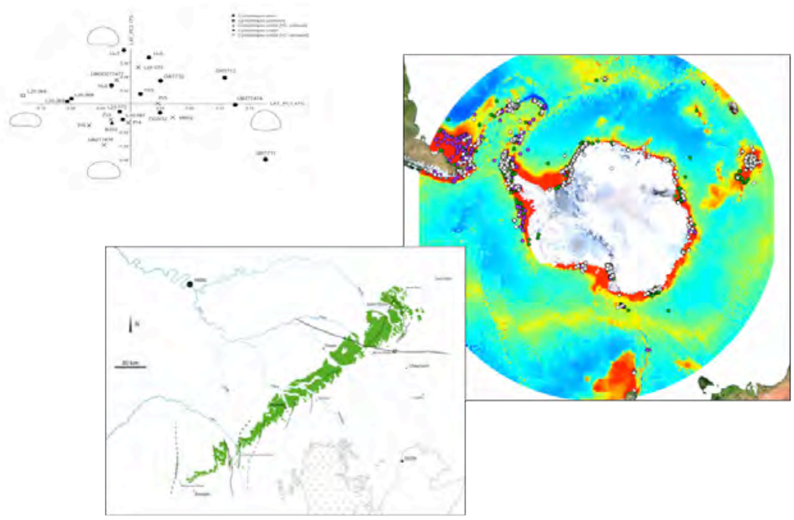
HABILITATION A DIRIGER DES RECHERCHES

ANALYSE MACROECOLOGIQUE DE LA BIODIVERSITE MARINE FOSSILE ET ACTUELLE

L'EXEMPLE DES ECHINIDES



Thomas Saucède

- 17 Mars 2014 -

Composition du jury :

Philippe Janvier, Directeur de Recherche CNRS, Muséum National d'Histoire Naturelle, Paris
Gilles Escarguel, Maître de Conférences HDR, université Lyon 1
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Bruno Faivre, Professeur, université de Bourgogne, Dijon
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"The past decade has seen the flowering of a bold and distinctive research programme in ecology that is concerned with thinking big. It is the ecology of wide expanses of space, long periods of time and large numbers of taxa. In a word, coined by Jim Brown and Brian Maurer, it is the discipline of macroecology"

Blackburn & Gaston 2003

RESUME

Ce mémoire est une synthèse de mes travaux de recherche réalisés au cours des onze années écoulées depuis la soutenance de ma thèse de doctorat. Il présente mes thématiques de recherche, les principaux résultats obtenus et constitue aussi une prospective pour la réalisation de mes projets futurs. Mes recherches portent sur l'analyse macroévolutive et macroécologique de la diversité fossile et actuelle des échinides. Ce groupe constitue un modèle d'étude de la biodiversité marine que j'aborde à différentes échelles taxinomiques et géographiques, ainsi qu'à travers des contextes variés, de la diversification des échinides irréguliers au Jurassique aux espèces abyssales et antarctiques actuelles. Mes thématiques de recherche s'articulent autour de l'étude des dimensions phylogénétiques, morphologiques, écologiques et biogéographiques de la diversité des échinides. Après une brève introduction, le premier chapitre du mémoire présente les spécificités du modèle d'étude, le choix des données traitées et les problématiques analytiques associées. Mes thématiques de recherche sont ensuite abordées dans trois chapitres consacrés à (1) l'étude de la structuration phylogénétique, (2) la caractérisation de la disparité morphologique et (3) l'analyse biogéographique et macroécologique de faunes d'échinides. En guise de conclusion, le dernier chapitre reprend mes principaux projets de recherche et les résume en soulignant la complémentarité des thématiques abordées.

Mots clés : Antarctique, biodiversité marine, biogéographie, disparité morphologique, échinides, Jurassique, macroécologie, macroévolution, phylogénie.

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Mes recherches sont adossées à plusieurs programmes scientifiques : ANR ANTFLOCKS coordonné par Guillaume Lecointre, BIANZO coordonné par Ann Vanreusel, ECOS-*Sud* Chili coordonné par Elie Poulin et Jean-Pierre Féral, PROTEKER coordonné par Jean-Pierre Féral et REVOLTA coordonné par Marc Eléaume. Elles ont également bénéficié du soutien du SCAR, de l'université de Bourgogne, de la région Bourgogne et du réseau de station marine ASSEMBLE.

TABLE DES MATIERES

BILAN D'ACTIVITE

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Né le 21 avril 1974
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Service national effectué en 1996-1997
Maître de Conférences (36ème section du CNU), classe normale, 4ème échelon
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CURSUS UNIVERSITAIRE

- Maître de Conférences à l'Université de Bourgogne - Dijon [2006-...]
- Attaché Temporaire d'Enseignement et de Recherche à l'Université J. Fourier - Grenoble [2002-2004]
- Thèse de Doctorat de l'université de Bourgogne [2002] - allocation de recherche (MNERT) - prix de l'Association Paléontologique Française [2003]
- Baccalauréat série C [1992] - Tours

PRODUCTION SCIENTIFIQUE ET ENCADREMENT

1. Liste des travaux publiés

Etudiant de thèse co-encadré souligné d'un trait simple; étudiants de master et de licence co-encadrés soulignés d'un trait double.

Articles soumis

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Le nom du conférencier est souligné.

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Le Pelvé S & **Saucède T**. Intérêt des données fossiles en biogéographie : exemple de l'échinide *Arbacia.*

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Díaz A, Féral J-P, David B, **Saucède T** & Poulin E. Echinoids of the genus *Sterechinus* from the southern ocean: evolutionary pathways between shallow and deep-sea and a possible connection with subantarctic benthos.

2010 53 Reunión Anual de la Sociedad de Biología de Chile y 4 Reunión anual Sociedad Chilena de Evolución, Santa Cruz, Chili.
Díaz A, Féral J-P, David B, **Saucède T** & Poulin, E. Procesos de diversificación del género *Sterechinus* (Echinoidea) en las zonas profundas y someras del Océano Austral.

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David B, Lecointre G. et al. The Antarctic Continental Shelf as a species flocks generator.

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2010 7th European Conference on Echinoderms, Goettingen, Allemagne.
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2009 13th International Echinoderm Conference, Hobart, Tasmanie.
Díaz A, Féral J-P, David B, **Saucède T** & Poulin E. Evolutionary pathway among Shallow and deep-sea urchins *Sterechinus* in the Southern Ocean.

2009 CAML Final Symposium, Gênes, Italie.
Hardy C, David B, Rigaud T, De Ridder C & **Saucède T**. Biodiversity and colonization of Antarctic cold waters: the importance of symbioses associated to echinoids.

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2009 Congrès de l'Association Paléontologique Française, Lille.
Saucède T, François E, Eble G & David B. Evolution des architectures apicales chez les échinides atélostomes : caractérisation par des réseaux de connectivité.

2008 20th International Congress of Zoology, Paris.
David B, Manjón-Cabeza ME, Moya F, Choné T, **Saucède T** & De Ridder C. The impact of global warming on polar seas: expected changes on Antarctic Echinoid fauna and forecasts for the future?

2008 20th International Congress of Zoology, Paris.
Hardy C, Rigaud T, David B, De Ridder C & **Saucède T**. Biodiversity and colonization of Antarctic cold waters: the importance of symbioses associated to echinoids.

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Saucède T & Villier L. The environmental context of spatangoids (Echinodermata: Echinoidea) evolution in the Early and Mid Cretaceous.

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David B, **Saucède T**, Alibert P & Laurin B. Asymétrie fluctuante sur une boîte. Les plaques d'*Echinocardium flavescens*.

2001 6th European Conference on Echinoderms, Banyuls.
Saucède T, Mooi R & David B. The strange apical system of the genus *Pourtalesia* (Holasteroida, Echinoidea): ontogeny and evolution.

2000 Journées de la Société Française de Systématique, Paris.
David B, Mooi R & **Saucède T**. Elucidation de phylogenèses fossiles par des données actuelles, la preuve par 5.

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Féral J-P, Ameziane N, David B, Poulin E, De Ridder C, Beurier J-P, Roca J-C, Chenuil A, Marschal C, Eleaume M, **Saucède T**, Diaz A & Manatura C. PROTEKER: Setup of a coastal underwater observatory in Kerguelen Islands.

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Kašparová E, **Saucède T** & Janko K. Is life history the main constrain shaping the population structure of species ?

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Pierrat B, **Saucède T** & David B. Biogeography and macroecology of Antarctic and sub-Antarctic Echinoids.

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1999 Colloque Bio Geo Images 99, Dijon.
Viguier B, **Saucède T**, Rouget I & Neige P. Mapping function : from morphology to landmark-based morphometry. Meaning of landmarks versus taxon.

4. Encadrements et co-encadrements d'étudiants

Co-encadrement de thèse de doctorat

Co-encadrant (50%) de la thèse de Benjamin Pierrat (septembre 2008-décembre 2011), intitulée : Macroécologie des échinides de l'océan Austral. Distribution, Biogéographie et Modélisation. Contrat doctoral, université de Bourgogne, Ecole Doctorale E2S (actuellement en CDD IE).

Master 2

Stéven Le Pelvé (janvier-juin 2013). Phylogéographie du genre *Arbacia* : apport des données fossiles. Stage de Recherche, Master 2 GBS, Paléontologie, université de Bourgogne. Encadrement : 100%.

Jonathan Edwards (janvier-juin 2012). Influence de l'échantillonnage sur la diversité. Cas des ammonites du Toarcien de la carrière de Belmont (Bas-Beaujolais, Rhône). Stage de Recherche, Master 2 GBS, Paléontologie, université de Bourgogne. Co-encadrement : 50%.

Damien Gendry (janvier-juin 2010). Le genre *Neseuretus* (Trilobita, Ordovicien Moyen et Supérieur). Exemple des faunes du Synclinorium du Ménez-Belair (Massif Armoricain, France). Stage de Recherche, Master 2 PPP, Paléontologie, université de Rennes 1. Co-encadrement : 30%.

Clotilde Hardy (janvier-juin 2009). Importance des oursins cidaridés pour la biodiversité des communautés benthiques en Antarctique. Stage de Recherche, Master 2 GSA, Ecologie, université de Bourgogne. Co-encadrement : 30%.

Claire Samant (janvier-juin 2008). La variation morphologique chez *Phyllobrissus gresslyi* (Cassiduloida) et *Coenholectypus macropygus* (Holectypoida), deux échinides irréguliers de la formation hauterivienne des calcaires à spatangues (bassin de Paris, France). Stage de Recherche, Master 2 GBS, Paléontologie, université de Bourgogne. Co-encadrement : 50%.

Master 1

Stéven Le Pelvé (février-mai 2012). Phylogéographie du genre *Arbacia* : apport des données fossiles. Stage de Recherche, Master 1 GBS, Paléontologie, université de Bourgogne. Encadrement : 100%.

Jonathan Pouteaux (février-mai 2012). Analyse de la distribution d'espèces d'oursins irréguliers de la Formation des "Calcaires à Spatangues" (Hauterivien, sud-est du bassin de Paris). Stage de Recherche, Master 1 GBS, Paléontologie, université de Bourgogne. Encadrement : 100%.

Thibaut Daveine (février-mai 2011). Etude paléobiogéographique des faunes d'oursins fini-Crétacé et cénozoïques de l'océan Austral. Stage de Recherche, Master 1 GBS, Paléontologie, université de Bourgogne. Encadrement : 100%.

Morvan Desvignes (février-mai 2010). Etude des assemblages fauniques d'échinodermes des plates-formes carbonatées de Normandie et du Boulonnais, de l'Aalénien au Callovien. Stage de Recherche, Master 1 GBS, Paléontologie, université de Bourgogne. Encadrement : 100%.

Fabien Contigliani (février-mai 2009). Etude paleoécologique des environnements aaléniens de Villaine-la-Carelle : aspects sédimentologiques et paléontologiques. Stage de Recherche, Master 1 GBS, Paléontologie, université de Bourgogne. Encadrement : 100%.

Jean-Paul Rullman (février-mai 2009). Diversité des faunes ectosymbiotiques portées par les oursins cidaridés vivant au large de la Terre Adélie (Antarctique). Stage de Recherche, Master 1 BOP, Ecologie, université de Bourgogne. Co-encadrement : 50%.

Clotilde Hardy (janvier-juin 2008). Importance des oursins cidaridés et de leurs ectosymbiotes pour la biodiversité benthique en Antarctique. Stage de Recherche, Master 1 BOP, Ecologie, université de Bourgogne. Co-encadrement : 30%.

Autres encadrements

De 2007 à 2013, encadrement de 16 étudiants de Licence 2 et 3 des Sciences de la Terre et de Licence 3 de Biologie-Géologie dans le cadre de stages bibliographiques obligatoires et de stages de recherche réalisés à l'initiative des étudiants.

ACTIVITES DE RECHERCHE ET RAYONNEMENT

1. Porteur de projets de recherche financés

- PhyMorA - *Phylogeography and morphological differentiation in the genus Arbacia (Echinoidea, Arbaciidae) off the coasts of Chile* [2011]
  Financement et logistique : ASSEMBLE (Association of European Marine Biological Laboratories)

- COSIE - *Contribution des oursins et de leurs symbiotes à la diversité benthique des Iles Eparses* [2011-2013]
  Financement et logistique : programme inter-organismes "Iles Eparses" (AAMP, CNRS, FRB, Ifremer, IPEV, IRD, MNHN, Taaf)

- Biodiversité marine au passage Jurassique Inférieur - Jurassique Moyen : étude de la macrofaune benthique des gisements aaléniens et bajociens de la Sarthe [2009]
  Financement : Bonus Qualité Recherche – université de Bourgogne

2. Participation à des projets de recherche nationaux et internationaux

- BIANZO I et II - *Biodiversity of the Antarctic Zoobenthos* [2002-2010]
  Financement : Fonds de la Recherche Scientifique Belge
  Coordinatrice : A. Vanreusel (section de biologie marine, université de Gand, Belgique)

- ANTFLOCKS - *The Antarctic shelf as a species flocks generator* [2008-2011]
  Financement *:* programme blanc de l'ANR
  Coordinateur : G. Lecointre (UMR 7138, MNHN, Paris)

- *Origine et évolution de la faune marine Antarctique* [2007-2009]
  Financement : ECOS-*Sud* Chili
  Coordinateurs: E. Poulin (lab. d'écologie, université du Chili) et J.-P. Féral (UMR 6540 DIMAR, Marseille)

- PROTEKER - *Impact du changement global sur le benthos et les habitats marins des îles Kerguelen* [2011-2015]
  Financement et logistique : IPEV (Institut polaire français Paul Emile Victor)
  Responsable: J.-P. Féral (UMR 6540 DIMAR, Marseille)

- *Les oursins, facteur structurant de la biodiversité* [2012-2013]
  Financement : région Bourgogne
  Responsable : B. David (UMR 6282 Biogéosciences, Dijon)

- REVOLTA - *Ecological Ressources and valorisation using a Long Term Observatory in Terre Adelie* [2013-2017]
  Financement et logistique : IPEV (Institut polaire français Paul Emile Victor)
  Responsable: M. Eléaume (UMR 7208 BOREA – MNHN/CNRS/IRD/PARIS VI)

3. Participation à des campagnes océanographiques

- Campagne *BENTART-06* [2 mois, 01/2006-02/2006]
  Financement et logistique : programme CGL2004-21006-E du gouvernement espagnol
  Responsable : A. Ramos Martos (Instituto Español de Oceanografía, Vigo, Espagne)

- Campagne *ANTARKTIS-XXIII/8* [3 mois, 10/2006-01/2007]
  Financement et logistique : Alfred Wegener Institute (AWI)
  Responsable : J. Gutt (AWI, Bremerhaven, Allemagne)

- Campagne *JR230* en Antarctique [3 mois, 10/2009-01/2010]
  Financement et logistique : British Antarctic Survey (NERC)
  Responsable : D. Barnes (British Antarctic Survey, Cambridge, Angleterre)

- Campagne PROTEKER 2013 [2 mois, 11/2013-12/2013]
  Financement et logistique : IPEV (Institut polaire français Paul Emile Victor)
  Responsable: J.-P. Féral (UMR 6540 DIMAR, Marseille)

4. Expertise

Rapporteur pour les revues *Alcheringa*, *Bulletin de la Société Zoologique de France*, *Journal of Systematic Palaeontology, Marine Biodiversity, Polar Biology, Zoosystema*, *Zoological Journal of the Linnean Society* et *Zootaxa.*

5. Conférencier invité

- Titre : *Modelling the distribution of Antarctic echinoids* (21 avril 2011)
  Station de biologie marine de Las Cruces, Chili

- Titre : *Modelling the distribution of Antarctic echinoids* (12 avril 2011)
  Laboratoire d'écologie appliquée, Universidad Catolica del Norte, Coquimbo, Chili

- Titre : *Biodiversity and colonization of Antarctic cold waters* (19 mai 2009)
  CAML (Census of Antarctic Marine Life) Final Symposium, Gênes, Italie

- Titre : *Biodiversité et biogéographie des faunes d'échinides antarctiques* (16 février 2009)
  Département des Sciences de la Terre, université Claude Bernard Lyon 1, France

- Titre : *French Research in the Antarctic & the study of marine biodiversity* (9 octobre 2008)
  Université de Málaga, Espagne

- Titre: *Origin and evolution of irregular echinoids* (14 septembre 2005)
  Museum für Naturkunde, Berlin, Allemagne

- Titre : *The environmental context of spatangoid (Echinodermata: Echinoidea) evolution in the Early and Mid Cretaceous* (21 avril 2005)
  Université Joseph Fourier, Grenoble

- Titre : *Analyse de la radiation des oursins irréguliers jurassiques* (5 avril 2004)
  Université Pierre et Marie Curie, Paris

- Titre : *Origine et évolution des oursins irréguliers* (3 décembre 2002)
  Université Joseph Fourier, Grenoble

RESPONSABILITES COLLECTIVES

- Responsable du parcours Paléontologie du M2 Recherche Géobiosphère, université de Bourgogne [2008-2009]

- Responsable de la Licence 3 des Sciences de la Terre et de l'Environnement, université de Bourgogne [2010-…]

- Responsable de l'offre de formation 2012-2016 de la mention Sciences de la Terre et de l'Environnement de l'université de Bourgogne pour les 3 années de Licence

- Membre élu du Conseil de l'UFR des Sciences de la Vie, de la Terre et de l'Environnement de l'université de Bourgogne [2012-...]

- Membre élu de la commission pédagogique de l'UFR des Sciences de la Vie, de la Terre et de l'Environnement, université de Bourgogne [2013-...]

ACTIVITES D'ENSEIGNEMENT

Avant ma nomination à Dijon au poste de maître de conférences, j'ai enseigné de 1998 à 2004 au sein des équipes pédagogiques des universités de Dijon et de Grenoble en tant que doctorant vacataire puis attaché temporaire d'enseignement et de recherche. Je suis intervenu dans les différentes années de Licence et de Master des filières des Sciences de la Terre et de la filière de préparation aux métiers de l'enseignement dans les disciplines de la géologie (cartographie, pétrographie et géologie sédimentaire, paléontologie et micropaléontologie).

Depuis 2006, j'enseigne dans tous les niveaux de licence et de master de la filière des Sciences de la Terre de l'UFR SVTE de l'université de Bourgogne. Outre les enseignements de cours magistraux, travaux dirigés et travaux pratiques dispensés (voir tableau ci-dessous), j'ai participé à l'encadrement de nombreux stages de terrain (entre 10 et 20 jours par an) et à la mise en place de certains d'entre eux dans tous les niveaux d'enseignement de la filière. Les disciplines enseignées couvrent la géologie générale et la cartographie (niveau licence), la paléontologie et la palichnologie (niveaux licence et master).

Depuis 2010, je suis responsable de la Licence 3 mention Sciences de la Terre et de l'Environnement de l'UFR SVTE pour laquelle j'ai mis en place plusieurs actions (stages étudiants, journées d'information et rencontres avec des professionnels dans le cadre du Programme Réussite en Licence).

ANNEES	HEURES COURS MAGISTRAUX	HEURES TRAVAUX DIRIGES	HEURES TRAVAUX PRATIQUES	TOTAL HEURES ENSEIGNEMENT
1998-2004	*78*	*36*	*244*	*358*
2006-2007	5	76	186	267
2007-2008	6	58	187	251
2008-2009	8	73	171	252
2009-2010	7	122	131	260
2010-2011	6	29	196	231
2011-2012	10	50	159	219
2012-2013	11	42	139	192

DIFFUSION DES CONNAISSANCES AUPRES DU PUBLIC

2013 **Conférencier invité** au Muséum d'Histoire naturelle de Dijon sur la biodiversité ancienne

2013 "**Nuit des chercheurs**" sur les mondes inconnus (abyssaux et antarctiques), université de Bourgogne, Dijon

2013 **Exposition** sur les Pôles, université de Bourgogne, Le Creusot

2011 Interventions au **collège** et à la **MJC** de Venarey-lès-Laumes (21) sur la recherche en Antarctique

2010 Invité à l'**émission** de la chaîne de télévision dijonnaise *VOOTV*: "le Grand RendezVoo"

2010 Rencontres anuelles de l'**Association** échinologique Française, Auxerre

2008 Invité à l'**émission** de *RADIO CAMPUS* "le microscope et la blouse", Dijon

2008 **Fête de la Science**, Dijon

2008 **Conférencier invité** au Muséum d'Histoire naturelle de Dijon

2008 **Conférencier invité** à la Nuit des Musées, Auxerre

2007 "**Café des Sciences**" sur la recherche en Antarctique, Dijon

2007 **Exposition** sur les Pôles, université de Bourgogne, Dijon

2007 **Fête de la Science**, Dijon

2007 Rédaction de **communiqués de presse** pour la **Société Cousteau** et la **Fondation Polaire Internationale**

2006 "**Nuit des chercheurs**" sur la biodiversité, université de Bourgogne, Dijon

ANALYSE MACROECOLOGIQUE DE LA BIODIVERSITE MARINE FOSSILE ET ACTUELLE

L'EXEMPLE DES ECHINIDES

AVANT-PROPOS

A l'issue de onze années écoulées depuis la soutenance de ma thèse de doctorat, le temps semble être venu de faire un bilan de mes travaux scientifiques passés et de poser avec cohérence la base de mes projets à venir. Le développement de mes recherches actuelles ainsi que la perspective de nouveaux projets et collaborations scientifiques m'invitent à cet exercice de synthèse et de prospective qui me semble correspondre à la définition de l'Habilitation à Diriger des Recherches.

Sur la base d'homologies alors nouvellement établies (Mooi *et al.* 1994), ma thèse de doctorat intitulée "Origine et évolution vers l'extrême des échinides irréguliers - Un nouveau modèle d'homologie, l'Extraxial Axial Theory, clef d'interprétation de la structure des appareils apicaux" avait un double objectif : clarifier notre connaissance de l'origine et des premières phases de diversification du groupe des échinides irréguliers (Saucède *et al.* 2001, 2003b, 2007) et identifier les homologies squelettiques au sein d'un groupe d'échinides irréguliers très dérivé, les holastéroïdes abyssaux, en mettant en évidence les profondes restructurations qui ont accompagné l'évolution de leur squelette (Saucède *et al.* 2001, 2003a, 2004). Mes travaux de thèse ont consisté en l'étude conjointe de données morphologiques fossiles et actuelles, et m'ont permis de me familiariser avec certaines méthodes d'analyse phylogénétique. L'étude conjointe de faunes actuelles et fossiles a depuis lors continué à alimenter mes travaux de recherche.

Quatre années après la fin de ma thèse, mon accession au corps des maîtres de conférences a coïncidé avec l'opportunité de pouvoir rejoindre, à un an d'intervalle, deux campagnes océanographiques dans l'océan Austral. Ma participation à ces deux campagnes a été le point de départ de plusieurs projets de recherche et de nouvelles collaborations scientifiques adossés à des programmes internationaux. Initialement embarqué dans ces missions océanographiques en tant que spécialiste de la systématique et de la morphologie des échinides, groupe commun des communautés benthiques antarctiques, mes collaborations avec des collègues biologistes m'ont permis de me familiariser avec de nouveaux outils (génétique), méthodes et catégories d'analyse (phylogéographie, biogéographie historique et écologie marine). Grâce à ces travaux et collaborations portant sur l'étude des faunes antarctiques, j'ai commencé à aborder des thématiques macroécologiques, bien que mes recherches aient principalement abouti à la publication de travaux de biogéographie. L'étude de la dynamique de la biodiversité nécessitait que la dimension temporelle, c'est-à-dire l'évolution de la distribution des faunes soit explicitement prise en compte dans mes analyses, et non pas seulement les dimensions spatiales et phylogénétiques. Cette dernière étape est actuellement en passe d'être franchie ; elle constituera une part majeure de mes travaux futurs. Partant de l'analyse macroévolutive d'échinides irréguliers, puis passant par l'écologie marine et la biogéographie de faunes d'échinides actuelles, mes projets en cours et futurs me permettent, pour ainsi dire, de 'boucler la boucle' et d'opérer un retour aux données paléontologiques, à travers une approche macroécologique qui intègre les études de faunes fossiles et actuelles.

Evidemment, l'ordre chronologique de publication de mes travaux ne reflète qu'en partie la description très linéaire que je viens d'en faire. Pour diverses raisons, mes projets ont régulièrement eu tendance à se croiser et se superposer plutôt qu'à se succéder selon une logique thématique implacable. Ce mémoire a en partie vocation à les réunir selon une organisation thématique, et non chronologique, en quatre chapitres de longueurs très inégales. Mes projets de recherche futurs y sont intégrés suivant la même logique thématique ; ils ne font donc pas l'objet de parties distinctes, mais sont bien identifiés comme "projets et perspectives" et clairement distingués des sections dédiées à mes "principaux résultats". Après une brève introduction, un premier chapitre est dédié à mes objets et modèles d'étude, ainsi qu'aux problématiques méthodologiques rencontrées. Ce premier chapitre aurait presque pu constituer une introduction générale mais il s'en distingue par les développements et perspectives méthologiques abordés. Les trois chapitres suivants présentent mes travaux de recherche selon trois volets dédiés respectivement à l'étude des dimensions phylogénétique (chapitre 2), morphologique (chapitre 3), biogéographique et macroécologique (chapitre 4) de la biodiversité actuelle et fossile. Certaines redondances entre chapitres étaient inévitables, l'approche macroécologique ayant pour vocation à intégrer les trois dimensions abordées dans des analyses jointes. Ainsi, analyses phylogénétiques, biogéographiques et macroécologiques sont abordées à deux reprises, mais selon des angles différents, dans les chapitres 2 et 4. En guise de conclusion, une courte synthèse de mes projets de recherche constitue le dernier chapitre de ce mémoire. Elle me permet de souligner la forte complémentarité qui caractérise les différentes thématiques de recherche abordées.

INTRODUCTION

L'approche macroécologique cherche à identifier, quantifier et analyser les facteurs environnementaux et historiques qui structurent la distribution spatiale de la biodiversité, actuelle et fossile, ainsi qu'à scénariser les modifications éventuelles associées aux changements environnementaux (Brown 1995, Gaston & Blackburn 2000, Briggs 2007). Son réel apport tient au fait qu'elle permet de réconcilier les approches écologiques et historiques de la biogéographie (Briggs 2007), et qu'elle a recours à des outils mathématiques et statistiques pour analyser la distribution de la biodiversité. L'approche macroécologique s'inscrit également dans une démarche macroévolutive qui implique d'étudier, ou pour le moins, de tenir compte de l'évolution de la biodiversité sur des temps longs. En ce sens, l'étude conjointe de données fossiles et actuelles permet d'enrichir les débats au sein de la discipline (Maguire & Stigall 2008, Malizia & Stigall 2011, Hendricks *et al.* 2008). La précision et la qualité des informations collectées dans les écosystèmes actuels permettent de mieux cerner le fonctionnement des écosystèmes anciens; l'étude de l'évolution de ces derniers alimente en retour les modèles prédictifs, qui décrivent les changements attendus dans les écosystèmes actuels (Svenning *et al.* 2011, Varela *et al.* 2011).

Les échelles spatiales, taxinomiques et temporelles auxquelles les analyses sont réalisées sont déterminantes dans la mesure où facteurs environnementaux et historiques n'interviennent pas de façon identique sur la dynamique locale des populations et sur les dynamiques régionales ou globales des communautés (Austin & Van Niel 2011, Blois *et al.* 2013). A l'échelle locale, la dynamique démographique des populations est fortement contrôlée par des déterminants physiques, chimiques et par les interactions biotiques; les variations d'abondance et de distribution des populations fluctuant sous l'effet de ces facteurs sur des temps courts (Pearson & Dawson 2003, Lomolino *et al.* 2006, Chatfield *et al.* 2010, Gogina *et al.* 2010, Soberón 2010, Bentlage *et al.* 2013). A large échelle et faible résolution spatiales, le poids des interactions biotiques est généralement considéré comme négligeable au regard des facteurs abiotiques qui se combinent à l'histoire évolutive des clades et aux processus géodynamiques pour déterminer les motifs biogéographiques (Ricklefs 2004, Bond & Chase 2002, Anderson & Martinez-Mayer 2004, Lomolino *et al.* 2006, Cheung *et al.* 2009, Saupe *et al.* 2012, Bentlage *et al.* 2013, Blois *et al.* 2013).

Dans le contexte actuel d’évolution climatique et de changements environnementaux rapides, l'approche macroécologique permet d’identifier les déterminants environnementaux à l'origine de la distribution de la biodiversité, d’estimer la sensibilité des espèces à leur environnement, et donc leur vulnérabilité potentielle face à ses changements. Comparés au domaine continental (milieux terrestre et d’eau douce), le domaine marin, et les mers polaires en particulier, ont été relativement peu étudiés en macroécologie. Cependant, les changements climatiques actuels impactent d’ores et déjà de façon sensible les environnements (Smith & Stammerjohn 2001, Quale *et al.* 2002) et le fonctionnement des écosytèmes marins (Moline *et al.* 2004, Ainley *et al.* 2005, Barnes 2005, Burrows *et al.* 2011, Gutt *et al.* 2012). Les développements et progrès actuels permettent cependant d’entrevoir une amélioration dans la précision des données collectées, des surfaces couvertes et de la performance des outils d’analyse (Wedding *et al.* 2008, Dawson 2011, Tyberghein *et al.* 2012).

La mise en oeuvre des analyses macroécologiques nécessite de pouvoir disposer de phylogénies robustes (Faith 1994, Webb *et al.* 2002, Ricklefs 2006, Wiens *et al.* 2011, Condamine *et al.* 2013). Les relations phylogénétiques entre clades étant connues, l’étude de leur disparité morphologique permet alors d’éclairer les processus macroévolutifs à l’origine de leur diversité (Wills 1994, Foote 1997, 1999, Neige 2003, Erwin 2007, Ruta 2009, Wills *et al.* 2012, Gerber 2013). L’intégration des composantes phylogénétiques, morphologiques, temporelles, spatiales et environnementales constitue le cœur de l’approche macroécologique (Donoghue & Moore 2003, Lomolino 2006, Pearman *et al.* 2008, Wiens 2012).

L'approche macroécologique constitue à la fois un cadre cohérent, un fil directeur, et l'objectif de mes travaux de recherche. Ce mémoire d'HDR me donne l'opportunité de les rassembler et de les ordonner en éclairant les principales thématiques traitées (tableau 1): phylogénie (chapitre 2), disparité morphologique (chapitre 3), biogéographie descriptive, écologique et historique (chapitre 4), et macroécologie (chapitre 4). Ces différentes thématiques me permettent d'aborder l'étude de la biodiversité selon différents angles ; elles représentent aussi des composantes complémentaires pour comprendre la dynamique de la biodiversité. C'est dans cette approche macroécologique que mes travaux passés et mes projets trouvent leur cohérence.

Thématiques	**Descriptif taxinomique, spatial et temporel**	**Publications**
Phylogénies	Genre *Nucleopygus*, France, Cénomanien	Saucède & Néraudeau 2006
	Sous-classe Irregularia, Monde, Jurassique	Saucède *et al*. 2007
	Faune benthique, Antarctique Est, Actuel	Dettai *et al*. 2011
Disparité morphologique et macroévolution	espèce *Calymne relicta*, Atlantique, Actuel	Saucède *et al*. 2009
	genre *Neseuretus* (trilobite), massif Armoricain, Ordovicien	Gendry *et al*. 2013
	genre *Nucleolites*, bassin de Paris, Jurassique	Moyne *et al*. 2004
	genre *Cyclolampas*, France, Jurassique	Saucède *et al*. 2013a
	genres *Salvaster*, *Pygolampas*, bassin de Paris, Hauterivien	Saucède *et al*. 2012
	classe Echinoidea, Monde, fossile et Actuel	Laffont *et al*. 2011
	classe Echinoidea, Monde, fossile et Actuel	David *et al*. 2009
Biogéographie descriptive	Classe Echinoidea, bassin de Paris, Hauterivien	Benetti *et al*. 2013
	Classe Echinoidea, mer de Bellingshausen, Actuel	Moya *et al*. 2012
	Classe Echinoidea, Antarctique Ouest, Actuel	Saucède 2008
	Classe Echinoidea, océan Austral, Cénozoïque	Saucède *et al*. 2013b
	Classe Echinoidea, océan Austral, Actuel	Pierrat *et al*. 2012a
	Classe Echinoidea, océan Austral, Actuel	Saucède *et al*. sous presse a
	Classes Echinoidea, Bivalvia, Gastropoda, océan Austral	Pierrat *et al*. 2013
	Faunes benthiques, mer de Bellingshausen, Actuel	Saiz *et al*. 2008
	Faunes benthiques, mer d'Amundsen, Actuel	Linse *et al*. 2013
	Faunes benthiques, océan Austral, Actuel	De Broyer *et al*. sous presse
Biogéographie écologique	Espèces d'échinides, Péninsule Antarctique, Actuel	Hardy *et al*. 2011
	Genre *Sterechinus*, océan Austral, Actuel	Pierrat *et al*. 2012b
	Ordre Spatangoida, Tethys, Crétacé	Saucède & Villier 2005
	Classe Echinoidea, mer de Bellingshausen, Actuel	Moya *et al*. 2012
	Communautés benthiques, mer de Bellingshausen, Actuel	Saiz *et al*. 2008
	Faunes marines, Péninsule Antarctique, Actuel	Gutt *et al*. 2011
	Faunes marines, océan Austral, Actuel	Gutt *et al*. 2012
Biogéographie historique et phylogéographie	Populations *Nacella concinna* (gastéropode), ouest Antarctique, Actuel	González-Wevar *et al*. 2013
	Espèces d'échinides, Péninsule Antarctique, Actuel	Hardy *et al*. 2011
	Genre *Sterechinus*, océan Austral, Actuel	Díaz *et al*. 2011
	Classe Echinoidea, océan Austral, Cénozoïque	Saucède *et al*. 2013b
	Classes Echinoidea, Bivalvia, Gastropoda, océan Austral, Actuel	Pierrat *et al*. 2013
	Phyla marins, océan Austral, Actuel	Lecointre *et al*. 2013
	Faunes marines, Péninsule Antarctique, Actuel	Gutt *et al*. 2011
	Faunes marines, océan Austral, Cénozoïque	Saucède *et al*. sous presse b
Macroécologie	Faunes marines, océan Austral, Actuel	Gutt *et al*. 2012

Tableau 1. Synthèse de mes thématiques de recherche, des objets et échelles d'études, et liste des publications associées.

CHAPITRE I.

MODELES D'ETUDE, NATURE ET QUALITE DES DONNEES

1. Le modèle « oursin » : échinides actuels et fossiles

1.1. Choix du modèle d'étude

Hormis deux études récentes sur les trilobites (Gendry *et al.* 2013) et les gastéropodes (González-Wevar *et al.* 2013), mes travaux de recherche s'appuient exclusivement sur l'étude du groupe des échinides. Initialement, c'est en tant que spécialiste des échinides, de leur anatomie, systématique, écologie et évolution que j'ai pu intégrer un certain nombre de programmes de recherche pluri-disciplinaires (ANR ANTFLOCKS, programmes REVOLTA, BIANZO, PROTEKER) et participer à plusieurs campagnes océanographiques dans l'océan Austral (campagnes BENTART'06, ANTXXIII/8 et JR230). L'origine de cette spécialisation tient à mes sujets de recherche de DEA et de thèse et aux projets de mes anciens encadrants (Rich Mooi et Bruno David). La poursuite de mes recherches sur le même modèle des échinides tient aux opportunités qui m'ont été offertes. Mes collaborations récentes (Gendry *et al.* 2013, González-Wevar *et al.* 2013) et ma participation à plusieurs campagnes océanographiques sous l'étiquette de biologiste 'benthologue' m'ont cependant permis d'étendre mes investigations à d'autres groupes d'invertébrés fossiles et actuels.

Le registre fossile des échinides est relativement bien documenté depuis la fin du Trias et le début du Jurassique, périodes d'apparition des groupes souches dans lesquels s'enracinent les clades actuels. Cette relative richesse du registre fossile m'a permis d'intégrer données fossiles et actuelles dans des analyses des diversités morphologique, écologique et taxinomique des échinides. A l'instar de collègues paléontologues, zoologistes et écologistes spécialistes de groupes taxinomiques, la spécialisation pour les échinides m'a autorisé à aborder l'étude du groupe à partir de données de différentes natures (fossiles, actuelles, biogéographiques, biostratigraphiques, morphologiques et génétiques) et d'en tirer des conclusions d'ordre méthodologique. A titre d'exemple, l'étude conjointe d'espèces fossiles et actuelles me permet d'évaluer la qualité de l'information morphologique portée par les espèces fossiles et d'en tirer des enseignements pour les interprétations paléo-autécologiques et taxinomiques.

L'interprétation des motifs de diversité et de leur évolution présente une portée limitée en l'absence d'analyses comparatives qui intègrent l'étude de groupes taxinomiques différents. L'étude des motifs biogéographiques en fournit un très bon exemple : les hypothèses de vicariance ne sont vérifiées que si la concomitance entre divergence évolutive et mise en place de barrières biogéographiques est démontrée indépendamment dans des groupes taxinomiques éloignés phylogénétiquement (Lomolino *et al.* 2006, Crisp *et al.* 2011, Ebach & Tangney 2007). Un nombre croissant de mes travaux a donc porté sur des études comparatives de données « échinides » et de données provenant d'autres groupes taxinomiques. Réalisés dans le cadre de collaborations auxquelles j'ai contribué en tant que spécialiste des échinides (Saiz *et al.* 2008, Gutt *et al.* 2011 ; Dettai *et al*. 2011, Gutt *et al*. 2012, Saucède *et al.* sous presse a, Lecointre *et al*. 2013, Linse *et al.* 2013), ces travaux permettent de comparer les informations tirées de groupes taxinomiques à l'écologie et à l'histoire évolutive contrastées (Pierrat *et al.* 2013). Enfin, certaines de mes collaborations actuelles portent sur l'étude de modèles biologiques autres que les échinides (gastéropodes, trilobites) ; elles correspondent à une évolution de mon champ de compétence dans les domaines de la biogéographie (Gonzalez-Wevar *et al.* 2013, Saucède *et al.* sous presse b) et des analyses morphologiques (Gendry *et al.* 2013).

1.2. Spécificités du modèle d'étude

Cette partie a pour but de présenter brièvement les principales spécificités de mon modèle d'étude, les échinides, afin d'aider le lecteur à se familiariser avec ce modèle et à saisir les contraintes et conditions de mise en oeuvre de mes travaux. L'ancienneté et la richesse de l'histoire évolutive des échinides (malgré un registre fossile inévitablement inégal et par nature parcellaire), les liens existant entre leur diversification et l'évolution des environnements anciens, la présence de nombreux caractères morphologiques, sont autant de particularismes qui m'ont permis d'aborder l'étude macroécologique et macroévolutive des échinides à travers des thématiques de recherche complémentaires.

Histoire évolutive

L'histoire évolutive des échinides a été fortement marquée par la crise biologique de la fin du Paléozoïque, quelques rares taxons seulement passant la limite Permien - Trias (Lewis & Ensom 1982). Ces derniers ont fortement conditionné la diversification du groupe après la crise, l'évolution des échinides post-paléozoïques étant en profonde rupture avec celle des formes paléozoïques (Kier 1974, 1982, 1984, Fell 1966, Durham 1966, Lewis & Ensom 1982, Smith 1978, 1984). La diversité des échinides augmente fortement dès le Trias Supérieur avec l'apparition des premiers Cidaroidea, Diadematacea et Echinacea. Elle s'accroît encore au Jurassique Inférieur avec les premiers représentants des Irregularia (échinides irréguliers), puis au Jurassique Supérieur avec les premiers Echinothuriacea (Fell 1966, Kier 1977, Smith 1984, 1988). Connus dans le registre fossile depuis le Jurassique Inférieur (Jesionek-Szymanska 1970), les échinides irréguliers connaissent plusieurs périodes de forte diversification morphologique au Jurassique, au Crétacé et au Paléogène (Thierry & Néraudeau 1994, Kier 1974). Au Jurassique Moyen, cette diversification est associée à la colonisation des environnements de plate-forme distale et à l'exploitation des ressources nutritives dans les fonds marins à sédiments meubles et granulométrie fine (Thierry 1984, Thierry & Néraudeau 1994, Thierry *et al.* 1997, Barras 2008). Au Crétacé Inférieur, les holastéroïdes (ordre des Holasteroida) et les spatangues (ordre des Spatangoida) font leur apparition dans le registre fossile. Ces deux ordres vont se diversifier dans l'ensemble des mers du globe, à toutes les latitudes et profondeurs et constituent aujourd'hui encore une part majeure de la diversité de la classe. L'étude des clades d'échinides actuelles et fossiles aux échelles macroécologiques et macroévolutives béneficie donc d'un cadre historique relativement bien documenté et ancien, notamment depuis le Jurassique Moyen pour les échinides irréguliers.

Particularismes écologiques et spécificités de la biodiversité marine

L'étude des échinides, organismes marins benthiques, est en grande partie conditionnée par des particularismes liés au monde marin et à la recherche en paléoécologie et écologie marine. L'état actuel de notre connaissance du monde marin et la performance des moyens d'investigation et des outils d'analyse déterminent les limites dans lesquelles la recherche sur les organismes marins peut être réalisée. Comparée au domaine continental (milieux terrestre et d'eau douce), notre connaissance du monde marin est très parcellaire. Outre les contraintes d'échantillonnage des données actuelles, en particulier dans les mers polaires et les domaines océaniques profonds, les limites des outils et moyens d'analyse disponibles constituent également de réelles contraintes. Les développements et progrès actuels permettent cependant d'entrevoir une amélioration dans la précision des données collectées, des surfaces d'analyse couvertes et de la performance des outils d'analyse (Wedding *et al.* 2008, Dawson 2011, Tyberghein *et al.* 2012).

Comparée au domaine continental, la faible richesse spécifique globale du monde marin est une caractéristique qui permet de souligner ses principaux particularismes écologiques et biogéographiques. Pourquoi y a-t-il si peu d'espèces marines par rapport aux espèces continentales (Hutchinson 1957) ? On compte en effet huit fois plus d'espèces sur les continents que dans les océans (entre 235 000 et 250 000 espèces marines ont été décrites sur 1,9 million d'espèces au total, soit 13 %). A surfaces égales, les continents ont une densité d'espèces 14 fois supérieure à celle des océans (relation espèce-surface) et entre 60 et 600 fois supérieure à volumes d'habitats égaux (relation espèce-volume), les estimations variant selon les sources (Bœuf 2007, CoML 2010, Boeuf 2011, Dawson 2012, Goulletquer *et al.* 2013). Les principales explications avancées soulignent la faible productivité primaire des océans, la complexité moindre de leurs habitats, le moins grand nombre de radiations coévolutives (ex : angiospermes-insectes en domaine continental), les faibles vitesses évolutives des groupes, la plus grande taille des populations, la quasi-absence à la fois de barrières biogéographiques imperméables et de réelles limites à la dispersion, le moins grand nombre de spécialisations écologiques et des aires de distribution plus vastes (voir Dawson 2012 pour revue).

La faible richesse spécifique du monde marin ne doit pas occulter d'autres données de diversité (abondance, écologie, biologie fonctionnelle et histoire évolutive) dont l'inventaire est à la fois très incomplet et difficile à réaliser (Dawson 2012, Goulletquer *et al.* 2013). Ainsi, les biomasses marines peuvent être considérables (le phytoplancton seul représenterait la moitié de la biomasse mondiale) et les régions très contrastées (déserts pélagiques contrastant avec les riches zones benthiques côtières). La diversité phylogénétique est importante (sur les 31 grands phylla actuels, 12 sont exclusivement marins) et ancienne par rapport au domaine continental (la biodiversité continentale est apparue il y a environ 440 millions d'années, mais l'explosion du nombre d'espèces est relativement récente et remonte à environ 110 millions d'années) (Bœuf 2007, Wedding *et al.* 2008, Goulletquer *et al.* 2013).

L'importante connectivité du monde marin a fortement conditionné les modalités évolutives des espèces. Ainsi, les exemples de spéciation allopatrique par vicariance sont rares (Waters 2008) alors que la présence de nombreuses discontinuités biogéographiques diffuses (ex : embouchure de l'Amazone, larges étendues océaniques de l'Atlantique et du Pacifique, front polaire antarctique, discontinuités du sud-est pacifique) a favorisé les phénomènes de spéciations parapatriques et péripatriques, dans lesquels les processus de dispersion (par diffusion, le long de corridors, à travers des filtres, sur de longues distances, discontinus ou aléatoires) sont déterminants (Dawson 2012, Bowen *et al.* 2013, Goulletquer *et al.* 2013).

Les échinides représentent une classe d'invertébrés marins benthiques de modeste richesse spécifique à l'échelle globale. A titre de comparaison, environ 900 espèces d'échinides actuelles (5000 fossiles) ont été décrites (Smith *et al.* 2006) contre 70000 espèces de gastéropodes et 20000 espèces de bivalves actuelles (Brusca & Brusca 2003). Bien qu'exclusivement restreints au milieu marin (comme toutes les autres classes d'échinodermes actuelles et fossiles) leur modeste richesse spécifique et leur plan anatomique original font souvent oublier l'importance de leurs diversités écologique et morphologique. Les espèces d'échinides se distribuent dans l'ensemble des océans et mers à salinités normales du monde, à toutes les profondeurs et latitudes, dans des provinces et habitats variés. Très dépendants des facteurs édaphiques (granulométrie, qualité et quantité de matière organique sur et dans les premiers centimètres de sédiment), il présentent des modes de nutrition (carnivores, dépositivores, algivores, omnivores, suspensivores), de reproduction et de développement variés (phases larvaires ou développement direct, larves planctotrophes ou lecitotrophes, planctoniques ou démersales, espèces dispersives ou incubantes). Cette diversité écologique s'accompagne d'une forte diversité morphologique qui s'exprime à la fois par de nombreux caractères structuraux du squelette (relations topologiques entre éléments du squelette) et par des caractères associés aux fonctions biologiques de nutrition, de respiration et de locomotion (fonctions associées de façon non exclusive aux appendices : pieds ambulacraires, pédicellaires, piquants et sphéridies).

Qualité du registre fossile

La qualité des informations fossiles disponibles et accessibles sur les échinides est très variable et sa nature parcellaire très inégale selon les taxons. La qualité du registre dépend bien sûr du niveau de préservation des environnements marins anciens. Le choix d'étudier les faunes d'environnements extrêmes (Antarctique et océan profond) s'accompagne inévitablement d'une importante lacune dans les informations fossiles. Ainsi, à de rares exceptions près (Kikuchi & Nikaido 1985, Gaillard *et al.* 2012), notre connaissance des faunes d'échinides profonds (faunes abyssales et hadales) s'appuie essentiellement sur les espèces actuelles et sur les représentants fossiles des phases précoces de diversification des clades dans les environnements de plate-forme distale (Smith 2004, Smith & Stockley 2005). Dans le même ordre d'idée, les échinides antarctiques fossiles ne sont connus depuis l'Aptien que par une vingtaine de taxons; contraste saisissant avec les 80 espèces de l'océan glacial actuel et réelle limite pour l'étude de leur diversité passée (Saucède *et al.* 2013b).

Les données d'occurrence fossiles sont également affectées par le caractère différentiel des processus taphonomiques qui dépendent des milieux et modes de vie des taxons. Cette inégalité du registre fossile existe à des niveaux taxinomiques variés, les radiations adaptatives à l'origine des grands clades impliquant une spécialisation pour certains milieux. Ainsi, les échinides irréguliers endobenthiques des environnements de faible hydrodynamisme tendent à bénéficer d'un meilleur registre fossile que les formes régulières épi-benthiques d'environnements exposés (Kier 1974). La diversité des échinides irréguliers du Jurassique Moyen est donc mieux documentée que celle des échinides cidaridés des environnements récifaux de la même période (Thierry & Néraudeau 1994).

Enfin, l'intégration de données actuelles et fossiles dans mes recherches a été très clairement conditionnée par les différences de nature entre espèces paléontologiques (morphologiques) et biologiques (morphologiques, écologiques et génétiques). L'identité morphologique a toujours primé sur les données paléoécologiques et stratigraphiques quand il s'est agi de définir des espèces fossiles. En l'absence d'arguments morphologiques objectifs, les distinctions géographiques et stratigraphiques parfois déjà observées autrefois par certains auteurs (Cotteau 1857-1878, 1862-1867, Valette 1908, Corroy 1925, Rat *et al.* 1987) ont été généralement révisées et mises en synonymie. Cette simplification 'opérationnelle' de la systématique des espèces d'échinides fossiles n'entraîne pas nécessairement une plus juste estimation des richesses spécifiques fossiles, l'écophénotypisme (différences morphologiques intra-spécifiques) étant par exemple rarement pris en compte dans les études (David 1985, Néraudeau 1995, Saucède *et al.* 2012, 2013b). Elle ne permet pas non plus d'éviter une certaine distortion du signal de diversité fossile, particulièrement gênante quand il s'agit de traiter des signaux fossiles et actuels dans une même étude (Saucède *et al.* 2013b). En effet, outre les pertes partielles ou totales des informations écologiques et génétiques, la diagnose des espèces fossiles repose sur une information morphologique partielle. L'information morphologique portée par les appendices (pédicellaires, piquants, sphéridies, pieds ambulacraires) et l'information de couleur étant généralement perdues lors de la fossilisation. Or, les données génétiques d'une étude récente (Diaz *et al.* 2011) et de travaux en cours confirment la pertinence et la précision de l'information morphologique portée par les appendices pour identifier à la fois les différenciations et les relations phylétiques entre espèces proches. A l'inverse, l'information portée par les caractères structuraux du squelette est plus facilement conservée chez les fossiles. Elle est généralement utilisée à des niveaux taxinomiques de rangs supérieurs à celui de l'espèce. La valeur diagnostique de ce type de caractère a cependant été démontrée au niveau spécifique pour certains clades (espèces de spatangues schizasteridés, Madon-Senez 1998, David *et al.* 2005).

Ateliers	**Collecte des données**		**Nature des données**				**Travaux publiés**
	origine	**descriptif**	**occurrence**	**abondance**	**morphologie**	**génétique**	
Echinides irréguliers jurassiques	terrain	Aalénien - Bajocien, Le Faye (Sarthe)	✗				5, 9, 24
		Lias - Bajocien, Amellago (Maroc)	✗				
		Jurassique Moyen et Supérieur, Côte d'Or, Nièvre, Haute-Marne, Saône et Loire	✗		✗		
	collections publiques	universités (Dijon, Lyon, Rennes, Grenoble, Poitiers, Berkeley); musées (MNHN Paris, CAS San Francisco, Boulogne-sur-Mer, Lille, Grenoble)	✗		✗		
	collections privées	Dudicourt, Clavel, Votat, Boursicot, Nicolleau, Ronnat	✗		✗		
	publications	littérature	✗		✗		
Echinides irréguliers crétacés	terrain	Hauterivien, bassin de Paris	✗	✗	✗		6, 8, 23, 29
		Cénomanien-Turonien, Tunisie	✗				
	collections publiques	universités (Dijon, Rennes, Grenoble)	✗		✗		
	collections privées	Robert	✗		✗		
	publications	littérature	✗				
Echinides austraux	terrain	campagne Bentart - Antarctique	✗	✗		✗	10, 11, 14, 15, 16, 18, 19, 20, 21, 22, 25, 26, 28, 31, 32, 33, 34
		campagne ANT XIII/8 - Antarctique	✗			✗	
		campagne JR230 - Antarctique	✗			✗	
		station Las Cruces - Chili	✗		✗	✗	
		station Rothera - Antarctique	✗		✗	✗	
	collections publiques	universités (Dijon, Concepcion, Santiago, Coquimbo), instituts (BAS, NIWA, GNS Sciences), musées (MNHN, Buenos Aires, Melbourne, Sydney, Malaga, Gène)	✗		✗	✗	
	publications	base de données (Echinide, SOMBASE, FRED)	✗				
		littérature	✗		✗		
Echinides abyssaux	collections publiques	instituts (CAS, NIWA, Shirshov), universités (Dijon), musée (MNHN)	✗		✗		13
	publications	littérature	✗		✗		

Tableau 2. Origine et nature des données collectées pour les différents modèles d'étude. Les numéros des publications associées suivent l'ordre de la liste fournie dans la partie "Bilan d'activité".

2. Nature, origine et qualité des données

Mes activités de recherche reposent essentiellement sur l'acquisition et l'analyse de données d'occurrence spatiale, d'occurrence stratigraphique, d'abondance et de morphologie. Dans mes travaux de macroécologie, données spatiales et morphologiques sont comparées aux données environnementales (paramètres des environnements marins actuels) et paléoenvironnementales (sédimentologiques et paléontologiques), dans le cadre d'approches corrélatives visant à caractériser les particularismes écologiques des espèces. Ces approches nécessitent de disposer de phylogénies robustes et d'un cadre systématique révisé et cohérent. Les analyses phylogénétiques réalisées reposent sur l'identification et l'analyse de l'information phylétique portée par les données morphologiques ; dans le cas des espèces actuelles, les données morphologiques ont été confrontées aux données génétiques dans le cadre de collaborations avec des collègues biologistes (tableau 2).

2.1. Nature des données

Données d'occurrence et d'abondance

Les données d'occurrence fournissent des informations sur la distribution spatiale des taxons actuels et fossiles ainsi que sur la distribution stratigraphique des taxons fossiles. Données d'occurrence spatiales et stratigraphiques ont été analysées conjointement dans une étude portant sur la biogéographie des faunes australes et son évolution au cours du Cénozoïque (Saucède *et al.* 2013b). Dans mes autres travaux, données spatiales et stratigraphiques, fossiles et actuelles, ont fait l'objet d'études séparées.

Les données d'occurrence spatiale consistent en des données géoréférencées de présence seule, la nature de l'échantillonnage ne permettant généralement pas de disposer de données d'absence fiables. Les conséquences analytiques seront développées dans le chapitre 4. La géolocalisation des données est le plus souvent acquise directement lors de l'échantillonnage sur le terrain ou par l'intermédiaire de collègues pour le matériel, publié ou non, de collections récentes. Dans le cas du matériel de collections anciennes, le géoréférencement est réalisé postérieurement à la collecte des spécimens sur la base des localités mentionnées, la précision et la qualité des données s'en trouvant diminuée. Dans tous les cas, la cohérence de l'information (toponymies incertaines, confusion entre données de longitude et de latitude) a été contrôlée par comparaison avec les données de distribution et d'habitat déjà acquises, ou par recoupement avec les informations stratigraphiques et géologiques disponibles dans le cas des taxons fossiles. En cas de doute, les données ne sont pas prises en compte. Rares sont les missions d'échantillonnage qui ont permis de vérifier la fiabilité des données de localisation, les preuves d'absence de taxons fossiles ou actuels étant difficiles à obtenir. Cela n'a été possible que dans le cas d'espèces très communes (exemple de l'espèce littorale *Tetrapygus niger* mentionnée en Patagonie mais jamais retrouvée malgré de nombreuses plongées).

J'ai pu participer à deux études réalisées à partir de données d'abondance: l'étude de la distribution d'échinides fossiles du bassin de Paris et l'étude de l'endofaune actuelle de la mer de Bellingshausen (Antarctique) (Saiz *et al.* 2008). L'information écologique portée par les données d'abondances absolues est beaucoup plus pertinente que celle des données d'abondances relatives, et ces dernières plus pertinentes que les données de présence seule (Pulliam 2000, Bahn & McGill

2013). Cependant, en l'absence de données d'abondances disponibles fiables, des procédures permettent d'utiliser les données de présence seule (modèles de niche) pour identifier les préférences écologiques des espèces (Pearce & Ferrier 2001, Varela *et al.* 2011, Aguirre-Gutiérrez *et al.* 2013, Bahn & McGill 2013). L'acquisition des données d'abondance requiert en outre un effort d'échantillonnage conséquent, rarement conciliable avec les contraintes de temps et de moyens imposés par les études à larges échelles. Dans le cas des d'échinides fossiles du bassin de Paris, une campagne d'échantillonnage exhaustive de plusieurs mois avait été réalisée par B. David en 1984 dans un seul niveau fossilifère, sur une centaine de sites couvrant une superficie d'environ 20 km sur 250 km (figure 1.1). Quelques sites tests ré-échantillonnées 25 ans plus tard dans le cadre de l'encadrement d'un stage de Master 2 (Samant 2008) m'ont permis de tester la représentativité et la reproductibilité des données d'abondance relative. Dans le cas de l'échantillonnage avec carottier boîte en mer de Bellingshausen, la nature de l'endofaune étudiée (meiofaune principalement), l'outil d'échantillonnage utilisé (carottier), ainsi que les réplicats systématiques réalisées, très coûteux en temps, personnes et énergie, ont permis de contrôler la reproductibilité et la fiabilité des données d'abondance absolue et relative. De telles campagnes d'échantillonnage sont très difficiles à mettre en œuvre à une telle échelle spatiale.

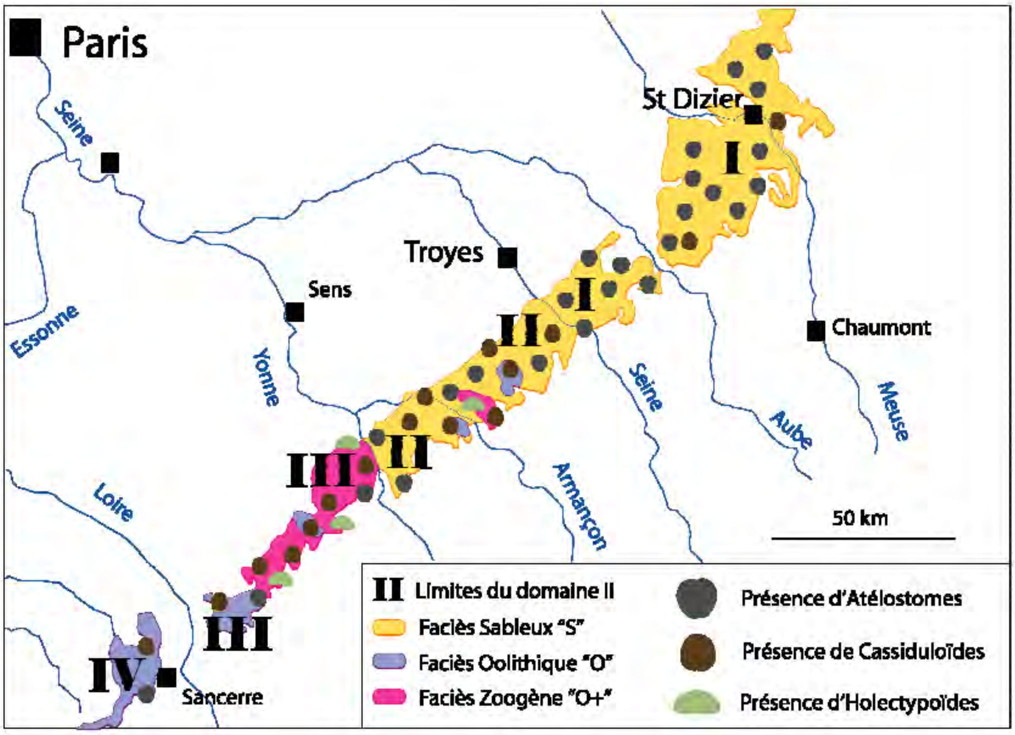


Figure 1.1. Echantillonnage de données d'abondance relative le long de la zone d'affleurement hauterivienne (d'après Samant 2008).

Les données d'occurrence stratigraphique collectées sur le terrain (pour l'étude des échinides irréguliers jurassiques et crétacés) ou à partir de collections récentes permettent généralement d'avoir une précision d'analyse proche de la zone d'ammonite pour les espèces européennes. Cette précision est largement suffisante, l'extension stratigraphique des espèces d'échinides fossiles étant souvent de l'ordre du sous-étage, voire au-delà (Thierry 1984, Thierry & Néraudeau 1994, Thierry *et al.* 1997). Les informations stratigraphiques tirées de collections anciennes ou de la littérature mentionnent souvent le nom des formations géologiques qui en Europe permettent d'approcher une précision de l'ordre du sous-étage. Dans le cas des données d’occurrence d’espèces non-européennes issues de collections et de publications, la précision est souvent moindre et les équivalences difficiles à établir avec précision (cas des équivalences stratigraphiques entre Formations australiennes, néo-zélandaises et sud-américaines, Saucède *et al.* 2013b). L’analyse des données au niveau du genre permet en partie de limiter l’impact des incertitudes biostratigraphiques sur les résultats (Saucède *et al.* 2013b).

Dans le cadre de mes travaux de macroécologie, les données d’occurrence spatiales ont été comparées aux informations environnementales afin de définir la préférence écologique des espèces. Les données environnementales ont été acquises parfois à partir de prélèvements ponctuels sur le terrain (Saiz *et al.* 2008, Moya *et al.* 2012), mais elles ont été le plus souvent tirées de publications (bases de données et données de la littérature) ou acquises sous forme de cartes environnementales (couches SIG issues de sources variées, voir chapitre 4). Il s’agit selon les cas de données catégorielles (ex : nature des sédiments, granulométrie) ou continues (ex : profondeur, température). La résolution et la précision des données dépendent de leur origine et de leur nature ; relativement bonnes pour les données de terrain (données ponctuelles), elles le sont moins pour les données ponctuelles extrapolées à une surface (cartes SIG) et les données de modélisation (précision de l’ordre de 0,5 degré de latitude et de longitude à l’échelle de l’océan Austral).

Données morphologiques

Les données morphologiques utilisées ont été acquises à partir de spécimens collectés sur le terrain, de matériel de collections, ou d’informations tirées de publications. Chez les échinides, l’information morphologique est portée par un grand nombre de caractères différents (figure 1.2): dimensions et formes du contour du test (Saucède *et al.* 2013a), topologie des contacts entre plaques du squelette (Laffont *et al.* 2011, Saucède *et al.* 2012), forme et dimension des appendices (piquants, pédicellaires, sphéridies, rosettes des pieds ambulacraires) et de la lanterne d’Aristote (Saucède *et al.* 2007, Díaz *et al.* 2011) et position des organes (tubercules, fascioles, périprocte, péristome, pores génitaux, pores ambulacraires – voir Saucède & Néraudeau 2006, Saucède *et al.* 2007). L’information de couleur est également utilisée comme caractère diagnostique pour un grand nombre d’espèces d’échinides réguliers (Mortensen 1935, 1940). Les différentes méthodes d'acquisition et d'observation des données dépendent des parties anatomiques étudiées : pied à coulisse et analyses de contour pour le test, simple loupe binoculaire pour les caractères structuraux du squelette et la majorité des appendices, microscope électronique pour les plus petits organes (pédicellaires, clavules et sphéridies) jusqu'à l'étude en tomographie des microstructures squelettiques (observations réalisées en collaboration avec des collègues de Chicago et d’Uton aux Etats Unis). La qualité de l’information phylétique apportée par les données morphologiques varie selon les caractères, les clades et le niveau taxinomique des analyses. Les appendices et la couleur peuvent permettre de résoudre les relations de parenté entre espèces d'échinides réguliers. A l'inverse, les caractères structuraux de la couronne (topologie des plaques) ne permettront de résoudre les relations entre espèces que chez certains échinides irréguliers. La nature des caractères morphologiques porteurs d’information phylétique est aussi un facteur déterminant pour la performance des reconstitutions phylogénétiques fossiles. L’absence de fossilisation de certains caractères de la vestiture (pédicellaires et piquants en place) peut rendre vaine la résolution des relations de parenté de certains groupes fossiles (cas des Cidaridae jurassiques).

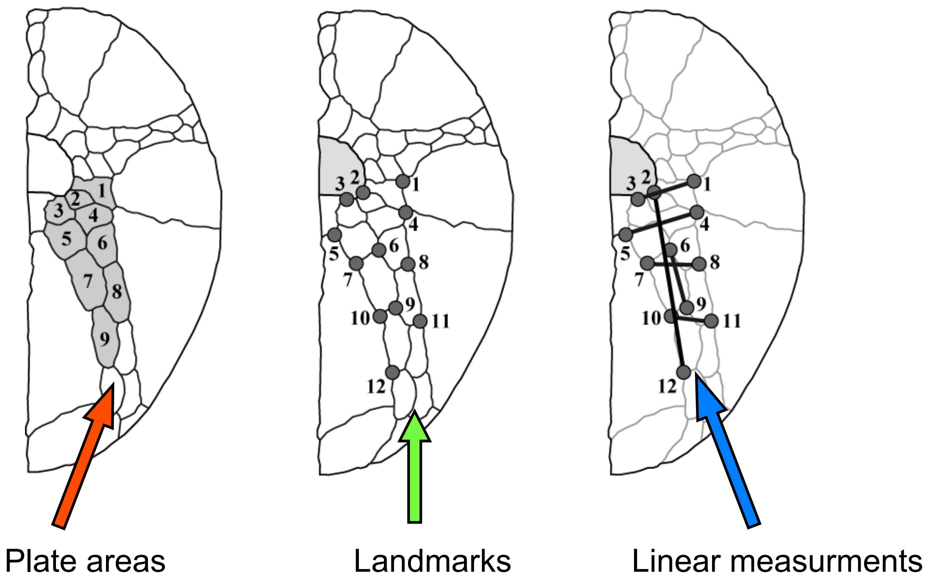


Figure 1.2. Exemples de caractères morphologiques pouvant être définis à partir du test des échinides (moitié gauche de face orale du spatangue *Echinocardium cordatum*, d'après Saucède *et al.* 2006).

La diversité (nature et nombre) des caractères morphologiques portés par les échinides (Smith *et al.* 2006), et en particulier par les échinides irréguliers (diversité de forme, d'architecture de plaques, de vestiture), est riche d'informations utilisables pour les reconstitutions phylogénétiques et les études de diversité (taxinomique et morphologique) actuelles et passées. Malgré la mauvaise préservation de certains caractères et la perte partielle d'information, l'intégration des informations actuelles et fossiles permet en outre d'interpréter l'évolution de la diversité morphologique passée sous son aspect de diversité fonctionnelle, de discuter des processus macroécologiques sous-jacents et de caractériser les assemblages et les écosystèmes anciens (Villéger *et al.* 2008, 2011, Mason & Bello 2013).

Malgré la diversité des caractères morphologiques disponibles chez les espèces d'échinides actuelles, cette diversité n'égale pas celle des caractères portés par les gènes, et les distances morphologiques entre taxons ne sont pas directement transposables de façon linéaire en distances phylétiques. Dans le cas de mes travaux sur les échinides austraux, l'étude des caractères morphologiques des taxons actuels a été souvent associée à celle des données génétiques (tableau 2) dans le cadre de collaborations avec des collègues biologistes (voir la partie consacrée aux données génétiques ci-dessous). La confrontation des données morphologiques et génétiques a été réalisée dans des analyses comparatives. Ces dernières, loin de démontrer le manque d'intérêt des données morphologiques porteuses de relativement peu de caractères phylétiques informatifs comparées aux données génétiques, utilisent l'information morphologique pour différents objectifs:

(1) En premier lieu, les données morphologiques revêtent un intérêt d'ordre opérationnel quand il s'agit d'identifier clairement les espèces à séquencer, de contrôler le référencement des données dans les bases de données génétiques (genbank) et d'avoir une première idée qualitative de la proximité phylétique entre espèces (et ainsi éviter des choix maladroits d'outgroups et de séquences analysées). A posteriori, la morphologie permet d'identifier clairement les espèces sur le terrain, sur la base de caractères morphologiques diagnostiques.

(2) D'autre part, certains caractères morphologiques peuvent être porteurs d'information phylétique non identifiée par les analyses génétiques ; elle peut alors contribuer à une meilleure résolution des relations de parenté (Nylander *et al.* 2004, Smith *et al.* 2006).

(3) La différentiation morphologique entre taxons peut être reportée sur les arbres de relations de parenté afin d'identifier les processus écologiques à l'origine des différentiations ou d'interpréter les contextes de la différentiation, en particulier quand ces caractères sont liés à des fonctions biologiques. Le manque de congruence éventuelle entre signaux morphologiques et génétiques renseigne alors sur l'histoire évolutive des caractères (Nylander *et al.* 2004). Dans le cas des espèces cryptiques, l'absence de différentiation morphologique est une information importante en soi pour identifier les processus écologiques impliqués.

(4) Enfin, l'information morphologique permet d'intégrer des données fossiles dans les phylogénies, données qui peuvent fournir des estimations des dates de divergence indépendantes.

Données génétiques

Lors de mon travail sur le terrain, la récolte d'échinides actuels est généralement suivie de la fixation des spécimens et/ou de leurs tissus (muscles situés à la base des piquants le plus souvent) dans l'éthanol et de leur congélation pour analyses génétiques ultérieures. Les analyses génétiques sont réalisées dans le cadre de collaborations avec des collègues biologistes des universités d'Aix-Marseille, de Santiago (Chili) et de l'Académie des Sciences de République Tchèque. Les analyses réalisées ont surtout utilisé les marqueurs mitochondriaux COI (Cytochrome c Oxidase 1) et ARN ribosomique 16S et les marqueurs nucléaires ITS (Internal Transcribed Spacer) et ARN ribosomique 28S. Les données génétiques obtenues par les collègues m'ont fourni des informations cruciales pour la reconstitution des phylogénies et la compréhension de l'histoire biogéographique des faunes australes (Diaz *et al.* 2011). Les analyses en cours portent sur la reconstruction des relations phylétiques au sein de quatre familles d'échinides austraux (Echinidae, Schizasteridae, Cidaridae et Arbaciidae). La résolution des phylogénies à partir des données génétiques présentent un double intérêt dans mes travaux : la révision systématique des espèces et l'identification ou la confirmation de caractères morphologiques porteurs d'information phylétique, indépendamment des analyses de parcimonie réalisées à partir des données morphologiques seules (figure 1.3). En outre, les analyses génétiques réalisées sur un nombre suffisant de spécimens d'une même espèce et échantillonnés en différents sites nous ont permis de cartographier la structuration génétique de populations (phylogéographie) et de tester la robustesse d'hypothèses biogéographiques (voir chapitre 4).

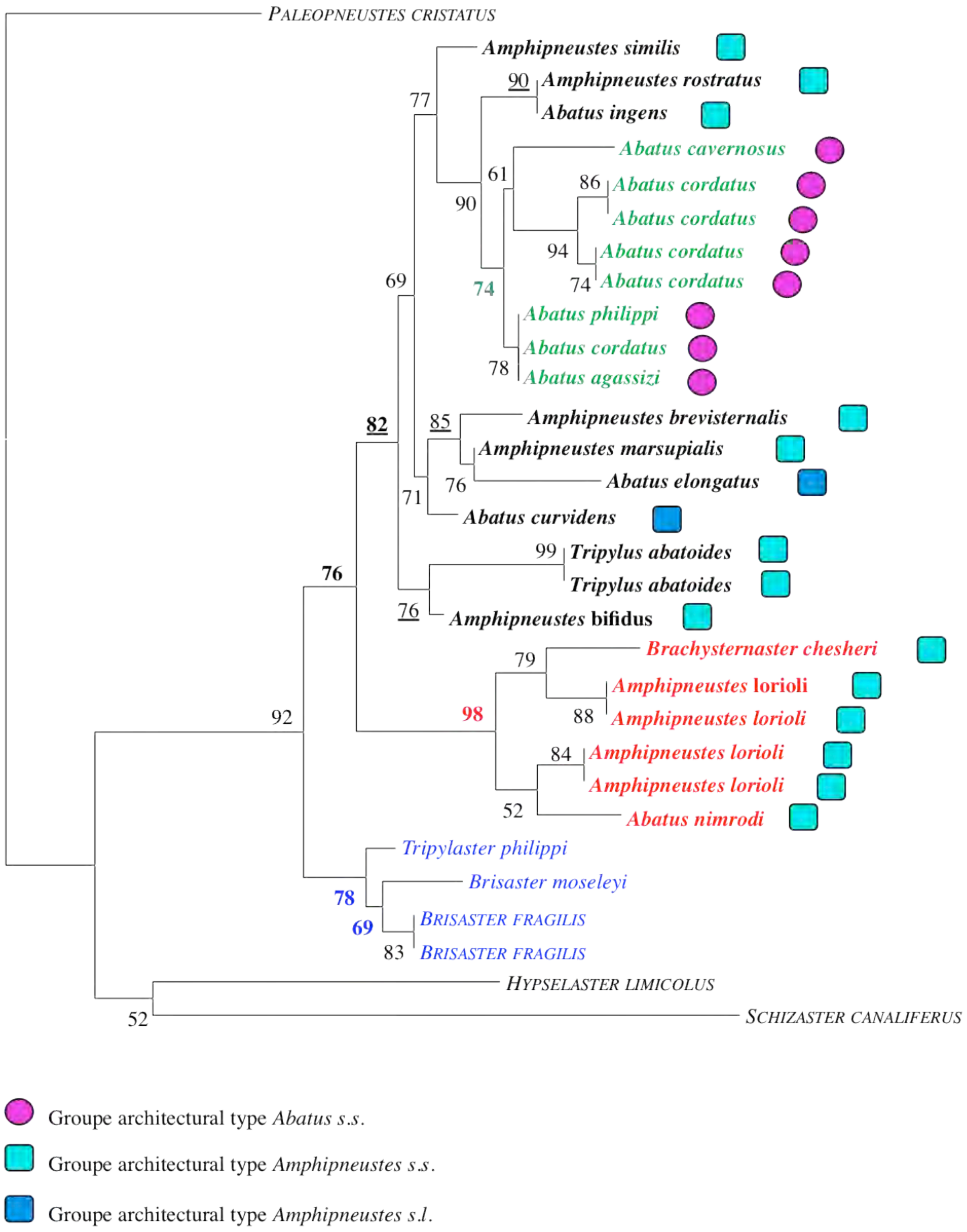


Figure 1.3. Comparaison entre groupes morphologiques (architecture des plaques du test) et phylogénie établie à partir des paires de bases 55 à 300 du gène COI (étude en cours sur les Schizasteridae antarctiques).

2.2. Origine et qualité des données

Les données utilisées proviennent de missions d'échantillonnage que j'ai réalisées sur le terrain, de données acquises à partir de spécimens de collections, et de données tirées de la littérature (tableau 2). Les données acquises sur le terrain constituent un jeu de données dont je peux directement contrôler la reproductiblité, ou tout du moins en avoir une idée. Parmi les missions d'échantillonnage que j'ai réalisées, ou auxquelles j'ai participé, un premier ensemble a eu pour but de compléter et de vérifier des jeux de données déjà constitués à partir de spécimens de collections et de publications (faunes d'échinides austraux, échinides crétacés du bassin de Paris). Un deuxième ensemble de missions avait pour objectif de réaliser des études très ciblées afin d'analyser localement la relation entre contexte sédimentaire, composition des faunes échinides (échinides jurassiques de la Sarthe, du Maroc, échinides crétacés de Tunisie), et variations morphologiques de ces faunes (échinides crétacés du bassin de Paris).

L'analyse des motifs de diversité à large échelle implique de pouvoir disposer de grands jeux de données qui nécessiteraient des campagnes d'échantillonnage de terrain trop nombreuses et coûteuses à la fois en temps et en moyens. J'ai donc eu recours à l'analyse de données collectées aussi (et surtout!) par d'autres depuis parfois plus d'un siècle et demi. La qualité des données anciennes est par nature plus difficilement contrôlable que celle des données collectées par des collaborateurs en activité. L'hétérogénéité des données issues d'origines variées a d'importantes conséquences pour la qualité des analyses réalisées et nécessite une vérification permanente afin d'homogénéiser au mieux les bases de données constituées (Pierrat *et al.* 2012a, Benetti *et al.* 2013). L'acquisition de données de collections et de la littérature m'ont cependant permis d'acquérir suffisamment de données de régions parfois difficilement accessibles (échinides antarctiques).

Données issues de matériel collecté sur le terrain

- Collecte du matériel biologique :

Depuis 2006, j'ai pu participer à des missions d'échantillonnage de matériel biologique dans le cadre de trois missions océanographiques dans l'océan Austral et de deux séjours de travail en station marine au Chili et en Terre de Graham (Péninsule antarctique). Ma participation aux missions océanographiques avait pour but d'acquérir de nouvelles données de distribution sur les échinides, dans des secteurs encore peu étudiés de l'océan Austral (mer de Bellingshausen, secteur de Larsen), et de disposer de nouveau matériel pour obtenir des données morphologiques et génétiques. Outres les nombreuses collaborations scientifiques développées, ces longues missions (plus de six mois cumulés) m'ont permis de constituer un jeu de données qui a été exploité dans le cadre du co-encadrement d'une thèse de doctorat (Pierrat 2011), de l'encadrement de trois stages de Master (Hardy 2008, 2009, Rullmann 2009), et valorisé par plusieurs publications (tableau 2).

Les missions océanographiques ont été réalisées dans le cadre de programmes nationaux, programme espagnol du ministère de la recherche (campagne Bentart, 2005-2006), projet allemand de l'Institut Alfred Wegener (mission ANT XXIII/8, 2006-2007) et projet britannique du British Antarctic Survey (campagne JR230, 2009-2010). Elles étaient également adossées à de grands programmes internationaux de recensement de la biodiversité marine antarctique pilotés par le

Scientific Committee on Antarctic Research (volet Census of Antarctic Marine Life du programme Census of Marine Life, Alexander *et al.* 2011) et par le comité de l'Année Polaire Internationale (2007-2008). Elles ont consisté en la collecte de données (échantillonnage et observation) sur la diversité des faunes benthiques en de nombreuses localités (figures 1.4a, b & c) et à l'aide d'outils de prélévement et d'observation variés : chaluts Agassiz, benthique, supra-benthique, carottier boîte, caméras sous-marines OFOS (*Ocean Floor Observation System*) et robots ROV (*Remotely Operated Vehicle*). La nature des outils utilisés et les superficies étudiées ont surtout permis d'acquérir des données d'occurrence d'espèces (à de rares exceptions près: voir le paragraphe consacré aux données d'abondance ci-dessus). Le travail des outils d'échantillonnage sur les fonds marins revêt un caractère aléatoire (position et contact du chalut avec le fond peu contrôlables), surtout à grande profondeur (jusqu'à 3000 m), et ne permet pas de contrôler l'homogénéité des surfaces échantillonnées. D'autre part, l'utilisation fréquente de chaluts à grande ouverture (plusieurs mètres) sur de longues durée de temps (plusieurs dizaines de minutes) implique un échantillonnage hétérogène d'habitats variés pour lesquels des réplicats sont peu pertinents (zones couvertes par les stations et limites des stations difficilement estimables). Des protocoles d'échantillonnage plus contraints ont cependant permis de répondre en partie à ces problèmes (figure 1.5). La comparaison des faunes collectées par les chaluts Agassiz et benthique a également démontré l'importance du biais d'échantillonnage lié aux outils utilisés, chaque station n'étant pas échantillonnée par l'ensemble des outils disponibles. Enfin, les contraintes météorologiques et les conditions de glace ont parfois rendu difficiles l'accès à certains sites, la mise à l'eau des outils et la réalisation des plans d'échantillonnage préalablement établis (jamais pleinement réalisée dans les faits !). Les données d'occurrence recueillies n'ont donc pu être exploitées qu'à large échelle spatiale. L'utilisation des moyens vidéo d'observation du fond marin a surtout fourni des renseignements sur les habitats et les communautés échantillonnées (OFOS et ROV), l'identification des espèces à partir des images enregistrées étant généralement impossible (caractères diagnostiques visibles à la loupe binoculaire uniquement).

Outres les missions océanographiques, deux séjours en station marine m'ont permis de prélever du matériel biologique ciblé pour des analyses morphologiques et génétiques qui participaient à des projets de phylogénies et d'analyses biogéographiques. Le séjour d'étude dans la station marine de Las Cruces (Chili) a donné lieu à des collectes des spécimens de l'espèce d'échinide *Tetrapygus niger*. Elle s'est déroulée dans le cadre d'un financement européen ASSEMBLE en avril 2011. Enfin, le séjour dans la station de Rothera (Terre de Graham) faisait suite à la mission JR230 (janvier 2010) et j'ai pu échantillonner des spécimens de l'espèce d'échinide *Sterechinus neumayeri* (Díaz *et al.* 2011) et du gastéropode *Nacella concinna* (González-Wevar *et al.* 2013).

Figure 1.4a. Quelques représentants communs des communautés benthiques antarctiques régulièrement échantillonnés (mission JR 230). De gauche à droite et de haut en bas : isopodes, échinide, éponge, holothurie, polychète, astérie, cnidaire, holothurie, chaetognathe, notothénioïdes, céphalopodes, crinoïde, amphipode, ophiure et pycnogonide.

Figure 1.4b. Quelques outils d'échantillonnage. De gauche à droite : chalut Agassiz, drague à roche et carottier boîte (mission BENTART'06).

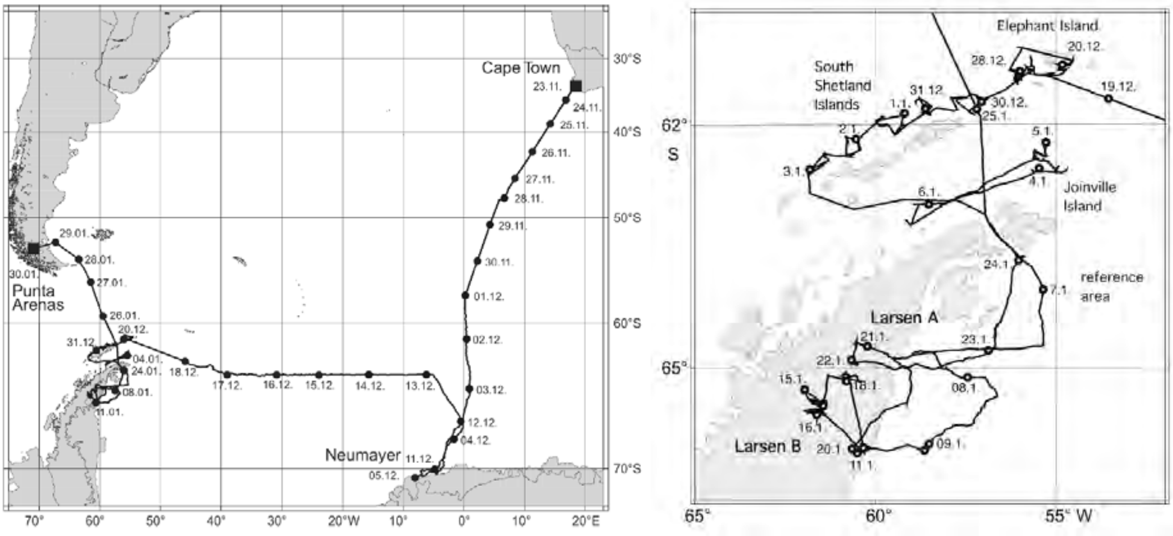


Figure 1.4c. Itinéraire général (gauche) et parcours détaillé (droite) du navire océanographique allemand *Polarstern* réalisé depuis l'Afrique du Sud vers l'Antarctique Est, la Péninsule Antarctique puis le Chili de novembre 2006 à janvier 2007 (mission ANTXXIII/8).

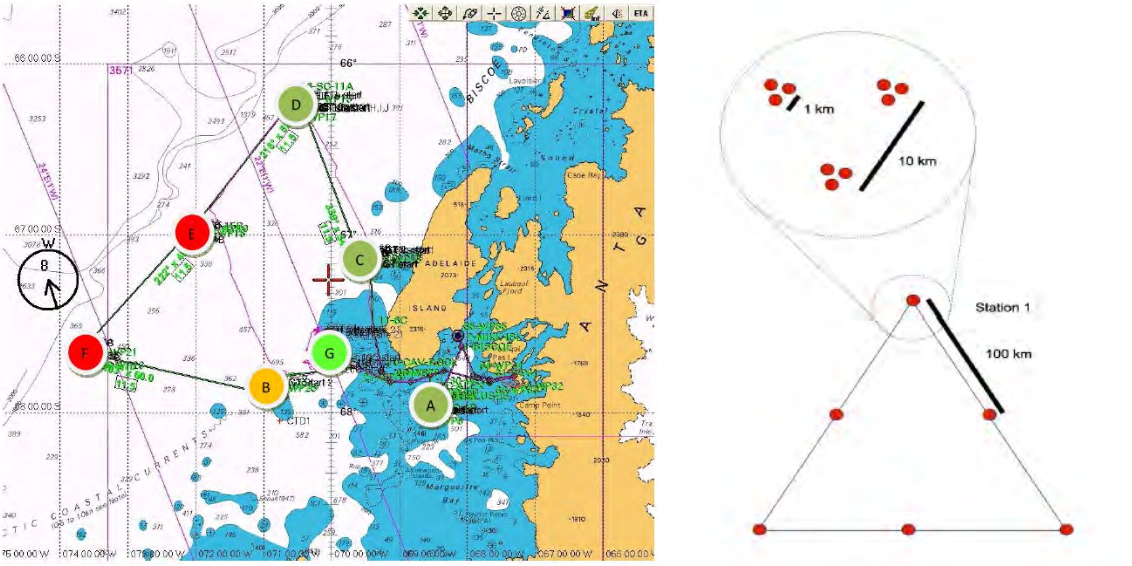


Figure 1.5. Exemple de protocole d'échantillonnage par chalutage consistant en trois réplicats réalisés respectivement à 1 km, 10 km et 100 km d'intervalle en six localités contrastées des zones internes, moyennes et distales du plateau continental (mission anglaise JR230 de janvier 2010 réalisée le long de la côte ouest de la Péninsule Antarctique; la localité G a remplacé la localité B alors couverte de glace et inaccessible).

- Collecte du matériel fossile :

Plusieurs missions de collecte de matériel fossile ont eu lieu depuis 2005. Elles ont eu pour objectif commun de collecter des spécimens d'échinides irréguliers dans leur contexte sédimentaire en des sites et dans des niveaux bien ciblés, connus (ou récemment découverts) pour leur caractère fossilifère. Les spécimens collectés ont permis d'étudier le lien entre faunes d'échinides et contexte paléoenvironnemental à l'échelle locale (échelle du site) ou régionale (zone d'affleurement des formations), pour des niveaux et régions généralement peu étudiés. Des coupes sédimentologiques ont été levées (avec leurs données sédimentologiques), la position stratigraphique des spécimens notée ; les datations ont été établies à l'aide des faunes d'ammonites.

Une première mission d'une semaine (avril 2010) dans des niveaux pliensbachiens et bajociens de la région d'Amellago (Haut Atlas Marocain) a été réalisée en collaboration avec C. Durlet (Biogéosciences, Dijon). Les niveaux pliensbachiens correspondent à des environnements de plate-forme distale riches en bivalves 'lithiotidés', gastéropodes et cidaridés. Les niveaux bajociens correspondent à des environnements de plate-forme interne riches en faunes de mollusques et échinides Acrosaleniidae. Ces niveaux ont livré un spécimen du plus ancien représentant connu d'échinide atélostome (*Orbignyana ebrayi*), groupe jurassique d'échinide irrégulier à l'origine des spatangues et holastéroïdes actuels.

Une seconde mission d'échantillonnage a eu lieu dans les niveaux aaléniens et bajociens de la Sarthe (figure 1.6). Ces niveaux correspondent aux premières incursions marines du Jurassique Moyen dans la région et représentent des environnements marins proximaux (conglomérats, grès, calcaires gréseux grossiers, bioclastiques puis oolitiques) mal datés, riches en échinides et en échinides irréguliers Pygasteridae et Galeropygidae en particulier. La découverte d'ammonites a permis de préciser le cadre biostratigraphique et de positionner la limite Aalénien-Bajocien. La succession des faunes d'échinides a été étudiée dans le cadre de l'encadrement d'un stage de Master 1 (Contigliani 2009). Plusieurs missions de quelques jours ont été réalisées en collaboration avec P. Courville (Géosciences, Rennes) et C. Durlet (Biogéosciences, Dijon).

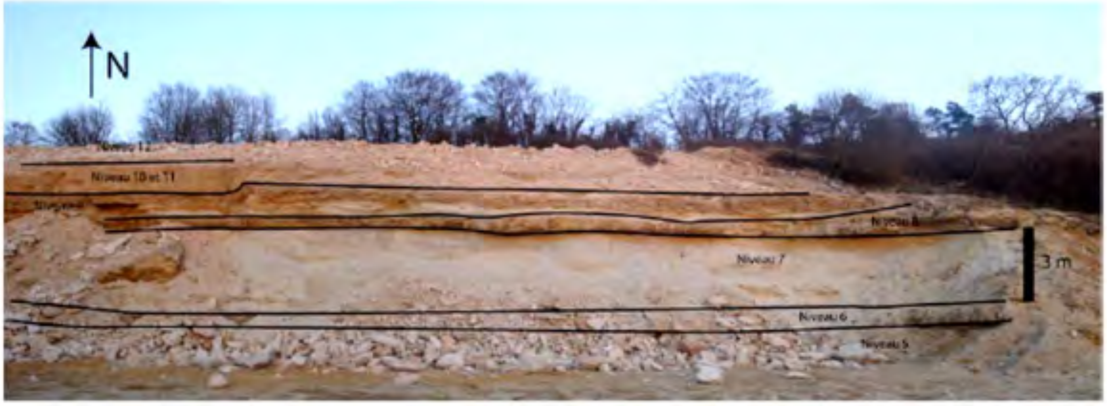


Figure 1.6. Niveaux aaléniens fossilifères de la Sarthe (coupe du Faye).

Une troisième mission a consisté en un échantillonnage d'échinides le long de plusieurs coupes connues de l'Aptien, Cénomanien et Turonien du Nord Ouest Tunisien, coupes datées grâce aux faunes d'ammonites (Chihaoui *et al.* 2010) et riches en échinides irréguliers (spatangues et holastéroïdes principalement). Cette mission d'une semaine a été réalisée en avril 2005 en collaboration avec A. et H. Arnaud, et E. Jaillard du laboratoire LGCA de Grenoble. Elle a permis de collecter une faune diversifiée d'échinides irréguliers dans des paléo-environnements de plate-forme distale. Des missions de terrain plus récentes réalisées par les collègues ont complété l'inventaire de la faune d'échinides déjà collectée. L'identification et la révision systématique de cette faune sont toujours en cours.

Plusieurs journées d'échantillonnage ont eu lieu dans les niveaux hauteriviens du Sud-Est du bassin de Paris (Formation des Calcaires à Spatangues) dans le cadre de l'encadrement d'un stage de Master 2 (Samant 2008). La collecte de spécimens en des sites de faciès contrastés (calcaires marneux à composante oolitique, bioclastique ou gréseuse) avait pour objectif de tester la relation entre variabilité morphologique et environnement sédimentaire chez deux espèces d'échinides irréguliers abondantes : *Coehnolectypus macropygus* et *Phylobrissus greslyi*. La collecte de nombreux spécimens suffisamment bien préservés a permis l'analyse des variations de formes par analyse de contour (analyse de Fourier) et a montré l'existence de différences de forme entre les échantillons des faciès gréseux d'une part, oolitiques et bioclastiques d'autre part.

Enfin, des journées ou demi-journées d'échantillonnage ponctuelles ont eu lieu régulièrement dans les niveaux du Jurassique Moyen et Supérieur de Côte d'Or, Nièvre, Haute-Marne et Saône-et-Loire. Les spécimens collectés alimentent une base de données toujours en cours de constitution sur la distribution des échinides en fonction des contextes sédimentaires.

Données issues de collections

Une grande partie des données de distribution et des données morphologiques provient de spécimens de collections publiques et privées. Les spécimens de collections privées et une partie des spécimens de collections publiques ont été récoltés par des collègues et personnes avec qui je collabore régulièrement, ce qui me permet de m'assurer de l'origine (localisation et position stratigraphique) des spécimens. A l'inverse, les spécimens de collections anciennes ne me permettent pas toujours de connaître l'origine du matériel avec précision (absence de données de localisation précises). Les spécimens de collection interviennent dans les analyses morphologiques réalisées dans le cadre de révisions systématiques de taxons actuels et fossiles (Saucède *et al.* 2009, 2012, 2013a).

Une partie des spécimens de collections publiques étudiés provient de missions océanographiques (tableau 2). Les données recueillies alimentent une base de données (http://ipt.biodiversity.aq/resource.do?r=antarctic_subantarctic_and_cold_temperate_echinoid_data base). Celle-ci est consultable en ligne; elle inventorie les données de distribution des échinides austraux au sud de 35°S (Pierrat *et al.* 2012). Cette base de données comporte actuellement plus de 6200 données géoréférencées de 149 espèces nominales (révision toujours en cours).

Le matériel fossile de collections publiques et privées me fournit des données d'occurrence pour l'étude des espèces jurassiques et crétacées (tableau 2). Une partie de ces données alimente une base de données, actuellement consultable en ligne (http://ipt.pensoft.net/ipt/resource.do?r=hauterivian_echinoids_of_the_paris_basin), et qui inventorie la distribution des échinides hauteriviens du bassin de Paris. Cette base de données a été en partie constituée dans le cadre d'un stage d'étudiant de L3 (Benetti *et al.* 2013). Cette base comporte des données de distribution géographique de 26 espèces d'échinides réguliers et irréguliers couvrant une surface d'environ 250 km sur 20 km, et comportant plus de 600 données d'occurrence. La systématique des espèces a été révisée et publiée (Saucède *et al.* 2012).

Données tirées de la littérature

Les données tirées de publications me permettent de compléter les données d'occurrence fossiles et actuelles acquises sur le terrain et en collection. Ce type de données ne permet pas toujours un très bon contrôle de sa fiabilité, en particulier en l'absence d'illustrations.

Outre les données tirées de la littérature, j'ai eu recours à l'utilisation de bases de données déjà constituées pour réaliser des analyses comparatives à large échelle (impliquant des jeux de données importants) entre espèces d'échinides actuelles et fossiles, ou entre les échinides et d'autres groupes taxinomiques pour lesquels je ne possédais aucune donnée. Ainsi, des données d'occurrence ont été obtenues à partir de la base de données *SOMBASE* (Southern Ocean Molluscs Data Base, Griffiths *et al.* 2003) pour une analyse biogéographique comparative entre faunes d'échinides, et faunes de bivalves et de gastéropodes de l'océan Austral (Pierrat *et al.* 2013a). *SOMBASE* a également fourni les données utilisées dans une analyse de modélisation de niche réalisée à l'échelle des communautés (travail en cours). Une base de données fossile, la base *FRED* (the Fossil Record Electronic Database, Geological Society of New Zealand & GNS Science) m'a également permis d'accéder à des données de distribution d'échinides fossiles de Nouvelle-Zélande pour une analyse biogéographique (Saucède *et al.* 2013b).

3. Les différents ateliers

Le matériel étudié depuis ma thèse peut être classé en quatre grands ateliers. Chacun de ces ateliers me permet de décrire et d'analyser la diversité des échinides au travers de quatre radiations réalisées dans des contextes distincts : radiation jurassique à l'origine des premiers échinides irréguliers, spécialisation des échinides irréguliers au Crétacé, diversification d'échinides dans des environnements aux conditions extrêmes, en Antarctique et en milieu abyssal. Les différents contextes environnementaux (plates-formes carbonatées, environnement marin glacial, domaine abyssal et hadal) et historiques (domaine téthysien jurassique et crétacé, ouvertures océaniques et isolement de l'océan Austral au Cénozoïque) de ces radiations me permettent de tester les rôles respectifs de l'environnement et des contingences historiques dans la diversification du groupe.

3.1. Echinides irréguliers jurassiques

Connus dans le registre fossile depuis le Sinémurien, les échinides irréguliers connaissent une importante phase de diversification au Jurassique Moyen et au Jurassique Supérieur. Cette diversification importante du groupe est associée à la colonisation des environnements de plate-forme distale et à leur capacité à se nourrir de la matière organique contenue dans les sédiments fins. L'étude de l'origine du groupe et de ses principales relations phylétiques avait été initiée durant ma thèse de doctorat. Les relations phylétiques étant aujourd'hui mieux connues et l'évolution des caractères mieux cernée, mes projets actuels visent à caractériser plus précisément l'évolution de la diversité morphologique du groupe et à étudier en particulier le caractère adaptatif de sa radiation, en analysant la part de diversité fonctionnelle au sein du signal de disparité morphologique (chapitre 3).

Thèmes de recherche. Les articles publiés abordent les domaines de la phylogénie et de la systématique, tandis que mes projets actuels consistent en une analyse macroécologique et macroévolutive de la diversification morphologique du groupe.

Acquisition des données. Les données comprennent des occurrences géographiques et stratigraphiques ainsi que des informations morphologiques acquises au niveau spécifique. La majeure partie des données d'occurrence provient de la littérature, tandis que les données morphologiques ont été majoritairement acquises à partir de spécimens de collections. Données d'occurrence et données morphologiques ont été complétées par des études ciblées sur le terrain : niveaux aaléniens et bajociens de la Sarthe, Lias et Bajocien du Haut Atlas Marocain, terrains jurassiques de Bourgogne (tableau 2).

Publications associées : Moyne *et al.* 2004, Saucède *et al.* 2007, Saucède *et al.* 2013a

3.2. Echinides irréguliers crétacés

Trois ordres d'échinides irréguliers apparaissent lors de nouvelles phases de diversification du groupe au Crétacé Inférieur et Supérieur : les Cassiduloida, les Holasteroida et les Spatangoida. Le premier ordre connaît une importante diversité au Mésozoïque, puis décline au cours du Cénozoïque jusqu'à nos jours. Les deux derniers ordres regroupent la majorité des espèces d'échinides irréguliers actuelles. La forte diversification de ces trois groupes au Crétacé, et en particulier celle des Cassiduloida constitue le cadre d'études macroécologiques ciblées sur les liens existant entre diversité taxinomique, morphologique et caractéristiques des habitats.

Thèmes de recherche. L'étude des échinides crétacés a donné lieu à des publications d'analyses phylogénétiques et de travaux de systématique. S'appuyant sur les résultats de ces travaux, mes projets actuels consistent maintenant en une approche macroécologique pour étudier la distribution et la diversité des espèces en lien avec la diversité de leur habitat.

Acquisition des données. Des missions de terrain ont permis de compléter des données anciennes tirées de la littérature et d'acquérir des données de distribution et des données morphologiques à partir d'échinides de l'Hauterivien du bassin de Paris ainsi que de l'Albien et du Cénomanien de Tunisie. Mes projets actuels portent cependant en grande partie sur l'étude de la Formation des Calcaires à Spatangues qui correspond à des niveaux calcaréo-argileux comportant différents faciès, déposés dans le sud-est du bassin de Paris à l'Hauterivien inférieur (Crétacé inférieur); cette Formation a livré une échinofaune abondante et diversifiée (26 espèces appartenant à 16 familles différentes, parmi lesquelles 13 espèces d'échinides réguliers et 13 espèces d'irréguliers) qui permet d'étudier les liens entre diversité de ces faunes et diversité des habitats.

Publications associées : Saucède & Villier 2005, Saucède & Néraudeau 2006, Saucède *et al.* 2012, Benetti *et al.* 2013

3.3. Faunes d'échinides antarctiques

Les échinides antarctiques présentent une forte richesse taxinomique et une forte diversité morphologique. La majorité des espèces est représentée par deux familles (Schizasteridae et Cidaridae) dont la diversité est expliquée par la radiation que les deux groupes connaissent sur le plateau continental antarctique dès l'Eocène. La diversification importante de ces deux familles est accompagnée d'un isolement géographique (modèle de radiation en bouffées d'espèces) et d'adaptations et traits d'histoire de vie originaux (espèces incubantes). Les échinides antarctiques représentent un modèle d'évolution en « vase clos » relatif, dans un contexte environnemental original (océan glacial).

Thèmes de recherche. Mes travaux et projets actuels répondent majoritairement à des problématiques de biogéographie et de macroécologie.

Acquisition des données. Toutes les données de distribution tirées de la littérature ont été exploitées afin de constituer une base de données régulièrement mise à jour à partir de données de collections vérifiées et de données originales issues de campagnes de collecte en mer.

Publications associées : Saucède 2008, Saiz *et al.* 2008, Gutt *et al.* 2011, Hardy *et al.* 2011, Díaz *et al.* 2011, Dettai *et al.* 2011, Gutt *et al.* 2012, Pierrat *et al.* 2012a, Moya *et al.* 2012, Pierrat *et al.* 2012b; Pierrat *et al.* 2013, Saucède *et al.* 2013b, Lecointre *et al.* 2013, Saucède *et al.* sous presse (a & b)

3.4. Faunes d'échinides abyssaux

Au sein des échinides irréguliers, l'ordre des Holasteroida se spécialise majoritairement pour les environnements marins profonds dès la fin du Crétacé. Il connait alors une radiation originale en milieu abyssal, radiation qui s'accompagne de modifications morphologiques profondes analogues (mais non homologues) à celles présentées par les premiers irréguliers au Jurassique (atrophie du système ambulacraire, déstructuration du squelette, explosion de la disparité morphologique). L'originalité des formes abyssales actuelles semble ne pouvoir s'expliquer que par le relâchement de contraintes morphogénétiques, plutôt que par des phénomènes d'adaptation. A l'instar des échinides antarctiques, les holastéroïdes abyssaux fournissent donc un modèle d'évolution dans un environnement extrême, associé à une très forte diversification morphologique, et non simplement taxinomique come chez les échinides antarctiques.

Thèmes de recherche. Une seule étude a été publiée après mes travaux de thèse. Elle aborde des aspects de systématique et présente une analyse morpho-fonctionnelle. Mes projets à venir visent à mieux caractériser la diversité morphologique originale de ces formes, en ciblant les caractères structuraux (relations topologiques entre éléments du squelette). Il s'agit donc d'une problématique principalement macroévolutive.

Acquisition des données. Les rares données disponibles consistent en des données morphologiques d'espèces actuelles qui proviennent de la littérature et de matériel étudié en collection.

Publicatios associée : Saucède *et al.* 2009

4. Projets en cours et perspectives

4.1. Modèles biologiques

Certains de mes travaux intègrent des données qui concernent d'autres groupes taxinomiques que les échinides (Saiz *et al.* 2008, Gutt *et al.* 2011, Dettai *et al.* 2011, Gutt *et al.* 2012, Saucède *et al.* sous presse b, Lecointre *et al.* 2013, Linse *et al.* 2013). Ces travaux permettent de comparer les informations tirées de groupes taxinomiques à l'écologie et à l'histoire évolutive contrastées (Pierrat *et al.* 2013) dans les domaines de la biogéographie (Gonzalez-Wevar *et al.* 2013) et de l'analyse de l'information morphologique (Gendry *et al.* 2013). Cette ouverture vers d'autres groupes devrait se poursuivre dans mes projets futurs, en particulier dans mes travaux de biogéographie (biogéographie historique, biorégionalisation et écorégionalisation) qui nécessitent de tester les correspondances entre divergence évolutive et phénomènes géodynamiques à travers différents phyla.

4.2. Campagnes de terrain

Ma participation à des campagnes en mer dans l'océan Austral me permettra de continuer à compléter des jeux de données toujours très parcellaires, tout en abordant des problématiques biogéographiques et macroécologiques plus ciblées. Ainsi, de prochaines missions d'échantillonnage dans l'océan Austral sont d'ores et déjà programmées. Une première mission autour des îles subantarctiques Kerguelen (programme PROTEKER 2013-2015 soutenu par l'*IPEV*) est prévue dès l'hiver 2013-2014 (figure 1.7). A l'aide de moyens d'échantillonnage, de mesure et d'observation complémentaires (plongée en scaphandre autonome, utilisation de chaluts benthiques, de ROV, mesures *in situ* de paramètres océanographique), cette mission me permettra de récolter des données écologiques et de distribution précises sur les échinides et les communautés benthiques autour de l'archipel. L'analyse macroécologique de ces données s'appuiera sur des modèles de niche utilisant des données d'abondance d'espèces clés, et des modèles basés sur des données de présence seule. L'étude sera également couplée à des analyses isotopiques ^{13}C et ^{15}N permettant de caractériser la niche isotopique d'espèces ciblées. Un projet analogue devrait avoir lieu dans les années à venir en Terre Adélie où un autre programme auquel j'émarge est déjà en cours de réalisation (programme REVOLTA 2014-2015 financé par l'*IPEV*).

A plus large échelle spatiale, une future campagne allemande de l'Institut Alfred Wegener (programme SYSTCO en 2016-2017) devrait me permettre de participer à l'échantillonnage de l'océan Austral profond entre le sud de l'Afrique du Sud et les côtes de l'Antarctique de l'Est. En outre, mon implication précoce dans cette future campagne m'a autorisé à proposer un projet qui vise à mieux connaître les faunes d'échinides de l'île Marion (*Pseudechinus marionis*) et à préciser les relations phylogéographiques de ces faunes. Certaines îles subantarctiques ont en effet pu constituer des zones-refuges durant les derniers maxima glaciaires (Gonzalez-Wevar *et al.* 2013). L'identification de ces zones doit permettre de mieux cerner les dynamiques biogéographiques récentes dans l'océan Austral.

Des campagnes de terrain portant sur du matériel fossile auront lieu dans le bassin de Paris. Le projet a pour objectif de modéliser l'évolution écologique d'espèces d'échinides grâce à des modèles de niche reposant sur la corrélation entre données d'occurrence fossiles et données sédimentologiques. La lignée des échinides collyritidés et les niveaux du Callovien (-165 à – 161 millions d'années) à l'Oxfordien (-161 à -155 millions d'années) seront plus particulièrement ciblés. La zone d'étude couvrira une bande d'environ 250 km de long, depuis le département des Vosges au NE à celui de l'Yonne au SW, sur une centaine de sites d'étude. Les données sédimentologiques sont déjà en grande partie connues mais elles nécessiteront d'être précisées et complétées par la collecte de matériel supplémentaire sur le terrain et l'étude de microfaciès.

Figure 1.7. Localités étudiées et moyens mis en œuvre (chaluts, filets, ROV et plongée) dans le cadre du programme PROTEKER prévu fin 2013 aux îles Kerguelen.

CHAPITRE II.

ETUDE DE LA STRUCTURATION PHYLOGENETIQUE DE LA BIODIVERSITE

L'analyse de la structuration phylogénétique de la biodiversité nous renseigne sur l'histoire évolutive des clades. Elle fournit un cadre historique et constitue une étape analytique préalable pour la compréhension des processus macroécologiques et macroévolutifs à l'origine de la biodiversité (Faith 1994, Purvis & Hector 2000, Webb *et al.* 2002, Wiens & Graham 2005, Ricklefs 2006, Eaton *et al.* 2008, Pearman *et al.* 2008, Wiens *et al.* 2011, Condamine *et al.* 2013).

De nombreux travaux de biogéographie et de macroécologie se sont intéressés à l'analyse de la distribution spatiale de la biodiversité au regard de sa structuration phylogénétique, la connaissance des relations de parenté entre taxons permettant également d'analyser les contraintes phylétiques associées aux caractères morphologiques et autécologiques (Nylander *et al.* 2004, Cavender-Bares *et al.* 2009, Roquet *et al.* 2009, Beck *et al.* 2012, Wiens 2012). En macroécologie, les principales problématiques portent sur les rapports entre conservatisme écologique et évolution, ainsi que sur les liens existant entre diversité des clades et structuration phylogénétique des caractères autécologiques. A titre d'exemple chez les échinides antarctiques : pourquoi les familles les plus diversifiées présentent-elles tant d'espèces incubantes (Poulin *et al.* 2002, David *et al.* 2005, Pearse *et al.* 2007) ? Quelles sont les autres innovations morphologiques associées ? Sont-elles liées à certaines fonctions biologiques (respiration, locomotion, nutrition) ?

La biogéographie historique a vocation à intégrer les informations phylogénétiques dans l'analyse des grands motifs de distribution spatiale de la biodiversité (Donoghue & Moore 2003, Lomolino 2006, Wiens 2012). Elle permet d'aborder l'étude de l'origine et de l'évolution géographique de grands clades. Elle se distingue en cela de la phylogéographie qui concerne l'étude des relations génétiques entre populations et donc l'évolution de la biodiversité sur des périodes de temps relativement courtes, généralement restreintes à l'Holocène (Pearman *et al.* 2008). Les principales problématiques abordées en biogéographie historiques portent sur les liens existant entre isolement géographique et diversité, et plus généralement, sur la recherche de congruences entre motifs biogéographiques et phylogénétiques (SanMartín & Ronquist 2004, Kissling *et al.* 2012). Ainsi, quel est le centre d'origine des grands clades ? Les clades les plus diversifiés ont-ils une plus large distribution ? Au contraire, diversité, monophylétisme et endémisme sont-ils associés comme dans le cas des modèles de diversification en bouffées d'espèces (Ribbink 1984, Eastman & McCune 2000, Lecointre *et al.* 2013)?

L'étude des relations phylétiques passe par la construction de phylogénies. Dans mes travaux, c'est naturellement la distribution des caractères morphologiques entre taxons qui me permet de reconstituer l'histoire évolutive des clades (Ronquist 2004), la proximité phylétique entre espèces étant déduite du partage d'états de caractères communs ou synapomorphies (Pearman *et al.* 2008). Dans la plupart des analyses macroécologiques, l'étude de la distribution des caractères (ou états de caractères) morphologiques au sein des phylogénies est utilisée pour discuter des processus écologiques associés à l'évolution des taxons (spéciation, dispersion et extinction). En paléontologie, les reconstructions phylogénétiques reposent presque exclusivement sur l'analyse des données morphologiques. Cependant, l'analyse intégrante de phylogénies moléculaires (établies grâce aux représentants actuels des clades) et morphologiques (incluant représentants actuels et fossiles) permet d'étudier la congruence entre des données de natures différentes, issues de sources indépendantes. Outre la possibilité d'intégrer des taxons fossiles dans les phylogénies, l'analyse conjointe de données morphologiques et génétiques permet une validation croisée des phylogénies (De Queiroz *et al.* 1995, Nylander *et al.* 2004, Smith *et al.* 2006).

Une partie de mes travaux d'après thèse ont consisté à déterminer et analyser les relations phylétiques entre taxons, à différents niveaux hiérarchiques : des analyses intra-spécifiques (González-Wevar *et al.* 2013) aux analyses inter-spécifiques voire entre grands clades (Saucède & Néraudeau 2006, Saucède *et al.* 2007). Ces différents niveaux taxinomiques ont déterminé également l'extension temporelle des analyses. La corrélation entre échelles taxinomique et temporelle d'analyse est évidente ; elle a déjà été soulignée plus haut lors de la distinction faite entre biogéographie historique et phylogéographie. Finalement, la dimension spatiale (biogéographie) était peu présente dans mes premiers travaux d'après thèse ; elle s'est progressivement imposée comme une nécessité dans mes travaux récents et dans mes projets dévolus aux analyses macroécologiques.

Le cœur de mes projets actuels repose sur la comparaison et l'intégration des informations morphologiques et génétiques dans des analyses phylogénétiques jointes. Ces analyses me permettent de tester la pertinence des reconstructions phylogénétiques par des validations croisées. Le recours aux données morphologiques me permet aussi de pouvoir tenir compte des informations paléontologiques, les données fossiles permettant (1) de pourvoir en partie aux pertes d'informations biogéographiques et morphologiques dans les lignées fossiles sans représentants actuels et (2) de calibrer dans le temps les divergences entre clades.

1. Structuration phylogénétique et macroévolution

La connaissance des phylogénies est un préalable à la compréhension des phénomènes macroévolutifs. Ainsi, l'étude des caractéristiques morphologiques des taxons au regard de leurs relations de parenté permet d'identifier les contraintes phylogénétiques (plésiomorphies) qui conditionnent l'apparition d'adaptations et d'innovations (Price & Carr 2000, Webb *et al.* 2002). La résolution des phylogénies permet de déterminer l'origine unique ou multiple des groupes taxinomiques, autrement dit de déterminer les contraintes phylétiques associées aux phases de diversification. L'étude de la distribution des caractères morphologiques au sein des phylogénies, et en particulier ceux associés à certaines fonctions biologiques permet de caractériser les phénomènes évolutifs et écologiques sous-jacents (Price & Carr 2000, Wiens & Graham 2005, Eaton *et al.* 2008, Pearman *et al.* 2008).

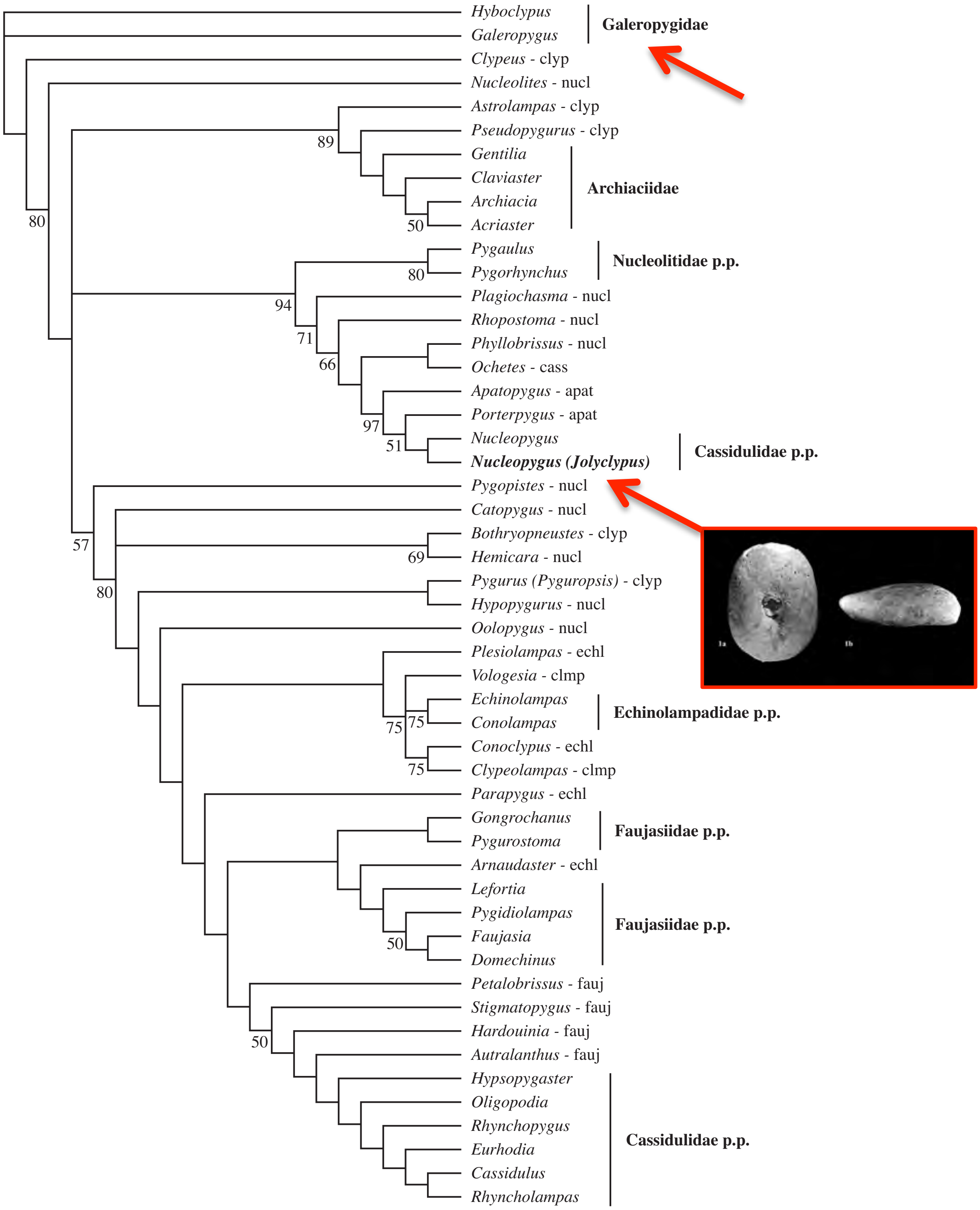


Figure 2.1. Résultat de l'analyse phylogénétique incluant l'espèce cénomanienne *Nucleopygus jolyi*. L'espèce (flèche et encart rouges) présente des convergences morphologiques avec la famille jurassique des Galeropygidae (flèche rouge) dans laquelle elle était initialement placée (d'après Saucède & Néraudeau 2006).

Principaux résultats

Apport des phylogénies à la compréhension de la radiation des échinides irréguliers

Suite à mes travaux de thèse, l'analyse phylogénétique (en parcimonie) des genres d'échinides irréguliers jurassiques a permis de déterminer l'origine unique du clade (sous-classe des Irregularia) à partir d'un ancêtre régulier et la structuration phylétique du groupe en trois principaux clades (Saucède *et al.* 2007). L'origine unique du groupe est associée à une contrainte phylogénétique (déplacement du périprocte) qui aboutira à des convergences entre les principaux clades (séparation du périprocte hors de l'appareil apical réalisée dans les différents groupes indépendamment) et à des innovations morphologiques touchant des caractères associés aux fonctions biologiques de nutrition (pores ambulacraires), de locomotion (piquants) et de respiration (pore ambulacraires). Ces innovations soulignent le caractère adaptatif de cette radiation. La radiation des échinides irréguliers s'inscrit en effet dans le contexte de la diversification de nombres de groupes d'invertébrés marins endobenthiques au début du Mésozoïque (Vermeij 1977, Wagner *et al.* 2006), diversification associée à l'exploitation des ressources nutritives présentes dans les sédiments marins.

A l'inverse, la présence de caractères en apparence plésiomorphes au sein de groupes dérivés, peut entraîner une mauvaise interprétation du signal de diversité en l'absence de phylogénies robustes (convergence entre taxon éteint et taxon dérivé). L'analyse phylogénétique incluant une espèce d'échinide cénomanien (Crétacé), considérée à tort comme le dernier représentant d'un groupe connu initialement au seul Jurassique, a montré que l'espèce appartenait en fait à un groupe dérivé crétacé, mais présentait des convergences avec le groupe jurassique (Saucède & Néraudeau 2006). Une fois encore, le caractère adaptatif de cette convergence a été souligné : il correspond à une paedomorphose et une réduction de taille (progenèse, Gould 1977), interprétées comme des adaptations à des environnements à sédiments fins (figure 2.1).

Publications associées : Saucède & Néraudeau 2006, Saucède *et al.* 2007

Projets et perspectives

L'océan Austral et les domaines océaniques profonds constituent des environnements aux forts particularismes abiotiques (température, couverture de glace, pression, obscurité). Ces particularimes impliquent l'existence de fortes contraintes qui ont conditionné la diversification de leurs faunes et favorisé les phénomènes adaptatifs, ainsi que l'émergence d'innovations (résistance au gel, incubation), les faunes étant apparues dans des contextes différents (origine anté-glaciaire pour les faunes antarctiques, origine sur les plateaux continentaux pour certaines faunes abyssales). Aujourd'hui, mes perspectives de recherche, déjà en cours de développement pour certaines (échinides antarctiques) ou encore à l'état de projet pour d'autres (échinides abyssaux), portent sur l'analyse des liens existant entre contraintes phylogénétiques, diversité taxinomique et morphologique au sein de clades d'échinides diversifiés dans ces milieux extrêmes. Elles doivent permettre de mieux comprendre les phénomènes macroévolutifs qui ont structuré la diversité de faunes d'échinides aux morphologies souvent originales (Saucède *et al.* 2004, 2007).

Phylogénie et diversification des échinides abyssaux

Les holastéroïdes abyssaux présentent des caractéristiques anatomiques uniques qui incluent une importante restructuration du squelette (David 1987, Smith 2004, Saucède *et al.* 2004) et l'apparition d'une vestiture originale (Saucède *et al.* 2009). L'absence de phylogénies robustes impliquant des taxons actuels et fossiles limite la compréhension des processus évolutifs associés à la radiation de ce groupe qui a colonisé les milieux abyssaux au Paléogène (Smith 2004, Smith & Stockley 2005). L'analyse des liens entre histoire évolutive, contraintes phylétiques et innovations morphologiques permettrait de mieux comprendre les mécanismes de diversification du groupe dans un contexte théorique de relachement de la pression sélective. Ce relachement serait la conséquence d'une diminution de la dépense énergétique due aux fonctions biologiques de respiration, de locomotion et de nutrition (Childress 1995, Seibel et Drazen 2007), fonctions dont l'évolution avait déjà conditionnée la diversification des échinides irréguliers au Jurassique.

Phylogénies et diversification des échinides antarctiques

La diversité des échinides antarctiques est dominée par deux familles : les Schizasteridae et les Cidaridae comprennent en effet 65% des espèces d'échinides (David *et al* 2005, Pierrat *et al.* 2012a). Or, si la monophylie des représentants exclusivement antarctiques de ces deux familles ne fait plus de doute (Lecointre *et al* 2013), la systématique (au niveau genres et espèces) et les relations phylétiques au sein des familles sont encore mal établies (Dettai *et al.* 2011). Comment alors interpréter les phénomènes macroévolutifs et macroécologiques parfois anciens (Eocène) à l'origine de la diversité encore mal quantifiée de ces deux familles (Pearse *et al.* 2007, Saucède *et al.* 2013b) ? Comment tester la part du climat (refroidissements fini-eocènes et miocènes, cycles glaciaires plio-pleistocènes) et de l'évolution océanographique (isolement relatif des eaux de surface antarctiques et mise en place des grands courants circum-antarctiques) dans ces processus de diversification ?

Des analyses phylogénétiques sont déjà en cours et sont soutenues par plusieurs programmes (ECOS-*Sud*, Ceamarc, ANR Antflocks, REVOLTA), réalisés dans le cadre de collaborations avec des collègues biologistes (Santiago du Chili, Marseille). Ces travaux devraient aboutir dans les deux années à venir aux premières publications portant les liens entre structuration phylogénétique et diversité morphologique et écologique. A plus longue échéance, l'analyse comparative de la diversification de ces deux familles et des autres familles d'échinides antarctiques intégrant les structurations phylogénétiques doit participer à mieux caractériser la biodiversité marine antarctique. Ce type de projet rejoint des préoccupations très actuelles portant sur la biologie de la conservation, l'évolution de la biodiversité (Gutt *et al.* 2012 ; Lecointre *et al.* 2013) et la création d'aires marines protégées (programmes PROTEKER et REVOLTA) ; préoccupations à l'origine des programmes internationaux (CAML – Census of Antarctic Marine Life, AnTERA – Antarctic Thresholds Ecosystem Resilience and Adaptation , AntEco – Antarctic Ecosystem), qui soutiennent les recherches sur la biodiversité marine antarctique.

2. Structuration phylogénétique, biogéographie et macroécologie

La macroécologie tend à l'intégration des approches de biogéographies écologique et historique ; elle a pour but de déterminer les facteurs environnementaux et historiques qui structurent les motifs de distribution de la biodiversité à large échelle de temps et d'espace (Brown 1995; Gaston & Blackburn 2000; Briggs 2007, Passy 2012). Cependant, l'apport du cadre phylogénétique à l'étude de la biodiversité a surtout été marqué par les développements de la biogéographie cladistique qui fournit un cadre méthodologique pour tester les hypothèses biogéographiques (Futuyma 1997, Lomolino *et al.* 2006, Ebach & Tangney 2007). Finalement, c'est la prise en compte des dimensions à la fois phylogénétiques, temporelles et spatiales, ainsi que des processus écologiques et évolutifs qui permet de mieux comprendre l'ensemble des phénomènes à l'origine de la biodiversité actuelle (Donoghue et Moore 2003, Lomolino *et al.* 2006, Pearman *et al.* 2008, Wiens 2012).

Principaux résultats

L'océan Austral, et le plateau continental antarctique en particulier, possède une faune marine qui a surpris les océanographes du vingtième siècle par son niveau de diversité. Il a depuis lors été parfois qualifié de *point chaud* de biodiversité. Est-ce réellement le cas ? En quelques chiffres, l'océan Austral sensu stricto (c'est-à-dire les eaux situées au sud du courant circum-polaire antarctique) héberge environ 5% de la biodiversité marine mondiale, pour une couverture de 8% des surfaces océaniques (Zwally *et al.* 2002, Linse *et al.* 2006, Griffiths 2010, Ingels *et al.* 2012) – mais il contient 9% des espèces mondiales d'échinides, soit 82 espèces sur 950 décrites) (Smith 2006, Pierrat *et al.* 2012a). La diversité marine antarctique est en fait très contrastée selon les groupes et niveaux taxinomiques considérés (Eastman & McCune 2000; Crame 2004; Clarke 2008; Clarke & Crame 2010; Krug *et al.* 2010; Ingels *et al.* 2012) et la richesse spécifique très contrainte phylogénétiquement (Eastman & McCune, 2000; Clarke & Crame, 2010, Lecointre *et al.* 2013). D'autre part, cette biodiversité doit être considérée au regard des caractéristiques physiographiques de l'océan austral. Ainsi, la biodiversité du plateau continental antarctique excède très largement celle de l'Arctique, mais le plateau est vaste (12% des surfaces de plateaux à l'échelle mondiale) quoique profond (principalement situé sous la zone photique - Aronson *et al.* 2008). A l'inverse, les lignes de côte antarctiques ne représentent que 4% des zones côtières mondiales, principales sources de biodiversité, mais la diversité des habitats côtiers est extrêmement pauvre à cause de la présence de glace et de la quasi absence d'apports continentaux (Eastman & McCune 2000, Rogers 2007, Clarke & Crame 2010). Ainsi, l'exemple de la biodiversité marine antarctique illustre parfaitement la nécessité de prendre en compte les informations phylogénétiques, écologiques et géographiques afin de comprendre son origine et son histoire.

Quelle est l'origine de la biodiversité benthique antarctique et quels sont les phénomènes macroécologiques (c'est-à-dire écologiques et biogéographiques) impliqués ? Comment la biodiversité antarctique a-t-elle répondu aux principaux changements environnementaux passés ? Une partie de mes travaux actuels tente de répondre à ces questionnements, en prenant pour principal sujet d'étude les échinides antarctiques. Dans mes recherches, je tente d'intégrer les dimensions phylogénétiques, temporelles, spatiales et écologiques à différentes échelles dans une approche que l'on pourrait qualifier de biogéographie historique intégrée pour reprendre la formule de Donoghue et Moore (2003).

Phylogéographie

Structure génétique des populations de patelle antarctique et histoire biogéographique récente

En phylogéographie, l'étude de la structure spatiale des variations génétiques intra-spécifiques permet de reconstituer l'histoire récente et de tester des scénarios démographiques - extinction, dispersion, expansion - possibles (Hewitt 2000, 2004, Maggs *et al.* 2008, Allcock & Strugnell 2012). A l'échelle des populations, sur des échelles de temps courtes (derniers milliers d'années) et des échelles spatiales régionales (Patagonie, îles subantarctiques, Péninsule antarctique), l'étude en collaboration des motifs de variation génétique (COI) entre populations du gastéropode *Nacella concinna* nous permet de proposer un scénario biogéographique alternatif à ceux proposés jusqu'ici.

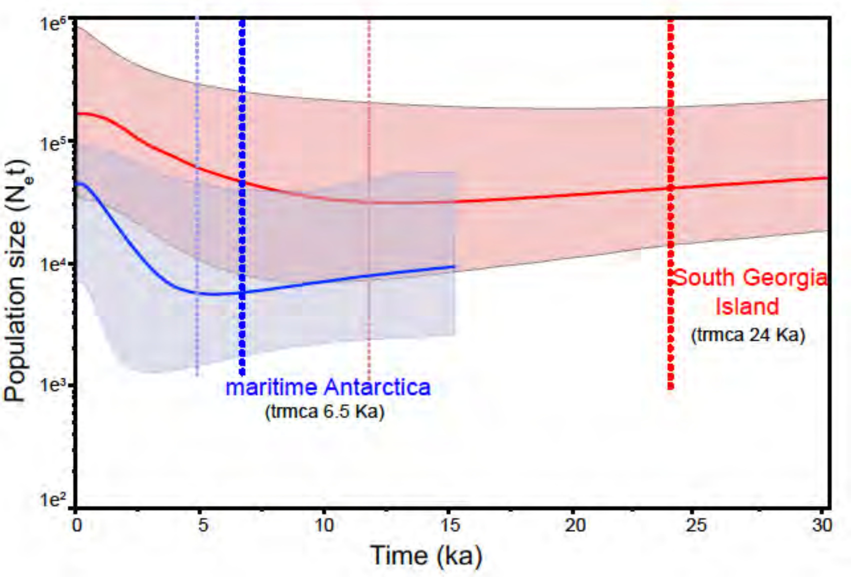


Figure 2.2. Modèle d'évolution démographique des populations de patelle antarctique (*Nacella concinna*) de Géorgie du Sud et d'Antarctique maritime depuis 30000 ans (González-Wevar *et al.* 2013).

Les indices sédimentologiques d'extension des calottes glaciaires sur le plateau continental antarctique lors des périodes de maximum glaciaire ont posé la question de la survie des faunes benthiques dans des zones de refuges (Grobe & Mackensen 1992, Brey *et al.* 1996, Thatje *et al.* 2005), refuges à partir desquels la faune benthique aurait ensuite recolonisé le plateau continental après le retrait glaciaire (Thatje *et al.* 2005, Aronson *et al.* 2008). Certaines études ont démontré la possibilité de refuges en milieu profond (Hunter & Halanych 2008, Raupach *et al.* 2010, Janosik *et al.* 2011, Allcock & Strugnell 2012), alors que d'autres suggèrent l'existence de zones de refuge *in-situ*, le long des côtes antarctiques (Thornhill *et al.* 2008, Raupach *et al.* 2010, Díaz *et al.* 2011). L'analyse des variations génétiques et de leur structure spatiale chez la patelle antarctique *Nacella concinna* suggère au contraire l'extinction totale des populations antarctiques lors du dernier maximum glaciaire (LGM), leur survie au sein de zones de refuge péri-antarctiques (Géorgie du Sud), et leur expansion démographique post-LGM le long des côtes antarctiques (figure 2.2).

Publication associée : González-Wevar *et al.* 2013.

Biogéographie historique

Structure phylogénétique, origine et histoire évolutive des faunes antarctiques

La phylogéographie n'a pas vocation à étudier les phénomènes macroévolutifs en temps profond. En ignorant les événements de divergence et les processus évolutifs anciens, la généralisation de l'histoire évolutive récente à des périodes de temps anciennes (plusieurs millions d'années) tend à fausser notre perception de la dynamique de la biodiversité (Pearman *et al.* 2008, Morlon *et al.* 2011). Ainsi, la structure de la biodiversité antarctique ne peut être entièrement expliquée par les dynamiques démographiques associées aux derniers cycles glaciaires. A titre d'exemple, l'origine des clades d'échinides antarctiques remonte au moins à la fin de l'Eocène (Saucède *et al*. 2013b), période de grand renouvellement faunique à l'échelle globale, mais début aussi de l'isolement du plateau continental antarctique (Lautrédou *et al*. 2010).

En biogéographie historique, de nombreuses études cherchent à décrire, comprendre et expliquer l'originalité de la biodiversité marine antarctique ; les deux problématiques abordées sont la recherche des centres d'origine biogéographiques par l'étude des affinités fauniques et phylétiques entre biorégions, et la mise en évidence des processus écologiques et évolutifs associés (Clarke & Crame 1997, Eastman & McCune 2000, Held 2000, Rogers 2007, Briggs 2003, Gage 2004, Clarke *et al.* 2005, Brandt *et al.* 2007, Pearse *et al.* 2007, Strugnell *et al.* 2008, Lecointre *et al.* 2013).

Afin d'expliquer les affinités existant entre une partie de la faune du plateau continental antarctique et celle des bassins océaniques profonds environnants, de nombreux auteurs (Clarke & Crame 1997, Held 2000, Rogers 2007, Briggs 2003, Gage 2004, Clarke *et al.* 2005, Brandt *et al.* 2007, Strugnell *et al.* 2008) ont proposé deux hypothèses biogéographiques alternatives.

- Selon le scénario de la submergence, ces affinités fauniques résulteraient du fait que le plateau fonctionne comme une source de diversité pour les bassins océaniques environnants.
- Selon l'autre scénario, le scénario de l'émergence, les affinités fauniques démontreraient une origine profonde de la biodiversité du plateau continental (Menzies *et al.* 1973, Zinsmeister & Feldmann 1984, Clarke & Crame 1989, Brandt 1991, 1992, Crame 1999, Brandt *et al.* 2007, Aronson *et al.* 2008).

L'analyse des relations phylétiques entre espèces du genre d'échinide *Sterechinus* nous a amené à décrire des motifs incompatibles avec les deux scénarios proposés jusqu'ici (figure 2.3). Ils suggèrent plutôt un isolement ancien des espèces antarctiques (anté-Pliocène), puis une colonisation des bassins profonds depuis les aires subantarctiques (Díaz *et al.* 2011).

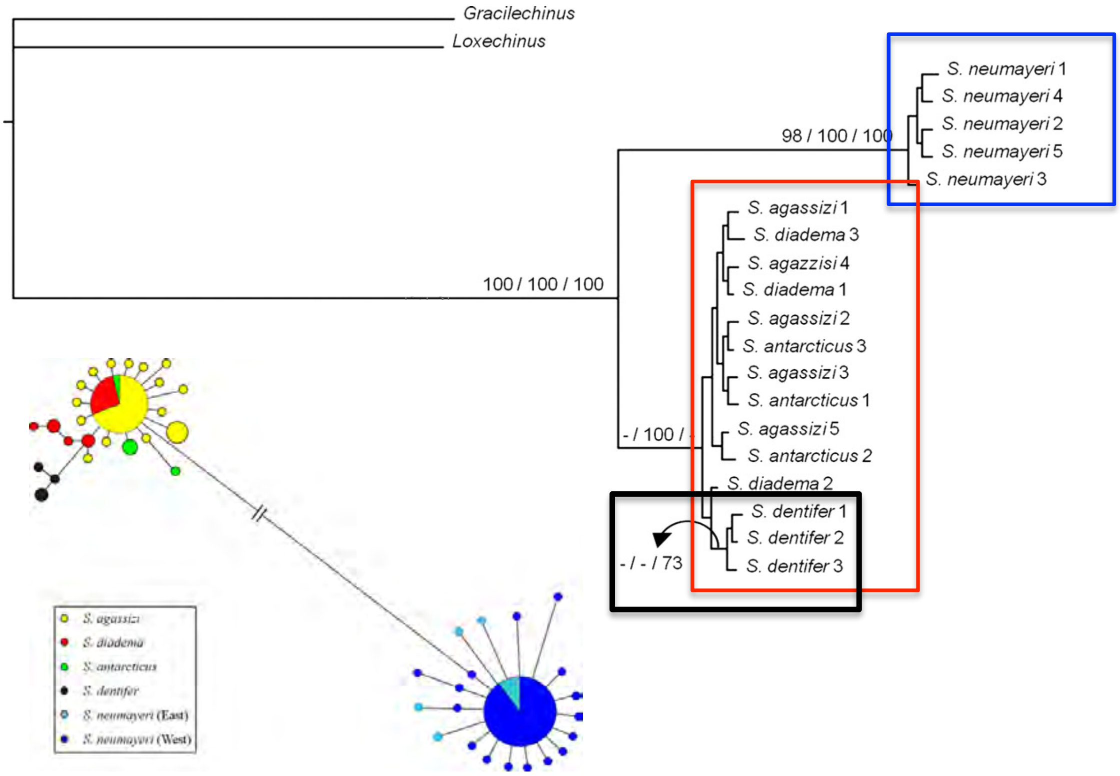


Figure 2.3. Réseau d'haplotypes et relations phylétiques (COI, méthode bayésienne) entre les espèces du genre *Sterechinus* exclusivement antarctiques (bleu), subantarctiques (rouge, jaune et vert) et profondes (noir) (d'après Díaz *et al.* 2011).

Le concept de *bouffées d'espèces*, ou *species flocks* (Ribbink 1984), illustre parfaitement la nécessité d'étudier les liens existant entre structures phylogénétiques, phénomènes macroévolutifs et distributions spatiales des clades. Les bouffées d'espèces résultent de la diversification extrêmement rapide d'espèces endémiques étroitement apparentées entre elles, très diversifiées écologiquement et très nombreuses (*speciosity*) par rapport au reste de leur habitat. L'étude du phénomène consiste en la recherche de motifs de diversité qui répondent aux critères historiques et écologiques suivants : groupements d'espèces monophylétiques, endémiques, présentant une forte richesse spécifique, des diversités morphologique et écologique importantes et dominantes (en terme de biomasse) dans leurs habitats (Ribbink 1984, Greenwood 1984, Eastman & McCune 2000). Le plateau continental antarctique présente des similitudes en terme d'isolement, de profondeur et d'âge avec certains lacs dans lesquels des bouffées d'espèces ont déjà été décrites (Ribbink 1984, Greenwood 1984). Quelques études ont donc cherché à identifier des bouffées d'espèces en Antarctique (Eastman & McCune 2000), malgré le paradigme très répendu d'un milieu marin diffusif défavorable à leur existence (Greenwood 1984, Lecointre *et al.* 2013). Dans le cadre d'un programme de l'ANR (ANR Antflocks), une étude menée en collaboration avec de nombreux collègues (Lecointre *et al.* 2013) sur la base des analyses phylogénétiques en cours (Dettai *et al.* 2011, Díaz *et al.* 2011) nous a permis de montrer que contrairement au paradigme retenu, les bouffées d'espèces ne sont pas rares en domaine marin puisqu'on dénombre 17 clades identifiés parmi les groupes de poissons, d'échinodermes et de crustacés analysés. Le plateau continental antarctique joue certainement un rôle de générateur de biodiversité dans l'océan Austral. Cette étude nous a permis d'affiner les critères d'identification des bouffées d'espèces et de proposer un protocole opératoire qui donne priorité aux critères historiques (monophylétisme, endémisme, richesse spécifique) sur les critères écologiques (diversité morphologique, écologique et prédominance dans les habitats). Pour les échinides, deux clades répondant favorablement aux critères historiques seuls ont été identifiés chez les Cidaridae et les Schizasteridae (Lecointre *et al.* 2013). Ces résultats constituent un point de départ nous incitant à mieux décrire la diversité écologique et phylétique des échinides pour comprendre les processus à l'origine des motifs de diversité observés.

Publications associées : Dettai *et al.* 2011, Díaz *et al.* 2011, Lecointre *et al.* 2013

Projets et perspectives

Parmi les développements de la biogéographie, la biogéographie cladistique est la discipline qui a apporté les outils méthodologiques permettant de tester des hypothèses biogéographiques (spéciation, duplication, extinction et dispersion) grâce à l'analyse topologique de cladogrammes (Futuyma 1997, Lomolino *et al.* 2006, Ebach & Tangney 2007). La biogéographie cladistique a été l'objet de critiques, portant non pas sur le principe des analyses topologiques, mais soulignant la nécessité de tenir compte également des informations temporelles (âge des divergences), sans lesquelles seules des *pseudo-congruences* entre cladogrammes pouvaient être obtenues. La critique a porté également sur le besoin de développer des analyses intégratives et non pas simplement multiplier les analyses indépendantes (Donoghue et Moore 2003, Lomolino *et al.* 2006, Pearman *et al.* 2008, Wiens 2012).

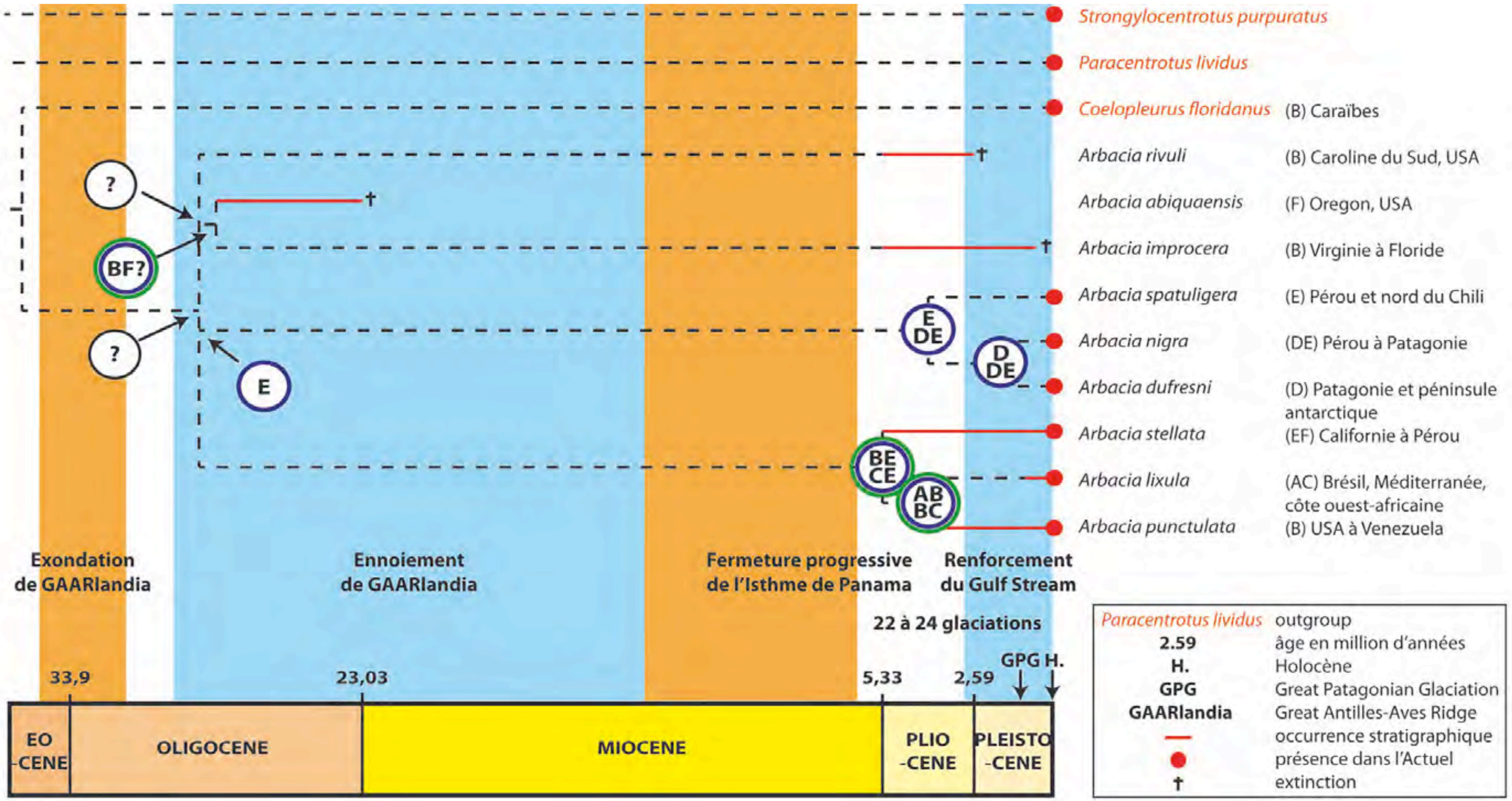


Figure 2.4. Arbre de relations de parenté entre espèces d'Arbaciidae actuelles et fossiles établi grâce à des analyses morphologiques et génétiques (COI), et intégrant des informations paléontologiques, stratigraphiques, biogéographiques et des tests d'hypothèse de vicariance (cercles verts) et de dispersion (cercles bleus) au regard de l'évolution de la zone Caraïbe (GAARlandia, isthme de Panama, Gulf Stream) et patagonienne (glaciations).

Analyses phylogénétiques et macroécologiques intégrées de faunes d'échinides

Les analyses intégrant les informations morphologiques et génétiques pour la reconstitution des phylogénies, et non pas la simple projection des caractères morphologiques sur des arbres moléculaires (Mooi & Gill 2010), doivent permettre de produire des phylogénies fiables et de tester des hypothèses biogéographiques sur la base de congruences réelles entre cladogrammes (De Queiroz *et al.* 1995, Nylander *et al.* 2004, Smith *et al.* 2006, Morlon *et al.* 2011). En outre, l'utilisation de données fossiles indépendantes permet de calibrer les temps de divergence entre sous-clades, et de remédier à la perte d'information biogéographique et morphologique pour les lignées fossiles sans représentants actuels (Nylander *et al.* 2004, Smith *et al.* 2006, Beck *et al.* 2012)

Les modalités et la pertinence des approches intégrant différentes sources d'informations phylogénétiques ont suscité de vifs débats d'ordre épistémologique (Mooi & Gill 2010, Farris & Carpenter 2011, Faith *et al.* 2011, 2012), mais la nécessité de telles approches a été réaffirmée pour combler le fossé existant entre utilisateurs de phylogénies moléculaires et utilisateurs de phylogénies morphologiques. Les informations morphologiques ne sont le plus souvent discutées qu'au regard des phylogénies moléculaires, considérées comme seules porteuses des vraies relations phylogénétiques ; le signal phylogénétique porté par les données morphologiques est donc encore largement négligé, sauf quand ces données sont les seules disponibles (Smith *et al.* 2006, Mooi & Gill 2010, Morlon *et al.* 2011). Plusieurs études ont cependant montré que dans les analyses phylogénétiques, les données morphologiques pouvaient être utilisées au même titre que les données moléculaires pour définir des états de caractères (Smith *et al.* 2006, Morlon *et al.* 2011). La nature et la qualité des différentes informations doit alors être simplement et clairement évaluée au préalable (Mooi & Gill 2010).

Mes collaborations avec des collègues biologistes (Santiago du Chili) ont abouti a un projet de recherche portant sur l'étude d'échinides américains et antarctiques de la famille des Arbaciidae (espèces des genres *Arbacia* et *Tetrapygus*) et des Echinidae (espèces des genres *Sterechinus*, *Dermechinus* et *Gracilechinus*). Ce projet consiste en une analyse macroécologique intégrant informations génétiques, morphologiques, biogéographiques et paléontologiques. Le signal phylogénétique porté par les caractères morphologiques est analysé en tant que tel et intégré dans des analyses comparatives (figure 2.4). L'analyse morphologique permet également la prise en compte des données paléontologiques. Ce projet a été déjà donné lieu à un programme de recherche financé par le réseau de station marine ASSEMBLE et à l'encadrement de stages de recherche en Master (Le Pelvé 2012, 2013). Il devrait déjà permettre la soumission de publications dès 2014.

Relations phylogénétiques et évolution des niches écologiques

La macroécologie a pour but de déterminer les facteurs environnementaux et historiques qui structurent la distribution de la biodiversité dans le temps et l'espace, ainsi que de scénariser les modifications éventuelles associées aux changements environnementaux (Brown 1995, Gaston & Blackburn 2000). Elle intègre donc les composantes historiques et écologiques de la biogéographie (Briggs 2007), souvent traitées indépendamment dans les analyses respectivement de biogéographie cladistique et de modélisation de niche écologique (et des modèles de distribution d'espèces associés).

Le domaine marin, et les mers polaires en particulier ont été relativement peu étudiés en macroécologie, alors que les changements climatiques actuels impactent d'ores et déjà de façon sensible les environnements (Smith & Stammerjohn 2001; Quale *et al.* 2002) et le fonctionnement des écosytèmes marins polaires (Moline *et al.* 2004, Ainley *et al.* 2005, Barnes 2005, Burrows *et al.* 2011). La réponse des espèces à ces modifications rapides de leur environnement physique (ex. hausse des températures, glissements saisonniers) et biotique (espèces invasives) est fortement conditionnée par leur conservatisme écologique. Depuis une dizaine d'années, les débats sur le rôle du conservatisme écologique des espèces dans les processus d'adaptation et plus généralement de spéciation, ont été renouvelés par le développement d'approches quantitatives (Peterson *et al.* 1999, Graham *et al.* 2004, Warren *et al.* 2008). La majorité des études met en évidence l'existence d'une évolution écologique sur des échelles de temps importantes, et principalement à des niveaux taxonomiques supérieurs à celui de l'espèce (voir Peterson 2011 pour une synthèse), alors que d'autres soulignent la fréquence de la différenciation écologique dans le processus de spéciation (e.g. Graham *et al.* 2004). La spéciation géographique (vicariance) précède-t-elle donc toujours la différenciation écologique qui ne serait alors qu'une conséquence d'un isolement écologique (Peterson *et al.* 1999)? Ou l'innovation écologique est-elle partie prenante dans le processus de spéciation (Graham *et al.* 2004)? L'étude du conservatisme écologique ouvre donc la voie à l'intégration des informations phylogénétiques, géographiques et écologiques (Peterson *et al.* 1999, Graham *et al.* 2004) dans des analyses comparatives des relations entre diversité écologique, distribution géographique et distances phylogénétiques (Warren *et al.* 2008).

Sur la base de connaissances déjà acquises sur la distribution géographique et les caractéristiques écologiques des échinides antarctiques (David *et al.* 2005, Pierrat *et al.* 2012a), ce deuxième projet aura pour objectif de comparer la diversité écologique modélisée d'espèces d'échinides (Gutt *et al.* 2012, Pierrat *et al.* 2012b) au regard de leurs relations phylogénétiques, dans le contexte de la diversification en bouffées d'espèces des Cidaridae et des Schizasteridae (Lecointre *et al.* 2013). La modélisation de niche déjà en cours concerne au moins une vingtaine d'espèces (voir le chapitre 4 – manuscrit en préparation). L'aboutissement des analyses phylogénétiques en cours devrait avoir lieu en 2014-2015. Le présent projet pourrait donc être réalisable à partir de 2015.

CHAPITRE III.

ANALYSE DE LA DISPARITE MORPHOLOGIQUE

L'analyse de la diversité morphologique (ou disparité morphologique) consiste en la caractérisation des formes et de leur évolution. L'approche morphologique a suscité beaucoup moins de travaux et d'attention que les mesures génétiques et taxinomiques de la biodiversité (Roy & Foote 1997, Wills 1998, Purvis & Hector 2000, Goulletquer *et al.* 2013). Elle permet cependant de rendre compte de caractéristiques ontogénétiques (contraintes du développement) et écologiques (caractères fonctionnels) qui ne sont pas décrites par les approches génétiques, taxinomiques et phylogénétiques. Diversités morphologique, taxinomique et phylogénétique sont en partie liées mais peu redondantes. Les analyses dédiées à la diversité morphologique peuvent donc fournir un signal complémentaire de celui de la diversité taxinomique (Foote 1997, Roy & Foote 1997, Wills *et al*. 2012). Classiquement, les études portant sur l'évolution de la (paleo)-biodiversité au cours du temps combinent ces différentes approches pour éclairer les processus associés à la dynamique évolutive de la biodiversité (Wills *et al.* 1994, Foote 1997, 1999, Neige 2003, Erwin 2007, Ruta 2009, Wills *et al.* 2012). Les éventuelles discordances entre signaux de diversité morphologique et taxinomique ont ainsi permis d'éclairer par exemple, les phénomènes macroévolutifs associés aux événements d'extinction (sélectivité) et de diversification (radiations adaptatives) passés (Foote 1997, Wills *et al.* 2012, Gerber 2013).

Ce chapitre présente mes travaux et projets spécifiquement dévolus à l'analyse morphologique de la biodiversité qui comporte classiquement deux volets :

1. la différenciation morphologique entre espèces pour laquelle je présente mes résultats de taxinomie et de systématique,

2. l'évolution de la disparité morphologique au cours du temps qui constitue l'objet de mes projets actuels et futurs.

Dans ce deuxième volet, l'étude de la disparité des échinides actuels et fossiles est abordée dans ses dimensions ontogénétiques (analyse des contraintes morphologiques induites par le développement) et fonctionnelles (analyse des caractères morphologiques associés aux fonctions biologiques).

L'analyse de la disparité morphologique soulève également des questions d'ordre méthodologique portant sur la taxinomie, sur la nature des caractères morphologiques à prendre en compte, ainsi que sur les méthodes d'analyse à employer (Roy & Foote 1997, Foote 1997, Laffont *et al.* 2011, Wills *et al.* 2012, Gerber 2013). Les questions d'ordre taxinomiques sont en partie abordées dans le premier volet. Dans le deuxième volet, l'étude des caractères morphologiques repose sur l'analyse des corrélations entre caractères, et de leurs variations ; elle s'appuie également sur la connaissance actuelle du développement et de l'écologie des échinides. La quantification des variations de forme est réalisée à l'aide de méthodes de morphométrie (analyse de contour et points homologues) et d'outils mathématiques tirés de la théorie des graphes (analyses topologiques entre éléments du squelette). L'analyse et la quantification de la diversité morphologique sont réalisées dans un cadre multidimensionnel (espaces morphologiques).

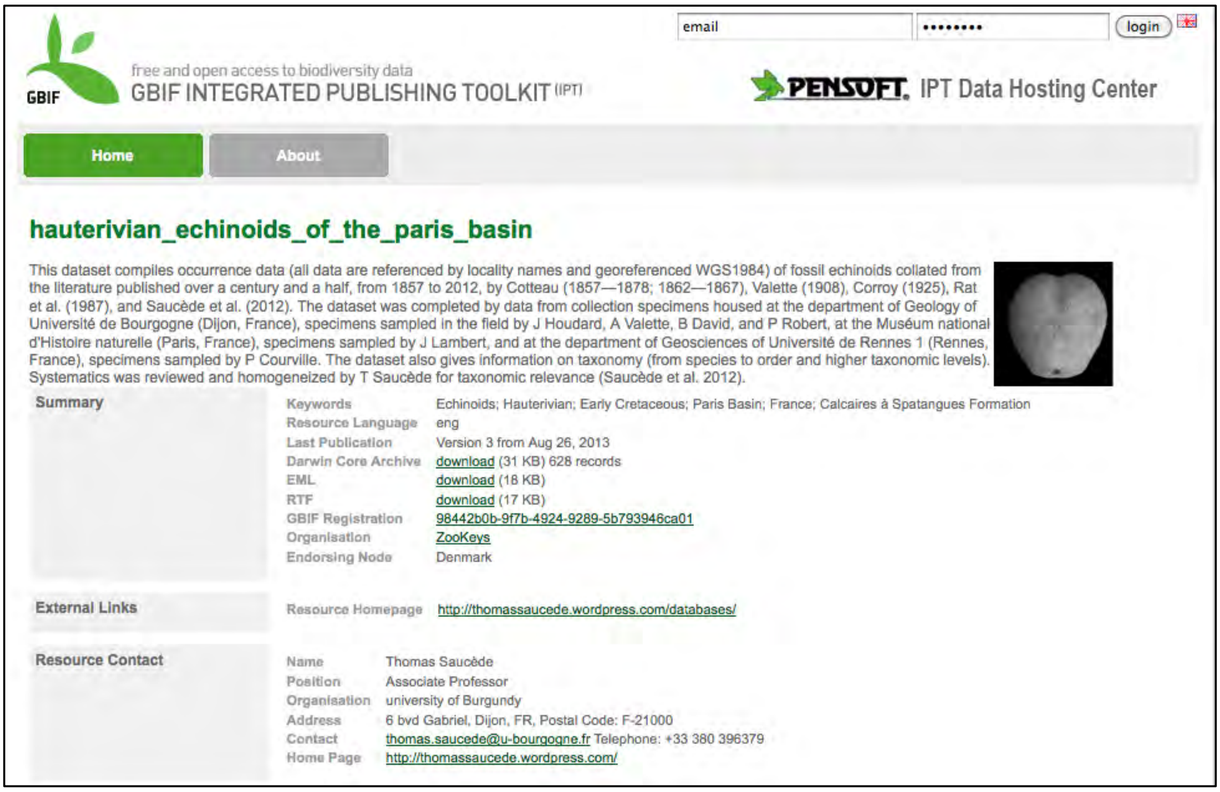
1. Différenciation morphologique et implications taxinomiques

La révision systématique et la description de nouveaux taxons sont un préalable aux études sur la biodiversité. Elles permettent de définir les « unités-clés » identifiables pour une meilleure estimation de la diversité taxinomique mais fournissent également un cadre taxinomique aux analyses de la diversité morphologique (Roy & Foote 1997, Goulletquer *et al.* 2013). Mes travaux d'analyse de la diversité morphologique m'ont naturellement amené à la révision de la systématique d'espèces actuelles et fossiles. Dans le cas des espèces actuelles, se pose la question de la congruence entre caractères morphologiques et données génétiques (Mayr 1963, Novo *et al.* 2012b). Dans le cas des fossiles, les données morphologiques sont les seules disponibles et ne portent qu'une partie de l'information morphologique initialement présente chez les organismes vivants. Mes travaux en cours sur l'étude de la différenciation morphologique entre espèces d'échinides actuelles indiquent que l'expression des différenciations morphologiques inter-spécifiques concerne souvent des organes perdus lors de la fossilisation (vestiture). Au contraire, certains caractères structuraux du squelette ainsi que la forme du test, conservés sur les spécimens fossiles, sont le lieu d'expression à la fois de variations inter- et intra-spécifiques, telles que celles résultant de l'écophénotypisme (Kanazawa 1992, Néraudeau 1992, Saucède & Néraudeau 2006). Notre connaissance de l'expression phénotypique chez les espèces actuelles m'invite donc à une certaine prudence quand il s'agit de tirer des conclusions taxinomiques à partir de l'étude des variations morphologiques fossiles seules.

Principaux résultats

Analyses morphologiques et implications taxinomiques en paléontologie

Ma contribution à la systématique des échinides fossiles comprend trois publications. Une quatrième publication porte sur la révision d'un genre de trilobite, travail réalisé en collaboration dans le cadre du co-encadrement d'un stage de Master 2 recherche (Gendry 2010). Ces travaux de systématique reposent sur l'observation et l'analyse qualitative et quantitative de variations morphologiques. Concernant les échinides, ils m'ont amené à réviser la position systématique d'une forme cénomanienne problématique (Saucède & Néraudeau 2006), étude déjà abordée dans le chapitre précédent consacré aux analyses phylogénétiques. La faune d'échinides de l'Hauterivien du bassin de Paris a également attiré mon attention par sa richesse spécifique (54 espèces décrites) et sa diversité taxinomique (22 genres, 14 familles, 9 ordres). L'abondance et la distribution des espèces variant selon la lithologie et la nature des faciès, cette faune constitue un cas d'étude intéressant pour des analyses macroécologiques. La révision des espèces initialement décrites s'est avérée cependant un préalable nécessaire à toute étude macroécologique. Elle m'a permis de décrire deux nouveaux genres et espèces d'échinides mais aussi de revoir la richesse spécifique à la baisse, avec seulement 26 espèces (Saucède *et al.* 2012, Benetti *et al.* 2013). Une base de données a été constituée dans le cadre de la révision systématique de ces espèces. Elle comporte 628 données d'occurrence géoréférencées. Ces données sont désormais disponibles en ligne (Benetti *et al.* 2013) via un portail GBIF (Global Biodiversity Information Facility) (figure 3.1) .



hauterivian_echinoids_of_the_paris_basin

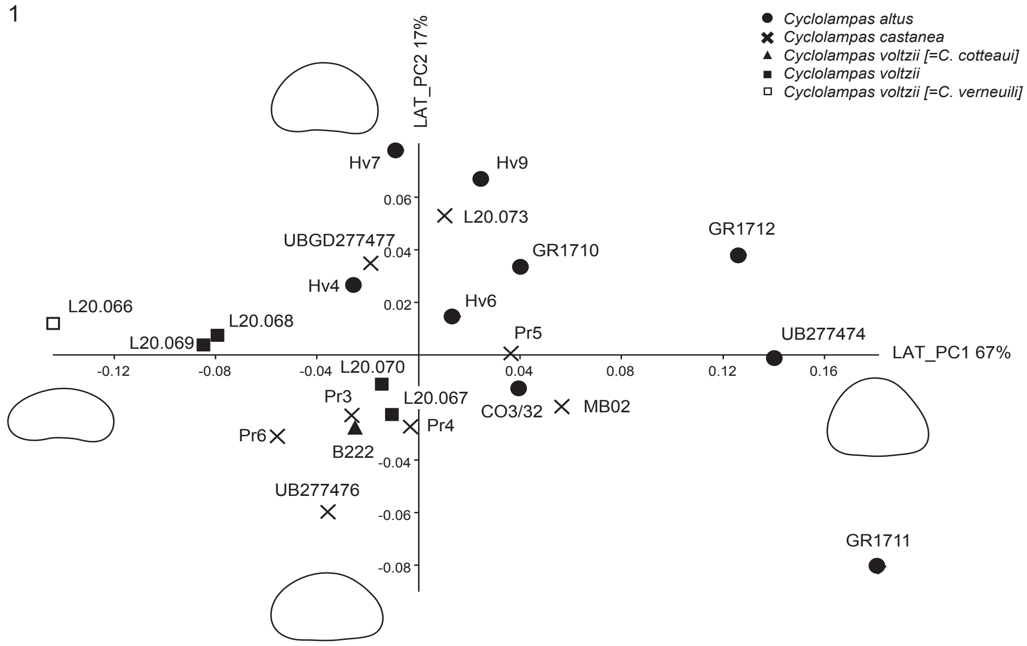
This dataset compiles occurrence data (all data are referenced by locality names and georeferenced WGS1984) of fossil echinoids collated from the literature published over a century and a half, from 1857 to 2012, by Cotteau (1857—1878; 1862—1867), Valette (1908), Corroy (1925), Rat et al. (1987), and Saucède et al. (2012). The dataset was completed by data from collection specimens housed at the department of Geology of Université de Bourgogne (Dijon, France), specimens sampled in the field by J Houdard, A Valette, B David, and P Robert, at the Muséum national d'Histoire naturelle (Paris, France), specimens sampled by J Lambert, and at the department of Geosciences of Université de Rennes 1 (Rennes, France), specimens sampled by P Courville. The dataset also gives information on taxonomy (from species to order and higher taxonomic levels). Systematics was reviewed and homogeneized by T Saucède for taxonomic relevance (Saucède et al. 2012).

Summary	Keywords	Echinoids; Hauterivian; Early Cretaceous; Paris Basin; France; Calcaires à Spatangues Formation
	Resource Language	eng
	Last Publication	Version 3 from Aug 26, 2013
	Darwin Core Archive	download (31 KB) 628 records
	EML	download (18 KB)
	RTF	download (17 KB)
	GBIF Registration	98442b0b-9f7b-4924-9289-5b793946ca01
	Organisation	ZooKeys
	Endorsing Node	Denmark
External Links	Resource Homepage	http://thomassaucede.wordpress.com/databases/
Resource Contact	Name	Thomas Saucède
	Position	Associate Professor
	Organisation	university of Burgundy
	Address	6 bvd Gabriel, Dijon, FR, Postal Code: F-21000
	Contact	thomas.saucede@u-bourgogne.fr Telephone: +33 380 396379
	Home Page	http://thomassaucede.wordpress.com/

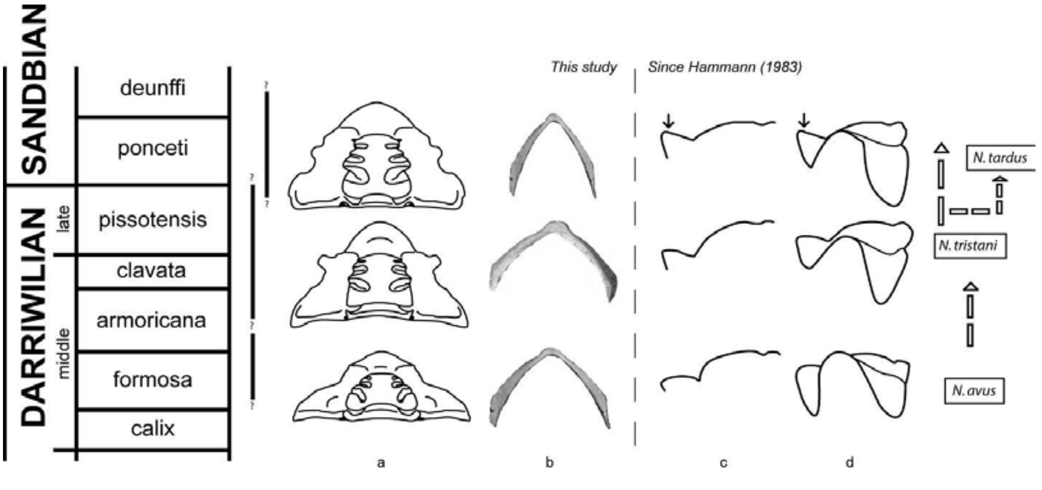
Figure 3.1. Capture d'écran d'un portail d'accueil GBIF donnant accès à la base de données publiée sur la distribution et la systématique des échinides hauteriviens du bassin de Paris.

Mes autres travaux de taxinomie s'appuient sur la quantification des variations morphologiques à l'aide de méthodes morphométriques (analyses de contours et de points homologues). Le genre d'échinide jurassique *Cyclolampas* comportait de nombreuses espèces décrites à partir de spécimens uniques sur la base de subtiles différences de forme. La découverte de nombreux spécimens du genre dans deux sites de Charente et de Bourgogne a révélé l'existence d'une importante variation morphologique intra-populationnelle. Très peu de caractères morphologiques permettant de différencier les espèces, seules des analyses des contours de test (par transformée de Fourier) ont permis d'analyser les variations morphologiques (figure 3.2). Les résultats ont montré que les caractères utilisés initialement pour différencier les espèces du genre correspondaient en fait à l'expression de variations morphologiques intra-populationnelles. Ils m'ont amené à réviser la systématique du genre et à décrire une nouvelle espèce (Saucède *et al.* 2013a).

Le genre de trilobite *Neseuretus* possède au contraire de nombreux caractères morphologiques identifiables qui présentent des variations entre spécimens de niveaux stratigraphiques différents. L'utilisation conjointe de mesures de biométrie classique (mesures de longueurs et d'angles) et de morphométrie (analyses de contours et de points homologues) a permis de décrire l'ensemble de ces variations morphologiques et de mettre évidence leur succession au cours du temps (figure 3.3). Les implications taxinomiques de cette étude ont permis de contribuer à la révision du genre (Gendry *et al.* 2013).



<u>Figure 3.2</u>. Analyse en Composantes Principales (plan des deux premières composantes) des variations de contour du test, quantifiées par transformée de Fourier, au sein du genre d'échinide jurassique *Cyclolampas* (Saucède *et al.* 2013a).



<u>Figure 3.3</u>. Succession stratigraphique des espèces de trilobite du genre *Neseuretus* de l'Ordovicien Moyen et Supérieur (Gendry *et al.* 2013). La révision systématique des espèces repose sur l'analyse de nombreux caractères morphologiques du céphalon, thorax et pygidium grâce à plusieurs méthodes de biométrie et de morphométrie géométrique.

Ces travaux de taxinomie et de systématique ont montré la difficulté que constitue la définition de caractères et d'états de caractères à partir de l'interprétation d'informations morphologiques réduites (ex : simples variations de contour de tests). Elles ont aussi montré la nécessité de disposer de suffisamment de spécimens pour quantifier et interpréter les variations de forme en l'absence de caractères morphologiques discrets fiables. Enfin, la pertinence et la signification des espèces paléontologiques identifiées doit être testée au regard d'autres sources d'information telles que les informations de temps, ou stratigraphiques (évolution des formes au cours du temps) et paléoécologiques (caractères autécologiques).

Publications associées : Saucède & Néraudeau 2006, Saucède *et al.* 2012, Saucède *et al.* 2013a, Gendry *et al.* 2013, Benetti *et al.* 2013

Travaux en cours, projets et perspectives

Variations morphologiques et concept biologique de l'espèce

Le découplage entre évolution morphologique et évolution génétique présente un profond intérêt en biologie évolutive, comme le montre le nombre d'études portant sur les espèces cryptiques (différenciation génétique seule) (Knowlton 1993, Hunter & Halanych 2008, McGuigan & Sgro 2009, Xavier *et al.* 2010, Lindner *et al.* 2011, Hemery *et al.* 2012, Novo *et al.* 2012a, 2012b, Waeschenbach *et al.* 2012). Il engendre aussi cependant des difficultés opérationnelles quand il s'agit de définir des caractères morphologiques permettant d'identifier les espèces. Cela est particulièrement vrai chez les invertébrés (Knowlton 1993, Waeschenbach *et al.* 2012, Novo *et al.* 2012b) qui présentent parfois peu de caractères et d'états morphologiques identifiables, des degrés de variations morphologiques intra- et inter-spécifiques recouvrants, ainsi que des phénomènes de convergence adaptative à l'origine d'homoplasies (Novo *et al.* 2012a). Les arguments formulés contre le concept morphologique de l'espèce ne sont pas nouveaux (Mayr 1963), le consensus actuel allant vers une systématique et une taxinomie multidisciplinaires qui intègrent les dimensions morphologique, moléculaire, écologique et géographique de l'espèce (Puillandre *et al.* 2012, Novo *et al.* 2012a).

En préalable à mes travaux de phylogénie et de biogéographie (Díaz *et al.* 2011, Moya *et al.* 2012, Pierrat *et al.* 2013), l'identification des espèces d'échinides australes récoltées sur le terrain ou consultées en collection (Pierrat *et al.* 2012a) ainsi que l'étude de leurs variations morphologiques ont révélé qu'une révision systématique de nombre d'entre elles était nécessaire, en particulier au sein de quatre principales familles : Arbaciidae, Echinidae, Schizasteridae et Cidaridae. Toutes les espèces étudiées présentent une part de variation morphologique inter-spécifique congruente avec les données génétiques disponibles (et en cours d'analyse), l'autre part correspondant à des variations intra-spécifiques qui concernent des caractères identifiés originellement comme diagnostiques d'espèces morphologiques et/ou géographiques (Díaz *et al.* 2011). A la différence de nombres d'invertébrés marins (Knowlton 1993, Xavier *et al.* 2010, Lindner *et al.* 2011, Waeschenbach *et al.* 2012) - dont des échinodermes (Hunter & Halanych 2008, Hemery *et al.* 2012) - aucune espèce cryptique d'échinide n'a encore été identifiée, peut-être en raison d'analyses insuffisantes, de particularismes anatomiques et phénotypiques (quantité de caractères morphologiques identifiables, forte canalisation), peut-être aussi en raison de phénomènes écologiques (fortes capacités de dispersion, larges niches écologiques) ou de phénomènes évolutifs (dérive génétique et dynamique démographique lentes). La différenciation morphologique entre espèces d'échinides concerne des caractères associés aux fonctions biologiques de locomotion, de nutrition et de respiration (Arbaciidae, Echinidae, Cidaridae), mais parfois aussi des caractères structuraux du squelette (Schizasteridae). Ces travaux de systématique s'accompagnent d'une réflexion sur la signification des congruences entre variations morphologiques et différences génétiques en termes de processus écologiques et de contraintes du développement, et ce en lien étroit avec les analyses phylogénétiques en cours. Ils doivent se concrétiser dans les années qui viennent par plusieurs notes, les notes de systématique intégrant l'analyse des composantes génétiques (travaux en collaboration), morphologiques, écologiques et géographiques.

Seul le travail en cours sur le genre *Sterechinus* est présenté ici à titre d'exemple, car il est le plus abouti pour le moment. Six espèces morphologiques avaient été originellement attribuées au genre *Sterechinus* (*S. neumayeri*, *S. antarcticus*, *S. diadema*, *S. dentifer*, *S. agassizi* et *S. bernasconiae*). A l'exception de trois espèces strictement antarctiques, elles sont distribuées dans les eaux antarctiques, subantarctiques et sud-américaines (Chili et Argentine), dans des régions distinctes (Mortensen 1943), de quelques mètres à plusieurs milliers de mètres de profondeur (Pierrat *et al.* 2012a). L'analyse des fortes variations morphologiques présentes chez les six espèces nous a permis de montrer que tous les caractères diagnostiques utilisés pour différencier les espèces jusqu'ici étaient l'objet de variations inter- et intra-spécifiques confondues chez cinq des six espèces, la morphologie des pédicellaires (vestiture) permettant uniquement de différencier trois groupes morphologiques. La sixième espèce s'est révélée appartenir à un autre genre (*Gracilechinus*). L'étude morphologique nous a donc permis d'individualiser trois groupes morphologiques principalement répartis selon des profondeurs et des températures différentes. Ces trois groupes morphologiques ne correspondent pas aux espèces géographiques originellement identifiées. A la différence d'espèces cryptiques (Hunter & Halanych 2008, Hemery *et al.* 2012, Novo *et al.* 2012b), l'environnement (profondeur, température et dynamique océanographique) semble être ici le facteur clé de la différenciation morphologique et non la géographie. Ces résultats ont été confirmés par des analyses génétiques réalisées sur le marqueur COI par des collègues chiliens (Díaz *et al.* 2011). Ils doivent faire l'objet de publications à partir de 2014 (figure 3.4).

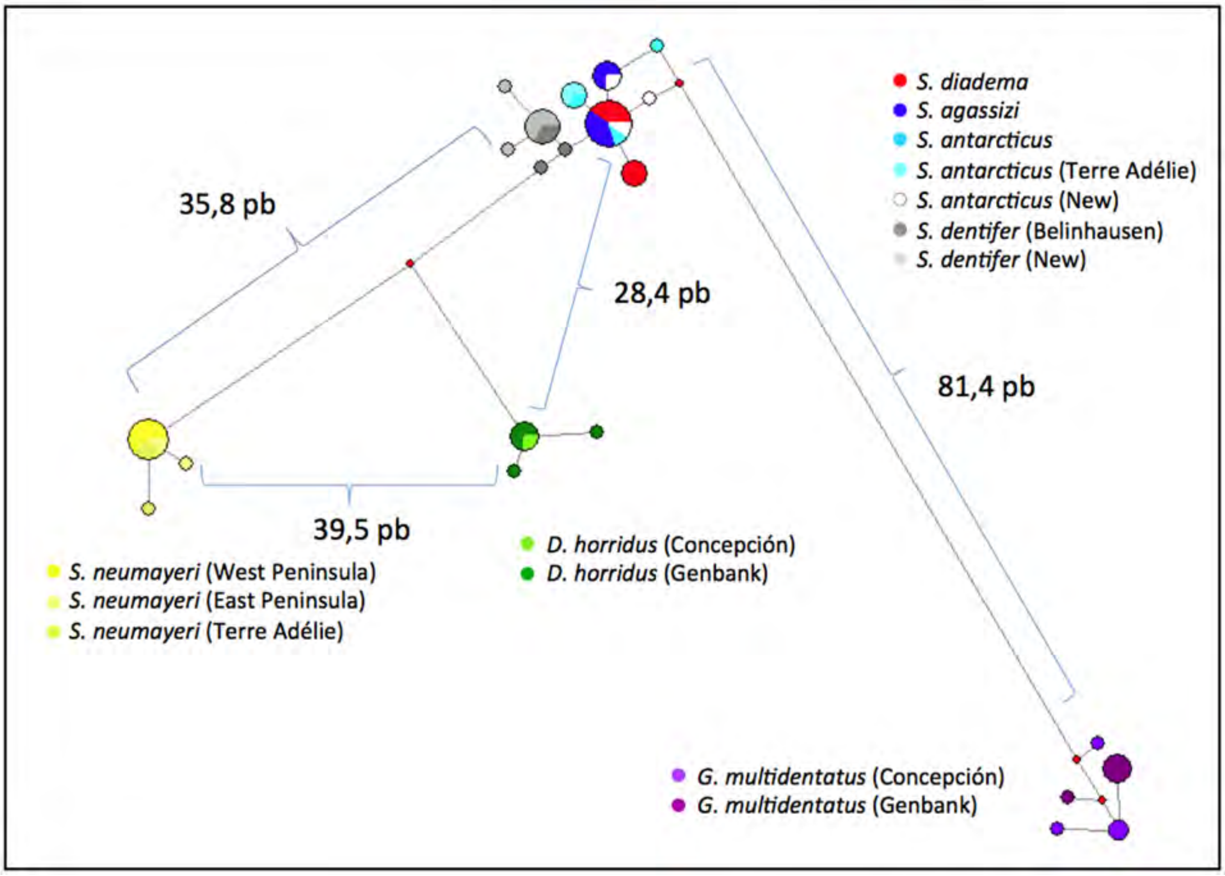


Figure 3.4. Réseau d'haplotypes (COI) des espèces d'Echinidae de l'océan Austral (étude en cours).

2. Analyse et évolution de la disparité morphologique

L'étude de la disparité morphologique permet d'éclairer certains facteurs fonctionnels, ontogénétiques et historiques (contingences historiques ou stochasticité) à l'origine de la biodiversité (Jablonski 2000, Gerber 2013). A la suite de mes travaux de thèse sur l'origine et la diversification des échinides irréguliers, j'ai pu montrer l'existence d'une corrélation dans la disparité morphologique entre caractères associés à des fonctions biologiques (nutrition, locomotion et respiration) d'une part, et entre caractères associés à la structuration interne du squelette d'autre part, caractères fonctionnels et structuraux semblant en grande partie découplés. A partir de cette constatation, deux projets de recherche ont été initiés il y a quelques années (voir David *et al.* 2009, Laffont *et al.* 2011) mais n'ont pas encore fait l'objet de publications : le premier a déjà abouti à des résultats qui doivent être publiés, le second va pouvoir être bientôt développé dans le cadre d'un stage de Master 2.

Le premier projet porte sur l'étude des contraintes structurales s'exerçant sur le squelette (plaques apicales) des échinides irréguliers, et sur leur évolution du Jurassique à l'Actuel. Il a pour objectif de mieux comprendre un aspect de l'évolution des contraintes du développement associé à la diversification des échinides irréguliers. Le second projet porte sur les liens entre diversifications écologique et morphologique, à travers l'étude de la composante fonctionnelle (richesse fonctionnelle) de la diversité morphologique des échinides jurassiques (Foote 1997, Villéger *et al.* 2011). Dans ces deux projets, l'analyse des données a et doit avoir lieu dans un cadre multidimensionnel (espaces morphologiques) dont l'intérêt a été démontré par de nombreuses études depuis une vingtaine d'années (Foote 1993, Wills *et al.* 1994, Roy & Foote 1997, Gould 2002, Erwin 2007, Villéger *et al.* 2011). En outre, l'utilisation de données fossiles et actuelles permet d'étudier le recouvrement entre diversités morphologiques de périodes et /ou clades différents, et de les comparer avec la diversité actuelle, souvent plus forte car mieux documentée. L'absence de recouvrement, ou le recouvrement partiel des diversités, nécessite des interprétations *ad hoc* et permet de mettre en évidence une évolution des contraintes structurales (Villéger *et al.* 2011, Wills *et al.* 2012).

Travaux en cours, projets et perspectives

2.1. Disparité morphologique et contraintes structurales

Ce premier projet porte sur l'étude des contraintes structurales du squelette des échinides irréguliers, et en particulier des irréguliers atélostomes, depuis leur origine au Jurassique jusqu'aux espèces actuelles qui composent une part importante des faunes d'échinides.

Les facteurs structuraux internes qui déterminent en partie la disparité morphologique, correspondent à des contraintes ontogénétiques dont l'évolution peut être étudiée par l'étude des niveaux et motifs d'intégration entre caractères (Jablonski 2000, Gerber 2013). Cette étude de l'intégration entre caractères morphologiques est ici abordée par l'analyse des motifs de connexion entre éléments du squelette, car ces motifs résultent des relations ontogénétiques entre éléments. Les motifs de connexion entre entités anatomiques sont essentiels pour identifier les unités anatomiques et les homologies entre clades (Rieppel 1988, Rasskin-Gutman 2003). Or, peu d'études de diversité morphologique se sont intéressées aux motifs de connexion en tant que niveau d'organisation morphologique à part entière (Rasskin-Gutman & Buscalioni 2001, Rasskin-Gutman 2003, Esteve-Altava *et al.* 2012). Les limites entre entités anatomiques apparaissent automatiquement suite à leur expansion au moment de la croissance des organismes; elles constituent alors un niveau d'organisation morphologique supérieur. En retour, ces motifs de connexion ont des répercussions sur les entités elles-mêmes en contraignant leur forme et leur développement (Rasskin-Gutman 2003). L'étude des motifs de connexion est donc importante pour comprendre les phénomènes impliqués dans la morphogenèse.

Ici, les motifs de connexion entre éléments du squelette ont été étudiés grâce aux outils mathématiques associés à la théorie des graphes. En effet, les entités anatomiques peuvent être symbolisées par les sommets de graphes et les contacts entre elles par des arrêtes (figure 3.5). La théorie des graphes fournit alors un cadre et des moyens de caractérisation et de quantification de ces motifs. Ce type d'approche a déjà été utilisé dans le cas d'études portant sur l'architecture et l'évolution du squelette de vertébrés (Rasskin-Gutman & Buscalioni 2001, Rasskin-Gutman 2003, Esteve-Altava et *al.* 2012). Tout comme les vertébrés, le squelette des échinides est composé de nombreux éléments squelettiques dont la connectivité constitue une composante morphologique d'importance pour comprendre leur évolution (figure 3.5). Ainsi, l'origine et la diversification des échinides irréguliers ont été accompagnées d'une importante restructuration de leur squelette, et en particulier de sa partie apicale (Jesionek-Szymanska 1963, Mintz 1968, Kier 1974, Smith 1984, Saucède *et al.* 2007). L'architecture des plaques apicales a surtout été étudiée dans le cadre de travaux de systématique, mais elle peut également éclairer un aspect de l'évolution morphologique des échinides (Kier, 1974, Saucède *et al.* 2004, 2007).

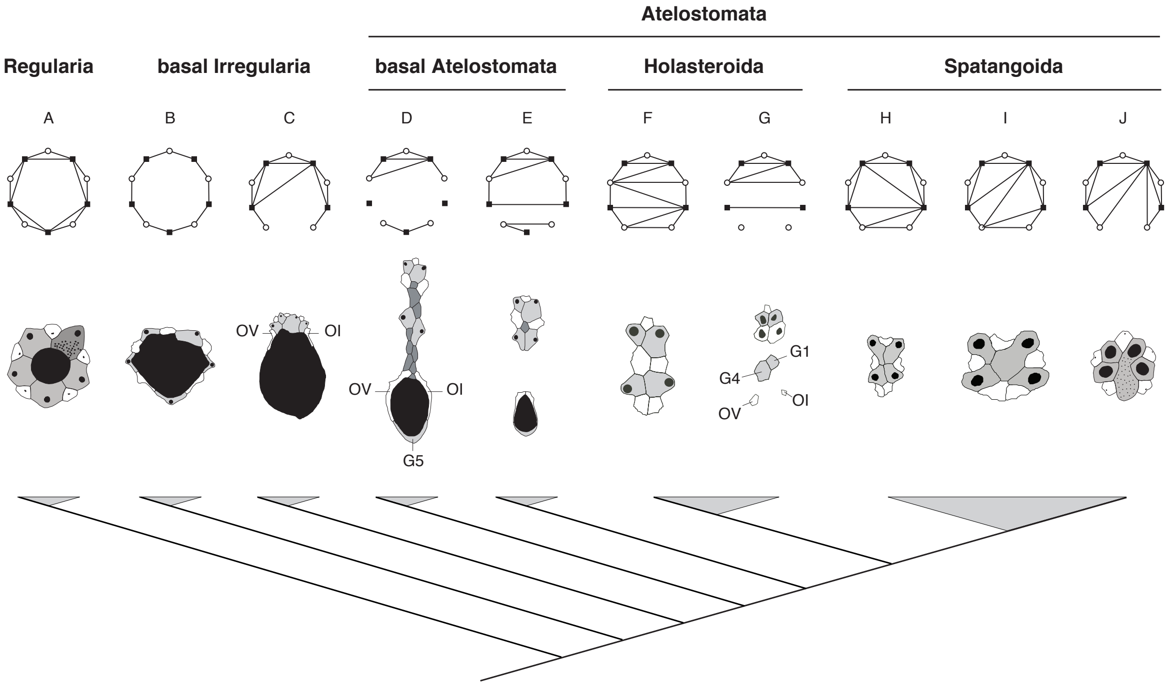
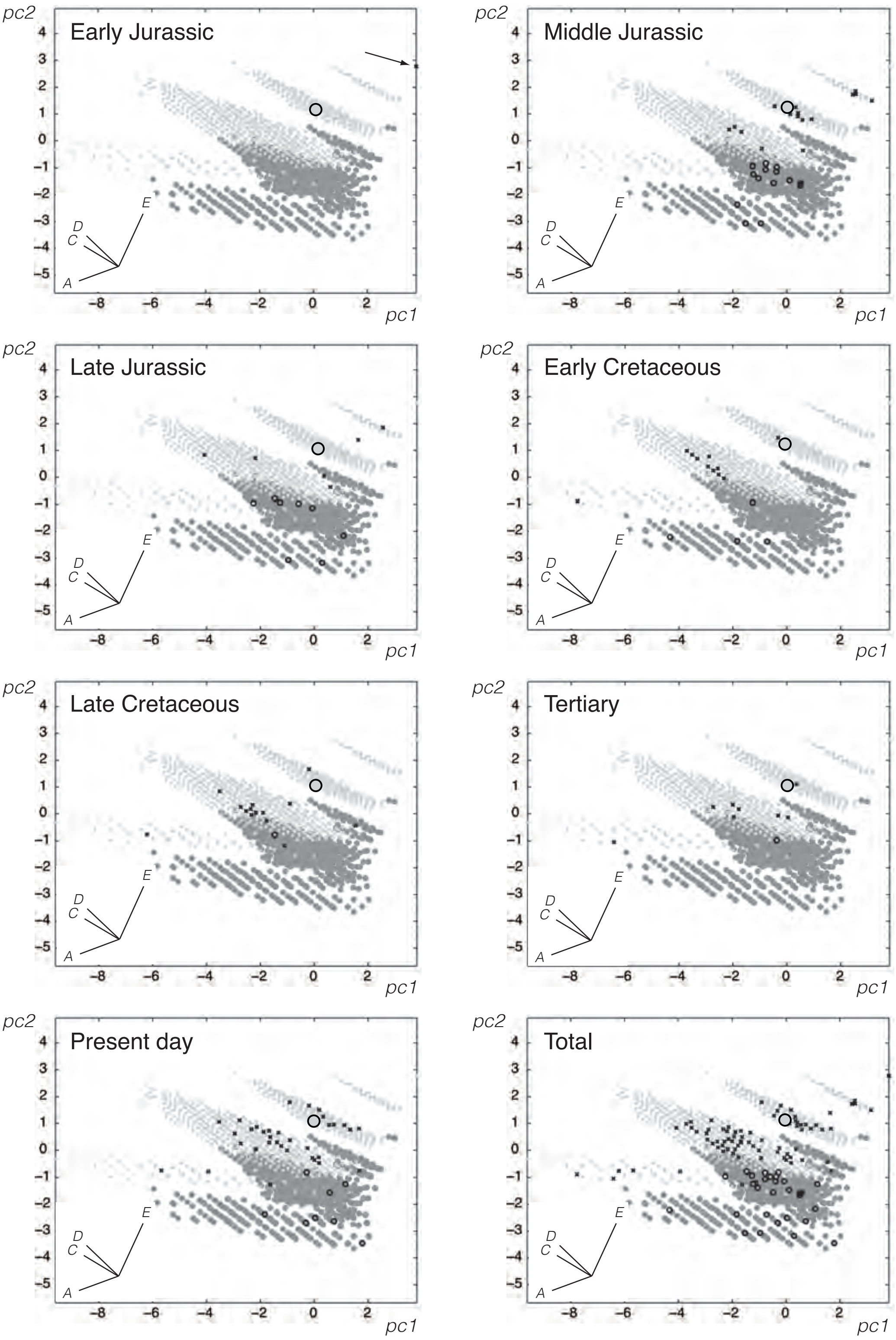


Figure 3.5. Synthèse des relations de parenté entre grands groupes d'échinides irréguliers, ici représentés par des structures apicales typiques. Les liaisons entre plaques apicales peuvent-être symbolisées à l'aide de graphes, et leurs variations analysées grâce aux outils mathématiques fournis par la théorie des graphes (étude en cours).

Les premiers résultats montrent que les connexions entre éléments du squelette apical des échinides irréguliers ne sont pas distribuées de façon isotrope entre plaques, et que la fréquence des motifs de connexion varie entre sous-clades et entre périodes. Ces motifs sont en effet le résultat de contraintes structurales (sans doutes développementales) qui ont évolué depuis les premiers échinides irréguliers jurassiques jusqu’aux formes actuelles (figure 3.5). Des espaces morphologiques (ou topologiques) ont été constuits à partir d’indices de compacité, d’excentricité, d’asymétrie et de complexité qui permettent de quantifier les propriétés topologiques des motifs de connexion. Dans ces espaces topologiques, la diversité topologique ne se recouvre que partiellement entre sous-clades et entre périodes, témoignant de l'évolution des motifs architecturaux au cours du temps (figure 3.6).



Early Jurassic

Middle Jurassic

Late Jurassic

Early Cretaceous

Late Cretaceous

Tertiary

Present day

Total

Figure 3.6. Evolution de la diversité topologique des appareils apicaux chez les échinides irréguliers atélostomes (figurés noirs) depuis le Jurassique inférieur. Les simulations (gris clair et foncé) représentent la portion "réalisable" (réaliste) des espaces topologiques (analyses en composantes principales), portion plus ou moins représentée chez les échinides au cours du temps (étude en cours).

2.2. Disparité morphologique et diversité fonctionnelle

La diversité fonctionnelle correspond à un niveau d'étude de la biodiversité qui suscite actuellement un intérêt scientifique renouvelé en écologie et biologie de la conservation (Purvis et Hector 2000, Mason *et al.* 2005, Villéger *et al.* 2008, 2010, Mason & Bello 2013, Goullectquer *et al.* 2013). La diversité fonctionnelle correspond à l'ensemble des processus, fonctions et caractéristiques biologiques des espèces qui composent une communauté (Mason & Bello 2013). Elle permet d'aborder des problématiques écologiques récurrentes qui concernent les mécanismes à l'origine de la composition des communautés et des écosystèmes (Mason *et al.* 2005, Mason & Bello 2013). En l'absence d'une connaissance exhaustive de la diversité taxinomique, elle assure une mesure de la biodiversité qui permet de rendre compte de la structure écologique des communautés et des écosystèmes. Elle permet d'évaluer leur stabilité face aux changements environnementaux actuels et à leurs conséquences telles que les phénomènes d'extinction et d'invasion d'espèces. Les espèces ayant des fonctions écologiques distinctes et complémentaires au sein des écosystèmes, l'extinction ou l'invasion d'une, ou de plusieurs espèces a nécessairement des répercussions sur le fonctionnement de ces écosystèmes. Les écosystèmes les plus diverses d'un point de vue fonctionnel (c'est-à-dire ceux qui présentent une plus grande variété d'interactions positives et complémentaires entre espèces) sont alors considérés comme étant les plus stables face aux changements environnements, bien que quelques exceptions aient été mises en évidence (Purvis & Hector 2000, Petchey & Gaston 2006, Goullectquer *et al.* 2013). En outre, au sein d'un écosystème, la forte diversité écologique d'un groupe fonctionnel peut avoir une action de facilitation pour les autres groupes, en renforçant leur stabilité (Purvis & Hector 2000).

La diversité fonctionnelle peut être mesurée à l'échelle locale (*diversité alpha*), on parle alors de *richesse fonctionnelle* (Villéger *et al.* 2008), elle peut aussi être comparée entre communautés contemporaines (*diversité béta*) ou entre périodes de temps différentes (*turnover*) afin d'en étudier l'évolution (Villéger *et al.* 2011, Mason & Bello 2013). Quelques travaux ont abordé l'étude de la diversité fonctionnelle à l'échelle de plusieurs groupes, ainsi que son évolution entre des périodes-clés (Cambrien, Dévonien, Actuel). Ces travaux reposent sur l'étude de la disparité morphologique de caractères associés à des fonctions biologiques essentielles (Villéger *et al.* 2011, Wills *et al.* 2012). Les taux de recouvrement ou de juxtaposition au sein d'espaces fonctionnels entre les disparités de groupes ou périodes différentes (Villéger *et al.* 2011, Mason & Bello 2013), renseignent alors sur l'évolution de la diversité fonctionnelle, en particulier dans le cadre de phénomènes de radiation ou d'extinction. La comparaison des niveaux de diversité fonctionnelle avec ceux de diversité phylogénétique renseigne également sur le conservatisme écologique des communautés (Mason & Bello 2013).

Ce second projet a pour but d'étudier l'évolution de la diversité fonctionnelle des échinides irréguliers au Jurassique, période-clé de leur diversification. Il doit consister en l'analyse de la disparité morphologique des caractères associés aux fonctions biologiques de locomotion (tubercules), de nutrition (pores adoraux, inclinaison et position du péristome) et de respiration (pores adoraux). L'étude comparée de la diversité fonctionnelle des échinides dans le cadre de phylogénies robustes comprenant échinides réguliers et irréguliers, doit permettre de démontrer le caractère adaptatif, ou tout du moins éclairer la dimension écologique de la diversification des échinides irréguliers au Jurassique, diversification en lien avec l'évolution paléoenvironnementale de l'époque, à savoir le développement des milieux circalittoraux carbonatés colonisés par les échinides irréguliers.

CHAPITRE IV.

ANALYSE DE LA DISTRIBUTION SPATIALE DE LA BIODIVERSITE

BIOGEOGRAPHIE ET MACROECOLOGIE

L'approche macroécologique a pour double objectif de déterminer les facteurs environnementaux et historiques qui structurent la distribution de la biodiversité dans le temps et dans l'espace, ainsi que de scénariser les modifications éventuelles associées aux changements environnementaux (Brown 1995, Gaston & Blackburn 2000, Briggs 2007). Dans le contexte actuel d'évolution climatique et de changements environnementaux rapides, cette approche suscite un réel engouement auprès des biologistes confrontés aux enjeux de la conservation, mais plus largement aussi auprès des écologistes et paléontologues intéressés par les sciences de l'évolution. L'identification des déterminants environnementaux à l'origine de la distribution des espèces permet en effet d'estimer leur sensibilité à leur environnement, et donc leur vulnérabilité potentielle face aux changements qu'il subit. La vulnérabilité des espèces peut être évaluée sur la base de notre connaissance de leurs exigences écologiques, mais aussi à partir de l'analyse de leur distribution spatiale. Compte tenu de la rapidité et de l'ampleur des changements actuels, en particulier en domaine marin (Burrows *et al.* 2011), les méthodes fondées sur l'analyse à large échelle de la corrélation spatiale entre caractéristiques environnementales et distribution des espèces ont été privilégiées pour estimer les exigences écologiques de ces espèces (Cheung *et al.* 2009). Au delà de la biogéographie descriptive, l'étude de la distribution spatiale des espèces revêt donc un intérêt macroécologique puisqu'elle permet de caractériser les niches écologiques des espèces. L'utilisation des données spatiales permet également de prédire et de rétro-prédire les distributions respectivement futures et passées des espèces sur la base du postulat d'équivalence de niche et du conservatisme écologique des espèces (voir Broennimann *et al.* 2007, Zurell *et al.* 2009, Elith *et al.* 2010, Blois *et al*. 2013, Collevatti *et al.* 2013 pour des tests et critiques de cette approche). La biogéographie descriptive constitue donc un préalable à la caractérisation des déterminants historiques (Svenning *et al.* 2011, Varela *et al.* 2011, Pierrat *et al.* 2012b, Stigall 2012, Blois *et al.* 2013). L'approche corrélative fait actuellement l'objet de nombreuses critiques (qui seront discutées plus bas), mais ces critiques soulignent aussi l'intérêt opérationnel qu'elle présente et concluent souvent en définissant le cadre et les conditions dans lesquels l'approche corrélative devrait être pratiquée (Austin *et al.* 2006, Broennimann *et al.* 2007, Barve *et al.* 2011, Svenning *et al.* 2011, Varela *et al.* 2011, Blois 2012, Tessarolo 2012, Aguirre-Gutierrez *et al.* 2013, Attorre *et al*. 2013, Bahn & McGill 2013, Bentlage *et al.* 2013, Gutt *et al.* 2013, Sheppard 2013).

1. Description des motifs biogéographiques

La biogéographie descriptive concerne la description des motifs de distribution des taxons et des communautés ; elle est une étape préalable aux analyses macroécologiques dont l'objet est d'identifier les facteurs de contrôle et les processus biogéographiques impliqués dans la dynamique de la biodiversité (Briggs 2007, Saucède *et al.* sous presse b). L'échelle spatiale à laquelle ces motifs sont décrits est déterminante pour les analyses macroécologiques qui suivent, dans la mesure où facteurs environnementaux et historiques n'interviennent pas de façon identique sur la dynamique des populations locales et sur celle des espèces ou des clades aux échelles régionales et globales. Echelles spatiale, taxinomique et temporelle sont souvent interdépendantes dans les analyses. Ainsi, l'analyse des motifs biogéographiques à l'échelle d'un océan ne permettra pas de révéler l'impact des hétérogénéités environnementales sur la distribution des populations, mais soulignera le rôle des déterminants physiques, physiographiques et historiques à l'échelle des espèces et des clades. A une telle échelle spatiale, la plupart des espèces présenteront un temps de réponse aux déterminants physiques qui sera supérieur à celui de l'analyse ; cette dernière pourra alors souligner l'importance du processus de dispersion pour expliquer les motifs observés. A l'échelle des clades, processus macroévolutifs et géodynamiques seront déterminants.

Plusieurs de mes travaux ont consisté en l'analyse des motifs de distribution de faunes benthiques antarctiques à différentes échelles taxinomiques (des populations aux clades), spatiales et temporelles (tableau 3). Les mers australes ont été relativement peu étudiées en macroécologie, alors que les changements climatiques actuels impactent d'ores et déjà de façon complexe le fonctionnement de leurs écosytèmes (Moline *et al.* 2004, Ainley *et al.* 2005, Barnes 2005). Malgré des difficultés d'échantillonnage évidentes (Bentlage *et al.* 2013), l'analyse biogéographique de l'océan Austral permet d'explorer une grande variété d'habitats aux diversités et complexités parfois importantes (Clarke & Johnson 2003), et aux conditions environnementales extrêmes. Elle implique également de tenir compte de particularismes et de processus originaux qui incluent l'existence d'une couverture de glace saisonnière, du courant circumpolaire antarctique et du front polaire, ainsi que d'adapations originales des espèces à cet environment unique (Gutt *et al.* 2012).

Principaux résultats

Analyse de la distribution spatiale de faunes benthiques à l'échelle régionale

Plusieurs de mes travaux ont porté sur l'étude de la distribution spatiale d'organismes benthiques à l'échelle des communautés (méio-, macro- et mégafaune) et à l'échelle de régions maritimes antarctiques. Ces travaux s'appuient sur des données de terrain issues de quatre missions d'échantillonnage réalisées en Antarctique de l'Ouest (mers de Bellingshausen et d'Amundsen et secteur de Larsen), dans des secteurs jusque là peu étudiés car difficilement accessibles. Ces études décrivent les motifs de répartition spatiale des assemblages fauniques, leur composition, leur richesse taxinomique et leur abondance (incluant une estimation de leur biomasse) depuis les secteurs internes du plateau continental jusqu'aux secteurs externes réprésentés par le talus continental et les bassins océaniques profonds. L'étude des motifs de distribution à l'échelle régionale est un préalable aux interprétations environnementales présentées dans le paragraphe suivant. L’échelle d’étude permet également d’appréhender la dynamique de la diversité régionale sur des temps très courts (quelques années) en lien avec des perturbations environnementales fortes (rupture de plates-formes de glace).

Modèle d'étude	Echelle taxinomique	Echelle spatiale			
		échelle régionale	plusieurs régions	échelle océanique	globale
ACTUEL	espèce		espèce de gastéropode : *Nacella concinna* - ouest Antarctique (30)	espèces d'échinides de l'océan Austral (19, 28)	
	genre			*Sterechinus* - océan Austral (16, 22)	*Arbacia*
	classe	échinides de mer de Bellingshausen (21) et de Larsen (15)	échinides ouest-antarctiques	échinides antarctiques (20, 32)	
	plusieurs classes		échinides, bivalves et gastéropodes d'Antarctique de l'ouest	échinides, bivalves et gastéropodes de l'océan Austral (25); faune marine antarctique (28)	
	communauté	benthos, Mer de Bellingshausen (11), Larsen (14), Mer d'Amundsen (31)			
FOSSILE (ponctuel : zone d'ammonite)	classe	échinides hauteriviens du bassin de Paris (29)			
FOSSILE (évolutif : 70 Ma)	classe			échinides de l'océan Austral - fini-Crétacé à Actuel (26)	

Tableau 3. Synthèse de mes travaux décrivant les motifs biogéographiques de faunes benthiques antarctiques à différentes échelles taxinomiques, spatiales et temporelles. Les numéros renvoient à mes publications et suivent l'ordre de la liste fournie dans la partie "Bilan d'activité".

L’étude à l’échelle des communautés couvre un grand nombre de taxa (25 classes représentées pour la mission Bentart’06, 32 classes pour BIOPEARL II, 15 phyla pour JR230). Toutes les études soulignent l’existence de diversités contrastées entre les domaines internes du plateau continental plus riches et plus diversifiés, et les domaines de plateau externes, de talus et de bassin présentant certaines affinités fauniques ainsi que des communautés moins riches et moins diversifiées (communautés dominées à 90% par les foraminifères dans les bassins). Des particularismes régionaux et locaux sont cependant présents, comme l’existence d’un gradient croissant de densité d’est en ouest en Mer de Bellingshausen, des assemblages originaux autour de l’île Pierre I^{er} et des contrastes fauniques entre régions (cas des mers de Ross et d’Amundsen pourtant voisines). La mégafaune benthique du plateau interne est souvent dominée par les échinodermes en termes de biomasse, d'abondance et de diversité, les échinides étant très largement présents. Par exemple, 17 espèces soit 22% de l'échinofaune antarctique ont été échantillonnés en une mission en mer de Bellingshausen, doublant le nombre des espèces d'échinides répertoriées dans cette région jusque là. Au sein des échinides, les distributions sont malgré tout contrastées, principalement en lien avec les caractéristiques trophiques des espèces (distribution des spécialistes plus restreinte par rapport aux généralistes plus largement distribués, plus fréquents et plus abondants).

L'étude menée dans le secteur de Larsen respectivement cinq ans et 12 ans après la rupture des deux plates-formes de glace a mis en évidence la faible diversité des assemblages benthiques (macro- et mégafaune) composés à la fois d'espèces pionnières, typiques des zones de plateau antarctique (*S. neumayeri* et *S. antarcticus* chez les échinides), et d'espèces interprétées comme les reliques de communautés ayant existé sous les plates-formes de glace (figure 4.1). La forte hétérogénéité spatiale des communautés suggère l'existence de perturbations localisées au-delà des zones de rupture des plates-formes de glace (raclage d'icebergs sur le fond) et des vitesses de réponse différentes des communautés entre les zones oligotrophes et les zones à forte production de biomasse (liée au domaine pélagique, où la biomasse est représentée par le krill, les poissons pélagiques et les mammifères marins).

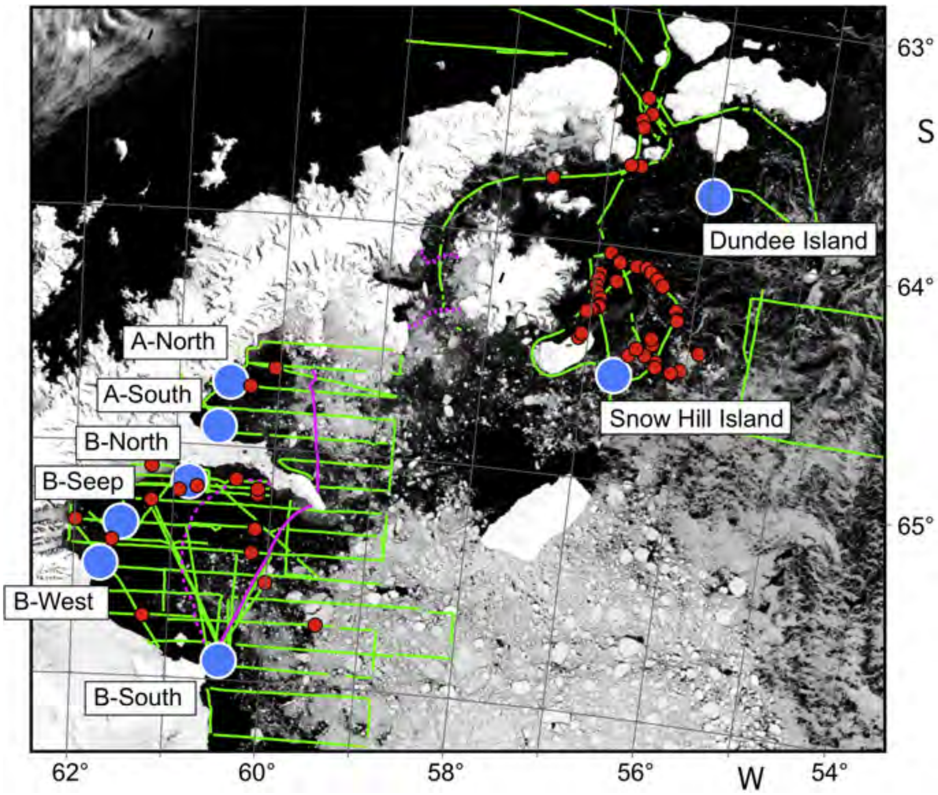


Figure 4.1. Vue satellite de la Péninsule Antarctique montrant les secteurs (points bleus), stations (points rouges) et transects (en vert) étudiés pour mettre en évidence l'impact de la rupture des plates-formes de glace sur les communautés benthiques (Gutt *et al.* 2011).

Publications associées : Saiz *et al.* 2008 (mer de Bellinghausen), Hardy *et al.* 2011 (secteur de Larsen), Gutt *et al.* 2011 (secteur de Larsen), Moya *et al.* 2012 (mer de Bellingshausen), Linse *et al.* 2013 (mer d'Amundsen).

Biorégionalisation à l'échelle de l'océan Austral

Une partir de mes travaux a concerné l'étude de la structuration spatiale au-delà de l'échelle régionale. L'objectif était de définir les motifs biogéographiques (ou phylogéographiques) entre régions antarctiques et péri-antarctiques (González-Wevar *et al.* 2013) à l'échelle de l'océan Austral (Pierrat *et al.* 2012a, Saucède *et al.* 2013b, Pierrat *et al.* 2013). Ces études m'ont permis d'aborder les motifs de distribution spatiale à des niveaux taxinomiques différents, de l'échelle de populations à celle de phyla.

A l'échelle des populations, l'étude avait pour but d'analyser la structuration spatiale de la diversité génétique chez la patelle antarctique *Nacella concinna* à travers l'étude de populations de la péninsule antarctique et des îles péri-antarctiques de l'arc de la Scotia. Les résultats ont montré l'existence de deux unités : (1) une unité à faible diversité génétique regroupant toutes les populations étudiées exceptée la population de Géorgie du Sud (île la plus septentrionnale de l'Arc de la Scotia), et (2) l'unité de la Géorgie du Sud à forte diversité génétique. La limite phylogéographique étant situé au milieu de l'Arc de la Scotia (González-Wevar *et al.* 2013).

Dans le cadre de la réalisation d'un *Atlas biogéographique de l'océan Austral* adossé aux programmes CAML (Census of Antarctic Marine Life – Alexander *et al.* 2011) et SCAR-MarBIN (Marine Biodiversity Information Network du SCAR), j'ai été sollicité pour la rédaction d'un chapitre consacré à la biogéographie des échinides antarctiques. A l'occasion de ce travail de synthèse, j'ai pu décrire les grands motifs biogéographiques de la classe à l'échelle de l'océan Austral et jusque 45° de latitude sud. La compilation des données publiées (Pierrat *et al.* 2012a) et des données d'occurrence géographique et bathymétrique acquises dans le cadre de mes missions m'a permis de caractériser également les motifs de richesses spécifique et générique (figure 4.2). Les richesses spécifique et générique des échinides sont les plus fortes sur le plateau continental antarctique, entre 100 et 1000 m de profondeur, où elles déterminent un gadient de richesse latitudinal original (Crame 2004), croissant entre 60° et 70° de latitude sud (limite sud du Front Polaire et des eaux subantarctiques). L'étude de la distribution des 126 espèces d'échinides référencées (Pierrat *et al.* 2012a) m'a permis de proposer une zonation latitudinale des espèces distinguant cinq zones : Haut Antarctique, Antarctique et subantarctique, subantarctique strict, Antarctique à tempérée froide et tempérée froide. Sans surprise, cette zonation reflète la structuration des masses d'eau. Elle caractérise 89% des espèces d'échinides, 11% seulement des espèces s'étendant au-delà des limites nord et sud des eaux subantarctiques, zone de fluctuation du Front Polaire.

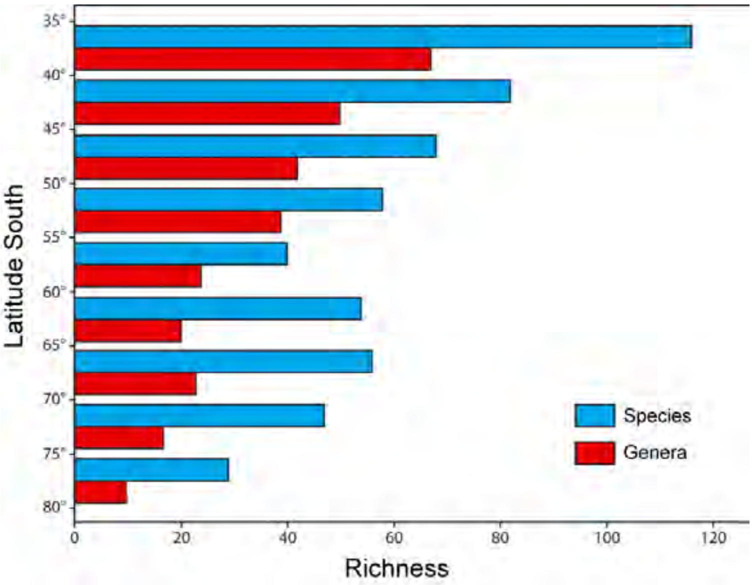


Figure 4.2. Gradients latitudinaux de richesse spécifique et générique des échinides de l'océan Austral montrant un pic de richesse spécifique entre 60° et 70° de latitude sud (Saucède *et al.* sous presse a).

Un second travail a étendu l'étude des motifs biogéographiques de la classe des échinides aux données fossiles, en comparant les affinités fauniques entre régions australes actuelles aux motifs biogéographiques anciens de trois étages géologiques pour lesquels des données d'occurrence d'échinides existent en Antarctique : le Maastrichtien, l'Eocène et le Miocène. L'analyse des données d'occurrence a été réalisée au niveau générique. Analyse des relations fauniques et tests de robustesse ont été réalisés par la méthode des réseaux de bootstraps traversants (BSN). Cette procédure permet de décrire à la fois la nature hiérarchique et/ou graduelle des relations fauniques entre régions (Brayard *et al.* 2007). Premier essai d'analyse quantitative à de telles échelles temporelle, taxinomique et spatiale pour cette région du monde, les résultats ont été discutés au regard des contextes océanographiques et tectoniques actuels et passés (figure 4.3). Ils ne concordent pas toujours avec les modèles couramment admis : ainsi, ils ne montrent pas l'existence, chez les échinides antarctiques, du provincialisme austral mis en évidence dans d'autres groupes à la fin du Crétacé et début du Cénozoïque (Zinsmeister 1979, 1981, Zinsmeister & Camacho 1980). A l'inverse, ils s'accordent sur d'autres points avec les études précédentes et montrent par exemple l'existence d'un isolement des faunes argentines au Miocène Inférieur (Del Rio 2002).

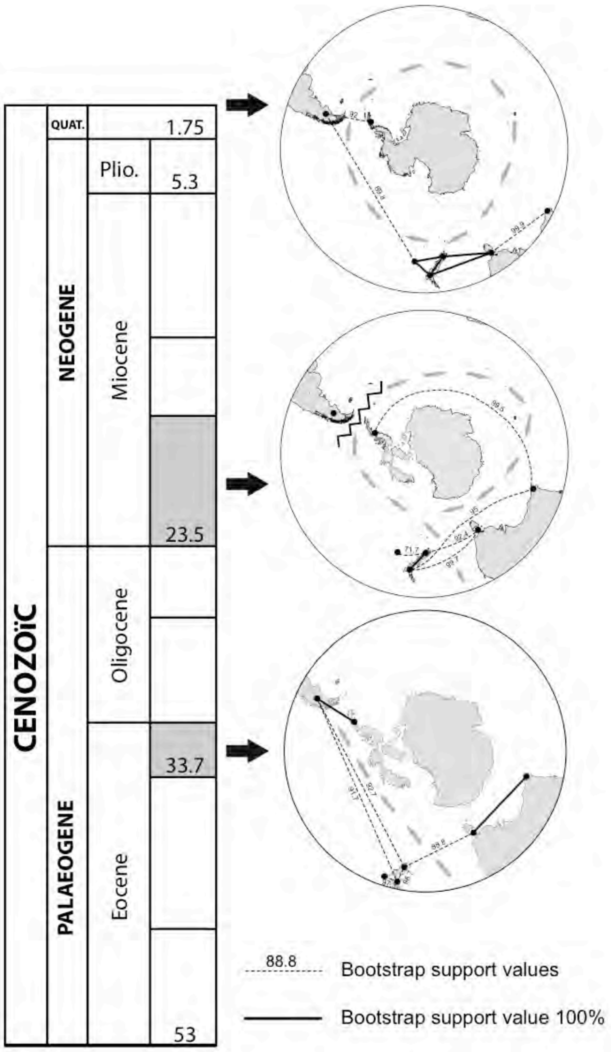


Figure 4.3. Affinités des faunes d'échinides entre régions australes à l'Eocène, Miocène et Actuel (traits pleins et pointillés) replacées dans leurs contextes océanographiques et paléogéographiques respectifs. Les flèches grises représentent les principaux courants océaniques (Saucède *et al.* 2013b).

L'analyse comparative des faunes actuelles d'échinides, de bivalves et de gastéropodes de l'océan Austral a permis d'intégrer dans une seule étude la description des motifs biogéographiques de plusieurs phyla. Cette analyse a été réalisée dans le cadre du co-encadrement de la thèse de B. Pierrat. La méthode BSN a été utilisée pour décrire les relations fauniques entre régions au sein des trois classes, aux niveaux de l'espèce et du genre, à partir de bases de données d'occurrence déjà constituées (Antarctic Echinoid Database, Pierrat *et al.* 2012a et Southern Ocean Mollusc Database, Griffiths *et al.* 2003). L'étude a permis de confirmer la structuration de l'océan Austral en grandes provinces fauniques tout en soulignant les particularismes phylétiques. Ainsi, bivalves et échinides montrent des motifs biogéographiques similaires structurés en trois grandes provinces : (1) néo-zélandaise, (2) sud-américaine et subantarctique, et (3) Antarctique. Les motifs présentés par les espèces et genres de gastéropodes diffèrent très clairement des deux autres clades ; ils montrent une structuration en cinq grandes provinces : (1) néo-zélandaise, (2) sud-américaine, (3) subantarctique orientale, (4) ouest-antarctique et (5) est-antarctique (Pierrat *et al.* 2013).

Publications associées : Saucède *et al.* sous presse a, Pierrat *et al.* 2012a, Saucède *et al.* 2013b, Pierrat *et al.* 2013, González-Wevar *et al.* 2013.

2. Etude des facteurs de contrôle

Les facteurs environnementaux et historiques qui déterminent la distribution des espèces interagissent entre eux de façon plus ou moins complexe et indirecte de sorte que la réponse des espèces peut être difficile à caractériser (Guisan & Zimmerman 2000, Phillips *et al.* 2006). D'autre part, les contributions respectives de ces facteurs de contrôle dépendent des échelles spatiale et temporelle d'analyse (Austin & Van Niel 2011, Blois *et al.* 2013). A l'échelle locale, la dynamique démographique des populations est fortement contrôlée par des déterminants physiques, chimiques et par les interactions biotiques; les variations d'abondance et de distribution des populations fluctuant sous l'effet de ces facteurs sur des temps courts (Pearson & Dawson 2003, Lomolino *et al.* 2006, Chatfield *et al.* 2010, Gogina *et al.* 2010, Soberón 2010, Bentlage *et al.* 2013). A large échelle et faible résolution spatiales, le poids des interactions biotiques est généralement considéré comme négligeable au regard des facteurs abiotiques qui se combinent à l'histoire évolutive des clades et aux processus géodynamiques pour déterminer les motifs biogéographiques (Ricklefs 2004, Bond & Chase 2002, Anderson & Martinez-Mayer 2004, Lomolino *et al.* 2006, Cheung *et al.* 2009, Saupe *et al.* 2012, Bentlage *et al.* 2013, Blois *et al.* 2013).

Dans mes travaux et projets actuels, l'étude des déterminants environnementaux et historiques à l'origine de la distribution des espèces a donc été guidée par deux nécessités : prendre en compte la complexité des relations entre facteurs structurants et identifier les rôles respectifs de ces facteurs aux différentes échelles spatiales, taxinomiques et temporelles.

2.1. L'environnement physique

De nombreuses procédures ont été développées pour analyser la distribution et la diversité des espèces en fonction de données environnementales (Guisan & Zimmermann 2000, Elith *et al*. 2006, Marmion *et al.* 2009). Parmi celles-ci, les modéles linéaires ne sont pas toujours les plus appropriés car les covariations entre variables environnementales sont souvent complexes et la réponse des espèces à ces covariations est fréquemment non-linéaires (effets de seuil et de saturation). Des méthodes ont donc été développées pour permettre d'utiliser des fonctions à la fois linéaires et non linéaires, de complexité plus ou moins grande, pour évaluer l'ensemble des relations entre variables et données de distribution (Austin 2002, Chatfield *et al.* 2010, Tong *et al.* 2013).

Parmi ces méthodes, l'approche corrélative par modélisation de niche permet de définir les exigences écologiques des espèces, en terme d'habitat, sur la base des corrélations spatiales entre paramètres de l'environnement et données de distribution des espèces (Phillips *et al*. 2006, Tsoar *et al.* 2007). Elle a pour but de créer des modèles de conditions environnementales favorables à l'existence d'une espèce ou d'une communauté (Guisan & Thuiller 2005) en estimant au mieux les niches écologiques (Phillips *et al.* 2006). Ceci implique que la distribution des espèces soit considérée à l'équilibre avec l'environnement physique, et que les actions anthropiques et/ou les interactions biotiques (prédation, compétition, facilitation et symbiose) ainsi que les processus biogéographiques et géodynamiques, ne soient pas pris en compte dans les modèles (Guisan & Thuiller 2005, Phillips *et al.* 2006). A l'inverse, l'approche dynamique consiste en des modèles écophysiologiques intégrant des relations mécanistes entre caractères fonctionnels et paramètres environnementaux pour modéliser l'étendue de la distribution potentielle des espèces (Kearney & Porter 2009, Buckley *et al.* 2010). Cette seconde approche a un meilleur pouvoir de prédiction car elle permet de décrire plus finement les niches potentielles des espèces et donc d'obtenir de meilleurs cartes de distribution potentielle après projection spatiale de ces niches (Sillero 2011). Cependant, les modèles dynamiques sont exigents en quantité et en qualité de données ; ils nécessitent de bien connaître l'écologie des espèces étudiées et de réaliser les études à des échelles spatiales réduites (Jeltsch *et al.* 2008). Ces contraintes constituent de réelles limites à leur utilisation (Angelitta 2009, Helmuth 2009). Les problématiques auxquelles essaient de répondre les analyses macroécologiques impliquent de disposer d'outils numériques opérationnels pour modéliser de façon rapide et à large échelle la distribution des espèces, ainsi que leur évolution face aux changements environnementaux actuels et passés. Tant que les mécanismes qui déterminent la réponse environnementale des espèces ne sont pas accessibles, ce qui est très souvent le cas pour les espèces marines, l'approche corrélative par modélisation de niche représente la procédure la plus opérationnelle (Botkin *et al.* 2007). Elle permet en outre des applications pratiques pour estimer rapidement la distribution de nombreuses espèces à large échelle spatiale (Elith & Leathwick 2009). D'autre part, les analyses réalisées à large échelle spatiale limitent également les erreurs et imprécisions liées aux biais d'échantillonnage locaux (Gutt *et al.* 2012). A partir de la connaissance de paramètres environnementaux actuels et de modèles d'environnements anciens et futurs il est alors possible de tester des scénarios biogéographiques passés et à venir.

Différentes terminologies sont utilisées pour nommer l'approche corrélative par modélisation de niche : "*species distribution modeling*" (modèles de distribution spatiale), "*ecological niche modeling*" (modèle de niche écologique), "*environmental niche modeling*" (modèle de niche environnementale), "*habitat suitability modeling*" (modèle d'habitat) ou "*bioclimate envelope modeling*" (modèle d'enveloppes bioclimatiques). Toutes ces terminologies ne sont pas exactement synonymes car, lorsqu'elles sont employées à bon escient, elles reflètent souvent des problématiques d'étude différentes (Huntley *et al.* 1995, Pearson & Dawson 2003, Pearson 2007). A titre d'exemple, les modèles d'enveloppes bioclimatiques ne s'intéressent qu'à un nombre limité de paramètres clés de l'environnement et n'ont pas pour objectif de modéliser de façon exhaustive l'ensemble des conditions environnementales définissant les habitats favorables aux espèces. Le terme de "*species distribution modeling*" est le plus couramment employé dans la littérature, bien que ce soit les habitats qui sont modélisés et non directement la distribution des espèces (Pearson 2007). Je préfère employer le terme de *modèle de niche* car le principe de ces modèles repose sur l'approximation de la niche fondamentale (ou niche potentielle) des espèces au sens d'Hutchinson (1957). La niche fondamentale a été définie comme l'ensemble des conditions environnementales permettant à une espèce de survivre et d'exister indéfiniment (Hutchinson 1957, Phillips *et al.* 2006, Pearson 2007). Il s'agit d'un concept opérationnel qui permet de décrire les relations entre biotopes et biocénoses. Ce concept sert de base aux modèles pour quantifier les relations entre paramètres environnementaux et distribution des espèces à larges échelles (Guisan & Zimmermann 2000, Peterson 2001, Guisan & Thuillier 2005, Wiens *et al.* 2009). La projection spatiale (distribution géographique) de la niche fondamentale permet de caractériser la distribution potentielle de l'espèce. En modélisant la niche fondamentale des espèces on peut donc proposer un modèle de distribution potentielle. Dans les faits, seule la niche potentielle des espèces peut-être modélisée à partir des variables environnementales existantes; elle constitue une approximation de la niche fondamentale. L'écart théorique entre la distribution réelle (cette distribution n'est connue que partiellement à partir des données de terrain collectées) et le modèle de distribution potentielle est alors expliqué par :

1. les biais d'échantillonnage
2. les imperfections des modèles (bien que limités par nature, les modèles doivent cependant constituer une aide à l'interprétation)
3. l'ensemble des facteurs géographiques, biotiques et historiques qui empêchent l'espèce d'occuper sa distribution potentielle (Peterson 2011).

La partie de la niche fondamentale réellement occupée par l'espèce est alors appelée la niche occupée (Barve *et al.* 2011). Elle diffère de la niche réalisée d'Hutchinson (1957) qui ne tient compte que des contraintes biotiques (Pearson 2007). Au final, la comparaison entre la distribution réelle connue et la distribution potentielle modélisée permet d'évaluer la sensibilité des espèces aux modifications attendues ou mesurées de leur environnement, mais aussi d'estimer les contributions respectives des facteurs environnementaux, biotiques et historiques dans la distribution réelle des espèces (figure 4.4).

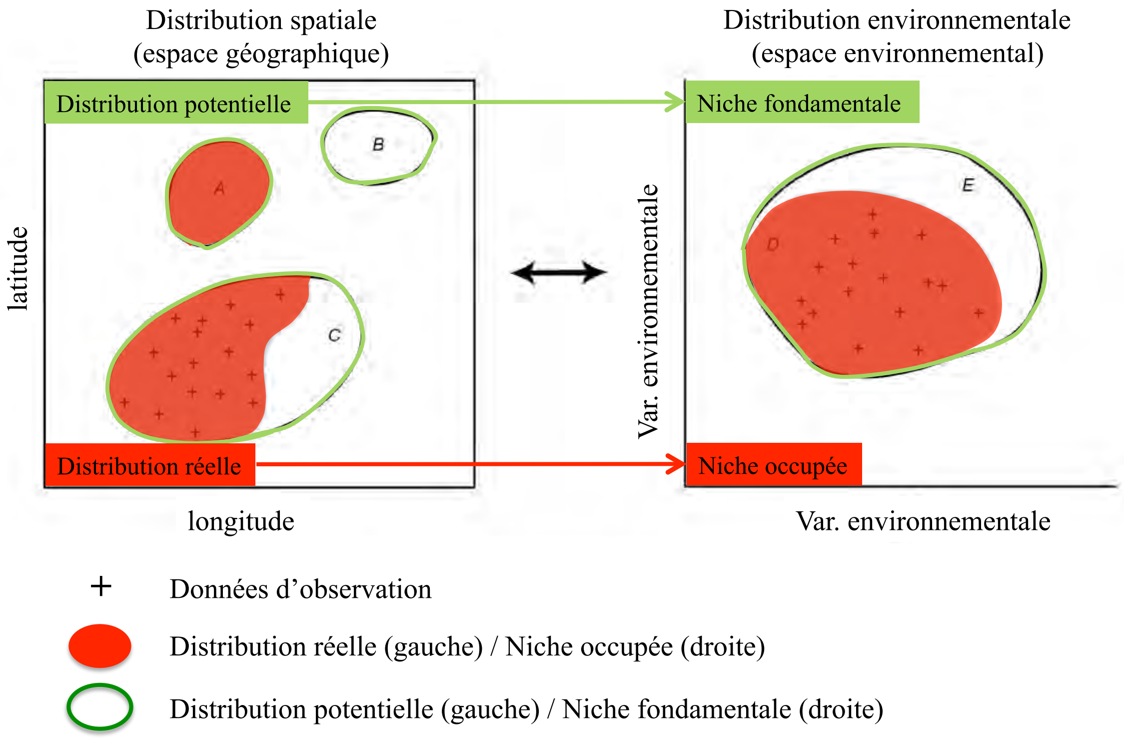


Figure 4.4. Relations entre données d'observation, distribution réelle, niche occupée, modèle de distribution potentielle et modèle de niche fondamentale. La différence entre la distribution réelle connue et la distribution potentielle modélisée permet d'évaluer la sensibilité des espèces et la contribution des facteurs environnementaux actuels dans leur distribution (adapté de Pearson 2007).

La distinction entre facteurs environnementaux et facteurs biotiques est parfois problématique (Pearson 2007). Les facteurs environnementaux peuvent être définis comme l'ensemble des variables qui possèdent une dynamique propre, indépendante de la présence et de la dynamique des populations. Au contraire, les facteurs biotiques sont directement liés à la dynamique des populations tels que les ressources nutritives et les interactions de type prédation, compétition ou facilitation (Barve *et al.* 2011). Certains aspects biotiques peuvent cependant être traités comme les variables environnementales et intégrés dans les modèles (Araújo & Luoto 2007, Heikkinen *et al.* 2007). Dans ce cas, la niche modélisée ne correspond plus exactement à la niche fondamentale, mais à une approximation de la niche réalisée (Hutchinson 1957). La différence entre niche réalisée et niche occupée peut alors être interprétée comme le résultat de contraintes géographiques (à la dispersion) et de contingences historiques (héritage de distributions passées).

Les différents types de modèles peuvent être distingués selon la nature des données traitées: données d'abondance, données de présence et d'absence, et données de présence seule. Les données d'abondance et de présence/absence permettent l'utilisation de modèles régressifs de type modèles linéaires généralisés (GLM) ou modèles additifs généralisés (GAM), modèles de réseaux de neurones artificiels (ANN) ou arbres de classification et de régression (CART) (Guisan *et al.* 2002, Thuiller *et al.* 2003). En milieu marin et en Antarctique en particulier, il est difficile d'obtenir des données quantitatives (abondance) et des données d'absence à large échelle; les données de présence seule sont donc le plus souvent les seules disponibles pour modéliser la distribution des espèces (Carpenter *et al.* 1993). D'autres modèles peuvent alors être utilisés, tels que les modèles génétiques (GARP) et les modèles d'entropie maximale (Maxent). Tous ces modèles reposent sur les mêmes fondements théoriques et présentent les mêmes limites méthodologiques (Gutt *et al.* 2012). Premièrement, ils supposent l'équilibre entre distribution des espèces et facteurs environnementaux. Ils ne tiennent pas compte de la dynamique des populations et s'éloignent en cela des processus écologiques. Ce postulat limite tout particulièrement la pertinence des modèles quand il s'agit de prédire la distribution d'espèces pour des conditions environnementales (futures ou passées) non réalisées actuellement, ou non réalisées dans la zone d'occurrence. La seconde limite tient au fait que les modèles de niche tendent à modéliser la niche fondamentale et donc ils supposent que tous les facteurs environnementaux conditionnant la survie et l'existence des espèces ont été pris en compte, ce qui n'est jamais réalisé. Cependant, les implications dépendent des objectifs d'étude initiaux (voir au dessus le cas des modèles d'enveloppes bioclimatiques). Enfin, la troisième limite est due au fait que les modèles de niche n'intègrent pas les processus qui lient changements environnementaux et variabilités génétique, phénotypique et comportementale d'une part, interactions biotiques, migration et dispersion d'autre part (Jeltsch *et al.* 2008, Angilletta 2009, Zurell *et al.* 2009, Somero 2010). Une alternative prometteuse pourrait être la fusion des approches corrélatives et dynamiques (Robinson *et al.* 2011). Cette "solution minimale" (Gutt *et al.* 2012) a déjà donné lieu à plusieurs travaux qui proposent de modéliser la dynamique des populations par une capacité de changements attribuée à chaque cellule de la zone de distribution selon son degré de congruence avec la niche fondamentale de l'espèce. Les processus modélisés font intervenir le recrutement et la migration des organismes (Cheung *et al.* 2008, 2009, Keith *et al.* 2008, Anderson *et al.* 2009, Zurell *et al.* 2012).

Principaux résultats

La plupart des études portant sur l'analyse de la distribution des espèces marines ont porté sur les zones littorales, à des échelles locales et régionales (MacLeod *et al.* 2008). Elles permettent de souligner l'importance de paramètres environnementaux tels que la profondeur, la salinité, et la nature des sédiments pour expliquer la distribution des espèces (Chatfield *et al.* 2010, Gogina *et al.*

2010); c'est le cas de la majorité des travaux portant sur l'étude de la distribution des faunes marines antarctiques (Griffiths *et al.* 2009). Ainsi, plusieurs de mes travaux ont consisté à caractériser la distribution d'espèces et d'assemblages benthiques à l'échelle locale et régionale (tableau 4). Les méthodes d'analyse employées (méthodes d'ordination) ont cependant montré leurs limites compte tenu de la complexité des relations entre variables environnementales et distribution des espèces.

A plus large échelle, les travaux réalisés dans le cadre du co-encadrement de la thèse de B. Pierrat m'ont permis d'analyser la distribution d'espèces d'échinides à l'échelle de l'océan Austral sur la base des relations existant entre distribution des espèces et facteurs environnementaux. La qualité de l'échantillonnage, la nature des données et la complexité des relations entre facteurs environnementaux et données de distribution ont imposé l'utilisation de l'approche corrélative par modélisation de niche. Les modèles de niche ont surtout été utilisés à large échelle pour les sytèmes terrestres, très peu ont été employés pour le milieu marin (Cheung *et al.* 2009, Elith & Leathwick 2009, Robinson *et al.* 2011). Nos travaux ont cependant permis de décrire les grands motifs biogéographiques des échinides antarctiques et subantarctiques (écorégionalisation), de déterminer les niches écologiques associées et d'explorer la contribution des principaux facteurs environnementaux.

facteurs de contrôle	échelle taxinomique	méthode	échelle spatiale	publications
profondeur, pente, température, couverture de glace, facteurs édaphiques (granulométrie, composants biogènes), facteurs biochimiques (salinité, azote, chlorophylle a)	espèce	modèles de niche (GARP, Maxent)	océan Austral	19, 22
profondeur, température, salinité, oxygène, facteurs édaphiques (granulométrie, MO, redox, carbonates), chlorophylle a	échinides et faune benthique	statistiques multivariées	mer de Bellingshausen	11, 21
sédimentation et glace	échinides et communautés marines	statistiques multivariées	régionale, Larsen	14
facteurs sédimentologiques	échinides	modèles de niche (GARP, Maxent, ENFA)	bassin de Paris	en cours
symbioses	échinides	biostatistiques	régionale, Larsen	15

Tableau 4. Synthèse de mes travaux portant sur l'étude du contrôle des facteurs de l'environnement physique sur la distribution des faunes à différentes échelles. Les numéros renvoient à mes publications et suivent l'ordre de la liste fournie dans la partie "Bilan d'activité".

Dans le cadre de l'étude des assemblages benthiques de la mer de Bellingshausen, la collecte des données de distribution et de diversité était associée à la mesure simultanée de paramètres physiques de l'environnement. Géolocalisation, profondeur, paramètres hydrographiques (température, salinité, concentrations en oxygène, en cholorophylle a ainsi qu'en particules en suspension - carbone et azote organiques) et paramètres édaphiques (granulométrie, contenu en matières organique, conditions d'oxydoréduction et teneur en carbonates) ont été mesurées pour chaque station. Cet échantillonnage simultané a permis de traiter conjointement l'ensemble des données environnementales grâce à des analyses multivariées non paramétriques (de type *Primer*, Clarke & Gorley 2001), et différentes méthodes d'ordination (MDS non paramétrique, classification hiérarchique et analyse canonique des correspondances). Les résultats montrent qu'à l'échelle de la mer de Bellingshausen, c'est la combinaison de la profondeur et de trois principaux facteurs édaphiques (conditions d'oxydoréduction, teneur en matière organique et granulométrie) qui explique le mieux la distribution des assemblages benthiques en général et des faunes d'échinides en particulier (figure 4.5). La combinaison de ces facteurs correspond en effet à une décroissance de la disponibilité des ressources nutritives avec la profondeur et avec l'éloignement du continent, les espèces généralistes à plus large niche écologique (ex : Echinidae) en sont les moins affectées (Saiz *et al.* 2008, Moya *et al.* 2012).

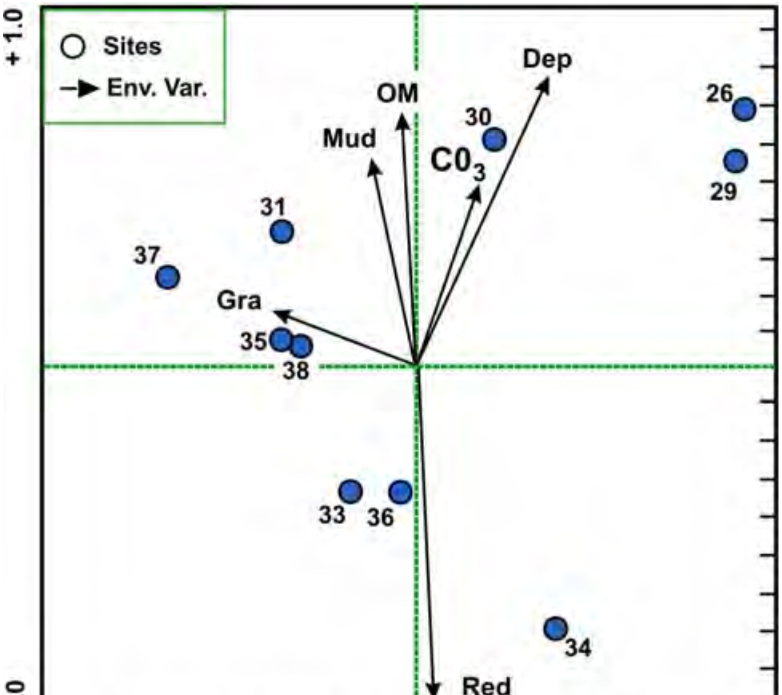


Figure 4.5. Analyse canonique des correspondances montrant la contribution de la profondeur (Dep) et de facteurs édaphiques (Red, OM, Mud, Gra) sur la composition des assemblages benthiques en mer de Bellingshausen (Saiz *et al.* 2008).

Analyse de données environnementales et de distribution à l'échelle de l'océan Austral

A l'échelle de l'océan Austral, les analyses macroécologiques ne pouvaient être réalisées à l'aide des méthodes multivariées et méthodes d'ordination utilisées dans les études régionales précédentes en raison de :

1. la qualité de l'échantillonnage - du point de vue de l'échantillonnage, il n'existait pas de jeu de données environnementales suffisamment complet qui couvre suffisamment de localités d'occurrence d'espèces. D'autre part, la majorité des données environnementales et de distribution provenaient d'échantillons prélevés en des temps différents, de sources de données très variées et présentaient une couverture très inégale de l'océan Austral.

2. la nature des données - le mode de collecte des données de distribution imposait de disposer d'un jeu de données de présence seule, les données d'absence étant en partie inconnues.

3. la complexité des covariations entre facteurs environnementaux - la complexité des covariations entre facteurs de l'environnement et la réponse en partie non linéaire des organismes nécessitait d'avoir recours à des algorithmes complexes, incluant fonctions linéaires et non linéaires.

L'analyse macroécologique des faunes d'échinides de l'océan Austral a été réalisée à l'aide des outils fournis par les systèmes d'information géographique et en ayant recours à des modèles de niches écologiques (Gutt *et al.* 2012, Pierrat et *al.* 2012b). Les données de distribution géoréférencées étant acquises (Pierrat *et al.* 2012a), les données environnementales couvrant l'ensemble de l'océan étaient disponibles sous la forme de cartes SIG de précision variable (du dixième au demi-degré de latitude et longitude) obtenues à partir de trois sources principales : la base de données créée pour les experts de l'IPCC (Intergovernmental Panel on Climate Change), ou GIEC en français (Groupe d'experts Intergouvernemental sur l'Evolution du Climat), l'Australian Antarctic Division et le British Antarctic Survey. Sur les 110 variables océanographiques disponibles, seules dix ont été retenues pour leur pertinence globalement reconnue pour l'écologie et la distribution des échinides, pour leur résolution spatiale (demi-degré), tout en veillant à éviter une trop forte corrélation entre variables (Philips *et al.* 2006). Deux procédures de modélisation ont été employées et comparées : Maxent (Phillips *et al.* 2006) et GARP (Stockwell & Peters 1999). L'utilisation de différentes procédures de modélisation permet en effet de contrôler, parmi d'autres moyens, la pertinence des modèles (Robinson *et al.* 2011, Aguirre-Gutierrez *et al.* 2013, Bahn & McGill 2013). Les deux procédures employées permettent de modéliser les niches écologiques et distributions potentielles à partir de données de présence seule, mais les algorithmes utilisés et les modes de calcul diffèrent.

Parmi tous les modèles de niche réalisés, seuls ont été publiés les modèles d'espèces aux relations phylogénétiques et écologiques contrastées. Une première publication présente les résultats de la modélisation de deux espèces proches du genre *Sterechinus* aux distributions connues contrastées : l'une est restreinte au plateau continental Antarctique, l'autre est répartie de l'Antarctique jusque 45° de latitude Sud (Pierrat et *al.* 2012b). A l'inverse, la seconde publication intègre les résultats de deux espèces, *Ctenocidaris perrieri* et *Amphipneustes lorioli*, éloignées phylogénétiquement (elles appartiennent à deux sous-classes différentes) et écologiquement (David *et al.* 2005) mais largement présentes sur l'ensemble du plateau continental antarctique (Gutt *et al.* 2012). Dans le cas des deux espèces proches, les résultats soulignent l'importance prépondérante de la profondeur pour expliquer la distribution de l'espèce la plus largement distribuée, alors que profondeur, couverture de glace et température des eaux de surface (en été) sont les trois facteurs contribuant à la distribution de l'espèce australe. Dans le cas des deux espèces éloignées phylognétiquement, les modèles présentent des résultats très similaires et soulignent l'importance de la profondeur, de la couverture de glace et de la température des eaux de surface en été pour la distribution des espèces. Des études antérieures avaient montré que la distribution des espèces d'échinides antarctiques semblait contôlée principalement par la profondeur et la nature des sédiments marins (Brey & Gutt, 1991, Jacob *et al.* 2003, David *et al.* 2005, Saiz *et al.* 2008, Moya *et al.* 2012). Les résultats obtenus grâce aux modèles de niche à l'échelle de l'océan Austral ne retiennent donc pas prioritairement les facteurs édaphiques mis en évidence précédemment. Cela peut signifier que ces facteurs ne sont pas déterminants à une telle échelle spatiale (ils sont à l'origine d'hétérogénéités régionales, limitées à certaines zones du plateau continental) et qu'ils sont, avec d'autres variables, en grande partie corrélés aux trois principaux facteurs retenus.

La comparaison entre données de distribution observées et distribution modélisées a permis de souligner les erreurs de commission des modèles (prédiction de présence fausse). Outre les limites de performance des modèles, ces erreurs peuvent aussi s'expliquer par le rôle potentiel joué par les déterminants biotiques (écart entre niche fondamentale et niche réalisée), océanographique et historique (contraintes et limites de dispersion) dont les modèles ne tiennent pas compte. Ainsi, l'aire de distribution modélisée pour les espèces de *Sterechinus* inclut le Plateau de Campbell et la Tasmanie alors que les espèces y sont vraissemblablement absentes (figure 4.6) d'après les nombreuses missions d'échantillonnage réalisées (Pierrat *et al* 2012b).

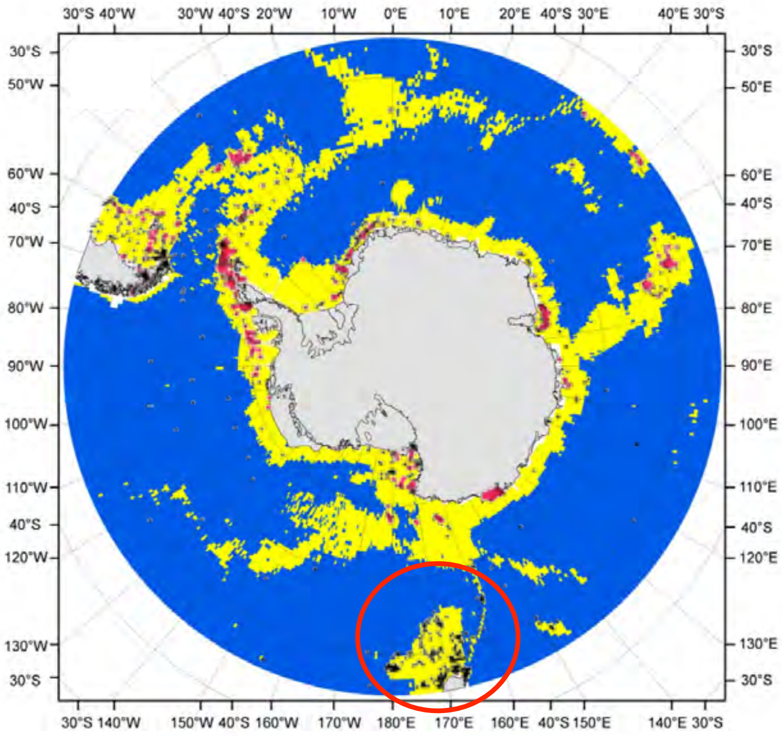


Figure 4.6. Carte de distribution potentielle seuillée (rouge : zones hautement favorables; jaune : zones favorables) de l'espèce *Sterechinus antarcticus* prédite au sud de la Nouvelle-Zélande (cercle rouge) alors qu'elle n'y a jamais été observée (points noirs) (modifié d'après Pierrat et *al.* 2012b).

Publications associées : Saiz *et al.* 2008, Gutt *et al.* 2011, Moya *et al.* 2012, Gutt *et al.* 2012, Pierrat et *al.* 2012b

Projets et perspectives

Mes projets actuels et perspectives de travail futurs concernent en grande partie l'analyse macroécologique par modélisation de niche. Dans le cadre de l'analyse des liens existant entre facteurs environnementaux et données de distribution d'espèces, trois projets complémentaires devraient être réalisés en priorité. Ils concernent (1) la meilleure prise en compte des contraintes méthodologiques imposées par les modéles de niche, (2) l'application de modèles de niche aux données fossiles et (3) l'extension de l'analyse de niche à l'échelle des communautés.

Perspectives méthodologiques

Le recours aux modèles de niche écologique pour analyser la distribution d'espèces s'accompagne d'un certain nombre de limites méthodologiques qui concernent l'échantillonnage, la nature des données et les procédures d'analyse.

Plusieurs études ont montré que les modèles de niche étaient très sensibles à la quantité, à l'hétérogénéité et à la distribution spatiale des données d'occurrence utilisées. La nécessité de disposer de suffisamment de points d'occurrence géoréférencés pour réaliser des modèles pertinents détermine souvent le choix des espèces analysées, indépendamment de leurs caractéristiques écologiques ou de leur représentativité au sein des communautés. Les résultats des modèles ne sont alors souvent éclairants que pour les espèces les plus communes seulement (espèces permettant de disposer de suffisamment de données d'occurrence). L'hétérogénéité des données d'occurrence utilisées détermine également un biais d'échantillonnage pour les valeurs environnementales correspondantes et considérées par les modèles comme représentatives d'habitats privilégiés pour les espèces. Enfin, le phénomène d'autocorrélation spatiale constitue une véritable limite aux modèles de niche (valeurs d'autant plus différentes qu'elles sont éloignées géographiquement), à la fois dans l'étude des relations entre données de distribution et données environnementales, mais aussi dans l'estimation de la performance des modèles (Bahn & McGill 2013). Ce phénomène est d'autant plus marqué que la zone d'étude est étendue au regard de la distribution des données d'occurrence des espèces. La prise en compte de toutes ces limites implique un travail préalable d'analyse des données utilisées (étude de la distribution des données et quantification de l'autocorrélation spatiale), et de comparaison avec les données modélisées, ainsi que la recherche de procédures de sélection des données de distribution et de l'étendue des zones d'études. Un développement possible consistera à étudier la distribution des espèces rares ou confinées géographiquement au regard des distributions modélisées afin de tester la représentativité des modèles. Enfin, l'analyse comparative des réponses environnementales et des corrélations entre variables de plusieurs modèles devra permettre en retour d'améliorer le choix des variables environnementales utilisées (Sheppard 2013).

La nature des données est également déterminante dans la performance des modèles. Les données d'abondance absolue et d'abondance relative fournissent de meilleures informations écologiques, et donc alimentent de modèles plus performants que les données de présence/absence et celles de présence seule (Bahn & McGill 2013). Un de mes projets consiste à comparer la performance de différents modèles obtenus à partir de ces quatre types de données, afin de s'assurer de la pertinence des modèles utilisant les données de présence seule. Les données fossiles de l'Hauterivien du bassin de Paris et les données actuelles issues de la campagne réalisée en mer de Bellinsghausen pourront être utilisées.

Enfin, du point de vue analytique, l'étude comparée des performances et des correspondances, environnementales et géographiques, entre modèles (ex : GARP, Maxent, ENFA) à travers différentes approches analytiques (discriminantes ou génétiques, déterminant des pseudo-absences ou non, par analyses séparées, consensus ou simultanées) permettra de tester la pertinence des modèles obtenus.

Modélisation de distributions fossiles

Peu d'études ont utilisé les modèles de niches pour analyser la distribution et caractériser les habitats de taxons ou communautés fossiles (Stigall & Libermann 2006, Stigall 2012). Quelques travaux portant sur des taxons et intervalles contrastés (équidés miocènes, arthropodes cambriens, brachiopodes ordoviciens) ont cependant démontré que la niche fondamentale d'espèces fossiles pouvait être approximée par des modèles de niche reposant sur la corrélation entre données de distribution des espèces et données géologiques utilisées comme estimateurs paléo-environnementaux (Maguire & Stigall 2008, Malizia & Stigall 2011, Hendricks *et al.* 2008).

L'utilisation de données de présence seule aux distributions spatiales discontinues est une contrainte dont les études macroécologiques doivent tenir compte dans l'analyse de la biodiversité fossile. L'utilisation de procédures de modélisation de niches associées aux outils SIG doit donc apporter une réponse méthodologique appropriée au traitement des données fossiles. L'utilisation des données fossiles et sédimentologiques déjà acquises sur la formation des Calcaires à Spatangues de l'Hauterivien du bassin de Paris (Benetti *et al.* 2013) permettra de tester la pertinence de différents modèles de niches au regard des données disponibles (abondance relative et présence seule). Au delà de la robustesse statistique des modèles, leur performance pourra être testée en comparant les distributions d'espèces prédites par les modèles avec les données de distribution réelles collectées sur le terrain (voir Hendricks *et al.* 2008 pour la procédure). Les modèles de distribution et les niches modélisées pourront être également confrontés aux informations paléobiologiques tirées de l'étude des variations morphologiques intra-spécifiques.

Modélisation à l'échelle des communautés

La réalisation de modèles de niche peut-être étendue à l'étude des communautés pour analyser la distribution de nombreuses espèces et définir des communautés ou assemblages d'espèces ainsi que des écorégions ou assemblages de sites favorables aux différentes communautés (Ferrier *et al.* 2002, Ferrier & Guisan 2006). A l'échelle des communautés, la démarche consiste en la méta-analyse de niches écologiques et de cartes de distribution d'espèces individuelles. Un projet actuellement en cours de développement (figure 4.7) consiste en l'analyse des espèces d'échinides, de bivalves et de gastéropodes de l'océan Austral avec un triple objectif :

1. définir des écorégions australes et identifier le rôle de facteurs environnementaux au regard des biorégions ou provinces déjà mises en évidence,
2. tester la spécificité des écorégions en analysant la distribution de différents groupes taxinomiques à différentes échelles phylogénétiques
3. identifier des communautés écologiques d'échinides (ainsi que leurs exigences et sensibilités écologiques).

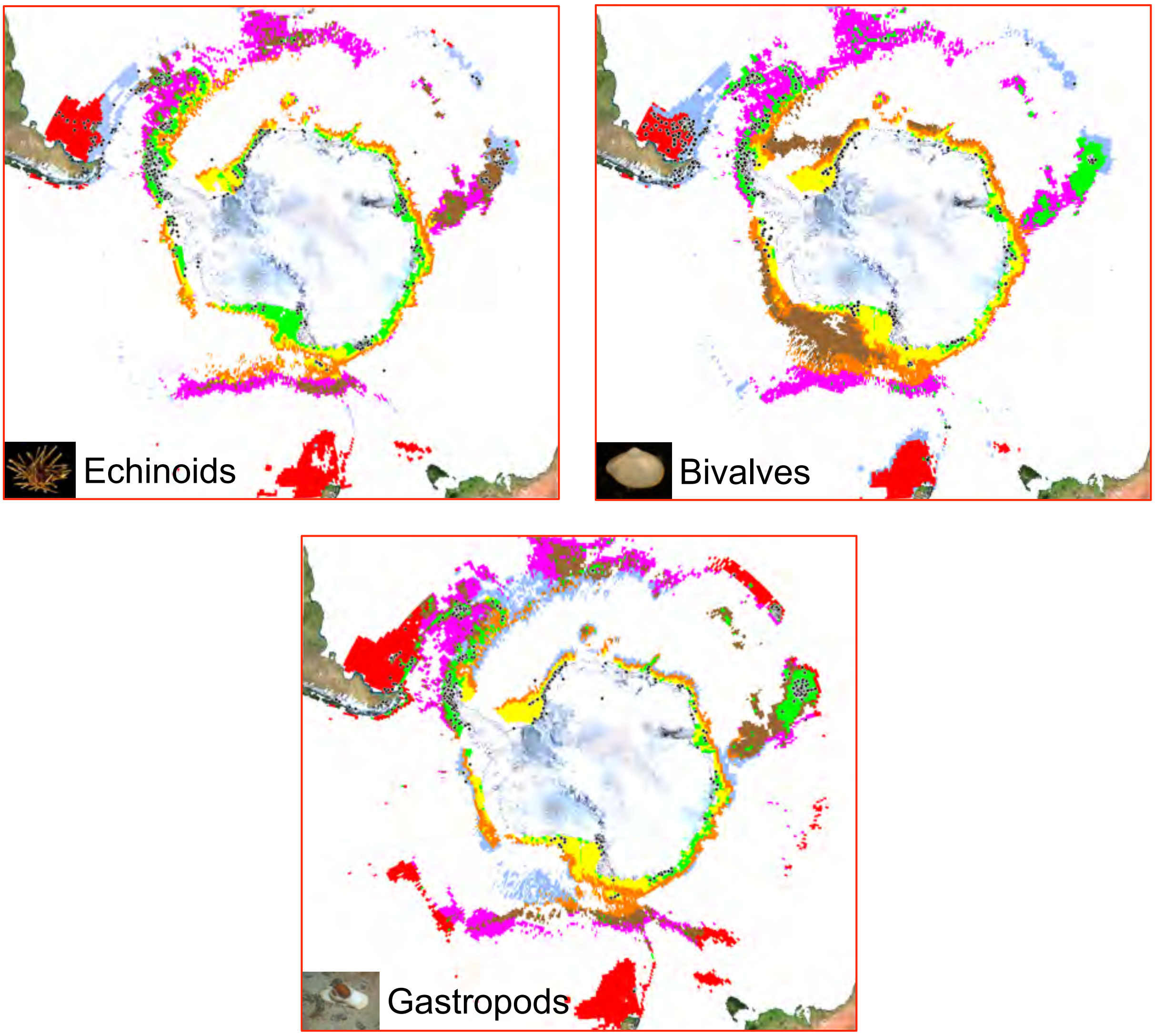


Figure 4.7. Ecorégions de l'océan Austral (rouge, marron, vert, bleu, violet, jaune et orange) d'après différents modèles de distribution établis pour les communautés d'échinides, de bivalves et de gastéropodes (étude en cours).

2.2. Rôle des interactions biotiques

Jusqu'à récemment, les approches macroécologiques ont surtout considéré les paramètres abiotiques, d'accès plus facile, pour établir des modèles de distribution d'espèces et d'écorégionalisation à l'échelle des communautés (Ferrier & Guisan 2006). Les facteurs biotiques, supposant l'introduction de paramètres d'interactions biologiques dans les modèles ont été peu explorés (modélisation de la niche réalisée d'Hutchinson). Les rôles respectifs de l'histoire évolutive et des interactions biotiques dans la structuration biogéographique des espèces à large échelle ont donné lieu à des débats contradictoires (Pigot & Tobias 2013). Des développements méthodologiques récents ont cependant montré la possibilité d'explorer et d'identifier le poids des interactions biotiques au regard des autres facteurs structurants de la biodiversité (Price & Kirkpatrick 2009, Pigot & Tobias 2013).

Principaux résultats

Importance des symbioses pour la diversité benthique locale

J'ai pu commencer à aborder l'étude des interactions biotiques entre espèces dans le cadre d'une approche macroécologique en analysant les relations symbiotiques entre invertébrés épibiontes et échinides cidaridés antarctiques (Hardy *et al.* 2011). Réalisés à l'occasion du co-encadrement de stages de Master (Hardy 2008, 2009; Rullmann 2009), ces travaux avaient pour objectif de tester l'importance des interactions biotiques (la symbiose dans ce cas) dans les processus de recolonisation du fond marin après des événements importants de perturbation des communautés benthiques. La diversité des épibiontes fixés aux piquants d'échinides a été étudiée chez une espèce pionnière du secteur de Larsen, *Notocidaris mortenseni*, zone récemment perturbée par la rupture de plates-formes de glace (voir ci-dessus). La diversité des épibiontes a été comparée à celle de secteurs non perturbés, ainsi qu'à celle des faunes sessiles fixées aux substrats minéraux durs. Les résultats ont montré que la richesse spécifique des épibiontes était plus faible dans le secteur de Larsen qu'ailleurs mais que les niveaux de diversité étaient similaires. Ils suggèrent aussi que des relations spécifiques et stables existent entre les épibiontes et les échinides, la composition des faunes sessiles fixées aux substrats minéraux étant davantage variable et dépendante de facteurs locaux. Enfin, les résultats indiquent que les symbioses associées aux échinides cidaridés pourraient contribuer à promouvoir la diversité benthique locale du secteur de Larsen en facilitant la recolonisation du fond marin.

Publication associée : Hardy *et al.* 2011

Projets et perspectives

Rôle des déterminants biologiques dans la distribution des échinides austraux

Au delà du cas particulier des relations symbiotiques et de leur importance pour la diversité locale, un projet consistera à étudier la structuration des motifs biogéographiques chez les échinides antarctiques, à diverses échelles spatiales, en explorant plus spécifiquement le rôle joué par les interactions biotiques (compétition, prédation et nutrition) au regard d'autres facteurs structurants. Il s'agira d'intégrer certains facteurs biologiques dans la modélisation de niche afin d'approcher au mieux la niche réalisée (au sens d'Hutchinson 1957) et d'affiner les modèles de distribution. Le poids des interactions biotiques pour expliquer les distributions à large échelle spatiale est généralement considéré comme négligeable au regard de certains facteurs abiotiques et des contingences historiques (Bond & Chase 2002, Anderson & Martinez-Mayer 2004, Saupe *et al.* 2012, Bentlage *et al.* 2013, Blois *et al.* 2013). Cependant, l'écart observé entre les distributions réelles et les modèles de distribution potentielle d'échinides déjà réalisés à l'échelle de l'océan Austral suggère que des phénomènes d'exclusion (compétition) entre espèces pourraient intervenir. Ainsi, l'absence des espèces de *Sterechinus* sur le Plateau de Campbell, en Tasmanie et sur les côtes chiliennes pourrait être liée à la présence dans ces mêmes régions d'une autre espèce (*Gracilechinus multidentatus*) proche phylogénétiquement et écologiquement (Pierrat *et al* 2012b).

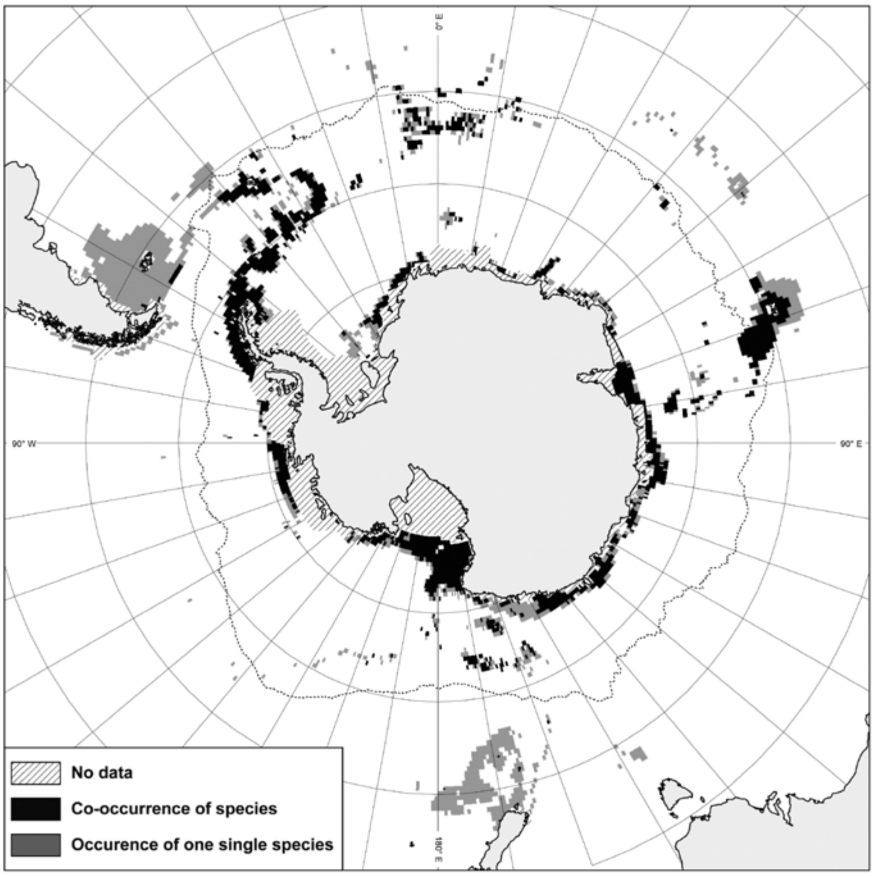


Figure 4.8. Modèle de co-occurrence (en noir) des deux échinides proches *S. antarcticus* et S. *neumayeri* dans l'océan Austral établi d'après leurs modèles de niches écologiques respectifs (Pierrat *et al* 2012b). Les distributions peuvent-être discutées au regard des proximités écologiques et phylétiques.

L'étude des interactions biotiques pourra être abordée entre espèces d'échinides proches (figure 4.8) (rôle de la compétition écologique pour les ressources testé au regard des distances écologiques et phylétiques entre espèces) ainsi qu'entre échinides et prédateurs connus (rôle de la prédation). Les espèces d'échinides ciblées seront celles dont le cadre phylogénétique a pu être précisé par les analyses moléculaires. L'importance de la prédation pourra être testée entre espèces d'échinides et d'étoiles de mer d'une part, entre échinides et gastéropodes d'autre part, groupes pour lesquels des bases de données d'occurrence sont disponibles (resources de SCAR-MarBIN). Les modèles de distribution obtenus à partir de facteurs abiotiques seuls pourront servir de références. L'influence des facteurs biotiques sera abordée via les écarts entre ces références et les nouveaux modèles qui intègrent les paramètres de compétition et de prédation, en suivant dans une premier temps les développements méthodologiques déjà disponibles (Price & Kirkpatrick 2009, Pigot & Tobias 2013).

2.3. Dynamique de la biodiversité : histoire des clades et de la Terre

Cette dernière partie concerne l'intégration des déterminants historiques dans les analyses macroécologique et biogéographique. Cela revient à tenter d'expliquer l'origine et l'évolution des motifs biogéographiques, en identifiant les processus macroévolutifs et macroécologiques à l'origine de la distribution de la biodiversité. Classiquement, deux processus sont invoqués en biogéographie historique : l'évolution – c'est-à-dire la spéciation (allopatrique, sympatrique, parapatrique ou péripatrique ; l'origine et la diversification des clades) et l'extinction (locale, régionale ou globale) – et la dispersion (Lomolino *et al.* 2006, Ebach & Tangney 2007, Rogers 2007, Clarke 2008, Pearse *et al.* 2009, Clarke & Crame 2010, Krug *et al.* 2010). Les développements méthodologiques réalisés en biogéographie cladistique ont amené à en distinguer quatre : spéciation par vicariance, duplication (spéciation sympatrique ou allopatrique au sein d'une même région d'étude), extinction et dispersion (Futuyma 1997, Lomolino *et al.* 2006, Ebach & Tangney 2007). Fondamentalement, la dynamique de la biodiversité résulte de changements induits par les processus géodynamiques et climatiques (Futuyma 1997, Rogers 2007, Clarke 2008, Pearse *et al.* 2009) ainsi que par l'évolution des facteurs biotiques, la réponse des espèces et des communautés aux changements environnements étant dépendante de leurs capacités à disperser et à s'apdater.

Principaux résultats

Analyse des processus biogéographiques dans l'océan Austral

Les principaux résultats de mes travaux portant sur la dynamique de la biodiversité concernent l'origine et l'évolution de la diversité des faunes d'échinides antarctiques (tableau 5). Ils ont déjà été présentés en grande partie dans le chapitre 2 consacré à la biogéographie historique, cette dernière ayant pour objectif d'intégrer les dimensions macroécologiques et phylogénétiques dans la compréhension de l'évolution de la biodiversité (Donoghue & Moore 2003, Lomolino 2006, Pearman *et al.* 2008, Wiens 2012).

Taxons	Période	Facteurs géodynamiques	Publications
Nacella concinna	Holocène	climat	30
Echinides antarctiques	Crétacé-Tertiaire	climat, océan, tectonique	26
Echinides, bivalves et gastéropodes antarctiques	Pleistocène-Actuel	climat, océan	25
Sterechinus	Miocène-Actuel	climat, océan	16
Echinides et faunes marines antarctiques	Actuel	climat	14, 15

Tableau 5. Liste de mes travaux abordant l'étude de la dynamique de la biodiversité et des processus géodynamiques associés. Les numéros renvoient à mes publications et suivent l'ordre de la liste fournie dans la partie "Bilan d'activité".

Ma participation à la réalisation de l'*Atlas biogéographique de l'océan Austral* (CAML, SCAR-MarBIN) déjà présenté plus haut, a également consisté en la rédaction d'un chapitre de synthèse sur les processus biogéographiques et leur illustration dans l'océan Austral. L'analyse des nombreuses études publiées sur ce thème m'a amené à identifier les liens existant entre facteurs climatiques, géodynamiques et océanographiques d'une part, et dynamique de la biodiversité marine antarctique d'autre part, au travers des principaux événements d'extinction, de spéciation, de diversification et de dispersion des clades depuis le Jurassique jusqu'à nos jours. J'y souligne l'importance de la longue histoire de la fragmentation du Gondwana, de la mise en place par phases successives de l'isolement du continent antarctique et de l'océan Austral, ainsi que de son évolution climatique. La reconstitution des dynamiques climatiques et océanographiques (rythmicité, cyclicité et intensité) m'est apparue essentielle pour comprendre les différentes réponses de la biodiversité passée.

Publications associées : Díaz *et al.* 2011, Hardy *et al.* 2011, Gutt *et al.* 2011, Pierrat *et al.* 2013, González-Wevar *et al.* 2013, Saucède *et al.* sous presse b

Projets et perspectives

Je présente ici deux projets de recherche qui me permettront d'entreprendre les analyses macroécologiques par modélisation de niche dans une dimension temporelle : l'étude de la dynamique macroécologique des espèces et des communautés pourra alors être enfin pleinement abordée. Des modèles de niche et de distribution prédictifs et rétro-prédictifs seront réalisés et testés en prenant l'exemple des échinides antarctiques actuels (modèles prédictifs futurs) et de lignées d'échinides irréguliers jurassiques (modèles rétro-prédictifs).

Modéles prédictifs de la distribution des faunes d'échinides austraux

Le réchauffement climatique actuel affecte déjà de façon sévère les mers polaires (Burrows *et al.* 2011, Gutt *et al.* 2012). Dans ce contexte, les effets des changements climatiques sur les faunes d'échinides antarctiques et sur leur distribution sont inconnus. En particulier, l'évolution des relations entre espèces d'Amérique du Sud et celles d'Antarctique de l'Ouest reste incertaine. Ce premier projet a pour objectif de préciser la capacité des échinides antarctiques à réagir aux changements environnementaux à venir. A l'aide des outils SIG et de modèles de niche, il doit permettre de proposer des modèles prédictifs de distribution des espèces d'échinides et en particulier de traiter des relations entre espèces d'Amérique du Sud potentiellement invasives, et espèces endémiques antarctiques. A terme, l'objectif est de proposer un modèle de distribution permettant d'appréhender l'impact plausible des changements climatiques sur les faunes d'échinides antarctiques. Les principaux modèles prédictifs de variables environnementales sont mis à disposition par le PCMDI (Program for Climate Model Diagnosis and Intercomparison) grâce à une base de données (WCRP CMIP3 multi-model dataset) initialement créée pour les experts du GIEC. Cette base de données propose des modèles d'évolution climatique concernant de nombreuses variables océaniques (Solomon *et al.* 2007). La résolution spatiale des cartes du WCRP CMIP3 étant faible (200 km sur 150 km pour les océans), la base de données Bio-ORACLE (Ocean Rasters for Analysis of CLimate and Environment) permettra de fournir des modèles prédictifs complémentaires et de meilleure résolution spatiale (cellules de 9,2 km de côté), pour 23 paramètres environnementaux, jusque 70° de latitude sud (Tyberghein *et al*. 2012).

Etude du conservatisme écologique de lignées fossiles

La réponse des espèces aux modifications de leurs environnements physique (ex. hausse des températures, glissements saisonniers) et biotique (espèces invasives) est fortement conditionnée par leur conservatisme écologique (Broennimann *et al.* 2007). Depuis une dizaine d'années, les débats sur la place du conservatisme écologique des espèces dans les processus d'adaptation et plus généralement de spéciation ont été renouvelés par le développement d'approches quantitatives (Peterson *et al.* 1999, Graham *et al.* 2004, Warren *et al.* 2008). La majorité des études mettent en évidence l'existence d'une évolution écologique sur des échelles de temps importantes, et principalement à des niveaux taxonomiques supérieurs à celui de l'espèce (voir Peterson 2011 pour une synthèse), alors que d'autres soulignent la fréquence de la différenciation écologique dans le processus de spéciation (e.g. Graham *et al.* 2004). La spéciation géographique (vicariance) précède-t-elle donc toujours la différenciation écologique qui ne serait alors qu'une conséquence d'un isolement écologique (Peterson *et al.* 1999)? L'innovation écologique est-elle partie prenante dans le processus de spéciation (Graham *et al.* 2004)? Face à des études parfois contradictoires, du fait d'hypothèses de travail et d'approches différentes, l'évaluation des modèles proposés ne doit pas reposer uniquement sur leur robustesse statistique, mais aussi sur leur réalisme biologique (Warren *et al.* 2008). Très peu d'études quantitatives portant sur le conservatisme écologique utilisent les données paléontologiques (Stigall & Liebermann 2006, Stigall 2012), alors que paradoxalement, celles-ci permettent de tester la pertinence des modèles sur des temps d'évolution importants. Quelques travaux ont démontré que la niche fondamentale d'espèces fossiles pouvait être modélisée (Maguire & Stigall 2008, Malizia & Stigall 2011, Hendricks *et al.* 2008). Ce second projet a pour double objectif de :

1. modéliser l'évolution écologique d'espèces d'échinides par des modèles de niche (GARP et Maxent) et

2. établir les liens entre évolution des niches écologiques et évolution des espèces, afin de préciser le conservatisme écologique de ces espèces dans un contexte de changements environnementaux.

Le conservatisme écologique sera testé entre espèces d'une lignée évolutive bien connue d'échinides irréguliers fossiles, celle des collyritidés (Thierry & Néraudeau 1994), sur une période de temps couvrant environ 10 millions d'années, du Callovien (-165 à – 161 millions d'années) à l'Oxfordien (-161 à -155 millions d'années) avec une précision de l'ordre du million d'années (précision de la zone d'ammonites). La lignée des collyritidés s'inscrit dans le contexte de forte diversification des échinides irréguliers au Jurassique moyen et supérieur (Saucède *et al.* 2007), intervalle correspondant à une augmentation générale du niveau marin (Thierry & Néraudeau 1994). La zone d'étude couvrira une bande d'environ 250 km de long, depuis le département des Vosges au NE à celui de l'Yonne au SW. Une centaine de sites d'étude sont concernés, sites dont la faune fossile et les données sédimentologiques sont disponibles (collections et littérature), le cadre stratigraphique étant précisé grâce aux faunes d'ammonites étudiées. Pour la période de temps ciblée, ces sites recouvrent des environnements marins contrastés, depuis des environnements de plate-forme à des environnements profonds, ayant subi d'importants changements (approfondissements, changements de polarité proximal-distal) au passage Jurassique moyen-Jurassique supérieur.

SYNTHESE DES PROJETS DE RECHERCHE

Pour des raisons pratiques, ce mémoire est structuré en différents chapitres dans lesquels j'ai abordé indépendamment l'étude des dimensions phylogénétiques, morphologiques et biogéographiques de la biodiversité. Certaines redondances étaient cependant inévitables, à la fois dans la présentation de mes principaux résultats et dans celle de mes projets. Elles reflètent les profondes connexions qui lient ces trois dimensions de la biodiversité, l'approche macroécologique ayant pour objectif de les intégrer dans des analyses jointes afin de mieux comprendre la dynamique de la biodiversité actuelle et passée. Ce court chapitre de conclusion a pour objectif de synthétiser brièvement mes principaux axes de recherche à venir, en soulignant leur complémentarité dans une approche macroécologique intégrante, et en présentant un échéancier qualitatif de leur mise en œuvre (tableau 6).

AXES de RECHERCHE	projets à 2 ans	projets sur 10 ans
Phylogénies	Echinides antarctiques	Holastéroïdes abyssaux
Disparité morphologique	Disparité topologique	Disparité morphologique et macroévolution des faunes d'échinides austraux
	Diversité fonctionnelle de lignées d'échinides jurassiques	Diversités fonctionnelles et structurales de la radiation des échinides irréguliers
Macroécologie	Evolution des niches écologiques d'échinides irréguliers jurassiques	Structure de la diversité écologique des faunes d'échinides austraux

Tableau 6. Echéancier qualitatif de réalisation de mes projets de recherche.

La caractérisation des processus macroécologiques et biogéographiques à l'origine des clades et de leur diversité (ex : modèles de radiation adaptative, de diversification en bouffées d'espèces, phénomènes de vicariance et de dispersion) nécessite de disposer de phylogénies robustes (Faith 1994, Webb *et al.* 2002, Ricklefs 2006, Wiens *et al.* 2011, Condamine *et al.* 2013). La résolution des relations phylogénétiques entre échinides constitue en effet une condition nécessaire pour la réalisation de mes projets de recherche en macroécologie et en biogéographie. C'est le cas de mes projets portant sur l'étude des échinides antarctiques et des holastéroïdes abyssaux, pour lesquels je ne dispose pas encore de phylogénies suffisamment robustes et complètes. Les relations phylogénétiques entre espèces d'échinides antarctiques sont actuellement en cours d'analyse dans le cadre de collaborations avec des collègues molécularistes. Ces travaux étant déjà bien avancés, des phylogénies complètes, reposant à la fois sur des données moléculaires et morphologiques, devraient être obtenues au cours de l'année à venir (2014-2015). L'analyse phylogénétique des holastéroïdes abyssaux est quant à elle beaucoup moins avancée. Depuis une dizaine d'années, j'acquière régulièrement des données morphologiques qui devraient me permettre de réaliser et de disposer d'une phylogénie relativement complète au cours de la prochaine décennie.

Les relations phylogénétiques entre clades étant connues, l'étude de leur disparité morphologique permet d'éclairer les processus macroévolutifs à l'origine de leur diversité (Wills *et* *al.* 1994, Foote 1997, 1999, Neige 2003, Erwin 2007, Ruta 2009, Wills *et al.* 2012, Gerber 2013). Mes projets de recherche portant sur l'étude de la disparité morphologique d'échinides fossiles et actuels peuvent s'appuyer sur des phylogénies établies dans mes travaux précédents (Saucède & Néraudeau 2006, Saucède *et al.* 2007) ou tirées de travaux publiés par d'autres (Smith *et al.* 2006, Barras 2008, Kroh & Smith 2010). Une partie de ces projets est déjà en cours de réalisation, les premiers résultats devant être publiés dès 2014 (analyse de la disparité topologique du squelette des échinides à l'aide des graphes). Ces travaux se prolongeront dans les années à venir selon deux axes principaux :

1. l'identification des processus macroévolutifs à l'origine des grands clades d'échinides austraux (Arbaciidae, Echinidae, Schizasteridae et Cidaridae), intégrant données morphologiques et génétiques

2. la caractérisation des facteurs structuraux (contraintes internes) et fonctionnels (radiation adaptative) associés à la diversification des échinides irréguliers, du Jurassique à l'Actuel.

L'intégration des dimensions phylogénétiques, temporelles, spatiales et environnementales, constitue le cœur de l'approche macroécologique qui vise à déterminer les facteurs environnementaux et historiques structurant la distribution de la biodiversité dans le temps et dans l'espace (Brown 1995, Gaston & Blackburn 2000, Briggs 2007). Cette approche intégrante permet de mieux comprendre l'ensemble des phénomènes à l'origine de la biodiversité (Donoghue & Moore 2003, Lomolino *et al.* 2006, Pearman *et al.* 2008, Wiens 2012). Mes projets de recherche en macroécologie reposent sur l'emploi de modèles de niches écologiques (dimensions environnementales et spatiales), sur leur projection cartographique et la caractérisation de leur évolution (dimension temporelle). A la différence de mes précédents travaux, ces projets me permettront d'aborder véritablement l'étude des dynamiques macroécologiques d'espèces et de communautés d'échinides, à travers des procédures de modélisation prédictives (échinides antarctiques actuels) et rétro-prédictives (échinides irréguliers jurassiques).

L'intégration des informations phylogénétiques prend ici toute son importance. Elle concerne deux projets de recherche :

1. la caractérisation de l'évolution des niches écologiques de lignées d'échinides fossiles, dans le cadre de leur diversification au Jurassique

2. l'étude comparative de la diversité écologique d'échinides antarctiques actuels (Cidaridae et Schizasteridae), au regard de leurs relations phylogénétiques, dans un contexte de diversification en bouffées d'espèces.

Ces projets devraient être réalisables à partir de 2015. Ils seront mis en œuvre en tenant compte de façon systématique des différentes contraintes méthodologiques imposées par les modèles de niche. Ces modèles seront réalisés à l'échelle de communautés d'échinides et seront testés au regard des déterminants environnementaux et biologiques.

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Palaeobiogeography of Austral echinoid faunas: a first quantitative approach

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Abstract: Few studies have been devoted to the palaeobiogeography of Antarctic echinoids, all of them analysing and discussing distribution patterns in a qualitative way. The present work aims at exploring the evolution of palaeobiogeographic relationships of Austral echinoid faunas through four time intervals, from the Maastrichtian to the present day, using a quantitative approach: the Bootstrapped Spanning Network procedure. Analyses were successfully performed and improve our knowledge of biogeographic relationships between the different Austral regions. Biogeographic maps were produced that can be easily and intuitively discussed. Our results mostly agree with palaeobiogeographic studies performed on other benthic invertebrates and are congruent with the palaeogeographic evolution of Antarctica. However, two main points markedly contrast with other works: there is no evidence of an Austral provincialism at the end of the Cretaceous and early Cenozoic, and echinoid data suggest isolation of southern Argentina from other Austral regions, including Antarctica, in the Early Miocene.

Earth history has had a deep influence on the evolution of the biosphere and consequently on the distribution of life through time. Regarding the Southern Ocean, the final break-up of Gondwana followed by the onset of the southern Pacific and Antarctic circumpolar surface currents during the Cenozoic have had a determinant role explaining the biogeography and diversity of modern Austral faunas (Zinsmeister 1979, 1981; Zinsmeister & Camacho 1980; Beu *et al.* 1997; Del Rio 2002; Pearse *et al.* 2009). Such events are considered to have promoted the two biogeographic processes that have long been invoked to explain the geographically discontinuous distribution patterns of taxa on Earth, namely (1) divergence by vicariance, an outcome of the fragmentation of Gondwana, and (2) dispersal, alternatively promoted or restricted in particular directions by southern surface currents. Both processes have probably worked in unison to shape the modern distribution of Austral faunas (Pearse *et al.* 2009).

Stressing the similarities among the gastropod faunas of Australasia, Antarctica and southern South America in the Late Cretaceous and early Palaeogene, Zinsmeister postulated the existence of a unique Austral faunistic province at that time, the so-called Weddellian province (Zinsmeister 1979, 1981; Zinsmeister & Camacho 1980). Then, the final break-up between Australia and Antarctica along with the northward drift of Australia and New Zealand to warmer conditions by the Late Eocene was associated with the appearance of distinctive faunas in these two latter regions. Faunal connections between Antarctica and southern South America persisted until the Drake Passage opened to depth about the Eocene–Oligocene boundary (Zinsmeister 1981; Beu *et al.* 1997; Scher & Martin 2006; Lawver *et al.* 2011). The onset of a southern Pacific surface current followed by the Antarctic circumpolar current in the Late Eocene was also considered to have influenced the evolution of Austral biogeography (Beu *et al.* 1997; Pearse *et al.* 2009). Hence, Beu *et al.* (1997) and Del Rio (2002) highlighted the existence of faunal similarities between New Zealand and southern South America owing to both eastward and westward dispersals from the Oligocene to the Holocene, while Pearse *et al.* (2009) stressed the role of the Antarctic circumpolar current in promoting speciation within brooding clades of the Southern Ocean.

Most palaeobiogeographic studies of Upper Cretaceous and Cenozoic Austral benthic invertebrates have been based on bivalve and gastropod faunas (Zinsmeister 1979; Zinsmeister & Camacho 1980; Crame 1996; Beu *et al.* 1997; Stilwell *et al.* 2004; Beu 2009), whereas few have considered fossil data across other benthic invertebrate groups such as brachiopods and echinoderms (Zinsmeister 1981). With only approximately 20 fossil species recorded in Antarctica so far, echinoids could appear at first sight as non-informative for palaeobiogeographic purposes. However, most fossils collected in the northern tip of the Antarctic Peninsula for more

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than one century are Maastrichtian, Late Eocene and Early Miocene in age, namely three key time periods to document respectively the situation before the Gondwanan final break-up, the outcome of the northward continental drift of Australia and New Zealand, and the biogeographic consequences of the opening of the Drake Passage and setting up of the Antarctic circumpolar current. Fossil echinoids of the same time periods are recorded in southern Argentina, South Australia and New Zealand, so that the evolution of palaeobiogeographic relationships among these nowadays distinct parts of Gondwana can be investigated using echinoid data. Although palaeobiogeographic relationships among Austral fossil echinoid faunas were formerly discussed (Hotchkiss 1982; Néraudeau *et al.* 2000; Néraudeau & Mathey 2000), it was only in a qualitative way. The present work aims at exploring the palaeobiogeographic relationships through the three time periods mentioned above and comparing them with the present-day situation using the same quantitative approach.

Material and method

Fossil data and taxonomic issues

The three studied geological periods (the Maastrichtian, Late Eocene and Early Miocene) are known in the southern high latitudes from stratigraphic levels that crop out in Antarctica (Table 1), southern Argentina, Australia and New Zealand. The time resolution of the analysis was determined by the biostratigraphic resolution and incompleteness of the known Antarctic (Table 1) and Argentinian fossil record. Seven areas were determined where fossil deposits from the three studied time periods crop out: the western part of the Antarctic Peninsula (including The James Ross basin and King George island), southern Argentina (Patagonia), southeastern and southwestern Australia, Chatham Island, and North and South New Zealand. Present-day distribution data correspond to echinoid samples collected during oceanographic campaigns led in close nearshore marine areas (Fig. 1).

Analyses were performed at genus level to make up for systematic bias and low stratigraphic resolution. Material from GNS Science in Lower Hutt (New Zealand) and from the Museo Argentino de Ciencas Naturales in Buenos Aires (Argentina) was examined to check on systematic reliability and consistency, a recurrent issue in palaeobiogeographic studies (Brayard *et al.* 2007). This was completed with data from the literature (Table 1) and from the online database FRED (Fossil Record Electronic Database) for fossil echinoids from New Zealand. Present-day occurrence data come from the updated version of the Antarctic Echinoid Database (David *et al.* 2005), which integrates most records collected during oceanographic cruises led in the Southern Ocean until 2003. They were augmented by new records collected during cruises led in Antarctica since 2003 (ANTXXIII/8, BENTART, 2003, 2006 and JR230) and with northern data collected as far as latitude 35°S. Specimens housed in public collections were examined (National Institute of Water and Atmospheric Research in Wellington, Museo Argentino de Ciencas Naturales in Buenos Aires, Melbourne Museum in Melbourne, Australian Museum in Sydney). The dataset used in this work corresponds to species occurrences recorded off the land areas where fossil deposits crop out. It covers the parts of continental shelves that best fit with the location of fossil sampling areas (Fig. 1).

Palaeobiogeographic analyses

Regional similarities were analysed using the Bootstrapped Spanning Network (BSN) procedure, namely a non-hierarchical clustering method recently developed for palaeobiogeographic studies and efficient for identification of both biogeographic groupings and transitional areas (Brayard *et al.* 2007). This approach gives a simple, intuitively legible picture of the nested as well as gradational taxonomic similarity relationships, hence providing a good synthesis (and additional insights) between hierarchical clustering and ordination in reduced space results. Associated with each occurrence matrix, a dissimilarity matrix was here computed using the Bray & Curtis (1957) coefficient, which gives a double weight to shared presences and thus relative underweight to absence and unique occurrence as an indication of faunal differences (Brayard *et al.* 2007). Similarity relationships were displayed as a connected network supported by 10 000 bootstrap iterations giving confidence intervals for each connection between bioregions (see Brayard *et al.* 2007 for an exhaustive description of the procedure). Displayed on (palaeo)geographic maps, the BSN allows a robust appraisal of faunal exchange pathways, including faunal gradients or reticulated biogeographic structures. BSN were computed using the software BSN v. 1.0 (Brayard *et al.* 2007) and results were visualized using the program PAJEK v. 1.07 (Batagelj & Mrvar 2005).

A total of 845 fossil occurrences, which correspond to the different locations and geological time periods for which a genus is recorded (17 for the Antarctic Peninsula, 69 for southern Argentina, 316 for South Australia, 33 for Chatham island, 244 for North New Zealand and 166 for South New Zealand) and 3158 present-day occurrences

Table 1. *Fossil echinoids identified in Antarctica, from Late Cretaceous to Early Miocene*

Echinoid taxa	Synonym	Geologic Formation	Time period	Location	Literature consulted
Abatus kieri McKinney, McNamara & Wiedman, 1988	*?Schizaster antarcticus* Lambert, 1910	La Meseta	Late Eocene	Seymour Island	Lambert, 1910; McKinney, McNamara & Wiedman, 1988
Almucidaris durhami Blake & Zinsmeister, 1991		López de Bertodano	Maastrichtian	Seymour Island	Blake & Zinsmeister, 1991
Austrocidaris seymourensis Radwanska, 1996		La Meseta	Eocene	Seymour Island	Radwanska, 1996
Cyathocidaris erebus Lambert, 1910			Maastrichtian	Seymour Island	Lambert, 1910
Cyathocidaris nordenskjoeldi Lambert, 1910		López de Bertodano	Maastrichtian	Seymour Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
Cyathocidaris patera Lambert, 1910		López de Bertodano	Maastrichtian	Seymour Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
Giraliaster lorioli (Lambert, 1910)	*Holaster lorioli* Lambert, 1910	Snow Hill	Maastrichtian	Snow Hill Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
Hemiaster (Bolbaster) vomer (Lambert, 1910)	*Vomeraster vomer* Lambert, 1910	Snow Hill	Maastrichtian	Snow Hill Island	Lambert, 1910; Néraudeau, Crame & Kooser, 2000
Huttonechinus antarctica Néraudeau, Crame & Kooser, 2000		Santa Marta	Late Cretaceous	James Ross Island	Néraudeau, Crame & Kooser, 2000
?Iheringiella sp.			Late Eocene	Black Island, McMurdo Sound	Hotchkiss & Fell, 1972
Micraster aff. regularis Arnaud, 1883		Santa Marta	Late Cretaceous	James Ross Island	Néraudeau, Crame & Kooser, 2000
Nordenskjoeldaster antarctica Lambert, 1910		Snow Hill	Maastrichtian	Snow Hill Island	Lambert, 1910; Bernasconi, 1959
Nordenskjoeldaster australis Néraudeau, Crame & Kooser, 2000		Santa Marta	Campanian	James Ross Island	Néraudeau, Crame & Kooser, 2000
?Notocidaris sp.		Cape Melville	Early Miocene	King George Island	Jesionek-Szymanska, 1987
?Schizaster sp.		Cape Melville	Early Miocene	King George Island	Jesionek-Szymanska, 1987
?Sterechinus sp.	*?Isechinus sp.* Gazdzicki & Wrona, 1982	Cape Melville	Early Miocene	King George Island	Jesionek-Szymanska, 1987
Stigmatopygus andersoni (Lambert, 1910)	*Cassidulus andersoni* Lambert, 1910	La Meseta	Eocene	Seymour Island	Lambert, 1910; McKinney, McNamara & Wiedman, 1988

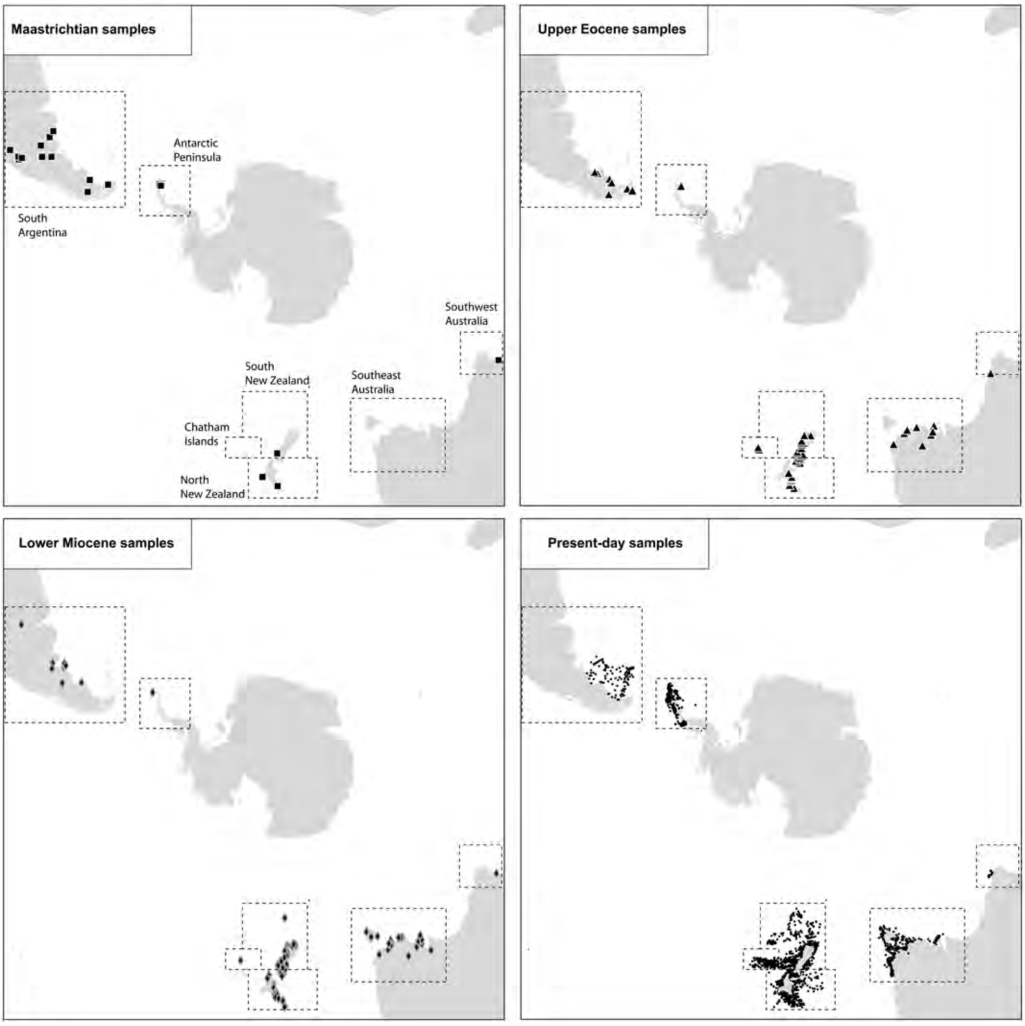

Fig. 1. Location of sampling sites for the Maastrichtian (squares), Late Eocene (triangles), Early Miocene (diamonds) and present day (solid circles).

(465 for the Antarctic Peninsula, 115 for southern Argentina, 704 for South Australia, 186 for Chatham island, 843 for North New Zealand and 845 for South New Zealand) were included within our final dataset and analysed (Fig. 1).

Fossil record and taxonomic richness

Genus richness values contrasted between both studied areas and time periods (Fig. 2). Overall, the total genus richness increases from 15 genera recorded in the Maastrichtian to 42 in the Late Eocene and 65 in the Early Miocene. The total present-day richness is represented by 165 genera. The incompleteness of our knowledge of the fossil record is obvious and could potentially bias the analyses. To assess this potential bias, the correlation significance between taxonomic dissimilarities and richness differences was addressed using a Mantel test. The test was performed between the matrix of taxonomic dissimilarities and the matrix of richness differences computed for each pairwise comparison between regions as the ratio of richness difference to total richness. The correlation value is 0.5 and significance was tested ($p < 0.01$; 5000 bootstrap iterations) using the software PAST v. 1. 92 (Hammer *et al.* 2001). Taxonomic dissimilarities are thus partly explained by richness differences. The relationship between faunal similarities and genus richness can be

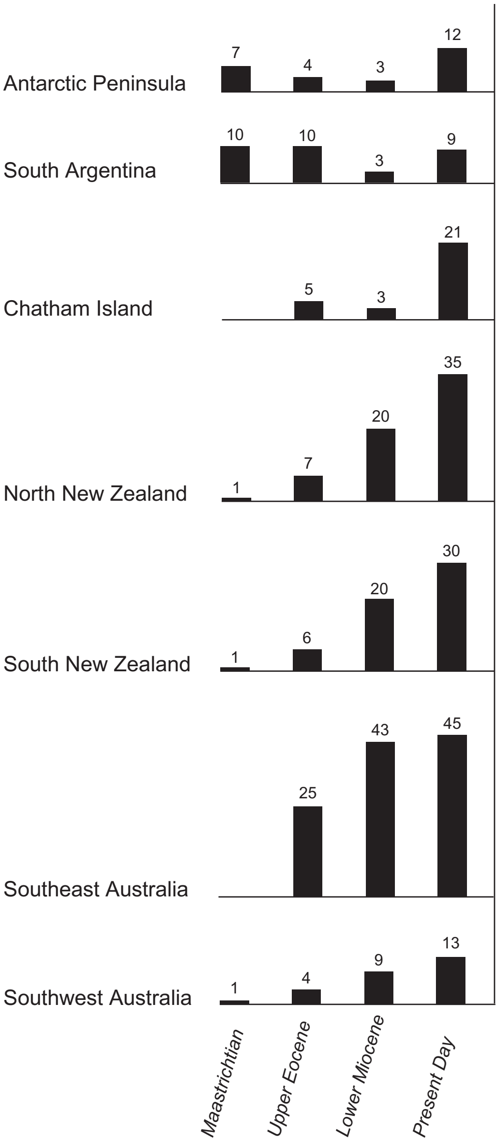

Fig. 2. Genus richness values for the seven studied areas and four time intervals.

interpreted either as biogeographically significant (e.g. provincialism and regional burst of diversity) or as a result of the uneven quality of data.

This stands out clearly when richness values are compared with the number of occurrences that increases from the Maastrichtian to the present day. On Chatham Island, in southern Argentina and the Antarctic Peninsula, richness values decrease from the Maastrichtian to the Early Miocene, then increase to the present day. Richness values and the number of fossil deposits investigated in the Antarctic Peninsula and Chatham Island vary in the same way; richness variation can therefore be interpreted as an outcome of collecting biases and should be interpreted with caution. However, in southern Argentina richness values do not seem to be correlated with the number of sampling sites, which are the most numerous for the Early Miocene (13) and Present Day (115), whereas richness values are the lowest for these time periods (Fig. 2). Therefore, the low richness values of the Early Miocene and present day in southern Argentina do not seem to be entirely determined by sampling biases and probably correspond to a distinctive biogeographic context. The low Argentinian richness sharply contrasts with the burst of echinoid richness recorded in the Late Eocene and Early Miocene of Australia and New Zealand (Fig. 2). These high richness values reflect the radiation of several regular and irregular families already documented in previous works (Philip & Foster 1971, 1977; Zinsmeister & Camacho 1980; Hotchkiss 1982) and obviously show up compared with the situation in the Maastrichtian, a period characterized by a poor fossil record in these regions.

Palaeobiogeographic relationships

BSN analyses were successfully performed and bootstrap support values stress robust, significant connections between regions despite the unevenness of fossil and present-day data. In Figure 3, faunal similarities among studied areas are shown as a connected network for each time period. Bold lines correspond to robust connections with a 100% confidence interval whereas weaker connections are depicted as dashed lines associated with their respective bootstrap support values.

Maastrichtian

Fossil faunas of the Maastrichtian remain insufficiently known and all computed faunal similarities are weak or not sufficiently contrasted. Thus, no robust network was computed nor displayed for this time period.

Despite the limited fossil record, especially in Australia and New Zealand, a qualitative survey of the echinoid faunas of the Late Cretaceous suggests the predominance of cosmopolitan genera with European (Boreal and Tethyan) affinities. Some authors also pointed out taxonomic similarities between faunas of West Antarctica and southern Argentina (Furque & Camacho 1949; Bernasconi 1954; Hotchkiss 1982). This is evidenced by the common occurrence of the genera *Cyathocidaris*, *Nordenskjoeldaster* and *Hemiaster* in both regions.

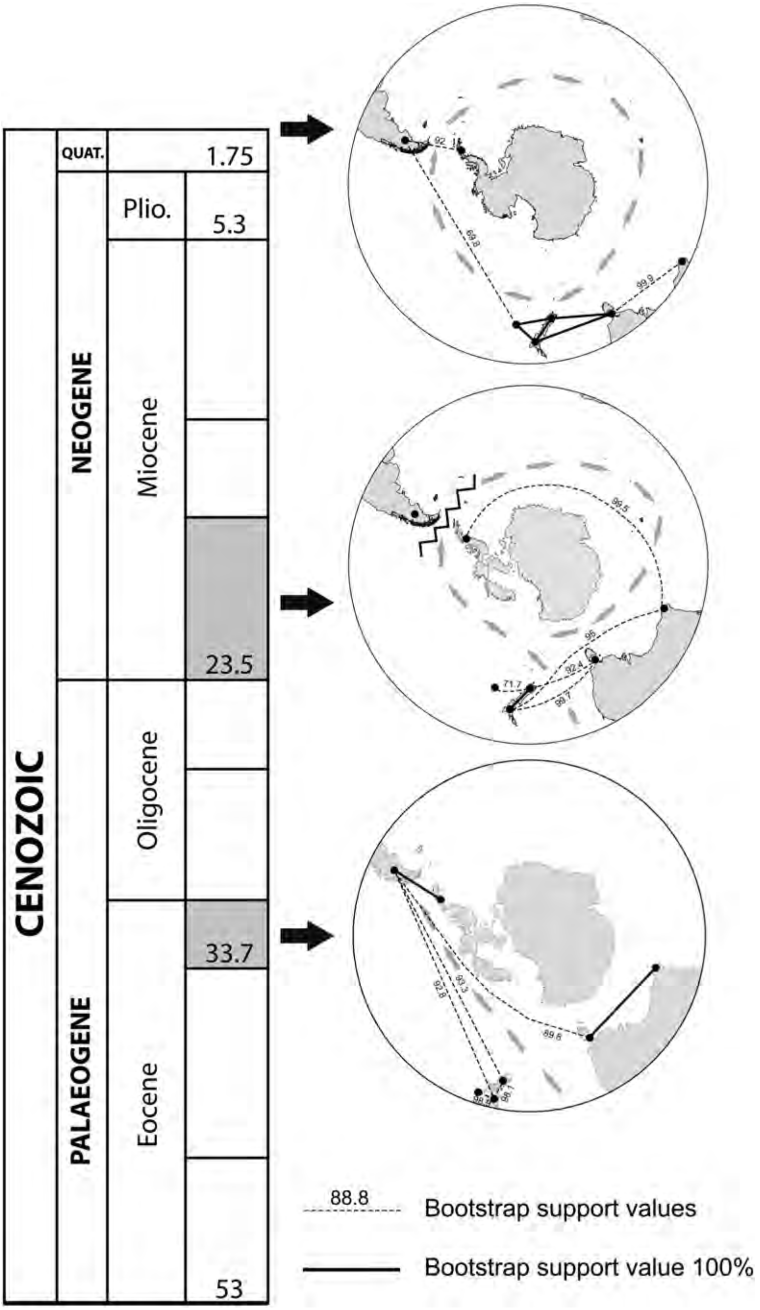

Fig. 3. Bootstrapped spanning networks showing echinoid faunal similarities for the Late Eocene, Early Miocene and present day (ages in millions of years ago). Connection robustness is given by bootstrap support values. Zigzag line symbolizes the biogeographic isolation of southern Argentina from Austral areas in the Early Miocene. Grey arrows depict the position and direction of the southern Pacific (Late Eocene) and Antarctic circumpolar (Early Miocene and present day) surface currents. Map background and current position modified from Lawver & Gahagan (2003).

Faunal connections between southern Argentina and New Zealand are also evidenced by the common presence of *Cyathocidaris* and *Diplodetus* in both regions.

Zinsmeister (1979) proposed the existence of the so-called Weddellian faunistic province to account for these faunal similarities along the southern margins of the Pacific at the end of the Cretaceous and early Cenozoic. The Gondwanan break-up and the prevalence of shallow-water seaways between land masses is considered to have promoted the origination and diversification of marine invertebrates in the SW Pacific Ocean. These taxa spread readily to the east in the early Cenozoic (Zinsmeister & Camacho 1980). This hypothesis is mostly supported by biogeographic studies of Struthiolariidae gastropods (Zinsmeister 1979; Zinsmeister & Camacho 1980). Néraudeau *et al.* (2000) highlighted echinoid faunal similarities between Boreal, Tethyan and Austral regions in the Late Cretaceous, contrasting markedly with Zinsmeister's hypothesis of a distinctive Austral province. The high level of echinoid cosmopolitanism at the end of the Cretaceous is documented by the occurrence of the following European genera in Austral areas: *Micraster* (Antarctic Peninsula), *Hemiaster* (Antarctic Peninsula), *Cyathocidaris* (Antarctic Peninsula, southern Argentina and New Zealand), *Echinocorys* (Australia), *Holaster* (southern Argentina) and *Nucleopygus* (southern Argentina) (Néraudeau & Mathey 2000). Unlike Struthiolariidae gastropods (Zinsmeister & Camacho 1980), the sparse echinoid data do not show any evidence of Austral provincialism during the Maastrichtian. A SW Pacific origin of Austral echinoid faunas followed by an eastward dispersal to South America is also not supported.

Late Eocene

BSN results for the Late Eocene show strong connections between southern Argentina and the Antarctic Peninsula on the one hand, and between southeastern and southwestern Australia on the other (Fig. 3). Trans-Pacific connections between southern Argentina and southeastern Australia as well as between southern Argentina and New Zealand are also well supported.

Previous studies of Austral echinoid faunas have suggested the existence of faunal affinities between southern Argentina and Antarctica in the Late Eocene (Bernasconi 1959; Hotchkiss & Fell 1972; Néraudeau *et al.* 2000). This is congruent with Zinsmeister's (1981) study that alluded to the Austral affinity of mollusc, echinoid and brachiopod faunas from southern Argentina. This strong connection between the two areas is typically exemplified by the occurrence of the shallow-water cassiduloid *Stigmatopygus* in both regions. This supports the existence of shallow-water seaways between the two areas during the Late Eocene (Zinsmeister 1981).

Philip & Foster (1971, 1977) and Zinsmeister & Camacho (1980) documented a burst of faunal diversity in Australia and New Zealand in Eocene times. The faunas are interpreted as either of Austral (Philip & Foster 1977) or Indo-Pacific origin (Zinsmeister & Camacho 1980). The diversity and distinctiveness of Australian echinoid faunas are mostly due to cassiduloid and spatangoid irregular echinoids and to the regular family Temnopleuridae, whereas faunal affinities between Chatham Island and New Zealand are the result of holasteroid occurrences (*Giraliaster* and *Corystus*). Foster & Philip (1978) also stressed the existence of recurrent echinoid trans-Tasman dispersals from southeastern Australia to New Zealand throughout the Cenozoic. This is not supported for the Late Eocene in the present analysis (Fig. 3).

The genera *Schizaster*, *Linthia*, *Austrocidaris* and *Prionocidaris* (the Patagonian species '*Cidaris' antarctica* Loriol (1902) and '*Cidaris' julianensis* Loriol (1902) show strong similarities with species of the genus *Prionocidaris* to which they are herein assigned) have a widespread distribution that supports long-distance connections from Australia to southern Argentina (*Schizaster* and *Linthia*) and to the Antarctic Peninsula (*Austrocidaris*) as well as between New Zealand and southern Argentina (*Prionocidaris*). These southern Trans-Pacific connections between southern Argentina, New Zealand and southeastern Australia are consistent with geographic and oceanographic reconstructions for that time (Lawver & Gahagan 2003) and congruent with other palaeontological studies based on echinoids (Hotchkiss 1982) and molluscs (Beu *et al.* 1997; Del Rio 2002). These connections can be interpreted either as an inheritance of the Zinsmeister's (1979) Weddellian province, which could explain the distribution of the genus *Schizaster*, mentioned in South Argentina in the Late Cretaceous (Parma & Casadio 2005), or as the result of dispersal through the cool surface current that circulated along the Pacific margin of Antarctica (Zinsmeister 1979; Beu *et al.* 1997; Lawver & Gahagan 2003). The genus *Schizaster* has a worldwide distribution and is mainly known as a typical Mediterranean and Tethyan echinoid of the Eocene–Miocene time period. Therefore, the wide austral distribution of the genus cannot be considered an inheritance of the Weddellian province. The same is true for the genus *Linthia*, which is probably of Turonian origin from France (D. Néraudeau pers. comm.). The current that circulated along the Pacific margin of Antarctica is considered to have initiated late in the Eocene (Fig. 3) when the shelf of the South Tasman Rise started to subside (Lawver & Gahagan 2003) and to have favoured the westward dispersal of taxa that are unknown in Austral areas before the Eocene. This could explain the widespread distribution of the genera *Austrocidaris* and *Prionocidaris*.

In spite of the existence of long-distance connections from Australia to the Antarctic Peninsula, most genera are less widely distributed. Within the family Schizasteridae, if genera such as *Schizaster* and *Linthia* are distinguished by a widespread distribution, other genera are restricted to only one region, such as *Abatus* in the Antarctic Peninsula and *Kina* in New Zealand. The origination of the two genera *Abatus* and *Kina* from a schizasterid ancestor along with their endemism could suggest a divergent evolution within the family, an obvious outcome of continental drift. However, phylogenetic relationships within the Schizasteridae require clarification, especially between the genus *Abatus* and its South African relatives. Only marsupiate species with sunken petals were assigned to the genus. They might be closely related to non-Antarctic and non-marsupiate species, and a genus can be represented by marsupiate species in a region of the world ocean, and non-marsupiate species in other areas (Dudicourt *et al.* 2005).

Early Miocene

The most noticeable result of the BSN analysis performed for the Early Miocene is the faunal isolation of southern Argentina from other Austral regions, including a south Pacific disconnection between southern Argentina and New Zealand. Results also show a direct connection between southwestern Australia and New Zealand, and a faunal disconnection between southeastern and southwestern Australia. An unexpected but robust relationship between the Antarctic Peninsula and southwestern Australia is also highlighted (Fig. 3).

The isolation of southern Argentina is partly congruent with Del Rio (2002), who highlighted the Caribbean affinity of part of Lower Miocene Patagonian molluscs. However, a faunal connection between Patagonia and New Zealand was also stressed by Del Rio (2002) and Beu *et al.* (1997). Based on echinoid data, there is no evidence so far for such a connection, despite the establishment of the Antarctic circumpolar current at the Eocene–Oligocene boundary and the possibility of subsequent westward dispersal from New Zealand (Beu *et al.* 1997; Lawver & Gahagan 2003). The fossil record is weak in southern Argentina and Antarctica (only three echinoid genera are known in Argentina and West Antarctica; Table 1), but the faunal distinctiveness between these two areas is well supported by the occurrence of peculiar South American faunas. In southern Argentina, echinoids are typically represented by the clypeasteroid family Monophorasteridae (*Amplaster* and *Monophoraster*) and the genus *Abertella* (Hotchkiss 1982; Mooi *et al.* 2000). These echinoids are unknown from other Austral areas. Hotchkiss & Fell (1972) postulated an Antarctic affinity of southern Argentinian clypeasteroids after the discovery of the genus *Iheringiella* in the Upper Eocene of East Antarctica, but interestingly Mooi *et al.* (2000) excluded the latter genus from the family Monophorasteridae, which is unequivocally restricted to South America. Moreover, the occurrence of the genus *Iheringiella* in the Upper Eocene of Antarctica (Hotchkiss & Fell 1972) is suspect (Table 1) considering that the only known specimen consists of a fragment without diagnostic features and that the genus is recorded from Miocene deposits in South America (R. Mooi pers. comm.). In Australia, the diversification of clypeasteroid echinoids gave rise to the families Fossulasteridae, Scutellinoididae and Arachnoididae. Diversity of Australasian echinoids is also typified by cassiduloids (e.g. *Pisolampas*), spatangoids (e.g. *Eupatagus*) and cidaroids (e.g. *Goniocidaris*). The southwestern Australian genera *Cardabia* and *Tripneustes* are absent in southeastern Australia, while the latter is present in New Zealand and Chatham Island. This supports the direct connection between southwestern Australia and New Zealand, and the faunal disconnection between southeastern and southwestern Australia. However, the genus *Tripneustes* is known from Miocene deposits of Switzerland and France, so that its absence from southeastern Australia could be due to incomplete sampling.

The robust relationship between the Antarctic Peninsula and southwestern Australia is mostly supported by the widespread distribution of the genus *Schizaster* (except in southern Argentina where the genus is not so far recorded in the Early Miocene). This widespread distribution extends back to the Late Eocene, the genus being recorded worldwide (see discussion above). Therefore, the robust relationship between the Antarctic Peninsula and southwestern Australia in the Early Miocene can be interpreted as an inheritance of distribution patterns of the past, and not as the result of contemporary faunal connections. This interpretation is corroborated by the divergent evolution of cidarid echinoids, which gave rise to distinct genera between Antarctica and Australia in the Early Miocene. For example, the genus *Goniocidaris* is first recorded in the Lower Miocene of New Zealand and Australia whereas in Antarctica, cidarids are known by the genus *Notocidaris*. The two genera diversified in different areas during the Neogene, the genus *Notocidaris* being mostly restricted to the Antarctic continental shelf (except for one Recent species in New Zealand), whereas *Goniocidaris* species spread to the Indo-Pacific region (Mortensen 1928; David *et al.* 2005). The geographically limited evolution and diversification of the genus *Notocidaris* in Antarctica supports the relative isolation of the continent from Australasia.

Present day

The comparison of BSN results for present day faunas with those of previously studied time intervals highlights the strong affinity between Australian and New Zealand modern faunas, including those of Chatham Island. The present day configuration also displays a relatively well-supported connection between southern Argentina and the Antarctic Peninsula, and the existence of a weak faunal connection between southern Argentina and Chatham Island (Fig. 3).

The similarity of echinoid faunas between Australia and New Zealand may be explained by the existence of recurrent trans-Tasman faunal exchanges between southeastern Australia and New Zealand throughout the Cenozoic (Foster & Philip 1978). Spatangoid echinoids are highly diversified in Australia and New Zealand (e.g. Maretiidae, Brissidae, among others), but most are restricted to these areas and have no representative in Antarctica or southern Argentina.

The relatively well-supported connection between southern Argentina and the Antarctic Peninsula across the Scotia Arc has been extensively documented in previous studies across various benthic groups, from bivalves and gastropods to polychaetes and isopods (e.g. Hedgpeth 1969; Linse *et al.* 2006; Clarke *et al.* 2007; Brandt *et al.* 2009). Based on echinoids, the connection can be explained by the extended latitudinal range of the schizasterid genera *Abatus* and *Tripylus*, and of the echinid genus *Sterechinus*. The three genera are represented by high Antarctic, Subantarctic and southern Argentinian cold-temperate species (David *et al.* 2005; Diaz *et al.* 2011), and are absent from Australasia. They are only known as fossils in the Upper Eocene (*Abatus*) and Lower Miocene (*Sterechinus*) of the Antarctic Peninsula, which suggests a West Antarctic or Subantarctic (see Diaz *et al.* 2011) origin, then dispersal through the Antarctic circumpolar current downstream of Drake Passage, in the Scotia Arc and southernmost Argentina, as well as in the Weddell Sea (Pearse *et al.* 2009). However, the occurrence of *Abatus* in the Upper Eocene of the Antarctic Peninsula (McKinney *et al.* 1988) might predate the full opening of the Drake Passage, in which case the genus could have migrated to South America before the full establishment of the Antarctic circumpolar current through the shallow waters that separated the two continents.

The existence of a weak faunal connection between southern Argentina and Chatham Island has been demonstrated by previous authors (Beu *et al.* 1997; Del Rio 2002) to have occurred since the Oligocene owing to dispersal through the Antarctic circumpolar current. In the present work, this circum-Antarctic dispersal is only supported by the occurrence of the Subantarctic and cool-temperate genera *Austrocidaris* and *Pseudechinus*, which are present off the coasts of southern Argentina, New Zealand and Chatham Island. *Pseudechinus* first occurs in the Cenozoic of Australia and New Zealand and then in the Pliocene of South America. This suggests the Australasian origin of the genus followed by circum-Antarctic dispersal to the west after the Early Miocene. The genus *Austrocidaris* is known as fossils in the Upper Eocene of West Antarctica, southern Argentina and Australia, and is supposed also to have dispersed from Australia in the Late Eocene (see discussion above).

Conclusion

Our results largely agree with previous biogeographic studies on echinoids and other benthic invertebrates. However, two main points contrast markedly with previous works: (1) there is no evidence of an Austral provincialism of echinoid faunas at the end of the Cretaceous and early Cenozoic – data instead suggest the cosmopolitanism of Austral echinoids that show Boreal and Tethyan affinities; (2) there is no evidence of faunal exchanges between New Zealand and southern Argentina in the Early Miocene – data better support a Caribbean affinity of southern Argentinian faunas as well as the presence of a biogeographic barrier between southern Argentina and other Austral regions. This result remains difficult to elucidate as it postdates the onset of the Antarctic circumpolar current, but it may be related to the transient intense glaciation that took place in Antarctica at the Oligocene-Miocene boundary (Rogers 2007). More fossil data are needed to confirm or invalidate this preliminary result.

In spite of the relative incompleteness of our knowledge of the echinoid fossil record at southern high latitudes, our results show that palaeobiogeographic relationships among echinoid faunas can be studied using a quantitative approach and not just qualitatively discussed. The quantitative analyses performed in this work improved our knowledge of the albeit still unclear biogeographic relationships between the different Austral regions. Moreover, the newly obtained biogeographic maps can be easily and intuitively discussed. More sampling efforts are needed though to improve understanding of the observed palaeobiogeographic relationships. Data from Madagascar, southern Chile and South Africa (Zululand) should be included in the future so as to complete this large-scale palaeobiogeographic analysis of Austral echinoid faunas.

Between the two biogeographic processes invoked to explain the distribution patterns of taxa, our interpretations usually favoured dispersal over vicariance. Two arguments support this lack of balance. First, biogeographic patterns of Australasian and Argentinian faunas have been deeply conditioned by the importance of immigration (Warren *et al.* 2009) from their respective northern areas. This is well typified by the Caribbean affinity of Argentinian echinoids in the Early Miocene or the Indo-Pacific affinity of Australian and New Zealand echinoids in the Late Eocene. Second, demonstration of the divergent evolution of taxa from an ancestral group by vicariance requires reliable phylogenies. The diversity of extant Antarctic echinoids is mostly due to the families Schizasteridae and Cidaridae, which are predominantly composed of endemic species (David *et al.* 2005). However, the origin of this diversity is not fully understood, as phylogenetic relationships with echinoids of other Austral regions remain unclear.

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ORIGINAL ARTICLE

Comparative biogeography of echinoids, bivalves and gastropods from the Southern Ocean

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ABSTRACT

Aim Biogeographical patterns within three classes, the Echinoidea, Bivalvia and Gastropoda, were investigated in Antarctic, sub-Antarctic and cold-temperate areas based on species occurrence data. Faunal similarities among regions were analysed to: (1) test the robustness of the biogeographical patterns previously identified in bivalves and gastropods; (2) compare them with the biogeographical patterns identified for echinoids; and (3) evaluate the reliability of the biogeographical provinces previously proposed, depending on the taxa and taxonomic levels analysed.

Location The Southern Ocean, sub-Antarctic islands and cold-temperate areas south of 45° S latitude at depths of < 1000 m.

Methods Taxonomic similarities among 14 bioregions were analysed using a non-hierarchical clustering method, the bootstrapped spanning network (BSN) procedure. Taxonomic similarities were analysed within the three classes at species and genus levels.

Results The previously identified large-scale biogeographical entities are clarified. Echinoid and bivalve faunas are structured mainly according to three faunal provinces: (1) New Zealand, (2) southern South America and sub-Antarctic islands, and (3) Antarctica. Gastropod faunas group into five provinces: (1) New Zealand, (2) southern South America, (3) east sub-Antarctic islands, (4) West Antarctica, and (5) East Antarctica. Strong faunal relationships between bioregions perfectly match the flows of the Antarctic Circumpolar and Antarctic Coastal currents. Moreover, the legacy of the climatic and palaeoceanographic history of Antarctica is revealed by trans-Antarctic faunal affinities, thereby strongly supporting hypotheses of past marine seaways that would have connected both the Amundsen–Bellingshausen area to the Weddell Sea and the Weddell Sea to the Ross Sea.

Main conclusions A significant advantage of the BSN procedure lies in the possibility of identifying both biogeographical groupings and transitional areas; that is, both strong connections and groupings between bioregions. The method has also proved to be efficient for identifying potential faunal exchange pathways and dispersal routes, both present and past, by fitting networks to oceanographic and palaeogeographical maps.

Keywords

Antarctic, bootstrapped spanning network, dispersal, sub-Antarctic, trans-Antarctic seaway, vicariance.

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INTRODUCTION

Biogeographical studies have been the subject of renewed interest in the last few decades, as evidenced by the emergence of new analytical approaches and procedures (Cox & Moore, 2000; Lomolino *et al.*, 2006). In addition, present-day distribution patterns can be rooted in ever more precise historical data (palaeogeographical, palaeoclimatic and palaeoecological), allowing revised interpretations (Cox & Moore, 2000; Lomolino *et al.*, 2006; Pearse *et al.*, 2009). However, many studies rely on clustering approaches, which appear particularly well suited to detecting hierarchical relationships among bioregions but ignore the gradations between them.

The Southern Ocean represents 8% of the world's ocean surface area and is now known to harbour about 5% of the Earth's marine metazoan diversity (Zwally *et al.*, 2002; Linse *et al.*, 2006; Ingels *et al.*, 2011). Owing to their distinctive ecological traits (e.g. specific reproduction strategies, slow growth rates), profound adaptations to unique environmental conditions (e.g. near-freezing water temperatures, ice-scouring, seasonal sea-ice cover, seasonal variation of food resources) and relatively high levels of endemism (Starmans & Gutt, 2002; Clarke, 2008), Antarctic marine organisms are considered to be particularly vulnerable to the environmental changes that are expected in the future. However, the strength of the predicted impact might depend on the taxa and ecological levels investigated, from individual species to communities (Dierssen *et al.*, 2002; Poulin *et al.*, 2002; Quayle *et al.*, 2002; Clarke & Johnston, 2003; Pörtner, 2006; Ingels *et al.*, 2011).

At a broad spatial scale, benthos in the Southern Ocean has long been structured by the Antarctic Polar Front (or Antarctic Convergence) and the Antarctic Circumpolar Current (ACC), and by the Pleistocene glacial–interglacial cycles (Lawver & Gahagan, 2003; Griffiths *et al.*, 2009). The Antarctic Polar Front, which closely matches the northern boundary of the Southern Ocean (at about 50° S latitude), constitutes the main biogeographical barrier to the northward dispersal of marine organisms distributed in the upper water layer. The ACC and the deep-sea basins that surround Antarctica also contribute to the isolation of Antarctic taxa from faunas of sub-Antarctic and cold-temperate shallow-water regions. Faunal exchanges among these regions can, however, occur through the Scotia Arc and, to a lesser extent, through island shelves and seamounts located south of New Zealand (Montiel, 2005; Linse *et al.*, 2006; Brandt *et al.*, 2009).

Our knowledge of Antarctic marine biodiversity has increased significantly since the first biogeographical studies were undertaken in the Southern Ocean (Ekman, 1953; Powell, 1965; Hedgpeth, 1969). UNESCO (2009) identified several benthic provinces based on depth, and it has been suggested that the lower bathyal zone could be subdivided into an Antarctic and a sub-Antarctic province, while the abyssal plain could be partitioned into an East Antarctica and a West Antarctic province. Recent biogeographical studies based on various benthic taxa (e.g. De Broyer & Jazdzewski, 1996; Linse *et al.*, 2006; Clarke *et al.*, 2007; Rodriguez *et al.*, 2007; Barnes & Griffiths, 2008; Griffiths *et al.*, 2009, 2011) have analysed taxonomic similarities among the bioregions previously identified around the Antarctic continental shelf (Hedgpeth, 1969). The conclusions were that the Antarctic continental shelf was composed of a single province and that high Antarctic faunas were evenly distributed around the continent (Barnes & De Grave, 2001; Griffiths *et al.*, 2009). Few studies, however, have integrated data from adjacent regions such as southern South America, South Australia, New Zealand and South Africa, which would place Antarctic biogeography into the wider geographical context of the Southern Ocean (Barnes & Griffiths, 2008; Griffiths *et al.*, 2009). The existence of a distinct sub-Antarctic benthic province has been suggested, with various islands and island groupings showing faunal affinities with either southern South America or New Zealand (Linse *et al.*, 2006; Griffiths *et al.*, 2009). Potential faunal connections between southern South America and West Antarctica have also been highlighted (Montiel, 2005; Linse *et al.*, 2006; Brandt *et al.*, 2009).

Bivalves and gastropods are among the best-documented benthic clades in the Southern Ocean. Occurrence data collected for more than a century during oceanographic expeditions were collated into the Southern Ocean Molluscan Database SOMBASE (Griffiths *et al.*, 2003). Contrasting biogeographical patterns were shown between bivalves and gastropods (Linse *et al.*, 2006; Barnes & Griffiths, 2008; Griffiths *et al.*, 2009), suggesting the possibility of different evolutionary histories between the two groups. As biogeographical patterns may depend upon the biological group analysed (Barnes & Griffiths, 2008; Griffiths *et al.*, 2009), Clarke (2008) proposed that biogeographical studies should be extended to other marine groups. The Antarctic echinoid fauna is phylogenetically distant from molluscs and well diversified in the Southern Ocean, with about 80 species accounting for *c.* 10% of the global echinoid species richness (David *et al.*, 2005b). It therefore appears to be appropriate for such a biogeographical study.

In this work, faunal similarities between regions were analysed in echinoids, bivalves and gastropods at species and genus levels using a newly developed quantitative approach, the bootstrapped spanning network (BSN) procedure (Brayard *et al.*, 2007, 2009). Initial objectives were: (1) to test the robustness of the biogeographical patterns previously identified in bivalves and gastropods; (2) to compare them with the biogeographical patterns to be identified in echinoids; and (3) to evaluate the reliability of the biogeographical provinces previously proposed, depending on the taxa and taxonomic levels analysed. The large-scale analysis of three diversified groups of high taxonomic rank (i.e. classes) at two taxonomic levels is expected to target preferentially the weight of oceanographic history in present biogeographical patterns. The importance of regional environmental conditions cannot be ignored, but they are expected to show contrasting contributions depending on the taxonomic level analysed.

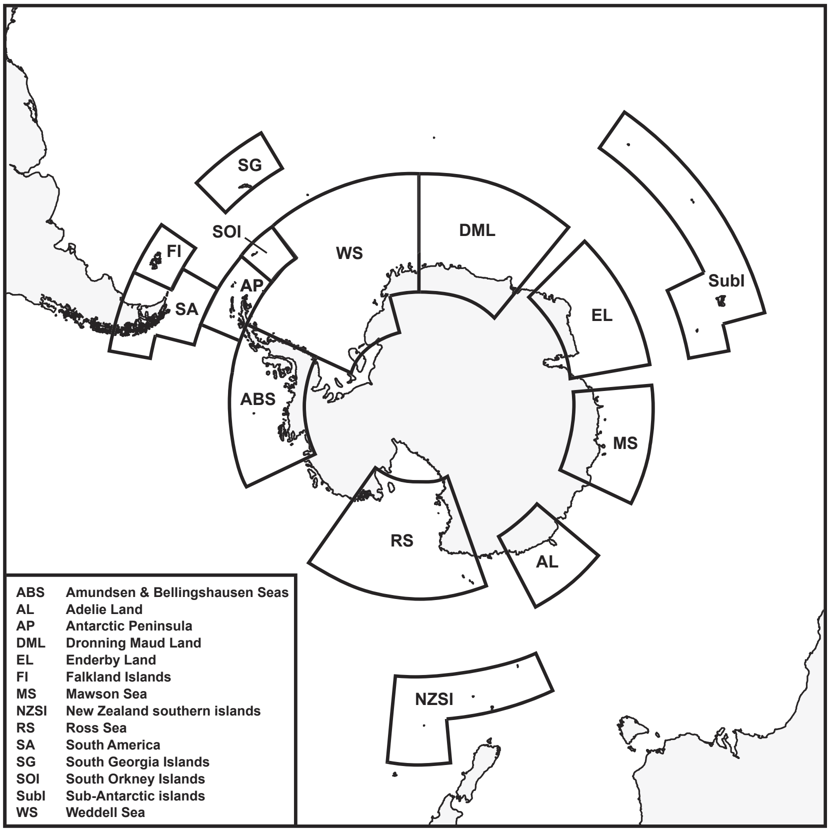

Figure 1 The 14 studied bioregions defined south of latitude 45° S, modified from Hedgpeth (1969), Linse *et al.* (2006) and Griffiths *et al.* (2009).

MATERIALS AND METHODS

Studied areas and bioregionalization

Echinoid, bivalve and gastropod biogeographical patterns of Antarctic, sub-Antarctic and cold-temperate areas were investigated south of 45° S latitude at depths ranging from the shoreline to the Antarctic continental break (1000 m depth). Fourteen bioregions were defined with a latitudinal and longitudinal accuracy of 5° (Fig. 1); they were adapted from Hedgpeth (1969) and from more recent studies (Linse *et al.*, 2006; Barnes & Griffiths, 2008; Griffiths *et al.*, 2009). Three cold-temperate bioregions were considered: the southern tip of South America (SA), the Falkland Islands (FI) and New Zealand southern islands of the Campbell Plateau (NZSI). Sub-Antarctic bioregions include South Georgia (SG) and an eastern bioregion composed of Prince Edward, Crozet, Bouvet, Kerguelen and Heard islands (SubI). Antarctic bioregions consist of the northern tip of the Antarctic Peninsula (AP), South Orkney Islands (SOI), the Weddell Sea (WS), Dronning Maud Land (DML), Enderby Land (EL), the Mawson Sea (MS), Adelie Land (AL), the Ross Sea (RS), and the assemblage composed of the Amundsen and Bellingshausen seas (ABS).

Occurrence data

Echinoid occurrence data were compiled from the Antarctic Echinoid Database (David *et al.*, 2005a), which integrates most records collected during oceanographic cruises carried out in the Southern Ocean until 2003. Data were updated with new records sampled during cruises conducted in Antarctica since 2003 and with data from as far north as 45° S latitude (Pierrat *et al.*, 2012). The updated echinoid dataset now comprises a total of 2671 occurrences (Fig. 2, Table 1). Bivalve and gastropod occurrence data were gathered through the online Southern Ocean Mollusc Database (SOMBASE; Griffiths *et al.*, 2003). SOMBASE includes 3505 and 7135 occurrences for bivalves and gastropods, respectively (Table 1), and is complete enough to be used in relevant large-scale biogeographical works (Linse *et al.*, 2006; Clarke *et al.*, 2007; Barnes & Griffiths, 2008; Griffiths *et al.*, 2009).

Finally, occurrence data were compiled for each group at the species and genus levels. Data include 35 genera and 85 species of echinoids, 103 genera and 250 species of bivalves, and 233 genera and 704 species of gastropods (Table 1).

Biogeographical analyses

Faunal similarities are usually studied using methods of multivariate analyses that identify spatial boundaries between species-level, genus-level or family-level assemblages. Biogeographical classifications aim at defining discontinuities among bioregion groupings and usually ignore the identification of transitional areas among distinct biogeographical units (Brayard *et al.*, 2007; UNESCO, 2009). In this study, taxonomic similarities among bioregions were analysed using

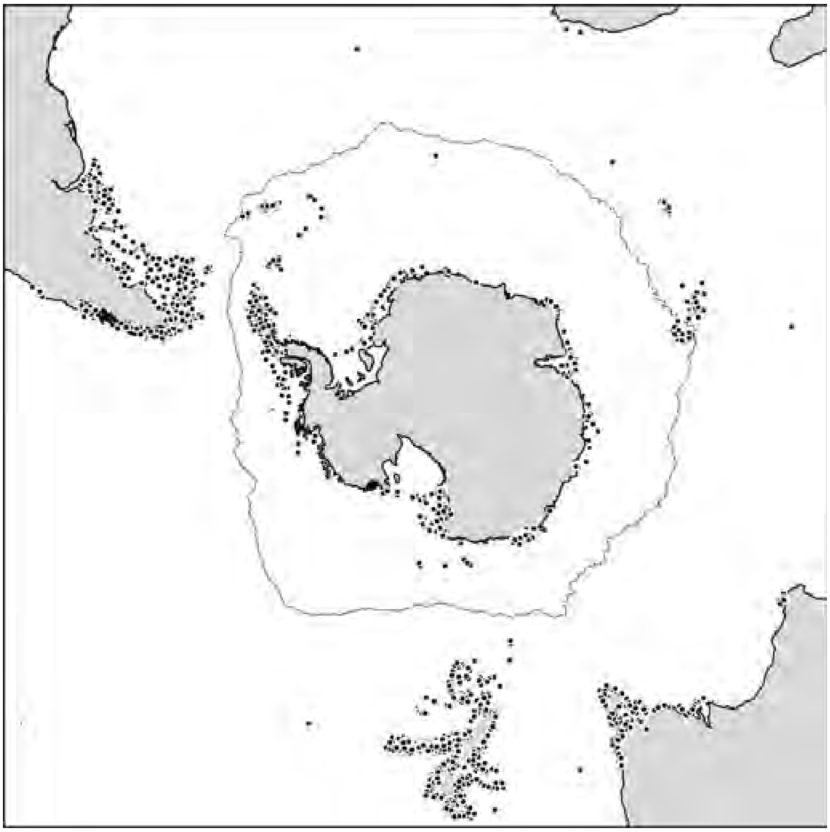

Figure 2 Distribution of echinoid occurrence data compiled from the updated Antarctic Echinoid Database (Pierrat *et al.*, 2012). The dataset comprises a total of 2671 occurrences and integrates records collected during oceanographic cruises carried out in the Southern Ocean and as far north as 45° S latitude.

Table 1 Numbers of genera and species of echinoids, bivalves and gastropods recorded in this study and occurrence data for each taxon for each of the 14 studied bioregions in the Southern Ocean. Echinoid occurrence data were compiled from the updated Antarctic Echinoid Database (Pierrat *et al.*, 2012), which integrates most records collected during oceanographic cruises carried out in the Southern Ocean and as far north as 45° S latitude. Bivalve and gastropod occurrence data were gathered through the online Southern Ocean Mollusc Database (SOMBASE; Griffiths *et al.*, 2003).

	Echinoidea			Bivalvia			Gastropoda		
	No. of genera	No. of species	Occurrence data	No. of genera	No. of species	Occurrence data	No. of genera	No. of species	Occurrence data
ABS	10	27	219	14	20	66	28	39	84
AL	8	24	192	23	32	175	42	69	359
AP	14	39	479	29	50	386	67	107	365
DML	6	16	33	11	11	18	50	93	220
EL	8	26	198	22	34	80	60	98	194
FI	11	16	168	39	60	222	79	146	372
MS	8	18	53	16	19	51	37	49	93
NZSI	13	16	84	42	61	179	55	90	203
RS	12	30	293	46	67	697	90	160	1207
SA	12	18	271	55	84	332	68	108	377
SG	11	16	104	29	47	206	65	128	587
SOI	11	24	98	25	33	94	60	85	165
SubI	11	12	127	42	40	109	57	114	1735
WS	14	34	352	33	65	890	89	186	1174

ABS, Amundsen and Bellingshausen seas; AL, Adelie Land; AP, Antarctic Peninsula; DML, Dronning Maud Land; EL, Enderby Land; FI, Falkland Islands; MS, Mawson Sea; NZSI, New Zealand southern islands; RS, Ross Sea; SA, South America; SG, South Georgia; SOI, South Orkney Islands; SubI, sub-Antarctic islands; WS, Weddell Sea.

the BSN procedure, a non-hierarchical clustering method that has recently been developed for palaeobiogeographical studies and allows identification of both biogeographical groupings and transitional areas (Brayard *et al.*, 2007, 2009). This approach yields a simple, intuitively comprehensible picture of the nested as well as gradational taxonomic similarity relationships. Associated with each occurrence matrix, a dissimilarity matrix was computed using the Bray–Curtis coefficient (Bray & Curtis, 1957), which gives a double weight to shared presences and a simple weight to absence and unique occurrence as an indication of faunal differences. Similarity structures were displayed as a connected network, which is a set of interlinked nodes represented by bioregions and supported by bootstrap replications (10,000 replicates were computed here) that give confidence intervals for each connection between bioregions (see Brayard *et al.*, 2007). Within a BSN, the robustness of connections is evaluated by bootstrap support values (BSVs). When it is fitted on geographical maps, the BSN allows a quantitative appraisal of faunal exchange pathways, including faunal gradients or reticulated biogeographical structures. BSNs were computed using the software BSN 1.0 (Brayard *et al.*, 2007), and results were visualized using the program PAJEK 1.07 (Batagelj & Mrvar, 2005).

RESULTS

Echinoid biogeographical patterns

The analysis of echinoid networks (Fig. 3a,b) reveals the existence of distinct biogeographical entities, although boundaries between these entities are not sharp barriers to faunal dispersal and are marked only by a relative drop in faunal similarities. In the echinoid species network (Fig. 3a), the Campbell Plateau bioregion (NZSI) shows a connection with the Ross Sea (RS). However, this relationship is not well supported, and the Campbell Plateau appears isolated from other bioregions of the Southern Ocean. Sub-Antarctic bioregions (SG and SubI) and those of southern South America (SA and FI) are strongly connected to each other (BSV > 85%) in a west–east pattern. They connect with West Antarctica through South Georgia (SG) and the South Orkney Islands (SOI), but this connection is weakly supported (BSV = 69%), suggesting faunal dissimilarities between sub-Antarctic bioregions and West Antarctica. Antarctic bioregions are strongly connected to each other (BSV > 95%) following a marked circum-Antarctic pattern, except for a strong discontinuity between the Weddell Sea (WS) and Dronning Maud Land (DML). The network structure suggests the existence of two sub-provinces, the West Antarctic (SOI, AP, WS, ABS) and East Antarctic (AL, MS, EL and DML), connecting through the Ross Sea. Interestingly, the Amundsen and Bellingshausen seas (ABS) are strongly related to the Weddell Sea (WS), although these bioregions are separated from each other by the landmass and ice sheets of the Antarctic Peninsula.

The echinoid genus network (Fig. 3b) differs from the species BSN in the detail of connections between bioregions, except for the relative remoteness of the Campbell Plateau. Two main biogeographical entities are indicated: (1) the connection between the bioregions of southern South America and the east sub-Antarctic bioregion (BSV = 76.2%); and (2) a robust circum-Antarctic link between Antarctic bioregions. The weak link between entities (1) and (2) is located between east sub-Antarctic bioregions (SubI) and South Georgia (BSV = 58.6%), the latter being strongly related to Enderby Land (BSV = 99.3%). Within the Antarctic bioregions, there is a discontinuity between Adelie Land (AL) and the Ross Sea (RS), the latter being connected to bioregions of West Antarctica. Enderby Land (EL) appears central within connected East Antarctic bioregions, whereas the South Orkney Islands (SOI) are central within connected West Antarctic bioregions. Finally, as in the species network, the Admunsen and Bellingshausen seas (ABS) and the Weddell Sea (WS) are strongly interconnected.

Bivalve biogeographical patterns

In the bivalve species network (Fig. 3c), the southern South America and sub-Antarctic bioregions are connected to each other following a west–east link, as for the echinoid species network. However, these connections are not very robust and undermine the significance of a wide southern South American and sub-Antarctic province for bivalve species. The Campbell Plateau (NZSI) is weakly connected to the Ross Sea, showing again the relative isolation of this bioregion. Antarctic bioregions are connected to each other (BSV > 84%) following a circum-Antarctic pattern interrupted by a discontinuity between the Weddell Sea (WS) and Droning Maud Land (DML), just as in the echinoid species network. The structure of the bivalve network does not show two distinct Antarctic provinces because the bioregions form a continuous structure with no partition between east and west. The Amundsen and Bellingshausen seas are weakly connected to the Antarctic Peninsula (AP), suggesting a higher level of endemism in this bioregion.

In the genus-level BSN, the east sub-Antarctic bioregion is strongly connected to bioregions of the Scotia Arc through South Georgia (SG), and directly to the Falkland Islands (FI) (Fig. 3d). The west–east pattern formed by the links between South American and sub-Antarctic bioregions is obvious, but sub-Antarctic bioregions are more strongly connected to West Antarctica than to the Falkland Islands through the South Orkney Islands (BSV > 95%). As in the bivalve species BSN, sub-Antarctic islands and South American bioregions do not seem to form a unique province. West Antarctic bioregions (SOI, AP and WS) are strongly connected (BSV = 100%). They connect East Antarctic bioregions (AL, MS, EL and DML) through the Antarctic Peninsula (AP) and Adelie Land (AL). Interestingly, the Ross Sea shows more affinities with the Weddell Sea, to which it is connected (BSV = 99.7%). The two bioregions are today separated by the West Antarctic Ice Sheet, much of the West Antarctic landmass being below sea level. A similarly unexpected connection reveals affinities between the Amundsen and Bellingshausen seas and Enderby Land, although the link is only moderately supported (BSV = 75.4%).

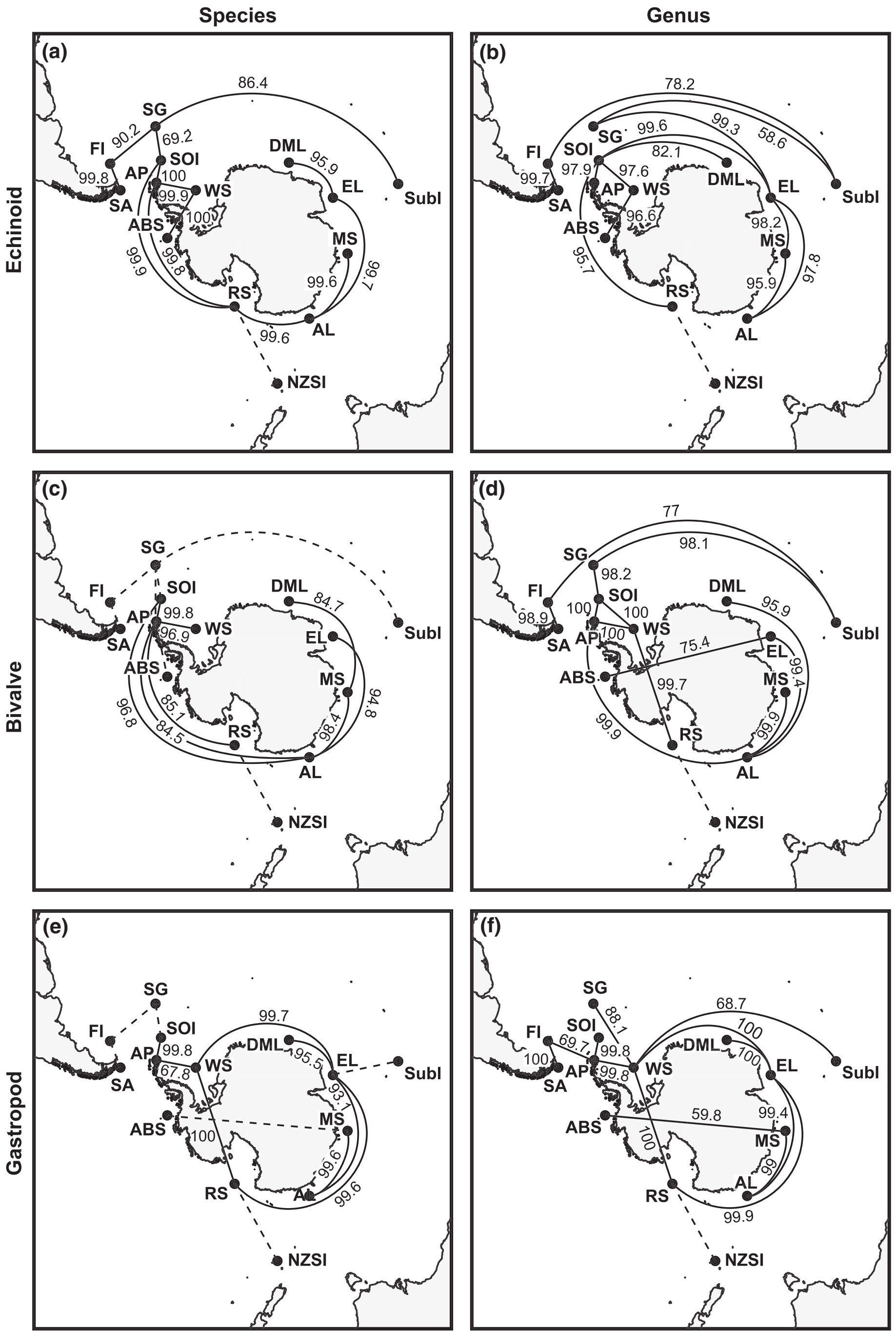

Figure 3 Bootstrapped spanning networks performed at species and genus levels for (a, b) echinoids, (c, d) bivalves and (e, f) gastropods from the Southern Ocean. Robust connections are represented as solid lines, and their associated bootstrap support values are indicated. Dashed lines correspond to weak connections. Abbreviations as in the inset in Fig. 1.

Gastropod biogeographical patterns

In the gastropod species BSN, the Campbell Plateau is weakly connected to other bioregions, as are sub-Antarctic islands and southern South American bioregions (Fig. 3e). The weak connection between east sub-Antarctic islands and Enderby Land (EL) departs from the patterns previously documented. The South Orkney Islands (SOI) and Antarctic Peninsula (AP) are strongly related to each other (BSV = 99.8%) and connect the Weddell Sea (WS) through a weak linkage (BSV = 67.8%). Other Antarctic bioregions are all strongly connected following both a circum- and a trans-Antarctic pattern. Therefore, the Weddell and Ross seas are strongly related to each other (BSV = 100%) through a trans-Antarctic connection. The gastropod species network clearly highlights the partition of Antarctica into two distinct provinces:

Table 2 Pairwise comparisons between genus- and species-level bootstrapped spanning networks (BSNs) of echinoids, bivalves and gastropods from the Southern Ocean. Values correspond to the number of similar connections between networks over a total of 14 connections per network. Highest similarity values between pairs are in bold.

	Echinoid species	Echinoid genera	Bivalve species	Bivalve genera	**Gastropod species**
Echinoid species	–	–	–	–	–
Echinoid genera	8	–	–	–	–
Bivalve species	**10**	6	–	–	–
Bivalve genera	8	8	9	–	–
Gastropod species	9	5	8	7	–
Gastropod genera	7	5	6	7	**10**

(1) a ‘small’ West Antarctic province restricted to the Antarctic Peninsula and South Orkney Islands, and (2) an extended East Antarctic province including the Weddell and Ross seas. Finally, the Amundsen and Bellingshausen seas appear to be partially disconnected from other Antarctic bioregions.

Patterns of gastropod species and genus networks are very alike (Fig. 3e,f, Table 2). The genus network is distinguished from that for the species only by a weak connection between the east sub-Antarctic islands and the Weddell Sea and a robust connection between South Georgia (SG) and the Weddell Sea (WS). However, the pattern remains identical to the gastropod species BSN, with a weak connection between southern South America and West Antarctica (BSV = 69.7%) and an unusual position of the Amundsen and Bellingshausen seas (BSV = 59.8%). The gastropod genus network shows the partition of Antarctica into a small west (AP, SOI) and a wide east (WS, DML, EL, MS, AL, RS) province. In addition, the Weddell Sea appears as central for faunal exchanges between Antarctic and sub-Antarctic bioregions.

DISCUSSION

Dispersal and the role of Antarctic surface currents

The echinoid species network provides a perfect case study to illustrate the good match between faunal connections and the locations of Antarctic surface currents (Fig. 4). While the ACC constitutes an eastward dispersal vector for faunas from southern South America, sub-Antarctic islands and the Scotia Arc region (Pearse *et al.*, 2009), the flow of the Antarctic Coastal Current could have triggered dispersal over the

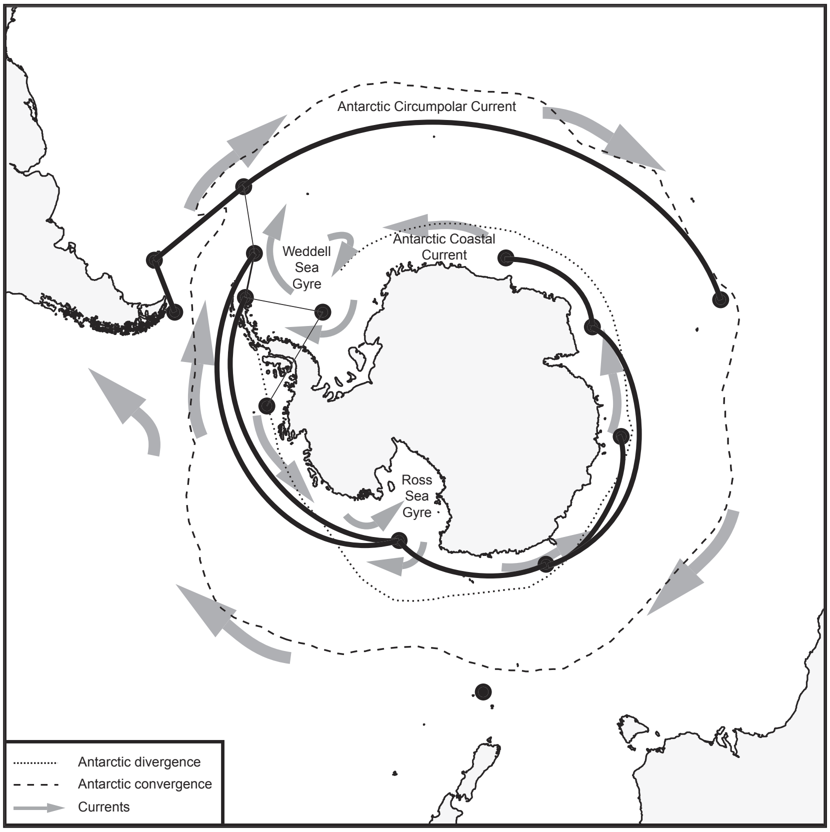

Figure 4 The bootstrapped spanning network based on echinoid species occurrence data compiled from the updated Antarctic Echinoid Database (Pierrat *et al.*, 2012) and fitted to the map of the Southern Ocean, with the positions of the main surface currents (Antarctic Circumpolar and Coastal currents) and approximate positions of the principal frontal zones. Connections depicted with bold lines can be interpreted to result from dispersal through surface currents.

Antarctic shelf and promoted the circum-Antarctic connection between bioregions. This continuous circumpolar distribution has been interpreted as an outcome of prevailing stable oceanographic conditions and the long-term influence of Antarctic surface currents (Barnes & De Grave, 2001; Griffiths *et al.*, 2009; Pearse *et al.*, 2009). However, in all bivalve and echinoid networks, an apparent discontinuity to circum-Antarctic dispersal is present between the Weddell Sea and Dronning Maud Land, which were never connected to each other. The absence of a connection between the Weddell Sea and East Antarctic bioregions could be explained by the action of the Weddell Sea gyre that might constitute a physical barrier to faunal dispersal (Fig. 5). The importance of the Weddell Sea gyre as an apparent barrier to gene flow was previously highlighted by Linse *et al.* (2006), while other studies emphasize the similarity of benthic assemblages in the two bioregions (e.g. Gutt & Koltun, 1995).

The historical legacy of Cenozoic trans-Antarctic seaways

Depending on the taxonomic group and level of biogeographical analyses performed, the Amundsen and Bellingshausen seas show faunal affinities with either the Weddell Sea (echinoids), Enderby Land and the Antarctic Peninsula (bivalves) or the Mawson Sea (gastropods). The Amundsen and Bellingshausen seas were little investigated until recently (Saiz *et al.*, 2008; Moya *et al.*, 2012), and more sampling efforts are needed before robust biogeographical hypotheses can be proposed (Linse *et al.*, 2006; Clarke *et al.*, 2007; Griffiths *et al.*, 2009). This could account for the weak and contrasting connections present in bivalve and gastropod networks. The relative remoteness of these two seas from other Antarctic bioregions still needs to be confirmed (Griffiths *et al.*, 2009).

Echinoid data show robust affinities between the Amundsen and Bellingshausen seas and the Weddell Sea, although the two bioregions are now separated by a continuous ice sheet and exhibit contrasting environmental conditions. This recurrent trans-Antarctic relationship at both the species and the genus level cannot be interpreted except by a long-term but recently disrupted faunal connection between the two sides of the Antarctic Peninsula. When superimposing the echinoid species BSN onto the Pleistocene palaeogeographical map of Antarctica (Fig. 5), it would appear that faunal connections between the Weddell Sea and the Amundsen and Bellingshausen seas could be explained by a trans-Antarctic seaway and currents that existed between the two areas at that time (Pollard & DeConto, 2009). Still more distant faunal affinities between now remote bioregions of the Antarctic shelf have previously been reported for molluscs between the Ross Sea and the Weddell Sea (Linse *et al.*, 2006; Barnes & Hillenbrand, 2010). As similar environmental conditions prevail in these two bioregions, similar benthic assemblages might logically have become established as a result of circum-Antarctic dispersal (Starmans *et al.*, 1999). However,

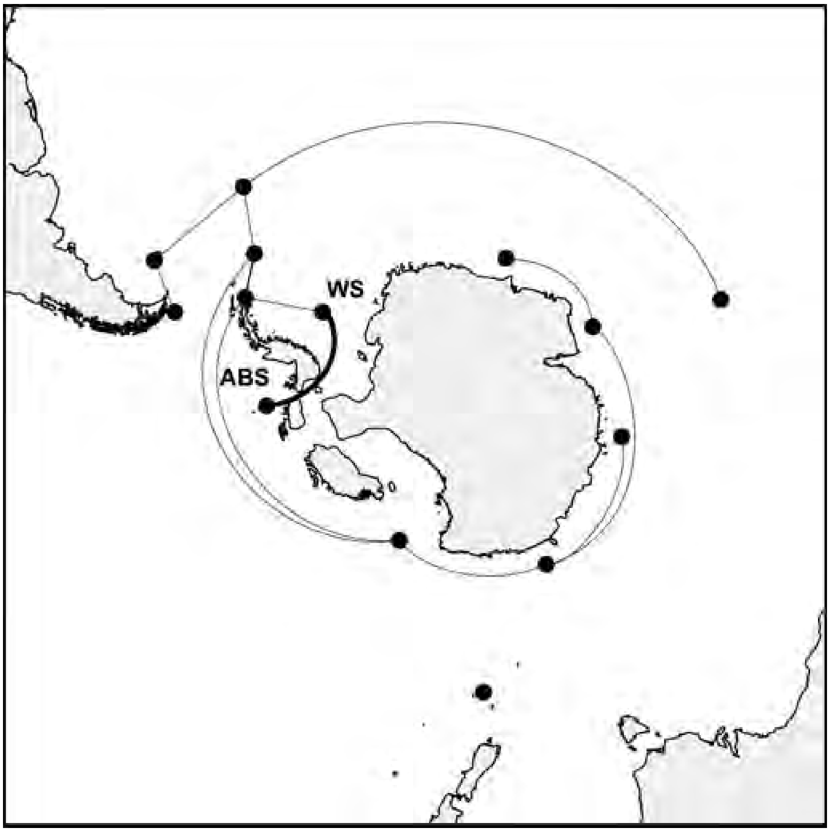

Figure 5 The bootstrapped spanning network for echinoid species fitted to the Antarctic palaeogeographical map of the Pleistocene showing potential faunal connections (bold line) between the Weddell Sea (WS) and Amundsen and Bellingshausen seas (ABS) that probably occurred through trans-Antarctic seaways when the West Antarctic Ice Sheet collapsed (modified from Pollard & DeConto, 2009).

the recurrence of faunal similarities within different taxonomic groups and at different taxonomic levels has also been explained by the existence of a trans-Antarctic seaway that connected the two bioregions and separated East Antarctica from continental fragments of West Antarctica from the Eocene to the mid-Miocene (Linse *et al.*, 2006). The Weddell –Ross connection is here also supported in gastropod and bivalve networks (Fig. 3d–f). Although the existence of a past trans-Antarctic seaway is suggested by trans-Antarctic connections in all the BSNs, the link between the Weddell Sea and the Amundsen and Bellingshausen seas during the Pleistocene is shown only by the echinoid data. Mollusc occurrence data recently collected in the Amundsen and Bellingshausen seas (K. Linse, British Antarctic Survey, Cambridge, pers. comm.) might confirm this trans-Antarctic recent connection.

Faunal provinces of the Southern Ocean

Despite biogeographical discrepancies between taxa and taxonomic levels, the distribution and robustness of faunal connections among the 14 bioregions highlight the existence of recurrent biogeographical patterns. Depending on the taxonomic group considered, results suggest that the Southern Ocean can be split two different ways: into three faunal provinces when based on echinoid and bivalve biogeography, namely New Zealand, southern South America plus sub-Antarctic islands, and Antarctica; or into five provinces when based on gastropod biogeography, namely New Zealand, southern South America, east sub-Antarctic islands, West Antarctica, and East Antarctica.

All biogeographical patterns show a connection between the southern islands of New Zealand and the Ross Sea, but this link is never robustly supported. In the literature, faunal affinities between the two bioregions have been reported only for cheilostomate bryozoans (Griffiths *et al.*, 2009). New Zealand faunas seem to be largely isolated from sub-Antarctic and Antarctic bioregions. This suggests that: (1) there is no dispersal from sub-Antarctic islands towards New Zealand southern islands, although the ACC flows south of the Campbell Plateau; and (2) the Antarctic Polar Front may constitute an efficient biogeographical barrier to faunal exchanges between the southern islands of New Zealand and the Ross Sea (Bargelloni *et al.*, 2000).

Regarding bivalve and echinoid biogeographical patterns, bioregions of southern South America and the sub-Antarctic islands tend to form a single entity, at both the genus and the species level (Fig. 3). Although the details and robustness of connections differ, most connections are similar between taxonomic levels in the two taxonomic groups. Faunal affinities between sub-Antarctic and South American bioregions have previously been reported in various taxonomic groups (Barnes & De Grave, 2001; Montiel, 2005; Linse *et al.*, 2006; Rodriguez *et al.*, 2007; Griffiths *et al.*, 2009) and interpreted to result from larval dispersal through the ACC. This hypothesis is also supported by molecular analyses (González-Wevar *et al.*, 2010; Díaz *et al.*, 2011). This might imply that these faunas have planktonic larvae or that long-distance and passive rafting in the ACC of strictly benthic species without planktonic larvae can occur (Pearse *et al.*, 2009; Leese *et al.*, 2010).

Echinoid and bivalve networks show the grouping of Antarctic bioregions into a single circum-Antarctic province, although with a discontinuity between the Weddell Sea and east Antarctic bioregions. In contrast to former biogeographical schemes (Ekman, 1953; Hedgpeth, 1969), the grouping of Antarctic bioregions into a single province agrees with most recent studies (Barnes & De Grave, 2001; Rodriguez *et al.*, 2007; Griffiths *et al.*, 2009, 2011). However, gastropod networks show a grouping of bioregions into a small West Antarctic and a wide East Antarctic province, with the two provinces connecting or overlapping in the Weddell Sea. This biogeographical pattern fits well with the results of Griffiths *et al.* (2009).

Comparative biogeography across taxa and taxonomic levels

Pairwise comparisons between networks show that the most similar networks are echinoid and bivalve species networks on the one hand, and gastropod species and genus networks on the other (Table 2). In the Southern Ocean, gastropods are represented by many species (e.g. eight times as many species as echinoids) that show different ecological requirements and potentially complex biogeographical patterns, but the relative similarity between gastropod species and genus networks implies that common factors might have been constant enough through time to result in common biogeographical patterns. Unlike gastropod networks, bivalve and echinoid species networks are more similar to each other than species and genus networks within each taxon. Echinoid and bivalve species may in part share either a common history or common ecological traits, or both, with regard to the oceanographic and climatic evolution of the Southern Ocean. In contrast, and regardless of potential biases of systematics, the relative discrepancy evident between species and genus networks within those two taxa invites consideration of oceanographic and climatic changes that might have constrained bivalve and echinoid geographical evolution.

Differences between gastropod and bivalve biogeographical patterns have been highlighted in previous studies (Linse *et al.*, 2006; Griffiths *et al.*, 2009). Gastropod species and genera of east sub-Antarctic islands show affinities with those of the Antarctic continental shelf. Considering the proximity between east sub-Antarctic islands and the Antarctic continent, gastropods were considered to have potentially colonized the Kerguelen Plateau from the Antarctic shelf, or vice versa (Frey *et al.*, 2000; Griffiths *et al.*, 2009). In contrast, the discovery of biogeographical similarities between bivalves and echinoids is new. In both taxa, faunal similarities between east sub-Antarctic islands and west sub-Antarctic and South American islands (South Georgia and the Falkland Islands) can be interpreted as the result of a common history and similar ecological traits. The hypothesis of range expansion by dispersal of propagules through the ACC fulfils historical, oceanographic and ecological criteria. As the ACC flows in an eastward direction, faunas would be conveyed towards downstream locations, from southern South America towards sub-Antarctic islands. However, dispersal through the ACC may have varied in intensity through time, or is not ancient enough to have shaped genus and species biogeography in the same way. Although still uncertain, the opening date of the Drake Passage is considered to fall in the late Eocene or early Oligocene (*c.* 34 Ma), while full establishment of the ACC is dated to the middle Miocene (*c.* 15 Ma; Lawver & Gahagan, 2003; Crame, 2004). Faunal connections between South America and east sub-Antarctic islands may not have occurred until that time, while most extant echinoid genera were established in Antarctica as early as the late Eocene and early Miocene (Hotchkiss & Fell, 1972; Hotchkiss, 1982; Pearse *et al.*, 2009).

CONCLUSIONS

Large-scale biogeographical studies have already proved to be useful when based on different taxonomic groups and levels (Linse *et al.*, 2006; Griffiths *et al.*, 2009). In this work, the comparative analysis of mollusc and echinoid distributions performed at species and genus levels clarifies the large-scale biogeographical entities previously identified (Linse *et al.*, 2006; Barnes & Griffiths, 2008; Griffiths *et al.*, 2009). The differences previously reported between bivalve and gastropod biogeographical patterns are supported (Linse *et al.*, 2006; Griffiths *et al.*, 2009), and the new results obtained for echinoids show how phylogenetically distant clades such as the Echinoidea and Bivalvia can show similar biogeographical patterns. The significant advantage of the BSN procedure lies in the possibility of identifying both biogeographical groupings and transitional areas; that is, both strong connections and groupings among bioregions. This is particularly relevant for the connection between South America and Antarctica through sub-Antarctic islands. The method also proved efficient for identifying potential faunal exchange pathways and dispersal routes, both past and present, by the fitting of networks to oceanographic and palaeogeographical maps. Therefore, the hypotheses of past marine seaways that would have connected both the Amundsen–Bellingshausen area to the Weddell Sea and the Weddell Sea to the Ross Sea are supported (Linse *et al.*, 2006; Barnes & Hillenbrand, 2010).

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BIOSKETCH

Benjamin Pierrat is a marine ecologist with broad interests in macroecology and biogeography. His PhD thesis, supervised by Bruno David and Thomas Saucède focused on the impact of climate change on the distribution of Antarctic echinoids using different biogeographical and ecological approaches (analysis of faunal similarities and ecological niche modelling procedures).

Author contributions: T.S. and B.D. conceived the ideas; B.P., T.S. and B.D. collected the data; B.P and A.B. analysed the data; and B.P. and T.S. led the writing.

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A REVISION OF THE RARE GENUS *CYCLOLAMPAS* (ECHINOIDEA) USING MORPHOMETRICS WITH DESCRIPTION OF A NEW SPECIES FROM THE UPPER CALLOVIAN OF BURGUNDY (FRANCE)

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ABSTRACT—The discovery of a new species, *Cyclolampas altus* new species in the upper Callovian of Burgundy (France) leads to the systematic revision of the rare echinoid genus *Cyclolampas* Pomel, 1883. Two morphometric approaches are used jointly to describe and quantify variations in test shape: the analysis of linear measurements and the Elliptic Fourier shape analysis. Both analyses yield congruent results that highlight the amplitude of within-species variations and quantify the part due to allometry. Along with the description of *C. altus*, the systematic position of species formerly assigned to the genera *Pygorhytis* Pomel, 1883 and *Cyclolampas* is amended. Previously attributed to the genus *Pygorhytis*, *Cyclolampas castanea* (Desor, 1858) is reassigned to the genus *Cyclolampas* on the base of new observations. Conversely, the examination of the Bajocian species *Pygorhytis kiliani* (Lambert, 1909) and *Pygorhytis gillieroni* Desor in Desor and de Loriol, 1872, which were previously assigned to *Cyclolampas* now supports their taxonomic reassignment to the genus *Pygorhytis*. Finally, the two species *Cyclolampas verneuili* (Cotteau, 1870) and *Cyclolampas cotteaui* Mintz, 1966 (nomen nudum) are considered junior synonyms of the genus type species *Cyclolampas voltzii* (Agassiz, 1839). The questioned origin date of the genus, estimated either to the Bajocian or to the Oxfordian, is now clearly established to be upper Callovian. These new results fit well with the overall scheme of atelostomate echinoid evolution and migration to deep-sea environments during the Middle and Upper Jurassic.

INTRODUCTION

THE LATE Triassic biotic crisis deeply affected echinoid diversity, which recovered during the Early Jurassic (Sprinkle, 1983; Kier, 1984) but markedly increased later in the Middle Jurassic (Thierry and Néraudeau, 1994). Diversity dynamics of post-Triassic echinoids is closely related to the evolution of irregular echinoids; originating in the Early Jurassic (Jesionek-Szymanska, 1970; Kier, 1974; Smith, 1984; Smith and Anzalone, 2000; Saucède et al., 2007), they gave rise to an initial burst of diversity in the Middle Jurassic as early as the Aalenian (Thierry and Néraudeau, 1994). One third of the species of irregular echinoids recorded in the Middle Jurassic belong to the atelostomates, a subgroup of irregulars that expanded its distribution range to open-water environnements and colonized soft, fine-grained sediments (Thierry, 1984; Barras, 2008) from the shallows to deep shelves as soon as the Bajocian (Thierry, 1984; Thierry et al., 1997). In the Upper Jurassic, the overall diversity of irregular echinoids decreased (Thierry et al., 1997) while many atelostomates migrated and specialized to deep basin environments (Thierry and Néraudeau, 1994; Gaillard et al., 2011), well before the end Cretaceous origination of deep-sea modern faunas (Smith, 2004; Smith and Stockley, 2005). Recent findings have documented such a specialization to deep-sea habitats in the Oxfordian atelostomate *Tithonia oxfordiana* Gaillard, Néraudeau and Thierry, 2011 (Gaillard et al., 2011). Our understanding of the evolution of atelostomates is therefore highly dependent on our knowledge of deep-sea and open-water deposits of the Middle and Late Jurassic (Thierry et al., 1997).

The genus *Cyclolampas* is part of those atelostomate echinoids that migrated into the deep-sea in the Upper Jurassic. Interestingly, it was mostly known by a few specimens from Switzerland and Southeast of France where deep-sea basin deposits of the Upper Jurassic had long been investigated (Desor, 1858; Cotteau, 1874; Mintz, 1966).

While early irregular echinoids still retained the apical plate pattern of regular echinoids, namely with the periproct enclosed within the apical system (Jesionek-Szymanska, 1970; Smith and Anzalone, 2000), one key morphological innovation associated with their subsequent diversification was the achievement of the so-called ‘exocyclic’ pattern, in which the periproct and apical plates, genitals and oculars are completely disjuncted (Kier, 1974; Smith, 1984). The evolutionary trend of the periproct to move away from the apical system has been achieved progressively in the different subgroups of irregulars independently throughout the Jurassic (Jesionek-Szymanska, 1963; Mintz, 1966; Saucède et al., 2007).

It is now assumed that the genus *Cyclolampas* evolved from the genus *Pygorhytis* through the achievement of the exocyclic pattern (Mintz, 1966; Barras, 2007). However, estimations of the origin of the genus are conflicting as either in the Bajocian (Thierry and Néraudeau, 1994) or the Oxfordian (Mintz, 1966). This would make the exocyclic pattern appearance alternatively early or late in the ‘pygorhytine’ evolutionary lineage as compared to the achievement of the process near the end of the Middle Jurassic in other taxa (Thierry, 1974). Therefore, the validity of the conflicting origin dates of the genus is questioned, all the more so as *Cyclolampas* is characterized by a poor fossil record.

Despite a poor fossil record, two species were initially assigned to the genus *Cyclolampas* and recognized by most authors: *Cyclolampas voltzii* (Agassiz, 1839) and *Cyclolampas verneuili* (Cotteau, 1870). The two species were described from badly preserved specimens and were distinguished with little precision on the bases of detailed differences in test shape, namely test height and profile, ambital outline and distance between the periproct and posterior ocular plates (Cotteau, 1870; Mintz, 1966). These vague differences led to some confusion over species identification (Beurlen, 1934; Mintz, 1966), which, along with uncertainties in the stratigraphic position of most specimens contributed to hinder evolutive assumptions (Mintz, 1966). Six supplementary species were referred to as *Cyclolampas*: *Cyclolampas bernensis* (Ooster, 1865), *Cyclolampas assulatus* (Schauroth, 1865), *Cyclolampas gillieroni* (Desor in Desor and de Loriol, 1872), *Cyclolampas suevicus* (Quenstedt, 1875), *Cyclolampas kiliani* (Lambert, 1909), and *Cyclolampas cotteaui* Mintz, 1966 (nomen nudum) but these species were not all recognized by previous authors (Lambert and Thiéry, 1924) or not formally discussed (Mintz, 1966; Thierry and Néraudeau, 1994).

The recent discovery of a new species of *Cyclolampas*, *Cyclolampas altus* n. sp., from the upper Callovian of Burgundy (France) leads to the systematic revision of the genus, including the redescription and taxonomic reassignment of certain species within the genera *Pygorhytis* and *Cycolampas*, and to reconsider its stratigraphic range. The number of specimens collected in the field sheds light on the amplitude of within-species variations that question the systematics of the genus and lead to reconsider the diagnostic characters used to discriminate among *Cyclolampas* species so far. This work presents 1) a systematic revision of the genus *Cyclolampas*, including the description of a new species and new observations of congeneric species, and 2) a quantitative morphological study of *Cyclolampas* species that joins the tools of biometry and those of geometric morphometrics.

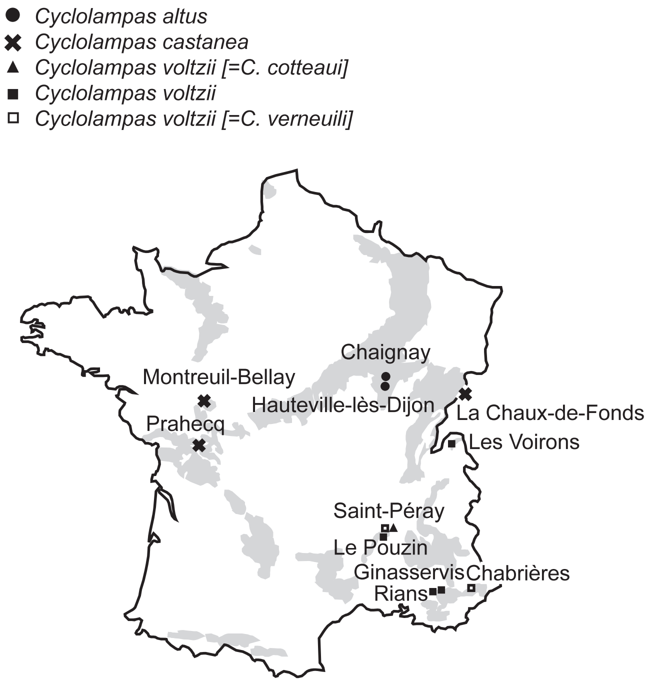


FIGURE *1*—Map of France showing the localities where studied specimens of *Cyclolampas* Pomel, 1883 and specimens from the literature were collected. Shaded gray corresponds to the main areas where the Middle and Upper Jurassic crop out.

MATERIAL AND GEOLOGICAL SETTING

The specimens of *Cyclolampas altus* n. sp. described in this work were collected in the Oolite Ferrugineuse Formation (OFF) at two localities in Burgundy (Côte d'Or, France). Eleven specimens were collected by the authors and Y. Ronnat at Hauteville-lès-Dijon (N 47°22′00″, E 4°59′44″), among which nine were preserved well enough for study; an additional specimen was collected by Prof. P. Neige at Chaignay (N 47°28′39″, E 5°4′16″) (Fig. 1; Table 1). The OFF is composed of a limestone-marl complex, a few decimeter to a few meter thick, characterized by the relative frequence and abundance of ferruginous ooliths (Rémond et al., 1992). Dated from the upper Callovian to the middle Oxfordian, the OFF was deposited under open-water conditions and reduced sedimentation rates and shows many unconformities along with local facies variations (Collin et al., 1999). It is rich in a diversified and abundant pelagic (ammonites, belemnites) and benthic (bivalves, gastropods, brachiopods, echinoids, crinoids) invertebrate macrofauna that gave rise to many biostratigraphical and paleontological studies (Bonnot et al., 1984; Bonnot et al., 1992; Bonnot, 1996; Bonnot and Marchand, 1994; Scoufflaire et al. 1997). At Hauteville-lès-Dijon and Chaignay, the layer where specimens of *C. altus* were collected is composed of a gray ferrugineous limestone, devoid of ooliths, and likely deposited under the storm-wave base as attested by the localized absence of hummocky cross stratifications. The associated ammonite fauna is abundant and clearly dates the layer to the upper Callovian (Quenstedtoceras lamberti zone, Quenstedtoceras lamberti subzone): *Quenstedtoceras lamberti* (Sowerby, 1819), *Peltoceras schroederi* Prieser 1937, *Euaspidoceras subbabeanum* (Sintzov, 1888 sensu Jeannet 1951), *Alligaticeras sp*., *Grossouvria sp*., *Hecticoceras paulowi* (de Tsytovitch, 1911), *Sublunuloceras discoides* (Spath, 1928), *Distichoceras bicostatum* (Stahl, 1824), *Horioceras baugieri* (d'Orbigny, 1847). The rest of the macrofauna is composed of echinoids (*Rhabdocidaris sp*., *Collyrites bicordata* (Leske, 1778), *Stomechinus sp*., *Diplopodia sp*. and *Holectypus sp*.), nautiles (*Pseudaganides sp*.), bivalves (*Ostrea sp*., *Gryphaea sp*., *Flabellomya sp*., *Goniomya sp*., *Entolium sp*., *Chlamys sp*.), gastropods *(Pleurotomaria sp*.), brachiopods (*Thurmanella sp., Moeschia sp., Gallienithyris sp.*) and crinoids (*Millecrinus sp*.).

Four specimens of *Cyclolampas castanea* were collected by P.-Y. Boursicot from fine limestone deposits at Montreuil-Bellay (N 47°08′47″, W 0°08′05″) in Pays de la Loire (Maine-et-Loir, France). Two of them are sufficiently well-preserved to be studied (Table 1). The levels where the specimens were collected also yielded the echinoid species *Tithonia praeconvexa* Jesionek-Szymanska, 1963 and *Collyrites elliptica* (Lamarck, 1816) and were dated to the upper Callovian (Peltoceras athleta zone, Collotia collotiformis subzone, Collotia collotiformis horizon) with the following ammonite fauna: *Peltoceras retrospinatum* Gérard and Contaut, 1936, *Euaspidoceras raynaudi* Bonnot, 1996, *Collotia collotiformis* (Jeannet, 1951), *Collotia fraasi* (Oppel, 1857), *Kosmoceras irwingi* Bonnot and Marchand, 1997, *Subgrossouvria sp*., *Grossouvria evexa* (Quenstedt, 1885), *Sublunuloceras virguloides* Gérard and Contaut, 1936, *Brightia canaliculata* (Quenstedt, 1849), *Paralcidia couffoni* Gérard and Contaut, 1936 and *Distichoceras complanatoides* (Quenstedt, 1887). Eighteen other specimens of *C. castanea* were collected by P. Nicolleau from marl deposits at Prahecq (N 46°15′34″, W 0°20′41″) in Poitou-Charentes (Deux-Sèvres, France). Most of them are affected by diagenetic distortion so that only four of them could be analyzed (Fig. 1; Table 1). In the same levels, the associated echinoid fauna is composed of *Collyrites elliptica* (Lamarck, 1816), *Disaster* (?) *moeschi* Desor, 1858 and *Polydiadema inaequale* (Agassiz, in Agassiz and Desor, 1846). The levels are also rich in ammonites, crinoids, and belemnites and were dated to the Quenstedtoceras lamberti zone, Quenstedtoceras lamberti subzone (upper Callovian) (P. Nicolleau, personal commun., 2001).

The other specimens of *Cyclolampas* examined, *C.voltzii* and *C. castanea,* come from collections of the Muséum national d'Histoire naturelle (MNHN) in Paris (France) and University of

TABLE *1*—Origin of studied specimens: FC, Daniel Fournier private collection, Grenoble, France; MNHN, Muséum national d'Histoire naturelle de Paris; UCMP, University of California, Berkeley, Museum of Paleontology; PYB, Pierre-Yves Boursicot private collection, Villedieu-la-Blouère, France; PN, Philippe Nicolleau private collection, Aiffres, France; UBGD, Université de Bourgogne; GR, Géosciences Rennes.

Species	Studied samples	Number of specimens	Location	Stratigraphic position
Pygorhytis kiliani (Lambert, 1909) (=*Pygomalus kiliani* Lambert, 1909)	FC - V01	1	Villar-d'Arène, Hautes-Alpes, France	upper Bajocian
Cyclolampas voltzii (Agassiz, 1839)	MNHN - L20.054, L20.068	2	Rians, Var, France	upper Oxfordian (Bimammatum Zone)
	MNHN - L20.069	2	Ginasservis, Var, France	upper Oxfordian (Bimammatum Zone)
	MNHN - L20.070	1	Rians/Ginasservis, Var, France	upper Oxfordian (Bimammatum Zone)
	MNHN - L20.067	1	Le Pouzin, Ardèche, France	Oxfordian
Cyclolampas voltzii (Agassiz, 1839) (=*Cyclolampas verneuili* [Cotteau, 1870])	MNHN - L20.063	1	Saint-Péray, Ardèche, France	lower Kimmeridgian (Platynota Zone)
	MNHN - L20.064	1	Chabrières, Hautes Alpes, France	middle Oxfordian (Transversarium Zone)
	MNHN - L20.065	1	Tizroutine (Djebel Zaghouan), Tunisia	upper Oxfordian
	MNHN - L20.066	1	Hadjer Abbès, Morocco	Tithonian
Cyclolampas voltzii (Agassiz, 1839) (=*C. cotteaui* Mintz, 1966)	UCMP - B222/10574	1	Saint-Péray, Ardèche, France	?lower Kimmeridgian (Platynota Zone)*
Cyclolampas castanea (Desor, 1858) (=*Collyrites castanea* Desor, 1858)	MNHN - L20.073	1	Chaux-de-Fonds, Neuchâtel canton, Switzerland	middle-upper Callovian
	PYB - UBGD 277477, MB02	2	Montreuil-Bellay, Maine-et-Loire, France	upper Callovian (Athleta Zone)
	UBGD 277476, PN - Pr1, Pr3, Pr4, Pr5, Pr6	6	Prahecq, Deux-Sèvres, France	upper Callovian (Lamberti Zone)
Cyclolampas altus n. sp.	UB - CO3/32	1	Chaignay, Côte d'Or, France	upper Callovian (Lamberti Zone)
	GR-PC.1710, GR-PC.1711, GR-PC.1712, UBGD 277474, UB - Hv4, Hv6, Hv7, Hv8, Hv9	9	Hauteville-lès-Dijon, Côte d'Or, France	upper Callovian (Lamberti Zone)

* The Callovian age given by Mintz (1966) is dubious (see discussion for more details).

California Museum of Paleontology (UCMP) in Berkeley (USA) (Table 1).

SYSTEMATIC PALEONTOLOGY

Terminology.—The definition of morphological terms used in the systematics section follows the Treatise of Invertebrate Paleontology (Durham and Wagner 1966, p. U251–U256).

Specimen repositories.—Université de Bourgogne (UBGD) in Dijon (France), Géosciences Rennes (GR) in Rennes (France), Muséum national d'Histoire naturelle (MNHN) in Paris (France) and University of California Museum of Paleontology (UCMP) in Berkeley (USA).

Stem group ATELOSTOMATA Zittel, 1879
Family COLLYRITIDAE d'Orbigny, 1853
Genus CYCLOLAMPAS Pomel, 1883

Type species.—Dysaster voltzii Agassiz, 1839 (by subsequent designation of Lambert and Thiéry, 1924), Oxfordian, Montagne des Voirons (Haute-Savoie, France).

Included species.—*Cyclolampas voltzii* (Agassiz, 1839), *Cyclolampas castanea* (Desor, 1858) and *Cyclolampas altus* n. sp.

Diagnosis.—Apical system exocyclic (posterior ocular plates and periproct not in direct contact) and disjuncted, the anterior part located slightly posterior to the test morphological apex, the posterior part located at test posterior margin. Phyllodes with pore pairs organized in three columns per half ambulacrum.

Description.—Apical side regularly convex to subconical, especially in large specimens. Ambital outline subcircular to slightly elongate. Oral side almost flat, a little pulvinate. Interambulacrum 5 faintly swollen and rounded to the posterior margin, bicarinated near the periproct. Apical system disjuncted, the anterior part not located at the test morphological apex but slightly posterior. Several complemental plates connect the two portions of the apical system and usually prevent direct contact between anterior ocular plates II and IV. The posterior part of the apical system is located at test posterior margin, posterior ocular plates and periproct connected by catenal plates, not in direct contact (exocyclic condition). Periproct oval, subambital in position, flush with test. Ambulacra narrow, composed of tiny round pores aborally. Apical extremity of posterior ambulacra distinctly curved backwards. Pores enlarged and increased in number on the oral side. Phyllodes with occluded plates and pore pairs organized in three columns per half ambulacrum, but no widening of ambulacra. Peristome subcircular in shape, central in position to slightly excentric anteriorly. Presence of tiny tubercles evenly distributed all over the test, a little larger and scrobiculate on the oral side.

Occurrence.—Callovian of France, Switzerland, former Soviet Union; Oxfordian of France, Switzerland, Tunisia; Kimmeridgian of France; Tithonian of Morocco, Spain, Italy, Poland.

Remarks.—The absence of direct contact between the periproct and posterior ocular plates is the only diagnostic character that unequivocally distinguishes the genus *Cyclolampas* from *Pygorhytis* (Mortensen, 1950; Mintz, 1966; Barras, 2007). During the evolution of basal irregular echinoids, the periproct and posterior ocular plates progressively broke up and moved apart following a recurrent process that took place within the different irregular lineages throughout the Jurassic (Jesionek-Szymanska, 1959, 1963; Kier, 1974; Smith, 1984; Saucède et al., 2007). Thierry (1974) then Moyne et al. (2007) described this phenomenon across the anagenetic evolution of the chronospecies of the genera and subgenera *Pygomalus, Collyrites* and *Cardiopelta* through the Middle and Upper Jurassic. Despite the gradational nature of the process leading to the exocyclic condition, they considered exocyclism a diagnostic character differentiating the subgenera *Pygomalus* and *Collyrites*. This character is actually unmistakable and proved taxonomically operative in this latter lineage. A similar position is adopted here to differentiate between the two

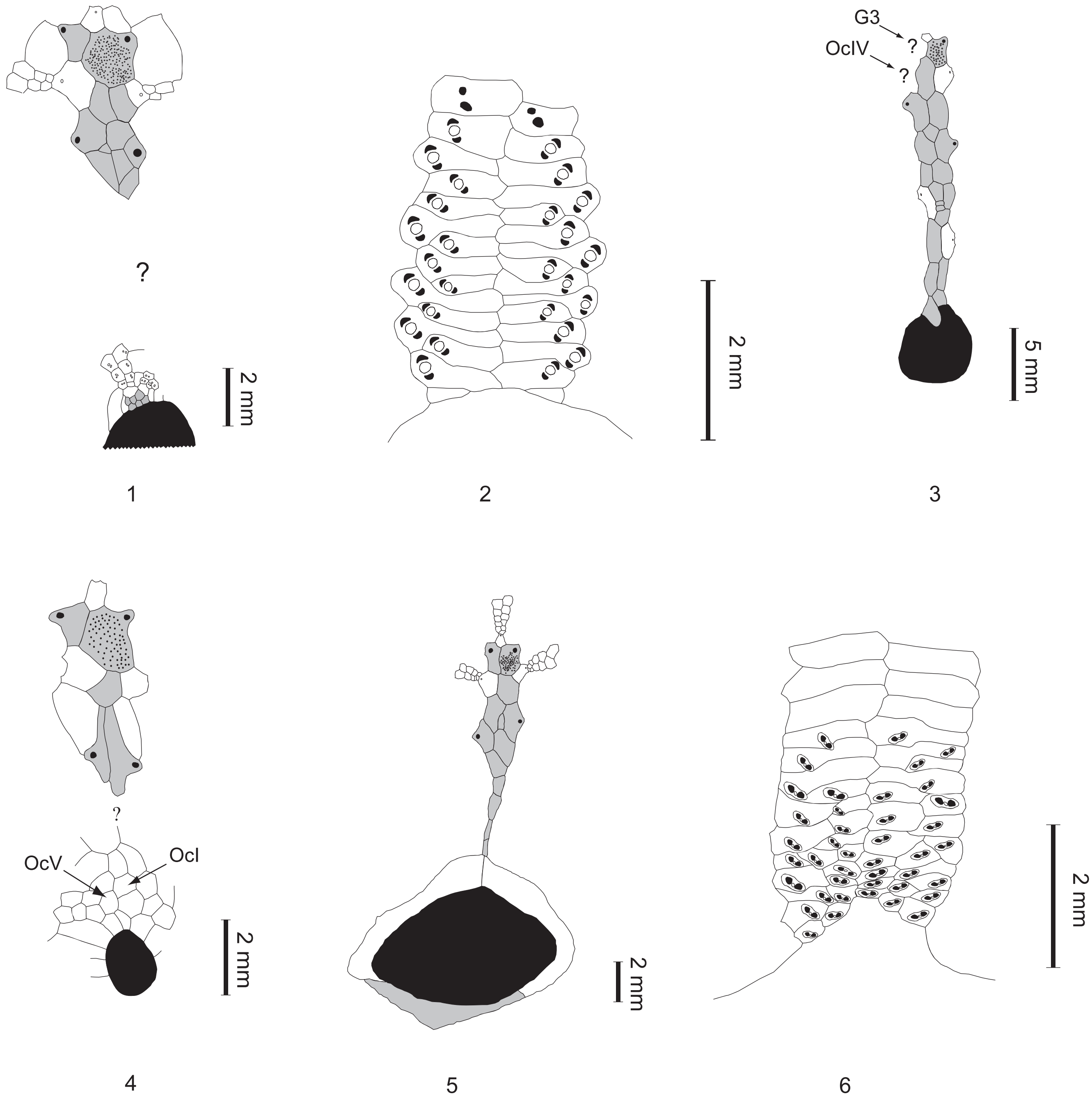


FIGURE 2—Apical and phyllode plate patterns: *1*, apical plates of *C. altus*, GR-PC.1710; *2*, phyllodes of ambulacrum I in *C. altus*, UBGD 277474; *3*, apical plates of *Cyclolampas verneuili* (Cotteau, 1870), after Solovejv 1971, fig. 18v-g; *4*, apical plates of *Cyclolampas castanea* (Desor, 1858), UBGD 277476; *5*, apical plates and periproct of *Pygorhytis kiliani* (Lambert, 1909), FC V01; *6*, phyllodes of ambulacrum IV in *P. kiliani*, FC V01.

genera of the *Pygorhytis*–*Cyclolampas* lineage, thus following on previous authors (Mortensen, 1950; Mintz, 1966; Barras, 2007).

Eight nominal species had been referred to as *Cyclolampas* in the literature (Table 1). In Thierry and Néraudeau (1994), two species from the Bajocian of France and Switzerland were attributed to *Cyclolampas*. The first one is *Pygorhytis gillieroni* Desor in Desor and de Loriol, 1872 from the lower Bajocian (Stephanoceras humphresianum zone) of Bulle (Fribourg, Switzerland). Very little is known about this species. However, Desor's illustrations and description suggest that the periproct contacts posterior oculars and that the species is very close to *Pygorhytis ringens* (Agassiz, 1835), from which it differs by a more rounded shape and a truncate overhanging posterior end, with an inframarginal downward facing periproct. Until new data are available, the direct contact between the periproct and posterior ocular plates supports the assignment of the species to the genus *Pygorhytis*, to which it was initially attributed (Desor and de Loriol, 1872). *Pygorhytis kiliani* (Lambert, 1909) from the upper Bajocian of Villar-d'Arène (Hautes-Alpes, France) was initially assigned to the genus *Pygomalus* (Lambert, 1909). The holotype has been lost, but new specimens were discovered by B. Clavel and D. Fournier (personal commun., 2004) at the type locality. The species was then transferred to the genus *Cyclolampas* in Thierry and Néraudeau (1994), on the base of the newly

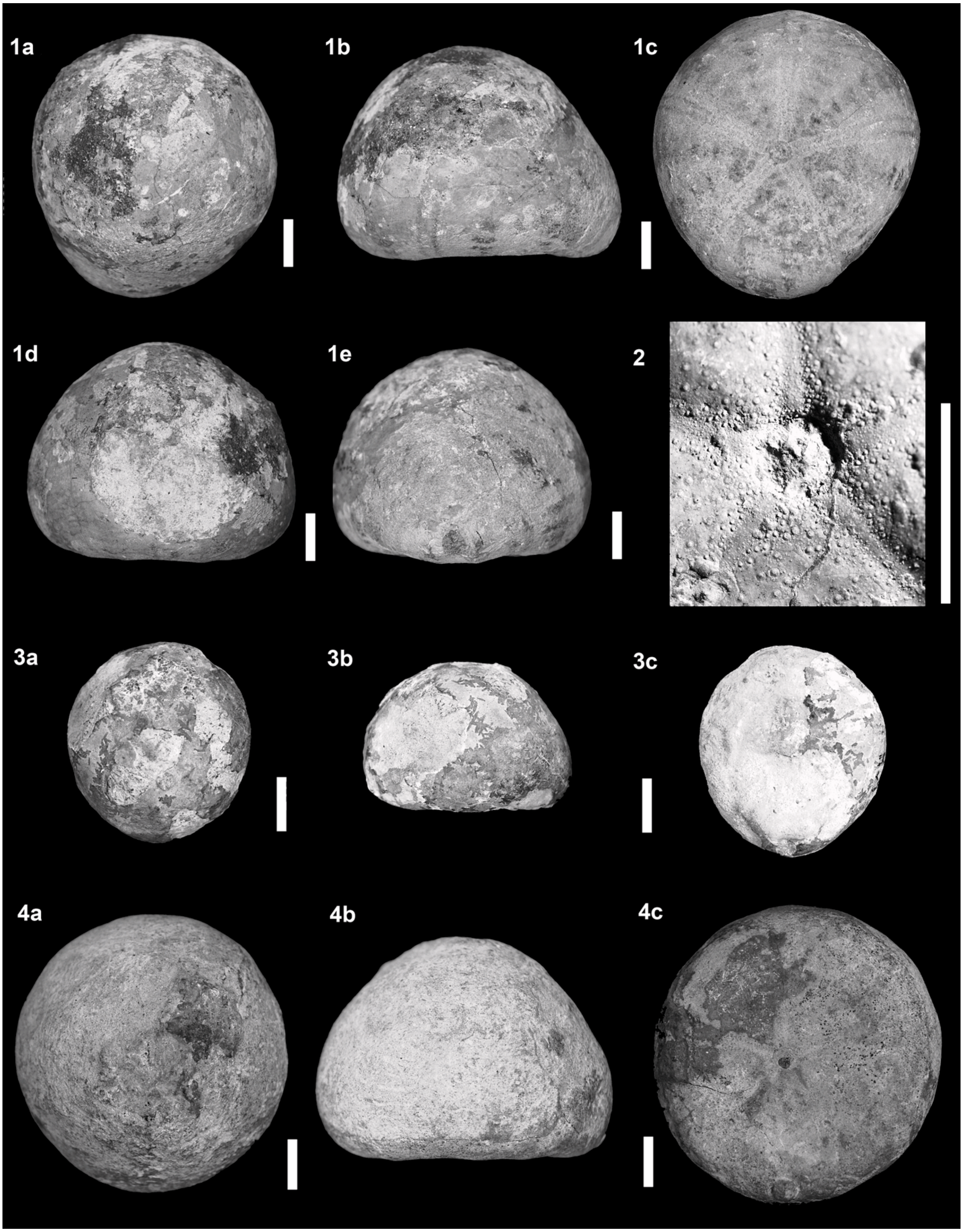
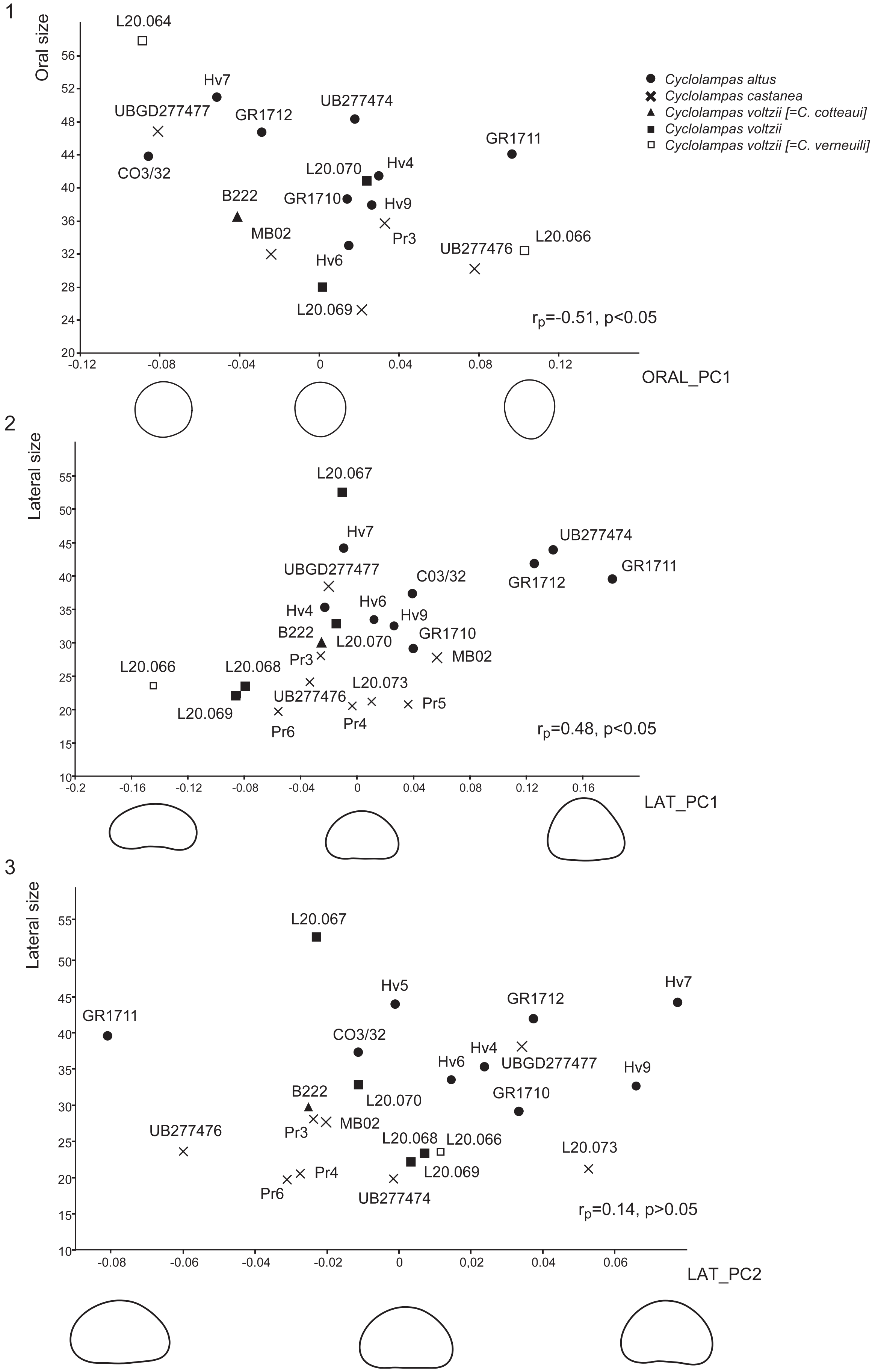


FIGURE *3*—Photographs of specimens of *Cyclolampas altus* n. sp. from the upper Callovian of Hauteville-lès-Dijon (Côte-d'Or, France): *1a–1e*, respectively: apical view, lateral view, oral view, frontal view, posterior view, syntype GR-PC.1711; *2*, peristome detail, syntype UBGD 277474; *3a–3c*, respectively: apical view, lateral view, oral view, syntype GR-PC.1710; *4a–4c*, respectively: apical view, lateral view, oral view, GR-PC.1712. Scale bars=10 mm.


1
Oral size
ORAL_PC1
L20.064
Hv7
UBGD277477
GR1712
UB277474
GR1711
CO3/32
L20.070
Hv4
B222
GR1710
Hv9
Pr3
MB02
UB277476
L20.066
Hv6
L20.069
r_p=-0.51, p<0.05
● Cyclolampas altus
✖ Cyclolampas castanea
▲ Cyclolampas voltzii [=C. cotteaui]
■ Cyclolampas voltzii
□ Cyclolampas voltzii [=C. verneuili]
2
Lateral size
LAT_PC1
L20.067
Hv7
UB277474
UBGD277477
GR1712
GR1711
C03/32
Hv6
Hv4
Hv9
B222
L20.070
GR1710
Pr3
MB02
L20.066
L20.068
L20.073
UB277476
L20.069
Pr5
Pr4
Pr6
r_p=0.48, p<0.05
3
Lateral size
LAT_PC2
L20.067
Hv5
Hv7
GR1712
GR1711
CO3/32
Hv4
Hv6
UBGD277477
Hv9
B222
L20.070
GR1710
Pr3
MB02
UB277476
L20.068
L20.066
L20.073
Pr4
L20.069
Pr6
UB277474
r_p=0.14, p>0.05

discovered specimens but neither an illustration or description was provided to support this result. One of the newly collected specimens could be examined for the present work. Our observations don't agree with the assignment of the specimen to *Cyclolampas*. Though extremely distorted, the specimen clearly shows an endocyclic apical pattern, the periproct being in direct contact with posterior ocular plates and surrounded by these latter (Fig. 2.5). Pore pairs of phyllodes are arranged into triads in each half ambulacrum (Fig. 2.6) as already mentionned in Lambert's description of the type material (Lambert, 1909). The joined occurrence of these two characters suggest that the species should be assigned to the genus *Pygorhytis*, as already suggested by Mintz (1966), but more well-preserved material is needed to check for potential synonymy with other species of the genus. *Collyrites bernensis* Ooster, 1865 had been attributed to the genus *Cyclolampas* by Lambert and Thiéry (1924). Ooster's illustration indeed suggests that the species could be attributed to the genus *Cyclolampas* but new material is needed to support this view. *Clypeus suevicus* Quenstedt, 1875 had been referred to as *Cyclolampas* by Lambert and Thiéry (1924) but the species is poorly illustrated and it is difficult to confirm the assignement of the species to *Cyclolampas* so far (Mintz, 1966). Finally, *Galerites assulatus* Schauroth, 1865 has been synonymized with *C. verneuili* (Quesntedt, 1875; Mintz, 1966) but we could not confirm the synonymy.

All three species herein included in the genus *Cyclolampas*, namely *C. voltzii*, *C. castanea*, and *C. altus* show important within-species variations in test shape, mostly in test height and test ambital outline as well as in the distance between posterior ocular plates and the periproct. Our results show that these characters are partly size-dependent and that the ambital outline along with the distance that separates posterior oculars and the periproct are not valid characters to discriminate among species. The three *Cyclolampas* species are identified below using a differential diagnosis based on two diagnostic characters: the relative test height and profile.

CYCLOLAMPAS ALTUS new species
Figures 2.1, 2.2, 3

Diagnosis.—Test extremely inflated in height, conical in shape. Test height about 70% of test length on average. Maximum height positionned at about the middle of test length.

Description.—Mean test length 50.1 mm, varying from 39.3 to 58.7 mm, mean test width 46.3 mm (93% of test length), varying from 35.1 to 56.2 mm and mean test height 34.5 mm (70% of test length), varying from 26.8 to 41.3 mm. Ambital outline subcircular (Fig. 3.4a, 3.4c) to ovate (Fig. 3.3a, 3.3c), or slightly elongate posteriorly (Fig. 3.1a, 3.1c). In lateral view, apical side domed (Fig. 3.1b, 3.3b) or subconical (Fig. 3.4b) with a low ambitus (at the lowest third of test height); oral side flat, a little pulvinate.

Apical system disjuncted, the anterior part not located at the test morphological apex but a little posteriorly, the posterior part of apical system at test posterior margin (Fig. 2.1). There are four perforated genital plates, gonopores not flush with genital plates but opening on top of a little cone at short distance above plate surface. Complemental plates present between bivium and trivium, within which they prevent direct contact between the anterior oculars II and IV and between the genitals 1 and 4. Apical system exocyclic, periproct and posterior ocular plates connected by catenal plates.

Periproct subambital in position, flush with test. Peristome central to slightly anterior. Ambulacra narrow aborally, non petaloid with tiny round pores. Apical extremity of posterior ambulacra distinctly curved backwards. Ambulacral pores enlarged on the oral side, increasing in size and number near the peristome to form phyllodes with no widening of ambulacra. Phyllodes a little depressed, containing occluded plates and enlarged pores that are arranged in three columns per half ambulacrum (Fig. 3.2). Pores crescent-shaped, pores of a pair not conjugate but separated by a node (Fig. 2.2). Adoral end of ambulacra and peristome a little sunken. Plastron protosternous. Interambulacrum 5 swollen near the posterior margin, forming a faint keel that is sulcate near the periproct.

Etymology.—From the Latin *altus*, meaning high, referring to the relative high test of the species.

Syntypes.—Specimens GR-PC.1710, GR-PC.1711, UBGD 277474 housed in the paleontological collections of GR (GR-PC.1710, GR-PC.1711) and UBGD (UBGD 277474), Middle Jurassic, upper Callovian (Quenstedtoceras lamberti Zone), Oolite ferrugineuse Formation, Hauteville-lès-Dijon (N 47°22′00″, E 4°59′44″) in Burgundy (Côte d'Or, France). Three syntypes were designated as representative of the characteristic, important shape variation between specimens of *C. altus*.

Occurrence.—Upper Callovian (Quenstedtoceras lamberti zone) at Hauteville-lès-Dijon (N 47°22′00″, E 4°59′44″) and Chaignay (N 47°28′39″, E 5°4′16″) in Burgundy (Côte d'Or, France).

Remarks.—The notable test height and shape of *C. altus* clearly distinguishes the species from other congeneric species. Specimens of *C. altus* differ markedly between each other, however, in test relative height and shape with the ambital outline varying from acuminate to circular (Fig. 3.1–3.4). These morphological variations were partly correlated to size (see the morphological analysis section below), the largest specimens tending to be the highest and most circular in outline, whereas small specimens tend to be the lowest and most acuminate (Fig. 4.1, 4.2). Shape differences between specimens of *C. altus* are thus interpreted as within-species variations that were likely caused by growth allometry in part. More material and sampling sites are needed for these variations to be fully understood. It is noteworthy that similar within-species variations were observed in other congeneric species (see the morphological analysis section below).

CYCLOLAMPAS VOLTZII (Agassiz, 1839)
Figures 2.3, 5.1–5.3

1839 *Dysaster voltzii* AGASSIZ, p. 8, pl. 4, figs. 11–13.
1842 *Dysaster voltzii* (Agassiz); DESOR, p. 25, pl. 1, figs. 18–21.
1847 *Dysaster voltzii* (Agassiz); AGASSIZ and DESOR, p. 139.
1858 *Collyrites voltzii* (Agassiz); DESOR, p. 207.
1859 *Collyrites voltzii* (Agassiz); WRIGHT, p. 326.
1865 *Collyrites voltzii* (Agassiz); OOSTER, p. 54.
1867 *Collyrites voltzii* (Agassiz); COTTEAU, p. 89, pl. 20.
1870 *Collyrites verneuili* COTTEAU, p. 272, pl. 39, figs. 7, 8.
1872 *Collyrites voltzii* (Agassiz); DESOR and DE LORIOL, p. 376, pl. 59, fig. 12.
1874 *Collyrites verneuili* (Cotteau); COTTEAU, p. 511, pl. 139, figs. 9, 10.
1875 *Disaster voltzii* (Agassiz); QUENSTEDT, p. 575, pl. 84, fig. 23.
1883 *Cyclolampas verneuili* (Cotteau); POMEL, p. 51.

FIGURE 4—Linear regression between size and component score values: *1*, size versus PC1 scores of the oral shape analysis, $r_{\text{Pearson}} = -0.51$, $p < 0.05$; *2*, size versus PC1 scores of the lateral shape analysis, $r_{\text{Pearson}} = 0.48$, $p < 0.05$; *3*, size versus PC2 scores of the lateral shape analysis, $r_{\text{Pearson}} = 0.14$, $p > 0.05$.

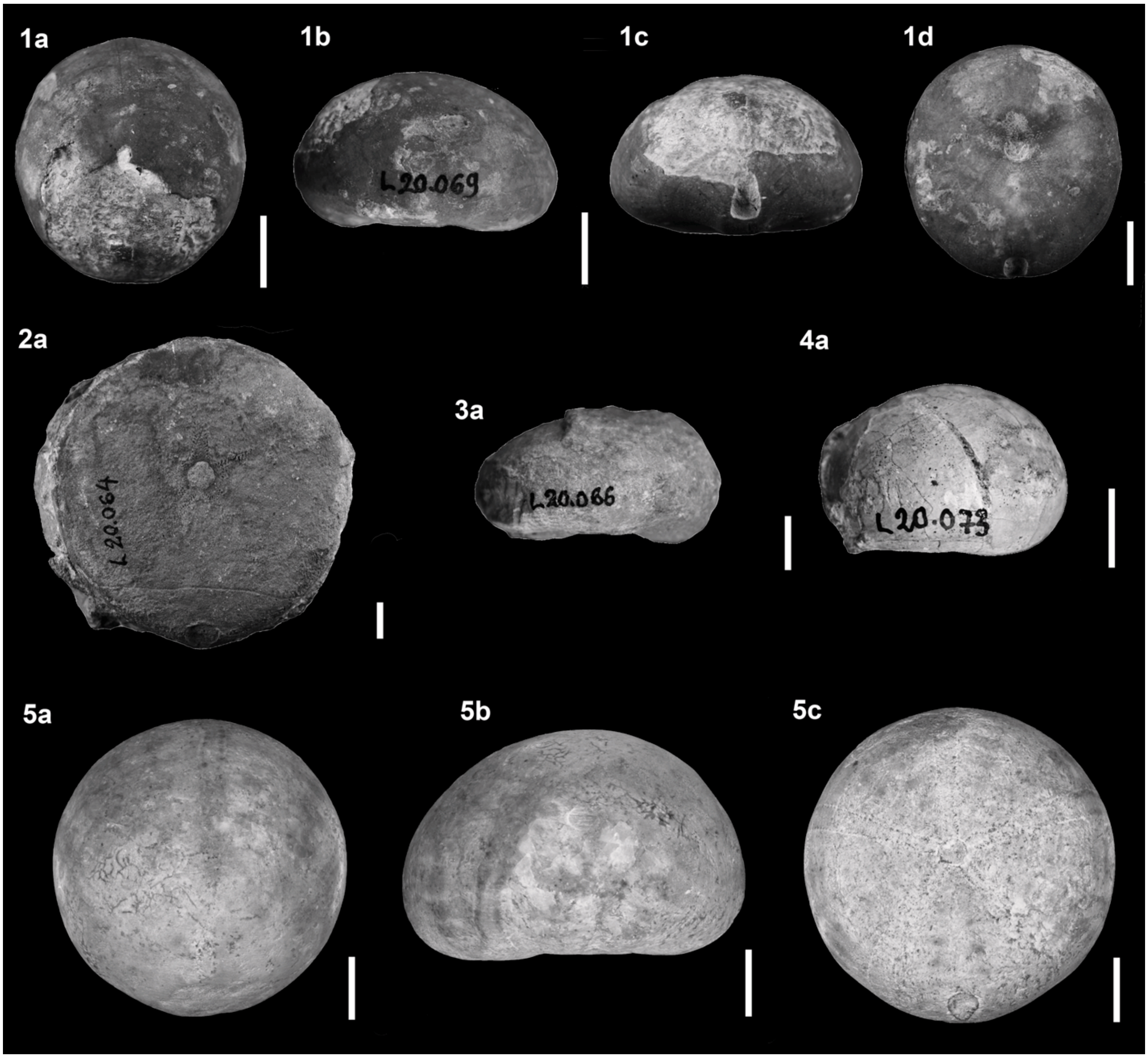


FIGURE 5—Photographs of specimens of *Cyclolampas voltzii*: *1a–1d*, respectively: apical view, lateral view, posterior view, oral view, MNHN L20.069; *2a*, oral view, MNHN L20.064; *3a*, lateral view, MNHN L20.066; *4a*, *Cyclolampas castana*, lateral view, MNHN L20.073; *5a–5c,* respectively: apical view, lateral view, oral view, UBGD 277477. Scale bars=10 mm.

1896 *Cyclolampas voltzi* (Agassiz); GAUTHIER, p. 19.

1924 *Collyrites (Cyclolampas) voltzi* (Agassiz); LAMBERT and THIERY, p. 391.

1924 *Collyrites (Cyclolampas) verneuili* (Cotteau); LAMBERT and THIERY, p. 39.

1929 *Collyrites (Cyclolampas) voltzii* (Agassiz); DEECKE, p. 502.

1929 *Collyrites (Cyclolampas) verneuili* (Cotteau); DEECKE, p. 502.

1933 *Cyclolampas verneuili* (Cotteau); LAMBERT, p. 59.

1934 *Cyclolampas voltzi* (Agassiz); BEURLEN, p. 59, figs. 6a, 6b.

1934 *Cyclolampas verneuili* (Cotteau); BEURLEN, p. 61, fig. 6c.

1950 *Cyclolampas voltzii* (Agassiz); MORTENSEN, p. 17, figs. 16, 17.

1950 *Cyclolampas verneuili* (Cotteau); MORTENSEN, p. 18.

1966 *Cyclolampas verneuili* (Cotteau); MINTZ, 1966, p. 81, pls. 1, 2.

1966 *Cyclolampas voltzii* (Agassiz); WAGNER and DURHAM, p. 526, fig. 414.

1966 *Cyclolampas voltzii* (Agassiz); MINTZ, p. 81.

1966 *Cyclolampas cotteaui* MINTZ, p. 83, pls. 1, 4, figs. 10, 11 (nonem nudum).

1971 *Cyclolampas verneuili* (Cotteau); SOLOVJEV, p. 49, fig. 18.

1971 *Cyclolampas voltzii* (Agassiz); SOLOVJEV, p. 48, fig. 18.

Diagnosis.—Test moderately high, though variable, test height

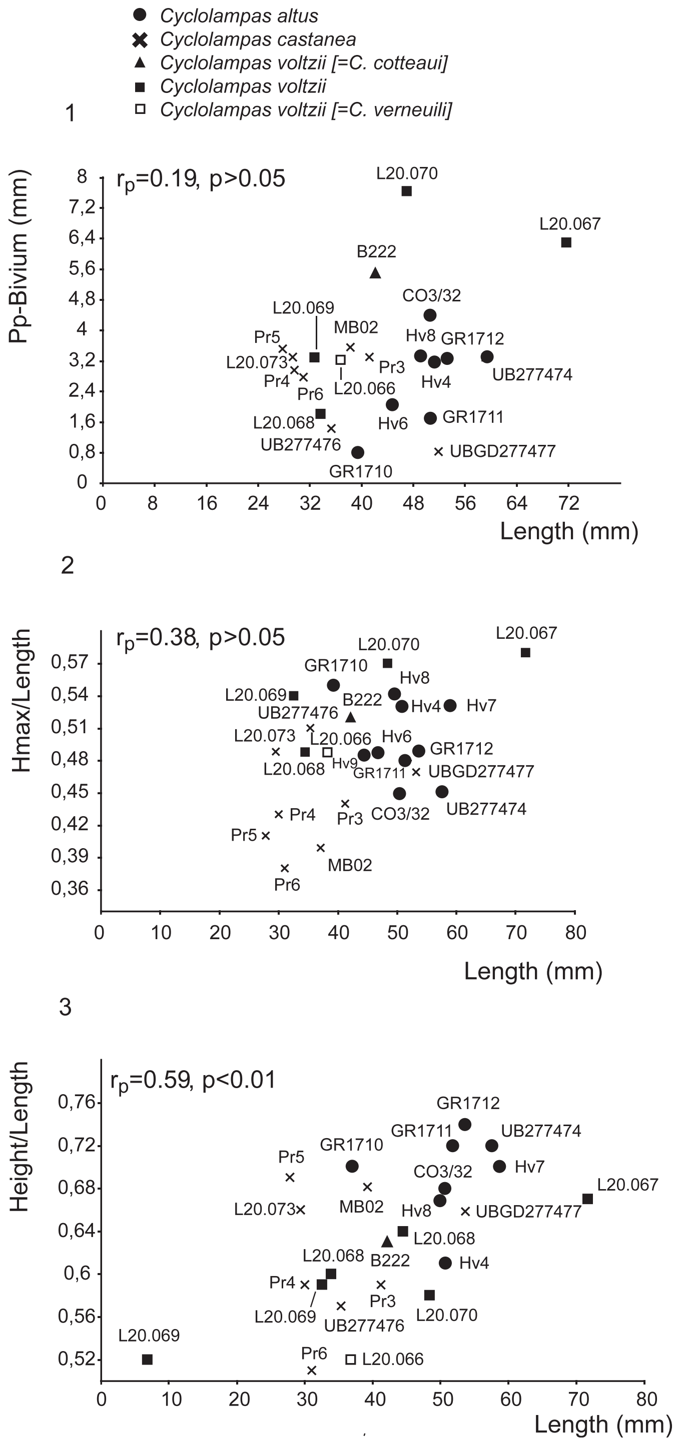


FIGURE 6—Linear measurements taken on echinoid tests: *1–3*, linear regression with length as independent variable and distance periproct-bivium, $r_{\text{Pearson}} = 0.19$, $p > 0.05$, maximum height relative position, $r_{\text{Pearson}} = 0.38$, $p > 0.05$, and relative height, $r_{\text{Pearson}} = 0.59$, $p < 0.01$ as dependent variables, respectively.

about 60% of test length on average. Apex excentric posteriorly, maximum height positionned at about 55% of test length.

Material.—See Table 1 for material examined.

Occurrence.—Montagne des Voirons (Haute-Savoie, France), Oxfordian.

Remarks.—*Cyclolampas verneuili* and *C. cotteaui* are here considered two subjective junior synonyms of *C. voltzii*. Each of these two synonymous species had been established and described after the observation of one single, badly preserved and incomplete specimen (Cotteau, 1870; Mintz, 1966). Each specimen had been considered to differ from *C. voltzii* by subtle differences in test shape. Compared to the first descriptions of *C. voltzii* (Agassiz, 1839; Desor, 1842), Cotteau's (1870) specimen would distinguish by a more acuminate outline, higher test profile, less backwards curved posterior ambulacra and a greater distance between posterior ocular plates and periproct. Mintz (1966) recognized three *Cyclolampas* species. The first one corresponds to *C. voltzii* as illustrated in Agassiz (1839),

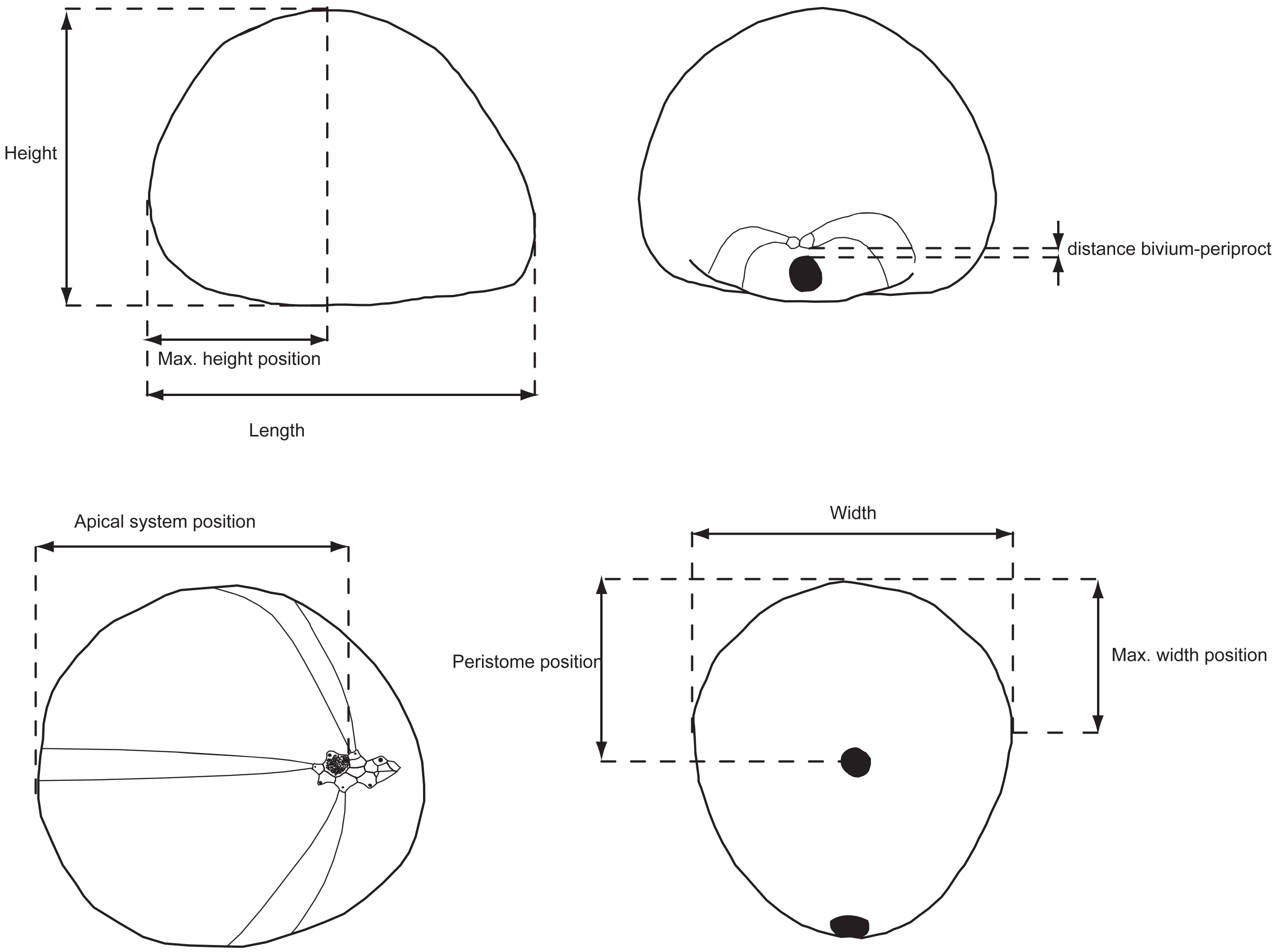


FIGURE 7—Linear measurements taken on the test for the biometric analysis.

characterized by a circular, non acuminate ambital outline, a low test profile and a short distance between the periproct and posterior oculars. The second corresponds to *C. verneuili* as illustrated in Cotteau (1870), characterized by an acuminate test, higher, sub-conical test profile and a greater distance between the periproct and the bivium. Finally, he established a third species, *C. cotteaui* for a specimen (UCMP B-222) that combines characters of the two former species, namely a high test profile and an acuminate ambital outline as in *C. verneuili*; a short distance between the periproct and posterior oculars as in *C. voltzii*. Here we consider that specimens previously identified as *C. verneuili* and *C. cotteaui* fall inside the variation range of *C. voltzii*, in which characters such as test height, ambital profile and distance between posterior oculars and the periproct vary among specimens (see the morphological analysis section below). Moreover, *C. cotteaui* was established by Mintz (1966) and only discussed in his unpublished Ph.D. thesis so that it should be considered a nomen nudum and not a valid species name following Article 13 of the International Commission of Zoological Nomenclature (1999). The fact that specimens assigned to *C. cotteaui* combine the respective diagnostic characters initially attributed to either *C. verneuili* or *C. voltzii* show that some characters may vary independently. Variations in test height and ambital outline (acuminate to circular) were actually correlated to size, the largest specimens being the highest and most circular in outline, whereas small specimens tend to be the lowest and the most acuminate (Figs. 4.1, 4.2, 6.3). Conversely, variation of distance between periproct and posterior oculars doesn't seem to vary with size (Fig. 6.1). These results show that ambital shape and distance between periproct and posterior oculars should no longer be considered as diagnostic characters to differentiate among *Cyclolampas* species.

Mintz (1966) designated Cotteau's drawing (1874) of a specimen of *C. voltzii* from the upper Oxfordian of Rians (Var, France) as the holotype for his species and made a hypotype from the specimen he observed (UCMP B-222). He attributed the latter to the Callovian from Saint-Péray (Crussol) in Ardèche (France) but gave no more information as to the origin of the specimen. The upper Callovian substage being unkown at Saint-Péray, Mintz's specimen would belong to the lower or middle Callovian. Considering that there is no other specimen of *Cyclolampas* known until the upper Callovian in either Europe or North Africa, considering the age of the holotype of *C. cotteaui* (upper Oxfordian) and considering the age of other specimens of *Cyclolampas* collected at Saint-Péray (lower Kimmeridgian), including Cotteau's specimen of *C. verneuili* (Cotteau, 1870), the presumed low stratigraphic position of Mintz's specimen seemed very unlikely to us. It is much more probable that specimen UCMP B-222 dates from the lower Kimmeridgian (Table 1). The presumed low stratigraphic position of Mintz's specimen of *C. cotteaui* certainly matched his view, as he regarded *C. cotteaui* as more "primitive" than *C. voltzii* and *C. verneuili*.

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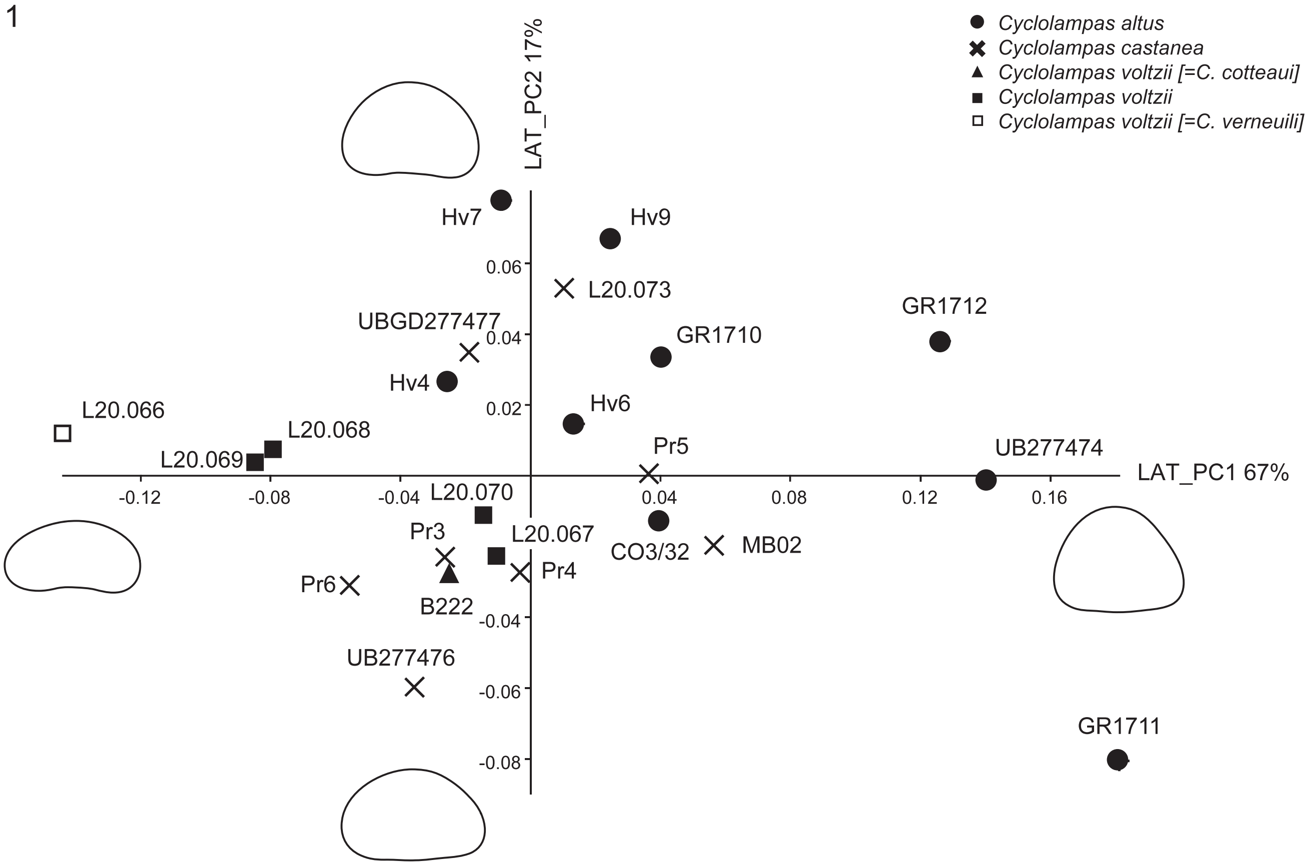

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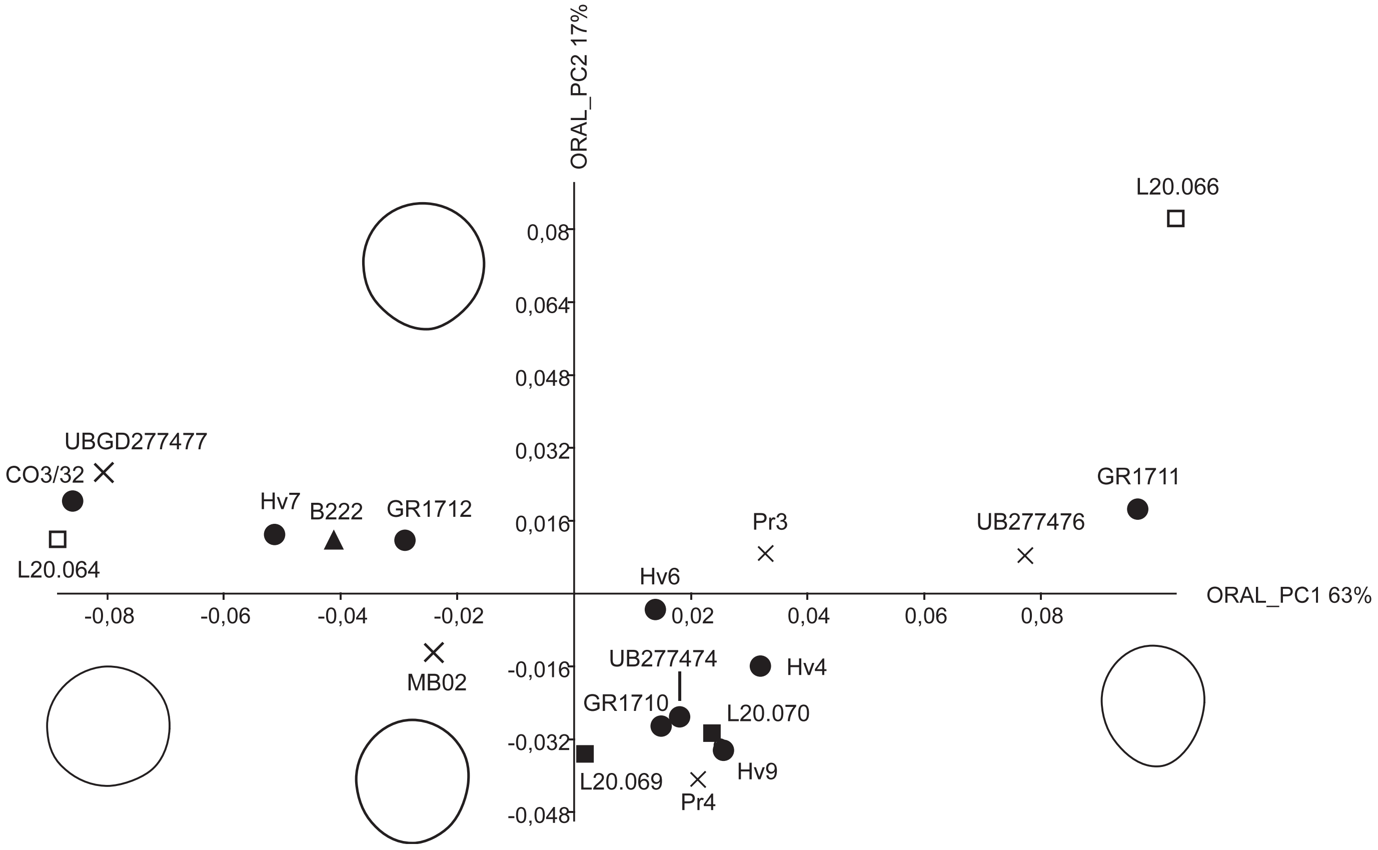

FIGURE *8*—Principal component analyses: *1*, analysis performed for lateral views; *2*, analysis performed for oral views.

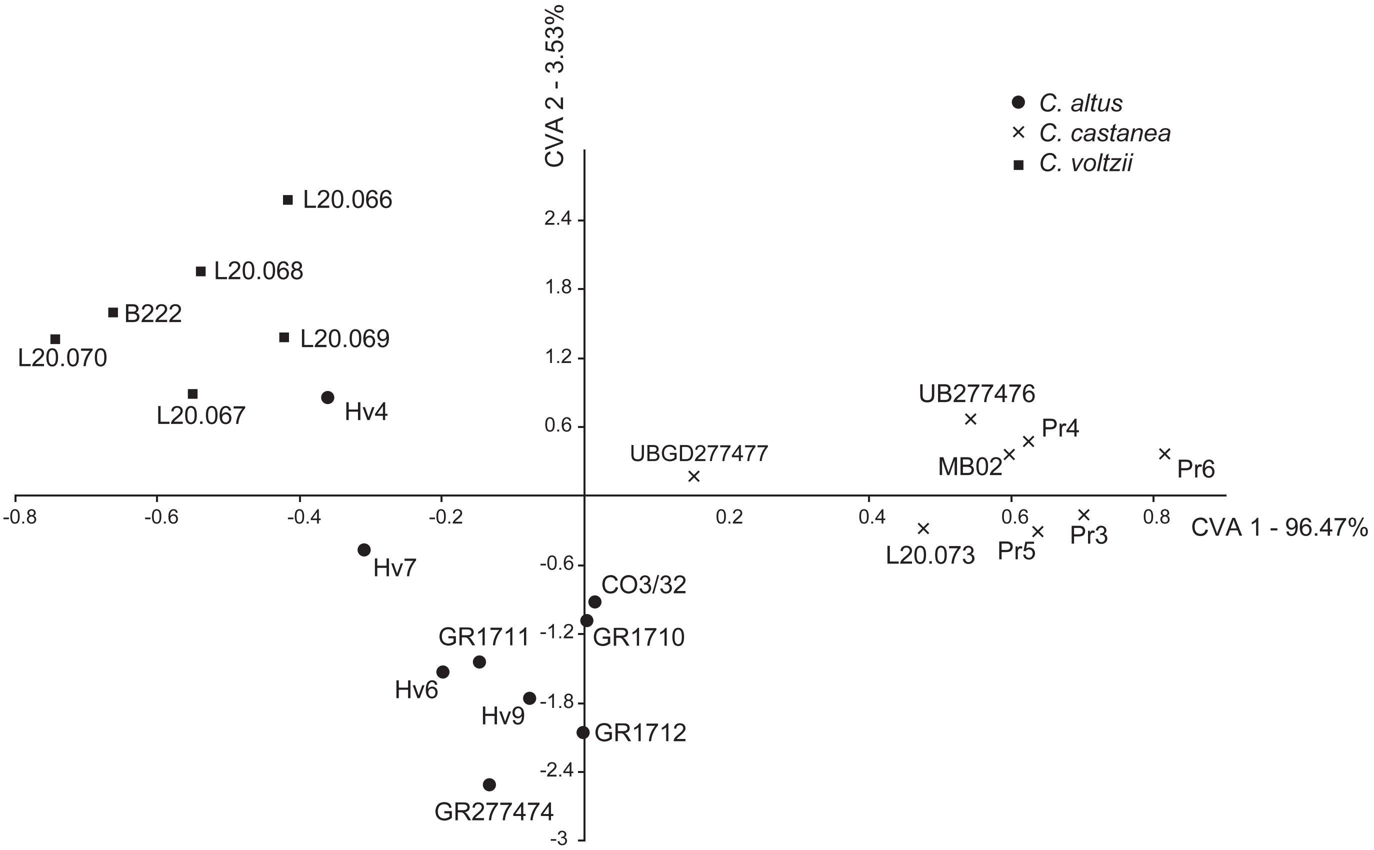

FIGURE 9—Canonical Variates Analysis (CVA) scatter plot performed for the lateral shape analysis.

CYCLOLAMPAS CASTANEA (Desor, 1858)
Figures 2.4, 5.4, 5.5

1858 *Collyrites castanea* DESOR, p. 207.
1859 *Collyrites castanea* (Desor); WRIGHT, p. 326.
1867 *Collyrites castanea* (Desor); COTTEAU, p. 69, pl. 15, figs. 1–9.
1872 *Collyrites castanea* (Desor); DESOR and DE LORIOL, p. 359, pl. 57, figs. 9–11.
1883 *Pygorhytis castanea* (Desor); POMEL, p. 50.
1893 *Pygorhytis tumulus* GREGORY, p. 11, pl. 2, figs. 6, 7.
1924 *Pygomalus castanea* (Desor); LAMBERT and THIERY, p. 391.
1924 *Pygomalus tumulus* (Gregory); LAMBERT and THIERY, p. 391.
1929 *Collyrites castanea* (Desor); DEECKE, p. 488.
1929 *Collyrites tumulus* (Gregory); DEECKE, p. 502.
1934 *Pygorhytis castanea* (Desor); BEURLEN, p. 57, fig. 3g.
1966 *Pygorhytis castanea* (Desor); MINTZ, p. 78.
1971 *Pygorhytis castanea* (Desor); SOLOVJEV, p. 48, pl. 3, fig. 17.

Diagnosis.—Test moderately high, height about 60% of test length on average. Apex a little anterior in position, with maximum height positionned at about 45% of test length.

Material.—See Table 1 for material examined.

Occurrence.—Chaux-de-Fonds (Neuchâtel, Switzerland), Callovian.

Remarks.—*Cyclolampas castanea* was initially assigned to the genus *Collyrites* (Desor, 1858) until it was transferred to *Pygomalus* (Lambert and Thiéry, 1924) then to *Pygorhytis* (Mintz, 1966). Because of incomplete illustrations and descriptions of the posterior part of the test, it turned out to be difficult to assign the species to either of the latter genera. The type specimen of *C. castanea* could not be examined but observation of other specimens showed that periproct and posterior oculars are disjuncted in *C. castanea*. This character, along with the presence of phyllodes composed of three series of pores per half-ambulacrum imply that the species must be reassigned to the genus *Cyclolampas* as already suggested by Gregory (1893) and Mintz (1966).

For the time being, we will here follow Solovjev (1971) and consider *Pygorhytis tumulus* Gregory, 1893 from the Callovian of Cutch (India) as a subjective junior synonym of *C. castanea*, considering that the low test profile of *P. tumulus* falls inside the range of variation of *C. castanea*. New material is however being revised that would question this synonymy (Kroh, personal commun., 2012).

As in the two congeneric species, specimens of *C. castanea* show shape variations that are partly size-dependent, the largest specimens being the highest and most circular in outline, whereas small specimens tend to be the lowest and the most acuminate (Figs. 4.1, 4.2, 6.3).

MORPHOLOGICAL ANALYSES

Previous studies showed how difficult it is to interpret shape variations within and among *Cyclolampas* species. This is mostly caused by the scarcity of well-preserved specimens. In order to discriminate between intra- and inter-specific variations, morphological variations within and between species were examined using two approaches: a biometric analysis based on linear measurements taken on echinoid tests and an outline shape analysis of photographed specimens using the Elliptic Fourier transform method. In figures and Table 1, the distinction among

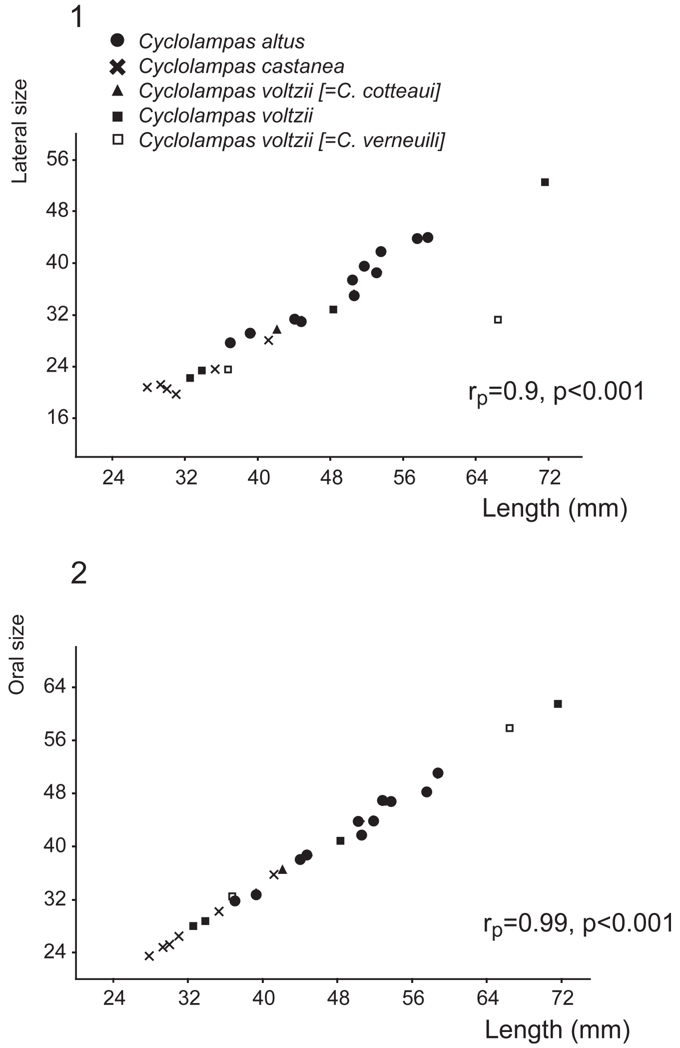

FIGURE *10*—Linear regression with length as independent variable and lateral and oral sizes as dependent variables: *1,* length versus lateral size, $r_{\mathrm{Pearson}} = 0.90$, $p < 0.001$; *2*, length versus oral size, $r_{\mathrm{Pearson}} = 0.99$, $p < 0.001$.

the specimens formerly assigned to the species *C. verneuili* and *C. cotteaui* is provided so as to help the reader evaluate the relevance of our taxonomic conclusions.

Biometric analysis.—Thirty specimens, which belong to the three *Cyclolampas* species herein recognized were sufficiently preserved to measure linear characters using a digital caliper (Table 1). The eight following variables were measured, corresponding to the morphological characters that were discussed by previous authors: test length, test height, test width, maximum heigth position, maximum width position, peristome and apical system positions along with the distance taken between the aboral edge of the periproct and posterior oculars (Fig. 7). A complete measurement set was not obtained for all specimens, as some have broken parts. The ratio between raw measures and test length was then computed for all variables to correct for size effect. Morphological differences between species were tested by performing a one-way ANOSIM (ANalysis Of SIMilarities) for each variable using the software PAST v. 1.93 (Hammer et al., 2001). The ANOSIM is a non parametric test of significance between groups (Clarke, 1993). In analogy with the MANOVA, this test is based on comparing any kind of distance between groups with distances within groups. Contrary to the MANOVA, the ANOSIM doesn't require similar sample sizes, normal distribution of values nor similar variances (Hammer et al., 2001). The ANOSIM was performed using the Euclidean distance and the significance of differences between groups was computed by permutations among groups with 10,000 replicates.

Only three variables discriminate significantly among the three species: test length, test relative height (Height/Length), and maximum heigth relative position (Hmax/Length) (Fig. 6.2, 6.3). Length differences among species was tested higly significant with the ANOSIM ($p<0.005$), but pairwise comparisons betwen species are only significant between *C. altus* and *C. castanea* ($p<0.01$, Bonferroni corrected). The ANOSIM performed on Hmax/Length is highly significant ($p<0.01$), but pairwise comparisons between species are only significant between *C. castanea* and *C. voltzii* ($p<0.05$, Bonferroni corrected). The test maximum height is positioned backward in *C. voltzii* (Hmax/Length values ~0.55), it is frontward in *C. castanea* (Hmax/Length values ~0.45), though it is variable within both species. In this respect, specimens of *C. altus* seem to be intermediate (Hmax/Length values ~0.50) between the two other species (Fig. 6.2). The correlation between Hmax/Length and Length (Spearman's correlation test) was not significant (r_s=0.38, $p>0.05$), showing no significant effect of allometry. The ANOSIM performed on test relative height is highly significant ($p<0.01$). Pairwise comparisons between species are significant between *C. altus* and the two other species ($p < 0.05$, Bonferroni corrected) and show that the test is significantly higher in *C. altus* (Height/

Length ~0.70) than in the two other species (Height/Length ~0.60). The test relative height was correlated to Length (Spearman's r_s=0.59, p<0.01), though with a low correlation value (Fig. 6.3). This shows that relative height differences between specimens are partly due to allometry. Therefore, height differences between *C. altus* and *C. castanea* can be partly explained by size differences between the two species.

Mintz (1966) partly discriminated the former species *C. cotteaui* and *C. verneuili* from other specimens of *C. voltzii* on the base of differences in the distance between the periproct and posterior oculars. Our results don't support this distinction, as differences among species in the distance between the periproct and posterior oculars were not tested significant (ANOSIM with p>0.05) and the correlation with test length was not tested significant either (Fig. 6.1). The material examined shows that the distance between the periproct and posterior oculars is highly variable within *Cyclolampas* species and that it is independent of size. Overall, morphological differences between the specimens formerly attributed to *C. verneuili* and *C. cotteaui* on the one hand, and other specimens of *C. voltzii* on the other hand could not be tested statistically as there are too few measurable specimens at hand. However, graphics examination suggests no conspicuous differences among the former species, whatever the character analyzed (Fig. 6.1–6.3).

Outline shape analysis.—The performed biometric analysis showed that *Cyclolampas* species can be discriminated between each other using pairwise comparisons of test relative height and maximum height position, but none of these linear characters can discriminate between all three species at the same time. This is partly due to important intra-specific variations but it also questions the relevance of the morphological descriptors used so far.

Many studies have demonstrated the relevance and discussed the merits of Fourier shape analysis in morphometric studies of those fossil organisms for which robust homologous landmarks cannot be defined (Crampton, 1995; Crônier et al., 1998; Haines and Crampton, 2000; Dommergues et al., 2007, among many others). In this morphometric method, the whole outline shape of organisms can be analyzed (not just a linear measure taken between two points) regardless of size differences. In *Cyclolampas*, the simple ovoid test shape and the absence of morphological traits for robust homologous landmarks to be defined makes the Fourier shape analysis a promising approach for the analysis of morphological variations within the genus.

Both lateral and ambital outlines were analyzed to take into account most of the morphological differences described by previous authors. Twenty-one specimens were well enough preserved to be photographed in apical view, 19 in oral view, and 23 in lateral view. Full color photographs were transformed into binary black and white images and outline shapes were analyzed using the software SHAPE version 1.3 (Iwata and Ukai, 2002) based on elliptic Fourier descriptors. Size was normalized and specimens aligned according to test length.

In Fourier-related analyses, the overall outline is expressed by low frequency functions while sharp details are depicted by middle- and high-frequency functions along with the analytical noise due to the positioning of specimens when they are photographed. Therefore, a limited number of harmonics must be analyzed to limit the contribution of the analytical error. This is determined as the best compromise between a low analytical error and a reliable description of the original outline, as estimated by the Fourier power (Crampton, 1995). The number of harmonics to be retained for the analysis was here determined by comparing measurement error to true morphological variations among specimens. Measurement error was assessed positioning and taking photos of all specimens twice for each view, and shape analyses were performed independently. Then measurement error was expressed as the proportion of variance due to among-replicate variations following Bailey and Byrnes (1990). Derived from a one-way Model II ANOVA, this method consists in decomposing the total variance into a within-specimen variance (S^2_{intra}) that represents the part of the variance due to measurement variations between replicates (measurement error), and an among-specimen variance (S^2_{inter}) due to true morphological variations among specimens. Then the percentage of measurement error (%ME) is defined as:

$$\%\text{ME} = 100 \times \frac{S^2_{\text{within}}}{S^2_{\text{within}} + S^2_{\text{among}}}$$

Measurement error was computed from Fourier coefficients of the 10 first harmonics. Values are relatively high and variable among harmonics, with a mean value of 18% in lateral view, 32% in oral view, and 51% in apical view. Regarding the high error value computed for the latter view, only lateral and oral outlines were analyzed. The number of harmonics to consider for the analysis was determined by the inflexion point on the curve depicting the cumulative Fourier power as a function of the harmonic order (for more details, see Renaud and Michaux, 2003). The five and four first harmonics were retained for the oral and lateral views respectively. In order to highlight main shape variations, a principal component analysis (PCA) was performed from the Variance/Covariance matrix of normalized Fourier coefficients for each view using the software SHAPE. Outlines were also reconstructed and displayed on the PCA score plots (Fig. 8.1, 8.2) to help visualize shape variation accounted for by each principal component. The two reconstructed outlines here correspond to the mean score value of the respective component plus and minus twice the standard deviation (equals to the eigenvalue square root), the scores on the remaining components remaining zero (Iwata and Ukai, 2002).

The two first components of the PCA computed for the lateral view account for 88% of total variance, the first and second components corresponding to 67% and 21% of total variance respectively (Fig. 8.1). Specimens of *C. altus* are mostly distributed towards positive score values of both components, specimens of *C. voltzii* towards negative score values of the first component and specimens of *C. castanea* are somehow intermediate in distribution. Reconstructed outlines show that main shape variation among specimens concerns the test relative height (PC1), whereas the presence of a shape either symmetrical and domed, or on the contrary slightly acuminate posteriorly is secondary (PC2). The distribution of specimens suggests that shape height could be a discriminant character between species (PC1), whereas test assymetry could be interpreted as a result of intra-specific variation (PC2). In order to test for the significance of shape differences among species, a one-way MANOVA (Multivariate ANalysis Of VAriance) was performed from Fourier coefficients of the first four harmonics using the software PAST version 1. 92 (Hammer et al., 2001). Tests for multivariate normality of coefficient distribution showed that distribution kurtosis departs from normality, moreover variances-covariances values are not similar among harmonic coefficients. Coefficients were therefore normalized prior to the analysis. The "species effect" was tested significant (Wilks' lambda significant with p<0.001), showing significant differences of mean shapes among the three species. In addition to the one-way MANOVA, a Canonical Variates Analysis (CVA) was performed so as to search for the maximal and second to maximal separation between all three species as in a discriminant analysis (Hammer et al., 2001). A scatter plot was produced where specimens are displayed along the two first canonical axes (Fig. 9). About 96% of total variance was accounted for by the first canonical axis along which *C. castanea* best discriminates from the two other species. The two other species differentiate from each other along the second axis that only accounts for 3.53% of total variance. In addition, one specimen of *C. altus* (Hv4) is distributed within specimens of *C. voltzii*. This specimen has indeed a particularly low test profile and is also plotted close to *C. voltzii* specimens in the PCA plot (Fig. 8.1). MANOVAs are usually considered as powerful tests but the validity of the procedure performed on non-normal variable-based data, though normalized prior to analysis, was questioned by Warton and Hudson (2004). The chosen alternative was to use distance-based data and less powerful but robust tests. Hence, two analyses: a one-way ANOSIM and a NP MANOVA (Non-Parametric MANOVA) were performed on raw (non normalized) harmonic coefficients using PAST, with the Chord distance chosen as the distance measure (considered as the most appropriate distance measure for morphometric variables and non euclidean spaces after Legendre and Legendre, 1998). In both analyses, shape differences were tested significant among species ($p<0.001$, with 10,000 permutations) and pairwise comparisons (Bonferroni-corrected p values) showed significant differences ($p<0.001$) between two species only: *C. voltzii* and *C. altus*. This is not congruent with the results obtained with the CVA. In both analyses shape differences among species were tested significant, but the two analyses don't seem to emphasize the same shape differences.

The two first components of the PCA performed for the oral view account for 80% of total variance, with 63% and 17% for the first and second components respectively (Fig. 8.2). All specimens are evenly distributed all along the first component and no clear partition can be seen between species. On the second component, one *C. voltzii* specimen (L20.066) appears as an outlier with a marked acuminate shape whereas other specimens show low score values, either positive or negative, with no distinction between species. A one-way MANOVA was performed from normalized coefficients of the first five harmonics so as to test for species differences, but it was not tested significant (Wilks' Lambda $p>0.05$). The ANOSIM and NPMANOVA were not tested significant either. Shape analysis of the oral view clearly highlights the importance of intra-specific shape variation within *Cyclolampas* species. It is noteworthy that these differences don't either match the distinction previously made between the former species *C. verneuili*, *C. cotteaui* and other specimens of *C. voltzii*. Reconstructed outlines of both components show that intra-specific variation is expressed by more or less wide or acuminate shapes within all three species.

Shape variations and size.—Morphological analyses have shown that variation of test height among *Cyclolampas* specimens is partly due to an allometric relationship between test height and length (Fig. 6.3). In order to estimate the part of shape variation due to shape allometry, the correlation and significance of the regression between shape variations and size were computed using PAST. Size was quantified as the square root of lateral and oral area estimates, not only to take into account test length but also width and height for size estimates of oral and lateral view, respectively. Using the parameters of L = test length, H = test height, and W = test width, size was estimated in lateral view (a) and oral view (b) as follows:

$$\text{(a)} \qquad \frac{\sqrt{\left(\pi(\mathrm{L}/4+\mathrm{H}/2)^2\right)}}{2}$$

$$\text{(b)} \qquad \sqrt{\pi(\mathrm{L4}+\mathrm{W}/4)^2}$$

Linear regressions between test length and size estimates (Fig. 10.1, 10.2) were both tested highly significant ($p<0.001$) but the value of the correlation coefficient is lower for the lateral view ($r_{\mathrm{Pearson}}=0.90$, Fig. 10.1) than for the oral view ($r_{\mathrm{Pearson}}=0.99$, Fig. 10.2). This suggests that morphological variations are more pronounced in lateral view than in oral view. Size differences between species was tested for both views using the Kruskal-Wallis test proposed in the software PAST (this test doesn't require data normality). For both views, size difference was tested significant ($p<0.05$) and pairwise comparisons (Mann-Whitney test) showed that only *C. castanea* and *C. altus* differ significantly from each other ($p<0.05$, Bonferroni corrected). This agrees with the results of the analysis performed on test length (Fig. 6).

Size estimates was plotted as a function of principal component scores of the PCA performed on oral and lateral views (Fig. 4.1–4.3). Both mean and extreme outline reconstructions are shown along their respective components to help visualize shape variations. In oral view (Fig. 4.1), the linear regression between size and PC1 scores was tested significant ($p<0.05$) but the correlation value is low ($r_{\mathrm{Pearson}}=-0.51$). The regression between size and PC2 scores was not tested significant. This shows that oral shape is partly determined by test size, the largest specimens tending to be the most circular, while the smallest specimens are the most acuminate. However, an important part of shape variation remains unexplained. In lateral view (Fig. 4.2, 4.3), the linear regression between size and PC1 scores was tested significant ($p<0.05$) whereas it is not significant between size and PC2 scores (Fig. 4.3). Lateral shape is partly determined by size ($r_{\mathrm{Pearson}}=0.48$), the largest specimens being the highest. Biometric and shape analyses herein agree with each other.

CONCLUSION

In the present work, the discovery of a new species of *Cyclolampas*, *C. altus* n. sp., led to the systematic revision of the genus and to the taxonomic reassignment of the following species within the genera *Pygorhytis* and *Cycolampas*. Previously attributed to the genus *Pygorhytis*, *C. castanea* was reassigned to the genus *Cyclolampas* on the base of new observations. Conversely, the examination and revision of the Bajocian species *Pygorhytis kiliani* and *Pygorhytis gillieroni*, which were previously assigned to *Cyclolampas* (Thierry and Néraudeau, 1994), now support their taxonomic reassignment to the genus *Pygorhytis*. Finally, *Cyclolampas verneuili* and *Cyclolampas cotteaui* are considered junior synonyms of the genus type species *Cyclolampas voltzii*.

The joint use of linear measurements and tools of geometric morphometrics highlighted the amplitude of within-species variations, a likely source of confusion over taxonomic identification of *Cyclolampas* species so far (see Mintz, 1966 for further discussion). Morphological variations are partly size-dependent: variations in test height and ambital outline (acuminate to circular) were significantly correlated to size differences between specimens, the largest specimens being the highest and the most circular in outline, whereas the smallest specimens tend to have the lowest profiles and to be the most acuminate. Because ambital shape variations occur within all three species and because the respective variation ranges widely overlap, the ambital shape should no longer be considered a diagnostic character to differentiate between *Cyclolampas* species. Conversely, test height varies both within and among species, but among-species differences exceed the range of within-species variations. Test relative height and profile shape are the two diagnostic characters that were retained to differentiate among the three species. Shape analyses are congruent with results of the biometric approach and show that *C. altus* is intermediate in maximum height position between *C. castanea* and *C. voltzii*, whereas it discriminates from the two other species with its higher test (Figs. 4, 6).

The systematic revision of *Cyclolampas* implies that the recognized stratigraphic range of the genus now extends from the upper Callovian to the Tithonian. This new stratigraphic distribution is more congruent with our knowledge of the evolutionary history of atelostomates, as compared to the conflicting former ones (Bajocian versus Oxfordian origin). In particular, the morphological and ecological evolution of the genus does fit with the overall scheme of atelostomate evolution. Hence, the genus *Cyclolampas* likely evolved from a 'pygorhytine' ancestor through the achievement of the total breakup between the periproct and apical plates (Mintz, 1966; Barras, 2007). This event took place by the end of the Middle Jurassic, as it did occur in other atelostomate lineages (Thierry, 1974; Moyne et al., 2007). In addition, the origin of the genus in deep-shelf environments of the Callovian and subsequent migration to deep-sea basins during the Oxfordian agree with the overall scenario of atelostomate specialization and migration to deep-sea environments during the Upper Jurassic (Thierry, 1984; Thierry and Néraudeau, 1994; Thierry et al., 1997; Barras, 2008).

The habitat of atelostomate echinoids changed significantly in the Upper Jurassic when most genera specialized to deep-sea environments. In the Middle Jurassic, atelostomates evolved the capability to feed on the organic content of fine-grained sediments through the evolution of penicillate tubefeet, a key innovation that triggered the diversification of the group then favored its migration to deep-sea environments during the Upper Jurassic (Thierry, 1984; Barras, 2008). In the Upper Cretaceous and early Cenozoic atelostomates colonized deep-sea environments on a second time (Smith and Stockley, 2005). The increase of surface water productivity and the consequent increase of organic delivery to deep-sea environments very likely promoted atelostomate migration on that time (Smith and Stockley, 2005). On both occasions, it seems that the decisive factor of atelostomate evolution and dispersal to the deep sea was the access to new food resources (Smith and Stockley, 2005; Barras, 2008). The presence of *C. altus* n. sp. in the upper Callovian of Burgundy is not a random occurrence either. Whatever the prevailing ecological context at the origin of *C. altus*, it should be related to the biogeographic template of Burgundy at that time. Interestingly, the Callovian corresponded to a time of relative high sea level in western Europe. In Burgundy, this led to the weakening of the biogeographic barrier formerly constituted by epicontinental platforms between Boreal and Tethyan biotas as evidenced by the mixing of their respective ammonite faunas (Dommergues and Marchand, 1988; Thierry, 1988). The relative high sea level along with the weakening of biogeographic barriers could have promoted both the specialization of benthic taxa to deep-sea environments and then, their southward or eastward dispersal to deep-sea basins of the Tethyan or Boreal realms. This could hold true for the origin of *Cyclolampas* in western Europe and its dispersal to the southern and eastern deep-sea basins of Europe and North Africa during the Late Jurassic.

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Description of two new fossil echinoids (Echinodermata: Echinoidea) from the Early Hauterivian (Early Cretaceous) of the Paris Basin (France)

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Abstract

Two new echinoid genera and species, *Salvaster roberti* gen. et sp. nov. and *Pygolampas edita* gen. et sp. nov. are described. They were collected in the Calcaires à Spatangues Formation (CSF) that consists of limestone and clay sediments deposited in the southeast of the Paris Basin (France) during the Early Hauterivian (Early Cretaceous). The CSF is dated from the *Acanthodiscus radiatus* chronozone, a time-interval of overall high sea level in Western Europe, but it yields a rich shallow-water fossil fauna mostly represented by benthic invertebrates. Of the 54 echinoid species ever described in the CSF, 26 species are recognized here. They are distributed into 16 different families, among which regular (13 species) and irregular (13 species) echinoids are represented in equal proportion. This work confirms the high level of echinoid diversity in the CSF for that time-period.

Key words: Hauterivian, Holasteroida, Cassiduloida, systematics, new genus, new species

Résumé

Deux nouveaux genres et espèces d'échinides, *Salvaster roberti* gen. et sp. nov. et *Pygolampas edita* gen. et sp. nov. provenant de la Formation des Calcaires à Spatangues (CSF) sont décrits. La CSF correspond à des sédiments calcaréo-argileux déposés dans le sud-est du bassin de Paris (France) à l'Hauterivien inférieur (Crétacé inférieur). Ces dépôts sont datés de la chronozone à *Acanthodiscus radiatus*, un intervalle de temps qui a correspondu à un haut niveau marin général en Europe de l'Ouest. La CSF a pourtant livré une riche faune fossile d'environnement marin peu profond, principalement représentée par des invertébrés benthiques. Parmi ceux-ci, 54 espèces d'échinides ont été décrites au total, mais seules 26 sont ici reconnues. Ces espèces appartiennent à 16 familles différentes, parmi lesquelles échinides réguliers (13 espèces) et irréguliers (13 espèces) sont représentés à proportion égale. La présente étude confirme le haut niveau de diversité de la faune d'échinides de la CSF par rapport aux autres dépôts connus au Crétacé inférieur.

Mots clés: Hauterivien, Holasteroida, Cassiduloida, systématique, nouveau genre, nouvelle espèce

Introduction

The 'Calcaires à Spatangues' Formation (CSF) consists of shallow marine sediments deposited in the southeast of the Paris Basin (France) during the very Early Hauterivian (Early Cretaceous) at the maximum of a second order sea level rise (Bulot *et al.* 2000; Courtinat *et al.* 2006; Bodin *et al.* 2009). Preserved deposits of near-shore and shallow marine environments are not common for that time-interval in Western Europe where deep-sea basin and deep shelf sediments predominate (Canérot & Cuny 1982; Rat *et al.* 1987; van de Schootbrugge *et al.* 2000). Deposits of the CSF yield a diversified, speciose and locally abundant fossil fauna, essentially composed of benthic invertebrates among which echinoids are common and locally very abundant (Cornuel 1841; Rat *et al.* 1987;

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Courtinat *et al.* 2006). In that respect, the CSF is a window on the little known benthic communities that thrived in shallow marine environments in the Hauterivian.

Fossil richness of the CSF has attracted the attention of palaeontologists since the middle of the nineteenth century (Cotteau 1851, 1857–78; Valette 1908; Corroy 1925; Rat *et al.* 1987; Walter 1996). Palaeontologists described up to 54 nominal species of echinoids in the CSF in all, although not all of them were recognized by one single author at a time (Table 1) and more than half of these 54 species (26 species) were described based on a type specimen collected in the CSF. However, many species are geographically restricted and morphologically little differentiated. Authors of the nineteenth century and beginning of the twentieth did not integrate the modern concepts of intraspecific shape variation, ecophenotypism nor growth allometry. Hence, Rat *et al.* (1987) recognized only nine species of irregular echinoids of the 28 ever identified in the CSF. This suggests that two-thirds of the species ever identified in the CSF might not be valid.

In this work, we describe two new species and genera of echinoids and we report a third species that was not recorded in the CSF so far. We examined also the 54 species previously described in the literature based on specimens both collected in the field and housed in reference collections so as to better assess the echinoid diversity of the CSF. The echinoid fauna of the CSF was described with details by Cotteau (1851, 1857-78) and later revised by Valette (1908) and Corroy (1925). As most species are not restricted to the CSF, taxonomy and species distribution were also discussed with great details by several other authors in the late 19th and early 20th century (Desor 1855–1858; Cotteau 1857–78; Lambert 1894; Savin 1905). Therefore, the two new taxa only are fully described, discussed and illustrated in the present work.

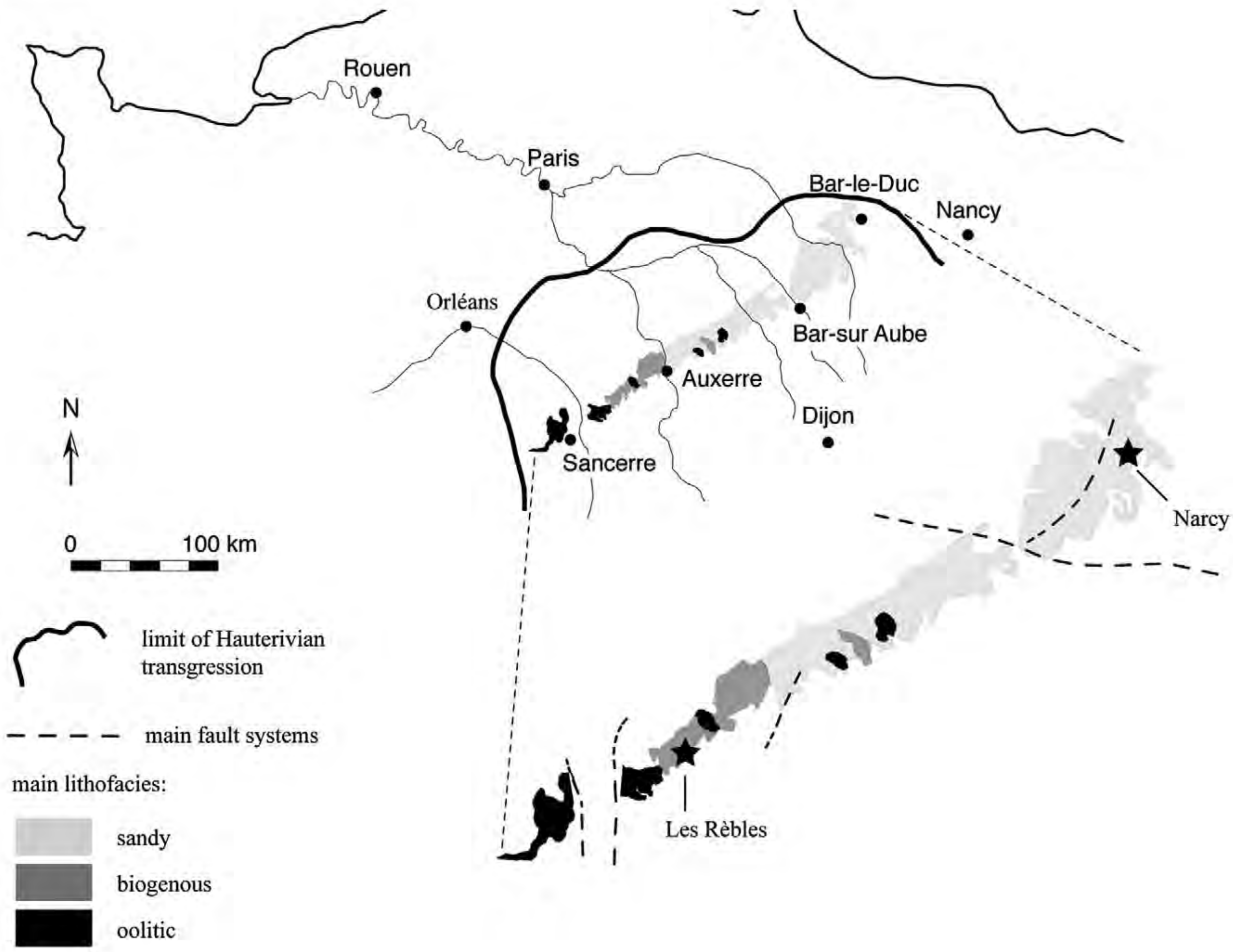

FIGURE 1. Map showing the area of the Paris Basin (France) where the Calcaires à Spatangues Fm crops out, along with the limit of the Hauterivian transgression and main fault systems (modified after Courtinat et al. 2006). Distribution of main lithofacies as defined by Rat *et al.* (1987). Black stars show type localities where new taxa, *Salvaster roberti* gen. et sp. nov. (Les Rèbles) and *Pygolampas edita* gen. et sp. nov. (Narcy) were collected.

TABLE 1. Echinoid species from the Calcaires à Spatangues Fm. recognized in this paper with key synonymies, corresponding literature and source of description/illustration. Public collections where the examined material is deposited are mentioned in the right-hand column: Houdard, Valette and David collections are housed at Université de Bourgogne in Dijon (France); Lambert collection is housed at Muséum national d'Histoire naturelle in Paris (France). Original material collected in the field for the present work is deposited at Université de Bourgogne and Geosciences Rennes (France). Underlined names in bold indicate taxa known only from the CSF.

Families (regular echinoids)	Currently accepted names	Cotteau (1857-1878)	Valette (1908)	Corroy (1925)	Material examined
Cidaridae Gray, 1825	***Plegiocidaris salviensis* (Cotteau, 1851)**	*Rhabdocidaris salviensis* (Cotteau, 1851)	*Aulacocidaris salviensis* (Cotteau, 1851)	*Aulacocidaris salviensis* (Cotteau, 1851)	Houdard, Lambert
Cidaridae Gray, 1825	*Plegiocidaris lardyi* (Desor, 1855)	*Cidaris lardyi* Desor, 1855	*Cidaris lardyi* Desor, 1855	*Cidaris lardyi* Desor, 1855 *Plegiocidaris lineolata* (Cotteau, 1862)	Valette, Lambert, David
Cidaridae Gray, 1825	*Plegiocidaris' friburgensis* (de Loriol, 1873)	-	-	*Plegiocidaris friburgensis* (de Loriol, 1873)	Valette
Cidaridae Gray, 1825	*Plegiocidaris muricata* (Roemer, 1836)	*Cidaris muricata* Roemer, 1836 *Cidaris hirsuta* Marcou, 1847	*Cidaris muricata* Roemer, 1836	-	Houdard, Valette, Lambert
Hemicidaridae Wright, 1857	*Pseudocidaris clunifera* (Agassiz, 1836)	*Hemicidaris clunifera* (Agassiz, 1836) *Hemicidaris neocomiensis* Cotteau, 1851	*Pseudocidaris clunifera* (Agassiz, 1836)	*Pseudocidaris clunifera* (Agassiz, 1836)	Houdard, Valette
Emiratiidae Ali, 1990	*Loriolia rotularis* (Agassiz, 1836)	*Pseudodiadema rotulare* (Agassiz, 1836) *Pseudodiadema picteti* Cotteau, 1857	*Tiaromma rotulare* (Agassiz, 1836)	*Trochotiara rotularis* (Agassiz, 1836)	Valette, David
Emiratiidae Ali, 1990	*Loriolia bourgueti* (Agassiz, 1840)	*Pseudodiadema bourgueti* (Agassiz, 1840)	*Trochotiara bourgueti* (Agassiz, 1840) *Loriolia foucardi* (Cotteau, 1851)	*Trochotiara bourgueti* (Agassiz, 1840) *Loriolia foucardi* (Cotteau, 1851)	Houdard, Valette, David
Emiratiidae Ali, 1990	*Tetragramma autissiodorensis* (Cotteau, 1851)	*Pseudodiadema autissiodorense* (Cotteau, 1851) *Pseudodiadema neocomiense* Cotteau, 1857 *Cyphosoma neocomiense* (Cotteau, 1857) *Pseudodiadema raulini* Cotteau, 1851 *Pseudodiadema robinaldinum* Cotteau, 1851	*Diplopodia autissiodorensis* (Cotteau, 1851) *Polypodia raulini* (Cotteau, 1851) *Phymosoma loryi* (Gras, 1852)	*Tetragramma autissiodorense* (Cotteau, 1851) *Phymosoma neocomiense* (Cotteau, 1857) *Diplopodia elegans* Corroy, 1925 *Diplopodia houdardi* (Lambert & Thiéry, 1910)	Houdard, Valette, Lambert, David
Stomechinidae Pomel, 1883	*Stomechinus fallax* (Agassiz, 1840)	*Psammechinus fallax* (Agassiz, 1840)	*Psammechinus rathieri* (Cotteau, 1851) *Psammechinus montmollini* (Desor, 1858)	*Psammechinus rathieri* (Cotteau, 1851) *Glyptechinus montmollini* (Desor, 1858)	this work: UBGD 277468
Acropeltidae Lambert & Thiery, 1914	*Goniopygus peltatus* (Agassiz, 1836)	*Goniopygus peltatus* (Agassiz, 1836)	*Polygoniopygus intricatus* (Agassiz, 1838)	*Goniopygus peltatus* (Agassiz, 1836)	Houdard
Arbaciidae Gray, 1855	*Codiopsis lorini* Cotteau, 1851	*Codiopsis lorini* Cotteau, 1851	*Codiopsis lorini* Cotteau, 1851	-	Houdard
Saleniidae L. Agassiz, 1838	*Hyposalenia stellulata* (Agassiz, 1838)	*Hyposalenia stellulata* (Agassiz, 1838) *Peltastes stellulatus* (Agassiz, 1838)	*Peltastes courtauti* Cotteau, 1851	*Hyposalenia stellulata* (Agassiz, 1838)	Houdard, Valette
Pedinidae Pomel, 1883	***Hemipedina minima* (Cotteau, 1851)**	*Hemipedina minima* (Cotteau, 1851)	*Hemipedina minima* (Cotteau, 1851)	-	-
Families or higher (irregular chinoids)	Currently accepted names	Cotteau (1857-1878)	Valette (1908)	Corroy (1925)	Material examined
Holectypidae Lambert, 1899	*Coenholectypus macropygus* (Agassiz, 1836)	*Holectypus macropygus* (Agassiz, 1836)	*Holectypus macropygus* (Agassiz, 1836)	*Holectypus macropygus* (Agassiz, 1836)	Valette, David
Conulidae Lambert, 1911	*Globator incisa* (Agassiz, in Desor 1842)	*Pyrina incisa* (Agassiz, in Desor 1842)	*Pseudopyrina incisa* (Agassiz, in Desor 1842)	*Pygopyrina incida* (Agassiz, in Desor 1842) *Pseudopyrina pygea* (Agassiz, 1839)	Valette
Clypeidae Lambert, 1898	*Pygurus montmollini* (Agassiz, 1836)	*Pygurus montmolini* (Agassiz, 1836)	*Pygurus montmollini* (Agassiz, 1836)	*Echinopygus montmolini* (Agassiz, 1836)	Houdard, Valette, David
Pygaulidae Lambert, 1905	*Plagiochasma olfersii* (Agassiz, 1836)	*Echinobrissus olfersii* (Agassiz, 1836) *Nucleolites archiaci* Cotteau, 1851	*Trematopygus olfersii* (Agassiz, 1836) *Trematopygus archiaci* (Cotteau, 1851)	*Trematopygus olfersi* (Agassiz, 1836) *Trematopygus archiaci* (Cotteau, 1851)	Houdard, David
Pygaulidae Lambert, 1905	*Pygorhynchus obovatus* (Agassiz, 1836)	*Botriopygus obovatus* (Agassiz, 1836) *Botriopygus minor* (Agassiz, 1836)	*Botriopygus obovatus* (Agassiz, 1836)	*Pygorhynchus obovatus* (Agassiz, 1836) *Pygorhynchus minor* (Agassiz, 1836)	Houdard, Valette, David
Nucleolitidae Agassiz & Desor, 1847	***Nucleolites salviensis* Cotteau, 1851**	*Echinobrissus salviensis* (Cotteau, 1851)	*Clitopygus salviensis* (Cotteau, 1851)	*Clitopygus salviensis* (Cotteau, 1851)	this work: UBGD 277469
Nucleolitidae Agassiz & Desor, 1847	*Phyllobrissus gresslyi* (Agassiz, 1839)	*Phyllobrissus gresslyi* (Agassiz, 1839) *Phyllobrissus ebrayi* Cotteau, 1859	*Phyllobrissus gresslyi* (Agassiz, 1839) *Phyllobrissus ebrayi* Cotteau, 1859	*Phyllobrissus gresslyi* (Agassiz, 1839) *Phyllobrissus ebrayi* Cotteau, 1859	Houdard, Valette, David
Nucleolitidae Agassiz & Desor, 1847	*Clypeopygus paultrei* (Cotteau, 1851)	*Clypeopygus paultrei* (Cotteau, 1851) *Clypeopygus robinaldinus* (Cotteau, 1851)	*Clypeopygus paultrei* (Cotteau, 1851) *Clypeopygus robineaui* (Cotteau, 1851)	*Clypeopygus paultrei* (Cotteau, 1851) *Clypeopygus robineaui* (Cotteau, 1851)	Valette, David
Neognathostomata Smith, 1981	***Pygolampas edita***	-	-	-	this work: GR-PC.1709
Atelostomata Zittel, 1879	*Disaster subelongatus* (d'Orbigny, 1853)	-	-	-	this work: UBGD 277470
Meridosternata Loven, 1883	***Salvaster roberti***	-	-	-	this work: UBGD 277467
Cardiasterina Pomel, 1883	*Pseudholaster intermedius* (Goldfuss, 1829)	*Holaster intermedius* (Goldfuss, 1829) *Holaster conicus* d'Orbigny, 1853	*Holaster intermedius* (Goldfuss, 1829) *Holaster conicus* d'Orbigny, 1853	*Holaster intermedius* (Goldfuss, 1829) *Holaster conicus* d'Orbigny, 1853	Houdard, Valette, Lambert, David
Toxasteridae Lambert, 1920	*Toxaster retusus* (Lamarck, 1816)	*Echinospatagus cordiformis* Breynius, 1732 *Echinospatagus neocomiensis* (d'Orbigny, 1853)	*Toxaster retusus* (Lamarck, 1816) *Toxaster neocomiensis* d'Orbigny, 1853	*Toxaster retusus* (Lamarck, 1816) *Toxaster neocomiensis* d'Orbigny, 1853 *Toxaster michelini* Cotteau, 1851	Valette , David

Material and methods

Echinoid specimens were sampled in the field by several collectors, mainly by P. Robert and P. Courville over a period of about 30 years at more than 100 localities where the CSF crops out, from Bar-le-Duc in the northeast of the Paris Basin to Sancerre in the southwest (Fig. 1). In addition to the specimens collected in the field, material from Houdard, Valette, Lambert and David collections was examined (Table 1). Houdard, Valette and David collections are part of the geological collections of Université de Bourgogne (UBGD, Dijon, France); Lambert collection is housed at the Muséum national d'Histoire naturelle (Paris, France). Specimens of almost all echinoid species ever recorded in the CSF were examined (Table 1), but type material was not studied. Measurement of holotypes was made with vernier callipers to within an error of 0.1 mm. Drawings of apical and adoral plate structures were made using a binocular microscope equipped with a camera lucida. New type material was photographed along with specimens of the rare species collected in the field that were not represented in the surveyed collections (Figs. 2, 4, 6).

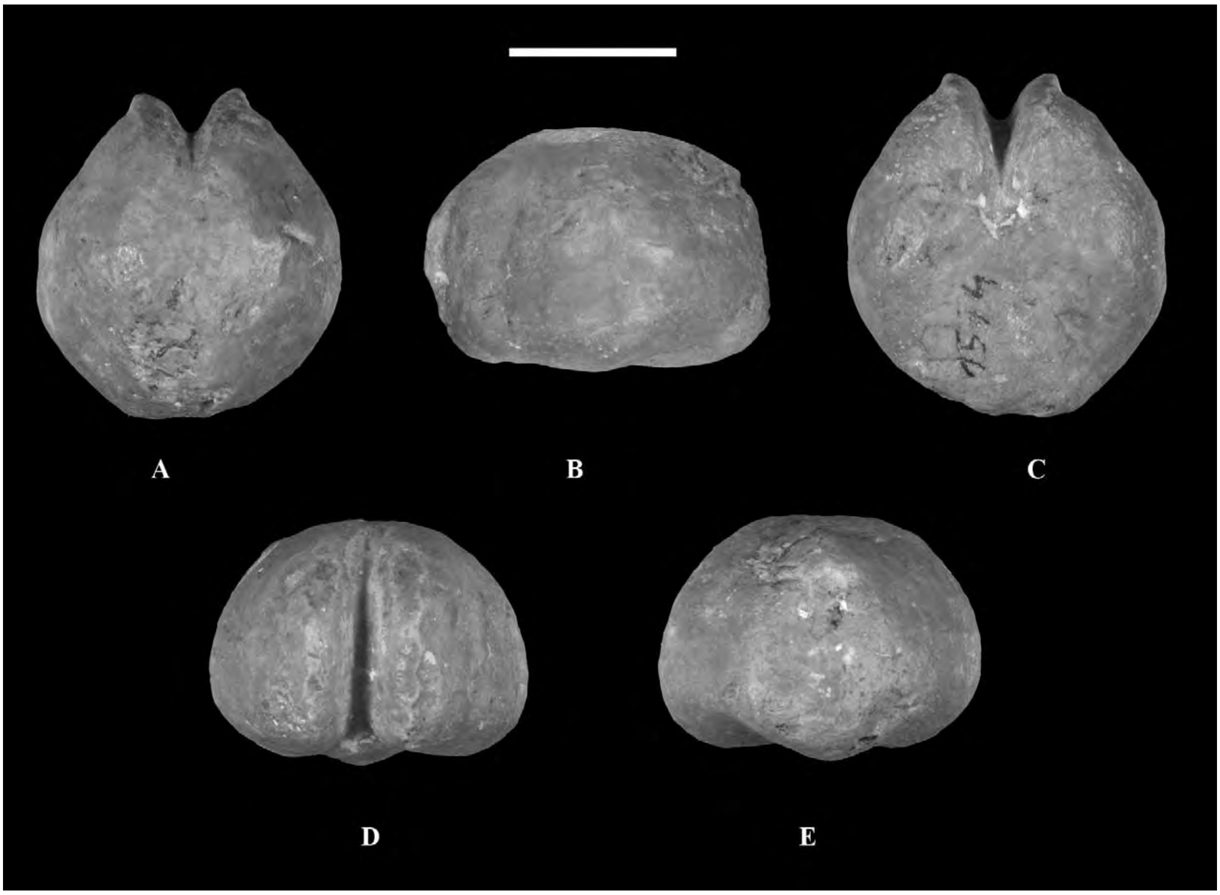

FIGURE 2. A-E, *Salvaster roberti* gen. et sp. nov., holotype, UBGD 277467, Calcaires à Spatangues Fm, Saint-Sauveur; apical (A), lateral (B), oral (C), frontal (D) and posterior (E) views of test, x2.2. Scale bar: 10 mm.

Geological setting and stratigraphy

The CSF crops out in the southeast of the Paris Basin, from Bar-le-Duc in the northeast to Sancerre in the southwest (Fig. 1). It is dated from the *Acanthodiscus radiatus* chronozone (early Early Hauterivian) according to the cephalopods collected: *Acanthodiscus radiatus* (Bruguière 1789), *Leopoldia leopoldina* group (d'Orbigny 1841) and *Cymatoceras pseudoelegans* (d'Orbigny 1840) (Cornuel 1841; Mégnien & Mégnien 1980; Magniez-Jannin 1984; Rat *et al.* 1987; Reboulet *et al.* 2009). The CSF is composed of limestone and clay deposits, only a few meter thick (ca. 0.5 to 8 m) with dominant bioclastic lithofacies (Rat *et al.* 1987). The average palaeo-depth was moderate (approximately few meters to ca. 20-30 m) based on dinoflagellates, foraminifer and bryozoan assemblages and the overall sedimentation rate was low as suggested by the abundance of worn ferruginous bioclasts and ooliths (Rat *et al.* 1987; Walter 1996; Courtinat *et al.* 2006). However, lithology is geographically contrasted. In the northeast, the CSF consists of a finely sorted, sandy and argillaceous limestone that is characterized by few biogenous components and rare fossils. Towards the southeast, sediments is enriched in ferruginous oolites and biogenous components, as palaeo-depth and siliciclastic inputs decreased. Locally, sediments can be particularly enriched in bioclasts and constitute the so-called 'biogenous' lithofacies (Rat *et al.* 1987). Sediments of the CSF were deposited in a shallow marine gulf opened towards the southeast and structured by three main fault systems (Fig. 1): the Loire, Puisaye-Auxerrois and Bray-Vittel systems (Rat *et al.* 1987; Walter 1994; Courtinat *et al.* 2006). The spatial distribution of lithofacies along with the associated foraminiferan fauna suggest the existence of shallow, inner-shelf and shoal deposit environments in the southwest, while palaeo-depth increased towards the northeast where outer-shelf environments prevailed (Magniez-Jannin 1984; Rat *et al.* 1987).

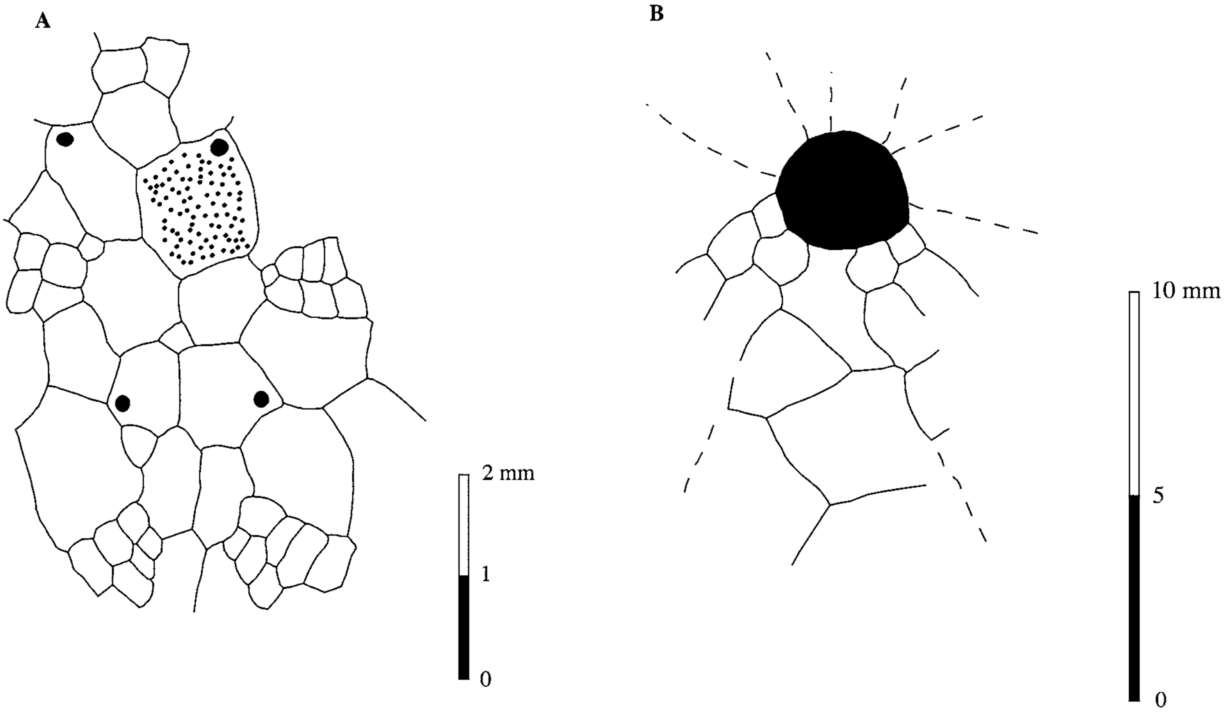

FIGURE 3. A–B, drawings of plate pattern in *Salvaster roberti* gen. et sp. nov., holotype, UBGD 277467; apical system (A) and plastron (B).

In biogenous lithofacies, fossil richness and abundance are outstanding (Rat *et al.* 1987). Fossils are mainly represented by a speciose and abundant benthic macrofauna (ca. 600 different nominal species ever described) that contrasts with the few pelagic and necto-benthic organisms collected (few fish and reptile teeth and vertebrae, ammonites, nautiles and belemnites). The benthic fauna is composed of many foraminiferans, serpulids, bivalves, gastropods, brachiopods, bryozoans, corals, sponges, crustaceans and echinoderms (Cornuel 1841; Corroy 1925; Magniez-Jannin 1984; Walter 1994, 1995, 1996). Irregular echinoids and specially spatangoids are the most abundant echinoderms (Table 1), as suggested by the name of the formation.

S. roberti gen. et sp. nov. was collected in a coarse-grained, bioclastic limestone with ferruginous ooliths. The associated fauna is characterized by the abundance and richness of endobenthic bivalves (*Trigonia*, *Exogyra*, *Lima*, *Pholadomya*) and rare gastropods (Naticidae, Apporaidae), cephalopods (*A. radiatus*), brachiopods and corals. The echinoid fauna is particularly rich and abundant (Table 2). *P. edita* gen. et sp. nov was collected in a sandy limestone lithofacies. The associated macrofauna is represented by bivalves (*Exogyra couloni*, *Panopaea neocomiensis*), cephalopods (*A. radiatus*, *L. leopoldina* group, *C. pseudoelegans*, *Acroteuthis subquadrata* (Roemer, 1836)), corals, bryozoans, annelids and brachiopods. In addition to *P. edita* gen. et sp. nov, echinoids are also represented in respective order of abundance by *Toxaster retusus*, *Pseudholaster intermedius*, *Phyllobrissus gresslyi*, *Pygurus montmollini* and *Plagiochasma olfersii* (Table 2).

TABLE 2. Echinoid species from the Calcaires à Spatangues Fm. collected in new type localities. New taxon names are underlined and in bold.

Higher taxonomic ranks	Les Rèbles	Narcy
Emiratiidae Ali, 1990	*Loriolia bourgueti* (Agassiz, 1840)	_
Emiratiidae Ali, 1990	*Tetragramma autissiodorensis* (Cotteau, 1851)	_
Saleniidae L. Agassiz, 1838	*Hyposalenia stellulata* (Agassiz, 1838)	_
Holectypidae Lambert, 1899	*Coenholectypus macropygus* (Agassiz, 1836)	_
Clypeidae Lambert, 1898	*Pygurus montmollini* (Agassiz, 1836)	*Pygurus montmollini* (Agassiz, 1836)
Pygaulidae Lambert, 1905	*Plagiochasma olfersii* (Agassiz, 1836)	*Plagiochasma olfersii* (Agassiz, 1836)
Pygaulidae Lambert, 1905	*Pygorhynchus obovatus* (Agassiz, 1836)	_
Nucleolitidae Agassiz & Desor, 1847	*Phyllobrissus gresslyi* (Agassiz, 1839)	*Phyllobrissus gresslyi* (Agassiz, 1839)
Nucleolitidae Agassiz & Desor, 1847	*Clypeopygus paultrei* (Cotteau, 1851)	_
Nucleolitidae Agassiz & Desor, 1847	_	***Pygolampas edita* gen. et sp. nov.**
Stem group Atelostomata Zittel, 1879	*Disaster subelongatus* (d'Obigny, 1853)	_
Stem group Meridosternata Lovén, 1883	***Salvaster roberti* gen. et sp. nov.**	_
Cardiasterina Pomel, 1883	*Pseudholaster intermedius* (Goldfuss, 1829)	*Pseudholaster intermedius* (Goldfuss, 1829)
Toxasteridae Lambert, 1920	*Toxaster retusus* (Lamarck, 1816)	*Toxaster retusus* (Lamarck, 1816)

Systematics

Systematics follows Kier (1962), Durham et al. (1966), Smith (1984) and Kroh and Smith (2010).

Class Echinoidea Leske, 1778
Cohort Irregularia Latreille, 1825
Superorder Microstomata Smith, 1984
Series Atelostomata Zittel, 1879
Order Holasteroida Durham & Melville, 1957
Stem group Meridosternata
Salvaster gen. nov.

Type species. *Salvaster roberti* gen. et sp. nov., by monotypy.

Etymology. Masculine gender. After the Latin “Salvator” (saver), from which the city name of Saint-Sauveur-en-Puisaye (close to the type locality) has derived, and “aster” (star).

Diagnosis. Ambulacrum III deeply sunken, forming a conspicuous and narrow frontal groove running from the apex down to the peristome. Adjoining interambulacra 2 and 3 forming sharp keels. Periproct supramarginal.

Salvaster roberti gen. et sp. nov.

Figures 2A–E & 3A–B

Holotype. The holotype and only known specimen is UBGD 277467 (Figs. 2 and 3) housed in the geological collections of Université de Bourgogne (Dijon, France).

Type locality. Collected by P. Robert at “Les Rèbles” (47°35’N, 03°13’E) near Saint-Sauveur-en-Puisaye, Yonne, France; Early Cretaceous, Hauterivian, *Acanthodiscus radiatus* chronozone, Calcaires à Spatangues Formation.

Etymology. After the last name of Mr. P. Robert who collected the specimen in the field in November 1995.

Diagnosis. As for the genus, by monotypy.

Description. Test length is 21.5 mm, test width 19.4 mm and test height 14.2 mm. In apical view, test outline ovate, deeply indented anteriorly (Fig. 2A). In lateral view, gross shape rectangular with apical side inflated and convex (Fig. 2B). Lateral flanks gently and evenly curved towards the ambitus. Ambitus low, situated at the lowest third of test height. Ambulacrum III deeply sunken, forming a conspicuous and narrow frontal groove running from the apex down to the peristome (Fig. 2C–D). Groove vertical at the ambitus, evenly curved below towards the peristome and above towards the apex. Groove adjoining interambulacra 2 and 3 forming sharp keels on each side. Posterior end of test truncated, vertical and narrow, with two weak posterior bulges, visible in oral view (Fig. 2C). Oral surface grooved with depressed ambulacra.

Apical system nearly central, the distance between the apical centre and the anterior side is 47% of test length. There are ten apical plates: four genital plates, five ocular plates and one supplementary plate (Fig. 3A). Plates arranged in the intercalary pattern, which means that anterior genitals 2 and 3 are separated from posterior genitals 1 and 4 by oculars II and IV (Fig. 3A). Supplementary plate located between the anterior ocular pair II and IV, and the posterior genital pair 1 and 4. Each genital perforated by one gonopore. Genital 2, the largest apical plate, is forming the madreporite.

Periproct supramarginal, oval, vertical and flush with the test. It is located at the top of the posterior side (Fig. 2E). Peristome circular in outline and anterior in position, the distance to the anterior side is ca. 40% of test length. The peristome slightly faces in anterior direction.

Ambulacra flush with test above the ambitus. Ambulacral plates much smaller than interambulacral plates. Small, simple ambulacral pore-pairs, the two columns equally developed, but pores mostly indistinct. Paired interambulacra composed of rectangular plates, wider than high adorally. Plastron raised and slightly keeled, protosternous with plating behind the labrum biserial and undifferentiated (Fig. 3B). Next plates progressively enlarged backwards. Apical side covered with few and evenly scattered tubercles. Inner margin of the anterior groove more densely tuberculated, as well as the oral side, mostly on interambulacral plates. Fascioles are not available.

Remarks. The intercalary apical plating of *S. roberti* gen. et sp. nov. is a diagnostic feature of the order Holasteroida and the protosternous plastron a plesiomorphic condition present in the stem group Meridosternata (Smith 2004). Despite a very peculiar test shape, *S. roberti* gen. et sp. nov. has most affinities with the genus *Pseudholaster* Pomel (1883), which is known from the Hauterivian to the Paleocene and its type species *Pseudholaster bicarinatus* (Agassiz, in Agassiz & Desor 1847) from the Albian and Cenomanian (Smith & Wright 2003; Smith 2004). Both genera present a deep frontal groove running from the apex to the peristome, although the interambulacra adjoining the frontal sulcus do not form such a sharp keel in *Pseudholaster* spp. as compared to *S. roberti* gen. et sp. nov.. In both genera, the peristome is oval, slightly inclined and typically facing to the anterior, and the protosternous plastron is slightly keeled. *Pseudholaster* spp. differ by their cordate test shape, almost petaloid ambulacra and the absence of supplementary plates in the apical system. *Taphraster campicheanus* (Cotteau 1858), a ‘basal holasteroid’ from the Hauterivian of Switzerland is also characterized by a deep frontal groove (Smith 2004). However, *T. campicheanus* is different from *S. roberti* in its slightly depressed paired ambulacra and downward projecting subanal region. Details of the apical and plastron plating of *T. campicheanus* are insufficiently known to precise its potential affinity with *S. roberti* gen. et sp. nov..

In *S. roberti* gen. et sp. nov., the most distinctive feature is the presence of a very deep and sharply rimmed frontal groove. The occurrence of a frontal groove is not that atypical in atelostomates. It is closely related to the way echinoids feed and is a convergent, more or less pronounced character in atelostomates (Smith 1984, 2004). It appeared independently in the Collyritidae (*Cardiolampas*, *Cardiopelta* and *Proholaster*) and the Tithoniidae (*Tithonia* and *Tetraromania*) as soon as the Middle Jurassic and was present in all species of Collyritidae by the Early Cretaceous (*Cardiopelta* and *Proholaster*). In the Holasteroida, a deep and vertical frontal groove evolved independently in the Cretaceous and Paleocene representatives of the Cardiasterina Pomel 1883 and ‘stegasterid’ (Smith 2004).

Series Neognathostomata Smith, 1981
Stem group Neognathostomata
Genus *Pygolampas* gen. nov.

Type species. *Pygolampas edita* sp. nov., by monotypy

Etymology. Feminine gender. After the Greek "pygo-" (rear end; the posterior part of the body) and "lampas" (lamp, the Ancient Greek torch). The genus name refers to the tapered rear of the test; "lampas" standing for echinoid, as it usually does in cassiduloid genus names.

Diagnosis. Apical system monobasal, with 3 gonopores (genital pore 3 absent). Petals unequal, the posterior pair and anterior petals sub-parallel, open distally and gradually ending, anterior pair closing distally. Phyllodes with one inner and one outer pore-pair series.

Pygolampas edita gen. et sp. nov.

Figures 4 A–F and 5 A–B

Holotype. The holotype and only known specimen is GR-PC.1709. It is housed in collections of the department of Earth Sciences, Géosciences, Université de Rennes 1 (Rennes, France).

Type locality. Collected by P. Courville near Narcy (48°58'N, 05°10'E), Haute Marne, France; Early Cretaceous, Hauterivian, *Acanthodiscus radiatus* chronozone, Calcaires à Spatangues Formation.

Etymology. After the Latin "editus, a, um" (high, elevated) that refers to the high test morphology.

Diagnosis. As for the genus, by monotypy.

Description. Test length is 38.3 mm, test width 32.9 mm and test height 28 mm. In apical view, test outline pentagonal, with anterior margin rounded, greatest width posterior to centre and posterior margin pointed, almost rostrate (Fig. 4A, C). In lateral view (Fig. 4B), test highly inflated adapically, flat adorally. Test dome-shaped in frontal view, with very low ambitus, situated at the lowest third of test height (Fig. 4D). Oral side depressed.

Apical system anterior, distance between apical centre and front side 38% of test length. Apical system monobasal, covered with hydropores, with three genital pores, genital pore 3 is absent. Periproct inframarginal, oval, flush with test, tilted downwards (not visible in apical view). Peristome sub-central, the distance to the anterior side ca. 48% of test length, pentagonal in shape and depressed (Fig. 4C).

FIGURE 4. A–E, *Pygolampas edita* gen. et sp. nov., holotype, GR-PC.1709, Calcaires à Spatangues Fm, Narcy; apical (A), lateral (B), oral (C), anterior (D) and posterior (E) views of test, x1.2; F, detail of apical system and petals in apical view, x1.7. Scale bars: 10 mm.

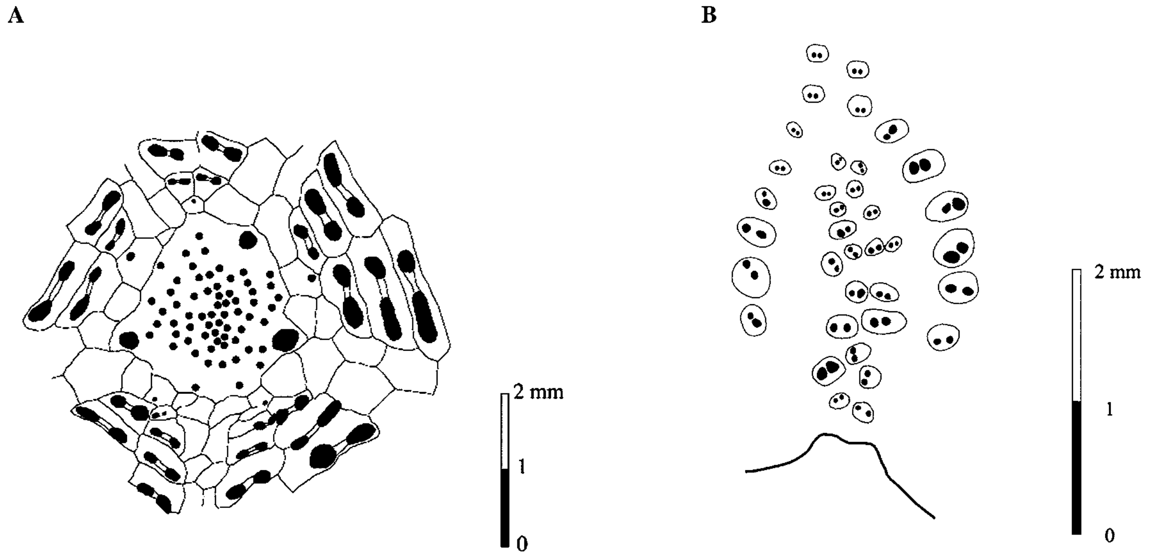

FIGURE 5. A–B, drawings of apical plate pattern (A) and phyllopores of ambulacrum IV (B) in *Pygolampas edita* gen. et sp. nov., holotype, GR-PC.1709.

Petals flush with test, anterior petal and posterior petal pairs open adorally, ending gradually and tapering aborally; anterior petal pair bowed, closing adorally and tapering both adorally and aborally. About 20 pore pairs in a petal. Pore pairs located near the adoral boundary of ambulacral plates. Pores conjugate, the adradial pore of each pore-pair is very elongate, slit-like. There are no pore pairs in each ambulacral plate beyond petals (except in the phyllodes).

Phyllodes well-developed, bowed, broad, pore pairs conjugate, distinct inner series of about 10 pore pairs in each half ambulacrum and outer series of about seven pore pairs. Inner (peradial) or lowermost (adoral) pore of a pore pair the same size as the outer (adradial) or uppermost (aborally) pore respectively. No buccal pores are present. Bourrelets slightly developed.

The test is covered with small scrobicular tubercles that slightly increase in size adorally. No naked area in interambulacrum 5 on the oral side is present.

Remarks. In *P. edita* gen. et sp. nov., test shape is quite atypical for neognathostomate echinoids in the Early Cretaceous. It seems to foreshadow the morphologies of ‘gitolampadid’ (e.g. *Gitolampas lamberti* Checchia-Rispoli, 1921) and ‘pygurid’ neognathostomates (e.g. *Pyguropsis noetlingi* de Loriol, 1899), which evolved at first in the Upper Cretaceous and show typical subpentagonal test outlines with rounded margins, planar oral surfaces (but sunken towards the peristome), domed to subconical upper surfaces and tapering posterior ends. However, *P. edita* gen. et sp. nov. differ from both ‘gitolampadid ‘ and ‘pygurid echinoids by the presence of three gonopores and absence of buccal pores. The presence of short and strongly bowed phyllodes with well-developed inner and outer series of pore-pairs, slightly developed bourrelets, no buccal pores and the absence of oral naked granular zone in interambulacrum 5 are diagnostic characters of ‘catopygids’ (Kier 1962; Smith & Wright 2000), a group of cassiduloids with no representative recorded in the CSF so far. However, *P. edita* gen. et sp. nov. differ from ‘catopygids’ by its high rostrate test shape and monobasal apical system with 3 gonopores. According to Kier (1962), cassiduloids might have evolved monobasal apical systems not until the end of the Cretaceous. The discovery of *P. edita* gen. et sp. nov. in the Early Hauterivian challenges this classic evolutionary scheme.

P. edita gen. et sp. nov. is also very similar in test shape, apical system and ambulacral pores to some ‘pliolampadid’ echinoids (e.g. *Pliolampas vassalli* (Wright, 1855) and *Studeria elegans* (Laube, 1869)), which evolved in the Cenozoic (Kier, 1962). In *P. edita* gen. et sp. nov., *P. vassalli* and *S. elegans*, the test is inflated with rounded margins, pointed posterior end and flat oral surface (but sunken towards the peristome). The apical system is monobasal with three gonopores (gonopore 3 absent), ambulacral pores are conjugate in petals, single beyond petals and bourrelets weakly developed. *P. edita* gen. et sp nov differ from the two other species by the absence of both buccal pores and single pored phyllodes, two derived features which appeared at first in the Upper Cretaceous (Kier 1962).

P. edita gen. et sp. nov is characterized by a unique composition of morphological characters, either derived (monobasal apical system with three gonopores) or ancestral (presence of double pored phyllodes and absence of buccal pores). As it does not fit into any other generic diagnosis, a new genus name was established.

Remarks on the diversity of the echinoids in the CSF

Of the 54 nominal species previously described in the CSF, 23 species were considered taxonomically and undoubtedly distinguishable in the present work (Table 1). Although the taxonomic status of some taxa is in need of comprehensive and thorough revision, all species names that are currently recognized are listed in table 1 along with corresponding key synonymies. In addition, three more species were identified in the present work, among which two are new to science, *S. roberti* gen. et sp. nov. and *P. edita* gen. et sp. nov., and one, *D. subelongatus* is reported in the CSF for the first time (Tables 1–2). According to the material examined in the present work, the echinoid species richness in the CSF would stand at least at 26 species, which is about one-half of the total number of echinoid species ever described in the CSF. However, this still makes the CSF an echinoid-rich formation for that time-period.

The 26 species identified in the CSF are distributed into 16 different families, among which regular (13 species) and irregular (13 species) echinoids are represented in equal proportion (Table 1). These echinoid richness and diversity partly reflect the diversity of habitats that may have occured in the CSF, especially in coarse-grained biocastic lithofacies characterized by the highest levels of richness and diversity (Rat *et al.* 1987). Hence, species such as *Codiopsis lorini* Cotteau 1851 and *Pseudocidaris clunifera* (Agassiz 1836) were usually restricted to shallow sub-recifal habitats (Masrour *et al.* 2004), while other regular echinoids, such as *H. stellulata* and atelostomates may have also inhabited circalittoral environments.

Diversity of irregular echinoids in particular was correlated to sediment grain size (Rat *et al.* 1987). Irregular echinoids are not all capable to feed on finely sorted sediments. Unlike atelostomate echinoids such as spatangoids that evolved penicillate tube feet and are capable to feed on both finely sorted and coarse-grained sediments, cassiduloids and holectypoids can only feed on coarse-grained sediments (Telford & Mooi 1996). Accordingly, Rat et al. (1987) identified four distinct bioregions based on echinoid assemblages that are also characterized by different lithofacies. From the northeast to the southwest, he distinguished (1) a first area characterized by finely sorted and detritic limestones where the atelostomate species *T. retusus* and *Pseudholaster intermedius* constitute 95% to 100% of echinoid assemblages, (2) a transition area with highly variable assemblages, (3) an area with ferruginous and oolitic limestones where the cassiduloids *C. paultrei*, *Pygorhynchus obovatus* and *Pygurus montmollini* are especially abundant and frequent, and (4) an area with argillaceous limestone and marl deposits where specimens of *T. retusus* represents more than 80% of echinoids.

With seven species and genera, cassiduloids represent the richest and most diversified echinoid group of the CSF. This is consistent with the overall scheme of cassiduloid diversity, the group and specially nucleolitids being globally well-diversified in the Early Cretaceous (Kier 1962). Most cassiduloids are particularly abundant and frequent in coarse-grained biocastic lithofacies of the CSF (Rat *et al.* 1987).

T. retusus, *Pseudoholaster. intermedius* and *Phyllobrissus gresslyi* are the most frequent and abundant echinoids of the CSF (Rat *et al.* 1987). They are widely distributed and occur in different lithofacies and bioregions. In these three species in particular, within-species variations in test shape were previously interpreted as taxonomically significant, leading to the creation of several nominal species (Table 1). On the contrary, Rat et al. (1987) interpreted these variations as the result of growth allometry and ecophenotypism controlled by environmental parameters such as sediment grain-size and palaeo-depth.

Unlike the three latter species, four taxa are particularly unfrequent in the CSF: *Stomechinus fallax* (Agassiz 1840), *Nucleolites salviensis* (Cotteau 1851) and *Disaster subelongatus* (d'Orbigny 1853) (see all Fig. 6A–I) and *Hemipedina minima* (Cotteau 1851). These species were represented by no specimen in the surveyed collections. Specimens of *S. fallax*, *N. salviensis* and *D. subelongatus* were collected by P. Robert and are illustrated herein (Fig. 6A–I). *D. subelongatus* is reported in the CSF for the first time, the species being known previously from Neocomian deposits of the South of France, Turkmenistan, Crimea and North Africa (Solovjev 1971). Three specimens were collected by P. Robert at three localities in Yonne: Venoy (where the figured specimen UBGD 277470 was collected), Gy-l'Evêque and Les Rèbles.

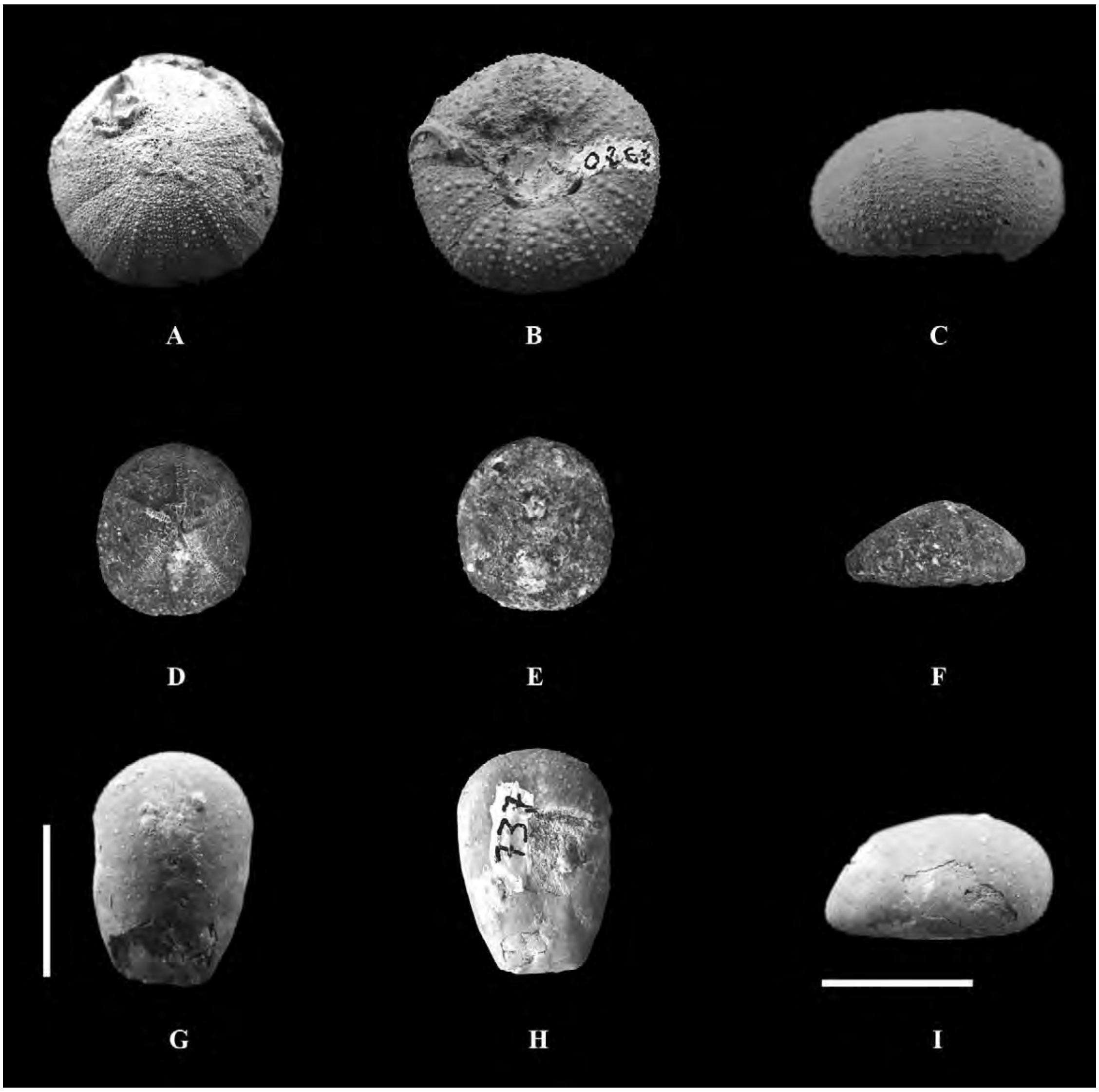

FIGURE 6. A–C, *Stomechinus fallax* (Agassiz, 1840), UBGD 277468, Auxerre, apical (A), oral (B) and lateral (C) views. D–F, *Nucleolites salviensis* (Cotteau, 1851), UBGD 277469, L'Orme du Pont, apical (D), oral (E) and lateral (F) views. G–I, *Disaster subelongatus* (d'Orbigny, 1853), UBGD 277470, Venoy, apical (G), oral (H) and lateral (I) views; x2. Scale bars: 10 mm.

While five echinoid species only seem to be restricted to the CSF (Table 1), others were widely distributed in the Hauterivian. In particular, nine species were identified in Early Hauterivian deposits of the Atlantic High Atlas of Morocco, namely *H. stellulata*, *P. clunifera*, *L. foucardi*, *T. autissiodorensis*, *C. lorini*, *Globator incisa* (Agassiz in Desor 1842), *P. obovatus* and *T. retusus*, although *T. retusus* only is reported there as soon as the *Acanthodiscus radiatus* chronozone (Masrour *et al.* 2004). In Morocco, this time-interval corresponds to marl deposits that might not have constituted suitable habitats for other species.

Conclusion

In Western Europe, the so-called 'Neocomian transgression' corresponds to a second order sea level rise that is associated to the drowning of carbonate platforms previously developed along the northern margin of the Tethys. Initiated in the Valanginian, the transgression reached its peak in the Early Hauterivian (*Acanthodiscus radiatus* chronozone) as evidenced by faunal exchanges between Boreal and Tethyan biotas (Bulot *et al.* 2000; Courtinat *et al.* 2006; Bodin *et al.* 2009). The oceanographic connection between Boreal and Tethyan realms was accompanied by the mixing of cold (Boreal) and warm (Tethyan) water masses and by the prevalence of homogenized and overall cool water temperatures in both realms (Bodin *et al.* 2006, 2009). Finally, continental weathering also intensified, causing an increase in nutrient mobilization and leading to high nutrient concentrations in seawater. This shift from oligotrophic to mesotrophic marine conditions impacted carbonate producing communities, which would have shifted from photozoan, or coralgal dominated communities ('blue water' lithofacies) to heterozoan, low diversity associations ('green water lithofacies) dominated by bryozoans, sponges and crinoids (Schootbrugge van de *et al.* 2000; Föllmi *et al.* 2006).

In the shallow marine gulf of the Paris Basin where sediments of the CSF were deposited, environmental conditions have favoured the presence of an abundant, rich and diversified echinoid fauna. The 'green water' lithofacies model with heterotrophic carbonate producing communities seems to apply to the CSF, in which coral beds are patchy and little extended, whereas bioclastic lithofacies and benthic groups such as bryozoans and sponges predominate (Rat *et al.* 1987; Walter 1996). However, the 'low diversity' community model mentioned by Schootbrugge van de et al. (2000) does not reflect exactly CSF diversity levels. Masse et al. (2009) described platform carbonates that were deposited under oligotrophic conditions in the Marseille region (south of France) at that time period. They solved the apparent contradiction with the heterozoan carbonate model proposed for the northern Tethys considering that the model applied to deep-sea communities and was not representative of overall, constant mesotrophic conditions. The CSF does not correspond to the photozoan platform carbonates described by Masse et al. (2009) for the Marseille region, may be as sediments were deposited further north where the influence of Boreal water masses was more determinant. The CSF sediments were deposited in shallow-water mesotrophic environments that albeit allowed for the development of a rich and diversified benthic fauna.

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ORIGINAL PAPER

Environmental control on the structure of echinoid assemblages in the Bellingshausen Sea (Antarctica)

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Abstract The Bellingshausen Sea is one of the most remote and least surveyed seas of the Southern Ocean, so that little was known about benthic communities and those factors that determine community structuring until recently. The present work aims at characterizing the structure and spatial distribution of echinoid assemblages in the Bellingshausen Sea, as well as identifying the environmental factors that determine assemblage structuring. Echinoids were collected at 32 stations using an Agassiz trawl, at depths of 86–3,304 m, during BENTART oceanographic expeditions led in 2003 and 2006. Sediment and bottom water properties were analysed using an USNEL-type box corer and a Neil Brown Instrument System Mark III CTD, respectively. Echinoids were found at all stations, except Peter I Island. Seventeen species were identified, representing 22 % of the echinoid species present in the Southern Ocean and increasing twofold the number of species recorded in the Bellingshausen Sea so far. The echinoid fauna is dominated by the very abundant species *Sterechinus antarcticus*. Depth is the key factor that determines the nature of echinoid assemblages, which are mainly divided into the continental shelf, the slope and the deep-sea basin. In addition, sediment properties, namely redox values, organic matter and mud content, best match species dispersion on the shelf. Sediment properties affect echinoid distribution depending on species food range and feeding strategy. As it might be expected, sediment properties more strongly influence specialist feeders (Schizasteridae and Cidaridae) than generalists (Echinidae).

Keywords Abiotic factors · Antarctic · Bellingshausen Sea · Benthos · Diversity · Echinodermata · Echinoidea

Introduction

The echinoid fauna is an important component of Antarctic benthic communities. Sea urchins were frequently sampled from the shallows of the continental shelf to deeper waters of the break, and down to abyssal plains of the Southern Ocean (Arnaud et al. 1998; Barnes and Brockington 2003; David et al. 2005; Brandt et al. 2007; Linse et al. 2008). There are around 80 species of Antarctic echinoids, most of which are endemic to the Southern Ocean (ca. 68 % of sp.). Most species (ca. 65 %) belong to two families: the Cidaridae (20 sp.) and the Schizasteridae (30 sp.), the remaining species being distributed within seven other families (David et al. 2005).

At family level, ecological requirements seem to be essentially determined by feeding strategies, while species of the same family may be distributed with different depth ranges (Brey and Gutt 1991; De Ridder et al. 1992; Jacob et al. 2003; David et al. 2005). In such organisms, and especially those species that are deposit-feeders, we may expect an important influence of sediment granulometry and organic content on echinoid distribution and

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assemblages too (Nichols 1959; Kanazawa 1992). In addition, factors such as biotic processes of the water column (seasonality of primary and secondary productions) and physical parameters (depth and co-varying factors, currents, ice cover, iceberg scouring, sea–floor morphology and sediment characteristics) could determine the abundance, richness or diversity of echinoid assemblages. The co-varying and interrelated contributions of those parameters may differ according to the type of habitat (shallow waters, deep continental shelf or abyssal plains) and to the scale of the study (in time, space and taxonomy). Hence, Antarctic benthic communities seem to match the classic model of shallow-shelf habitats often being tightly coupled to water column processes when both intense seasonality and short pelagic food webs occur (Thrush et al. 2006).

Finally, biological specificities such as reproduction strategies (brooding or larval broadcasting), dispersal capabilities and recruitment seem to influence community structuring (Gutt and Schikan 1998; Bowden 2005; Matallanas and Olaso 2007; Aldea et al. 2008; Hétérier et al. 2008; Linse et al. 2008), especially in the deep-sea where the patchy distribution of communities shows no clear relationships with depth or any other physical factor (Linse et al. 2007; Hétérier et al. 2008).

The present study focuses on the echinoid fauna of the Bellingshausen Sea (BS). Located between Thurston Island to the west and Marguerite Bay to the east (from 70°W to 100°W), the BS is one of the least investigated Antarctic areas by marine biologists, mainly due to remoteness and ice prevalence most parts of the year (Fairbridge 1966; Turner and Owens 1995; Grotov et al. 1998; Clarke and Johnston 2003). Therefore, echinoids of the Bellingshausen Sea were only known by eight species that had been collected over 80 years during four scientific expeditions in the period between 1897 (RV *Belgica*) and 1973 (RV *Hero*). The physical environment of the BS remains poorly documented as well, thereby limiting understanding of species distribution patterns (Gutt et al. in press).

In 2003 and 2006, BENTART expeditions were devoted to sampling in the BS; they have led to a great improvement in our knowledge of the benthos, now available through many scientific publications (García Raso et al. 2005; Matallanas and Olaso 2007; Rios and Cristobo 2007; Troncoso et al. 2007; Aldea et al. 2008; Eakin et al. 2008; García Raso et al. 2008; Troncoso and Aldea 2008; Sáiz-Salinas et al. 2008; Varela and Ramos-Esplá 2008; O'Loughlin et al. 2009). The present work is an attempt to improve our knowledge of echinoid diversity in the BS by addressing the three following questions. (1) Is the Bellingshausen Sea extremely impoverished in echinoids due to unsuitable environmental conditions? (2) What is the structure of echinoid assemblages there? (3) Which are the environmental factors that influence the structure and spatial distribution of echinoid assemblages?

Materials and methods

Field sampling

Sampling was done during BENTART expeditions (Spanish Antarctic Research Program) of the RV 'Hespérides' from January to March 2003 and from January to February 2006. Samples were collected at 32 stations between 86 and 3,304 m depth (Fig. 1; Table 1), using an Agassiz trawl with horizontal and vertical openings of 2.01 and 1.12 m, respectively, and a 10-mm mesh size (Ramos 1995; Arnaud et al. 1998). A USNEL-type box corer with a maximum breakthrough of 60 cm and an effective sampling area of 0.25 m^2 (Sáiz-Salinas et al. 2008) was used for infaunal organisms and sediments. Hydrographic casts were made with a Neil Brown Instrument System Mark III CTD, and water sampling at different depth was done with Niskin bottles. Suprabenthic samples were collected with a modified Macer-GIRO Q sledge (Carter and Hunter 1994). This sledge was equipped with three superimposed nets (0.5 mm mesh size).

Echinoid systematics

Echinoids were sorted, identified at species level, counted and fixed in 70 % ethanol for further investigations. Taxonomy was based on morphological characters of the test, pedicellariae and spines as described in David et al. (2005).

Environmental data

Nine environmental variables were measured in order to know the water column and bottom features. Sediment redox profiles were analysed immediately after sampling. Redox values were measured with an Orion ORP 9678 electrode coupled to an Orion 3 Star Portable pH meter. A standard ORP solution (Orion 967861) was used as a reference. Analyses of sediment granulometry (gravels %, sand %, mud %) and organic deposit (OD %) were performed following the standard methods detailed in Eleftheriou and McIntyre (2005) and Bale and Kenny (2005). Three granulometric fractions were defined following Wentworth's classification (1922). The total organic deposit (OD %) was estimated from the sediment weight loss after 4 h heating in an oven at 450 °C (see Sáiz-Salinas et al. 2008 for further details).

A 24-bottle Rosette sampler system was used to collect water samples, and a Neil Brown Instrument System Mark III CTD (conductivity, temperature, depth) with additional oxygen and fluorescence sensors was attached at the bottom of the Rosette. The Rosette sampler is equipped with 10-dm^3 Niskin bottles.

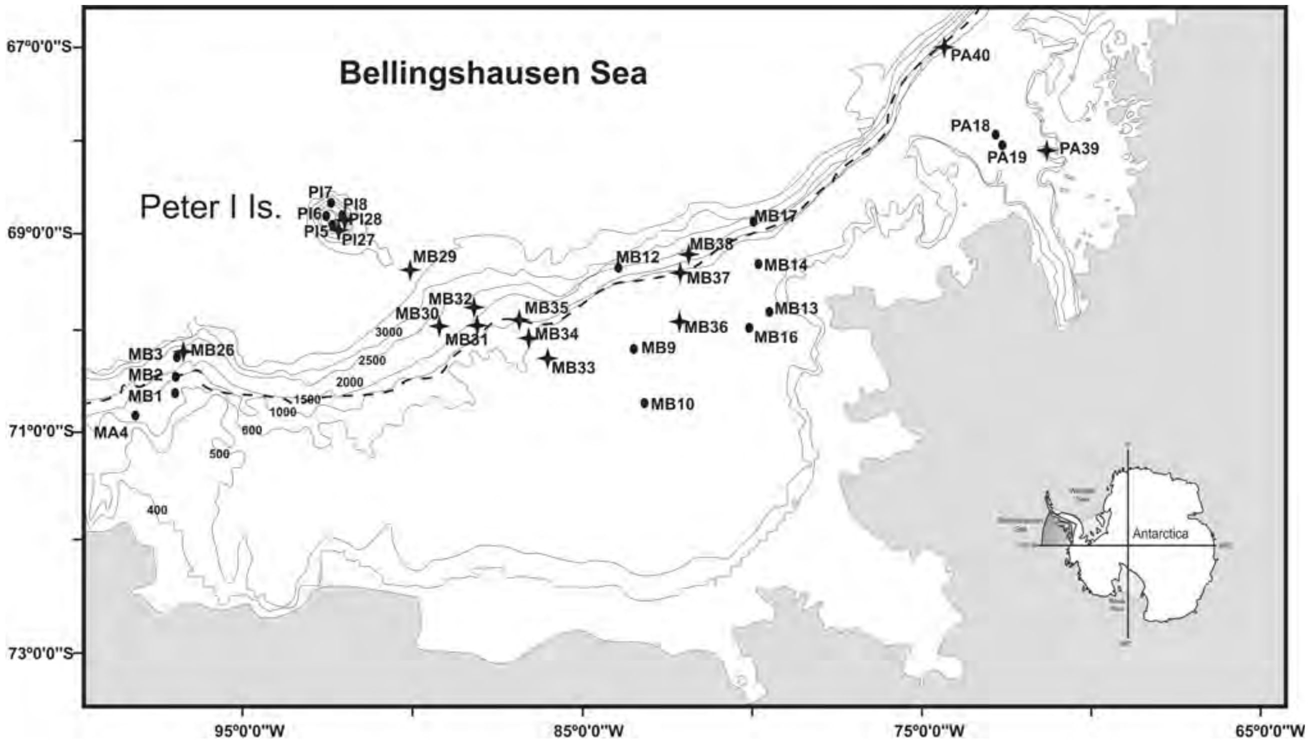


Fig. 1 Sampling area and stations of expeditions Bentart'03 (*points*) and Bentart'06 (*crosses*). *Dashed line* ice cover limit

The Rosette and CTD were deployed, and bottles were closed at predetermined depths. Water samples were used for inorganic nutrient analyses, for the suspended particulate matter (organic carbon and nitrogen), chlorophyll a (Chl a) and oxygen concentration determinations.

Data analyses

Echinoid species were classified according to their frequency across samples, which is a surrogate to evaluating their importance in the community. It is based on the percentage frequency of occurrence across all stations that is computed and classified into four categories: ubiquitous species (>20 % of stations), very common species (between 10 and 20 %), common species (between 5 and 10 %) and rare or accidental species (<5 %) (Mora 1980; Manjón-Cabeza and García Raso 1994; Manjón-Cabeza and Ramos 2003).

To investigate the structure of echinoid assemblages, similarities between samples were computed by a hierarchical cluster analysis using the UPGMA agglomerative algorithm (Sneath and Sokal 1973; RMACOQUI ver. 1.0 software Olivero et al. 2011).

It was made on the similarity matrix of the Baroni–Urbani coefficients calculated from presence/absence data (Baroni-Urbani and Buser 1976). The robustness of each cluster was supported by a test of biological significance of the boundaries between echinoid assemblages (McCoy et al. 1986). Strong and weak boundaries were defined between assemblages following McCoy et al. (1986). A strong boundary separates two significantly different clusters with no species in common. A weak boundary separates two significantly different clusters that share common species. When boundaries are not significant, it means that species distribution is homogeneous in the studied area. Boundary analysis follows Olivero et al. (1998).

Stations were plotted using a correspondence analysis and a canonical correspondence analysis computed from the presence/absence matrix and based on the eigenvalues of χ^2 distances between all data points (Ter Braak and Prentice 1988; Hennebert and Lees 1991; Legendre and Legendre 1998), using PAST—paleontological statistics, ver. 1.181 computer program (Hammer et al. 2001). Once identified, the environmental variables that best matched echinoid significant assemblages were selected to run a canonical correspondence analysis (CCA). They were used to define ordination axes on which echinoid data (with both stations and specimens) were plotted. Environmental variables were plotted as well as correlations with ordination axes.

Results

A total of 1,913 specimens of echinoids were examined for this work, and 17 species representing 6 families and 5

Table 1 List of stations with species, environmental data and other data as abundance (per species and per station) (N), species richness (S) and occurrence

Abrev.	Spcies/stations	MB1	MB2	MB3	MB4	PI5	PI6	PI7	PI8
Order Cidaroida									
Family Cidaridae									
AE	*A. eltaniana* Mooi et al., 2000								
CP	*C. perrieri* Koehler, 1912								
CS	*C. speciosa* Mortensen, 1910								
NG	*N. gaussensis* Mortensen, 1909								
NL	*N. lanceolata* Mooi et al., 2000			1	1				
NM	*N. mortenseni* (Koehler, 1900)			1	1				
Order Echinoida									
Family Echinidae									
SA	*S. antarcticus* Koehler, 1901	5	105	8					
AD	*S.* Koehler, 1926								
Order Echinothuioidea									
Family Echinothriidae									
KA	*K. asterias* (A. Agassiz, 1881)								
Order Holasteroida									
Family Plexechinidae									
PP	*P. planus* (Mironov, 1978)		9						
Family Pourtalesiidae									
PD	*P. debilis* (Koehler, 1926)								
Order Spatangoida									
Family Schizasteridae									
ABE	*A. elongatus* (Koehler, 1908)								
AL	*A. lorioli* Koehler, 1901								
AR	*A. rostratus* (Koehler, 1926)								
AS	*A. similis* Mortensen, 1936								
TC	*T. cordatus* (Koehler, 1912)								
TA	*T. abatoides* (H. L. Clark, 1925)								
N	Abundance (number of specimens)	5	114	10	2	0	0	0	0
N (%)	Abundance (%)	0.26	5.96	0.52	0.10	0.00	0.00	0.00	0.00
S	Species richness	1	2	3	2	0	0	0	0
Lat	Latitude (°)	70.64	70.49	70.29	70.87	68.9	68.8	68.7	68.8
Lon	Longitude (°)	95.17	95.24	95.20	98.44	90.6	90.8	90.7	90.4
D	Depth (m)	523	726	1,432	426	124	220	370	86
OD	Organic deposit (%)	4.808	5.019	5.417	4.56	1.43	1.35	1.85	1.23
G	Gravels (%)	11.15	40.3	14.03	14.18	0.25	0.65	0.08	0.13
S	Sand (%)	32.68	24.48	47.33	31.53	18.6	23.9	11.8	74.1
M	Mud (%)	56.2	35.25	38.6	54.3	81.1	75.5	88.2	25.8
R	Redox	252.2	289.3	259.8	271.3	199	123	175	156
T	Temperature (°C)	1.29	1.049	0.658	1.368	−0.4	1.49	1.87	−1
Sl	Salinity (ups)	34.74	34.74	34.73	34.73	34.2	34.6	34.7	34
O_2	Oxygen (mmol/L)	203	204.9	213.3	197.6	253	199	190	307

Table 1 continued

Abrev.	Spcies/stations	MB9	MB10	MB12	MB13	MB14	MB16	MB17	PA18
Order Cidaroida									
Family Cidaridae									
AE	*A. eltaniana* Mooi et al., 2000								
CP	*C. perrieri* Koehler, 1912								
CS	*C. speciosa* Mortensen, 1910								
NG	*N. gaussensis* Mortensen, 1909								1
NL	*N. lanceolata* Mooi et al., 2000								
NM	*N. mortenseni* (Koehler, 1900)				2	1			2
Order Echinoida									
Family Echinidae									
SA	*S. antarcticus* Koehler, 1901	30	28	2	25	26	12		17
AD	*S.* Koehler, 1926							11	
Order Echinothuioidea									
Family Echinothriidae									
KA	*K. asterias* (A. Agassiz, 1881)								
Order Holasteroida									
Family Plexechinidae									
PP	*P. planus* (Mironov, 1978)						1		
Family Pourtalesiidae									
PD	*P. debilis* (Koehler, 1926)								
Order Spatangoida									
Family Schizasteridae									
ABE	*A. elongatus* (Koehler, 1908)								
AL	*A. lorioli* Koehler, 1901	3	1						
AR	*A. rostratus* (Koehler, 1926)								
AS	*A. similis* Mortensen, 1936								
TC	*T. cordatus* (Koehler, 1912)								
TA	*T. abatoides* (H. L. Clark, 1925)								
N	Abundance (number of specimens)	33	29	2	27	27	13	11	20
N (%)	Abundance (%)	1.73	1.52	0.10	1.41	1.41	0.68	0.58	1.05
S	Species richness	2	2	1	2	2	2	1	3
Lat	Latitude (°)	70.24	70.74	69.40	69.82	69.35	69.99	68.92	67.96
Lon	Longitude (°)	81.77	81.49	82.22	77.75	78.07	78.32	78.24	71.06
D	Depth (m)	540	494	2,043	608	492	906	1,947	355
OD	Organic deposit (%)	4.05	5.957	3.811	4.639	3.678		1.979	
G	Gravels (%)	8.833	2.475	8.833	30.1	9.25	33.7	33.7	
S	Sand (%)	36.1	23.1	36.1	26.77	27.43	23.78	23.78	
M	Mud (%)	55.07	74.43	55.07	43.2	63.35	42.52	42.52	
R	Redox	260	261.8	266	240.5			224.7	
T	Temperature (°C)	1.152	1.112	0.816	1.148				
Sl	Salinity (ups)	34.74	34.74	34.73	34.74				
O_2	Oxygen (mmol/L)	197.8	197.2	215.6	187.5				

Table 1 continued

Abrev.	Spcies/stations	PA19	MB26	PI27	PI28	MB29	MB30	MB31	MB32	MB33
Order Cidaroida										
Family Cidaridae										
AE	*A. eltaniana* Mooi et al., 2000									
CP	*C. perrieri* Koehler, 1912	3								
CS	*C. speciosa* Mortensen, 1910									
NG	*N. gaussensis* Mortensen, 1909									
NL	*N. lanceolata* Mooi et al., 2000									
NM	*N. mortenseni* (Koehler, 1900)									
Order Echinoida										
Family Echinidae										
SA	*S. antarcticus* Koehler, 1901							5	31	555
AD	*S.* Koehler, 1926		4				48			
Order Echinothuioidea										
Family Echinothriidae										
KA	*K. asterias* (A. Agassiz, 1881)					1				
Order Holasteroida										
Family Plexechinidae										
PP	*P. planus* (Mironov, 1978)		7				8	36		
Family Pourtalesiidae										
PD	*P. debilis* (Koehler, 1926)							2		
Order Spatangoida										
Family Schizasteridae										
ABE	*A. elongatus* (Koehler, 1908)									
AL	*A. lorioli* Koehler, 1901									
AR	*A. rostratus* (Koehler, 1926)									1
AS	*A. similis* Mortensen, 1936	1								
TC	*T. cordatus* (Koehler, 1912)	1								
TA	*T. abatoides* (H. L. Clark, 1925)									
N	Abundance (number of specimens)	5	11	0	0	1	56	43	31	556
N (%)	Abundance (%)	0.26	0.58	0.00	0.00	0.05	2.93	2.25	1.62	29.06
S	Species richness	3	2	0	0	1	2	3	1	2
Lat	Latitude (°)	68.07	70.24	69	68.9	69.43	69.98	69.95	69.80	70.27
Lon	Longitude (°)	70.95	95.04	90.4	90.3	88.44	87.52	86.32	86.54	84.19
D	Depth (m)	517	1,920	1,873	1,191	3,304	1,814	1,426	1,849	438
OD	Organic deposit (%)		1.991			8.916	5.31	7.005		4.017
G	Gravels (%)		1.331			1.543	0	58.38		20.11
S	Sand (%)		89.73			13.27	27.78	11.68		48.17
M	Mud (%)		8.935			85.19	72.22	29.95		31.72
R	Redox		178.9			262.1	207.8	187.7		290.2
T	Temperature (°C)		0.551			0.385	0.724	0.563		
Sl	Salinity (ups)		34.7			34.7	34.71	34.7		
O_2	Oxygen (mmol/L)		216.9			109.7	211.3	214.4		

Table 1 continued

Abrev.	Spcies/stations	MB34	MB35	MB36	MB37	MB38	PA39	PA40	*N*	N (%)	O (%)
Order Cidaroida											
Family Cidaridae											
AE	*A. eltaniana* Mooi et al., 2000						27	1	28	1.464	6.25
CP	*C. perrieri* Koehler, 1912								3	0.157	3.13
CS	*C. speciosa* Mortensen, 1910			1					1	0.052	3.13
NG	*N. gaussensis* Mortensen, 1909								1	0.052	3.13
NL	*N. lanceolata* Mooi et al., 2000			1					3	0.157	9.38
NM	*N. mortenseni* (Koehler, 1900)			1			2	2	12	0.627	25.00
Order Echinoida											
Family Echinidae											
SA	*S. antarcticus* Koehler, 1901	23	12	30	559	2	70	100	1,645	85.991	62.50
AD	*S.* Koehler, 1926								63	3.293	9.38
Order Echinothuioidea											
Family Echinothriidae											
KA	*K. asterias* (A. Agassiz, 1881)								1	0.052	3.13
Order Holasteroida											
Family Plexechinidae											
PP	*P. planus* (Mironov, 1978)	52				4			117	6.116	21.88
Family Pourtalesiidae											
PD	*P. debilis* (Koehler, 1926)								2	0.105	3.13
Order Spatangoida											
Family Schizasteridae											
ABE	*A. elongatus* (Koehler, 1908)	10					1		11	0.575	6.25
AL	*A. lorioli* Koehler, 1901	8		1					13	0.680	12.50
AR	*A. rostratus* (Koehler, 1926)								1	0.052	3.13
AS	*A. similis* Mortensen, 1936								1	0.052	3.13
TC	*T. cordatus* (Koehler, 1912)	1							2	0.105	6.25
TA	*T. abatoides* (H. L. Clark, 1925)	9							9	0.470	3.13
N	Abundance (number of specimens)	103	12	34	559	6	100	103	1,913	Specimens	
N (%)	Abundance (%)	5.38	0.63	1.78	29.22	0.31	5.23	5.38			
S	Species richness	6	1	5	1	2	4	3	17	Species	
Lat	Latitude (°)	70.14	69.93	69.94	69.44	69.23	68.13	66.96			
Lon	Longitude (°)	84.86	85.18	80.41	80.86	80.07	69.59	72.58			
D	Depth (m)	603	1,117	560	495	1,324	167.1	402			
OD	Organic deposit (%)	1.799	7.36	8.507	5.703	5.981					
G	Gravels (%)	0	47.65	33.15	35.37	65.69					
S	Sand (%)	87.79	14.63	6.124	43.5	7.113					
M	Mud (%)	12.21	37.72	60.72	21.2	27.2					
R	Redox	326	260.7	289	244	298.2					
T	Temperature (°C)	1.173		1.188	1.309	0.862					
Sl	Salinity (ups)	34.71		34.71	34.72	34.71					
O_2	Oxygen (mmol/L)	198.8		192.9	193.7	210.5					

orders were identified (Table 1). This is 22 % of the total number of species recorded in the Southern Ocean and only three families are absent: the Arbaciidae, Urechinidae and Temnopleuridae.

New records and distribution data

Very few specimens of *Sterechinus dentifer, Kamptosoma asterias* and *Plexechinus planus* were previously recorded in the Southern Ocean (David et al. 2005, Fig. 2). The present new records increase significantly the biogeographic distribution and bathymetric range known so far. *K. asterias* is a new record in the Ross quadrant, and its depth range now extends from 3,304 m to 4,200 m. *S. dentifer* is new in the Weddell and Ross quadrants, and its depth range has been increased towards deeper waters, from 1,600 to 1,920 m. *P. planus* is a new record in the Ross quadrant, and its depth range has been increased from 603 to 1,152 m. Interestingly, the two last species were sampled in relatively high abundance as compared to previous records, and *P. planus* is even classified as ubiquitous (22 %) on the continental break and deep shelf of the Bellingshausen Sea (Fig. 3).

Abundance and species richness

Overall abundance values (*N* %) were rather low, except for high values at two stations [MB33 (29.06 %) and MB37 (29.2 %)], which are mainly due to high local abundance by specimens of *Sterechinus antarcticus* [MB33 (555 specimens) and MB37 (559 specimens)] (Figs. 3, 4). The next most abundant species were *P. planus* (117 specimens) and *S. dentifer* (63 specimens) (Fig. 3a, b, c). Highest values of species richness (S) were recorded at stations close to the ice shelf [MB34 (6 species) and MB36 (5 species)], while no echinoids were found at stations off Peter I Island during the two surveys (Fig. 4). The three most frequent families are the Echinidae, Schizasteridae and Cidaridae (Fig. 3b), for which samples are characterized either by the exclusive occurrence of a single species at almost all stations (Echinidae) or by a non-exclusive turnover among several species (Cidaridae and Schizasteridae) (Table 1).

Of the 17 species recorded, three species were classified as ubiquitous (>20 %): *S. antarcticus*, *Notocidaris mortenseni* and *P. planus*; three as very common (between 10 and 20 %)*: Amphipneustes lorioli, Notocidaris lanceolata* and *S. dentifer*; three as common (between 5 and 10 %):

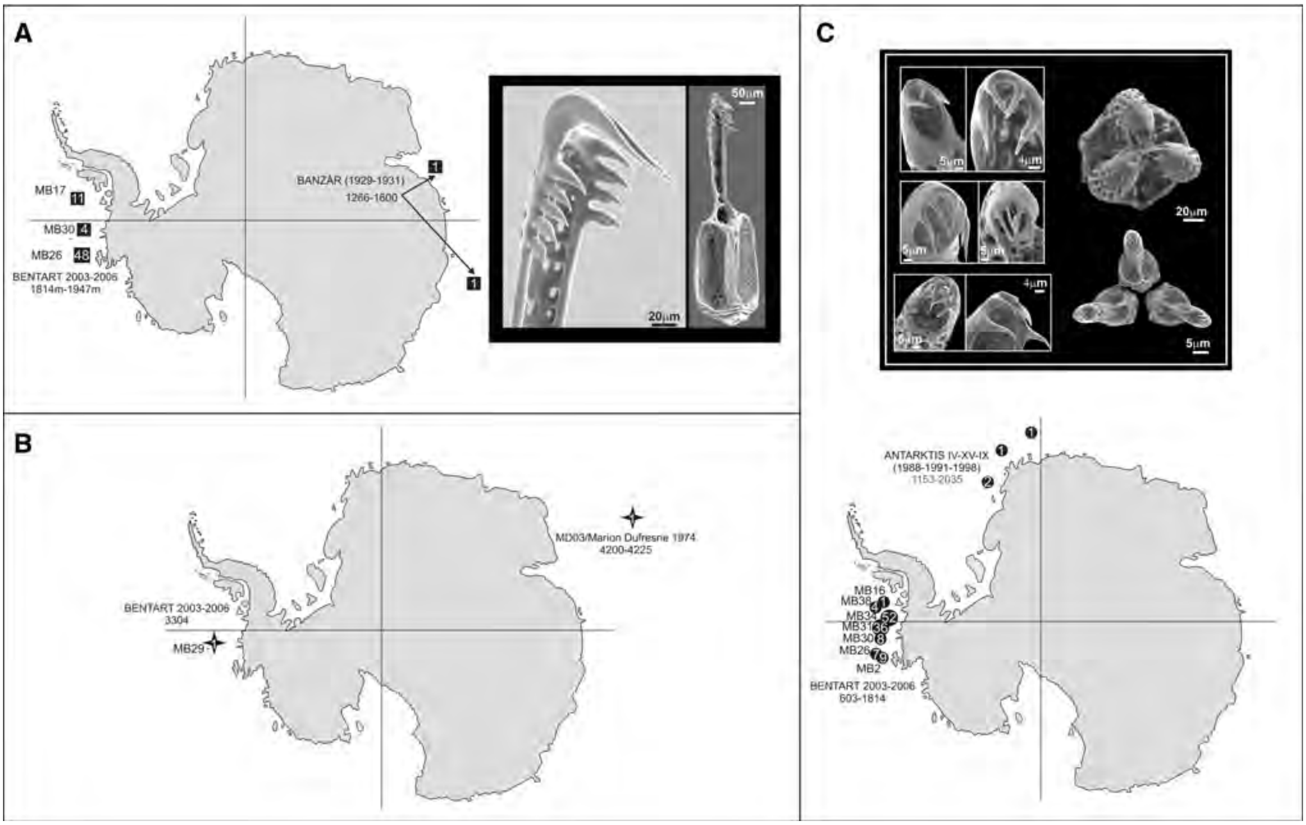


Fig. 2 Antarctic maps showing former and new records for *S. dentifer* (**a**), *K. asterias* (**b**) and *P. planus* (**c**) along with abundance data, BENTART stations and names of former expeditions (number of the specimens recollected at each station). SEM *pictures* of pedicellariae of *S. dentifer* (*bottom left*) and *P. planus* (*top left*). See also Table 1

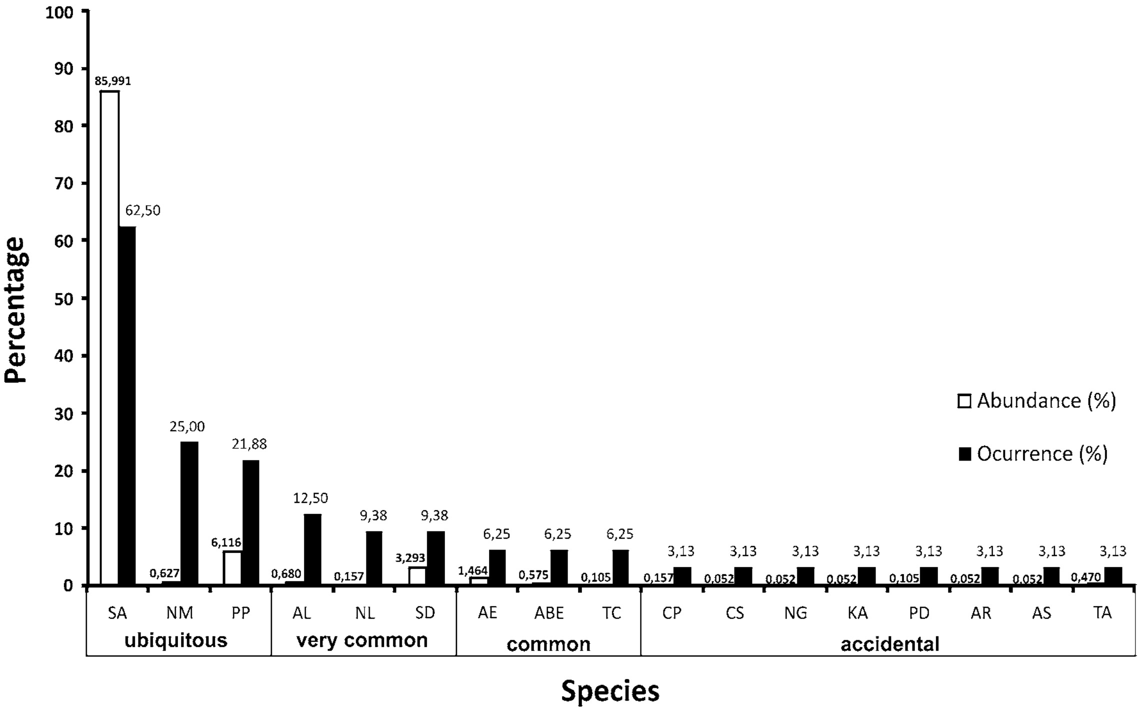


Fig. 3 Relative abundance (N %) and occurrence (%) across stations. Species ranking and classification according to the percentage frequency of occurrence (D): ubiquitous species (Ci > 20 %); very common species (10 % < Ci < 20 %); common species (5 % < Ci < 10 %); and rare or accidental species (Ci < 5 %) (Mora 1980; Manjón-Cabeza and García Raso 1994; Manjón-Cabeza and Ramos 2003). For abbreviations, see Table 1

Aporocidaris eltaniana, *Tripylus cordatus* and *Abatus elongatus*; eight (i.e. 47 % of species) as accidental species (<5 %): *Ctenocidaris perrieri, Ctenocidaris speciosa, Notocidaris gaussensis, Tripylus abatoides, Amphipneustes rostratus, Amphipneustes similis, A. lorioli* and *K. asterias*; and *Pourtalesia debilis* (Fig. 3d).

Fig. 4 Total abundance data (*right*) and species richness (*left*). Stations ordered by longitude from *left* (west) to *right* (east)

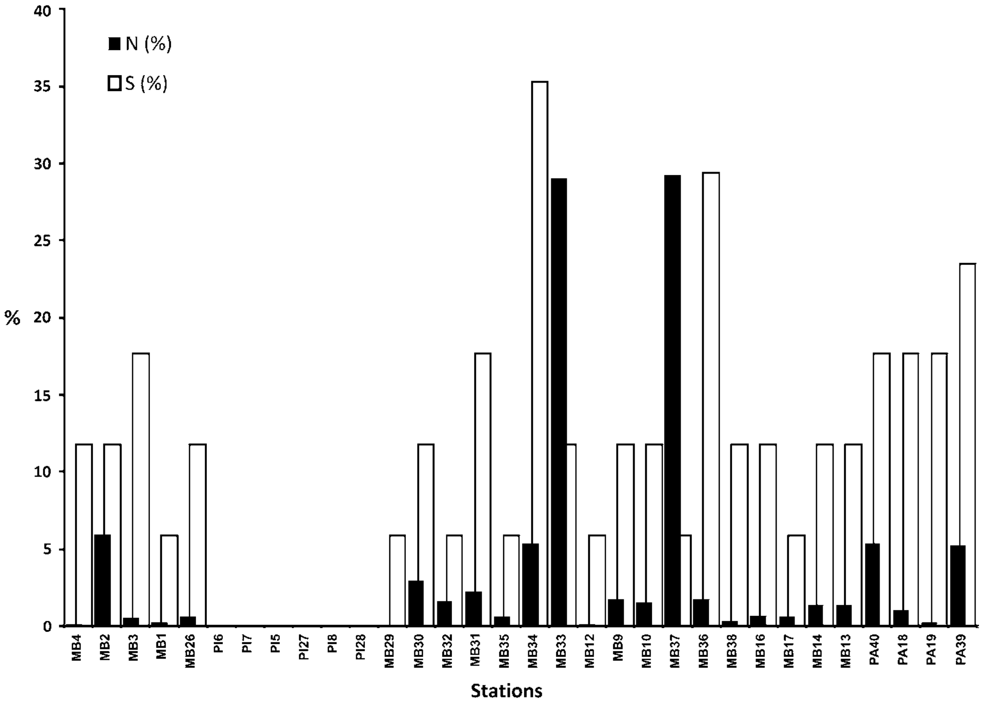
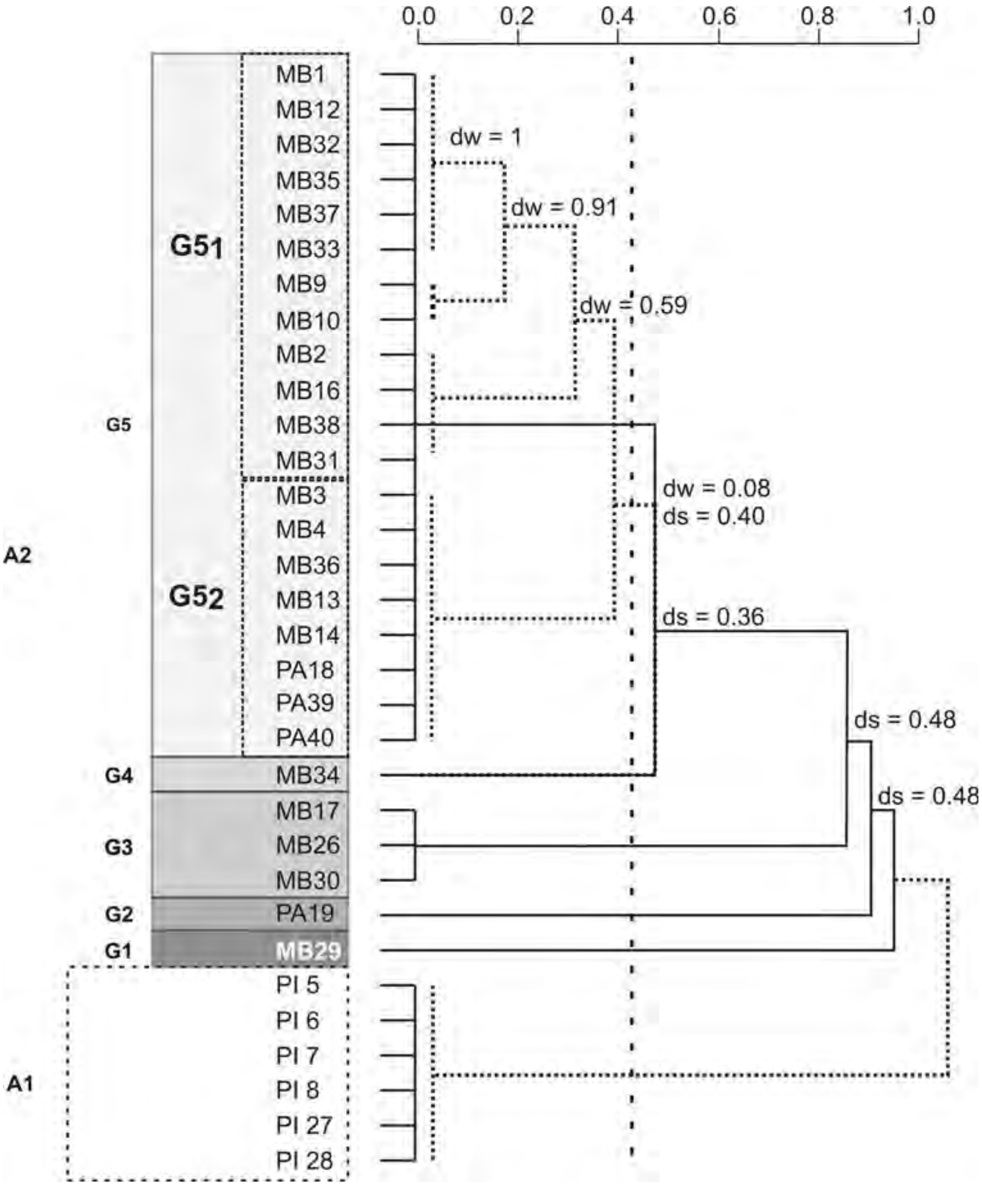


Fig. 5 Qualitative analysis of similarity (Baroni–Urbani index and UPGMA agglomeration algorithm). The segregations versus aggregations are explained in the text ("Results"). *dw* Significant weak boundary, *ds* significant soft boundary



Echinoid assemblages

The cluster analysis (Fig. 5) shows a clear partitioning between two well-defined areas: A1 (Peter I Island) and A2, stations with low values of species richness except for two of them (MB34 and MB36) (Figs. 3, 6). In the A2 grouping, cluster (Fig. 5) and correspondence (Fig. 8) analyses show the existence of five distinctive assemblages separated by strong boundaries and two subgroups by a weak boundary. Species composition of echinoid assemblages is characterized as follows.

A1	All the stations of Peter I Island are devoid of echinoids
A2	All the other stations of the Bellingshausen Sea are clustered into the five following assemblages:
G1	The only true abyssal station characterized by the exclusive presence of *K. asterias*
G2	Station characterized by two species that are absent from other stations: *A. similis* and *C. perrieri*. Echinidae (*S. antarcticus* and *S. dentifer*) are absent
G3	Three stations characterized by low abundance and species richness values, and the presence of the deep Echinidae *S. dentifer*
G4	Station characterized by high abundance and richness values (Figs. 4, 7). Species richness is provided by Schizasteridae and abundance values due to the Plexechinidae *P. planus* and the Echinidae *S. antarcticus*. Cidaridae are absent from the station

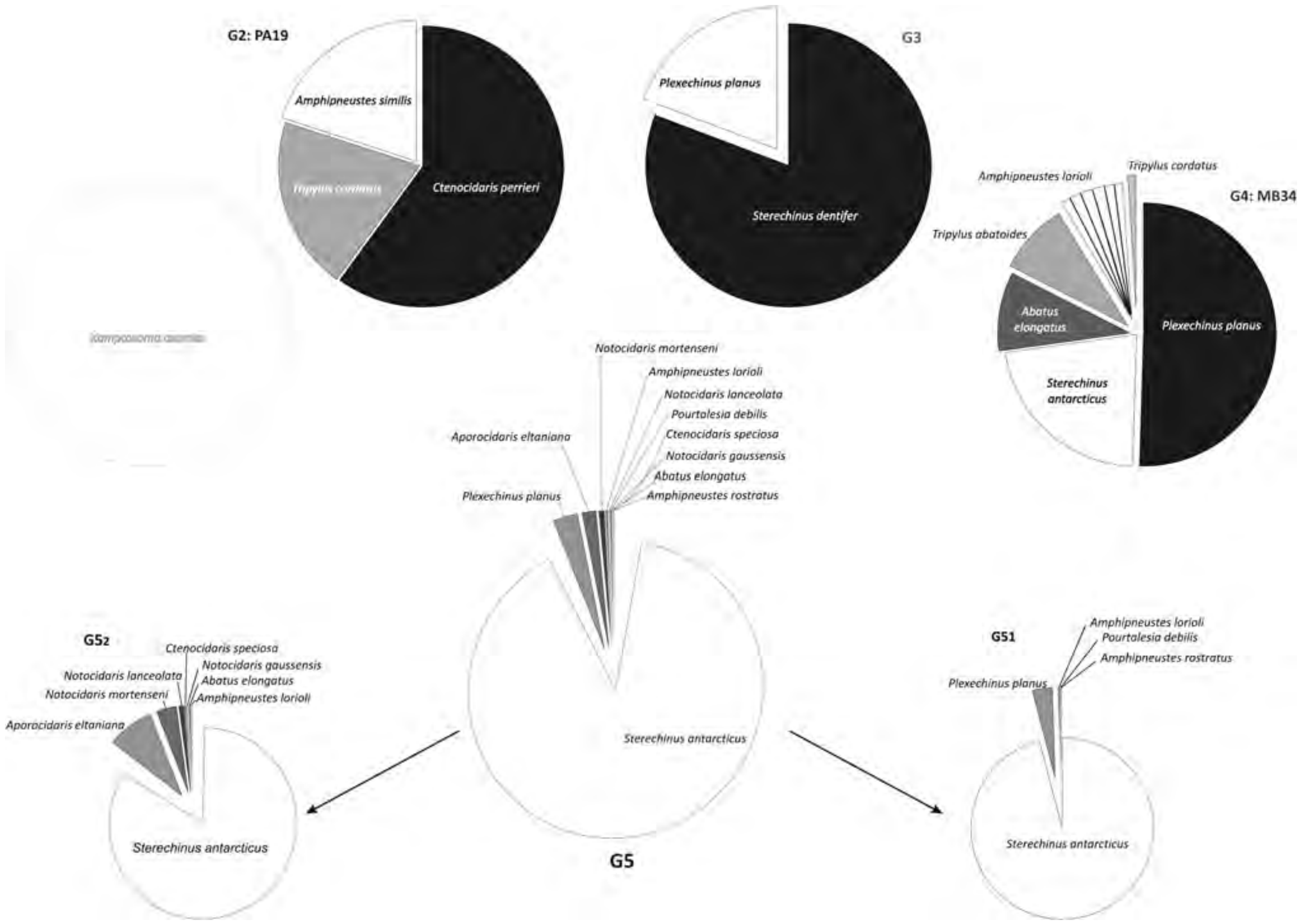
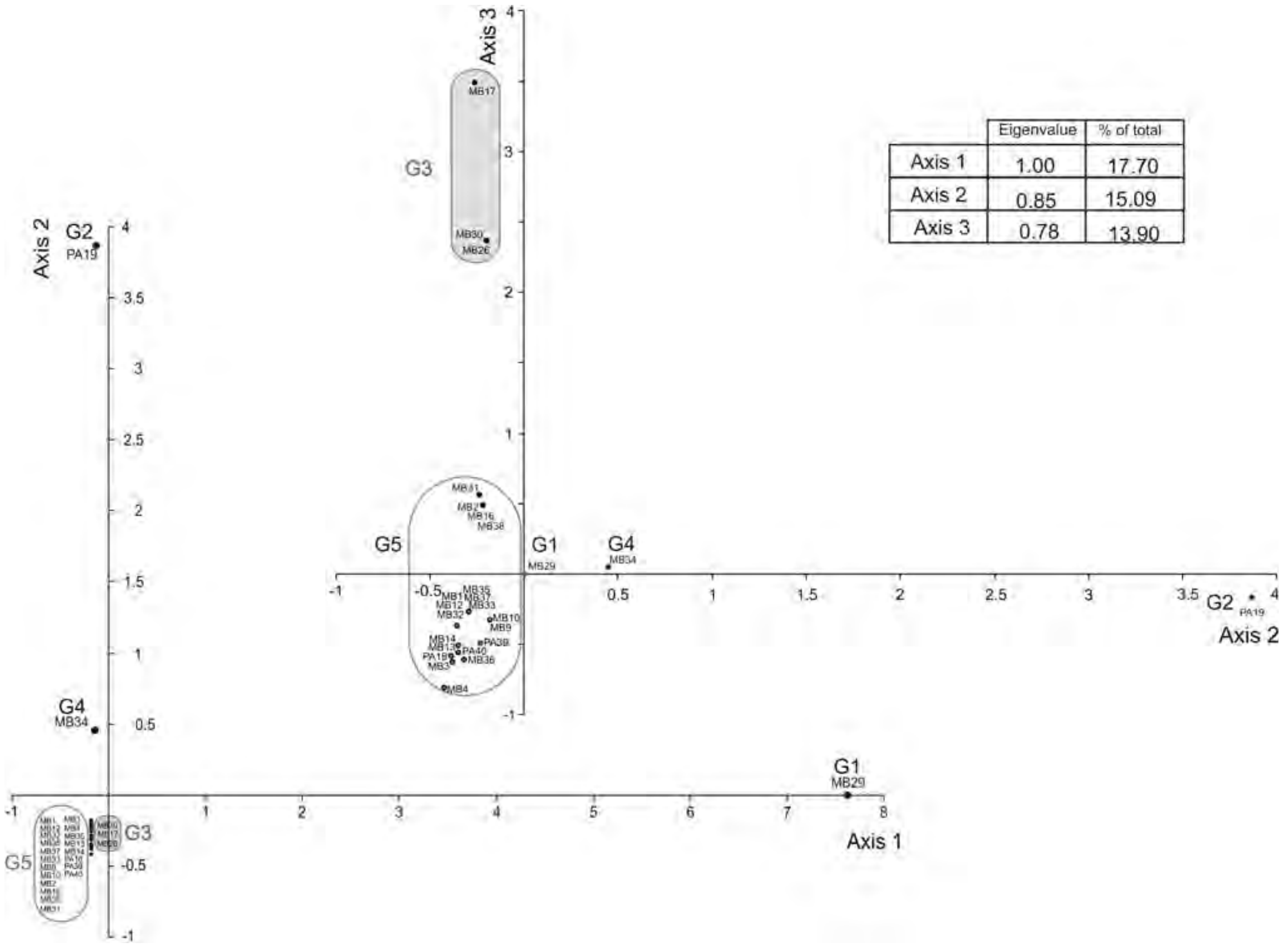


Fig. 6 Composition (abundance %) of echinoid assemblages as defined by the hierarchical cluster analysis and supported by the Baroni–Urbani coefficients

G5	Abundance is dominated by the Echinidae *S. antarcticus*. No distinction is shown on first axes of the CA (Fig. 8), though the two following subsets are separated by a weak boundary (Fig. 5):
G5(1)	The common feature is the low species richness, only one or two species associated with the ubiquitous *S. antarcticus*, most often *P. planus* or *A. lorioli* depending on depth
G5(2)	Stations characterized by high values of species richness (Figs. 4, 7), mainly due to Cidaridae

The environmental control of echinoid assemblages

Depth, sediment redox values, mud and OD % contents were retained as explanatory variables, and a CCA analysis was carried out to project biotic data in the space of the four environmental variables herein (Fig. 8). Stations from Peter I Island were excluded from the analysis as the CCA does not support that all variable values equal ‘0’. The two first axes (eigenvalues: $\lambda_1 = 0.60$; $p < 0.001$ and $\lambda_2 = 0.36$; $p = 0.006$ with 10,000 replicate permutation test) clearly show a good match between the four selected environmental variables and echinoid assemblages (Fig. 8). Depth appears as the main factor that controls the dividing of echinoid assemblages into the deep-sea (G1), the slope (G3) and the continental shelf (G4 + G5). Redox values, mud and OD % contents seem to control the partitioning of assemblages on the continental shelf (between G4 and G5, and within G5). Echinoid species were plotted on the two first axes of the CCA to visualize their respective environmental preferences. The main distinction can be made between species exclusive of the deep basin (*K. asterias*), those of the continental slope (*S. dentifer*), the deep species present both on the slope and the shelf (*P. planus*) and species exclusive of the shelf (*S. antarcticus,* Schizasteridae and Cidaridae). Cidaridae are mainly distinguished by their preference for sediments rich in mud and organic matter whereas Schizasteridae are more frequent in low-organic sandy sediments.



	Eigenvalue	% of total
Axis 1	1.00	17.70
Axis 2	0.85	15.09
Axis 3	0.78	13.90

Fig. 7 Correspondence analysis. Groups were defined by the hierarchical cluster analysis and supported by the Baroni–Urbani coefficients

Discussion

Is the Bellingshausen Sea really impoverished in echinoids?

The BS is sometimes considered as a vast 'benthic desert' controlled by oligotrophic conditions (Sáiz-Salinas et al. 2008; San Vicente et al. 2009) and intense iceberg traffic (Peck et al. 1999; Gutt 2000). In the Weddell and Ross Seas, dense 3-D communities of filter feeders have been reported, while such a spatial complexity and diversity of habitats seem to be absent from the BS (San Vicente et al. 2009). During BENTART expeditions, eleven new records were added to the catalogue of echinoid species present in the BS. The total number of echinoid species now recorded in the BS is nineteen that is almost 25 % of Antarctic echinoid species. At least for echinoids, the BS is not particularly impoverished compared with previous considerations.

The absence of echinoids off Peter I Island is remarkable and contrasts with other taxa that were sampled there: fish (Matallanas and Olaso 2007), suprabenthic fauna (San Vicente et al. 2009), decapods (García Raso et al. 2005) gastropods and bivalves (Aldea et al. 2008; Troncoso and Aldea 2008). However, the low values of benthic species richness and of diversity reported (Matallanas and Olaso 2007; San Vicente et al. 2009) along with high local abundance of a few species (Troncoso and Aldea 2008) suggest the prevalence of peculiar ecological conditions. The absence of echinoids could be explained either by unsuitable physical or unfavourable biological conditions, or both. The importance of passive dispersal of larvae by currents to colonization processes were emphasized by Matallanas and Olaso (2007). Brooding is a common feature of many Antarctic echinoids, but frequent species such as *S. antarcticus*, *S. dentifer* and *P. planus* are indirect developers with mobile larvae (Brey and Gutt 1991; David et al. 2005), and recent investigations showed that non-brooders (echinoids) can disperse and colonize shallow waters of remote areas after ice-shelf collapse and intense ice disturbance (Saucède 2008). Peter I Island is a volcanic island that acts as a topographic barrier to currents and shifts the course of the westward-flowing bottom current in

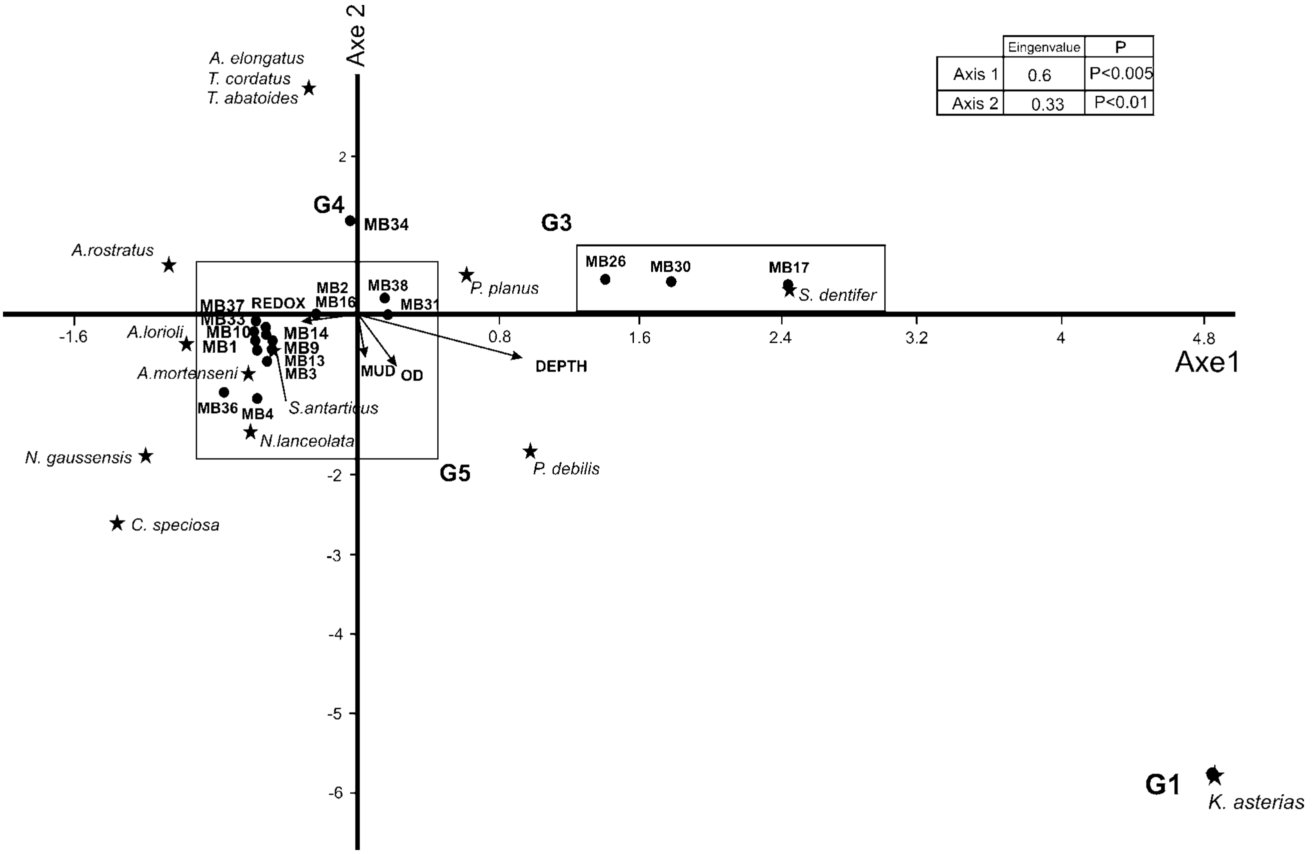


Fig. 8 Canonical correspondence analysis (CCA). Eigenvalues are $\lambda_1 = 0.60$ ($p = 0.0016$) and $\lambda_2 = 0.33$ ($p = 0.0075$) for the two first axes (significance tested by 10,000 replicate permutations). Groups were defined by the hierarchical cluster analysis and supported by the Baroni–Urbani coefficients

the BS (Scheuer et al. 2006). Current conditions are unlikely to affect dispersal of echinoid larvae to Peter I, as it does not seem to impede dispersal of other taxa. The prevalence of low-organic sediments, low salinity and redox values in Peter I island might reduce the survival of settling echinoid larvae, although echinoids occur under comparable conditions elsewhere.

At the moment, the absence of echinoids is best explained by local benthic conditions, characterized by low-organic sediments along with low salinity and redox values, which might impede echinoid settlement and survival off Peter I Island.

What is the structure of echinoid assemblages?

The structure of echinoid assemblages is essentially related to the distribution and abundance of Echinidae: *S. dentifer* on the continental break and *S. antarcticus* on the continental shelf. The abyssal echinoid *K. asterias* characterizes the deep-sea basin. On the continental shelf, assemblages are determined by cidarid distribution. Schizasteridae and Cidaridae are by far the most diversified echinoid families in the Southern Ocean (David et al. 2005). Schizasteridae were collected at all stations of the continental shelf, whereas Cidaridae were sometimes missing. Interestingly, Schizasteridae and Cidaridae were not collected outside the shelf, though both families are represented by deep-sea species in the Southern Ocean (David et al. 2005).

Abundance, species richness and diversity values are low in the deep-sea basin and on the continental break (Figs. 3, 7), but there is no significant trend of decreasing values with depth on the continental shelf. This is consistent with previous results on bivalves and gastropods (Aldea et al. 2008).

Which are the environmental factors that best match the structure and spatial distribution of echinoid community?

Depth and sediment characteristics, mainly redox values, organic and mud contents have been reported to be controlling benthic assemblages on the continental shelf of the BS (Sáiz-Salinas et al. 2008; Troncoso and Aldea 2008; San Vicente et al. 2009). Current intensity, bottom morphology and ice disturbance (iceberg scouring) have been pointed out too (Starmans et al. 1999; Gutt 2000; Barry et al. 2003; Sáiz-Salinas et al. 2008), while others noticed the importance of life strategies and dispersal capabilities (Aldea et al. 2008; Matallanas and Olaso 2007).

Depth is the factor that best discriminates among main echinoid assemblages, which are divided into the deep-sea basin, the continental slope and the shelf. On the shelf, sediment characteristics—redox values, organic and mud contents—best explain the distribution patterns of Schizasteridae and Cidaridae. The significant contribution of sediment characteristics on echinoid distribution can be explained by differences in food ranges and feeding strategies among echinoid families that feed and live on the sediment. This is also explained by a stronger control of sediment characteristics on the distribution of specialist feeders (Schizasteridae and Cidaridae) than on that one of generalists (Echinidae) (Jacob et al. 2003; David et al. 2005). Schizasteridae are deposit-feeders that are able to plough and burrow into the sediment, and some can tolerate relatively low-organic sandy substrates. In contrast, Cidaridae are epibenthic echinoids and mostly scavengers that are more dependent on the biomass and type of organic deposits (animal matter or organic detritus) present on the sea floor (De Ridder and Lawrence 1982; David et al. 2005).

In the present work, depth just discriminates between the two species of Echinidae, *S. antarcticus* and *S. dentifer* but not among species of Cidaridae nor Schizasteridae. The genus *Sterechinus* is the only Antarctic representative of the family Echinidae and is represented by three species—*Sterechinus neumayeri*, *S. antarcticus* and *S. dentifer*—which occupy different depth ranges (Brey and Gutt 1991; David et al. 2005). Patterns of distribution among species of Schizasteridae and Cidaridae are much less clear (David et al. 2005).

Conclusion

This study shows how complex it can be to interpret distribution patterns when different factors—herein, depth and sediment characteristics—interfere at different scales (geographic and taxonomic) to control biotic assemblages.

On a large scale, the impact of environmental parameters such as depth and sediment characteristics on benthic assemblages has been questioned (Gutt 2000). In the BS, echinoid assemblages were partly explained by those parameters. However, complementary studies of other parameters might help understand more clearly the relationship between those patterns and environmental parameters.

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Evolutionary pathways among shallow and deep-sea echinoids of the genus *Sterechinus* in the Southern Ocean

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ABSTRACT

Antarctica is structured by a narrow and deep continental shelf that sustains a remarkable number of benthic species. The origin of these species and their affinities with the deep-sea fauna that borders the continent shelf are not clear. To date, two main hypotheses have been considered to account for the evolutionary connection between the faunas: (1) either shallow taxa moved down to deep waters (submergence) or (2) deep-sea taxa colonized the continental shelf (emergence). The regular sea urchin genus *Sterechinus* is a good model to explore the evolutionary relationships among these faunas because its five nominal species include Antarctic and Subantarctic distributions and different bathymetric ranges. Phylogenetic relationships and divergence times among *Sterechinus* species were established using the COI mitochondrial gene by assuming a molecular clock hypothesis. The results showed the existence of two genetically distinct main groups. The first corresponds exclusively to the shallow-water Antarctic species *S. neumayeri*, while the second includes all the other nominal species, either deep or shallow, Antarctic or Subantarctic. Within the latter group, *S. dentifer* specimens all formed a monophyletic cluster, slightly divergent from all other specimens, which were mixed in a second cluster that included *S. agassizi* from the continental shelf of Argentina, *S. diadema* from the Kerguelen Plateau and *S. antarcticus* from the deep Antarctic shelf. These results suggest that the deeper-water species *S. dentifer* and *S. antarcticus* are more closely related to Subantarctic species than to the shallow Antarctic species *S. neumayeri*. Thus, for this genus, neither the submergence nor emergence scenario explains the relationships between Antarctic and deep-sea benthos. At least in the Weddell quadrant, the observed genetic pattern suggests an initial separation between Antarctic and Subantarctic shallow species, and a much later colonization of deep water from the Subantarctic region, probably promoted by the geomorphology of the Scotia Arc.

1. Introduction

The Southern Ocean comprises the southernmost waters of the World Ocean south of 60°S latitude, as designated by the International Hydrographic Organization in 2000. It also marks the Antarctic Treaty System. However, we consider as a more likely biological (or biogeographical) limit the Antarctic Circumpolar Current (ACC) which is the largest wind-driven current on Earth. It goes all the way around the globe and connects the Atlantic, Pacific and Indian Oceans. The ACC is a massive flow of water that acts as a barrier separating the Southern Ocean from more northern oceans. The current extends from the sea surface to depths of 4000 m and can be more than 200 km wide. Usually, the ACC encompasses all water masses from the ocean surface down to the sea floor (Witworth, 1988). It is a very cold current with temperatures ranging from −1 to 5 °C depending on the time of the year, and with speeds up to 3.7 km per hour. However, the ACC is not a uniform current. It consists of a series of fronts that are associated with deep jets distributed in the meridian direction and encircling the Antarctic continent. The Southern Ocean has several unique environmental characteristics, such as presenting little stratification within the water column and being the main source of cold water for the deep zones of all the oceans (Brandt et al., 2007).

The marine fauna of the Southern Ocean substantially differs from that of other regions due to the geological history of the Antarctic continent and the extreme environmental conditions to which species are subjected (Clarke, 1983; Aronson and Blake, 2001; Peck, 2002). The isolation of the fauna began with the fragmentation and dispersion of the blocks that formed the Gondwana supercontinent and finished with the opening of the Drake Passage. Lawver and Gahagan (2003) stated that the Drake's Passage was definitely open by 28.5 Ma. It is also stated that it was probably open to deep-water circulation as early as 30 Ma (Barker and Burrell, 1977; Barker and Thomas, 2004) or 31 ± 2 Ma

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(Lawver and Gahagan, 2003). Other recent estimates place this opening at approximately 24 Ma, near the time of the Oligocene-Miocene boundary (Pfuhl and McCave, 2005; Lyle et al., 2007). After the effective separation of South America from the Antarctic Peninsula, three types of barriers were installed around the Antarctic Continent: geographic, oceanographic and bathymetric (Lawver et al., 1992; Crame, 1999; Clarke and Barnes, 2005; Pfuhl and McCave, 2005; Tripati et al., 2005). These barriers have helped produce a rich endemic fauna on the continental shelf and slope that surrounds the Antarctic continent (Poulin et al., 2002; Clarke and Johnston, 2003; Clarke et al., 2005; Thatje, 2005). Griffiths et al. (2009) considered it as a differentiated biogeographic province, with only a few internal differences between the Eastern and Western regions. The Antarctic continental shelf is quite narrow and unusually deep, about 450 m and up to 1000 m in some places; its macrobenthic fauna is characterized by a high diversity (Brey et al., 1994), that probably includes more than 15,000 species (Gutt et al., 2004), mainly polychaetes, bryozoans, pycnogonids, amphipods and echinoderms (Clarke and Johnston, 1996). Another notable characteristic of the fauna is that it has eurybathic species compared to the continental shelf fauna of other continents (Brey et al., 1996).

In spite of the isolation established millions of years ago, Arntz et al. (2005) suggested a strong biogeographic union between the marine benthic faunas of the Antarctic Peninsula and the Magellanic region, explained by the geologic history of the two continents. Dell (1972) recognized the possibility of interchange of species after the separation of the continents, arguing that the ACC and the Polar Front would not have acquired sufficient intensity at the beginning of the tectonic process (Barker and Thomas, 2004; Hassold et al., 2009). Also, the reports of larvae and adult individuals of a group historically absent from the Antarctic convergence in 2002 (zoea larvae of brachyuran decapods and individuals of the spider crab *Hyas aranaeus*) have led several authors to suggest a re-establishment of connection between the faunas of Antarctica and South America due to a weakening of the current (Thatje and Fuentes, 2003; Tavares and De Melo, 2004). Although the studies of Thatje and Fuentes (2003) and Tavares and De Melo (2004) emphasized their observations in the current climatic situation, in which anthropogenic interference may play a fundamental role (e.g., climatic change, ballast water transport), they also opened the debate about possible contacts between faunas during the interglacial periods of the Pleistocene as a consequence of oceanographic changes during these episodes. More generally, some authors have suggested that neither the ACC nor the PF are absolute barriers (Stanchowicz et al., 2002; Page and Linse, 2002), while others hypothesized the existence of cryptic species rather than a permeability of the PF barrier (Thornhill et al., 2008).

Based on the similarity between the marine benthic fauna of the Antarctic continental shelf and that of the surrounding deep areas, many authors have proposed a continuity of the benthic fauna by means of the abyss, which would allow a connection with the Subantarctic and Magellan zones (Clarke and Crame, 1997; Held, 2000; Rogers, 2000; Briggs, 2003; Gage, 2004; Clarke et al., 2005, Brandt et al., 2007; Strugnell et al., 2008). The wide bathymetric distribution of the isopod crustaceans in the Southern Ocean revealed a complex evolutionary history, which has opened a discussion on the evolutionary relationships between shallow-water and deep-water faunas in the Antarctic Ocean (Menzies et al., 1973). Two main hypotheses have been proposed to explain the evolutionary relations of these faunas: (1) evolutionary polar submergence, in which taxa moved from shallow water to deeper waters; and (2) evolutionary polar emergence, in which taxa colonized the continental shelf from the deeper waters (Menzies et al., 1973; Zinsmeister and Feldmann, 1984; Clarke and Crame, 1989; Brandt, 1991, 1992; Crame, 1999; Brandt et al., 2007; Aronson et al., 2008).

The climatic history of the Antarctica with its successive glacial periods may suggest that the submergence hypothesis would be more effective in order to explain evolutionary relationships between congeneric species belonging to the two faunas. Sedimentary registers indicated that during the glacial periods the continental ice extended farther than the border of the continental shelf (Grobe and Mackensen, 1992), thus the survival of the benthic communities would only have been possible on the slope or in the depths (Brey et al., 1996). This suggests that the wide bathymetric distribution of the species of the Antarctic continental shelf reflects the oscillations in the extension of the ice shelf, supposing that these were the species that could re-colonize the shelf when the ice receded during the following interglacial period (Thatje et al., 2005; Aronson et al., 2008). Physiological adaptations (i.e. to pressure) in order to survive during these periods of deep-water refuges for shallow-water species were hypothesized (Clarke and Johnston, 2003); these adaptations could be the key to the colonization of the deeper zones. However, the emergence hypothesis cannot be discarded, since the constant physical regime of the Antarctic Ocean, which is close to the conditions in deep water, would allow colonization of the shallow zone by benthic species of the deep ocean (Dayton and Oliver, 1977; Brandt et al., 2007). In addition, as Berkman et al. (2004) suggested, the similarity between deep-water and shallow-water habitats may have been greater during glacial periods. The presence of an extensive ice field on the shelf and continental slope would have changed the conditions of sedimentation and greatly reduced the light and primary productivity, allowing the colonization of the continental shelf by abyssal organisms (Berkman et al., 2004). Brandt et al. (2007) suggested that the advance and retreat of the shelf ice during the succession of glacial-interglacial cycles, which pushed species to the deeper ocean or caused their extinction, would have caused a combination of emergence and submergence in the margins of the Antarctic.

Spatial analyses of genetic lineages are necessary in order to reconstruct the evolutionary history of Antarctic species. However, studies of this type are relatively scarce in Antarctica, due to the logistic difficulty in obtaining representative samples of populations and species, especially from deep waters. The programs “Evolution and Biodiversity in Antarctica: the response of life to change” (EBA), “Census of Antarctic Marine Life” (CAML), and the development of the International Polar Year (2007-2009) have facilitated such studies. They contributed to the inventory of current biodiversity and improved our understanding of the Antarctic marine ecosystem, by means of multi-scale studies and promoting cooperation among investigators. These efforts have facilitated phylogenetic studies in the last few years; most efforts have been concentrated on crustaceans, fish and mollusks, and have allowed us to tackle wider questions about habitat colonization, patterns of occurrence of species and the evolution of adaptations (Stanchowicz et al., 2002). However, studies that examine the evolutionary relationships between shallow and deep-sea faunas of the Antarctic Ocean are still scarce (Held, 2000; De Mesel et al., 2006; Brandt et al., 2007; Strugnell et al., 2008).

The regular sea urchin genus *Sterechinus* (family Echinidae, order Echinoida) is represented by five nominal species distinguished by morphological and biogeographical criteria. Fertilization is external and development includes a planktonic larva (Bosch et al., 1987). Three of the five species are found all around Antarctica: *S. neumayeri* (Meissner, 1900) is the most abundant regular echinoid in shallow waters (Clarke., 1992); its depth ranges from a few meters to 810 m; *S. antarcticus* (Koehler, 1901) is dominant below 450 m, although it has a wide bathymetric range (30 – 2000 m); while *S. dentifer* (Koehler, 1926) has a much more restricted and deeper range (1200 – 1600 m) (David et al., 2005a). The Subantarctic species are *S. diadema* (Studer, 1876), which is considered as endemic to the Kerguelen shelf between 15 and

750 m, and *S. agassizii* (Mortensen, 1910) found between 55° and 35°S along the Argentinian continental shelf and characterized by a wide bathymetric distribution (10 to about 1000 m, most typically at about 200 m) (David et al., 2005a). These contrasting geographic and depth ranges make this genus a good model: (1) to determine when Antarctic and Subantarctic marine faunas loosed contact and started to follow independent evolutionary histories; and (2) to elucidate the evolutionary relationships between shallow and deep-water faunas in the Southern Ocean, testing both hypotheses of polar submergence and emergence.

2. Material and methods

Specimens of *S. neumayeri* were obtained from the shallow zone of the Antarctic Peninsula and the eastern region of this continent, while *S. diadema* and *S. agassizi* were obtained from the Kerguelen Archipelago and the continental shelf of Argentina, respectively. In the case of deep-water species, *S. dentifer* were dredged from Bellinghausen Sea, while *S. antarcticus* samples were obtained from both the Antarctic Peninsula and East Antarctica (Fig. 1, Table 1).

2.1. Extraction, amplification and sequencing

Total DNA was extracted from gonadal tissue or spines of 193 specimens using the salt method (Aljanabi and Martínez, 1997). PCR was used to amplify the mitochondrial Cytochrome Oxidase gene, using the primers described by Lee et al. (2004), LCOI1490 (5′– TCTA CAA ACC ACA ARG AYA TTG G -3′) and HCOIN (5′– CCC ATT GAA AGA ACG TAG TGA AAG TG -3′). A fragment of 945 bp was amplified, which corresponds to a part of the COI gene of *S. neumayeri*, from nucleotide 65 to 1009 (Genbank accession AY275548, size 1077 pb). However, due to the low quality of samples from the Subantartic region (degraded DNA), it was necessary to design intermediate primers from the sequences obtained in *S. neumayeri*; ERZin-F (5′- GAC CGA CTG CCC TTA TTT -3′) and ERZin-R (5′- CTC GCT TTC CTG AGT AGT -3′). Polymerase chain reactions (PCR) were carried out in a Thermo PxE 0.5 thermocycler using Taq DNA polymerase (Invitrogen, Recombinant, 500 U) under standard amplification conditions with 25 μL of reaction volumes. Each reaction tube contained: 1 μL (approx 10 ng) of genomic DNA extract, 2.5 μL 10XPCR buffer, 1.5 Mm $MgCl_2$, 2.5 μL 10 mM each dNTP, 10 picomoles of each primer, 0.2 U Taq polymerase. After 7 min of initial heating at 95 °C, amplification was performed in 35 repetitions of a three-step cycle (denaturation, 95 °C for 1 min; annealing, 58 °C for 1.5 min; extension, 72 °C for 1.5 min) and a final extension for 10 min. PCR products were purified with Qiagen Qiaquick columns and the sequencing was done by the Korean company Macrogen, in an ABI 3100 automatic sequencer (Applied Biosystems); the sequences obtained were aligned with the programs Proseq v. 2.91 (Filatov, 2002) and ClustalX 1.8 (Thompson et al., 1997).

Table 1
Number of sequences obtained and analyzed of species of the genus *Sterechinus*.

Species	Geographic origen	Number of sequences
Sterechinus neumayeri	Antarctic Peninsula	116
	Terre Adélie (East Antarctic)	15
Sterechinus antarcticus	Antarctic Peninsula	3
	Terre Adélie (East Antarctic)	2
Sterechinus dentifer	Antarctic Peninsula	4
Sterechinus diadema	Kerguelen Island	13
Sterechinus agassizi	Argentinian continental shelf	40

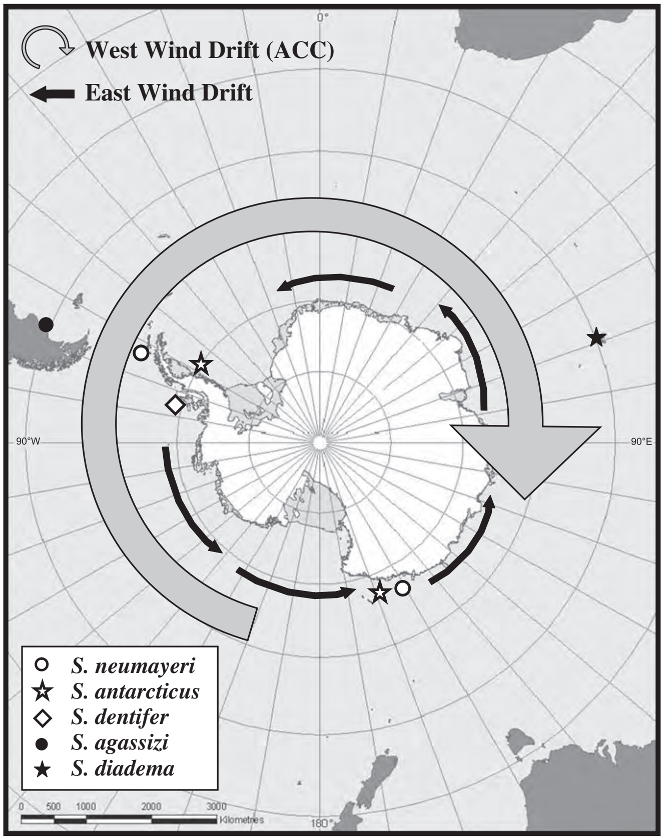

Fig. 1. Sample collection sites of species of the genus *Sterechinus*. The two different arrows indicate the main oceanographic currents of the Southern Ocean.

2.2. Genealogical and phylogenetic relations among shallow and deep-water species

The genealogical relations among haplotypes of the shallow and deep-water species were graphed by median joining using the program Network 4.1.5 (Röhl, 2002). In addition, we calculated the pairwise genetic p-distances between pairs of morphospecies with the program Arlequin 3.1 (Excoffier et al., 2005).

For phylogenetic reconstruction within *Sterechinus* we used as outgroup two species of the same family Echinidae: *Gracilechinus multidentatus* (Genbank access EU869929.1) and *Loxechinus albus* (Genbank access AY275550.1). Phylogenetic trees were constructed by maximum parsimony (MP) and maximum likelihood (ML) methods using PAUP* program (version 4.0b10; Swofford, 1999). For MP all sites were treated as unordered characters with equal weight, using the heuristic search method with the addition of ordered sequences and branch swapping (TBR Branch Swapping algorithm). ML analysis was carried out using the substitution model of sequence evolution HKY+I inferred from ModelTest (Posada and Crandall, 1998). Support for branches was estimated using bootstrap re-sampling with 1000 replicates in MP and ML analyses (Felsenstein, 1981). We also performed Bayesian phylogenetic analyses with the program MrBayes v.3.1.2 (Huelsenbeck and Ronquist, 2003), using the substitution model GTR+G as recovered by the MrModeltest program (Nylander, 2004). This method estimates the posterior probability that each taxon recovered is a monophyletic unit. All the Markov Chain Monte Carlo analyses (MCMC) were performed twice, using independent runs with random trees for a total of 5×10^6 generations. Trees were sampled every 500 generations and the first 1000 trees discarded; the rest were used to construct a consensus phylogram with the majority rule and posterior probability for the nodes. Phylogenetic reconstructions for all search criteria were performed with a subsample of the most representative haplotypes of each species.

2.3. Divergence time estimation

Divergence times among *Sterechinus* species were estimated with BEAST version 1.5.3 (Drummond and Rambaut, 2007), using the two substitution rates of COI sequence calibrated by Lee et al. (2004), 0.51 and 0.72% Ma^{-1}, for species of the family Echinidae. This is a Bayesian Markov chain Monte Carlo method that incorporates a strict clock model and for this reason, the heterogeneity of evolutionary rates among the branches was checked by the log likelihood ratio test (Felsenstein, 1981) between the clock-enforced ML tree and the non-enforced ML tree ($-\mathrm{lnL}=2601.6390$ and $-\mathrm{lnL}=2597.9814$, respectively), using DAMBE (Xia and Xie, 2001). We assumed a Yule speciation process, as recommended for species-level phylogenies (Drummond and Rambaut, 2007). The HKY+I substitution model was used for the two substitution rates, and we used default prior distributions for all other parameters. Each independent analysis was performed with MCMC chain runs for 50 million generations and the parameters were sampled every 1000 generations.

For each BEAST analysis, the divergence time and its confidence interval for the species of the *Sterechinus* was assessed using the software Tracer Version 1.5 (Drummond and Rambaut, 2007).

3. Results

3.1. Genealogical relations among shallow- and deep-water species from Antarctic and Subantarctic regions

The haplotype network of the shallow- and the deep-water species of the genus *Sterechinus* showed the existence of two highly divergent groups, separated by 56 fixed substitutions. The first group included all haplotypes of the shallow Antarctic species *S. neumayeri*, while the second gathered all haplotypes of shallow subantarctic species as *S. diadema* from the Kerguelen Archipelago and *S. agassizii* of the Argentinian continental shelf, as well as those species typically found in deep water, *S. dentifer* and *S. antarcticus* (Fig. 2). The network showed that haplotypes of deep-water species have a much closer relation with the shallow-water species of the Subantarctic region than with the shallow-water Antarctic species *S. neumayeri*. While *S. antarcticus* shared the most frequent haplotype with the Subantarctic group, the four specimens of *S. dentifer* clustered into a differentiated haplogroup. The p-distance values showed that *S. neumayeri* had about 5% sequence difference with all other species of the genus, while the rest of the species (deep Antarctic and shallow Subantarctic) had values of less than 0.7% (Table 2). Considering only shallow-water species, large p-distance values separated Subantarctic and the Antarctic species (about 6%), while the values between samples of *S. neumayeri* from the East and West Antarctic and between S. *diadema* and *S. agassizi* were only 0.08% and 0.03%, respectively (Table 2).

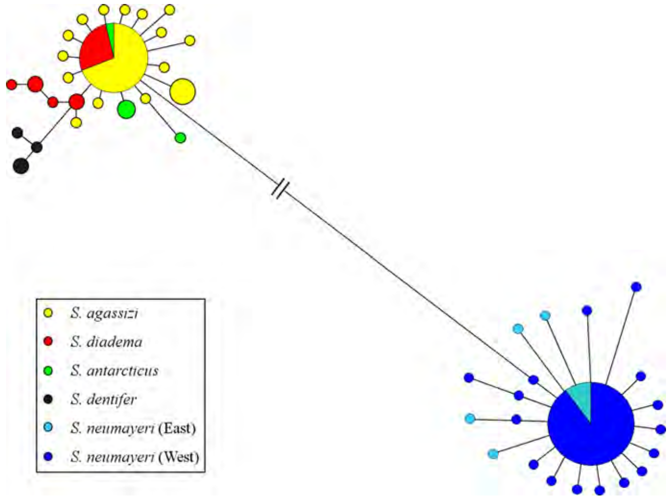

Fig. 2. Median Joining Haplotype network showing the genealogical relations among all species of the genus *Sterechinus*.

Table 2
Pairwise p-distances values (above diagonal), among species of the genus *Sterechinus.*

Species	*S. neumayeri*	*S. agassizi*	*S. diadema*	*S. antarcticus*	*S. dentifer*
S. neumayeri	----	5.99	5.95	5.94	5.96
S. agassizi	-	----	0.20	0.24	0.60
S. diadema	-	-	----	0.24	0.51
S. antarcticus	-	-	-	----	0.65
S. dentifer	-	-	-	-	----

3.2. Phylogenetic relations among shallow and deep-water species

The length of the section of the COI gene obtained for the species of *Sterechinus* was 774 pb. Of these sites, 210 were variable and 110 were informative for parsimony. The nucleotide composition was 27.14% A, 21.95% C, 18.24% G and 32.67% T. The substitution saturation test showed that the COI sequences are not saturated ($\mathrm{Iss}=0.2945 < \mathrm{Iss.c}=0.7363$; $\mathrm{df}=463$ $p < 0.0001$), which validates their use in phylogeny. The maximum parsimony (MP) analysis found 10 equally parsimonious trees, with a consistency index of 0.8228, homoplasy index of 0.1772 and retention index of 0.8260. The tree topology shows two well-differentiated groups; one includes the haplotypes of *S. neumayeri* and the other has the rest of the species, corroborated by a 100% bootstrap value (Fig. 3). Within the latter group the tree shows a subgroup which includes *S. diadema*, *S. agassizi* and *S. antarcticus*, however with low bootstrap support. Maximum likelihood analysis (ML) of the sequences with the ModelTest parameters and the Bayesian analysis resulted in a tree with similar topology that distinguishes the two major clades described above. All three methods, based on different assumptions, produced similar trees in terms of branching and the robustness of the same nodes (Fig. 3). The genus *Sterechinus* appears monophyletic and, among the five nominal, formerly described, species, only *S. neumayeri* is monophyletic.

3.3. Divergence time estimation

Results from BEAST Program dating analyses estimated the beginning of the divergence among the two main clades between 5.6 and 7.9 M (substitution rates 0.72 and 0.51% Ma^{-1}, respectively), in the late Miocene. The confidence interval for the greater substitution rate is 4.01 – 7.19 Ma, whereas the slower rate is 5.77 – 10.27 Ma.

4. Discussion

The phylogenetic analysis of the genus *Sterechinus* showed two main clades. One corresponds to all individuals of the shallow-water Antarctic species *S. neumayeri*, which fulfills the criteria of a phylogenetic species. The second clade gathers specimens belonging to the four other nominal species. Among them, only individuals of *S. dentifer* (Antarctic deep-sea species) form a haplogroup slightly differentiated from other species of the clade. Specimens of

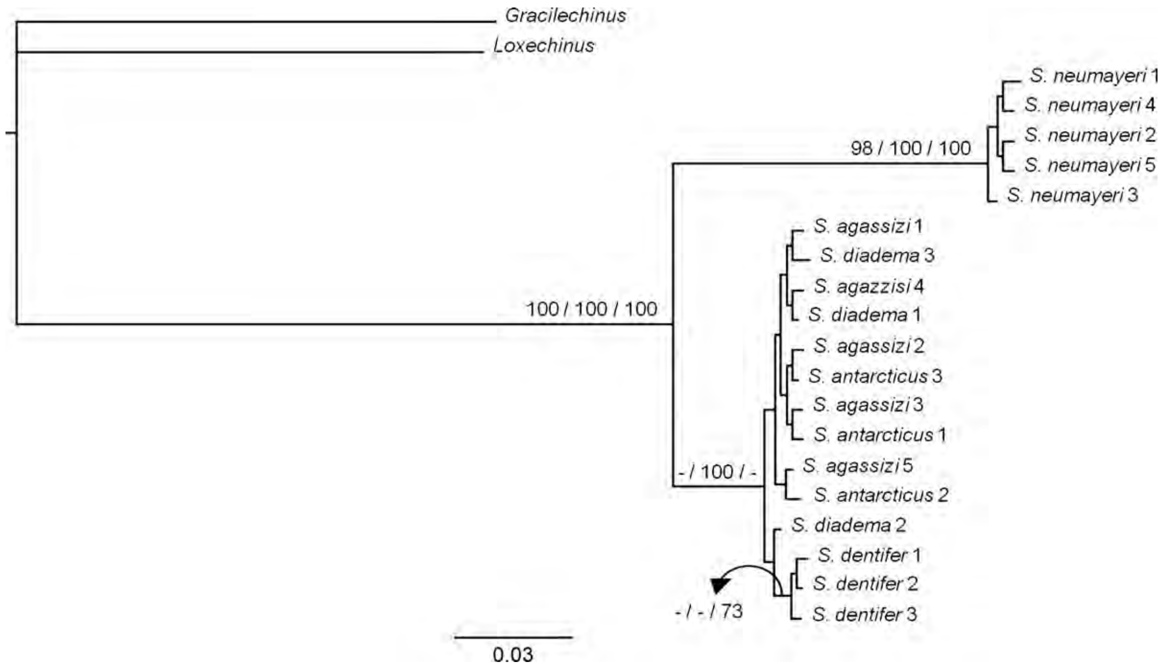

Fig. 3. The Bayesian inference (BI) tree of the COI sequences obtained for the genus *Sterechinus*. The branch support values are from ML and MP bootstrap (1000 repetitions) and BI analyses.

S. diadema, S. agassizii and *S. antarcticus* do not separate into different haplogroups but form one single genetic entity and do not fulfill the criteria for distinguishing different phylogenetic species. The distinctions between *Sterechinus* species were so far grounded on architectural (plate pattern), general shape and appendages characters (Mortensen, 1943; David et al., 2005b). However, those supposedly distinctive characters are rather subtle, and their ranges of variation tend to overlap making the separation between species unclear. The most conspicuous distinction concerns *S. dentifer*, which displays characteristic pedicellariae. For the other species, part of the identification of specimens by former authors relied generally on few specimens, therefore without appraisal of variation, and sometimes also on geographic criteria (Clark, 1925). The four nominal species of the second clade appear now to be much more similar from a phylogenetic point of view, so that they could be possibly clumped into a single entity, all the more that there is few support to distinguish them as already suggested (David et al., 2005b). This absence of genetic differences challenges the status of *S. diadema*, *S. antarcticus*, and *S. agassizii* as separate species. The case of *S. dentifer* is still pending, considering the low number of specimens analyzed, due to the scarcity of deep-sea samples.

Within the first clade, the absence of phylogeographic structure of *Sterechinus neumayeri* could reflect the existence of past or present connectivity sufficient to impede any divergence processes, even at the scale of thousands of kilometers. This fact indicates that these distant populations have not been isolated, at least as regard as the mutation time scale of the COI gene (around 250.000–175.000 years, considering 0.51% and 0.74%, respectively). According to the oceanographic characteristics of the Southern Ocean, past or even present connectivity may have been facilitated by the East Wind Drift, which flows counterclockwise around the continent (Fig. 1). Such connectivity would be also explained by an important dispersion capacity and possible long permanence in the water column of its larval stages. Based on temporal samples in the Antarctic Peninsula, Bowden et al. (2009) estimated that the development time of *S. neumayeri* larvae could reach four months. Moreover, Marsh et al. (2001) showed that larvae of the same species have an extremely low metabolism, which may allow them to remain for up to a year in the plankton (D. Manahan, personal communication). In the shallow Subantarctic, samples from the Argentinian continental shelf and from Kerguelen Plateau correspond to distinct nominal species, *S. agassizi* and *S. diadema*, albeit weakly morphologically differentiated. However, we found no evidence for an ongoing divergence process between them and this may reflect the existence of past or recent contacts between South America and Kerguelen Islands driven by the ACC. In this regard, Moyano (1999) proposed the existence of a high connectivity within the Subantarctic ecosystem, emphasizing the Magellan Straits region as a zone united form a zoogeographical point of view with the circum-austral Subantarctic region by the West Wind Drift. More recent molecular studies performed on other marine benthic organisms are in agreement with our results, showing recurrent and modern gene flow among Subantarctic regions in *Ostrea chilensis* (Ó Foighil et al., 1999), *Macrocystis pyrifera* (Coyer et al., 2001), *Mytilus* spp. (Gérard et al., 2008), and *Durvillaea antarctica* (Fraser et al., 2009).

Based on our results and recent studies of shallow Antarctic and Subantarctic benthos, we propose a model of two rings of connectivity (Antarctic and Subantarctic two-ring model) which includes two large routes of dispersion: (1) the ACC (historically referred to as West Wind Drift), which would connect the Subantarctic zones, and (2) the Antarctic Costal Current (East Wind Drift) which surrounds the Antarctic. These rings may have maintained a degree of connectivity sufficient to avoid the process of molecular divergence between their populations (Fig. 1). Genetic relationships among Antarctic shallow and deep-sea *Sterechinus* species do not support either of the two hypotheses of submergence or emergence previously proposed to explain the biogeographic and evolutionary relationships between the two Antarctic benthos. Deep specimens identified as *S. antarcticus* and *S. dentifer* that were collected close to the Antarctic Peninsula and East Antarctica form a single haplogroup together with the specimens from Argentina and Kerguelen. Moreover, individuals recognized as *S. antarcticus* share the main haplotype with both subantarctic shallow species. These results are congruent with the suggestion of Mortensen (1936) and David et al. (2005b), who proposed, based on morphological characters, that *S. antarcticus*, *S. agassizi* and *S. diadema* may be closely related and may correspond to local phenotypes of a single species. In the case of the four individuals collected in the deepest zone, identified as *S. dentifer*, three new haplotypes cluster in a slightly divergent clade (p-distance less than 1%). Compared with the divergence found between *S. neumayeri* and all other samples, this low value may indicates a recent divergence between *S. dentifer* and the group composed of *S. agassizii*, *S. diadema* and *S. antarcticus*. These results contrast with previous studies on the relationship between Antarctic and deep-sea fauna. While some groups such as pectinid bivalves (Berkman et al., 2004) fit the emergence hypothesis, others such as deep-water foraminiferans (*Epistominella*, Pawlowski et al., 2007), serolid isopods (Held, 2000) and octopuses (Strugnell et al. 2008) match the submergence hypothesis. Based on the extensive sampling effort of the ANDEEP project, Brandt et al. (2007) found that a combination of the processes of submergence and emergence would explain satisfactorily the evolutionary relationships among isopod families.

In this context, our work does not support either the emergence or submergence hypothesis, but provides evidence of an evolutionary relationship between deep-sea and subantarctic shallow fauna. A possible scenario to explain the evolutionary pathways between shallow and deep-sea *Sterechinus* spp. may first involve an initial separation between shallow Antarctic and Subantarctic species by the end of the Miocene, and secondly a later colonization of the deep ocean from the Subantarctic zone, probably promoted by the geomorphology of the Scotia Arc (Thompson, 2004). Then the colonization of the abyssal area extended to the slope and deep part of the Antarctic continental shelf, where the highly divergent species *S. neumayeri* and *S. antarcticus* are now found in sympatry. In this scenario and according to our divergence time estimation, the divergence between the shallow-water species of *Sterechinus* from the Antarctic and Subantarctic regions would have begun at the end of the Miocene and/or the beginning of the Pliocene. Page and Linse (2002), who used the 16S gene, indicated a similar separation time for gastropod species of the genus *Limatula* (*L. ovalis* and *L. pygmaea*); about 5.8–8 Ma. More recently, González-Wevar et al. (2010) revealed the diversification of the limpet genus *Nacella* in the Southern Ocean and estimated the appearance of the main *Nacella* lineages between 9.3 ± 1.5 and 5.4 ± 1.1 Ma in Antarctica, Central Chile, Magellan and Kerguelen Provinces. Divergence time between geminate Antarctic and South American species may have occurred even later, as proposed by Hunter and Halanych (2008) for the brittle star *Astrotoma.* These results strongly suggest that Antarctic and Subantarctic benthic populations of invertebrates with long-lived larvae could have maintained connectivity long after the physical separation of the continents and the formation of the ACC. Different lines of evidence show that the time period that we propose in this paper for the divergence of the faunas (Miocene-Pliocene transition) involved particular events, such as an exceptionally cold period which would have generated a new and important expansion of the ice cap in the western part of the Antarctic continent (Kennett and Barker, 1990; Zachos et al., 2001; Gersonde and Censarek, 2006). Crame (1999) suggested that the rapid development of the ice cap between 6.2 and 4.8 Ma would have produced a change in the velocity of the circum-Antarctic current (Barker and Thomas, 2004; Hassold et al., 2009). According to this interpretation, the interruption of gene flow between populations of *Sterechinus* may correspond to the installation of an effective oceanographic barrier, probably linked to an intensification of the ACC (see Thornhill et al., 2008). Additionally, our results support the absence of gene flow between the regions during the Pliocene and Pleistocene (5 Ma to present), in spite of episodes of possible weakening of the current during the repeated inter-glacial periods. The reduction in ice extension, along with a probable homogenization of sea water temperatures, has not been sufficient to create a viable bridge for the interchange between the Antarctic Peninsula and the Magellanic region. Finally, the intensification of the oceanographic barrier, which occurred at about 5 Ma, may have produced a definitive separation between shallow species of the two regions, in spite of a high, but different dispersal capacity of the planktonic larvae.

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Ectosymbiosis associated with cidaroids (Echinodermata: Echinoidea) promotes benthic colonization of the seafloor in the Larsen Embayments, Western Antarctica

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ABSTRACT

Ice-shelf collapses in the Larsen A and B embayments along the Weddell side of the Antarctic Peninsula resulted in new open-water areas that are likely reorganizing benthic communities. It is a natural laboratory to assess colonization of the sea bottom under new conditions. We tested the hypothesis that the epibionts associated to cidaroid echinoids could promote or enhance the colonization of hard surfaces. In fact, being vagile, cidaroids might improve dispersal capabilities of the sessile animals that are attached to their spines, e.g., promoting the colonization of areas where the fauna has been eradicated by iceberg scouring. If this hypothesis is correct, pioneer sessile species present locally on stones might have affinities with ectosymbionts on cidaroids, and the sessile fauna present both on cidaroids and stones should be more similar in the Larsen embayments than in undisturbed areas. We therefore compared sessile species living on cidaroids with those living on stones in three areas: Larsen A and B embayments and two undisturbed and geographically different areas, Atka Bay and Elephant Island. Overall, richness, evaluated as 'morphotypes' richness, was lower in the Larsen area than in other areas, but levels of species diversity were similar among the three zones. The estimate of similarity between assemblages (using the C_{22} index of Chao et al., 2008) also suggests that cidaroid epibionts are either species-specific or specific to cidaroids, while the composition of sessile fauna on stones is more variable and probably dependent on local factors. In the two undisturbed areas, sessile fauna are highly different between stones and cidaroids. This contrasts with the Larsen embayments where cidaroids share more than 80% of epibionts with the surrounding stones. These results suggest that ectosymbioses linked to cidaroids strongly contribute to benthic colonization of the seafloor in the Larsen enbayments. With time, secondary successions are expected to occur, increasing the difference between epibiotic communities on cidaroids and those on stones, and lead to the situations observed in unperturbed sites.

1. Introduction

Biodiversity has a paramount role in the ecosystems functioning (Duffy et al., 2007), and the dynamics of colonization of new habitats is of particular interest in assessing processes of recovery. However, the onset of ecosystem settlement in newly free areas is often difficult to assess. Well-studied cases concern large-scale catastrophic events (such as volcanic eruptions, forest fires, hurricanes, meteorite impacts) that caused the complete destruction of life and former habitats (Brown and Lomolino, 1998; Thornton et al., 2001; Rampino and Koeber, 2006). Small-scale disturbances can be equally important by removing, for instance, dominant plants or animals and modifying inter-specific competition inside a community. Such disturbances occur in terrestrial (e.g., falling trees in tropical forests) and in aquatic ecosystems (e.g., predatory sea-stars removing dominant mussels on intertidal rocky shores) (Brown and Lomolino, 1998). Few studies have been carried out in the marine realm (Tomascik et al., 1996; Lock et al., 2009). For instance, benthos recovery after human-induced disturbances has been investigated (including in the deep sea). In addition to small-scale recolonization studies of artificial trays devoid of fauna (e.g., Kline and Stekoll, 2001), a broad-scale attempt was made in the Peru trench at 4150 m depth (Thiel et al., 2001). This disturbance covered an area of 10 km^2 in which 2 km^2 sections were intensively disrupted to 10–15 cm depth. Seven years later, the macrofaunal taxa had largely recovered (Borowski, 2001), with an enhanced heterogeneity and, for some taxa, even greater abundances than before (Bluhm, 2001).

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Recolonization takes time. Early stages correspond to the settlement of pioneers in discrete patches that then expand and coalesce. Later stages involve species replacements. For plants on lava, the pioneer colonization stage lasts more than 20 years (Abe, 2006; Cutler et al., 2008). For corals it takes fewer than five years for diversification to begin (Tomascik et al., 1996). For a complex ecosystem, complete recolonization might take centuries (Rampino and Koeber, 2006; Cutler et al., 2008). In contrast, deep-sea benthos may show a rapid colonization of physically disturbed seafloor presumably because the sediment disruption enhances food accessibility, at least for deposit feeders (Ingole et al., 2005).

The recent changes in the Larsen ice shelves along the Weddell side of the Antarctic Peninsula provide an opportunity to observe the effects of large-scale disturbances due to ice melting. After a period of steady retreat, concomitant with ice thinning up started in the late 1980s, the ice shelves of Larsen A (to the north) and Larsen B (central embayment) collapsed in 1995 and 2002, respectively. This last event corresponds to the largest surface of ice shelf ever disintegrated, equalling a surface of more than 3000 km^2 which rapidly collapsed over a few weeks (Shepherd et al., 2003; Rack and Rott, 2004). Each collapse event released a huge amount of thick ice that scoured the seafloor down to several hundred meters depth. In the two years after the collapse and disappearance of the buttressing ice shelf, ice discharge from ice streams has increased 3–8 fold, producing many large icebergs (Rignot et al., 2004; Scambos et al., 2004). Discharge of these icebergs has slowed to a new equilibrium (Rott et al., 2007). The impact of iceberg scouring on the benthos has been well characterized in Antarctica (Gutt et al., 1996; Smale et al., 2008), and it is known that in the Weddell Sea, even in 'standard' conditions, ice scouring prevented the Antarctic benthos from reaching maturity and can affect up to the 20% of the seafloor (Gutt and Starmans, 2001). Therefore, the catastrophic events recorded in Larsen A and B can be expected to have dramatically impacted the benthos and, especially, the sessile organisms formerly present under the ice shelves.

Studies of recovery after intense ice disturbances showed that a variety of factors may affect the successive stages of settlement of Antarctic benthic communities. These include dispersal capabilities and growth rates of colonizing species, as well as competition between species (Teixido et al., 2004, 2007). Teixido et al. (2007) also suggested ectosymbiosis might contribute to benthic colonization.

The general role of symbiotic relationships in early stages of the process of species colonisation is still unclear. In plants, mutualist relationships may be either an advantage for early colonization (e.g., mycorrhization facilitates resources acquisition in pioneers, Cuenca and Lovera, 1992), or a limiting factor (e.g., plants and pollinators need synchronicity, Shanahan et al., 2001). Ectosymbiosis, the inter-specific relationship in which a species (the symbiont) lives on another species (the basibiont), whatever the nature of the relationship, is suspected to facilitate colonization (Hétérier et al., 2008). Ectosymbiosis has been identified as a key factor that structures benthic communities in the Antarctic as it decreases the level of competition between benthic species for hard substrates which are often scarce (Gutt and Schickan, 1998). The most studied Antarctic basibionts are bivalves (Cerrano et al., 2009) and cidaroid echinoids (Hétérier et al., 2008; Linse et al., 2008; Cerrano et al., 2009). Primary spines of cidaroids lack an epithelium, thereby providing an accessible hard substrate for numerous sessile species (David et al., 2009). As they harbour sessile species distinct from those attached to the surrounding stones, cidaroids are expected to play a key role in maintaining and possibly enhance biodiversity in deep environments of Weddell Sea (Hétérier et al., 2004, 2008). A similar role is suggested to occur in shallow waters as well (Linse et al., 2008).

Ectosymbionts are thought to promote the colonization of disturbed marine areas because dispersion is improved through the mobility of their basibionts (Cerrano et al., 2006). The collapse of Larsen A and B offered the opportunity to study the early stages of colonization of newly vacated large areas of the seafloor. In this regard, two different dynamics may occur, allowing to test two alternative hypotheses. According to the first one, if sessile species attached to cidaroids are species-specific (this is the case in deep waters, see Hétérier et al., 2008), they must be the primary-colonizers. When these primary-colonizers subsequently colonize the surrounding area, the community settled on stones should reflect the ectosymbiotic community living on cidaroids. This pattern should depart from unperturbed situations, where sessile communities of stones and cidaroids usually differ (Hétérier et al., 2008). An alternative hypothesis is that sessile species colonizing the newly vacated area of Larsen firstly settle on stones and, only secondarily, on the spines of cidaroids. In this latter case, primary-colonizers should be composed by generalist sessile species, and the sessile fauna settled on cidaroids in new colonized areas should differ from that of undisturbed areas. These two alternative hypotheses are here tested through a comparative study of the sessile organisms fixed on rocks versus those fixed on cidaroids, in three contrasting areas: the impacted Larsen embayments and two relatively undisturbed control sites located on each side of the Weddell Sea.

2. Material and methods

Sampling was done during the expedition *ANTARKTIS-XXIII/8* of the RV '*Polarstern*' in the Weddell Sea and South Shetlands from November 2006 to January 2007 (Gutt, 2008). Cidaroids and stones were collected, during the same trawl, on the continental shelf, using either a Bottom or an Agassiz trawl. On the whole, a total of 15 stations, distributed in the three contrasting areas between 146 and 391 m deep: one station at the entrance of Atka Bay in the East Weddell Sea, five stations in Larsen A and B embayments (where ice shelves recently collapsed) and nine stations off Elephant Island (Fig. 1, Table 1). In each station, both substrates (stones and cidaroids) were collected during the same trawl.

All collected cidaroids were studied. Spine length, test diameter, and height were measured with digital vernier calliper to the precision of a tenth of a millimeter. Cidaroid size was estimated using a size index determined as the sum of the test height and lengths of the longest aboral spine and the longest adoral spine. Many parameters may affect the quality and integrity of samples. For example, the bottom type, the trawl size and the trawling time may lead to the damage of the collected cidaroids in different ways and, above all, by breaking their spines. Therefore, a Kruskal–Wallis test was performed to test whether the number of spines found on collected cidaroids was the same in all three areas. Moreover, a Wilcoxon Signed Ranks Test was used to assess the evenness of the number of specimens sampled by the two types of trawl.

To obtain 'biotic' (cidaroids) and 'abiotic' (stones) substrates of comparable size, only stones with a size within the size range of cidaroids (i.e. between 10 and 100 mm) were taken into account. Because trawls sometimes collect stones in large numbers, a random sub-sample of about a hundred stones was considered for the analyses. All studied stones were measured, considering the largest measure as stone length, and its perpendicular measure as stone width. A size index was calculated by multiplying length by width. Finally, each encrusted stones and cidaroid specimens were fixed (separately) in 95% ethanol for further analysis and subsequent identification of their sessile organisms.

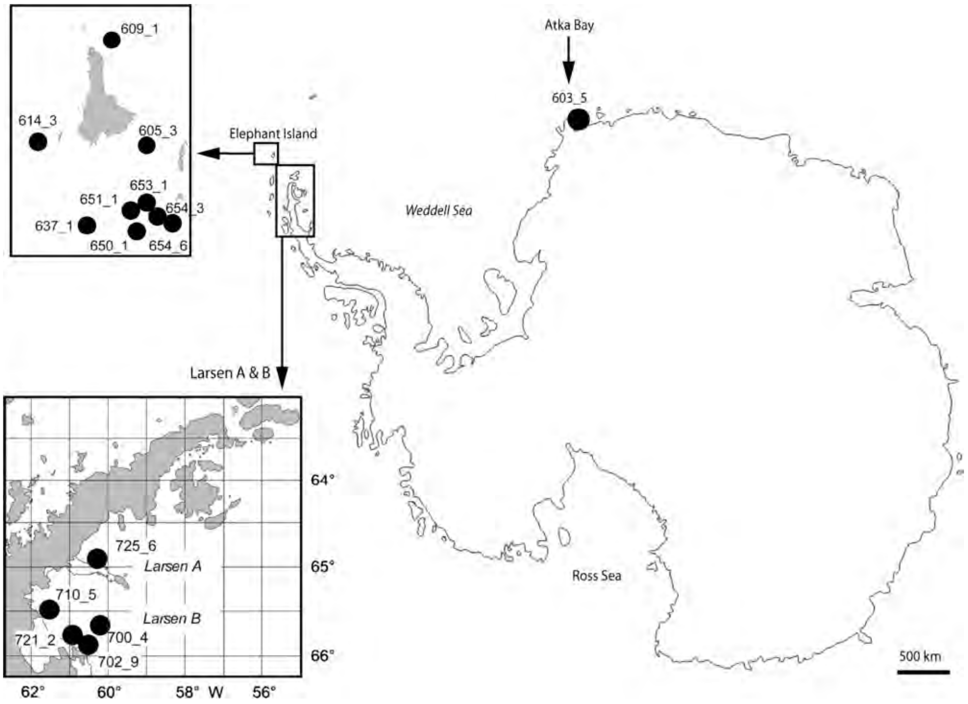

Fig. 1. Map of Antarctica with location of sampling stations (black dots) in Atka Bay, Larsen A and B and Elephant Island (black circles show precise station locations). Modified after Gutt (2008).

Table 1
Sampling station position, average depth, used trawl and number of stones and cidaroids sampled in each with the proportion of individuals colonized by at least one sessile species.

Station	Position		Average depth (m)	Trawl	Area	Number of individuals						Proportion of colonized individuals		
						S	C					S	C	P
							Am	Cp	Cg	Nm	Rt			
PS69/603_5	70°30.99′S	08°48.08′W	285.5	AGT	AB	49	0	15	1	1	3	0.67	1.00	0.0003
PS69/605_3	61°20.33′S	55°31.53′W	145.8	AGT	EI	96	15	0	0	3	26	0.24	1.00	< 0.0001
PS69/609_1	61°12.04′S	54°37.10′W	317.4	BT										
PS69/614_3	60°52.37′S	55°29.80′W	253.3	AGT										
PS69/637_1	61°05.31′S	56°14.65′W	391.3	BT										
PS69/650_1	61°17.41′S	56°12.28′W	322.3	BT										
PS69/651_1	61°17.42′S	55°58.46′W	305.7	BT										
PS69/653_1	61°18.54′S	55°57.92′W	359.1	BT										
PS69/654_3	61°21.52′S	56°02.28′W	353.6	AGT										
PS69/654_6	61°22.80′S	56°03.84′W	342.5	AGT										
PS69/700_4	65°55.40′S	60°19.95′W	438.6	AGT	L	138	0	0	0	6	0	0.33	1.00	0.03
PS69/702_9	65°57.85′S	60°28.42′W	218.2	AGT										
PS69/710_5	65°32.86′S	61°38.33′W	240.6	AGT										
PS69/721_2	65°55.41′S	60°34.01′W	296.6	AGT										
PS69/725_6	64°54.80′S	60°37.46′W	180.6	AGT										

AB: Atka Bay, EI: Elephant Island, L: Larsen. AGT: Agassiz trawl, BT: Bottom trawl. S: stones, C: cidaroids, Am: *Aporocidaris milleri*, Cg: *Ctenocidaris gigantea*, Cp: *Ctenocidaris perrieri*, Nm: *Notocidaris mortenseni*, Rt: *Rhynchocidaris triplopora*. *P*: Likelihood ratio χ^2 testing for the difference in the proportion of colonized individuals between stones and cidaroids in each area. The number of individuals pertains for each area. For EI and L areas, they are cumulated numbers of several stations.

Identification and counting of sessile organisms present both on cidaroid spines and stone surfaces was made in the laboratory with the aid of a stereomicroscope. Most epibionts were determined at least to the class level, and at a lower taxonomic level when possible. Because of the diversity of the sessile organisms present, very few could be determined to the species level. The solution adopted was to determine ‘morphotypes’ and consider them as species proxies for further analyses. The prevalence of sessile organisms on cidaroids or stones was calculated as the ratio of the number of colonized individuals to the total number of individuals (Table 1). Abundance data were obtained by counting the number of individuals attached to each colonized substrate (cidaroid or stone). For colonial species (e.g., sponges, bryozoans, hydrozoans), for which the notion of ’individual’ is ambiguous, it is conservative to consider that a single colony was founded by only one propagule and that each spatially discrete colony represents one single event of colonization (Hétérier et al., 2008). Species abundance distribution (SAD) of sessile assemblages was analysed according to the methods reviewed by McGill et al. (2007). Such methods are independent of taxon identity and result more robust for comparison of communities that do or do not share species (or morphotypes). By using these methods, it is possible to capture most of the information in rank-abundance plots (McGill et al., 2007). Abundance data on a $\log_{10}$ scale were plotted against the rank for each morphotype, from the most abundant (Rank 1) to the least abundant, and the distributions were inspected visually to look for differences between communities (Whittaker, 1965; Krebs, 1989; Magurran, 2004).

Data were analysed using indices for richness ($\hat{S}_{ACE}$), diversity ($\hat{H}$) and similarity (C_{22}) as suggested by Chao and Lee (1992), Lee and Chao (1994), Chao and Shen (2003), and Chao et al. (2008). These indices, calculated using the software SPADE (Chao and Shen, 2009), are an extension of classical indices used in community ecology (Krebs, 1989). They take into account ’unseen’ species, as estimated by the probability of missing rare species and computed from abundance-based data. These indices use replicates to compute confidence intervals which make possible comparisons of heterogenous data. To obtain these indices for a given sampling station, we used individual cidaroids or stones as replicates for describing the cidaroid or stone assemblages respectively (as suggested by Shaw and Dobson (1995) for host–parasite relationships). Therefore, the width of the confidence intervals computed will depend on the number of cidaroids and stones collected at a given station. When the number of replicates (cidaroids and stones) collected at a station was too low, one single index was computed for all stations in a zone (Table 1). Finally, a 95% confidence interval (CI) based on 200 bootstrap iterations was obtained for each index. The estimate of S, the richness index of a given assemblage, was obtained using the abundance-based coverage estimator $\hat{S}_{ACE}$ (Chao and Lee, 1992). The estimate of H, the alpha diversity index of a given assemblage, was obtained using the extended Shannon index $\hat{H}$ of Chao and Shen (2003) based on the frequency and abundance of species. Finally, the estimate of similarity between assemblages used the non-parametric index C_{22} of Chao et al. (2008) that is derived from a Morisita index. Comparisons of average C_{22} values between cidaroids and stones for all the sampling stations were tested using a Wilcoxon test, and not just estimated according to 95% CI of C_{22} values. Statistical analyses were made using the softwares SPADE (Chao and Shen, 2009) and JMP (SAS Institute).

3. Results

On the whole, 70 cidaroid specimens were collected: 20 in Atka Bay, 44 off Elephant Island and six in Larsen areas. Cidaroids belonged to five species with different spine morphologies: *Ctenocidaris gigantea* (H.L. Clark, 1925), *Ctenocidaris perrieri* Koehler, 1912, *Notocidaris mortenseni* (Koehler, 1900), *Rhynchocidaris triplopora* Mortensen, 1909 and *Aporocidaris milleri* (A. Agassiz, 1898). *R. triplopora* and *N. mortenseni* are widely distributed all around Antarctica (David et al., 2005). We only found one species in Larsen, *N. mortenseni* (Table 1). Comparison among cidaroids showed that the number of spines found on collected cidaroids was the same in all three areas (for *N. mortenseni* and *R. triplopopra;* Kruskal–Wallis $Z=1.63$, $p=0.44$). Moreover there was no significant difference in the number of cidaroids sampled by the two types of trawl in Elephant Island area (Wilcoxon Signed Ranks Test, $W=14.5$, $p=0.32$). We therefore considered our samples similar in quality among the different areas.

In the three geographic zones, stones were always more abundant than cidaroids. However, while all cidaroid spines had ectosymbionts, only a small fraction of stones had sessile animals (Table 1). It is likely that some bare stones were partially buried into the mud as they were collected, the sediment cover preventing them from being colonized by epizoans. However, there was no evidence to generalize this fact to the majority of them. One hundred and seventeen morphotypes (hereafter called ‘species’) belonging to 10 taxa were counted in the three geographic areas. Bryozoans were the dominant group in terms of number of species (Fig. 2). Protozoans were numerically dominant in number of individuals, but showed a lower diversity (Fig. 2). Plots of the species abundance distribution (SAD) showed no major difference between the different geographic zones (Fig. 3). There were always numerical dominant species (500–1000 individuals) and a slight excess of rare species. Nevertheless, there were more rare species in the Atka Bay station than in others and the Larsen zone had slightly fewer species than the other two (Fig. 3).

Sessile species richness is higher on cidaroids (all species grouped) than on stones in Atka Bay and Elephant Island zones, while no significant differences were found in Larsen (Fig. 4A). The estimated total richness is also lower in Larsen than in the two other zones. Diversity shows contrasting patterns among the

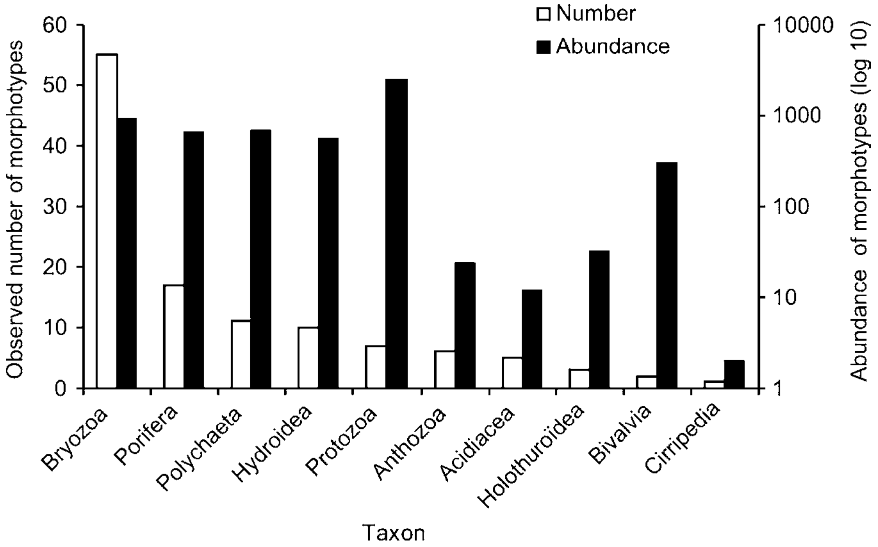

Fig. 2. Total number (white bars) and abundance (black bars) of morphotypes found in the 10 sessile taxa, in all sites and all substrate types.

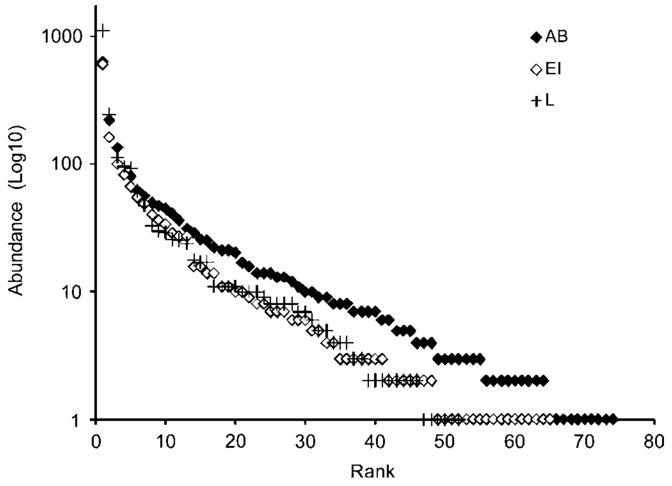

Fig. 3. Species abundance distribution (rank-abundance plot) of total sessile fauna for the three zones (fauna found on both stones and cidaroids). AB: Atka Bay, EI: Elephant Island, L: Larsen.

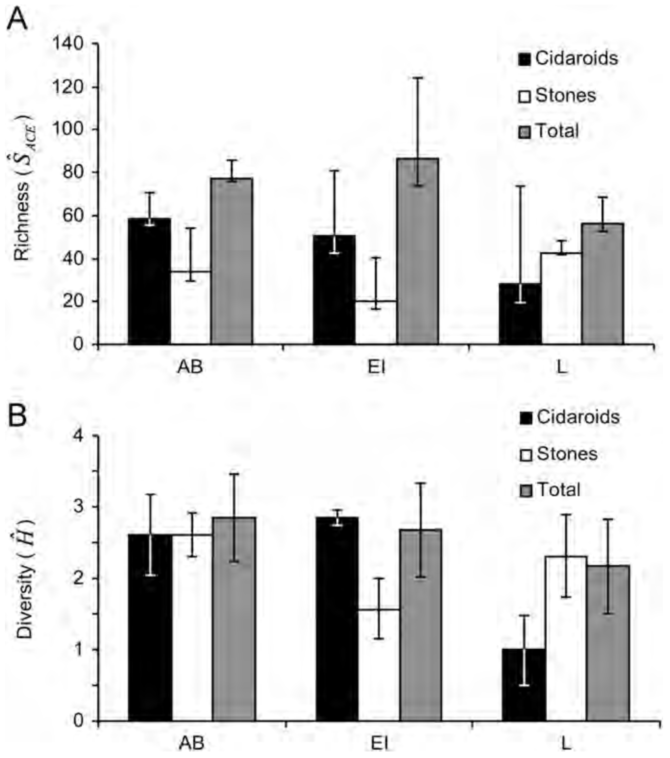

Fig. 4. Characteristics of sessile fauna within each geographic zone: (A) estimate of species richness ($\hat{S}_{ACE}$) according to the type of substrate and (B) estimate of specific diversity ($\hat{H}$) according to the type of substrate. For each zone, the total of all cidaroid species is considered. AB: Atka Bay, EI: Elephant Island, L: Larsen. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

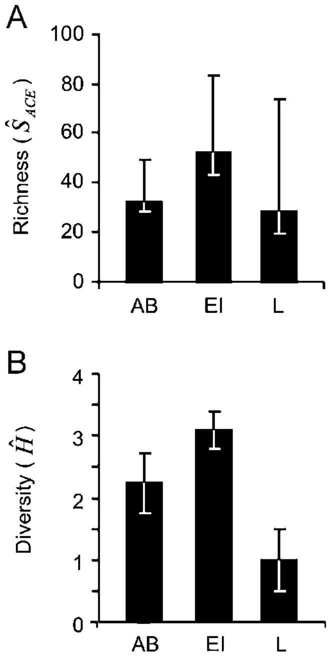

Fig. 5. Characteristics of sessile fauna fixed on *Notocidaris mortenseni* within each geographic zone: (A) estimate of species richness ($\hat{S}_{ACE}$) and (B) estimate of specific diversity ($\hat{H}$). AB: Atka Bay, EI: Elephant Island, L: Larsen. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

three zones (Fig. 4B). While no pattern was found between stones and cidaroids in Atka Bay, diversity was lower on stones than on cidaroids at Elephant Island. The reverse pattern was found in Larsen. Global diversities are not significantly different between the three zones but ectosymbiont diversity found on cidaroids in Larsen is lower than in the two other stations (Fig. 4B). Since the different zones harboured different cidaroid species, this difference might be due to differences in the qualities of substrate provided by these different species. We therefore compared Richness and Diversity for the only cidaroid species present in all three zones. The ectosymbiont richness on *N. mortenseni* is not significantly different between stations, while overall diversity is much lower in Larsen than in other zones (Fig. 5).

The similarity between sessile communities was compared at three different levels. We first compared, within each zone, the similarities of fauna between the different types of substrates (e.g., between stones and a given species of cidaroid, or between two cidaroid species). In Atka Bay and Elephant Island, similarities are much higher between the different cidaroid species than between stones and cidaroids (Fig. 6), with the exception of the low similarity between *R. triplopora* and *C. perrieri* in Atka Bay. In Larsen, the level of similarity between stones and cidaroids is significantly higher than in the two other zones and is at the same level (around 80%) as similarities between cidaroid species at the two other zones (Fig. 6). We then compared the similarities in sessile fauna between the different geographic zones. This was done for the substrates common to the three zones, i.e. the cidaroid *N. mortenseni* and stones. Sessile fauna living on *N. mortenseni* is highly similar between zones, while similarities of the fauna fixed on stones are very low and always significantly lower than those between cidaroids (Fig. 7). The similarity of the fauna fixed on stones between Larsen and Elephant Island is nevertheless higher than for the other comparisons (Fig. 7).

4. Discussion

We only found one cidaroid species in Larsen, *Notocidaris mortenseni*. Its epibiotic fauna is less diverse but as rich as the one found on stones. In addition, the two faunas are very similar since approximately 80% of species are common to the two substrates. This last result contrasts sharply with what is found in the two other zones, where similarities between the epibiotic fauna present on cidaroids and the one present on stones are very low. Hétérier et al. (2008) found a similar pattern in the Weddell Sea at deeper stations (depth > 1000 m), where general

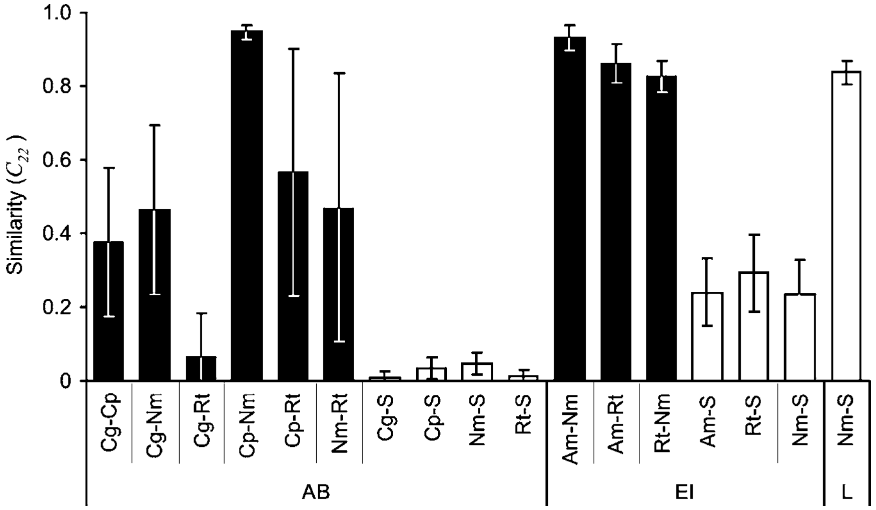

Fig. 6. Inter-substrate pairwise similarities (C_{22}) of sessile fauna at each geographic zone. AB: Atka Bay, EI: Elephant Island, L: Larsen. Am: *Aporocidaris milleri*, Cg: *Ctenocidaris gigantea*, Cp: *Ctenocidaris perrieri*, Nm: *Notocidaris mortenseni*, Rt: *Rhynchocidaris triplopora*, S: stones. Black bars stand for similarities between cidaroids, white bars for similarities between cidaroid and stone. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

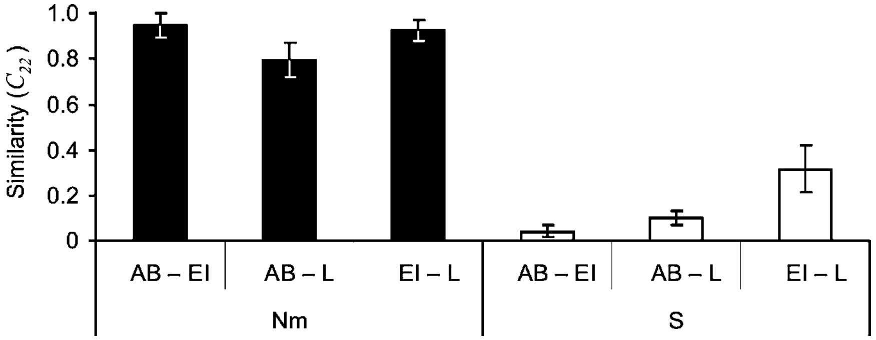

Fig. 7. Similarities (C_{22}) of sessile fauna between the different geographic zones, according to the substrate types. AB: Atka Bay, EI: Elephant Island, L: Larsen. Only substrates common to the 3 zones were considered. Nm: *Notocidaris mortenseni*, S: stones. Error bars are 95% confidence intervals based on 200 bootstrap iterations.

biodiversity is low (Clarke and Johnston, 2003). The present study extends the conclusions of Hétérier et al. (2008) to shallower environments, showing that sessile species harboured by cidaroids are complementary with those living on stones and that ectosymbiosis makes an important contribution to biodiversity in the Antarctic.

A striking result in the present study is that the epibiotic communities on *N. mortenseni* are very similar among the three distantly related geographic zones while the epibiotic communities on stones are very different. This means that the structure of the stone-borne epibiotic communities relies upon local environmental factors while cidaroid epibiosis is highly species-specific.

Overall, sessile communities are poorer in terms of number of species in the Larsen areas freed after the ice shelves collapse, while community diversities ($\hat{H}$) are very similar in all three zones. This means that colonization is not just the action of a few dominant pioneer species, but that numerically various species contribute to increasing local diversity (otherwise a much lower diversity would have been found in Larsen). Cerrano et al. (2006) proposed that ectosymbiosis might facilitate the colonization of an ecosystem by sessile organisms after a perturbation, because living substrates (basibionts) are actively motile while mineral substrates are not.

Two observations suggest that colonizing processes of Larsen bottoms are helped by the presence of *N. mortenseni*: (1) in Larsen the epibionts found on *N. mortenseni* are similar to those found in the other studied sites, and (2) these Larsen cidaroids share more than 80% of their epibionts with the surrounding stones. This means that cidaroids might have colonized Larsen bottoms as adults and that cidaroid epibionts have settled in the surroundings via their propagules, producing a local sessile community (i.e. on stones and other hard substrates). This would support the hypothesis of Cerrano et al. (2006) that ectosymbiosis might facilitate the colonization of an ecosystem by sessile organisms. Appearance of *N. mortenseni* in the Larsen area may also have resulted from larval dispersal without direct involvement in the settlement of ectosymbionts. Indeed, planktonic larvae of cidaroids are not colonized by epibionts, nor are juveniles because their spines are still protected by an epithelium. Therefore, adult *N. mortenseni* are likely the main agents in the dispersion of epibiotic species. Our results also suggest that the 20% of the species specificity to stones might be due to local recruitment. Similarities of the sessile faunas fixed on stones in Larsen and Elephant Island, which are in relative proximity, are very high. This contrasts with the situation between Larsen and Atka Bay that are more distant. These two simultaneous sources of recruitment could explain the high diversity of epibionts in this recently perturbed ecosystem. With time, secondary successions with new colonization and species replacement will most probably occur on stones (and other abiotic hard substrate in the area) rather than on cidaroids (their epibiotic communities being rather specific and constant). This could thus increase the difference between cidaroid and stone epibiotic communities and lead to the usual situation observed in unperturbed sites (see Hétérier et al., 2008) where epibiotic communities differ for stones and cidaroids.

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The morphology, ontogeny, and inferred behaviour of the deep-sea echinoid *Calymne relicta* (Holasteroida)

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The deep-sea holasteroid *Calymne relicta* was first described from a few fragments discovered by the HMS 'Challenger' in the Bermuda abyssal plain more than a century ago. In addition to re-examining the type material, we describe herein new specimens from unpublished material collected between 3720 and 4860 m during three scientific expeditions that took place on both sides of the North Atlantic between 1966 and 1991. The new material includes juvenile and adult specimens in sufficiently good preservational state to allow a full redescription, including all types of appendages, some of which have never been described. These new observations confirm the atypical characteristics of *C. relicta*, including test morphology and spines that have no equivalent in other extant taxa. We explore in detail characteristics of this species that were almost impossible to interpret previously. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **155**, 630–648.

ADDITIONAL KEYWORDS: appendages – Calymnidae – functional morphology – spines – systematics.

INTRODUCTION

The deep-sea is the largest contiguous habitat on Earth, covering more than 60% of its surface. This habitat provides a variety of extreme environments and situations to analyse, as it is much more multifaceted than previously thought (Gage & Tyler, 1991). Many deep-sea forms have drastically modified their physiology, morphology, or behaviour to cope with high pressures (Sebert, 2002), darkness (Douglas, Partridge & Marshall, 1998), extreme temperatures (from cold bottoms to warm hydrothermal vents [Segonzac, De Saint Laurent & Casanova, 1993; Lee, 2003]), oxygen depletion (Levin, 2003), or scarcity of resources (Corbari, Sorbe & Massabuau, 2005). Bizarre fishes (Heezen & Hollister, 1971), cirrate octopuses (Roper & Brundage, 1972), swimming elasipodid holothurians (Ohta, 1985), or the recently discovered armoured sea snail (Warén *et al.*, 2003) are emblematic of peculiar morphologies present in the deep-sea. Such oddities are illustrative of adaptive strategies, including exaptations (Gould & Vrba, 1982). However, they may also suggest a release of selective competition among organisms (David, 1990), thereby allowing the expression of morphologies that may have been counter-selected in other environments.

Echinoids contribute significantly to this list of highly transformed animals. Among these are the Holasteroida, an almost exclusively deep-sea order of irregular urchins. Bottle- and amphora-shaped pourtalesiids are probably the most unusual of all sea urchins (David, 1988; Saucède, Mooi & David, 2004). Not only do holasteroids exhibit strange morphologies but they have also developed some of the most extreme behaviours encountered in echinoids. Examples include the internally brooding *Antrechinus* (Mooi & David, 1993) and the symbiont-laden *Cystocrepis* (David *et al.*, 2003b).

Calymne relicta Thomson, 1877 was dredged from the Bermuda abyssal plain more than a century ago, during the HMS 'Challenger' cruise. The original material consisted only of a few fragments briefly

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described in the 'Challenger' reports (Thomson, 1877; Agassiz, 1881). These same fragments were recently redescribed by Smith (2004), providing an accurate but limited description of the test architecture. However, no precise depictions of the appendages (spines and pedicellariae) exist.

Previous treatments of *C. relicta* hinted at an atypical morphology departing even from that of other deep-sea holasteroids. However, this work was unable to say anything about *Calymne*'s mode of life (Lovén, 1883; Mortensen, 1907, 1950; Smith, 2004). During the 'Atlantis' cruise (1966), additional material was collected in the same geographic area in which the original material was found, as well as in other parts of the North Atlantic (Soviet cruises ranging from 1983 to 1991). This new material (Table 1) included juveniles and adults in sufficiently good preservational state to allow a full redescription of *C. relicta*, including all types of appendages. With the new material, we are able to add considerably to our understanding of divergent morphology of deep-sea echinoids. Therefore, we can explore in detail characteristics of this species that were almost impossible to interpret previously, and to propose an interpretation of its behaviour and habits.

MATERIAL AND METHODS

In addition to re-examining the type material, we studied six juvenile specimens and isolated fragments collected in 1966 from the Bermuda area during the 'Atlantis' cruise. These specimens were identified by R.H. Chesher, but never published. In addition, we had access to all the specimens collected by 0.25 m^2 grab during two Russian cruises in 1983 and 1991 on both sides of the North Atlantic (Fig. 1, Table 1).

Terminology of external appendages and test features is that of Mooi & David (1996). Spines, pedicellariae, and other external features were examined and drawn using the methods of Mooi & David (1996) and David & Mooi (2000).

SYSTEMATIC DESCRIPTION

Several very delicate specimens of *Calymne* were taken in an almost complete state during the Russian cruises. The excellent condition of this material is attributed to the fact that the 0.25 m^2 grab took specimens still enveloped in the cushioning ambient substrates.

FAMILY CALYMNIDAE MORTENSEN, 1907

In the most recent revision of holasteroid echinoids, Smith (2004) identified a clade, Calymnidae, comprising the Recent genera *Calymne* and *Sternopatagus* as

Table 1. Complete listing of all known specimens of *Calymne*. Except for the syntypes (NHM 81.11.22.46), all specimens were hitherto unpublished. *type material

Cruise	Station date	Sampling area	Depth	Sampling device	Institution catalogue number	Material [length]
HMS 'Challenger'	Station 54 27.05.1873	'north of the Bermudas' (Mortensen, 1950) – –	4846 m	–	Natural History Museum, London NHM 81.11.22.46	*2 fragmented adult specimens [23 mm; 28 mm]
RV 'Atlantis II' cruise 24	Station 122 21.08.1966	North of Bermuda lat: 35°05.0'N–35°52.0'N long: 64°57.5'W–64°58.0'W	4833 m	Epibenthic trawl	Museum of Comparative Zoology, Harvard MCZ 8571	6 juvenile specimens [1.3–11.3 mm] 2 fragmented adult specimens [30 mm; 40–50 mm]
RV 'Akademik Kurchatov' cruise 37	Station 3787 25.07.1983	NW of Amper Seamount lat: 35°50.5'N long: 13°00.3'W	4860 m	Grab [layer: 0–50 mm]	Shirshov Institute of Oceanology, Moscow –	1 adult specimen [28 mm]
RV 'Akademik Mstislav Keldysh' cruise 23	Station 2462 03.07.1991	Newfoundland Basin lat: 41°45.08'N long: 49°55.85'W	3720 m	Grab [layer: 0–50 mm]	Shirshov Institute of Oceanology, Moscow –	1 juvenile specimen [13.8 mm]

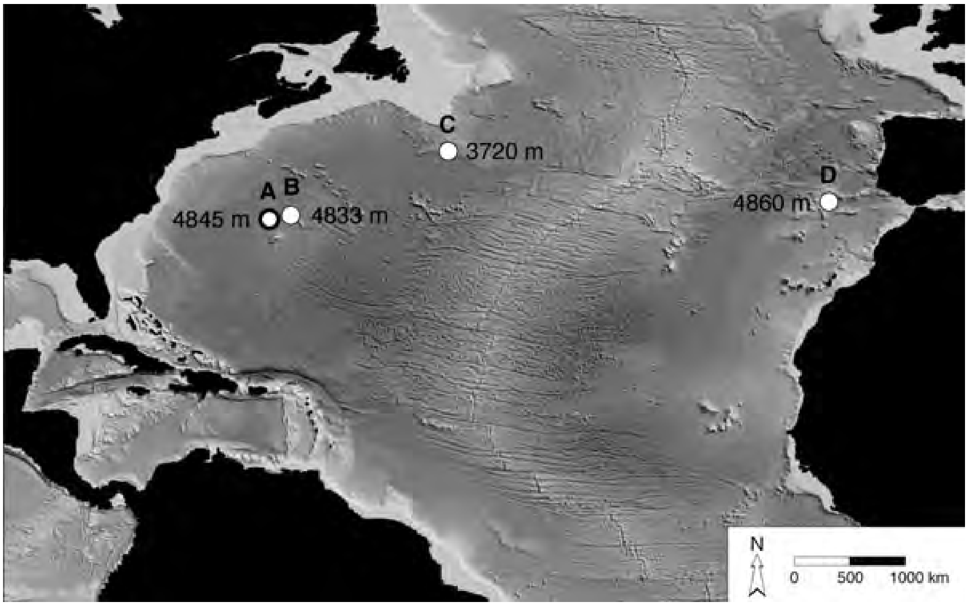

Figure 1. Map of northern Atlantic Ocean showing localities and depths from which *Calymne relicta* has been collected. A, type locality of specimen in Natural History Museum, London. B, R/V 'Atlantis II' cruise 24, station 122. C, R/V 'Akademik Mstislav Keldysh', cruise 23, station 2462. D, R/V 'Akademik Kurchatov', cruise 37, station 3787.

well as the fossil genera *Pseudoffaster*, *Sanchezaster*, and *Chelonechinus*. Some of the relationships among those taxa were already supported by the phylogenies proposed by David (1988). However, these placements were based on gross morphology and plate architecture, and did not take into account appendages that can be of the utmost importance (Mortensen, 1907). Moreover, some features of *Calymne* lead us to question the phylogeny proposed by Smith (2004) and the composition of the family Calymnidae. The genera referred by Smith (2004) to the family Calymnidae differ very significantly from each other in numerous characters. Examples of heterogeneous expressions of character states within the family include, but are not restricted to: peristome flush with the test or at the end of a deep groove; marginal fasciole well developed or absent; apical system disjunct or not; ambulacra with single or paired pores; test thin or thick; plastron continuous or disjunct. That these extremes in such basic characters can exist in a single clade is, to say the least, somewhat perplexing. Therefore, for the moment we will follow Clark (1917, 1925), Mortensen (1907, 1950) and Wagner & Durham (1966) in regarding *C. relicta* as the only species in the family Calymnidae, which is characterized by: (1) a meridosternous plastron; (2) amphiplacous anterior interambulacra (in interambulacra 2 and 3, the first plate is followed by a pair of plates); (3) a well-developed marginal fasciole; (4) a peristome flush with the test; (5) ambulacra with single pores; (6) highly specialized spines (as described below).

GENUS *CALYMNE* THOMSON, 1877

Diagnosis

Test of adults very high, ovoid in aboral view, and compressed laterally with low ambitus; anterior end rounded without frontal groove; posterior end almost vertically truncated. Large spoon-shaped spines present on plastronal area; frills of large paddle-shaped spines around periproct and aborally on the posterior end; subanal tuft of large pointed spines.

Other significant features are important in identification of the genus but are present in other holasteroids and therefore not diagnostic for *Calymne* alone. These are as follows. Orthosternous plastron with small labrum in contact with sternal plate; interambulacra 1 and 4 meridoplacous, interambulacra 2 and 3 amphiplacous in adults; anterior and posterior pairs of genital plates separated by pair of ocular plates; two gonopores on genital plates 2 and 3. Uniporous ambulacra. Peristome flush with test; periproct supramarginal, located at top of posterior face. Marginal orthofasciole crossing plates 5.a.4 and 5.b.5. Rostrate pedicellariae of three types; ophicephalous pedicellariae umbrella-shaped; triphyllous pedicellariae present; tridentate and globiferous pedicellariae absent.

Genotype and only known species: *Calymne relicta*.

CALYMNE RELICTA THOMSON, 1877

Calymne relicta – Thomson, 1877: 397, figs 102–103; Agassiz, 1881: 155–157, pls XXXIV, XXXIX 24–26, XL 63–65, XLIII 24, XLIV 47, 48; Lovén, 1883: 90; Mortensen, 1907: 53–54, 86, text-fig. 7, pls X 5, 6, 30; Clark, 1917: 125; Clark, 1925: 188; Mortensen, 1950: 127–131; Mooi & David, 1996: figs 9p, 12k; Smith, 2004: 146–149, text-fig. 7.

Diagnosis

As for the genus.

RESULTS

GENERAL FEATURES AND PLATE ARCHITECTURE

Size

Juveniles collected during the R/V 'Atlantis' cruise (MCZ 8571) range between 1.3 and 11.3 mm in length. Test lengths of two adult specimens (30.0 mm and between 40.0 and 50.0 mm respectively) were estimated from fragments (MCZ 8571). The adult from the R/V 'Akademik Kurchatov' cruise was 28.0 mm long, 23.2 mm wide, and 25.0 mm high. The young specimen from the R/V 'Akademik Mstislav Keldysh' cruise was 13.8 mm long. As in most deep-sea holasteroids, the test is very thin and extremely fragile.

Colour

Either dry (after fixation or preservation) or wet (still in ethanol) the test is beige, tube feet are darker beige, primary spines are white, and miliary spines are translucent. However, the test and spines of the specimen collected by the 'Challenger' were described as being pale green (Agassiz, 1881; Clark, 1925).

Shape of the test

The test of adults is high, ovoid in aboral view, and compressed laterally, with a low ambitus (Fig. 2C, D). In contrast, the lateral view shown by Agassiz (1881: plate 34, test length (TL) of about 30 mm) is low, and therefore departs from that of our specimens. This can be accounted for by the fact that Agassiz's figure was compiled from fragments of different specimens and not likely to be an accurate reconstruction in all respects. A low profile is more typical of a juvenile specimen. Maximum width is approximately half-way along the anterior-posterior axis, but posterior to the peristome and the apical system (Fig. 2A, B). The anterior margin of the test is gently rounded and smoothly joins the domed aboral surface, which extends posteriorly in a broad, aboral ridge (Fig. 2E). Maximum height is about two-thirds of the length towards the posterior of the test, where the aboral surface forms a broad, barely distinguishable bulge. The posterior is vertically truncate except for a weakly developed rostrum below the ambitus. The oral surface is flat in the anterior region, but is developed into a wide keel in the posterior part along the midline. The anterior, unpaired ambulacrum is slightly sunken adorally, with this trough shallowing near the anterior margin until it is flush with the rest of the test at the ambitus.

Apical system

In adult specimens the apical system is more or less elongate, but with considerable alteration of the typical holasteroid pattern [apical plates from left and right sides joining along the midline to form a biserial pattern, as described in Mooi & David (1996)]. In *Calymne*, the posterior genitals (1 and 4) and posterior oculars (I and V) are stretched along the midline of the apical surface. The posterior genitals can even be uniserially arranged (Fig. 3A). In the anterior part of the apical system, genital 3 may be separated from ocular IV by plates of interambulacrum 3. Such a pattern is reminiscent of that in *Plexechinus* and *Urechinus* (Mooi & David, 1996). In all the juvenile specimens examined (up to 11.3 mm long), apical plates are biserially arranged and organised according to the typical holasteroid pattern (Fig. 3B). Therefore, in *Calymne*, apical structures become progressively stretched and redistributed during ontogeny. The overall pattern and degree of stretching differ among specimens, and do not seem dependent on test size alone. The same phenomenon has been observed in several species of deep-sea holasteroids (Saucède *et al.*, 2004; Smith, 2004). Gonopores are present only on genital plates 2 and 3; posterior genitals lack pores. Genital plate 2 is the largest genital and is perforated by a few hydropores.

Peristome and periproct

The peristome is small, circular, slightly depressed, and tilted to face somewhat anteriorly. It is situated anteriorly, distant from the anterior edge by about 20% of the test length. The peristomial membrane contains numerous small platelets, with the mouth opening slightly displaced toward the posterior margin of the peristome (Fig. 4A). The periproct is longitudinally ovate, high on the posterior surface. The adoral margin of the periproct is bounded by interambulacral plates 5.a.7/5.b.8 and the aboral margin by plates 5.a.10/5.b.10 (Fig. 4B, D).

Ambulacra and interambulacra

Ambulacra are all similar and flush with the test, except for the aforementioned oral portion of ambulacrum III. Aborally, ambulacral plates are large and similar in size to the interambulacral plates (that is, there are no traces of petaloids) (Fig. 4C). Tube feet are mounted on minute unipores, situated near the centre of the ambulacral plates. Distal to the phyllopodia near the mouth, tube feet are rudimentary,

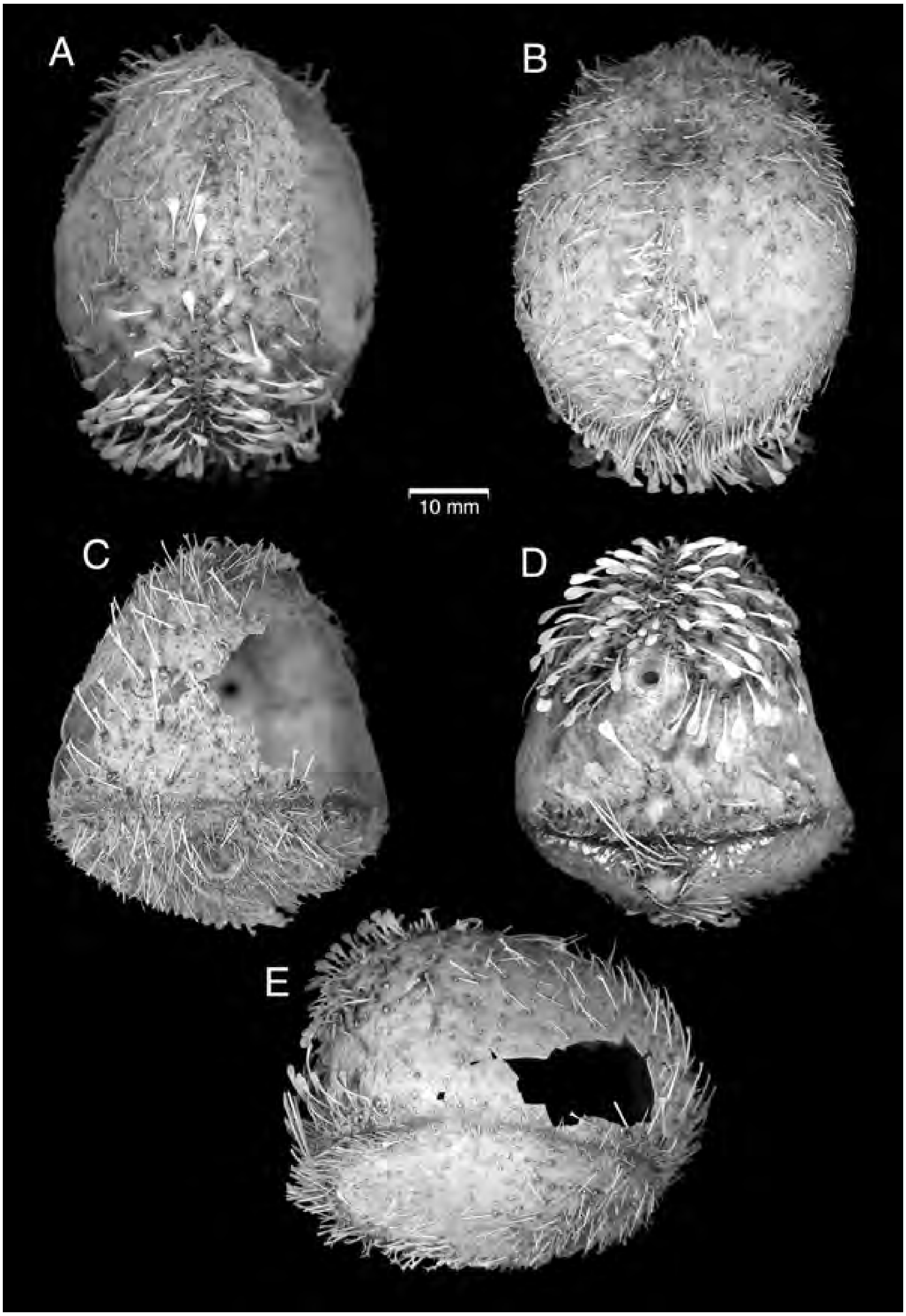

Figure 2. Specimen from R/V 'Akademik Kurchatov' cruise 37, station 3787. A, aboral surface. B, oral surface. C, anterior surface. D, posterior surface. E, right side.

appearing in preserved material as small, darkened knobs. Proximal to the peristome, the tube feet on the basicoronal ambulacral plates are developed into penicillate phyllopodia, each of which possesses about ten rudimentary digitations.

The plating in interambulacrum 5 is orthosternous (Fig. 4A). The labral plate (5.1) is followed by a single, large sternal plate (5.b.2); both plates are always in contact. Laterally, the labrum contacts the first or second ambulacral plate, and the sternal plate reaches the second or third ambulacral plate. The sternal plate is followed by a pair of elongate, symmetrical episternal plates (5.a.2 and 5.b.3) then by a pair of elongate and non-alternating post-episternal

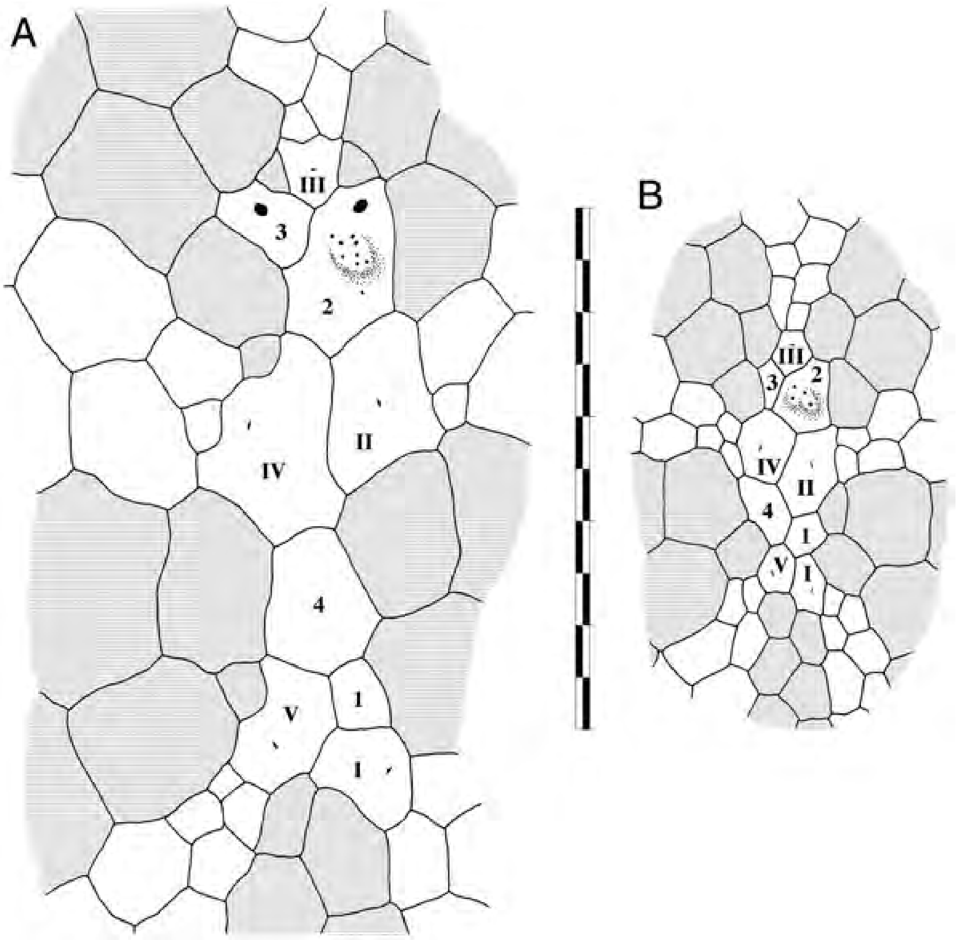

Figure 3. Apical system plate architecture of *Calymne relicta* (MCZ 8571) from R/V 'Atlantis' cruise 24, station 122, anterior towards top of page, interambulacral plates shaded, apical plates labelled according to Lovén's system. A, adult specimen approximately 30 mm long. B, juvenile specimen (lacking gonopores) 11.3 mm in test length.

plates (5.a.3 and 5.b.4), at which point the plates alternate. The plate pattern in interambulacra 1 and 4 is meridoplacous (plates 1.1 and 4.1 followed by a single plate). Interambulacra may be disjunct (Fig. 4A): interambulacral plates 1.1 and 1.b.2 disjunct (ambulacral plates I.b.2 and II.a.2 in contact) and interambulacral plates 4.1 and 4.b.2 disjunct (ambulacral plates IV.b.2 and V.a.2 in contact). The plating in interambulacra 2 and 3 is amphiplacous: plates 2.1 and 3.1 are followed by biserially arranged and regularly alternating plates.

APPENDAGES

Spine morphology

Spines are more diverse in size and shape than in any of the known holasteroids. Ten different types can be identified, including primary spines, miliary spines, and clavulae (spines of the fasciole) (see Mooi & David, 1996; David & Mooi, 2000 for terminology). Primary spines include four types of long, slender spines (L1–L4) and four different types of spatulate spines (S1–S4). In all types of spines, the shaft is longitudinally striated by ribs that run from the tip almost to the base, where the spine is progressively more expanded and finally surrounded by distinct buttresses which flare out into the more or less enlarged and asymmetric milled ring. In spines of the L-type, the milled ring is slightly asymmetric, a little enlarged on the concave side of the curved shaft or bent extremity of the spine. In contrast, spines of the S-type are characterized by highly asymmetric rings, greatly enlarged on the convex side of the curved extremity of the shaft. The different types of spines are diversified and distributed on the test as follows [spine lengths are taken from the adult specimen from the R/V 'Akademik Kurchatov' cruise (station 3787)].

Spines of type L1 are up to 8.0 mm long. They are smooth and the same diameter for nearly their entire

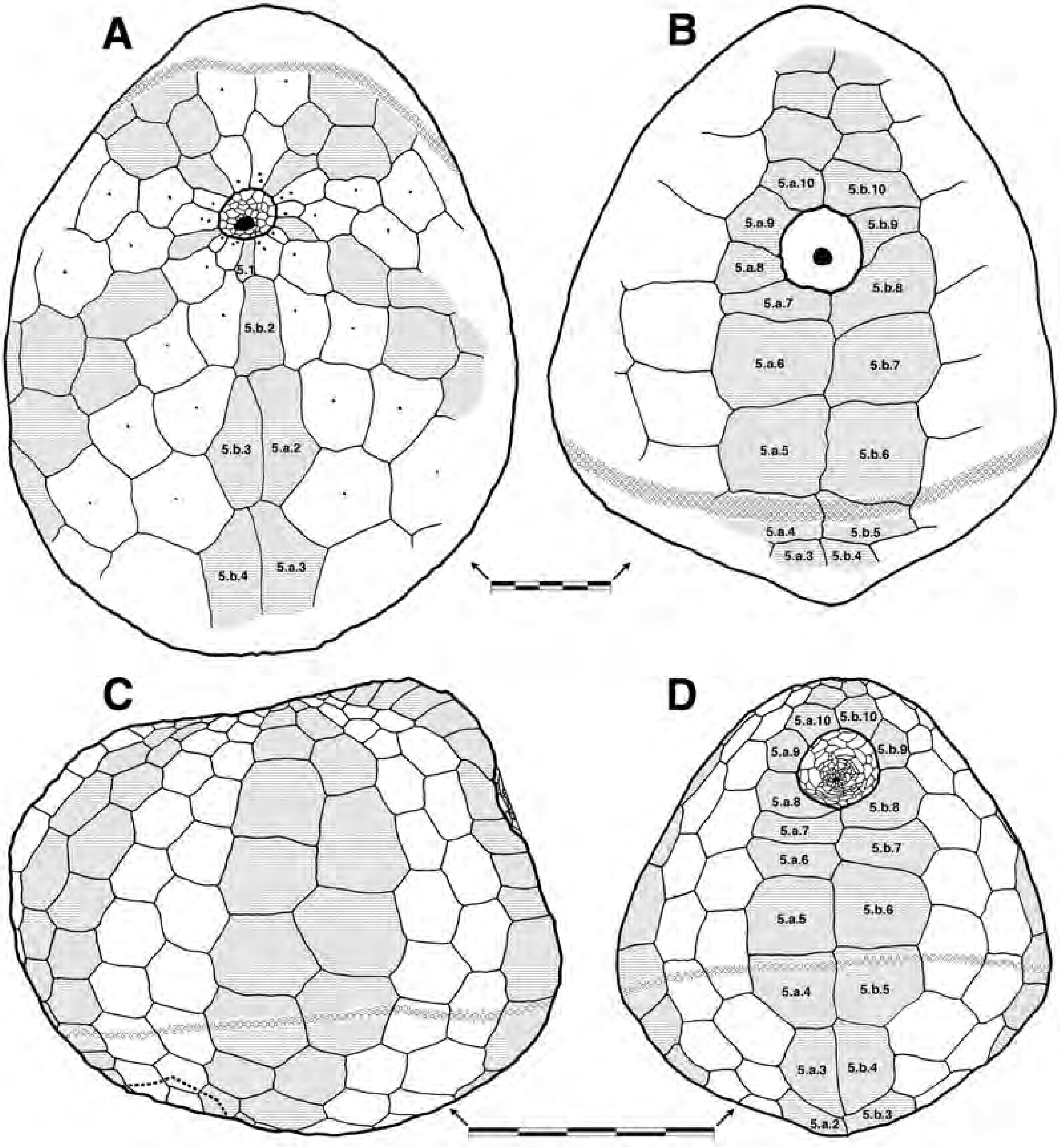

Figure 4. Plate architecture of *Calymne relicta*. For each, the fasciole is indicated by bands of small, open circles, the interambulacra are shaded, mouth and anal openings are black, some plate sutures are omitted because they were not visible on the specimen. The plates of the posterior interambulacrum are numbered according to Lovén's rule. Scale bars are 5 mm long. A, oral surface of adult specimen from R/V 'Akademik Kurchatov' cruise 37, station 3787, anterior towards top of page. B, posterior surface of specimen in (A). C, left side of specimen from MCZ 8571, R/V 'Atlantis' cruise 24, station 122, position of mouth indicated by dashed line. D, posterior surface of specimen in (C), viewed slightly more from the oral surface than view shown in (B).

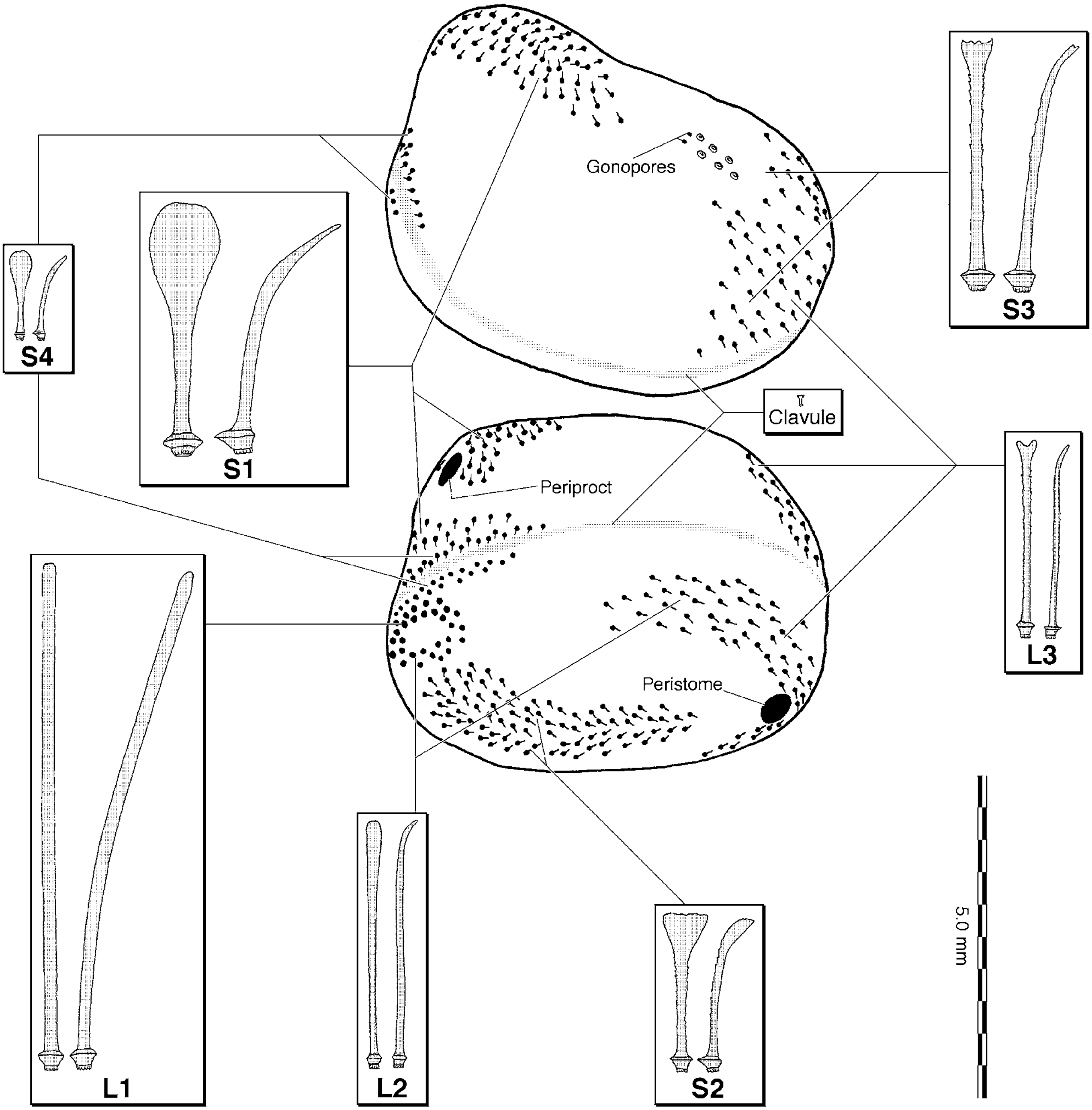

Figure 5. Location of spine types on *Calymne relicta* plotted on specimen from R/V 'Akademik Kurchatov' cruise 37, station 3787. For each view of entire specimen, the orientation of the power stroke as suggested by tubercle asymmetry is indicated by the direction of the small lines leading away from the dot. The upper drawing of the entire specimen is an oblique view from the anterior-dorsal, anterior to the right. The lower drawing of the entire specimen is an oblique view from the posterior-ventral, anterior to the right. Shaded bands indicate the position of the fasciole. For each spine drawing (except for the clavule), the image on the left is a 'frontal' view, the one on the right is a 'side' view. Scale bar at lower right is for the spines, which are all drawn to scale.

length, slightly curved, with a rounded tip. These spines are located on the posterior end of the test, just beneath the marginal fasciole, where they are curved upwards (Fig. 5). The spines are set into a circular arc, bounding adapically the small posterior rostrum. In the adapical part of the anterior ambulacrum, five large and closely packed tubercles are arranged in two straight lines, with two tubercles on the left side of the test and three on the right side. Unfortunately, we were unable to observe the spines that once articulated on these adapical tubercles in adults. Only the base of a single one of these spines (on an adapical tubercle) is preserved and shows that the spine was large. However, in a juvenile (station 2462, cruise 23 of the R/V 'Akademik Mstislav Keldysh'), a spine is preserved on one of these adapical tubercles; it is smooth and narrows gradually from its base to the flattened and slightly widened tip. At 49% of the test length, this is the longest spine on this specimen. It is more than a third longer than the L1 spines located beneath the marginal fasciole.

Spines of type L2 are about 4.0 mm long, with a smooth shaft and a slightly bent tip shaped into a flattened, oar-like terminus. The L2 spines are common on the oral, apical, and posterior surfaces of the test (Fig. 5). Posteriorly, they are present just distal to the plastron, where they form a half circle along the lower part of the posterior rostrum, bending upward. They change progressively into L1 spines towards the upper part of the half circle (described above); from this point they are present all over the oral surface, bending towards the anterior except on the posterior ambulacra in which L2 spines tend to be smaller, with their tips bending posteriorly. In the aboral region, they are located antero-laterally, and are bent posteriorly.

Type L3 spines are 2.5 to 3.0 mm long, and have a flattened, curved, and bifid terminal widening. The distal part of the shaft is thorny on the two sides of the bifid tip (Fig. 6A, B). L3 spines are present on the oral, aboral, and anterior surfaces of the test (Fig. 5). They are bent posteriorly in aboral regions and anteriorly in the adoral area.

Type L4 spines are short, with a length ranging between 1.5 and 2.0 mm. They have a pointed, slightly bent tip. The shaft is smooth at the base and thorny towards and on the concave side of the bent tip (Fig. 6C). L4 spines are scattered all over the test, except posteriorly. The tip is bent forward on the anterior and adoral parts of the test, and backward on the posterior and apical parts.

Spines of type S1 are up to 4.1 mm in length and are distinctly paddle-shaped (Fig. 6D), with a curved and broad tip (up to 1.0 mm wide). The entire spine is smooth. S1 spines are distributed on the posterior and aboral sides of the test into two distinct series (Fig. 5). The first series is a posterior, narrow band located just above the marginal fasciole. This series widens below the periproct and is separated by a 'naked' area (covered only by miliary spines) from the second series, which is a set of densely packed S1 spines that extends to the lateral edges of the periproct and aborally onto the posterior curvature of the test. These closely spaced S1 spines form a conspicuous posterior tuft (Fig. 2D). In the first series, spine curvature is orientated upward while shafts of the second series are curved downward, radiating from the posterior edge of the aboral surface, where the test forms a broad, low bulge.

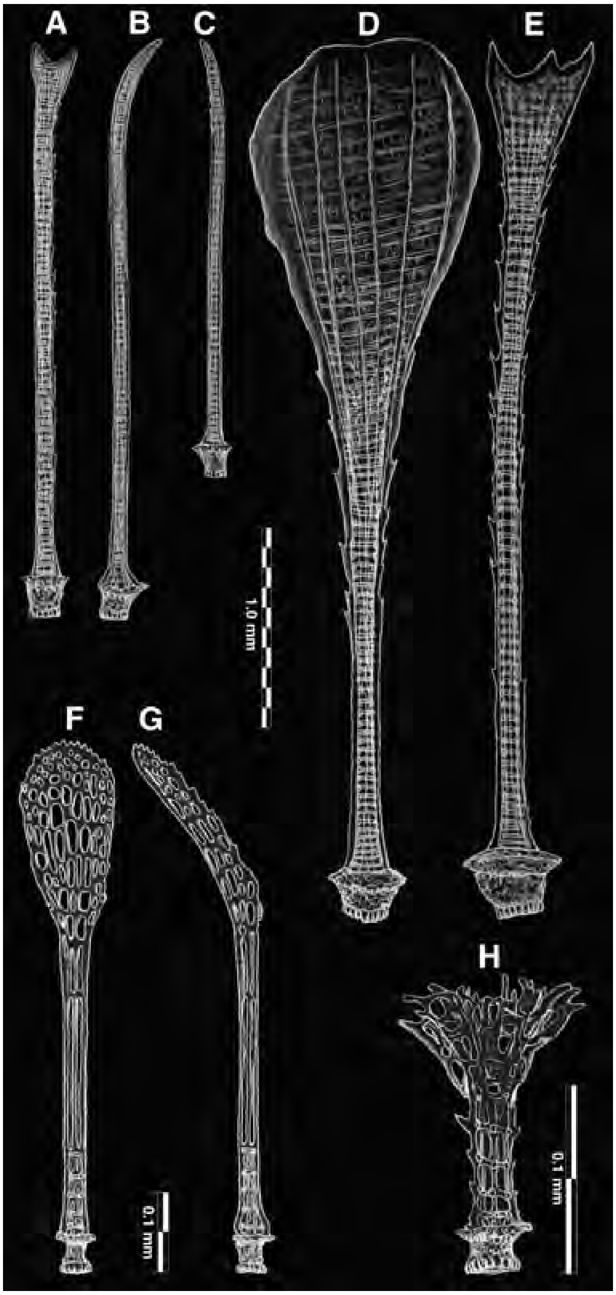

Figure 6. Drawings of spines of *Calymne relicta*, depicted as viewed with transmitted light microscopy. Scale bar at uppermost refers to (A)–(E), at lower left to (F) and (G), at lower right to (H). A, 'frontal' view of type L3. B, 'side' view of type L3. C, 'side' view of type L4. D, 'frontal' view of type S1. E, 'frontal' view of type S3. F, 'frontal' view of miliary. G, 'side' view of miliary. H, clavule from fasciole.

Spines of type S2 are thick and short, ranging between 2.7 and 2.8 mm in length. The tip is spatulate, concave, and truncated to form a shape like the proximal half of a spoon's ladle. The margin of the spatulate terminus is slightly serrate. The shaft is smooth on its convex side, and thorny on the other surfaces. S2 spines are present exclusively on the plastron, with the tips curved posteriorly (Fig. 5).

Spines of type S3 are about 4.0 mm long and possess a concave, terminal widening with a serrated margin. The shaft is smooth on the convex side, but thorny elsewhere (Fig. 6E). S3 spines are located on the anterior face of the test from the apical system to the oral surface, and are abundant above the marginal fasciole (Fig. 5). All these spines are curved upward above the marginal fasciole. However, adorally, they are orientated backward.

Spines of type S4 are small, spatulate spines about 1.5 mm long. They are located on the posterior part of the test, both above and below the marginal fasciole (Fig. 5). Those located above the fasciole are curved so as to point upward, whereas those below are pointed downward.

Miliary spines have a long and very slender shaft which terminates in a broad, flattened expansion (Fig. 6F, G). They are bent just at the point where the shaft starts flattening. As Mortensen (1907: 54) pointed out: 'miliary spines have the point widened so as to form a broad, fenestrated plate, finely serrate along the outer edge'. Miliary spines are present all over the test. However, they are especially abundant on the aboral surface, above the marginal fasciole. In contrast, they are rare on the oral surface and on the sides of the test.

Clavulae have a short shaft that terminates in very broad, crown-shaped terminal expansion (Fig. 6H). These expansions can be as wide as 0.6–0.8 times the length of the clavulae. The marginal fasciole is well developed and easily distinguished, with up to eight series of regularly arranged clavulae. Miliary tubercles that support these clavulae are very distinct from other miliaries of the test and form a true orthofasciole (*sensu* Néraudeau, David & Madon, 1998). The fasciole follows the ambitus, delineating the boundary between the oral and aboral surfaces, and passes well below the periproct (Figs 2D, 5). In adult specimens, the fasciole passes over the second pair of plates in ambulacrum III (plates III.a.2 and III.b.2) and over interambulacral plates 5.a.4 and 5.b.5 beneath the periproct (Fig. 4A, B). In interambulacrum 5, the position of the fasciole is the same in juvenile and adult specimens, but in ambulacrum III its position differs with ontogeny (see below).

Pedicellariae and sphaeridiae

As in previous studies on other species of holasteroids (Mortensen, 1950; Mooi & David, 1996; David & Mooi, 2000), rostrate, triphyllous, and ophicephalous pedicellariae were identified. However, in *Calymne*, tridentate and globiferous pedicellariae were not found.

Calymne is distinguished by well-developed rostrate pedicellariae which vary in shape and size, and which are apparently more numerous in adult (station 3787) than in juvenile specimens (station 2462). Mortensen (1907, 1950) recognized two different types of rostrate pedicellariae. However, we could distinguish four types according to their size, relative length and width of the distal part of the blade, number and size of terminal teeth, and morphology of the basal part. Type 1 rostrate pedicellariae have valves about 0.4 mm in length, and a width/length (W/L) ratio (W/L of valve) of about 0.7 (Fig. 7A). Valves have a short middle constriction and a wide blade with about ten large, undifferentiated teeth. Margins of the basal part are serrated and a few thorns are developed on the stem (Fig. 7B). Type 1 rostrates are located on the oral surface and around the periproct. Type 2 rostrates have valves about 0.25 to 0.4 mm long, with a long, slender middle part and a relatively narrow blade with about ten large, undifferentiated teeth (Fig. 7C). The W/L ratio is about 0.5, and the distal part is longer than the basal part. Margins of the base are smooth as is the stem. Type 2 rostrates are found mainly on the aboral surface. Type 3 rostrates differ from type 2 only in possessing a wider blade with about 20 small, undifferentiated teeth (Fig. 7D). Type 4 rostrates are rare, found only near the peristome, and consist of minute valves about 0.2 mm long, with a W/L ratio of about 0.5.

Ophicephalous pedicellariae are found on both adult and juvenile specimens. They are especially numerous on the aboral side of the juvenile specimen collected by the R/V 'Akademik Mstislav Keldysh' (Station 2462). Ophicephalous pedicellariae have an elongated distal part of the valve, with a contrastingly very narrow, smooth proximal area, and a highly serrate, parasol-shaped terminal margin with about 16 downward-directed, needle-like teeth (Fig. 7E). The stems of these ophicephalous pedicellariae are extremely truncated, and less than 30% of the length of the valves themselves. The umbrella-shaped pedicellariae of *Calymne* are comparable to those observed in the Pourtalesiidae (Mooi & David, 1996). Some differences exist, however: *Echinocrepis* has short valves; *Cystocrepis* and *Ceratophysa* have medium-length valves; and *Echinosigra* and *Pourtalesia* have long valves (Mironov, 1973).

Triphyllous pedicellariae were found around the peristome and above the periproct, and differ from ophicephalous and rostrate in having a long, muscu-

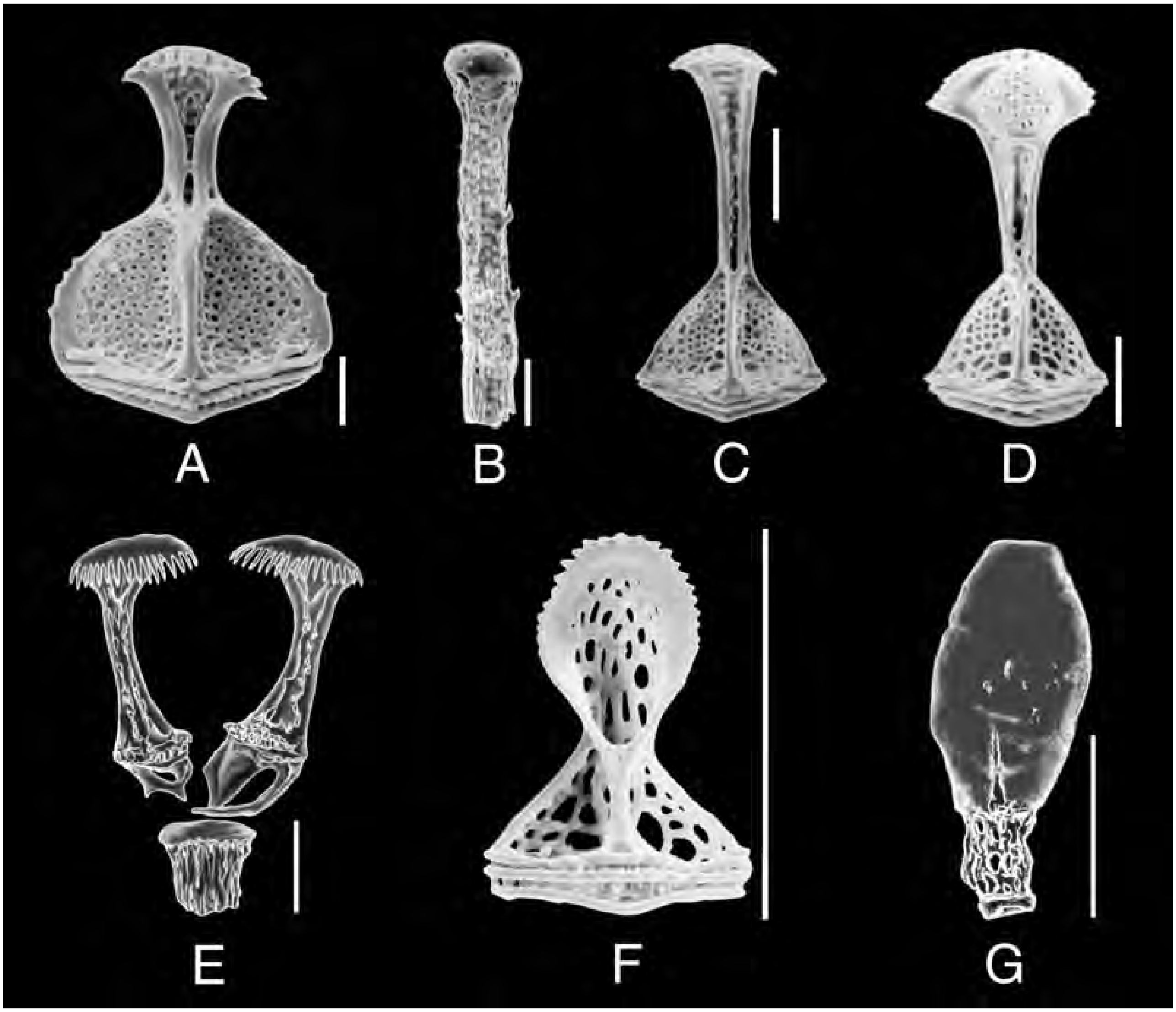

Figure 7. Pedicellariae of *Calymne relicta*. A, scanning electron micrograph (SEM) of interior view of type 1 rostrate valve. B, SEM of interior view of type 1 rostrate stem. C, SEM of interior view of type 2 rostrate valve. D, SEM of interior view of type 3 rostrate valve. E, drawing of two of the three valves of an ophicephalous pedicellaria showing position in life relative to the stem. F, SEM of interior view of triphyllous valve. G, drawing of sphaeridium. Scale bars 0.1 mm.

lar, hollow, fluid-filled neck between the valves and the stem. In *Calymne* the neck is one to three times the length of the valves. The valve is short and has evenly spaced, very small teeth, all of which are approximately the same size. The tip of the valve is rounded (Fig. 7F).

Smooth, slightly elongate sphaeridiae (Fig. 7G) occur around the peristome, one or two per plate. In the posterior ambulacra, sphaeridiae can be found distal to the peristome up to the fourth ambulacral plate.

ONTOGENETIC DATA

During cruises of the R/V 'Atlantis' and 'Akademik Mstislav Keldysh', entire, undamaged juveniles ranging between 1.3 and 13.8 mm long were collected. The size range, as well as the presence of very early stages of growth represented by the smallest specimens, permit analysis of the morphological changes occurring during postlarval growth of *Calymne relicta*.

The earliest stages (Fig. 8A) to which we had access were collected by the R/V 'Atlantis II', and represent a just-postlarval imago that is somewhat elongated and comparable to young, early postmetamorphic *Echinocardium cordatum* (Gordon, 1927) and *Pourtalesia miranda* (David, 1987). At this stage, the periproct is still partly enclosed by the apical system, reminiscent of adult early Jurassic Irregularia (Jesionek-Szymanska, 1959; Saucède, Mooi & David,

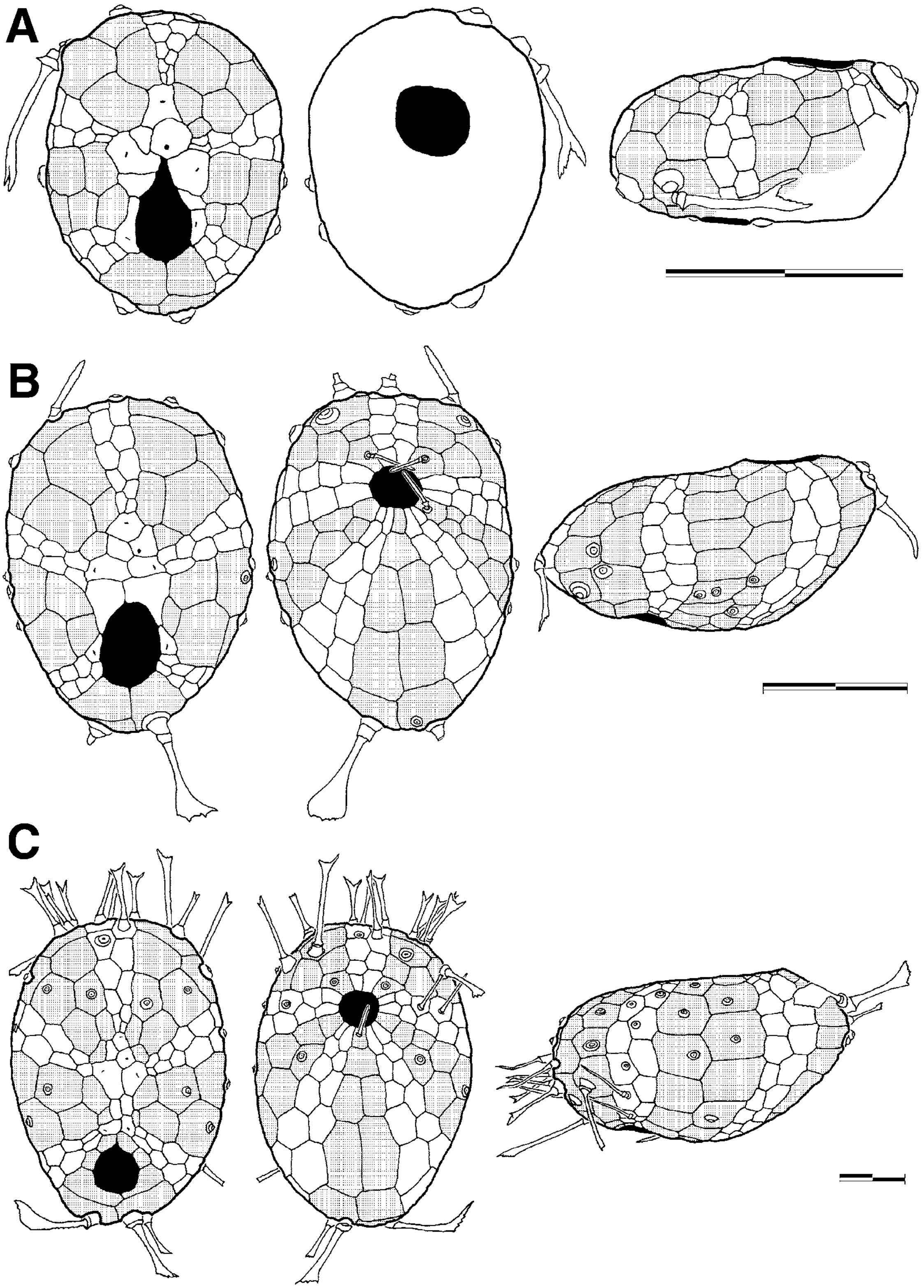

Figure 8. Ontogeny of *Calymne relicta* from MCZ 8571, R/V 'Atlantis' cruise 24, station 122. For each set of drawings, from left to right: apical view, oral view, and left side. The periproct and peristome are in black, and the interambulacral plates are shaded. In some specimens, the sutures are omitted because they were not discernible, and only primary tubercles are shown (some still with spines attached). All scale bars are 1 mm long. A, just-postlarval imago. B, very small juvenile. C, larger juvenile with periproct separated from apical system.

2007). The peristome is already in a slightly anterior position. Large bifid spines are present at the ambitus on the anterior edge.

At sizes of about 2.5 mm (Fig. 8B), the test is more elongated. The apical side is flattened, whereas the oral side is swollen behind the peristome. The periproct is still partly enclosed by the posterior part of the apical system, which is displaced posteriorly; it is separated from the peristome by about six plates. The plastron is conspicuously orthosternous, the labrum being in contact with a single sternal plate, while the other interambulacra are still all amphiplacous. Large tubercles encircle the test at the ambitus. Large spatulate spines (of S1 or S2 types) are present posteriorly; bifid spines occur anteriorly.

Although the general shape of the test does not change, important architectural changes occur by the time the young *Calymne* reaches 5.0 mm in length (Fig. 8C). The periproct is now separated from the apical system by one pair of interambulacral plates, and the apical system itself is configured in the typical holasteroid pattern. On the oral surface, the paired posterior interambulacra (1 and 4) remain meridoplacous. Large tubercles are now present in all regions of the test except the plastronal area. Numerous bifid spines adorn the anterior part of the test, while spatulate spines occur posteriorly. There is still no trace of a fasciole. Marginal spination seems completely undifferentiated and it has not been possible to identify any clavulae that might correspond to early stages of fasciole formation.

At 10.0 mm, the test profile has drastically changed, being much more elevated and less elongated (Fig. 4C, D). Changes occur almost exclusively on the upper part of the test and can be related to the high rate of production of new plates in the posterior interambulacrum (5), the periproct now being separated from the apical system by six pairs of plates. The periproct occupies an upper position on the vertical, posterior face. The oral surface remains relatively unchanged. A well-developed marginal fasciole is clearly visible all around the test (it crosses interambulacrum 5 on plates 5.a.4/5.b.5, and ambulacrum III on plates III.a.4/III.b.4); the clavulae are distinct, and have the characteristic crown-shaped tips. Hence, the fasciole forms when the test is between 5 and 10 mm long according to processes which still remain to be precisely identified.

Further development builds upon the previous trends with only minor modifications. The oral surface becomes more flat and parallel with the aboral surface. The apical system continues to elongate and eventually becomes disjunct. In ambulacrum III, the fasciole is shifted lower, passing over plates III.a.2 and III.b.2 in adults, whereas in interambulacrum 5, the position exhibited in earlier stages is maintained.

HABITAT

Determination of the physical environment in which specimens of *C. relicta* have been collected is a prerequisite for any behavioural interpretation. In particular, the nature of the sea bottom is a determinant factor in the ecology of irregular echinoids (Nichols, 1959a; Smith, 1980a; Kanazawa, 1992; Telford & Mooi, 1996). *Calymne* is an exclusively deep-sea form with a known depth range of 3720 to 3860 m. Characteristics of the sea bottom are precisely known only for station 2462, cruise 23 of the R/V ‘Akademik Mstislav Keldysh’. The sediment is compact, viscous, dark-grey with dark-brown spots, and composed of clays and silts with the addition of numerous sand grains. The carbonate ($CaCO_3$) content is between 24.0 and 25.5%, comprising mostly foraminiferans and coccoliths. Some biogenic siliceous inclusions are present. The associated fauna includes hexactinellids, bryozoans, and polychaetes. More generally, the deep-sea bottom is soft with a superficial thixotropic layer of deep-sea marine snow covering the mud itself. Marine snow is made up of macroaggregates particularly rich in organic matter (bacteria, dead phyto- and zooplankton, faecal pellets) sinking from the upper layers of the water column. Marine snow is a major nutrient delivery system to the deep-sea benthic fauna (Turley, 2002).

DISCUSSION

SPINE MORPHOLOGY AND ACTION

Relationships among spine morphology, location, and function have been studied in detail in spatangoids (Nichols, 1959a; Kier & Grant, 1965; Chesher, 1968; Smith, 1980a, b; Kanazawa, 1992). A major precept of these works is that the preferred direction of the power stroke of spines can be deduced from the direction in which areoles (area around tubercles at which spine muscles insert) are enlarged and displaced (Nichols, 1959a; Smith, 1980a; Kanazawa, 1992).

In *Calymne*, the aboral surface is densely covered by miliary spines, but primary spines are relatively sparse over most of this surface (particularly on the sides of the test) except for the posterior region. This low spine density is typical of deep-sea epifaunal holasteroids. In contrast, aboral spines are more densely distributed in infaunal, irregular echinoids living in muddy substrates. This is the case for the extant deep-sea burrowing spatangoids *Aceste bellidifera*, *Aeropsis rostrata*, *Hemiaster expergitus*, and *Brisaster latifrons* (Smith, 1980a; David & Sibuet, 1985; Kanazawa, 1992). In the latter species, the aboral spine canopy is implicated in maintaining the ceiling of burrows and in keeping a free space for ciliary currents between the test surface and the sediment much as in other burrowing Irregularia (Mooi, 1986).

In *Calymne*, five large tubercles are grouped just anterior to the apical system on the adapical plates of ambulacrum III, indicating the presence of five large spines. In burrowing spatangoids (e.g. *Echinocardium cordatum* and *Moira atropos*), large apical spines are raised to form an upwardly directed tuft that helps to maintain the apical funnel that allows water to enter and oxygenate the burrow. Moreover, apical funnel-building tube feet are present for compaction and mucus-plastering activity of the apical tuft (Nichols, 1959a; Kanazawa, 1992). However, when these echinoids are exposed on the sea bottom, these long apical spines no longer form an erect tuft but lie flattened posteriorly over the aboral surface and the apical system (Smith, 1980a).

In *Calymne*, apical and funnel-building tube feet are absent, and the low density of spines suggests that aboral food collection is not a primary function of the apical spination. In our opinion, the biserial arrangement of the five apical tuft spines in *Calymne* is not consistent with maintenance activity at the base of a funnel. Instead, our observations suggest that the long apical spines over the two gonopores probably function as a protective canopy.

The anteriormost, or frontal surfaces of *C. relicta* are densely populated by several types of spines, including types L2, L3, and S3 (Fig. 2C). All are about the same length, and are more or less mixed together. Throughout this region, smaller primary spines (L4) are present in between the larger spines. Starting at the apical system, the arrangement consisting of one large spine per plate continues down ambulacrum III, but the five large apical spines are replaced by S3 spines that are in turn replaced by smaller L3 spines at the ambitus. S3 spines are also replaced laterally by the L3 type (Fig. 5). Above the fasciole, the areoles of all the frontal primary spines are enlarged adorally, indicating a downward power stroke, whereas spines located below the fasciole are constructed so as to perform an antagonistic, aborally directed stroke (Fig. 5).

Infaunal spatangoids tend to have frontal spines that are used for excavating or scraping on the facing wall of a burrow, and it is thought that the general motion of the spines is in a horizontal stroke (Gale & Smith, 1982; Kanazawa, 1992). Strokes in opposite directions on either side of a fasciole exist in some spatangoids (e.g. *Brissopsis lyrifera*, Smith, 1980a), but in these cases, the peripetalous fasciole is located far above the ambitus and spine morphology is completely different from that observed in *Calymne* (Smith, 1980a; Hollertz & Duchêne, 2001). In *Calymne*, L2, L3, and S3 spines have widened tips – an uncommon feature in scraping spines. Frontal spines of the oddly shaped, deep-sea mud-burrower *Aceste bellidifera* are enlarged at their tips as well, but differ from those of *Calymne* in exhibiting a probably horizontal power stroke.

Latero-dorsal spines are represented by spine types L2, L3, and L4, which are sparsely distributed (Fig. 5). Generally, these spines are used in burrowing species to support the top of the burrow and maintain a space for water circulation (Gale & Smith, 1982; Kanazawa, 1992). In *Calymne*, the shape and low density of latero-dorsal spines are not suited for such a function. Similarly placed spines in epifaunal spatangoid species are involved in defence and/or righting of the test (Kanazawa, 1992), but they tend to be more robust than those observed in *Calymne*.

When the test is viewed directly at the posterior bulge, the spatulate spines radiate outwards from either side of the mid-line in two wide frills separated by a region of aligned or 'combed' spines (Fig. 2A, D). In these frills, all spines of type S1 (either located on the apical side or more posteriorly, around the periproct) have areoles that are asymmetrically enlarged in a direction converging on the highest point of the test, which corresponds to the aforementioned posterior bulge (Fig. 5). Therefore, S1 spines of the posterior frills are constructed to move in such a way as to converge on the posterior bulge of the test. That is, there is a posteriorly directed movement of aboral spines and an aborally directed movement of lateral and posterior spines. This arrangement is very unusual and probably unique in echinoids.

Calymne's orthofasciole is wide (eight miliary rows) and bears strongly differentiated clavulae (Fig. 6H). By analogy with spatangoids, it is likely that this orthofasciole is involved in water circulation over the test, a water current being generated by the epithelial ciliation especially developed along the clavulae. The ciliary current maintains a flow of oxygenated water close to the test, sweeps the surface of the test clean, and forces waste and other unwanted material under the test (Nichols, 1959a; De Ridder & Lawrence, 1982). In some species, this current may provide food particles as well (De Ridder & Lawrence, 1982). Currents can be reinforced by the ciliary action of miliary spines that are densely distributed aborally (Nichols, 1959a; Stephenson, 1963; Smith, 1980a). In spatangoids, clavulae are also implicated in mucus secretion by glands present in the epithelium of the clavulae to help shield the test surface from the ambient sediment (Nichols, 1959b). In *Calymne*, nothing is known about the mucus-secreting properties of the crown-shaped clavulae, which are very different in shape from clavulae in which mucus-secreting cells have been detected (Nichols, 1959b).

Marginal fascioles are uncommon in Recent sea urchins. Unfortunately they occur in animals for which no direct knowledge of their behaviour is known (e.g. the spatangoids *Linopneustes excentricus*, *L. spectabilis*, and *Pericosmus macronesius*, and the holasteroid *Sternopatagus sibogae*). Some Cretaceous species also have marginal fascioles (*Infulaster*, *Hagenowia*, *Offaster*, and *Pseudoffaster*). The fossil holasteroids *Infulaster* and *Hagenowia* supposedly lived almost completely buried in carbonaceous mud, although their fasciole was in a marginal position and was morphologically less specialized than that of *Calymne* (Gale & Smith, 1982).

Posteriorly, the fasciole and the spine types S1 and S4 that border it on both sides (Fig. 5) display a pattern similar, although not at the same places on the test, to that in the deep-sea, mud-dwelling spatangoid *Aceste bellidifera*. In that species, large and small spatulate spines, very similar in shape to S1 and S4 spines of *Calymne*, are organised in two parallel bands on each side of a peripetalous fasciole, with the largest spines turned outward on the distal side of the fasciole. In burrowing spatangoids, spines surrounding the fasciole seem to transfer mucus towards the aboral and lateral surfaces of the test (Smith, 1980a). The situation is not completely the same in *Calymne*, as S1 and S4 spines are not distributed all along the fasciole, but only along its posterior portion. Therefore, it is likely that a mucous veil cannot be formed all over the test. If this is among their functions, S1 and S4 spines could be involved in developing a mucous coating specifically for the posterior part of the test. This would implicate these spines in isolating the test surface of the posterior region from the surrounding sediment.

The subanal tuft of *Calymne* includes spines that are curved gently upward, and lower spines (L2) with flattened extremities (Figs 2E, 5). In spatangoids, the subanal tuft is associated with a funnel used as a sanitary drain into which a cleansing ciliary current is directed (Smith, 1980a; De Ridder & Lawrence, 1982). In most burrowing species, this subanal sanitary drain is also associated with a subanal fasciole, which is absent in *Calymne*. However, the sector of the marginal fasciole near the tuft is likely to play a role similar to that of the subanal fasciole of spatangoids. Therefore, the subanal tuft of *Calymne* suggests the existence of a subanal funnel, further implying that this region of the test is below the sediment surface for at least some of the time.

The plastron of *Calymne* is covered by large, asymmetric tubercles bearing S2 spines (Fig. 2B). In spatangoids, plastronal spines are generally spatulate, and tend to be wider in mud- than in sand-dwellers (Smith, 1980a). However, they are rarely widened to such an extent as in *Calymne* (Fig. 6D). Similar spatulate spines are also present in the deep-sea spatangoids *Aeropsis rostrata* and *Aceste bellidifera*, although they are slightly different in shape. Plastron spines are involved in locomotion (Nichols, 1959a; Stephenson, 1963; Smith, 1980a).

Calymne is unique among holasteroids and spatangoids because the asymmetric enlargement of areoles and the orientation of S2 spine curvatures imply a surprising but unmistakable preferred stroke toward the front of the test (Fig. 5). This unusual orientation is the reverse of that normally seen in spatangoid plastronal regions. Plastronal spines push backward in all species, generally in an oar-like movement, causing forward locomotion (Nichols, 1959a; Stephenson, 1963; Fischer, 1966; Smith, 1980a; Kanazawa, 1992). In *Calymne*, plastronal spines seem to make the test move or tilt backward, at least temporarily.

Calymne's ventro-lateral spines are sparse and represented by types L2, L3, and L4 (Fig. 5). In spatangoids with large, locomotory, plastronal spines, ventro-lateral spines are generally used to move sediment upward and/or backward from beneath the test (Smith, 1980a; Kanazawa, 1992). When burrowing spatangoids are exposed at the surface of the sediment, ventro-lateral spines are also used for rapid burial (Kier & Grant, 1965; Kanazawa, 1992, 1995; Hollertz & Duchêne, 2001).

The tips of L2 and L3 spines are widened and curved forward, an orientation compatible either with a frontward scraping stroke (primary or preferred stroke) or a backward propulsive thrust (secondary stroke). In the latter case, the propulsive thrust would make the test move forward, at least for some of the time. A propulsive function of ventro-lateral spines has been observed in some spatangoids (e.g. *Lovenia elongata*) in which plastronal spines are reduced in number and size and cannot provide an effective thrust. In those spatangoids, both locomotion and excavation are performed by ventro-lateral spines (Kanazawa, 1992).

IS *CALYMNE* EPIFAUNAL OR INFAUNAL?

Recent holasteroids are all deep-sea forms and consequently little is known about their behaviour (but see Southward *et al.*, 1976; Rice *et al.*, 1979; David & Sibuet, 1985; Lauermann & Kaufmann, 1998; David *et al.*, 2003b). Nevertheless, functional and ecological interpretations have been reliably deduced from studies of functional anatomy (Mironov, 1975, 2008). There are, of course, problems with this approach for some groups. These are exemplified by the case of soft-bodied 'regular' echinoids, the echinothurioids, which have fleshy aboral spines. Few could have speculated accurately about the functions of these spines without direct observations (Emson & Young, 1998).

Morphology-based interpretations of the mode of life of atypical irregular echinoids such as *Calymne* are necessarily hypothetical, and require confirmation by vehicle-based direct observation (Southward *et al.*, 1976; David & Sibuet, 1985; Lauermann & Kaufmann, 1998). Fortunately, in irregular sea urchins, many characteristics of the test permit inferences concerning their behaviour and *Calymne* is no exception. When morphological characters are considered, comparisons with analogous (and sometimes even homologous) structures found in spatangoids – the closest relatives of holasteroids (Mintz, 1968; Smith, 1984) – take functional analysis from the realm of speculation to that of testable hypotheses. Correlations between actual behaviour of spatangoids and their functional morphology have been studied in detail and continue to provide reliable results supported by ecological observations (Nichols, 1959a; Kier & Grant, 1965; Chesher, 1968; Smith, 1980a, b; Kanazawa, 1992).

We feel that observations such as the ones provided above concerning the test and appendages permit robust, testable hypotheses regarding the mode of life of echinoids, because so many of their vital functions, such as locomotion, burial, respiration, and excretion are directly related to skeletal characteristics (Smith, 1984). The most significant morphological features of *Calymne* that might inform these hypotheses are: the high arch of the test when viewed in profile, the anterior placement of the mouth, the relatively high placement of the periproct on the posterior face of the test, the occurrence of a marginal fasciole, plastronal spines with an apparent reverse power stroke, a subanal tuft, and posterior spine frills on either side of an aboral, posterior bulge in the test.

The first step in interpreting *Calymne*'s behaviour is to determine its living position relative to the sea floor. The only robust data we have concern one young specimen found within the first 5 cm of the upper sediment layer in station 2462, cruise 23 of the R/V ‘Akademik Mstislav Keldysh’. Unfortunately, this is not sufficient to determine with precision *Calymne*'s living position. The problem is confounded by the fact that juveniles of some echinoids can exploit levels in the sediment different from those of their corresponding adults. In addition, interpretations of the position in life for *Calymne* in particular are made more difficult because seemingly incompatible characters occur together: specialized spines evocative of burrowing forms co-occur with general features unsuited for a permanent infaunal position. From that, it is necessary to consider several hypotheses regarding *Calymne*'s mode of life and ability to burrow.

Calymne is characterized by a high test profile (Fig. 2C–E). Such a high, inflated test camber is found in other extant deep-sea holasteroids such as the pourtalesiid genera *Echinocrepis* and *Cystocrepis*, and in fossils such as *Echinocorys*, all of which have been observed or inferred to be epifaunal, or at most, shallow burrowers (Stephenson, 1963; Mironov, 1975, 2008; Southward *et al.*, 1976; Lauermann & Kaufmann, 1998; David *et al.*, 2003b). Moreover, the epifaunal lifestyle is a common behaviour among holasteroids, although the fossil genus *Infulaster*, with its exceptional morphology, has been interpreted to be infaunal (Gale & Smith, 1982). Among spatangoids, most species are burrowers, with the exception of certain epifaunal deep-sea species (e.g. *Linopneustes murrayi*, *Genicopatagus affinis*) which evolved high test profiles and ambulacra with less well-developed petaloids (Mortensen, 1950; Fischer, 1966; Smith, 1980b; Kanazawa, 1992; David *et al.*, 2003a). These morphological features have been interpreted to be correlated with an evolutionary return from an infaunal habit to life at the surface of the sea floor (Fischer, 1966; Kanazawa, 1992).

A high test profile and a sparse aboral spine canopy seem incompatible with complete burrowing. Moreover, the anterior ambulacrum of mud-burrowers is distinguished by the presence of specialized organs and structures involved in nutrition and burrowing: penicillate tube feet and/or an oral groove with specialized spines (De Ridder, Jangoux & De Vos, 1987). In *Calymne*, the absence of such specialized structures in the anterior ambulacrum is congruent with an epifaunal hypothesis. The presence of a marginal fasciole suggests that *Calymne* is partly buried, at least up to the ambitus just above the fasciole. Concomitantly, the low marginal position of *Calymne's* fasciole does not support a completely infaunal mode of life either. Generally, spatangoid burrowers that lack an aboral fasciole can live buried only in gravels or coarse sands, whereas all mud-burrowers possess an aboral fasciole (Smith, 1980a). Therefore, while the functional significance of marginal fasciole remains poorly understood, the absence of an aboral fasciole in *Calymne* prevents us from suggesting that this echinoid is a deep burrower. The presence of a subanal tuft as well as of spatulate spines on both sides of the fasciole (on the posterior side) reinforces the hypothesis of partial burrowing. Taking into account the upper frills of large spatulate spines at the posterior of the test, the direction of stroke, and the considerably enlarged S1 spines, we suggest a function related to sediment or particle (deep-sea marine snow) transfer over the posterior part of the test or more likely, to a pushing action against the sediment.

INFERRED BEHAVIOUR

Most benthic deep-sea animals cannot, energetically speaking, ‘afford’ a sessile lifestyle. In fact, most of the adaptations to the abyssal benthic lifestyle seem directed towards enhanced mobility in order to exploit opportunistically the occasional rich marine snowfall or patchy distributions of otherwise sparse nutrients. This principle is manifested in several diverse echinoderms: swimming elasipodid holothuroids 'leaping' from place to place (Ohta, 1985); swimming aspidochirote holothuroids undulating above the bottom (Rice *et al.*, 1979); other holothuroids that can walk on enlarged podia (pers. observ.); crawling crinoids (Fujita, Ohta & Oji, 1987); and fast-moving, lightly constructed echinothurioid sea urchins with hooves on their spines (Emson & Young, 1998).

These observations reinforce the likelihood that *Calymne* is epifaunal. However, any such hypothesis of an epifaunal lifestyle must also accommodate the unorthodox position of the fasciole and two groups of spines. First, the occurrence of a marginal fasciole and of a subanal tuft implies that *Calymne* might live partly buried, the flat oral surface shallowly ploughing the sea floor, mouth-first. In this interpretation, the subanal tuft may be used to stabilize the test on the unstable deep-sea mud. Second, the function of the upper-posterior frills of large spines is difficult to envisage in the context of well-known echinoid behaviours. A superficial examination might lead to a first hypothesis involving cleaning of the test or a covering reaction, but this would depart significantly from all direct observations made on other deep-sea holasteroids (Rice *et al.*, 1979; David *et al.*, 2003b). A second hypothesis would suggest that the frills help overturned specimens to right themselves. Although it might seem unusual to evolve a specialized spination for this purpose alone, this hypothesis is supported by the shape of the test. It is very high, and therefore likely to be unstable in nearly any current regime, and lacks robust lateral spines that would otherwise perform this righting function. This hypothesis could also explain the spatulate shape of the spines, which is ideally suited for pushing against sediment.

The forward motion of *Calymne* almost undoubtedly results from the coordinated strokes of L2 and L3 spines located on the oral surface. In these spines, curvature is orientated forward, allowing efficient contact and thrust upon the substrate. During locomotion, plastronal S2 spines can rest perpendicular to the test without producing any forward stroke, but would participate in stabilizing the test. The shallow burial could be accomplished by the combined strokes of plastronal (S2) spines, frontal spines (S3), and ventro-lateral L2 and L3 spines. In this scenario, while ventro-lateral spines excavate that part of the sediment located beneath the test, their action is assisted by a slight rocking movement of the test. This movement, facilitated by the thixotropy of the substrate, would be achieved by the antagonistic and coordinated actions of plastronal and frontal spines. These spines would tilt the test alternatively frontward through action of the frontward stroke of plastronal spines, and then backward by the downward stroke of frontal spines. Rocking movements have already been observed in *Brissopsis lyrifera* and wedge-shaped spatangoids that rock while burrowing in muddy substrates (Kanazawa, 1992; Hollertz & Duchêne, 2001). If we accept that *Calymne* is partially infaunal, we might envisage that it uses the phyllopodia to gather and transfer food from the relatively rich upper marine snow layers to the anteriorly placed mouth. One might even suggest that as *Calymne* does so, it is tilted upward to bring the mouth closer to the upper layers. This rocking behaviour could in fact help to orientate the animal to initiate this 'tilted ploughing'.

In *Calymne*, the combination of atypical morphological characters is a challenge to the functional morphological approach, particularly given the lack of detailed knowledge of deep-sea environments. Nevertheless, such morphological inference for function should not be the domain of palaeontology alone. For extant organisms that inhabit environments that remain relatively unexplored, it is necessary to develop hypotheses and even predictions concerning behaviour in order to develop a context for the unusual morphologies these animals represent. With further data from direct deep-sea observation, the soundness of such analyses can only be improved.

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Phylogeny and origin of Jurassic irregular echinoids (Echinodermata: Echinoidea)

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Abstract – A phylogenetic analysis of Jurassic irregular echinoids is realized to explore the origin and early evolution of this important subset of echinoids. The phylogeny is based on 39 characters and considers data from apical system architecture, the corona including tuberculation and spines, Aristotle's lantern, and general test shape. Results corroborate the monophyly of Irregularia, and clarify the phylogenetic interrelationships existing between the main groups of irregular echinoids. Specializations of the Aristotle's lantern, spines, tubercles and phyllodes constitute the apomorphies for different taxa, as for the whole of Irregularia. The phylogenetic signal yielded by these characters highlights the importance of the environmental context of the origin and diversification of irregular echinoids. The definition of 'irregularity' is re-examined, rejecting exocyclism and characters of the apical system as appropriate synapomorphies, and stressing the importance of other characters, particularly the high density and small size of tubercles and spines. A new clade name, Infraclypeidae [P], and phylocode designations (stem-based diagnoses) are proposed for the clades Irregularia, Eognathostomata, Microstomata, Neognathostomata and Atelostomata. Other groupings formerly used (Pygasteroida, Galeropygidae and Menopygidae) are considered paraphyletic.

Keywords: Irregularia, Echinoidea, phylogeny, systematics, Jurassic.

1. Introduction

1.a. Irregular echinoids

The mass extinction that took place at the end of the Permian deeply affected echinoid diversity. Only two lineages survived the event (Kier, 1965, 1968, 1974, 1977, 1984; Fell, 1966; Smith, 1984; Smith & Hollingworth, 1990). Once past the 'Palaeozoic' crisis, echinoid diversity recovered through significant evolutionary radiation and rapid morphological diversification (Kier, 1974, 1982; Smith, 1978*b*, 1984). The echinoids therefore played a much more prominent role in Mesozoic echinoderm diversity than they did previously (Erwin, 1993). Diversity increased from the Early Jurassic (Sprinkle, 1983) with the appearance of a large and important group of echinoids: the irregular sea urchins, recognized as the clade Irregularia Latreille, 1825 (Kier, 1977, 1982; Smith, 1984, 1988). This clade includes forms as diverse as the present-day lamp urchins, heart urchins and sand dollars, and constitutes nearly 60 % of extant and extinct species of echinoids (calculated after Kier, 1974). The appearance of irregular sea urchins thus contributes greatly to the general recovery and expansion of echinoid diversity that occurs within the global context of the 'Mesozoic Marine Revolution' (MacLeod, 2003; Vermeij, 1977, 1995).

The establishment of an anterior–posterior axis of secondary bilateral symmetry in the otherwise pentaradial tests of the Irregularia distinguishes them from the other globose sea urchins (sometimes referred to as 'regular' urchins), and places the radiation of irregular sea urchins among the most significant events in the evolution of echinoids. The establishment of secondary bilateral symmetry is associated with the migration of the periproct (the area which surrounds the anus) from the summit of the test toward the posterior margin. This migration accompanies other morphological innovations such as the anteriorly placed mouth, the single-direction locomotory systems with spines specialized to produce an efficient power-stroke, the sophisticated particle-picking mechanism that provides continuous access to fresh and abundant supplies of food, and the miniaturization of almost all external appendages such as spines and podia. All these morphological innovations are strongly linked with the colonization and the adaptation to new ecological niches, determined by the nature of the sea bottom where irregular sea urchins live. Irregular echinoids are exclusively microphagous species that can only ingest small nutrient-bearing particles (De Ridder & Lawrence, 1982). This feeding behaviour implies a specialization of the body form and appendages for feeding and moving upon or inside soft sediments (Kier, 1974; Smith, 1981; Kanazawa, 1992; Telford & Mooi, 1996).

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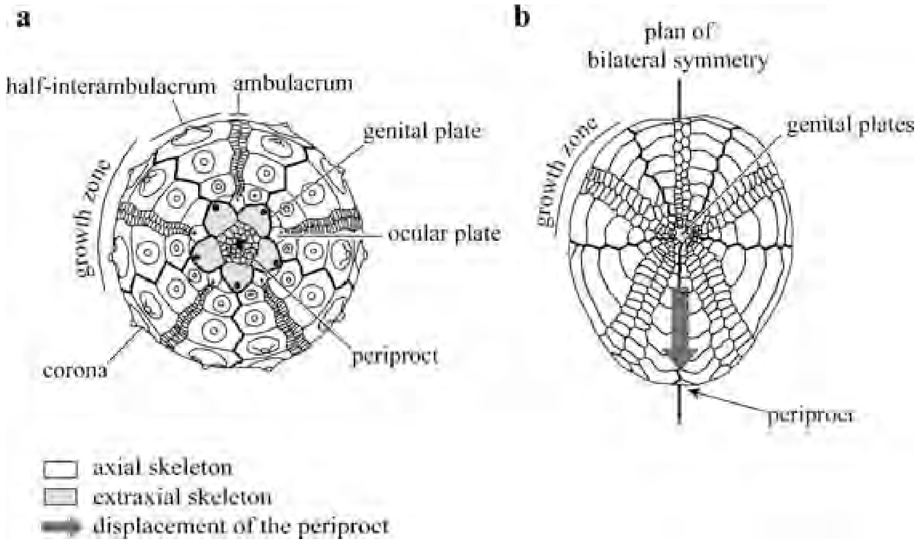

Figure 1. According to the Extraxial–Axial Theory, the echinoid test is constructed almost entirely from axial elements organized into five growth zones. In regular echinoids, the periproct is enclosed within the apical system, a composite structure that gathers ocular (axial elements) and genital (extraxial elements) plates that surround the periproct (extraxial elements) (a, from David & Mooi, 1999). Conversely, in irregular echinoids, the migration of the periproct leads to a breaking of the extraxial region into two distinct units: the genital plates that stay in an apical position, and the periproct that move towards the margin of the test (b).

David & Mooi (1996) have proposed a new system for interpretation of the body wall components among echinoderms (David & Mooi, 1998, 1999; David, Mooi & Telford, 1995; Mooi & David, 1997, 1998). This new system (the Extraxial-Axial Theory, or EAT) bases the recognition of homologies on the embryology and the ontogeny of structures (David & Mooi, 1996, 1998; Mooi, David & Marchand, 1994). It identifies two major body wall categories in the Echinodermata: axial and extraxial. The identification of these two distinct body wall regions permitted the establishment of new homologies pertaining to all echinoderms. In some cases, it also led inexorably to drastic challenges of previous phylogenetic hypotheses (David & Mooi, 2000; Mooi & David, 1998).

Echinoids are unique among the echinoderms because the entire coronal part of the test consists of axial body wall (Mooi, David & Marchand, 1994). The extraxial region is restricted and indeed constricted to the scales present on the periproctal membrane and to the genital plates (Fig. 1). The axial region of the corona is organized into five growth zones that form and continue to grow in accordance with the 'Ocular Plate Rule' (OPR). Following this mechanism, each growth zone is closely associated with an ocular plate and consists of an ambulacrum surrounded by two half-interambulacra, one on each side of the ambulacrum. New ambulacral and interambulacral plates are formed next to the ocular plate. Plates are shifted away from the apical system and the ocular plate as new plates are added at the edge of the oculars between the oculars and the rest of the plate column.

The apical system is a composite structure that associates ocular (axial element) and genital (extraxial element) plates that surround the periproct (extraxial) in 'regular' echinoids (Fig. 1a). In irregular echinoids, the migration of the periproct leads to a 'breaking' of the apical system as the periproct moves out of the circle formed by the genital and ocular plates. This phenomenon is called exocyclism. Exocyclism entails a disruption of the echinoid's small remaining extraxial region into two distinct units: (1) genital plates that remain in the apical position; (2) the periproct and its associated scales that move toward the margin (and in some cases all the way to the oral surface) of the test (Fig. 1b). Therefore, the diversification of irregular echinoids is associated with exocyclism that corresponds to a disruption of the extraxial part of the body into two separate areas.

1.b. Previous works and systematics

According to Melville & Durham (1966), irregular echinoids constitute a morphological (and not taxonomic) group or grade that can be distinguished from 'regular' forms by the position of the periproct outside the apical system (exocyclism), by the predominance of bilateral symmetry in test outlines, and by the absence of the Aristotle's lantern in many of them. Variation in expression of test outline and the Aristotle's lantern implies that these characters cannot constitute absolute criteria for establishment of a natural group of irregular echinoids. In addition, Durham & Wagner (1966) use the terms 'irregular' and 'exocyclic' as synonyms. These terms refer to tests with the periproct located outside the apical system and supposedly contrast with 'regular' and 'endocyclic' which refer to tests with the periproct located within the apical system. Finally, irregular, or exocyclic, groupings are recognized to be polyphyletic, the subclass rank of the group is abandoned, and 'irregular echinoid' is retained only as an informal division (Melville & Durham, 1966).

At the same time, Jesionek-Szymanska (1959) and Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) showed that the boundary between regularity and irregularity is not so definite. The morphological changes from the regular to the irregular condition occurred in stages, so that many Jurassic irregular echinoids display intermediate morphologies between regularity and fully manifested irregularity (Jesionek-Szymanska, 1963; Mintz, 1968). Therefore, according to these authors, some Jurassic irregular echinoids are still endocyclic (the periproct is located within the apical system), and exocyclism and irregularity are not good synonyms. If we consider restriction of the concept of irregularity (exocyclism in which the periproct moves significantly away from the centre of the apical system so that it eventually loses contact with it) to the clade that we now consider the Irregularia, we are still left with evidence suggesting that some form of exocyclism (that is, at least some movement of the periproct away from the center of the apical system in the direction of interambulacrum 5) occurred at least seven times in independent lineages of 'regular' echinoids (Saucède, Mooi & David, 2003). Consequently, exocyclism is not a sufficient criterion to define irregularity. Repeated movements of the periproct toward and into interambulacrum 5 could be seen as supporting the plural origin of irregular echinoids, as suggested by Melville & Durham (1966).

As a morphological character of irregular echinoids, exocyclism was given great taxonomic weight in the 19th and the beginning of the 20th century, but the question of the origin of the group, whether unique or plural, was not necessarily tackled. Some authors considered exocyclism to be of major taxonomic importance and placed irregular echinoids in a unique category (Desor, 1855–1858; Wright, 1855–1860; Zittel, 1876–1880; Gregory, 1900). For others, the presence or absence of the Aristotle's lantern was of paramount importance, and echinoids were divided accordingly into those that lack a lantern (the atelostomes) and those that possess one (the gnathostomes). Even in cases when irregular echinoids were recognized, they were split within two distinct groups according to the presence or absence of the Aristotle's lantern (Pomel, 1869, 1883; Lambert & Thiéry, 1909–1925). Finally, certain authors (e.g. Duncan, 1889) did not make a distinction between regular and irregular forms, and species that we now recognize as irregular taxa were scattered among widely disparate groups.

The position favouring the plural origin of irregular echinoids prevailed for most authors of the 20th century. Hawkins (1922) was the first to tackle the question of the origin of irregular echinoids. He derived them from 'regular' echinoids through two independent lineages and two possible ancestors: (1) the Microstomata (*sensu* Smith, 1984) through the genus *Pseudopygaster* Hawkins, 1922 (= *Loriolella* Fucini, 1904) on the one hand, and (2) the Eognathostomata (*sensu* Smith, 1981) through the genus *Plesiechinus* Pomel, 1883 on the other hand.

Mortensen (1948) proposed independent origins for the two families composing the Eognathostomata: the Pygasteridae Lambert, 1899 and the Holectypidae Lambert, 1899. His assumption relied on the absence of tubercle crenulation in certain species of Pygasteridae (as in the 'regular' Pedinidae Pomel, 1883), contrasting this condition with the crenulate tubercles of Holectypidae (as in the 'regular' Diadematidae Gray, 1855). However, he maintained both families, Holectypidae and Pygasteridae, in the same order, and all irregular echinoids in a unique subclass. Later, Jesionek-Szymanska (1970) and Rose & Olver (1984) showed that Pygasteridae have primitive crenulate tubercles, and that crenulation tends to disappear in derived species of *Pygaster* Agassiz, 1836.

In spite of this, the hypothesis of irregular polyphyly has especially been supported by studies of the Aristotle's lantern. These studies followed initial work by Jackson (1912), and the first observations on the Aristotle's lantern and associated structures in irregular echinoids were published on the Eognathostomata (Hawkins, 1934). Durham & Melville (1957) used lantern and tooth morphology to derive irregular echinoids from aulodont and stirodont regular ancestors through three distinct lineages: (1) the Pygasteroida Durham & Melville, 1957, (2) the Gnathostomata Zittel, 1879 (holectypoids and clypeasteroids) and (3) the Atelostomata Zittel, 1879. They concluded that the group Irregularia is polyphyletic and should be abandoned, a position which prevailed in the widely followed *Treatise on Invertebrate Palaeontology* (Durham, 1966). The independence of pygasteroids and holectypoids was also supported by Melville's work (1961) on tooth shape. He compared the apparent triangular shape of teeth in the genus *Pygaster* (pygasteroid) to the keeled teeth of the genus *Holectypus* Desor, 1842 (holectypoid). Consequently, he derived the pygasteroids from regular aulodont echinoids (the Pedinidae), and all other irregular echinoids from stirodonts. Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) derived pygasteroids from among the Pedinidae, and proposed a stirodont ancestor for the Microstomata in which the lantern is absent (Mintz, 1968). Hess (1971) also classified the keeled teeth of *Holectypus* as of stirodont affinity, but Philip (1965) suggested an aulodont origin for the lantern of holectypoids, which he derived from the Diadematidae. However, Philip (1965) did not give an opinion on the origin of other irregular echinoids. Märkel (1978) presented independent origins for the three irregular orders that possess a lantern, namely: the Cassiduloida Claus, 1880, the Holectypoida Duncan, 1889, and the Clypeasteroida Agassiz, 1872. Jensen (1981), founding her position on the study of teeth microstructure and ambulacral composition, grouped the orders Pygasteroida and Pedinoida Mortensen, 1939 (aulodont regular echinoids) into the superorder Pedinaceae. She made this the sister group of all other irregular echinoids, which then constitute a monophyletic assemblage.

The hypothesis of the polyphyletic origin of irregular echinoids was first challenged by Kier (1974), who showed that the morphology of the lantern and teeth is similar in the genera *Pygaster* and *Holectypus*, but he did not draw any conclusions about their origin. Smith (1981) showed that all irregular echinoids possess the same type of lantern with diamond-shaped teeth, a type already present in a 'regular' species (*Eodiadema* aff. *minutum* (Buckman, 1845) *in* Strickland & Buckman, 1845) which was in turn related to aulodont echinoids. He also considered the genera *Pygaster* and *Holectypus* to be closely related and to constitute the sister group of all other Irregularia. Smith's view has been followed by successive authors (Rose, 1982; Rose & Olver, 1988; Anzalone, Teruzzi & Smith, 1999; Smith & Anzalone, 2000; Solovjev & Markov, 2004).

Basically, all previous works on the origin of irregular echinoids rely on the study of the four following characters: (1) the position of the periproct with respect to the apical system; (2) the Aristotle's lantern; (3) tubercle crenulation; and (4) the organization of ambulacral plates. Depending on each author and their views of a character's relative importance, these characters have fomented arguments both for and against the unique origin (that is, the monophyly) of irregular echinoids. However, Kier's (1974) and Smith's (1981, 1982) findings that the irregulars are monophyletic based on lantern morphology are seldom questioned.

Even if the monophyly of Irregularia is no longer challenged, a broader definition of irregularity taking into account all of the above-mentioned features is needed. In addition, phylogenetic relationships among irregular taxa as well as the relationship with regular echinoids remain imprecise. Clarification of phylogenetic relationships is an essential stage of understanding the processes by which irregularity is achieved. Through this understanding, a much better picture will develop of the most important radiation of post-'Palaeozoic' echinoids.

2. Materials and methods

2.a. Taxon selection

Fossil taxa are of extreme interest when trying to resolve phylogenies because they bear morphological information of phylogenetic significance that is often absent in extant taxa (Benton, Wills & Hitchin, 2000; Wagner, 2000; Smith, 2001). Moreover, extant taxa are sometimes so different morphologically, when evolution has been rapid enough to accumulate large numbers of apomorphies along a given lineage, that comparisons only among extant forms can be misleading. Uncovering phylogenies necessitates the study of intermediate morphologies, and these are often inherent in the fossil record (Rieppel, 1994).

In the Lower Jurassic, the very earliest irregular echinoids, such as '*Plesiechinus*' *hawkinsi* Jesionek-Szymanska, 1970 (Sinemurian of Nevada) and *Loriolella ludovicii* Meneghini, 1867 (Pliensbachian of Italy), still display the pattern observed in regular echinoids, namely a periproct enclosed by the genital and ocular plates (Jesionek-Szymanska, 1970; Smith & Anzalone, 2000). However, the periproct becomes displaced from the centre of the apical system (becomes more eccentric) during growth and tends to 'stretch' the genital plate in interambulacrum 5 and adjacent ambulacral oculars of the apical system in which the periproct is enclosed. By definition, these genital and ocular plates become posterior elements of the apical system. In later forms, such 'stretching' culminates in disruption of the ring of apical plates and actual migration of the periproct away from the apical system. This trend appears to be progressive over a large span of time ranging from Early Jurassic to Late Jurassic times, and exocyclism therefore appears to have been achieved gradually in irregular echinoids (Jesionek-Szymanska, 1963; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966). By contrast, in Recent irregular echinoids, periproct migration begins during early ontogeny before the closure of the apical system, and posterior plates show little or no evidence of elongation (Gordon, 1926). Therefore, apical structures of the first irregulars are very informative; they display the intermediate patterns lacking even in the early ontogeny of extant forms, and are therefore essential to the comprehension of the processes of periproct migration, and to determine if these processes are homologous in all irregulars.

Homoplasy in morphological characters is a common feature of invertebrate phylogenies (Moore & Willmer, 1997; Wills, 1998). They sometimes constitute evidence for the adaptation of species to similar habits and habitats (Stewart, 1993; Suter, 1994). At other times, they are evidence that hypotheses of homology among the characters in question require reassessment. Phylogenies of echinoids are no exception, and parallel evolution in apical structure has been stressed by several authors (Jesionek-Szymanska, 1963; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Kier, 1974; Saucède, Mooi & David, 2003; Solovjev & Markov, 2004), and more generally for numerous traits within the Cassiduloida (Kier, 1962, 1966; Suter, 1994; Smith, 2001; Wilkinson, Suter & Shires, 1996). The probability of homoplasy increases if too many fossil taxa are selected over too long

Table 1. List of species used for character coding

Taxon	Stratigraphic range	Collection
Caenocidaris cucumifera (Agassiz, 1840)	Upper Toarcian–Upper Bajocian	Gras, Saucède
Acrosalenia hemicidaroides Wright, 1851	Bajocian–Lower Callovian	Saucède
Farquharsonia crenulata Kier, 1972	Bathonian	
Diademopsis bowerbankii Wright, 1851	Hettangian–Sinemurian	
Eodiadema minutum (Buckman, 1845) *in* Strickland & Buckman, 1845	Upper Sinemurian–Lower Pliensbachian	
Atlasaster jeanneti Lambert, 1937	Sinemurian	Collignon
'*Plesiechinus*' *hawkinsi* Jesionek-Szymanska, 1970	Upper Sinemurian	
Plesiechinus ornatus (Buckman, 1845) *in* Strickland & Buckman, 1845	Aalenian–Bajocian	Clavel, Lambert, UB
Pygaster gresslyi Desor, 1842	Middle Oxfordian–Upper Tithonian	Clavel, Cotteau, Courville, UB, Lambert
Pileus hemisphaericus Desor, 1856	Oxfordian	Lambert, Votat
Holectypus depressus (Leske, 1778)	Bathonian–Callovian	CAS, Cassel, UB, Votat
Loriolella ludovicii (Meneghini, 1867)	Lower Domerian	
Eogaleropygus microstoma (Lambert, 1933)	Middle Toarcian	
Galeropygus agariciformis (Wright, 1851)	Upper Toarcian–Bathonian	UB, UCMP
Hyboclypus caudatus Wright, 1851	Bajocian–Bathonian	Courville, Dailly, Dudicourt, UB
Centropygus petitclerci Lambert, 1901	Upper Aalenian	Clavel
Clypeus plotii Leske, 1778	Upper Bajocian–Lower Callovian	CAS, Courville, Dudicourt, Mooi, UCMP
Pygurus depressus Agassiz *in* Agassiz & Desor, 1847	Bathonian–Upper Callovian	Collignon
Nucleolites clunicularis (Phillips, 1829)	Bathonian–Lower Callovian	Courville; UCMP
Pseudosorella orbignyana Cotteau, 1855	Middle Oxfordian–Lower Tithonian	Lambert
Menopygus nodoti (Cotteau, 1859)	Bathonian	Clavel, Collignon, Cotteau, Dudicourt
Pyrinodia guerangeri (Cotteau, 1862)	Bajocian	
Infraclypeus thalebensis Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891	Tithonian	Courville, Enay, Clavel
Desorella elata (Desor, 1847) *in* Agassiz & Desor, 1847	Upper Oxfordian	Lambert
Pachyclypus semiglobus (Münster, 1829) *in* Goldfuss, 1826–1844	Lower Kimmeridgian	Lory
Orbigniana ebrayi (Cotteau, 1874)	Upper Bajocian	Clavel, Lambert
Pygorhytis ringens (Agassiz, 1839)	Upper Bajocian–Middle Callovian	UCMP, UP
Cyclolampas kiliani (Lambert, 1909)	Upper Bajocian	Fournier
Pygomalus ovalis (Leske, 1778)	Upper Bajocian–Middle Bathonian	Thierry
Collyrites elliptica (Lamarck, 1791) *in* Bruguière, 1816	Upper Bathonian–Upper Callovian	Gras, UB
Disaster moeschi Desor, 1858	Callovian	
Metaporinus sarthacensis Cotteau, 1860	Upper Bathonian–Middle Callovian	Votat
Tithonia praeconvexa Jesionek-Szymanska, 1963	Upper Callovian	Clavel, UCMP

Location of consulted collections: Caillet – Claude Bernard University, Lyon; Collignon – Bourgogne University, Dijon; Cotteau – Claude Bernard University, Lyon; Courville – University of Rennes; Dailly – Claude Bernard University, Lyon; Dudicourt – University of Rennes; Enay – Claude Bernard University, Lyon; Fournier – Joseph Fourier University, Grenoble; Gras – Museum of Grenoble; Lambert – Museum National d'Histoire Naturelle (MNHN), Paris; Lory – Museum of Grenoble; Saucède – Joseph Fourier University, Grenoble; Thierry – Bourgogne University, Dijon; Votat – University of Rennes; CAS – California Academy of Sciences, San Francisco; UB – Bourgogne University, Dijon; UCMP – University of California Museum of Paleontology, Berkeley; UP – University of Poitiers.

an interval of time (Sanderson & Donoghue, 1989; Suter, 1994; Smith, 2001) or if the selected terminal taxa are too distant from the origination time of the group. These problems foster the phenomena of long branch attraction and character exhaustion (Wagner, 1995, 2000). The alternative is a careful selection of taxa relevant to the question and from key time intervals (Stewart, 1993; Smith, 2001).

Taxa used in the present study were chosen exclusively from the Jurassic. In fact, they originate as close as possible to the lowermost Jurassic, the supposed earliest occurrence of irregular echinoids. Therefore, representatives of the orders Spatangoida Claus, 1876, Holasteroida Durham & Melville, 1957 (*sensu* Smith, 1984), Clypeasteroida, Oligopygoida Kier, 1967 and Neolampadoida Philip, 1963 were not considered in the analysis, as they originated in the Early Cretaceous and the Palaeogene (Kier, 1962, 1974; Smith, 1984, 2004; Eble, 1998, 2000; Mooi, 1990; Jeffery, 2001; Villier *et al.* 2004). In a recent study (Barras, in press), certain Jurassic irregular echinoids are included within the orders Spatangoida and Holasteroida. Pending further investigations, we will follow herein the definition of these orders as formulated by Smith (1984).

Taking into account the taxonomic level of the analysis, we selected 33 species representative of 32 genera covering the morphological range expressed during the Jurassic part of the radiation (Table 1). The selection was performed according to availability of material, quality of preservation (with the intention of minimizing missing data), and stability of taxonomic nomenclature. Poorly known genera or those judged to be so similar as to be almost synonymous with other genera were not included.

To resolve the origin of irregular echinoids and to test their monophyly, four species have been selected among 'regular' echinoids to represent the possible stem groups of irregular echinoids as suggested by previous authors. *Diademopsis bowerbankii* Wright,

Table 2. Data matrix

Characters	1	/6	/11	/16	/21	/26	/31	/36
Caenocidaris cucumifera	00000	00000	00000	00000	00020	01000	00010	0000
Acrosalenia hemicidaroides	00010	00100	01000	00210	00000	00000	00010	2000
Farquharsonia crenulata	00010	00000	01000	00200	00000	00000	000?0	1000
Diademopsis bowerbankii	??0?0	00?00	0?000	00100	00000	00010	10000	1000
Eodiadema minutum	??0?0	00?00	00000	00100	00000	00000	00000	3100
Atlasaster jeanneti	00010	00000	01000	00110	00000	00010	100?0	??00
'Plesiechinus' hawkinsi	11010	00?00	01010	00101	00000	00120	001?0	3101
Plesiechinus ornatus	11021	00011	01010	10300	00000	00120	01110	3101
Pygaster gresslyi	11021	00011	03010	10301	00000	00120	01110	3102
Pileus hemisphaericus	10021	00011	13010	10301	00000	00220	111?0	3100
Holectypus depressus	10021	00011	13012	00301	00000	00120	01100	3101
Loriolella ludovicii	?10??	00??0	01010	11000	10011	01100	00001	??01
Eogaleropygus microstoma	?101?	00??0	01000	10011	1002?	00221	??1?1	3111
Galeropygus agariciformis	01011	00110	01000	21011	1011?	10221	02101	3112
Hyboclypus caudatus	01011	00110	01000	21011	10022	10221	02101	3121
Centropygus petitclerci	11111	00111	02000	21012	1012?	10221	02101	3101
Clypeus plotii	11111	00001	03000	21012	1012?	10221	02101	3102
Pygurus depressus	10121	00001	13002	11012	10122	10221	02101	3102
Nucleolites clunicularis	11111	02011	13000	21022	1012?	10221	02101	3121
Pseudosorella orbignyana	11121	00001	13000	21022	1012?	00221	02101	3111
Menopygus nodoti	01011	00110	01000	20000	00012	00221	021?1	??01
Pyrinodia guerangeri	000?1	00111	13000	0?000	000??	00221	0?1?1	??21
Infraclypeus thalebensis	000?1	01111	12002	11001	00121	00221	021?1	??01
Desorella elata	000?1	01111	12001	11000	00111	00221	0?1?1	??21
Pachyclypus semiglobus	000?1	00011	13001	0?00?	00???	00221	021?1	??21
Orbignyana ebrayi	01011	10110	02100	21010	1002?	10221	02101	??21
Pygorhytis ringens	01111	00100	02101	11011	10021	10221	02101	??21
Cyclolampas kiliani	01111	20100	02101	01010	1002?	11221	02101	??22
Pygomalus ovalis	11111	20010	02100	10020	10022	10221	02101	??20
Collyrites elliptica	11111	21011	12101	01021	11022	10221	02101	??21
Disaster moeschi	11111	00000	03101	00000	1102?	11221	02101	??21
Metaporinus sarthacensis	10111	00001	12101	00021	1102?	10221	02101	??20
Tithonia praeconvexa	01111	00000	02101	00020	11021	10221	02101	??20

Character states are described in the text.

1851 was chosen as the earliest representative of the Diadematacea Duncan, 1889. The genus appeared as early as the end of the Triassic (Bather, 1911; Kier, 1977; Smith, 1988) and is considered a representative of the stem group from which all the Irregularia and Stirodonta Jackson, 1912 originated (Smith, 1981). The Aristotle's lantern of *D. bowerbankii* was precisely described by Hawkins (1934), and is among the oldest known of the aulodont type (Kier, 1974; Jensen, 1981). The species *Acrosalenia hemicidaroides* Wright, 1851 was selected as the representative of the Stirodonta, which has been considered a possible ancestor for certain groups of, or for all, the irregular echinoids (Durham & Melville, 1957; Melville, 1961; Durham, 1966; Jesionek-Szymanska, 1963; Mintz, 1968). The genus *Acrosalenia* Agassiz, 1840 appeared as early as the Early Jurassic (Jensen, 1981), and is thought to contain the first stirodonts. The family Acrosaleniidae Gregory, 1900 is characterized by an eccentric periproct and the presence of one or several supplementary plates in the apical system (Fell, 1966). *Farquharsonia crenulata* Kier, 1972 belongs to the family Diadematidae, which has been considered the possible stem group of holectypoids (Mortensen, 1948; Philip, 1965), pygasteroids (Hawkins, 1912, 1922), galeropygoids (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) or of all the Irregularia (Jesionek-Szymanska, 1963; Smith, 1981). *F. crenulata* is characterized by an eccentric periproct within the apical system. Finally, *E. minutum* has been placed as the sister group of the Irregularia (Smith, 1981, 1984). *Caenocidaris cucumifera* (Agassiz, 1840), a representative of Cidaroidea Claus, 1880, was chosen as outgroup to root the trees. The Cidaroidea diverged from other post-'Palaeozoic' echinoids as early as the end of the Triassic (Kier, 1974, 1977; Smith, 1981, 1990).

2.b. Character coding

The high taxonomic level of the analysis required a selection only of characters relevant to the question under consideration (as recommended by Stewart, 1993), that is, early evolution of the major irregular taxa. Therefore, selected characters deal with general structures of the test common to all taxa in the analysis, and are not subject to variation at the species level.

A set of 39 characters was coded (Table 2) and organized into the following four main categories, which are themselves broken down into subcategories that deal with specific features within some of these categories. (1) The first 16 characters concern the apical system, the periproct and the relationships between both structures. Character coding relies partly on the interpretation of apical disruptions and periproct migration according to the Extraxial-Axial Theory (e.g. character 3), a model that is general enough to allow comparison between morphologically distant taxa (such as regular and irregular echinoids). (2) The next 18 characters (17–34) deal with structures of the corona, including the ambulacra, interambulacra, peristome, tuberculation and spines. (3) Three characters (35–37) concern the Aristotle's lantern. (4) The last two characters (38, 39) deal with the overall shape of the test.

2.c. Tree computing methods

We used the software PAUP 4.0b10 (Swofford, 2000) to perform a parsimony analysis. Because of the large size of the data matrix (Table 2), trees were computed using the heuristic search algorithm and the ACCTRAN optimization criterion. Character states were unordered. One hundred replicates with random taxon addition sequences were performed to make sure that the taxon addition order used by software PAUP 4.0b10 does not hinder the discovery of other trees of shortest length. Parsimony indices were also obtained with PAUP 4.0b10, and indices of stratigraphic congruence were computed with the software GHOSTS 2.4 (Wills, 1999*b*). Three indices of stratigraphic congruence were calculated: Stratigraphic Consistency Index (SCI: Huelsenbeck, 1994), Relative Completeness Index (RCI: Benton, 1994), and Gap Excess Ratio (GER: Wills, 1999*a*) tests for index values were computed by randomization according to the procedure described in the software GHOSTS 2.4 (Wills, 1999*b*).

2.d. Character analysis

2.d.1. Genital and ocular plates (characters 1–5)

Plate columns and, in some cases, even individual plates making up the test of a given sea urchin can be homologized to those of any other urchin. A numbering system based on the cycle of radii and interradii around the peristome was devised by Lovén (1874) as summarized in David, Mooi & Telford (1995) to refer precisely to specific plates and plate columns. We use this system to identify specific plates in the apical system and the coronal skeleton. Also, to save space, we often omit the term 'plate' in reference to a specific element. For example, 'genital plate 2' can be abbreviated to 'genital 2'.

Genital 2 (which contains the madreporite) is differentiated from other genital plates by the presence of tiny, often numerous, pores (the hydropores) (Fig. 2a) that lead to the stone canal and thereby to the ring canal of the water vascular system. In 'regular' echinoids, genital 2 is roughly the same size as other genital plates (Fig. 2b). In irregular echinoids, genital 2 tends to increase in size in correlation with the degree to which hydropores are developed (Fig. 2c) (Kier, 1974). Finally, in some irregular echinoids, genital 2 expands so much that it completely separates oculars I and II and genital 1 on one side from oculars III–V and genitals 3 and 4 on the other (ethmolytic apical systems) (Durham & Wagner, 1966) (Fig. 2d).

In some forms, periproct migration is accompanied by a stretching of posterior apical plates, namely genital 5 and ocular plates I and V (Fig. 2e). Posterior oculars are stretched considerably to maintain contact between the periproct and the apical system, but they regain something close to their original shape in taxa whose periproct is completely dissociated from the apical system (Fig. 2a). Genital 5 is the most distorted plate as the periproct moves away from the apical system. In the first irregulars, this extraxial plate is crushed between the posterior rim of the periproct and the axial plates of interambulacrum 5 (Fig. 2e). Subsequently, the plate is progressively incorporated into the periproctal area, and it finally atrophies and almost disappears in more derived forms (Jesionek-Szymanska, 1959, 1963). Gordon (1926) showed that in some extant irregulars, genital 5 is present but extremely reduced in size among the scales of the periproctal membrane.

According to previous authors, the apical system of pygasteroids should be distinguished from that of other irregular echinoids by non-elongated posterior oculars and by the absence of genital 5 incorporated to the posterior rim of the periproct (Hawkins, 1912; Jesionek-Szymanska, 1963; Smith, 1981, 1984). However, this is contradicted by personal observations of different species (*Plesiechinus ornatus* (Buckman, 1845) *in* Strickland & Buckman, 1845; *Pygaster trigeri* Cotteau, 1857 *in* Cotteau & Triger, 1855–1869; *Pygaster laganoides* Agassiz, 1839; *Pygaster joleaudi* Besairie & Lambert *in* Lambert, 1933*a*; *Pygaster umbrella* Agassiz, 1839 and *Pygaster gresslyi* Desor, 1842) showing that posterior oculars are really elongated in these species (Fig. 2f), and that genital 5 can be present on the posterior rim of the periproct, as observed in a juvenile specimen of *P. trigeri* (Bathonian of Sarthes, France; collection of Votat). This supports Gordon's (1926) hypothesis that genital 5 is incorporated into the periproctal area in all irregular echinoids. Perforated by a gonopore in regular echinoids, genital plate 5 loses the gonopore in the first irregulars (but it is still present in '*P.*' *hawkinsi*) when the plate begins to be distorted. A fifth gonopore reappears several times in the evolutionary history of irregular echinoids: in the Cretaceous holectypoids and in at least three separate clades in the Cenozoic clypeasteroids.

In endocyclic echinoids, whether 'regular' or irregular, posterior ocular plates are separated by the periproct and genital plate 5 (Fig. 2b). In exocyclic echinoids, periproct migration out of the apical system leaves a 'free space' within the apical ring, which is filled either by additional plates or by the rearrangement of standard apical plates according to various patterns that depend on the taxa considered. Posterior oculars are separated by supplementary plates in stem irregulars (Fig. 2g), but are brought closer and finally contact each other in more derived taxa (Fig. 2h). However, in ethmolytic apical structures, posterior oculars do not come into contact because genital plate 2 is extended posteriorly between them (Fig. 2d). The extension of genital plate 2 is independent of periproct migration. Therefore, the separation of posterior oculars was coded in different ways depending on whether they are separated by supplementary plates or by genital plate 2.

1. Development of the genital plate 2: 0, all genital plates of nearly the same size; 1, genital 2 enlarged.
2. Elongation of posterior ocular plates: 0, posterior ocular plates short; 1, posterior ocular plates elongated (much longer than wide).

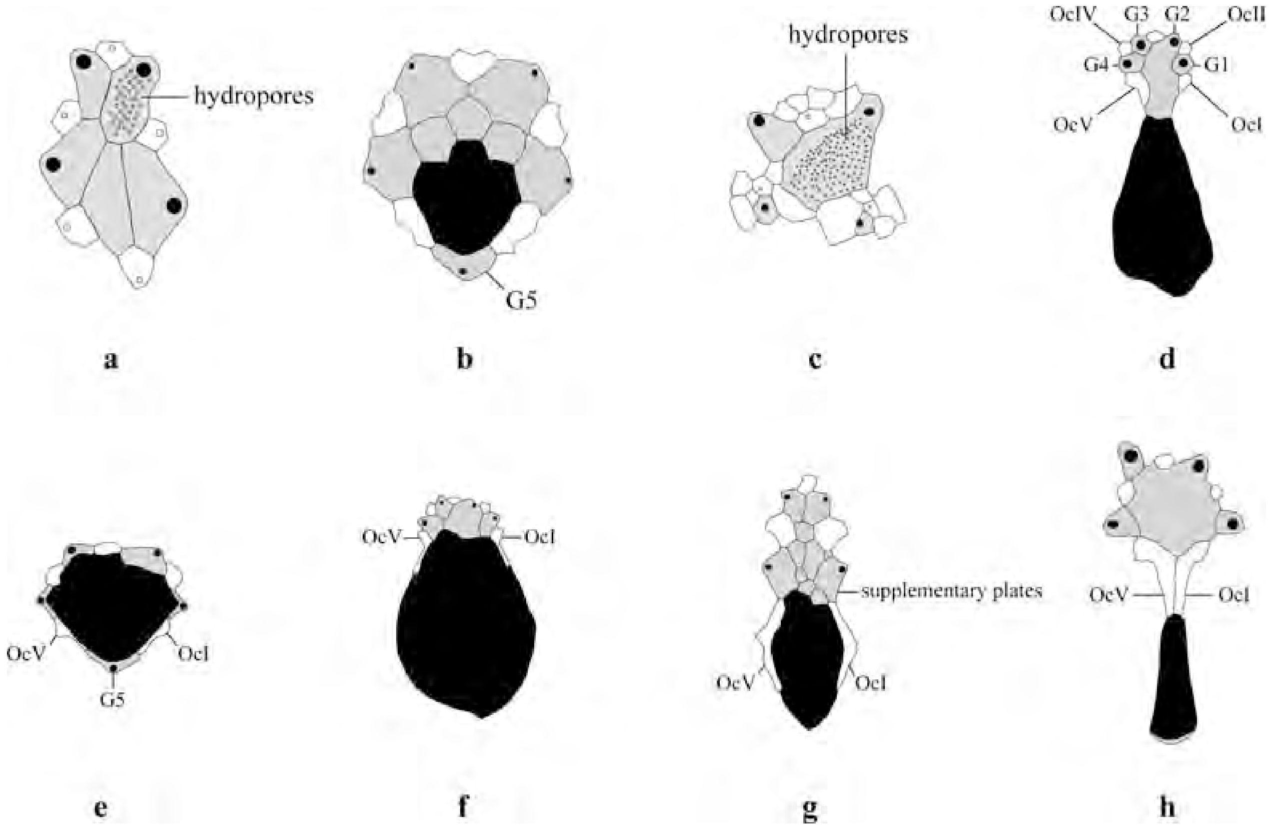

Figure 2. Characters involving genital and ocular plates. (a) *Pachyclypus semiglobus*: hydropores are not widespread and genital 2 is approximately of the same size as other genital plates; posterior oculars do not contact the periproct and are not elongated. (b) *Acrosalenia hemicidaroides*: all genitals have the same size, genital 5 excepted. (c) *Metaporinus sarthacensis*: hydropores are widespread and genital 2 is the largest genital plate. (d) *Pseudosorella orbignyana*: in ethmolythic apical systems, apical plates are separated by the significant extension of genital 2. (e) '*P.' hawkinsi*: posterior oculars and genital 5 are elongated, and genital 5 is 'crushed' between the axial plates of the corona and the periproct. (f) *Pygaster gresslyi*: posterior ocular plates are elongated. (g) *Hyboclypus caudatus*: posterior oculars are separated from each other by the periproct and supplementary plates. (h) *Clypeus plotii*: posterior ocular plates are in contact with each other.

3. Contact between posterior ocular plates: 0, ocular plates completely separated by the periproct or by supplementary plates; 1, ocular plates in contact (or separated by genital plate 2 in ethmolytic apical structures).
4. Development of genital plate 5: 0, genital plate 5 well developed and not deformed; 1, genital plate 5 crescent-shaped, lying at the lower side of the periproct; 2, genital plate 5 lacking or reduced.
5. Perforation of genital plate 5: 0, genital plate 5 bearing a gonopore; 1, genital plate 5 not bearing a gonopore.

2.d.2. *Supplementary plates (characters 6–9)*

In all Jurassic irregular taxa, the breakout and migration of the periproct is associated with formation of supplementary (or complementary) plates inside the apical system. Supplementary plates first appear in the fossil record in the genus *Galeropygus* Cotteau, 1856 (the earliest, known species of *Galeropygus* is *Galeropygus lacroixi* Lambert, 1924 from the Upper Pliensbachian, but the type specimen appears to be missing from Lambert's collections; the earliest, preserved apical system is from *G. agariciformis* (Wright, 1851) from the Upper Toarcian), and they progressively disappear in all taxa during the Late Jurassic, once the periproct and the apical system are completely separated (except in holectypoids). Contrary to some previous descriptions (Jesionek-Szymanska, 1963; Fell, 1966), and in spite of their infrequent preservation, we have found supplementary plates in pygasteroids (Hawkins, 1944) and in holectypoids (Fig. 3a). The apical system of *Holectypus* has long been interpreted to be composed of five genital plates, the fifth genital plate lacking a gonopore in the Jurassic (Wagner & Durham, 1966). However, considering the apical disruptions induced by periproct migration, and the presence of two or three supplementary plates in the species *Holectypus hemisphaericus* Desor *in* Agassiz & Desor, 1847, it seems more likely that the fifth imperforate 'genital' plate of *Holectypus* and *Pileus* Desor, 1856 is a supplementary plate. The term 'genital' used by most authors actually refers to a function recovered by Cretaceous holectypoids (the plate is again perforated by a gonopore (Wagner & Durham, 1966)), and does not refer to a homology with the posterior genital 5 of other taxa. Supplementary plates are also present in some 'regular' taxa (e.g. Acrosaleniidae) characterized by a very eccentric position of the periproct within the apical system (Fig. 3b).

Supplementary plates are formed inside the apical system. They do not originate in contact with ocular plates, they generally present no precise structural pattern, and they

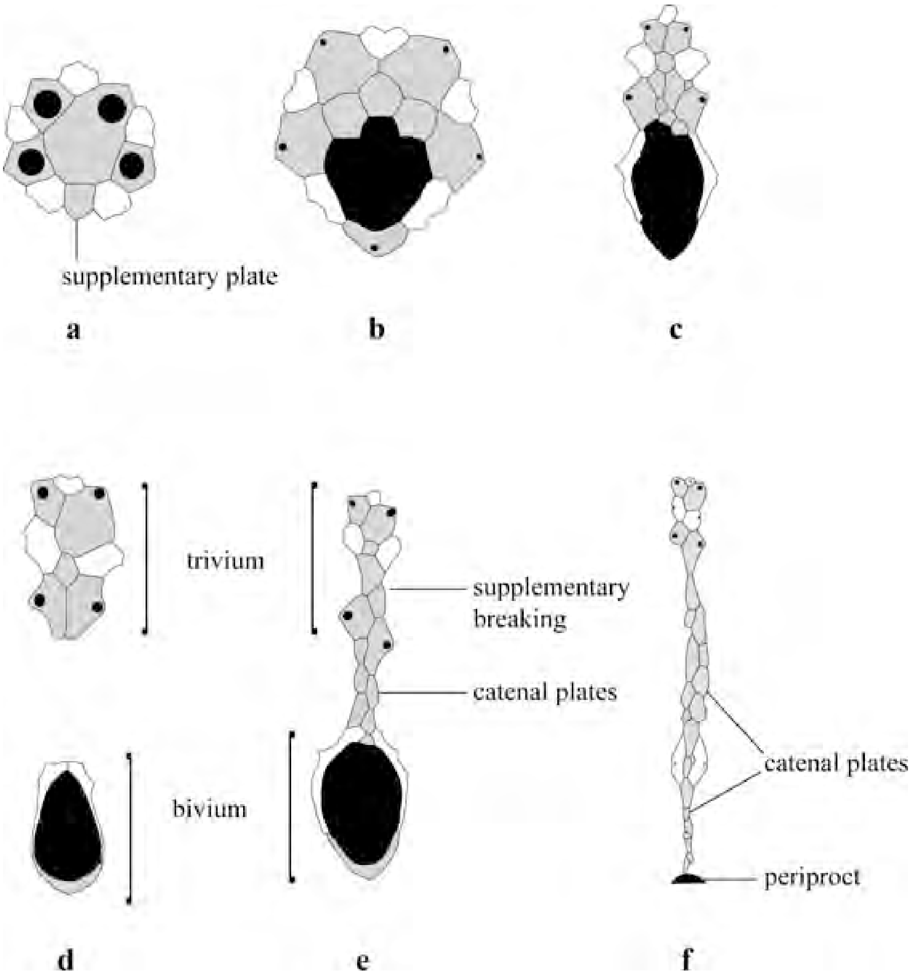

Figure 3. Characters involving supplementary plates. (a) *Holectypus depressus*: genital plate 5 is replaced by a supplementary plate. (b) *Acrosalenia hemicidaroides*: the ‘regular’ family Acrosaleniidae is characterized by the presence of several supplementary plates in the anterior part of the apical system. (c) *Hyboclypus caudatus*: supplementary plates fill the space created by periproct migration. (d) *Pygorhytis ringens*: in the first Atelostomata, the apical system is broken into an anterior part (trivium) and a posterior part (bivium). (e) *Orbigniana ebrayi*: a supplementary rupture is present within the trivium. (f) *Collyrites elliptica*: catenal (supplementary) plates are present between the trivium and the bivium as well as between the bivium and the periproct.

are variable in size and number irrespective of specimen size. In view of their pattern and position with respect to other apical plates, we consider supplementary plates as elements of the extraxial skeleton. They are present either in the anterior or posterior part of the apical system, and generally fill the free space created by the departure of the periproct (Fig. 3c). In Jurassic Atelostomata, the stretching of the apical system results in breakage into an anterior sub-unit, the trivium (composed of three ocular and four genital plates), and a posterior sub-unit, the bivium (composed of two ocular plates) (Fig. 3d). These two sub-units are connected by a row of supplementary plates, called catenal plates (Durham & Wagner, 1966), and aligned along the III-5 axis in certain taxa (*Orbigniana ebrayi* (Cotteau, 1874) *in* Gotteau, Péron & Gauthier, 1873–1891; *Cyclolampas kiliani* (Lambert, 1909)) (Fig. 3e). Supplementary plates may also link posterior oculars to the periproct (e.g. in *Infraclypeus* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891 and *Collyrites* Desmoulins, 1835). In this case, we assign the term catenal to these plates as well (Fig. 3f).

6. Supplementary plates between the bivium and the trivium: 0, no supplementary plates between the bivium and the trivium; 1, supplementary plates in continuous row of catenal plates between the bivium and the trivium; 2, supplementary plates in irregular plating between the bivium and the trivium.
7. Supplementary plates between the posterior ocular plates and the periproct: 0, no supplementary plates between the posterior ocular plates and the periproct; 1, supplementary plates forming a catenal row between the posterior ocular plates and the periproct; 2, supplementary plates in irregular plating between the posterior ocular plates and the periproct.
8. Supplementary plates between the anterior ocular plates: 0, no supplementary plates between the anterior ocular plates; 1, supplementary plates present between the anterior ocular plates.
9. Supplementary plates between the posterior ocular plates: 0, no supplementary plates between the posterior ocular plates; 1, supplementary plates present between the posterior ocular plates.

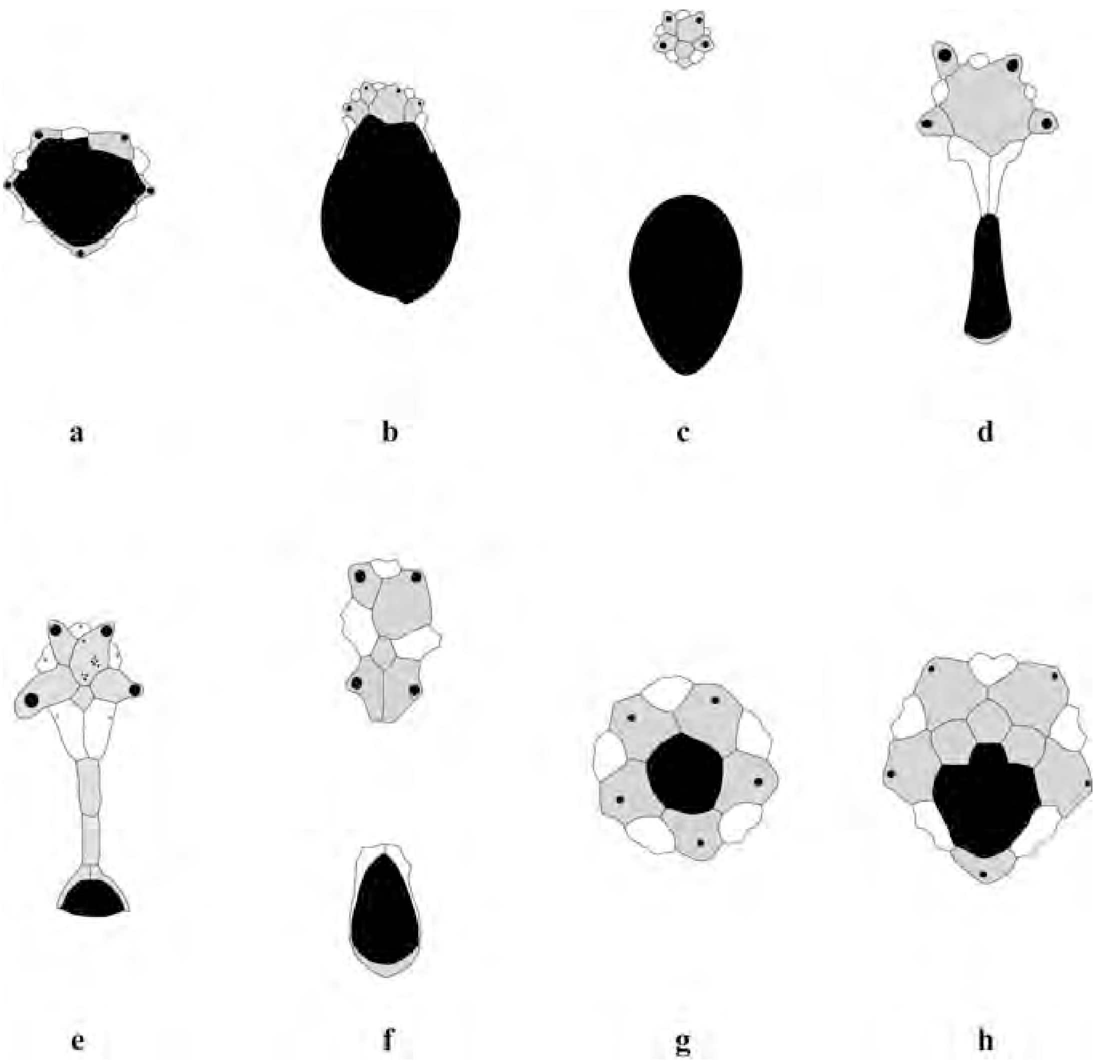

Figure 4. Relationships between the periproct and the apical system. (a) *'Plesiechinus' hawkinsi*: the periproct is still enclosed within the apical system, but posterior apical plates are stretched by the onset of periproct migration. (b) *Pygaster gresslyi*: posterior ocular plates are elongated but do not contact genital 5, the apical system is exocyclic. (c) *H. hemisphaericus*: the periproct is isolated within the axial plates of the corona. (d) *Clypeus plotii*: posterior oculars still contact the periproct but the anterior apical plates are already grouped together. (e) *Nucleolites clunicularis*: posterior oculars do not contact the periproct and the apical plating forms a compact structure. (f) *Pyrorhytis ringens*: the apical plating of the trivium forms an intercalary structure. (g) *Caenocidaris cucumifera*: the apical plating forms a dicyclic structure. (h) *Acrosalenia hemicidaroides*: the apical plating forms a hemicyclic structure.

2.d.3. Relationships between periproct and apical system (characters 10–13)

In 'regular' echinoids, two distinct patterns in apical structure can be recognized: (1) they are said to be dicyclic when genital and ocular plates form two concentric circles around the periproct, with no ocular joining the periproctal rim (Fig. 4g), and (2) they are monocyclic or hemicyclic when at least some ocular plates form part of the inner circle around the periproctal rim (Fig. 4a, h) (Durham & Wagner, 1966).

Durham & Melville's (1966) definition of exocyclism (that is, tests with the periproct located outside the apical system) is not precise enough to be applied to early irregular echinoids which are characterized by apical structures intermediate between the common endocyclic and exocyclic systems. Therefore, we refine Durham & Melville's (1966) definition of exocyclism as the contact between the periproct and the axial plates of interambulacrum 5. This contact is made possible by the breaking of the apical rim (between posterior oculars and genital 5) and the periproct's movement out of the apical circle (as suggested by the term exocyclism).

Exocyclism is realized progressively in many taxa (Jesionek-Szymanska, 1963), first by the breakage between the posterior oculars and genital 5, then by the progressive movement of the periproct away from posterior oculars which stretch before losing all contact with the periproct (Fig. 4c, d). Once they lose this contact, apical plates begin to group together and fill the space created by periproct removal. Therefore, apical plates begin to group together in the anterior part of the apical system, even when the periproct is still in contact with posterior ocular plates (Fig. 4e). This pattern is present in Cassiduloida and basal Atelostomata. Then, posterior ocular plates tend to group together with the anterior part of the apical system once they lose contact with the periproct (Jesionek-Szymanska, 1963; Thierry, 1974) (Fig. 4e). Finally, exocyclism results in the isolation of the extraxial periproct embedded within a growth zone boundary, between the axial plates of interambulacrum 5 and distant from other extraxial elements (that is, the genitals) (Fig. 4c).

The grouping of apical plates is achieved in two different ways, leading to two types of apical patterns: (1) the intercalary (or elongate) structure (Fig. 4f) in which genital plates 1 and 4 are not in contact with the periproct, and genital plate 2 does not contact genital plate 4; and (2) the compact structure (Fig. 4d, e) in which genital plates 1 and 4 are not in contact with the periproct, and genital plate 2 contacts genital plate 4.

10. Endo- and exocyclism: 0, periproct not in contact with interambulacrum 5 (endocyclic state); 1, periproct in contact with the interambulacrum 5 (exocyclic state).
11. Contact between the posterior ocular plates and the periproct: 0, periproct in contact with the posterior ocular plates (or with the posterior genital plates when the ocular plates are exsert); 1, periproct not in contact with the posterior ocular plates.
12. Structure of the apical system: 0, apical system dicyclic, genital and ocular plates forming two concentric circles around the periproct, no ocular joining the periproctal rim; 1, apical system monocyclic or hemicyclic, at least some ocular plates participate in the inner circle around the periproctal rim; 2, apical system intercalary, genital plates 1 and 4 not in contact with the periproct, and genital plate 2 not in contact with genital plate 4; 3, apical system compact, genital plate 2 in contact with genital plate 4.
13. Disjunction of the apical system: 0, posterior ocular plates and genital plates 1 and 4 in contact; 1, posterior ocular plates and genital plates 1 and 4 disjunct.

2.d.4. *The periproct (characters 14–16)*

The periproct is large in pygasteroids and holectypoids, as well as in *L. ludovicii* (Smith & Anzalone, 2000) (Fig. 5a, b). In these taxa, it occupies a much larger surface than the rest of the apical disc. In contrast, the periproct is relatively smaller in all other irregular echinoids, with a surface area nearly the same size as the rest of the apical disc (Jesionek-Szymanska, 1963) (Fig. 5c, d).

In numerous Jurassic irregulars, the periproct remains on the apical side of the test. This position is described as supramarginal. However, in the majority of menopygids and Atelostomata, the periproct migrates posteriorly to the margin of the test, and is said to be marginal. It can even reach the oral side (as in *Holectypus*, *Pygurus* Agassiz, 1839, and *Infraclypeus* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891) and become inframarginal.

In 'regular' echinoids and holectypoids, the periproct is flush with the test, whereas it is depressed in pygasteroids, in *L. ludovicii* and *Eogaleropygus microstoma* (Lambert, 1933*b*) (Jesionek-Szymanska, 1978; Smith & Anzalone, 2000). The periproct is vertical and located at the bottom of a deep anal groove in galeropygoids, cassiduloids and early atelostomates.

14. Size of the periproct: 0, surface of the periproct smaller than or of nearly the same size as the apical disc; 1, surface of the periproct much larger than the apical disc.

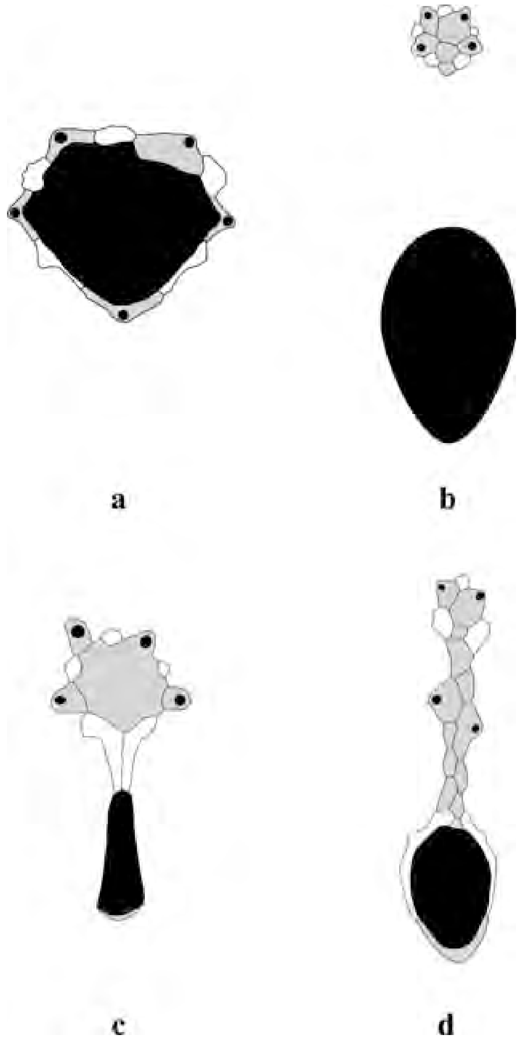

Figure 5. Characters of the periproct. In (a) (*'Plesiechinus' hawkinsi*) and (b) (*Holectypus hemisphaericus*), the periproctal area exceeds the area filled by apical plates. In (c) (*Clypeus plotii*) and (d) (*Orbigniana ebrayi*), the periproctal area is smaller or approximately equals the area filled by apical plates.

15. Position of the periproct: 0, periproct supramarginal; 1, periproct marginal; 2, periproct inframarginal.
16. Attitude of the periproct: 0, periproct flush with the test; 1, periproct in a slight anal groove; 2, periproct vertical and in a steep anal groove.

2.d.5. *Ambulacra (characters 17–21)*

Kier (1974) reviewed the evolution of plate compounding throughout the Mesozoic. Originating in Late Triassic cidaroids, plate compounding diversified gradually during the Mesozoic and corresponds to an increase in the number of elementary ambulacral plates. Kier interpreted the evolution of plate compounding as a mechanism by which echinoids could increase the number of tube feet (sensation, locomotion and food collection), while maintaining the size of ambulacral tubercles and spines (protection against predation). Because of miniaturization of their spines, most irregular taxa are distinguished by simple ambulacral plating, except in pygasteroids and holectypoids which retain plate compounding of the plesiechinid type. Jensen (1981) distinguished between the plesiechinid type of plate compounding in Pygasteroida (which she related to the early diadematoid type), from the pattern present in Holectypoida (the holectypid type). This was an argument to make Eognathotomata polyphyletic, but in designating these as separate types and therefore essentially as autapomorphies for each of these groups, Jensen obviated the possibility that they could contain phylogenetic information. Herein, we follow Kier (1974) in considering that holectypoids and pygasteroids share the same type of compounded plates.

Petaloids are absent in the earliest irregular echinoids, although ambulacral pores are slightly elongated in '*P.' hawkinsi*, pygasteroids and holectypoids (Jesionek-Szymanska, 1970). Petaloid ambulacra became strongly developed in cassiduloids (and especially in the genera *Clypeus* Leske, 1778 and *Pygurus*) as early as the Middle Jurassic, with the outer pore of the pore pairs elongated into a narrow slit. Petals were slightly developed later on in Atelostomata, but to a lesser extent. Pore morphology and tube foot morphology are closely linked (Smith, 1978*a*, 1980*a*). Petaloid evolution corresponds to a specialization of aboral tube feet that allows irregular echinoids to conduct gas exchange more efficiently, especially in relation to new living habits such as burrowing, a more intense activity than grazing (Kier, 1974) that also results in reduced exposure to ambient water flow.

The appearance of phyllodes corresponds to an increase in number, specialization and enlargement of adoral ambulacral pores. The function of phyllodes is to enhance efficiency of tube feet for food gathering (particle picking) in irregular echinoids (Telford & Mooi, 1996) or for attachment in 'regular' echinoids. Whatever the function, phyllodes were considered homologous structures in 'regular' and irregular echinoids by Kier (1974). Phyllodes are present in 'regular' echinoids as early as the Early Jurassic (in pedinoids). In pygasteroids, phyllodes are very similar to those of pedinoids. In galeropygoids and first cassiduloids, phyllopodia became larger and arranged in arcs of three. This increase in size and number is correlated with a modification of adoral ambulacral plating (demi-plates and reduced plates) that allows crowding of the pores in the region near the peristome. Phyllode arrangement is used in systematics. For example, the families Clypeidae Lambert, 1898 and Nucleolitidae Agassiz & Desor, 1847 are distinguished according to their phyllopodial patterns (Kier, 1962). Phyllodes are also differentiated in the first Atelostomata which inherited the arrangement of phyllopodes in arcs of three (Jesionek-Szymanska, 1963). However, menopygids have been distinguished from galeropygoids mainly by the absence of phyllodes (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Rose & Olver, 1988).

17. Depression of ambulacra: 0, ambulacra not depressed on the oral side; 1, ambulacra depressed on the oral side.
18. Compounded plates (ambulacral units composed of several elemental plates bound together by a single large primary tubercle): 0, simple ambulacral plating, ambulacra composed throughout of simple plates; 1, compound plating of diadematoid type, unit of three plates bound together; 2, compound plating of acrosaleniid type, a simple plate alternates with two plates bound together; 3, compound plating of plesiechinid type, each plate overlained by two tubercles that bind it to two different units.
19. Structure of the adoral part of the ambulacra: 0, ambulacra composed only of primary plates adorally, that is plates with an adradial (contact with the interambulacral column) and a perradial suture (contact with the neighbouring ambulacral column); 1, ambulacra composed adorally of reduced plates intercalated between primary plates, and pore pairs arranged in triads; 2, ambulacra composed adorally of reduced plates intercalated between primary plates, and pore pairs not arranged in triads.
20. Petals: 0, petals not differentiated, partitioned isopores aborally; 1, petals slightly developed, enlarged and specialized pore pairs aborally; 2, petals well developed, enlarged and elongated anisopores, outer pores in a narrow slit.
21. Phyllodes: 0, phyllodes not differentiated, ambulacral pores not specialized near the peristome; 1, phyllodes with specialized ambulacral pore pairs near the peristome.

2.d.6. Interambulacra (characters 22, 23)

Atelostomata are distinguished from other irregular echinoids by differentiation in the size of their adoral interambulacral plates (Devriès, 1960; Kier, 1974). However, the earliest Atelostomata (*O. ebrayi*, *C. kiliani*, *Pygomalus ovalis* (Leske, 1778) and *Pygorhytis ringens* (Agassiz, 1839)) still lack this differentiation (Jesionek-Szymanska, 1963; Kier, 1974). Such a differentiation first appeared in the Upper Bathonian (as in *Collyrites elliptica* (Lamarck, 1791) *in* Bruguière, 1816) by the enlargement of the first plate of interambulacrum 5, thereby forming the labrum (Jesionek-Szymanska, 1963; Mintz, 1968). For Kier (1974), this differentiation was related to the evolution of heart-shaped tests with wide peristomes in Atelostomata. Very early in ontogeny, the relative positions of interambulacral plates become nearly fixed on the oral side so that test and peristomial growth is almost exclusively accommodated by the enlargement of adoral plates.

Galeropygoids and cassiduloids evolved an outward bulging of the basicoronal interambulacral plates to form the so-called bourrelets. Bourrelets are present, although slightly developed, in certain menopygids as well. As early as the Middle Jurassic, bourrelet development is particularly significant in cassiduloids in which bourrelets intrude into the peristome (e.g. *Clypeus*), and might have been involved in food gathering. These structures are covered by many small tubercles and tiny spines which some have hypothesized were used to push particles up into the peristome (Kier, 1962; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966). However, Telford & Mooi (1996) observed no such function of the bourrelets in extant *Cassidulus* Lamarck, 1801, in which podia were the sole agents of food transfer into the mouth. Spines were never employed in food manipulation, and bourrelet spination was actually moved out of the way to admit particles being manipulated by the phyllopodia.

22. Differentiation of oral interambulacral plates: 0, basicoronal interambulacral plates not differentiated; 1, enlarged basicoronal interambulacral plates.
23. Bourrelets (doming of the interambulacra near the peristome): 0, bourrelets absent; 1, bourrelets present.

2.d.7. Peristome (characters 24–27)

Buccal notches and the perignathic girdle are structures internal to the peristome and associated with the function of the Aristotle's lantern (Melville & Durham, 1966). They are present in 'regular' echinoids (buccal notches are absent in cidaroids) and in the irregular pygasteroids and holectypoids (Kier, 1974) but disappear as the lantern is lost in the Microstomata. The earliest Microstomata retain relics of buccal notches and of a perignathic girdle as marks of their 'regular' origin. Relics can be found in menopygids (Rose & Olver, 1988), in *L. ludovicii* (Smith & Anzalone, 2000), and in some Atelostomata and galeropygoids (Kier, 1962; Jesionek-Szymanska, 1963).

In Microstomata, the anterior displacement of the peristome accompanies the appearance of bilateral symmetry of the test. Anterior shifting of the peristome can be related to the adoption of burrowing and infaunal living habits that necessitated an exclusive forward motion of echinoids to facilitate the ingestion of particles gathered from the sediment (Kier, 1974).

24. Buccal notches: 0, buccal notches well developed; 1, small residual buccal notches; 2, buccal notches absent;
25. Perignathic girdle (internal processes for attachment of muscles supporting the lantern): 0, perignathic girdle complete; 1, perignathic girdle atrophied, no longer functional; 2, perignathic girdle absent.
26. Position of the peristome: 0, peristome close to a central position; 1, peristome anterior.
27. Depression of the peristome: 0, peristome depressed; 1, peristome flush with the test.

2.d.8. Tubercles and spines (characters 28–34)

Kier (1974) and Smith (1981) observed a trend toward the reduction in size and increase in number of tubercles and spines in the evolution of post-'Palaeozoic' echinoids. The greatest decrease in size of spines occurs with the appearance of irregular echinoids. In the earliest irregular, '*P.*' *hawkinsi*, tubercles of the oral side are of the same size in ambulacra and interambulacra, whereas the later *L. ludovicii* still retains large interambulacral tubercles and spines (Smith & Anzalone, 2000). Nevertheless, in succeeding irregular echinoids, tubercles and spines are of the same size in ambulacra and interambulacra. The decrease in tubercle size and their correlated increase in number became more pronounced in Microstomata as early as the Pliensbachian, and is noticeable in the genus *Galeropygus* in which there are many more tubercles than in *Plesiechinus* (Kier, 1974, 1982; Smith, 1978*b*). In pygasteroids and holectypoids, tubercles are ordered in concentric rows all over the test. The areoles, depressions around the tubercles for attachment of muscles controlling movement of spines, are asymmetrical around tubercles of the oral side. The asymmetry is radially arranged all over the oral side, so that there is no specialization to accommodate the power stroke by the muscle during movement in a particular direction (Smith, 1980*b*). Conversely, the increase in tubercle number in Microstomata goes along with an unordered arrangement of tubercles on the test, but the asymmetry of areoles is organized in accordance with the bilateral symmetry of the test and is a specialization for forward and unidirectional movement of echinoids. It is related to the adaptation of Microstomata to moving upon or within the sediment in a single direction (Smith, 1978*b*, 1980*b*).

Crenulation, the ribbing or lobation of the perimeter of the tubercle's platform below the mamelon, evolved once but has been lost several times in the evolution of regular echinoids (Lewis & Ensom, 1982). In the Introduction to the present work, it was noted that Mortensen (1948) used the crenulation of tubercles as a criterion to argue for the independent origin of holectypoids and pygasteroids, whereas Jesionek-Szymanska (1970), as well as Rose & Olver (1984), showed that crenulation could not be used to demonstrate the independent origin of these groups. In fact, tubercles are originally crenulated in irregular echinoids, and all the Microstomata have crenulated tubercles (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966).

The internal structure of spines differs among echinoids but is constant in a given species (Hyman, 1955) or even at higher taxonomic levels such as genera or families (Melville & Durham, 1966). The internal structure of spines is used in the systematics of 'regular' echinoids. In particular, some 'regular' taxa evolved solid spines, whereas they are hollow in others as well as in irregular echinoids, excepted in pygasteroids. Hence, pygasteroids possess solid spines, whereas spines are hollow in holectypoids (Smith, 1981).

28. Density of primary tubercles on ambulacral plates: 0, one single large primary tubercle on each ambulacral plate (or compound plate); 1, two or three 'primary' tubercles on each ambulacral plate near the ambitus; 2, numerous 'primary' tubercles on each ambulacral plate near the ambitus.
29. Density of primary tubercles on interambulacral plates: 0, one single large primary tubercle on each interambulacral plate; 1, two or three 'primary' tubercles on each interambulacral plate near the ambitus; 2, numerous 'primary' tubercles on each interambulacral plate near the ambitus.
30. Ordering of primary tubercles: 0, primary tubercles ordered in concentric rows all over the test; 1, primary tubercles not ordered in concentric rows.
31. Crenulation of primary tubercles (tubercles with ribbed periphery): 0, primary tubercles crenulate; 1, primary tubercles smooth.
32. Symmetry of areoles (depression for attachment of muscles supporting and controlling movement of spines): 0, areoles with a radial symmetry on the oral side; 1, areoles with bilateral symmetry, the long axis arranged radially on the oral side; 2, areoles with bilateral symmetry, the long axis arranged anterior to posterior on the oral side.
33. Size of spines: 0, large primary spines; 1, short and slender primary spines.
34. Internal structure of spines: 0, hollow primary spines; 1, solid primary spines.

2.d.9. Aristotle's lantern (characters 35–37)

The importance of the Aristotle's lantern for the systematics of irregular echinoids was discussed in the Introduction. Smith (1981, 1982) showed that irregular echinoids and *E. minutum* evolved diamond-shaped teeth from the aulodont type (grooved teeth) by paedomorphosis (McNamara, 1982). Similarly, *E. minutum*, the holectypoids and juvenile cassiduloids (cassiduloids lose the lantern as adults) have wide pyramids derived from the narrow pyramids of aulodont echinoids (e.g. *Diademopsis* Desor, 1855).

35. Presence of the lantern: 0, Aristotle's lantern present in adults; 1, Aristotle's lantern absent in adults.
36. Type of teeth: 0, teeth of cidaroid type; 1, grooved teeth; 2, keeled teeth; 3, teeth diamond-shaped in cross-section.
37. Type of pyramids: 0, narrow pyramids; 1, wide pyramids.

2.d.10. Shape of the test (characters 38, 39)

The choice of coding characters linked to the shape of the echinoid test (profile and outline) in a phylogenetic analysis may seem questionable. Indeed, at a species level, such characters are known to be 'sensitive' to environmental variations (Néraudeau, 1995), and their significance for taxa discrimination may be reproved. For example, in several Cretaceous irregular groups (such as archiaciids, holectypoids and hemiasters), the shape of the test appears related to sediment granulometry, to the depth of burrowing, and to water depth (Nichols, 1959; Smith & Paul, 1985; Zaghbib-Turki, 1989; Néraudeau & Moreau, 1989). However, because of the taxonomic level of the present analysis along with the antiquity and the originality of first irregular echinoids, it seemed relevant to consider the possible phylogenetic significance of test shape. Furthermore, Kier (1974) noted a change in the general shape of the echinoid test with the appearance of irregular echinoids. He correlated this change to the migration of the periproct outside the apical system. Indeed, tests of irregular echinoids can be elongated and display a bilateral symmetry that distinguishes them from 'regular' echinoids (Smith, 1981). However, in earliest irregular echinoids, tests are wider than long and the bilateral symmetry is not so conspicuous (e.g. '*P.*' *hawkinsi* and *G. agariciformis*). Elongated tests did not appear before the Middle Jurassic in Microstomata. The elongation and bilateral symmetry of the test are related to the adaptation of irregular echinoids to a unidirectional mode of locomotion (Kier, 1974; Smith, 1978*b*, 1981, 1984). Irregular echinoids also evolved flattened tests, particularly pronounced in the cassiduloids *Clypeus* and *Pygurus* (Kier, 1974).

38. Marginal outline of the test: 0, circular outline, length and width of the test more or less equal; 1, widened outline, test wider than long; 2, elongated outline, test longer than wide.
39. Profile of the test: 0, high, rounded test; 1, low, rounded test; 2, low, flattened test.

3. Results

3.a. General results

The parsimony analysis found 156 shortest trees with a length of 151 steps. Completion of 100 replicates with random taxon addition sequences did not reveal the existence of other trees of equal shortest length. We used a majority-rule consensus tree to summarize this set of trees (Fig. 6). Phylogenetic relationships among taxa are almost all resolved, with the exception of two polytomies: one involves the 'regular' echinoids *A. hemicidaroides* Wright, 1851 and *F. crenulata* Kier, 1972 and the other concerns the derived irregular taxa *Clypeus plotii* Leske, 1778, *Pygurus depressus* Agassiz *in* Agassiz & Desor, 1847, *Nucleolites clunicularis* (Phillips, 1829) and *Pseudosorella orbignyana* Cotteau, 1855. Most of the nodes are well supported (Fig. 6); the uncertainties (4 nodes out of 28) lying within the relationships among crown cassiduloids (one node) and atelostomates (three nodes). Parsimony indices (CI = 0.391, RI = 0.738, RC = 0.288, HI = 0.609) fall within the ranges of values obtained in previous cladistic analyses carried out on irregular echinoids (Suter, 1994; Smith & Anzalone, 2000; Smith, 2001, 2004; Villier *et al.* 2004). These recurrent and relatively low values reveal the importance of homoplastic state changes in these phylogenetic analyses of primitive fossil forms (Suter, 1994; Villier *et al.* 2004).

The overall aspect of the majority-rule consensus tree is clearly asymmetric, with a paraphyletic assemblage constituted by stem 'regular' taxa, and a monophyletic group corresponding to the Irregularia (clade 1). The question of whether to include *E. minutum* in the Irregularia or not is discussed below. This monophyletic assemblage is organized into four sub-units corresponding to the four main recognized groups of Jurassic irregulars: the Eognathostomata (clade 2), the menopygids (excluding *Menopygus nodoti* (Cotteau, 1859)) (clade 4), the Neognathostomata Smith, 1981 (clade 5), and the Atelostomata (clade 6). The last three clades are themselves united to form a sixth grouping, the Microstomata (clade 3). The monophyly of Irregularia is well-supported (decay index ≥ 3, bootstrap value = 90 %), and departs from Jensen's analysis (1981) but agrees with all other, more recent cladistic works (Smith, 1981, 1984; Rose & Olver, 1988; Smith & Anzalone, 2000; Solovjev & Markov, 2004).

3.b. Main clades

3.b.1. Clade 1

All recognized irregular taxa in the analysis are strongly related and form the clade Irregularia (Fig. 6). The clade is supported by the following synapomorphies: relatively large size of the periproct (character 14), high density of primary tubercles on ambulacral and interambulacral plates (characters 28 and 29), shortening of primary spines (character 33), *L. ludovicii* excepted (characterized by large primary spines attached to a primary tubercle, one to each interambucral plate), and a relatively low test camber (character 39). The relatively large surface area of the periproct is seen in the very first irregulars ('*P.*' *hawkinsi* and *L. ludovicii*), as well as in the Eognathostomata (Clade 2). However, all other irregulars possess a relatively small periproct. Similarly, a low test profile characterizes basal taxa, but presents numerous reversions in more derived groups. On the contrary, characters related to appendages, namely the increased number of primary tubercles and shortened primary spines (characters 28, 29 and 33), exhibit relatively low levels of homoplasy and are shared both by all basal and terminal irregular taxa (*L. ludovicii* excepted).

The diamond-shaped teeth (character 36) and narrow pyramids (character 37) are states shared by *E. minutum* and

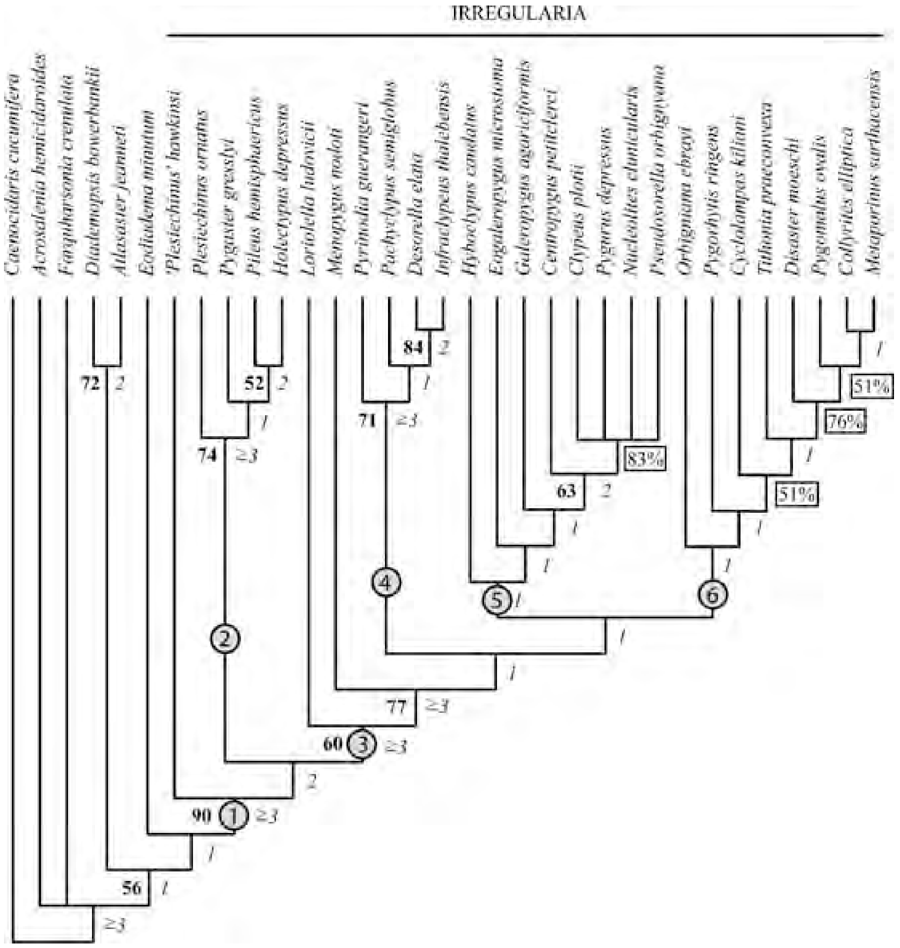

Figure 6. Fifty per cent majority-rule consensus tree of the 156 equally parsimonious cladograms computed from the data matrix of Table 2. *Caenocidaris cucumifera* is the outgroup. Clades discussed in the text are designated by encircled numbers. Four nodes are not fully supported; their support is given as percentage values in squares. Bootstrap values are indicated in bold on the left of each branch; Bremer support values are in italics on the right of each branch.

lantern-bearing irregulars (Smith, 1981), and are features that led Smith (1984) to include *E. minutum* in the Irregularia. *E. minutum* shares two other characters with irregular echinoids: the elongation of posterior ocular plates (character 2) and the development of genital plate 2 (character 1). However, these two characters show important homoplastic changes within the Irregularia (Fig. 7).

'P.' hawkinsi shares the apomorphic characters of other irregular taxa: a relatively large periproct (character 14), and specialization of appendages (characters 28, 29 and 33). Previous authors (Jesionek-Szymanska, 1970; Smith, 1981; Kier, 1982) also considered *'P.' hawkinsi* to be the first representative of irregular echinoids on the basis of its morphological affinities (overall shape and plesiechinid type of compound plating) with pygasteroids (*Plesiechinus*, *Pygaster,* and *Pileus*). However, '*P.' hawkinsi* differs from pygasteroids and other early irregular taxa in three character states: the perforated genital plate 5 (character 5), the absence of supplementary plates (character 9) and a periproct that is not depressed (character 16).

Atlasaster jeanneti Lambert, 1937 is discussed herein because Lambert (1931, 1937) considered this taxon to be an early irregular representative on the basis of what turns out to be an erroneous interpretation of its apical system. *A. jeanneti* possesses none of the apomorphic characters of irregular echinoids, and in the consensus tree, it is placed close to the regular echinoid *D. bowerbankii*, with which it shares smooth primary tubercles (character 31) and the presence of two primary tubercles on interambulacral plates (character 29). More investigations are needed to determine the precise phylogenetic position of *A. jeanneti*, but the present results indicate that it should be considered an early representative of the 'regular' Diadematacea, lacking any phylogenetic affinity with irregular echinoids.

3.b.2. Clade 2

Clade 2 (Fig. 6) is fairly well-supported (decay index ≥ 3) and corresponds to the superorder Eognathostomata as described by Smith (1981), the sister group of all other irregular echinoids ('*P.' hawkinsi* excepted). Apomorphies of the clade are: genital plate 5 reduced or lacking (character 4), exocyclic apical system (character 10), plesiechinid compound plating (character 18), bilaterally symmetric and radially ordered areoles (character 32) and solid primary spines (character 34). As for Clade 1, characters related to specialization of appendages (characters 18 and 32) distinguish the Eognathostomata from other irregular taxa, whereas other character changes (4, 10 and 34) are homoplastic within the Irregularia. The overall morphology of '*P.' hawkinsi* is very close to 'pygasteroid' representatives of the Eognathostomata, as already discussed above. Although *Plesiechinus* can be considered a possible ancestor for the clade, as a representative of basal irregular echinoids,

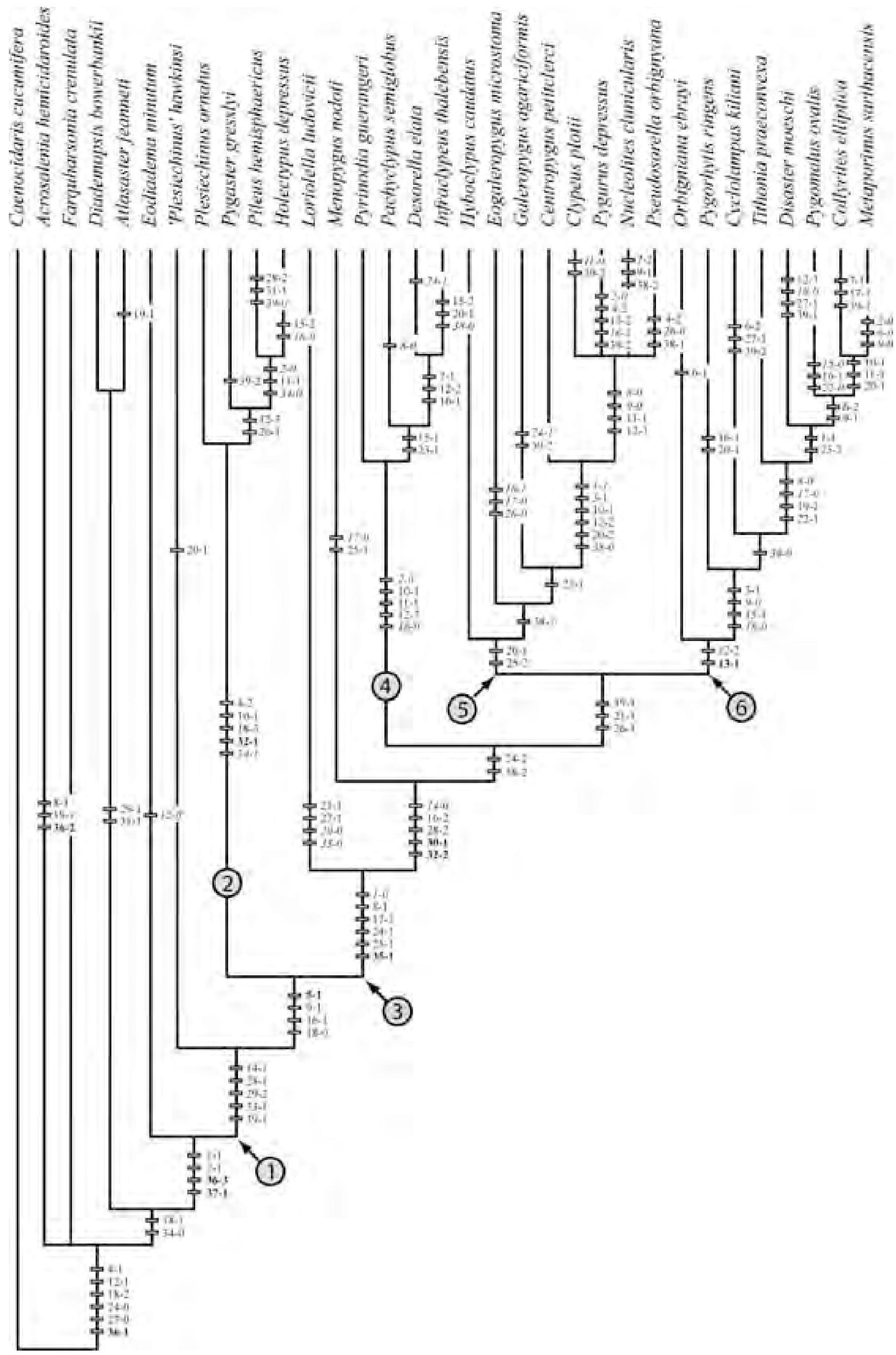

Figure 7. List of character state changes in the majority rule consensus tree. For example: 36-1 = change to state 1 of character 36. Non-homoplastic character changes are in bold; reversals are in italics. Clades discussed in the text are designated by encircled numbers.

it cannot be included in the Eognathostomata because of the plesiomorphic state of the apical system and of the periproct. For the most part, in publications before the 1980s, 'pygasteroid' and 'holectypoid' echinoids were considered completely independent lineages stemming from unrelated 'regular' groups (Durham & Merville, 1957; Melville, 1961; Philip, 1965; Durham, 1966; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Märkel, 1978; Jensen, 1981). In contrast, our analysis supports Smith's view (1981, 1984) and considers 'pygasteroid' and 'holectypoid' echinoids as sister groups in a distinct, monophyletic assemblage. Moreover, our results do not support the traditional dichotomy between 'pygasteroids' and 'holectypoids'. Instead, the taxa *Pileus* (a traditional 'pygasteroid') and *Holectypus* ('holectypoid') form a well-supported clade, excluding the paraphyletic 'pygasteroids' *Plesiechinus* and *Pygaster* (Fig. 6).

3.b.3. Clade 3

Clade 3 (Fig. 6) encompasses all irregular echinoids not included in the Eognathostomata and that lack compounded ambulacral plates (reversion to the most plesiomorphic state of character 18), do not possess an Aristotle's lantern as adults (character 35), and do not have a complete and functional perignathic girdle and buccal notches (characters 24 and

25). This clade corresponds to the superorder Microstomata as described by Smith (1984). Other character changes that distinguish basal Microstomata are highly homoplastic. These are: development of genital plate 2 (character 1), supplementary plates between anterior oculars (character 8), and the depression of ambulacra (character 17).

The basal taxon of the clade is *L. ludovicii,* which is distinguished from other Microstomata by a mosaic of plesiomorphic and apomorphic features (Smith & Anzalone, 2000). Plesiomorphic features that separate it from other taxa in the clade concern the appendages and the periproct. *L. ludovicii* is characterized by a single, large primary spine on each interambulacral plate (characters 29 and 33), ordered primary tubercles with radially symmetric areoles (characters 30 and 32), and a relatively large periproct that is not arranged vertically in a deep anal groove (characters 14 and 16).

Clade 3 differs slightly from the superorder Microstomata as defined by Smith (1984). First, relics of buccal notches and of the perignathic girdle (characters 24 and 25) are present in basal taxa and constitute the apomorphic state for the clade, whereas these structures were considered absent by Smith (1984). Moreover, the present clade includes the 'menopygids' (the genus *Menopygus* and Clade 4) and *L. ludovicii*, taxa not formally included by Smith (1984). This extension of Microstomata agrees with Rose & Olver (1988) and Solovjev & Markov (2004), whereas Smith & Anzalone (2000) consider *L. ludovicii* as the sister taxon of Microstomata.

3.b.4. Clade 4

Clade 4 includes all Microstomata that do not possess specialized ambulacral plates and pores adorally (characters 19 and 21). This description corresponds to the family Menopygidae Lambert & Thiéry, 1911 as it was redescribed by Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966), except for the exclusion of *M. nodoti*. The absence of specialized ambulacral plates and pores adorally distinguishes 'menopygids' from other Microstomata but is not an attribute only of 'menopygids'. For example, Eognathostomata also lack specialized phyllodes, a plesiomorphic character state within the Irregularia. Characters at the base of Clade 4 (characters 2, 10, 11, 12 and 16) are apomorphic character states of the apical system but display numerous homoplastic changes within the Microstomata (Fig. 7). Within Clade 4, some species, such as *Desorella elata* (Desor, 1847) *in* Agassiz & Desor, 1847 and *Pachyclypus semiglobus* (Münster, 1829) *in* Goldfuss, 1826–1844, could be more closely related (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Rose & Olver, 1988), but previous analyses gave too much weight to homoplastic characters of apical structures. Until new material is described, we have no robust argument either to separate *Pyrinodia guerangeri* (Cotteau, 1862) from the other three species or to split the clade formed by these four taxa.

The exclusion of *M. nodoti* from the clade is an essential difference from previous works (Lambert & Thiéry, 1911; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Rose & Olver, 1988), especially as the genus *Menopygus* gave its name to the family Menopygidae. *M. nodoti* differs from other 'menopygids' by lack of adoral depression in the ambulacra (character 17), by relics of the perignathic girdle (character 25), and by plesiomorphic character states of the apical system (characters 2, 10, 11, 12 and 16). As discussed above, these characters display important homoplastic changes among the Microstomata.

Rose & Olver (1988) excluded *P. guerangeri* from the Menopygidae and put it in *incertae sedis*, because of the lack of both an intercalary apical system and anal groove. However, *P. semiglobus* exhibits these states as well (a compact apical system and absence of anal groove), even though it is included in the family by the same authors (Rose & Olver, 1988).

3.b.5. Clade 5

Clade 5 comprises Microstomata with compound ambulacral plates adorally and differentiated phyllodes (characters 19 and 21), as well as an anteriorly placed mouth (character 26). However, members of Clade 5 do not have intercalary or disjunct apical systems (characters 12 and 13). In addition, they have differentiated petals (character 20) and no perignathic girdle (character 25), these characters being homoplastic at the level of Irregularia. Clade 5 corresponds to the series Neognathostomata of Smith (1981).

At the base of the Neognathostomata is a paraphyletic assemblage formed by the so-called 'galeropygoids' that includes the genera *Hyboclypus* Agassiz, 1839, *Eogaleropygus* Jesionek-Szymanska, 1978*,* and *Galeropygus* Cotteau, 1856 (Mortensen, 1948; Kier, 1962; Mintz, 1968; Smith, 1981; Jesionek-Szymanska, 1978). This small paraphyletic group of three taxa partly corresponds to the family Galeropygidae Lambert *in* Lambert & Thiery, 1911 (elevated to the ordinal rank by Mintz (1968)). 'Galeropygoids' constitute the stem group of other Neognathostomata that correspond to the orders Cassiduloida Claus, 1880 *sensu* Mintz (1968), and Clypeasteroida Agassiz, 1872.

Mortensen (1948), Mintz (1968) and Smith (1981) included *Centropygus petitclerci* Lambert, 1901 in the Galeropygidae, whereas it is placed in *incertae sedis* by Kier (1962). This taxon possesses differentiated petals and bourrelets (characters 20 and 23) as well as an exocyclic apical system (character 10). All three of these apomorphic states bring *C. petitclerci* closer to the order Cassiduloida, of which it constitutes the basal taxon, than to the paraphyletic stem group formed by 'galeropygoids'. The order Cassiduloida is supported by numerous synapomorphies, however, it gave rise to the Clypeasteroida in the Palaeogene and is paraphyletic *de facto* (Smith, 1981, 1984; Mooi, 1990; Suter, 1994; Smith, 2001). Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) also included the poorly known species *Jolyclypus jolyi* (Gauthier, 1898) of the Cenomanian within the 'galeropygoids'. However, observation of several newly collected specimens suggests that this species (not included herein) displays close affinities with the genus *Nucleopygus* Agassiz, 1840 from the Upper Cretaceous.

Within the 'cassiduloids', the families Clypeidae Lambert, 1898 (including *C. plotii* and *P. depressus*) and Nucleolitidae Agassiz & Desor, 1847 (*N. clunicularis* and *P. orbignyana*) are not differentiated (Fig. 6). This result agrees with Suter's (1994) phylogenetic analysis of cassiduloids that showed the importance of homoplasies between both families. On the contrary, Kier (1962) differentiated the two families according to petal shape and number of pores in the phyllodes.

3.b.6. Clade 6

Clade 6 includes Microstomata with both a disjunct apical system (character 13) and intercalary apical structure (character 12) and corresponds to the series Atelostomata.

Although they are considered diagnostic characters of the order Disasteroida Mintz, 1968, characters 12 and 13 undergo reversion in more derived Disasteroida. That is, the apical disjunction is resorbed before the appearance of Cretaceous forms, and compact apical structures appear as early as the Middle Jurassic in *Disaster moeschi* Desor, 1858. What most distinguishes derived Disasteroida from more basal ones (*O. ebrayi*, *P. ringens,* and *C. kiliani*) is the differentiation in size and shape of adoral interambulacral plates (character 22). This differentiation became even more pronounced during the Cretaceous, corresponding to a new phase of diversification that gave rise to the orders Holasteroida Durham & Melville, 1957 (*sensu* Smith, 1981) and Spatangoida Claus, 1876. The differentiation of interambulacral plates is a synapomorphy shared by the three orders Disasteroida, Holasteroida and Spatangoida which constitute the Atelostomata (Devriès, 1960; Fischer, 1966; Mintz, 1968; Kier, 1974; Smith, 1981).

Disasteroida have been subdivided into different families or subfamilies, depending on configuration of apical structures and degree to which the peristome and ambulacra can be depressed (Beurlen, 1934; Jesionek-Szymanska, 1963; Mintz, 1968; Solovjev, 1971; Smith, 1984). However, most of these different taxonomic subdivisions have not been supported by cladistic analyses and seem to constitute paraphyletic grades (however, see Barras (in press) concerning the family Tithoniidae). In the present analysis, three different families can be identified, namely the Tithoniidae Mintz, 1968 (*Tithonia* Pomel, 1883 and *Metaporinus* Agassiz, 1844), Collyritidae d'Orbigny, 1853 (*Collyrites* and *Pygomalus* Pomel, 1883) and Pygorhytidae Lambert, 1909 (*Orbigniana* Ebray, 1860, *Pygorhytis* Pomel, 1883 and *Cyclolampas* Pomel, 1883), all of which constitute paraphyletic groupings.

3.c. Homoplasy levels for key features

Parsimony indices for each character show that values differ considerably according to the character set analysed. Accordingly, characters coding for plate structures of apical systems show high homoplasy values. In particular, the appearance of supplementary plates (characters 6, 7, 8 and 9) and the relationships between the periproct and the posterior plates of the apical system (characters 2 and 11) have the highest levels of homoplasy. Only two characters show low levels of homoplasy and depart significantly from patterns shown by other characters of the apical disc: the loss of perforation in genital 5 (character 5), an apomorphy of all irregulars except '*P.' hawkinsi*, and the disjunction between bivium and trivium (character 13), an apomorphy of the Atelostomata. Most characters describing the density and the organization of tubercles (characters 28, 29, 30 and 32) as well as spine size (character 33) also show low homoplasy values. Highest values are obtained in characters coding for the Aristotle's lantern (characters 35, 36 and 37). Remaining characters show high values of homoplasy; they describe the shape and the position of periproct, the peristome, plate and pore structure of ambulacra and interambulacra, and the overall shape of the test.

3.d. Completeness of the fossil record and stratigraphic congruence

The congruence with stratigraphic range data is sometimes regarded as an additional test of phylogenetic inferences (Wagner, 2000; Benton, Wills & Hitchin, 2000; Pol, Norell & Sidall, 2004). We do not consider stratigraphy as a test of topology in the same way that character distributions are, because the nature of the evidence is totally different. However, we believe that detection of stratigraphic incongruence might point to the need for additional investigations (examination of new fossils and reanalysis of characters). Among the three indices calculated, Relative Completeness Index (RCI) = 13.73, Stratigraphic Consistency Index (SCI) = 0.61, Gap Excess Ratio (GER) = 0.80 (the tested values were significantly different from a random distribution with 0.1 % uncertainty), only the Gap Excess Ratio (GER) value falls within the range of values calculated for echinoids in previous analyses (Benton, Hitchin & Wills, 1999; Villier *et al.* 2004).

Comparisons between raw values of analyses on different taxonomic groups are to be considered cautiously (Pol, Norell & Sidall, 2004), however, it is noticeable that only the Gap Excess Ratio (GER) values obtained in our analysis correspond to values obtained in other works (Benton, Hitchin & Wills, 1999; Villier *et al.* 2004). An explanation may come from the fact that we have selected some taxa of the Lower Jurassic, where the fossil record of echinoids is particularly uneven (Thierry *et al.* 1997; Smith & Anzalone, 2000) and ghost ranges are potentially significant for primitive irregular echinoids. Consequently, low values obtained for the Relative Completeness Index (RCI) are not surprising. On the contrary, the Gap Excess Ratio (GER), that is, the proportion of the total ghost range imposed by the contraints of the cladogram, is not necessarily affected by significant ghost ranges (Wills, 1998). Moreover, the Stratigraphic Consistency Index (SCI) values have been shown to be more sensitive to tree topology than Gap Excess Ratio (GER) values (Benton, Hitchin & Wills, 1999; Wagner, 1995; Pol, Norell & Sidall, 2004), and the majority-rule consensus tree (Fig. 6) shows a pectinate topology with basal taxa characterized by stratigraphic ranges not drastically older than the ranges of terminal taxa.

Our choice of representative species implies the existence of numerous gaps and conflicts between the tree topology and the stratigraphy, as the stratigraphic range of the species selected as representative of a certain combination of characters does not always correspond to the origination date of the clades (most of the irregular clades are supposed to have originated during the Early Jurassic but are poorly known before the Bajocian). For example, *M. nodoti* (Bathonian) is a basal taxon of Microstomata, although more derived species like *E. microstoma* (Middle Toarcian) have an earlier known stratigraphic

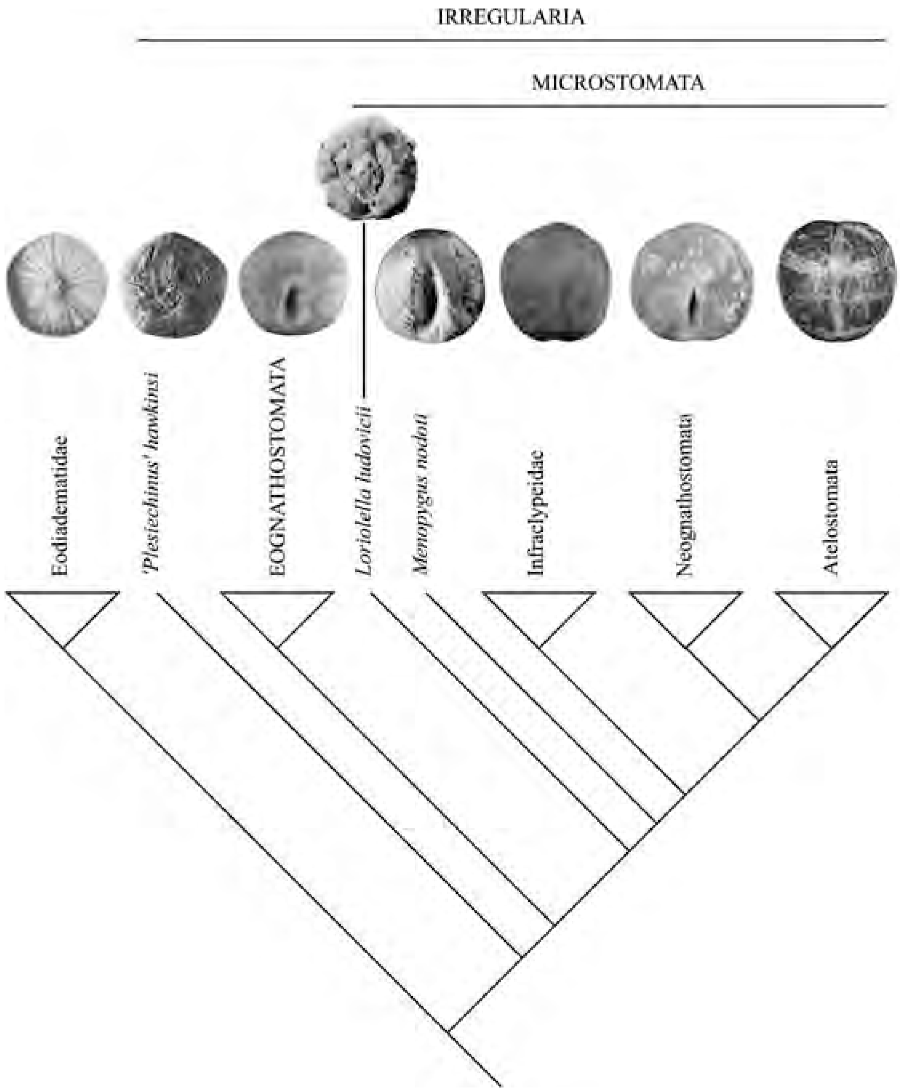

Figure 8. Synthetic representation of the majority rule consensus tree, showing the five main clades of Irregularia. Picture captions from left to right: *Eodiadema minutum*, from Wright, 1855–1860; *'Plesiechinus' hawkinsi,* from Jesionek-Szymanska, 1970; *Pygaster gresslyi*, Votat private collection; *Loriolella ludovicii*, from Smith & Anzalone, 2000; *Menopygus nodoti*, from Rose & Olver, 1988; *Infraclypeus thalebensis*, Clavel private collection; *Centropygus petitclerci*, Claude Bernard University; *Pygomalus analis*, from B. Martin-Garin, unpub. M.Sc. thesis, Univ. Dijon, 2000.

origination. Another example is the basal taxon of Neognathostomata*, Hyboclypus caudatus* Wright, 1851 (Bajocian–Bathonian), which is younger than more derived Neognathostomata such as *G. agariciformis* (Upper Toarcian–Bathonian) or *C. petitclerci* (Upper Aalenian).

4. Taxonomic implications

The present phylogenetic analysis corroborates the monophyly of the Irregularia as well as the other higher taxonomic groupings established by Smith (1984), namely the superorders Eognathostomata and Microstomata, and the series Neognathostomata and Atelostomata (Fig. 8). The analysis also supports the paraphyly of the family 'Galeropygidae' already suspected by previous authors (Kier, 1962; Mintz, 1968). Unlike those of previous workers (Durham & Melville, 1957; Melville, 1961; Fell, 1966), our results suggest the paraphyly of the order 'Pygasteroida'. We also consider the family Menopygidae as a paraphyletic grouping (as opposed to the classifications of Lambert & Thiéry (1911), Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) and Rose & Olver (1988)). All these changes have implications for the way in which we classify sea urchins. We have chosen herein to make reference to PhyloCode principles in the designation of taxa (De Queiroz & Gauthier, 1990, 1992, 1994, among many others), and to rely on stem-based diagnoses of the form, 'the most inclusive clade containing one or more component taxa but excluding others'. PhyloCode designations are restricted to the six main clades discussed above, all being retained in the strict consensus of the 156 trees. The PhyloCode is designed so that it can be used concurrently with the rank-based codes (Cantino & De Queiroz, 2004), and PhyloCode designations do not invalidate publication criteria as presently established for traditional systematics. As the PhyloCode has not gained universal acceptance for the time being, we have decided herein to give traditional taxonomic designations as well.

PhyloCode designation:
Irregularia [P] Latreille, 1825 (converted clade name)

Diagnosis. The largest monophyletic group containing '*P.' hawkinsi* Jesionek-Szymanska, 1970 but excluding *E. minutum* (Buckman, 1845) *in* Strickland & Buckman, 1845.

Traditional taxonomic designation:
Cohort Irregularia Latreille, 1825 *sensu* Smith, 1981
Remarks. Smith (1984) included *E. minutum* in a new family, the Eodiadematidae, which he considered the first representative of the Irregularia. Members of the Eodiadematidae possess the diamond-shaped teeth of Irregularia, but do not share the other synapomorphies of the clade (that is, the relatively large size of the periproct and the specialization in size and number of spines). We restrict herein the usage of Irregularia to preserve traditional usage, and to hone the description of the group to include those forms that have numerous miniaturized spines and a relatively large periproct. However, we recognize the close affinity between Eodiadematidae and Irregularia. Eodiadematidae certainly constitute the stem group of Irregularia, but are not considered as their first representatives (Fig. 8). Therefore, we do not include *E. minutum* and the family Eodiadematidae within the Irregularia. A consequence of the origin of the Irregularia from a common ancestor with the Eodiadematidae is that 'regular' echinoids do not form a natural grouping, but a paraphyletic stem group for Irregularia. The common term 'regular' remains convenient to designate non-irregular echinoids, but as a taxonomic concept, it is bankrupt.

The basal and oldest known representative of the Irregularia is '*P.' hawkinsi*. This species already has the specialized spines and an overall morphology close to the Eognathostomata and to the species arranged under the generic names *Plesiechinus* and *Pygaster*. '*P.' hawkinsi* is plesiomorphic for characters that concern phyllodes and the structure of the apical system. In contrast, the second oldest known irregular species, *L. ludovicii*, displays large interambulacral spines but specialized phyllodes and a more derived apical structure than '*P.' hawkinsi*. This suggests that the very first irregulars, which radiated during the Early Jurassic, should display a mosaic of plesiomorphic and apomorphic features. As demonstrated by Smith (1978*b*) and Smith & Anzalone (2000), this mosaic depends on the relative degree of specialization of first irregulars for both deposit feeding (*L. ludovicii*) and an infaunal life-style ('*P.' hawkinsi*).

Contrary to Lambert's description (1931, 1937), *A. jeanneti* possesses no synapomorphies with the Irregularia and nothing to justify maintaining it within that clade.

PhyloCode designation:
Eognathostomata [P] Smith, 1981 (converted clade name)

Diagnosis. The largest monophyletic group containing *P. ornatus* (Buckman, 1845) *in* Strickland & Buckman, 1845, but excluding *L. ludovicii* (Meneghini, 1867).

Traditional taxonomic designation:
Superorder Eognathostomata Smith, 1981

Remarks. Because '*P.' hawkinsi* is the basal taxon of the Irregularia, the genus *Plesiechinus* is *de facto* paraphyletic. Consequently, the order Pygasteroida justified by Durham & Melville (1957) and Melville (1961), and including the genera *Plesiechinus*, *Pygaster,* and *Pileus*, is also paraphyletic. Moreover, the clade formed by *P. gresslyi*, *Pileus hemisphaericus* and *Holectypus depressus* (Leske, 1778) makes Pygasteroida paraphyletic as well. However, a more detailed analysis at a lower taxonomic level is needed to determine the precise position of the species within the genera *Plesiechinus*, *Pygaster* and *Pileus*. Concerning 'pygasteroid-like' species, this could lead to the partial abandonment of the generic name *Plesiechinus* in favor of the name *Pygaster*. In this case, the name *Plesiechinus* would be maintained only for the species '*P.' hawkinsi,* as already suggested by Smith (http://www.nhm.ac.uk/palaeontology/echinoids/).

PhyloCode designation:
Microstomata [P] Smith, 1984 (converted clade name)

Diagnosis. The largest monophyletic group containing *L. ludovicii* (Meneghini, 1867) but excluding *P. ornatus* (Buckman *in* Strickland & Buckman, 1845).

Traditional taxonomic designation:
Superorder Microstomata Smith, 1984

Remarks. We include *L. ludovicii* in the Microstomata, of which it represents the earliest form. *M. nodoti* and the clade formed by other menopygids are included in the Microstomata as well, and form a paraphyletic basal grouping. The crowngroup of the Microstomata is subdivided into two sister groups formed by the Neognathostomata and the Atelostomata (Fig. 8).

PhyloCode designation:
Infraclypeidae [P] (new clade name)

Diagnosis. The largest monophyletic group containing both *Infraclypeus thalebensis* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891 and *P. guerangeri*

(Cotteau, 1862) but excluding *H. caudatus* Wright, 1851.

Traditional taxonomic designation:
Family Infraclypeidae, new family

Type genus: *Infraclypeus* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891

Other genera included: *Pyrinodia* Pomel, 1883, *Desorella* Cotteau, 1855 and *Pachyclypus* Desor, 1858

Diagnosis. Microstomata with an exocyclic apical system and that do not possess specialized ambulacral plates and pores adorally, that is to say, without differentiated phyllodes.

Remarks. The former Menopygidae here constitutes a paraphyletic grouping, and its diagnosis must be changed. *Menopygus* displays a more derived tuberculation and apical structure than *Loriolella*, but does not have synapomorphies with other 'menopygids'. In the present analysis, four menopygids form a clade supported by homoplastic characters, but excluding *M. nodoti* (Fig. 8). As *Menopygus* was the type genus of the former family Menopygidae, we are forced to provide a new name for the 'menopygids' of Clade 4. We propose the most derived genus of the clade, and its type species *I. thalebensis*, as the source for that name, and call the new clade the Infraclypeidae [P].

PhyloCode designation:
Neognathostomata [P] Smith, 1981 (converted clade name)

Diagnosis. The largest monophyletic group containing *H. caudatus* Wright, 1851 but excluding *O. ebrayi* (Cotteau, 1874) *in* Gotteau, Péron & Gauthier, 1873–1891.

Traditional taxonomic designation:
Series Neognathostomata Smith, 1981

Remarks. The Galeropygidae is a paraphyletic grouping and constitutes the stem group of Cassiduloida. 'Galeropygoids' share the plesiomorphic character states of Neognathostomata, such as the absence of bourrelets, and differ fundamentally from basal Atelostomata only by a non-disjunct apical system. In particular, the species *H. caudatus* and *O. ebrayi* (a basal atelostomate) are very similar except for the disjunction of the apical system. This close affinity between certain basal Neognathostomata and basal Atelostomata explains why both clades are more weakly supported (Bremer support = 1, Fig. 6) than the other clades defined herein (Fig. 8). However, basal Neognathostomata and basal Atelostomata are distinguished by a non-homoplastic, unequivocal character dealing with apical structure (disjunction of the apical system) and no confusion is possible. Therefore, phylocode designations are proposed herein for the monophyletic groups Atelostomata and Neognathostomata.

PhyloCode designation:
Atelostomata [P] Zittel, 1879 (converted clade name)

Diagnosis. The largest monophyletic group containing *O. ebrayi* (Cotteau, 1874) *in* Gotteau, Péron & Gauthier, 1873–1891, but excluding *H. caudatus* Wright, 1851.

Traditional taxonomic designation:
Series Atelostomata Zittel, 1879 *sensu* Smith, 1981

Remarks. The Disasteroida is the only representative of the Atelostomata in the Jurassic. It constitutes the stem group of Holasteroida and Spatangoida, which necessarily makes the Disasteroida in the original sense paraphyletic. Within the 'disasteroids', our results do not support the monophyly of Pygorhytidae, Collyritidae and Tithoniidae.

5. Discussion

5.a. Exocyclism and irregularity

Results of our analysis reinforce Smith's conclusions (1981, 1984) concerning the monophyly of Irregularia and the phylogenetic interrelationships existing between the main groups of irregular echinoids (Fig. 8). Moreover, our results permit better assessment and placement of the evolutionary events at the origins of the principal subsets of irregular echinoids, particularly concerning the evolution of apical structures. Therefore, it can be established from the eccentric position of the periproct within the apical circle that the migration of the periproct out of the apical system started at the outset of the origins of the group (in '*P.*' *hawkinsi*). However, the complete separation between the periproct and the rest of the apical system (= true exocyclism) occurred several times independently, at different times, following different morphological patterns within the different irregular clades as early as the Early Jurassic (in Eognathostomata) and as late as the Late Jurassic (in Microstomata). Therefore, irregularity and exocyclism are not perfectly synonymous terms (Jesionek-Szymanska, 1959; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966), and true exocyclism cannot be considered an apomorphy of Irregularia to the exclusion of all 'regular' endocyclic echinoids. Irregularity must be defined by characters of the corona as well, namely the high density and small size of tubercles and spines, and not only by characters of the apical system. The appearance of irregularity is a unique event, accompanied by changes in both the corona and the apical system, whereas exocyclism has occurred independently along several lineages, and does not serve to characterize any single clade. This interpretation relies explicitly on the distribution of evolutionary events in a phylogeny, using several features to support each node instead of relying on the more classical idea of using a single, sometimes superficial feature to describe a large and complex taxonomic assemblage.

5.b. Adaptation and homoplasy

The evolution of the first irregular echinoids was achieved through important morphological changes concerning both external and internal features and plate architecture. The external features concerned were spines, tubercles, ambulacral pores (phyllodes and petals) and the periproct, and internal features include the Aristotle's lantern. These features are related to the biological functions of locomotion, nutrition and breathing, and their evolution is controlled by phylogenetic constraints. Adaptive characters are sometimes associated with high levels of homoplasy in irregular echinoids (Suter, 1994; Villier *et al.* 2004). However, our results would show that most of these 'adaptive' characters provide an excellent phylogenetic signal when they are not coded as superficial similarities, but as features that are analysed with phylogenetic definitions of homology firmly in mind. Specialization of the Aristotle's lantern, spines, tubercles and phyllodes constitute apomorphies for the different taxa, and even for the entire Irregularia. The phylogenetic signal yielded by these characters stresses the importance of the environmental context of the origin and diversification of irregular echinoids. The palaeoenvironmental context of the appearance of irregular echinoids is the colonization of new habitats that forced a rapid diversification of the group during the Early Jurassic (Kier, 1974, 1982; Smith, 1978*b*, 1984). Smith (1981) interpreted the reduction in size and the increase in number of spines and tubercles as an adaptation of the first irregular echinoids to locomotion in soft bottom environments and to an infaunal life-style (Smith, 1984). According to Rose & Olver (1984), this is a first step in the specialization of irregular echinoids, and it allows determination of a morphological and stratigraphic boundary between regularity and irregularity.

Smith & Anzalone (2000) showed that the first known Microstomata, *L. ludovicii*, retained large primary interambulacral tubercles and spines. This constitutes evidence of an epifaunal life-style. However, *L. ludovicii* had already adopted a deposit-feeding habit (small peristome, atrophy of the Aristotle's lantern and specialization of ambulacral pores adorally). In contrast, the Eognathostomata retained the lantern to collect the organic component of particles at the surface of the sediment in spite of the fact that they could have lived buried in the sediment (Smith, 1978*b*, 1984). Therefore, in Microstomata, it seems that there has been a rapid and early specialization to deposit-feeding before the appearance of an infaunal or semi-infaunal behaviour. As early as the end of the Liassic, the Microstomata (e.g. *Galeropygus*) possessed specialized tubercles (with asymmetric areoles), a bilateral symmetry of the test, and prominent phyllodes. These characters are adaptations for burrowing (Kier, 1974; Smith, 1978*b*, 1984) and show that at that time, unlike the Eognathostomata, the Microstomata no longer lived semi-epifaunally. Therefore, the two main clades of the Irregularia, the Eognathostomata and the Microstomata, adopted two different strategies in the adaptation to new ecological niches. This explains why adaptative characters are phylogenetically informative in separating the clades.

Periproct migration has an adaptative significance as well. It has been constrained, initiated or fostered by environmental factors (Smith, 1984). However, it accompanies disruptions of apical structures that are developmentally (David, 1990) or epigenetically controlled. This is true only for (1) the whole clade of the Irregularia, characterized by a stretching of posterior oculars and genital 5 in basal taxa, and for (2) basal Atelostomata, distinguished by the disjunction of the apical system into a bivium and a trivium. However, all other characters showed numerous homoplastic changes and illustrate an iterative evolutionary scheme within main irregular clades. For example, vertical orientation of the periproct occurred five times, and the appearance of supplementary plates, the disappearance (atrophy) of genital 5 and exocyclism was realized independently in almost all of the main clades. Unlike Suter's work (1994) on Cassiduloida, this high level of homoplasy cannot be directly interpreted as a result of adaptation to the external environment. This instead suggests invocation of a 'structuralist' explanation, namely internal constraints that limit the disparity of apical structures, as advocated by Rieppel (1989). These constraints may derive from the conservative morphogenetic processes and hierarchical structure of ontogenetic processes (Rieppel, 1989), that is, epigenesis. To sum up, the evolution of the first irregular echinoids (evolution of plate, lantern and appendage features) illustrates the interplay between functionalist (external) and structuralist (internal) factors (Wake, 1989).

5.c. The Extraxial–Axial Theory

The reduction of extraxial body wall and the correlated increase in axial body wall is a general pattern in echinoderm evolution, and particularly in echinoids in which the extraxial region is extremely reduced (David & Mooi, 1996, 1998). In irregular echinoids, the restructuring of the extraxial region (periproct and genital plates), delimited by the axial corona, is realized through a secondary and temporary development of the extraxial part of the body wall within the apical system. It is realized either by the significant increase in periproct size in the Eognathostomata and early Microstomata such as *L. ludovicii* (Smith & Anzalone, 2000), or by the pronounced development of supplementary plates in the Microstomata. However, once the periproct has moved down interambulacrum 5 and becomes separated from the apical system, the extraxial component is again reduced. Therefore, the evolution of the apical system of the first irregular echinoids is realized through a temporary (Early and Middle Jurassic) change in the ratio between the extraxial and the axial components of the body wall. This is yet another example of the fact that the interaction of the two major components of the body wall of echinoderms plays an integral role even in those forms in which the extraxial component is the most reduced: the echinoids.

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