Changes in radula and jaw during life stages of *Eucobresia diaphana* (Draparnaud, 1805) (Gastropoda, Pulmonata, Vitrinidae)

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For a better understanding of the changing feeding pattern of *Eucobresia diaphana* (Draparnaud, 1805) during its life cycle, the radula and jaw of juvenile and adult specimens were studied by using scanning electron microscopy. The feeding pattern was observed during fieldwork and in an experimental setting.

The radula and jaw of adult *E. diaphana* resemble the descriptions and figures given in the literature. The most striking characteristics of the juvenile radulae, apart from the smaller number of teeth and rows and their small size, are (1) the slow development of the central teeth, (2) the varied shape of the laterals and (3) the irregular number of cones and cusps on those laterals. In juvenile specimens, the median projection of the jaw still consists of two parts. After the summer season, the jaw and radula are fully grown. The changes during the maturation are illustrated and discussed. Adult *Eucobresia diaphana* appear to be omnivorous, whereas juvenile specimens have a more herbivorous feeding pattern. The juvenile teeth may also have a special function during hatching.

Key words: Vitrinidae, *Eucobresia diaphana*, radula, jaw, shells, feeding pattern, life cycle, Netherlands.

Introduction

In The Netherlands, *Eucobresia diaphana* (Draparnaud, 1805) has been found in the region of Nijmegen, at a few locations in the southern part of the province of Limburg and in both the national park 'De Biesbosch' and the national landscape 'Het Groene Woud' in the province of Noord-Brabant (Arends & Pouderoyen, 1957; Gittenberger et al., 1984; Bruyne et al., 2003; Margry & Boesveld, 2009; Margry, 2013). Since the first record of *E. diaphana* in Het Groene Woud (Margry & Van Roessel, 2004), several aspects of the biology and ecology of this species have been studied. On 8.i.2009 a clutch of eggs was found and observed during the days that followed. After the hatching of the first eggs on 29.i.2009, the development of the snails was followed till the last juvenile died on 6.iv.2009. The juveniles lived on wet particles of sand and loam with remains of the eggs, moss, algae, fungal hyphae and nematodes. It could not be determined which parts of these potential foods were eaten.

Vitrinid snails may be herbivorous, omnivorous or carnivorous (Hesse, 1923: 7; Dorsman & De Wilde, 1929: 73; Barker, 2004: 309). In Gastropoda, the feeding pattern is reflected in the appearance of the radula and jaw (Solem, 1974; Hausdorf, 1998; Barker, 2001; 2004). The jaw of *E. diaphana* is

oxygnathic, with a median projection in the cutting edge (Hesse, 1923: 14; Van Benthem Jutting, 1933: 272; Ehrmann, 1956: 11; Barker, 2004: 307). Wiegmann gave a length of 0.98 mm (Hesse, 1923: 14). In *Eucobresia* Baker, 1929, the radula is dichoglossan (Giusti et al., 2011: 352). Most descriptions of the radula of *E. diaphana* are based on the unpublished "Sämtliche Manuskripte über die Vitrinen" from F. Wiegmann, with about 500 to 600 figures with accompanying text about the anatomy of Vitrinidae (Eckardt, 1914; Wagner, 1915; Hesse, 1923). Eckardt (1914) found more transverse rows than Hesse (1923), and Wagner (1915) regarded the bicuspid transitional teeth as marginals. Other numbers of radula elements are all about the same. Only Eckardt (1914) also studied two specimens himself (Table 1). The tricuspid central tooth has a mesocone and two equal ectocones, the ca. 11 tricuspid lateral teeth have an elongated mesocone, one narrow endocone and a smaller ectocone, two transitional bicuspid laterals have no endocones but a – sometimes hardly visible – ectocone, and the ca. 23 marginals are monocuspid and become gradually smaller close to the edge (Eckardt, 1914; Hesse, 1923).

Figures of the teeth of *E. diaphana* are shown in Eckardt (1914: 271, 274) and Wagner (1915: pl. 13 fig. 107). Those figures are largely based on the manuscript of Wiegmann. According to Hesse (1923: 88), Wagner (1915) however made inaccurate copies of Wiegmann's drawings.

Eckardt (1914: 270) concluded, that the number of teeth and rows is variable within the species and depending on maturity. He emphasized that, for the study of the radula, adult animals should be taken. He furthermore mentioned that in radulae of juvenile Vitrinidae (cf. *Vitrina pellucida* (Müller, 1774)) of just a few days before hatching, already 15 rows of teeth could be found.

In this study different life stages of the radula and jaw of *E. diaphana* are compared to their shells and literature. The findings are related to observations on the food taken.

Methods

All life stages of this species were collected in the Scheeken, a wet poplar forest in the municipality of Best, The Netherlands, in the national landscape Het Groene Woud (51°32′ N - 05°23′ E). All specimens were conserved in the freezer. From adult specimens besides the radula and the jaw, the shell and the genital tract were preserved most of the times as well.

To achieve juvenile specimens, clutches of eggs were collected and kept in the refrigerator (5°C); every day their development was observed. Hatched animals were conserved separately in tubes in the freezer. For further study, the shells and jaws were removed and the radulae were extracted with a 10% KOH solution. The age of these snails is

Reference	R3	L3	T2	M1 Bicuspid	M1 monocuspid	Transverse rows	Remarks
Wiegmann, according to Eckardt (1914)	1	11	2		25	92-103	
Wiegmann, according to Wagner, (1915)	1	10		2	20-23		
Wiegmann, according to Hesse (1923)	1	11	2		25	79-95	Length of crown is 0.0312 mm Length of Jaw is 0.98 mm
Specimen Inselsberg (Eckardt, 1914: 270)	1	9	2		23-24	71	
Specimen Inselsberg (Eckardt, 1914: 270)	1	8	2		22	73	

Table 1. Number of teeth and rows of the radula of *Eucobresia diaphana* according to several authors, allegedly after the manuscript of Wiegmann and for the two specimens studied by Eckardt (1914).

R3 = tricuspid central tooth (rachis), L3 = tricuspid lateral teeth, T2 = transitional bicuspid lateral, M1 = marginals.

Number of specimen (+ part of radula concerned in detail)	Age [assumed age]	collecting date	Shell mm	Jaw mm	R3 µm	L3 number	L3 µm	Djuv	T2 number	M1 number	Transverse rows	Longitudal rows	Figure		
													Radula	Jaw	shell
20110102.1.1h (anterior part)	1 day	-	-	-	5	0	10	4-5	-	-	30-	9-11	1, 2	-	-
20110102.1.1h (posterior part)	1 day	-	-	-	5	3	10	5-6	-	-	-	17-19	1, 3	-	-
20110102.1.1g (anterior part)	1 day	-	0.95	-	0-11	0	12	4	-	-	-	6-	-	-	-
20100225.1.1k (anterior part)	3 days	-	-	-	10	1-2	10	4-5	-	-	35-	11-15	4	-	-
20100225.1.1k (posterior part)	3 days	-	-	-	10	3-4	11	4-5	-	-	-	15-19	-	-	-
20110226.1	[3 days]	26.ii.2011	1.22	-	11	1-2	11	4-5	-	-	-	11-15	5	-	-
20100225.1.1e	2 weeks	-	1.17	0.20	12	2-3	12	5-6	-	-	-	15-17	6	14	-
20090423.1b	[2 months]	23.iv.2009	1.34	-	13	6	13	2	4-	-	-	25-	-	-	-
20090423.1c	[2 months]	23.iv.2009	1.41	-	14	6	14	1	3	?	-	21-	7	-	-
20120614.1A.1b	[4 months]	14.vi.2012	2.37	0.42	18	7-8	18	1	2	?	-	21-	-	15	17, 18
20120614.1e	[4 months]	14.vi.2012	2.67	0.44	18	7-8	18	1	1	12-	-	43-	8	-	-
20120614.1A.1a	[5 months]	14.vi.2012	3.19	0.52	20	7-8	20	1	1	10-	-	39-	-	-	-
20120813.1B.1b	[6 months]	13.viii.2012	2.82	0.47	-	8-9	-	1	1	14-	-	49-	-	16	-
20081009.1A.1b	[9 months]	9.x.2008	5.47	0.85	24	11	26	-	1-2	20	62-	65-67	13	-	-
20081106.1B.1b	[10 months]	6.xi.2008	6.77	0.84	-	-	-	-	-	-	-	-	-	-	-
20081106.1C.1a	[10 months]	6.xi.2008	7.12	0.82	-	-	-	-	-	-	-	-	-	-	-
20081119.1.1a	[10 months]	19.xi.2008	7.88	-	24	12	26	-	1-2	20	47-	67-69	9-12	-	-
20090108.1A.1b	[11 months]	8.i.2009	6.35	0.95	-	-	-	-	-	-	-	-	-	-	-

Table 2. Specimens of *Eucobresia diaphana* in assumed order of their age with details on age, date of collecting, measurements of shells, teeth and jaws, number of teeth and rows and corresponding figures. 10- = at least 10, R3 = central tooth, L3 = laterals, T2 = transitional teeth, M1 = marginals, Djuv = deviating juvenile teeth. The age is given in days and weeks. If the age is estimated on the basis of the date of collecting, it is given between brackets.

known and given in days and weeks. The age of the other animals had to be estimated and is indicated between brackets.

Photos are made with a Jeol JSM-7600 F Field Emission Scanning Electron Microscope. Shells, radulae, jaws and alcohol material of the genital tract are kept in the collection of the author. Measurements of the shells were taken with a calliper to the nearest 0.1 mm. Measurements of the jaws and teeth are taken from the photos.

For the study of the feeding pattern, animals were observed during fieldwork. Also specimens were kept in tubes together with earthworms (Oligochaeta) and, once, with a part of an unidentified slug, and studied during several days. From a few stomachs the contents were studied.

The terminology is in conformity with Solem (1973, 1974) and Barker (2004). Anterior and posterior is limited to the ends of the radula. Juvenile teeth on both sides of the central teeth are called laterals, without indicating to what extent those teeth are homologous with the adult laterals.

Results

Radula and jaw.— In Table 2 the details of the specimens are given in assumed order of their age.

The radulae of juvenile specimens of one day old have a bi- or tricuspid central tooth, with all cusps almost equally large or the start of a longer mesocone . In the first developed, thus oldest row on the anterior part of the radula on each side of the central tooth only four or five teeth are present. These teeth have an irregular number of cusps and cones or are, more to the edge, just a plate without any cusp. In the posterior part, all cusps of the central tooth are larger than in the oldest rows but still smaller than the other teeth on both sides. In these rows a few laterals already have the adult form. The other teeth towards the edge have more cusps, are triangular with a few gradually diminishing cusps, have one elongated cone, or are rectangular plates only. The crown of the elongated cusp of the innermost lateral teeth in the 14th row measures about 11 μm (Figs. 1-3)

In the radula of the three days old snail the central teeth in the anterior part have a mesocone, which is about as long as the mesocone of the laterals (Figs. 4, 5). In these transverse rows only two laterals with an adult appearance are present. About thirty transverse rows to the posterior end, already three laterals have this form. In this radula in total about 35 transverse rows could be counted. The crown of the elongated cusps of the central tooth and the adjacent laterals on the anterior part measure about 10 μm and 11 μm, respectively.

In the radula of the two weeks old juvenile the central teeth and the laterals have the same appearance as in the radula of the three days old specimen. The crown of the elongated cusp of both the central tooth and the adjacent lateral measures about 12 - 13 μm (Fig. 6).

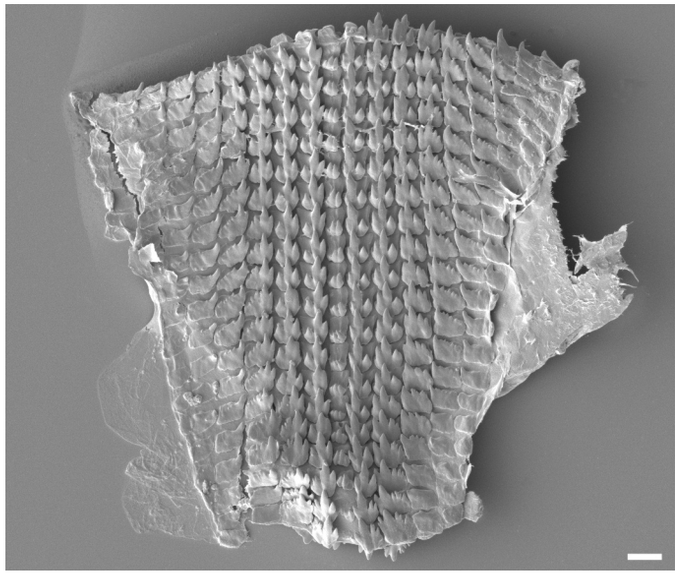
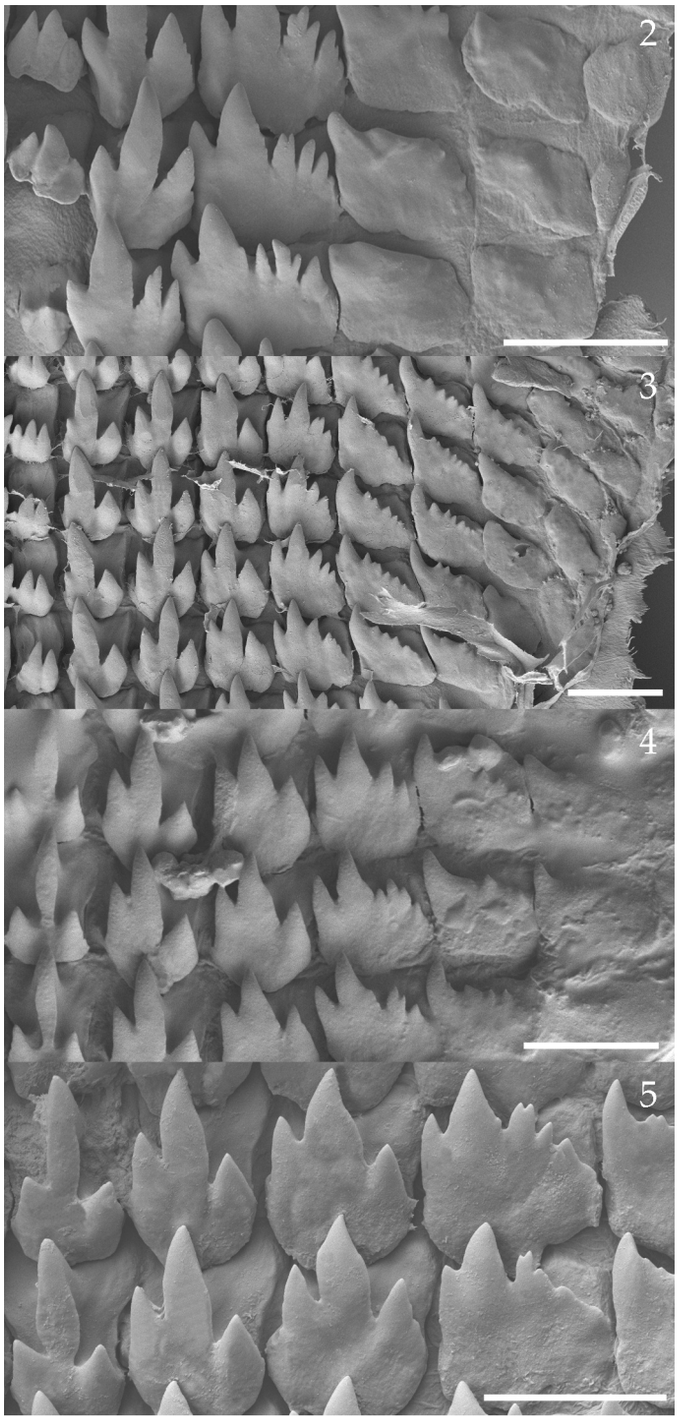
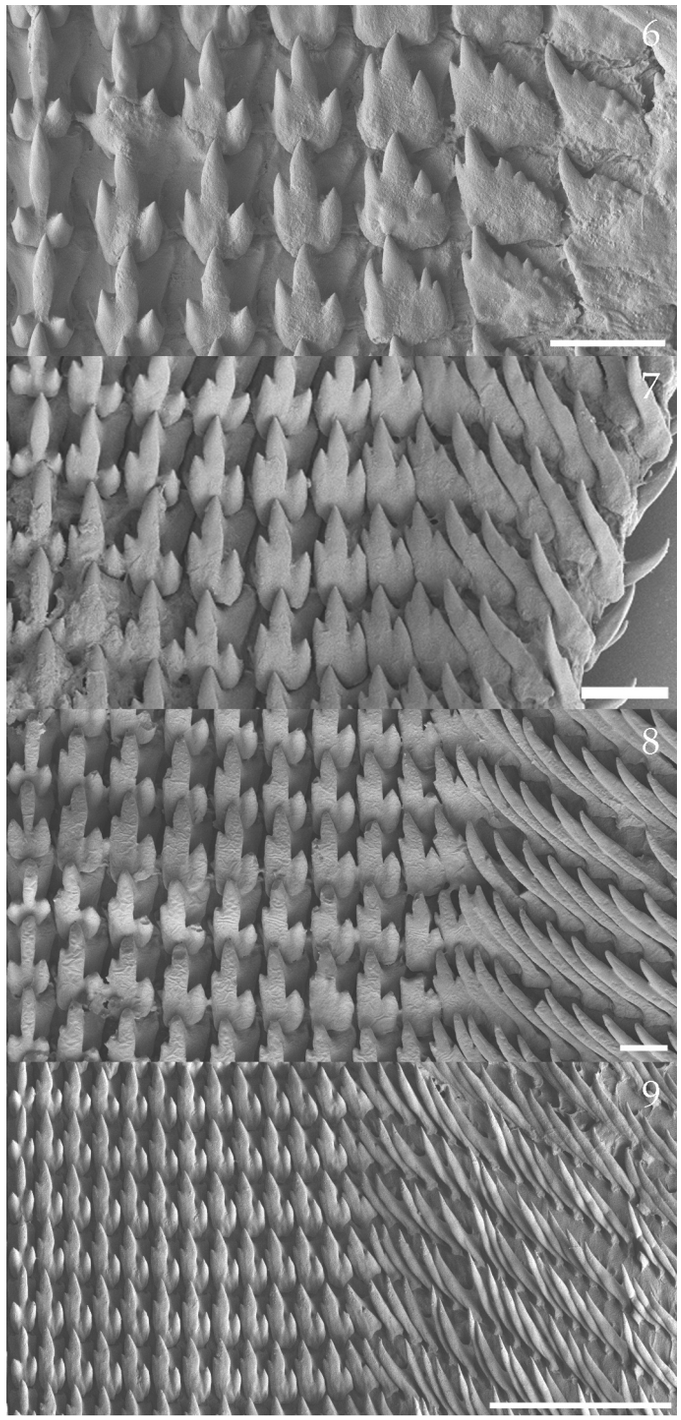


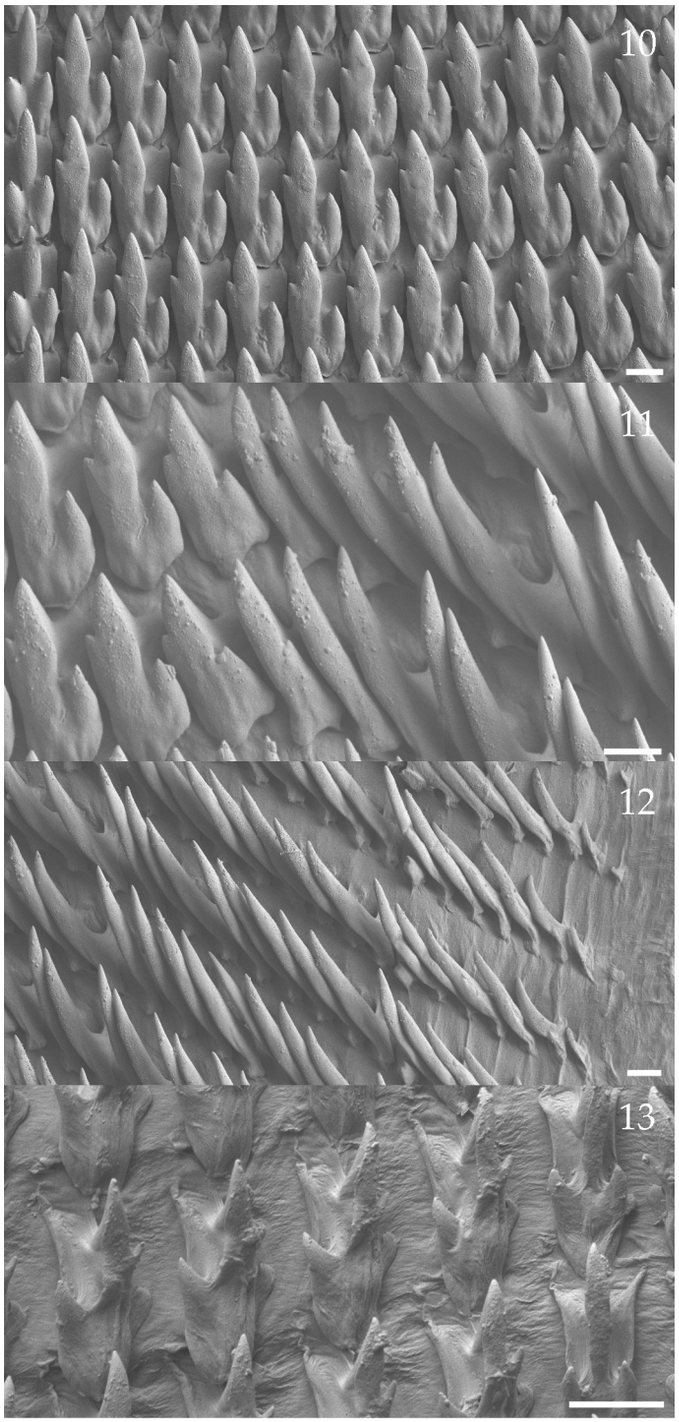
Fig. 1. Complete radula of an one day old individual (20110102.1.1h) of *Eucobresia diaphana.* Scale bar 10 μm.

Figs 2-9. Radulae of *Eucobresia diaphana*. **2**, anterior part (one day old); **3**, posterior part (one day old); **4**, anterior part (three days old, 20100225.1.1k); **5**, central part (February, about three days old, 20110226.1); **6**, central part (two weeks old, 20100225.1.1e); **7**, central part (April, about two months old, 20090423.1c); **8**, central part (June, about four months old, 20120614.1e); **9**, central part (November, about ten months old, 20081119.1.1a). Scale bars 10 μm (Figs 2-8), 100 μm (Fig. 9).





MARGRY, C.J.P.J. – Radula and jaw of *Eucobresia diaphana*



During the first months of their life, the deviating juvenile teeth in the new transverse rows more and more get the appearance of the adult lateral teeth. The last deviating teeth seem to change gradually in bicuspid teeth while the number of marginals is increasing. In older specimens only two bicuspid teeth remain and the number of marginals comes to its maximum (Figs. 7,8).

The radula of both adult specimens have a central tooth with an elongated mesocone and two smaller ectocones. The ca. eleven lateral teeth have an elongated mesocone, a large ectocone, and a longer, but narrow endocone. One or two transitional lateral teeth have a more or less narrow ectocone and sometimes a very small endocone as well. The ca. 20 marginals only have one elongated mesocone. Towards the outer edge of the row these marginals become gradually smaller (Figs. 9-12). On the posterior end of the radula the teeth are not fully developed (Fig. 13), whereas they are worn on the anterior end. In the centre of the radula the crown of the mesocone of the central tooth and the adjacent lateral tooth measure about 24 μm and 26 μm respectively.

From the jaw of the specimen of two weeks old the median projection still consists of two parts (Fig. 14). In somewhat older jaws the fusion of these two parts is almost complete (Fig. 15). In fully grown jaws no separate parts can be seen (Fig. 16).

Radula, jaws and shells. — The protoconch from juveniles from one day old has three quarters or almost one whorl with a microsculpture of irregular rows of pits, which enter the nucleus. In June the shell has 1.5 whorls (Fig. 17, 18). In August, when the radula is almost completed, the shell has 1.7 to 2 whorls. A specimen collected 9.x.2008, thus about nine months old, with a complete radula, has a shell with 2.2 whorls.

Feeding pattern.— During fieldwork on 21.i.2010 one adult specimen was observed eating from cow manure (*Bos*

Figs 10-13. Radulae of *Eucobresia diaphana*. **10-12**, November, about ten months old (20081119.1.1a). **10**, detail of central teeth; **11**, detail of transitional teeth; **12**, detail of lateral teeth; **13**, almost mature teeth on the posterior part (October, 20081009.1A.1b). Scale bars 10 μm.

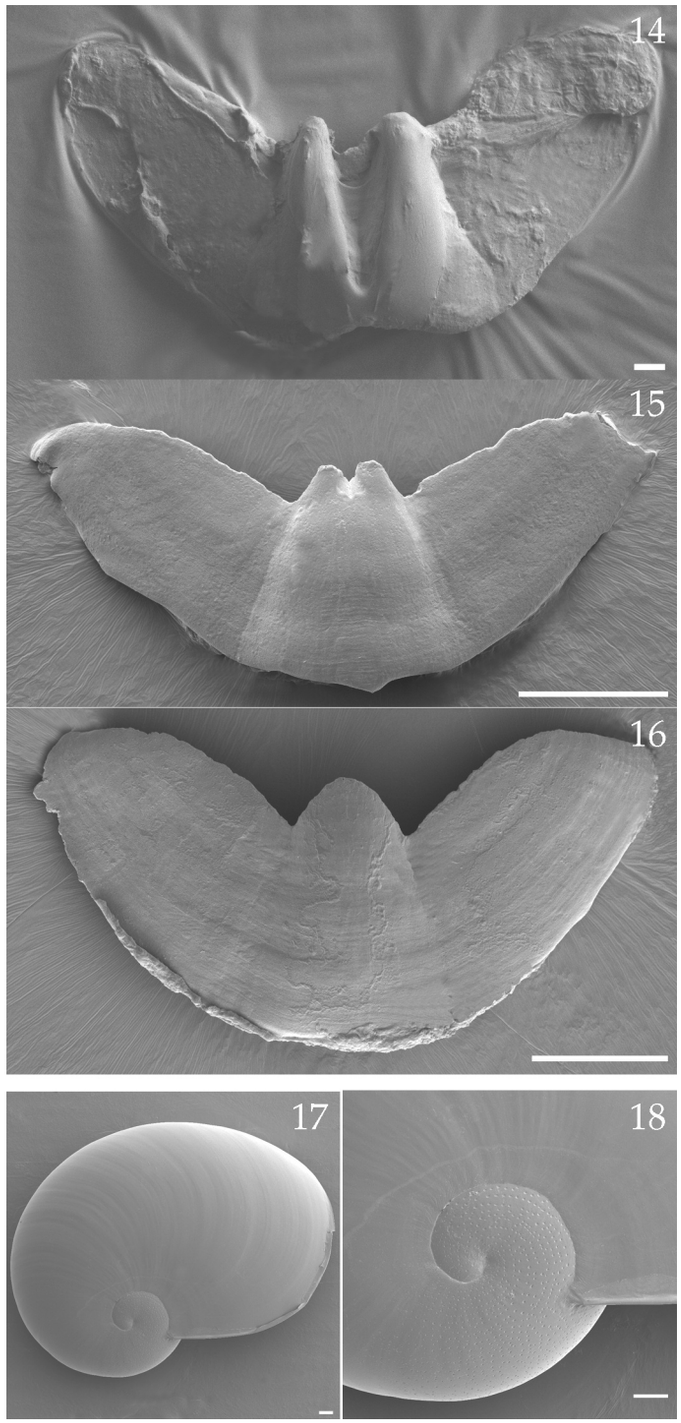
taurus Linnaeus, 1758 cv. Aberdeen Angus). On 4.ii.2010 an adult specimen was feeding on a dropping, which is typical for Microtidae (Diepenbeek, 1999) (Fig. 19). On 4.xii.2011 an adult was feeding on the remnants of an unidentified mushroom. On 28.ii.2009 a juvenile was found with a green content in the stomach visible through the skin. During a photo session on 28.xii.2011 an adult snail could be followed while gnawing on the petiole of a poplar leave (Fig. 20). During feeding, the tentacles are almost completely withdrawn and the jaw can be seen moving.

In dissected adults, collected 28.xii.2008 and 25.i.2009, green parts were found in the stomach. In this part of the season only green moss is available. In adults from 19.ii.2008 and 8.i.2009 no green parts could be found in the stomach or intestine. The stomach from an adult from 25.i.2009 contains a little green particle and several empty eggs, which according to their form and surface look very similar to the eggs from *E. diaphana*.

One adult from 8.i.2009 was kept in a tube together with three juvenile earthworms. After a few days, only two worms were present. It is not known if the third worm was eaten dead or alive. One adult from 21.i.2010 was kept with a live juvenile earthworm. The next day the worm was split into two parts, both of which still moving. One day later, both parts were eaten. Another adult from that date eat a dead earthworm and an adult from 4.ii.2010 ate a part of a dead slug.

Discussion and conclusions

The radulae of the adult specimens closely resemble those figured and described by Eckardt (1914), Wagner (1915) and Hesse (1923). Eckardt found less lateral teeth and the specimens from the Scheeken have less marginal teeth, but those



Figs 14-18. Jaw and shell of *Eucobresia diaphana*. **14-16**, dorsal side of jaw. **14**, two weeks old (20100225.1.1.e); **15**, about four months old (June, 20120614.1A.1b); **16**, about six months old (August, 20120813.1B.1b). **17-18**, shell, about four months old (June, 20120614.1A.1b). **17**, dorsal side of shell; **18**, detail of protoconch.
Scale bars 10 μm (Fig. 14), 100 μm (Figs 15-18).

Figs 19-20. Adult *Eucobresia diaphana*. **20**, eating on dropping; **21**, eating from detritus on the petiole of a poplar leave (photographs: I. Margry).

differences can be seen as intraspecific variation. The length of the central and adjacent lateral teeth closely match the length which is given by Wiegmann (Hesse, 1923: 18) although it is not certain whether Wiegmann took measurements of the crown or another part of the tooth.

Next to the lower number of teeth and rows and the small size of the teeth, the most striking characteristics of the juvenile radulae are (1) the slow development of the central teeth, (2) the varied shape of the laterals and (3) the irregular number of cones and cusps on those laterals.

Intraspecific variation in the radula related to maturation has been reported before. Hubendick (1945) mentioned de differences between juvenile and adult radulae of *Lymnaea limosa* (L.) (cf. *Radix balthica* Linnaeus, 1758). For *Lehmannia valentiana* (Férussac, 1823) Waldén (1962) described the variation in the number of teeth both in the transverse and the longitudinal rows during post-embryogenesis until the maturity. He also found changes in the form and length of the teeth. Jungbluth et al. (1981) studied 38 species of slugs and argued that the radulae from pulmonates cannot be used as a taxonomical character due to several reasons, including the variability during individual growth. Waldén (1962) and Jungbluth et al. (1981: 22) also described the change during maturation from polydenticular to oligodenticular teeth: the older the animal, the less polydenticular and increasingly more bi- and monocuspid teeth are found. Waldén (1962: 87, fig. 18) demonstrated de teeth of a transverse row of the radula from a juvenile specimen of *Limax tenellus* (Müller, 1774). In this specimen, triangular lateral teeth with elongated cones could be recognised.

Solem (1974) explained the special role of the central tooth in the interlock system. In juvenile *E. diaphana,* the role of the central teeth seems insignificant next to the rather large adjacent teeth. More research on the functioning of the radula is necessary in order to understand the specific role of those central teeth and the delay of their development in juvenile specimens.

In Fig. 13 the final part of maturation of a radula is illustrated. It shows teeth that are not yet fully developed. Those teeth still were in the radula sac for hardening by incorporation of organic compounds and minerals. Barker (2001: 222) described how this process is affected by cells of the upper epithelium. According to Solem (1974) the whole radular ribbon grows forward at a rate of five to six transverse rows per day for browsing and plant eating species, and two rows per day in some carnivores. The total number of transverse rows also depends on the disappearing by wear at the anterior part. In juvenile specimens this will be less than the growth forwards. Only in adults, are the rates of disintegration and formation of the radula in balance (Barker, 2001: 213). *E. diaphana* will probably have a fully mature radula at the end of the July decline, the period of rest as described by Umiński (1983). The snails are about five to six months old

then. The radulae of adult animals from October and November, when the snails are about nine to ten months old, are fully developed. However, the sexual maturity of those snails differs. The albumen gland of the animal collected 9.x.2008, with a shell length of 5.47 mm, is hardly developed and the talon is entirely visible. From the animal collected 19.xi.2008, with a shell length of 7.88 mm (!), the albumen gland is fully developed and the talon totally embedded. Thus, the radula will probably be fully developed already before the maturation of the genitals starts.

The maturation of the jaw occurs simultaneously with that of the radula. In the jaw of a two weeks old juvenile specimen, the two initial plates of the jaw can be identified. In pulmonates the evolution of the jaw directs towards fusion of the jaw plates (Barker 2004: 373). In his study on specimens of *Semilimax pyrenaicus* (A. Férussac, 1821), Bowell (1908: 98) could not find any indication of a bilateral origin, but he most likely studied adult specimens. Hesse (1923: 14) described Vitrinidae with aberrant jaws with a two-piece end on the median projection. This observation is most likely based on immature specimens.

According to Hausdorf (1998) the loss of endo- and ectocones of the marginal teeth can be seen as an adaptation from a pure herbivorous to an omnivorous diet. Carnivory has been linked with various morphological characters, including the reduction or even loss of the central and lateral teeth, elongation of unicuspid, aculeate marginals and a reduction of the jaw (Solem, 1974; Hausdorf, 1998; Barker, 2004). Adult specimens of *E. diaphana* show a typical omnivorous radula with a prominent jaw. In contrast, juvenile specimens lack the carnivorous elements and the jaw is not fully developed. According to Barker (2001: 232), the jaw is less developed when animals graze soft substrates like algae. This would suggest that juvenile specimens of *E. diaphana* are adapted to a herbivorous life. In view of this assumption, it is not surprising that a juvenile was found (28.ii.2009, in the Scheeken) with green contents in the intestine, clearly visible because of the transparency of the body.

Observations in the field and in experiments prove that adult *E. diaphana* is omnivorous, Their feeding on mosses, live and dead earthworms, cow manure and droppings, fits in the general descriptions of food from Vitrinidae (Hesse, 1923: 7; Dorsman & De Wilde, 1929: 73; Frömming, 1954; Ehrmann, 1956; Barker, 2004: 309). Attacking earthworms was only known for *Vitrina pellucida* (O.F. Müller, 1774) (Hesse, 1923; Dorsman & De Wilde, 1929; Frömming, 1954). It could not be confirmed that the ovophagy concerns real cannibalism. The empty eggs in the stomach kept their typical lemon-shaped form, even after investigation with tweezers. In one snail, after gnawing on a petiole, the poplar leave was studied; the gnawed part was missing the soft brown layer, i.e. the decaying part of the leave, which fits with the description of Hesse (1923: 7), who mentioned detritus as a part of the food.

In addition to a role during feeding, the juvenile radula has a special function in hatching. During the observation of eggs in January 2009, the hatching of a specimen of *E. diaphana* could be followed. Inside the egg, the embryo pulled on the wall in order to make an opening. Then, during hatching, the embryo used the radula. Firm teeth with many cusps were helpful and might be a prerequisite in this struggle to the outside world.

For a better understanding of the changes during embryogenesis and maturation of the radulae and jaws of Vitrinidae in general, and *E. diaphana* in particular, more data are needed. This will also be helpful in the study on the hypothesized change in food preferences during the life cycle of these animals. It would also be of great value if the manuscript with all the many figures and notes of F. Wiegmann would become available again.

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