

# Phylogeny, biogeography and systematics

Hans WINKLER

**Abstract:** After a historical overview of woodpecker systematics, a short account of the systematic relationships within the Piciformes and Picidae is given. The honeyguides (Indicatoridae) are the sister group of the woodpeckers (Picidae). Further members of the order are the barbets (Megalaimidae, Lybiidae, Capitonidae), toucans (Ramphastidae), puffbirds (Bucconidae) and jacamars (Galbulidae). Three subfamilies are currently recognized, with the Picinae containing the greatest number of species in five tribes. The Picidae do not occur in the Australo-Papuan region. South East Asia, Northern South America and equatorial Africa form the diversity hotspots of the family. Woodpecker plumage characteristics have misled systematists repeatedly. Molecular methods have uncovered many cases of parallel evolution and begin to help to understand plumage variation due to habitat variables and social mimicry. The new scoring system used in the checklist by del HOYO et al. (2014a) does not account for these facts. The species list presented here thus does not comply with all the changes in this new checklist.

**Key words:** Piciformes, Picidae, phylogeography, taxonomy, species delimitation, HBW checklist.

## A brief history of woodpecker classifications from Aristotle to the 20<sup>th</sup> century

### The beginnings

BRUCE (2003) gave a splendid introduction to the fascinating history of bird classification that also contains a few references to woodpeckers. SIBLEY & AHLQUIST (1972) and MOORE & MIGLIA 2009 discussed the historical development of the systematics of woodpeckers and allies in greater detail.

Aristotle classified all passerines (with the exception of swallows and martins) together with woodpeckers and other smaller birds, but also recognized their special attributes, such as the hard bill. Modern systematics began with the works of Carl Linnaeus or Linné. Three species of woodpeckers appear 1740 in the 2<sup>nd</sup> edition (*Picus niger*, *P. viridis*, *P. varius*) and were placed between the cuckoos (*Cuculus* which also included the wryneck!) and treecreepers (*Certhia*) and the nuthatch (*Sitta*). Toe arrangement, bill shape and climbing behavior seem to have been the criteria for this placement. He maintained the close relationship between woodpeckers and cuckoos even in the 10<sup>th</sup> edition (1758) by putting the latter in the 'Picae' which also contained parrots and hummingbirds. *Picus* followed *Jynx* (wryneck) in the sequence of species.

ILLIGER (1811) listed seven orders of birds, 'Scansores' or climbing birds, 'Ambulatores' or walking birds,

'Raptatores' or birds of prey, 'Rasores' or scratching birds, 'Cursores' or runners, 'Grallatores' or waders, and 'Natatores' or swimming birds. He recognized five families within the 'Scansores': 'Psittacini' (parrots), 'Serrati' (birds with serrated bills, e.g. toucans or trogons), 'Amphiboli' (those with an opposable toe, e.g. puffbirds and cuckoos), 'Sagittilingues' (birds with arrow shaped tongues) and the 'Syndactyli' (birds with stitched together toes, kingfishers, jacamars). The wrynecks and woodpeckers were part of the 'arrow-tongues'. Clearly, morphological features were important for establishing similarities and hence classification. Squabbles about priorities and plagiarism characterize the early 19<sup>th</sup> century as well as attempts to reflect 'divine order' in the classification of organisms (BRUCE 2003). The woodpeckers were grouped together with the passeriform birds in a group named 'Sylvicolae', forest birds, by VIEILLOT (1816). William SWAINSON (1837) listed them after the parrots and before the treecreepers, and presented many figures on foot and bill characters. Within the family Picidae, he recognized the Picinae or true woodpeckers, and the Buccoinae into which he classified the wrynecks and piculets, and *Bucco* and *Oxyrynchus* (now an obsolete name referring to the Sharpbill *Oxyruncus* in the Suboscines). It was GLOGER (1834) who made it clear that woodpeckers and passerine birds should be put into different orders because of the pronounced anatomical differences especially in the syrinx, and *Picus* and *Jynx* appear between cuckoos and the Hoopoe (*Upupa epops*), with *Picus* being divided into tree-living and ant-eating woodpeckers.

By the second half of the 19<sup>th</sup> century knowledge on the anatomy of birds had increased substantially, and collectors around the world sent specimens to the big national museums. In a list based on the holdings of the bird collection of the British Museum by GRAY (1869) jacamars, hoopoes and rollers are still found within the Passeres. The woodpeckers, however were placed by this author far away from those groups in the ‘Scansores’ with the parrots and cuckoos, and also the barbets and toucans (GRAY 1870). Extensive anatomical work spurred several authors to produce new classifications. GARROD (1874) recognized the similarities between the woodpeckers and barbets, but had other coraciiform birds, such as the puffbirds, bee-eaters and jacamars still within the Passeriformes. However, FÜBRINGER (1888) put together the honeyeaters (Indicatoridae), toucans (Ramphastidae) and the woodpeckers in the Pici. On the other side of the Atlantic, Elliot COUES, one of the great American ornithologists of the 19<sup>th</sup> century, had studied the anatomy of woodpeckers quite thoroughly (see BOCK, this volume), placed them between cuckoos and parrots, but did not consider other relationships because of his focus on North American birds (COUES 1884). He listed the Pileated Woodpecker right after the Ivory-billed Woodpecker, but did recognize the considerable differences in toe proportions and arrangement between the genera these species represent. He also grouped the pied woodpeckers together (including *Picoides*), followed by *Melanerpes* and *Sphyrapicus*, and finally *Colaptes*.

At the turn of the 20<sup>th</sup> century Richard B SHARPE undertook to catalogue the then already enormous bird collection of the British Museum, both as author and editor. The Catalogue treats the woodpeckers as part of the ‘Picariae’, not in volume 19 that deals with the ‘Scansores and Coccyges’, and hence the honeyguides, barbets, cuckoos and turacos, and reserved volume 18 solely for the treatment of the woodpecker family as part of the Scansores by HARGITT (1890). This volume lists all the 50 genera recognized at that time and which all were represented at the British Museum. Then, the collection held almost 8000 woodpecker specimens of 385 species and subspecies. Using modern names, the list begins with the African Ground Woodpecker, immediately followed by American *Colaptes* (not including Cuban *ferndinae* positioned between *Dinopium* and *Celeus* in this arrangement of species). Then a mixture of Eurasian *Picus*, *Chrysophlegma*, one species of *Dinopium* (*rafflesi*, the other species of this genus were grouped with *Micropternus* and *Meiglyptes*), American *Piculus* and African *Campethera* continue the list. The pied woodpeckers follow the genera *Melanerpes*, *Sphyrapicus*. Interestingly, the Lesser Spotted Woodpecker is embedded within the smaller American pied

woodpeckers, the Middle Spotted Woodpecker far away from the Great Spotted Woodpecker and close to the Yellow-crowned Woodpecker and *Dendropicos*. HARGITT also seems to have recognized the closer link between *Chrysocolaptes* and *Campephilus*, as well as between *Dryocopus* (*Mulleripicus*) and American representatives of *Dryocopus*. There were, of course, also taxonomic decisions that one cannot reconcile with the modern system.

The system of birds used in the 20<sup>th</sup> century had several „fathers“ (BRUCE 2003) of which one was Hans Friedrich GADOW who presented a detailed account of the anatomy of birds (1891) and consequently a system (1893) that was very influential with respect to the higher classification of birds and included an overview of the previous attempts on a higher classification of birds. The woodpeckers were put into the Coraciiformes and Pici which comprised the families Galbulidae, Capitonidae, Ramphastidae, and Picidae with the subfamilies Jynginae and Picinae. He deviated slightly from FÜBRINGER (1888) in the placement of the honeyguides which he considered a subfamily of the barbets.

Two influential projects on the classification of birds should be briefly mentioned here. One was the very influential list of higher taxa (down to the family level) by F. Alexander WETMORE (e.g. 1930, 1960), and the other the checklist by James L. PETERS which respected all taxonomic levels down to the subspecies and served as an important reference in the bird collections around the world. With regard to the higher classification, these lists were derived from GADOW’S. In WETMORE (1930, 1960) the woodpeckers and honeyguides had a similar position as in GADOW (1893). The Peters-list from 1948 (reprinted 1964) split the order Piciformes into the suborders Galbulae and Pici, with the latter containing only one family, the Picidae. It treated the honeyguides as a family that together with the barbet family (without the toucans) comprised the superfamily Capitonoidea. Three subfamilies, the Jynginae (wrynecks), Picumninae (piculets) and Picinae (true woodpeckers), constituted the woodpecker family. Like in HARGITT (1890), the Picinae started with *Geocolaptes* and *Colaptes*. However, *ferndinae* which was put into a monotypic genus (*Nesoceleus*), was already part of the group of species that today comprise the genera *Colaptes* and *Piculus*. The puzzling insular species *Sapheopipo noguchii* (Okinawa) and *Xiphidiopicus percussus* (Cuba) got a place between the three toed woodpeckers and *Dendropicos*. The large woodpeckers in *Dryocopus* and *Campephilus* were set far apart, the former, together with *Mulleripicus*, in the vicinity of *Picus*, the latter at the end of the sequence of species together with *Blythipicus* and *Chrysocolaptes*.

## Prioritizing plumage colors and behavior: the system of Lester L. SHORT

Konrad LORENZ pioneered the idea that behavioral traits could be treated like morphological ones in phylogenetic and systematic inference. He demonstrated this with a phylogeny of ducks that he based solely on courtship behavior using the comparative method he had learned from morphologists and which basically was the antecedent of cladistics (LORENZ 1941). With the exception of the vocalizations of songbirds, behavior had never played an important role in systematics. The systems outlined above rested on anatomy and plumage characteristics. Lester L. SHORT took up the Herculean task not only study woodpeckers in all the great bird collections of the world and collecting specimens himself, but also to observe their behavior and record vocalizations in the wild. He laid down his results in numerous papers and summarized them in his monography (SHORT 1982). There, he also presented a new system of woodpeckers that rested largely on plumage characteristics, and partly on behavior. This system differed in some points radically from what had been produced so far. Two aspects characterize his approach, first the high priority he assigned to plumage color and patterns, and lumping species in large genera. Within genera he adhered to the concept of the superspecies (= *Artenkreis* of RENSCH 1926; see also MAYR & SHORT 1970, HAFFER 1986). A superspecies unites monophyletic lineages of allopatric species (MAYR 1963, AMADON 1966). With 33 species *Picoides*, the pied woodpeckers, became the largest genus, and one of the largest in birds (BOCK & FARRAND 1980), comprising the genera *Picoides* and *Dendrocopos* of PETERS (1948). Asian *Micropternus* was merged into South-American *Celeus* and all the large black woodpeckers formed the tribe Campephilini. *Mulleripicus* was seemingly a problem and put together with other Asian, largely grey and black, 'derived' woodpeckers into the Meiglyptini. Convinced that the yellow shafts of the central tail feathers in African woodpeckers could not have evolved independently, the large genera *Campethera* and *Dendropicos* became the tribe Campetherini, ignoring other differences, such as the role of the malar stripe as sexual badge. The work of other people on anatomy, convergence and plumage features (BOCK & MILLER 1959, GOODWIN 1968, CODY 1969, GOODGE 1972) did not deter SHORT from prioritizing plumage colors and behavior, and his interpretation of them (SHORT 1982, pp. 41-42). This system was intended to be based on similarities, phylogenetic relationships were formulated only vaguely and certainly not in the parlance of cladistics (e.g., *Sapheopipo* shows tendencies toward both *Picus* and *Blythipicus*."; SHORT 1982, p. 42). Another example would be his evaluation of the relationships between African and South Ameri-

can Woodpeckers (SHORT 1970, 1982, VUILLEUMIER & ANDORS 1993). Altogether, this new arrangement of species and genera was an admirable attempt to include behavior and other non-museum features in a natural system of birds.

For some time this system became the standard for woodpecker classification in handbooks and other publications. WINKLER et al. (1995) followed it, and so had SIBLEY & MONROE (1990) who, however, split with OUELLET (1977) most of the Eurasian *Picoides* again as *Dendrocopos*, leaving the American pied and three-toed woodpeckers in *Picoides* (see also BROWNING 2003, HOGSTAD 2008). Although it had already become evident that Short's system cannot be upheld, it was still used in WINKLER & CHRISTIE (2002) as well.

## The molecular revolution

SIBLEY & AHLQUIST 1972 conducted the first major study that used biochemical data to infer phylogenetic relationships in birds. The starch gel electrophoretic patterns of the egg white proteins of 816 species of non-passerine formed the base for their comparisons. With respect to the position of the woodpeckers, they did not come up with conclusive results. They did recognize that barbets and woodpeckers are allied and differ substantially from other non-passerine groups. However, they did not recover a relationship between the woodpeckers and honeyguides, and pointed out similarities to the cuckoos for the latter but none to the barbets. They concluded furthermore that the closest relatives of the woodpeckers may be found among the passerines.

In 1990, SIBLEY & AHLQUIST presented the first comprehensive phylogeny of birds based on DNA data. Phylogenetic inference in this study was constrained because the method they used, DNA-DNA hybridization, required that samples had to be compared biochemically for obtaining genetic distances making it infeasible to compare each sample with all the other ones. This invited speculations based on other, not always clearly stated sources. The survey included only four American woodpecker species, not sufficient for a comprehensive revision of the relationships within the Picidae. Consequently, SIBLEY & MONROE (1990) followed SHORT (1982) and OUELLET (1977) for the classification of woodpeckers. The cladistic analyses of mycological and osteological characters by SWIERCZEWSKI & RAIKOW 1981 and SIMPSON & CRACRAFT 1981 had already established the sister group relationship between the honeyguides and woodpeckers and the DNA-DNA hybridization data confirmed this result.

Soon after DNA-sequencing methods became widely available, researchers hastened to study the phylogenetic relationships among birds with this new

method. The results of the first such studies in woodpeckers immediately revealed that their classification needed thorough revision (PRYCHITKO & MOORE 1997; DEFILIPPIS & MOORE 2000; PRYCHITKO & MOORE 2000; WEIBEL & MOORE 2002a, 2002b). Although the main objective of the paper by PRYCHITKO & MOORE (1997) was not to present a comprehensive molecular phylogeny of woodpeckers and hence treated only five species, it already revealed that the Golden-olive Woodpecker (*Piculus* 'rubiginosus) is actually a flicker (*Colaptes*; see also MOORE et al. 2010) and not a member of *Piculus* as in SHORT (1982). SHORT & MORONY (1970) and SHORT (1982). GOODGE (1972) had suggested that sapsuckers are closely related to *Melanerpes*, whereas SWIERCZEWSKI & RAIKOW 1981 had concluded that they former are sister to the pied woodpeckers (*Picoides*, *Dendrocopos*, and allies). DEFILIPPIS & MOORE 2000 resolved this issue by showing that the sapsuckers are genetically closer to *Melanerpes*. The papers by WEIBEL & MOORE (2002a, 2002b, 2005) seriously challenged parts of the plumage-based classification of Short (1982), with showing that the American branch of his genus *Picoides* is closely related to *Veniliornis* which he had placed with *Colaptes-Piculus*. They also revealed that the Eurasian Lesser Spotted Woodpecker (*Picoides* 'minor) is closely linked with small American pied woodpeckers within which the Downy and Hairy Woodpecker (*Picoides* 'pubescens, 'P.' villosus) were shown to be not as closely related as assumed previously. Thus, convergence in picid plumage color began to emerge as a severe problem for the SHORT (1982) classification on the one hand, and a fascinating puzzle for understanding its evolutionary background on the other.

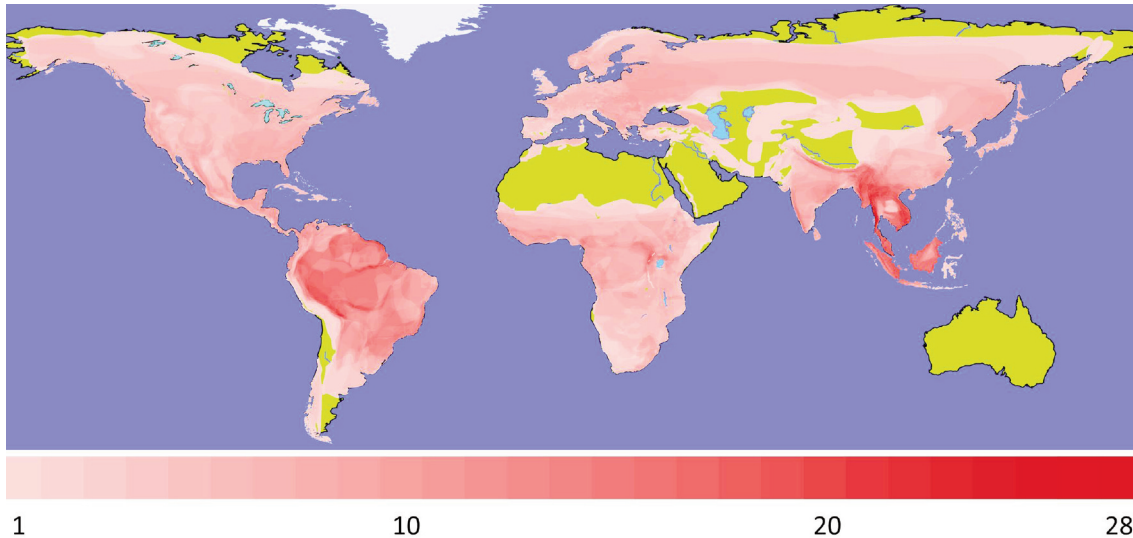
The Okinawa Woodpecker (*Sapheopipo* 'noguchii) was another case of how coloration and possibly also rapid evolution on islands had misled taxonomists. It was put into the monotypic genus *Sapheopipo* with uncertain affinities (e.g. PETERS 1948) because structural traits of bill, feet, and wings seemed similar to those in *Dendrocopos*, while coloration and habits reminded ornithologists of *Picus* (YAMASHINA 1941, GOODWIN 1968, GOODGE 1972, SHORT 1973a, 1982). WINKLER et al. (2005) finally discovered that this species is indeed a member of the genus *Dendrocopos* with *D. leucotos* (White-backed Woodpecker) as close relative.

WEBB & MOORE (2005) were the first to cover all the important woodpecker genera (30 species) in a molecular study using three mitochondrial genes. The results delivered the decisive blow to the traditional classification. *Mulleripicus* was shown to be close to *Dryocopus*, the close ties between *Campethera* and *Picus* became evident (because of an error, the position of

*Geocolaptes* was not correctly assigned), *Chrysocolaptes* and *Campephilus* with their distinct toe arrangement (BOCK & MILLER 1959) became sister groups, and a new clade was established that included *Melanerpes*, *Sphyrapicus*, and the pied woodpeckers with *Veniliornis* as their tropical relatives. Although these results were bound to topple over the previous coloration-based classification, one plumage character, namely the malar as sexual badge exhibited a strong phylogenetic signal. WEBB & MOORE (2005) made the unfortunate move to erect new Tribus, luckless because the names they proposed violated nomenclatural rules.

Soon thereafter, more and more papers appeared that refined those results and which increasingly included nuclear DNA as well (BENZ et al. 2006, FUCHS et al. 2006, 2007). *Blythipicus*, in agreement with its morphology, became part of the *Chrysocolaptes-Campephilus* clade, *Micropternus* was allied with its Asian relatives again (*Meiglyptes*) after Short had united it with South-American *Celeus*, and *Hemicircus* emerged as a clade that has branched off the main tree early in the cladogenesis of the woodpeckers (FUCHS et al. 2007; supported also by morphology: MANEGOLD & TÖPFER 2012). *Dinopium*, as already suspected by CODY (1969), was moved away then from its look-alike *Chrysocolaptes* and kept a position close to *Gecinulus* (FUCHS et al. 2007, WINKLER et al. 2014). Molecular data uncovered two more striking cases of plumage convergence. The first case concerned the Asian Darjeeling Woodpecker (*Dendrocopos darjellensis*, a close relative of the Great Spotted Woodpecker *D. major*), and the Crimson-breasted Woodpecker (*D. cathpharius*, close to the Lesser Spotted Woodpecker and the Downy Woodpecker; WINKLER et al. 2014), and the second one involved the genera *Campephilus*, *Dryocopus*, and *Celeus* in South America (LAMMERTINK et al. 2015). That the yellow shafts of the tail feathers of *Campethera* and *Dendropicos* are due to convergence, had already been shown by WEBB & MOORE (2005), however, FUCHS & PONS (2015) added more evidence and provided interesting information on the relationships between the pied woodpeckers and *Dendropicos*. FUCHS et al. (2013) uncovered also an intriguing case of horizontal or reticulate phylogenetic relations: they presented evidence for an early hybridization event between the ancestors of *Campephilus* and *Melanerpes*.

The latest additions to woodpecker phylogenetics used supermatrix approaches (SANDERSON et al. 1998, BININDA-EMONDS 2004, YANG & RANNALA 2012) combining molecular data from 112 and 179 species respectively, about three quarters of all the known species (DAVIS & PAGE 2014, DUFORT 2015). The latter paper includes also divergence time estimates.



**Fig. 1:** Species density of the woodpeckers of the world. Based on data provided by BirdLife International and NatureServe (2014). Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA. Color bar indicates the number of species.

The development of taxonomy and phylogenetics of woodpeckers shows, if anything, that most plumage color patterns are very unreliable characters for classification because they are labile, correlate with environmental clines, habitat background color, more or less so with genetic isolation, and are often subject to convergence (SHORT 1967, CODY 1969, JACKSON 1970a, MENDEL & JACKSON 1977, WEIBEL & MOORE 2002a, WIEBE & BORTOLOTTI 2001, 2002, WEIBEL & MOORE 2005, MOORE et al. 2006, SENEVIRATNE et al. 2012, GRAHAM & BURG 2012, PRUM 2014, FERNANDO & SENEVIRATNE 2015). As long as not all species have studied thoroughly, the possibility of further surprising findings thus remains.

With all that progress made, the approach suggested in a recent paper by TOBIAS et al. (2010) potentially plunges woodpecker systematics back to its stone age. Ornithology once at the frontier of evolutionary biology and the biological species concept seems to move away from contemporary science (WATSON 2005). The scoring system by TOBIAS et al. (2010) has unfortunately rather insensibly been applied in the checklist by DEL HOYO et al. (2014a) with consequences for woodpecker taxonomy that will be discussed at the end of this chapter. The positive aspect of this development is that problematic cases are more or less explicitly spelled out and will hopefully stimulate further research and critical reappraisal of woodpecker classification.

## Biogeography

DARWIN in his 1859 „Origin of Species“ did not fully appreciate the role of biogeography for understanding speciation and diversification processes. Later researchers became more and more aware of the important relationships between phylogeny and biogeography.

The breakthrough came with MAYR (1963) who stressed the role of geographical barriers in speciation processes. The renewed interest in phylogenetic research that came with cladistics and later with molecular phylogenetic methods lead also to an increased interest in biogeographical patterns, plate tectonics and the respective role of vicariance and dispersal for speciation (CRACRAFT 1982, WILEY 1988, RIPLEY & BEEHLER 1990, RONQUIST 1997, EDWARDS & BEERLI 2000), among other things, and finally to the research field of Phylogeography (AVISE 2000, KNOWLES 2004).

ILLIGER (1816) presented arguably the first biogeography of birds in which he also addressed the question of the relationship between relatedness and geography (p. 236). He recognized that the woodpeckers are not occurring in Australia, but, strangely enough, claimed that New Zealand is home to two species of ‘*Picus*’.

Extant woodpeckers inhabit the Americas, Eurasia, and Africa (Fig. 1). They are missing from Madagascar. Weber’s Line, a modification of Wallace’s line, describes approximately the south-eastern border to the Australian region which neither woodpeckers nor their closest allies have reached (MAYR 1944). Weber’s Line includes not only woodpecker inhabited islands such as Sulawesi and Lombok within the Oriental region, but also Timor which has not been colonized by woodpeckers.

BLACKBURN et al. (1998) conducted the first study on the overall biogeographical patterns in woodpeckers: The distribution of range sizes was skewed (see also GASTON 1998, GASTON & HE 2002), with most species ranging over small areas only, and the largest ranges were found in the North of the American and Eurasian continents (see also HUSAK & HUSAK 2003). They also found that body size bears on the number of sympatric species. Greater diversity in body size correlates with

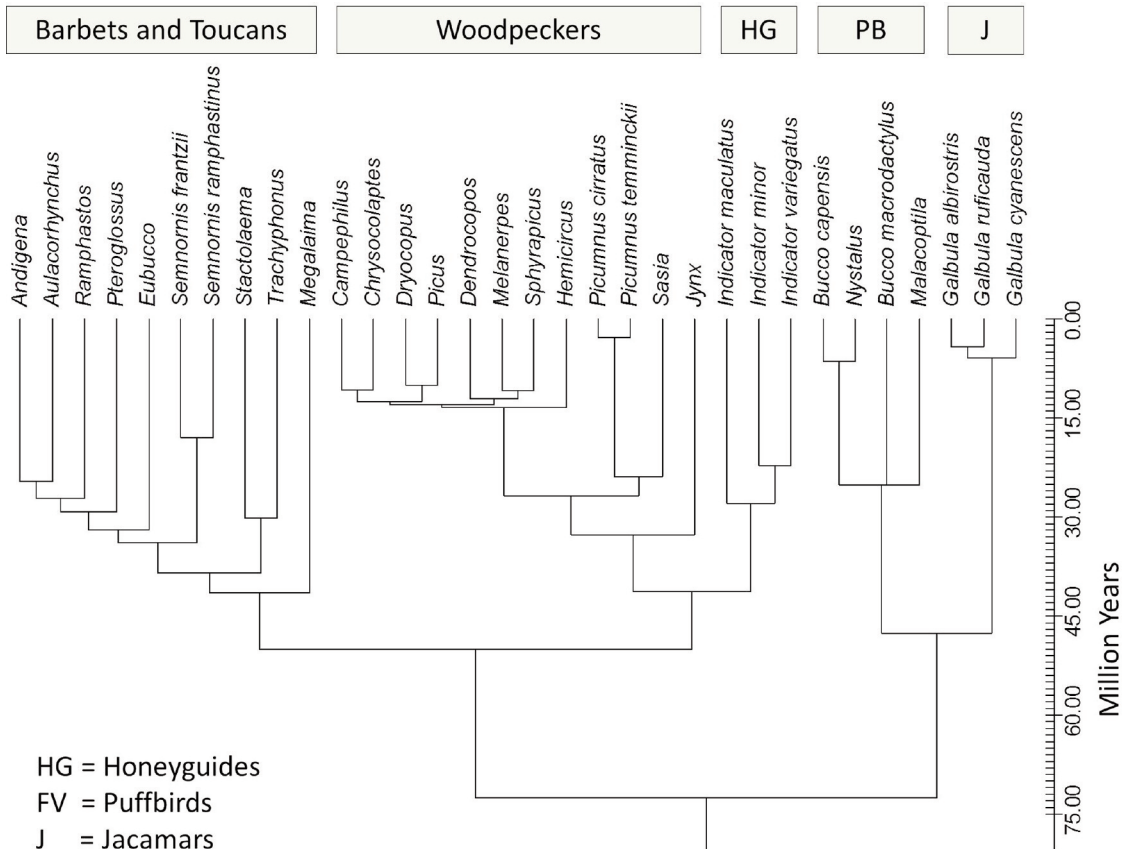
more range overlap. On a smaller scale, FRETWELL (1978) analyzed species packing in North American woodpeckers. Woodpecker communities, according to his analysis, can pack more species by adding middle-sized species. SHORT (1978) could confirm this pattern for a tropical forest in Malaysia where 13 sympatric species ranged from 9 to 430g, with seven species weighing between 50 and 100g. As in many other organisms, woodpeckers exhibit a clear latitudinal diversity gradient. The tropical and subtropical forests of South-East Asia, South and Central America, and equatorial Africa harbor the greatest number of species (Fig. 1; MIKUSI SKI 2006). However, latitudinal extent and latitude do not correlate as in some other bird families (KOLEFF & GASTON 2001). The number of subspecies within species tends also to be higher at low latitudes (MARTIN & TEWKSBURY 2008, p. 2279, Fig. 2). With respect to the new biogeographic regions suggested by HOLT et al. (2013), woodpeckers are most diverse in the Oriental and Neotropical regions. Woodpecker relations in the Sino-Japanese Region, especially around the Himalayas (MARTENS et al. 2011, FJELDSÅ 2013) need to be carefully revised (WINKLER et al. 2014), because it has been not properly sampled in studies like the one by ZINK et al. (2002a) or PERKTAS & QUINTERO (2013).

MAYR (1946) listed the woodpeckers among the strictly land bird families that are widespread or evenly distributed and therefore make biogeographical analysis with respect to their origin difficult. He concluded that the origin of woodpeckers most likely was the New World, although he had to admit that their closest relatives are of Old World origin. Any exercise in historical biogeography that is intended to retract the origin of woodpeckers has to take into account that transoceanic colonization is exceedingly unlikely in this family. SHORT (1982) suggested a New World origin for the woodpeckers. Two facts seem to support this view. Firstly, the Neotropics are rich in woodpecker diversity, especially the piculets, considered a basal lineage, radiated into many species there. Secondly, the primitive Antillean Piculet of the Picinae may also be used as an argument for a New World Origin (BENZ 2006).

Fossil finds (MAYR 2001, MANEGOLD & LOUCHART 2012) and the distribution of the honeyguides, now recognized as the sister group of woodpeckers (see above), suggest an Old World origin of woodpeckers. Furthermore, a tropical Asian origin of woodpeckers would explain the biogeography and genetic patterns of extant species best (BLACKBURN et al. 1998, FUCHS et al. 2007, ERICSON 2012). With *Hemicircus* as basal as the Antillean Piculet (FUCHS et al. 2007), the New World occurrence constitutes a weaker argument for a New World origin of woodpeckers.

Given the new phylogenies and the limited dispersal abilities of woodpecker, the intercontinental exchange between Asia and the Americas must have taken place over the Bering land bridge which represented a land connection from the Mesozoic (over 70 million years before present) until the late Miocene and Pliocene (HOPKINS 1967, ELIAS et al. 1996, ELIAS & BRIGHAM-GRETTE 2013) Migration across this land bridge was feasible during most of the Tertiary when temperate and subtropical forests covered the area (DONOGHUE & MOORE 2003, SWANSON 2003), allowing primates and other land vertebrates to cross (e.g. SMITH et al. 2006, SPINKS & SHAFFER 2009, LI et al. 2015). A broad bridge opened also when sea levels dropped significantly during the Quaternary. Parts of Alaska and Eastern Siberia were free of glacial ice then because of dry climatic conditions (ELIAS & BRIGHAM-GRETTE 2013). FUCHS et al. (2007) suggested that the New World and Africa were colonized from Asia during the Middle Miocene. According to their analyses, diversification of the main clades started after the Mid-Miocene Climatic Optimum (ZACHOS et al. 2008). Faunal exchange across the Beringian landbridge was certainly not unidirectional. The ancestor of the Lesser Spotted and the Crimson-breasted Woodpecker most likely came from North America (see phylogeny in WINKLER et al. 2014), and in the *Dryocopus-Celeus-Colaptes* clade exchange may have taken place in both directions. Some of the groups involved (e.g. Piculets, ivory-billed woodpeckers) are not represented by extant species in northern Eurasia or North America and there is no fossil evidence that their ancestors have occurred in either area (MOORE et al. 2010).

The intercontinental split between the Eurasian and the American Three-toed Woodpecker took place in the Late Pliocene or Early Pleistocene (ZINK et al. 1995, 2002a, DROVETSKI et al. 2010). Their phylogenetic relationships with small Asian pied woodpeckers (e.g. *kizuki*, *moluccensis*) suggest an Asian origin for the three-toed woodpeckers (WINKLER et al. 2014). More local tectonic and volcanic processes create islands and land bridges with significant biogeographic consequences. Glaciation cycles are associated with sea-level oscillations which create land bridges at low levels and separate continuous populations at high ones. Archipelagoes, such as the Antilles in the New World or Sundaland in Southeast Asia, narrow stretches of land like the Isthmus of Panama in Central America or the Isthmus of Kra on the Malayan Peninsula are especially subject to these dynamic processes (MARSHALL & LIEBHERR 2000, VORIS 2000, HUGHES et al. 2003, WOODRUFF 2003, DE BRUYN et al. 2004, BACON et al. 2015).



**Fig. 2:** Within order relationships of the Piciformes based on sequences of mitochondrial (*ND2*, *cytb*) and nuclear DNA (*RAG1*, *TGF $\beta$ 2*,  $\beta$ -fibrinogen intron 2, myoglobin intron 2) covering 6453 positions. The following species entered the computations: *Andigena cucullata*, *Aulacorhynchus prasinus*, *Ramphastos toco*, *Pteroglossus azara*, *Eubucco bourcierii*, *Semnornis frantzii*, *S. ramphastinus* (Capitonidae and Ramphastidae); *Stactolaema olivacea*, *Trachyphonus usambiro* (Lybiidae); *Megalaima virens* (Megalaimidae); *Bucco capensis*, *B. macrodactylus*, *Nystalus maculatus*, *Malacoptila semicincta* (Bucconidae); *Galbula albirostris*, *G. ruficauda*, *G. cyanescens* (Galbulidae); *Indicator maculatus*, *I. minor*, *I. variegatus* (Indicatoridae); and finally *Campephilus melanoleucos*, *Chrysocolaptes lucidus*, *Dryocopus pileatus*, *Picus viridis*, *Dendrocopos major*, *Melanerpes carolinus*, *Sphyrapicus varius*, *Hemicircus canente*, *Picumnus cirratus*, *P. temminckii*, *Sasia ochracea*, and *Jynx torquilla* for the Picidae. In addition, *Alcedo leucogaster* (Alcedinidae), *Athene cunicularia* (Strigidae), *Todus angustirostris* (Todidae), *Merops nubicus* and *M. viridis* (Meropidae) served as outgroup. Analysis with MrBayes (RONQUIST et al. 2012), two Million generations, GTR-Inverse Gamma model of nucleotide substitution. Chronogram obtained with r8s (SANDERSON 2003) and the following calibration points: 80 Million years for continental separation of *Malacoptila* and *Picus*, 72.5 Million years for the *Picus*-*Pteroglossus* split (PACHECO et al. 2011) and 13.4 Million years for the *Hemicircus*-*Picus* divergence (FUCHS et al. 2007). See DUFORT 2015 for a more detailed chronogram of the Picidae.

Several studies analyzed the phylogeographic processes that were associated with the diversification within genera. VOOUS (1947) tried to link glaciations with (sub)speciation in the European pied woodpeckers, focusing largely on the history of the Great Spotted Woodpecker. His conclusions could not be corroborated by later analyses (WINKLER 1979, GARCIA-DELREY et al. 2007, PERKTAS & QUINTERO 2013, WINKLER et al. 2014, FUCHS & PONS 2015). As in other cases involving woodpeckers, plumage colors turned out to be a very undependable basis for comparisons. The sapsuckers (*Sphyrapicus*) can serve as an example of how climate change and Pleistocene glaciation drove diversification and partial isolating mechanisms restrict gene flow (BROWNING 1977, JOHNSON & ZINK 1983, JOHNSON &

JOHNSON 1985, CICERO & JOHNSON 1995, WEIR & SCHLUTER 2004). The work of SELANDER & GILLER (1963) on Central American *Melanerpes* (Centurus) woodpeckers and BAPTISTA'S (1978) study of *Colaptes* (*Piculus*) in this region have never been revised using modern methods (see also MOORE et al. 2010). *Melanerpes* is still poorly known. Other Neotropical genera have received some attention and the available data on *Celeus* (BENZ & ROBBINS 2011) and *Veniliornis* (MOORE et al. 2006) invite further studies. The genus *Campephilus* would also deserve more phylogeographic investigations (FLEISCHER et al. 2006). The Greater Sundas and Malayan peninsula formed a contiguous landmass during low sea levels (VORIS 2000). The subsequent splits in warmer periods between islands and at

the Isthmus of Kra resulted, for instance, in the separation of *Sasia ochracea* and *S. abnormis* about five Million years BP (FUCHS et al. 2006). Taking this value to calibrate the divergence in the mitochondrial cytochrome *b* gene (data from GenBank, distance based on the JUKES-CANTOR estimator), one obtains 2.26% divergence per million years which is higher than the often used universal 2% rate (GARCÍA-MORENO 2004; but see PEREIRA & BAKER 2006). However, values calculated with model corrected distances tend to be higher (PÄCKERT et al. 2007), and the value of 2.08% for the uncorrected genetic divergence comes much closer to the „universal“ rule. Applying the latter value to the divergence time of the pair *Sphyrapicus varius* and *Melanerpes carolinus*, the estimate would be 6.52 million years (Messinian, Miocene; INTERNATIONAL COMMISSION ON STRATIGRAPHY 2009) which differs substantially from the estimate by NAHUM et al. (2003) who used a more distant calibration point for their genetic data, namely the divergence of Galliformes and other neognaths (PATON et al. 2002), resulting in a value of  $36.9 \pm 6.1$  million years (Eocene/Oligocene).

Widespread species offer the opportunity to evaluate the relationships between local conditions, phenotypic variation and population genetics. And, they also may serve as cases for discussing these aspects in a taxonomical context. Woodpeckers offer several such more or less well studied examples. For instance, the hybridization zone between the western and eastern forms of the Northern Flicker with all its implications is one of the best studied among birds (SHORT 1965, BOCK 1971, MOORE & BUCHANAN 1985, MOORE & KOENIG 1986, MOORE et al. 1991, MOORE & PRICE 1993, WIEBE 2000, WIEBE & BORTOLOTTI 2001, 2002, FLOCKHART & WIEBE 2009). The substantial clinal variation in morphological features of the Hairy Woodpecker (*Leuconotopicus villosus*) has been studied quantitatively by JACKSON (1970a). KLICKA et al. (2011) presented an insightful study of the genetic structure of this widespread American species. They could show that latitude and above all topography contribute to mitochondrial haplotype diversity. The similar, but smaller Downy Woodpecker (*Dryobates pubescens*) shows similar trends although the genetic differentiation seems to be weaker than in the former species (BALL & AVISE 1992, PULGARÍN-RESTREPO & BURG 2012).

## The origin of the woodpeckers

### The Piciformes

As has been shown in the previous section, morphological analyses (SWIERCZEWSKI & RAIKOW 1981, SIMPSON & CRACRAFT 1981) and molecular data (SIBLEY&

AHLQUIST 1990) suggest, that woodpeckers, honeyguides (Indicatoridae) and the barbets and toucans descended from a common stock. Classical morphological analyses, biochemical data of proteins and DNA all support the notion that the closest relatives of the woodpeckers are the honeyguides with which they are then linked to the barbets. ZELENKOV (2007), however, suggested that the mousebirds (Coliiformes) are closer to the Piciformes than the Coraciiformes on the basis of leg and foot morphology. Fig. 2 depicts a tree based on a concatenation analysis that included several piciform families and important picid tribes, with owls and several coraciiforms as outgroups. It confirms the present view on the Piciformes according to which this order comprises the honeyguides (Indicatoridae), barbets (Megalamidae, Lybiidae, Capitonidae), toucans (Ramphastidae), puffbirds (Bucconidae) and jacamars (Galbulidae). This also agrees with the results of recent molecular studies of the Aves (HACKETT et al. 2008, JARVIS et al. 2014, PRUM et al. 2015).

### The fossil record

The fossil history of woodpecker before the Pliocene is not well known. The maybe earliest record of a woodpecker, early Miocene at least, is a contour feather preserved in amber from the Dominican Republic (LAYBOURNE et al. 1994). There is another report on a feather in Baltic amber that BACHOFEN-ECHT (1949) likened to feathers of small woodpeckers, such as the Lesser Spotted Woodpecker (he used the name *Picus minor* what led to some misunderstanding regarding the genus by later authors, e.g. GRIMALDI & CASE 1995). This type of amber could originate from the Eocene, but stemmed more likely from lower Oligocene strata. Some records referring to the Eocene, Oligocene and Miocene may have been wrongly assigned to woodpeckers (BRODKORB 1970). French upper Oligocene/Miocene deposits contained two fossil bird species that were described as woodpeckers by MILNE EDWARDS (1869-1874), but later studies revealed that this assignment to the Picidae was wrong (CRACRAFT & MORONY 1969, BALLMANN 1969). Other French Miocene and Eocene fossils originally described as woodpeckers seem not to be picids either (CRACRAFT & MORONY 1969, BRODKORB 1970). However, DE PIETRI et al. (2011) claim to have found the earliest definite record of a woodpecker in the early Miocene of Saulcet, France. The species, *Piculoides saulcetensis*, was represented solely by the distal end of a tarsometatarsus and was probably about the size of a Lesser Spotted Woodpecker. UMANSKAJA (1981) described a specimen from the late Miocene of the Ukraine as *Picus peregrinabundus* that may represent a woodpecker, however the generic designation needs to be revised (DE PIETRI et al. 2011, MLÍKOVSKÝ 2002), and



a middle sized woodpecker fossil was discovered in Italy that belongs to the same period (BALLMANN 1976).

A fossil, unearthed in South Africa, is remarkable in several respects (MANEGOLD & LOUCHART 2012, MANEGOLD et al. 2013). It comprises several bones and dates back to the early Pliocene and does not resemble extant African woodpeckers. *Australopicus nelsonmandelai* represents a woodpecker that seems to be most closely related to *Dryocopus*, a genus not represented in Africa today. FEDDUCIA & WILSON (1967) described a small fossil woodpecker from the lower Pliocene in Kansas as *Pliopicus brodkorbi*. Its relationships with modern species need to be reevaluated. CRACRAFT & MORONY (1969) reported on another lower Pliocene species, *Palaeonerpes shorti*, based on a distal end of a tibiotarsus that was uncovered in Nebraska. This fossil somewhat resembled modern *Melanerpes* species. Another lower Pliocene undescribed woodpecker fossil from Nebraska showed features found in modern flickers (*Colaptes*, WETMORE 1931). Woodpeckers that already closely resemble modern woodpeckers were found in the Upper and Middle Pliocene deposits of Hungary (*Picus pliocaenicus*, *Dendrocopos praemedius*; KESSLER 2014). VON BUCHHOLZ (1986) found a woodpecker cavity among petrified remains of an early Pliocene forest. However, he erroneously attributed it to the Eocene (NATIONS et al. 2009). An as yet undescribed fossil cavity was collected by H. BIEBACH (pers. comm.) between Cairo and the Bahariya Oasis and may be from the early or middle Miocene (cf. EL-SAADAWIA et al. 2004). The cavity was most likely produced by a woodpecker about the size of a Eurasian Green Woodpecker.

Modern woodpeckers are well represented in Pleistocene strata in central Europe (JÁNOSSY 1974, MLÍKOVSKÝ 2002). *Bathoceleus hypalus* from the Upper Pleistocene of the Bahamas, apparently not related closely to extant species, was found on New Providence Island together with remains of the West Indian Woodpecker which has also been found on Great Exuma Island (BRODKORB 1959, WETMORE 1937). BERNSTEIN (1965) found at least four Antillean Piculets in a late Pleistocene deposit on Hispaniola and 11 Hispaniolan Woodpeckers. These fossils and other evidence indicate that the woodpeckers of the West Indies arrived from North America, Central America and South America during periods of low sea levels (BRODKORB 1959, CRUZ 1974). The Sandia Cave, New Mexico, contained Northern Flicker bones in a late Pleistocene (dated about 12,000 B.P.) site (BRASSO & EMSLIE 2006).

## A classification of the woodpeckers of the world

The history of biology and the classification of plants and animals and other creatures are tightly interwoven. Classification always reflects the current state of biological knowledge and what is thought to be biologically relevant. It also signifies what the people who devise a certain classification think what the use and benefits of their system should be. Classifications attempt to arrange a diversity of entities into sets of classes based on similarities possessed by the included individual entities; similarity simply meaning that the description of one entity agrees largely with the description of the other (MAYR & BOCK 2002). Disagreements among biologists concern mainly what type of description should be relevant and have a priori greater information content (MAYR 1965). Thus, a classification system, such as the one of ARISTOTLE, may include not only biological, but also philosophical agenda (ROMERO 2012). Ever since DARWIN (1859, chapter 13), biologists struggled to include common descent into a „natural“ classification of organisms. In its extreme, by ignoring all other aspects (contra DARWIN) except descent, this led to „cladification“ (MAYR & BOCK 2002).

One of the most important properties of a classification is its role in information storage and retrieval. This is the reason why not only taxonomists have considered stability one of the chief merits of a good classification (MAYR & BOCK 2002). However, requests to formally stabilize the system of birds (The president of the 14<sup>th</sup> IOC, David Lack, failed with such a proposal at this IOC at Oxford) have rightly been declined by taxonomists even at a time when indeed the general impression might have been that the classification of birds has basically reached its conclusion. Molecular and information processing techniques have revolutionized our knowledge about phylogenetic relationships and in its course classifications. Within birds this revolution affected mainly the Passeriformes, but all other groups to a lesser or greater degree as well. Our understanding of the relationships among woodpeckers, although well defined as a group, did not form an exception.

Modern integrative taxonomy should be based on natural taxa, those that share the greatest number of attributes (MAYR 1965). It also has to be consistent with phylogenetic and to some degree biogeographic evidence. Principles of utility and also stability should also be observed. The final part of this section will provide a taxonomic list of woodpeckers that hopefully complies with these requirements. The paragraphs that follow should inform about the important developments in our knowledge about woodpecker phylogeny and biogeography which form the justification for the species list in

Tab. 2 and which should particularly be compared with the handbook and checklist by DEL HOYO et al. (2014ab).

## Family Picidae

The grouping and gross phylogenetic relationships of woodpecker subfamilies seem rather clear. The wrynecks (Jynginae) are a very distinct sister group to the remaining woodpeckers, containing two major radiations, the diminutive piculets (Picumninae) and the true woodpeckers constituting the largest subfamily, the Picinae. These subfamilies represent deep branches in the woodpecker phylogeny that are between 20 and more than 30 Million years old (DUFORT 2015) corresponding to the Oligocene and early Miocene (INTERNATIONAL COMMISSION ON STRATIGRAPHY 2009).

### Subfamily Jynginae

The two wryneck species probably represent an old lineage of woodpeckers that has branched off very early from the one that eventually led to the true woodpeckers. They form one superspecies with an Old World distribution. They are cryptically colored, with brown, grey and black patterns matching the structure of a typical bark surface. They move along branches in a rather passerine style and frequently descend to the ground. The foot is a zygodactyl, yoke-shaped, four-toed perching foot. The feathers of these sexually monomorphic birds are soft. This is particularly true for the long tail feathers, which are more or less rounded at the tips. The short bill is slightly curved and pointed. The nostrils are round and exposed, and only partly covered by feathering. The tip of the tongue is only slightly pointed, smooth and without any barbs. With this kind of a bill they cannot excavate their own nest. But they do breed in natural cavities and old woodpecker holes. Ants form the major part of their diet.

### Subfamily Picumninae

The piculets exhibit many specializations that characterize woodpeckers. The feature that distinguishes them most conspicuously from other woodpeckers is their tail with short and only slightly pointed feathers. The plumage is soft, and brown to greenish colors with black markings dominate. Forehead and crown, which are more or less densely spotted and streaked bear the signals for sexual recognition with orange or red in males and with white in most females. They move rapidly along thin branches, may hammer vigorously and with stamina. In all these activities the tail is rarely used as a prop. As in most woodpeckers, the nostrils are covered by feathers, and the bill is pointed, slightly curved on the culmen, and compressed laterally. The long tongue has a rounded tip with fine bristles. They are

able to excavate their own breeding holes. Calls are not unlike those of other woodpeckers and some species drum.

The African Piculet and two Asian piculets have been treated as two separate genera, *Verreauxia* and *Sasia*, in PETERS 1948. SHORT (1982) united all three species in *Sasia*. However, molecular studies and the fact that the African species has only eight, rather than ten, rectrices justifies maintaining two separate genera. Together, they form the basal group within the subfamily (FUCHS et al. 2006). All three species of this genus possess a bare area around the eye, they lack white tail stripes, and they are further distinguished by a very round cross-section of the upper mandible, and by zygodactyl feet with a greatly reduced (African Piculet) or absent (White-browed Piculet) first toe. The remaining piculets occur in Asia (one species) and South America.

The Asian Speckled Piculet is very similar to its American congeners. It shares a unique color pattern, laterally converging white bars on the outer and a white stripe on the central tail feathers, with the South American species. While many other features may be convergent due to the diminutive size of these species, SHORT (1982) saw no obvious reason why this particular tail pattern should have evolved independently. The molecular study of FUCHS et al. (2006) confirmed this reasoning, and showed that the Asian species is sister to all the American ones. Because the morphological differences are small, these authors recommended not to resurrect the genus *Vivia* for the Asian species, and this proposal is followed here. Within the South American piculets, species limits and taxonomy are still far from clear. Scant knowledge about behavior and ecology in many parts of the continent, considerable geographic variation within species and relatively frequent interbreeding (see SHORT 1982) hinder firm conclusions. These tiny woodpeckers differentiated only recently, significantly later than for instance *Colaptes* (DUFORT 2015). Thus many South American piculets are closely related, hybridize (SHORT 1982, NETO 1995, TAVARES et al. 2011) and the may form but a few (super)species as suspected by SHORT (1982). As has been shown in a recent study of the piculets of Venezuela, more data may change our conception of these woodpeckers in many ways. The Golden-spangled Piculet (*Picumnus exilis*) comprises several, apparently distinct forms (RÉGO et al. 2014) which, however, are given not species rank here. Subspecies *nigropunctatus* treated as a genuine species in DEL HOYO et al. (2014a) is a junior synonym of *P. squamulatus obsoletus* considered a genuine species by RÉGO et al. (2014). While stories like that are not so rare in avian and woodpecker taxonomy it underscores the point that still much has to be done with regard to the

systematics of South American Piculets. Similar confusion existed in the subspecific designation within the Ochraceous Piculet (*P. limae*) and between this form and the Tawny Piculet (*P. fulvescens*). Here we include the subspecies *saturatus*, formerly in *limae*, as conspecific with *P. fulvescens*.

The monotypic genus *Nesocittes* has been traditionally included in the Picumninae, but is treated here as a Tribe within the Picinae (see below).

### Subfamily Picinae

The true woodpeckers are characterized by unique features of the bill, tongue and skull, as well as by distinctive variants of the zygodactyl toe arrangement and by a specialized tail. These features and details of the molting pattern as well as their early development are intimately related to their habits. These are characterized by the foraging mode that to a lesser or stronger degree includes subsurface feeding that mainly is carried out on trees, but in some form has changed or complemented into digging up ant or termite nests on the ground. This predominant foraging mode goes along with their hole nesting habits. Woodpeckers excavate their own nesting holes mainly into dead wood. Some ground foraging species dig their nests into the ground. Woodpeckers hop along branches and their climbing style derives from this locomotor pattern (WINKLER 1972). The typical structural adaptations found in woodpeckers are all connected with these habits. The central feathers of the noticeably graduated tail are strong and pointed with especially strong shafts and vanes and with stiff barbs. They are more or less clearly curved forwards at the tip. These characteristics are best developed in medium sized to large arboreal species. The bill is slightly curved in some genera, but is straight in most species with ridges and with a pointed or chisel-like tip. In most species the nostrils are protected by covering feathers. The exceptionally long tongue has a barbed tip, with a high diversity of barb arrangements among species. The length of the tongue and the arrangement of the tongue-bones also vary greatly (LUCAS 1895, LEIBER 1907, STEINBACHER 1934, 1935, 1941, 1955, 1957). Most or all species have large mucus secreting salivary glands producing a sticky mucus that coats the tongue tip to trap food particles. Woodpeckers are most diverse in southern Asia and on South America (SHORT 1982). But they are also widespread in the Holarctic region, and in Africa. Within these true woodpeckers several tribes are recognized.

SHORT (1982) had split the true woodpeckers into six tribes. The Colaptini (flickers and allies) and Melanerpini (e.g. Acorn Woodpecker and Red-headed Woodpecker, Sapsuckers) comprise seven genera that

are confined to the New World with one exception, the colaptine Rufous Woodpecker (*Celeus brachyurus*) which lives in Asia. The Picini (e.g. Green Woodpecker, Flamebacks) occur with seven genera in the Palaearctic and Orientalis only, so do the tropical Meiglyptini (e.g. Buff-necked Woodpecker *Meiglyptes tukki*) with three genera. The Campephilini include two genera of large woodpeckers, the 'logcocks' (*Dryocopus*) and ivory-bills (*Campephilus*), with the latter being confined to the Americas while the former is widespread in Eurasia as well. Finally according to this view, the Campetherini occur on all continents because of the widespread genus *Dendrocopos-Picoides*. As has been discussed in the preceding sections, this classification has been shaken up thoroughly. The following paragraphs will introduce the five tribes recognized now (WINKLER et al. 2014).

### Tribe Nesocittini

The Antillean Piculet seems to be rather isolated from all other true woodpeckers and inhabits the Caribbean island of Hispaniola since at least 24 million years (see above). Its bill is long, slightly curved and pointed, and some morphological features suggest a closer relationship to other Picinae than to the Picumninae (GOODGE 1972, KIRBY 1980). The behavior reminds more of a barbet or a vireo (songbird) than of a woodpecker (SHORT 1974). Molecular data suggest it represents a very old stock, maybe together with *Hemicircus* the last remnant of an once widespread picid lineage (BENZ et al. 2006, WINKLER et al. 2014, DUFORT 2015) showing features that relate to that Asian genus as well as to other Picinae in a mixture of primitive and derived characters (MANEGOLD & WHITE 2014).

### Tribe Hemicircini

The genus *Hemicircus* contains two rather small species, which are predominantly black and white and which are crested too. The bill is of medium length, rather straight, chisel-tipped, indicating strong pecking habits. The tail appears even shorter than in *Nesocittes*. But it is stiff and it is slightly bent forwards near the tip. The fourth toe is longer than the front toes and the first is about half its length. Broadly, its morphology represents early adaptations to drilling and true woodpecker-like climbing (MANEGOLD & TÖPFER 2012).

The males of the Grey-and-buff Woodpecker (*H. concretus*) have much red in the crest, whereas the females show only traces of cinnamon or red. The sexual dimorphism of the other species, the Heart-spotted Woodpecker (*H. canente*) is unique among woodpeckers in that the male has a black face, crown and crest, while the female's forehead and frontal part of the crown are white.

DEL HOYO et al. (2014a) distinguishes a third species, *H. sordidus* from *concretus*, now named Red-crested Woodpecker, according to their scoring of plumage characteristics. They suggest using the vernacular name previously assigned to *concretus*, namely Grey-and-buff Woodpecker, to this new species, and reserve Red-crested Woodpecker for *concretus* which occurs on Java only while *sordidus* is distributed from south Myanmar, peninsular Thailand, Sumatra and Borneo. This is an interesting hypothesis, but with no further biological information not deemed sufficient here for recognizing this split as valid.

### Tribe Campephilini

SHORT (1982) considered the Campephilini to be an offshoot of the Colaptini. They themselves are thought to be connected with the Campetherini (see below). This was largely based on the assumption that *Dryocopus* is part of this tribe. Indeed, *Campephilus* and *Dryocopus* have many features in common. Species of both genera are large, and are boldly colored with black and white and a greater or lesser amount of red. The large woodpeckers of the genus *Campephilus* are all crested to a greater or lesser extent and their sexual badges are found mainly on the crown and affect crest coloration and the malar region. The chisel-tipped bill is long and straight, the nostrils well protected and covered by feathers. The tail is long and stiff, and curved forwards towards the tip, which is strong and pointed. All toes are long, the fourth significantly longer than the front toes. They are directed forward in climbing and the tarsus may closely touch the climbing substrate (BOCK & MILLER 1959). The similarity in head and hind limb musculature and toe arrangement (BOCK & MILLER 1959, GOODGE 1972) to South-Asian Flamebacks (*Chrysocolaptes*), and to some degree *Blythipicus*, were not considered diagnostic by SHORT (1982). CODY (1969) had listed several features including morphology, feeding habits and vocalizations that separate *Dryocopus* and *Campephilus* and presumed that the similarities in color patterns are due to convergence and social mimicry. The anatomical similarities between *Chrysocolaptes* and *Campephilus*, however, would be difficult to explain on the basis of convergence (GOODGE 1972, p. 82). Molecular studies (DEFILIPPIS & MOORE 2000, PRYCHITKO & MOORE 2000, WEBB & MOORE 2005, BENZ et al. 2006, FUCHS et al. 2007, WINKLER et al. 2014, DUFORT 2015) and a recent analysis of osteological characters (MANEGOLD & TÖPFER 2012) have broadly confirmed the results of BOCK & MILLER (1959), CODY (1969) and GOODGE (1972).

This tribe thus comprises the genera *Blythipicus*, *Chrysocolaptes*, and *Campephilus*. WINKLER et al. (2014) included the monotypic genus *Reinwardtipicus* (species

*validus*) into *Chrysocolaptes* while DEL HOYO et al. (2014a) kept it as a separate genus. SHORT (1982) recognized its *Campephilus*-like foot and placed this species close to *Blythipicus*, away from *Chrysocolaptes*.

The populations of the *Chrysocolaptes lucidus* complex pose a formidable taxonomic challenge because of its highly diverse plumage patterns and size variation. Many of them are strictly insular and DEL HOYO et al. (2014a) split *lucidus* into seven species (see also COLLAR 2011). A compromise based on scattered genetic (WINKLER et al. 2014) and biological (voice) evidence and biogeography is followed here. Referring to the names used in DEL HOYO et al. (2014a), *guttacristatus* (including *stricklandi* although voice may be distinctive; RASMUSSEN & ANDERTON 2005), *strictus* and *lucidus* (includes all Philippine forms which seem not to differ strongly in their vocalizations; G. GORMAN pers. Comm.). As pointed out by DEL HOYO et al. (2014a) (see RASMUSSEN & ANDERTON 2005), *C. guttacristatus socialis* could be a valid species too. However, the whole complex needs a thorough and comprehensive revision before continuing with any further taxonomic speculations

Relationships within *Campephilus* are largely uncontentious. However, DEL HOYO et al. (2014a) decided to assign species rank to the *splendens* subspecies of *C. haematogaster*. The reasons given, some minor plumage differences and a rather problematic (homology) account of the vocalizations, and the unclear geographical relationships with *haematogaster* are not convincing. Subspecies *nelsoni* of *C. guatemalensis* (W Mexico) seems to be more distinct than plumage patterns suggest (WINKLER et al. in prep.). FUCHS et al. (2013) uncovered a most intriguing relationship to *Melanerpes* that probably is due to an ancient gene transfer via hybridization.

### Tribe Picini

The Picini represent a worldwide radiation of woodpeckers. This tribe now includes *Campethera* from the former tribe Campetherini and *Dryocopus* from the former Campephilini (see above) and excludes *Chrysocolaptes* and *Blythipicus*, as well as *Sapheopipo*, now listed in the next tribe in the genus *Dendrocopos*.

Ground feeding is common in this group and ants form the typical diet. The corresponding adaptations are a straight to slightly curved and more or less pointed bill and a long tongue. The tail is long and stiff. Sexual color dimorphism affects crown and/or a moustachial stripe. Some species have conspicuous crests. Green color, sexual markings on the crown, and a small crest are also the characteristics of the two *Gecinulus* species. They both are bamboo specialist. Their short bill is

slightly curved, but the chisel-tip and the rather broad base indicate that they frequently hammer. The nostrils are covered with feathers. The tail is soft and broad, which may be a secondary adaptation for climbing on bamboo. These woodpeckers possess three toes of about equal length. The South Asian genus *Dinopium* is largely sympatric with similar looking *Chrysocolaptes* (Campephilini). The bill in this genus is short to moderately long, curved, and the tip is pointed to slightly chisel-tipped. The slit-like nostrils are only partly covered by feathers. The tail is fairly soft, long and somewhat curved. The first is short to very short and rudimentary (and completely absent in two species). The dominant plumage colors are green, red, golden to yellow, black and white plumage. All species are crested and sexual color differences pertain to the crown and affect also the malar stripe. Five species of *Dinopium* are recognized here, with *everetti* assigned species status following DEL HOYO et al. (2014a) (see also WINKLER et al. 2014). Although *psarodes* from Sri Lanka is distinct because of its reddish coloration (possibly mimicking the local subspecies of *Chrysocolaptes guttacristatus*), hybridization with other forms of *benghalense* is extensive (FREED et al. 2015) and, contrary to DEL HOYO et al. (2014a), it is not given species status here.

The African genus *Campethera* (here subsumed under *Geocolaptes*, Tab. 2) shares many characteristics with South American *Colaptes*, *Piculus* and *Celeus*. Generally, plumage in these two groups is often greenish and the underparts are barred or spotted and that pattern can easily shift between bars and spots in both groups. Other details in plumage coloration, e.g. yellow tail shafts or malar stripes as the bearers of sexual signals are also shared. The greatest plumage similarities are exhibited by the young of these groups. *Piculus* and *Campethera* both have large mandibular glands, similar features in the tracheal and other muscles with some similarities to *Celeus* as well, and both have peculiar asymmetric testes. The African Ground Woodpecker *Geocolaptes olivaceus* which up to recently represented a monotypic genus is embedded into „*Campethera*“ according to molecular data (G. FUCHS pers. comm., DUFORT 2015). Its special features are related to its ground foraging. The long and curved bill and the moderately stiff tail feathers render them as typical ground foragers. Compared with its arboreal relatives, the plumage colors are dull. Like in flickers, flight feathers have yellow shafts. Its social behavior too probably evolved convergent to some of the terrestrial flickers. To avoid paraphyly, the Ground Woodpecker either has to be included into *Campethera*, or the whole group has to be split into three genera. Tab. 2 lumps all species into one genus which by priority has to be *Geocolaptes*

(SWAINSON, 1832) rather than *Campethera* (GRAY, 1841). FUCHS & BOWIE (2015) suggested convincingly to split *caroli* and *nivosa* in two species each based on genetic analyses and biogeography. However, not all subspecies were sampled and thus species limits cannot be defined yet unambiguously. The split of *nivosa* also needs careful reanalysis of plumage characteristics. For these reasons, these splits have not been entered in Tab. 2.

*Gecinulus* has been varying considered monotypic (SHORT 1982) or containing two species (PETERS 1948, WINKLER & CHRISTIE 2002, DEL HOYO et al. 2014ab). There is a small zone of contact in northern Thailand and possibly northern Laos in which hybridization occurs (ROUND et al. 2012). Gene flow seems to be restricted though and two species, *grantia* and *viridis*, are recognized here pending further research proves otherwise.

The wide ranging Grey-faced Woodpecker *Picus canus* has been split into three species in DEL HOYO et al. (2014a). Species *Picus canus* according to this decision occurs from France to northern China and includes subspecies *jessoensis* (E Siberia to Hokkaido) and *griseiventris* (Korea). The new species *guerini* is thought to comprise the adjoining southern populations in the Sino-Himalayan region and includes subspecies *hessei* and *tan-colo*, among others. Finally, the geographically isolated and dark-reddish form *dedemi* from the mountains of Sumatra is given species rank too (DEL HOYO et al. 2014a). There is clearly more variation in the southern populations than in the temperate zones. However, variation appears to be largely clinal and related to humidity and temperature. Birds of warmer and more humid zones appear to be generally darker. Plumage colors also vary by age and season (GREENWAY 1940) and there appear to be many intermediates among populations (GREENWAY 1940, VAURIE 1959, SHORT 1982). Looking at the maps in DEL HOYO et al. (2014a), there seems to be a zone of overlap in China's Hebei province between *canus* and *guerini*, not commented on by the authors. All together, the separation of *guerini* and *canus* as species appears to be rather arbitrary. This case needs certainly more study. The spectacular colors of *dedemi* would suggest species status for this insular population when one applies a purely phenomenological scoring system. One can also speculate that the isolation would have been long lasting enough to generate differences that would be sufficient to guarantee genetic isolation upon a hypothetical secondary contact with other populations. DEL HOYO et al. (2014a) correctly pointed out that subspecies *tan-colo* from Hainan and Taiwan is questionable because it seems rather unlikely that these two geographically well separated insular populations share a recent common

**Table 1:** Disentangling the former *Celeus* species *elegans*, *lugubris* and *flavescens*. Past species-subspecies designation follows SHORT (1982). Reordering based on published (BENZ & ROBBINS 2011, LAMMERTINK et al. 2015) and additional own unpublished *cytb* and *ND2* sequences.

Former species	subspecies	Current species	Distribution
<i>elegans</i>	<i>elegans</i>	<i>elegans</i>	French Guiana, Surinam, NE Brazil
<i>elegans</i>	<i>hellmayri</i>	<i>elegans</i>	Easternmost Venezuela, Guyana, Surinam
<i>elegans</i>	<i>deltanus</i>	<i>elegans</i>	Amacuro Delta, Venezuela
<i>elegans</i>	<i>leotaudi</i>	<i>elegans</i>	Trinidad
<i>elegans</i>	<i>jumana</i>	<i>lugubris</i>	E Colombia, Venezuela, NW Brazil, N Bolivia, Amazonian Brazil to Mato Grosso
<i>elegans</i>	<i>citreopygius</i>	<i>lugubris</i>	E Ecuador, E Peru
<i>lugubris</i>	<i>lugubris</i>	<i>lugubris</i>	W-central Mato Grosso, E Bolivia
<i>lugubris</i>	<i>kerri</i>	<i>lugubris</i>	Paraguay, southernmost Mato Grosso
<i>flavescens</i>	<i>flavescens</i>	<i>flavescens</i>	Parana, E Paraguay, Brazil south from São Paulo and Rio de Janeiro
<i>flavescens</i>	<i>ochraceus</i>	<i>ochraceus</i>	Lower Amazon region, Maranhão, Ceara, Piauh, E Bahia
<i>flavescens</i>	<i>intercedens</i>	<i>flavescens</i>	Goias, Minas Gerais, W Bahia

history. The overt similarity of these two peripheral forms (SHORT 1982) may be due to convergence.

Short sequences (307 bp) of the mitochondrial *cytb* gene provided some further information on genetic distances (JUKES-CANTOR corrected). Nominate *canus* (Vienna, Austria) differed from *jessoensis* (Hebei) not at all, from *tanco* (Taiwan, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands, No.53587) by 0.3%, from *dedemi* (Sumatra, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands, No. 10315) by 2.3%, and from *hessei* (N Myanmar, Natural History Museum Vienna No. 45512) by 3.3%. The greatest difference found, 4.4%, was between *hessei* and *dedemi*, the latter differing from *tanco* by 2.7%. To put these differences into perspective, some values for the same section of *cytb* among populations of the *Picus viridis* group may be illustrative. The greatest difference (7.5%) in this group was between *vaillantii* and *sharpei*, while *sharpei* and *viridis* differed by 2.7 to 3.7% only, and *vaillantii* and *viridis* by 4.7 to 5.1%. All this shows that there is much to be done with respect to the relationships in the *canus* group. Species *guerini* seems not to be a valid one, however, *hessei* may well be part of a distinct species that has to be described and defined yet. In passing, it should be noted that already earlier researchers have pointed out its distinct coloration (GREENWAY 1940, VAURIE 1959, SHORT 1982) and vocalization (RASMUSSEN & ANDERTON 2005). Given this analysis, only *dedemi* can be accepted as a genuine species (as part of a *canus* superspecies) so far. Any other split between *canus* populations is not justified yet, but will probably be necessary upon further studies especially of *hessei*.

The Eurasian Green Woodpecker *Picus viridis* has been studied much better than the former species. DEL HOYO et al. (2014a) followed PERKTAS et al. 2011 and split it into three species, with the Iberian and North African populations each given species rank. But, they kept the genetically distinct (PERKTAS et al. 2011) and geographically most isolated population from the Zagros Mountains of Iran (*innominatus*) in *viridis* because of only subtle plumage differences. However, the isolation of this Iranian population took place much more recently than that of the Iberian one (PERKTAS et al. 2011). PONS et al. (2010) suggested to separate *vaillantii* as a species while keeping subspecies status for *sharpei*. Gene flow at the contact zone between *sharpei* and *viridis* in France as well as vocalizations (FAURÉ 2013; HW pers. observations) support this decision (see Tab. 2).

MOORE et al. (2010) sorted out the genera *Piculus* and *Colaptes* exemplifying once more how woodpecker coloration can be strongly driven by habitat characteristics, with forest and ground living species in each genus converging with respect to the background coloration within their respective habitats. The taxonomic treatment of the forms within the genus *Colaptes* by DEL HOYO et al. (2014a) illustrates their conception most clearly (see also REMSEN 2015) which bases species delimitation mostly on plumage characteristics and ignores intermediate forms and hybridization. As already pointed out, the relationships between red and yellow-shafted forms of the Northern Flicker (here treated as one species, *Colaptes auratus*) are well studied and are a good example of extensive gene flow without any significant isolating mechanisms in operation (see above). The relationships among the more southern and Central American populations are complex (SHORT 1967), and their relationships with related groups certainly need further research and the relationships between *C. chrysoides*, *C. a. mexicanoides* and *C. auratus* clarified. There is no reason to separate *melanolaimus* from *Colaptes melanochloros*. Variation is extensive and so is hybridization along contact zones (SHORT 1972b). Splitting of *Colaptes rivolii* into two species (*rivolii* and *atriceps*) needs more data than those presented by DEL HOYO et al. (2014a). Data in GenBank seem all to refer to *C. r. atriceps*; some obviously wrong location references present difficulties, however. A further split in DEL HOYO et al. (2014a), the one between *C. campestris* and *C. campestroides* (see SHORT 1972b), is also not recognized in Tab. 2. Assigning species status to *cinereicapillus* of *Colaptes rupicola* may be justified (DEL HOYO et al. 2014a) because plumage differences are obvious and calls seem to be different as well (SHORT 1972b). However, more biological information is needed to accept this taxonomic decision.

The Central and South American complex of *Colaptes rubiginosus* is difficult to evaluate (BAPTISTA 1978). Splitting *C. aeruginosus* as a species seems to be justified on the basis of coloration and vocalization and genetics and its sister species is *auricularis* rather than *rubiginosus* which presumably has *atricollis* as closest relative (MOORE et al. 2010, DUFORT 2015). If it turns out that all Central American „*rubiginosus*“ form one species, it would have to be named *yucatanensis* for priority reasons and *aeruginosus* would not be a valid name (cf. DUFORT 2015). Genetic analyses of the complex will have to sample all parts of these species' ranges to get a better idea of their phylogeography (DUFORT 2015). Only then it has to be shown whether further species need to be recognized; the splits proposed by DUFORT (2015) thus seem to be premature.

The genera *Mulleripicus* and *Dryocopus* have been shown to be closely related and form a monophyletic clade (WINKLER et al. 2014, DUFORT 2015). The populations of the northern and southern Philippines seem to be quite distinct (DUFORT 2015) and recognizing the southern *fuliginosus* populations as full species again (as in PETERS 1948) appears to be well justified (COLLAR 2011, DEL HOYO et al. 2014a). Although recognizing three genera may be justified (*Mulleripicus* and *Dryocopus* in the Old World, *Hylatomus* in the New World), Tab. 2 list all the New and Old World species as *Dryocopus*. DEL HOYO et al. (2014a) recognize subspecies *fuscipennis* of *D. lineatus* as a separate species. Its coloration seems to be correlated with its arid habitat and it certainly would be interesting to study it more closely. However, current knowledge does not justify treating it as a species. Rare *D. schulzi* is little known, hybridizes with *lineatus* (SHORT 1982) and its taxonomic status may therefore need reconsideration.

The genus *Celeus* is morphologically characterized by a short to medium bill that can be slightly curved to straight. In contrast to *Dryocopus*, there is no feathering over the nostrils (SHORT 1982). Taxonomy and historical biogeography of several species were treated by SHORT (1972a, 1973b) and HAFFER (1969). Recent genetic analyses clarified relationships within the genus (BENZ & ROBBINS 2011). Subspecies *obrieni* of *spectabilis* described by SHORT (1973b) is now recognized as a valid species and is like *spectabilis* a bamboo specialist (KRATTER 1998, DE SOUSA AZEVEDO et al. 2013, LEITE et al. 2013). *Celeus undatus* and *C. grammicus* are genetically very similar (BENZ & ROBBINS 2011; own unpublished data), form a wide contact zone, and are treated as single species in Tab. 2. The complex interrelations in the *elegans* group are summarized in Tab. 1. SHORT (1972a) had already noticed that *elegans* and *lugubris* hybridize in the Mato Grosso. The suggestion that *Celeus lugubris cit-*

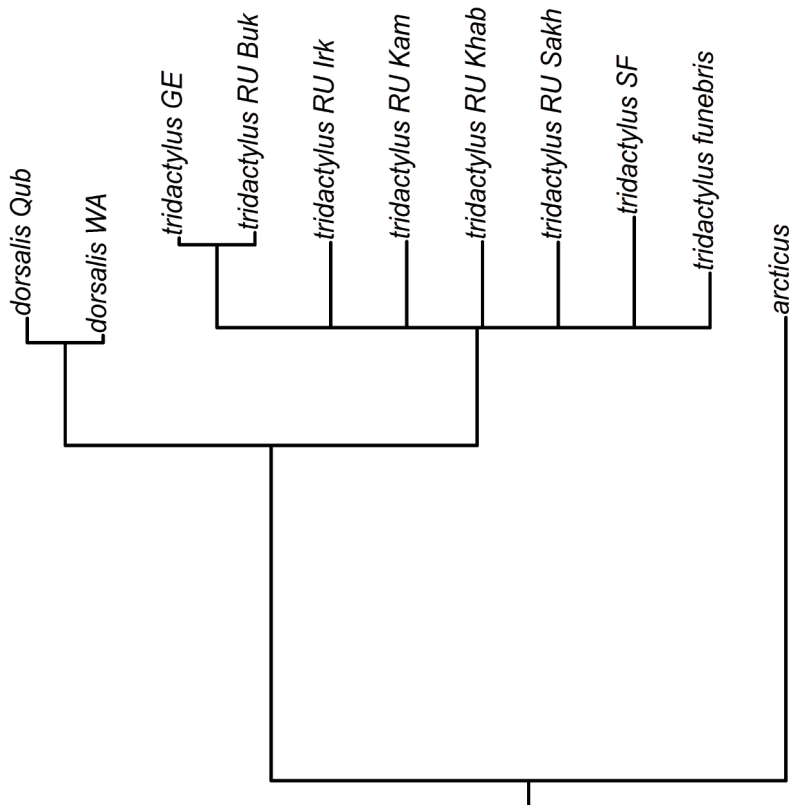
*ropygius* may be a valid species (DEL HOYO et al. 2014a) is not supported at all by genetic data available to me.

### Tribe Melanerpini

The Melanerpini, according to SHORT'S (1982) reasoning, derive from the same old ancestral group as the Colaptini and Campetherini. New molecular data support this notion (summarized in DUFORT 2015) and suggest the Picini (which now encompass those tribes) as sister group. And there is a relationship with the Campephilini due to an ancient hybridization event (FUCHS et al. 2013).

The Melanerpini comprise three genera that are restricted to the New World which include moderately specialized and hence very generalistic and successful woodpeckers. These American woodpeckers command all typical woodpecker locomotor styles and most species are excellent flyers. In fact, several species cover long distances in open areas regularly, some are short distance migrants and the sapsuckers are genuine long distance migrants. So, it is neither surprising that fly-catching is an important foraging technique in some species (LEONARD & HEATH 2010), nor that this group has successfully colonized all major Caribbean Islands. There some endemic species have evolved. The niche breadth of these woodpeckers is further augmented with a more or less well developed ecological and morphological sexual dimorphism, particularly on islands (SELANDER 1966, BOCK 1970, WALLACE 1974, MARTINDALE 1983, CRUZ & JOHNSTON 1984, MARTINDALE & LAMM 1984). The bill is long, usually pointed and slightly to strongly curved, and can be used for excavating, probing and taking fruit, acorns and nuts, and an occasional nestling bird or lizard. The various species are either boldly patterned in black and white with red and yellow, or exhibit finer black and white horizontal barrings. However, no clear cut line can be drawn between these two types of patterning. Sexual differences in plumage coloration are either well marked or absent. In this there is no convincing relationship with sociality, since there are completely monomorphic species like the Guadeloupe Woodpecker that are not more inclined to social life than other species. Juvenile birds differ from adults more conspicuously than in most woodpeckers. Sociality, living in family groups, or even in cooperative groups with complex interrelations is widespread in this group. Many species are frugivorous, take nuts and seed, and the most specialized sapsucking woodpeckers are found in this tribe. Most species are not only conspicuous visually, but also strike as being garrulous and loud.

The large genus *Melanerpes* was formerly split in two major groups, the ladder-backed *Centurus* and the



**Fig. 3:** Phylogenetic relationships among *Picoides* woodpeckers. Analysis based on published (ZINK et al. 2002b, WINKLER et al. 2014) mitochondrial sequences (*cytb*, *ND2*; 1993bp) and unpublished ones based on samples provided by Peter PECHACEK from Germany and China. Analyses with MrBayes (RONQUIST et al. 2012), two Million generations, HKY85 model of nucleotide substitution. Branches with support lower than 80% were collapsed. Abbreviations: Qub Quebec, Canada; WA Washington, USA; RU Buk Bukukun, Russia; RU Irk Irkutsk Russia; RU Kam Kamchatka Peninsula, Russia; RU Khab Khabarovsk, Russia; RU Sakh Sakhalin Island, Russia; SF Finland.

boldly patterned *Melanerpes*. There are many intermediate stages between these extremes, the group is in all respects rather uniform, so distinguishing several genera does not seem to be justified (SHORT 1982). The four species of North American sapsuckers, *Sphyrapicus*, were placed within this tribe because of many anatomical, behavioral and ecological similarities (GOODGE 1972, SHORT 1982). Meanwhile, there is overwhelming evidence from molecular data, too, that these birds are indeed close relatives of *Melanerpes* (DEFILIPPIS & MOORE 2000, WEBB & MOORE 2005, BENZ et al. 2006, OVERTON & RHOADS 2006, FUCHS et al. 2013). They show similar color patterns and the juvenile plumage may also be distinct. Sexual dimorphism well expressed or absent. All species are more or less migratory and the sapsucking habit is well developed. Sapsuckers show their greatest diversification along the western mountains and coast of North America. Analysis of their DNA has clarified the relationships. Williamson's Sapsucker is closest to the ancestral species. The Yellow-bellied Sapsucker (*S. varius*) is a widespread distinct

species. The sapsuckers of the Northwest do hybridize sometimes, but genetic analysis supports their specific status, with *S. ruber* probably the most recently evolved one. On Cuba and its nearby islands lives the Cuban Green Woodpecker that has assigned a genus of its own, *Xiphidiopicus*. It is a very green species that, however, exhibits a color pattern that is very reminiscent of the one of sapsuckers to which it seems to be related (OVERTON & RHOADS 2006). The Cuban Green Woodpecker does not show some of the more derived morphological character states that are common to *Melanerpes* and *Sphyrapicus*, however. It lacks, for instance, a characteristic tie between certain tendons of the toes (GOODGE 1972). It remains to be shown whether this indicates that this little known species represents the remnant of an ancestral species or whether it has secondarily lost these specializations again during its long, separate island evolution.

The second group of woodpeckers within the tribe occurs on all continents inhabited by woodpeckers and contains several widespread and familiar species. It has sometimes recognized as a tribe of its own, the Dendropicini (FUCHS & PONS 2015). This group comprises (DEL HOYO et al. 2014a) the genera *Picoides*, *Yungipicus*, *Leiopicus*, *Dendropicos*, *Dendrocopos*, *Dryobates*, *Leucontopicus* and *Veniliornis* in Table 2. These woodpeckers share many features with *Melanerpes* and *Sphyrapicus* including omnivorous diet, sapsucking, and differing degrees of ecological sexual dimorphism (e.g. KILHAM 1965, LIGON 1968, JACKSON 1970b, KOCH et al. 1970, HOGSTAD 1976, 1993, 2008, STENBERG & HOGSTAD 2004, KOTAKA et al. 2006). With respect to the generic assignment of species to genera, I do not follow completely FUCHS & PONS (2015), and do not recognize *Dendrocoptes* for *auriceps*, *medius* and *dorae* and leave them rather together with *mahrattensis* in *Leiopicus* (Table 2; cf. WINKLER et al. 2014).

The Three-toed Woodpecker, in the classical conception, covers a huge Holarctic range. Recent molecular data strongly urge to split the North American forms as a separate species, the American Three-toed Woodpecker *Picoides dorsalis* from the Eurasian populations (ZINK et al. 2002b). Substantial geographic separation and distinct coloration would justify separating *P. t. funebris* as a separate species at a first glance. This is exactly what DEL HOYO et al. (2014a) did, however, at the same time not recognizing *dorsalis* anymore because of plumage similarities with North Eurasian birds. This birdwatcher view would lead to paraphyly (Fig. 3) unless three species would be created, and employing some consistency, even the Alpine-Carpathian populations would deserve species rank (*alpinus*) then. In Tab. 2 only two species, namely *tridactylus* and *dorsalis* are listed.



Wholly African are the 15 species of the genus *Dendropicos* recognized in Tab. 2, which also often show some greenish coloration too, and which seem generally more arboreal than the other small African woodpeckers of the genus *Campethera*. Hence, they possess strong claws, and the bill is only slightly curved. Sexual dichromatism pertains to the crown or nape which are not red in females. White frontal markings occur in females of the Bearded Woodpecker (*D. namaquus*) only. As in *Campethera*, the underside may be plain, spotted, barred or streaked. Some species show extended red coloration there. The yellow shafts of the central tail feathers are a feature that is common to both African genera. Species *obsoletus* which was assumed to be more closely related to small Asian woodpeckers (*Yungipicus moluccensis* and its relatives, SHORT 1982) has been shown by FUCHS & PONS (2015) and DUFORT (2015) to be well embedded in *Dendropicos*.

WINKLER et al. 2014 suggested to re-establish genus *Dryobates* for the small American pied woodpeckers (*pubescens*, *nutallii*, *scularis*) and argued on the basis of molecular data that the Old World species *minor* and *cathpharius* have to be included too (see also BROWNING 2003, FUCHS & PONS 2015). The latter species has been split by DEL HOYO et al. (2014a) into two allopatric species (*cathpharius*, *pemyii*) which is an interesting working hypothesis.

Based on molecular data and other information the genus *Leuconotopicus* for several American pied woodpecker species (*borealis*, *villosus*, *stricklandi*, *albolavatus*) had to be resurrected (DEL HOYO et al. 2014a; cf. WINKLER et al. 2014, FUCHS & PONS 2015) into which *fumigatus*, the Smoky-brown Woodpecker, had to be moved from closely related, but separate, *Veniliornis* (MOORE et al. 2006). DEL HOYO et al. (2014a) separated *L. arizonae* and *L. stricklandi* that previously had been considered conspecific on the basis of their ecology and behavior

(DAVIS 1965, SHORT 1982) without presenting any new evidence.

The striking plumage similarities between *Dryobates* and *Leuconotopicus*, i.e. between the Hairy and the Downy Woodpecker, are due to convergence or social mimicry, or both (WEIBEL & MOORE 2005, PRUM 2014).

The genus *Veniliornis*, containing 13 Central and South American species, shows many similarities with the pied woodpeckers. The bill of *Veniliornis* is well adapted for excavating, strong and straight, with ridges and slit-like, feather-covered nostrils. They have green and often more or less red upperparts, which distinguishes them from the pied woodpeckers, but strongly reminds of some of the African woodpeckers. Sexual markings are on the crown which is bright red in males and dark, sometimes streaked pale olive in females, but never at the malar as in the Picini. The arboreal morphology, in the past, had been attributed to convergent evolution with the pied woodpeckers. New molecular studies have unanimously shown that these features correspond to common ancestry, but plumage characteristics that were used to place this genus near *Colaptes* and *Campethera* (SHORT 1970, 1982) are actually the convergent ones. I include now *Veniliornis frontalis* (Dot-fronted Woodpecker, *Perlstirnspecht*) treated as a separate species by SHORT (1982), WINKLER et al. (1995), WINKLER & CHRISTIE (2002) and (DEL HOYO et al. 2014ab) into *Veniliornis passerinus* (see MOORE et al. 2006, KERR et al. 2009) and agree, with SHORT (1982) that these two forms need to be better studied at their zone of contact where they seem to hybridize. Molecular data from the central parts of the *passerinus* range in Amazonia would be very helpful too.

**Table 2:** A list of the woodpeckers of the world. See text for details.

Scientific name	English name	Deutscher Name	Comment
<b>Subfamily Jynginae</b>	<b>Wrynecks</b>	<b>Wendehälse</b>	
<i>Jynx torquilla</i>	Eurasian Wryneck	Wendehals	
<i>Jynx ruficollis</i>	Rufous-necked Wryneck	Rotkehl-Wendehals	
<b>Subfamily Picumninae</b>	<b>Piculets</b>	<b>Weichschwanzspechte</b>	
<i>Verreauxia africana</i>	African Piculet	Graubauch-Mausspecht	
<i>Sasia abnormis</i>	Rufous Piculet	Malaienmausspecht	
<i>Sasia ochracea</i>	White-browed Piculet	Rötelmausspecht	
<i>Picumnus innominatus</i>	Speckled Piculet	Tüpfelzergspecht	
<i>Picumnus nebulosus</i>	Mottled Piculet	Braunbrust-Zergspecht	
<i>Picumnus rufiventris</i>	Rufous-breasted Piculet	Rotbauch-Zergspecht	
<i>Picumnus exilis</i>	Golden-spangled Piculet	Goldschuppen-Zergspecht	
<i>Picumnus lafresnayi</i>	Lafresnaye's Piculet	Lafresnaye-Zergspecht	
<i>Picumnus aurifrons</i>	Bar-breasted Piculet	Goldstirn-Zergspecht	

Table 2: continued

Scientific name	English name	Deutscher Name	Comment
<i>Picumnus fuscus</i>	Rusty-necked Piculet	Rotnacken-Zwergspecht	see Parker & Rocha O. 1991
<i>Picumnus sclateri</i>	Ecuadorian Piculet	Braunohr-Zwergspecht	
<i>Picumnus squamulatus</i>	Scaled Piculet	Schuppenzwergspecht	Includes <i>Picumnus nigropunctatus</i>
<i>Picumnus pumilus</i>	Orinoco Piculet	Orinokozwergspecht	
<i>Picumnus minutissimus</i>	Guianan Piculet	Däumlingspecht	
<i>Picumnus varzeae</i>	Varzea Piculet	Varzeazwergspecht	
<i>Picumnus steindachneri</i>	Speckle-chested Piculet	Perlenbrust-Zwergspecht	
<i>Picumnus cirratus</i>	White-barred Piculet	Zebrazwergspecht	
<i>Picumnus dorbygnianus</i>	Ocellated Piculet	Orbigny-zwergspecht	
<i>Picumnus albosquamatus</i>	White-wedged Piculet	Weißschuppen-Zwergspecht	
<i>Picumnus pygmaeus</i>	Spotted Piculet	Fleckenzwergspecht	
<i>Picumnus spilogaster</i>	White-bellied Piculet	Weißbauch-Zwergspecht	
<i>Picumnus temminckii</i>	Ochre-collared Piculet	Temminckzwergspecht	
<i>Picumnus olivaceus</i>	Olivaceous Piculet	Olivrücken-Zwergspecht	
<i>Picumnus granadensis</i>	Greyish Piculet	Braunrücken-Zwergspecht	
<i>Picumnus fulvescens</i>	Tawny Piculet	Fahlzwergspecht	
<i>Picumnus limae</i>	Ochraceous Piculet	Ockerzwergspecht	
<i>Picumnus castelnaui</i>	Plain-breasted Piculet	Gelbbauch-Zwergspecht	
<i>Picumnus subtilis</i>	Fine-barred Piculet	Cuzcowergspecht	
<i>Picumnus cinnamomeus</i>	Chestnut Piculet	Zimtwergspecht	
<b>Subfamily Picinae</b>	<b>True woodpeckers</b>	<b>Echte Spechte</b>	
Tribe Nesocitini	Antillean woodpeckers	Hüpfspechte	
<i>Nesocites micromegas</i>	Antillean Piculet	Hüpfspecht	
Tribe Hemicircini			
<i>Hemicircus concretus</i>	Grey-and-buff Woodpecker	Kurzschwanzspecht	Includes <i>H. sordidus</i>
<i>Hemicircus canente</i>	Heart-spotted Woodpecker	Rundschwanzspecht	
Tribe Campephilini	Ivory-bills	Elfenbeinschnäbel	
<i>Blythipicus rubiginosus</i>	Maroon Woodpecker	Maronenspecht	
<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	Rotohrspecht	
<i>Reinwardtipicus validus</i>	Orange-backed Woodpecker	Reinwardtspecht	
<i>Chrysocolaptes guttacrastatus</i>	Greater Flameback	Goldmantel-Sultanspecht	The species has been split in various species in the list of DEL HOYO et al. 2014. See text for a discussion of the species limits recognized here.
<i>Chrysocolaptes strictus</i>	Javan Flameback	Javasultansspecht	
<i>Chrysocolaptes lucidus</i>	Philippine Flameback	Philippinen-Sultanspecht	
<i>Chrysocolaptes festivus</i>	White-naped Woodpecker	Goldschulterspecht	
<i>Campephilus haematogaster</i>	Crimson-bellied Woodpecker	Blutbauchspecht	Includes <i>C. splendens</i>
<i>Campephilus principalis</i>	Ivory-billed Woodpecker	Elfenbeinspecht	includes <i>bairdii</i>
<i>Campephilus imperialis</i>	Imperial Woodpecker	Kaiserspecht	
<i>Campephilus magellanicus</i>	Magellanic Woodpecker	Magellanspecht	
<i>Campephilus leucopogon</i>	Cream-backed Woodpecker	Weißmantelspecht	
<i>Campephilus rubricollis</i>	Red-necked Woodpecker	Rothalsspecht	
<i>Campephilus robustus</i>	Robust Woodpecker	Scharlachkopfspecht	
<i>Campephilus pollens</i>	Powerful Woodpecker	Zimtbindenspecht	
<i>Campephilus melanoleucos</i>	Crimson-crested Woodpecker	Schwarzkehlspecht	
<i>Campephilus gayaquilensis</i>	Guayaquil Woodpecker	Guayaquilspecht	
<i>Campephilus guatemalensis</i>	Pale-billed Woodpecker	Königspecht	
Tribe Picini			
<i>Micropternus brachyurus</i>	Rufous Woodpecker	Rötelspecht	
<i>Meiglyptes tristis</i>	Buff-rumped Woodpecker	Braunbürzelspecht	
<i>Meiglyptes jugularis</i>	Black-and-buff Woodpecker	Dommelspecht	
<i>Meiglyptes tukki</i>	Buff-necked Woodpecker	Tukkispecht	

Scientific name	English name	Deutscher Name	Comment
<i>Gecinulus grantia</i>	Pale-headed Woodpecker	Blasskopf-Bambusspecht	
<i>Gecinulus viridis</i>	Bamboo Woodpecker	Rotscheitel-Bambusspecht	
<i>Dinopium rafflesii</i>	Olive-backed Woodpecker	Olivrückenspecht	
<i>Dinopium benghalense</i>	Black-rumped Flameback	Orangespecht	
<i>Dinopium shorii</i>	Himalayan Flameback	Himalaya-Feerrückenspecht	
<i>Dinopium javanense</i>	Common Flameback	Feerrückenspecht	
<i>Dinopium everetti</i>	Spot-throated Flameback	Philippinen-Feerrückenspecht	
<i>Chrysophlegma miniaceum</i>	Banded Woodpecker	Mennigspecht	
<i>Chrysophlegma mentale</i>	Checker-throated Woodpecker	Tropfenkehlspecht	
<i>Chrysophlegma flavinucha</i>	Greater Yellownape	Gelbnackenspecht	
<i>Geocolaptes abingoni</i>	Golden-tailed Woodpecker	Goldschwanzspecht	Includes <i>mombassica</i>
<i>Geocolaptes notatus</i>	Knysna Woodpecker	Knysnaspecht	
<i>Geocolaptes caroli</i>	Brown-eared Woodpecker	Braunohrspecht	
<i>Geocolaptes nivosus</i>	Buff-spotted Woodpecker	Termitenspecht	
<i>Geocolaptes olivaceus</i>	Ground Woodpecker	Erdspecht	
<i>Geocolaptes punctuliger</i>	Fine-spotted Woodpecker	Punktchenspecht	
<i>Geocolaptes bennettii</i>	Bennett's Woodpecker	Bennettspecht	Includes <i>scriptoricaudus</i>
<i>Geocolaptes nubicus</i>	Nubian Woodpecker	Nubierspecht	
<i>Geocolaptes cailliautii</i>	Green-backed Woodpecker	Tüpfelspecht	
<i>Geocolaptes maculosus</i>	Little Green Woodpecker	Goldmantelspecht	
<i>Geocolaptes tullbergi</i>	Tullberg's Woodpecker	Kehlbindenspecht	
<i>Picus chlorolophus</i>	Lesser Yellownape	Gelbhaubenspecht	
<i>Picus puniceus</i>	Crimson-winged Woodpecker	Rotflügelspecht	
<i>Picus awokera</i>	Japanese Woodpecker	Japangrünspecht	
<i>Picus canus</i>	Grey-faced Woodpecker	Grauspecht	Includes <i>guerini</i> See text
<i>Picus dedemi</i>	Sumatran Woodpecker	Sumatragrauspecht	for details
<i>Picus erythrogygus</i>	Black-headed Woodpecker	Rotbüzelspecht	
<i>Picus vaillantii</i>	Levaillant's Woodpecker	Vaillantspecht	
<i>Picus viridis</i>	Eurasian Green Woodpecker	Grünspecht	Includes <i>sharpei</i>
<i>Picus squamatus</i>	Scaly-bellied Woodpecker	Schuppengrünspecht	
<i>Picus xanthopygaeus</i>	Streak-throated Woodpecker	Hindugrünspecht	
<i>Picus rabieri</i>	Red-collared Woodpecker	Halsbandspecht	
<i>Picus viridanus</i>	Streak-breasted Woodpecker	Burmagrünspecht	
<i>Picus vittatus</i>	Laced Woodpecker	Netzbauchspecht	
<i>Dryocopus pileatus</i>	Pileated Woodpecker	Helmspecht	
<i>Dryocopus lineatus</i>	Lineated Woodpecker	Linienspecht	
<i>Dryocopus schulzi</i>	Black-bodied Woodpecker	Schwarzbauchspecht	
<i>Dryocopus martius</i>	Black Woodpecker	Schwarzspecht	
<i>Dryocopus javensis</i>	White-bellied Woodpecker	Weißbauchspecht	
<i>Dryocopus hodgei</i>	Andaman Woodpecker	Andamanenspecht	
<i>Dryocopus fuliginosus</i>	Southern Sooty Woodpecker	Philippinenspecht	
<i>Dryocopus funebris</i>	Northern Sooty Woodpecker	Trauerspecht	
<i>Dryocopus fulvus</i>	Ashy Woodpecker	Celebesspecht	
<i>Dryocopus pulverulentus</i>	Great Slaty Woodpecker	Puderspecht	
<i>Celeus loricatus</i>	Cinnamon Woodpecker	Rotkehlspecht	
<i>Celeus torquatus</i>	Ringed Woodpecker	Schwarzbrustspecht	
<i>Celeus ochraceus</i>	Ochre-backed Woodpecker	Blondschoffspecht	
<i>Celeus flavescens</i>	Blond-crested Woodpecker	Gelbschoffspecht	
<i>Celeus elegans</i>	Chestnut Woodpecker	Fahlkopfspecht	
<i>Celeus lugubris</i>	Pale-crested Woodpecker	Blasskopfspecht	
<i>Celeus castaneus</i>	Chestnut-colored Woodpecker	Kastanienspecht	
<i>Celeus undatus</i>	Waved Woodpecker	Olivbüzelspecht	Includes <i>grammicus</i>
<i>Celeus galeatus</i>	Helmeted Woodpecker	Wellenohrspecht	Moved from <i>Dryocopus</i> ; see main text.
<i>Celeus flavus</i>	Cream-colored Woodpecker	Strohspecht	
<i>Celeus spectabilis</i>	Rufous-headed Woodpecker	Zimtkopfspecht	

**Table 2:** continued

Scientific name	English name	Deutscher Name	Comment
<i>Celex obrieni</i>	Kaempfer's Woodpecker	Kaempferspecht	
<i>Piculus chrysochloros</i>	Golden-green Woodpecker	Bronzespecht	
<i>Piculus leucolaemus</i>	White-throated Woodpecker	Weißkehlspecht	
<i>Piculus flavigula</i>	Yellow-throated Woodpecker	Gelbkehlspecht	
<i>Piculus collopiterus</i>	Stripe-cheeked Woodpecker	Panamaspecht	
<i>Piculus simplex</i>	Rufous-winged Woodpecker	Zimtflügelspecht	
<i>Piculus litae</i>	Lita Woodpecker	Litaspecht	
<i>Piculus aurulentus</i>	Yellow-browed Woodpecker	Weißbrauenspecht	
<i>Colaptes fernandinae</i>	Fernandina's Flicker	Kubaspecht	
<i>Colaptes auratus</i>	Northern Flicker	Goldspecht	
<i>Colaptes chrysoides</i>	Gilded Flicker	Wüstengoldspecht	
<i>Colaptes rivolii</i>	Crimson-mantled Woodpecker	Rotmantelspecht	
<i>Colaptes melanochloros</i>	Green-barred Woodpecker	Grünbindenspecht	
<i>Colaptes pitius</i>	Chilean Flicker	Bänderspecht	
<i>Colaptes rupicola</i>	Andean Flicker	Andenspecht	
<i>Colaptes punctigula</i>	Spot-breasted Woodpecker	Tüpfelbrustspecht	
<i>Colaptes campestris</i>	Campo Flicker	Feldspecht	
<i>Colaptes auricularis</i>	Grey-crowned Woodpecker	Graukappenspecht	
<i>Colaptes aeruginosus</i>	Bronze-winged Woodpecker	Veracruz-Olivmantelspecht	
<i>Colaptes rubiginosus</i>	Golden-olive Woodpecker	Olivmantelspecht	
<i>Colaptes atricollis</i>	Black-necked Woodpecker	Graustirnspecht	
Tribe Melanerpini			
<i>Sphyrapicus thyroideus</i>	Williamson's Sapsucker	Kiefernsoftlecker	
<i>Sphyrapicus varius</i>	Yellow-bellied Sapsucker	Gelbbauch-Saftlecker	
<i>Sphyrapicus nuchalis</i>	Red-naped Sapsucker	Rotnacken-Saftlecker	
<i>Sphyrapicus ruber</i>	Red-breasted Sapsucker	Feuerkopf-Saftlecker	
<i>Xiphidiopicus percussus</i>	Cuban Green Woodpecker	Blutfleckspecht	
<i>Melanerpes candidus</i>	White Woodpecker	Weißspecht	
<i>Melanerpes lewis</i>	Lewis's Woodpecker	Blutgesichtsspecht	
<i>Melanerpes herminieri</i>	Guadeloupe Woodpecker	Guadeloupespecht	
<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	Rotkopfspecht	
<i>Melanerpes formicivorus</i>	Acorn Woodpecker	Eichelspecht	
<i>Melanerpes pucherani</i>	Black-cheeked Woodpecker	Schläfenfleckspecht	
<i>Melanerpes chrysauchen</i>	Golden-naped Woodpecker	Buntkopfspecht	Includes <i>pulcher</i> , treated as a species in DEL HOYO et al. 2014
<i>Melanerpes cruentatus</i>	Yellow-tufted Woodpecker	Gelbbrauenspecht	
<i>Melanerpes flavifrons</i>	Yellow-fronted Woodpecker	Goldmaskenspecht	
<i>Melanerpes cactorum</i>	White-fronted Woodpecker	Kaktusspecht	
<i>Melanerpes chrysogenys</i>	Golden-cheeked Woodpecker	Goldwangenspecht	
<i>Melanerpes hypopolius</i>	Grey-breasted Woodpecker	Graukehlspecht	
<i>Melanerpes pygmaeus</i>	Yucatan Woodpecker	Yucatanspecht	
<i>Melanerpes rubricapillus</i>	Red-crowned Woodpecker	Rotkappenspecht	
<i>Melanerpes hoffmannii</i>	Hoffmann's Woodpecker	Hoffmannspecht	
<i>Melanerpes uropygialis</i>	Gila Woodpecker	Gilaspecht	
<i>Melanerpes superciliaris</i>	West Indian Woodpecker	Bahamaspecht	
<i>Melanerpes portoricensis</i>	Puerto Rican Woodpecker	Scharlachbrustspecht	
<i>Melanerpes striatus</i>	Hispaniolan Woodpecker	Haitispecht	
<i>Melanerpes radiolatus</i>	Jamaican Woodpecker	Jamaikaspecht	
<i>Melanerpes aurifrons</i>	Golden-fronted Woodpecker	Goldstirnspecht	
<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	Carolinaspecht	
<i>Melanerpes santacruzi</i>	Velasquez's Woodpecker	Velasquezs Specht	Consists of all former „ <i>aurifrons</i> “ sub-species from Veracruz south
<i>Picoides arcticus</i>	Black-backed Woodpecker	Schwarzrückenspecht	
<i>Picoides tridactylus</i>	Eurasian Three-toed Woodpecker	Dreizehenspecht	Includes <i>funebri</i> as a subspecies. See main text and Fig. 3.

Scientific name	English name	Deutscher Name	Comment
<i>Picoides dorsalis</i>	American Three-toed Woodpecker	Fichtenspecht	
<i>Yungipicus temminckii</i>	Sulawesi Woodpecker	Temminckspecht	
<i>Yungipicus maculatus</i>	Philippine Woodpecker	Scopolispecht	
<i>Yungipicus ramsayi</i>	Sulu Pygmy-Woodpecker,	Suluspecht	
<i>Yungipicus nanus</i>	Brown-capped Woodpecker	Braunscheitelspecht	
<i>Yungipicus moluccensis</i>	Sunda Woodpecker	Sundaspecht	
<i>Yungipicus canicapillus</i>	Grey-capped Woodpecker	Grauscheitelspecht	
<i>Yungipicus kizuki</i>	Pygmy Woodpecker	Kizukispecht	
<i>Leiopicus mahrattensis</i>	Yellow-crowned Woodpecker	Gelbscheitelspecht	
<i>Leiopicus auriceps</i>	Brown-fronted Woodpecker	Braunstirnspecht	
<i>Leiopicus medius</i>	Middle Spotted Woodpecker	Mittelspecht	See FUCHS & PONS 2015 for another suggestion
<i>Leiopicus dora</i>	Arabian Woodpecker	Araberspecht	
<i>Dendropicos elachus</i>	Little Grey Woodpecker	Wüstenspecht	
<i>Dendropicos poecilolaemus</i>	Speckle-breasted Woodpecker	Tropfenspecht	
<i>Dendropicos abyssinicus</i>	Abyssinian Woodpecker	Wacholderspecht	
<i>Dendropicos fuscescens</i>	Cardinal Woodpecker	Kardinalspecht	
<i>Dendropicos gabonensis</i>	Gabon Woodpecker	Gabunspecht	
<i>Dendropicos lugubris</i>	Melancholy Woodpecker	Düsterspecht	
<i>Dendropicos stierlingi</i>	Stierling's Woodpecker	Stierlingspecht	
<i>Dendropicos namaquus</i>	Bearded Woodpecker	Namaspecht	
<i>Dendropicos pyrrhogaster</i>	Fire-bellied Woodpecker	Rotbauchspecht	
<i>Dendropicos xantholophus</i>	Golden-crowned Woodpecker	Scheitelfleckspecht	
<i>Dendropicos elliotii</i>	Elliot's Woodpecker	Elliot'specht	
<i>Dendropicos obsoletus</i>	Brown-backed Woodpecker	Braunrückenspecht	
<i>Dendropicos goertae</i>	Grey Woodpecker	Graubrustspecht	
<i>Dendropicos spodocephalus</i>	Grey-headed Woodpecker	Graukopfspecht	
<i>Dendropicos griseocephalus</i>	Olive Woodpecker	Goldrückenspecht	
<i>Dendrocopos hyperythrus</i>	Rufous-bellied Woodpecker	Braunkehlspecht	
<i>Dendrocopos macei</i>	Fulvous-breasted Woodpecker	Isabellbrustspecht	
<i>Dendrocopos analis</i>	Freckle-breasted Woodpecker	Sprenkelbrustspecht	The taxon „ <i>macei</i> “ in FUCHS & PONS 2015 refers to <i>analis</i> only.
<i>Dendrocopos atratus</i>	Stripe-breasted Woodpecker	Streifenbrustspecht	
<i>Dendrocopos leucotos</i>	White-backed Woodpecker	Weißrückenspecht	
<i>Dendrocopos owstoni</i>	Amami Woodpecker	Riukiuspecht	DEL HOYO et al. 2014 separate this insular form from <i>leucotos</i> based on coloration only. There are no other biological data to compare this form with other subspecies of <i>D. leucotos</i> .
<i>Dendrocopos noguchii</i>	Okinawa Woodpecker	Okinawaspecht	
<i>Dendrocopos assimilis</i>	Sind Woodpecker	Tamariskenspecht	
<i>Dendrocopos syriacus</i>	Syrian Woodpecker	Blutspecht	
<i>Dendrocopos leucopterus</i>	White-winged Woodpecker	Weißflügelspecht	
<i>Dendrocopos major</i>	Great Spotted Woodpecker	Buntspecht	
<i>Dendrocopos darjellensis</i>	Darjeeling Woodpecker	Darjeeling-Specht	
<i>Dendrocopos himalayensis</i>	Himalayan Woodpecker	Himalajaspecht	
<i>Dryobates pubescens</i>	Downy Woodpecker	Dunenspecht	
<i>Dryobates nuttallii</i>	Nuttall's Woodpecker	Nuttall-Specht	
<i>Dryobates scalaris</i>	Ladder-backed Woodpecker	Texas-specht	
<i>Dryobates cathpharius</i>	Crimson-breasted Woodpecker	Rotbrustspecht	includes <i>pernyii</i>
<i>Dryobates minor</i>	Lesser Spotted Woodpecker	Kleinspecht	
<i>Leuconotopicus borealis</i>	Red-cockaded Woodpecker	Kokardenspecht	
<i>Leuconotopicus fumigatus</i>	Smoky-brown Woodpecker	Rußspecht	
<i>Leuconotopicus villosus</i>	Hairy Woodpecker	Haarspecht	
<i>Leuconotopicus stricklandi</i>	Strickland's Woodpecker	Stricklandspecht	Includes <i>arizonae</i> (see main text)
<i>Leuconotopicus albolavatus</i>	White-headed Woodpecker	Weißkopfspecht	

Table 2: continued

Scientific name	English name	Deutscher Name	Comment
<i>Veniliornis chocoensis</i>	Choco Woodpecker	Chokospecht	
<i>Veniliornis cassini</i>	Golden-collared Woodpecker	Goldnackenspecht	
<i>Veniliornis kirkii</i>	Red-rumped Woodpecker	Blutbürzelspecht	
<i>Veniliornis spilogaster</i>	White-spotted Woodpecker	Perlbauchspecht	
<i>Veniliornis mixtus</i>	Chequered Woodpecker	Streifenschwanzspecht	
<i>Veniliornis lignarius</i>	Striped Woodpecker	Strichelkopfspecht	
<i>Veniliornis sanguineus</i>	Blood-colored Woodpecker	Blutrückenspecht	
<i>Veniliornis passerinus</i>	Little Woodpecker	Sperlingsspecht	Includes <i>frontalis</i> (see main text)
<i>Veniliornis callonotus</i>	Scarlet-backed Woodpecker	Scharlachrückenspecht	
<i>Veniliornis dignus</i>	Yellow-vented Woodpecker	Gelbbauchspecht	
<i>Veniliornis nigriceps</i>	Bar-bellied Woodpecker	Bindenbauchspecht	
<i>Veniliornis affinis</i>	Red-stained Woodpecker	Blutflügelspecht	
<i>Veniliornis maculifrons</i>	Yellow-eared Woodpecker	Goldohrspecht	

## References

- AMADON D. (1966): The superspecies concept. — *Systematic Zoology* **15**: 246-249.
- AVISE J.C. (2000): *Phylogeography. The history and formation of species.* — Harvard University Press, Cambridge, Massachusetts. viii+447 pp.
- BACHOFEN-ECHT A. (1949): *Der Bernstein und seine Einschlüsse.* — Springer-Verlag, Wien. 204 pp.
- BACON, C.D., SILVESTRO D., JARAMILLO C., SMITH B.T., CHAKRABARTY P. & A. ANTONELLI (2015): Biological evidence supports an early and complex emergence of the Isthmus of Panama. — *Proceedings of the National Academy of Sciences of the United States of America*: doi: 10.1073/pnas.1423853112
- BAER W. (1903): *Untersuchungsergebnisse von Mageninhalten verschiedener Vogelarten.* — *Ornithologische Monatschrift* **28**: 262-268.
- BALL R.M. Jr & J.C. AVISE (1992): Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. — *The Auk* **109**: 626-636.
- BALLMANN P. (1969): Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. — *Zitteliana* **1**: 5-58.
- BALLMANN P. (1976): Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien), zweiter Teil. — *Scripta Geologica* **38**: 1-59.
- BAPTISTA L.F. (1978): A revision of the Mexican *Piculus* (Picidae) complex. — *Wilson Bulletin* **90**: 159-181.
- BENZ B.W. & M.B. ROBBINS (2011): Molecular phylogenetics, vocalizations, and species limits in *Celeus* woodpeckers (Aves: Picidae). — *Molecular Phylogenetics and Evolution* **61**: 29-44.
- BENZ B.W., ROBBINS M.B. & A.T. PETERSON (2006): Evolutionary history of woodpeckers and allies (Aves: Picidae): Placing key taxa on the phylogenetic tree. — *Molecular Phylogenetics and Evolution* **40**: 389-399.
- BERNSTEIN L. (1965): Fossil birds from the Dominican Republic. — *Quarterly Journal of the Florida Academy of Sciences* **28**: 271-284.
- BININDA-EMONDS O.R.P. (2004): The evolution of supertrees. — *Trends in Ecology and Evolution* **19**: 315-322.
- BLACKBURN T.M., GASTON K.J. & J.H. LAWTON (1998): Patterns in the geographic ranges of the world's woodpeckers. — *Ibis* **140**: 626-638.
- BOCK C.E. (1970): The ecology and behavior of the Lewis' Woodpecker (*Asyndesmus lewis*). — *University California Publications in Zoology* **92**: 1-100.
- BOCK C.E. (1971): Pairing in hybrid flicker populations in eastern Colorado. — *The Auk* **88**: 921-924.
- BOCK W.J. & J. FARRAND Jr (1980): The number of species and genera of recent birds: a contribution to comparative systematics. — *American Museum Novitates* **2703**: 1-29.
- BOCK W.J. & W. DEW. MILLER (1959): The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. — *American Museum Novitates* **1931**: 1-45.
- BOYD M. & K. ELLISON (2004): Golden-fronted Woodpecker consumes Northern Mockingbird nestling. — *Bulletin of the Texas Ornithological Society* **37**: 25-27.
- BRASSO R.L. & S.D. EMSLIE (2006): Two new late Pleistocene avifaunas from New Mexico. — *The Condor* **108**: 721-730.
- BRODKORB P. (1959): Pleistocene birds from New Providence Island, Bahamas. — *Bulletin of the Florida State Museum, Biological Sciences* **4**: 349-371.
- BRODKORB P. (1970): The paleospecies of woodpeckers. — *Quarterly Journal of the Florida Academy of Sciences* **33**: 132-136.
- BROWNING M.R. (2003): The generic distinction of pied woodpeckers. — *Western Birds* **34**: 97-107.
- BRUCE M. (2003): A brief history of classifying birds. — In: DEL HOYO J., ELLIOTT A. & D. CHRISTIE (eds), *Handbook of the Birds of the World.* — Lynx Edicions, Barcelona: 11-43.
- CICERO C. & N.K. JOHNSON (1995): Speciation in sapsuckers (*Sphyrapicus*): III. Mitochondrial-DNA sequence divergence at the cytochrome-*b* locus. — *The Auk* **112**: 547-563.
- CODY M.L. (1969): Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. — *The Condor* **71**: 222-239.
- COLLAR N.J. (2011): Species limits in some Philippine birds including the Greater Flameback *Chrysocolaptes lucidus*. — *Forktail – Journal of Asian Ornithology* **27**: 29-38.
- COUDRAIN V., ARLETTAZ R. & M. SCHAUB (2010): Food or nesting place? Identifying factors limiting Wryneck populations. — *Journal für Ornithologie* **151**: 867-880.

- COUES E. (1884): Key to North American Birds. Second Edition. — Estes and Lauriat, Boston, MA. 863 pp.
- CRACRAFT J. (1982): Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. — *American Zoologist* **22**: 411-424.
- CRACRAFT J. & J.J. MORONY Jr (1969): A new Pliocene woodpecker, with comments on the fossil Picidae. — *American Museum Novitates* **2400**: 1-8.
- CRUZ A. (1974): Distribution, probable evolution, and fossil record of West Indian Woodpeckers (Picidae). — *Caribbean Journal of Science* **14**: 183-188.
- CRUZ A. & D.W. JOHNSTON (1984): Ecology of the West Indian Red-bellied Woodpecker on Grand Cayman Island: distribution and foraging. — *Wilson Bulletin* **96**: 366-379.
- DARWIN C. (1859): On the origin of species by means of natural selection; or, the preservation of favoured races in the struggle for life. — John Murray, London. 502 pp.
- DAVIS K.E. & R.D.M. PAGE (2014): Reweaving the tapestry: a supertree of birds. — *PLOS Currents Tree of Life* **1**: doi: 10.1371/currents.tol.c1af68dda7c999ed9f1e4b2d2df7a08e
- DE BRUYN M., NUGROHO E., HOSSAIN M.M., WILSON J.C. & P.B. MATHER (2004): Phylogeographic evidence for the existence of an ancient biogeographic barrier: the Isthmus of Kra Seaway. — *Heredity* **2004**: 1-9.
- DE PIETRI V., MANEGOLD A., COSTEUR L. & G. MAYR (2011): A new species of woodpecker (Aves; Picidae) from the early Miocene of Saulcet (Allier, France). — *Swiss Journal of Palaeontology* **130**: 307-314.
- DE SOUSA AZEVEDO L., ALEIXO A., SANTOS M.P., SAMPAIO I., SCHNEIDER H., VALLINOTO M. & P.S. DO RÉGO (2013): New molecular evidence supports the species status of Kaempfer's Woodpecker (Aves, Picidae). — *Genetics and Molecular Biology* **36**: 192-200.
- DEFILIPPIS V.R. & W.S. MOORE (2000): Resolution of phylogenetic relationships among recently evolved species as a function of amount of DNA sequence: An empirical study based on woodpeckers (Aves: Picidae). — *Molecular Phylogenetics and Evolution* **16**: 143-160.
- DEL HOYO J., COLLAR N.J., CHRISTIE D.A., ELLIOTT A. & L.D.C. FISHPOOL (2014a): HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 1 (Non-passerines). — Lynx Edicions, Barcelona. 904 pp.
- DEL HOYO J., ELLIOTT A., SARGATAL J., CHRISTIE D.A. & E. de JUANA (2014b): Handbook of the Birds of the World Alive. <http://www.hbw.com>. — Lynx Edicions, Barcelona.
- DENIS D., TORRELLA L., JIMÉNEZ A. & K. BEOVIDES (1999): Observación de Carpinteros Verdes (*Xiphidiopicus percussus*) depredando huevos de garzas (Aves: Ardeidae). — *El Pitirre* **12**: 95.
- DIAMOND J. (1990): Alone in a crowded universe. — *Natural History* **6/90**: 30-34.
- DONOGHUE M.J. & B.R. MOORE (2003): Toward an integrative historical biogeography. — *Integrative and Comparative Biology* **43**: 261-270.
- DROVETSKI S.V., ZINK R.M., ERICSON P.G.P. & I.V. FADEEV (2010): A multilocus study of pine grosbeak phylogeography supports the pattern of greater intercontinental divergence in Holarctic boreal forest birds than in birds inhabiting other high-latitude habitats. — *Journal of Biogeography* **37**: 696-706.
- DUFORT M.J. (2015): An augmented supermatrix phylogeny of the avian family Picidae reveals uncertainty deep in the family tree. — *Molecular Phylogenetics and Evolution* **94**: 313-326.
- DUNNING J.B. Jr (1993): CRC Handbook of avian body masses. — CRC Press, Boca Raton, Florida. pp.
- EDWARDS S.V. & P. BEERLI (2000): Gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. — *Evolution* **54**: 1839-1854.
- ELIAS S.A. & J. BRIGHAM-GRETTE (2013): Glaciations: Late Pleistocene glacial events in Beringia. — In: ELIAS S. (eds), *Encyclopedia of Quaternary Science*. 2<sup>nd</sup> ed. — Elsevier, Amsterdam: 191-201.
- ELIAS S.A., SHORT S.K., NELSON C.H. & H.H. BIRKS (1996): Life and times of the Bering land bridge. — *Nature* **382**: 60-63.
- EL-SAADAWIA W., YOUSSEF S.G. & M.M. KAMAL-EL-DIN (2004): Fossil palm woods of Egypt: II. Seven Tertiary Palmoxydon species new to the country. — *Review of Palaeobotany and Palynology* **129**: 199-211.
- ERICSON P.G.P. (2012): Evolution of terrestrial birds in three continents: biogeography and parallel radiations. — *Journal of Biogeography* **39**: 813-824.
- FEDDUCIA A. & R.L. WILSON (1967): Avian fossils from the lower Pliocene of Kansas. — *Occ. Papers Mus. Zool. Univ. Michigan* **655**: 1-6.
- FERNANDO S.P. & S.S. SENEVIRATNE (2015): Quantitative analysis of the variation of plumage colouration in *Dinopium* flame-back complex of Sri Lanka. — *Wildlanka* **3**: 61-67.
- FLEISCHER R.C., KIRCHMAN J.J., DUMBACHER J.P., BEVIER L., DOVE C., ROTZEL N.C., EDWARDS S.V., LAMMERTINK M., MIGLIA K.J. & W.S. MOORE (2006): Mid-Pleistocene divergence of Cuban and North American ivory-billed woodpeckers. — *Biology Letters* **0490**: 1-4.
- FLOCKHART D.T.T. & K.L. WIEBE (2009): Absence of reproductive consequences of hybridization in the Northern Flicker (*Colaptes auratus*) hybrid zone. — *The Auk* **126**: 351-358.
- FREED L.A., WARAKAGODA D., CANN R.L., SIRIVARDANA U. & U. HETTIGE (2015): A hybrid swarm of *Dinopium* woodpeckers in Sri Lanka. — *The Wilson Journal of Ornithology* **127**: 13-20.
- FRETWELL S. (1978): Competition for discrete versus continuous resources: tests for predictions from the MacArthur-Levins models. — *The American Naturalist* **112**: 73-81.
- FRUGIS S., MALAGUZZI G., VICINI G. & P. CRISTINA (1988): Guida ai Picchi del mondo. — Museo Regionale di Scienze Naturali, Torino. 350 pp.
- FÜBRINGER M. (1888): Untersuchungen zur Morphologie und Systematik der Vögel: zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. Band 2: Allgemeiner Theil, Resultate und Reflexionen auf morphologischem Gebiete, systematische Ergebnisse und Folgerungen. — T.J. van Holkema, Amsterdam. Pp. 837-1717.
- FUCHS J. & R.C.K. BOWIE (2015): Concordant genetic structure in two species of woodpecker distributed across the primary West African biogeographic barriers. — *Molecular Phylogenetics and Evolution* **88**: 64-74.
- FUCHS J., OHLSON J.I., ERICSON P.G.P. & E. PASQUET (2006): Molecular phylogeny and biogeographic history of the piculets (Piciformes: Picumninae). — *Journal of Avian Biology* **37**: 487-496.
- FUCHS J., OHLSON J.I., ERICSON P.G.P. & E. PASQUET (2007): Synchronous intercontinental splits between assemblages of

- woodpeckers suggested by molecular data. — *Zoologica Scripta* **36**: 11-25.
- FUCHS J. & J.M. PONS (2015): A new classification of the Pied Woodpeckers assemblage (Dendropicini, Picidae) based on a comprehensive multi-locus phylogeny. — *Molecular Phylogenetics and Evolution* **88**: 28-37.
- FUCHS J., PONS J.M., LIU L., ERICSON P.G.P., COULOUX A. & E. PASQUET (2013): A multi-locus phylogeny suggests an ancient hybridization event between *Campephilus* and melanerpine woodpeckers (Aves: Picidae). — *Molecular Phylogenetics and Evolution* **67**: 578-588.
- GADOW H. (1891): Vögel. I. Anatomischer Theil. — In: BRONN H.G. (eds), H.G. Bronns Klassen und Ordnungen des Tierreichs wissenschaftlich dargestellt in Wort und Bild. — C.F. Winter'sche Verlagshandlung, Leipzig: 1-1008.
- GADOW H. (1893): Vögel. II. Systematischer Theil. — In: BRONN H.G. (eds), H.G. Bronns Klassen und Ordnungen des Tierreichs wissenschaftlich dargestellt in Wort und Bild. — C.F. Winter'sche Verlagshandlung, Leipzig: 1-303.
- GARCIA-DELREY E., DELGADO G., GONZALES J. & M. WINK (2007): Canary Island great spotted woodpecker (*Dendrocopos major*) has distinct mtDNA. — *Journal für Ornithologie* **148**: 531-536.
- GARCÍA-MORENO J. (2004): Is there a universal mtDNA clock for birds? — *Journal of Avian Biology* **35**: 465-468.
- GARROD A.H. (1874): On certain muscles of birds and their value in classification. Part II. — *Journal of Zoology* **42**: 111-123.
- GASTON K.J. (1998): Species-range size distributions: products of speciation, extinction and transformation. — *Philosophical Transactions of the Royal Society of London B Biological Sciences* **353**: 219-230.
- GASTON K.J. & F. HE (2002): The distribution of species range size: a stochastic process. — *Proceedings of the Royal Society of London, Series B Biological Sciences* **269**: 1079-1086.
- GENISE J.F., STRANECK R.J. & P.L. HAZELDINE (1993): Sapsucking in the White-fronted Woodpecker *Melanerpes formicivorus*. — *Ornithologia Neotropical* **4**: 77-82.
- GERMAN NATIONAL ACADEMY OF SCIENCES LEOPOLDINA (2014): Challenges and Opportunities of Integrative Taxonomy for Research and Society – Taxonomic Research in the Era of OMICS Technologies. — Deutsche Akademie der Naturforscher Leopoldina e.V. Nationale Akademie der Wissenschaften (German National Academy of Sciences), Halle/Saale. 54 pp.
- GLOGER C.L. (1834): Vollständiges Handbuch der Naturgeschichte der Vögel Europas mit besonderer Rücksicht auf Deutschland. Erster Theil, die deutschen Landvögel enthaltend. — August Schulz, Breslau. lvi+600 pp.
- GOODGE W.R. (1972): Anatomical evidence for phylogenetic relationships among woodpeckers. — *The Auk* **89**: 65-85.
- GOODWIN D. (1968): Notes on woodpeckers (Picidae). — *Bulletin of the British Museum (Natural History) Zoology* **17**: 1-44.
- GORMAN G. (2014): Woodpeckers of the World. The Complete Guide. — Christopher Helm / Bloomsbury Publishing Plc, London. 528 pp.
- GRAHAM B.A. & T.M. BURG (2012): Molecular markers provide insights into contemporary and historic gene flow for a non-migratory species. — *Journal of Avian Biology* **43**: 1-17.
- GRAY G.R. (1869): Hand-List of Genera and Species of Birds, distinguishing those contained in the British Museum Part 1, Accipitres, Fissirostres, Tenuirostres, and Dentiostres. — Trustees of the British Museum, London. xx+404 pp.
- GRAY G.E. (1870): Hand-List of Genera and Species of Birds, distinguishing those contained in the British Museum. Part 2, Conirostres, Scansores, Columbae, and Gallinae. — Trustees of the British Museum, London. xv+278 pp.
- GREENWAY J.C., Jr (1940): Oriental forms of *Picus canus*. — *The Auk* **57**: 550-560.
- GRIMALDI D. & G.R. CASE (1995): A feather in amber from the Upper Cretaceous of New Jersey. — *American Museum Novitates* **3126**: 1-6.
- HACKETT S.J., KIMBALL R.T., REDDY S., BOWIE R.C.K., BRAUN E.L., BRAUN M.J., CHOJNOWSKI J.L., COX W.A., HAN K.L., HARSHMAN J., HULLDLESTON C.J., MARKS B.D., MIGLIA K.J., MOORE W.S., SHELDON F.H., STEADMAN D.W., WITT C.C. & T. YURI (2008): A phylogenomic study of birds reveals their evolutionary history. — *Science* **320**: 1763-1767.
- HADOW H.H. (1973): Winter ecology of migrant and resident Lewis Woodpeckers in Southeastern Colorado. — *The Condor* **75**: 210-224.
- HAFFER J. (1969): Speciation in Amazonian forest birds. — *Science* **165**: 131-137.
- HAFFER J. (1986): Über Superspezies bei Vögeln. — *Annalen des Naturhistorischen Museums Wien, Serie B (Botanik und Zoologie)* **88/89**: 147-166.
- HANULA J.L. & R.T. ENGSTROM (2000): Comparison of red-cockaded Woodpecker (*Picoides borealis*) nestling diet in old-growth and old-field longleaf pine (*Pinus palustris*) habitats. — *American Midland Naturalist* **144**: 370-376.
- HANULA J.L. & K.E. FRANZREB (1995): Arthropod prey of nestling Red-cockaded Woodpeckers in the upper coastal plain of South Carolina. — *Wilson Bulletin* **107**: 485-495.
- HARGITT E. (1890): Catalogue of the Birds in the British Museum. XVIII. Catalogue of the Picariae in the Collection of the British Museum. Scansores, containing the family Picidae. — Trustees of the British Museum, London. xv+597 pp.
- HAZLER R., DRUMTRA D.E.W., MARSHALL M.R., COOPER R.J. & P.B. HAMEL (2004): Common, but commonly overlooked: Red-bellied woodpeckers as songbird nest predators. — *Southeastern Naturalist* **3**: 467-474.
- HESS C.A. & F.C. JAMES (1998): Diet of the Red-cockaded Woodpecker in the Apalachicola National Forest. — *Journal of Wildlife Management* **62**: 509-517.
- HOGSTAD O. (1976): Sexual dimorphism and divergence in winter foraging behaviour of Three-toed Woodpeckers *Picoides tridactylus*. — *Ibis* **118**: 41-50.
- HOGSTAD O. (1993): Why is the Three-toed Woodpecker (*Picoides tridactylus*) more sexually dimorphic than other European Woodpeckers? — *Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg* **67**: 109-118.
- HOGSTAD O. (2008): Sexual bill dimorphism supports separation of the woodpecker genera *Dendrocopos* KOCH (1816) in the Palaeartic and *Picoides* LACÉPÈDE (1799) in the Nearctic. — *Ornis Norvegica* **31**: 183-188.
- HOLT B.G., LESSARD J.P., BORREGAARD M.K., FRITZ S.A., ARAÚJO M.B., DIMITROV D., FABRE P.H., GRAHAM C.H., GRAVES G.R., JONSSON K.A., NOGUÉS-BRAVO D., WANG Z., WHITTAKER R.J., FJELDÅ J. & C. RAHBEK (2013): An update of Wallace's zoogeographic regions of the world. — *Science* **339**: 74-78.



- HOPKINS D.M. (1967): The Cenozoic history of Beringia - A synthesis. — In: HOPKINS D.M. (eds), The Bering Land Bridge. — Stanford University Press, Stanford, CA: 451-481.
- HUGHES J.B., ROUND P.D. & D.S. WOODRUFF (2003): The Indo-Chinese-Sundaic faunal transition at the Isthmus of Kra: an analysis of resident forest bird species distributions. — *Journal of Biogeography* **30**: 569-580.
- HUSAK M.S. & A.L. HUSAK (2003): Latitudinal patterns in range sizes of New World woodpeckers. — *Southwestern Naturalist* **48**: 61-69.
- IBARRA-CERDEÑA C.N., ÑIGUEZ-DÁVALOS L.I. & V. SÁNCHEZ-CORDERO (2005): Pollination ecology of *Stenocereus queretaroensis* (Cactaceae), a chiropterophilous columnar cactus, in a tropical dry forest of Mexico. — *American Journal of Botany* **92**: 503-509.
- ILLIGER C. (1811): *Prodromus systematis mammalium et avium*. — C. Salfeld, Berlin. xviii+301 pp.
- ILLIGER J.K.W. (1816): *Tabellarische Uebersicht der Vertheilung der Vögel über die Erde*. — *Abhandlungen der Kaiserlichen Akademie der Wissenschaften in Berlin, Physikalische Klasse* **1812-13**: 222-236 (ix Tables).
- INTERNATIONAL COMMISSION ON STRATIGRAPHY (2009): *International Stratigraphic Chart*.
- JACKSON J.A. (1970a): Character variation in the Hairy Woodpecker (*Dendrocopos villosus*). Ph. D. dissertation. — University of Kansas, Lawrence, Kansas. 340 pp.
- JACKSON J.A. (1970b): A quantitative study of the foraging ecology of Downy Woodpeckers. — *Ecology* **51**: 318-323.
- JÁNOSSY D. (1974): Die mittelpleistozäne Vogelfauna von Hundsheim (Niederösterreich). — *Sitzungsberichte der Österr. Akademie der Wissenschaften, Mathem.-naturw. Kl., Abt. I* **182**: 211-257.
- JARVIS E.D., MIRARAB S., ABERER A.J., LI B., HOUE P., LI C., HO S.Y.W., FAIRCLOTH B.C., NABHOLZ B., HOWARD J.T., SUH A., WEBER C.C., DA FONSECA R.R., LI J., ZHANG F., LI H., ZHOU L., NARULA N., LIU L., GANAPATHY G., BOUSSAU B., BAYZID M.S., ZAVIDOVYCH V., SUBRAMANIAN S., GABALDÓN T., CAPELLA-GUTIÉRREZ S., HUERTA-CEPAS J., REKEPALLI B., MUNCH K., SCHIERUP M., LINDOW B., WARREN W.C., RAY D., GREEN R.E., BRUFORD M.W., ZHAN X., DIXON A., LI S., LI N., HUANG Y., DERRYBERRY E.P., BERTELSEN M.F., SHELDON F.H., BRUMFIELD R.T., MELLO C.V., LOVELL P.V., WIRTHLIN M., SCHNEIDER M.P.C., PROSDOCIMI F., SAMANIEGO J.A., VELAZQUEZ A.M.V., ALFARO-NÚÑEZ A., CAMPOS P.F., PETERSEN B., SICHERITZ-PONTEN T., PAS A., BAILEY T. et al. (2014): Whole-genome analyses resolve early branches in the tree of life of modern birds. — *Science* **346**: 1320-1331.
- JOHNSON N.K. & C.B. JOHNSON (1985): Speciation in sapsuckers (*Sphyrapicus*): II. Sympatry, hybridization, and mate preference in *S. ruber daggetti* and *S. nuchalis*. — *The Auk* **102**: 1-15.
- JOHNSON N.K. & R.M. ZINK (1983): Speciation in sapsuckers (*Sphyrapicus*): I. Genetic differentiation. — *The Auk* **100**: 871-884.
- KERR K.C., LIJTMAR D.A., BARREIRA A.S., HEBERT P.D.N. & P.L. TUBARO (2009): Probing evolutionary patterns in neotropical birds through DNA barcodes. — *PLoS ONE* **4**: e4379.
- KESSLER J.E. (2014): Fossil and subfossil bird remains and faunas from the Carpathian Basin. — *Ornis Hungarica* **22**: 65-125.
- KILHAM L. (1965): Differences in feeding behavior of male and female Hairy Woodpeckers. — *Wilson Bulletin* **77**: 134-145.
- KIRBY V.C. (1980): An adaptive modification in the ribs of woodpeckers and piculets (Picidae). — *The Auk* **97**: 521-532.
- KLICKA J., SPELLMAN G.M., WINKER K., CHUA V. & B.T. SMITH (2011): A phylogeographic and population genetic analysis of a widespread, sedentary North American bird: The Hairy Woodpecker (*Picoides villosus*). — *The Auk* **128**: 346-362.
- KNOWLES L.L. (2004): The burgeoning field of statistical phylogeography. — *J. evol. Biol.* **17**: 1-10.
- KOCH R.F., COURCHESNE A.E. & C.T. COLLINS (1970): Sexual differences in foraging behavior of White-headed Woodpeckers. — *Bulletin Southern California Academy of Sciences* **69**: 60-64.
- KOJIMA K. & S. MATSUOKA (1985): Studies on the food habits of four sympatric species of woodpeckers II: Black woodpecker *Dryocopus martius* from winter to early spring. — *Tori* **341**: 1-6.
- KOLEFF P. & K.J. GASTON (2001): Latitudinal gradients in diversity: real patterns and random models. — *Ecography* **24**: 341-351.
- KOTAKA N., OZAKI K., TOGUCHI Y., KINJO M. & K. ISHIDA (2006): Extraordinary sexual differences in foraging niche in the Okinawa Woodpecker on a subtropical island. — *Journal für Ornithologie* **147**: 196.
- KRATTER A.W. (1998): The nests of two bamboo specialists—*Celeus spectabilis* (Rufous-headed Woodpecker) and *Cercomacra manu* (Manu Antbird). — *Journal of Field Ornithology* **69**: 37-44.
- LAMMERTINK M., KOPUCHIAN C., BRANDL H.B., TUBARO P.L. & H. WINKLER (2015 in press): A striking case of deceptive woodpecker colouration: the threatened Helmeted Woodpecker *Dryocopus galeatus* belongs in the genus *Celeus*— *Journal of Ornithology*. doi: 10.1007/s10336-015-1254-x
- LAYBOURNE R.C., DEEDRICK D.W. & F.M. HUEBER (1994): Feather in amber is Earliest New World fossil of Picidae. — *Wilson Bulletin* **106**: 18-25.
- LEIBER A. (1907): *Vergleichende Anatomie der Spechtzunge*. *Zoologica* No. 51. — E. Schweizerbart, Stuttgart. 84 pp.
- LEITE G.A., FIGUEIRA R.T.P.D.G.M.J.E. & J.H.C. DELABIE (2013): Foraging behavior of Kaempfer's Woodpecker (*Celeus obrieni*), a bamboo specialist. — *The Condor* **115**: 221-229.
- LEONARD D.L. Jr & J.A. HEATH (2010): Foraging strategies are related to skull morphology and life history traits of *Melanerpes* woodpeckers. — *Journal für Ornithologie* **151**: 771-777.
- LI J.T., WANG J.S., NIAN H.H., LITVINCHUK S.N., WANG J., LI Y., RAO D.Q. & S. KLAUS (2015): Amphibians crossing the Bering Land Bridge: Evidence from holarctic treefrogs (*Hyla*, Hylidae, Anura). — *Molecular Phylogenetics and Evolution* **87**: 80-90.
- LIGON J.D. (1968): Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. — *The Auk* **85**: 203-215.
- LINNAEUS C. (1740): *Systema Naturae in quo naturae regna tria naturae, secundum, classes, ordines, genera et species, systematicae proponuntur*. — Gottfr. Kiesewetter, Stockholm. ii+80 pp.
- LINNAEUS C. (1758): *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. — Holmiae. (Salvius), Stockholm. iv+824 pp.

- LÖHRL H. (1972): Zum Nahrungserwerb beim Buntspecht (*Dendrocopos major*). — Anzeiger der ornithologischen Gesellschaft Bayern **11**: 248-253.
- LORENZ K. (1941): Vergleichende Bewegungsstudien an Anatiden. — Journal für Ornithologie **79** (Sonderheft): 194-294.
- LUCAS F.A. (1895): The tongues of woodpeckers. — Bulletin Division of Ornithology and Mammalogy U. S Department of Agriculture **7**: 35-42.
- MANEGOLD A. & A. LOUCHART (2012): Biogeographic and paleoenvironmental implications of a new woodpecker species (Aves, Picidae) from the early Pliocene of South Africa. — Journal of Vertebrate Paleontology **32**: 926-938.
- MANEGOLD A., LOUCHART A., CARRIER J. & A. ELZANOWSKI (2013): The Early Pliocene avifauna of Langebaanweg (South Africa): a review and update. — In: GÖHLICH U.B. & A. KROH (eds), Paleornithological Research 2013. Proceed. 8<sup>th</sup> Internat. Meeting Society of Avian Paleontology and Evolution. — Verlag Naturhistorisches Museum Wien, Vienna: 135-152.
- MANEGOLD A. & T. TÖPFER (2012): The systematic position of *Hemicircus* and the stepwise evolution of adaptations for drilling, tapping and climbing up in true woodpeckers (Picinae, Picidae). — Journal of Zoological Systematics and Evolutionary Research **51**: 72-82.
- MANEGOLD A. & J. WHITE (2014): Morphologische Anpassungen an das Klettern und Hacken beim Hüpfspecht *Nesocittes micromegas* (Picidae, Piciformes) dargestellt mit Hilfe der Computertomografie. — Die Vogelwarte **52**: 324-325.
- MARSHALL C.J. & J.K. LIEBHERR (2000): Cladistic biogeography of the Mexican transition zone. — Journal of Biogeography **27**: 203-216.
- MARTENS J., TIETZE D.T. & M. PÄCKERT (2011): Phylogeny, biodiversity, and species limits of passerine birds in the Sino-Himalayan region—A critical review. — Ornithological Monographs **70**: 64-94.
- MARTIN P.R. & J.J. TEWKSBURY (2008): Latitudinal variation in sub-specific diversification of birds. — Evolution **62**: 2775-2788.
- MARTINDALE S. (1983): Foraging patterns of nesting Gila woodpeckers. — Ecology **64**: 888-898.
- MARTINDALE S. & D. LAMM (1984): Sexual dimorphism and parental role switching in Gila Woodpeckers. — Wilson Bulletin **96**: 116-121.
- MAYR E. (1944): Wallace's Line in the light of recent zoogeographic studies. — Quarterly Review of Biology **19**: 1-14.
- MAYR E. (1946): History of the North American bird fauna. — Wilson Bulletin **58**: 1-68.
- MAYR E. (1963): Animal Species and Evolution. — Belknap - Harvard University Press, Cambridge, MA. 602 pp.
- MAYR E. (1965): Numerical phenetics and taxonomic theory. — Systematic Zoology **14**: 73-97.
- MAYR E. & W.J. BOCK (2002): Classifications and other ordering systems. — Journal of Zoological Systematics and Evolutionary Research **40**: 169-194.
- MAYR E. & L.L. SHORT (1970): Species taxa of North American birds. A contribution to comparative systematics. — Publ. Nuttall Ornithol. Club **9**: 1-127.
- MAYR G. (2001): The earliest fossil record of a modern-type piciform bird from the late Oligocene of Germany. — Journal für Ornithologie **142**: 2-6.
- MENGEL R.M. & J.A. JACKSON (1977): Geographic variation of the Red-cockaded Woodpecker. — The Condor **79**: 349-355.
- MERMOD M., REICHLIN T.S., ARLETTAZ R. & M. SCHAUB (2009): The importance of ant-rich habitats for the persistence of the Wryneck *Jynx torquilla* on farmland. — Ibis **151**: 731-742.
- MIKUSIŃSKI G. (2006): Woodpeckers: distribution, conservation, and research in a global perspective. — Annales Zoologici Fennici **43**: 86-95.
- MILNE EDWARDS A. (1869-1874): Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Tom. 2. — Librairie de G. Mason, Paris. 632 pp.
- MLIKOVSKÝ J. (2002): Cenozoic Birds of the World Part 1: Europe. — Ninox Press, Praha. 417 pp.
- MOORE W.S. & D.B. BUCHANAN (1985): Stability of the Northern Flicker hybrid zone in historical times: Implications for adaptive speciation theory. — Evolution **39**: 135-151.
- MOORE W.S., GRAHAM J.H. & J.T. PRICE (1991): Mitochondrial DNA Variation in the Northern Flicker (*Colaptes auratus*, Aves). — Molecular Biology and Evolution **8**: 327-344.
- MOORE W.S. & W.D. KOENIG (1986): Comparative reproductive success of Yellow-shafted, Red-shafted and hybrid flickers across a hybrid zone. — The Auk **103**: 42-51.
- MOORE W.S. & K.J. MIGLIA (2009): Woodpeckers, toucans, barbets, and allies (Piciformes). — In: HEDGES S.B. & S. KUMAR (eds), The Timetree of Life. — Oxford University Press, : 445-450.
- MOORE W.S., OVERTON L.C. & K.J. MIGLIA (2010): Mitochondrial DNA based phylogeny of the woodpecker genera *Colaptes* and *Piculus*, and implications for the history of woodpecker diversification in South America. — Molecular Phylogenetics and Evolution **58**: 76-84.
- MOORE W.S. & J.T. PRICE (1993): The nature of selection in the Northern Flicker Hybrid zone and its implications for speciation theory. — In: HARRISON R.G. (eds), Hybrid zones and the evolutionary process. — Oxford University Press, New York: 196-225.
- MOORE W.S., WEIBEL A.C. & A. AGIUS (2006): Mitochondrial DNA phylogeny of the woodpecker genus *Veniliornis* (Picidae, Picinae) and related genera implies convergent evolution of plumage patterns. — Biological Journal of the Linnean Society **87**: 611-624.
- MUSCHKETAT L.F. & K.F. RAQUÉ (1993): Nahrungsökologische Untersuchungen an Grünspechten (*Picus viridis*) als Grundlage zur Habitatpflege. — Beih. Veröff. Natursch. Landschaftspf. Bad.-Württ. **67**: 71-81.
- NAHUM L.A., PEREIRA S.L., DE CAMPOS FERNANDES F.M., MATIOLI S.R. & A. WAJNTAL (2003): Diversification of Ramphastinae (Aves, Ramphastidae) prior to the Cretaceous/Tertiary boundary as shown by molecular clock of mtDNA sequences. — Genetics and Molecular Biology **26**: 411-418.
- NATIONS J.D., SWIFT R.L., CROXEN F. & R. BETTS (2009): Stratigraphic, Sedimentologic, and Paleobotanical Investigations of Terrace Gravels, U.S. Army Yuma Proving Ground. Contributed Report CR-09-A. — Arizona Geological Survey, Tucson. vi+91 pp.
- NETO F.L. (1995): Um h'brido entre *Picumnus cirratus temminckii* e *P. albosquamatus guttifer* (Piciformes: Picidae). — Ararajuba **3**: 68-69.
- OHL M. (2014): Principles of taxonomy and classification: current procedures for naming and classifying organisms. — In: HENKE W., HARDT T. & I. TATTERSALL (eds), Handbook of Paleoanthropology. — Springer-Verlag, Berlin, Heidelberg: 141-166.

- OJEDA V. (2003): Magellanic woodpecker frugivory and predation on a lizard. — *Wilson Bulletin* **115**: 208-210.
- OJEDA V.S. & M.L. CHAZARRETA (2006): Provisioning of Magellanic Woodpecker (*Campephilus magellanicus*) nestlings with vertebrate prey. — *The Wilson Journal of Ornithology* **118**: 251-254.
- ONIKI Y. & E.O. WILLIS (1998): Nesting of Yellow-fronted Woodpeckers, *Melanerpes flavifrons* (Picidae). — *Ornithologia Neotropical* **9**: 81-85.
- OUELLET H. (1977): Relationships of woodpecker genera *Dendrocopos* KOCH and *Picoides* LACÉPÈDE, (Aves, Picidae). — *Ardea* **65**: 165-183.
- PACHECO M.A., BATTISTUZZI F.U., LENTINO M., AGUILAR R.F., KUMAR S. & A.A. ESCALANTE (2011): Evolution of modern birds revealed by mitogenomics: timing the radiation and origin of major orders. — *Molecular Biology and Evolution* **28**: 1927-1942.
- PÄCKERT M., MARTENS J., TIETZE D.T., DIETZEN C., WINK M. & L. KVIST (2007): Calibration of a molecular clock in tits (Paridae) – Do nucleotide substitution rates of mitochondrial genes deviate from the 2% rule? — *Molecular Phylogenetics and Evolution* **44**: 1-14.
- PADIAL J.M., MIRALLES A., DE LA RIVA I. & M. VENCES (2010): The integrative future of taxonomy. — *Frontiers in Zoology* **7**: 16.
- PARKER T.A. III & O. ROCHA O. (1991): Notes on the status and behaviour of the Rusty-necked Piculet *Picumnus fuscus*. — *Bulletin of the British Ornithologists' Club* **111**: 91-92.
- PATON T., HADDRATH O. & A.J. BAKER (2002): Complete mitochondrial DNA genome sequences show that modern birds are not descended from transitional shorebirds. — *Proceedings of the Royal Society of London, Series B Biological Sciences* **269**: 839-846.
- PONS J.M., OLIOSO G., CRUAUD C. & J. FUCHS (2010): Phylogeography of the Eurasian green woodpecker (*Picus viridis*). — *Journal of Biogeography* **38**: 311-325.
- PEREIRA S.L. & A.J. BAKER (2006): A mitogenomics timescale for birds detects variable phylogenetic rates of molecular evolution and refutes the standard molecular clock. — *Molecular Biology and Evolution* **23**: 1731-1740.
- PERKTAS U., BARROWCLOUGH G.F. & J.G. GROTH (2011): Phylogeography and species limits in the green woodpecker complex (Aves: Picidae): multiple Pleistocene refugia and range expansion across Europe and the Near East. — *Biological Journal of the Linnean Society* **104**: 710-723.
- PERKTAS U. & E. QUINTERO (2013): A wide geographical survey of mitochondrial DNA variation in the great spotted woodpecker complex, *Dendrocopos major* (Aves: Picidae). — *Biological Journal of the Linnean Society* **108**: 173-188.
- PETERS J.L. (1948): Check-list of birds of the world, vol. VI. — Harvard Univ. Press, Cambridge, Mass. xi+259 pp.
- PRUM R.O. (2014): Interspecific social dominance mimicry in birds. — *Zoological Journal of the Linnean Society* **172**: 910-941.
- PRUM R.O., BERV J.S., DORNBURG A., FIELD D.J., TOWNSEND J.P., LEMMON E.M. & A.R. LEMMON (2015): A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. — *Nature* **526**: 569-573.
- PRYCHITKO T.M. & W.S. MOORE (1997): The utility of DNA sequences of an intron from the  $\beta$ -fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). — *Molecular Phylogenetics and Evolution* **8**: 193-204.
- PRYCHITKO T.M. & W.S. MOORE (2000): Comparative evolution of the mitochondrial cytochrome *b* gene and nuclear  $\beta$ -fibrinogen intron 7 in woodpeckers. — *Molecular Biology and Evolution* **17**: 1101-1111.
- PULGARÍN-RESTREPO P.C. & T.M. BURG (2012): Genetic signals of demographic expansion in Downy Woodpecker (*Picoides pubescens*) after the last North American Glacial Maximum. — *PLoS ONE* **7**: e40412.
- RASMUSSEN P.C. & J.C. ANDERTON (2005): *Birds of South Asia: The Ripley guide. vol. 2 (Attributes and status)*. — Lynx Edicions, Barcelona. 688 pp.
- RÊGO M.A., DEL-RIO G. & L.F. SILVEIRA (2014): A taxonomic review of *Picumnus exilis* (Aves: Picidae) reveals an underestimation of Piculet species diversity in South America. — *Journal für Ornithologie* **155**: 853-867.
- REMSEN J.V. Jr (2015): *HBW and BirdLife International Illustrated Checklist of the Birds of the World Volume 1: Non-passerines* Josep del Hoyo and Nigel J. Collar 2014. — *Journal of Field Ornithology* **86**: 182-187.
- RENSCH B. (1926): Der Rassenkreis der Felsenschnecke *Campylaea zonata* Studer. — *Zoologischer Anzeiger, Jena* **67**: 253-263.
- REPASKY R.R., BLUE R.J. & P.D. DOERR (1991): Laying Red-cockaded Woodpeckers cache bone fragments. — *The Condor* **93**: 458-461.
- RIPLEY S.D. & B.M. BEEHLER (1990): Patterns of speciation in Indian birds. — *Journal of Biogeography* **17**: 639-648.
- ROMERO A. (2012): When whales became mammals: the scientific journey of cetaceans from fish to mammals in the history of science. — In: ROMERO A. & E.O. KEITH (eds), *New Approaches to the Study of Marine Mammals*. — InTech. Available from: <http://www.intechopen.com/books/new-approaches-to-the-study-of-marine-mammals/when-whales-became-mammals-the-scientific-journey-of-cetaceans-from-fish-to-mammals-in-the-history-o>.
- RONQUIST F. (1997): Phylogenetic approaches in coevolution and biogeography. — *Zoologica Scripta* **26**: 313-322.
- RONQUIST F., TESLENKO M., VAN DER MARK P., AYRES D.L., DARLING A., HÖHNA S., LARGET B., LIU L., SUCHARD M.A. & J.P. HUELSENBECK (2012): MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. — *Systematic Biology* **61**: 539-542.
- RUDOLPH D.C., CONNER R.N. & R.R. SCHAEFER (1991): Yellow-bellied Sapsuckers feeding at Red-cockaded Woodpecker resin wells. — *Wilson Bulletin* **103**: 122-123.
- RUGE K. (2014): Der Dreizehenspecht (*Picoides tridactylus*) am Feldberg – Eine Einführung. — *Die Vogelwarte* **52**: 82-83.
- SANDERSON, M.J. (2003): R8s: inferring absolute rates of evolution and divergence times in the absence of a molecular clock. — *Bioinformatics* **19**: 301-302.
- SANDERSON M.J., PURVIS A. & C. HENZE (1998): Phylogenetic supertrees: assembling the trees of life. — *Trends in Ecology and Evolution* **13**: 105-109.
- SANDOVAL L., BIAMONTE E. & A. SOLANO-UGALDE (2008): Previously unknown food items in the diet of six neotropical bird species. — *The Wilson Journal of Ornithology* **120**: 214-216.
- SCHLICK-STEINER B.C., STEINER F.M., SEIFERT B., STAUFFER C., CHRISTIAN E. & R.H. CROZIER (2010): Integrative taxonomy: a multisource approach to exploring biodiversity. — *Annual Review of Entomology* **55**: 421-438.

- SENEVIRATNE S.S., TOEWS D.P.L., BRELSFORD A. & D.E. IRWIN (2012): Concordance of genetic and phenotypic characters across a sapsucker hybrid zone. — *Journal of Avian Biology* **43**: 119-130.
- SELANDER R.K. (1966): Sexual dimorphism and differential niche utilization in birds. — *The Condor* **68**: 113-151.
- SHORT L.L. (1965): Hybridization in the flickers (*Colaptes*) of North America. — *Bulletin of the American Museum of Natural History* **129**: 307-428.
- SHORT L.L. (1967): Variation in Central American Flickers. — *Wilson Bulletin* **79**: 5-21.
- SHORT L.L. (1970): The affinity of African with Neotropical woodpeckers. — *Ostrich* **8** (suppl.): 35-40.
- SHORT L.L. (1971): The evolution of terrestrial woodpeckers. — *American Museum Novitates* **2467**: 1-23.
- SHORT L.L. (1972a): Relationships among the four species of the superspecies *Celeus elegans* (Aves, Picidae). — *American Museum Novitates* **2487**: 1-26.
- SHORT L.L. (1972b): Systematics and behavior of South American flickers (Aves, *Colaptes*). — *Bulletin of the American Museum of Natural History* **149**: 1-109.
- SHORT L.L. (1973a): Habits, relationships, and conservation of the Okinawa Woodpecker. — *Wilson Bulletin* **85**: 5-20.
- SHORT L.L. (1973b): A new race of *Celeus spectabilis* from eastern Brazil. — *Wilson Bulletin* **85**: 465-467.
- SHORT L.L. (1974): Habits of three endemic West Indian Woodpeckers (Aves, Picidae). — *American Museum Novitates* **2549**: 1-44.
- SHORT L.L. (1978): Sympatry in woodpeckers of lowland Malayan forest. — *Biotropica* **10**: 122-133.
- SHORT L.L. (1982): *Woodpeckers of the World*. — Delaware Museum of Natural History, Greenville, Delaware. xiii+676 pp.
- SHORT L.L. & J.J. MORONY Jr (1970): A second hybrid Williamson's × Red-naped Sapsucker and an evolutionary history of sapsuckers. — *The Condor* **72**: 310-315.
- SIBLEY C.G. & J.E. AHLQUIST (1972): A comparative study of the egg white proteins of non-passerine birds. *Bulletin* 39. — Peabody Museum of Natural History, Yale University, New Haven, Conn. vi+276 pp.
- SIBLEY C.G. & J.E. AHLQUIST (1990): Phylogeny and classification of birds. A study in molecular evolution. — Yale University Press, New Haven & London. 976 pp.
- SIBLEY C.G. & B.L. MONROE (1990): *Distribution and Taxonomy of Birds of the World*. — Yale University Press, New Haven, London. 1111 pp.
- SIMPSON S.F. & J. CRACRAFT (1981): The phylogenetic relationships of the Piciformes (Class Aves). — *The Auk* **98**: 481-494.
- SMITH T., ROSE K.D. & P.D. GINGERICH (2006): Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. — *Proceedings of the National Academy of Sciences of the United States of America* **103**: 11223-11227.
- SPINKS P.Q. & H.B. SHAFFER (2009): Conflicting mitochondrial and nuclear phylogenies for the widely disjunct *Emys* (Testudines: Emydidae) species complex, and what they tell us about biogeography and hybridization. — *Systematic Biology* **58**: 1-20.
- STEINBACHER J. (1934): Untersuchungen über den Zungenapparat indischer Spechte. — *Journal für Ornithologie* **82**: 399-408.
- STEINBACHER J. (1935): Über den Zungenapparat südafrikanischer Spechte. — *Orn. Mber.* **43**: 85-89.
- STEINBACHER J. (1941): Weitere Untersuchungen über den Zungenapparat afrikanischer Spechte. — *Orn. Mber.* **49**: 126-137.
- STEINBACHER J. (1955): Zur Morphologie und Anatomie des Zungenapparates brasilianischer Spechte. — *Senckenbergiana Biologica* **36**: 1-8.
- STEINBACHER J. (1957): Über den Zungenapparat einiger neotropischer Spechte. — *Senckenbergiana Biologica* **38**: 259-270.
- STYRSKY J.D. & J.N. STYRSKY (2003): Golden-fronted Woodpecker provisions nestlings with small mammal prey. — *Wilson Bulletin* **115**: 97-98.
- SWAINSON W. (1837): *The Natural History and Classification of Birds*. Vol. II. — Longman, Rees, Orme, Brown, Green & Longman, London. v+398 pp.
- SWANSON D.K. (2003): A comparison of taiga flora in north-eastern Russia and Alaska/Yukon. — *Journal of Biogeography* **30**: 1109-1121.
- SWIERCZEWSKI E.V. & R.J. RAIKOW (1981): Hind limb morphology, phylogeny, and classification of the Piciformes. — *The Auk* **98**: 466-480.
- TAVARES E.S., GONÇALVES P., MIYAKI C.Y. & A.J. BAKER (2011): DNA barcode detects high genetic structure within Neotropical bird species. — *PLoS ONE* **6**: e28543.
- TOBIAS J.A., SEDDON N., SPOTTISWOODE C.N., PILGRIM J.D., FISHPOOL L.D.C. & N.J. COLLAR (2010): Quantitative criteria for species delimitation. — *Ibis* **152**: 724-746.
- TSCHINKEL W.R. (2002): The natural history of the arboreal ant, *Crematogaster ashmeadi*. — *Journal of Insect Science* **2**: 12.
- UMANSKAJA A.S. (1981). Miocenove pticy Zapadnogo Pričernomor'ja USSR. Soobščenie II. [Miocene birds of western Pričernomor'e. Communication II.] *Vestnik Zoologii*, **17**: 17-21. (In Russian).
- VASCONCELOS M.F., D'ANGELO NETO S. & F.E. VIANA (2008): The white-browed woodpecker *Piculus aurulentus* (TEMMINCK, 1821) (Aves: Picidae) as a potential seed disperser of *Myrsine umbellata* MART. (Myrsinaceae). — *Lundiana* **9**: 159-160.
- VAURIE C. (1959): Systematic notes on Palearctic birds, No. 34; Picidae: The genera *Picus* and *Dryocopus*. — *American Museum Novitates* **1945**: 1-21.
- VEILLOT L.P. (1816): *Analyse d'une nouvelle ornithologie élémentaire*. — A. Belin, Paris. 70 pp.
- VILLARD P. & C. PAVIS (1998): Diet of nestling Guadeloupe Woodpeckers. — *Journal of Field Ornithology* **69**: 415-418.
- VON BUCHHOLZ H. (1986): Die Höhle eines Spechtvogels aus dem Eozän von Arizona, USA (Aves, Piciformes). — *Verhandlungen des naturwissenschaftlichen Vereins in Hamburg (Neue Folgen)* **28**: 5-25.
- VOOUS K.H. Jr (1947): On the history of the distribution of the genus *Dendrocopos*. — *Limosa* **20**: 1-142.
- VORIS, H.K. (2000): Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. — *Journal of Biogeography* **27**: 1153-1167.
- VUILLEUMIER F. & A.V. ANDORS (1993): Avian biological relationships between Africa and South America. — In: GOLDBLATT P. (eds), *Biological relationships between Africa and South America*. — Yale University Press, New Haven & London: 289-328.

- WALLACE R.A. (1974): Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. — *The Condor* **76**: 238-248.
- WATSON D.M. (2005): Diagnosable versus distinct: Evaluating species limits in birds. — *BioScience* **55**: 60-68.
- WEBB D.M. & W.S. MOORE (2005): A phylogenetic analysis of woodpeckers and their allies using 12S, Cyt b, COI nucleotide sequences (class Aves; order Piciformes). — *Molecular Phylogenetics and Evolution* **36**: 233-248.
- WEIBEL A.C. & W.S. MOORE (2002a): A test of a mitochondrial gene-based phylogeny of woodpeckers (Genus *Picoides*) using an independent nuclear gene, -fibrinogen intron 7. — *Molecular Phylogenetics and Evolution* **22**: 247-257.
- WEIBEL A.C. & W.S. MOORE (2002b): Molecular phylogeny of a cosmopolitan group of woodpeckers (Genus *Picoides*) based on *COI* and *cyt b* mitochondrial gene sequences. — *Molecular Phylogenetics and Evolution* **22**: 65-75.
- WEIBEL A.C. & W.S. MOORE (2005): Plumage convergence in *Picoides* woodpeckers based on a molecular phylogeny, with emphasis on convergence in Downy and Hairy Woodpeckers. — *The Condor* **107**: 797-809.
- WEIR J. & D. SCHLUTER (2004): Ice sheets promote speciation in boreal birds. — *Proceedings of the Royal Society of London, Series B Biological Sciences* **271**: 1881-1887.
- WEISSHAUPT N., ARLETTAZ R., REICHLIN T.S., TAGMANN-IOSET A. & M. SCHAUB (2011): Habitat selection by foraging Wrynecks *Jynx torquilla* during the breeding season: identifying the optimal habitat profile. — *Bird Study* **58**: 111-119.
- WETMORE A. (1930): A systematic classification for the birds of the world. — *Proceedings of the United States National Museum* **76** (24): 1-8.
- WETMORE A. (1931): Record of an unknown woodpecker from the Lower Pliocene. — *The Condor* **33**: 255-256.
- WETMORE A. (1937): Bird remains from cave deposits on Great Exuma Island in the Bahamas. — *Bulletin of the Museum of Comparative Zoology at Harvard College* **80**: 427-441.
- WETMORE A. (1960): A classification of the birds of the world. — *Smithsonian Miscellaneous Collections* **139**: 1-37.
- WIEBE K.L. (2000): Assortative mating by color in a population of hybrid Northern Flickers. — *The Auk* **117**: 525-529.
- WIEBE K.L. & G.R. BORTOLOTTI (2001): Variation in colour within a population of northern flickers: a new perspective on an old hybrid zone. — *Canadian Journal of Zoology* **79**: 1046-1052.
- WIEBE K.K. & G.R. BORTOLOTTI (2002): Variation in carotenoid-based color in Northern Flickers in a hybrid zone. — *Wilson Bulletin* **114**: 393-400.
- WINKLER H. (1972): Beiträge zur Ethologie des Blutspechts (*Dendrocopos syriacus*). Das nicht-reproduktive Verhalten. — *Zeitschrift für Tierpsychologie* **31**: 300-325.
- WINKLER H. (1979): Bemerkungen zum Maurenspecht, *Picoides major numidus*. — *Journal für Ornithologie* **120**: 290-298.
- WINKLER H., CHRISTIE D.A. & D. NURNEY (1995): Woodpeckers: A Guide to the Woodpeckers, Piculets and Wrynecks of the World. — Pica Press, Sussex. 406 pp.
- WINKLER H. & D. CHRISTIE (2002): Family Picidae (woodpeckers). — In: DEL HOYO J., ELLIOTT A. & J. SARGATAL (eds), *Handbook of the Birds of the World*. — Lynx Edicions, Barcelona: 296-555.
- WINKLER H., GAMAUF A., NITTINGER F. & E. HARING (2014): Relationships of Old World woodpeckers (Aves: Picidae) – new insights and taxonomic implications. — *Annalen des Naturhistorischen Museums Wien, Serie B (Botanik und Zoologie)* **116**: 69-86.
- WILEY E.O. (1988): Vicariance biogeography. — *Annual Review of Ecology and Systematics* **19**: 513-542.
- WOODRUFF D.S. (2003): The location of the Indochinese-Sundaic biogeographic transition in plants and birds. — *Natural History Bulletin of the Siam Society. Bangkok* **51**: 97-108.
- YAMASHINA Y. (1941): On the three endemic birds on the Ryukyu Islands. — *Trans. Bio.-Geogr. Soc. Japan* **3**: 319-328.
- YANG Z. & B. RANNALA (2012): Molecular phylogenetics: principles and practice. — *Nature Reviews Genetics* **13**: 303-314.
- ZACHOS J.C., DICKENS G.R. & R.E. ZEEBE (2008): An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. — *Nature* **451**: 279-283.
- ZELENKOV N.V. (2007): The structure and probable mechanism of evolutionary formation of the foot in piciform birds (Aves: Piciformes). — *Palaeontological Journal* **41**: 290-297.
- ZINK R.M., ROHWER S., ANDREEV A.V. & D.L. DITTMANN (1995): Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. — *The Condor* **97**: 639-649.
- ZINK R.M., DROVETSKI S.V. & S. ROHWER (2002a): Phylogeographic patterns in the Great Spotted Woodpecker (*Dendrocopos major*) across Eurasia. — *Journal of Avian Biology* **33**: 175-178.
- ZINK, R.M., ROHWER S., DROVETSKI S., BLACKWELL-RAGO R.C. & S.L. FARRELL (2002b): Holarctic phylogeography and species limits of Three-toed Woodpeckers. — *The Condor* **104**: 167-170.

## Address of the author:

Prof. Dr. Hans Winkler  
 Konrad-Lorenz-Institut of Ethology  
 Department of Integrative Biology and Evolution  
 Veterinary University Vienna  
 Savoyenstraße 1A  
 A-1160 Wien, Austria  
 E-mail: hans-christoph.winkler@oeaw.ac.at

# ZOBODAT - [www.zobodat.at](http://www.zobodat.at)

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Denisia](#)

Jahr/Year: 2015

Band/Volume: [0036](#)

Autor(en)/Author(s): Winkler Hans Christoph

Artikel/Article: [Phylogeny, biogeography and systematics 7-35](#)