

Relationships of Old World woodpeckers (Aves: Picidae) – new insights and taxonomic implications

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Abstract

The paper presents a phylogeny of Old World woodpeckers based on mitochondrial (cytochrome b, 12S rRNA). It complements published phylogenies of this group in several important aspects. A species that was formerly treated as part of the core group of pied woodpeckers of the genus *Dendrocopos*, turned out to be the closest relative of the Eurasian lesser spotted woodpecker (*Dryobates minor*), itself a representative of an American radiation. We identified the brown-fronted woodpecker, a bird of the Himalayan foothills, as the closest relative of the predominantly European middle spotted woodpecker. The latter is a close relative of the yellow-crowned woodpecker, widely distributed over India and other parts of South Asia. We include these three species in the genus *Leiopicus* (with species *medius*, *auriceps*, and *mahrattensis*). Further taxonomic recommendations resulted from analyses based on a short fragment of the cytochrome b gene. Among these is the inclusion of the genus *Mulleripicus* into *Dryocopus* that is represented both in the New and Old World. We present further details of our suggested taxonomy that covers the whole family Picidae in Appendix 2. Open questions concern, among others, the exact phylogenetic relationships of the two African woodpecker clades with Asian woodpeckers, and the phylogeographical and taxonomic structure of the great spotted woodpecker (*Dendrocopos major*) and its closest allies.

Key words: Picidae, phylogeny, woodpeckers, taxonomy.

Zusammenfassung

Diese Arbeit präsentiert eine auf Abschnitten des mitochondrialen Genoms (cytochrome b, 12S rRNA) basierende Phylogenie altweltlicher Spechte. Diese enthält im Vergleich zu bisher erschienen Phylogenien dieser Gruppe einige wichtige Ergänzungen. Eine bisher aufgrund offensichtlich konvergenter Gefiedermerkmale den eigentlichen Buntspechten (Gattung *Dendrocopos*) zugerechnete Art stellte sich als Schwesterart des Kleinspechts (*Dryobates minor*) heraus, der einer amerikanischen Radiation angehört. Als nächster Verwandter des vorwiegend in Europa vorkommenden Mittelspechts wurde der am Fuße des Himalayas vorkommende Braunstirnspecht identifiziert, der mit dem in Indien und anderen Bereichen Südasiens weit verbreitete Gelbscheitelspecht unmittelbar verwandt ist. Die drei Arten fassen wir in der Gattung *Leiopicus* (mit den Arten *medius*, *auriceps* und *mahrattensis*) zusammen. Weitere taxonomische Vorschläge ergaben sich aus phylogenetischen Analysen, die in erster Linie auf einem kurzen Abschnitt des cytochrome b Gens beruhen. Darunter befindet sich die Einordnung der Spechte der Gattung *Mulleripicus* in *Dryocopus*, die in der alten und neuen Welt vertreten ist. Weitere Details der neuen, von uns vorgeschlagenen Taxonomie werden präsentiert. Offene Fragen betreffen unter anderem die genauen

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phylogenetischen Beziehungen der zwei afrikanischen Stammlinien der Spechte zu den asiatischen Spechten und die phylogenetische, biogeografische und taxonomische Struktur der Verwandtschaftsgruppe des Buntspechts (*Dendrocopos major*).

Introduction

Woodpeckers represent one of the most diverse non-passeriform radiations with at least 28 genera and 216 species (SHORT 1982, WINKLER et al. 1995, WINKLER & CHRISTIE 2002). Despite being highly specialized in several morphological features, and in this respect rather uniform, they successfully colonized Africa, Asia, the Americas, and Europe, including some islands. They have, however, not colonized Madagascar and stopped basically at the Wallace's Line (there are two species on Sulawesi), and therefore do not occur in New Guinea and Australia. Woodpeckers are found in a variety of forests and woodlands, including rainforests and deserts with few trees or cacti. Some species in South America and Africa inhabit areas without trees and dig their nests into the ground. The habitat requirements of several species and concerns about their conservation have made them important target and flagship species particularly for forest habitats. However, quite a few species and subspecies still survive in small continental and island populations.

The apparent morphological uniformity of woodpeckers led researchers to base their classification primarily on plumage characteristics (SHORT 1982). However, recent analyses of molecular data have shown that the current classification of woodpeckers needs thorough revision (PRYCHITKO & MOORE 1997, DEFILIPPIS & MOORE 2000, PRYCHITKO & MOORE 2000, WEIBEL & MOORE 2002ab, WINKLER & CHRISTIE 2002, ZINK et al. 2002ab, WINKLER et al. 2005, WEBB & MOORE 2005, BENZ et al. 2006, BENZ & ROBBINS 2011, FUCHS et al. 2006, 2007, 2008, 2013). This implies that zoogeographical relations and patterns of adaptation and convergence within the family Picidae have to be critically re-examined as well. Both the New World and the Old World have been suggested as origin for the woodpeckers (SHORT 1982, BLACKBURN et al. 1998). Fossil finds (MAYR 2001) and the distribution of the honeyguides, now recognized as the sister group of woodpeckers (SWIERCZEWSKI & RAIKOW 1981, SIBLEY & AHLQUIST 1990, JOHANSSON & ERICSON 2003, PRYCHITKO & MOORE 2003), suggest an Old World origin of woodpeckers. However, an Asian origin of woodpeckers would explain the biogeography of extant species best (BLACKBURN et al. 1998). WINKLER & CHRISTIE (2002) also discuss the arguments for a possible African origin.

Undoubtedly, Asia contains the morphologically most diverse array of woodpeckers, represented by more than a dozen genera (WINKLER & CHRISTIE 2002). SHORT (1982) proposed the first comprehensive phylogenetic hypothesis regarding the relationships among these genera which was almost exclusively based on plumage characters and some behavioral data. Its details were at variance with other morphological and anatomical data (BOCK & MILLER 1959, BOCK 1963, GOODGE 1972), and even with interpretations of plumage patterns (GOODWIN 1968). MOORE and his collaborators provided the first molecular data that were suitable to shed some light into this confusing situation (PRYCHITKO & MOORE 1997, DEFILIPPIS & MOORE 2000, PRYCHITKO & MOORE 2000, WEIBEL & MOORE 2002a, 2002b, WEBB & MOORE 2005). Additional molecular evidence came from recent papers by BENZ et al. (2006), FUCHS et al. (2006, 2007, 2008, 2013), BENZ & ROBBINS (2011), and MANEGOLD & TÖPFER (2012) presented a cladistic analysis of 69 osteological characters and 18 picid species.

Dispersal abilities of woodpeckers are low. There are a few migratory species in North America. In Asia there is only one form (*Dendrocopos hyperythrus subrufinus*) that migrates, but it does not cross deserts or the sea. Although woodpeckers have difficulties in crossing physical or ecological barriers, they do expand ranges within a short time over great distances, provided suitable habitat is more or less contiguous. The Syrian woodpecker (*D. syriacus*) spread from Turkey to the Baltic Sea within a century. The black woodpecker (*Dryocopus martius*) in Europe and the pileated (*D. pileatus*) and red-bellied woodpecker (*Melanerpes carolinus*) in North America are quickly regaining areas formerly lost due to anthropogenic factors (GLUTZ & BAUER 1980, FOSTER et al. 2002). Huge areas occupied by genetically undifferentiated populations hallmark such range expansions (BALL & AVISE 1992, ZINK et al. 2002a).

Plate tectonics and global climate changes have not only determined the phylogeny of woodpeckers on an intercontinental scale (FUCHS et al. 2007, 2008), they affected woodpecker evolution in Asia throughout the Tertiary and Quaternary, too. Especially SE Asia's complex tectonic history (HALL 2002) and the profound effects that Pleistocene sea level changes had on the configuration of land and sea (VORIS 2000) created many opportunities for speciation by vicariance.

In this paper we present our analyses of Old World woodpeckers that complement previous findings of other authors, point out some problems that have not been resolved yet, and discuss taxonomic implications.

Material and methods

Samples: The 78 specimens investigated and the sequences from GenBank which were included in the analyses are listed in Appendix 1. Blood and tissues from muscle, skin samples (toe pad) were obtained in the field and from museum material. Furthermore, we used feather samples in two cases, and in one we were provided with already extracted DNA.

DNA extraction, amplification, sequencing: DNA extractions from museum material (skin from the foot pads) and feathers were performed in a 10% Chelex (Biorad) solution containing proteinase K (0.5 mg/ml). After incubation (4 h, 50°C, with agitation) solutions were heated to 95°C for 5 min and centrifuged for 1 min. The supernatant was purified using the QIAquick PCR Purification Kit (QIAGEN) with a final volume of 50 µl elution buffer. DNA from fresh tissue was extracted with the DNeasy tissue kit (QIAGEN) following the manufacturer's instructions. All the materials used for handling the skin or feather samples were irradiated with UV light prior to use. Negative controls were used in all procedures. PCR amplifications were carried out with an Eppendorf Thermocycler in a volume of 25 µl, containing 1 unit Dynazyme DNA polymerase (Finnzymes OY), 0.5 µM of each primer, and 0.2 mM of each dNTP. The solutions were heated to 95°C (2 min) and then put through 30 reaction cycles: 95°C (10 s), 58°C (10 s), 72°C (30 s), followed by a final extension at 72°C (5 min). For PCR reactions with DNA from fresh tissue 50–200 ng were used as template DNA. Optimal amounts of template DNA of Chelex extractions were determined empirically (2–10 µl of the DNA solution). Negative controls were carried out to screen for contaminated reagents: (1) control extractions (without DNA) instead of template; (2) reaction with H₂O instead of template. We

amplified entire mitochondrial genes for cytochrome b (cytb) and 12S rRNA (12S) with external primers (Appendix 1). For some samples two additional internal primer pairs for the 12S gene with overlap of at least 50 bp of adjacent fragments were used. In several cases, when only DNA of bad quality from museum specimens was available, we amplified a shorter fragment of the cytb gene (cytb-s) with an additional internal primer. These sequences served as basis for comparisons among closely related species. For *Dendrocopos auriceps*, 25 nucleotides at the 5' end of the 12S gene could not be determined, probably due to mutated primer binding sites in the tRNA-Phe gene. Therefore, a nested primer had to be used for this taxon, resulting in a slightly shorter sequence. PCR products were extracted from agarose gels using the Qiaquick Gel Extraction Kit (Qiagen) and sequenced directly (using the same primers as for PCR amplification) or cloned (TOPO TA Cloning Kit, Invitrogen). Sequencing of both strands was performed by MWG-Biotech (Ebersberg, Germany). The sequences are registered under the GenBank accession numbers given in the Appendix 1.

Phylogenetic analysis: Alignments were produced with MUSCLE version 3.8 (EDGAR 2004) and optimized manually. For the 12S alignment 31 sites were excluded from further analysis because they could not be aligned unambiguously. Phylogenetic analyses were undertaken for each gene independently (cytb: 930 bp, 12S: 969 bp) and in combination employing maximum likelihood ML (PHYML version 3.1, GUINDON et al. 2010) as well as with Bayesian analysis using MrBayes 3.2 (RONQUIST & HUELSENBECK 2003). The hLRT (hierarchical likelihood ratio test) implemented in ModelTest 2.1.4 (POSADA & CRANDALL 1998, DARRIBA et al. 2012) selected the GTR+I+G model for the full cytb – 12S data set, consistent with previous studies on cytb and 12S sequences in woodpeckers (WEBB & MOORE 2005). For the Bayesian analyses the data set was partitioned by genes, with the GTR+I+G model specified for each partition. All analyses were run for 2.000.000 generations with four Markov chains and uniform priors under default heating values sampling every 100 generations. The first 200,000 generations were discarded as burn-in. Checking with Tracer 1.5 (RAMBAUT & DRUMMOND, 2009) confirmed that stationarity of likelihoods was achieved before that point. Nodes with posterior probabilities less than 80% were collapsed. Partial trees based on short fragments of the cytb gene (cytb-s, 307 bp) were calculated with the PHYML, with either the HKY or GTR substitution model, depending on the results of ModelTest.

Results and discussion

Phylogeny based on combined cytb and 12S sequences

The complete data set (cytb and 12S) comprised 52 taxa. A tree inferred from a two-partitioned Bayesian analysis is depicted in Fig. 1. In this tree representatives of 21 (out of 28) currently recognized genera of the Picidae (WINKLER & CHRISTIE 2002) are represented. Old World wryneck (*Jynx torquilla*) splits from the basal node, followed by branches comprising piculets of the genera *Sasia* (Old World) and *Picumnus* (Old and New World). The next branch places *Nesocittes micromegas* as sister taxon to the Picinae. The remaining taxa, comprising the true woodpeckers, are divided into three major clades.

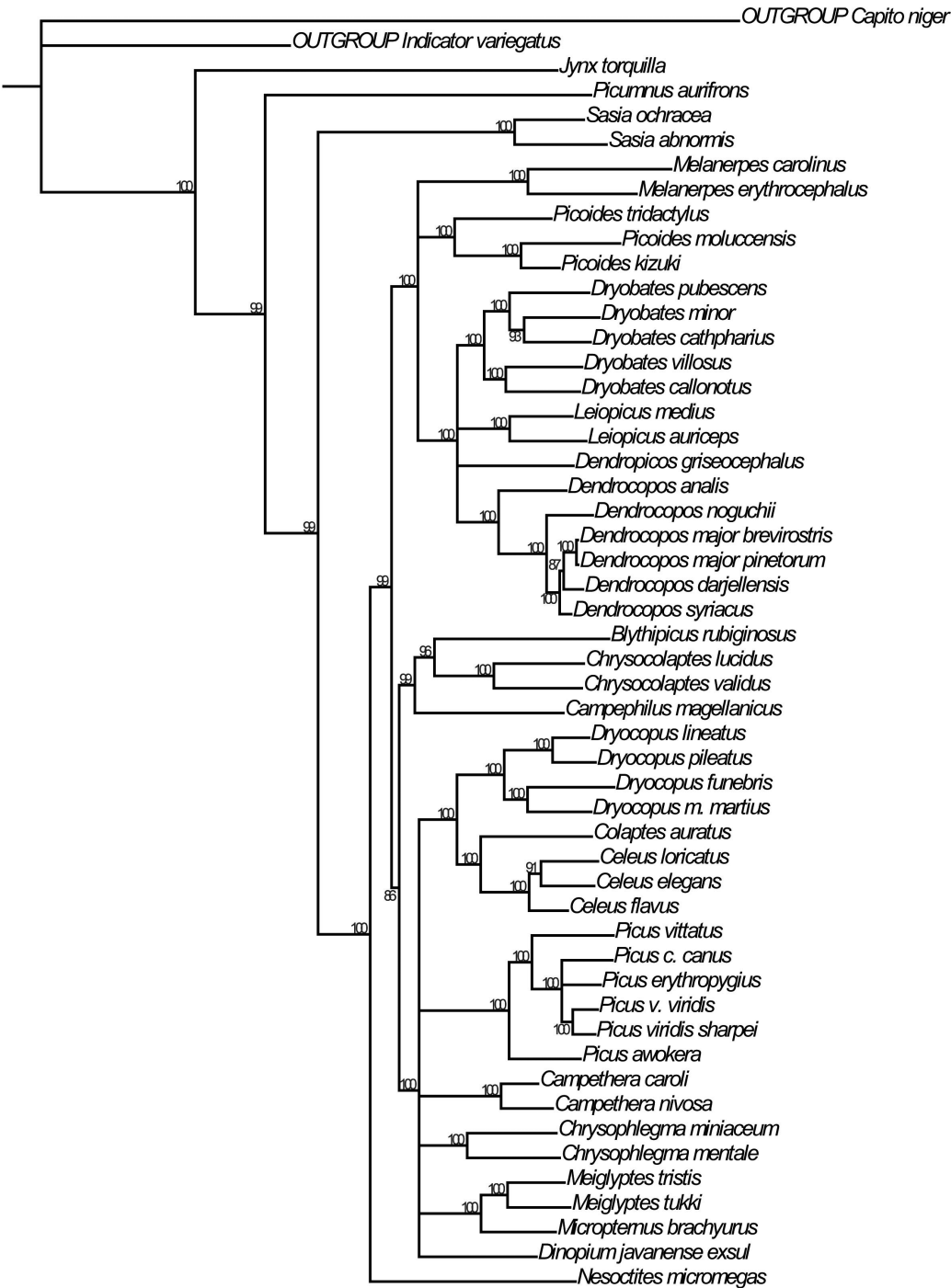


Fig. 1: Phylogenetic tree based on BI analysis of the combined cyt b and 12 S sequences. Taxon names refer to those suggested in Appendix 2. Numbers at the nodes are posterior probabilities expressed as percentages.

The first clade contains small to medium sized American and Eurasian species. The second clade holds the so called ivory-bills (CODY 1969). The remaining third clade comprises a diverse array of species, representing among others the logcocks (*Meglyptes*, *Micropternus*, *Dinopium*, *Dryocopus*; see CODY 1969) and ground foraging groups such as *Colaptes* and *Picus*.

The phylogeny in Fig. 1 corroborates and expands the results of previous molecular studies of woodpecker phylogenetic relationships (WEIBEL & MOORE 2002ab, WEBB & MOORE 2005, BENZ et al. 2006, FUCHS et al. 2006, 2007, 2008, 2013). It confirms that African woodpeckers (genera *Campethera* and *Dendropicos*) belong to two different lineages, that *Micropternus brachyurus* is related to *Meglyptes*, that *Mulleripicus* is embedded in *Dryocopus*, and that *Chrysocolaptes* together with *Blythipicus* are related to the New World ivory-bills (genus *Campephilus*). This study also corroborates that the plumage similarities of Asian *Dinopium* and *Chrysocolaptes* are due to convergence and not common descent.

Our analysis revealed new insights in the complex relationships within the pied woodpeckers (genera *Dendrocopos* and *Picoides*), including a new case of plumage parallelism. The great spotted woodpecker (*D. major*) and its relatives form a well supported monophyletic group to which *D. macei* also belongs. The close relationship between *D. leucotos*, *D. noguchii* and *D. major* has already been discussed by WINKLER et al. (2005). New is that the Darjeeling woodpecker (*D. darjellensis*) is a member of the *D. major* - lineage. Our results revealed an unexpected new case of convergent plumage parallelism: The crimson-breasted woodpecker (*D. cathpharius*) and the largely sympatric and somewhat bigger Darjeeling woodpecker form such a pair with striking plumage convergence, however, the former species has turned out to be a relative of the lesser spotted woodpecker (*D. minor*) which is part of the American pied woodpecker radiation (WEIBEL & MOORE 2002ab). Based on vocalizations, WINKLER & SHORT (1978) have already noted that the vocalizations of *D. cathpharius* differ from the larger *D. darjellensis* which were thought to be related because of plumage similarities.

SHORT (1982) subdivided the subfamily Picinae, the true woodpeckers, in six tribes (Melanerpini, Campetherini, Colaptini, Campephilini, Picini, Meglyptini) which clearly became obsolete with the new molecular studies. WEBB & MOORE (2005) proposed a new division into tribes that quickly was adopted by other authors (e.g. BENZ et al. 2006, FUCHS et al. 2008, 2013, MANEGOLD & TÖPFER 2012). However, besides being linguistically clumsy, the new names suggested by WEBB & MOORE (2005) are not based on available generic names (see DUBOIS 2006, p. 176). Thus "Malarpicini" and "Megapicini" are considered as not valid here, and we replace them with Picini (stem derived from the genus *Picus*) and Campephilini (name giving genus *Campephilus*) in the taxonomic overview presented in the Appendix 2. We also rather discard Dendropicini of WEBB & MOORE (2005) and Picoidini suggested by WINKLER (2009). We retain the Melanerpini (SHORT 1982) which would include SHORT's original tribe, part of his Campetherini and Colaptini (see Appendix 2). Within this tribe, *Melanerpes*, *Sphyrapicus*, and *Xiphidiopicus* form a distinct clade. The isolated position of *Hemicircus* (FUCHS et al. 2007, 2013, MANEGOLD & TÖPFER 2012) justifies putting the two species of this genus into a monogeneric tribe.

Our results suggest that *D. macei* is at the base of the *D. major* – *darjellensis* – *leucotos* clade, which is clearly at variance with the notion that *D. auriceps* is part of the *D. macei*

superspecies (SHORT 1982). Instead *D. auriceps* turns out to be related with the Eurasian middle spotted woodpecker (*D. medius*), and *D. mahrattensis* (FUCHS et al. 2007). RASMUSSEN & ANDERTON 2005 split *macei* into two species on the basis of coloration, size, and vocalizations. We could only sequence (short cytb) one specimen of the nominate form, which is clearly distinct from *analisis*. Thus we follow this suggestion and treat subspecies *westermani* and *macei* as belonging to species *macei* and the subspecies *longipennis*, *andamanensis* and *analisis* to species *analisis*.

Besides the *D. major*, *D. medius*, and the *D. minor* clades, there is a group of very small woodpeckers in the east and southeast of Asia that includes many island forms. They form a clade that contains not only *D. kizuki* and *D. moluccensis*, but also *D. canicapillus* and *D. maculatus* (WEIBEL & MOORE 2000a). A further species is *temminckii* of which we could analyze the short cytb section which places this insular form (Sulawesi and small neighboring islands) in that clade as well. The three-toed woodpeckers of Eurasia and North America (*Picoides tridactylus*, *P. dorsalis*, *P. arcticus*) form the sister clade to the smaller Asian forms. Possible taxonomic consequences would be to place both groups into two separate genera, namely *Yungipicus* (BONAPARTE, 1854) and *Picoides* (LACÉPÈDE, 1799; cf. WOLTERS 1975-1982), or in one genus. We adopted the latter option (see Appendix 2). African *Dendrocopos* are embedded in "*Dendrocopos*" and appears therefore not to be the sister group of *Dendrocopos* and *Picoides* as implied by the current classification. According to our results the small East and South Asian *Dendrocopos* form the sister group to all the other pied woodpeckers and *Dendrocopos*.

The middle spotted woodpecker and its allies

FUCHS et al. (2007) showed that the middle spotted woodpecker is related to the yellow-crowned woodpecker, and our analyses add the brown-fronted woodpecker to this clade for which the generic name *Leiopicus* BONAPARTE, 1854 is available (WINKLER 2009). This genus thus comprises now the species *medius* (Iran to Europe), *mahrattensis* (India, Sri Lanka, Myanmar, Thailand), and *auriceps* (northern Indian subcontinent). Phylogenies obtained from cytb and cox1 (not shown) both comprise the same topology, with *mahrattensis* at the base and *auriceps* and *medius* as sister species. The small and isolated population of *mahrattensis* in Thailand has not been genetically sampled yet.

The great spotted woodpecker and its allies

Our data show complex relationships that were to some degree already indicated by PERKTAS & QUINTERO (2013). These authors, however, did not include *darjellensis*, *himalayensis*, and *leucopterus* in their analysis of 352bp of the mitochondrial ND2 gene. They concluded that *major* should be split into several species, as especially the Chinese and Japanese populations were rather distinctive. They also had included one specimen from Iran that also seemed to be quite distant and considered by them also representing a possible separate species. Since *Dendrocopos leucopterus* occurs not too far from their sampling site in northern Iran, the relationships between these populations should be clarified before implementing such taxonomic changes. Unfortunately, the one ND2 sequence of *D. leucopterus* produced by us aligned at a section of the gene not covered by the sequences of PERKTAS & QUINTERO (2013). However, we did obtain sequences based on samples from China, Japan for *major* and from Nepal for *D. darjellensis*. Comparison with the sequences deposited in GenBank by PERKTAS & QUINTERO (2013) confirmed

the distinctness of the Chinese and Japanese populations and clustered *D. darjellensis* within the specimen from China and Myanmar. Clearly, more research has to be done at population level. At the moment we regard it as premature to designate (phylogenetic) species based on these short ND2 (352 bp, PERKTAS & QUINTERO 2013) and short cytb (301 bp, this study) sequences. At any rate, *D. darjellensis* may then be just a subspecies of a new Sino-Himalayan pied woodpecker species that has yet to be named.

Relationships within the Picini

SHORT (1982) already saw the similarity between *Celeus* and *Dryocopus*, but nevertheless placed them into different tribes. The species intermediary between these two genera, he suggested, would be the Helmeted Woodpecker (*Dryocopus galeatus*; WINKLER et al. 1995 erroneously used '*magellanicus*' instead of '*galeatus*' in their discussion of this relationship). Our data confirm the relationships of *Dryocopus* with *Celeus* and *Colaptes/Piculus* and support the notion of an American origin of the former. The phylogeny presented in Fig. 1 adds proof to the notion that the rufous woodpecker (*Micropternus brachyurus*) of the Old World cannot be merged into the New World genus *Celeus* as SHORT (1982) had suggested on the basis of plumage characters and life history (cf. BENZ et al. 2006). The rufous woodpecker's sister group clearly is the genus *Meiglyptes* (BENZ et al. 2006, FUCHS et al. 2006, 2008, 2013). Our phylogeny is the first that contains all three species (Fig. 1).

Little is known still about the placement of the genus *Gecinulus*. SHORT (1982) merged the different populations into one species *Gecinulus grantia*, the bamboo woodpecker. WINKLER et al. (1995) kept the traditional split into two species *G. grantia* (Nepal to China) and *G. viridis* (Malaysia). The analyses of FUCHS (2007) suggest a close relationship with *Dinopium*.

The position of the golden-backed woodpeckers, genus *Dinopium*, within the Picini is still not fully resolved. Certainly they are only distant relatives of the very similar looking flamebacks of the genus *Chrysocolaptes* (see CODY 1969). Within *Dinopium*, some relationships are still not resolved. Of the four species recognized traditionally, one, *D. rafflesii*, has not been sampled genetically yet. The suggestion to split the subspecies *everetti* from the island Palawan as a full species finds some support from the data available to us. This and other insular populations may deserve to be raised to species rank in future studies.

Widespread *Picus canus* and *P. viridis* show interesting phylogeographic relationships. The latter species and its closest relatives have been treated in recent studies (PONS et al. 2010, PERKTAS et al. 2011). Our data do not yet allow for a complete phylogeny of *Picus*. The phylogeny shown in Fig. 1 justifies to split the species *miniaceus* and *mentalis* from *Picus* and put them into a separate genus *Chrysophlegma*, as suggested by FUCHS et al. (2008). A short cytb sequence (FUCHS et al. 2008) also supports including *flavinucha* into this genus.

Dryocopus

Our study confirms the close relationship of *Dryocopus* and *Mulleripicus*. Previous analyses (e.g. FUCHS et al. 2008) did not resolve the relationships between American and Old World *Dryocopus*. Here we showed for the first time that Old World *Dryocopus*

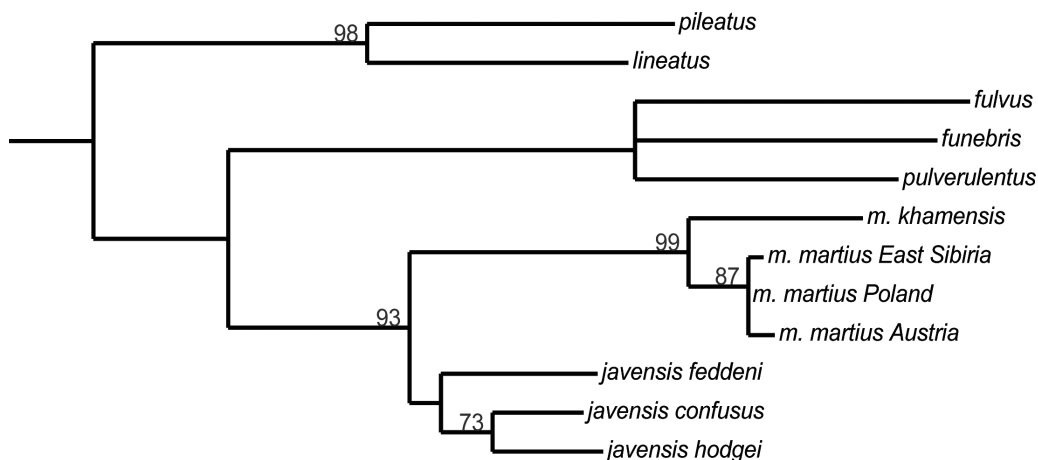


Fig. 2: Relationships within the genus *Dryocopus*. Phylogeny based on cytb-s sequences. Bootstrap values are given at the nodes. *Blythipicus rubiginosus* was used as outgroup. Species *pileatus* occurs in N America, *lineatus* in C and S America. Species *fulvus* (Sulawesi), *funebris* (Philippines), and *pulverulentus* (N India, continental SE Asia, Greater Sundas) were formerly placed into the genus *Mulleripicus*. Species *martius* is split into a Chinese (*khamensis*) and N Eurasian branch (n nominate). In the South it is replaced by *javensis*. Subspecies *feddeni* is continental (Thailand, Myanmar, Malaysia) and *confusus* (Luzon) as well as species *hodgei* (Andamans) are island forms.

and *Mulleripicus* are closer to each other than either is to the American species (Fig. 1, Fig. 2.). Hence *Mulleripicus* has to be merged into *Dryocopus*. We prefer not to split the genus *Dryocopus* in an American and Old World clade taxonomically. The island form *hodgei* from the Anadammans is usually considered as a species (SHORT 1982) which is confirmed here. As Fig. 2 shows, *confusus* from Luzon, and possibly some of the other island forms, deserve species status by the same token. We also claim species status to the isolated Chinese form *khamensis* of the black woodpecker which is well separated from the nominate *martius* form.

Chrysocolaptes

The former genus *Reinwardtipicus* is closely related and merged here with *Chrysocolaptes*. The genus contains a further species that occurs on the Indian subcontinent (WINKLER et al. 1995). No genetic data of this species (*C. festivus*) were available to us. The relationships within the species *C. lucidus* need further studies. The phylogeny presented in Fig. 3 is a first attempt to get some insights in the relationships within this species that contains many island populations which may deserve species rank (COLLAR 2011).

African woodpeckers

The cytb sequence of *Geocolaptes* used by WEBB & MOORE (2005) and BENZ et al. (2006) and deposited under AY940801 in GenBank represents *D. minor* and has now been deleted from GenBank due to sample contamination (see also FUCHS et al. 2007). Its relationship to *Campethera* has been established by FUCHS et al. (2007, 2008),

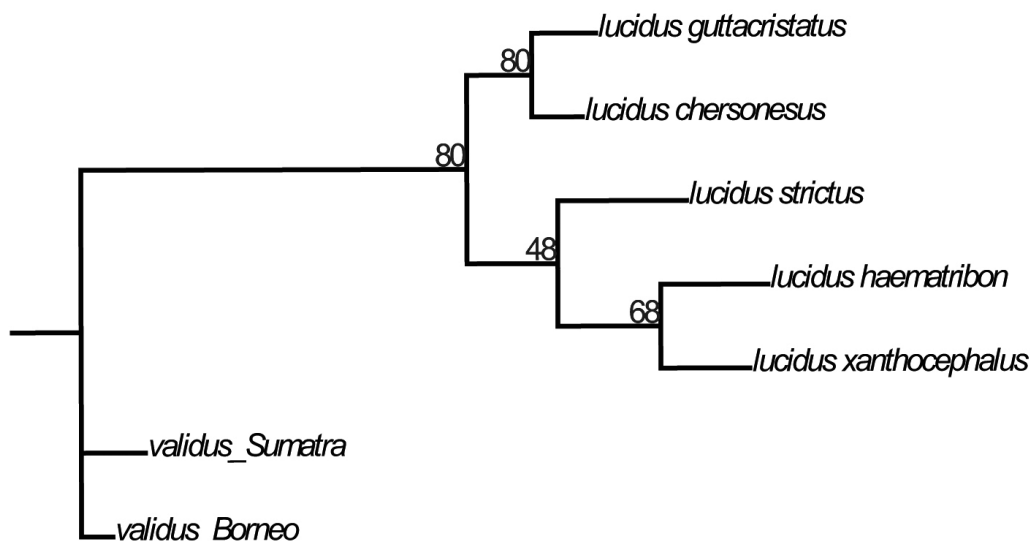


Fig. 3: Relationships within the genus *Chrysocolaptes*. Phylogeny based on short cytb-sequences. Bootstrap values are given at the nodes. *Blythipicus rubiginosus* was used as out-group. Subspecies *guttacristatus* is continental (N India, Nepal, China, Indochina), *chersonesus* occurs in Malaysia, Sumatra and W Java, *strictus* is confined to E Java, *haematribon* is insular (N Philippines, e.g. Luzon), and so is *xanthocephalus* (C Philippines, e.g. Negros).

confirmed by our study, and corroborates previous taxonomies (SHORT 1982). Our data indicate that *Leiopicus* and *Dendropicus* may be sister clades (cf. phylogenies in FUCHS et al. 2013), but this has to be studied in greater detail. An open and interesting question is the position of the Arabian woodpecker (*D. doraë*) which may link these two groups not only geographically. More studies on the genera *Dendropicus* and *Campethera* are clearly needed, and they would have to include *D. doraë* and another African species that is currently placed in a monotypic genus *Ipophilus* with species *obsoletus* (WOLTERS 1975–1982, DICKINSON & REMSEN 2013).

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Appendix 1

Specimens of woodpeckers used in this study.

Taxon	Tissue	Voucher no, source	Geographic origin, year of collection	Sequence	Accession No.
<i>Jynx torquilla</i>	bl	H. Winkler	Austria, Illmitz, 2008	12S, cytb	KF766011, KF765948
<i>Sasia abnormis</i>	mu	LSUMNS B 38548	Malaysia, Borneo, Sabah	12S, cytb	KF766012, KF765949
<i>Sasia o. ochracea</i>	mu	AMNH PRS 2435	Vietnam, Tay Con Linh, 2000	12S, cytb	KF766013, KF765950
<i>Picumnus aurifrons</i>	GB	LSUMNS 18479/18254	Bolivia, Santa Cruz	12S, cyb	AY940761 ^a , AY942888 ^a
<i>Nesocites m. micromegas</i>	mu	AMNH NKK 1095	Dominican Republic, La Altagracia, 1998	12S, cytb	KF766014, KF765951
<i>Campephilus magellanicus</i>	sk	V. Ojeda	Argentina, Patagonia, 2005	12S, cytb	KF766016, KF765952
<i>Blythipicus rubiginosus</i>	mu	LSUMNS B 36332	Malaysia, Crocker Range	12S, cytb	KF766015, KF765953
<i>Chrysocolaptes lucidus</i>	GB	ZMUC p815		12S, cytb	AY940745 ^a , AY940797 ^a
<i>C. l. guttacrastatus</i>	sk	NMW 45.503	Myanmar, Mandalay, 1937	cytb-s	KF765954
<i>C. l. chersonesus</i>	sk	RMNH 3894	Indonesia, Sumatra, Deli, 1915	cytb-s	KF765955
<i>C. l. strictus</i>	sk	RMNH 23300	Indonesia, Java, Bandi, 1939	cytb-s	KF765956
<i>C. l. haematribon</i>	sk	RMNH 99719-6	Philippines, Luzon, Dalton Pass, 1986	cytb-s	KF765957
<i>C. l. xanthocephalus</i>	sk	RMNH 99717	Philippines, Negros, Basay, Bayawan, 1964	cytb-s	KF765958
<i>C. validus xanthopygius</i>	mu	LSUMNS B 38653	Malaysia, Borneo, Kinabalu	12S, cytb	KF766017, KF765959
<i>C. v. xanthopygius</i>	sk	RMNH 28202-40	Indonesia, Sumatra, Deli, Boven, 1920	cytb-s	KF765960
<i>Dinopium javanense exsul</i>	sk	NMW 85216	Indonesia, Bali, captivity	12S, cytb	KF766018, KF765961
<i>Micropternus brachyurus badiosus</i>	mu	LSUMNS B-47165	Malaysia, Borneo, Sabah	12S, cytb	KF766019, KF765962
<i>Meiglyptes tristis grammithorax</i>	mu	LSUMNS B 36352	Malaysia, Borneo, Crocker Range	12S, cytb	KF766020, KF765963
<i>Meiglyptes t. tukki</i>	mu	LSUMNS B 47045	Malaysia, Borneo, Kinabalu	12S, cytb	KF766021, KF765964
<i>Chrysophlegma miniaceum</i>	GB	LSUMNS 1153		12S, cytb	AY940765 ^a , AY940811 ^a
<i>Chrysophlegma mentale</i>	mu	LSUMNS B 36478	Malaysia, Trusmadi	12S, cytb	KF766022
<i>Campepthera nivoso herberti</i>	mu	AMNH ALP 066	Central African Rep., Bayanga, 1998	12S, cytb	KF766023, KF765965
<i>Campepthera c. caroli</i>	mu	AMNH ALP 004	Central African Rep., Bayanga, 1998	12S, cytb	KF766024, KF765966
<i>Picus viridanus</i>	sk	RMNH 12560	Thailand, Nikhé, 1946	cytb-s	KF765967
<i>P. s. squamatus</i>	sk	NMW 68.240	Pakistan, Karakoram, 1958	cytb-s	KF765968
<i>P. awokera</i>	mu	LSUMNS B 16980	Japan, Fukui, Imajo	12S, cytb	KF766025, KF765969
<i>P. vittatus</i>	mu	G. Nikolaus	Indonesia, Java	12S, cytb	KF766031, KF765973
<i>P. v. viridis</i>	mu	M. Riesing	Austria, Lower Austria, 2003	12S, cytb	KF766026, KF765970

Taxon	Tissue	Voucher no, source	Geographic origin, year of collection	Sequence	Accession No.
<i>P. v. sharpei</i>	mu	MNCN/ADN 3700	Spain, Otenuelo del Valle, Madrid, 2003	12S, cytb	KF766027, KF765971
<i>P. c. canus</i>	bl	K. Michalek (KLIVV100)	Austria, Vienna, 1995	12S, cytb	KF766029, AY701057 ^c
<i>P. erythropygus nigrigenis</i>	mu	AMNH PRS 555	captivity	12S, cytb	KF766028, KF765972
<i>Colaptes auratus</i>	GB	WSU 86-10.1/81-7.1	USA, Kentucky	12S, cytb	AY940740 ^a , AY942881 ^a
<i>Celeus l. torricatus</i>	mu	LSUMNS B-100060	Ecuador, El Placer	12S, cytb	KF766032, KF765975
<i>Celeus elegans citreopygus</i>	mu	ZMUC P1823/136665	Ecuador, Napo, Laguna Anangu, 1995	12S, cytb	KF766034, KF765976
<i>Celeus flavus peruvianus</i>	mu	LSUMNS B 4214	Peru, Loreto	12S, cytb	KF766033, KF765977
<i>Dryocopus p. pileatus</i>	GB	WSU 86w-3.4/1.5	USA, Texas/California	12S, cytb	AY940751 ^a , AY942885 ^a
<i>D. lineatus</i>	GB	LSUMNS 6660/ WSU 95-1.3	Bolivia, Santa Cruz	12S, cytb	AY940750 ^a , AY940800 ^a
<i>D. javensis feddeni</i>	sk	NMW 45.502	Myanmar, Mandalay, 1937	cytb-s	KF765978
<i>D. j. confusus</i>	sk	NMW 90.629	Philippines, Luzon, 1989	cytb-s	KF765979
<i>D. hodgei</i>	sk	ZMB 64549	India, Middle Andaman Island, 1964	cytb-s	KF765980
<i>D. m. martius</i>	sk	NMW 82.429	Austria, Upper Austria, Leonstein, 1987	cytb-s	KF765981
<i>D. m. martius</i>	fe	NMW 2004/00	Poland, Bialowieza, 2003	cytb	KF765982
<i>D. m. martius</i>	mu	NMW 96.495	Russia, E Siberia, Solnechny, 2001	12S, cytb	KF766035, KF765983
<i>D. m. khamensis</i>	sk	ZMB 35.226	China, Tschou-tou, 1928	cytb-s	KF765984
<i>D. fulvus</i>	sk	ZMB1999.1116	Indonesia, Sulawesi, 1931	cytb-s	KF765985
<i>D. fulvus</i>	sk	ZMB1999.1117	Indonesia, Sulawesi, 1931	cytb-s	KF765986
<i>D. funebris mayri</i>	GB	ZMUC p703	Philippines, Luzon, Hamut, 1991	12S, cytb	AY940757 ^a , AY940805 ^a
<i>D. pulverulentus harterti</i>	sk	ZMB 40.108	Myanmar, Prome, 1937	cytb-s	KF765987
<i>Melanerpes carolinus</i>	GB	WSU 86w-1.4	USA, Kentucky	12S, cytb	AY940755 ^a , AY942886 ^a
<i>M. erythrocephalus</i>	GB	WSU 86w26			AY940756 ^a , AY940804 ^a
<i>Picoides t. tridactylus</i>	mu	NMW 96.333	Russia, Chitinskaya Oblast, Bukukun, 2004	12S, cytb	KF766036, AY863147 ^c
<i>P. m. moluccensis</i>	mu	AMNH PRS 695	Singapore	12S, cytb	KF766037, KF765988
<i>P. kizuki iijimae</i>	DNA	N. Kuroda	Japan, Hokkaido, Sapporo, 2000	12S, cytb	KF766039, KF765990
<i>P. temminckii</i>	sk	ZMB 34.2523	Indonesia, Celebes, Lambanang, 1931	cytb-s	KF765991
<i>Dendropicos griseocephalus</i>	GB	UWBM 471		12S, cytb	AY940749 ^a , AY942884 ^a
<i>Leptopicus maharattensis</i>	sk	RMNH 4938	Sri Lanka, Kalkutara Distr., 1921	cytb-s	KF765995
<i>L. auriceps</i>	mu	AMNH JGG 992	Nepal, Kipsung, 1993	12S, cytb	KF766040, KF765993,
<i>L. auriceps</i>	sk	ZMB 26.272	India, Chakrata, Kulu, 1912	cytb-s	KF765994
<i>L. m. medius</i>	mu	H. Winkler	Austria, Vienna, Wilhelminenberg, 2003	12S, cytb	KF766043, KF765997

Taxon	Tissue	Voucher no, source	Geographic origin, year of collection	Sequence	Accession No.
<i>Dryobates pubescens</i>	GB	WSU 86w-5.5	USA, Texas	12S, cytb	AF173562 ^b , AF389325 ^d
<i>Dryobates villosus</i>	GB	WSU 86w-14.4/10.7	USA, California/Arizona	12S, cytb	AY940768 ^a , AY942890 ^a
<i>Dryobates callonotus</i>	GB	LSUMNS B5175		12S, cytb	AY940771 ^a , U83297 ^e
<i>Dryobates minor hortorum</i>	bl	KLIVV B	Germany, Mecklenburg-Vorpommern, Galenbecker See, 2000	12S, cytb	KF766041, KF765992
<i>Dryobates c. cathpharius</i>	mu	J. Martens, MAR 90176	Nepal, Myagdi Dist., 1995	12S, cytb	KF766042, KF765998
<i>D. c. cathpharius</i>	sk	ZMB 76.180	India, Sikkim, Gantok, 1939	cytb-s	KF765999
<i>Dendrocopos hyperythrus</i>	sk	ZSM 62.374	Nepal, Ting Sang La,	cytb-s	KF766000
<i>D. m. macei</i>	sk	ZFMK 24.04.3683	Nepal, Raniban, Balaju, 1964	cytb-s	KF766005
<i>D. macei longipennis</i>	sk	ZMB 39.67	Myanmar, Ryndaw, 1938	cytb-s	KF766001
<i>D. analis</i>	mu	H. Siebenrock	Malaysia (?), captivity, 2005	cytb	KF766003
<i>D. analis</i>	mu	G. Nikolaus	Indonesia, Java	12S, cytb	KF766044, KF766004
<i>D. atratus</i>	sk	ZMB 39.70	Myanmar, Mt. Victoria, 1938	cytb-s	KF766006
<i>D. noguchii</i>	mu	K. Ispida / N. Kuroda	Japan, Kumigami Vill., Okinawa, 2000	12S, cytb	KF766046, AY701060 ^f
<i>D. syriacus</i>	bl	K. Michalek (KLIVV 183)	Austria, Lower Austria, Perchtoldsdorf, 1995	12S, cytb	KF766049
<i>D. d. darjellensis</i>	mu	AMNH JGG 1085	Nepal, Gongga, 1993	12S, cytb	KF766050, KF766007
<i>D. m. brevirostris</i>	mu	NMW 93.965	Russia, Lake Baikal, Swatoi-Nos, 2001	12S, cytb	AY701065 ^c , KF766008
<i>D. m. pinetorum</i>	mu	NMW Sk 7.277	Austria, Lower Austria, Gars / Kamp, 1997	12S, cytb	KF766048, AY701064 ^e
<i>D. m. stresemanni</i>	mu	J. Martens, MAR03251	China, Yunnan, Zhongdian, 2002	cytb	KF766008
<i>Indicator variegatus</i>	GB	FMNH 355280		12S, cytb	AY940753 ^a , AY940802 ^a
<i>Capito niger</i>	GB	LSUMNS B4805/3560		12S, cytb	AY940747 ^a , AY940799 ^a

Material for DNA-extraction (Tissue): mu muscle, sk skin from the foot pads of study skins, bl blood, fe feather. Voucher numbers are given for tissues and museum specimens (AMNH American Museum of Natural History, N.Y.; FMNH Field Museum of Natural History, Chicago; KLIVV Konrad Lorenz-Institute for Comparative Ethology, Vienna; MNCN/ADN Museo Nacional de Ciencias Naturales, Madrid; NMW Museum of Natural History Vienna; UWBM University Washington Burke Museum; ZFMK Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn; LSUMNS Louisiana State University, Museum of Natural Sciences, Baton Rouge; RMNH Naturalis, Leiden; ZMB Zoological Museum Berlin; ZMUC Zoological Museum, University of Copenhagen; ZSM Zoologische Staatssammlung, Munich). Accession numbers of sequences determined in the present study and sequences obtained from GenBank (GB) are listed. Sequence (cytb, 12S) s: short section. References for GenBank accession No.: ^a WEBB & MOORE (2005), ^b TUNEN et al. (2003), ^c WINKLER et al. (2005), ^d WEIBEL & MOORE (2002), ^e MOORE & DEFILIPPIS 1997. Additional ND2 and cox1 sequences can be found under the following accession numbers: KF765946, KF765947, KF766009, KF766010. Two cytb sequences of *Leiotopius mahrattensis* have accession numbers KF765995, KF765996.

Appendix 2

Recommendations for the classification of woodpeckers with focus on Old World woodpeckers. The Howard-Moore list edited by DICKINSON & REMSEN (2013) follows in part a splitting approach at the genus level pioneered by WOLTERS (1975-1982), whereas in other instances they adopted SHORT's (1982) list who was a "lumper", and subsumed, for instance, a wide range of Old and New World species into one huge genus *Picoides*. Here, we try to follow a moderate course that lies somewhat in between extreme lumping and splitting, and that changes traditional usage as little. In cases where there are no changes with respect to genus – species associations compared to the Howard-Moore list, we only present genera. Taxa are ordered with respect to where they branch off in the phylogeny.

Picidae

Jynginae

Jynx LINNAEUS, 1758

Picumninae

Verreauxia HARTLAUB, 1836 [1 species, Africa]

Sasia HODGSON, 1837 [2 species, Asia]

Picumnus TEMMINCK, 1825 [26 species, S America]

Picinae

Nesocitini¹

Hemicircini²

Hemicircus SWAINSON, 1837 [2 species S, Asia]

Campephilini³

Campephilus GRAY, 1840 [9 extant plus 2 recently extinct species, Americas]

Blythipicus BONAPARTE, 1854 [2 species, S Asia]

Chrysocolaptes BLYTH, 1843⁴ [3 species, S, SE Asia]

Picini⁵

Dinopium RAFINESQUE, 1814 [4⁶ species, S, SE Asia]

Gecinulus BLYTH, 1845 [2 species, S, SE Asia]

Micropternus BLYTH, 1845 [1 species, S, SE Asia]

Meiglyptes SWAINSON, 1837 [2 species, S Asia]

Chrysophlegma GOULD, 1850 [3 species, S Asia]

Geocolaptes SWAINSON 1982 [1 species, S Africa]

Campeothera GRAY, 1841 [11 species, Africa]

Picus LINNAEUS, 1758 [12 species, Eurasia, N Africa]

Piculus VON SPIX, 1824 [6 species, C, S America]

¹ Represents a single New World species on Hispaniola (*Nesocitites micromegas*). May deserve subfamily rank.

² Like the previous tribe, may deserve subfamily rank.

³ Corresponds to "Megapicini" of WEBB & MOORE (2005).

⁴ We include *Reinwardtipicus* BLYTH, 1854.

⁵ Corresponds to "Malarpicini" of WEBB & MOORE (2005).

⁶ We leave *everetti* as a subspecies of *javanense*. However, revision of all the island forms in the genus may raise it together with others to species status.

- Colaptes* VIGORS 1825 [12 species, N, C, S America]
Celeus BOIE, 1831 [12 species, C, S America]
Dryocopus BOIE, 1826⁷ [8 Old and 4 New World species]
 Melanerpini⁸
Sphyrapicus S.F. BAIRD, 1858 [4 species, N America]
Xiphidiopicus BONAPARTE, 1854 [1 species, Cuba]
Melanerpes SWAINSON, 1832 [23 species, Americas]
Picoides LACÉPÈDE, 1799 [6 species in Asia and 2 in N America]⁹
tridactylus, *temminckii*, *kizuki*, *maculatus*, *canicapillus*, *moluccensis* in the Old World.
Dendropicos MALHERBE, 1849 [15 species]¹⁰
Leopicus BONAPARTE, 1854 [3 species, Eurasia]
mahrattensis, *auriceps*, *medius*
Dryobates BOIE, 1826 [2 species in Eurasia, 23 in the Americas]¹¹
minor and *cathpharius* in the Old World.
Dendrocopos KOCH, 1816 [12 species in Eurasia and N Africa]
hyperythrus, *atratus*, *macei*, *analisis*, *noguchi*, *leucotos*, *assimilis*, *syriacus*, *darjellensis*, *major*, *leucopterus*, *himalayensis*.

⁷ We include *Mulleripicus* BONAPARTE, 1854 which is kept as a separate genus in the Howard-Moore list. However, if this is maintained, Old and New World *Dryocopus* have to be split, with the latter subsumed as *Hylatomus* BAIRD, 1858 (see WOLTERS 1975-1982).

⁸ See the comments in the Howard-Moore list (DICKINSON & REMSEN 2013). WINKLER (2009) suggested to keep Melanerpini and Picoidini separate. We follow the Howard-Moore list (DICKINSON & REMSEN 2013) here.

⁹ See notes under *Dryobates*.

¹⁰ We keep the genus as in SHORT (1982). There is no justification so far for the former splits still maintained in the new Howard-Moore list (DICKINSON & REMSEN 2013). We also include *dorae* (placed in *Picoides* by SHORT 1982) and *obsoletus*, although their position remains unclear and subject to change.

¹¹ At present, we include species that were formerly put into *Picoides* and *Veniliornis*. If one wants to split, a possible grouping would be *Dryobates* for the small American and Eurasian species, and *Leuconotopius* for the remaining species.

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