THE GENERIC DISTINCTION OF PIED WOODPECKERS

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ABSTRACT: The ten species of New World four-toed woodpeckers (*scalaris*, *nuttallii*, *pubescens*, *villosus*, *stricklandi*, *arizonae*, *borealis*, *albolarvatus*, *lignarius*, and *mixtus* and the two boreal three-toed species (*arcticus* and *tridactylus*), currently combined in the genus *Picoides*, differ, in addition to the number of toes, in modifications of the skull, ribs, the belly of the pubo-ischio-femoralis muscle, head plumage, and behavior. I recommend that the generic name *Dryobates* be reinstituted for the New World four-toed woodpeckers.

There are three general morphological groups of pied woodpeckers, a group of nine four-toed species of the New World, a group of 22 four-toed species of the Old World, and a group of two three-toed species straddling both regions. I refer to these groups of pied woodpeckers beyond as the New World, Old World, and three-toed groups. The three-toed species have long been in the genus *Picoides* Lacépède, 1799, but the four-toed groups have been combined at the generic level in different ways. All four-toed pied woodpeckers were long included in the genus *Dryobates* Boie, 1826, later changed to *Dendrocopos* Koch, 1816 an earlier name (Voous 1947, A.O.U. 1947, Peters 1948). Despite the difference in number of toes, *Dendrocopos* was combined with *Picoides* because of general similarities in anatomy (Delacour 1951, Short 1971a), plumage and behavior (Short 1974a), and vocalizations (Winkler and Short 1978). The A.O.U (1976) followed this merger of the genera. On the basis of skeletal characters Rea (1983) was skeptical of the merger, but he did not provide details. On the other hand, Ouellet (1977), concluding that the two genera differ in external morphology and some behaviors and vocalizations, separated the Old World four-toed woodpeckers in *Dendrocopos* and three-toed and New World four-toed woodpeckers in *Picoides*. The A.O.U. (1987, 1998), Sibley and Monroe (1990), and most European authors (e.g., Hogstad 1978, Cramp 1985, Aulen and Lundberg 1991) followed Ouellet (1977). More recently, analysis of DNA sequences of the genes for cytochrome oxidase I, cytochrome b (Weibel and Moore 2002a), and ß-fibrinogen intron 7 (Weibel and Moore 2002b) suggest that *Picoides* (sensu Short 1982) consists of several groups of species.

In discussing the characters on which he based his classification of woodpeckers, Short (1982) commented that anatomical studies are unreliable because of the lack of analyses of various structures' functions. Burt (1930), however, had found a positive correlation between certain modifications in the skull and habits of woodpeckers. Spring (1965) concluded that the loss of the hallux and a reduced angle of cranial kinesis are probably modifications for a woodpecker's peck to deliver a blow of maximum impact. Kirby (1980) concluded that woodpeckers with wider ribs are adapted to more frequent and harder pecking than species with narrow ribs and that the pattern of increasing rib width follows that of increasing specialization in the skull in species characterized by Burt (1930).

Burt (1930) discussed as a modification in the skull of woodpeckers the meeting of the frontal bone (forehead of the cranium) and the superior processes of the premaxillary (base of the maxilla), which forms a so-called cranio-facial angle. He qualitatively ranked the three-toed pied woodpeckers as having a more acute angle than the four-toed New World species. The frontal bones of both groups, and of the distinct (Zusi and Marshall 1970) genus *Sphyrapicus*, the sapsuckers, fold toward the cranium (Burt 1930).

Another modification in the skull is the relative distance between the lateral parts of the frontal bone that bulge anteriorly and the anterior center of the bone (Figure 1). Here I summarize this distance and other measurements of the skull, with other anatomical and behavioral information, to determine differences and similarities among pied woodpeckers.

METHODS

I examined skeletons including skulls and an associated femur of 17 of the 22 species of Old World four-toed pied woodpeckers, all species of New World four-toed pied woodpeckers except the Checkered Woodpecker (*Picoides mixtus*) of South America, both species of three-toed pied

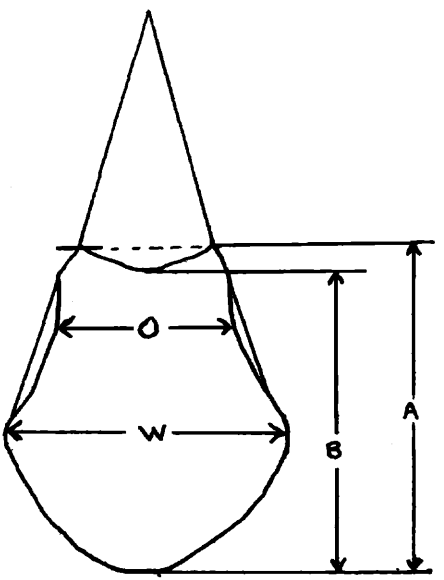

Figure 1. Diagrammatic dorsal view of a woodpecker skull showing distances measured. A, distance from the medial base of the most posterior part of the occiput to the anterior lateral corners of the frontal bone; B, distance, measured medially, from the most posterior part of the occiput to center of the anterior margin of the frontal bone. The craniofacial distance formula, normalized for the size of the bird, is expressed by (*A* – *B*)/femur length(100). Two measurements of widths of the skull: W, maximum width; O, width at the orbits.

woodpeckers (the Three-toed, *P. tridactylus*, and the Black-backed, *P. arcticus*), all species of *Sphyrapicus*, and three species of the African genus *Dendropicos* (sensu Short 1982) (Table 1). The last genus was included because *Picoides* and *Dendropicos* are probably closely related (Short 1971b). On each skull I measured the distance along the midline between the most anterior point of the frontal bone in its center and the most anterior (farther anterior) point of the frontal bone at its lateral corners. I did this by subtracting the length of the cranium, measured medially from the base of the occiput to the center of the most anterior part of the frontal bone (B in Figure 1), from the distance from the medial base of the occiput to the lateral corners of the most anterior part of the frontal bone (A in Figure 1). To avoid possible bias caused by the species' varying sizes (Kirby 1980, Rising and Somers 1989), I divided A – B by femur length. Thus, the formula (A – B)/femur(100) gives a value that, for brevity, I refer to as facial distance. The sexes were combined because the characters addressed in the study are not sexually dimorphic. I also compared maximum skull width (W in Figure 1) and dorsal skull width between the orbits (O in Figure 1), divided by length of femur. SYSTAT (Wilkonson 1989) was used for the statistical analyses. For the species omitted from this analysis, no skeleton including an intact skull and at least one femur was available from the numerous museums surveyed.

RESULTS AND DISCUSSION

In the three-toed pied woodpeckers the facial distance is greater than in the four-toed species. The average facial distance for both three-toed species is at least 2.5 greater than in any four-toed species, and individual variation yields only minimal overlap with only one of the four-toed species, the Old World Lesser Spotted Woodpecker (*Dendrocopos minor*) (Tables 1 and 2). The skull shapes of the two groups are distinct visually; a skull is readily identifiable as that of a three-toed or a four-toed woodpecker without the facial distance being measured (Figure 2). Facial distances of New World and Old World four-toed woodpeckers (Table 2), sapsuckers (mean 5.18, range 2.89–7.50, $n = 8$) and the available species of *Dendropicos* (mean 3.63, range 1.32–6.77, $n = 4$) are similar to one another and do not overlap those of the three-toed woodpeckers.

The width of the skull (Figure 1) in all pied woodpeckers is similar. The width of the skull of species of *Dendropicos* (0.84 to 0.95) and *Sphyrapicus* (Figure 3) is similar in both genera and narrower than in the pied species. The width of the skull at the orbits (Figure 1) is similar in the four-toed pied woodpeckers. This variable is greater in the three-toed species and in *Sphyrapicus*, whereas in *Dendropicos* it is narrower than in the other woodpeckers measured.

Principal-components analysis, based on facial distance, widths, and lengths of the skull (Figure 1) of the pied woodpeckers, revealed extensive overlap in canonical factors 1 and 2 of the Old and New World four-toed species (Figure 4). The three-toed pied woodpeckers and *Sphyrapicus*, however, differ from each other, and both differ from four-toed pied woodpeckers (Figure 4).

Table 1 Cranio-facial Distance of Adult Three- and Four-toed Pied Woodpeckers and Some Related Species

Species	*n*	Range	Mean ± SD[a]
Old World four-toed woodpeckers (*Dendrocopos*)			
Sulawesi (*temmincki*)	1		3.30
Philippine (*maculatus*)	3	3.16–5.56	4.07
Brown-capped (*nanus*)	1		4.86
Pygmy (*kizuki*)	1		5.33
Gray-capped (*canicapillus*)	2	3.82–4.69	4.23
Lesser Spotted (*minor*)	5	7.60–9.43	8.50
Fulvous-breasted (*macei*)	1		3.45
Stripe-breasted (*atratus*)	2	1.40–2.90	2.10
Yellow-crowned (*mahrattensis*)	1		7.40
Darjeeling (*darjellensis*)	1		4.16
Rufous-bellied (*hyperythrus*)	1		5.80
Middle Spotted (*medius*)	3	3.90–4.90	4.40
White-backed (*leucotos*)	1		4.09
Himalayan (*himalayensis*)	1		4.16
Sind (*assimilis*)	1		5.82
Syrian (*syriacus*)	2	5.20–6.80	6.00
Great Spotted (*major*)	5	3.89–5.33	4.80
New World four-toed species (*Dryobates*)			
Striped (*lignarius*)	1		6.34
Ladder-backed (*scalaris*)	23	2.23–5.40	4.20 ± 1.20
Nuttall's (*nuttallii*)	6	2.71–5.59	4.70
Downy (*pubescens*)	22	2.98–7.59	5.10 ± 1.30
Red-cockaded (*borealis*)	10	3.41–6.53	4.60 ± 1.81
Strickland's (*stricklandi*)[b]	9	2.55–6.01	4.90
Hairy (*villosus*)	24	2.25–7.05	5.30 ± 1.20
White-headed (*albolarvatus*)	5	4.61–8.48	7.30
Three-toed species (*Picoides*)			
Three-toed (*tridactylus*)	10	8.60–13.83	11.10 ± 1.58
Black-backed (*arcticus*)	8	10.08–13.25	11.14
Sapsuckers (*Sphyrapicus*)			
Yellow-bellied (*varius*)	3	7.32–2.89	4.45
Red-naped (*nuchalis*)	2	7.07–7.50	7.29
Red-breasted (*ruber*)	1		3.77
Williamson's (*thyroideus*)	2	3.38–6.37	4.88
African pied woodpeckers (*Dendropicos*)			
Golden-crowned (*xantholophus*)	1		4.00
Bearded (*namaquus*)	1		1.32
Cardinal (*fuscescens*)	1		6.77
Gray (*goertae*)	1		2.42

[a]Standard deviation (SD) calculated for $n > 9$.

[b]Includes Arizona Woodpecker (*arizonae*).

Table 2 Comparison of Three- and Four-toed Pied Woodpeckers

Character	Three-toed	Four-toed		Source[a]
		New World	Old World	
Cranio-facial distance[b]				
Mean	11.34	4.86	4.37	1
SD	1.39	1.34	1.00	
Range (males)	8.85–11.3	2.23–8.48	1.30–6.06	
Width of first sternal rib[c]				
Mean	14.7	11.3	12.1	2
Range	14.6–14.8	11.7–12.6	9.6–13.9	
Bellies of pubo-ischio-femoralis muscle	fused	separate	—	3
Head-turned and head-bobbing displays	lacking	present	present	4
Clutch size	2.8–3.2	3.8–4.6	—	5

[a]1. This study. Data summarized in Table 1.
2. Kirby (1980); V. C. Kirby (unpubl. data). Data from Black-backed, Three-toed, six New World four-toed, and nine palearctic four-toed woodpeckers.
3. Swierczewski and Raikow (1981). Data from Black-backed, White-headed, and Downy Woodpeckers.
4. Short (1971b).
5. Koenig (1987). Clutch sizes are ranges from mean clutch size adjusted for latitude. All North American species included.

[b]Quantities in millimeters × 100.

[c]Normalized for size of the bird by being divided by length of femur.

The first thoracic rib (Kirby 1980, V. C. Kirby unpubl. data), averages wider in the three-toed species than in the four-toed species (Table 2), and measurements (normalized for size of the bird by being expressed as a fraction of femur length) do not overlap. Other anatomical studies also suggest differences between three- and four-toed woodpeckers. Swierczewski and Raikow (1981) found that the bellies of the pubo-ischio-femoralis muscle are separate in the Downy (*P. pubescens*) and White-headed (*P. albolarvatus*) Woodpeckers, both New World species, but are fused in all other woodpeckers they compared, including the three toed species (Old World four-toed species omitted from this study). The muscle flexor perforans et perforatus digiti III is modified in the three-toed species. The three- and four-toed species differ also in several other characters related to the three-toed species' loss of the hallux (Table 2; Swierczewski and Raikow 1981).

Plumage patterns on the heads of pied woodpeckers, although species-level characters, provide useful taxonomic information (Short 1974b:40; 1976) and suggest differences of groups of species. Most male three-toed and New World four-toed woodpeckers differ in the position and extent of a red or yellow patch on the head. The patch is on the nape of most New World four-toed males but it is on the crown of the three-toed species.

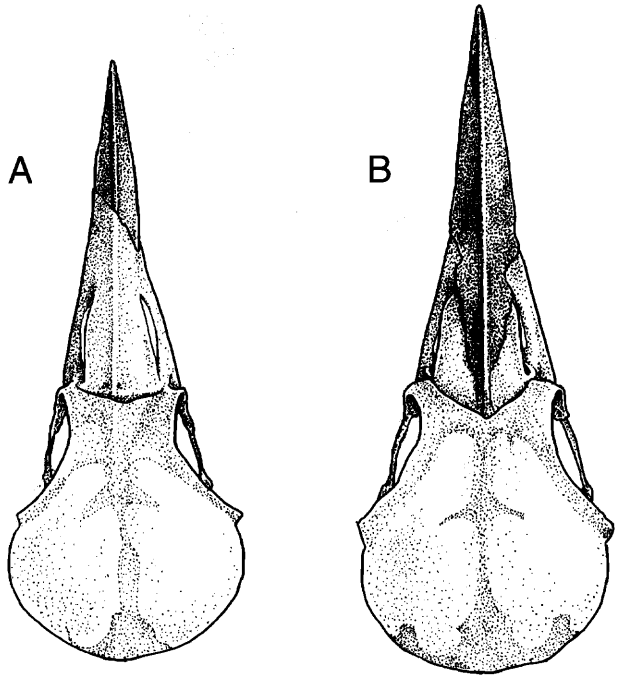

Figure 2. Dorsal views of skulls of pied woodpeckers, showing the difference in shape of forehead between the four-toed species, exemplified by a Hairy Woodpecker (A; SDNHM 41367), and the three-toed species, exemplified by a Black-backed Woodpecker (B; SDNHM 41833). The difference in the extent of dark on the maxilla is the result only of variation in the amount of ramphotheca remaining on the bill after preparation.

Illustration by Jennifer V. Zee

Because the patch is on the back of the head in four-toed woodpeckers, in defense from conspecifics, females facing out from a nest or roost cavity are at an advantage because they look like males (Kilham 1983); sexes of the three-toed species facing out from a cavity are probably more readily distinguished by conspecifics because the patch is on the top of the head. Crest-raising in woodpeckers, exposing yellow, red, black, or white in males, is used in sexual recognition and threat displays (Short 1982). Displays that expose the small red area on the nape in males of the Downy and Hairy (*P. villosus*) would seem to require frequent movements of the head; the large yellow crown in males of the three-toed species would be relatively visible by conspecifics, with or without frequent movements of the head. Short's (1982) survey of behavior of pied woodpeckers suggests, qualitatively, that the Downy and Hairy Woodpeckers display more side-to-side head movements and less frontal exposure of the head (Bill-Lowered Posture; Short 1982) than do the Three-toed or Black-backed Woodpeckers. Short's

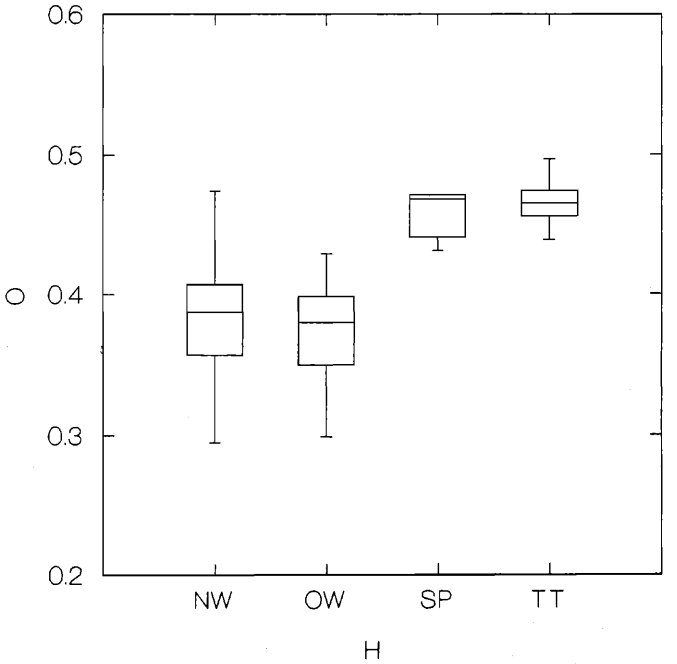

Figure 3. Maximum width and width at orbit of pied woodpeckers and sapsuckers. NW, New World four-toed species; OW, Old World four-toed species; SP, sapsuckers; TT, three-toed species.

(1982) descriptions of the head displays of the Ladder-backed Woodpecker (*P. scalaris*), the only New World four-toed species with red on most of the crown in males, seem more similar to those of the closely related (Short 1971a) Downy Woodpecker than to those of the three-toed species. Although this difference may be unrelated to head pattern and or color, paired three-toed woodpeckers are more antagonistic to each other than are New World four-toed species (Kilham 1966, Short 1982).

Genetic studies by Weibel and Moore (2002a, b) did not include nine species of Old World four-toed pied woodpeckers addressed in my study and included fewer species of *Dendropicos* and *Sphyrapicus*. However, my study did not include the Checkered Woodpecker because specimens were unavailable, and I did not compare the neotropical genus *Veniliornis*, which Weibel and Moore (2002a) considered, with *Dendropicos*, to be close to or nested within *Picoides*. Phylogenetic trees generated from sequences of three genes (Weibel and Moore 2002a, b) suggest relationships among the pied woodpeckers but these do not include all taxa and are not yet conclusive. Weibel and Moore (2002b) concluded that there are three New World groups of *Picoides*: the large species, including the White-headed, Hairy, Strickland's (*P. stricklandi*) and Red-cockaded (*P. borealis*), the small

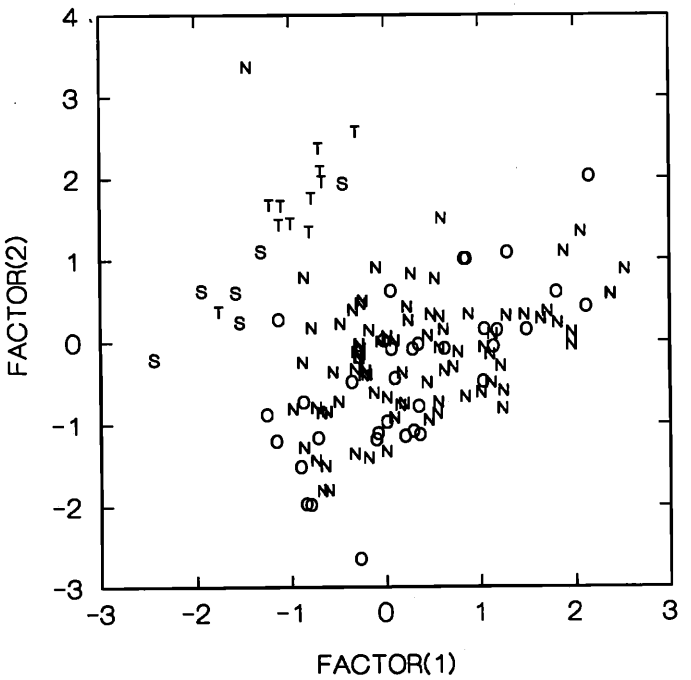

Figure 4. Principal-components analysis of skull measurements of pied woodpeckers and sapsuckers. O, Old World four-toed species; N, New World four-toed species; T, three-toed species; S, sapsuckers.

species, including Nuttall's (*P. nuttallii*), Ladder-backed, and Downy, along with the Lesser Spotted Woodpecker from the Old World), and a neotropical group, including the Striped (*P. lignarius*), Checkered, and the genus *Veniliornis*). Weibel and Moore (2002b) considered *Dendropicos*, with the White-backed (*Dendrocopos leucotos*) and Great Spotted (*D. major*) Woodpeckers, to be "clearly closely related to the New World group," but did not state which group, and that the three-toed and remaining four-toed pied woodpeckers are another distinct group.

CONCLUSIONS AND TAXONOMIC RECOMMENDATIONS

Contrary to Short (e. g., 1974b, 1982), morphological characters of skeletons, regardless of function, serve to identify species groups in woodpeckers (see Olson 1972). Anatomical characters (Spring 1965, Kirby 1980) are also related to behavior (contra Short 1982). The number of toes between groups of pied woodpeckers has long been considered unimportant generically (e.g., Delacour 1951, Short 1971a). However, that character is among many that distinguish the three- and four-toed pied woodpeckers

(Table 2, Figure 3). Furthermore, comparisons of measurements of the skulls of pied woodpeckers reveal that the three-toed woodpeckers differ (Figures 3 and 4) and may be easily identified visually (Figure 2).

Hypotheses (Mengel 1970, Bock and Bock 1974, Short 1971a, Ouellet 1977) speculating on the origin and evolution of pied woodpeckers have emphasized the origin of the three-toed species in North America. Three-toed and four-toed woodpeckers differ from one another more than was generalized by Short (1982), and it is reasonable to believe that three-toed and New World four-toed woodpeckers could have evolved independently. Weibel and Moore (2002a) inferred there were three invasions of Eurasian species.

Although Old World and New World four-toed woodpeckers are similar anatomically (Table 2, Figures 3 and 4), the two groups differ externally and behaviorally (see Ouellet 1977 and others) and karyotypically (Shields 1982, who compared only the Downy, Hairy, Great Spotted, and Lesser Spotted Woodpeckers). My data show multiple generic-level morphological differences between three-toed and New World four-toed woodpeckers, suggesting that they are inappropriately considered congeneric. These differences are more pronounced than those between the New World and Old World four-toed woodpeckers (presently considered to represent different genera), but Ouellet (1977), followed by and substantiated by others (e.g., see Cramp 1985), presented compelling evidence for separation of these two four-toed groups. The three-toed species differ from the New World and Old World four-toed species anatomically, in plumage color of the head, and in some behaviors. Although three-toed and many four-toed Old World pied woodpeckers are similar in three genes (Weibel and Moore 2002a, 2002b), the two groups differ anatomically and behaviorally Ouellet 1977; this study). Four-toed pied woodpeckers from the New and Old Worlds are similar in the anatomical characters addressed in this study but differ genetically (Weibel and Moore 2002a, 2002b), thus supporting Ouellet (1977).

Determining whether the genetic groups (Weibel and Moore 2002b:255) represent distinct genera requires increasing the number of taxa and genes compared, not to mention setting generic limits on genetic data. Further genetic and morphologic studies should help define the pied woodpeckers generically. From this study I conclude that the pied woodpeckers represent three good genera and recommend that the generic name *Dendrocopos* continue to apply to the Old World four-toed species of pied woodpeckers. I also recommend that *Picoides* apply only to the three-toed pied woodpeckers and that the generic name *Dryobates* (type species *pubescens*) be used for the North American four-toed species, the Ladder-backed, Nuttall's, Downy, Hairy, Strickland's, Arizona (*arizonae*), Red-cockaded, White-headed, and provisionally for the South American species, the Striped and Checkered (*lignarius* and *mixtus*).

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