



Higher classification of New World parrots (Psittaciformes; Arinae), with diagnoses of tribes

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We offer here a diagnosed higher-level classification of New World parrots to reflect relationships inferred from a consensus of recent DNA-based phylogenies and morphological and behavioral studies. General understanding of the position of New World parrots among the Psittaciformes through the later 20th century stems from Smith's (1975) exhaustive review of structural morphology and behavior, which supplanted previous hypotheses (e.g. Verheyen 1956; Boetticher 1959; Brereton 1963; Wolters 1975). In his study, which covered over 54 genera, including 20 of the roughly 31 from the New World (Collar 1997; Dickinson 2003), Smith (1975) concluded that the New World parrots were monophyletic. Moreover, he considered the New World parrots sufficiently divergent from other parrots to be accorded subfamily rank because they share several unique morphological and behavioral characters, including imperforate neonatal ear canals, double-sided "dyck texture" (Dyck 1971) pigmentation of remiges, lack of cutaneous pigmentation, and one-legged copulatory stance.

All studies based on DNA sequence data have subsequently corroborated the monophyly of New World parrots (Miyaki *et al.* 1998, de Kloet & de Kloet 2005, Tokita *et al.* 2007; Wright *et al.* 2008, Schweizer *et al.* 2011, Kirchman *et al.* 2012, Schirtzinger *et al.* 2012). Furthermore, most found them sister to the African psittacine parrots (*Psittacus*, *Poicephalus*), a relationship robustly supported in the two studies with broadest sampling (Schweizer *et al.* 2011, Schirtzinger *et al.* 2012). Sibley and Ahlquist (1990: fig. 361) had earlier recovered the same result from DNA-DNA hybridisation.

Although the timing of divergences within the parrots is hampered by a lack of well-recognized fossil calibrations within crown lineages, the geographic isolation of New World from Old World parrots is almost certainly ancient. Wright *et al.* (2008) calculated two different divergence dates for New World from Old World parrots based on alternative calibrations. One calibration, based on geological dating of the separation of New Zealand from Australia, produced a date of ca. 55 mya (early Eocene) for this split, and the other, based on a fossil of a stem parrot lineage, produced a date of ca. 35 mya (early Oligocene). Schweizer *et al.* (2011) calculated a divergence date for this separation of ca. 30 mya (Oligocene), based on a number of fossil calibrations external to the parrots. Any of these divergence dates would make the New World parrot lineage older than many non-passerine lineages treated as families in traditional classifications.

Joseph *et al.* (2012) expressed the sister relationship of the New World group and the African psittacine parrots by placing them in a family of their own, Psittacidae, in which each was ranked as a subfamily. They also showed that the valid subfamily name for the New World group under the International Code of Zoological Nomenclature (ICZN 1999), hereafter the Code, was Arinae G.R. Gray 1840 (1825), replacing Macrocerinae Vigors, 1825. We accept this classification of relationships and its nomenclature.

Within the Arinae, supra-generic groupings have been varied and contentious, particularly among the early morpho-behavioral reviews. Verheyen (1956) broke them up into the two groups, the attenuate-tailed (macaws, conures and allies) and round-tailed (amazons and allies) parrots, that Salvadori (1891), Thompson (1899), and others had long recognized. Brereton (1963) proposed radically different relationships and combined all New World parrots in a group among the Old World cockatoos and psittaculine parrots (superfamily Cacatuoidea), except for a small cluster comprising the genera *Forpus*, *Psilopsiagon*, and *Bolborhynchus*, a grouping that proved prescient. These last genera he placed as a distinct group among the Australasian lorries and broad-tailed parrots, which were themselves part of his larger superfamily Platycercoidea. They share a common form of the temporal fossa and auditory meatus with other members of Brereton's (1963) Platycercoidea, and they scratch-preen the head indirectly, over the wing, not under as in

other New World parrots. Smith (1975), followed by Collar (1997) and Dickinson (2003), in turn accepted no groups (tribes) at all among New World parrots, nor did Peters (1937). This was because of exceptions and mixed combinations of traits across the genera. The studies of Salvadori, Thompson, Verheyen and Brereton, analytical though they may have been, were essentially intuitive, based on an eclectic choice of characters with little consideration of their function or potential for adaptive convergence.

Molecular studies, nevertheless, have not only corroborated the traditional long/attenuate- and short/rounded-tailed groups in New World parrots, but also have affirmed the distinctiveness of *Forpus* and *Bolborhynchus* and its allies (Brereton 1963). Joseph *et al.* (2012) used the molecular phylogenies of Miyaki *et al.* (1998), Tavares *et al.* (2006), and Wright *et al.* (2008) to separate the two traditional groups as tribes, despite admitted gaps in taxon sampling; they also predicted that filling those gaps might require recognition of additional tribes. Schirtzinger *et al.* (2012) have now generated a phylogeny of 117 species of parrots (Aves: Psittaciformes) based on DNA sequences of two mitochondrial genes and two nuclear introns. It covered all recognized family groups (Smith 1975, Sibley & Monroe 1990, Collar 1997, Rowley 1997, Dickinson 2003, Joseph *et al.* 2012) and included members of 29 of the 33 living and recently extinct genera of New World parrots (Dickinson 2003, Remsen *et al.* 2012). The four missing genera were the extinct *Conuropsis* and three monospecific genera: *Alipiopsitta*, *Ognorhynchus*, and *Pionopsitta sensu stricto*.

Schirtzinger *et al.* (2012) recovered four primary monophyletic lineages among New World parrots, the first, second and third completely resolved with posterior probabilities of 1.0 and 100% maximum likelihood bootstrap support. They were: (1) a group of four genera of small, mostly green “parrotlets” (*Touit*, *Psilopsiagon*, *Bolborhynchus*, *Nannopsittaca*), which was sister to all other groups; (2) the parrotlet genus *Forpus* alone; (3) the traditional attenuate-tailed group (*Ara* and allies); and (4) the traditional round-tailed group (*Amazona* and allies). These lineages are consistent with those found by Tavares *et al.* (2006), drawn from more limited generic and genetic sampling and not as strongly supported. They are also corroborated by Kirchman *et al.* (2012), who found 1.0 posterior probability support for lineages 1, 3, and 4, albeit with less complete sampling than Schirtzinger *et al.* (2012). Kirchman *et al.* (2012) were able to place *Conuropsis* among the attenuate-tailed lineage 3. Only the study of Wright *et al.* (2008) is partly discrepant. Its phylogeny separated lineages 2, 3 and 4, but, screening only two genera of lineage 1 (*Touit*, *Nannopsittaca*), clustered them in lineage 4 with weak support.

Lineages 1 and 2 do not appear to have been recognized in modern or historic classifications, although Brereton (1963) did group both in one separate family, which he referred to as both Forpidae and Amoropsittacidae (see below). As a group, genera in lineage 1 have also never been identified as closely related. In Ridgway's (1916) detailed dichotomous key to New World parrots, *Nannopsittaca* and *Touit* (then *Urochroma*) are paired but appear in a different branch of the key than do *Bolborhynchus* and *Psilopsiagon*, which are paired as well (also Wolters 1975). The absence of any obvious external characters uniting the two pairs explains why: their species are almost all small, green, short-tailed parrotlets that resemble those of *Forpus* and *Brotogeris*, among which they were traditionally split in linear classificatory sequences (Peters 1937, Wolters 1975, Sibley & Monroe 1990, Collar 1997). Despite external similarities, *Forpus* nevertheless differs internally in lacking a furcula and an *Musculus ambiens*, whereas *Brotogeris* lacks a uropygial gland and preen-scratches directly under the wing, traits characteristic of the amazons and allies (Brereton 1963; see diagnoses below).

A consensus of these data leads us to recognize the four lineages as distinct tribes. These are diagnosed in the classification below, based on morphological and behavioral character states drawn from Verheyen (1956), Brereton (1963), and Smith (1975). We append the component genera in a linear sequence based on the convention that (1) the branch with the fewest genera is listed first for each node of molecular phylogenies, (2) for terminal pairs of genera, the genus with the fewest species is listed first, and (3) for polytomies or terminal pairs of taxa with the same number of species, the genus listed first in traditional sequences (*e.g.* Collar 1997, Dickinson 2003) is listed first. Genera not sampled by Schirtzinger *et al.* (2012) or Kirchman *et al.* (2012) are placed in their traditional positions with respect to the sampled genera. For circumscription of genera, see Remsen *et al.* (2012) and references therein, except for the partitioning of the genus *Aratinga* into four genera, which follows Remsen *et al.* (2013).

The formal names employed for the tribes, one so far unused other than by its author, need explanation. Use of Arini and Androglossini Sundevall, 1872, for lineages 3 and 4, comprising macaws and allies and amazons and allies respectively, is based on Joseph *et al.* (2012). Amazonini Mathews & Iredale, 1920, based on *Amazona* Lesson, 1830, which is the in-use senior synonym of *Androglossus* Sundevall, 1872, may have been introduced in place of Androglossini before 1961, but its use (*e.g.* Verheyen 1956; Wolters 1975) is evidently too rare to satisfy the requirements of prevailing usage under Article 40.2 of the Code. The availability of Forpini Brereton, 1963, for the blue-winged parrotlets of lineage 2 was established by Bock (1994).

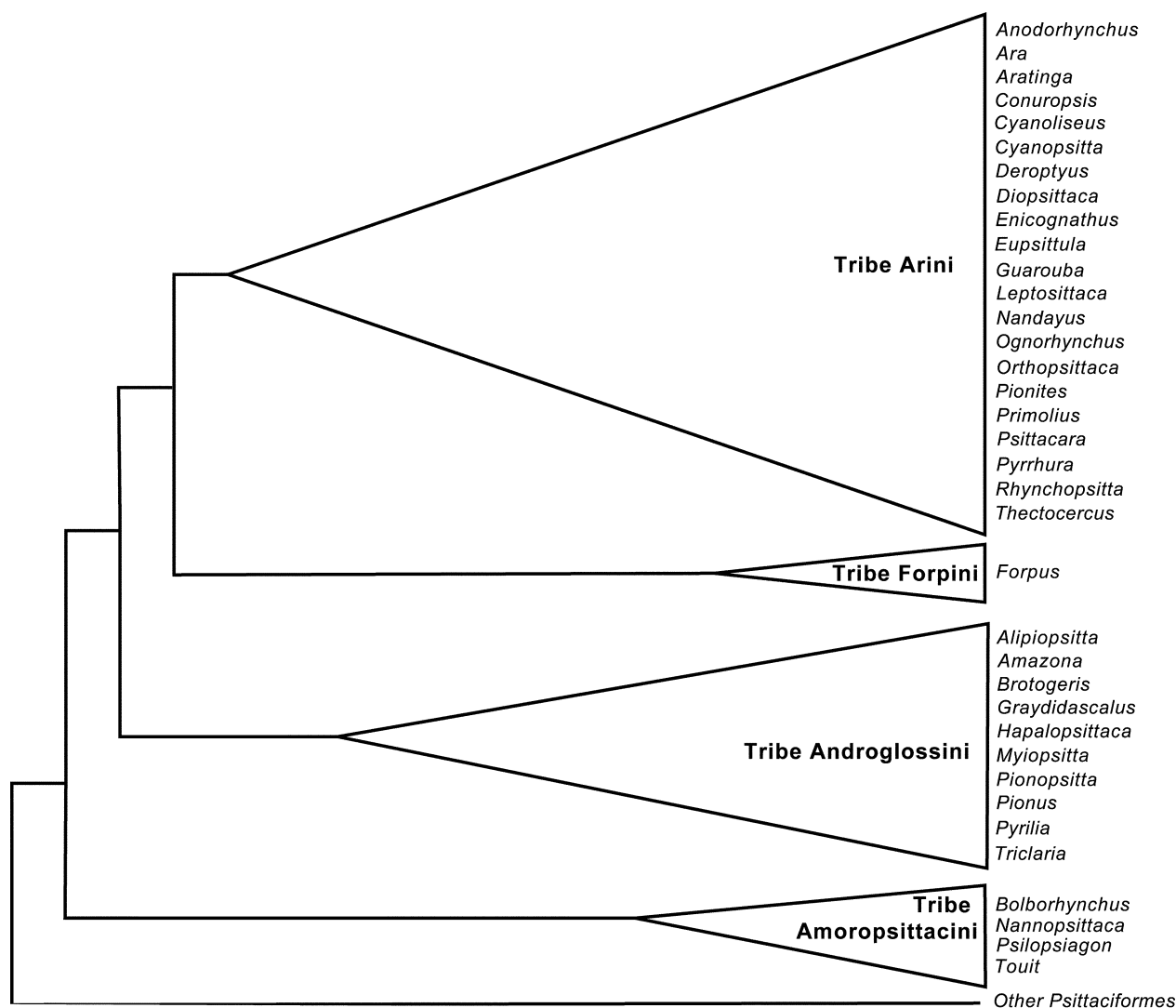


FIGURE 1. Cladogram showing the composition of and relationships among the four tribes of Neotropical parrots proposed here. Topology based on Schirtzinger (2011).

A name for lineage 1 (*Touit*, *Psilopsiagon*, *Nannopsittaca* and *Bolborhynchus*) has apparently only been recorded by Brereton (1963), and then perhaps as an unwitting error. In his review of parrot systematics, Brereton (1963) introduced two family-group names for lineage 1 plus *Forpus*, both of which he combined in a single family (see above). The names were Forpidae (p. 509), based on *Forpus* Boie, 1858, and Amoropsittidae (p. 515, sic = Amoropsittacidae), based on *Amoropsittaca* Richmond, 1915; the latter genus (type species *Arara ayмара* D'Orbigny) is today synonymized with *Psilopsiagon* Ridgway, 1912 (Collar 1997; Dickinson 2003). Both names are available by reference to included genera and descriptive characters given in Table 5 of Brereton's paper (ICZN 1999: Articles 11.7 and 13.1). Evidently unaware that he had introduced different names for the same family in different sections of his paper, Brereton treated both as valid. Under Art. 24 of the Code, precedence of one name over the other may be resolved by the first reviser rule if both names refer to the same taxon. Yet that circumstance no longer applies if lineage 1 is split at family-group rank from lineage 2, as here: it leaves each name available and valid for the tribe that includes its type genus. Amoropsittacini is therefore validly available for lineage 1 under Article 40.1 of the Code, with its original spelling corrected under Articles 29.3, 32.5.3 and 35.4.1.

Dickinson & Remsen (2013) have since used the above information in their treatment of New World parrots; and in doing so they have selected the tribe name Amoropsittacini to take priority over the simultaneously published name Forpini should their taxa ever be merged exclusively at the same family-group rank (p. 365, footnote 12). Here we take the opportunity to correct several errors and ambiguities in Dickinson & Remsen's (*l.c.*) account of these nominal taxa:

(1) p. 356, footnote 12: the emendation of spelling refers to Amoropsittacini, not Forpini, for reasons given in the paragraph above;

(2) p. 391, item 2.1.(6): the spelling of the tribe name “Amauropsittacini” and its type genus “*Amauropsittacus*” are mis-spellings of Amoropsittacini and *Amoropsittacus* respectively.

Suprageneric Classification of New World Parrots, with Diagnoses of the Tribes

Subfamily ARINAE G.R. Gray, 1840 (1825), *A List of the Genera of Birds*, with an indication of the typical species of each genus, p. 51. R. & J.E. Taylor, London—type genus *Ara* Lacépède, 1799.

Tribe AMOROPSITTACINI Brereton, 1963, *Proceedings of the XIII International Ornithological Congress*, p. 515. Ithaca, New York – type genus *Amoropsittaca* Richmond, 1915 (= *Psilopsiagon* Ridgway, 1912).

Small, short- and acute- to round-tailed green parrots with naked cere, sometimes discolorous cap and breast or broad red sash in outer rectrices, and which are sometimes sexually dimorphic (*Psilopsiagon*, *Touit*); temporal fossa shallow, ill-defined, and weakly muscled; auditory meatus part-closed posteriorly and crescentic; orbital ring incompletely ossified, with prefrontal extension vestigial; furcula present; *M. ambiens* present; uropygial gland well-developed; head-preening indirect, by foot over wing. **NOTE:** Anatomical traits based on *Psilopsiagon* and *Bolborhynchus*.

Genera: *Touit* Gray, 1855; *Psilopsiagon* Ridgway, 1912; *Bolborhynchus* Bonaparte, 1857; *Nannopsittaca* Ridgway, 1912.

Tribe FORPINI Brereton, 1963, *Proceedings of the XIII International Ornithological Congress*, p. 509. Ithaca, New York – type genus *Forpus* Boie, 1858

Very small, stumpy- and rounded-tailed, uniformly green parrots with naked cere, usually blue remiges and sometimes back, and which are sexually dimorphic to varying degrees; temporal fossa moderately deep and well-defined and moderately muscled; auditory meatus part-closed posteriorly and crescentic; orbital ring incompletely ossified, with prefrontal extension vestigial; furcula absent; *M. ambiens* absent; uropygial gland well-developed; head-preening indirect, by foot over wing.

Genera: *Forpus* Boie, 1858.

Tribe ARINI G.R. Gray, 1840 (1825)

Small-medium to large, usually acutely medium- to long-tailed variably coloured parrots with feathered or naked cere, and which are sexually monomorphic; temporal fossa well and deeply defined, and strongly muscled; auditory meatus open and square-shaped; orbital ring completely or almost completely ossified by extension of prefrontal (except *Anodorhynchus*); furcula present; *M. ambiens* usually present; uropygial gland well-developed; head-preening direct, by foot under wing. **NOTE:** *Leptosittaca*, *Guarouba*, *Diopsittaca*, *Cyanopsitta*, *Orthopsittaca*, and *Primolius* not scored for anatomical or behavioral traits.

Genera: *Pionites* Heine, 1890; *Deroytus* Wagler, 1832; *Pyrrhura* Bonaparte, 1856; *Enicognathus* G.R. Gray, 1840; *Cyanoliseus* Bonaparte, 1854; *Anodorhynchus* Spix, 1824; *Rhynchopsitta* Bonaparte, 1854; *Eupsittula* Finsch, 1868 (see Remsen *et al.* 2013 for resurrection of this genus); *Conuropsis* Salvadori, 1891; *Aratinga* Spix, 1824; *Cyanopsitta* Bonaparte, 1854; *Nandayus* Bonaparte, 1854 (for inclusion in *Aratinga* see Remsen *et al.* 2013); *Orthopsittaca* Ridgway, 1912; *Primolius* Bonaparte, 1857; *Ara* Lacépède, 1799; *Leptosittaca* Berlepsch & Stolzmann, 1894; *Ognorhynchus* Bonaparte, 1857; *Guarouba* Lesson, 1830; *Diopsittaca* Ridgway, 1912; *Thectocercus* Ridgway, 1916 (see Remsen *et al.* 2013 for resurrection of this genus); *Psittacara* Vigors, 1825.

Tribe ANDROGLOSSINI Sundevall, 1872, *Methodi Naturalis Avium Disponendarum Tentamen*, p. 69. Samson & Wallin, Stockholm—type genus: *Androglossus* Sundevall, 1872

Small to medium, usually round-tailed, green parrots with usually naked cere, commonly vari-coloured heads, and which are, except for *Triclaria* and several species of *Amazona*, sexually monomorphic; temporal fossa usually well and deeply defined, and strongly muscled; auditory meatus open and square-shaped; orbital ring variably ossified by extension of prefrontal; furcula present; *M. ambiens* absent; uropygial gland usually atrophied; head preening direct, by foot under wing. **NOTE:** *Hapalopsittaca*, *Alipiopsitta*, and *Pionopsitta* not scored for anatomical or behavioral traits.

Genera: *Myiopsitta* Bonaparte, 1854; *Brotogeris* Vigors, 1825; *Pionopsitta* Bonaparte, 1854; *Triclaria* Wagler, 1832, *Hapalopsittaca* Ridgway, 1912, *Pyrilia* Bonaparte, 1856, *Pionus* Wagler, 1832, *Graydidascalus* Bonaparte, 1854, *Alipiopsitta* Caparroz & Pacheco, 2006, *Amazona* Lesson, 1830.

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