

# The phylogenetic affinities of the parrot taxa *Agapornis*, *Loriculus* and *Melopsittacus* (Aves: Psittaciformes): hypotarsal morphology supports the results of molecular analyses

Gerald Mayr

Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25,  
D-60325 Frankfurt a.M., Germany. Email: Gerald.Mayr@senckenberg.de

**Abstract.** The interrelationships between the currently recognised subtaxa of parrots (Psittaciformes) are poorly understood and even monophyly of some is not well established. A recent phylogenetic analysis of nuclear gene sequences strongly supports a previously unrecognised clade including *Agapornis* (lovebirds), *Melopsittacus* (Budgerigar), Cyclopsittini (fig-parrots) and Loriini (lories). In the present study it is shown that these taxa also share a unique derived morphology of the hypotarsus, which further occurs in *Loriculus* (hanging-parrots) and *Micropsitta* (pygmy-parrots). It is hypothesised that *Agapornis*, *Loriculus*, *Micropsitta*, Cyclopsittini, *Melopsittacus* and Loriini form a clade for which the name Loricoloriinae is proposed. The presence of an ossified arcus parahyalis on the hyoid bone further suggests a clade including Cyclopsittini, *Melopsittacus* and Loriini, which also gained support from analysis of molecular data.

## Introduction

The phylogeny of the parrots (Psittaciformes) is still very poorly understood. The interrelationships between the subtaxa recognised by Rowley (1997) and Collar (1997) are virtually unresolved and even monophyly of some has not been convincingly established. This is especially true for the Australasian Platycercini (platycercine or broad-tailed parrots) and the Old World Psittaculini (psittaculine or red-billed parrots). With the exception of a second underwing-covert stripe as a possible apomorphy of Platycercini (Courtney 2002), no morphological apomorphies present throughout all members of these taxa have been identified, and their traditional diagnoses are to a large degree based on geographical distribution and external characteristics, such as tail-length and coloration of the bill (e.g. Smith 1975). Not surprisingly, the few molecular studies that have a sufficiently broad taxon sampling do not support monophyly of Platycercini and Psittaculini as currently recognised (Christidis *et al.* 1991; de Kloet and de Kloet 2005; Astuti *et al.* 2006).

Although earlier authors noted several anatomical and behavioural characters of potential phylogenetic significance (e.g. Garrod 1874; Beddard 1898; Mivart 1895; Thompson 1899; Mudge 1903; Glenny 1955; Brereton 1963; Homberger 1980; Güntert 1981), some of these show considerable variation in closely related psittaciform taxa. For example, a closed orbital ring is present in some individuals of *Eclectus roratus* (Eclectus Parrot) but absent in others, and the furcula is complete in *Psephotus dissimilis* (Hooded Parrot) but lacks the extremities sternalis in *P. haematonotus* (Red-rumped Parrot).

Still, not all anatomical characters of potential phylogenetic significance were recognised by earlier authors and the significant variation in hypotarsal morphology was only recently described in more detail by Mayr and Göhlich (2004). In particular, these authors noted that Loriini (lories) and Cyclopsittini

(fig-parrots), as well as the species of *Agapornis* (lovebirds) and *Loriculus* (hanging-parrots) share a highly characteristic derived morphology of the hypotarsus. A similar hypotarsal morphology also occurs in *Melopsittacus undulatus* (Budgerigar).

*Melopsittacus* has been assigned to the Platycercini by most earlier authors, whereas *Agapornis* and *Loriculus* have usually been placed in the Psittaculini. Following tradition, Mayr and Göhlich (2004) noted that the hypotarsal morphology of *Melopsittacus* can be derived from that of the Platycercini, which likewise exhibit a characteristic pattern of the hypotarsal canals. However, a recent analysis of sequences of the Z-chromosomal spindlin gene by de Kloet and de Kloet (2005) provided strong support for a clade combining *Agapornis* + (*Psittaculirostris* (fig-parrots) + (*Melopsittacus* + Loriini)). A clade including these taxa and *Micropsitta* (pygmy-parrots) was also retained in an earlier phenetic analysis of allozyme variation by Christidis *et al.* (1991: Fig. 1) (see Fig. 1).

These observations place hypotarsal morphology in a new context and in the present study the morphological and molecular evidence are brought together. In addition, the previously unknown hypotarsi of *Micropsitta* as well as *Lathamus discolor* (Swift Parrot) and *Pezoporus wallicus* (Ground Parrot), two enigmatic species of the Platycercini, are described in order to evaluate the phylogenetic affinities of these taxa.

## Materials

Hypotarsi of the following parrot species were examined (all in the collection of Forschungsinstitut Senckenberg; nomenclature and classification after Rowley 1997 and Collar 1997):

**Cacatuini:** *Cacatua* (*C. galerita*, *C. goffini*, *C. leadbeateri*, *C. moluccensis*, *C. ophthalmica*, *C. pastinator*, *C. sulfurea*,

*C. tenuirostris*), *Callocephalon fimbriatum*, *Calyptorhynchus funereus*, *Eolophus roseicapillus*, *Nymphicus hollandicus*, *Probosciger aterrimus*.

**Loriini:** *Chalcopsitta cardinalis*, *Charmosyna* (*C. josefinae*, *C. papou*, *C. rubronotata*, *C. placentis*), *Eos* (*E. cyanogenia*, *E. histrio*, *E. reticulata*), *Glossopsitta concinna*, *Neopsittacus pullicauda*, *Oreopsittacus arfaki*, *Trichoglossus* (*T. chlorolepidotus*, *T. haematodus*, *T. ornatus*).

**Psittrichadini:** *Psittrichas fulgidus*.

**Nestorini:** *Nestor notabilis*.

**Strigopini:** *Strigops habroptilus*.

**Micropsittini:** *Micropsitta pusio*.

**Cyclopsittini:** *Cyclopsitta diophthalma*, *Psittaculirostris* (*P. desmarestii*, *P. edwardsii*).

**'Platyercini':** *Barnardius zonarius*, *Cyanoramphus novaezelandiae*, *Eunymphicus cornutus*, *Lathamus discolor*, *Melopsittacus undulatus*, *Neophema* (*N. chrysogaster*, *N. elegans*, *N. pulchella*, *N. splendida*), *Neopsephotus bourkii*, *Northiella haematogaster*, *Pezoporus wallicus*, *Platyercus* (*P. adscitus*, *P. elegans*, *P. eximius*, *P. icterotis*), *Prosopieia tabuensis*, *Psephotus* (*P. dissimilis*, *P. haematonotus*, *P. varius*).

**'Psittaculini':** *Agapornis* (*A. canus*, *A. fischeri*, *A. lilianae*, *A. nigrigenis*, *A. personata*, *A. roseicollis*, *A. taranta*), *Alisterus* (*A. amboinensis*, *A. chloropterus*, *A. scapularis*), *Aprosmictus erythropterus*, *Eclactus roratus*, *Geoffroyus geoffroyi*, *Loriculus* (*L. galgulus*, *L. stigmatus*), *Polytelis* (*P. alexandrae*, *P. anthopleps*, *P. swainsonii*), *Psittacula* (*P. alexandri*, *P. cyanocephala*, *P. eupatria*, *P. himalayana*, *P. krameri*), *Psittinus cyanurus*, *Tanygnathus lucionensis*.

**Psittacini:** *Coracopsis vasa*, *Poicephalus* (*P. cryptoxanthus*, *P. gulielmi*, *P. meyeri*, *P. rufiventris*, *P. senegalus*), *Psittacus erithacus*.

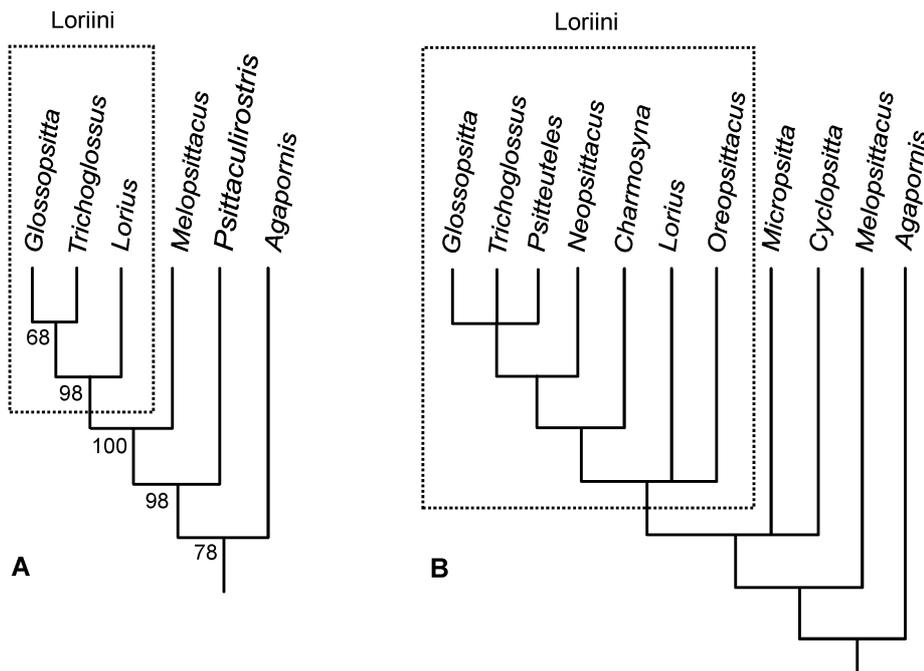
**Arini:** *Amazona* (*A. aestiva*, *A. amazonica*, *A. arausiaca*, *A. autumnalis*, *A. brasiliensis*, *A. festiva*, *A. imperialis*, *A. ochro-*

*cephala*, *A. pretrei*, *A. rhodocorytha*, *A. versicolor*, *A. vinacea*, *A. vittata*, *A. xanthops*), *Anodorhynchus hyacinthinus*, *Ara* (*A. ararauna*, *A. chloroptera*, *A. macao*, *A. rubrogenys*), *Aratinga* (*A. acuticaudata*, *A. leucophthalmus*, *A. pertinax*, *A. solstitialis*, *A. wagleri*, *A. weddellii*), *Bolborhynchus lineola*, *Brotogeris* (*B. chrysopterus*, *B. cyanoptera*, *B. jugularis*, *B. pyrrhopterus*, *B. versicolorus*), *Cyanoliseus patagonus*, *Diopsittaca nobilis*, *Enicognathus* (*E. ferrugineus*, *E. leptorhynchus*), *Forpus* (*F. coelestis*, *F. conspicillatus*, *F. crassirostris*), *Guarouba guarouba*, *Myiopsitta monachus*, *Nandayus nenday*, *Pionites melanocephala*, *Pionopsitta pileata*, *Pionus sordidus*, *Pyrrhura* (*P. cruentata*, *P. leucotis*, *P. molinae*, *P. peralta*, *P. picta*).

## Results

The hypotarsus is a structure on the proximal end of the tarsometatarsus which guides the tendons of the flexor muscles of the toes. Most psittaciform birds possess a hypotarsus with two canals for the deep flexor tendons, i.e. those of *musculus flexor hallucis longus* (fhl) and *musculus flexor digitorum longus* (fdl) (Fig. 2A, B). The tendons of the superficial flexor tendons, i.e. those of *musculus flexor perforatus digiti II* (pII), *musculus flexor perforans et perforatus digiti II* (ppII), *musculus flexor perforatus digiti III* (pIII), *musculus flexor perforans et perforatus digiti III* (ppIII), and *musculus flexor perforatus digiti IV* (pIV), are not usually enclosed in bony canals.

This pattern of hypotarsal canals, or slight modifications thereof (Mayr and Göhlich 2004), occurs in most extant psittaciform taxa, including the Nestorini (the species of *Nestor* (Kea (*N. notabilis*) and kakas)), Strigopini (*Strigops habroptilus* (Kakapo)), Cacatuini (cockatoos), Psittacini (Afrotropical parrots) and most Arini (New World parrots, in which the canals of the deep flexor tendons often fuse). From outgroup comparisons with other birds and Eocene stem-group representatives of



**Fig. 1.** Molecular phylogenies in comparison. (A) Simplified detail of a cladogram resulting from an analysis of intron sequences of the Z-chromosomal spindlin gene (de Kloet and de Kloet 2005: fig. 1); bootstrap support values are indicated above the nodes. (B) Simplified detail of an UPGMA phenogram resulting from an analysis of allozyme variation of 21 protein loci (Christidis *et al.* (1991: fig. 1).

the Psittaciformes (Mayr and Daniels 1998) it can be concluded that it represents the plesiomorphic condition.

In contrast, and as detailed by Mayr and Göhlich (2004), the hypotarsi of *Agapornis*, *Loriculus*, *Melopsittacus* and the Loriini are characterised by the formation of a large canal that encompasses most of the superficial flexor tendons, i.e. those of ppII, pIII, ppIII and pIV (Fig. 2F, G, J). In *Agapornis*, *Loriculus* and the Loriini, this canal also includes the tendon of pII and, in the latter, the canals of the superficial and deep flexor tendons usually fuse to form a large canal for all flexor tendons (Fig. 2J).

The same derived hypotarsal morphology occurs in *Micropsitta* (Fig. 2H), whose hypotarsus is for the first time examined in the present study and resembles that of *Melopsittacus*. The hypotarsus of the Cyclopsittini is also very similar to that of the above taxa but the plantar wall of the canal for the superficial flexor tendons is incompletely closed (Fig. 2I).

The previously undescribed hypotarsus of *Lathamus discolor* closely resembles the derived type found in the platycercine taxa *Platycercus* (rosellas), *Northiella* (*N. haematogaster* (Blue Bonnet)), *Eunymphicus* (*E. cornutus* (Horned Parakeet)), *Cyanoramphus* (parakeets), *Prosopiea* (shining-parrots), *Barnardius* (ringnecks), and *Psephotus* (grass parrots), in which the superficial tendons (pIII, ppIII and pIV) are situated in a deep sulcus (Fig. 2C, D). In contrast to the taxa listed above, these tendons are not enclosed in a bony canal which also encompasses the tendon of ppII.

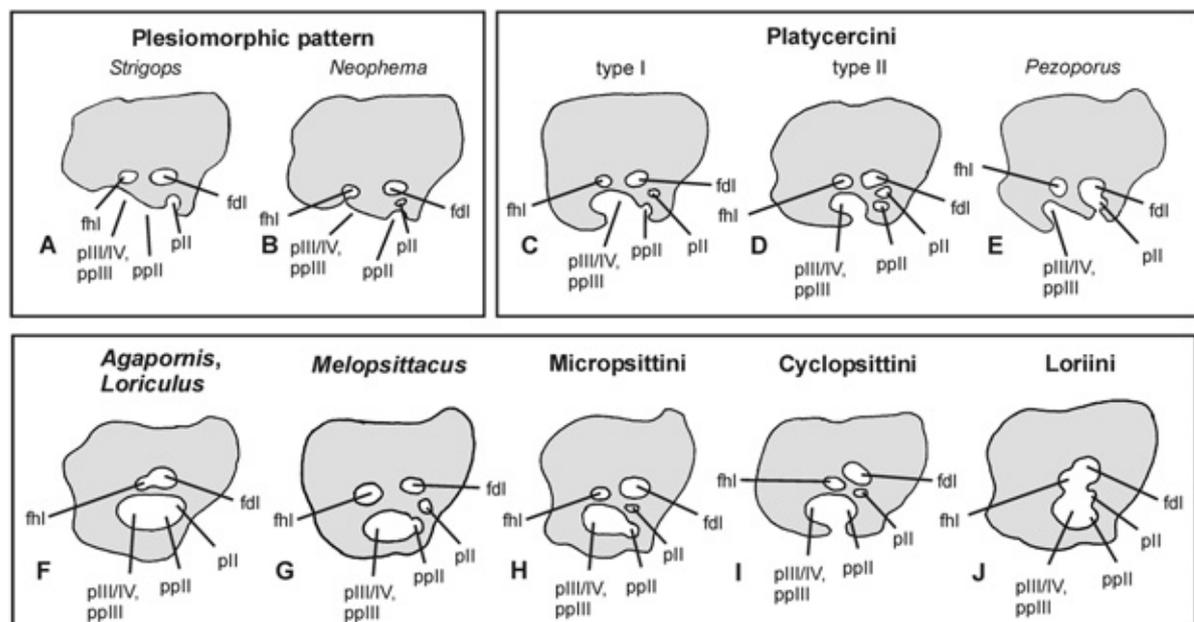
Within the examined Platycercini this derived hypotarsal morphology is absent in *Neophema* (grass parrots) and

*Neopsephotus* (*N. bourkii* (Bourke's Parrot)). In *Pezoporos wallicus* (Fig. 2E) the tendons of pIII, ppIII and pIV are not enclosed in a canal as in *Melopsittacus* but situated in a sulcus as in the platycercine taxa listed above.

## Discussion

The strongest evidence for the correctness of a phylogenetic hypothesis comes from congruence among independent datasets (e.g. Mayr 2008). As noted above, a clade including *Agapornis*, *Melopsittacus*, Cyclopsittini and Loriini was supported by analyses of allozyme variation and nuclear gene sequences (Christidis *et al.* 1991; de Kloet and de Kloet 2005). The study of Christidis *et al.* (1991) also recovered *Micropsitta* as part of this clade, and the formation of a bony canal for the superficial flexor tendons (ppII, pIII, ppIII and pIV) provides further morphological evidence for a clade comprising these taxa, including *Micropsitta*, as well as *Loriculus*, which was not included in the studies of Christidis *et al.* (1991) and de Kloet and de Kloet (2005).

The Cyclopsittini were considered closely related to the Loriini by earlier authors (e.g. Smith 1975), but a clade including all of the above taxa has not been proposed before. Holyoak (1973) suggested that the Platycercini, Loriini and Nestorini form a monophyletic group, but did not list unambiguous apomorphies of a clade including these taxa (see also Smith 1975). The Nestorini exhibit the plesiomorphic hypotarsal morphology (i.e. the superficial flexor tendons pIII, ppIII and pIV are not situated in a sulcus or canal) and the analysis of de Kloet and de Kloet (2005) strongly supports sister-group relationship



**Fig. 2.** Comparison of parrot hypotarsi (left tarsometatarsus, not to scale): (A) *Strigops habroptilus*; (B) *Neophema elegans*; (C) Platycercini, type I (*Eunymphicus*, *Cyanoramphus*, *Psephotus* [part]); (D) Platycercini, type II (*Platycercus*, *Prosopiea*, *Lathamus*, *Barnardius*, *Psephotus* [part]); (E) *Pezoporos wallicus*; (F) *Loriculus stigmatus*; (G) *Melopsittacus undulatus*; (H) *Micropsitta pusio*; (I), *Cyclopsitta diophthalma* (Cyclopsittini); and (J) *Trichoglossus haematodus* (Loriini). The canals and grooves for the flexor tendons are indicated by the following abbreviations: fhl – musculus flexor hallucis longus; fdl – musculus flexor digitorum longus; pII – musculus flexor perforatus digiti II; ppII – musculus flexor perforans et perforatus digiti II; pIII/IV – musculi flexores perforati digitorum III et IV; ppIII – musculus flexor perforans et perforatus digiti III.

between a clade including Nestorini and Strigopini, and all other extant Psittaciformes.

*Melopsittacus* has been assigned to the Platycercini by most previous authors (e.g. Holyoak 1973; Smith 1975; Homberger 1980; Collar 1997). However, this hypothesis has not been convincingly established with derived characters. Homberger (1980: p. 165) assumed that some of the lingual and palatal adaptations of *Melopsittacus* for a granivorous diet evolved independently from those of typical Platycercini, and that 'concerning neither the palate nor the tongue, *Melopsittacus* exhibits non-adaptive characters shared with other Platycercini' (my translation). Brereton (1963) assigned *Melopsittacus* to his taxon 'Pezoporidae', together with *Pezoporus* and *Geopsittacus*. These three taxa lack the derived A-2-s carotid artery pattern found in all other platycercine parrots except *Neophema* and *Neopsephotus* (Glenny 1955; Smith 1975: table 2). As detailed above, *Melopsittacus* and *Pezoporus* are clearly distinguished from each other in hypotarsal morphology, with *Pezoporus* showing the derived pattern of 'core-Platycercini' (all platycercine taxa investigated in this study except *Neophema*, *Neopsephotus*, and *Melopsittacus*). Although a molecular analysis by Leeton *et al.* (1994) showed *Pezoporus* to be more closely related to *Melopsittacus* than to *Platycercus*, this study was based on a rather small taxon sampling and no representatives of the Loriini were included.

*Agapornis* and *Loriculus* were assigned to the Psittaculini by many earlier authors (e.g. Smith 1975; Collar 1997). Again, this classification appears to have been strongly influenced by geographical distribution and external characteristics, such as the red bill of the males which does, however, not occur in all species of *Agapornis* and *Loriculus* and is also found in some Loriini. Brereton (1963) classified *Agapornis* and *Loriculus* into his 'Micropsittidae', which also included *Micropsitta*, whereas Homberger (1980) retained *Agapornis* in the Psittaculini but assigned *Loriculus* to a monotypic 'family'. The only comprehensive molecular analysis in which *Loriculus* was included resulted in a sister-group relationship between *Loriculus* and *Psittitrichas* (Astuti *et al.* 2006). A sister-group relationship between these two taxa received, however, very low bootstrap support and *Agapornis* and *Melopsittacus* were not included in the study.

To the best of my knowledge, there is thus no published evidence that strongly conflicts with a clade that includes *Agapornis*, *Loriculus*, *Melopsittacus*, *Micropsitta*, the Cyclopsittini and Loriini, for which I propose the term Loricoloriinae, with the type genus *Loriculus*.

Unfortunately, hypotarsal morphology does not offer convincing clues concerning the relationships within this clade. The analysis of de Kloet and de Kloet (2005) supports a clade including *Melopsittacus*, the Cyclopsittini and Loriini, to the exclusion of *Agapornis* (Fig. 1A), which is in concordance with the fact that the hyoid bone of these taxa exhibits an arcus parahyalis, a derived character which otherwise occurs only in the Nestorini (Mivart 1895; Holyoak 1973). The wings of the adult males of *Melopsittacus*, the Cyclopsittini and most Loriini further bear a pale stripe across their ventral side (Holyoak 1973; Smith 1975). *Melopsittacus* and the Cyclopsittini share a completely closed orbital ring but as this feature evolved several times independently within Psittaciformes its homology needs

to be tested in a more inclusive analysis, which is beyond the scope of this study.

The hypotarsal morphology of 'core-Platycercini', in which the tendons of pIII, ppIII and pIV are situated in a deep sulcus, may be homologous to that of the Loricoloriinae, in which these tendons are enclosed in a bony canal. Indeed, a clade including the sampled taxa of 'core-Platycercini' and Loricoloriinae, as well as *Neopsephotus* (in a polytomy with 'core-Platycercini' and Loricoloriinae) was retained in an analysis of de Kloet and de Kloet (2005: fig. 3), in which the phylogenetic significance of sequence indels was taken into account. Future studies will have to show whether it is also recovered in analyses of other molecular data.

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