Parrot interrelationships – morphology and the new molecular phylogenies

Gerald Mayr

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

Abstract.   Molecular analyses have started to provide a congruent picture of parrot interrelationships but the affinities of some taxa remain uncertain and there have been few attempts to correlate the new molecular phylogenies with anatomical characters. In the present study, anatomical features that were traditionally used to classify parrots are mapped onto the molecular tree topologies. Some characters show a high degree of homoplasy but the distributions of others correlate well with the molecular phylogenies. The morphology of the hypotarsus indicates a clade including the core-Platycercini and Loricoloriinae excluding *Neophema* and *Neopsephotus*. The lack of the ambiens muscle suggests a sister-group relationship between *Coracopsis* and *Psittrichas*, whose affinities are not congruently resolved by molecular data; a derived pattern of the carotid arteries indicates a position of these two taxa within a clade including *Psittacus*, *Poicephalus* and the Arini. Within the Arini, a clade including the long-tailed New World parrots is supported by the derived presence of unusually small narial openings, whereas a clade including some of the short-tailed taxa is supported by the loss of the ambiens muscle.

Introduction

Parrots (Psittaciformes) are one of the most species-rich groups of non-passeriform birds, but for a long time their interrelationships remained poorly understood. Recently, however, four molecular analyses with a broad sampling of taxa were published, with good agreement in the resulting tree topologies (de Kloet and de Kloet 2005; Tokita *et al*. 2007; Wright *et al*. 2008; Schweizer *et al*. 2010). These analyses are based on independent ribosomal, mitochondrial and nuclear sequence data, and some clades are highly supported and congruently obtained (Fig. 1).

In general, these studies found a sister-group relationship between the clade (*Strigops* + *Nestor*) and all other Psittaciformes, with the Cacatuini (cockatoos) branching next as the sister group of all of the remaining Psittaciformes except *Strigops* and *Nestor*. (In the analysis of Schweizer *et al. Strigops* was not included, and the study of de Kloet and de Kloet did not find a basal position of the Cacatuini.) Astuti *et al*. (2006) also found a sister-group relationship between the Cacatuini and all other included parrots , but the taxon sampling of this study was not dense and most nodes of the resulting phylogeny received only low support values.

All four analyses (de Kloet and de Kloet 2005; Tokita *et al*. 2007; Wright *et al*. 2008; Schweizer *et al*. 2010) further supported a sister-group relationship between the African taxa *Psittacus* and *Poicephalus* and the monophyletic Arini (New World parrots), as well as a clade including Loriini (lories), Cyclopsittini (fig-parrots) and the non-monophyletic 'Platycercini' (platycercine or broad-tailed parrots) and 'Psittaculini' (psittaculine or red-billed parrots). *Melopsittacus*, traditionally classified in the 'Platycercini', is the sister taxon of the Loriini, whereas a clade including *Agapornis* and *Loriculus*, which were traditionally

classified in the 'Psittaculini', is the sister group of the *Melopsittacus*–Cyclopsittini–Loriini clade.

Still, however, these phylogenies contain several poorly resolved or conflicting clades, and little attempt has been made to correlate the molecular results with morphological characters. A notable exception is the study of Tokita *et al*. (2007), who mapped the presence of a closed suborbital arch and a well-developed musculus pseudomasseter on a molecular tree topology, and found that both features, which may or may not be functionally correlated (Zusi 1993; Tokita *et al*. 2007), exhibit a high degree of homoplasy. Mayr (2008) noted that hypotarsal morphology supports a clade including *Micropsitta*, *Agapornis*, *Loriculus*, *Melopsittacus*, Cyclopsittini and Loriini, for which the term Loricoloriinae was proposed.

Earlier morphologists identified various anatomical features of potential phylogenetic significance within parrots (e.g. Beddard 1898; Thompson 1899; Glenny 1955; Holyoak 1973; Smith 1975; Homberger 1980; Güntert 1981). In the present study, some of these characters are mapped onto the phylogenetic framework provided by the new molecular analyses in order to identify potential apomorphies of psittaciform clades, and to evaluate the extent of homoplasy of some morphological features in a well-defined avian group.

Materials and methods

Skeletons of the following parrot species were examined (all in the collection of Forschungsinstitut Senckenberg):

Strigopini: *Strigops habroptilus*;

Nestorini: *Nestor notabilis*;

Cacatuini: *Cacatua* (*galerita*, *goffini*, *leadbeateri*, *moluccensis*, *ophthalmica*, *pastinator*, *sulphurea*, *tenuirostris*), *Callocephalon fimbriatum*, *Calyp-*
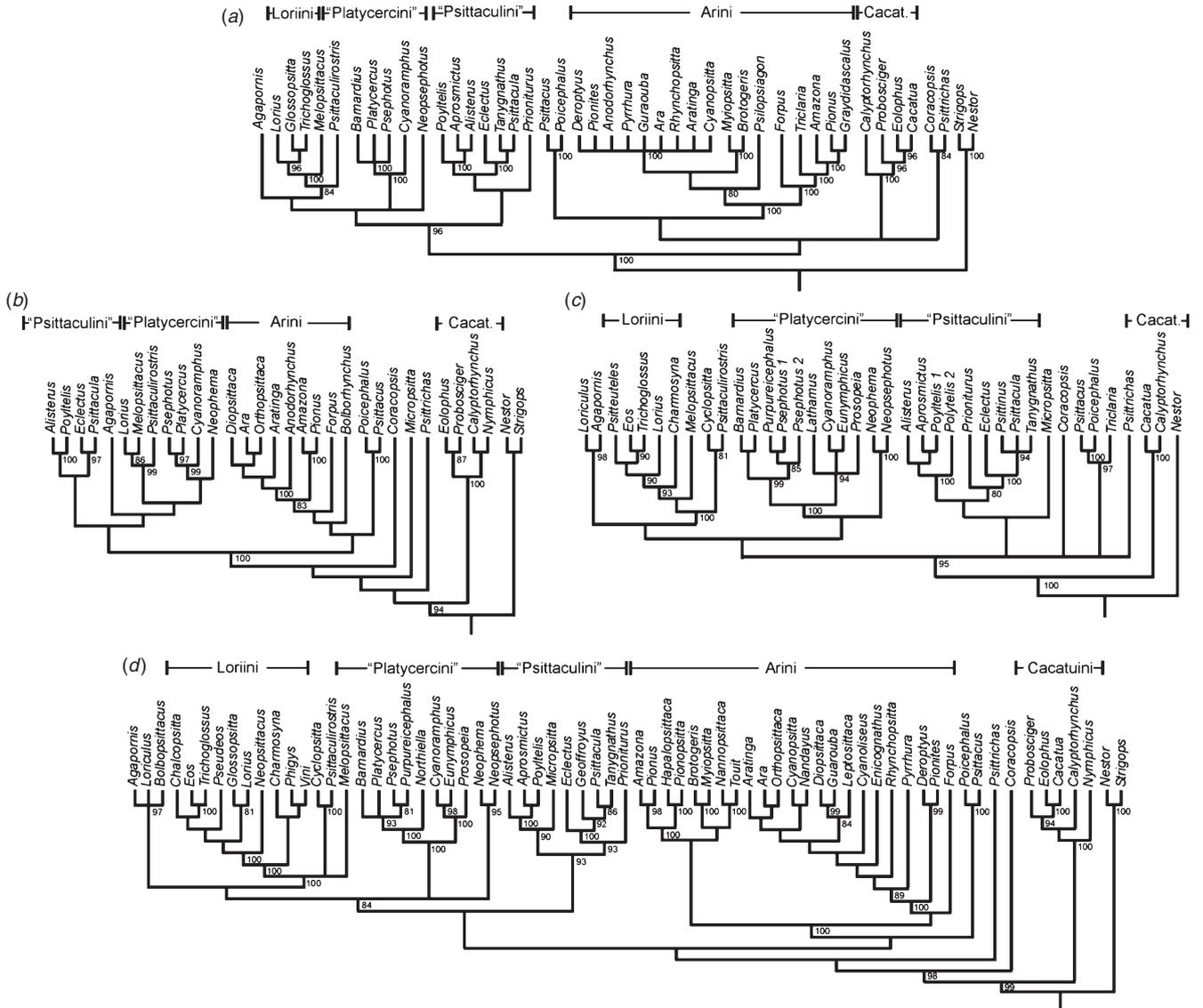
Fig. 1. Molecular phylogenies in comparison. (*a*) Consensus tree resulting from a maximum-likelihood analysis of Z-chromosomal spindlin sequences (after de Kloet and de Kloet 2005: fig. 3; maximum parsimony trees were not shown in the study). (*b*) Maximum likelihood cladogram resulting from an analysis of 12S and 16S rRNA (after Tokita *et al.* 2007; maximum parsimony trees were not shown in the study). (*c*) Strict consensus tree resulting from a maximum parsimony analysis of nuclear c-mos, RAG-1, and ZENK sequences (after Schweizer *et al.* 2010: fig. 2). (*d*) Strict consensus tree resulting from a maximum parsimony analysis of sequences of the mitochondrial cytochrome oxidase I and NADH dehydrogenase 2 genes, and the nuclear tropomyosin α-subunit intron 5, rhodopsin intron 1, and transforming growth factor β-2 (after Wright *et al.* 2008: fig. 1). Numbers next to the nodes indicate bootstrap support values >80% as given in the original publications.

torhynchus funereus, *Eolophus roseicapillus*, *Nymphicus hollandicus*, *Probosciger aterrimus*;

Psittrichadini: *Psittrichas fulgidus*;

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

Arini: *Amazona* (*aestiva*, *amazonica*, *arausiaca*, *autumnalis*, *brasiliensis*, *festiva*, *imperialis*, *ochrocephala*, *pretrei*, *rhodocorytha*, *versicolor*, *vinacea*, *vittata*, *xanthops*), *Anodorhynchus hyacinthinus*, *Ara* (*ararauna*, *chloroptera*, *macao*, *rubrogenys*), *Aratinga* (*acuticaudata*, *leucophthalmus*, *pertinax*, *solstitialis*, *wagleri*, *weddellii*), *Bolborhynchus lineola*, *Brotogeris* (*chrysopterus*, *cyanoptera*, *pyrrhopterus*, *versicolorus*), *Cya-*

noliseus patagonus, *Enicognathus* (*ferrugineus*, *leptorhynchus*), *Forpus* (*coelestis*, *conspicillatus*), *Geoffroyus geoffroyi*, *Guarouba guarouba*, *Myiopsitta monachus*, *Nandayus nenday*, *Pionites melanocephala*, *Pionopsitta pileata*, *Pionus sordidus*, *Primolius couloni*, *Pyrrhura* (*cruentata*, *leucotis*, *perlata*, *picta*);

'Psittaculini': *Agapornis* (*canus*, *lilianae*, *nigrigenis*, *personata*, *roseicollis*), *Alisterus* (*amboinensis*, *chloropterus*, *scapularis*), *Aprosmictus erythropterus*, *Eclectus roratus*, *Loriculus* (*galgulus*, *stigmatus*), *Polytelis* (*alexandrae*, *anthopeplus*, *swainsonii*), *Psittacula* (*alexandri*, *cyanocephala*, *eupatria*, *himalayana*), *Psittinus cynanurus*, *Tanygnathus lucionensis*;

Micropsittini: *Micropsitta bruijnii*;

'Platycercini': *Barnardius* (*barnardi*, *zonarius*), *Cyanoramphus novaezelandiae*, *Eunymphicus cornutus*, *Melopsittacus undulatus*, *Neophema* (*chrysogaster*, *elegans*, *pulchella*, *splendida*), *Neopsephotus bourkii*, *Northiella haematogaster*, *Platycercus* (*elegans*, *eximius*, *icterotis*), *Prosopeia tabuensis*, *Psephotus* (*chrysopterygius*, *haematonotus*);

Cyclopsittini: *Cyclopsitta* (*diophthalma*, *gulielmitertii*), *Psittaculirostris* (*desmarestii*, *edwardsii*);

Loriini: *Chalcopsitta cardinalis*, *Charmosyna* (*papou*, *rubronotata*, *placentis*), *Eos* (*cyanogenia*, *histrio*, *reticulata*), *Glossopsitta concinna*, *Lorius hypoinochrous*, *Neopsittacus pullicauda*, *Oreopsittacus arfaki*, *Pseudeos fuscata*, *Trichoglossus haematodus*, *Vini* (*australis*, *peruviana*).

Nomenclature of the extant taxa follows Rowley (1997) and Collar (1997) (which is consistent with Christidis and Boles 2008 for Australian taxa). Non-osteological characters were taken from the literature. Ancestral character states were reconstructed with Mesquite 2.71 using the parsimony criterion (Maddison and Maddison 2009).

The tree used for the character reconstructions is based on the well-supported and taxon-rich phylogeny of Wright *et al.* (2008: fig. 1), with the following modifications: (a) following Schweizer *et al.* (2010), *Cyclopsittini* and *Melopsittacus* are shown as successive sister taxa of Loriini (these three taxa were placed in a polytomy in the Wright *et al.* 2008 analysis); (b) following Schweizer *et al.* (2010), *Barnardius* and *Platycercus* were shown as sister taxa (placed in a polytomy in the Wright *et al.* 2008 analysis); (c) *Psittinus*, which was not included in the Wright *et al.* (2008) study, was added and placed in a polytomy with *Geoffroyus*, *Tanygnathus*, and *Psittacula*, because its position was not fully resolved in the Schweizer *et al.* (2010) study; (d) *Coracopsis* and *Psittrichas* were placed in a polytomy because of their highly variable position in the studies of de Kloet and de Kloet (2005), Tokita *et al.* (2007), Wright *et al.* (2008), and Schweizer *et al.* (2010); (e) the phylogeny of the New World taxa is after Tavares *et al.* (2006: fig. 2) because Arini were less comprehensively sampled by Wright *et al.* (2008) and Schweizer *et al.* (2010); (f) *Callocephalon* and *Oreopsittacus*, which were not included in any of the recent molecular analyses, were tentatively added.

Results

Plesiomorphic features of Strigops, Nestor, and Cacatuini

Strigops, *Nestor* and the species of the Cacatuini are the only extant Psittaciformes with a distinctly bifurcated spina externa of the sternum, which is narrow in all other crown group Psittaciformes (Fig. 2). Beddard (1898: p. 260) further noted that *Strigops*, *Nestor* and the Cacatuini are distinguished from other parrots in that the musculus deltoideus major is, as usually, larger than the m. deltoideus minor, whereas these muscles are either of equal size in other parrots, or the m. deltoideus minor is larger. Beddard (1898: p. 255) also listed differences in the morphology of the syrinx between *Strigops* and the Cacatuini and the rest of the examined parrots (*Nestor* was not studied). In the former two taxa the 'first semi-rings of the bronchi [=cartilagines bronchosyringeales] are weak and cartilaginous, and are usually separated from each other by considerable tracts of membrane' (Beddard 1898: p. 255), whereas in the other taxa (*Amazona*, *Pionus*, *Psittacus*, *Poicephalus*, *Tanygnathus*, *Polytelis*, *Eos*, *Trichoglossus*,

Lorius, *Platycercus* and *Prosopeia*) they are 'as a rule ossified, and are frequently more or less fused together' (Beddard 1898: p. 256). The topology of the trees resulting from the molecular phylogenies suggests that a bifurcated spina externa, a large musculus deltoideus major, and weak and cartilaginous cartilagines bronchosyringeales are plesiomorphic traits of crown group Psittaciformes.

So far, no morphological features were published that convincingly support a clade including *Strigops* and *Nestor*, and a sister-group relationship between the latter and all other Psittaciformes. The apparatus hyobranchialis of *Nestor* is, however, distinguished from that of other parrots by proportionally longer ossa epibranchialia, which, by outgroup comparisons with other neornithine birds, are a plesiomorphic trait (the ossa epibranchialia are very short and stout in other parrots; Fig. 2). As already noted by Thompson (1899), the quadratum of *Strigops* exhibits a proportionally longer processus orbitalis than that of all other Psittaciformes, which have unusually short processus orbitalis and that are unquestionably a derived feature (Fig. 2).

Size of the narial openings

Boles (1993) described several features of the upper bill of parrots and noted that the narial openings of some Cacatuini (*Calyptorhynchus*, *Probosciger*) and Arini (*Anodorhynchus*, *Ara*, *Aratinga*, *Cyanoliseus*, *Enicognathus*, *Myiopsitta*, *Pionites*, *Pyrrhura*, *Rhynchopsitta*) are unusually small (Fig. 2). As shown in Fig. 3a the distribution of small nostrils corresponds well with the molecular phylogenies, which indicate that they represent an apomorphy of a clade including long-tailed Arini: *Anodorhynchus*, *Ara*, *Aratinga*, *Cyanoliseus*, *Enicognathus*, *Pionites*, *Pyrrhura* and *Rhynchopsitta*, and evolved convergently in *Myiopsitta*.

Hyoid apparatus

The apparatus hyobranchialis of *Melopsittacus*, the Cyclopsittini, Loriini and *Nestor* exhibits an arcus parahyalis, that is, the processus parahyales fuse dorsally and form an osseous arch (Mivart 1895; Fig. 2). According to the molecular phylogenies this feature is an apomorphy of a clade including *Melopsittacus*, the Cyclopsittini and Loriini, and evolved convergently in *Nestor* (Fig. 3b).

Incomplete furcula

In several parrots the furcula lacks an extremitas sternalis, so that the scapi clavicularum are separated. Such reduction of the extremitas sternalis occurs in *Strigops*, *Forpus*, *Micropsitta*, *Agapornis*, *Melopsittacus* and all other taxa of the traditional 'Platycercini' except *Prosopeia*, *Eunymphicus* and *Lathamus* (Smith 1975), as well as in *Oreopsittacus* (Loriini; *contra* Smith 1975, who erroneously considered the furcula of this taxon to be complete). The 'platycercine' taxon *Psephotus* varies, with a complete furcula being present in, for example, *Psephotus dissimilis*, but absent in *P. haematonotus*. According to the molecular phylogenies, the extremitas sternalis was reduced at least nine times (Fig. 4a), in: (1) *Strigops*; (2) *Forpus*; (3) *Micropsitta*; (4) *Agapornis*; (5) *Melopsittacus*; (6) *Oreopsittacus*; (7) the stem species of the *Neopsephotus–*
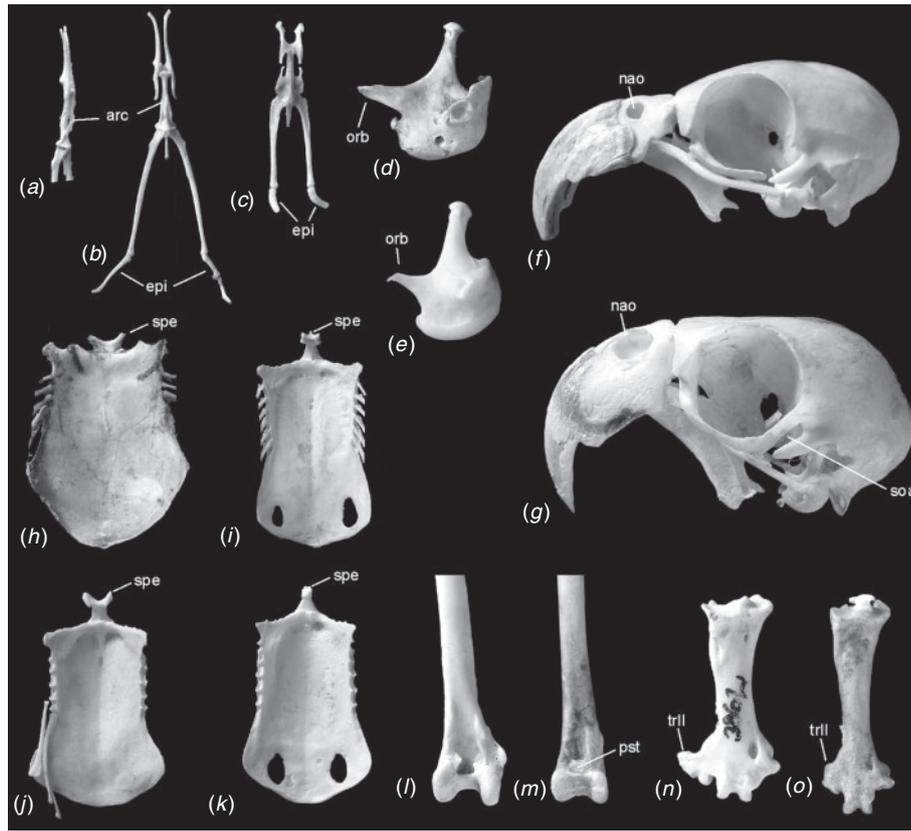
Fig. 2. (*a–c*) Apparatus hyobranchialis of: (*a*, *b*) *Nestor notabilis* (Nestorini) and (*c*) *Polytelis anthopeplus* ('Psittaculini'). (*d*, *e*) Quadratum of: (*d*) *Strigops habroptilus* (Strigopini) and (*e*) *Ara nobilis* (Arini). (*f*, *g*) Narial opening of: (*f*) *Pionites melanocephala* (Arini) and (*g*) *Pionus sordidus* (Arini). (*h–k*) Spina externa of the sternum of: (*h*) *Strigops habroptilus*; (*i*) *Nestor notabilis*; (*j*) *Cacatua sulphrea* (Cacatuini); and (*k*) *Ara nobilis*. (*l*, *m*) Distal tibiotarsusand (*n*, *o*) tarsometatarsus of: (*l*, *n*) *Tanygnathus lucionensis* ('Psittaculini') and (*m*, *o*) *Polytelis anthopeplus*. Figures not to scale. Abbreviations: arc, arcus parahyalis; epi, os epibranchiale; nao, narial opening; orb, processus orbitalis; pst, pons suprantendineus; soa, suborbital arch; spe, spina externa; tmII, trochlea metatarsi II.

Neophema clade; (8) *Cyanoramphus*; and (9) the stem species of the clade including *Psephotus*, *Barnardius*, *Platycercus* and *Northiella*. The variation of the morphology of the furcula in parrots was considered to be of little phylogenetic significance by Smith (1975), and loss of an extremitas sternalis indeed occurred too often to be of great phylogenetic significance. Stegmann (1964) assumed that reduction of the furcula is correlated with a size increase of the crop, and this hypothesis is supported by the fact that within the 'Platycercini' the furcula is incomplete in granivorous taxa, whereas it is complete in the nectarivorous and frugivorous species, which feed on softer and easily digestible plant matter (*Prosopeia*, *Eunymhicus* and *Lathamus*; Collar 1997).

Supratendinal bridge of tibiotarsus

Among the well-known variations in psittaciform osteology is the incomplete ossification, or even complete lack, of the pons supratendineus on the distal tibiotarsus, which to the best of my knowledge is here for the first time surveyed across a comprehensive taxonomic sampling. This bridge is incompletely ossified

in: *Tanygnathus*, *Psittacula*, *Psittinus*, *Geoffroyus* and *Eclectus* among the studied 'Psittaculini'; *Psittacus* (Psittacini); *Primolius*, *Nandayus*, *Aratinga*, *Cyanoliseus* and *Pionites* among the Arini; and *Callocephalon* and *Calyptorhynchus* among the Cacatuini. It is completely absent in *Poicephalus* (Psittacini), and *Bolborhynchus*, *Ara*, *Anodorhynchus*, *Myiopsitta*, *Pionopsitta*, *Pionus*, and *Amazona* (Arini). The condition in *Pyrrhura* and *Guarouba* (Arini) and *Cacatua* and *Eolophus* (Cacatuini) varies. Character mapping indicates that the supratendinal bridge was reduced in (1) the stem species of the *Eclectus–Geoffroyus–Psittinus–Tanygnathus–Psittacula* clade and (2) the stem species of the clade including *Psittacus*, *Poicephalus* and the Arini, and has been regained in *Guarouba*, *Enicognathus*, *Forpus* and *Brotogeris* (Arini) (Figs 2, 4*b*).

Morphology of the hypotarsus

Most psittaciform birds possess a hypotarsus with only two canals for the deep flexor tendons; the tendons of the superficial flexor are not enclosed in bony canals. As described by Mayr (2008), *Micropsitta*, *Agapornis*, *Loriculus*, *Melopsittacus* and
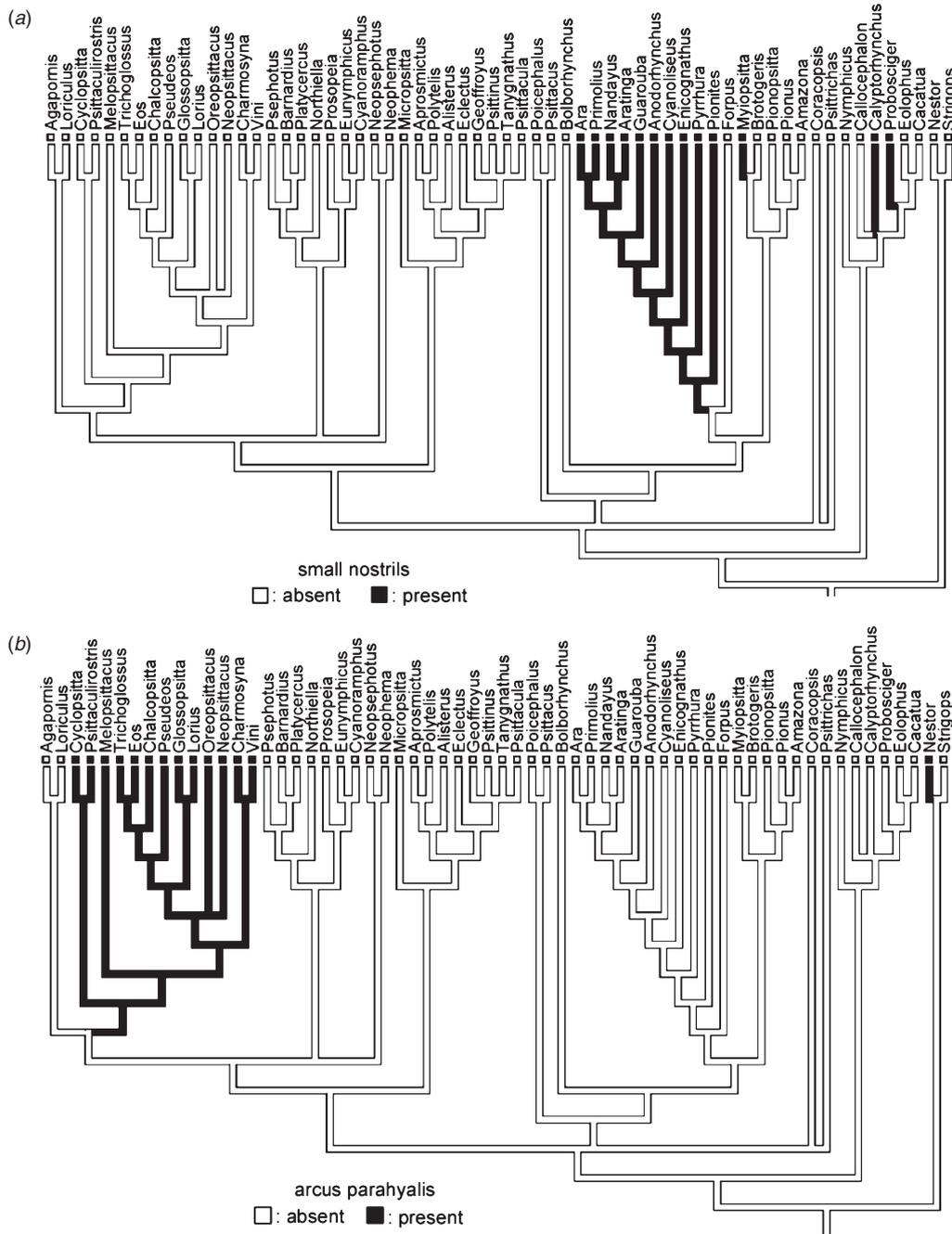
Fig. 3. Distribution of (*a*) small nostrils and (*b*) an arcus parahyalis. Phylogeny of the Old World taxa after Wright *et al*. (2008) with some modifications after Schweizer *et al*. (2010), as described in the Materials and methods. Phylogeny of the New World taxa after Tavares *et al*. (2006). The position of *Callocephalon* and *Oreopsittacus*, which were not included in the above studies, is tentative. Squares below the taxon names indicate character states.

the Loriini are characterised by a derived hypotarsal morphology in which the tendons of the flexores perforati digitorum III and IV muscles and those of the flexor perforans et perforatus digiti III muscle are situated in a large bony canal (Fig. 5). In Cyclopsittini and the core-Platycercini (*Pezoporus*, *Psephotus*, *Barnardius*, *Platycercus*, *Northiella*, *Prosopeia*, *Lathamus*, *Eunymphicus* and *Cyanoramphus*) these tendons run in a deep

sulcus (the condition in *Geopsittacus* is not known). A sulcus for the above tendons also occurs in *Bolborhynchus* and *Pionopsitta* (both Arini). According to the molecular phylogenies inclusion of the superficial flexor tendons in a closed canal evolved three times independently, in: (1) *Micropsitta*; (2) the *Agapornis–Loriculus* clade; and (3) the clade (*Melopsittacus* + Loriini) (Fig. 5).
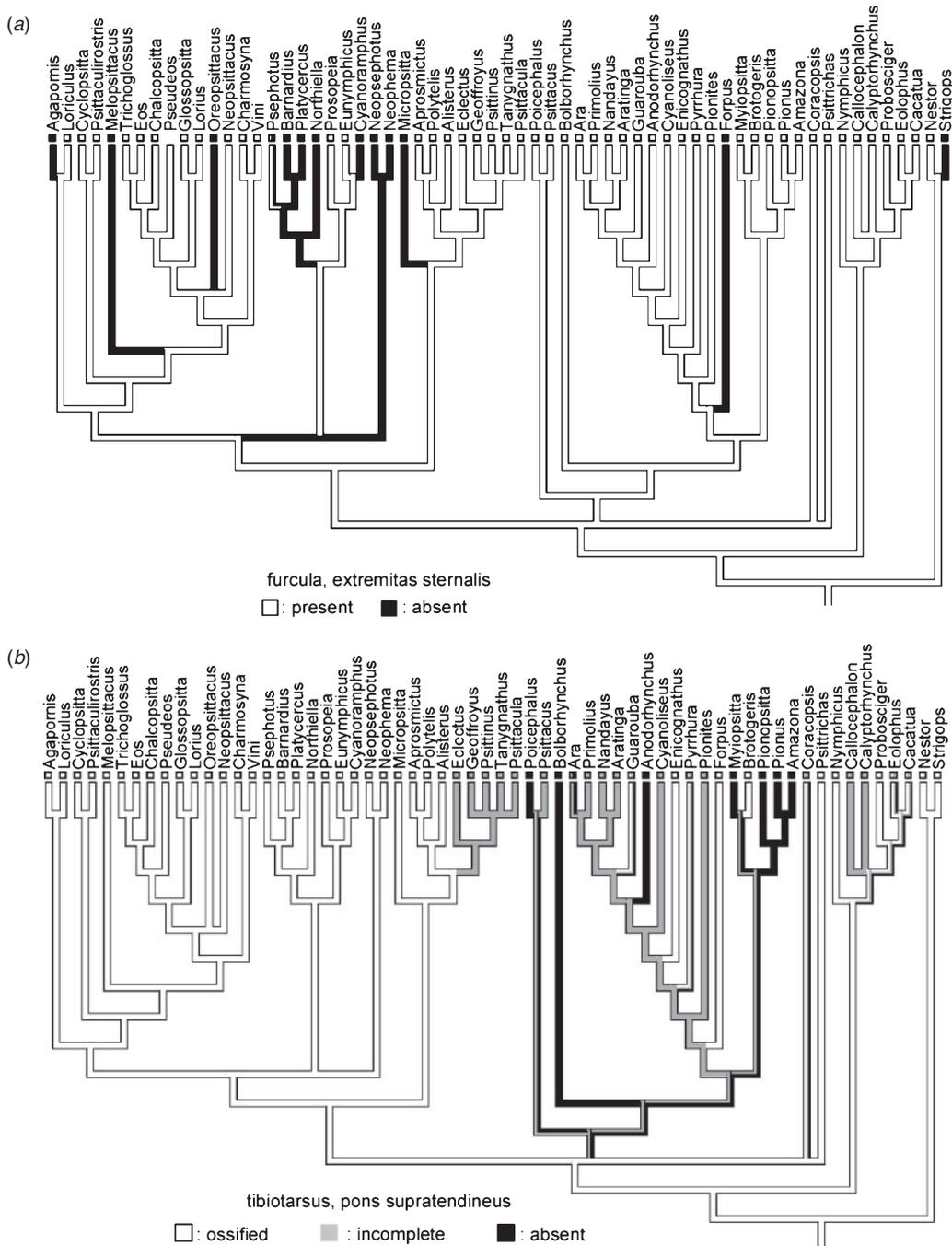
Fig. 4. Distribution of (*a*) an incomplete furcula and (*b*) an incompletely ossified supratendinal bridge. Phylogeny as in Fig. 3. Squares below the taxon names indicate character states; missing square denotes an unknown character state.

Carotid formula

Variation in the morphology of the carotid arteries was among the major characters used by earlier authors to classify parrots (e.g. Garrod 1874; Beddard 1898). Two main patterns can be distinguished: the plesiomorphic morphology, with two carotid arteries in the usual position, which was termed A-1 by Glenny (1955), and a derived pattern, termed A-2-s (Glenny 1955), in which the left carotid artery is a superficial

vessel (a special case is represented by *Cacatua* (Cacatuini), in which the right carotid artery is reduced). Most parrots exhibit the plesiomorphic A-1 pattern. The derived A-2-s pattern is present in *Nestor*, the traditional 'Platycercini' except for *Geopsittacus*, *Neophema*, *Neopsephotus* and *Melopsittacus*, as well as in *Coracopsis*, *Psittrichas*, *Psittacus*, *Poicephalus* and all Arini (Glenny 1955; Smith 1975) (Fig. 6*a*).
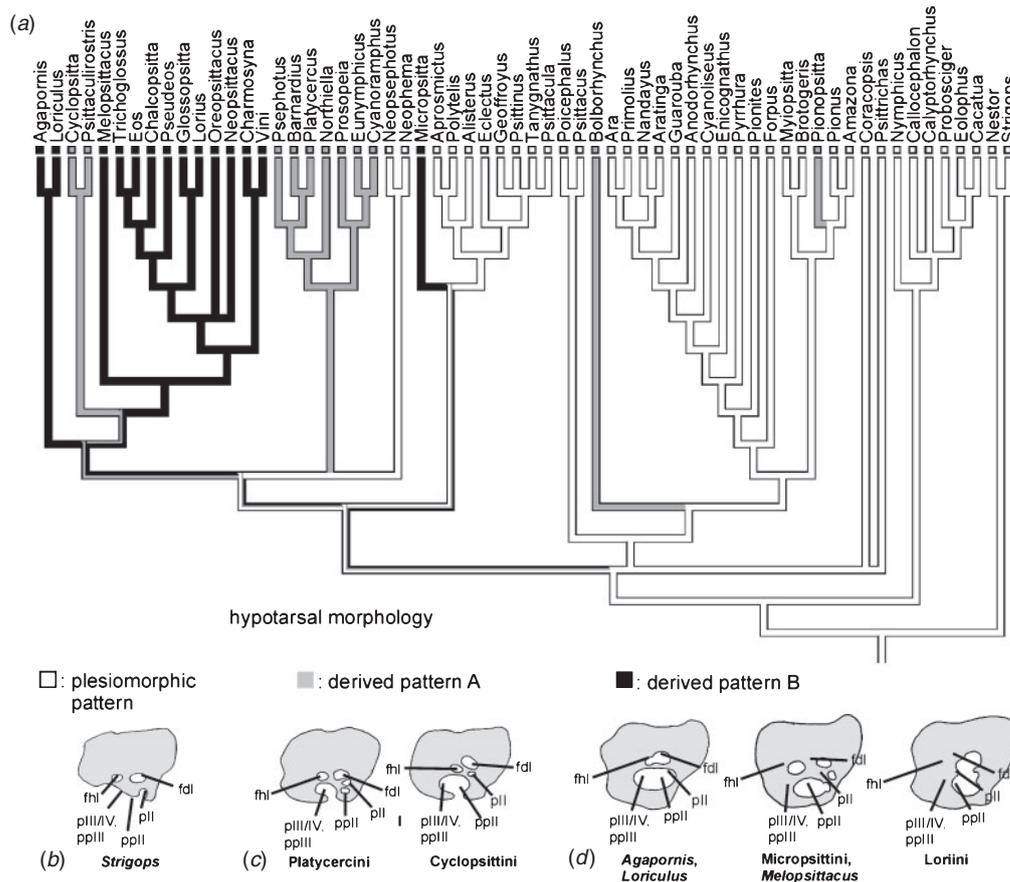
Fig. 5. (*a*) Distribution of hypotarsal morphology. (*b*) Plesiomorphic pattern. (*c*) Derived pattern with tendons of pIII/IV and ppIII situated in sulcus. (*d*) Derived pattern with tendons of pIII/IV and ppIII enclosed in canal. Phylogeny as in Fig. 3. Squares below the taxon names indicate character states. Abbreviations for hypotarsal canals/furrows: pII, tendon of musculus flexor perforatus digiti II; ppII, tendon of musculus flexor perforans et perforatus digiti II; pIII, tendon of musculus flexor perforatus digiti III; ppIII, tendon of musculus flexor perforans et perforatus digiti III; pIV, tendon of musculus flexor perforatus digiti IV.

If *Coracopsis* and *Psittrichas* are successive sister taxa of all other Psittaciformes except the Cacatuini, *Nestor* and *Strigops*, as suggested by the analyses of Wright *et al*. (2008), one has to assume a five-fold origin of the A-2-s type, in: (1) *Nestor*; (2) *Psittrichas*; (3) *Coracopsis*; (4) the core-Platycercini; and (5) a clade including *Psittacus*, *Poicephalus* and Arini. However, the affinities of *Coracopsis* and *Psittrichas* have not yet been convincingly established with molecular data (see Discussion), and a more parsimonious explanation for the distribution of the derived A-2-s type would be a three-fold origin in (1) *Nestor*; (2) the core-Platycercini; and (3) a clade including *Coracopsis*, *Psittrichas*, *Psittacus*, *Poicephalus* and Arini.

Ambiens muscle

As noted by Garrod (1874), parrots are among the few higher level avian taxa that exhibit variation in the development of the ambiens muscle, whose presence is plesiomorphic for neornithine birds. The ambiens muscle has been reported present in at least some individuals of *Strigops* (other individuals lack the muscle, e.g. Beddard 1898), *Nestor*, *Psittacus*, *Poicephalus*, *Ara*, *Aratinga*, *Pionites*, *Bolborhynchus* and *Psilopsiagon* (Beddard 1898;

Brereton 1963) (note that Beddard's '*Psittacula*' is now *Forpus*, whereas *Psittacula* as recognised today is listed as '*Palaeornis*'). Underlying the molecular phylogenies, this muscle was thus lost in: (1) the Cacatuini; (2) *Coracopsis* and *Psittrichas* (either independently two times or in the stem species of a clade including the two taxa; see Discussion); (3) *Forpus*; (4) *Pyrrhura*; (5) a clade including the short-tailed New World parrots (*Myiopsitta*, *Brotogeris*, *Pionopsitta*, *Pionus*, *Amazona*); and (6) the clade including the 'Psittaculini', 'Platycercini', Cyclopsittini and Loriini (Fig. 6*b*).

Discussion

Character mapping shows that some morphological features recognised by earlier authors, such as the presence of a suborbital arch (Tokita *et al*. 2007) and the reduction of the extremitas sternalis of the furcula (Fig. 4*a*), exhibit a high degree of homoplasy and are not suited for reconstruction of the interrelationships of higher level psittaciform taxa. The distribution of the derived states of other characters, however, correlates well with the molecular tree topology.
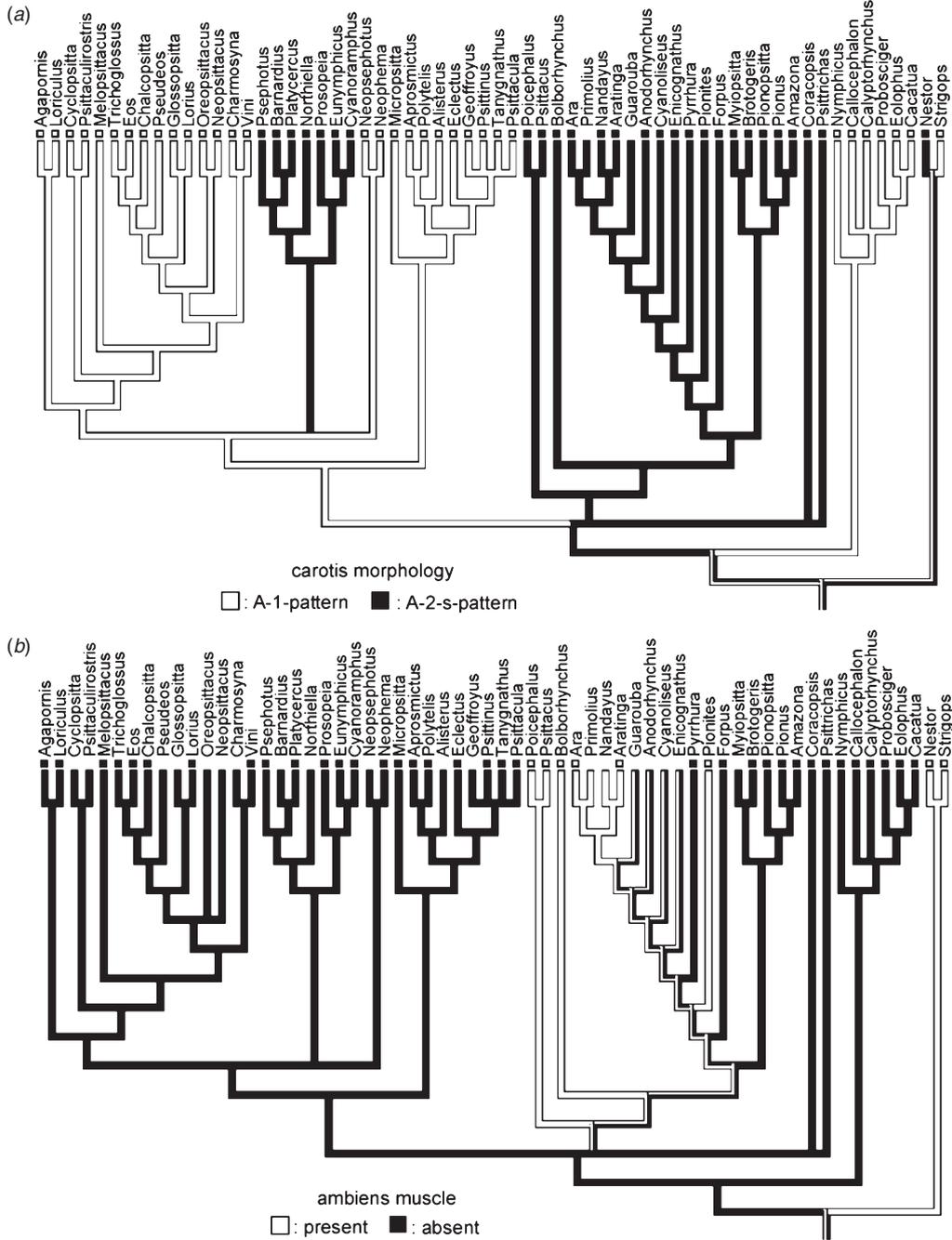
Fig. 6. Distribution of (*a*) the carotid artery type (after Glenny 1955; Smith 1975) and (*b*) the development of the ambiens muscle (after Beddard 1898; Brereton 1963). Phylogeny as in Fig. 3. Squares below the taxon names indicate character state; missing squares denote unknown character states.

For example, the well-supported clade including the Cyclopsittini, *Melopsittacus* and the Loriini resulting from the molecular analyses confirms the homology of the arcus parahyalis of the hyobranchial apparatus of these birds, and supports Homberger's (1980) hypothesis that the granivorous adaptations of *Melopsittacus* evolved independently from those of other 'platycercine' taxa. A clade including the psittaculine taxa *Tanygnathus*, *Psittacula*, *Psittinus*, *Geoffroyus* and *Eclectus* is supported by the

reduction of the supratendinal bridge on the tibiotarsus, which is entire in other psittaculine taxa. Reduction of this bridge may be functionally correlated with the unusually large and medially directed trochlea metatarsi II on the tarsometatarsus of the former five taxa (Fig. 2).

Mayr (2008) considered it possible that the derived hypotarsus shared by the Loricoloriinae and core-Platycercini is homologous, that is that the stem species of the clade including these taxa

had a hypotarsus in which the tendons of the flexores perforati digitorum III and IV and flexor perforans et perforatus digiti III muscles were situated in a deep sulcus. Whether this hypothesis holds depends on the position of *Neophema* and *Neopsephotus*, whose plesiomorphic hypotarsal morphology supports a position outside a clade including the other 'Platycercini' and the Loricoloriinae. The molecular analyses do not congruently resolve the affinities of these two taxa, and whereas *Neophema* and *Neopsephotus* indeed resulted outside the core-Platycercini–Loricoloriinae clade in one of the analyses of de Kloet and de Kloet (2005: fig. 1), they were shown to be the sister taxon of a clade including *Agapornis*, *Loriculus* and *Bolbopsittacus* in the analysis of Wright *et al*. (2008: fig. 2) and placed as the sister taxon of core-Platycercini in the analyses of Tokita *et al*. (2007) and Schweizer *et al*. (2010). Clearly, more data are needed to resolve convincingly the affinities of *Neophema* and *Neopsephotus*, but current evidence does at least not strongly contradict their position outside a clade including the core-Platycercini and Loricoloriinae.

Leeton *et al*. (1994) found a clade formed by *Pezoporus* and *Geopsittacus*, which were not included in the new molecular analyses, to be the sister group of *Neophema*, but their study included a limited taxon sampling, and the resulting tree topology conflicts with that of the new molecular phylogenies in several aspects. The hypotarsus of *Geopsittacus* is not known, but that of *Pezoporus* shows the derived morphology characteristic of the core-Platycercini (Mayr 2008). Because *Pezoporus* lacks the derived A-2-s pattern of the carotid arteries, it is most likely the sister group of a clade including *Psephotus*, *Purpureicephalus*, *Barnardius*, *Platycercus*, *Northiella*, *Prosopeia*, *Lathamus*, *Eunymphicus* and *Cyanoramphus*.

A caveat has to be placed on the phylogenetic significance of the morphology of the hypotarsus, because *Micropsitta*, which exhibits the derived pattern found in the Loricoloriinae (Mayr 2008), was found to be a sister taxon of the core-Psittaculini in the analyses of Wright *et al*. (2008: fig. 2) and Schweizer *et al*. (2010), and was even placed within that taxon in one of the trees of Wright *et al*. (2008: fig. 1). A sister-group relationship between *Micropsitta* and the core-Psittaculini is also supported by the analysis of Hackett *et al*. (2008), in which, however, only a few psittaciform taxa were included. Although protein electrophoresis indicates a position of *Micropsitta* within the Loricoloriinae (Christidis *et al*. 1991), and *Micropsitta* is like the Loricoloriinae in the reduction of the extremitas sternalis of the furcula, the congruent evidence from the above studies indicates that these features evolved convergently to the condition seen in the Loricoloriinae.

The Madagascan taxon *Coracopsis* was considered to be most closely related to the African *Psittacus* and *Poicephalus* by earlier authors (e.g. Smith 1975), and Brereton (1963) even included *Psittrichas* in his Psittacidae (a group including *Psittacus*, *Poicephalus*, *Coracopsis*, *Psittrichas* and *Prosopeia*). The affinities of *Coracopsis* and *Psittrichas* are not unambiguously resolved by the molecular data. Whereas *Psittrichas* branches before *Coracopsis* in the phylogeny of Tokita *et al*. (2007), the reverse is the case in Wright *et al*.'s (2008) phylogeny, and both taxa are found to be sister groups in the analysis of de Kloet and de Kloet (2005), with only the latter topology receiving bootstrap support above 80%. Bayesian analysis of Schweizer *et al*.'s (2010) data

also supported a sister-group relationship between *Coracopsis* and *Psittrichas*, but the clade was not retained in a parsimony analysis, in which both taxa were placed in a polytomy. From a morphological point of view, a sister-group relationship between *Coracopsis* and *Psittrichas* is indicated by the fact that both taxa lack the ambiens muscle. *Coracopsis* and *Psittrichas* further share the derived A-2-s pattern of the carotid arteries with the African taxa *Poicephalus* and *Psittacus* and the Arini, and morphological data are thus more consistent with a sister-group relationship between a clade (*Coracopsis* + *Psittrichas*) and a clade including *Poicephalus*, *Psittacus* and Arini.

Although the interrelationships of several New World taxa remain unresolved, molecular data strongly support a clade including the short-tailed taxa *Amazona*, *Pionus* and *Pionopsitta*, and indicate that this clade is most closely related to a group including *Brotogeris* and *Myiopsitta* (Tavares *et al*. 2006; Wright *et al*. 2008). With regard to these taxa, the tree topology resulting from the molecular analyses correlates well with the distribution of the ambiens muscle in New World parrots, which is lost in *Amazona*, *Pionus*, *Pionopsitta* and *Brotogeris* (the status of this muscle in *Myiopsitta* is not known; Fig. 6*b*). Molecular data also strongly support a clade including the long-tailed taxa *Anodorhynchus*, *Ara*, *Aratinga*, *Cyanoliseus*, *Enicognathus*, *Pionites*, *Pyrrhura* and *Rhynchopsitta* (Tavares *et al*. 2006; Wright *et al*. 2008), which is supported morphologically by the occurrence of very small narial openings in these birds (Fig. 3*a*). *Forpus* occurred as sister taxon of the short-tailed New World parrots in the analysis of de Kloet and de Kloet (2005) but is more closely related to the long-tailed taxa in the analyses of Tavares *et al*. (2006), Tokita *et al*. (2007), and Wright *et al*. (2008). *Forpus* lacks the ambiens muscle but because the status of this muscle is not known for many long-tailed Arini, morphological data do not convincingly inform the systematic affinities of this parrotlet.

Despite the significant increase in our knowledge of the interrelationships among parrots in recent years, there are still several distinctive psittaciform taxa that have not been included in any of the recent analyses and whose anatomy is also poorly known. Apart from *Geopsittacus* and *Pezoporus* (see above), this is true for the New Guinean taxon *Psittacella*, which is traditionally included in the 'Psittaculini' but which was reported as a sister taxon of the 'Platycercini' in one analysis of several presented by Christidis *et al*. (1991). Because the 'Psittaculini' are clearly distinguished from most 'Platycercini' in hypotarsal morphology, the osteology of *Psittacella* may contribute to a determination of its affinities, once skeletons become available. The same applies for *Bolbopsittacus*, which formed a clade with *Agapornis* and *Loriculus* in the analysis of Wright *et al*. (2008), with the latter two having a distinctive hypotarsal morphology (Mayr 2008). Further, more data are needed on the distribution of the ambiens muscle in the Arini, and it is to be hoped that future systematists continue to study the anatomy of parrots, whose potential for the resolution of phylogenetic issues still appears to be underutilised.

Acknowledgements

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