A new parrot from the Miocene of Germany, with comments on the variation of hypotarsus morphology in some Psittaciformes

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ABSTRACT. A new taxon of parrot (Psittaciformes) is described from the Middle Miocene of Southern Germany. *Bavaripsitta ballmanni* gen. et sp. n. is known from an almost complete tarsometatarsus which resembles the corresponding bone of some small Psittaculini (*Polytelis*, *Alisterus*) and Platycercini (e.g., *Psephotus* spp.) in general shape and morphology. Although the new taxon cannot be assigned to any of the modern groups of parrots, together with other fossil specimens it shows that there was a considerable diversity of parrots in the Lower and Middle Miocene of the Old World. Our study further provides the first detailed survey on the variation of hypotarsus morphology within extant Psittaciformes. A derived hypotarsal structure is described that supports monophyly of a clade including the genera *Psephotus*, *Eunymphicus*, *Cyanoramphus*, *Northiella*, *Prosopeia*, *Barnardius*, *Platycercus*, and *Melopsittacus*, to the exclusion of *Neophema* and *Neopsephotus* (all Platycercini). Also well characterized by a derived morphology of the hypotarsus are Loriinae and Cyclopsittacini. A shared derived hypotarsal morphology may further support sister group relationship between *Agapornis* and *Loriculus* (Psittaculini).

KEY WORDS : Aves, Psittaciformes, *Bavaripsitta ballmanni* gen. et sp. n., Miocene, Nördlinger Ries, hypotarsus, phylogeny.

INTRODUCTION

Parrots (Psittaciformes) are a morphologically quite uniform group of birds, which today has its greatest diversity in the Australasian and Neotropic region. Crown group parrots (i.e. the taxon comprising the last common ancestor of all extant Psittaciformes as well as all its extant and extinct descendants) are currently divided into the Australasian Cacatuidae and the Psittacidae (del HOYO et al., 1997). Within the Psittacidae, COLLAR (1997) distinguished two subgroups, the Australasian Loriinae (Lories) and the Psittacinae. The latter include the New Zealandian Nestorini (Kea and Kaka) and Strigopini (Kakapo), the New Guinean Psittrichadini (Pesquet's parrot), the Australasian Platycercini (platycercine Parrots), Cyclopsittacini (Fig parrots), and Micropsittini (pygmy-parrots), the Psittacini (Afrotropical parrots), the Psittaculini (psittaculine parrots), which occur in large parts of the Old World, and the Neotropic Arini (New World parrots).

Although a good fossil record exists for Eocene stem group representatives of the Psittaciformes (i.e. more basal taxa outside the crown group, see MAYR & DANIELS, 1998, MAYR, 2002), fossil crown group parrots still are very rare. Most Tertiary remains are from Miocene deposits of Europe. The first taxon described is *Archaeopsittacus verreauxi* from the Lower Miocene of France (MILNE-EDWARDS, 1867-1871), which is known from a complete tarsometatarsus and a few other referred bones, and which was tentatively referred to the Psittaculini by MLÍKOVSKÝ (1998). Also known from a tarsometatarsus is *Xenopsitta fejfari*, which was reported by MLÍKOVSKÝ (1998) from the Lower Miocene of the Czech Republic and which was considered by this author to be a member of the Psittacini. CHENEVAL (2000) described isolated bones, including an incomplete tarsometatarsus, of a parrot from the Middle Miocene of France which he referred to as *Pararallus dispar* (Milne-Edwards, 1869-71). According to MLÍKOVSKÝ (1998) this name is not available for the parrot remains that he (MLÍKOVSKÝ, 2002) instead listed as *Psittacus lartetianus* Milne-Edwards, 1872. However, the distal humerus selected by CRACRAFT (1973) as lectotype of *Pararallus dispar* is part of the syntypical series that includes the proximal tarsometatarsus selected by MLÍKOVSKÝ (2002) as lectoype of *Psittacus lartetianus* (contra MLÍKOVSKÝ 1998); a lectotype can only be changed by decision of the International Commission of Zoological Nomenclature (we thank C. Mourer-Chauviré for drawing our attention to this). HEIZMANN & HESSE (1995) further mentioned the presence of parrots in the Middle Miocene deposits of Steinheim in Germany.

Only a few Tertiary psittaciform taxa have been described from non-European localities. WETMORE (1926) assigned a humerus from the Miocene of Nebraska to a new species of the recently extinct taxon *Conuropsis*, and TONNI & NORIEGA (1996) described a well-preserved skull from the Pliocene of Argentina as a new species of the extant taxon *Nandayus*. From fossil deposits in Australia, BOLES (1993) described a rostrum of a Miocene

cockatoo and, also from Australia, BOLES (1998) identified Pliocene remains of the budgerigar, *Melopsittacus undulatus*.

Here we describe a tarsometatarsus of a fossil parrot from the Middle Miocene (about 15-13.5 million years ago, see STEININGER, 1999) freshwater deposits of the Nördlinger Ries in Germany. The occurrence of parrots at this site was already noted by BALLMANN (1979, 1983) and HEIZMANN & HESSE (1995), but the specimens have remained undescribed until now. We further comment on the variation of hypotarsus morphology in some extant Psittaciformes.

MATERIAL AND METHODS

Skeletons of the following representatives of the Psittaciformes in the collection of Forschungsinstitut Senckenberg, the Staatssammlung für Anthropologie und Paläoanatomie München, and the collection of Jürgen Bosch (Seewald-Besenfeld, Germany) were examined : Cacatuidae : *Cacatua* (*galerita, leadbeateri, moluccensis, sulphurea*), *Callocephalon fimbriatum, Eolophus roseicapillus, Nymphicus hollandicus, Probosciger aterrimus.* Psittacidae : Loriinae : *Chalcopsitta cardinalis, Charmosyna* (*papou, rubronotata, placentis*), *Eos* (*cyanogenia, histrio, reticulata*), *Lorius domicellus, Neopsittacus pullicauda, Oreopsittacus arfaki, Trichoglossus haematodus, Vini australis*; Psittrichadini : *Psittrichas fulgidus*; Nestorini : *Nestor notabilis*; Strigopini : *Strigops habroptilus*; Cyclopsittacini : *Cyclopsitta diophthalma, Psittaculirostris* (*desmarestii, edwardsii*); Platycercini : *Barnardius barnardi, Cyanoramphus novaezelandiae, Eunymphicus cornutus, Melopsittacus undulatus, Neophema* (*chrysogaster, elegans, pulchella, splendida*), *Neopsephotus bourkii, Northiella haematogaster, Platycercus* (*elegans, eximius, icterotis*), *Prosopeia tabuensis, Psephotus* (*chrysopterygius, haematonotus*); Psittaculini : *Agapornis* (*fischeri, lilianae, nigrigenis, personata, roseicollis*), *Alisterus* (*amboinensis, chloropterus, scapularis*), *Eclectus roratus, Loriculus stigmatus, Polytelis* (*alexandrae, anthopeplus, swainsonii*), *Prioniturus platurus, Psittacula* (*alexandri, cyanocephala, eupatria, himalayana*), *Psittinus cynanurus, Tanygnathus lucionensis*; Psittacini : *Coracopsis vasa, Poicephalus* (*cryptoxanthus, 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*), *Cyanoliseus patagonus, Diopsittaca nobilis, Enicognathus* (*ferrugineus, leptorhynchus*), *Forpus* (*coelestis, conspicillatus*), *Geoffroyus geoffroyi, Guarouba guarouba, Myiopsitta monachus, Nandayus nenday, Pionites melanocephalus, Pionus sordidus, Pyrrhura* (*cruentata, leucotis, perlata, picta*).

Nomenclature and classification of the extant taxa follow ROWLEY (1997) and COLLAR (1997). Anatomical terminology follows BAUMEL & WITMER (1993) and VANDEN BERGE & ZWEERS (1993); measurements are in millimeters.

SYSTEMATIC PALEONTOLOGY

Psittaciformes Wagler, 1830
Bavaripsitta gen. n.
(Figs. 1A-D, 2A)

Type species : *Bavaripsitta ballmanni* gen. et sp. n.

Etymology : The name is derived from *Bavaria* (Lat.) : bavaria, and *psitta*, a diminutive of *Psittacus*.

Differential diagnosis : The tarsometatarsus of *Bavaripsitta* gen. n. differs from the corresponding bone of :

– all Nestorini and Strigopini in being much smaller and in the presence of a well-developed medial foramen vasculare proximale.

– Psittrichadini in being much smaller and less stout; in *Psittrichas* the canals of the deep flexor tendons are further fused to form a single canal.

– all Cacatuidae, Arini, and Psittacini investigated in this study in being less stout and in the presence of a well developed medial foramen vasculare proximale. In many Arini the canals of the deep flexor tendons (i.e., those of musculus flexor digitorum longus and m. flex. hallucis longus) are further fused to form a single canal.

– all Loriinae and Cyclopsittacini, all Platycercini included in this study except *Neophema* and *Neopsephotus*, some Psittaculini (*Prioniturus, Agapornis, Loriculus*), as well as *Bolborhynchus* (Arini) in the plesiomorphic morphology of the hypotarsus (see discussion and Figs. 1 and 3). In the derived (see discussion) condition present in the aforementioned taxa there is a large sulcus plantar to the canals of the deep flexor tendons, which confines the tendons of musculus flexor perforans digiti III and of the musculi flexores perforati digitorum III et IV (Figs. 3A-I); the tendon of musculus flexor perforatus digiti II is enclosed in a bony canal. The hypotarsus of the Loriinae and of *Agapornis* and *Loriculus* is further modified in that the canals of the deep flexor tendons are fused and the sulcus plantar thereof is closed to form a large canal (Figs. 3B, C, F).

– *Neophema* and *Neopsephotus* (Platycercini) in that the medial rim on the plantar surface of the trochlea metatarsi II is more pointed and medially protruding. In both extant taxa the medial foramen vasculare proximale is further strongly reduced and in *Neopsephotus* the trochlea metatarsi III protrudes much farther distally relative to the other trochleae.

– Micropsittini (of which only skins were available for comparison) in its much larger size. According to MLÍKOVSKÝ (1998 : 338), the hypotarsus of *Micropsitta* exhibits the derived condition found in the Loriinae (see above) and thus differs from that of *Bavaripsitta* gen. n.

– all Psittaculini investigated in this study in the absence of a sulcus for the tendon of musculus flexor perforatus digiti II; it is also much smaller than all studied Psittaculini except *Agapornis* spp. and *Loriculus* spp. The trochlea metatarsi II of *Bavaripsitta* gen. n. is further not greatly enlarged and not strongly medially protruding as in *Psittacula, Psittinus, Tanygnathus, Geoffroyus,* and *Eclectus* (see Fig. 2F).
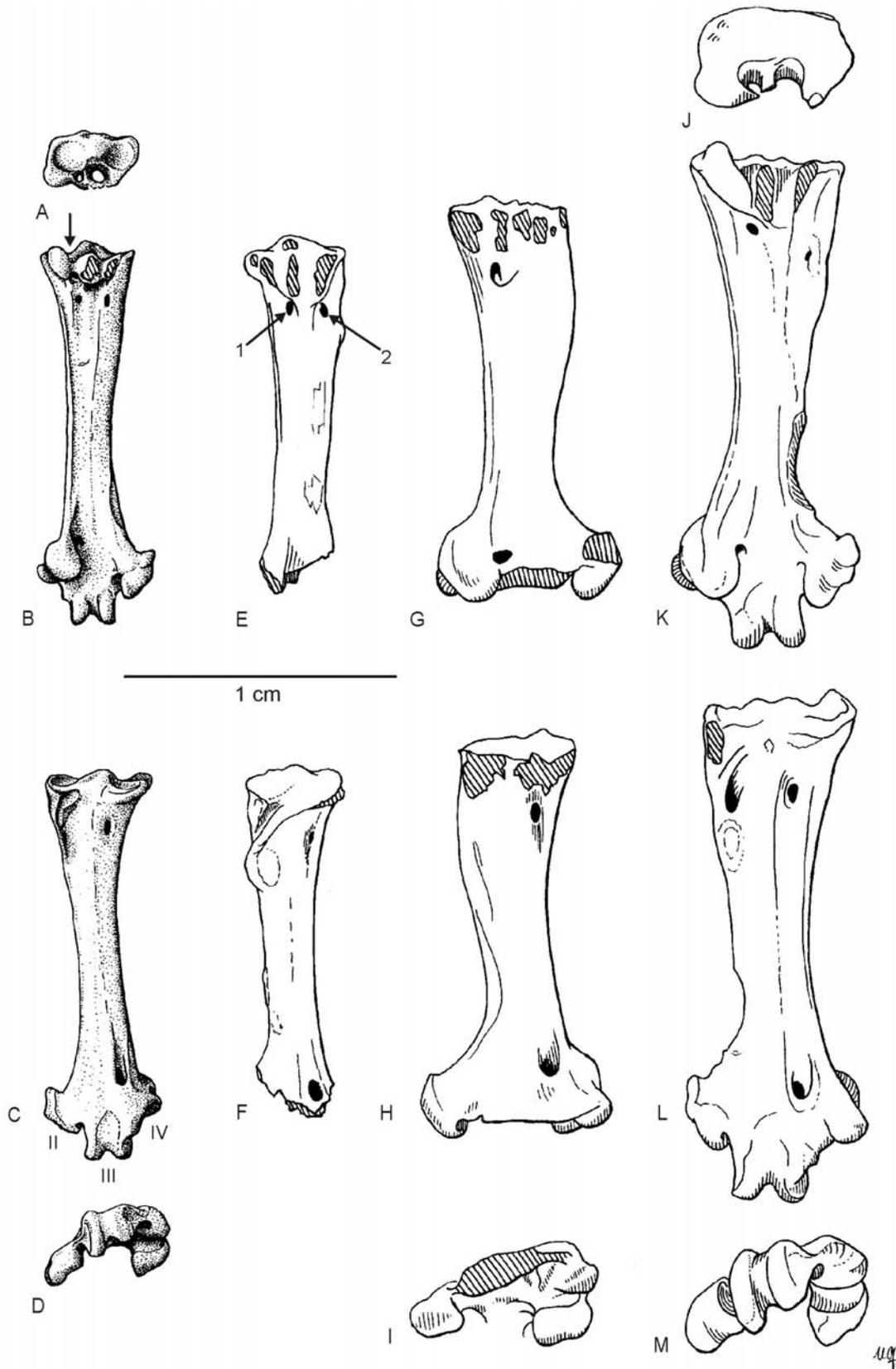
Fig. 1. – Tarsometatarsus of fossil parrots in comparison. (A-D) *Bavaripsitta ballmanni* gen. et sp. n. (holotype), (E, F) *Pararallus dispar* (Milne-Edwards, 1869) (reversed to appear to be from the left side), (G-I) *Xenopsitta fejfari* MLíKOVSKÝ, 1998 (reversed to appear to be from the left side, after MLíKOVSKÝ, 1998), (J-M) *Archaeopsittacus verreauxi* (Milne-Edwards, 1871). A, J, proximal end in proximal view, B, E, G, K, plantar view, C, F, H, L, dorsal view, D, I, M, distal end in distal view. The arrow in B indicates the canal for musculus flexor hallucis longus, which in *Bavaripsitta* gen. n. is not closed plantarly over its entire length, the arrows in E point to the lateral (1) and medial (2) foramen vasculare proximale. The trochleae metatarsorum II-IV are indicated by Roman numerals.
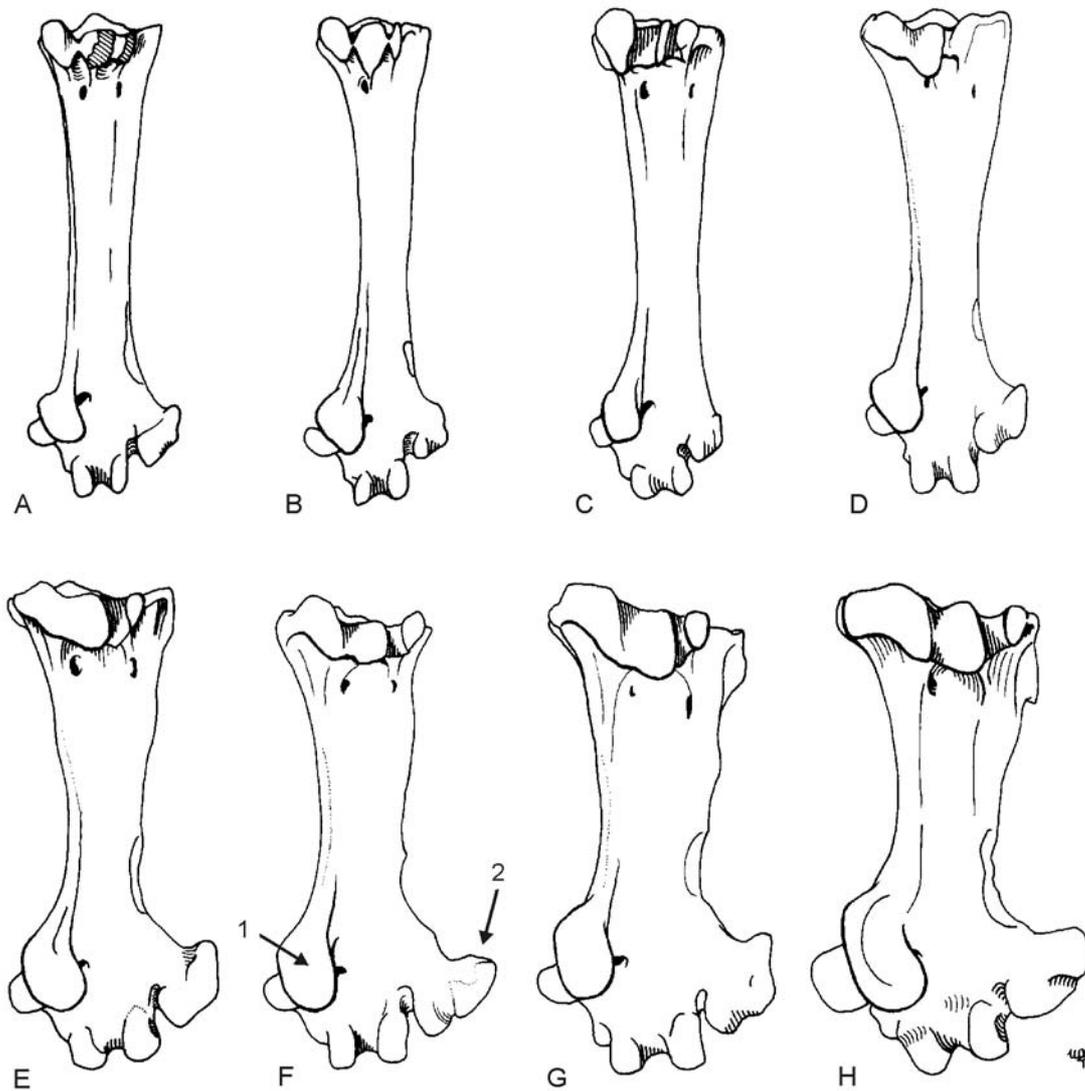
Fig. 2. – Left tarsometatarsus of some psittaciform birds in comparison (plantar view). (A) *Bavaripsitta ballmanni* gen. et sp. n. (holotype), (B) *Neophema elegans* (Platycercini), (C) *Psephotus haematonotus* (Platycercini), (D) *Alisterus scapularis* (Psittaculini), (E) *Coracopsis vasa* (Psittacini), (F) *Tanygnathus lucionensis* (Psittaculini), (G) *Amazona xanthops* (Arini), (H) *Cacatua moluccensis* (Cacatuidae). The arrows indicate the large trochlea accessoria (1) which is a synapomorphy of crown-group Psittaciformes, and the trochlea metatarsi II (2) which is exceptionally large in *Psittacula*, *Psittinus*, *Tanygnathus*, *Geoffroyus*, and *Eclectus* (Psittaculini). Not to scale.

– the Lower Miocene *Archaeopsittacus* Milne-Edwards, 1871 and *Xenopsitta* Mlíkovský, 1998 in being much smaller, less stout, trochlea metatarsi II with medial rim on plantar surface more pointed and medially protruding; it further differs from *Xenopsitta* in the presence of a well-developed medial foramen vasculare proximale.

– the Middle Miocene taxon *Pararallus dispar* (Cheneval, 2000, contra Mlíkovský, 1998, 2002) in the proximo-distally shorter hypotarsus, the less medially protruding tuberositas musculi tibialis cranialis, and the fact that the canal for musculus flexor hallucis longus is not completely closed over its length.

Remarks : Our taxon sampling includes 57 of the 84 extant psittaciform genera recognized by Rowley (1997) and Collar (1997). Fourteen of the missing genera are Neotropic, and it is unlikely for biogeographic reasons that *Bavaripsitta* n. gen. is congeneric with one of these taxa. Of the following 13 Old World taxa no skeletons were available for comparisons : *Calyptorhynchus* (Cacatuidae), *Pseudeos*, *Psitteuteles*, *Phigys*, *Glossopsitta* (Loriinae), *Micropsitta* (Micropsittini), *Bolbopsittacus* (Cylopsittacini), *Purpureicephalus*, *Lathamus*, *Pezoporus*, *Geopsittacus* (Platycercini), *Psittacella*, *Aprosmictus* (Psittaculini). All of these taxa occur either in Australia, New Guinea or on Southeast Asian islands and it is also not very likely that one is most closely related to a Miocene parrot from Germany.

Bavaripsitta ballmanni gen. et sp. n.

Holotype : Almost complete left tarsometatarsus, housed in the Bayerische Staatssammlung für Paläontologie und Geologie, München, collection number BSP 1970 XVIII 899 (Fig. 1A-D).

Type locality and horizon : Steinberg in the Nördlinger Ries, Germany (see BALLMANN, 1979 and HEIZMANN & FAHLBUSCH, 1983 for information on the locality), Middle Miocene (stratigraphic unit MN6, see HEIZMANN & HESSE, 1995). The specimen is from a single block of travertine, which contained several thousand vertebrate remains and which probably represented a filling of a Karstic cavity in the Tertiary limnic sinter of Nördlinger Ries.

Etymology : The species has been named after Peter Ballmann in recognition of his work on the fossil birds from Nördlinger Ries. The specimens described here were picked out of the fossil material from Steinberg and first identified as parrots by him.

Diagnosis : Same as for genus.

*Tentatively referred specime*n : Distal end of right humerus from the same block of travertine as the holotype, housed in Bayerische Staatssammlung für Paläontologie und Geologie, München, collection number BSP 1970 XVIII 900.

Measurements (in mm) : Tarsometatarsus (holotype) : maximum length, 13.6, proximal width, 3.5, distal width, 4.2. Humerus (referred specimen BSP 1970 XVIII 900) : distal width 4.7.

Description and comparison : The holotypical tarsometatarsus is about the size of the corresponding bone of the extant *Melopsittacus undulatus*. In general shape and proportions it resembles the tarsometatarsus of extant *Polytelis* spp. (Psittaculini) and, apart from the plesiomorphic morphology of the hypotarsus (see below), many Platycercini (e.g. *Neophema*, *Psephotus* spp.). Many other extant Psittaciformes have a stouter tarsometatarsus with wider proximal and distal ends (Fig. 2, the relative squatness of the tarsometatarsus of parrots does not appear to be significantly related to allometric changes due to different body size). Compared to other fossil parrots, the tarsometatarsus of *Bavaripsitta ballmanni* gen. et sp. n. is most similar to that of *Pararallus dispar* (CHENEVAL, 2000), which differs, however, in the morphology of the hypotarsus (see differential diagnosis and Fig. 1B, E).

The impressiones retinaculi extensorii on the dorsal surface of the proximal end are distinct and border a marked sulcus as in most extant Psittaciformes. The tuberositas musculi tibialis cranialis is situated at the medial margin of the shaft. There are two foramina vascularia proximalia, whereas in many of the extant taxa investigated (e.g., *Psittacus*, *Poicephalus*, most Cacatuidae, Arini, and Platycercini), the medial foramen vasculare proximale is greatly reduced or completely absent.

The hypotarsus of *B. ballmanni* is proximo-distally short and encloses two canals for the tendons of musculus flexor digitorum longus and m. flexor hallucis longus. Unlike most extant Psittaciformes (Fig. 3), there is no well-developed sulcus/canal for the tendon of musculus flexor perforatus digiti II. The canal for musculus flexor hallucis longus is not closed plantarly over its entire length, as in extant *Neophema*, but unlike virtually all other modern parrots we examined. The hypotarsus of *B. ballmanni* lacks a deep sulcus or canal for the tendons of musculus flexor perforans digiti III and of the musculi flexores perforati digitorum III et IV, which is found in all

extant Loriinae and Cyclopsittacini, all Platycercini included in this study except *Neophema* and *Neopsephotus*, some Psittaculini (*Prioniturus*, *Agapornis*, *Loriculus*), and *Bolborhynchus* (Arini) (see discussion).

At the distal end of the bone, the trochlea metatarsi II does not bear a well-developed sulcus, in contrast to, e.g., *Melopsittacus* or *Alisterus*. This trochlea is further not greatly enlarged and not strongly medially protruding as in the probably closely related (e.g. SMITH, 1975; HOMBERGER, 1980; CHRISTIDIS et al., 1991) extant taxa *Psittacula*, *Psittinus*, *Tanygnathus*, *Geoffroyus*, and *Eclectus* (Psittaculini, see Fig. 2F). As in all crown group Psittaciformes (see MAYR, 2002), the trochlea metatarsi III is slightly asymmetric with the lateral rim being smaller than the medial one. The rims are narrow and widely separated, delimiting a marked sulcus. The trochlea metatarsi IV bears a large trochlea accessoria, which exhibits the unmistakable highly derived morphology typical of crown group Psittaciformes (Fig. 2, see also MAYR, 2002). The trochlea accessoria does not reach farther distally than the trochlea metatarsi IV. The fossa metatarsi I is essentially situated on the plantar surface of the bone whereas it is located on the medial margin of the shaft in many extant Psittaciformes.

The tentatively referred humerus is slightly larger than the corresponding bone of the extant *Melopsittacus undulatus* and closely resembles the distal humerus of extant Psittaciformes, which is very similar in the members of this taxon.

DISCUSSION

Archaeopsittacus, *Xenopsitta*, and the new taxon *Bavaripsitta* show distinct differences in the morphology of the tarsometatarsus (Fig. 2) that indicate there already was a considerable diversity of parrots in the Miocene of the Old World. Unfortunately, assignment of these fossils to any of the modern taxa is hindered by the absence of diagnostic derived features in the known bones (mainly tarsometatarsi).

Almost certainly, a hypotarsal morphology as exemplified by *Archaeopsittacus* and *Bavaripsitta* (the hypotarsus of *Xenopsitta* is broken) is plesiomorphic within crown group Psittaciformes, i.e. only the deep flexor tendons (those of musculus flexor digitorum longus and m. flex. hallucis longus) are enclosed in bony canals and are well separated. With slight modifications, this type of hypotarsus (Fig. 3K) occurs in numerous unrelated psittaciform taxa (Fig. 3J-L) and can be derived from the condition in fossil stem group Psittaciformes in which the hypotarsus bears two sulci for the deep flexor tendons (MAYR & DANIELS, 1998 : text-fig. 5, MAYR, 2002 : fig. 6).

Surprisingly, although there are many comparative studies on parrot morphology (e.g., VERHEYEN, 1956; BRERETON, 1963; HOLYOAK, 1973; SMITH, 1975; HOMBERGER, 1980; GÜNTERT, 1981), the striking variation in the structure of the hypotarsus received virtually no attention. MLÍKOVSKÝ (1998 : 338) appears to be the first to have briefly mentioned hypotarsal variation in some Psittaciformes, but his description is not very detailed and contains some inaccuracies (for example, he erroneously
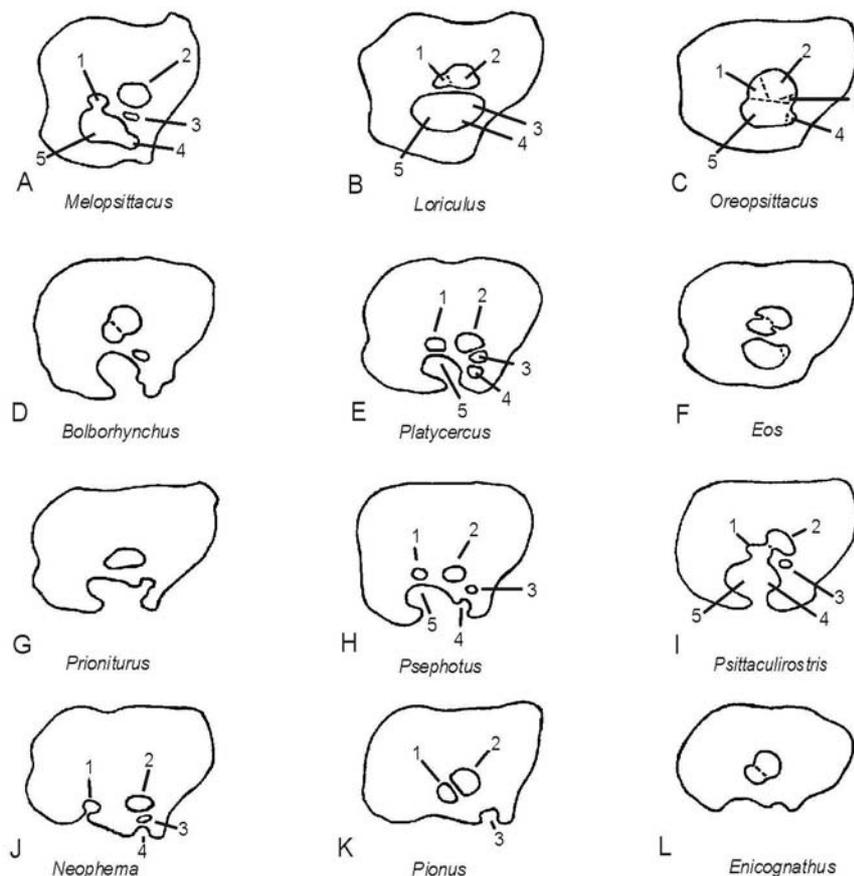
Fig. 3. – Different types of hypotarsi of extant parrots in comparison (left tarsometatarsus). (A) *Melopsittacus undulatus* (Platycercini), (B) *Loriculus stigmatus* (Psittaculini), (C) *Oreopsittacus arfaki* (Loriinae), (D) *Bolborhynchus lineola* (Arini), (E) *Platycercus elegans* (Platycercini), (F) *Eos reticulata* (Loriinae), (G) *Prioniturus platurus* (Psittaculini), (H) *Psephotus haematonotus* (Platycercini), (I) *Psittaculirostris desmarestii* (Cyclopsittacini), (J) *Neophema elegans* (Platycercini), (K) *Pionus sordidus* (Arini), (L) *Enicognathus leptorhynchus* (Arini). Not to scale; the dashed lines indicate non-ossified membranes. The numerals indicate the canals and grooves for the tendons of : 1 - musculus flexor hallucis longus, 2 - m. flex. digitorum longus, 3 - m. flex. perforatus digiti II, 4 - m. flex. perforans et perforatus digiti II, 5 - m. flex. perforans digiti III and musculi flexores perforati digitorum III et IV.

considered the hypotarsus of *Nymphicus*, *Psittrichas*, and New World parrots to be similar to that of the Loriinae).

Well characterized by a derived hypotarsal morphology are the Loriinae (Figs. 3C, F) and Cylopsittacini (Fig. 3I). In these taxa, the canals for the deep flexor tendons (m. flexor hallucis and m. flexor digitorum) are fused, and the superficial tendons are situated in a canal (Loriinae) or in a nearly closed, deep sulcus (Cyclopsittacini).

A hypotarsal morphology identical to that of the Loriinae is also found in *Agapornis* and *Loriculus* (Fig. 3 B) and may support a close relationship between these two taxa that are currently (e.g., COLLAR, 1997) classified into the Psittaculini (pro, e.g., BRERETON, 1963; contra, e.g., HOMBERGER, 1980).

Within the Platycercini, a derived hypotarsal morphology in which the tendons of musculus flexor perforans digiti III and musculi flexores perforati digitorum III et IV are situated in a deep sulcus (Fig. 3 E, H) is found in the genera *Psephotus*, *Eunymphicus*, *Cyanoramphus*, *Northiella*, *Prosopeia*, *Barnardius*, *Platycercus* and supports monophyly of these taxa (pro, e.g., RENZONI & WATTERS,

1972; HOLYOAK, 1973; HOMBERGER, 1980, 1991; contra, e.g., BRERETON, 1963 [who included *Prosopeia* in the Psittacini]; SMITH, 1975 [who included *Prosopeia* in the Psittaculini]; CHRISTIDIS et al., 1991; MIYAKI et al., 1998). A slightly modified, similar hypotarsus is also found in *Melopsittacus* (Fig. 3A) and supports inclusion of this taxon into the Platycercini (pro, e.g., RENZONI & WATTERS, 1972; HOLYOAK, 1973; HOMBERGER, 1980; COLLAR, 1997; contra, e.g., CHRISTIDIS et al., 1991; MIYAKI et al., 1998). *Neophema* (Fig. 3J) and *Neopsephotus*, however, which are generally also classified in the Platycercini (e.g., SMITH, 1975; GÜNTERT, 1980; HOMBERGER, 1980; COLLAR, 1997) exhibit the presumably plesiomorphic (see above) morphology of the hypotarsus.

Although *B. ballmanni* is clearly distinguished from all other known psittaciform taxa (see differential diagnosis), because of the absence of diagnostic derived characters it cannot be reliably assigned to any of the extant psittaciform taxa. Hypotarsal morphology clearly prevents classification of the fossil taxon into the Loriinae, Cyclopsittacini, and Platycercini except *Neophema* and

Neopsephotus. However, being plesiomorphic it does not give positive clues on the phylogenetic affinities of this taxon. A closer relationship between *Bavaripsitta* and the Neotropic Arini or Australian Cacatuidae is not supported by the morphology of the tarsometatarsus and also not very likely for biogeographic reasons. As detailed in the differential diagnosis, *Bavaripsitta* is further distinguished from any of the extant African (*Psittacus*, *Poicephalus*, *Agapornis*, *Psittacula*) or continental Eurasian (*Psittacula*, *Loriculus*) psittaciform taxa. Apart from being smaller and slightly more slender, in its overall shape and morphology, the tarsometatarsus of *B. ballmanni* most closely resembles that of *Polytelis* and *Alisterus* (Psittaculini - as noted above, in the other studied taxa of the Psittaculini the trochlea metatarsi II is greatly enlarged). However, these similarities (relatively slender tarsometatarsus, morphology of the hypotarsus and the distal end of the bone) may well be plesiomorphic within crown group Psittaciformes, as the tarsometatarsus of *Bavaripsitta* for example also exhibits similar proportions to that of Eocene stem group representatives of the Psittaciformes (see MAYR & DANIELS, 1998; MAYR, 2002).

Assignment of *Archaeopsittacus* to the Psittaculini (MLíKOVSKÝ, 1998) was also based on plesiomorphic characters, i.e. the presence of the medial foramen vasculare proximale and the similar morphology of the hypotarsus. Although the tarsometatarsus of *Archaeopsittacus* does resemble that of some extant Psittaculini (compare Figs. 1K and 2D), the phylogenetic position of this taxon needs to be substantiated with derived characters as it is conceivable that certain Psittaculini (*Polytelis* and *Alisterus*) retained a primitive tarsometatarsal morphology. Apart from a smaller trochlea metatarsi II, the tarsometatarsus of *Archaeopsittacus* for example also resembles that of the Madagascan *Coracopsis* (Fig. 2E).

Assignment of *Xenopsitta* to the Psittacini (MLíKOVSKÝ, 1998) which include the African genera *Coracopsis*, *Poicephalus*, and *Psittacus* was based on the "general shape" of the bone and on the absence of the medial foramen vasculare proximale (which is also reduced in *Psittacus* and *Poicephalus* but present in *Coracopsis*). As far as comparable, the incomplete tarsometatarsus of *Xenopsitta* indeed resembles the corresponding bone of *Psittacus* and a close relationship to some of the African parrots would also not be unlikely for biogeographic reasons. However, at least judging from the illustration in MLíKOVSKÝ (1998), the tarsometatarsus of *Xenopsitta* also appears to have a similar shape to that of, e.g. *Tanygnathus*, *Amazona*, or *Cacatua* (compare Figs. 1 and 2) and the medial foramen vasculare proximale is reduced in many unrelated taxa of modern Psittacidae (see above).

Knowing the exact systematic position of the European psittaciform taxa unquestionably would be of great interest concerning the biogeography and early evolution of parrots. However, due to our incomplete understanding of the relationship between the extant taxa and the limited fossil material available, we do not consider it possible to reliably assign either *Bavaripsitta*, *Xenopsitta*, or *Archaeopsittacus* to any taxon of modern parrots. Just because of its great implications such an assignment needs to be based on well-defined derived characters, such as the

modifications of the hypotarsus described in this study, rather than on overall morphology and general shape of few bones.

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