A New Stem Parrot from the Green River Formation and the Complex Evolution of the Grasping Foot in Pan-Psittaciformes

ARTICLE

A NEW STEM PARROT FROM THE GREEN RIVER FORMATION AND THE COMPLEX EVOLUTION OF THE GRASPING FOOT IN PAN-PSITTACIFORMES

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ABSTRACT—Deposits from the Fossil Butte Member of the Green River Formation preserve exceptional fossils from one of the most diverse Paleogene avifaunas worldwide. Stem lineage parrots are well represented in this avifauna. Here we report a new species of Pan-Psittaciformes (crown clade parrots and their stem lineage relatives). The new species shares several features with extant parrots that are not present in the contemporaneous clades Halcyornithidae and Messelasturidae, including a wider pelvis, deeper trochlea cartilaginis tibialis, and larger pygostyle. Morphology of the foot suggests strong grasping ability and an arboreal ecology. Phylogenetic analysis of a combined data set of morphological and molecular sequence data resulted in limited support for a sister-group relationship between the new taxon and Quercypsittidae as well as a previously unrecognized clade including Vastanavidae, Halcyornithidae, and Messelasturidae. Regardless of whether this phylogeny or alternate hypotheses are preferred, a complex history of character evolution is inferred for key features related to the zygodactyl grasping foot within Pan-Psittaciformes.

INTRODUCTION

As recently as the 1980s, parrots were thought to have one of the least complete fossil records of any avian group (Olson, 1985; Mayr, 2009). Over the past few decades, however, a diverse assemblage of Eocene–Oligocene fossils have been identified as stem lineage representatives of the parrot total group Pan-Psittaciformes. Fossils identified as stem parrots primarily on the basis of the morphology of the zygodactyl foot are well known from the Eocene–Oligocene of Europe and North America. These include the Halcyornithidae (six species), Quercypsittidae (two species), *Psittacopes lepidus*, and several unnamed species from the London Clay Formation (Mourer-Chauviré, 1992; Mayr and Daniels, 1998; Dyke and Cooper, 2000; Mayr, 2002, 2009; Ksepka et al., 2011). Halcyornithidae were prevalent in the Eocene of North America and Europe. Although they share many derived features associated with the zygodactyl foot with crown clade psittaciforms, they lack most of the specializations of the beak that characterize extant parrots and also exhibit primitive features of the wing (e.g., a longer, more curved humerus without a markedly projected crista deltopectoralis). The diminutive *Psittacopes* and the Quercypsittidae are both supported as closer relatives of extant parrots based on additional synapomorphies of the hind limb skeleton (Mayr, 2002; Ksepka et al., 2011). *Psittacopes* also lacks most key features of the skull of crown clade parrots and has been considered a more generalized feeder (Mayr, 2009). Quercypsittidae are known only from postcranial remains, making inferences of their ecology more difficult. These fossil taxa indicate that although Pan-Psittaciformes diversified during the Paleogene, they probably occupied different niches than extant parrots.

Surprisingly, some fossil taxa previously allied with other avian clades have recently been linked to Pan-Psittaciformes through new discoveries of more complete material. The Messelasturidae (two species), formerly considered to be related to hawks (Peters, 1994) or owls (Mayr, 2005), were recently hypothesized to be the sister taxon of Halcyornithidae (Mayr, 2011). Messelasturids are characterized by a hooked beak, deep mandible, and raptorial claws, which together suggest a raptorial ecology. Another enigmatic group, the semi-zygodactyl Vastanavidae (two species) of India, was originally considered to be of uncertain affinities (Mayr et al., 2007) but is now hypothesized to represent a basal divergence within Pan-Psittaciformes (Mayr et al., 2010). Less can be surmised about the habits of the vastanavids, which are known from only a few elements of the skeleton.

In this contribution, we report a new specimen from the Fossil Butte Member of the early Eocene Green River Formation representing a new species of Pan-Psittaciformes. The Fossil Butte Member comprises lacustrine deposits formed within the boundaries of Fossil Lake, which during the Eocene was part of a major freshwater lake system surrounded largely by paratropical lowland forest (Grande, 1994; Buchheim, 1998; Cushman, 1999). The Green River Formation is renowned for often spectacularly preserved vertebrate and invertebrate fossils (e.g., de Carvalho et al., 2004; Conrad et al., 2007; Hilton and Grande, 2008; Simmons et al., 2008; Chaboo and Engel, 2009; Engel, 2011) and the Fossil Butte Member in particular has yielded a remarkably diverse fossil avifauna (e.g., Grande, 1984; Olson, 1987; Mayr, 2000; Olson and Matsuoka, 2005; Clarke et al., 2009; Ksepka and Clarke, 2010a; Weidig, 2010). Three species of Pan-Psittaciformes are already known from the Fossil Butte avifauna, including the messelasturid *Tynskya eocaena* and the halcyornithids *Cyrilavis olsoni* and *Cyrilavis colburnorum* (Feduccia and Martin, 1976; Mayr, 2000; Ksepka et al., 2011).

Institutional Abbreviations—**AMNH**, Department of Ornithology, American Museum of Natural History, New York,

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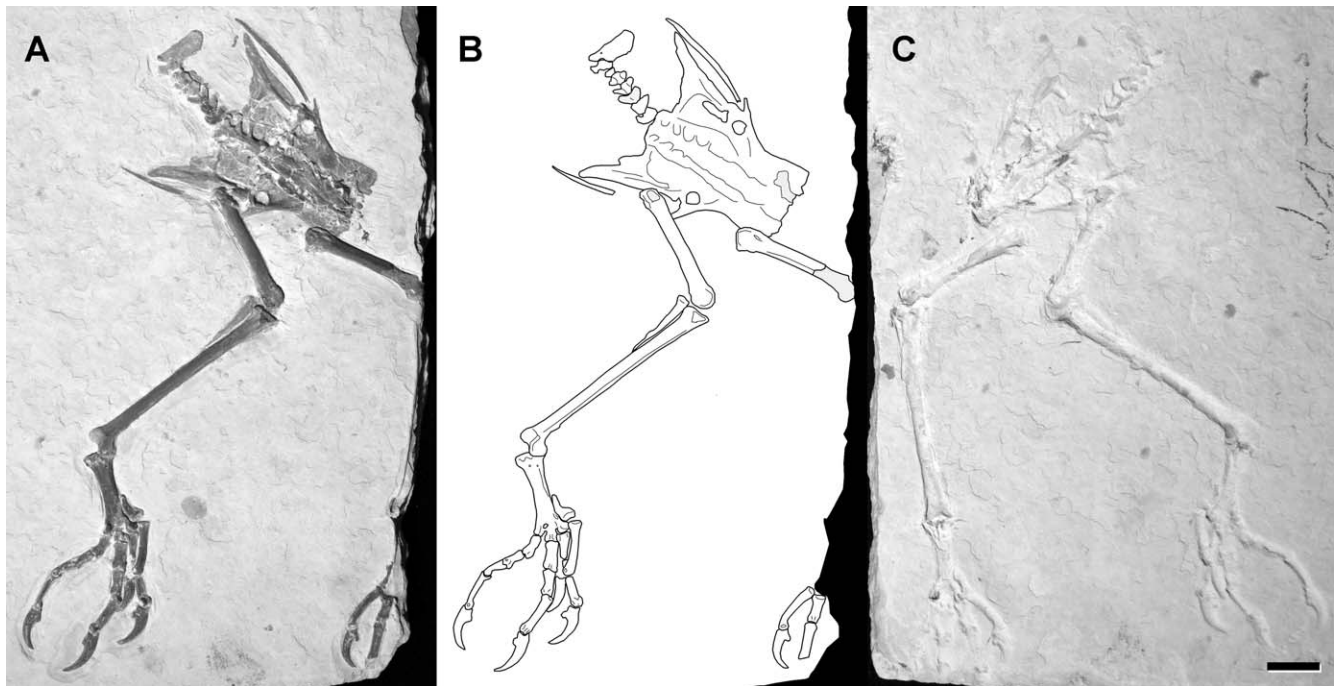
FIGURE 1. Holotype of *Avolatavis tenens*. **A**, main slab (UWGM 39876a); **B**, line drawing of main slab; **C**, counterslab (UWGM 39876b). Scale bar equals 1 cm.

SYSTEMATIC PALEONTOLOGY

PAN-PSITTACIFORMES Mayr, 2011
AVOLATAVIS TENENS, gen. et sp. nov.
(Figs. 1–3)

Holotype—UWGM 39876a and b (Fig. 1). The primary slab (UWGM 39876a) preserves the articulated pelvis, caudal vertebral series, and complete left hind limb. Much of the right hind limb is missing in UWGM 39876a, but impressions on the

FIGURE 2. Details of the pelvis of *Avolatavis tenens* (UWGM 39876a). **Abbreviations**: **ac**, acetabulum; **f**, foramen in pygostyle; **fil**, foramen ilioischiadicum; **p**, pubis; **st**, strut bounding fossa renalis; **su**, suture between ilium and synsacrum. Scale bar equals 1 cm.

FIGURE 3. Details of the hind limb of *Avolatavis tenens* (UWGM 39876a). **Abbreviations**: **fl**, flange at lateral end of hypotarsus; **fvd**, foramen vasculare distale; **fvpl**, lateral foramen vasculare proximale; **fvpm**, medial foramen vasculare proximale; **gr**, groove on tr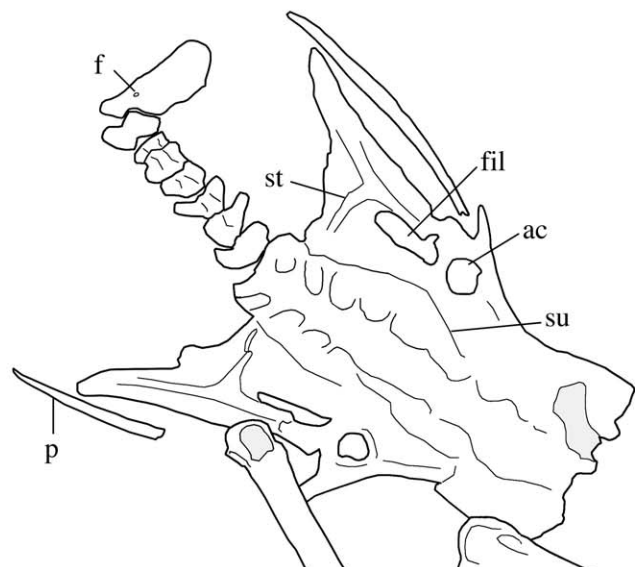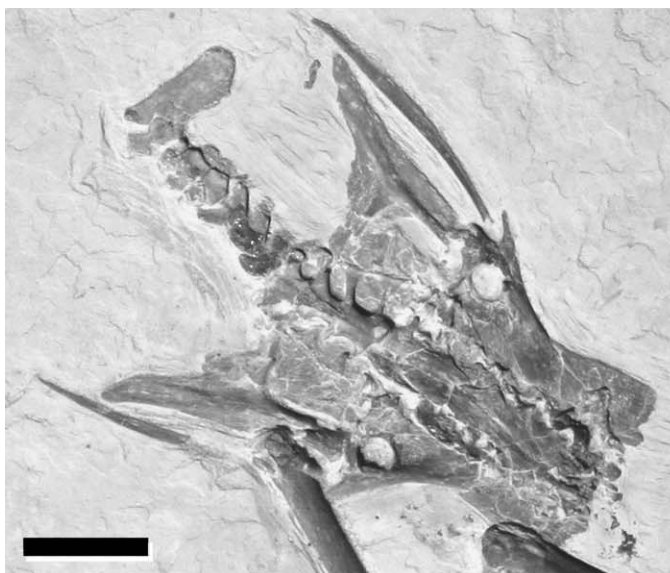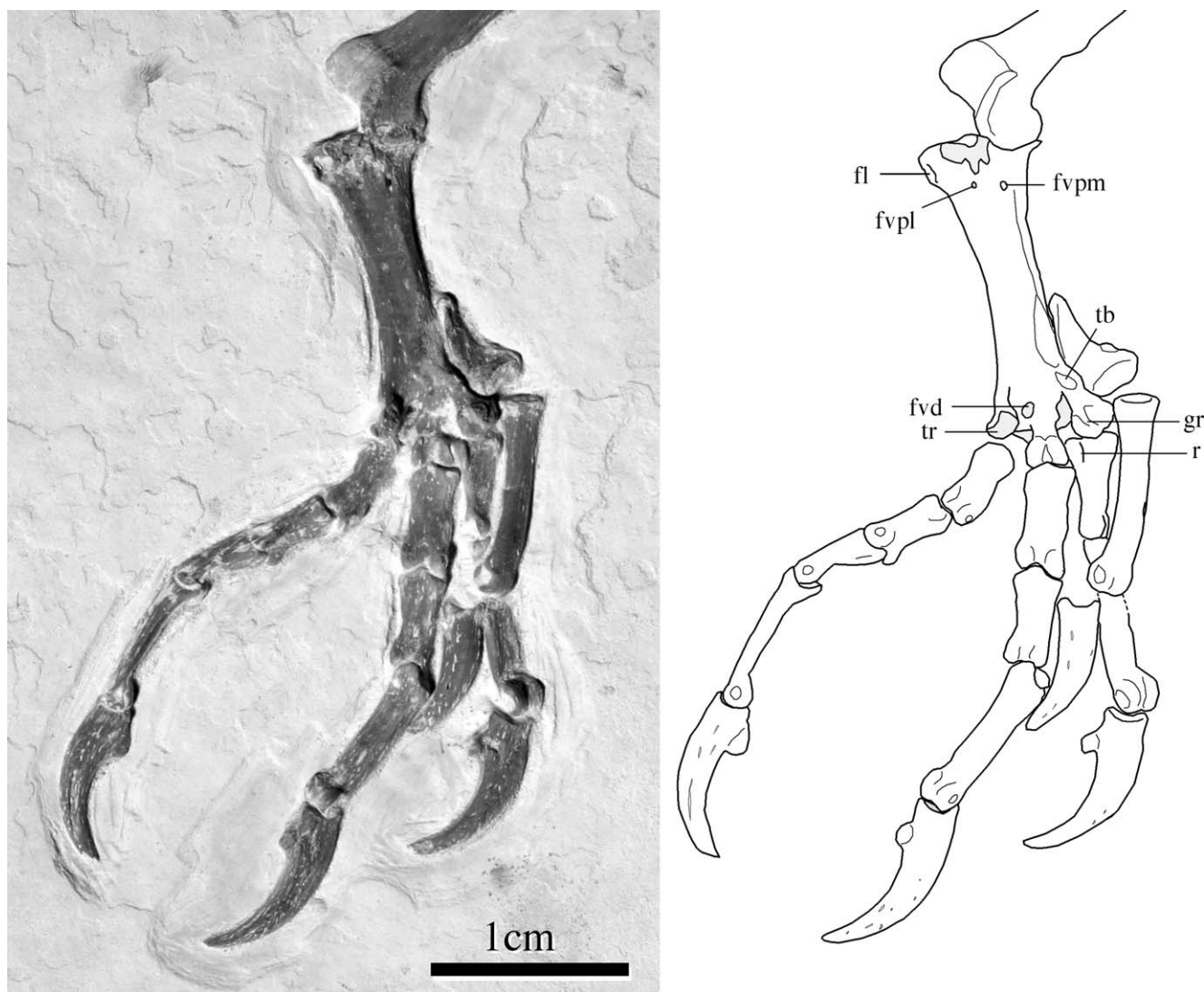ochlea metatarsi II; **tb**, plantar tubercle at base of metatarsal II; **tr**, broken base of flange or trochlea accessoria of metatarsal IV.

counterslab (UWGM 39876b) indicate that it was articulated prior to exposure. A latex peel records details of the elements of the right hind limb, which are preserved as natural molds in the counterslab.

Etymology—*Avolatavis* from the Latin *avolare* ('to fly away' or 'to vanish') and *avis* ('bird'), referring to the fact that this is one of many avian species to have disappeared from North America since the Eocene; *tenens* from the Latin participle for 'grasping,' referring to the strong foot.

Type Locality and Horizon—Locality I of Grande and Buchheim (1994), Fossil Butte Member, Green River Formation. The fossil-bearing beds at the Fossil Butte Member are approximately 51.66 ± 0.09 Ma in age based on $^{40}Ar/^{39}Ar$ dates from an overlying tuff deposit (Smith et al., 2008). Beds at Locality I are composed of laminated micrites from nearshore facies (F-2 deposits of Grange and Buchheim, 1994). This locality has yielded several fossil birds, including an undescribed specimen of *Gallinuloides wyomingensis* (D.T.K. and J.A.C., pers. observ.), an indetermi-

nate species of Zygodactylidae (Weidig, 2010), and several undescribed specimens.

Measurements (all in mm)—Pelvis: width at cranial end, 16.3; width at acetabula, 23.7; width at caudal tips of ischia, 32.8. Pygostyle: maximum height, 10.6. Lengths of limb elements: femur, 24.7; tibiotarsus, 40.8; tarsometatarsus, 17.1; metatarsal I, 5.1. Lengths of pedal phalanges: I-1, 9.8; II-1, 9.1; II-2, 4.6; III-1, 5.0; III-2, ~4.8; III-3, 8.5; IV-1, 4.4; IV-2, 3.9; IV-3, 3.9; IV-4, 7.7.

Diagnosis—Presence of a pronounced, ovoid tubercle on the plantar surface of the base of trochlea metatarsi II is an autapomorphy of *Avolatavis tenens* among Pan-Psittaciformes. Additional differential diagnosis as follows: differs from *Quercypsitta* in the stouter tarsometatarsus (proximal width = 35% of total length in *Avolatavis*, versus 28% in *Quercypsitta*) and absence of a sulcus located proximal to the incisura intertrochlearis medialis on the dorsal face of the shaft. Differs from Halcyornithidae, Messelasturidae, and Vastanavidae in wider pelvis (unknown in vastanavids), trochlea cartilaginis tibialis forming very deep

(proximodistally) concavity, and absence of a crista medianoplantaris of the tarsometatarsus. Additional differences from halcyornithids include presence of a well-developed sulcus at midline of the articular surface of trochlea metatarsi II and pedal digits of subequal robustness (versus digit III markedly more robust than digit II). Additional differences from messelasturids include a narrower trochlea metatarsi III. Additional differences from vastanavids include a shallow (versus deeply concave) fossa metatarsi I, presence of a well-developed sulcus at midline of the articular surface of trochlea metatarsi II, trochlea metatarsi II extending well distal to level of trochlea metatarsi IV (versus subequal projection), and a strongly ginglymoid trochlea metatarsi III with a deep (versus shallow) dorsal sulcus. *Avolatavis* differs from *Psittacopes lepidus* in much larger size (tibiotarsus ∼60% longer), in the proximal displacement of the lateral foramen vasculare proximale relative to the medial foramen vasculare proximale of the tarsometatarsus, and in that the proximal three phalanges of pedal digit IV are markedly shorter than the penultimate phalanx (versus subequal in length). *Avolatavis* differs from extant parrots in that the rims of trochlea metatarsi III are less widely spaced relative to one another and symmetrical (versus medial rim more extensively plantarly projected), the pedal digits are of subequal robustness (versus digit III markedly more robust than digit II), and the proximal phalanx of digit IV lacks pronounced ventral flanges, which form a nearly enclosed canal for the flexor tendon.

Avolatavis can be excluded from other semi-zygodactyl and zygodactyl clades by pronounced differences in other regions of the hind limb skeleton. *Avolatavis* differs from the extinct Sandcoleidae in the unexpanded (versus greatly enlarged) tuberculum musculi gastrocnemialis lateralis of the femur, straight (versus medially bowed) tibiotarsus, plantarly located (versus medially located) fossa metatarsi I, and unabbreviated (versus highly abbreviated) proximal phalanx of digit II. *Avolatavis* differs from the extinct Zygodactylidae in the stout (versus gracile and greatly elongated) tarsometatarsus and abbreviated (versus unabbreviated) proximal pedal phalanges. *Avolatavis* differs from *Eurofluvioviridavis* (Aves incertae sedis), which also has a stout grasping foot, in lacking that taxon's characteristic very large trochlea metatarsi II and by having much less strongly reduced proximal pedal phalanges. *Avolatavis* differs from *Parvicuculus* (Aves incertae sedis) by lacking a crista medianoplantaris and having a much smaller foramen vasculare distale.

Comment—The new fossil is assigned to the parrot total group based on the following features: (1) deep trochlea cartilaginis tibialis of the tibiotarsus, (2) squat shape of the tarsometatarsus, (3) semi-zygodactyl or zygodactyl foot, and (4) the proportions of the pedal phalanges (proximal three phalanges of digit IV subequal in length to penultimate phalanx). Character 2 is optimized as a synapomorphy of Pan-Psittaciformes and character 1 is optimized as a synapomorphy of a more exclusive clade within Pan-Psittaciformes in the phylogenetic analysis presented below. Although some of these features are also observed in taxa outside of Pan-Psittaciformes, the new fossil can be excluded from other superficially similar avian taxa as outlined in the diagnosis above.

Description—Seven small free caudal vertebrae are present in addition to the pygostyle, but are rather poorly preserved (Fig. 2). Most extant parrots have five free caudal vertebrae (excluding the pygostyle), though we observed four in *Rhynchopsitta pachyrhyncha* and six in *Platycercus elegans* and *Eclectus roratus*. The pygostyle in the fossil is complete and strongly resembles that of extant parrots, bearing a tall blade and a squared incision for articulation with the proceeding caudal vertebra. A small distal foramen perforates the blade near the caudoventral margin. Presence, size, and position of this foramen vary in extant parrots.

The pelvis is complete and is exposed in ventral view (Fig. 2). The cranial iliac blades are relatively narrow and are flat and horizontally oriented as preserved. Sutures between the ilia and synsacrum are clearly visible and it seems likely these elements were incompletely fused as in other species of Pan-Psittaciformes. Foramina intertransversaria are not visible and are either absent or very small. The pubis is long and rod-like. It approaches but does not contact the distal end of the ischium. The caudal margin of the ischium extends markedly beyond the level of the first caudal vertebra and tapers to a blunt, triangular point. A transversely oriented caudal strut extends from the synsacrum to the ischium, suggesting that a shallow fossa renalis was enclosed.

Both femora are preserved. The left femur is exposed in medial aspect, though the head is broken off. The right femur is exposed in lateral aspect and lacks a portion of the distal end. A shallow depression is present on the caudal face of the shaft at the level of the head. In both elements, the shaft is very straight, as in extant parrots. The medial surface is smooth, lacking discernable muscle insertion scars. The medial condyle is craniocaudally narrow and bears a shallow pit in the center of the condyle.

The left tibiotarsus is exposed at an oblique angle so that the medial and caudal surfaces are visible (Fig. 3). Although the right tibiotarsus has been lost, a latex peel taken from the impression on the counterslab reviews some additional morphologies of the distal end. The crista cnemialis lateralis is very weakly projected. At the distal end, the groove in the trochlea cartilaginis tibialis is deep and bounded by sharp rims, particularly on the medial side. The fibula is approximately one-third the length of the tibiotarsus and has a flattened medial surface.

The left tarsometatarsus is complete (Fig. 3), but only a few fragments of the right tarsometatarsus are intact. Overall proportions of the tarsometatarsus are stout compared to most other avian clades, though more slender than in most extant parrots (e.g., *Cacatua* or *Amazona*). The tarsometatarsus is slightly shorter than in the smallest individuals of *Quercypsitta sudrei* reported by Mourer-Chauviré (1992). Details of the hypotarsus are not clearly observable because some fragments of bone were damaged during splitting of the slab and remain embedded in the counterslab. For this reason, it is not clear whether sulci or enclosed hypotarsal canals for the deep flexor tendons were present. Nevertheless, the hypotarsal crests and/or canals did not extend very far distally along the plantar face of the shaft. The lateral foramen vasculare proximale is displaced well proximal of its medial counterpart, as in extant parrots, *Quercypsitta*, and *Vastanavis*, but unlike other stem psittaciforms. A sharp, strong flange projects plantarly from the proximolateral margin of the tarsometatarsus. A similar structure is present in falconids (e.g., *Falco*). In extant parrots, this flange appears to be assimilated into the lateral border of the hypotarsal canals.

A slight ridge is developed at the medioplantar margin of the shaft, giving this margin a squared appearance. In many extant parrots, the medioplantar margin is gently rounded, and a slight ridge is instead developed along the lateroplantar margin. The plantar face of the shaft is flat, lacking a crista medianoplantaris (present in Halcyornithidae, Messelasturidae, and Vastanavidae). A shallow, proximodistally elongate fossa metatarsi I is located on the plantar surface of the shaft. This configuration is similar to that in *Quercypsitta*. In *Vastanavis*, as well as most extant parrots, fossa metatarsi I is placed on the medial margin of the shaft. This fossa is also much deeper in *Vastanavis* than in *Avolatavis*, whereas the fossa depth varies in extant parrots. Metatarsal I is preserved nearly in articulation; its trochlea is retracted from the level of trochleae metatarsorum II and IV in what appears to be close to life position. As in extant parrots the element is stout, but in contrast to most extant species the articular surface of trochlea metatarsi I is smooth rather than bearing a midline sulcus. A small tubercle is present on the medial border of the plantar surface of the shaft, just proximal to the trochlea metatarsi I. This tubercle appears to homologous to a more proximally placed tubercle that is present in extant parrots.

Trochleae metatarsi II and IV are plantarly deflected. As in *Quercypsitta*, but in contrast to *Vastanavis*, trochlea IV is shorter (in distal extent) than trochlea II. Trochlea metatarsi II is asymmetrical in plantar view, with a pronounced medioplantar flange. The articular surface of trochlea metatarsi II is similar to that in *Vastanavis* and *Quercypsitta* in bearing a shallow groove on its plantar surface. Trochlea metatarsi II is plantarly flat in most extant parrots, though several taxa possess a deeper groove that extends onto the dorsal surface of the trochlea (e.g., *Melopsittacus* and *Tanygnathus*; Mayr and Göhlich, 2004). A pronounced, ovoid tubercle occurs on the plantar surface of the base of trochlea II, starting at the distal margin of fossa metatarsi I and extending to the level of the dorsal border of the foramen vasculare distale. This feature is not observed in other species of Pan-Psittaciformes and is considered autapomorphic for *Avolatavis tenens*. Trochlea metatarsi III is relatively narrow and is also deeply grooved. Trochlea metatarsi IV has a 'stalked' base as in extant zygodactyl birds, including parrots. Trochlea metatarsi IV preserves a strong projection on its lateral margin, though because the tip is broken off, it remains impossible to determine with certainty whether this projection ended as a wing-like flange as in messelasturids and vastanavids or represents the incomplete base of a fully separated trochlea accessoria as in other pan-psittaciforms. A latex peel taken from the voids preserved in the counterslab confirms that this flange was nearly, if not completely, reversed. A foramen vasculare distale is present.

Although the dorsal surface of the tarsometatarsus is still embedded in the matrix of the main slab, the canalis interosseus distalis appears to have been incomplete—i.e., there appears to be a distal bridge of bone separating the foramen vasculare distale from the incisura intertrochlearis lateralis on the dorsal surface of the tarsometatarsus, but no corresponding bridge of bone on the plantar surface appears to have been present. If this interpretation is correct, the conformation differs from *Quercypsitta* in which the canalis foramen vasculare distale is separated from the incisura intertrochlearis lateralis by a distal bridge of bone on the plantar side, but not on the dorsal side.

All of the toes are preserved in articulation on the left side. Digits II–IV are each individually longer than the tarsometatarsus. All phalanges are preserved in nearly complete articulation in the left foot, save that the claw of the hallux is displaced, and the ungual of digit II has been reversed. The proximal phalanx of the hallux is the longest of the pedal phalanges, but nonetheless the hallux is much shorter than the remaining digits. Digits III and IV are subequal in length and are notably longer than digit II. The phalanges of the digits are of essentially equal robustness, as in *Psittacopes lepidus*. In halcyornithids and extant parrots, the phalanges of digits III and IV are more robust than those of digit II (proportions in *Quercypsitta* remain unknown). The proximal phalanx of II has a strong ventral ridge located at the lateral margin of the proximal end. The ventral surfaces of the proximal phalanges of digits III and IV lack the deep grooves and/or canals for the flexor tendons that are present in extant parrots. The proximal three phalanges of digit IV are reduced in length compared to the penultimate phalanx. All phalanges have deep foveae ligamentorum collateralia. The unguals of all digits are elongate, relatively straight, and lack lateral sulci. The flexor tubercles are knob-like and distally displaced. The ungual of the hallux is partly obscured at the tip but does not appear to have been longer than the proximal phalanx of that digit.

PHYLOGENETIC ANALYSIS

Methods

We expanded a recent combined morphology and molecular sequence data set from a previous study of Pan-Psittaciformes (Ksepka et al., 2011) by incorporating the fossil taxa *Avolatavis*, *Vastanavis*, and *Messelastur*. A total of 19 taxa in Pan-Psittaciformes were sampled including 11 fossil taxa and eight extant parrots. All taxa were coded at the species level to facilitate inclusion of sequence data and accurately represent character variation, with one exception. *Vastanavis* is known only from isolated specimens that hinder direct assignments at the species level. We combined codings from the holotype and referred coracoids of *Vastanavis eocaena* with codings from tarsometatarsi and other elements assigned to *Vastanavis* sp. by Mayr et al. (2010) in the primary analysis. We also conducted a supplemental analysis using only the codings from the holotype of *Vastanavis eocaena*. The messelasturid *Tynskya eocaena* was excluded from the primary analyses due to a lack of informative codings obtainable from the nearly complete but very badly preserved holotype (see Mayr, 2000). Inclusion of this taxon results in a near total lack of resolution among the stem Pan-Psittaciformes in the strict consensus tree. Outgroup taxa included nine species representatives from Coliiformes, Falconidae, and Passeriformes, three taxa that have been recovered as the extant sister taxon of Psittaciformes in recent analyses (Mayr and Clarke, 2003; Ericson et al., 2006; Hackett et al., 2008; Mayr, 2011). Specimens examined and references consulted for scoring are provided in Appendix 1.

The total evidence data set contains 105 morphological characters (Appendices 2 and 3). Molecular sequence data from cytochrome *b*, RAG-1, and the third intron of the Z-chromosomal spindlin gene were included for extant taxa. GenBank accession numbers of sequences are provided in Table 1. Alignments from cytochrome *b* and RAG-1 sequences were created manually and alignments from the Z-chromosomal spindlin gene used in the analysis of de Kloet and de Kloet (2005) were obtained from the authors. A nexus file of the combined matrix is available electronically as Supplementary Data 1 (online at www.tandfonline.com/UJVP).

A branch and bound search was conducted in PAUP4.0b10 (Swofford, 2003) with morphological and molecular characters weighed equally and branches of minimum length 0 collapsed. A second analysis was conducted using only the morphological data set. Bremer support values were calculated via branch and bound searches for suboptimal trees.

Results

Analysis of the combined data set yielded three most parsimonious trees (tree length [TL] = 2769 steps, retention index [RI] = 0.617, rescaled consistency index [RC] = 0.448) (Fig. 4). Analysis of the morphology data set yielded six most parsimonious trees (TL = 246 steps, RI = 0.784, RC = 0.401). The strict consensus trees from the morphological and combined analyses are identical in topology except that a branch uniting the extant parrots *Amazona* and *Cyanoliseus* was recovered in the combined analysis but collapsed in the morphological analysis. Aside from the addition of three new fossil species, relationships agree with those previously reported using an earlier version of this data set (Ksepka et al., 2011) Thus, we focus discussion on the placement of these taxa below.

Our results support a novel basal clade uniting *Vastanavis*, *Messelastur*, and Halcyornithidae. This clade is supported by two unambiguous synapomorphies in our result: a deep and cup-shaped cotyla scapularis on the coracoid and presence of a short crista medianoplantaris of the tarsometatarsus. The first character is potentially plesiomorphic given that a deep cotyla is observed in stem lineage fossil representatives of many clades and is present in outgroups of Aves (e.g., *Ichthyornis* and *Apsaravis*). It is also known to be homoplastic within Pan-Psittaciformes (Ksepka et al., 2011). The second character shows less homoplasy within Aves. Although present in some taxa within Piciformes and 'Coraciiformes' (e.g., Alcedinidae, Meropidae, Upupiformes, Coracii, Galbulae), this feature is absent in all proposed close relatives of Pan-Psittaciformes.

TABLE 1.   GenBank accession numbers and references for sequence data.

Taxon	RAG-1	Cytochrome *b*	Spindlin Z
Colius striatus	AF294669 (Johansson et al., 2001)	U89175 (Espinosa de los Monteros, 2000)	—
Urocolius macrourus	—	AY274033 (Sorenson et al., 2003)	AY741658 (de Kloet and de Kloet, 2005)
Acanthisitta chloris	AY056975 (Barker et al., 2002)	AY325307 (Harrison et al., 2004)	—
Tyrannus tyrannus	AF143739 (Groth and Barrowclough, 1999)		—
Gracula religiosa	AY307193 (Cibois and Cracraft, 2004)		AY0955502 (de Kloet and de Kloet, 2005)
Falco sparverius	EU233235 (Wink et al., unpublished)	EU233114 (Wink et al., unpublished)	—
Herpetotheres cachinnans	AY461402 (Griffiths et al., 2004)	U83319 (Griffiths, 1997)	—
Micrastur semitorquatus	AY461404 (Griffiths et al., 2004)	U83314 (Griffiths, 1997)	—
Nestor meridionalis	—	AF346390 (Weidig et al., unpublished)	AY741653 (de Kloet and de Kloet, 2005)
Calyptorhynchus funereus	GQ505229 (Schweizer et al., 2010)		AY741640 (de Kloet and de Kloet, 2005)
Cacatua sulphurea	—	AF313750 (Schliebusch et al., 2001)	AY741620 (de Kloet and de Kloet, 2005)
Amazona farinosa	DQ143346 (Tavares et al., 2006)	AY283475 (Ottens-Wainright et al., 2003)	—
Cyanoliseus patagonus	DQ143334 (Tavares et al., 2006)	DQ143283 (Tavares et al., 2006)	AY741636 (de Kloet and de Kloet, 2005)
Lorius lory	—	AB177952 (Astuti et al., 2006)	AY741616 (de Kloet and de Kloet, 2005)
Trichoglossus haematodus	—	AB177942 (Astuti et al., 2006)	AY741615 (de Kloet and de Kloet, 2005)
Melopsittacus undulatus	DQ143354 (Tavares et al., 2006)	DQ467903 (Boon et al., 2008)	AY741622 (de Kloet and de Kloet, 2005)

A previous phylogenetic analysis by Mayr et al. (2010) did not fully resolve the position of *Vastanavis* within Aves. Nonetheless, the authors of that study considered a basal placement within Pan-Psittaciformes to be the most likely position for Vastanavi-
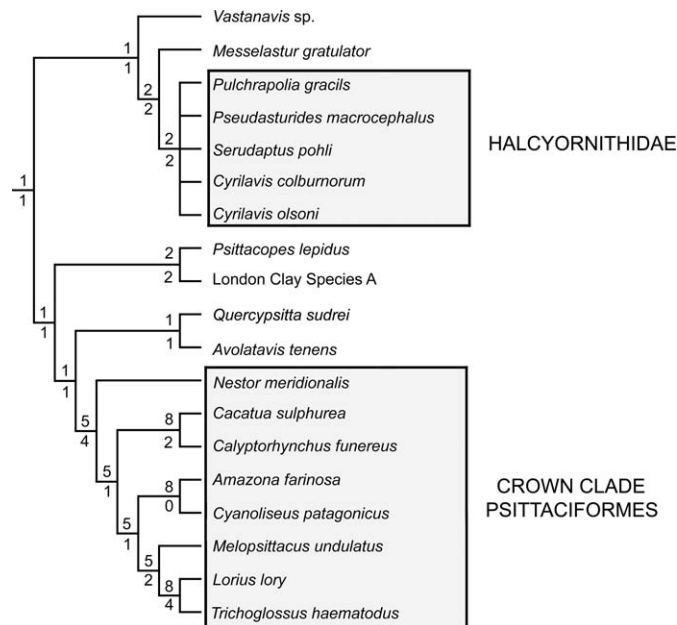

FIGURE 4.   Strict consensus tree (TL = 2769 steps, RI = 0.617, RC = 0.448) from combined analysis of 106 morphological characters and sequence data from cytochrome *b*, RAG-1, and the third intron of the Z-chromosomal spindlin gene. The strict consensus tree from the analysis using only the morphological data set is congruent except that one additional branch is collapsed. Bremer support values for the combined tree are placed above the appropriate branches, and Bremer support values for the morphological tree are placed below the appropriate branches. Note that the single branch that was not recovered in the morphological analysis is indicated by a Bremer value of 0.

dae. Shifting *Vastanavis* to an alternate position as the basal-most taxon in Pan-Psittaciformes costs only a single additional step, and so we consider the position of this taxon to be open to further debate. Furthermore, we note that when only codings from the holotype coracoid of *Vastanavis* are included in the analysis, many branches collapse in the strict consensus and the position of *Vastanavis* relative to other basal Pan-Psittaciformes is unresolved. Resolving the relationships of *Vastanavis* with confidence will probably not be possible without more complete specimens that could, for example, reveal whether the skull and wing also shared unique features with Messelasturidae and Halcyornithidae.

Quercypsittidae is placed in a second clade, including *Psittacopes*, an unnamed taxon from the London Clay Formation (Species A of Mayr and Daniels, 1998), and extant Psittaciformes, in agreement with previous studies (Mayr and Daniels, 1998; Mayr et al., 2010; Ksepka et al., 2011). Five character states are optimized as unambiguous synapomorphies for this clade, including a rounded sternal carina, short and straight humerus, inflated crista bicipitalis of the humerus, trochlea cartilaginis tibialis deep distally, and a large trochlea accessoria that is separated from the main body of trochlea metatarsi IV. Only the last two of these characters can be confirmed in *Quercypsitta* and only the third can be confirmed in *Avolatavis,* because many elements remain unknown for these taxa. A sister-group relationship between *Avolatavis* and *Quercypsitta* is supported by a single unambiguous synapomorphy, presence of a well-developed sulcus on trochlea metatarsi II. Relationships among the sampled extant parrot species are the same as those reported by Ksepka et al. (2011) and agree with recent molecular hypotheses (de Kloet and de Kloet, 2005; Wright et al., 2008; Schweizer et al., 2010; White et al., 2011; see discussion of morphological and molecular congruence in Mayr, 2010) with regard to placement of Strigopidae as the sister taxon to all other crown parrots and identification of a subsequent split between Cacatuidae and Psittacidae.

DISCUSSION

With the addition of *Avolatavis tenens*, Pan-Psittaciformes is recognized as one of the most diverse clades in the Green River
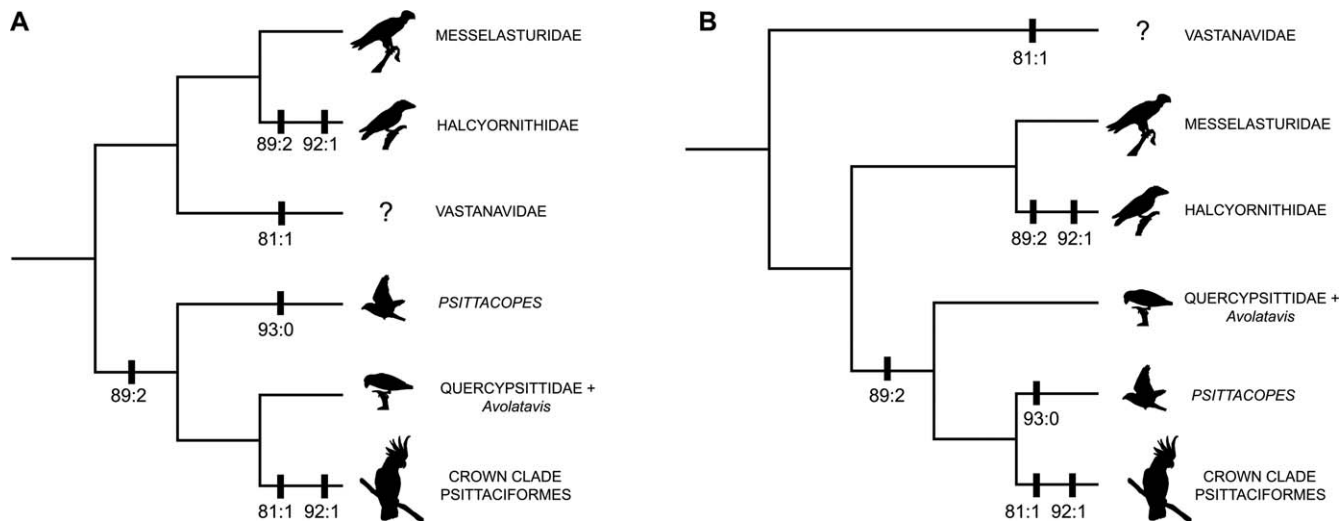
FIGURE 5. Alternate hypotheses for Pan-Psittaciformes phylogeny mapping key characters of the grasping foot that evolved multiple times within the clade. **A**, phylogeny from the analysis presented in this paper; **B**, phylogeny preferred by Mayr et al. (2010), with *Avolatavis* inserted based on results presented in this paper. Character numbers correspond to the phylogenetic matrix: **81(1)**, fossa metatarsi I shifted to medial face of tarsometatarsus; **89(2)**, presence of fully developed trochlea accessoria of metatarsal IV; **92(1)**, pedal digits III–IV robust and digit II gracile; **93(0)**, proximal 3 phalanges of digit IV subequal in length to penultimate phalanx (reversal from greatly abbreviated).

avifauna. Four species of stem lineage parrots are now known from the nearly contemporaneous deposits of the Fossil Butte Member: the halcyornithids *Cyrilavis olsoni* and *Cyrilavis colburnorum*, the messelasturid *Tynskya eocaena*, and *Avolatavis tenens*. Although diverse, stem psittaciforms do not appear to have been particularly abundant. Only the taxon *Cyrilavis colburnorum* is known from more than a single individual, compared to more common taxa such as the stem roller *Primobucco*, the stem frigatebird *Limnofregata*, and the 'Messel rail' *Messelornis*, each of which are known from at least 10 skeletons (Davis and Briggs, 1998; Olson and Matsuoka, 2005; Ksepka and Clarke, 2010b; Smith, 2010).

Morphologies of the foot of *Avolatavis tenens* strongly suggest an arboreal lifestyle, though wing shape remains unknown. The penultimate phalanx of each pedal digit is the longest phalanx, as in most extant arboreal birds (Hopson, 2001). Notably, the flightless parrot *Strigops habroptilus* (the Kakapo) does not exhibit such proportions (Hopson, 2001), though it should be recognized that this taxon is capable of climbing high into trees when feeding. The skeleton of *Avolatavis tenens* also shares several features with extant parrots that are not present in halcyornithids or messelasturids, including a wider pelvis, deeper trochlea cartilaginis tibialis, and larger pygostyle, that together suggest differences in locomotor attributes between the three clades of Green River pan-psittaciforms. Interestingly, the pedal digits of *Avolatavis tenens* are similar in robustness, whereas in the more basal halcyornithids and extant parrots the phalanges of digits III and IV are markedly more robust than those of digit II. *Psittacopes lepidus* and messelasturids also share the condition observed in *Avolatavis tenens*. This optimization suggests that more robust digit III and digit IV evolved independently in halcyornithids and crown psittaciforms, presumably as modifications related to climbing or grasping. The pygostyle is small in halcyornithids, messelasturids, and *Psittacopes*. Notably, this element is lost in all Messel specimens of halcyornithids, including several that are otherwise nearly completely articulated (Hoch, 1988; Mayr, 1998), possibly indicating a weak connection to the synsacrum (Ksepka et al., 2011). In *Avolatavis tenens*, the pygostyle is large and compares well to that of similarly sized extant parrots, suggesting that the tail may have been longer

or more expanded compared to that in other Paleogene stem psittaciforms.

A complex history for many of the characters associated with a grasping foot is required given the distribution of features exhibited in *Avolatavis tenens* and other stem taxa regardless of the phylogenetic hypothesis that is preferred for Pan-Psittaciformes (Fig. 5). Our results suggest that disparity between the robustness of digits II and III/IV arose independently within Halcyornithidae and crown Psittaciformes, that a medially placed metatarsal I arose independently within Messelasturidae and crown Psittaciformes, and that a fully developed trochlea accessoria must have evolved separately in halcyornithids and in the clade uniting *Psittacopes*, Quercypsittidae, and crown Psittaciformes (alternatively, it may have evolved near the base of Pan-Psittaciformes and been secondarily lost in the raptorial Messelasturidae). The shortening of the proximal pedal phalanges, a character otherwise exhibited in all fossil and extant pan-psittaciforms and associated with a grasping foot in birds (Hopson, 2001), appears to have been secondarily reversed in *Psittacopes lepidus*. Clearly, the evolutionary journey towards modern parrots involved multiple side branches and a complex series of character transformations rather than a straightforward march.

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APPENDIX 1. Specimens examined and literature consulted for observations made in the text and for phylogenetic character codings

Acanthisitta chloris	MNZ 26466
Colius striatus	AMNH 4756, 4496, 8954
Falco sparverius	NCSM 16607
Gracula religiosa	USNM 432042, 432708
Herpetotheres cachinnans	USNM 18445, 18446
Micrastur semitorquatus	USNM 13492, 13493
Sandcoleus copiosus	USNM 433912, 433913, 433973–434025
Tyrannus tyrannus	NCMS 18530, 19066, 5864
Urocolius macrourus	AMNH 24231, USNM 491889
Amazona farinosa	AMNH 16053
Aratinga aurea	NCSM 4198
Avolatavis tenens	UWGM 39876a and b
Cacatua sulphurea	AMNH 9040
Calyptorhynchus funereus	SMF 7252
Cyanoliseus patagonus	USNM 227500, 227501
Cyrilavis colburnorum	FMNH PA 722, 754, 766
Cyrilavis olsoni	USNM 424075 (cast of holotype)
Eclectus roratus	NCSM 11670
London Clay Species A	Mayr and Daniels, 1998
Loriculus galgulus	NCSM 20880
Lorius lory	USNM 557119, 557120
Melopsittacus undulatus	NCSM 7692, NCSM 21920
Messelastur gratulator	Peters, 1994; Mayr, 2005, 2011
Nestor meridionalis	AMNH 61008
Neophema pulchella	USNM 614463
Nymphicus hollandicus	NCSM 10044
Platycercus elegans	AMNH 9220
Pseudasturides macrocephalus	WDC-C-MG 94
Psittacopes lepidus	SMF-ME 1279; Mayr and Daniels, 1998
Pulchrapollia gracilis	Dyke and Cooper, 2000; Mayr, 2002
Quercypsitta sudrei	Mourer-Chauviré, 1992
Rhynchopsitta pachyrhyncha	NCSM 17979
Serudaptus pohli	WDC-C-MG 201
Strigops habroptilus	USNM 18275, 289424
Trichoglossus haematodus	AMNH 27531, FMNH 337369
Vastanavis eocaena and *V*. sp.	Mayr et al., 2007, 2010

APPENDIX 2. Descriptions of characters used in phylogenetic matrix.

(1) Rostrum, length: approximately one-half skull length (0); approximately one-third total skull length (1).

(2) Rostrum, bifurcated groove running from region of cere to culmen: absent (0); present (1). This feature was considered diagnostic for Psittaciformes by Boles (1993).

(3) Rostrum, tomial edge of upper beak: smooth (0); notched (1).

(4) Bony nares, shape: ovoid (0); round (1).

(5) Bony nares, orientation: directed laterally (0); directed dorsolaterally (1); directed dorsally (2).

(6) Internarial septum: absent (0); present (1).

(7) Nasals/premaxillae at zona flexorius craniofacialis: relatively smooth or slightly indented (0); with marked swelling at midline (1). This character was identified as a synapomorphy of Cacatuidae by Boles (1993).

(8) Lacrimal, processus supraorbitalis: does not project above orbit (0); enlarged, pointed, and caudally projected above orbit (1).

(9) Frontals, interorbital region: much narrower than skull at level of quadrate (0); wide, interorbital region subequal to skull width at level of quadrate (1).

(10) Fossa temporalis: widely separated on dorsal surface of skull (0); extend to approach one another at the midline or contact at a crest (1).

(11) Bony ring formed by contact between processus postorbitalis and lacrimal: absent (0); present (1). Taxa in which the processus postorbitalis and lacrimal closely approach one another but do not fully contact were scored (1) for this analysis.

(12) Bony ring formed by contact between processus zygomaticus and lacrimal: absent (0); nearly complete (1); complete (2). Ordered.

(13) Bony ring ('temporal fenestra') formed by contact between processus zygomaticus and processus postorbitalis: absent (0); present (1).

(14) Palatine, orientation of pars lateralis: horizontal (0); vertical (1).

(15) Palatine, processus maxillaris, articulation with premaxilla: processus maxillaris fuses with maxilla at rostral end (0); rostral end of processus maxillaris condyle-like, articulating with socket in premaxilla (1).

(16) Quadrate, processus oticus in caudal aspect: mediolaterally wide (0); narrow and pillar-like (1). A slender quadrate was considered to be a synapomorphy of crown parrots by Mayr and Daniels (1998).

(17) Quadrate, condylus medialis and pterygoideus: separate (0); fused (1).

(18) Mandible, length: subequal to upper beak in length (0); markedly shorter than upper beak (1). This mismatch between the lengths of the upper and lower beaks is a major feature contributing to the 'parrot-shaped' beak of extant Psittaciformes (Mayr and Daniels, 1998).

(19) Mandible, depth: shallow (0); deep, approaching the depth of the upper beak at midpoint (1).

(20) Mandible, fenestra rostralis mandibulae: absent or minute perforation (0); large, ovoid opening (1).

(21) Mandible, fenestra caudalis mandibulae: small, foramen-sized perforation (0); large, ovoid opening (1).

(22) Atlas, processus ventralis: short (0); elongated and caudally projected (1).

(23) Cervical vertebrae, number: 10 (0); 11 (1); 12 (2). Ordered. For purposes of scoring this character all vertebrae bearing a free rib are considered thoracic vertebrae.

(24) Presacral vertebrae, number: 17 (0); 18 (1); 19 (2); 20 (3). Ordered.

(25) Pygostyle: short, height approximately equal to the length of the proceeding two free caudal vertebrae (0); large, height approximately equal to length of proceeding four free caudal vertebrae (1).

(26) Furcula: fully fused (0); clavicles remain separate (1).

(27) Furcula, omal end: mediolaterally flattened and unspecialized (0); with distinct laterally projecting facies articularis acrocoracoidea (1); mediolaterally flattened and forms wide triangular expansion (2).

(28) Furcula, apophysis furculae: absent or a barely perceptible ridge (0); small process (1); large, mediolaterally flattened diamond-shaped expansion (2).

(29) Sternum, spina externa: cranially directed (0); craniodorsally directed (1); dorsally directed (2). Ordered. This character was considered synapomorphic for Psittaciformes by Mayr and Daniels (1998) but is also present in Passeriformes.

(30) Sternum, spina externa: narrow and blade-like (0); cranial apex widened (1); cranial apex strongly widened and bifurcated (2). Ordered.

(31) Sternum, processus craniolateralis: craniolaterally directed (0); laterally directed (1).

(32) Sternum, apex carinae: rounded (0); pointed (1).

(33) Sternum, caudal incisurae/fenestrae: none (0); two (1); four (2). Ordered.

(34) Sternum, caudal incisurae/fenestrae: open caudally (0); closed caudally forming fenestrae (1).

(35) Coracoid, facies articularis clavicularis: unexpanded (0); greatly expanded so as to overhang the sulcus supracoracoideus (1).

(36) Coracoid, pneumatic foramen on underside of processus acrocoracoideus: absent (0); present (1).

(37) Coracoid, cotyla scapularis: cup-shaped (0); flattened (1).

(38) Coracoid, foramen nervi supracoracoidei: present (0); absent (1).

(39) Coracoid, processus procoracoideus: well developed (0); highly reduced or absent (1).

(40) Coracoid, processus lateralis: present (0); highly reduced or absent (1).

(41) Scapula, acromion: shortened (0); elongate (1).

(42) Scapula, pneumatic foramen on dorsal surface between facies articularis humeralis and acromion: absent (0); present (1).

(43) Humerus, caput humeri: relatively low and lozenge-shaped (0); hemispherical, with strong proximal projection (1).

(44) Humerus, crista bicipitalis: unexpanded (0); inflated and proximodistally expanded (1).

(45) Humerus, crista deltopectoralis: smoothly curving and moderately projected (1); triangular, with pronounced cranial projection (1).

(46) Humerus, fossa pneumotricipitalis: pneumatic foramen absent (0); pneumatic foramen present (1).

(47) Humerus, caudal face, scar for retinaculum m. scapulotriceps: well separated from caput (0); extending nearly to base of caput (1).

(48) Humerus, shaft: relatively elongate and curved (0); short and straight (1).

(49) Humerus, processus supracondylaris dorsalis: obsolete, weakly projected tubercle (0); well-developed process (1).

(50) Ulna, cotyla dorsalis lateral margin hooked in lateral view: absent (0); present (1).

(51) Ulna, cotyla dorsalis continuous with incisura radialis: absent (0); present (1).

(52) Ulna, cotyla ventralis greatly: unexpanded (0); greatly expanded and extending onto olecranon (1).

(53) Ulna, depressio radialis: shallow depression (0); deep and pit-like (1).

(54) Carpometacarpus, processus pisiformis: centrally placed (0); shifted cranially (1).

(55) Carpometacarpus, processus extensorius: moderately projected (0); elongate and sharply projected, approaching width of trochlea carpalis in length (1).

(56) Carpometacarpus, shape: metacarpal III straight, narrow spatium intermetacarpale (0); metacarpal III bowed, wide spatium intermetacarpale (1).

(57) Phalanx II-1: internal indicus process: weak or absent (0); strongly projected (1).

(58) Alular claw: present (0); absent (1).

(59) Pelvis, width at level of acetabulum: broad (0); narrow (1).

(60) Pelvis, ala preacetabularis ilii fuses to crista spinosa synsacri: no (0); yes (1).

(61) Pelvis, sutura iliosynsacralis: obliterated (0); incompletely fused (1).

(62) Femur, tuberculum gastrocnemius lateralis: unexpanded (0); greatly enlarged (1).

(63) Tibiotarsus, crista cnemialis lateralis: unhooked (0); hooked so that tip points distally (1).

(64) Tibiotarsus, ridge at medial side of proximal end of shaft, opposite crista fibularis: absent (0); present (1).

(65) Tibiotarsus pons supratendineus: ossified (0); cartilaginous (1).

(66) Tibiotarsus, depth distal groove in trochlea cartilaginus tibialis: shallow (0); deep (1).

(67) Fibula, length: short (0); long, fused to and extending almost to distal end of the tibiotarsus (1).

(68) Tarsometatarsus, shape: slender, ratio of length to proximal width >4.0 (0); stout, ratio of length to proximal width <4.0 (1).

(69) Tarsometatarsus, hypotarsus, pathway for tendon of m. flexor hallucis longus: sulcus (0); canal (1).

(70) Tarsometatarsus, hypotarsus, pathway for tendon of m. flexor digitorum longus: sulcus (0); canal (1).

(71) Tarsometatarsus, hypotarsus, deep plantar tendons (m. flexor hallucis longus and m. flexor digitorum longus): in individual sulci/canals (0); share a common canal (1).

(72) Tarsometatarsus, hypotarsus, large common canal housing tendons of m. flexor perforans et perforatus digiti III and m. flexores perforati digitorum III et IV: absent (0); present, fully enclosed (1). This large canal was noted as a possibly synapomorphy of *Agapornis*, *Loriculus*, *Micropsitta*, *Melopsittacus*, Cyclopsittini, and Loriini by Mayr (2008).

(73) Tarsometatarsus, hypotarsus, pathway for tendon of m. flexor perforatus digiti II: no bony pathway (0); in a sulcus (1); enclosed in a canal (2). Ordered. This large canal was noted as a possibly synapomorphy of *Agapornis*, *Loriculus*, and Loriini by Mayr (2008).

(74) Tarsometatarsus, hypotarsus, large common canal housing the tendons of m. flexor perforatus digiti II, m. flexor perforans et perforatus digiti II, m. flexores perforati digitorum III et IV, and m. flexor perforans et perforatus digiti III: absent (0); present (1).

(75) Tarsometatarsus, hypotarsus, some canal housing only the tendon of m. flexor perforatus digiti II: absent (0); present (1).

(76) Tarsometatarsus, proximal part of shaft, dorsal surface: concave, with pronounced fossa infracotylaris dorsalis (0); flattened or convex (1).

(77) Tarsometatarsus, foramina vascularia proximalia: both medial and lateral foramina present (0); only medial foramen present (1); only lateral foramen present (2); both absent (3).

(78) Tarsometatarsus, foramina vascularia proximalia, relative position: at same level (0); lateral foramen more proximal (1); medial foramen more proximal (2).

(79) Tarsometatarsus, tuberositas tibialis cranialis: placed near midline of shaft (0); placed near the medial margin of the shaft (1).

(80) Tarsometatarsus, crista medianoplantaris: absent (0); short crista, restricted to proximal third of tarsometatarsus (1); powerfully projected crista, extending nearly to midpoint of tarsometatarsus (2).

(81) Tarsometatarsus, placement of fossa metatarsi I: on posterior face of shaft (0); on medial face of shaft (1).

(82) Tarsometatarsus, depth of fossa metatarsi I: shallow indentation (0); deep concavity (1).

(83) Tarsometatarsus, size trochlea metatarsi II: small (0); greatly enlarged (1).

(84) Tarsometatarsus, trochlea metatarsi II, proximally directed process projecting from proximomedial edge: absent (0); present (1).

(85) Tarsometatarsus, trochlea metatarsi II, articular face: smooth or weakly grooved (0); with well-developed sulcus at midline (1).

(86) Tarsometatarsus, trochlea metatarsi III, shape in distal view: mediolateral and dorsoplantar dimensions subequal (0); much wider mediolaterally (1).

(87) Tarsometatarsus, rims of trochlea metatarsi III: symmetrical (0); medial rim more extensively plantarly projected than lateral rim (1).

(88) Tarsometatarsus, tubercle on lateral edge of the base of trochlea metatarsi III: absent (0); present (1).

(89) Tarsometatarsus, trochlea metatarsi IV: unmodified (0); with plantarly projected, wing-like flange (1); with fully developed trochlea accessoria (2). Ordered.

(90) Tarsometatarsus, trochlea metatarsi IV separated from trochlea accessoria by deep furrow: absent (0); present (1). This character is considered non-comparable for taxa lacking a trochlea accessoria.

(91) Tarsometatarsus, canalis interosseus distalis: completely enclosed (0); plantarly open (1); dorsally open (2). *Vastanavis* is coded 0/1 reflecting variability described by Mayr et al. (2010).

(92) Pedal digits, relative robusticity of digits II and III: comparable (0); phalanges of digit III much more robust than those of digit II (1).

(93) Pedal phalanges, proximal 3 phalanges of digit IV: individually longer than or subequal to phalanx IV-4 (0); much shorter than digit IV-4 (1).

(94) Pedal phalanx IV-1, fully closed or nearly closed bony canal for flexor tendon on ventral surface: absent (0); present (1).

(95) Pedal unguals: relatively long (0); strongly shortened (1).

(96) Pedal unguals, sulci neurovasculares present on lateral surface: absent (0); present (1).

(97) Tendon of m. extensor digitorum longus, accessory branch to hallux: absent (1); present (1). This branch is known to occur only in Coliiformes and Psittaciformes (Berman and Raikow, 1982).

(98) Plumage, sexual dimorphism: no dimorphism, adult female and male plumage identical (0); slight dimorphism (1); strong dimorphism (2). State 2 is introduced to accommodate the marked difference in the outgroup species *Falco sparverius*. Codings follow Forshaw (2006).

(99) Plumage, Dyck texture in feathers: absent (0); present (1). Green and blue feather color is created by texture of the feather barbs (Dyck, 1971) in most parrots, but this texture is absent in Cacatuidae (Auber and Mason, 1955; Auber, 1957).

(100) Feathered head crest: absent (0); present (1). Codings follow Forshaw (2006).

(101) Remiges, band creates pale stripe on underside of wing in female or both sexes: absent (0); present (1). *Nestor*

parrots have a barred pattern of underwing coloration that we consider non-homologous to the derived state. Codings after Holyoak (1973) and Forshaw (2006).

(102) Tongue, brush-tip: absent (0); present (1). Codings follow Smith (1975) and Forshaw (2006) in considering the slightly modified tongues of *Lathamus* and *Loriculus* non-homologous to the extreme brush-tip morphology of Loriinae (contra Holyoak, 1973).

(103) Gall bladder: absent (0); present (1). A small gall bladder is present in Cacatuidae (Beddard, 1898; Smith, 1975).

(104) Uropygial gland (oil gland): absent (0); present (1). Codings follow Collar (1997) and Rowley (1997).

(105) Incubation: by female only (0); by both parents (1). Codings follow Smith (1975).

APPENDIX 3. Morphological character matrix (multistate codings indicate polymorphism: A = 0/1, B = 1/2).

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                                         10        20        30        40        50
Sandcoleus copiosus        0?0010?0?0000????00?0??0???00?12001000001000?010
Urocolius macrourus        10001100000000000001022000200012000111100100101 10
Colius striatus            10001100000000000001022000000012000?111100100101 10
Herpetotheres cachinnans   100101011000000000010122001000011101100?0100010011
Micrastur semitorquatus    1000110100000000000023001000011101100?0100010011
Falco sparverius           100101010000000000010023001000111101110100001 10011
Acanthisitta chloris       0000?0?0?0000000000?1???00?2?20?20001111??000??01?
Tyrannus tyrannus          0000100000000010000002200221201100011010000010110
Gracula religiosa          0000100000000010000010220022120010011111?0?1?010111
Vastanavis                 ????????????????????????0?0?????00010000????????
Quercypsitta sudrei        ?????????????????????????????00010?0??????????
Avolatavis tenens          ?????????????????????0??????????????????????????
Messelastur gratulator     1??0???1??000????000???01?0????????0?00??1?0000?01?
Pulchrapollia gracilis     ?????????????????0??????????????????????????0??0?
Cyrilavis olsoni           ???????1??????????00?????000??1??????????1?000?00?
Cyrilavis colburnorum      0001001010000??0?0000???1000???1200000001000??00?
Pseudastur. macrocephalus  1?00?0010100000?0?0000??1?000???120??10??1?00?00?
Serudaptus pohli           0?00????01000??0?000?????001?1120??????10?00??00?
Psittacopes lepidus        ??00??00??????0?00?1???10?12??0200?11?????10??11?
London Clay Species A      1??0??000??????0?1????001??????0?11??0?0?00??1?
Cacatua sulphurea          1111011010121111111001110000221001111000011111101
Calyptorhynchus funereus   1111011010110111111001110000?21001111000011111101
Amazona farinosa           11111100101101111110011?0000211011111110000011110101
Cyanoliseus patagonus      111010001011011111110110000021101111110000011110101
Lorius lory                11112100101011111110021000121101111110000011110101
Trichoglossus haematodus   111121001001011111100121000021101111110000011110101
Melopsittacus undulatus    11112100101211111110011010?201011111110000011110101
Nestor meridionalis        110001001001011111110121000022101111110000011111101
                                         60        70        80        90       100  105
Sandcoleus copiosus        ?10?01?00?1100001 10????00110110010001?0??????????????
Urocolius macrourus        0101?10101010101000010000001?10100010001?001?00110100?11
Colius striatus            0101010101010100001 0000001?10100010001?001000100100?11
Herpetotheres cachinnans   0001101?01000?001000000000002020000100 01?001?00010000??1
Micrastur semitorquatus    0011100001000100100000000000202110010001?001000010000??0
Falco sparverius           00110010010000000000002101010001?001000000200001?1
Acanthisitta chloris       ?0????0??00??1?00?01100100?0?1000000000?1???0?010000?11
Tyrannus tyrannus          100100110010100000110020100210000000000?100001000000?10
Gracula religiosa          10?1000100101100001100201002100000000000?100001000000111
Vastanavis                 ??????0??????????10100?00001111100000001?A????1?????????
Quercypsitta sudrei        ??????????????01?1??????00110000100121 2???????????????
Avolatavis tenens          ????????0??????101???????01?000001 00???101000?????????
Messelastur gratulator     ??1000?A10???000?10?00000???110?00?1??1??01?0?????????
Pulchrapollia gracilis     10100?0?????0?1???1000000?000?10????001??11?????????????
Cyrilavis olsoni           ???000001??0?????0?????????01?1??0?0?????111?0?????????
Cyrilavis colburnorum      ????00010????00?00?????01?11?????????21?01?????????
Pseudastur. macrocephalus  ??10?00110??0000????????000110?00???20?11?11?????????
Serudaptus pohli           ??1?00?10???1?001???????????????????????22?11?00?????????
Psittacopes lepidus        ????0011????1??10?????????00?00??????21?00?1?????????
London Clay Species A      ?0?001????????01?10000000000?00000?001211??11?????????
Cacatua sulphurea          0001101001100111011100B0012?1011110012111110?100100111
Calyptorhynchus funereus   0001101?01100111011100B0012??010110?112111110?110100110
Amazona farinosa           0001101?011001101111010001111101121111110?101000000
Cyanoliseus patagonus      0001101?011001010111001012?1011100?112111110?101000010
Lorius lory                0001101?011001010111112101 3?10101101121111100101011010
Trichoglossus haematodus   0001101?011001010111121010010101101121111100101011010
Melopsittacus undulatus    0001101?01100101001120010110000111112111100101010010
Nestor meridionalis        0001101?011001010111001 2?101001001121111 1?0111000001?
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