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

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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 trochea 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 Tunyska 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,
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; fvm, medial foramen vasculare proximale; gr, groove on trochlea 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 40Ar/39Ar 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 indeterminate 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
rostr. Presence, size, and position of this foramen vary in extant par- 
thal foramen perforates the blade near the caudoventral margin. A small dis- 
that of extant parrots, bearing a tall blade and a squared incision 
tus pachyrhyncha and six in 
2). Most extant parrots have five free caudal vertebrae (exclud- 
addition to the pygostyle, but are rather poorly preserved (Fig. 
qual projection), and a strongly ginglymoid trochlea metatarsi III 
tending well distal to level of trochlea metatarsi IV (versus sube- 
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 ar- 
ticular surface of trochlea metatarsi II, trochlea metatarsi II ex- 
tending well distal to level of trochlea metatarsi IV (versus sube- 
quai 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 pha- 
lanax (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 plantarily 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 Sand- 
coleidae in the unexpanded (versus greatly enlarged) tuberculum 
musculi gastrocnemialis lateralis of the femur, straight (versus 
medially bowed) tibiotarsi, 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 un- 
abbreviated) 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 Parvicinculus 
(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 tibiotarsi, (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 opti- 
mized 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 (exclud- 
ing the pygostyle), though we observed four in Rhynchospitta 
pachyrhyncha and six in Platyceurus elegans and Eclectus rora- 
tus. 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 dis- 
tal foramen perforates the blade near the caudoventral margin. 
Presence, size, and position of this foramen vary in extant par- 
rots. 
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 mar- 
gin of the ischium extends markedly beyond the level of the first 
caudal vertebra and tapers to a blunt, triangular point. A trans- 
versely 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 mediolateral 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 
mediolateral 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 enemialis 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 mediolateral surface. 

The left tarsometatarsus is complete (Fig. 3), but only a few 
fragments of the right tarsometatarsus are intact. Overall propor- 
tions of the tarsometatarsus are stout compared to most other 
avian clades, though more slender than in most extant par- 
rots (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 sulei 
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 plantarily 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 Vastanavi- 
dae). A shallow, proximodistally elongate fossa metatarsi I is lo- 
cated on the plantar surface of the shaft. This configuration is 
similar to that in Quercypsitta. In Vastanavis, as well as most ex- 
tant parrots, fossa metatarsi I is placed on the mediolateral 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 re-
tracted 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 mediolateral 
margin of the plantar surface of the shaft, just proximal to the trochlea 
metatarsi I. This tubercle appears to homologous to a more prox- 
imally placed tubercle that is present in extant parrots.
Trochlea metatarsi II and IV are plantarily 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 plantarily flat in most extant parrots, though several taxa possess a deeper groove that extends onto the dorsal surface of the trochlea (e.g., *Melopsitta* and *Tanygnathus*; Mayr and Göhlich, 2004). A pronounced, oval 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 vascular distale. This feature is not observed in other species of Pan-Psittaciformes and is considered autapomorphic for *Avolutavis 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 extended 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 vascular 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 vascular distale from the incisura intertrocchlearis 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 vascular distale is separated from the incisura intertrocchlearis 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 *Psittacocetes 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.

**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 *Avolutavis*, *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 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 (Swoford, 2003) with morphological and molecular characters weighted 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 metastatic 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 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.

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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 medianoplataris 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, Coraci, Galulacea), this feature is absent in all proposed close relatives of Pan-Psittaciformes.
TABLE 1. GenBank accession numbers and references for sequence data.

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<td>U63314 (Griffiths, 1997)</td>
</tr>
<tr>
<td>Nestor meridionalis</td>
<td>—</td>
<td>AF346390 (Weidig et al., unpublished)</td>
</tr>
<tr>
<td>Calyptorhynchus funeratus</td>
<td>GQ505229 (Schweizer et al., 2010)</td>
<td>—</td>
</tr>
<tr>
<td>Cacatua sulphurea</td>
<td>—</td>
<td>AF313750 (Schliebusch et al., 2001)</td>
</tr>
<tr>
<td>Amazonia farinosa</td>
<td>DQ143346 (Tavares et al., 2006)</td>
<td>AY283475 (Ottens-Wainright et al., 2003)</td>
</tr>
<tr>
<td>Cyanoliseus patagonus</td>
<td>DQ143334 (Tavares et al., 2006)</td>
<td>DQ143283 (Tavares et al., 2006)</td>
</tr>
<tr>
<td>Lorius lory</td>
<td>—</td>
<td>AB177942 (Astuti et al., 2006)</td>
</tr>
<tr>
<td>Trichoglossus haematodus</td>
<td>—</td>
<td>AB177952 (Astuti et al., 2006)</td>
</tr>
<tr>
<td>Melopsittacus undulatus</td>
<td>DQ143354 (Tavares et al., 2006)</td>
<td>DQ467903 (Boon et al., 2008)</td>
</tr>
</tbody>
</table>

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 Vastanavis. 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 share unique features with Messelasturidae and Halcyornithidae.

Quercypsittidae is placed in a second clade, including Ptilocercus, 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 accessorius that is separated from the main body of trochlea metatarsi IV. Only the last two of these characters can be confirmed in Quercypsittis and only the third can be confirmed in Avolatavis, because many elements remain unknown for these taxa. A sister-group relationship between Avolatavis and Quercypsittis 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...
Avifauna. Four species of stem lineage parrots are now known from the nearly contemporaneous deposits of the Fossil Butte Member: the halcyornithids Cyrilavisolsoni and Cyrilaviscolburnorum, the messelasturid Tynskyaeocaena, and Avolativas tenens. Although diverse, stem psittaciforms do not appear to have been particularly abundant. Only the taxon Cyrilaviscolburnorum is known from more than a single individual, compared to more common taxa such as the stem roller Primobucco, the stem frigatebird Limnopterigata, and the ‘Messel rail’ Messelorntis, 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 Avolativas 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 Avolativas 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 Avolativas 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 Avolativas 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 Avolativas 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 Avolativas 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 accessorius 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.

ACKNOWLEDGMENTS

We thank B. Breithaupt and L. Grande for providing locality data and access to specimens considered in this study. Acquisition of the latex peel of the counter slab and additional preparation of the specimen was skillfully undertaken by A. Shinya. J. Dean, L. Fuller, J. Gerwin, H. James, G. Mayr, W. Simpson, P. Sweet, T. Trombone, and D. Willard generously accommodated access to comparative materials. We thank G. Mayr for comments on the manuscript and R. Cartwright for assistance with latinization of the species name. This project was supported by National Science Foundation Division of Earth Sciences grants 0938199 to J.A.C. and 0719943 to L. Grande: “Collaborative Research: Integrated Study of an Exceptional Avifauna from the Eocene Green River Formation: New Data on Avian Evolution and Taphonomy.”
LITERATURE CITED


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

| Acanthisita 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 |
| Sandeoleus copiosus | USNM 433912, 433913, 433973–434025 |
| Tyrannus tyrannus | NCSM 18530, 19066, 5864 |
| Urococulus macrourus | AMNH 24231, USNM 491889 |
| Amazona farinosa | AMNH 10583 |
| Araatinga aurea | NCSM 4198 |
| Avosetis tenens | UWGM 39876a and b |
| Catatua sulphurea | AMNH 9040 |
| Calyptorhynchus funereus | SMF 7252 |
| Cyanoloxus patagonicus | USNM 227500, 227501 |
| Cyralis colburrorum | FMNH PA 722, 754, 766 |
| Cyralis olsoni | USNM 424075 (cast of holotype) |
| Eclectus roratus | NCSM 11670 |
| London Clay Species A | Mayr and Daniels, 1998 |
| Loricus galgalus | NCSM 20880 |
| Lorrus lory | USNM 557119, 557120 |
| Melopsittacus undulatus | NCSM 7692, NCSM 21920 |
| Nestor meridionalis | AMNH 61008 |
| Neophema pulchella | USNM 614463 |
| Nyphicus hollandsicus | USNM 10044 |
| Philecyon elegans | AMNH 9220 |
| Pseudaristides macrocephalus | WDC-C-MG 94 |
| Psittacos pespidus | SMF-ME 1279, Mayr and Daniels, 1998 |
| Pulchrorhynchus gracilis | Dyke and Cooper, 2008, Mayr, 2002 |
| Quercysita sudrei | Mourer-Chauviré, 1992 |
| Rhyhchopita pachyrrhyncha | NCSM 17979 |
| Seradapitus poli | WDC-C-MG 201 |
| Sittipha hainlensis | USNM 18275, 289424 |
| Tachyclossos 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, tomal edge of upper beak: smooth (0); notched (1).
(4) Bony nares, shape: ovoid (0); round (1).
(5) Bony nares, orientation: directed laterally (0); directed dorso-laterally (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 mandibulæae: absent or minute perforation (0); large, ovoid opening (1).
(21) Mandible, fenestra caudalis mandibulæae: small, foramensized 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.
(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 articulares acrocoracoidea (1); mediolaterally flattened and forms wide triangular expansion (2).
(28) Furcula, apophysis furculæ: 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 cranialateralis: cranialaterally 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 claviculares: unexpanded (0); greatly expanded so as to overhang the sulcus supracrescoideus (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 supracrescoidei: present (0); absent (1).
(39) Coracoid, processus procoroacoideus: 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 spatum intermetacarpale (0); metacarpal III bowed, wide spatum 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: 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 cartilaginis 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 digitii III and m. flexores perforati digitiorum 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 Lorini by Mayr (2008).

(73) Tarsometatarsus, hypotarsus, pathway for tendon of m. flexor perforator 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 Lorini by Mayr (2008).

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

(75) Tarsometatarsus, hypotarsus, some canal housing only the tendon of m. flexor perforator digitii 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).

(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 (0); present (1). This branch is known to occur only in Columiformes 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 bars (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 _Lorinae_ (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).

| Character | Sandcoleus copiosus | Urocolius macrourus | Colius striatus | Herpetotheres cachinnans | Micrastur semitorquatus | Falco sparverius | Acanthisitta chloris | Tyrannus tyrannus | Gracula religiosa | Vastanavis | Quercypsitta sudrei | Avolatavis tenens | Cyrilavis olsoni | Cyrilavis colburnorum | Pseudastur. macrocephalus | Serudaptus pohli | Pulchrapollia gracilis | Cyrilavis grata | Psittacopes lepidus | London Clay Species A | Cacatua sulphurea | Calyptorhynchus funereus | Amazona farinosa | Cyanoliseus patagonus | Lorius lory | Trichoglossus haematodus | Melopsittacus undulatus | Nestor meridionalis |
|-----------|---------------------|---------------------|----------------|--------------------------|------------------------|----------------|-------------------|-------------------|----------------|-------------|-------------------|----------------|----------------|----------------|-------------------|----------------|-------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| 10        | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |
| 20        | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |
| 30        | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |
| 40        | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |
| 50        | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |
| 100       | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |
| 105       | 0                   | 1                   | 1              | 1                        | 0                      | 1              | 0                 | 1                 | 1             | 0           | 0                 | 0              | 0              | 0               | 0                 | 0              | 1                 | 0               | 0              | 0              | 1               | 1              | 1                 | 1               | 1              | 0              | 1               | 0              | 0               | 0              |