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A taxonomic and anatomic assessment of the extinct Zygodactylidae (Aves) from the Green River Formation of Wyoming and placement of Zygodactylidae within Aves

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A taxonomic and anatomic assessment of the extinct Zygodactylidae (Aves) from the Green River Formation of Wyoming and placement of Zygodactylidae within Aves

by

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Abstract

A taxonomic and anatomical assessment of the extinct Zygodactylidae (Aves) from the Green River Formation of Wyoming and placement of Zygodactylidae within Aves

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Birds are the most diverse extant group of terrestrial vertebrates, and relationships amongst major extant and extinct avian lineages remain hotly debated. A clade of Aves which has received limited attention is the extinct Zygodactylidae, a species-rich group of perching birds that possess a foot with a retroverted fourth toe, an elongate tarsometatarsus and a large intermetacarpal process in the wing. Specimens currently included within Zygodactylidae previously were thought to be sister taxa to songbirds (Passeriformes) or woodpeckers and allies (Piciformes). Zygodactylids were most abundant during the Eocene in North America and Europe and persisted to the Early Miocene. Five exceptionally preserved fossils from the Early Eocene Green River Formation of Wyoming are described, and provide insights into the interrelationships of zygodactylid taxa and the position of the clade within Aves.

In an attempt to resolve systematic relationships within zygodactylids, and the position of the clade within Aves, I conducted two sets of phylogenetic analyses. The first focused on clarifying relationships within Zygodactylidae. Each taxon was evaluated for 37 morphological characters. Resulting strict consensus cladograms yield topologies in which two of the new Green River specimens are positioned in a clade within *Zygodactylus*, a taxon previously known only from the Early Oligocene and Early Miocene of Europe. The second set of analyses sought to assess which extant avian lineage is most closely allied with Zygodactylidae. Those analyses used a dataset of 135 characters evaluated for 57 species and a supraspecific terminal, Zygodactylidae. Scoring of Zygodactylidae was based on morphological observations from all described taxa within Zygodactylidae. The extant species sample was chosen to evaluate previously proposed hypotheses of relationships between Zygodactylidae and other avian clades and included songbirds, parrots and 43 species from the coraciiform-piciform clade (e.g., woodpeckers, galbulids, rollers and motmots). Outgroup species were iteratively swapped to determine if outgroup choice affected recovered estimates of zygodactylid relationships within Aves. Zygodactylidae is the sister taxon to songbirds in the resultant tree topologies. These results forward our understanding of the relationship between Zygodactylidae and Passeriformes within Aves.

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1.1: INTRODUCTION

Birds are one of the most diverse groups of land vertebrates, though relationships amongst major extant and extinct avian lineages remain poorly understood. One clade that has received limited attention is Zygodactylidae, an extinct, comparatively species-rich group of enigmatic perching birds that possess unique morphologic adaptations (Mayr, 2008, 2009). Taxa within Zygodactylidae are zygodactyl, possessing a retroverted fourth toe and associated trochlea accessoria on the distal tarsometatarsus. They also possess an elongate tarsometatarsus and large intermetacarpal process in the wing (Brodkorb, 1971; Mayr, 2008). The interrelationships of described Zygodactylidae were not studied previously. Specimens currently included within Zygodactylidae previously were allied with woodpeckers and their relatives (Piciformes; Mayr, 1998), songbirds (Passeriformes; Mayr, 2004, 2008), and even rollers (Coracii; Feduccia and Olson, 1979). Most recently Mayr (2008) proposed that *Primozygodactylus*, *Primoscens* and *Zygodactylus* were closely related and comprised a clade, Zygodactylidae. Zygodactylids are most abundant in Eocene deposits in North America and Europe, though proposed parts of the clade are known from the Oligocene and Early Miocene of Europe (Mayr, 2008). Exceptionally preserved newly discovered fossils from the Early Eocene Green River Formation of Wyoming are herein described, and are found to be taxa within Zygodactylidae. The relationships of these specimens are analyzed along with other taxa within this clade, representing the first systematic analysis to evaluate the interrelationships of species assigned to Zygodactylidae, and to test the monophyly of that taxon.

In this chapter, I describe five specimens from the Fossil Butte Member of the Green River Formation (Grande, 1984). All of the described specimens from the Green River Formation Green River are referable to Zygodactylidae based on apomorphies, and two (FMNH PA 726 and UWGM 40705) are recovered in analyses as a new species of Zygdactylidae.

1.2: TAXONOMIC HISTORY OF ZYGODACTYLIDAE

The clade name Zygodactylidae was originally proposed by Brodkorb (1971) for fragmentary material from the lower Miocene of Germany and the middle Miocene of France (*Zygodactylus grivensis* Ballman, 1969a; *Zygodactylus ignotus* Ballman, 1969b). Prior to Mayr (2008), Zygodactylidae sensu Brodkorb (1971) included only *Zygodactylus ignotus* and *Zygodactylus grivensis*. However, the taxa *Primozygodactylus major* Mayr 1998, *Primozygodactylus danielsi* Mayr 1998, *Primozygodactylus ballmani* Mayr 1998, and *Primoscens minutus* Harrison and Walker 1977 were assigned to the taxon 'Primoscenidae' sensu Harrison and Walker (1977; Mayr, 1998), based on the presence of a pronounced trochlea accessoria, elongate tarsometatarsus and pronounced unfused intermetacarpal process (Mayr, 1998), all characters also shared by *Zygodactylus ignotus* and *Zygodactylus grivensis*.

The name 'Primoscenidae' was originally coined at the identification of a new species from a single carpometacarpus (*Primoscens minutus* Harrison and Walker 1977) from the Early Eocene London Clay Formation (see Fig. 1.1). This specimen was noted by Harrison and Walker (1977) for its prominent intermetacarpal process and general similarities with Passeriformes. *Primoscens minutus* was the only species assigned to Primoscenidae when Mayr (1998) referred 18 specimens to 'Primoscenidae,' although isolated elements in a private collection from the London Clay had been proposed to belong to Primoscenidae (Fig. 1.2:I; Daniels personal communication cited by Feduccia, 1999). The specimens referred by Mayr (1998) were from the Middle Eocene deposits of Messel in Germany, as well as the early Eocene Green River Formation in North America and the late Palaeocene/early Eocene Fur Formation of Denmark. Three new 'Primoscenidae" species, *Primozygodactylus danielsi*, *Primozygodactylus major*, and *Primozygodactylus ballmani*, were identified (Mayr, 1998).

More recently, *Zygodactylus luberonensis* Mayr 2008 (Fig 1.2:III), a new species of Zygodactylidae, was described in Mayr (2008) based on a nearly-complete specimen (SMF Av 519) found in the early Oligocene lacustrine deposits of the Luberon area in Southern France. This taxon was found to possess not only the zygodactyl foot typical of 'primoscenids' and zygodactylids, but shared with 'Primoscenidae,' amongst other characters, a ventrally displaced insertion of the *m. brachialis* on the humerus, a large dorsal supracondylar process, and a well-developed intermetacarpal process that was unfused with metacarpal III. These similarities were determined by Mayr (2008) to warrant synonymizing 'Primoscenidae' with Zygodactylidae, rendering 'Primoscenidae' a junior synonym of Zygodactylidae. However, the accessory trochlea on the tarsometatarsus was proposed to be more bulbous and distally-extending in *Zygodactylus* (now with an Eocene-Miocene distribution) than in *Primoscens* and *Primozygodactylus*, indicating possible subclades within Zygodactylidae.

Researchers placed zygodactylids within several extant avian taxa. Despite the apparent zygodactyl condition of *Zygodactylus grivensis* and *Zygodactylus ignotus* (both known only from distal tarsometatarsal and tibiotarsal fragments), Ballman (1969a, b) was unsure of the appropriate taxonomic assignment for these taxa. He doubted they were most closely related to the extant clade Piciformes, which also have a zygodactyl foot condition. Instead, he suggested possible passeriform affinities for *Zygodactylus ignotus*. The assignment of Zygodactylidae to Piciformes was proposed by by Harrison and Walker (1977), and they also asserted that 'primoscenid' *Primoscens minutus* represented a basal passeriform. *Zygodactylus grivensis* was tentatively suggested as a member of Piciformes by Simpson and Cracraft (1981) based on the presence and structure of the accessory trochlea (Fig. 1.2:IV). They argued that the size and position of the accessory trochlea was more similar to the piciform subclade Pici than to Galbulidae or to Bucconidae, and suggested *Zygodactylus* might be a part of Pici. They also noted "[t]he morphology of *Z. grivensis* is unique, however, and an assignment of this form to a particular suborder [within Piciformes] is difficult (Simpson and Cracraft, 1981: 492)." In 1998, Mayr specifically considered *Zygodactylus* a sister taxon to Pici, and 'Primoscenidae' as the sister taxon to that clade within crown-group Piciformes. It should be noted that Mlíkovský's (1996) referral of extinct taxa *Procolius* and *Quercypsitta* to Zygodactylidae has not been supported by subsequent researchers and these taxa appear unrelated to each other or to the other proposed Zygodactylid species (Mayr, 2009).

Only a single published phylogenetic analysis has been published which focused on the relationships of 'Primoscenidae' and Zygodactylidae. This analysis, performed by Mayr (2004), used morphological characters and 17 supraspecific taxa representing major avian subclades. Resultant tree topologies from the analysis showed a sister-taxon relationship between Passeriformes and a clade composed of Zygodactylidae and 'Primoscenidae' (prior to the recognition of 'Primoscenidae' as a junior synonym of Zygodactylidae by Mayr, 2008). The matrix was reanalyzed by Mayr (2008) with additional morphological data from *Zygodactylus luberonensis*; this reanalysis provided further justification for a sister-taxon relationship between Passeriformes and a supraspecific terminal 'Zygodactylidae'. See Table 1.1 for a summary of the taxonomic history of Zygodactylidae.

1.3: GEOLOGIC SETTING

The Green River Formation crops out into portions of Wyoming, Colorado and Utah (Fig. 1.1). The formation spans the Late Paleocene to the Middle to Late Eocene, and possesses the most species-rich paleontological record known from the North American Tertiary aquatic communities (Grande, 1984, 1994).

The Green River Formation is comprised of lacustrine deposits from three lakes. Numerous fossil specimens, including those described herein, have been found in the Fossil Butte Member of the Formation. The Fossil Butte Member includes deposits of the smallest and most short-lived of the three lakes, Fossil Lake, which is located in present day Wyoming (Grande, 1984). The Fossil Butte Member has yielded spectacular collections of trace fossils, articulated vertebrates, and non-vertebrates, including multiple squamates and mammals (Grande, 1994; Grande and Buchheim, 1994).

Most of the known avian diversity in the Green River Formation is from the Fossil Butte Member (Grande, 1994) and includes stem representatives of mousebirds (Coliiformes; Ksepka and Clarke, 2010), rollers (Coracii; Kespka and Clarke, 2010), parrots (Pan-Psittaciformes; Ksepka et al., 2011), frogmouths (Podargiformes; Nesbitt et al., 2011), and galliforms (Galliformes; Mayr and Weidig, 2004) among at least twelve named species and an array of as-yet-unpublished forms.

When the fossil-rich beds of the Fossil Butte Member (FBM) were deposited, the lake was likely freshwater (Grande, 1994). The FBM is bounded above by a k-spar tuff, which was dated to 51.66 ±0.09 Ma with $^{40}Ar/^{39}Ar$ spectrometry (Smith et al., 2008), providing constraint on the minimum age for the unit. Estimates of the rate of deposition suggest that fossils were deposited in a short timeframe of several thousand years (Grande and Buchheim, 1994).

1.4: MATERIALS AND METHODS

Five specimens from the Fossil Butte Member of the Green River Formation, Tynsky Quarry (Locality H, F-2 Facies of Grande and Buchheim, 1994), near Kemmerer, Lincoln County, Wyoming, USA, are described herein. They are FMNH PA 726, FMNH PA 757, FMNH PA 770, UWGM 40705 and UWGM 41363. Comparative materials used are listed below.

Osteological terminology follows English equivalents of the Latin in Baumel and Witmer (1993). Measurements (Tables 1.2, 1.3, 1.4 and 1.5) represent the maximum linear length of the bone along its longitudinal axis in millimeters, unless otherwise stated. Measurements were taken with digital calipers to the nearest 1/10th of a millimeter. Measurements were taken from personal observations except for those from Weidig (2004; USNM 299821, WDC-CGR-014, NAMAL 2000-0217-004). Scorings for *Acanthisitta chloris* (YPM ORN 110797) were obtained from high-resolution computed tomography scans, courtesy of Department of Organismic and Evolutionary Biology at Harvard University and Bhart-Anjan Bhullar.

The phylogenetic evaluation of described taxa and other fossil zygodactylids (section 1.6, 1.7 and 1.8) follows Section1.5. For purposes of systematic paleontology, nine described fossils were compared. The extinct taxa examined for this analysis were *Primozygodactylus enjooae* (SMF-ME 1074, holotype), *Primozygodactylus major* (SMF-ME 799, SMF-1758 [holotype]), *Primozygodactylus danielsi* (SMF-ME 2522 [holotype], SMF-ME 1269, SMF-ME 1817, HLMD-Me 15550, HLMD-Me 10206), *Primozygodactylus ballmani* (SMF-ME 2108 [holotype], HLMD-Me 15396), *Primoscens minutus* (BMNH A 4681, holotype), *Zygodactylus luberonensis* (SMF-Av 519, holotype), *Zygodactylus ignotus* (Ballman, 1969a), *Zygodactylus grivensis* (Ballman, 1969b) and both specimens of *Eozygodactylus americanus* (USNM 299821 [holotype] and WDC-CGR-014 [paratype]). I did not personally examine *Eozygodactylus americanus*, *Primoscens minutus Zygodactylus ignotus* and *Zygodactylus grivensis*, but I did see the other taxa.

1.5: INSTITUTIONAL ABBREVIATIONS

FMNH, Field Museum of Natural History, Chicago, Il, USA; HLMD, Hessisches Landes-Museum, Darmstadt, Germany; NAMAL, North American Museum of Ancient Life, Lehi, Utah, USA; SMF, Forschunginstitut Senckenberg, Frankfurt am Main, Germany; USNM, United States National Museum, Washington, DC, USA; UWGM, University of Wyoming Geological Museum, Laramie, WY, USA; WDC, Wyoming Dinosaur Center, Thermopolis, WY, USA.

1.6: SYSTEMATIC PALEONTOLOGY OF FMNH PA 726 AND UWGM 40705

Aves Linnaeus, 1758

Zygodactylidae Brodkorb, 1971

Emended diagnosis: Proposed synapomorphies include four previously identified characters from Mayr (2008) and one newly identified character. The wording of the following four character descriptions was modified slightly for clarity. The carpometacarpus has a distinct intermetacarpal process that is unfused to metacarpal III (Characters 18 and 19, Appendix I) and a distinct protuberance on the anterior margin of metacarpal II close to its midpoint (Character 17, Appendix I; Fig. 1.8, 'processus dentiformis'; Mayr, 2004). The tarsometatarsus distinctly exceeds the humerus in length (Character 31, Appendix I). The furcula possesses a broad, subtriangular omal end (Character 4, Appendix I). A ventrally bowed jugal bar (Character 2, Appendix I; Fig. 1.4) was determined from the present study to be a local synapomorphy of the clade. Mayr (2008) also considered the presence of a hypotarsus with two bony canals, well-developed cnemial crests on the tibiotarsus, and the presence of a lateral plantar crest on the tarsometatarsus to be diagnostic of Zygodactylidae, but those features are highly homoplastic within Aves (Livezey and Zusi, 2001, 2007) and are of more limited utility.

Taxonomic remarks: 'Primoscenidae' is considered a junior synonym of Zygodactylidae (as proposed by Mayr, 2008).

Taxa included: *Zygodactylus ignotus* Ballman 1969a, *Zygodactylus grivensis* Ballman 1969b, *Zygodactylus luberonensis* Mayr 2008, *Primoscens minutus* Harrison and Walker, 1977, *Primozygodactylus danielsi* Mayr 1998, *Primozygodactylus ballmani* Mayr 1998, *Primozygodactylus major* Mayr 1998, *Primozygodactylus enjooae* Mayr and Zelenkov 2009, and *Eozygodactylus americanus* Weidig 2010.

Zygodactylus Ballman, 1969

Emended diagnosis: This taxon is characterized by a unique combination of characters (Mayr, 2008), including proposed autapomorphies, which are designated by an '*' below. There is a distinct convexity on lateral tarsometatarsal margin just proximal to the metatarsal IV trochlea (Fig. 1.10; Character 29*, Appendix 1), and a bulbous and distally elongate accessory trochlea on metatarsal IV (Character 34*, Appendix I; Fig. 1.10). The coracoid is narrow and elongate, and the procoracoid process is reduced (Character 7, Appendix 1). The humerus possesses a tuberculate dorsal supracondylar process separated from the humeral shaft by a small notch (Characters 10 and 11, Appendix 1; Fig. 1.8). Metacarpal III extends distally far beyond metacarpal II (Character 22, Appendix 1). Character 29 was considered an autapomorphy of *Zygodactylus* by Mayr (2008), and character 34 was considered an autapomorphy of *Zygodactylus* by Ballmann (1969a, b) and Mayr (2004). These characters are also recovered as autapomorphies of *Zygodactylus* in this analysis.

Zygodactylus n. sp.

Type specimen. FMNH PA 726, a partially articulated skeleton (Fig. 1.3, 1.4C, 1.5, 1.6, 1.7, 1.8, 1.9C, 1.10).

Type Locality. Tynsky Quarry (Locality H, F-2 Facies of Grande and Buchheim, 1994), near Kemmerer, Lincoln County, Wyoming, USA.

Referred specimen. UWGM 40705, a partially articulated pectoral girdle (Fig. 1.14 and 1.15) from Locality J, F-2 Facies described by Grande and Buchheim (1994).

Type Horizon: Eocene Green River Formation, Fossil Butte Member. Etymology: *Zygodactylus* n. sp.

Diagnosis: FMNH PA 726 is unique amongst taxa assigned to Zygodactylidae in having a femur which is shorter than the humerus (Character 12, Appendix I), and an ungual on digit III which is more that 25% the size of the sum of the remaining digits (Character 38, Appendix I). These characters can be assessed in most described Zygodactylidae, save the fragmentary *Primoscens minutus*, *Zygodactylus ignotus* and *Zygodactylus grivensis*.

Differential diagnosis: *Zygodactylus* n. sp. is distinguished from the holotype of *Eozygodactylus americanus* by the presence of a protuberance ("dentiform process") on the mid-shaft of the dorsal margin of metacarpal II (Weidig, 2010; Character 17, Appendix I); lateral trabeculae of the sternum which do not extend posterior to the medial trabeculae (Character 8, Appendix I). *Zygodactylus* n. sp. differs from *Zygodactylus ignotus* in possessing a shorter tarsometatarsus (measurement from Mayr, 2008). *Zygodactylus* n. sp. also differs from *Zygodactylus grivensis* in possessing a shorter accessory trochlea. The accessory trochlea of *Zygodactylus* n. sp. is more similar to that of *Zygodactylus luberonensis* both in the somewhat shorter accessory trochlea and in the presence of a marked sulcus on the plantar surface of the convexity on the proximal end of metatarsal trochlea IV (Mayr, 2008).

Additional differentia: The presence of a distinct expansion on the anterolateral distal tarsometatarsus, just proximal of the metatarsal IV trochlea present in *Zygodactylus* n. sp. (Fig. 1.10), was considered by Mayr (2008) as autapomorphic for *Zygodactylus*. It is absent in all other extinct and extant taxa examined for this study save *Zygodactylus grivensis* and *Zygodactylus ignotus*, supporting this assessment and placement of FMNH PA 726 within *Zygodactylus*. This feature is absent in all taxa assigned to

Primozygodactylus, *Primoscens*, but the relevant region is not preserved in *Eozygodactylus americanus* and thus cannot be assessed for that taxon. The stouter coracoid with a more expanded sternal margin clearly distinguishes *Zygodactylus* n. sp. from *Zygodactylus luberonensis*. As in *Primozygodactylus* but not *Zygodactylus luberonensis*, *Zygodactylus* n. sp. possesses a medial flange on the coracoid (Fig. 1.9); this feature appears to be variably present in passeriforms and piciforms. Unfortunately WDC-CGR-014, the paratype of *Eozygodactylus americanus,* has only a poorly preserved coracoid on which features are difficult to discern, and no coracoid is preserved in USNM 299821, the holotype of *Eozygodactylus americanus*.

Zygodactylus n. sp. is generally similar both in measurements and morphology to the holotype and paratype of *Eozygodactylus americanus*, (USNM 299821 and WDC-CGR-014, respectively), from the Fossil Butte Member of the Green River Formation. However, the carpometacarpus is well-preserved in both specimens, and it is clear that no dentiform protuberance is present on metacarpal II in either specimen of *Eozygodactylus americanus*; a distinct dentiform protuberance is visible in *Zygodactylus* n. sp. A dentiform process is also present in *Primoscens minutus*.

1.6.1: Description: FMNH PA 726, holotype specimen of *Zygodactylus* n. sp.

FMNH PA 726 (Fig. 1.3-1.10) comprises a complete skull and articulated postcranial skeleton. Though crushed, the skull and cervical vertebrae remain in articulation. Most of the right forelimb is absent, and much of the synsacrum is broken and crushed, obscuring morphology in those regions. However, the left forelimb and both hind limbs are present, articulated, and relatively uncrushed.

Cranial Elements

The dorsal border of the frontal, braincase and portions of the quadrate and lacrimal/ectethmoid complex are severely crushed (Fig. 1.4C). The dorsal premaxillae are relatively straight, and curve slightly downward at the tip of the beak. As in other parts of Zygodactylidae, the narial openings are elongate, approximately rectangular in shape, and approaching three quarters of the overall rostrum length, (i.e., the holotype of *Eozygodactylus americanus*, USNM 299821; Fig. 1.11). The posterior and anterior-most portions of the narial openings are slightly fractured, which may slightly distort their shape slightly. Within Aves, thin and elongate rectangular openings also are seen in Columbiformes and some passeriforms. The antorbital fenestrae open just adjacent to the posterior-most edge of the narial openings with the narial bar nearly vertical in orientation. This condition contrasts with the substantial overlap of fenestrae and narial openings, and strongly angled narial bar seen in some parts of Coracii (e.g., *Coracias garrulus*). The specimen appears to have lacked an ossified nasal septum, as was noted previously for *Primozygodactylus*, passeriforms and some Piciformes (namely members of Picidae; e.g., Mayr, 2009), and in contrast to the ossified nasal septae seen in many parts of Coracii and other members of Piciformes (specifically Galbulidae and Bucconidae; Clarke et al., 2009). Thin, barely-visible segments of bone within the exposed narial opening may represent portions of vomer (visible in this region through the narial openings in multiple avian taxa, including *Bombycilla cedrorum*).

Scleral ossicles are preserved in the orbit, though many are missing or shifted out of articulation (Fig. 1.4, 3C). Other ossicles are crushed, though the margins of five are distinctly visible. The relative ossicle sizes and shapes appear similar to those of HLMD-Me 15396 (?*Primozygodactylus ballmanni*; Fig. 21 of Mayr, 1998). Overlying the dorsal edge of the posterior mandible is a thin and ventrally bowed jugal, which is obscured just anterior to the quadrate. The quadrate is three-dimensionally preserved, and the orbital process of the quadrate is visible. That process is relatively short in comparison to the condition in extant Passeriformes, though unfortunately no quadrates of other zygodactylids are preserved. The braincase and more anterior portions of the skull are severely crushed. However, a minute postorbital process is visible (similar in size and appearance to the same process in some passeriforms, e.g., *Tyrannus forficatus*).

Mandible

The mandible is exposed in left lateral view (Fig. 1.4C). The mandibular symphysis is short, and the posterior portion of the mandible is deflected ventrally. The posterior mandibular ramus curves ventrally from approximately its midpoint but appears slightly upturned where it terminates with an abbreviated retroarticular process. An elongate depression is developed on the posterolateral mandible, though it is unclear whether this is a morphological feature or the result of crushing and distortion. What may be a posterior mandibular fenestra (or possibly breakage) is present slightly anterior to the lateral mandibular process; however, USNM 299821, the paratype of *Eozygodactylus americanus* lacks this fenestra. Due to the possibility of breakage on this feature, it is coded as '?' in Appendix II. The lateral mandibular process of these specimen is a relatively small tubercle at the apex of a tiny crest coming off of the posterior-most portion of the mandible. The retroarticular process is small.

Vertebral Column

The many of the anterior cervical vertebrae (Figs. 1.4C, 1.5, 1.6) are badly crushed, rendering morphological features indiscernible, and making the identification of the atlas and axis difficult. At least thirteen individual cervical vertebrae are visible, and at least twenty-one total presacral vertebrae. At least two free caudals are present. Most Passeriformes have seven caudal vertebrae (Bochenski et al., 2011), though *Primozygodactylus danielsi* possessed five caudal vertebrae (Mayr, 1998). A pygostyle is not preserved. There is no indication of a notarium, and the synsacrum is crushed and distorted.

Sternum

The sternum is visible in dorsal view and partially obscured by ribs, matrix, and some crushing on the right side (Fig. 1.5). Posterior segments of the intermediate trabeculae are preserved as impressions, though the lateral trabeculae are intact. As in the holotype of *Eozygodactylus americanus* (USNM 299821), and specimens of *Primozygodactylus* (HLMD-Me 15396, HLMD-Me 10206 and WN 89609; Fig. 24 of Mayr 1998), the sternum is broad, and exhibits four deep incisures. The lateral and intermediate trabeculae are approximately equal in posterior extent. By contrast, the lateral trabeculae extend farther posteriorly than the intermediate trabeculae in *Eozygodactylus americanus* (USNM 299821). The posterior tips of the trabeculae exhibit slight mediolateral expansion, but not as extensive as in USNM 299821, especially as compared to the lateral trabeculae. The relatively broad external rostral spine is developed on the anterior edge of the sternum between the coracoids (Fig. 1.9). That spine was reconstructed as comparatively narrow in primozygodactylids by Mayr (1998). In extant Passeriformes, the feature is typically bifid (Manegold, 2008). In Piciformes this feature is typically bifid as well. The left coracoid is visible in dorsal view (Fig. 1.5). In contrast with Piciformes, Trogoniformes, and some Coracii, no sternal notch is present. The presence of a sternal notch has been considered a localized autapomorphy of Piciformes by Mayr et al. (2003).

The coracoid is not as slender as *Zygodactylus luberonensis*, and has a small acrocoracoid process that is partly obscured, though visible in dorsal view. A portion of the sternal articulation of the right coracoid is visible and is broad compared to *Zygodactylus luberonensis*. A flange (Fig. 1.9) is located on the distomedial portion of the coracoid, as with all described coracoids of *Primozygodactylus* (Mayr, 1998; Mayr, 2009) although this feature is not present in *Zygodactylus luberonensis* (Mayr, 2008). The flange appears to be variably present in passeriforms and piciforms.

Scapula

The scapula (Fig. 1.5) is relatively short and moderately-recurved with a tapering distal tip and moderately well-developed acromion process similar to that of *Primozygodactylus danielsi* (e.g., holotype specimen SMF-ME 2522; Fig. 22, Mayr, 1998), and is indistinguishable from the scapula of the *Eozygodactylus americanus* holotype (USNM 299821). The acromion is not bifurcated as it is in most extant passeriforms (save Eurylaimidae and Cotingidae; Olson, 1971).

Furcula

A thin bone adjacent to the right side of the left humerus, appears to be a part of the left furcular ramus (Fig. 1.8) while just medial to the right coracoid a second narrow element appears to be a part of the right ramus. The ramus looks narrow and, as far as comparisons are possible for such a fragmentary element, appears similar to UWGM 40705. Further, thin furcular rami are typical of Passeriformes and Piciformes.

Humerus

The right and left humeri of the specimen are exposed in posterior view (Figs. 1.5, 1.8). Although the left humerus is comparatively well exposed, only the posterodorsal edge of the right humerus is visible, partially obscured by the right scapula. A capital incisure is exposed on the left humerus. The bicipital crest is short. In contrast to the more well-projected deltopectoral crest seen in *Primozygodactylus danielsi* (Fig. 25 of Mayr, 1998), the deltopectoral crest of FMNH PA 726 is expanded and of relatively moderate size, a condition seen in the holotype of *Eozygodactylus americanus* (USNM 299821), *Primozygodactylus* sp. indet. WN 88583A, and the holotype of *Primozygodactylus danielsi* holotype (SMF-ME 2522). The ventral tubercle is prominent, as with USNM 299821 and specimens *Primoscens* sp. (WN 87558A) and the holotype of *Primozygodactylus danielsi* (SMF-ME 2522; see Mayr, 1998).

The left humeral shaft is crushed, such that its midpoint width cannot reliably be assessed (Fig. 1.8). The curvature of the shaft appears to be less than that seen in the holotype of *Eozygodactylus americanus* (USNM 299821), though the curvature of FMH PA 726 may be an artifact of the aforementioned crushing. On the distal humerus, a well-projected dorsal supracondylar process is visible, which was suggested by Mayr (2008) to be a local synapomorphy of a clade containing *Zygodactylus* and Passeriformes (though this feature is present in Piciformes as well). The projection and size of the process is similar in appearance to that of the zygodactylid WN 92747 ('Primoscenidae' indet., Mayr, 1998: Fig. 25) and *Zygodactylus luberonensis* (Mayr, 2008) in that it is projected on a short stalk with a small notch separating it from the shaft. By contrast, it is somewhat more dorsally directed than in the holotype and paratype of *Eozygodactylus americanus* (USNM 299821 and WDC-CGR-014). Substantial crushing obscures detail on the relative development of the *m. scapulotriceps* and *m. humerotriceps* grooves. The flexor process is well projected and bulbous, similar in size and build to that in WN 92747 ('Primoscenidae' indet., Mayr 1998) and extant Passeriformes (e.g., *Turdus merula*).

Ulna and Radius

The left ulna is comparatively well exposed in oblique dorsal view, and a moderately pointed olecranon process is visible. The right ulna is not exposed. The proximal end of the left ulna is obscured by the humerus. The ulna is longer than the humerus, as in *Zygodactylus luberonensis*, Pici, *Primozygodactylus danielsi* (SMF 2522), ?*Primozygodactylus ballmanni* (HLMD-Me 15396), *Primozygodactylus major* (SMF-Me 1758), and holotype and paratype of *Eozygodactylus americanus* (USNM 299821 and WDC-CGR-014). Passeriformes, by contrast, exhibit ulnae shorter than, approximately equal to, or longer than the humerus. As in WDC-CGR-014, the ulna is shorter than the tarsometatarsus, unlike the condition seen in *Primozygodactylus* in which the ulna is longer or subequal to the tarsometatarsus (Weidig, 2010). These proportions in FMNH PA 726 contrast to the generally elongate ulna but short tarsometatarsus seen in many extant passeriforms and piciforms.

Although the olecranon of the ulna in Passeriformes and Piciformes is elongate and pointed (Manegold, 2008), the olecranon of FMNH PA 726 is comparatively shorter. However, it is contrasted with the even more abbreviated olecranon noted in examined specimens of non-piciform parts of the large Coraciiformes +Piciformes clade (Hackett et al., 2008).

Carpometacarpus

The left carpometacarpus is exposed in dorsal view, partially covered proximally by the ulna and radius. The right carpometacarpus is not visible. This specimen has a large intermetacarpal process (Fig. 1.8), as with all previously described taxa within Zygodactylidae for which a carpometacarpus is preserved, and taxa such as extant Passeriformes and Piciformes. In contrast to all extant Passeriformes and some Piciformes, the intermetacarpal process is not fused to the third metacarpal, though it does contact this metacarpal. A carpometacarpal protuberance ('processus dentiformis' of Mayr, 2004) is present on the anterior surface of metacarpal II, as in Passeriformes, *Zygodactylus luberonensis* and *Primoscens minutus*, though contra *Primozygodactylus*. A carpometacarpal protuberance on the medial dorsal-most margin of the carpometacarpus also is found in the extinct Eocene sylphornithids (Mayr, 2004) and some kingfishers (Boles, 1997).

The third metacarpal projects farther distally than metacarpal II, which is present in an array of avian taxa including most extant passeriforms (Manegold, 2008), *Zygodactylus luberonensis*, *Zygodactylus ignotus*, extant galbulids and the extinct sylphornithids (Mayr, 2004). This contrasts with *Primozygodactylus* (e.g., *Primozygodactylus danielsi,* SMF 2522; Mayr, 2004: Fig. 5) and *Primoscens minutus*, in which metacarpals II and III are approximately equal in distal extent. The distal carpometacarpus is poorly preserved in the holotype of *Eozygodactylus americanus*, USNM 299821. However, in that specimen the third metacarpal and second metacarpal appear to end at approximately the same point, as in extant members of Pici and the three species of *Primozygodactylus* in which carpometacarpi are preserved (*Primozygodactylus ballmani* [SMF-ME 2108], *Primozygodactylus danielsi* [e.g., SMF-ME 2522b, SMF-ME 1269] and *Primozygodactylus major* [SMF-ME 1758]).

Manual Phalanges

The manual phalanges are exposed on the left side (Fig. 1.8). The first digit has two phalanges; a small claw is present. Phalanx I:1 is comparable in size and appearance to the phalanges in the holotype and paratype of *Eozygodactylus americanus* (USNM 299821 and WDC-CGR-014). It is more gracile and longer than phalanx I:1 in *Primozygodactylus* (e.g., *Primozygodactylus danielsi*, SMF 2522). Taxa within *Primozygodactylus*, including *Primozygodactylus enjooae* and *Primozygodactylus danielsi*, also possess a manual digit I:2, though none were preserved in USNM 299821 or WDC-CGR-014. *Zygodactylus luberonensis* has a well-preserved phalanx I:2 that is virtually identical in size and appearance to that seen in FMNH PA 726. While non-preservation of such a delicate ungual cannot definitively speak to its presence or absence, it is interesting to note its presence in both FMNH PA 726 and *Zygodactylus luberonensis*, but it was not observed in specimens of *Eozygodactylus americanus* specimens (USNM 299821, WDC-CGR-014) with apparently similar quality of preservation. Phalanx II:2 is shorter than II:1 and relatively narrow. Phalanx III:1 also is narrow, and the flexor tubercle is inconspicuous. In these morphologies the phalanx resembles *Primozygodactylus danielsi* and *Primozygodactylus enjooae* (Mayr, 2009). All Passeriformes examined for this study have much more abbreviated and broad II:2, and the piciforms have a pronounced flexor tubercle on III:1. Phalanx II:1 is generally shorter and the III:1 flexor tubercle more well developed in Alcidinidae, Meropidae, Motmotidae, and Coraciidae. A proximally projected process on the anteroproximal tip of II:1, present in Piciformes (Mayr, 2004), is not present.

Pelvic Girdle

Portions of both the right and the left anterior iliac blades are visible in dorsal view with squared anterior margins (Fig. 1.6). The proximal half of the right femur appears to lie in articulation with the acetabulum, although the distal portion of element appears to lie under the rest of the pelvic elements. A well-developed dorsolateral iliac crest is present. The posterior terminus of the ischium, visible on the left side, extends significantly beyond the terminus of the crest and is strongly angled ventrally. The tip of the left ischium shows an anteriorly deflected tip. The left pubis is visibly rod-like and extends just farther than the ischium. A large ischiopubic fenestra is present. In these morphologies, it is similar to some extant Passeriformes (e.g., *Turdus migratorius*). Although an open obturator foramen was identified as an apomorphy of WDC-CGR-014 (Weidig 2010), unfortunately this feature is not preserved in FMNH PA 726 (though this feature is widespread in Aves).

Tibiotarsus

The left tibiotarsus is exposed in lateral view while the right is exposed in medial view (Fig. 1.7). The fibula lies in articulation with the proximal left tibiotarsus. The tibiotarsus is the longest hind limb element, as in *Primozygodactylus*, in previously described species of *Zygodactylus*, and *Eozygodactylus americanus* paratype specimen WDC-CGR-014. The cranial cnemial crest, especially visible on the right tibiotarsus, is pronounced and well projected anteriorly. That condition is also seen in WDC-CGR-014, *Zygodactylus luberonensis* and all specimens of *Primozygodactylus* in which the element is preserved. However, it is slightly more weakly projected than the cranial cnemial crest in the leg of a small zygodactylid specimen which was assigned to Zygodactylidae gen. indet. sp. indet. by Weidig (2010; UWGM 21421; Fig. 1.12). The proximal condyles for articulation of the femur project posteriorly relative to the tibiotarsal shaft, in a conformation similar to Passeriformes. The cnemial crest is not hooked, in contrast to most Passeriformes, Piciformes and *Zygodactylus luberonensis*. It also does not appear to be hooked in the *Eozygodactylus americanus* paratype (WDC-CGR-014).

Tarsometatarsus

The left tarsometatarsus is exposed in lateral view but the right is exposed in medial view (Fig. 1.10). The presence of trochlea accessoria, and the preservation of the fourth toe in a retroverted position on both the right and left foot, strongly suggest that FMNH PA 726 was zygodactyl. The tarsometatarsus is thin and elongate, as with Passeriformes, Piciformes, the paratype of *Eozygodactylus americanus* (WDC-CGR-014), other Zygodactylidae species (e.g., *Zygodactylus luberonensis*, *Primozygodactylus danielsi*, *Primozygodactylus ballmani*, *Primozygodactylus major*), *Gracilitarsus mirabilis*, and an array of other avian taxa that are otherwise quite distinct from the new species (e.g., some parts of Charadriiformes, Gruoidea, Ciconiiformes). However, relative to humeral and ulnar length the tarsometatarsus is longer in FMNH PA 726 than *Gracilitarsus mirabilis*, species of *Primozygodactylus* and most taxa of Passeriformes examined for this study. The right proximal tarsometatarsus is partially visible in plantar view, and shows at least one ossified hypotarsal canal. The medial hypotarsal crest is visible on both the left and right tarsometatarsus (Fig. 1.7), though details are difficult to ascertain due to crushing. The hypotarsus is large and well projected plantarly with a deep medial parahypotarsal fossa as in other *Primozygodactylus* and *Zygodactylus* taxa with preserved tarsometatarsi. The intercotylar eminence is relatively diminutive.

Metatarsal I is visible on the right foot and is relatively abbreviated (Fig. 1.10). The trochlea of metatarsal III extends farthest distally, and metatarsal II extends distally beyond metatarsal IV. Well-preserved accessory trochleae on the Metatarsal IV trochleae are visible on both feet, in lateral view on the left limb and plantar view on the right. The accessory trochlea is extremely well-projected plantarly, as in *Zygodactylus luberonensis*, though in contrast described specimens of *Primozygodactylus*. However, contra passeriforms and Coracii, and in accordance with the paratype of *Eozygodactylus americanus* (WDC-CGR-014), the metatarsal III trochlea projects distal to the metatarsal II and IV trochleae. As mentioned above, FMNH PA 726 exhibits a previously-proposed apomorphy of *Zygodactylus* (Mayr, 2008): a distinct convexity on lateral tarsometatarsal margin just proximal to the metatarsal IV trochlea (Fig. 1.10; Character 29, Appendix 1). This specimen also exhibits a feature proposed by Mayr (2008) as an apomorphy of *Zygodactylus luberonensis*: the presence of a marked sulcus on the plantar surface of the proximal end of trochlea metatarsi IV bordering the aforementioned lateral tarsometatarsal convexity (Fig 1.10; Mayr, 2008; Character 29, Appendix 1). These features are absent in all taxa of Passeriformes, Piciformes and outgroup taxa examined for this study. A small plantar ala is also developed on the trochlea of metatarsal IV.

Pedal Phalanges

As with *Zygodactylus luberonensis* and the paratype of *Eozygodactylus americanus* (WDC-CGR-014), the phalanges are much more gracile, and the unguals less recurved, than those of *Primozygodactylus* (Fig. 1.10; Fig. 2 in Mayr and Zelenkov, 2009). Digit III is longest and digit II is shortest. Digit I is relatively elongated with a slightly recurved ungual. The digits are longer and thinner than all described specimens of *Primozygodactylus* (Table 1.5), though they are similar in size and proportions to WDC-CGR-014 and *Zygodactylus luberonensis* (SMF-Av-519, Fig 1.2III; Mayr, 2008: Fig. 2). Several unguals are slightly longer (Table 1.5) than those of WDC-CGR-014, *Zygodactylus luberonensis*, *Primozygodactylus danielsi* and *Primozygodactylus enjooae*. As in all Zygodactylidae, unguals exhibit a pronounced neurovascular sulcus (Mayr, 1998, 2008, 2009). An apomorphy of *Zygodactylus* n. sp. is the ratio of the ungual length of digit III in relation to the remainder of the phalanges of digit III. In FMNH PA 726 the ungual is more that 25% the size of the sum of the remainder of the digit's phalanges, whereas in all other zygodactylids, and *Acanthisitta chloris* the ungual is less than 25% of the remainder of the sum of the phalanges of the digit.

1.6.2: Description: UWGM 40705, referred specimen of *Zygodactylus* n. sp.

UWGM 40705 comprises a partial pectoral girdle and left limb in dorsal view (Fig. 1.13 and 1.14). The left humerus is broken at midshaft. The furcula is visibly thin with breakage at the omal ends. A rounded furcular apophysis is apparent. This contrasts starkly with the blade-like furcular apophysis of most passeriforms and some piciforms, as well as *Primozygodactylus danielsi* (SMF-ME 2091, SMF-ME 2553; Mayr, 1998), though a rounded furcular apophysis is seen in an unnamed species of *Primozygodactylus* (WN 89609; Mayr, 1998). To date, no described specimen of *Zygodactylus* has a preserved furcular apophysis (Mayr, 2008). The scapula is similar in shape and proportion to that of FMNH PA 726, *Zygodactylus luberonensis*, and holotype of *Primozygodactylus danielsi* (SMF-ME 2522), though the acromion process and humeral articular facet are more widely separated in the holotype of *Primozygodactylus major* (SMF-ME 1758). As in other zygodactylids, the acromion is not bifurcate. The sternal coracoidal margin is expanded and the coracoid shaft is narrow.

The sternum is preserved in dorsal view, and as with FMNH PA 726 the sternum is stocky and broad, with four deep incisures. An external rostral spine appears to be developed. The lateral and intermediate trabeculae exhibit approximately equal posterior extension, as in FMNH PA 726. The lateral trabeculae extend slightly posterior to the medial ones in the holotype (USNM 299821) and paratype (WDC-CGR-014) of *Eozygodactylus americanus*.

As in the holotype of *Zygodactylus* n. sp. (FMNH PA 726), other within Zygodactylidae, Passeriformes, Piciformes and other 'higher land birds', the carpometacarpus possesses a large intermetacarpal process that contacts metacarpal III, though in contrast with passeriforms and some piciforms the intermetacarpal process is not fused with the minor metacarpal. A prominent dentiform process is notable on the along the mid-shaft of metacarpal II. A dentiform process is present in the holotype specimen of *Zygodactylus* n. sp., *Zygodactylus luberonensis,* extant passeriforms and piciforms (Manegold, 2008; Mayr, 2008). It is absent in *Primozygodactylus* (Mayr, 1998) and the holotype and paratype specimens of the other Fossil Butte zygodactylid taxon, *Eozygodactylus americanus* (Weidig 2010).

1.7 SYSTEMATIC PALEONTOLOGY OF FMNH PA 770 AND EMENDED DIAGNOSIS OF *EOZYGODACTYLUS AMERICANUS*

Aves Linnaeus, 1758

Zygodactylidae Brodkorb, 1971

Eozygodactylus americanus Weidig 2010.

Type specimen: USNM 299821, partially articulated skeleton, lacking pelvis and hind limbs.

Paratype specimen: WDC-CGR-014, articulated postcranial skeleton (skull not preserved).

Type Locality: Tynsky Quarry (Locality H, F-2 Facies of Grande and Buchheim, 1994), near Kemmerer, Lincoln County, Wyoming, USA Type Horizon: Green River Formation, Fossil Butte Member.

Emended diagnosis: *Eozygodactylus americanus* was diagnosed by Weidig (2010) by the presence of a humerus with a large dorsal supracondylar process (Character 15, Appendix I), manual digit III:1 widened into a small tubercle (Character 22, Appendix I), and pelvis with an open obturator foramen (Character 25, Appendix I). A pronounced dorsal supracondylar process is also present in *Zygodactylus luberonensis*, *Zygodactylus* n. sp., and undescribed zygodactylid WN 92747 (Mayr, 1998). The distal widening of manual digit III:1 also is present in *Zygodactylus* n. sp., though this state also variably observed within Passeriformes (e.g., *Troglodytes troglodytes*). Though an open obturator foramen is locally apomorphic for Zygodactylidae, that feature can only be assessed in *Primozygodactylus danielsi*, *Primozygodactylus ballmani* and *Primozygodactylus major* due to poor preservation in other specimens. An open obturator foramen is widespread within Aves (Livezey and Zusi, 2007).

Due to a lack of access to these specimens, I could not determine further apomorphies for the taxon *Eozygodactylus americanus*. I note that measurements for the holotype of *Eozygodactylus americanus* (USNM 299821) and the paratype (WDC-CGR-014) are somewhat different (Table 1.4). The holotype has a well-preserved skull but the hind limbs were not preserved, whereas the paratype has no skull but has preserved hind limbs. More detailed examination of these two specimens and the recovery of more comparative material may reveal that the paratype and holotype are actually different taxa. However, such an analysis is outside the scope of this project.

Differential diagnosis: *Eozygodactylus americanus* can be distinguished from *Zygodactylus luberonensis*, *Zygodactylus* n. sp., and *Primoscens minutus* in the absence of a dentiform process on the carpometacarpus of the former (Character 17, Appendix I). The paratype of *Eozygodactylus americanus* (WDC-CGR-014) can be distinguished from *Zygodactylus* n. sp. additionally by meristic differences; pedal ungual III:4 is less than 25% of the sum of the length of the proximal three phalanges of digit III. Further, the paratype of *Eozgodactylus americanus* does not share the foreshortened femur of *Zygodactylus* n. sp. (Table 1.4, 1.5).

Referred specimen: FMNH PA 770, slab a and b, partial pelvic girdle and articulated legs and feet (Fig. 1.15 and 1.16), from Locality H, F-2 Facies described by Grande and Buchheim (1994).

Diagnosis: FMNH PA 770 shares with WDC-CGR-014 elongate toes and gracile unguals (Character 36, Appendix I), and almost identical measurements (Table 1.4). Further, despite an appearance similar to FMNH PA 726, FMNH PA 770 shares with WDC-CGR-014 an ungual on pedal digit III which is less than 25% the length of the sum of the lengths of the remaining three phalanges (Character 38, Appendix I).

1.7.1: Description: FMNH PA 770, referred specimen of *Eozygodactylus americanus*

Slab a, which contains most of FMNH PA 770, comprises posterior thoracic vertebrae, free caudal vertebrae, a pygostyle, pelvic girdle, and complete right and left hind limbs exposed in right lateral view. The tip of the right ischium is preserved as an impression. The bone at the tarsometatarsal and tibiotarsal epiphyses is differently textured, “punky”, with a distinct preservational style. It is possible that this specimen represents a sub-adult individual. Slab b is primarily impressions of the opposite side of the specimen, with a few fragments of preserved bone, including the right ungual of digit III and portions of proximal phalanges II and III and several fragments of the distal tarsometatarsus of the left limb. Unless otherwise stated, descriptions below focus on the substantially more complete slab a.

The preacetabular ilium is partially visible adjacent to the crushed synsacral vertebrae. Impressions of what are inferred to be postacetabular iliac blades are visible. The pelvis is poorly preserved due to crushing and a large break in the slab. However, the morphology of the right pubis and ischium appears similar to FMNH PA 726. The pygostyle is neither enlarged nor disc-shaped as in piciforms and coliiforms (Character 28, Appendix II), and is lacking the pronounced dorsal notch of trogoniforms. A pygostyle was not previously discernable in any described specimen of Zygodactylidae.

The femur is similar in width to *Zygodactylus n. sp.* (FMNH PA 726; Fig. 1.3). The tibiotarsus is thin and elongate, longer than the tibiotarsus of *Primozygodactylus*, though slightly shorter than *Zygodactylus n. sp.* (FMNH PA 726) and almost identical to the tibiotarsal length of the paratype specimen of *Eozygodactylus americanus* (WDC-CGR-014). Limb proportions between *Zygodactylus* n. sp. and *Eozygodactylus americanus* are somewhat different (see Table 1.2). Although detailed structures are not visible on the distal tarsometatarsi of this specimen, the pedal phalanges are articulated and exceptionally preserved. An accessory trochlea is not visible due to crushing, so definitive assertion of zygodactyly is not possible. However, on both feet digits II and III are visible only in dorsal view, while digit IV on the right foot is preserved in palmar view, suggesting digit IV’s retroversion. The phalanges are elongated and thin, as with the paratype of *Eozygodactylus americanus* (WDC-CGR-014), *Zygodactylus luberonensis* (SMF Av 519), and *Zygodactylus* n. sp. (FMNH PA 726), in contrast to the more stout phalanges of *Primozygodactylus*. The pedal unguals are short and only weakly recurved, as with *Zygodactylus* and the paratype of *Eozygodactylus* n. sp., and in sharp contrast to the large and more recurved pedal unguals seen in *Primozygodactylus*, and all specimens of Passeriformes and Piciformes viewed for this study.

1.8: SYSTEMATIC PALEONTOLOGY OF FMNH PA 757 AND UWGM 40363: SPECIMENS CONSIDERED ZYGODACTYLIDAE INDET.

Of the five Fossil Butte Member specimens treated here, two (FMNH PA 757, UWGM 40363) are referred to Zygodactylidae indet. They cannot with confidence be referred to either of the two Zygodactylidae species previously named from the Fossil Butte Member, because the only preserved characters on these specimens are cranial.

Referred Specimens: FMNH PA 757 (Fig. 1.17; Fossil Butte Member of the Green River Formation; Locality H, F-2 Facies of Grande and Buchhein, 1994), skull and anterior cervical vertebrae; UWGM 40363 (Fig. 1.18; Fossil Butte Member of the Green River Formation; Locality J, F-2 Facies of Grande and Buchhein, 1994), isolated skull.

Basis for referral: FMNH PA 757 is referable to Zygodactylidae based on the presence of a rectangular narial opening (Character 1, Appendix I), a ventrally bowed jugal (Character 2, Appendix 1), and a narial opening greater than 50% of the length of the rostrum (Character 3, Appendix I). Further similarities shared by these specimens with Zygodactylidae include an absence of an internarial septum, the presence of thin nasal bars, and a recurved beak tip with pitting on the tip. Cranium length, rostrum length, and length of the narial opening are close in both specimens to the holotype of *Eozygodactylus americanus* (USNM 299821) and *Zygodactylus* n. sp. (Table 1.4).

1.8.1: Description of FMNH PA 757

FMNH PH 757 is an exquisitely preserved skull in left lateral view with several anterior cervical vertebrae preserved in articulation (Fig 1.17). The premaxilla is uncrushed anteriorly, and shows numerous neurovascular pits and canals at the tip of the rostrum. Similar pits and canals are also visible in FMNH PA 726 and UWGM 40636 (Fig. 1.4), but are poorly preserved. As in FMNH PA 726 and USNM 299821, the premaxillae are straight with a very slight downward curve near the rostrum tip. The narial openings are elongated and rectangular and encompass more than half of the total rostrum length. The narial bar is slightly angled with the anterior tip of the antorbital fenestra nearly even with, but just slightly anterior to, the posterior-most edge of the narial opening. The specimen shares with the holotype of *Eozygodactylus americanus* (USNM 299821) and the holotype of *Zygodactylus* n. sp. (FMNH PA 726) an elongated narial opening that lacks an ossified nasal septum. The nasofrontal hinge is well demarcated. An interorbital septum is largely absent; the development of the mesethmoid appears to be weak. Its preserved shape is nearly identical to that in the holotype of *Zygodactylus* n. sp. (FMNH PA 726).

Scleral ossicles are visible in the orbit, though many are shifted out of articulation. The margins of six are distinctly visible, and the relative ossicle sizes and shapes are not markedly different from those of FMNH PA 726. Overlying the dorsal edge of the posterior mandible is a thin and ventrally bowed jugal. The outline of the quadrate is visible in rough articulation to the jugal. Its orbital process, like that of FMNH PA 726, is more abbreviated than in comparison to most Passeriformes. The preservation on the orbital process in other zygodactylids is too poor for comparison. The braincase and anterior portions of the skull are crushed. Interestingly, this specimen preserves some of the hyoid apparatus. Though the preserved parts of the left ceratobranchial and epibranchial are not helpful for comparisons with other zygodactylids (for whom no hyoid material is described), this does suggest that this specimen may have lacked modified extant ceratobranchial and especially epibranchial elongation, as seen in Piciformes.

1.8.2: Description of UWGM 40363

This specimen consists of a single partial skull in left lateral view, with no postcranial elements (Fig. 1.18). The posterior portion of the braincase is missing. The anterior wall of the braincase appears ossified. The nares may overlap with the antorbital fenestra, though a significant amount of breakage obscures that region in the specimen. The mandible is poorly preserved. Bone of the rostral tip is preserved, but posteriorly, only impressions remain. The impression of the posterior ramus of the mandible is deflected ventrally. The scleral ossicles remain articulated in the posterior-most portion of the orbit, and consist of four articulated ossicles and at least one ossicle touching the dorsal-most portion of the skull. A possible scleral ossicle is present below that, near what might be a fragment of the lacrimal.

1.9: SUMMARY OF THE SYSTEMATIC REVISION OF NEW FOSSIL BUTTE MEMBER ZYGODACTYLIDS

UWGM 40705, here referred to *Zygodactylus* n. sp., was tentatively assigned to *Eozygodactylus americanus* by Weidig (2010). UWGM 40705 is strikingly similar in preserved morphology, size, and proportions with the holotype and referred specimen of *Eozygodactylus americanus* and the holotype of Zygodactylus n. sp. However, it shares with the holotype specimen of *Zygodactylus* n. sp. (FMNH PA 726) a mid-shaft protuberance on the anterior margin of metacarpal II (Character 17, Appendix I; 'processus dentiformis', Mayr 2004). A dentiform process is absent in the holotype (USNM 299821) and paratype (WDC-CGR-014) of *Eozygodactylus americanus*, as well as *Primozygodactylus*. However, it is present in *Zygodactylus luberonensis* and *Primoscens minutus*. FMNH PA 770, here referred to *Eozygodactylus americanus*, possesses the elongate, narrow toes and weakly curved pedal unguals seen in *Zygodactylus* n. sp. (FMNH PA 726), in the *Eozygodactylus americanus* paratype (WDC-CGR-014; Weidig, 2010), and *Zygodactylus luberonensis*. These specimens all exhibit the elongate tarsometatarsus and pronounced cnemial crests seen in all known zygodactylids.

FMNH PA 770 exhibits a tibiotarsal length shorter than that the holotype of *Zygodactylus* n. sp. (FMNH PA726), but consistent with the paratype of *Eozygodactylus americanus* (WDC-CGR-014; Table 1.4). Pedal digit lengths (Table 1.5) in the paratype of *Eozygodactylus americanus* and FMNH PA 770 are almost identical. FMNH PA 770 differs from *Zygodactylus* n. sp. and agrees with the *Eozygodactylus americanus* paratype in the ratio of the ungual of digit III to the sum of the length of the remaining phalanges of digit III (Character 38, Appendix I). Referral to *Eozygodactylus americanus* is supported if the referral of the paratype to that species is supported. However, in the absence of more complete specimens the referral of FMNH PA 770 to *Eozygodactylus americanus* remains tentative.

UWGM 40363 and FMNH PA 757 preserve only cranial material, and due to similarities in beak size, narial construction and head shape with the holotype of *Eozygodactylus americanus* and the holotype of *Zygodactylus* n. sp. (FMNH PA 726), as well as similarities with *Primozygodactylus danielsi*, *Primozygodactylus ballmani* and *Primozygodactylus major*, they are here referred to as Zygodactylidae genus indeterminate, species indeterminate. Narial opening size, beak length and cranium length are nearly identical to the dimensions of the holotype of *Zygodactylus* n. sp. (FMNH PA 726) and holotype of *Eozygodactylus americanus* (USNM 299821; Table 1.4). The similarity in the shape and size (Fig. 1.4) of these skulls is striking. UWGM 40363 and FMNH PA 757 share with both the holotype of *Zygodactylus* n. sp. (FMNH PA 726) and the holotype specimen of *Eozygodactylus americanus* (USNM 299821) an approximately rectangular narial opening (Character 1, Appendix I), a ventrally bowed jugal (Character 2, Appendix 1), and a narial opening greater than 50% of the length of the rostrum (Character 3, Appendix I); all of these characters have a restricted distribution in Aves.

1.10: PHYLOGENETIC ANALYSIS ADDRESSING THE RELATIONSHIPS AMONG SPECIES AND SPECIMENS OF ZYGODACTYLIDAE

Thirty-eight characters (Appendix I) for 21 taxa were coded for phylogenetic analysis using MacClade (Maddison and Maddison, 1992). Characters were either assembled from observation or, where noted, previous analyses (i.e., Mayr, 2004 and

Clarke et al., 2009). Additional characters were taken in part from observations by Ashley (1941), Zelenkov (2007), Manegold (2008), Mayr (2008), and Weidig (2010), as noted in Appendix I. Six multistate characters appear to form a natural set of evolutionary steps and were ordered (Slowinski, 1993; Characters 6, 9, 11, 12, 16, and 31, Appendix I). Multiple analyses were run using PAUP*4.0b10 (Swofford, 2003). A branch-and-bound search strategy was used, with 1000 replicates and 100 random sequence additions per replicate (TBR). Iterative outgroup swapping to determine the stability of ingroup relationships, taking into account different hypotheses of the position of Zygodactylidae in Aves, which was a secondary point of inquiry here. Bootstrap support values from 1000 replicates (100 random sequence additions per replicate) were computed, with bootstrap scores greater than 50% noted in Fig. 1.20 a, b and c.

All previously named Zygodactylidae species and FMNH PA 726 (*Zygodactylus* n. sp.) were scored for this analysis (Table 1.6). However, when all taxa and Green River specimens described herein were included, no resolution was found. This was likely due to the presence of so many fragmentary specimens, resulting in terminals with few scored characters, which were operational taxonomic equivalents that served only to decrease resolution (Wiens, 2003). Iterative outgroup swapping was performed with basal parrots (*Nestor* spp.), Piciformes, and two separate passerine terminals, one of which included scorings for both oscines and suboscines and one of which recorded only scorings for the sister taxon of oscines plus suboscines, *Acanthisitta chloris* (Barker et al., 2002; Ericson et al, 2003; Ericson et al., 2006; Suh et al., 2011). Dense sampling of the comparatively species rich crown-clades of Passeriformes and Piciformes was outside the scope of this analysis, and supraspecific terminals were employed for both groups.

Passeriformes scorings were obtained from the following taxa: *Tyrannus tyrannus*, *Thamnophilus caerulescens*, *Corvus bracnyrunchus*, *Menura novahollandiae*

(Table 2.1). These taxa were chosen so as to sample both suboscine and oscine passeriforms. *Acanthisitta chloris* was scored separately, and placed in its own terminal, due to its probable sister-group relationship to the clade containing both oscines and suboscines (Barker et al., 2002; Ericson et al., 2006; Suh et al., 2011). Piciformes scorings were obtained from *Dryocopus pileatus*, *Colaptes auratus*, *Galbula ruficada* and *Chelidoptera tenebrosa* (Table 2.1). Psittaciformes *Nestor meridionalis* and *Nestor notabilis* were chosen for this analysis due to their basal placement within Psittaciformes (Miyaki et. al, 1998; Wright et. al, 2008; Ksepka et. al, 2011). Meristic data were obtained from measurements of *Nestor notabilis* from Livezey (1992), and additional morphological data was obtained from Ksepka et. al (2011) for *Nestor meridionalis*. These scorings were then combined into a supraspecific *Nestor* spp. terminal.

1.11: RESULTS

The results of the previous analyses are presented in Fig. 1.20 (a, b and c). Ingroup topology remained relatively consistent, though when the tree was rooted with Psittaciformes, *Zygodactylus luberonensis* was placed in a polytomy with the Green River Formation Zygodactylidae taxa and the four species of *Primozygodactylus*. *Zygodactylus* n. sp. specimens FMNH PA 726 and FMNH PA 770 were recovered as the sister taxon to a clade comprised of the paratype of *Eozygodactylus americanus* (WDC-CGR-014) and holotype (USNM 299821). In all other outgroup sampling scenarios, the holotype of *Eozygodactylus americanus* (USNM 299821) and paratype (WDC-CGR-014) specimens were recovered in a clade as a sister taxon to *Zygodactylus* n. sp. Relationships amongst species of *Primozygodactylus* were widely varied in each analysis, sometimes forming a clade (20b:C, D), but more often individual taxa were nested within other species of *Primozygodactylus* (20c:E, 20a:A).

1.12: DISCUSSION

FMNH PA 726 shares a number of synapomorphies of *Zygodactylus* within the Zygodactylidae (e.g., plantarly prominent accessory trochlea on Metatarsal IV, and the presence of a marked sulcus on the plantar surface of a lateral convexity just proximal to the metatarsal IV trochlea). FMNH PA 726 is recognized as the holotype specimen of a new species within *Zygodactylus*, *Zygodactylus* n. sp.. It is the earliest known occurrence of *Zygodactylus*, previously known only from European Oligocene and Miocene deposits. Because the paratype and holotype specimens of *Eozygodactylus americanus* (WDC-CGR-014 and USNM 299821) were not available for direct study, morphological inferences are restricted to images and observations published by Weidig (2010). Although USNM 299821 and WDC-CGR-014 share a number of similarities with *Zygodactylus* n. sp., phylogenetic analyses and character data are consistent with *Eozygodactylus americanus* as a distinct taxon. For example, a dentiform process appears absent in the holotype and paratype of *Eozygodactylus americanus* and femoral measurements are distinct (in the paratype specimen) from *Zygodactylus* n. sp. The nearly-identical skull morphology of *Zygodactylus amercanus* holotype USNM 299821 and FMNH PA 726, as well as the elongate tarsometatarsus, thin toes and weakly curved unguals of WDC-CGR-014, and the presence of an intermetacarpal process in all three specimens support referral to *Zygodactylus*.

UWGM 40705 was referred to *Eozygodactylus americanus* by Weidig (2010), a referral that is not supported by morphological evidence, especially when compared with FMNH PA 726. While UWGM 40705 is poorly preserved, a distinct dentiform process is visible on the carpometacarpus, present in *Zygodactylus* n. sp. and *Primoscens minutus* (Mayr, 2008) but absent in *Eozygodactylus americanus* and *Primozygodactylus* (Mayr, 1998). UWGM 40705 has no scoreable characters in common with *Zygodactylus ignotus*, but while an assignment to this taxon cannot be ruled out, *Zygodactylus ignotus* was from the Lower Miocene of Germany (Ballman, 1969a), making assignment to this taxon unlikely.

It was noted by Mayr and Zelenkov (2009) that *Zygodactylus luberonensis* possessed proportionally longer legs than other Eocene zygodactylids, straighter ungual phalanges and a pedal digit III measuring only slightly less that the tarsometatarsus length. *Zygodactylus* n. sp. and the paratype of *Eozygodactylus americanus* (WDC-CGR-014) have straight pedal ungual phalanges and a pedal digit III/tarsometatarsus length ratio of 0.89 and 0.96 respectively (Table 1.2). A ratio of 0.90 is seen in *Zygodactylus luberonensis* (Mayr, 2008). Further, as in *Zygodactylus luberonensis*, the trochlea accessoria is more bulbous than the trochlea accessoria of *Pici* or other zygodactylids. Thus, the expanded, posteriorly-extending trochlea does not necessarily represent, as Zelenkov (2007: 295) proposed, a "continuous evolutionary sequence" through time between *Primozygodactylu*s and *Zygodactylus*, but instead suggests that both tarsometatarsal modifications existed concurrently within Zygodactylidae.

As *Zygodactylus* n. sp. and *Eozygodactylus americanus* resemble *Zygodactylus luberonensis* in some limb proportions (Table 1.2), bulbous accessory trochlea and weakly curved toes, it is possible that these taxa occupied a similar ecological niche. Rüggerberg (1960) suggested that the presence of elongate pedal phalanges and weakly curved unguals was correlated with primarily terrestrial taxa (e.g., sandpipers, roadrunners). Given the pronounced gracility of these taxa's phalanges, and the elongate pedal phalanges, a more terrestrial ecology is thus a possibility. However, Mayr (2008) pointed out that a specialized food-manipulation use related to the highly modified accessory trochlea is a possible explanation for the zygodactyl condition.

The results of the analysis and the presence of apomorphies (e.g., a marked convexity on the lateral tarsometatarsal margin of the anterior margin of trochlea metatarsi IV, Character 28, Appendix I) lend strong support to the inclusion of FMNH PA 726 within *Zygodactylus*. The results also lend support to an affiliation of holotype and paratype specimens of *Eozygodactylus americanus* (USNM 299821 and WDC-CGR-014) with *Zygodactylus*, because these specimens possess the elongate, delicate toes and weakly curved pedal unguals (Character 37, Appendix I), a large dorsal supracondylar process separated from the shaft by a notch (Character 9, Appendix I), and overall meristic similarities (Tables 1.2, 1.3, 1.4, 1.5). More detailed analyses of those specimens may reveal that *Eozygodactylus* is a junior synonym of *Zygodactylus*. Given the presence of varied measurements between the holotype and the paratype of *Eozygodactylus americanus*, and the absence of hind limbs for comparison in USNM 299821, further analyses may indicate that these two specimens do not represent a single species.

1.13: SUMMARY AND CONCLUSIONS

Although interrelationships amongst Zygodactylidae remain poorly understood, Zygodactylidae was recovered as a monophyletic clade in this analysis. More detailed taxon sampling and the discovery of future specimens will assist in bringing clarity to our understanding of relationships within Zygodactylidae. *Zygodactylus* n. sp. is recovered persistently in a clade with the other Green River Formation Zygodactylidae. The apomorphy-based assignment of FMNH PA 726 and UWGM 40705 to *Zygodactylus* greatly increases the known biogeographical range of *Zygodactylus*, which had only previously been found in European deposits (Mayr, 2008). Physical examinations of the holotype and paratype of *Eozygodactylus americanus* (USNM 299821 and WDC-CGR-014 respectively) will determine whether *Eozygodactylus* is a junior synonym of *Zygodactylus*.

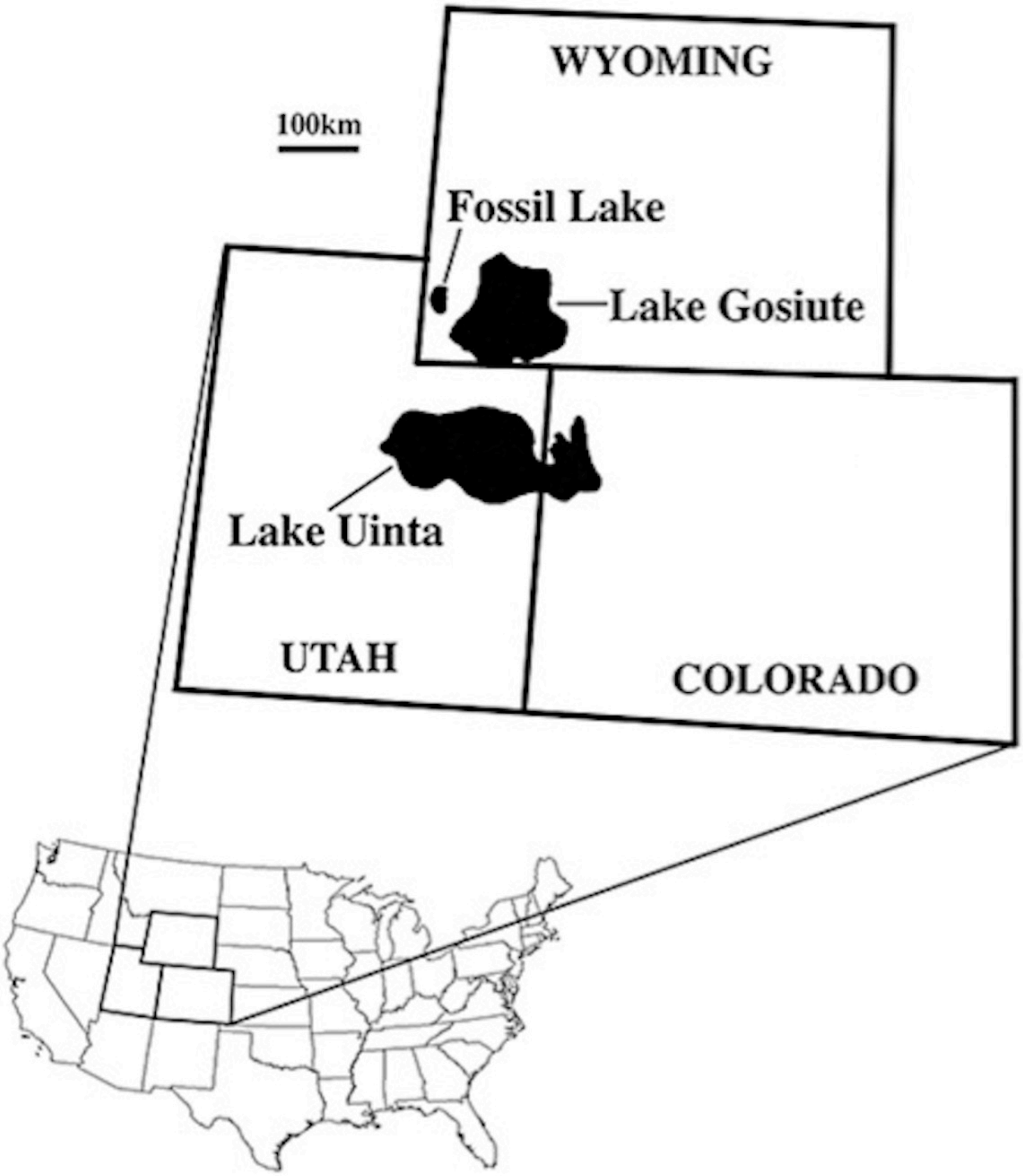


Figure 1.1: Map of the USA showing the Green River lake system during the late early Eocene (Ksepka and Clarke, 2010; reprinted with permission of the authors).

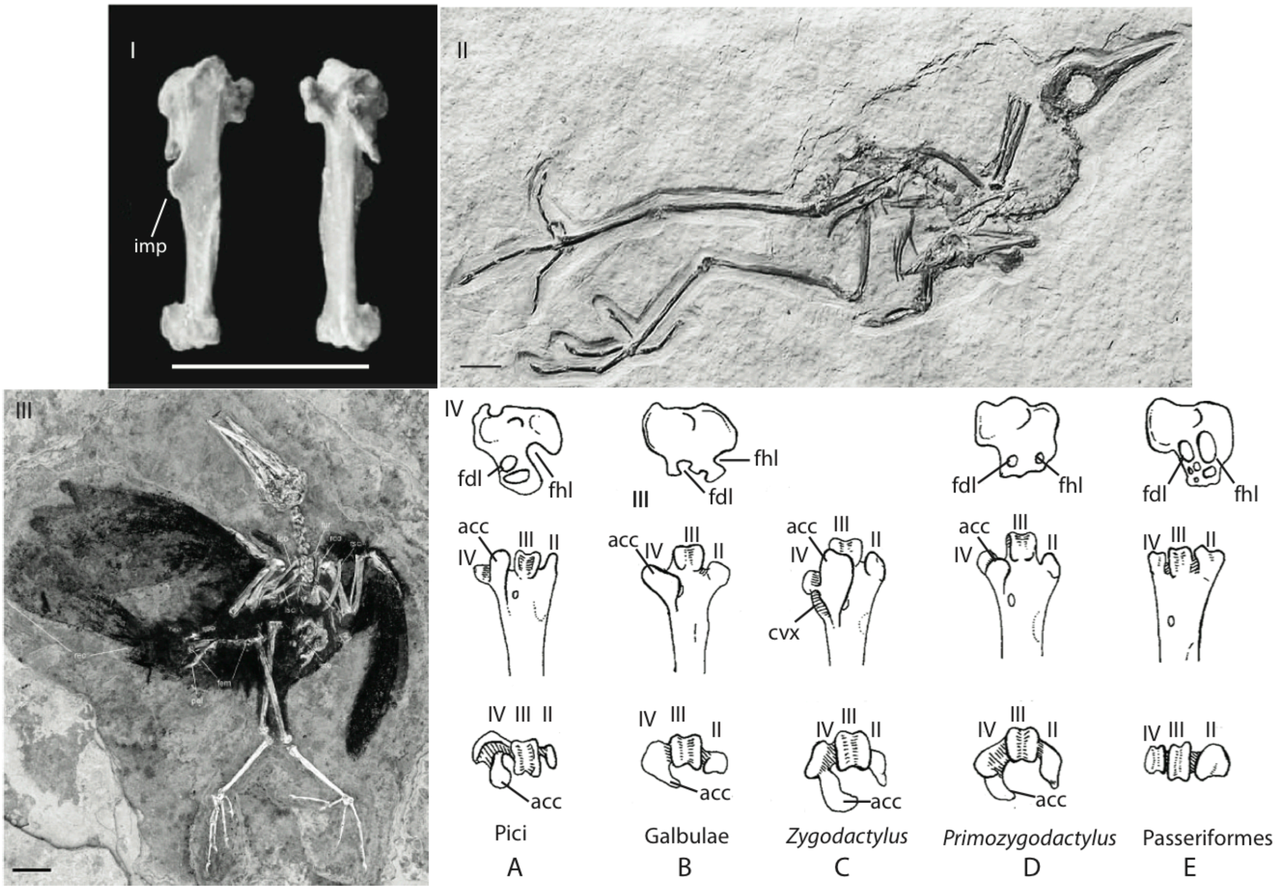


Figure 1.2: I: BMNH A 4681, right carpometacarpus of *Primoscens minutus* Harrison and Walker 1977 from the Early Eocene London Clay. Abbreviation: **imp** – intermetacarpal process. A) posterodorsal view; B) anteroventral view. Scale bar is equal to 0.5cm. Image from Mayr (2009). II: WDC-CGR-014, paratype of *Eozygodactylus americanus* Weidig 2010 (image modified from Weidig, 2010). Scale bar is equal to 1cm. The skull is fabricated. III: SMF Av 519, *Zygodactylus luberonensis* Mayr 2008, from the Early Oligocene of southern France (image from Mayr, 2008). Scale bar is equal to 10mm. Fig. IV Proximal, palmar and distal views of tarsometatarsi. Figure modified from Mayr (2004). A) Pici (Piciformes); B) Galbulae (Piciformes); C) *Zygodactylus*; D) *Primozygodactylus*; E) Passeriformes. Note the bulbous metatarsal IV accessory trochlea typical of *Zygodactylus*.

Figure 1.3: Photograph of FMNH PA 726, the holotype of *Zygodactylus* n. sp., from the Green River Formation in Wyoming. Shown in left lateral view. Scale bar equals 1cm.

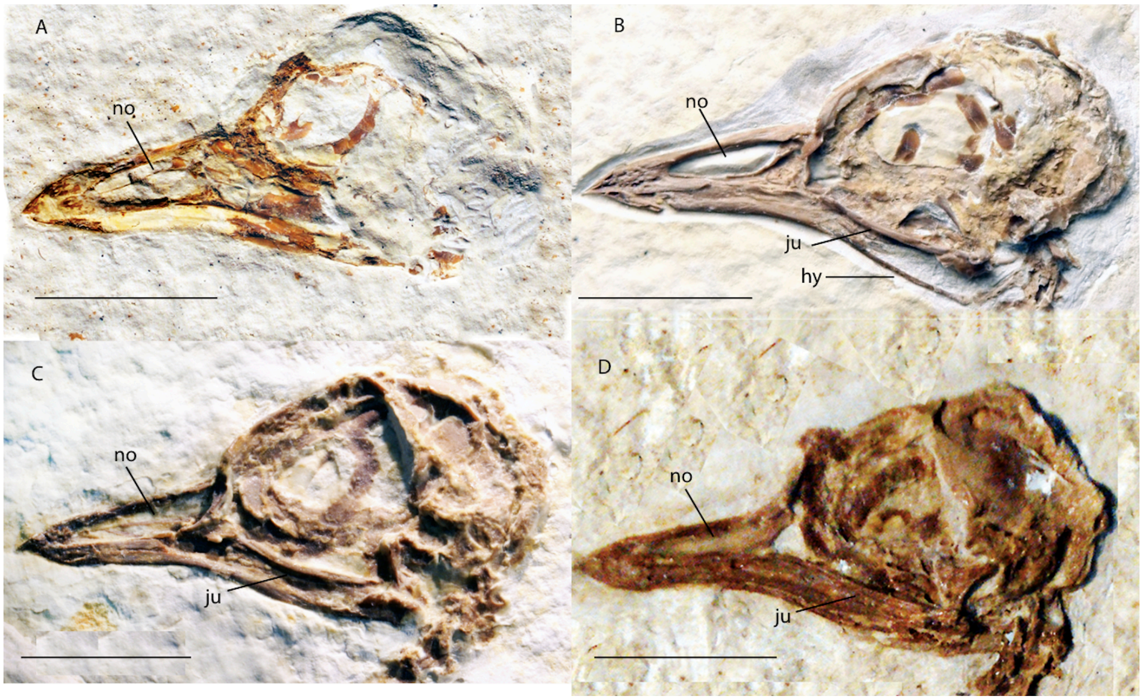


Figure 1.4: Crania of Green River Formation specimens referred to Zygodactylidae, shown in left lateral view. A) UWGM 40363, referred to Zygodactylidae gen. indet. sp. indet. B) FMNH PA 757, referred to Zygodactylidae gen. indet sp. indet.; C) FMNH PA 726, *Zygodactylus* n. sp.; D) USNM 299821, *Eozygodactylus americanus* Weidig 2010. Abbreviations: **hy** – hyoid; **ju** – jugal; **no** – narial opening. Scale bar equals 1cm.

Figure 1.5: Pectoral girdle of FMNH PA 726, *Zygodactylus* n. sp. Abbreviations: **cor** – coracoid; **ltr** – lateral trabecula; **mtr** – medial trabecula; **sca** – scapula. Scale bar is equal to 1cm.

Figure 1.6: Pelvic girdle of FMNH PA 726, *Zygodactylus* n. sp. Abbreviations: **ccc** – cranial cnemial crest; **isc** – ischium; **lfe** – left femur; **pai** – preacetabular ilium; **pub** – pubis. Scale bar is equal to 1cm.

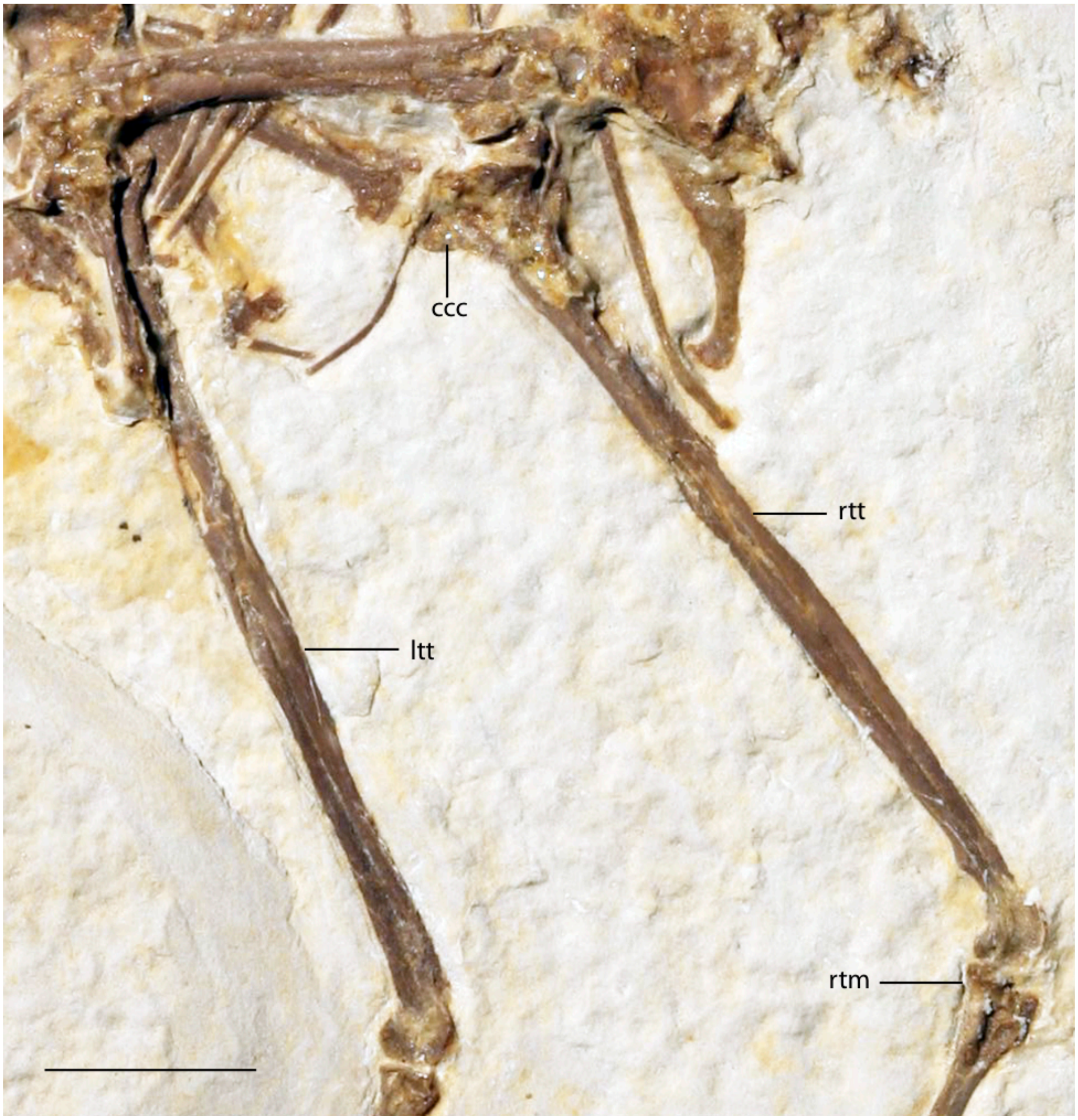


Figure 1.7: Tibiotarsi of FMNH PA 726, *Zygodactylus* n. sp. Abbreviations: **ccc** – cranial cnemial crest; **itt** – left tibiotarsus; **rtm** – right tarsometatarsus; **rtt** – right tibiotarsus. Scale bar is equal to 1cm.

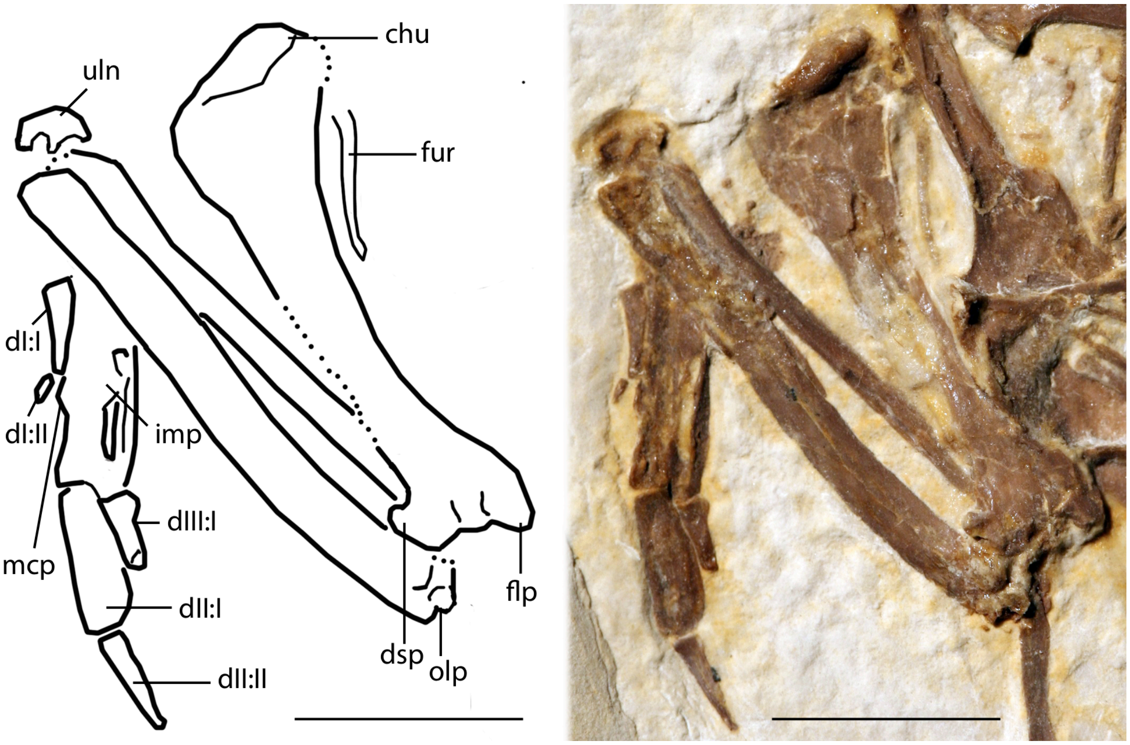


Figure 1.8: Line-drawing and photo of the left forelimb of FMNH PA 726, *Zygodactylus* n. sp. Note the distinct dorsal supracondylar process and large intermetacarpal process. Abbreviations: **chu** – caput humerus; **dI:I** – manual digit one, phalanx one; **dI:II** – manual digit one, phalanx two; **dIII:I** – manual digit three, phalanx one; **dII:I** – manual digit two, phalanx one; **dII:II** – manual digit two, phalanx two; **dsp** – dorsal supracondylar process; **flp** – flexor process; **mpr** – metacarpal protuberance ('dentiform process' of Mayr, 1998); **olp** – olecranon process; **uln** – ulnare. Scale bar is equal to 1cm.

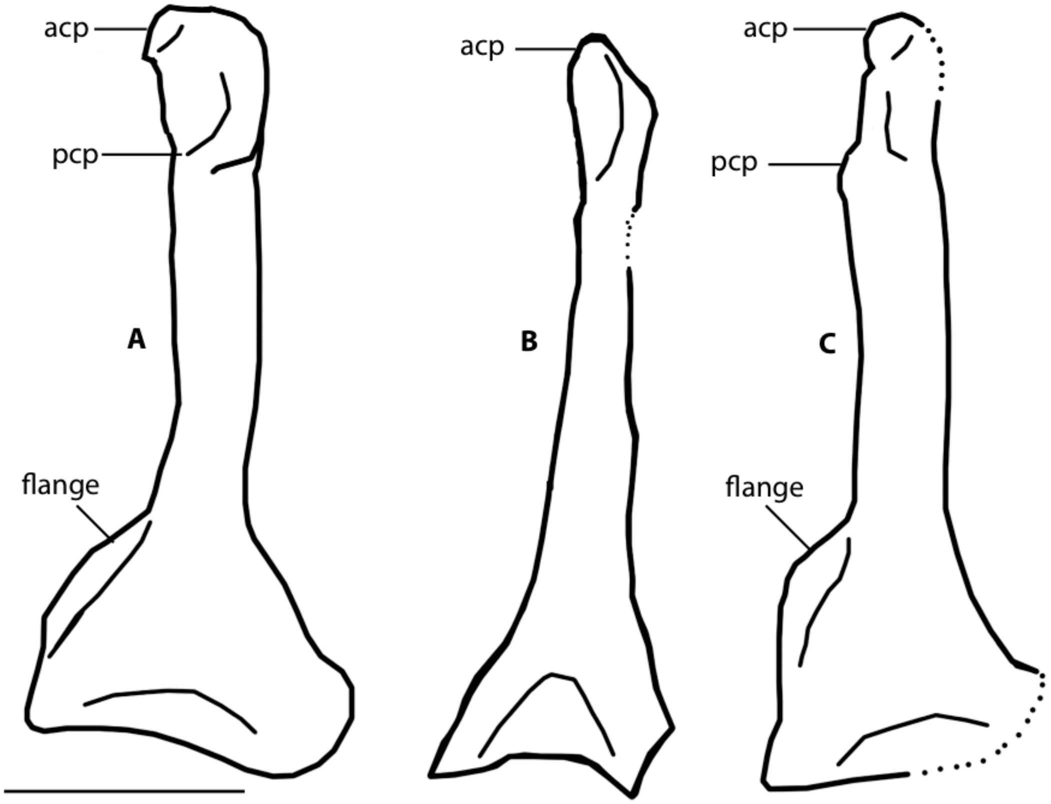


Figure 1.9: Dorsal view of right coracoids from: A, *Primozygodactylus danielsi*, SMF 2552 (Mayr, 1998)*;* B, *Zygodactylus luberonensis*, SMF Av 519 (Mayr, 2008)*;* C, FMNH PA 726, *Zygodactylis* n. sp. Note flange on medial side of coracoid. Abbreviations: **acp** – acrocoracoid process; **prp** – procoracoid process. Scale bar is equal to 5mm.

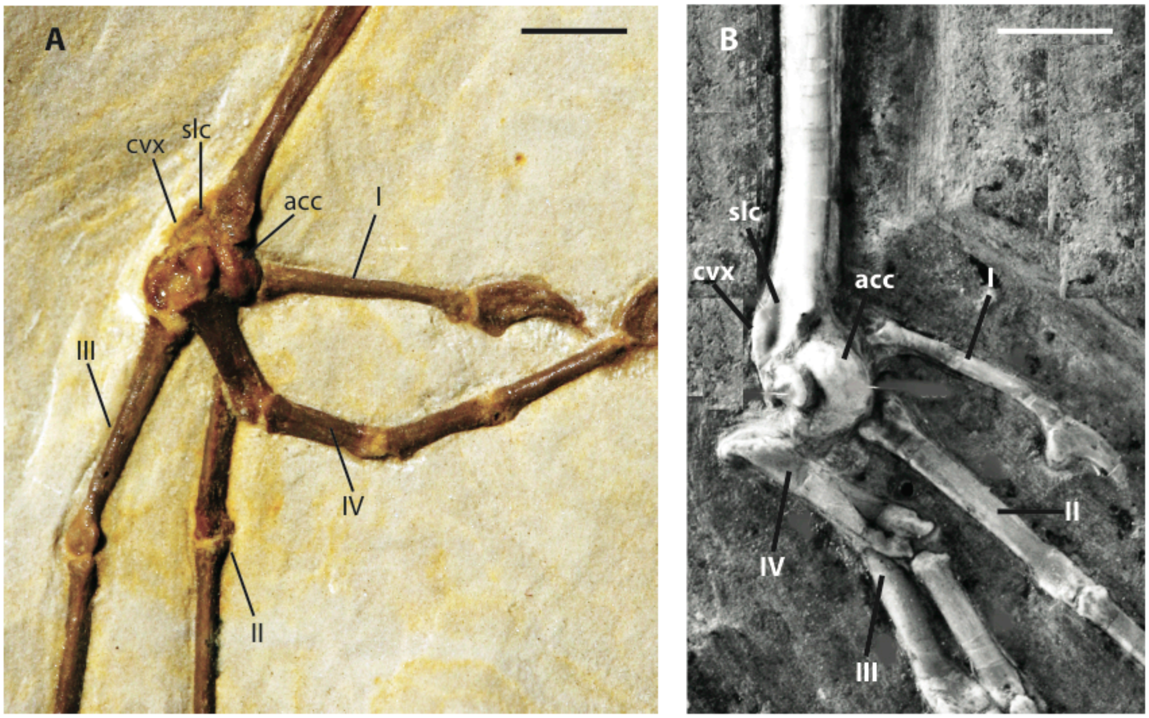


Figure 1.10: Distal left tarsometatarsi in lateroplantar view. A) FMNH PA 726, *Zygodactylis* n. sp.; B) *Zygodactylus luberonensis*. SMF Av 519. Abbreviations: **I, II, III, IV**: digits one, two, three, and four, respectively; **acc**: trochlea accessoria; **cvx**: convexity on anterolateral margin; **slc**: sulcus on plantar surface of anterolateral convexity (a synapomorphy of *Zygodactylus luberonensis* and *Zygodactylus* n. sp.; photograph of B from Mayr, 2008). Scale bar is equal to 5mm.

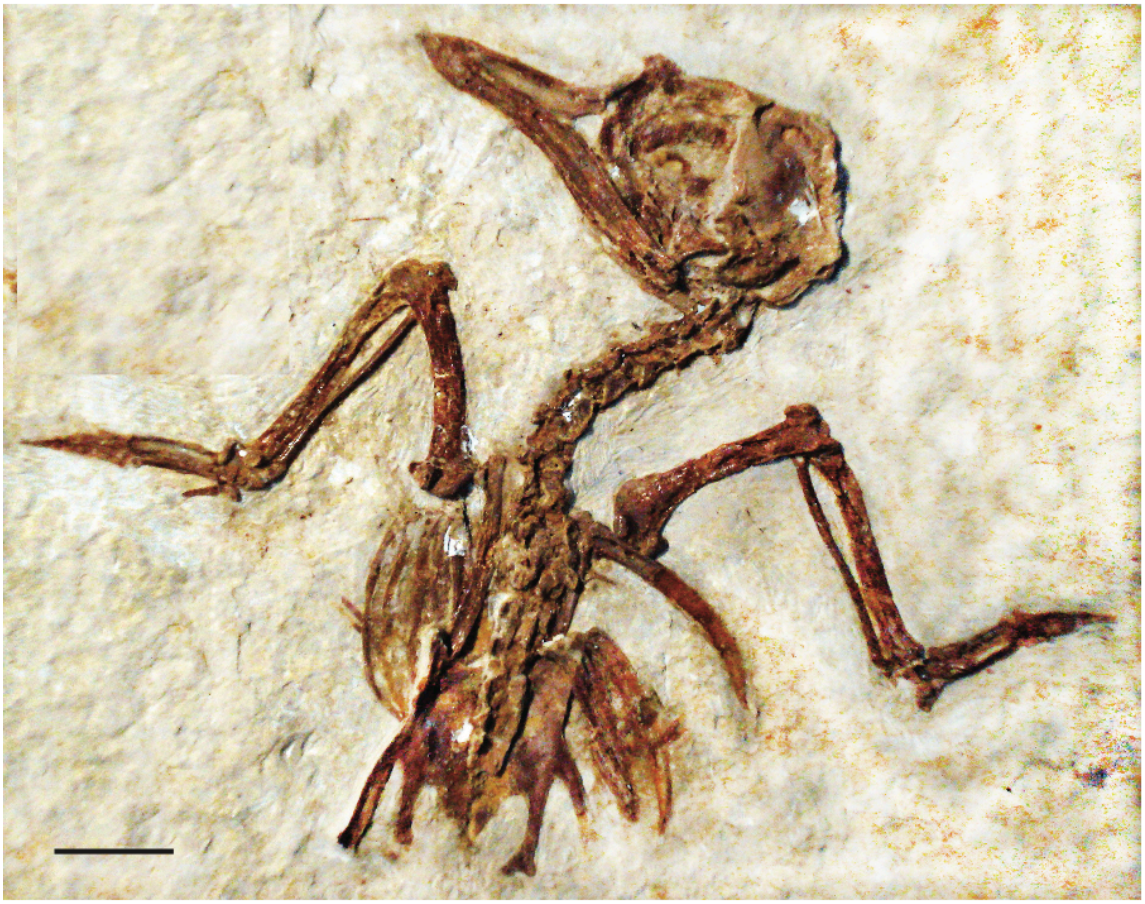


Figure 1.11: USNM 299821, holotype specimen of *Eozygodactylus americanus* Weidig 2010. Scale bar is equal to 1cm.

Figure 1.12: UWGM 21421, Zygodactylidae gen. indet. Weidig 2010. Note the massive cranial cnemial crest and the retroverted digit I and digit IV. Abbreviations: **ccc** – cranial cnemial crest; **DI, DII, DIII, DIV**: digits one, two, three, and four, respectively. Scale bar is equal to 1cm.

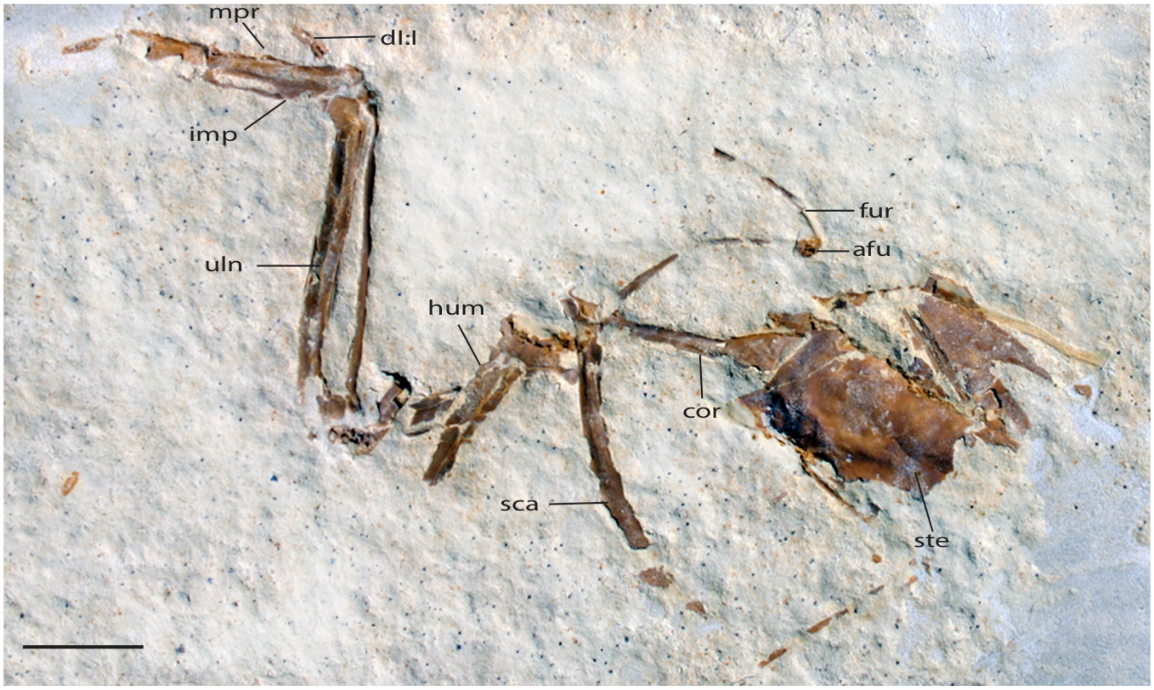


Figure 1.13: UWGM 40705 slab a, referred to *Zygodactylus* n. sp. Right forelimb, sternum and pectoral elements. Abbreviations: **afu** – apophysis furculae; **cor** – coracoid; **dI:I** – digit one, phalanx one; **fur** – furcula; **uln** – ulna; **hum** – humerus; **imp** – intermetacarpal process; **mpr –** metacarpal process; **sca** – scapula; **ste** – sternum. Scale bar is equal to 1cm.

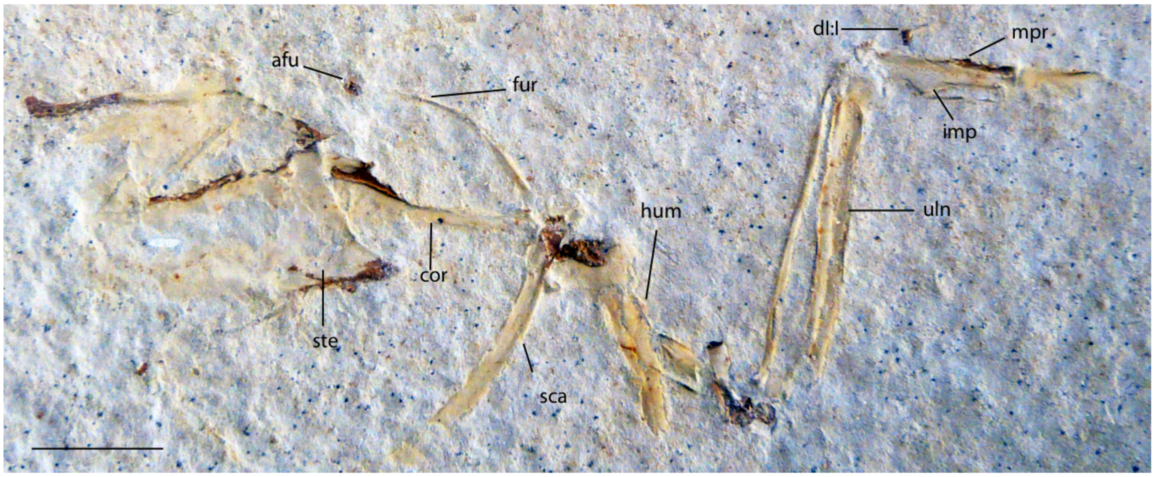


Figure 1.14: UWGM 40705 slab b, referred to *Zygodactylus* n. sp. Right forelimb, sternum and pectoral elements. Abbreviations: **afu** – apophysis furculae; **cor** – coracoid; **dI:I** – digit one, phalanx one; **fur** – furcula; **uln** – ulna; **hum** – humerus; **imp** – intermetacarpal process; **mpr –** metacarpal process; **sca** – scapula; **ste** – sternum. Scale bar is equal to 1cm.

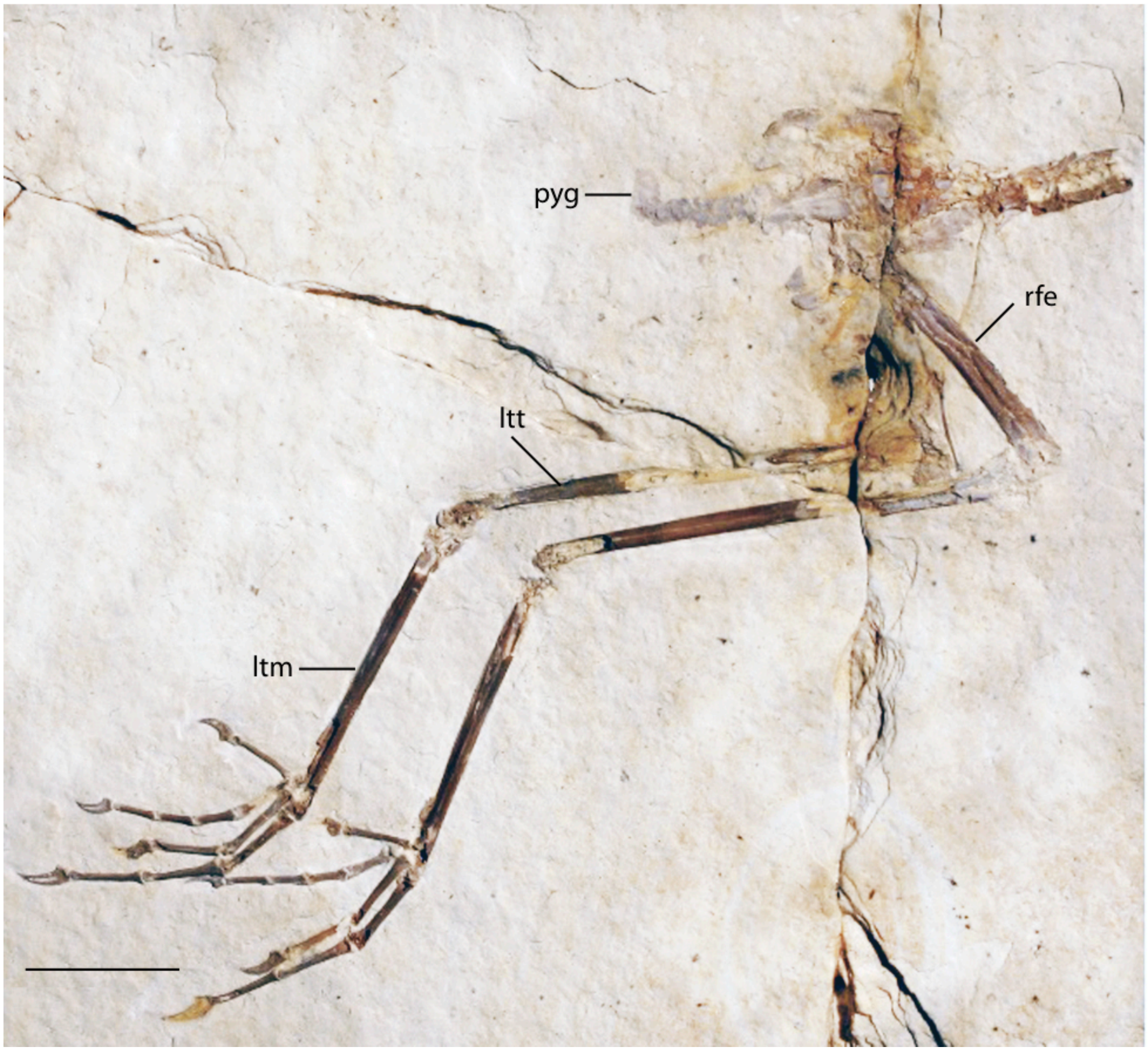


Figure 1.15: FMNH PA 770 slab A, tentatively referred to *Eozygodactylus americanus* Weidig 2010. Exposed in right lateral view. Abbreviations: **ltm** – left tarsometatarsus; **ltt** – left tibiotarsus; **pyg** – pygostyle; **rfe** – right femur. Scale bar is equal to 1cm.

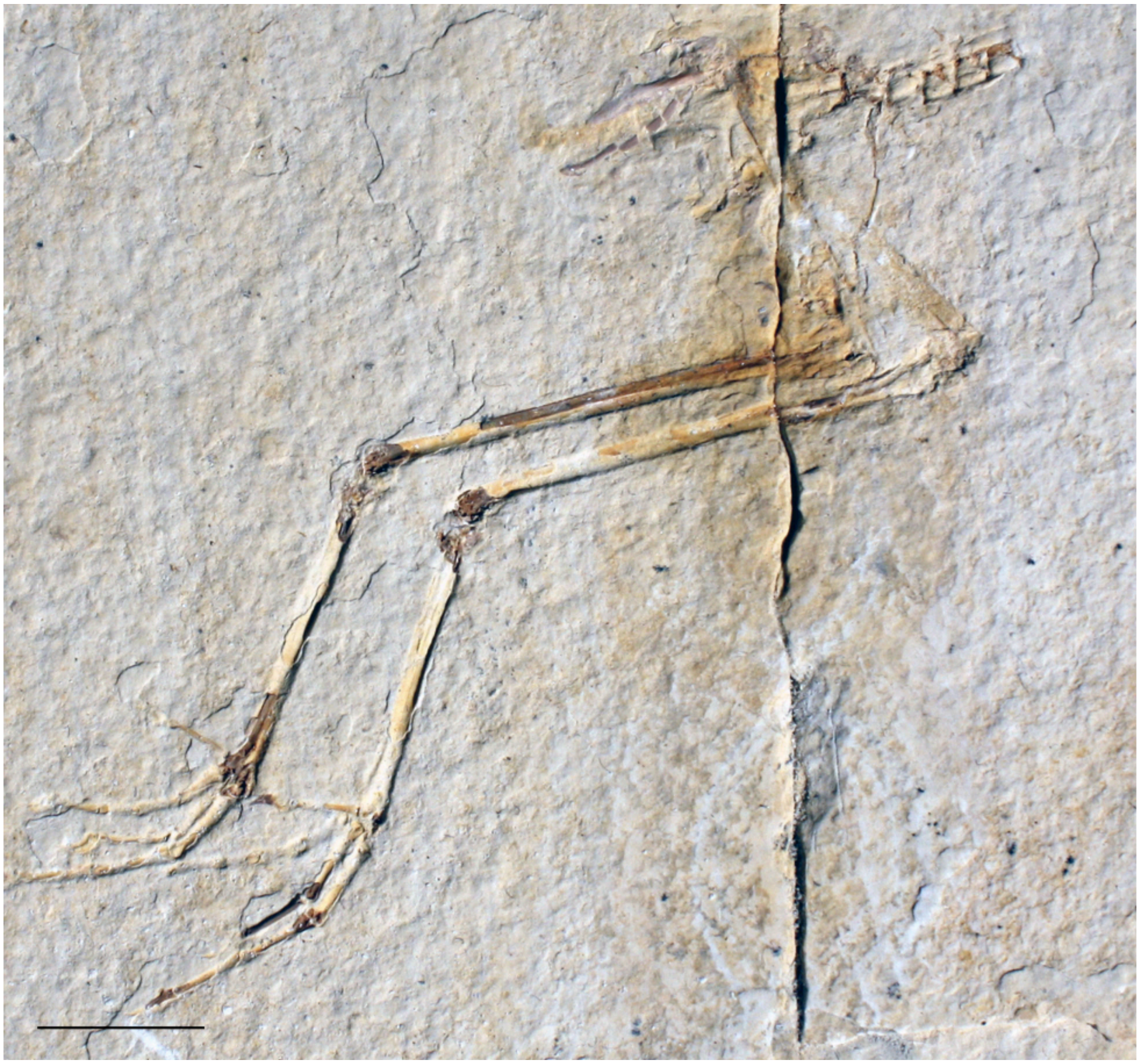


Figure 1.16: FMNH PA 770 slab B, tentatively referred to *Eozygodactylus americanus* Weidig 2010. Exposed in right lateral view. Scale bar is equal to 1cm.

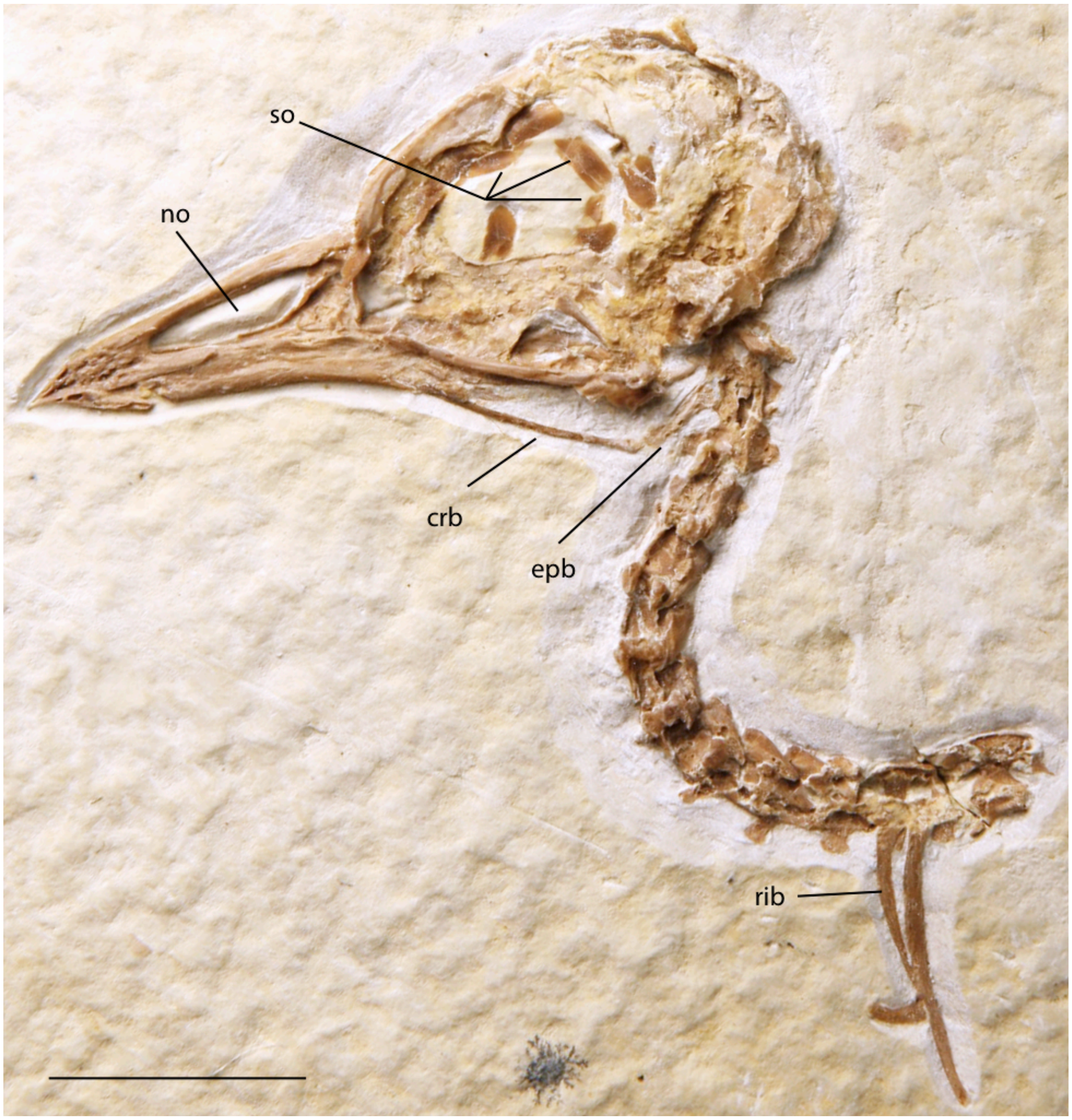


Figure 1.17: FMNH PA 757, referred to Zygodactylidae gen. indet sp. indet. Abbreviations: **crb** – ceratobranchial; **epb** – epibranchial; **no** – narial opening; **so** – scleral ossicles. Scale bar equals 1cm.

Figure 1.17: FMNH PA 757, referred to Zygodactylidae gen. indet sp. indet. Abbreviations: **crb** – ceratobranchial; **epb** – epibranchial; **no** – narial opening; **so** – scleral ossicles. Scale bar equals 1cm.

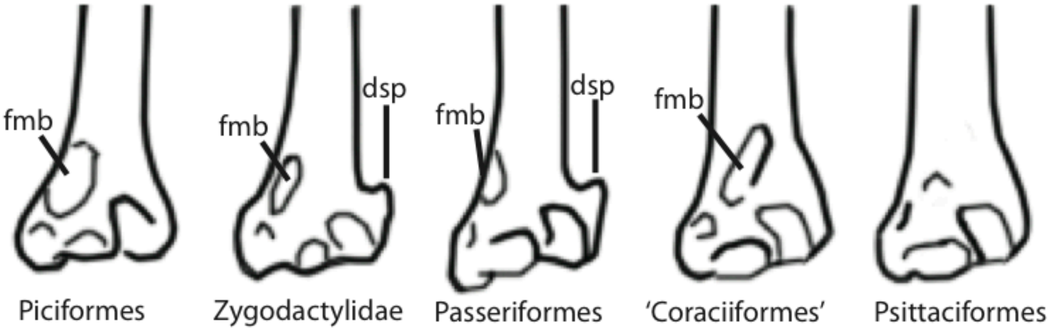


Figure 1.19: Distal end of left humeri (anterior view). Note medially situated scar on the origin of the *m. brachialis* in Zygodactylidae and Passeriformes (Character 43, Appendix II) and prominent dorsal supracondylar process of both Passeriformes and Zygodactylidae (Character 44). Abbreviations: **fmb** –*m. brachialis* fossa; **dsp** – dorsal supracondylar process. Specimens used: Piciformes: *Dryocopus pileatus*; Zygodactylidae: *Zygodactylus grivensis* (from Mayr, 2004); Passeriformes: *Menura novaehollandiae*; 'Coraciiformes': *Coracias caudata*; Psittaciformes: *Lorius garrulus*.

Figure 1.20a: Strict consensus trees of branch-and-bound analyses of named zygodactylid taxa. Each tree represents an iterative outgroup swap. Bolded branches indicate taxa from the Green River Formation, and bootstrap values are noted. A) 'Caprimulgiformes' set as outgroup, with all outgroup taxa included. MPTs=8, TL=80, CI=0.588, RI=0.612; B) Supraspecific terminal representing oscine and suboscine Passeriformes is rooted as the outgroup. MPTs=3, TL=43, CI=0.814, RI=0.778.

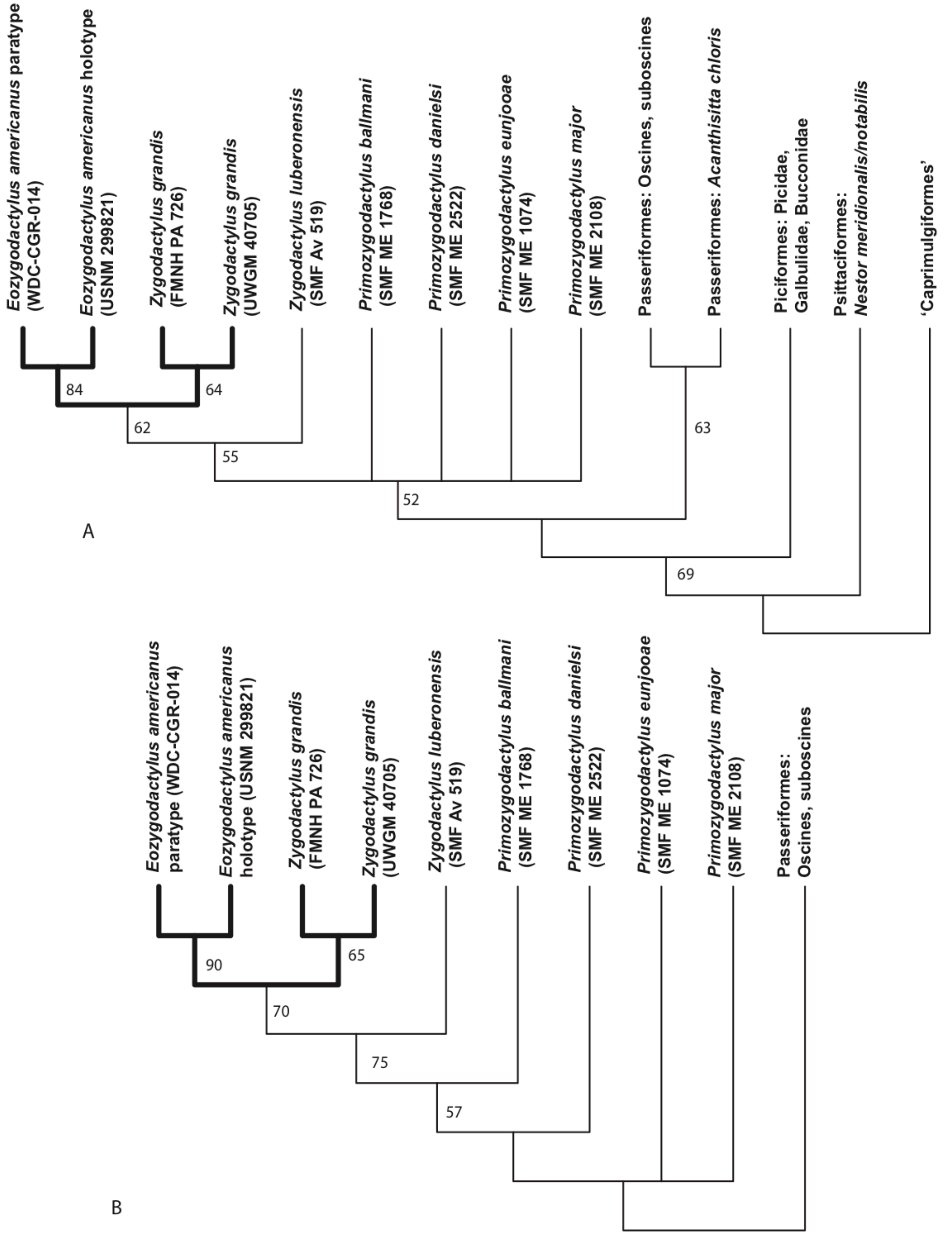
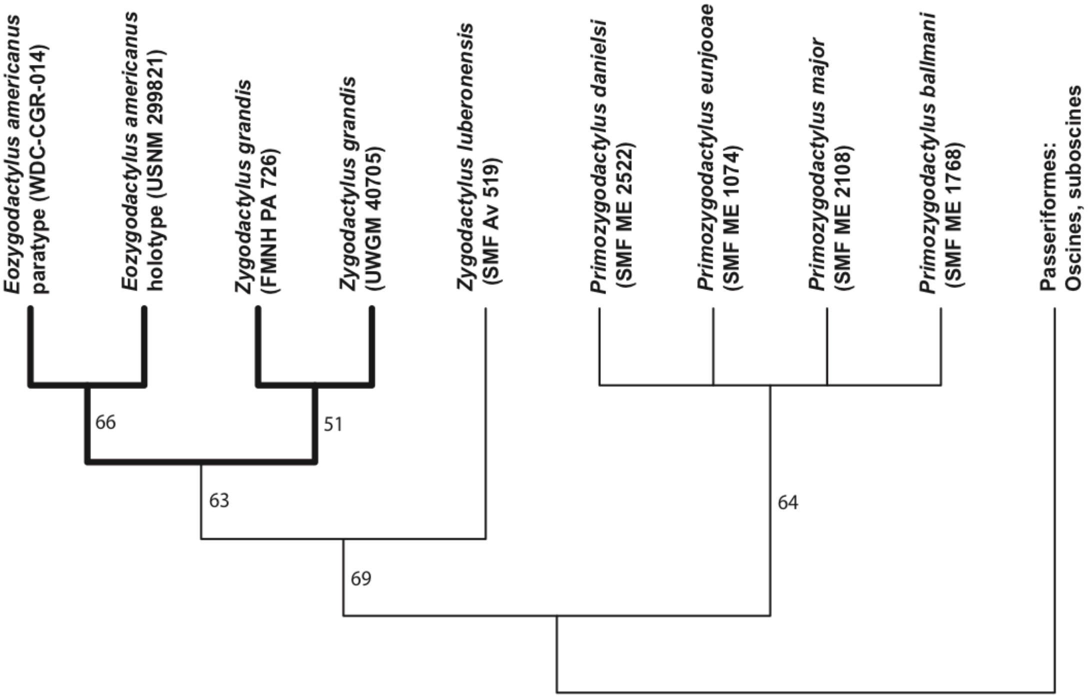
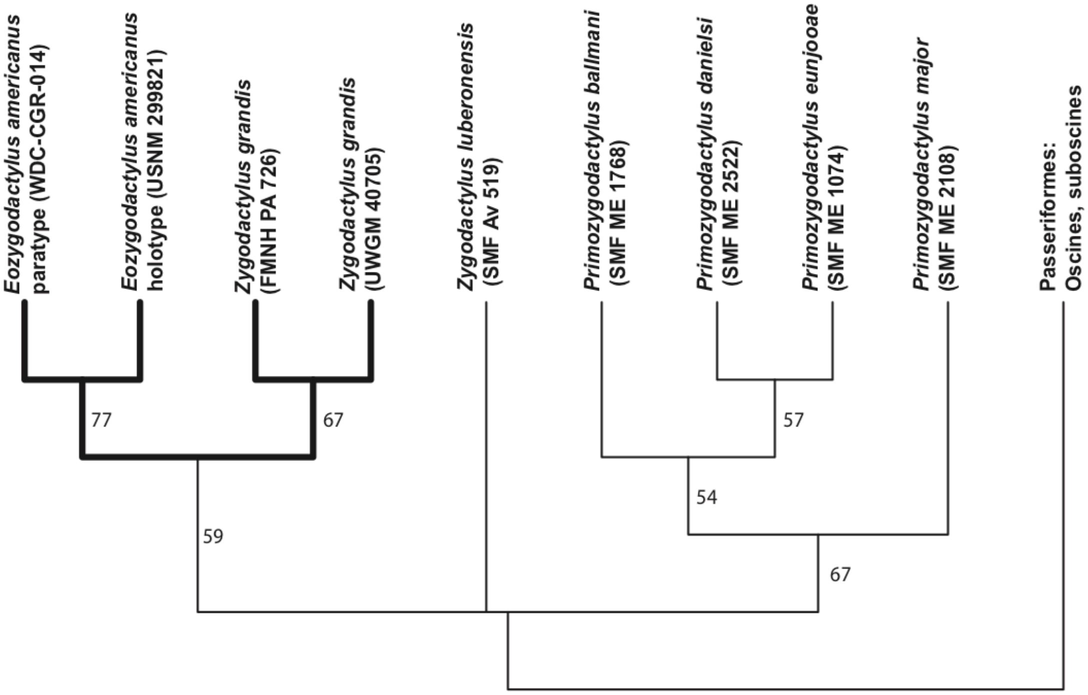

Eozygodactylus americanus paratype (WDC-CGR-014)
Eozygodactylus americanus holotype (USNM 299821)
Zygodactylus grandis (FMNH PA 726)
Zygodactylus grandis (UWGM 40705)
Zygodactylus luberonensis (SMF Av 519)
Primozygodactylus ballmani (SMF ME 1768)
Primozygodactylus danielsi (SMF ME 2522)
Primozygodactylus eunjooae (SMF ME 1074)
Primozygodactylus major (SMF ME 2108)
Passeriformes: Oscines, suboscines
Passeriformes: *Acanthisitta chloris*
Piciformes: Picidae, Galbulidae, Bucconidae
Psittaciformes: *Nestor meridionalis/notabilis*
'Caprimulgiformes'
84
64
62
55
52
63
69
A
Eozygodactylus americanus paratype (WDC-CGR-014)
Eozygodactylus americanus holotype (USNM 299821)
Zygodactylus grandis (FMNH PA 726)
Zygodactylus grandis (UWGM 40705)
Zygodactylus luberonensis (SMF Av 519)
Primozygodactylus ballmani (SMF ME 1768)
Primozygodactylus danielsi (SMF ME 2522)
Primozygodactylus eunjooae (SMF ME 1074)
Primozygodactylus major (SMF ME 2108)
Passeriformes: Oscines, suboscines
90
65
70
75
57
B

Figure 1.20b: Strict consensus cladograms from analyses of specimens of named zygodactylid taxa and specimens of the proposed new species. Each tree represents an iterative outgroup swap. Bolded branches indicate taxa from the Green River Formation, and bootstrap values are noted. C) *Acanthisitta chloris*, sister taxon to the group containing oscine and suboscine Passeriformes (e.g., Ericson, 2004) rooted as outgroup. MPTs=7, L=40, CI=0.875, RI=0.833. D) Supraspecific node representing combined scorings for *Nestor meridionalis* and *Nestor notabilis* rooted as outgroup. MPTs=5, L=48, CI=0.854, RI=0.781.


Eozygodactylus americanus paratype (WDC-CGR-014)
Eozygodactylus americanus holotype (USNM 299821)
Zygodactylus grandis (FMNH PA 726)
Zygodactylus grandis (UWGM 40705)
Zygodactylus luberonensis (SMF Av 519)
Primozygodactylus danielsi (SMF ME 2522)
Primozygodactylus eunjooae (SMF ME 1074)
Primozygodactylus major (SMF ME 2108)
Primozygodactylus ballmani (SMF ME 1768)
Passeriformes: Oscines, suboscines
66
51
63
69
64

C


Eozygodactylus americanus paratype (WDC-CGR-014)
Eozygodactylus americanus holotype (USNM 299821)
Zygodactylus grandis (FMNH PA 726)
Zygodactylus grandis (UWGM 40705)
Zygodactylus luberonensis (SMF Av 519)
Primozygodactylus ballmani (SMF ME 1768)
Primozygodactylus danielsi (SMF ME 2522)
Primozygodactylus eunjooae (SMF ME 1074)
Primozygodactylus major (SMF ME 2108)
Passeriformes: Oscines, suboscines
77
67
57
54
59
67

D

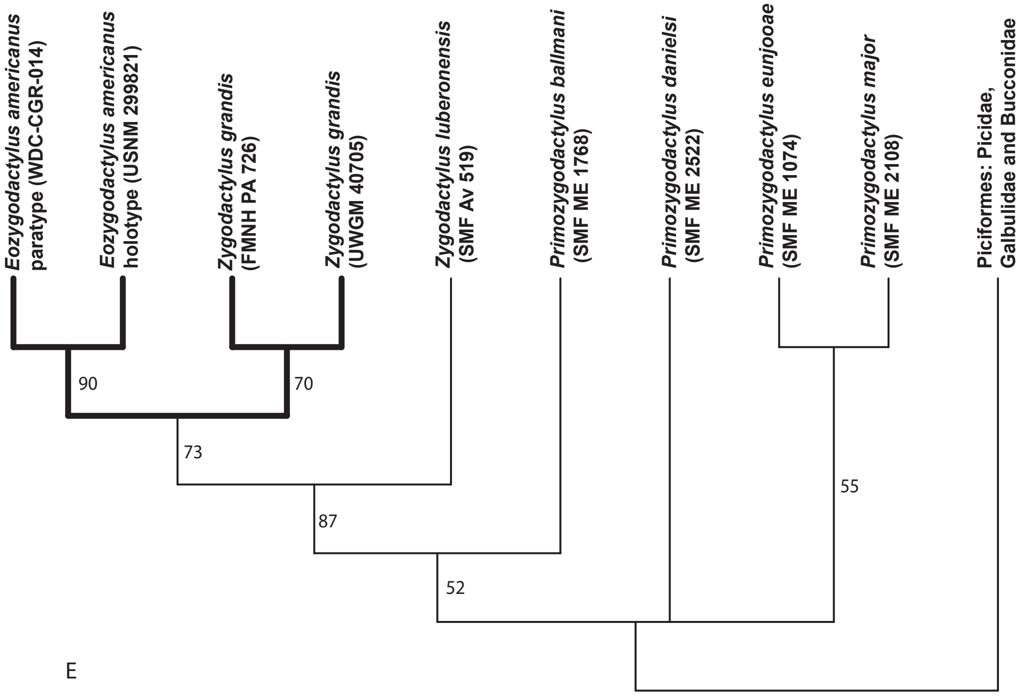


Figure 1.20c: Strict consensus cladogram resulting from a branch-and-bound analysis of named zygodactylid taxa. Bolded branches indicate taxa from the Green River Formation, and bootstrap values are noted. E) Supraspecific node representing Piciformes rooted as outgroup. MPTs=1, L=43, CI=0.814, RI=0.765. For all trees except B, a clade is formed by *Zygodactylus luberonensis*, *Z.* n. sp. and the holotype and paratype of *Eozygodactylus americanus*.

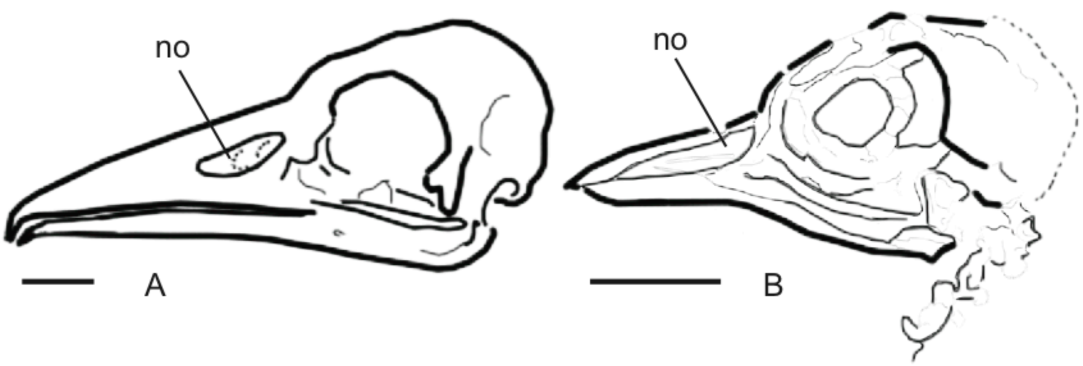


Figure 1.21: Line drawings of A) *Coracias garrulus*, and B) the holotype of *Zygodactylus* n. sp., from the Green River Formation in Wyoming. Shown in left lateral view. Note the ovoid narial opening (state 1, Appendix I) in A and the semi-rectangular narial opening (state 0, Appendix I) in B. Scale bars equal 1cm.

Table 1.1: Previous assessments of the affinities of taxa within Zygodactylidae.

Taxon	**Source**	**Taxonomic assignment**
Zygodactylus ignotus, Z. grivensis	Ballman, 1969a, b	Unsure, *Z. ignotus* possibly passeriform
Zygodactylus	Harrison and Walker, 1977	Piciformes
'Primoscenidae'	Harrison and Walker, 1977	Passeriformes
Zygodactylus	Simpson and Cracraft, 1981	Piciformes
'Primoscenidae'	Mayr, 1998	Piciformes
Zygodactylidae *sensu* Harrison and Walker 1977 + 'Primoscenidae'	Mayr, 2004	Sister clade to Passeriformes
Zygodactylidae *sensu* Mayr 2008	Mayr, 2008	Sister clade to Passeriformes

Table 1.2: Ratios of measurements for European zygodactylids and North American zygodactylids. Abbreviations: **CM** – Carpometacarpus; **F** - Femur; **HU** - Humerus; **TM** - Tarsometatarsus; **TT** - Tibiotarsus; **UL** – Ulna.

	HU:UL	**HU:CM**	**HU:F**	**HU:TM**	**UL:TT**	**UL:TM**	**CM:TM**	**TT:TM**
Eozygodactylus americanus, (holotype, USNM 299821)	0.88	1.91	-	-	-	-	-	-
Eozygodactylus americanus, (paratype WDC-CGR-014)	0.94	1.95	0.87	0.79	0.56	0.83	0.40	1.40
Zygodactylus n. sp. (holotype, FMNH PA 726)	0.96	2.20	1.23	0.87	0.57	0.92	0.40	1.57
Primozygodactylus danielsi (holotype, SMF-ME 2522)	0.88	2.13	1.0	0.89	0.72	1.02	0.42	1.43
Primozygodactylus major (SMF-ME 2108)	0.92	2.24	1.15	1.03	0.79	1.11	0.46	1.41
Primozygodactylus ballmani (SMF-ME 1768)	0.88	2.23	1.0	0.84	0.72	0.95	0.38	1.33
Zygodactylus luberonensis (holotype, SMF Av 519)	0.95	2.0	0.87	0.70	0.52	0.70	0.35	1.42

Table 1.3: Measurements of Green River Formation and European zygodactylid specimens. All measurements are in mm and represent the maximum linear length of the bone along its longitudinal axis.

	***Zygodactylus* n. sp. (holotype, FMNH PA 726)**	***Eozygodactylus americanus* (*FMNH* PA 770**	***Euzygodactylus americanus* (holotype, USNM 299821)**	***Euzygodactylus americanus* (paratype, WDC-CGR-014)**	***Zygodactylus luberonensis* (holotype, SMF Av 519)**	***Primozygodactylus danielsi* (holotype, SMF-ME 2522)**	***Primozygodactylus major* (SMF-ME 1758)**	***Primozygodactylus ballmani* (SMF-ME 1758)**	***Primozygodactylus eunjooae* (holotype, HLMD–Me 10206)**
Humerus	18.6	—	16.8	17.2	17.2	16.5	28.4	21.0	—
Ulna	19.3	—	19.0	18.2	18.1	18.3	31.1	22.9	—
Carpometacarpus	8.5	—	8.8	8.8	8.6	8.2	12	9.0	—
Femur	15.1	16.9	—	19.7	19.5	16.5	24.6	20.8	17.5
Tibiotarsus	33.6	30.4	—	30.6	34.7	27.4	39.0	33.0	29.8
Tarsometatarsus	21.4	20.9	—	21.8	24.5	19.6	28.0	24.6	21.0

Table 1.4: Measurements of Green River Formation zygodactylid specimens. All measurements are in millimeters, left/right. Beak length is measured from the tip of the premaxilla to just anterior to the frontal. Narial opening is measured from the furthest anterior point of the narial opening to the furthest posterior point of the narial opening. Other lengths taken from points of greatest distance. Measurements from WDC-CGR-014 and USNM 299821 from Weidig (2010). Specimens preceeded by '*' are herein referred to Zygodactylidae genus indeterminate, species indeterminate.

	Zygodactylus grandis **holotype FMNH PA 726**	***Zygodactylus grandis*** **UWGM 40705**	***Eozygodactylus americanus*** **paratype WDC-CGR-014**	***Eozygodactylus americanus*** **holotype USNM 299821**	***Eozygodactylus americanus*** **FMNH PA 770**	***UWGM 21421**	***FMNH PA 757**	***UWGM 40363**
Cranium length	21.1	—	—	~19	—	—	18.9	~17.6
Rostrum length	13.8	—	—	~13	—	—	13.3	12.9
Narial opening	~9.0	—	—	~8	—	—	7.1	6.3
Coracoid	13.7/-	—	13.8/~13.1	—	—	—	—	—
Humerus	18.3/~18.6	~18.9	-/~17.2	16.8/16.8	—	—	—	—
Ulna	19.3/-	18.1	~18.2/-	~19.0/~19.1	—	—	—	—
Carpometacarpus	~8.5/-	7.7	8.8/-	-/8.8	—	—	—	—
Femur	15.1/-	—	19.7/-	—	~16.9/-	-/~12.0	—	—
Tibiotarsus	33.0/33.6	—	-/30.6	—	30/4/30/.1	-/21.5	—	—
Tarsometatarsus	21.4/20.2	—	21.7/21.8	—	20.9/20.5	-/13.5	—	—

Table 1.5: Dimensions of pedal phalanges from known Green River Formation and European zygodactylids for comparison. Measurements are in millimeters, left/right. Measurements from WDC-CGR-014 and SMF-2522 from Weidig (2010) and Mayr (1998) respectively.

	I1	**I2**	**II1**	**II2**	**II3**	**III1**	**III2**	**III3**	**III4**	**IV1**	**IV2**	**IV3**	**IV4**	**IV5**
Eozygodactylus americanus paratype WDC-CGR-014	5.4/~5.6	2.5/~2.0	-/5.9	5.1/5.2	2.9/~ 2.2	~6.0/~4.6	5.7/5.7	4.7/4.8	~2.7/3.3	-/2.7	2.8/2.9	2.6/2.6	2.6/2.6	-/-
Eozygodactylus americanus FMNH PA 770	4.7/4.1	2.3/2.1	6.1/6.0	4.4/4.7	2.7/2,7	5.5/5.8	5.4/5.2	4.4/4.6	3.0/3.0	~4.5/4.0	2.8/2.5	2.1/2.3	3.0/2.8	2.3/2.4
Zygodactylus n. sp. FMNH PA 726	4.6/4.3	2.6/2.7	-/5.2	4.7/4.6	3.0/3.0	6.0/5.8	5.0/5.2	4.2/4.4	3.8/3.9	2.7/2.8	2.7/2.5	2.7/2.5	3.3/3.4	2.5/2.8
Zygodactylus luberonensis SMF Av 519	4.6	2.1	6.5	4.6	2.7	7.1	6.5	5.4	3.1	5.2	4.0	3.7	3.1	2.6
Primozygodactylus danielsi SMF 2522,	4	2.4	4.8	4.3	2.4	5.7	4.9	4.3	2.6	2.9	2.9	2.5	2.5	2
Zygodactylidae gen. indet. sp. indet. UWGM 21421	-	-	-	2.9	1.9	2.9	~2.6	~2.3	-	-	-	-	-	-

Table 1.6: Chapter 1 Morphological Character Matrix – Characters 0-38. When polymorphisms are present, they are coded here as follows: A – 0/1; B – 0/2; C:1/2; D: 2/3.? Indicates missing data.

	1 0	2 0	3 0	3 8
Eozygodactylus americanus USNM 299821 (holotype)	000?021021	0-101-0101	?1001?--??	??-?1---
Eozygodactylus americanus WDC-CGR-014 (paratype)	??-?021021	00??100100	??00?01???	100?1000
Eozygodactylus americanus FMNH PA 770	??-???????	??????????	??????2??1	?0001000
Zygodactylus n. sp. FMNH PA 726	000?021121	-2?0101101	1110??1101	10001001
Zygodactylus n. sp. UWGM 40705	????0?1121	?2????1101	?1????????	?????-??
Zygodactylidae, UWGM 21421	??????????	??????????	??????2???	?00?1-0?
Zygodactylidae, FMNH PA 757	000???????	??????????	??????????	?????-??
Zygodactylidae, UWGM 40363	000???????	??????????	??????????	?????-??
Zygodactylus luberonensis SMF Av 519	0?01000-11	-011101101	10100?1101	10-01000
Zygodactylus ignotus Ballman 1968a	??????????	??????????	??????1111	?000?-??
Zygodactylus grivensis Ballman 1969b	??????????	??????????	??????????	?00??-??
Primoscens minutus BMNH A 4681	??????????	??????110?	0?????????	?????-??
Primozygodactylus danielsi SMF ME 2522	0001011110	1110111100	0010010001	10010110
Primozygodactylus eunjooae SMF ME 1074	??-1--1---	--1?1-1???	?0-0??-000	?0011110
Primozygodactylus major SMF ME 2108	0001111110	111012110?	?010?10000	20011110
Primozygodactylus ballmani SMF ME 1768	000?-11-10	1110101??1	?010?1000?	10011110
Passeriformes: Tyrannidae, Corvidae, Thamnophilidae	A0A11000CA	1D1A1C1110	?00B102000	A11-11C1
Piciformes: Picidae, Galbulidae, Bucconidae	1111110111	1210110110	?00A?10001	000011C1
Passeriformes: *Acanthisitta chloris*	0101???-11	021-10?111	?A0??12000	111-1120
Psittaciformes: *Nestor meridionalis/notabilis*	1010130-0-	21000000-1	?002?11001	00001?2?
Caprimulgiformes: *Caprimulgus vociferus*	1100010-00	02000200-?	?0?0?0000-	001-100-

Chapter 2: A Phylogenetic Analysis of Aves Incorporating Zygodactylidae

2.1: INTRODUCTION

In Chapter 1, a taxonomic assessment of relationships within Zygodactylidae sensu Mayr (2008) was discussed. A new species of *Zygodactylus* is described and interrelationships within Zygodactylidae were evaluated through an analysis of morphological characters. However, the position of Zygodactylidae within Aves remains unclear – determining the position of Zygodactylidae within Aves is the focus of this chapter. Zygodactylidae represents one of the more diverse clades of Aves during the Eocene of North American and Europe (Mayr, 2009), and may be valuable to understanding the pattern and timing of avian radiation. To assess the position of Zygodactylidae within Aves, I employed the morphological dataset used by Clarke et al. (2009), in addition to a handful of independently assessed characters and other characters modified from those described by Mayr (2004),

2.2: PREVIOUS PHYLOGENETIC WORK

Recent studies using morphological characters and molecular sequence data resolved some taxonomic controversies, but also created additional confusion regarding higher-level avian relationships. For example, although molecular sequence data repeatedly established Acanthisittidae as the sister taxon to a clade containing all other Passeriformes (e.g., Ericson et al., 2002, 2004; Barker et al., 2002, 2004; Livezey and Zusi, 2007; Hackett et al., 2008; Worthy et al., 2010; Pacheco et al., 2011; Suh et al., 2011), molecular sequence data also recently recovered a well-supported relationship between passeriforms and parrots (e.g., Hackett et al., 2008, Suh et al., 2011). The limited analyses performed to assess the relationships of Zygodactylidae and of subclades within Zygodactylidae also resulted in confusion regarding the status of the clade's sister taxon (Mayr, 2004, 2008, 2009).

Taxa within of Zygodactylidae were primarily proposed by previous researchers as most closely related to passeriforms or to piciforms (as summarized by Ballman, 1969a, b; Harrison and Walker, 1977; Mayr, 1998, 2004, 2008). This was a less-contentious assertion prior to recent molecular analyses, because Piciformes and Passeriformes had been considered sister taxa based on forelimb morphology since the late 1800s (e.g., Raikow, 1982; Barker et al., 2004). However, recent research suggests passeriforms and piciforms are less closely related that previous researchers had proposed (e.g., Hackett et al., 2008, Suh et al., 2011). Analyses of molecular sequence data by Ericson et al. (2004, 2006), Hackett et al. (2008), Suh et al. (2011) and other researchers (e.g., Barker et al., 2004) have recovered Passeriformes in a subclade containing not Piciformes, but instead Psittaciformes (parrots) and Falconiformes (falcons). Piciformes, wrested from their association with Passeriformes, was more recently recovered as nested within Coraciiformes, a clade including alcediniform birds, hoopoes, bee-eaters, rollers, and other traditional "higher land birds" (e.g., Mayr et al., 2003; Mayr, 2004; Hackett et al., 2008; Clarke et al., 2009).

A close relationship between Zygodactylidae and the extant Piciformes (who also have zygodactyl foot structure) appeared foregone to many researchers (e.g., Olson, 1975; Simpson and Cracraft, 1981). To date, only two systematic analyses (Mayr, 2004; Mayr 2008, both using the same dataset) have been performed which were focused on determining the position of Zygodactylidae within Aves. In each of those studies, support was found for a sister-group relationship between Passeriformes and Zygodactylidae, with Piciformes nested within 'Coraciiformes.' This relationship was supported in Mayr's (2004, 2008) analyses by the presence of a furcula with well-developed, blade-like apophysis furculae (Character 2, Appendix II), and a furcula with the omal end with well-developed and wide acrocoracoid and acromial processes which forms a plate-like and triangular omal extremity (Character 30, Appendix II). It was further supported by the presence of a carpometacarpus with the ventral part of the carpal trochlea cranio-caudally narrow and proximo-distally elongate, slanting caudally towards the midline of the caudal side, with a well-marked caudal carpal fovea (Mayr, 2004; this character was excluded from this project), a tarsometatarsus with well-developed plantar crests (Character 6, Appendix II), and a hypotarsus with a bony canal for the tendon of *m. flexor hallucis longus* (Character 6, Appendix II). Character 6 was not recovered as a supporting character for that clade in my analyses. Characters 2 and 30 are also seen in piciforms, along with a large intermetacarpal process and a medially-situated scar on the origin of the *m. brachialis* (Fig. 1.21; Mayr, 2004).

2.3: MATERIALS AND METHODS

Taxon Sampling

I sampled species exemplars for avian higher taxa. If a species used by Hackett et al. (2008) was unavailable for study, the closest-related available species was substituted (e.g., although a complete skeleton of *Thamnophilus punctatus*, the species sampled by Hackett et al. [2008], was unavailable for study, *Thamnophilus caerulescens* was accessible for this study).

I included taxa within Passeriformes, including acanthisittids, oscines and suboscines. Acanthisittidae is typically considered the sister taxon to the clade containing oscines and suboscines (Ericson et al., 2002; Barker et al., 2002, 2004; Livezey and Zusi, 2007; Hackett et al., 2008; Worthy et al., 2010; Pacheco et al., 2011; Suh et al., 2011). Suboscine Passeriformes are typified by a less-complex syrinx than oscines, a distinctive columella, and apparent differences in cognitive ability (Ames, 1971; Feduccia, 1975; Kroodsma and Konichi, 1991).

Five passeriform taxa were scored for this analysis. Scorings for A*canthisitta chloris* (YPM ORN 110797) were obtained by x-ray computed tomography scans courtesy of the Department of Organismic and Evolutionary Biology at Harvard University and Bhart-Anjan Bhullar. All other extant taxa were directly evaluated for osteological characters (Tables 2.2, 2.3), though all myological and plumage scores were obtained from the dataset published by Clarke et al. (2009). This sampling is limited given the 9,000+ extant species of Passeriformes (Table 2.1). Sampling for Zygodactylidae involved scorings from all zygodactylid specimens described in Chapter 1, in addition to all named species of Zygodactylidae. The named zygodactylid taxa are *Primozygodactylus enjooae* (SMF-ME 1074, holotype), *Primozygodactylus major* (SMF-ME 799, SMF-1758 [holotype]), *Primozygodactylus danielsi* (SMF-ME 2522 [holotype], SMF-ME 1269, SMF-ME 1817, HLMD-Me 15550, HLMD-Me 10206), *Primozygodactylus ballmani* (SMF-ME 2108 [holotype], HLMD-Me 15396), *Primoscens minutus* (BMNH A 4681, holotype), *Zygodactylus luberonensis* (SMF-Av 519, holotype), *Zygodactylus ignotus* (Ballman, 1969a), *Zygodactylus grivensis* (Ballman, 1969b) and both specimens of *Eozygodactylus americanus* (USNM 299821 [holotype] and WDC-CGR-014 [paratype]). I did not personally examine *Eozygodactylus americanus*, *Primoscens minutus Zygodactylus ignotus* and *Zygodactylus grivensis*, though the other taxa listed above were.

Major clades in Hackett et al. (2008) including several traditional orders were labeled by letter (Fig. 2.1a, 2.1b, Table 2.1). Clade F of Hackett et al. (2008) contains Passeriformes, 'Coraciiformes' (including Piciformes), Psittaciformes, Coliformes, Strigiformes, Accipitridae, Falconiformes, *Leptosomus* and Cathartidae. Although previous authors suggested that Zygodactylidae may be related to various avian clades (including Coracii [Olson and Feduccia, 1979], Piciformes [Ballman, 1969a; Mayr, 1998], and Passeriformes [Ballman, 1969b; Harrison and Walker, 1977; Mayr, 2004]), none of the proposed relationships justify ingroup sampling outside of Clade F. Thus, Accipitridae from Clade F is used as an outgroup taxon, and focus is on taxa within Clade F, excluding Cathartidae, Strigiformes, Falconidae and *Leptosomus*. Caprimulgiformes is also included as an outgroup taxon because it was used in Clarke et al. (2009), though it was not recovered within Clade G by Hackett et al. (2008). Taxa within "Coraciiformes" (*sensu* Hackett et al., 2008) were well-sampled by Clarke et al. (2009), and I used the taxa and scorings used in Clarke et al. (2009; Appendix 2). All taxa and specimen numbers not within Zygodactylidae are listed in Table 2.1.

As is typical of extinct taxa, for each species-level taxon of Zygodactylidae substantial missing data were noted. Thus, to maximize available data, a supraspecific "Zygodactylidae" was created using scorings from all known available taxa. When multiple states were found in distinct Zygodactylidae species, or other taxa, characters were scored as polymorphic (e.g., 0/1). Though this can result, amongst other issues, in characters being rendered uninformative (Prendini, 2001), most of the taxa within Zygodactylidae are fragmentary and individually preserve too few characters, leading to poorly-resolved trees (Wiens, 2003).

Software Implemented

Fifty-seven taxa were coded for 135 characters (Appendix II) using MacClade (Maddison and Maddison, 1992). Characters were from Clarke et al. (2009), Mayr (2004), Maurer and Raikow (1981), and Swierczewski and Raikow (1981) were used, in addition to a handful of characters I describe as new (noted in Appendix II). Four characters which appear to form a natural set of evolutionary steps were ordered (Slowinski, 1993; Appendix II). Analyses were run using PAUP*4.0b10 (Swofford, 2003). Heuristic analyses were performed. Tree bisection and reconnection (TBR) was used as the branch-swapping algorithm for the search. Two outgroups were tested to determine the stability of ingroup relationships. Bootstrap support values from 1000 replicates (100 random sequence additions per replicate) were computed, with bootstrap scores greater than 50% noted on Figures 2.2, 2.3 and 2.4. The constraint tree seen in Fig. 2.4 and discussed below was built in MacClade (Maddison and Maddison, 1992), and exported into PAUP*4b10 (Swofford, 2003).

Constraint Tree Protocols

In addition to the analyses outlined above, a constraint tree was employed to determine where Zygodactylidae would fall when topologies from recently recovered relationships of Aves were enforced. Relationships of higher-level taxa and passeriforms in this study were based on relationships reported by Hackett et al. (2008). Species-level relationships among ‘Coraciiformes’ were based on the strict consensus tree of the two most parsimonious trees from a combined analysis of both morphological and molecular data for that clade (Clarke et al., 2009: Fig. 2.1b). When hypothesized relationships differed between Clarke et al., 2009, and Hackett et al., 2008, results hypothesized by Clarke et al. (2009) were used.

2.4: RESULTS

Topology in the unconstrained analysis differed from hypotheses present by Hackett et al. (2008) and Clarke et al. (2009), but major groups of Aves are still retained (for a summary, see Fig. 20a and 20b). Piciformes is recovered as a monophyletic clade within "Coraciiformes," and Galbulidae and Bucconidae are recovered as sister taxa to Picidae.

Zygodactylidae is recovered as a sister taxon to Passeriformes in all analyses, including those with the constraint tree, and *Acanthisitta chloris* is recovered as the sister taxon to oscine and suboscine passeriforms (Figure 2.2, 2.3, 2.4).

Contra most recent analyses (e.g., Ericson et al., 2002; Barker et al., 2002, 2004; Livezey and Zusi, 2007; Hackett et al., 2008; Worthy et al., 2010; Pacheco et al., 2011; Suh et al., 2011), Psittaciformes is recovered within Coracii. Fossil rollers *Primobucco perneri*, *Primobucco mcgrewi*, *Primobucco frugilegus* and *Eocoracias brachyptera* receive no resolution in this analysis and fall out in a polytomy basal to all other ingroup taxa sampled. When Caprimulgiformes is excluded and Accipitridae is employed as the only outgroup, *Geranopterus alatus* and *Paracoracias occidentalis* also fall out into a basal polytomy in relation to ingroup taxa. Oddly, Coliiformes are resolved as the sister taxon to Trogoniformes, and the clade containing mousebirds and trogons is found as a sister taxon to the clade containing Zygodactylidae and passeriforms.

The analysis, using Caprimulgiformes and Accipitridae as outgroups, produced 252 most parsimonious trees. The strict consensus tree is shown in in Fig. 2.2. Excluding

Caprimulgiformes, the analysis produced 1180 most parsimonious trees (MPTs). The strict consensus tree excluding Caprimulgiformes can be viewed in Fig. 2.3.

Significant (~>50%) bootstrap support was not recovered for the Coliiformes + Trogoniformes clade, but the clade containing Zygodactlidae and Passeriformes received bootstrap support of 79 when Caprimulgiformes is included, and 71 when excluded (Figs. 21 and 22). The analysis with a constraint tree also recovered Zygodactylidae as the sister taxon to Passeriformes (Fig. 2.4). An analysis of the dataset employing the constraint tree produced six most parsimonious trees.

2.5: DISCUSSION

Recovery of Zygodactylidae as the sister to Passeriformes in these analyses appears to be driven largely by pectoral girdle characters. Synapomorphies of the clade containing Zygodactylidae and Passeriformes optimized in both the constrained and unconstrained analyses include an elongate, posteriorly expanded and sheet-like furcular apophysis (Character 29, Appendix II; note the pronounced sheet-like furcular apophysis in *Zygodactylus* n. sp. UWGM 40705, Figs. 1.13 and 1.14) and acrocoracoid and acromion processes on the coracoid well-developed and wide, forming a plate-like triangular omal extremity (Character 30, Appendix II). They also include a medio-distally oriented *m. brachialis* scar in the humerus (Character 43, Appendix II; Fig. 1.18), the presence of a pronounced dorsal supracondylar process on the humerus (Character 44, Appendix II; Fig. 1.8), and an elongated, narrow olecranon of the ulna (though the olecranon is less elongated in Zygodactylidae than extant Passeriformes; Character 46, Appendix II; Fig. 1.8).

None of the aforementioned characters are unique for the clade containing Passeriformes and Zygodactylidae within Clade F (Hackett et al., 2008). That is, Character 29, Appendix II, is seen also in Coliiformes; 30, 43 and 44 (Appendix II) are also seen in Piciformes, 49 and 46 (Appendix II) are seen in Piciformes and Upupidae, and 48 is seen in Piciformes and some Coracii. This degree of homoplasy within the dataset and taxa of Clade F is likely one of the confounding factors in previous taxonomic assignments of Zygodactylidae. However, the placement of Zygodactylidae as a sister taxon to Passeriformes in this study accords with results presented by Mayr (2004, 2008) and hypotheses by other researchers (e.g., Olson, 1985; Mayr, 1998, 2004, 2009).

I did not find support for a relationship between Psittaciformes and Passeriformes. Placement of Psittaciformes with Coracii was supported by four characters. The presence of a greatly medially expanded lacrimal (Character 11) is shared by *Coracias caudata*, *Coracias garrulus*, *Eurystomus orientalis*, *Uratelornis chimaera*, *Atelornis pittoides, Brachypteracias leptosomus* and Psittaciformes, as well as the clade containing motmots, todies, and kingfishers. It is also present in Accipitridae. The presence of an elongate postorbital process on the skull which is touching or nearly touching the jugal bar (Character 15, Appendix II) is a similar condition to Coracii is seen some Piciformes (taxa within Galbulae but not Pici or Bucconidae) and some Psittacidae. The presence of a strongly raised intramuscular line on the sternum (Character 36) is shared by all taxa within the clade containing *Uratelornis chimaera*, *Atelornis pittoides*, *Brachypteracias leptosomus* and Psittaciformes. The presence of a projection on the proximoventral end of the carpometacarpus is seen not only in Coracii but also Meropidae, *Tockus erythrorhynchus*, *Aceros undulates*, and Zygodactylidae (though this feature is not visible due to the position of the ulna in *Zygodactylus* n. sp.). Within Clade F of Hackett et al.

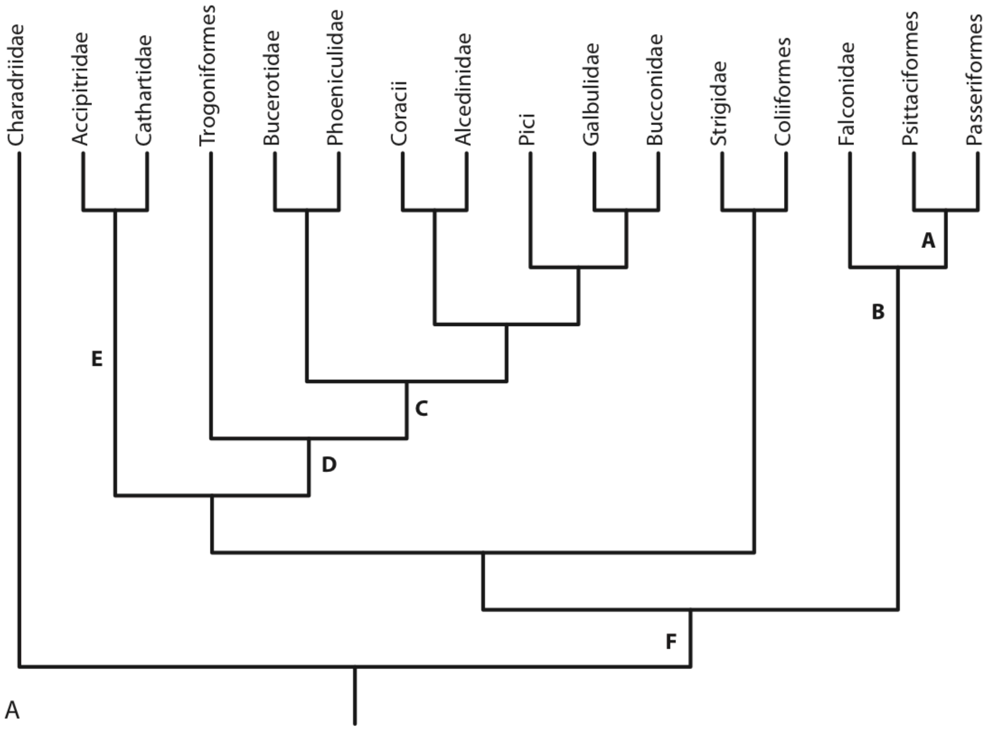
(2008), a concave, distal margin to the metatarsal trochlea II, which gives the trochlea a hooked appearance in ventral view (Character 53, Appendix II), is apomorphic for the clade containing *Uratelornis chimaera*, *Atelornis pittoides*, *Brachypteracias leptosomus* and Psittaciformes. The unique position of Psittaciformes as being nested within Coraciiformes in this analysis may be an artifact of inadequate taxon sampling or poor character choice, since most of the characters used in this analysis were not focused on Psittaciformes. The presence of zygodactyly in Psittaciformes, and forelimb and skull morphology of that group, is markedly different from that seen in 'Coraciiformes,' and no genetic data support such a relationship (Ericson et al., 2004, 2006; Hackett et al., 2008). Future analyses should focus on better sampling and further homology assessment for Psittaciformes.

Researchers have long asserted that due to tendonal arrangements and other morphological differences, zygodactyly arose independently in all extant clades which zygodactyly is known (i.e., Cuculiformes, Piciformes and Psittaciformes; Gadow and Selenka, 1891; Maurer and Raikow, 1981; Sibley and Ahlquist, 1990). If Zygodactylidae was being consistently recovered as a sister taxon to Piciformes, it might be suggested that zygodactyly was the ancestral condition in a clade containing both Piciformes and Zygodactylydae. However, the recovery of Zygodactylidae as a sister taxon to Passeriformes, in addition to the recovery by other researchers of Psittaciformes as a sister taxon to a clade containing both Passeriformes and Zygodactylidae, suggest a substantial plasticity in pedal morphology for taxa within Clade F of Hackett et al. (2008). This possible plasticity also was discussed by Mayr (2009). It is still possible that more detailed character and taxon sampling will reveal that Zygodactylidae is not the sister taxon of Passeriformes, though morphological data herein and noted by other researchers provide sufficient character data to hypothesize that the taxon falls somewhere within the passeriform-piciform-‘coraciiform’ nexus.

2.6: SUMMARY AND CONCLUSIONS

As was proposed by Mayr (2004, 2008, 2009), I recovered character support for a sister-taxon relationship between Zygodactylidae and Passeriformes. As Passeriformes is the most species-rich clade of Aves known (Sibley and Ahlquist, 1990), and as the taxon is often the focus of detailed systematics research relevant to all of Aves, this recovered topology is pertinent to much systematic analyses that focus on crown-clade Aves. However, this project was limited in scope and did not involve broad taxon sampling within Passeriformes. The project also did not focus on sampling and character choice for Psittaciformes. The topology recovered by Ericson et al. (2006), Hackett et al. (2008), Suh et al. (2011) and others which shows Psittaciformes as the sister taxon of Passeriformes was not recovered in this project, and instead a novel association of Coracii with Psittaciformes was recovered. It is clear that future research will need to focus on increased taxon sampling and deeper morphological analyses of the aforementioned taxa.

Figure 2.1a: Two trees showing recent phylogenetic analyses of avian relationships. A) A simplified version of relationships resolved by analysis of molecular sequence data by Hackett et al. (2008). Note the position of Passeriformes relative to Psittaciformes. Letters within the tree indicate Hackett et al.'s (2008) clade designation, used herein for convenient shorthand. B) Clades recovered from analysis by Mayr, 2004, 2008. This is the only analysis previously performed which included Zygodactylidae.

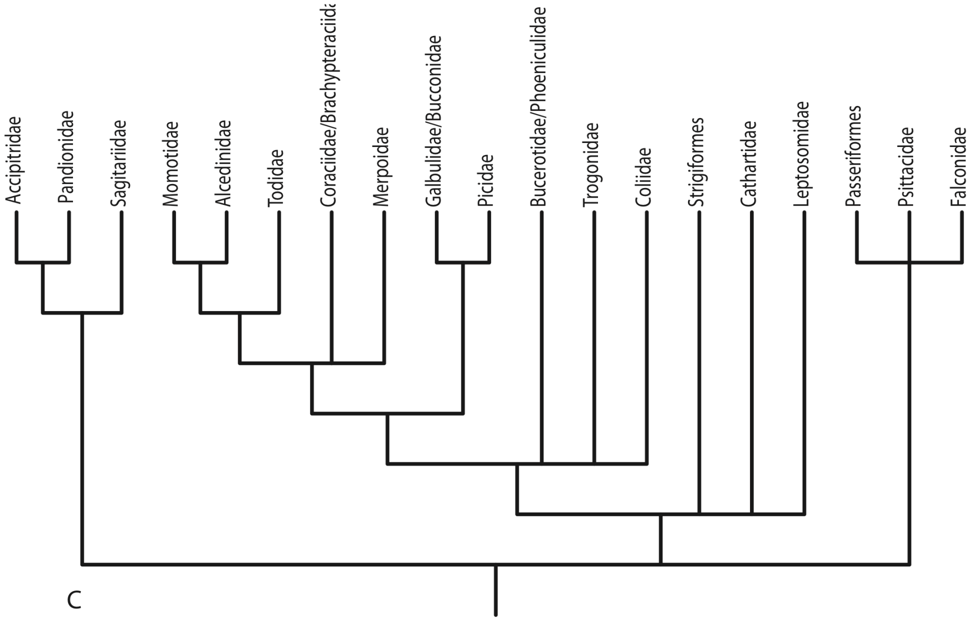

Charadriidae
Accipitridae
Cathartidae
Trogoniformes
Bucerotidae
Phoeniculidae
Coracii
Alcedinidae
Pici
Galbulidae
Bucconidae
Strigidae
Coliiformes
Falconidae
Psittaciformes
Passeriformes
A
B
E
C
D
F

A


Tinamidae
Caprimulgiformes
Coracii/dae/
Brachypteracidae
Alcedinidae
Bucerotidae/
Upupidae
Galbulidae/Pici
Coliiformes
Passeriformes
Zygodactylidae

B

Figure 2.1b: Two more recent analyses of modern avian taxa. C) A simplified tree from the molecular sequence analysis performed by Ericson et al. (2006). D) Relationships recovered from analyses of a combined molecular and morphological dataset by Clarke et al. (2009). Note the position of Piciformes nested within taxa traditionally included in Coraciiformes.


Accipitridae
Pandionidae
Sagitariidae
Momotidae
Alcedinidae
Todidae
Coraciidae/Brachypteraciida
Merpoidae
Galbulidae/Bucconidae
Picidae
Bucerotidae/Phoeniculidae
Trogonidae
Coliidae
Strigiformes
Cathartidae
Leptosomidae
Passeriformes
Psittacidae
Falconidae
C

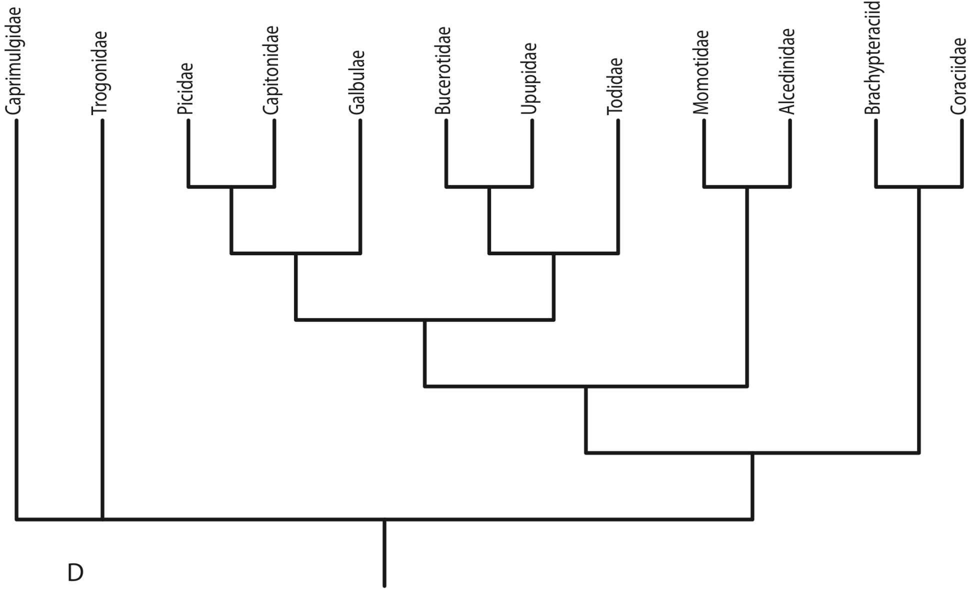

Caprimulgidae
Trogonidae
Picidae
Capitonidae
Galbulae
Bucerotidae
Upupidae
Todidae
Momotidae
Alcedinidae
Brachypteraciidae
Coraciidae
D

Figure 2.2: Strict consensus cladogram of 252 most parsimonious trees (MPTs) 433 steps in length. The tree statistics are: CI=0.360, RI=0.769, RC=0.277. Note the position of Zygodactylidae relative to Passeriformes. The Zygodactylidae + Passeriformes clade is supported by the following characters: 29 (3), 30 (2), 43 (0), 44 (1/2), 46 (1), and 48 (1). The clade containing Psittaciformes and Coracii is supported by 11(1), 15 (0), 36 (1), 50 (0) and 53 (0). See Appendix II for character descriptions.

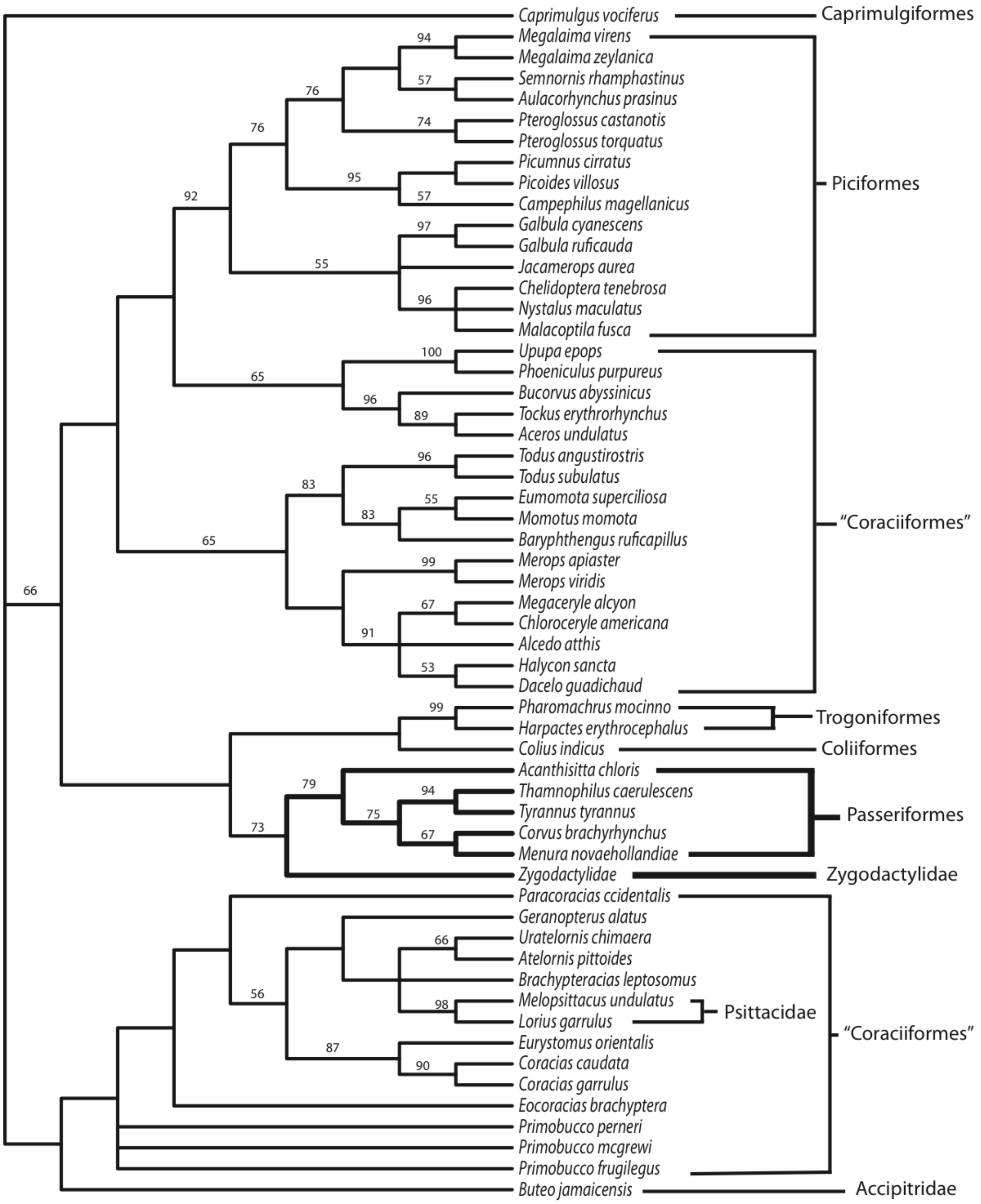

Caprimulgus vociferus
Caprimulgiformes
94
Megalaima virens
Megalaima zeylanica
57
Semnornis rhamphastinus
Aulacorhynchus prasinus
76
76
74
Pteroglossus castanotis
Pteroglossus torquatus
Picumnus cirratus
95
Picoides villosus
57
Campephilus magellanicus
Piciformes
92
97
Galbula cyanescens
Galbula ruficauda
55
Jacamerops aurea
Chelidoptera tenebrosa
96
Nystalus maculatus
Malacoptila fusca
100
Upupa epops
Phoeniculus purpureus
65
96
Bucorvus abyssinicus
89
Tockus erythrorhynchus
Aceros undulatus
96
Todus angustirostris
83
Todus subulatus
55
Eumomota superciliosa
83
Momotus momota
Baryphthengus ruficapillus
"Coraciiformes"
65
99
Merops apiaster
Merops viridis
66
67
Megaceryle alcyon
Chloroceryle americana
91
Alcedo atthis
53
Halycon sancta
Dacelo guadichaud
99
Pharomachrus mocinno
Harpactes erythrocephalus
Trogoniformes
Colius indicus
Coliiformes
Acanthisitta chloris
79
94
Thamnophilus caerulescens
75
Tyrannus tyrannus
Passeriformes
67
Corvus brachyrhynchus
73
Menura novaehollandiae
Zygodactylidae
Zygodactylidae
Paracoracias ccidentalis
Geranopterus alatus
66
Uratelornis chimaera
Atelornis pittoides
Brachypteracias leptosomus
56
98
Melopsittacus undulatus
Lorius garrulus
Psittacidae
"Coraciiformes"
87
Eurystomus orientalis
90
Coracias caudata
Coracias garrulus
Eocoracias brachyptera
Primobucco perneri
Primobucco mcgrewi
Primobucco frugilegus
Buteo jamaicensis
Accipitridae

Figure 2.3: Strict consensus cladogram of 1180 most parsimonious trees (MPTs) 422 steps in length. The tree statistics are: CI=0.370, RI=0.773 RC=0.286. Caprimulgiformes excluded in this analysis.

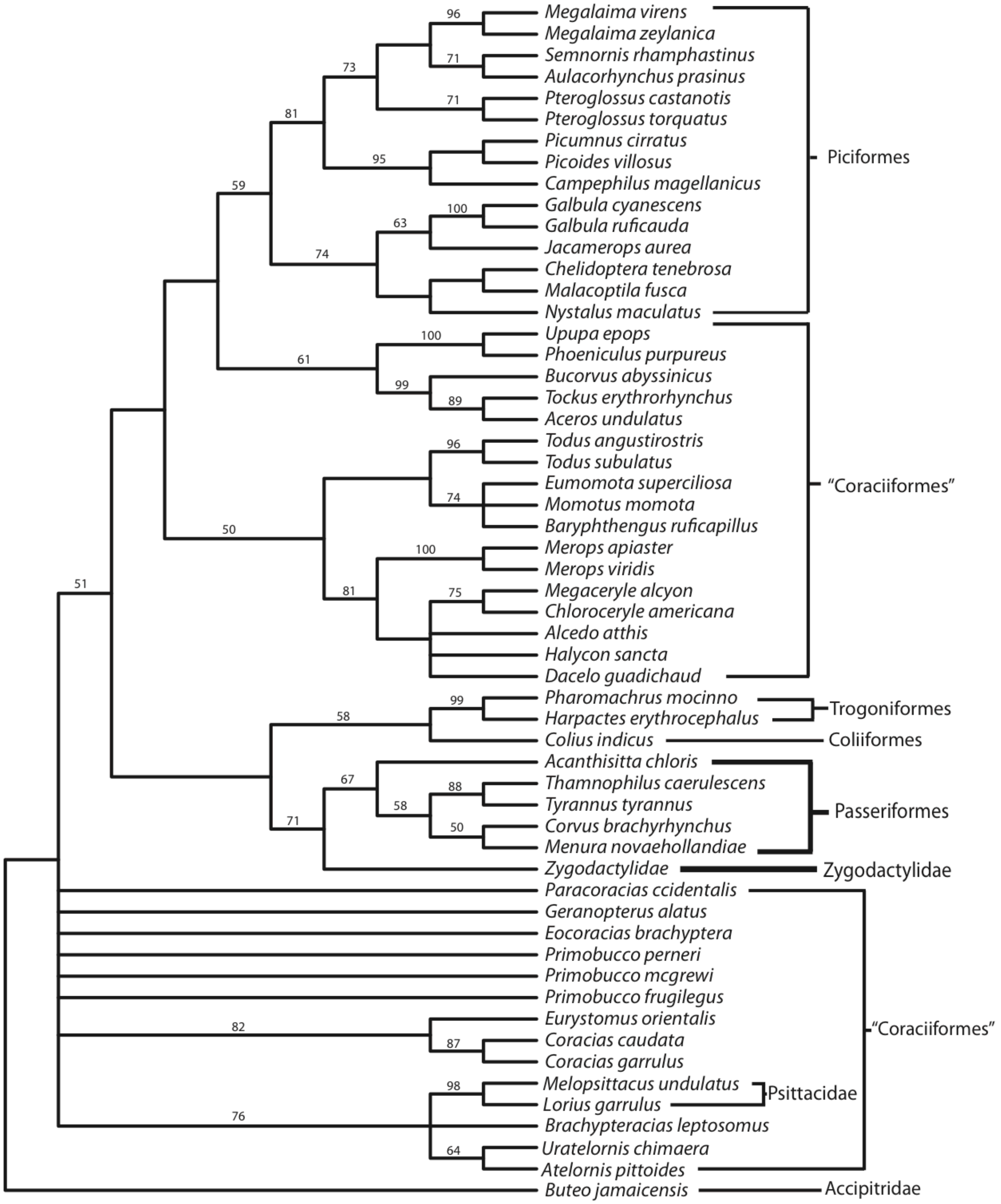

Megalaima virens
Megalaima zeylanica
Semnornis rhamphastinus
Aulacorhynchus prasinus
Pteroglossus castanotis
Pteroglossus torquatus
Picumnus cirratus
Picoides villosus
Campephilus magellanicus
Galbula cyanescens
Galbula ruficauda
Jacamerops aurea
Chelidoptera tenebrosa
Malacoptila fusca
Nystalus maculatus
Piciformes
Upupa epops
Phoeniculus purpureus
Bucorvus abyssinicus
Tockus erythrorhynchus
Aceros undulatus
Todus angustirostris
Todus subulatus
Eumomota superciliosa
Momotus momota
Baryphthengus ruficapillus
Merops apiaster
Merops viridis
Megaceryle alcyon
Chloroceryle americana
Alcedo atthis
Halycon sancta
Dacelo guadichaud
"Coraciiformes"
Pharomachrus mocinno
Harpactes erythrocephalus
Trogoniformes
Colius indicus
Coliiformes
Acanthisitta chloris
Thamnophilus caerulescens
Tyrannus tyrannus
Corvus brachyrhynchus
Menura novaehollandiae
Passeriformes
Zygodactylidae
Zygodactylidae
Paracoracias ccidentalis
Geranopterus alatus
Eocoracias brachyptera
Primobucco perneri
Primobucco mcgrewi
Primobucco frugilegus
Eurystomus orientalis
Coracias caudata
Coracias garrulus
Melopsittacus undulatus
Lorius garrulus
Psittacidae
Brachypteracias leptosomus
Uratelornis chimaera
Atelornis pittoides
"Coraciiformes"
Buteo jamaicensis
Accipitridae
96
71
73
71
81
95
59
100
63
74
100
61
99
89
96
74
50
100
81
75
51
99
58
67
88
58
50
71
82
87
98
76
64

Figure 2.4: Phylogenetic analysis using Hackett et al. (2008) and Clarke et al. (2009) as backbone constraints. Strict consensus cladogram of 6 most parsimonious trees (MPTs) 479 steps in length (CI=0.326, RI=0.730, RC=0.238). Zygodactylidae composite terminal is recovered as the sister taxon to Passeriformes. The Zygodactylidae + Passeriformes clade is supported by the following characters: 29 (3), 30 (2), 43 (0), 44 (2), 46 (1) and 48 (1). See Appendix II for details.

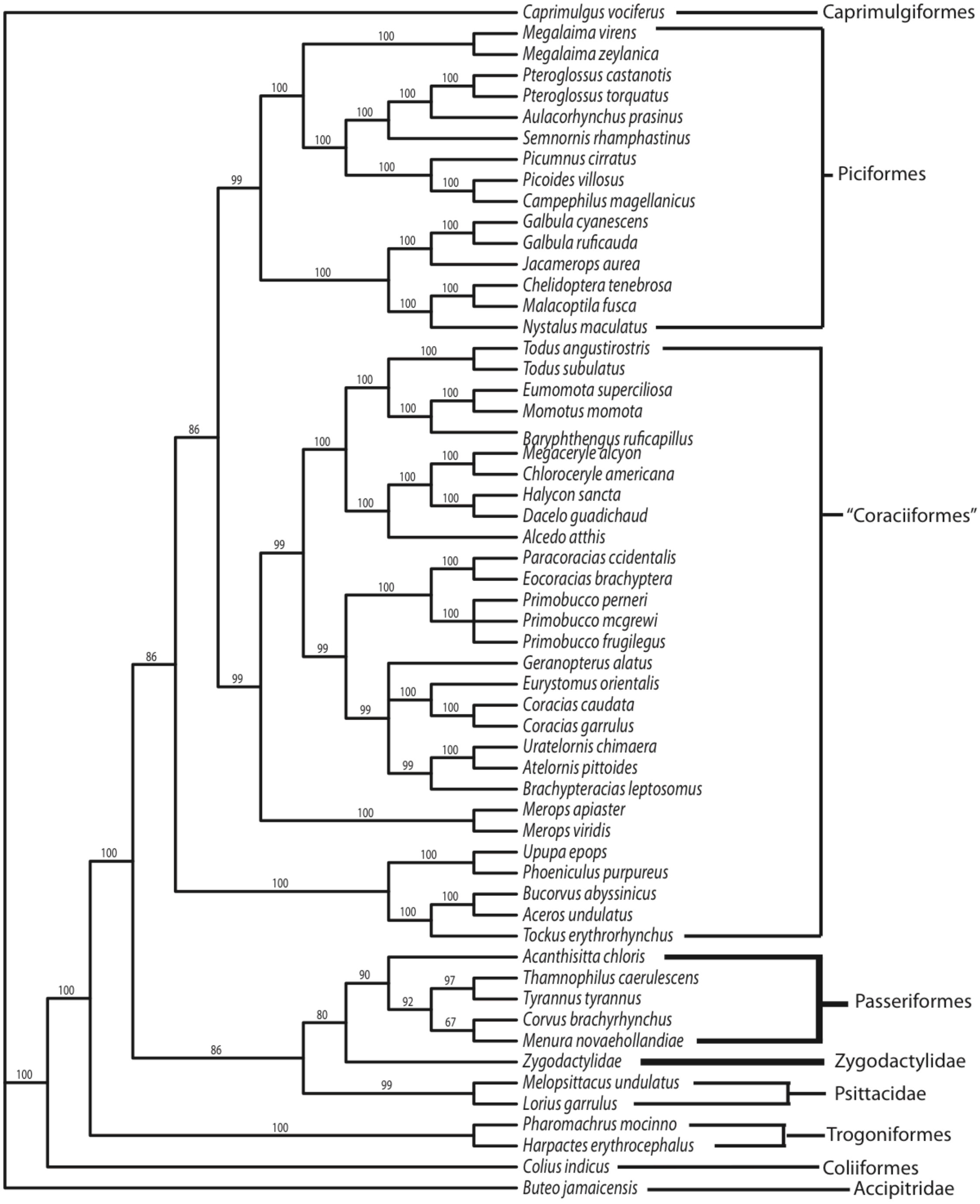

Caprimulgus vociferus
Caprimulgiformes
100
Megalaima virens
Megalaima zeylanica
100
Pteroglossus castanotis
100
100
Pteroglossus torquatus
100
Aulacorhynchus prasinus
100
Semnornis rhamphastinus
Picumnus cirratus
100
99
Picoides villosus
100
Campephilus magellanicus
Piciformes
100
Galbula cyanescens
100
Galbula ruficauda
Jacamerops aurea
100
100
Chelidoptera tenebrosa
100
Malacoptila fusca
Nystalus maculatus
100
Todus angustirostris
Todus subulatus
100
100
Eumomota superciliosa
100
Momotus momota
86
Baryphthengus ruficapillus
100
Megaceryle alcyon
100
Chloroceryle americana
100
Halycon sancta
100
100
Dacelo guadichaud
"Coraciiformes"
Alcedo atthis
99
100
Paracoracias ccidentalis
Eocoracias brachyptera
100
Primobucco perneri
100
Primobucco mcgrewi
Primobucco frugilegus
99
86
Geranopterus alatus
99
Eurystomus orientalis
100
Coracias caudata
100
99
Coracias garrulus
100
Uratelornis chimaera
99
Atelornis pittoides
Brachypteracias leptosomus
100
Merops apiaster
Merops viridis
100
Upupa epops
100
Phoeniculus purpureus
100
Bucorvus abyssinicus
100
Aceros undulatus
100
Tockus erythrorhynchus
Acanthisitta chloris
90
97
Thamnophilus caerulescens
100
Tyrannus tyrannus
92
Passeriformes
80
Corvus brachyrhynchus
67
Menura novaehollandiae
86
Zygodactylidae
Zygodactylidae
100
Melopsittacus undulatus
99
Lorius garrulus
Psittacidae
Pharomachrus mocinno
100
Trogoniformes
Harpactes erythrocephalus
Colius indicus
Coliiformes
Buteo jamaicensis
Accipitridae

Table 2.1: The 57 exemplar species used to represent taxa in the analysis in Chapter 2. See Figure 16 for clade locations by Hackett et al. (2008). *Φ* following a taxon indicates that taxon is extinct.

Specimen number	**Species**	**Taxon**	**Hackett Clade**
YPM ORN 110797	*Acanthisitta chloris*	Acanthisittidae - Passeriformes	A
FMNH 24542	*Tyrannus tyrannus*	Suboscine – Passeriformes	A
TMM M-10459	*Thamnophilus caerulescens*	Suboscine – Passeriformes	A
TMM M-10399	*Corvus brachyrynchus*	Oscine – Passeriformes	A
FMNH 336751	*Menura novaehollandiae*	Oscine – Passeriformes	A
FMNH 96161	*Melopsittacus undulatus*	Psittaciformes	B
TMM M-10376	*Lorius garrulus*	Psittaciformes	B
TMM M-10348	*Buteo jamaicensis*	Falconiformes	F
FMNH 291250	*Megalaima virens*	Piciformes	C
AMNH 28186	*Megalaima zeylanica*	Piciformes	C
AMNH 8599	*Pteroglossus castanotis*	Piciformes	C
AMNH 2994	*Pteroglossus torquatus*	Piciformes	C
AMNH 7088	*Aulacorhynchus prasinus*	Piciformes	C
AMNH 4340	*Semnornis ramphastinus*	Piciformes	C
AMNH 23882	*Picumnus temminckii*	Piciformes	C
AMNH 18859	*Picoides villosus*	Piciformes	C
AMNH 6706	*Campephilus magellanicus*	Piciformes	C
FMNH 314855	*Dryocopus pileatus*	Piciformes	C
FMNH 289330	*Galbula cyanescens*	Piciformes	C
AMNH 25635	*Galbula ruficauda*	Piciformes	C
FMNH 397899	*Jacamerops aurea*	Piciformes	C
AMNH 19269	*Chelidoptera tenebrosa*	Piciformes	C
AMNH 25635	*Malacoptila fusca*	Piciformes	C
AMNH 25636	*Nystalus maculatus*	Piciformes	C
AMNH 25419	*Todus angustirostris*	“Coraciiformes”	C
AMNH 25467	*Todus subulatus*	“Coraciiformes”	C
AMNH 10295	*Eumomota superciliosa*	“Coraciiformes”	C
AMNH 4807	*Momotus momota*	“Coraciiformes”	C
AMNH 6669	*Baryphthengus ruficapillus*	“Coraciiformes”	C

AMNH 27237	*Megaceryle alcyon*	“Coraciiformes”	C
AMNH 10170	*Chloroceryle americana*	“Coraciiformes”	C
AMNH 28154	*Halycon sancta*	“Coraciiformes”	C
AMNH 457	*Dacelo guidichaud*	“Coraciiformes”	C
AMNH 23570	*Alcedo atthis*	“Coraciiformes”	C
AMNH 30572	*Paracoracias occidentalis* ϕ	“Coraciiformes”	C
HMLD 10474	*Eocoracias brachyptera* ϕ	“Coraciiformes”	C
AMNH 56581	*Primobucco perneri* ϕ	“Coraciiformes”	C
USNM 336284	*Primobucco mcgrewi* ϕ	“Coraciiformes”	C
SMF 3507	*Primobucco frugilegus* ϕ	“Coraciiformes”	C
USNM 347415	*Eurystomus orientalis*	“Coraciiformes”	C
AMNH 1471	*Coracias caudata*	“Coraciiformes”	C
AMNH 2141	*Coracias garrulus*	“Coraciiformes”	C
SMF 4571	*Uratelornis chimaera*	“Coraciiformes”	C
FMNH 427333	*Atelornis pittoides*	“Coraciiformes”	C
FMNH 431181	*Brachypteracias leptosomus*	“Coraciiformes”	C
AMNH 9627	*Merops apiaster*	“Coraciiformes”	C
AMNH 449	*Merops viridis*	“Coraciiformes”	C
AMNH 27075	*Upupa epops*	“Coraciiformes”	C
AMNH 10211	*Phoeniculus purpureus*	“Coraciiformes”	C
AMNH 1770	*Bucorvus abyssinicus*	“Coraciiformes”	C
USNM 19687	*Aceros undulatus*	“Coraciiformes”	C
USNM 321102	*Tockus erythrorhynchus*	“Coraciiformes”	C
AMNH 4673	*Pharomachrus mocinno*	Trogoniformes	D
FMNH 25539	*Harpactes erythrocephalus*	Trogoniformes	D
AMNH 25712	*Colius indicus*	Coliiformes	F
NCSM 15171	*Caprimulgus vociferus*	Caprimulgiformes	L

Table 2.2a: Chapter 2 Morphological Character Matrix – Characters 0-70, 0/1 polymorphism denoted by ‘A’.

	10	20	30	40	50	60	70
Caprimulgus - vociferus	1000000000	0000000100	000001?010	0001000001	0100000000	-000000011	0000000101
Megalaima - virens	0010010000	0?-1100001	000011?102	1001000100	1012212110	-100001001	0011000101
Megalaima zeylanica	0010010000	0?-1100001	0000110102	1001000100	1012212110	-100001001	0011000101
Pteroglossus castanotis	-10001-10-	-1-1101102	000001?102	0101000100	1012212010	-100001001	0011000101
Pteroglossus torquatus	-10001-10-	-1-1101102	0000010102	0101000100	1012212010	-100001001	0011000101
Todus angustirorstris	1000101010	1000001112	100011?000	1?01000100	0002201110	-100010001	00000?0101
Todus subulatus	1000101010	1000001112	1000110000	1?01000100	0002201010	-100010001	0000000101
Galbula cyanescens	0000001001	0001100102	?00011?101	0010?10100	0012211010	-100001001	1000000111
Galbula ruficauda	0000001001	0001100102	000011?101	0010?10100	0012211010	-100001001	1000000111
Paracoracias occidentalis	11?0-010-1	00--2011-0	?0-?-?10??	?-0---0100	?00000000-	-0-0?0001?	?-0-??0---
Geranopterus alatus	?-0----?--	-?--21??--	??-?-?---?	1000------	?0000--011	010?0?00?-	?---???-10
Eocoracias brachyptera	?0?--0-0-1	00--201?-0	?0-?-?-00?	??00---100	?000001001	-000?0001?	?-0-??010-
Primobucco perneri	10?-0010-1	-0--1-??-0	?0-?-?1-0?	??-0----00	?000000001	-0-000000?	?-0-??01--
Primobucco mcgrewi	10?0-0-0-1	-0--10-1-0	-000----00	??-0-00100	0000000001	000000000?	?-0-??01--
Primobucco frugilegus	10?-0010-1	-0--101?-0	?00?-?--0?	??-0------	?0000--00-	-0-0?0000?	?---??0---
Eurystomus orientalis	1110011001	1010211000	0000111000	1100000100	0100000011	1000000011	0000000110
Coracias caudate	1110011001	1010211001	0000111010	1100000100	0100000011	1000000011	0000000110

Table 2.2b: Chapter 2 Morphological Character Matrix – Characters 0-70, 0/1 polymorphism denoted by ‘A’.

	10	20	30	40	50	60	70
Coracias garrulus	1110011001	1010211001	0000111010	1100000100	0100000011	1000000011	0000000110
Uratelornis chimaera	?110001001	10002110-1	000011?01?	1100010100	0000001111	011000?001	0010001110
Brachypteracias leptosomus	1110001001	10002111-1	0000111010	1000010100	0000001111	1110000001	0010000110
Atelornis pittoides	1110001001	10002110-1	0000111010	1000010100	0000001111	0110000001	0010001110
Merops apiaster	0010000000	0000000012	0000110000	1100001100	0000001001	0100000001	1000000101
Merops viridis	0010000000	0000000012	000011?000	1100001100	0000001001	0100000001	1000000101
Eumomota superciliosa	100000001-	-1-0101112	1000110000	1001000110	0000201010	-100000001	0000000101
Momotus momota	000000101-	-1-0101112	1000110000	1101000110	0000201010	-100000001	0000000101
Baryphthengus ruficapilla	000000101-	-1-0101?12	1000110000	1001000110	0000001010	-100000001	0000000101
Megaceryle alcyon	0011001001	1010000012	0000110000	1000000100	0000001010	-100000010	0000000111
Alcedo atthis	0011001001	1010000012	0000110000	1010000100	0000201010	-100000011	0000000111
Halycon sancta	0011001001	1010101012	0000110000	1000000100	0000001010	-100000011	0000000111
Dacelo guidichaud	0011001001	1020101012	0000110000	1000000100	0000001010	-100000011	0000000111
Chloroceryle Americana	0011001001	1010000012	0000111000	1000000100	0000000010	-100000010	?000000111
Upupa epops	100101100-	-1-1000002	000002?101	0110001101	0000211120	-101110111	1100110101
Phoeniculus purpureus	100101100-	-1-1000002	0000120101	0110001101	?000212120	-101110111	0101110101
Bucorvus abyssinicus	--000-1?00	0--1101102	0010010101	0100001101	0000201020	-100000000	?100100101
Tockus erythrorhynchus	--000-1?00	0--1101102	0010?1?101	0?10?01101	010020?021	010???00??	0000100101
Aceros undulates	--00001?00	0--1101102	001001?101	0110001101	0100200021	0100000011	0000100101
Semnornis ramphastinus	-11001-00-	-1-1001101	000011?102	0101000100	1000211010	-101001001	0001011101

Table 2.2c: Chapter 2 Morphological Character Matrix – Characters 0-70, 0/1 polymorphism denoted by ‘A.’

	10	20	30	40	50	60	70
Coracias garrulus	1110011001	1010211001	0000111010	1100000100	0100000011	1000000011	0000000110
Uratelornis chimaera	?110001001	10002110-1	000011?01?	1100010100	0000001111	011000?001	0010001110
Brachypteracias leptosomus	1110001001	10002111-1	0000111010	1000010100	0000001111	1110000001	0010000110
Atelornis pittoides	1110001001	10002110-1	0000111010	1000010100	0000001111	0110000001	0010001110
Merops apiaster	0010000000	0000000012	0000110000	1100001100	0000001001	0100000001	1000000101
Merops viridis	0010000000	0000000012	000011?000	1100001100	0000001001	0100000001	1000000101
Eumomota superciliosa	100000001-	-1-0101112	1000110000	1001000110	0000201010	-100000001	0000000101
Momotus momota	000000101-	-1-0101112	1000110000	1101000110	0000201010	-100000001	0000000101
Baryphthengus ruficapilla	000000101-	-1-0101?12	1000110000	1001000110	0000001010	-100000001	0000000101
Megaceryle alcyon	0011001001	1010000012	0000110000	1000000100	0000001010	-100000010	0000000111
Alcedo atthis	0011001001	1010000012	0000110000	1010000100	0000201010	-100000011	0000000111
Halycon sancta	0011001001	1010101012	0000110000	1000000100	0000001010	-100000011	0000000111
Dacelo guidichaud	0011001001	1020101012	0000110000	1000000100	0000001010	-100000011	0000000111
Chloroceryle Americana	0011001001	1010000012	0000111000	1000000100	0000000010	-100000010	?000000111
Upupa epops	100101100-	-1-1000002	000002?101	0110001101	0000211120	-101110111	1100110101
Phoeniculus purpureus	100101100-	-1-1000002	0000120101	0110001101	?000212120	-101110111	0101110101
Bucorvus abyssinicus	--000-1?00	0--1101102	0010010101	0100001101	0000201020	-100000000	?100100101
Tockus erythrorhynchus	--000-1?00	0--1101102	0010?1?101	0?10?01101	010020?021	010???00??	0000100101
Aceros undulates	--00001?00	0--1101102	001001?101	0110001101	0100200021	0100000011	0000100101
Semnornis ramphastinus	-11001-00-	-1-1001101	000011?102	0101000100	1000211010	-101001001	0001011101

Table 2.3a: Chapter 2 Morphological Character Matrix – Characters 71-135, 0/1 polymorphism denoted by ‘A.’

	80	90	100	110	120	130	135
Caprimulgus - vociferus	00?000????	??????????	?????????0	?0??????00	0?0???????	??000??00	00000
Megalaima - virens	100?00????	??????????	??????????	??????????	??????????	????????1?	??0??
Megalaima zeylanica	100?00????	??????????	???110000?	?0?000??00	?01110-110	?1?1??0011	010?1
Pteroglossus castanotis	100000????	??????????	??????????	??????????	??????????	????????1?	??0??
Pteroglossus torquatus	100000????	??????????	???110000?	?0?000??0?	?011101010	?1?1??0011	010?1
Todus angustirorstris	011010????	??????????	??????????	??????????	??????????	????????0?	??00?
Todus subulatus	0110100000	01000100?1	100???1?01	?000101001	0?1???????	111110??00	11001
Galbula cyanescens	100000????	??????????	??????????	??????????	??????????	????????1?	??00?
Galbula ruficauda	100000????	??????????	???0000101	?0?1000?1-	0100011001	?000??011?	01000
Paracoracias occidentalis	01?0?0????	??????????	??????????	????0?????	??????????	??????????	???-?
Geranopterus alatus	01?-?-????	??????????	??????????	??????????	??????????	??????????	???-?
Eocoracias brachyptera	01?0?0????	??????????	??????????	??????????	??????????	??????????	???-?
Primobucco perneri	?1???0????	??????????	??????????	??????????	??????????	??????????	???-?
Primobucco mcgrewi	0??0?0????	??????????	??????????	??????????	??????????	??????????	???-?
Primobucco frugilegus	??????????	??????????	??????????	??????????	??????????	??????????	???-?
Eurystomus orientalis	0100000000	0100000000	00000???01	0001000001	0?0???0000	000000?100	00000

Table 2.3b: Chapter 2 Morphological Character Matrix – Characters 71-135, 0/1 polymorphism denoted by 'A.'

	80	90	100	110	120	130	135
Coracias caudate	0100000000	0100000000	000??????0	0000000001	0?0???????	000000??00	0000?
Coracias garrulus	0100000000	0100000000	000???1?00	0000000001	0?0???????	000000??00	00000
Uratelornis chimaera	010000????	??????????	??????????	??????????	??????????	????????0?	??00?
Brachypteracias leptosomus	010000????	??????????	??????????	??????????	??????????	????????0?	??000
Atelornis pittoides	010000????	??????????	??????????	??????????	??????????	????????0?	??00?
Merops apiaster	0110100100	0100000001	000???0001	010100101-	??1???????	111010??00	11000
Merops viridis	011010????	??????????	??????????	?1????????	??????????	????????0?	??00?
Eumomota superciliosa	0110100000	0100000001	100??????1	0001000000	0?1???????	111110??00	11010
Momotus momota	0110100000	0100000001	100???1001	0001000000	0?1???????	111110??00	11010
Baryphthengus ruficapilla	0110100000	0100000001	100??????1	0001000000	0?1???????	111110??00	11000
Megaceryle alcyon	0110100100	0100010001	000??????1	0101000001	0?1???????	101111??00	10001
Alcedo atthis	011010????	?100??00?1	000???0001	?1???00?01	??1???????	????????0?	?1001
Halycon sancta	011010????	?100??00?1	000???0001	?1???00?01	??1???????	????????0?	?000?
Dacelo guidichaud	0110100100	0100010001	000??????1	0101000001	0?1???????	101010??00	1100?
Chloroceryle Americana	0110100100	0100010001	000??????1	0101000001	0?1???????	101111??00	11001
Upupa epops	0101101100	0010001101	121???0011	000110001-	0?1???????	101110??00	01001
Phoeniculus purpureus	011110????	?010??11?1	121???0001	?0???00?1-	??????????	????????0?	?1001
Bucorvus abyssinicus	0100001011	1101100001	010??????1	101011011-	1-1???????	000010??00	01001
Tockus erythrorhynchus	010?101011	1101100011	020???1001	101011011-	1-1???????	000010??00	01001

Table 2.3c: Chapter 2 Morphological Character Matrix – Characters 71-135, 0/1 polymorphism denoted by ‘A.’

	8 0	9 0	1 0 0	1 1 0	1 2 0	1 3 0	1 3 5
Aceros undulates	0100101011	1101100011	010??????1	101011011-	1-1???????	000010??00	01001
Semnornis ramphastinus	100000????	??????????	???1100010	?0?0000?00	0011100110	01?1??0011	01001
Aulacorhynchus prasinus	100000????	??????????	???1000010	?0?0000?00	0011100110	01?1??0011	01001
Picumnus cirratus	1?0?00????	??????????	???1110000	?0?1110?01	0011000010	01?1??0011	0100?
Picoides villosus	100100????	??????????	???1110000	?1?1110?01	0011000010	01?11?-011	01101
Campephilus magellanicus	100100????	??????????	???1110000	?0?1110?01	0011000010	01?1??0011	01101
Jacamerops aurea	100?00????	??????????	???0001101	?1?100??1-	0100011001	?0?0??0111	010?0
Pharomachrus mocinno	0000?1????	?000??10?1	000???1?01	?1???00?00	??0???????	????????2?	?1000
Harpactes erythrocephalus	0000?11000	0000001001	000??????1	01010000?0	0?0???????	000100??20	01000
Chelidoptera tenebrosa	100000????	??????????	???0000101	?0?100??1-	0110010001	?0?0??1111	010?0
Nystalus maculatus	100000????	??????????	???0000100	?0?100??01	0110010001	?0?0??1111	0?0?0
Chelidoptera tenebrosa	100000????	??????????	???0000100	?0?100??00	0110000001	?0?0??111?	010?0
Nystalus maculatus	000100????	??????????	??????????	??????????	??????????	??????????	?????
Malacoptila fusca	111000????	??????????	??????????	??????????	??????????	????????0?	??00?
Acanthisitta chloris	111000????	??????????	??????????	??????????	??????????	??????????	?????

Table 2.3d: Chapter 2 Morphological Character Matrix – Characters 71-135, 0/1 polymorphism denoted by ‘A.’

	8 0	9 0	1 0 0	1 1 0	1 2 0	1 3 0	1 3 5
Melopsittacus undulates	000100????	??????????	??????????	??????????	??????????	??????????	?????
Lorius garrulus	000100????	??????????	??????????	??????????	??????????	??????????	?????
Thamnophilus caerulescens	000100????	??????????	??????????	??????????	??????????	??????????	?????
Trannus tyrannus	100000????	??????????	???1000010	?0?0000?00	0011100110	01?1??0011	01001
Corvus brachyrhynchus	1?0?00????	??????????	???1110000	?0?1110?01	0011000010	01?1??0011	0100?
Menura novaehollandiae	000100????	??????????	??????????	??????????	??????????	??????????	?????
Zygodactylidae	110000????	??????????	??????????	??????????	??????????	??????????	?????
Colius indicus	0???00????	??????????	??????????	??????????	??????????	??????????	?????
Buteo jamaicensis	010000????	??????????	??????????	??????????	??????????	??????????	?????

Appendix I: characters implemented for analysis in Chapter 1

Characters were developed in the course of this research unless otherwise noted.

1. Skull: narial opening: approximately rectangular (0); ovoid (1). See Fig. 1.21.

2. Skull: jugal: bowed ventrally (0); straight or concave (1). See Fig. 1.4, 1.21.

3. Skull: narial opening: greater than 50% the length of rostrum (0); equal to or less than 50% the length of the rostrum (1). See Fig. 1.21.

4. Furcula, omal extremity: reduced, outline linear (0); wide, subtriangular omal extremity (1). Character 9 of Mayr (2004). Zygodactylidae is characterized by a wide subtriangular omal extremity (Mayr, 2008). Figure 5C in Mayr (2008)

5. Scapula: acromion, size: moderate (0); large (1).

6. Coracoid: procoracoid process, size: completely reduced (0); developed but moderate size, projecting approximately ¼ the width of the coracoid shaft (1); large, projecting approximately half the width of the coracoid shaft (2); projecting more than ½ the width of the coracoid shaft (3). Ordered. Wording simplified and state (3) added from character 11 of Mayr (2004). State 0 is present in *Zygodactylus*. State 2 is present in *Nestor notabilis*. State 0 and 1 visible in Fig. 1.9.

7. Coracoid: medial side: flange absent, margin straight (0); flange present, margin convex (1). State 1 is present in *Primozygodactylus*, the holotype of *Zygodactylus* n. sp. (FMNH PA 726). Character first noted by Mayr (2008). See Fig. 1.9.

8. Sternum: lateral trabeculae, posterior tip: extends posteriorly beyond tips of medial trabeculae (0); of same length or slightly shorter than medial trabeculae (1). State 0 is seen in the holotype of *Eozygodactylus americanus* (USNM 299821). State 1 is seen in the holotype of *Zygodactylus* n. sp. (FMNH PA 726).

9. Humerus: size of dorsal supracondylar process: absent or a very small nub (0); well-developed but small (1); large, separated from shaft by a small notch (e.g., *Zygodactylus luberonensis*, *Zygodactylus* n. sp., *Eozygodactylus americanus*; 2). Noted by Manegold (2008). See Fig. 1.19.

10. Humerus: direction of dorsal supracondylar process: parallel to shaft of humerus (0); laterally directed in relation to humeral shaft (1). See Fig. 1.19.

11. Humerus: bicipital crest, size: moderate (0); large (1); Exceptionally large, pointed (e.g., Psittaciformes; 2). Ordered.

12. Humerus:femur ratio: femur longer than humerus (0); femur subequal to humerus (1); femur smaller than humerus (2). Ordered.

13. Humerus*: m. brachialis* origin medially situated (0); laterally situated (1). State (0) is typical of Passeriformes, described zygodactylids, Piciformes and Coliiformes. Noted in Ashley (1941). Modified from character 16 of Mayr (2004).

14. Humerus: humeral head: narrow in posterior view (0); globose (1). Markedly more globose in *Zygodactylus luberonensis* than in *Zygodactylus* n. sp.

15. Humerus: flexor process: short nub extending only slightly distal to the ventral condyle (0); markedly projecting distal to ventral condyle (1). State 0 is seen in Psittaciformes. State 1 is seen in *Zygodactylus* n. sp. See Fig. 1.19.

16. Ulna:tarsometatarsus ratio: ulna shorter than tarsometatarsus (0); ulna subequal to tarsometatarsus (1); ulna longer than tarsometatarsus (2). Ordered.

17. Carpometacarpus: dorsal margin: protuberance mid-shaft (‘dentiform process’ of Mayr, 1998): absent, dorsal margin straight (0). Present, protuberance mid-shaft (1). The holotype and paratype specimens of *Eozygodactylus americanus* have no mid-shaft protuberance, differentiating that specimen from *Zygodactylus* n. sp. Character 46 of Clarke et al. (2009). See Fig. 1.8.

18. Carpometacarpus: intermetacarpal process: absent (0); present (1). Modified from Character 47 of Clarke et al. (2009).

19. Carpometacarpus: intermetacarpal process: if present, unfused to minor metacarpal (as in Zygodactylidae; 0); fused to minor metacarpal (e.g., Passeriformes, Piciformes; 1). Modified from Character 47 of Clarke et al. (2009).

20. Carpometacarpus: metacarpal III: somewhat curved, concave dorsally (0); straight (1).

21. Carpometacarpus: metacarpal III: subequal to metacarpal II (0); longer than metacarpal II (1). Modified from Character 24 of Mayr (2004).

22. Manual digit III, phalanx I: posterior margin: straight or slightly tapered (0); widened into a small tubercle (1). This character is present in both the holotype of *Zygodactylus* n. sp. (FMNH PA 726) and the holotype of *Eozygodactylus americanis* (USNM 299821), as well as in some Passeriformes (e.g., *Troglodytes aeclon*). Noted by Weidig (2010). See Fig. 1.8.

23. Manual digit I, phalanx II: absent (0); present (1); State 1 found in *Zygodactylidae*.

24. Manual digit II, phalanx I: smooth and linear ventrally (0); hooked ventrally, as in galbulids (1); convex ventrally, as in *Melopsittacus* (2). Modified from Character 56 of Clarke et al. (2009).

25. Manual digit II, phalanx II: >50% length of digit II, phalanx I (0); ≤50% length of phalanx II, digit I.

26. Pelvis: obturator foramen: open (0); closed (1). This character is highly variable in Passeriformes and most Aves. Weidig (2010) stated that this is an apomorphy of *Eozygodactylus*.

27. Tibiotarsus: cranial cnemial crest, anterior projection: less than anteroposterior width of shaft of tibiotarsus (0); subequal to width of shaft of tibiotarsus (1); larger than width of shaft of tibiotarsus (2). Wording and number of states modified from Character 39 of Mayr (2004).

28. Tarsometatarsus, anterior end of trochlea metatarsi IV: marked convexity on lateral tarsometatarsal margin: present (0); absent (1). This character is autapomorphic for *Zygodactylus* (Mayr, 2008).

29. Tarsometatarsus: a marked sulcus on the plantar surface of the proximal end of trochlea metatarsi IV bordering the lateral tarsometatarsal convexity (Fig 9; Mayr, 2008).

30. Tarsometatarsus: trochlea metatarsi II: plantarly directed projection: absent (e.g., Passeriformes); 0); present (e.g., Piciformes; 1). Character 40 of Mayr (2004).

31. Tarsometatarsus: shorter than humerus (0); subequal to humerus (1); exceeding humerus in length (2). This character is widely variable within Passeriformes, though the tarsometatarsus is uniformly longer than the humerus in Zygodactylidae. Ordered. Modified from Character 34 of Mayr (2004).

32. Tarsometatarsus, posterior: metatarsal trochlea arranged such that plantar surface is concave (0); is aligned linearly, does not form concave plantar surface (1). State 0 is present in Zygodactylidae and Piciformes, and state1 is present in Coracii and Passeriformes. Commented on by Zelenkov (2007).

33. Tarsometatarsus, accessory trochlea: absent (0); present (1). Clarke et al. (2009), character 69.

34. Tarsometatarsus, trochlea accessoria (if present): bulbous, reaches at least to middle of trochlea metatarsi III (e.g., *Zygodactylus*; 0); does not reach to trochlea metatarsi III (e.g., *Primozygodactylus*; 1). Noted by Mayr (2004).

35. Pedal phalanx II, phalanx I: less than 1/3 the length of phalanx II, digit II; longer than 1/3 the length of phalanx II, digit I. State 1 is an apomorphy for *Primozygodactylus danielsi*.

36. Pedal digit III: tarsometatarsus ratio: $\geq$85% (0); <85%.

37. Pedal unguals: degree of curvature: slight to absent (0); moderate (1); pronounced curve such that phalanx is (2). Noted by Mayr (2008). State 0 is seen in *Zygodactylus*, and state 1 is present in *Primozygodactylus*. State 2 is seen in Passeriformes such as *Acanthisitta chloris* and *Turdus migratorius*.

38. Pedal ungual III:IV: <25% of the sum of the length of the proximal three phalanges of digit III; ≥25% of the sum of the length of the proximal three phalanges of digit III. State 1 is autapomorphic for *Zygodactylus* n. sp. (FMNH PA 726) within Zygodactylidae.

Appendix II: Characters implemented for analysis for Chapter 2

Osteological

1. Skull: relationship of external naris and antorbital fenestra: do not overlap in lateral view (0); naris overlaps antorbital fenestra posteriorly (1). Character 1 of Clarke et al. (2009). State 1: Seen in bucorvids, *Picumnus*, todies, *Coracias*. Variable in passerines, seems linked to beak robusticity.

2. Skull: external naris, shape, lateral view: ovoid (0); roughly triangular with a flat ventral margin (1); elongate and approximately rectangular (2). Modified from character 2 of Clarke et al. (2009), to encompass the state (2) seen in some passerines, *Zygodactylus* n. sp. (FMNH PA 726) and other zygodactylids.

3. Skull: temporal fossae, dorsal extent: widely separated (0); approach each other at midline (1).State 1 seen in alcedinids, *Coracias*. Character 3 of Clarke et al. (2009).

4. Skull: palatine, posterolateral margin, posteriorly directed spine-like processes: absent (0); present (1). Character 4 of Clarke et al. (2009).

5. Skull: anterior wall of braincase: largely ossified (0); almost completely unossified (1). Character 5 of Clarke et al. (2009).

6. Skull: external naris, division by a thin bony septum: undivided (0); divided (1; e.g. Cracraft, 1971: Fig. 1). Discussed in Mayr and Mourer-Chauviré (2000). Character 6 of Clarke et al. (2009).

7. Skull: internarial septum, largely or completely ossified: absent (0); present (1).

Discussion in Mayr et al. (2004). Character 7 of Clarke et al. (2009).

8. Skull: beak grossly inflated: absent (0); present (1). Character 8 of Clarke et al. (2009).

9. Skull: upper beak, cutting edge of rhamphotheca finely serrated: absent (0); present (1). Character 9 of Clarke et al. (2009).

10. Skull: lacrimal, head: small (0); greatly enlarged (1); fused with frontals (2). Character 10 of Clarke et al. (2009), which was herein modified to include the fusion of the lacrimal to the frontal as in Pici and Bucerotidae noted by Mayr et al. (2003).

11. Skull: lacrimal, descending process: unexpanded (0); greatly medially expanded (1). Character 11 of Clarke et al. (2009); similar to character 2 of Mayr (2004).

12. Skull: lacrimal: present, unreduced (0); greatly reduced or absent (1) Character 12 of Clarke et al. (2009).

13. Skull: lacrimal, posterior margin of head in dorsal view: straight (0); concave, with small posterior point (1); concave with large posterior point (2). Ordered. Character 13 of Clarke et al. (2009).

14. Skull: ectethmoid, greatly expanded and plate-like, dorsal margin fused with frontals: no (0); yes (1). Character 14 of Clarke et al. (2009); Character 3 of Mayr (2004).

15. Skull: postorbital process: short (0); elongate, but well-separated from jugal bar (1); elongate, touching or nearly touching jugal bar (2). Ordered. See discussion

by Mayr et al. (2004). Character 15 of Clarke et al. (2009).

16. Skull: postorbital process, development of an anterior process: absent (0); present (1). See discussion in Livezey and Zusi (2007). Character 16 of Clarke et al. (2009).

17. Skull: zygomatic process, weak or absent: (0); long and thin (1); abbreviated and tab-like (2). Character 17 of Clarke et al. (2009).

18. Skull: palatine, posterior margin: concave (0); convex (1). Character 18 of Clarke et al. (2009).

19. Skull: columella, large hollow bulbous basal footplate area with large fenestra on one side: absent (0); present (1). Scorings are based on Feduccia (1975a, b). See also Mayr and Clarke (2003) and Livezey and Zusi (2006: 61). Character 19 of Clarke et al. (2009). Character 6 of Mayr (2004), where the character was noted as autapomorphic for suboscine Passeriformes.

20. Mandible: mandibular symphysis: short, approximately one-fifth of mandible length or less (0); moderate length, up to one-third of mandible length (1); extensive, more than one-third of mandible length (2). Character 20 of Clarke et al. (2009). State 0 and 1 are variably present in passerines.

21. Mandible: deep incision between medial process and retroarticular process in dorsal view (Olson, 1976): absent (0); present (1). Character 21 of Clarke et al. (2009).

22. Mandible: posterior mandibular fenestra: absent (0); large opening (1). Present but small (2) Character 22 of Clarke et al. (2009).

23. Atlas and axis: separate (0); fused into single element in adult (1). Character 23 of Clarke et al. (2009).

24. Atlas: transverse foramen: absent (0); present (1). Character 24 Clarke et al. (2009).

25. Axis: transverse foramen: absent (0); present (1). Character 25 of Clarke et al. (2009).

26. Presacral vertebrae: more than 19 (0); 19 (1); 18 (2). Character 26 of Clarke et al. (2009), similar to character 8 of Mayr (2004).

27. Pygostyle: anterior border of lamina: absent or small (0); notch present (1); circular perforation with bony anterior rim (2). Character 27 of Clarke et al. (2009).

28. Pygostyle: discus: unmodified (0); shield-like with sharply defined ridge-like lateral margins (1); discus enlarged, with large dorsal and ventral projections (this state encompasses the unique morphology seen in Coliiformes; 2); discus not enlarged, but dorsal and ventral projections prominent (e.g., Menura; 3) See Mayr et al. (2003). Modified from character 28 of Clarke et al. (2009) to encompass state 3; also similar to character 7 of Mayr (2004).

29. Furcula: apophysis: absent or small, blunt tubercle (0); blade-like projection (1); diamond-shaped (2); large sheet-like expansion (3); small, sharp point (e.g., mousebirds, *Menura*; 4). Character 29 of Clarke et al. (2009), modified to include states 3 and 4.

30. Furcula: omal end: unmodified (0); widened with blunt, slightly convex and short acrocoracoid and acromion processes (1); acrocoracoid and acromion processes well developed and wide, forming plate-like omal extremity of subtriangular shape (2). Character 30 of Clarke et al. (2009); similar to character 9 of Mayr (2004).

31. Scapula: acromion process: single (0); bifurcated, with additional medial process (1) Character 31 of Clarke et al. (2009); similar to character 14 of Mayr (2004). Typically bifurcated in suboscines.

32. Scapula: pneumatic foramen on anterior part of acrocoracoid process: absent (0); present (1). Character 32 of Clarke et al. (2009).

33. Coracoid: bony bridge connecting procoracoid process and acrocoracoid process: absent (0); present (1). Character 33 of Clarke et al. (2009).

34. Coracoid: procoracoid process: well developed (0); greatly reduced (1). Character 34 of Clarke et al. (2009); same as character 11 of Mayr (2004). Somewhat developed in *Acanthisitta*, but greatly reduced in most suboscines and oscines.

35. Coracoid: distinct process overhanging supracoracoid sulcus: absent (0); present (1) See Mayr (1999) for discussion of this feature. Character 35 of Clarke et al. (2009).

36. Sternum: clearly defined and strongly raised intramuscular line: absent (0); present (1). This character was discussed by Cracraft (1971). Character 36 of Clarke et al. (2009).

37. Sternum: internal spine: absent (0); present (1). Character 37 of Clarke et al.

(2009).

38. Sternum: external spine: absent (0); present (1). Character 38 of Clarke et al. (2009).

39. Sternum: posterior incisures: open (0); closed, forming fenestrae (1). Character 39 of Clarke et al. (2009).

40. Sternum: posterior incisures: four (0); two (1). Character 40 of Clarke et al. (2009); character 15 of Mayr (2004).

41. Clavicles: fused, forming furcula (0); unfused (1). Character 41 of Clarke et al. (2009).

42. Humerus: bicipital crest: unenlarged (0); expanded, extending far distally (1). This character was discussed by Cracraft (1971). Character 42 of Clarke et al. (2009).

43. Humerus: *fossa musculi brachilalis*: medio-distally situated (0); latero-distally situated with weakly developed ventral margin (1). Latter state typical of passerines, zygodactylids, mousebirds; noted by Ashley (1941). Modified from character 16 of Mayr (2004).

44. Humerus: distal: supracondylar process: absent or small nub (0); present, but only moderately developed (e.g., suboscines, Menurae, acanthisittids (1); pronounced, e.g., oscines (2). Noted by Manegold (2008).

45. Ulna, feather papillae: absent or faint (0); moderately raised knobs (e.g., *Thamnophilus*); prominent raised knobs (1). Character 43 of Clarke et al. (2009).

46. Ulna, olecranon: blunt (0); elongated and narrow (1). Character 44 of Clarke et al. (2009); similar to character 19 of Mayr (2004), in passerines the olecranon is typically quite elongated and pointed.

47. Ulnare, rami: ventral ramus (crus longus) longer than dorsal ramus (crus brevis) (0); subequal (1); dorsal ramus longer than ventral ramus (2). Character 45 of Clarke et al. (2009).

48. Carpometacarpus: metacarpal II, anterior protuberance at midshaft (protuberentia metacarpalis; Baumel and Witmer, 1993; dentiform process of Mayr, 2004): absent (0); present (1). Character 46 of Clarke et al. (2009).

49. Carpometacarpus: intermetacarpal process: absent or weak (0); well developed (1); well-developed and fused with minor metacarpal (2), absent, but tendon of *m. extensor carpi ulnaris* inserting in position of intermetacarpal process (3). Character states 0, 1, 3 advocated by Mayr et al. (2004), distinguish between the taxa that lack an intermetacarpal process and retain a primitive insertion of the extensor ulnaris tendon, and those that lack the process but show the apomorphic displaced insertion of the tendon. A detailed discussion of this feature was provided by Stegmann (1963). Modified from Character 47 of Clarke et al. (2009). Ordered.

50. Carpometacarpus: metacarpal III with ventrally protruding projection on ventral side of proximal end: absent (0); present (1). Character 48 of Clarke et al. (2009). Equivalent to Character 23 of Mayr (2004) but worded differently.

51. Carpometacarpus: foramen in ventrally protruding projection from metacarpal III: absent (0); present (1). See Mayr and Mourer-Chauviré (2000). For taxa lacking

the projection this character is considered noncomparable. Character 49 of Clarke et al. (2009).

52. Carpometacarpus: metacarpals II and III subequal in length (0); metacarpal III projects significantly distal to metacarpal II (1). Character 50 of Clarke et al. (2009).

53. Carpometacarpus: portion of carpal trochlea proximal to metacarpal III: present (0); absent, creating concave distal margin to trochlea and giving the trochlea a hooked appearance in ventral view (1). See Mayr and Mourer-Chauviré (2000: fig. 10). Character 51 of Clarke et al. (2009).

54. Carpometacarpus: metacarpals II and III: separated by moderate intermetacarpal space (0); metacarpal III strongly bowed, creating a wide space (1). Character 52 of Clarke et al. (2009).

55. Carpometacarpus: ridge continuing distally from pisiform process to metacarpal III; absent (0); present (1). This character was discussed by Mayr (2000). Character 53 of Clarke et al. (2009).

56. Carpometacarpus: posterior margin of metacarpal III: smooth (0); undulating (1). Character 54 of Clarke et al. (2009).

57. Manual digit II, phalanx I: large proximally directed process on ventral side: absent (0); present (1). Character 55 of Clarke et al. (2009). Character 26 of Mayr (2004).

58. Manual digit II, phalanx I: proximally hooked process projects from posterior edge of distal end (Mayr, 2004: fig. 5c): absent (0); present (1). Character 56 of

Clarke et al. (2009).

59. Manual digit II, phalanx I: internal index process: small, does not surpass the distal articular surface for digit II, phalanx II (0); well developed, surpasses distal articular surface for digit II, phalanx II (1). Character 57 of Clarke et al. (2009).

60. Pelvis: pectineal tubercle: present, well developed (0); weak or absent (1). Character 58 of Clarke et al. (2009).

61. Pelvis: anterior iliac blades: dorsal margin free from vertebrae (0); reduced in size and fused with vertebral transverse processes to form flat, horizontal surface (1). This character was discussed by Simpson and Cracraft (1981). Character 59 of Clarke et al. (2009). Encompasses character 28 of Mayr (2004).

62. Femur: pneumatic foramen on anterolateral surface of proximal end: absent (0); present (1). Character 60 of Clarke et al. (2009).

63. Tibiotarsus: anterior cnemial crest: weakly anteriorly projected (0); strongly projected (1). This feature was discussed by Cracraft (1971). Character 61 of Clarke et al. (2009).

64. Tibiotarsus: anterior cnemial crest continuous with ridge along medial edge of the shaft, paralleling the fibular crest (1). Character 62 of Clarke et al. (2009).

65. Tarsometatarsus: bony canal enclosing tendons of *m. flexor hallucis longus*: absent (0); present (1). Character 63 of Clarke et al. (2009).

66. Tarsometatarsus: ossified extensor retinaculum: absent (0); present (1). Character 64 of Clarke et al. (2009). Also character 35 of Mayr (2004).

67. Tarsometatarsus: shorter than humerus (0); elongate, surpassing humerus in length (1). Modified from Character 65 of Clarke et al. (2009) and Character 34 of Mayr (2004). In all known zygodactylids, the tarsometatarsus is extremely elongate.

68. Tarsometatarsus: well-developed medial plantar crest: absent (0); present (1). Character 66 of Clarke et al. (2009). This represents a portion of character 36 of Mayr (2004).

69. Tarsometatarsus: distal vascular foramen: moderate size (0); greatly enlarged (1). Discussed by Mayr and Mourer-Chauviré (2000). Character 67 of Clarke et al. (2009).

70. Tarsometatarsus: distal interosseal canal: present, canal open on plantar side, forming a deep, narrow sulcus between trochlea III and IV (0); absent (1). Clarke et al. 2009, character 68. Discussed in Mayr and Mourer-Chauviré (2000) and used in Mayr et al. (2004), as well as Mayr (2004).

71. Tarsometatarsus: large accessory trochlea on trochlea IV: absent (0); present (1). Character 69 of Clarke et al. (2009).

72. Tarsometatarsus: trochlea IV reaching almost as far distally as trochlea III and rotund in lateral view: absent (0); present (1). See Mayr et al. (2004). Character 70 of Clarke et al. (2009).

73. Pedal digit I, phalanx 1: proximal end: unexpanded (0); greatly expanded medially (1). See discussion by Mayr (1998: fig. 20). Character 71 of Clarke et al. (2009), Character 45 in Mayr (2004).

74. Pedal digit I, phalanx 1: length relative to other proximal phalanges: moderate length, e.g. subequal to pedal digit III, phalanx 1 (0); elongate, twice the length of proximal phalanx of digit III. Character 72 of Clarke et al. (2009). Character 46 in Mayr (2004).

75. Foot syndactyl: no (0); yes (1). Character 73 of Clarke et al. (2009).

76. Foot heterodactyl: no (0); yes (1). Character 74 of Clarke et al. (2009). State 1 is apomorphic of Trogonidae.

Myological

77. *Pectoralis pars propatagialis*, *pars longus*: fleshy (0); tendinous (1). Character 6 of Maurer and Raikow (1981). Character 75 of Clarke et al. (2009).

78. *Tensor propatagialis*: single belly (0); two bellies (1). Character 7 of Maurer and Raikow (1981). Character 76 of Clarke et al. (2009).

79. *Tensor propatagialis*, *pars longus*: present (0); absent (1). Character 8 of Maurer and Raikow (1981). Character 77 of Clarke et al. (2009).

80. *Deltoideus major*, scapular anchor: present (0); absent (1). Character 10 of Maurer and Raikow (1981). Character 78 of Clarke et al. (2009).

81. *Deltoideus minor*, insertion: anterior to supracoracoideus tendon (0); distal to supracoracoideus tendon (1); directly onto tendon (2). Character 79 of Clarke et al. (2009).

82. *Scapulotriceps*, *ligamentum tricipitale*: present (0); absent (1). Character 15 of

Maurer and Raikow (1981). Character 80 of Clarke et al. (2009).

83. *Expansor secondariorum pars cubtiti*: present (0); absent (1). Character 16 of Maurer and Raikow (1981). Character 81 of Clarke et al. (2009).

84. *Flexor digitorum profundus*: two heads (0); one head (1). Character 18 of Maurer and Raikow (1981). Character 82 of Clarke et al. (2009).

85. *Extensor carpi radialis*, origin: one head (0); two heads (1). Character 19 of Maurer and Raikow (1981). Character 83 of Clarke et al. (2009).

86. *Extensor carpi ulnaris*, origin: separate from *ectepicondylo-ulnaris* (0); origins fused (1). Character 20 of Maurer and Raikow (1981). Character 84 of Clarke et al. (2009).

87. *Extensor digitorum communis* origin: from humerus only (0); from humerus and radius (1). Character 21 of Maurer and Raikow (1981). Character 85 of Clarke et al. (2009).

88. *Extensor digitorum communis* insertion on alular phalanx: present (0); absent (1). Character 22 of Maurer and Raikow (1981). Character 86 of Clarke et al. (2009).

89. *Ectepocondylo-ulnaris*, origin: single tendon (0); two tendons (1). Character 23 of Maurer and Raikow (1981). Character 87 of Clarke et al. (2009).

90. *Extensor longus digiti major pars distalis*: present (0); absent (1). Character 24 of Maurer and Raikow (1981). Character 88 of Clarke et al. (2009).

91. *Extensor longus alulae*, radial head: present (0); absent (1). Character 25 of

Maurer and Raikow (1981). Character 89 of Clarke et al. (2009).

92. *Interosseus dorsalis*: bipennate (0); unipennate (1); absent (2). Character 90 of Clarke et al. (2009).

93. *Interosseus ventralis*: bipennate (0); unipennate (1). Character 29 of Maurer and Raikow (1981). Character 91 of Clarke et al. (2009).

94. *Iliotibialis cranialis* origin: single head (0); two heads (1). Character 1 of Swierczewski and Raikow (1981). Character 92 of Clarke et al. (2009).

95. *Femorotibialis externus pars distalis*: present (0); absent (1). Character 8 of Swierczewski and Raikow (1981). Character 93 of Clarke et al. (2009).

96. *Femorotibialis internus*: two bellies (0); one belly (1). Character 9 of Swierczewski and Raikow (1981). Character 94 of Clarke et al. (2009).

97. *Flexor cruris lateralis* and *flexor cruris medialis* tendons of insertion: connected (0); separate (1). Character 12 of Swierczewski and Raikow (1981). Character 95 of Clarke et al. (2009).

98. *Flexor cruris medialis* origin: from ischium (0); from ischium and pubis (1). Character 14 of Swierczewski and Raikow (1981). Character 96 of Clarke et al. (2009).

99. *Iliofemoralis internus*: present (0); absent (1). Character 20 of Swierczewski and Raikow (1981). Character 97 of Clarke et al. (2009).

100. *Iliotibialis lateralis*, acetabular part: fleshy (0); apneurotic (1); absent (2).

Character 98 of Clarke et al. (2009).

101. *Iliotrochantericus caudalis*, origin: dorsal iliac crest (0); spinal crest of synsacrum (1). Character 32 of Maurer and Raikow (1981). Character 99 of Clarke et al. (2009).

102. *Flexor cruris lateralis pars accesoria femoralis*: present (0); absent (1). Character 33 of Maurer and Raikow (1981). Character 100 of Clarke et al. (2009).

103. *Pubo-ischio-femoralis*, *pars medialis*: undivided (0); divided (1). Character 35 of Maurer and Raikow (1981). Character 101 of Clarke et al. (2009).

104. *Pubio-ischio-femoralis*: bellies separate (0); fused (1). Character 36 of Maurer and Raikow (1981). Character 102 of Clarke et al. (2009).

105. *Obturatorius lateralis pars dorsalis*: present (0); absent (1). Character 37 of Maurer and Raikow (1981). Character 103 Clarke et al. (2009).

106. *Obturatorius medialis*: oval (0); triangular (1). Character 38 of Maurer and Raikow (1981). Character 104 of Clarke et al. (2009).

107. *Gastrocnemius pars medialis*: single head (0); two heads (1). Character 39 of Maurer and Raikow (1981). Character 105 of Clarke et al. (2009).

108. *Gastrocnemius pars medialis*: origin from medial surface of tibiotarsus (0); origin from posterior surface of tibiotarsus (1). Character 40 of Maurer and Raikow (1981). Character 106 of Clarke et al. (2009).

109. *Fibularis longus*: present (0); absent (1). Character 42 of Maurer and Raikow

(1981). Character 107 of Clarke et al. (2009).

110. *Fibularis longus*, long branch, connecting to *flexor perforatus digiti III* tendon: present (0); absent (1). Character 41 of Maurer and Raikow (1981). This character is coded '?' in taxa lacking *fibularis longus*. Character 108 of Clarke et al. (2009).

111. *Fibularis brevis*, tibiotarsal ligament: present (0); absent (1). Character 25 of Swierczewski and Raikow (1981). Character 109 of Clarke et al. (2009).

112. *Plantaris*: present (0); absent (1). Character 110 of Clarke et al. (2009).

113. *Plantaris*, belly: short (0); long (1). Character 32 of Swierczewski and Raikow (1981). Character 111 of Clarke et al. (2009).

114. *Popletius*: present (0); absent (1). Character 43 of Maurer and Raikow (1981).Character 112 of Clarke et al. (2009).

115. *Extensor digitorum longus tendon*, first bifurcation: distal (0); proximal (1). Character 21 of Swierczewski and Raikow (1981). Character 113 of Clarke et al. (2009).

116. *Extensor digitorum longus*, tendinous slip to digit IV: absent (0); present (1). Character 22 of Swierczewski and Raikow (1981). Character 114 of Clarke et al. (2009).

117. *Flexor perforatus digiti* II, tendon: perforated by *flexor perforans et perforatus digiti II* and *flexor hallucis longus* tendons (0); not perforated (1). Character 26 of Swierczewski and Raikow (1981). Character 115 of Clarke et al. (2009).

118. *Flexor perforatus digiti* II: present (0); absent (1). Character 27 of Swierczewski and Raikow (1981). Character 116 of Clarke et al. (2009).

119. *Flexor perforans et perforatus digiti* II tendon perforated by *flexor hallucis longus* tendon: perforated (0); not perforated (1). Character 28 of Swierczewski and Raikow (1981). Character 117 of Clarke et al. (2009).

120. *Flexor perforatus digiti* III: two tendons of origin (0); one tendon of origin (1). Character 30 of Swierczewski and Raikow (1981). Character 118 of Clarke et al. (2009).

121. *Extensor brevis digiti* III: present (0); absent (1). Character 49 of Maurer and Raikow (1981). Character 119 of Clarke et al. (2009).

122. *Extensor brevis digiti* IV: present (0); absent (1). Character 50 of Maurer and Raikow (1981). Character 120 of Clarke et al. (2009).

123. *Abductor digiti* II: present (0); absent (1). Character 47 of Maurer and Raikow (1981). Character 121 of Clarke et al. (2009).

124. *Adductor digiti* II: present (0); absent (1). Character 48 of Maurer and Raikow (1981). Character 122 of Clarke et al. (2009).

125. *Abductor digiti* IV: present (0); absent (1). Character 51 Maurer and Raikow (1981). Character 123 of Clarke et al. (2009).

126. Vinculum of *flexor perforatus digiti* III and IV: absent (0); present (1). Character 52 of Swierczewski and Raikow (1981). Character 124 of Clarke et al. (2009).

127. *Flexor hallucis brevis*, tendon insertion: single (0); bifurcate (1). Character 37 of Swierczewski and Raikow (1981). Character 125 of Clarke et al. (2009).

128. *Abductor digiti* IV, retinaculum on trochlea IV: absent (0); present (1). Character 42 of Swierczewski and Raikow (1981). Character 126 of Clarke et al. (2009).

129. Deep plantar tendons, type (after George and Berger, 1966): type V (0); type VI (1); type VIII (2). Character 127 of Clarke et al. (2009).

130. *Flexor hallucis longus*: arises by one or two heads (0); arises by three heads (1). Character 128 of Clarke et al. (2009).

131. *Flexor hallucis longus*: supplies hallux (0); tendon excluded from hallux (1). Character 56 of Maurer and Raikow (1981). Character 129 of Clarke et al. (2009).

Plumage

132. Wing feathering: diastataxic (0); eutaxic (1). Scorings are based on Stephan (1970) and Bostwick and Brady (2002). Character 130 of Clarke et al. (2009).

133. Retrices highly stiffened: absent (0); present (1). Character 48 of Swierczewski and Raikow (1981). Character 131 of Clarke et al. (2009).

134. Central retrices with racquet-shaped tips: absent (0); present (1). Character 132 of Clarke et al. (2009).

135. Uropygial gland: naked or minutely tufted (0); tufted (1). Scorings are based on Johnston (1988). Character 133 of Clarke et al. (2009).

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