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Calcardea junnei Gingerich, 1987 from the late Paleocene of North America is not a heron, but resembles the early Eocene Indian taxon *Vastanavis* Mayr et al., 2007

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Abstract.—We revisit the holotype of *Calcardea junnei* Gingerich, 1987 from the latest Paleocene (Clarkforkian) of the Willwood Formation (Wyoming, USA). The species is based on a partial skeleton and was originally assigned to the Ardeidae (herons). As we show, this classification cannot be upheld and *Calcardea* Gingerich, 1987 more closely resembles the taxon *Vastanavis* Mayr et al., 2007 (Vastanavidae), a parrot-like bird from the early Eocene of India. Even though *C. junnei* is a large bird, its long wings and short tarsometatarsus argue against a predominantly terrestrial way of living, and the morphology of the tarsometatarsus and pedal phalanges instead suggest strong grasping feet. We conclude that an assignment of *Calcardea* to the landbird clade (Telluraves) is better supported than its classification into the waterbird clade (Aequornithes), which includes Ardeidae and other 'ciconiiform' and 'pelecaniform' taxa. *Calcardea junnei* is one of the oldest known representatives of Telluraves and its morphology shows plesiomorphic features, which contributed to its previous misidentification as a heron. *Calcardea* exhibits a distinctive osteology and affords a glimpse of a previously unknown late Paleocene avian morphotype.

Introduction

The sediments of the Willwood Formation in Wyoming (USA) have yielded a significant number of avian fossils, and the described diversity includes specimens of the palaeognathous Lithornithidae (Houde, 1988), the large, flightless Gastornithidae (Andors, 1992), the enigmatic, long-legged Geranoididae (Cracraft, 1969; Mayr, 2016), and the coliiform Sandcoleidae (Houde and Olson, 1992). However, most of these fossils stem from early Eocene strata of the Bighorn Basin, and of the above-listed taxa, only two species of the Lithornithidae (*Lithornis promiscuous* Houde, 1988 and *L. plebius* Houde, 1988) and one species of the Sandcoleidae (*Sandcoleus copiosus* Houde and Olson, 1992) were reported from earlier (late Paleocene) strata of Clarks Fork Basin.

The only further avian species that was described from the late Paleocene of Clarks Fork Basin is *Calcardea junnei* Gingerich, 1987, which was originally assigned to the Ardeidae (herons). This classification was already disputed by Mayr (2009, 2016), who raised the possibility that *C. junnei* could be related to the Geranoididae, of which only leg bones are known from early Eocene strata of the Willwood Formation.

Calcardea junnei is represented by a partial skeleton including fragments of several major limb bones. Despite its incomplete preservation, some bones of the holotype exhibit a distinctive morphology, and here we revisit the fossil and comment on its phylogenetic affinities.

Materials and methods

The holotype of *Calcardea junnei* was excavated in 1985 and the limestone matrix of the specimen was partially dissolved in 10% formic acid (Gingerich, 1987). Several vertebrae and other bone fragments of the specimen were prepared further at the Royal Belgian Institute of Natural Sciences. Following immersion in 7–10% acetic acid for 30–60 min, the bones were rinsed in water for at least four times longer than their immersion in acid. Finally, the bones were treated with Paraloid B72 to consolidate and protect them against oxidation.

Repositories and institutional abbreviations.—The fossils are deposited in the American Museum of Natural History, New York, USA (AMNH), the H.N.B. Garhwal University, Department of Geology, Uttarakhand, India (GU/RSR/VAS), the Institut für Geologische Wissenschaften und Geiseltalmuseum of Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany (IGWuG), and the University of Michigan, Museum of Paleontology, Ann Arbor, USA (UM).

Systematic paleontology

Aves Linnaeus, 1758
?Telluraves sensu Yuri et al., 2013
Calcardea Gingerich, 1987

Type species.—*Calcardea junnei* Gingerich, 1987, by original designation, monotypic.

Calcardea junnei Gingerich, 1987
Figures 1–4

Holotype.—UM 76882: partial skeleton including two cervical vertebrae (one nearly complete, the other consisting of a caudal fragment), a thoracic vertebra, a caudal vertebra*, a partial synsacrum*, a right coracoid lacking the midsection of the shaft and small portions of both ends, the damaged omal extremity of the left coracoid, the fragmentary extremitas cranialis of the right scapula, a cranial fragment of the sternum, the caput humeri and proximal section of the shaft of the left humerus, a fragment of the caput humeri and the cranioventral section of the distal end of the right humerus, the fragmentary proximal end of a ?left radius*, a portion of the distal section of the shaft of the right tibiotarsus*, fragments of both tarsometatarsi, two pedal phalanges, as well as other unidentifiable fragments. (Asterisks mark bones identified for the first time in the present study.)

Occurrence.—Head of Big Sand Coulee, Clarks Fork Basin, limestone lens J of University of Michigan locality SC-29 (discovery site), Park County, Wyoming, USA (Gingerich, 1987). Latest Paleocene, Clarkforkian North American Land Mammal Age, subzone Cf-3; 56.2–55.8 Myr (Secord et al., 2006; Manz and Bloch, 2015).

Description.—The most complete bone of the *Calcardea junnei* holotype is the right coracoid, which only lacks the midsection of the shaft (restored with plaster in the specimen) and small portions of the omal and sternal ends including the processus procoracoideus and the processus lateralis (Fig. 1.1–1.3). Of the left coracoid, the incomplete extremitas omalis is preserved. The bone exhibits a deeply excavated cotyla scapularis. The facies articularis humeralis is long and shows little lateral prominence. Most of the facies articularis clavicularis is broken, but the remaining portion indicates that it was overhanging the sulcus coracoideus. In the dorsal portion of the sulcus coracoideus, there is a small pneumatic opening in the section, where the extremitas omalis bends medially (Fig. 1.3). The bone exhibits a small foramen nervi supracoracoidei, which is located close to the medial margin of the shaft. The broken extremitas sternalis is positioned somewhat offset from the main axis of the shaft of the bone. The angulus medialis appears to have been prominent, although its tip is broken. The facies interna of the crista articularis sternalis is well developed. The processus lateralis is missing. Compared to extant taxa, the coracoid of *Calcardea* shows a resemblance to the corresponding bone of the Ardeidae (Fig. 1.7), Ciconiidae (Fig. 1.8), and Otididae (Fig. 1.9), but as already noted by Mayr et al. (2007), it also corresponds well with the coracoid of the early Eocene parrot-like taxon *Vastanavis* Mayr et al., 2007 (Fig. 1.4, 1.5; see Discussion).

Gingerich (1987) noted that the shape of the nearly complete cervical vertebra (Fig. 2.1–2.6) is highly unusual and not matched by any extant avian taxon. Gingerich (1987) considered this vertebra to be the seventh cervical, but here we regard its exact position in the vertebral column to be uncertain. As detailed by Gingerich (1987), this vertebra is characterized by

a derived shape of the facies articularis cranialis, which extends onto the dorsal side of the corpus and has a slightly convex surface (Fig. 2.1). In most extant birds, this articulation facet is saddle-shaped and cranially directed, but the sixth and seventh cervical vertebrae of Psittaciformes (parrots), e.g., *Strigops habroptila* Gray, 1845 (Fig. 2.8) and some Strigiformes (owls), e.g., *Bubo scandiacus* (Linnaeus, 1758) (Fig. 2.9) exhibit a morphology like *Calcardea*. Another characteristic feature of the specimen is the presence of prominent tori dorsales of the zygapophyses caudales, which in lateral view form a marked caudal step and create a distinct dorsal fossa immediately cranial of the lacuna interzygapophysialis (Fig. 2.3, 2.6). Similarly, elevated tori dorsales occur on the caudalmost cervical vertebrae of, e.g., Phoenicopteriformes (flamingos), Podicipediformes (grebes), and some Gruiformes (e.g., Gruidae [cranes]); in these birds, the respective vertebrae otherwise, however, have a different shape and are much shorter. In caudal view, the facies articularis caudalis is dorsoventrally deep but mediolaterally narrow, which contrast with the opposite condition in most extant birds. The sulcus caroticus on the ventral surface of the vertebra is mediolaterally narrow. In addition to this nearly complete cervical vertebra, the holotype includes the fragmentary caudolateral portion of another cervical vertebra, which has not been previously mentioned. This vertebra also features a prominent torus dorsalis, but otherwise it is too fragmentary for meaningful comparisons.

The holotype furthermore comprises a thoracic vertebra, which has not yet been described and likewise exhibits a distinctive morphology (Fig. 2.10, 2.11). A notable feature of the specimen is the presence of large pneumatic openings on the lateral surfaces of the vertebral body. Such openings have a restricted distribution among extant birds and are not to be confused with the deep fossae present in some taxa (e.g., Charadriiformes and Procellariiformes). Equally large foramina only occur in the anseriform Anhimidae, whereas smaller foramina are present in the gruiform Gruidae and some species of the accipitriform Cathartidae, e.g., *Cathartes aura* (Linnaeus, 1758). The thoracic vertebra of *Calcardea* is furthermore acoelous, with essentially flat cranial and caudal articulation facets. This morphology contrasts sharply with the condition found in most extant birds, in which the thoracic vertebrae are heterocoelous and have saddle-shaped articular surfaces. Acoelous vertebrae are found in the Sphenisciformes (penguins), the suliform Phalacrocoracidae (cormorants) and Anhingidae (anhingas), but also in some Psittaciformes (e.g., *Strigops* Gray, 1845, *Anodorhynchus* Spix, 1824). The corpus of the thoracic vertebra of *Calcardea* lacks a processus ventralis.

The largest fragment of the synsacrum (Fig. 3.8) stems from the central section and comprises 6–7 fused vertebrae. In addition, there is the caudalmost end of the synsacrum, which consists of two vertebrae with their dorsal sections incompletely fused. The fragmentary caudal vertebra preserved in the holotype lacks a processus ventralis (Fig. 2.12, 2.13).

The fragmentary scapula (Fig. 3.1) does not allow a meaningful description and lacks features of taxonomic significance. The main characteristics of the cranial fragment of the sternum (Fig. 3.2, 3.3) were described by Gingerich (1987), who noted that the bone exhibits overlapping sulci coracoidei and a well-developed spina externa. Although the condition of the sulci
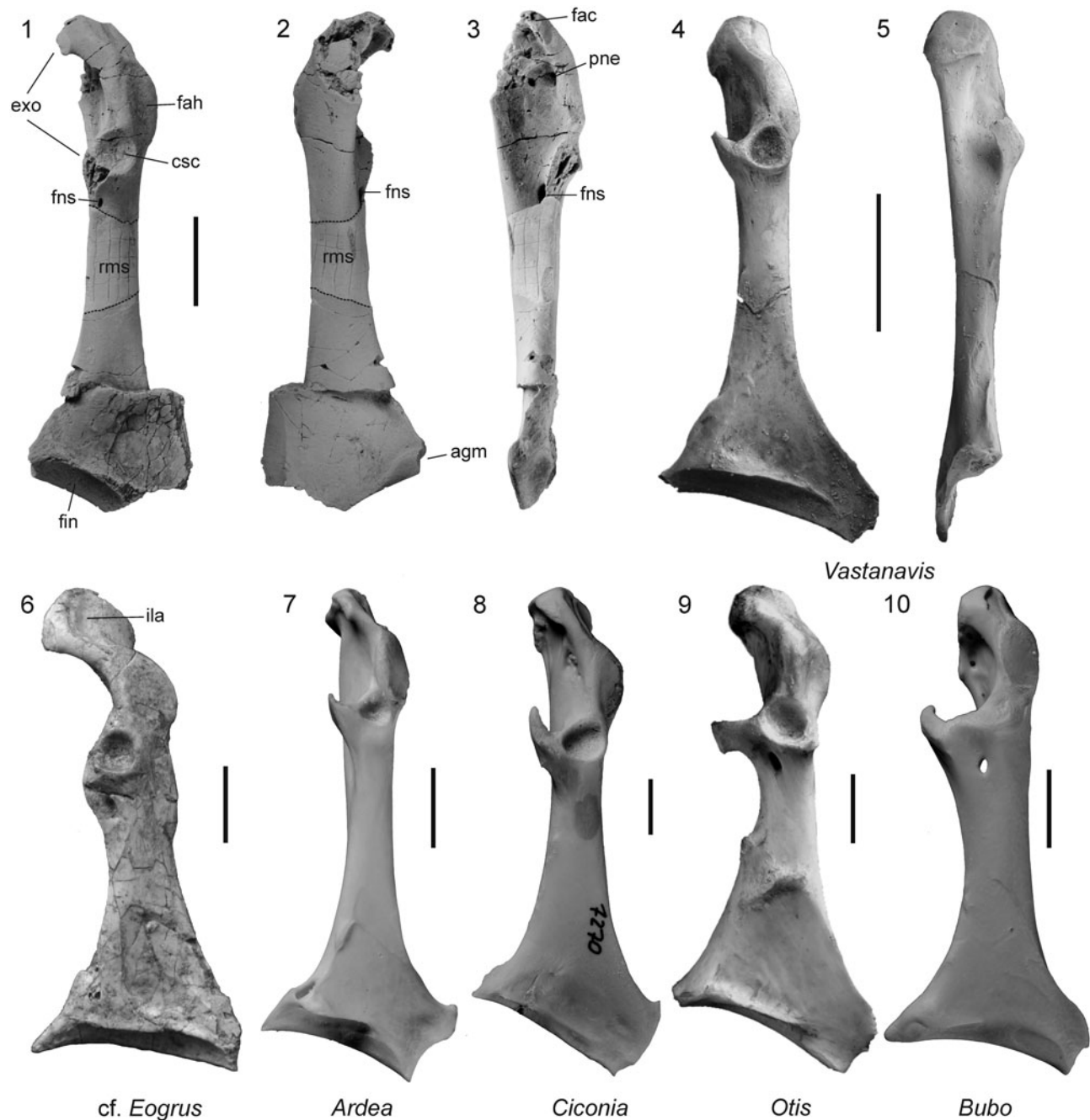
Figure 1. *Calcardea junnei* Gingerich, 1987 from the late Paleocene of the Willwood Formation (Wyoming, USA), coracoid of the holotype (UM 76882) in comparison to the coracoids of various extant and fossil taxa: (**1–3**) *Calcardea junnei*, right coracoid in dorsal (**1**), ventral (**2**), and medial (**3**) views (dotted black lines delimit the restored midsection of the shaft); (**4, 5**) *Vastanavis eocaena* Mayr et al., 2007 from the early Eocene Vastan Lignite Mine in India in dorsal (**4**) and medial (**5**) views (GU/RSR/VAS 1254, mirrored to ease comparisons); (**6**) *Eogrus aeola* Wetmore, 1934 (Eogruidae), tentatively referred left coracoid (AMNH 2941, mirrored to ease comparisons) from the middle Eocene of Inner Mongolia (China); (**7**) Great Egret, *Ardea alba* Linnaeus, 1758 (Ardeidae); (**8**) White Stork, *Ciconia ciconia* (Linnaeus, 1758) (Ciconiidae); (**9**) Great Bustard, *Otis tarda* Linnaeus, 1758 (Otididae); (10) Snowy Owl, *Bubo scandiacus* (Linnaeus, 1758) (Strigiformes). The fossil bones in (**1–5**) were coated with ammonium chloride. agm = angulus medialis; csc = cotyla scapularis; exo = extremitas omalis; fac = facies articularis clavicularis; fah = facies articularis humeralis; fin = facies interna of crista articularis sternalis; fns = foramen nervi supracoracoidei; ila = impressio ligamenti acrocoracohumeralis; pne = pneumatic opening in sulcus coracoideus; rms = restored midsection of shaft. Scale bars = 10 mm.

coracoidei indeed resembles the morphology found in the Ardeidae, the spina externa is dorsoventrally flat and mediolaterally broad and therefore very unlike the mediolaterally compressed and blade-like spina externa of the Ardeidae.

The fragmentary left humerus includes the caput humeri (Fig. 3.4) and the proximal section of the shaft (Fig. 3.5).

Preserved parts indicate a bone of similar overall proportions to the humerus of, e.g., extant Cathartidae (and many other taxa with a humerus morphology like New World vultures). The cranioventral portion of the distal end of the right humerus (Fig. 3.6) is also part of the *Calcardea* holotype. When first described, this was erroneously considered to be the "external
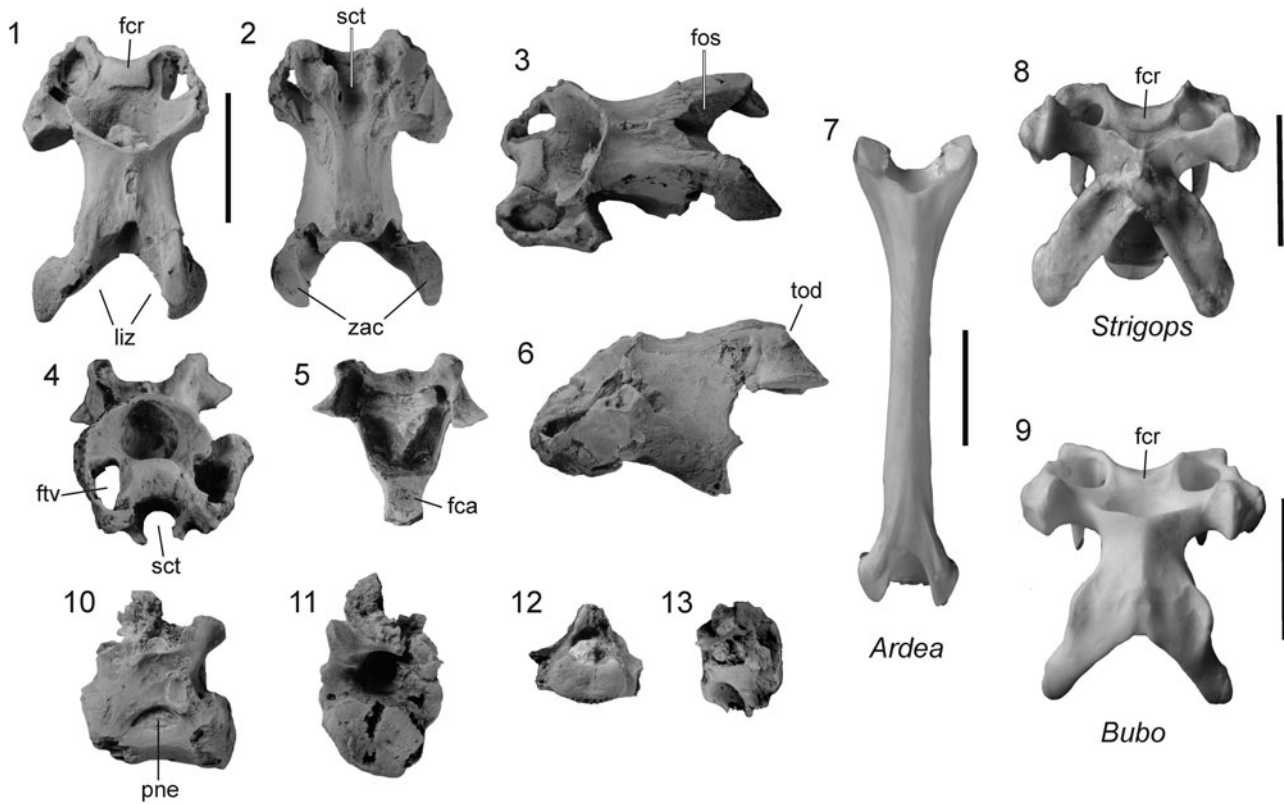
Figure 2. *Calcardea junnei* Gingerich, 1987 from the late Paleocene of the Willwood Formation (Wyoming, USA), vertebrae of the holotype (UM 76882): (**1–6**) nearly complete cervical vertebra in dorsal (**1**), ventral (**2**), laterodorsal (**3**), cranial (**4**), caudal (**5**), and lateral (**6**) views; (**7–9**) sixth cervical vertebrae of the Great Egret, *Ardea alba* Linnaeus, 1758 (Ardeidae) (**7**), the Kakapo, *Strigops habroptila* Gray, 1845 (Psittaciformes) (**8**), and the Snowy Owl, *Bubo scandiacus* (Linnaeus, 1758) (Strigiformes) (**9**); (**10, 11**) thoracic vertebra in left lateral (**10**) and caudal (**11**) views; (**12, 13**) caudal vertebra in caudal (**12**) and dorsal (**13**) views. The fossil bones were coated with ammonium chloride. fca = facies articularis caudalis; fcr = dorsally bulging facies articularis cranialis; fos = fossa formed by prominent tori dorsales; ftv = foramen transversarium; liz = lacuna interzygapophysialis; pne = pneumatic opening; sct = sulcus caroticus; tod = torus dorsalis; zac = zygapophysis caudalis. Scale bars = 10 mm; same scale for (**1–6, 10–13**).

condyle with ectepicondylar prominence" (Gingerich, 1987, p. 299). This latter bone fragment bears a pronounced fossa on the cranial surface of the epicondylus ventralis; unlike in the Ardeidae, the tuberculum supracondylare ventrale is proximodistally short. The proximal end of the ?left radius (Fig. 3.7)—the only other wing bone preserved in the *C. junnei* holotype—resembles the proximal radius of, e.g., *Bubo bubo* Linnaeus, 1758 (Strigiformes), but does not exhibit features of particular phylogenetic significance.

Another bone fragment is here identified as the distal section of the shaft of the right tibiotarsus, which is broken immediately before the condyles (Fig. 4.11, 4.12). The bone exhibits a small tubercle on the medial side of the cranial surface, which is likely to be the medial attachment site for the tuberositas retinaculi extensori; this tubercle appears to have been in a far proximal position, as it is in, e.g., extant Psittaciformes and Strigiformes. Only the most proximal section of the sulcus extensorius is preserved and it cannot be determined whether a pons supratendineus was present. Although the distal end of the bone is missing, the proportions of the preserved section of the shaft suggest a mediolaterally wide and craniocaudally narrow distal end. A further 19 mm long bone fragment, which exhibits a low crest along one side, could represent a portion of the proximal tibiotarsus with the crista fibularis.

Fragments of both tarsometatarsi are preserved, with the right one represented by a major section of the shaft lacking both ends (Fig. 4.1, 4.2) and the left one by a distal end with broken trochleae and a portion of the shaft (Fig. 4.3–4.7). The shaft of the more complete right tarsometatarsus widens proximally and its distal end is broken just proximal of the onset of the trochleae, with a small portion of the sulcus extensorius preserved. The proximal end is broken distal of the hypotarsus and neither foramina vascularia proximalia nor the tuberositas musculi tibialis cranialis are preserved. The shaft section of the left tarsometatarsus is broken at approximately the same proximal level and also lacks traces of the hypotarsus and other diagnostic structures. From the proportions of the preserved fragment of the right tarsometatarsus, it can be inferred that ∼ 60–75% of the bone are preserved. Overall, the tarsometatarsus of *Calcardea* would therefore have been comparatively short and of similar proportions to the tarsometatarsus of the coliiform *Sandcoleus copiosus* (see introduction) or extant Cathartidae (New World vultures). The preserved portion of the shaft is dorsoplantarly flat and lacks any indication of a crista medianoplantaris. A shallow and narrow tendinal sulcus runs along the plantar surface of the distal end of the bone, between the fused metatarsals II and III (Fig. 4.1). Although the trochleae of both tarsometatarsi are broken and missing, the left tarsometatarsus
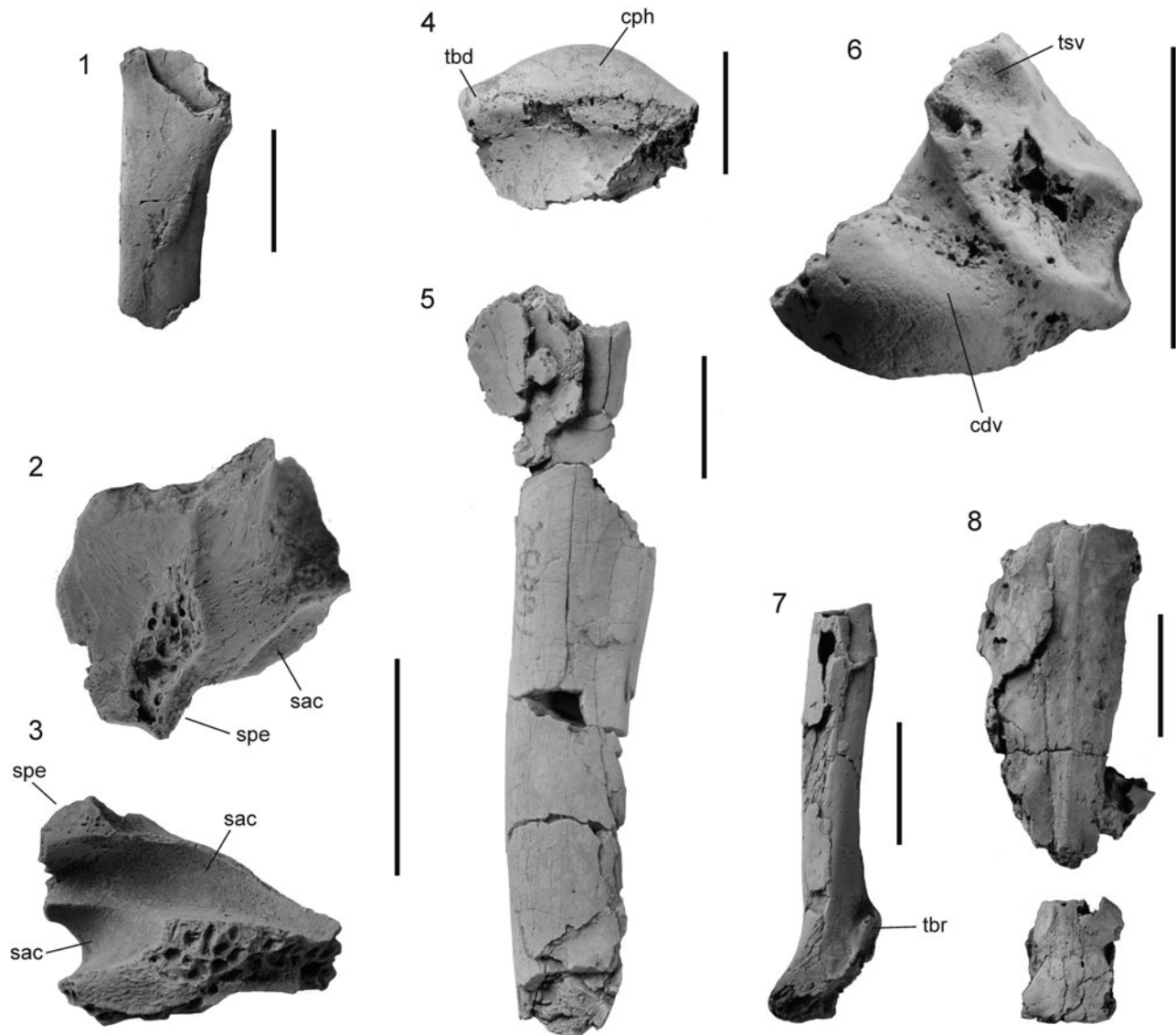
Figure 3. *Calcardea junnei* Gingerich, 1987 from the late Paleocene of the Willwood Formation (Wyoming, USA), diverse bone fragments of the holotype (UM 76882): (**1**) fragmentary extremitas cranialis of right scapula in lateral view; (**2, 3**) cranial fragment of the sternum in ventral (**2**) and cranial (**3**) views; (**4, 5**) left humerus, fragment of proximal end (**4**) and proximal section of shaft (**5**) in caudal view; (**6**) ventrodistal fragment of the right humerus in cranial view; (**7**) fragmentary proximal end of the ?left radius; (**8**) two fragments of the synsacrum in ventral view. All bones were coated with ammonium chloride. cdv = condylus ventralis; cph = caput humeri; sac = sulcus articularis coracoideus; spe = spina externa; tbd = tuberculum dorsale; tbr = tuberculum bicipitale radii; tsv = tuberculum supracondylare ventrale. Scale bars = 10 mm.

preserves the section immediately proximal to them. In this specimen, the proximal portion of the foramen vasculare distale is visible, and the distal fragment of the left tarsometatarsus shows an indistinct fossa metatarsi I, which is located on the medial surface of the tarsometatarsus. Based on the proportions of this fragment, the distal end of the bone must have been fairly wide, with a medially prominent trochlea metatarsi II (Fig. 4.8). In distal view, the distal portion of the left tarsometatarsus shows that the trochlea metatarsi II was not significantly wider than the trochlea metatarsi IV (Fig. 4.7). The broken ends of the tarsometatarsus fragments furthermore show that the bone was remarkably thick walled and that the bone cortex was traversed by numerous canals. In proximal view, the shaft of the right tarsometatarsus allows the recognition of the three metatarsals, which are well separated by thin osseous sheets in the interior

of the bone. Because the distal end of the humerus exhibits well-defined osteological structures, incomplete fusion of the metatarsals is unlikely to indicate a subadult condition.

The two pedal phalanges (Fig. 4.13–4.16) are short and stout and, hence, clearly distinguished from the long and slender pedal phalanges of the Ardeidae. The phalanges are notably large and robust in relation to the size of the tarsometatarsus, which indicates unusually strong feet. The exact identity of the phalanges is difficult to determine, but both are likely to belong to either digit 2 or digit 3.

Measurements (in mm).—Right coracoid, maximum length as preserved, 58.0. Right tibiotarsus, preserved distal width of fragment, 9.2; estimated original distal width of bone, ~10. Right tarsometatarsus, preserved length of fragment, 29.7;
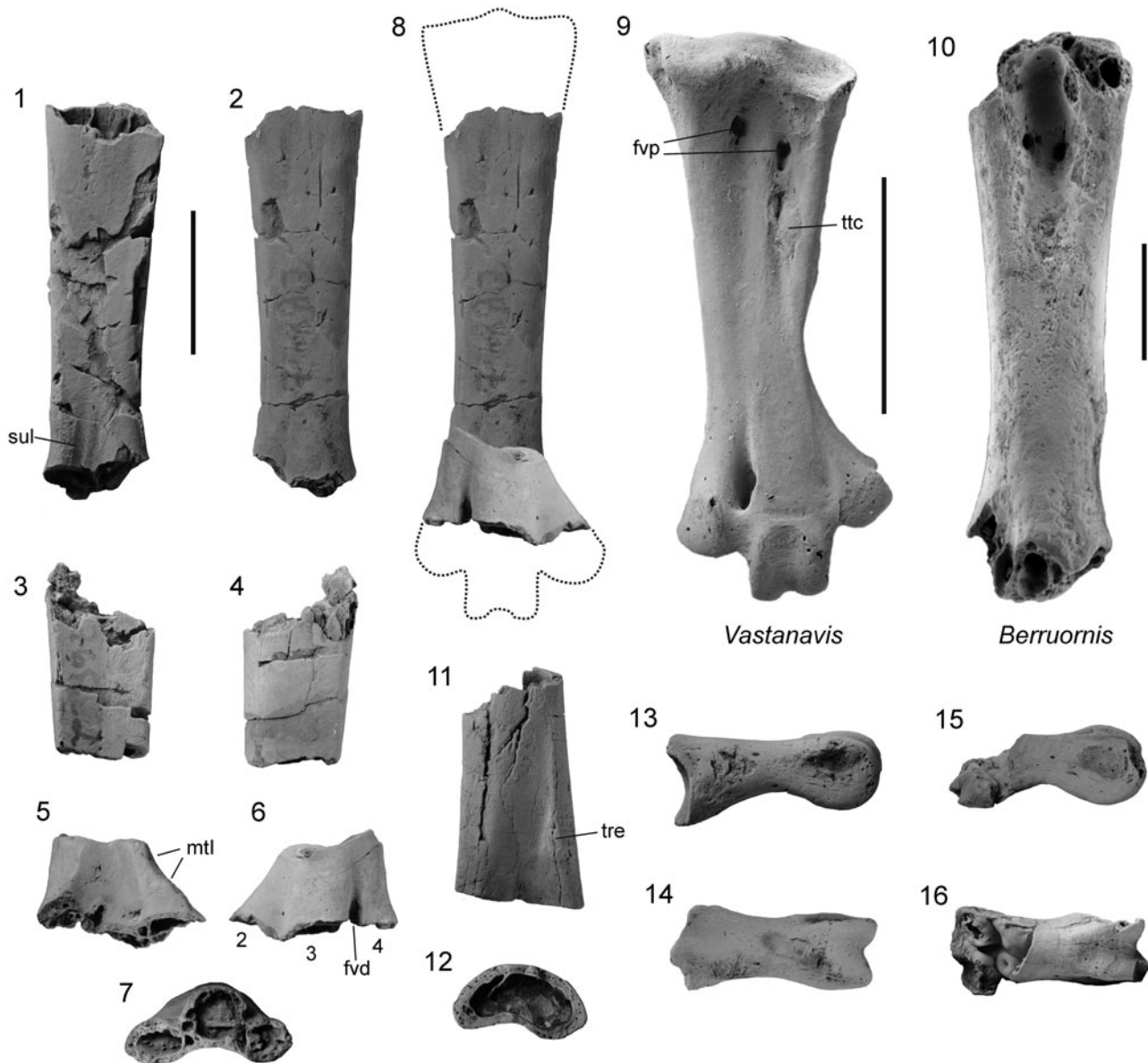
Figure 4. *Calcardea junnei* Gingerich, 1987 from the late Paleocene of the Willwood Formation (Wyoming, USA), leg bones of the holotype (UM 76882): (**1, 2**) shaft section of the right tarsometatarsus in plantar (**1**) and dorsal (**2**) views; (**3, 4**) shaft section of the left tarsometatarsus in plantar (**3**) and dorsal (**4**) views; (**5–7**) fragmentary distal end of the left tarsometatarsus in plantar (**5**), dorsal (**6**, with bases of the broken trochleae numbered), and distal (**7**) views; (**8**) tentative reconstruction of the original shape of the tarsometatarsus with the shaft of the right tarsometatarsus and the mirrored distal fragment of the left tarsometatarsus superimposed, and with dotted lines indicating the reconstructed shape of the bone; (**9**) tarsometatarsus of *Vastanavis* sp. (GU/RSR/VAS 1809); (**10**) holotype tarsometatarsus of *Berruornis halbedeli* Mayr, 2007 from the Paleocene of Walbeck (IGWuG WAL01.2001); (**11, 12**) distal section of the shaft of the right tibiotarsus in cranial (**11**) and distal (**12**) views; (**13, 14**) and (**15, 16**) two pedal phalanges in lateral (**13, 15**) and dorsal (**14, 16**) views. All fossil bones were coated with ammonium chloride. fvd = foramen vasculare distale; fvp = foramina vascularia proximalia; mtI = fossa metatarsi I; sul = sulcus on plantar surface of distal tarsometatarsus; tre = tuberositas musculi tibialis cranialis; ttc = tuberositas retinaculi extensori. Scale bars = 10 mm; same scale for all except (**9, 10**).

estimated total length of bone, 40–50. Left tarsometatarsus, preserved distal width, 11.5; estimated total width, 13–15.

Remarks.—The holotype of *Calcardea junnei* consists of a partial postcranial skeleton, but so far only the most diagnostic bones have been described and no photographs of the specimens have been published. Like many other vertebrate remains from the Willwood Formation (see Bloch and Boyer, 2001), the fossil was found in a freshwater limestone lense (Gingerich, 1987). There are no duplicate elements in the material and all bone fragments match in their sizes, so it is

reasonable to assume that they stem from the same individual. In several instances, fragments of the same bone are markedly differently colored, which indicates that they were embedded in a fractured state and fossilized in different microenvironments that led to a differential staining of the isolated fragments.

Discussion

The skeletal morphology of *Calcardea junnei* does not indicate close affinities to the Ardeidae, from which most bones of the

fossil species are clearly distinguished. Gingerich (1987) listed the overlapping sulci coracoidei in support of ardeid affinities, but this feature occurs in too many distantly related avian taxa to be of great phylogenetic significance (apart from their well-known presence in many aquatic and semiaquatic birds, overlapping sulci coracoidei are, for example, found in Falconidae and Musophagidae; see Mayr and Clarke, 2003, character 69). Even though the coracoid shows a resemblance to the corresponding bone of the Ardeidae, it exhibits a foramen nervi supracoracoidei (absent in herons) and has a proportionally longer omal extremity (compare Fig. 1.1 and 1.7). The tarsometatarsus of *C. junnei* lacks a well-developed, semicircular fossa metatarsi I, which is a derived feature of herons (Mayr et al., 2018a). Its shortness, which is evident from the proportions of the preserved fragments, furthermore conflicts with classification in the Ardeidae or any other taxon of the waterbird clade (Aequornithes), which includes the traditional ciconiiform and pelecaniform birds (Mayr, 2011). The cervical vertebra of *C. junnei* differs entirely from that of the Ardeidae in its proportions (compare Fig. 2.1 and 2.7). The short pedal phalanges likewise do not support closer affinities of *Calcardea* to the Ardeidae, which have very long toes with elongate phalanges.

As mentioned in the Introduction, Mayr (2009, 2016) considered the possibility that *Calcardea* is a representative of the Geranoididae, which is among the more abundant bird families in early Eocene strata of the Willwood Formation. However, the short tarsometatarsus clearly precludes the assignment of *C. junnei* to the very long-legged Geranoididae. The coracoid of the Geranoididae is unknown, and even though the coracoid of *Calcardea* shows superficial similarity to that of the closely related Eogruidae from the Eocene of Asia (Fig. 1.6), it has a proportionally shorter extremitas omalis, a less conspicuous foramen nervi supracoracoidei, and a less distinct impressio ligamenti acrocoracohumeralis.

Mayr et al. (2007) already noted that the coracoid of *Calcardea* resembles that of *Vastanavis* (Vastanavidae), a well-represented avian taxon from the early Eocene (~ 54.5 Ma) Cambay Shale Formation of the Vastan and Tadkeshwar Lignite mines in western India (Mayr et al., 2007, 2010, 2013; Smith et al., 2016). Fossils of similar taxa also were reported from the early Eocene of Europe and North America (Mayr et al., 2010; Mayr, 2015). *Vastanavis* is a parrot-like bird, but its exact affinities are not well resolved and a recent analysis placed it outside Psittacopasseres, the clade including Psittaciformes and Passeriformes (Mayr, 2015).

Our direct examination of the *C. junnei* holotype corroborates the similarity of the coracoid to that of *Vastanavis*; shared features include the straight extremitas omalis and rounded processus acrocoracoideus, the similar shape of the facies articularis humeralis, and the deeply excavated and circular cotyla scapularis. The coracoid of *Calcardea* differs from that of *Vastanavis* in that the medial surface of the sulcus coracoideus is more deeply excavated, the extremitas omalis is somewhat longer, and the shaft of the bone exhibits a small foramen nervi supracoracoidei. Mayr et al. (2007) furthermore considered the crista articularis sternalis of *Calcardea* to be oriented more obliquely to the longitudinal axis of the coracoid shaft, although this difference might be an artifact of the somewhat dislocated extremitas sternalis of the bone. The tarsometatarsus of *Calcardea*

agrees with that of *Vastanavis* in its flat plantar surface, the dorsoplantarly compressed shaft, and the medially situated fossa metatarsi I (which forms a concave facet in *Vastanavis*), but the bone is proportionally narrower than the tarsometatarsus of *Vastanavis* (Fig. 4.8, 4.9). The preserved fragments of the humerus and tibiotarsus resemble the corresponding bones of *Vastanavis*, but both elements are too incomplete for meaningful comparisons. The sizes of the vertebrae, coracoid, and distal tibiotarsus of *C. junnei* are comparable to those of a Hyacinth Macaw, *Anodorhynchus hyacinthinus* (Latham, 1790), which is one of the largest extant parrots. *Calcardea junnei* was therefore distinctly larger than the two known species of *Vastanavis*; the coracoid measures 31 mm in *V. cambayensis* Mayr et al., 2010 and 35–39 mm in *V. eocaena* Mayr et al., 2007, and the tarsometatarsus of *Vastanavis* has a length of 23–24 mm (Mayr et al., 2010, 2013).

As detailed above, the vertebrae of *Calcardea* show a resemblance to those of both Psittaciformes and Strigiformes. The tarsometatarsus shaft of *Calcardea* also has similar proportions to that of the strigiform taxon *Berruornis* Mourer-Chauviré, 1994 from the late Paleocene of Europe (Fig. 4.10; Mourer-Chauviré, 1994; Mayr, 2002, 2007). However, *Berruornis* represents an even larger bird and has a mediolaterally wider trochlea metatarsi II. The proportionally narrower trochlea metatarsi II (as inferred from the remains of this trochlea on the distal end of the left tarsometatarsus of the holotype) also distinguishes *C. junnei* from the North American Protostrigidae, of which one species, *Eostrix mimica* (Wetmore, 1938), was found in the Wasatch Formation of Wyoming, which is coeval in age to early Eocene strata of the Willwood Formation (Wetmore, 1938). The coracoids of *Berruornis* and protostrigid owls is unknown, but the coracoid of *Calcardea* is quite unlike the known coracoids of other fossil and extant Strigiformes, in which the foramen nervi supracoracoidei is larger, the facies articularis humeralis more dorsally directed, and a shallow facies articularis scapularis rather than a cotyla scapularis is present (Fig. 1.10).

With an estimated humerus length of 110–130 mm and a tarsometatarsus length of 40–50 mm, *Calcardea junnei* had long wings and comparatively short legs, which indicates that it was not a predominantly terrestrial bird. In its proportions and with regard to the essentially flat plantar surface, the tarsometatarsus resembles that of birds with well-developed grasping capabilities and strong flexor tendons, such as parrots, owls, and diurnal birds of prey. However, because critical parts of the *C. junnei* skeleton remain unknown, e.g., the distal end of the tarsometatarsus as well as the shapes of the beak and the ungual phalanges, inferences on the possible foraging habits and diet of the species cannot be drawn.

We conclude that *Calcardea* is not a representative of the Ardeidae and has no significance in reconstructing the origin of this clade. Compared with the known early Paleogene avian taxa, *Calcardea* is most similar to the geologically slightly younger (by 2 million years) *Vastanavis*, but owing to the fragmentary condition of the holotype and only known specimen of *C. junnei*, we cannot exclude the possibility that the similarities to *Vastanavis* are due to the retention of plesiomorphic features. In any case, the available evidence conforms best with a tentative assignment of *Calcardea* to Telluraves, the clade formed

by diurnal birds of prey and the arboreal landbirds (Yuri et al., 2013). Our classification is mainly based on the overall morphology of the bones, but even though no autapomorphy of Telluraves has yet been identified, a dorsoplantarly flat tarsometatarsus is a derived characteristic that is only present in representatives of this clade.

Mayr (2017, p. 93, 204) hypothesized that deforestation after the K/Pg impact might have caused the extinction the Mesozoic Enantiornithes and enabled the radiation of arboreal Neornithes, most of which belong to the Telluraves (these conclusions were reinforced by Field et al., 2018, who overlooked the earlier study). Previously known Paleocene representatives of Telluraves include stem group representatives of Cariamiformes (seriemas; Alvarenga, 1985) and Strigiformes (Rich and Bohaska, 1981; Mourer-Chauviré, 1994; Mayr, 2002, 2007), as well as putative stem group representatives of Coliiformes (mousebirds; Ksepka et al., 2017) and Psittacopasseres (Mayr et al., 2018b). All of these fossils were assigned to extant clades within Telluraves and so far no truly archaic representatives of Telluraves have been found. Although the exact affinities of *Calcardea* can only be determined through the identification of further fossils, the taxon exhibits a distinctive osteology and affords a glimpse of a previously unknown late Paleocene avian morphotype. We consider it possible that the morphology of the North American taxon is close to the plesiomorphic bauplan of Telluraves, but well-based inferences on the evolutionary significance of *Calcardea* must await more complete fossils; it is to be hoped that future discoveries shed more light on this unusual bird.

Acknowledgments

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