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A New Avian Species with Tubercle-bearing Cervical Vertebrae from the Middle Eocene of Messel (Germany)

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ABSTRACT. A new avian species, *Perplexicervix microcephalon* n.gen. and n.sp., is described from the Middle Eocene of Messel in Germany. It is most unusual in that the cervical vertebrae of five of the six known specimens bear numerous bony tubercles. Such tubercles were also reported from another avian fossil from the Messel deposits, which is a representative of the extinct taxon Idiornithidae. Although the osteology of *P. microcephalon* is not known well enough for a reliable phylogenetic assignment, the new species clearly does not belong to the Idiornithidae. Compared to extant birds, it agrees with Anhimidae and Cathartidae in some osteological features. The origin of the vertebral tubercles remains mysterious. The fact that these structures are now known from two unrelated avian taxa supports previous assumptions, that they represent a pathologic condition. Not in line with this assumption, however, is their occurrence in all specimens referred to *P. microcephalon*, in which cervical vertebrae are preserved.

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Peters (1995) described a remarkable skeleton of a large bird from the Middle Eocene of Messel in Germany as *Idiornis tuberculata*. This species belongs to the Idiornithidae, stem lineage representatives of the Cariamidae. Apart from being the most complete skeleton of an idiornithid, it is of particular interest in that the cervical vertebrae and few other bones are covered by numerous small tubercles of enigmatic origin and significance.

Such tubercles were subsequently also reported on the cervical vertebrae of two other bird specimens from Messel, and on a cervical vertebra from the Quercy fissure fillings in France (Mayr, 2007). Both Messel fossils consist only of skulls with a few cervical vertebrae, and belong to a bird that is smaller than *I. tuberculata*. Because of their fragmentary preservation, a taxonomic and phylogenetic assignment was not possible. Concerning the origin of the tubercles, Mayr (2007) concluded that they most likely are of pathologic origin and document a Paleogene avian disease without a modern counterpart.

Here I describe new fossil birds from Messel which can be referred to the same species as the above-mentioned skulls. One of them is a fairly complete skeleton that was unknown to me in 2007, and has the cervical vertebrae and few other bones likewise covered with numerous small tubercles.

Material and methods

Osteological terminology follows Baumel & Witmer (1993). Measurements are in millimetres and indicate the maximum length of the bone along its longitudinal axis; the length of the claws was measured from the tip of the tuberculum extensorium to the apex phalangis. Institutional abbreviations: SMF—Forschungsinstitut Senckenberg, Frankfurt am Main; HLMD—Hessisches Landesmuseum, Darmstadt.

Systematic paleontology

Neognathae incertae sedis

Perplexicervix n.gen.

Type species. *Perplexicervix microcephalon* n.sp.

Diagnosis. *Perplexicervix* n.gen. is characterized by the following features: (1) skull small in comparison to postcranial skeleton; (2) beak short, triangular in dorsoventral view, with a straight culmen, sigmoid tomia, and a slightly hooked tip; (3) surface of cranium with marked pores and furrows; (4) well-developed processus basipterygoidei present; (5) processus extensorius of carpometacarpus prominent and with broadly rounded tip; (6) tarsometatarsus elongate with short trochleae metatarsorum II et IV; (7) hallux long. Characters (2), (3), and (5) are considered autapomorphies of the new taxon.

Etymology. From *perplexus* (Lat.): incomprehensible, and *cervix* (Lat.): neck, in reference to the curious tubercles on the cervical vertebrae.

Perplexicervix microcephalon n.gen. and n.sp.

Holotype. SMF-ME 11211a+b (partially dissociated skeleton lacking the left leg; Fig. 1a).

Referred specimens. SMF-ME 3548 (skull with atlas, axis, and third vertebra; Fig. 2a), SMF-ME 10846a+b (skull and cranialmost six cervical vertebrae; Fig. 2c), SMF 2559a+b (partial postcranial skeleton; Fig. 3), HLMD-Me 14996a+b (postcranial skeleton; Fig. 1b). There is a further, uncatalogued skeleton of *Perplexicervix microcephalon* in the collection of B. Pohl (Groß-Bieberau, Germany), which also exhibits numerous tubercles on the cervical vertebrae (Fig. 4).

Type locality and horizon. Messel near Darmstadt, Germany; lower Middle Eocene (MP 11; about 47 Ma).

Diagnosis. As for genus.

Measurements. SMF-ME 11211a+b (holotype): Skull, 56.6; humerus ca. 73 (right; visible through the transparent reverse of the slab); ulna, ca. 85 (right), 79.5 (right); carpometacarpus, 40.5 (left), ca. 40 (right); femur, 45.2 (right); tibiotarsus, ca. 71 (?) (right; calculated by adding the lengths of the two broken halves); tarsometatarsus, ca. 60 (?) (right; calculated by adding the lengths of the two

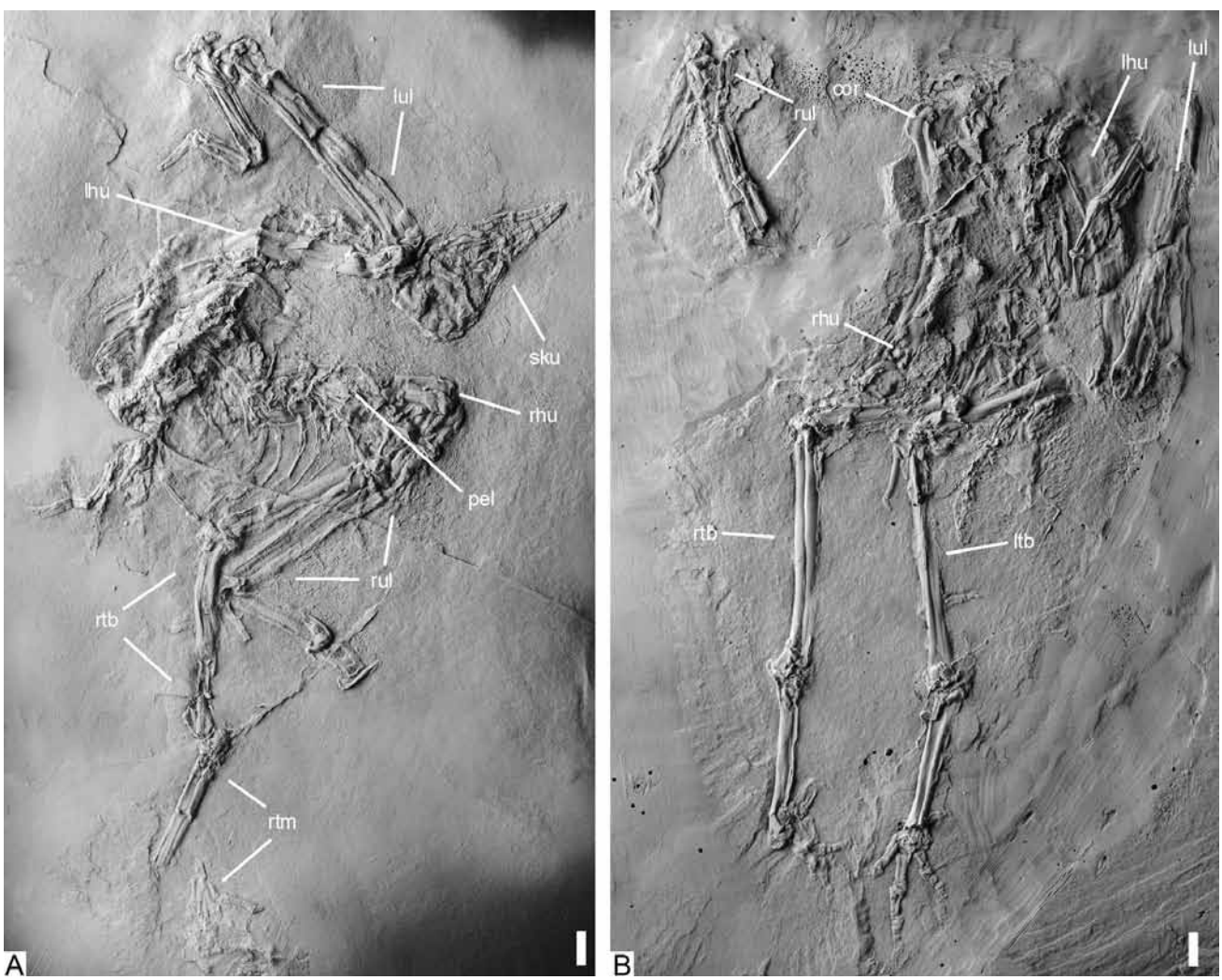

Figure 1. *Perplexicervix microcephalon* n.gen. and n.sp. (*A*) holotype (SMF-ME 11211a); (*B*) HLMD-Me 14996a. Abbreviations: *cor*—coracoid, *lhu*—left humerus, *ltb*—left tibiotarsus, *lul*—left ulna, *pel*—pelvis, *rhu*—right humerus, *rtb*—right tibiotarsus, *rtm*—right tarsometatarsus, *rul*—right ulna, *sku*—skull. Coated with ammonium chloride to enhance contrast; scale bars equal 10 mm.

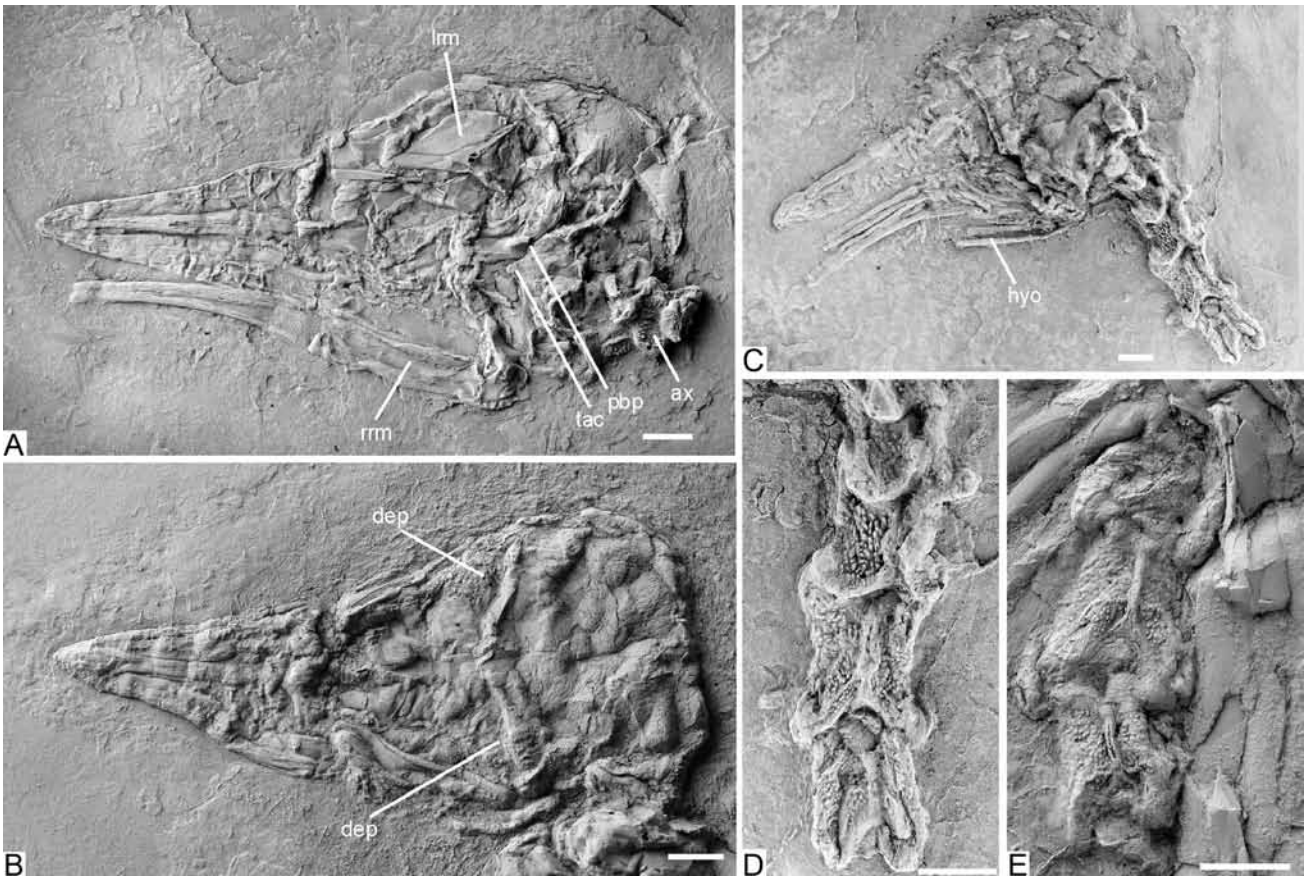

Figure 2. *Perplexicervix microcephalon* n.gen. and n.sp., skull (*A–C*) and cervical vertebrae (*D, E*). (*A*) SMF-ME 3548 (ventral view); (*B*) holotype (SMF-ME 11211a; dorsal view); (*C*) SMF-ME 10846a (lateral view); (*D*) holotype (SMF-ME 11211a); (*E*) referred specimen SMF-ME 10846a. Abbreviations: ax—axis, dep—depressions on cranium (see text), hyo—hyoid bone, lrm—left ramus mandibulae, pbp—processus basipterygoideus, rrm—right ramus mandibulae, tac—tuba auditiva communis. Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

broken halves); pedal phalanges: I1, ca. 11.0. SMF 2559a+b: humerus, 80.9 (left); ulna, 84.0 (left); carpometacarpus, 43.0 (left); tibiotarsus, ca. 74.7 (left), ca. 81.0 (right). HLMD-Me 14996a+b: humerus, ca. 80.5 (left), ca. 82 (right); ulna, ca. 85–87 (right); carpometacarpus, ca. 43.5 (right); femur, ca. 46.5 (left), ca. 45 (right); tibiotarsus, ca. 75.5 (left), ca. 75.5 (right); tarsometatarsus, ca. 52 (left), ca. 51.5 (right); pedal phalanges (HLMD-Me 14996a): I1, ca. 12.5 (right); I2, ca. 5 (right); II1, ca. 13.5 (?) (left); III1, ca. 13 (left); III2, ca. 8.5 (left); IV1, ca. 6.5 (?) (left); IV2, ca. 4.5 (left). Pohl specimen: Skull, ca. 61; humerus, ca. 73 (left), ca. 80 (right); ulna, 86.5 (right); carpometacarpus, 40.2 (left); tibiotarsus, ca. 73 (right); tarsometatarsus ca. 51.5 (right). SMF-ME 10846a: Skull, 56.5. SMF-ME 3548: Skull, 66.5.

Etymology. Derived from *micro* (Gr.): small, and *cephalon* (Gr.): head, in reference to the small skull of the new species.

Description and comparisons

As in the Anhimidae (Anseriformes), Galliformes and Columbiformes, the skull is very small in relation to the body. It is also of similar overall proportions to the skull of the Anhimidae and, in dorsal view, becomes gradually narrower towards the tip of the beak. The beak itself is short and, in dorsal view, has a triangular shape. In lateral view (SMF-ME 10846a), it is rather low dorsoventrally, with a straight culmen, sigmoid tomia, and a slightly hooked tip. The narial openings are very long and almost reach into the tip of the beak. The ossa maxillaria are widely separated.

The ventral surface of the skull is exposed in SMF-ME 3548. In this specimen well-developed processus basipterygoidei can be discerned which resemble those of the Cathartidae. The caudal wall of the cavum tympanicum forms a cone-like projection, just caudal to the alae parasphenoidales (SMF-ME 3548), which indicates that the fossa parabasalis, i.e., the depression in which the ostia canalis carotici et ophthalmicus externus are located, was laterally open. Also in SMF-ME 3548, a tuba auditiva communis can be discerned and the lamina parasphenoidalis bears marked pores. As noted previously (Mayr, 2007), there are some low and blunt bony tubercles on the basicranium of SMF-ME 3548. The processus parasphenoidales laterales are well developed.

Perplexicervix microcephalon lacks processus supraorbitales. In the holotype, the dorsal surface of the cranium appears to be elevated caudal of the orbitae, and is contrasted from the rostral portion by a distinct, V-shaped step (Fig. 2b). Although this may be an artifact of preservation, the symmetry of this feature rather indicates that it reflects the true morphology of the cranium, i.e., that either the caudal portion of the cranium was unusually elevated or the rostral

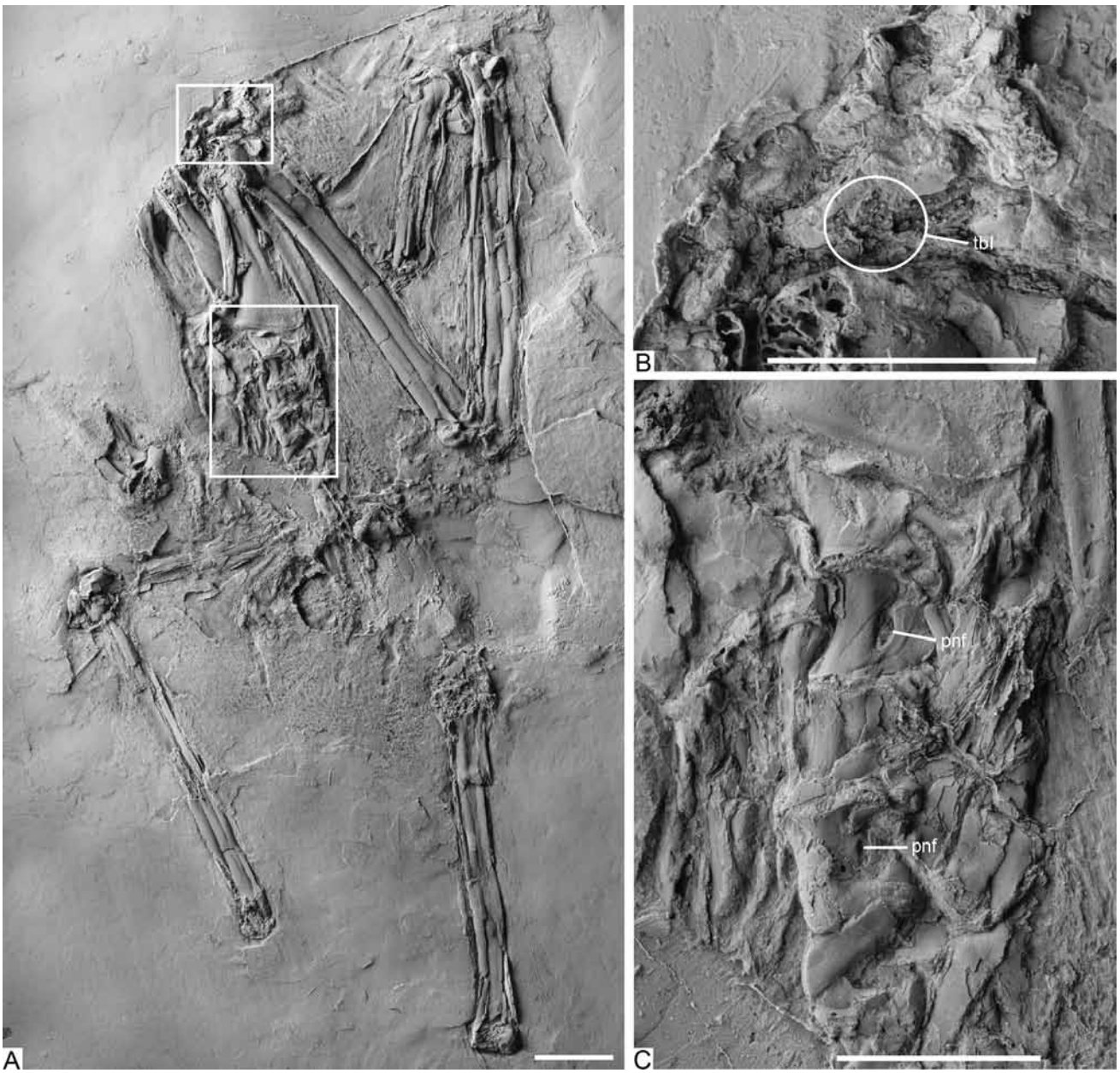

Figure 3. *Perplexicervix microcephalon* n.gen. and n.sp. (*A*) referred specimen SMF-ME 2559a, the framed areas indicate the details shown in *B* and *C*; (*B*) detail of cervical vertebrae; (*C*) detail of thoracic vertebrae. Abbreviations: *tbl*—tubercles on cervical vertebrae, *pnf*—pneumatic foramen. Coated with ammonium chloride to enhance contrast; scale bars equal 10 mm.

portion depressed. In all specimens, the surface of the cranium exhibits large pores and marked furrows (see also Mayr, 2007).

The processus postorbitalis is short, the processus zygomaticus wide, square, and with a truncated tip as in Cathartidae. As far as this can be discerned in the crushed skulls, the fossae temporales appear to have been shallow.

In SMF-ME 3548 the processus oticus of the left quadratum can bee seen in cranial view (Mayr, 2007: fig. 2a), whereas only a small portion of the capitulum oticum of the right quadratum is visible. The processus oticus resembles that of the White-tailed Kite *Elanus leucurus* (Accipitridae); as in the latter, the articulation facet of the capitulum oticum extends onto the cranial surface of the processus oticus. The incisura intercapitularis is very shallow.

The rami mandibulae are dorsoventrally narrow and particularly slender in their distal half; the pars symphysialis (visible through the reverse of the transparent slab of SMF-ME 11211a) is very short, its length is about equal to the depth of the narrow distal section of the rami mandibulae. Fenestrae mandibulae are absent. The caudal part of the mandible bears a well-developed processus medialis.

The cervical vertebrae of section II of Boas (1929) are long and exhibit shallow lacunae interzygapophysiales and elongate, ridge-like processus spinosi (SMF-ME 10846a). At least the fourth cervical vertebra lacks an osseous bridge from the processus transversus to the processus articularis caudalis (arcus interzygapophysialis of Livezey & Zusi, 2006:133) (SMF-ME 10846a). Whether this bridge was present on the third cervical vertebra cannot be clearly discerned (SMF-ME 10846a)—if it was, the enclosed foramen must have been

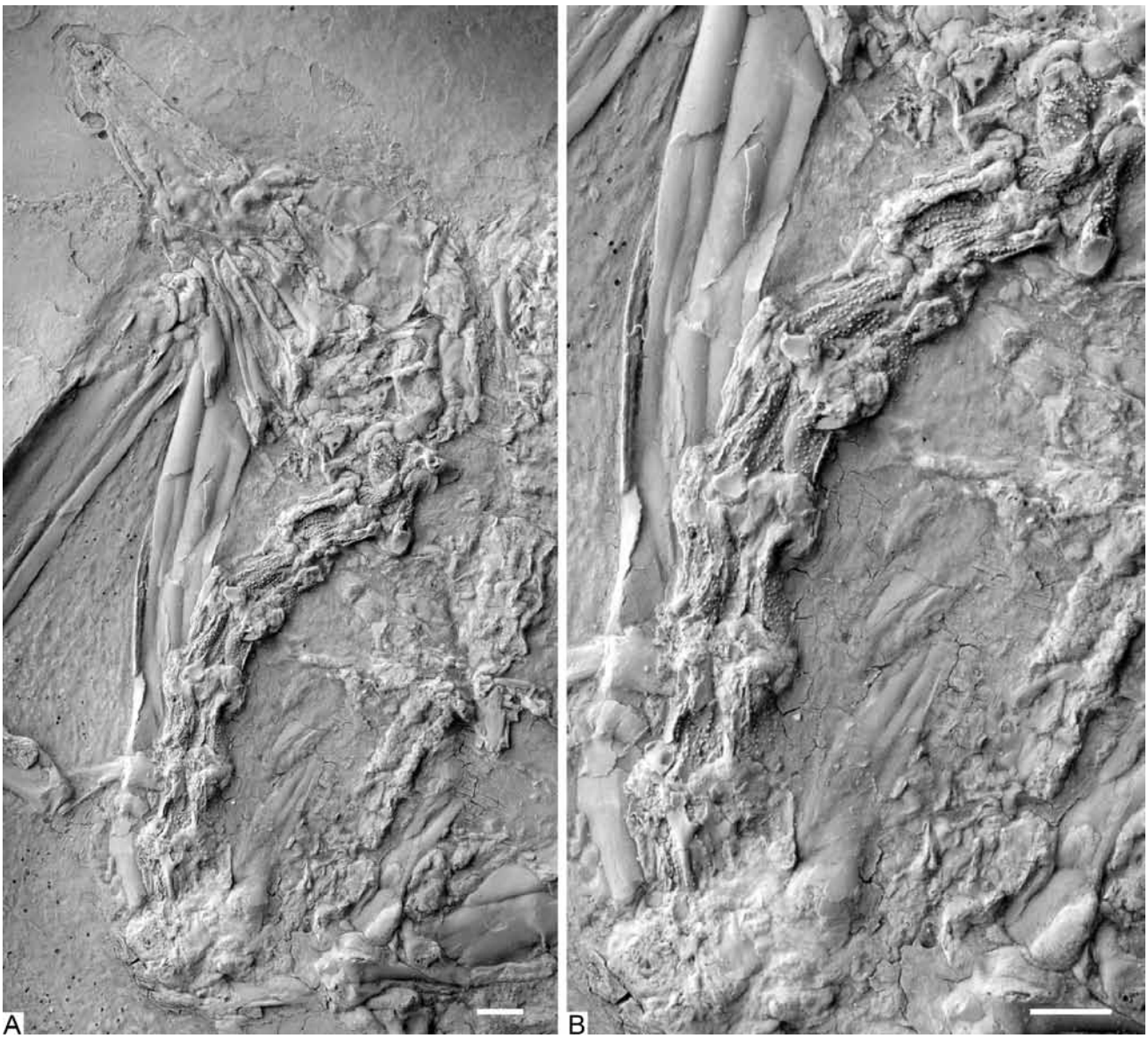

Figure 4. *Perplexicervix microcephalon* n.gen. and n.sp., skull and cervical vertebrae of Pohl specimen (*A*), and detail of cervical vertebrae (*B*). Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

very small. In all specimens except HLMD-Me 14996a+b, in which they are not preserved, the cervical vertebrae are densely covered with numerous small tubercles (Fig. 2). The morphology of these tubercles in the referred specimens SMF-ME 10846 and SMF-ME 3548 was described by Mayr (2007), and this description also matches the tubercles in the other specimens. In the privately owned specimen in the Pohl collection it can be seen that the tubercles cover the first nine cervical vertebrae (Fig. 4). The thoracic vertebrae lack tubercles. As in extant Anhimidae, they exhibit a pneumatic foramen on the lateral surface of the corpus (SMF-ME 11211a, SMF-ME 2559a; Fig. 3c).

The robust and broadly rounded processus acrocoracoideus of the right coracoid can be seen in ventral view in HLMD-Me 14996a (Fig. 5a); in its shape it resembles the processus acrocoracoideus of the Otididae. Although only a small portion of the dorsal surface of the extremitas sternalis is visible in HLMD-Me 14996b, distinct muscle striae can be discerned.

The cranial end of the left scapula is exposed in lateral view in HLMD-Me 14996b (Fig. 5b). The acromion is short and there is a well-developed tuberculum coracoideum which indicates the presence of a cup-like cotyla scapularis on the coracoid.

In the holotype only the poorly preserved distal portions of the humeri are visible, and more details of the bone can be discerned in SMF-ME 2559a and HLMD-Me 14996a+b. Being fairly elongate, with a rather narrow proximal and a wide distal end, it resembles the humerus of the Cathartidae in its proportions. There crista deltopectoralis is long but not very prominent, and there seems to have been a convex crista bicipitalis (HLMD-Me 14996a, left side). The small tuberculum dorsale is visible on the left humerus of HLMD-Me 14996b. The distal end only allows the recognition of the ventrally protruding epicondylus ventralis, which bears two marked pits on its ventral surface (HLMD-Me 14996a, SMF-ME 2559a).

The ulna exceeds the other limb bones in length, but only

Figure 5. *Perplexicervix microcephalon* n.gen. and n.sp., selected skeletal elements. (*A*) extremitas omalis of right coracoid in ventral view (HLMD-Me 14996a); (*B*) cranial end of left scapula (HLMD-Me 14996b); (*C*) distal end of right humerus in cranial view (HLMD-Me 14996b); (*D*) left manus of holotype (SMF-ME 11211a); (*E*) left wing (HLMD-Me 14996a). Abbreviations: *cmc*—carpometacarpus, *hum*—humerus, *pex*—processus extensorius; *tbc*—tuberculum coracoideum, *uln*—ulna. Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

few details of its articular ends can be discerned. The cotyla ventralis seems to have been shallow and the olecranon is short (SMF-ME 11211a, SMF-ME 2559a). In the holotype, the poorly preserved distal end of the left ulna is exposed in ventral view and allows the recognition of a short condylus dorsalis and a small tuberculum carpale. The small condylus dorsalis can also be seen on the right ulna of HLMD-Me 14996a and in SMF-ME 2559a.

The carpometacarpus is slender and fairly long, of similar overall proportions to that of Cathartidae. The prominent processus extensorius has a broadly rounded tip (Fig. 5d) and resembles that of the Turkey Vulture, *Cathartes aura*. The os metacarpale minor is straight, the spatium intermetacarpale narrow, and the symphysis metacarpalis distalis fairly long.

The phalanx digiti alulae is long and lacks an ungual phalanx. The phalanx proximalis digiti majoris exhibits a small processus internus indicis of similar shape to that of *Cathartes aura* (SMF-ME 11211a).

The pelvis of SMF-ME 11211a is visible in ventral view. There are low tubercles on what I consider to be a portion of the left ischium.

The femur of the holotype bears tubercles on the lateral surface of the proximal end and the midsection of the shaft. Although these are somewhat less pronounced than the tubercles on the cervical vertebrae, they are nevertheless very distinct. Such tubercles are absent on the corresponding parts of the fairly well-preserved femora of the referred specimen HLMD-Me 14996a+b.

The tibiotarsus of the holotype is broken in its distal part and the two portions are displaced against each other, thus probably indicating a fracture rather than a breakage due to diagenetic processes. The cristae cnemiales are well developed, and the crista cnemialis cranialis appears to have been proximally protruding (SMF-ME 2559a, right tibiotarsus). The condyles are widely separated and dorsoventrally low, the condylus medialis being smaller than the condylus lateralis; whether an ossified pons supratendineus was present cannot be discerned (SMF-ME 2559a).

The tarsometatarsus of the holotype is broken in its distal fourth and the two parts are dislocated and turned against each other (Fig. 6a); the proximal portion of the bone is visible in plantar view, whereas the dorsal surface of the distal fragment is exposed. In HLMD-Me 14996a+b the left tarsometatarsus is embedded in a dorsoventral position, whereas the right one can be seen in mediolateral view.

The tarsometatarsus of *P. microcephalon* is long and

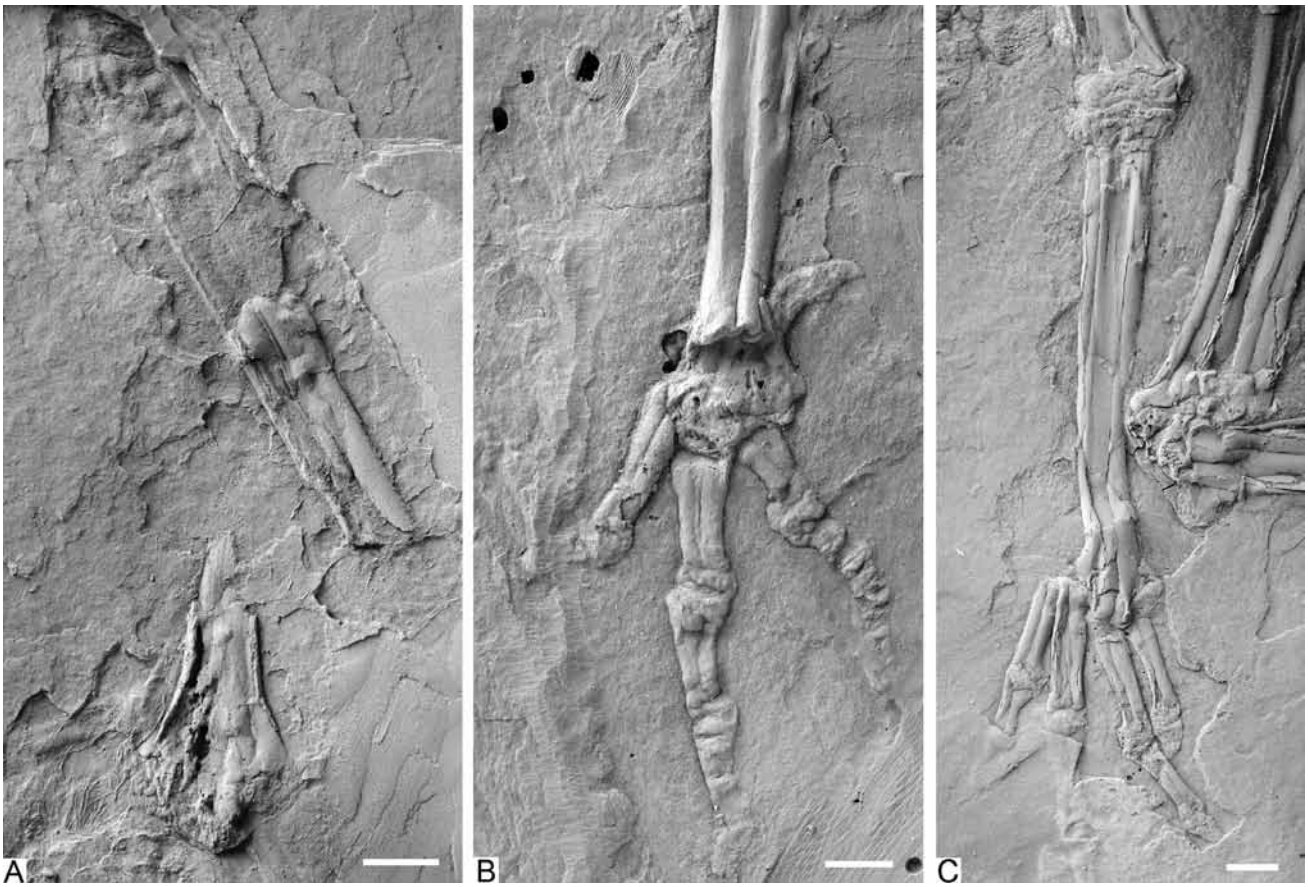

Figure 6. *Perplexicervix microcephalon* n.gen. and n.sp., foot. (*A*) holotype (SMF-ME 11211b), right side; (*B*) HLMD-Me 14996a, left side; (*C*) Pohl specimen, right side. Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

slender, the shaft of equal width over most of its length, becoming only slightly narrower distally. The distal end itself is wide and appears to have had a fairly symmetrical shape, with short trochleae metatarsorum II et IV. The hypotarsus is visible through the reverse of the transparent slab of SMF-ME 11211a, but in this specimen it can only be discerned that it bears wide and shallow grooves. The better preserved plantar surface of the left hypotarsus is visible in HLMD-Me 14996b. It has a triangular outline and bears two low ridges, the lateral one of which is larger, and in the medial portion there is a small, nearly closed sulcus. The foramen vasculare distale cannot be discerned in HLMD-Me 14996; in the holotype, there is a large ovate opening in the area of this foramen which does, however, not perforate the bone and seems to be a preparation artifact.

In the holotype only a resin mould of the long hallux is preserved, and in HLMD-Me 14996a+b the toes are badly deformed, which makes it difficult to discern the length of some phalanges (Fig. 6b). However, at least the proximal phalanges of the second and third toes are of average proportions. Next to the lateral side of the left tarsometatarsus of HLMD-Me 14996a, there is a narrow elongate bone, which I interpret as the os metatarsale I.

In SMF-ME 11211a faint shadows of the right wing feathers are visible and, as preserved, the outermost primary measures about 110 mm. Remains of the long wing feathers are also preserved in HLMD-Me 14996a+b, but do not allow a meaningful description.

Discussion

Perplexicervix microcephalon n.gen. and n.sp. measures only about half of the size of *Idiornis tuberculata* (length of tibiotarsus ca. 71 versus 130 mm), and exhibits very different limb proportions. Whereas the ulna is only slightly longer than the cranium in *I. tuberculata* (the beak of this species is unknown), the bone measures nearly 1.5 times the length of the entire skull in *P. microcephalon* (the absolute lengths are 79.5–85 mm in the holotype of *P. microcephalon* versus only 64 mm in the holotype of the much larger *I. tuberculata*). *Perplexicervix microcephalon* is further distinguished from *Idiornis* in the morphology of the carpometacarpus (proportionally much shorter and with a bowed os metacarpale minus in *Idiornis*) and coracoid (in *Idiornis* the processus acrocoracoideus is connected by an osseous bridge with the processus procoracoideus), as well as the proportionally shorter tarsometatarsus.

The presence of a tuba auditiva communis and a bicondylar processus oticus of the quadrate support a position of *P. microcephalon* within neognathous birds (e.g., Cracraft, 1988). Within extant Neognathae, functional processus basipterygoidei occur in galloanserine birds, some Procellariiformes and Charadriiformes, Columbiformes, Cathartidae, Sagittariidae, Strigiformes, Trogonidae, and some taxa of the Strisores sensu Mayr (2010), i.e., the clade including nightjars, swifts, hummingbirds, and allies. Of these taxa, *P. microcephalon* most closely resembles

the anseriform Anhimidae and the Cathartidae in overall morphology, but the incomplete knowledge of its osteology does not allow an reliable phylogenetic assignment of the peculiar fossil species. Occurrence of processus basipterygoidei and pneumatic openings on the bodies of the thoracic vertebrae in particular indicates affinities to the Anhimidae, and there remains a possibility that *P. microcephalon* is related to as yet undescribed putative early Eocene Anhimidae (Mayr, 2009).

Specimen SMF-ME 3548 is notably larger than the holotype, but the small number of known specimens does not allow an unambiguous assessment whether this indicates specific difference or sexual dimorphism in size. The long wings indicate that *P. microcephalon* was capable of sustained flight. Judging from the relatively wide and short beak, which only has a very slightly hooked tip, *P. microcephalon* may have fed on either plant matter or soft-bodied invertebrates.

The origin and significance of the vertebral tubercles remains mysterious. Their presence in two avian species without close relationship is in agreement with earlier assumptions, that these unusual structures are of pathologic origin (Mayr, 2007; see also Peters, 1995). This hypothesis gets further support from the fact that small tubercles are present on the femur of the holotype, but absent on the femora of HLMD-Me 14996a+b. As I have detailed previously (Mayr, 2007), the regular structure and symmetric distribution of the tubercles may indicate a systemic, i.e., metabolic or endocrine, disorder. If they were caused by, for example, high doses of phytohormones or an extinct group of pathogens, there may well have been an accumulation within taxonomically restricted avian groups with a similar feeding ecology or habitat. However, in conflict with a pathologic origin is the fact that these tubercles occur in all specimens of *P. microcephalon* with preserved cervical vertebrae, i.e. in no less than five of the six known specimens. If the tubercles represent a true morphological feature, it is difficult to imagine what function they may have fulfilled, and why similar structures are unknown from extant birds.

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