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JUVENILE SPECIMENS OF THE PTEROSAUR *GERMANODACTYLUS CRISTATUS*, WITH A REVIEW OF THE GENUS

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ABSTRACT—Two juvenile specimens of the pterodactyloid pterosaur *Germanodactylus cristatus* are identified from the Solnhofen Limestone of southern Germany. The specimens had been referred to the nominal species *Pterodactylus kochi* and *P. micronyx*. They have edentulous tips on the upper and lower jaws; their skulls are taller and less elongate and have fewer teeth than similarly sized specimens assigned to *P. antiquus* and *P. micronyx*; and they have tall neural spines on their cervical vertebrae. In addition, they exhibit a distinctive suite of skeletal proportions that distinguishes them from similarly sized specimens assigned to *P. antiquus* and *P. micronyx*. The specimens do not exhibit any trace of a cranial crest, which supports the interpretation that the cranial crest developed late in ontogeny, probably as the individual approached skeletal and/or sexual maturity. The taxonomy of *Germanodactylus* is reviewed and revised diagnoses are presented.

INTRODUCTION

Germanodactylus cristatus, heretofore known only from the holotype specimen (BSP 1892.IV.1), has been one of the rarest pterosaur species from the Upper Jurassic Solnhofen Limestone of southern Germany. The holotype specimen was originally described by Plieninger (1901), who noted that the upper and lower jaw tips were edentulous and that it exhibited a sagittal crest extending upward from the posterior part of the premaxillae above the orbit and naso-antorbital fenestra. Plieninger, in an admirable feat of lumping, referred the specimen to *Pterodactylus kochi*, noting that the skeletal proportions were similar to those of the holotype of *P. kochi* and interpreting the absence of a cranial crest in the holotype as the result of preparation damage or sexual dimorphism. Similarly, Plieninger interpreted the lack of edentulous jaw tips in small specimens assigned to *P. kochi* as an ontogenetic difference. Wiman (1925) presumably disagreed with Plieninger's interpretation and erected the species *Pterodactylus cristatus* for BSP 1892.IV.1 without any discussion. Young (1964) erected the genus *Germanodactylus* for the specimen on the grounds that it differed from all other *Pterodactylus* specimens in the presence of edentulous jaw tips and the cranial crest. He seems to have been unaware that Wiman had erected the species *P. cristatus* for the specimen, and therefore referred to the specimen as *Germanodactylus kochi*. Kuhn (1967), perhaps also unaware of Wiman's species name, figured the specimen as *P. kochi* and considered *P. kochi* to be the type species of Seeley's (1871) genus *Diopecephalus*, which Kuhn suggested was characterized by edentulous jaw tips and the presence of the cranial crest. Thus, Kuhn thought that *Diopecephalus* had priority over *Germanodactylus*. Wellnhofer (1968) considered *Diopecephalus* to be invalid, and so as part of his revision of all Solnhofen pterodactyloids (Wellnhofer, 1970), he reviewed the species under the new combination *Germanodactylus cristatus*, referred *P. rhamphastinus* to the genus *Germanodactylus* in large part because it also had a cranial crest (crests were not yet known in *P. longicollum* and *Ctenochasma*), and presented diagnoses of the genus and species.

Bennett (1996) described the presence of year-classes in pterosaurs from the Solnhofen Limestone and argued that immature specimens assigned to the small nominal species of *Pterodactylus* (i.e., *P. antiquus, P. kochi, P. micronyx*, and *P. elegans*) were juveniles of the species represented by large mature specimens assigned to *Germanodactylus, Ctenochasma*, *Gnathosaurus*, and *P. longicollum*. I attempted to match up small and large species and concluded that *P. antiquus, P. kochi, P. longicollum, Germanodactylus cristatus*, and *G. rhamphastinus* represented juveniles and adults of two or three biological species; however, I put off formal taxonomic revision pending a thorough restudy of the pertinent specimens. After further consideration, I concluded that *Germanodactylus* was distinct from *Pterodactylus* because of the edentulous jaw tips, reduced number of teeth arranged with smaller, more slender teeth anteriorly and robust laterally compressed conical teeth posteriorly, large naso-antorbital fenestra, maxillary tooth row extending under the naso-antorbital fenestra, and distinctive metacarpal IV:wing phalanx 1 proportions (Bennett, 2002).

Recent restudy of the Solnhofen pterodactyloids resulted in the identification of two juvenile specimens of *Germanodactylus cristatus*—one had previously been referred to *Pterodactylus kochi* (now considered a junior synonym of *P. antiquus* [Jouve, 2004]), while the other had been referred to *P. micronyx*. This demonstrates how similar juveniles of different Solnhofen pterodactyloids are and also how difficult the task of correctly matching juvenile and adult specimens may be. This paper documents the juvenile specimens and presents a taxonomic revision of *Germanodactylus*.

Institutional Abbreviations: BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts; PTH, Philosophisch-Theologische Hochschule, Eichstätt; and SoS, JuraMuseum (Solnhofen Sammlung), Eichstätt.

JUVENILE SPECIMENS

SoS 4593

This specimen was referred to *Pterodactylus kochi* (Wellnhofer, 1970, Specimen #9 with old catalog number PTH 29.III.1950). It is a complete skeleton of a small individual preserved in right lateral view with the forelimbs folded together under the body, the wingfingers extended posteriorly to lie near the feet, and the hindlimbs flexed together under the body. Wellnhofer (1970, pp. 27–31, Abb. 6, Taf. 6, fig. 2–3) thoroughly described the specimen and therefore redescription is unnecessary, except to note differences in observation and damage to the specimen since Wellnhofer's description.

Wellnhofer's reconstruction of the skull (1970, Abb. 6) illustrated the tip of the premaxillae as blunt, but it is bilaterally compressed and tapers to a sharp point (Fig. 1). There are ten teeth in the upper jaw—note that there is a small, vaguely tooth-shaped mass of calcite between the third and fourth teeth. The fifth and sixth teeth are a mature tooth and its small erupting replacement, respectively. Wellnhofer stated the premaxillary-maxillary suture was clearly visible and found three premaxillary teeth and seven maxillary teeth, and in his reconstruction he illustrates a small posterior tooth under the naso-antorbital fenestra. I agree that the suture is clearly visible for much of its length, but based on my examination, and ignoring the replacement tooth, there are four premaxillary teeth and five maxillary teeth. I did not find a tooth under the naso-antorbital fenestra. The second and fourth premaxillary teeth seem to have blunted tips, and the second through fourth maxillary teeth have broken or truncated tips. Wellnhofer stated there were nine dentary teeth, but based on my examination the lower jaw preserves eight teeth which occlude between the upper teeth, again ignoring the replacement tooth. The dentary teeth are not blunted or truncated. Careful microscopic examination of the jaws, including tilting the slab so as to look up at the ventral surface of the premaxilla and down at the dorsal surface of the dentary failed to identify any tooth, broken tooth base, empty alveolus, or any other evidence of teeth on the tips of the jaws. Thus, the jaw tips are edentulous and taper to sharp points.

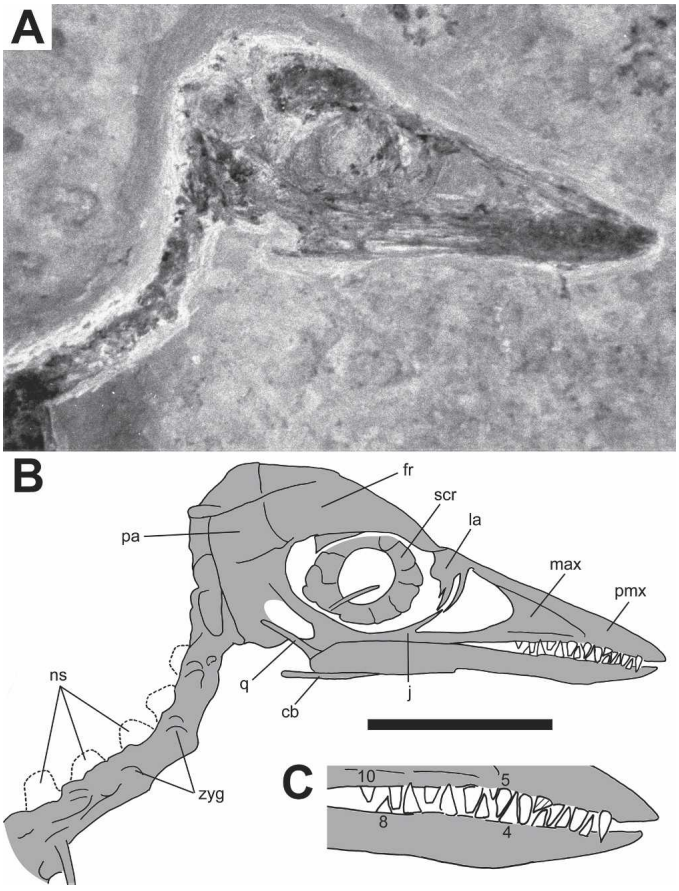

FIGURE 1. **A,** photograph and **B,** camera lucida drawing of the skull and cervical vertebrae of *Germanodactylus cristatus*, SoS 4593, in right lateral view. **C,** inset shows details of the dentition with tooth numbering. Skull length is 25.7 mm. **Abbreviations: cb**, ceratobranchial; **fr**, frontal; **j**, jugal; **la**, lacrimal; **max**, maxilla; **ns**, tall neural spines (outlines based on Wellnhofer [1970]); **pa**, parietal; **pmx**, premaxilla; **q**, quadrate; **scr**, sclerotic ring; **zyg**, zygapophyses. Hatching in **C** represents a calcitic mass. Scale bar for **A** and **B** equals 10 mm; scale bar for **C** equals 5 mm.

The jugal process of the lacrimal curves posteriorly to approach the anteriorly directed and upward curving lacrimal process of the jugal. The quadrate is slanting backward at an angle of about 40° above horizontal. A moderately robust ceratobranchial is partially visible under the posterior end of the right ramus of the mandible, and extends some distance behind the retroarticular process.

Wellnhofer (1970) described and illustrated the specimen as having tall neural spines on the cervical vertebrae, but when I examined the specimen in June 2002 all the spines were gone, leaving behind clearly visible irregular broken bases of the neural spines of the third and fourth cervical vertebra. There was fine limestone dust on the specimen and the posterior margin of the skull and cervical series seemed to have been freshly excavated. Thus, it would seem that someone, in an attempt to further prepare or clean up the cervical region, destroyed the neural spines.

SoS 4006

This specimen was referred to *Pterodactylus micronyx* (Wellnhofer, 1970, Specimen #31 with old catalog number PTH 1957/52) and was figured (Wellnhofer, 1970, Abb. 6, Taf. 7, fig. 3) but not described. The slab has the number 1957/52a on it, which implies that there is a counterpart slab "b," but I did not see one. The specimen is a complete skeleton of a small individual preserved in right lateral view with the forelimbs folded together under the body, the wingfingers extended posteriorly, and the hindlimbs splayed out more or less as in flight. The quality of preservation of the bone is such that fine details such as sutures are impossible to make out.

The premaxillae and dentaries have sharply pointed tips (Fig. 2). There are seven teeth in the upper jaw with no sign of replacement teeth, and seven teeth in the mandible with the fifth tooth close behind the fourth and presumably a replacement tooth. The anterior teeth are slender and sharply pointed, and the more posterior teeth are more robust. The third dentary tooth is broken or truncated. Careful microscopic examination of the jaws, including tilting the slab so as to look up at the ventral

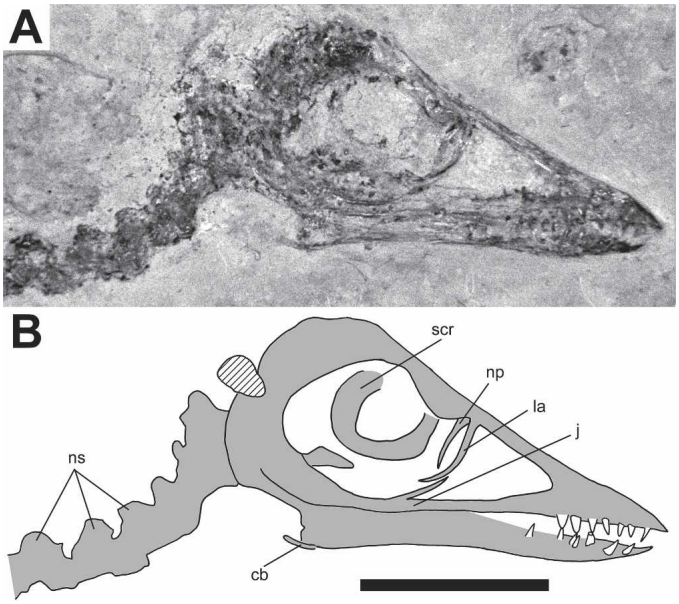

FIGURE 2. **A,** photograph and **B,** camera lucida drawing of the skull of and cervical vertebrae of *Germanodactylus cristatus*, SoS 4006, in right lateral view. Skull length is 26.5 mm. **Abbreviations**: **cb**, ceratobranchial; **j**, jugal; **la**, lacrimal; **np**, nasal process; **ns**, tall neural spines; **scr**, sclerotic ring. Hatching represents a calcitic mass. Scale bar equals 10 mm.

surface of the premaxilla and down at the dorsal surface of the dentary failed to identify any tooth, broken tooth base, empty alveolus, or any other evidence that teeth would have been present on the tips of the jaws. Thus, the jaw tips are definitely edentulous and taper to sharp points. The posterior end of a ceratobranchial is visible below and behind the end of the mandible.

The skull is relatively tall. There is a very faint sclerotic ring, that seems to have been poorly ossified. The jugal process of the lacrimal curves posteriorly to approach the anterosuperiorly directed lacrimal process of the jugal. Medial to the jugal process of the lacrimal is a slightly curved nasal process. The quadrate is slanting backward at an angle of about 35° above horizontal.

The cervical vertebrae have tall neural spines, but no other notable features can be discerned. The carpus and tarsus are largely unossified. The left tarsus preserves a small single ossicle that probably represents the astragalus (Fig. 3). Metatarsal (Mt) I and II are about the same length, and Mt III and IV are progressively shorter. The first phalanx of pedal digit II is much shorter than the first phalanx of digit I, and the first phalanges of digits III and IV increase in length such that the length of the first phalanx of digit IV is equivalent to that of digit I.

STATISTICAL ANALYSES

Measurement data for SoS 4006 and 4593 were compared to specimens assigned to *Pterodactylus antiquus* (Wellnhofer's [1970] Specimens 1–8, 10–28) and *P. micronyx* (Wellnhofer's [1970] Specimens 29, 30, 32–44). Wellnhofer's (1970) measurement data of the specimens were used where possible because they have been used in other analyses, and in most cases my measurements of the specimens do not differ significantly from Wellnhofer's. The measurement data were analyzed using Principal Components Analysis with the statistical package SPSS 11.5 for Windows (SPSS Inc., Chicago).

The measurement data are also presented graphically in graphs that are in the spirit of the "Nopcsa curves" of Wiman (1925; see also Nopcsa, 1923), but differ in that they are based on the absolute measures of skeletal elements rather than the size relative to the humerus and are not spaced out vertically on the graph (Fig. 4); they are hereafter referred to as Modified Nopcsa Curves. As a consequence of using absolute measures and not spacing them out vertically, similarly-sized specimens clump together, and the graph permits comparison of the lengths of individual elements, the proportions of different specimens, and evaluation of the isometry or allometry of adjacent elements within a sample of a species. Measurement data of SoS 4006 and 4593 are plotted against each other, and against those of similarly-sized specimens assigned to *P. antiquus* (Wellnhofer's [1970] Specimens 6–8, 10, 11) and *P. micronyx* (Wellnhofer's [1970] Specimens 29, 30, 32–35).

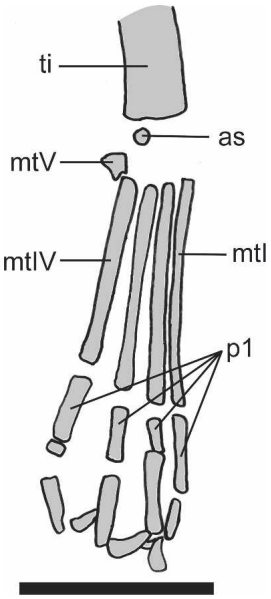

FIGURE 3. Left tarsus and pes of *Germanodactylus cristatus*, SoS 4006. **Abbreviations**: **as**, astragalus; **mtI, mtIV**, and **mtV**, metatarsals **I, IV**, and **V**, respectively; **p1**, first phalanges of digits I-IV. Scale bar equals 5 mm.

RESULTS

The results of the Principal Components Analysis are shown in Figure 5. The plots of the two juveniles with specimens assigned to *Pterodactylus antiquus* show that the two specimens plot close to one another and are on the periphery of the scatter of points. The plots of the two juveniles with specimens assigned to *P. micronyx* also show that the two specimens plot close to one another, but they are not easily distinguished from the *P. micronyx* specimens, and in the plot of Components 2 and 3 they are right in the middle of the scatter of points.

The Modified Nopcsa Curves are shown in Figure 4. The curve plotting SoS 4593 and similarly-sized *P. antiquus* specimens shows that SoS 4593 differs from the *P. antiquus* specimens in that the *praecaudale Rumpfwirbelsäule* (PCRW; = combined length of dorsal and sacral vertebrae) is relatively much longer, and is absolutely longer than the skull, whereas in the *P. antiquus* specimens the skull is considerably longer than the PCRW. At the same time, the proportions of the fore- and hindlimbs are

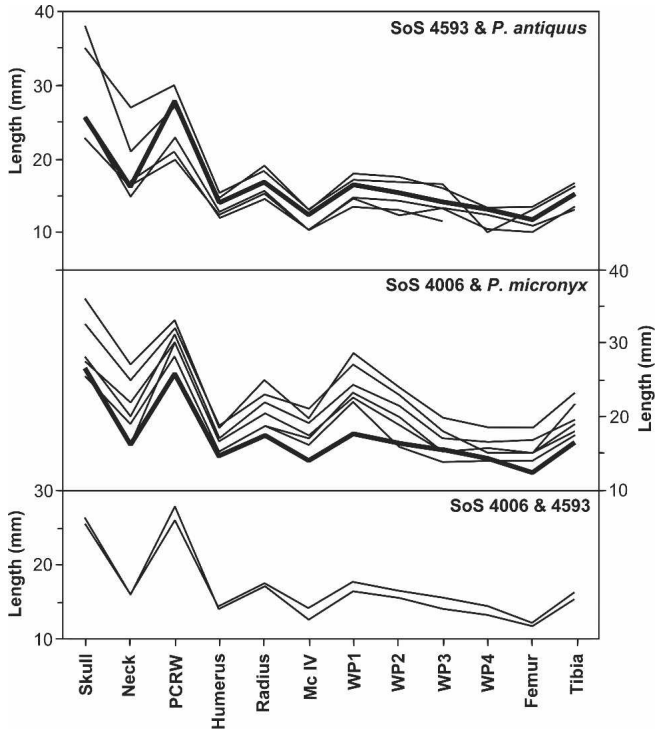

FIGURE 4. Modified Nopcsa Curves of skeletal proportions based on measurement data from Wellnhofer (1970). At top, *Germanodactylus cristatus*, SoS 4593 (heavy line), plotted with similarly sized *Pterodactylus antiquus* specimens (light lines); scale at left. In the middle, *G. cristatus*, SoS 4006 (heavy line), plotted with similarly sized specimens assigned to *P. micronyx* (light lines); scale at right. At bottom, SoS 4006 and 4953 plotted together; scale at left. See text for explanation. **Abbreviation**: **PCRW**, *praecaudale Rumpfwirbelsäule* (= combined length of dorsal and sacral vertebrae).

quite similar in SoS 4593 and the *P. antiquus* specimens. The curve plotting SoS 4006 and similarly-sized specimens assigned to *P. micronyx* shows that the proportions of the skull, neck, PCRW, and humerus are quite similar in SoS 4006 and the *P. micronyx* specimens, and some of the *P. micronyx* specimens have a PCRW longer than the skull like SoS 4593. However, SoS 4006 differs considerably from the *P. micronyx* specimens in the proportions of the wing. The radius, metacarpus, and first wing phalanx are considerably shorter than the *P. micronyx* specimens and the ratios of the wing phalanges is quite different. The curve plotting SoS 4006 and 4593 shows that the two specimens are very similar, and given their differences from the curves of similarly-sized assigned to *P. antiquus* and *P. micronyx* specimens, it supports the idea that SoS 4006 and 4593 are distinct from both species.

DISCUSSION

The juveniles, SoS 4006 and 4593, share a short, tall skull with sharply pointed edentulous jaw tips, low number of teeth with the posterior teeth relatively large and robust, backward curving jugal process of the lacrimal, anterosuperiorly directed lacrimal process of the jugal, quadrate slanting at 35–40° above horizontal, prominent ceratobranchial, and tall neural spines on the cervical vertebrae. When they are compared to a similarly sized specimen of *Pterodactylus antiquus* (SMNS 81775, Fig. 6), the *P. antiquus* specimen has a longer, lower skull, toothed jaw tips, greater number of teeth with the posterior teeth decreasing in size, straight roughly vertical jugal process of the lacrimal, quadrate reclined at no more than 10° above horizontal, and low neural spines. Likewise, when they are compared to a similarly sized specimen *of P. micronyx* (BSP 1935.I.50; see Wellnhofer, 1970, Abb. 8), although the *P. micronyx* specimen has a rather tall skull, the superior margin is concave and the angle of the quadrate is quite low, and although there are a similar number of teeth, the jaw tips are not edentulous and the teeth are much more slender. In addition, the Modified Nopcsa curves show that the two specimens are very similar to one another, and both differ markedly from similarly-sized specimens assigned to *P. antiquus* and *P. micronyx*.

The holotype of *Germanodactylus cristatus* has a relatively short, tall skull with sharply-pointed edentulous jaw tips, large naso-antorbital fenestra, steeply inclined quadrate, relatively low tooth count arranged with smaller, more slender teeth anteriorly and robust laterally compressed conical teeth posteriorly, and maxillary tooth row extending under the naso-antorbital fenestra. The two juvenile specimens share most of those features with the holotype, and those features they do lack (i.e., large naso-antorbital fenestra and maxillary tooth row extending under the fenestra) are merely ontogenetic differences. Unfortunately, the cervical vertebrae of the holotype are not preserved in a position that shows the morphology of the neural spines. Based on the similarities, and in particular the sharply-pointed edentulous jaw tips, SoS 4006 and 4593 are referred to *G. cristatus*.

The pedal morphology of *Germanodactylus cristatus* with Mt

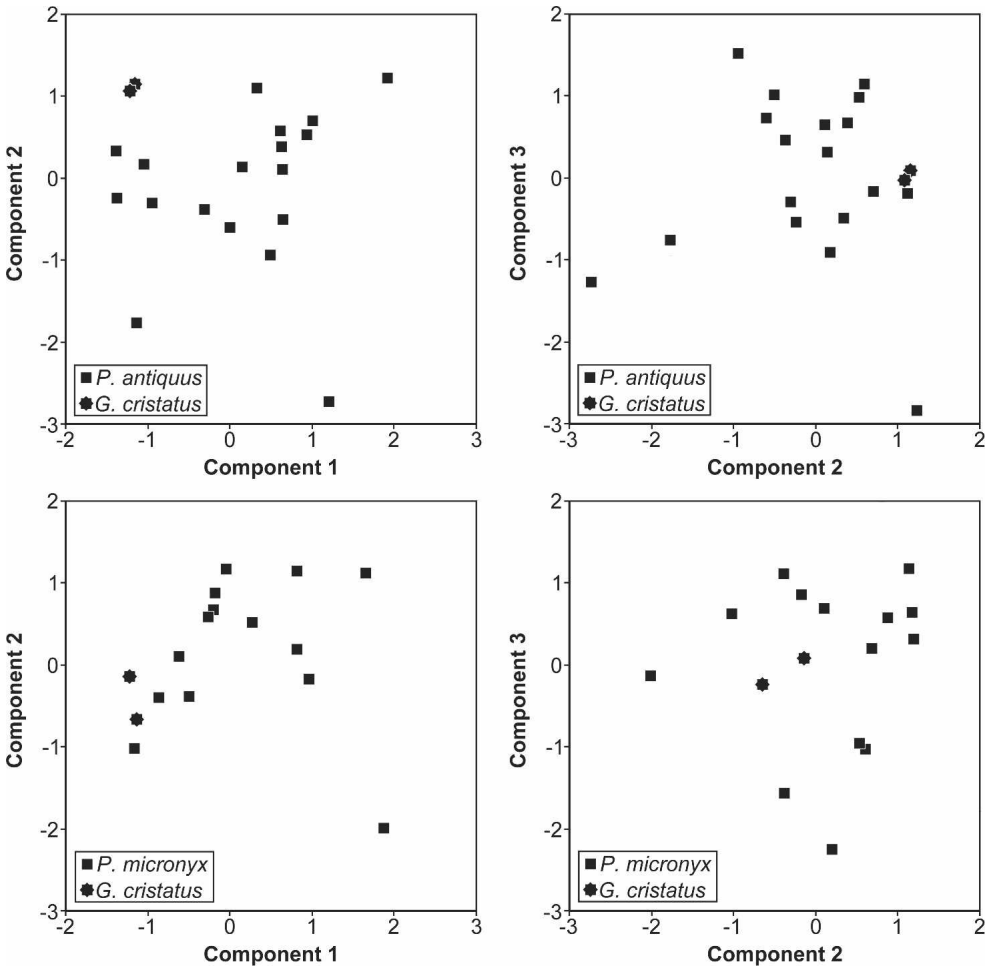

FIGURE 5. Plots of components 1 and 2, and 2 and 3 from the Principal Components analyses of specimens of *Pterodactylus antiquus*, *P. micronyx*, and *Germanodactylus cristatus*.

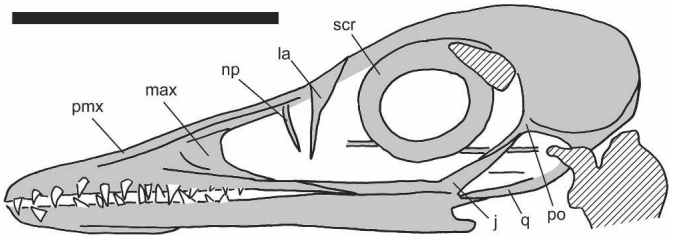

FIGURE 6. Camera lucida drawing of *Pterodactylus antiquus*, SMNS 81775, in left lateral view. Skull length is 23.9 mm. **Abbreviations: j**, jugal; **la**, lacrimal; **max**, maxilla; **np**, nasal process; **pmx**, premaxilla; **po**, postorbital; **q**, quadrate; and **scr**, sclerotic ring. Hatching represents a calcitic mass. Scale bar equals 10 mm.

III and IV progressively shorter than Mt I and II, and unequal length first phalanges of digits I-IV is similar to that of *Pterodactylus antiquus*, and markedly different from juveniles of *Ctenochasma elegans* and juveniles assigned to *P. micronyx* (probably juveniles of *Gnathosaurus subulatus* [Bennett, 1996]), in which Mt I-IV are nearly equal in length as are the first phalanges of digits I-IV. In SoS 4006 the first phalanx of digit II (II-P1) is 48% of the first phalanx of digit I (I-P1) length, and in SoS 4593 the II-P1 is 61% of the I-P1 length, whereas in most specimens of *P. antiquus* the II-P1 is 62–69% of the I-P1 length; however, it is not clear if this difference is significant.

The condition of the teeth of the two juveniles of *Germanodactylus cristatus* is intriguing. Both of them are preserved with their mandibles in articulation, yet both have teeth that appear blunted or truncated, perhaps as a result of wear or damage to the tooth tips from biting hard objects. Other juvenile pterodactyloids from Solnhofen do not seem to show similar blunting or truncation. Bakhurina (1993) and Unwin (2003) suggested a line of descent from *Germanodactylus* to *Dsungaripterus*, which has edentulous jaw tips, low crushing posterior teeth, and exhibits truncated teeth as a result of wear presumably from feeding on bivalved mollusks. Although I have argued against Bakhurina's and Unwin's phylogenetic scenario (Bennett, 2003a), it is possible that the ecological scenario is valid, and *G. cristatus* may have fed on hard-shelled prey. In addition, the prominent ceratobranchials of the juveniles may indicate that the tongue had a greater role in feeding than in the longer-jawed *Pterodactylus antiquus*.

It is interesting that both juvenile specimens of *Germanodactylus cristatus* were collected from the quarry at Workerszell, which lies roughly 4.5 km NNW of Eichstätt, whereas no other pterosaurs mentioned in Wellnhofer's (1970, 1975) revisions of the Solnhofen Limestone pterosaur fauna came from there. This may be pure coincidence, but it is also possible that that locality was close to a breeding colony of *G. cristatus* and so accumulated unlucky hatchlings or that the local environment was particularly to the liking of hatchling *G. cristatus* such that they congregated in the area. It is also possible that the quarry at Workerszell is in a particular horizon laid down when *G. cristatus* was particularly abundant.

SYSTEMATIC PALEONTOLOGY

Order PTEROSAURIA Kaup, 1834
Suborder PTERODACTYLOIDEA Plieninger, 1901
Family PTERODACTYLIDAE Bonaparte, 1838
Genus *GERMANODACTYLUS* Young, 1964

Type Species—*Pterodactylus cristatus* Wiman, 1925.

Included Species—*Pterodactylus cristatus* Wiman, 1925; *Ornithocephalus ramphastinus* Wagner, 1851.

Distribution—Lower Tithonian of Solnhofen Limestone, Malm Zeta 2, Solnhofen, Eichstätt, and Workerszell, Bavaria, Germany, and Mornsheimer Limestone, Malm Zeta 3, Daiting, Bavaria, Germany.

Diagnosis—Pterodactyloids with the anterior skull tapering evenly to a rather sharply pointed premaxillary jaw tip, 4–5 premaxillary teeth and 8–12 maxillary teeth per side, maxillary teeth laterally compressed cones with oval cross-sections and more robust than the premaxillary teeth, posterior maxillary teeth not significantly reduced in size (unlike the condition in *Pterodactylus*), relatively steep quadrate, naso-antorbital fenestra more than twice as long as the orbit, neck length approximately two thirds of skull length, and metacarpus shorter than the antebrachium.

Remarks—Based on Plieninger's (1901) description of BSP 1892.IV.1 and his assignment of that specimen to *Pterodactylus kochi*, Young (1964) erected the genus *Germanodactylus* for the species *P. kochi* on the grounds that it differed from all other *Pterodactylus* species in the presence of edentulous jaw tips and the cranial crest. Kuhn (1967) felt that Seeley's (1871) genus *Diopecephalus* had priority over *Germanodactylus*, while Wellnhofer (1968, 1970) dismissed *Diopecephalus* in favor of *Germanodactylus* on the grounds that Seeley was unaware of BSP 1892.IV.1 when he erected *Diopecephalus* and that the genus was based on a character that was not present in the referred specimens.

Wellnhofer's (1970) diagnosis of the genus included the characters "premaxillary crest above naris and orbit," "jugal process perpendicular to inferior border of the maxilla," and "bones of the pectoral and pelvic girdles fused," which I have discarded. These characters are essentially ontogenetic characters reflecting the maturity of the type specimens of the included species. All Solnhofen pterodactyloids developed cranial crests at maturity (Bennett, 2002), thus possession of a cranial crest is not diagnostic of *Germanodactylus*. Likewise, the bones of the pectoral and pelvic girdles fused in mature individuals of all pterodactyloids (Bennett, 1993, 1996). The lacrimal process of the jugal in the juvenile specimens described above is anteriorly directed and curving upward, whereas it is vertical and straight in BSP 1892.IV.1, so the orientation changes through ontogeny. In addition, the orientation of the lacrimal process in mature specimens of *Germanodactylus* does not seem to be significantly different from that of large specimens of *Pterodactylus* and *Ctenochasma*.

Kuhn's (1967) interpretation that the name *Diopecephalus* had priority over the name *Germanodactylus* needs to be reexamined. Seeley (1871) suggested the name *Diopecephalus* in a footnote:

> "Another unnamed generic type is typified by *Pterodactylus longicollum, P. rhamphastinus*, and the two species included under the name *P. kochi*. In this genus the middle hole of the skull is entirely wanting. For it I suggest the name *Diopecephalus*." (Seeley, 1871: 35)

By "the two species included under the name *P. kochi*" Seeley presumably meant the holotype specimen of *P. kochi* (Wagner, 1837, = SM 404 & BSP AS.XIX.3) and the type specimen of *P. scolopaciceps* (von Meyer, 1859, = BSP AS.V.29), according to Wellnhofer (1968) the only two specimens known as *P. kochi* at the time. It is now clear that *G. rhamphastinus* is not congeneric with either *P. kochi* or *P. longicollum*, and that *P. kochi* and *P. longicollum* are not congeneric (Bennett, 2003b). Thus, the specimens that Seeley thought typified his proposed genus pertained to what are now considered to be three different genera, but he did not designate a type species. The character "middle hole of the skull is entirely wanting" (i.e., complete confluence of the naris and antorbital fenestra) is a synapomorphy of the Pterodactyloidea and does not characterize any single genus. Seeley, may have been unaware that the nasal process was a median ossification, and may have thought that the naris and

antorbital fenestra were still partially separated in *P. antiquus* by the nasal process on the one hand, and that *P. longicollum*, *P. rhamphastinus*, and *P. kochi* differed from it in the complete confluence of the openings on the other. The holotype of *P. kochi* has a prominent nasal process, but it is clearly not lying on the plane of the lateral margin of the naso-antorbital fenestra, and so Seeley may have correctly interpreted it as not separating the naris and antorbital fenestra, whereas no nasal process is visible in the holotype of *P. scolopaciceps*. Regardless, neither the fact that the character proposed by Seeley does not diagnose a genus nor the fact that Seeley did not designate a type species invalidates the name *Diopecephalus*.

By 1901, Seeley had modified his view somewhat, and designated *Pterodactylus kochi* as the type species of *Diopecephalus*:

> "In the species named *P. kochi*, which I regard as the type of a distinct genus, there are large teeth in the front of the jaw corresponding to those of Pterodactylus [sic], and behind these a smaller series of teeth extending back under the nostril, which approaches close to the orbit of the eye, without any indication of a separate antorbital vacuity. On those characters the genus *Diopecephalus* was defined." (Seeley, 1901: 168)

Although Seeley published the previous statement the same year that Plieninger published the description of BSP 1892.IV.1 as *P. kochi,* he made no mention of edentulous jaws or a premaxillary crest, so he did not include it in his conception of *P. kochi* and probably was unaware of Plieninger's specimen. Seeley (1901) referred to *P. longicollum* as *Cycnorhamphus fraasi*, thus viewing it as congeneric with *C. suevicus*, whereas *P. rhamphastinus* was only briefly mentioned without any suggestion that it belonged in *Diopecephalus*. Seeley's 1901 statement is essentially compatible with his 1871 statement in that in both Seeley stated that specimens assigned to *P. kochi* represented a genus distinct from *Pterodactylus*, but in 1901 he clearly designated *P. kochi* as the type species of the new genus. Therefore, *Diopecephalus* is a junior synonym of *Pterodactylus*. Kuhn (1967) felt that *Diopecephalus* could be applied to Wiman's *P. cristatus* and recently some individuals have suggested that the name *Diopecephalus* should be applied to *P. longicollum*, but Seeley's designation of *P. kochi* as type species prevents both possibilities.

GERMANODACTYLUS CRISTATUS (Wiman, 1925)

Pterodactylus kochi Wagler: Plieninger, 1901:65.
Pterodactylus cristatus Wiman, 1925:17.
Germanodactylus kochi (Wagler): Young, 1964:251.
Diopecephalus kochi (Wagler): Kuhn, 1967:34.
Germanodactylus cristatus (Wiman): Wellnhofer, 1970:64.

Holotype—BSP 1892.IV.1. Original description by Plieninger (1901).

Horizon and Locality—Solnhofen Limestone, Malm Zeta 2, Eichstätt, Germany.

Paratypes—None.

Distribution—Solnhofen Limestone, Malm Zeta 2, Eichstätt and Workerszell (~4.5 km NNW of Eichstätt), Germany.

Diagnosis—Species of *Germanodactylus* with the anterior 8–10% of the upper and lower jaws edentulous and tapering to short points, roughly 13 and 12 teeth in the upper and lower jaws, respectively.

Referred Specimens—SoS 4006, 4593, and an undescribed specimen at the Staatliches Museum für Naturkunde Karlsruhe.

Remarks—The five names in the synonymy were all applied to BSP 1892.IV.1.

GERMANODACTYLUS RHAMPHASTINUS (Wagner, 1851)

Ornithocephalus ramphastinus, Wagner, 1851:4.
Pterodactylus rhamphastinus (Wagner): von Meyer, 1859:54.
Diopecephalus rhamphastinus (Wagner): Seeley, 1871:35.
Pterodactylus rhamphastinus (Wagner): Lydekker, 1888:8.
Germanodactylus rhamphastinus (Wagner): Wellnhofer, 1970:66.

Holotype—BSP AS.I.745

Horizon and Locality—Mornsheimer Limestone, Malm Zeta 3, Daiting, Germany.

Paratypes—None.

Distribution—Solnhofen Limestone, Malm Zeta 2, Solnhofen, Germany; and Mornsheimer Limestone, Malm Zeta 3, Daiting, Germany.

Diagnosis—Species of *Germanodactylus* with toothed jaw tips and roughly 16 and 15 teeth in the upper and lower jaws, respectively.

Referred Materials—MCZ 1886 (Bennett, 2002).

Remarks—Wagner (1851) spelled the specific name "*ramphastinus*" because the large head and neck reminded him of the Toucan:

> "Höchst auffallend ist neben der ungewöhnlichen Grösse dieses Exemplares das auffallende Uebergewicht, welches der gewaltige Schädel und die langen und starken Knochen des Halses über den kleinen schwachen Rumpf behaupten; es erinnert diess einigermassen an die grossschnäbligen und ziemlich langhalsigen Pfefferfresser [Ramphastos], wesshalb ich auch dieser neuen Art den Namen Ornithocephalus ramphastinus beigelegt habe." (Wagner, 1851:4)

If Wagner had created the species name "*ramphastinus*" by combining the Greek *rhamphos* (meaning "beak") with the Greek *steinos* (meaning "narrow"), then his omission of the "h" might have required emendation to properly latinize it. However, because he was clearly modifying the generic name *Ramphastos* by adding the Latin *-inus* (meaning "resembling") to describe the new species as "toucan-like", Wagner's spelling would be acceptable under the ICZN. Meyer (1859) reviewed the species and noted that it was so-named because of its resemblance to the toucan, but Meyer spelled both names with "h"'s (i.e., "*Rhamphastos*" and "*rhamphastinus*") without stating that he intended to emend the spelling. All subsequent authors (e.g., Seeley, 1871, 1901; Plieninger, 1929; Wellnhofer, 1970, 1978) have spelled the name "*rhamphastinus*" and attributed that spelling to Wagner (1851), and so according to the ICZN the widespread attribution of "*rhamphastinus*" to Wagner (1851) makes it a justified emendation.

Wellnhofer (1970) listed three additional species names in his synonymy (i.e., *Pterodactylus medius*, *P. dubius*, and *P. propinquis medius* [sic]) marked with question marks, but those species were based on specimens that were lost during World War II. Münster (1831) described and illustrated *P. medius* that consisted of an incomplete skull, trunk skeleton, girdles, humeri, and femora. The specimen was relatively large, and the pelvic bones seem to have been fused, which suggests the specimen was mature, but there seems to have been no evidence of a cranial crest. The skull lacked edentulous jaw tips, and Münster stated there were 16 conical teeth in the mandible; however, there was at least one empty alveolus and assuming uniform tooth spacing there would have been at least 17 mandibular teeth. The anterior teeth were smaller than the more posterior teeth, but based on Münster's illustration the posteriormost teeth were also rather small. Thus, *Pterodactylus medius* was similar to the holotype of *G. rhamphastinus* and may have been conspecific, but differed in

somewhat in its dentition and without the specimen at hand it is impossible to conclude that it was.

Wagner (1851) described *Pterodactylus dubius*, which consisted of an articulated incomplete vertebral column (1st dorsal through anterior caudals) associated with somewhat disarticulated dorsal ribs, sternum, and pelvic girdle including prepubes. The specimen was relatively large, but was clearly immature as the pelvic bones were not fused at all. The specimen lacked a skull, and so there is no reason to think that it pertained to *G. rhamphastinus* rather than some other pterodactyloid.

Wagner (1858) described *Pterodactylus propinquis*, which included an incomplete skull lacking the orbital and braincase regions, preserved in left lateral view, but clearly showing a cranial crest. Wellnhofer (1970) stated that it was based on the same specimen as Münster's *P. medius*, but Wagner gives different measurements for the two species, so they must have been based on different specimens. The mandible of *P. propinquis* was toothed to the tip, the naso-antorbital fenestra was quite large, and the single posterior maxillary tooth was large and robust. Although the evidence is equivocal, the specimen may have pertained to *G. rhamphastinus*, in which case it would be a junior synonym of *G. rhamphastinus*.

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