

ON THE TAXONOMIC STATUS OF *CYCNORHAMPHUS* AND *GALLODACTYLUS* (PTEROSAURIA: PTERODACTYLOIDEA)

S. CHRISTOPHER BENNETT

Department of Systematics and Ecology and Natural History Museum,
University of Kansas, Lawrence 66045-2454

ONE OF THE rarest pterosaurs from the Upper Jurassic Solnhofen Limestone of southern Germany is *Pterodactylus suevicus*. Only two specimens are known: the holotype, consisting of a virtually complete skeleton described by Quenstedt (1855); and a second specimen, consisting of only postcranial elements described by Wagner (1858) and lost during World War II (Wellnhofer, 1970). Seeley (1870) noted that *P. suevicus* differed from *P. antiquus*, the type species of *Pterodactylus*, in a number of significant points. Therefore, he placed *P. suevicus* in a new genus, *Cycnorhamphus*. Seeley (1870:111) gave the following diagnosis of *Cycnorhamphus*:

“Nares very small, looking upward from a swan-like beak. The middle hole of the skull very large and elongated and lateral. Neck long. Wing-metacarpal long. Four joints in wing-finger. Ilium widening in front. Epipubic bones meeting mesially. The type is *Pterodactylus suevicus* (Quenstedt).”

The character “nares very small” was the result of a misinterpretation of depressions on the premaxillae that probably resulted from crushing, and “middle hole of the skull” referred to the confluent naris and antorbital fenestra, which Seeley apparently considered the antorbital fenestra alone.

Fraas (1878) described a new pterosaur specimen from the Solnhofen Limestone (Staatliches Museum für Naturkunde, Stuttgart [=SMNS] 5802) and referred it to *Pterodactylus suevicus*, but did not comment on Seeley’s genus. Subsequently,

Seeley (1891) argued that Fraas’s specimen was specifically distinct from, although congeneric with, Quenstedt’s holotype of *P. suevicus* and so named it *Cycnorhamphus fraasii*. Seeley (1901) reviewed the genus *Cycnorhamphus*, which included *Pterodactylus suevicus* and *C. fraasii*, and commented on the important characters of *P. suevicus* (Seeley, 1901:169–171) that warranted generic separation:

“*Pterodactylus suevicus* differs from the typical pterodactyle in having a rounded, flattened under surface to the lower jaw, instead of the common condition of a sharp keel in the region of the symphysis. The beak also seems flattened and swan-like, and the teeth are limited to the front of the jaw. There appear to be some indications of small nostrils, which look upward like the nostrils of *Rhamphorhynchus* [sic], but this may be a deceptive appearance, and the nostrils are large lateral vacuities, which are in the position of antorbital vacuities, so that there would appear to be only two vacuities in the side of the head in these animals. The distinctive character of the skeleton in this genus is found in the extraordinary length of the metacarpus and in the complete ossification of the smaller metacarpal bones throughout their length. The metacarpal bones are much longer than the bones of the fore-arm, and about twice the length of the humerus. The first wing phalange is much longer than the others, which successively and rapidly diminish in length, so that the third is half the length of the first. There are differences in the pelvis; for the anterior process of the ilium is very short, in comparison with its length in the genus *Pterodactylus* [sic]. And the long stalk of the prepubic bone with its great hammer-

headed expansion transversely in front gives those bones a character unlike other genera, so that *Cynorhamphus* [sic] ranks as a good genus, easily distinguished from Cuvier's type, in which the four bones of the wing are more equal in length, and the last is more than half the length of the first; while the metacarpus in that genus is only a little longer than the humerus, and much shorter than the ulna."

At the same time, Plieninger (1901) noted that he considered *Cynorhamphus* a junior synonym of *Pterodactylus* because he considered all toothed pterodactyloid species in which the scapula did not articulate with a notarium to belong to *Pterodactylus*. Plieninger (1907) later restudied the type specimen of *Pterodactylus suevicus* and restated his position that the separation from *Pterodactylus* was completely unwarranted. He noted that the "swan-like beak" was the result of crushing of the specimen, that the "small nares" were the result of Seeley's misinterpretation of the specimen, and that the reduction in length of the more distal wing phalanges was size-related and present in other large pterosaurs. He concluded that *P. suevicus* differed from other *Pterodactylus* species only in the less sharply pointed beak, teeth restricted to anterior part of the jaws, and the proportions of wing bones, and that those differences were insufficient for generic separation. In addition, he noted that Fraas's specimen, the holotype of *Cynorhamphus fraasii*, could be referred to *Pterodactylus longicollum*. Thus, *C. fraasii* is a junior synonym of *P. longicollum*. Wellnhofer (1970) concurred with Plieninger's rejection of the genus *Cynorhamphus* on the grounds that it was based on characters that were not sufficient for generic separation or were not present in the specimen, but rather misinterpretations of the morphology. It is important to note here that Plieninger and Wellnhofer argued that *Cynorhamphus* was a junior synonym of *Pterodactylus*, and not that the name was unavailable.

A specimen of a similar pterosaur from Canjuers in southern France was described by Fabre (1976) as a new species and genus, *Gallodactylus canjuersensis*. The specimen was like *Pterodactylus suevicus* in that it lacked a premaxillary crest and had what was termed an occipital chignon, a parietal crest extending up and back from the occipital region of the skull. Fabre gave three diagnostic characters of the genus *Gallodactylus*: no premaxillary crest; parietal crest; and size greater than that of *Pterodactylus sensu stricto* [= *P. antiquus*?]. Fabre transferred *P. suevicus* and *P. longicollum* to *Gallodactylus* because both were supposed to have parietal crests. Fabre noted that Plieninger (1907) and Wellnhofer (1970) had considered the name *Cynorhamphus* invalid because it was based on cranial characters that were misinterpretations of the morphology. However, Fabre seemed not to have appreciated that Plieninger and Wellnhofer argued that *P. suevicus* was congeneric with *P. antiquus*, rather than that the name *Cynorhamphus* was unavailable. Subsequently, Wellnhofer (1978) accepted the genus *Gallodactylus* and the referral of *P. suevicus* to it. Wellnhofer, however, retained *P. longicollum* in the genus *Pterodactylus* because it differs from *P. suevicus* and *G. canjuersensis* in that it did not seem to have a parietal crest, had distinctly different dentition, and its scapulocoracoid was fused. This interpretation of the taxonomy was also used by Wellnhofer (1991).

There is now general agreement that *Pterodactylus suevicus* and *Gallodactylus canjuersensis* are congeneric with each other but not with *P. antiquus*, the type of the genus *Pterodactylus* (Wellnhofer, 1970, 1978; Fabre, 1976; Bennett, in press). *Pterodactylus suevicus* and *G. canjuersensis* both differ from *P. antiquus* in skull shape, dentition restricted to the anterior parts of the jaws, presence of a parietal crest, and the apparent absence of a premaxillary crest. The non-fusion of the scapulocoracoid, long considered a diagnostic character of *Pterodactylus* (Welln-

hofer, 1970, 1978), is an ontogenetic character of no taxonomic significance (Bennett, 1993, in press), and the types of both species are immature (personal observ.). *Pterodactylus suevicus* and *G. canjuersensis* both have small parietal crests extending up and back from the occipital region, but *P. longicollum* shows no trace of such a crest and, in fact, the Eichstätt specimen of *P. longicollum* has a premaxillary crest like that of *Gnathosaurus* (Bennett, in press).

The name *Cynorhamphus* is available because Seeley (1870) identified the type species of the genus and listed those characters that he thought differentiated it from *Pterodactylus*. It does not matter that some of those characters (e.g., small nares) are not present in the type species or that some (e.g., swan-like beak) are open to interpretation. The name *Cynorhamphus* is valid because it is the oldest available generic name other than *Pterodactylus* that has been applied to the species *Pterodactylus suevicus*. The name *Cynorhamphus* has priority over *Gallodactylus*. *Cynorhamphus* is not a *nomen oblitum* because all authors after Seeley (e.g., Plieninger, 1901, 1907, 1929; Piveteau, 1955; Romer, 1956; von Huene, 1956; Wellnhofer, 1970) until Fabre (1976) treated the name as available, although they considered it a junior subjective synonym of *Pterodactylus*. Thus, when it was determined that *P. suevicus* was not congeneric with *Pterodactylus antiquus*, *Cynorhamphus* should have been adopted.

SYSTEMATIC PALEONTOLOGY

Order PTEROSAURIA Kaup, 1834

Suborder PTERODACTYLOIDEA Plieninger, 1901

Family PTERODACTYLIDAE Bonaparte, 1838

Genus CYNORHAMPHUS Seeley, 1870

Type species.—*Pterodactylus suevicus* QUENSTEDT, 1855.

Included species.—*Pterodactylus suevicus* QUENSTEDT, 1855; *Gallodactylus canjuersensis* FABRE, 1976.

Distribution.—Lower Tithonian of Nusplingen, Württemberg and Eichstätt, Bavaria in Germany; and upper Portlandian of Canjuers in France.

Diagnosis.—Pterodactyloids with a short parietal crest extending up and back from the occipital region of the skull, but lacking a premaxillary crest.

Remarks.—The genus *Gallodactylus* had been included in the Pterodactylidae (Fabre, 1976; Wellnhofer, 1978); however, it is likely that the Pterodactylidae are paraphyletic, although the relationships of the Jurassic pterodactyloids are not properly understood (Howse, 1986; Unwin, 1992; Bennett, 1994, in press). The specimens of *C. suevicus* were said to come from the "Unteres Untertithon" (=lower Lower Tithonian) by Wellnhofer (1978), while Fabre (1976) stated that the holotype of *C. canjuersensis* came from the upper Portlandian, thus the latter species is probably stratigraphically younger than the former.

CYNORHAMPHUS SUEVICUS (Quenstedt, 1855)

Pterodactylus württembergicus QUENSTEDT, 1854:270.

Pterodactylus suevicus QUENSTEDT, 1855:34.

Pterodactylus württembergicus Quenstedt. VON MEYER 1855, p. 809.

Pterodactylus (Ornithocephalus) eurychirus WAGNER, 1858, p. 444.

Cynorhamphus suevicus (Quenstedt), SEELEY, 1870, p. 237.

Gallodactylus suevicus (Quenstedt), FABRE, 1976, p. 40.

Holotype.—Geologisch-Paläontologisches Institut, Tübingen (=GPIT) "Orig. Quenstedt 1855, Taf. 1," described by Quenstedt (1855) and Plieninger (1907).

Horizon and locality.—Nusplingen Limestone, Malm Zeta 1, Nusplingen, Württemberg, Germany.

Paratypes.—None.

Distribution.—Nusplingen Limestone, Malm (=lower Ti-

thonian) Zeta 1, Nusplingen, Württemberg, and the Solnhofen Limestone, Malm Zeta 2, Eichstätt, Bavaria, Germany.

Diagnosis.—Parietal crest extends up and back with rounded margin; teeth long, thin, and confined to the anterior 20 percent of the jaws; humerus and tibia relatively longer than in *Cycnorhamphus canjuersensis*.

Referred materials.—One specimen formerly in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, described by Wagner (1858), and lost during World War II.

Remarks.—All names in the synonymy except *Pterodactylus* (*Ornihocephalus*) *eurychirus* were applied to the holotype, the latter name was applied to the second specimen, now lost. The name "*Pterodactylus württembergicus*" was used by Quenstedt in a letter, but was not considered by him to be the specific name; he used *Pterodactylus suevicus* when the description of the specimen was published in the following year (see Wellnhofer [1970] for a discussion and more complete synonymy).

The diagnosis above is modified from that of Wellnhofer (1978). Wellnhofer's diagnosis also included the length of the cervical vertebrae, shape of the sternum, non-fusion of the scapulocoracoid, metacarpus significantly longer than the forearm, and the diminution in the length of wing phalanges 1–4. The short cervical vertebrae and elongate metacarpus are shared with *Cycnorhamphus canjuersensis* and may have been plesiomorphic for the genus. The shape of the sternum and the non-fusion of the scapulocoracoid are ontogenetic characters and are not taxonomically informative (Bennett, 1993, in press), indicating instead that the specimen is immature. Other evidence of immaturity includes unfused humeral epiphyses and visible sutures on the syncarpals and on the extensor tendon process of wing phalanx 1. The proportions of the wing phalanges differ somewhat between *C. suevicus* and *C. canjuersensis*, but the sample is too small to indicate whether the difference is significant. The two specimens of *C. suevicus* had very similar proportions, while according to my measurements of *C. canjuersensis* wing phalanx 2 is slightly longer and wing phalanx 4 is slightly shorter relative to wing phalanx 1 than in *C. suevicus*.

CYCNOTHAMPHUS CANJUERSSENSIS (Fabre, 1976)

Gallodactylus canjuersensis FABRE, 1976, p. 40–41.

Holotype.—Museum National d'Histoire Naturelle, Paleontologie, Paris (=MNHN) CNJ-71, described by Fabre (1976).

Horizon and locality.—Upper Portlandian of Canjuers, France.

Paratypes.—None.

Diagnosis.—Parietal crest extends straight backward, not back and up as in *Cycnorhamphus suevicus*, and has a trapezoidal margin; confluent naris and antorbital fenestra twice as long as the orbital diameter; temporal fenestra smaller than in *C. suevicus*; and humerus and tibia relatively shorter than in *C. suevicus*.

Referred materials.—None.

Remarks.—The diagnosis above is modified from Fabre (1976). Fabre included other characters as well: obturator foramen opening onto the puboischiadic suture, and wing phalanx 4 considerably shorter than wing phalanx 3. The fact that the obturator foramen opens onto the puboischiadic suture is merely an ontogenetic character of no taxonomic significance. I was unable to confirm that wing phalanx 4 is significantly shorter than in *Cycnorhamphus suevicus*. Fabre gave the lengths of wing phalanges 3 and 4 as 94 and 60 mm, respectively. However, my examinations of the specimen indicate that wing phalanx 4 is poorly preserved, but is at least 74 mm long. Thus, it is at least 0.82 times the length of wing phalanx 3; compared to 0.91 and 0.87 in the two specimens of *C. suevicus*, respectively (Well-

nhofer, 1970). Looked at another way, wing phalanx 4 is at least 0.48 times the length of wing phalanx 1, compared to 0.55 and 0.53 in the two specimens of *C. suevicus*, respectively. Based on the single specimen of *C. canjuersensis* and its poorly preserved wing phalanx 4, I think there is insufficient evidence to view the apparent differences in length as taxonomically significant.

The species is known from a single specimen, which like the holotype of *Cycnorhamphus suevicus* is immature based on the unfused pectoral and pelvic girdles, extensor tendon process of wing phalanx 1, and proximal tarsals. It is not clear whether the species is distinct from *C. suevicus*. The direction and shape of the cranial crest and the overall size and proportions of the specimens are characters that may vary with ontogenetic age. However, one morphological feature that may be of specific importance is the shape of the jaws. Fabre (1976) reconstructed the upper jaw as curving upward anteriorly and the lower jaw as curving downward anteriorly, such that the dentigerous parts of the jaws did not closely approach when the mandible was adducted, and the teeth were reconstructed as larger and more widely spaced than in *C. suevicus*. The jaws of the specimen are poorly preserved; although they appear to curve as Fabre reconstructed them and there are a number of subcircular holes in the dentary that might be interpreted as alveoli, I am not convinced that those features are not artificial. However, for the present it seems best to accept Fabre's reconstruction and view the specimen as specifically distinct from *C. suevicus*.

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