

REVISION OF THE EARLY CRETACEOUS *CORDICEPHALUS* FROM ISRAEL AND AN ASSESSMENT OF ITS RELATIONSHIPS AMONG PIPOID FROGS

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ABSTRACT—Because many fossil pipoid anurans have been described during the past 35 years from Cretaceous deposits in South America and Africa, it is appropriate to revisit some of the earlier ones to have been discovered, viz., *Cordicephalus gracilis*, *C. longicostatus*, and *Thoraciliacus rostriceps* from Israel. Careful examination of *Cordicephalus*, based on study of previously, as well as newly, prepared specimens, reveals the existence of only one species. *Cordicephalus gracilis* is redescribed and compared with *Thoraciliacus*, and the phylogenetic relationships of these genera to other living and fossil pipoid frogs are investigated in a parsimony analysis. *Thoraciliacus* is basal to a clade containing *Cordicephalus*, *Palaeobatrachus*, and all other living and fossil pipids; however, the placement of *Cordicephalus* with respect to *Palaeobatrachus* and Pipidae is unresolved. Both *Thoraciliacus* and *Cordicephalus* retain the primitive state for several pipid synapomorphies involving the condition of the vomers, parasphenoid, and presence of a tympanosquamosal bone. In contrast to *Thoraciliacus*, however, *Cordicephalus* is characterized by several derived characters including possession of an otic capsule modified to accommodate a Eustachian tube and depressed, fully ossified opisthocoelous vertebrae. Despite their lack of many pipid specializations, both *Thoraciliacus* and *Cordicephalus* seem to possess many morphological features that typically are associated with aquatic habits. Among these are possession of a flat skull with a short rostrum, short axial column, and relatively long metapodials.

INTRODUCTION

The first report of frog remains from a lacustrine Early Cretaceous bed at Maktesh Ramon, an erosional valley in the central Negev Desert, was a brief note by Nevo (1956). In a later contribution, Nevo (1968) described and formally named three species based on numerous, mostly articulated adult specimens preserved either as limonitic-replaced skeletons or colored imprints. Nevo referred *Thoraciliacus rostriceps*, *Cordicephalus gracilis*, and *C. longicostatus* to Pipidae. At that time, Pipidae included living representatives, as well as several fossil taxa, the taxonomic place of which was unresolved. Further, Nevo (1968) proposed that *Thoraciliacus* was related to several extinct South American and African pipoids. However, he proposed that *Cordicephalus* was related to the extant African *Xenopus*, thereby suggesting an early dichotomy of the pipid lineage from common ancestors in Jurassic or even Triassic times. Despite the wealth of information in Nevo's paper, it has become increasingly evident that many osteological features of *Cordicephalus* and *Thoraciliacus* should be revisited and redescribed to foster a better understanding of the early evolutionary history of pipoids (Báez, 1996; Báez and Trueb, 1997). It was necessary to re-examine this significant material before we could compare these anurans with other extinct and extant taxa, and describe the acquisition of the derived, and in some instances, bizarre features that characterize the living pipids (Cannatella and Trueb, 1988; Trueb et al., 2000) in a phylogenetic context. *Thoraciliacus rostriceps* was redescribed by Trueb (1999); herein, we redescribe and evaluate the systematic relationships of *Cordicephalus*. This study is based on the examination of the material assigned to *Cordicephalus gracilis* and *C. longicostatus* by Nevo (1968), and some additional material that was given to The University of Kansas Biodiversity Research Center by the Hebrew University from a series of uncatalogued specimens in their collections. The latter specimens were prepared and proved pivotal for our interpretation of the cranial anatomy of *Cordicephalus*. We conclude that all these remains pertain to a single species, *C. gracilis*.

We also discuss the phylogenetic relationships of *Cordicephalus* and *Thoraciliacus* among pipoid taxa as a result of a parsimony analysis based on previous studies (Báez and Trueb, 1997; Báez and Pugener, 2003).

In this paper we follow the supraspecific taxonomy of Ford and Cannatella (1993), who restricted the name Pipidae to the crown group, including the last common ancestor of the living taxa and all of its descendants. These authors applied the stem-based name Pipimorpha to those taxa that are more closely related to living Pipidae than to living *Rhinophrynus*.

Institutional Abbreviations—**HUJZ**, Hebrew University, Jerusalem, Department of Zoology; **KU**, University of Kansas Natural History Museum and Biodiversity Research Center; **KUVP**, KU, Division of Vertebrate Paleontology; **LIHUBA**, Laboratorio de Investigaciones Herpetológicas (Vertebrados), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires; **PVL**, Instituto Miguel Lillo, Tucumán, Argentina.

SYSTEMATIC PALEONTOLOGY

AMPHIBIA Linnaeus, 1758
ANURA Rafinesque, 1815
PIPOIDEA Fitzinger, 1843
CORDICEPHALUS Nevo, 1968

Type Species—*Cordicephalus gracilis* Nevo, 1968.

Diagnosis—As for *Cordicephalus gracilis*, the only known species.

CORDICEPHALUS GRACILIS Nevo, 1968
(Figs. 1–8)

Cordicephalus gracilis Nevo, 1968:269.

Cordicephalus longicostatus Nevo, 1968: 272. [Holotype—HUJZ F171 from Lower Cretaceous of western Maktesh Ramon, Israel (30°32'20" N, 34°43'36" E; 1236/9945 [Israel Topo-



FIGURE 1. *Cordicephalus gracilis*, holotype (HUJZ F165). **A**, Left counterpart (HUJZ F165a). **B**, Right counterpart (HUJZ F165b). Note that the counterparts are not clear dorsal and ventral impressions. Instead, each represents an incomplete frontal section through the specimen, with the right counterpart being dorsal to the left. Obvious signs of postmortem displacement are indicated by the position of the pelvic girdle relative to the sacral diapophyses and the relative positions of the long bones of the hind limbs. The snout is incomplete, lacking nasals and premaxillae. See interpretative drawing in Figure 2.

graphical Map]); collected by Eviatar Nevo in 1954]. New synonymy.

Holotype—HUJZ F165a,b, a partially complete skeleton (ca. 30.5 mm in snout–vent length) preserved on two slabs as part and counterpart. It lacks the rostral part of the skull, parts of the pectoral girdle, and the phalangeal elements of the manus. HUJZ F165a is more complete than the counterpart (F165b), which lacks most of the cranium (Figs. 1A, B, 2).

Type Locality—Amphibian Hill, western Makhtesh Ramon, southern Negev, Israel (30°32'20" N, 34°43'36" E; 1236/9945 [Israel Topographical Map]).

Type Horizon and Age—Lacustrine deposit with an alternating sequence of light and dark laminations intercalated in a volcanoclastic unit that now is referred to the Hatira Formation (Mateer et al., 1992; Gvirtzman et al., 1996). Basalt flows, which have a representative ^{40}Ar – ^{39}Ar age of 118.0 ± 1.5 Ma (Gvirtzman et al., 1996), underlie and overlie the frog-bearing beds. This suggests an Aptian age for the frogs, according to the Mesozoic timescale of Gradstein et al. (1995).

Referred Specimens—HUJZ F149, F151a,b, F153a, F154, F155a,b, F157–59, F160a,b, F161a,b, F162a,b, F163–64, F165a,b, F166, F169, F170a,b, F171a,b, F172a,b, F173a,b, F174a,b, F175,

F176a,b, F177–78, F179a,b, F182, F184, F184a,b, F185, F185a,b, F187–88, F189a,b, F190–92, F193a,b, F194–97, F198a,b, F199a,b, F200a,b, F201a, F202a,b, F203–05, F206a,b, F207a, F208, F209, F209a, F251a,b, F252a,b,c, KUVF 127543–46.

Emended Diagnosis—Moderately small pipimorph frog (ca. 30 mm snout–vent length) that differs from other currently known members of this group in the following combination of characters: dentate maxillary arcade with pedicellate, bicuspid teeth; large, anteriorly located, edentulous vomers; seven discrete presacral vertebrae with opisthocelous, depressed centra; transverse processes of two posterior presacrals arched (or strongly angled at midlength) anteriorly, and almost as long as sacral diapophyses.

DESCRIPTION

Cranium

The skull of *Cordicephalus gracilis* is almost as wide as long, with the length being measured from the tip of the snout to the posterior margins of the otic capsules. The greatest width of the skull seems to be posterior to the maxilla in the area of the anterior parts of the otic capsules (Figs. 1–4). The rostral (pre-orbital) region is short; it represents about one fifth of the total

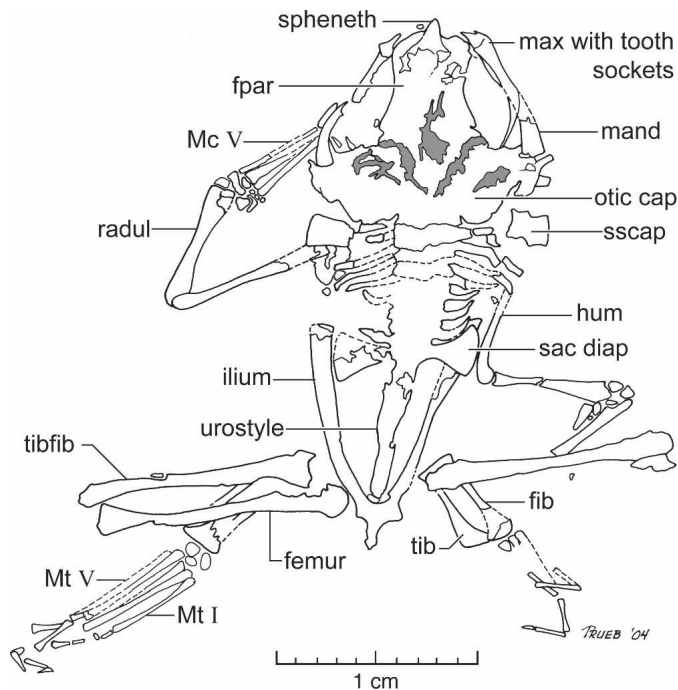


FIGURE 2. *Cordicephalus gracilis*, holotype (HUIJZ F165a). Drawing of the holotype shown in Figure 1A. Gray areas indicate matrix and impressions of margins of bones are show with dashed lines. It was not possible to reconstruct the distal part of the right foot. **Abbreviations:** cap, capsule; fib, fibulare; fpar, frontoparietal; hum, humerus; mand, mandible; max, maxilla; Mc, metacarpal; Mt, metatarsal; radul, radioulna; sac diap, sacral diapophysis; spheneth, sphenethmoid; sscap, suprascapula; tib, tibiale; tibfib, tibiofibula.

length of the skull. Among the notable features of the skull are the following: large otic capsules; azygous frontoparietal; relatively deep nasals that cover the entire rostrum; dentate, incomplete maxillary arcade; long, lanceolate parasphenoid lacking posterolateral alae; triradiate pterygoid articulating with the maxilla in the posterior part of the orbit; large, edentate vomers; and anterolateral ossification of the sphenethmoid in the region of the planum antorbitale. Neopalatines and quadratojugals are absent (Fig. 4).

Endocranium

Sphenethmoid—Because most specimens are crushed, it is difficult to describe the structure of the anterior braincase. The sphenethmoid is best represented in KUVF 127543–44 (Figs. 5, 6), in which the ventral surface of the bone is exposed. Although the sphenethmoid is not especially well preserved in these specimens, its shape and anterior relationships are reasonably clear. Anterolaterally, there are robust rami formed by ossification of the planum antorbitale on each side. The ossification extends at least three quarters of the distance to the maxilla, thereby forming a robust brace between the maxillary arcade and the braincase (Fig. 6). The ossified planum is thick ventrally and has a significant dorsal component, indicating that a stout bony wall separated the orbit from the olfactory capsule. Owing to the elaboration of the sphenethmoid in the area of the planum, the orbitonasal foramen was bordered completely in bone. As revealed by HUIJZ F170a, b, and F197, the sphenethmoid has a significant anteromedial process that suggests that the septum nasi was at least partially ossified. The degree of ossification in this region implies that the olfactory foramina are bound in bone.

In the midorbital region, the body of the sphenethmoid is

wide, having a broadly rounded ventral surface on which the cultriform process of the parasphenoid rests. The lateral walls of the braincase are not vertical; instead, they slope dorsolaterally to meet the ventral margin of the frontoparietal (e.g., HUIJZ F170b; KUVF 127544; Figs. 4, 5). The sphenethmoid terminates in the posterior region of the orbit and was not synostotically united with the prootic posteriorly. The optic foramen could not be identified unequivocally in any of these specimens; either the foramen is obscured by the crushed bone or it was located at the posterior margin of the sphenethmoid in the posterior part of the orbit. In most specimens exposed in dorsal view, the sphenethmoid is concealed by the platelike frontoparietal. However, in a few specimens lacking the frontoparietal (e.g., HUIJZ F170a, 197), a well-defined frontoparietal fontanelle circumscribed anteriorly by the bony sphenethmoid is visible; this arrangement is typical of most non-pipid anurans. Moreover, the configuration of the sphenethmoid, along with its extensive ossification, suggests that in *Cordicephalus*, the orbital region of the skull was formed by cartilage replacement bone as in most anurans.

Prootics and Exoccipitals—The occipital and otic regions are crushed in all specimens and their shapes are distorted in most. Nonetheless, the preservation of prominent epiotic eminences in nearly all individuals suggests that the endochondral prootic and exoccipital bones were synostotically united to form the otic capsule. The otic capsules in a few specimens (e.g., HUIJZ F190, F191) are sufficiently well preserved to determine that each capsule, at the level of its anterior margin, was about equal in width to the frontoparietal. The anterior margin of each capsule is more or less straight and slopes away from the frontoparietal in a posterolateral direction. Laterally, each capsule bears a modest crista parotica that is wider anteriorly than posteriorly. The posterior margins of the otic capsules (in the region of the epiotic eminence) extend posterior to the occipital condyles. The otic region is large and its overall shape can be characterized as rectangular. Nearly all the specimens are too damaged to determine whether the foramen magnum was complete in bone (and the exoccipitals thus fused to one another dorso- and ventromedially).

In two specimens (KUVF 12743–44), there are indications of a low, rounded ridge extending obliquely across the ventral surface of each otic capsule anterolateral to the inner ear region. The mediolateral extent of these ridges is difficult to estimate owing to the poor preservation of the region, although fragments of the parasphenoid corpus between the otic capsules indicate that they did not reach the midline. The ridge, together with the depression anteriorly adjacent to it, may have accommodated the Eustachian tube. The fenestra ovalis is located on the lateral margin of the otic capsule, at about its midlength.

The contribution of the prootic to the lateral margin of the braincase in the orbital region is difficult to assess. The consistency and frequency of the breakage planes separating the otic capsule from the braincase, along with the configuration of the sphenethmoid, suggest that the prootic was not synostotically united with the sphenethmoid anteriorly, and that the two elements were separated by cartilage in life. In one specimen (KUVF 127544; Fig. 5), there is a notch in the edge of the prootic dorsal to its articulation with the parasphenoid; this may represent the bony margin of the prootic foramen. The exact condition of the occipital condyles could not be determined. The partial remains of the right condyle in HUIJZ F188, taken together with the several atlases preserved (e.g., HUIJZ F191; KUVF 127543–44), suggest that the condyles were not widely separated, had articular surfaces with a slight medial orientation, and were short.

Pleural Apparatus—The stapes is visible in several specimens (e.g., HUIJZ F161b, F165a, F170a, F189a), but it is best preserved in HUIJZ F188, in which the element is in situ (Nevo, 1968:plate 11B, *C. longicostatus*). The expanded base seems to

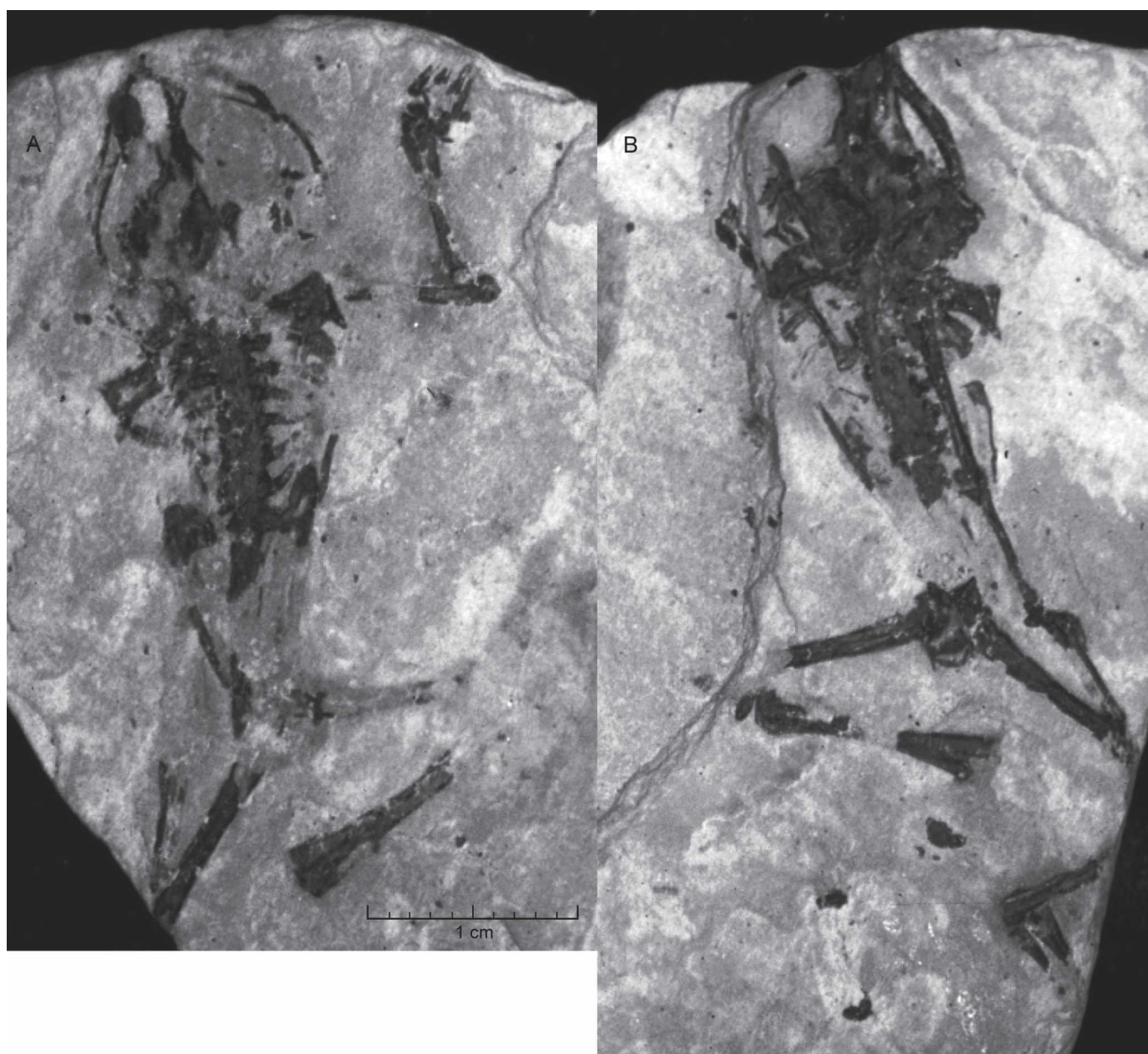


FIGURE 3. *Cordicephalus longicostatus*, holotype (HUJZ F171). **A**, Left counterpart (HUJZ F171a). **B**, right counterpart (HUJZ F171b). Note that the counterparts are not clear dorsal and ventral impressions; each represents an incomplete frontal section through the specimen, with the right counterpart being dorsal to the left. The distal expansion of the scapula is clear in both sections. The maxilla and coracoid are well represented in the right counterpart.

represent the pars interna plectri (= footplate). The stylus, or pars media plectri, is cylindrical; the basal third of the stylus is oriented anterolaterally, whereas the distal two thirds is directed more anteriorly.

Exocranium

Nasals—These paired, laminar bones are not well preserved in any of the specimens examined—probably owing to their delicate nature. Parts of the bones are visible in ventral aspect in KUV 127543 (Fig. 6) and HUJZ F191. The nasals seem to be relatively deep and to lack distinct rostral processes; medially, the anteromedial margins of the nasals are in broad contact with one another (Fig. 4). The anterior margins of the nasals more or

less conform to the arc of the maxillary arcade and extend from the preorbital process of the pars facialis of the maxilla anteromedially to the tip of the snout above the premaxillae. The posterolateral margin of each nasal extends from the frontoparietal to the maxilla and seems to have overlain the dorsal margin of the ossified planum antorbitale, thereby forming a complete bony anterior orbital margin. These portions of the nasals are in close contact with the facial lobe of the maxillae (Fig. 4).

Frontoparietal—This azygous, well-ossified bone forms the main roof of the skull (Figs. 1A, 2); although it is fragmented or obscured by other elements in many specimens, it is possible to discern its general features. The anterior margin of the frontoparietal is rounded (e.g., HUJZ F179) and completely overlaps the anterior margin of the braincase. Posteriorly, the frontopa-

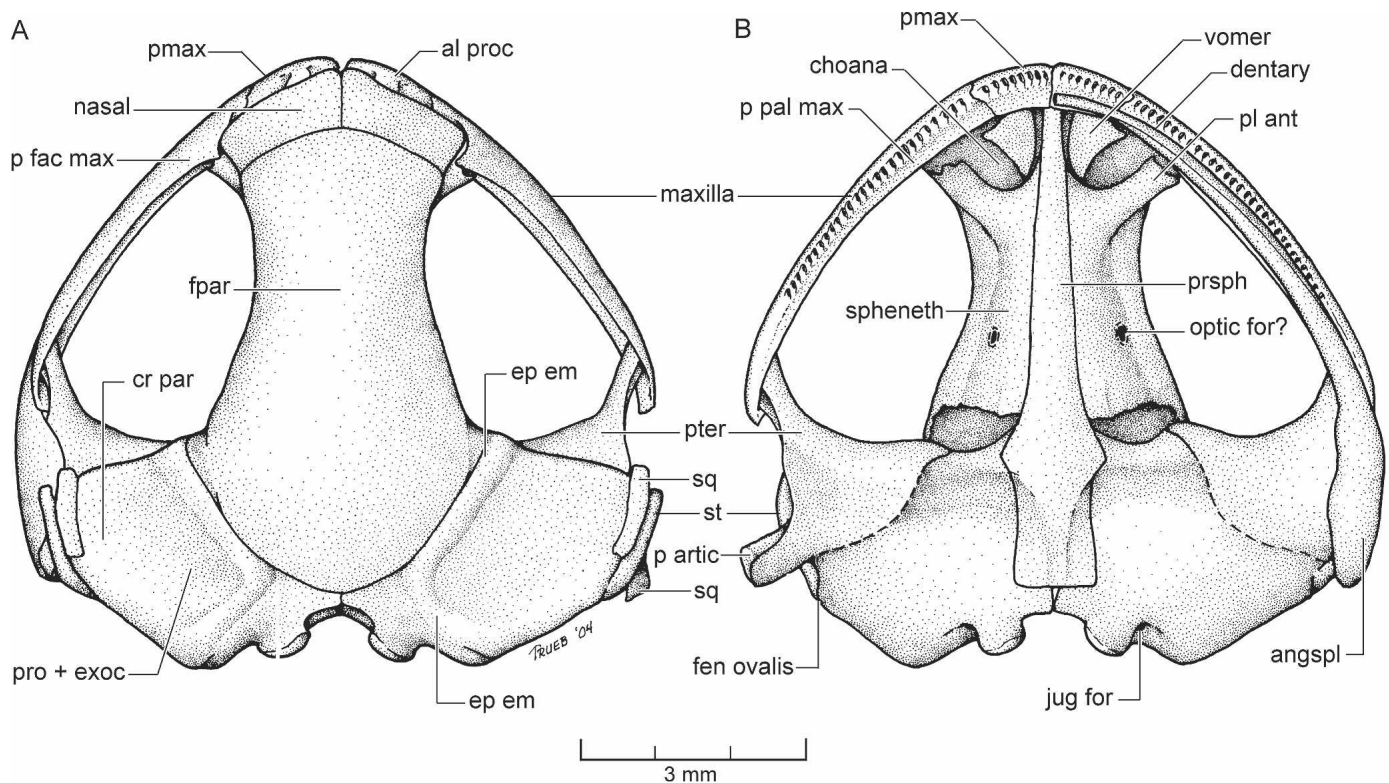


FIGURE 4. *Cordicephalus gracilis*, reconstruction of skull in dorsal (A) and ventral (B) aspects. Only the left side of the mandible is depicted. The locations of the teeth are shown by empty sockets, the number of which is not exact. Note that the optic foramen is indicated with a dashed line, owing to our uncertainty of the position of this structure. **Abbreviations:** **al proc**, alary process of premaxilla; **angspl**, angulosphenial; **cr par**, crista parotica; **ep em**, epiotic eminence of otic capsule; **fen ovalis**, fenestra ovalis; **fpar**, frontoparietal; **jug for**, jugular foramen; **optic for?**, questionably, the optic foramen; **p artic**, pars articularis of palatoquadrate; **p fac max**, pars facialis of maxilla; **p pal max**, pars palatina of maxilla; **pl ant**, planum antorbitale; **pmax**, premaxilla; **pro + exoc**, fused prootic and exoccipital; **prsph**, parasphenoid; **pter**, pterygoid; **spheneth**, sphenethmoid; **sq**, squamosal; **st**, stapes.

rietal overlies the medial part of each otic capsule in the region of the epiotic eminence (Fig. 4). The marginal flanges of the frontoparietal seem to be slightly deflected over the epiotic eminences, with the medial portion of the bone between these structures being more or less flat (e.g., KU 127543–44). There is no evidence of crests in the region. In some specimens, the frontoparietal is missing and the braincase is exposed dorsally (HUIJZ F201, 197, 170; Nevo, 1968:plate 9F), whereas in others, the bone is shifted forward (HUIJZ 252; KU 127543); this suggests that the frontoparietal was not fused to the underlying elements. The orbital margin of the frontoparietal is concave. The bone may be slightly flared laterally at the anterior end of the orbit in the region of the plana antorbitale; it narrows slightly in the mid-orbital region and then becomes progressively wider posteriorly. Its greatest width (ca. 33% greatest skull width) is at the anterior margin of the otic capsules, where the lateral margins of the frontoparietal recurve to form a rounded posterior margin (e.g., HUIJZ F161b, F179a, F188, F191; KUVF 127543; Fig. 6). At this level, the frontoparietal is about 36% wider than it is at the anterior margin of the orbit, and about 63% wider than it is at its narrowest point in the orbital area.

There is no evidence of thickened supraorbital margins or supraorbital flanges on the frontoparietal. In one specimen (HUIJZ F190), there is a small hole in the frontoparietal; although this might represent the pineal foramen, the structure is not evident in any other specimen that we examined. The braincase is evident in two specimens preserved in ventral view (KUVF 127543–44; Figs. 5, 6); in both of the latter, fragments of the dorsolateral braincase are displaced and preserved beside the sphenethmoid. These bones are thought to represent the bilat-

eral vertical flanges (i.e., laminae perpendiculares) of the frontoparietal that articulate with, or are fused to, the lateral walls of the sphenethmoid to form a complete girdle of bone in the orbital region. If this interpretation is correct, then the cranium of *Cordicephalus* must have been relatively high, rather than depressed, in lateral profile.

Vomers—Remains of these paired dermal bones that underlie the olfactory capsules were unquestionably identified in two specimens—KUVF 127543 and 127544 (Figs. 5, 6); they are best preserved in the latter. Each vomer is a large, edentate, triangular element that flanks the anterior end of the cultriform process of the parasphenoid. The anterior ramus is broad and lies posteriorly adjacent to the pars palatina of the premaxilla. A short prechoanal process is directed toward the pars facialis of the maxilla; a distinct postchoanal process is absent.

Parasphenoid—This dermal bone is not preserved in its entirety in any specimen examined. However, the presence of fragments with distinct, smooth boundaries (e.g., KUVF 127543–44) suggests that the parasphenoid was not fused to the sphenethmoid and otic capsules above, and permits us to reconstruct its general shape. The narrow cultriform process extends from the posterior part of the orbit to the premaxillae anteriorly (HUIJZ F165a, F179a, F252c; KUVF 127543–44; Fig. 4). The corpus of the parasphenoid lacks subotic alae; its posterior margin is located near the ventral margin of the foramen magnum. In KUVF 127543, short, laterally directed processes and crescent-shaped muscle scars are present and bilaterally symmetrical on each side of the parasphenoid corpus at the level of the anterior margin of the otic capsules. The base of the corpus is about the same width as the basal part of the cultriform process.

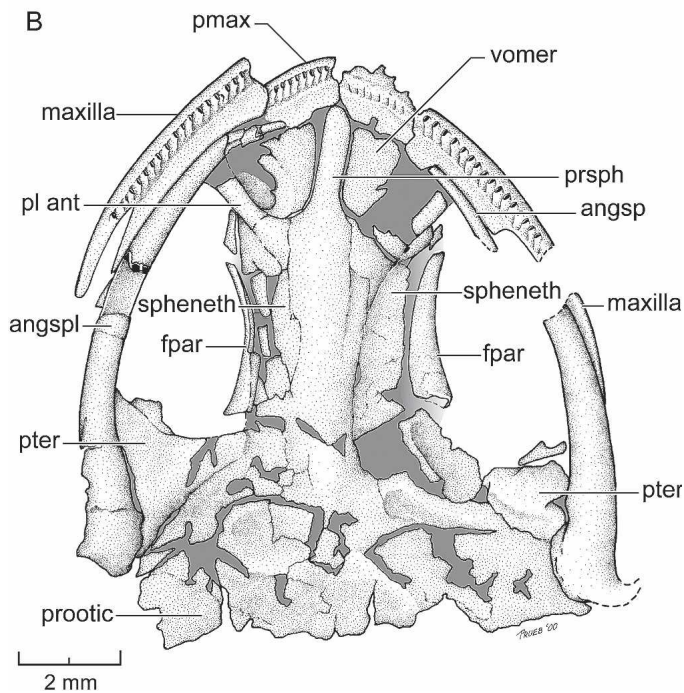


FIGURE 5. *Cordicephalus gracilis*, KUV 127544. **A**, Photograph of head of specimen. **B**, interpretative rendering of skull. Bones are stippled and matrix is indicated in gray. Broken sections of bone are hatched. In this ventral view, parts of the maxillae and premaxillae as well as the mandibles are evident. The vomers (right nearly complete) flank the cultriform process of the parasphenoid. Ossification of the planum antorbitalis is obvious, and the right pterygoid is especially well preserved. The contributions of the lamina perpendicularis of the frontoparietal and the sphenethmoid to the left side of the braincase are evident. **Abbreviations:** angspl, angulosphenial; fpar, frontoparietal; pl ant, planum antorbitalis; pmax, premaxilla; prsph, parasphenoid; pter, pterygoid; spheneth, sphenethmoid.

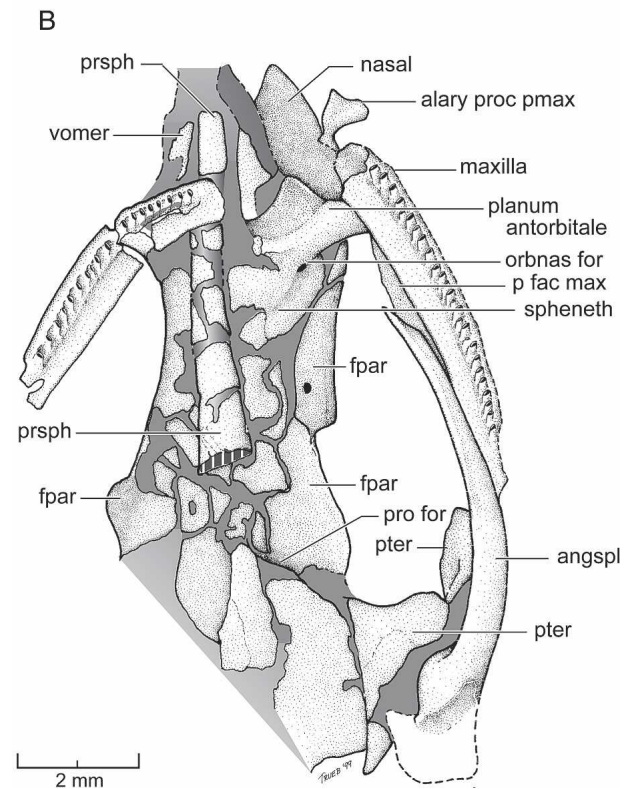
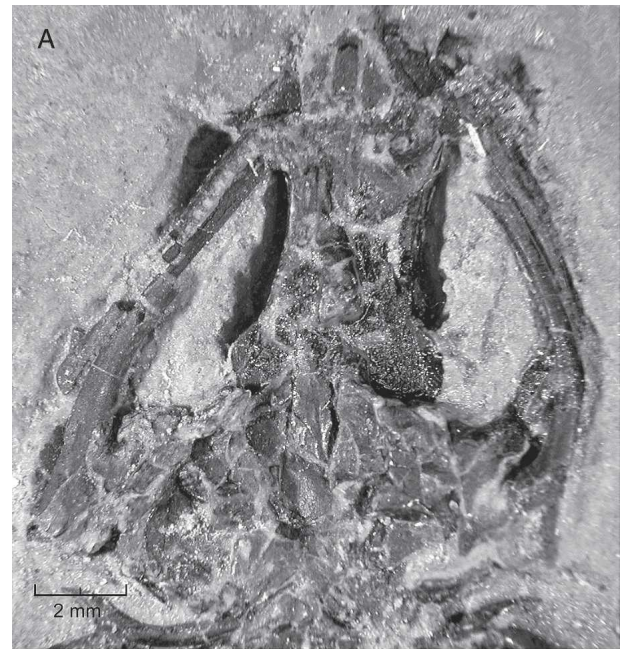


FIGURE 6. *Cordicephalus gracilis*, KUV 127543. **A**, photograph of head of specimen. **B**, interpretative rendering of skull; the right edge of the block was elevated to maximize the exposure of the left side of the braincase. Bones are stippled and matrix is indicated in gray. Broken sections of bone are hatched. In this ventral view, both maxillae are evident, but the right maxilla is broken. Parts of the vomers flank the anterior end of the parasphenoid. The ventral surface of part of the left nasal is visible anteriorly, along with the alary process of the premaxilla (anterior aspect). Fragments of the cultriform process of the parasphenoid lie on top of an elevated ridge of sediment; part of the corpus of the parasphenoid may be visible posteriorly between the otic capsules. **Abbreviations:** angspl, angulosphenial; fpar, frontoparietal; orbnas, orbitonasal; p fac max, pars facialis of maxilla; proc, process; pro for, prootic foramen; prsph, parasphenoid; pter, pterygoid; spheneth, sphenethmoid.

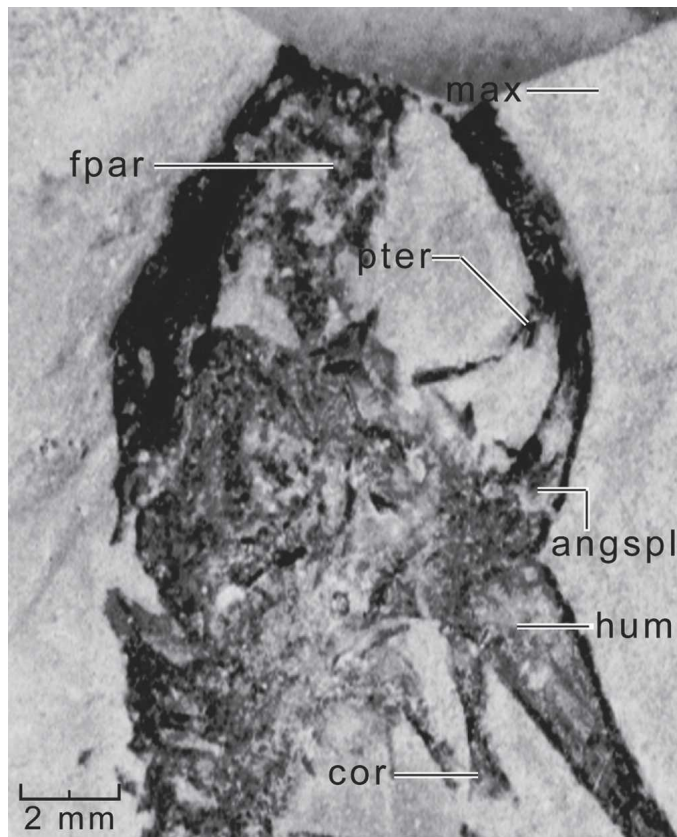


FIGURE 7. *Cordicephalus gracilis* (HUIJZ F283). Detail of head and anterior postcranial skeleton. The smooth arc of the upper jaw and mandible is clearly visible at the right, along with the anterior margin of the pterygoid in the posterior part of the orbit. The posterior position of the jaw articulation is evident. The slender coracoid bone lies to the left of the humerus. **Abbreviations:** *angspl*, angulosplenial; *cor*, coracoid; *fpar*, frontoparietal; *hum*, humerus; *max*, maxilla; *pter*, pterygoid.

Septomaxillae—In the type of *Cordicephalus longicostatus* (HUIJZ F171a), there is a small, triradiate element anteriorly adjacent to the snout. This may represent an isolated septomaxilla.

Premaxillae—The premaxillae are preserved in KUVF 127543 and 127544 (Figs. 5, 6). In the latter specimen, the bones are visible in ventral view in their natural position. The pars dentalis is well developed and seems to have borne eight teeth. The margins of the deep partes palatinae are slightly irregular in KUVF 127544, but smooth in the nearly complete premaxilla preserved in KUVF 127543 (Fig. 6). Based on these specimens, it seems that the width of the pars palatina increases slightly toward the midline of the skull in *Cordicephalus*; however, a conspicuous median palatine process and a posterolateral process are absent. The premaxillae seem to have articulated with each other in a straight medial articulation, and each bone seems to have had a broad, slightly oblique articulation with the maxilla without overlap of the respective partes palatinae. In KUVF 127544, the well-developed premaxillary alary process is preserved. Viewed anteriorly, the pair of alary processes diverge laterally from each other; in addition, the processes are inclined slightly anteriorly in lateral profile. The base of the alary process is about 30% the mediolateral width of the premaxilla and the height of the process is about half the width of the bone. The dorsal margin of the alary process is slightly concave, and the process is more expanded at its dorsolateral corner than at its dorsomedial corner.

Maxillae—These bones are best preserved in HUIJZ F165a (holotype of *C. gracilis*), F170a, F171a (holotype of *C. longicostatus*), F193a, and KUVF 127543–44. The maxilla has a well-developed pars dentalis that supported about 25 teeth, based on counts of tooth sockets. Few specimens preserve the dentition; however, it was possible to observe that the teeth are pedicellate and bicuspid in KUVF 127543. From its broad articulation with the premaxilla, the robust maxilla extends to the posterior region of the orbit, where it terminates freely (Fig. 4). The relatively wide pars palatina is evident in KUVF 127543–44 (Figs. 5, 6). This lingual shelf, the edge of which is rounded, is broadest anteriorly at its articulation with the pars palatina of the premaxilla and narrows posteriorly, but it is present at the posterior end of the bone. The pars facialis is low anteriorly; it increases in height in the region of the planum antorbitale, where it forms a distinct, low preorbital process at the anterior margin of the orbit. The anterior extension of the pars facialis beyond the articular surface of the pars palatina of the maxilla suggests that the maxilla might have slightly overlapped the lateral part of the premaxilla (Fig. 4).

Suspensory Apparatus

Pterygoid—In most specimens, this triradiate bracing bone is crushed and obscured by the stout lower jaw. The anterior ramus is short and stout; it extends anterolaterally from the otic capsule to articulate with the maxilla in the angle formed by the partes palatina and facialis near the distal end of the maxilla in the posterior third of the orbit (e.g., HUIJZ F190). The association of the lateral margin of the pterygoid with the adjacent mandible in KUVF 127544 suggests that there may have been a shallow ventral flange at the base of the anterior ramus. The short posterior ramus also is present in KUVF 127544 (Fig. 5), but the mandible obscures its relationship with the palatoquadrate. In the same specimen, as well as in KUVF 127543, pieces of bone overlap the ventral surface of the anterolateral otic capsule; these may be fragments of the pterygoid. The pterygoid seems to have been broadly triangular and to have covered the anterolateral portion of the otic capsule.

Squamosal—There are few remains that can be identified unequivocally as squamosals. The best example is HUIJZ F189a, in which the squamosal is isolated along the lateral margin of the otic capsule. In this dorsal exposure, the head of the squamosal is visible as a slender bone; the zygomatic ramus is broken, but the otic ramus seems to be complete. The stapes protrudes beneath the otic ramus and the ventral ramus of the squamosal; the ventral ramus of the squamosal is a slender, straight ventral projection that must have invested the lateral surface of the palatoquadrate cartilage. Thus, the bone seems to have been T-shaped, rather than conch-shaped, in lateral aspect; from this, we can infer that a tympanosquamosal bone was absent. The zygomatic ramus is relatively short and acuminate in HUIJZ F190.

Mandible

The lower jaw is preserved in many specimens (e.g., HUIJZ F179a, F190–91, F193a, and F252a; Figs. 1, 2, 4, 5, 7). Usually, the posterior part of the mandible is represented more clearly than the anterior part (e.g., KUVF 127543–44, Fig. 5). In some specimens (e.g., HUIJZ F161b, F165a), the mandible is displaced anteriorly with respect to the rest of the skull. These specimens reveal that the lower jaw was relatively massive, especially posteriorly, and arcuate, with no indication of recurvature. The angulosplenial has a shallow, but distinct, coronoid flange, which usually is visible adjacent to the lateral margin of the pterygoid (KUVF 127543). There is no evidence of mentomeckelian bones [= mentomandibulars of Nevo (1968)]. The articulation of the jaw seems to have been located posteriorly, at approximately the level of the fenestra ovalis.

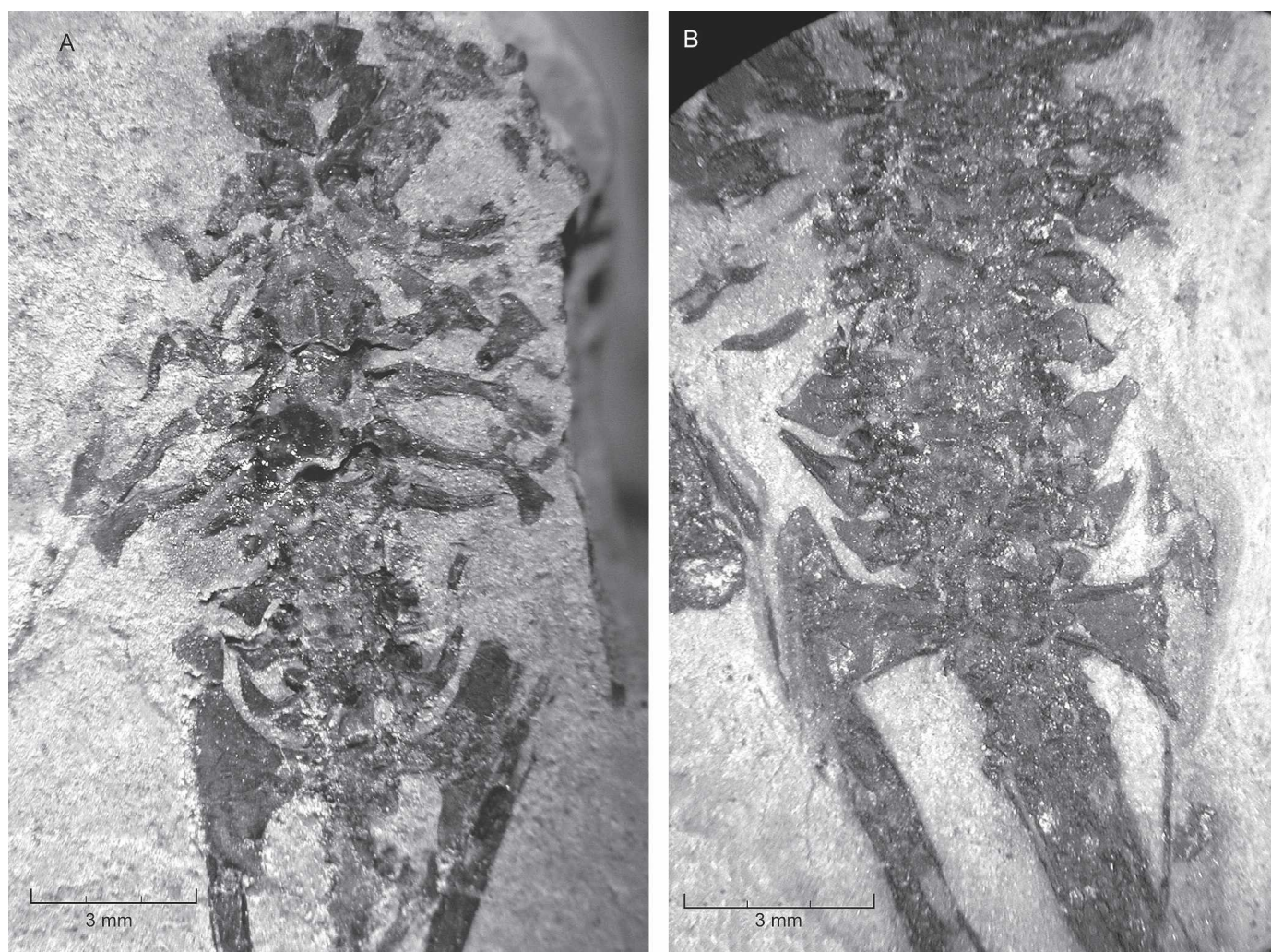


FIGURE 8. Dorsal aspects of the vertebral columns of (A) *Cordicephalus gracilis* (KUPV 127545) and (B) *Thoraciliacus rostriceps* (KUPV 127550). In *Cordicephalus*, the transverse processes of all presacral vertebrae except Presacral VI are complete on one or both sides, and the left sacral diapophysis is clearly represented. The differences in the shapes of the transverse processes of the posterior presacral vertebrae and the sacral diapophyses in the genera are clearly evident.

Hyobranchial Apparatus

In one specimen (KUPV 127545), a pair of small, slender bones that are slightly expanded at their proximal ends is preserved near the skull. These bones are oriented diagonally and lie anterolateral to the atlantal centrum. They are identified as the posteromedial processes of the hyoid.

Axial Column

Presacral Vertebrae—The vertebral column consists of seven presacral vertebrae. Because the first vertebra bears well-developed transverse processes in all specimens examined for this trait (e.g., HUIZ F191; KUPV 127543, 127545; Fig. 8), we consider the first presacral to represent the fusion of Presacrals I and II. The presence of a nerve foramen anterior to the left atlantal transverse process in KU 127544 supports this conclusion. The vertebral columns are crushed or sectioned in most specimens; thus, it is difficult to describe some features in detail, such as the nature of the articulation between pre- and postzygapophyses. The vertebral centra are relatively flat in ventral aspect (e.g., KUPV 127544–45); those of Presacrals III–V are somewhat broader than long, whereas the three posterior presacral

centra are as broad as long. The posterior articular facets are concave, whereas the anterior ones appear to be convex in several slightly disarticulated centra (e.g., KUPV 12743, 127545); this strongly suggests an opisthocoelous condition.

The transverse processes of *Cordicephalus* are extraordinarily well developed, as is apparent in HUIZ F191 and KUPV 127544–45 (Figs. 8, 9). Other specimens (e.g., HUIZ F160a, F161b, F165a, F171a,b, F177, F190, F252a; KUPV 127543) have impressions or remains of the transverse processes of some, but not all, presacral vertebrae. The robust transverse processes on the atlas (Presacral I + II) are unusual in their length and in having a nearly sigmoid configuration (Fig. 8); the overall width of this vertebra is equal to, or slightly greater than, that of the sacrum (e.g., HUIZ F165; KUPV 127545). The transverse processes of Presacrals III and IV are about equal in length and approximately 175% the length of the atlantal transverse processes. These transverse processes arch posteriorly and have a characteristic wavy shape that varies slightly among specimens examined. The proximal third or fourth of the processes of Presacrals III, IV, and occasionally V, extends laterally from the centrum and frequently is distinctly constricted at its midlength; the thickening probably represents the point of ankylosis of ribs

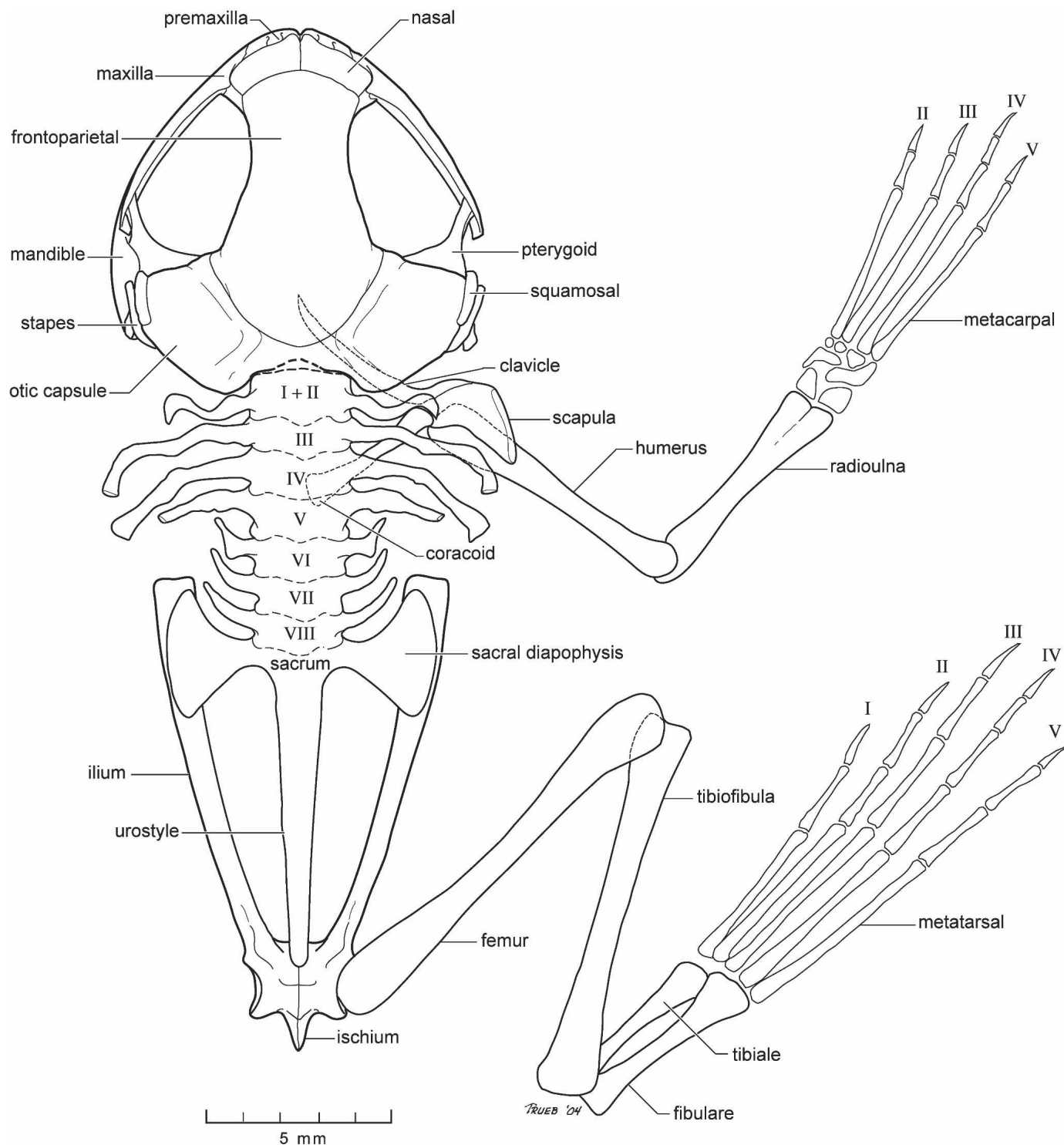


FIGURE 9. *Cordicephalus gracilis*, reconstruction of the skeleton in dorsal aspect. Dashed lines indicate proposed reconstructions or, in the case of the pectoral girdle, bones lying ventral. Digits are numbered I–V and presacral vertebrae are identified by Roman numerals. The relationship between the sacrum and urostyle is indeterminate. Similarly, the configuration of the neural arches and the presence or absence of imbrication is unknown.

to the transverse processes during development (e.g., HUIZ F161b). The distal ends of these processes are somewhat dilated and blunt. The transverse processes of Presacral V are long, equal to or even greater in length than those of the atlas (HUIZ F158, F165, F197; KUPV 127545), and are oriented laterally. The

proximal halves of the transverse processes of Presacral VI (Fig. 8) are oriented posterolaterally (HUIZ F191) or laterally (KUPV 127543), but in some specimens (e.g., HUIZ F191, 161b), the distal halves may be directed anterolaterally owing to a nearly 90° flexion in each process, which terminates in an acu-

minate tip. The transverse processes of Presacrals VII and VIII are slender, arched (or angled—e.g., F150a), and oriented anterolaterally. The vertebral profile in decreasing order of width is, as follows: III \approx IV $>$ I + II \approx V $>$ sacrum $>$ VI $>$ VII \approx VIII. Well-developed, rounded prezygapophyses are visible slightly anterior and adjacent to the base of the corresponding transverse processes in several specimens in which the vertebral column is exposed in ventral view (e.g., KUVF 127543, 127545).

Sacrum—The sacrum is composed of a single vertebra. The sacral diapophyses are dilated, with the convex lateral margins that usually are more than five times the width of the base of each diapophysis (e.g., KUVF 127543, 127545; Figs. 1, 8, 9), although in some specimens, they are less dilated (e.g., HUIJZ F190–91). The overall width of the sacrum is narrow, being less than that of Presacral V, but more than that of Presacrals VI–VIII. The distance between the anterolateral corners of the sacral diapophyses is slightly greater than that between the posterolateral corners. Both the anterior and posterior edges of the sacral diapophyses are curved.

Urostyle—The urostyle is moderate in length, being slightly shorter than the presacral vertebral column (Fig. 8). The relationship between the sacrum and urostyle is unclear. In some specimens (e.g., HUIJZ F165a,b, F171a; KUVF 127543, 127545), the elements seem to be fused to each other. This condition also is suggested by HUIJZ F190, in which the presacral segment is disarticulated from the rest of the vertebral column, and the sacrum and urostyle are shifted in one piece. In other specimens (e.g., HUIJZ F179b, F191), there seems to be a monocondylar articulation between the two elements. In most specimens examined, the urostyle lacks transverse processes; however, a small transverse process lies posterior to the left sacral diapophysis in KUVF 127543. Occasionally, the neural arches of one or two postsacral vertebrae are present in the anterior part of the urostyle (e.g., KUVF 127545). The urostyle is too crushed to determine the presence or absence of a dorsal crest. It is apparent (e.g., HUIJZ F165a,b) that the blunt distal tip was about half the width of the proximal end of the element.

Appendicular Skeleton

Pectoral Girdle—Components of the pectoral girdle usually are disassociated, although parts of the scapula, coracoid, and clavicle are preserved in ventral aspect in many specimens. The clavicles, usually represented by their lateral parts, are anteriorly concave and moderately acuminate medially (e.g., HUIJZ F200a, F206b; KUVF 127543; Figs. 3, 6, 7, 9). The lateral portion of each clavicle, at the level of the articulation of the bone with the scapula, is distinctly convex anteriorly and acuminate laterally. The clavicle has a broad articulation with the anterior margin of the pars acromialis of the scapula. The girdle doubtless was arciferous, although the epicoracoid cartilages might have been fused in the midline in the “pseudofirmisternal” condition described by Cannatella and Trueb (1988).

The coracoids, or parts of the bones, commonly are preserved (e.g., HUIJZ F 171b, F176a, F191, F200a, F252a; KUVF 127543; Figs. 3, 9). The bone is straight and expanded at both ends; the glenoid end seems slightly wider than the sternal terminus owing to the presence of a small protuberance that is associated with the posterior margin of the clavicle near the articulation of these bones with the scapula. The ends of the coracoid are about two and half times wider than the midshaft width of the bone.

The scapula is well preserved in KUVF 127543. It is a robust element, with a distinctive, almost rhomboidal shape (Fig. 9). The anterior margin of the scapula is more or less straight, rather than anteriorly concave; thus, the shaft of the bone does not have a “waist” or a bow-shape. The scapula is wider laterally than medially owing to its evident posterior projection. The length of the lateral margin is about two and one-half times that of the

head of the scapula, but only about 80% of the width of the bone. The pars acromialis is well developed and overlain anteriorly by the lateral end of the clavicle; the pars acromialis seems to have been separated from the posterior pars glenoidalis by a short groove, rather than a distinct notch. The medial margins of the partes acromialis and glenoidalis articulated with the lateral end of the coracoid.

The cleithrum seldom is clearly visible as an element distinct in the fragmentary remnants of the suprascapular blade (Figs. 1–3). Frequently, the bone is represented by the proximal portion that articulates with the lateral margin of the scapula. The proximal cleithrum bears an anterior prong (Fig. 3) that might have enclosed the leading edge of the suprascapular cartilage in a groove (e.g., HUIJZ F171a, 189a); however, it is impossible to determine the overall shape of the suprascapula, which, therefore, is omitted from the reconstruction of *Cordicephalus* depicted in Figure 9.

Forelimb and Manus—The humerus is best preserved in HUIJZ F165b, F171b, F177, F197b, F190, and F191, in which it usually is preserved in lateral or medial aspect. The bone is long, straight, and slender; the caput humeri (head) is well developed, spherical, and about 30% wider than the distal width of the bone at the level of the humeral ball (= eminentia capitata of Gaupp [1896]; = capitate eminence of Nevo [1968]). The symmetry of the proximal half of the humerus suggests that if a crista medialis or deltoid crest (= crista ventralis of Gaupp [1896]) were present, they were poorly developed. The eminentia capitata, or humeral ball, at the distal end of the bone seems to have been large and to have composed most of the distal width of the humerus.

The radioulna frequently is at least partially preserved. Among the most informative examples are HUIJZ F165a, F170a, and F190. In HUIJZ F190, the olecranon process and large cotyle (= sigmoid cavity) for the humeral ball are obvious in profile. The proximal width of the radioulna is about 75% that of its distal width; the midshaft width of the slender bone is a little less than half the distal width. A distinct sulcus intermedialis indicating the plane of fusion of the radius and ulna is evident on the dorsal surface of the distal third of the radioulna.

Parts of the carpus are preserved in HUIJZ F165a, F170a, F190, and F193. The best preservation is in F190, in which the left carpus seems to be complete and the right carpus is distally complete; both are in dorsal aspect. There are two large, proximal elements associated with the end of the left radioulna (Figs. 1, 2); the preaxial bone is identified as the radiale and the postaxial element as the ulnare. Following the nomenclatural scheme of Fabrezi (1992) and Fabrezi and Alberch (1996), we identified the bone lying distal to the radiale as Element Y. Distal to the ulnare along the postaxial margin is another good-sized element that reaches the base of Metacarpal V and is identified herein as Distal Carpal 5. A distal carpal is associated with the base of each of the other metacarpals (Distal Carpals II–IV); the bone at the base of Metacarpal IV is the largest of these elements. In the right carpus, there is an additional, small bone medial to the base of Metacarpal II; this may represent a prepollex—an element that is missing from the left carpus of this specimen. The metacarpals (well preserved in the right hand) seem extraordinarily long, being about 75% the length of the radioulna. In decreasing order, their lengths are II $>$ IV = V $>$ III. The phalangeal formula is 2-2-3-3 and the terminal phalanges are acuminate.

Pelvic Girdle—Although parts of the ilial shafts frequently are preserved (e.g., HUIJZ F165a, b, F177, F189a, F191; KUVF 127543, 127545, 127546), we did not encounter a well-preserved acetabular portion of the ilium exposed in lateral view. The best overall preservation of the entire pelvic girdle is in the holotype of *Cordicephalus gracilis* (HUIJZ 165a,b; Figs. 1, 2). The dorsal profile of the pelvic girdle describes a broad V-shape and the anterior ends of the ilia extend only a short distance beyond the

sacral diapophyses (Fig. 9). The width of the pelvic girdle at the anterior ends of the ilia is about 60% of the total length of the ilium. The ilial shafts lack any indication of prominent flanges or crests and probably were oval in cross section (e.g., KUPV 127545). A well-developed but low and broad-based dorsal prominence is located at the posterior end of the ilial shaft. A moderate supracetabular expansion that did not extend beyond the dorsal margin of the prominence seems to have been present. The modest infra-acetabular expansion has a distinct ventral component, but the presence of an inter-ilial tubercle cannot be confirmed. The ischia seem to have been long, with their anterior-posterior expansion being about equal to the length of the acetabulum. The acetabulum seems to have been oval and completed ventrally by a flat, bony pubis. The dorsal margin of the acetabulum is flat and the ischium appears to have been expanded dorsally, although the extent of this expansion could not be determined.

Hind Limb and Pes—Parts of the hind limb are especially well represented in HUIJZ F151b, F165a,b, F177, F201a, and F251b. The femur seems to be slightly sigmoid (e.g., HUIJZ F165, F197a) and clearly longer than the tibiofibula. Both ends of the femur are expanded about equally. The tibiofibula is robust and straight with equally expanded ends. The tibiale (= astragalus of some authors) and fibulare (= calcaneum of some authors) are evident in HUIJZ F165a, b, F177, and F251b. These bones seem to be distally fused in the first specimen, but separate in the two latter individuals; this might represent a trait that is ontogenetically or sexually variable. The fibulare is the more robust and longer bone of the two. The distal tarsus was too poorly preserved in all specimens that we examined to allow us to describe it completely. At least three distal tarsals are preserved in the holotype (Figs. 1, 2). The largest of these elements lies distal to the tibiale; because of its size, it is identified as a slightly displaced Element Y of Shubin and Alberch (1986). The medium-sized element that occurs distal to it, between the bases of Metatarsal II and III, seems to correspond to Distal Tarsal III, whereas the other bone medial to the tibiale probably is part of the prehallux. The metatarsals are elongated; the longest (Metatarsal V) is clearly longer than the tibiofibula. The lengths of the metatarsals decrease in the following order: V > III > IV > II > I. A phalangeal formula could not be determined. The terminal phalanges are long and pointed.

THE TAXONOMIC STATUS OF *CORDICEPHALUS LONGICOSTATUS*

Nevo (1968) acknowledged the similarity of the two species of *Cordicephalus* and distinguished *C. longicostatus* from *C. gracilis* primarily on the bases of the larger size of the former (31.44 vs. 26.05 mm of mean SVL, respectively) and cranial features. These include the following (condition in *C. gracilis* in parentheses): (1) Nasals subquadrangular (crescentic bars); (2) rostrum small, triangular (no rostrum); (3) anterior margin of sphenethmoid shallow (sphenethmoid with long, triangular anterior process); (4) slender, vase-shaped frontoparietals (vaselike); (5) parasphenoid “apparently” lacking processes on base of blade and hilt (wide rear portion of parasphenoid with lateral processes both anteriorly and posteriorly); and (6) otic capsules subquadrangular (ellipsoidal). Among postcranial characters, Nevo cited long ribs (medium to long), sacral diapophyses broadening abruptly distally (broadening gradually), cleft scapula (uncleft), suprascapular blade rounded posteriorly (suprascapular blade triangular), and interilial angle 30° (45°). In his descriptions of the pectoral girdles, Nevo (1968) described the coracoid of *C. gracilis* as having equally expanded sternal and glenoidal ends, in contrast to that of *C. longicostatus*, which he described as having the sternal end wider than the glenoidal end.

We failed to find consistency in these putative differences

among the specimens that we examined. For example, frontoparietals of similar shapes and proportions are present in some specimens ascribed to *Cordicephalus gracilis* and some belonging to *C. longicostatus* (compare figures 9C and 10 A, B of Nevo, 1968). In no specimen of *C. longicostatus* available to us is the corpus of the parasphenoid well enough preserved to ascertain the absence of processes at the base of the blade in this species. Also, gradually expanding sacral diapophyses occur in HUIJZ F188, 193, 252, referred to *C. longicostatus*, whereas, conversely, sacral diapophyses that might be described as broadening abruptly are present in specimens labeled as *C. gracilis* (e.g., HUIJZ F165, F190). Additionally, in some specimens of *C. longicostatus* (e.g., HUIJZ F176; Nevo, 1968:plate 10 B) in which the coracoid is well preserved, relative expansion of the sternal end with respect to the glenoidal end resembles that of the coracoid of *C. gracilis* (e.g., Nevo, 1968:plate 10 A). Moreover, there is obvious variation in these diagnostic characters among the specimens that were identified as each of these species. In this regard, it should be noted that the bones frequently are fractured and partially covered by the fine-grained sediment. In most instances, this causes the bones to have outlines that do not correspond to their actual shapes and is the source of some of this apparent variation.

Nevo is to be complimented on his attempt to avoid typology by quantifying data in a morphometric analysis, but based on our examination of the specimens, it seems that it would be extraordinarily difficult to obtain meaningful, repeatable measurements from these fossils. Moreover, we have no reason not to assume that this population of anurans included both sexes, as well as subadults. Thus, many perceived differences simply may reflect sexual dimorphism and ontogenetic variation in size and degree of ossification that is known to occur in Recent taxa. Lacking persuasive characters by which to distinguish these two species, it seems conservative and prudent to synonymize them. Here-with, we place *Cordicephalus longicostatus* Nevo, 1968, in the synonymy of *Cordicephalus gracilis* Nevo, 1968.

COMPARISONS AND TAXONOMIC PLACEMENT

Our interpretations of several features of *Cordicephalus gracilis* differ from those of Nevo (1968). In his interpretation of the holotype of this species (op. cit.:fig. 6), he illustrated a portion of the sphenethmoid exposed dorsally between the frontoparietal and the nasals. In the holotype (HUIJZ F165 a), the frontoparietal is exposed in ventral view and its anterior margin lies in front of (i.e., anterior to) the anterior part the braincase (excluding the septum nasi) formed by the sphenethmoid (Figs. 1A, 2). Nevo apparently interpreted the anterior margin of the sphenethmoid, along with the ossified portion of the septum nasi, to represent the posterior edges of the nasals. This observation led him to the conclusion that the sphenethmoid was exposed dorsally between the frontoparietal and nasals, as shown in his reconstruction of the skull of *C. gracilis*. We found no evidence of this configuration of the dorsal skull table among the specimens that we examined.

Owing to our extensive preparation of some specimens, we determined that the vomers are larger and located more anteriorly (Fig. 4) than depicted by Nevo's (1968:fig. 7) restoration of these bones. Also, we could not corroborate the presence of a distinct process at the posterior end of the parasphenoid in either *Cordicephalus* or *Thoraciliacus*.

Nevo (1968:269) described the nasals of *Cordicephalus gracilis* as well-developed, elongated, crescentic bars that overlie the premaxillae. This is an accurate description of his rendering of the type (HUIJZ F165; fig. 6), but the nasals were misidentified in this specimen, as described above.

Nevo (1968:269) considered the pterygoids to be well-developed bones, characterized by their curved anterior exten-

sion in *Cordicephalus gracilis*. He thought that the shape of the pterygoids, together with the supposedly arched lower jaw, impart a heartlike shape to the skull. We were unable to corroborate the presence of a pterygoid bearing a long anterior ramus in any of the specimens that we examined; therefore, we consider the anterior pterygoid ramus to be a much shorter process that meets the maxilla at the posterior third of the orbit. In addition, we prepared mandibles that are preserved in three dimensions (e.g., Fig. 6) and found them not to be strongly bowed.

Our interpretation of the vertebral column differs significantly from that of Nevo (1968) in the absence of a free atlas; in all specimens that we examined, Vertebrae I and II are fused. Nevo also reported that Presacals II–V bear free ribs, as shown in his interpretation of the holotype (op. cit.:fig. 6, but see Figs. 1, 2, 8). Some evidence of the ankylosis of the transverse processes of these vertebrae and corresponding ribs occurs in a few specimens (e.g., KUV 127543–45), but we observed no free ribs in individuals that we judged to be mature based on size and degree of ossification.

The nature of the articulation between the urostyle and sacrum is difficult to interpret because this region is poorly preserved in available specimens. Nevo (1968) observed that the sacrum articulated with the urostyle via a monocondylar articulation, and that there may be as many as two postsacra. We observed similar variation, in addition to apparent fusion between the sacrum and urostyle in some specimens.

Nevo (1968) considered the pectoral girdle of *Cordicephalus gracilis* to be arciferal with strongly arched clavicles, straight coracoids that are equally expanded at both ends, and a small, approximately triangular scapula that is uncleft. However, in his discussion of variation, he cited examples of cleft scapulae in *C. gracilis*, whereas that of "*C. longicostatus*" is cleft in the few specimens that he attributed to this species.

A total of nine free carpal elements, including a small distal carpal at the base of Metacarpal V, was reported as characteristic of *Cordicephalus* (Nevo, 1968); however, we were not able to corroborate the presence of this small bone.

According to Nevo (1968), *Cordicephalus* is distinguished from the sympatric monotypic genus *Thoraciliacus*, by the following features of *Cordicephalus*: a more slender skeleton, ilia diverging to form a triangle, shorter ischia, heart-shaped skull lacking a prominent rostrum, quadrate anteriorly placed, arcuate mandibles and anterior rami of pterygoids, more elongated otic capsules, third rib longer than second, arcuate transverse processes of Vertebrae VII and VIII, and longer humerus and radioulna. However, some of these putative distinguishing traits are based on misinterpretations of the state present either in *Cordicephalus* or in *Thoraciliacus*, as discussed below.

In comparison with the braincase of *Thoraciliacus*, that of *Cordicephalus* is considerably more ossified. This is evident in the extensive ossification in the region of the antorbital planes and septum nasi of the latter. The short maxillary preorbital processes of *Cordicephalus*, in contrast to the long processes of *Thoraciliacus*, may be correlated with this great anterolateral ossification of the neurocranium in *Cordicephalus*. Additionally, in *Cordicephalus*, the nasal capsule floor is invested ventrally by extensive vomers for which there is no evidence in *Thoraciliacus* (Nevo, 1968; Trueb, 1999). The premaxillae of *Cordicephalus* are narrower than those of *Thoraciliacus*, although these bones bear well-developed, distally expanded alary processes in both taxa (contra Trueb, 1999). *Cordicephalus* and *Thoraciliacus* have long parasphenoids that bear short processes at the level of the anterior margin of the otic capsules, as examination of recently prepared material of *Thoraciliacus* (e.g., KUV 127555) demonstrated, contrary to previous statements (Trueb, 1999). Despite this similarity, the corpus of the parasphenoid is wider in *Thoraciliacus* than in *Cordicephalus*, and we did not observe marked scars on the ventral surface of the bone in examples of *Thora-*

ciliacus. The examination of specimens of *Cordicephalus* preserved in three dimensions allowed us to verify that the venter of the otic capsules is excavated anteriorly, probably to provide space for the Eustachian tubes. In addition, the pterygoids seem to have floored these excavations laterally. In *Thoraciliacus* the ventral surfaces of the otic capsules are not modified to accommodate the Eustachian tubes according to Trueb (1999).

In both taxa, the skull is longer than the vertebral column, excluding the urostyle. However, as noted by Nevo (1968), *Cordicephalus* possesses a more gracile skeleton than *Thoraciliacus*, with proportionally longer forelimbs and hind limbs. Parenthetically, it should be noted that, in the reconstruction of *Thoraciliacus* by Trueb (1999), the hind limb is erroneously shown at a smaller scale than the rest of the skeleton. Also, the second pair of ribs is directed posteriorly, as noted by Nevo (1968), and not curved anteriorly as depicted by Trueb (1999). One of the most characteristic features of *Cordicephalus* is the long, arcuate transverse processes on Presacals VII and VIII, which in *Thoraciliacus* are shorter and broad-based (Fig. 9). The vertebral centra appear round in cross section and notochordal in *Thoraciliacus*, whereas those of *Cordicephalus* are more flattened and posteriorly concave. These taxa differ in the shape of the sacral diapophyses; those of *Cordicephalus* are narrower proximally and with distal margins more distinctly curved than in *Thoraciliacus*. In turn, this difference in the shape of the sacral diapophyses seems to be correlated with the shape and length of the ilia. The shafts are relatively longer and form a narrower angle when the bones are articulated in *Thoraciliacus* than in *Cordicephalus*.

To assess the phylogenetic placement of *Cordicephalus*, a parsimony analysis was conducted with PAUP 4.0b10 (Swofford, 2002). This analysis is based largely on those published by Báez and Pugener (2003), and Báez and Harrison (2005). However, a few characters have been re-evaluated and re-scored when necessary, as discussed below. We also scored the characters for the extant *Bombina* (*B. variegata* KU 80894; LIHUBA 402) and for *Thoraciliacus*. The 56 characters, equally weighted, are described in Appendix 1 and the taxon-character matrix in Appendix 2.

Careful preparation and close examination of specimens of *Cordicephalus* enabled us to score Characters 17 (maxillary antorbital process), 20 (septomaxilla), 25 (posteromedial extent of parasphenoid), and 28 (pterygoid knob) (Appendix 1), the states of which have been considered unknown in this taxon in a previous analysis (Báez and Harrison, 2005). Likewise, Character 9 (antorbital plane) was rescored as "0" for *Cordicephalus*, which was previously regarded as possessing completely ossified antorbital planes (Báez and Pugener, 2003), because there is reasonable evidence for distally cartilaginous planae. We also included an additional character: ossification of mentomeckelians (Character 35), although there is some controversy over the presence of these bones in *Palaeobatrachus*. These bones have been reported in this taxon (Špinar, 1972; Estes and Reig, 1973), but Cannatella and de Sá (1993) questioned their bony nature. In most specimens of *Palaeobatrachus* exposed in ventral aspect examined for this trait, the dentaries lie flat on their medial surfaces, thereby making it difficult to determine the presence or absence of these small bones. However, mentomeckelian bones partially fused to the long dentaries are clearly present in *Palaeobatrachus* sp. (KU 124976) and in *P. grandipes* (specimen 35b of the Špinar collection, National Museum, Prague; AMB pers. obs.).

Character 16 of the present analysis merits comment. The disposition of the maxillary connection to the premaxilla was used by Cannatella and Trueb (1988) in their phylogenetic analysis of the extant pipids. These authors considered the condition in which the pars facialis of the maxilla slightly overlaps the premaxilla as a derived state for pipids. Subsequently, Báez and

Trueb (1997) noted that some overlap occurs in non-pipid frogs and redefined the character so as to evaluate whether the anterior maxillary pars facialis extends to, or overlaps, the premaxillary process. Henrici (1998) also considered the presence of a maxilla that overlaps the premaxilla to be a synapomorphy that unites pipids and palaeobatrachids in her analysis of the taxonomic position of *Rhadinosteus parvus*, possibly a pipoid, from the Upper Jurassic of Utah. Finally, Báez and Harrison (2005) took into account both the shape of the anterior maxillary pars facialis and the presence of overlap. However, examination of the anterior portion of the maxillary pars facialis and its relationship with the premaxilla in the taxa included herein indicates that the maxilla extends onto the premaxilla in *Bombina* (e.g., *B. variegata*) and *Discoglossus* (e.g., *D. pictus*, PVL unnumbered specimen), as well as in other discoglossids examined for this trait but not included in this analysis (e.g., *Barbourula busuangensis* KU 79003; *Alytes cisternasii*, PVL unnumbered specimen). In *Bombina*, the maxillary pars facialis forms a distinct articulating process that overlaps the premaxilla, but this process is not as long and pointed as is in most pipids and *Palaeobatrachus*. In living hylomorphs, the maxillae lack a distinct pointed process, but their anterior ends are in contact with each other, completely overlapping the reduced premaxillae. Although in the Eocene *Singidella* from Tanzania, the anterior ends of left and right maxillae are not in contact, they are narrowly separated and widely overlap the premaxillae (Báez and Harrison, 2005).

With regard to the coronoid process of the angulosplenial

(Character 35), Cannatella and Trueb (1988) noted that it is broad and expanded into a blade-like flange in extant pipids, unlike the coronoid processes of *Rhinophrynus* (Trueb, 1996) and *Palaeobatrachus* (Hossini and Rage, 2000), which are small or moderately developed. However, we observed some variation between these extreme conditions.

The phylogenetic analysis yielded six most parsimonious trees of 111 steps (CI: 0.640, RI: 0.840) using the branch-and-bound search strategy. These hypotheses differ in the alternate position of *Cordicephalus* as the sister taxon of the clade formed by Pipidae and the Tertiary *Palaeobatrachus*, or as the sister taxon of *Palaeobatrachus*. These most-parsimonious trees also differ in the placement of some South American xenopodinomorph taxa within Pipidae, the interrelationships of which remain ambiguous as in previous analyses (Báez and Pugener, 2003; Báez and Harrison, 2005; Trueb et al., 2005). A strict consensus of the six most-parsimonious trees is presented in Figure 10. Support for the nodes has been estimated by decay indices (Bremer, 1994) and by bootstrap percentages based on 1000 replicates; the corresponding values are indicated on the cladogram (Fig. 10).

Cordicephalus shares with other pipimorphs several unambiguous synapomorphies: short nasal region (2), incomplete maxillary arcade (19), long parasphenoid (24), free ribs in larvae but fused to transverse processes in adults (46), ossified pubis (55). Although this evidence corroborates that *Cordicephalus* clearly is a member of Pipimorpha (sensu Ford and Cannatella, 1993), its placement with respect to Pipidae and *Palaeobatrachus* remains unresolved in the present analysis.

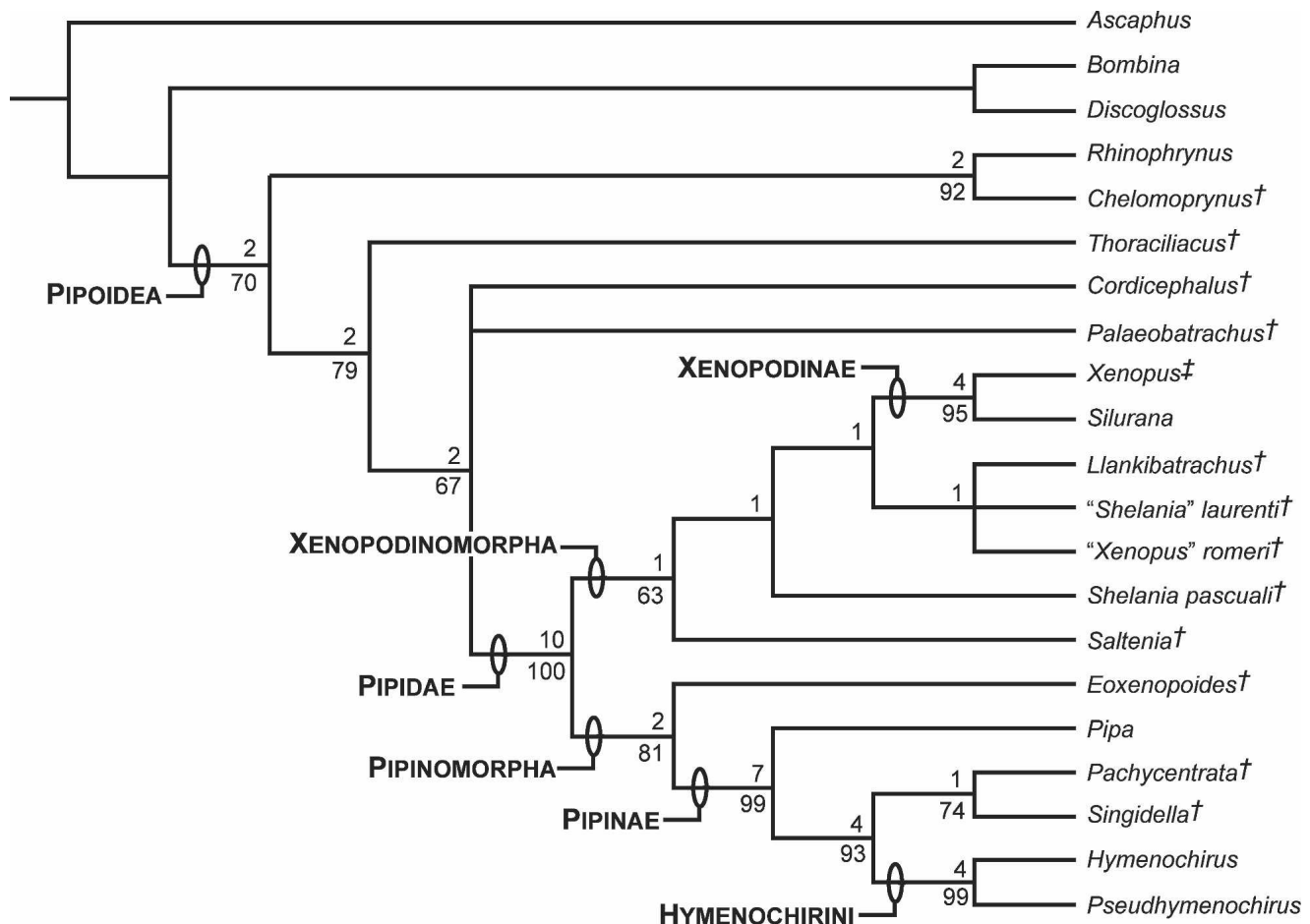


FIGURE 10. Strict consensus of the six most-parsimonious trees obtained in the analysis. Bremer values for clades are shown above the stems and bootstrap values are below the stem. Extinct frogs are indicated by daggers.

Thoraciliacus rostriceps, in turn, seems to represent a more basal pipimorph lineage relative to a clade that includes *Cordicephalus*, *Palaeobatrachus*, and the crown Pipidae (Fig. 10). This conclusion contrasts with those of previous analyses based on the data offered by Nevo (1968), in which, although lying outside the crown group, *Thoraciliacus* and *Cordicephalus* form a clade (Báez, 1981; Henrici, 1998). Both taxa from Israel retain the primitive state for several pipid synapomorphies (laminar septomaxillae [20], vomers postchoanal in position or absent [21], parasphenoid incorporated into the braincase floor [22], conch-shaped tympanosquamosal [26]; however, this restudy of *Cordicephalus* revealed significant differences from *Thoraciliacus*). The presence of modified venters of the otic capsules to house the Eustachian tubes (12) and depressed (41), opisthocoealous (42) presacral centra in *Cordicephalus* support its more crownward position within Pipimorpha. In *Thoraciliacus*, the condition of the presacral centra seems to resemble that of *Rhinophrynus* in that the ontogenetically late opisthocoealy is preceded by incompletely ossified centra with concave articular facets anteriorly and posteriorly (Trueb, 1999).

CONCLUSIONS

Both *Thoraciliacus* and *Cordicephalus* possess features that traditionally have been considered adaptive for an aquatic mode of life, such as a flat skull, long parasphenoid that supports the short nasal capsules, reduced number of presacrals by fusion of the atlas and second vertebra, and relatively long metapodials that suggest extensive webbing, (Noble, 1954; Nevo, 1968; Trueb, 1996). However, these taxa lack many other derived cranial as well as postcranial features that occur in extant pipids (Cannatella and Trueb, 1988), some of which may also be related to their fully aquatic habits.

The excavated venter of the otic capsules of *Cordicephalus* suggests that it had longer Eustachian tubes than in terrestrial frogs and reflects a modification of the braincase for underwater hearing (Elepfandt, 1996) earlier in pipimorph history than previously thought. By contrast, the retention of T-shaped squamosals indicates that its ears were not as specialized to detect underwater sound as those of living pipids, which have a complete bony framework for the tympanic membrane.

Nevo (1968) suggested that *Cordicephalus* lacks many aquatic specializations in the pelvis present in *Thoraciliacus*. Our study corroborated that there are significant differences in the postcranial skeleton of these two species. Some of these features have been identified as part of a single iliosacral functional complex, the characteristics of which are important in locomotor behavior in extant frogs (Emerson, 1979, 1982). *Cordicephalus* has moderately expanded sacral diapophyses with distinctly curved lateral margins, which contrast with the straighter diapophyseal margins of *Thoraciliacus*. Although the lateral borders of the sacral diapophyses may have been completed in cartilage in life, this slight difference in shape occurs together with relatively shorter ilia and longer posterior transverse processes in *Cordicephalus* than in *Thoraciliacus*. Unfortunately, we were not able to determine the pattern of the ilio-lumbaris muscle attachment to identify the type of iliosacral articulation (Emerson, 1979) in each of these fossil species. The great variation in the position of the articulation of the sacrum with the iliac shafts in *Thoraciliacus rostriceps* suggests that the predominant movement in this species was an anteroposterior sliding in the horizontal plane, which has been shown to be advantageous for swimming (Palmer, 1960; Emerson and de Jongh, 1980). In contrast, *Cordicephalus* usually preserves the sacral diapophyses articulated at the anterior ends of the ilia, as noted by Nevo; this might be the result of a different type of iliosacral articulation, which enabled the frog to perform considerable lateral rotation at the iliosacral joint. If this were the case, then *Cordicephalus* might have had a wide locomotor repertoire.

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- (10) Margins of the optic foramina: 0, composed of cartilage and sphenethmoidal ossification; 1, composed completely of sphenethmoidal ossification.
- (11) Floor of the braincase in the orbital region: 0, rounded; 1, distinctly angled.
- (12) Eustachian canal: 0, absent; 1, present as deep furrow in prootic; 2, present as shallow anterior depression in prootic.
- (13) Inferior perilymphatic foramina: 0, present, not ventral to jugular foramina; 1, present, ventral to jugular foramina; 2, absent.
- (14) Superior perilymphatic foramina: 0, present; 1, absent.
- (15) Premaxilla, palatine process: 0, not daggerlike; 1, daggerlike.
- (16) Maxilla, pars facialis: 0, not or slightly overlapping premaxilla; 1, overlapping premaxilla with pointed process that reaches alary process; 2, nearly or completely covering premaxilla anteriorly.
- (17) Maxilla, antorbital process: 0, absent; 1, present.
- (18) Maxilla, partes in the orbital region: 0, distinct; 1, not distinct.
- (19) Maxillary arcade: 0, complete; 1, incomplete.
- (20) Septomaxillae: 0, small and complex; 1, large and arcuate.
- (21) Vomers: 0, medial to the choanae; 1, posterior to choanae only; 2, absent.
- (22) Parasphenoid, relationship to braincase: 0, not fused; 1, partially or completely fused.
- (23) Parasphenoid, alae: 0, present; 1, absent.
- (24) Parasphenoid, anterior extent: 0, not reaching maxillary arcade; 1, reaching maxillary arcade.
- (25) Parasphenoid, posteromedial extent: 0, extending near ventral margin of foramen magnum; 1, ending well anteriorly to ventral margin of foramen magnum.
- (26) Squamosal, shape: 0, T-shaped without stapedial process; 1, T-shaped with stapedial process; 2, conch-shaped.
- (27) Squamosal, zygomatic ramus: 0, well developed; 1, reduced or absent.
- (28) Pterygoid knob: 0, absent; 1, present.
- (29) Pterygoid, position of anterior ramus: 0, medial to maxilla; 1, abutting maxilla; 2, dorsal to maxilla; 3, anterior ramus absent.
- (30) Pterygoid, medial ramus: 0, present, lacking indentation; 1, present, with indentation; 2, absent.
- (31) Pterygoid, configuration in otic region: 0, not expanded; 1, expanded to form an otic plate.
- (32) Pterygoid, contact between medial ramus and parasphenoid: 0, limited or no contact; 1, extensive contact.
- (33) Pterygoid, fusion of pterygoid and otic capsule: 0, not fused; 1, fused.
- (34) Angulosplenial, coronoid process: 0, poorly developed; 1, blade-like.
- (35) Mentomeckelian bone: 0, present; 1, absent.
- (36) Jaw articulation, position: 0, lateral to otic capsule; 1, at anterior margin of otic capsule.

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APPENDIX 1

List of the 56 osteological characters and their states in adult frogs used in the parsimony analysis. See text for explanation. The data matrix is presented in Appendix 2.

Cranial Characters

- (1) Skull shape in lateral profile: 0, rounded; 1, wedge-shaped.
- (2) Length of rostrum: 0, one-third, or more, of skull length; 1, one quarter, or less, of skull length.
- (3) Nasals: 0, paired; 1, fused.
- (4) Frontoparietals and nasals, relationship: 0, not overlapping; 1, overlapping.
- (5) Frontoparietals: 0, paired; 1, fused.
- (6) Frontoparietals, posterolateral extensions: 0, absent; 1, present.
- (7) Frontoparietal fontanelle, anterior margin: 0, sphenethmoidal ossification composes anterior margin; 1, anterior margin cartilaginous.
- (8) Olfactory foramina: 0, bound completely or partially in bone; 1, bound in cartilage.
- (9) Planum antorbitale: 0, partially or completely cartilaginous; 1, completely ossified/mineralized between sphenethmoid medially and maxillary arcade laterally

Hyobranchium

- (37) Posteromedial process, length: 0, length less than half anteroposterior length of lower jaw; 1, length more than half anteroposterior length of lower jaw.
- (38) Posteromedial process, anterior end: 0, wider than posterior end; 1, narrower than posterior end.
- (39) Parahyoid bone: 0, present; 1, absent.
- (40) Ceratohyal (= hyale): 0, not ossified; 1, ossified.

Postcranial Characters

- (41) Vertebral centra, shape: 0, cylindrical; 1, depressed.
- (42) Vertebral centra, articulation facets: 0, notochordal; 1, opisthocoelous; 2, procoelous.

	Character																																			
Taxon	5						10						15						20						25						30					
<i>Ascaphus</i>	0	0	0	0	0	0	0	2	1	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0					
<i>Bombina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Chelomophrynus</i>	0	?	0	?	1	0	?	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	1	0	?	?	?					
<i>Cordicephalus</i>	0	1	0	0	1	0	0	0	0	?	0	2	?	?	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0					
<i>Discoglossus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0					
<i>Eoxenopoides</i>	0	1	0	1	1	0	0	0	1	1	1	1	?	?	0	1	0	1	1	?	1	1	1	1	0	2	1	0	2	0	0					
<i>Hymenochirus</i>	1	1	0	0 ¹	1	0	1	0	1	1	1	2	0	1	2	0	1	1	1	1	2	1	0	1	2	1	0	3	0	0	0					
<i>Llankibatrachus</i>	0	1	0	1	1	0	?	?	?	?	1	0	1	?	?	0	?	1	1	1	1	?	1	1	1	0	2	0	1	2	1					
<i>Pachycentrata</i>	1	?	?	?	1	1	?	0	1	1	1	1	?	?	?	?	?	?	?	?	2	1	1	0	1	?	?	0	?	?	?					
<i>Palaeobatrachus</i>	0	1	0	0	1	0	0	0	0	0	1	2	0	0	0	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0					
<i>Pipa</i>	1	1	0	1	1	0	1	0	0	1	1	1	2	0	0	1	0	1	1	1	2	1	1	1	1	2	1	0	2	0	0					
<i>Pseudhymenochirus</i>	1	1	0	?	1	0	1	0	1	1	1	1	2	0	1	2	0	1	1	1	2	1	1	0	1	2	1	0	3	0	0					
<i>Rhinophrynus</i>	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	2	0					
<i>Saltenia</i>	?	1	0	1	1	0	0	0	0	1	0	1	?	?	?	0	1	1	?	1	?	1	1	1	0	2	1	1	0	?	?					
"Shelania" laurenti	0	?	0	1	1	0	0	0	0	1	0	1	1	1	?	?	1	1	1	?	1	1	1	?	0	2	?	1	?	?	?					
<i>Shelania pascuali</i>	0	1	1	1	1	0	0	0	0	1	0	1	?	?	?	0	1	1	1	1	1	1	1	1	0	2	0	1	0	1	0					
<i>Silurana</i>	0	1	0	1	1	0	1	1	0	1	0	1	0	1	0	1	0	1	1	1	2	1	1	1	0	2	0	1	2	1	0					
<i>Singidella</i>	1	1	0	?	1	1	?	0	1	1	1	1	?	?	?	0	2	0	1	1	1	2	1	1	0	1	2	1	0	2	0					
<i>Thoraciliacus</i>	0	1	0	1	1	0	?	?	?	0	0	0	?	?	?	0	?	1	?	1	?	0	0	1	1	0	0	0	0	0	0					
<i>Xenopus</i>	0	1	1	1	1	0	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	2	0	1	2	1	0					
"Xenopus" romeri	0																																			