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CRANIAL ANATOMY, ONTOGENY, AND RELATIONSHIPS OF THE LATE CARBONIFEROUS TETRAPOD *GEPHYROSTEGUS BOHEMICUS* JAEKEL, 1902

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ABSTRACT—We review the cranial morphology of the Late Carboniferous terrestrial tetrapod *Gephyrostegus bohemicus* from the coal deposits of the Nýřany Basin in the Czech Republic. *Gephyrostegus* is known from several skulls ranging in length from about 25 mm to about 58 mm (holotype). The narrow skull is about twice as long as wide and shows a well-ossified quadrate and articular, but no evidence of braincase ossification. Autapomorphic features include a pustular ornamentation on some skull table bones, and a plate-like tabular process exhibiting a fine dorsal pitting. *Gephyrostegus* shares with *Brukter-erpeton fiebigi* (Late Carboniferous, Germany) the presence of low, anteromedially to posterolaterally orientated sharp ridges on the posteroventral surface of the vomer. It shares with seymouriamorphs a rectangular, transverse pterygoid process and closely packed, radially arranged rows of small denticles on the palate. A phylogenetic analysis retrieves Gephyrostegidae (*Gephyrostegus*, *Brukbererpeton*) as sister group to Seymouriamorpha, although this wider clade receives low bootstrap support.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

A wealth of tetrapod taxa, most with body lengths of around 140 mm, have been described from Nýřany and Třemošná (Plzeň-Manětín Basin, Czech Republic). Among them, the genus *Gephyrostegus* was last described in detail by Carroll (1970), with some amendments by Panchen (1970). According to Carroll (1970:305), *Gephyrostegus* "represents the morphological pattern expected in the group of anthracosaurs which gave rise to reptiles," and forms a branch of the anthracosaurs separate from embolomeres (here, 'anthracosaur' refers to the group that includes eoherpetontids and embolomeres; Holmes, 1984, 1989; Smithson, 1985; Panchen and Smithson, 1988; Ruta and Clack, 2006; Ruta and Coates, 2007). Its robust postcranium and gracile limbs suggest a terrestrial animal, in contrast to the largely aquatic embolomeres. Although Carroll's conclusions on the affinities of this taxon have been superseded by cladistic studies, in many of these *Gephyrostegus* has appeared as a stem amniote, often crownward of embolomeres (e.g., Clack and Finney, 2005; Ruta and Clack, 2006; Ruta and Coates, 2007).

Given the significance ascribed to this genus, it is unfortunate that Carroll was unable to complete his studies (see below) and had to rely on only two specimens rendered as peels. He also included descriptions and figures of some of the other Nýřany tetrapods: *Diplovertebron punctatum*, *Eusauropleura digitata*, and *Solenodonsaurus janenschi*. These are dealt with briefly below, but are not otherwise described. Carroll provided detailed drawings of *Gephyrostegus*, a full skeletal reconstruction, and two alternative skull reconstructions based on the two specimens studied. As a consequence, they showed differences from

each other. We have been able to study additional specimens unavailable to Carroll, and unrecognized until recently. Our re-description aims to reconcile the conflicting skull reconstructions in Carroll and to provide a new cladistic analysis incorporating our new observations on the cranial morphology of *Gephyrostegus* and of a range of other taxa not available to Carroll. Our cladistic analysis also includes characters from the postcranium. However, these will be detailed in a separate work on the postcranial osteology of the Carboniferous Czech anthracosaurs. Below, we provide a detailed historical background to research on this faunistic assemblage.

HISTORICAL BACKGROUND

Since their first description (Fritsch, 1885a, 1885b), the small anthracosaurs from Nýřany and Třemošná have often been invoked in relation to the origin of amniotes and other amniote-like groups, such as seymouriamorphs (e.g., Panchen and Smithson, 1988; Lee and Spencer, 1997). The specimens are dispersed across several museums, and the political history of the 20th century has meant that they were not all readily accessible to most potential researchers. Most previous studies have been based on one to four specimens and no author has attempted to incorporate all of the determinate material in a single description. The material discussed here has a complicated history, having been described as five different species in four different genera. One publication (Brough and Brough, 1967) added some basal amniotes to the hypodigm, but these were later removed (Carroll, 1970). Because the full taxonomic and descriptive history of this material has never been reviewed, we take the opportunity to outline it here. The material originally described by Antonín Frič (or Anton Fritsch), referred to by his Fritsch Original (Fr. Orig.)

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numbers, is held in the National Museum, Prague, and now has NMP catalog numbers.

Fritsch had collected some of this material from the mine at Nýřany in the 1870s, but did not mention it in his first report on the fauna (Frič, 1876). By the time he had completed the first part of his monumental 'Fauna der Gaskohle und der Kalksteine der Permformation Böhmens' (Fritsch, 1879), he had recognized some of the vertebrate material as distinctive and gave advanced notice of the taxon *Diplovertebron punctatum* diagnosed by its double centra. This and other taxa listed on pages 26–32 of the first part of 'Fauna der Gaskohle' have generally been treated as nomina nuda, being insufficiently diagnosed.

The first full description of anthracosaur-like material from the Plzeň-Manětín Basin was published by Fritsch (1885a:11–13, pls. 50, 52–53). Two specimens from Nýřany (Fr. Orig. 96 and 128) were described as *Diplovertebron punctatum* in the monotypic family Diplovertebridae. Fr. Orig. 128 is a large slab with much of a single, completely disarticulated skeleton. Fr. Orig. 96 bears a few well-preserved, mostly postcranial, isolated elements. One source of confusion in Fritsch's description is that he (Fritsch, 1885a:11) noted that the small slab (Fr. Orig. 96) was figured in plates 50 and 52, and the large slab (Fr. Orig. 128) was figured in plates 50 and 53. Plate 53 is indeed entirely composed of material from Fr. Orig. 128, but is captioned in error as Fr. Orig. 96. We should also note that in plate 52, figure 2, the Fr. Orig. 96 engraving has been subject to considerable artistic license, involving substantial material rearrangement relative to its configuration on the original slab. At this stage, Zittel's (1887–1890) vertebra-based tetrapod classification had not yet appeared, and Fritsch seems to have regarded *Diplovertebron* as a small temnospondyl-like form but with embolomerous vertebrae. He made no attempt to reconstruct the skull from the isolated elements available to him. Fritsch (1885b:pl. 62, fig. 5a) also figured a small anthracosaur pelvis (Fr. Orig. 314) from Nýřany, which he identified as a damaged jaw element of the temnospondyl *Nyrania trachystoma*. Ten years later, Fritsch (1895:121, pl. 128, figs. 9–11) established the binomen *Hemichthys problematica* for a skull in counterpart (Fr. Orig. 207) from Třemošná, described as a possible fish. At that time, he had no skull material of *Diplovertebron punctatum* that would have allowed him to make a comparison. The *Hemichthys* specimen is in fact a small anthracosaur skull. Finally, in the last part of 'Fauna der Gaskohle,' Fritsch (1901:89–90, pl. 162, figs. 5–8) described a small, articulated tail with heavy scalation (Fr. Orig. 208) from Třemošná under the binomen *Nummulosaurus kolbii*. The tail is clearly embolomerous. There is a string of trunk vertebrae on the same slab, although their association is uncertain and they appear to belong to an aïstopod (Panchen, 1970:55). Fritsch had clearly been unlucky in that he never encountered an articulated, small anthracosaur specimen from Nýřany or Třemošná, and so had no basis for uniting the various fragmentary specimens that he had described.

Jaekel (1902:127, text-fig. 1) described the first recognizable articulated specimen of a Nýřany anthracosaur from counterparts of a skull and anterior postcranial skeleton deposited in the Museum für Naturkunde, Humboldt University, Berlin, and named it *Gephyrostegus bohemicus*. There was sufficient morphological information to allow Jaekel to consider the affinities of this taxon, which he regarded as an intermediate between stegocephalians (primitive amphibian-grade tetrapods) and cotylosaurs (primitive amniote-like and basal amniote tetrapods). Since Jaekel's paper, the Plzeň-Manětín Basin anthracosaurs have generally been discussed in terms of their possible ancestry to later amniote or near-amniote groups.

By this time, Zittel's (1887–1890) classification of early tetrapods based on their vertebral construction was in wide use. Case (1911:79) first suggested that the original *Diplovertebron* was an embolomere. This view was put more robustly by Watson (1926), who had acquired a further small but articulated

specimen from Nýřany (DMSW B.65) for his own collection. He concluded that not only was it a small example of Jaekel's *Gephyrostegus*, but also that both were the same as Fritsch's first-described anthracosaur, *Diplovertebron punctatum*. Data from these specimens allowed Watson (1926:figs. 29–31) to provide a fairly complete reconstruction of *Diplovertebron punctatum* (= *Gephyrostegus bohemicus*) as a small Nýřany anthracosaur.

In the 1930s, Watson's research assistant, Margaret Steen, published several papers dealing with Permo-Carboniferous amphibians. In one of these, Steen (1938) reviewed the Nýřany and Třemošná tetrapods. Steen (1938:239, text-fig. 25) briefly redescribed Fritsch's *Diplovertebron* material as an anthracosaur, giving the correct specimen numbers to the material and figures, and also designating Fr. Origs. 96 and 128 as (para)types. At this stage, she presumably agreed with Watson's association of the Jaekel and Watson specimens, because she mentioned DMSW B.65 as being part of this taxon. Later in the same work, Steen (1938:261) categorized *Nummulosaurus kolbii* as an indeterminate embolomere. However, she did not mention *Hemichthys problematica*, presumably assuming that it was a fish. By 1938, the published situation was that there was a single small Nýřany anthracosaur, *Diplovertebron punctatum*, and a range of indeterminate specimens. Romer (1947) followed this interpretation broadly, but suggested that *Diplovertebron* might be a primitive seymouriamorph with residual anthracosaurian features. Romer (1947:268) also noted the similarity of the *Nummulosaurus* tail vertebrae to those of *Diplovertebron*, and was the first (Romer, 1947:106) to recognize that Fritsch's *Nyrania* jaw element was an anthracosaur pelvis.

After leaving Watson's employ and marrying Professor James Brough, Steen wrote three other papers in the 1940s, one of which discussed *Gephyrostegus*. As was well known to their contemporaries, the three manuscripts co-authored by Brough and Brough contradicted several of Watson's views on tetrapod relationships and phylogeny, and could not be published until 1967, when Watson's influence had declined. Brough and Brough (1967) added four other specimens from Nýřany to the hypodigm of *Gephyrostegus bohemicus*, namely, the type of *Solenodonsaurus janenschi* Broili, 1924, a second *Solenodonsaurus* described by Pearson (1924), as well as two undescribed specimens from Prague. They treated *Gephyrostegus* as a primitive seymouriamorph unrelated to Fritsch's *Diplovertebron punctatum*, and regarded Watson's juvenile specimen as a different species, which they named *Gephyrostegus watsoni*.

At the same time as Brough and Brough were publishing their work, Carroll had started on a further revision of *Gephyrostegus*. Unfortunately, his study in Prague in 1968 was cut short after 2 days by the Russian invasion, and he was not able to study much of the Prague material firsthand. Consequently, his work was largely based on non-Prague material and on a cast of Fr. Orig. 96. A major conclusion of Carroll's work was that all four specimens newly associated with *Gephyrostegus* by the Broughs actually belonged to other taxa. Thus, the two *Solenodonsaurus* specimens reverted to being a distinct basal amniote taxon (Carroll, 1970:292–301), and the two undescribed specimens from Prague were reidentified as romeriid captorhinomorphs. The latter were later fully redescribed as *Brouffia orientalis* and *Coelostegus prothales* (Carroll and Baird, 1972), and are now placed in the family Protorothyrididae. Carroll's revision of *Gephyrostegus* thus reverted to the original Jaekel and Watson specimens plus one previously undescribed postcranium from Berlin. Carroll regarded *Gephyrostegus* as an anthracosaur-captorhinomorph intermediate or an anthracosaur taxon that was of the structural type ancestral to basal amniotes. Unfortunately, he was not able to study any of Fritsch's material directly, and was only able to study Fr. Orig. 96 from a cast, concluding that this specimen was a small but typical embolomere. He proposed Fr. Orig. 96 as the only specimen of *Diplovertebron punctatum*, disregarding the more

anatomically complete Fr. Orig. 128. Panchen (1970) followed this arrangement, formally naming Fr. Orig. 96 as the lectotype of *D. punctatum*, and recording it as an eogyrinid "based on weak and mostly negative evidence" (Panchen, 1970:53). Thus, neither Carroll nor Panchen had examined Fr. Orig. 128 in Prague, and both were confused by the misprinted caption to Fritsch's plate 53. Disregarding the correct numbers published by Steen, who had examined the material, they erroneously argued for there being two blocks numbered Fr. Orig. 96. In fact, the larger of the two *Diplovertebron* blocks is unambiguously Fr. Orig. 128, and always has been.

Little work has been carried out on *Gephyrostegus* since Carroll. Godfrey and Reisz (1991) described a previously unrecorded vertebral column (NMP M.3609) from Nýřany as a fourth *G. bohemicus* specimen and documented the atlas-axis complex in more detail, concluding that it was consistent with Carroll's interpretation of *Gephyrostegus* as a relict primitive anthracosaur.

Thus, the current published status of the Nýřany and Třemošná anthracosaurs is as follows: *Gephyrostegus* is based on four specimens and interpreted as a small relict anthracosaur, possibly close to seymouriamorphs (Romer, 1947; Brough and Brough, 1967) or amniotes (Carroll, 1970); *Diplovertebron* is based on a single specimen and appears to be a small embolomere (Carroll, 1970; Panchen, 1970); and *Hemichthys* has not been studied since Fritsch's description. Several other specimens (including Fr. Orig. 128) in Prague and Vienna are available for a reevaluation of the material from the Plzeň-Manětín Basin.

Nomenclature and Validity of the Name *Gephyrostegus bohemicus*

It may be noted that the binomina were published in the following sequence:

Diplovertebron punctatum Fritsch, 1885a
Hemichthys problematica Fritsch, 1895
Nummulosaurus kolbii Fritsch, 1901
Gephyrostegus bohemicus Jaekel, 1902
Gephyrostegus watsoni Brough and Brough, 1967

Hence, *Gephyrostegus bohemicus* is the fourth name to be applied to an anthracosaur from the Plzeň-Manětín Basin, with *G. watsoni* as a junior synonym of it. What of the other three? Regardless of its determinability, *Hemichthys problematica* has not been claimed as a valid definable taxon since 1895, when it was named. In the fourth edition of the International Code on Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999: 28), Rule 23.9.1 states that "prevailing usage must be maintained when the following conditions are both met: 23.9.1.1 the senior synonym . . . has not been used as a valid name after 1899 and 23.9.1.2 when . . . the junior synonym . . . has been used for a taxon as a presumed valid name, in at least 25 works, published by at least 10 authors in the preceding 50 years and encompassing a span of not less than 10 years." *Gephyrostegus bohemicus* is the prevailing usage and has been extensively used by many authors since 1902 and particularly since 1970. Consequently, *Hemichthys problematica* is a nomen oblitum even though it is a senior synonym of *G. bohemicus*. The same rule cannot be applied to *Nummulosaurus kolbii* because it was published in 1901, 2 years later than the critical date for this rule. Its status will depend on new detailed comparisons between the specimen and caudal vertebrae of *Gephyrostegus* and *Diplovertebron*. The *Diplovertebron punctatum* status will also depend on reevaluations of all preserved postcrania, including those not previously described.

MATERIALS AND METHODS

We examined specimens and casts. In the largest, best-preserved specimen (the holotype), most cranial bones are articulated and visible in both dorsal and ventral aspects, and the skull roof and palatal bones of other, partially disarticulated specimens retain most of their original anatomical positions. Skull length (SL; sum of sagittal lengths of nasal, frontal, parietal, and post-parietal) ranges from about 58 mm in MB Am. 718 a (holotype; Fig. 1), to about 25 mm in UMZC T.1222a (Carroll, 1970:figs. 3, 4). Skull drawings are based on tracings of enlarged, high-resolution photographs. Small details were drawn with a camera lucida (Leica M205 C binocular stereomicroscope).

Phylogenetic analyses were run in PAUP* (version 4.0b10; Swofford, 2003) on a Pentium PC and on a Macintosh Power-Book with heuristic search (1000 random stepwise addition sequence replicates; tree bisection-reconnection branch-swapping algorithm, saving one tree in memory from each replicate; successive swapping on all trees in memory with multiple tree saving option in effect; ACCTRAN optimization). The results were printed using TreeView (Page, 1996).

Institutional Abbreviations—UMZC, University Museum of Zoology, Cambridge, U.K.; **DMSW**, D. M. S. Watson Collection, University of Cambridge, Cambridge, U.K.; **MB**, Humboldt University, Natural History Museum, Berlin, Germany; **NMP**, National Museum, Prague, Czech Republic.

Anatomical Abbreviations—a.Co, anterior coronoid; **a.Me.fe**, anterior Meckelian fenestra; **An**, angular; **Ar**, articular; **De**, dentary; **de.fa**, dentary fang; **Ecpt**, ectopterygoid; **Fr**, frontal; **Ju**, jugal; **i.lam.La**, internal lamina of lacrimal; **It**, intertemporal; **La**, lacrimal; **la.can**, lacrimal canal; **m.Co**, middle coronoid; **Mx**, maxilla; **Na**, nasal; **occ.fl**, occipital flange; **pal.ra.Pt**, palatal ramus of pterygoid; **Par**, prearticular; **p.Co**, posterior coronoid; **Pfr**, prefrontal; **p.Me.fe**, posterior Meckelian fenestra; **Pmx**, premaxilla; **Po**, postorbital; **Pp**, postparietal; **pr.Ta**, tabular process; **Psp**; postsplenial; **Pt**, pterygoid; **Qj**, quadratojugal, **Qu**, quadrate; **qu.ra.Pt**, quadrate ramus of pterygoid; **San**, surangular; **sot.pl**, sclerotic plates; **Sp**, splenial; **Sq**, squamosal; **sq.fl**, squamosal flange; **St**, supratemporal; **Ta**, tabular; **tr.pr.Pt**, transverse process of pterygoid; **v.l.Pp**, ventral lamella of postparietal; **v.l.Qj**, ventral lamella of quadratojugal; **v.s.Fr**, ventral surfaces of frontals.

SYSTEMATIC PALEONTOLOGY

TETRAPODA Goodrich, 1930
GEPHYROSTEGIDA Jaekel, 1911
GEPHYROSTEGIDAE Jaekel, 1909

Included Species—*Gephyrostegus bohemicus* Jaekel, 1902; *Bruktererpeton fiebigi* Boy and Bandel, 1973.
Diagnosis—Characters shared with seymouriamorphs: rectangular transverse pterygoid process; anterior triangular wedge-like process of parasphenoid; radiating rows of small palatal denticles. Plesiomorphic character also found in anthracosaurs: non-sutural cheek–skull table junction. Characters of uncertain polarity: tooth crown bases without striations; intercentrum height about one-third of pleurocentrum height; pleurocentra incomplete dorsally; 24 presacral vertebrae; absence of dorsal iliac process; chevron-like pattern of long and narrow gastralia.

GEPHYROSTEGUS Jaekel, 1902

Generic Diagnosis—As for the only species, *Gephyrostegus bohemicus* Jaekel, 1902.
Type Species—*Gephyrostegus bohemicus* Jaekel, 1902.

GEPHYROSTEGUS BOHEMICUS Jaekel, 1902

(Figs. 1–7)

Diplovertebron punctatum Fritsch, 1885a:11, pl. 53, partim Carroll, 1970:non pl. 52 (lectotype).
Hemichthys problematica Fritsch, 1895:121, pl. 128, figs. 9–11. Nomen oblitum.
Gephyrostegus bohemicus Jaekel, 1902:127, fig. 1 (original description).

Diplovertebron punctatum Fritsch, 1885a: Watson, 1926:238, figs. 29, 30, partim Carroll, 1970, non Fritsch, 1885a:pl. 52 (lectotype).

Gephyrostegus bohemicus Jaekel, 1902: Brough and Brough, 1967:147, fig. 2A, B.

Gephyrostegus watsoni Brough and Brough, 1967:158, fig. 9.

Gephyrostegus bohemicus Jaekel, 1902: Carroll, 1970:268, figs. 1, 2.

Holotype—MB Am. 718 a, 719 b, skull and partial postcranium on counterpart blocks (Figs. 1, 2).

Referred Material—NMP M.885 (Fr. Orig. 207), articulated skull in right lateral view, holotype of *Hemichthys problematica* Fritsch, 1895; UMZC T.1337, partially disarticulated skull, counterpart of NMP M.885; NMP M.398-1, part of articulated skull; NMP M.377, skull in palatal view; UMZC T.1222a (DMSW B.65), almost complete skeleton of small individual, holotype of *Gephyrostegus watsoni* Brough and Brough, 1967.

Horizon, Locality, and Age—Plattenkohle of Humboldt Mine, Nýřany, Plzeň-Manětín Basin, Czech Republic, Asturian (Upper Moscovian), Late Carboniferous (Němejc, 1952).

Diagnosis—Character shared with *Bruktererpeton*: anteromedial to posterolateral ridges on palatine anteroventral surface, extending in part onto vomer. Possible autapomorphies: pustular ornamentation of skull roof bones; plate-like tabular process with shallow dorsal pits.

DESCRIPTION

Skull

General Features—Unless noted otherwise, taxon bibliographic references are reported only when taxon names are first mentioned. The contribution of various bones to skull openings are not described in detail, and the reader is referred to the figures for basic bone relationships. The narrow, parabolic skull (Fig. 6A) is almost twice as long as wide. The elliptical, dorsolateral orbits are situated at about skull midlength. The pineal foramen is situated posterior to the orbits and aligned with the intertemporal midlength. The jaw articulation projects slightly behind the tabular posterior corner. The gently concave skull table is deeply embayed posteriorly in dorsal aspect and widest at the level of the anterior margin of the postparietals. The steep cheeks are deepest at the level of the quadratojugal-jugal contact and meet the skull table at an angle of about 60°, forming a non-sutural posterodorsal contact. The 'otic notch' is triangular in lateral aspect. Except for the slightly interdigitating jugal-squamosal and jugal-quadratojugal sutures, most skull roof sutures are simple. The shape and size of some antimeric bones may differ (e.g., intertemporal). The dermal skull roof of small specimens shows pits and short grooves on the ossification centers and low ridges and grooves peripherally (Figs. 5, 7). The holotype's skull table bones show irregular pustules on their ossification centers (Figs. 1, 6A, 7A) and radiating grooves peripherally. No external sensory grooves are visible. Immediately anterior to the basipterygoid articulation, the medial margin of the pterygoid is shallowly embayed. More anteriorly, a narrow slit between the medial pterygoid margins and the lateral margins of the long parasphenoid cultriform process is visible, such that the palate approaches the 'closed' type.

Skull Roof and Sclerotic Ring—The elongate nasal processes of the premaxillae (Figs. 1, 2, 6A, 7A) bear small digitiform extensions along their slightly diverging dorsal ends, which accommodate the anterior-most nasal tips. The dorsoventrally narrow, long maxillary ramus has a shallow posterior depression for the articulation with the maxilla. The anteroposteriorly broad, internal supradental shelf forms the anterior margin of the exochoanal fenestra. Fragments in the left exonarial fenestra of NMP M.885

may be remnants of a crushed septomaxilla. A plate-like element tucked between lacrimal and premaxilla in the left exonarial fenestra of NMP M.398-1 may be either a septomaxilla or the anterior-most portion of a palatal bone (Fig. 5).

The elongate nasal is slightly shorter than the frontal (Figs. 1, 3, 5, 6A, 7A), mediolaterally broader anteriorly than posteriorly, and narrowly wedged between frontal and prefrontal. In NMP M.398, the right nasal overlaps a large underlying lamella of the left nasal (Fig. 5). The elongate frontal (Figs. 1, 3, 5, 6A, 7A) is widest in its midlength, narrowing rapidly both anteriorly (where it is deeply wedged between the nasals) and posteriorly (where it forms a short contact with the parietal).

The triangular prefrontal forms the deep, sharp-edged anteromedial orbit margin (Figs. 1, 3, 5, 6A, 7A), and fits anteriorly into a shallow posterolateral notch of the nasal. Unlike in previous accounts (e.g., Jaekel, 1902; Carroll, 1970), the long, narrow, and dorsoventrally deep posterior ramus of the prefrontal meets the stout anterior ramus of the postfrontal along a short, oblique suture situated between the middle and posterior one-thirds of the frontal length. In the holotype, the prefrontal posterior ramus is hidden underneath the disrupted adjacent medial margin of the frontal, giving the false impression that this margin is deep and enters the orbit.

The crescent-like postfrontal (Figs. 1, 6A, 7A) slightly underlaps the postorbital laterally, as revealed by the shape of the slightly displaced left postorbital of MB Am. 719 b (Fig. 2).

The lateral margin of the elongate parietal (Figs. 1, 5, 6A) is deeply wedged between the bones of the lateral temporal series. The large, subcircular pineal foramen is aligned with the intertemporal midlength. Bone proportions on the exposed ventral skull roof surface of UMZC T.1222a suggest that the intertemporal and supratemporal overlapped the underlying lamellae of the parietal (cf. *Discosauriscus austriacus*; Klembara, 1997). In NMP M.398-1, the left side of the skull shows a subdivided parietal in the form of a subelliptical bone in the position normally occupied by the medial-most intertemporal portion and the adjacent part of the parietal (Fig. 5; cf. Klembara, 1993, 1994; Klembara et al., 2002; Klembara and Ruta, 2004a).

The lateral margin of the posteriorly elongate, triangular intertemporal (Figs. 1, 5, 6A, 7A) fits into a distinct groove along the postorbital medial margin (well preserved in NMP M.398-1 and in the holotype) (Figs. 1, 5).

The posteriorly elongate, triangular supratemporal has a strong dorsal ridge (more strongly developed on the right intertemporal of the holotype) near its lateral margin (Figs. 1, 2, 4A, B, 6A, 7A) that continues on the intertemporal. An anteroposterior ventral groove, delimited medially by a strong ridge (e.g., see left supratemporal of MB Am. 719 b; Fig. 2), would accommodate a convex dorsal articular facet of the squamosal (e.g., UMZC T.1222a) in life. The squamosal-supratemporal contact may have been mobile in life. The ventral ridge may have prevented medial displacement of the squamosal in life. There is no robust otic flange extending ventrally from the supratemporal posterolateral margin, contra Carroll (1970:fig. 6).

The long, narrow, anterolateral ventral lamella of the obliquely elongate tabular (Figs. 1, 2, 4–6A, 7A) underlies the posteromedial portion of the supratemporal. At the level of the posterior extremity of the supratemporal, the tabular curves slightly medially. A small, rectangular, plate-like process extends from the tabular posterolateral corner (well preserved in UMZC T.1337 and MB Am. 718 a). It is slightly thinner dorsoventrally than the tabular itself. Its dorsal surface—continuous with the tabular ornamented surface—is finely pitted (e.g., UMZC T.1337; Fig. 4). The smooth posterior tabular margin extends into a large, posteroventrally inclined occipital flange (also seen in ventral view in MB Am. 719 b; Fig. 2). This joins medially a similar flange from the postparietal posteromedial margin.
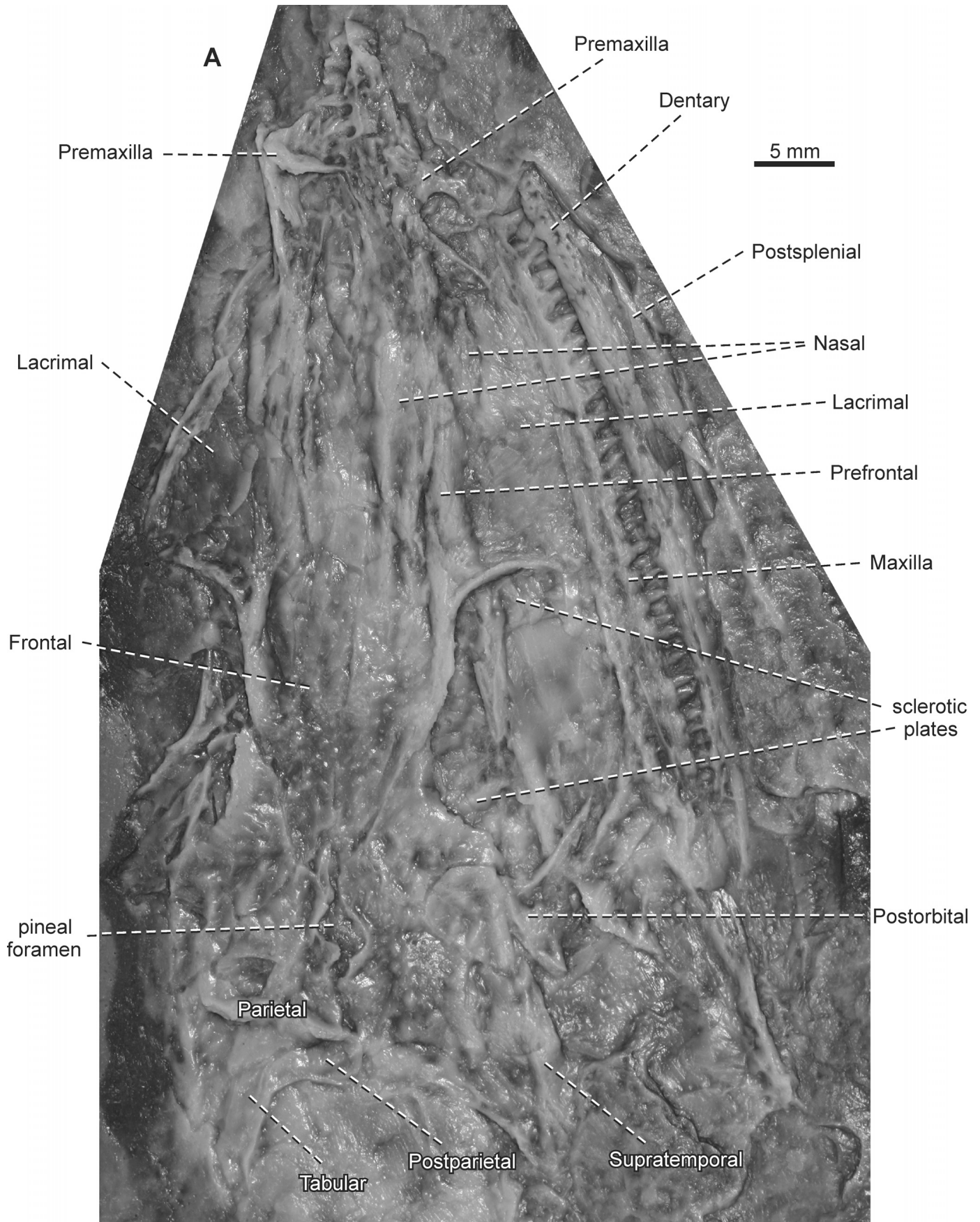
FIGURE 1. *Gephyrostegus bohemicus* Jaekel, 1902; holotype MB Am. 718 a. Photograph (**A**) and drawing (**B**) of skull and right lower jaw in dorsal view. *(Continued)*
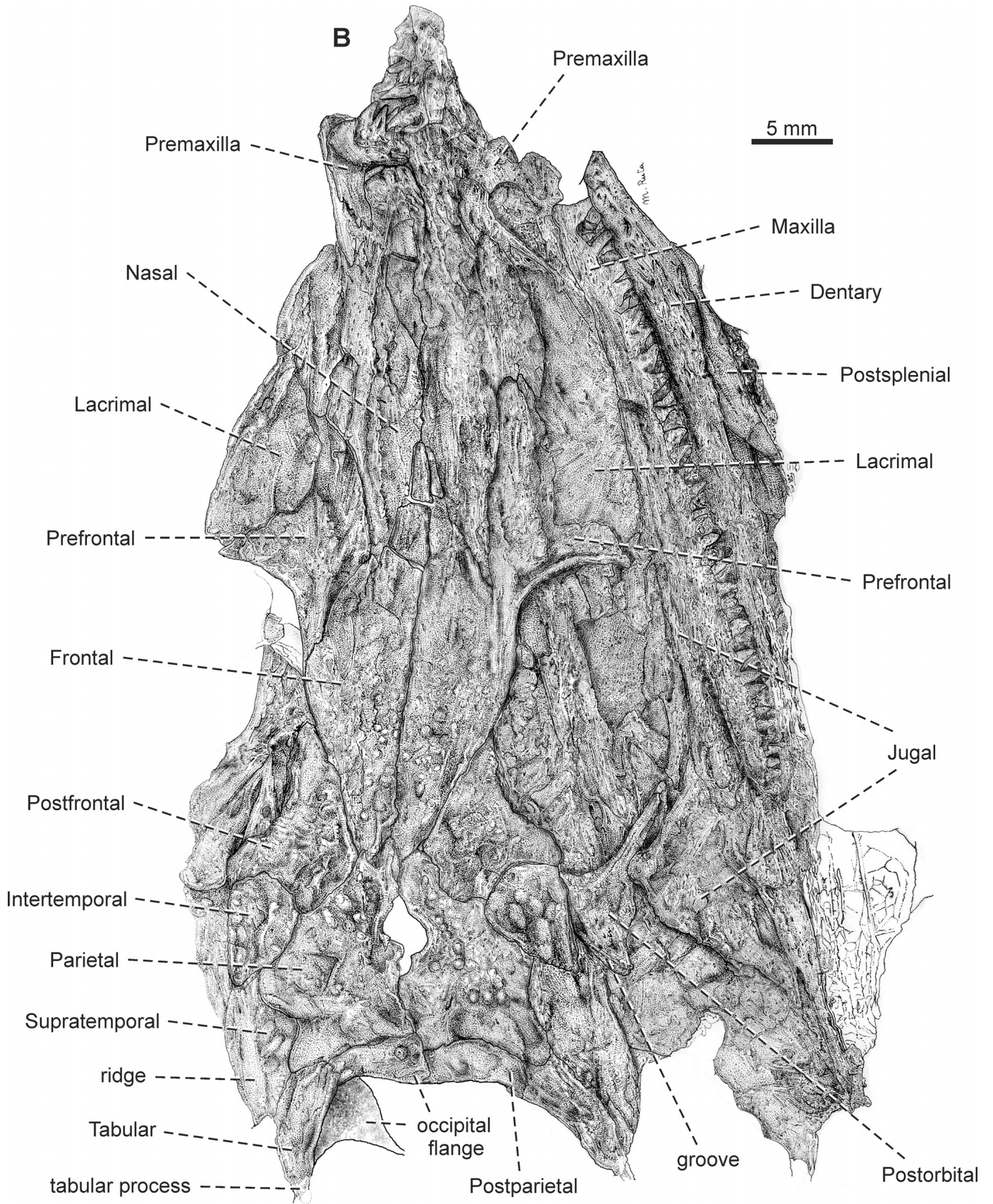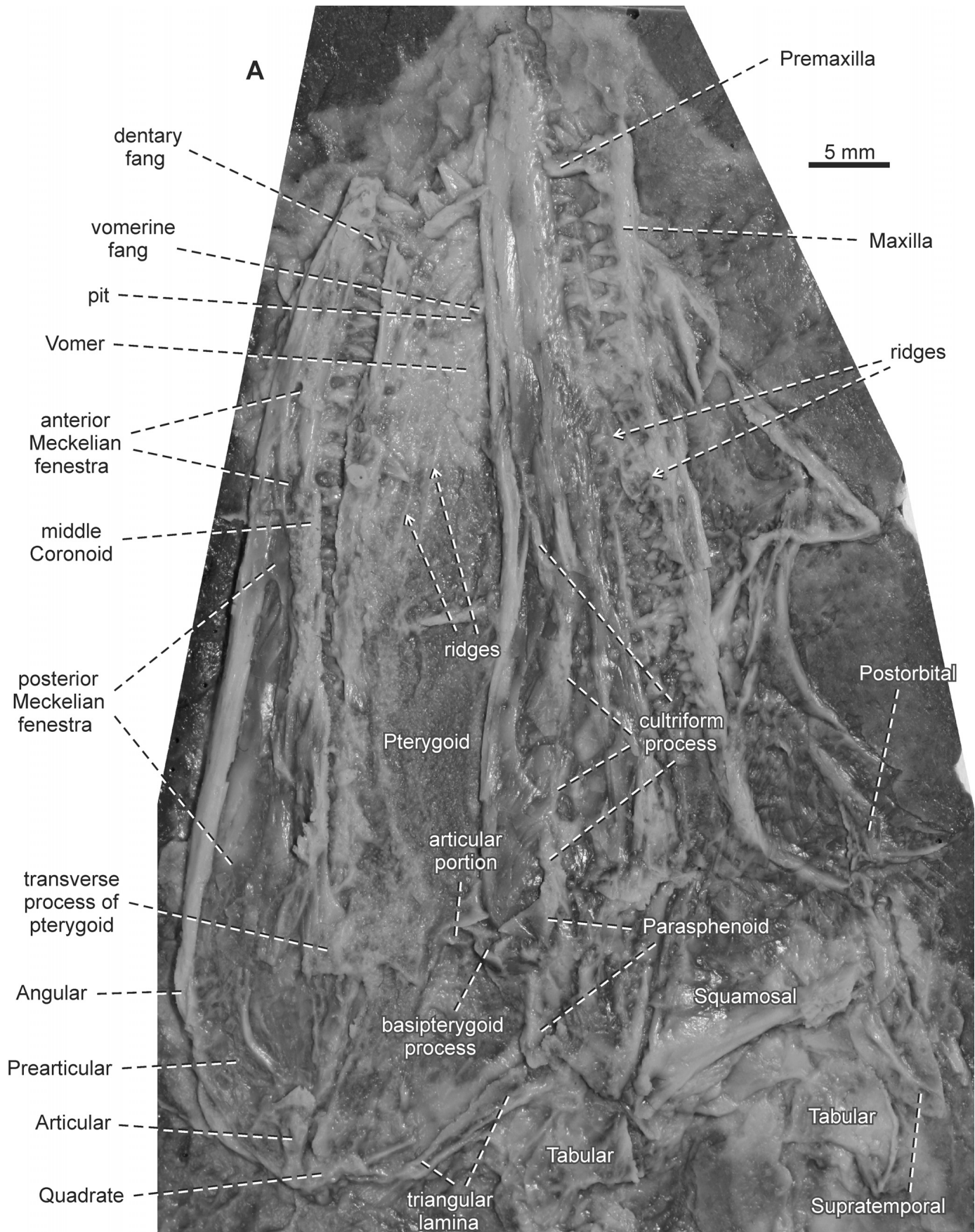
FIGURE 1. (Continued)

FIGURE 2.   *Gephyrostegus bohemicus* Jaekel, 1902; holotype MB Am. 719 b. Photograph (**A**) and drawing (**B**) of skull and right lower jaw in ventral view. *(Continued)*
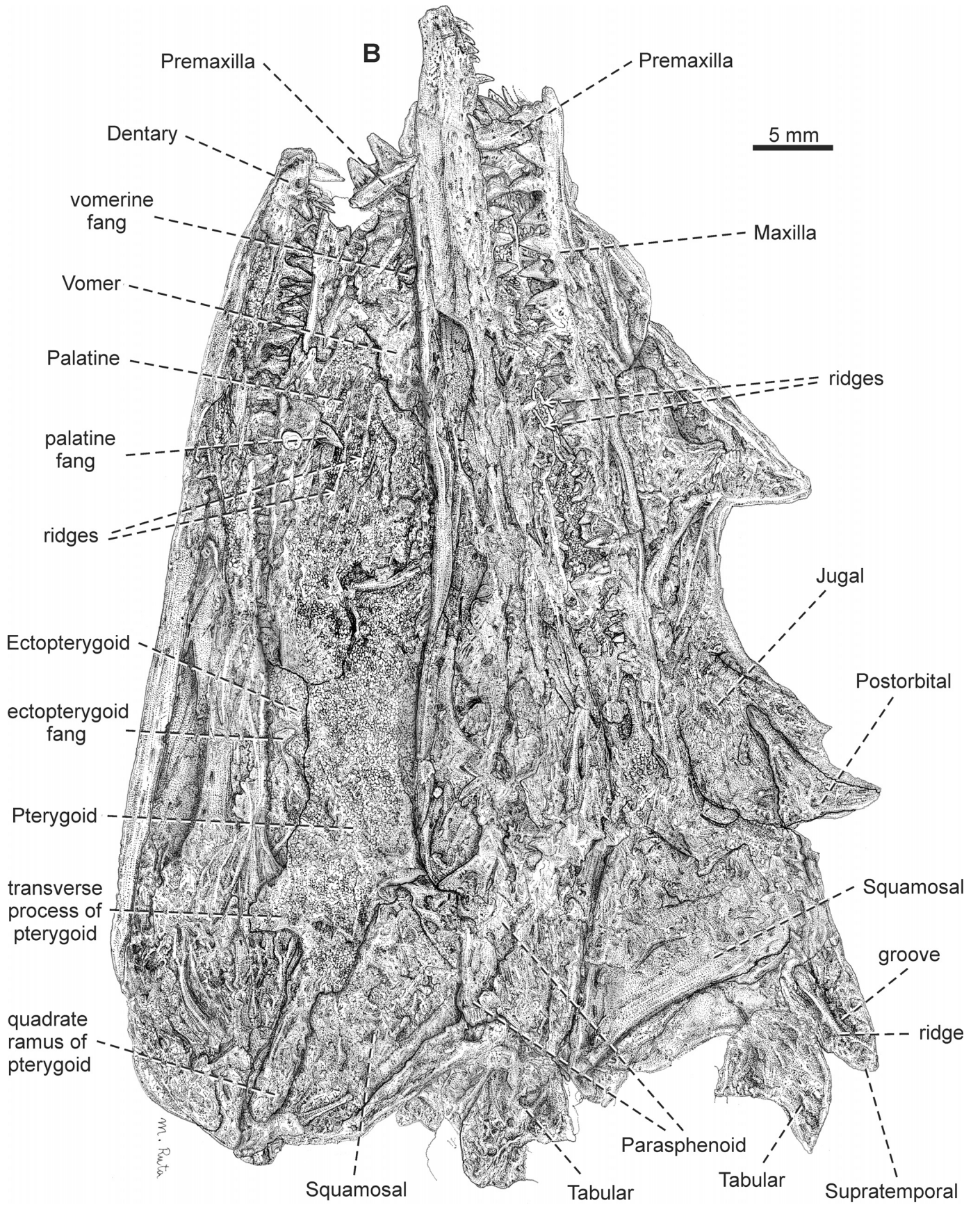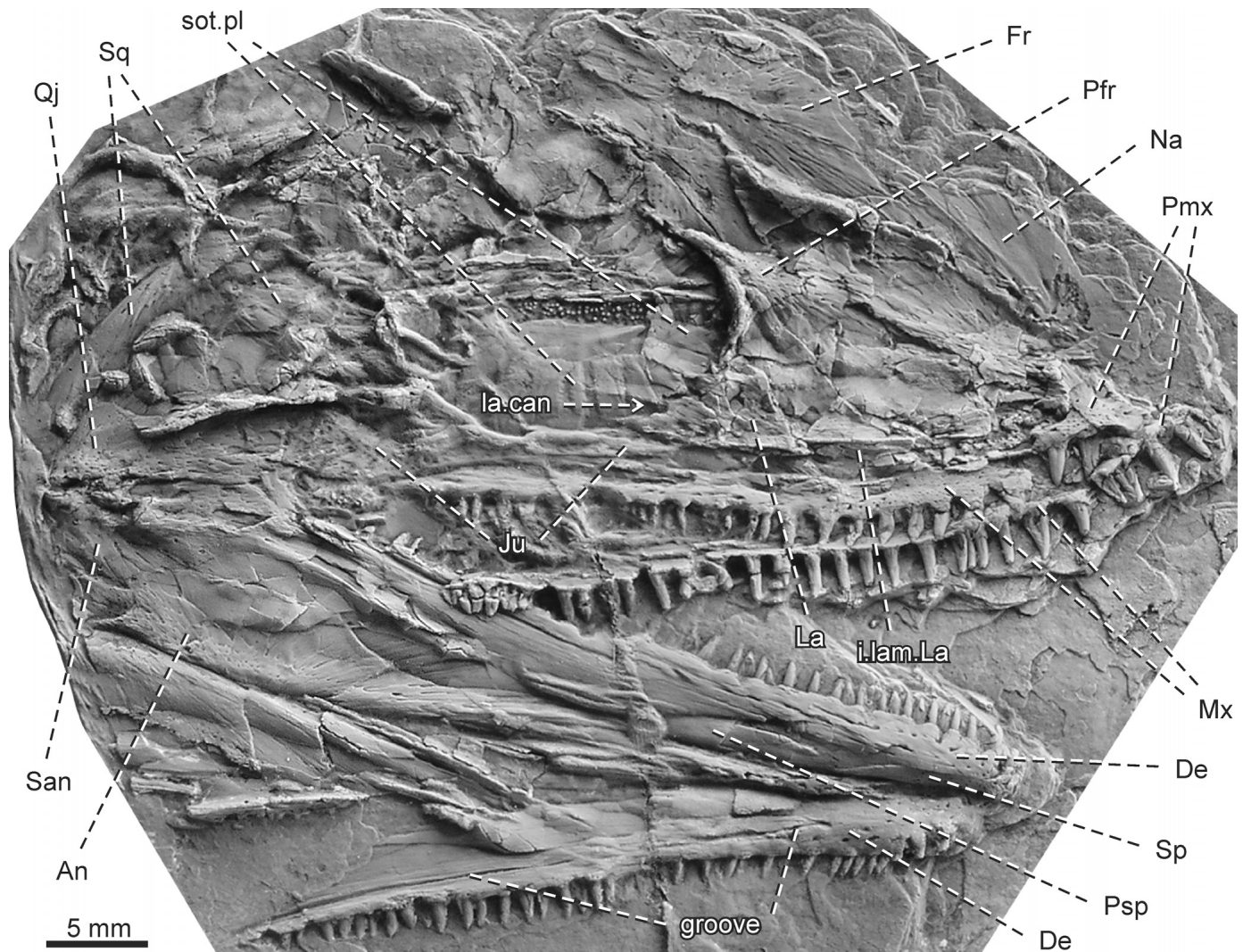
FIGURE 2. (Continued)

FIGURE 3. *Gephyrostegus bohemicus* Jaekel, 1902; NMP M.885. Photograph of galvanoplastic cast of skull and lower jaws in right lateral view produced by Fritsch and described as *Hemichthys problematica* (Fritsch, 1985).

The mediolaterally elongate postparietal is slightly shorter than the tabular (Figs. 1, 2, 4A, B, 5, 6A, 7A). The medial portion of the left postparietal has a large lamella underlying the right postparietal (UMZC T.1337; Fig. 4A, B). The flange is broadest medially, narrows gradually laterally, and becomes very reduced at the bone midlength.

The long, slender maxilla (Figs. 1–4A, B, 5–7A) is deepest in its midlength, underlies the anterior two-thirds of the jugal (contra Carroll, 1970:fig. 6A; reconstructed point contact between maxilla and quadratojugal), and has a prominent supradental shelf.

The long, large lacrimal bears a short suborbital process (Figs. 1, 3, 5, 6A, 7A). In NMP M.885, the ventral margin of the bone shows a groove and produces a ventromedial internal lamella (Fig. 3). In life, the groove would accommodate the dorsal margin of the maxilla, whereas the internal lamella would be adpressed to the internal maxillary surface, as in *Discos-auriscus* and *Karpinskiosaurus secundus* (Klembara, 2011). The lacrimal orbital margin shows a broad opening for the nasolacrimal canal (Fig. 3), which is subdivided into two halves by a small and short septum (best visible in NMP M.398-1), as in *Discos-auriscus*.

The long, dorsoventrally narrow suborbital ramus of the jugal (Figs. 1–4A, B, 5–7A) ends anteriorly in an acuminate tip underlying the lacrimal suborbital process. Dorsally, the jugal is wedged between the postorbital ventral process and the squamosal. Posteroventrally, the jugal forms a broad, triangular plate with a free ventral margin.

The straight medial margin of the triangular postorbital (Figs. 1, 2, 4A, B, 5, 6A, 7B) fails to reach the supratemporal. The long, narrow lateroventral ramus of the postorbital terminates in a point. Its small anteromedial process contacts the postfrontal, and extends slightly anterior to the orbit posterior margin

The large quadrilateral squamosal (Figs. 2–4A, B, 5, 6A, 7A) bears an anteroposteriorly elongate and subelliptical dorsal facet for the articulation with the ventral side of the skull table, similar to that of *Pholiderpeton scutigerum* (Clack, 1983:fig. 12). The straight posterior edge of the squamosal forms an angle of about 45° with the horizontal and carries a smooth 'otic' flange. The flange is narrow and trough-like anterodorsally, widens gradually and becomes shallower posteroventrally, and wraps around the quadrate dorsolateral portion. In MB Am. 719 b, a long and posteroventrally narrowing triangular lamina on the squamosal
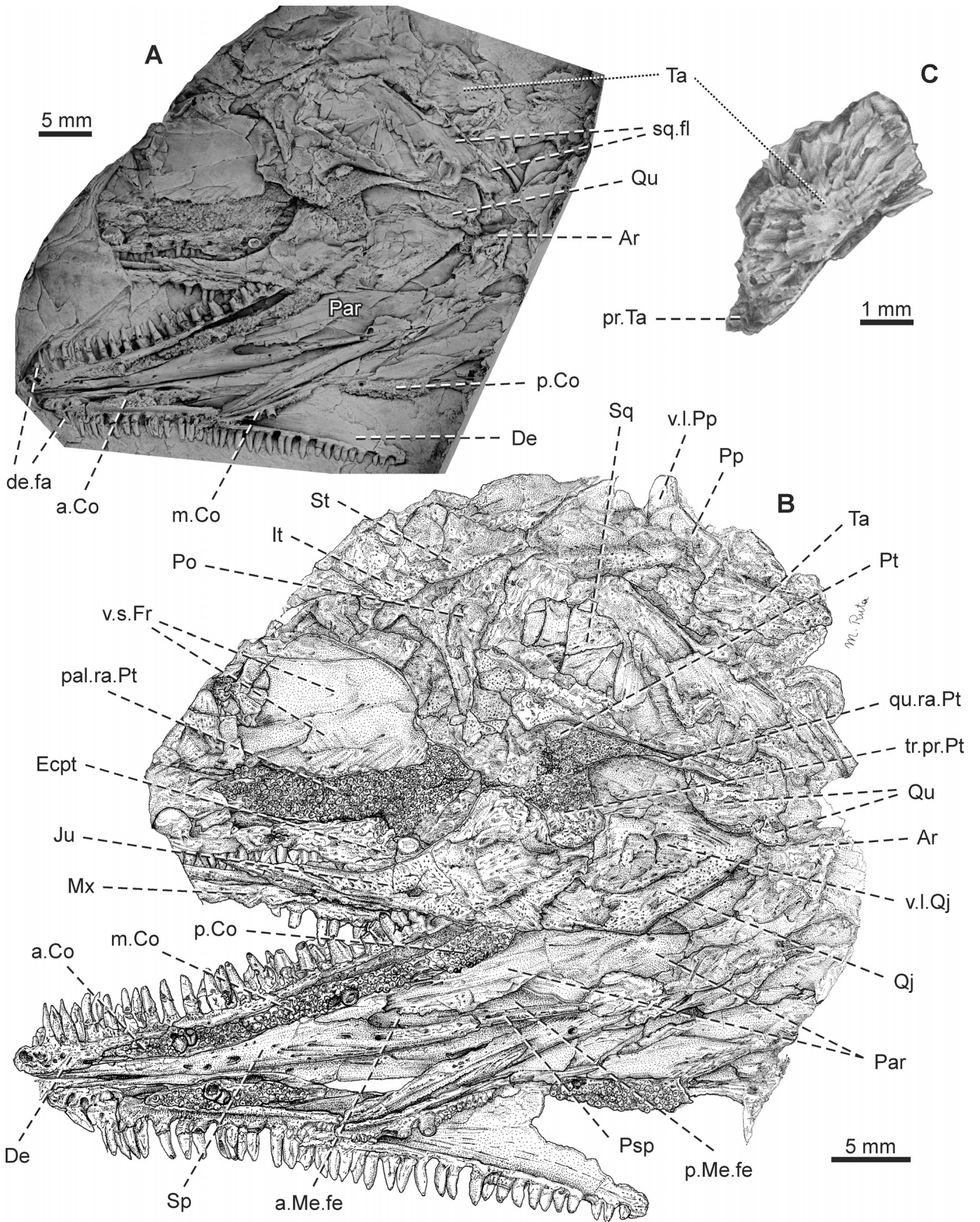
FIGURE 4. *Gephyrostegus bohemicus* Jaekel, 1902; UMZC T.1337. Photograph (**A**) and drawing (**B**) of cast of skull and lower jaws in left lateral view described by Fritsch as *Hemichthys problematica* (Fritsch, 1895). **C**, drawing of isolated left tabular in dorsal view.
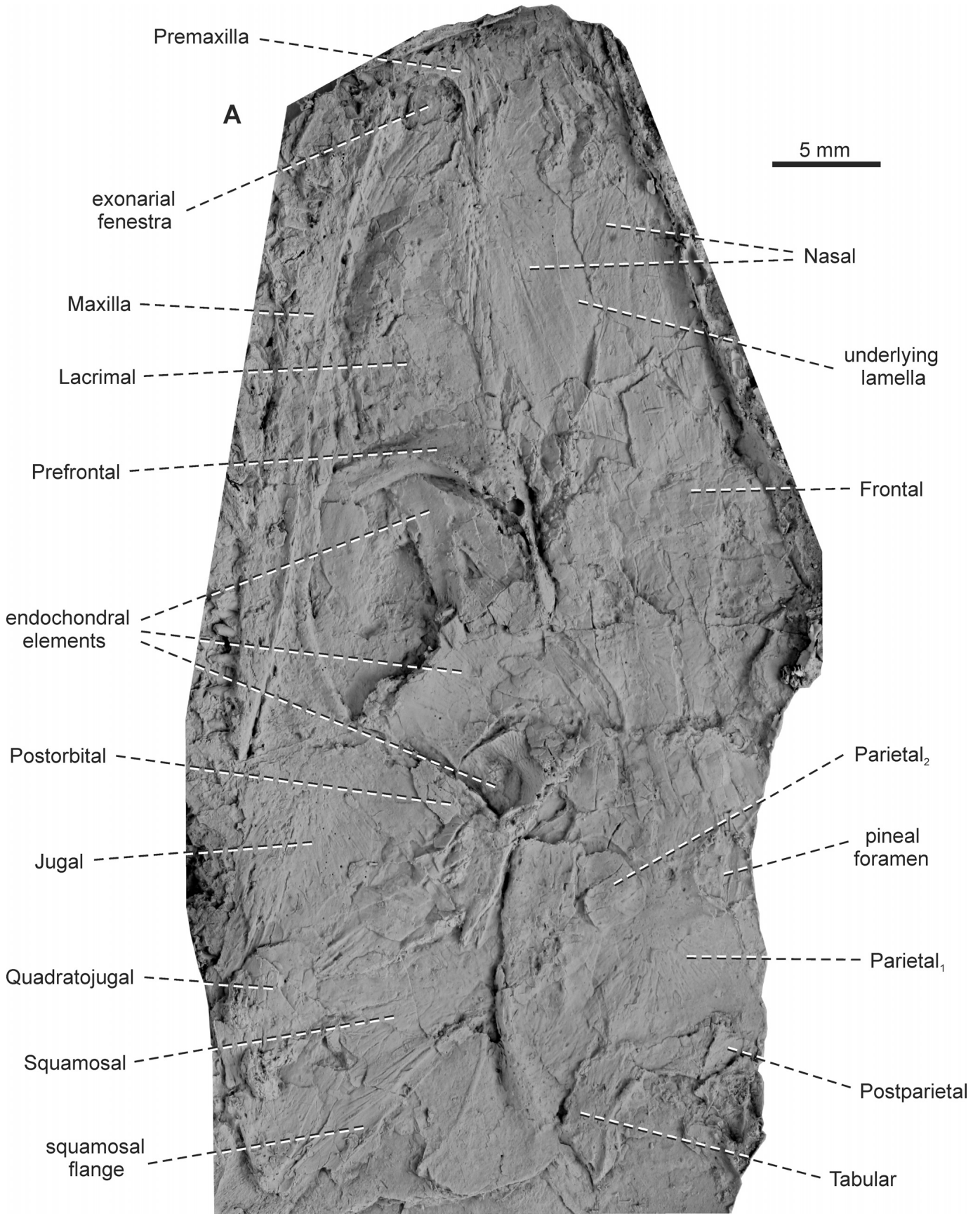
FIGURE 5. *Gephyrostegus bohemicus* Jaekel, 1902; NMP M.398-1. Photograph (**A**) and drawing (**B**) of skull in left lateral view. *(Continued)*
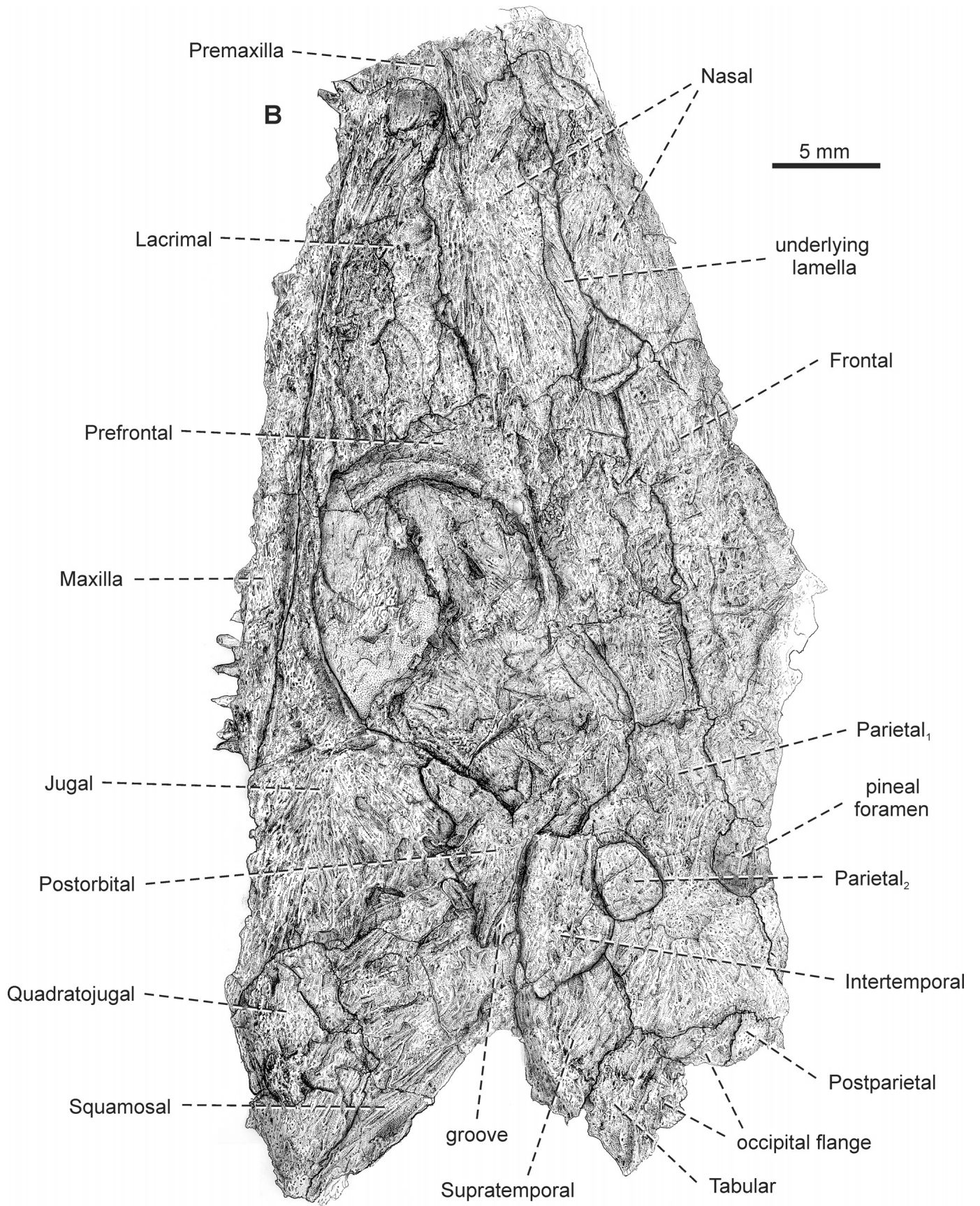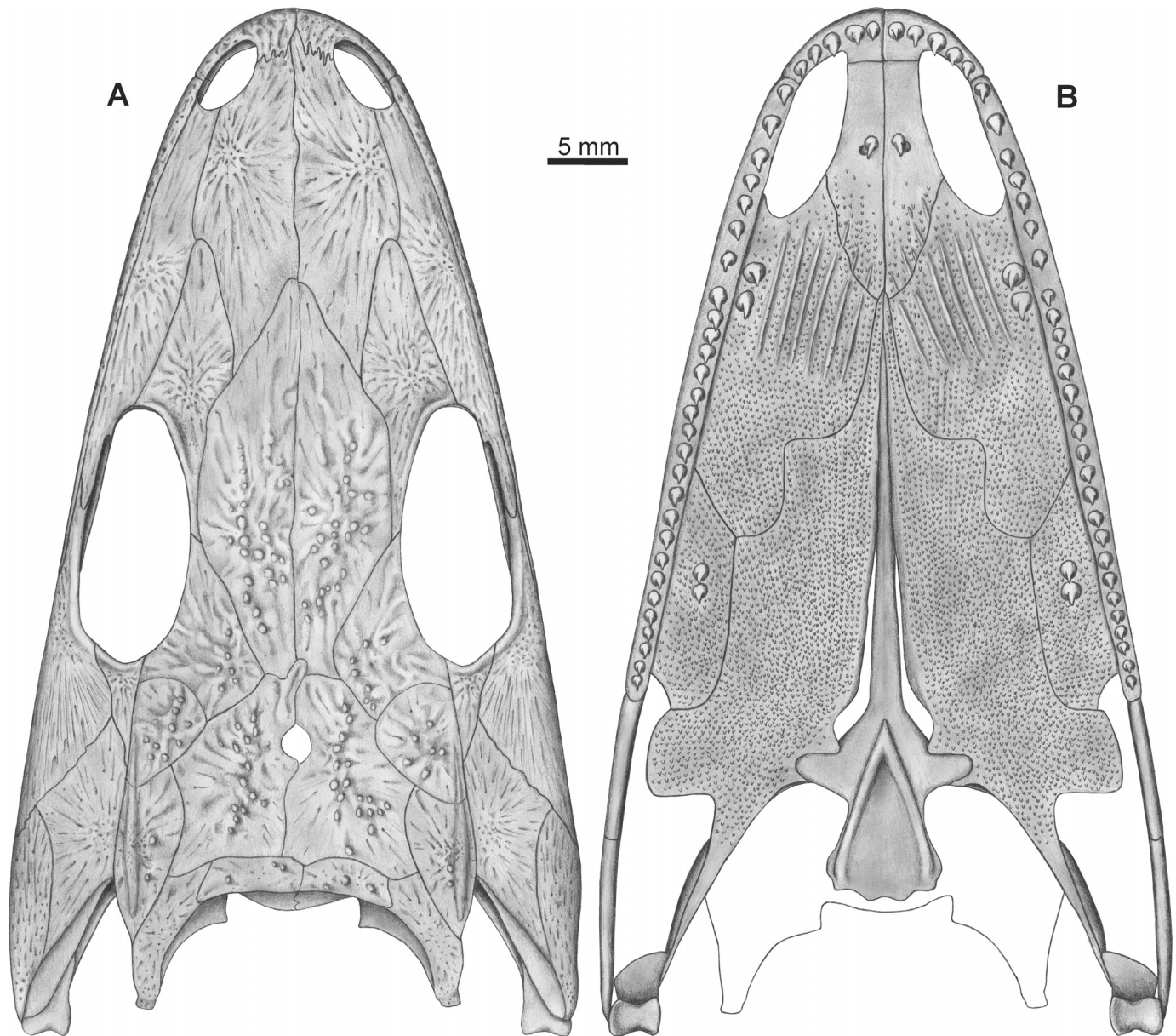
FIGURE 5. (Continued)

FIGURE 6.   *Gephyrostegus bohemicus* Jaekel, 1902. Reconstruction of skull in dorsal (**A**) and ventral (**B**) views.

internal surface is aligned with the posterior margin of the smooth 'otic' flange (Fig. 2). Based on its position, this lamina may be homologous to the flange extending medially from the posterodorsal internal portion of the squamosal in *Pholiderpeton* (Clack, 1987:fig. 1a) and to the crest observed on the posterior internal part of the squamosal in *Discosauriscus austriacus* (Klembara, 1997:fig. 13). In *D. austriacus*, a tall ascending lamina of the pterygoid quadrate ramus abuts against this crest. The triangular lamina of *Gephyrostegus* is likely to represent a broken off flange extending medially from the posterointernal squamosal surface. This interpretation is supported by the preservation of NMP M.885, in which the dorsoventrally compressed posterior margin of the squamosal (seen in lateral view) is slightly raised due to the flange on its inner side (Fig. 3).

The posteroventral internal part of the large and elongate quadratojugal (Figs. 3–7A) articulates with the quadrate.

The sclerotic ring, best preserved in NMP M.885 (Figs. 1, 3, 7A), may have included up to 15–20 subrectangular plates, each showing a narrower centrifugal and a broader centripetal edge. Externally and moving clockwise along the ring, each plate overlaps a shallow depression on the centripetal part of the adjacent radial margin of the following plate.

Palate—The lateral palatal bones are long and plate-like. The vomers meet mid-ventrally along their entire lengths (Figs. 2, 4, 6B), delimiting the anteromedial margin of the exochoanal fenestra. This margin is slightly longer than the deeply incised exochoanal margin of the palatine. The long palatine-vomer suture runs anterolaterally to posteromedially. Posteriorly, the vomer joins the anterior extremity of the parasphenoid cultriform process. Slightly anterior to its midlength, the vomer carries a fang and a replacement pit.

The palatine (Figs. 2, 6B) is mediolaterally wider in its anterior two-thirds than in its posterior one-third and forms a sinuous suture with the pterygoid palatal ramus. Along the oblique palatine-ectopterygoid suture, the ectopterygoid underlies a smooth, short dorsal lamina of the palatine. Two large
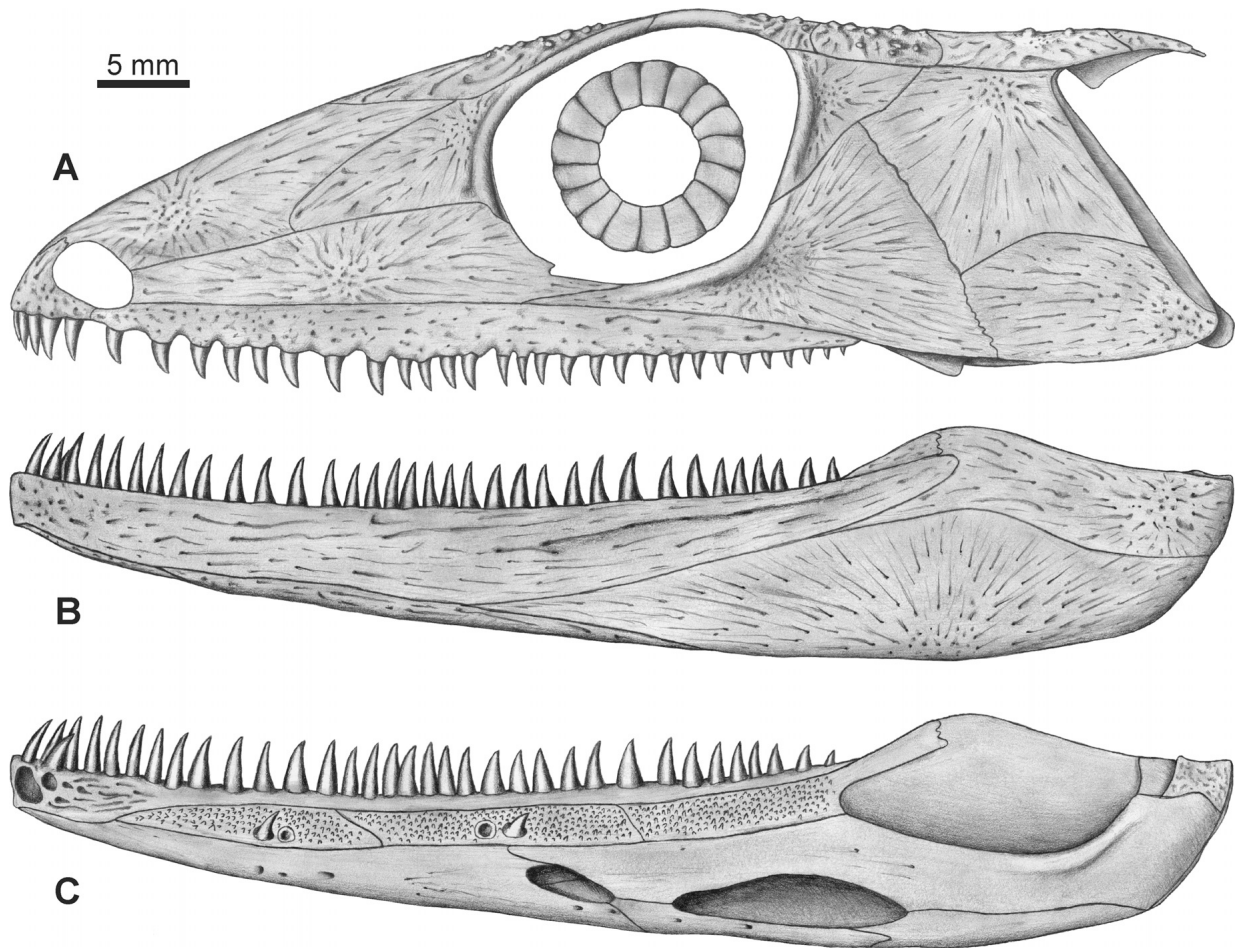
FIGURE 7. *Gephyrostegus bohemicus* Jaekel, 1902. **A**, reconstruction of skull in lateral view; **B**, **C**, lower jaw in lateral (**B**) and medial (**C**) views.

anterolateral fangs occur close to the palatine-maxilla suture. The anterior portion of the palatine and the posterior portion of the vomer bear oblique ridges (Fig. 2). In reptiliomorphs, similar ridges occur only on the posteroventral vomer surface of *Bruktererpeton* (Boy and Bandel, 1973), but we cannot ascertain whether ridges are present also on the palatine. These ridges may be a synapomorphy of *Gephyrostegus* and *Bruktererpeton*.

The ectopterygoid (Figs. 2, 4A, B, 6B) forms a long suture with the pterygoid palatal ramus and a short suture with the pterygoid transverse process. Two fangs occur slightly anterior to the ectopterygoid midlength.

The pterygoid palatal ramus (Figs. 2, 4A, B, 6B) narrows gradually to a point anteriorly, where it joins its antimere along a short tract. Its well-developed, rectangular transverse process is similar to that of most seymouriamorphs (e.g., White, 1939; Klembara, 1997; Klembara and Ruta, 2004a, 2005a; Klembara et al., 2007). The basicranial fossa is situated at the level of the process midlength. Immediately anterior to the basicranial articulation, the medial margin of the palatal ramus is slightly embayed, and a very narrow space was probably present between the palatal ramus and the parasphenoid cultriform process. The anteroventral margin of the robust quadrate ramus extends slightly ventrally (e.g., UMZC T.1337; Fig. 7A). The quadrate ramus is a dorsoventrally orientated plate, although its dorsal-most extent cannot be seen. However, the flange on the internal surface of the squamosal posterior-most portion (see above) suggests that, as in other seymouriamorphs, a tall ascending lamina of the ptery-

goid quadrate ramus was present. The posteromedial half of the quadrate ramus bears short ridges and grooves.

The triangular parasphenoid plate (Figs. 2, 6B) bears a distinct, wedge-like process, similar to that in seymouriamorphs (see below), although its anterior portion is not as deep as in the latter group. The process is deepest anteriorly, immediately anterior to the level of the basipterygoid processes. Its posteriorly diverging lateral margins become gradually lower and mediolaterally broader, and fade out on the posterolateral portions of the plate. These margins delimit a ventral depression that becomes gradually shallower posteriorly. The parasphenoidal extensions to the basipterygoid processes are large. Short processes project laterally from the plate's posterolateral margins. Two additional small processes project from its posterior margin.

Ossifications of Palatoquadrate and Stapes—Neither the epipterygoid nor the stapes can be observed. The well-preserved left quadrate of the holotype and of UMZC T.1337 (Figs. 2, 4A, B) show clearly subdivided condyles: a massive lateral convex portion is separated by a shallow groove from a more gracile, narrower medial portion. The quadrate forms a medially narrowing anterodorsal plate, the medial wall of which articulates with the pterygoid quadrate ramus.

Neural Endocranium—The right basipterygoid process of MB Am. 719 b (Fig. 2) is the only identifiable endochondral element of the neural endocranium. Two additional unidentified fragments are visible in the posterior portion of the left orbit in NMP M.398-1 (Fig. 5). Carroll's (1970:fig. 5A above left) basisphenoid,

opisthotic, and prootic are likely to be, respectively, the right atlas neural arch, the axis in dorsal aspect, and an axial intercentrum. Carroll's (1970:fig. 1 and fig. 5A, below middle) basioccipital may in fact consist of a partial left atlas neural arch, atlas pleurocentrum, and atlas intercentrum.

Lower Jaw

The medial aspect of the lower jaw (Figs. 1–4A, B, 7B, C) was redescribed by Ahlberg and Clack (1998). Here, we add new data. The straight anterior symphysial margin of the dentary is orientated dorsoventrally. The dorsoventrally narrow posterior extremity of the dentary extends slightly posterior to the interdigitating surangular–posterior coronoid suture (this suture is visible both medially and laterally; Fig. 3B, C). The dentary ornamentation, best preserved in MB Am. 719 b and NMP M.885, consists of pits of different sizes, short grooves, and rugosities anteriorly (Figs. 1, 3B). Several large foramina open anteroposteriorly below the dentary dorsal margin. A long and uninterrupted groove (?oral sulcus; ?canal for blood vessel) runs immediately ventral to the bone dorsal margin in its posterior part (Fig. 3B). The lateral surface of the dentary bears narrow anteroposterior grooves, but is otherwise smooth. The dentary produces a deep lamina immediately posterior to the subelliptical symphysis. The surface of this lamina is densely covered in longitudinal grooves and ridges. A large pit lies immediately behind the symphysis. Additional pits can be seen more posteriorly. The ventral margin of the lamina forms a sinuous suture with the splenial, posterior to which the lamina narrows gradually posteriorly and forms straight sutures with the coronoids.

The large, distinctly ornamented angular (Figs. 2, 3, 7B, C) shows grooves and ridges in its ventrolateral portion, at the level of the surangular–posterior coronoid suture, from which point they radiate peripherally. The posterior portion of the bone shows a medial lamina joining the prearticular posteroventral wall and contributing to the posteroventral margin of the posterior Meckelian fenestra.

The long, deep surangular (Figs. 3, 7B, C) is overlapped anteriorly by the dentary and produces a pointed process wedged between dentary and angular. The surangular ossification center shows distinct pits and rugosities. Radiating grooves originating from these pits diminish gradually at about the surangular midlength. The posterior, deep part of the bone surrounds the articular, meeting the prearticular posterodorsal margin medially (Fig. 7B, C).

The posterior extremity of the large, elongate splenial (Figs. 2–4A, B, 7B, C) underlies the anterior end of the postsplenial. The ornamented portion of the splenial lateral surface forms a narrow strip covered in distinct pits anteroventrally, from which short grooves extend posteriorly. The splenial medial surface forms a large plate (Fig. 4A, B) extending slightly posterior to the jaw midlength. Its pointed anterior end reaches the ventral portion of the symphyseal region, but does not participate in the symphyseal articulation. The dorsal margin of this plate is sutured with the anterior and middle coronoids. Dorsal to the anterior Meckelian fenestra, the splenial meets the anterior end of the prearticular; ventral to the fenestra, it is sutured with the postsplenial. In lateral view, the postsplenial forms a long suture with the dentary and a slightly shorter suture with the angular (Figs. 1, 3, 4A, B, 7B, C). Pits and short ridges occur in the anterior part of the bone. The postsplenial medial lamina forms both the short posteroventral margin of the anterior Meckelian fenestra and most of the ventral margin of the posterior Meckelian fenestra. Between the fenestrae, it contacts the prearticular. Its posterior end fits into the angular medial lamina.

The posterodorsal and ventromedial walls of the subrectangular articular (Figs. 2, 4A, B, 7B, C) are covered by surangular and prearticular, respectively. The prearticular forms most of the

posteromedial half of the lower jaw (Figs. 2, 4A, B, 7C). Its subquadrangular posterior part is separated by a constriction from the narrower, anterior part. The latter forms a distinct, medially directed dorsal flange along the posteromedial margin of the adductor fossa. The prearticular delimits the dorsal margins of both Meckelian fenestrae and meets the posterior and middle coronoids along a straight suture. Its anterior extremity, wedged between middle coronoid and splenial, extends slightly anterior to the anterior Meckelian fenestra, at about middle coronoid midlength. The rectangular, plate-like coronoids (Figs. 2, 4A, B, 7C) differ slightly in length, the anterior coronoid being the shortest, the posterior the longest.

Dentition

The tips of the slender, conical marginal teeth curve slightly posteriorly. The tooth bases do not bear distinct grooves (dentine infolding), contra Carroll (1970). The absence of such grooves is exceptional among reptiliomorphs. The premaxilla bears five teeth (NMP M.885). The number of preserved maxillary teeth ranges from 26 in NMP M.885 to about 29 in MB Am. 719 b, which also shows several empty alveoli. In the smaller UMZC T.1222a, there are about 35 preserved teeth, but many fewer empty alveoli. Two fangs occur on each marginal palatal bone (a single fang plus replacement pit on the vomer of MB Am. 719 b) (Fig. 2). Closely packed rows of small denticles radiate out from the region immediately lateral to the pterygoid articular portion and extend onto most of the palate, including the spaces between the oblique ridges (Figs. 2, 6B).

The dentary has about 40 tooth positions, including empty alveoli, and one dentary fang lingual to the anterior-most teeth (Figs. 2, 4A, B, 6B, C). The coronoids are entirely covered in small denticles (except on the posterior ascending ramus of the posterior coronoid). The anterior and middle coronoids carry a pair of fangs situated near their midlengths.

SKULL RECONSTRUCTIONS

Relative to Carroll's two skull reconstructions (1970:fig. 6A, based on the holotype, and fig. 6B, based on the smaller UMZC T.1222), ours differ in several features (Figs. 6, 7). His two reconstructions (A and B, hereafter) differ in the nature of the relationship between the pre- and postfrontal: in neither did they meet, but they were more widely separated in B than in A. In our reconstruction, they form a narrow contact over the orbit midpoint. The postorbital is more extensive in A than in B. Our reconstruction agrees more closely with B. Carroll's A shows a very narrow quadratojugal, B a more extensive one. Again, ours agrees more closely with B. Other differences include the shape of the lacrimal-prefrontal contact and its contribution to the exonarial fenestra. A shows a septomaxilla, for which we find no evidence and a distinct lacrimal excavation into the prefrontal, not present in our reconstruction. Palatal differences include the relationships of the palatine, vomer, and pterygoid. In our reconstruction, the vomers just meet the pterygoids in the midline and the palatines, though broad, are narrowly separated by the narrow anterior pterygoid ends. In A, the vomers and pterygoids are separated by a broad contact between the paired palatines, whereas in B, vomers and pterygoids form a broad contact and the palatines are narrow. Carroll's palate reconstructions show a much less extensive transverse process of the pterygoid compared with ours. Our version of the lower jaw has a much longer entry of the dentary, and a much smaller entry of the third coronoid, into the surangular crest.

ONTOGENY

Skull lengths vary from 25 (UMZC T.1222a; Carroll, 1970) to 58 (MB Am. 718 a; Fig. 1) mm, with middle-sized specimens (e.g.,

UMZC T.1337, NMP M.398-1, and NMP M.377) estimated at about 35–40 mm. In UMZC T.1222a, neither the quadrate nor the articular are ossified. Also, its vertebrae are poorly ossified and the carpals and tarsals are unossified. In the middle-sized UMZC T.1337, by contrast, both the quadrate and the articular are ossified. In the largest skull, however, no other braincase ossifications have been identified with certainty apart from the basipterygoid processes of the basisphenoid. As described by Carroll (1970), the largest specimen has ossified tarsals and girdles. In early tetrapods, ossified tarsals are usually attributed to adults. If the largest *Gephyrostegus* specimen is an adult, then the absence of braincase ossifications is surprising. Remnants of ossifications may be tucked between the skull roof and the posterior part of the palate (a bulge in the area of the basipterygoid processes may provide some circumstantial evidence). If most of the braincase was cartilaginous, then *Gephyrostegus* would be comparable to the large terrestrial temnospondyl *Acanthostomatops vorax* (Witzmann and Schoch, 2006).

DISCUSSION

Two early tetrapods assigned to the family Gephyrostegidae require brief comments. One of these, the North American Late Carboniferous *Eusauropleura digitata* (Cope, 1868), was last reviewed by Carroll (1970), based on two specimens lacking cranial elements. Our own initial observations of the *Gephyrostegus* postcranium suggests to us that the supposed gephyrostegid-like features of *Eusauropleura* are questionable. We reserve a detailed treatment of those features in a separate paper. The second tetrapod to be considered is *Bruktererpeton fiebigi* Boy and Bandel, 1973, known from a partially preserved skeleton from the early Late Carboniferous of Germany. Boy and Bandel's attribution of *Bruktererpeton* to Gephyrostegidae appears to be correct. The two taxa resemble each other in their skull proportions, orbit position, morphology of the skull roof, possession of a large, rectangular pterygoid transverse process, presence of oblique palatal ridges, tooth size and shape, and postcranial and scale morphology. However, several cranial traits distinguish them.

Unlike *Gephyrostegus*, *Bruktererpeton* has no distinct anterolateral nasal lappet. Also, its anteroposteriorly broad, lateromedially abbreviated tabular is shorter than the postparietal, whereas the long, narrow tabular of *Gephyrostegus* is longer than the postparietal. *Bruktererpeton* lacks a tabular process, but a small, dorsally ornamented, plate-like process is present in *Gephyrostegus*. There are about 10 premaxillary teeth in *Bruktererpeton*, but only five in *Gephyrostegus*. The tooth crown bases of *Bruktererpeton* are expanded lingually and the mesial portion of their mid-crowns and labial and lingual portions of their apex are flat. In contrast, *Gephyrostegus* has conical teeth.

Autapomorphies of *Gephyrostegus*

Gephyrostegus differs from all other reptiliomorphs in showing pustular ornamentation on the skull roof bones and an ornamented tabular process, which requires discussion. The process is small, subquadrangular, and plate-like, and bears small shallow dorsal pits. In embolomeres (e.g., *Neopteroplax*: Romer, 1963; *Palaeoherpeton*: Panchen, 1964; *Pholiderpeton*: Clack, 1987) and *Silvanerpeton* (Ruta and Clack, 2006), the posterolateral corner of the tabular resembles a slender and pointed horn. In *Proterogyrinus* (Holmes, 1984), the tabular has two posterolateral processes, a dorsal process covered in shallow pits (a continuation of the tabular ornamented portion) and a ventral process with a smooth dorsal area. In *Eoherpeton* (Smithson, 1985), the tabular carries a blunt, conical tabular horn somewhat similar to that in *Bruktererpeton*. In seymouriamorphs, a plate-like, quadrangular process projects from the posterolateral portion of the tabular ventral surface (Laurin, 1995, 1996; Klembara, 1997, 2005, 2009a; Bulanov, 2003; Klembara and Ruta, 2004a, 2004b, 2005a,

2005b; Klembara et al., 2005, 2006, 2007). A plate-like tabular process—distinct from the tabular itself—is absent in diadectomorphs (Moss, 1972; Fracasso, 1987; Berman et al., 1992, 1998, 2004, 2010; Berman, 2000). The process of *Gephyrostegus* corresponds in position to the dorsal horn of *Proterogyrinus* (continuation of the tabular ornamented surface), resembles that of seymouriamorphs in being plate-like, and is unique in its fine dorsal pitting.

Comparisons with Seymouriamorphs, Anthracosaurs, and Diadectomorphs

The cranial anatomy of *Gephyrostegus* is very similar to that of anthracosaurs. Similarities include the shape and configuration of the skull table bones and the non-sutural supratemporal-squamosal contact. In other respects, *Gephyrostegus* resembles seymouriamorphs and, to some extent, diadectomorphs. Three features are relevant to our comparisons.

The first feature is the pterygoid transverse process. The transverse process of rectangular shape of *Gephyrostegus* is shared with seymouriamorphs. In anthracosaurs, this process is either absent or protruding slightly laterally (e.g., *Proterogyrinus*, *Silvanerpeton*). In diadectomorphs, its posterolateral corner extends more or less ventrally and posteriorly (e.g., *Diadectes absitus*: Berman et al., 1998; *Tseajaia*: Moss, 1972; *Limnoscelis*: Fracasso, 1987, Berman et al., 2010; *Orobates* [in this taxon, the process is anteroposteriorly narrow and lateromedially elongate]: Berman et al., 2004).

The second feature is the anterior triangular, wedge-like process on the parasphenoid carrying a dorsoventrally deep, sharp anterior crest. In reptiliomorphs, this process is present only in seymouriamorphs (Klembara, 1997; Klembara and Ruta, 2004a, 2005a; Klembara et al., 2005, 2006, 2007). In *Proterogyrinus*, a triangular, wedge-like structure without the sharp anterior crest occurs anteriorly on the parasphenoid plate (Holmes, 1984). In *Diadectes absitus* (Berman et al., 1998) and *Orobates pabsti* (Berman et al., 2004), the anterior triangular part of the plate becomes gradually low dorsoventrally and continues smoothly into the cultriform process.

The third feature is the presence of closely packed, radiating rows of small denticles on the palatal bones. In *Gephyrostegus*, these rows originate from the region immediately lateral to the pterygoid articular portion. In anthracosaurs, a fine denticle shagreen covers the ventral surface of the pterygoids and/or other palatal bones (e.g., *Proterogyrinus*, *Silvanerpeton*), but the denticles never form rows. All seymouriamorphs show variably developed ridges covered with rows of small denticles and intercalated with grooves (e.g., Klembara, 1997; Klembara and Ruta, 2004a, 2005a; Klembara et al., 2005, 2006, 2007). In the largest *Discosauriscus austriacus* specimens, the ridges disappear, but densely arranged radiating denticle rows persist (Klembara, 1997, 2009b). Both seymouriamorphs and *Gephyrostegus* show such rows, but no diadectomorph does.

Phylogenetic Analysis

Although the phylogenetic position of *Gephyrostegus* was examined in several large-scale analyses of early tetrapods (e.g., Vallin and Laurin, 2004; Clack and Finney, 2005; Ruta and Coates, 2007; Clack and Klembara, 2009), it became necessary to reconsider its affinities in light of a focused 'reptiliomorph' character set that also includes the new and revised data presented here. We use the results from a new cladistic analysis to highlight the instability of certain groups that have long been implicated in the debate of amniote origins.

In some earlier analyses, *Gephyrostegus* was placed firmly on the amniote stem, with little variations in its placement relative to other putative stem-amniote groups. For example, Clack and Finney (2005) placed *Gephyrostegus* immediately crownward
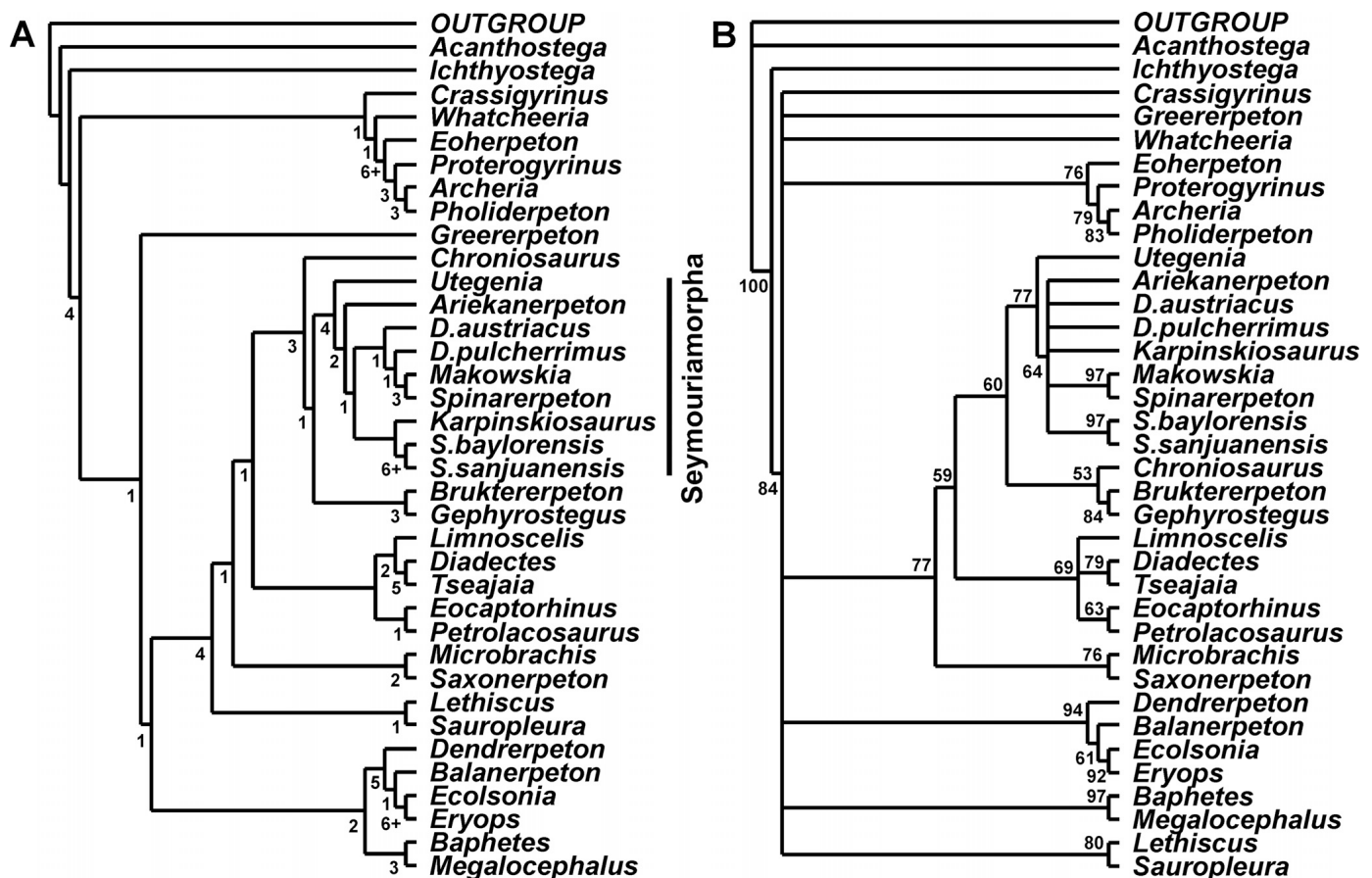
FIGURE 8. Phylogenetic analysis. **A**, the most parsimonious tree recovered by PAUP* version 4.0b10 from a heuristic search of 37 taxa and 156 characters; **B**, bootstrap percentages on a 50% majority-rule consensus tree.

of embolomeres as a sister taxon to (Seymouriamorpha, Microsauria). Ruta and Coates (2007) found similar results, with a paraphyletic Gephyrostegidae nested between anthracosaurs and seymouriamorphs in a diverse array of stem-amniote taxa that also included the majority of lepospondyls. In a slightly modified form, this pattern was also found by Clack and Klembara (2009), with Gephyrostegidae forming a grade group next to an assemblage of seymouriamorphs, basal crown amniotes, and microsaurs.

Here, we use an amended, enlarged, and refined version of a data matrix first published by Klembara and Ruta (2004b), with new data from Klembara (2011). The matrix consists of 37 taxa coded for 156 morphological characters. Characters 15, 47, and 92 are redefined relative to those in Klembara (2011); character 156 is new (Supplementary Data, Appendix S1).

We found one most parsimonious tree (length 615 steps; consistency index = 0.3626; retention index = 0.6739; rescaled consistency index = 0.2443) (Fig. 8A), rooted on a hypothetical, all-zero outgroup (Supplementary Data, Appendix S2). The tree shows several established and some new features, including novel branching patterns as well as hypotheses of relationships that were postulated, but never tested, in previous papers (e.g., see position of *Whatcheeria*). *Gephyrostegus* and *Brukterpeton* form sister taxa, as in Ruta et al. (2003) but unlike in Ruta and Coates (2007). The monophyletic Gephyrostegidae is sister group to Seymouriamorpha. *Utegenia* and *Ariekanerpeton* form successively more closely related taxa, in that sequence, to remaining seymouriamorphs. (*Karpinskiosaurus*, *Seymouria*) is sis-

ter group to (*Discosauriscus* [paraphyletic] (*Makowskia*, *Spinarerpeton*)). *Chroniosaurus* is sister taxon to ((*Gephyrostegus*, *Bruktererpeton*) Seymouriamorpha). This larger clade joins (Diadectomorpha, Amniota), with *Captorhinus* and *Petrolacosaurus* as crown amniotes. Two novel patterns relate to the positions of lepospondyls and anthracosaurs. Thus, nectrideans and microsaurs appear as successive sister groups to the clade ((Chroniosuchia (Gephyrostegidae, Seymouriamorpha)), (Diadectomorpha, Amniota)). Anthracosaurs emerge as stem tetrapods (cf. Laurin, 1998) at the apex of a clade that also includes *Crassigyrinus* and *Whatcheeria*. The position of *Whatcheeria* reflects Lombard and Bolt's (1995) earlier hypothesis of its close affinity to the anthracosaurs. Baphetidae and Temnospondyli form sister groups. Colosteidae (*Greererpeton*) are crownward of (*Crassigyrinus* (*Whatcheeria*, Anthracosauria)) on the tetrapod stem. The phylogenetic position of chroniosuchians remains elusive, despite recent work on this group. Clack and Klembara (2009) placed *Chroniosaurus* in a polytomy with *Silvanerpeton*, an anthracosaur clade, and a clade of remaining reptiliomorphs. Schoch et al. (2010) retrieved microsaurs and chroniosuchians as a clade at the apex of a branching sequence that consisted of *Limnoscelis*, *Seymouria*, and *Gephyrostegus* more basally. This wider group was placed in a polytomy with *Silvanerpeton* and other anthracosaurs. Buchwitz et al. (2012) placed chroniosuchians as the sister taxon to the microsaur *Asaphestera*. This clade formed a large polytomy with various reptiliomorphs and other tetrapods. Our results are consistent with the mosaic of gephyrostegid and seymouriamorph traits in *Chroniosaurus*. A

bootstrap analysis (1000 replicates) provides strong support for Seymouriamorpha but very low support for (Gephyrostegidae, Seymouriamorpha) (Fig. 8B).

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