On a small *Cochleosaurus* described as a large *Limnogyrinus* (Amphibia, Temnospondyli) from the Upper Carboniferous of the Czech Republic

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Limnogyrinus elegans (Fritsch) is the most primitive micromelerpetontid temnospondyl from the Upper Carboniferous of Nýřany, Czech Republic. A recent revision of the taxon by Werneburg (1994) attributed to this species a skull in dorsal aspect which was significantly larger than any previously reported and showed evidence of snout elongation. Restudy of this specimen demonstrates it to be a skull, visible in ventral aspect, of a juvenile of *Cochleosaurus bohemicus*, a more primitive edopoid temnospondyl, which is frequent in the Nýřany assemblage. Werneburg's diagnosis of *Limnogyrinus* is revised and the problems of constructing ontogenetic series are discussed.

Key words: Amphibia, Temnospondyli, Dissorophoidea, Carboniferous, Czech Republic.

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Introduction

The Micromelerpetontidae is a small family of temnospondyl amphibians described from the Late Carboniferous and Early Permian limnic basins of central Europe. Micromelerpetontids had been described as "branchiosaurs" for much of the 20th century and assumed to be either branchiosaurids or larvae of other temnospondyl groups, but were first recognised as a natural group of dissorophoids by Boy (1972). The family now comprises three genera: *Micromelerpeton* from the Lower Permian of Germany and France, *Branchierpeton* from the Stephanian and Lower Permian of Germany and the Czech Republic, and the more primitive *Limnogyrinus* from the Upper Westphalian of the Czech Republic and the Stephanian of Germany. Micromelerpetontids were small temnospondyls with abbreviated snouts, long bodies and short limbs and may have been paedomorphic. Most micromelerpetontid specimens, of all genera, represent individuals with skull lengths of 25 mm or less, but Boy (1995: 443) and Boy and Sues (2000: 1167) have reported larger *Micromelerpeton* specimens with more elongate skulls up to 47 mm in length from the Niederkirchen Beds of Germany. These may represent an early *Micromelerpeton* morphotype that underwent transformation to a terrestrial adult, in contrast to other *Micromelerpeton* assemblages that remained as small aquatic individuals (Boy 1995).

Specimens of the most primitive micromelerpetontid from the Westphalian D of Nýřany, Czech Republic were initially variously described by Fritsch as referred specimens of *Branchiosaurus salamandroides* (Fritsch 1879), the type of "*Limnerpeton*" *elegans*, and referred specimens of other species of *Limnerpeton* (Fritsch 1881). They continued to be confused with other taxa by Bulman and Whittard (1926) as *B. salamandroides*, by Romer (1947) as *Potomochoston salamandroides* and by Boy (1972) and Milner (1980) as *Limnerpeton laticeps*. Milner (1986) recognised *elegans* as the senior species name for the Nýřany micromelerpetontid, placed it in the new genus *Limnogyrinus* and diagnosed it briefly. The first coherent descriptions of *Limnogyrinus elegans* from multiple specimens were by Werneburg (1989, 1994) using material from the National Museum, Prague and the Museum of Humboldt University, Berlin. Most of Werneburg's specimens fell clearly into the concept of *L. elegans* as diagnosed by Milner. However, one cranial specimen, introduced in Werneburg's 1994 description, was significantly larger and longer-snouted than any other described previously and suggested that *Limnogyrinus elegans* might have an adult morphology which was different from the typical smaller material. As part of our on-going study of systematics and ontogeny in early dissorophoids, we examined this specimen during a visit to the National Museum in Prague in 2001 and our conclusions are presented here.

Institutional abbreviations.—BMNH, Department of Palaeontology, The Natural History Museum, London, England; MB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; NMP, National Museum, Prague, Czech Republic.

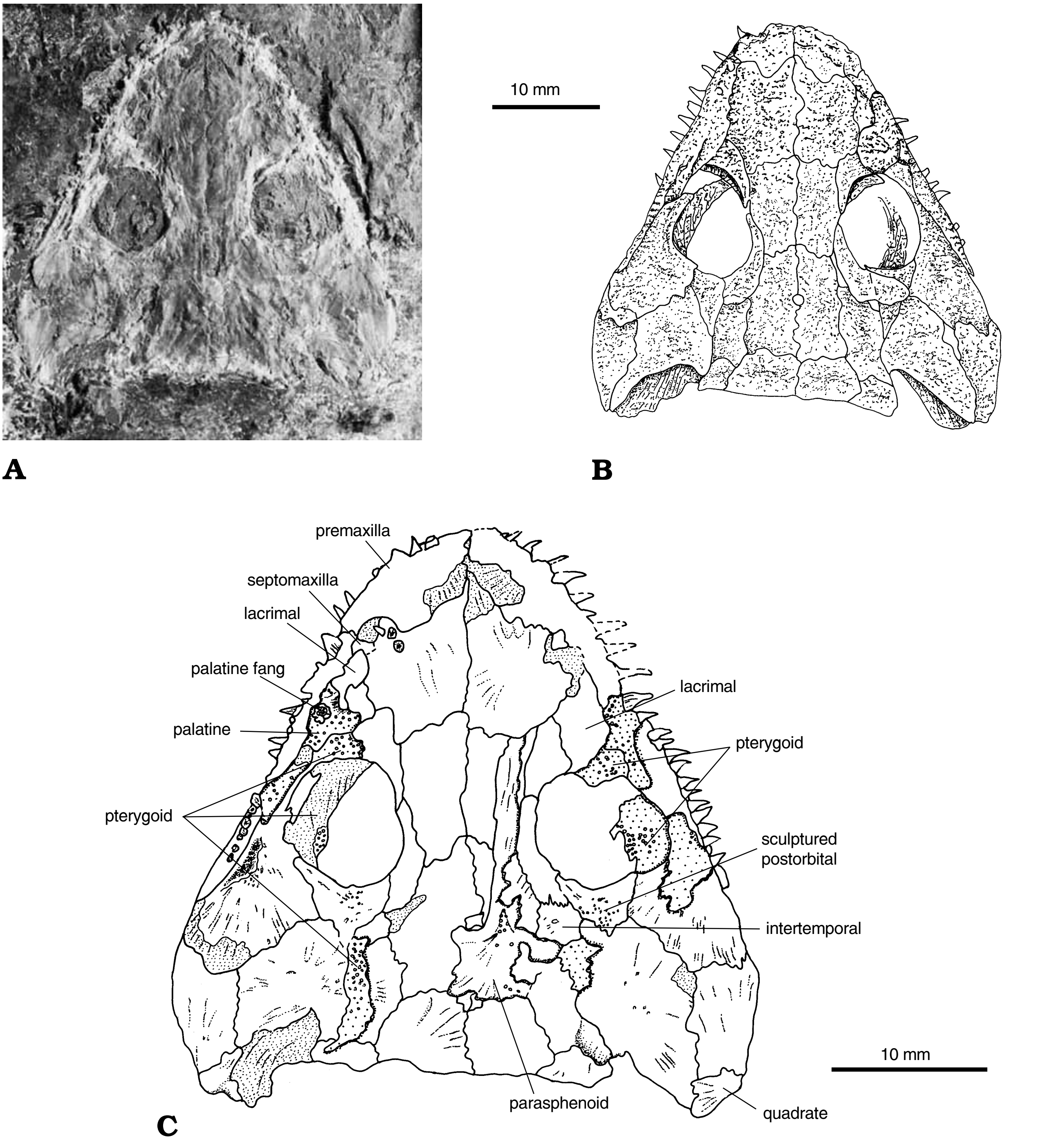

Fig. 1. *Cochleosaurus bohemicus* Fritsch. NMP M4225 from Nýřany, Czech Republic. **A**. Photograph of specimen. **B**. Werneburg's (1994: fig. 6) interpretation as a large specimen of *Limnogyrinus elegans*. This copy of Werneburg's figure has been reversed to simplify comparison with Fig. 1C. **C**. Specimen reinterpreted as a small *Cochleosaurus* skull in palatal aspect.

Description

Locality and horizon.—From Nýřany, Czech Republic; Gaskohle, Nýřany Member, Westphalian D, Late Carboniferous.

Material.—NMP M4225, a slab bearing a single small skull, about 36 mm long (Fig. 1A–C). Specimen previously figured as NMP We 5 by Werneburg 1994 (fig. 6, and as a reconstruction in fig. 1b). Werneburg's figure of the specimen is reversed and appears to have been made from a latex cast.

Morphology.—NMP M4225 comprises a single slab of coal bearing a small skull preserved as original bone. It has not been acid-etched and only a few regions are represented as moulds, presumably where bone adhered to a counterpart slab. Werneburg (1994: 463) gave its length as 32.2 mm but it was found by the authors to be 36 mm in length. Adhering fragments of latex indicated that the specimen had been cast prior to our examination, and we suspect that Werneburg worked from a cast that may have shrunk slightly. The specimen is depicted as seen in Fig. 1A and as interpreted by us in Fig. 1C. A copy of Werneburg's interpretation, reversed for ease of comparison, is given in Fig. 1B. In the following description, the terms left and right refer to the original topology of the skull, reversed because it is seen in ventral view.

Werneburg depicted the specimen as a skull visible in dorsal aspect and with the skull roof surface bearing faint surface markings (Fig. 1B), as is typical in some micromelerpetontids (*Limnogyrinus*, *Branchierpeton*). In fact, the specimen is a skull visible in ventral aspect, the faint markings being the normal pattern seen on the ventral surface of most temnospondyl skull elements. We can be confident of this interpretation for three reasons:

1) Where the skull roofing bone has been exfoliated (central premaxillary region, right jugal and squamosal), the moulds of more robust dermal sculpture can be seen on the coal surface (Fig. 1C).

2) Palatal elements are superimposed on the skull roof. Under a low angle of illumination, a parasphenoid is visible, as are parts of the both palatines and pterygoids (Fig. 1C). These bear denticles and a tusk is visible in the right palatine, so they are certainly exposed in ventral aspect.

3) In the posterior region of the right maxilla, the stumps of a row of teeth can be seen facing out of the specimen on top of the bone of the maxilla (Fig. 1C). In Werneburg's figure (Fig. 1B), these are depicted as a series of sculpture pits on the dorsal surface of the maxilla.

Much of the morphology of this specimen is that of a typical primitive temnospondyl and the following description focuses on features of interest as seen in Fig. 1C.

The premaxillae are large elements occupying the anterior third of the snout. Each has space for about 12 long recurved teeth, of which up to eight are present. The external nares are small and set well back along the snout. The maxillae are long narrow straight bones bearing large recurved teeth anteriorly and smaller conical teeth posteriorly. There is space for about 25 teeth on each maxilla. The right lacrimal almost contacts the external naris but is separated from it by a poorly preserved septomaxilla. The left lacrimal appears to border the orbit margin, although the pterygoid obscures much of this contact. There is a prefrontal-postfrontal common suture excluding the frontal from the orbit margin. The postfrontal is a small bone and does not have the lateral extension behind the orbit attributed to it by Werneburg. The postorbital is unusual in bearing pitting all over its ventral surface unlike the other skull roof bones. The jugal is highly expanded posteriorly and extends to the jaw margin separating the maxilla from the quadratojugal. The right jugal shows the sutural connection to the ectopterygoid as a roughened surface. The quadratojugal is roughly rectangular and on both sides of the skull, the quadrate is visible as a block of bone behind the quadratojugal. The squamosal is a large element and the complete left squamosal shows the tympanic embayment to have been a shallow structure with a possible deeper notch close to the tabular. The right squamosal is damaged and the apparent large tympanic embayment figured by Werneburg is actually the broken edge of an exfoliated piece of squamosal, the mould of the dorsal dermal sculpture being visible on the underlying matrix. The skull table is of typical primitive temnospondyl configuration. Intertemporals are present, unambiguously on the right side where the intertemporal-supratemporal suture can be seen. The skull table bones have the "stepped" configuration common in primitive temnospondyls whereby the postparietals are deep square structures while the tabulars are narrow strips of bone. The parietals are consequently stepped forwards from the supratemporals. A pineal foramen is present.

The palate is represented by some elements which have been compressed onto the underside of the skull roof, but can be seen under low-angle illumination and recognised by the presence of denticle fields. Within the orbits, they are represented by bone fragments or moulds where the bone has detached. The vomers are hardly represented but a poorly defined patch of the right vomer is present bearing the vomerine fangs at the level of the external nares. Part of both palatines and anterior pterygoids are present and show the palatines to have been excluded from the interpterygoid vacuity margin by broad palatine rami of the pterygoids. The anterior margin of the right palatine clearly forms the concave border of the choana. The lateral edge of this border bears the palatine fang+pit. Fragments of bone further back may represent ectopterygoids or parts of the pterygoids, but cannot be precisely identified. The pterygoids are represented by fragments of the broad palatine rami and by a section of the right quadrate ramus. The parasphenoid comprises a small square basal plate and a slender cultriform process. The small right carotid foramen can be seen. There are denticles over most of the visible surface of the palatines and pterygoids and a triangular batch of denticles at the base of the cultriform process.

Systematic position

We identify NMP M4225 as a juvenile of *Cochleosaurus bohemicus* for the following reasons.

1) The presence of intertemporal ossifications, together with pterygoids extending broadly forwards to exclude the palatines from the interpterygoid vacuities indicate that this is a primitive temnospondyl, either an edopoid (e.g., Fig. 2A, B), a stem-dvinosaurian *sensu* Yates and Warren 2000 (= trimerorhachoid) or one of the miscellaneous basal temnospondyls (*Dendrerpeton*, *Balanerpeton*, *Capetus* or an undescribed form). It is not a dissorophoid or stem-stereospondyl.

2) The presence of long premaxillae with a stepped medial edge and small posteriorly set external nares, together with a small tympanic embayment close to the tabular, and a slender cultriform process, show this to be an edopoid *sensu* Milner (1980) i.e. a clade comprising the Edopidae and

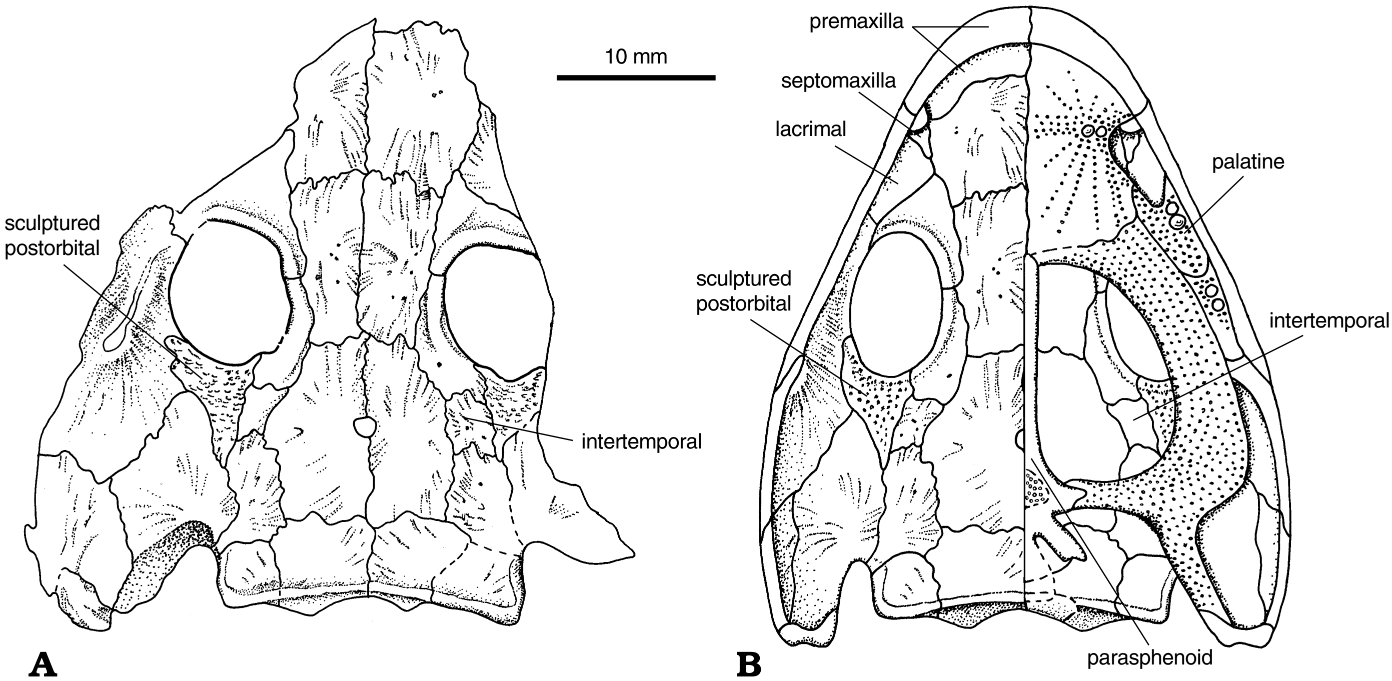

Fig. 2. *Cochleosaurus bohemicus* Fritsch. **A**. NMP M525 ("*Dendrerpeton deprivatum*") = Fritsch Orig. 32, interior of skull roof. **B**. Original composite reconstruction of small skull based on BMNH R2823 (palate), MB Am.25 (extent of interpterygoid vacuities in small skull) and NMP M525 (interior of skull roof).

Cochleosauridae. The premaxillary configuration is a derived character for the clade, and precludes the specimen from being a juvenile of the Nýřany taxon *Capetus* which possesses small premaxillae. The tympanic embayment and cultriform process are primitive characters, contrasting with derived conditions in stem-dvinosaurians.

3) The jugal extending to the jaw margin between the maxilla and the quadratojugal is a cochleosaurid character (Fig. 2B), though it does occur elsewhere in the temnospondyls. The sculptured ventral surface of the postorbital is known only in *Cochleosaurus bohemicus*, the type cochleosaurid, which occurs frequently in the Nýřany assemblage (Fig. 2A, B). *Cochleosaurus* is also characterised by postparietal lappets but these have not developed in the juveniles (Fig. 2A, B) and need not be expected in a specimen as small as NMP M4225. The large recurved premaxillary teeth are also a feature of *Cochleosaurus* in the context of the Nýřany fauna.

In conclusion, the specimen is not the largest *Limnogyrinus elegans* skull in dorsal aspect, but a juvenile *Cochleosaurus bohemicus* skull in ventral aspect.

Discussion

Transferring this specimen from the hypodigm of *Limnogyrinus* to that of *Cochleosaurus* has several implications. Its addition to the described *Cochleosaurus* juveniles is beyond the scope of this note and will be discussed by the junior author (SES) in a future paper forming part of her revision of *Cochleosaurus bohemicus*. The removal from *Limnogyrinus* will be discussed here.

The most obvious consequence of removing this specimen from the hypodigm of *Limnogyrinus* concerns the maximum size attained by this genus. We have seen no *Limnogyrinus* skull more than 21 mm in total length. Of the two larger specimens identified by Werneburg, one is the specimen discussed here, the other is the holotype—a disarticulated skull which he estimated to be 27 mm in length. In a revision of the species of *Limnerpeton*, we remeasured this specimen and concluded that it represents a skull of 18–20 mm length (Milner and Sequeira 2003). Several *Limnogyrinus* skulls fall in the 18–21 mm size range and this is either the adult size, or represents an abundant age-class, with the adult still completely unknown.

A second consequence concerns the skull roof component of Werneburg's diagnoses of *Limnogyrinus* and of *L. elegans*. These should be minimally amended as follows:

Limnogyrinus

Emended diagnosis.—Genus of micromelerpetontid growing to 21 mm skull length. Orbits situated in anterior of skull. Prefrontal-postfrontal contact. Parietals shorter than supratemporals and with anteriorly situated pineal foramen. Postparietals are slender wide ossifications, and tabulars even more slender strip-like elements. Posterior edge of skull table concave and at the level of the supratemporal-tabular suture. Occipital shelf a medial structure of paired ossifications.

L. elegans

Emended diagnosis.—A species of *Limnogyrinus* with the following characters: Skull length from 7–21 mm. Orbits situated in the anterior half of the skull. Snout short and blunt.

Frontals short. Postfrontal expanded posterolaterally. Postorbital as long as wide. Maxilla with 35–40 teeth, the fifth from the frontal is enlarged. Occipital shelf is a narrow strip or forms paired lappets.

The remainder of each diagnosis is unaffected, Werneburg's palatal, mandibular and postcranial characteristics being taken from genuine *Limnogyrinus* specimens.

The third consequence concerns our understanding of dissorophoid ontogeny. There has been a recent resurgence of interest in the growth series of early amphibians and the information that they may convey about the origins of metamorphosis (Carroll et al. 1999; Boy and Sues 2000; Steyer 2000; Schoch 2001 and in press). Plausible growth series of single taxa are still very infrequent in the fossil record, so it is most important that those which appear to be present are genuine, and not composed of more than one genus, otherwise there is no prospect of making sense of the ontogeny of early tetrapods. Steyer (2000: 459) discussed this as a problem of associating larvae with named adults. In this instance, the problem is actually the misassociation of a large specimen with named smaller specimens. This problem is particularly acute in the study of the temnospondyls of the Nýřany assemblage because there are at least six genera present (*Cochleosaurus*, *Capetus*, *Branchiosaurus*, *Limnogyrinus*, *Platyrhinops*, and *Mordex*). Thus, although the Nýřany tetrapod assemblage is rich in temnospondyl larvae and juveniles and a potentially important source of ontogenetic series, its richness in taxa means that the specimens have to be described and studied with greater rigour.

Finally, the reidentification of this specimen has implications for phylogenetic analyses of dissorophoid relationships. These are in a state of flux (Boy 1981; Milner 1990; Daly 1994). Micromelerpetontids have been argued to be the sister-group to the Branchiosauridae (Boy 1981: fig. 5), a distinct primitive offshoot of the Dissorophoidea (Milner 1990) and have been associated with the Amphibamidae as a part of that family (Daly 1994). If the most primitive micromelerpetontid genus were to be represented in analyses by character-states found in a cochleosaurid skull, it is likely that micromelerpetontids would appear to be extremely primitive dissorophoids for entirely spurious reasons. They might also ultimately "attract" the Micromelerpetontidae and possibly the Dissorophoidea towards long-snouted temnospondyls in phylogenetic analyses, on the same incorrect basis. This is a good reason for not conducting phylogenetic analyses from information taken from the literature.

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