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Revision of the amphibian genus *Limnerpeton* (Temnospondyli) from the Upper Carboniferous of the Czech Republic

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The Late Carboniferous amphibian genus *Limnerpeton* Fritsch, 1881 is revised on the basis of the type specimens of the eight original species described by Fritsch using material from Nýřany, Třemošná and Kounov, now in the Czech Republic. The type species *Limnerpeton modestum* is a *nomen dubium* restricted to a mandible that almost certainly belongs to an amphibamid temnospondyl but is not critically diagnostic. “*Limnerpeton*” *laticeps* and “*Limnerpeton*” *macrolepis* lectotypes are both small individuals of the same taxon as the later described *Mordex calliprepes* Steen, 1938 and thus form part of the hypodigm of *Mordex laticeps* comb. nov. “*Limnerpeton*” *elegans* is now *Limnogyrinus elegans* and is a member of the temnospondyl family Micromelerpetontidae. “*Limnerpeton*” *obtusatum* is a specimen of the microsauro *Microbrachis pelikani*. “*Limnerpeton*” *dubium* is an indeterminate tetrapod, probably either a temnospondyl or a pelycosaur. “*Limnerpeton*” *difficile* is a *nomen dubium* but the type is probably a small specimen of the tuditanomorph microsauro *Crinodon limnophyes*. “*Limnerpeton*” *caducum* is almost certainly a specimen of the ophiderpetontid aistopod *Oestocephalus granulatus*. Several other described small temnospondyls from Nýřany are discussed and shown to be specimens of either *Limnogyrinus elegans*, *Mordex laticeps* or Amphibamidae *incertae sedis*. The tetrapod fauna at Nýřany includes four dissorophoid temnospondyls as proposed by Milner (1986) but with two changes in nomenclature. They comprise the branchiosaurid *Branchiosaurus salamandroides*, the micromelerpetontid *Limnogyrinus elegans*, the amphibamid *Platyrhinops* cf. *lyelli* and the primitive trematopid *Mordex laticeps*. These represent four of the five major dissorophoid families and demonstrate that the group had already diversified by the late Westphalian.

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

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Introduction

During the Carboniferous, tetrapods diversified to give some 40–50 major lineages of amphibians and primitive amniotes, most of which have been described from a small number of species-rich Late Carboniferous assemblages. Much of this material was collected in the 19th century during the era of manual coal-mining. The Late Carboniferous vertebrate assemblages from mines at Nýřany, Třemošná and Kounov in Bohemia (now part of the Czech Republic) were initially described by Anton Fritsch (= Frič in his 1876 publication) between 1876 and 1901. Many of Fritsch’s taxa have subsequently been revised, but there remains a large quantity of undescribed material from Nýřany in museum collections in central Europe.

Fritsch named some 50–60 genera and species of amphibian and reptile from his Bohemian material, and most of his taxa have either been validated by subsequently described material, or shown to be junior synonyms of other taxa. However, the genus *Limnerpeton* Fritsch, 1881, and its eight con-

stituent species, have never been thoroughly revised since Fritsch’s work, and *Limnerpeton* has generally been viewed as a repository for a series of poorly characterised and probably indeterminate small tetrapods with skulls in the 15–30 mm range. The aim of this paper is to redescribe, refigure and evaluate the systematic position of the type and principal figured specimens of Fritsch’s eight species of *Limnerpeton*, and is based on first-hand examination of almost all of the surviving material. The opportunity is taken to refigure and comment on two other small “branchiosaur” specimens from Nýřany which were referred to *Branchiosaurus salamandroides* by Bulman and Whittard (1926) but are small specimens of *Limnogyrinus elegans*.

Taxonomic history

In 1876, Anton Fritsch published an initial listing of tetrapods from several newly discovered Permo-Carboniferous sites in Bohemia. The listed forms were not illustrated and

type specimens were not designated but the taxa were given binomial names and defined by 3–4 line descriptions. These included some characteristics, together with the locality and horizon of each specimen. These published names and limited diagnoses are valid in the context of the ICZN definitions of valid taxonomy in pre-1931 publications (International Commission on Zoological Nomenclature 1999 Article 12.1). They were clearly intended to be brief taxonomic diagnoses and Fritsch's names have been widely accepted as dating from this paper in later revisions. In that paper (Frič 1876: 73), one small amphibian mandible from Nýřany was named *Microdon modestus*, and this later became the type species of *Limnerpeton*.

In 1879, Fritsch published the first of 15 parts of his monumental "Fauna der Gaskohle und Permformation Böhmens", this part including an extended introductory section in which he listed the taxa that he intended to describe fully in successive parts of this treatise. This listing consists purely of binomina and localities and many of the names published there are nomina nuda. The list (Fritsch 1879: 28) included not only *Microdon modestus* from Nýřany, but also *M. laticeps* and *M. latissimus* from Nýřany and *M. sp.* from Kounová (now Kounov). In the following year, Fritsch became aware that the name *Microdon* was preoccupied, noting a previous use by Agassiz for a pycnodont fish (in fact, the first and valid use of the name *Microdon* was by Meigen 1803: 275 for a dipteran insect). Consequently, when Fritsch described his amphibian material fully in 1881, he did so under the new generic name *Limnerpeton*. The eight species of *Limnerpeton* described by Fritsch comprised *L. modestum*, *L. laticeps*, *L. macrolepis*, *L. elegans*, *L. obtusatum*, *L. difficile*, and *L. caducum* from Nýřany (plus one *L. laticeps* specimen from Třemošná), and *L. dubium* from Kounov. Fritsch's earlier nomen nudum, *M. laticeps* had clearly become *L. laticeps* but it is unclear which described species is the definitive successor to the nomen nudum *M. latissimus*. One might speculate that it is the broad-skulled *L. obtusatum* but Fritsch left no clue in his work. Fritsch placed the genus in the monogeneric family Limnerpetidae and both family and genus were described as "Stegocephalians with a long salamander-like body, wide frog-like head and large orbits situated anteriorly in the skull. The parasphenoid is like that of branchiosaurids, the vertebrae are amphicoelous with a distinctly developed (neural) spine. Ribs short and slightly curved. Numerous small, similar-sized teeth, sometimes finely grooved around the point, otherwise smooth with a large pulp cavity. The back is well-ossified and scales are present" (Fritsch 1881: 147). Viewed from the modern systematic perspective, this diagnosis could cover a wide range of small tetrapods, although the branchiosaurid-like parasphenoid and short ribs are both temnospondyl characters that, in principle, should have restricted the constituent taxa to temnospondyls.

Stehlík (1924) reported five specimens of *L. obtusatum* in the collection of the Geological Institute of Masaryk University, Brno, but his descriptions and single figure are not informative and it is unclear whether his material was correctly at-

tributed or not. Steen (1938) reexamined Fritsch's material and gave a brief redescription of *L. laticeps*. She concluded that the Třemošná specimen of this species was an adelospondyl (= microsaur) while the Nýřany specimen was "a different taxon". She listed all other *Limnerpeton* species as indeterminate, though noting that *L. obtusatum* was a lepospondyl, *L. elegans* was a lepospondyl or adelospondyl, and *L. macrolepis* was a labyrinthodont.

Romer (1945) revised the Kounov material, comparatively with the assemblages from the Texas Lower Permian. His interpretation of the Kounov material was based on examination of Fritsch's figures, rather than the original material, and also undertaken with the aim of "lumping" diverse specimens into a small number of lightly defined taxa. *Limnerpeton dubium* was placed in synonymy with *Dendrerpeton foveolatum* and these and other specimens referred with doubt to the genus *Onchiodon* (as *Onchiodon? foveolatum*, Romer 1945: 433) on the basis of general resemblance ("some at least pertains to a typical rhachitome", Romer 1947: 136). Romer (1947) gave consideration to only one Nýřany *Limnerpeton* species, placing *L. laticeps* in synonymy with *Branchiosaurus salamandroides* and *Potomochoston limnaios* as the binomen *Potomochoston salamandroides*.

Brough and Brough (1967) redescribed *Limnerpeton obtusatum* as a distinct species of the microsaur genus *Microbrachis*, *M. obtusatum*, and subsequently Carroll and Gaskill (1978) have argued that this species is a junior synonym of *Microbrachis pelikani*, while Werneburg (1994) suggested that it is a specimen of the microsaur *HylopleSION longicostatum*.

Boy (1972) suggested that the Nýřany *L. laticeps* was an early member of the dissorophoid temnospondyl family Micromelerpetontidae. Milner (1986) concluded that *L. laticeps* was a member of the dissorophoid genus *Amphibamus*, and that *L. elegans* was the senior name of the Nýřany micromelerpetontid, transferring it to the new genus *Limnogyrinus*. The latter conclusion has been followed by Werneburg (1989, 1994). Clack and Milner (1994) referred most of the Nýřany "Amphibamus" material to the Linton taxon as *Platyrrhinops cf. P. lyelli* but excluded the type of *Limnerpeton laticeps*, leaving it as a specimen of uncertain status.

The current published situation is that only one of Fritsch's species appear to have a relatively unequivocal taxonomic status, namely *L. elegans* as *Limnogyrinus elegans*—a primitive micromelerpetontid from Nýřany. *L. obtusatum* is argued to be either a junior synonym of *Microbrachis pelikani* or of *HylopleSION longicostatum*; *L. laticeps* and *L. dubium* are small temnospondyls of uncertain systematic position, while *L. modestum* (the type species), *L. macrolepis*, *L. difficile*, and *L. caducum*, are nomina dubia based on specimens which have not been studied in detail since Fritsch described them.

Institutional abbreviations.—BMNH, Department of Palaeontology, The Natural History Museum, London; ČGH, acquisition catalogue, National Museum, Prague, Czech Republic;

DMSW, D.M.S. Watson collection (now part of UMZC collection); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; NMP, National Museum, Prague, Czech Republic; UMZC, University Museum of Zoology, Cambridge University, England.

Descriptions

Holotype and lectotype specimens.—The first and major section of this systematic review is restricted to the holotype and lectotype specimens of each of the eight species of *Limnerpeton*, as the status of each species depends solely on the type specimens. Referred specimens and non-lectotypic syntypes are considered in a later section. In the following review, the species are discussed in the same sequence that they were described by Fritsch (1881). Consequently we have not incorporated any higher systematics but place all the taxa in a single higher systematic framework following the descriptions. For each species, the proposed correct identity is presented in the line following Fritsch's original binomen.

Limnerpeton modestum Frič (1876), 1881 *nomen dubium*

= *Amphibamidae incertae sedis*

Fig. 1.

Microdon modestus Frič 1876: 73.

Microdon modestus Frič; Fritsch 1879: 28.

Limnerpeton modestum (Frič); Fritsch 1881: 147, pl. 27: 7, text-fig. 88.

Limnerpeton modestum (Frič); Steen 1938: 263.

Limnerpeton modestum (Frič); Werneburg 1994: 464.

Holotype: NMP M464 (= Fritsch Orig. 15; ČGH 3007), a small block of coal bearing a right mandible exposed in lateral aspect, and lacking the articular region (Fig. 1). This specimen, a mandible with 44 teeth, was specifically mentioned in Fritsch's 1876 description and so constitutes the holotype. Fritsch (1879: 148, pl. 27: 6, 8) reported a dermal scale and a small palatal element on the same slab as this jaw, but neither of these are now visible on this specimen. Pyritic decay has caused the loss of some of the coal on the surface of the slab, and these two specimens must be presumed to be lost. The holotype jaw appears to be situated on a stable coal surface and is not in imminent danger of destruction.

Locality and horizon: From the Humboldt Mine, Nýřany, Czech Republic; Gaskohle, Nýřany Member, Westphalian D, Late Carboniferous.

Description.—The specimen is a right mandibular ramus exposed in lateral aspect (Fig. 1). Most of it is represented by original bone, but in the articular region, the bone is lost and only a natural mould in the coal remains. The bone surface is damaged with many flakes exfoliated, but some surface detail is preserved on each of the visible bones. The mandible would have been about 31.5 mm long when complete. It was long and slender with a low coronoid process and an articulation set at about the same level as the tooth row.

The dentary is relatively slender and bears light antero-posterior striations. It bears a large number of small closely

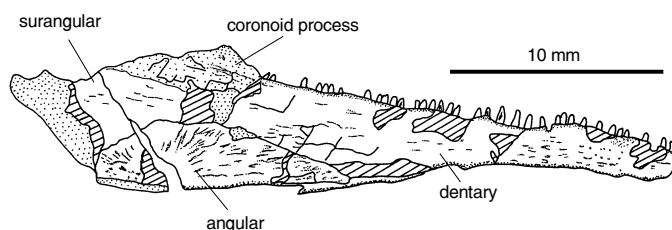


Fig. 1. *Limnerpeton modestum* Fritsch *nomen dubium*. NMP M464 (Fritsch Orig. 15), holotype right mandible, from Nýřany, Czech Republic. In this and the following figures, hatching represents broken bone surface and stipple represents bone impression on matrix.

spaced teeth with columnar sides and short bluntly pointed crowns. Because of damage to various teeth that are represented by stumps, there is an element of subjectivity in a tooth-count. Fritsch counted 44 teeth in the mandible but we could not see more than 36 standing teeth. However, if one attempts a more comprehensive count of teeth plus spaces, with some estimates for damaged sections, there appears to have been space for 60–64 teeth in the mandible, with perhaps two-thirds present at any one time. Damaged teeth show no trace of labyrinthodont infolding. About one third of the distance from the anterior end of the tooth-row, the teeth seem to have been slightly longer and more pointed than the anterior or posterior teeth.

The splenials are not recognisable, but the angular is a prominent element. It occupies much of the posteroventral region of the mandible and bears more pronounced striate-radiate dermal ornament than the other bones. Dorsal to it, part of a lightly striated surangular is present. Dorsal to the preserved part of the surangular is the natural mould of part of the medial region of the coronoid process. Posterior to this is the articular region, also represented by a mould in which the profile of the articular cotyle can be determined.

Systematic position.—The mandible must have belonged to a tetrapod with a skull of 30–35 mm length and most Nýřany tetrapods would have had individuals, adult or juvenile, that fell within this size, one exception being the nectridean *Scincosaurus* in which the skull was smaller even in the largest known individuals. The radiating sculpture on the angular, the prominent coronoid process and the relatively long slender anterior region of the mandible suggest a temnospondyl. The non-infolded nature of the teeth is not problematic to this interpretation as tiny dissorophoid temnospondyls have non-labyrinthine teeth. The only Nýřany temnospondyls in which the dentary has space for up to 64 small teeth are the amphibamid *Platyrhinops* (ca. 68 teeth per ramus) and the genus *Mordex* (ca. 74 teeth per ramus). In *Platyrhinops*, the teeth are blunt and slightly expanded as in *L. modestum*, whereas as in *Mordex* they are pointed and incurved in large specimens. In conclusion, the type of *Limnerpeton modestum* is the mandible of an amphibamid temnospondyl. Clack and Milner (1994) assigned the more complete Nýřany amphibamid specimens to *Platyrhinops* cf. *lyelli*. This specimen is not sufficiently

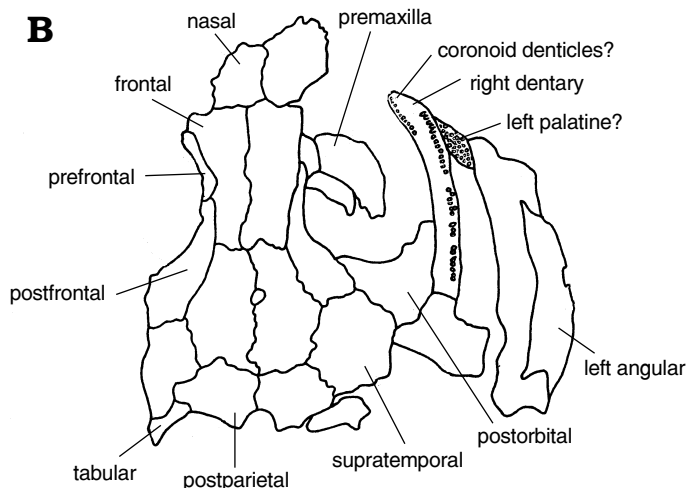
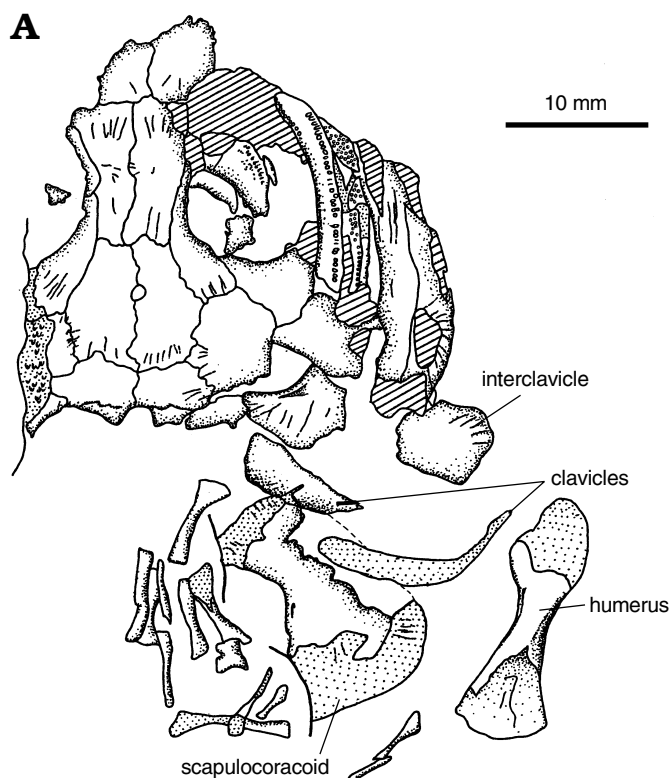


Fig. 2. *Mordex laticeps* comb. nov. NMP M470 (Fritsch Orig. 94), lectotype specimen of “*Limnerpeton*” *laticeps*, from Nýřany, Czech Republic. A. Skull and anterior postcranial skeleton. B. Key to skull elements.

determinate below family level for the genus to be made the senior synonym of *Platyrhinops*; *Limnerpeton modestum* is a *nomen dubium* and can only ever be attributed to better material with doubt. However for faunal and ecological studies, it may be associated with *P. cf. lyelli* for practical purposes.

“*Limnerpeton*” *laticeps* Fritsch, 1881
= *Mordex laticeps* (Fritsch) comb. nov.

Figs. 2, 3.

Taxonomic note.—Fritsch described this species on the basis of two syntypic specimens, one (Orig. 94) from Nýřany and one (Orig. 246) from Třemořná. It was perceived by Steen (1938) and Romer (1947) that the two syntypes represented separate taxa and Romer (1947: 143) treated the Nýřany specimen as the lectotype although he did not formally designate it as such. Milner (1986) formally designated the Nýřany specimen as the lectotype of *Amphibamus laticeps*. There was insufficient space to give reasons for that decision in that publication, but they are: (i) that the taxon was originally intended to be based on a Nýřany specimen (Fritsch 1879: 28); (ii) that the plate of the Nýřany specimen has page priority over that of the Třemořná specimen; (iii) that the Nýřany specimen is still intact while the Třemořná specimen has been destroyed by pyritic decay, although it is represented by galvanotypes; (iv) that the Nýřany specimen is larger and more structurally informative than the Třemořná specimen and hence more suitable as

a lectotype. The Třemořná specimen is discussed in a later section.

Microdon laticeps Fritsch 1879: 28 nomen nudum.

Limnerpeton laticeps Fritsch 1881: 148–151, pl. 31: 1, text-fig. 92, non pl. 36: 1, text-figs. 89–91.

Limnerpeton laticeps Fritsch; Steen 1938: 261 partim!.

Potomochoston salamandroides (Fritsch); Romer 1947: 146, non Fritsch, non Steen.

Amphibamus laticeps (Fritsch); Milner 1986: 672.

Amphibamus laticeps (Fritsch); Werneburg 1994: 464–465.

“*Limnerpeton*” *laticeps* (Fritsch); Clack and Milner 1994: 188.

Lectotype (after Milner 1986): NMP M470/471 (= Fritsch Orig. 94; St.123), a skull in ventral aspect and a partial postcranial skeleton in counterpart. The specimen comprises three blocks of coal and a galvanotype of one block. NMP M470 comprises the anterior half of the specimen with the bone preserved as figured by Fritsch (1881: pl. 31) and in this work (Fig. 2A), a second fitting slab bearing the posterior half of the specimen in which the bone has been etched away to leave a mould in the coal, and a galvanotype made from the acid-etched posterior slab (Fig. 3A). NMP M471 is the counterpart block corresponding to the posterior end of the anterior block and the entire posterior block (Fig. 3B). It does not include any cranial material. It should be noted that Fritsch’s pl. 31 incorporates substantial rearrangement of the postcranial elements to fit his plate format. In the original specimen, the skeleton topology is still represented across the slab despite some disarticulation.

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

Description.—The skeleton of this specimen is disarticulated but the various elements have been only slightly displaced. The skull, which does not survive in counterpart, is repre-

sented by the underside of the greater part of the skull roof, with one detached bone in the orbit (Fig. 2). The palate is largely missing but both mandibles are crushed together superimposed on the left cheek region. Immediately behind the skull are several elements of the pectoral girdle together with one humerus and numerous neural arches and ribs. On the posterior counterpart slabs are more neural arches and trunk ribs, some forelimb elements, the right half of the pelvis and many elements of the hind limbs. Dermal scales are scattered throughout the slabs and are still in associated sheets around the posterior trunk region.

The skull would have been about 33 mm in midline length and is that of a small dissorophoid with large orbits and a short broad skull table. The bones are described as they appear in ventral aspect. An impression of some of the sculpture on the dorsal surface of the right supratemporal is preserved and shows honeycomb-type pitting with no trace of striations. There were squarish nasals, elongate frontals showing a slight expansion at the anterior end, and narrow prefrontals that extended back to meet the postfrontals, excluding the frontals from the orbit margin. The postfrontals have narrow anterior extensions and a relatively expanded ovoid posterior region. The parietals were large rhomboidal elements, narrower anteriorly next to the interorbital region. The pineal foramen is relatively large and situated just anterior to the middle of the interparietal suture. There are no intertemporals, and the supratemporals are large square elements, extending posteriorly behind the level of the parietals. The postparietals are wide rectangular bones, about half the area of the parietals and narrowing laterally where they extend behind the supratemporals. Each postparietal bears an occipital flange bordering the foramen magnum. The left tabular is present though slightly detached. It was a small element separated widely from the parietal. It bore a tiny posteriorly directed process on its posterolateral corner. The lateral edge overlapping the otic notch region had a convex expansion. The left postorbital was a triangular bone, wider than long and apparently only slightly wedged between the supratemporal and squamosal. Part of a large left squamosal is visible. It appears to have a concave posterior edge forming the anterior margin of a large otic notch but this region is damaged.

In the left orbit is a lump of bone, most of which appears to be a marginal tooth-bearing element seen in dorsal aspect. No teeth are visible but it has a smooth, apparently natural convex margin next to which is a row of parallel pits. There may be a fragment of a second bone sutured to the opposite side of this bone. It resembles the dorsal surface of the premaxilla and maxilla in other small temnospondyls and appears to be the right premaxilla with an attached nasal fragment. It is taken to be the greater part of a robust and distinctive premaxilla.

No part of the palate is clearly visible but there are several pieces of densely denticulate bone wedged between the two mandibles. These cannot be identified but from their position are probably pieces of the palatine and pterygoid, or possibly ectopterygoid. They demonstrate that the lateral palatal bones bore a dense covering of denticles.

Parts of the middle and posterior regions of both mandibles are present. The tooth-bearing strip of bone overlying the outer edge of the left orbit appears to be the right dentary together with part of a denticle-bearing coronoid. The preserved fragment of dentary has space for about 36 teeth. The tooth bases and positions suggest that the dentary teeth were small, equal in size and closely spaced. Medial to the tooth row is a distinct shelf, apparently the medial surface of the dentary on which the coronoids would have been situated. At the anterior end is a row of denticles, distinctly smaller than the main tooth row, and this is presumably a row of coronoid denticles. The left mandible is represented by the entire posterior region, which is severely crushed. The angular is visible in ventral aspect and can be recognised by its dermal ornament in the form of radiating striations. Behind it in the coal is a mould of the articular, visible as its bilobed condylar surface.

Clack and Milner (1994), following the unpublished thesis of Milner (1974), noted the presence of several branchial ossicles behind the skull of this specimen. More recent examination shows these to be small dorsal osteoderms, also found thinly scattered over the rest of the slab. There is no trace of branchial ossicles on this specimen.

The axial skeleton is disarticulated but not much scattered. One articulated series of four trunk vertebrae are 13.8 mm in total length. The distance from the back of the skull to the ilium is 74 mm which suggests a presacral column of about 22 vertebrae. The disarticulated nature of the specimen makes this a crude estimate but both the skull and the pelvis were substantial elements and might not have moved far. At any rate, this is unlikely to have been an unusually long-bodied temnospondyl. The neural arches are present as separately ossified halves with very low neural spines and distinct anterior and posterior zygapophyses. The middle trunk series bear prominent rib articulations. In the same middle trunk region, at least two isolated intercentra can be seen. They have been dorsoventrally flattened and appear as small ovals of bone, pointed at both ends and with a medial suture, implying that the intercentrum has recently ossified from two separate halves.

Ribs are scattered throughout the postcranial skeleton. The trunk ribs are relatively small and straight or slightly curved. The anterior trunk ribs, represented by a clump of ribs just behind the skull, are larger with expanded heads. One or two pairs situated next to the pectoral girdle, have slightly expanded distal shafts. No uncinat processes are visible. The posterior trunk ribs are shorter, thinner and unossified distally. Close to the pelvis are four caudal haemal arches, each comprising a pair of rod-like bones fused to give an articulating surface proximally and terminating together as a fused point distally (Fig. 3).

The pectoral girdle is represented by the partly hidden interclavicle, both clavicles, and both scapulocoracoids, also each partly hidden (Fig. 2). No cleithra could be recognised although it is possible that the cleithral shafts might be present, unrecognized, in amongst the anterior trunk ribs. The

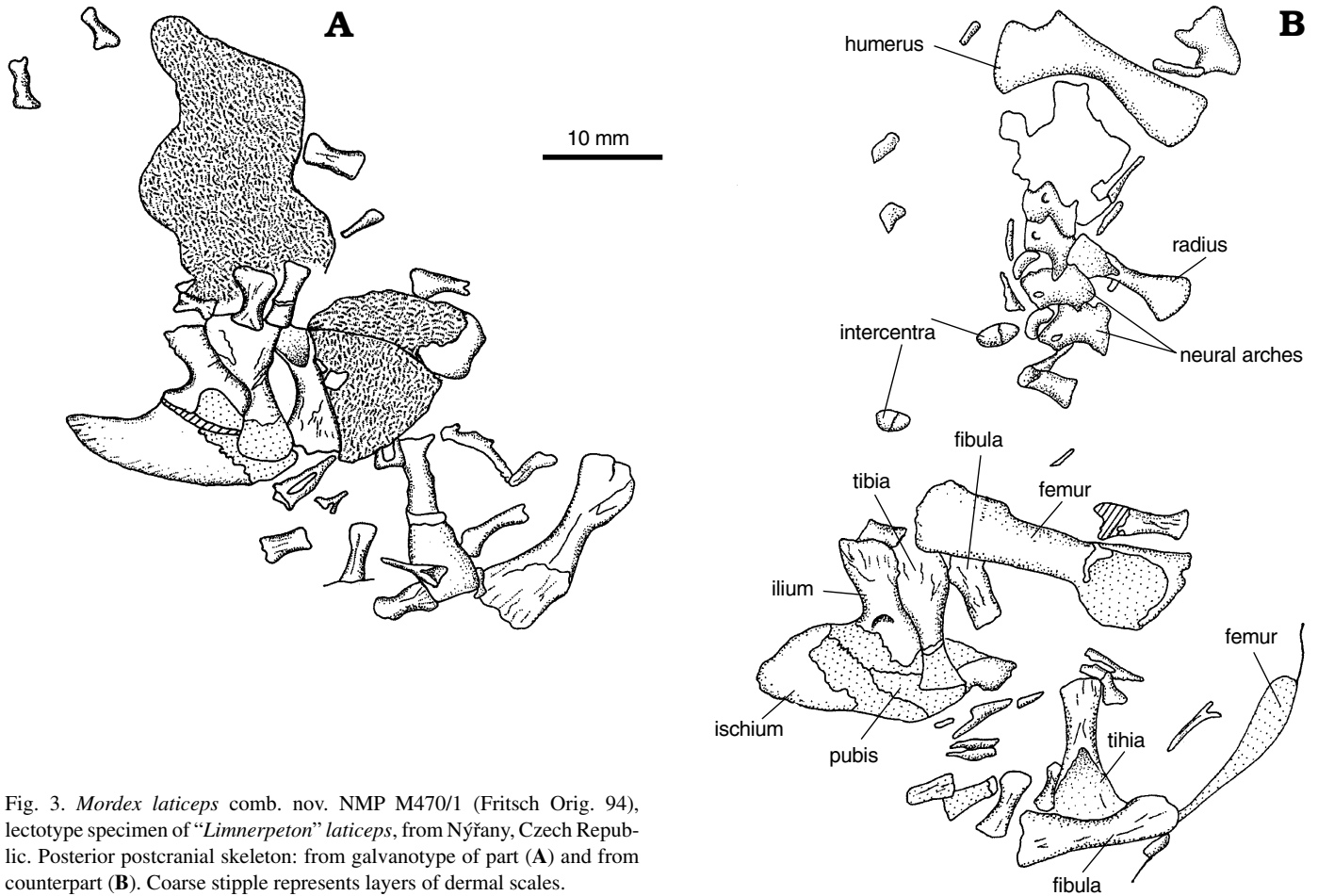


Fig. 3. *Mordex laticeps* comb. nov. NMP M470/1 (Fritsch Orig. 94), lectotype specimen of "*Limnerpeton*" *laticeps*, from Nýřany, Czech Republic. Posterior postcranial skeleton: from galvanotype of part (A) and from counterpart (B). Coarse stipple represents layers of dermal scales.

interclavicle is a small rhomboid, about as long as wide and fully ossified. It is visible in internal aspect and the nature of its dermal ornament is unknown. The clavicles are long structures with narrow blades and the articulated dermal pectoral girdle would have been a narrow strut-like structure rather than a large plate-like structure. The scapulocoracoids are fully ossified, an unusual feature in such a small temnospondyl. Each scapulocoracoid is a flat element with a broad crescent shape or kidney shape (Fig. 2). There is a thickened strut extending down the posterior concave edge and a foramen on the edge of the posteroventral extension of the coracoid. The only anterior limb elements that can be identified are the humeri and a radius. The left humerus, close to the skull is a slender element comparable in proportions to those of branchiosaurids and dissorophids. Neither end is greatly expanded and no supinator process is visible. The right humerus, partway down the trunk, is similar and is accompanied by a slender radius.

The lateral face of the right side of the pelvic girdle is visible on both counterparts (Fig. 3). The right elements, ilium, ischium and pubis are sutured together, an unusual feature in a small temnospondyl. The ilium bears a large acetabulum and a relatively stout posterodorsally directed dorsal shaft. The dorsal shaft is simple with no caudal process and only a slight suggestion of dorsal expansion. The pubis is repre-

sented by a poorly defined patch of bone, as if it were just in the process of ossification. The ischium is fully ossified and is a large slightly curved plate of bone extending well behind the ilium (Fig. 3). It appears to have extended forwards under the pubis, which is wedged between it and ilium so that much of the area immediately below the acetabulum is occupied by the pubis. The femur is relatively large but the only specimen is too poorly preserved to permit useful observations to be made. Both sets of tibiae and fibulae are present. The tibia is the larger element, relatively straight with highly expanded proximal end and a less expanded distal end. The smaller fibula is slightly bowed and is expanded principally at the distal end. Numerous pedal phalanges are scattered around the posterior part of the specimen.

Large numbers of dispersed and clumped scales are associated with this specimen. There appear to have been both dorsal osteoderms and ventral gastralia present. The dorsal osteoderms are very small circular structures while the gastralia are larger ovoid scales with a thickening along one edge. None of the patches of scales appears to have remained in a life position and there are some dense clusters of scales in the region of the posterior abdomen and pelvis as if some patches of skin had been folded in this region. The animal was evidently covered both dorsally and ventrally with substantial dermal scales.

Systematic position.—This specimen is clearly a small temnospondyl, the configuration of the skull roof, the crescentic intercentra, and the very short ribs, all supporting this identification. The short broad skull, the wide skull table lacking intertemporal ossifications and the small interclavicle, all indicate that it is a dissorophoid, either one of the four well-established dissorophoid taxa from Nýřany, or a representative of a fifth taxon. At various times it has been associated with branchiosaurid and amphibamid specimens (Romer 1947), micromelerpetontid specimens (Boy 1972) and amphibamid specimens (Milner 1986, Werneburg 1994), but its cranial proportions do not correspond to those of *Platyrhinops* of equivalent size (Clack and Milner 1994). The nine characteristics that permit “*L.*” *laticeps* to be associated with one of the defined dissorophoid taxa at Nýřany are as follows.

(1) *Premaxilla.*—The critical synapomorphy that permits “*Limnerpeton*” *laticeps* to be associated with one of the four known dissorophoids from Nýřany is the robust premaxilla. This characterises *Mordex* and can be seen in the type specimen of *M. calliprepes* (Steen 1938: text-fig. 42). *Platyrhinops*, *Limnogyrinus* and *Branchiosaurus* all have premaxillae with a much narrower tooth-bearing marginal ramus surmounted by a narrow alary process. In *Mordex*, the enlarged premaxillae appear to compensate structurally for the extended narial vacuities.

No other characteristic of the lectotype of “*L.*” *laticeps* is as critically diagnostic for synonymy with *Mordex calliprepes* but several are of restricted distribution and in permutation support this identification. The most relevant are as follows.

(2) *Dermal sculpture.*—The small area of skull roof represented as a natural mould, shows it to have borne honeycomb pitting with no striations. This is found in *Platyrhinops* and *Mordex* but not in *Limnogyrinus* or *Branchiosaurus*.

(3) *Supratemporal shape.*—The supratemporal is square, not elongate. This is found in *Platyrhinops*, *Mordex* and *Branchiosaurus* but not in *Limnogyrinus* which has elongate supratemporals.

(4) *Interorbital width.*—The orbits are closely spaced, the interorbital width being less than one orbit width. This is found in *Branchiosaurus* (which does not reach the size of “*L.*” *laticeps*) and in *Limnogyrinus* and small *Mordex* below 50 mm skull length (which do) but in *Platyrhinops*, the interorbital width is already greater than the orbit width at 30 mm skull length.

(5) *Denticulation of palate.*—The lateral elements of the palate bear a dense array of denticles. This is comparable to the situation in *Platyrhinops* and *Mordex*, but such denticle fields are not found in *Branchiosaurus* or *Limnogyrinus*.

(6) *Scapulocoracoid.*—The scapulocoracoid is fully ossified. For this to have happened in a dissorophoid with a 30 mm skull is indicative of a terrestrial animal with a fully ossified pectoral girdle such as might be expected in *Mordex* or *Platyrhinops* but not *Limnogyrinus* or *Branchiosaurus*.

(7) *Humerus length.*—The humerus is a substantial elongate element with no visible supinator process and of a type

found only in some dissorophoid families. The humeri of *Platyrhinops*, *Mordex* and *Branchiosaurus* all have this shape but that of *Limnogyrinus* is a shorter more compact bone.

(8) *Pelvis.*—In the pelvis, the ilium and ischium are co-ossified and ossification of the pubes has commenced. For ossification of the pelvis to have taken place in a dissorophoid with a 30 mm skull is strongly indicative of a terrestrial adult with a fully ossified pelvis such as might be expected in *Mordex* or *Platyrhinops* but not *Limnogyrinus* or *Branchiosaurus*.

(9) *Dermal scales.*—The specimen bears several patches of fully ossified dermal scales, presumably representing skin patches. Such scales are not found in *Platyrhinops* of similar size.

Conclusion.—*Mordex calliprepes* is the only established dissorophoid taxon in which the permutation of character-states found in “*Limnerpeton*” *laticeps* is found. Although the “*L.*” *laticeps* lectotype does not have the snout region to permit the presence of the characteristic *Mordex* elongate naris to be seen, it does possess the distinctive premaxilla. There is no conflict then, in combining the two taxa in synonymy, with “*L.*” *laticeps* as the senior species name and *Mordex* characterising the genus. It is unfortunate that the type specimen of “*L.*” *laticeps* shows fewer of the diagnostic character-states than the type of *M. calliprepes*, but history imposes this resolution, given that *laticeps* has at least one diagnostic feature.

“*Limnerpeton*” *macrolepis* Fritsch, 1881
= *Mordex laticeps* (Fritsch) comb. nov.

Figs. 4, 5.

Limnerpeton macrolepis Fritsch 1881: 151–152, pl. 32: 1–5.

Limnerpeton macrolepis Fritsch; Steen 1938: 263–264.

Amphibamus laticeps (Fritsch); Milner 1986: 672.

Limnerpeton macrolepis Fritsch; Werneburg 1994: 464.

Taxonomic note: Fritsch described this species on the basis of four syntypic specimens from Nýřany, namely Orig. 134a, b, Orig. 234, Orig. 242, and Orig. 243. No subsequent worker has revised or discussed this material in detail and as first revisers, we designate Orig. 134 as the lectotype because (i) the plate illustrating it has page priority over the others, (ii) it is the most complete specimen and bears most morphological information.

Lectotype (selected here): NMP M472 (= Fritsch Orig. 134a, b; ČGH 3005), counterpart slabs bearing a small disarticulated skeleton. The specimen was figured by Fritsch 1881: pl. 32: 1–5. The slab figured by Fritsch as Orig. 134a (pl. 32: 1) is intact though with some pyrite decay (Fig. 4). The counterpart slab figured as Orig. 134b (pl. 32: 2) is now represented only by the left half as figured by Fritsch, the right half being lost (Fig. 5A).

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

Description.—The specimen comprises a small skeleton in which the skull is completely disarticulated, as is the postcranium. Despite the chaotic appearance of Fritsch’s figure, there is a broad sequence from cranial to pelvic elements across the slab (Figs. 4, 5A), and there is no doubt that a sin-

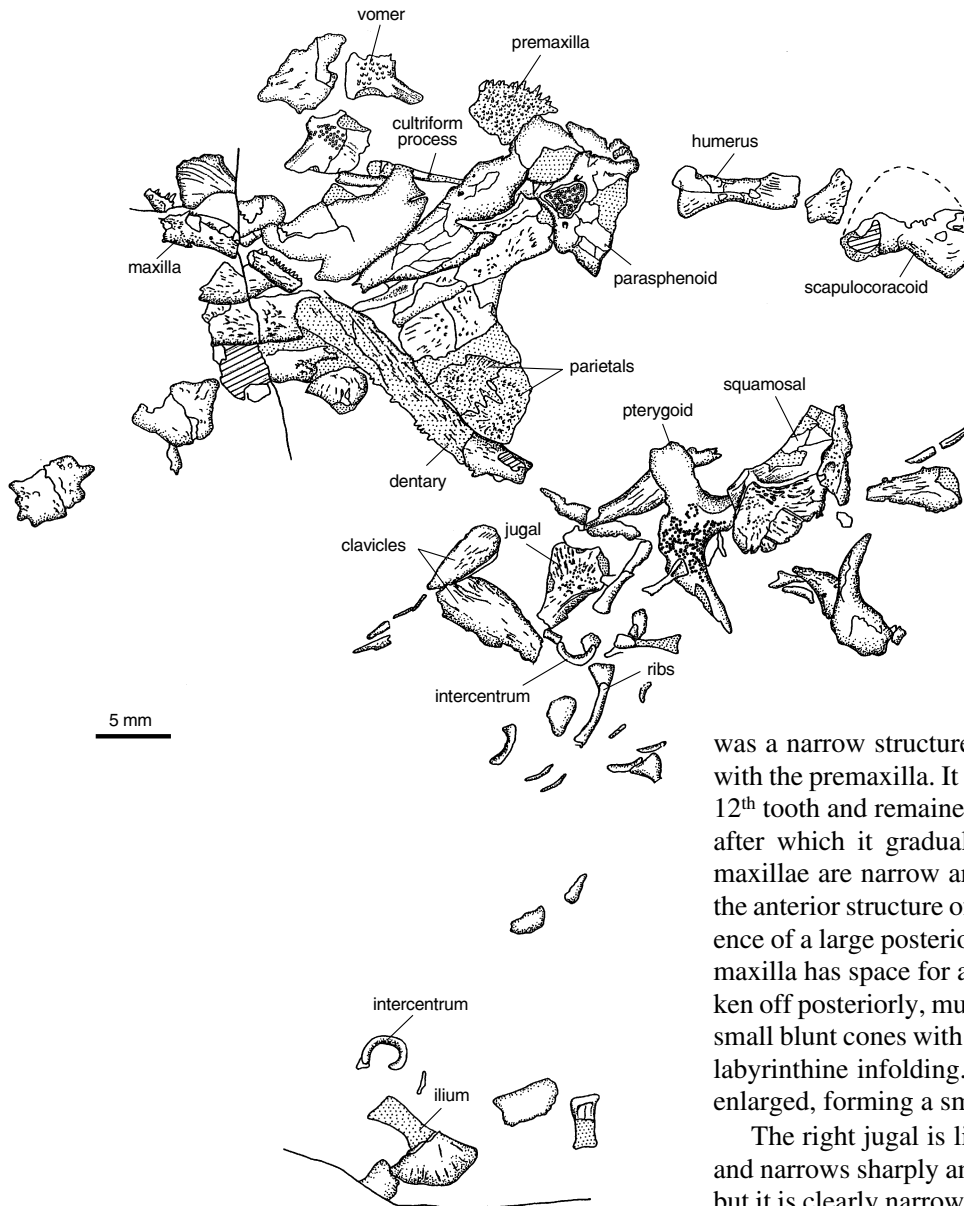


Fig. 4. *Mordex laticeps* comb. nov. NMP M472 (Fritsch Orig. 134a), lectotype specimen of "*Limnerpeton*" *macrolepis*, from Nýřany, Czech Republic. Complete specimen on main part.

gle small temnospondyl was the source of this specimen. The following description is based almost entirely on Orig. 134a, which is the most informative specimen. None of the counterpart remains on Orig. 134b is comparably informative. This account does not attempt to identify and described all the visible material but concentrates on those elements which are both recognisably preserved and of systematic value.

The left premaxilla is preserved as an impression at one end of a clump of cranial elements (Fig. 4). It is very comparable to that in the holotype of *Mordex calliprepes*, being a massive blocky structure bearing at least 15 small teeth and possibly up to 20. The anterior tip and posterior edges are damaged. The dermal surface was covered in dense honeycomb pitting. The right maxilla is present although broken. It

was a narrow structure anteriorly with only a small contact with the premaxilla. It became deeper back to the level of the 12th tooth and remained so back to the level of the 20th tooth after which it gradually narrowed. Usually temnospondyl maxillae are narrow anteriorly for only a short distance but the anterior structure of this maxilla is suggestive of the presence of a large posteriorly extending naris as in *Mordex*. The maxilla has space for at least 40 small teeth and, as it is broken off posteriorly, must have borne at least 50. The teeth are small blunt cones with large pulp cavities and no evidence of labyrinthine infolding. The 6th and 7th from the anterior are enlarged, forming a small pseudocanine peak (Fig. 4).

The right jugal is lightly sculptured on its dorsal surface and narrows sharply anteriorly. The anterior tip is broken off but it is clearly narrowing to a point, a condition characterising dissorophoids. The parietals are still in articulation. They are slightly elongate rectangles bearing honeycomb pitting. The pineal foramen is a wide oval about a third of the length from the anterior and behind it is an extremely undulating interparietal suture. The left squamosal has a broadly triangular anterior dermal surface with a strongly concave posterior edge (Fig. 5B). It clearly bordered a very large tympanic notch, which must have been a circular structure larger than the dermal region of the squamosal. The long quadrate ramus of the squamosal is incomplete but suggests a quadrate position behind the level of the back of the skull table.

Two damaged denticle-bearing plates of bone near the premaxilla appear to be the vomers (Fig. 4). No vomerine fangs are visible but the denticles are densely packed where preserved. Both bones possess smooth concave edges that appear to be the anterior margins of the interpterygoid vacuities. The left pterygoid is relatively complete (Fig. 4). The ventral face of the central region and the palatine ramus are

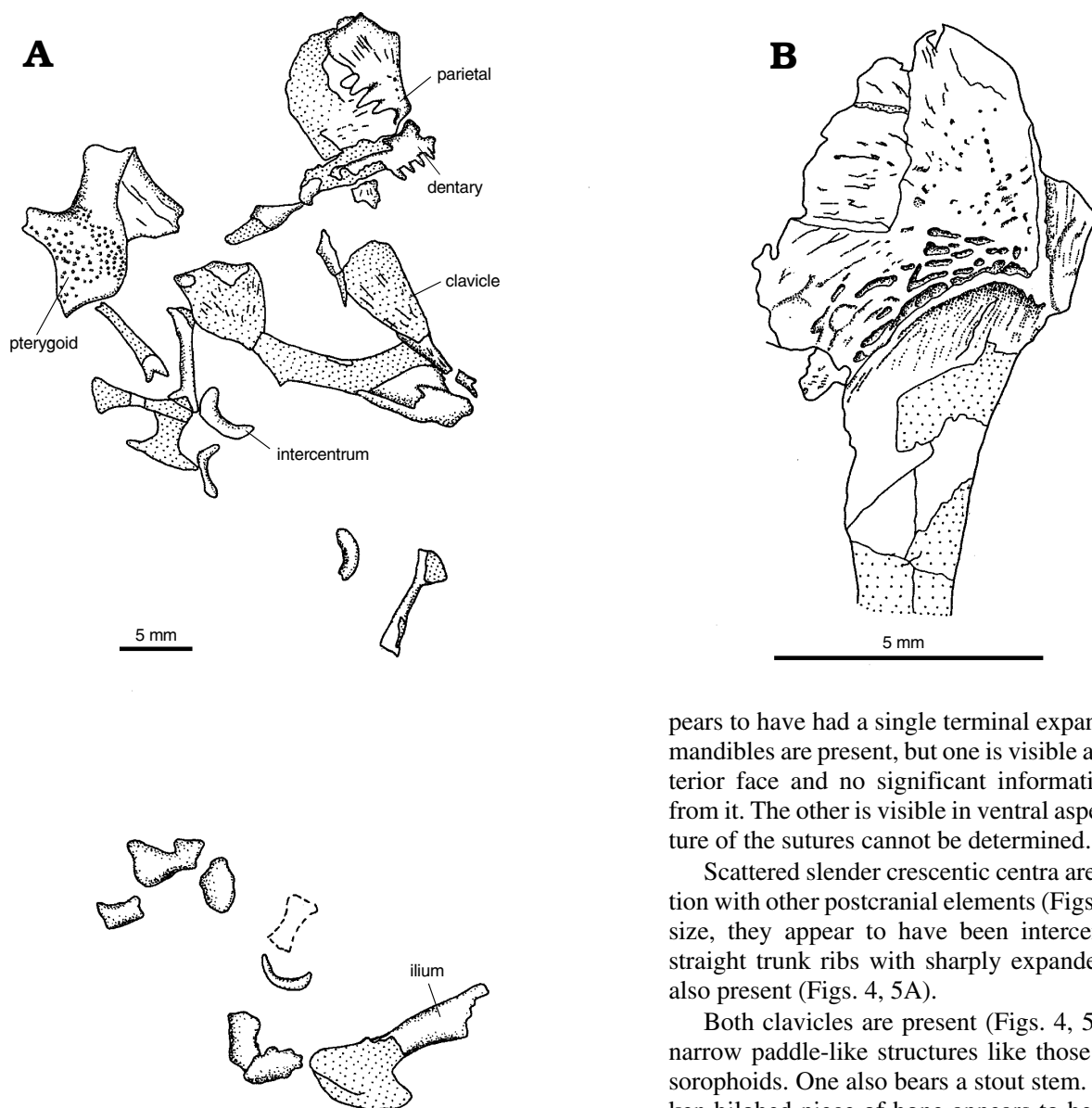


Fig. 5. *Mordex laticeps* comb. nov. NMP M472 (Fritsch Orig. 134), lectotype specimen of "*Limnerpeton*" *macrolepis*, from Nýřany, Czech Republic. A. Counterpart specimen (Orig. 134b). B. Left squamosal, part of Orig. 134a (shown complete in Fig. 4).

covered in a dense sheet of denticles. The palatine ramus widens from an anterior point suggesting that the palatine narrowed posteriorly and that the ectopterygoid may have been narrow. The quadrate ramus is broad but may have been crushed from a vertical to a horizontal plane. The basiptyergoid process is broad but the surface for articulation with the basisphenoid is obscured by the overlapping squamosal. The parasphenoid is largely visible in ventral aspect (Fig. 4). The broadly rectangular basal plate bears a sharply defined triangle of denticles at its junction with the cultriform process. Carotid foramina with elongate entry grooves are present on either side of the denticle patch. The cultriform process is relatively slender. Anteriorly it is damaged but ap-

pears to have had a single terminal expansion. Both crushed mandibles are present, but one is visible as a very cracked interior face and no significant information can be derived from it. The other is visible in ventral aspect but the exact nature of the sutures cannot be determined.

Scattered slender crescentic centra are present in association with other postcranial elements (Figs. 4, 5A). From their size, they appear to have been intercentra. Several short straight trunk ribs with sharply expanded single heads are also present (Figs. 4, 5A).

Both clavicles are present (Figs. 4, 5A). The blades are narrow paddle-like structures like those of most other dissorophoids. One also bears a stout stem. A crushed and broken bilobed piece of bone appears to be the thick posterior strut of a broken scapulocoracoid (Fig. 4). It is unusual for a scapulocoracoid to be ossified in such a small temnospondyl, but this also occurs in the type of *Mordex laticeps* redescribed above. The anterior convex area is lost and the posterior thickened region is preserved with the original concave posterior edge visible. Next to it is a humerus, a relatively long slender element with no visible supinator process and little expansion of the ectepicondylar region. One ilium is present split between the two counterparts (Figs. 4, 5A). It has a clear ventral sutural surface and has not coossified with ischium or pubis. The dorsal blade is simple and slightly expanded dorsally. Ventral scales are present scattered across the slabs.

Systematic position.—"*Limnerpeton*" *macrolepis* is clearly another small dissorophoid. The very large tympanic notch, the large numbers of marginal teeth, the extensive denticulation of the palatal elements and the ossified scapulocoracoid identify it as either *Platyrhinops* or *Mordex*. The massive premaxilla, the unusual shape of the anterior maxilla

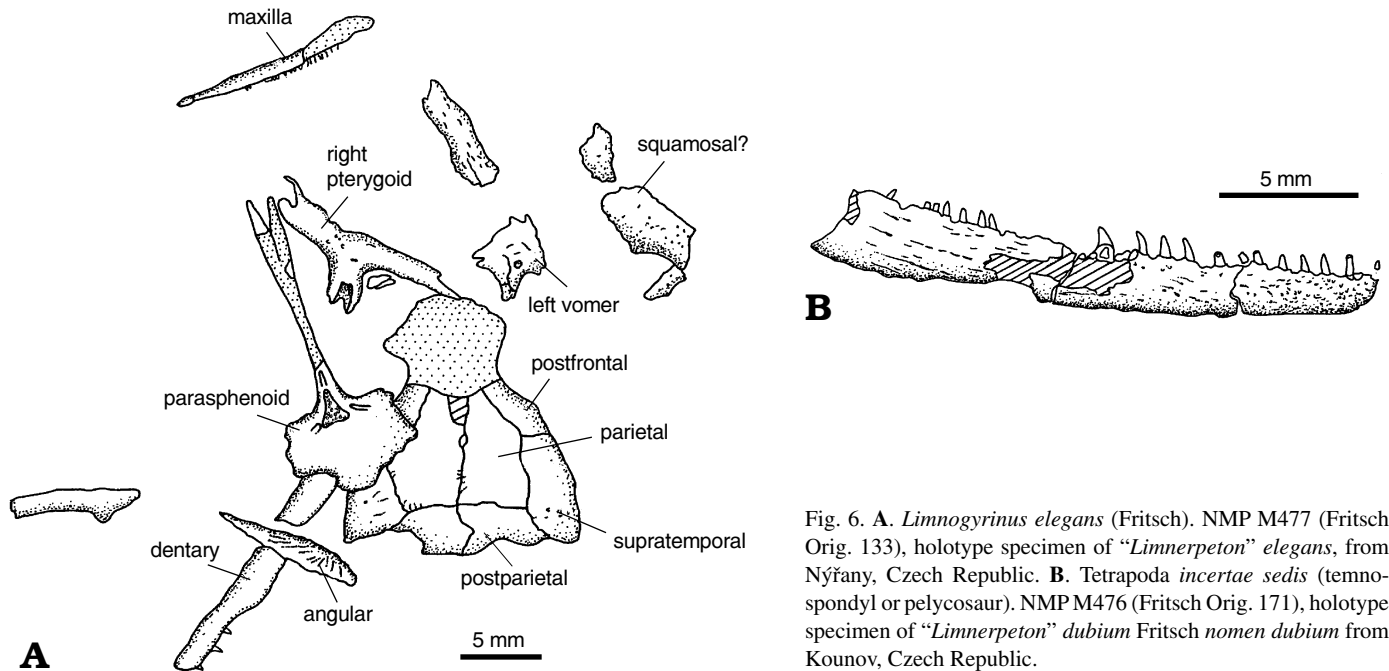


Fig. 6. **A.** *Limnogyrinus elegans* (Fritsch). NMP M477 (Fritsch Orig. 133), holotype specimen of “*Limnerpeton*” *elegans*, from Nýřany, Czech Republic. **B.** Tetrapoda *incertae sedis* (temnospondyl or pelycosaur). NMP M476 (Fritsch Orig. 171), holotype specimen of “*Limnerpeton*” *dubium* Fritsch *nomen dubium* from Kounov, Czech Republic.

and the presence of dermal scales identify it as *Mordex*. The species name *macrolepis* is preceded by *laticeps* in the *Limnerpeton* section of Fritsch’s work. This species therefore falls within the synonymy of the new combination *Mordex laticeps* as discussed above.

“*Limnerpeton*” *elegans* Fritsch, 1881
= *Limnogyrinus elegans* (Fritsch) Milner, 1986.

Fig. 6A.

Limnerpeton elegans Fritsch 1881: 152–154, pl. 34: 1–14, text-fig. 93.

Limnerpeton elegans Fritsch; Steen 1938: 264.

Limnerpeton Fritsch; Boy 1972: 38.

Limnogyrinus elegans (Fritsch); Milner 1986: 672–673.

Limnogyrinus elegans (Fritsch); Werneburg 1989: 26, figs. 8, 11, 15.

Limnogyrinus elegans (Fritsch); Werneburg 1994: 459–464, Abb. 5, 7c.

Holotype: NMP M477 (= Fritsch Orig. 133), a block bearing scattered cranial and postcranial elements of a small temnospondyl (Fig. 6A). The specimen is coated in preservative and would otherwise have disintegrated. There is also the galvanotype NMP M1057 made from the counterpart that is now lost, presumed destroyed, and in which several elements in the specimen can be seen in a more complete state.

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

Description.—The surviving counterpart and the galvanotype both show a cluster of cranial elements at one end of the slab, comprising a skull table, a maxilla, the parasphenoid, a vomer, a pterygoid and fragments of a mandible (Fig. 6A). This part of the material was figured by Werneburg (1994: fig. 5). Trailing away from the cranial material are a series of small low neural arches, fragments of ribs and a few phalanges and scales. These tell us nothing of significance about the specimen and the following description is restricted to the cranial material. If

Micromelerpeton-like proportions are assumed, the skull would have been about 18 mm in midline length.

The skull table is preserved in articulation with the frontals but lacking the tabulars. The frontals are elongate rectangles, and the postfrontals are posteriorly expanded, there being no intertemporals. The postfrontals probably sutured with the prefrontals, although this is not absolutely certain in this specimen. The parietals are relatively large and the pineal foramen is situated about one third of the way along the interparietal suture. The supratemporals are clearly anteroposteriorly elongate elements, almost twice as long as it is wide, and the postparietals are narrow elements extending behind the parietals and partway behind each supratemporal. The posteromedian region of each postparietal appears to be anteroposteriorly deep on the original specimen but this is the occipital extension of the postparietals. Anterior to the skull table, there are four scattered isolated dermal bones. All are broken and none is readily identifiable. The largest one is probably a squamosal as it is too large to represent any other dermal element outside the skull table. The right maxilla is also present, having drifted slightly further away from the skull table. It is a low slender bone, pointed posteriorly and resembling that of *Micromelerpeton* (Boy 1972: fig. 4p). Traces of about twenty very small pointed teeth are present but there would have been space for over thirty teeth on the maxilla.

Three palatal elements are present, namely a left vomer, a right pterygoid and a parasphenoid. The vomer appears to be exposed in palatal aspect. It is a squarish bone with a straight medial edge, a shallowly concave posterior edge where it bordered the interpterygoid vacuity and a sharper concavity in the lateral edge marking the choanal rim. The choana must have been relatively large and anteroposteriorly elongate.

The anterior edge of the vomer was convex and presumably followed the outline of the snout tip behind the premaxilla. There is the base of one fang situated medial to the antero-medial corner of the choana. The pterygoid is a right pterygoid visible in palatal aspect, evidenced by the presence of a few denticles in the central region of the bone where the rami meet. The palatine ramus is elongate slender and relatively straight and terminates in a point as in *Micromelerpeton*. The basiptyergoid ramus is bilobed around a ventral opening as in *Micromelerpeton* (Boy 1972: fig. 7). The quadrate ramus is slightly shorter and broader than the palatine ramus. The parasphenoid is exposed in palatal aspect. The basal plate is broadly rectangular with a convexity along the posterior edge. In its anteromedial region at the base of the cultriform process is a triangular patch of denticles flanked by the carotid foramina. The denticle patch extends only a short way along the cultriform process. The cultriform process is slender, narrowing anteriorly to just over half its length and then gradually widening. At the anterior end it divides into two elongate anteriorly directed lobes which presumably overlay the vomers.

To the left of the skull table are scattered elements of a mandible including a dentary bearing tiny pointed teeth, an elongate angular bearing finely striate ornament, and a possible articular. The mandible appears to have been a slender structure but little else can be said about it.

Systematic position.—Authors such as Boy (1972) and Milner (1980) had referred the abundant Nýřany micromelerpetontid material to *Limnerpeton laticeps*. However the “*L.*” *elegans* type specimen was recognised as the senior name-bearing specimen of the Nýřany micromelerpetontid by Milner (1986) on the basis of the elongate supratemporals, the parasphenoid with a small denticle field and a maxilla with space for 30–40 teeth. Milner assigned the species to the new genus *Limnogyrinus*, and the type of *L. elegans* was incorporated in a redescription by Werneburg (1994).

“*Limnerpeton*” *obtusatum* Fritsch, 1881
= *Microbrachis pelikani* Fritsch, 1876

Limnerpeton obtusatum Fritsch 1881: 154–156, pl. 35: 1–7, text-figs. 94–98.

Limnerpeton obtusatum Fritsch; Steen 1938: 263.

Microbrachis obtusatus (Fritsch); Brough and Brough 1967: 132–136, pl. 14, text-figs. 1–3.

Microbrachis pelikani Fritsch 1876; Carroll and Gaskill 1978: 115, fig. 83E.

Hyloplezion longiscutatum (Fritsch 1876) 1883; Werneburg 1994: 464 (non Fritsch).

Holotype and only specimen: The original specimen (Fritsch Orig. 236) is lost, as noted by Steen (1938: 263), and may have been destroyed as a result of the manufacture of galvanotype copies. Many galvanotypes survive including NMPM639 and BMNH R359 (studied by Brough and Brough 1967).

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

Description.—Unlike most other *Limnerpeton* species, *L.*

obtusatum has been the subject of subsequent study and redescription. This specimen was figured and redescended from the surviving galvanotype by Brough and Brough (1967) and Carroll and Gaskill (1978) as cited above, and no purpose would be served by repeating their work. One comment is apposite. Brough and Brough (1967: 132) noted that the galvanotype specimen of *L. obtusatum* differed in several details from the original specimen figured by Fritsch, and they suggested that, in the process of making successive galvanotypic copies electrolytically, the specimen may have lost superficial structures to reveal underlying structures in later copies. There is another possibility. Fritsch was clearly concerned not to risk the entire destruction of his original material and almost all of the specimens that he used to make galvanotypic copies, existed in counterpart. His frequent practice appears to have been to acid-etch one counterpart for the manufacture of copies (and removing some layers of bone), while leaving the better counterpart intact for posterity. The usual outcome does seem to have been that the counterpart used for galvanotyping was destroyed while the untouched counterpart survives. In some cases, both counterparts survive, and the appearance of a specimen with surviving bone is quite different from that of the electrotypes taken from an acid-etched mould of its counterpart. This has two consequences. Firstly the differences between the specimen as figured by Fritsch and the surviving galvanotypes may actually be the differences of two counterpart specimens treated differently. Secondly, it is possible that the counterpart of *L. obtusatum* figured by Fritsch still survives unrecognised in the large uncatalogued collection at the NMP. In the process of studying the temnospondyl material from Nýřany, ARM has fortunately been able to relocate lost counterparts of the types of *Branchiosaurus salamandroides* (reported lost by Werneburg 1986: 682) and “*Dendrerpeton deprivatium*” (reported lost by Steen 1938: 245). We have not attempted to look for a counterpart of *L. obtusatum* but its continued existence is a possibility.

Systematic position.—The identification of “*L.*” *obtusatum* as a large microbrachomorph microsaur is uncontroversial but there are two interpretations of its precise identity in the recent literature. Carroll and Gaskill (1978: 115–117) referred it to *Microbrachis pelikani* whereas Werneburg (1994: 464) referred it to *Hyloplezion longiscutatum*.

Carroll and Gaskill (1978) discussed the type specimen and noted that it largely comprised the skull roof of a large specimen seen in ventral aspect. They concluded that the differences between it and other *Microbrachis* specimens claimed by Brough and Brough were mostly attributable to the different exposure and to misidentification of some elements. Comparison of the skull of “*L.*” *obtusatum* as figured by Brough and Brough (1967: fig. 1a) with the skulls of *Microbrachis* and *Hyloplezion* as figured by Carroll and Gaskill (1978: fig. 106) shows the tabular-postparietal configuration to be identical to that of *Microbrachis* and distinct from that of *Hyloplezion*. Furthermore, the left squamosal

and quadratojugal of “*L.*” *obtusatum* (figured as pectoral girdle by Brough and Brough) bear dermal sculpture like those of *Microbrachis*, whereas the skull of *Hyloplezion* is unsculptured.

Werneburg (1994: 464) did not make reference to Brough and Brough’s (1967) or Carroll and Gaskill’s (1978) interpretations of this taxon but suggested that the type of “*L.*” *obtusatum* was *Hyloplezion longicostatum*, based on the presence of more than 30 presacral vertebrae and the appearance of the dorsal scales. The presacral counts of *Microbrachis* and *Hyloplezion* are 38 and 30 respectively (Carroll and Gaskill 1978: 169) and both have very similar dorsal scales of typical microsaurian type. The two characteristics cited by Werneburg apply to *Microbrachis* as much as *Hyloplezion*. In view of the specific cranial resemblances of “*L.*” *obtusatum* to *Microbrachis pelikani*, it is concluded, following Carroll and Gaskill, that “*L.*” *obtusatum* is a junior synonym of that species.

“*Limnerpeton*” *dubium* Fritsch, 1881 *nomen dubium*
= *Tetrapoda incertae sedis* (temnospondyl or pelycosaur)

Fig. 6B.

Microdon sp. Fritsch 1879: 28.

Limnerpeton dubium Fritsch 1881: 157, pl. 33: 4, 5.

Limnerpeton dubium Fritsch; Steen 1938: 263.

Onchiodon? foveolatum (Fritsch); Romer 1945: 432–433, *non* Fritsch.

Limnerpeton dubium Fritsch; Werneburg 1994: 464.

Holotype and only specimen: NMP M476 (= Fritsch Orig. 171), the anterior region of a right dentary exposed in lateral aspect (Fig. 6B).

Locality and horizon: From Kounov, 30 km northwest of Prague, Czech Republic. Kounov Member, Slaný Formation in the Rakovnick Basin, late Stephanian B, Late Carboniferous.

Description.—The specimen is a broken right dentary exposed in lateral aspect (Fig. 6B). It is incomplete posteriorly but the preserved section is 20.2 mm long. About 20 teeth are preserved but the preserved element has space for about 47 teeth. The posterior end of the element is broken off, but to judge by the small size of the posterior teeth, the bone is nearly complete and would have been only slightly longer with space for a few more teeth. The dentary was a relatively slender element for a small tetrapod and bore a dense concentration of foramina over the anterolateral surface. These foramina thin out further back where they are accompanied by anteroposterior streaking and small grooves. The impression is of an anterior centre of ossification and posterior growth in the dentary.

The teeth are unlike those of other *Limnerpeton* species in that they are sharply pointed, slightly elongate cones and distinctly recurved. They are neither closely spaced, nor parallel sided. Each has a raised rim of bone around its base. There is little evidence of differentiation of tooth size beyond the usual reduction in size of the posterior teeth, although one tooth in the middle of the dentary, appears to be distinctly larger than any other. This tooth has a large pulp cavity and no trace of labyrinthine infolding.

Systematic position.—Romer’s combination of several Kounov specimens as ?*Onchiodon foveolatum* appears to have been little more than a proposal to reduce the “typical rhachitome” taxa from Kounov to a single taxon, and *L. dubium* was placed here without any specific explanation. The assignment to *Onchiodon*, then seen as the European eryopid counterpart to *Eryops*, seems to have been primarily part of an agenda to interpret the Kounov fauna as equivalent to that of the Texas Red-Beds. Other authors have been content to leave the specimen as a *nomen dubium*. The Kounov fauna does include both terrestrial and aquatic tetrapod taxa, so almost any Permo-Carboniferous family could, in principal, be present.

The dentary of *L. dubium* with about 50 roughly alternating recurved teeth and spaces is unlike that of any microsauro, neotridian or herbivorous amniote. The raised bases to the teeth, and the highly foraminate and pitted surface to the bone suggest a small terrestrial animal, either a temnospondyl or a pelycosaur.

The dentary has the general proportions and appearance that of a small temnospondyl and the tooth number and curvature are appropriate. A particular feature of both eryopid and trematopid temnospondyls is the development of pseudocanine teeth partway along the length of the dentary and there is some suggestion of this in this specimen in that the tooth in position 23 and the spaces on either side of it are slightly enlarged. Against the temnospondyl interpretation is the absence of any suggestion of labyrinthodont infolding in such conical teeth, either visible in section or in the form of grooves running around the bases of the teeth. Comparably small *Cochleosaurus* dentaries bear teeth that already possess distinct simple infolding (SES personal observation).

The alternative interpretation is that the dentary might be that of a small carnivorous pelycosaur-grade synapsid. Such an identity would be consistent with the absence of infolding in the teeth. The slender curved dentary and narrow recurved teeth occur in ophiacodonts and haptodontine sphenacodonts. Sphenacodontine and edaphosaurid pelycosaur fragments have been recognised in the Kounov fauna, and the presence of a haptodontine or an ophiacodont would not be surprising. However the pitted surface of the dentary is unlike that seen in pelycosaurs and more temnospondyl-like. Furthermore, the presence of raised tooth-bases resembles that in eryopids but not pelycosaurs where a labial lamina hides the tooth bases in labial aspect.

In conclusion, “*Limnerpeton*” *dubium* cannot be assigned to a specific tetrapod group with confidence and must remain a *nomen dubium*, pending a more focused study on the entire Kounov assemblage.

“*Limnerpeton*” *difficile* Fritsch, 1881 *nomen dubium*
= ?*Crinodon limnophyes* (Steen 1938) Carroll and Gaskill, 1978

Fig. 7A.

Limnerpeton difficile Fritsch 1881: 157–158, text-figs. 99, 100.

Limnerpeton difficile Fritsch; Steen 1938: 264.

?*Limnogyrinus elegans* (Fritsch); Werneburg 1994: 465.

Holotype and only specimen: NMP M618 (= Fritsch Orig. 193), a slab bearing a poorly preserved skull fragment (Fig. 7A₁) and a broken mandible (Fig. 7A₂). The material was described and figured by Fritsch 1881: 157–158 and text-figs. 99, 100. Fritsch's p. 157 reference to a figure on pl. 30 is an error.

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

Description.—The specimen comprises a very poorly preserved middle region of a skull roof and a partial mandible situated a few centimetres from it. The skull is now not so well preserved as Fritsch's figure suggests. The same area of bone is still present but the moulds of lost bone around the periphery are not as distinct as Fritsch 1881 indicated.

The skull would have been about 14–18 mm midline length, has relatively large orbits and was probably broad and rounded, seen from above (Fig. 7A₁). The bone appears to be smooth and unornamented and it is unclear whether the skull is exposed in dorsal or ventral aspect. Several bones are preserved incompletely including a prefrontal, both frontals, postfrontals and parietals and a postorbital, together with tiny scraps of a nasal, a jugal and a supratemporal. The jugal (figured as a postorbital by Fritsch) has a characteristic shape with a spike-like narrow anterior process, flaring out posteriorly into a squarish plate of bone. The anterior spike is still visible but the rest of the bone is represented by poor impression and the original element may have been exfoliated from the slab at some stage in its history. The frontals were rectangular elements and were probably excluded from the orbit margin by a prefrontal-postfrontal contact. The pineal figured by Fritsch at the anterior end of the interparietal suture, appears to be an artifact of damage, the more substantial edge of the pineal foramen being visible about halfway along the right parietal. There is no certainly identifiable palatal material, the pterygoid and cultriform process figured by Fritsch appearing very ambiguous in the specimen. There is thus no clear evidence of the construction of either the palate or the otic region. There are a few platelets of bone in right orbit that might be palpebral or palatal ossicles.

The tooth-bearing element was identified by Fritsch as a maxilla bearing 13 teeth. It appears to be an anterior mandible, largely dentary, visible in medial aspect (Fig. 7A₂). There are 14 teeth visible but allowing for spaces and a damaged region of the dentary, there is space for at least 21–22 teeth altogether. The teeth appear to have been non-labyrinthine blunt cones, slightly backwardly directed, but not so sharp or recurved as suggested by Fritsch (1881: text-fig. 100b). The teeth gradually reduce in size from anterior to posterior.

Systematic position.—This specimen has generally been ignored although Werneburg (1994: 465) suggested that it might be a poor specimen of *Limnogyrinus elegans* based on the presence of the palpebral elements (scleroticalpflaster) which are otherwise not known in Nýřany small temnospondyls.

"*L.*" *difficile* had a short broad skull and is clearly either a dissorophoid temnospondyl or a tuditanomorph microsauro.

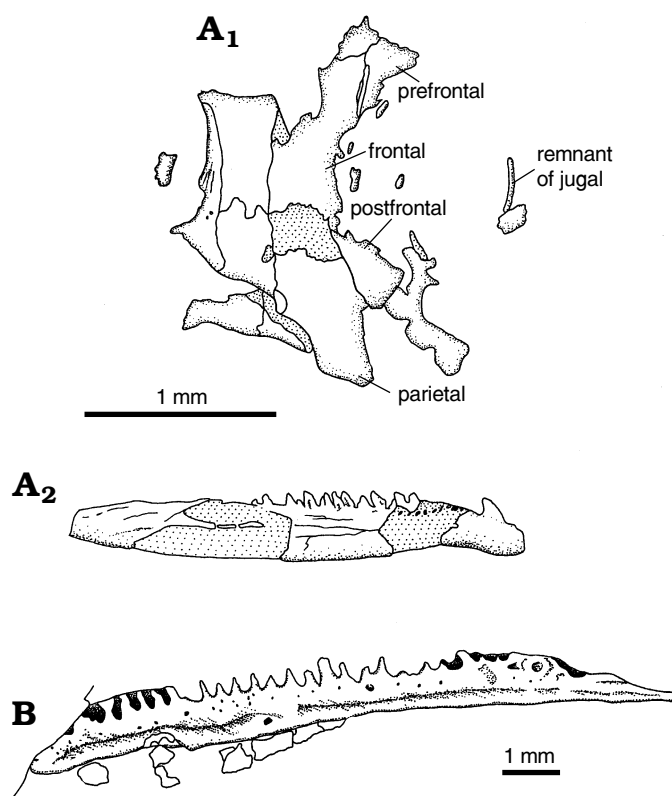


Fig. 7. A. ?*Crinodon limnophyes* (Watson). NMP M618 (Fritsch Orig. 193), holotype specimen of "*Limnerpeton*" *difficile* Fritsch, from Nýřany, Czech Republic. Skull fragment (A₁). Mandible, not in original orientation (A₂). B. *Oestocephalus granulosis* (Fritsch). NMP M619 (Fritsch Orig. 194), holotype specimen of "*Limnerpeton*" *caducum* Fritsch, from Nýřany, Czech Republic.

There is no significant resemblance to the skulls of the baphetids, edopoid temnospondyls, nectrideans, aistopods, microbrachomorph microsaur, anthracosaurs or amniotes known from Nýřany. The presence of a mandible with space for up to 22 blunt conical teeth restricts the possible attributions. Of the Nýřany dissorophoid temnospondyls, *Mordex* has space for up to 75 dentary teeth (Milner 1986), *Platyrhinops* has space for up to 68 (Clack and Milner 1994), *Limnogyrinus* has space for about 40 and *Branchiosaurus* has space for about 35. Of these genera, only *Platyrhinops* has blunt conical teeth. However among the Nýřany tuditanomorph microsaur, *Crinodon* has space for 28 blunt conical teeth on each dentary, *Ricnodon* about 20 simple peg-like teeth and *Sparodus* about 17 stout crushing teeth (Carroll and Gaskill 1978).

Not only does *Crinodon limnophyes* most closely resemble "*L.*" *difficile* in tooth count and shape, but it also possesses prominent palpebral ossifications (Carroll and Gaskill 1978: 10, 11), consistent with the platelets visible in "*L.*" *difficile*. The jugal of *Crinodon* also specifically resembles that of "*L.*" *difficile* in having a slender spike-like anterior process and a posterolateral flare that substantially separates

the maxilla from the quadratojugal. The remaining visible bones of the skull roof are entirely consistent with attribution to a tuditanomorph microsauro, but this is a measure of poor preservation as they are equally consistent with attribution to a dissorophoid temnospondyl.

In conclusion, the visible morphology of "*Limnerpeton*" *difficile* is most consistent with its identification as a tuditanomorph microsauro and, on the basis of its dentition, jugal shape and palpebral ossifications, with *Crinodon limnophyes*. It is not so determinate that the species should be made the senior synonym of *C. limnophyes*; it can only ever be attributed to better material with doubt. However for faunal and ecological studies, it may be associated with *C. limnophyes* for practical purposes.

"*Limnerpeton*" *caducum* Fritsch, 1881

= *Oestocephalus granulosus* (Fritsch, 1880) Carroll, 1998

Fig. 7B.

Limnerpeton? *caducum* Fritsch 1881: 158, text-fig. 101.

Limnerpeton caducium (sic) Fritsch; Steen 1938: 263.

Limnerpeton? *caducum* Fritsch; Werneburg 1994: 464.

Holotype and only specimen: NMP M619 (= Fritsch Orig. 194), a right dentary exposed in ventral aspect (Fig. 7B), together with a broken rib. The dentary was described and figured by Fritsch (1881) as a left maxilla. Apart from the listing by Steen (1938) with the erroneous spelling *Limnerpeton caducium*, and a mention by Werneburg (1994), no other author has referred to it.

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

Description.—The principal element appears to be a right dentary, about 13 mm in length, in which the teeth are all missing and which is exposed in dorsal aspect with the ventrolateral edge either buried or eroded (Fig. 7B). The eroded tooth positions, most of which have a dental foramen medial to them, suggest that there was space for over 31 teeth in the dentary, and probably about 40. There are no bases of teeth, labyrinthodont or simple. The dentary is partly obscured at the anterior end, but the anteromedial corner appears to be rounded. On the medial side of the tooth positions is a distinct shelf that runs back about three-quarters of the length of the dentary. Posteriorly the dentary narrows to a point, the posterior region being an extension of the medial shelf rather than the tooth-bearing lateral edge. There appear to be several fragments of another element medial to the anterior half of the dentary. This appears to have been an elongate strip of bone and may represent a splenial.

Close to the dentary is a very small broken rib bearing a slender lateral extension, too poorly preserved to merit illustration. Fritsch interpreted this as a rib with widely separated tuberculum and capitulum but it appears to be a central portion of a rib shaft bearing a slender uncinat process, almost perpendicular to the shaft.

Systematic position.—This specimen appears to comprise the right dentary and a rib of an aïstopod tetrapod of the fam-

ily Ophiderpetontidae. The valid name for the ophiderpetontid from Nýřany is *Oestocephalus granulosus* (Fritsch, 1881), see Carroll et al. (1998: 180). *Oestocephalus* is a genus of long-skulled ophiderpetontid known from the Late Carboniferous assemblages from Newsham, Nýřany, Linton, Cannelton, Mazon Creek and Kounov. The material is described under four species but critical species-level diagnoses have not been made (Carroll et al. 1998) and the following comparisons are made with *Oestocephalus* specimens from Nýřany, Linton and Mazon Creek as figured in the recent literature and examined by the senior author.

The relatively straight, long shallow dentary with a slight medial curvature anteriorly and a lingual shelf corresponds to that of *Oestocephalus*. The lingual shelf can be seen in the type specimen of *O. amphiuminus* figured by Carroll (1998: fig. 4A). Most aïstopod specimens retain some dentary teeth but where they are lost, the condition resembles that in *L. caducum*. The apparent deep sockets where the teeth have cleanly broken off or been lost can be seen in some *O. amphiuminus* from Linton (Carroll 1998: fig. 8A). The presence of space for up to 40 teeth also corresponds to the condition in a small *Oestocephalus* skull. In large *O. amphiuminus* from Linton, there is space for about 50 teeth in each dentary (Carroll et al. 1998: 169) but this is in specimens with 30 mm long dentaries (Carroll et al. 1998: fig. 97). In a smaller *Oestocephalus* specimen from Mazon Creek (Carroll 1998: fig. 3D, E) there is space for about 40 teeth in a 16 mm dentary, only slightly larger than that of *L. caducum*, indicating that the tooth-count is the same in a similar-sized dentary. The elongate bone represented by fragments along the anterior lingual margin of the *L. caducum* dentary is consistent in size and position with the splenial of *Oestocephalus* (Carroll 1998: fig. 3E).

The rib appears to be a broken anterior trunk rib of an aïstopod in which there is a laterally directed slender uncinat process. McGinnis (1967: fig. 13) figured an anterior precaudal rib (MCZ 2204) of *Phlegethontia* with a very similar configuration. No other small Carboniferous tetrapods have such ribs.

The few known specimens of *Oestocephalus granulosus* from Nýřany are all of small individuals with skulls measurably in the 10–20 mm length range or consistent with that size, so the specimen of *L. caducum* would fall in this size range. We suggest that *L. caducum* can be treated as a junior synonym of the aïstopod *Oestocephalus granulosus* previously described by Fritsch in 1880, unless future work were to demonstrate the presence of two ophiderpetontids at Nýřany, in which case it might revert to *nomen dubium* status.

Significant referred specimens

Fritsch Orig. 246 ("*L. laticeps*" syntype)

= *Mordex laticeps*

Locality and horizon: From Třemořná, Czech Republic; Plattelkohle, Nýřany Member, Westphalian D, Late Carboniferous.

Material.—NMP M639 (= Fritsch Orig. 246). This was an articulated skeleton on a block of coal, now destroyed by pyritic decay. We can confirm that this specimen is certainly destroyed rather than lost, as in 1978, ARM was able to examine the pyritised block with some residual traces of the specimen. There are many galvanotypes of this specimen including NMP M1060. The specimen was incorporated in the description of *L. laticeps* by Fritsch (1881: 148–151, pl. 36: 1 and text-figs. 90, 91). Apart from being briefly discussed as a possible adelospondyl (= microsaur) by Steen (1938: 261) and Romer (1947: 143), no other author has referred to it directly.

Systematic position.—The specimen as figured by Fritsch (1881: pl. 36: 1) comprised an articulated skeleton about 70 mm in length, including a skull about 18 mm in length. It was the skeleton of a small dissorophoid temnospondyl with poorly or unossified centra, short straight ribs and a parasphenoid with a broad basal plate and a long rod-like cultriform process. The tail was substantially complete and comprised at least 21 caudal vertebrae. Steen (1938) and Romer (1947) suggested that this specimen was a microsaur, presumably because Fritsch figured traces of two apparent large centra in the posterior trunk. However the palate and rib structure are those of a temnospondyl and ossified centra are absent from most of the column, an unlikely situation in a small microsaur, the group being characterised by early ossification of centra (Carroll 1989). It seems likely that Fritsch's "centra" were counterpart neural arches seen in internal aspect.

There were about 21 presacral vertebrae and the humeri were elongate, both of which indicate that it was not a specimen of the micromelerpetontid *Limnogyrinus elegans* (25–26 presacrals and short humerus) *contra* Werneburg (1994). The large number of closely packed small dentary teeth and the large deep otic notch demonstrate that it is either a *Platyrhinops* or a *Mordex* larva and not a *Branchiosaurus* (fewer elongate marginal teeth, shallow notch and rarely reaching 18 mm skull length). The presence of prominent gastralia and the radius and ulna significantly shorter than the humerus show that it is not *Platyrhinops* but likely to be a juvenile of *Mordex laticeps*. It thus probably has the same taxonomic identity as the lectotype. Identification is by a process of elimination rather than by possession of unambiguous synapomorphies, so cannot be certain. Nevertheless there are no characteristics of the specimen that contradict this identity.

Fritsch Orig. 234 ("*L. macrolepis*" syntype)
= *Limnogyrinus elegans*

Fig. 8.

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

Material.—NMP M473 (= Fritsch Orig. 234). This specimen comprises a skull, pectoral girdle and scales on a single small slab (Fig. 8), and was figured by Fritsch 1881: pl. 33: 1.

Description.—NMP M473 appears as an enigmatic jumble of bones in Fritsch's figure, but is actually a small skull with displaced mandibles and associated pectoral girdle (Fig. 8).

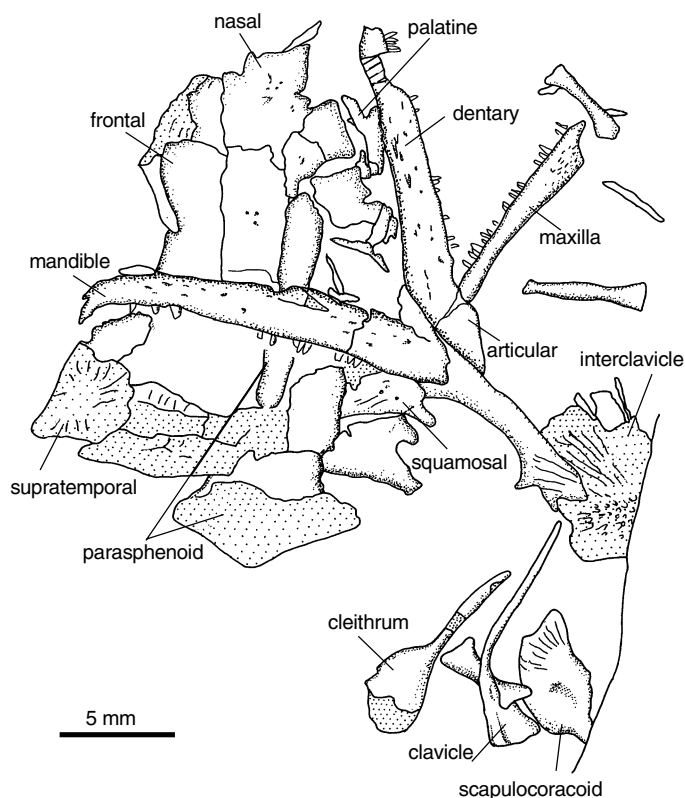


Fig. 8. *Limnogyrinus elegans* (Fritsch). NMP M473 (Fritsch Orig. 234), specimen of "*Limnerpeton*" *macrolepis*, from Nýřany, Czech Republic.

The skull is about 18 mm midline length and mainly comprises the skull roof visible in ventral aspect, together with a detached left maxilla, left palatine and fragments of the parasphenoid. The skull roof is partly obscured by other elements and partly represented by impression in the underlying coal. One nasal is more or less complete and shows this to have been an almost square bone. Both frontals are present and these are rectangular bones, about twice as long as wide. Prefrontals extend backwards lateral to the frontals but it is not clear whether they contact the postfrontals or not. The skull table can be seen in outline but only the supratemporal shape can be distinguished. The right supratemporal is represented as an impression on the coal and is an elongate element, at least one and a half times as long as wide. Part of the left squamosal is visible and suggests the presence of a large squamosal embayment. A large element just behind the squamosal has not been identified. The maxilla is a low slender bone bearing finely striate sculpturing on its dermal surface. It was slightly deeper anteriorly narrowing concavely to a point where it met the premaxilla ventral to the external naris. It bears a large number of small, closely spaced, elongate pointed teeth. At least twenty teeth are present on the maxilla but there was space for at least thirty teeth.

The left palatine is visible as a small bilobed element wedged between the left prefrontal and the dentary. It had a triangular body and two small anterior rami bracketing the

posterior region of the choana. No trace of a palatine fang can be seen but the preservation is poor. The parasphenoid is represented by the middle portion of the shaft of the cultriform process and by some traces of the posterior region of the basal plate.

The right mandible is represented by the dentary and the articular in articulation, while the left dentary is accompanied some poorly defined postdentary elements of the left mandible. The mandible was about 22 mm long. The dentary is long and slender and bears light pitting over its lateral surface. The teeth are small, pointed and slightly elongate. Only scattered teeth are present but their size and spacing suggests that there was space for 45–55 teeth in each dentary. The posterior region of the left dentary is largely obscured but a slightly raised coronoid region is exposed. Behind the right dentary is the articular seen in internal aspect. There is a long adductor fossa margin marked by a slightly concave dorsal edge, followed by the articular condyle seen in medial aspect.

The pectoral material present includes the moulds of most of the interclavicle and the right cleithrum, together with the right clavicle, the scapular region of the scapulocoracoid and the humerus (Fig. 8). The interclavicle was a rhomboid, slightly longer than wide and relatively large for that of a small dissorophoid. It bore pitting on the medial dermal surface and long anteroposterior striations along the anterior region. The cleithrum and clavicle are relatively similar. The cleithrum may be recognised by its moderately expanded oval blade and a stout stem about the same length as the blade. The cleithrum blade appears to have been about one quarter of the area of the interclavicle. Only the base of the expanded clavicular blade is visible, recurved where it would have capped the interclavicle, and attached to a longer stem than the cleithrum. The scapulocoracoid was poorly ossified and the preserved portion appears to be the reniform scapular region. The humerus is relatively small and narrow-waisted, and the ends were probably not fully ossified, appearing concave.

Systematic position.—Orig. 234 appears to be a poorly preserved specimen of the micromelerpetontid *Limnogyrinus elegans*. It is a dissorophoid with light striate dermal sculpture, elongate supratemporals, a relatively large interclavicle with anterior spikes, and space for 30 small, slightly columnar teeth on the maxilla and 45–55 on the dentary. These features all identify it as *Limnogyrinus elegans* in contrast to the other Nýřany dissorophoids.

Fritsch Origs. 242, 243 (“*L. macrolepis*” syntypes)
= Amphibamidae *incertae sedis*

Fig. 9.

Material.—NMP M474 (= Fritsch Orig. 243), a small maxilla (Fig. 9A, B), figured by Fritsch 1881: pl. 33: 2. NMP M475 (= Fritsch Orig. 242), a small maxillary fragment, figured by Fritsch 1881: pl. 33: 3.

These two specimens are both jaws that appear to have belonged to amphibamid temnospondyls. NMP M474 (Fig. 9A) is an isolated right maxilla about 14 mm long, with space

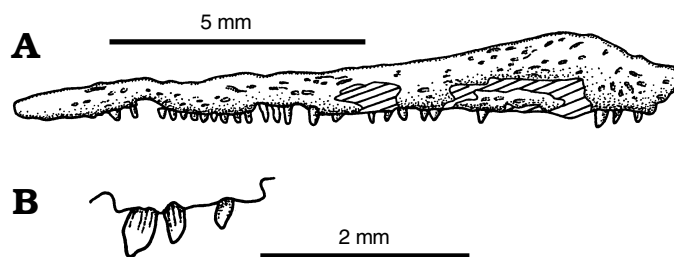


Fig. 9. Amphibamidae *incertae sedis*. NMP M474 (Fritsch Orig. 243), a right maxilla, syntype of “*Limnerpeton*” *macrolepis*, from Nýřany, Czech Republic. A. Entire specimen. B. Anterior teeth showing shape and pseudo-canine condition.

for about 55 teeth, approximately half of which are present. The maxilla is slender, slightly expanded anteriorly and bears fine striations over its outer surface. The teeth are flattened labio-lingually with blunt tips and grooves extending up from the base (Fig. 9B). The tooth shape is that of a *Platyrhinops*-like amphibamid although the teeth cannot be distinguished as bicuspid or monocuspid. The specimen is not strictly determinate but, like the holotype of *Limnerpeton modestum*, appears to belong to the Amphibamidae. NMP M475 is a tiny fragment of maxilla or dentary bearing five teeth that are closely packed blunt cones bearing terminal striations. They also most closely resemble the teeth of *Platyrhinops lyelli* and this is probably also a fragment of an amphibamid tooth-bearing bone.

Bulman and Whittard’s “*B. salamandroides*” material
= *Limnogyrinus elegans*

Fig. 10.

Locality and horizon: Both from Nýřany, Czech Republic; Gaskohle, Nýřany Member, Westphalian D, Late Carboniferous.

Material.—UMZC T17, anterior region of a small temnospondyl in palatal aspect (Fig. 10A) figured by Bulman and Whittard (1926: text-fig. 5B) as D.M.S. Watson specimen no. 17. UMZC T18, a small temnospondyl in lateral and ventral aspect (Fig. 10B) figured by Bulman and Whittard (1926: text-fig. 5A) as D.M.S. Watson specimen no. 18.

Systematic position.—These two specimens were described and figured by Bulman and Whittard (1926) as examples of *Branchiosaurus salamandroides*. They were referred to *Limnogyrinus elegans* by Milner (1986) and listed in the synonymy of *Limnogyrinus elegans* by Werneburg (1994). UMZC T17 was figured by Bulman and Whittard as a reconstructed palate with an unusually marked basal plate to the parasphenoid. This is in fact a large interclavicle superimposed on the basal plate and the markings are those of the dermal surface of the interclavicle with the semi-circular slots for the overlapping clavicles (Fig. 10A). The large squarish interclavicle, narrow clavicles and relatively small humeri, and cultriform process with a denticle patch at its base, all indicate that this is a specimen of *Limnogyrinus elegans*. The suggestion of a row of lateral palatal teeth in Bulman and

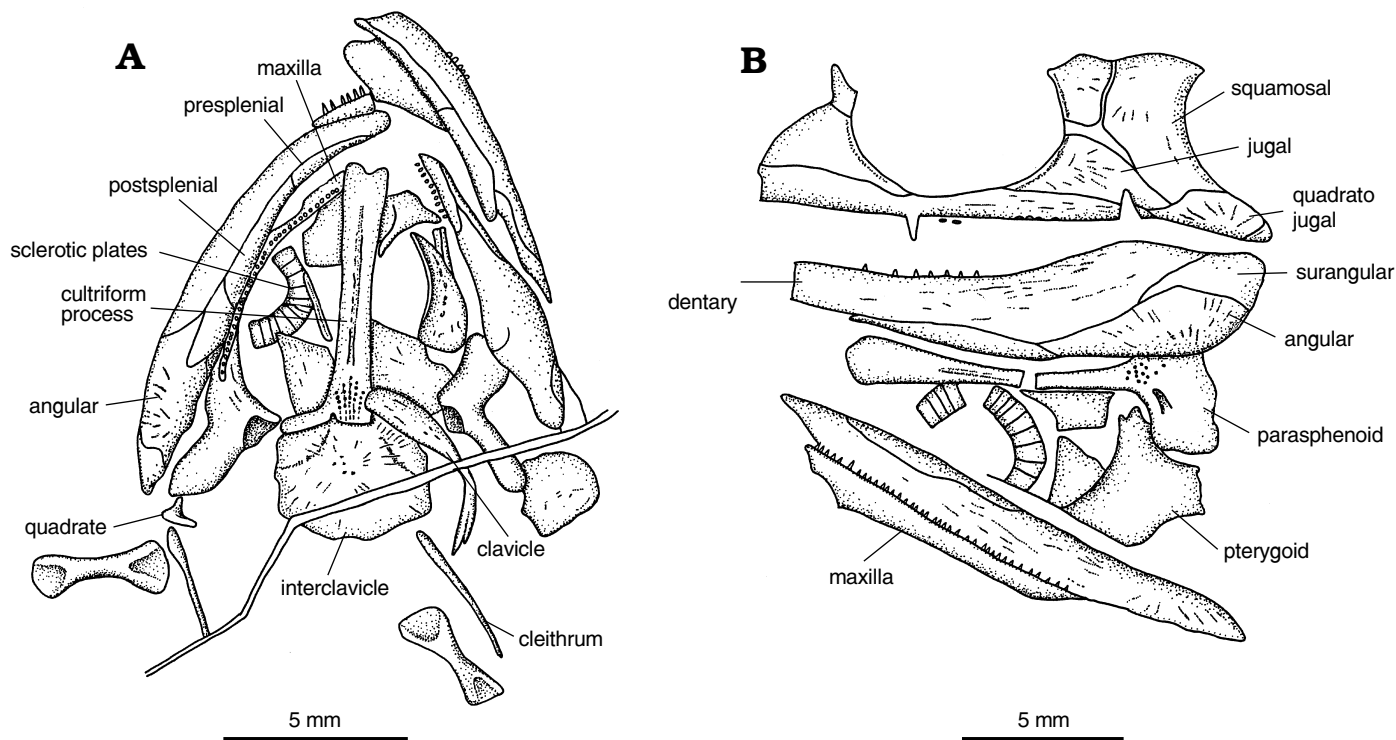


Fig. 10. *Limnogyrinus elegans* (Fritsch). A. UMZC T17 from Nýřany, Czech Republic. Specimen figured as *Branchiosaurus salamandroides* by Bulman and Whittard (1926: text-fig.5B). B. UMZC T18 from Nýřany, Czech Republic. Specimen figured as *Branchiosaurus salamandroides* by Bulman and Whittard (1926: text-fig.5A).

Whittard's reconstruction is based on the right maxillary dentition seen end on and superimposed on the palate (Fig. 10A). UMZC T18 was figured as a posterior left side of skull but the complete postcranium is present. The maxilla bears about 40 spaced teeth and the parasphenoid has a patch of denticles at the base of the cultriform process (Fig. 10B). These are both characteristics of *Limnogyrinus elegans* and not *Branchiosaurus salamandroides* and this specimen can be identified unambiguously as another *Limnogyrinus*. Neither of Bulman and Whittard's specimens is *Branchiosaurus salamandroides* and should be disregarded in considerations of that taxon.

Stehlík's "*L. obtusatum*" specimens

Locality and horizon: All from Nýřany, Czech Republic; Gaskohle, Nýřany Member, Westphalian D, Late Carboniferous.

Material.—Five specimens in the collection of the Geological Institute of Jan Masaryk University, Brno, described by Stehlík (1924). The collection still exists (J. Klembara pers. comm.) but we have not had the opportunity to examine this material.

Comment.—Stehlík described five specimens (as Specimens 1–5) which he attributed to *L. obtusatum*. Unfortunately his descriptions are not very informative, neither is his only figure (Stehlík 1924: fig. 6) of an ilium and hind limb. However, Stehlík categorised *Limnerpeton* as a lepospondyl rather than a phyllospondyl (as most small or juvenile temnospondyls

were then classified) which suggests that his material may have been microsaurian. He noted that the interclavicle "ran backwards into a flat, quite broad spur", which could be a description of the posteromedial spike of bone found in the interclavicle of forms such as *Microbrachis*. Fritsch's *obtusatum* specimen proved to be a *Microbrachis* and it seems possible that at least some of Stehlík's specimens were *Microbrachis* as well.

Discussion

The results of this study may be summarised in terms of the revised taxonomic identities, as follows.

Temnospondyli: Dissorophoidea

Amphibamidae.—*Limnerpeton modestum* is based on an amphibamid mandible and two of the referred "*L.*" *macrolepis* specimens are amphibamid maxillae or fragments. None is convincingly determinate below family level. However the types of "*Limnerpeton*" *laticeps* and "*L.*" *macrolepis* are not amphibamids as previously suggested (Milner 1986). There are fewer amphibamid specimens from Nýřany than hitherto believed but still at least six specimens that appear to represent a species indistinguishable from *Platyrhinops lyelli* from Linton, Ohio (Clack and Milner 1994).

Trematopidae.—The senior author has been preparing a redescription of *Mordex calliprepes* based on three specimens, namely the type—a 40 mm long skull—and parts of two much larger skulls (Milner 1986). One of the most significant conclusions from the present work is that several other small temnospondyls are juveniles or larvae of this taxon. These certainly include the lectotypes of “*L.*” *laticeps* and “*L.*” *macrolepis*, and several of Fritsch’s key *Branchiosaurus salamandroides* specimens together with the referred “*L.*” *laticeps* from Třemošná. The recognition of these specimens as *Mordex* juveniles not only requires a new combination for the taxon with *laticeps* as the senior species name, but also reveals a possible growth series (skulls from 9 mm to 120 mm) of a primitive dissorophoid with a large terrestrial adult. This will be described and discussed in a later publication.

Micromelerpetontidae.—As well as the type of *Limnogyrinus elegans*, a referred specimen of “*L.*” *macrolepis* belongs here, as do Bulman and Whittard’s two *Branchiosaurus* specimens.

Branchiosauridae.—The removal of Bulman and Whittard’s specimens from the hypodigm of *B. salamandroides* was already noted by Werneburg (1994). The discovery that several of the middle-sized dissorophoids are part-grown specimens of *Mordex laticeps*, leads to the possibility that some of the small material attributed to *Branchiosaurus salamandroides* may be larval *Mordex*. Work in progress by the authors confirms that this is so and that a major reassessment of *B. salamandroides* is necessary.

Aïstopoda

Ophiderpetontidae.—“*Limnerpeton*” *caducum* appears to be a further specimen of the small ophiderpetontid *Oestocephalus granulatus* known from a small number of specimens in the Nýřany assemblage.

Microsauria

Tuditaniae.—“*Limnerpeton*” *difficile* appears to be a second small specimen of the tuditanid microsauro *Crinodon limnophyes* previously known only from a single large skull.

Microbrachidae.—“*Limnerpeton*” *obtusatum* is a specimen of the common microsauro *Microbrachis pelikani* as argued by Carroll and Gaskill (1978).

Tetrapoda incertae sedis

The identity of “*Limnerpeton*” *dubium* from Kounov is unresolved in the absence of more complete material from this locality.

Although this may seem a rather pedantic exercise in interpreting a series of poor 19th century name-bearing specimens, it is necessary because of some of the taxonomic and faunal implications of the results. Firstly, this material was named early in the study of the Nýřany fauna and there was

the potential that some of the “*Limnerpeton*” species might prove to be senior synonyms of other taxa. This is unambiguously so in the case of “*Limnerpeton*” *laticeps* which proves to be the senior species name for the genus *Mordex*. Other species are either junior synonyms or insufficiently determinate to be made senior synonyms.

Secondly, some of this material, including the non-type specimens discussed here, has been misassigned to other taxa by Bulman and Whittard (1926), Milner (1980, 1986), and Werneburg (1994), and this has complicated attempts to understand the precise anatomy of this assemblage of the most basal members of several dissorophoid families. Until the most primitive branchiosaurids, micromelerpetontids, amphibamids and trematopids can be described and defined unambiguously, we stand little chance of establishing the interrelationships of the dissorophoid families. This study is the first stage in a planned program of redescription of these four taxa in order to understand dissorophoid origins and relationships.

Thirdly, the identification and reidentification of these specimens shifts our perception of the content of the Nýřany assemblage from the assessments of frequency proposed by Milner (1980, 1986). It appears that there were several small *Mordex* specimens, larvae or juveniles, hitherto unrecognised, whereas the amphibamid *Platyrhinops* is actually more rare and represented by only 4–5 specimens. Several specimens assigned to *Branchiosaurus* are actually *Limnogyrinus* or tiny *Mordex* and strictly determinate *Branchiosaurus* specimens are probably less common than previously believed.

The tetrapod fauna at Nýřany includes four dissorophoid temnospondyls as proposed by Milner (1986). They comprise the primitive branchiosaurid *Branchiosaurus salamandroides*, the primitive micromelerpetontid *Limnogyrinus elegans*, the amphibamid *Platyrhinops* cf. *lyelli* and the primitive trematopid *Mordex laticeps*. These represent four of the five major dissorophoid families and demonstrate that the group had already diversified by the late Westphalian. The Nýřany dissorophoids are less structurally diverse than their later relatives but it is likely that stem-dissorophoids will eventually be found in the early Westphalian.

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