

# A REVISION OF PARAMBLYPTERID AND AMBLYPTERID ACTINOPTERYGIANS FROM UPPER CARBONIFEROUS–LOWER PERMIAN LACUSTRINE DEPOSITS OF CENTRAL EUROPE

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**ABSTRACT.** The descriptions and diagnoses of the type species of *Paramblypterus*, *Paramblypterus decorus*, and the type species of *Amblypterus*, *Amblypterus latus*, which is very similar to *Paramblypterus*, are revised. The skulls of *Paramblypterus decorus*, *P. duvernoyi*, and *A. latus* are restored in three-dimensional models, and their diagnoses are emended. Intra-specific variation of *P. decorus* and *P. duvernoyi* concerns dermohyal, ‘suborbital’ and extrascapular bones, and dermohyal, rostral, parietal and extrascapular bones, respectively. Owing to poor preservation, patterns of variation could only be recognised in one specimen of *A. latus* regarding the extrascapular series and the posterior edges of the scales. All data on *Amblypterus* and *Paramblypterus* were entered into a PAUP analysis. Fifty taxa of lower actinopterygians were analysed for 57 characters. According to this analysis, *Paramblypterus* and *Amblypterus* are contained in the same family, the Amblypteridae. *P. gelberti* and *P. duvernoyi* are the sister group of *P. rohani* and *P. decorus*, and the genus *Paramblypterus* is the sister taxon of the genus *Amblypterus*.

**KEY WORDS.** morphology, intra-specific variation, systematics, lower actinopterygians, amblypterids, paramblypterids, Permo-Carboniferous.

PARAMBLYPTERID and amblypterid fishes are the most abundant fish fossils in Upper Carboniferous–Lower Permian lacustrine deposits of Europe (Agassiz 1833; Goldfuss 1847; Egerton 1850; Heckel 1861; Weiss 1864; Traquair 1877; Sauvage 1888, 1894; Woodward 1891; Fritsch 1895; Gardiner 1963; Blot 1966; Heyler 1969; 1976; Stamberger 1976, 1993; Gad 1988). Even though they are of great importance for our understanding of early actinopterygian evolution, their morphology and ecology have not yet been described in detail. Most of the specimens are poorly preserved, especially in the snout region. This study presents a comprehensive cladistic analysis of these fishes, with new information on certain genera that have not been included in previous studies.

Depending on the author, *Amblypterus* and *Paramblypterus* either belong to two families (Blot 1966; Heyler 1976; Stamberger 1976, 1993; Gad 1988) or are united in one family, the Amblypteridae (Gardiner 1963). This discussion was caused by Gardiner (1963), who revised the genus *Amblypterus* without having examined the type specimen, since it was thought to be lost. Instead, he examined new specimens without designating a neotype. The subgenus *Paramblypterus* was given generic rank by Blot (1966), who put it in a monotypic family of its own, the Paramblypteridae, with *Paramblypterus decorus* as the type species. When Heyler (1976) rediscovered the type specimen of *Amblypterus lateralis* (synonym *A. latus*) for a revision of the genus *Amblypterus*, he noticed that it did not match the description of *Amblypterus* given by Gardiner (1963), but instead resembles *Paramblypterus*. Therefore, the definition of either *Amblypterus* or *Paramblypterus* became ambiguous and the question of whether they belong in a single or separate families remained to be solved. *Paramblypterus rohani* from the Krknose Piedmont Basin of the Czech Republic and *Paramblypterus gelberti* from the Saar-Nahe Basin of south-west Germany were revised by Stamberger (1976) and Gad (1988) respectively and, for lack of a clear diagnosis of *Amblypterus*, were included in the genus *Paramblypterus*. *P. rohani* (Heyler 1971) has also been described from Surmoulin, France. Stamberger

(1993) assigned certain specimens from the Krknose Piedmont Basin of the Czech Republic to the species *P. gelberti*. Other *Paramblypterus* species such as *P. caudatus*, *P. luridus*, *P. obliquus*, and *P. reussi* from the Czech Republic (Stamberg 1973, 1976), and *P. comblei* and *P. gaudryi* from France (Heyler 1969), are known from only a few specimens, which makes it difficult to evaluate their species designation.

In this study, the type species of both *Paramblypterus* (*P. decorus*) and *Amblypterus* (*A. latus*) are revised as a basis for the revision of the genera *Paramblypterus* and *Amblypterus*. The skull and snout region of *Paramblypterus decorus* and *Amblypterus latus*, and the palate of *P. gelberti* are reconstructed. The intraspecific variation of the skull of these species is documented and compared to *Paramblypterus* species described earlier. In addition, the postcranial elements of *Paramblypterus duvernoyi* are reconstructed. Skulls of *P. decorus* and *A. latus* are reconstructed and their descriptions are revised. Data obtained from the revision of *P. duvernoyi*, *P. gelberti*, *P. decorus*, and *Amblypterus latus* were entered into a PAUP analysis in an attempt to resolve their ambiguous systematics.

#### GEOLOGY AND PALAEOECOLOGY

The Rotliegend (Lower Permian) of the Saar-Nahe Basin is divided into an upper part consisting of the red beds after which it is named, and where lake sediments are rare, and a lower part which is of greyish colour and in which lake deposits are abundant (Boy 1994). These lake deposits yield a rich fauna (Boy 1976). Up to now, molluscs (Boy 1976), crustaceans (Boy 1976; Martens 1984), chondrichthyans (e.g. Hampe 1989, 1994), acanthodians (Heidtke 1990), certain actinopterygians (Gardiner 1963; Gad 1988; Schindler 1993), lungfishes (Heidtke 1986), 'osteolepiforms' (Schultze and Heidtke 1986), and amphibians (e.g. Boy 1972, 1978) have been described. The Saar-Nahe Basin was the largest area of subsidence of the Lower Rotliegend and covered at least 100 by 40 km along the southern margin of the Rheinische Schiefergebirge (Boy 1994). Irregular subsidence caused depressions of differing sizes, where water was trapped and lakes started to form (Boy 1994). During the Early Permian, central Europe was located at 10–20 degrees North, and the climate is thought to have been tropical to subtropical (Boy, pers. comm. 1998). Depending on the locality, specimens are preserved either complete or disarticulated (Boy 1998). In the profundal facies of the lakes, fine lamination shows that sedimentation rates were low and currents were absent on the bottom (Boy, pers. comm. 1998). Completely articulated skeletons indicate that the lake was deep, because in tropical climates pressure of overlying waters, which increase with the depth of a lake, prevent bodies from floating upwards and being damaged. In contrast, fossils from shallower lakes, i.e. not deeper than 10–20 m, are preserved disarticulated because they floated. High abundances of disarticulated, but otherwise unaffected specimens, point to periods of low sedimentation rate. On the other hand, areas of high sedimentation rates yield few fossils because they are too widely scattered. Distinct patterns in the arrangement of disarticulated fossils are a result of predation or the action of currents and can be identified as such (Elder and Smith 1984).

Except for specimens of *Paramblypterus decorus*, which are from the Commentry Basin, the fossil fishes examined here are from the Saar-Nahe Basin. They are from stratigraphically high units of the Lower Rotliegend, the Lauterecken-Odernheim Formation, which has been divided into ten units by Boy *et al.* (1990). The lakes that are dealt with here belong to the three topmost units (L-O 8–L-O10), and to one lower unit, L-O 6 (Text-fig. 1).

#### *Paramblypterus gelberti*

Lake Pfarrwald and Lake Jeckenbach yield specimens of this species. Sediments of Lake Jeckenbach consist of very finely laminated black shales containing a certain amount of carbonate detritus (Boy *et al.* 1990). The lake was deep and large, about 22–80 km in diameter. The litho- and biofacies of Lake Pfarrwald, which are known from only a few localities, are similar to those of Lake Jeckenbach (Boy *et al.* 1990).

#### *Paramblypterus duvernoyi*

Specimens examined here are from Lake Odernheim, Lake Kappeln, Lake Klauswald, and phases I and II of Lake Humberg.

| Ma  | global stratigraphy | European stratigraphy | group                     | abbr.                | lakes  |
|-----|---------------------|-----------------------|---------------------------|----------------------|--|
| 290 | Sakmarian           | Saxonian              | Nahe Group                | N4<br>N3<br>N2<br>N1 | Lake Sobernheim<br>Lake Jakobsweiler   |
|     |                     |                       | Thallichtenberg Formation | T                    | Lake Boos  |
|     |                     |                       | Oberkirchen Formation     | Ob                   |  |
|     |                     |                       | Disibodenberg Formation   | D                    | Lake Körborn   |
|     |                     |                       |                           | L-O10                | Lake Humberg ★   |
|     |                     |                       | Odernheim Formation       | L-O9                 | Lake Klauswald ★<br>Lake Pfarrwald ★<br>Lake Kappeln ★                       |
|     |                     |                       |                           | L-O8                 | Lake Ruthweiler<br>Lake Odernheim ★  |
|     |                     |                       | Jeckenbach Formation      | L-O7                 |  |
|     |                     |                       |                           | L-O6                 | Lake Jeckenbach ★<br>Lake Niederkirchen<br>Lake Raumbach                     |
|     |                     |                       |                           | L-O5                 |  |
|     |                     |                       |                           | L-O4                 | Lake Breitenheim<br>Lake Ulmet   |
|     |                     |                       |                           | L-O3                 | Lake Meisenheim<br>Lake Grumbach<br>Lake Schorrenwald<br>Lake Wiesweiler     |
|     |                     |                       | Lauterecken Formation     | L-O2<br>L-O1         |  |
|     |                     |                       | Quirnbach Formation       | Q                    | Lake Roßbach<br>Lake Hohenöllen<br>Lake Immetshausen<br>Lake Stiehlberg      |
|     |                     |                       | Wahnwegen Formation       | W                    | Lake Nerzweiler  |
|     |                     |                       | Altenglan Formation       | A                    | Lake Hirschfeld<br>Lake Reckweilerhof  |
|     |                     |                       | Remigiusberg Formation    | R                    | Lake Theisbergstegen<br>Lake Gimbsbach                                       |
| 300 | Gzhelian            | Stephanian            | Breitenbach Formation     | BR                   | Lake Godelhausen<br>Lake Altenkirchen<br>Lake Habach<br>Lake Oberw.-Tiefenb. |

TEXT-FIG. 1. Sequence of lakes of the Lower Rotliegend (Lower Permian) of southwest Germany.

*Lake Odernheim.* This lake was fairly large and stretched across 760 km<sup>2</sup> (Stapf 1990). Its depositional environment was similar to that of Lake Jeckenbach and Lake Kappeln (Boy, pers. comm. 1998).

*Lake Kappeln.* The very finely layered sediments of Lake Kappeln consist of black shales containing a certain amount of carbonate detritus (Boy *et al.* 1990). The lake was deep and large, about 22–80 km in diameter with an anoxic bottom layer (Boy 1994).

*Lake Klauswald.* Sediments of this lake are restricted to small areas. Owing to the limited availability of localities, its geology and ecology have not yet been studied in detail. Lake Klauswald was supposedly fairly deep and yields either completely preserved or fragmented fossils (Boy, pers. comm. 1998).

*Lake Humberg.* This is the largest of the lakes examined here, having covered an area of 3400 km<sup>2</sup> (Stapf 1990). Its deposits can be found throughout the Saar-Nahe Basin but they are best known in the north-eastern part (Boy 1994). Lake Humberg existed over a longer period of time than the other lakes, and according to Boy (1994) four depositional stages can be distinguished. In phase I, the lake was deepest and similar to lakes Jeckenbach and Kappeln. In phase II, sedimentation stayed essentially the same, but less carbonate detritus was deposited.

#### *Amblypterus latus*

This species is found in phase IV of Lake Humberg. This phase lasted over a longer period of time than the other stages (Boy, 1994). Owing to subsiding of the basin, the lake deepened. Sedimentation was dominated by deltaic influence, causing thicker, alternating laminae of clay and finely grained silt (Boy *et al.* 1990). The beds are as much as 10–20 m thick; these are the so-called ‘Lebacher Toneisensteinlager’ where most of the fossils are preserved in siderite nodules.

#### *Paramblypterus decorus*

Specimens are from Lake Commentry, which lies in the Commentry Basin west of Lyon within the Massif Central of France. The basin arose along a fault caused by the Hercynian Orogeny during the Late Carboniferous (Blot 1966) where tectonic activity resulted in subsidence of the area and the formation of limnic basins (Poplin 1994). The palaeoenvironment was fluvial, lacustrine, and swampy with equatorial conditions (Poplin 1994). Lake Commentry covered an area of 10 × 3 km (Blot 1966). Fossils are often preserved in phosphate nodules (Poplin 1994).

### SYSTEMATIC PALAEONTOLOGY

*Institutional abbreviations.* Specimens examined are deposited in the following museums and collections: BMNH, The Natural History Museum, London; BSM, Bayrische Staatssammlung für Geologie und Paläontologie, Munich; GPIM, Geologisch-Paläontologisches Institut Mainz; MHNC, Museum Historiae Naturalis Casselense, Kassel; MB, Museum für Naturkunde der Humboldt-Universität, Berlin; MNHN, Muséum National d’Histoire Naturelle, Paris; NHM/LfN, Landessammlung für Naturkunde Rheinland-Pfalz, Naturhistorisches Museum Mainz; PIB, Paläontologisches Institut, Bonn; PMNB, Pfalzmuseum für Naturkunde, Bad Dürkheim; SMF, Forschungsinstutit und Natur-Museum Senckenberg, Frankfurt/Main; USGP, Université de Strasbourg, Laboratoire de Géologie et Paléontologie; MSS, Museum der Saarbergwerke.

*Preparation and reconstruction of specimens.* All specimens are preserved as compressions flattened during fossilisation. Surface structure, such as sculpturing of the skull roofing bones and scales, is present on many specimens. A Wild M8 and a Cetis microscope equipped with a camera lucida were used to draw the specimens. The best preserved specimens of *P. decorus*, *P. duvernoyi*, and *A. latus* were used for three-dimensional restoration-drawings. The drawings of the bones were transferred onto thin paper which was melted onto plates of bees’ wax. The bones were cut out and re-assembled in three-dimensional models which were then photographed. Line drawings of the photographs were made, enlarged, redrawn with wax pencils and ink and reduced to their original size.

*Measurements.* Frequently, the depth of maxilla, opercle, and subopercle, or length of the head have been used for diagnosis (e.g. Lowney 1980; Kazantseva-Selezneva 1981a). This did not work for paramblypterid species examined here, because the shapes of the bones are either too variable or disarticulated. Instead, drawings of the bones to be examined were digitised in AUTOCAD 12 and the area and circumference were calculated. For establishing D-values, the outlines of the scales were also digitised

TABLE 1. Terminology of dermal cranial bones.

| Terminology used here      | Terminology used elsewhere  |
|----------------------------|---|
| Dermosphenotic 1           | Dermosphenotic (e.g. Kazantseva-Selezneva 1981b)  |
| Dermosphenotic 2           | (Superior) infraorbital (e.g. Stemberg 1976; Blot 1966)   |
| Jugal 1                    | (Inferior) infraorbital (e.g. Gardiner 1963; Schindler 1993)  |
| Jugal 2                    | (Posterior) infraorbital (e.g. Gardiner 1967; Gad 1988)   |
| Lacral                     | (Anterior) infraorbital (e.g. Gardiner 1963; Gad 1988)  |
| Lateral extrascapulars 2–4 | Postparietals (e.g. Blot 1966)  |
| 'Nasal' or 'nasal 1'       | Nasal (e.g. Nielsen 1942)   |
| 'Nasal 2'                  | Supraorbital or superoantorbital (e.g. Heyler 1969; Stemberg 1976)                                    |
| 'Nasal 3'                  | Antorbital (e.g. Lund and Poplin 1997)  |
| Parietal                   | Frontal (e.g. Long 1988)  |
| Postparietal               | Parietal (e.g. Taverne 1997)  |
| Premaxilla                 | Rostro-premaxillo-antorbital (e.g. Poplin and Lund 1997)  |
| Supratemporal              | Intertemporo-supratemporal, dermopterotic, or tabular (e.g. Jessen 1968; Schaeffer 1984; Lowney 1980) |

in Autocad 12 and their area calculated. D-values can be used to distinguish shapes by comparing the area of a circle with the same circumference (L) as the object in question (Schmidt-Kittler 1984, 1986). D is a descriptive parameter which equals the area of the according circle divided by the area of the shape (F).

$$D = \frac{L^2}{4\pi \cdot F}$$

Objects with an area similar to that of a circle have D-values close to 1. More complex shapes lead to higher D-values. Trunk length (TL) was measured from the posterior margin of the supracleithrum to the centre of the caudal fin. The first ten scales posterior to the supracleithrum were measured for establishing the 10S (i.e. 10 scale rows) parameter. The caudal peduncle was measured where it is narrowest. Body depth was measured posterior to the skull where the body is deepest. Scales were counted along the lateral line: (1) from supracleithrum to caudal scale inversion; (2) from supracleithrum to the origin of the fins; and (3) between ridge scales of dorsal and pelvic fin. Where possible, fin rays were counted at the base of the fins.

### Terminology

The terminology follows Arratia and Schultze (1991) and Arratia and Cloutier (1996). Other terminologies set off by quotation marks, except for the 'nasal', refer to earlier works (e.g. Blot 1966; Heyler 1969) and employ the common terminology for paramblypterid fishes. Different terminologies are currently being used for dermal cranial bones (e.g. Arratia and Cloutier 1996; Poplin and Lund 1997). Corresponding terminology to that adopted herein is listed in Table 1. Where species other than *Paramblypterus* and *Amblypterus* are used for comparison, the terminology used in the relevant publication is given in parentheses, e.g. the supratemporal (dermopterotic) of *Paramblypterus comblei*. Bone terminology adopted herein differing from common usage is explained below.

*Nasal, supraorbital, and preorbital.* *Cheirolepis* is the only actinopterygian fish species that has three bones lateral to the rostral element(s) (Pearson 1982; Arratia and Cloutier 1996). However, *Paramblypterus* has a very similar bone arrangement. In most actinopterygians only one bone lateral to the rostral, the 'nasal', borders the anterodorsal margin of the orbit. If the bone arrangement in *Cheirolepis* is taken as the primitive condition, it appears that the 'nasal' is a compound bone formed by fusion of the nasal with the supra- and preorbital, which split up secondarily in *Paramblypterus*. Among *Paramblypterus*, different proportions of these bones can be observed, and in one specimen of *P. duvernoyi* three bones are actually present lateral to the rostral (Dietze 1999, fig. 5B, D, I), which further corroborates this assumption. Therefore, the term 'nasal' is applied for the compound bone, and 'nasal 1–3' for elements considered split up secondarily.

*Supratemporal, intertemporal, and dermosphenotic.* In Devonian species of lower actinopterygians, such as *Cheirolepis trailli*, *Howqualepis rostridens*, or *Moythomasia nitida*, supratemporal, intertemporal, and dermosphenotic are present (Jessen 1968; Pearson 1982; Long 1988). Subsequently, the intertemporal gets either fused to dermosphenotic or supratemporal, or is lost. However, owing to different proportions of supratemporal and dermosphenotic, it is impossible to determine what part of the intertemporal bone fused to which bone, or if it had fused to any bones at all. In the absence of ontogenetic evidence, if an intertemporal bone is absent the bones present are identified as dermosphenotic and supratemporal for the anterior and posterior element, respectively. If two bones are present anterior to the supratemporal without either resembling an intertemporal element, they are identified as dermosphenotic 1 and dermosphenotic 2 according to their topography.

*Jugal.* The jugal starts out as a single element among lower actinopterygians, e.g. *Cheirolepis* (Pearson and Westoll 1979), *Mimia* or *Moythomasia* (Gardiner 1984), and subsequently is split in two, e.g. *Cornuboniscus* (White 1939), ‘Fubarichthys’ (Lowney 1980) or *Karaoungaria* (Kazantseva-Selezneva 1981b). Accordingly, these bones are referred to as jugal 1 and jugal 2 for the ventral and dorsal element, respectively.

*Premaxilla.* If two bones are present between lacrimal, rostral, and ‘nasal’ or corresponding elements, they are commonly referred to as rostropremaxillary and antorbital depending on the course of the infraorbital canal and the presence of teeth (e.g. Poplin and Lund 1997). Accordingly, if only one element is present, it is identified as premaxillo-antorbital. However, if the bone arrangement of Devonian taxa is the plesiomorphic condition it appears to be the other way around. Devonian actinopterygians have a single, tooth-bearing bone forming the anteriormost part of the jaw margin between lacrimal, rostral, and ‘nasal’ or corresponding elements (e.g. Jessen 1968; Pearson 1982; Long 1988; Arratia and Cloutier 1996). This is further corroborated by the course of the infraorbital sensory canal, which in *Cheirolepis trailli* branches on the premaxilla and not on the pre- or antorbital (Pearson 1982). Accordingly, if two bones are present they are identified as anterior/posterior premaxilla or ventral/dorsal premaxilla, depending on how they are divided. This applies to the species used for establishing relationships among lower actinopterygians. In *Paramblypterus* and *Amblypterus* an undivided premaxilla is present.

*Remarks.* Dermohyals are identified by being fused to the hyomandibula. In the material examined, usually most of the hyomandibula is covered by the dermohyal(s) and surrounding bones and only a small portion of it can be observed. In one specimen (Dietze 1999, fig. 2A) the dorsal portion of the hyomandibula with the dermohyal attached to it can be seen.

In general, ‘median’ refers to unpaired elements, e.g. ‘median gular’, along the midline, whereas ‘medial’ is used where more than one element is present. Since the extrascapular along the midline can be divided, it is called ‘medial extrascapular’.

Class OSTEICHTHYES Huxley, 1880  
Subclass ACTINOPTERYGII Cope, 1887  
Family AMBLYPTERIDAE Romer, 1945

*Emended diagnosis.* Medial extrascapular single. Medium or deep maxillary plate. ‘Spiracular’ bone present. Single premaxilla. Two jugals. Two dermosphenotics. Laniary teeth absent; maxillary and dentary teeth in one series. Mouth terminal. Little ornamentation of scales.

#### Genus PARAMBLYPTERUS Sauvage, 1888

*Emended diagnosis.* Genus of amblypterid that differs from the other genus in the family (*Amblypterus*) by the following characters: ‘Nasal’ split up secondarily. Dermohyal not present as a single ossification. More than two ‘suborbitals’. Seven to nine branchiostegal rays. Gap between opercular series and skull roofing bones absent. Duplication of the extrascapular series present. Scales serrated weakly, with little ornamentation.

*Type species.* *Paramblypterus decorus* (Egerton, 1850) designated by Blot, 1966.

*Species included.* *Paramblypterus duvernoyi* (Agassiz, 1833), *Paramblypterus gelberti* (Goldfuss, 1847), *Paramblypterus decorus* (Egerton, 1850), and *Paramblypterus rohani* (Heckel, 1861). Other nominal species in the genus (*P. caudatus*, *P. comblei*, *P. gaudryi*, *P. luridus*, *P. obliquus*, and *P. reussi*) either represent junior synonyms, or are known too poorly to allow for a comparison.

### *Paramblypterus decorus* (Egerton, 1850)

Text-figures 2–4, 5c, 6–7

- 1850    *Palaeoniscus decorus* Egerton, p. 7.
- 1877    *Amblypterus decorus* Traquair, p. 558.
- 1966    *Paramblypterus decorus* (Sauvage); Blot, p. 16.

*Holotype.* BMNH-P 607 and counterpart BMNH-P 3420, London. Well preserved specimen of 152 mm trunk length wanting part of the tail, which is present on the counterpart impression.

*Type locality.* Commentry, France.

*Type horizon.* La Grande Couche de Commentry, Middle Stephanian, Upper Carboniferous.

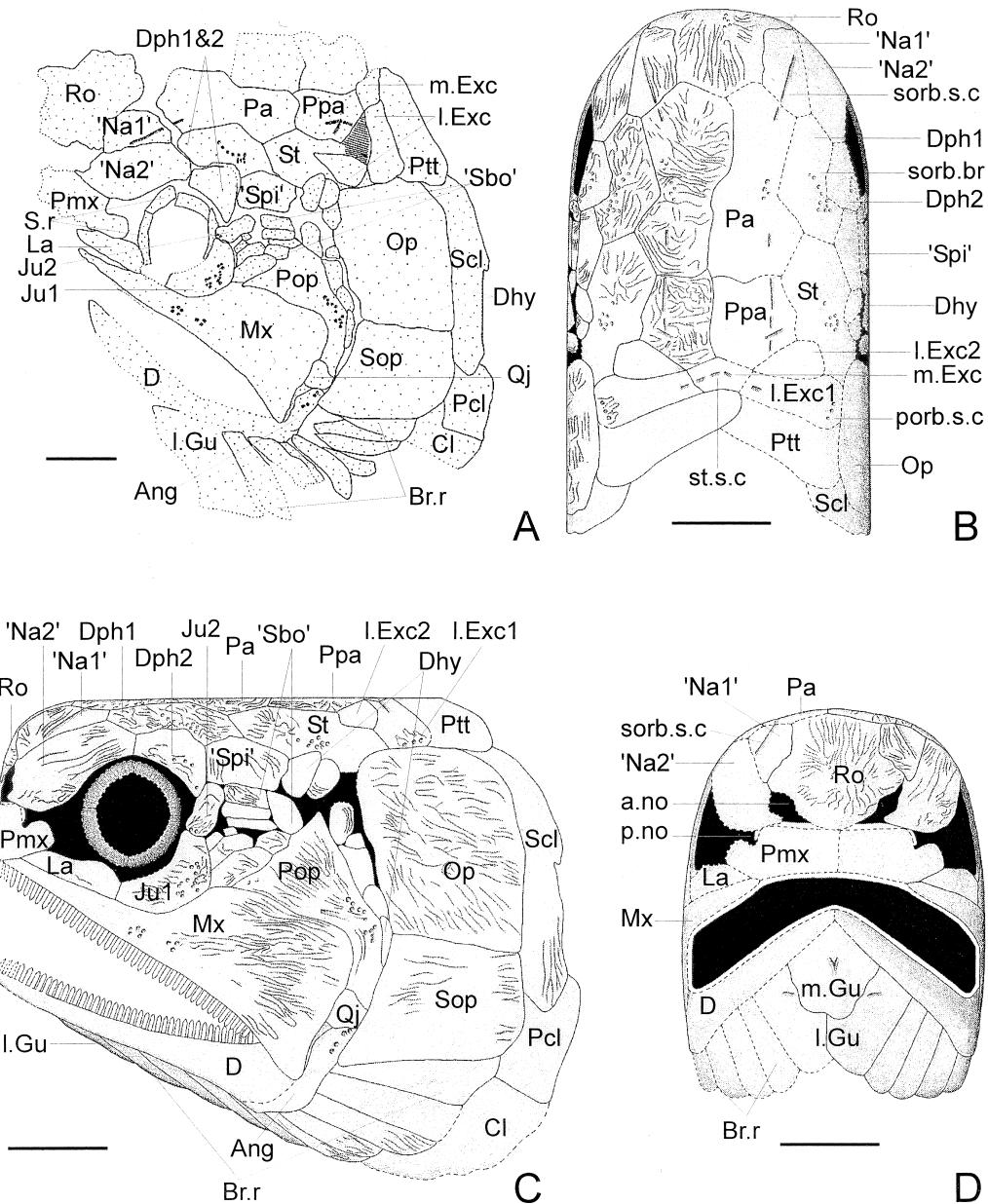
*Material.* 83 specimens from Lake Commentry; trunk length of specimens 66–245 mm.

*Emended diagnosis as combination of characters.* All bones of the skull ornamented densely. Parietal process absent. Rostral flaring anteriorly. Almost equal sized dermosphenotic 1 and supratemporal. Sturdy sclerotic bones present. Six to nine ‘suborbital’ bones. Maxillary plate of medium depth. Premaxilla contacts lacrimal ventrally. Seven to ten dermohyal bones. Dermosphenotic 1 contacts ‘nasal 1’. Jugal 2 contacts ‘spiracular’. ‘Spiracular’ angular. Nine branchiostegal rays. Postcleithral region variable; up to three enlarged scales ventral to postcleithrum. 46 or 47 scale rows along lateral line. Scales weakly serrated.

### *Description*

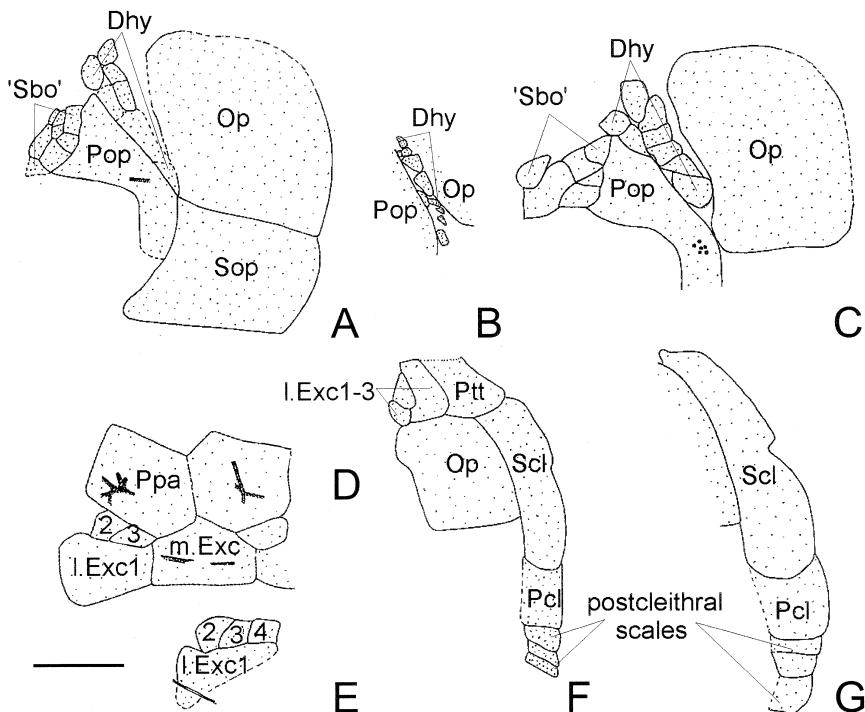
*Skull roof* (Text-fig. 2A–B). The parietals articulate with dermosphenotic 1 and the anterior portion of the supratemporal laterally. The posterior margins of the postparietals suture to the additional lateral extrascapulars laterally and to the single medial extrascapular medially. Up to three additional lateral extrascapulars can be present in *P. decorus* (Text-fig. 3D–F). Dermosphenotic 1 is boomerang-shaped and sutures to the parietal medially, to ‘nasal 1’ anteriorly, to ‘nasal 2’ anterolaterally, to the dermosphenotic 2 laterally, to the ‘spiracular’ posterolaterally, and to the supratemporal posteriorly. The supratemporal lies lateral to the parietals and postparietals, anterolateral to extrascapular 1 and 2, anterodorsal to the opercle, and to two dorsal dermohyal elements and the ‘spiracular’. The ‘spiracular’ is large and rectangular. It contacts the dermosphenotic 2 anteriorly, dermosphenotic 1 anterodorsally, supratemporal postero-dorsally, one dermohyal element posteriorly, two ‘suborbital’ bones ventrally, and jugal 2 anteroventrally. All of the skull roofing bones are ornamented with a layer of ganoin.

*Cheek* (Text-fig. 2A–C). The orbit, which bears a sturdy sclerotic ring, is surrounded posteriorly by dermosphenotic 2, and jugals 1 and 2, anteroventrally by the premaxilla, and ventrally by the lacrimal. Dermosphenotic 2 articulates with a ventral notch of dermosphenotic 1 dorsally, and with the ‘nasal 2’ anteriorly. An oval shaped jugal 2 and a crescent shaped jugal 1 suture to dermosphenotic 2 ventrally. The lacrimal sutures to jugal 1 anteriorly. Posterior to jugal 1 and jugal 2 about 6–9 loosely arranged ‘suborbitals’, which are bordered by the preopercle posteriorly, the maxilla ventrally, the jugals anteriorly, and the ‘spiracular’ dorsally (Text-figs 2A, C, 3A, C). The posterior elements fit in a concavity of the preopercle whereas the anterior elements are arranged loosely. The largest and ventralmost ‘suborbital’, jugal 1, and lacrimal suture to the maxilla. All of the cheek bones except for the smaller ‘suborbitals’ are ornamented with a layer of ganoin.



TEXT-FIG. 2. *Paramblypterus decorus*. A, line drawing of specimen MNHN1962-1. B, restoration of the skull; specimen MNHN1962-1, dorsal view. C, lateral view. D, anterior view, teeth omitted; broken lines indicate reversed and broken parts. Scale bar represents 10 mm.

**Snout** (Text-fig. 2A–C). *P. decorus* has a blunt snout. A single median rostral lies anterior to the parietals. The dorsal half of the rostral is almost square and sutures to the paired 'nasal 1'. Towards the anterior, the rostral flares laterally where it is in contact with the paired 'nasal 2'. It then tapers towards the anterior, thus, together with 'nasal 2', enclosing the anterior nostril. Unlike the arrangement of *P. gelberti* and *P. duvernoyi*, 'nasal 1' does not contact the premaxilla, but sutures to the rostral, 'nasal 2', dermosphenotic 1, and parietal. Owing to poor preservation, the exact



TEXT-FIG. 3. Variation of *P. decorus*. A–C, dermohyal region; MNHN1889-36-9D38, MNHN1889-36-31, MNHN1-262B. D–E, extrascapular series; MNHN1329b, MNHN1257b. F–G, enlarged postcleithral scales; MNHN1-262, MNHN 1889-36-293V. Scale bar represents 10 mm.

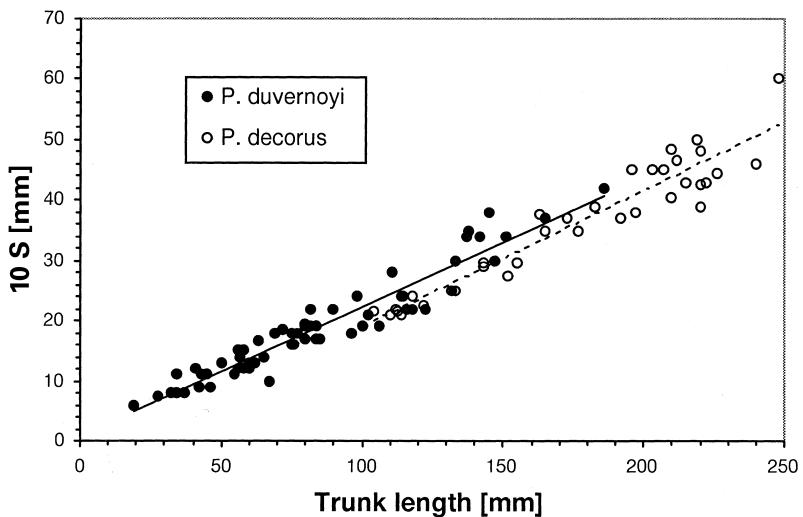
outline of the premaxilla could not be determined and it might have been deeper and longer. The posterior half of each premaxilla articulates with the lacrimal posteroventrally, 'nasal 2' dorsally, and maxilla ventrally. Premaxilla and 'nasal' 2 enclose a notch for the posterior nostril. All of the snout bones are ornamented with a layer of ganoin. Since the surface of the premaxillae is preserved too poorly, it could not be determined whether it is ornamented or not. Until now, the absence of the premaxilla had been considered a synapomorphy of paramblypterid fishes (Gad 1988).

*Opercular series* (Text-figs 2A, c, 3A–c). Dorsally, the opercle sutures to supratemporal, lateral extrascapular, and posttemporal, but it does not come in contact with the additional lateral extrascapulars. This region is variable concerning the number and shape of elements present (Text-fig. 3A–c). Seven to ten dermohyal elements lie anterior to the opercle and posterior to the preopercle (Text-figs 2A, c, 3A, c). The narrow ventral portion of the preopercle and its wider anterior part form an angle of less than 90 degrees owing to a relatively low maxillary plate. Anteriorly, the preopercle is gently concave where it sutures to the 'suborbitals'. Between preopercle and lower jaw, the quadratojugal articulates with both bones. The surface of the quadratojugal is not preserved and it could not be determined whether it was ornamented or not. The branchiostegal series is composed of about nine lanceolate branchiostegals. Posterior to the symphysis between the dentaries lies a single median gular. Apart from some elements of the dermohyal series, all of the cheek bones are ornamented with a layer of ganoin.

*Lower jaw.* The lower jaw is well preserved in one specimen only. It is likely that all of its surface was ornamented with ridges of enamel. The posterior part of the dentary articulates with the angular, of which only the dorsal part is preserved completely (Text-fig. 2A).

*Palate.* No palatal bones were preserved in any of the specimens examined.

*Dentition.* Dentary, maxilla, and probably premaxilla bear teeth. In paramblypterid fishes preservation of teeth is poor

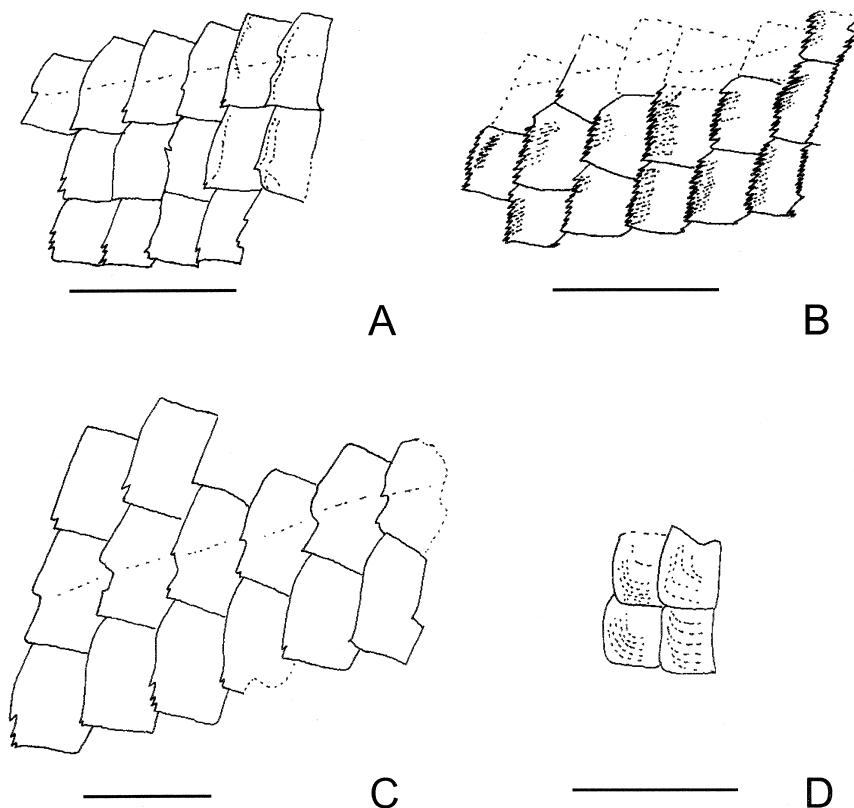


TEXT-FIG. 4. Allometric scale growth of *Paramblypterus decorus* (dotted line) and *Paramblypterus duvernoyi* (solid line); 10S = 10 scale rows.

in general, and teeth on the premaxilla were observed only on one premaxilla of a specimen of *P. duvernoyi* (Dietze 1999, fig. 5j). Contrary to Blot (1966), the teeth of *P. decorus* are similar to those of *P. gelberti* and *P. duvernoyi*. Because of poor preservation, the exact number of teeth could not be determined and therefore are drawn schematically for the reconstruction. The teeth of specimen MNHN-PA considered as belonging to the dentary by Blot (1966, pl. 9B) instead appear to me to be coronoid teeth. The same picture shows what has often been referred to as tubular dentine, a rough surface on the ventral margin of the maxilla where the teeth were embedded (Blot 1966; Heyler 1969; Poplin and Heyler 1993). In my opinion, the so-called ‘tubular dentine’ is merely an effect caused by impressions of dentary and maxillary teeth, and the rough surface is not part of the maxilla but is caused by the teeth of both sides having been pressed against each other. Moreover, the teeth of *Paramblypterus* appear to have been very fragile and probably caved in during fossilisation, an appearance that formerly further supported the suggestion of tubular dentine. However, casts of this region show rows of closely set teeth dislocated from the maxilla, but no loose bony material in which the teeth were embedded. The same feature can be observed in specimens of *A. latus* that are preserved in nodules.

*Sensory canals and pit-lines* (Text-fig. 2). Postorbital, supratemporal, supraorbital, infraorbital and operculomandibular sensory canals can be followed either by pores or grooves. The postorbital canal can be observed on the lateral extrascapulars only, where it divides into infraorbital and a supratemporal branch. The supratemporal canal runs medially along the lateral extrascapulars and crosses the medial extrascapular. The supraorbital canal runs anteriad slightly lateral to the midline of each postparietal and parietal. It enters ‘nasal 1’ at the midline and runs ventrolaterally towards ‘nasal 2’. Since no grooves or pores can be observed on the premaxilla it is not clear if it ended on the nasals or continued further on ventrally. The infraorbital canal runs anteriad at the midline of the supratemporal and along the ventral margin of dermosphenotic 1. It continues parallel to the orbit margin on dermosphenotic 2 along jugal 2 and jugal 1. Pores of a supraorbital branch running anterodorsally on dermosphenotic 1 are present. An ethmoidal commissure could not be observed in any of the specimens. The operculomandibular canal runs along the posterior margin of the ventral portion of the preopercle. On its dorsal part, it divides into a preopercular branch parallel to the dorsal margin of the preopercle, and a jugular branch parallel to the ventral margin of the preopercle. No pores were preserved on the quadratojugal or dentary. Pit-lines are present on the preopercle, the gulars, and on the postparietals.

*Pectoral girdle* (Text-figs 2A, C, 3F–G). Posttemporal, supracleithrum, and postcleithrum articulate with the posterior margins of the extrascapulars and the opercular series. The supracleithrum has a small rounded process in its overlap area with the posttemporal (Text-fig. 3G). The postcleithrum has an articulation surface in its dorsal portion, where it is overlapped by the supracleithrum. The region ventral to the postcleithrum is variable. Ventral to the postcleithrum three enlarged postcleithral scales can be present (Text-fig. 3F–G). They are rectangular in outline, almost as long as the



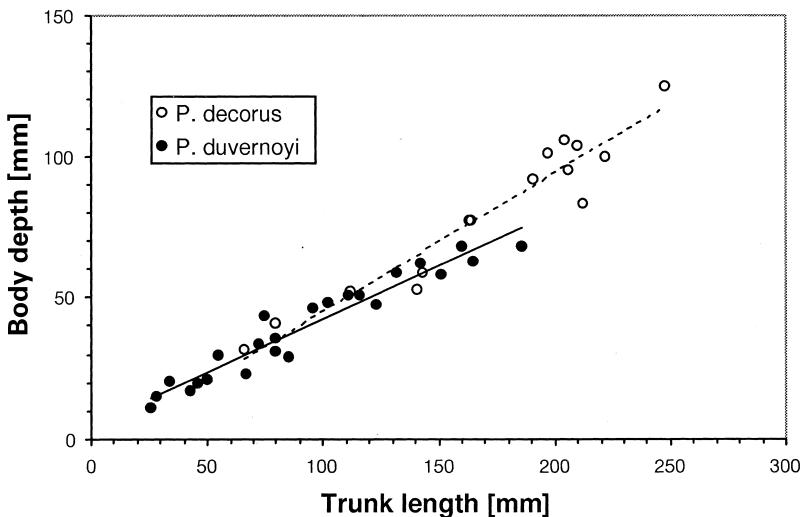
TEXT-FIG. 5. Detail of squamation. A, *Paramblypterus duvernoyi*. B, *P. gelberti*. C, *P. decorus*. D, *Amblypterus latus*. Scale bar represents 5 mm.

postcleithrum, and their dorsoventral height is smaller than that of the scales of the body. The exact outline of the cleithrum could not be determined due to poor preservation and covering of postcleithral elements. No clavicles could be observed in any of the specimens. Preservation of the pectoral girdle is poor and the surface is not preserved on any bones.

**Postcranial skeleton.** Specimens with a trunk length of 66–245 mm were examined. Scale growth is allometric (Text-fig. 4). Serrated scales are present in *P. decorus* (Text-fig. 5c), but difficult to evaluate, since the posterior edges are usually broken. The surface of the scales bears weak ridges and is otherwise smooth. Three unpaired ridge scales precede the dorsal fin. Three or four basal scutes are present anterior to the anal fin. The dorsal margin of the caudal fin is covered with similar, but more elongated scales. 46 or 47 scale rows between supracleithrum and the inclination of the scales anterior to the caudal fin were counted along the lateral line. There are 8–10 scale rows above and 13–15 scale rows below the lateral line. The position of the lateral line appears to vary among specimens. However, the overall number of 25 scale rows seems to be constant. Caudal peduncle and maximum body depth show allometric growth (Text-figs 6–7). Growth of the caudal peduncle in *P. decorus* and *P. duvernoyi* is similar in specimens up to 75 mm trunk length. However, in larger specimens depth of the body and caudal peduncle is larger in specimens of *P. decorus*.

The pectoral fin is small and rectangular. The number of lepidotrichia of the pectoral fin could not be established precisely due to poor preservation. According to Blot (1966), there are at least 24 lepidotrichia present. The pelvic fin inserts in advance of the dorsal fin. It is rectangular as well, but somewhat larger than the pectoral fin, and 24 or 25 lepidotrichia are present. Both pectoral and pelvic fins bear fringing fulcra on their leading edges.

The dorsal fin is posterior to the middle of the body and slightly in advance of the anal fin. It is triangular



TEXT-FIG. 6. Body depth in relation to trunk length for *Paramblypterus decorus* and *P. duvernoyi*.

and bears  $39 \pm 1$  lepidotrichia. The anal fin is triangular and includes 34 or 35 lepidotrichia. The caudal fin is heterocercal and bears a caudal flap on its dorsal lobe. The number of lepidotrichia present could not be established due to poor preservation. Fringing fulcra are present on the leading edge of both midline fins and the ventral caudal lobe.

#### *Paramblypterus duvernoyi* (Agassiz, 1833)

Text-figures 5A, 7, 8A, 9–11, 12B–D, F, 13C–G, 17–19

- 1833 *Palaeoniscus duvernoyi* (Agassiz), p. 45.  
 1891 *Amblypterus duvernoyi* (Giebel); Woodward, p. 440.  
 1976 *Paramblypterus duvernoyi* (Agassiz); Boy, p. 43.

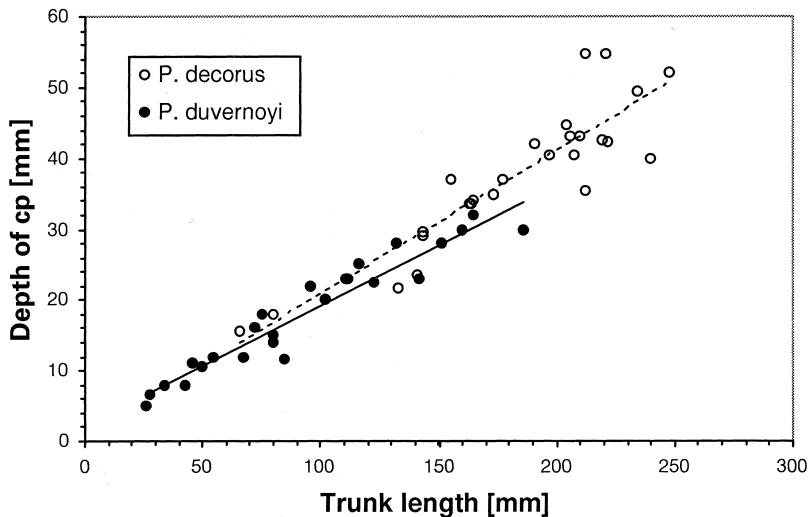
*Type material.* Agassiz 1833, vol. 2, tab. 7, figs 1–5; two specimens with a trunk length of approximately 93 mm and 125 mm. It has not been possible to locate the type material.

*Type locality.* Münsterappel, TK 1:25,000, Blatt 6213 Kriegsfeld.

*Type horizon.* Kappeln-Schwarzschieferbank, L-O 9 (Text-fig. 1), Lower Rotliegend, Autunian, Lower Permian, Germany (Boy *et al.* 1990).

*Material.* 112 specimens from Lake Odernheim (L-O 8), 47 specimens from Lake Kappeln (L-O 9), 30 specimens from Lake Klauswald (L-O 9), 124 specimens from Lake Humberg, phases I and II (L-O 10); trunk length of specimens 19–220 mm.

*Emended diagnosis as combination of characters.* Distinct ornamentation of parietals, postparietals, extrascapulars, posttemporals, dermosphenotics, supratemporals and supracleithra. Parietals with variable lateral process. One or two medial extrascapular(s). Additional lateral extrascapulars contact opercle. Rostral tapering anteriorly. Sclerotic bones absent. Six ‘suborbital’ bones. Maxillary plate deep. One or two dermohyal bones. ‘Spiracular’ rounded. Opercular and subopercular areas and D-values different from those of *P. gelberti*. Eight branchiostegal rays. D-values of scales 1·4 to 2·0. Area of serrated scales narrowing towards anal fin.  $41 \pm 2$  scale rows along lateral line.



TEXT-FIG. 7. Caudal peduncle (cp) in relation to trunk length for *Paramblypterus decorus* and *P. duvernoyi*.

### Remarks

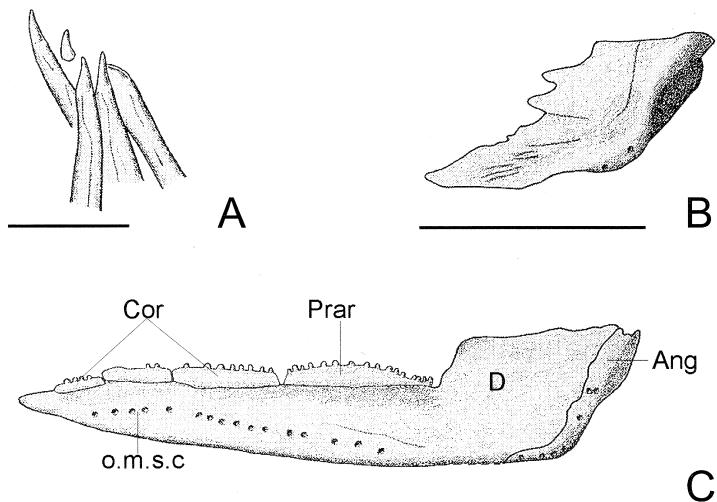
The skull and its ontogenetic and intraspecific variation have been described in Dietze (1999), and only additional information is given here.

**Dentition** (Text-fig. 8). Dentary, maxilla, and premaxilla bear teeth. They are slender, pointed structures (Text-fig. 8A) bearing an acrodin cap (Ørvig 1978), which usually is not preserved. Supposedly, the shafts of the teeth were composed of a thin dentine layer surrounding a wide pulp cavity which caved in during fossilisation. This caused a secondary groove running dorsoventrally along the midline of the teeth. Coronoids and prearticular bear short and rounded teeth (Text-fig. 8C). In most specimens, the teeth were poorly preserved or not present at all, so the exact number of teeth could not be determined.

**Palate.** Parasphenoid, entopterygoid, ectopterygoid, metapterygoid, and quadrate are present. The palatal bones are identical in *P. duvernoyi* and *P. gelberti*. The palate for *P. duvernoyi* was reconstructed using *P. gelberti* as a model and is discussed there.

**Pectoral girdle** (Dietze 1999, fig. 1c). The posttemporals lie posterior to the medial and lateral extrascapulars. Supracleithrum, postcleithrum, and cleithrum lie posterior to the opercular series which covers the anterior portion of these bones. The postcleithrum has an articulation surface in its dorsal portion where the supracleithrum overlaps. The cleithrum has an articulation surface in its dorsal part where the postcleithrum fits on. A ‘postspiracular’ is present only in one small specimen, where it was located between posttemporal, opercle, and supracleithrum (Dietze 1999, fig. 4). Two disarticulated clavicles of *P. duvernoyi* could be observed (Text-fig. 9A–B). The clavicle consists essentially of two parts: a flat ventral expanse, which curves inward ventrally, and a dorsal portion which is triangular in outline and tapers dorsally. In lateral view, narrow ridges of ganoin are present on its dorsal portion, which are also present on the cleithrum. In medial view, the dorsal part bears a sturdy ridge where it articulated with the cleithrum. Since they are of almost identical shape as in *Mimia toombesi* or *Moythomasia durgaringa* (Gardiner, 1984), it is likely that their arrangement is similar. Moreover, a bone closely resembling the interclavicle of these species (see Gardiner 1984, p. 375, fig. 130; p. 379, fig. 134) could be observed (Text-fig. 9C). It is lanceolate in outline with serrated edges in its middle part. Ventrally, a ridge runs along the midline with small grooves next to it. The dorsal surface is smooth. Posttemporal, supracleithrum, postcleithrum, cleithrum are ornamented with ridges and tubercles, but not as intensely as the skull roofing bones.

**Postcranial skeleton.** Until now, *Paramblypterus* has often been described as deep bodied (e.g. Blot 1966). This interpretation may have been caused by postmortem bursting and spreading out of the scales. However, the



TEXT-FIG. 8. A, teeth of *Paramblypterus duvernoyi*; specimen GPIM-M5819. B, left angular of *P. gelberti* in lateral view; specimen GPIM-M2267. C, left dentary of *P. gelberti* in lateral view; specimen GPIM-M2291. Scale bar represents 1 mm (A) and 10 mm (B, C).

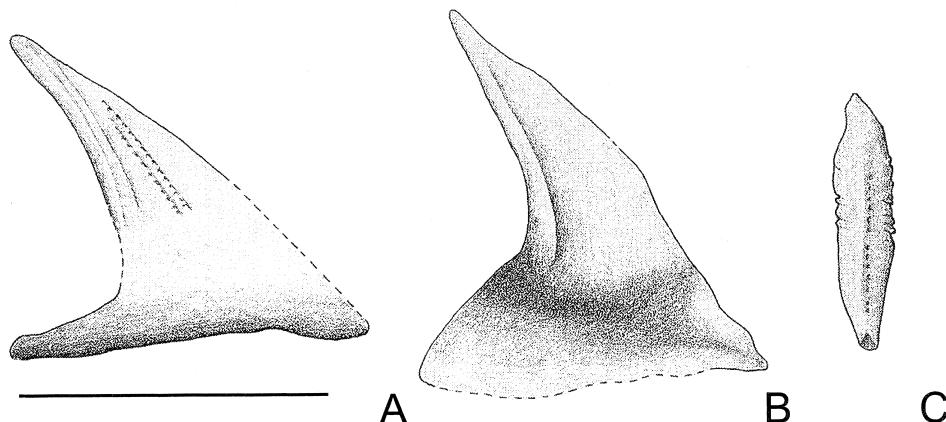
reconstruction of the whole fish (Text-fig. 10) shows a fairly slender body with only a little hump posterior to the paired posttemporals.

Specimens with a trunk length of 19–220 mm were examined. Scale growth shows allometry (Schmidt-Nielsen 1984). Broken specimens suggest that this species reached a trunk length of more than 220 mm. The scales below the lateral line and tapering towards the anal fin are serrated and bear fine ridges that run anterodorsally from the serrations (Text-fig. 5A). Serrations and ridges are most prominent posterior to postcleithrum and cleithrum. Scales yield D-values (Schmidt-Kittler 1984, 1986) between 1.4 and 2.0. The area on the body bearing serrated scales appears to be reduced during ontogeny, but more complete specimens are needed to corroborate this observation.

Three to four unpaired ridge scales precede the dorsal fin and two ridge scales precede the anal fin. The ridge scales of the dorsal fin are smooth; the ridge scales of the anal fin bear accretion lines and can be serrated. The dorsal margin of the caudal fin is covered by 4–5 basal scutes followed by a series of elongated scutes. The surface of the scutes is smooth. Below the lateral line, the dorsoventral height of the scales on the body decreases progressively. Whereas scales on the body are deeper than long, scales on the belly are longer than deep. Along the lateral line,  $42 \pm 2$  scale rows between supracleithrum and the insertion of the fins, there are approximately 28 scale rows to the dorsal fin,  $8 \pm 1$  scale rows to the pelvic fin, and  $23 \pm 1$  scale rows to the anal fin. The location of the lateral line appears to vary among specimens. However, the overall number of 23 scale rows seems to be constant. Caudal peduncle and maximum body depth show allometric growth throughout (Text-fig. 11). In larger specimens, caudal peduncle and body depth are lower than in specimens of *P. decorus*, but are very similar in specimens of *P. duvernoyi* and *A. latus*.

The pectoral fin is small and rectangular. Fused lepidotrichia of the marginal rays are present at the origin of the pectoral fin on specimens PMNB-WÖR 66 and GPIM-M2964. The pelvic fin inserts in advance of the dorsal fin. It is rectangular as well, but somewhat larger than the pectoral fin, and  $20 \pm 2$  lepidotrichia are present. Both pectoral and pelvic fin bear fringing fulcra on their leading edges.

The dorsal fin is posterior to the middle of the body and starts slightly in advance of the anal fin. It is triangular and bears  $34 \pm 2$  lepidotrichia. The anal fin is triangular and includes about 34 lepidotrichia. The caudal fin is heterocercal and bears a caudal flap on its dorsal lobe. The number of lepidotrichia present is  $20 \pm 2$  for the ventral lobe. Fringing fulcra are present on the leading edge of both midline fins and the ventral caudal lobe. In adult specimens, the rays of all fins bifurcate halfway to two-thirds along their length up to three times. The first ray that reaches the distal portion of the fins does not bifurcate in any of the fins. For reconstruction of the whole fish (Text-fig. 10), the number of fin rays of the pectoral and caudal fin were estimated, since they were not preserved completely in any of the specimens examined.



TEXT-FIG. 9. *Paramblypterus duvernoyi*; specimen GPIM-M4972. A, right clavicle in lateral view. B, left clavicle in medial view. C, interclavicle in ventral view. Scale bar represents 10 mm.

#### Comparison with *Paramblypterus decorus*

Whereas *P. duvernoyi* has a short, rounded snout with a fairly upright suspensorium, the snout of *P. decorus* is drawn out and more blunt. The bones are connected loosely in *P. duvernoyi*, but they are articulated more closely in *P. decorus*. The rostral of *P. duvernoyi* tapers anteriorly, but it flares in specimens of *P. decorus*. ‘Nasal 1’ does not contact the premaxilla in *P. decorus*, but does so in *P. duvernoyi*. A sclerotic ring is present in *P. decorus*, but is absent in *P. duvernoyi*. The posterior part of the premaxilla of *P. duvernoyi* lies broadly on the maxilla, whereas the premaxilla has only a small contact with the maxilla in *P. decorus*. The posterior expansion of the maxilla is deeper in *P. duvernoyi* than in *P. decorus*. *P. duvernoyi* has a process on the parietals, which is not present in *P. decorus*. Dermosphenotic 1 is smaller than the supratemporal in *P. duvernoyi*, whereas these bones are almost equal sized in *P. decorus*. Dermosphenotic 1 sutures to ‘nasal 1’ in *P. decorus*, but it does not do so in *P. duvernoyi*. As in *P. duvernoyi*, duplication of the lateral extrascapulars is present in *P. decorus*. However, it seems that the dorsalmost additional lateral extrascapular arises first in *P. decorus*, whereas the ventralmost appears first in *P. duvernoyi*. *P. duvernoyi* has fewer dermohyal and suborbital elements than *P. decorus*. In contrast to *P. decorus*, enlarged postcleithral scales have not been observed in specimens of *P. duvernoyi*. Serration of scales is similar in *P. duvernoyi* and *P. decorus* and yield D-values (Schmidt-Kittler, 1984, 1986) between 1.4 and 2.0. Scale allometry of *P. duvernoyi* differs from *P. decorus* in that equal sized specimens have larger scales (Text-fig. 4). In specimens larger than 60 mm and 75 mm, growth of body depth and caudal peduncle increases faster in specimens of *P. decorus* than of those of *P. duvernoyi* (Text-figs 6–7). Except for the anal fin, fewer lepidotrichia are present in the fins of *P. duvernoyi* than of *P. decorus*.

#### *Paramblypterus gelberti* (Goldfuss, 1847)

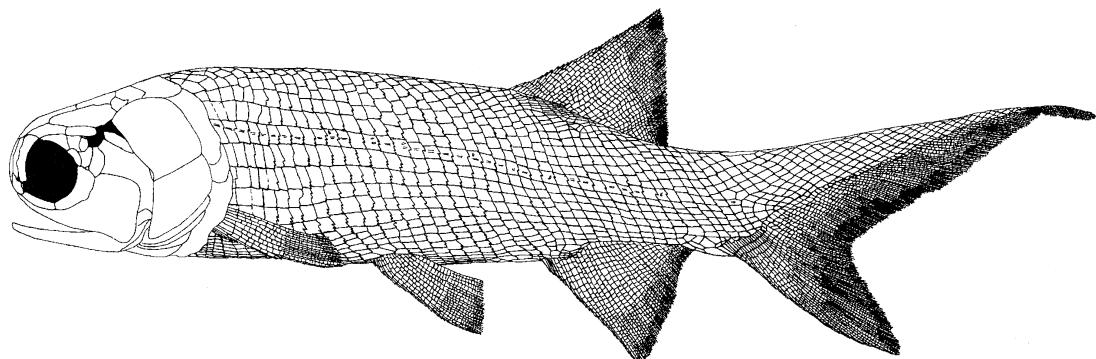
Text-figures 5B, 8B–C, 12E, G–H, 13A–B

- 1847 *Palaeoniscus gelberti* (Goldfuss), p. 17.
- 1891 *Amblypterus gelberti* (Traquair); Woodward, p. 447.
- 1976 *Paramblypterus gelberti* (Goldfuss); Boy, p. 43.
- 1988 *Paramblypterus gelberti* (Goldfuss); Gad, p. 149.

*Holotype*. BSM 1871 II 1, Munich. Specimen of 120 mm trunk length with well-preserved trunk and wanting head, which is present on the counterpart impression.

*Type locality*. Pfarrwald at Heimkirchen.

*Type horizon*. Pfarrwald-Bank, L-O 9 (Text-fig. 1), Lower Rotliegend, Autunian, Lower Permian, Germany (Boy *et al.* 1990).



TEXT-FIG. 10. Restoration of *Paramblypterus duvernoyi*, teeth omitted. Scale bar represents 10 mm.

*Material.* 76 specimens from Lake Pfarrwald (L-O 9), 30 specimens from Lake Jeckenbach (L-O 6); trunk length 35·5–151 mm.

*Emended diagnosis as combination of characters.* Little ornamentation of parietals, postparietals, extrascapulars, posttemporals, dermosphenotics, supratemporals and supracleithra. Parietals with lateral process. One or two medial extrascapular(s). Additional lateral extrascapulars do not contact opercle. Rostral tapering anteriorly. Sclerotic bones absent. Five ‘suborbital’ bones. Maxillary plate deep. One to three dermohyal bones. ‘Spiracular’ rounded. Eight branchiostegal rays. D-values of scales higher than 2·0.  $42 \pm 2$  scale rows along lateral line. Area of serrated scales on body not tapering towards anal fin. Ornamentation of scales fairly prominent.

#### Remarks

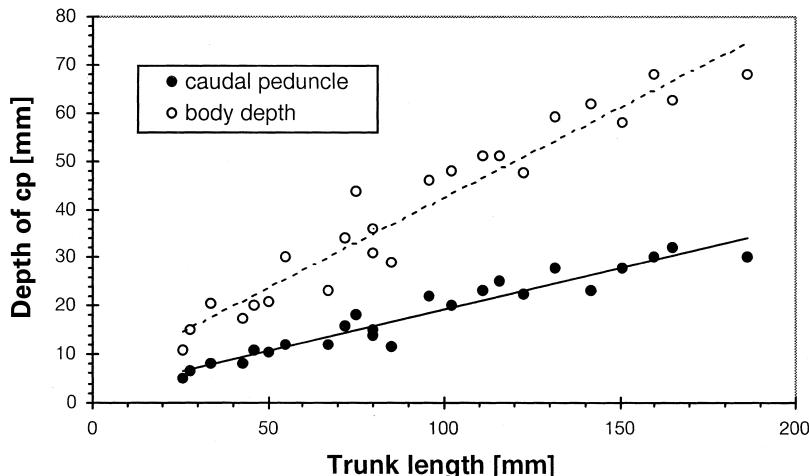
The skull and postcranial elements of *P. gelberti* have been described and compared to *P. duvernoyi* in detail earlier (Dietze 1999). Therefore, only differences in squamation and the description of the palate are given here.

*Squamation.* Serration of the scales might serve as a means to distinguish *P. gelberti* and *P. duvernoyi*. In *P. duvernoyi* the part of the body bearing serrated scales appears to decrease during ontogeny so that serrated scales are confined to the area posterior to the skull, whereas the degree of serration stays the same in specimens of *P. gelberti*. Moreover, scales of *P. duvernoyi* (Text-fig. 5A) are usually serrated less heavily and bear fewer ridges than scales of *P. gelberti* (Text-fig. 5B). Accordingly, D-values for scales of *P. gelberti* are usually higher than 2·0, whereas D-values for scales of *P. duvernoyi* are below 2·0. However, these features might prove difficult given the poor preservation of postcranial elements of *P. gelberti*.

*Palate* (Text-figs 12–13). In *Polypterus*, the palatoquadrate ossifies as separate elements, with the metapterygoid and quadrate ossifying first and the remainder only late in ontogeny (Arratia and Schultze 1991). Apart from metapterygoid and quadrate, no features of the palatoquadrate could be observed in *Paramblypterus*. It is likely that the palatoquadrate and associated elements of *Paramblypterus* developed in a way similar to *Polypterus*, and are not preserved, because they had not yet ossified.

The entopterygoid (Text-fig. 12A–C, G–H) sutures laterally to the dermopalatines and slopes dorsomedially where it contacts the parasphenoid body halfway along its length. Posteriorly, it sutures to the metapterygoid. It bears a wavy ledge where the dermopalatines fit on. Its ventral face is covered with small rounded granular teeth, except for a smooth margin anteriorly and dorsally. Its dorsal face is smooth.

The metapterygoid (Text-fig. 12A, D–H) is oriented like the entopterygoid. It sutures to the ectopterygoid laterally and slopes dorsomedially towards the parasphenoid. Anteriorly, it sutures to the entopterygoid, and contacts the



TEXT-FIG. 11. Caudal peduncle and body depth in relation to trunk length for *Paramblypterus duvernoyi*.

quadrate posterodorsally. Its ventral face is covered with small rounded granular teeth, except for a smooth margin posteriorly and dorsally. The dorsal face of the metapterygoid bears a ridge which runs parallel to its ventral margin and sends off a branch that runs dorsad about midway of the bone.

Lateral to the entopterygoid and medial to the maxilla lie three dermopalatines (Text-fig. 12A, H) which are arranged in a row. The posteriormost dermopalatine has a tiny protuberance posteriorly where it fuses to the ectopterygoid. The dermopalatines are covered completely with granular teeth on their ventral face.

The ectopterygoid (Text-fig. 12A, F–H) lies lateral to the metapterygoid and medial to the maxilla. The ectopterygoid has an anterior notch, where the caudalmost dermopalatine articulates. Posteriorly, it has a tiny protuberance. It is of rectangular shape and all of its ventral face bears granular teeth.

The parasphenoid has well-developed ascending processes (Text-fig. 13) which point dorsally. In dorsal view (Text-fig. 13A), the opening of the bucco-hypophysial canal and two grooves, which correspond to the course of the parabasal canal, can be observed. On its ventrolateral surface (Text-fig. 13B), two spiracular grooves run along the ascending processes to the centre of the parasphenoid. The parasphenoid body is somewhat bilaterally asymmetrical and variable in outline (Text-fig. 13C–G). The ventral surface bears a tooth patch of granular teeth. The tooth patch extends along the middle two thirds of the parasphenoid. Anteriorly, the tooth patch covers about one third of the bone and flares towards the ascending processes.

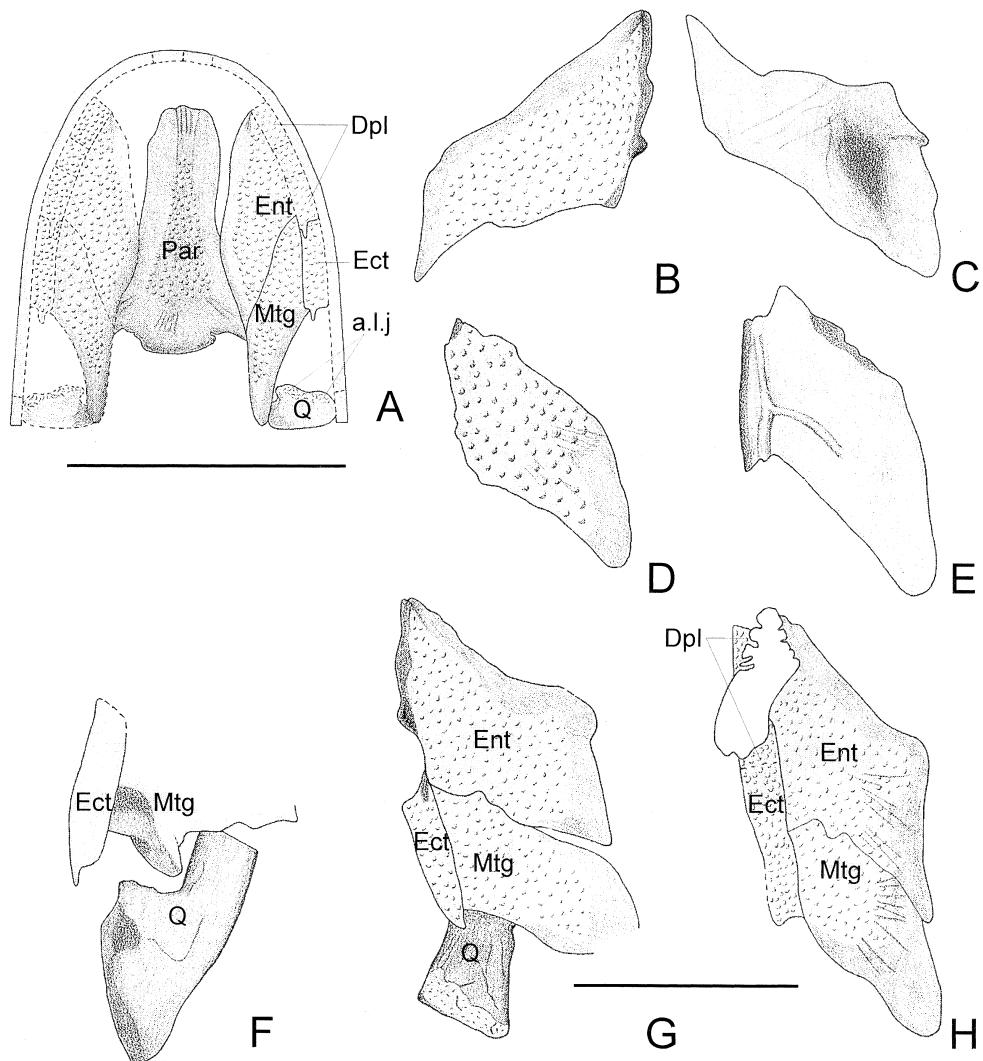
The quadrate (Text-fig. 12A, F–G) is a small element and together with metapterygoid and ectopterygoid encloses the adductor fossa. Ventrally, it bears the cartilaginous articulation for the lower jaw. Its dorsal portion is smooth and contacts the posteroventral margin of the metapterygoid.

A vomer was not found in any of the specimens.

#### Genus AMBLYPTERUS Agassiz, 1833

*Emended diagnosis as combination of characters.* Distinct ornamentation of parietals, postparietals, extrascapulars, posttemporals, dermosphenotics, and supratemporals. No parietal process. Single pairs of lateral extrascapulars. Rostral probably tapering anteriorly (Gardiner 1963). Delicate sclerotic bones present. ‘Nasal’ present as single ossification. ‘Nasal’ borders the orbit anteriorly. Supratemporal more than twice as long as dermosphenotic 1. Dermosphenotic 1 and dermosphenotic 2 contact ‘nasal’. Single dermohyal. Two ‘suborbitals’. Maxillary plate deep. Ten branchiostegal rays. Postcleithrum absent. Posterior edges of scales straight, bearing concentric striae.  $40 \pm 2$  scale rows along lateral line.

*Type species.* *Amblypterus latus* Agassiz, 1833; designated by Woodward, 1891.



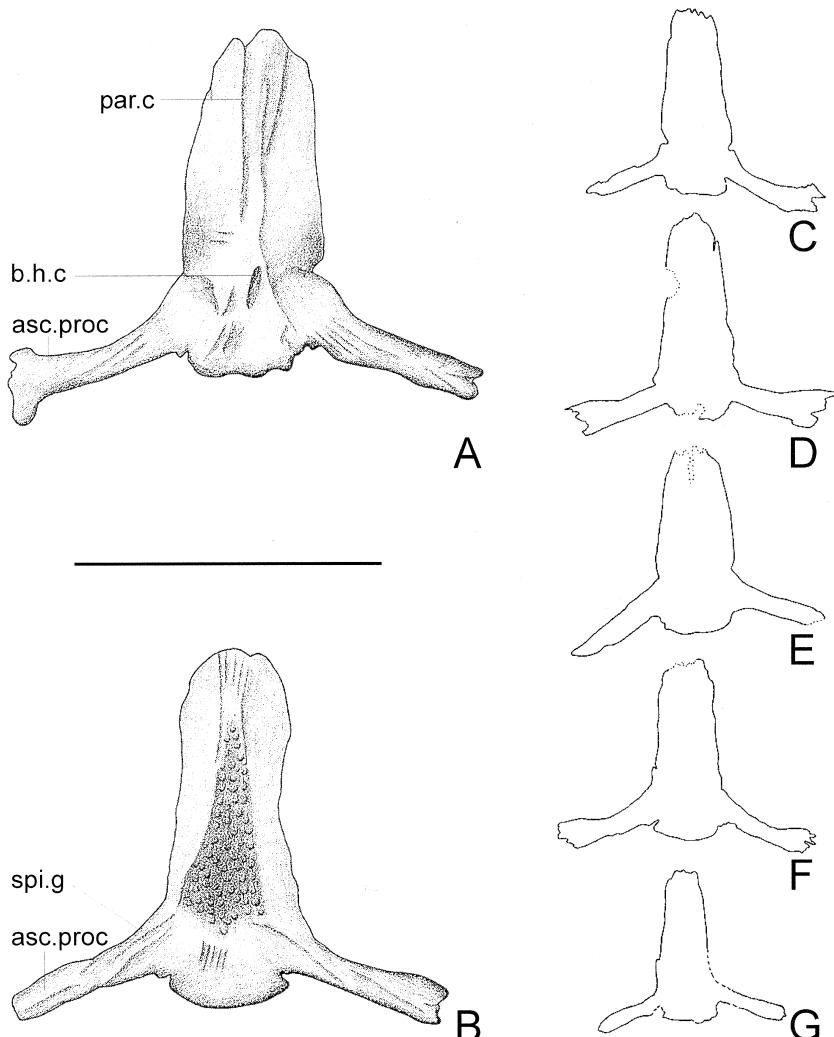
TEXT-FIG. 12. A, restoration of the palate of *Paramblypterus duvernoyi* and *P. gelberti* in ventral view; specimens GPIM-M2248 and GPIM-M2315. B, left entopterygoid in ventral view; GPIM-M4972. C, left entopterygoid in dorsal view; GPIM-M4972. D, right metapterygoid in ventral view; GPIM-M4907/3. E, right metapterygoid in dorsal view; GPIM-M2267. F, right metapterygoid, ectopterygoid, and quadrate in dorsal view; GPIM-M5811. G, right entopterygoid, metapterygoid, ectopterygoid, and quadrate in ventral view; GPIM-M5263. H, right entopterygoid, dermopalatines, metapterygoid, and ectopterygoid in ventral view; GPIM-M2291. B-D, F, *P. duvernoyi*. E, G-H, *P. gelberti*. Scale bars represent 10 mm.

*Species included. Amblypterus latus* Agassiz, 1833.

*Amblypterus latus* Agassiz, 1833.

Text-figures 5D, 14–19

1833    *Amblypterus latus* Agassiz, p. 37.



TEXT-FIG. 13. Paraspheonoid. A, dorsal view; GPIM-M2267. B, ventral view; GPIM-M2248. C, PMNB-WÖR66. D, GPIM-M4973. E, GPIM-M4972. F, GPIM-M5813. G, GPIM-M4907. A-B, *P. gelberti*. C-G, *P. duvernoyi*. Scale bar represents 10 mm.

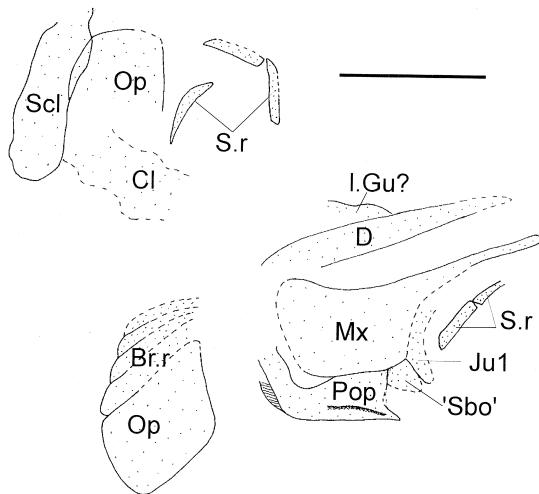
- 1877 *Amblypterus lateralis*, (Agassiz); Traquair, p. 552.  
 1976 *Paramblypterus lateralis* (Agassiz); Boy, p. 41.

*Holotype*. Lost; syn. *A. lateralis* (Agassiz, 1833), VP 1301 (St 21), USGP Strasbourg. Complete specimen of 75 mm trunk length with poorly preserved skull.

*Type locality*. Lebach, Saarbrücken.

*Type horizon*. Humberg-Bank (phase IV), L-O 10 (Text-fig. 1), Lower Rotliegend, Autunian, Lower Permian, Germany (Boy *et al.* 1990).

*Material*. 73 specimens from Lake Humbach, phase IV (L-O 10); trunk length of specimens 34–128 mm.



TEXT-FIG. 14. Line drawing of type specimen of *Amblypterus lateralis*; USGP-VP 1301 (St 21). Scale bar represents 10 mm.

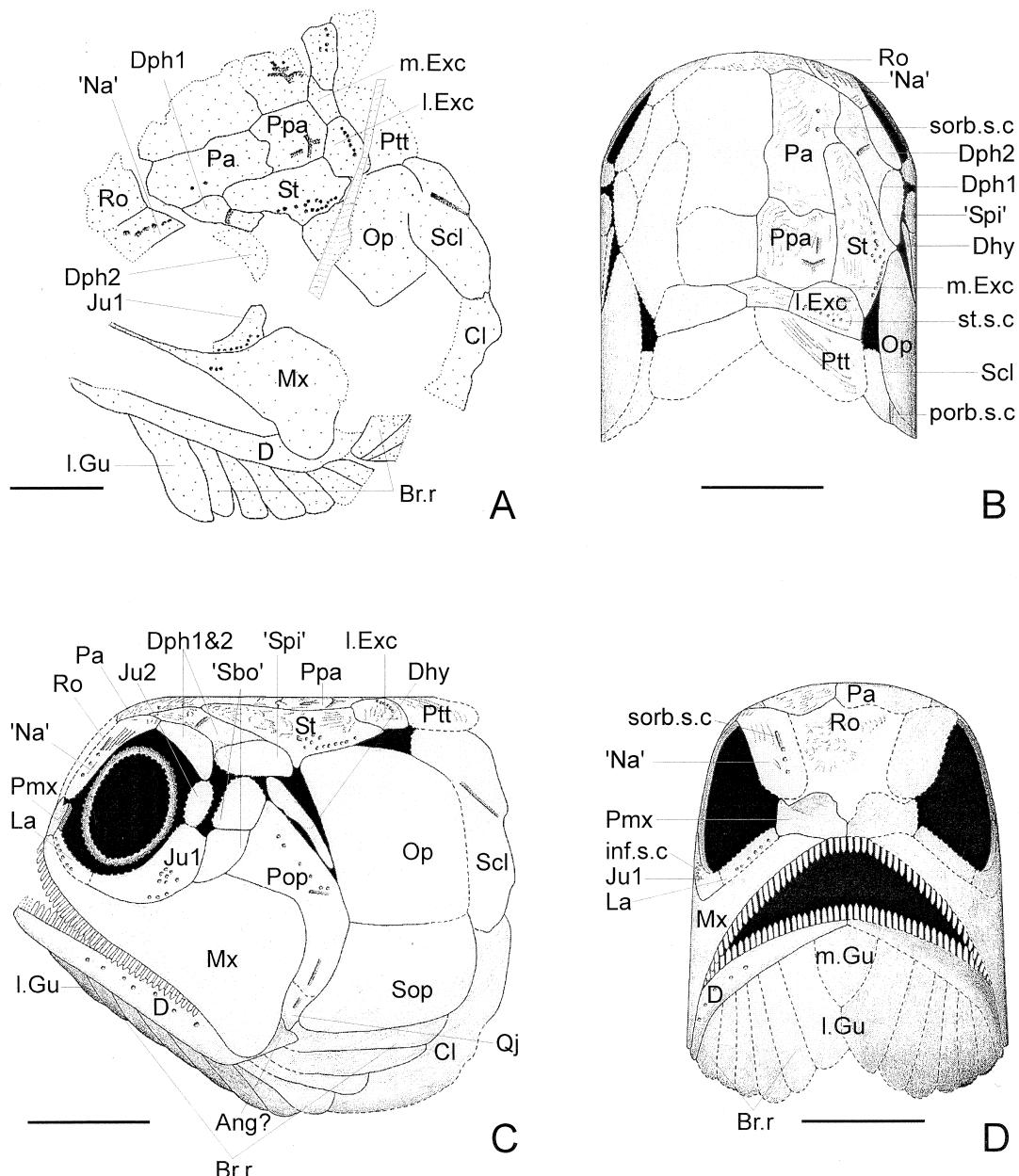
**Remarks.** As mentioned earlier, there has been some confusion about what is an *Amblypterus* and what is a *Paramblypterus* as a result of insufficient descriptions and inapplicable diagnoses. This was further complicated by the loss of the type specimen of *A. latus* and the fact that Gardiner (1963) did not designate a neotype when revising the genus. However, the type specimen of *A. lateralis* (Text-fig. 14), which Woodward (1891) regarded as synonymous with *A. latus*, still exists. Unfortunately, Agassiz's description of *A. latus* does not allow for corroboration of *A. lateralis* as a synonym for *A. latus*. However, Agassiz (1833, vol. 2, tab. 4f) pictured the type specimen of *A. latus* bearing a sclerotic ring and having smooth scales. Sclerotic ring elements are present in the holotype of *A. lateralis*, but have not been observed in any of the specimens of *P. duvernoyi* from Lake Humburg. As concerns the description of the type specimen of *A. lateralis* by Heyler (1976, p. 20), part of it does not match the specimen. Heyler pictured it having one suborbital element in his text-figure 1, and three suborbital elements in his text-figure 2, the former of which I found to match the specimen (Text-fig. 14). Since there is no evidence of the type specimen of *A. lateralis* being different from *A. latus*, it is appropriate to acknowledge these species as synonymous for the time being.

**Diagnosis.** As for genus.

#### Description

**Skull roof** (Text-fig. 15A–B). The parietals do not bear a distinct lateral process between dermosphenotic 1 and supratemporal. The postparietals are more or less square in outline and half as long as the parietals. The single medial extrascapular sutures with the postparietals anteriorly, and laterally with the lateral extrascapulars which are of elongated trapezoidal shape. Usually no additional lateral extrascapulars are present. Only the largest specimen examined (PIB-2) has additional lateral extrascapulars. Dermosphenotic 1 and the supratemporal lie laterally to the parietal and postparietal. The supratemporal is elongate and bears a ventrolateral process that articulates between opercle and 'spiracular'. Except for the 'spiracular', all skull roofing bones are ornamented with tubercles and ridges of ganoin.

**Cheek** (Text-fig. 15A, c). The orbit, which bears a delicate sclerotic ring, is surrounded posteriorly by dermosphenotic 2, and jugals 1 and 2, and anteroventrally by lacrimal and premaxilla. Dermosphenotic 2 sutures with dermosphenotic



TEXT-FIG. 15. *Amblypterus latus*. A, line drawing of specimen SMF-75P. B, Restoration of the skull; specimens SMF75P and Mb-f3809b, dorsal view. C, lateral view. D, anterior view; broken lines indicate reversed parts. Scale bars represent 10 mm.

1 dorsally and the 'nasal' anteriorly as it does in *P. decorus*. The oval shaped jugal 2 and the crescent shaped jugal 1 articulate ventrally to dermosphenotic 2. Two fairly big and rounded 'suborbitals' abut posterior to jugal 1 and jugal 2. The maxilla articulates with the ventral 'suborbital', jugal 1, and lacrimal dorsally. In contrast to the description by Gardiner (1963, p. 293), the maxilla has a posteroventrally elongated margin. This is

similar to the maxilla of *P. gelberti* and *P. duvernoyi* and unlike that seen in elonichthyid fishes. In *Elonichthys* (Schindler, 1993) the maxilla is low, more angular and the posterior expansion is not set off as distinctly as in *Paramblypterus*. The surface of the bones of the cheek is preserved too poorly to evaluate whether they are ornamented or not. The surface of the 'suborbitals' appears to have been smooth.

**Snout** (Text-fig. 15A, D). A single median rostral articulates laterally with the 'nasal'. It is likely to have formed by the fusion of supraorbital, preorbital, and nasal, since this bone occupies the position of supra- and preorbital, but also bears the supraorbital sensory canal. The exact outline of the rostral could not be observed in any of the specimens examined (however, see Gardiner 1963). Since the articulation of the 'nasal' with both dermosphenotics is clearly seen on the specimens used for reconstruction (Text-fig. 15A), the arrangement of the bones could be restored even with part of the rostral missing. However, it is not clear whether the snout bones of *A. latus* articulated only loosely as in *P. gelberti* and *P. duvernoyi*, or had a flaring rostral as in *P. decorus*, or neither. The posterior portion of the premaxilla lies on the maxilla and articulates with the lacrimal posteriorly and the 'nasal' dorsally. Due to the poor preservation of the snout, the position of neither anterior nor posterior nostril could be determined. The 'nasal' and those parts of the rostral that are preserved are covered with narrow ridges and tubercles.

**Opercular series** (Text-fig. 15A, C). The opercle articulates with the supratemporal and leaves a gap enclosed by supratemporal, extrascapular, and posttemporal dorsally, supracleithrum posteriorly, and opercle ventrally. A single dermohyal, which is narrow and elongate, lies anteriorly to the opercle. Anteroventrally of the dermohyal abuts the preopercle. The preopercle has a narrow ventral and a widening anterior portion. It sutures dorsoposteriorly to the maxilla. The anterior margin of the preopercle bears two convex indentations where the 'suborbitals' suture. The shape of the dorsal margin of the quadratojugal is not known. However, the presence of the sensory canal allowed for identification of this bone. The median gular was not preserved in any of the specimens examined, and for the reconstruction it was assumed that it was similar in outline and arrangement to *Paramblypterus*, given the adjacent elements. The branchiostegal series was preserved completely in one specimen only, where ten branchiostegal rays were present. They are lancelet-like bones as in *Paramblypterus*, but more delicate. Since the surface of the bones in the opercular series is not preserved, it is not possible to determine whether they were ornamented or not.

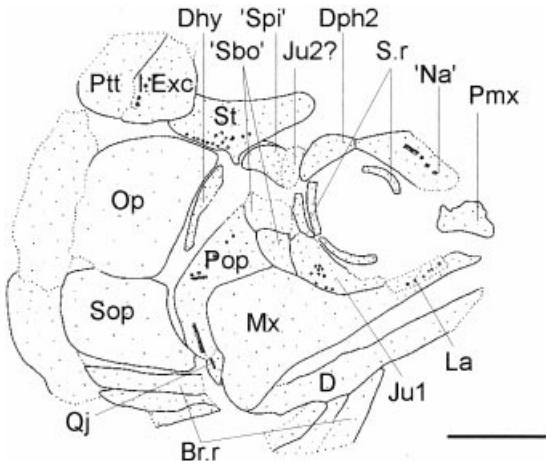
**Lower jaw.** Preservation of the lower jaw is poor, and it is unclear whether an angular was present or not. Coronoids could be observed, but the outline of the bones could not be determined because of poor preservation.

**Palate.** On specimen BMNH-P3459 and counterpart BMNH-P980 a faint impression of a parasphenoid is present. Except for the outline of ascending processes, no details could be made out. No other palatal bones could be observed in the specimens examined.

**Dentition.** Dentary, maxilla, and premaxilla (specimen BMNH-14536) bear teeth. Short, rounded teeth belonging to the coronoids are present in the lower jaw (specimen BMNH-2900b). It appears that teeth of *Amblypterus* resemble those seen in *Paramblypterus* (Text-fig. 8A, C). Preservation of teeth is poor, and the exact number of teeth could only be estimated and were drawn schematically in the reconstruction.

**Sensory canals** (Text-fig. 15). Postorbital, supratemporal, supraorbital, infraorbital, and operculomandibular sensory canals are indicated either by pores and grooves. The postorbital canal enters the dorsal part of the supracleithrum, runs anterodorsally along the posttemporal, and divides into infraorbital and supratemporal branches on the lateral extrascapulars. The supratemporal canal runs along the posterior margin of the lateral extrascapular and probably crossed the medial extrascapular. The supraorbital canal runs anteriorly along the lateral margins of postparietal and parietal. It continues passing somewhat off the midline through the 'nasal'. The infraorbital canal runs along the ventral margin of the supratemporal, and curves ventrally through the posterior margin of dermosphenotic 1. No pores could be observed on dermosphenotic 2, but the canal probably passed through the midline of jugal 2 and jugal 1, and continued through the lacrimal anteriorly. An ethmoidal commissure was not observed in any of the specimens. The operculomandibular canal runs along the midline of the ventral portion of the preopercle, divides into the preopercular canal parallel to the dorsal margin of the preopercle, and the jugular canal parallel to the ventral margin of the anterior portion of the preopercle. It passes along the midline of the quadratojugal, and continues anteroventrally on the dentary. Pit-lines are present on the preopercle, quadratojugal, and postparietals.

**Pectoral girdle** (Text-figs 15A, C, 16). Posttemporal, supracleithrum, and cleithrum articulate with the posterior margins of extrascapulars and the opercular series. The supracleithrum slips underneath the opercle anteriorly, and underneath the



TEXT-FIG. 16. *Amblypterus latus*, line drawing of Mb-f3809b. Scale bar represents 10 mm.

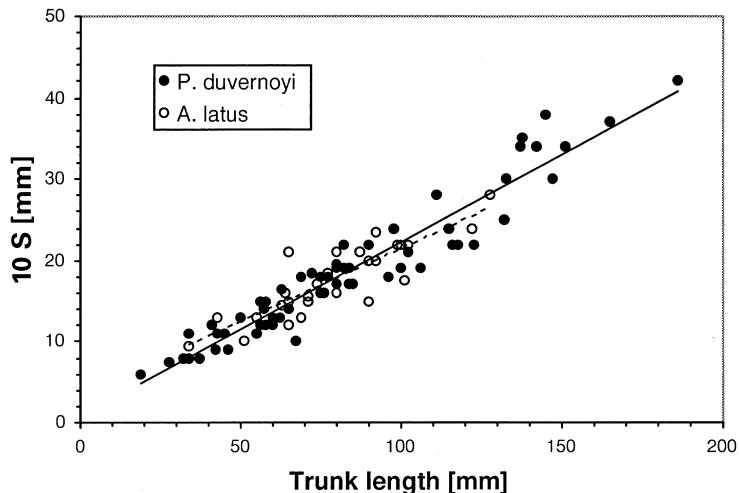
posttemporal dorsally. A postcleithrum was not observed in any of the specimens examined. The cleithrum has an articulation surface in its dorsal part for the supracleithrum. The ventral portion of the cleithrum is not preserved.

**Postcranial skeleton.** Specimens with a trunk length of 34–128 mm were examined. Scale growth is allometric (Text-fig. 17). The scales are smooth with concentric growth lines (Text-fig. 5d). Normally, the posterior edges of the scales are straight. However, specimen PIB-2 not only has additional lateral extrascapulars but also serrated scales, both of which might be related to its size. The serration of the scales is difficult to evaluate because the specimen is broken. Since the specimen is not complete, the area of serrated scales on the body could not be determined. The surface of the scales appears to bear fine ridges. About 3–4 unpaired ridge scales precede the dorsal fin and two basal scutes precede the anal fin. The dorsal margin of the caudal fin is covered with more elongated scales. Caudal peduncle and maximum body depth show allometric growth (Text-figs 18–19). 38–42 scale rows from supracleithrum to the inclination of the scales anterior to the caudal fin are present along the lateral line. There are approximately 11 scale rows above and 14 scale rows below the lateral line resulting in an overall number of 25 scale rows in *A. latus*. Growth of scales, caudal peduncle, and body depth are very similar in *A. latus* and *P. duvernoyi* (Text-figs 17–19) and cannot be used to distinguish these species. Morphological differences are discussed below.

The pectoral fin appears to be small and rectangular. The pelvic fin is small and in advance of the dorsal fin. Both fins bear fringing fulcra on their leading edges. The dorsal fin is triangular and inserts posterior to the middle of the body and slightly in advance of the anal fin. The anal fin is triangular as well. The caudal fin is heterocercal. Fringing fulcra are present on the leading edges of dorsal and anal fin, and the ventral lobe of the caudal fin. Size and position of the fins appears to be similar to that of *P. duvernoyi*, but are difficult to evaluate precisely because of poor preservation. Accordingly, it was not possible to establish the number of fin rays present. Distally, the fin rays bifurcate approximately three times in adult specimens.

#### Comparisons with Paramblypterus

Duplication of lateral extrascapulars is present in *Paramblypterus*, but not in specimens of *Amblypterus*. The supratemporal of *Amblypterus* has a ventral protuberance which has not been observed in *Paramblypterus*. Two, six, and 6–9 ‘suborbitals’ are present in *Amblypterus*, *P. duvernoyi*, and *P. decorus*, respectively. Anterior to the parietal lies an unpaired rostral, a paired ‘nasal 1’, and a paired ‘nasal 2’ in *Paramblypterus*, whereas only one set of ‘nasals’ is present in *Amblypterus*. There are one, 1–3, and 7–10 dermohyal elements present in *Amblypterus*, *P. duvernoyi*, and *P. decorus*, respectively. The branchiostegal series is composed of approximately ten, eight, and nine branchiostegal rays in *Amblypterus*, *P. duvernoyi*, and *P. decorus*, respectively. A postcleithrum is present in *Paramblypterus*, but is absent in *Amblypterus*. Whereas scales are serrated in *Paramblypterus*, the posterior edges of scales of *Amblypterus* are straight. Scales of *Paramblypterus* may have fine ridges. In contrast, scales of *Amblypterus* are smooth with concentric striae. Accordingly, D-values of scales are lower in *Amblypterus* (1·2) than in *Paramblypterus* (between 1·4 and 2·0).



TEXT-FIG. 17. Allometric scale growth of *Amblypterus latus* (dotted line) and *Paramblypterus duvernoyi* (solid line); 10S = 10 scale rows.

*Paramblypterus caudatus*, *Paramblypterus luridus*, *Paramblypterus obliquus*, *Paramblypterus reussi*

*Type locality*. Kostalov, district Semily, Czech Republic.

*Type horizon*. Rudnik Horizon, Semily Formation, lowermost Permian, Czech Republic (Stamberg 1973, 1976).

*Remarks*. Two specimens of *Paramblypterus caudatus* (Heckel, 1861) are known (Stamberg 1976). Apart from the presence of a postcleithrum, its reconstruction closely resembles that of *P. rohani*, which has only one jugal. Given the small sample size and the variation of the *Paramblypterus* species described above, *P. caudatus* and *P. rohani* might be synonymous.

The holotype of *Paramblypterus luridus* (Heckel, 1861) is poorly preserved and the only specimen known so far. According to Stamberg (1976), this species might be synonymous with *P. rohani*.

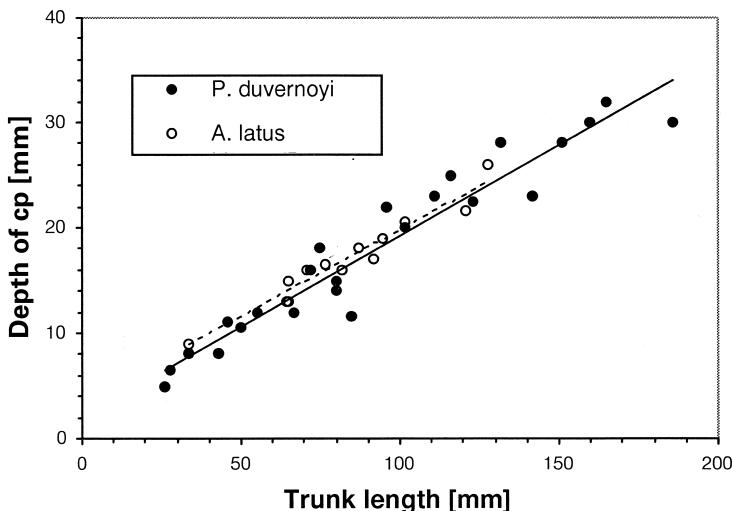
Again, only the holotype of *Paramblypterus obliquus* (Heckel, 1861) has been described (Stamberg 1976). It was considered to be a different species according to the obliquity of its scale rows, which according to Stamberg (1976) is a result of deformation of the specimen. He suggested that this species is synonymous with *P. rohani* as *P. luridus*.

*Paramblypterus reussi* (Heckel, 1861) is known only from its holotype (Stamberg 1976). Features such as shape of the trunk, parietal process, and maxilla are considered to be distinct features of this species (Stamberg 1973). However, it is likely that *P. reussi* is also synonymous with *P. rohani*.

According to the specimens available (Stamberg 1973, 1976), these species cannot be distinguished from, and might be synonymous with *P. rohani*, whose type locality is likewise Kostalov. The same applies to specimens that have been assigned to the species *P. gelberti* by Stamberg (1993). Moreover, *P. rohani* is very similar to *P. duvernoyi*, and if it were not for the single jugal even they would be difficult to tell apart.

*Paramblypterus comblei*, *Paramblypterus gaudryi*, (?)*Paramblypterus rohani*

*Type locality*. Autun Basin, France.



TEXT-FIG. 18. Caudal peduncle (cp) in relation to trunk length for *Amblypterus latus* (dotted line) and *Paramblypterus duvernoyi* (solid line).

Type horizon of *P. comblei*. Faisceau de Molloy, Stephanian C, uppermost Carboniferous (Boy and Schindler in press).

Type horizon of *P. gaudryi*. La Couche d' Igornay, Stephanian D/Autunian, uppermost Carboniferous (Boy and Schindler in press).

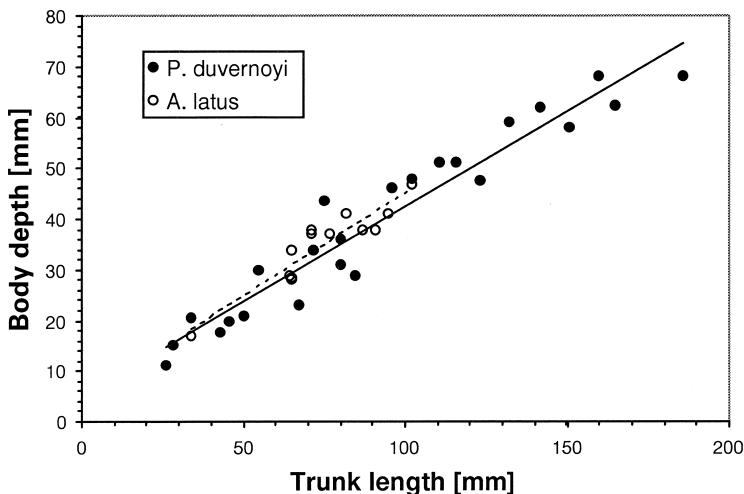
Locality of (?)*P. rohani*. La Grande Couche de Surmoulin, uppermost Carboniferous/lowermost Permian (Boy and Schindler in press).

**Remarks.** Two specimens and two fragments of *Paramblypterus comblei* (Heyler 1969) were described and considered to be a new species according to features such as shape of the maxilla and opercle, and size of 'nasal 2' (supraorbital) and supratemporal (dermopterotic) (Heyler 1969). Taking into account the intra-specific variation described above, these characters bear little validity for keying out paramblypterid species. What is figured of *P. comblei* (Heyler 1969, p. 68, fig. 9) closely resembles specimens of *P. decorus* (Heyler, 1969).

*Paramblypterus gaudryi* (Sauvage, 1890) is known only from its holotype, which is an incomplete specimen (Heyler 1969). According to Heyler (1969), it differs from other *Paramblypterus* species in the shape of the maxilla, a rather obliquely oriented opercle, an oblique suture between opercle and subopercle, and the subopercle being deeper than the opercle. Except for the latter character, none of these features would suffice to key out this species from other *Paramblypterus* species.

Except for the high subopercle of *P. gaudryi*, none of the diagnostic features given by Heyler (1969) stands up to the intra-specific variation described for *Paramblypterus*. It is likely that *P. comblei* and possibly *P. gaudryi* are junior synonyms of *P. decorus*.

Specimens from France assigned to *P. rohani* (Heyler 1971) are disarticulated for the most part. Certain skull bones are not known at all. For their dissimilarity with *P. decorus*, Heyler considered these specimens to belong to *P. rohani*. However, skull roofing bones, such as parietal, postparietal, dermosphenotic 1, and supratemporal, of the species from Surmoulin bear drawn out processes unlike anything described for either *P. rohani* or *P. duvernoyi*. Even though certain bones of *Paramblypterus* are very variable in shape, the outline of the bones of *P. rohani* from France (Heyler 1971) appear to be beyond the scope of intraspecific variation. Ornamentation of the skull bones is similar to that of *P. decorus*, but this species lacks processes entirely. The rostral of specimen MNHN-Sur179 resembles that of *P. decorus*, but



TEXT-FIG. 19. Body depth in relation to trunk length for *Amblypterus latus* (dotted line) and *Paramblypterus duvernoyi* (solid line).

is somewhat less ornamented. Unless transitional bone arrangements from any of the species described above can be established, it is impossible to include this species in either of the *Paramblypterus* species.

#### RELATIONSHIPS

The relationships of amblypterid and/or paramblypterid fishes have been dealt with earlier by Gardiner (1963, 1967a), Blot (1966), Heyler (1969, 1976), Stemberg (1976), Lowney (1980), Schaeffer (1984), Gad (1988), and Gardiner and Schaeffer (1989). According to Gardiner (1963, 1967a) both *Amblypterus* and *Paramblypterus* belong to the Amblypteridae, whereas Blot (1966), Heyler (1969, 1976) and Stemberg (1976) placed *Amblypterus* in the Amblypteridae, and *Paramblypterus* in the Paramblypteridae. Owing to the questionable reconstruction of *Amblypterus*, Lowney (1980) and Gad (1988) considered the Paramblypteridae only. According to Gardiner and Schaeffer (1989), *Paramblypterus* belongs to the so-called 'Pteronisculus-Group', which includes *Acrolepis*, *Dicellopype*, *Nematoptychius*, *Pteronisculus* and *Turseodus*; this group is interchangeable with the so-called 'Boreosomus-Group', which includes *Boreosomus* and *Ptycholepis*. Gardiner and Schaeffer (1989) placed *Amblypterus* in either the 'Belichthys-Group' or 'Amblypterus-Group', the former containing *Belichthys*, *Commentrya*, *Cornubonisicus*, *Gonatodus*, *Phanerosteon*, and 'Rhadinichthys' *carinatus*, the latter containing *Amblypterus*, *Gyrolepidotes*, *Oxypteriscus*, *Pseudogonatodus*, and *Rhadinichthys ornatissimus*. However, because of the limited size of samples, insufficient descriptions, ambiguous definition of species due to loss of type specimens, and the poor preservation of these fish species, their relationships could not be resolved sufficiently. Data obtained in this study by examination of large samples of both *Amblypterus* and *Paramblypterus*, and a revision of their type species, have finally allowed a detailed analysis of their relationships as well as their interrelationships with other lower actinopterygians. This study is focused on the relationships of amblypterid-paramblypterid fishes; other taxa will not be discussed in detail.

Taxa included in this analysis are based on sufficiently described species of the 'Pteronisculus/Boreosomus-Group' and 'Belichthys/Amblypterus-Group' established by Gardiner and Schaeffer (1989). Taxa described by Kazantseva-Seleznova (1981b) were included, since they are often left out of analyses of lower actinopterygians. Lowney (1980) considered paramblypterids to be related to certain Bear Gulch species, which therefore were added to the analysis. In addition, certain taxa that were revised recently, such as *Cyranorhis* (Lund and Poplin 1997), *Wendichthys* (Lund and Poplin 1997), *Elonichthys* (Schindler

1993), *Coccocephalus* (Poplin and Veran 1996), *Cheirolepis* (Arratia and Cloutier 1996), *Howqualepis* (Long 1988), and *Osorioichthys* (Taverne 1997) were included.

Characters such as presence of the postcleithrum, absence of fringing fulcra, number of branchiostegal rays, number of ‘suborbitals’, presence of pineal foramen, parietal/postparietal length, presence of an interclavicle, presence of a ‘postspiracular’, presence of an intertemporal bone, orientation of the suspensorium, presence of a quadratojugal, presence of a caudal flap on the tail, presence of an ascending process on parasphenoid, presence of a sclerotic ring, presence of an accessory opercle, and peg and socket articulation of the scales, were used earlier in analyses of lower actinopterygians where their plesiomorphic condition had been established (Gardiner 1967a, b, 1984; Patterson 1973; Pearson 1982; Lauder and Liem 1983; Gardiner and Schaeffer 1989; Coates 1993; Arratia and Cloutier 1996; Coates 1998, 1999). The remaining characters, such as division of the jugal, dermosphenotic, and premaxilla, or the nature of the extrascapular series, resulted from observation of certain features present in the species that are included in this analysis.

This is a broad preliminary analysis based primarily on the literature for lower actinopterygians other than the Amblypteridae (see Appendix for complete list of references). Detailed redescription of many other lower actinopterygians is necessary for a better understanding of their interrelationships. Therefore, this does *not* represent a revision of the relationships of all taxa included. The objective of this analysis is to establish relationships of the Amblypteridae, especially to those taxa they were considered to be related to earlier (e.g. Gardiner and Schaeffer 1989). Again, I emphasise that characters of taxa other than the Amblypteridae rely on data from the literature without examination of the actual specimens.

#### *Relationships of the Amblypteridae*

In this analysis, the distribution of 57 characters among 50 taxa was determined using PAUP version 3.1.1 (Swofford 1993). All characters were run unordered with delayed transformation (DELTRAN) as character optimisation. A heuristic search was carried out using the branch-swapping algorithm. *Cheirolepis trailli* (Pearson 1982), a basal actinopterygian, was used as the outgroup. PAUP resulted in 330 most parsimonious trees with each having a tree length of 408. The strict consensus tree is illustrated in Text-figure 20. Each parsimonious tree has a consistency index (CI) of 0.24, and a retention index (RI) of 0.57. Apparently, the low consistency index is related to a high degree of homoplasy among lower actinopterygians. Evaluation of high numbers of taxa generally result in low consistency indices (Sanderson and McDonoghue 1989).

All 330 most parsimonious trees resulted in a monophyletic group containing [[[Amblypteridae + *Acrolepis sedgwicki*] + *Cornuboniscus budensis*] + *Belichthys minimus*] + *Dicellopype macrodentata*]]. This group formed a polytomy with three other monophyletic groups in the strict consensus tree (Text-fig. 20). The Amblypteridae were resolved completely with [*P. decorus* + *P. rohani*] being the sister group of [*P. duvernoyi* + *P. gelberti*], and *Paramblypterus* being the sister taxon of *Amblypterus*. Even though several polytomies are present in the strict consensus tree (Text-fig. 20), the position of the Amblypteridae within the lower actinopterygians is unambiguous for the taxa that have been analysed. The Amblypteridae are most similar to *Acrolepis sedgwicki*, *Cornuboniscus budensis*, *Belichthys minimus*, and *Dicellopype macrodentata*, which are Late Permian, Early Carboniferous, and two Early Triassic taxa respectively. Various analyses were run with reduced data sets (see Appendix) excluding taxa with many uncertainties. All analyses resulted in the same topology concerning the Amblypteridae.

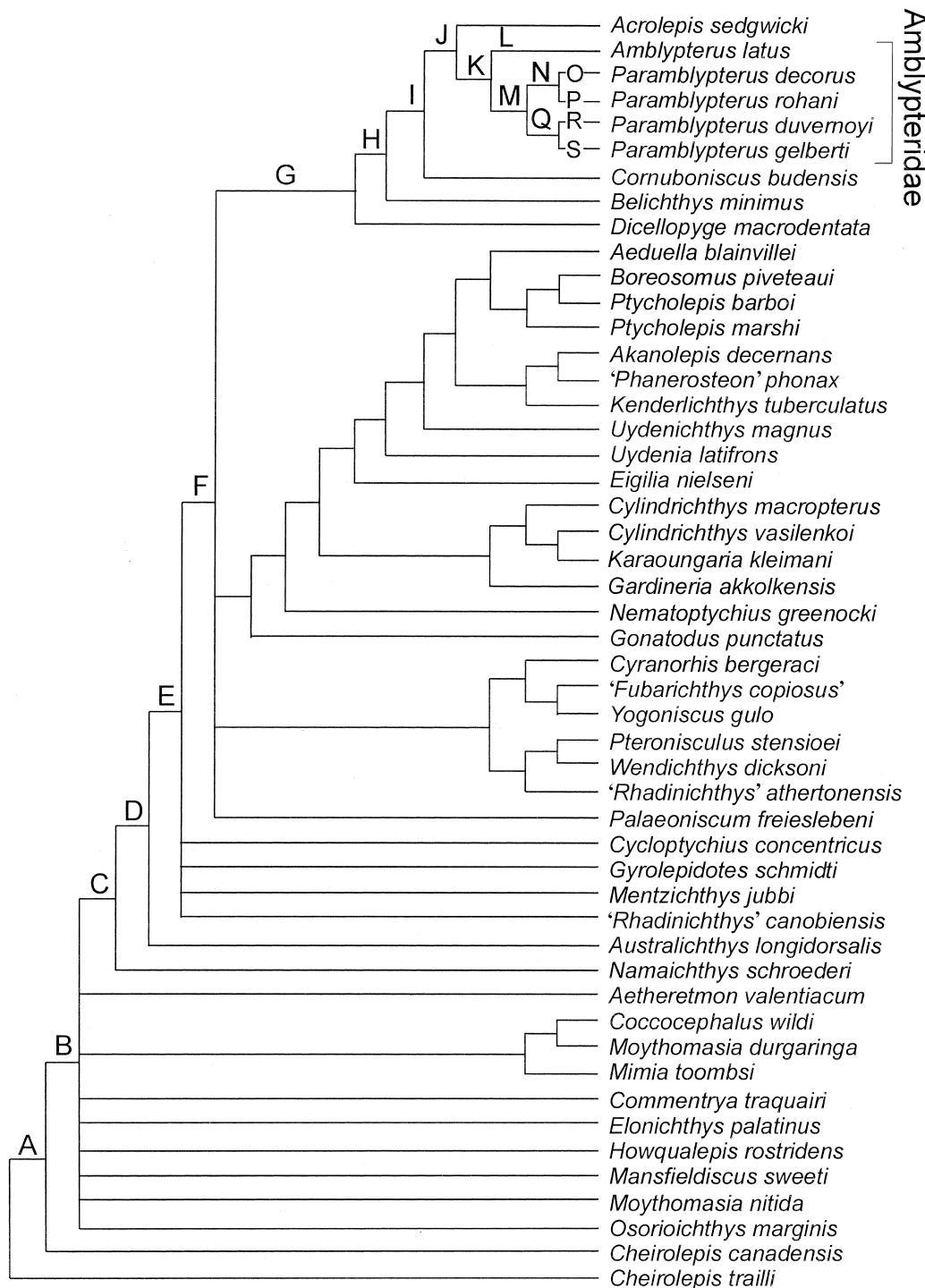
Since this study is focused on the relationships of *Amblypterus* and *Paramblypterus*, only nodes J through S which concern the Amblypteridae and their sister taxon are discussed here.

Node J is supported by the following characters:

Character 27 [0 → 1]: dentary and maxilla teeth in one series (ci = 0.167).

Character 38 [0 → 1]: snout bluntly rounded (ci = 0.100).

Character 42 [1 → 0]: opercle deeper than subopercle (ci = 0.250).



TEXT-FIG. 20. Strict consensus tree of 50 taxa analyzed for 57 characters showing the relationship of the Amblypteridae and certain lower actinopterygians.

These have low consistency indices. Moreover, character 42 represents a reversal, thus further weakening the support of this branch. This node separates the Amblypteridae and *Acrolepis sedgwicki* from the remainder of the taxa. *Acrolepis sedgwicki* closely resembles *Amblypterus latus*, but is not known completely, which may explain this grouping.

Node K is supported by the following characters. Amblypteridae.

- Character 2 [0→2]: single medial extrascapular (ci = 0.250).
- Character 7 [2→1]: parietal up to twice as long as postparietal (ci = 0.154).
- Character 16 [0→1]: dermosphenotic 2 contacts 'spiracular' (ci = 1.000).
- Character 18 [0→2]: 'spiracular' round (ci = 0.667).
- Character 31 [1→0]: quadratojugal present (ci = 0.143).
- Character 32 [0→2]: rostral tapering (ci = 0.200).
- Character 50 [0→1]: surface of scales smooth (ci = 0.500).

Three of these seven characters have consistency indices of 0.500 and higher. Apart from *Cheirolepis*, this represents the best supported branch of this analysis. It separates *Acrolepis sedgwicki* from the Amblypteridae and confirms the family Amblypteridae.

Node L is supported by the following characters. *Amblypterus latus*.

- Character 10 [1→2]: supratemporal more than two times longer than dermosphenotic 1 (ci = 0.133).
- Character 14 [1→0]: dermosphenotic 1 contacts 'nasal' (ci = 0.100).
- Character 15 [0→1]: dermosphenotic 2 contacts 'nasal' (ci = 0.333).
- Character 22 [0→2]: jugal 2 does not contact 'spiracular' (ci = 0.667).
- Character 23 [0→1]: 'suborbitals' contact jugal 2 (ci = 0.200).
- Character 45 [1→0]: gap between opercular and skull roofing bones present (ci = 0.143).
- Character 46 [0→1]: postcleithrum absent (ci = 0.100).
- Character 49 [0→1]: posterior edges of scales straight (ci = 0.333).

Two of these eight characters represent reversals. However, fairly high consistency indices of characters 15, 22, and 49 serve to corroborate this genus.

Node M is supported by the following characters. Genus *Paramblypterus*.

- Character 4 [0→1]: additional lateral extrascapulars do not contact opercle (ci = 0.222).
- Character 11 [0→1]: ventral protuberance of supratemporal absent (ci = 0.167).
- Character 19 [1→2]: three to six 'suborbitals' (ci = 0.300).
- Character 33 [1→2]: 'nasal' split up secondarily (ci = 1.000).
- Character 39 [0→1]: nine or eight branchiostegal rays (ci = 0.250).
- Character 41 [0→1]: dermohyal not single (ci = 0.250).

None of these six characters has any reversals. Character 33 appears to be a true synapomorphy of paramblypterid fishes. In comparison to other nodes, the fairly high consistency indices further confirm this genus.

Node N is supported by the following characters. *P. decorus* + *P. rohani*.

- Character 5 [0→1]: postparietal does not contact lateral extrascapular 1 (ci = 0.125).
- Character 12 [2→1]: anterior third of supratemporal contacts parietal (ci = 0.222).
- Character 18 [2→1]: 'spiracular' angular (ci = 0.667).
- Character 25 [2→1]: medium maxillary plate (ci = 0.250).
- Character 26 [1→0]: ventral margin of maxilla straight (ci = 0.125).

Since all but one of these represents reversals, this node does not seem to be supported particularly well. However, certain data of *P. decorus* and *P. rohani* not known as yet might further corroborate this branch.

Node O is supported by the following characters. *P. decorus*.

- Character 6 [1 → 0]: parietal long and rectangular (ci = 0.200).  
 Character 10 [1 → 0]: equal length of supratemporal and dermosphenotic 1 (ci = 0.133).  
 Character 19 [2 → 3]: more than six ‘suborbitals’ (ci = 0.300).  
 Character 22 [0 → 1]: jugal 2 contacts ‘spiracular’ (ci = 0.667).  
 Character 29 [1 → 0]: gape long (ci = 0.200).  
 Character 30 [1 → 0]: suspensorium oblique (ci = 0.400).  
 Character 32 [2 → 1]: rostral flaring (ci = 0.200).  
 Character 37 [0 → 1]: premaxilla contacts lacrimal ventrally (ci = 0.167).  
 Character 43 [1 → 2]: supratemporal contact opercle caudoventrally (ci = 0.167).  
 Character 44 [0 → 1]: enlarged postcleithral scales present (ci = 0.167).  
 Character 53 [1 → 0]: dense skull ornamentation (ci = 0.125).

Seven of these 11 characters represent reversals. Within the Amblypteridae, the number of ‘suborbitals’, the contact of the jugal 2 to the ‘spiracular’, the flaring rostral, the premaxilla contacting the lacrimal ventrally, enlarged postcleithral scales, and dense skull ornamentation serve to distinguish *P. decorus* from other species of the genus. However, owing to homoplasy of these features among lower actinopterygians, these differences do not show in this analysis.

Node P is supported by the following characters. *P. rohani*.

- Character 4 [1 → 2]: additional lateral extrascapulars contact opercle (ci = 0.222).  
 Character 7 [1 → 2]: parietal more than two times longer than postparietal (ci = 0.154).  
 Character 8 [0 → 1]: parietal process present (ci = 0.500).  
 Character 17 [2 → 1]: dermosphenotic 2 does not contact ‘suborbitals’ (ci = 0.222).  
 Character 20 [1 → 0]: jugal not split (ci = 0.222).  
 Character 23 [2 → 0]: ‘suborbitals’ do not contact jugal 2 (ci = 0.200).  
 Character 24 [2 → 1]: ‘suborbitals’ do not contact maxilla (ci = 0.222).  
 Character 39 [1 → 2]: seven or fewer branchiostegal rays (ci = 0.250).  
 Character 46 [0 → 1]: postcleithrum absent (ci = 0.100).  
 Character 55 [0 → 1]: sclerotic ring absent (ci = 0.111).

Four of these ten characters are reversals.

Node Q is supported by the following characters. *P. duvernoyi* + *P. gelberti*.

- Character 8 [0 → 1]: parietal process present (ci = 0.500).  
 Character 10 [1 → 2]: supratemporal more than twice as long as dermosphenotic 1 (ci = 0.133).  
 Character 16 [0 → 2]: dermosphenotic 2 does not contact ‘spiracular’ (ci = 1.000).  
 Character 17 [2 → 1]: dermosphenotic 2 contacts ‘suborbitals’ (ci = 0.222).  
 Character 21 [1 → 2]: jugal 1 contacts ‘suborbitals’ posteriorly (ci = 0.231).  
 Character 22 [0 → 2]: jugal 2 does not contact ‘spiracular’ (ci = 0.667).  
 Character 55 [0 → 1]: sclerotic ring absent (ci = 0.125).

As mentioned earlier (Dietze 1999), *P. duvernoyi* and *P. gelberti* are very similar species. In all analyses, they were grouped together, and had a branch support of 100 per cent when bootstrapped. Seven characters support this group with high consistency indices of character 8, 16 and 22.

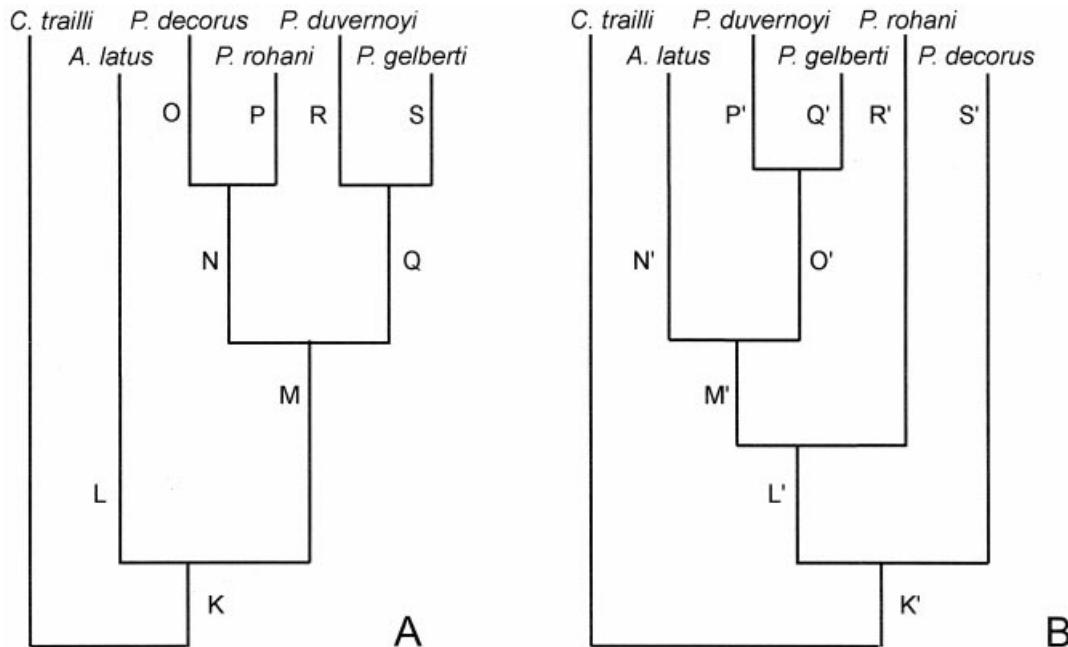
Node R is supported by the following character. *P. duvernoyi*.

- Character 4 [1 → 2]: additional lateral extrascapulars contact opercle (ci = 0.222).

This node is supported by only one character, thus confirming the similarity of *P. duvernoyi* and *P. gelberti*.

Node S is supported by the following characters. *P. gelberti*.

- Character 43 [1 → 0]: supratemporal does not contact opercle (ci = 0.167).  
 Character 53 [1 → 2]: little skull ornamentation (ci = 0.125).



TEXT-FIG. 21. Separate analysis of the Amblypteridae, character states at nodes. A, *Paramblypterus* is the sister taxon of *Amblypterus*: Node K, 1[1], 2[2], 6[1], 7[1], 9[1], 12[1], 13[1], 16[1], 18[1], 20[1], 21[1], 24[2], 25[1], 27[1], 28[1], 29[2], 30[1], 32[1], 40[1], 43[1], 48[1], 50[1], 53[1], 54[1], 56[1], 57[1]; Node L, 10[2], 15[1], 17[2], 19[1], 22[2], 23[1], 26[1], 33[1], 34[1], 38[1], 46[1], 49[1]; Node N, 5[1], 12[1], 18[1], 25[1]; Node P, 4[2], 7[2], 8[1], 10[1], 20[0], 24[1], 39[2], 46[1], 55[1]; Node Q, 8[1], 10[2], 16[2], 21[2], 22[1], 23[2], 26[1], 34[1], 38[1], 55[1]; Node R, 4[2]; Node S, 43[0], 53[2]; Node O, 6[0], 17[2], 19[3], 22[1], 29[0], 30[0], 32[1], 37[1], 43[2], 44[1], 53[0]. B, *P. decorus* is the sister taxon of the remaining species of the Amblypteridae: Node K', 1[1], 2[2], 7[1], 9[1], 11[1], 12[1], 13[1], 14[1], 15[2], 16[1], 18[1], 21[1], 24[2], 25[1], 27[1], 28[1], 33[2], 40[1], 41[1], 45[1], 48[1], 50[1], 56[1], 57[1]; Node L', 6[1], 17[1], 19[2], 29[1], 30[1], 43[1], 53[1], 54[2]; Node N', 11[0], 14[0], 15[1], 17[2], 19[1], 23[1], 33[1], 41[0], 45[0], 46[1], 49[1]; Node O', 8[1], 16[2], 21[2], 23[2], 39[1], 55[1]; Node Q', 4[1], 43[0], 53[2]; Node R', 4[2], 5[1], 7[2], 8[1], 10[1], 24[1], 39[2], 46[1], 55[1]; Node S', 4[1], 5[1], 17[2], 19[3], 20[1], 22[1], 32[1], 37[1], 39[1], 43[2], 44[1]; Node M', 10[2], 12[2], 18[2], 20[1], 22[2], 25[2], 26[1], 32[2], 34[1], 38[1].

As for the previous node, few characters support this branch, which indicates the difficulty in keying out *P. gelberti* and *P. duvernoyi*.

**Remarks.** Until now, *Amblypterus* species were keyed out according to the reconstruction given by Gardiner (1963), which differs completely from *Paramblypterus*. However, his reconstruction shows an elonichthyid type of maxilla in *Amblypterus*, which in fact is not present. In contrast, the maxilla of *Amblypterus* is similar to *Paramblypterus*, thus resulting in a reconstruction close to paramblypterid species. When analysed separately, this similarity became even more obvious. *Amblypterus* appears among *Paramblypterus* species (Text-fig. 21B), and the genus *Paramblypterus* appears to be called into question. However, features supporting this are related to the feeding apparatus, and resemble adaptations for improved suction feeding, such as an oblique suspensorium or a short gape. In contrast, characters which support the genus *Paramblypterus* are not related to a certain morphological construction (Text-fig. 21A). Moreover, certain features which result in a separation of *Amblypterus* and *Paramblypterus* appear much earlier in the overall analysis.

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## APPENDIX

*Anatomical abbreviations*

a.l.j, articulation for lower jaw; a.no, anterior nostril; Ang, angular; asc.proc, ascending process; b.h.c, bucco-hypophysial canal; Br.r, branchiostegal rays; Cl, cleithrum; Cor, coronoid; c.par, parasphenoid body; D, dentary; Dhy, dermohyal; Dpl 1–3, dermopalatines 1–3; Dph 1 & 2, dermosphenotic 1 and 2; Ect, ectopterygoid; Ent, entopterygoid; inf.s.c, infraorbital sensory canal; Ju 1 & 2, jugal 1 and 2; I.Exc 1–4, lateral extrascapular 1–4; I.Gu, lateral gular; La, lacrimal; m.Exc, medial extrascapular; m.Gu, median gular; Mx, maxilla; Mtg, metapterygoid; 'Na', compound bone consisting of nasal, pre- and supraorbital, which is split up secondarily in *Paramblypterus*; 'Na 1–3', secondarily split up 'nasal'; Op, opercle; Pa, parietal; Par, parasphenoid; par.c, parabasal canal; Pcl, postcleithrum; Pmx, premaxilla; p.no, posterior nostril; Pop, preopercle; porb.s.c, postorbital sensory canal; Ppa, postparietal; Prar, prearticular; Ptt, posttemporal; Q, quadrate; Qj, quadratojugal; Ro, rostral; 'Sbo', suborbital; Scl, supracleithrum; Sop, subopercle; Sorb, supraorbital; sorb.br, supraorbital branch; sorb.s.c, supraorbital sensory canal; 'Spi', 'spiracular'; spi.g, spiracular groove; S.r, sclerotic ring elements; St, supratemporal; st.s.c, supratemporal sensory canal.

*List and definition of characters used for analysis*

Character polarity was determined using outgroup comparison. *Cheirolepis trailli* (Pearson 1982) was used as the outgroup and character states present in this species were considered plesiomorphic.

1. Pineal foramen [0 = present; 1 = absent].
2. Medial extrascapular [0 = absent; 1 = paired; 2 = single]. The extrascapular series starts out with a single pair of lateral extrascapulars, e.g. *Cheirolepis trailli* (Pearson 1982), which divides further into medial and lateral extrascapulars. Subsequently, the medial pair of extrascapulars fuses.
3. Expansion of maxilla set off posteriorly [0 = yes; 1 = no].
4. Additional lateral extrascapular [0 = absent; 1 = present, without contact to opercle; 2 = present, contact to opercle]. Depending on whether the duplication of the extrascapular series is present, their contact to the opercular series is determined.
5. Postparietal contacts lateral extrascapular 1 [0 = yes; 1 = no].
6. Shape of postparietal [0 = long and rectangular; [1 = square; 2 = narrow and rectangular].
7. Length of parietal in relation to length of postparietal [0 = equal length of parietal and postparietal; 1 = parietal up to twice as long as postparietal; 2 = parietal more than twice as long as postparietal].
8. Parietal process between supratemporal and dermosphenotic [0 = absent; 1 = present].
9. Intertemporal bone [0 = present; 1 = absent]. As mentioned earlier, an intertemporal is present in Devonian species, such as *Cheirolepis trailli*, *Howqualepis rostridens*, and *Moythomasia nitida* (Pearson 1982; Long 1988;

- Jessen 1968). Subsequently, the intertemporal either becomes fused to dermosphenotic or supratemporal, or is lost. However, because of different proportions of the supratemporal and dermosphenotic, it is impossible to determine what part of the intertemporal bone fused to which bone, or if it had fused to any bones at all. Therefore, if a separate ossification of the intertemporal could not be accounted for, it was coded absent.
10. Length of supratemporal in relation to length of dermosphenotic [0 = equal length of supratemporal and dermosphenotic; 1 = supratemporal longer than dermosphenotic; 2 = supratemporal more than two times longer than dermosphenotic].
  11. Ventral protuberance of the supratemporal [0 = present; 1 = absent]. As can be seen in *Amblypterus* (Text-fig. 15c), the lateral margin of the supratemporal can be drawn out which refers to the protuberance and is coded 0. If the lateral margin is straight it is coded 1.
  12. Contact of supratemporal and parietal [0 = absent; 1 = anterior third of supratemporal contacts parietal; 2 = more than anterior third of supratemporal contacts parietal].
  13. Dermosphenotic split in two [0 = no; 1 = yes].
  14. Dermosphenotic or dermosphenotic 1 contact 'nasal' or 'nasal 1' [0 = yes; 1 = no].
  15. Dermosphenotic 2 contacts 'nasal' or 'nasal 1' [0 = dermosphenotic 2 absent; 1 = yes; 2 = no].
  16. Dermosphenotic 2 contacts 'spiracular' [0 = 'spiracular' absent; 1 = yes; 2 = no].
  17. Dermosphenotic 2 contacts 'suborbitals' [0 = 'suborbitals' or dermosphenotic 2 absent; 1 = yes; 2 = no].
  18. Shape of 'spiracular' [0 = 'spiracular' absent; 1 = angular; 2 = round].
  19. Number of 'suborbitals' present [0 = less than two; 1 = two; 2 = three to six; 3 = more than six].
  20. Jugal split [0 = no; 1 = in two; 2 = in three].
  21. Contact of jugal or jugal 1 to 'suborbitals' [0 = 'suborbitals' absent; 1 = posteriorly; 2 = posterodorsally; 3 = no contact].
  22. Jugal 2 contacts 'spiracular' [0 = 'spiracular' absent; 1 = yes; 2 = no].
  23. 'Suborbitals' contact jugal 2 [0 = jugal 2 absent; 1 = yes; 2 = no].
  24. 'Suborbitals' contact maxilla [0 = 'suborbitals' absent; 1 = no; 2 = yes].
  25. Shape of posterior expansion of maxillary plate [0 = low; 1 = medium; 2 = deep]. The character state of the maxillary plate was determined by dividing the depth of the maxilla by its length. Low, medium, and deep maxillary plate have a ratio of less than 0.25, between 0.25 and 0.35, and higher than 0.35 respectively. However, maxillary plates are extremely irregular in outline, and this character may be difficult to reproduce exactly. Still, I decided to include it because different depths of the maxilla are an obvious feature of lower actinopterygians.
  26. Ventral margin of maxilla [0 = straight; 1 = curved]. The ventral margin of the maxilla was considered straight if the angle enclosed by the ventral and the posteroventral margin of the maxilla does not exceed 5 degrees. As already explained for the preceding character, exact measurements are difficult owing to the varying shape of the maxilla and might be affected by subjectivity.
  27. Dentary and maxillary teeth in two series [0 = yes; 1 = no].
  28. Laniary teeth present [0 = yes; 1 = no].
  29. Gape [0 = long; 1 = short]. Gape length was calculated by dividing the length of the mouth opening to the anteriormost part of the jaw margin by the length from the posterior margin of the opercle to the anteriormost part of the jaw margin. For long and short gapes the ratio is equal or higher than 0.5 and lower than 0.5 respectively. Again, this character might prove difficult to reproduce exactly.
  30. Orientation of suspensorium [0 = oblique; 1 = less oblique; 2 = ± vertical]. Orientation of approximately 45 degrees to the horizontal (reflected by the orientation of the preopercle) was considered oblique. Angles between 45 and 70 degrees were coded 2, and more obtuse-angled suspensoria were regarded as almost vertical. Since the orientation of the preopercle served to determine the angle and not the actual orientation of the suspensorium, this character is based on the assumption of a close relationship of preopercle and underlying suspensorium, which is not established for all the species used in this analysis.
  31. Quadratojugal present [0 = yes; 1 = no].
  32. Rostral [0 = straight; 1 = flaring; 2 = tapering]. If the rostral bone neither widened nor narrowed anteriorly it was considered straight and coded 0. A rostral was identified as flaring and coded 1 if it widened anteriorly as is the case in *P. decorus* (Text-fig. 2d). If the rostral narrowed anteriorly it was coded 2.
  33. Supraorbital, preorbital, and nasal [0 = not fused; 1 = fused to 'nasal'; 2 = split up secondarily into 'nasals 1–3']. The supraorbital, preorbital, and nasal are present lateral to the rostral in *Cheirolepis trailli* (Pearson 1982) and *Cheirolepis canadensis* (Arratia and Cloutier 1996). In most of the other species included in this analysis, only one bone, the 'nasal', is present lateral to the rostral, which is thought to contain all three elements. This bone is secondarily split up into two or three elements, the 'nasals 1–3'.
  34. 'Nasal' or nasal contacts premaxilla [0 = no; 1 = yes].
  35. Preopercle with distinct anterior and ventral portion [0 = yes; 1 = no].

36. Division of premaxilla [0 = premaxilla not divided; 1 = anteriorly/posteriorly; 2 = ventrally/dorsally].
37. Contact of premaxilla to lacrimal [0 = posteriorly; 1 = ventrally; 2 = none].
38. Shape of snout [0 = blunt, with rostrum; 1 = bluntly rounded]. Many primitive actinopterygians have a blunt snout that is flat or drawn out anteriorly: this is character state 0. If the snout is rounded anteriorly it is coded as 1.
39. Number of branchiostegal rays present [0 = ten or more; 1 = nine or eight; 2 = seven or fewer].
40. Angle enclosed by ventral and anterior portion of preopercle [0 = angle wider than 90 degrees; 1 = angle narrower than 90 degrees].
41. Dermohyal present as a single ossification [0 = yes; 1 = no; 2 = dermohyal absent].
42. Depth of suboperculum and opercle [0 = opercle deeper than subopercle; 1 = opercle lower than subopercle]. Opercular and subopercular depths were established by following the length of the dorsal portion of these bones and at right angles measuring the longest possible distance to their ventral margin. This parameter proved difficult when edges were slightly convex or protuberances were present, but it did not affect the relation of the depths of these bones.
43. Contact of supratemporal to opercle [0 = none; 1 = ventrally; 2 = ventrocaudally].
44. Enlarged postcleithral scales [0 = absent; 1 = present].
45. Gap between opercular series and skull roofing bones [0 = present; 1 = absent].
46. Postcleithrum [0 = present; 1 = absent].
47. Interclavicle [0 = present; 1 = absent].
48. ‘Postspiracular’ [0 = present; 1 = absent].
49. Posterior edges of scales [0 = serrated; 1 = straight; 2 = not applicable].
50. Surface of scales smooth [0 = no; 1 = yes; 2 = not applicable].
51. Fringing fulcra present [0 = no; 1 = not on all fins; 2 = on all fins].
52. Caudal flap present [0 = yes; 1 = no].
53. Skull ornamentation [0 = dense; 1 = moderate; 2 = little].
54. Ascending process on parasphenoid [0 = absent; 1 = small; 2 = true].
55. Sclerotic ring present [0 = yes; 1 = no].
56. Accessory opercle present [0 = yes; 1 = no].
57. Peg and socket articulation of scales present [0 = no; 1 = yes; 2 = not applicable].

*Taxa entered into PAUP analysis, their stratigraphical distribution and reference*

*Acrolepis sedgwicki*; U. Permian, Great Britain; Aldinger 1937. *Aeduella blainvillei*; L. Permian, France; Heyler 1969. *Aetherthmon valentiacum*; L. Carboniferous, Scotland; White 1927. *Akanolepis decernans*; U. Carboniferous, Russia; Kazantseva-Selezneva 1981b. *Australichthys longidorsalis*, L. Carboniferous, South Africa; Gardiner 1969. *Belichthys minimus*, L. Triassic, Australia; Hutchinson 1975. *Boreosomus pivotteaui*; Triassic, Greenland; Nielsen 1942. *Cheirolepis canadensis*; U. Devonian, Canada; Arratia and Cloutier 1996. *Cheirolepis trailli*; M. Devonian, Scotland; Pearson 1982. *Coccocephalus wildi*; U. Carboniferous, Great Britain; Poplin and Veran 1996. *Commentrya traquairi*; U. Carboniferous, France; Blot 1966. *Cornuboniscus budensis*; L. Carboniferous, Great Britain; White 1939. *Cycloptychius concentricus*, L. Carboniferous, Great Britain; Moy-Thomas and Dyne 1938. *Cylindrichthys macropterus*; L. Permian, Russia; Kazantseva-Selezneva 1981b. *Cylindrichthys vasilenkoi*; L. Permian, Russia; Kazantseva-Selezneva 1981b. *Cyranorhis bergeraci*; L. Carboniferous, North America; Lund and Poplin 1997. *Dicellopype macrodentata*; L. Triassic, Australia; Hutchinson 1975. *Eigilia nielseni*; U. Permian, Russia; Kazantseva-Selezneva 1981b. *Elonichthys palatinus*; L. Permian, Germany; Schindler 1993. ‘*Fubarichthys copiosus*’; L. Carboniferous, North America; Lowney 1980. *Gardiniera akkolkensis*; U. Permian, Russia; Kazantseva-Selezneva 1981b. *Gonatodus punctatus*; L. Carboniferous, Scotland; Gardiner 1967b. *Gyrolepidotes schmidti*; Carboniferous?, Russia; Matveeva 1958. *Howqualepis rostridens*; U. Devonian, Australia; Long 1988. *Karaoungaria kleimani*; L. Permian, Russia; Kazantseva-Selezneva 1981b. *Kenderlichthys tuberculatus*; U. Carboniferous, Russia; Kazantseva-Selezneva 1981b. *Mansfieldiscus sweeti*; L. Carboniferous, Australia; Long 1988. *Mentzichthys jubbi*; L. Carboniferous, South Africa; Gardiner 1969. *Mimia toombsi*; U. Devonian, Australia; Gardiner 1984. *Moythomasia durgaringa*; U. Devonian, Australia; Gardiner 1984. *Moythomasia nitida*; U. Devonian, Germany; Jessen 1968. *Namaichthys Schroederi*; U. Carboniferous, South Africa; Gardiner 1962. *Nematoptychius greenocki*; L. Carboniferous, Scotland; Gardiner 1963. *Osorioichthys marginis*; U. Devonian, Belgium; Taverne 1997. *Palaeoniscum freieslebeni*; U. Permian, Germany and Great Britain; Aldinger 1937. *Paramblypterus duvernoyi*; L. Permian, Germany; Dietze 1999. *Paramblypterus gelberti*; L. Permian, Germany; Dietze 1999. *Paramblypterus rohani*; U. Carboniferous, Czech Republic; Stemberg 1976. ‘*Phanerosteon*’ *phonax*; L. Carboniferous, North America; Lowney 1980. *Pteronisculus stensioei*; Triassic, Greenland; Nielsen 1942. *Ptycholepis barboi*; M. Triassic, Switzerland; Bürgin 1992. *Ptycholepis marshi*; U. Triassic, North America; Schaeffer *et al.* 1975. ‘*Rhadinichthys*’ *athertonensis*; L. Carboniferous, North America; Lowney 1980. *Rhadinichthys canobiensis*; L. Permian, Great

Britain; Moy-Thomas and Dyne 1938. *Uydenia latifrons*; L. Carboniferous, Russia; Kazantseva-Selezneva 1981b. *Uydenichthys magnus*; L. Permian, Russia; Kazantseva-Selezneva 1981b. *Wendichthys dicksoni*; L. Carboniferous, North America; Lund and Poplin 1997. *Yogoniscus gulo*; L. Carboniferous, North America; Lowney 1980.

#### *Material examined*

The Natural History Museum, London; all prefixed BMNH- (22658, 2900b, 36128, 44082, P10263, P10265, P12099, P14536, P28487a/b, P29285, P3420, P3457, P3458a, P3458b, P3459, P3475a, P607, P6195, P6195, P797, P978, P979, P980, P994). Bayrische Staatssammlung für Geologie und Paläontologie, Munich (BSM 1871 II 1). Geologisch-Paläontologisches Institut Mainz; all prefixed GPIM- (1, 10–19; 2, 20–25, 26a/b, 27–29; 3, 30–39; 4, 40–49; 5, 50–59; 6, 60–64; 7; 8; 9; F375; M1098; M1211; M1214; M1217; M1220; M1223–M1225; M1229; M1233; M1235; M1238–M1239; M1241; M1244–M1246; M1248; M1250; M1252; M1255; M1257–M1259; M1281, M1300; M1325; M1405; M1409; M1411–M1412; M1414; M1421; M1423; M1425; M1446; M1575; M1593; M1595–M1596; M1604; M1606; M1609; M1616–M1617; M1623–M1624; M1626; M1628–M1631; M1636a/b; M1639; M1642; M1662; M1666; M1669a/b; M1797b; M1799; M1801; M1807; M1820; M1838b; M1839a/b; M1840a/b; M1841a/b; M1842a/b; M1843; M1851; M1853; M1855; M1868a/b; M1869a/b; M1870a/b; M1887a/b; M1889–M1891; M1893a/b; M1894a/b; M1896; M1939, M1962; M2009; M2134; M2136; M2248; M2249; M2257–M2258; M2259a/b; M2260a/b; M2261; M2263; M2264a/b; M2265a/b; M2267–M2270; M2272–M2273; M2275; M2276a/b; M2277–M2294; M2295a/b; M2296; M2298; M2300–M2302; M2303a/b; M2305a/b; M2306; M2309–M2316; M2317a/b; M2318; M2319a/b; M2320–M2322; M2324–M2328; M2330–M2334; M2825–M2826; M2964; M3380; M3950; M3953; M3958–M3960; M4238–M4239; M4246; M4294; M4300; M4309; M4314; M4408; M4469; M4887–M4888; M4905, M4905/1, M4905/2; M4907, M4907/1–4; M4915; M4937; M4939; M4947; M4954–M4955; M4959; M4961; M4962, M4962/1–3; M4963; M4966; M4971–4972, M4972/1–2; M4973–M4975; M4994; M5174; M581; M5810–M5811; M5819–M5822; P111b). Museum Historiae Naturalis Casselense, Kassel (MHNC, 2 specimens without institutional number). Museum für Naturkunde der Humboldt-Universität, Berlin; all prefixed MB- (f1504–f1505, f15415a/b, f2528, f304a/b, f3794b, f3795, f3796a/b, f3797, f3799a/b, f3800a/b, f3801, f3802a/b, f3803–f3805, f3806a/b, f3809a/b, f614a, f9.III.1900, I00321, I00326b, I00402a, 10 specimens without institutional number). Muséum National d'Histoire Naturelle, Paris; all prefixed MNHN- (1, 8, 5D, 094, 230, 283B, 366A, 371, 425A, 430B, 451, 466, 509, 630, 647, 1044, 1255B, 1257B, 1262, 1329, 1334, 1340B, 10124, 10724, 093, 1/130B, 1/144, 1/262B, 1/203, 190417, 19551262, 195812, 19582, 19587, 195814, 195820, 19591, 19614, 19611, 19621, 1889362g, 1889365, 18893614, 18893627, 18893618, 18893621, 18893622A, 18893620, 18893622D, 18893628, 18893629, 18893631, 18893636M, 188936293V, 18893625431, 18893638292, 18893642332, 188936BA, 188936269D39, PA, 1606, COM20, COM49, COM51, COM53, COM147, COM157, 456D, 537, 598, 1/208, 1/263, 1/268, 1/304, 600, G120/1, G120/2, 1/264, Sur179, 1/53, 1/12B, Sur179). Landessammlung für Naturkunde Rheinland-Pfalz, Naturhistorisches Museum Mainz; all prefixed NHM/LfN- (PW199566L-S, PW199567L-S, PWL1985/4, 1 specimen without institutional number); Paläontologisches Institut, Bonn (PIB, 10 specimens without institutional number). Pfalzmuseum für Naturkunde, Bad Dürkheim; all prefixed PMNB- (BGC112, FJC26, FJC6, FJC8, FJC73–FJC76, FJC78, GRE10, PDC97–PDC98, ROT391, WÖR27, WÖR56, WÖR66). Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt/Main; all prefixed SMF- (P75a/b, R497, 498). Université de Strasbourg, Laboratoire de Géologie et Paléontologie; all prefixed USGP- (St21, St23, St25, St27–St29). Museum der Saarbergwerke, Saarbrücken (MSS, 5 specimens without institutional number).

#### *Reduced data sets*

1. *Amblypterus latus*, *Boreosomus piveteaui*, *Cheirolepis canadensis*, *Cheirolepis trailli*, *Commentrya traquairi*, *Cyranorhis bergeraci*, *Elonichthys palatinus*, ‘*Fubarichthys copiosus*’, *Gonatodus punctatus*, *Howqualepis rostridens*, *Mansfieldiscus sweeti*, *Mimia toombsi*, *Moythomasia durgaringa*, *Moythomasia nitida*, *Palaeoniscum freieslebeni*, *Paramblypterus decorus*, *Paramblypterus duvernoyi*, *Paramblypterus gelberti*, ‘*Phanerosteon*’ *phonax*, *Pteronisculus stensioei*, *Ptycholepis barboi*, *Ptycholepis marshi*, *Rhadinichthys canobiensis*, ‘*Rhadinichthys*’ *athertonensis*, *Wendichthys dicksoni*, *Yogoniscus gulo*.
2. *Amblypterus latus*, *Boreosomus piveteaui*, *Cheirolepis canadensis*, *Cheirolepis trailli*, *Commentrya traquairi*, *Cyranorhis bergeraci*, *Elonichthys palatinus*, ‘*Fubarichthys copiosus*’, *Gonatodus punctatus*, *Palaeoniscum freieslebeni*, *Paramblypterus decorus*, *Paramblypterus duvernoyi*, *Paramblypterus gelberti*, ‘*Phanerosteon*’ *phonax*, *Pteronisculus stensioei*, *Rhadinichthys canobiensis*, *Wendichthys dicksoni*, *Yogoniscus gulo*.

#### *Character data matrix*

Numbers in parentheses refer to polymorphic characters (variable within species). Uncertainties are entered as ‘?’

|                                     | 1–5          | 6–10      | 11–15     | 16–20     | 21–25     | 26–30     | 31–35     | 36–40     | 41–45     | 46–50        | 51–57            |
|-------------------------------------|--------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|--------------|------------------|
| <i>Acrolepis sedgwicki</i>          | 1 0 0 1 0    | 1 2 0 1 1 | 0 2 1 1 2 | ? ? ? ? 1 | ? ? ? ? 2 | 1 1 1 1 1 | 1 0 1 ? 0 | ? ? 1 0 1 | 0 0 1 ? 1 | 0 ? 1 0 0    | 2 ? 0 ? ? 1 1    |
| <i>Aeduella blainvilliei</i>        | 1 1 1 1 1    | 0 1 0 1 0 | 1 1 1 0 2 | 0 ? 2 3 0 | 1 ? ? 2 0 | 0 1 1 1 2 | 1 0 1 ? 1 | ? ? 1 2 0 | 2 0 1 0 1 | 1 ? 1 1 1    | 1 1 2 ? 1 1 1    |
| <i>Aetherichthys valentiacum</i>    | 1 0 0 0 ?    | 0 ? ? 0 ? | ? ? ? ? ? | ? ? ? 2 ? | 1 ? ? 1 1 | 0 0 0 0 0 | ? ? ? ? 0 | ? ? ? 0 1 | 0 0 1 0 ? | 0 ? ? 0 0    | 2 1 0 2 0 1 1    |
| <i>Akanolepis decernans</i>         | 1 0 1 0 0    | 0 1 0 1 0 | 1 0 1 1 1 | 0 0 0 0 1 | 0 0 0 0 1 | 0 ? ? 1 1 | 2 0 1 1 1 | 2 0 1 2 1 | 0 1 1 ? 1 | ? ? ? 1 0    | ? ? 1 ? ? 1 1    |
| <i>Amblypterus latus</i>            | 1 2 0 0 0    | 1 1 0 1 2 | 0 2 1 0 1 | 1 2 2 1 1 | 1 2 1 2 2 | 1 1 1 1 1 | 0 2 1 1 0 | 0 0 1 0 1 | 0 0 1 0 0 | 1 ? 1 1 1    | 2 ? 1 2 0 1 1    |
| <i>Australichthys longidorsalis</i> | 1 0 0 0 0    | 1 2 0 1 2 | 1 2 0 0 0 | 0 0 0 1 0 | 1 0 0 2 1 | 0 0 0 0 0 | 2 0 1 1 0 | 0 0 0 0 1 | 0 0 1 0 0 | 1 ? 1 0 0    | ? ? 0 ? 1 1 1    |
| <i>Belichthys minimus</i>           | 1 0 0 0 0    | 1 2 0 1 1 | 0 2 ? 0 ? | 0 ? 0 1 ? | ? ? ? 1 0 | 0 ? ? 0 0 | 1 0 1 1 0 | 2 1 1 0 0 | 0 1 1 0 1 | 1 ? 1 ? 0    | 1 0 1 ? 1 1 1    |
| <i>Boreosomus pivateui</i>          | 1 1 1 0 0    | 0 2 0 1 0 | 1 1 1 0 2 | 0 2 0 2 1 | 2 0 2 1 0 | 0 1 1 1 2 | 1 0 1 1 1 | 0 1 0 1 0 | 0 0 1 0 0 | 1 ? 1 0 0    | 2 1 1 2 0 1 1    |
| <i>Cheirolepis canadensis</i>       | 0 0 0 0 0    | 0 0 0 1 0 | 1 0 0 1 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 ? 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 1 0    | 1 0 0 0 0 0 0    |
| <i>Cheirolepis trailli</i>          | 0 0 0 0 0    | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0    | ? 0 0 0 0 0 0    |
| <i>Coccocephalus wildi</i>          | 1 1 0 1 1    | 0 2 0 1 1 | 1 1 1 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 1 0 0 0 0 | 1 0 1 1 0 | 0 0 0 ? 0 | 0 0 0 ? ? | ? ? 1 ? ?    | ? ? 1 1 ? 1 ?    |
| <i>Commentrya traquairi</i>         | 1 1 0 1 1    | 1 2 0 1 0 | 1 1 0 0 0 | 0 0 0 2 1 | 1 0 2 2 0 | 0 0 0 0 0 | 0 ? 1 1 0 | 1 0 0 1 0 | 0 0 1 0 0 | 0 2 0 0 0    | 2 0 0 ? 0 1 1    |
| <i>Cornuboniscus budensis</i>       | 1 0 0 0 0    | 1 2 0 1 0 | 0 2 1 1 2 | 0 2 0 1 1 | 1 0 2 1 2 | 0 0 0 1 1 | 2 0 1 1 0 | 0 0 0 0 1 | 0 1 0 1 1 | 0 ? 1 0 0    | 1 0 1 ? 0 1 1    |
| <i>Cycloptychius concentricus</i>   | 1 0 0 0 0    | 1 2 0 1 1 | 0 2 0 0 0 | 0 0 0 1 0 | 1 0 0 2 0 | 1 0 0 0 0 | 1 0 1 1 0 | 0 0 0 0 0 | 0 0 1 0 0 | 0 ? 1 0 ?    | 2 1 1 ? 1 1 1    |
| <i>Cylindrichthys macropterus</i>   | 1 1 0 0 1    | 0 1 0 1 1 | 1 1 1 1 1 | 0 2 0 1 1 | 1 0 2 2 0 | 0 ? ? 0 0 | 1 0 1 1 0 | 1 0 1 0 0 | 1 0 1 0 1 | 0 ? 1 0 0    | ? ? ? 2 1 0 1    |
| <i>Cylindrichthys vasilenkoi</i>    | 1 1 0 1 1    | 1 2 0 1 2 | 1 2 1 1 1 | 0 2 0 2 1 | 1 0 2 2 0 | 1 ? ? 0 0 | 1 0 1 1 0 | 1 0 0 0 0 | 1 0 1 0 1 | 0 ? 1 0 0    | ? ? ? 2 1 0 1    |
| <i>Cyranorhis bergeraci</i>         | 1 1 0 0 0    | 1 2 0 1 2 | 1 2 1 1 1 | 0 1 0 1 0 | 1 0 0 2 0 | 1 1 1 0 0 | 1 2 1 1 0 | 0 1 0 0 0 | 0 0 1 0 1 | 1 2 0 0 0    | 2 0 0 ? 0 1 1    |
| <i>Dicelopogye macrodentata</i>     | 1 ? 0 0 1    | 2 2 0 1 0 | 0 2 1 0 2 | 0 2 0 1 1 | 2 0 2 2 0 | 1 0 1 0 0 | 2 0 1 1 0 | 1 0 0 0 0 | 0 1 1 0 1 | 0 ? 1 0 1    | 2 1 0 ? 0 (01) 1 |
| <i>Eigilia nielseni</i>             | 1 1 0 0 0    | 0 2 0 1 0 | 1 1 1 0 1 | 0 1 0 1 1 | 2 0 2 2 0 | 1 ? ? 0 0 | 1 0 1 1 0 | 1 1 1 0 0 | 1 0 1 0 1 | 1 ? 1 0 0    | 2 1 ? ? 1 1 1    |
| <i>Elonichthys palatinus</i>        | 1 1 0 0 0    | 0 1 0 1 0 | 1 0 0 1 0 | 0 0 0 2 0 | 1 0 0 2 0 | 1 0 0 0 0 | 1 0 1 0 0 | 1 0 0 0 0 | 0 0 1 ? 0 | 1 ? 0 0 0    | 0 1 1 2 0 0 1    |
| ' <i>Fubarichthys copiosus</i> '    | 1 0 0 0 0    | 1 2 0 1 2 | 0 2 1 1 1 | 0 2 0 3 1 | 1 0 0 2 0 | 1 1 0 0 0 | 1 2 1 0 0 | 2 0 0 0 0 | 1 0 1 0 1 | 0 ? 0 0 0    | 2 0 1 2 0 1 1    |
| <i>Gardineria akkolkensis</i>       | 1 1 0 0 0    | 0 2 0 1 1 | 1 1 1 1 1 | 0 2 0 1 1 | 2 0 2 2 0 | 1 ? ? 0 0 | 1 0 1 1 0 | 1 0 1 0 0 | 1 0 1 0 1 | 0 ? 1 0 0    | 2 1 ? ? 1 0 1    |
| <i>Gonatodus punctatus</i>          | 1 0 0 0 0    | 1 2 0 1 1 | 1 1 1 0 2 | 0 1 0 1 0 | 2 0 0 2 0 | 1 1 1 0 0 | 1 0 1 0 0 | 1 0 0 0 0 | 1 0 0 0 1 | 1 ? 1 0 0    | 2 1 0 ? 0 1 1    |
| <i>Gyrolepidotes schmidti</i>       | 1 0 0 0 0    | 1 1 0 1 2 | 1 2 0 0 0 | 0 0 0 1 0 | 2 0 0 2 0 | 1 ? ? 1 0 | 1 0 1 1 0 | 0 2 1 1 0 | 0 0 1 0 1 | 1 ? 1 0 0    | 2 1 ? ? 0 1 1    |
| <i>Howqualepis rostridens</i>       | 0 0 0 0 0    | 0 1 0 0 0 | 1 1 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 1 1 0 | 0 0 0 0 0 | 0 0 1 0 0 | 0 1 0 0 0    | 0 0 0 2 0 1 1    |
| <i>Karaoungaria kleimani</i>        | 1 1 0 0 1    | 0 1 0 1 2 | 1 2 1 0 1 | 0 1 0 2 1 | 1 0 2 2 0 | 1 ? ? 0 0 | 1 2 1 1 0 | 1 0 1 0 0 | 1 0 1 1 1 | 0 ? 1 0 0    | 2 1 2 ? 0 0 1    |
| <i>Kenderlichthys tuberculatus</i>  | 1 0 0 0 0    | 0 1 0 1 2 | 1 1 1 1 2 | 0 2 0 1 1 | 1 0 2 2 1 | 0 ? ? 1 1 | 1 0 1 1 0 | 1 0 1 2 1 | 2 0 1 0 1 | 1 ? 1 0 1    | ? ? 1 ? 1 1 1    |
| <i>Mansfieldiscus sweeti</i>        | 1 0 0 0 0    | 0 1 0 1 0 | 1 1 0 0 0 | 0 0 0 0 0 | 2 0 0 1 0 | 0 0 0 0 0 | 0 0 1 1 0 | 2 0 0 0 0 | 0 0 0 0 0 | 1 ? 0 0 0    | 2 1 0 ? 0 0 1    |
| <i>Mentzichthys jubbi</i>           | 1 0 0 0 0    | 1 2 0 1 2 | 0 2 0 0 0 | 0 0 0 1 0 | 1 0 0 2 0 | 1 0 0 0 0 | 2 0 1 1 0 | 0 0 0 0 0 | 0 0 1 0 0 | 0 ? 1 1 0    | 2 1 0 ? 2 1 1    |
| <i>Mimia toombsi</i>                | 0 0 0 0 0    | 0 0 0 0 0 | 1 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 1 0 0 0 0 | 0 0 1 1 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0    | 2 0 0 1 0 1 1    |
| <i>Moythomasia durgaringa</i>       | 0 1 0 0 1    | 0 0 0 1 1 | 1 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0 | 1 0 0 0 0 | 0 0 1 1 0 | 0 1 0 0 0 | 0 0 0 0 0 | 0 0 0 0 0    | ? ? 0 1 0 1 1    |
| <i>Moythomasia nitida</i>           | 0 1 0 0 0    | 0 0 0 0 0 | 1 0 0 0 0 | 0 0 0 0 0 | 0 0 0 0 1 | 0 0 0 0 0 | 1 0 1 1 0 | 0 0 0 0 0 | 0 0 1 0 1 | 0 0 0 0 0    | 0 0 0 0 0 0 0 1  |
| <i>Namaichthys Schroederi</i>       | 1 1 0 0 0    | 1 2 0 1 2 | 1 2 0 0 0 | 0 0 0 2 0 | 1 0 0 2 0 | 0 0 0 0 0 | 1 0 1 1 0 | 0 0 0 0 0 | 0 0 0 0 0 | 0 ? 1 0 0    | ? ? 1 ? 1 1 1    |
| <i>Nematoptychius greenocki</i>     | 1 0 0 0 0    | 0 1 0 1 1 | 1 1 1 0 1 | 0 2 0 1 1 | 1 0 2 2 0 | 1 0 0 0 0 | 1 0 1 1 0 | 1 0 0 0 0 | 2 0 0 0 0 | 0 ? 1 ? 1    | ? ? 0 ? 0 1 1    |
| <i>Osorioichthys marginis</i>       | 1 1 0 0 0    | 0 0 0 0 1 | 1 1 0 0 0 | 0 0 0 0 0 | 2 0 0 2 0 | 0 1 1 0 0 | 0 2 1 1 0 | 0 1 0 0 0 | 0 1 1 1 1 | 0 0 0 0 0    | 1 ? ? ? 0 1 1    |
| <i>Palaeoniscum freieslebeni</i>    | 1 1 0 0 0    | 1 2 0 1 2 | 1 2 1 1 2 | 0 2 0 1 2 | 1 0 2 2 0 | 1 0 1 0 0 | 1 0 1 1 0 | 0 1 0 0 0 | 2 0 1 0 1 | 0 ? 1 0 0    | 2 1 2 ? 0 1 1    |
| <i>Paramblypterus decorus</i>       | 1 2 0 1 1    | 0 1 0 1 0 | 1 1 1 1 2 | 1 2 1 3 1 | 1 1 1 2 1 | 0 1 1 0 0 | 0 1 2 0 0 | 0 1 0 1 1 | 1 0 2 1 1 | 0 ? 1 0 1    | 2 0 0 ? 0 1 1    |
| <i>Paramblypterus duvernoy</i>      | 1 (12) 0 2 0 | 1 1 1 1 2 | 1 2 1 1 2 | 2 1 2 2 1 | 2 2 2 2 2 | 1 1 1 1 1 | 0 2 2 1 0 | 0 0 1 1 1 | 1 0 1 0 1 | 0 0 1 0 (01) | 2 0 1 2 1 1 1    |
| <i>Paramblypterus gelberti</i>      | 1 (12) 0 1 0 | 1 1 1 1 2 | 1 2 1 1 2 | 2 1 2 2 1 | 2 2 2 2 2 | 1 1 1 1 1 | 0 2 2 1 0 | 0 0 1 1 1 | 1 0 0 0 1 | 0 0 1 0 (01) | 2 0 2 2 1 1 1    |

|                                      | <b>1–5</b> | <b>6–10</b> | <b>11–15</b> | <b>16–20</b> | <b>21–25</b> | <b>26–30</b> | <b>31–35</b> | <b>36–40</b> | <b>41–45</b> | <b>46–50</b> | <b>51–57</b>  |
|--------------------------------------|------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|---------------|
| <i>Paramblypterus rohani</i>         | 1 2 0 2 1  | 1 2 1 1 1   | 1 1 1 1 2    | 1 1 1 2 0    | 1 0 0 1 1    | 0 1 1 1 1    | ?? 2 ? 0     | ?? ? 2 1     | 1 0 1 0 1    | 1 ? 1 0 1    | 2 ? 1 2 1 1 1 |
| <i>'Phanerosteon' phonax</i>         | 1 0 0 0 0  | 1 2 0 1 2   | 1 1 1 1 2    | 0 0 0 0 1    | 0 0 0 0 2    | 0 1 0 1 2    | 0 0 1 1 0    | 1 1 0 1 1    | 0 0 1 1 1    | 1 ? 1 2 2    | 0 1 1 1 0 1 2 |
| <i>Pteronisculus stensioei</i>       | 1 1 0 1 1  | 1 2 0 1 2   | 1 2 1 0 1    | 0 2 0 1 1    | 1 0 2 2 0    | 1 1 1 0 0    | 0 0 1 1 0    | 1 1 1 0 0    | 1 0 0 0 0    | 0 1 0 ? (01) | 1 ? 1 2 0 1 1 |
| <i>Ptycholepis barboi</i>            | 1 1 1 0 1  | 1 2 0 1 0   | 1 1 1 0 2    | 0 2 0 3 1    | 2 0 2 2 0    | 0 1 1 0 2    | 1 1 1 1 1    | 0 1 1 2 0    | 0 0 0 0 0    | 0 ? 1 0 0    | 2 1 0 ? 0 1 1 |
| <i>Ptycholepis marshi</i>            | 1 0 1 0 0  | 0 2 0 1 0   | 1 1 1 0 2    | 0 2 0 3 1    | 2 0 2 2 0    | 0 1 1 1 2    | 1 0 1 1 1    | 0 0 1 2 0    | 0 0 1 0 1    | 1 ? 1 0 0    | 2 1 0 ? 0 1 1 |
| <i>'Rhadinichthys' athertonensis</i> | 1 0 0 0 0  | 1 2 0 1 2   | 1 2 1 0 1    | 0 2 0 1 0    | 1 0 0 2 0    | 1 1 1 0 0    | 1 1 1 0 0    | 0 0 0 0 0    | 0 0 1 0 1    | 0 1 0 0 1    | 2 0 1 2 0 1 1 |
| <i>Rhadinichthys canobiensis</i>     | 1 1 0 0 0  | 1 2 0 1 2   | 0 2 0 0 0    | 0 0 0 1 0    | 2 0 0 2 0    | 1 0 0 0 0    | 1 1 1 1 0    | 0 0 0 0 0    | 0 0 1 0 1    | 0 ? 1 0 (01) | 2 1 0 ? 1 1 1 |
| <i>Uydenia latifrons</i>             | 1 1 0 0 0  | 1 1 0 1 1   | 1 1 1 0 1    | 0 1 0 1 1    | 1 0 1 2 0    | 1 ?? 0 0     | 1 2 1 1 0    | 1 0 0 2 0    | 0 0 1 0 1    | 1 ? 1 0 1    | 2 1 1 ? 1 1 1 |
| <i>Uydenichthys magnus</i>           | 1 1 0 0 0  | 0 1 0 1 2   | 1 1 1 1 2    | 0 1 0 1 0    | 1 0 0 2 0    | 1 ?? 0 0     | 1 0 1 1 0    | 1 1 1 1 0    | 0 0 2 0 1    | 1 ? 1 0 0    | 2 1 ?? 1 1 1  |
| <i>Wendichthys dicksoni</i>          | 1 1 0 1 0  | 2 2 0 1 2   | 1 2 1 0 1    | 0 2 0 1 0    | 3 0 0 1 0    | 1 1 1 0 0    | 1 0 1 1 0    | 0 1 1 0 0    | 0 0 1 0 1    | 0 ? 0 0 1    | 2 0 1 2 0 1 1 |
| <i>Yogoniscus gulo</i>               | 1 0 0 0 0  | 1 2 0 1 2   | 1 2 1 1 1    | 0 2 0 3 0    | 1 0 0 2 1    | 1 0 1 0 0    | 1 1 1 1 0    | 2 0 0 0 1    | 1 0 1 1 1    | 0 ? 1 0 0    | 2 0 0 2 0 1 1 |