

NEW DATA ON THE OSTEOLOGY OF THE ACTINOPTERYGIAN FISH *AMBLYPTERUS* AND THE RELATIONSHIP BETWEEN *AMBLYPTERUS* AND *PARAMBLYPTERUS*

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Abstract. The relationship between the actinopterygian genera *Amblypterus* and *Paramblypterus* from the Early Permian sediments of Central and Western Europe are resolved. Firstly a historical summary is presented of the various opinions on the position of *Amblypterus* and *Paramblypterus*, and secondly the results of the my own studies of the type specimen of *Amblypterus lateralis* and other material from the Saar Basin. New data on the osteology of *Amblypterus latus* including a new reconstruction of the head and body are introduced. A comparison of the species from the Saar Basin including the species *Amblypterus latus* and *A. lateralis* with the type species of *Paramblypterus decorus*, *Paramblypterus duvernoy* and *Paramblypterus rohani* supports the author's opinion of the close relationship between the genera *Amblypterus* and *Paramblypterus*.

■ Actinopterygii, *Amblypterus*, *Paramblypterus*, osteology, Permian

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Introduction

Fishes of the family Amblypteridae comprise the most numerous component of the actinopterygians in the Early Permian sediments of the limnic basins of Central and Western Europe. Amblypteridae markedly exceed other actinopterygians in the majority of localities in the basins of the Bohemian Massif, the French Massif Central and German basins. Localities where members of other families dominate are quite rare. The estimation that the specimens of Amblypteridae form at least 90% of the actinopterygian population in the Early Permian sediments of the limnic basins of the Bohemian Massif and are numerous in other Permian basins of Central and Western Europe will not be far from the truth. Thus it follows that species and genera of the family Amblypteridae belong to those first described in the papers about Carboniferous and Permian actinopterygians, and the discussions on position of the species of the type genus of *Amblypterus* and relationship to other genera including the genus *Paramblypterus*, appear simultaneously. A number of previous authors (Troschel 1857, Traquair 1877–1914, 1877, Woodward 1891, Gardiner 1963, Blot 1966, Boy 1976, Heyler 1969, 1976, Gad 1988, Dietze 1999, 2000) have considered the position of the genus *Amblypterus* and its relationship to other genera, namely to *Paramblypterus*.

Several species from the Bohemian Early Permian were formerly included in the genus *Amblypterus* or *Paramblypterus*. After studying the type material in depth, and in spite of the number of papers published about the relationship between *Amblypterus* and *Paramblypterus* I can present a different view of the situation. The relationship between the two

genera can be resolved on the basis of my own study of the type specimen of *Amblypterus lateralis* and other material currently considered as *A. latus* and *A. lateralis* from Saar Basin, and a comparison with the species of *Paramblypterus*, namely *P. decorus*, *P. duvernoy* and *P. rohani*.

History

Romer (1945) erected the family Amblypteridae with designation of the type genus *Amblypterus*, but without any other description. The genus *Amblypterus* was originally described much earlier by Agassiz (1833). The first short description published in vol. 2, p. 3 can be quoted: “All fins very large compose from numerous lepidotrichia. Pectoral fins very large, anal large, dorsal fin opposite to the space between the ventral and anal fins, anterior margin of the fins with small pointed lepidotrichia beside the dorsal lobe of the caudal fin. Medium-sized scales.”

Agassiz at the same time refers to vol. 1, pl. A, fig. 3. Agassiz (1833) mentioned on page 4 five species included in the genus *Amblypterus*:

1. *Amblypterus macropterus*
2. *Amblypterus eupterygius*
3. *Amblypterus lateralis*
4. *Amblypterus latus*
5. *Amblypterus olfersi*

A conception of the genus *Amblypterus* is introduced by Agassiz in his reconstruction on pl. A, fig. 3. It is obvious that the reconstruction has very large pectoral fins, a low anal fin with its long base similar to *Amblypterus eupterygius*. Agassiz submitted a thorough description of the

genus *Amblypterus* on pp. 28–31, and compared it with the genus *Catopterus*. He pointed out the difference in the relative size of the fins and in the position of the dorsal fin, being opposite to the anterior margin of the anal fin and to the space between the anal and ventral fins. He remarked on the close relationship between *Amblypterus* and *Palaeoniscus* (in the shape of the fins and in their relationship position), but that they differ in the structure of the lepidotrichia and in the formation of the fins as a whole. He considered the relatively enormous size of the fins to be a feature of the genus. Agassiz characterized *Amblypterus* as having a fusiform body shape, more or less concave dorsally above the space between the pectoral and ventral fins. The caudal fin is short but relatively large. The scales are of a rhombic shape, smooth in some species, and grooved in others. The fins are very large, consisting of lepidotrichia: dorsal fin 30–50 lepidotrichia, anal fin 30–50 lepidotrichia, ventral lobe of the caudal fin 25–30 lepidotrichia, dorsal lobe of the caudal fin 80–100 lepidotrichia, pectoral fin 20–30 lepidotrichia.

The position of the fins is considered to be an important feature of the genus, the dorsal fin is not at the midpoint but is positioned posteriorly, where the trunk decreases in size as it becomes the caudal fin. It is opposite to the anterior margin of the anal fin and to the space between the anal and ventral fins. The anal fin commences opposite to the middle of the dorsal fin or slightly posteriorly. The ventral fins are set anteriorly to the anterior margin of the dorsal fin. There is nothing about the bones of the skull except the mouth which is formed from large jaws, and along their entire margin they are equipped with extremely minute teeth arranged in a brush-like manner.

As was mentioned above, Agassiz (1833) described five species and included in the genus *Amblypterus*: *A. macropterus* (pp. 31–35), *A. eupterygius* (pp. 36–37), *A. latus* (pp. 37–38), *A. lateralis* (p. 39) and *A. olfersii* (p. 40). It was Agassiz who already distinguished two species with smooth scales (*A. lateralis* and *A. latus*), and two species with sculptured scales (*A. macropterus* and *A. eupterygius*) in his description.

Agassiz (1833–43) later also assigned to the genus *Amblypterus* the species *A. agassizii* MÜNST. (pp. 105–106), *A. nemopterus* (pp. 107–109), *A. punctatus* (pp. 109–110), and *A. striatus* (pp. 111–112).

Giebel (1848) distinguished between *Amblypterus* species having smooth scales: *Amblypterus duvernoy* (consistent with *Palaeoniscus duvernoy* AG. 1833, pp. 45–47), *Amblypterus latus* and *A. lateralis*; and those with sculptured scales: *Amblypterus macropterus*, *A. eupterygius*, *A. agassizii*, *A. nemopterus*, *A. punctatus*, *A. striatus*, *A. olfersii* and others.

Troschel (1857) also differentiated between *Amblypterus* species, initially described from the Saar Basin as having sculptured or smooth scales, and placed them into two groups:

1. Sculptured scales: *A. macropterus* and *A. eupterygius*
2. Smooth scales: *A. lateralis* and *A. latus*

It is of note that Troschel (1857) characterized the species *A. macropterus* and *A. eupterygius* as having sculptured scales but also large conical teeth whereas the species from the second group with smooth scales have brush-like teeth. Troschel retained the species *A. lateralis*

and *A. latus* in the genus *Amblypterus* with respect to one of Agassiz's characteristics of the genus *Amblypterus*, that is the minute brush-like teeth, whereas he erected a new genus *Rhabdolepis* for the species with large conical teeth and sculptured scales. Characteristics of the *Amblypterus* are after Troschel (1857, p. 18): brush-like teeth on the jaws, numerous teeth on the palate, robust smooth scales, large fins and small fulcral scales.

Traquair (1877) considered the species *Amblypterus latus* to be a typical representative of the genus *Amblypterus* and he pointed out differences from the genus *Palaeoniscus*. At the same time he did not find any differences in *Palaeoniscus duvernoy*, and he recommended this species to be included in the genus *Amblypterus*. He described elsewhere in the text (1877, p. 558) a group of the fishes for which *Palaeoniscus duvernoy* is a typical representative, and he included it in the genus *Amblypterus*. He also included in this group the species *P. duvernoy*, *P. vratislaviensis* and *P. lepidurus* as described by Agassiz, species *P. dimidiatus*, *P. elongatus*, *P. tenuicauda*, *P. gibbus* and *P. opisthopterus* as described by Troschel (1857), species *P. gelberti* described by Goldfuss (1847), species *P. decorus*, *P. arcuatus*, *P. beaumonti*, as described by Egerton (1850), and also the species *P. rohani*, *P. caudatus*, *P. obliquus*, *P. reussii* and *P. luridus* as described by Heckel (Heckel and Kner 1861) from the Krkonoše Piedmont Basin.

Sauvage (1888) described the history of the genus *Amblypterus*, and also considered *A. latus* to be the type of the genus *Amblypterus*. He included in *Amblypterus*, in addition to the original species, new species *A. renaulti*, *A. commentryi*, *A. elaveris*, *A. euryi* and *A. fayoli*. He similarly summarised the history of *Amblypterus* in his other papers (Sauvage 1890, 1893) and he described the new species included in the genus *Amblypterus*.

Woodward's treatise from 1891 is significant. He regarded *A. latus* as the type of the genus *Amblypterus*, and he considered *A. lateralis* to be a synonym of *A. latus*. He borrowed the specimens from the Natural History Museum, London for his studies. Woodward (1891) also assigned to the genus *Amblypterus* the species *A. traquairi* WOODWARD, *A. beaumonti* (EGERTON), *A. decorus* (EGERTON), *A. arcuatus* (EGERTON), *A. reussii* (HECKEL), *A. blainvillei* (AG.), *A. voltzii* (AG.) and *A. duvernoy* (AG.). He included the specimens which were regarded as synonyms of *A. duvernoy* (*A. vratislaviensis* (AG.), *A. lepidurus* (AG.), *A. gibbus* (TROSCHEL), *A. dimidiatus* (TROSCHEL), *A. tenuicauda* (TROSCHEL), *A. elongatus* (TROSCHEL), *A. opisthopterus* (TROSCHEL), *A. rohani* (HECKEL), *A. obliquus* (HECKEL), and *A. caudatus* (HECKEL). He added several species into the genus *Amblypterus* but several others were added with some uncertainty. Agassiz's original species *A. macropterus* and *A. eupterygius* were included by Woodward (1891) in the genus *Elonichthys* but as the species *Elonichthys macropterus*.

Traquair (1877–1914) alluded in his anatomical description of palaeoniscids to some anatomical features of the genus *Amblypterus*, and he referred to his reconstruction of *A. latus* on pl., 2, fig. 1. It is necessary to note that this reconstruction is much more elaborate in comparison with that of Agassiz (1833, pl. A, fig. 3), and differs in several features. Traquair (1877–1914) drew a smaller pectoral fin,

a shorter anal fin base, a triangular shape for both the anal and dorsal fins, and less numerous scale rows. The bones of the head indicate the operculum to have had a square shape, the maxilla a rounded posterior maxillary plate, and the jaws to possess minute teeth of equivalent size. It is necessary to point out that the maxilla, preoperculum and suborbital bones which are very similar to the later reconstruction by Gardiner (1963) which will be discussed further. It is not clear from the text which of the specimens served as a model.

Fritsch (1894) accepted the diagnosis of the genus *Amblypterus* (p. 94) by Woodward (1891), after Troschel (1857) and Traquair (1877). He remarked (p. 94) however that the diagnosis was uncertain. Fritsch (1894, 1895) included in the genus *Amblypterus* the following species: *A. verrucosus* FRITSCH, *A. duvernoy* (AGASSIZ), *A. vratislaviensis* (AGASSIZ), *A. rohani* (HECKEL), *A. luridus* (HECKEL), *A. obliquus* (HECKEL), *A. caudatus* (HECKEL), *A. lepidurus* (AGASSIZ), *A. reussii* (HECKEL), *A. feistmanteli* FRITSCHE, *A. zeidleri* FRITSCH and *A. angustus* (AGASSIZ).

Aldinger (1937) made reference to three species of the genus *Amblypterus* including *A. latus* from the Early Permian of Saarbrücken, but only within the context of the scale structure.

Gardiner (1963) revised the type species *Amblypterus latus*, he also provided a diagnosis of the family Amblypteridae ROMER, 1945 and a new diagnosis of the genus *Amblypterus*. GARDINER (1963, pp. 291–294) submitted a description of *A. latus* together with a reconstruction of the head. It is reported in the text that he used 18 specimens from the Natural History Museum, London in his research, but did not study the type specimens of *A. latus* or *A. lateralis*, and no neotype was determined. *A. lateralis* is included in *A. latus* as a synonym. The reconstruction of *A. latus* as exhibited by Gardiner is however at variance with the existing type species of *A. lateralis* and other material relating to *A. latus* or *A. lateralis*, as later studies proved.

Blot (1966) produced in his paper an excellent description and reconstruction of *Paramblypterus decorus* from the Carboniferous sediments of Commentry Basin. He deduced from the reconstruction and description of *A. latus* by Gardiner (1963) that *Amblypterus* and *Paramblypterus* were quite different genera. Blot (1966) introduced a diagnosis for the genus *Paramblypterus*, and also established a new family, Paramblypteridae. The type species *Paramblypterus decorus* for the genus *Paramblypterus* was initially described by Egerton (1850) as *Palaeoniscus decorus*, later Traquair (1877) referred to it as *Amblypterus decorus* and finally Sauvage (1888) considered it a subgenus, *Paramblypterus*, included within the genus *Amblypterus*. However, Blot (1966) included an excellent description and reconstruction of the type species *Paramblypterus decorus*, and his paper is an outstanding resource for understanding the actinopterygians of the genus *Paramblypterus*.

In his survey of Permo-Carboniferous actinopterygians Lehman (1966) published a reconstruction of *Amblypterus latus* in the sense of Gardiner (1963) and a reconstruction of *Paramblypterus decorus* in the sense of Blot (1966). These entirely distinct reconstructions of the animals which are essentially similar were thus introduced to science.

Heyler elaborated on the genera *Amblypterus* and *Paramblypterus* in several papers. Heyler (1969) summarised the history of the genus *Amblypterus*, and remarked on the description presented by Gardiner (1963) and that Gardiner did not look at the type and that his reconstruction differs in generic features from the type of *A. lateralis* VP 1301, which was studied by Heyler in Strasbourg. Heyler confirmed that it is impossible to find the type specimen of *A. latus*, but all revising authors (Agassiz, Traquair, Troschel, Woodward) considered *A. lateralis* to be very similar or the same as *A. latus*, and for this reason *A. lateralis* should be the type species of *Amblypterus* instead of the missing *A. latus*. Heyler (1969) presented a description and reconstruction of *Amblypterus latus* according to Gardiner's conception of *Amblypterus latus*, and he later (Heyler 1976) suggested a new name, *Gardinerichthys latus* for this animal, for the reason that it differs entirely from the genus *Amblypterus*.

Heyler (1976) submitted a history of the genus *Amblypterus* in more detail, including a description of the type specimen of *A. lateralis* and other material deposited in the collection of the University in Strasbourg.

Heyler (1997) again summarised the historical publications and gave his opinion on the *Amblypterus* and *Paramblypterus* question. He stated that *Amblypterus lateralis* and *Paramblypterus* were unquestionably close. However he considers *Amblypterus* and *Paramblypterus* to be two different genera.

Finally Dietze (2000) presented results of a study of *Amblypterus*, namely *A. latus* respectively *A. lateralis*. She provided a new diagnosis of *Amblypterus* on the basis of 73 specimens and the holotype of *A. lateralis*. She also revised the type species *Paramblypterus decorus*, and published an emended diagnosis of the genus *Paramblypterus*. Dietze (2000) considered the genera *Amblypterus* with the type species *A. latus* (*A. lateralis* as its synonym) and *Paramblypterus* with the type species *P. decorus*, to be separate and included in the family Amblypteridae ROMER, 1945. She enumerated (Dietze 2000, p. 949) several distinguishing features of *Amblypterus* and *Paramblypterus*:

1. The duplicate extrascapular bones in *Paramblypterus* are absent in *Amblypterus*.
2. The lateroventral process on the dermopterotic in *Amblypterus* is not developed in *Paramblypterus*.
3. Nasal 1 and nasal 2 (nasal 2 is superorbital anterior in the sense of Blot 1966) is present in *Paramblypterus*. Nasal 2 is absent in *Amblypterus*.
4. A postcleithrum is present in *Paramblypterus* but not in *Amblypterus*.
5. Scales on *Paramblypterus* can have slight mounds, but are smooth with concentrically arranged incremental lines in *Amblypterus*.

Heyler (2000) noted briefly the relationship between *Amblypterus* and *Paramblypterus* in his survey of the Stephanian and Autunian actinopterygians of the French Massif Central. He included *A. lateralis* as *Paramblypterus lateralis* in the family Paramblypteridae (erected by Blot 1966) and in the order Paramblypteriformes (erected by Heyler 1969). He abandoned the genus *Amblypterus* and family Amblypteridae for several reasons:

- a. Inaccurate original assignation of the genus *Amblypterus* by Agassiz.

- b. Confusion caused by the reconstruction of *Amblypterus latus* presented by Gardiner (1963).

Prof. Daniel Heyler communicated to me by a letter dated 15.4.2002 his personal opinion regarding this research and suggested reserving the name *Amblypterus latus* for species which demonstrate the features which were described and figured by Gardiner (1963), and that the species *Amblypterus lateralis* should be transferred to the genus *Paramblypterus* because this genus is well defined.

There was no reference to the reconstruction published by Gardiner and Schaeffer (1989) and designated as *Paramblypterus decorus* after Blot (1966) and Štamberg (1976). This published reconstruction by Gardiner and Schaeffer (1989, fig. 9D) is very misleading. I have never published any reconstruction and the results of studies of *Paramblypterus decorus* and paramblypterids from the Permian of the Bohemian Massif significantly differ from *Paramblypterus decorus* from the Carboniferous of the French Massif Central. In my opinion, the above mentioned reconstruction is of an animal which is still unknown to this time from Permo-Carboniferous sediments.

We can reach several conclusions based on the historical opinions summarised in the research on the genera *Amblypterus* and *Paramblypterus*:

1. Reconstruction of the type species *Amblypterus latus* in the sense of Gardiner (1963) showed an animal quite distinct from *A. latus* or *A. lateralis* initially described by Agassiz from the Saar Basin (Heyler 1969, 1976, 1997, 2000; Dietze 2000).
2. The genus *Amblypterus* represented by the type species *Amblypterus latus*, or more precisely *A. lateralis* and the genus *Paramblypterus* with the type species *P. decorus* are separate although very similar genera within the family Amblypteridae (Heyler 1997, Dietze 2000, Schindler 2007).
3. *Amblypterus* and *Paramblypterus* are identical genera, and the generic name *Paramblypterus* should be used (Heyler 2000). The genus *Amblypterus* should have been abandoned due to the inaccurate original assignation of the genus *Amblypterus* by Agassiz, the type specimen of the type species *A. latus* is lost, and great confusion was caused by the description and reconstruction of *Amblypterus latus* presented by Gardiner (1963) which does not conform to any fish from the Saar Basin. The term Amblypteridae should have been abandoned for the same reason. The terms *Amblypterus* and Amblypteridae should be reserved for the actinopterygians described by Gardiner (1963), if these specimens exist. The species *Amblypterus lateralis*, which includes a holotype, should be considered to be *Paramblypterus lateralis* and included in the family Paramblypteridae HEYLER, 1969 as the genus *Paramblypterus* has been clearly identified (Heyler 2000).

Results of anatomical studies of *Amblypterus* and relationship between *Amblypterus* and *Paramblypterus*

There are several opinions on the position of the genus *Amblypterus* and relationship between *Amblypterus* and *Paramblypterus* as the previous section described. For this

reason the present paper is focused on my own study of accessible material and presents a different opinion regarding the topic. The result of my own studies of Agassiz's genus *Amblypterus* material is presented and it supports the results of Heyler (1976, 2000), Dietze (2000) and others. These publications are used at the end of this section in the comparison of the characteristics of *Paramblypterus* as published by Blot (1966), Heyler (1969), Štamberg (1976) and Dietze (2000).

The studied material referred to below is from Lebach nodules:

1. The *Amblypterus lateralis* holotype figured by Agassiz (1833, pl. 4, fig. 1) deposited in the University of Strasbourg under No. VP 1310 (Plate 1, fig. 1), (Heyler's number – St 21).
2. Collection from the University of Strasbourg, Nos VP 1305; VP 1301a, b; VP 1302 a, b; VP 1303; VP 1304 a, b.
3. Collection deposited in The Natural History Museum, London (BMNH), namely Nos. P 978; P 14536; P 979; P 3458; P 29006; P 359; P 22658; P 36128; P 44082.
4. Collection deposited in the Humboldt University Museum in Berlin, namely Nos. MB. f. 3809; MB. f. 1504; MB. f. 14396; MB. f. 14400; MB. f. 14394; MB. f. 14395; MB. f. 3796; MB. f. 3798; MB. f. 3800; MB. f. 3806; MB. f. 3805; MB. f. 3799.
5. Collection deposited in the Goldfuss-Museum in Bonn (GM), namely Nos. P 1125, P 1127, P 1130, P 1180, P 1271, P 1755 etc.
6. Collection deposited in the National Museum, Prague (NMP), Nos. M 1762/61/2688; M 1762/61/2691; M 1762/61/2690; 1762/61/2692; M 1762/61/2693; M 1762/61/2689; SC 117, Sc 118.

The type specimen *Amblypterus lateralis*

AGASSIZ, 1833

Study of the type specimen of *Amblypterus lateralis* (No VP 1310) is an important first step (Plate 1, fig. 1).

Specimen VP 1310 is approximately 145 mm in total length with the caudal extremity of the caudal fin missing. The trunk is partly preserved, moderately convex dorsally anteriorly to the dorsal fin. Smooth scales have a straight, not denticulated posterior margin (in those specimens preserved sufficiently well for study of their posterior margin). Clearly visible concentrically arranged growth lines are present where the upper ganoin layer is missing. The approximate scale count is:

$$\frac{28}{10 \ 21 \ 39} \ 43$$

Three or four large ridge scales are in front of the dorsal fin, one pair of large scales is in front of the anal fin. The paired fins are well developed, relatively large but smaller than the dorsal and anal fins. Lepidotrichia are articulated along their whole length, and branch dichotomically. The anal fin is triangular, and the same size as the dorsal fin. The dorsal fin is composed of 35 lepidotrichia.

The maxilla has a large oblong maxillary plate. The length/ height ratio of the maxillary plate is 1.3. The weak lower jaw contains the remains of minute teeth. The preoperculum bends anteriorly, and its anteroventral margin curves around

the maxillary plate forming an angle of 90°. The dorsal region of the preoperculum extends anteriorly whereas the anterior does not reach the level of the anterior margin of the maxillary plate. The anterior margin of the dorsal region of the preoperculum is concave with several small suborbital bones anteriorly. Four suborbital bones were found, but more were probably developed. The jugal borders the orbit posteroventrally, and lies anteriorly from the maxillary plate. Two fragments of the sclerotical bones were found in the ventral region of the orbit, but they were in fact more numerous. The suboperculum is of oblong shape, length greater than height. The remains of three branchiostegal rays are preserved.

Results of study of other *Amblypterus latus* material

The study of comparative material specified in the introduction to this section is presented. The findings supplement our knowledge of the species *Amblypterus latus* published recently by Dietze (2000).

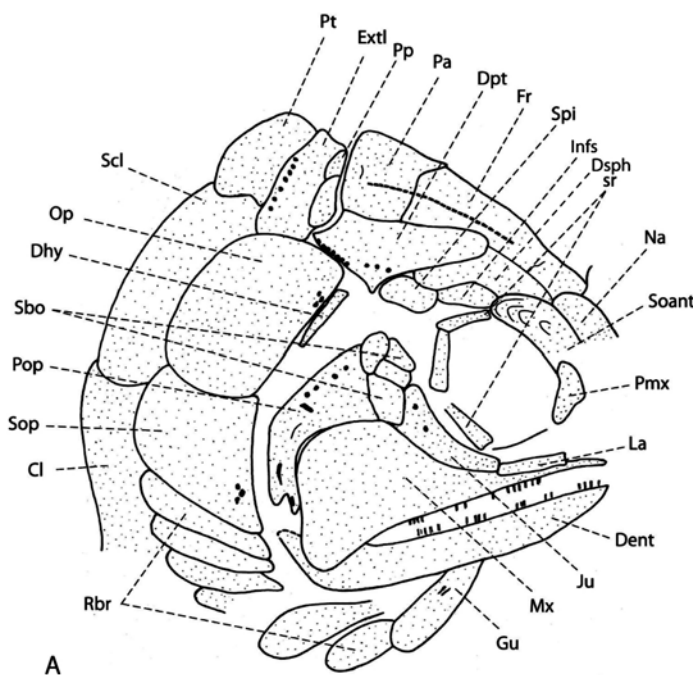
Skull roof. The interfrontal and interparietal sutures are straight. Two postparietal bones (additional lateral extrascapulars in the sense of Dietze 2000) lie posteriorly to the parietals, and are squeezed between the posterior process of the dermopterotic and the extrascapular lateral lying posteriorly (text-fig.1). Postparietal bones occur frequently. A dermopterotic with lateral process projecting between the opercular and spiracular (text-figs. 1–4) is also documented in several specimens.

Rostral region. A pair of postrostral bones, a pair of nasal bones, supraorbital anterior and premaxilla compose the rostral region. The supraorbital anterior was previously described by Blot (1966) in *Paramblypterus decorus*, and was later recorded by several later authors in other

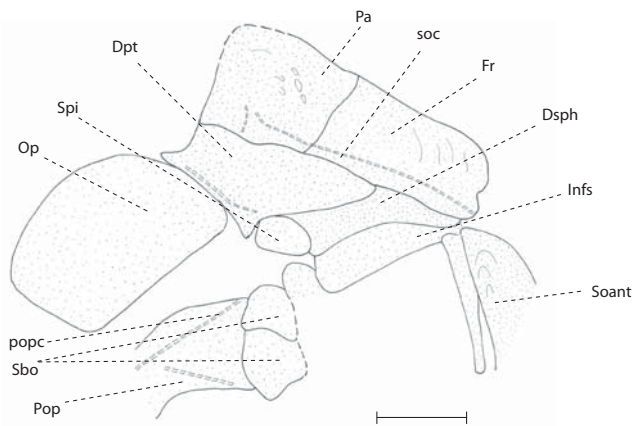
paramblypterids. The well preserved supraorbital anterior in specimens MB f. 3809b (text-fig. 1) and BMNH – P 14536 (text-fig. 4) is a dorsoventrally elongated bone of oval shape flanking the orbit anteriorly. The bone is ornamented in its dorsal region with conspicuous mounds parallel to the margin of the bone. No remains of the sensory canal are recognisable. The supraorbital anterior is in contact dorsoposteriorly with the infraorbital superior and with the dermosphenotic. The dermosphenotic totally separates the supraorbital anterior from the frontal. The premaxilla is partly preserved anteroventrally to the supraorbital anterior in MB f. 3809 and nearly complete in M 1762/61/2692, with a sickle-shaped form. The ventral margin of the bone is denticulated and forms the medial section of the mouth. Premaxilla posterior region borders slightly with the orbit anteroventrally, and in addition to the maxilla it is also in contact with lacrimal, and dorsally with the supraorbital anterior. However, this group of bones had not been found together in any of the studied specimens.

The sclerotic ring in the orbit probably consists of five thin bones, an assumption made from fragments in the specimens MB f. 3809, BMNH – P 3458a and the holotype VP 1310. The supraorbital anterior, and partly also the premaxilla, border the orbit anteriorly, infraorbital superior dorsally, jugal, infraorbital posterior and lacrymal posteriorly and ventrally. Between the orbit and preoperculum can be developed only two suborbital bones as described Dietze (2000) on MB f. 3796b, or there can be four or more small suborbital bones as can be seen in specimens VP 1310, VP 1301 or MB f. 3809.

Jaws. The maxilla deserves special attention. It was clearly figured earlier by Dietze (2000), and its diagnostic features markedly distinct from those figured by Gardiner (1963) which were revised several times by Heyler (1969, 1976, 1997, 2000). The maxilla is of a typical shape with



Text-fig. 1. *Amblypterus latus* AGASSIZ, 1833. Pen and ink drawing (A) and photo (B) of the skull in lateral view. Mb. F. 3809b, scale bar represents 10 mm. Cl – cleithrum; Dent – dentalosphenial; Dhy – dermohyal; Dpt – dermopterotic; Dsph – dermosphenotic; Extl – extrascapular lateral; Fr – frontal; Gu – gular; Infs – infraorbital superior; Ju – jugal; La – lacrimal; Mx – maxilla; Na – nasal; Op – operculum; Pa – parietal; Pmx – premaxillar; Pop – preoperculum; Pp – postparietal; Pt – posttemporal; Rbr – branchiostegal rays; Sbo – suborbital; Scl – supracleithrum; Soant – supraorbital anterior; Sop – suboperculum; Spi – spiracular; sr – sclerotic ring.

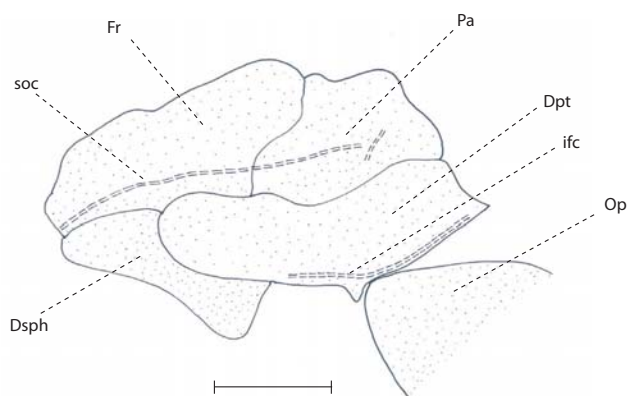


Text-fig. 2. *Amblypterus latus* AGASSIZ, 1833. The skull roof, bones of the check and operculum. MB. f. 3796, scale bar represents 5 mm. Dpt – dermopterotic; Dsph – dermosphenotic; Fr – frontal; Infs – infraorbital superior; Op – operculum; Pa – parietal; Pop – preoperculum; popc – preopercular canal; Sbo – suborbital; Soant – supraorbital anterior; soc – supraorbital canal; Spi – spiracular.

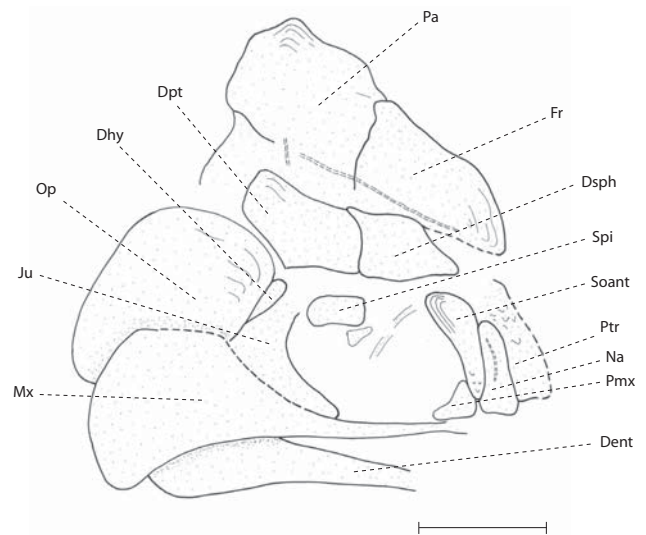
large maxillary plate. There are some differences in its length/height ratio when we consider the shape of the maxillary plate. The holotype of *A. lateralis* (VP1310) has a maxillary plate length/height ratio of 1.3, it is a relatively long maxillary plate. The maxillary plate is shorter in specimens MB f 3809b, BMNH – P 36128, VP 1305 and is very short with a length/height ratio of nearly 1 in the specimen NMP – M 1762/61/2688. The maxillary plate is in all specimens very large and high. The type of maxillary plate (long and low) which was described Gardiner (1963) is unknown in the *A. latus* or *A. lateralis* material from Lebach. None of the maxillary plates show any significant prolongation ventroposteriorly. It is however necessary to draw attention to the significant length/height variation, from 1 to 1.3. The reason can probably be due to the variation in the shape of the maxillary plate or in its deformation during the course of fossilization.

The lower jaw is relatively weak and slightly bent anteriorly.

Dentition. Dentition on the lower and upper jaws consists of minute sharply pointed teeth attached to long tubules. These tubules are clustered together in several rows



Text-fig. 3. *Amblypterus latus* AGASSIZ, 1833. The skull roof in dorsal view. MB. F. 3799b, scale bar represents 5 mm. Dpt – dermopterotic; Dsph – dermosphenotic; Fr – frontal; ifc – infraorbital canal; Op – operculum; Pa – parietal; soc – supraorbital canal.

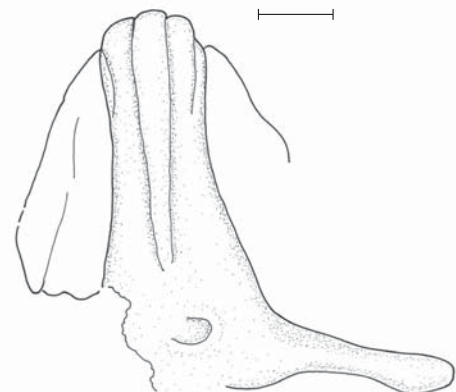


Text-fig. 4. *Amblypterus latus* AGASSIZ, 1833. Jaws and the bones of the check in lateral view, the skull roof in dorsal view. BMNH P 14536, scale bar represents 5 mm. Dent – dentalosplenial; Dhy – dermohyal; Dpt – dermopterotic; Dsph – dermosphenotic; Fr – frontal; Ju – jugal; Mx – maxilla; Na – nasal; Op – operculum; Pa – parietal; Pmx – premaxillar; Ptr – postrostral; Soant – supraorbital anterior; Spi – spiracular.

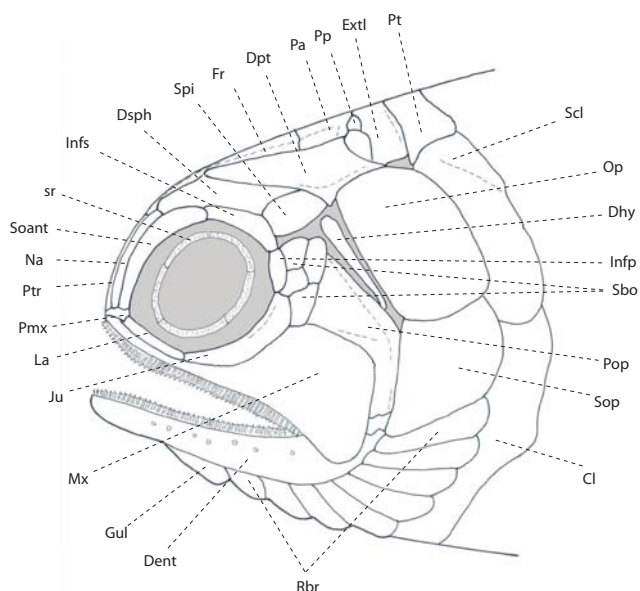
(BMNH – P 3458b, BMNH – P 979b, GM – P 1271, VP 1305). Small, strong, sharply pointed teeth without tubules are on the coronoids of the lower jaw (GM – P 1271).

Opercular apparatus. The operculum is an oblong shape with round corners. The suboperculum extends anteroventrally into a blunt process. The anterior margin of the suboperculum is at least one third longer than the posterior. Eight branchiostegal rays are present (BMNH – P 122658, BMNH – P 15415, MB. f. 3800), paired gular lateral (BMNH – P 22658, MB.f. 3809b), and the gular medial in NMP – M1762/61/2691 is a relatively large wide bone, moderately orocaudally elongated. The remains of the sensory canals are not preserved. A small dorsoventrally elongated dermohyal is crushed between the anterior margin of the operculum and dorsoposterior margin of the preoperculum (BMNH – P 14536, MB f. 3809).

Palatal bones. The parasphenoid is visible in samples MB f. 3796, BMNH – P 44082 (text-fig. 5) plus others processus cultriformis and paired processus ascendens, whereas the corpus parasphenoidis ends just behind the processus ascendens similarly as in *Paramblypterus duvernoy* and *P. rohani*.

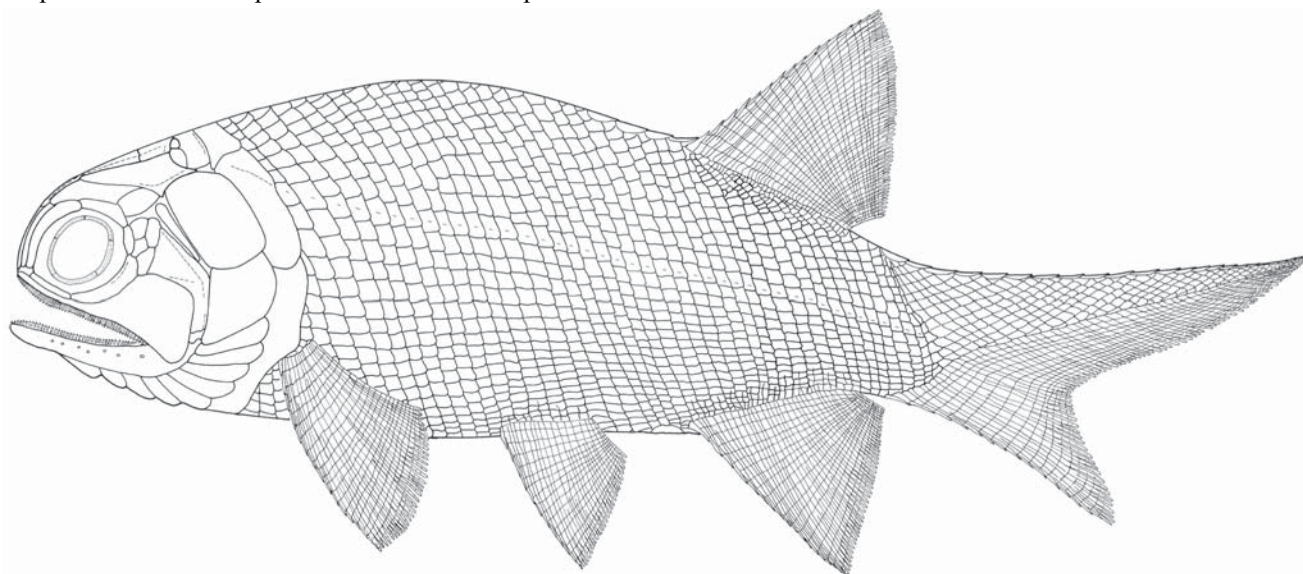


Text-fig. 5. *Amblypterus latus* AGASSIZ, 1833. Parasphenoid in dorsal view. BMNH P 44082, scale bar represents 2 mm.



Text-fig. 6. *Amblypterus latus* AGASSIZ, 1833. Reconstruction of the skull in lateral view, x 2.1, original. Original. Cl – cleithrum; Dent – dentalosplenic; Dhy – dermohyal; Dpt – dermopterotic; Dsph – dermosphenotic; Extl – extrascapular lateral; Fr – frontal; Gul – gular lateral; Infp – infraorbital posterior; Infs – infraorbital superior; Ju – jugal; La – lacrimal; Mx – maxilla; Na – nasal; Op – operculum; Pa – parietal; Pmx – premaxillar; Pop – preoperculum; Pp – postparietal; Pt – posttemporal; Ptr – postrostral; Rbr – branchiostegal rays; Sbo – suborbital; Scl – supracleithrum; Soant – supraorbital anterior; Sop – suboperculum; Spi – spiracular; sr – sclerotic ring.

Body and fins. The fusiform body has a conspicuously arched dorsal portion in the region above the space between the pectoral and pelvic fins. The body height is 3.5 times body length, and the length of the head is 4.2 times the total body length. It is necessary to point out the relatively large size of paired and unpaired fins. The paired fins are a little smaller than the unpaired fins, but they are large compared with the body of *Paramblypterus decorus* and other well-known paramblypterids. The pectoral fin is well preserved in Mb f. 14396. It has 21 mm long lepidotrichia whereas the longest lepidotrichia of the dorsal and anal fins are 22 mm. The pectoral fin is well preserved also in other specimens



Text-fig. 7. *Amblypterus latus* AGASSIZ, 1833. Reconstruction of the body, x 1.0, original.

eg. BMNH – P 14536. The base of the pelvic fin extends over the length of five or six scale rows. The dorsal fin is large, and its base extends over the length of ten scale rows, and it borders the areas with small scales. The dorsal fin contains about 40 segmented and dichotomically branched lepidotrichia. The anal fin also borders on the area with small scales, and its base extends over the length of 13 scale rows. The anal fin consists of 40 segmented and dichotomically branched lepidotrichia. The leading edge of the paired and unpaired fins consists of fulcral scales.

Paired and unpaired fins of *Paramblypterus rohani* are however much smaller in relation to the body size. The base of the pelvic fin extends over the length of 4 to 4.5 scale rows, and it consists of approximately 19 lepidotrichia. The base of the dorsal fin extends over the length of 8 scale rows, and it contains 25 – 30 lepidotrichia. The anal fin extends over 8 – 9 scale rows, and it comprises 30 lepidotrichia.

The approximate scale count in the studied specimens of *Amblypterus latus* is:

$$\frac{27}{9 \ 21 \ 37} \ 42$$

Comparing the genera *Amblypterus* and *Paramblypterus*

A summary of the newly obtained results from the study of the genus *Amblypterus*, including the results published by Dietze (2000) are compared with the characteristics of the genus *Paramblypterus* published by Blot (1966), Heyler (1969), Štamberg (1976), Dietze (2000) and the present study.

Dietze (2000, p. 949) presented the following differences in features of *Amblypterus* and *Paramblypterus*:

1. Duplication of lateral extrascapulars (postparietals in this paper) is present in *Paramblypterus*, but missing in *Amblypterus*.
2. The supratemporal (dermopterotic in this paper) of *Amblypterus* has a ventrolateral protuberance which has not been observed in *Paramblypterus*.
3. Two suborbitals are present in *Amblypterus*, six suborbitals in *Paramblypterus duvernoyi* and 6-9 suborbitals in *Paramblypterus decorus*.

4. Only one paired nasal forms the snout in *Amblypterus*, whereas nasal 1 and nasal 2 (supraorbital anterior in this paper) form the snout in *Paramblypterus*.
5. One dermohyal is present in *Amblypterus*, 1-3 in *Paramblypterus duvernoy* and 7-10 dermohyal elements in *Paramblypterus decorus*.
6. A postcleithrum is present in *Paramblypterus*, but is absent in *Amblypterus*.
7. The scales of *Paramblypterus* have fine ridges and their posterior margin is serrated whereas the scales of *Amblypterus* are smooth with concentric striae and their posterior margin is straight.
8. D-values (see Dietze 2000, p. 931; 949) of scales are lower in *Amblypterus* (1.2) than in *Paramblypterus* (between 1.4 and 2.0).

Further study of the *Amblypterus* material showed that some characters which had been considered exclusive for *Paramblypterus* were also present in *Amblypterus*. It is therefore not possible to consider these characters to be specific to only one of these two genera:

Considering:

Point 1. Postparietal bones (duplication of lateral extrascapular in the sense of Dietze 2000) are certainly developed at least in some specimens of *Amblypterus* (text-fig. 1).

Point 2. Ventrolateral protuberance of the dermopterotic (supratemporal in the sense of Dietze 2000) is distinct also in young specimens of *Paramblypterus rohani*, and thus it is not a unique character of *Amblypterus*.

Point 3. The holotype of *Amblypterus lateralis* exhibits three suborbital bones, specimen MB. f 3809b has four (text-fig. 1).

Point 4. A supraorbital anterior (nasal 2 after Dietze 2000) is also present in *Amblypterus* (text-figs 1, 2, 4).

Point 6. A postcleithrum is present in *P. rohani* from the Krkonoše Piedmont Basin NMP – P 1893, but is absent in many other specimens.

Only the following differences can be found when distinguishing between *Amblypterus* from *Paramblypterus*:

– Only one dermohyal present in *Amblypterus*, more dermohyals in *Paramblypterus*;

– Scales of *Paramblypterus* carry fine mounds on their outer surface, and the posterior margin of the scales is denticulated, whereas the scales of *Amblypterus* are smooth with concentric growth striae, and the posterior margin of the scales is not denticulated. I consider this character to be of weak predicative value as *Amblypterus* preserved in nodules usually has the posterior margin of the scales missing, and Dietze (2000) also described a denticulated posterior margin on the scales of a large specimen of *Amblypterus*.

– D-values (see Dietze 2000, p. 931; 949) of scales are lower in *Amblypterus* (1.2) than in *Paramblypterus* (between 1.4 and 2.0).

– Large paired and unpaired fins in *Amblypterus*. The fins of *Paramblypterus* (*P. decorus*, *P. duvernoy*, *P. rohani*) are smaller in relation to the size of the body.

The reconstructions of the head and body (text-figs 6, 7) of *A. latus* represent the author's conception of its anatomy, shape of the body and position of the fins. Summarizing the

results of previous studies of *Amblypterus* and *Paramblypterus* by other authors (Dietze, Heyler, Boy and others) and the new results obtained in this study, demonstrate the minute distinction between *Amblypterus* (fishes from Lebach described as *Amblypterus latus*, *A. lateralis*) on one side, and fishes of the genus *Paramblypterus* (described as *Paramblypterus decorus*, *P. duvernoy*, *P. rohani*, etc.) on the other. On the contrary many more characters have been found to be common for both *Amblypterus* (represented by *A. latus* and *A. lateralis*) and *Paramblypterus* (represented by *P. decorus*, *P. duvernoy* and *P. rohani*). In particular the following consistent features should be noted:

1. Shape of the upper jaw with the maxillary plate.
2. Type of dentition formed by tubular teeth.
3. Presence of the supraorbital anterior in the nasal region.
4. Configuration of the skull roof.
5. Configuration of the cheek including suborbital bones, preoperculum, inclination of the suspensorium.
6. Configuration of the opercular apparatus.

The enumerated features convinced me that *Amblypterus* and *Paramblypterus* are very similar genera. The above mentioned differences between these two genera are more likely characteristics of the separate species rather than being genera specific. I suggest keeping both genera separate for the present time for two reasons; firstly, the differences mentioned above, and secondly to prevent further confusion evoked by integration of the two genera and according to the rule of the priority, using the genus name *Amblypterus*.

Conclusions

Conclusions from the historical summary and new studies of the *Amblypterus* and *Paramblypterus* genera relationship are as follows:

1. *Amblypterus latus* which was described and figured by Gardiner (1963) shows an animal quite distinct from *A. latus* or *A. lateralis* initially described by Agassiz from the Saar Basin.
2. New studies of specimens of *Amblypterus latus* or *A. lateralis* produced new data on the osteology, mainly the presence of supraorbital anterior, postparietal bones and numerous suborbital bones. All these osteological features are typical for *Paramblypterus decorus*, *P. duvernoy* and *P. rohani*.
3. Newly described osteological features conspicuously converge the two genera but I propose keeping the two genera separate for the present.
4. An emended diagnosis for *Amblypterus* (DIETZE, 2000): Distinct ornamentation of frontals, parietals, extrascapulars, posttemporals, dermosphenotics and dermopterotics. No frontal process. Small postparietals can be present. Single pair of lateral extrascapulars. The supraorbital anterior borders the orbit anteriorly, and it contains the rostral region in addition to the postrostral and nasal. Dermopterotic more than twice the length of the dermosphenotic. Delicate sclerotic bones present. Maxillary plate deep. Numerous identical minute teeth on the jaws, consisting of long tubules tipped with fine sharply pointed teeth. More than two suborbitals. Single dermohyal. Operculum higher than the suboperculum. From 8 to 10 branchiostegal rays. Postcleithrum absent.

Posterior edges of scales straight, bearing concentric striae. 40–42 scale rows along the lateral line. Fins large.

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Explanations of the plates

PLATE 1

Amblypterus latus AGASSIZ, 1833

1. Holotype VP 1310 of *Amblypterus lateralis* AGASSIZ, 1833; x 1.0.
2. Specimen VP 1302; x 1.0.
3. Specimen BMNH P 14536; x 1.0.

PLATE 2

1. *Paramblypterus* sp. Specimen MHK 81638 from the Krkonoše Piedmont Basin, locality Arnultovice, x 1.2.
2. *Paramblypterus rohani* (HECKEL, 1861) and *Neslovicella elongata* (ŠTAMBERG, 2010). Specimen P 167 (Municipal Museum in Nová Paka) from the Krkonoše Piedmont Basin, locality Košťálov, x 0.6.
3. *Paramblypterus rohani* (HECKEL, 1861). Specimen MHK 81398 from the Krkonoše Piedmont Basin, locality Rybnice, x 0.6.

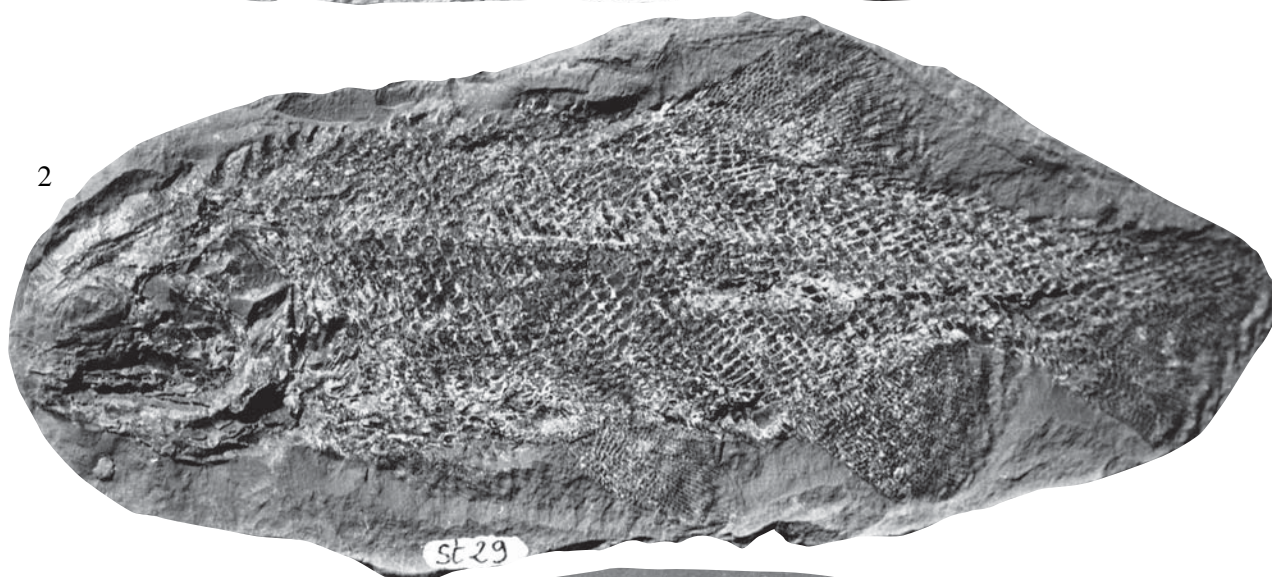


PLATE 2

