



NEW GENUS AND SPECIES OF THE FAMILY AEDUELLIDAE (ACTINOPTERYGII) FROM THE LOWER GOLDLAUTER FORMATION (ASSELIAN, LOWER PERMIAN) OF THE THURINGIAN FOREST (GERMANY)

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Abstract: A new aeduellid actinopterygian *Amelangia ornata* gen. et sp. nov. is described from the Lower Goldlauter Formation of the Thuringian Forest (Lower Permian, Germany). Distinguishing characters of the newly described taxon are a large dermosphenotic, an unusually large number of suborbital bones, a maxilla with a low maxillary plate, a distinct sculpture consisting of tubercles on the operculum and suboperculum, the presence of a single branchiostegal ray, and a pectoral fin with a scaly basal lobe. The preserved characters place the new genus close to the genera *Aeduella* and *Bourbonnella*. The newly described genus and species is similar to an isolated operculum and suboperculum recovered from the Lower Permian of the Krkonoše Piedmont Basin in the Bohemian Massif.

Key words: Actinopterygii, Aeduellidae, anatomy, Lower Permian, Thuringian Forest

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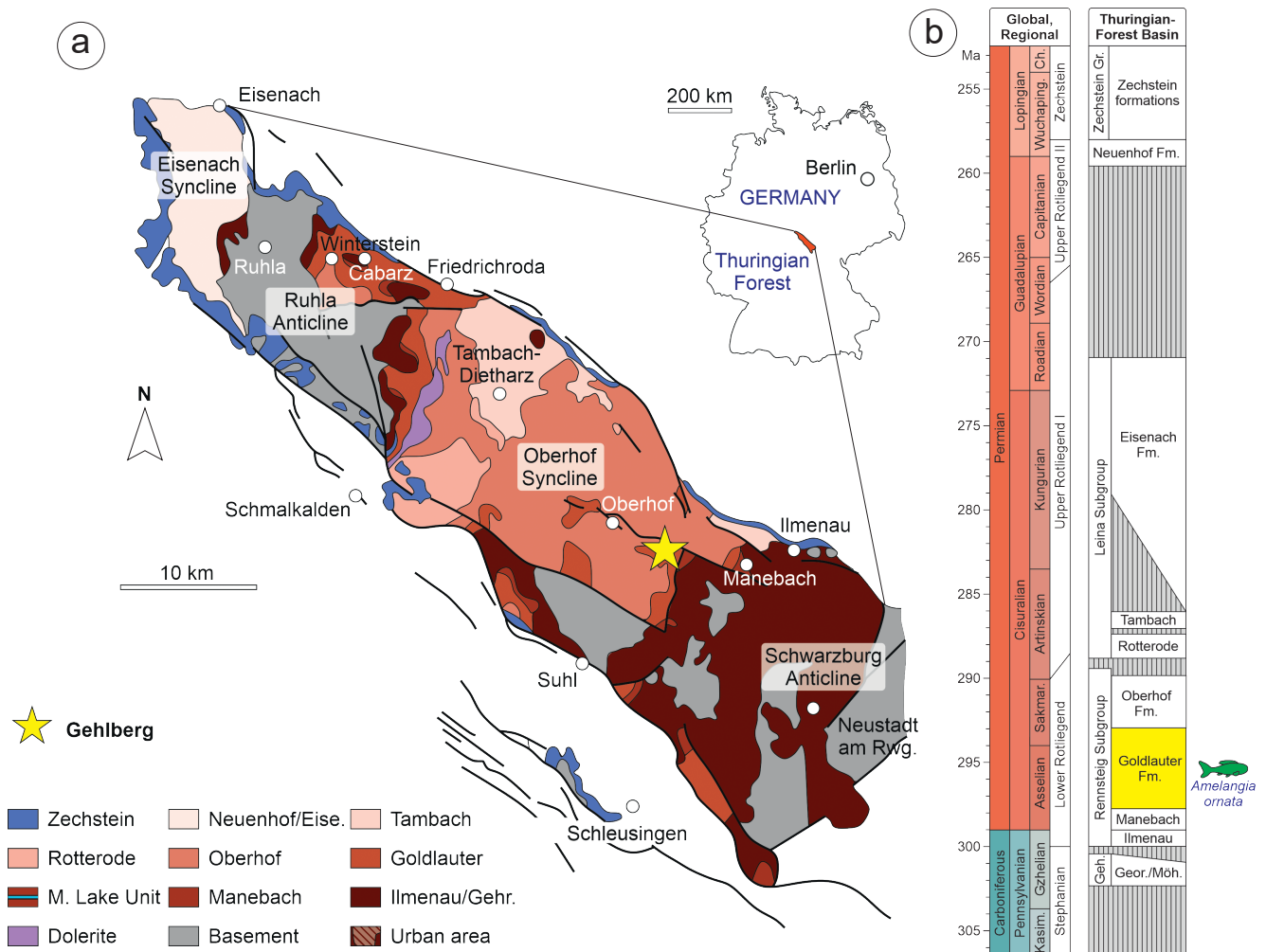
Introduction

Actinopterygians of the family Aeduellidae appears to be a homogeneous group, characterized by a set of features of which the most striking are the maxilla with a posterior plate of triangular shape, slender teeth with tubules, supraorbital canal passing from parietal to dermopterotic, mosaic of small suborbitals between orbit and opercular bones, high operculum and suboperculum, and a small number of branchiostegal rays. Actinopterygii, currently classified in the family Aeduellidae, are known in the literature from as far back as the works of Blainville (1818) and Agassiz (1833). However, it was not until Westoll (1937) that the situation improved significantly – he clearly recognized the distinctive features that characterize these individuals, and established the new genus *Aeduella* with the species *Aeduella blainvillei* (AGASSIZ, 1833). Subsequently, Romer (1945) established the family Aeduellidae on the basis of this genus, and then Heyler (1969) described other species belonging to the family Aeduellidae from the Permian sediments of the French Massif Central. Gradually, more new records and species of aeduellids were discovered from the Saar-Nahe Basin (Heyler 1991, Poplin 2001, Poplin and Dutheil 2005), northern Switzerland (Bürgin 1990), Puertollano Basin in

Spain (Forey and Young 1985), North America (Gottfried 1987, Mickle 2011), eastern European Russia (Yankevich and Minich 1998), and the Bohemian Massif (Štamberg 2002, 2007, 2010). Records of these interesting fishes are continuously increasing (Štamberg 2013, 2018) and so far, 16 species belonging to the family Aeduellidae are known from sediments of the Upper Carboniferous and Lower Permian. One species of aeduellid fish *Westollia crassa* (POHLIG, 1892) has been described from the deposits of the Thuringian Forest. This species is only known from the Gottlob Quarry locality in Friedrichroda (Štamberg, submitted) from sediments of the Upper Goldlauter Formation (Schneider et al. 2020). The newly described species from the Lower Goldlauter Formation extends the species list of the family Aeduellidae.

Geology

Fish specimen NHMS-Am4219 was discovered near Gehlberg in the Thuringian Forest Basin (Text-fig. 1a), in the up to 800 m thick Goldlauter Formation (Asselian – possible earliest Sakmarian, Lower Permian; Text-fig. 1b). During that time, reddish-brown, coarse clastic fan deposits formed at the edges of the basin. The fans interfinger distally with



Text-fig. 1. a: geological map of Thuringian Forest, including positions of finding locality Gehlberg (asterisk). Modified from Lütznier et al. (2012) and Trümper et al. (2023). b: Late Palaeozoic lithostratigraphy of Thuringian Forest area, with levels of volcanic deposits indicated. Modified after Schneider et al. (2020), but see Lütznier et al. (2020) for new, contrasting radioisotopic ages. Abbreviations: Ch. – Changhsingian, Fm. – Formation, Geh. – Gehren Subgroup, Geor. – Georgenthal Formation, Gr. – Group, Kasim. – Kasimovian, Möh. – Möhrenbach Formation, Sakmar. – Sakmarian, Wuchiaping. – Wuchiapingian.

red alluvial plain sandstones and siltstones, fluvio-lacustrine brownish to grey sandstones, and lacustrine laminated shales in the center of the basin. These mostly black shales were deposited in lakes alternately dominated by acanthodians/xenacanthids and palaeoniscids/amphibians (Schneider et al. 2019). The holotype was recovered from a layer of greenish-gray clayey siltstone, belonging to the Lower or Middle *Acanthodes* horizon of the Lower Goldlauter Formation (Asselian). This sedimentary sequence extends from the Pochwerksgrund near Suhl-Goldlauter in the south, over the area at the Sperbersbach near the Schmücke up to the west of Gehlberg in the north.

Material and methods

A part and counterpart of the holotype were available for study. These specimens are stored under the number NHMS-Am4219 in the collection of the Naturhistorisches Museum Schloss Bertholdsburg Schleusingen in Germany. The specimens were partly prepared using a Krantz pneumatic needle. Drawing was prepared with SN 20 Zeiss stereomicroscope, coupled with camera lucida. Photographs

were taken with a Nikon D800 with lens AF Micro Nikkor 60 mm, 1 : 2.8D.

Two naming conventions are used for the skull roof bones of the actinopterygian fishes: one based on tradition, and one based on homology with tetrapods (Schultze et al. 2021). Both are used at present in literature for two paired bones of the skull roof. The traditional names frontal and parietal are used here to be consistent with the nomenclature used for other Aeduellidae (Heyler 1969, Poplin 2001, Poplin and Dutheil 2005, Mickle 2011, Štamberg 2007, 2010, 2018). The description terminology of the dermosphenotic and dermopterotic follow the nomenclature proposed by Poplin (2004).

Institutional abbreviations

- NHMS Naturhistorisches Museum Schloss Bertholdsburg Schleusingen, Germany (coll. Numbers: NHMS-Am)
- MNH Museum of Eastern Bohemia in Hradec Králové, the Czech Republic

Systematic palaeontology

Subclass Actinopterygii COPE, 1877

Family Aeduellidae ROMER, 1945

Amelangia gen. nov.

Type species. *Amelangia ornata* sp. nov.

Etymology. In honour of Andree Amelang from Stützerbach near Ilmenau who discovered the holotype. He is a successful fossil collector for the Schleusingen Natural History Museum (NHMS).

Diagnosis. As for the type species.

Amelangia ornata sp. nov.

Text-figs 2, 3

Holotype. Specimen NHMS-Am4219 (part and counterpart) deposited in Naturhistorisches Museum Schloss Bertholdsburg Schleusingen; Germany.

Etymology. Ornātus – derived from the sculpture decorating the surface of the operculum, suboperculum and branchiostegal ray.

Material. Only the type specimen is known.

Diagnosis. Aeduellid fish with a total length of about 12 cm. Orbit surrounded posteriorly by three small infraorbitals, dorsally by a large dermosphenotic, anteriorly by a sickle-shaped supraorbital anterior with distinct ridges. Many small suborbital bones and narrow dermohyal present anterior to operculum. Maxilla with low maxillary plate is triangular. Depth of maxillary plate 3.1 times total length of maxilla. Only one branchiostegal ray present. A distinct sculpture consisting of tuberculations covers surface of operculum, suboperculum, and partially the branchiostegal ray. Pectoral fin sits on small lobe covered with scales. Base of dorsal fin sits on field of small scales. Segments of lepidotrichia of dorsal fin have sigmoidal sutures between them. Scale count:

28

10 - -

Type locality. Gehlberg, sports area, Thuringian Forest, Germany.

Type horizon. Lower Goldlauter Formation, Asselian, Thuringian Forest Basin.

Description. Positive and negative impressions of the individual show the skull and the anterior part of the trunk, including the pectoral, ventral and dorsal fins (Text-fig. 2a, b). It can be assumed, by comparing with the proportions of the body of *Aeduella blainvillei*, that the individual reached a total length of about 12 cm. The maximum depth of the body (25 mm) is reached in the area between the pectoral and pelvic fins.

Skull roof. The bones of skull roof are not completely preserved (Text-fig. 3a, b). The right frontal, which is broad and short, is partially preserved. The specimen shows fine remains of numerous tuberculations, suggesting that the surface of the frontal was originally decorated with very

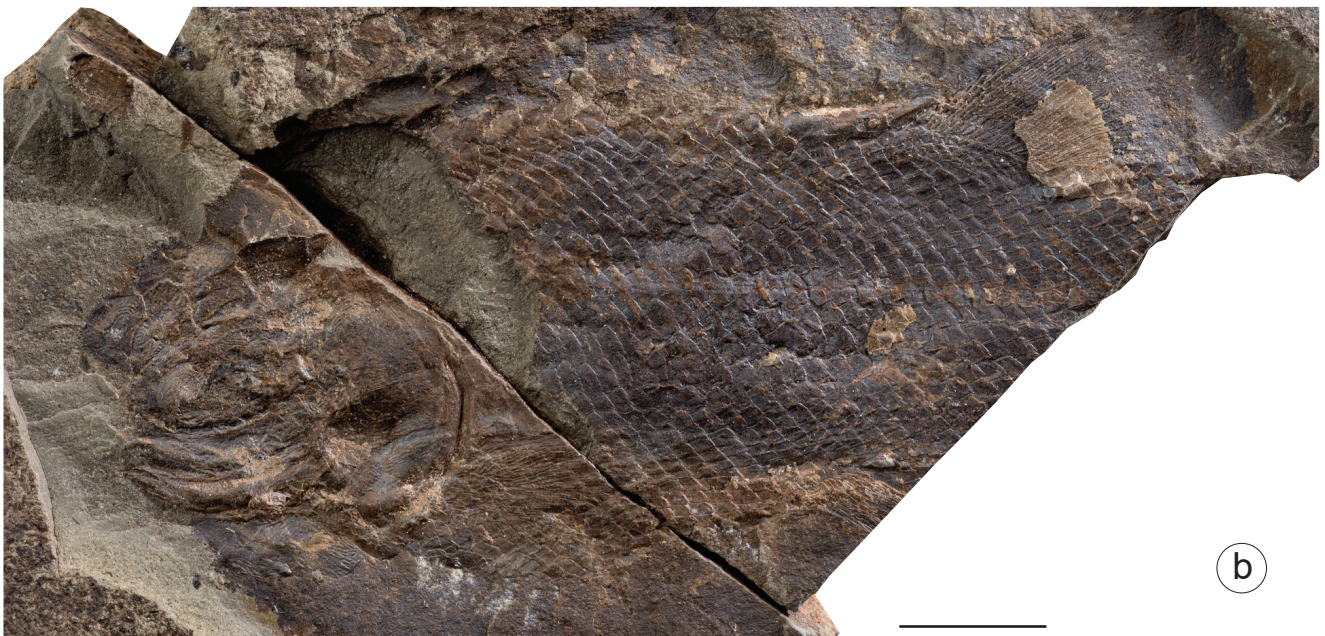
numerous distinct tubercles, and anteriorly with short ridges oriented parallel to the anterior margin. A short section of the supraorbital canal is located in the anterior part of the bone, near its lateral margin. The right parietal on the specimen is longer than it is wide, and no sculpture or remnants of sensory canals are preserved on the parietal. The large dermosphenotic lining the lateral margin of the frontal is the best-preserved bone of the skull roof. It extends posteriorly to the level of the frontal contact with the parietal, and abuts the dermopterotic posteriorly. The lateral margin is slightly concave, and flanks the orbit dorsally. The dermosphenotic forms a lateral process in its posterior part, then gradually narrows anteriorly, where it contacts the supraorbital anterior. On the dorsal surface of the bone, several ridges parallel to the lateral margin of the bone are preserved. Posterior to the dermosphenotic is a somewhat preserved rectangular dermopterotic, which flanks the parietal laterally. Neither the sculpture nor the sensory canals are preserved. The bones posterior to the parietal and dermopterotic are completely indistinct, except for a small rectangular bone that is probably part of a band of extrascapular bones. A fragment of the bone anteriorly to the frontal Štamberg interprets to be nasal.

The circumorbital series (Text-fig. 3a, b) consists of, in addition to the dorsally situated dermosphenotic, the supraorbital anterior and antorbital anteriorly, jugal ventrally, and three smaller infraorbital bones posterior to the orbit. The supraorbital anterior is a slightly sickle-shaped bone, with the posterior margin ringing the orbit. The supraorbital anterior bears distinct ridges arranged concentrically parallel to the margins of the bone. The holotype preserves the supraorbital anterior of both the right and left sides (Text-fig. 3a, b). The antorbital is preserved anterior to the supraorbital anterior. A fragment of an anteroposteriorly elongated narrow jugal lines the dorsal margin of the suborbital portion of the maxilla ventral to the orbit. The posterior margin of the orbit is flanked by three small infraorbitals in the space between the posterior end of the jugal and the lateroventral margin of the dermosphenotic process. Across the orbit is an impression of a skeletal fragment appearing as a band of five small bones laid in a single line. It can be assumed that these are fragments of circumorbital bones from the left side of the skull (Text-fig. 3a, b). The articulation of this skeletal fragment is probably due to the course of the infraorbital canal and the short outlying canals. A similar structure on the bones can be observed in *Aeduella blainvillei* illustrated by Heyler (1969: pl. 21, fig. 2).

Cheek. The area between the orbit and opercular bones is filled with numerous small suborbital bones (Text-fig. 3a, b). Nine small oval-shaped bones can be found on the specimen. Between the suborbital bones and the operculum is a fragment of a dorsoventrally extended dermohyal. Several suborbital bones from the left side of the skull are displaced anteriorly to the skull roof bones. The position and shape of the preoperculum is very indistinct. The maxilla is typically aeduellid, narrow anteriorly and progressively deeper posteriorly. The posterior portion of the maxilla is relatively low, and its depth is 3.1 times the total length of the maxilla. The anterior part of the maxilla has numerous well-developed tubular teeth, consisting of a tube and a small pointed tooth at the end of the tube. The same teeth are preserved on the mandible. The teeth on the upper and lower jaw are of the same size and closely spaced.



a



b

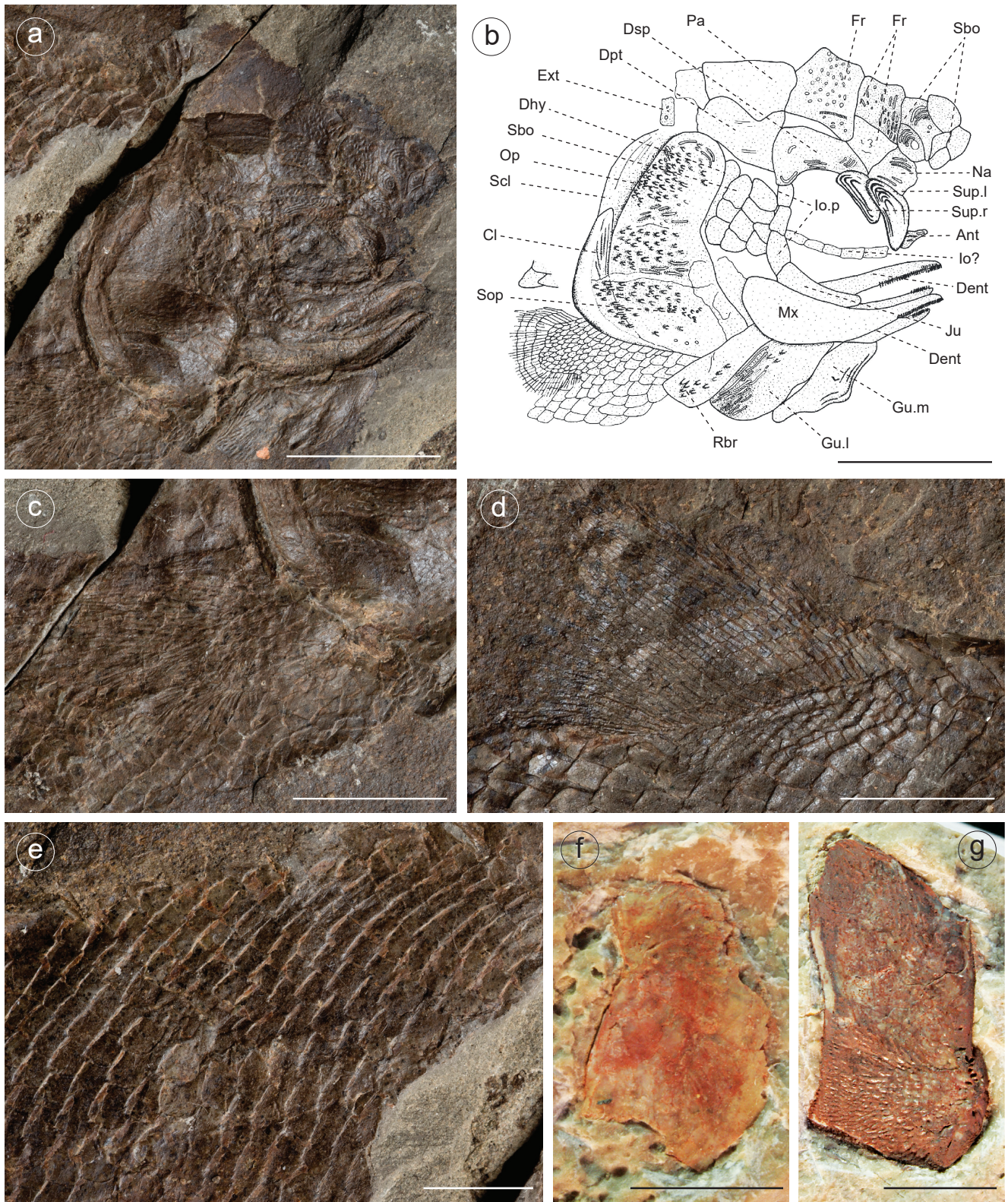
Text-fig. 2. *Amelangia ornata* gen. et sp. nov. Part (a) and counterpart (b) of the holotype NHMS-Am4219. Gehlberg (Thuringian Forest, Germany; Lower Goldlauter Formation, Asselian). Scale bars 10 mm.

Opercular apparatus. The operculum, suboperculum, branchiostegal ray, and lateral and median gulars form the dermal bones of the opercular apparatus (Text-fig. 3a, b). The operculum is rounded in its dorsal part, markedly extended dorsoventrally, whereas the dorsal part of the operculum is angular and inclined anteriorly. There is an imperfectly preserved border between the operculum and suboperculum. Both bones bear numerous tuberculations, with their spike-like apices directed posteriorly and covering the entire surface of the operculum and suboperculum. One branchiostegal ray lies between the suboperculum and the lateral gular. The small tuberculations on the branchiostegal ray have the same shape as on the suboperculum and operculum. The lateral gular anterior to the branchiostegal ray is almost twice the area of the branchiostegal ray. The lateral half of the outer surface of the bone bears numerous long and short ridges parallel to the lateral margin of the bone. The medial margin of the lateral

gular forms a fold where the convex part of the lateral margin of the median gular fits. The median gular is approximately rhombic in shape, antero-posteriorly elongated and much narrower than the lateral gular. In the medial part of the bone, the impression of the pit line of the gular is visible.

Shoulder girdle. Only a narrow fragment of the supracleithrum is visible posterior to the operculum. An arcuate cleithrum lining the suboperculum extending to the operculum is evident posterior to the opercular bones.

Fins. The pectoral fin sits on a small lobe covered with minute scales (Text-fig. 2b, c). The anterior margin of the fin is turned dorsally. The lepidotrichia are articulated, and the anterior margin of the fin is protected by the terminal pointed segments of the lepidotrichia. The pelvic fin is small, sitting on four vertical scale rows, and its base begins behind the tenth scale row. The number of lepidotrichia is indeterminate. The dorsal fin is very well preserved. Its base



Text-fig. 3. a–e: *Amelangia ornata* gen. et sp. nov., Holotype NHMS-Am4219 from Gehlberg (Thuringian Forest, Lower Goldlauter Formation, Asselian), scale bars 5 mm. a, b: Photograph and drawing of skull. c: Lobe of pectoral fin. d: Dorsal fin with field of minute scales along base of fin. e: Scales in anterior part of body including scales of lateral sensory line. f–g: Aedeuclid fish cf. *Amelangia ornata*, from Tatobity (Krkonoše Piedmont Basin, Chotěvice Formation, Asselian), scale bars 5 mm. f: Left operculum in lateral view, MHK-G 67. g: Right suboperculum in lateral view with numerous tubercles, mainly in ventral half of bone, MHK-G 66. Abbreviations: Ant – antorbital, Cl – cleithrum, Dent – dentary, Dhy – dermohyal, Dpt – dermopterotic, Dsp – dermosphenotic, Ext – extrascapular, Fr – fragments of the right frontal, Gu.l – lateral gular, Gu.m – median gular, Io.p – infraorbitals posteriorly from orbit, Io? – probably fragments of infraorbitals, Ju – jugal, Mx – maxilla, Na – nasal, Op – operculum, Pa – parietal, Rbr – branchiostegal ray, Sbo – suborbital, Scl – supracleithrum, Sop – suboperculum, Sup.l – supraorbital anterior – left, Sup.r – supraorbital anterior – right.

begins behind the 28th scale row and extends over the six scale rows. There is a very distinct field of small scales along the base of the dorsal fin (Text-fig. 3d). The fin is composed of 25 lepidotrichia, which are articulated and divide dichotomously distally. The distal parts of the lepidotrichia are separated from each other. The sutures between the segments of lepidotrichia are sigmoidal.

Squamation. The scales on the side of the body are rectangular, and the largest scales are those in the anterior part of the body, on the flank, in rows along the lateral sensory line (Text-fig. 3e). Their size decreases posteriorly. The posterior margin of the scales is serrated. The serrated margin is particularly well developed in the scales on the anterior portion of the fish, and the number of serrations on the posterior margin of the scale decreases towards the posterior portion of the fish. The outer margin of the scales is not sculptured, except for incremental lines parallel to the posterior margin of the scales. Scales bearing the lateral sensory canal are preserved on the entire preserved body fragment. There are 8 scales in a vertical row anterior to the dorsal fin, dorsally to the lateral sensory line. Four large dorsal scutes are developed in front of the dorsal fin.

Relationships to other Aeduellidae

In the newly described species, though only some skull bones are preserved, the bones that are present are informative. The preserved bones on the skull and characters on the body of the fish clearly show typical aeduellid characters (Heyler 1969, Poplin and Dutheil 2005, Štamberg 2007, 2010, 2018), such as the triangular maxilla, the dentition on the jaws formed by so-called tubular teeth consisting of a tube and a small, sharply pointed tooth perched on it, a deep operculum, and a small number of branchiostegal rays. In stature, the described specimen belongs to medium-sized aeduellids, such as *Aeduella blainvillei* (AGASSIZ, 1833), *Bourbonnella guilloti* HEYLER, 1967, *Bourbonnella hirsuta* ŠTAMBERG, 2007, *Decazella vetteri* (HEYLER, 1964), *Platysella poplinae* HEYLER, 2002, *Platysella lallyi* HEYLER et POPLIN, 1983 and *Schaeffeevus sulcatus* YANKEVICH AND MINICH, 1998.

Several characters place the described species close to *Aeduella blainvillei*, particularly the shape of the maxilla: it has a low plate, whose depth is 3.1 times the total length of the maxilla. In *Aeduella blainvillei*, this ratio varies from 3 to 4 (Heyler 1969, Štamberg 2018), whereas this ratio is 2.5 in *Bourbonnella guilloti* (HEYLER, 1969) and 2.2 in *Bourbonnella hirsuta* (ŠTAMBERG, 2007). The small aeduellid *Neslovicella rzehaki* (ŠTAMBERG, 2007) from the Bohemian Massif also has a deeper posterior part of the maxilla relative to its total length: 2.25 (Štamberg 2007), likewise *Westollia crassa* (POHLIG, 1892) known from Gottlob Quarry in Friedrichroda (Goldlauter Formation, Thuringian Forest) has this ratio of 2–2.3 (Štamberg, submitted). Another character of *Aeduella blainvillei* is the presence of only one branchiostegal ray. In all other species of the family Aeduellidae, except *Bourbonnella guilloti*, two branchiostegal rays are present. The sculpture on the opercular bones in the newly described species is very distinctive. A similar sculpture, but much less pronounced, has been described in some specimens of *Aeduella blainvillei* from the Bourbon l'Archambault Basin (Štamberg 2018:

figs 30, 31). The list of identical characters with *Aeduella blainvillei* is completed by the identical number (25) of lepidotrichia composing the dorsal fin.

Other characters which are valid for the newly described species and *Aeduella blainvillei*, but which are also known in other species of the family Aeduellidae and especially in species of the genus *Bourbonnella*, are a relatively large orbit flanked dorsally by a large triangular dermosphenotic (Heyler 1969), a sickle-shaped supraorbital anterior, and numerous suborbital bones in the region between the operculum and infraorbital bones. Of the characters found on the trunk, the small lobe covered with small scales on which the pectoral fin sits and the array of small scales on the base of the dorsal fin are particularly important. These characters are characteristic of both the genus *Aeduella* and *Bourbonnella*. The scales on the body of the fish are only partially preserved, but it is quite clear that the scale count differs from that of *Aeduella blainvillei* or *Decazella vetteri*, and conversely is similar to species of the genus *Bourbonnella*. There were probably 10 scale rows between the supracleithrum and the beginning of the base of the pelvic fin, and 28 scale rows towards the beginning of the dorsal fin, compared to *Aeduella blainvillei* where 7–8 scale rows were reported (Heyler 1969) between the supracleithrum and the beginning of the pelvic fin, and 22 ± 1 scale rows towards the beginning of the dorsal fin. In *Decazella vetteri*, these numbers are 8 to the ventral fin and 24 to the dorsal fin (Heyler 1969), whereas in *Bourbonnella guilloti* they are 9–10 rows to the ventral fin and 28–29 rows to the dorsal fin (Heyler 1969). In *Bourbonnella hirsuta* there are 12 rows to the ventral fin and 28 rows to the dorsal fin (Štamberg 2007).

Important features that characterize the newly described species are the distinctive sculpture formed by tuberculations, whose spike-like apices are directed posteriorly and cover the operculum, suboperculum and partly the branchiostegal ray, to give these bones a spiked appearance. A rather distinct sculpture formed by ridges and flat tubercles is not only on the supraorbital anterior, but also preserved in the frontal and lateral gular. Of the bones surrounding the orbit, the three small infraorbital bones forming the posterior margin of the orbit are characteristic.

The distinctive sculpture on the bones of the opercular apparatus, consisting of tuberculations with apices directed posteriorly in the species described here, is unique among fishes of the family Aeduellidae. In this respect, the finding of an isolated suboperculum and operculum (Text-fig. 3f, g) of the aeduellid type in the Chotěvice Formation (Asselian) of the Bohemian Massif of the Krkonoše Piedmont Basin is interesting (Štamberg et al. 2019). The surface of the operculum is considerably abraded, but the very well preserved suboperculum (Text-fig. 3g) shows densely arranged tuberculations on its surface, namely on the ventral half of the bone, with spike-like apices directed posteriorly. This is a sculpture entirely consistent with the species *Amelangia ornata* gen. et sp. nov. Due to the absence of other bones that would allow a closer comparison with *Amelangia ornata* gen. et sp. nov., the finding of the operculum and suboperculum from the Chotěvice Formation of the Krkonoše Piedmont Basin can only be considered as fragments of a species close to *Amelangia ornata* gen. et sp. nov.

Conclusion

The newly described, only partially preserved aedeullid fish *Amelangia ornata* gen. et sp. nov. presents a number of characters typical of the family Aedeullidae, and in support of a close relationship with the genera *Aedeulla* and *Bourbonnella*. The holotype shows an upper jaw with a low triangular maxillary plate, a large dermosphenotic lining the dorsal margin of the orbit, a large number of small suborbital bones, only one branchiostegal ray, the pectoral fin perched on a small lobe covered with scales, the dorsal fin perched on array of small scales composed of 25 segmented lepidotrichia. Segments of lepidotrichia have sigmoidal sutures. Unlike *Aedeulla blainvillei*, three small infraorbitals posterior to the orbit are present, the outer surface of the operculum, suboperculum and part of branchiostegal ray is covered with numerous distinct tuberculations. Another distinction from *Aedeulla blainvillei* is the considerably greater number of scale rows between the supracleithrum and ventral fin, and between the supracleithrum and dorsal fin base. These scale row counts are more similar to what is seen in the genus *Bourbonnella*. Based on the comparison of the above characters, the new specimen is considered to be a new genus and species of *Amelangia ornata* gen. et sp. nov., with close relationships to both *Aedeulla* and *Bourbonnella*. With the first taxon from the family Aedeullidae, *Westollia crassa*, recorded from the Upper Goldlauter Formation (Štamberg, submitted), this new description of *Amelangia ornata* serves as a second representative of this family from the Lower Goldlauter Formation of the Thuringian Forest Basin.

An isolated suboperculum known from the Lower Permian sediments of the Krkonoše Piedmont Basin showing identical characters to the sculpture on the newly described *Amelangia ornata* can be considered an aedeullid fish cf. *Amelangia ornata*.

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