A new actinopterygian species of *Igornichthys* Heyler, 1972 from the Permian of the Krkonoše Piedmont Basin (Bohemian Massif, Czech Republic), and its relationship to the actinopterygians of other European Permo-Carboniferous basins

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ABSTRACT
A new actinopterygian species from lacustrine Lower Permian deposits of the Krkonoše Piedmont Basin (Bohemian Massif, Czech Republic) is assigned to the genus *Igornichthys* Heyler, 1972. Present study of this new species reveals several anatomical structures that markedly advance our knowledge and make the generic diagnosis of *Igornichthys* more precise. Characters that include sharply pointed spines on the scales, a supraorbital sensory canal continuing from the frontal on to the dermopterotic, a maxilla with the maxillary plate protruding at a ventro-posteriorly angle, dentition forming a single row of similar conical teeth, and an oblong operculum are diagnostic of the new species. *Igornichthys* is placed within Igornichthyidae Heyler, 1977 together with *Igornella* Heyler, 1969, *Setlikia* Štamberg & Zajíc, 1994 and *Commentrya* Sauvage, 1888 from the Stephanian and Lower Permian of the French Massif central and the Bohemian Massif. Analysis of the anatomical features of *Igornichthys* and other members of Igornichthyidae demonstrates clear differences from other actinopterygians occurring in the lacustrine basins of the Carboniferous and Lower Permian. The occurrence of very closely related species within *Igornichthys* and genera included in Igornichthyidae and Amblypteridae Romer, 1945, documents an extensive interconnection among the lacustrine basins of the French Massif central, the Saar Nahe Basin and the Bohemian Massif in the Late Carboniferous and particularly in the Early Permian.

KEY WORDS
Early Permian,
Bohemian Massif,
Actinopterygii,
morphology,
new species.

RÉSUMÉ
*Une nouvelle espèce d'*Igornichthys *du Permien du Bassin de Krkonoše Piedmont (Massif Bohémien, République Tchèque), et ses relations avec les actinoptérygiens d'autres bassins européens permo-carbonifères.*
L'étude de cette nouvelle espèce révèle plusieurs structures anatomiques remarquables qui complètent nos connaissances et affinent la diagnose du genre *Igornichthys* Heyler, 1972. Cette nouvelle espèce est caractérisée notamment par des écailles présentant des tubercules très pointus, un canal sensoriel supraorbitaire continu du frontal au dermoptérotique, un maxillaire avec sa plaque qui s'étend ventro-postérieurement, une denture composée d'une seule rangée de dents similaires et coniques, et d'un opercule oblong. *Igornichthys* compose la famille des Igornichthyidae Heyler, 1977 avec *Igornella* Heyler, 1969, *Setlikia* Štamberg & Zajíc, 1994 et *Commentrya* Sauvage, 1888 du stéphanien et permien inférieur du Massif central français et du Massif de Bohême. L'analyse des caractères anatomiques montre qu'*Igornichthys* et les Igornichthyidae sont nettement différents des autres actinoptérygiens des bassins lacustres du carbonifère et du permien inférieur. L'apparition d'espèces très proches du genre *Igornichthys* et des genres d'Igornichyidae et d'Amblypteridae Romer, 1945 témoigne d'une forte interconnection entre les bassins lacustres du Massif central français, de la Sarre et de Bohême durant le carbonifère supérieur et plus particulièrement durant le permien inférieur.

MOTS CLÉS
Permien inférieur,
Massif de Bohême,
Actinopterygii,
morphologie,
espèce nouvelle.

INTRODUCTION

Actinopterygian fish of the genus *Igornichthys* Heyler, 1972 from the Lower Permian of the Autun Basin (French Massif central) were discussed by Heyler (1969, 1972). These actinopterygians, along with specimens of the genus *Igornella* Heyler, 1969 from the same deposits of the Autun Basin, were assigned by Heyler (1972) to the proximity of Aeduellidae. The course of the supraorbital canal is consistent with that in Aeduellidae Heyler, 1969, that was given as support for his assignment. However, conspicuous differences in the maxilla, teeth, parietal and the type of the sculpture of the scales are similar to the Triassic genus *Brookvalia* Wade, 1933, and Heyler (1977) subsequently placed Igornichthyidae within the new order Brookvaliiformes Heyler, 1977. According to Heyler (2000), the family Igornichthyidae includes: *Igornichthys doubingeri* Heyler, 1972 and *Igornella comblei* Heyler, 1969 from the Lower Permian of the Autun Basin, *Igornella montcellensis* Heyler & Poplin, 1994 from the Stephanian of Montceau-les-Mines, and *Commentrya traquairi* Sauvage, 1888 from the Stephanian of Commentry. Štamberg & Zajíc (1994) included *Setlikia bohemica* Štamberg & Zajíc, 1994 from the Upper Carboniferous of the Kladno-Rakovník Basin (Bohemian Massif) as a species and genus within the family Igornichthyidae. Recent extensive study of Lower Permian deposits of the Krkonoše Piedmont Basin (Bohemian Massif) provided the author of this paper with abundant new actinopterygian material including a juvenile specimen of *Igornichthys*. The anatomical characters of this specimen significantly extends our knowledge of this genus and an analysis comparing the anatomical characters of Carboniferous and Permian actinopterygians from the Bohemian Massif, Saar Basin and French Massif central is now possible.

GEOLOGICAL CONTEXT

The intramontane Krkonoše Piedmont Basin occupies the north-eastern region of the Bohemian Massif. The area of the basin is more than 1100 km², and the maximum thickness of the volcano-sedimentary basin fill in its central part is nearly 1800 m. The basin was formed as a part of a system of basins that opened in the Bohemian Massif during the late phases of the Variscan orogeny. Deposition within the basin started during the Westphalian D (Moscovian), and continued to the Early Permian (Sakmarian). The youngest units (Saxonian to Triassic) are preserved only in the eastern part of the basin (Trutnov-Náchod subbasin) (Prouza & Tásler 2001). The Lower Permian filling is represented by the Vrchlabí Formation (Asselian) along with the important fossiliferous Rudník Member. The Rudník Member represents on average a 40-60 m thick succession of lacustrine grey mudstone with layers of black claystone, carbonate, sandstone and conglomerate. Present outcrops indicate the east-west extent of the Rudník Member is more than 30 km in length, and has a surface area of approximately 300-500 km², although it could be much larger, on the order of 1000 km² (Martínek *et al.* 2006). The occurrence of actinopterygians, and other vertebrates, is restricted to a lacustrine bituminous gray-black calcareous claystone, which outcrops in one or two beds in numerous localities along the northern border of the Krkonoše Piedmont Basin between the villages Semily and Rudník, and repeatedly in the short strip between villages Košťálov and Kundratice. The most common species in all of the studied Rudník Member localities is *Paramblypterus rohani* (Heckel, 1861) of the family Amblypteridae Romer, 1945. *Neslovicella elongata* Štamberg, 2010, a member of the Aeduellidae is rarer than *Paramblypterus rohani.* The small predatory actinopterygian *Letovichthys* Štamberg, 2007 is rare and known only from a total of five specimens. An isolated occurrence of another small predatory actinopterygian, *Igornichthys*, comes from a single locality, Příkrý "Hoňkův creek".

Štamberg & Zajíc (2008) added both invertebrates and vertebrates to the Rudník Member faunal record. They found that the invertebrate fauna contains abundant conchostracans and a syncarid crustacean, *Monicaris rudnicensis* Štamberg, 2000. The fish fauna includes an acanthodian, *Acanthodes gracilis* (Beyrich, 1848), and a xenacanthid shark, *Bohemiacanthus carinatus* (Fritsch, 1890). The amphibian fauna includes *Ptyonius bendai* Fritsch, 1895, *Melanerpeton* sp., and *Archegosaurus dyscriton* (Steen, 1938). *Sagenodus tardus* Fritsch, 1899, a rare dipnoan fish, also occurs within the Rudník Member fauna. The Příkrý "Hoňkův creek" locality that produced the new species of *Igornichthys* also contains the actinopterygian *Paramblypterus rohani*, isolated acanthodian spines and scales, isolated xenacanthid shark spines, abundant conchostracans and *Monicaris rudnicensis*, a syncarid crustacean.

METHODS

The descriptive terminology used in this paper conforms to that adopted by Grande & Bemis (1998) with observations, drawings, measurement methods and some terms after Štamberg (2007). The descriptions of the fin structures correspond with that of Arratia (2008). An SEM Hitachi S-3700N was used for the study and documentation of suitable scales and tooth microsculpture.

Abbreviations

Cl	cleithrum;
Dent	dentary;
Dpt	dermopterotic;
Dsph	dermosphenotic;
Ext	extrascapular;
Fr	frontal;
Gul	gular lateral;
infc	infraorbital canal;
Io	infraorbital;
La	lacrymal;
Na	nasal;
Mx	maxilla;
Op	operculum;
Pa	parietal;
Par	parasphenoid;
poc	preopercular canal;

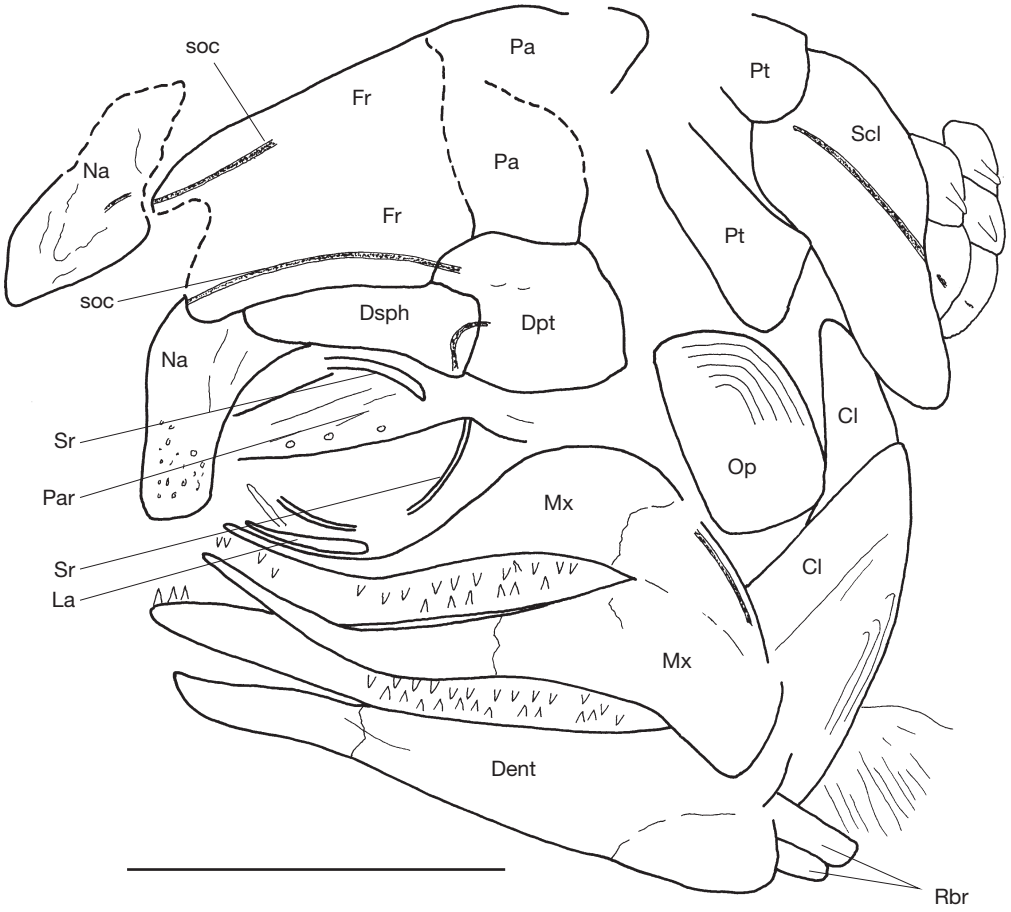

FIG. 1. — *Igornichthys bohemicus* n. sp., skull in left lateral view, holotype MHK 30866. The outlines of the bones, which are ill-defined, are marked with dashed lines. Abbreviations: see Methods. Scale bar: 5 mm.

Pop	preoperculum;
Pp	postparietal;
Pt	posttemporal;
Rbr	branchiostegal rays;
Rpr	rostropostrostral;
Scl	supracleithrum;
Soant	supraorbital anterior;
soc	supraorbital canal;
Sop	suboperculum;
Sr	sclerotic ring.

SYSTEMATIC PALEONTOLOGY

Order BROOKVALIIFORMES Heyler, 1977

Family IGORNICHTHYIDAE Heyler, 1977

TYPE GENUS. — *Igornichthys* Heyler, 1972.

INCLUDED GENERA. — *Igornichthys* Heyler, 1972; *Igornella* Heyler, 1969; *Commentrya* Sauvage, 1888; *Setlikia* Štamberg & Zajíc, 1994.

DIAGNOSIS. — The skull roof has large frontals, small parietals and large dermopterotics. The supraorbital canal traverses from the frontal to the dermopterotic and not to the parietal. The teeth are of intermediate size and sharply pointed. The sculpture on the scales forms one or two large and sharply pointed spines that are postero-ventrad oriented.

REMARKS

Heyler (1977) erected the family Igornichthyidae in his text but did not include a diagnosis. The here given diagnosis was compiled and based primarily on Heyler (1969, 1977).

Genus *Igornichthys* Heyler, 1972

TYPE SPECIES. — *Igornichthys doubingeri* Heyler, 1972.

INCLUDED SPECIES. — *Igornichthys doubingeri* Heyler, 1972; *I. bohemicus* n. sp.

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION. — Lower Permian, Autunian Basin, Krkonoše Piedmont Basin.

EMENDED DIAGNOSIS. — Supraorbital canal traverses across the frontal to the dermopterotic. One long dermosphenotic dorsally borders the orbit. Maxilla with a large maxillary plate and conspicuous postero-ventral angle, and strong mandibular. Operculum of oblong shape. Branchiostegal rays narrow and numerous. Body elongated. The outer surface of the scales is ornamented with one or two sharply pointed spines that are oriented in postero-ventrad direction.

REMARKS

The first description of *Igornichthys* introduced by Heyler (1969) included the following diagnosis of the

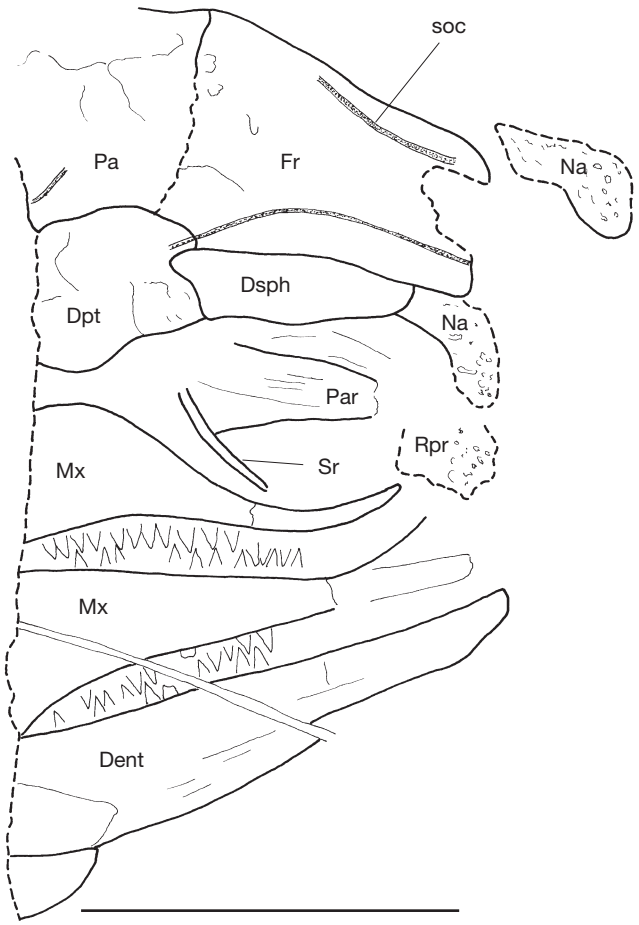

Fig. 2. — *Igornichthys bohemicus* n. sp., outprint of the skull in left lateral view, holotype MHK 30866. The outlines of the bones, which are ill-defined, are marked with dashed lines. Abbreviations: see Methods. Scale bar: 5 mm.

genus: "Maxillaire à plaque postérieure assez forte, se courbant vers le bas en arrière ; mandibule forte, non élevée à l'arrière ; opercule et sous-opercule assez étroits ; préopercule de forme imprécise, mais courbant en avant en sa partie supérieure ; rayons branchiostèges étroits et nombreux ; corps allongé, pelvienne s'attachant vers la 9e rangée d'écailles ; écailles portant une ornementation très particulière formée d'une ou deux pointes dirigées postérieurement et un peu vers le bas, plaquées sur la surface de l'écaille". Heyler (1969) unfortunately neglected to designate a type species, but resolved this situation when he designated *Igornichthys doubingeri* Heyler, 1972 as the type species of the genus *Igornichthys* Heyler, 1972. According to the International Code of Zoological nomenclature (ICZN: art. 11.9.3) this is considered an unavailable name, and the genus *Igornichthys* became valid after the designation of the type species in 1972. Heyler (1969) thus provided a diagnosis of the genus *Igornichthys* only from the characters of *I. doubingeri*. The current author is convinced that the new species from the Bohemian Massif belongs to the genus *Igornichthys*, but differs in some characters from the type species.

Igornichthys bohemicus n. sp.
(Figs 1-10)

Igornichthys sp. – Štamberg 1994: 21, fig. 2; 2013: 167, 168.

Holotype. — Specimen MHK 30866 (part and fragment of the counterpart) with relatively well preserved bones of the head and anterior region of the trunk. The holotype is deposited in the Museum of Eastern Bohemia in Hradec Králové.

Etymology. — Bohemicus, -a, um (Lat.); after the region of the Czech Republic.

Material examined. — Holotype only.

Type locality. — Rybnice "Hoňkův creek", 50°36'59.47N, 15°23'08.80E, Semily District, Krkonoše Piedmont Basin, Czech Republic.

Stratigraphic horizon and age. — Rudník Member, Vrchlabí Formation, Asselian, Early Permian.

Diagnosis. — Supraorbital canal traverses from the frontal to the dermopterotic. Large orbit with thin sclerotic bones. Demosphenotic narrow and elongated. One row of straight, conical marginal teeth of uniform shape and size. Dorsally convex operculum with rounded edges and a straight ventral border. The deep of the operculum is 1.7 × that of the length. There are 12 scale rows anterior to the origin of the pelvic fin. Anterior margins of the pelvic and anal fins are "protected" by fulcra of the procurrent rays. Terminal segments of rays together with fringing fulcra are forming the leading edge. Lepidotrichia of the pectoral fin are unsegmented.

Description

The referred holotype specimen of the new species of *Igornichthys* represents a small subadult that is approximately 50 mm in total length. The overall specimen is reasonably well preserved including jaws with teeth, bones of the skull roof, operculum and dermal bones of the shoulder girdle. The trunk shows well the squamation and also the structure of the pectoral, pelvic and anal fins. The posterior part of the body is missing.

Body form

The body is fusiform and only slightly convex in the anterior portion (Fig. 3A). The skull length represents *c.* ⅕ of the total length of the body.

Head

The head contains a conspicuously large orbit with a length that equals one third of the entire head. There are fragments of three sclerotic bones which are gently bent and narrower on their distal ends (Figs 1; 2; 3B). Complete sclerotic ring that probably consists of four sclerotic bones. The dorso-ventrad elongated nasal is sculptured with tubercles and borders the orbit anteriorly. The nasal is dorso-posteriad in contact with dermosphenotic and frontal, and separates the orbit from the frontal. A narrow lacrymal borders the ventral rim of the orbit. The bones between the posterior maxillary plate and the orbit are not clearly visible. The dermosphenotic borders the orbit dorsally. It is antero-posteriad elongated, anteriorly narrow and broadens gradually posteriad. The infraorbital sensory canal is preserved over a short distant only, it trav-

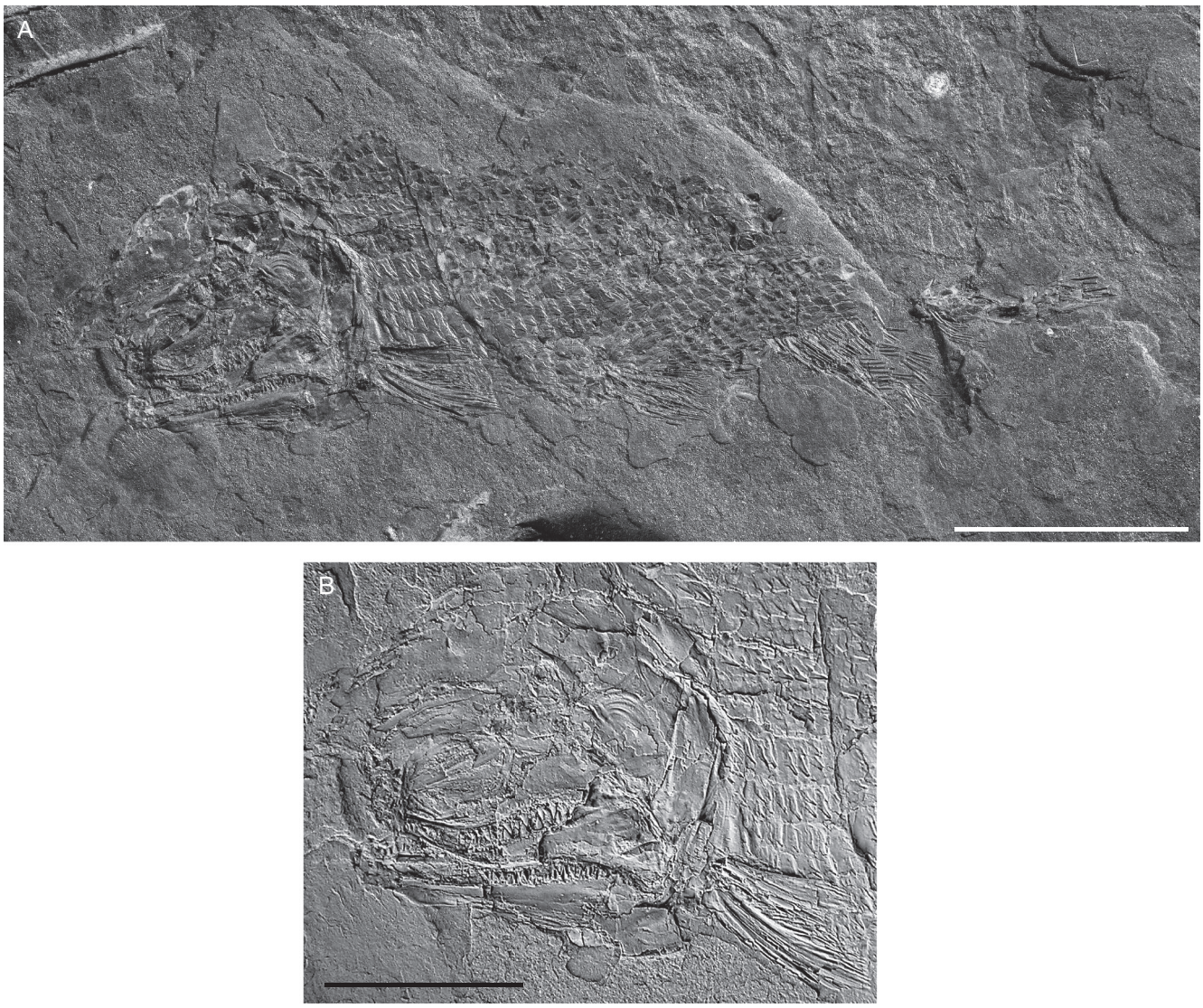

Fig. 3. — *Igornichthys bohemicus* n. sp., holotype MHK 30866: **A**, left view of the whole specimen; **B**, detail of the skull in left lateral view. Scale bars: 5 mm.

erses from the dermopterotic to the dermosphenotic. It is bent at a 90° angle, and appears to continue posterior to the orbit. The dermopterotic is wider and shorter than the dermosphenotic. It is placed posteriorly and in line with it. The frontal is the largest skull roof bone that is seen. It is laterally bordered with the demosphenotic, and the posterior part of the lateral margin of the frontal is in contact with dermopterotic. A conspicuous supraorbital sensory canal passes from the anterior margin of the frontal along the lateral margin of the bone, and slightly bends when laterally traversing to the dermopterotic. The interfrontal suture is not clear. A parietal that is twice as short as the frontal, is seen only in incomplete outline. The jaws are well preserved. The maxilla has a narrow and long anterior part that markedly elevates posteriad. The posterior part forms a maxillary plate of oblong shape with a downwardly protruding postero-ventral angle. The maxilla represents 2.4 × the length of the maxillary plate. The depth of the maxillary plate including the postero-ventral angle represents 3 × the length of the maxilla. The lower jaw is strong, anteriorly narrow and posteriorly moderately elevated. Dentition on the upper and lower jaws forms a single row of straight, conical teeth of equal size and shape. The teeth have a relatively wide base, and their height is twice that of the base. Tooth surfaces are smooth (Fig. 6). The teeth are in a single row, and interlock when the jaws are closed. There are 24-27 marginal teeth along each half of the jaw. The height of the teeth compared to the depth of the skull in front of the opercular series (Poplin & Heyler 1993) yields a ratio of 40.

The palatal bones are provided with small and sharply pointed teeth, several of which are preserved. A parasphenoid fragment is preserved that shows a strong lateral ascending process in the dorsal part of the orbit. The ventral surface of the processus cultriformis was likely tooth-bearing, as evidenced by a number of circular broken bases (Fig. 1). Circular broken bases of the teeth demonstrate much smaller teeth than are on the jaws. The preoperculum is partially preserved; it is anteriorly bent along the dorso-posterior rim of the maxillary. A portion of the preopercular canal extends along the posterior margin of

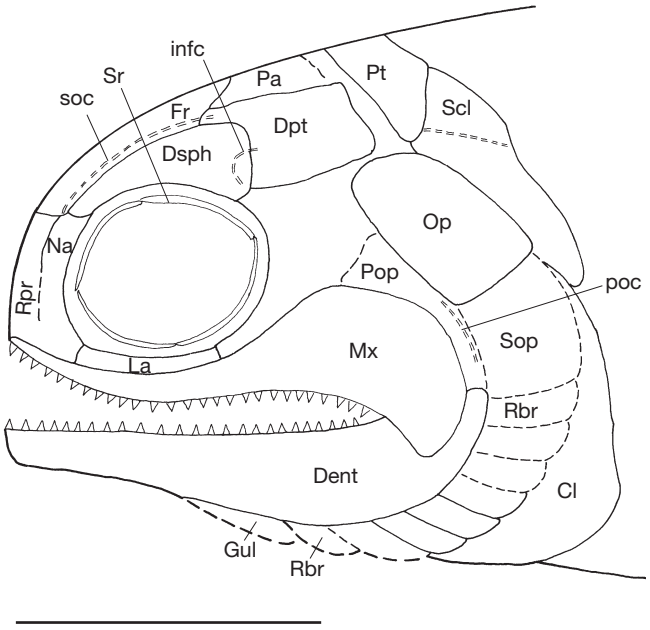

FIG. 4. — *Igornichthys bohemicus* n. sp., reconstruction of the skull in left lateral view. The outlines of the bones, which are ill-defined, are marked with dashed lines. Abbreviations: see Methods. Scale bar: 5 mm.

the preoperculum. The operculum is oblong in shape, and its depth is 1.7 × that of the length. The axis of the operculum (Štamberg 2007) is inclined at an angle of about 50°. The operculum is rounded in the dorsal region, and the ventral margin is straight with rounded corners. The suboperculum is unknown, and fragments of three narrow branchiostegal rays posterior to the lower jaw indicate that there were several branchiostegal rays in the operculo-gular apparatus. There is an outline of a large post-temporal that extends onto the dorsal rim of the operculum. The extrascapular bones are unknown. The supracleithrum is dorso-ventrad elongated, and is taller than the operculum. The ventral region of the supracleithrum reaches the cleithrum. A lateral sensory canal traverses across the dorsal region of the supracleithrum diagonally. The cleithrum is strong and broadly exposed laterally. The cleithrum and the operculum are mutually shifted during fossilization (Figs 1; 3). Acute dorsal end of the supracleithrum reached the ventral border of the operculum beyond the life of the animal (Fig. 4).

Fins

The pectoral fin is preserved showing unsegmented lepidotrichia along the entire length. The lepidotrichia are not dichotomically branched in the distal portion. The leading edge of the pectoral fin shows a terminal section of six procurrent rays. A partially preserved, small, pelvic fin is proximally placed slightly closer to the origin of the anal fin than to the pectoral. There are 12 scale rows anterior to the origin of the pelvic fin and 23 scale rows anterior to the origin of the anal fin. The anal fin is triangular in shape. The lepidotrichia of the pelvic and anal fins are segmented along their entire length. These segments are narrow and very long, which indicates that this is subadult specimen.

The rays of the anal fin have no more than eight segments. The leading edges of both fins show protective terminal segments of rays together with less numerous fringing fulcra (Fig. 9E, F). Some segments show a very fine microsculpture on their ganoine surface. The basal segments of the anal fin have ridges that are short, fine and linearly arranged (Fig. 9D).

Squamation

The scales and their sculpture show important characteristic features. The surfaces of the scales have conspicuous spines. The spines in the central region of the scales generally have a wide base, and are pointed posteriad and slightly downwards. Each scale shows only a single spine (Figs 7A, B, D, E; Fig. 8A), although two spines do occur on scales in the rows ventral to the lateral line scales behind the head (Fig. 3B), and in the fifth and twentieth rows (Figs 7C; 8B). All trunk scales including those from the lateral sides, ventral sides and the posterior region of the body are equipped with the spines. The spines are absent only from the scales of the lateral sensory line. It is not clear if they were present or absent from behind the anal fin as these scales are not preserved. The surface of the spines is distinct from that of the surrounding scale surface. The scale surfaces are rough, which indicates bone tissue. The spine surfaces are covered with a thickened ganoin layer that bears fine ridges. These ridges are linearly arranged, oriented parallel to the axis of the spine, and set 4 µm apart (Fig. 7F). The microsculpture was partially removed in the course of fossilization. There are 12 vertical scale rows between the supracleithrum and the origin of the pelvic fin. There are roughly 23 scale rows between supracleithrum and the origin of the anal fin. Eight horizontal scale rows are below and five horizontal scale rows are above the lateral line in the level of the begin of the pelvic fin.

There is a fragment of a ventral scute at the lower peduncle in front of the caudal fin. It contains a flat ridge on its surface that shows a thickened ganoine layer with well-preserved microsculpture. The microsculpture is formed by short ridges that are linearly arranged. These ridges are 4.5 µm apart, and show a gentle flabelliform fork (Fig. 9A-C). The remainder of the scute has a rough surface indicative of bone. The above observations suggest the ganoine is limited to the spines only.

DISCUSSION

The new species exhibits characters of the genus *Igornichthys*. The most important of these are the typical scale sculpture, a supraorbital sensory canal that traverses from the frontal to the dermopterotic, a maxilla with a large maxillary plate that is postero-ventrad prolonged to a processus and marginal conical teeth. *Igornichthys* is presently known as: *I. doubingeri* (Heyler, 1972) from the Igornay Formation of Autun Basin (Permian), *Igornichthys* sp. (Schindler 2007) from an isolated scale in the Saar Basin (Permian), and *I. bohemicus* n. sp. from the Krkonoše Piedmont Basin (Asselian, Vrchlabí Formation) of the Bohemian Massif (this paper). *Igornichthys bohemicus* n. sp. substantially adds to our knowledge of the genus *Ig-*

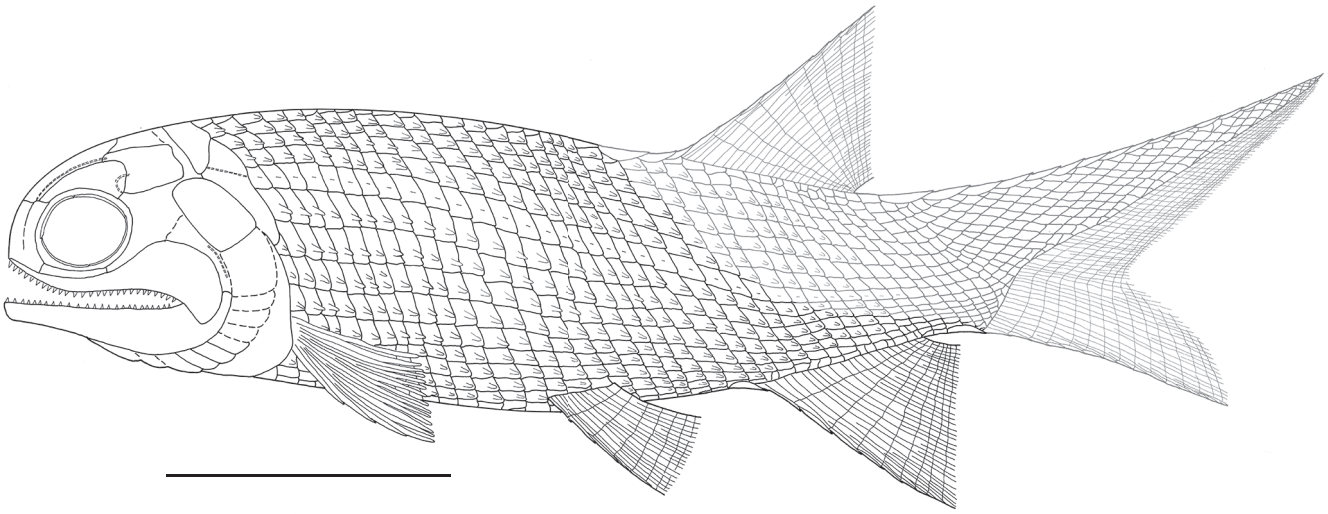

FIG. 5. — *Igornichthys bohemicus* n. sp., reconstruction of the body in left lateral view. Posterior part of the body which is not preserved is grey. Scale bar: 5 mm.

ornichthys. This new species demonstrates some characters previously described by Heyler (1969), but also adds new information regarding the skull roof including the course of the supraorbital canal. The course of the supraorbital canal in *I. bohemicus* n. sp. confirms its affinity with *Igornella* (Heyler, 1969), *Setlikia* (Štamberg & Zajíc, 1994) and *Commentrya* (Blot, 1966). *Igornichthys bohemicus* n. sp. is erected by the author based on the dentition, position and the shape of the operculum, and the origin of the pelvic fin, which are distinct from *I. doubingeri*.

Heyler (1969) described *I. doubingeri* as showing an alternation of large and smaller teeth on the jaws. *Igornichthys bohemicus* n. sp., in contrast, has marginal teeth that are of equal shape and size. Unlike those in *I. doubingeri*, the teeth of *I. bohemicus* n. sp. are arranged in a single row. Interestingly, both species of *Igornichthys* represent subadult specimens that are from 50-80 mm in total length, and the long ray segments and an absence of dichotomisation in these structures support this conclusion. *Igornichthys* combines some anatomical features that are separately seen in several actinopterygian families of the Carboniferous and Permian basins of the French Massif central, Bohemian Massif and Saar Nahe Basin. The skull roof bones in *Igornichthys* are noticeably similar to those of other actinopterygians. The dermosphenotic in *Igornichthys* is narrow and long (Fig. 10D). It carries the angle of the infraorbital sensory canal and according to the definition of Poplin (2004) belongs to a group of actinopterygians with one dermosphenotic that extends over the orbit. The dermosphenotic is prolonged over the orbit, and its shape and position is similar to Aeduellidae (Fig. 10A, B) (Heyler 1969; Poplin & Dutheil 2005; Štamberg 2007, 2010) and *Commentrya traquairi* Sauvage, 1888 (Blot 1966). It conforms in position and shape with *Letovichthys tuberculatus* Štamberg, 2007 from the Bohemian Massif. However, it differs in absence of infraorbital canal dichotomization, which is known in *L. tuberculatus.* Conversely, other species of the family Igornichthyidae, *Igornella comblei* and *Setlikia bohemica,* have another ventral dermosphenotic (infraorbital after Štamberg & Zajíc 1994; supraorbital? after Heyler 1969) between the dermosphenotic and the orbit. The position and shape of the dermosphenotic is quite distinct in Amblypteridae. It is triangular in shape and separated from the orbit by the infraorbital and nasal (Blot 1966; Heyler 1969; Dietze 1999, 2000; Štamberg 1976, 2013).

The course of the supraorbital canal is another important character in Carboniferous and Permian actinopterygians. It generally traverses the frontal and passes to the parietal in most actinopterygians (Amblypteridae, Elonichthyidae, Rhabdolepidae, and others). The supraorbital canal in *Igornichthys*, and other taxa within Igornichthyidae including *Commentrya*, passes from the frontal to the dermopterotic. The same course of the supraorbital canal is observed in Aeduellidae (Heyler 1969; Poplin & Dutheil 2005; Štamberg 2007, 2010) and also in *Commentrya traquairi* (Blot, 1966) that is a taxon of the Igonichthyidae. The shape of the maxilla and the type of dentition is another important feature of Permo-Carboniferous actinopterygians. The maxilla of *Igornichthys* has a distinctive maxillary plate with a prominent postero-ventral angle. This characteristic is also present in taxa belonging to Elonichthyidae Aldinger, 1937 and Rhabdolepidae Gardiner, 1963 of the Saar Basin and Bohemian Massif (Gardiner 1963; Schindler 1993, 2007; Štamberg 1991, 2010). Amblypterids also have a well-developed maxillary plate but the plate is deeper and without a prominent postero-ventral angle (Heyler 1969; Štamberg 1976; Dietze 1999, 2000). Aeduellids have a maxillary plate of triangular shape (Heyler 1969, 1991; Štamberg 2007, 2010).

The dentition in Carboniferous and Permian actinopterygians shows morphological variation. The marginal teeth in aeduellids and amblypterids form as very small tubular teeth that are closely set and form a narrow brush on the jaws (Blot 1966, Poplin & Heyler 1993). *Igornichthys bohemicus* n. sp. has small, but strongly conical, marginal teeth

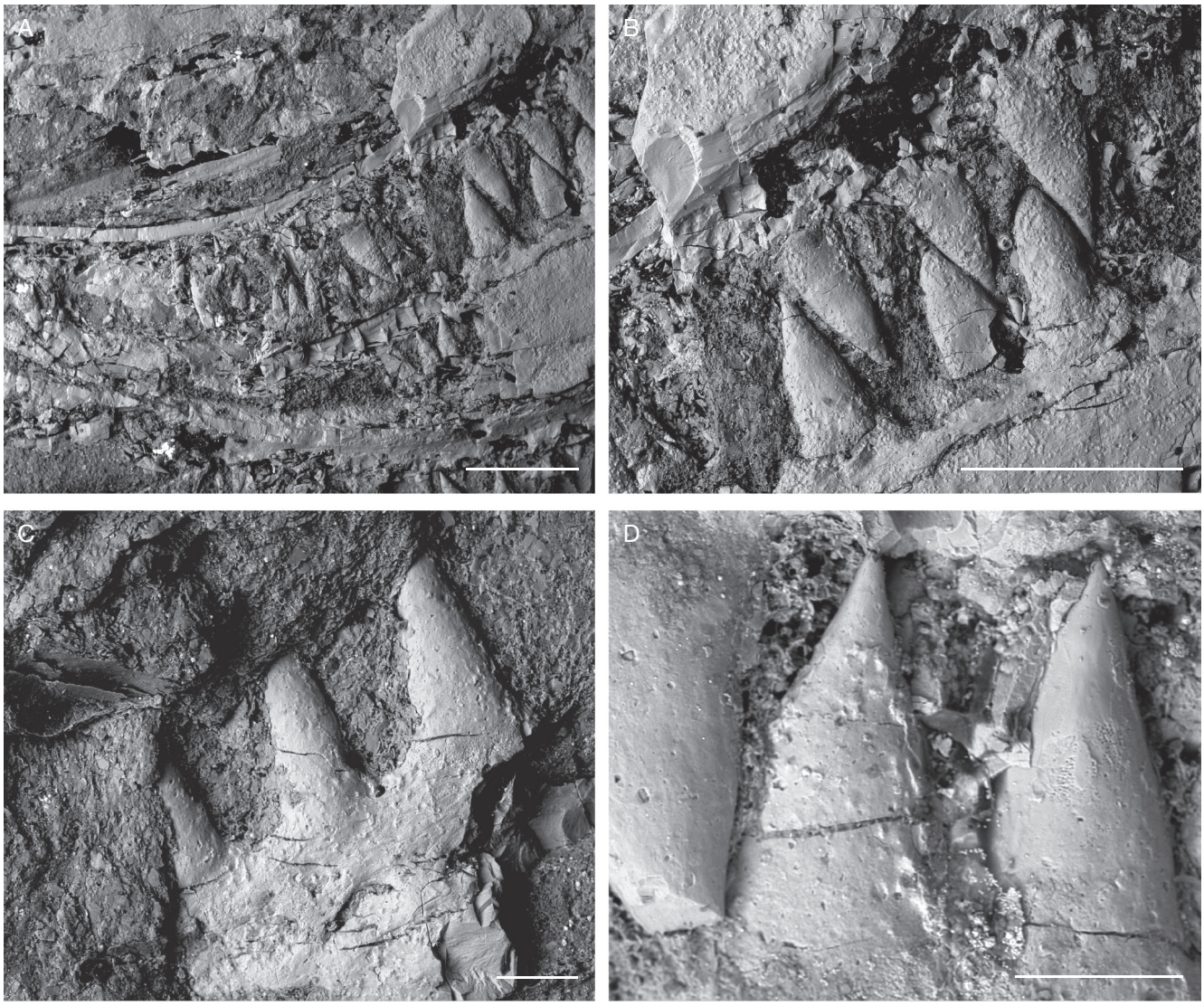

FIG. 6. — *Igornichthys bohemicus* n. sp., holotype MHK 30866: **A**, general view of the teeth of upper and lower jaws; **B**, detail of the teeth of the upper and lower jaws, which interlock, when the jaws are closed; **C**, detail of the teeth of the anterior region of the lower jaw; **D**, detail of the teeth of the lower jaw. Scale bars: A, B, 500 µm; C, D, 100 µm.

in one row. *Igornichthys doubingeri* has similar teeth which were described by Heyler (1969) as alternating with much smaller ones. Genus *Letovichthys* from the Lower Permian of the Bohemian Massif has teeth in two rows. The teeth in the inner row are large and sharply pointed, and those in the outer row are small and numerous. These tooth rows are seen also in *Meisenheimichthys* Schindler, 1993 from the Saar Nahe Basin (Schindler 1993, 2007) and the large carnivore *Progyrolepis* (Fritsch, 1895) from the Bohemian Massif (Štamberg 1991) and Buxières-les-Mines (Poplin 1999). The ratio of tooth height to the depth of the skull in front of the opercular series provides a somewhat precise appraisal of the relative size of the teeth (Poplin & Heyler 1993). The ratio found in *I. bohemicus* n. sp. is 40, which is about the same as *Letovichthys tuberculatus* from the Bohemian Massif. The stout laniary teeth in *Progyrolepis speciosus* (Frič, 1875) differ in having a ratio of 20.

The operculum of *Igornichthys* is closely similar in shape to that of amblypterids. It is not exceedingly deep or anteriorly bent as that of aeduellids, but is oblong and dorsally rounded with a straight ventral rim. Ventrally it is not as narrow as the operculum in *Meisenheimichthys* from the Saar Basin (Schindler 2007) or in *Progyrolepis speciosus* (Frič, 1876) and "*Elonichthys*" *krejcii* (Fritsch, 1895) from the Bohemian Massif (Štamberg 1991).

The discovery of microsculpture in some scales and segments of the lepidotrichia in *Igornichthys bohemicus* n. sp. is another important character. These small tubercles are typical for ganoine surface (Schultze 2016), and they have been observed on the scales of Mesozoic and Recent holostean and polypterids. Arrangement and shape of the microtubercles could be diagnostic feature for determination of isolated scales of Permo-Carboniferous actinopterygians, as already Meunier *et al.* (1986), Gayet & Meunier (2001) have dem-

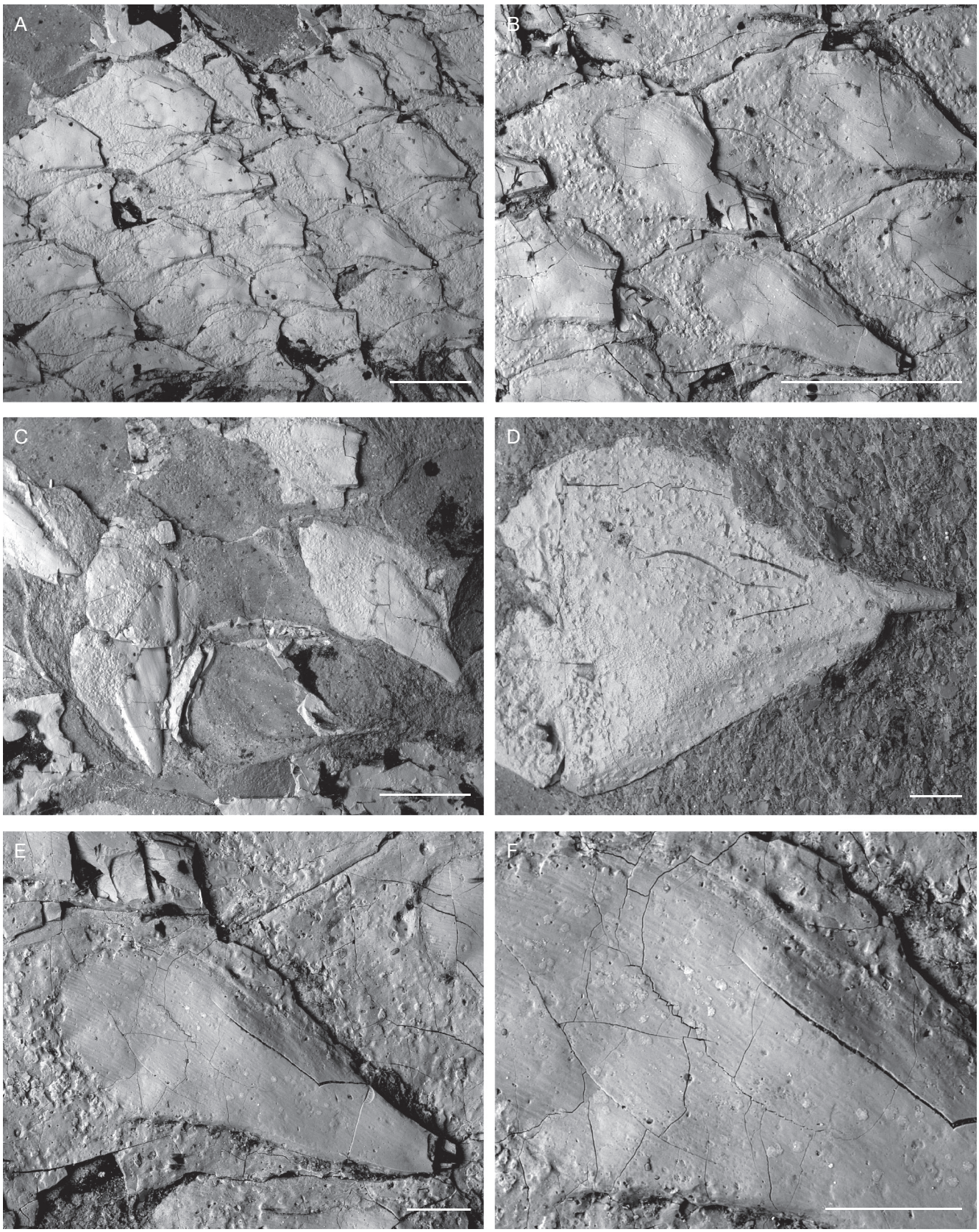

FIG. 7. — *Igornichthys bohemicus* n. sp., holotype MHK 30866, scales on the left lateral side of the body: **A**, scales from rows 23-27 with conspicuous spines; **B**, detail of the scales from rows 25-27 with single spine; **C**, scales with two spines; **D**, detail of the scale with single spine in medial view; **E**, detail of the scale from row 27 with microsculpture of spines, whereas the surrounding scale surface is rough, which indicates bony surface; **F**, detail of the microsculpture on the spine of the previous scale. Scale bars: A, B, C, 500 µm; D, E, F, 100 µm.

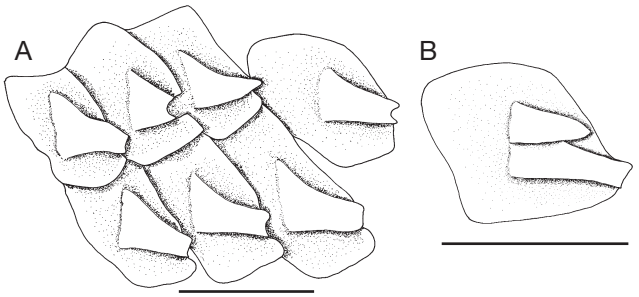

FIG. 8. — *Igornichthys bohemicus* n. sp., holotype MHK 30866: **A**, scales with one spine sharply pointing in posterior direction and slightly downwards on each scale; **B**, scale with two sharply pointed tubercles. Scale bars: 1 mm.

onstrated for recent and fossil genera of Lepisosteiformes and Polypteriformes. *Igornichthys bohemicus* n. sp. demonstrates microtubercles which have form of a short ridges slightly elongated in antero-posterior direction. The microtubercles of the same shape described Štamberg (2016) in "*Elonichthys*" sp. Microtubercles conspicuously elongated in antero-posteriad direction figured already Richter (1995) in the scales of *Palaeoniscum freieslebeni* Blainville, 1818 and S*trepheoschema fouldenensis* White, 1927 and Štamberg (2016) in *Progyrolepis heyleri* Poplin, 1999, while the scales of aeduellid *Spinarichthys dispersus* (Fritsch, 1894) have microtubercles of circular shape (Štamberg 2016: fig. 12B).

The relationship between *Igornichthys* and *Igornella* deserves special consideration. Heyler (1969) described the new genus and species *Igornella comblei* together with *Igornichthys* from the same deposits of the Autun Basin. The holotype and other specimens of *Igornella comblei* well demonstrate the rostral region and the skull roof, and partially the opercular region. The jaws and branchiostegal rays are presently unknown in comparison with *I. doubingeri*. By contrast the skull roof and rostral region are presently unknown in *I. doubingeri*. The additional description of another species *Igornella montcellensis* (Heyler & Poplin, 1994) did not complete our knowledge in this respect. What is presently known is that the genera *Igornichthys* and *Igornella* have the same sculpture on the scales. Heyler (1969, 2000) has already known that these genera are not clearly separated. *I. bohemicus* n. sp. shows new data about the skull roof and documents a correspondence in the course of the supraorbital canal with *Igornella comblei*. Although *Igornichthys* and *Igornella* show several important features in common, it is not possible to synonymize them for the following reasons: *Igornella comblei* has an infraorbital (ventral dermosphenotic after Poplin 2004) between the orbit and the dermosphenotic, which is missing in *I. bohemicus* n. sp.; and the operculum of *Igornichthys* is 1.7 × deeper than long, whereas it is only slightly deeper in comparison to its length in *Igornella comblei*. A similar situation exists between *I. bohemicus* n. sp. and *Setlikia bohemica* (Fig. 10C) from the Bohemian Massif. *S. bohemica* shows similarity in its rostral region to *Igornella comblei* by having a skull roof with a triangular parietal and a supraorbital canal that traverses from the frontal to the dermopterotic and the second dermosphenotic. This species certainly belongs to Igornichthyidae, although information about the upper jaw, dentition and squamation are unfortunately missing.

The present discussion presents evidence that the anatomical characters of the Igornichthyidae differ substantially from the Amblypteridae, Aeduellidae, Elonichthyidae that occupied basins of the French Massif central, Saar Nahe Basin and Bohemian Massif in the Late Carboniferous and Early Permian. Representatives of Igornichthyidae have a set of characters that are known separately in other families, namely: supraorbital canals that transverse from the frontal to the dermopterotic; maxilla with a large maxillary plate of oblong shape and a postero-ventral angle; small but strong conical teeth fixed to the jaws; operculum of oblong shape that does not narrow ventrad or dorsad; and the sculpture on the scales form one or two large spines pointing posteriad and slightly downwards.

The family Igornichthyidae Heyler, 1977 is at present represented by the following species and occurrences:
– *Igornichthys doubingeri* Heyler, 1972 – French Massif central, Permian, Autunian Basin, Igornay Member (Heyler 1969, 1977, 2000);
– *Igornichthys bohemicus* n. sp. – Bohemian Massif, Krkonoše Piedmont Basin, Lower Permian, Asselian, Vrchlabí Formation, Rudník Member;
– *Igornichthys* sp. – Saar Nahe Basin, Lower Permian, Asselian, Remigiusberg Formation, Theisbergstegen See (Schindler 2007);
– *Igornella comblei* Heyler, 1969 – French Massif central, Permian, Autunian Basin, Igornay Member (Heyler 1969, 1977, 2000);
– *Igornella montcellensis* Heyler & Poplin,1994 – French Massif central, Montceau-les-Mines Basin, Stephanian B (Heyler & Poplin 1994; Heyler 2000);
– *Setlikia bohemica* Štamberg & Zajíc, 1994 – Bohemian Massif, Kladno-Rakovník Basin, Stephanian B, Slaný Formation, Ledce Member (Štamberg & Zajíc 1994);
– *Commentrya traquairi* Sauvage, 1888 – French Massif central, Commentry Basin, Stephanian (Blot 1966).

The enumerated species illustrate that there was an interchange of actinopterygian fauna among the Bohemian Massif and the French Massif central including the Saar Nahe Basin in Germany. The Permo-Carboniferous environments of the Bohemian Massif, the French Massif central and the Saar Nahe Basin are mostly interpreted as freshwater deposits (Poplin 1994; Roscher & Schneider 2006; Boy & Schindler 2012). Reinterpretation of the environments as marine or influenced by marine in the above mentioned basins was published more recently (Soler-Gijón & Moratalla 2001; Schultze & Soler-Gijón 2004; Schultze 2009). Species composition of the Permian fauna in basins evokes in my opinion their spread in fluvio-lacustrine system. Extensive fluvio-lacustrine systems made possible the migration of actinopterygians in the Stephanian B, as documented by the closely related species *Igornella montcellensis* from Montceau-les-Mines (French Massif central) and *Setlikia bohemica* from the Bohemian Massif. Communication among the lacustrine basins was much more extensive during the Carboniferous

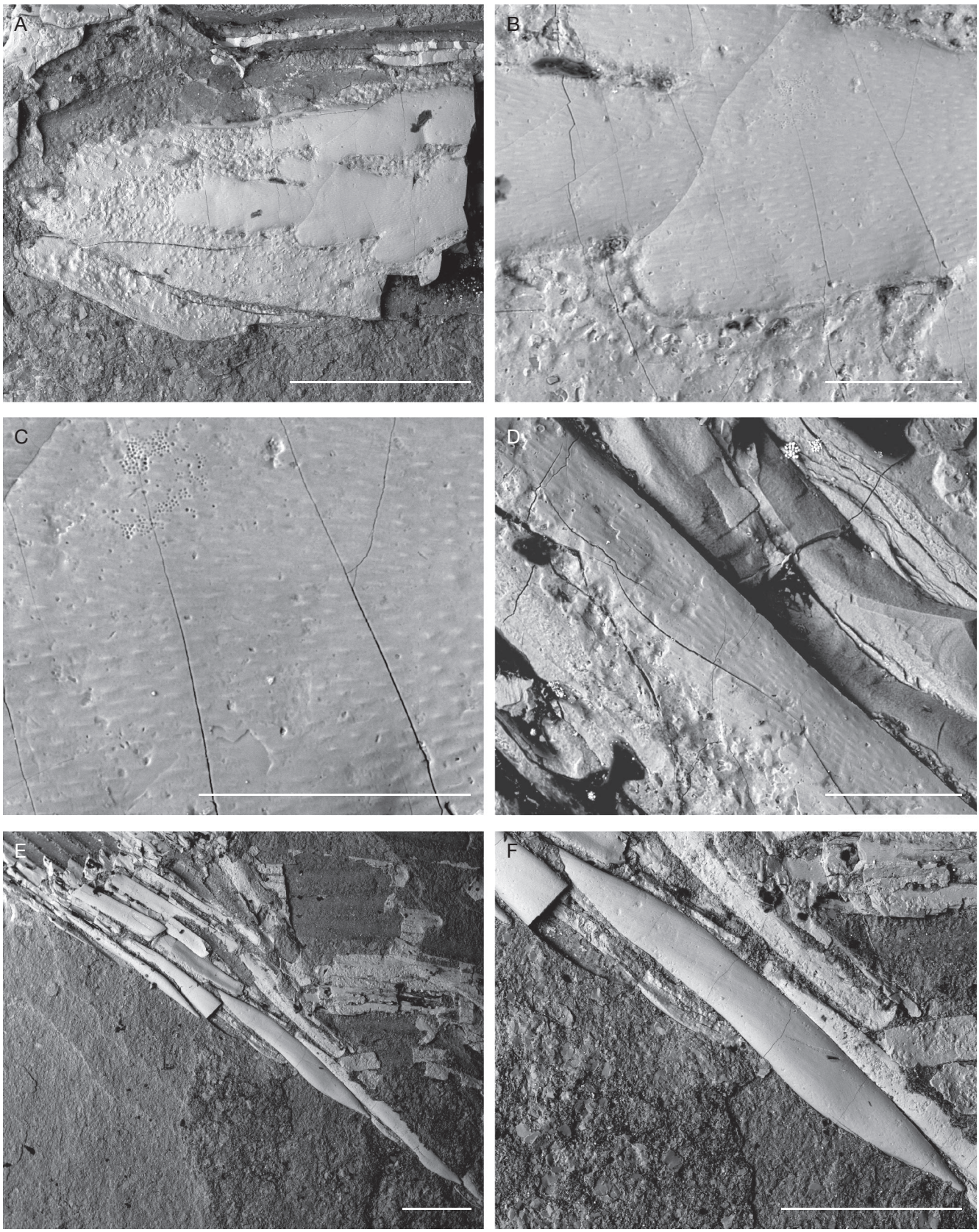

FIG. 9. — *Igornichthys bohemicus* n. sp., holotype MHK 30866: **A**-**C**, ventral scute from the caudal peduncle, which shows the sculpture of flat ridges on its surface (**A**) and microsculpture formed by short ridges and tubercles that are linearly arranged (**B**, **C**); **D**, basal segments of the anal fin with fine microsculpture on their surface; **E**, the leading edge of the anal fin with fulcral scales; **F**, detail of the fulcral scale on the leading edge of the anal fin. Scale bars: A, E, F, 500 µm; B, C, D, 100 µm.

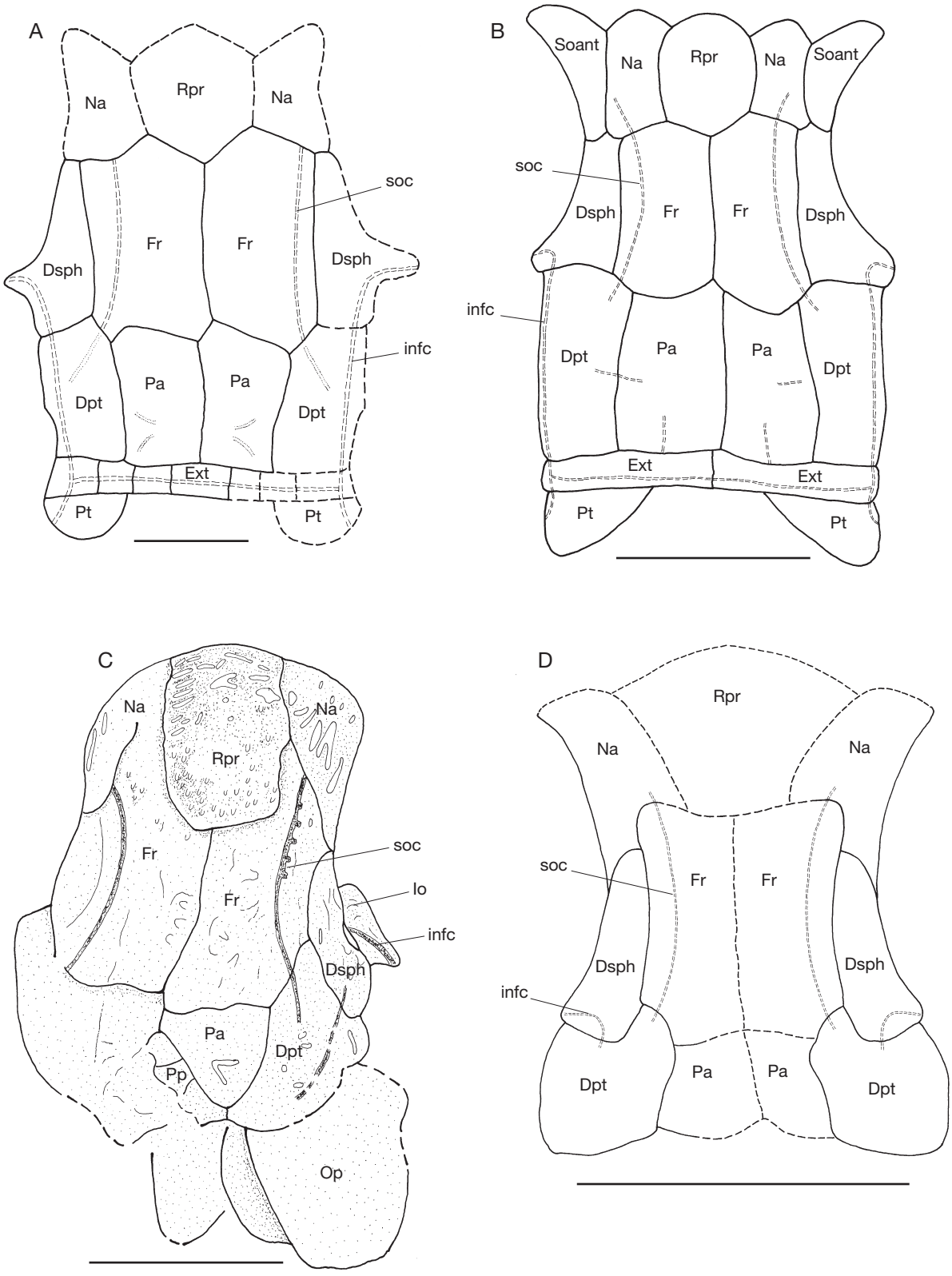

FIG. 10. — Reconstructions of the skull in dorsal view of some Aeduellidae and Igornichthyidae. The outlines of the bones, which are ill-defined, are marked with dashed lines: **A**, *Aeduella blainvillei* (Agassiz, 1833), after Heyler (1969); **B**, *Neslovicella rzehaki* Štamberg, 2007, after Štamberg (2007); **C**, *Setlikia bohemica* Štamberg & Zajíc, 1994, after Štamberg & Zajíc (1994); **D**, *Igornichthys bohemicus* n. sp. Abbreviations: see Methods. Scale bars: 1 cm.

and Early Permian transition and into the Permian. The genus *Igornichthys* occurs during this time in basins of both massifs and the Saar Nahe Basin. This fact has previously been discussed in connection with occurrences of the same or closely related genera and species of Aeduellidae and Amblypteridae in the basins of the French Massif central, the

Saar Nahe Basin and the Bohemian Massif (Heyler 1969; Štamberg 2006). The occurrence of *Igornichthys*, and abundant occurrences of *Paramblypterus* Sauvage, 1877 illustrate an extensive interconnection of the above mentioned Lower Permian basins at the time of deposition of the Vrchlabí Formation (Krkonoše Piedmont Basin), Igornay Formation and Surmoulin Formation (Autun Basin) and Remigiusberg Formation and Meisenheimichthys Formation in the Saar Nahe Basin.

CONCLUSION

This paper is a continuation of the study of new actinopterygians in the Lower Permian deposits of the lacustrine basins of the Bohemian Massif. A new actinopterygian species, *Igornichthys bohemicus* n. sp., is described from Lower Permian sediments of the Krkonoše Piedmont Basin (Bohemian Massif, Czech Republic). Anatomical characters of the new species expand our knowledge of the genus *Igornichthys*. Incorporation of this new data along with the preceding observations clarify the diagnosis of *Igornichthys* and Igornichthyidae. A distinction among the Igornichthyidae and other co-occurring actinopterygian taxa in the Lower Permian basins of the Bohemian Massif, French Massif central and Saar Nahe Basin is thus made possible. It's now clear from an analysis of anatomical characters that representatives of *Igornichthys* and Igornichthyidae have a set of characters (skull roof with supraorbital canal traversing from the parietal to the dermopterotic, shape of the upper jaw with postero-ventral angle on the maxillary plate, type of dentition, sculpture on the scales) that are known separately in other families such as Aeduellidae, Amblypteridae and Elonichthyidae. The occurrence of very closely related species of the genus *Igornichthys* and genera of Igornichyidae and Amblypteridae Romer, 1945 document a rather extensive interconnection among the lacustrine basins of French Massif central, Saar Nahe Basin and Bohemian Massif in the Late Carboniferous and particularly in the Early Permian.

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