Saurichthys and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution

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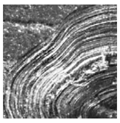

A new marine fish assemblage from the late Smithian (Olenekian, Early Triassic) *Anasibirites* beds of the Thaynes Formation collected near Georgetown (Bear Lake County, south-east Idaho, USA) comprises actinopterygians (*Saurichthys* cf. *elongatus*, Actinopterygii indet.), sarcopterygians (Actinistia indet.), and possibly chondrichthyans. We review the global fossil record of the Triassic lower actinopterygian *Saurichthys*, which is used herein for a case study of trends in morphological adaptations as well as variations in palaeogeographic distribution and diversity dynamics of Early Mesozoic fishes. In the Early Triassic, *Saurichthys* already occupied a top position in marine food webs, with some species achieving body lengths of up to 1.5 m. Distribution of morphological characters in *Saurichthys* during the Triassic suggests trends towards a reduction in squamation, stiffening of the fins and axial skeleton, shortening of the postorbital portion of the cranium, and reduction in the number of dermal skull bones. The postcranial adaptations in particular helped to improve the fast-start ability of these ambush predatory fishes. The palaeogeographic range of *Saurichthys* changed from a virtually global distribution in the Early Triassic (indicating rapid dispersal within marine and freshwater ecosystems after the end-Permian mass extinction) to an occurrence mainly restricted to the north-western Tethys in the Late Triassic, and also towards increasing rarity within continental deposits. Modifications in the palaeogeographic distribution were accompanied by successive loss in global species richness and were possibly related to intra-Triassic extinction events, environmental alterations and/or competition. • Key words: Saurichthyidae, Osteichthyes, coelacanth scale, biotic recovery, biodiversity, cosmopolitanism, extinction, palaeobiogeography, morphological trends.

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Marine Early Triassic fishes from the United States are sparse and for the most part not well documented (Wilson & Bruner 2004, Brinkmann *et al.* 2010). Occurrences are mainly restricted to the Candelaria Hills in south-western Nevada (Brinkmann *et al.* 2010; Romano *et al.* in prep.), and the Bear Lake area in Idaho (Fig. 1A, B). Although Early Triassic fishes have also been reported from Tiglukpuk Creek (Killik-Itkillik region, Alaska) by Patton & Tailleur (1964), these remains come from the shale member of the Shublik Formation and are of Middle Triassic rather than Early Triassic age (Detterman *et al.* 1975, Embry *et al.* 2002).

Early Triassic fishes from Bear Lake Valley in south-east Idaho have been known since the onset of the last century, when Evans (1904) first described a chondrichthyan fin spine belonging to *Nemacanthus elegans* (see Maisey 1977) from Paris Canyon (Fig. 1C). However, fossil fishes from Bear Lake County have received very little attention since that time. First, Tanner (1936) briefly described several specimens of a deep-bodied ray-finned fish from the Woodside Formation (Dienerian, Induan, see *e.g.* Reeside *et al.* 1957) of Paris Canyon (Fig. 1C), for which he erected a new genus and species, *Haywardia jordani.* Schaeffer &

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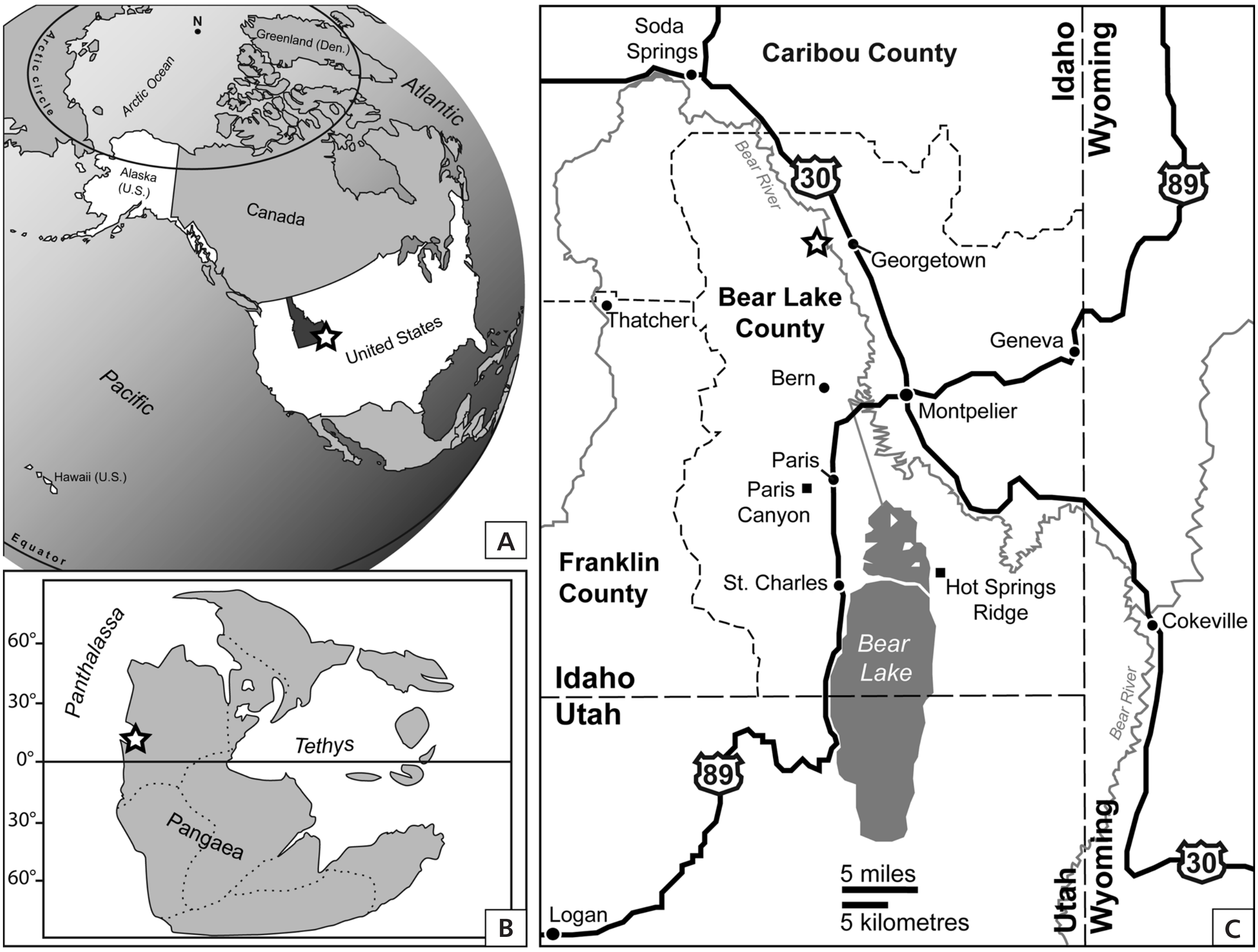


Figure 1. Geographic position of the locality (indicated by the white star) near Georgetown in northern Bear Lake County (Idaho, USA) where the new fish fossils have been collected; A – in present-day North America (Idaho shown in dark grey). • B – in Pangaea during the Early Triassic. • C – in Bear Lake County, south-east Idaho.

Mangus (1976) tentatively synonymised *H. jordani* with *Bobasatrania canadensis* (Lambe, 1914). Nevertheless, *B. canadensis* is mainly characterized by fin morphology and the fins are very poorly preserved in Tanner's (1936) material (pers. obs. CR 2012). *H. jordani* may well represent a bobasatraniform, but a revision of the type specimens is necessary to clarify their taxonomic affiliation. Second, Youngquist (1952) mentioned the presence of isolated hybodontoid shark remains near the mouth of Paris Canyon (Fig. 1C). Later, Dunkle (pers. comm. *in* Schaeffer & Mangus 1976, p. 552) identified remains of *Laugia*, *Birgeria*, *Bobasatrania*, and a perleidid from various Early Triassic deposits in the Bear Lake area. However, Dunkle's specimens have neither been described nor illustrated and their collection numbers and repositories are unknown, which makes it difficult to verify these occurrences. There are no fish remains from the Early Triassic of Bear Lake Valley among the collections of the Cleveland Museum of Natural History (M. Ryan, pers. comm. to CR 2010), where Dunkle worked during part of his career. Finally, Mutter & Rieber (2005) reported an ichthyodorulite from the Hot Springs ridge (Fig. 1C) north-east of Bear Lake Hot Springs belonging to a new ctenacanthoid shark (*Pyknotylacanthus spathianus*), and a few indeterminable actinopterygian remains preserved with the fin spine. This material was collected from the *Columbites parisianus* Zone (*C. parisianus* bed, Jenks in press) of the Middle Shale unit of the Thaynes Formation (Fig. 2), which is of early Spathian age (Guex *et al.* 2010) and probably equivalent to the stratigraphic level of Youngquist's (1952) chondrichthyan remains.

Here we present a new Early Triassic ichthyofauna from Bear Lake County, whose stratigraphic age is intermediate to that of the material of Tanner (1936) and that described by Youngquist (1952) and Mutter & Rieber (2005). Study of Early Triassic fishes from Bear Lake County and the Candelaria Hills is important because at the time of deposition both sites were located close to the

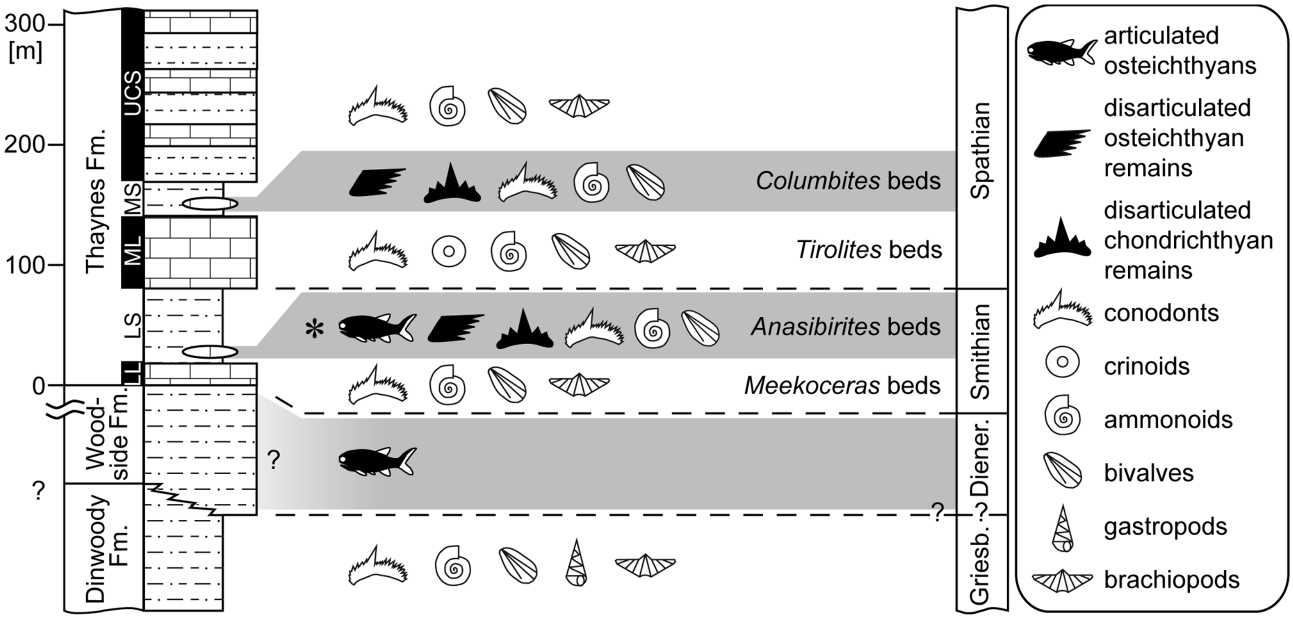


Figure 2. Simplified stratigraphic log showing important fossil-bearing levels in the Early Triassic of Bear Lake County (Idaho, USA) and adjacent areas (after Kummel 1943, 1954; Mutter & Rieber 2005; Newell & Kummel 1942; Tanner 1936; Youngquist 1952; this study). The position of the new fish assemblage described herein is marked by an asterisk. See text and Kummel (1943, 1954) for further details on the stratigraphy of the study area. Lithological units of the Thaynes Formation (after Kummel 1954): LL – Lower Limestone; LS – Lower Shale; ML – Middle Limestone; MS – Middle Shale; UCS – Upper Calcareous Siltstone. Time scale: Griesb. – Griesbachian; Diener. – Dienerian.

equator (Fig. 1B) and, thus, the south-eastern Panthalassa – a part of this super-ocean for which we so far have no record of Early Triassic fishes (Brinkmann *et al.* 2010, López-Arbarello 2004). Knowledge regarding Early Triassic fish faunas from North America is crucial to understand the recovery patterns of chondrichthyan and osteichthyan fishes of the eastern Panthalassa after the end-Permian mass extinction. Here we take advantage of the well-known and globally distributed Triassic actinopterygian *Saurichthys*, also present in the new fish assemblage from Bear Lake County, as a case example for trends in palaeogeographic distribution, diversity dynamics and morphological adaptations.

Geological setting

The fish fossils described herein were collected in an exposure of the Lower Shale unit of the Thaynes Formation located about 3.6 km (*ca* 2.25 miles) west of Georgetown (Bear Lake County, Idaho, USA; Fig. 1C) on the steep bluff immediately west of the Bear River and north of the Narrows Road (east 1/2 of Section 10, T11S, R43E). They are preserved in calcareous concretions that are found *in situ* among the upper portion of the *ca* 0.5 m thick *Anasibirites* beds. The *Anasibirites* beds are well-developed at the Georgetown locality and are situated about 1 m above the Lower Limestone unit of the Thaynes Formation (Fig. 2). The co-occurrence of the *Anasibirites* ammonoid fauna with the fishes constrains the age of the new ichthyofauna to the late Smithian (Brühwiler *et al.* 2010, Silberling & Tozer 1968). This age determination is confirmed by the presence of the conodont *Scythogondolella milleri* within the same layer. The fishes are found together with bivalves of the genus *Leptochondria.* Remains of the ichthyosaur *Cymbospondylus* have been described from the same locality, but their exact stratigraphic position within the Thaynes Formation is uncertain (Massare & Callaway 1994).

The Early Triassic sedimentary history of the study area is marked by three transgression-regression cycles (Paull & Paull 1993) probably controlled by global sea-level changes (Embry 1997). After the rapid transgression at the beginning of the Triassic (Griesbachian and Dienerian), marine shales, siltstones, and limestones of the Dinwoody Formation (Fig. 2), whose maximum thickness is found north of Bear Lake (Kummel 1954), accumulated in a Permian depression. Following the Dienerian sea-level fall, red beds of the Woodside Formation (Fig. 2) developed in shallower parts of the basin. At the beginning of the Smithian, a new rapid transgression is documented by the deposition of the Lower Limestone unit of the Thaynes Formation, containing the *Meekoceras* ammonoid fauna. Fine clastics and limestones characterize the subsequent lithological units of the 750 to 1070 m thick Thaynes Formation (Fig. 2), as defined by Kummel (1943, 1954), indicating a less important shallowing trend during the later part of the Smithian and the Spathian. Marine sedimentation ceased when the shoreline moved westwards after a last, moderate transgression in the middle Spathian (Paull & Paull 1993).

Material and methods

The fish material from the late Smithian of Bear Lake County (south-east Idaho, USA; Fig. 1) described below is deposited at the Palaeontological Institute and Museum, University of Zurich (PIMUZ), Switzerland. The specimens represent at least three distinct taxa: *Saurichthys* cf. *elongatus* Stensiö, 1925 (PIMUZ A/I 3900, Figs 3, 4), Actinopterygii indet. (PIMUZ A/I 3902, Fig. 5), and Actinistia indet. (PIMUZ A/I 3901, Fig. 6). The presence of chondrichthyans is evidenced by a piece of fossilized cartilage found in the same horizon (PIMUZ A/I 3903). Individuals A/I 3900 and A/I 3903 were collected in June 2009 during a field trip by CR, WB, and JJ, whereas specimens A/I 3901 and A/I 3902 were collected by JJ over 30 years earlier. All fossils have been consolidated with Elvacite acrylic resin. The depth of focus of the photographs of the fossils was improved using the open source stacking software CombineZP.

The three-dimensionally preserved cranium PIMUZ A/I 3900 (*Saurichthys* cf. *elongatus*, Fig. 3) was scanned with X-ray computed tomography (Kak & Slaney 1988) with a spatial resolution of 30 μm. This procedure was conducted at the Swiss Federal Laboratories for Materials Testing and Research (Empa). Although the contrast was insufficient for a digital 3D reconstruction, four cross-section images were generated that show the external shape and internal features of the skull (Fig. 4). The employed cone beam setup consists of an X-ray tube 'XT9160-TXD' from Viscom, a high precision rotation table 'UPR-160F air' mounted on a XYZ stage made of three linear stages 'LS-270' from Micos and an X-ray flat panel detector 'C7942' from Hamamatsu. The X-ray tube 'XT9160-TXD' was operated with an acceleration voltage of 120 kV and a cathode current of 80 μA. The resulting source spectrum was further hardened with a lead filter of 50 μm thickness so that the dynamic range of the detector was used in an optimal way. A 1 mm thick Al filter was mounted in front of the flat panel detector in order to suppress scattered low energy X-rays. The 2240 × 2368 pixels of the detector were binned 2 × 2 so that the effective pixel size was 100 μm. The sample and flat panel detector were mounted at distances of 150 mm and 500 mm from the source, respectively. A total of 720 transmission images with an individual exposure time of 5.6 s were recorded from different angles distributed evenly over 360 degrees. The projected images were corrected for pixel errors, offset and pixel gain before a beam-hardening correction was applied. Finally, the three-dimensional distribution of the attenuation coefficient was calculated by means of a filtered back projection Feldkamp algorithm (Feldkamp *et al.* 1984, Kak & Slaney 1988).

For the taxonomic interpretation of PIMUZ A/I 3900, we measured distances on the skull (see Fig. 7) of this specimen as well as cranial remains of other Triassic saurichthyids (Table 1). Skull bone terminology for *Saurichthys* follows Rieppel (1985) and Mutter *et al.* (2008). Open nomenclature is used in the sense of Bengtson (1988).

The peculiar skull and body morphology of the Triassic lower actinopterygian (*sensu* Gardiner *et al.* 2005) *Saurichthys* (see Fig. 8 and Discussion) makes even fragmentary material easily identifiable at least at genus level, thereby reducing the risk of being overlooked in the field and in collections. On account of this, the palaeogeographic distribution of *Saurichthys* can be considered as well-documented. For the analyses of saurichthyid palaeogeography and diversity (see Discussion), we grouped the marine occurrences of *Saurichthys* (listed in Table 2) into different palaeobiogeographic regions (see Fig. 9) according to their stratigraphic, palaeogeographic, and palaeoenvironmental relationships. For the Early Triassic, we distinguish the following palaeobiogeographic regions: the Boreal Sea province (Spitsbergen, Bjørnøya, Greenland, Ellesmere Island in Arctic Canada, Magadan district of far-east Russia), the Rybinsk epicontinental basin (Russia, Upper Volga region), the north-western Tethys region (Mangyshlak peninsula of Kazakhstan, Volgograd region of Russia), the eastern Tethys province (China, Jiangsu), the southern Tethys province (Nepal, north-western and south-western Madagascar, Himachal Pradesh in India), and the eastern Panthalassa region (Alberta and British Columbia in Canada, Idaho in the USA). The Anisian occurrences are grouped as follows: France (Lorraine), the Netherlands, Germany (Brandenburg, Franconia, Lower Saxony, Thuringia), and Poland (Upper Silesia) are referred to the epicontinental Germanic Basin (Buntsandstein, Muschelkalk); the Swiss-Italian boundary area (Besano and Monte San Giorgio) and Slovenia to the north-western Tethys province; China (Guizhou, Yunnan) to the eastern Tethys region; and USA (Nevada) to the eastern Panthalassa region. The Ladinian occurrences were combined into the following palaeobiogeographic regions: Austria (Carinthia), Israel, Kazakhstan (Caspian depression), Slovenia, Spain (Catalonia), Swiss-Italian boundary area (Besano-Viggiù and Monte San Giorgio), Switzerland (Graubünden), Turkey (western Taurus), and Saudi Arabia are part of the north-western Tethys region; Germany (Franconia, Württemberg) belongs to the Germanic Basin (Muschelkalk, Keuper); and China (Guizhou, Yunnan) to the eastern Tethys province. Carnian occurrences are grouped into the Germanic Basin (Germany, Württemberg), the Boreal Sea province (Bjørnøya, Svalbard archipelago, Norway), and the north-western Tethys region, which includes Austria (Lower Austria), Italy (Fiuli-Venezia Giulia), and Spain (Catalonia). For the Norian-Rhaetian interval, occurrences in Austria (Tyrol, Upper Austria) and Italy (Campania, Fiuli-Venezia Giulia, Lombardy) are merged into the north-western Tethys province. Continental occurrences of *Saurichthys* (listed in Table 3) are all treated as individual localities in Fig. 9. Statistical analyses were performed using PAST (Hammer *et al.* 2001).

Institutional abbreviations. – BSPM – Bayerische Staatssammlung für Paläontologie, Munich, Germany; CGS – Chengdu Center of China Geological Survey, Sichuan; CMN – Canadian Museum of Nature, Ottawa, Ontario; GBA – Geological Survey of Austria, Vienna; MGUH – The Natural History Museum of Denmark, Copenhagen; PIMUZ – Palaeontological Institute and Museum, University of Zurich, Switzerland; PMU – Palaeontological collections, Museum of Evolution, Uppsala University, Sweden.

Anatomical abbreviations. – ad.pr. – antero-dorsal process of scale; An – angular bone; D – dentary bone; Db – dermal bones on the medial side of the palatoquadrate; Dp – dermopterotic bone; Ds – dermosphenotic bone; eth.ca. – ethmoidal canal; Ex – extrascapular bone; ex.n. – anterior and posterior exonarine opening; Ff – fringing fulcra; Fr – frontal bone; Har – haemal arch; Hs – haemal spine; La – lachrymal bone; M – mandible; md – mid-dorsal scale row; md.pr. – mid-dorsal process of scale (peg); ml – mid-lateral scale row; mv – mid-ventral scale row; Mx– maxilla; Na – nasalo-antorbital bone; Nar – neural arch; Nc – neurocranium; Not – notochord; Ns – neural spine; Pa – parietal bone; Pop – praeoperculum; pop.ca. – praeopercular canal; prz – praezygapophysis; Ps – parasphenoid; Qj – quadratojugal; Rpm – rostro-praemaxilla; Sa – supraangular bone; Sc – supracleithrum; so.ca. – supraorbital canal; temp.ca. – temporal canal; vl – ventro-lateral scale row.

Systematic palaeontology

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
[*sensu* Rosen *et al.* 1981]
Infraclass Actinopteri Cope, 1872 [*sensu* Patterson 1982]
Family Saurichthyidae Owen, 1860 [*sensu* Stensiö 1925]

Genus *Saurichthys* Agassiz, 1834 [*sensu* Mutter *et al.* 2008]

Type species. – *Saurichthys apicalis* Agassiz, 1834 from the Middle Triassic (Ladinian; Emmert 1977) of Bayreuth, Germany.

Saurichthys cf. *elongatus* Stensiö, 1925
Figures 3, 4

Lectotype of S. elongatus *Stensiö, 1925.* – Designated here, PMU P.271, Palaeontological collections, Museum of Evolution, Uppsala University, Sweden (Stensiö 1925: pl. 22, fig. 4, pl. 23, figs 1–2, pl. 25, figs 3–4; pl. 34, fig. 1). We select PMU P.271 as the lectotype because Stensiö's (1925) description of *Saurichthys elongatus* is based to a great extent on this specimen.

Type horizon and locality. – 'Fish horizon' (Smithian, *e.g.* Weitschat & Dagys 1989), Lusitaniadalen Member, Vikinghøgda Formation, Spitsbergen, Svalbard archipelago, Norway.

Material. – PIMUZ A/I 3900 consists of three parts: a three-dimensionally preserved skull with components of the shoulder girdle (A/I 3900a; Figs 3, 4), the counterpart of the dermal skull roof (A/I 3900b), and the counterpart of the right mandible (A/I 3900c). The right side of the skull (A/I 3900a) was exposed at the surface of the nodule and is slightly damaged due to weathering.

Description. – The skull of PIMUZ A/I 3900 (part a) is fairly complete. Only the tip of the snout and the operculars are missing. A/I 3900a is about 95 mm long and at the level of the orbit approximately 20 mm high. The rostrum, from the anterior margin of the orbit to the tip of the jaws, had an estimated length of *ca* 65 mm. The mandible was roughly 110 mm long, indicating a total body length of *ca* 300 to 400 mm (see Griffith 1959, Rieppel 1992).

A/I 3900a is gently deformed only in its posterior portion but otherwise still expresses the original shape of the head (Fig. 3A–D). The skull exhibits a more or less trapezoidal cross-section within its postorbital portion (Fig. 4X_3–X_4). Within the praeorbital part, the transverse section of the skull is on the other hand rather ovoid, with its height distinctly exceeding its breadth. In the posterior part of the skull, the dermal cranial roof is horizontally arranged and quite flat. Above the orbits, the skull roof forms a broad, longitudinal channel with conspicuous, oblique lateral flanks (Figs 3D, 4X_1). In the rostral portion, the skull roof is flat along its midline, but bends equably downwards towards its flanks. The lateral side of the cranium is gently convex within most of the postorbital portion, but somewhat concave in the orbital and posterior part of the praeorbital sections. Further rostrally, the lateral surface of the skull becomes convex again. Ventrally, the lateral surfaces of the cranium converge (Figs 3, 4).

The postorbital part of the dermal cranial roof is mainly formed by the large, paired dermopterotic bones, which cover an area reaching from the level of the posterior end of the orbits to about the level of the jaw joints (Fig. 3A).

Laterally, the dermopterotic bones extend to the margins of the dermal skull roof. Behind the dermopterotic bones lie two much smaller elements, the extrascapulae, whose outlines are visible on part b of A/I 3900. The dermopterotic bones antero-laterally border the dermosphenotic bones. The boundary between these two bones is straight, albeit slightly serrated. The dermopterotic and dermosphenotic bones anteriorly adjoin the large frontal bones. Both frontal bones possess a small postero-medial process, with which they separate the most anterior portions of the adjacent dermopterotic bones (Fig. 3A). Although the state of preservation of the parietal bones is very poor, these elements seem to have a similar size and relative position among the bones of the dermal skull roof as in other species of *Saurichthys*, *i.e.* behind the frontal bones and between the anterior parts of the dermopterotic bones (see *e.g.* Mutter *et al.* 2008; Rieppel 1980a, 1985; Stensiö 1925). The medial margins of the frontal bones and the parietal bones cannot be seen in A/I 3900 and it is possible that both of these paired elements are fused together.

The rostrum is shaped by the anterior portions of the frontal bones, the nasalo-antorbital bones, and the lachrymal bones, but predominantly by the large, unpaired rostro-praemaxilla (Fig. 3A, B). The rostro-praemaxillary bone extends from the area of the external narial openings to the tip of the snout and reaches its maximal height at a distance from the orbit that is about twice as long as that between the orbit and the external narial openings. From there, the height of the rostro-praemaxilla decreases both anteriorly and posteriorly. Caudally, the rostro-praemaxilla borders the frontal, nasalo-antorbital, lachrymal and maxillary bones. The frontal and nasalo-antorbital bones both have a considerable anterior extension. These cranial elements have their rostral ends at approximately the same level, which is around the point of maximal height of the rostro-praemaxilla. The nasalo-antorbital bone contains the anterior and posterior narial openings (Fig. 3A, B). The anterior narial opening is much larger than the posterior one and has an oblong shape. Its vertical axis is distinctly longer than its horizontal component. The posterior narial opening is rather uniformly shaped. The small lachrymal bone is sandwiched between the nasalo-antorbital bone dorsally and the anterior process of the maxilla ventrally, and its boundary with the anteriorly located rostro-praemaxilla is deeply serrated (Fig. 3B).

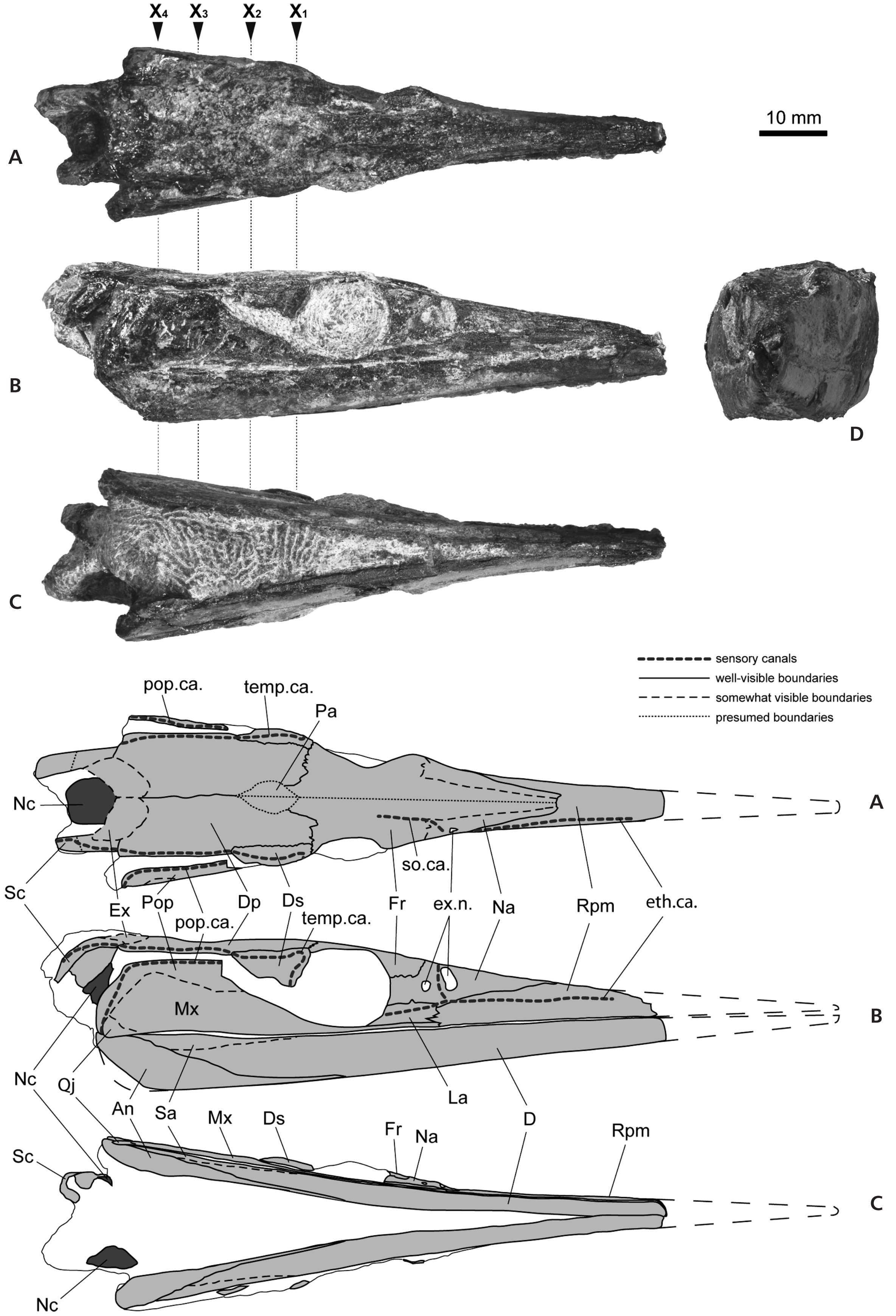
The cheek region is formed by three bones: the maxilla, the praeoperculum, and the quadratojugal. The maxillary bone has the typical palaeoniscoid shape, *i.e.* it consists of a large postorbital plate and a long and narrow anterior process that rostrally extends to the level of the exonarine openings (Fig. 3B). Behind and above, the maxilla adjoins the boomerang-shaped praeoperculum. However, the suture between the praeoperculum and the maxillary bone is not well visible. In a postero-ventral position to the maxilla lies the small quadratojugal, which has an approximately triangular outline (Fig. 3B, C).

The lateral wall of the lower jaw is composed of the very large dentary bone and the much smaller angular bone and supraangular bone (Fig. 3B, C). The boundaries between these three elements are best seen on part c of specimen A/I 3900. The posterior margin of the angular bone is slightly damaged (Fig. 3B). Both the angular bone and the supraangular bone have a considerable rostral extension. The angular bone anteriorly extends to about the level of the centre of the orbital opening, while the supraangular bone rostrally reaches approximately to the level of the posterior margin of the orbit. Additionally, a slight protrusion is present on the postero-dorsal part of the lower jaw formed by the angular bone (A/I 3900c). Within the posterior part of the skull, the height of the mandible is much lower than that of the upper jaw (only about one third of the entire height of the rear portion of the cranium). The left and the right branches of the lower jaw anteriorly meet in an acute angle. Posteriorly, the two hemimandibles gently curve laterally as they diverge (Fig. 3C). Branchiostegal rays are absent.

The large orbits are each bounded by the frontal bone dorsally and antero-dorsally, the nasalo-antorbital and lachrymal bones anteriorly, the long and slender anterior process of the maxilla ventrally, and the dermosphenotic bone postero-dorsally (Fig. 3). It is not known whether supra- and infraorbital ossifications were present. The sclerotic ring is not preserved.

Of the sensory canals of the head, only the temporal canal, the supraorbital canal, the ethmoidal canal, and the praeopercular canal are visible in A/I 3900 (Fig. 3A–C). The lateral line canal pierces the supracleithrum posteriorly. It thereafter penetrates the dermopterotic bone through its postero-lateral corner, continues as the temporal canal close to the lateral margin of this bone and then proceeds through the dermosphenotic. Near the rostral end of the dermosphenotic, the canal bends ventrally and then runs parallel to the anterior margin of this bone, and it most likely continued behind and below the eye. Further

Figure 3. *Saurichthys* cf. *elongatus* Stensiö, 1925: Three-dimensionally preserved skull of specimen PIMUZ A/I 3900 (part a) from the late Smithian of Bear Lake County (Idaho, USA). • A–D – skull in dorsal, lateral, ventral, and anterior view. Drawings with identification of bones and anatomical structures shown below. The length of the rostrum, indicated by the widely-spaced dashed line, is estimated based on the inclination of the dorsal and ventral margins and the width of the upper and lower jaw at the anterior end of the fragment. The approximate positions of the four μCT generated transverse sections of the skull (see Fig. 4) are indicated (X_1–X_4).


X4
X3
X2
X1
10 mm
A
B
C
D
sensory canals
well-visible boundaries
somewhat visible boundaries
presumed boundaries
pop.ca.
temp.ca.
Pa
Nc
A
Sc
Ex
Pop
pop.ca.
Dp
Ds
temp.ca.
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Fr
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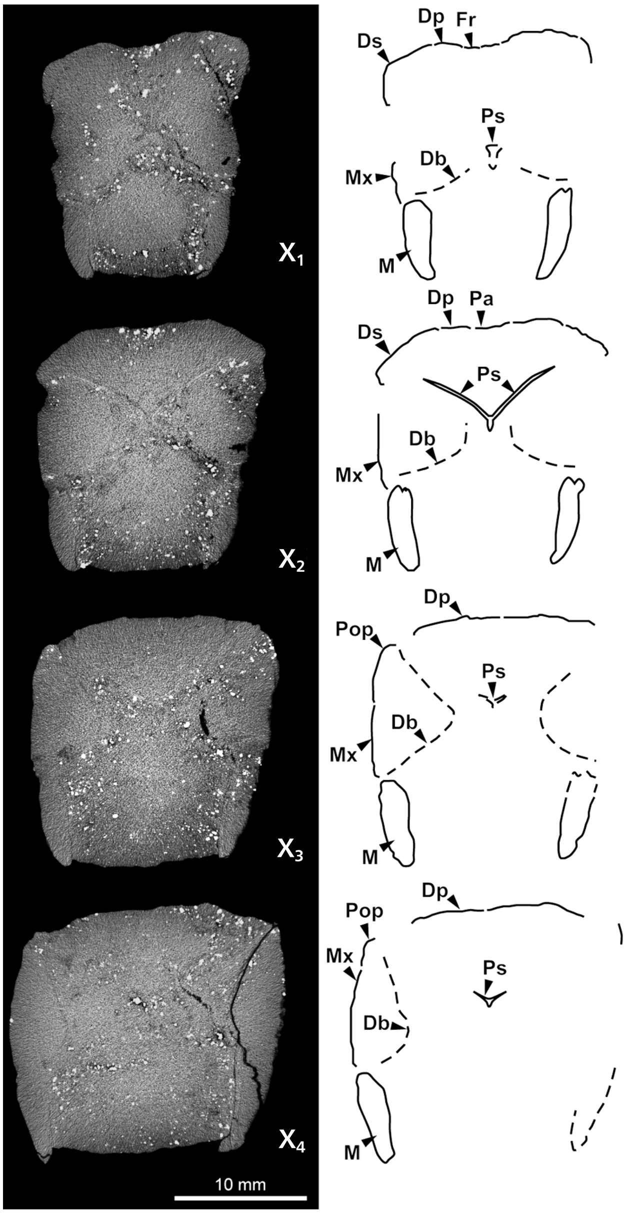

Figure 4. *Saurichthys* cf. *elongatus* Stensiö, 1925: µCT generated transverse sections through the postorbital portion of PIMUZ A/I 3900a from the late Smithian of Bear Lake County (Idaho, USA), with line drawings thereof. The approximate positions of the four section planes X_1–X_4 are shown in Fig. 3.

rostrally, the canal enters the lachrymal bone and continues in the nasalo-antorbital bone. The right supraorbital canal is seen above the external narial openings. The supraorbital canal laterally resumes between the external narial openings and fuses with the infraorbital canal and the ethmoidal canal in the nasalo-antorbital bone. The latter runs along the lateral side of the rostrum in anterior direction. The praeopercular sensory canal passes along the upper margin of the praeoperculum and then continues posteriorly through the ventral shank of this bone.

Parts of the occipital portion of the neurocranium are visible at the caudal end of A/I 3900a (Fig. 3A–C). However, the state of preservation of the neurocranium precludes a detailed description. Of the gill skeleton, presumably one of the epibranchials is visible on the left side of A/I 3900a. Other cranial elements such as the dermal bones on the medial side of the palatoquadrate and the parasphenoid are visible on µCT generated transverse sections of the skull (Fig. 4). The parasphenoid is clearly seen on the µCT images. This bone has a distinct crest issuing from its ventral side and large but antero-posteriorly short ascending processes behind the orbits (Fig. $4X_2$). Further caudally, the parasphenoid is very narrow. The dermal bones on the medial side of the palatoquadrate form a deeply convex wall that extends far into the mouth, especially in the part immediately behind the orbits.

Preservation of the dermal shoulder girdle of specimen A/I 3900 is very incomplete. Fragments of both supracleithra are found *in situ* and still attached to the dermal cranial roof (Fig. 3).

Remarks. – The skull proportions of PIMUZ A/I 3900 from Bear Lake County are very similar to those of the lectotype of *Saurichthys elongatus* Stensiö, 1925 (PMU P.271; Stensiö 1925, pl. 22, fig. 4, pl. 23, figs 1, 2, pl. 25, figs 3, 4, pl. 34, fig. 1) from the Smithian 'fish horizon' of Spitsbergen, Svalbard archipelago, Norway (see Table 1). There are also resemblances in the cranial bone pattern between these approximately equally-sized specimens (Fig. 7). Based on these similarities, we suggest that PIMUZ A/I 3900 and PMU P.271 belong either to the same species or to two closely related ones (see Discussion).

Actinopterygii indet.
Figure 5

Material. – PIMUZ A/I 3902.

Description. – Specimen PIMUZ A/I 3902 is a nearly complete but heavily weathered mid-sized actinopterygian, of which the *ca* 120 mm long trunk and parts of the dorsal, anal, and pelvic fins are preserved. The maximum depth of the specimen (*ca* 45 mm) is reached shortly anterior to the dorsal fin. Based on the depth at the anterior end of the fossil, it seems probable that the shoulder girdle and skull were positioned immediately in front (Fig. 5).

The squamation of A/I 3902 is composed of rhombic scales (Fig. 5A), which are seen from their internal side. The scales are arranged in oblique rows running from antero-dorsally to postero-ventrally. At least 40 scale rows are discernable. The angle between the scale rows and the longitudinal body axis is about 60 degrees in the anterior part and roughly 50 degrees within the caudal portion of

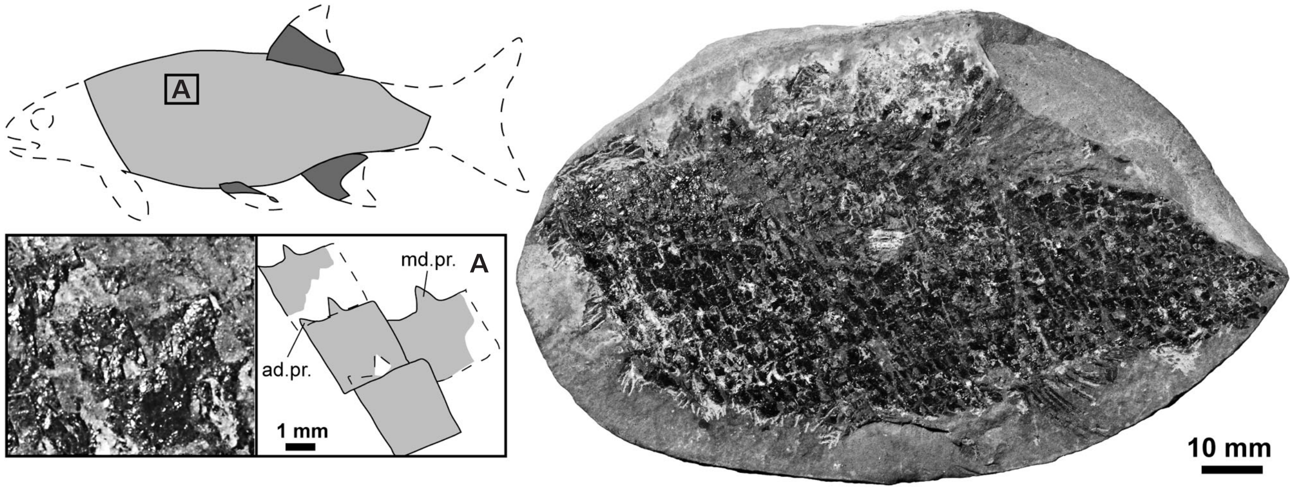

Figure 5. Actinopterygii indet.: PIMUZ A/I 3902 (right) from Bear Lake County (Idaho, USA), showing a portion of the trunk of a medium-sized actinopterygian (top left). The skull, the pectoral girdle, and the caudal fin are missing. Anterior is left. • A – magnified detail of the squamation.

the trunk. As typical for many lower actinopterygians, the largest scales are found in the anterior part of the mid-flank region, and scale size gradually decreases towards the more caudally situated rows. Scales within the lateral part of each row are generally higher than broad, albeit not very distinctly. In contrast, those scales in the ventral and dorsal regions of the trunk are slightly broader than high. The transition between these two morphotypes is continuous. In the anterior part of the body, the scales possess a large, acute mid-dorsal process, as well as an appropriate groove on their medial side near their ventral end (peg-and-socket articulation). A second process is developed at the antero-dorsal corner of the scales of the anterior body portion. The bases of the dorsal and antero-dorsal processes of each scale are separated by a short distance (Fig. 5A). Scales on the caudal peduncle lack peg-and-socket articulation. Concentric growth lines are visible in some of the rhombic scales.

The pelvic fins of A/I 3902 are located closer to the anal fin than to the pectoral girdle: eight scale rows behind the anterior end of the fossil and seven scale rows in front of the anal fin. Although only the very basal parts of the pelvic fins are preserved, it is evident that these fins had a very short baseline. Indeed, their base only spans the breadth of two scale rows, and the proximal part only includes five fin rays. A lanceolate basal fulcrum is located just anterior to the pelvic fins.

The virtually opposing anal and dorsal fins are very long-based compared to the pelvic fins (Fig. 5). The bases of each of these fins extend over approximately nine scale rows. The anal fin encompasses about twelve lepidotrichia. Several fringing fulcra cover the leading margin of its first lepidotrichium. The dorsal fin begins approximately four scale rows behind the anal fin and about ten scale rows behind the pelvic fins. The lepidotrichia of the dorsal and anal fin are robust and separated by small interspaces. At least nine fin rays can be discerned in each of these fins. The lepidotrichia of all preserved fins are repeatedly segmented. The basal segments of the anal and dorsal fin are much longer than the distal ones and the more posterior lepidotrichia are distally ramified.

Remarks. – Regarding the structure of the scales and fins, specimen PIMUZ A/I 3902 resembles basal holosteans. However, its incomplete preservation precludes a more specific taxonomic interpretation.

Subclass Sarcopterygii Romer, 1955
Infraclass Actinistia Cope, 1871 [*sensu* Forey 1998]

Actinistia indet.
Figure 6

Material. – PIMUZ A/I 3901. The specimen represents an isolated actinistian scale, preserved as part and counterpart, A/I 3901a (Fig. 6) and A/I 3901b.

Description. – The scale is *ca* 27 mm long and up to 18 mm wide and its outline is generally ovoid. It is twice dorsoventrally constricted, once near its anterior end and once immediately behind its centre. The scale is slightly arched towards laterally and there is a depressed area next to the focus. Within this concavity is a distinct ridge (Fig. 6A).

The lateral surface of the scale can be divided into two parts: a large anterior area, which *in vivo* was covered by the adjacent scales, and a small posterior region that contains the dermal ornamentation. The anterior area is about twice as large as the free field (Fig. 6A). The basal plate of A/I 3901 is obliquely to horizontally sectioned and the

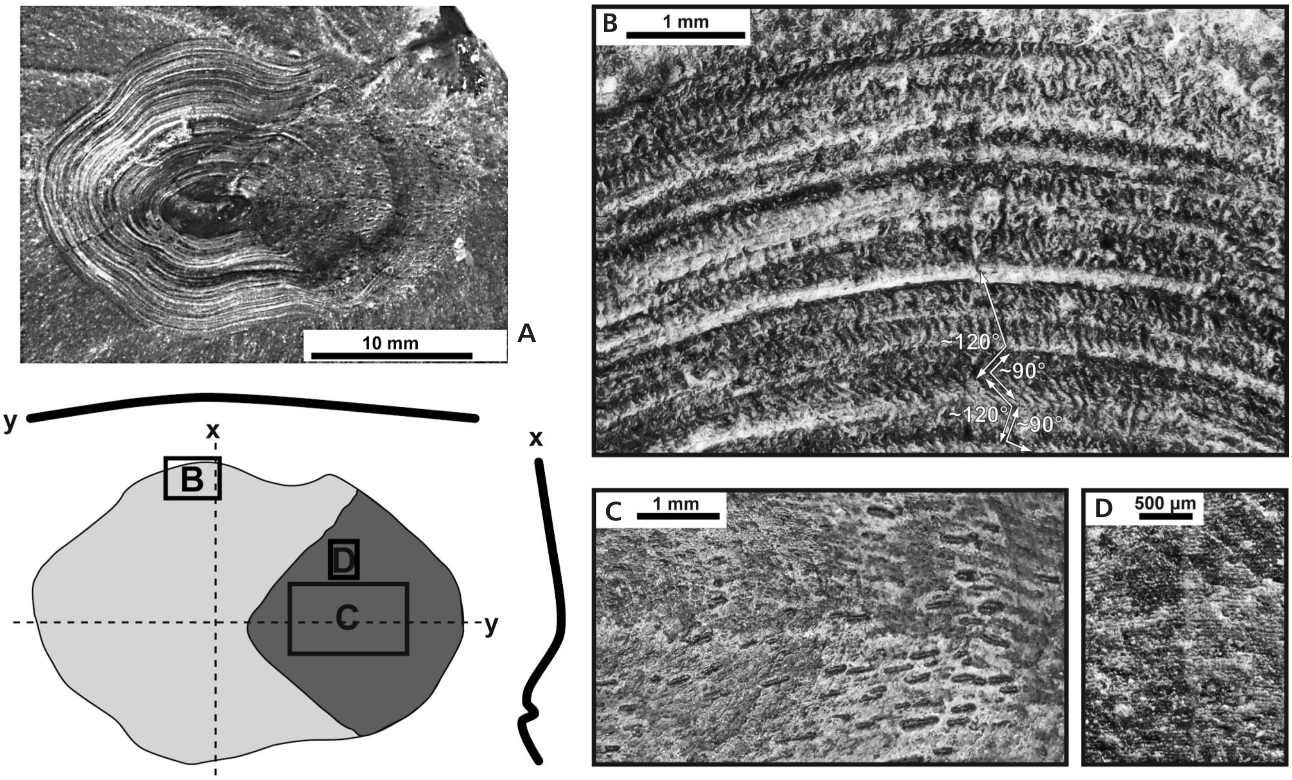

Figure 6. Actinistia indet.: PIMUZ A/I 3901 from Bear Lake County (Idaho, USA), an isolated actinistian scale, preserved on two complementary parts, a and b. • A – part a of PIMUZ A/I 3901 and drawing thereof below. Anterior is left. The three-dimensional shape of the scale is indicated by its approximate transversal (x) and longitudinal (y) cross sections. • B – magnified detail of the basal plate of A/I 3901 showing the arrangement of the collagen fibre bundles, with indicated approximate angle between two consecutive layers. • C – close-up of the free field showing the ornamentation consisting of oblong, medio-laterally flattened tubercles. • D – larger magnification of the free field of the scale, revealing numerous very fine, parallel ridges between the tubercles.

concentric growth lines are well visible within the anterior field (Fig. 6A). The growth rings correspond to successively accreted layers of isopedine (*sensu* Meunier 1987) and the arrangement of the collagen fibre bundles within these layers is still preserved (Fig. 6B). The collagen fibre bundles run parallel within a given layer but change their orientation from layer to layer in a regular pattern. In some parts of the anterior field of A/I 3901, a periodic pattern can be discerned in the arrangement of the collagen fibre bundles of the subsequent layers of the basal plate: the angle between the fibre bundles of two successive layers alternates between *ca* 90 and 120 degrees (Fig. 6B).

The free field has a rhomboid outline and it reaches from the posterior part of the focus to the hind margin of the scale. The ornamentation of the free field consists of small tubercles and of very fine ridges intermediate to the tubercles (Fig. 6C, D). The tubercles on the free field are generally oblong and medio-laterally flattened. They are more or less antero-posteriorly oriented and usually separated from one another by wide gaps. However, they sometimes may also occur in clusters (Fig. 6C). Tubercles are only developed in proximity to the longitudinal axis and along the caudal margin of the scale but are absent in the antero-lateral regions of the free field. The delicate ridges between the tubercles run parallel in antero-posterior direction and cover the entire area of the free field (Fig. 6D).

Remarks. – Actinistians are known since the Devonian and they reached their highest generic richness in the Early Triassic, with at least 12 valid genera (Forey 1998, Schultze 2004, Tong *et al.* 2006, Wendruff & Wilson 2012). Today, these lobe-finned fishes are represented by the 'living fossil' *Latimeria*.

The majority of Early Triassic actinistians exhibit ornamentation upon the free field that consists of distinct ridges running in antero-posterior direction. These ridges may be continuous or interrupted. Scale ornamentation consisting of tubercles is rare. Among Early Triassic actinistians, scale ornamentation of continuous longitudinal ridges is found in *Axelia* (Stensiö 1921, pl. 16, figs 5, 7), *Laugia* (*e.g.* Stensiö 1932, pl. 1–4), *Mylacanthus* (Stensiö 1921, pl. 18, fig. 1), *Piveteauia* (Lehman 1952, pl. 3, fig. c), *Rebellatrix* (Wendruff & Wilson 2012, fig. 1), *Rhabdoderma madagascariensis* (Lehman 1952, pl. 5, fig. d), *Scleracanthus* (Stensiö 1921, pl. 19, fig. 2), *Whiteia nielseni* (Forey 1998, fig. 11.19), *Whiteia woodwardi*

(Lehman 1952, pl. 5, figs a, c), *Wimania sinuosa* (Stensiö 1921, fig. 30) and *Wimania*? *multistriata* (Stensiö 1921, pl. 8, figs 4–6, pl. 9, fig. 1). Interrupted ridges are characteristic for the scales of *Chaohuichthys* (Tong *et al.* 2006, fig. 15) from the Early Triassic of China (Anhui).

Tuberculated scale ornamentation is observed among Early Triassic actinistians in *Sinocoelacanthus* Liu, 1964, *Sassenia tuberculata* (Stensiö 1921, pl. 10, fig. 2) and *Whiteia tuberculata* (see Lehman 1952, pl. 5, fig. b). In *S. tuberculata*, the tubercles are minute and close-set. Those of specimen PIMUZ A/I 3901 (Fig. 6D) are also small but well-separated by wide interspaces – apart from a few clusters. In *W. tuberculata*, the tubercles are widely-spaced as in A/I 3901 but distinctly larger. Moreover, the tubercles of *W. tuberculata* are equably distributed over the entire free field, whereas those of A/I 3901 are restricted to the central part and posterior margin of the free field.

Differences in scale ornamentation patterns are useful for distinguishing actinistian taxa (Forey 1998, Rieppel 1980b). However, one must bear in mind that ornamentation varies between scales on different parts of the body. The same is true for the shape of the scale and the relative size and form of the free field. Specimen A/I 3901 is distinctly bent in transverse section (Fig. 6A), which may indicate that its original location on the animal was near the base of one of its fins. Regarding the ornamentation of the scale, A/I 3901 shows closest affinities to *S. tuberculata* and *W. tuberculata* and might represent one of these species.

Some microstructural features that characterize A/I 3901 can still be found in the extant *Latimeria*. The corrugations of the free field of A/I 3901 (Fig. 6D), which are probably a structure of the external layer, resemble similar structures on the scales of *Latimeria* (Meunier *et al.* 2008, figs 1–3; Miller 1979, fig. 13). The arrangement of the collagen fibre bundles of the basal plate of A/I 3901 (Fig. 6B) is also comparable to that seen in *Latimeria*, where they are organized in a 'twisted plywood' fashion (Giraud *et al.* 1978, Meunier *et al.* 2008).

Discussion

Saurichthys cf. *elongatus*, the best-preserved member of the new late Smithian fish assemblage from Bear Lake County (Idaho, USA), is an early representative of the lower actinopterygian *Saurichthys* Agassiz, 1834. *Saurichthys* is the most species-rich genus of the Saurichthyidae Owen, 1860 (*sensu* Stensiö 1925) and is found in marine and freshwater deposits of Triassic age around the world (*e.g.* Beltan & Tintori 1980, Kogan *et al.* 2009, Mutter *et al.* 2008, Rieppel 1985). At least some Middle and Late Triassic species are known to have been viviparous (Bürgin 1990, Bürgin *et al.* 1991, Griffith 1977, Renesto & Stockar 2009, Rieppel 1985).

Besides *Saurichthys*, the family Saurichthyidae also comprises the monotypic *Eosaurichthys* Liu & Wei, 1988 from the marine Late Permian of Zhejiang (southern China), and *Saurorhynchus* Reis, 1892, consisting of a couple of species from marine Early Jurassic deposits of Europe and North America (*e.g.* Gardiner 1960, Neuman & Wilson 1985, Thies 1985). Other proposed saurichthyid genera have been synonymised with either *Saurichthys* ("*Ichthyorhynchus*" Bellotti, 1857; "*Belonorhynchus*" Bronn, 1858 in part; "*Giffonus*" Costa, 1862; "*Stylorhynchus*" Martin, 1873; "*Brevisaurichthys*" Beltan, 1972; "*Systolichthys*" Beltan, 1972), or with *Saurorhynchus* ("*Belonorhynchus*" in part; *Belonostomus* Agassiz, 1834 in part; "*Acidorhynchus*" Stensiö, 1925; "*Gymnosaurichthys*" Berg, 1940) by subsequent authors (*e.g.* Cartanyà 1999, Gardiner 1960, Mutter *et al.* 2008, Reis 1892, Rieppel 1985, Stensiö 1925, Kogan *et al.* in prep.). Recently, Wu *et al.* (2011) placed three new species from the Anisian (Middle Triassic) of southern China in the genus *Sinosaurichthys* erected by them mainly on account of the shoulder girdle morphology and the position and orientation of the pectoral fin, which points more dorsally than in *Saurichthys*. Wu *et al.* (2011) interpreted these characters, among others, as indicative of a surface-cruising lifestyle, as opposed to the ambush predator behaviour of most other saurichthyids. Nevertheless, considering the various morphological congruencies with *Saurichthys*, we doubt that these differences justify the erection of a new genus. The validity of *Sinosaurichthys* needs to be evaluated by further studies. For the purpose of our analyses (see below), we preliminarily treat the species included in "*Sinosaurichthys*" by Wu *et al.* (2011) as species of *Saurichthys*.

In general appearance, *Saurichthys* resembles the phylogenetically unrelated extant garfish (*Belone belone*) in having a long, slender body with far posteriorly positioned pelvic, anal, and dorsal fins (the latter two opposing each other), a symmetrical caudal fin, and an elongated head that normally measures more than one fourth of the total body length (see Gardiner 1960; Griffith 1959, 1962; Rieppel 1985, 1992; Stensiö 1925; Woodward 1888, 1890, 1895; Fig. 8). Standard length of fully grown individuals ranges from *ca* 15 cm (*e.g.* Griffith 1959, Kogan *et al.* in prep.) to more than 1.5 m (*e.g.* Martin *et al.* 1991, Mutter *et al.* 2008). The scales of *Saurichthys* are arranged in an even number of longitudinal rows that in most species do not cover the complete trunk. The equally long upper and lower jaws taper forward in a long, pointed rostrum (Fig. 8). The maxillary bone is palaeoniscoid-shaped with an extended postorbital plate and a narrow anterior process. This bone sutures with the rostro-praemaxilla in front of the orbit (Stensiö 1925). The jaws are typically ornamented with oblique striae and armed with conical teeth of two or three size classes. The teeth are characterized by a striated basal portion and a smooth enamel cap (Agassiz

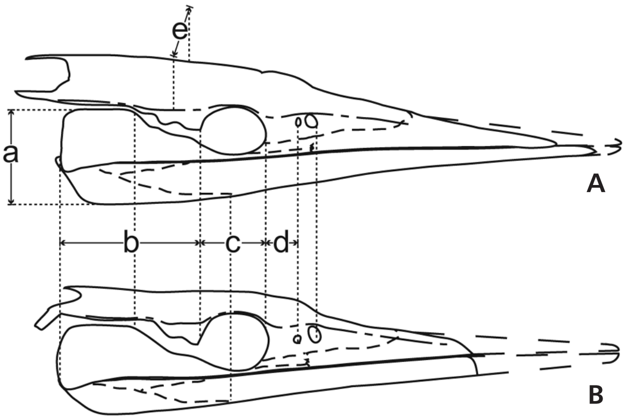

Figure 7. Comparison of the skulls of *Saurichthys elongatus* and *Saurichthys* cf. *elongatus.* • A – PMU P.271, lectotype of *S. elongatus* Stensiö, 1925 from the Smithian of Spitsbergen, Svalbard archipelago, Norway (after Stensiö 1925, pl. 23, fig. 1). • B – PIMUZ A/I 3900 (*S.* cf. *elongatus*) from the late Smithian of Bear Lake County, Idaho, USA. Both specimens are approximately the same size. Measured distances (a–e) used to calculate skull proportions (compare Table 1): a – maximal distance between upper margin of praeoperculum and the ventral margin of the angular bone; b – distance between jaw joint and posterior border of orbital opening; c – length of orbit; d – distance between anterior margin of the orbit and the posterior narial opening; e – maximal width of the skull at the level of the dermosphenotic bones.

1833–1843; Gardiner 1960; Griffith 1959; Rieppel 1985, 2000; Stensiö 1925; Woodward 1888, 1890, 1895). Isolated teeth with the aforementioned features that are found in Late Permian (*e.g.* Tverdokhlebov *et al.* 2005) and Triassic strata are often ascribed to *Saurichthys*, but their taxonomic affiliation is mostly controversial (*e.g.* Gardiner 1960, Griffith 1962, Stensiö 1919, Storrs 1994).

The phylogenetic relationships of *Saurichthys* are still not well resolved. While some cladistic analyses indicate that *Saurichthys* is more closely related to neopterygians than to any other group of recent actinopterygians (*e.g.* Coates 1999, fig. 9a), most place *Saurichthys* together with *Birgeria* near the base of Acipenseriformes (*e.g.* Coates 1999, fig. 9c; Gardiner & Schaeffer 1989, Gardiner *et al.* 2005, Rieppel 1992).

Saurichthys cf. *elongatus* and the Smithian saurichthyids of Spitsbergen

In his monograph on Early Triassic saurichthyids from Spitsbergen (Svalbard archipelago, Norway), Stensiö (1925) described numerous articulated but incomplete remains and assigned them to either *Saurichthys wimani* (Woodward, 1912) or to one of three new species that he erected, *S. ornatus*, *S. elongatus* and *S. hamiltoni.* He referred at least fourteen specimens to *S. elongatus*, mainly on account of (1) their small body size, and (2) resemblances in their dermal bone ornamentation. Similar criteria were used by Stensiö (1925) to distinguish the other Spitsbergen saurichthyids. For example, *S. ornatus* was basically diagnosed by its large body size and, as the name already implies, the conspicuous ornamentation of its skull bones. However, the use of body size and dermal bone ornamentation for taxonomy appears problematic. First, body size should only be used to characterize a fossil taxon if it is already well-distinguished by other traits. Second, it has been shown that the pattern of ornamentation on the dermal skull bones of several lower actinopterygians varies during ontogeny (*e.g.* Ørvig 1978) and this also seems to be true for *Saurichthys curionii* from the Middle Triassic of Monte San Giorgio and Besano, Swiss-Italian boundary area (pers. obs. CR 2010).

We have attempted to design a morphometric scheme for the classification of *Saurichthys* skulls (Fig. 7). Our preliminary morphometric analysis (see Table 1) revealed high 'intraspecific' variability in skull proportions within *S. elongatus* and *S. ornatus*. For instance, the ratio between the height and length of the postorbital part of the skull (a/b in Fig. 7 and Table 1) is *ca* 0.5 in PMU P.271 (*S. elongatus*, lectotype), P.284 (*S. ornatus*), P.286 (*S. ornatus*), and PIMUZ A/I 3900 (*S.* cf. *elongatus*). In contrast, the ratio between the height and the length of the cheek is approximately two-thirds in specimens PMU P.260 (*S. elongatus*), P.262 (*S. wimani*), and P.316 (*S. ornatus*), and *ca* 0.8 in PMU P.885 (*S. elongatus*) (compare Stensiö 1925, pls 1–34; Table 1).

These differences in skull proportions plus the weak diagnostic potential of body size and patterns of dermal bone ornamentation suggest inadequacies in the current taxonomic framework of the aforementioned species. A comprehensive taxonomic revision of the Early Triassic saurichthyids from Spitsbergen is needed, which is, however, beyond the scope of the present paper. Furthermore, the applicability of the selected skull proportions for the differentiation of species has to be tested on additional material of *Saurichthys*. Nonetheless, the high variability in the postorbital part of the skull between the better-known species of *Saurichthys* and evolutionary trends within it (see below) appear promising for the new scheme.

Saurichthys: morphological trends

A commonly accepted phylogenetic model explaining the diversity and evolution of saurichthyid species is still lacking (*e.g.* Schmid & Sánchez-Villagra 2010). While attempts have been made to arrange the morphological changes in time lines (*e.g.* Rieppel 1992), other authors emphasized the lack of a linear trend ('orthogenesis' of Beltan & Janvier 1978, Beltan & Tintori 1980) in the evolution of *Saurichthys*.

Table 1. Ratios between specific distances on the skull of specimens referred to various species of *Saurichthys*. The measured distances on the skull (a–e) are illustrated in Fig. 7. The length of the orbit (c [mm]) is here used as an indicator for relative body size. Sources: Stensiö (1925), Rieppel (1985), Mutter *et al.* (2008), and pers. obs. of CR.

Species	Specimen	c	b/c	a/c	a/b	d/c	e/a
Saurichthys cf. *elongatus*	PIMUZ A/I 3900	12.85	2.24	1.57	0.52	0.37	0.97
S. elongatus	PMU P.271	12.70	2.22	1.53	0.52	0.49	0.92
	PMU P.260	12.73	2.43	1.75	0.62	0.40	–
	PMU P.885	14.58	1.66	1.44	0.81	0.12	–
	PMU P.263	18.90	2.09	1.81	0.58	0.51	–
S. ornatus	PMU P.286	23.90	2.50	1.80	0.52	0.31	–
	PMU P.284	24.10	3.00	1.92	0.49	0.60	1.07
	PMU P.316	24.40	3.50	2.72	0.64	–	–
S. cf. *ornatus*	MGUH-VP-994	11.90	2.00	1.52	0.58	0.33	1.07
S. wimani	PMU P.262	19.60	2.70	1.96	0.63	0.41	–
S. hamiltoni	PMU P.281	21.67	3.39	2.33	0.69	–	0.75
S. toxolepis	CMN 12288	15.30	2.30	1.37	0.46	0.68	1.01
S. curionii	PIMUZ T 4451	3.36	1.90	1.48	0.78	–	–
	PIMUZ T 4104	11.65	1.17	1.00	0.86	0.33	–

Albeit erratic, the distribution of several cranial and postcranial characters in these fishes does follow a trend-like general pattern. For instance, the length of the postorbital part of the skull is larger than or equal to its maximum height in most Early Triassic species of *Saurichthys*, but relatively shorter in many later forms (Mutter *et al.* 2008, Wu *et al.* 2009; Table 1, Fig. 8A). Another cranial trend is reported for the bending of the mandibular rami (Mutter *et al.* 2008): while the branches of the lower jaw are straight or only gently curved in the Early Triassic *Saurichthys* cf. *ornatus*, *S. toxolepis* (see Mutter *et al.* 2008), *S. madagascariensis* (pers. obs. IK 2011), and *Saurichthys* cf. *elongatus* (Fig. 3C), they are notably bent outwards at the level of the orbits in the Middle Triassic *S. curionii* (see Rieppel 1985). The elements of the dermatocranium of *Saurichthys* are reduced in number compared to other contemporaneous lower actinopterygians (Griffith 1959, Rieppel 1985), and a great diversity in cranial anatomy is already observed within Early Triassic species (Mutter *et al.* 2008; see also Table 1). During the Triassic, further reduction in the number of skull bones takes place. For example, the eye is surrounded by eight separate bones in the Early Triassic *S. madagascariensis* but only by a single sclerotic ring in Late Triassic forms (Griffith 1959; Piveteau 1944–1945; Rieppel 1980a, 1985).

The squamation of *Saurichthys* (Fig. 8A) conspicuously differs from the condition seen in most contemporaneous actinopterygians, where it consists of rhomboid scales with peg-and-socket articulation that are arranged in sub-vertical rows (compare *e.g.* Fig. 5). *Saurichthys*, in contrast, is characterised by longitudinal rows of ganoid scales arranged along the dorsal, ventral and lateral midlines (*e.g.* Stensiö 1925; Woodward 1890, 1895). The earliest forms also had scales in dorso-lateral and ventro-lateral positions (Kogan 2011, Lehman 1952, Liu & Wei 1988, Nielsen 1936, Rieppel 1980a, Stensiö 1925), and at least one paired file of ventro-lateral scales was present in most Early and Middle Triassic species (Kogan *et al.* 2009, Mutter *et al.* 2008, Rieppel 1985, Wu *et al.* 2011, Zhang *et al.* 2010). In the latest Triassic species of *Saurichthys*, only the mid-ventral and mid-dorsal scale rows are present (*e.g.* Griffith 1962, Schmid & Sánchez-Villagra 2010; Fig. 8A), and the body of the Early Jurassic *Saurorhynchus brevirostris* is completely devoid of scales (Hauff 1938, Gardiner 1960, Thies 1985). The scales of saurichthyids become generally smaller and thinner during the evolution of these fishes (pers. obs. IK 2011). Moreover, the scales of the mid-dorsal and mid-ventral rows (except the always enlarged interlocking scutes of the caudal peduncle) change their outline from broad and heart-shaped in early species to lanceolate or spiniform in the Late Triassic forms (Fig. 8A).

The axial skeleton of *Saurichthys* is composed of paired dorsal and ventral elements arranged around the persistent notochord (Fig. 8B). Ossified vertebral centra are not developed. The dorsal elements (neural arches) approach a number of 200 pairs and are roughly T-shaped. Each neural arch has a slender vertical body that is laterally convex and anteriorly and posteriorly concave, a rounded base, and two processes, one pointing antero-dorsally and the other postero-dorsally. The process directed antero-dorsally is usually referred to as the praezygapophysis, which serves for the articulation with the preceding vertebral element. The relative length of the praezygapophyses generally increases during the Triassic (Fig. 8B), giving a greater lateral stability to the vertebral column especially in

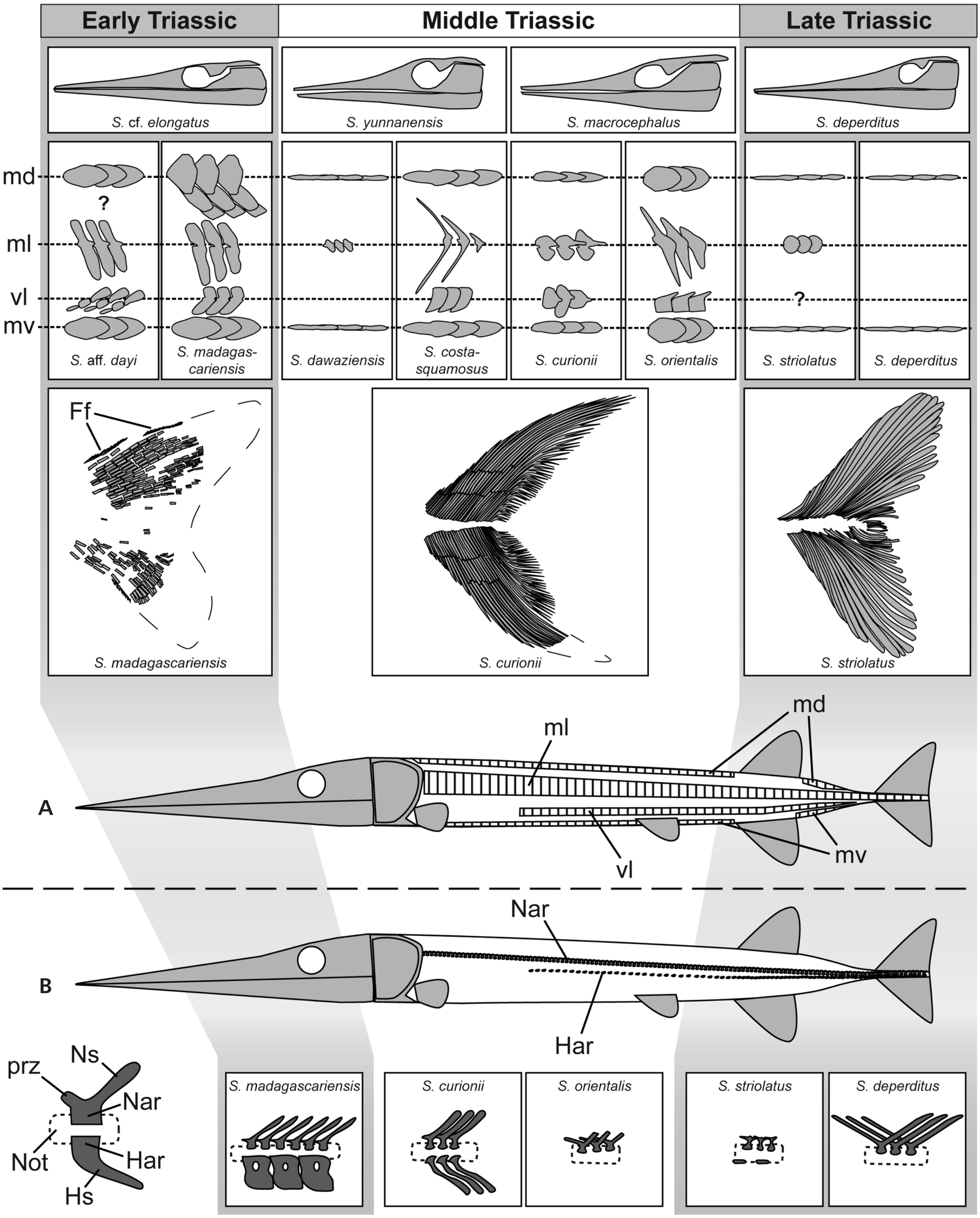

Figure 8. General morphology and distribution of several skeletal characters among some of the better-known species of the lower actinopterygian *Saurichthys* during the Early, Middle and Late Triassic (see text for more details). Schematic drawings of anatomical parts of the different species are not to scale. Anterior is always left. • A – the external appearance of a generalised *Saurichthys* with sketches showing the morphology of the skull (top; based on PIMUZ A/I 3900, CGS LPV-2088, PIMUZ T 3805, BSPM 1910/1/8), squamation (middle; after various specimens), and caudal fin (bottom; based on MGUH 30235, PIMUZ T 4154, GBA 2006/097/0012). • B – the course, structure, and diversity of the vertebral column (after various specimens). With the exception of the Middle Triassic *S. orientalis*, all pictured species are known from marine deposits. Compiled after Griffith (1959), Kogan (2011), Kogan *et al.* (2009), Lehman (1952), Rieppel (1985), Tintori (1990), Wu *et al.* (2009), Zhang *et al.* (2010), this study, and pers. obs. of CR and IK.

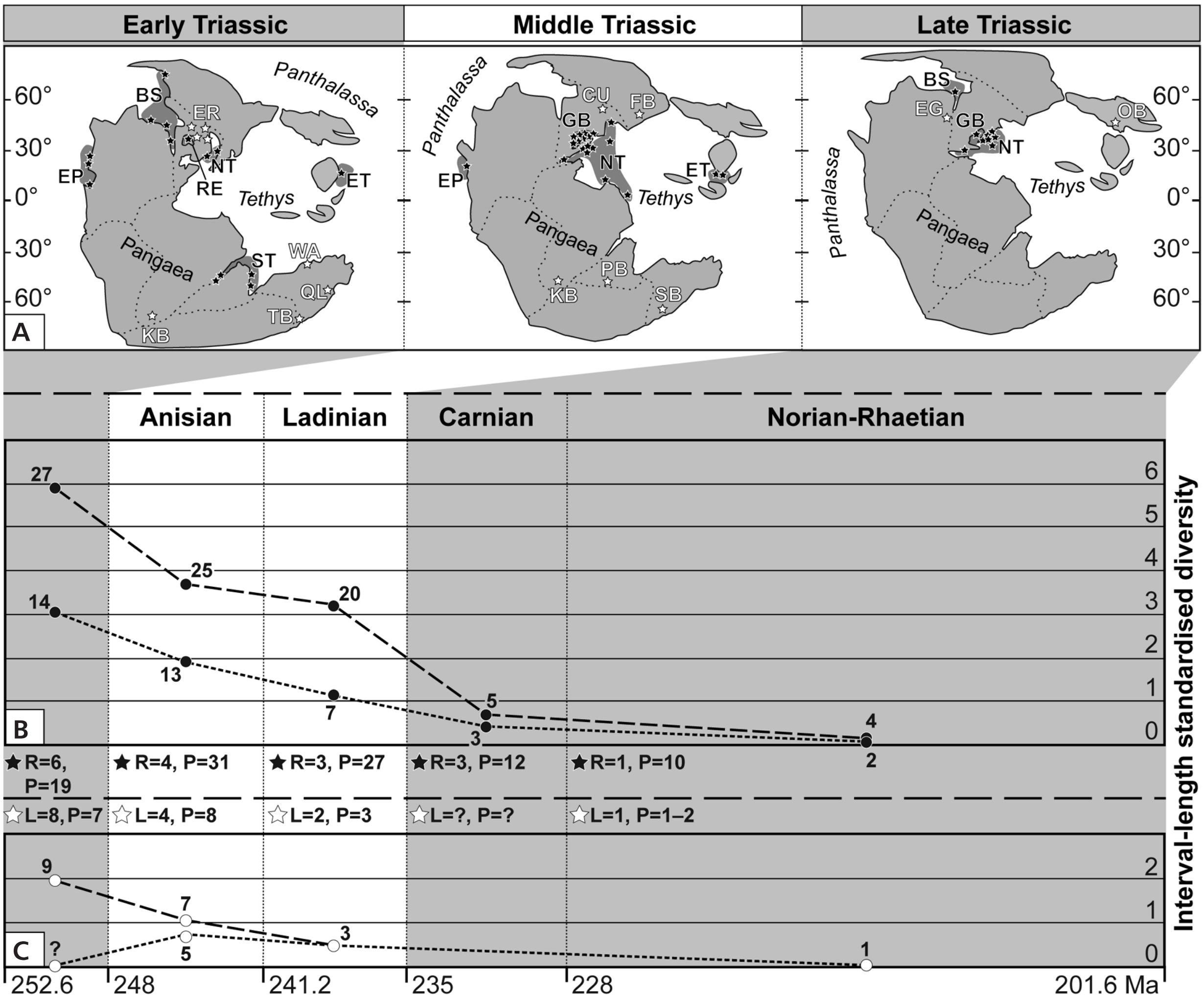

Figure 9. Palaeogeographic distribution and global diversity of the lower actinopterygian *Saurichthys* during the Early, Middle, and Late Triassic (data listed in Tables 2, 3). • A – palaeogeographic distribution within the marine (black stars) and continental realm (white stars) during the different epochs of the Triassic (see Material and methods for more information). Marine occurrences are grouped into the following palaeobiogeographic regions (dark grey areas; compare Table 2): BS – Boreal Sea; EP – eastern Panthalassa; ET – eastern Tethys; GB – Germanic Basin; NT – north-western Tethys; RE – Rybinsk epicontinental basin; ST – southern Tethys. Continental localities (not grouped, compare Table 3): CU – Russia – Cis-Ural; EG – East Greenland; ER – European Russia (Moscow syncline, Mezen syncline, Vyatka-Kama depression, southern Cis-Ural); FB – Fergana Basin (Madygen, Kyrgyzstan); KB – Karoo Basin; OB – Ordos Basin; PB – Pranhita-Godavari Basin (India, Andhra Pradesh); QL – Queensland; SB – Sydney Basin; TB – Tasmanian Basin; WA – Western Australia. Palaeogeographic maps modified from Paleomap project. • B – interval-length standardized species richness (*i.e.* number of species per million years) of *Saurichthys* within marine deposits, and • C – interval-length standardized species richness of *Saurichthys* within freshwater deposits during the Early Triassic, the Middle Triassic (Anisian, Ladinian), and the Late Triassic (Carnian, Norian-Rhaetian phase). The stippled line in B and C indicates maximal diversity (including species in open nomenclature), and the dotted line represents minimal species richness (excluding species in open nomenclature). Values of standardised diversity always plotted in the middle of each interval together with the total number of species known from that interval. Information on the numbers of marine palaeobiogeographic regions (R), number of individual localities (L – for freshwater localities), and approximate amount of publications containing descriptions of *Saurichthys* (P – data after Tables 2, 3) per interval are given within the figure. Interval duration estimates are based on boundary ages after Brack *et al.* (2005), Mundil *et al.* (2004), Ovtcharova *et al.* (2006), Schaltegger *et al.* (2008), and Walker & Geissman (2009).

the posterior part of the body (Tintori 1990). The postero-dorsally directed processes could be neural arches, postzygapophyses or both. The ventral elements (haemal arches) are normally restricted to the posterior body portion and their number relates to respective dorsal elements as either 1:1 or 1:2 (*e.g.* Rieppel 1985, Stensiö 1925, Tintori 1990, Woodward 1895). They are rather box-shaped in lateral view in Early Triassic forms (*e.g.* Lehman 1952, Stensiö 1925), but can be more diversely shaped or even unossified in later ones (*e.g.* Rieppel 1985, pers. obs. IK 2011; Fig. 8B). The vertebral column is not upturned into the upper caudal lobe as in most other lower actinopterygians, but continues straight to the posterior margin of the caudal fin, whose lepidotrichia directly articulate with the respective neural and haemal arches. The dorsal and anal fins are supported by about five to fifteen endoskeletal radials, which are considerably less numerous than the respective lepidotrichia (*e.g.* Rieppel 1985, Stensiö 1925).

The structure of the fins of *Saurichthys* is also not typical compared to most other lower actinopterygians. While the pectoral fins are mostly small and fan-shaped (but see Wu *et al.* 2011) and their lepidotrichia always unsegmented, the fin rays of the pelvic, dorsal, anal, and caudal fins exhibit a general decrease in the degree of segmentation during the evolution of saurichthyids (Rieppel 1985, 1992; Schmid & Sánchez-Villagra 2010). The lepidotrichia of both the pelvic and the unpaired fins consist of numerous segments in most early forms (*e.g.* Kogan 2011, Lehman 1952, Liu & Wei 1988, Stensiö 1925, Woodward 1890), but are unsegmented in many Late Triassic species (*e.g.* Griffith 1959, 1977; Fig. 8A) as well as in the Early Jurassic *Saurorhynchus* (*e.g.* Hauff 1938). Even though unsegemented pelvic, dorsal, anal, and caudal fin rays are already present in some Early Triassic species, such as *Saurichthys dayi* and *S. toxolepis* (see Mutter *et al.* 2008), and segmented unpaired fins characterize the Late Triassic *S. deperditus* (see Bassani 1895, Griffith 1962, Tintori & Gozzi 2005), the proportion of forms with reduced fin segmentation generally increased during the Triassic.

Where preserved, the caudal fin is symmetrical (abbreviate-diphycercal, Griffith 1959) in saurichthyids, but there is evidence of a larger epaxial lobe in some early forms like *S. madagascariensis* (Lehman, 1952, pers. obs. IK 2011). In some forms, the hindmost fin rays of both the upper and the lower lobe build a small third, median or terminal lobe (Rieppel 1985; pers. obs. of IK 2011 on material of *S. striolatus*). Fringing fulcra are often present on the leading margin of all fins in early saurichthyids (Lehman 1952, Liu & Wei 1988, Stensiö 1925), but are absent in forms of Middle Triassic or younger age (*e.g.* Rieppel 1992; Fig. 8A), except for a few species from the Middle Triassic of southern China (Wu *et al.* 2009, 2011).

The non-linear pattern of morphological changes in saurichthyids during the Triassic speaks in favour of a cladogenetic mode of evolution (see Rieppel 1992, fig. 13). Besides the shortening of the postorbital portion of the head and the reduction of the number of dermal cranial bones, the dominant morphological changes were the loss in scales and fin ray segmentation (*e.g.* Mutter *et al.* 2008; Rieppel 1985, 1992; Schmid & Sánchez-Villagra 2010). The last-mentioned modifications are directly linked to the swimming and chasing behaviour (see *e.g.* Webb *et al.* 1992), which together with the successive stiffening of the vertebral column (Tintori 1990) led to an enhanced fast-start performance in later forms of *Saurichthys* and the Early Jurassic *Saurorhynchus*.

Based on the observed trends towards a reduced dermal skeleton, we can infer that saurichthyids are derived from a more general lower actinopterygian ancestor with, for instance, full body squamation, segmented lepidotrichia in all fins (Schmid & Sánchez-Villagra 2010), fringing fulcra on all fins, and a more common cranial bone pattern. In this context, the proposition that reduced body armour (Coates 1999, Gardiner *et al.* 2005) and absence of fringing fulcra (Coates 1999) are synapomorphies of *Saurichthys* and recent sturgeons (mainly based on the use of the better known but more derived Middle Triassic species of *Saurichthys* for character establishment) is misleading. Although Acipenseridae have five longitudinally arranged scale rows (Bemis *et al.* 1997) that may superficially resemble those of saurichthyids (albeit the latter always have an even number of files), the squamation pattern in Polyodontidae is very different: in these fishes scales are only present on the upper caudal lobe. Furthermore, acipenserids and polyodontids possess a truly heterocercal caudalis, while the tail fin of saurichthyids is abbreviate-diphycercal already in the earliest species (*e.g.* Liu & Wei 1988). Accepting that acipenserids and polyodontids form a monophyletic clade (see *e.g.* Bemis *et al.* 1997), it seems that the reduction in squamation in this group happened in convergence with saurichthyids, a factor that should be taken into account in future cladistic analyses.

Saurichthys: palaeogeographic trends

Many authors have reported occurrences and even erected new species of *Saurichthys* based solely on isolated teeth and/or tiny jaw fragments (see *e.g.* Agassiz 1833–1843, Schmid 1861, Winkler 1880). Since the taxonomic affiliation of such material is uncertain (*e.g.* Gardiner 1960, Stensiö 1919, Storrs 1994; see also above), we restrict our palaeogeographic overview of *Saurichthys* only to reports of more complete, diagnostic material. The fossil record of *Saurichthys* within different intervals of the Triassic is listed in Table 2 for the marine realm and in Table 3 for the non-marine domain.

In the Early Triassic, *Saurichthys* was widely distributed in marine and freshwater environments at both high and low palaeolatitudes (Fig. 9A). *Saurichthys* is known from the marine Early Triassic of East Greenland, Spitsbergen and Bjørnøya (Svalbard archipelago, Norway), Canada (Alberta, British Columbia, Nunavut), the USA (Idaho), Russia (Magadan district, Volgograd region), Kazakhstan, Nepal, China (Jiangsu), and north-western and south-western Madagascar (*e.g.* Beltan & Janvier 1978, Jin 2006, Lehman *et al.* 1959, Minikh 1981, Mørk *et al.* 1990, Mutter *et al.* 2008, Nielsen 1936, Novikov *et al.* 2002, Piveteau 1944–1945, Stensiö 1925, this study). Moreover, during recent fieldwork in the Himalaya (Spiti Valley, Himachal Pradesh, India) a lower jaw fragment of a saurichthyid was discovered in Dienerian strata (PIMUZ A/I 4145, Brinkmann *et al.* in prep.). Minikh (1981, 1982) reported four species from the Olenekian (Smithian?) Rybinsk Formation of Tikhvinskoye (Upper Volga region), which at that time was considered to be of freshwater origin (*e.g.* Sennikov 1996). However, most authors now agree that these sediments were deposited in an epicontinental basin under marine conditions (*e.g.* Arefyev *et al.* 2009, Lozovsky 1987, Minikh & Minikh 2005).

From the non-marine Early Triassic, *Saurichthys* has been described from South Africa, European Russia (Moscow syncline, Mezen syncline, Vyatka-Kama depression, southern Cis-Ural), and Australia (Queensland, Tasmania, Western Australia) (*e.g.* Bender 2008; Bender & Hancox 2004; Dziewa 1980; Minikh 1981, 1983; Turner 1982; Warren 1980) (Fig. 9A).

During the Middle Triassic, *Saurichthys* was still widely distributed (Fig. 9A), with its highest diversity being found in the Tethys. *Saurichthys* is among the most abundant and diverse fishes of the marine Middle Triassic localities of Yunnan and Guizhou (southern China; Lombardo *et al.* 2011; Wu *et al.* 2009, 2011; Zhang *et al.* 2010), and the Monte San Giorgio and Besano-Viggiù region (Swiss-Italian boundary area; Rieppel 1985, 1992; Tintori & Lombardo 1999). Moreover, it is known from the marine Middle Triassic of Nevada (USA), Graubünden (Switzerland), Austria, Slovenia, Spain, France, Germany, Poland, the Netherlands, Israel, and Turkey (*e.g.* Agassiz 1833–1843, Bachmayer & Warch 1959, Beltan *et al.* 1979, Bürgin *et al.* 1991, Cartanyà 1999, Eck 1865, Firtion 1934, Furrer 2009, Hagdorn & Mutter 2011, Hennig 1909, Hilzheimer 1930, Hitij *et al.* 2010, Jin 2006, Martin *et al.* 1991, Münster 1839, Oosterink 1986, Rieppel *et al.* 1996, Sander *et al.* 1994, Schmid 1846). Frech (1903–1908) described two species (*S. lepidosteoides*, *S. latifrons*) from the lowermost Muschelkalk of Upper Silesia (Poland), in sediments transitional from Spathian to Anisian according to current bio- and magnetostratigraphic dating (*e.g.* Nawrocki & Szulc 2000; J. Szulc, pers. comm. to IK 2012). Additionally, Kear *et al.* (2010) reported from central Saudi Arabia jaw fragments possibly referable to *Saurichthys*, which are probably of Ladinian age (B.P. Kear, pers. comm. to CR 2012). Minikh (1992) found remains of *Saurichthys* in supposedly non-marine strata near Lake Inder in the Caspian depression (Kazakhstan), but the depositional environment of this site is now considered as coastal marine (A.V. Minikh, pers. comm. to IK 2012).

Within Middle Triassic continental deposits, *Saurichthys* has been reported from South Africa, Andhra Pradesh (India), New South Wales (Australia), southern Cis-Ural (Russia), and Kyrgyzstan (Griffith 1978; Jain 1984; Kogan *et al.* 2009; Minikh 1992; Ritchie 1981, 1987; Sytchevskaya 1999; Turner 1982; Wade 1935; Woodward 1890) (Fig. 9A). Mutter *et al.* (2008) listed *Saurichthys* from the non-marine Middle Triassic of Argentina, which is erroneous (A. López-Arbarello, pers. comm. to IK 2009).

The palaeogeographic distribution of *Saurichthys* during the Late Triassic was mainly restricted to the Tethys (Fig. 9A). *Saurichthys* has been described from the marine Late Triassic of Austria, Italy, Germany, Spain, and Bjørnøya (Svalbard archipelago, Norway) (*e.g.* Beltan & Tintori 1980; Böhm 1903; Fortuny *et al.* 2011; Griffith 1977; Kner 1867; Oertle 1928; Tintori 1990, 1998; Tintori *et al.* 1985). Additionally, Khorana & Tirkey (1977) described a bone fragment supposedly belonging to *Saurichthys* from the Late Triassic of Jammu and Kashmir (India). However, this is a misidentification (J.W. Schneider, pers. comm. to IK 2012). Jaw fragments from the marine Rhaetian of England that have been ascribed to *Saurichthys* by various authors were later summarized by Storrs (1994) under the parataxon *Severnichthys*.

Reports from Late Triassic continental deposits (Fig. 9A) are sparse and controversial. Fragments possibly referable to *Saurichthys* from East Greenland were mentioned by Jenkins *et al.* (1994). Chou & Liu (1957) described an incomplete skeleton of *S. huanshenensis* and other fish remains from freshwater deposits of Hengshan (Shaanxi, northern China). Although Chou & Liu (1957) dated this fish assemblage as Early Triassic, more recent workers refer to it as Late Triassic (Chang & Miao 2004, Jin 2006, Liu *et al.* 1999).

Our compiled data on saurichthyid palaeobiogeography suggest two main trends in the distribution of these fishes. The first trend consists of a change from a virtually global distribution in the Early Triassic (except South America and Antarctica) to an occurrence that was basically restricted to the north-western Tethyan realm in the Late Triassic (Fig. 9A, Tables 2, 3). Although this observation may be linked to the paucity of palaeoichthylogical sites for the marine Late Triassic, which are mainly limited to Europe and China (*e.g.* Chang & Miao 2004, Jin 2006, Tintori 1998), the fact that *Saurichthys* has not yet been reported from the marine Late Triassic of China (*e.g.* Chang & Miao 2004, Wang *et al.* 2009) may be indicative of a restricted palaeogeographic distribution at that time. In fact, the range of *Saurichthys* near the end of the Triassic already resembles that of the Early Jurassic *Saurorhynchus*, which is only known from marine deposits of Euramerica (*e.g.* Firtion & Schneider 1975, Neuman & Wilson 1985, Thies 1985).

The second trend recognized in saurichthyid palaeogeography is increasing rarity within freshwater deposits (Fig. 9A, Table 3). During Early and Middle Triassic times, *Saurichthys* inhabited major freshwater systems of Gondwana (*e.g.* Karoo basin of southern Africa, Sydney basin in south-east Australia) and Laurasia (Cis-Ural and European Russia, Madygen in south-west Kyrgyzstan). However, *Saurichthys* is largely absent from Late Triassic non-marine environments, such as the vast fluvio-lacustrine systems of the USA (*e.g.* Newark, Chinle, and Dockum Groups; see *e.g.* Milner *et al.* 2006, Olsen *et al.* 1982), and South America (*e.g.* Ischigualasto-Villa Uniòn and Cuyo

Table 2. The fossil record of *Saurichthys* (including "*Sinosaurichthys*" from the Middle Triassic of Yunnan and Guizhou, southern China) from marine and brackish deposits within the Early, Middle, and Late Triassic, with important references. Only diagnostic finds are incorporated, and occurrences of isolated teeth are omitted. Individual occurrences are grouped into palaeobiographic regions (R, compare Fig. 9 and corresponding figure caption) according to their stratigraphic, palaeogeographic, and palaeoenvironmental context (see Material and methods).

Epoch	Stage/Substage (Stratigraphy)	Occurrence (R)	Species	Material	References
Early Triassic	Griesbachian	Greenland (BS)	*S.* aff. *dayi, S.* cf. *ornatus*	skulls, body fragments	Kogan (2011), Mutter *et al.* (2008), Nielsen (1936)
	Dienerian	India, Himachal Pradesh (ST)	*Saurichthys* sp.	lower jaw fragment	Brinkmann *et al.* (in prep.)
	Dienerian–Smithian	Madagascar (north-west) (ST)	*S. madagascariensis, S. piveteaui, S. stensioei*	skulls, body fragments, complete specimens	Beltan (1968), Lehman (1952), Piveteau (1944–1945)
	?	Madagascar (south-west) (ST)	*S.* "*madagascariensis*"	body fragments, complete specimens	Lehman *et al.* (1959), Rieppel (1980a)
	Smithian	Norway, Svalbard (Spitsbergen and Bjørnøya) (BS)	*S. elongatus, S. hamiltoni, S. ornatus, S. wimani, Saurichthys* sp.	skulls, body fragments	Mørk *et al.* (1990), Stensiö (1925), Woodward (1912)
	?	Canada, Alberta (EP)	*S. dayi, Saurichthys* sp.	skull fragment, complete specimens	Raymond (1925), Schaeffer & Mangus (1976)
	?	Canada, British Columbia (EP)	*S. dayi, S. toxolepis, Saurichthys* sp.	skulls, body fragments, complete specimens	Mutter *et al.* (2008), Schaeffer & Mangus (1976)
	Smithian	Canada, Nunavut (Ellesmere Island) (BS)	*Saurichthys* sp.	skull fragment	Schaeffer & Mangus (1976)
	Smithian	USA, Idaho (EP)	*Saurichthys* cf. *elongatus*	skull	this study
	Olenekian (Smithian?)	Russia, Upper Volga region (RE)	*S. eximius*, *S. obrutchevi*, *S. proximus*, *S. tertius*	skulls, scales	Minikh (1981, 1982)
	Olenekian (Spathian?)	Kazakhstan (Mangyshlak peninsula) (NT)	*Saurichthys* sp.	skull	Minikh (1981)
	Olenekian	Russia, Far East (BS)	*Saurichthys* sp.	skeleton	Minikh (1981)
	Olenekian	Russia, Volgograd region (NT)	*Saurichthys* sp.	jaw fragments	Novikov *et al.* (2002)
	Olenekian	China, Jiangsu (ET)	*Saurichthys* sp.	?	Jin (2006)
	?	Nepal (ST)	*S. nepalensis*	skull	Beltan & Janvier (1978)
Middle Triassic	Spathian-Anisian boundary (Lower Muschelkalk)	Poland, Upper Silesia (GB)	*S. latifrons, S. lepidosteoides*	skulls	Eck (1865), Frech (1903–1908)
	Anisian (Upper Buntsandstein)	France, Lorraine (GB)	*S. daubreei*	complete specimen	Firtion (1934)
	Anisian (Upper Buntsandstein)	Germany, Franconia (GB)	*Saurichthys* sp.	skulls, complete specimens	Bashkuev *et al.* (2012)
	Anisian (Upper Buntsandstein)	Germany, Brandenburg (GB)	*Saurichthys* sp.	lower jaw	Hilzheimer (1930)
	Anisian (Lower Muschelkalk)	The Netherlands (GB)	*S.* "*tenuirostris*", *Saurichthys* sp.	complete specimens	Oosterink (1986)
	Anisian (Middle Muschelkalk)	Germany, Brandenburg (GB)	*Saurichthys* sp.	skulls	Hennig (1909)
	Anisian (Middle Muschelkalk)	Germany, Lower Saxony (GB)	*Saurichthys* sp.	jaw fragments	Schultze & Möller (1986)
	Anisian (Middle Muschelkalk)	Germany, Thuringia (GB)	*S. tenuirostris*	skulls	Meyer (1849), Münster (1839), Reis (1892), Schmid (1846)
	Anisian (Upper Muschelkalk)	Poland, Upper Silesia (GB)	*S.* "*tenuirostris*"	skull fragments	Eck (1865)
	Anisian	China, Guizhou (ET)	*Saurichthys* sp.	?	Jin (2006)
	Anisian	China, Guizhou (ET)	"*Sinosaurichthys*" *longipectoralis*	complete specimens	Wu *et al.* (2011)
	Anisian	China, Yunnan (ET)	*S. dawaziensis*, *S. yunnanensis*, *Saurichthys* sp.	complete specimens	Lombardo *et al.* (2011), Wu *et al.* (2009), Zhang *et al.* (2010)

Table 2. continued

Epoch	Stage/Substage (Stratigraphy)	Occurrence (R)	Species	Material	References
Middle Triassic	Anisian	China, Yunnan (ET)	"*Sinosaurichthys*" *longimedialis*, "*S.*" *minuta*	complete specimens	Wu *et al.* (2011)
	Anisian	USA, Nevada (EP)	*Saurichthys* sp.	skull fragments, scales	Rieppel *et al.* (1996), Sander *et al.* (1994)
	Anisian	Slovenia (NT)	*Saurichthys* sp.	complete specimens	Hitij *et al*. (2010)
	Anisian–Ladinian	Swiss-Italian boundary area (Besano and Monte San Giorgio) (NT)	*S. costasquamosus* (= *S.* "*robustus*" in part), *S. curionii* (= *S.* "*robustus*" in part, *S.* "*stoppanii*", *S.* "*intermedius*"), *S. macrocephalus* (= *S.* "*robustus*" in part), *S. paucitrichus, Saurichthys* sp.	skull and body fragments, complete specimens	Alessandri (1910), Bassani (1886), Bellotti (1857, 1873), Bürgin (1990), Griffith (1959), Deecke (1889), Renesto & Stockar (2009), Rieppel (1985, 1992), Tintori & Lombardo (1999)
	Ladinian	Switzerland, Graubünden (NT)	*S. costasquamosus, S. curionii, Saurichthys* sp.	complete specimens	Bürgin *et al.* (1991)
	Ladinian	Slovenia (NT)	*Saurichthys* sp.	complete specimens	Hitij *et al*. (2010)
	Ladinian	Austria, Carinthia (NT)	*Saurichthys*? sp.	jaw fragment	Bachmayer & Warch (1959)
	Ladinian (Upper Muschelkalk)	Germany, Franconia (GB)	*S. apicalis*	skull, rostrum fragments	Agassiz (1833–1843, 1834), Münster (1839), Reis (1892)
	Ladinian	Spain, Catalonia (NT)	*S.* aff. *costasquamosus, S.* aff. *curionii, Saurichthys* sp.	complete specimens	Beltan (1972), Cartanyà (1999)
	Ladinian	Israel (NT)	*Saurichthys* sp.	rostra	Martin *et al.* (1991), Rieppel (2000)
	Ladinian	Kazakhstan, Caspian Depression (NT)	*Saurichthys ultimus*	skull fragments	Minikh (1992)
	Ladinian	Turkey, western Taurus (NT)	*Saurichthys* sp.	rostrum	Beltan *et al.* (1979)
	Ladinian	Saudi Arabia (NT)	*Saurichthys*? sp.	rostrum fragments	Kear *et al.* (2010)
	Ladinian (Lower Keuper)	Germany, Franconia (GB)	*S. gypsophilus*	skull fragment	Reis (1892)
	Ladinian (Lower Keuper)	Germany, Württemberg (GB)	*Saurichthys* sp.	rostrum fragments	Hagdorn & Mutter (2011)
	Ladinian	China, Guizhou (ET)	*Saurichthys* sp.	?	Jin (2006)
	Ladinian	China, Yunnan (ET)	*Saurichthys* sp.	?	Jin (2006)
Late Triassic	Carnian	Norway, Svalbard (Bjørnøya) (BS)	*Saurichthys*? sp.	jaw fragment	Böhm (1903)
	Carnian (Middle Keuper)	Germany, Württemberg (GB)	*S. irregularis*	skull fragments	Oertle (1928), Seegis (1997)
	Carnian	Italy, Friuli-Venezia Giulia (NT)	*S. striolatus*	complete specimens	Bronn (1858), Griffith (1959), Kner (1866), Woodward (1895), Zittel (1887–1890)
	Carnian	Austria, Lower Austria (NT)	*S. calcaratus*	body fragments, complete specimen	Bürgin (1990), Griffith (1977)
	Carnian	Spain, Catalonia (NT)	*Saurichthys* sp.	skull and body fragments	Fortuny *et al.* (2011), Lehman (1964)
	Norian	Italy, Campania (NT)	*S. deperditus*	body fragments	Bassani (1892, 1895), Costa (1862), Tintori *et al.* (1985)
	Norian	Italy, Friuli-Venezia Giulia (NT)	*Saurichthys* sp.	complete specimens	Tintori (1990)
	Norian	Italy, Lombardy (NT)	*S. deperditus, S. seefeldensis, Saurichthys* sp.	body fragments, complete specimens	Beltan & Tintori (1980), Tintori (1990)
	Norian	Austria, Tyrol (NT)	*S. seefeldensis*	skull (lost?), body fragments	Kner (1867), Zittel (1887–1890)
	Norian	Austria, Upper Austria (NT)	*S. deperditus* (= *S.* "*krambergeri*")	complete specimen	Griffith (1962), Tintori & Gozzi (2005)

basins; López-Arbarello 2004), and the Early Jurassic saurichthyid *Saurorhynchus* is exclusively known from marine deposits (*e.g.* Gardiner 1960, Neuman & Wilson 1985, Thies 1985).

The diminishing palaeogeographic range of saurichthyids during the Triassic was paralleled by a pronounced decrease in their global species richness. This tendency is well-documented in the marine record (Fig. 9B) and, even though the data are scarcer, is also seen in the continental record (Fig. 9C). Despite the much longer duration of the Late Triassic, only a very few species have been described from this epoch compared to the Early and Middle Triassic. For instance, the average number of marine species per million years in the Early Triassic is 7–8 times higher than in the Carnian and over 38 times higher than in the Norian-Rhaetian inverval (Fig. 9B, C). Since we could not find a significant correlation between marine species richness and the number of substantial publications on saurichthyids (compare Table 2, Fig. 9) we conclude that the diversity decrease during the Triassic is not influenced by research effort. There is a correlation between counts of marine species and the number of palaeobiogeographic regions (see Material and Methods for definitions) per interval (Spearman's ρ/Kendall's τ, $p < 0.05$) but none between number of marine species and occurrences (see Table 2, Fig. 9). There may be a Lagerstätten effect, since the number of productive sites for the Late Triassic is lower than that for the Early and Middle Triassic. Nevertheless, we emphasise that the conspicuous morphological diversity (disparity) of Early and Middle Triassic saurichthyids seen, for example, within skull shape, fin structure, and squamation, is not observed among the Late Triassic forms (Fig. 8, see also above). We therefore conclude that the decline in saurichthyid diversity between the Early and Late Triassic is generally authentic.

We furthermore note the disappearance of the plesiomorphic saurichthyid morphotypes from the marine realm during the Early to Middle Triassic transition. To these morphotypes we refer forms that show all or most of the following attributes: (1) relatively long postorbital skull portion, (2) well-developed squamation with deep mid-lateral and broad mid-dorsal and mid-ventral scales, (3) repeatedly segmented fin rays, and (4) presence of fringing fulcra. These basal morphotypes are abundant in Early Triassic strata, but absent from marine deposits of Middle Triassic or younger age (Fig. 8). However, similar fin and squamation constellations can be found in non-marine species from the Middle Triassic of Australia (Woodward 1890), and Kyrgyzstan (Kogan *et al.* 2009; Fig. 8A) as well as in the possibly Late Triassic *S. huanshenensis* from northern China (Chou & Liu 1957; Wu F.X., pers. comm. to IK 2011). Hence, it seems that freshwater systems may have served as *refugia* for some archaic saurichthyids, thus helping them survive into the Middle and possibly even the Late Triassic.

The global distribution of *Saurichthys* and many other fish genera during the Early Triassic (*e.g.* Brinkmann *et al.* 2010) resembles patterns described for ammonoids of the same epoch. Ammonoids show repeated phases of increased cosmopolitanism during the Early Triassic, which have been linked to the recurrent emergence of a flat latitudinal sea-surface temperature gradient (see *e.g.* Brayard *et al.* 2006, Brühwiler *et al*. 2010, Galfetti *et al.* 2007). Such episodes of diminished temperature difference between higher and lower palaeolatitudes (*e.g.* during the late Smithian), in combination with reduced interspecific competition due to the effects of the end-Permian mass extinction, possibly enabled pole-ward range extensions of *Saurichthys* during Early Triassic times. The loss in global species richness and the disappearance of the basal saurichthyid morphotypes in the marine realm near the end of the Early Triassic may be related to two extinction events in the aftermath of the end-Permian mass extinction: the Smithian-Spathian boundary event (*e.g.* Galfetti *et al.* 2007), and the Spathian-Anisian boundary extinction (Brayard *et al.* 2006, Bucher 1989). The extinction event near the end of the Smithian, which is better researched, is known to have strongly decimated nekto-pelagic clades such as conodonts and ammonoids (*e.g.* Brühwiler *et al.* 2010, Orchard 2007). This event, which took place approximately 2 million years after the main extinction pulse near the Permian-Triassic boundary (Mundil *et al.* 2004, Ovtcharova *et al.* 2006), might have also affected marine saurichthyids and other fishes. The successive global diversity loss and increasingly restricted palaeogeographic distribution of *Saurichthys* (Fig. 9B, C; Tables 2, 3) may be linked to climatic changes (*e.g.* Preto *et al.* 2010), and/or to increasing competition with more advanced fishes and marine reptiles (*e.g.* ichthyosaurs, sauropterygians) that evolved during the early Mesozoic. However, further research is necessary to test these scenarios.

Conclusions

Even though the occurrence of Early Triassic fishes in Bear Lake County in south-east Idaho (USA) has been known for over a century, fossil fish assemblages from this area have largely remained unstudied (see introduction). Only a few fish taxa have been properly described and figured in the literature (Evans 1904, Mutter & Rieber 2005, Tanner 1936) and more research is needed to better understand these assemblages. The new marine ichthyofauna presented herein is the first fish assemblage reported from the Smithian of the United States. Since the Bear Lake area was situated within equatorial palaeolatitudes during the Early Triassic (Fig. 1B), it also represents one of the

Table 3. The fossil record of *Saurichthys* from freshwater deposits within the Early, Middle and Late Triassic (compare Fig. 9), with important references. Only diagnostic finds are incorporated, and occurrences of isolated teeth are omitted. Abbreviations for the continental occurrences (L) indicated in Fig. 9A are given in brackets (see caption of Fig. 9 for further details).

Epoch	Stage/Substage	Occurrence (L)	Species	Material	References
Early Triassic	Spathian	South Africa (KB)	*Saurichthys* sp.	jaw fragments	Bender & Hancox (2004)
	Olenekian	Russia, Moscow syncline (ER)	*Saurichthys* sp.	skull fragments	Minikh (1981)
	?	Russia, Mezen syncline (ER)	*Saurichthys* sp.	jaws, jaw fragments	Minikh (1983)
	?	Russia, Vyatka-Kama depression (ER)	*S.* "*vjuschkovi*", *Saurichthys* sp.	jaw fragments	Minikh (1983)
	?	Russia, southern Cis-Ural (ER)	*Saurichthys* sp.	skull fragments	Minikh (1983)
	?	Australia, Queensland (QL)	*Saurichthys* cf. *gigas*	rostrum fragment	Turner (1982)
	?	Australia, Tasmania (TB)	*Saurichthys* sp.	skull fragments	Bender (2008), Dziewa (1980)
	?	Australia, Western Australia (WA)	*Saurichthys* sp.	?	Turner (1982), Warren (1980)
Middle Triassic	Anisian	Australia, New South Wales (SB)	*S. gigas, S. gracilis* (= *S.* "*elegans*"), *S. parvidens*	complete specimens	Ritchie (1981, 1987), Wade (1935, 1939), Woodward (1890)
	Anisian	South Africa (KB)	*Saurichthys* sp.	jaw fragment	Griffith (1978)
	Anisian	India, Andhra Pradesh (Pranhita-Godavari Valley) (PB)	*Saurichthys* cf. *madagascariensis*	rostrum fragment	Jain (1984)
	Anisian-Ladinian	Russia, southern Cis-Ural (CU)	*S. dongusensis,* *S. ultimus*	skull fragments	Minikh (1992)
	Ladinian	Kyrgyzstan (FB)	*S. orientalis*	complete specimens	Kogan *et al.* (2009), Sytchevskaya (1999)
Late Triassic	?	Greenland (EG)	*Saurichthys*? sp.	rostrum fragment	Jenkins *et al.* (1994)
	Rhaetian?	China, Shaanxi (Ordos Basin) (OB)	*S. huanshenensis*	body fragment	Chou & Liu (1957)

southernmost localities for eastern Panthalassan fishes from that epoch. The presence of a saurichthyid in the late Smithian of Bear Lake County that resembles the lectotype of *Saurichthys elongatus* Stensiö, 1925 from the Smithian 'fish horizon' of Spitsbergen (Boreal Sea province, see Fig. 9) may indicate a wider palaeogeographic range of *S. elongatus* than previously thought. However, a revision of the type material of *S. elongatus* and additional fossils are required to clarify the taxonomic status of the Idaho specimen.

To our present knowledge, Saurichthyidae Owen, 1860 (*sensu* Stensiö 1925) were the first fishes to have developed an elongated, streamlined body with posteriorly placed fins and long, slender jaws. This specialised morphology enabled *Saurichthys* Agassiz, 1834 to become an important piscine predator (*e.g.* Lombardo & Tintori 2005), which already occupied a top position within marine food webs in the Early Triassic, as is well-exemplified by the large body sizes of *S. dayi* and *S. ornatus* (>1.2 m standard length; see Mutter *et al*. 2008, Stensiö 1925). Saurichthyids also achieved their highest species richness and a virtually global distribution shortly after the end-Permian mass extinction. In the Early and Middle Triassic, *Saurichthys* occurred in both marine and fluvio-lacustrine environments at low and high palaeolatitudes. However, its distribution seemingly became more and more restricted to Euramerica towards the end of the Triassic (Fig. 9A), a trend that continued into the Early Jurassic with the saurichthyid *Saurorhynchus* Reis, 1892 (Gardiner 1960, Neuman & Wilson 1985, Thies 1985).

Cosmopolitanism and relatively high species richness of saurichthyids in the Early Triassic concur with the general faunal dispersal at that time. They may be related to recurrent episodes of a flat palaeolatitudinal sea-surface temperature gradient (*e.g.* Brayard *et al.* 2006) and reduced interspecific competition in the wake of the end-Permian mass extinction. The progressive restriction of saurichthyids to the north-western Tethyan realm accompanied by loss in global species richness could be a consequence of successive changes in global climate (see *e.g.* Preto *et al.* 2010), which partially led to extinction events within and at the end of the Triassic (*e.g.* Bucher 1989, Galfetti *et al.* 2007, Schaltegger *et al.* 2008). Among the victims of such extinction events were possibly the plesiomorphic saurichthyid morphotypes (see Discussion) that disappeared from marine environments during the late Early Triassic. The reduction in distribution and diversity of saurichthyids from the Early Triassic onwards, which contrasts the general trend towards increasing diversity within fishes during the Triassic (*e.g.* Friedman & Sallan

2012), could also be linked to increasing competition (*e.g.* with holosteans and teleosts) but the significance of this factor must be further explored.

Important morphological transformations in *Saurichthys* can be summarized as: the reduction of cranial ossifications, the shortening in the cheek region of the skull, the stiffening of the vertebral column and fins, and the gradual weight reduction of the integument of the trunk (Fig. 8). At least the postcranial trends have a great functional significance in enhancing the fish's fast-start capability and, thus, its efficiency as an ambush predator (see Rieppel 1985, 1992; Tintori 1990, 1998). The disappearance of saurichthyids in the late Early Jurassic despite this increasing specialisation may possibly uncover evolutionary limits set by the basal organization of these fishes. The saurichthyid morphotype, however, independently arose later in several groups of fishes from the extinct aspidorhynchids and dercetids to the extant lepisosteids and belonids, and can therefore be considered successful.

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