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European Journal of Taxonomy 321: 1–29
https://doi.org/10.5852/ejt.2017.321
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2017 · Maxwell E.E. & Stumpf S.

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Research article

urn:lsid:zoobank.org:pub:490DE895-000D-4995-9FAC-1F50DEB0DD0F

Revision of *Saurorhynchus* (Actinopterygii: Saurichthyidae) from the Early Jurassic of England and Germany

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Abstract. Saurichthyidae is a speciose group of fishes, ranging from the Late Permian to the Middle Jurassic. Early Jurassic saurichthyids are usually considered morphologically less disparate and taxonomically less diverse than their Triassic counterparts, consisting of only two valid species. These were historically differentiated almost entirely based on cranial ratios, and both had stratigraphic ranges spanning the Early Jurassic. Here, we revise the Early Jurassic saurichthyid fishes of Europe based on restudy of the type material of *Saurorhynchus brevirostris* (Woodward, 1895) and *S. acutus* (Agassiz, 1844). We identify four species based on cranial osteology: *S. acutus, S. brevirostris, S. anningae* sp. nov., and *S. hauffi* sp. nov. *Saurorhynchus brevirostris* and *S. anningae* sp. nov. are known from the Sinemurian of England only, whereas *S. acutus* and *S. hauffi* sp. nov. share a broad European distribution during the Toarcian, from southwestern Germany to England. *Saurorhynchus anningae* sp. nov. and *S. brevirostris*, in particular, show disparity in such ecomorphologically important traits as cranial fineness, and tooth and jaw morphology. In contrast, *S. acutus* and *S. hauffi* sp. nov. show much lower levels of disparity, differing from each other in nostril morphology, dermal ornamentation, and position of the lateral extrascapular. The new species do not increase diversity estimates for *Saurorhynchus* in either the Sinemurian or Toarcian interval.

Keywords. Early Jurassic, Actinopterygii, Saurichthyidae, Posidonienschiefer Formation, Charmouth Mudstone Formation.

Maxwell E.E. & Stumpf S. 2017. Revision of *Saurorhynchus* (Actinopterygii: Saurichthyidae) from the Early Jurassic of England and Germany. *European Journal of Taxonomy* 321: 1–29. https://doi.org/10.5852/ejt.2017.321

Introduction

Saurichthyidae is a speciose group of fishes, ranging from the Late Permian to the Middle Jurassic (Romano *et al.* 2012; Maxwell 2016). The genus *Saurichthys* Reis, 1892 encompasses all other named genera in phylogenetic analyses, but due to the long stratigraphic range and number of species, subgenera – monophyletic clades within *Saurichthys* – have been maintained for convenience (Maxwell

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et al. 2015). Jurassic saurichthyids are all considered to belong to the monophyletic *Saurorhynchus* species group (see Kogan 2016 for discussion of the higher taxonomic name *Saurorhynchus* Reis, 1892), and are known almost exclusively from Europe, with a single reported occurrence from the Toarcian of Canada (Neuman & Wilson 1985; reviewed by Maxwell 2016).

Saurichthyids are interpreted as piscivores based on both gastric contents and functional morphology (Rieppel 1985; Kogan *et al.* 2015; Renesto & Stockar 2015; Argyriou *et al.* 2016), and this is equally true of *Saurorhynchus* (Urlichs *et al.* 1994). However, Early Jurassic species of *Saurorhynchus* appear to have been much smaller than some of their Triassic relatives (~30–50 cm vs >100 cm in length (Romano *et al.* 2012)), and thus potentially occupied a lower trophic position. Although most saurichthyids have a long, slender body shape, *Saurorhynchus* is one of the deepest-bodied members of the clade (Maxwell *et al.* 2015). It is known from fully marine deposits only (Romano *et al.* 2012).

Historically, several species of *Saurorhynchus* have been proposed. Agassiz (1844) described *S. acutus* based on a partial skull from the Toarcian of Whitby, UK. He also named *"Aspidorhynchus" walchneri* from the Toarcian of Baden, Germany, and *S. anningiae* from the Sinemurian of Lyme Regis, UK. The latter names were unaccompanied by descriptions, figures, or cited specimens and so are *nomina nuda*. Woodward (1895) later described a second valid species, *S. brevirostris*, based on a skull from the Sinemurian (Forey *et al.* 2010) of Lyme Regis.

Material of *Saurorhynchus* from the Southwest German Basin is by far the most abundant and best studied of the global occurrences. The material from Württemberg was first reported as *Aspidorhynchus walchneri* (Quenstedt 1843) and subsequently figured under the names *Belonostomus acutus* and *Saurorhynchus acutus* (Quenstedt 1856–1858; Reis 1892). However, Woodward (1895) later included all the Toarcian material from Württemberg in his new Sinemurian species *Belonorhynchus brevirostris*. When Hauff (1938) reviewed the material from Holzmaden (Württemberg), he agreed with the species-level assessment of Woodward and classified the majority as *S. brevirostris* based on the short, deep mandible. The problem of holotypes and referred material coming from very different time intervals was compounded when Gardiner (1960) referred the bulk of the Sinemurian specimens of *Saurorhynchus* to *S. acutus*. Thus, a situation was created where two species, distinguished primarily based on cranial fineness, had stratigraphic ranges spanning the Early Jurassic. This situation is especially problematic since relative cranial length, and fineness in particular, is a common axis of morphological differentiation among closely related saurichthyids (Maxwell *et al.* 2015).

Clarification of the alpha taxonomy of *Saurorhynchus* is desirable for several reasons. As the youngest representative of Saurichthyidae, a better understanding of morphology within this species group will be helpful in understanding loss of diversity and disparity within the family as a whole. From a more practical perspective, a good description of the material from the classic localities of Germany and England will provide a list of characters useful for accurately identifying new finds, and thus for testing hypotheses relating to Early Jurassic biogeography and actinopterygian diversity. Moreover, *Saurorhynchus* falls in two very different positions in saurichthyid phylogeny depending on which species is studied: namely outside of the Middle Triassic Tethyan radiation when coded based on Sinemurian material referred to *S. acutus* (Wu *et al.* 2013), or nested within a clade of Middle-Late Triassic European species when coded based on Toarcian material referred to *S. brevirostris* (Maxwell *et al.* 2015). A detailed morphological study has the potential to reveal new phylogenetically informative characters that may help stabilize the position of the *Saurorhynchus* species group within Saurichthyidae. The objective of the current work is to clarify the taxonomic and morphological diversity of Early Jurassic saurichthyids from the UK and Germany following restudy of the type material of the two currently accepted species, *S. acutus* and *S. brevirostris*. We identify discrete morphological characteristics for use in specific identification of Early Jurassic saurichthyids.

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Material and methods

Specimens of *Saurorhynchus* from the following collections were studied, measured and photographed:

GG = Institut für Geographie und Geologie, Ernst-Moritz-Arndt-Universität Greifswald
GPIT = Geologisch-Paläontologisches Institut Tübingen
GZG = Geowissenschaftliches Zentrum, Georg-August-Universität Göttingen
MHH = Urwelt Museum Hauff
NHMUK = Natural History Museum, London
NLMH = Niedersächsisches Landesmuseum Hannover
NMB = Staatliches Naturhistorisches Museum Braunschweig
PMU = Palaeontological collections, Museum of Evolution, Uppsala University
SMNS = Staatliches Museum für Naturkunde Stuttgart

Stratigraphic and geographic provenance were also noted, where available.

Skull bones are described using the established terminology for Saurichthyidae (e.g., Rieppel 1985) in order to facilitate comparisons within the family; however please note that some of the terminology does not reflect homology with more distantly related groups (e.g., sarcopterygians). Saurichthyids are characterized by a marginal dentition composed of large teeth alternating with smaller teeth (Griffith 1978). We use the term "laniary teeth" to refer to these larger teeth. We use the term "incisivlücken" (Hauff 1938) to describe the depressions along the marginal premaxilla and dentary into which the tips of the opposing laniary teeth fit when the jaws are closed.

Geology

Early Jurassic saurichthyids are known from three formations in Germany and two from the UK, all fully marine. Less productive localities are known in France, Belgium, Luxembourg, and Canada (reviewed by Maxwell 2016); these will not be discussed here.

United Kingdom

Charmouth Mudstone Formation. The *Saurorhynchus* material from the area around Lyme Regis re-examined in the present study consists of historical collections, and thus generally lacks specific stratigraphic information. Based on lithological comparisons, Forey *et al.* (2010) surmised that this material originated from the Black Ven Mudstone Member of the Charmouth Mudstone Formation (?*Caenisites turneri* to *Echioceras raricostatum* Zones; latest early Sinemurian to late Sinemurian).

Whitby Mudstone Formation. As with the material from Lyme Regis, the Toarcian material from Whitby also lacks detailed stratigraphic context. However, potential provenance is restricted to the Whitby Mudstone Formation (early to middle Toarcian, *Dactylioceras tenuicostatum, Harpoceras serpentinum,* and *Hildoceras bifrons* Zones) (e.g., Benton & Spencer 1995).

Germany

Numismalismergel Formation. The Numismalismergel Formation is a succession of marls and marly limestones extending from the *Uptonia jamesoni* Zone to the *Amaltheus stokesi* Subzone (early Pliensbachian to earliest late Pliensbachian) (Arp 2012). This formation has yielded a single *Saurorhynchus* lower jaw (SMNS 96082) exposed as part and counterpart in a broken geode from the Eastern Swabian Alb locality of Hüttlingen.

Posidonienschiefer Formation. In southwestern Germany, the Posidonienschiefer Formation consists of marls, marly clays, and intercalated limestones, and spans three early to middle Toarcian ammonite zones: the *tenuicostatum, serpentinum,* and *bifrons* Zones (Riegraf *et al.* 1984). It was deposited over

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2.7–2.88 million years (Boulila *et al.* 2014). In the latest *tenuicostatum* Zone (*Dactylioceras semicelatum* Subzone), continuous deposition of organic-rich laminated black shales began, and continued through most of the *serpentinum* Zone (Röhl *et al.* 2001). Condensation horizons occur in the latest *serpentinum* Zone and the earliest *bifrons* Zone (Kauffman 1978; Röhl *et al.* 2001). The Posidonienschiefer Formation in the Southwest German Basin has been regionally subdivided into a series of beds denoted by Roman numerals with Arabic numerals as subscript. See Riegraf *et al.* (1984) for a correlation between this scheme and the ammonite zonation.

In southwestern Germany, specimens of *Saurorhynchus* are known from the latest *tenuicostatum* Zone to the end of the *serpentinum* Zone (see Hauff 1938 for approximate stratigraphic distribution and raw abundance data), a range of approximately 1.5–1.62 million years (Boulila *et al.* 2014). Most of the material consists of isolated skulls and skull fragments, strongly compressed and exposed in lateral view; however, rare articulated specimens have been recovered (Hauff 1938; Urlichs *et al.* 1994).

Material of *Saurorhynchus* is also known from the Posidonienschiefer Formation in northwestern Germany (Wunnenberg 1928; Thies 1985), from the area around Braunschweig and from the time-equivalent "Green Series" of Grimmen, northeastern Germany. Where detailed stratigraphic information is available, this material originates from the *Eleganticeras elegantulum* and *Cleviceras exaratum* Subzones of the *serpentinum* Zone. Many of the specimens described by Thies (1985) are in private collections and not accessible for study, with the exception of NLMH 70598 (specimen SWG 1 of Thies), GZG.V.27931 (352-1 of Thies), GZG.V.27932 (352-2 of Thies), and GZG.V.27933 (352-3 of Thies).

Jurensismergel Formation. The Jurensismergel Formation consists of alternating marls and marly limestones of late Toarcian age (Nitsch *et al.* 2015). It is relatively poor in vertebrate fossils. A single partial saurichthyid rostrum recovered from the lower part of this formation is non-diagnostic below family level (SMNS 96946); a partial skull is also known from the locality of Mistelgau on the eastern edge of the Southwest German Basin (Schulbert 2013).

Results

The type material of both currently recognized species, *Saurorhynchus acutus* and *S. brevirostris*, is from the UK. Here, we briefly review the two currently accepted species, before providing detailed descriptions for two new species identified during restudy of the referred material.

Actinopterygii Cope, 1887
Saurichthyidae Owen, 1860
Saurorhynchus Reis, 1892

Saurorhynchus acutus (Agassiz, 1844)
Figs 1A, 2D, 4D, 5A–B

Belonostomus acutus Agassiz, 1844: 142, pl. 47a, fig. 4.
Acidorhynchus brevirostris Stensiö, 1925, partim: 176.

Acidorhynchus brevirostris – Hauff 1938, partim: pl. 22, fig. d. — Wenz 1967: pl. II, fig. A.

Revised diagnosis

Anterior narial opening narrow and elongate; maxilla strongly dorsoventrally compressed and ventrally deflected suborbitally such that the contact with the premaxilla occurs at an angle; posterior dorsal skull parallel to the long axis of the skull; postorbital segment approximately equal in length to the maximum depth of the lower jaw; parasphenoid edentulous ventral to the orbit; foramen for the internal carotid

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and efferent pseudobranchial arteries centered within the basisphenoid (sensu Wenz 1967); lateral extrascapular fused to lateral dermopterotic and not extending dorsal to the hyomandibula; posterior edge of the mandible strongly sinusoidal; angle between the posterior and ventral edges of the mandible less than 80 degrees; subnarial laniary dentition absent; acrodin caps of the posterior laniaries straight.

Material studied

Holotype

UNITED KINGDOM: Toarcian of Whitby (NHMUK PV P 4268, Fig. 1A).

Referred material

GERMANY: all referred material consists of isolated skulls. Bisingen (SMNS 56923, Fig. 5A); Holzmaden (SMNS 57039 (Fig. 5B), SMNS 88007); Holzmaden, εII_3 (PMU 30009); Holzmaden, εII_4 (SMNS 50924, MHH 17); Holzmaden, εII_6 (SMNS 55324, PMU 30010); Ohmden (NHMUK PV P 3792, NHMUK PV P 36222, NHMUK PV P 36223, SMNS 55319, SMNS 87738, GPIT/OS/133); Ohmden, εII_3 (SMNS 51009); Ohmden, εII_4 (SMNS 50268); Ohmden, εII_5 (SMNS 96927, SMNS 96927); Schandelah, *serpentinum* Zone (GZG.V.27932).

Description

Saurorhynchus acutus is anatomically very similar to the Toarcian *S. hauffi* sp. nov., described in detail in a subsequent section. The following brief description is designed only to differentiate the two species, to clarify general osteological nomenclature within *Saurorhynchus*, and to describe parts of the anatomy not preserved in *S. hauffi* sp. nov.

No well-preserved postcranial material is available for *Saurorhynchus acutus*. Skull length (tip of rostrum to jaw joint, and corresponding to the length of the dermatocranium when measured along the dorsal midline) of the largest referred specimen is 125 mm (Appendix 1). Assuming similar proportions to *S. hauffi* sp. nov., fork length is estimated at 44 cm for large individuals of *S. acutus*. All the skulls examined in the course of this study were severely compressed, making the cranial sutures difficult to differentiate.

There is no clear evidence for interrostral bones. The anterior narial opening is an elongate anteroventrally inclined slit. When the skull is viewed dorsolaterally, it is evident based on the orientation and lipping along the anterior external narial opening that it is functionally situated more dorsally than the posterior narial opening. The suborbital bar of the maxilla is strongly dorsoventrally compressed ventral to the orbit and is also ventrally deflected such that it meets the rostropremaxilla at an angle ventral to the external narial opening. This creates the impression of proportionately large, round orbits. The suture between the maxilla and premaxilla is interdigitating, differing from some of the Toarcian material of *Saurorhynchus* from France and Northern Germany (Wenz 1967; Thies 1985). In some specimens, the ornamentation on the skull roof is drastically reduced and simplified, consisting mainly of pitting and being slightly more reticular only in the region of the parietals (e.g., Fig. 5B).

Unlike in *S. brevirostris,* the dorsal skull roof extends posteriorly without strong dorsal deflection. The element sutured to the posterolateral dermopterotic has been documented in *Saurorhynchus* by several authors, and has been variously interpreted as the squamosal (Reis 1892), fused suprascapular-supracleithrum (Gardiner 1960), or extrascapular (Hauff 1938). It does not participate in the cranial midline, and extends slightly further posteriorly than the dermopterotic. We interpret this element as a lateral extrascapular, following the discussion about the homology in Kogan & Romano (2016). The posterior elongation of the skull roof in *S. acutus* relative to *S. hauffi* sp. nov. is partly accomplished through the posterior displacement of the lateral extrascapular relative to the dermopterotic (Fig. 5B, D). The lateral extrascapular and the dermopterotic are fused, such that it is difficult to see the suture

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Fig. 1. Holotype specimens of Early Jurassic saurichthyids. **A**. *Saurorhynchus acutus* (Agassiz, 1844) (NHMUK PV P 4268). **B**. *Saurorhynchus brevirostris* (Woodward, 1895) (NHMUK PV OR 40726). **C**. *Saurorhynchus anningae* sp. nov. (NHMUK PV P 3791). **D–E**. *Saurorhynchus hauffi* sp. nov. (SMNS 55057). Scale bars: A, C = 20 mm; E = 50 mm. Photos A–C © The Trustees of the Natural History Museum, London.

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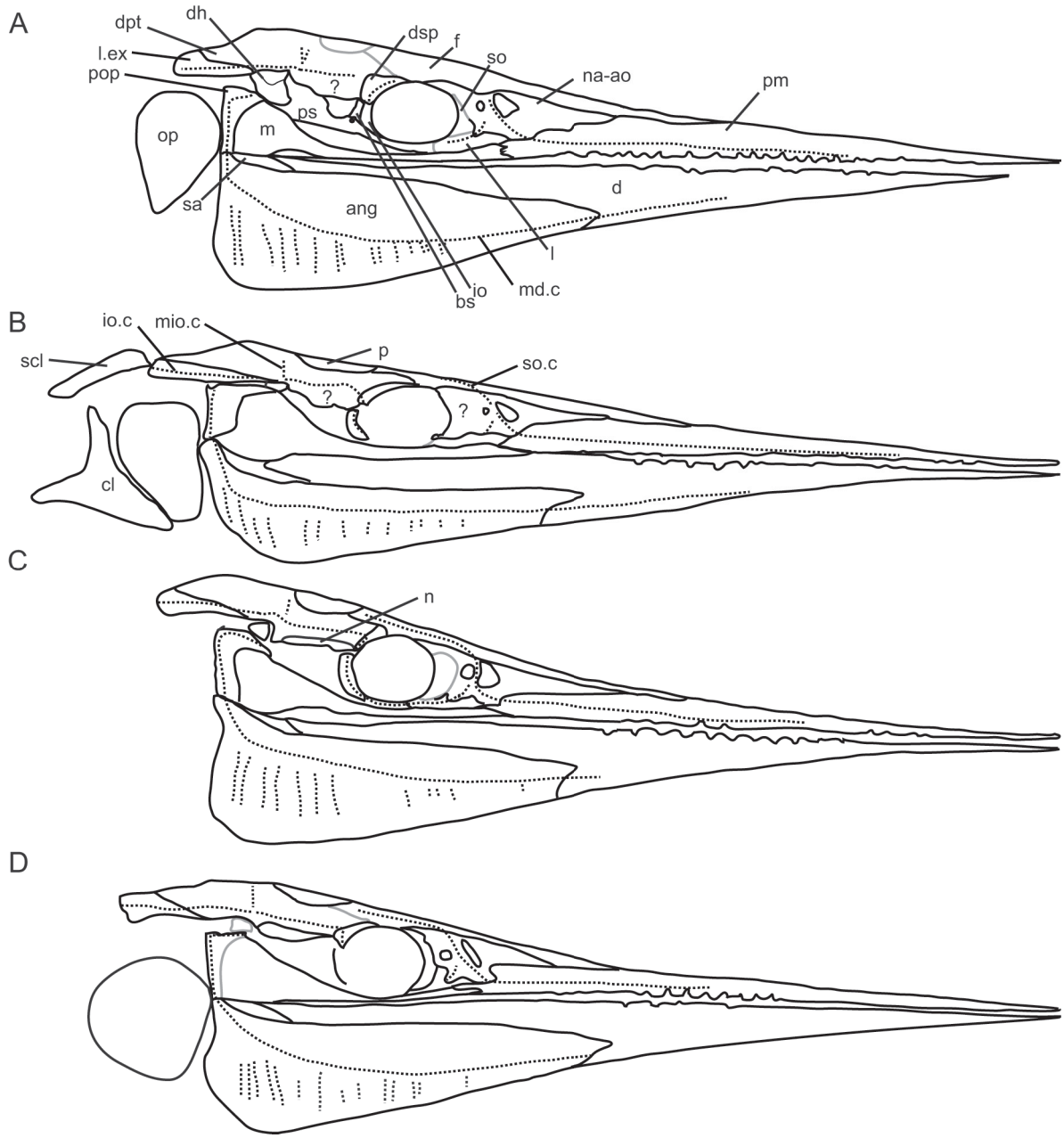

Fig. 2. Reconstruction of the dermal skull in Early Jurassic saurichthyids. **A**. *Saurorhynchus brevirostris* (Woodward, 1895). **B**. *Saurorhynchus anningae* sp. nov. **C**. *Saurorhynchus hauffi* sp. nov. **D**. *Saurorhynchus acutus* (Agassiz, 1844). Not to scale. Dashed lines indicate sensory canals, grey lines indicate bones that were present but where the exact location of the sutural contact is unclear, and question marks indicate areas of uncertainty. Abbreviations: ang = angular; bs = basisphenoid; cl = cleithrum; d = dentary; dh = dermohyal; dpt = dermopterotic; dsp = dermophenotic; f = frontal; io = infraorbital; io.c = infraorbital sensory canal; l = lacrimal; l.ex = lateral extrascapular; m = maxilla; md.c = mandibular sensory canal; mio.c = medial branch of the infraorbital sensory canal; n = neomorph; na-ao = nasaloantorbital; op = opercle; p = parietal; pm = rostropremaxilla; pop = preopercle; ps = parasphenoid; sa = supraangular; scl = supracleithrum; so = supraorbital; so.c = supraorbital sensory canal.

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along parts of its length. On the ventral surface of the dermal skull roof, two ridges run longitudinally between the orbits, dividing the interorbital surface into thirds. On the lateral side of the ridges, numerous foramina are located between the ridge and the ventral surface of the frontals. Such ridges have been interpreted as part of the neurocranium in the orbitotemporal region (Maxwell *et al.* 2016). The space between these ridges is filled with broken, cancellous bone tissue.

The palate is exposed in a single specimen (SMNS 50924). The dermopalatine extends as far anteriorly as the posterior external narial opening. It is convex in ventral view, broadening in a medial direction. It bears denticles; these are smaller and blunter than those of the other tooth-bearing elements. Anteriorly, it articulates with the maxilla laterally; posteriorly it articulates with the parasphenoid medially and, posterior to this, the entopterygoid. There is no lateral palatal foramen, but because the parasphenoid is not anteriorly expanded, a medial foramen exists between the anterior dermopalatine and parasphenoid. The ectopterygoid is very small and triangular. The portion of the parasphenoid posterior to the anterior edge of the orbit is edentulous; more anteriorly it bears small denticles.

The anteriormost point of the angular is located on the ventral half of the lower jaw. The ventral part of the angular-dentary suture is posteroventrally angled and straight, forming a simple 'v'. The teeth are largest at the midpoint of the rostrum and become much smaller anteriorly. In no specimens was corrugation of the collar ganoine observed.

The opercle is preserved in a single specimen (PMU 30010). This element is 13.6 mm high and 13.9 mm long, and ornamented with elongate pits radiating from the palatoquadrate articulation. In overall shape it is more ovate than in *Saurorhynchus brevirostris*.

Remarks

Woodward (1895) outlined a series of characters to diagnose *S. acutus*, the majority of which cannot be observed in the type material and were drawn from observation of specimens from the much older Charmouth Mudstone Formation. Upon re-examination of the type material, Woodward (1899) clarified that the posterior (backwards) extension of the skull roof was the main feature uniting the Toarcian type and Sinemurian referred specimens, even though he had reservations that a species was likely to have such a long stratigraphic range.

Our observations suggest that the type specimen of *S. acutus* can be unambiguously differentiated from the older Sinemurian material by the short distance between the posterior edge of the orbit and the articular facet for the hyomandibula relative to the length of the orbit. These measurements fall along a single anteroposterior line, and thus are not expected to be significantly influenced by distortion. In addition, the narial opening in the holotype specimen of *S. acutus* is narrower than in the material from the Charmouth Mudstone. The syntype specimen figured by Agassiz (1844), NHMUK PV P 961a and its (unfigured) counterslab NHMUK PV P 36219 are non-diagnostic below family level. The holotype is consistent with a large number of specimens of *Saurorhynchus* from the Toarcian of Germany, and when the additional anatomical information present in this referred material is considered it becomes clear that large differences exist between the Sinemurian and Toarcian specimens. The revised diagnosis is constructed based on the referred material from Germany, as well as on the holotype.

Occurrence

Early Jurassic, Toarcian, Whitby (type locality); Toarcian, *tenuicostatum* Zone, *semicelatum* Subzone to *serpentinum* Zone, Baden-Württemberg, Germany; *serpentinum* Zone, Lower Saxony, Germany (referred material).

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Saurorhynchus brevirostris (Woodward, 1895)
Figs 1B, 2A, 4B–E, 6A

Belonorhynchus brevirostris Woodward, 1895, partim: 17–18, pl. II, fig. 2.

Saurorhynchus brevirostris – Forey *et al.* 2010: 352, pl. 65, fig. 6.

Revised differential diagnosis

The diagnosis is constructed based on the holotype and referred material housed at the NHMUK. This species can be differentiated from all other *Saurorhynchus* species by the following combination of characters: short, deep skull, overbite consistently present (overbite slight or absent in *S. acutus*); posterior dorsal skull roof deflected dorsally relative to the long axis of the skull (parallel in *S. acutus*); postorbital segment approximately equal in length to the depth of the lower jaw; anterior narial opening large and triangular in outline with the apex directed toward the mandible (narrow and elongate in *S. acutus*); foramen for the internal carotid and efferent pseudobranchial arteries positioned posterolaterally within the basisphenoid, exposing the large foramen of the ophthalmica magna artery on the anterolateral surface of the basisphenoid; posterior edge of the mandible weakly sinusoidal (strongly sinusoidal in *S. acutus*); angle between the posterior and ventral edges of the mandible less than 80 degrees; subnarial laniaries well-developed with acrodin caps directed lingually (subnarial laniaries absent and all acrodin caps straight in *S. acutus*); mandibular sensory canal closer to the dorsal than ventral edge of the posterior mandible. Opercle strongly wedge-shaped; lateral supracleithrum bearing prominent anterior process pierced by a foramen; pectoral radials well-ossified.

Material studied

Holotype

UNITED KINGDOM: Lyme Regis (NHMUK PV OR 40726) (Fig. 1B). A skull with partial pectoral girdle preserved in lateral view. This specimen is probably from the Charmouth Mudstone Formation, Black Ven Mudstone Member, latest early Sinemurian to late Sinemurian (Forey *et al.* 2010).

Remarks

Here we restrict usage of *S. brevirostris* to material from the Lower Lias. The anterior tip of the holotype skull is missing, but in the largest referred specimen skull length (tip of rostrum to jaw joint) is 86 mm (Suppl. Table 1). Assuming similar proportions to *S. hauffi* sp. nov., fork length is estimated at up to 30 cm for *S. brevirostris*.

Saurorhynchus anningae sp. nov.
urn:lsid:zoobank.org:act:F16C4AFF-4A3B-4C35-8902-F95446F9B1EB
Figs 1C, 2B, 3A, 4A, 6B, 7A

Belonorhynchus acutus – Woodward, 1890: pl. 8, fig. 7. — Woodward 1895, partim: 14–15, pl. 2, fig. 1.
Acidorhynchus acutus – Stensiö 1925: 178, fig. 58.
Saurorhynchus acutus – Gardiner 1960, partim: 272–280, figs 19–21. — Forey *et al.* 2010: 350–352, pl. 65, fig. 5.

Etymology

Name modified from that derived by Agassiz (1844) in honour of Mary Anning, an important fossil collector from Lyme Regis.

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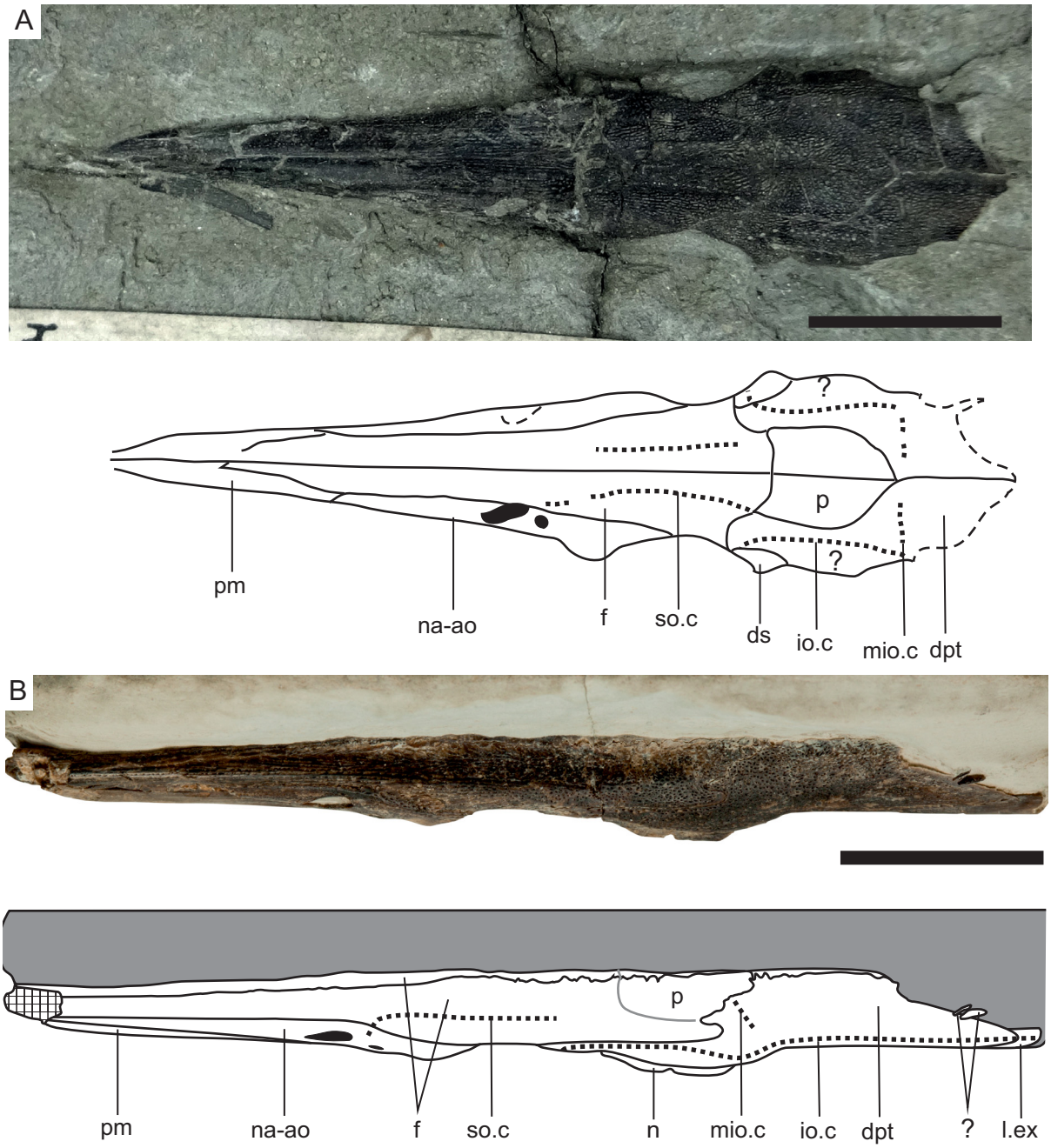

Fig. 3. Dorsal skull roof. **A**. *Saurorhynchus anningae* sp. nov. (NHMUK PV P 964); note that this skull has been dorsoventrally compressed. **B**. *Saurorhynchus hauffi* sp. nov., three-dimensionally preserved skull GG 20001. Fine dashed lines indicate sensory canals, large dashes indicate broken or incomplete areas; grey lines indicate bones that were present but where the exact location of the sutural contact is unclear, and question marks indicate areas of uncertainty. Abbreviations: dpt = dermopterotic; dsp = dermophenotic; f = frontal; io = infraorbital; io.c = infraorbital sensory canal; l.ex = lateral extrascapular; mio.c = medial branch of the infraorbital sensory canal; n = neomorph; na-ao = nasaloantorbital; p = parietal; pm = rostropremaxilla; so.c = supraorbital sensory canal. Scale bars = 10 mm. A. Photo © The Trustees of the Natural History Museum, London.

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Material studied

Holotype

UNITED KINGDOM: a skull and pectoral girdle preserved in lateral view (NHMUK PV P 3791, Fig. 1C).

Stratum typicum

UNITED KINGDOM: Lower Lias. Based on lithological comparisons, most likely the Black Ven Member of the Charmouth Mudstone Formation (Forey *et al*. 2010).

Locus typicus

UNITED KINGDOM: Lyme Regis, Dorset.

Differential diagnosis

This species can be differentiated from all other species of *Saurorhynchus* by the following combination of characters: slender, elongate skull (length to depth greater than in *S. brevirostris*); posterior dorsal skull roof essentially parallel to the long axis of the skull; postorbital segment much longer than the depth

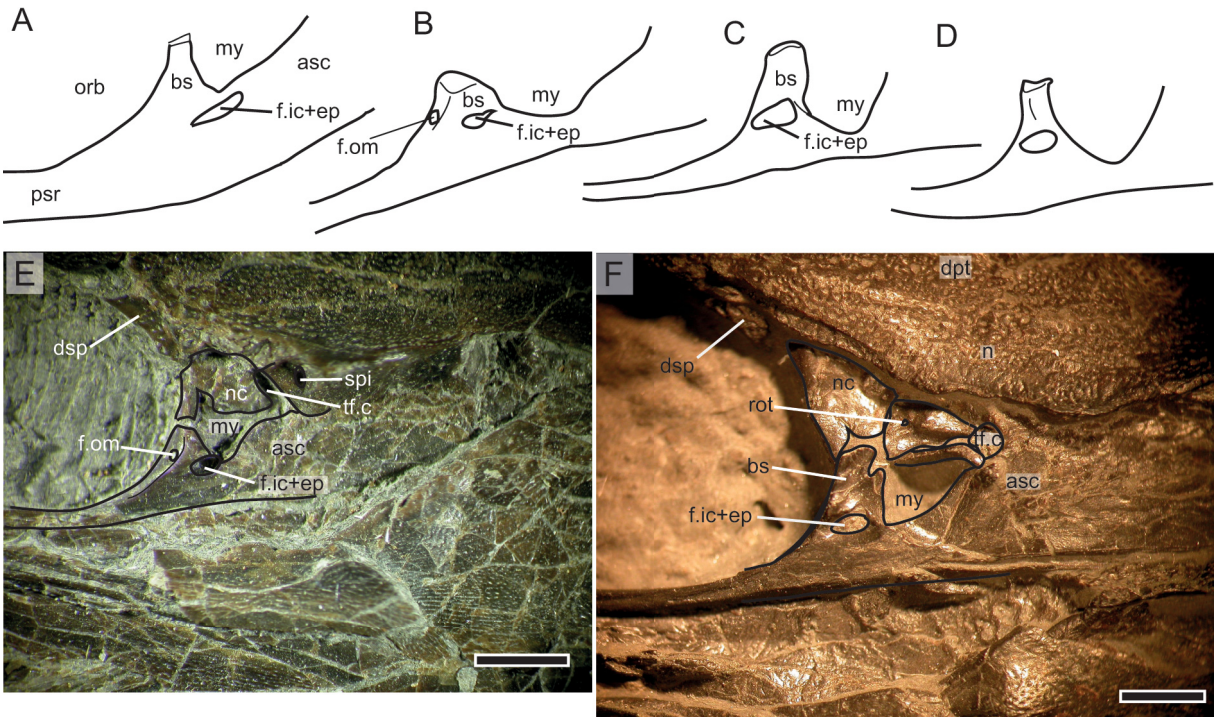

Fig. 4. Orbitotemporal region, illustrating variation in the braincase of Early Jurassic saurichthyids. **A**. *Saurorhynchus anningae* sp. nov. (based on NHMUK PV P 36227). **B, E**. *Saurorhynchus brevirostris* (Woodward, 1895) (photo pertains to NHMUK PV P 4878, mirrored). **C, F**. *Saurorhynchus hauffi* sp. nov. (photo is of SMNS 51888, mirrored). **D**. *Saurorhynchus acutus* (Agassiz, 1844) (based on SMNS 87737). Abbreviations: asc = ascending process of the parasphenoid; bs = basisphenoid; dpt = dermopterotic; dsp = dermosphenotic; f.ic+ep = foramen for the internal carotid artery and efferent pseudobranchial artery; f.oma = f.om = foramen for the great ophthalmic artery; my = posterior myodome; n = neomorph; nc = neurocranium; orb = orbit; psr = parasphenoid rostrum; rot = foramen for the lateral otic ramus; spi = ventral opening of the spiracular canal; tf.c = trigeminofacial chamber. Scale bars: E–F = 2 mm. E. Photo © The Trustees of the Natural History Museum, London.

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of the lower jaw (almost double) and double the length of the orbit (unlike in *S. acutus*); anterior external narial opening teardrop shaped, widening ventrally; parasphenoid rostrum bearing small denticles ventral to the orbit; foramen for the internal carotid and efferent pseudobranchial arteries displaced posteriorly relative to the basisphenoid and almost entirely enclosed by the parasphenoid (unlike in *S. brevirostris, S. acutus*); posterior edge of mandible straight or only weakly sinusoidal, becoming gradually rounded ventrally; angle between the posterior and ventral edges of the mandible greater than 90 degrees; acrodin caps of posterior laniaries not directed lingually (unlike in *S. brevirostris*); opercle roughly triangular in shape, tapering ventrally.

Description

The material referred herein to *S. anningae* sp. nov. has been well-described by Gardiner (1960) as *S. acutus*. The following description focuses on details in which our interpretations differ from those of Gardiner, or those structures for which additional details can be noted.

The holotype skull is only 89 mm long, however the largest skull referable to *S. anningae* sp. nov. is 137 mm in length (Suppl. Table 1). Assuming similar proportions to *S. hauffi* sp. nov., fork length is estimated at 48 cm in the largest individuals.

The antorbital rostrum is composed of the rostropremaxilla, nasaloantorbitals, and frontals. There are two external narial openings, the anterior of which is teardrop shaped and somewhat narrower than reconstructed by Gardiner. The posterior narial opening is small and circular in outline. The suture between the maxilla and premaxilla occurs ventral to the nares. Between the maxilla and the nasaloantorbital is an extremely weakly ossified area that would have borne the infraorbital canal. This space corresponds to the lacrimal, and is more anteriorly extensive than in Gardiner's reconstruction. Gardiner noted interrostral elements in some of the specimens he examined; we could not confirm the presence of these separate ossifications during restudy of the material. He also noted separate nasal and antorbital ossifications; this observation appears to be based on post-mortem breakage.

The frontal plays a small role in the dorsal edge of the orbit (Fig. 3A). Posterior to the lateral frontal is a small, triangular dermosphenotic, which carries the infraorbital sensory canal and excludes the dermopterotic from the orbit. Ventral to the dermosphenotic is a curved element forming the posterior edge of the orbit and carrying the infraorbital sensory canal; this was identified by Gardiner as the dermosphenotic but is here considered to be the penultimate infraorbital. In some of the most heavily ossified specimens, this element can be quite robust and heavily ornamented.

The lateral extrascapular extends as far anteriorly as the hyomandibula-dermopterotic articulation, unlike in *S. acutus*, and more anteriorly than in Gardiner's reconstruction. A dermohyal is present, fused to the lateral surface of the dorsal hyomandibula (as noted by Gardiner 1960). The opercle is also as described by Gardiner.

None of the specimens examined in the present study had a well-preserved ascending process of the parasphenoid, so the posterior position of the foramen for the orbital artery could not be confirmed. Anterior to the ascending process, the parasphenoid bears denticles along its ventral surface. In lateral view, the foramen for the internal carotid and efferent pseudobranchial arteries lies ventral to the opening for the posterior myodome (Fig. 4A), rather than ventral to the anterior basisphenoid as in Toarcian species (Wenz 1967; Thies 1985).

The mandible consists of three elements in lateral view: the dentary, angular and supraangular. The configuration of the angular-dentary suture reconstructed by Gardiner (1960) is incorrect, as argued

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elsewhere (Griffith 1962). The angular is extensively exposed along the lateral lower jaw, and extends anteriorly approximately as far as the anterior edge of the nasaloantorbital.

The dentary and rostropremaxilla bear large (laniary) teeth, each flanked by a pair of smaller teeth. Laniary teeth are all positioned well anterior to the external narial openings. The posteriormost laniary teeth have relatively straight crowns with acrodin caps, which fit into corresponding pits in the opposite jaw (incisivlücken). Among the posteriormost laniary teeth, the upper teeth overlap the dentary, resulting in incisivlücken on the lateral lower jaw, whereas the lower jaw is slightly narrower and so the laniaries do not project outside the mouth, resulting in an absence of incisivlücken on the lateral surface of the posterior premaxilla (Fig. 6B). The largest teeth are found in the middle of the tooth row; the anteriormost laniary teeth are quite small, similar in size to the flanking teeth. All teeth consist of an acrodin cap, a lightly corrugated region of collar enamel, and an uncorrugated base. Plicidentine appears to be developed around the very base of the tooth, but does not form external ridges above the level of the jawbone. The difference in tooth shape observed between posterior and anterior teeth in *S. brevirostris* is absent.

Few specimens are available with well-preserved postcrania. The holotype specimen preserves a discrete supracleithrum bearing ornamentation on its external surface (Fig. 1C). A triradiate cleithrum is also present. NHMUK PV P 3790 preserves the most complete postcranium. The neural arch-like elements are small and blocky, similar to those of many saurichthyids. Anteriorly, neural spines are small or absent, and elongate anterior and posterior zygapophyses overlap to form a lattice. In the region around the median fins, neural spines appear to be present, but poor preservation makes this homology interpretation questionable. Haemal spines are preserved in a 1:1 relationship with the neural arch-like elements along the posterior part of the block, dorsal to some poorly preserved anal axonosts. The haemal spines are elongate and bifurcate ventrally. Only a single scale row is present anterior to the median fins, the mid-dorsal scale row (Fig. 7A). The scales are smooth and needle-like, tapering at their anterior and posterior ends. Posterior to the anal axonosts, a mid-ventral scale row is also present.

Remarks

Agassiz (1844: 143 in pt. 2) originally coined the name "*Belonostomus anningiae*" for specimens of *Saurorhynchus* from the Lower Lias of the UK, but failed to describe the material or identify a holotype. Subsequently, Woodward (1888) figured a non-diagnostic specimen as *B. anningiae*, but did not provide a description either and subsequently synonymized *B. anningiae* with *Saurorhynchus acutus* (Woodward 1895). Thus, the name *Saurorhynchus anningiae* is considered a *nomen nudum*, and is still available for the longirostrine material from the Charmouth Mudstone Formation (Sinemurian) of the UK as per the original intention of Agassiz.

Occurrence

This species is currently known from the "Lower Lias" of Lyme Regis and Charmouth (UK) only. Based on lithological comparisons, Forey *et al.* (2010) surmised that the material of *S. anningae* sp. nov. at the NHMUK originated from the Black Ven Mudstone Member of the Charmouth Mudstone Formation (?*turneri* to *raricostatum* Zones; latest early Sinemurian to late Sinemurian). The single specimen for which more specific stratigraphic provenance is available, NHMUK PV P 27569 from the *Oxynoticeras oxynotum* Zone (late Sinemurian), falls within this range.

Saurorhynchus hauffi sp. nov.
urn:lsid:zoobank.org:act:CF1D94D7-EE54-4E13-B059-97C2536D27FA
Figs 1D–E, 2C, 4C, F, 5C–D, 6C, 7B–D

Belonostomus acutus Quenstedt, 1856–1858: pl. 29, fig. 8.

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Belonorhynchus brevirostris Woodward, 1895: 18 (partim).

Belonorhynchus brevirostris –Woodward 1899: fig. 1
Acidorhynchus brevirostris – Hauff 1938 partim: pl. 22, figs b,c. — Thies (1985) partim: pl. 1, figs 1, 5.
Saurorhynchus brevirostris – Hauff & Hauff 1981: fig. 76. — Urlichs *et al.* (1994): fig. 79. — Böttcher (1998): fig. 7.15.

Etymology

Named in honour of Bernhard Hauff, whose doctoral dissertation described the saurichthyid fishes from the Holzmaden region.

Material studied

Holotype

GERMANY: Articulated skeleton lacking median and pelvic fins (SMNS 55057, Fig. 1D). Although the skull of this specimen is not perfectly preserved, it was selected as the holotype based on the presence of extensive postcranial material.

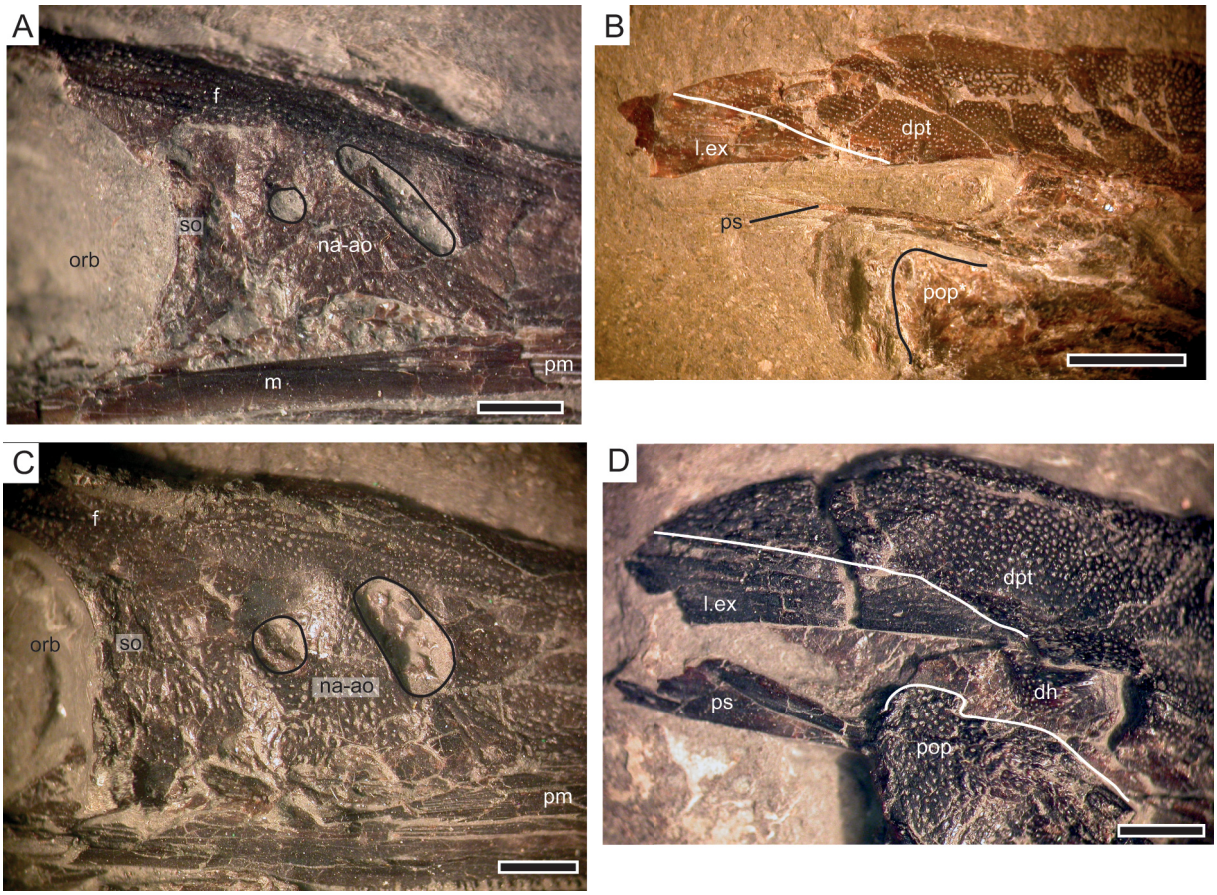

Fig. 5. Characters distinguishing *Saurorhynchus acutus* (Agassiz, 1844) and *S. hauffi* sp. nov. **A**. *S. acutus*, narial region (SMNS 56923). **B**. *S. acutus*, lateral extrascapular-dermopterotic contact (SMNS 57039). **C**. *S. hauffi* sp. nov., narial region (SMNS 51888). **D**. *S. hauffi* sp. nov., lateral extrascapular-dermopterotic contact (SMNS 53980, mirrored). Abbreviations: dpt = dermopterotic; dh = dermohyal; f = frontal; l.ex = lateral extrascapular; m = maxilla; na-ao = nasaloantorbital; orb = orbit; pm = rostropremaxilla; pop = preopercle; pop* = damaged preopercle; ps = parasphenoid; so = supraorbital. Scale bars: A, C–D = 2 mm; B = 5 mm.

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Referred material

GERMANY: all referred material consists of isolated skulls, unless otherwise noted. Bad Boll, $\varepsilon II_{10–12}$ (SMNS 96878/1); Dotternhausen, εII_4 (SMNS 51007, Fig. 6C); Dotternhausen, εII_6 (SMNS 58394); Haverlahwiese, *elegantulum* Subzone (NLMH 70598); Holzmaden, εII_3 (MHH 2); Holzmaden, εII_4 (SMNS 55302); Grimmen, *exaratum* Subzone (GG 20001, Fig. 3B); Ohmden (SMNS 53980, Fig. 5D); Ohmden, εII_3 (SMNS 50075); Ohmden, εII_4 (SMNS 51888, Figs 4F, 5C); Schandelah, *exaratum* Subzone (GZG.V.27931); Schandelah, *serpentinum* Zone, articulated skeleton, caudal region and median fins absent (NMB 373).

UNITED KINGDOM: Whitby, Toarcian (NHMUK OR 39153).

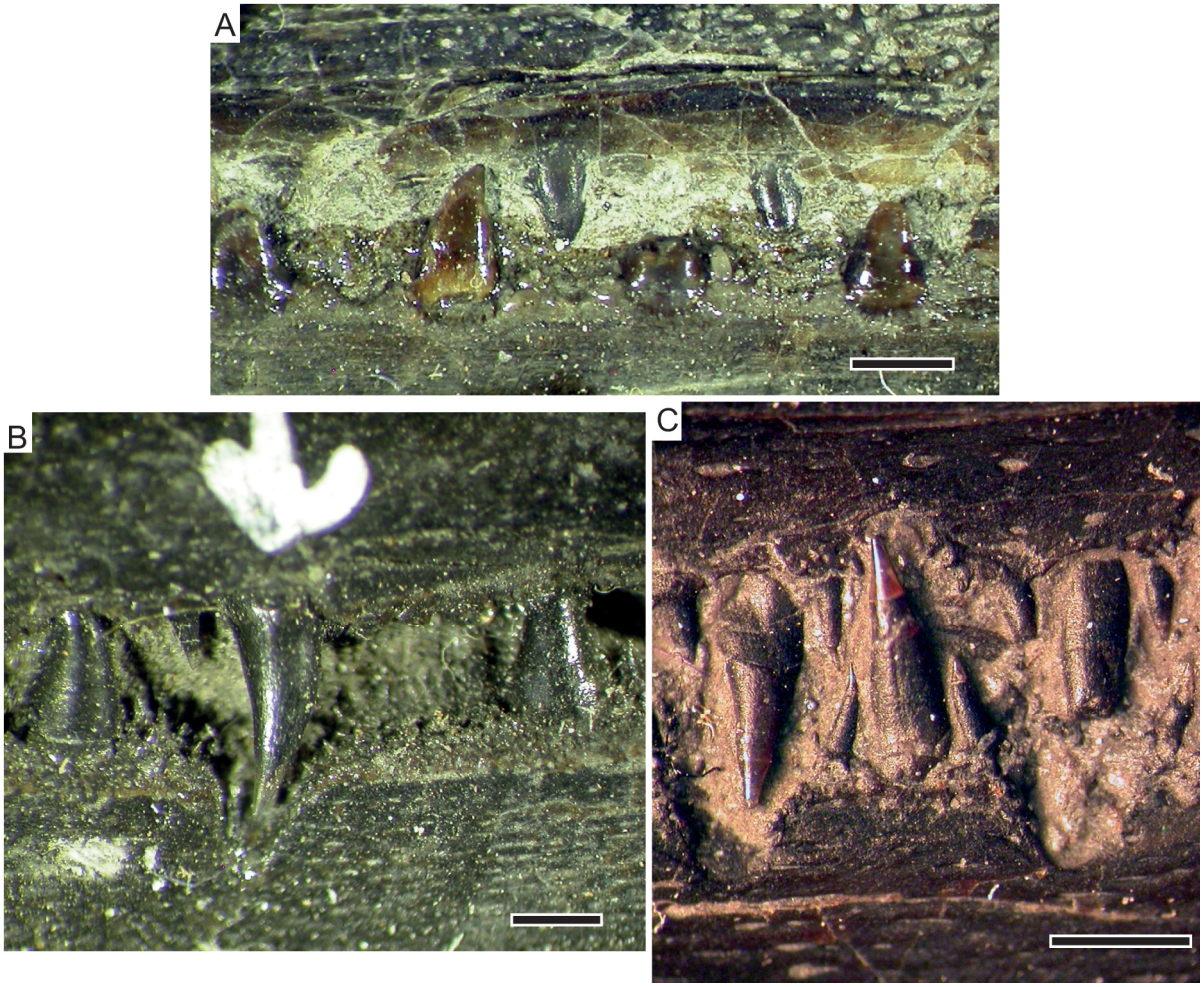

Fig. 6. Posteriormost laniary dentition. **A**. *Saurorhynchus brevirostris* (Woodward, 1895) (NHMUK PV P 4878), note the lingually curved crowns. **B**. *Saurorhynchus anningae* sp. nov. (NHMUK PV P 27569), note the incisivlücke associated with the premaxillary laniary tooth and the absence of lateral crypts associated with the two flanking mandibular laniaries. Photos © The Trustees of the Natural History Museum, London. **C**. *S. hauffi* sp. nov. (SMNS 51007), mid-rostral dentition illustrating the relationship between the incisivlücken, laniaries, and flanking smaller teeth. Scale bars: 1 mm

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Stratum typicum

GERMANY: Posidonienschiefer Formation, horizon εII4 (uppermost *semicelatum* Subzone-lowermost *exaratum* Subzone).

Locus typicus

GERMANY: Zell unter Aichelberg, Baden-Württemberg.

Differential diagnosis

This species can be differentiated from all other *Saurorhynchus* species by the following combination of characters: short, deep skull; posterior dorsal skull roof deflected dorsally relative to the long axis of the skull (parallel in *S. acutus* and *S. anningae* sp. nov.); postorbital segment approximately equal in length to the depth of the lower jaw (approximately twice as long in *S. anningae* sp. nov.); overbite slight or absent (unlike in *S. brevirostris*); maxilla not ventrally deflected under the orbit (unlike in *S. acutus*); coarse, reticular ornamentation on the dermal bones of skull roof (ornamentation reduced in *S. acutus*); parasphenoid edentulous ventral to the orbit (unlike in *S. anningae* sp. nov.); foramen for the internal carotid and efferent pseudobranchial arteries centered ventral to the anterior basisphenoid and oriented laterally (unlike in *S. anningae* sp. nov. and *S. brevirostris*); foramen for the ophthalmica magna artery situated between two ridges on the anterior surface of the basisphenoid (anterior surface of basisphenoid flat and foramen oriented anterolaterally in *S. brevirostris*); posterior edge of mandible strongly sinusoidal (straight or only weakly sinusoidal in *S. brevirostris* and *S. anningae* sp. nov.); angle between the posterior and ventral edges of the mandible less than 80 degrees (more than 90 degrees in *S. anningae* sp. nov.); mandibular sensory canal positioned along the dorsal half of the posterior mandible; anterior narial opening ovate (elongate in *S. acutus*); subnarial laniary teeth absent (unlike in *S. brevirostris*); lateral supracleithrum bearing prominent anterior process pierced by a foramen.

Description

As with *S. anningae* sp. nov., material now attributed to *Saurorhynchus hauffi* sp. nov. has been previously described (Hauff 1938; Thies 1985). However, as much of the material on which the initial descriptions were based is referable to *S. acutus*, a redescription is necessary. *S. hauffi* sp. nov. exhibits lower jaw lengths of up to 115 mm (Suppl. Table 1); this would correspond to a fish approximately 40 cm in length.

The rostropremaxilla is the dominant bone in the rostrum, dorsoventrally compressed at the anterior tip and becoming strongly laterally compressed posteriorly. The posterior rostropremaxilla bears a ventral process that forms an overlapping suture with the maxilla ventral to the external narial openings, as well as a dorsal process that approaches the anterior narial opening. Between these two processes, an anterior ventral process of the nasaloantorbital bearing the sensory canal is enclosed. The rostropremaxilla is ornamented with longitudinal grooves. Incisivlücken are lacking at the anteriormost tip. The rostropremaxilla bears approximately 30 laniary teeth. The anterior teeth are very small, and become progressively larger towards the midpoint of the jaw. The sensory pit line runs along the lateral surface of the premaxilla immediately dorsal to tooth row. The sensory pits become increasingly obscured by incisivlücken anteriorly. The presence or absence of interrostrals could not be confirmed.

The maxilla extends anteriorly as far as the first laniary tooth. The suborbital bar is dorsoventrally compressed and bears denticles on its occlusal surface. Posterior to the orbit and anterior to the deepest point of the posterior lamina, a small concave embayment is present along the ventral edge of the maxilla. The postorbital lamina is ornamented with pits, the more posterior of which are elongated in such a way that they appear directed towards the suborbital bar.

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The nasaloantorbital is triangular in lateral view. The posterior end encloses two external narial openings: a small, round posterior opening and a large, oval to reniform anterior opening (Fig. 5C). Between the two narial openings runs the supraorbital sensory canal. This canal splits into two branches ventrally; the junction is contained within the nasaloantorbital. Because the lacrimal is often damaged or missing, the ventral edge of the nasaloantorbital is often clearly exposed and has a complex morphology dictated by the orientation of the canals. There is no evidence for separate ossifications of the nasal and antorbital. The nasaloantorbital articulates with the frontal dorsally and the premaxilla ventrally. Ornamentation can be quite strong in the around the narial openings, but becomes reduced anteriorly. Between the posterior narial opening and the orbit is an area of strong dermal ornamentation associated with an element posterior to the nasaloantorbital and excluding it from contact with the anterior orbital margin. This element appears to be anamesic and is tentatively identified as a supraorbital.

The orbital series is heavily ossified. The frontal is not excluded from the dorsal edge of the orbit (Fig. 3B), in contrast to previous reconstructions (Hauff 1938; Thies 1985). The lacrimal is weakly

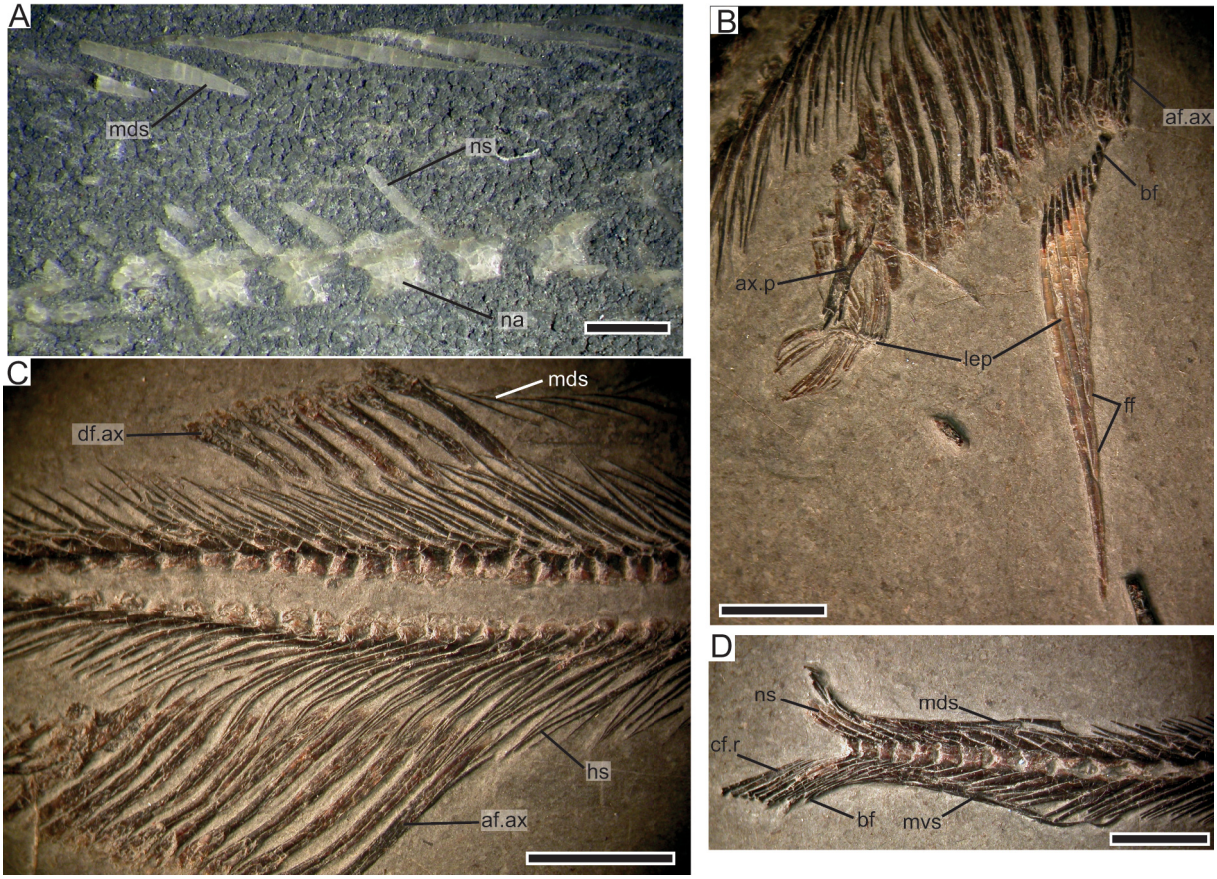

Fig. 7. Postcranium, Early Jurassic saurichthyids. **A**. *Saurorhynchus anningae* sp. nov., neural arches and squamation in the posterior abdominal region (NHMUK PV P 3790). **B–D**. *Saurorhynchus hauffi* sp. nov., SMNS 55057. **B**. Lepidotrichia of the anal fin. **C**. Relationship between the neural and haemal arches and the axonosts. **D**. Caudal peduncle. Abbreviations: af.ax = axonosts of the anal fin; ax.p = axonost plate; bf = basal fulcra; cf.r = caudal fin radials; df.ax = axonosts of the dorsal fin; ff = fringing fulcra; hs = haemal spine; lep = lepidotrichia; mds = mid-dorsal scale row; mvs = mid-ventral scale row; na = neural arch; ns = neural spine. Scale bars: A = 1 mm, B–D = 5 mm. A. Photo © The Trustees of the Natural History Museum, London.

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ossified and anteroposteriorly elongate, articulating with the maxilla ventrally, premaxilla anteriorly, and nasaloantorbital and supraorbital dorsally. It transmits the infraorbital sensory canal.

The dermosphenotic is variable in size, and forms the posterodorsal edge of the orbit. It carries the infraorbital canal. Ventral to the dermosphenotic, an elongate infraorbital forms the majority of the posterior orbit and carries the sensory canal. Infraorbitals along the ventral edge of the orbit are extremely weakly ossified (just a thin tube of bone surrounding the infraorbital canal, not in direct articulation with more anterior or posterior elements), and as such are rarely preserved.

Posterior to the dermosphenotic and fused with the lateral dermopterotic, an elongate, anamesic element is sometimes preserved. As with the dermosphenotic, it is somewhat variable in terms of size. It is often missing, and even when present the sutural contact can be very difficult to see. This element is most similar to the "supraspiracular plate" of *Birgeria groenlandica* Stensiö, 1932 in shape, position, and the absence of a sensory canal (Nielsen 1949). The ventral dermosphenotic in *B. stensioei* Aldinger, 1931 (Romano & Brinkmann 2009) was later homologized with the "supraspiracular plate" of *B. groenlandica*, however the ventral dermosphenotic should contact the infraorbital and carry the infraorbital canal (Poplin 2004), which the elongate element in *S. hauffi* sp. nov. does not. We tentatively consider this element to be a neomorph.

The dermopterotic is a broad dorsally convex sheet of bone making up the posterior skull roof (Fig. 3B). A descending process forms an interdigitating suture with the ascending process of the parasphenoid, and creates a notch into which slots the posterior end of the neomorph. Ornamentation generally consists of pits. There is an elongate pore medial to the hyomandibular contact indicating that the medial process of the infraorbital sensory canal was present. Anterior to this canal are the parietals. These form a large, oval ossification. Ornamentation is reticular. No evidence of sensory canals or pores could be detected.

An elongate lateral extrascapular is sutured to the lateral dermopterotic, dorsal to the hyomandibula (Fig. 5D). It transmits the posterior infraorbital canal. A medial extrascapular is also present, and together they form a v-shaped articulation with the dermopterotic.

A dermohyal was present, as the dorsal portion of the hyomandibular bears the pitted ornamentation characteristic of dermal bones (Fig. 5D). A prominent posteriorly oriented joint surface on the ventrolateral dermopterotic articulates with the hyomandibula.

The palate is not exposed in any of the skulls attributable to this species, however the parasphenoid is often well-exposed in lateral view. The parasphenoid rostrum is curved and edentulous ventral to the orbit; the posterior stem is straight and dorsally displaced. The ascending process of the parasphenoid projects dorsolaterally, and is ornamented with fine striations. The foramen for the ophthalmic artery is closer to the anterior than posterior edge of the ventral ascending process (Fig. 1D). There is no expanded tooth plate ventral to the ascending process, and the entire parasphenoid posterior to the anterior margin of the orbit is edentulous. The posterior stem of the parasphenoid is broad. Anteriorly, a central ridge and two lateral ridges are present on the ventral surface of the posterior stem; posteriorly the central ridge diminishes such that it is absent at the posterior end.

Posterior to the orbit, the large foramen for the internal carotid and efferent pseudobranchial artery is contained within the basisphenoid (Fig. 4C, F). In one specimen (SMNS 55302) this foramen is subdivided into anterior and posterior components by a pillar of bone. On the anterior surface of the basisphenoid, the large foramen for the ophthalmica magna artery is recessed in a groove laterally bordered by cristae. Posterior to the basisphenoid, the space between the ascending process and basisphenoid has been interpreted as the posterior myodome. The posterior myodome appears to be roofed by an

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independent ossification dividing the posterior myodome from the trigeminofacialis chamber. Dorsal to this ossification, the foramen for the ramus oticus lateralis emerges from the neurocranium.

The preopercle is relatively narrow, with the dorsal ramus being narrower than the posterior ramus. It carries the preopercular sensory canal. Unlike previous reconstructions (Hauff 1938; Gardiner 1960; Thies 1985), it is clear that the preopercular sensory canal runs along the length of the dorsal ramus as well as the posterior ramus, as in *Saurichthys*. The dorsal edge of the preopercle bears two tiny processes, the anterior of which is directed dorsoanteriorly and the posterior of which is directed anteromedially. These presumably articulate with the hyomandibula. The suture between the posterior ramus of the preopercle and the maxilla is easy to differentiate based on the change in the direction of ornamentation at the suture. The quadratojugal is rectangular in shape and meets the maxilla anteriorly and the preopercle dorsally and posteriorly. It contacts the articular ventromedially.

The lateral lower jaw consists of four elements: a tiny articular, a small supraangular, an expanded angular, and the dentary. The articular is in contact with the supraangular anteriorly. The dorsal portion of the angular is very thin and often eroded, making it appear that the sensory canal is located near the dorsal edge of this element. However, that is not the case. The mandibular sensory canal is contained entirely within the angular, and runs closer to the occlusal jaw margin than the ventral edge. It gives rise to descending canals. The posterior edge of the angular is strongly sinusoidal, and projects posterior to the jaw joint. The angular is also strongly ornamented with pitting and some reticulation; there are a series of "growth lines" running parallel to the ventral edge. The dentary itself has a woody texture, with the grain oriented parallel to the long axis of the mandible. The ventral part of the angular-dentary suture begins as at a posteroventrally angle dorsally, but becomes deflected ventrally.

The laniary teeth are simple cones bearing an acutely pointed acrodin cap, and in general appear to be entirely unornamented and lack any differentiation between tooth base and "collar ganoine" (Fig. 6C). However, a single specimen (SMNS 51007) does show extremely faint corrugation of the collar region. We consider that its small maximum tooth size is possibly a reason for restricted expression of corrugation in the collar region (the specimens of *S. anningae* sp. nov. that clearly show a corrugated collar region are among the largest specimens, far larger than the largest *S. hauffi* sp. nov.). Some variability in the degree of expression must also be assumed (Gardiner 1960).

Postcranium

Paired fins. The supracleithra are seldom preserved. They appear to be thin and relatively straight dorsally, ventrally bearing a prominent anterior process that is pierced by a foramen on its medial surface. There is no equivalent to this ventral anterior process of the supracleithrum within *Saurichthys*, but this morphology is shared with *S. brevirostris*. The cleithra are triradiate, with a robust posterior ramus. The paired fins are even more rarely preserved. In NMB 373, the pectoral fins are triangular in shape, with the longest and most robust lepidotrichia located close to the leading edge of the fin. A precise count of lepidotrichia is not possible. In no specimens referred to *S. hauffi* sp. nov. are pelvic fins preserved.

Axial skeleton. The following description is based on SMNS 55057. Sixty-three abdominal and 117 caudal neural arch-like elements are preserved anterior to the caudal fin, for a total of 180 (90 vertebral segments). As indicated by the low abdominal neural arch count, the abdominal-caudal transition is displaced anteriorly relative to the anal fin (Fig. 1D). The neural arch-like elements consist of a short, robust base, a moderately long prezygapophysis and a long, tapering neural spine. The medial surface of alternating neural arches is pierced by a foramen for the intersegmental vessel (Wu *et al.* 2015). The neural spines become longer more posteriorly in the column, and become forked immediately anterior to the insertion for the dorsal fin. Posterior to the dorsal fin, the neural spines are not forked for a short distance, but become bifurcated again and posteriorly inclined towards the caudal fin. The haemal spines

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are short, robust hooks anteriorly, lying dorsal to the gastric mass. Some of them are also bifurcated in this region. They lengthen at the end of the abdominal cavity, and become bifurcated or even trifurcated dorsal to the anal fin (Fig. 7C). Posterior to the anal fin, the haemal spines become shorter, more robust, and posteriorly inclined.

Median fins. The median fins are not complete. Eight elongate dorsal axonosts are preserved in the holotype, and no dorsal lepidotrichia. The anteriormost axonost is not differentiated relative to more posterior axonosts. Twelve anal axonosts are preserved; again the anteriormost is not differentiated (Fig. 7B). The two forks of the neural and haemal spines insert on either side of an axonost. There is a gap between the axonosts and the lepidotrichia, and a single roundish, extremely weakly ossified baseost is preserved posteriorly. Four basal fulcra are present. The preserved lepidotrichia are unsegmented and are not distally bifurcated. Fringing fulcra are present, with an arrangement similar to that described by Stensiö (1925) for the pelvic fins of *S. ornatus*, but differing in that the fringing fulcrum and distal lepidotrichium appear to be fused, especially rostrally. When fused, a suture is present between the fulcra and underlying lepidotrichia. The posterior anal fin consists of finer, soft rays. A heavily ossified element associated with more poorly ossified endochondral fragments is also preserved in this region. It is bilaterally symmetrical, forked anteriorly with each of the two rami bifurcating again. The posterior end bears three small projections, with the medial projection being slightly longer than the other two. This element is tentatively interpreted as the axonost plate (Fig. 7B), based on comparisons in shape and position with the same element in *Birgeria* (Schwarz 1970). Caudal radials are preserved, but lepidotrichia are missing.

Squamation. The only scale row present anterior to the median fins is the mid-dorsal scale row. Scales in this row are elongate, needle-like, and unornamented (Fig. 7C). Posterior to the median fins, no scales are present, unlike in *S. anningae* sp. nov. in which, at minimum, the mid-ventral row is ossified. Immediately anterior to the caudal fin, the caudal peduncle is encased in robust mid-dorsal and mid-ventral scales, which grade into basal fulcra posteriorly (Fig. 7D). The scales in the caudal peduncle are more robust than the abdominal scales, but are also smooth in texture.

Occurrence

Early Jurassic, Toarcian, *tenuicostatum* Zone, *semicelatum* Subzone to *serpentinum* Zone, Baden-Württemberg, Germany; *serpentinum* Zone, Lower Saxony, Germany; *exaratum* Subzone, Western Pomerania, Germany; Toarcian, Whitby, UK.

Saurorhynchus sp.

Material studied

GERMANY: Numismalismergel jaw (SMNS 96082).

Remark

SMNS 96082 is the only Pliensbachian record of *Saurorhynchus* of which we are aware. Although clearly referable to *Saurorhynchus*, SMNS 96082 is distinct from *S. anningae* sp. nov. in the shape of the posterior mandible and position of the mandibular sensory canal, and also from *S. brevirostris,* in that the posterior edge of the mandible is more strongly sinusoidal. However, there are few features to differentiate SMNS 96082 from the Toarcian-aged *S. acutus* and *S. hauffi* sp. nov. One notable difference is the development of plicidentine, which is easily visible around all tooth bases in this specimen. In Toarcian saurichthyids, plicidentine, while present at least some of the time, does not appear to be as well-developed or consistently present. However, body size/absolute tooth size may be playing a role: with a mandibular depth of 23 mm, the Numismalismergel jaw ranks among the largest *Saurorhynchus*

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skulls from southwestern Germany (Suppl. Table 1; Hauff 1938). As in the Toarcian material, the collar region of the teeth does not appear to be corrugated.

Comparing the jaw depth to other Toarcian *Saurorhynchus* skulls, a skull length of between 114 mm (based on PMU 30009) and 143 mm (Hauff 1938) is predicted, which would result in an estimated fork length of 40–50 cm.

Discussion

Given the high degree of morphological and size similarity, as well as geographic and stratigraphic overlap between *S. hauffi* sp. nov. and *S. acutus*, it is important to examine whether differences between these two taxa are not attributable to intraspecific variation or dimorphism. Hauff (1938) acknowledged this high degree of morphological variation within Toarcian saurichthyids from Baden-Württemberg, but was unable to identify discrete characters with which to delineate species. Variation in narial morphology is poorly documented among saurichthyid fishes, but does not appear to be pronounced within Triassic species or even between closely related species (Rieppel 1985). The shape of the anterior narial opening in *S. acutus* is unique among saurichthyids. In addition to the shape of the narial opening, differences in the position of the lateral extrascapular and reduced dermal ornamentation in *S. acutus* mean that it is in practice not too difficult to distinguish *S. acutus* and *S. hauffi* sp. nov. based on cranial remains. It is possible that more abundant postcranial remains for both species will reveal more concrete information regarding how these two highly similar taxa coexisted in apparent sympatry.

Within the material referred to *S. acutus*, two distinct patterns of cranial ornamentation are present: a reduced pattern and a more clearly developed pattern. This reduced pattern was described in a Toarcian saurichthyid by Woodward (1899), who attributed the reduction to abrasion during preparation. Abrasion cannot be ruled out among the Posidonia Shale material, especially as several specimens show clear tooling marks from preparation, however since all *S. acutus* skulls show reduced ornamentation relative to *S. hauffi* sp. nov., it is possible that these differences in ornamentation may later prove to be of taxonomic relevance.

In contrast to the relative ecomorphological homogeneity of the Toarcian species, the Sinemurian-aged *S. anningae* sp. nov. and *S. brevirostris* are clearly differentiated based on a multitude of features, including cranial fineness, tooth morphology, and body size. *S. brevirostris* is smaller (~30 cm fork length vs ~50 cm fork length in *S. anningae* sp. nov.) and shows heterodonty between the anterior and posterior teeth, as well as a pronounced overbite. Moreover, *S. brevirostris* has a shorter, deeper skull than *S. anningae* sp. nov., as well as a narrower, more ventrally tapered opercle. The opercular shape differences observed between *S. anningae* sp. nov. and *S. brevirostris* correlate well with those associated with variation in body fineness in saurichthyids (Wilson *et al.* 2015), implying that *S. brevirostris* may also have had a shorter, deeper body than *S. anningae* sp. nov. Differences in morphology and proportions are unlikely to be related to ontogeny, since there is overlap in size between the smallest specimens of *S. anningae* sp. nov. and mid-sized specimens of *S. brevirostris* (Suppl. Table 1).

Saurorhynchus anningae sp. nov. is the most divergent from the other *Saurorhynchus* species in a suite of morphological features including anatomy of the orbitotemporal region, specifically the position of the foramen for the internal carotid and efferent pseudobranchial arteries (Fig. 4). The polarity of this feature is unclear, but differs from the other three species. However, *S. anningae* sp. nov. also demonstrates a suite of features that are almost certainly plesiomorphic, based on their wide distribution among Triassic saurichthyids, such as the shape of the posterior and posteroventral mandible, denticles on the parasphenoid rostrum ventral to the orbit, and squamation developed further anteriorly in the caudal region.

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Saurorhynchus hauffi sp. nov. also exhibits some unusual features not previously identified in the species group, including retention of fringing fulcra on the median fins (Fig. 7B). These structures were observed and described as a ganoine layer overlying the anterior distal lepidotrichia (Thies 1985). This character could not be evaluated in other species of *Saurorhynchus* as none of the fins are well-preserved. Their presence in a Jurassic saurichthyid is somewhat unexpected (Romano *et al.* 2012), and may have implications for the position of the *Saurorhynchus* species group within saurichthyid phylogeny.

This variation within fishes referred to *Saurorhynchus* may be responsible for the two very different positions of the *Saurorhynchus* species group in phylogenetic analyses of Saurichthyidae, namely outside of the Middle Triassic Tethyan radiation when coded based on *S. anningae* sp. nov. (Wu *et al.* 2013), or nested within a clade of Middle–Late Triassic European species when coded based on *S. hauffi* sp. nov. (Maxwell *et al.* 2015). The four Early Jurassic species discussed here are united by the presence of a dermohyal, dorsal position and multiple descending branches of the mandibular sensory canal and the pattern of dermal ornamentation composed of pitting and reticulation with a reduced or absent ganoine layer rather than parallel ganoine ridges and tubercles, to the exclusion of all Triassic saurichthyids, including other species in the *Saurorhynchus* species group. Bifurcating haemal spines (observed in *S. hauffi* sp. nov. and *S. anningae* sp. nov.) may also unite this group, although the postcranial axial skeleton is unknown for *S. acutus* and *S. brevirostris*. The 'v'-shape of the angular-dentary suture, presence of incisivlücken, pattern of the dentition consisting of a laniary tooth flanked by a pair of smaller teeth, and unsegmented lepidotrichia are all found in some of the other members of the *Saurorhynchus* species group, i.e., *Saurorhynchus deperditus*, *S. striolatus*, and *S. calcaratus* (E.E.M. pers. observ.; Griffith 1959, 1962, 1977).

Taphonomy

Beardmore & Furrer (2016b) analyzed the taphonomy of saurichthyid fishes from the Middle Triassic Monte San Giorgio lagerstätte, and this study provides a basis for comparison with the taphonomic patterns observed for the Posidonia Shale saurichthyids. Specifically, Beardmore & Furrer (2016b) report frequent isolation of the head unit from the postcranium, then loss of the opercles, followed by loss of the mandible. This taphonomic gradient is associated with increasing water depth and decreasing sedimentation rates between the two formations studied (Meride and Besano Formations). The low degree of skeletal completeness observed in the Posidonienschiefer Formation saurichthyids, combined with high prevalence of the head unit in isolation, agrees well with the findings of Beardmore & Furrer (2016b) for the Besano Formation in terms of preservation, water depth, and sedimentation. In the latest *tenuicostatum* Zone, a time corresponding to a sea level lowstand (Röhl & Schmid-Röhl 2005), water depths are estimated at 50 m or less in the southwest German Basin, gradually deepening to 100–150 m by the latest *serpentinum* Zone (Riegraf *et al.* 1984; Röhl *et al.* 2001). Sedimentation rates for the *serpentinum* Zone are estimated at an average of 2 mm compacted sediment / kyr at the Holzmaden locality (Martill 1993), an order of magnitude less than that of the Besano Formation and potentially explaining the much lower frequency of complete specimens and skull units associated with opercles, or even mandibles, in the Posidonienschiefer Formation. Additional loss of completeness may be related to current activity (Hofmann 1958; Brenner & Seilacher 1978; Kauffman 1978, 1981; Riegraf *et al.* 1984; Beardmore *et al.* 2012; Reisdorf *et al.* 2012; Beardmore & Furrer 2016a).

Palaeobiogeography

Both of the *Saurorhynchus* species from the Southwest German Basin (*S. acutus* and *S. hauffi* sp. nov.) are also represented in the Toarcian fish fauna from the Northwest German Basin and the Cleveland Basin (Whitby, UK). Although the skulls from Whitby lack detailed locality information, the holotype skull is in matrix containing a mass occurrence horizon of the bivalve *Pseudomytiloides dubius*, suggesting a stratigraphic origin from the *serpentinum* Zone, *exaratum* Subzone (Caswell & Coe 2013), and thus is probably coeval with the material from Germany. In other words, both species shared a broad

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distribution in Europe in the Toarcian immediately following the onset of the early Toarcian Oceanic Anoxic Event. This pattern of broad faunal distribution within Europe during the *serpentinum* Zone in particular has been noted for ammonites, fishes, and some marine reptiles (Godefroit 1994; Benson *et al.* 2011; Dera *et al.* 2011; Wretman *et al.* 2016; Konwert & Stumpf 2017), but see Maisch & Ansorge (2004) who argue in favour of faunal provincialism.

Conclusion

Four valid species of saurichthyid fishes are confirmed as present in the Early Jurassic of Europe, *Saurorhynchus acutus, S. anningae* sp. nov., *S. brevirostris* and *S. hauffi* sp. nov. Of these, *S. brevirostris* and *S. anningae* sp. nov. are known only from the Sinemurian of England, whereas *S. acutus* and *S. hauffi* sp. nov. are restricted to the Toarcian but share a broad distribution within Europe. All species are characterized by unambiguous discrete morphological features that will be of assistance in identifying new finds of *Saurorhynchus* and improving our understanding of diversity and disparity in the youngest saurichthyids.

Acknowledgments

Thanks to E. Bernard (NHMUK), I. Werneburg (GPIT), A. Gehler (GZG), A. Richter (NLMH), R. Kosma (NMB), and B. Kear and J.O. Ebbestad (PMU) for access to collections, and O. Maaß for preparation of SMNS 96927. Comments by reviewers J. Kriwet and I. Kogan improved the manuscript. S.S. was supported by a PhD scholarship from the state of Mecklenburg-Western Pomerania.

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Manuscript received: 27 September 2016
Manuscript accepted: 9 January 2017
Published on: 23 May 2017
Topic editor: Christian de Muizon
Desk editor: Kristiaan Hoedemakers

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Appendix 1. Select cranial measurements for Early Jurassic species of *Saurorhynchus* Reis, 1892.

Specimen	Lower jaw length	Lower jaw max. depth	Antorbital (rostral) length	Opercle length	Opercle depth
***Saurorhynchus acutus* (Agassiz, 1844)**					
NHMUK PV P 4268 (holotype)	–	–	84	–	–
SMNS 88007	–	–	71	–	–
SMNS 55319	95	16	72	–	–
SMNS 56923	84	–	64	–	–
SMNS 55324	93	–	70	–	–
SMNS 87738	–	–	59	–	–
SMNS 51009	125	–	92	–	–
SMNS 50924	96	16	78	–	–
SMNS 57039	102	17	78	–	–
SMNS 96927	–	–	69	–	–
SMNS 96927	–	–	70	–	–
NHMUK PV P 3792	111	18	84	–	–
NHMUK PV P 36222	110	19	84	–	–
NHMUK PV OR 19668	100	–	74	–	–
NHMUK PV OR 22528	87	–	68	–	–
NHMUK PV P 36223	91	–	71	–	–
GPIT 05/133	–	21		–	–
GZG.V.27932	–	18		–	–
PMU 30009	114	25	84	–	–
PMU 30010	91	–	72	14	14
***Saurorhynchus brevirostris* (Woodward, 1895)**					
NHMUK PV OR 40726 (holotype)	>82	14	>57	10	13
NHMUK PV P 36233	80 (jaw joint to rostral tip = 86 mm)	13	64	–	–
NHMUK PV P 4878	74 (jaw joint to rostral tip = 77 mm)	12	56	–	–
NHMUK PV OR 39866	52 (jaw joint to rostral tip = 54 mm)	9	37	–	–
NHMUK PV P 36232	–	15	–	–	–
NHMUK PV OR 48007	–	–	62	–	–

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Specimen	Lower jaw length	Lower jaw max. depth	Antorbital (rostral) length	Opercle length	Opercle depth
***Saurorhynchus anningae* sp. nov.**					
NHMUK PV P 3791	89	10	65	9	13
NHMUK PV P 428	137	13	101	–	–
NHMUK PV P 36227	–	–	49	–	–
NHMUK PV P 3790	74	9	–	–	–
NHMUK PV P 36226	79	10	60	7	11
NHMUK PV OR 43054	96	13	75	–	–
NHMUK PV P 36228	94	12	–	–	–
***Saurorhynchus hauffi* sp. nov.**					
SMNS 55057 (holotype)	97	17	–	–	–
SMNS 96878/1	91	16	68	–	–
SMNS 55934	84	–	63	–	–
SMNS 95825	99	17	76	–	–
SMNS 51007	76	15	55	–	–
SMNS 53980	85	15	64	–	–
SMNS 51888	112	17	86	–	–
SMNS 50075	–	24	–	–	–
SMNS 55302	90	–	66	–	–
SMNS 55957	101	–	78	–	–
NHMUK PV OR 39153	95	13	70	–	–
NHMUK PV P 48441	115		87	–	–
GPIT 05/00833	103	16	77	–	–
GPIT 05/00831	85	–	62	–	–
GPIT 05/00832	92	–	68	–	–
GZG.V.27931	101	–	79	–	–
NLMH 70598	91	14	69	–	–
NMB 373	102	17	78	–	–

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: European Journal of Taxonomy

Jahr/Year: 2017

Band/Volume: 0321

Autor(en)/Author(s): Maxwell Erin E., Stumpf Sebastian

Artikel/Article: Revision of Saurorhynchus (Actinopterygii: Saurichthyidae) from the Early Jurassic of England and Germany 1-29