

A new long and narrow-snouted ichthyosaur illuminates a complex faunal turnover during an undersampled Early Jurassic (Pliensbachian) interval

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Abstract: Ichthyosaurian faunas before and after the Pliensbachian stage of the Early Jurassic are known from numerous, often complete fossils. The two faunas are very different taxonomically, with only one of the pre-Pliensbachian genera, but none of the species, persisting into the post-Pliensbachian (Toarcian). Pliensbachian ichthyosaurs are rare, yet this interval represents a critical and poorly understood time in ichthyosaurian evolution just c. 10 myr after the end-Triassic mass extinction. Thus, a new ichthyosaur from the mid-Pliensbachian of the Dorset coast of the UK, the most complete ichthyosaur known from that stage, is significant. *Xiphodracon goldencapensis* gen. et sp. nov. is characterized by a distinct combination of characters and several autapomorphies, including: a unique lacrimal with prong-like projections on its anterior edge, a prefrontal with projections that interdigitate with the nasal and

lacrimal, a wedge-shaped external naris with an anterodorsal constriction that forms a distinct foramen (shaped by the nasal, lacrimal and prefrontal), and a maxilla that forms almost the entire border of the external naris. Phylogenetic analyses indicate that *X. goldencapensis* is more closely related to the late Pliensbachian to Toarcian genus *Hauffiopteryx* than to earlier genera that continued into the Pliensbachian (e.g. *Leptonectes*, *Ichthyosaurus*), and forms a distinct clade (*Hauffiopterygia* nov.) within a monophyletic Leptonectidae. This indicates that a substantial faunal turnover in diversity occurred towards the end of the early Pliensbachian, leading to a major shift in composition towards a more typical Toarcian ichthyosaur fauna.

Key words: Ichthyosauria, Pliensbachian, Leptonectidae, Lower Jurassic, faunal turnover, *Xiphodracon*.

IN the UK, the west Dorset coast, from Lyme Regis east to Charmouth and Seatown, is renowned for the numerous ichthyosaurs that have been collected there for over 200 years. Specimens collected in the 19th century from the Lyme Regis area and from the area around Street (Somerset) make up the bulk of Early Jurassic ichthyosaur skeletons in British museums and universities, with many other specimens in museum collections worldwide. Most of the specimens lack detailed stratigraphic data, but are generally considered to be from the lower two stages (Hettangian and Sinemurian) of the Early Jurassic (McGowan 1974a, 1974b; McGowan & Motani 2003; Weedon & Chapman 2022). The exposures along the Dorset coast near Charmouth and Seatown, however, also include younger strata from the Pliensbachian Stage (Page 2010).

Pliensbachian ichthyosaurs from the UK are seemingly much rarer and less diverse than those from the

Sinemurian. *Ichthyosaurus anningae* and *I. conybeari* are known from the Jamesoni Zone of the lowest Pliensbachian (Lomax 2010; Bennett *et al.* 2012; Lomax & Massare 2015; Massare & Lomax 2016); whereas *Leptonectes moorei*, *L. solei* and *Temnodontosaurus platyodon* are known from the slightly higher Ibex Zone (McGowan & Milner 1999; Lomax & Massare 2018; Weedon & Chapman 2022).

Pliensbachian ichthyosaurs have also been reported from Europe but, as in the UK, they are rare and mostly represented by fragments. Specimens that can be assigned to genus or family include an incomplete forefin of *Leptonectes tenuirostris* from the mid-Pliensbachian Davoei Zone of Belgium (Godefroit 1992), a partial skeleton of *Leptonectes* sp. from the lower Pliensbachian Jamesoni Zone of Spain (Fernández *et al.* 2018), and a fragmentary leptonectid from the lower Pliensbachian Ibex Zone of Luxembourg (Fischer *et al.* 2022). The incomplete skull



FIG. 1. The holotype and only known specimen of the hauffiopterygian leptonectid, *Xiphodracon goldencapensis* (ROM VP52596) from Golden Cap, between Charmouth and Seatown, Dorset, UK. The skeleton is exposed in ventrolateral view. The skull has been fully prepared free of matrix whereas most of the skeleton is still in matrix. The left (upper) forefin has been prepared so that it is three-dimensionally preserved and projects upwards. Scale bar represents 20 cm.

and mandible of *Temnodontosaurus nuertingensis* from Germany is from the Jamesoni or Ibex Zone (Maisch & Hungerbühler 1997), whereas Hungerbühler & Sachs (1996) reported an incomplete skull and other fragments of a *Temnodontosaurus* sp. from the Davoei Zone of Germany. A small skull and fragmentary skeleton of *Hauffiopteryx typicus* has been found in the slightly higher Margaritatus Zone of Switzerland (Maisch & Reisdorf 2006; Maxwell & Cortés 2020). Notably, every Pliensbachian occurrence mentioned here, in both the UK and Europe, is for a single specimen.

This research describes a nearly complete specimen of a new genus and species of Pliensbachian ichthyosaur, *Xiphodracon goldencapensis*, from the west Dorset coast, UK, the most complete Pliensbachian ichthyosaur described thus far. It is stratigraphically higher than other Pliensbachian ichthyosaurs from the UK, and provides insight into the turnover of ichthyosaurian taxa towards the end of the Early Jurassic, a pivotal but poorly understood time in ichthyosaurian evolution.

Institutional abbreviations. ANSP, Academy of Natural Sciences, Philadelphia, PA, USA; BGS GSM, British Geological Survey, Keyworth, UK; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; BRLSI, Bath Royal Literary and Scientific Institution, Bath, UK; CHCC, Charmouth Heritage Coast Centre, Dorset, UK; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; NHMUK, Natural History Museum, London, UK; NMO, Naturmuseum Olten, Olten, Switzerland; ROM, Royal Ontario Museum, Toronto, Canada; SMNS, State Museum of Natural History Stuttgart, Stuttgart, Germany.

GEOLOGICAL SETTING & MATERIAL

The focus of this study is ROM VP52596, an almost complete skull and skeleton, missing one hindfin and the

posterior part of the tail (Fig. 1). The specimen comes from the shoreline area east of Golden Cap, between Charmouth and Seatown, Dorset, along the 'Jurassic Coast' of England, UK (Fig. S1). It derives from the Charmouth Mudstone Formation, Green Ammonite Member (lower part of the 'Green Ammonite Beds'), Bed 122c of Lang (1936), specifically from c. 1.5 to 2 m above Bed 121 (Belemnite Stone) of Lang (1928). It is from the Early Jurassic Davoei Zone, Maculatum Subzone of the early Pliensbachian (ROM archives; Barton *et al.* 2011; Phelps 1985; Page 2010; Weedon & Chapman 2022, p. 289; C. Moore & P. Davis, pers. comms 2025).

The specimen was discovered and initially prepared by Chris Moore of Charmouth, UK, and sold to the ROM in 2001, where preparation was completed by Ian Morrison. Most of the specimen is exposed in ventral view, consisting of multiple connecting blocks. The skull was removed from the matrix and prepared in three dimensions. The specimen has a total length of 218 cm, measuring from the tip of the snout to the last preserved vertebra and including the skull. However, it is missing most of the preflexural caudal vertebrae and all of the fluke. We estimate that it had a total length of c. 3.0 m. The skull is well-preserved in three dimensions, although it is dorso-ventrally crushed, which has altered the original shape of the orbit and skull roof. Most of the left and right sides of the skull, however, remain largely intact and sutures are well-defined, although some displacement is apparent. Some of the braincase elements, atlas-axis, both forefins, the left hindfin and the right femur are mostly free of matrix and can be examined in three dimensions.

In the matrix surrounding the right hyoid is a ?bony mass of unknown origin (Figs 2D, S2A, B). It is rounded, seemingly smooth, but appears to comprise 4–5 distinct contiguous segments that outwardly resemble very small distal fluke centra of an ichthyosaur or, perhaps, deformed fish centra (Fig. S2). Similarly, other ?bony

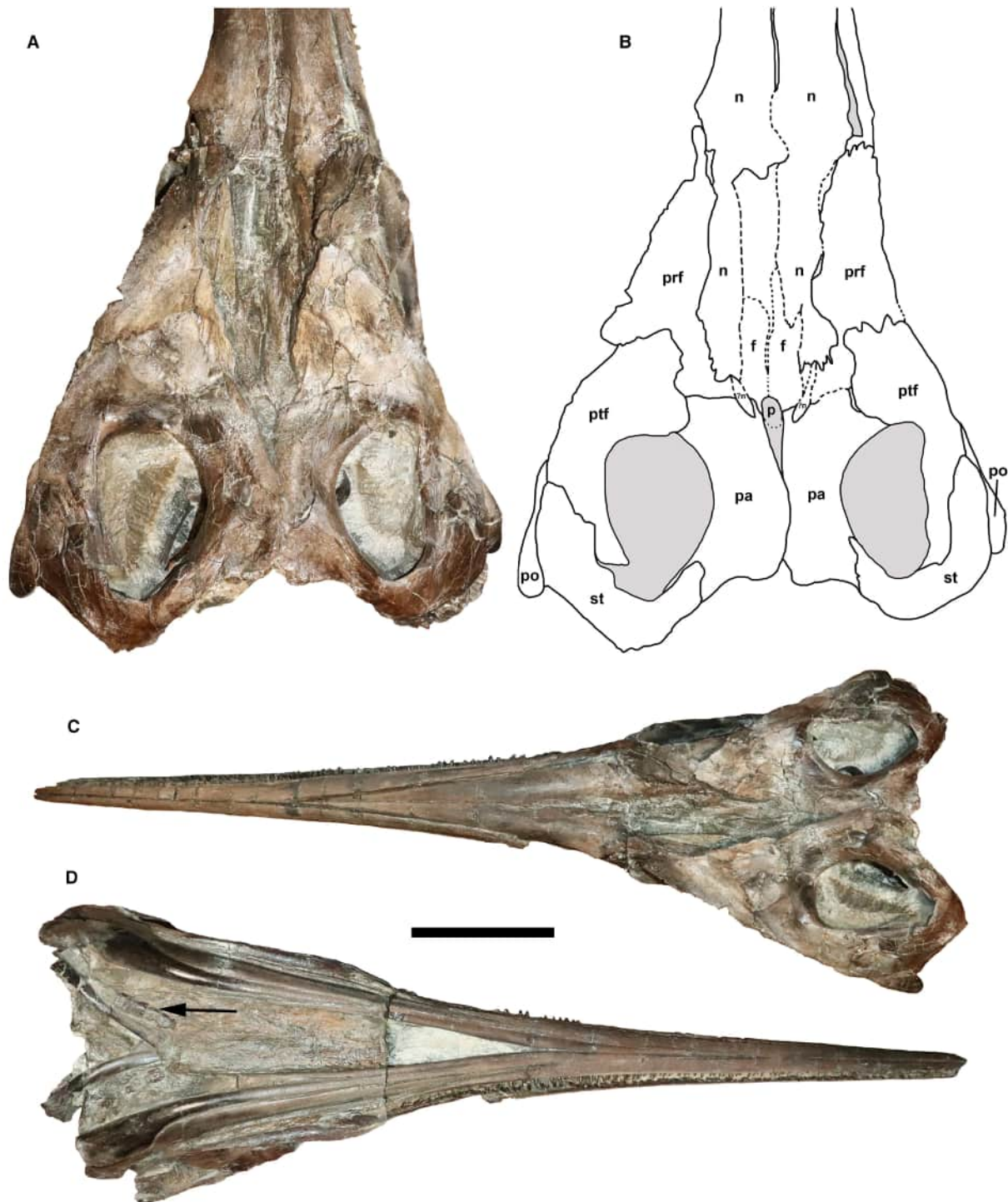


FIG. 2. Skull of *Xiphodracon goldencapensis* (ROM VP52596). Photograph (A) and interpretative illustration (B) of the skull roof in dorsal view. C, entire skull in dorsal view. D, ventral view of the same. Arrow points to a large ?bony mass of unknown origin. Abbreviations: f, frontal; n, nasal; p, pineal; pa, parietal; po, postorbital; prf, prefrontal; ptf, postfrontal; st, supratemporal. Scale bar represents 10 cm (C, D).

fragments are adjacent to the left hyoid. This bromalite material might represent a consumulite (Hunt & Lucas 2021).

A dark mass between the ribs might be stomach contents, but it is covered with a preservative that obscures finer details. Patches of what might be residual soft-tissue structures are

present along the vertebral column, some ribs, and a large patch is ventral to the right pelvic girdle and possibly around the hindfin. Both forefins had some soft tissue preservation around the fins (C. Moore, pers. comm. 2025), which was not evident on the specimen when we examined it.

METHOD

Two analyses were undertaken to determine the phylogenetic position of ROM VP52596, *Xiphodracon goldencapensis*: the first using equal weights parsimony and the second using implied weighting (see [Phylogenetic Analysis](#) below for details).

The matrix was based on that of Miedema *et al.* (2024), originally derived from Moon (2019). *Temnodontosaurus* spp. were rescored and *T. zetlandicus* was added as an OTU (operational taxonomic unit) based on Laboury *et al.* (2022) (Lomax *et al.* 2025). Specimens referred to *Hauffiopteryx typicus* were not merged into a single OTU, but were retained as three separate OTUs: (1) the material from Strawberry Bank; (2) the material from south-western Germany; and (3) the Pliensbachian skull from Switzerland. This decision was undertaken because there are several subtle differences between the material from the UK and that from Germany in the posteroventral cheek region that nonetheless affect character scoring. While these differences have been attributed to preservation or preparation (Maxwell & Cortés 2020), there is no strong disadvantage to maintaining the OTUs as distinct rather than scoring the characters as polymorphic.

Character 219 (number of 'complete' postaxial accessory digits in the forelimb) was rescored for all taxa. This character was scored by Moon (2019) based on a combination of Maisch & Matzke (2000, char. 89) and Fischer *et al.* (2011, char. 38), and was not revised in subsequent iterations of the matrix. This resulted in differences in scoring and homology assessment of digit V and what constituted a post-axial digit between non-parvipelvian, non-ophthalmosaurian parvipelvian, and ophthalmosaurian ichthyosaurs. In the revised character formulation, digit V (regardless of potential non-homology between parvipelvians and non-parvipelvians) was not scored as a postaxial accessory digit.

Character 129 (reduction of the dentition) was also rescored for all taxa, given that inconsistencies in scoring were noted during optimization of synapomorphies. Dentition was considered reduced if the teeth were non-functionally small (e.g. as in some specimens of *Stenopterygius* spp.) or reduced below a threshold value (relative crown size <0.13; 'minute teeth' *sensu* Fischer *et al.* 2016).

Three characters were treated as additive for logical reasons: 107, 153 and 219.

SYSTEMATIC PALAEONTOLOGY

ICHTHYOSAURIA de Blainville 1835

PARVPELVIA Motani 1999a

LEPTONECTIDAE Maisch 1998

HAUFFIOPTERYGIA nov.

LSID. <https://zoobank.org/NomenclaturalActs/f05b7088-1ee3-482e-a8a6-3538dc253f77>

Diagnosis. Mid-sized ichthyosaurs <3.5 m in length, characterized by a lack of contact between the nasal and postfrontal; participation of the prefrontal in the external narial opening; forefin with four digits; proximal limb elements polygonal; bicapitate dorsal ribs; lateral gastral elements extending at least two-thirds of the length of the dorsal region; and a rod-like ischium and pubis.

Genus *Xiphodracon* nov.

LSID. <https://zoobank.org/NomenclaturalActs/16d6aa3a-35a3-49d7-a1bf-173cc05a311a>

Derivation of name. Sword-like dragon. *Xipho-* derived from ancient Greek *xiphos* meaning 'sword or sword shaped' in reference to the long, narrow and sword-like snout, and *-dracon*, ancient Greek (*drakon*) and Latin (*dracō*) for 'dragon', in reference to ichthyosaurs having been informally and colloquially referred to as 'sea dragons' for over 200 years.

Diagnosis. As for the type and only species.

Xiphodracon goldencapensis sp. nov.

Figures 1–9

LSID. <https://zoobank.org/NomenclaturalActs/dc8f140d-11a1-4f7b-81ec-2dd0c7ed58bf>

Derivation of name. Sword-like dragon from Golden Cap. The species epithet *goldencapensis* refers to the location of discovery at Golden Cap, Dorset, England, UK.

Holotype. ROM VP52596, an almost complete skeleton comprising a three-dimensionally preserved skull, mandible and teeth, pectoral girdle, both forefins, pelvic girdle, parts of both hindfins, and most of the axial skeleton. A cast of ROM VP52596 is in the collections of the State Museum of Natural History Stuttgart, catalogued as SMNS 97790.

Type locality & horizon. East of Golden Cap, between Charmouth and Seatown, Dorset, UK, from the Early Jurassic, early Pliensbachian. Lias Group, Lower Lias Subgroup, Charmouth Mudstone Formation, Green Ammonite Member, Bed 122c (c. 1.5–2 m above Bed 121); Davoei Zone, Maculatum Subzone.

Diagnosis. A mid-sized, c. 3 m hauffiopterygian leptonectid with the following autapomorphies: anterodorsal border of triradiate lacrimal rugosely striated with prominent prong-like projections on its anterior edge; prefrontal anterior process with projecting structures that interdigitate with similar structures on nasal and dorsal lacrimal; posterodorsal foramen connected to the external naris; posterodorsal foramen formed by the nasal, prefrontal and lacrimal; small flange on the nasal and lacrimal forming a constriction that connects the foramen to the narial opening; anterodorsal part of the maxilla 'split' by the subnarial process of the premaxilla, creating dorsal and ventral processes; maxilla comprising almost entire ventral margin of naris, which is unique among Early Jurassic ichthyosaurs.

Xiphodracon goldencapensis is also characterized by the following unique combination of characters: dorsally oriented parietal flange, with pronounced ridge; elongate oval pineal foramen almost wholly surrounded by frontals, with small parietal contribution; extensive dorsal exposure of prefrontal making up a significant part of the mid-lateral skull roof; prefrontal extent excluding postfrontal from contact with the frontal; prefrontal contacting parietal; prefrontal anterior process dorsoventrally robust and bifurcated, participating in external narial opening; anteroposteriorly wide and robust postorbital tapering dorsally but not ventrally, making up more than half of posterior margin of orbit; anterior process of the maxilla extending only slightly beyond the narial opening; elongate squamosal, extending the entire length of the cheek; lateral exposure of posterior dentary very thin; splenial laterally exposed at the midpoint of the skull, ventral and anterior to the position of the naris; splenial and dentary making up a large portion of the mandible in ventral view; lateral exposure of angular tall posteriorly but decreasing abruptly and disappearing before middle of orbit; slender, delicate and relatively long snout as in all leptonectids but without an overbite; small, slender teeth with fine enamel ridges that extend almost to the smooth crown apex; narrow tooth roots with grooves that are continuous with some ridges on crown; extensive gastral basket, extending posterior to the 35th presacral; coracoid with deep anterior notch; robust coracoids much longer anteroposteriorly than mediolaterally wide; exceptionally long medial process of the interclavicle and very short transverse bar; humerus longer than wide, much wider distally than proximally with narrow shaft; highly reduced, centrally located dorsal trochanter; four digits in forefin (II–V); two digits (III, IV) in contact with intermedium; two digits (IV, V) in contact with ulnare; digits II and III more prominent than IV and V; radius larger than ulna; forefin with anteriorly notched radiale and distal carpal 2; pelvis tripartite; ischium longer than ilium, pubis and femur; femur much longer than wide, with distal end wider than proximal; four digits (II–V) in hindfin; anteriorly notched tibia and distal tarsal 2 (tibiale), metatarsal II and at least the first phalanx also notched.

Description of holotype

Disposition. The skeleton is exposed in ventral view, and preparation is inferred to have taken place from the underside based on the disposition of the left forefin, which would have

been projecting into the sediment at the time of burial (Fig. 1). However, despite the position of the forefins, the skull does not show obvious indicators of headfirst sea-floor arrival, with the crushing being restricted to perimortem fracturing of the mid-skull roof in a dorsoventral direction (Figs 2, 3, S3), and greater compressive force having been exerted on the right side of the skull than on the left (as deduced by the degree of compression and perimortem fracturing of the right jugal ventral to the orbit). See further details in *Palaeobiology*, below.

Skull. The skull is 64.2 cm long, measured in lateral view, and has a long, slender and narrow rostrum (preorbital ratio 0.67–0.68). A large orbit is filled by a mostly complete scleral ring on either side (Fig. 3).

The premaxillae are c. 80% of snout length (= preorbital rostrum length). The maxilla is broad and low, asymmetric, and somewhat triangular, with a large lateral exposure ventral to the naris (Fig. 3). It forms about two-thirds of the ventral margin of the naris, with a posterior contribution by the anterior process of the lacrimal. The maxilla is overlapped anterodorsally by the subnarial process of the premaxilla, resulting in an exposure of the maxilla dorsal and ventral to the process. The right side of the skull is better preserved and shows a narrow subnarial process of the premaxilla that clearly extends ventral to the narial opening but does not contribute to it. The subnarial process is separated from the lacrimal by the maxilla.

The maxilla forming most of the long, ventral border of the external naris is unusual in Lower Jurassic ichthyosaurs. In most cases, the lacrimal anterior process and premaxillary subnarial process (and sometimes the anterior process of the jugal) contact one another to separate the maxilla from the naris, as in *Ichthyosaurus*, *Protoichthyosaurus*, *Leptonectes* and *Temnodontosaurus* (McGowan & Motani 2003; Lomax *et al.* 2017a; Laboury *et al.* 2022; but see Lomax *et al.* 2020). However, in some specimens of *Stenopterygius* and *Hauffiopteryx* a small part of the maxilla contributes to the naris margin (Maxwell 2012a; Maxwell *et al.* 2012; Maxwell & Cortés 2020). Nevertheless, even in those examples, the maxillary contribution is not as extensive as seen in *Xiphodracon*. The large contribution of the maxilla to the narial margin (Fig. 3) is more similar to what occurs in more primitive Triassic taxa such as *Mixosaurus* and *Besanosaurus* (McGowan & Motani 2003; Bindellini *et al.* 2021) than to that in some ophthalmosaurians, in which the maxilla forms a broad contribution to the external narial opening posterior to the narial pillar (e.g. *Platypterygius australis*: Kear 2005) or ventral to the narial pillar, which may or may not be formed by the maxilla (e.g. *Simbirskiasaurus*, *Kyhytysuka*; Fischer *et al.* 2014; Cortés *et al.* 2021; see Campos *et al.* 2020 for a summary).

The posterior process of the maxilla does not extend far under the orbit in *Xiphodracon*, extending approximately as far posteriorly as the posterior lacrimal, but is largely concealed in lateral view by the jugal (Fig. 3A, B). The alveolar groove does not extend more than a few millimetres posterior to the posterior narial opening. The anterior process of the maxilla extends only slightly beyond the narial opening; the latter is like that observed in *Hauffiopteryx* (Maxwell & Cortés 2020).

The entire dorsal margin of the external narial opening, as well as the anterodorsal margin of the posterodorsal embayment

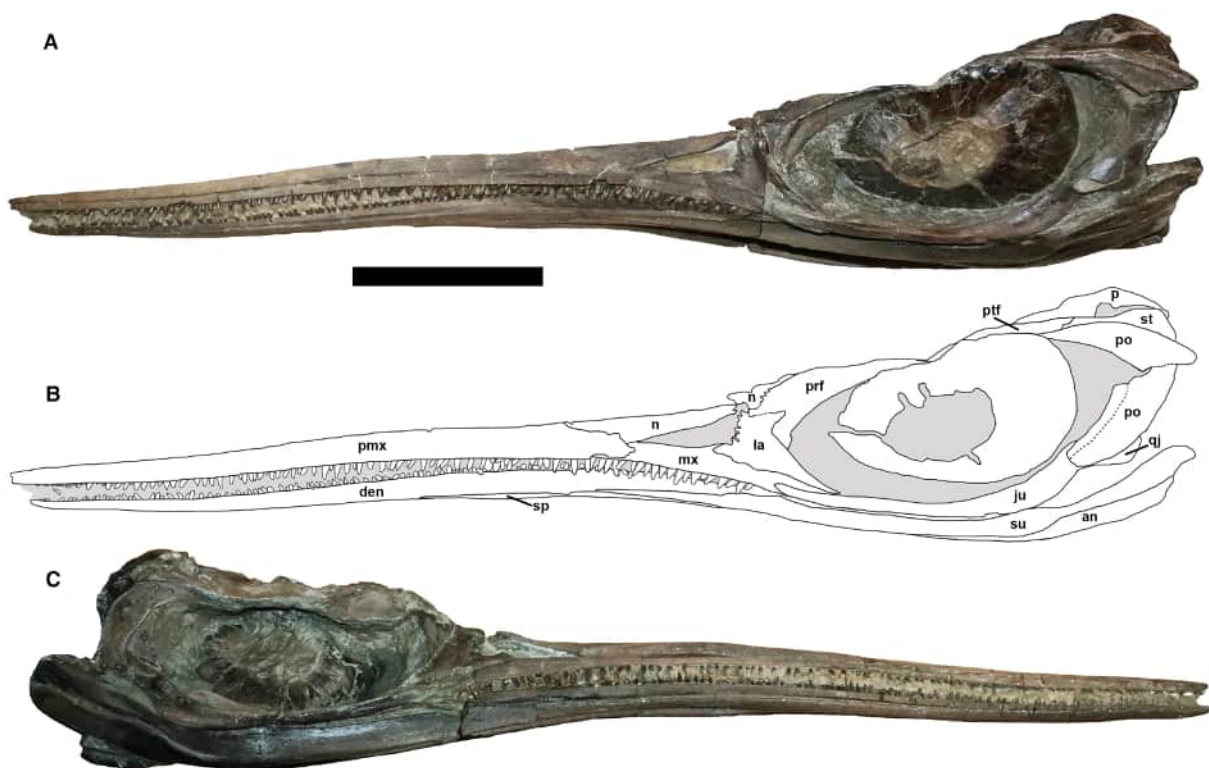


FIG. 3. Skull of *Xiphodracon goldencapensis* (ROM VP52596). Photograph (A) and interpretative illustration (B) in left lateral view. C, photograph of the right lateral view. Note the unusual, multi-prong projections on the anterodorsal margin of the lacrimal and similar but smaller interdigitating structures on the prefrontal (see also Fig. 4). *Abbreviations:* an, angular; den, dentary; ju, jugal; la, lacrimal; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; po, postorbital; prf, prefrontal; ptf, postfrontal; qj, quadratojugal; sp, splenial; st, supratemporal. Scale bar represents 10 cm.

(foramen) is formed by the nasal (Fig. 3). The supranarial process of the premaxilla extends posteriorly to about the anterior edge of the naris, but does not contribute to its margin. The nasals extend approximately one narial length beyond the external naris in lateral view, where they become covered by the especially long and narrow premaxillae, which encompass almost all of the lateral margin of the skull anterior to the external naris. The nasals comprise 59% of snout length in dorsal view; the remainder of which is occupied by the premaxilla (Fig. 2C). At the posterior margin of the external naris, the nasals ‘pinch’ mediolaterally and then widen again along the dorsal margin of the naris.

The posterior ends of the nasals are similarly dorsoventrally flattened as the frontals, at least in part, making the morphology difficult to discern (Fig. 2). However, both the left and right show some sort of interdigitating with the prefrontal posteriorly and form a broad contact with the prefrontal laterally. Each nasal appears to end posteriorly with an extension of a thin, slender ‘spur’ that seemingly interdigitates with the parietal (Fig. 2A, B).

The lacrimal is best preserved on the left side (Figs 3A, B, 4B). It is a triradiate element with a tall, wide dorsal process, a slightly longer ventroposterior process, and a shorter anterior process. Most notably, the entire anterodorsal border of the

lacrimal is rugosely striated and has as many as six ‘prongs’ projecting along its anterior edge (Figs 3A, B, 4B), a morphology that is unknown in any other ichthyosaurian taxa. More peculiar, a couple of the prongs bifurcate at their anterior end. Although the lacrimal is incomplete and damaged on the right side, the preserved dorsal and anterior margins have the same morphology as the left (Fig. 4B–D). Similarly, the right prefrontal clearly shows interdigitation with the nasal and the lacrimal. Thus, these features are not pathological (e.g. the result of bone remodelling) but instead may be related to the presence of salt glands (Massare *et al.* 2021).

The lacrimal forms most of the posterior margin of the large, wedge-shaped external naris, along with at least one-quarter to one-third of the posteroventral margin, as best observed on the left side (Figs 3A, B, 4B). However, at the posterodorsal corner of the nares is a noticeable circular region or foramen (Figs 3B, 4B–D). A small flange on the nasal and part of the lacrimal form a constriction that connects the foramen to the main, much larger portion of the narial opening. The foramen is bordered by the nasal, which has a noticeable circular indentation; the dorsal process of the lacrimal; and a minor contribution by the narial process of the prefrontal. The combination of characters is unusual, and the presence of a distinct upper foramen connected to the external naris is unique among Early Jurassic ichthyosaurs.

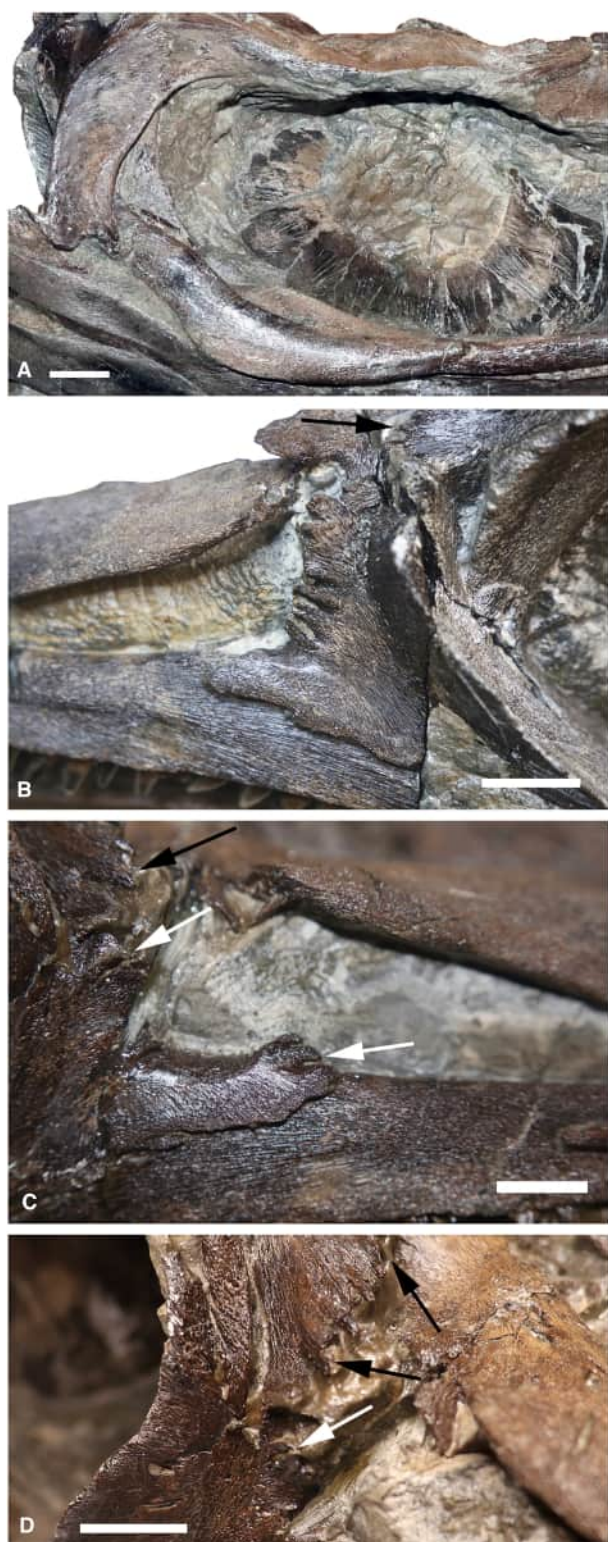


FIG. 4. The post-orbital and lacrimal–prefrontal regions of *Xiphodracon goldencapensis* (ROM VP52596). A, close-up of the right post-orbital region of the skull showing the tall, antero-posteriorly wide and robust postorbital that tapers dorsally but not ventrally and comprises more than half of the posterior margin of the orbit. B, close-up of the left narial region showing the wedge-shaped external naris with the posterodorsal foramen formed by the nasal, lacrimal and prefrontal; note the unusual, multi-prong (and sometimes bifurcating) projections on the anterodorsal margin of the lacrimal and similar structures on the prefrontal (arrow). C, similar view as in B but from the right side, showing the damaged, incomplete lacrimal but with the multi-prong projections (in B, C and D the black arrows indicate projections on the prefrontal; white arrows indicate projections on the lacrimal). D, oblique view of C but showing more detail of prefrontal projections and posterodorsal foramen. Scale bars represent: 2 cm (A); 1 cm (B–D).

Most of the features of the skull roof can be discerned (Fig. 2A, B). The prefrontal is best preserved on the left side of the skull. It comprises a significant part of the mid-lateral margin of the skull roof, which does not appear to be due to deformation although it is displaced on the right side (Fig. 2A, B). Notably, the prefrontal has extensive medial exposure and contacts the parietal, separating the nasal from the extensive anterior end of the postfrontal. Thus, the postfrontal does not contact the frontal. Although the medial-most edge is damaged, the prefrontal probably also does not contact the frontal. Motani (2005) noted this unusual prefrontal exposure in ROM VP52596. Similar morphology is known in *Stenopterygius* (Motani 2005; Maxwell *et al.* 2012) and in another isolated Lower Jurassic skull (NHMUK VP R15943; Motani 2005, fig. 1C, D; and Lomax *et al.* 2020, p. 648).

The prefrontal anterior process is dorsoventrally robust and bifurcated, with the posterior portion making a large contribution to the anterior orbital margin and the anterior portion exposed on the anterolateral surface of the skull and contributing to the margin of a posterodorsal foramen connected to the external narial opening (see below; Figs 2B, 3, 4B–D). The participation of the prefrontal in the external narial opening is shared only with *Hauffiopteryx* among Early Jurassic ichthyosaurs. The anterior portion of the prefrontal also has several projecting structures that are similar to those on the lacrimal, as observed on both sides (Figs 3B, 4B–D), which is unique among ichthyosaurs. The anterior process of the prefrontal forms about half the anterior margin of the orbit, excluding the lacrimal dorsal process from the orbit margin. Similar morphology is observed in *Ichthyosaurus somersetensis*, *I. larkini*, *Hauffiopteryx* and *Leptonectes*. In contrast, the lacrimal dorsal process has a substantial contribution to the orbital margin in *Ichthyosaurus communis* and *Stenopterygius* (McGowan & Motani 2003; Motani 2005; Maxwell 2012a; Maxwell *et al.* 2012; Massare & Lomax 2018a; Maxwell & Cortés 2020).

In lateral view the orbit is equally well preserved on either side, although it is deformed and some displacement has occurred (Fig. 3). The scleral rings are somewhat damaged by

Massare *et al.* (2021) reported similar structures in the posterior region of the naris in several Early Jurassic ichthyosaurs and suggested that they might be for a salt gland structure.

crushing, but consist of c. 17 ossicles (Fig. 3). Based on the better-preserved left orbit, the external diameter of the ring was 11.5 cm, and the internal diameter is estimated at 4.5 cm (retro-deformed: 5.1 cm internal horizontal $\times$ 3.9 cm vertical).

The postfrontal makes up about one-third of the dorsal margin of the orbit, with the posterior end of the prefrontal making up the remaining anterodorsal border. About two-thirds of the posterior margin of the orbit is made up of a tall, anteroposteriorly wide and robust, slightly curved postorbital that tapers dorsally but not ventrally, where it overlaps the jugal dorsal ramus (Figs 3, 4A). Although there is some displacement on either side of the skull, the right side probably represents the correct morphology for the postorbital. A narrow anterodorsal process of the postorbital comprises one-third of the dorsal margin of the orbit and separates the posterior half of the postfrontal from it (Fig. 4A). A small part of the dorsal margin of the postorbital is exposed on the skull roof, posterolaterally to the postfrontal (Fig. 2A, B). The dorsal exposure of the postorbital is best observed on the right side and could be autapomorphic, although this might also be exaggerated by the slight dorsoventral crushing of the skull.

In *Protoichthysaurus prostaialis* (Lomax *et al.* 2017a, 2020), the postorbital is a substantially large element that is anteroposteriorly wide, although not as tall as in ROM VP52596. In *Ichthysaurus anningae* the postorbital is roughly rectangular and comprises most of the posterior margin of the orbit (Lomax & Massare 2015). The postorbital morphology in ROM VP52596 also differs from the tall and narrow postorbital typically seen in *Hauffiopteryx*, *Leptonectes*, *I. somersetensis* and *I. conybeari*, for example (McGowan & Motani 2003; Massare & Lomax 2016; Lomax & Massare 2017; Maxwell & Cortés 2020).

The jugal comprises the entire ventral margin of the orbit except for a slight contribution from the ventroposterior (suborbital) process of the lacrimal, which has minor contact with the jugal ventrally (Fig. 3). The anterior process of the jugal extends just beyond the orbit margin, where it contacts the posterior process of the maxilla. It does not reach the external narial opening. The dorsal ramus of the jugal has a gentle bend and makes up the remaining one-third of the posterior margin of the orbit. The dorsal ramus of the jugal has a boss and prominent embayment along its posterior edge in the region of the glenoid (Fig. 3).

Both squamosals are preserved along the posterior skull. The squamosal is an elongate, very narrow triangle, tapering ventrally (Fig. 5D). It is very dorsoventrally tall, extending from the posterior skull roof to almost the quadrate facet. The squamosal forms the lateral and dorsal walls of the quadrate foramen. The elongate squamosal, extending the entire length of the cheek is shared only with *Suevoleviathan* and *Hauffiopteryx* among Early Jurassic ichthyosaurs (Maisch 2001, p.45; EEM pers. obs. 2024; BRLSI M1399, M1401).

The quadratojugal is exposed on the left side, although it is largely concealed by overlapping elements, specifically the squamosal (Fig. 5D). In lateral view it forms a concave ventral edge posterior to its articulation with the posterior jugal, framing a small infratemporal embayment. The quadratojugal is exposed primarily in posterior view, where it is overlapped by the squamosal laterally, and forms a defined quadrate process medially.

In the posterior dorsal skull roof the postfrontal comprises half of the anterior and practically all of the lateral margin of the upper temporal fenestra; the supratemporal comprises a small section of the posterior half of the lateral, all of the posterior, and just under half of the medial margin; and the parietal forms the rest of the medial margin and half of the anterior margin. The lateral ramus of the supratemporal is much longer than the medial ramus, despite the small contribution to the lateral temporal fenestra.

The frontals are dorsoventrally depressed inward, therefore their exact morphology is difficult to interpret, but they appear anteroposteriorly much longer than mediolaterally wide. The pineal foramen is an elongate oval and is almost wholly surrounded by the frontals, with a small parietal contribution along the posterior edge of the opening but this is unclear because of crushing/damage (Fig. 2A, B). It is also possible that the parietals overlap the posterolateral ends of the frontals. The position of the pineal in ROM VP52596 is similar to *Leptonectes*, *Temnodontosaurus*, *Stenopterygius* and *Protoichthysaurus* (McGowan & Motani 2003; Motani 2005; Maxwell *et al.* 2012; Lomax *et al.* 2020).

The ventrolateral edge of the supratemporal is especially robust and extensive, with a well-developed ventral ramus that contacts the dorsal process of the quadrate ramus of the pterygoid and medial surface of the quadrate. The ventral ramus is notched anteriorly, potentially the same structure as that interpreted as passage for a blood vessel in *Ophthalmosaurus* (Moon & Kirton 2016), although the anterior edge of the channel is not ossified in *Xiphodracon*. Posterior to the contact with the postfrontal, a section of the supratemporal is damaged and could be mistaken for a squamosal due to its trapezoidal shape; we interpret this as part of the supratemporal rather than a squamosal. Both parietals are complete and form a low sagittal crest. They seemingly diverge approximately halfway along their midline, forming an opening that is adjacent to (or part of) the pineal foramen (Fig. 2A, B). This feature is most similar to that seen in *Stenopterygius* (Motani 2005, fig. 2b), although it is possibly preservational in ROM VP52596.

Both quadrates are preserved, but are mostly concealed behind the postorbital and jugal (Fig. 5D). At the posterior end of the skull, in posterior view, the left quadrate is exposed a little more, but its morphology is hard to interpret because it is surrounded by matrix and other bones. It appears laterally concave with an apparent saddle-like shape and robust articular condyle.

The left pterygoid is poorly exposed in posterior view. The dorsal process of the quadrate ramus contacts the quadrate laterally.

Regarding the braincase, the supraoccipital, exoccipitals and basioccipital were fully prepared from the matrix. The basioccipital is noticeably wider than tall (Fig. 5A–C). It has a bulbous, circular occipital condyle that occupies about half of the posterior surface. In posterior view the extracondylar area is extensive, and mediolaterally wide (Fig. 5A); somewhat semicircular with distinctly flared lateral edges, but less so than seen in *Leptonectes* (Lomax & Massare 2012). A medial indentation in the extracondylar area is visible in posterior view. The lateral edge of the extracondylar area forms part of the stapedial facet. The opisthotic facet is substantially larger (about twice the size) than

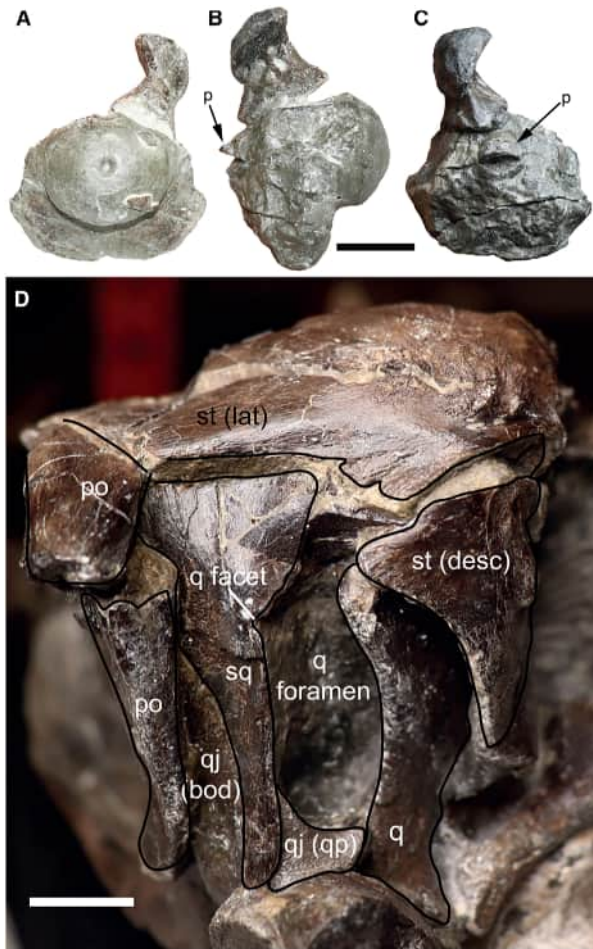


FIG. 5. A–C, basioccipital and right exoccipital of *Xiphodracon goldencapensis* (ROM VP52596) in: A, posterior; B, lateral; C, anterior view. D, left posterolateral cheek region of the skull. **Abbreviations:** p, basioccipital peg; po, postorbital; q, quadrate; qj (bod), body of the quadratojugal; qj (qp), quadrate process of the quadratojugal; q facet, quadrate facet on the squamosal; q foramen, quadrate foramen; sq, squamosal; st (desc), descending ramus of the supratemporal; st (lat), lateral ramus of the supratemporal. Scale bars represent 2 cm.

the stapedial facet. The condyle is demarcated from the extracondylar area by a distinct ridge. The extracondylar area is oriented primarily in the anteroposterior plane, appearing minimized in posterior view. This is similar to the configuration in *Hauffiopteryx* or *Temnodontosaurus*, for example, but different to the configuration in *Eurhinosaurus*, where the extracondylar area is expanded ventral to the condyle, or *Ichthyosaurus*, where it is more expanded both ventral and lateral to the condyle. The extent of the condyle and extracondylar area appears outwardly similar to what has been observed in many Early Jurassic taxa, such as *Ichthyosaurus* (McGowan & Motani 2003; e.g. NHMUK VP R6697), *Excalibosaurus* (McGowan 2003), *Leptonectes* (Lomax & Massare 2012), *Wahlisaurus* (Lomax 2016) and *Hauffiopteryx* (Maxwell & Cortés 2020).

The exoccipital facets are rectangular and separated by a ridge capped by a narrow anteroposterior surface that makes up the floor of the foramen magnum (Fig. 5B). A small basioccipital peg is present on the rugose anterior surface, as in Early Jurassic forms such as *Ichthyosaurus*, *Excalibosaurus* and *Stenopterygius* (Motani 1999a; McGowan 2003; Miedema & Maxwell 2019), although it is smaller. The peg is best observed in dorsal, anterior and lateral views (Fig. 5B, C). Although damaged ventrally, the dorsal portion of the peg is complete and can be seen projecting from the basioccipital in lateral view (Fig. 5B).

The right exoccipital is articulated with the basioccipital and is a short, wide element forming the lateral edges of the foramen magnum (Fig. 5A–C). The supraoccipital facet is broad and triangular and the medial edge is slightly concave. The left exoccipital is preserved on a separate block on the underside of the main skull block, where it is associated with the atlas–axis. The supraoccipital is preserved but is damaged, with the left half being the most complete (Fig. S4). It is convex and arched in anterior and posterior views and is wider than it is tall. It contacts the exoccipital along a broad facet. A pair of foramina are clearly exposed on the anterior surface and probably served for the passage of the endolymphatic ducts. When the supraoccipital is articulated with the left exoccipital and basioccipital, the exoccipital appears to contribute slightly more than half of the height of the margin of the foramen magnum. The descending rami of the supraoccipital are divergent. On the posterolateral surface of the supraoccipital, a clear impression of the membranous labyrinth is preserved; this is weakly triradiate.

Several bones are exposed at the posterior end of the skull, mostly in matrix, but displaced from life position. The left (and what might be the right) stapes is mediolaterally elongate, with a bulbous occipital head and seemingly tapered distal end (Fig. S4). Both robust opisthotics are preserved, but the left is partly concealed by other bones and matrix. The right, however, is exposed in ventrolateral view (Fig. S4), on a separate skull block (with the atlas–axis and other bones). The opisthotic has a well-defined ridge with a lip that delineates the basioccipital facet. A ?right prootic is preserved on the right side of the posterior skull in anterior view (Fig. S4). The ventral surface is rounded, whereas the dorsal surface is weakly pronounced into two processes, similar to the morphology described for *Stenopterygius* (Miedema & Maxwell 2019). The block containing the basioccipital originally filled part of the cavity dorsal to the prootic and was associated with it prior to preparation.

Mandible & dentition. The right and left mandible are nearly complete, with the left missing just a few millimetres of the anterior tip and the posteriormost part of the angular (Fig. 3). The lower jaw is 66.2 cm in length. In lateral view, at the posteriormost end, two-thirds of the exposure is surangular, one-third is angular (Fig. 3A, B). The posterolateral surangular bears a roughened, recessed surface, slightly dorsal to the angular facet. Anterior to the glenoid region, the surangular fossa is dorsally overhung by a sharp ridge.

Immediately anterior to the glenoid region, the angular increases in height and the surangular decreases until the anterior edge of the infratemporal embayment (= posterior jugal boss). The angular exposure greatly decreases at the posterior

orbit margin, and the surangular comprises most of the mandible under the orbit (Fig. 3A, B). The angular disappears at about the midpoint of the orbit in lateral view. Among Early Jurassic taxa the larger, more extensive angular exposure in posterolateral view is most similar to what occurs in *Temnodontosaurus*, *Leptonectes moorei* and, to a lesser extent, *Stenopterygius* (McGowan & Milner 1999; McGowan & Motani 2003; Maxwell 2012a). A large angular exposure is seen in ophthalmosaurians, but it extends much farther anteriorly in lateral view than in ROM VP52596 (e.g. McGowan & Motani 2003; Kear 2005; Druckenmiller *et al.* 2012; Moon & Kirton 2016). In ventral view the angular and surangular extend to approximately the same level as each other in *Xiphodracon*, approaching the posterior mandibular symphysis (Fig. 2D).

In lateral view the surangular is underlapped by a minor exposure of the splenial (Fig. 3), starting towards the anterior margin and extending well beyond the surangular exposure (by just under 10 cm). This lateral exposure can be seen on both sides of the lower jaw, therefore it is unlikely to be taphonomic. The splenial has a small lateral exposure on at least some Upper Jurassic ophthalmosaurians (e.g. Gilmore 1906; Druckenmiller *et al.* 2012; Moon & Kirton 2016), and a ventrally protruding splenial is also observed in *Hauffiopteryx altera* (Maxwell & Cortés 2020). The mandibular symphysis is 33.5 cm long (Fig. 2D), of which the splenial contributes 45% and the dentary 55% (18.5 cm). This differs from *Hauffiopteryx typicus*, in which the splenial forms a slightly greater proportion of the mandibular symphysis than the dentary, but also from *Temnodontosaurus*, in which the splenials extend almost to the anterior end of the mandible (Fraas 1913; Maxwell & Cortés 2020).

Both articulars are preserved: that on the right is best exposed and undamaged, whereas that on the left is broken posteriorly. The right articular is rather rounded in shape, and is only weakly concave medially. The prearticular facet is well-defined. The posterior edge of the right prearticular is preserved in articulation with the angular and articular.

Both hyoids are preserved and are slightly curved, rod-like bones (Figs 2D, S2). Although partly obscured, the anterior and posterior ends seem to be slightly flattened.

At its posterior end the dentary lateral exposure is long and narrow, represented by a sliver under the orbit in lateral view (Fig. 3A, B), first appearing just anterior to the midpoint of the orbit (best seen on the right side), similar to *Stenopterygius* and *Hauffiopteryx* (McGowan & Motani 2003; Maxwell & Cortés 2020). However, this is unlike *Ichthyosaurus* and *Protoichthyosaurus*, for example, in which the dentary exposure is deeper posteriorly (Lomax & Massare 2017, 2018) or *Leptonectes moorei* that has a shorter, distinctly blunt posterior end of the dentary (McGowan & Milner 1999). The dentary is not prominent until a point anterior to the maxilla, where the surangular exposure is small; the surangular disappears slightly anterior to the external naris. An irregular groove (the dentary fossa) extends the length of the dentary, from the posterior edge of the naris to almost the anterior tip. A similar, corresponding groove (premaxillary fossa) extends along the length of the premaxilla. No overbite is present, best observed in right lateral view (Fig. 3C).

The tooth crowns are small and slender (Figs 3, 6). The best preserved teeth show fine enamel ridges that extend almost to the smooth crown apex. The roots are narrow, not bulbous, and show grooves/infolds that are continuous with some of the ridges of the crown (Fig. 6). The enamel is thin, especially towards the base of the crown. The teeth are relatively similar in size and shape along the length of the jaw (Figs 3, 6), and many show signs of apical wear. Many teeth show evidence of malformation similar to that figured in *Stenopterygius* (Maxwell *et al.* 2022, fig. 5j), namely a bulge or 'swelling' of the root at the base of the crown on some teeth (Fig. 6). Because these teeth are interspersed with 'normal' teeth along the jaw, this malformation appears to reflect a discrete event (injury, disease) during the life of the animal that affected teeth during their development. A total of 15 (right side) and 18 (left side) maxillary teeth are preserved. The maxillary tooth row extends posteriorly to just anterior to the orbital margin.

Axial skeleton. The atlas–axis complex is disarticulated and lying between the mandibles on a separate block of matrix. The centra are fused, but can be differentiated by a shallow groove on the floor of the neural canal and a ridge on the lateral surface. On the ventral surface are facets for the atlantal and axial intercentra. The axial neural arch is damaged, but clearly robust. The atlantal neural arch was not medially fused to its contralateral element, nor to the axial arch. Only the right half was exposed, preserved in medial view; the left half remained in articulation with the axial arch (only base of neural arch visible). The pro-atlas process may be damaged, given that there appears to have been breakage in this region. The neural spine appears to have been reduced relative to that of the axis.

The preserved length of the vertebral column is 152.5 cm, measured along the vertebral column from the position of the atlas–axis to the posterior end of the specimen (Fig. 1). The precaudal length of the vertebral column is 116.0 cm, excluding the skull. Most of the cervical and dorsal centra are covered by ribs from the left side of the ichthyosaur. Ribs from the right side are preserved in articulation with the vertebral column, but ventrally compressed into a condensed mass that runs from the pectoral girdle to the caudal centra.

Two portions of the vertebral column are articulated: one segment adjacent and immediately posterior to the pectoral girdle, and a second segment in the posterior-most portion of the specimen (Fig. 1). The centra anterior to the pectoral girdle and those in the posterior dorsal region are not articulated.

There are 44 precaudal centra, counting the atlas–axis as two. The first caudal centrum (no. 45) is identified as the first centrum to have a single, elongated rib articulation (= synapophysis). A total of 13 caudal centra are preserved, but this is about one-third of the number that would be expected anterior to the tail bend (Buchholtz 2001, fig. 5), therefore a substantial portion of the tailstock is missing. Two much smaller caudal centra from near the apical region and a single, disarticulated, fluke centrum are preserved in the matrix adjacent to the distal end of the preserved vertebral column. Haemaphyses and ossified haemal arches are absent on the anterior caudal centra, unlike in *Ichthyosaurus* (McGowan & Motani 2003; Lomax & Massare 2017, fig. 4b) and *Eurhinosaurus* (von Huene 1928; EEM



FIG. 6. Representative dentition of *Xiphodracon goldencapensis* (ROM VP52596). A, maxillary teeth. B, a segment from a more anterior position in the rostrum. The tooth crowns are small, mostly slender and have fine enamel ridges that extend almost to the smooth crown apex. White arrows show examples of malformed teeth that bear a distinct bulge or swelling of the root at the base of the crown (compare with 'normal' teeth present). C, inset tooth represents another malformed tooth showing the distinctive bulge (black arrow). Scale bars represent 1 cm.

pers. obs. 2022). Anterior caudal centra are *c.* 2.6 cm long $\times$ 6 cm wide.

For two common Early Jurassic genera, *Stenopterygius* and *Ichthyosaurus*, the tailstock is *c.* 60% of the precaudal length of the vertebral column (Buchholtz 2001, table 1). If this specimen had similar proportions, the tailstock would have been *c.* 70 cm, giving an estimated preflexural length of the vertebral column of 186 cm. Thus the preflexural length of the specimen, including the skull, would have been *c.* 250 cm. This is a minimum estimate, however, because some Early Jurassic genera (*Eurhinosaurus*, *Suevoleviathan*, *Temnodontosaurus*) had tailstocks that were proportionally longer than in *Ichthyosaurus* and *Stenopterygius* (Buchholtz 2001, fig. 5). Exactly where *Xiphodracon* falls along this spectrum can be determined only with the discovery of additional specimens.

Cervical ribs are weakly bicipitate, with the two heads projecting slightly but connected by a sheet of bone. The dorsal ribs are strongly grooved on both the anterior and posterior surfaces in the shoulder region (figure-eight cross-section). Dorsal ribs

are more strongly bicipitate than the cervical ribs. Ribs decrease in length rapidly in the caudal region, becoming short and paddle-like.

The position of the left hindfin is about two centra posterior to the first caudal centrum, as determined based on the first synapophysis. This is likely to be taphonomic displacement of the hind fin, based on both a rapid decrease in rib morphology and rib curvature. The rib associated with the first synapophysis curves anteriorly at its distal end, indicating that the last dorsal centrum has been correctly identified.

Gastralia are preserved *in situ*, overlying the ribs and extending over at least two-thirds of the presacral length to approximately centrum 38, with those gastralia from the left side (a lighter colour) extending across the block posterior to the pectoral girdle (Fig. 1). A median gastral element is absent; 1–2 elements are present laterally. A single example of a laterally bifurcating element is preserved. The posterior extent of the gastralia is known only from *Hauffiopteryx* among Early Jurassic ichthyosaurs (Maisch 2008), although there is evidence that the

gastral basket in at least some specimens of *Ichthyosaurus* extends as far posteriorly (e.g. *I. somersetensis*, BRSMG Ce 16611; *I. communis*, CAMSM J35187 and MCZ 1494), and better documentation in Hettangian–Sinemurian taxa is warranted.

Pectoral girdle & forefin. The robust coracoids are exposed in ventral view (Fig. 7). There is a large, deep anterior notch, best seen on the left coracoid. *Temnodontosaurus*, *Leptonectes*, *Excalibosaurus*, *Eurhinosaurus*, *Hauffiopteryx* and *Stenopterygius* have coracoids with only an anterior notch (McGowan & Motani 2003; Maxwell & Cortés 2020), whereas *Ichthyosaurus* and *Protoichthyosaurus* have coracoids with both anterior and posterior notches (Lomax *et al.* 2017a; Massare & Lomax 2018a). The depth of the notch is comparable to what occurs in some *L. tenuirostris* specimens (e.g. BRLSI M3556, ANSP 17307, BGS GSM 51236), although it is quite variable for the species (DRL, JAM pers. obs. 2018, 2024). The deep anterior notch and overall coracoid morphology are very similar to the coracoid of *Excalibosaurus* (Fig. 7; ROM VP47697; DRL, JAM pers. obs. 2016, 2024). The scapular facet in *Xiphodracon* is less than half the length of the glenoid facet and at almost a 90° angle to it. The posterior edge of the coracoid is broadly curved, seen best on the left coracoid. The coracoids are about one-third longer anteroposteriorly than mediolaterally. The posterior end is notably mediolaterally broad and does not narrow (Fig. 7).

The scapula is much longer than the humerus (Fig. 7). The proximal end is much wider than the distal end, as in *Ichthyosaurus*, *Leptonectes* and *Stenopterygius* (McGowan & Motani 2003, fig. 70). The anterodorsal margin is broad in *Xiphodracon*, essentially fan shaped, whereas the distal end is only slightly expanded. A weak acromial process is present, best preserved on the left side.

The interclavicle and clavicle are articulated, but separated from the coracoids. The interclavicle is T shaped with a very long medial process that extends the entire length of the coracoids, and widens slightly at its posterior end (Fig. 7). The exceptionally long medial process may also be shared with *Excalibosaurus* (ROM VP47697; DRL, JAM pers. obs. 2016, 2024).

The transverse bar is very short, giving the anterior end an almost triangular shape. The clavicle is broad, almost wing-like medially, and narrows where it contacts the scapula. The right clavicle appears to have been fractured and rehealed just lateral to the facet for articulation with the scapular acromial process.

Both forefins are preserved, but the left one is at a c. 90° angle to the rest of the skeleton (Figs 1, 8). The humerus is longer than it is wide, and much wider distally than proximally (Fig. 8), similar to *Leptonectes*, *Temnodontosaurus* and *Stenopterygius* (Motani 1999b, figs 4–5; McGowan & Motani 2003, fig. 70). The distal edge is slightly elongated anteriorly, with a distinct facet at the anterior end, as sometimes occurs in *L. tenuirostris* (e.g. NHMUK VP R498, BGS GSM 118411, BRLSI M3575). The shaft is fairly narrow, less than half the width of the distal end at its narrowest point. The dorsal process is positioned above the midpoint of the radius, offset anteriorly from the centre with a highly reduced dorsal trochanter, and forms a sharp ridge that extends only a short distance along the length of the shaft (Fig. 8C). The deltopectoral crest is small and also anterior to the centre (Fig. 8D). Viewed proximally, the head of the humerus is roughly oval in shape and fairly flat, not bulbous. Neither process is prominent in this view. A distinct groove extends across more than half of the proximal region (Fig. 8E–G), separating the ventral and dorsal processes, best seen in anterior and posterior views, where the humeral head appears to be heart shaped (i.e. two lobes) (Fig. 8E, G). This probably represents pathological subsidence of the proximal joint surface.

There are four digits, with two digits (III, IV) in contact with the intermedium and two (IV, V) in contact with the ulnare (Fig. 8A, B) as in *Stenopterygius* (Motani 1999b; Maxwell 2012b), *Hauffiopteryx* (Maxwell & Cortés 2020) and some *Leptonectes tenuirostris* specimens (e.g. NHMUK VP R498, BRLSI M3575). Digits II and III are more prominent than digits IV and V. The phalanges of digits II, III and IV are anteroposteriorly elongated ovals, but digit V has circular phalanges that are noticeably smaller than those of the other digits (Fig. 8A, B). The morphology of the carpal and metacarpal rows and the relative prominence of the digits is similar to

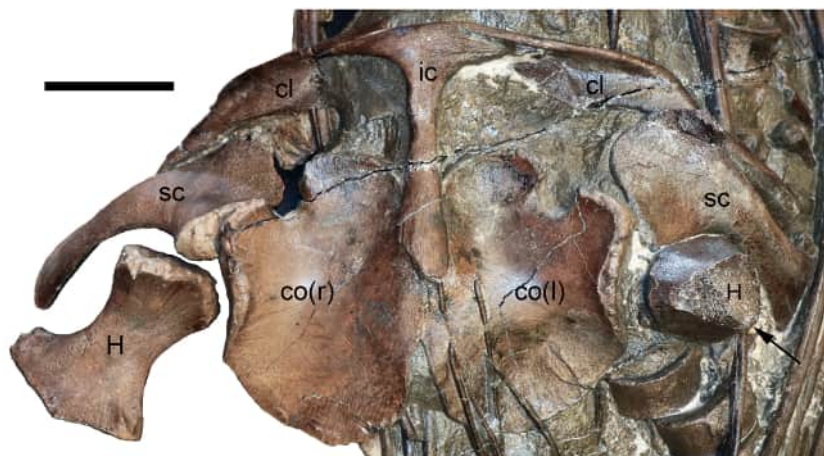


FIG. 7. Pectoral girdle of *Xiphodracon goldencapensis* (ROM VP52596) exposed in ventral view. Arrow points to the proximal region of the left humerus, which is preserved *in situ*. This articulates with the rest of the left forefin in Figure 8A. Abbreviations: cl, clavicle; co (r)/co (l), right and left coracoids; H, humerus; ic, interclavicle; sc, scapula. Scale bar represents 5 cm.

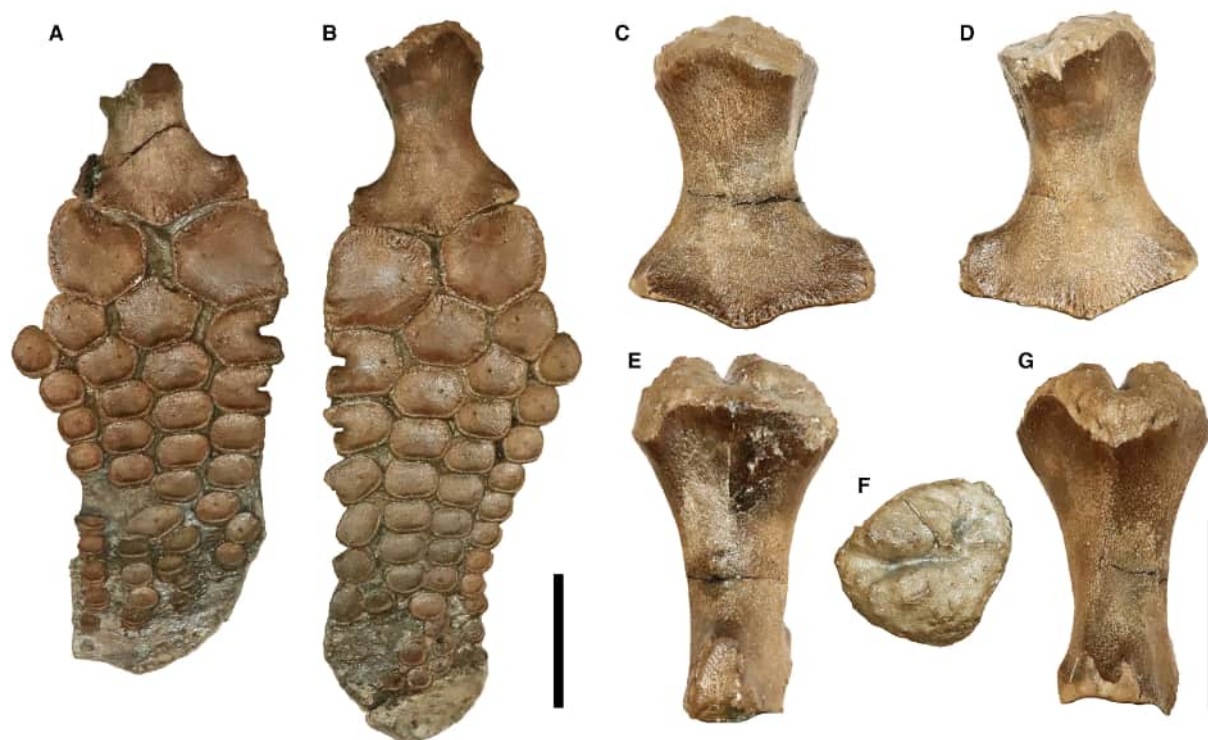


FIG. 8. Forefins of *Xiphodracon goldencapensis* (ROM VP52596). A, left forefin in ventral view, anterior to the right; note that the proximal region of this fin is preserved *in situ*, as can be observed in Figure 7. B, right forefin in ventral view, anterior to the left. C–G, right humerus in: C, dorsal; D, ventral; E, anterior; F, proximal; G, posterior view. Scale bars represent 5 cm (A–B; C–G).

Stenopterygius triscissus and the Late Triassic *Macgowania janiiceps* (McGowan 1996; Motani 1999b; Maxwell 2012b). The radius is noticeably larger than the ulna and has a small bump towards the anterodistal surface (in both radii) that might prove to be taxonomically useful. It is not notched, unlike some *Stenopterygius*, *Hauffiopteryx*, *Excalibosaurus*, some *Temnodontosaurus*, and *L. tenuirostris* specimens (Motani 1999b; McGowan 2003; McGowan & Motani 2003; Maxwell & Cortés 2020), but the radiale, distal carpal (and the metacarpal only on the right forefin) are notched anteriorly (Fig. 8A, B). This notching pattern is unique among leptonektids (including *Hauffiopteryx* spp.), which either always have a notched radius (with or without notching in other elements) or lack notching entirely (compare forefin morphologies in Fig. S5). However, intraspecific variation in notching occurs in some taxa (e.g. Maxwell *et al.* 2014). The fin elements are closely packed, in contact with one another on the right fin, but less so on the left fin. Many limb elements, including the propodials, bear vascular foramina on their dorsal and ventral surfaces (Fig. 8C–G); the significance of this is currently not understood. Lomax *et al.* (2017b) reported abundant foramina on most of the snout and postcranial skeleton of a neonate specimen of *Ichthyosaurus communis*. These foramina are not nearly as widespread on ROM VP52596, but instead occur as isolated foramina in the centre of the limb elements distal to the propodials (see below).

Pelvic girdle & hindfin. The pelvis is tripartite, as in most Early Jurassic ichthyosaurs. Both pelves are present, but the right

pelvis is the most complete, which is lying in a block of matrix, close to the mass of ribs and some distance from the vertebral column (Figs 1, 9D, E). The left pelvis is along the vertebral column, associated with the left hindfin. Both ischia and pubes are articulated, although one side is missing half of the pubis and the other side is missing half of the ischium (Fig. 9D, E). The complete (left) ischium is oblong, but with a robust proximal end, narrow shaft and an anteroposteriorly expanded distal end that is slightly wider than the proximal (Fig. 9E). The ischium is more than 10% longer than the ilium, pubis and femur. The pubis (right) is more slender than the ischium. The proximal and distal ends are slightly expanded relative to the shaft, which is especially narrow. A single, narrow ilium has only a subtle curvature (Fig. 9D). It is the shortest element in the pelvis and is also shorter than the femur. The morphology of the pelvis (specifically the slender elements that only slightly widen at the ends) is more similar to that of *Ichthyosaurus communis*, *I. breviceps* and *I. conybearei*, rather than the morphology of the more anteroposteriorly expanded bones observed in *Ichthyosaurus somersetensis*, *Leptonektes*, *Eurhinosaurus*, *Wahlisaurus* and *Temnodontosaurus*; or the fused ischiopubis in *Stenopterygius* or *Hauffiopteryx* (McGowan & Motani 2003; Maxwell 2012a; Massare & Lomax 2014, 2016; Lomax 2016; Lomax & Massare 2017; Maxwell & Cortés 2020).

The right hindfin is represented only by the femur. The articular surface shows weak subsidence, probably pathological, and there is a perimortem bite mark on the posterodorsal edge (Fig. 9B; see Palaeobiology, below, for discussion). The left

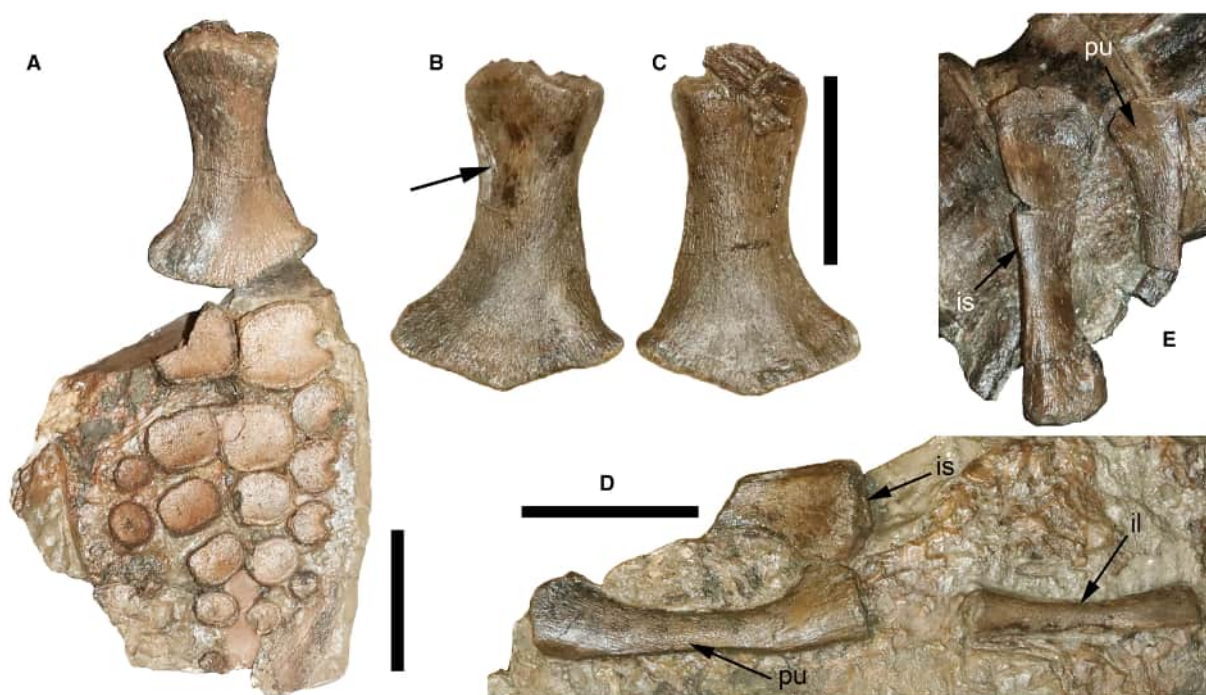


FIG. 9. Hindfin and pelvic girdle of *Xiphodracon goldencapensis* (ROM VP52596). A, left hindfin in ventral view, anterior to the right; note the notched tibia and additional notched elements. B–C, right and left femora, dorsal view; arrow points to a bite mark. D, the most complete pelvis (right). E, the incomplete left pelvis. *Abbreviations:* il, ilium; is, ischium; pu, pubis. Scale bars represent 3 cm (A; B–C; D–E).

hindfin is exposed in ventral view and appears to be nearly complete (Figs 1, 9A). Including the tibia, the anterior digit has five elements preserved. The femur is long, with only a minor anteroposterior expansion proximally and a constricted shaft that widens distally, forming a noticeably wide posterodistal expansion (Fig. 9B, C). In ventral view the ventral process is sharply offset anteriorly (Fig. 9A), whereas in dorsal view the dorsal process is highly reduced and is barely apparent (Fig. 9B, C). The proximal head is almost D shaped in anterior view, rugose, with a roughened bone texture, and is essentially flat rather than bulbous, with a slight depression attributed to subsidence of the proximal joint surface, probably due to pathology. When viewed distally only one long facet for both the tibia and fibula is evident, but in both dorsal and ventral views there is a distinct angle between the facets. The hindfin has four primary digits, but digit V is less prominent, smaller, and has more rounded elements (Fig. 9A). The tibia is notched, as is distal tarsal 2 (tibiale), metatarsal II and at least the first phalanx. As in the forefin, intraspecific variation might also occur in hindfin notching (Massare & Lomax 2018b). The tibia notch is an open C shape that is slightly proximodistally elongate. A notched tibia is known in a few Early Jurassic taxa, including *Leptonectes tenuirostris*, *Ichthyosaurus conybeari*, *Eurhinosaurus*, *Excalibosaurus*, *Hauffiopteryx*, *Suevoleiathan*, some species of *Temnodontosaurus*, and is variable intraspecifically in all Toarcian species of *Stenopterygius* (McGowan & Motani 2003; Maxwell *et al.* 2014; Massare & Lomax 2016; Swaby & Lomax 2020; Maxwell & Cortés 2020; Weedon & Chapman 2022). It is more common in taxa from the uppermost Lower Jurassic (Toarcian): those from

the ‘Upper Lias’ rather than the ‘Lower Lias’. Although the fibula is missing most of the proximal posterior region, it would have been slightly smaller than the tibia, paralleling the forefin, which has a larger radius than ulna (compare Fig. 8A, B with Fig. 9A). The astragalus is positioned between the distal tibia and fibula and appears to have had a broader contact with the tibia than the fibula. The anterodistal edge of the hindfin appears to preserve traces of soft tissue, preserved as a blackish brown layer (Fig. 9A).

Ontogenetic assessment. Although ROM VP52596 shows some osteologically immature characteristics, several osteological markers suggest that this individual was approaching skeletal maturity. The skull is dorsoventrally crushed in ROM VP52596, however, on the better preserved left side (Fig. 3A, B) the scleral ring does not completely fill the orbit, an osteologically mature characteristic (Fernández *et al.* 2005). Furthermore, the onset of fusion of certain cranial sutures (in particular, between the posterior premaxilla and maxilla on the right side of the skull) also suggest an individual that is close to skeletal maturity. The clearly delimited postparietal shelf and ridge, the posterior boss on the jugal almost in line with the horizontal ramus, well-developed interfrontal connection beginning to fuse, and relatively robust and well-ossified basioccipital peg suggest an osteological age between postnatal 2 and mature, probably closer to the latter, following the criteria of Miedema & Maxwell (2022).

Other widely used criteria for assessing maturity in ichthyosaurs (e.g. Kear & Zammit 2014; Lomax & Massare 2015; Delsett *et al.* 2017) are those documented by Johnson (1977) for fins of

Stenopterygius. Convex fin elements and space between proximal fin elements occur in immature *Stenopterygius* specimens (Johnson 1977). In ROM VP52596 the fin elements are flat, not convex. Some gaps are present between fingers proximally, which could be taphonomic, but the phalanges are closely packed (Fig. 8A, B). The convex humeral head further supports an argument for a mature individual (Fig. 8). However, the femur head is flat, and the shaft of the humerus and, to a lesser extent, the femur, has a rough sandpaper-like texture (Figs 8C–G, 9A–C), features found on osteologically immature individuals (Johnson 1977). Because the specimen still retains a few immature characteristics, we conclude that it is close to but not a fully osteologically mature individual.

Palaeobiology

The skeleton of ROM VP52596 provides information regarding the ecology of *Xiphodracon goldencapensis*. Gastric contents are preserved on the left side of the specimen, posterior to the coracoid. Their identification is supported by previous work suggesting that the ichthyosaurian stomach was positioned on the left side of the body (Böttcher 1989). The gastric contents consist of layers of buff coloured and blackish material; small brownish bone fragments consistent with actinopterygian fish bones and scales are mixed in. It is unclear whether cephalopod hooklets are also present in the black part of the mass. Identification of the fish remains requires more detailed examination and perhaps additional preparation.

Xiphodracon goldencapensis exhibits damage incurred to the skeleton throughout life, including a fractured clavicle (Fig. 7), ? avascular necrosis affecting at least three-quarters of the propodials (Figs 8, 9), and malformed teeth scattered along the dentition (Fig. 6). Pathologies affecting the forelimb and girdle are the most commonly described injuries among neoichthyosaurians (Pardo-Pérez et al. 2018). Previously, avascular necrosis was attributed to deep diving behaviour based on analogies with human divers (e.g. Motani et al. 1999). However, more recent literature on extant marine vertebrates suggests that avascular necrosis occurs when normal diving behaviour (not necessarily deep diving) is disrupted by a sympathetic nervous response (García-Párraga et al. 2018; Fahlman 2024), for instance an unsuccessful attack by a predator. Whether the putative avascular necrosis, clavicle fracture, or a third event resulted in the unusual dental malformations is unclear.

The cause of death of ROM VP52596 appears to have been a bite to the skull, inflicted by a large predator (Figs 3, S3). Clear tooth punctures on the skull roof cannot be differentiated, only general areas of radiating fracturing and more pronounced depression. It is possible that the skull was taphonomically distorted, although the rest of the skull and skeleton do not display similar distortion. Based on the size of ROM VP52596, a gape size of at least 15 cm was required to inflict the bite, and comparisons with *Stenopterygius* indicate that a gape of over 40 cm would have been required to consume an ichthyosaur of this size (Serafini et al. 2025). Potential Pliensbachian predators include only large individuals of the ichthyosaur *Temnodontosaurus*. In contrast, the bite mark on the dorsal surface of the right femur

is proportionately quite small (Fig. 9B), and can be attributed to scavenging activity.

PHYLOGENETIC ANALYSIS

The matrix discussed above (see Method, above) was analysed under equal weights parsimony implemented in TNT v1.6 (Goloboff & Morales 2023) using a New Technology search (50 iterations of the ratchet algorithm, drift algorithm default settings, minimum length found 100 times), followed by a traditional search using trees from RAM. This resulted in 10 000 most-parsimonious trees of length 1681. Resolution among parvipelvians was very poor; however *Xiphodracon* formed a clade with *Hauffiopteryx* spp. in the strict consensus solution, herein regarded as *Hauffiopterygia* nov. IterPCR was used to improve resolution and resulted in 38 taxa being pruned. The resulting topology was as optimized in previous versions of the matrix, with *Hauffiopteryx* + *Xiphodracon* and *Stenopterygius* forming successive outgroups to Ophthalmosauria (Figs 10, 11).

The second analysis used implied weighting, with $k = 12$ (as in the preferred tree featured in Laboury et al. 2022), and resulted in 34 trees of length 70.13811. This result shifted *Xiphodracon* + *Hauffiopteryx* spp. (= *Hauffiopterygia*) away from *Stenopterygius* spp. into a monophyletic Leptonectidae (Fig. 10). Because several aspects of this topology (specifically: more poorly known taxa resolved as earlier-diverging in their respective clades) indicated that missing data might be affecting phylogenetic position, extended implied weighting (EIW) was also implemented, resolving 164 trees of length 62.31733; the position of ROM VP52596 was not affected. A search ($k = 6$) under EIW produced 125 trees of length 89.7416; among Early Jurassic parvipelvians, *Xiphodracon* remained within Leptonectidae, but shifted into a position more closely related to *Leptonectes* spp.

RESULTS & DISCUSSION

Relationships of Early Jurassic parvipelvians

The relationship between *Xiphodracon goldencapensis* as sister taxon to *Hauffiopteryx* spp., forming a clade *Hauffiopterygia*, was consistently recovered in almost all analyses, supported by the following synapomorphies common to both the implied weights and equal weights topologies: lack of contact between the nasal and post-frontal; participation of the prefrontal in the external narial opening, two lateral gastral elements, and a rod-like ischium and pubis. However, equal weights and implied weights parsimony returned notably different solutions for the placement of *Hauffiopterygia*.

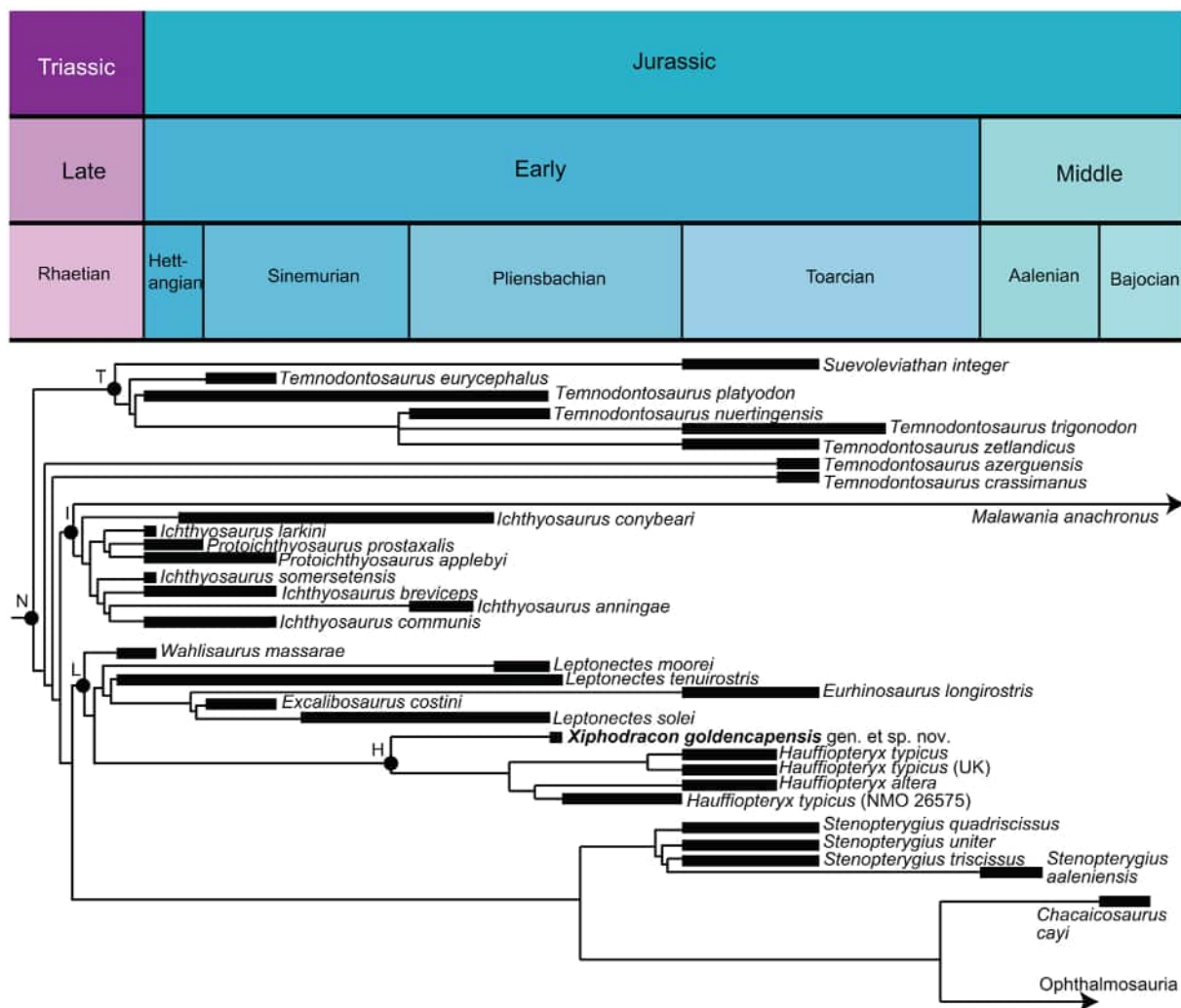


FIG. 10. Phylogenetic position of *Xiphodracon goldencapensis* under parsimony optimization. Strict consensus of 164 most-parsimonious trees of length 62,31733 recovered under extended implied weights parsimony ($k = 12$) and plotted against time. Abbreviations: H, Hauffiopterygia; I, Ichthyosauridae; L, Leptonectidae; N, Neoichthyosauria; T, Temnodontosauridae.

Equal weights parsimony recovered the classical arrangement of a monophyletic Stenopterygiidae (*sensu* Maisch 2008), with the *Hauffiopteryx* clade and *Stenopterygius* forming successive branches to Ophthalmosauria (Fig. 10). This topology has been recovered in previous analyses using both equal and implied weights parsimony optimization of the same matrix (e.g. Maxwell & Cortés 2020; Laboury *et al.* 2022), but has also been recovered from a quasi-independent dataset (Marek *et al.* 2015) and represents the current paradigmatic view.

Intriguingly, implied weights parsimony ($k = 12$) recovered Hauffiopterygia within a monophyletic Leptonectidae, with Leptonectidae representing the sister taxon of Baracromia (Fig. 10). Implied weights parsimony has been viewed as being analytically superior to equal weights parsimony (Goloboff *et al.* 2018), and this result ($k = 12$, EIW) represents our preferred topology

(Fig. 10). The relationship between *Hauffiopteryx* and Leptonectidae has received little phylogenetic support following the removal of the *Hauffiopteryx* skull from the Pliensbachian of Switzerland from the *Leptonectes tenuirostris* OTU, but is not new and dates from the earliest recognition of *Hauffiopteryx* as a distinct genus (Maisch 2008; see also Moon 2019).

Our preferred topology ($k = 12$ EIW) highlights several areas of uncertainty in the phylogenetic relationships of Early Jurassic ichthyosaurs (Fig. 10). In particular, we found Temnodontosauridae (including *Suevoleviathan*) to be the earliest-diverging neoichthyosaurian lineage, unlike other analyses addressing the relationships of Early Jurassic taxa using either implied weights (Laboury *et al.* 2022) or equal weights (Moon 2019; Maxwell & Cortés 2020; this study) that placed Ichthyosauridae in this position. This position of Temnodontosauridae has been recovered

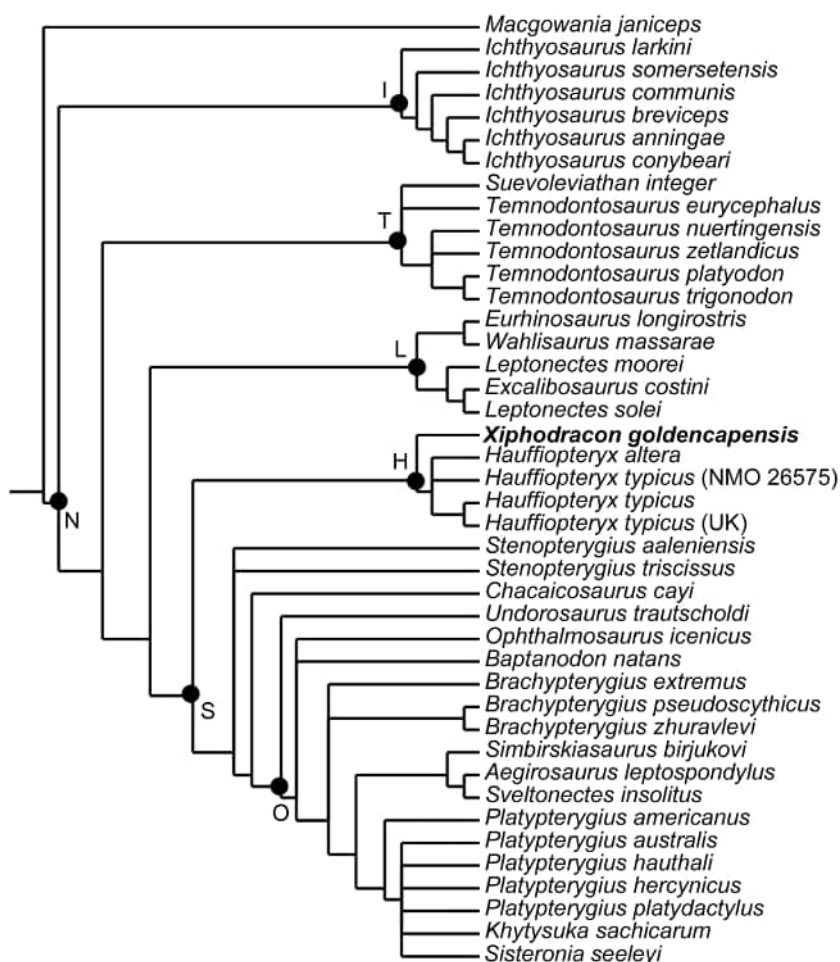


FIG. 11. Strict consensus of 10 000 most-parsimonious trees of length 1681 recovered under equal weights parsimony, unstable taxa pruned from the strict consensus using IterPCR. Abbreviations: H, Hauffiopterygia; I, Ichthyosauridae; L, Leptonectidae; N, Neoichthyosauria; O, Ophthalmosauria; S, Stenopterygiidae *sensu* Maisch 2008; T, Temnodontosauridae.

in some of the earliest phylogenetic studies of ichthyosaur relationships (Sander 2000; Maisch & Matzke 2000). It is important to note that we also do not recover a sister-group relationship between Ichthyosauridae + Baracromia or between *Temnodontosaurus* + Leptonectidae, as is typical of many analyses characterized by weak or genus-level taxon sampling among Early Jurassic parvipelvians (Motani 1999a; Fischer *et al.* 2013 and subsequent modifications of this matrix; Ji *et al.* 2016 and subsequent modifications of this matrix).

Our preferred topology highlights the relationship between poorly preserved and/or poorly known taxa, phylogenetic instability, and a basally diverging position within their respective lineages under implied weights parsimony (Fig. 11). Whereas in the preferred topology of Laboury *et al.* (2022), *Temnodontosaurus crassimanus* was the earliest-diverging temnodontosaurid and *T. azerguensis* was an early-diverging leptonectid, in our analysis both of these species were pulled from their

positions onto successive branches between Temnodontosauridae and Ichthyosauridae in the $k = 12$ EIW analysis, and were unresolved under equal weighting. Similarly, *Malawania* is resolved in our $k = 12$ EIW analysis as the earliest diverging ichthyosaurid, but was pruned in the analysis of Laboury *et al.* (2022), as well as in our equal weights analysis. Thus, its phylogenetic position is best interpreted as unresolved, although historically it has been recovered within Ichthyosauridae (Fischer *et al.* 2013).

Pelvic girdle evolution in Parvipelvina

One of the key characteristics of Neoichthyosauria, the monophyletic group to which almost all post-Triassic ichthyosaurs can be referred, is a reduced tripartite pelvic girdle (Sander 2000). The subsequent evolution of the clade featured increasing reduction and fusion of the ischium and pubis, with baracromian ichthyosaurs united by the

presence of an ischiopubis, which together with the ilium formed a bipartite pelvic girdle (McGowan & Motani 2003). The trend in pelvic reduction reached its peak by the Late Jurassic, with some ophthalmosaurians characterized by a bipartite pelvic girdle and complete loss of the obturator foramen (reviewed by Delsett *et al.* 2017).

In this context, as sister group to Baracromia, *Hauffiopteryx*, in which the ischium and pubis were fused laterally but not medially, has been interpreted as an early step in ischiopubis evolution (e.g. Maisch 2008). The phylogenetic placement of *Xiphodracon*, characterized by a tripartite pelvic girdle (Fig. 9D, E), rejects the stepwise hypothesis of ischiopubis evolution in *Hauffiopteryx* and Baracromia, and indicates that the shared bipartite pelvic girdle between *Hauffiopteryx* and baracromians is almost certainly the result of evolutionary convergence. This conclusion is not affected by the placement of Hauffiopterygia in either Leptonectidae or Stenopterygiidae *sensu* Maisch 2008.

Among leptonectids, intraspecific variation in both medial and lateral fusion of the ischium and pubis has been documented in *Leptonectes tenuirostris*, including right–left asymmetric fusion in an individual (McGowan 1989; Motani 1999a; Lomax & Massare 2012), as well as sometimes in *Ichthyosaurus* (McGowan & Motani 2003). Intraspecific variability in the fusion of the medial edge of the ischium and pubis is also documented in *Temnodontosaurus trigonodon*; however, lateral fusion is not observed in this taxon (McGowan 1979). Thus, it appears that prior to the evolution of an ischiopubis in Baracromia and *Hauffiopteryx*, partial fusion of pelvic elements existed as a variable morphology in all major groups of neoichthyosaurians.

Early Jurassic faunal turnover

Although Laboury *et al.* (2025) argued that the Late Triassic extinction had little effect on ichthyosaurian diversity,

none of the genera or species that existed before the extinction continued into the Jurassic, and several families disappeared. In the UK, the taxonomic diversity of ichthyosaurs increased fairly rapidly after the Late Triassic extinction eliminated some of the largest species known (e.g. Nicholls & Manabe 2004; Sander *et al.* 2022; Lomax *et al.* 2018, 2024). Thus the Early Jurassic began with a major change in taxonomic diversity of ichthyosaurs. However, there is evidence of turmoil within c. 10 myr following their recovery from the end-Triassic mass extinction, as showcased by a considerable taxonomic turnover.

This well-documented but poorly understood turnover in ichthyosaurian diversity occurred towards the end of the Early Jurassic, with the later Toarcian fauna being taxonomically different from the earlier Hettangian–Sinemurian fauna. Although two common families, Temnodontosauridae and Leptonectidae, continued from the earlier Sinemurian through the Pliensbachian and into the Toarcian, their composition changed (Figs 10–12). Within Temnodontosauridae, *Temnodontosaurus platyodon*, *T. eurycephalus* and *T. nuertingensis* became extinct, but new species appeared in the Toarcian: *T. trigonodon*, *T. crassimanus*, *T. ? acutirostris*, *T. zetlandicus* and *T. ? azerguensis* (Martin *et al.* 2012; Swaby & Lomax 2020; Laboury *et al.* 2022). Within Leptonectidae, *Leptonectes tenuirostris* as well as the rare species *L. solei*, *L. moorei* and *Excalibosaurus costini* became extinct, succeeded in the Toarcian by *Eurhinosaurs longirostris*, *Hauffiopteryx typicus* and *H. altera* (Maxwell & Cortés 2020). This turnover also resulted in the emergence of a new family, Suevoleviathanidae, and a new clade, Baracromia (which includes Stenopterygiidae) in the Toarcian (Figs 10, 12). Baracromia might have originated by the late Pliensbachian (McGowan 1978).

The picture is more complicated, however, with the disappearance of the once abundant Hettangian–Sinemurian Ichthyosauridae, represented by *Ichthyosaurus* and *Protoichthyosaurus*. Although Ichthyosauridae has not been found in the late Pliensbachian or Toarcian,

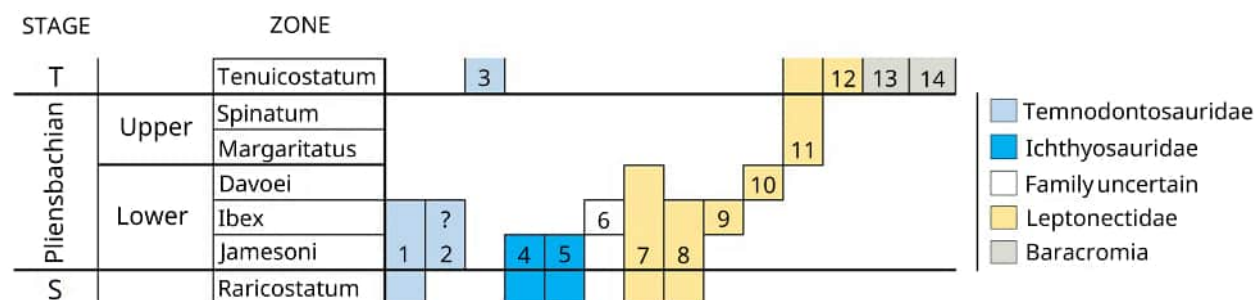


FIG. 12. Ichthyosaurian species in the Pliensbachian. Note that ichthyosaurian diversity in the last zone of the Sinemurian (S) and first zone of the Toarcian (T) stages are also shown. Temnodontosauridae: 1, *Temnodontosaurus platyodon*; 2, *T. nuertingensis*; 3, *T. trigonodon*. Ichthyosauridae: 4, *Ichthyosaurus anningae*; 5, *I. conybeari*. Family uncertain: 6, *Fernatator prenticei*. Leptonectidae: 7, *Leptonectes tenuirostris*; 8, *L. solei*; 9, *L. moorei*; 10, *Xiphodracon goldencapensis*; 11, *Hauffiopteryx typicus*; 12, *Eurhinosaurs longirostris*. Baracromia: 13, *Stenopterygius quadriscissus*; 14, *S. triscissus*.

Malawania anachronus from the Early Cretaceous of Iraq represents a link to Ichthyosauridae and thus requires a 'ghost lineage' in the Pliensbachian (Fischer *et al.* 2013).

A taxonomic turnover, however, was initiated in the Pliensbachian. Many fairly common and once abundant Hettangian–Sinemurian species (e.g. *I. communis*, *I. breviceps*, *P. prostaxalis*) as well as more rare ones (e.g. *T. eurycephalus*, *E. costini*, *P. applebyi*) did not survive beyond the Sinemurian (McGowan 1986, 2003; Weedon & Chapman 2022). However, five Sinemurian species (*L. tenuirostris*, *L. solei*, *I. anningae*, *I. conybeari*, *T. platyodon*) continued into the lower Pliensbachian (Figs 10, 12; Godefroit 1992; McGowan 1993; Lomax & Massare 2015, 2018; Massare & Lomax 2016; Weedon & Chapman 2022), a decrease in diversity, but at least a continuation of a Sinemurian-like fauna, as noted by Fischer *et al.* (2022). The lower Pliensbachian also saw the appearance of *T. nuertingensis* and *L. moorei*, although neither of them survived to the end of the lower Pliensbachian. *Leptonectes tenuirostris*, *L. moorei*, *L. solei* and *Xiphodracon goldencapensis* point to a diversification of the leptonectids in the Pliensbachian (Figs 10–12). However, *Hauffiopteryx typicus* is the only leptonectid reported from the upper Pliensbachian, and it continued into the Toarcian. The close relationship between *Xiphodracon* and *Hauffiopteryx* suggests that the turnover to a Toarcian fauna began towards the end of the lower Pliensbachian, with the upper Pliensbachian lacking any Sinemurian taxa.

Ichthyosaurian evolution and diversity is poorly understood in the Pliensbachian because specimens are rare (Fischer *et al.* 2021, fig. 1). Likewise, the exact stratigraphic position is known for relatively few specimens of Lower Jurassic ichthyosaurs from the UK in general. Hundreds of historic specimens lack detailed stratigraphic data and hence have the potential to substantially change the current picture of ichthyosaurian diversity through time if more specific geologic ages can be determined. Moreover, we have not incorporated the Pliensbachian material from western North America that includes taxonomically indeterminate vertebral material and the recently described *Fernatator prenticei* from British Columbia, Canada (McGowan 1978; Massare *et al.* 2025). Thus, Pliensbachian diversity is even higher than previously recognized.

Many historic specimens from the Lyme Regis–Charmouth localities have been assumed to derive from the well-collected Hettangian–Sinemurian exposures (McGowan 1974a, 1974b; McGowan & Motani 2003; Weedon & Chapman 2022), even though Pliensbachian strata are exposed in the area, further east along the coast. In fact, the first ichthyosaur to be unequivocally recorded from the Pliensbachian of the English Lower Jurassic was

reported only relatively recently (McGowan & Milner 1999).

The turnover in taxonomic diversity that appears to occur between the Sinemurian and Pliensbachian may be reflecting a gap in the data: the Pliensbachian strata in the Lyme Regis–Charmouth area might not have been collected as thoroughly as the older strata and hence do not appear as diverse. Another possibility is that the environment preserved in the Pliensbachian might have been more restrictive in some way from that of the Sinemurian, such that only a subset of the Sinemurian taxa were present. In any case, the mix of Sinemurian and Toarcian taxa in the Pliensbachian suggests a stepwise transition between the height of diversity in the Sinemurian to the entirely different and more typical Toarcian ichthyosaurian fauna (Figs 10, 12).

CONCLUSION

Xiphodracon goldencapensis gen. et sp. nov. is a hauffiopterygian leptonectid ichthyosaur from the Lower Jurassic (Pliensbachian) of Dorset, England, UK. The new taxon possesses autapomorphic features of the lacrimal, prefrontal and external narial region, as well as a unique combination of skull and postcranial characters shared with other taxa. It also has pathologies in the skull and postcranium and appears to have succumbed to predation. The holotype and only example is the most complete Pliensbachian ichthyosaur known thus far. Although Pliensbachian ichthyosaurs are rare, this discovery increases the number of Early Jurassic ichthyosaur genera to 12, with at least six genera (*Xiphodracon*, *Ichthyosaurus*, *Leptonectes*, *Hauffiopteryx*, *Temnodontosaurus* and *Fernatator*) recorded from the Pliensbachian.

The phylogenetic position of *Hauffiopteryx* has been debated since it was originally defined (Maisch 2008). The recovery of *Xiphodracon* as a member of the Leptonectidae, forming a new clade with *Hauffiopteryx*, Hauffiopterygia, has wider implications for the radiation and subsequent diversity of ichthyosaurs during this time (Figs 10–12). *Xiphodracon* helps to resolve the phylogenetic position of *Hauffiopteryx*, and ultimately elucidates a closer relationship between Leptonectidae and *Stenopterygius* than previously recognized (see also Srdic *et al.* 2021). Moreover, this relationship indicates that similarities in cranial architecture between *Hauffiopteryx* and leptonectids are more likely to be the result of common descent (contra Maxwell & Cortés 2020), whereas aspects of postcranial morphology shared with *Stenopterygius* (in particular, the presence of an ischiopubis) are more likely to be the result of evolutionary convergence.

Adding to the pool of Pliensbachian ichthyosaur diversity, *X. goldencapensis* provides new insights into the faunal turnover during the late Early Jurassic, a pivotal yet poorly understood time in ichthyosaurian evolution. The transition in the Early Jurassic from the diverse ichthyosaur fauna of the Sinemurian to the diverse, but entirely different fauna of the latest Early Jurassic (Toarcian) occurred in the Pliensbachian. The presence of multiple leptonectids suggests that there was a surge in leptonectid diversity in the Pliensbachian, analogous to the diversification of Ichthyosauridae in the Hettangian–Sinemurian. Common genera of the Sinemurian fauna (e.g. *Ichthyosaurus*, *Leptonectes*) continued into the early Pliensbachian, but disappeared before the late Pliensbachian (Figs 10–12). *Xiphodracon*, with strong affinities to *Haufiopteryx*, appeared in the last zone of the early Pliensbachian and represents the beginning of the transition to the Toarcian fauna, a major turnover in species-level diversity. Nevertheless, Pliensbachian specimens are rare, and new discoveries may alter our understanding, providing a more complex picture of faunal replacement and diversification during the Pliensbachian gap.

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Author contributions. **Conceptualization** DR Lomax (DRL), JA Massare (JAM); **Data Curation** DRL, JAM, EE Maxwell (EEM); **Formal Analysis** DRL, JAM, EEM; **Funding Acquisition** DRL; **Investigation** DRL, JAM, EEM; **Methodology** DRL, JAM, EEM; **Project Administration** DRL; **Validation** DRL, JAM, EEM;

Writing – Original Draft Preparation DRL, JAM; **Writing – Review & Editing** DRL, JAM, EEM.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <https://zoobank.org/References/CADD3324-680B-4E06-A710-6925BE6FB7C9>

The morphological matrix for this study is available in MorphoBank: <http://morphobank.org/permalink/?P6048>

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.70038>):

Appendix S1. Nexus file for morphological matrix.

Figure S1. Location map of *Xiphodracon goldencapensis*, ROM VP52596.

Figure S2. A close-up of the hyoid region of *Xiphodracon goldencapensis*, ROM VP52596, showing the bony mass of unknown origin.

Figure S3. Depth map of the skull of *Xiphodracon goldencapensis*, ROM VP52596.

Figure S4. Additional braincase elements of *Xiphodracon goldencapensis*, ROM VP52596.

Figure S5. Comparison of forefin notching in the Leptonectidae.

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