



A LONGIROSTRINE *TEMNODONTOSAURUS* (ICHTHYOSAURIA) WITH COMMENTS ON EARLY JURASSIC ICHTHYOSAUR NICHE PARTITIONING AND DISPARITY

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Abstract: We describe an almost complete ichthyosaur skeleton from the middle Toarcian (Lower Jurassic) of the Beaujolais foothills near Lyon, France, and assign it to *Temnodontosaurus azerguensis* sp. nov. This new species exhibits cranial peculiarities such as a thin, elongated and possibly edentulous rostrum, as well as a reduced quadrate. These characters indicate dietary preferences that markedly differ from other species referred to *Temnodontosaurus*, a genus previously considered as the top predator of the Early Jurassic seas. Despite a conservative postcranial skeleton, we propose that *Temnodontosaurus* is one of the most ecologically disparate genera of ichthyosaurs, including apex predators and now a soft prey longirostrine hunter. Ammonites collected from

the same stratigraphic level as the described specimen indicate that the new species is somewhat younger (*bifrons* ammonite zone) than the most known Toarcian ichthyosaurs and therefore slightly postdates the interval of severe environmental changes and marine invertebrate extinctions known as the Toarcian Oceanic Anoxic Event. The present study therefore raises the question of whether postcrisis recovery of vertebrate faunas, including the radiation of *Temnodontosaurus* into a new ecological niche, may have been a consequence of marine ecosystem reorganization across this event.

Key words: Ichthyosauria, Toarcian, anoxic event, jaw mechanics, *Temnodontosaurus*.

TEMNODONTOSAURUS Lydekker, 1889 is a genus of particularly large non-thunnosaurian neoichthyosaurs, reaching lengths in excess of 12 m (Godefroit 1993; Hungerbühler and Sachs 1996; Maisch and Matzke 2000). The genus is regarded as the top predator of the Early Jurassic seas, and the only Jurassic ichthyosaur for which a diet consisting mainly of vertebrate prey has been proposed (Massare 1987; Godefroit 1996), thanks to its large teeth exhibiting well-marked carinae (Massare 1987; Godefroit 1996; McGowan 1996; V. Fischer, pers. obs. on NHMUK R1157) and preserved gut containing marine reptile remains (Böttcher 1989). *Temnodontosaurus* is reported from many locations in the European archipelago, including sites now located in Germany (Theodori 1843; Huene 1922; Maisch and Matzke 2000), England (Huene 1922;

Godefroit 1994) and France (Gaudry 1892; Fischer *et al.* 2011). Despite an extensive 13-myr record covering a wide range of palaeoenvironments (Fischer *et al.* 2011), the colonization of a lower trophic level by *Temnodontosaurus* has never been documented.

Here, we report a large and nearly complete ichthyosaur from the Lafarge quarry in Belmont d'Azergues near Lyon (south-eastern France; Fig. 1) representing a new longirostrine and probably toothless *Temnodontosaurus* species. The specimen was found in 1984 by M. Dejob and Ms. Laurent, but has never been described in detail. Elmi and Rulleau (1991), in their detailed biostratigraphic analysis of the quarry, published an *in situ* photograph of the specimen. They identified the following ammonites in the belemnite-rich marlstone bed containing the ichthyosaur:

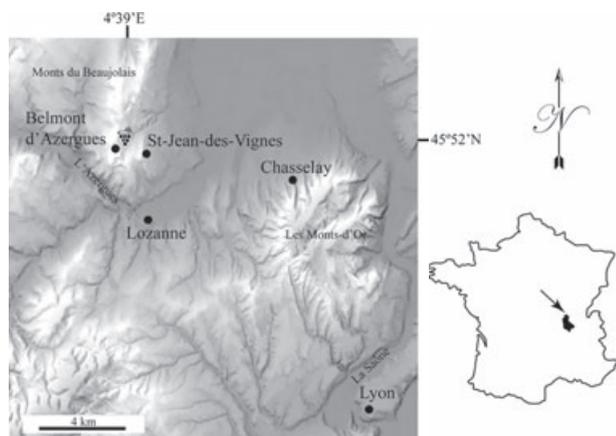


FIG. 1. Locality of the Belmont ichthyosaur from the Toarcian of Beaujolais, Rhône, France. The grape vine indicates the provenance of *Temnodontosaurus azerguensis* sp. nov.

Hildoceras apertum, *Harpoceras* sp., and *Pseudolioceras* aff. *lythense*, which indicate the *bifrons* subzone (*bifrons* zone, middle Toarcian; Elmi and Rulleau 1991).

Institutional abbreviations. NHMUK, Natural History Museum, London, England; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; MAMSPLP, Musée des Amis de la Mine in Saint-Pierre La Palud, Rhône department, France; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Anatomical abbreviations. at-ax, atlas-axis complex; bf, basioccipital facet; bp, basiptyergoid process; bo, basioccipital; bs, basisphenoid; cl, clavicle; d, dentary; eo, exoccipital; f, femur; fi, fibula; h, humerus; hf, hypoglossal foramen; hsc, impression of the horizontal semicircular canal; i, intermedium; il, ilium; interc, intercentrum; isch, ischium; j, jugal; pmx, premaxilla; pop, paraoccipital process; pvsc, impression of the posterior semicircular canal; op, opisthotic; pb, pubis; pt, pterygoid; q, quadrate; r, radius; sac, sacculus; sc, scapula; stp, stapes; t, tibia; u, ulna; ut, utriculus.

SYSTEMATIC PALAEOLOGY

Order ICHTHYOSAURIA de Blainville, 1835
Suborder NEOICHTHYOSAURIA Sander, 2000

Genus TEMNODONTOSAURUS Lydekker, 1889

Type species. *Temnodontosaurus platyodon* (Conybeare, 1822).

Emended diagnosis and comparison. Large (7–12 m) non-thunnosaurian (forefin and hind fin of comparable size; Motani, 1999) Neichthyosauria is characterized by a paired carotid foramen on the basisphenoid (unlike *Eurhinosaurus*, Maisch and Matzke, 2000; unknown for other members of the clade); maxilla with long anterior pro-

cess, extending as far as the nasal anteriorly (autapomorphic within non-thunnosaurian neichthyosaurians; V. Fischer, pers. obs.); constricted humerus (unlike *Eurhinosaurus* and *Excalibosaurus* McGowan, 2003; and *Suevoleviathan* Maisch, 1998a); forefin and hind fin composed of numerous hexagonal elements (unlike *Leptonectes solei* McGowan, 1993; and *Eurhinosaurus*, McGowan, 2003); at least two notches in the leading edge digit of forefin and hind fin (unlike *L. moorei* McGowan and Milner, 1999; *L. solei* McGowan, 1993; and *Suevoleviathan* Maisch, 1998a).

Stratigraphic range. Upper Hettangian–middle Toarcian (Lower Jurassic).

Temnodontosaurus azerguensis sp. nov.

Figures 2–6

Derivation of name. Derived from ‘Azergues’, the local name of the valley and river flowing near the Belmont quarry.

Comparative diagnosis. *Temnodontosaurus* is characterized by the following combination of characters: extremely slender and elongated rostrum (rostrum/skull length ratio = 0.69); narrow and shallow dental grooves; reduced lunate quadrate (ratio of quadrate anteroposterior length (measured directly dorsal to condyle) to mandible length = 0.066; 0.2199 in *T. eurycephalus*); reduced dorsal head of the exoccipital (shared with *T. platyodon*, Godefroit 1993); expanded posterior end of the pterygoid lamellae; elongate humerus (length/mid-shaft width ratio = 2.87); presence of an anterodistal leading edge on the humerus (shared with *T. trigonodon*, McGowan 1996); elongate femur (axial length/distal width ratio = 0.76) (shared with *T. trigonodon*, Gaudry 1892); absence of a spatium interosseum between tibia and fibula (shared with *T. trigonodon*, Böttcher 1989).

Type stratum. *Bifrons* zone, middle Toarcian, Lower Jurassic.

Type locality. Belmont d’Azergues, Rhône, France.

Holotype. An unnumbered and almost complete skeleton preserved with its ventral surface exposed (Fig. 2A). The specimen is cemented to a 10-m concrete slab on permanent display at Musée des Amis de la Mine in Saint-Pierre La Palud, Rhône department, France (MAMSPLP).

Comparative description

Skull. The skull is exposed in ventral view (Figs 2, 3), and it is nearly complete but crushed. The rostrum is extremely elongate

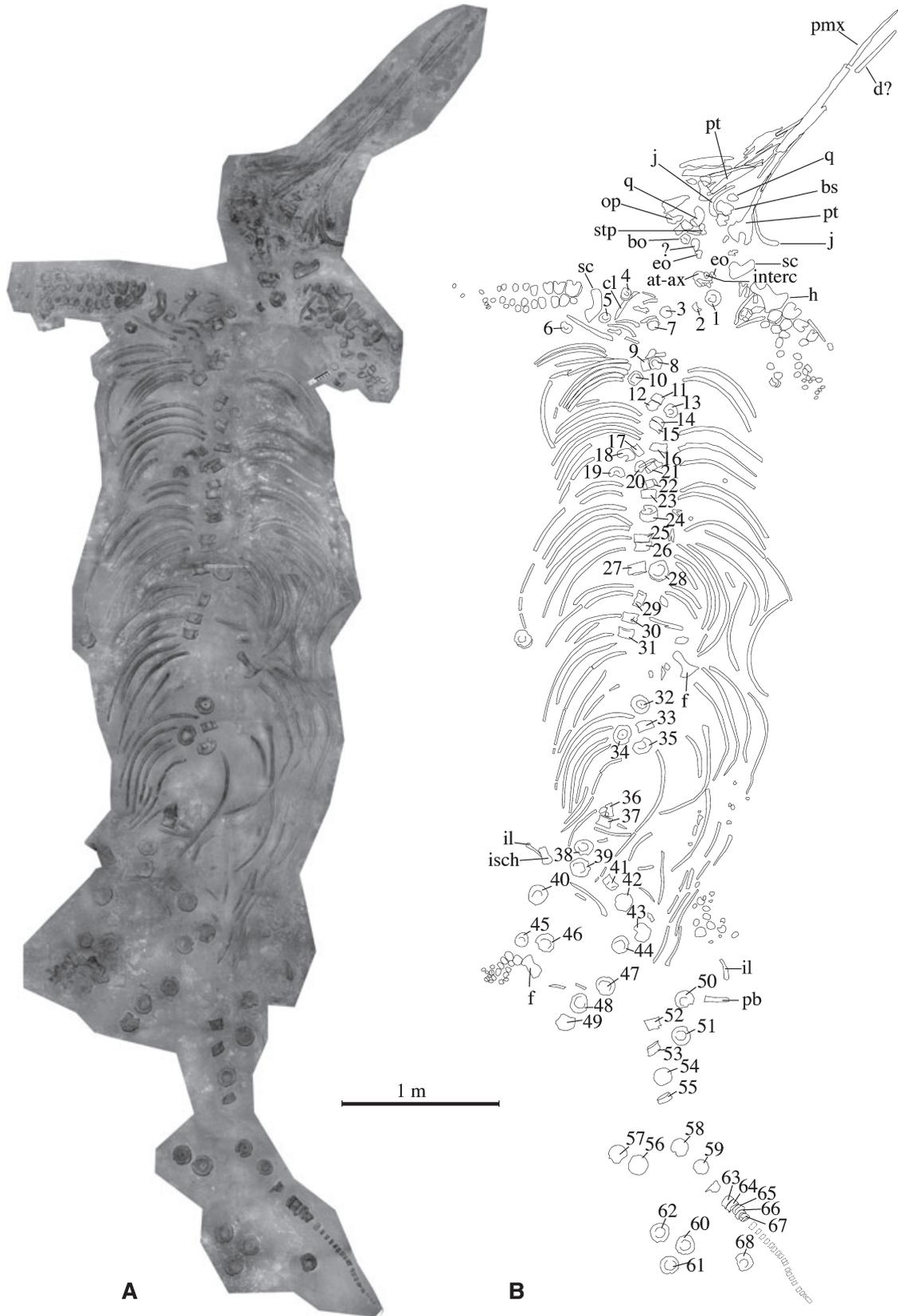


FIG. 2. *Temnodontosaurus azerguensis* sp. nov. from the Toarcian of Beaujolais (MAMSPLP) preserved in ventral view. A, photograph. B, line drawing of the skeleton.

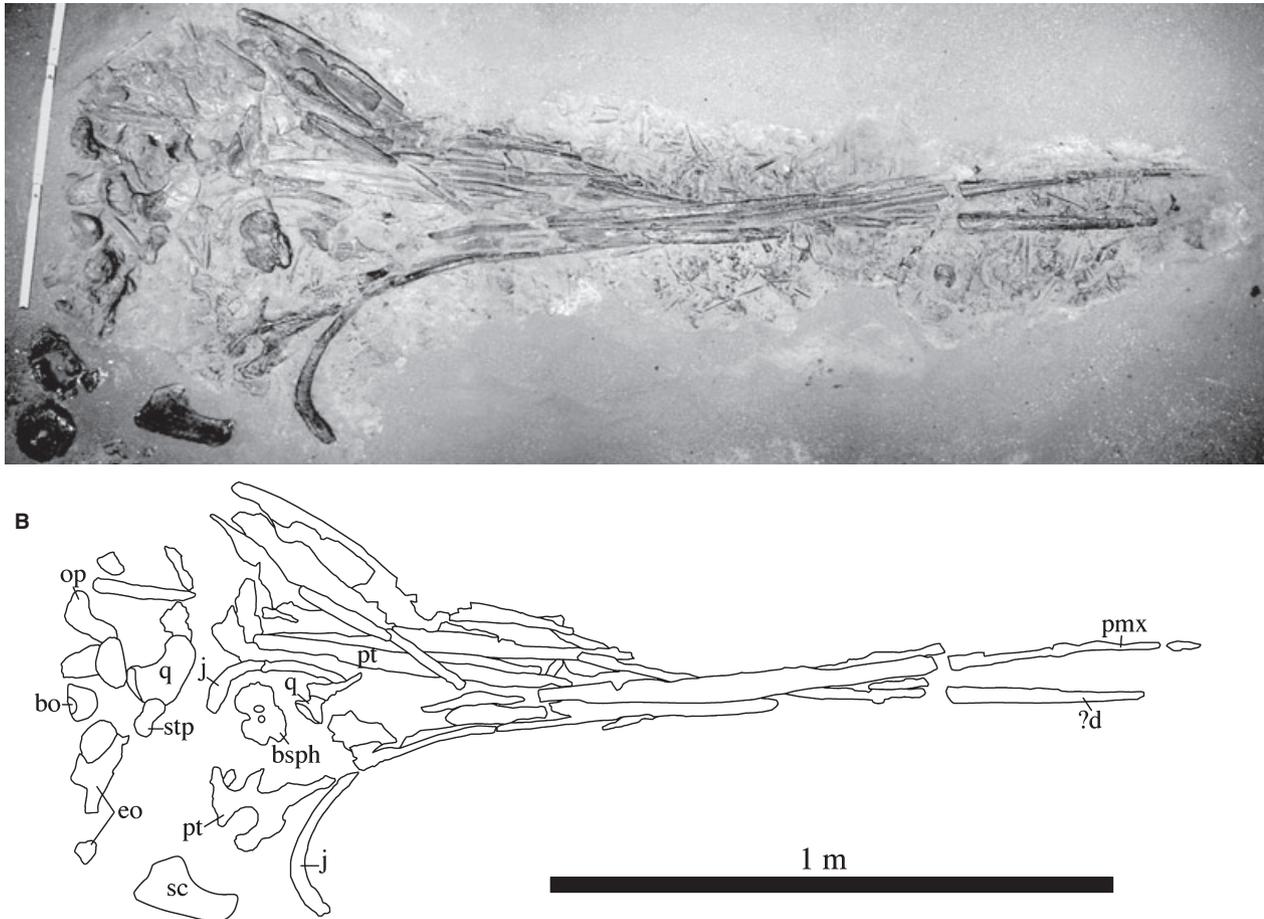


FIG. 3. Details of the skull of *Temnodontosaurus azerguensis* sp. nov. (MAMSPLP) in ventral view. A, photograph. B, line drawing.

(jaw length = 1.7 m; rostrum/skull length ratio = 0.69). Both the premaxilla and the dentary are preserved up to the very tip, but they cannot be distinguished from each other. They are thin and edentulous, although narrow and shallow dental grooves are present. Shallow depressions delimited by thin walls are present in the anterior part of the dental groove. The dental grooves are poorly preserved posteriorly and do not seem to widen and deepen posteriorly. Both jugals are complete; the anterior ramus of the jugal is a thin rod that is slightly dorsoventrally compressed. Its possible lateral surface bears a shallow longitudinal groove. The posterior ramus is thicker and exhibits a V-shaped ridge that tapers ventrally. The right quadrate is complete. It is small and crescent-shaped in lateral view with a deep, wide posterior notch. The lateral surface is smooth and slightly concave. The supratemporal head is slightly thickened. The quadrate condyle is small, triangular and restricted to the posterior half of the quadrate. Most elements of the palatal complex are present but cannot be precisely identified. The pterygoids are partly visible but badly crushed anteriorly (Fig. 4H). The pterygoid lamellae are unusual in exhibiting marked posterior processes (Fig. 4G), giving the pterygoid a Y shape posteriorly. The dorsal lamella of the pterygoid has shifted inwards because of diagenetic compression. The ventral surface of the basisphenoid is exposed (Fig. 2). It is hexagonal and the posterior end is weakly subdivided by a shallow groove.

The carotid foramen is deep, paired and set within the anterior half of the basisphenoid. Laterally, the basisphenoid forms thick but short basiptyergoid processes, and the anterior edge of the basisphenoid is straight. The parasphenoid is missing. The exoccipital is markedly hourglass-shaped. Its occipital foot is strongly expanded and is far larger than the dorsal head, as in *Ichthyosaurus* (McGowan 1973) or *Ophthalmosaurus* (Kirton 1983). The articular surface for the basioccipital is strongly convex and has a rugose texture. The shaft of the exoccipital forms the lateral wall of the foramen magnum and presumably the lateral wall of foramina jugularis, where two hypoglossal foramina are visible. The opisthotic is long and robust (Fig. 4C, D). The osseous labyrinth is similar to that described by McGowan (1973) in *Ichthyosaurus* and by Maisch (2002) in *Temnodontosaurus* cf. *trigonodon*, in having a deep, narrow dorsomedial impression of the posterior semicircular canal, a long and narrow lateral groove housing the horizontal semicircular canal, and a wide, shallow ventral depression housing the posteroventral part of the sacculus. Proximally, the opisthotic bears a flat articular surface for the basioccipital. The stapes is small and stout. Its occipital head is not markedly expanded.

Axial skeleton. The atlas-axis is complete, including a well-preserved axis intercentrum. The atlas-axis is pentagonal and its outer edge is markedly crenate. Both elements are very short (18

and 24 mm for the atlas and the axis, respectively) compared to the other centra (see below). The atlas is fused to the axis, but the suture between the elements remains visible, especially dorsally, where it slightly constricts the neural canal. Moreover, the

neural arch facets are not continuous from the atlas to the axis. Ventrally, the atlas-axis articulates with the stout, roughly triangular axis intercentrum. The anterior surface of the atlas is smooth and markedly convex whereas the posterior surface of the axis is rugose and slightly concave.

Most of the preserved centra exceed a diameter of 70 mm, the largest measuring 115 mm. The vertebral count is 73, but is largely underestimated, and most centra are disturbed and disarticulated. Generally, centra are very long (Data S1) and moderately amphicoelous. Both the diapophyses and parapophyses are set in the anterior half of the centra and are prominent. Numerous centra exhibit a single apophysis in a lateroventral position, indicating that diapophyses and parapophyses are fused in the posterior thoracic region, like all non-thunnosaurian neoichthyosaurs (Sander 2000). Some caudal centra have well-marked chevron facets.

Few neural arches are visible. The neural spine is thick and arises from a thick neural arch with a rounded articular surface. The post-zygapophyses are paired in all cervical neural arches. Posterior dorsal neural arches have anteroposteriorly elongated pedicles and unpaired zygapophyses.

Numerous ribs are complete and relatively undisturbed. Cervical ribs are small and conical. Only the anterior thoracic ribs are bicapitate. All ribs are robust and have a rounded to oval cross-section. Some exhibit longitudinal ridges on the anterior and posterior surfaces, but these are too shallow to give the ribs the usual figure-eight cross-section.

Appendicular skeleton. Both scapulae are incomplete, lacking their distal ends. The anterior edge of the scapula is rather straight whereas the posterior edge is markedly curved, as in many specimens of *Temnodontosaurus* (e.g. Gaudry 1892). Medially, the scapula bears a large, straight articular facet for the coracoid and a small glenoid contribution. A rod-like bone with a flattened, concavo-convex end is interpreted as the distal part of one of the clavicles.

The left humerus is exposed ventrally. Most of its capitulum is missing (Fig. 5A). The shaft is markedly elongated and constricted. The distal end is strongly expanded anteroposteriorly and dorsoventrally compressed. The total length of the humerus is 230 mm, its mid-shaft width is 80 mm and its distal width is 170 mm (length/width ratio = 1.35; length/mid-shaft width ratio = 2.87). The leading edge of the bone is deeply curved whereas the posterior edge has a less pronounced curvature. Distally, the humerus bears two elongated articular facets, for radius and ulna. The radial facet is slightly longer than the

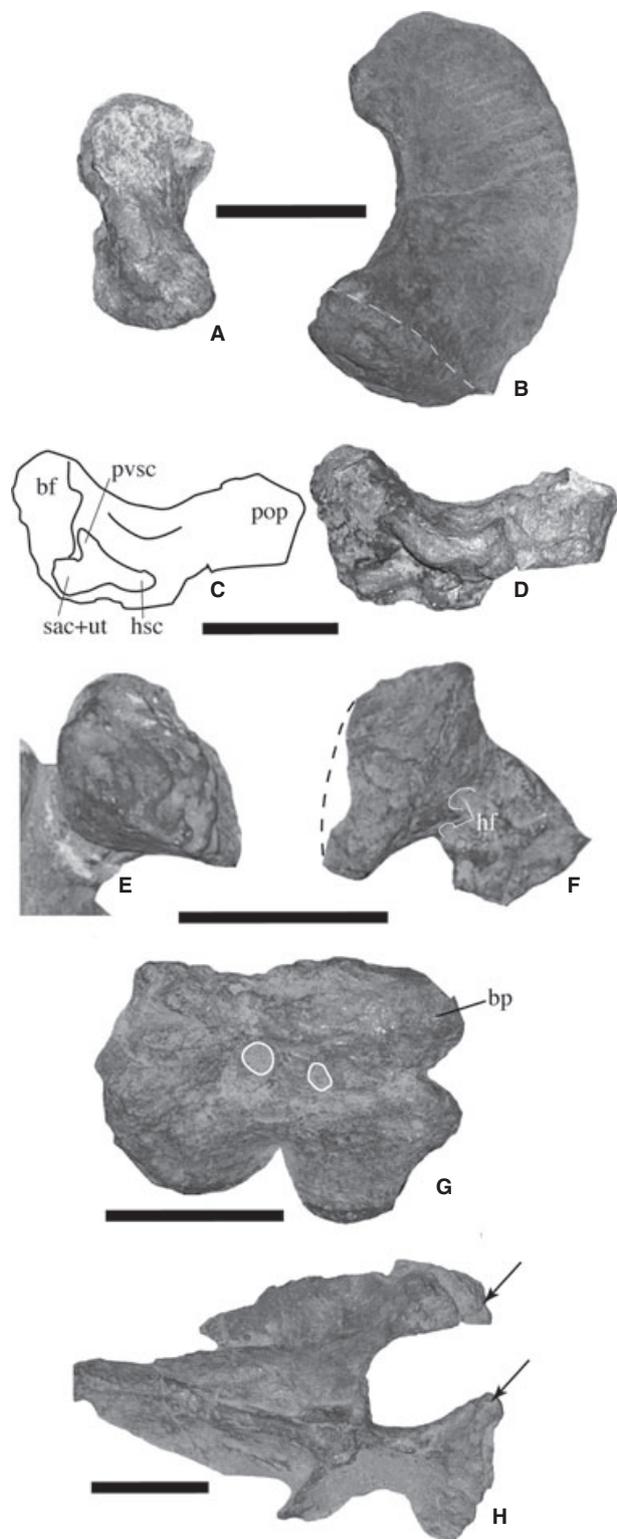


FIG. 4. Details of the anatomy of *Temnodontosaurus azerguensis* sp. nov. (MAMSPLP). A, right stapes in dorsoposterior view. B, right quadrate in lateral view showing the reduced articular condyle (highlighted by the stippled line) and anterior part of the pterygoid lamella. C–D, line drawing and corresponding left opisthotic in dorsomedial view. E–F, right and left exoccipitals in anterior view and medial views respectively, showing the expanded occipital foot. G, basisphenoid in ventral view – white circles indicate the paired ventral carotid foramina. H, distal portion of the left pterygoid with arrows pointing to the lamellae.

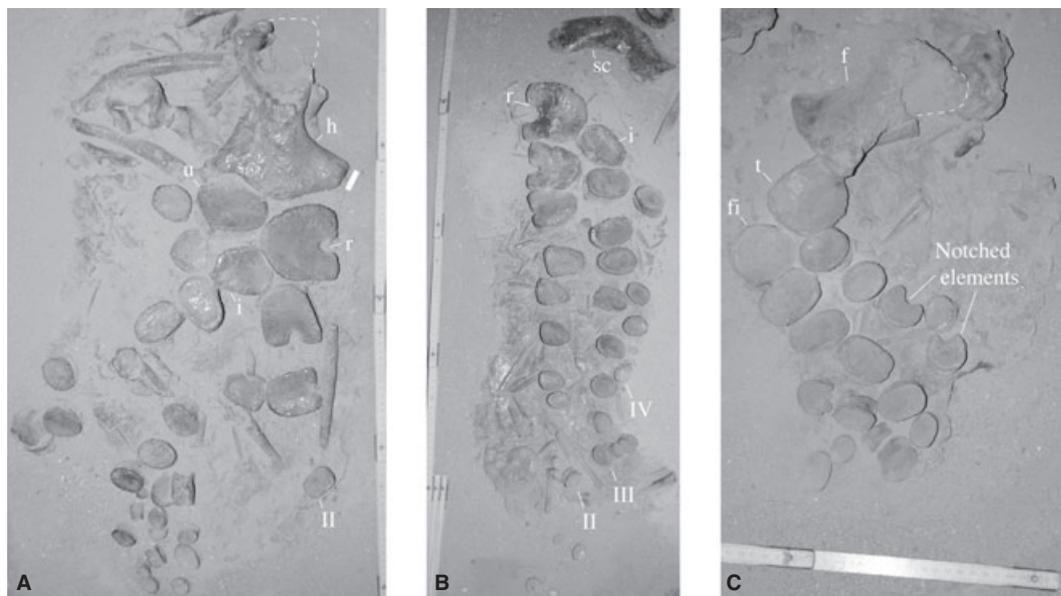


FIG. 5. Anatomy of the appendicular skeleton of *Temnodontosaurus azerguensis* sp. nov. (MAMSPLP). A, left forefin in ventral view – the thick white bar indicates the leading edge. B, right forefin in ventral view. C, right hind fin. When discernible, digit count is indicated.

ulnar facet. The radial facet is straight whereas the ulnar facet is superficially S-like in dorsal view, with a concave anterior portion and a slightly convex posterior portion.

Anterodistally, the humerus forms a prominent leading facet, with a straight edge similar to that of *T. trigonodon* (McGowan 1996). The radius and ulna are similar in size. The radius is large and polygonal, and it presents a small facet connecting to the ulna, meaning that there was a void (spatium interosseum) or cartilage because of the absence of a well-marked ridge between the radial and ulnar facet on the humerus. This facet is smaller than the intermedium facet. The anterior edge of the radius, the radiale and the first carpal are markedly notched in both forefins. Both forefins are tridactyle and apparently completely lack accessory digits. The maximum element count is nine, but it is largely underestimated because the distal ends of both forefins are disturbed. Proximal-most elements are hexagonal and have straight articular facets, but elements become oval distally. All elements are slightly hourglass-shaped in anterior view.

Elements of both sides of the pelvic girdle are preserved, including both ilia and the right ischium, which is a plate that is slightly constricted at mid-shaft. The ilium is slightly recurved and conical, tapering distally. The left ilium is 150 mm long and 39 mm wide. The left pubis is plate-like and slightly recurved.

Both femora are preserved. The femur is elongate (length 180 mm) and very widened at its distal end (138 mm, $L/W = 1.30$). The ventral process is strongly developed. The femur mimics the humerus in being elongate, constricted at mid-shaft and widely expanded distally. Distally, the femur bears two very elongated articular facets for the tibia and fibula. The hind fin is large, probably as large as the forefin given the size of the femur and the number of elements. This differs from some leptonectids such as *Leptonectes* (e.g. McGowan 1974; McGowan 1993) and *Excalibosaurus* (McGowan 2003), and from thunno-

saurian ichthyosaurs (Motani 1999). The right tibia and fibula are visible. These are large, flat and slightly polygonal. Elements then quickly become oval in shape. The hindfin is tridactyle, as in most non-thunnosaurian neoichthyosaurs. The proximal-most elements are not notched, whereas some disturbed smaller elements are, having a lunate shape.

DISCUSSION AND CONCLUSIONS

Affinities of the new species

A thorough revision of the genus *Temnodontosaurus* is beyond the scope of this study. Instead, we used the best and most up-to-date diagnoses found in the literature to build our diagnosis of *T. azerguensis*. We largely relied on that of Maisch and Matzke (2000); only McGowan and Motani (2003) proposed another diagnosis for *Temnodontosaurus*, but is mainly based on ratios and absolute size. We are confident that *T. azerguensis* can be assigned to the genus *Temnodontosaurus* for several reasons. *T. azerguensis* differs from all leptonectids and *T. platyodon* in having a tibia and fibula in contact (McGowan and Motani 2003; VF, pers. obs. on NHMUK 2003*, NHMUK R1158, IRSNB R122). The absence of an acromial process on the scapula of *T. azerguensis* differs from *L. tenuirostris* (McGowan and Motani 2003), *L. moorei* (McGowan and Milner 1999) and *Excalibosaurus* (McGowan 2003). The constricted humerus of *T. azerguensis* differs from *Excalibosaurus*, *Eurhinosaurus* (McGowan 2003) and *Suevolevi-*

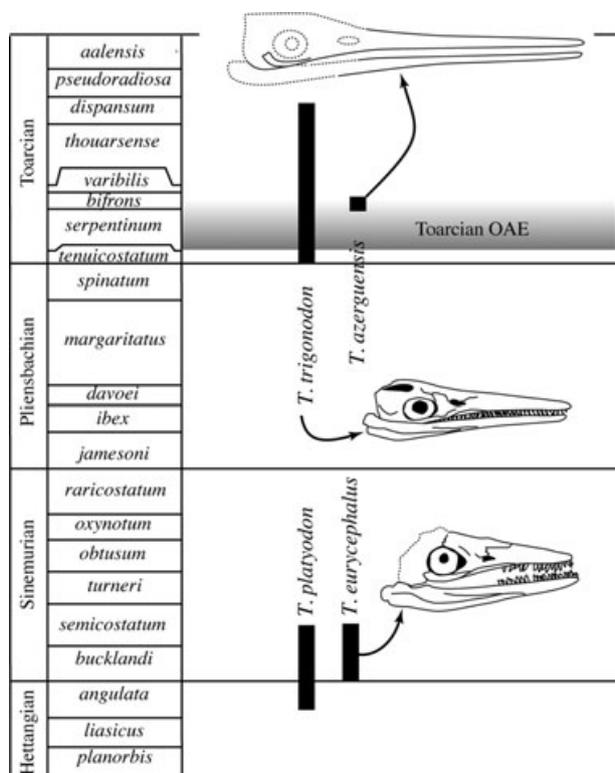


FIG. 6. Stratigraphic distribution at the level of the ammonite zone of the best-known species of *Temnodontosaurus* during the Early Jurassic, including the newly described species *T. azerguensis* sp. nov. The skull reconstructions are based on SMNS 15950 for *T. trigonodon*, NHMUK R1157 for *T. eurycephalus*, and based on MAMSPLP for *T. azerguensis* sp. nov. Stratigraphic ranges of *Temnodontosaurus* are based on Maisch and Matzke (2000) and McGowan and Motani (2003). Ammonite zones are not proportionate to absolute time.

athan (Maisch 1998a). The presence of at least two notched elements on the leading edge of the forefin of *T. azerguensis* differs from *Leptonectes* spp. (McGowan 1993, 2003; McGowan and Milner 1999) and *Suevoleiathan* (Maisch 1998a). The absence of a radio-ulnar foramen in *T. azerguensis* differs from *L. tenuirostris* (McGowan 1996; Godefroit 1992) and some specimens of *T. trigonodon* (McGowan 1996). The relatively long hind fin (as long as the forefin) of *T. azerguensis* differs from *L. tenuirostris* (McGowan and Motani 2003), *L. solei* (McGowan 1993) and *Excalibosaurus* (McGowan 2003). The presence of numerous phalanges and hexagonal proximal elements in *T. azerguensis* differs from *L. solei* (McGowan 1993) and *Eurhinosaurus* (McGowan 2003). The pelvic girdle is markedly different from that of *Suevoleiathan* in lacking the anterior pointed process on the ilium (Maisch 1998a). The basisphenoid is poorly known in non-thunnosaurian neioichthyosaurs, but it is not paired in *Eurhinosaurus* (Maisch and Matzke 2000) and

has only been described as paired in *Temnodontosaurus* (Huene 1922; Godefroit 1993; Maisch 2002). Although the skull of *T. azerguensis* is superficially similar to *Leptonectes*, this list of characters precludes any affinities with this taxon.

On the other hand, the basicranium and postcranial anatomy of the Belmont ichthyosaur are extremely similar to those described for *Temnodontosaurus* (e.g. McGowan 1996; Maisch and Matzke 2000; McGowan and Motani 2003) and is most similar to *T. trigonodon* (see Diagnosis). The Belmont ichthyosaur is, however, very different from *T. eurycephalus*, *T. trigonodon* and *T. platyodon* (Gaudry 1892; Godefroit 1993; McGowan and Motani 2003) in having a very slender rostrum and mandible, a reduced quadrate and in possibly being edentulous. No evidence for teeth could be detected in the Belmont ichthyosaur, nor in the surrounding sediment. The minimal disarticulation of the specimen favours the hypothesis that teeth were absent. The presence of dental grooves indicates that the specimen did probably possess teeth at some stage, perhaps earlier in ontogeny as known in other ichthyosaurs (Seeley 1874; McGowan 1979; Nicholls and Manabe 2004). In any case, the dental grooves of the Belmont ichthyosaur are reduced compared to those of similarly sized *Temnodontosaurus* (e.g. *T. platyodon*; Godefroit 1993), indicating the teeth – if any – would have been small, unlike other species of that genus.

The species '*Temnodontosaurus*' *acutirostris* (Owen, 1840) has also been described as a longirostrine taxon with a lunate quadrate and paired carotid foramen on the ventral surface of the basisphenoid (Huene 1952). Despite the possible erroneous generic attribution of that species (Maisch 2010), it does not correspond to the Belmont ichthyosaur by having an expanded dorsal head of the exoccipital (Fraas 1913), a much stouter and shorter humerus and femur with clearly separated radius, ulnar, fibular and tibial facets, up to 25 tightly packed hexagonal paddle elements per digit (Chapman and Doyle 2002), and a constricted ischium and pubis (Huene 1922), as shown by the re-discovery of the holotype (Chapman and Doyle 2002).

Temnodontosaurus nuertingensis (Huene, 1931) is a poorly known species from the Pliensbachian of Baden-Württemberg that was revised by Maisch and Hungerbühler (1997). Despite the scarcity of the material referred to this taxon, it differs from the Belmont ichthyosaur in having a much smaller skull (jaw length <1300 mm, considered by Maisch and Hungerbühler (1997) as a diagnostic feature), a thicker rostrum (Huene 1931) and moderately sized teeth (Huene 1931; Maisch and Hungerbühler 1997). The rest of the characters listed by Maisch and Hungerbühler (1997) refer to bones that are badly preserved or not preserved in the Belmont ichthyosaur. The characters observed in *T. nuertingensis*, if interpreted

as juvenile characters (especially those concerning small size and presence of teeth), could lend support to the hypothesis that *T. azerguensis* is an adult of *T. nuertingensis*. However, there is not a single feature uniting these two taxa and the Belmont ichthyosaur differs from all currently valid *Temnodontosaurus* species in the extremely elongated rostrum and mandible (Figs 2–3, 6), the Y shape of the posterior end of the pterygoid, the reduced condyle of the lunate quadrate, the elongated and constricted humerus, and an unconstricted ischium. Therefore, we refer the Belmont ichthyosaur to a new species, *T. azerguensis*.

Ecological diversity and cranial plasticity within the genus Temnodontosaurus

As depicted in the frontispiece of Sir Thomas Hawkins (1840), members of the genus *Temnodontosaurus* represent iconic monsters of the Jurassic seas. Their large size, sometimes surpassing 10 m in total length (McGowan 1996) and a massive dentition displaying bi- or trifaceted crowns suggest they were apex predators (Massare 1987, 1997). Despite a size and postcranial anatomy similar to other *Temnodontosaurus* species, *T. azerguensis* departs from this cranial morphology. As mentioned above, the rostrum is thin and elongated, the dental grooves are reduced and there is no evidence of teeth in the specimen or in the surrounding sediment. If teeth were present at all, their size would have been very small. The elongated and possibly edentulous rostrum of *T. azerguensis* have been ineffective for piercing or crushing hard-shelled or bony prey (Massare 1987). Instead, it resembles the rostra of *Stenopterygius*, basal Leptonectidae, some Ophthalmosauridae, and *Shastasaurus*, taxa for which a diet of small and soft prey has been inferred (Massare 1987, 1997; Godefroit 1996; Maisch 2008; Fischer *et al.* 2011; Sander *et al.* 2011).

Whereas comprehensive biomechanical studies of the jaws of ichthyosaurs have not been undertaken, both McGowan (1973) and Kear (2005) have attempted to reconstruct the musculature of the thunnosaurian ichthyosaurs *Ichthyosaurus communis* and *Platypterygius australensis*, respectively. According to these studies, the anterior part of the quadrate pterygoid lamella provides attachment for m. adductor mandibulae posterior, which is used in generating bite force and holding the jaw shut on prey (Kear 2005). From a mechanical point of view, a larger quadrate condyle grants the jaw joint a better resistance in dorsoventral loading situations (Kear 2005). *Temnodontosaurus azerguensis* differs from other *Temnodontosaurus* spp. by having a reduced anterior part of the quadrate pterygoid lamella, a reduced quadrate condyle and a much longer snout, a condition also seen in

Leptonectidae (e.g. Maisch and Matzke 2003; McGowan 2003). Taken together, these features indicate that *T. azerguensis* produced dramatically less bite force than other species of *Temnodontosaurus*.

Intragenetic variation in the length of the rostrum is common in Early Jurassic ichthyosaurs, such as *Leptonectes* and *Ichthyosaurus*, where both short-snouted (*L. moorei*, *I. breviceps*) and long-snouted (*L. tenuirostris*, *L. solei*, and *I. conybeari*) species are known. However, the extreme differences in snout length and possible bite force existing between *T. eurycephalus* and *T. azerguensis* indicates *Temnodontosaurus* was probably one of the most morphologically disparate genera of ichthyosaurs. Indeed, the size, skull shape, carinae-bearing teeth (V. Fischer pers. obs.) and preserved gut content of *T. platyodon*, *T. trigonodon* and *T. eurycephalus* indicate that these taxa occupied an apex predator niche (McGowan 1974; Massare 1987; Böttcher 1989; Godefroit 1996; McGowan 1996), whereas *T. azerguensis* is best regarded as a hunter of small and soft prey, even if the feeding ecology of other edentulous ichthyosaurs has been interpreted as suction feeding (Nicholls and Manabe 2004; and discussion in Sander *et al.* 2011). Other *Temnodontosaurus* species may have had a rather 'General' ecological niche (see guild definitions in Massare 1987). For example, *T. nuertingensis* has a long yet robust rostrum and medium sized, conical teeth (Huene 1931; Maisch and Hungerbühler 1997), although this species is too fragmentary to fully assess its ecology. *Temnodontosaurus azerguensis* typifies the high morphofunctional plasticity of the skull and rostrum of *Temnodontosaurus* (Fig. 6). On the other hand, the postcranial skeleton of this genus remains basically unmodified. This implies a clear decoupling between the diet and the hunting strategy: the morphological disparity of the rostrum illustrates exploitation of various food sources (e.g. Massare 1987), whereas modifications to the relative lengths of body parts and centrum shape have direct implications on swimming and hunting styles (Massare 1988; Motani *et al.* 1996; Buchholtz 2001). The latter traits are conservative throughout the evolution of *Temnodontosaurus*, and its unregionalized axial skeleton suggests that *T. azerguensis* was an agile, ambush hunter, as proposed for other species of the genus (Buchholtz 2001). In summary, the cranial and postcranial morphology of the Belmont ichthyosaur highlights the broad ecological spectrum occupied by *Temnodontosaurus*.

Stratigraphic and evolutionary significance

The ammonite specimens discovered in association with *T. azerguensis* constrain it to the basal *bifrons* zone and hence indicate that it is somewhat younger than most

Toarcian ichthyosaurs known. For instance, the large majority of Toarcian ichthyosaurs from south-western Germany have been discovered in the organic-rich laminated shales (Posidonienschiefer) near the transition between the *tenuicostatum* and *falciferum* ammonite zones, while a comparatively lower number of specimens have been reported from the *bifrons* zone (McGowan 1979; Hauff and Hauff 1981; Maisch 1998b, 2008; McGowan and Motani 2003). These deposits are thought to reflect the most dramatic lithological expression of severe environmental changes and marine invertebrate extinction related to the onset of an Oceanic Anoxic Event (T-OAE; e.g. Jenkyns 1988; Röhl *et al.* 2001; Cohen *et al.* 2007). On the contrary, both *T. azerguensis* and the marine reptile fauna from the Main Alum shale of Yorkshire are middle Toarcian in age (*bifrons* zone; Benton and Taylor 1984; Elmi and Rulleau 1991) and therefore postdate this event.

Interestingly, the marine Oceanic Anoxic Event (T-OAE) successions in Europe are, in contrast to immediately older and younger strata, noteworthy for the extreme scarcity or total absence of belemnites, suggesting the widespread development of inhospitable environmental conditions at that time (e.g. van de Schootbrugge *et al.* 2005; Hesselbo *et al.* 2007). Because numerous lines of evidence suggest that cephalopods constituted one of the main food resources of ichthyosaurs and other contemporaneous marine reptiles (e.g. Pollard 1968; Martill 1986; Böttcher 1989), it appears feasible that such transient changes in food resources had a significant impact on marine reptile faunal composition and could hence have favoured new niche exploration such as that exemplified by *T. azerguensis*. At present, however, ichthyosaur remains in post-*falciferum* strata of Europe are scarce and determining possible links between changes in source partitioning and marine vertebrate turnover cannot be assessed.

Thorne *et al.* (2011) pointed out that the diversity and disparity of ichthyosaurs after the end-Triassic mass extinction never attained the scale observed in the Triassic. The effects of the Oceanic Anoxic Event (T-OAE) on marine vertebrate fauna, if any, seem to have gone unnoticed so far. The present discovery however slightly expands the morphospace occupation of Liassic neoichthyosaurs and indicates that some of these ichthyosaurs explored various ecological niches during their evolutionary history, in contrast to most Triassic and post-Liassic ichthyosaur genera, for which ecological niche appears conservative in the evolutionary history of each genus. This may, however, be a consequence of inadequate sampling.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Measurements of skeletal elements of *Temnodontosaurus azerguensis*.

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