

Marine vertebrate remains from the Toarcian–Aalenian succession of southern Beaujolais, Rhône, France

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Abstract – A previously undocumented marine vertebrate fauna comprising ichthyosaur, plesiosaur, marine crocodilian and fish remains from the Toarcian–Aalenian succession at Lafarge quarry, southern Beaujolais (Rhône, France) is described on the basis of both historical collections and new discoveries. The taxonomic composition of the Lafarge quarry marine vertebrate assemblage highlights its cosmopolitan nature and strong relationships with taxa known from elsewhere in Europe. Several groups are recorded for the first time in the Toarcian–Aalenian succession of France, implying new palaeobiogeographic interpretations and prompting discussion of marine amniote diversity during this interval.

Keywords: diversity, France, Jurassic, marine vertebrates.

1. Introduction

The Early Jurassic period is marked by an episode of biological crisis that occurs towards the Pliensbachian–Toarcian boundary and continues into the early Toarcian (Little & Benton, 1995; Harries & Little, 1999; Macchioni & Cecca, 2002; Wignall, Newton & Little, 2005; Suan *et al.* 2008; Caswell, Coe & Cohen, 2009). This biotic crisis seems to have ensued from marked temperature changes and broadly coeval onset of seawater oxygen deficiency (Baudin, Herbin & Vandenbroucke, 1990; Harries & Little, 1999; Wignall, Newton & Little, 2005; Caswell, Coe & Cohen, 2009; Gómez & Goy, 2011), termed the Toarcian Oceanic Anoxic Event (T-OAE; Jenkyns, 1988). The impact of this crisis on the marine vertebrates, however, remains poorly understood (Benton, 1993).

Early Jurassic marine vertebrate history is particularly important, as this time witnessed the radiations of three major groups of successful marine amniotes, namely the thalattosuchian crocodiles, the neoichthyosaurian ichthyosaurs and the plesiosaurs (Benton,

1990*a, b*; Benson, Evans & Druckenmiller, 2012). Particularly diversified and abundant remains of marine amniotes have been recorded in Toarcian strata of western Europe, making the assemblages of this age the most diversified and well known of the Early Jurassic (e.g. Westphal, 1962; Benton & Taylor, 1984; Pierce & Benton, 2006; Delfino & Dal Sasso, 2006; Großmann, 2007; Bardet *et al.* 2008*a*; Bardet, Pereda Suberbiola & Ruiz-Omeñaca, 2008*b*; Maisch, 2008; Vincent & Smith, 2009; Vincent, 2011). In contrast, estimates of marine amniote diversity (e.g. Benson *et al.* 2010; Thorne, Ruta & Benton, 2011) infer a minimum at the beginning of the Middle Jurassic (Aalenian–Bajocian), although poor sampling from strata of this age (Bardet, 1994) implies artificial heterogeneity. Therefore, it is still unclear whether these diversity patterns reflect environmentally driven faunal turnover or simply result from a sampling bias.

In this context, the abundant invertebrate and vertebrate specimens spanning the whole Toarcian and part of the Aalenian stage from the Beaujolais area in France might provide clues about the diversity alteration through this critical interval. Indeed, thirty years of excavations in the Lafarge cement quarry in southern

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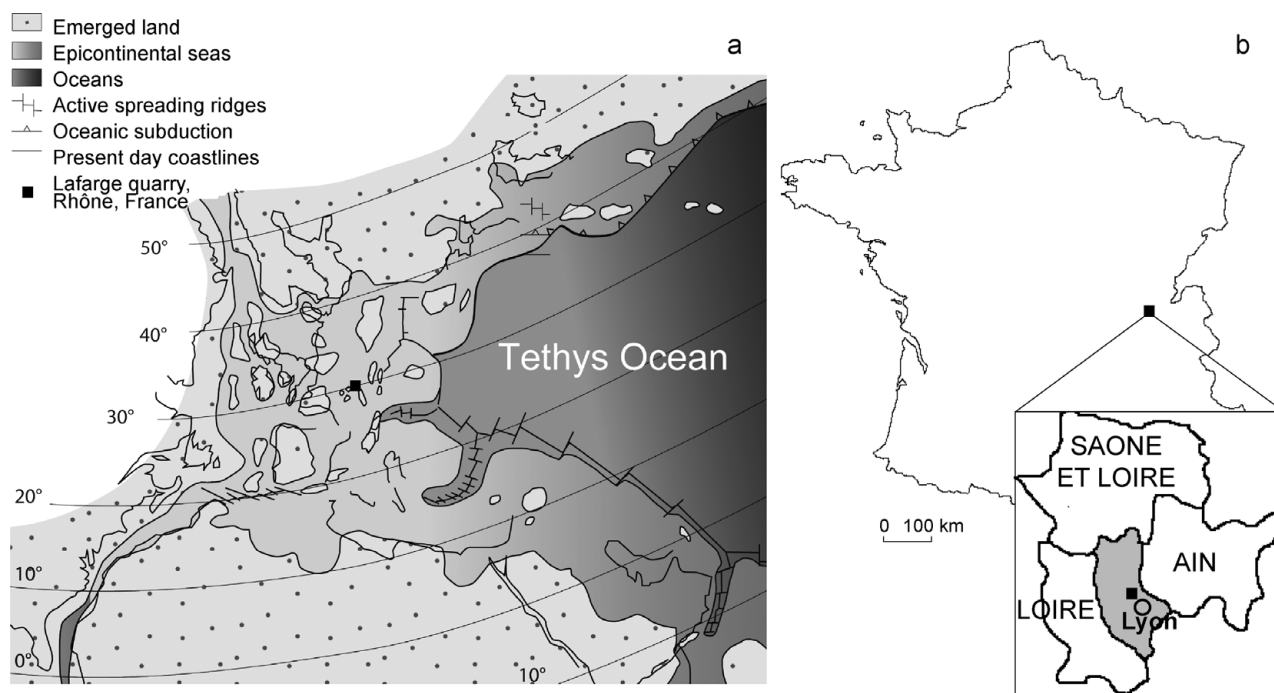


Figure 1. Location of the Toarcian–Aalenian succession of the Lafarge quarry. (a) Palaeogeography of the western margin of the Tethys Ocean during the Early Jurassic (from Suan *et al.* 2008) showing the position of the Lafarge quarry. (b) Regional position of the Lafarge quarry.

Beaujolais, France, as well as scientific exploration, have provided a wealth of new palaeontological and biostratigraphical data from the Lower and Middle Jurassic strata at this locality. Although the invertebrate fauna of the succession has been extensively studied (Elmi & Rulleau, 1991, 1993; Rulleau, 2006), the vertebrate associations and their occurrence throughout the succession have not been described. This paper relies on collected samples now stored at the nearby museum of Espace Pierres Folles in Saint-Jean-des-Vignes, Beaujolais and from recent field investigations of the Lafarge quarry site. An account and a brief description of the vertebrate fauna is presented for this succession: the presence of Chondrichthyes, Actinopterygii, Ichthyosauria, Plesiosauria and marine crocodilians is attested by cranial and postcranial elements, the first two taxa being newly reported at this locality, thus implying a potential for further recovery of complete material. This report adds a substantial comparative basis to the knowledge of contemporaneous marine vertebrates from Europe such as Holzmaden (Germany; Urlichs, Wild & Ziegler, 1994) and Yorkshire (England; Benton & Taylor, 1984), and helps to constrain the evolution of vertebrate fauna across the Early–Middle Jurassic transition.

Institutional abbreviations. GLAHM, – University of Glasgow, Hunterian Museum, Glasgow, Scotland, UK; MAMSPL – Musée des Amis de la Mine, Saint-Pierre-la-Palud, Rhône, France; MHNL – Muséum d'Histoire Naturelle de Lyon, Lyon, France; PF – Espace Pierres Folles, Saint-Jean-des-Vignes, Rhône, France.

2. Geological setting and lithostratigraphy

The Lafarge quarry, near the villages of Saint-Jean-des-Vignes, Belmont and Charnay (Beaujolais, Rhône, SE France), exposes a succession of fully marine strata of Toarcian to Bajocian age that were deposited at relatively shallow depths near the easternmost reach of the Massif Central (Fig. 1). The lithostratigraphy and ammonite biostratigraphy of the section were described by Elmi & Rulleau (1991, 1993). Excavations undertaken in 2009 and 2010 in the southern part of the quarry allowed new detailed observations and sampling of the Toarcian to lowermost Aalenian sequence, including the lower Toarcian interval, which is otherwise poorly represented in the quarry (Rulleau, 1997). The lower Toarcian is mainly represented by partly dolomitized, massive and yellowish argillaceous limestone beds interbedded with weathered yellow plastic clays ('Calcaires à *Ammonitella*'; Elmi & Rulleau, 1991). The first beds yielded specimens of *Dactyloceras* (*Orthodactylites*) diagnostic of the *tenuicostatum* zone, while overlying beds yielded abundant belemnite rostra and several ammonites diagnostic of the *serpentinum* ammonite zone (Fig. 2). This carbonate-rich interval is overlain by an interval ~2.5 m thick (from 2.7 to 5.3 m; 'Marnes inférieures'; Elmi & Rulleau, 1991) of dark grey, finely laminated calcareous marl (yellow and structureless when deeply weathered) presenting several millimetre-thick pyritic beds rich in vertebrate debris and belemnite rostra towards its base and equivalent to the classical 'Schistes Cartons' of the Paris Basin. The middle Toarcian sequence (*bifrons* zone to

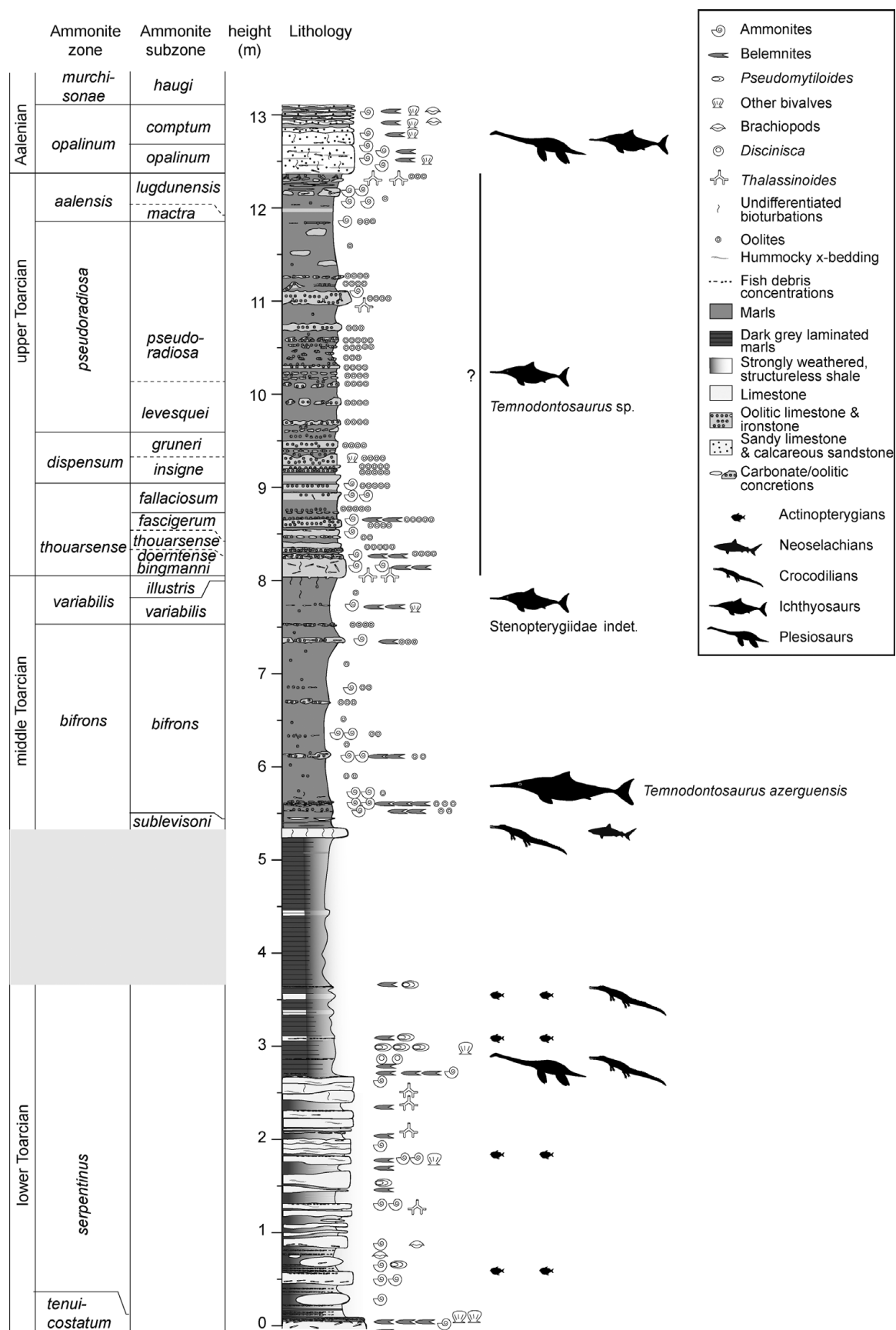


Figure 2. Stratigraphic log of the Toarcian section and base of the Aalenian at Lafarge quarry, Rhône, France together with the distribution of discovered vertebrates.

variabilis zone) is represented by an ~2.5 m interval of ammonite- and belemnite-rich purplish bioturbated marls ('Marnes médianes'; Elmi & Rulleau, 1991) with a few dispersed phosphatic oolites and interrupted by thin and discontinuous oolitic limestone beds. The upper Toarcian sequence, from 8 to 12.4 m, ('Marnes supérieures'; Elmi & Rulleau, 1991) consists of purplish to greenish grey bioturbated marls (deep red when weathered) that yielded abundant belemnites, bivalves and ammonites. Several massive, orange to reddish oolitic limestone beds occur towards the base, the lowermost of which being more prominent and especially rich in ammonites and belemnites ('Banc à *Haugia* et à *Grammoceras*'; Elmi & Rulleau, 1991). An intensively bioturbated, massive and sandy yellowish bioclastic limestone bed at 12.4 m ('Dalle à *Leioceras*'; Elmi & Rulleau, 1991) marks the base of the more calcareous and coarser sequence of the lower Aalenian (*opalinum* ammonite zone), which consists mainly of yellowish to pinkish sandy calcarenite and calcareous sandstone beds (Fig. 2).

3. Survey of the marine vertebrate material

3.a. Chondrichthyes

Chondrichthyan fossils occur in the middle Toarcian (MHNL 20103017), *bifrons* zone (PF Toa 623), *variabilis* zone? (PF Aal 323), through to the lower Aalenian (PF Aal 32 and PF Aal 312). Diagnostic elements include: two hybodontiform spines (PF Aal 321, Fig. 3a, b and PF Aal 323, Fig. 3c), a lateral tooth of *Asteracanthus* sp. (PF Aal 312; Fig. 3d), one *Hybodus* tooth (MHNL 20103017; Fig. 3e, f) and one neoselachian tooth (PF Toa 623; Fig. 3g).

PF Aal 323 (22 cm in length) is a nearly complete spine missing its tip. It is gently curved posteriorly and laterally flattened being taller (3 cm) than wide, the width decreasing from the base to the tip of the spine. Laterally, the spine is flanked by about 14 longitudinal ribs in the mid-region that seem to anastomose anteriorly to about 10 ribs. The dorsal and lateral areas of the base of the spine are devoid of ornamentation and correspond to the insertion area of the spine in the body of the shark. Although the presence of denticles on the ventral surface of the spine of PF Aal 321 cannot be assessed here due to the area being covered with sediment, the fin spine is overall very similar to that seen in *Hybodus*, *Asteracanthus*, *Lissodus* and *Acrodus* (Maisey, 1978); the presently described specimen could represent any of those taxa.

PF Aal 312 is a low crown plate-like tooth measuring 2.3 cm long and 1.1 cm wide. The root is not visible. In occlusal view, the crushing crown is nearly rectangular (slightly asymmetric) presenting a fine set of reticulations, a characteristic of a lateral tooth of *Asteracanthus* sp. (Rees, 2008). An occlusal crest is absent.

MHNL 20103017 is a large tooth crown belonging to the cladodont morphotype. It has a longitudinal length

of 2.5 cm and is 0.6 cm wide at the level of the central cusp. The crown is slightly asymmetric. It possesses one main central abraded cusp, which is flanked by one cusp then one cusplet mesially, and by one cusp then by two cusplets distally. Lingually, vertical ridges originate above the base of the crown, which is smooth and flattened. Labially, vertical ridges descend to the base of the crown. Here, the surface is irregular and ornamented with nodes. Labially and lingually, the ridges do not anastomose and meet near the apex of the cusps and cusplets. Medial and distal cusp apices are smooth. In occlusal view, a single longitudinal crest extends for the mesio-distal length of the crown. This tooth is attributed to *Hybodus* sp. because the crown is mesio-distally long and relatively low, by the presence of a large central cusp flanked by smaller cusplets, the presence of nodes on the labial side of the crown and the presence of an occlusal ridge extending for the entire mesio-distal length.

PF Toa 623 is a minute tooth (crown height = 3 mm) attached to the umbilicus of *Hildoceras bifrons*, within a shallow depression on the shell. The crown is taller than wide, triangular with a pointed apex and slightly curved labially. The root is broken. The shape of the crown indicates for the first time the presence of a neoselachian in the *bifrons* zone of the Lafarge quarry. The association of this tooth with an ammonite might indicate a trophic interaction, a case similar, though less obvious than a recently reported close association between hybodont teeth and ammonite (Vullo, 2011).

3.b. Actinopterygii

Actinopterygian remains from the Lafarge Quarry occur in the lower Toarcian *serpentinus* zone (MHNL 2013062, MHNL 2013064, PF Toa 472), through to the *bifrons* subzone of the middle Toarcian (MHNL 20103063). Diagnostic elements include an incomplete skull with parts of pectoral girdle and fins (MHNL 2013062; Fig. 3h), an isolated ganoid scale (MHNL 20103063; Fig. 3i), an ornamented bone fragment (MHNL 20103064; Fig. 3j) and incomplete posterior postcranial portions with pelvic and anal fins (PF Toa 472 and one unnumbered fragment; Fig. 3k–l).

MHNL 2013062 preserves a massive dentary showing a well-developed coronoid process located anteriorly, a quadrate-mandibular articulation placed below the posterior half of orbit, and a preopercle possessing two well-defined limbs forming a slightly obtuse angle; the vertical one is more elongated than the horizontal one (Fig. 3h). The preopercular sensory canal shows about eight or nine unbranched diverticula in the horizontal limb of the bone and two others in the vertical limb. This specimen can probably be referred to the genus *Leptolepis* on the basis of the general proportions of the skull, the very anterior position of the coronoid process and the shape of the preopercle. According to the diagnoses of Nybelin (1962, 1974), a preopercular sensory canal with a small number of unbranched diverticula is diagnostic of *L. normandica*,

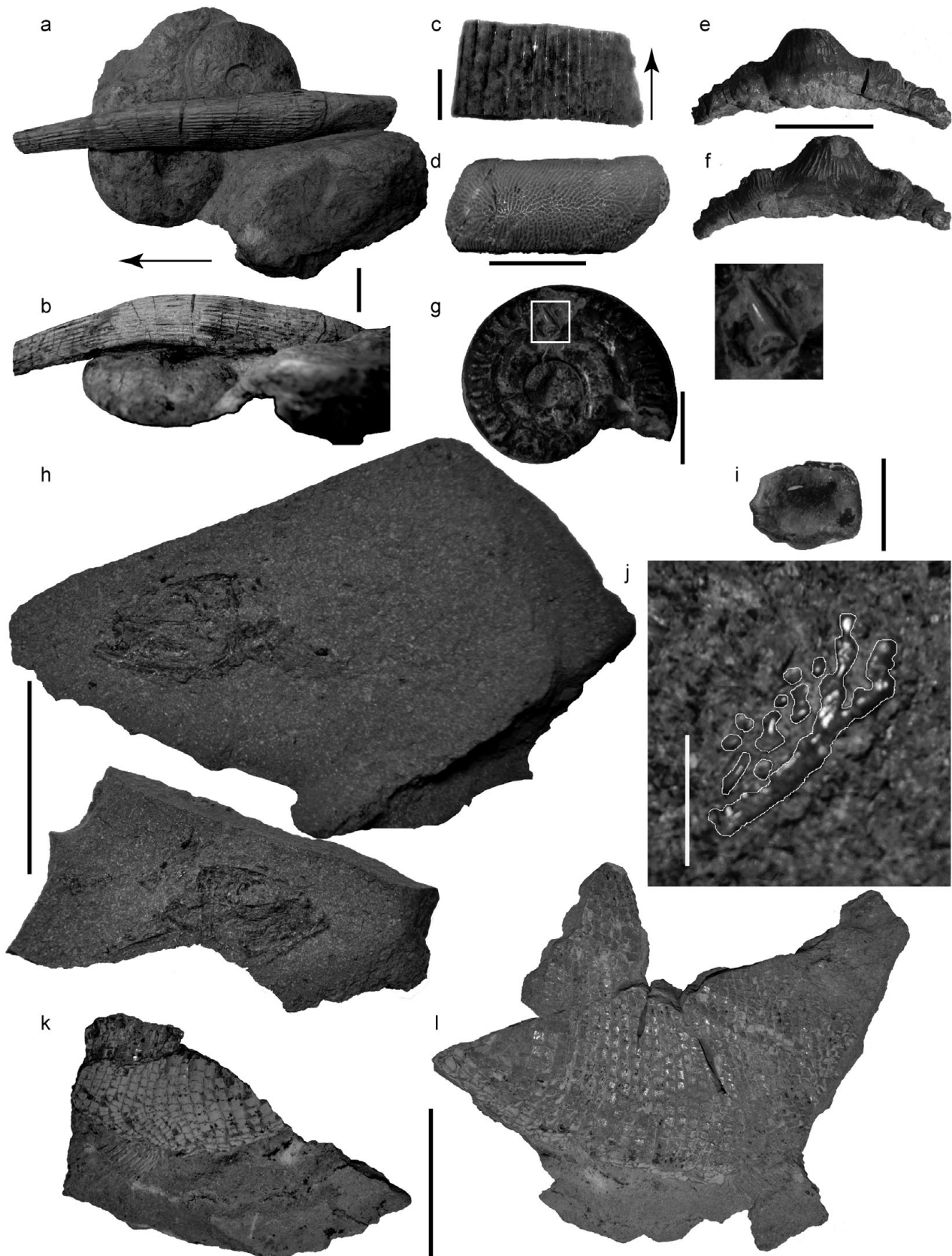


Figure 3. Chondrichthyan and actinopterygian remains from the Toarcian–Aalenian of Beaujolais, France. (a, b) Hybodontiform fin spine (PF Aal 321). (c) Fragment of hybodontiform fin spine (PF Aal 323). The arrows point toward the apex of the spines. (d) Low crown plate-like tooth of *Asteracanthus* sp. (PF Aal 312). (e, f) *Hybodus* tooth (MHNL 20103017). (g) Neoselachian tooth on ammonite (PF Toa 623) with enlargement of outlined area. (h) Skull of *Leptolepis* sp. (MHNL 20103062). (i) Ganoid scale (MHNL 20103063). (j) *Dapedium*-like cranial bone ornamentation (MHNL 20103064) outlined in white. (k) Postcranial part of ?*Dapedium* sp. (PF Toa 472). (l) Postcranial part of ?*Dapedium* sp. (unnumbered). Scale bars represent: (a, d, e, f, g, i, j) 1 cm; (c) 0.2 cm; (h) 3 cm; (k, l) 5 cm.

but better-preserved material is necessary to assert this specific determination.

MHNL 20103063 consists of a square-shaped scale without ornamentation and with surface and edges smoothed by erosion, possibly referable to *Lepidotes* or *Dapedium* (Fig. 3i). MHNL 20103064 consists of a ganoid specimen showing a rugae-like superficial bone ornamentation that is usually found on cranial bones of *Dapedium* or *Tetragonolepis* (Wenz, 1967; Thies, 1991). The incomplete posterior postcranial portions (PF Toa 472 and one unnumbered fragment; Fig. 3k, l) preserve fulcra that are present anteriorly to the insertion of the anal fin. Anal fin rays are thick and spaced. The body is covered by ganoid scales of different shape and size; the ones located close to the anal fin are the smallest. Scales located in the ventral or posterior part of the specimen are square-shaped or longer than high; other scales are higher than long. Some dorsal and ventral scale edges are wave-shaped. The shape of the ventral profile corresponds to a deep-bodied fish. Orientation and shape of scales suggest affinities with *Dapedium* (Agassiz, 1833–1844; Wenz, 1967).

3.c. Ichthyosauria

Ichthyosaurian remains occur in the Toarcian (PF Toa 514; PF Toa 467), *serpentinum* zone (MHNL 20103011), *bifrons* zone (MAMSPL uncatalogued), *variabilis* zone (MHNL 20103016), upper Toarcian (PF Toa 485), through to the lower Aalenian (PF Aal 308 and PF Aal 309). Diagnostic elements include: an almost complete skeleton (MAMSPL uncatalogued) of *Temnodontosaurus azerguensis* Martin *et al.* 2012; non-diagnostic cranial material (PF Toa 467); partial cranial material of *Temnodontosaurus* sp. (PF Toa 485); partial postcranial material of Thunnosauria indet. (PF Toa 514); partial postcranial material of non-thunnosaurian Neoichthyosauria (MHNL 20103011); partial postcranial material of Thunnosauria (MHNL 20103016); and partial cranial and postcranial material of Ichthyosauria indet. (PF Aal 309; PF Aal 308).

PF Toa 467 is a partial rostrum whose structure is clearly revealed in a transverse section (Fig. 4a). A deep and thin fossa praemaxillaris runs along the premaxilla. The nasals form a ridge-like convexity on either side of the dorsal surface and concealed beneath the overlapping premaxilla. The anterior part of the vomer is excluded from the palate by the premaxilla. The vomer contacts the lingual wall of the premaxilla and is buttressed ventrally by the palatal processes of the premaxilla. The lingual wall of the dentary is smaller than that of the premaxilla. Each dentary bears a shallow fossa dentalis. The splenial is curved and contacts the dentaries along a straight suture. The surangular is a very low and slender element. Its ventral part contacts the splenial. Tooth crowns are slender, pointed, and straight. The root is not bulbous.

PF Toa 485 is a pair of tooth-bearing bones here identified as the premaxillae (Fig. 4b). They surround a

large and rounded internal cavity, the central canal. The premaxilla is thick and its lateral surface exhibits a thin and shallow fossa praemaxillaris. The dental grooves are large. The nasals are present in the central canal as two thin convex elements. The teeth are large, thick, and rounded in cross-section. The crown is textured by deep and widely spaced apicobasal ridges, which extend on to the slightly bulbous root. This specimen is tentatively referred to *Temnodontosaurus* sp. based on the tooth morphology: *Temnodontosaurus* is the only genus of Liassic ichthyosaur combining large teeth with bulbous roots and deep apicobasal ridges (Godefroit, 1993; McGowan, 1996; pers. obs.); deep apicobasal ridges are also found in some species of *Ichthyosaurus* and *Suevoleviathan* but these taxa lack the bulbous roots (Godefroit, 1996; Maisch, 2001; pers. obs.). The precise position of the bed that yielded this specimen is not recorded. However, the matrix surrounding the specimen exhibits a highly distinctive red colour that is absent in the Aalenian and lower and middle Toarcian strata of the study site, but commonly found towards the top of the Toarcian sequence (see Section 2). These observations indicate that the specimen almost certainly comes from the upper Toarcian, though further attribution to a given ammonite zone is as yet impossible.

PF Toa 514 consists of a series of 20 centra, including posterior dorsal and caudal elements (Fig. 4c). They were found in a block, having being displaced before burial. Diapophyses and parapophyses are separated and lie at the ventral half of centrum, a feature of thunnosaurian ichthyosaurs (Sander, 2000). The only thunnosaurian ichthyosaurs known from the European Toarcian record appear to be stenopterygiids (*Stenopterygius* + *Hauffiopteryx*), but this assignation is made by default. Accordingly, the material is assigned to Thunnosauria indet.

MHNL 20103011 is a large and elongated propodial lacking the proximal half (Fig. 4d). The trochanters are low and do not extend further than mid shaft. The shaft is moderately constricted and the distal extremity is flat and anteroposteriorly expanded. Two large and flat facets are present distally. The specimen can be referred to as non-thunnosaurian Neoichthyosauria (Leptonectidae, *Temnodontosaurus*, *Suevoleviathan*) despite its incompleteness. Indeed, the humeri of non-thunnosaurian neoichthyosaurs lack prominent trochanters (e.g. McGowan & Motani, 2003). This is corroborated by the wide and flat distal end and the flat and elongated distal facets, which characterize the propodials of non-thunnosaurian neoichthyosaurs. Within this clade, the propodial closely resembles that of *Temnodontosaurus* (Godefroit, 1993; McGowan & Motani, 2003).

MHNL 20103016 is an incomplete femur with a partially preserved distal end (Fig. 4e). The femur is short and possesses a poorly developed dorsal trochanter and a prominent ventral ridge, both of which vanish before mid-shaft. The anterior surface is flat and triangular whereas the posterior surface is blade-like, as in thunnosaurian ichthyosaurs (e.g. *Ichthyosaurus*:

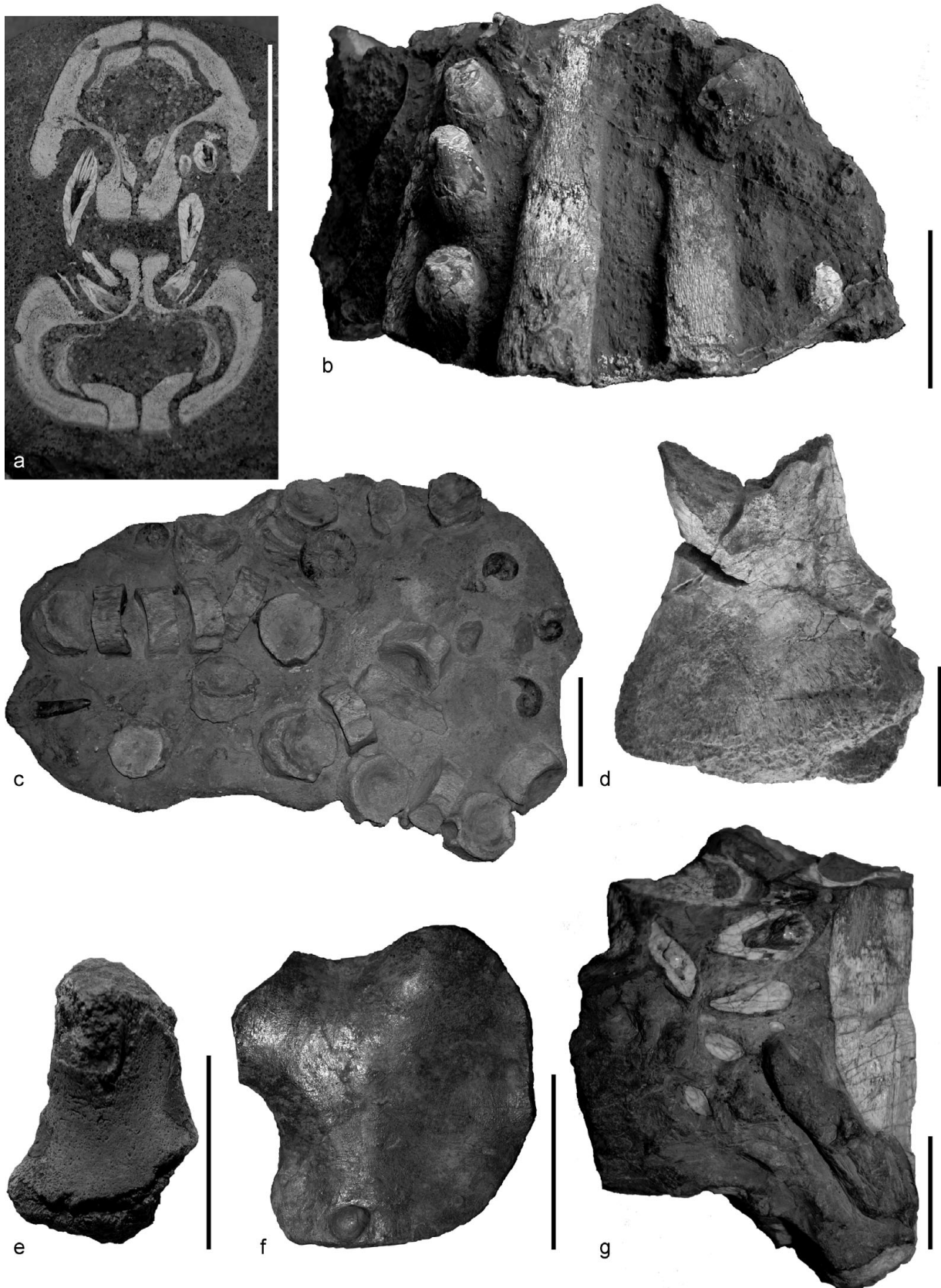


Figure 4. Ichthyosaurian remains from the Toarcian of Beaujolais, France. (a) Transverse section of a rostrum, Ichthyosauria indet. (PF Toa 467). (b) Cranial elements, *Temnodontosaurus* sp. (PF Toa 485). (c) Vertebrae, Thunnosauria indet. (PF Toa 514). (d) Humerus, non-thunnosaurian Neoichthyosauria indet. (MHNL 20103011). (e) Femur, Stenopterygiidae indet. (MHNL 20103016). (f) Coracoid, Ichthyosauria indet. (PF Aal 309). (g) Cranial elements, Ichthyosauria indet. (PF Aal 308). Scale bars represent: (a, b, d) 5 cm; (c, f) 10 cm; (e, g) 2.5 cm.

McGowan & Motani, 2003; Ophthalmosauridae: Andrews, 1910; Zammit, Norris & Kear, 2010; pers. obs.). Distally, there are two concave and oval articular facets. The anterior facet of the tibia appears to be slightly longer than that of the fibula. The surface of the femur is made of finished bone, which suggests maturity. The small size of the femur and its shape indicates that it belongs to Thunnosauria, a clade of derived ichthyosaurs with reduced hind limbs. As in some *Stenopterygius* specimens, and unlike *Ichthyosaurus*, the femur is short (proximal–distal distance) relative to its depth (dorsal–ventral distance) (McGowan & Motani, 2003; Caine & Benton, 2011). The femur also lacks the raised ridge in the distal part of the anterior surface seen in *Ichthyosaurus* (McGowan & Motani, 2003; Maxwell, Zammit & Druckenmiller, 2012). Accordingly, this specimen is tentatively referred to *Stenopterygiidae* indet.

PF Aal 309 is a coracoid of an indeterminate ichthyosaur (Fig. 4f). This fan-shaped element presents two lateral facets. The anterior one, for articulation with the scapula, is the longest. The posterior one represents the coracoidal contribution to the glenoid. The coracoid has a prominent emargination on its anterior edge, medial to the scapular facet and a second larger emargination on its lateral edge, posterior to the glenoid contribution. This specimen is referred to *Ichthyosauria* indet.

PF Aal 308 is a partial rostrum (Fig. 4g). The partially preserved dental grooves bear nine teeth. They are all very pointed and slender without constriction between the crown and the root. The root apparently had a somewhat rectangular, rather than rounded, cross-section and could indicate immaturity as in derived ichthyosaurs such as *Ophthalmosaurus icenicus* (VF, pers. obs. of GLAHM material). Nevertheless, tooth root cross-section is also known to vary with position along the jaw in other ophthalmosaurids (Kear, 2005) and therefore cannot be regarded as a robust indicator of osteological immaturity. This specimen is referred to *Ichthyosauria* indet.

3.d. Plesiosauria

Plesiosaur remains are rare in the Lafarge Quarry and occur in the Aalenian (PF Aal 186–187). Diagnostic elements include postcranial remains preserved in two incompletely prepared blocks of fine-grained, wine-coloured sandstone (PF Aal 186–187; Fig. 5). These remains (Fig. 5a) correspond to sub-articulated postcranial elements of a single individual and preserve dorsal vertebrae, ribs and girdle fragments. The six preserved dorsal vertebrae present well-rounded centra (Fig. 5b). All centra are slightly wider than long and high ($W > L > H$). The dorsal groove for the neural canal gives a slightly heart-shape to each centrum. The dorsal centra bear slightly concave articular surfaces with rugose margins. The facets for the ribs are placed high up and entirely bear by the neural arch. The lateral surfaces beneath the neural arch are concave. The neural arches

are strongly built and bear large pre- and postzygapophyses which are narrower than the centrum. The high neural spine is more than twice the height of the centrum, and blade-like, with a slightly convex apex. Several long and robustly recurved single-headed dorsal ribs are preserved. The bone girdle elements are flat and fragmentary, but their poor preparation and preservation preclude further determination.

3.e. Crocodylians

Crocodylian remains from the Lafarge Quarry occur in the Toarcian *serpentinum* zone (PF Toa 663; MHNL 20103014.2; MHNL 20103047), the *bifrons* zone (MHNL 20103015), and up into the upper Toarcian (PF Toa 468). Diagnostic elements include: two jaw fragments (PF Toa 663; Fig. 5c and MHNL 20103015; Fig. 5f), teeth (MHNL 20103014.2; Fig. 5d), one osteoderm (MHNL 20103047; Fig. 5e), vertebrae (PF Toa 470, MHNL 20103041; Figs. 5g–i), and a femur (PF Toa 468; Fig. 5j).

PF Toa 663 is a partial dentary preserving at least 14 alveoli with shallow cupular pits in between (Fig. 5c). The elongate and shallow bone bears circular and regularly spaced alveoli of similar size reminiscent of a non-diagnostic thalattosuchian.

The bone beds yielded several isolated crocodylian teeth (e.g. MHNL 20103014.2; Fig. 5d). They are relatively small, slender, curved and conical in shape. In addition to the mesiodistal carinae, they bear fine vertical ridges on their lingual and labial surfaces. Such piercing morphologies are seen in *Stenosaurosaurus*, *Platysuchus* or *Pelagosaurus* and are typical of longirostrine marine crocodylians, so no further identification can be advanced.

MHNL 20103047 is an osteoderm showing several ovoid and large pits and is rectangular in shape (Fig. 5e). The presence of a prominent lateral keel is reminiscent of the double row of osteoderms of the dorsal armour of non-eusuchian mesoeucrocodylians (see reconstructions in Salisbury & Frey, 2000). Among thalattosuchians, the presence of a dorsal keel may exclude an attribution to the genus *Pelagosaurus* (see specimens in Pierce and Benton, 2006; Lepage *et al.* 2008).

MHNL 20103015 is a piece of jaw presented in section and showing internal vacuities (Fig. 5f). The absence of the large narial duct and the presence of three pneumatic zones indicate that this jaw fragment represents the articulated dentaries. Its morphology is ovoid and dorsoventrally compressed, indicating a tubular snout. This trait, and the presence of three well-spaced alveoli, is reminiscent of longirostrine thalattosuchians.

PF Toa 470 and MHNL 20103041 are two isolated elongated, hourglass-shaped and mediolaterally compressed vertebral centra, interpreted as caudal centra. They lack a neural arch and spine (Figs 5g–i). They are reminiscent of the mesoeucrocodylian condition in being amphicoelous (Salisbury & Frey, 2000).

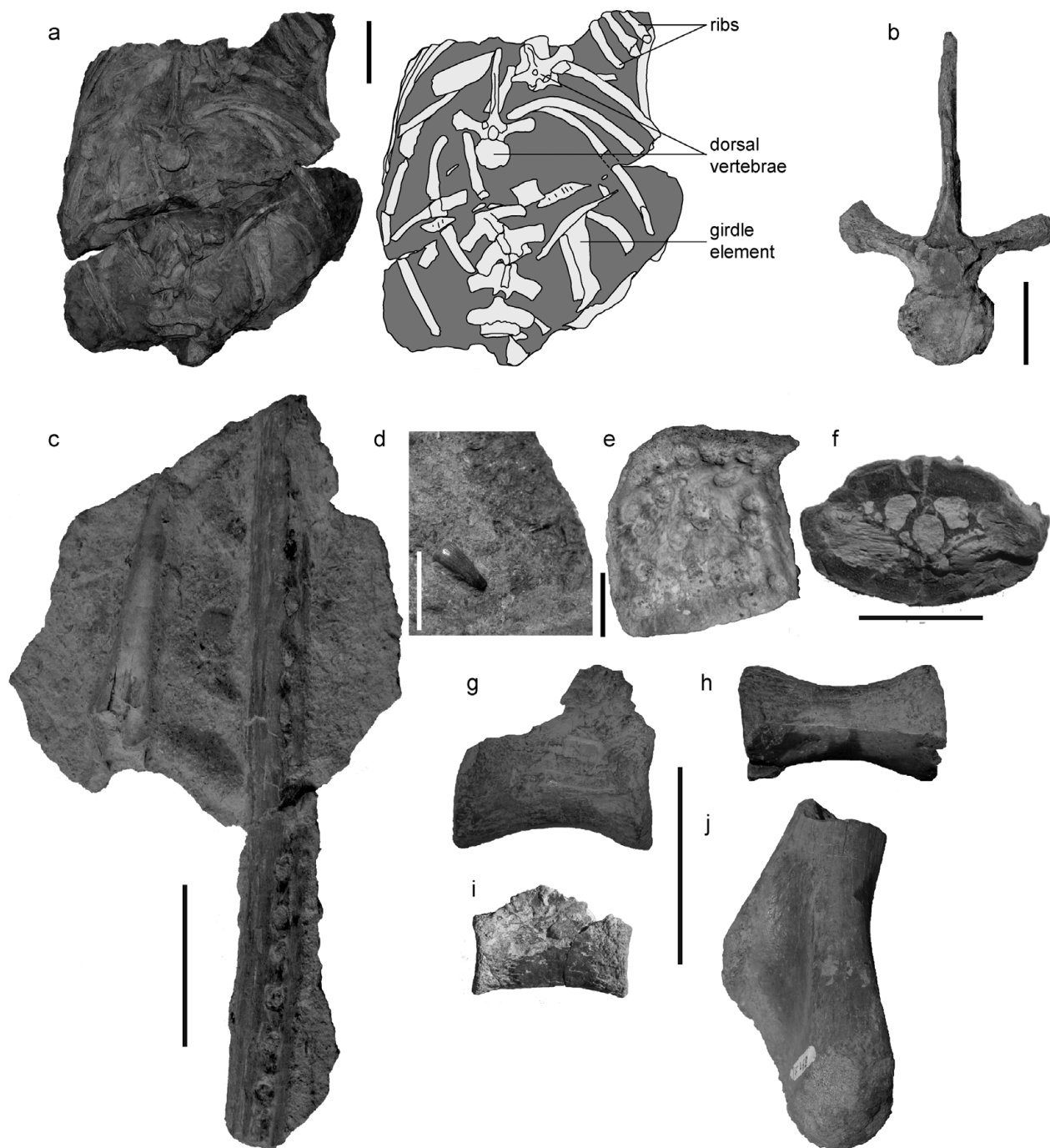


Figure 5. Plesiosaur and thalattosuchian crocodilian remains from the Toarcian and Aalenian of Beaujolais, France. (a) Photograph and line drawing, Plesiosauria indet. (PF Aal 186–187). (b) Dorsal vertebra (PF Aal 186–187). (c) Partial mandible, Thalattosuchia indet. (PF Toa 663). (d) Tooth, Crocodilia indet. (MHNL 20103014.2). (e) Osteoderm, Thalattosuchia indet. (MHNL 20103047). (f) Piece of jaw, Thalattosuchia indet. (MHNL 20103015). (g, h) Caudal vertebra, Thalattosuchia indet. (PF Toa 470) in (g) lateral and (h) ventral view; (i), caudal vertebra in lateral view, Thalattosuchia indet. (MHNL 20103041). (j) Partial distal part of a femur, Crocodilia indet. (PF Toa 468). Scale bars represent: (a) 10 cm; (b, c, g, h, i, j) 5 cm; (d, e, f) 1 cm.

PF Toa 468 is a proximal portion of a right curved femur. It presents a well-rounded condyle and a well expressed fourth trochanter (Fig. 5j).

4. Discussion

4.a. Stratigraphic range and implications for evolution of vertebrate diversity during the Early–Middle Jurassic

The Lafarge quarry site records an almost continuous Toarcian – lower Aalenian marine succession, which, in

contrast to other Toarcian exposures, yields abundant vertebrate remains throughout (Fig. 2). Indeed, due to regional unconformities, most of the upper Toarcian is missing in Yorkshire and SW Germany (e.g. Cope *et al.* 1980; Riegraf, 1985), where vertebrate remains have been almost exclusively reported from the *falciferum* (SW Germany) and basal *bifrons* (Yorkshire) ammonite zones (Benton & Taylor, 1984; Benton & Spencer, 1995; F. Großmann, unpub. Ph.D. thesis, Der Geowissenschaftlichen Fakultät der

Eberhard-Karls-Universität Tübingen, 2006). The complete Toarcian succession at the study site, with only 12 m of strata, appears highly condensed when compared to most coeval exposures and boreholes where the Toarcian, when complete, generally exceeds 50 m (de Graciansky *et al.* 1998). Much reduced sedimentation rates, as suggested by the exceptionally high invertebrate abundance (Rulleau, 2006), are likely to explain the high abundance of vertebrate remains in the whole Toarcian succession of the Lafarge quarry site. These remains are mainly isolated bones or teeth of marine vertebrates: actinopterygians, neoselachians, ichthyosaurians, plesiosaurians and marine crocodilians. Most cannot be identified at the infra-familial level, but some are tentatively identified at the generic level.

Ichthyosaur fossils outnumber crocodilians and plesiosaurs throughout the Toarcian–Aalenian succession of the Beaujolais foothills. These apparent marine vertebrate abundances appear similar to those documented in other less complete Toarcian marine successions from NW Europe (Yorkshire: Benton & Taylor, 1984; Benton & Spencer, 1995; Holzmaden: F. Großmann, unpub. Ph.D. Thesis, Der Geowissenschaftlichen Fakultät der Eberhard-Karls-Universität Tübingen, 2006) and Lower Jurassic strata of England (e.g. Benton & Spencer, 1995; Smith & Radley, 2007). One exception to these general trends is the dominance of crocodilians in Luxembourg, which might reflect the more proximal setting of this locality during the Early Jurassic period (P. Godefroit, unpub. Ph.D. thesis, Univ. catholique de Louvain, Faculté des Sciences, 1994). Although more specimens and finer stratigraphic resolution are needed to confirm these patterns in the southern Beaujolais, these observations suggest that no abrupt change in the relative composition of Jurassic marine reptile groups followed the Toarcian. Therefore, marine reptile assemblages appear relatively unaffected by the severe environmental changes (e.g. Hesselbo *et al.* 2007; Suan *et al.* 2010; Gómez & Goy, 2011) characterizing this interval.

Another significant feature of the Lafarge quarry vertebrate fauna is the occurrence of possible remains of *Temnodontosaurus* in upper Toarcian strata. Specimens attributed to this genus have previously been reported in strata from the Hettangian *angulata* ammonite zone to the middle Toarcian *bifrons* ammonite zone (McGowan & Motani, 2003), but its relatives are absent in younger levels. If correct, the attribution of the specimen PF Toa 485 to *Temnodontosaurus* thus extends the stratigraphic range of this genus substantially and suggests that its extinction horizon might not be related to the T-OAE. Similarly, the presence of a possible stenopterygiid (MHNL 20103016) in the *variabilis* zone is also stratigraphically significant, since this clade mainly occurs in the strata of the *tenuicostatum*, *falciferum* and *bifrons* ammonite zones in Germany and the UK (Maisch, 2008; Caine & Benton, 2011; Maxwell, 2012). Our new data, together with the recent description of two Aalenian *Stenopterygius* specimens (Maxwell, Fernández & Schoch, 2012) provide additional evi-

dence for the presence of the group after the T-OAE and suggest that its disappearance was also unrelated to the event.

In this context, the new material from the Aalenian is particularly significant in that it links the history of marine amniote groups through the Jurassic. Two groups have been recovered from the Aalenian stage of the Lafarge quarry, namely Plesiosauria and Ichthyosauria. Only scanty remains of plesiosaurs have been described from this stage in Germany and France (see Vincent, Bardet & Morel, 2007 and references therein). The specimen PF Aal 186–187 is thus one of the few plesiosaur fossils found in Aalenian strata worldwide (Gasparini, 1992; Vincent, Bardet & Morel, 2007; Kear, 2012) and the second most complete found in France (Vincent, Bardet & Morel, 2007). Similarly, Aalenian ichthyosaur remains have only been found in southern France (Arnaud, Monleau & Wenz, 1976) and Germany, where they are represented by one partial and one sub-complete specimen (Fernández, 1999; Maxwell, Fernández & Schoch, 2012) and near the Aalenian–Bajocian boundary in Argentina (Fernández, 2003). These specimens thus represent one of the few Aalenian ichthyosaurs found and described worldwide. New marine crocodilian material (isolated vertebrae; currently under mechanical preparation) has been recently (2011) collected from the lower Aalenian of the Lafarge quarry site, and potentially represents the first significant record of the group in the Aalenian. In summary, the Aalenian vertebrate remains presented here, although essentially represented by fragmentary material, are especially significant in that they permit the inference of marine amniote abundance through a poorly documented interval.

4.b. Palaeobiogeographic implications

The Lafarge quarry site provides interesting clues about the palaeobiogeography of marine vertebrates during the Early–Middle Jurassic transition. Indeed, since southern European sites have yielded isolated marine amniote remains but no association of contemporaneous ichthyosaurs, plesiosaurs and crocodilians (Sander & Bucher, 1993; Delfino & Dal Sasso, 2006; Bardet, Pereda Suberiola & Ruiz-Omeña, 2008b; Fischer, Guiomar & Godefroit, 2011; Smith, Araújo & Mateus, 2012), the Lafarge quarry succession preserves the southernmost vertebrate assemblage of this age. The occurrence of remains assignable to probable *Temnodontosaurus* and stenopterygiid at the study site indicates a broad similarity with German and English sites. In addition, the actinopterygian assemblage, formed by *Leptolepis* sp. and *Dapedium* or *Lepidotes*-like remains, is reminiscent of that from other well-known Lower Jurassic European localities, in France (La Caine, Sainte Colombe, see Wenz, 1967), Germany (Holzmaden), England (Lyme Regis, Whitby) and Belgium (Fontenoille, see Delsate, Duffin & Weiss, 2002). Chondrichthyans, represented by hybodontiforms and one neoselachian, similarly suggest a widespread distribution. These similarities reinforce

the idea that these free-swimming animals had rather a cosmopolitan distribution in European epicontinental seas near the early–middle Toarcian transition, consistent with coeval ammonite assemblages (Dera *et al.* 2011). However, this faunal homogeneity contrasts with the relatively strong palaeobiogeographic zonation suggested for certain groups of marine reptiles in Europe during the Toarcian (e.g. Maisch & Ansorge, 2004). The presence of different taxa at the various sites could be related to palaeolatitudinal temperature gradients, but is more likely correspond to discovery biases considering the relatively few documented specimens and the ammonite-zone-level diachronism of the marine reptile-yielding sites (Smith & Vincent, 2010; Benson, Ketchum & Noé, 2011). In this context, ongoing investigations of the almost complete and fossiliferous Toarcian–Aalenian succession in southern France will undoubtedly provide further valuable bases for reconstructing the palaeobiogeographical distribution of vertebrates among European epicontinental seas.

5. Conclusion

The completeness and temporal extension of the Lafarge quarry succession extends the stratigraphical range of the ichthyosaur genus *Temnodontosaurus* to the upper Toarcian and suggests the presence of stenopterygiids in the uppermost middle Toarcian. The reported occurrences of these successful taxa, combined with their apparent absence in Middle Jurassic strata, suggests that their disappearance occurred after the Toarcian and was unrelated to the T-OAE. Given the very seldom occurrence of marine vertebrates reported from the Middle Jurassic, it is difficult to determine whether the extinction of those taxa, diversified and abundant during the Early Jurassic, was gradual or rapid and potentially the result of severe environmental perturbations. Similarly, pre T-OAE specimens (i.e. from the upper Pliensbachian and lowermost Toarcian) are relatively scarce, hence preventing detailed reconstruction of extinction and diversification dynamics of marine vertebrates over this interval. In this context, the almost continuous record of vertebrate specimens from the biostratigraphically well-constrained marine succession described above, opens an interesting avenue of research for further high-resolution tracing of the evolution of vertebrate fauna across this key interval.

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