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Running header: Toarcian ichthyosaurs and the T-OAE

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Abstract: We report new ichthyosaur material excavated in lower Toarcian levels of the LafargeHolcim Val d'Azergues quarry in Beaujolais, SE France. A partially articulated skull and a smaller, unprepared but likely subcomplete skeleton preserved in a carbonate concretion are identified as stenopterygiids, a family of wide European distribution during the Early Jurassic. These specimens are among the finest preserved Toarcian exemplars known from Europe and in one of them, soft tissue preservation is suspected. Their state of preservation is attributed to the combination of prolonged anoxic conditions near the water-sediment interface and early carbonate cementation resulting from the activity of sulfate-reducing bacteria. We also present carbon and strontium isotope values obtained from the study site that allow detailed temporal comparisons with other Toarcian vertebrate-yielding sites and environmental perturbations associated with the Toarcian Oceanic Anoxic Event (T-OAE). These comparisons suggest that the relatively high abundance and good preservation state of Toarcian vertebrates was favoured by a prolonged period of low bottom water oxygenation and accumulation rates. The environmental conditions that prevailed during the T-OAE were probably responsible for the extensive nature of Lagerstätte-type deposits with exceptional preservation of marine organisms. Whether the T-OAE had a biological impact on marine vertebrates requires a precise chemostratigraphic context of the fossil record spanning the Pliensbachian–Toarcian interval.

'Supplementary material: [Geochemical dataset used in the present study including bulk sediment inorganic and organic carbon isotope composition ($\delta^{13}C$) and radiogenic strontium isotope ($^{87}Sr/^{86}Sr$) values of belemnites.] is available at XXX'.

The Early Jurassic Period was punctuated by severe environmental perturbations with paroxysmal events coinciding with rapid biotic extinctions and turnover among marine invertebrates across the transitions between the Pliensbachian-Toarcian stages and the *tenuicostatum-serpentinum* ammonite zones (Little & Benton 1995; Harries & Little 1999; Macchioni & Cecca 2002; Wignall *et al*. 2005; Suan *et al*. 2008; Caswell *et al*. 2009; Suan *et al*. 2010; Ruebsam *et al*. 2019). The early-middle Toarcian also witnessed the deposition of widespread laminated black shales resulting from a prolonged episode of warmth and decreased bottom water oxygenation, which may have favoured the preservation of abundant marine invertebrates and vertebrates (e.g. Martill 1993). The interval of most intense environmental perturbation recorded in strata spanning the uppermost part of the *tenuicostatum* ammonite zone to the top of the *serpentinum* ammonite zone is known as the Toarcian Oceanic Anoxic Event (T-OAE) (e.g. Jenkyns 1988; Baudin *et al*. 1990; Harries & Little 1999; Wignall *et al*. 2005; Caswell *et al*. 2009). Marine vertebrates were apparently little impacted by the T-OAE (Vincent *et al*. 2013; Maxwell & Vincent 2016), although the records for the time intervals pre- and post-dating these events are either scarce (Martin *et al*. 2012) or poorly constrained stratigraphically.

Ichthyosaur remains are certainly the most ubiquitous marine vertebrates found in Toarcian deposits of Europe with most iconic specimens reported from the Posidonienschiefer Formation of the Holzmaden area in SW Germany. The most spectacular exemplars include gravid females preserving soft tissues as well as stomach contents (Böttcher 1989; 1990) and individuals preserving integuments (Lindgren *et al*. 2018). Other remarkable finds include English specimens from Ilminster in Somerset (Caine & Benton 2011; Williams *et al*. 2015) or the Alum Shale Member in Yorkshire (Benton & Taylor 1984; McGowan & Motani 2003) but also specimens preserving soft tissues from the Hettangian/Sinemurian of Dorset (Martill 1995).

Lagerstätte-type deposits during the Toarcian have been described mainly from the Posidonienschiefer Formation in SW and NW Germany (Urlichs *et al*. 1994; Hauff *et al*. 2017), Strawberry Bank and Whitby in England (Benton & Taylor 1984; Benton & Spencer 1995; Williams *et al*. 2015), and, more recently, from the Ya Ha Tinda locality in Alberta, Canada (Martindale *et al*. 2017). Three of these localities (Posidonia Shale, Whitby and Ya Ha Tinda) are renowned for exceptionally-preserved vertebrates occurring in organic-rich shales. Most of these shale-hosted specimens, however, have been intensively impacted by burial compaction, which has exceeded 90% in such lithologies (Martill 1993), hence obscuring some important morphological features, including details of skull bone contacts (e.g. Fraas 1913). On the other hand, carbonate concretions with exceptional three-dimensional preservation have been reported from Strawberry Bank as well as in a number of other Toarcian localities (e.g. Normandy: Mazin 1988; northeastern Germany: Maisch & Ansorge 2004; Beaujolais: Vincent *et al*. 2013; Luxembourg: Vincent *et al*. 2019; see also Table 1). Vertebrates preserved in carbonate concretions are potentially important because they are comparatively less flattened than shale-hosted specimens. Given the established presence of soft tissues in Toarcian marine vertebrates (e.g. Lindgren *et al*. 2018), carbonate concretions may also be promising for three-dimensional reconstructions of soft tissues.

Regardless of their type of preservation, published Toarcian ichthyosaurs generally lack a precise stratigraphic control, with the exception of most SW German specimens that benefited from the early use of stratigraphic subdivisions of the Posidonia Shale (Hauff 1921). The infra-stage stratigraphic data of previous discoveries, if any, relied mostly on ammonite biostratigraphy (e.g. Benton & Taylor 1984; Godefroit 1994; Benton & Spencer 1995), in which resolution might be strongly limited by both the abundance of age-diagnostic species and the use of different bioevents in the various faunal provinces (Page 2003; McArthur *et al*. 2020). Similarly, it is yet unclear whether vertebrate-hosting carbonate concretions are bound to stratigraphically restricted horizons or occur randomly in Toarcian successions. In this context, the massive accumulation of high-resolution isotope data fostered by the growing interest for the T-OAE perturbations over the past decades could provide an independent temporal framework for past and future vertebrate discoveries. Such a multidisciplinary approach combining sedimentological, geochemical and palaeontological data has been successfully used to replace important vertebrate specimens in a detailed palaeoenvironmental and temporal framework and hence better constrain conditions favouring their preservation (Suan *et al*. 2013; Vincent *et al*. 2013; Vincent *et al.* 2020).

In this study, we briefly describe two new ichthyosaur specimens recovered from our fieldwork in the LafargeHolcim Val d'Azergues quarry of Beaujolais, SE France. We attempt to place the finds in a precise stratigraphic context using carbon and strontium isotopes, allowing detailed age comparisons with coeval ichthyosaur-yielding localities. We discuss the implications of our findings for the evolutionary response of ichthyosaurs to Early Jurassic perturbations and the significance of exceptional preservation, including that of soft tissues, for the prediction of similar discoveries within Toarcian deposits.

Institutional abbreviations

BRLSI, Bath Royal Literary and Scientific Institution, Bath; **LGL-TPE,** Laboratoire de Géologie de Lyon – Terre, Planètes, Environnements, Villeurbanne; **MHNL,** Muséum d'Histoire Naturelle de Lyon/Musée des Confluences de Lyon, Lyon; **MHH,** Museum Hauff, Holzmaden; **NHMUK,** Natural History Museum, London; **SMNS,** Staatliches Museum für Naturkunde, Stuttgart.

Lithology and biostratigraphy

A synthetic account of the Lower Jurassic sedimentary succession available at the LafargeHolcim Val d'Azergues quarry in Beaujolais (Rhône, SE France) is given below. More detailed information is available from previous works (Vincent *et al*. 2013; Suan *et al*. 2013). The quarry exposes a marine sequence from the lower Toarcian up to the upper Bajocian (Figs. 1, 2); the Toarcian – Aalenian lithostratigraphy and ammonite biostratigraphy having been described by Elmi & Rulleau (1991; 1993), and the complete succession was published by Rulleau (2006). Here, we focus on the most recent excavations undertaken by our team during the 2009–2013 campaigns, revealing new observations and samplings of the lower Toarcian interval, which was previously poorly known in the quarry (Rulleau 1997). The basalmost lower Toarcian strata include a 2.5 m-thick succession of dolomitized argillaceous yellowish limestone beds intercalated with yellow plastic clays. A temporary trench realized in the lowermost levels in 2013 confirmed that these lithologies are the weathered equivalent of grey, argillaceous limestone beds intercalated with dark grey laminated marls with high total organic carbon contents (up to 14% in weight; Charbonnier *et al*. 2020). This basal interval ('Calcaires Jaunes à Ammonitella' in Elmi & Rulleau 1991) includes the *tenuicostatum* and *serpentinum* ammonite zones (Elmi & Rulleau 1991; Suan *et al*. 2013). The *tenuicostatum* zone was documented only in the basal bed, which yielded various dactylioceratid ammonites of the *semicelatum* subzone (upper part of *tenuicostatum* Zone; e.g. *Dactylioceras* (*Orthodactylites*) *semicelatum*, *D*. (*O*.) *crosbeyi*). The overlying 40 cm of succession did not yield any ammonites. The presence of *Cleviceras elegans* in a bed 50 cm above the base of the section and especially the co-occurence of *C. elegans* with *Harpoceras serpentinum* in nodular layers 70 and 120 cm above the base already indicates the upper part of the *elegantulum* subzone (lower part of the *serpentinum* Zone, equivalent of the *exaratum* subzone, see Page 2003). *Cleviceras elegans* was collected also from beds 155 and 180 cm (bed with ichthyosaur specimen MHNL 20103062) above the base. However, this species can range up to the early *falciferum* subzone (e.g. Bécaud, 2006) so these beds can thus either represent the upper *elegantum* subzone or the lower *falciferum* subzone. First age-diagnostic ammonites of the *falciferum* subzone (upper part of the *serpentinum* Zone) represented by *Harpoceras pseudoserpentinum* and *Hildaites subserpentinum* occur in the uppermost bed, just below the dark marls. The yellowish limestone interval is capped by a distinctive, 2-3 cm thick packstone-grainstone horizon mainly consisting of fish debris and bivalves partly cemented by pyrite. The overlying 2.5 m-thick interval ('Marnes inférieures' in Elmi & Rulleau 1991) of dark grey, finely laminated and unfossiliferous calcareous marls, also often weathered into yellow plastic clays in the quarry (Suan *et al*. 2013), yielded only few, poorly preserved ammonites and hence lacks definitive ammonite zone assignment. Two fragmentary specimens of *Harpoceras falciferum* were collected about 90 cm above the base of the marly interval. Although this species is typical of the upper part of the *falciferum* subzone, its upper stratigraphic range limit is located in the *sublevisoni* subzone of the early *bifrons* Zone (e.g. Elmi *et al*. 1997). The calcareous nannofossil association and $^{87}Sr/^{86}Sr$ values (see below) indicate that this level with *H. falciferum* fragments probably belongs to the *sublevisoni* subzone. This marly interval is overlain by a 2.4 m-thick succession of intensively bioturbated marl containing iron ooids and abundant invertebrates, including age-diagnostic ammonites of the *bifrons* (middle Toarcian) and *variabilis* (upper Toarcian) ammonite zones and various vertebrate remains (e.g. Vincent *et al*. 2013). The base of this interval yielded the articulated skeleton of the ichthyosaur *Temnodontosaurus azerguensis* (Martin *et al*. 2012). Apart from the almost unfossiliferous interval of dark grey marls between 2.5 and 5.2 m, the investigated succession is relatively well-constrained biostratigraphically owing to its ammonite richness. Nannofossil data may offer additional temporal constraints. The first occurrence of *Watznaueria colacicchii*, recorded at 3.3 m in the ammonite-barren interval in the LafargeHolcim Val d'Azergues Quarry (Suan *et al*. 2013), has been recently shown to coincide with the base of the *bifrons* Zone in Portugal (Ferreira *et al*. 2019; base of nannofossil NTJ7b Zone). Pending future ammonite discoveries and further chemostratigraphic assessment (see below), the base of the *bifrons* Zone should hence certainly occur below that suggested by sparse ammonite record of *Harpoceras faciferum*, i.e., toward the lower half of the ammonite-barren interval.

The Posidonienschiefer Formation (Posidonia Shale; Lias epsilon) of Southwestern Germany has been divided into lower, middle, and upper components indicated by roman numerals (I-III), with beds within these larger subdivisions indicated using subscript. When comparing the biostratigraphy to the divisions recorded in the Southwest German Basin, we use the bed-level nomenclature and ammonite zone correlations detailed by Riegraf *et al*. (1984).

Material and methods

Fieldwork and specimen preparation. We report on two ichthyosaur specimens discovered during our palaeontological excavations in 2010 and 2012 at LafargeHolcim Val d'Azergues cement Quarry near Charnay in the Beaujolais hills (Rhône, France). Both specimens are reposited at the Musée des Confluences, Lyon, France. The first specimen (MHNL 20103062) was discovered in July 2010 in a thin limestone bed at 1.8 m during manual excavation of the interval between 1.6 and 2.5 m (*serpentinum* Zone). The second specimen was discovered in the material excavated mechanically by a bulldozer from the first 2.5 m of the measured interval in July 2012 (*serpentinum* ammonite Zone). MHNL 20103062 was prepared during 2013 by one of us (AC) at Institut des Sciences de l'Evolution, Université de Montpellier, alternating mechanical preparation and weak acetic acid baths in order to soften the sediment without damaging the bone surface. The second specimen (MHNL 20103364), preserved in a large carbonate concretion with possible soft tissues, awaits preparation and is temporarily deposited at LGL-TPE for ongoing study before its permanent curation at Musée des Confluences (MHNL). These recent findings extend the relatively rich record of ichthyosaurs of this site (Vincent *et al*. 2013), initiated in 1984 with the discovery of a subcomplete specimen, which was recently described and attributed to *Temnodontosaurus azerguensis* (Martin *et al.* 2012).

Chemostratigraphy. In order to place the recently discovered specimens from the LafargeHolcim Val d'Azergues quarry into a stratigraphic context, we analyzed the bulk sediment inorganic and organic carbon isotope composition as well as the strontium isotope composition of belemnites, all collected from the section that yielded the three ichthyosaur specimens. We also analyzed the inorganic carbon isotope composition of a sample collected from the carbonate concretion containing the specimen discovered in 2012 to narrow down its likely provenance. The stratigraphic log of the study site, modified from Suan *et al.* (2013) and updated with these new geochemical data (Supplementary Data), is shown in Figure 2.

A total of 43 samples (including the sample collected from the ichthyosaur-hosting carbonate concretion), consisting of both weathered and non-weathered sediment, were analyzed for their bulk carbonate carbon isotope ($\delta^{13}C_{carb}$) composition using an auto sampler MultiPrep™ system coupled to a dual-inlet GV IsoPrime™ isotope ratio mass spectrometer (IRMS). Each sample was powdered in an agate mortar and, depending on calcium carbonate contents, an aliquot of 200-2000 μg of the obtained powder was reacted with anhydrous, oversaturated phosphoric acid at 90°C for 20 min. Each analytical run contained international (NIST NBS19) and in-house standards (Carrara Marble) to monitor analytical precision and accuracy.

A total of 22 samples were analyzed for their organic carbon isotope composition ($\delta^{13}C_{TOC}$). To avoid potentially strong weathering biases on the measured $\delta^{13}C_{TOC}$ values (Suan *et al.* 2013), only samples that appeared non-weathered under visual examination (dark colour, absence of orange-brownish oxidation stains) were selected. Each sample was powdered in an agate mortar and decarbonated using 1N hydrochloric acid at ambient temperature overnight. Each sample was sequentially rinsed four times with deionized water, with 40 minutes between rinses to allow the sediment to settle, and oven-dried at 40°C. Between 0.5 and 1 mg of decarbonated powder was weighted into tin capsules and placed in a Pyrocube® elemental analyzer connected to an Elementar Isoprime® isotope-ratio mass spectrometer in continuous flow. Each analytical run contained four sets of international (IAEA-CH-7) and in-house standards (Caseine) to monitor analytical precision and accuracy. All carbon isotope results are reported relative to the 'Vienna Pee Dee belemnite' (VPDB). Based upon replicated analysis of standards, the precision of our measurements was better than ± 0.1‰ for $\delta^{13}C_{TOC}$ values and ± 0.05‰ for $\delta^{13}C_{carb}$ values.

We sampled five belemnites for radiogenic strontium analysis ($^{87}Sr/^{86}Sr$) from different levels in the lower and middle Toarcian interval. For each sample, the rostrum was broken into millimeter-size fragments to select the best-preserved portion of the samples. Fragments showing a strong radial fabric were subsequently picked (avoiding the apical line and external-most areas) under a binocular microscope and powdered in an agate mortar. About 2 mg of belemnite powder was dissolved in concentrated nitric acid and evaporated to dryness. All samples were retaken in 2M HNO_3 and purified through a strontium-specific resin (Sr-Spec Eichrom®). The obtained solution was analyzed for $^{87}Sr/^{86}Sr$ ratios at LGLTPE on a Neptune Plus multicollector ICP-MS (Thermo Scientific) during a single session in December 2014. Reference material (SRM-987) of known $^{87}Sr/^{86}Sr$ composition was repeatedly measured in the same analytical session. The standard SRM-987 gave an average value of 0.7100912 ± 0.00000356 (1SD, n = 5), which is within 0.0001568 of the value 0.710248 (McArthur *et al*. 2000). Belemnite values were adjusted accordingly and are listed in the Supplementary Data.

Results

Carbon and strontium isotope composition. The $\delta^{13}C_{carb}$ profile, although somewhat scattered, reveals a marked >3‰ decrease across the *tenuicostatum-serpentinum* zonal transition and a >4‰ increase between 0.3 and 1 m. The $\delta^{13}C_{TOC}$ values of non-weathered samples show minimal values (down to –32‰) at the very base of the *serpentinum* ammonite Zone, and a marked 2.4‰ increase between 0.3 and 0.6 m. These new records, when combined with previously published data from the same site (Suan *et al*. 2013; Fig. 2), show that the characteristic T-OAE negative carbon isotope excursion of the *serpentinum* Zone is restricted to the first 0.70 m of the studied section. In particular, the extremely low $\delta^{13}C_{TOC}$ values recorded between 0.3 and 0.5 m are comparable to those recorded in most other contemporary sections in the base of the T-OAE interval (–30 to –34‰) (Suan *et al*. 2016; 2018). The sedimentary matrix of the large carbonate concretion found during the excavation of the trench in the basal 2.5 m interval yielded a $\delta^{13}C_{carb}$ value of –3.88‰. Comparatively low values are only recorded in the interval comprised between 0.2 and 0.5 m at the very base of the *serpentinum* Zone in our composite $\delta^{13}C_{carb}$ profile, constraining its likely provenance (Fig. 2).

The obtained $^{87}Sr/^{86}Sr$ values for the analyzed Toarcian belemnites range between 0.70710095 and 0.707227, consistent with the range of values obtained for this interval in previous studies (McArthur *et al*. 2000; Bailey *et al*. 2003). Our $^{87}Sr/^{86}Sr$ profile records a marked shift toward more radiogenic values at the base of the measured section, the amplitude of which is compatible with that observed across the *tenuicostatum*-*serpentinum* transition in SW Germany and NE England (McArthur *et al*. 2000; Bailey *et al*. 2003). The belemnite specimen sampled in the argillaceous marl located 2 cm below the ichthyosaur specimen MHNL 20103062 yielded a $^{87}Sr/^{86}Sr$ value of 0.707194. Comparably high values are only found in the uppermost part of the *serpentinum* Zone in both German (Fig. 2b) and English sites (McArthur *et al*. 2000; Bailey *et al*. 2003), where the boundary between the *serpentinum-bifrons* zones is biostratigraphically better constrained than in the Val d'Azergues Quarry. In Yorkshire, such values occur immediately below the base of the Alum Shale Member (McArthur *et al*. 2000), which has yielded historically important marine vertebrate specimens (Benton & Taylor 1984). In the Val d'Azergues Quarry, the belemnite collected in the same bed as the *Temnodontosaurus azerguensis* specimen (Martin *et al*. 2012), *i.e.* in the *bifrons* ammonite subzone (*bifrons* zone), gave a $^{87}Sr/^{86}Sr$ value of 0.7072229. In Yorkshire, comparable values occur above the base of the *crassum* subzone, which correspond to the topmost part of the Alum Shale Member (*bifrons* zone; McArthur *et al*. 2000). The $^{87}Sr/^{86}Sr$ value of 0.707227 measured in the uppermost sample from the *variabilis* ammonite zone is consistent with values measured in the middle of the *variabilis* zone in Yorkshire. Within the temporal resolution allowed by the Toarcian strontium isotope stratigraphy (< 200 ka, McArthur *et al*. 2020), these $^{87}Sr/^{86}Sr$ data support the synchronicity of Subboreal and Submediterranean ammonite Subzones that have been respectively used in Yorkshire and SE France (Elmi *et al*. 1997; Page 2003). In summary, the obtained carbon and strontium isotope data enhance correlations with the classical localities of SW Germany (Fig. 2) and Yorkshire, hence enabling detailed relative dating of the various Toarcian ichthyosaur finds and their relationships with the coeval environmental perturbations (see below).

Description of Ichthyosaur MHNL 20103062. Specimen MHNL 20103062 preserves most of the skull and the anterior part of the mandible. The rostrum is complete with an antorbital length of 43 cm and a prenarial length of 35 cm. Despite being partly disarticulated, it preserves fine anatomical details including bones preserved in volume and sutures in the peri-orbital region. The left lateral side of the specimen is exposed. The skull lacks the posteriormost part of the braincase and is split along the sagittal axis. The right elements of the skull are disarticulated and have been displaced dorsally; the top of the right portion of the skull table faces laterally. Because the postorbital region in ichthyosaurs is short, a rough total skull length can be estimated and would not have surpassed 60 cm.

The large circular orbit measures 10 cm in diameter. It is bordered ventrally by the jugal, anteroventrally by the lacrimal, anteriorly and anterodorsally by the prefrontal and posteriorly by the postorbital. The left sclerotic ring is 9 cm in diameter and its aperture diameter is 3.6 cm. The aperture diameter to the orbital diameter versus skull length ratio of Fernández *et al*. (2005) compares well (0.23) with the values of other adult specimens of the genus *Stenopterygius*. The sclerotic ring is complete and articulated with 14 individual sclerotic plates. The plates overlap each other but there is no clockwise or anti-clockwise trend.

The premaxilla contributes to most of the rostrum. The lateral surface bears a set of small foramina that are placed at the level of a long groove that extends posteriorly on the lateral surface of the bone. There are no individualized tooth sockets, the implantation is aulacodont. There are at least 30 alveolar positions deduced by incipient concavities on the bone. The subnarial process of the premaxilla projects below the external nares but does not contact the anteriormost tip of the jugal, being separated from the ventral margin of the external nares by the underlying maxilla. The supranarial process of the premaxilla is short.

The maxilla separates the premaxilla and lacrimal from any contact. The maxilla contributes to the anterior ventral half of the external nares. The maxilla supports the premaxillary lamina anteriorly, and posterodorsally possesses a long sutural contact with the jugal. Dorsally, the maxilla contacts the lacrimal, separating the jugal from the external nares. In the anteriormost corner of the external nares, the maxilla contacts the descending process of the nasal. The maxillary tooth row stops below the orbit in the anteriormost orbital area.

The nasal contributes dorsally to the external naris for its entire length. Here, an overhanging crest projects laterally above the external naris (Fig. 3). Anteroventrally, the nasal descends along the anterior edge of the external nares, excluding the premaxilla from the external nares and suturing ventrally onto the maxilla. Posteriorly, in lateral view the nasal contacts the lacrimal and prefrontal. Because the skull is split in half, it is difficult to ascertain the presence of an internasal depression on the dorsal surface of the skull.

The lacrimal contributes to the posterior and posteroventral margins of the external nares. The anteriormost tip of the lacrimal consists of a delicate notch projecting medially to the maxilla, along the ventral border of the external nares. The lacrimal contacts the nasal dorsally, along the posterior margin of the external nares, excluding the prefrontal from the narial opening. This suture stops just below the dorsal edge of the external nares. The circumorbital area of the lacrimal is heavily vascularized. The ventral margin of the lacrimal mostly contacts the jugal, with the exception of its anterior part, which contacts the maxilla. The lacrimal has an oblique and indented suture with the prefrontal on the orbital margin.

The prefrontal forms the anterodorsal margin of the orbit. The bone is anteroposteriorly thin, preventing the nasal from reaching the orbital margin. As observed in dorsal view (Fig. 3), the prefrontal is constricted between the nasal and postfrontal and contacts the frontal and parietal near its medial margin.

The jugal anterior tip projects beyond the anterior margin of the orbits as a thin lamina. Here, it overlaps the maxilla ventrally and the lacrimal dorsally. The jugal forms the majority of the ventral border of the orbit; the anteroventral border of the orbit is made by a thin lamina of the lacrimal overlapping the jugal. The posterior portion of the jugal sends a short dorsal extension along the orbital edge as a mediolaterally flat ascending lamina.

Bones of the skull table include a complete right frontal and fragmentary left frontal, a right postfrontal, fragmentary left postorbital and right parietal. The anterior margin of the interfrontal foramen wedges between the posterior ends of the nasals. There is no extension of the interfrontal fossa on the nasal. This fossa is exclusively restricted to the frontals.

Both frontals are sutured in their posterior region, but for most of their length they never contact. Their dorsal surface is steeply inclined toward the midline where they accommodate the elongate interfrontal foramen. The frontals contact the nasal at the anterior edge of the interfrontal foramen. Laterally, the frontal contacts the prefrontal and posteriorly, it contacts the parietal. Posteriorly, the frontal forms the anterolateral margin of the pineal foramen as in most post-Triassic ichthyosaurs (Maisch & Matzke 2000). The pineal foramen preserves only its anterior portion, missing the posteriormost margin. It opens dorsally with an anteriorly rounded outline (about 0.7 cm in diameter) on the sagittal axis at the frontoparietal suture.

The postfrontal forms the anterior margin of the supratemporal fenestra where it consists of a thickened rim. Anterior to this rim, the rest of the dorsal surface of the postfrontal is concave. Its lateral area is triangular and overhangs the orbits laterally. The postfrontal contacts the prefrontal anteriorly along a sinuous suture. Posteromedially, it contacts the parietal.

The postorbital consists of a wide lamina that makes the posterior margin of the orbit and contacts the posterior ascending process of the jugal. On the posteriormost margin of the postorbital, a long lamina is observed and might correspond to a fragment of the squamosal or quadratojugal.

A small fragment of the right parietal is visible (Fig. 3). In its anterior portion, the parietal makes the lateral margin of the pineal foramen, and contacts the frontal anteriorly and also the postfrontal laterally. Although fragmented, the parietal appears to participate in the medial margin of the supratemporal fenestra.

The mandible has partially been recovered and includes the anteriormost rami of both dentaries. The dentary is a straight bone with a flat and long dentary symphysis. The tooth row is confluent for the entire preserved length.

A single tooth is still attached to the premaxilla but all other teeth were recovered detached from the premaxilla, maxilla and dentary in the surrounding sediment, the block revealing 10 detached teeth (Fig. 3). The crowns are narrow, pointed, slender, recurved and rounded in cross section (Fig. 4). The enamel surface bears no carinae and is unornamented. The root has the characteristic plicidentine morphology with deep furrows on the external surface giving the typical cauliflower outline in cross section. Roots are only slightly more than half the total length of the tooth.

Ichthyosaur from the carbonate concretion. The second specimen (MHNL 20103364, Fig. 5) was discovered during the summer of 2012 when a trench on the floor of the LafargeHolcim Val d'Azergues quarry was excavated thanks to heavyduty vehicles, allowing us to attain the lowest stratigraphic horizons available in the quarry (Figs. 1a, 5a). As presented above, this specimen, together with other carbonate concretions, originates from the base of the *serpentinum* ammonite zone. The ichthyosaur specimen is contained in a large carbonate concretion measuring about 50 cm in diameter. Breaks on its surface reveal an articulated skeleton with the extremity of the rostrum at one end (Fig. 5c), and opposite, a paddle (Fig. 5b) and a section in the thorax with articulated vertebral centra and ribs (Fig. 5d). The specimen is curled around one side of the carbonate concretion and sectioned at the level of the thorax, missing the tail. Nonetheless, the anterior part of the rostrum is sectioned and shows several tooth roots; opposite the rostrum on the carbonate concretion, the forefin is partly visible and displays at least four phalanges (Fig. 5b). The phalanges are not in contact and possess rounded edges. Those characters are compatible with the morphology of distal phalanges of stenopterygiids. The total body length of the specimen cannot be precisely measured but may not have surpassed one meter. Reddish to purple hues are observed within the rib cage and most likely represent remnants of soft tissues (Figs. 5d, e, f), to be investigated in future work, for example through X ray Computed Tomography in order to avoid destroying soft tissue during preparation.

Discussion

Affinities of the new finds. Currently recognized Toarcian ichthyosaur genera include *Eurhinosaurus*, *Hauffiopteryx*, *Temnodontosaurus*, *Stenopterygius* and *Suevoleviathan* (e.g. McGowan 1979; Godefroit 1994; McGowan & Motani 2003; Fischer *et al*. 2012; Caine & Benton 2012; Martin *et al*. 2012; Maxwell 2012; Moon 2017; Maxwell & Cortés 2020).

MHNL 20103062 does not preserve any postcranial elements, which are prominent in ichthyosaur diagnoses (Maxwell 2012). Ichthyosaurs from the Posidonia Shale are often preserved as flattened complete skeletons but details of their skull anatomy may be obscured by compression. As a consequence, diagnostic characters for species have been established on skull proportions and postcranial anatomy (McGowan 1979) with species delineation relying mostly on postcranial proportions (Maxwell 2012). Nevertheless, a number of cranial features can be compared with other Jurassic forms and help constrain the affinities of MHNL 20103062.

MHNL 20103062 can be differentiated from the large predatory species of the genus *Temnodontosaurus* in which the maxilla does not contribute into the ventral margin of the external narial opening, in contrast to that of MHNL 20103062 (Fig. 4). In toothed *Temnodontosaurus* species, the maxilla is excluded from the narial opening by the subnarial process of the premaxilla contacting the lacrimal and jugal (McGowan 1994; Maisch 1998a). In MHNL 20103062, the nasal does not contact the parietal posteriorly, contrary to species of the genus *Temnodontosaurus* (Maxwell *et al*. 2012; Ji *et al*. 2015). MHNL 20103062 can be differentiated from *T. azerguensis* in possessing teeth (Martin *et al*. 2012).

Eurhinosaurus longirostris is extremely derived among Toarcian ichthyosaurs, with its particularly elongate rostrum that parallels the morphology of extant billfishes and swordfishes (e.g. McGowan 1979). Although the rostrum is elongate in MHNL 20103062, it is comparatively much shorter than that of *E. longirostris*.

MHNL 20103062 can be differentiated from *Hauffiopteryx* based on the absence of participation of the prefrontal in the external narial opening (see Maxwell & Cortés, 2020). In addition, the pineal foramen is positioned between the supratemporal fenestrae in MHNL 20103062; it opens anterior to the supratemporal fenestrae in *Hauffiopteryx*. In *Hauffiopteryx*, the anterior margin of the supratemporal fenestra consists of the parietal (not of the postfrontal as in MHNL 20103062); the prefrontal is constricted between its lateral and medial parts in MHNL 20103062, but of uniform width in *Hauffiopteryx*; the comparatively shorter rostrum of *Hauffiopteryx* and its differential tooth size between fore and aft dentition, also differ from MHNL 20103062 (Maisch 2008; Caine & Benton 2011; Marek *et al*. 2015; Maxwell & Cortés 2020).

Suevoleviathan differs from MHNL 20103062 in that the lacrimal and subnarial process of the prefrontal exclude the maxilla from the ventral edge of the narial opening in lateral view, the descending process of the prefrontal is much more weakly developed, the medial process of the prefrontal contacting the parietal and frontal is absent in dorsal view, and the frontal contributes only to the anterior edge of the parietal foramen rather than forming the anterior and lateral edges (Maisch 1998b; 2001).

Other Early Jurassic ichthyosaurs such as the genera *Ichthyosaurus* and *Protoichthyosaurus* are distinct from MHNL 20103062, in that the tooth enamel in these genera bears a strongly ridged ornamentation, unlike in MHNL 20103062.

These genera also have a medial process of the prefrontal contacting both the parietal and frontal (see Lomax *et al*. 2020). This latter character is shared with the genus *Leptonectes* (Fig. 2 in Maisch & Matzke 2003). In MHNL 20103062, the anterior margin of the supratemporal fenestra consists of the postfrontal, without a large contribution from the parietal (unlike in *Leptonectes* and *Wahlisaurus*: Maisch & Matzke 2003; Lomax *et al*. 2018). In *Leptonectes tenuirostris*, the subnarial and supranarial processes of the premaxilla are subequal in length (McGowan & Motani 2003: fig. 69).

MHNL 20103062 can be identified as a member of the genus *Stenopterygius* on the basis of the following skull characters: In MHNL 20103062, the supranarial process of the premaxilla is substantially shorter than the subnarial process (Figs. 3, 4), a condition shared with the genus *Stenopterygius.* Since the work of Maxwell (2012), several species of *Stenopterygius* have been synonymized and we follow it, recognizing the genus *Stenopterygius* as containing four European species, *S. quadriscissus*, *S. uniter S. triscissus*, and *S. aaleniensis*, plus a South American one *S. cayi* (Fernández 1994). MHNL 20103062 differs from some specimens of *S. triscissus* (see specimen BRLSI M1409 studied by Caine & Benton 2011) in the lack of contact between premaxilla and lacrimal; however note that this feature varies intraspecifically in *Stenopterygius* (e.g., *S. triscissus*: compare Caine & Benton 2011: text-fig.3; Godefroit 1994: fig. 19). Also, the absence of contact between nasal and parietal contrasts with the state reported for some specimens of *S. triscissus* (Caine & Benton 2011), but not for others (Motani 2005). The contact reported by Caine & Benton (2011) is very thin in this juvenile specimen from Strawberry Bank; this character is likely to be intraspecifically variable. The pineal foramen opens in different ways among members of the genus *Stenopterygius*: (1) the pineal foramen is included between the supratemporal fenestrae; or (2) the pineal foramen opens just anterior to the supratemporal fenestrae. MHNL 20103062, many Curcy specimens (Mazin 1988 plate I; *S. triscissus*: NHMUK OR 33157(Caine & Benton 2011: text-fig. S3), Eudes-Deslongchamps 1877)) and an Ilminster *S. triscissus* specimen (BRLSI M1409) (Caine & Benton 2011) all share condition (1). Some Holzmaden *Stenopterygius* specimens in which the skull table is visible show condition (2) such as in some specimens of *S. quadriscissus* (MHH 1981/33 or SMNS 55933) or *S. triscissus* (SMNS 14846). Differences are also noted with *S. aaleniensis*, which possesses an embayment in the posterior dorsal corner of the external nares (Maxwell *et al*. 2012), absent in MHNL 20103062. MHNL 20103062 differs from the South American *S. cayi*, which lacks teeth (Fernández 1994). Tooth reduction is variably present in all three Toarcian species of *Stenopterygius*, with some adult specimens possessing unreduced dentition while others are functionally edentulous (Maxwell 2012; Dick & Maxwell 2015; Dick *et al*. 2016).

The specimen from the large carbonate concretion is unprepared and cannot be precisely identified beyond a tentative referral to Stenopterygiidae indet. based on the characters visible on the rostrum and forefin.

In conclusion, MHNL 20103062 is referable to the genus *Stenopterygius*, and because it is represented only by a skull, we refrain from further specific attribution and refer it to *Stenopterygius* sp.. However, the prenarial length of 35 cm is outside the range of *S. quadriscissus* (see Maxwell 2012), making referral to the latter species unlikely. The carbonate concretion specimen is a probable stenopterygiid, but this will have to be confirmed with further preparation.

Ichthyosaur preservation during the T-OAE. Preservation of marine vertebrates in Lower Jurassic carbonate concretions (as compiled in Table 1) is known at least since the discovery of the Strawberry Bank Lagerstätte (Lower Toarcian of Ilminster, Somerset) by Charles Moore in the late 1840s (Williams *et al*. 2015). This locality has yielded carbonate concretions containing finely preserved ichthyosaur skeletons that were studied much later (McGowan 1979) and only recently referred to *Stenopterygius triscissus* and *Hauffiopteryx typicus* (Caine & Benton 2011; Marek *et al*. 2015). Elsewhere, ichthyosaur skulls preserved in similar carbonate concretions have subsequently been reported from the Toarcian of Luxembourg with *Stenopterygius* (Godefroit 1994) and France including *Temnodontosaurus burgundiae* from Sainte-Colombe in Burgundy (Gaudry 1892) and specimens from Curcy-sur-Orne in Normandy (Dechaseaux 1954) including an acid prepared carbonate concretion containing a skull connected to postcranial elements of *Stenopterygius* (Mazin 1988). A 9-meter long complete individual of *Temnodontosaurus* (SMNS 50000) mostly preserved within a giant carbonate concretion was discovered from horizon epsilon II_6 between Zell unter Aichelberg and Ohmden (Böttcher 1989). Large carbonate concretions within the upper part of horizon epsilon II_4 yielded at least two specimens on display at the Dotternhausen Museum including *Stenopterygius* and *Hauffiopteryx* (Jäger 2005; Maxwell & Cortés 2020). A specimen of *Stenopterygius quadriscissus* (SMNS 4789) is not technically speaking within a concretion but hosts pyrite in the thoracic area and also originates from epsilon II_5 and was selected for histological analysis (Anderson *et al*. 2018). Additional skulls and fragmentary ichthyosaurian postcranial remains from the Holzmaden region preserved in concretions are also present in regional collections. The difficulty in preparing specimens from hard concretions partially accounts for the rarity of described specimens in the literature originating from nodular beds and also the heavily lithified epsilon II_5 level. In addition, *Stenopterygius* specimens in concretions do not typically preserve enough of the skeleton to allow referral to species, which requires relatively complete skeletons at present (but see *S. aaleniensis* in Maxwell *et al*. 2012). This results in a perceived gap in the fossil record of species in the genus (e.g. Fig. 2 in Maxwell 2012).

Williams *et al*. (2015) described the Strawberry Bank carbonate concretions as biomicritic mudstones to packstones containing invertebrate bioclasts. Carbonate concretions are often weathered to a yellowish colour, as is the surrounding sediment, although originally, the unaltered deposits were blue-grey (Moore 1866) with high organic content (Suan *et al*. 2013; Charbonnier *et al*. 2020). Under anoxic conditions, the presence of organic matter in mudstone boosts the formation of concretions early during diagenesis; microbial activity produces methane and carbon dioxide that provide the basis for carbonate precipitation and nucleation (Raiswell 1988; Raiswell & Fisher 2000; Marshall & Pirrie 2013). Within most Toarcian levels with organic-rich shales, specimens have undergone compaction and even if soft tissues have been positively identified, their flatness hides many morphological features. The interesting prospect is that levels with concretions are known within these organic-rich shales and due to their early diagenetic implementation, hold the potential of preserving vertebrate specimens, including soft tissues, in volume.

Several ichthyosaur specimens from the Toarcian of SW Germany and, to a lesser extent, of England are known to preserve soft tissue including skin and muscle fibers preserved as phosphatized or carbonized films (Fraas 1888; Martill 1993; Lingham-Soliar 1999). Ichthyosaurs with extensive soft tissue remains have been reported from a number of beds within the Posidonienschiefer Formation, predominantly in the laminated black shales extending from the upper part of the *tenuicostatum* Zone into the *serpentinum* Zone, specifically from epsilon II_1, (*semicelatum* subzone) to epsilon II_8 (*elegans* subzone), with most soft-tissue specimens originating from epsilon II_3–II_4 (Hauff 1921; Hofmann 1958; Keller 1992; Martill 1993). A slightly broader stratigraphic range for soft tissue preservation was presented by Heller (1966), including specimens from epsilon II_9 and epsilon II_{10} (*falciferum* subzone), suggesting that soft-tissue preservation, as concerns Toarcian deposits, may not be limited to laminated black shales and the epsilon II_5 laminated limestone. However, the best-preserved examples are from the laminated sediments. Recent studies using geochemical, ultrastructural and molecular tools have helped characterize the preservation of different soft tissue types from deposits of the Posidonienschiefer Formation in SW Germany. As such, a carbonate concretion from Dotternhausen containing an individual of *Stenopterygius* preserves structures resembling collagen as well as red and white blood cells (Plet *et al*. 2017); another *Stenopterygius* specimen preserved on a mudstone slab from the early Toarcian from Kromer Shale Quarry near Ohmden shows integument likely preserving blubber, melanophores as well as various lipids and proteins (Lindgren *et al*. 2018).

Our geochemical data ($\delta^{13}C$ and $^{87}Sr/^{86}Sr$) help to constrain the stratigraphic origin of the newly reported specimens. These data show that MHNL 20103062 comes from the middle part of the *serpentinum* ammonite zone, i.e. after the T-OAE carbon isotope excursion (Fig. 2). This specimen is partly disarticulated and not preserved in a carbonate concretion but at the base of a normally graded argillaceous limestone bed likely corresponding to a tempestite (Suan *et al*. 2013). The preparation of this specimen revealed a discontinuous, millimeter-sized crust of goethite covering the stratigraphically lowermost surface of the bones as well as the sediment located between the left and right premaxillae. This goethite crust, still partly visible as rust-coloured stains on and in between some bones in the prepared specimen (Fig. 3), likely corresponds to a completely oxidized pyrite crust. Comparable pyrite coatings described in some other Konservat Lagerstätten have been interpreted as a consequence of microbial degradation of organic-rich tissues (Muscente *et al*. 2017). The specimen therefore certainly did preserve soft tissues replaced by pyrite (subsequently weathered into goethite).

The geochemical data indicate that the oldest ichthyosaur specimen reported here and preserved in connection within a carbonate concretion was most likely derived from the very base of the *serpentinum* ammonite zone (Fig. 2) within the interval recording the T-OAE negative carbon isotope excursion. We highly suspect the preservation of soft tissue in the carbonate concretion specimen, as evidenced from oxidized features contained exclusively within the rib cage (Fig. 7d–f). In addition, chemo- and biostratigraphic constraints enable detailed temporal correlations between our finds from Beaujolais and coeval finds from SW Germany (Fig. 2).

At the scale of a given locality, there seems to be no specific horizon yielding complete specimens with soft tissues and a close examination of other similar (in age and sedimentological characteristics) paleontological localities may confirm this hypothesis. However, the occurrence of carbonate concretions containing marine vertebrates seems to correspond to the T-OAE interval, and depending on the thickness of the deposit as observed across European localities, several horizons with carbonate concretions may be recovered during this particular environmental perturbation. For example, the succession at LafargeHolcim Val d'Azergues quarry is condensed and such carbonate concretions were predicted to occur in the lower part of the *serpentinum* Zone, where the negative carbon isotope excursion is recorded. The original collector at Strawberry Bank only described one such horizon, and though the precise location of that quarry is enigmatic, this observation was corroborated by an excavation in close proximity in 2019 led by MW. As for the historical locality of La Caine, prospecting for carbonate concretions in the field will have to be undertaken. In Belgium and Luxembourg, several marine reptile specimens have been reported between the *tenuicostatum* and *serpentinum* ammonite zones (Godefroit 1994; Vincent *et al*. 2019), but a more detailed placement against carbon isotope stratigraphy established for this area (Ruebsam *et al*. 2016; Hermoso *et al*. 2014) would deserve further geochemical investigations of host sediments. At Holzmaden, the majority of the ichthyosaur fossil record stretches from epsilon II_1 to epsilon II_{10}, which corresponds to a large interval encompassing periods before, within and after the T-OAE (Maxwell & Vincent, 2016). Most of the Posidonia Shale facies in SW Germany consist of bituminous shales: the occurrence of carbonate concretions is reported from epsilon II_4, but most Toarcian ichthyosaurs from the Holzmaden area are preserved as flattened skeletons from the bituminous shale. Therefore, putting efforts into prospecting for marine vertebrates from nodular carbonate concretions of the T-OAE, notably in the level corresponding to the upper portion of epsilon II_4, will likely yield specimens preserved in volume, including soft tissues. Such a prospect is particularly appealing because the anatomical organization of internal soft organs is virtually unknown in ichthyosaurs and other marine reptiles of that age.

Early Jurassic evolution of ichthyosaurs in relation to the T-OAE. The youngest ichthyosaur skeleton from the LafargeHolcim Val d'Azergues quarry is *Temnodontosaurus azerguensis* from the base of the *bifrons* Zone, which is post-T-OAE. Here, we report stenopterygiids both within (base of *serpentinum* Zone) and after (middle of *serpentinum* Zone) the negative carbon isotopic excursion of the T-OAE. The T-OAE initiates near the limit of the *tenuicostatum* - *serpentinum* zones (Fig. 2). The oldest occurrence of the genus *Stenopterygius* has been recorded from epsilon I_2 level in Germany (Maxwell 2012), which corresponds to the base of the *tenuicostatum* zone. This suggests that *Stenopterygius* was already present just before the T-OAE. In SW Germany, *Stenopterygius* is particularly abundant in epsilon II_3 level (Maxwell 2012), i.e. the top of the *tenuicostatum* zone, which corresponds to the onset of the T-OAE. Bottom anoxic conditions are ideal to preserve marine faunas and this may explain the abundance of marine vertebrates preserved as complete skeletons from this lower Toarcian interval (Ulrichs *et al*. 1994). Marine vertebrates from the Toarcian of Yorkshire are equally abundant and finely preserved in bituminous shales within the *falciferum* subzone (Benton & Taylor 1984). Benton & Taylor (1984) state that the German fauna is older than the Yorkshire fauna, and a *falciferum* subzone for the Yorkshire fauna indicates that this marine assemblage is post-T-OAE. Ilminster specimens from the 'saurian and fish bed' are preserved in carbonate concretions collected from the *exaratum* subzone (Williams *et al*. 2015), which corresponds to the level that yielded the presently described carbonate concretion from Beaujolais containing the ichthyosaur specimen (MHNL 20103364). The carbonate concretion with the nicely preserved ichthyosaur from Curcy/La Caîne in Normandy comes from the *serpentinum* Zone, else known as the "Argiles à poissons" (Mazin 1988) but more precise stratigraphic details are unknown. Another nice skull preserved in volume (NHMUK PV OR 33157) comes from Curcy in Normandy and was originally mentioned and figured by Owen (1849) and by Caine & Benton (2011). Marine reptile discoveries from Belgium and Luxembourg were mostly recorded from the s*erpentinum* Zone, *exaratum* subzone (Godefroit 1994).

With the onset of the T-OAE, marine life experienced a major environmental perturbation with a well-documented impact on the invertebrate fauna (Little & Benton 1995; Harries & Little 1999; Macchioni & Cecca 2002; Wignall *et al*. 2005; Suan *et al*. 2008; Caswell *et al*. 2009). Although recent studies do not validate an extinction of marine vertebrates during the T-OAE (Vincent *et al*. 2013), it was statistically demonstrated that ichthyosaur body size was impacted (Maxwell & Vincent 2016). The rich fossil record from the Holzmaden area shows that the most recent levels of the *serpentinum* Zone contain the largest known specimens of the genus *Stenopterygius* (Maxwell & Vincent 2016) as well as the oldest known records of *Suevoleviathan*. The long skull of MHNL 20103062 (< 60 cm) and its stratigraphic position within the middle levels of the *serpentinum* Zone are consistent with these observations. The largest *Stenopterygius* specimens from Germany have a skull length of 72 cm for *S. uniter*, 67 cm for *S. triscissus* and 56 cm for *S. quadriscissus* (Maxwell & Vincent 2016). The Posidonia Shale has yielded hundreds if not thousands of vertebrate specimens, and indeed provides an ideal context to run such quantitative diversity analyses, but the impact of the T-OAE on marine faunas can be studied further elsewhere, contextualizing the fossil record with precisely dated occurrences, thanks to its apparent wide extension across Europe and also globally (Martindale *et al*. 2017).

Pre-T-OAE vertebrate fossils are important to understand marine diversity change in relation to the environmental perturbation of the Toarcian. For example, an apparent turnover can be identified between 'Lower Liassic' and 'Upper Liassic' ichthyosaur faunas (Hungerbühler & Sachs 1996), but growing evidence supports this turnover occurring in the Pliensbachian. During the Toarcian, *Stenopterygius* is the most abundant genus and seems to be the ecomorphological equivalent of the Pliensbachian genera *Ichthyosaurus* and *Leptonectes*. The youngest stratigraphically constrained occurrences of *Ichthyosaurus* are from the lower Pliensbachian strata of the UK (Lomax & Massare 2015; Massare & Lomax 2016); the youngest constrained records of *Leptonectes* are also from the lower Pliensbachian (*L. moorei* from the UK and more fragmentary remains attributable to *Leptonectes* from the UK, Belgium, Spain, and SW Germany: Fraas 1892 [see Maisch 2010]; Godefroit 1992; Fernández *et al*. 2018, McGowan & Milner 1999; Lomax & Massare 2018). The upper Pliensbachian specimen previously referred to *Leptonectes* (Maisch & Reisdorf 2006) has been reinterpreted as *Hauffiopteryx*, a genus best-documented from the Toarcian (Maxwell & Cortés 2020). An ischiopubis from the early-middle Liassic of the UK, cited by some authors as the earliest occurrence of *Stenopterygius* (McGowan 1978; Hungerbühler & Sachs 1996), is inconsistent with the Toarcian representatives of this genus based on the posteromedial orientation and large size of the obturator foramen, and incomplete lateral fusion between the ischium and pubis (McGowan 1978: pl.

2.3). As stated above, the occurrence of *Stenopterygius* in lowermost Toarcian strata (Maxwell 2012; Maxwell & Vincent 2016; this study) suggests that this genus was already present before the depositional record of the T-OAE started. Additional confusion in the distribution of Early Jurassic ichthyosaurs is caused by taxonomic identifications with a number of historical finds having been attributed to *Leptopterygius* von Huene 1922, a now obsolete genus name, which encompassed the different genera *Leptonectes*, *Suevoleviathan* and *Temnodontosaurus*. The Pliensbachian ichthyosaur record is poor and essentially originates from the lowest levels. Further sampling of this interval is important to understand evolutionary patterns during the Early Jurassic.

Conclusions

Our study highlights some future directions of research in order to clarify our understanding of faunal evolution in relation to a major environmental perturbation, i.e. testing the effects of the T-OAE on marine vertebrates, especially outside of the well-studied southwest German basin.

An apparent faunal transition may have occurred between lower Pliensbachian and Toarcian ichthyosaur assemblages. However, upper Pliensbachian strata are undersampled and the timing of this transition cannot be constrained yet. Whether the T-OAE may represent an abiotic influence as to the replacement of Pliensbachian ichthyosaurs by Toarcian ones seems unlikely considering that pre-T-OAE ichthyosaurs are apparently already represented by the genus *Stenopterygius*. This requires a precise stratigraphic and taxonomic context for each fossil individual to be recorded.

The taxonomy of Lower Jurassic ichthyosaurs is in critical need of a revision and several taxa may be synonymous. Despite numerous recent efforts (e.g. Lomax & Massare 2015; Maxwell & Cortés 2020), differences between *Leptonectes* and *Stenopterygius* are tenuous and ichthyosaur diversity may have been overlooked in a number of cases that still need to be identified. If Pliensbachian and Toarcian ichthyosaur faunas are homogeneous, then the impact of the T-OAE on these faunas remains minimal and an explanation of what triggered this faunal transition is still required.

Finally, we emphasize that the study of nodular carbonate concretions might reveal important information about soft tissue preservation, including the preservation of organs in three dimensions. As concerns marine vertebrates, this could correspond to a major advance to better understand the palaeobiology of these extinct animals and the adaptations of tetrapods from terrestrial to marine environments. Multidisciplinary approaches, such as that proposed in this work combining palaeontology, sedimentology and chemostratigraphy shall provide a solid framework to finely track the impact of environmental changes on marine vertebrates on both short- and long-term timescales. As an example, renewed field efforts can be directed at historical localities (e.g. La Caine or Strawberry Bank) that yielded exquisitely preserved specimens but where a detailed stratigraphic framework is lacking.

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Figure captions

Fig. 1. Photographs of the Belmont d'Azergues LafargeHolcim Val d'Azergues quarry, Beaujolais, France, taken during the 2013 fieldwork and contextualizing the area of discovery of *Stenopterygius* sp. remains described in this work. (a), general view of the quarry looking South from the hardground surface of the *variabilis* zone; (b), looking North, view of the trench realized through the *serpentinum* Zone where both *Stenopterygius* sp. finds were made; (c), aerial view (Googlemap) of the quarry identifying the areas of the inset photographs A and B.

Fig. 2. Lithological, biostratigraphic and geochemical data from Toarcian strata of (a) LafargeHolcim Val d'Azergues quarry in SE France and (b), Dotternhausen in SW Germany. The green band marks the interval of lowest carbon isotope values, i.e., the core of the negative carbon isotope excursion associated with the Toarcian Oceanic Anoxic Event. The stratigraphic position of ichthtyosaur specimens discussed in the text is indicated along the lithological log. The sedimentary matrix of the large carbonate concretion found during the excavation of the trench in the basal 2.5 m interval yielded a δ^{13}Ccarb value of –3.88‰. Comparatively low values are only recorded in the interval comprised between 0.2 and 0.5 m, enabling to narrow down its likely provenance. Correlations between the two sites were established using litho-,

bio- and chemostratigraphic features. Data for LafargeHolcim Val d'Azergues quarry from this study and Suan *et al*. (2013). Data for Dotternhausen from Bailey *et al*. (2003) and Suan *et al*. (2015). Epsilon levels from Hauff (1921) and Röhl *et al*. (2001).

Fig. 3. Photograph (a) and drawing (b) of the left lateral side of the skull of (MHNL 20103062) *Stenopterygius* sp. from the Toarcian of Beaujolais. Abbreviations: en, external nares; for, foramen; fr, frontal; iff, interfrontal foramen; ju, jugal; la, lacrimal; lac. sut., lacrimal suture; mx, maxilla; p, parietal; pfr, prefrontal; pif, pineal foramen; pmx, premaxilla; pof, postfrontal; qj, quadratojugal; sr, sclerotic ring; t, teeth. [Full page width]

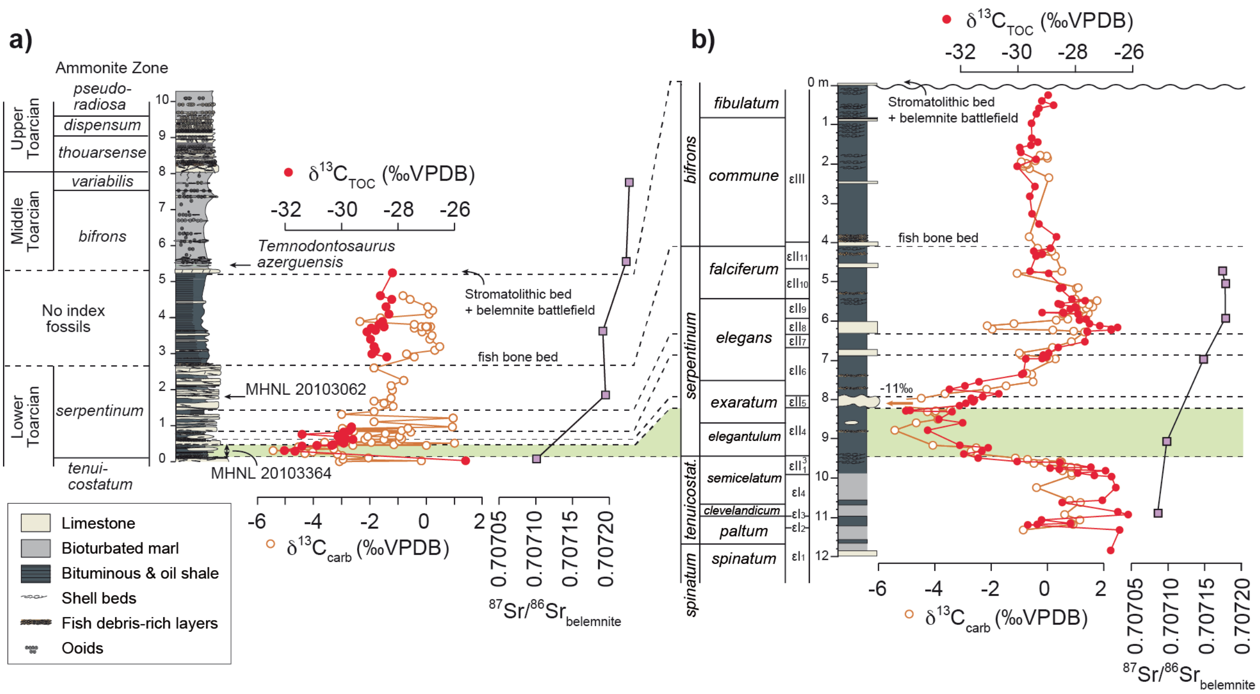
Fig. 4. Isolated tooth of *Stenopterygius* sp. (MHNL 20103062) from the Toarcian of Beaujolais in labial or lingual (a, b), mesial or distal (c, d) and basal (e) views. [Full page width]

Fig. 5. The nodular concretion (MHNL 20103364) (a) as recovered during fieldwork with * corresponding to (b), articulated phalanges; ** corresponding to (c), anterior tip of the rostrum with arrows corresponding to teeth in section; and *** corresponding to (d), section through the rib cage showing ribs and gastralia (arrows) delimiting an internal zone of purple hue suspected of representing oxidized organic matter together with close-ups (not to scale) of the purple hue within sediment (e) and around gastralia (f). Abbreviations: c, centrum; ga, gastralia. [Full page width]

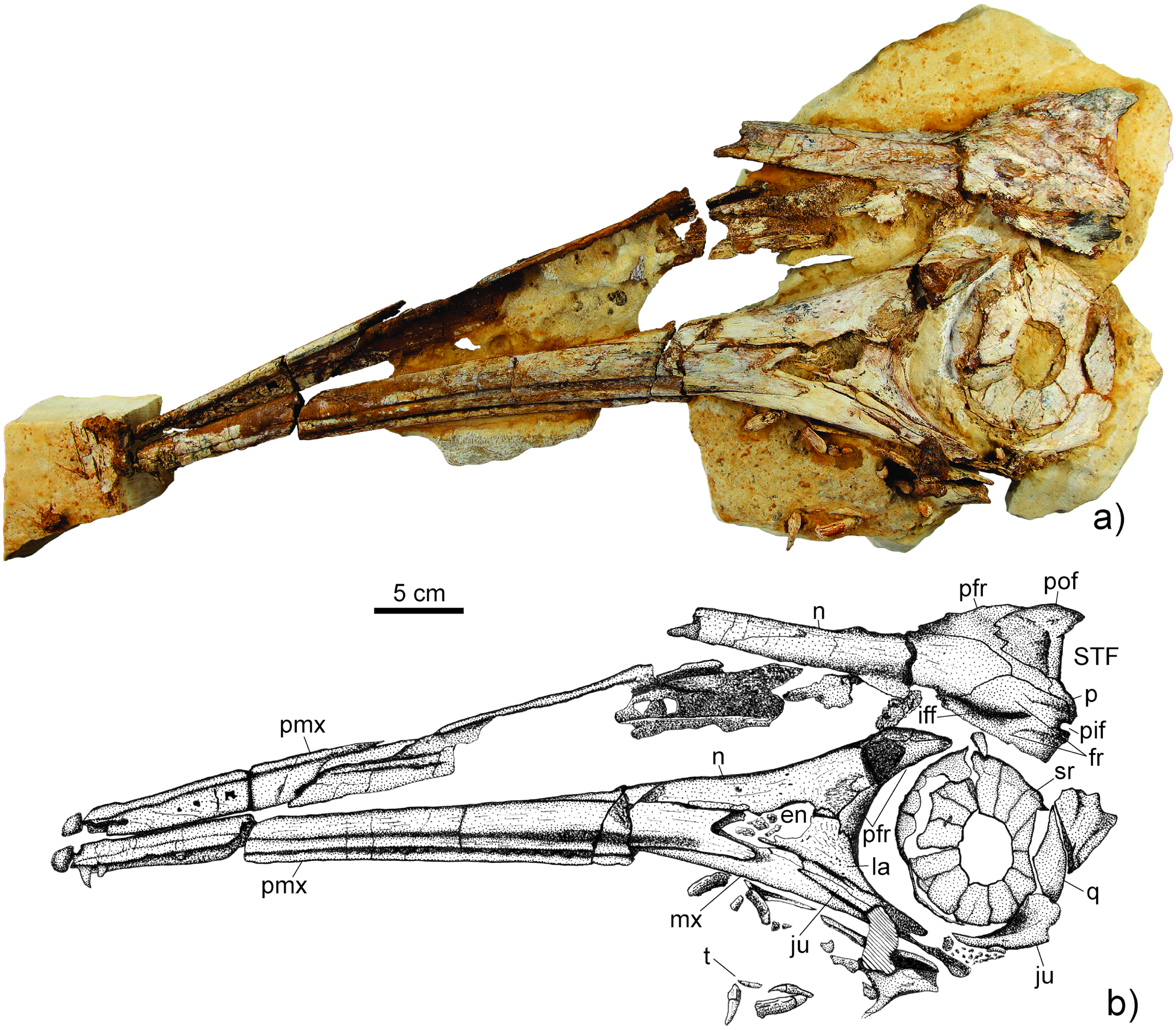
Table 1. List of early Toarcian localities with ichthyosaur-bearing carbonate concretions (AZ = Ammonite Zone).

Supplementary Data. Geochemical dataset used in the present study including bulk sediment inorganic and organic carbon isotope composition ($\delta^{13}C$) and radiogenic strontium isotope ($^{87}Sr/^{86}Sr$) values of belemnites.


a)
serpentinum
variabilis
b)
c)
N
variabilis
serpentinum
Google
100 m
Imagery ©2020 CNES / Airbus, Maxar Technologies, Map data ©2020
France
3D Earth view is not available



a)
Ammonite Zone
Upper Toarcian
Middle Toarcian
Lower Toarcian
pseudo-radiosa
dispensum
thouarsense
variabilis
bifrons
No index fossils
serpentinum
tenui-costatum
Temnodontosaurus azerguensis
MHNL 20103062
MHNL 20103364
Stromatolithic bed + belemnite battlefield
fish bone bed
δ13C TOC (‰VPDB)
δ13C carb (‰VPDB)
87Sr/86Sr belemnite
Limestone
Bioturbated marl
Bituminous & oil shale
Shell beds
Fish debris-rich layers
Ooids
b)
fibulatum
commune
falciferum
elegans
exaratum
elegantulum
semicelatum
clevelandicum
paltum
spinatum
bifrons
serpentinum
tenuicostat.
Stromatolithic bed + belemnite battlefield
fish bone bed
-11‰



a)
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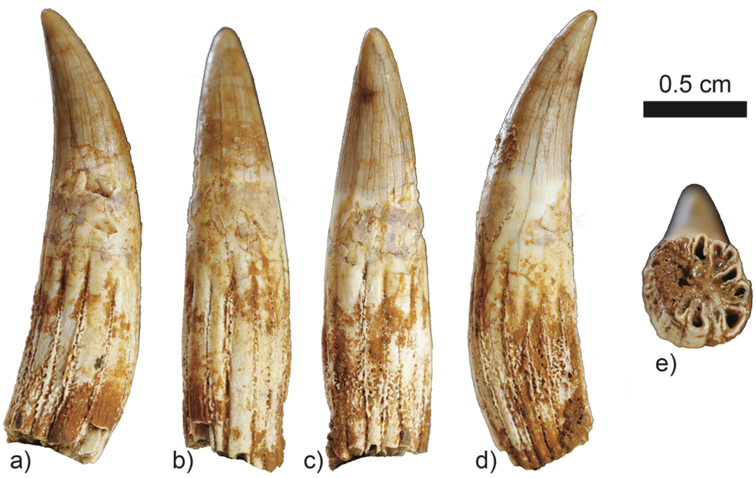
0.5 cm
a)
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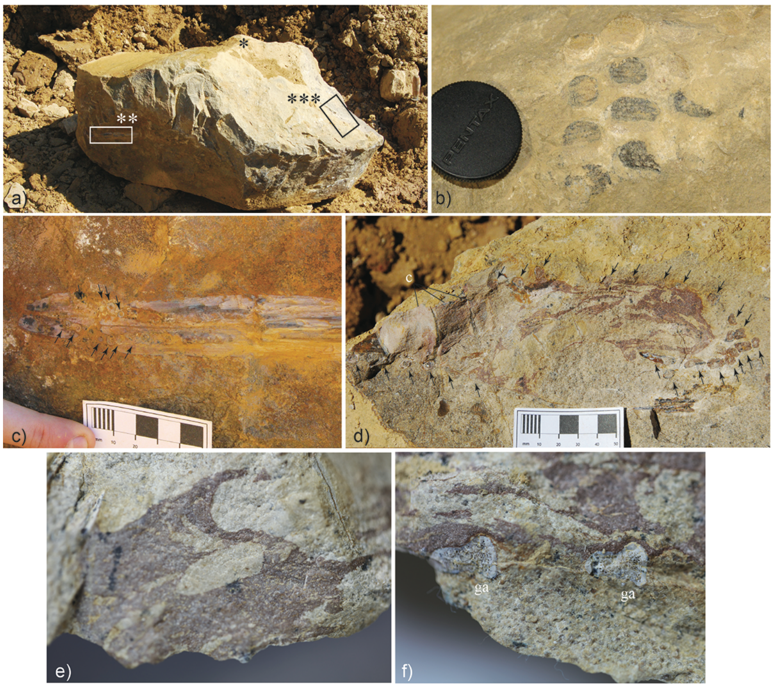
d)
e)


*
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Locality	**Taxa**
Strawberry Bank, Ilminster, Somerset, UK	*Stenopterygius triscissus*, *Hauffiopteryx typicus*
Whitby, Yorkshire, UK	various ichthyosaur species
Schistes de Grandcourt, Belgium and Luxembourg	*Stenopterygius* sp.
Sainte-Colombe, Burgundy, France	*Temnodontosaurus burgundiae*
Curcy-sur-Orne, Normandy, France	?*Stenopterygius*
Holzmaden area, Baden-Württemberg, Germany	*Temnodontosaurus, Stenopterygius, Hauffiopteryx*
Dotternhausen-Dormettingen, Baden-Württemberg, Germany	*Hauffiopteryx altera, Stenopterygius* sp.
Dobbertin and Grimmen, Mecklenburg-West Pomerania, Germany	*Stenopterygius* sp.
Staffelegg, Canton Aargau, Switzerland	*Eurhinosaurus longirostris*
Belmont, Beaujolais, France	*Stenopterygius* sp.

Table 1. List of early Toarcian localities with ichthyosaur-bearing carbonate concretions (AZ = Ammonite Zo

Stratigraphy	Stratigraphic Correlation	References
exaratum subzone, *serpentinum* AZ	post T-OAE	Williams et al. 2015
?	T-OAE not constrained	Benton and Taylor, 1984
exaratum subzone, *serpentinum* AZ	T-OAE not constrained	Godefroit, 1994
?*serpentinum* AZ	T-OAE not constrained	Gaudry, 1892
serpentinum AZ	T-OAE not constrained	Dechaseaux, 1954; Mazin, 1988
Base of *serpentinum* AZ (eII4-II6)	T-OAE and post-T-OAE	Böttcher, 1989; Keller 1992
Base of *serpentinum* AZ (eII4)	within T-OAE	Jäger, 2005, Keller 1992
Elegantulum subzone, *serpentinum* AZ	T-OAE not constrained	Maisch & Ansorge, 2004, Stumpf, 2016
bifrons or *variabilis* AZ	post T-OAE	Reisdorf et al. 2011
Base of *serpentinum* AZ	within T-OAE	this study

ne)

Lafarge Beaujolais

sample ID	Preservation	Composite height (m)	CaCO3 (wt. %)	TOC carb. free IRMS (wt.%)	SD	TOC (wt.%) IRMS	$\delta^{13}C_{TOC}$ (‰VPDB)	SD
PL-2013-1	Non-weathered	0.28	1.14	14.46	0.06	14.29	-31.67	0.05
PL-2013-2	Non-weathered	0.30	1.18	13.63	0.56	13.47	-32.05	0.05
DV01-2	Non-weathered	0.42	0.32	12.63		12.59	-31.40	0.01
DV02-2	Non-weathered	0.44	78.57	10.00		2.14	-30.35	
DV03-2	Non-weathered	0.46	69.34	8.94		2.74	-30.88	
DV04-2	Non-weathered	0.48	57.69	10.90		4.61	-30.30	
DV05-2	Non-weathered	0.51	79.26	10.89		2.26	-29.94	
DV06-2	Non-weathered	0.57	57.72	10.27	0.42	4.34	-30.06	0.03
DV07-2	Non-weathered	0.61	11.26	14.78		13.12	-29.59	
DV08-2	Non-weathered	0.64	15.47	13.65		11.54	-29.86	
DV09-2	Non-weathered	0.69	24.74	13.83		10.41	-30.14	
DV10-2	Non-weathered	0.75	1.29	10.21		10.07	-31.40	
DV11-2	Non-weathered	0.81	26.65	9.22		6.76	-29.93	
DV12-2	Non-weathered	0.85	27.81	12.55	0.28	9.06	-29.73	0.03
DV13-2	Non-weathered	0.92	54.43	16.92		7.71	-29.66	
DV14-2	Non-weathered	0.96	89.73	15.68		1.61	-29.66	
L 03	Non-weathered	2.90	27.37	3.42		2.48	-28.39	
L 04	Non-weathered	3.00	29.00	3.08		2.19	-28.93	
L 05	Non-weathered	3.10	31.75	2.89		1.97	-28.80	
L 06	Non-weathered	3.20	32.21	9.56		6.48	-28.85	
L 07	Non-weathered	3.40	43.68	9.67		5.45	-28.98	
L 08	Non-weathered	3.50	35.06					
L 09	Non-weathered	3.60	35.90	9.44		6.05	-29.09	
BB2-NW	Non-weathered	3.65	31.00	8.88		6.13	-28.80	
L 10	Non-weathered	3.70	39.37	10.33		6.26	-28.95	
MA-2013NW	Non-weathered	3.75	50.94	9.52		4.67	-28.51	
L 11	Non-weathered	3.80	53.13	10.41		4.88	-28.68	
L 12	Non-weathered	3.90	37.27	10.48		6.58	-28.54	
L 13	Non-weathered	4.00	30.34					
L 14	Non-weathered	4.10	26.06	12.18		9.01	-28.31	
L 15	Non-weathered	4.20	28.20					
L 16	Non-weathered	4.30	29.17	10.25		7.26	-28.43	
L 18	Non-weathered	4.50	29.75	9.74		6.84	-28.22	
L 19	Non-weathered	4.60	26.47	9.55		7.02	-28.62	
UAB-NW	Non-weathered	5.25	22.00	6.17		4.81	-28.20	
CHI-01	Weathered	0.00	60.43					
CHI-02	Weathered	0.06	68.56					
CHI-03	Weathered	0.11	58.53					
CHI-04	Weathered	0.16	4.74					
CHI-05	Weathered	0.20	4.26					
CHI-06	Weathered	0.23	17.93					
CHI-07	Weathered	0.26	8.93					
CHI-08	Weathered	0.30	28.60					
CHI-09	Weathered	0.35	14.83					
CHI-10	Weathered	0.40	26.24					
CHI-11	Weathered	0.47	73.12					
CHI-12	Weathered	0.53	75.49					
CHI-13	Weathered	0.62	8.19					
CHI-14	Weathered	0.70	12.37					
CHI-15	Weathered	0.78	12.58					

CHI-16	Weathered	0.84	69.55					
CHI-17	Weathered	0.92	93.60					
CHI-18	Weathered	1.10	86.84					
CHI-19	Weathered	1.30	89.53					
CHI-20	Weathered	1.40	27.09					
CHI-21	Weathered	1.54	84.63					
CHI-22	Weathered	1.68	29.11					
CHI-23	Weathered	1.77	82.41					
BB2-W	Weathered	3.65	28.00	0.14		0.10	-24.80	
UAB-W	Weathered	5.25	22.00	0.26		0.20	-25.40	
LI 01	Weathered	0.02	79.89	0.23		0.05	-25.51	
LI 02	Weathered	0.53	72.93	0.29		0.08	-28.20	
LI 04	Weathered	0.88	78.43	0.38		0.08	-29.55	
LI 05	Weathered	1.20	84.27					
LI 06	Weathered	1.62	83.96	1.84		0.30	-27.50	
LI 07	Weathered	1.98	90.84					
LI 08	Weathered	2.11	85.23					
LI 09	Weathered	2.26	89.45	0.77		0.08	-27.02	
LI 10	Weathered	2.61	93.12	1.19		0.08	-27.09	
Nodule 2012	Weathered							
CH11-224	Belemnite	0.02						
Ch09-023	Belemnite	1.83						
CH09-003	Belemnite	3.64						
BLH 01	Belemnite	5.61						
BLH 13	Belemnite	7.85						

$\delta^{13}C_{carb}$ (‰VPDB)	$\delta^{18}O_{carb}$ (‰VPDB)	**87Sr/86Sr**	**year of collection**	**Source**
			2013	This study
			2013	This study
			2013	This study
-2.54	-4.75		2013	This study
0.07	-3.44		2013	This study
-1.08	-4.04		2013	This study
1.06	-2.56		2013	This study
-0.89	-3.35		2013	This study
-1.44	-5.51		2013	This study
-0.81	-5.70		2013	This study
-0.90	-5.18		2013	This study
			2013	This study
-0.50	-5.13		2013	This study
-0.82	-5.47		2013	This study
-0.61	-5.04		2013	This study
0.96	-2.90		2013	This study
-0.42	-5.10		2009	Suan et al. (2013)
-0.70	-4.98		2009	Suan et al. (2013)
0.30	-5.14		2009	Suan et al. (2013)
0.48	-5.10		2009	Suan et al. (2013)
0.14	-4.76		2009	Suan et al. (2013)
0.21	-5.01		2009	Suan et al. (2013)
-0.15	-4.83		2009	Suan et al. (2013)
			2010	Suan et al. (2013)
-0.42	-4.82		2009	Suan et al. (2013)
			2013	This study
-0.42	-4.58		2009	Suan et al. (2013)
-2.36	-5.50		2009	Suan et al. (2013)
-1.63	-5.01		2009	Suan et al. (2013)
0.12	-5.11		2009	Suan et al. (2013)
0.23	-5.18		2009	Suan et al. (2013)
0.07	-5.05		2009	Suan et al. (2013)
-0.57	-5.02		2009	Suan et al. (2013)
-0.82	-5.14		2009	Suan et al. (2013)
			2010	Suan et al. (2013)
-3.08	-4.97		2011	This study
-2.95	-5.10		2011	This study
-2.05	-4.75		2011	This study
-2.98	-7.11		2011	This study
-3.15	-9.25		2011	This study
-4.32	-6.94		2011	This study
-4.05	-6.42		2011	This study
-5.45	-5.30		2011	This study
-3.28	-5.79		2011	This study
-4.54	-5.77		2011	This study
-3.31	-4.34		2011	This study
-1.97	-4.89		2011	This study
-2.19	-9.42		2011	This study
-2.09	-5.50		2011	This study
-1.46	-6.10		2011	This study

-2.60	-4.36		2011	This study
-3.00	-4.37		2011	This study
-1.88	-3.34		2011	This study
-3.02	-4.16		2011	This study
-1.87	-4.57		2011	This study
-1.15	-3.23		2011	This study
-1.80	-5.53		2011	This study
-1.21	-3.11		2011	This study
			2010	Suan et al. (2013)
			2010	Suan et al. (2013)
-0.18	-4.90		2009	Suan et al. (2013)
-3.60	-3.89		2009	Suan et al. (2013)
-2.83	-4.00		2009	Suan et al. (2013)
0.96	-2.50		2009	This study
-1.49	-3.27		2009	Suan et al. (2013)
-1.19	-3.08		2009	Suan et al. (2013)
-1.25	-4.48		2009	Suan et al. (2013)
-0.80	-2.40		2009	Suan et al. (2013)
-1.85	-2.23		2009	Suan et al. (2013)
-3.88	-4.18		2012	This study
		0.7071010	2011	This study
		0.7071948	2009	This study
		0.7071911	2009	This study
		0.7072229	2011	This study
		0.7072272	2011	This study