

Stenopterygiids from the lower Toarcian of Beaujolais and a chemostratigraphic context for ichthyosaur preservation during the Toarcian Oceanic Anoxic Event Running header: Toarcian ichthyosaurs and the T-OAE

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37 Lagerstätte-type deposits, marine reptiles, Ichthyosauria

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39 Abstract: We report new ichthyosaur material excavated in lower Toarcian levels of 40 the LafargeHolcim Val d'Azergues quarry in Beaujolais, SE France. A partially 41 articulated skull and a smaller, unprepared but likely subcomplete skeleton preserved 42 in a carbonate concretion are identified as stenopterygiids, a family of wide European 43 distribution during the Early Jurassic. These specimens are among the finest preserved 44 Toarcian exemplars known from Europe and in one of them, soft tissue preservation is 45 suspected. Their state of preservation is attributed to the combination of prolonged 46 anoxic conditions near the water-sediment interface and early carbonate cementation 47 resulting from the activity of sulfate-reducing bacteria. We also present carbon and 48 strontium isotope values obtained from the study site that allow detailed temporal 49 comparisons with other Toarcian vertebrate-yielding sites and environmental 50 perturbations associated with the Toarcian Oceanic Anoxic Event (T-OAE). These 51 comparisons suggest that the relatively high abundance and good preservation state of 52 Toarcian vertebrates was favoured by a prolonged period of low bottom water 53 oxygenation and accumulation rates. The environmental conditions that prevailed 54 during the T-OAE were probably responsible for the extensive nature of Lagerstätte-55 type deposits with exceptional preservation of marine organisms. Whether the T-OAE 56 had a biological impact on marine vertebrates requires a precise chemostratigraphic 57 context of the fossil record spanning the Pliensbachian-Toarcian interval. 58 59 'Supplementary material: [Geochemical dataset used in the present study including bulk sediment inorganic and organic carbon isotope composition (δ^{13} C) and 60

buck sedment morganic and organic carbon isotope composition (6°C) and

61 radiogenic strontium isotope (87 Sr/ 86 Sr) values of belemnites.] is available at XXX'.

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69 The Early Jurassic Period was punctuated by severe environmental perturbations with 70 paroxysmal events coinciding with rapid biotic extinctions and turnover among 71 marine invertebrates across the transitions between the Pliensbachian-Toarcian stages 72 and the tenuicostatum-serpentinum ammonite zones (Little & Benton 1995; Harries & 73 Little 1999; Macchioni & Cecca 2002; Wignall et al. 2005; Suan et al. 2008; Caswell 74 et al. 2009; Suan et al. 2010; Ruebsam et al. 2019). The early-middle Toarcian also 75 witnessed the deposition of widespread laminated black shales resulting from a 76 prolonged episode of warmth and decreased bottom water oxygenation, which may 77 have favoured the preservation of abundant marine invertebrates and vertebrates (e.g. 78 Martill 1993). The interval of most intense environmental perturbation recorded in 79 strata spanning the uppermost part of the *tenuicostatum* ammonite zone to the top of 80 the serpentinum ammonite zone is known as the Toarcian Oceanic Anoxic Event (T-81 OAE) (e.g. Jenkyns 1988; Baudin et al. 1990; Harries & Little 1999; Wignall et al. 82 2005; Caswell et al. 2009). Marine vertebrates were apparently little impacted by the 83 T-OAE (Vincent et al. 2013; Maxwell & Vincent 2016), although the records for the 84 time intervals pre- and post-dating these events are either scarce (Martin et al. 2012) 85 or poorly constrained stratigraphically.

86 Ichthyosaur remains are certainly the most ubiquitous marine vertebrates 87 found in Toarcian deposits of Europe with most iconic specimens reported from the 88 Posidonienschiefer Formation of the Holzmaden area in SW Germany. The most 89 spectacular exemplars include gravid females preserving soft tissues as well as 90 stomach contents (Böttcher 1989; 1990) and individuals preserving integuments 91 (Lindgren et al. 2018). Other remarkable finds include English specimens from 92 Ilminster in Somerset (Caine & Benton 2011; Williams et al. 2015) or the Alum Shale 93 Member in Yorkshire (Benton & Taylor 1984; McGowan & Motani 2003) but also 94 specimens preserving soft tissues from the Hettangian/Sinemurian of Dorset (Martill 95 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,

103 however, have been intensively impacted by burial compaction, which has exceeded 104 90% in such lithologies (Martill 1993), hence obscuring some important 105 morphological features, including details of skull bone contacts (e.g. Fraas 1913). On 106 the other hand, carbonate concretions with exceptional three-dimensional preservation 107 have been reported from Strawberry Bank as well as in a number of other Toarcian 108 localities (e.g. Normandy: Mazin 1988; northeastern Germany: Maisch & Ansorge 2004; Beaujolais: Vincent et al. 2013; Luxembourg: Vincent et al. 2019; see also 109 110 Table 1). Vertebrates preserved in carbonate concretions are potentially important 111 because they are comparatively less flattened than shale-hosted specimens. Given the 112 established presence of soft tissues in Toarcian marine vertebrates (e.g. Lindgren et al. 113 2018), carbonate concretions may also be promising for three-dimensional 114 reconstructions of soft tissues.

115 Regardless of their type of preservation, published Toarcian ichthyosaurs 116 generally lack a precise stratigraphic control, with the exception of most SW German 117 specimens that benefited from the early use of stratigraphic subdivisions of the 118 Posidonia Shale (Hauff 1921). The infra-stage stratigraphic data of previous 119 discoveries, if any, relied mostly on ammonite biostratigraphy (e.g. Benton & Taylor 120 1984; Godefroit 1994; Benton & Spencer 1995), in which resolution might be 121 strongly limited by both the abundance of age-diagnostic species and the use of 122 different bioevents in the various faunal provinces (Page 2003; McArthur et al. 2020). 123 Similarly, it is yet unclear whether vertebrate-hosting carbonate concretions are bound 124 to stratigraphically restricted horizons or occur randomly in Toarcian successions. In 125 this context, the massive accumulation of high-resolution isotope data fostered by the 126 growing interest for the T-OAE perturbations over the past decades could provide an 127 independent temporal framework for past and future vertebrate discoveries. Such a 128 multidisciplinary approach combining sedimentological, geochemical and 129 palaeontological data has been successfully used to replace important vertebrate 130 specimens in a detailed palaeoenvironmental and temporal framework and hence 131 better constrain conditions favouring their preservation (Suan et al. 2013; Vincent et 132 al. 2013; Vincent et al. 2020). 133 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-

137	yielding localities. We discuss the implications of our findings for the evolutionary		
138	response of ichthyosaurs to Early Jurassic perturbations and the significance of		
139	exceptional preservation, including that of soft tissues, for the prediction of similar		
140	discoveries within Toarcian deposits.		
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142	Institutional abbreviations		
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144	BRLSI, Bath Royal Literary and Scientific Institution, Bath; LGL-TPE, Laboratoire		
145	de Géologie de Lyon – Terre, Planètes, Environnements, Villeurbanne; MHNL,		
146	Muséum d'Histoire Naturelle de Lyon/Musée des Confluences de Lyon, Lyon; MHH,		
147	Museum Hauff, Holzmaden; NHMUK, Natural History Museum, London; SMNS,		
148	Staatliches Museum für Naturkunde, Stuttgart.		
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150	Lithology and biostratigraphy		
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152	A synthetic account of the Lower Jurassic sedimentary succession available at the		
153	LafargeHolcim Val d'Azergues quarry in Beaujolais (Rhône, SE France) is given		
154	below. More detailed information is available from previous works (Vincent et al.		
155	2013; Suan et al. 2013). The quarry exposes a marine sequence from the lower		
156	Toarcian up to the upper Bajocian (Figs. 1, 2); the Toarcian – Aalenian		
157	lithostratigraphy and ammonite biostratigraphy having been described by Elmi &		
158	Rulleau (1991; 1993), and the complete succession was published by Rulleau (2006).		
159	Here, we focus on the most recent excavations undertaken by our team during the		
160	2009–2013 campaigns, revealing new observations and samplings of the lower		
161	Toarcian interval, which was previously poorly known in the quarry (Rulleau 1997).		
162	The basalmost lower Toarcian strata include a 2.5 m-thick succession of dolomitized		
163	argillaceous yellowish limestone beds intercalated with yellow plastic clays. A		
164	temporary trench realized in the lowermost levels in 2013 confirmed that these		
165	lithologies are the weathered equivalent of grey, argillaceous limestone beds		
166	intercalated with dark grey laminated marls with high total organic carbon contents		
167	(up to 14% in weight; Charbonnier et al. 2020). This basal interval ('Calcaires Jaunes		
168	à Ammonitella' in Elmi & Rulleau 1991) includes the tenuicostatum and serpentinum		
169	ammonite zones (Elmi & Rulleau 1991; Suan et al. 2013). The tenuicostatum zone		
170	was documented only in the basal bed, which yielded various dactylioceratid		

171 ammonites of the semicelatum subzone (upper part of tenuicostatum Zone; e.g. 172 Dactylioceras (Orthodactylites) semicelatum, D. (O.) crosbeyi). The overlying 40 cm 173 of succession did not yield any ammonites. The presence of *Cleviceras elegans* in a 174 bed 50 cm above the base of the section and especially the co-occurence of C. elegans 175 with Harpoceras serpentinum in nodular layers 70 and 120 cm above the base already 176 indicates the upper part of the *elegantulum* subzone (lower part of the *serpentinum* 177 Zone, equivalent of the *exaratum* subzone, see Page 2003). Cleviceras elegans was 178 collected also from beds 155 and 180 cm (bed with ichthyosaur specimen MHNL 179 20103062) above the base. However, this species can range up to the early *falciferum* 180 subzone (e.g. Bécaud, 2006) so these beds can thus either represent the upper 181 *elegantum* subzone or the lower *falciferum* subzone. First age-diagnostic ammonites 182 of the *falciferum* subzone (upper part of the *serpentinum* Zone) represented by 183 Harpoceras pseudoserpentinum and Hildaites subserpentinum occur in the uppermost 184 bed, just below the dark marls. The yellowish limestone interval is capped by a 185 distinctive, 2-3 cm thick packstone-grainstone horizon mainly consisting of fish debris 186 and bivalves partly cemented by pyrite. The overlying 2.5 m-thick interval ('Marnes 187 inférieures' in Elmi & Rulleau 1991) of dark grey, finely laminated and 188 unfossiliferous calcareous marls, also often weathered into yellow plastic clays in the 189 quarry (Suan *et al.* 2013), yielded only few, poorly preserved ammonites and hence 190 lacks definitive ammonite zone assignment. Two fragmentary specimens of 191 Harpoceras falciferum were collected about 90 cm above the base of the marly 192 interval. Although this species is typical of the upper part of the *falciferum* subzone, 193 its upper stratigraphic range limit is located in the *sublevisoni* subzone of the early 194 bifrons Zone (e.g. Elmi et al. 1997). The calcareous nannofossil association and 195 ⁸⁷Sr/⁸⁶Sr values (see below) indicate that this level with *H. falciferum* fragments 196 probably belongs to the sublevisoni subzone. This marly interval is overlain by a 2.4 197 m-thick succession of intensively bioturbated marl containing iron ooids and abundant 198 invertebrates, including age-diagnostic ammonites of the *bifrons* (middle Toarcian) 199 and variabilis (upper Toarcian) ammonite zones and various vertebrate remains (e.g. 200 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 201 202 almost unfossiliferous interval of dark grey marls between 2.5 and 5.2 m, the 203 investigated succession is relatively well-constrained biostratigraphically owing to its 204 ammonite richness. Nannofossil data may offer additional temporal constraints. The

205 first occurrence of Watznaueria colacicchii, recorded at 3.3 m in the ammonite-barren 206 interval in the LafargeHolcim Val d'Azergues Quarry (Suan et al. 2013), has been 207 recently shown to coincide with the base of the bifrons Zone in Portugal (Ferreira et 208 al. 2019; base of nannofossil NTJ7b Zone). Pending future ammonite discoveries and 209 further chemostratigraphic assessment (see below), the base of the *bifrons* Zone 210 should hence certainly occur below that suggested by sparse ammonite record of 211 Harpoceras faciferum, i.e., toward the lower half of the ammonite-barren interval. 212 The Posidonienschiefer Formation (Posidonia Shale; Lias epsilon) of 213 Southwestern Germany has been divided into lower, middle, and upper components 214 indicated by roman numerals (I-III), with beds within these larger subdivisions 215 indicated using subscript. When comparing the biostratigraphy to the divisions 216 recorded in the Southwest German Basin, we use the bed-level nomenclature and 217 ammonite zone correlations detailed by Riegraf et al. (1984).

218

219 Material and methods

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221 Fieldwork and specimen preparation. We report on two ichthyosaur specimens 222 discovered during our palaeontological excavations in 2010 and 2012 at 223 LafargeHolcim Val d'Azergues cement Quarry near Charnay in the Beaujolais hills 224 (Rhône, France). Both specimens are reposited at the Musée des Confluences, Lyon, 225 France. The first specimen (MHNL 20103062) was discovered in July 2010 in a thin 226 limestone bed at 1.8 m during manual excavation of the interval between 1.6 and 2.5 227 m (serpentinum Zone). The second specimen was discovered in the material 228 excavated mechanically by a bulldozer from the first 2.5 m of the measured interval in 229 July 2012 (serpentinum ammonite Zone). MHNL 20103062 was prepared during 230 2013 by one of us (AC) at Institut des Sciences de l'Evolution, Université de 231 Montpellier, alternating mechanical preparation and weak acetic acid baths in order to 232 soften the sediment without damaging the bone surface. The second specimen 233 (MHNL 20103364), preserved in a large carbonate concretion with possible soft 234 tissues, awaits preparation and is temporarily deposited at LGL-TPE for ongoing 235 study before its permanent curation at Musée des Confluences (MHNL). These recent 236 findings extend the relatively rich record of ichthyosaurs of this site (Vincent *et al.* 237 2013), initiated in 1984 with the discovery of a subcomplete specimen, which was

recently described and attributed to *Temnodontosaurus azerguensis* (Martin *et al.*2012).

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241 **Chemostratigraphy.** In order to place the recently discovered specimens from the 242 LafargeHolcim Val d'Azergues quarry into a stratigraphic context, we analyzed the 243 bulk sediment inorganic and organic carbon isotope composition as well as the 244 strontium isotope composition of belemnites, all collected from the section that 245 yielded the three ichthyosaur specimens. We also analyzed the inorganic carbon 246 isotope composition of a sample collected from the carbonate concretion containing 247 the specimen discovered in 2012 to narrow down its likely provenance. The 248 stratigraphic log of the study site, modified from Suan et al. (2013) and updated with 249 these new geochemical data (Supplementary Data), is shown in Figure 2.

250 A total of 43 samples (including the sample collected from the ichthyosaur-251 hosting carbonate concretion), consisting of both weathered and non-weathered 252 sediment, were analyzed for their bulk carbonate carbon isotope ($\delta^{13}C_{carb}$) composition 253 using an auto sampler MultiPrep[™] system coupled to a dual-inlet GV IsoPrime[™] 254 isotope ratio mass spectrometer (IRMS). Each sample was powdered in an agate 255 mortar and, depending on calcium carbonate contents, an aliquot of 200-2000 μ g of 256 the obtained powder was reacted with anhydrous, oversaturated phosphoric acid at 257 90°C for 20 min. Each analytical run contained international (NIST NBS19) and in-258 house standards (Carrara Marble) to monitor analytical precision and accuracy.

259 A total of 22 samples were analyzed for their organic carbon isotope 260 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 261 262 visual examination (dark colour, absence of orange-brownish oxidation stains) were 263 selected. Each sample was powdered in an agate mortar and decarbonated using 1N 264 hydrochloric acid at ambient temperature overnight. Each sample was sequentially 265 rinsed four times with deionized water, with 40 minutes between rinses to allow the 266 sediment to settle, and oven-dried at 40°C. Between 0.5 and 1 mg of decarbonated 267 powder was weighted into tin capsules and placed in a Pyrocube[®] elemental analyzer connected to an Elementar Isoprime[®] isotope-ratio mass spectrometer in continuous 268 269 flow. Each analytical run contained four sets of international (IAEA-CH-7) and in-270 house standards (Caseine) to monitor analytical precision and accuracy. All carbon 271 isotope results are reported relative to the 'Vienna Pee Dee belemnite' (VPDB). Based 272 upon replicated analysis of standards, the precision of our measurements was better 273 than $\pm 0.1\%$ for $\delta^{13}C_{TOC}$ values and $\pm 0.05\%$ for $\delta^{13}C_{carb}$ values.

We sampled five belemnites for radiogenic strontium analysis (87Sr/86Sr) from 274 275 different levels in the lower and middle Toarcian interval. For each sample, the 276 rostrum was broken into millimeter-size fragments to select the best-preserved portion 277 of the samples. Fragments showing a strong radial fabric were subsequently picked 278 (avoiding the apical line and external-most areas) under a binocular microscope and 279 powdered in an agate mortar. About 2 mg of belemnite powder was dissolved in 280 concentrated nitric acid and evaporated to dryness. All samples were retaken in 2M 281 HNO₃ and purified through a strontium-specific resin (Sr-Spec Eichrom®). The 282 obtained solution was analyzed for ⁸⁷Sr/⁸⁶Sr ratios at LGLTPE on a Neptune Plus 283 multicollector ICP-MS (Thermo Scientific) during a single session in December 2014. 284 Reference material (SRM-987) of known ⁸⁷Sr/⁸⁶Sr composition was repeatedly 285 measured in the same analytical session. The standard SRM-987 gave an average 286 value of 0.7100912 ± 0.00000356 (1SD, n = 5), which is within 0.0001568 of the 287 value 0.710248 (McArthur et al. 2000). Belemnite values were adjusted accordingly 288 and are listed in the Supplementary Data.

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290 Results

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292 **Carbon and strontium isotope composition.** The $\delta^{13}C_{carb}$ profile, although somewhat 293 scattered, reveals a marked >3‰ decrease across the *tenuicostatum-serpentinum* zonal 294 transition and a >4‰ increase between 0.3 and 1 m. The $\delta^{13}C_{TOC}$ values of non-295 weathered samples show minimal values (down to -32%) at the very base of the 296 serpentinum ammonite Zone, and a marked 2.4‰ increase between 0.3 and 0.6 m. 297 These new records, when combined with previously published data from the same site 298 (Suan et al. 2013; Fig. 2), show that the characteristic T-OAE negative carbon isotope 299 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 0.5 300 301 m are comparable to those recorded in most other contemporary sections in the base 302 of the T-OAE interval (-30 to -34‰) (Suan et al. 2016; 2018). The sedimentary 303 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 304 305 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 ⁸⁷Sr/⁸⁶Sr values for the analyzed Toarcian belemnites range 308 between 0.70710095 and 0.707227, consistent with the range of values obtained for 309 310 this interval in previous studies (McArthur et al. 2000; Bailey et al. 2003). Our 311 ⁸⁷Sr/⁸⁶Sr profile records a marked shift toward more radiogenic values at the base of 312 the measured section, the amplitude of which is compatible with that observed across 313 the tenuicostatum-serpentinum transition in SW Germany and NE England (McArthur 314 et al. 2000; Bailey et al. 2003). The belemnite specimen sampled in the argillaceous 315 marl located 2 cm below the ichthyosaur specimen MHNL 20103062 yielded a 316 ⁸⁷Sr/⁸⁶Sr value of 0.707194. Comparably high values are only found in the uppermost 317 part of the serpentinum Zone in both German (Fig. 2b) and English sites (McArthur et 318 al. 2000; Bailey et al. 2003), where the boundary between the serpentinum-bifrons 319 zones is biostratigraphically better constrained than in the Val d'Azergues Ouarry. In 320 Yorkshire, such values occur immediately below the base of the Alum Shale Member 321 (McArthur et al. 2000), which has yielded historically important marine vertebrate 322 specimens (Benton & Taylor 1984). In the Val d'Azergues Quarry, the belemnite 323 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 ⁸⁷Sr/⁸⁶Sr value of 324 325 0.7072229. In Yorkshire, comparable values occur above the base of the crassum 326 subzone, which correspond to the topmost part of the Alum Shale Member (*bifrons* zone; McArthur et al. 2000). The ⁸⁷Sr/⁸⁶Sr value of 0.707227 measured in the 327 328 uppermost sample from the *variabilis* ammonite zone is consistent with values 329 measured in the middle of the variabilis zone in Yorkshire. Within the temporal 330 resolution allowed by the Toarcian strontium isotope stratigraphy (< 200 ka, 331 McArthur et al. 2020), these ⁸⁷Sr/⁸⁶Sr data support the synchronicity of Subboreal and 332 Submediterranean ammonite Subzones that have been respectively used in Yorkshire 333 and SE France (Elmi et al. 1997; Page 2003). In summary, the obtained carbon and 334 strontium isotope data enhance correlations with the classical localities of SW 335 Germany (Fig. 2) and Yorkshire, hence enabling detailed relative dating of the various 336 Toarcian ichthyosaur finds and their relationships with the coeval environmental 337 perturbations (see below).

338

339 Description of Ichthyosaur MHNL 20103062. Specimen MHNL 20103062

340 preserves most of the skull and the anterior part of the mandible. The rostrum is 341 complete with an antorbital length of 43 cm and a prenarial length of 35 cm. Despite 342 being partly disarticulated, it preserves fine anatomical details including bones 343 preserved in volume and sutures in the peri-orbital region. The left lateral side of the 344 specimen is exposed. The skull lacks the posteriormost part of the braincase and is 345 split along the sagittal axis. The right elements of the skull are disarticulated and have 346 been displaced dorsally; the top of the right portion of the skull table faces laterally. 347 Because the postorbital region in ichthyosaurs is short, a rough total skull length can 348 be estimated and would not have surpassed 60 cm.

349 The large circular orbit measures 10 cm in diameter. It is bordered ventrally by 350 the jugal, anteroventrally by the lacrimal, anteriorly and anterodorsally by the 351 prefrontal and posteriorly by the postorbital. The left sclerotic ring is 9 cm in diameter 352 and its aperture diameter is 3.6 cm. The aperture diameter to the orbital diameter 353 versus skull length ratio of Fernández et al. (2005) compares well (0.23) with the 354 values of other adult specimens of the genus Stenopterygius. The sclerotic ring is 355 complete and articulated with 14 individual sclerotic plates. The plates overlap each 356 other but there is no clockwise or anti-clockwise trend.

357 The premaxilla contributes to most of the rostrum. The lateral surface bears a 358 set of small foramina that are placed at the level of a long groove that extends 359 posteriorly on the lateral surface of the bone. There are no individualized tooth 360 sockets, the implantation is aulacodont. There are at least 30 alveolar positions 361 deduced by incipient concavities on the bone. The subnarial process of the premaxilla 362 projects below the external nares but does not contact the anteriormost tip of the jugal, 363 being separated from the ventral margin of the external nares by the underlying 364 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

area excluding the premaxilla from the external nares and suturing ventrally onto the

376 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 internasaldepression on the dorsal surface of the skull.

379 The lacrimal contributes to the posterior and posteroventral margins of the 380 external nares. The anteriormost tip of the lacrimal consists of a delicate notch 381 projecting medially to the maxilla, along the ventral border of the external nares. The 382 lacrimal contacts the nasal dorsally, along the posterior margin of the external nares, 383 excluding the prefrontal from the narial opening. This suture stops just below the 384 dorsal edge of the external nares. The circumorbital area of the lacrimal is heavily 385 vascularized. The ventral margin of the lacrimal mostly contacts the jugal, with the 386 exception of its anterior part, which contacts the maxilla. The lacrimal has an oblique 387 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 406 the anterior edge of the interfrontal foramen. Laterally, the frontal contacts the

407 prefrontal and posteriorly, it contacts the parietal. Posteriorly, the frontal forms the

408 anterolateral margin of the pineal foramen as in most post-Triassic ichthyosaurs

409 (Maisch & Matzke 2000). The pineal foramen preserves only its anterior portion,

410 missing the posteriormost margin. It opens dorsally with an anteriorly rounded outline

411 (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.

415 The postfrontal contacts the prefrontal anteriorly along a sinuous suture.

416 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

420 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.

428 A single tooth is still attached to the premaxilla but all other teeth were 429 recovered detached from the premaxilla, maxilla and dentary in the surrounding 430 sediment, the block revealing 10 detached teeth (Fig. 3). The crowns are narrow, 431 pointed, slender, recurved and rounded in cross section (Fig. 4). The enamel surface 432 bears no carinae and is unornamented. The root has the characteristic plicidentine 433 morphology with deep furrows on the external surface giving the typical cauliflower 434 outline in cross section. Roots are only slightly more than half the total length of the 435 tooth.

436

437 Ichthyosaur from the carbonate concretion. The second specimen (MHNL

438 20103364, Fig. 5) was discovered during the summer of 2012 when a trench on the

439 floor of the LafargeHolcim Val d'Azergues quarry was excavated thanks to heavy-

440 duty vehicles, allowing us to attain the lowest stratigraphic horizons available in the 441 quarry (Figs. 1a, 5a). As presented above, this specimen, together with other 442 carbonate concretions, originates from the base of the *serpentinum* ammonite zone. 443 The ichthyosaur specimen is contained in a large carbonate concretion measuring 444 about 50 cm in diameter. Breaks on its surface reveal an articulated skeleton with the 445 extremity of the rostrum at one end (Fig. 5c), and opposite, a paddle (Fig. 5b) and a 446 section in the thorax with articulated vertebral centra and ribs (Fig. 5d). The specimen 447 is curled around one side of the carbonate concretion and sectioned at the level of the 448 thorax, missing the tail. Nonetheless, the anterior part of the rostrum is sectioned and 449 shows several tooth roots; opposite the rostrum on the carbonate concretion, the 450 forefin is partly visible and displays at least four phalanges (Fig. 5b). The phalanges 451 are not in contact and possess rounded edges. Those characters are compatible with 452 the morphology of distal phalanges of stenopterygiids. The total body length of the 453 specimen cannot be precisely measured but may not have surpassed one meter. 454 Reddish to purple hues are observed within the rib cage and most likely represent 455 remnants of soft tissues (Figs. 5d, e, f), to be investigated in future work, for example 456 through X ray Computed Tomography in order to avoid destroying soft tissue during 457 preparation.

458

459 Discussion

460

461 Affinities of the new finds. Currently recognized Toarcian ichthyosaur genera

462 include Eurhinosaurus, Hauffiopteryx, Temnodontosaurus, Stenopterygius and

463 Suevoleviathan (e.g. McGowan 1979; Godefroit 1994; McGowan & Motani 2003;

464 Fischer et al. 2012; Caine & Benton 2012; Martin et al. 2012; Maxwell 2012; Moon

465 2017; Maxwell & Cortés 2020).

466 MHNL 20103062 does not preserve any postcranial elements, which are 467 prominent in ichthyosaur diagnoses (Maxwell 2012). Ichthyosaurs from the Posidonia 468 Shale are often preserved as flattened complete skeletons but details of their skull 469 anatomy may be obscured by compression. As a consequence, diagnostic characters 470 for species have been established on skull proportions and postcranial anatomy 471 (McGowan 1979) with species delineation relying mostly on postcranial proportions 472 (Maxwell 2012). Nevertheless, a number of cranial features can be compared with 473 other Jurassic forms and help constrain the affinities of MHNL 20103062.

474 MHNL 20103062 can be differentiated from the large predatory species of the 475 genus *Temnodontosaurus* in which the maxilla does not contribute into the ventral 476 margin of the external narial opening, in contrast to that of MHNL 20103062 (Fig. 4). 477 In toothed *Temnodontosaurus* species, the maxilla is excluded from the narial opening 478 by the subnarial process of the premaxilla contacting the lacrimal and jugal 479 (McGowan 1994; Maisch 1998a). In MHNL 20103062, the nasal does not contact the 480 parietal posteriorly, contrary to species of the genus Temnodontosaurus (Maxwell et 481 al. 2012; Ji et al. 2015). MHNL 20103062 can be differentiated from T. azerguensis 482 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*.

487 MHNL 20103062 can be differentiated from *Hauffiopteryx* based on the 488 absence of participation of the prefrontal in the external narial opening (see Maxwell 489 & Cortés, 2020). In addition, the pineal foramen is positioned between the 490 supratemporal fenestrae in MHNL 20103062; it opens anterior to the supratemporal 491 fenestrae in Hauffiopteryx. In Hauffiopteryx, the anterior margin of the supratemporal 492 fenestra consists of the parietal (not of the postfrontal as in MHNL 20103062); the 493 prefrontal is constricted between its lateral and medial parts in MHNL 20103062, but 494 of uniform width in *Hauffiopteryx*; the comparatively shorter rostrum of 495 Hauffiopteryx and its differential tooth size between fore and aft dentition, also differ 496 from MHNL 20103062 (Maisch 2008; Caine & Benton 2011; Marek et al. 2015; 497 Maxwell & Cortés 2020). 498 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).

505 Other Early Jurassic ichthyosaurs such as the genera *Ichthyosaurus* and 506 *Protoichthyosaurus* are distinct from MHNL 20103062, in that the tooth enamel in 507 these genera bears a strongly ridged ornamentation, unlike in MHNL 20103062. 508 These genera also have a medial process of the prefrontal contacting both the parietal 509 and frontal (see Lomax et al. 2020). This latter character is shared with the genus 510 Leptonectes (Fig. 2 in Maisch & Matzke 2003). In MHNL 20103062, the anterior 511 margin of the supratemporal fenestra consists of the postfrontal, without a large 512 contribution from the parietal (unlike in *Leptonectes* and *Wahlisaurus*: Maisch & 513 Matzke 2003; Lomax et al. 2018). In Leptonectes tenuirostris, the subnarial and 514 supranarial processes of the premaxilla are subequal in length (McGowan & Motani 515 2003: fig. 69).

516 MHNL 20103062 can be identified as a member of the genus *Stenopterygius* 517 on the basis of the following skull characters: In MHNL 20103062, the supranarial 518 process of the premaxilla is substantially shorter than the subnarial process (Figs. 3, 519 4), a condition shared with the genus Stenopterygius. Since the work of Maxwell 520 (2012), several species of Stenopterygius have been synonymized and we follow it, 521 recognizing the genus *Stenopterygius* as containing four European species, S. 522 quadriscissus, S. uniter S. triscissus, and S. aaleniensis, plus a South American one S. 523 cayi (Fernández 1994). MHNL 20103062 differs from some specimens of S. triscissus 524 (see specimen BRLSI M1409 studied by Caine & Benton 2011) in the lack of contact 525 between premaxilla and lacrimal; however note that this feature varies 526 intraspecifically in *Stenopterygius* (e.g., *S. triscissus*: compare Caine & Benton 2011: 527 text-fig.3; Godefroit 1994: fig. 19). Also, the absence of contact between nasal and 528 parietal contrasts with the state reported for some specimens of S. triscissus (Caine & 529 Benton 2011), but not for others (Motani 2005). The contact reported by Caine & 530 Benton (2011) is very thin in this juvenile specimen from Strawberry Bank; this 531 character is likely to be intraspecifically variable. The pineal foramen opens in 532 different ways among members of the genus *Stenoptervgius*: (1) the pineal foramen is 533 included between the supratemporal fenestrae; or (2) the pineal foramen opens just 534 anterior to the supratemporal fenestrae. MHNL 20103062, many Curcy specimens 535 (Mazin 1988 plate I; S. triscissus: NHMUK OR 33157(Caine & Benton 2011: text-536 fig. S3), Eudes-Deslongchamps 1877)) and an Ilminster S. triscissus specimen 537 (BRLSI M1409) (Caine & Benton 2011) all share condition (1). Some Holzmaden 538 Stenopterygius specimens in which the skull table is visible show condition (2) such 539 as in some specimens of S. quadriscissus (MHH 1981/33 or SMNS 55933) or S. 540 triscissus (SMNS 14846). Differences are also noted with S. aaleniensis, which 541 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).

547 The specimen from the large carbonate concretion is unprepared and cannot be 548 precisely identified beyond a tentative referral to Stenopterygiidae indet. based on the 549 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.

556

557 Ichthyosaur preservation during the T-OAE. Preservation of marine vertebrates in 558 Lower Jurassic carbonate concretions (as compiled in Table 1) is known at least since 559 the discovery of the Strawberry Bank Lagerstätte (Lower Toarcian of Ilminster, 560 Somerset) by Charles Moore in the late 1840s (Williams et al. 2015). This locality has 561 yielded carbonate concretions containing finely preserved ichthyosaur skeletons that 562 were studied much later (McGowan 1979) and only recently referred to 563 Stenopterygius triscissus and Hauffiopteryx typicus (Caine & Benton 2011; Marek et 564 al. 2015). Elsewhere, ichthyosaur skulls preserved in similar carbonate concretions

have subsequently been reported from the Toarcian of Luxembourg with

566 Stenopterygius (Godefroit 1994) and France including Temnodontosaurus burgundiae

567 from Sainte-Colombe in Burgundy (Gaudry 1892) and specimens from Curcy-sur-

568 Orne in Normandy (Dechaseaux 1954) including an acid prepared carbonate

569 concretion containing a skull connected to postcranial elements of *Stenopterygius*

570 (Mazin 1988). A 9-meter long complete individual of *Temnodontosaurus* (SMNS

571 50000) mostly preserved within a giant carbonate concretion was discovered from

572 horizon epsilon II₆ between Zell unter Aichelberg and Ohmden (Böttcher 1989).

573 Large carbonate concretions within the upper part of horizon epsilon II₄ yielded at

574 least two specimens on display at the Dotternhausen Museum including

575 Stenopterygius and Hauffiopteryx (Jäger 2005; Maxwell & Cortés 2020). A specimen

576 of Stenopterygius quadriscissus (SMNS 4789) is not technically speaking within a 577 concretion but hosts pyrite in the thoracic area and also originates from epsilon II₅ and 578 was selected for histological analysis (Anderson et al. 2018). Additional skulls and 579 fragmentary ichthyosaurian postcranial remains from the Holzmaden region preserved 580 in concretions are also present in regional collections. The difficulty in preparing 581 specimens from hard concretions partially accounts for the rarity of described 582 specimens in the literature originating from nodular beds and also the heavily lithified 583 epsilon II₅ level. In addition, Stenopterygius specimens in concretions do not typically 584 preserve enough of the skeleton to allow referral to species, which requires relatively 585 complete skeletons at present (but see S. aaleniensis in Maxwell et al. 2012). This 586 results in a perceived gap in the fossil record of species in the genus (e.g. Fig. 2 in 587 Maxwell 2012).

588 Williams et al. (2015) described the Strawberry Bank carbonate concretions as 589 biomicritic mudstones to packstones containing invertebrate bioclasts. Carbonate 590 concretions are often weathered to a yellowish colour, as is the surrounding sediment, 591 although originally, the unaltered deposits were blue-grey (Moore 1866) with high 592 organic content (Suan et al. 2013; Charbonnier et al. 2020). Under anoxic conditions, 593 the presence of organic matter in mudstone boosts the formation of concretions early 594 during diagenesis; microbial activity produces methane and carbon dioxide that 595 provide the basis for carbonate precipitation and nucleation (Raiswell 1988; Raiswell 596 & Fisher 2000; Marshall & Pirrie 2013). Within most Toarcian levels with organic-597 rich shales, specimens have undergone compaction and even if soft tissues have been 598 positively identified, their flatness hides many morphological features. The interesting 599 prospect is that levels with concretions are known within these organic-rich shales and 600 due to their early diagenetic implementation, hold the potential of preserving 601 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 II₁,

609 (*semicelatum* subzone) to epsilon II₈ (*elegans* subzone), with most soft-tissue

610 specimens originating from epsilon II₃–II₄ (Hauff 1921; Hofmann 1958; Keller 1992; 611 Martill 1993). A slightly broader stratigraphic range for soft tissue preservation was 612 presented by Heller (1966), including specimens from epsilon II₉ and epsilon II₁₀ 613 (falciferum subzone), suggesting that soft-tissue preservation, as concerns Toarcian 614 deposits, may not be limited to laminated black shales and the epsilon II₅ laminated 615 limestone. However, the best-preserved examples are from the laminated sediments. 616 Recent studies using geochemical, ultrastructural and molecular tools have helped 617 characterize the preservation of different soft tissue types from deposits of the 618 Posidonienschiefer Formation in SW Germany. As such, a carbonate concretion from 619 Dotternhausen containing an individual of Stenopterygius preserves structures 620 resembling collagen as well as red and white blood cells (Plet *et al.* 2017); another 621 Stenopterygius specimen preserved on a mudstone slab from the early Toarcian from 622 Kromer Shale Quarry near Ohmden shows integument likely preserving blubber, 623 melanophores as well as various lipids and proteins (Lindgren et al. 2018). 624 Our geochemical data (δ^{13} C and 87 Sr/ 86 Sr) help to constrain the stratigraphic 625 origin of the newly reported specimens. These data show that MHNL 20103062 626 comes from the middle part of the serpentinum ammonite zone, i.e. after the T-OAE 627 carbon isotope excursion (Fig. 2). This specimen is partly disarticulated and not 628 preserved in a carbonate concretion but at the base of a normally graded argillaceous 629 limestone bed likely corresponding to a tempestite (Suan et al. 2013). The preparation 630 of this specimen revealed a discontinuous, millimeter-sized crust of goethite covering 631 the stratigraphically lowermost surface of the bones as well as the sediment located 632 between the left and right premaxillae. This goethite crust, still partly visible as rust-633 coloured stains on and in between some bones in the prepared specimen (Fig. 3), 634 likely corresponds to a completely oxidized pyrite crust. Comparable pyrite coatings 635 described in some other Konservat Lagerstätten have been interpreted as a 636 consequence of microbial degradation of organic-rich tissues (Muscente et al. 2017). 637 The specimen therefore certainly did preserve soft tissues replaced by pyrite 638 (subsequently weathered into goethite). 639 The geochemical data indicate that the oldest ichthyosaur specimen reported 640 here and preserved in connection within a carbonate concretion was most likely 641 derived from the very base of the serpentinum ammonite zone (Fig. 2) within the 642 interval recording the T-OAE negative carbon isotope excursion. We highly suspect

643 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).

647 At the scale of a given locality, there seems to be no specific horizon yielding 648 complete specimens with soft tissues and a close examination of other similar (in age 649 and sedimentological characteristics) paleontological localities may confirm this 650 hypothesis. However, the occurrence of carbonate concretions containing marine 651 vertebrates seems to correspond to the T-OAE interval, and depending on the 652 thickness of the deposit as observed across European localities, several horizons with 653 carbonate concretions may be recovered during this particular environmental 654 perturbation. For example, the succession at LafargeHolcim Val d'Azergues quarry is 655 condensed and such carbonate concretions were predicted to occur in the lower part of 656 the serpentinum Zone, where the negative carbon isotope excursion is recorded. The 657 original collector at Strawberry Bank only described one such horizon, and though the 658 precise location of that quarry is enigmatic, this observation was corroborated by an 659 excavation in close proximity in 2019 led by MW. As for the historical locality of La 660 Caine, prospecting for carbonate concretions in the field will have to be undertaken. 661 In Belgium and Luxembourg, several marine reptile specimens have been reported 662 between the *tenuicostatum* and *serpentinum* ammonite zones (Godefroit 1994; 663 Vincent et al. 2019), but a more detailed placement against carbon isotope 664 stratigraphy established for this area (Ruebsam et al. 2016; Hermoso et al. 2014) 665 would deserve further geochemical investigations of host sediments. At Holzmaden, 666 the majority of the ichthyosaur fossil record stretches from epsilon II_1 to epsilon II_{10} , 667 which corresponds to a large interval encompassing periods before, within and after 668 the T-OAE (Maxwell & Vincent₇ 2016). Most of the Posidonia Shale facies in SW 669 Germany consist of bituminous shales: the occurrence of carbonate concretions is 670 reported from epsilon II₄, but most Toarcian ichthyosaurs from the Holzmaden area 671 are preserved as flattened skeletons from the bituminous shale. Therefore, putting 672 efforts into prospecting for marine vertebrates from nodular carbonate concretions of 673 the T-OAE, notably in the level corresponding to the upper portion of epsilon II₄, will 674 likely yield specimens preserved in volume, including soft tissues. Such a prospect is 675 particularly appealing because the anatomical organization of internal soft organs is 676 virtually unknown in ichthyosaurs and other marine reptiles of that age.

677

678 Early Jurassic evolution of ichthyosaurs in relation to the T-OAE. The youngest 679 ichthyosaur skeleton from the LafargeHolcim Val d'Azergues quarry is 680 Temnodontosaurus azerguensis from the base of the bifrons Zone, which is post-T-681 OAE. Here, we report stenopterygiids both within (base of serpentinum Zone) and 682 after (middle of *serpentinum* Zone) the negative carbon isotopic excursion of the T-683 OAE. The T-OAE initiates near the limit of the *tenuicostatum* - *serpentinum* zones 684 (Fig. 2). The oldest occurrence of the genus Stenopterygius has been recorded from 685 epsilon I₂ level in Germany (Maxwell 2012), which corresponds to the base of the 686 tenuicostatum zone. This suggests that Stenopterygius was already present just before 687 the T-OAE. In SW Germany, Stenopterygius is particularly abundant in epsilon II₃ 688 level (Maxwell 2012), i.e. the top of the *tenuicostatum* zone, which corresponds to the 689 onset of the T-OAE. Bottom anoxic conditions are ideal to preserve marine faunas 690 and this may explain the abundance of marine vertebrates preserved as complete 691 skeletons from this lower Toarcian interval (Ulrichs et al. 1994). Marine vertebrates 692 from the Toarcian of Yorkshire are equally abundant and finely preserved in 693 bituminous shales within the falciferum subzone (Benton & Taylor 1984). Benton & 694 Taylor (1984) state that the German fauna is older than the Yorkshire fauna, and a 695 falciferum subzone for the Yorkshire fauna indicates that this marine assemblage is 696 post-T-OAE. Ilminster specimens from the 'saurian and fish bed' are preserved in 697 carbonate concretions collected from the *exaratum* subzone (Williams *et al.* 2015), 698 which corresponds to the level that yielded the presently described carbonate 699 concretion from Beaujolais containing the ichthyosaur specimen (MHNL 20103364). 700 The carbonate concretion with the nicely preserved ichthyosaur from Curcy/La Caîne 701 in Normandy comes from the serpentinum Zone, else known as the "Argiles à 702 poissons" (Mazin 1988) but more precise stratigraphic details are unknown. Another 703 nice skull preserved in volume (NHMUK PV OR 33157) comes from Curcy in 704 Normandy and was originally mentioned and figured by Owen (1849) and by Caine & 705 Benton (2011). Marine reptile discoveries from Belgium and Luxembourg were 706 mostly recorded from the serpentinum Zone, exaratum subzone (Godefroit 1994). 707 With the onset of the T-OAE, marine life experienced a major environmental 708 perturbation with a well-documented impact on the invertebrate fauna (Little & 709 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 710 711 extinction of marine vertebrates during the T-OAE (Vincent et al. 2013), it was

712 statistically demonstrated that ichthyosaur body size was impacted (Maxwell & 713 Vincent 2016). The rich fossil record from the Holzmaden area shows that the most 714 recent levels of the *serpentinum* Zone contain the largest known specimens of the 715 genus Stenopterygius (Maxwell & Vincent 2016) as well as the oldest known records 716 of Suevoleviathan. The long skull of MHNL 20103062 (< 60 cm) and its stratigraphic 717 position within the middle levels of the *serpentinum* Zone are consistent with these 718 observations. The largest *Stenoptervgius* specimens from Germany have a skull length 719 of 72 cm for S. uniter, 67 cm for S. triscissus and 56 cm for S. quadriscissus (Maxwell 720 & Vincent 2016). The Posidonia Shale has yielded hundreds if not thousands of 721 vertebrate specimens, and indeed provides an ideal context to run such quantitative 722 diversity analyses, but the impact of the T-OAE on marine faunas can be studied 723 further elsewhere, contextualizing the fossil record with precisely dated occurrences, 724 thanks to its apparent wide extension across Europe and also globally (Martindale et 725 al. 2017).

726 Pre-T-OAE vertebrate fossils are important to understand marine diversity 727 change in relation to the environmental perturbation of the Toarcian. For example, an 728 apparent turnover can be identified between 'Lower Liassic' and 'Upper Liassic' 729 ichthyosaur faunas (Hungerbühler & Sachs 1996), but growing evidence supports this 730 turnover occurring in the Pliensbachian. During the Toarcian, *Stenopterygius* is the 731 most abundant genus and seems to be the ecomorphological equivalent of the 732 Pliensbachian genera *Ichthyosaurus* and *Leptonectes*. The youngest stratigraphically 733 constrained occurrences of Ichthyosaurus are from the lower Pliensbachian strata of 734 the UK (Lomax & Massare 2015; Massare & Lomax 2016); the youngest constrained 735 records of Leptonectes are also from the lower Pliensbachian (L. moorei from the UK 736 and more fragmentary remains attributable to *Leptonectes* from the UK, Belgium, 737 Spain, and SW Germany: Fraas 1892 [see Maisch 2010]; Godefroit 1992; Fernández 738 et al. 2018, McGowan & Milner 1999; Lomax & Massare 2018). The upper 739 Pliensbachian specimen previously referred to Leptonectes (Maisch & Reisdorf 2006) 740 has been reinterpreted as *Hauffiopteryx*, a genus best-documented from the Toarcian 741 (Maxwell & Cortés 2020). An ischiopubis from the early-middle Liassic of the UK, 742 cited by some authors as the earliest occurrence of *Stenopterygius* (McGowan 1978; 743 Hungerbühler & Sachs 1996), is inconsistent with the Toarcian representatives of this 744 genus based on the posteromedial orientation and large size of the obturator foramen, 745 and incomplete lateral fusion between the ischium and pubis (McGowan 1978: pl.

746 2.3). As stated above, the occurrence of *Stenopterygius* in lowermost Toarcian strata

- 747 (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
- 750 identifications with a number of historical finds having been attributed to
- 751 Leptopterygius von Huene 1922, a now obsolete genus name, which encompassed the
- 752 different genera Leptonectes, Suevoleviathan and Temnodontosaurus. The
- 753 Pliensbachian ichthyosaur record is poor and essentially originates from the lowest
- revels. Further sampling of this interval is important to understand evolutionary
- 755 patterns during the Early Jurassic.
- 756

757 Conclusions

758

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

768 ichthyosaurs are apparently already represented by the genus Stenopterygius. This

requires a precise stratigraphic and taxonomic context for each fossil individual to berecorded.

771 The taxonomy of Lower Jurassic ichthyosaurs is in critical need of a revision 772 and several taxa may be synonymous. Despite numerous recent efforts (e.g. Lomax & 773 Massare 2015; Maxwell & Cortés 2020), differences between Leptonectes and 774 Stenopterygius are tenuous and ichthyosaur diversity may have been overlooked in a 775 number of cases that still need to be identified. If Pliensbachian and Toarcian 776 ichthyosaur faunas are homogeneous, then the impact of the T-OAE on these faunas 777 remains minimal and an explanation of what triggered this faunal transition is still 778 required.

779

Finally, we emphasize that the study of nodular carbonate concretions might

780 reveal important information about soft tissue preservation, including the preservation 781 of organs in three dimensions. As concerns marine vertebrates, this could correspond 782 to a major advance to better understand the palaeobiology of these extinct animals and 783 the adaptations of tetrapods from terrestrial to marine environments. Multidisciplinary 784 approaches, such as that proposed in this work combining palaeontology, 785 sedimentology and chemostratigraphy shall provide a solid framework to finely track 786 the impact of environmental changes on marine vertebrates on both short- and long-787 term timescales. As an example, renewed field efforts can be directed at historical 788 localities (e.g. La Caine or Strawberry Bank) that yielded exquisitely preserved

- 789 specimens but where a detailed stratigraphic framework is lacking.
- 790 791

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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-,

1153 bio- and chemostratigraphic features. Data for LafargeHolcim Val d'Azergues quarry 1154 from this study and Suan et al. (2013). Data for Dotternhausen from Bailey et al. 1155 (2003) and Suan et al. (2015). Epsilon levels from Hauff (1921) and Röhl et al. 1156 (2001). 1157 1158 Fig. 3. Photograph (a) and drawing (b) of the left lateral side of the skull of (MHNL 1159 20103062) Stenoptervgius sp. from the Toarcian of Beaujolais. Abbreviations: en, 1160 external nares; for, foramen; fr, frontal; iff, interfrontal foramen; ju, jugal; la, lacrimal; 1161 lac. sut., lacrimal suture; mx, maxilla; p, parietal; pfr, prefrontal; pif, pineal foramen; 1162 pmx, premaxilla; pof, postfrontal; qj, quadratojugal; sr, sclerotic ring; t, teeth. [Full 1163 page width] 1164 1165 Fig. 4. Isolated tooth of Stenopterygius sp. (MHNL 20103062) from the Toarcian of 1166 Beaujolais in labial or lingual (a, b), mesial or distal (c, d) and basal (e) views. [Full 1167 page width] 1168 1169 Fig. 5. The nodular concretion (MHNL 20103364) (a) as recovered during fieldwork 1170 with * corresponding to (b), articulated phalanges; ** corresponding to (c), anterior tip of the rostrum with arrows corresponding to teeth in section; and *** 1171 1172 corresponding to (d), section through the rib cage showing ribs and gastralia (arrows) 1173 delimiting an internal zone of purple hue suspected of representing oxidized organic 1174 matter together with close-ups (not to scale) of the purple hue within sediment (e) and 1175 around gastralia (f). Abbreviations: c, centrum; ga, gastralia. [Full page width] 1176 1177 Table 1. List of early Toarcian localities with ichthyosaur-bearing carbonate 1178 concretions (AZ = Ammonite Zone). 1179 Supplementary Data. Geochemical dataset used in the present study including bulk 1180 1181 sediment inorganic and organic carbon isotope composition (δ^{13} C) and radiogenic 1182 strontium isotope (⁸⁷Sr/⁸⁶Sr) values of belemnites.











Sheet1

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

Sheet1

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
<i>bifrons</i> or <i>variabilis</i> AZ	post T-OAE	Reisdorf et al. 2011
Base of serpentinum AZ	within T-OAE	this study

Lafarge Beaujolais								
sample ID	Preservation	Composite height (m)	CaCO3 (wt. %)	TOC carb. free IRMS (wt.%)	SD	TOC (wt.%) IRMS	δ 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	1
DV03-2	Non-weathered	0.46	69.34	8.94		2.74	-30.88	1
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	<u> </u>
L 03	Non-weathered	2.90	27.37	3.42		2.48	-28.39	<u> </u>
L 04	Non-weathered	3.00	29.00	3.08		2.19	-28.93	<u> </u>
L 05	Non-weathered	3.10	31.75	2.89		1.97	-28.80	<u> </u>
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	<u> </u>
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					1
CHI-10	Weathered	0.40	26.24					1
CHI-11	Weathered	0.47	73.12		•			
CHI-12	Weathered	0.53	75.49					
CHI-13	Weathered	0.62	8.19					1
CHI-14	Weathered	0.70	12.37					1
CHI-15	Weathered	0.78	12.58					1

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			

δ 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)
0.10			2010	Suan et al. (2013)
-0.42	-4 82		2009	Suan et al. (2013)
0			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)
0.02	0.11		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
_3.78	_5 70		2011	This study
-3.20	-5.19		2011	This study
_2 21	_/ 3/		2011	This study
-3.31	-4.34		2011	This study
-1.97	-4.07		2011	This study
-2.19	-9.42		2011	This study
-2.09	-5.50		2011	This study
-1.40	-0.10		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
0.96	-2.50 -3.27		2009 2009	This study Suan et al. (2013)
0.96 -1.49 -1.19	-2.50 -3.27 -3.08		2009 2009 2009	This study Suan et al. (2013) Suan et al. (2013)
0.96 -1.49 -1.19 -1.25	-2.50 -3.27 -3.08 -4.48		2009 2009 2009 2009	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013)
0.96 -1.49 -1.19 -1.25 -0.80	-2.50 -3.27 -3.08 -4.48 -2.40		2009 2009 2009 2009 2009 2009	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013)
0.96 -1.49 -1.19 -1.25 -0.80 -1.85	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23		2009 2009 2009 2009 2009 2009 2009	This study Suan et al. (2013) Suan et al. (2013)
0.96 -1.49 -1.19 -1.25 -0.80 -1.85 -3.88	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23 -4.18		2009 2009 2009 2009 2009 2009 2009 2012	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) This study
0.96 -1.49 -1.19 -1.25 -0.80 -1.85 -3.88	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23 -4.18		2009 2009 2009 2009 2009 2009 2009 2012	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) This study
0.96 -1.49 -1.19 -1.25 -0.80 -1.85 -3.88	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23 -4.18	0.7071010	2009 2009 2009 2009 2009 2009 2012 2011	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) This study This study
0.96 -1.49 -1.19 -1.25 -0.80 -1.85 -3.88	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23 -4.18	0.7071010 0.7071948	2009 2009 2009 2009 2009 2009 2012 2011 2011	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) This study This study This study
0.96 -1.49 -1.19 -1.25 -0.80 -1.85 -3.88	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23 -4.18	0.7071010 0.7071948 0.7071911	2009 2009 2009 2009 2009 2009 2012 2011 2009 2009	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) This study This study This study This study
0.96 -1.49 -1.19 -1.25 -0.80 -1.85 -3.88	-2.50 -3.27 -3.08 -4.48 -2.40 -2.23 -4.18	0.7071010 0.7071948 0.7071911 0.7072229	2009 2009 2009 2009 2009 2009 2012 2011 2009 2009	This study Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) Suan et al. (2013) This study This study This study This study This study