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The Early Jurassic ichthyosaur *Stenopterygius* in the collections of the Museo di Scienze della Terra, Università di Catania (Italy)

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KEY WORDS - "Bonaventura Gravina" Collection, Ichthyosauria, Stenopterygius*, Early Jurassic, Toarcian, Southern Germany.*

ABSTRACT - The "Bonaventura Gravina" Collection of the Earth Science Museum of Catania (Italy) includes an ichthyosaur specimen of unknown geographic and stratigraphic provenance, age, and taxonomic determination. On comparison with other fossils from the same collection it was established that the specimen is from Böll, southwestern Germany; the ammonites preserved on the same slab indicate an early Toarcian age. Based on the available information it is suggested that it comes from the Early Jurassic Posidonia *Shale* (Posidonienschiefer)*, which is known worldwide for its ichthyosaur remains. A morphological comparison with Toarcian ichthyosaurs allowed the fossil remains to be referred to an adult specimen of* Stenopterygius*, a mid-sized ichthyosaur genus common in the Toarcian of Southern Germany. The phylogenetic analysis by parsimony supports this conclusion.*

RIASSUNTO - [L'ittiosauro *Stenopterygius* del Giurassico Inferiore nelle collezioni del Museo di Scienze della Terra dell'Università di Catania (Italia)] - *La provenienza geografica e stratigrafica, l'età e la tassonomia di un esemplare di ittiosauro conservato nella collezione "Bonaventura Gravina" del Museo di Scienze della Terra dell'Università di Catania erano ignote. L'esemplare studiato è presente in due lastre, una contenente resti del cranio e della mandibola, l'altra un segmento di colonna vertebrale e alcuni elementi scheletrici degli arti posteriori. Dal confronto con altri fossili dalla stessa collezione è stato possibile stabilire che i reperti provengono da Böll nel Baden-Württemberg (Germania sudoccidentale). Gli ammoniti conservati sul retro della lastra documentano la specie* Dactylioceras tenuicostatum *(Young & Bird, 1822) ed indicano un'età Toarciano inferiore. Resti del bivalve* Bositra *sono pure presenti. L'associazione di* D. tenuicostatum *e* Bositra *è tipica della formazione nota come "*Posidonia *Shale"* (Posidonienschiefer) *del Giurassico Inferiore, conosciuta in tutto il mondo per aver fornito numerosi resti di ittiosauri in un eccezionale stato di conservazione. Lo studio morfologico e il confronto con altri generi di ittiosauri del Toarciano hanno permesso di attribuire i reperti presenti nel Museo di Catania ad un esemplare adulto di* Stenopterygius*, un ittiosauro di taglia media comune nel Toarciano della Germania meridionale. L'analisi filogenetica conferma tale attribuzione.*

INTRODUCTION

Ichthyosaurs were marine reptiles with a global distribution from the Early Triassic (Olenekian) to the Late Cretaceous (late Cenomanian) (Motani, 1999, 2005). They were the sauropsids with the best adaptation to an aquatic lifestyle, possessing paddle-like limbs and hydrodynamic body morphology convergent with that of the tunniform osteichthyes in some derived forms (Motani, 1999; Sander, 2000). The "Bonaventura Gravina" palaeontological Collection of the Museo di Scienze della Terra of the Università di Catania consists of several hundred fossils donated to the University by Baron Bonaventura Gravina, a famous sicilian agronomist, just before his death in 1891 (Di Geronimo & Sciuto, 2004). Among the most outstanding specimens in the collection are two slabs of dark gray to blackish slate, each preserving partial ichthyosaur skeletal remains.

Unfortunately, all information about the acquisition, provenance, age and taxonomic determination of the material housed in the museum are missing. The original labels associated with the fossils are heavily damaged and largely unreadable.

The aim of this work is to assess the provenance and the age of these slabs, and to establish the identity of the ichthyosaur remains preserved inside.

MATERIAL AND METHODS

Two blackish slabs ("a" and "b"), some decimeters wide, are stored under the number MSTC 316467 (Figs 1-2). They preserve ichthyosaur bones and some bivalves and ammonites. The MSTC 316467a slab preserves part of the skull and lower jaws, while the MSTC 316467b slab preserves a segment of the axial skeleton, and some elements of the hind limbs as reported in Fig. 3. MSTC 316467 have been compared to other fossils in the collection to find those preserved on a similar type of rock. Samples of rock from both MSTC 316467 slabs and from other specimens with an apparently similar lithology have been analysed under the binocular microscope and compared to each other to confirm the belonging to the same lithotype. Finally, we investigated the labels associated to the fossils to assess the locality of provenance. Biostratigraphic support for the provenance of the ichthyosaur was also attempted.

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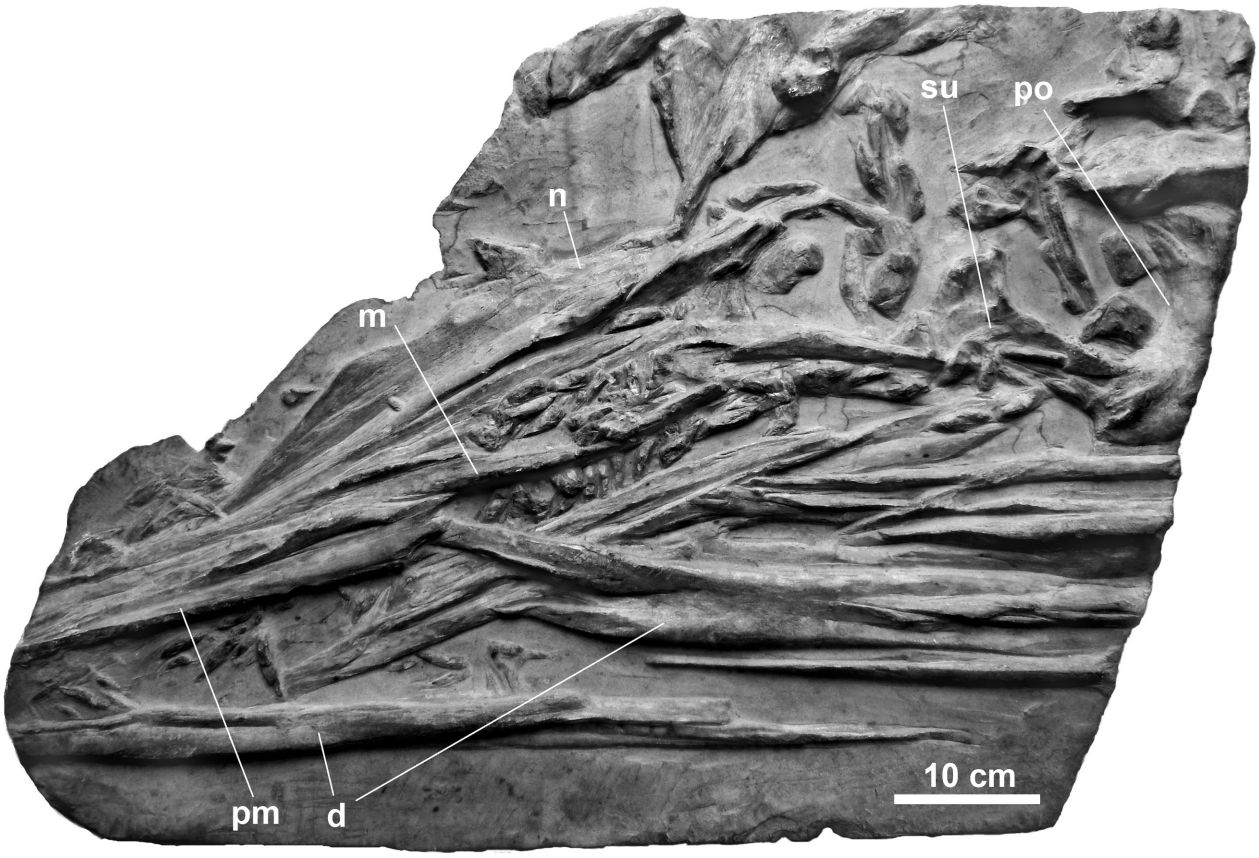

Fig. 1 - Slab MSTC 316467a preserving the skull and lower jaw bones of an adult specimen referable to *Stenopterygius* (Jaekel). Abbreviations: n, nasal; m, maxilla; pm, premaxilla; d, dentary; su, supratemporal; po, postorbital. Scale bar is 10 cm.

Although it is common for ichthyosaur specimens from the *Posidonia* Shale to be mounted on slabs of 'fleins' from other stratigraphic provenance for display (Maxwell, pers. comm.), the close examination of the slabs listed above confirmed that this is not the case.

Systematics used in this paper follow Motani (1999) adapted to the nomenclatural revision proposed by Maisch (2008) for *Stenopterygius* taxonomy. In order to test the phylogenetic affinities of the ichthyosaurian specimens described herein, we entered an Operational Taxonomic Unit (OTU) based on MSTC 316467 in a modified version of the data matrix of Maxwell et al. (2012), which differs for the inclusion of MSTC 316467 and the exclusion of the Aalenian species investigated in that study, *Stenopterygius aaleniensis* Maxwell, Fernàndez & Schoch, 2012. The data matrix used in Maxwell et al. (2012) allows to construct the most recent phylogenetic analysis focusing on species-level relationships of Early Jurassic ichthyosaurs thus

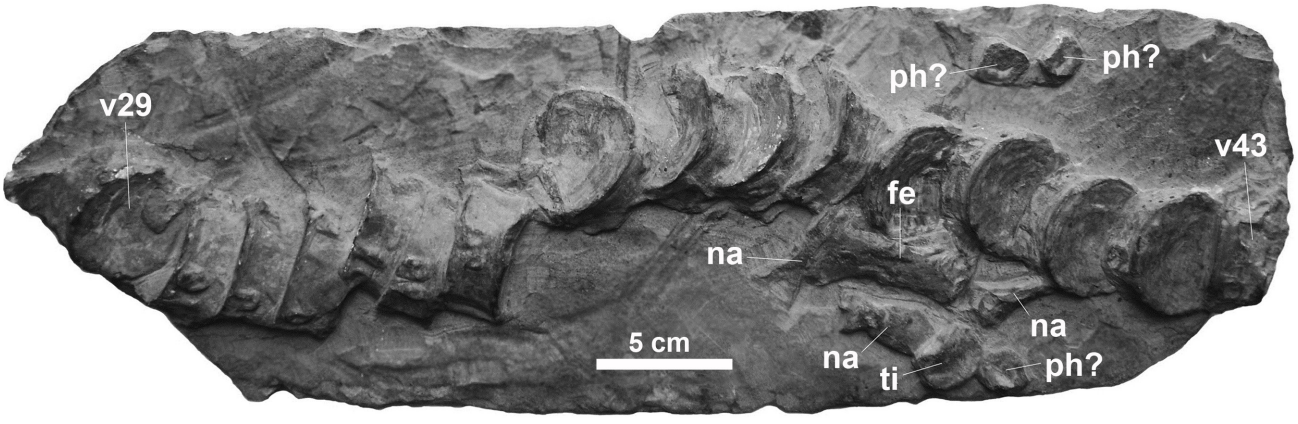

Fig. 2 - Slab MSTC 316467b containing elements of the axial skeleton and limbs of an adult specimen referable to *Stenopterygius* (Jaekel). Abbreviations: fe, femur; na, neural arch; ph?, undetermined phalanx; ti, tibia; v, vertebral series. Scale bar 5 cm.

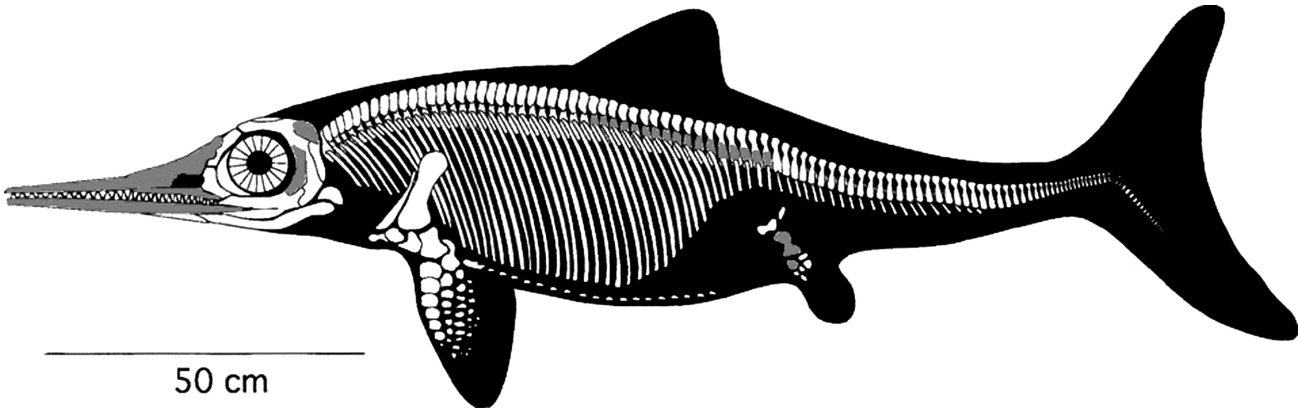

Fig. 3 - Skeletal reconstruction and body outline of MSTC 316467. In white, the missing elements. Modified from Sander (2000).

the more suitable to test the phylogenetic relationship of MSTC 316467. For more information on the phylogenetic analysis, see Maxwell et al. (2012). Character state codings for MSTC 316467 added to the data matrix of Maxwell et al. (2012) are: 2000????????????????????0 ???1??????????????????????????1??

The original data matrix used by Maxwell et al. (2012) is available at the link below:

www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0041692.s006la.

To test if both slabs bear the same specimen (or at least to the same species), two different OTUs, each with the codings of the ichthyosaur material contained in a single slab, were entered in the data matrix. The phylogenetic analysis by parsimony was run with TNT vers. 1.0 (Goloboff et al., 2008), while TreeView 1.6.6. (Page, 1996) was used to visualise the cladograms.

Ichthyosaur specimens from museums in Germany, which contain the largest and best sampled collections of *Stenopterygius* fossils (MHH, SMNS), and which have been studied by former authors to investigate the systematic and paleobiology of this taxon, could not be examined firsthand, so relevant data have been taken from the available literature (Maisch, 2008; Maxwell, 2012).

Institutional abbreviations - MHH, Museum Hauff, Holzmaden, Germany; MSTC, Museo di Scienze della Terra of the Università di Catania, Catania, Italy; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

PROVENANCE AND AGE

The fossil was purchased by Baron Bonaventura Gravina during the 19th century. The specimens were piled up in an attic, where humidity caused serious damages to the collection and in particular to the original labels (Sciuto & Campisi, 2000). The damaged labels from the back side of both slabs show some characters (W, ü, r) that, after comparison with MSTC 316466, a slab preserving an ammonoid from the same collection with a label reporting "Boll Würtemberg" [sic] as provenance, have been recognised as the same inscription. Böll is a town in Baden-Württemberg (SW Germany) close to the locality of Holzmaden that is famous for its fossil vertebrates and invertebrates preserved in the Early Jurassic *Posidonia* Shale (*Posidonienschiefer*; Oschmann, 1999; Grossmann, 2007). The *Posidonia* Shale of the Holzmaden area is one of the main sources of ichthyosaur remains in the world (e.g., Martill, 1993).

The back side of the slabs MSTC 316467 contains the same ammonoids preserved in MSTC 316466, which can be referred to *Dactylioceras tenuicostatum* (Young & Bird, 1822) (Giulio Pavia, pers comm. 2011; Fig. 4), the marker of the Tenuicostatum Zone (lowermost lower Toarcian).

The *Posidonia* Shale encompasses the Tenuicostatum-Bifrons ammonite zones (Riegraf et al., 1984). The slabs preserve also several shells of the pelagic pelecypod *Bositra* (Fig. 5), which was once known as *Posidonia*, and is the fossil defining the ichthyosaur-bearing unit of the Holzmaden area (Wild, 1990).

Finally, the slab MSTC 316465, which has a black shaly lithology similar to that of MSTC 316467, contains remains of the crinoids *Seirocrinus,* another common fossil in the *Posidonia* Shale of the Holzmaden area (Simms, 1986).

SYSTEMATIC PALAEONTOLOGY

Order Ichthyosauria de Blainville, 1835
Parvorder Merriamosauria Motani, 1999
Microorder Parvipelvia Motani, 1999
Division Neoichthyosauria Sander, 2000
Subdivision Thunnosauria Motani, 1999
Family Stenopterygiidae Woodward in von Zittel, 1932

Genus *Stenopterygius* Jaekel, 1904

Type species - *Stenopterygius quadriscissus* (Quenstedt, 1856)

Stenopterygius sp.

Material - MSTC 316467a and MSTC 316467b slabs.

Description - The cranial remains contained in the slab MSTC 316467a (Fig. 1) comprise both premaxillae, the left maxilla, the left dentary and a portion of the right

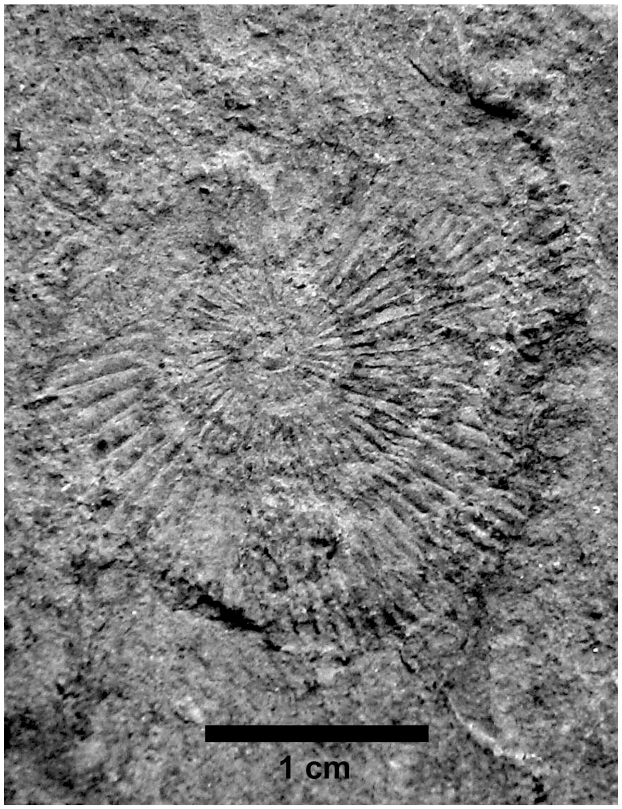

Fig. 4 - *Dactylioceras tenuicostatum* (Young & Bird, 1822), ammonite contained in the back side of MSTC 316467a.

one, many teeth, the right nasal, the left postorbital, the left supratemporal, and some sclerotic bones. The slab includes several overlapping cranial bone shards and fragments too incomplete to be identified. The left premaxilla overlaps the right one, hampering the description of the latter. Premaxillae are elongated, the preserved portion being 18 cm long and three cm high at the point where the bone bifurcates caudally in dorsocaudal and ventrocaudal processes that border the rostral margin of the external naris. The ventral margin of the processus subnarialis is broken. The maxilla is long and thin, without a prominent dorsal process. The ventral border is straight. The body of the maxilla does not increase in size caudally. The deepest point of the bone is at mid-length. The right nasal is exposed in dorsal view, showing a flat dorsal surface all along its extent, a straight medial margin without any trace of an internasal foramen and a sinuous lateral surface.

The exact morphology of the external naris is difficult to describe given the fragmentary and disarticulated nature of the material. However, the nasal ends caudally in a small caudolaterally oriented wing-like processus narialis. Caudally to this process, there is a quite straight border ascending caudodorsally that should represent the suture between the nasal and the lacrimal/prefrontal complex. Caudally the nasal ends in a thin supraorbital process, overlapped by bits of unidentified bones. A thick, ventrally wide, and "C" shaped postorbital is present near the circumorbital area, which also contains some scleral plates. There is a thin tetraradiate supratemporal dorsal to this area, showing a long ventral process. The dentary is broken in two pieces; some teeth are still present along the dentary margin. The dentary, which lacks its rostralmost tip, is long and thin, widening in dorsoventral length caudally to almost double in size the rostralmost width. Teeth are poorly preserved; the best is 23 mm long apicobasally, with slight apicobasal striations but without mesial and distal carinae. It lacks a clear constriction at the base of the crown.

The segment of vertebral column preserved in the second slab (MSTC 316467b, Fig. 2) consists of 16 centra and a few incomplete neural arches. The centra are amphicoelous and discoidal with a characteristic "ashtray" shape. The centra are 20-25 mm long, 60-65 mm high, and 45-50 mm wide. There is no contact between the diapophyses and the dorsal margin of the centra. The diapophyses and parapophyses are separated and appear as circular bumps on the lateral side of the centrum in most of the vertebrae, but they merge into a singular articular surface in the last three vertebrae. The left femur and tibia and at least three phalanges are preserved. The femur is exposed in dorsal view, parallel to the long axis of the vertebral column with its head pointing caudally. It is 67 mm long, 34 mm wide proximally, and 38 mm wide distally. It is constricted in its mid-section with a distal end distinct from the diaphysis, and is as wide distally as the proximal end. The tibia is a bean-shaped, rostrally notched element that is preserved close to the femur and is one third of its length. The damaged pedal phalanges occur close to the femur and tibia.

Remarks - The slabs containing the ichthyosaur bones are mounted together on a wood support. The labels associated with them, even though seriously damaged and largely unreadable, contain some characters (W, ü, r), located in specific positions, that are congruent with those of the complete inscriptions found in better preserved labels from other specimens in the same collection. This allowed to recognize the locality's name as "Böll Württemberg". A previous taxonomic determination as "*Ichthyosaurus*" can be also reconstructed from the labels where some letters are still visible, that are compatible with this name writing, in both slabs constituting MSTC 316467. The back of both slabs shows the same mollusk association. In addition, sections taken from both slabs

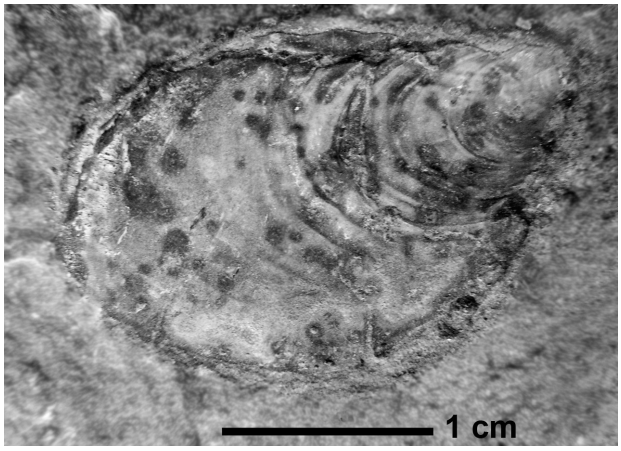

Fig. 5 - *Bositra* sp., bivalve contained in the back side of MSTC 316467a.

show the same type of lithology, confirming the belonging to the same stratigraphic horizon. The bones preserved in both slabs show the same type of preservation. These observations, considered in addition to the complementary nature between the content of the slabs (there are cranial bones in one slab and postcranial material in the other) suggest that the skeletal material could belong to the same species or even to the same specimen, although being preserved in two separate slabs.

Five ichthyosaur genera have been reported from the Lower Jurassic of Central Europe: *Suevoleviathan* Maisch, 1998, *Temnodontosaurus* Lydekker, 1889*, Eurhinosaurus* Abel, 1909, *Hauffiopteryx* Maisch, 2008 and *Stenopterygius* Jaekel, 1904. The latter one is represented by three Toarcian species: *Stenopterygius uniter* (von Huene, 1931)*, S. triscissus* (Quenstedt, 1856), and *S. quadriscissus* (Quenstedt, 1856). Attributed to the latter genus are also other species from younger layers and/or outside the Tethydean Bioprovince: *Stenopterygius cayi* (Fernández, 2007) from the Bajocian of Argentina and a newly described Aalenian species from Germany, *S. aaleniensis* (Maxwell et al., 2012).

Stenopterygius is a historically notorious fossil reptile, famous for the dead pregnant females associated with embryos (Böttcher, 1990; Deeming et al., 1993).

The premaxillae of MSTC 316467 are long and slender, as in *Stenopterygius,* and very different from the moderately robust premaxillae of *Temnodontosaurus* and *Suevoleviathan,* and the extremely slender rostrum of *Eurhinosaurus* that is several times longer than the postorbital skull length. The maxilla is a tiny splint of bone, contrary to the more prominent morphology observed in *Temnodontosaurus,* which has a maxilla constituting about half of the dental margin (McGowan, 1994: fig. 2).

The lower jaw is also prominent, being as long as the preserved portion of upper jaw, and unlike the reduced lower jaw in *Eurhinosaurus*.

The nasal has a caudolaterally oriented wing-like processus narialis that borders the caudodorsal margin of the external naris, as described in a specimen assigned to *Stenopterygius* cf. *quadriscissus* (Maisch & Ansorge, 2004). The supratemporal is slender, unlike *Hauffiopteryx* where it is a prominent bone (Caine & Benton, 2011). The tooth crowns are conical, with unornamented to slightly ridged enamel as in *Stenopterygius* (Maisch, 2008; Maxwell, 2012). Teeth in MSTC 316467 also lack carinae, unlike in *Temnodontosaurus* (Fraas, 1891; von Huene, 1922; McGowan, 1979; Maisch & Matzke, 2000) and show unexpanded roots and crowns without the characteristic "bumped" ornamentations found in *Suevoleviathan* (Maisch, 1998, 2010). Although longitudinal striations of the crowns are seldom reported in *Stenopterygius* specimens, this feature is considered diagnostic for *S. uniter* by Maisch (2008) contra Maxwell (2012), which points out that slightly ridged teeth are present in some large individuals of *S. quadriscissus*.

The vertebral anatomy of MSTC 316467 more closely resembles *Stenopterygius* and *Hauffiopteryx* than the other taxa. In *Temnodontosaurus*, the merging of parapophysis and diapophysis starts around the 3rd cervical vertebra (McGowan & Motani, 2003), while in MSTC 316467 the merging occurs close to the pelvic region, a pattern observed in *Stenopterygius* (McGowan & Motani, 2003; Maxwell et al., 2012). This merging position indicates that the preserved vertebral string is the segment of the dorsal vertebral column just cranial to the pelvic region, probably representing the 29th to the 45th vertebrae. This configuration is very similar to the pattern described for *S. aaleniensis* by Maxwell et al. (2012) and is consistent with the morphology described for *Stenopterygius* (Buchholtz, 2001). The femur resembles that of *Stenopterygius* in having a mid constricted shaft and a proximal end as wide as the distal one, unlike the femora in *Eurhinosaurus* and *Temnodontosaurus*, which have distal ends twice as wide as the proximal one (Maisch & Matzke, 2000: figs 26-27). In addition, the tibia is one third the femur length, as in *Stenopterygius*, while it is proportionally longer in *Eurhinosaurus* and *Temnodontosaurus*, being half the femur length in the latter genera (McGowan & Motani, 2003).

Maisch (2008) recognized the absence of teeth in adult individuals as a diagnostic character distinguishing between *Stenopterygius uniter* and *S. triscissus* from the edentulous once adult *S. quadriscissus*. However, as noted by Maxwell (2008), tooth size reduction and eventual loss of dentition is not a constant feature in this genus, as there are adult individuals of *S. quadriscissus* (SMNS 16811; Maxwell, 2012) that clearly had functional teeth.

Maxwell (2012) devised a metric scheme for distinguishing the species of *Stenopterygius* from the early Toarcian of southwestern Germany, recognizing three valid species: *S. quadriscissus*, *S. triscissus*, and *S. uniter*. Nevertheless, the suggested criteria are extremely difficult to apply to disarticulated specimens like those herein described, in which both the anterior and posteriormost portions of the rostrum and most of the hind limbs are missing, and the preserved elements are damaged.

Thus, the shape and proportions of the cranial bones, the morphology of the vertebrae, and the morphology of the appendicular elements support the assignment to *Stenopterygius*.

Confident of the morphometric data reported by McGowan (1973) and Maxwell (2012), given the preserved dentary portion of 300 mm in length, to which the missing postdentary portion and rostralmost tip of the bone must be added, we estimate a total length of 400-600 mm for the lower jaw of MSTC 316467.

The femur is 67 mm long, close to the upper size limit reported for *Stenopterygius triscissus* in the sample analyzed by Maxwell (2012; SMNS 14846: femoral length of 76 mm for a skull length of over 600 mm and total body length up to 350 cm) and approaching the largest specimen reported for *S. quadriscissus* (MHH 1981/33: femoral length of 77 mm for a jaw length of 702 mm and a total body length approximately 350 cm). In these samples, *S. triscissus* and *S. quadriscissus*, reached a rostrocaudal length around 350 cm, while *S. uniter* was the biggest species reaching 400 cm in length (SMNS 57532: femoral length of 82 mm for a jaw length of 702 mm). McGowan (1979) stated that the average body length of an adult *Stenopterygius* is 300-350 cm, reporting mature specimens of *S. quadriscissus* with jaw length of 405 mm. Thus, we estimate a total body length for MSTC 316467 at around this dimensional range and consider the specimen to be a mature individual.

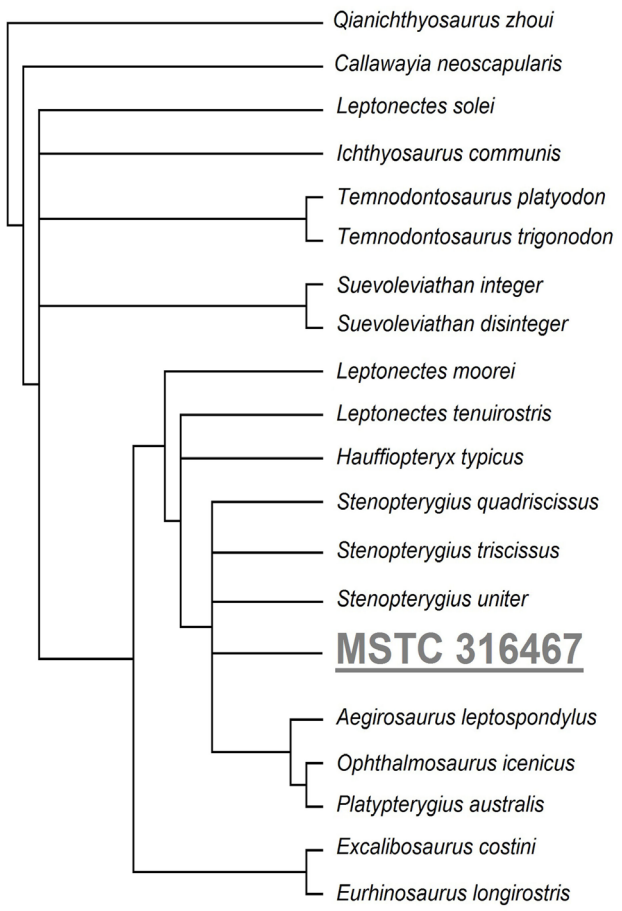

Fig. 6 - Strict consensus of the shortest trees recovered by the phylogenetic analysis, showing the relationships of MSTC 316467 among Lower Jurassic ichthyosaurs.

The phylogenetic analysis by parsimony recovered 27 shortest trees of 137 steps each (Consistency Index = 0.4964; Retention Index = 0.5036). The strict consensus of the 27 shortest trees recovered (Fig. 6), was in agreement with previous phylogenetic hypotheses (Maxwell et al., 2012).

Accordingly, the details of the resulted topology are not discussed here. Relevant to the aim of this study, a polytomy between all the *Stenopterygius* species was obtained, including MSTC 316467. When MSTC 316467 is codified as two different OTUs (one for each slab), the resulting topology concerning *Stenopterygius* consists in a sister group relationship between the cranial and the postcranial OTUs and the other *Stenopterygius* species, a result supporting the interpretation discussed above that assumes the two bone sets of MSTC 316467 as belonging to the same species of *Stenopterygius* (and probably even to the same specimen). As discussed throughout the text, the lack of a complete and articulated skull and hind limbs material does not permit the referral of MSTC 316467 to any of the known Toarcian species of *Stenopterygius.*

On the other hand, the association of *Seirocrinus*, *Bositra* and *D. tenuicostatum* strongly suggests that the material originates from the top of the Tenuicostatum Zone (*Dactylioceras semicelatum* subzone, the point of maximum abundance of *S. quadriscissus* [Riegraf et al., 1984; Röhl et al., 2001; Caswell et al., 2009; Maxwell, 2012]). Given that the first appearance of *Stenopterygius uniter* is not until the *Harpoceras falciferum* subzone (Maisch, 2008; Maxwell, 2012), this taxon can probably be ruled out as a possibility.

CONCLUSIONS

The ichthyosaur remains from the Museo di Scienze della Terra of the Università di Catania come from Böll (Baden-Württemberg, Germany). Their stratigraphic provenance is from the *Posidonia* Shale and more precisely from the lower Toarcian Tenuicostatum Zone. The morphological comparison with the five Early Jurassic genera *Eurhinosaurus*, *Temnodontosaurus*, *Suevoleviathan*, *Hauffiopteryx,* and *Stenopterygius* points to a referral to the latter taxon.

The specimen is represented by two slabs containing different sets of non-overlapping bones. The phylogenetic analysis by parsimony supports referral to *Stenopterygius* and is consistent with the interpretation of the two slabs as pertaining to the same specimen. Nevertheless, the scarcity of diagnostic elements prevents the assignment of MSTC 316467 to any of the known Toarcian *Stenopterygius* species.

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