Temnodontosaurus and *Stenopterygius* (Diapsida: Ichthyosauria) specimens in the Comiso Natural History Museum (Sicily, Italy)

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Abstract. The paleontological collection of the Comiso Natural History Museum (Sicily, Italy) includes two ichthyosaurian specimens from the Lower Jurassic Posidonia Shale (southwestern Germany). Based on comparative morphology, we refer them to *Temnodontosaurus* and *Stenop-terygius* both common genera in the Toarcian of Southern Germany.

Keywords: Ichthyosauria, Stenopterygius, Temnodontosaurus, Early Jurassic, Southern Germany.

INTRODUCTION

Ichthyosaurs were fish-shaped marine reptiles from the Mesozoic Era (252-66 million years ago; Motani, 1999; Motani, 2005) known since the early XIX century (Home, 1814) and made famous between scholars thanks to the sampling work by Mary Anning (McGowan, 1991). Ichthyosaurs were characterized by relatively large orbital fenestrae, hyperdactyly and hyperphalangy in the pectoral and pelvic fins, dorsal fin lacking a bony support, and heterocercal caudal fin (Motani 1999; McGowan & Motani, 2003), resulting in a body plan well-adapted to an aquatic environment (Carroll, 1988). The paleontological collection of the Comiso Natural History Museum includes two ichthyosaurian specimens coming from the *Posidonia* Shale Formation (Posidonienschiefer), a Toarcian (Early Jurassic) unit cropping out from southern Germany, notoriously known for the exceptionally preserved fossils of both vertebrate (fishes, ichthyosaurs, plesiosaur and several archosaurs) and invertebrates (bivalves, belemnoids, ammonites, crustaceans and crinoids) species, which are collected and sold to different collections all over the world (e.g., Martill, 1993).

MATERIALS AND METHOD

A blackish slab, stored as MSNC 4410/76, contains the remains of a moderately large ichthyosaur (4-6 m) exposed on one side of the slab (Fig. 1), and some traces of ammonites and bivalves on the opposite side (Fig. 2). The second specimen MSNC 4410/77 (Figs. 3, 4, 5) is a three dimensionally preserved ichthyosaur, including the skull and the lower jaw, cervical vertebrae and part of the pectoral girdle. No skeletal remains posterior to the pectoral girdle are preserved. The matrix of MSNC 4410/77 contains shells of bivalves (Fig. 6). Biostrati-

graphic support for the dating of the ichthyosaurs was also attempted and a morphological comparison with the known Toarcian ichthyosaur genera was attempted to identify the two specimens.

RESULTS

Biostratigraphy

The back side of the slab of specimen MSNC 4410/76 contains some traces of ammonites and bivalves. The ammonite is referred to *Harpoceras falcifer* (Sowerby, 1820) for the planispiral and partly involute shell in which the width of the last whorl increases suddenly, being about two and a half times higher than the previous whorl. In the shell, ribbing is very fine and falcoid; the umbilicus is relatively narrow and deeper with marked umbilical edge (Bendik, 2012). *Harpoceras falcifer* is the marker of the Falcifer Ammonoid Zone (middle lower Toarcian) (Riegraf et al., 1984). The bivalves show a concentric outer ornamentation and are referred to the pelagic pelecypod *Bositra*, once known as *Posidonia*, the fossil defining the ichthyosaur-bearing unit of the Holzmaden area (Wild, 1990). The specimen MSNC 4410/77shows an abundance of fossil shells referred to *Bositra* but lacks any trace of ammonite imprints, hampering a precise assignment to one of the Ammonoid Zones recognized in the *Posidonia* Shale.

Osteology

Specimen MSNC 4410/76 - Osteological remains from MSNC 4410/76 comprise the posterior portion of the left premaxilla, both nasals (lacking the anterior portions), prefrontals, postfrontals, scleral ossicles, right postorbital, right quadratojugal, right quadrate, right jugal, right squamosal, posterior portions of both right surangular and right angular, left supratemporal, both scapulae, vertebral column up to the 23rd vertebra with associated ribs, elements from the pectoral girdle and forefin. The posterior portion of the premaxilla shows a robust and triangular subnarial process, more elongated than the supranarial process, both bordering the ventral, the anterior and the anterodorsal margin of the external naris. The nasal fails to expand posteriorly and lacks a prominent wing-like process bordering dorsoposteriorly the external naris (as seen in Temnodontosaurus; Fischer et al., 2011). Posteriorly, the nasal diverges laterally creating a space that accommodates some fragment of the frontal. Fragments of both prefrontals are present, dorsoventrally thick and bordering the dorsal rim of the orbit. The frontal is preserved still in articulation with the nasal, showing a right angle articulation. Four scleral ossicles are present in articulation, wider dorsoventrally than anteroventrally. The postorbital is C shaped as is usual for ichthyosaurs (McGowan & Motani, 2003), slightly thicker both dorsally and ventrally, and maintaining a constant width along its entire extent. The posterior portion of the jugal is preserved, with a bowed dorsal margin, ventrally bordering the orbit and a wide quadrangular postorbital process. A roughly trapezoidal quadratojugal is fragmented into a ventral and a dorsal portion, articulating anteriorly with the postorbital. The quadrate is partially covered by the matrix and the proximal end of the left scapula, hampering the description of the whole element. From what can be observed it looks triangular in outline with a slightly concave anterior margin and an anterodorsally wide ventral process. The squamosal is triangular. There is a rectangular parietal, slightly curved laterally and three



Fig. 1 – MSNC 4410/76, ichthyosaur remains from the Lower Jurassic of Southern Germany attributed to *Temnodontosaurus*. Abbreviations: a, angular; ar, articular; bo, basioc-cipital; c, clavicle; j, jugal; lf, left frontal; ln, left nasal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; rf, right frontal; rn, right nasal; rsc, right scapula; sa, surangular; sq, squamosal; st, supratemporal; lsc, left scapula; sr, elements of the scleral ring; st, supratemporal; r, ribs; ph, phalages; vc, vertebral column; scale bar equals 5 cm.



Fig. 2 – ammonite from MSNC4410/76. It is referred to *Harpoceras falcifer* (Sowerby, 1820) that is the marker of the Falcifer Ammonoid Zone (middle lower Toarcian); the scale bar equals 1 cm.

time longer then wide. The supratemporal is massive, with the prefrontal process thicker than the parietal process, reciprocally oriented at 90°. The basioccipital includes an oval and robust occipital condyle and a wide extracondylar area mostly evident ventrally to the occipital condyle. A ventral longitudinal furrow runs along the extracondylar area. The posterior portion of the lower jaw is preserved, with the posterior portions of both angular and surangular still in articulation, covering laterally the articular, which is still set underneath the quadratojugal. The surangular is rather tall, with a prominent coronoid process. The angular is almost as wide dorsoventrally as the surangular, contributing to a relatively deep posterior end of the lower jaw. The articular is wider dorsoventrally than it is anterodorsally. A series of 23 vertebrae is preserved in articulation posterior to the skull. A fused atlas-axis complex is preserved. The suture between the two elements is more evident along the dorsolateral surface. The anteroventral margin of the atlas is blunt and reaches the ventralmost point at the ventral border of the entire complex, a morphology suggesting that the atlantal intercentrum is fused with the rest of the complex. The complex increases its height posteriorly in its anterior half, then it suddenly decreases posteriorly forming some sort of hump. All the remaining vertebrae have their lateral surfaces worn out and filled by matrix, the latter preserving the morphology of the centra and showing the costal articulations. The articular facets for the rib are well separated from each other, as shown by circular and well-spaced parapophyses and diapophyses and by dicephalous ribs at least up to the 12th vertebra. Some elements of the pectoral girdle are pre-



Fig. 3 – MSNC 4410/77, a specimen of small to middle-sized (1-3 m long) ichthyosaur from the Lower Jurassic of Southern Germany in lateral view. It is here referred to *Stemopterygius* sp. Abbreviations: a, angular; d, dentary; en, external naris; j, jugal; l, lacrimal; m, maxilla; n, nasal; pm, premaxilla; sa, surangular; sr, sclerotic ring; the scale bar equals 5 cm.



Fig. 4 – MSNC 4410/77 in ventral view. Abbreviations: c, clavicle; lar, left articular; ld, left dentary; lh, left hyoid; lsa, left surangular; pas, parasphenoid; rar, right articular; rd, right dentary; rh, right hyoid; r, ribs; rsa, right surangular; sc, scapula; vc, vertebral column: the scale bar equals 5 cm.





Fig. 6 - shell in MSNC 4410/77 referred to the pelagic pelecypod Bositra; the scale bar equals 1 cm.

served in the slab: both scapulae and a fragmentary clavicle. The scapula is strap-like with a wide proximal end lacking a pronounced acromial process.

Specimen MSNC 4410/77 - The skull of MSNC 4410/77 comprises premaxillae, maxillae, nasals, frontals, jugals, sclerotic bones, lacrimals, supratemporal, parasphenoid, dentaries, surangulars, angulars, articulars, hyoids, vertebrae, clavicles and a scapula. The premaxilla is elongate and bifurcates posteriorly into a dorsal and a ventral processes of same length, and bordering anteriorly the external naris. The conjoined nasals meet anteriorly at an acute angle, widening posteriorly, reaching the maximum width above the external naris. The nasals expand posterolaterally into wing-like processes, and posteriorly embrace the frontal along its anterolateral margin. The frontal sends a long nasal process anteriorly and borders the pineal foramen posteriorly. The maxilla is long and thin. The jugal is slightly deeper dorsoventrally than the maxilla, with a rounded orbital margin. It bears a dorsally straight lacrimal margin and a slightly wider quadratojugal process. The lacrimal is thin, with a rounded jugal process bordering dorsoventrally the orbit and a wider dorsal process conferring to the bone a triradiate shape. The dentary is thin, with a posterior process widely overlying the surangular. It occupies most of the dorsoventral extent of the caudal end of the lower jaw, covering most of the angular, which is long and thin, approaching anteriorly half the length of the surangular. The articular is exposed ventrally, still in articulation with the surangular-angular complex: it is box-shaped, mediolaterally wider than it is anteroventrally long. A thin parasphenoid is evident on the ventral side of the skull. In ventral view, some fragmented long and thin bones are preserved caudally to the parasphenoid, probably representing the hyoids. All the teeth are

missing from the dentigerous margin of the jaw, with the exception of a single tooth (Fig. 7) encased along the anteror margin of the right premaxilla. It is broken transversally, with a circular outline, lacking carinae and showing a faint apicobasally oriented ornamentation. The clavicles are long and joined medially, with a distinct ventral expansion to accommodate the interclavicle. The scapula is strap-like with an expanded fan-shaped proximal end, and a well pronounced acromial process. The third cervical vertebra is caudally exposed, showing a pentagonal outline. The remaining cervical centra are exposed dorsally showing the neurocentral articular facets.

DISCUSSION

Both ichthyosaur specimens herein described come from the Lower Jurassic of Central Europe, a paleobioprovince that has yielded to date five ichthyosaurian genera: *Suevoleviathan* Maisch, 1998, *Temnodontosaurus* Lydekker, 1889, *Eurhinosaurus* Abel, 1909, *Hauffiopteryx* Maisch, 2008 and *Stenopterygius* Jaekel, 1904. The premaxillae of MSNC 4410/76 are robust like in *Temnodontosaurus* and *Suevoleviathan*, differing from the relatively longer and slender rostra in *Stenopterygius*, *Eurhinosaurus* and *Hauffiopteryx*. In addition, the specimen MSNC 4410/76 shows the following combination of synapomorphies that is diagnostic of *Temnodontosaurus* (following the analysis in Fischer et al., 2011): the nasal lacks a well pronounced descending process on the dorsal border of the nares (character state 6.0); the nasal lacks a *processus temporalis* for the frontal (12.0); the squamosal is triangular in shape (14.0); the quadratojugal has extensive exposure (15.0); the basioccipital has a wide extracondylar area (17.0); the angular has extensive lateral exposure, so that it covers almost half of the dorsoventral



Fig. 7 – tooth encased along the rostral margin of the right premaxilla in MSNC 4410/77; the scale bar equals 1 cm.

depth of the caudal portion of the lower jaw (22.1); the scapula lacks a prominent acromion process (28.0). Furthermore, the relative robustness of the nasals, the jugal and the lower jaw exclude the identification as Temnodontosaurus azerguensis (Martin, Fischer, Vincent and Suan 2012). In addition, the features reported above, and in particular the deep lower jaw, allows the assignment of the specimen to Temnodontosaurus trigonodon (Theodori, 1843), a mediumto large-sized (up to 9 m in length) nektonic predator common in the Lower Jurassic of central Europe (mainly Germany and northern France; McGowan & Motani, 2003). The premaxilla in MSNC 4410/77 is relatively longer and less robust than in *Temnodontosaurus* but not as delicate as in Eurhinosaurus; and shows subequal caudodorsal and caudoventral processes as in *Stenopterygius.* The presence of a descending process of the nasal bordering dorsocaudally the external nares (character state 6.1 in Fischer et al., 2011) is shared by specimens assigned to Stenopterygius cf. quadriscissus (Quendstedt, 1856; see Maisch & Ansorge, 2004). Lateral exposure of the angular is minimal (character state 22.0) as in *Stenopterygius* and *Hauffiopteryx*; the scapula shows a prominent acromion process (28.1) as in *Stenopterygius*. The parietal foramen is surrounded almost entirely by the frontals, as in Stenopterygius (differing from Suevoleviathan and Temnodontosaurus, a feature shared with Hauffiopteryx; Maxwell et al., 2012). The maxilla is long and thin, as in *Stenopterygius*, contrary to the robust morphology in *Tem*nodontosaurus, which bears a maxilla constituting about half of the dental margin (McGowan, 1994: fig. 2). The lower jaw is not strongly reduced (unlike Eurhinosaurus; McGowan & Motani, 2003). The teeth are small with smooth enamel, as in *Stenopterygius* (a feature shared with Eurhinosaurus and Hauffiopteryx; Maisch, 2008; Maxwell, 2012), but clearly differing from the heavy ridged and labiolingually compressed *Temnodontosaurus* teeth (Fraas, 1891; von Huene, 1922; McGowan, 1979; Maisch & Matzke, 2000). The maxilla extends as far posteriorly as the lacrimal (a feature present in all species of *Stenopterygius*). The posterior edge of the external narial opening shows minimal dorsal deflection, as in Stenopterygius quadriscissus, S. triscissus, and S. uniter (Maxwell et al., 2012). Given the combination of character discussed, we are confident in assigning MSNC 4410/77 to the genus Stenopterygius. Given the lack of ammonites in the slab, and so in the absence of a biostratigraphic support for the dating of the specimen, and lacking the proper morphometric information to distinguish between different species of *Stenopterygius* (as devised by the metric scheme described in Maxwell, 2012), we cannot go under the genus level and assign MSNC 4410/77 to Stenopterygius sp.

CONCLUSIONS

The ichthyosaur remains from the Comiso Natural History Museum come from the Lower Jurassic of Southern Germany. MSNC 4410/76 comes from the Falcifer Ammonoid Zone (middle lower Toarcian), while we cannot infer a more precise biostratigraphic position for MSNC 4410/77, given the lack of ammonite remains associated with the ichthyosaur bones. The morphological comparison with the five Early Jurassic genera *Eurhinosaurus*, *Suevoleviathan*, *Hauffiopteryx*, *Stenopterygius* and *Temnodontosaurus*, points to a referral to the latter taxon for MSNC 4410/76 and more precisely to the species *T. trigonodon*, and to *Stenopterygius* for MSNC 4410/77, restored in Fig. 8.

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Fig. 8 – *Temnodontosaurus* and *Stenopterygius* digital restoration by paleoartist Fabio Manucci, scuba diver (-2 m long) as scale bar.

RIASSUNTO

Temnodontosaurus e *Stenopterygius* (Diapsida:Ichthyosauria) nel museo di Storia naturale di Comiso (Sicilia, Italia)

La collezione paleontologica del Museo di Storia Naturale di Comiso (Ragusa) include due esemplari di ittiosauri, rettili mesozoici adattati alla vita acquatica, provenienti dalla formazione degli Scisti a Posidonia. Questa unità stratigrafica, risalente al Toarciano (Giurassico inferiore), affiora nel Sud-Ovest della Germania, ed è nota per gli esemplari fossili splendidamente conservati di vertebrati (pesci, ittiosauri, plesiosauri e arcosauri) e invertebrati (bivalvi, belemniti, ammoniti, crostacei e crinoidi). Gli esemplari di ittiosauri della collezione del Museo di Storia Naturale di Comiso comprendono una lastra con resti del cranio, del cinto pettorale e della colonna vertebrale di un ittiosauro di medie dimensioni (MSNC 4410/76), un esemplare comprendente porzioni di cranio e scheletro assiale, conservato tridimensionalmente di minori dimensioni (MSNC 4410/77). L'associazione di molluschi (ammoniti e bivalvi) conservati nella prima lastra ha permesso di collocare biostratigraficamente l'esemplare nel Toarciano medio-inferiore (Zona ad Harpoceras falcifer), mentre l'assenza di ammoniti nel secondo esemplare non permette di risalire più in dettaglio nella datazione, riferita al Toarciano. Sulla base di comparazioni morfologiche con i taxa noti di ittiosauri del Giurassico inferiore europeo, è stato possibile attribuire i resti contenuti nella lastra al genere Temnodontosaurus, un macropredatore nectonico di dimensioni medio-grandi, mentre i resti del secondo individuo sono stati riferiti al genere Stenopterygius, predatore nectonico generalista di dimensioni medio-piccole. Nel presente studio è inclusa una ricostruzione dei due esemplari.

REFERENCES

- Abel O. (1909). Cetaceenshldien. I. Mitteilung: Das Skelett von *Eurhinodelphis cocheteuxi* aus dem Obermiozan von Antwerpen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften*, 118: 241-253.
- Bendík A. (2012). Ammonite fauna of subfamily Harpoceratinae Neumayr, 1875 from Jurassic Janovky and Adnet formations in the Velká Fatra Mts. (Central Slovakia). *Mineralia Slovaca*, 44: 285-294.

Carroll R.L. (1988). Vertebrate Paleontology and Evolution: W.H. Freeman and Company, New York, 251-260 pp.

- Fischer V., Masure E., Arkhangelsky M.S., Godefroit P. (2011). A new Barremian (Early Cretaceous) ichthyosaur from western Russia. *Journal of Vertebrate Paleontology*, 31: 1010-1025.
- Fraas E. (1891). Ichthyosaurier der süddeutschen Trias- und Jura- Ablagerungen. 81 pp. H. Laupp, Tübingen.
- Home E. (1814). Some account on the fossil remains of animal more nearly to fishes than any other class of animals. *Philosophical Transactions of the Royal Society*, 101: 571–577.
- Huene F.V. von (1922). Die Ichthyosaurier des Lias und ihre Zusammenhänge. 114 pp. Verlag von Gebrüder Borntraeger, Berlin.
- Jaekel O. (1904). Eine neue Darstellung von Ichthyosaurus. Zeitschrift der deutschen geologischen Gesellschaft, 56: 26-34.
- Lydekker R. (1889). Palaeozoology: Vertebrata. *In* Nicholson H.A. & Lydekker R. (ed.), A manual of palaeontology for the use of students with a general introduction on the principles of palaeontology. W. Blackwood: 889-1474.
- Maisch M.W. (1998). A new ichthyosaur genus from the Posidonia Shale (Lower Toarcian, Jurassic) of Holzmaden, SW-Germany with comments on the phylogeny of post-Triassic ichthyosaurs. *Neues Jahrbuch für Geologie und Paläontologie*, 209: 47-78.
- Maisch M.W. & Ansorge J. (2004). The Liassic ichthyosaur Stenopterygius cf. quadriscissus from the lower Toarcian of Dobbertin (northeastern Germany) and some considerations on lower Toarcian marine reptile palaeobiogeography. Palaontologische Zeitschrift, 78: 161-171.
- Maisch M.W. & Matzke A.T. (2000). The Ichthyosauria. Stuttgarter Beiträge zur Naturkunde Geologie und Paläontologie, 298: 1-159.
- Maisch M.W. (2008). Revision der Gattung Stenopterygius Jaekel, 1904 emend. von Huene, 1922 (Reptilia: Ichthyosauria) aus dem unteren Jura Westeuropas. Paleodiversity, 1: 227-271.
- Martill D.M. (1993). Soupy substrates: a medium for exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia*, 2: 77-97.
- Martin J.E., Fisher V., Vincent P., Suan G. (2012). A longirostrine *Temnodontosaurus* (Ichthyosauria) with comments on Early Jurassic niche partitioning and disparity. *Palaeontology*, 55: 995–1005.
- Maxwell E.E. (2012). New metrics to differentiate species of *Stenopterygius* (Reptilia: Ichthyosauria) from the Lower Jurassic of Southwestern Germany. *Journal of Paleontology*, 86 (1): 105-115.
- Maxwell E.E., Fernàndez M.S. & Schoch R.R. (2012). First diagnostic marine reptile remains from the Aalenian (Middle Jurassic): a new ichthyosaur from southwestern Germany. *PLoS ONE*, 7 (8): e41692.
- McGowan C. (1979). A revision of the Lower Jurassic ichthyosaurs of Germany with description of two new species. *Paleontographica*, 166: 93-135.
- McGowan C. (1991). Dinosaurs, Spitfires, and Sea Dragons. Cambridge, Harvard University Press, 365 pp.
- McGowan C. (1994). Temnodontosaurus risor is a juvenile of Temnodontosaurus platydon (Reptilia: Ichthyosauria). Journal of Vertebrate Paleontology, 4: 427-479.
- McGowan C. & Motani R. (2003). Ichthyopterygia *In* Sues H.D. (ed.), Handbook of Paleoherpetology, Verlag Dr. Friedrich Pfeil: 1-175.
- Motani R. (1999). Phylogeny of the Ichthyopterygia. Journal of Vertebrate Paleontology, 19: 472-495.
- Motani R. (2005). True skull roof configuration of *Ichthyosaurus* and *Stenopterygius* and its implications. *Journal of Vertebrate Paleontology*, 25: 338-342.
- Quenstedt F.A. (1856). Der Jura. H. Laupp, Tubingen, pp. 842.
- Riegraf W.V., Werner G. & Lorcher F. (1984). Der Posidonienschiefer. Biostratigraphie, Fauna und Fazies des südwestdeutschen Untertoarciums (Lias ε). *Ferdinand Enke*, Stuttgart, pp. 195.
- Sowerby J. (1820). The Mineral conchology of Great Britain. Taylor, London, 3: 254-271.
- Theodori C. (1843). Uebet einen kolossalen Ichthyosaurus trigonodon. Gelehrte Anzeigen der Koeniglich Bayerischen Akademie der Wissenschaften, München, 16: 906-911.
- Wild R. (1990). Holzmaden. In Briggs D.E.G. & Crowther P.R. (eds), Palaeobiology: a Synthesis, Blackwell Science: 282-285.