

The first ophthalmosaurid ichthyosaur from the Upper Jurassic of the Umbrian–Marchean Apennines (Marche, Central Italy)

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(Received 10 November 2015; accepted 4 May 2016; first published online 11 July 2016)

Abstract – The first ophthalmosaurid ichthyosaur from the Upper Jurassic deposits of the Central–Northern Apennines (Marche, Italy) is here described for the first time. The specimen is relatively complete and is referred to *Gengasaurus nicosiai* gen. et sp. nov. based on a unique combination of characters, including a peculiar condition of the preaxial accessory facet on the humerus. The faunal association of the ichthyosaur-bearing level indicates a late Kimmeridgian – earliest Tithonian age, and its finding contributes significantly to our knowledge of the diversity of Late Jurassic ichthyosaurs from the Western Tethys. Two shark teeth assigned to the order Hexanchiformes were also recovered in association with the ichthyosaur specimen, suggesting that scavenging of the carcass might have occurred. *Gengasaurus* can be referred to Ophthalmosauridae based on the reduced extracondylar area of the basioccipital, and the presence of a preaxial digit. It differs from *Ophthalmosaurus* spp. in several respects, including the shape of the posterior basisphenoid, the shape of the supraoccipital, the anteriorly deflected preaxial facet of the humerus, and a proximodistally shortened ulna. The new taxon actually shares diagnostic characters with both members of the two main lineages recovered in previous phylogenetic analyses, more nested within Ophthalmosauridae. The affinities of *Gengasaurus* to genera from both the northern and southern hemispheres also suggest that connectivity between pelagic habitats was high during the early Late Jurassic, allowing dispersal of some forms, followed by local, endemic divergence.

Keywords: Ophthalmosauridae, Jurassic, Western Tethys, Apennines, hexanchiform teeth.

1. Introduction

Ichthyosaurs were highly specialized marine reptiles, with a fish-like shape that facilitated rapid dispersal in an aquatic environment. First appearing in the Early Triassic, ichthyosaurs quickly achieved a global distribution, including the successful colonization of high-latitude habitats (Sander, 2000). In Europe, the Middle Triassic locality of Monte San Giorgio on the Swiss–Italian border, and Early and Middle Jurassic sites in the UK and Central Europe have particularly well-documented ichthyosaur faunas (Sander, 2000). However, Late Jurassic Southern European ichthyosaur occurrences are substantially less well documented relative to those of South America (reviewed by Fernández, 2007), Svalbard (e.g. Druckenmiller *et al.* 2012; Roberts *et al.* 2014) and Russia (reviewed by Storrs, Arkhangelsky & Efimov 2000), and there is a relative paucity of knowledge of the ichthyosaur fauna from the Western Tethys.

Diagnostic Late Jurassic ichthyosaur remains from Europe have been documented from the UK (Kimmeridge Clay; Tithonian), the Solnhofen Formation (Fm.) (Germany; Tithonian), and also the Kim-

meridgian of France (in urgent need of taxonomic reappraisal) (reviewed by Lennier, 1887; Kirton, 1983; Bardet & Fernández, 2000). Reports of more fragmentary remains, mostly referred to *Ophthalmosaurus* sp., span the Oxfordian–Tithonian interval of both the UK and Central Europe (Sauvage, 1902; Bardet, Corral & Pereda-Suberbiola, 1997; Danise, Twitchett & Matts, 2014). In this context, new localities, especially from the Southern European Tethyan margin, promise to be particularly informative.

With the exception of the Triassic Lagerstätte of Monte San Giorgio, the Italian fossil record of ichthyosaurs is particularly poor, and usually consists of a few disarticulated elements. Sirotti & Papazzoni (2002) described some Early Cretaceous remains from the Northern Apennines, south of Modena and Bologna; another rostrum belonging to *Platypterygius* sp. has recently been reported in Fornaciari *et al.* (2014) from the Lessini Mountains, near Verona, and a few vertebrae are reported from the Triassic of Sicily (Dal Sasso *et al.* 2014) and the Southern Alps (reviewed by Balini & Renesto, 2012). A few bone fragments, including two ribs and a partial rostrum belonging to ichthyosaurs, have been found on Monte Nerone (Apecchio, Pesaro Urbino, Marche, Italy) (I.P., pers. obs.), but the material is still undescribed.

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During the summer of 1976, a largely complete ichthyosaur specimen was discovered near Genga (Ancona, Marche, Italy) in an Upper Jurassic outcrop of the Marche Apennines.

After more than 20 years, a suitable location for the specimen was found at the Abbey of San Vittore di Genga, where it was finally prepared, and where it is still part of the exhibition. This specimen is probably one of the most complete ichthyosaur fossils ever found in Italy, and is the first Jurassic ichthyosaur from the Apennines, but since its discovery only a few studies have discussed the material, and none has dealt with its taxonomic affinities (Fastelli & Nicosia, 1980; De Marinis & Nicosia, 2000; Marino & Sacchi, 2002; Tintori *et al.* 2005). The history of this fossil has always been problematic, mainly because of the authorities' lack of attention to palaeontological findings (De Marinis & Nicosia, 2000).

During the Late Jurassic, the Umbrian–Marchean realm was characterized by pelagic deposition, and the sea-floor was dotted with numerous structural highs and lows, derived from the fragmentation and drowning of the pre-rifting Early Jurassic carbonate platform (e.g. Centamore *et al.* 1971; Farinacci *et al.* 1981; Santantonio, 1993, 1994). The ichthyosaur specimen comes from the 'Calcari ad aptici e Saccocoma' Fm. *sensu* Galluzzo & Santantonio (2002), and, based on the association of micro- and macrofossils (belemnites, aptychi, calpionellids and crinoids), it has been dated to the late Kimmeridgian – earliest Tithonian.

Here we describe the Genga ichthyosaur for the first time, and undertake detailed comparisons with other ophthalmosaurid ichthyosaurs.

2. Geological setting

2.a. The Jurassic of the Umbrian–Marchean Succession

In order to refine the stratigraphic position of the ichthyosaur, a detailed geological survey has been performed in the area, supported by palaeontological and microfacies analyses. The ichthyosaur was discovered near Genga (Ancona, Marche, Italy), in a small village called Camponoecchio, on the right side of the Esino River (Fig. 1). The specimen was embedded in Upper Jurassic pelagic deposits of the Umbrian–Marchean Succession (UMS) (Fig. 2), involved during the Neogene–Quaternary in the fold-and-thrust propagation of the Apenninic Chain (e.g. Centamore *et al.* 1971; Galluzzo & Santantonio, 2002; Scrocca, Doglioni & Innocenti 2003). The sedimentary succession starts with Hettangian–Sinemurian p.p. peritidal platform carbonate (Calcare Massiccio Fm.), followed by Lower Jurassic – Miocene pelagites and hemipelagites. The superposition of pelagic deposits on shallow water carbonates is due to an extensional tectonic phase which affected the Western Tethys during the Early Jurassic (see Centamore *et al.* 1971; Farinacci *et al.* 1981; Santantonio, 1993, 1994). This rifting stage related to the open-

ing of the Ligurian–Piedmont Ocean, dismembered the vast Calcare Massiccio carbonate palaeoplatfom and caused a complex submarine palaeotopography, consisting of structural highs and lows (e.g. Centamore *et al.* 1971; Farinacci *et al.* 1981; Santantonio, 1993, 1994). Tectonic subsidence caused the drowning of the hangingwall-block carbonate factories around the Hettangian–Sinemurian boundary, while horst-block factories drowned in the early Pliensbachian, also due to palaeoceanographic perturbation (Morettini *et al.* 2002; Passeri & Venturi, 2005; Marino & Santantonio, 2010; Santantonio & Carminati, 2011). The complex Early Jurassic architecture is highlighted by differences in facies and thickness of the syn- and post-rifting deposits: a thick (several hundred metres) pelagic carbonate and siliceous succession, with common gravity-flow deposits, characterizes the basinal areas, while thin (few tens of metres) cephalopod-rich, 'condensed' sediments were deposited on the tops of structural highs ('pelagic carbonate platforms' or PCPs – Santantonio, 1993, 1994) (Fig. 2). The Calcare Massiccio limestone was exposed at the footwall of the Jurassic faults in the form of submarine palaeoescarpments (Santantonio, 1993, 1994; Carminati & Santantonio, 2005; Santantonio & Carminati, 2011), and was gradually overlapped by basin-fill deposits. Calcare Massiccio olistoliths can be found embedded in the basinal successions due to episodic failures of the PCP margins. The contacts of the silica-rich pelagites with the Calcare Massiccio (a chert-free carbonate limestone) are marked by the occurrence of chert nodules and crusts linked with surficial to pervasive silicification of the Calcare Massiccio at the unconformity (Santantonio, Galluzzo & Gill, 1996). The palaeobathymetric differences existing between the top of the horst-blocks and the basins were levelled in the Early Cretaceous by the Maiolica Fm., and from this moment on, and until the Miocene, sedimentation became homogeneous at regional scale.

During the Late Jurassic, the area in which the ichthyosaur was found was characterized by several different PCPs surrounded by basins: Mount Murano (Galluzzo & Santantonio, 1994), Mount Scoccioni (Di Bucci *et al.* 1994) and Mount Valmontagnana – Mount Frasassi (Coltorti, 1980; Coltorti & Bosellini, 1980). Even Mount Revellone can likely be interpreted as a structural high (Guerrera & Tramontana, 2002), despite having been previously interpreted as an olistolith by Coltorti & Bosellini (1980). Its SW steep palaeoescarpment is perfectly exposed, and is overlapped by the chert-rich units from the Corniola to the Maiolica of the Camponoecchio basin. A small outcrop of Calcare Massiccio, surrounded and overlapped by the Calcari e Marne a Posidonia and Calcari Diasprigni deposits, characterizes the Il Sassone area (Fig. 1). This can be interpreted as a huge olistolith of Calcare Massiccio, embedded in the Middle Jurassic pelagites, related to gravity failures of the Mount Revellone or the Mount Scoccioni PCP margins during the deposition of the Calcari e Marne a Posidonia. Evidence of tectonic

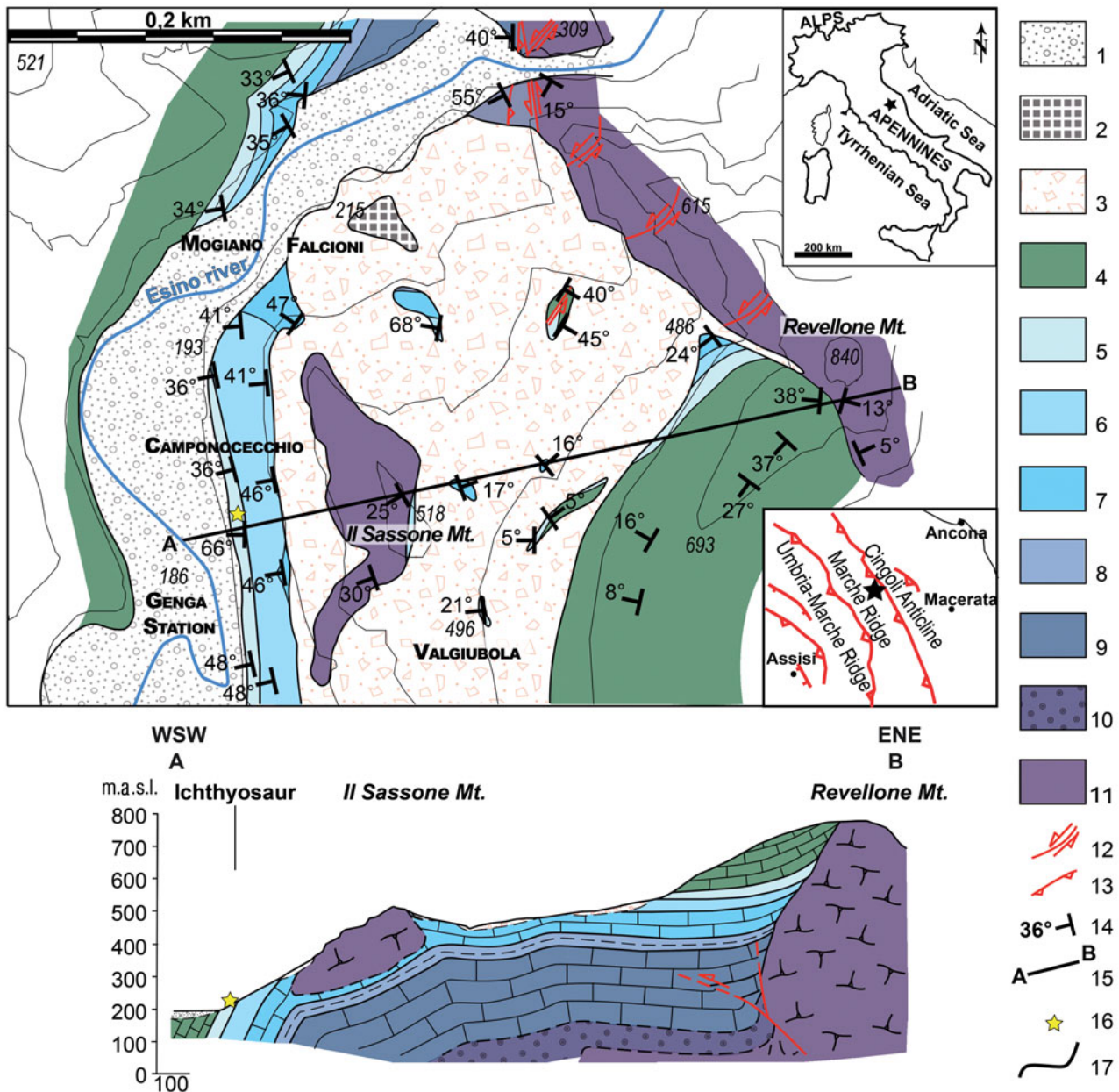


Figure 1. (Colour online) Geological map and section of the discovery site of MSVG 39617. Legend: (1) Alluvial deposits (Holocene–Pleistocene); (2) tufas (Holocene–Pleistocene); (3) detritus (Holocene–Pleistocene); (4) Maiolica Fm. (early Aptian – late Tithonian); (5) ‘Calcarei ad aptici e Saccocoma’ Fm. (early Tithonian – late Kimmeridgian); (6) ‘Calcarei Diasprigni’ Fm. (early Kimmeridgian – ?middle-late Bajocian); (7) ‘Calcarei e marne a Posidonia’ Fm. (?middle Bajocian – late Toarcian); (8) Rosso Ammonitico Fm. (Toarcian p.p.); (9) Corniola Fm. (early Toarcian – Sinemurian p.p.); (10) ‘Calcare Massiccio C’ informal unit (Hettangian–Sinemurian); (11) Calcare Massiccio Fm. (Hettangian); (12) strike-slip fault; (13) thrust; (14) bed attitude; (15) trace of the geological section; (16) exact point of discovery of MSVG 39617; (17) stratigraphic boundary.

instability during the Middle Jurassic in the area is abundant, with gravity-flows, slumps and breccias bearing clasts of Calcare Massiccio (Centamore *et al.* 1975; Galdenzi, 1986).

2.b. Stratigraphic position of the specimen

The ichthyosaur specimen was found *c.* 200 m SW of the Il Sassone olistolith, embedded in Upper Jurassic pelagites. The Upper Jurassic units building up the UMS are the Calcarei Diasprigni (lower Bajocian p.p. – lower Tithonian p.p.) and the lowermost part

of the Maiolica (lower Tithonian p.p. – lower Aptian) Fms. Fastelli & Nicosia (1980) attributed the beds in which the specimen was found to the Calcarei Diasprigni. This latter unit was formally subdivided by Cita *et al.* (2007) into two members: the ‘selciferous’ and ‘aptychi and Saccocoma limestones’ members. Galluzzo & Santantonio (2002) subdivided the ‘Calcarei Diasprigni’ into three formations, based on the lithogenetic role played by the fossiliferous content: (from bottom to top) ‘Calcarei e marne a Posidonia’ (latest Toarcian – ?late Bajocian; thin-shelled bivalves), ‘Calcarei Diasprigni’ (?late Bajocian – early Kimmeridgian;

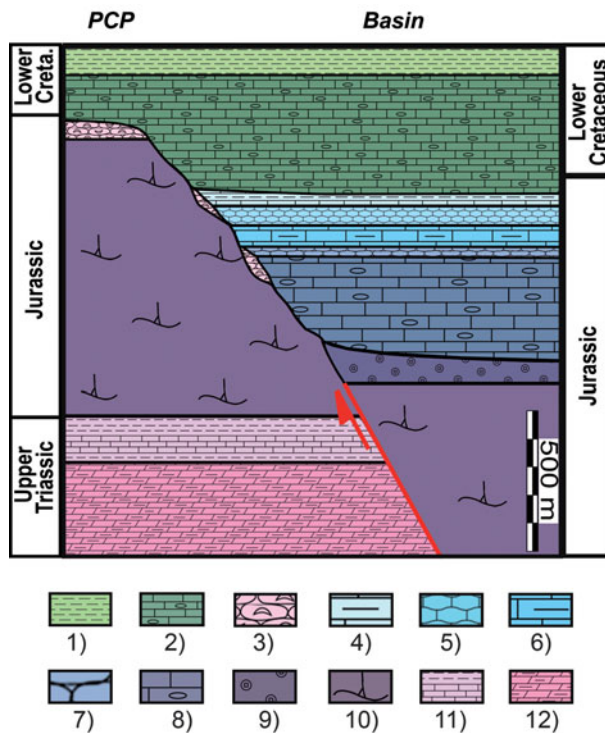


Figure 2. (Colour online) Simplified scheme of the Mesozoic stratigraphy of a typical PCP-basin system in the Umbrian–Marchean domain. Legend: (1) Marne a Fucoidi Fm. (Albian–early Aptian); (2) Maiolica Fm. (early Aptian – late Tithonian); (3) ‘Bugarone’ Group (early Tithonian – Sinemurian p.p.); (4) ‘Calcare ad Aptici e Saccocoma’ Fm. (early Tithonian – late Kimmeridgian); (5) ‘Calcare Diasprigni’ Fm. (early Kimmeridgian – ?middle-late Bajocian); (6) ‘Calcare e marne a Posidonia’ Fm. (?middle Bajocian – late Toarcian); (7) Rosso Ammonitico Fm. (Toarcian p.p.); (8) Corniola Fm. (early Toarcian – Sinemurian p.p.); (9) ‘Calcare Massiccio C’ informal unit (Hettangian–Sinemurian); (10) Calcare Massiccio Fm. (Hettangian); (11) Mount Cetona Fm. (Rhaetian p.p.); (12) Anidriti di Burano Fm. (Rhaetian p.p. – ?Norian). The red arrows indicate the Jurassic palaeofault.

radiolarians) and ‘Calcare ad aptici e Saccocoma’ (Kimmeridgian p.p. – lower Tithonian; crinoids and cephalopods). The ‘Calcare e marne a Posidonia’ are chert-rich limestones, in thin beds rich in posidoniid bivalves, and marlier near the base, while the ‘Calcare Diasprigni’ are polychrome thin-bedded, chert-rich limestones and cherts, apparently without macrofossils, and the microfauna characterized only by radiolarians. The ‘Calcare ad aptici e Saccocoma’ are green-reddish, chert-rich, thin-bedded limestones and marly limestones. The faunal association consists of macrofossils including *Saccocoma* spp., belemnites, aptychi, rhyncholites and echinoid fragments, while the microfauna is characterized by radiolarians and calcisphaerulids. Given the lithological similarity between the two formations (‘Calcare Diasprigni’ and ‘Calcare ad aptici e Saccocoma’), according to Galluzzo & Santantonio (2002), the boundary is placed at the occurrence of *Saccocoma* sp. The field analysis of the area, where the specimen was discovered, confirms the original obser-

vations of Fastelli & Nicosia (1980), and applying the stratigraphic subdivision of Galluzzo & Santantonio (2002) it became evident that the ichthyosaur comes from the ‘Calcare ad aptici e Saccocoma Fm.’ (Figs 1, 2). About 10 m below the ichthyosaur-bearing level, some belemnites were found, and in particular one complete specimen and a fragment of the alveolar region. The first one, ascribed to *Produvalia* cf. *monsalvensis* Gilliéron 1873 (Fig. 3e), has a middle Callovian to Oxfordian stratigraphic distribution, and is reported from SE France, Switzerland, SW Germany and Sicily (S Italy) (Mariotti, 2002). The alveolar fragment is typical of some duvaliid specimens (*Duvalia* sp.) (N. Mariotti, pers. comm. 2014). These data, coupled with the finding of rhyncholites (*Palaeoteuthis* sp. and *Leptocheilus* sp. fide Riegraf & Luterbacher, 1989), crinoid fragments (?*Cyrtocrinus* sp.: Fig. 3c) and aptychi (*Laevaptychus* sp.), and with the lack of *Saccocoma* sp., suggest a ?middle-late Oxfordian – early Kimmeridgian age for the horizon. The mass occurrence of *Saccocoma* sp. is an ecological event that at regional scale is dated at the latest early Kimmeridgian (e.g. Winterer & Bosellini, 1981; Cecca *et al.* 1990; Manni, Nicosia & Tagliacozzo 1997; Marino *et al.* 2004), and in the analysed area the first occurrence of *Saccocoma* sp. is recorded *c.* 4 m below the ichthyosaur-bearing level. In the Central and Northern Apennines, two species of *Saccocoma* are described: *S. tenella* and *S. vernioryi* (Nicosia & Parisi, 1979; Manni & Nicosia, 1984). *S. tenella* is the more abundant and has the longer stratigraphic range (upper Kimmeridgian – upper Tithonian) (Chiocchini *et al.* 2008). According to Manni & Nicosia (1984), presence of *S. vernioryi* is recorded from the lower to middle Tithonian on the Central–Northern Apennines, and it is less common than *S. tenella*; moreover, it also seems to be mainly typical of escarpment environments (A.C. pers. obs.), so its absence is unlikely to be due to ecological factors. By combining the two data points (i.e. first occurrence of *Saccocoma* sp. 4 m below the ichthyosaur level, and the lack of *S. vernioryi*), the horizon is at the oldest upper Kimmeridgian, and older than lower Tithonian.

Finally, another important datum to constrain the age of the new specimen is given by the lack of chitinous forms among calpionellids: according to Andreini, Caracuel & Parisi (2007), chitinoideids (e.g. *Chitinoidea* sp.) make their appearance all over the Tethys in the latest early Tithonian, and these forms were not recovered from the ichthyosaur bed.

In conclusion, the faunal assemblage of the ichthyosaur-bearing level includes belemnites (*Duvalia* sp.), aptychi (*Laevaptychus* sp., ?*Laevilamellaptychus* sp.: Fig. 3a, d), rhyncholites (*Leptocheilus* sp.: Fig. 3b), trace fossils (*Thalassinoides* sp., *Chondrites* sp.), radiolarians, calcisphaerulids and abundant *Saccocoma tenella* (Fig. 3a). These data, coupled with the absence of *S. vernioryi* and *Chitinoidea* sp., indicate a late Kimmeridgian – earliest Tithonian age for the new ophthalmosaurid.

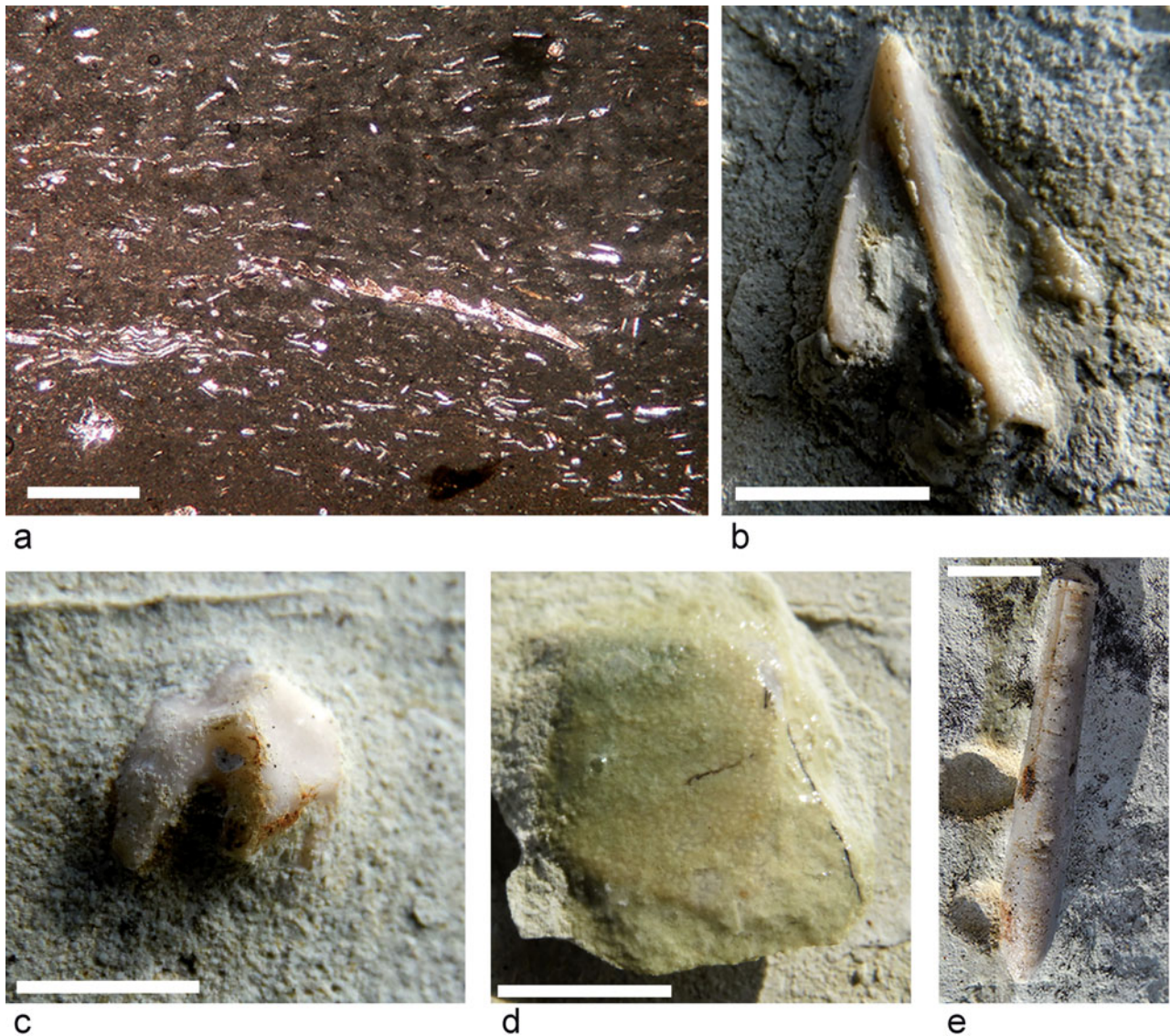


Figure 3. (Colour online) Micro- and macrofossils from the horizon where *Gengasaurus nicosiai* MSVG 39617 was found. (a) Thin-section of the slab on which the specimen lies: the micro-facies consists of a wackestone rich in fragments of *Saccocoma* sp. and radiolarians, and a section of an aptychus is visible in the central part of the picture; (b) *Leptocheilus* sp.; (c) *Cyrtocrinus* sp.; (d) tubular setting of the upper lamellar layer of *Laevaptychus* sp., sampled from the ichthyosaur-bearing bed; (e) specimen of *Produvalia* cf. *monsalvensis* Gilliéron 1873. Scale bar is (a) 2 mm, (b–e) 10 mm.

3. Material

The specimen consists of an almost complete skeleton crushed on a slab, and prepared from the top (i.e. stratigraphic side up). It consists of a disarticulated skull and an articulated vertebral column, extending from the atlas-axis to the anterior caudal region. The pectoral girdle and the forelimb are partially preserved, while the pelvic girdle and hindlimb are missing. There are two main gaps along the vertebral column that could be due to scavenging, taphonomic processes or erosion. Shark teeth have been recovered on the slab among the ichthyosaur remains, but due to the deep erosion of the bones it is difficult to establish the unambiguous presence of striations on the bone confirming interaction between the sharks and the carcass. Measurements of the specimen are provided in Table 1, and important ratios in Table 2.

Institutional abbreviations. GSM, Geological State Museum of the Russian Academy of Sciences named after V. I. Vernadsky (Moscow, Russia); MSVG, Museo di speleo-paleontologia e archeologia di San Vittore di Genga, Ancona, Marche, Italy; PMO, Palaeontological Museum Oslo, University of Oslo, Oslo, Norway; UPM, Undory Palaeontological Museum (Undory Village, Ulyanovsk region, Russia).

4. Systematic palaeontology

Order ICHTHYOSAURIA de Blainville, 1835
 Family OPHTHALMOSAURIDAE Baur, 1887
Gengasaurus gen. nov.

Etymology. Named after the town of Genga (Ancona, Marche, Italy), where the specimen was found, and ‘-saurus’, Greek for ‘lizard’.

Table 1. Skeletal element measurements of *Gengasaurus nicosiai* MSVG 39617. Values reported for the anterior and posterior precaudal vertebrae and for the anterior caudals are average measurements, while for the few preserved posterior caudals, direct measurements are given. Abbreviations: avg, average; d, diameter; d_{a-p} , diameter anterior–posterior; d_{d-v} , diameter dorsal–ventral; CH, centrum height; CL, centrum length; CW, centrum width; H, height; L, length; l, left; r, right; W, width; W_{dist} , width measured at the distal head of the bone; W_{mid} , width measured at the shaft of the bone; W_{prox} , width measured at the proximal head of the bone.

Element	Measurement (cm)
Mandible L	(r) 74.50; (l) 62.50; (avg) 68.50
Premaxilla L	30.00
Premaxilla H at mid-length	4.50
Gullet W	25.00 (estimated)
Sclerotic d_{a-p}	14.20
Sclerotic d_{d-v}	13.50
Hyoid shaft W	1.60
Precaudal region L	147.00 (from atlas-axis) (estimated)
Atlas-axis CH	5.60
Atlas-axis CW	5.37
Anterior precaudal CH	5.58
Anterior precaudal CL	2.52
Anterior precaudal neural spine H	6.80
Anterior precaudal neural spine W	2.35
Posterior precaudal CH	8.07
Posterior precaudal CL	2.79
Mid-posterior precaudal neural spine H	8.25
Mid-posterior precaudal neural spine W	2.95
Anterior caudal region L	105.5
Anterior caudal CH	7.43
Anterior caudal CL	3.00
Anterior caudal CH	5.22
Anterior caudal CW	4.22
Posterior caudal CH (preflexural)	3.60
Posterior caudal CW (preflexural)	4.00
Posterior caudal CH (postflexural)	2.00
Posterior caudal CW (postflexural)	2.40
Posterior caudal CH (postflexural)	1.78
Posterior caudal CL (postflexural)	1.39
Scapula W_{prox}	8.63
Scapula W_{mid}	3.71
Humerus L	13.06
Humerus W_{prox}	5.85
Humerus W_{mid}	5.18
Humerus W_{dist}	8.27
Humerus preaxial facet	1.45
Humerus radial facet	3.97
Humerus ulnar facet	3.67
Radius W_{prox}	3.69
Radius W_{mid}	4.77
Radius L	4.20
Ulna W_{prox}	3.62
Ulna W_{mid}	3.67
Ulna L	3.25

Type species. *Gengasaurus nicosiai* sp. nov.

Stratigraphy. Calcari ad aptici e Saccocoma Fm. (*sensu* Galluzzo & Santantonio, 2002), Umbrian–Marchean Succession, Central–Northern Apennines (Figs 1, 2).

Age. Late Kimmeridgian – earliest Tithonian (Fastelli & Nicosia, 1980; this study).

Diagnosis. As for the type and only species.

Table 2. Principal ratios between some elements of *Gengasaurus nicosiai* MSVG 39617 for body proportions. The values reported for the anterior and posterior precaudal vertebrae and for the anterior caudals are average measurements, while for posterior caudals the direct measurements of the few preserved ones are reported. Abbreviations: d, diameter; d_{a-p} , diameter anterior–posterior; d_{d-v} , diameter dorsal–ventral; CH, centrum height; CL, centrum length; CW, centrum width; H, height; L, length; W, width; W_{dist} , width measured at the distal head of the bone; W_{mid} , width measured at the shaft of the bone; W_{prox} , width measured at the proximal head of the bone.

Elements	Ratio
Premaxilla L / mandible L (snout ratio)	0.44
Premaxilla H / mandible L (snout depth ratio)	0.065
Mandible L / precaudal region L	0.47
Mandible L / anterior caudal region L	0.65
Sclerotic d_{a-p} / mandible L	0.21
Sclerotic d_{d-v} / mandible L	0.20
Sclerotic d_{a-p} / premaxilla L	0.47
Sclerotic d_{d-v} / premaxilla L	0.45
Humerus W_{prox} / L	0.45
Humerus W_{mid} / L	0.40
Humerus W_{dist} / L	0.63
Radius W_{mid} / L	1.14
Ulna W_{mid} / L	1.13
Anterior caudal region L / precaudal region L	0.72
Anterior precaudal CH/CL	2.21
Posterior precaudal CH/CL	2.89
Anterior caudal CH/CL	2.48
Posterior caudal (postflexural) CH/CL	1.28
Atlas CH/CW	1.04
Anterior caudal CH/CW	0.81
Posterior caudal (preflexural) CH/CW	0.90
Posterior caudal (postflexural) CH/CW	0.83

Gengasaurus nicosiai sp. nov.

Figures 4, 5, 6

Etymology. Named after Umberto Nicosia, professor and mentor of Palaeontology at the University of Rome ‘Sapienza’, who prepared the specimen in 1998–9, in the Abbey of San Vittore di Genga.

Holotype. MSVG 39617, a relatively complete individual preserved on a slab, with a disarticulated skull, part of the pectoral girdle, and an articulated vertebral column lacking the posterior caudal region.

Locality and horizon. Camponoecchio, Genga (Ancona, Marche, Italy), 43° 24' 28.05" N, 12° 58' 52.60" E. Calcari ad aptici e Saccocoma Fm. (*sensu* Galluzzo & Santantonio, 2002) (Fig. 1).

Diagnosis. The new taxon is distinguished from other ophthalmosaurid ichthyosaurs by the following unique combination of characters: basioccipital with reduced extracondylar area similar in extent to *Ophthalmosaurus* spp. (extracondylar area less reduced than in *Brachypterygius extremus*, *Arthropterygius chrisorum*: Kirton, 1983; Maxwell, 2010); supraoccipital and exoccipital contributing roughly equally to the foramen magnum (supraoccipital contribution far exceeds exoccipital contribution in *Ophthalmosaurus natans*; exoccipital contribution exceeding supraoccipital contribution in *O. icenicus*: Gilmore, 1905, 1906; Kirton, 1983); medial ramus of supraoccipital a thin bar (flat and plate-like in *O. icenicus*: Kirton, 1983); orbit relatively

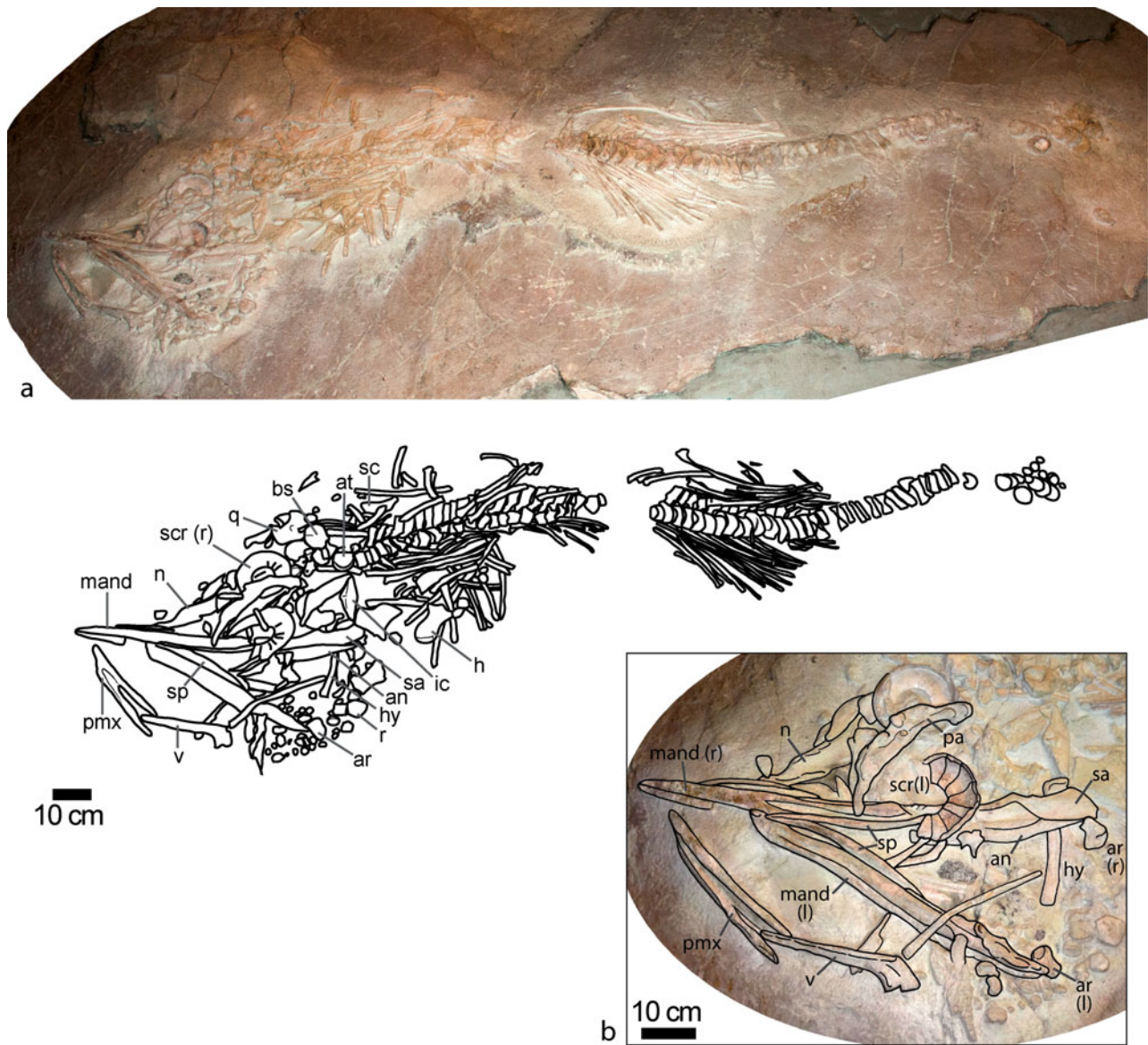


Figure 4. (Colour online) *Gengasaurus nicosiai* gen. et sp. nov., MSVG 39617, holotype and only known specimen, consisting of a relatively complete individual, with a disarticulated skull, partially articulated mandibles, part of the pectoral girdle, and a mostly articulated vertebral column, mostly visible in lateral view, from the atlas-axis to the anterior caudals. (a) The overall view of the specimen; (b) A closer view of palatal complex, skull roof, and mandible elements. Abbreviations: an, angular; ar, articular; at, atlas; bs, basisphenoid; h, humerus; hy, hyoid; ic, interclavicle; l, left; mand, mandible; n, nasal; pa, parietal; pmx, premaxilla; q, quadrate; r, right; sa, surangular; sc, scapula; scr, sclerotic ring; sp, splenial; v, vomer.

large (ratio between the sclerotic ring and mandible = 0.21); vertebrae in anterior caudal region not extremely shortened (centrum height:length <3.0; >3.0 in *O. icenicus*, *Arthropterygius chrisorum*: Massare *et al.* 2006; Maxwell, 2010); three articular facets on the humerus (only two facets present in *Nannopterygius enthekiodon* and *Cryopterygius kristiansenae*: Kirton, 1983; Druckenmiller *et al.* 2012), with the smallest located anteriorly for articulation with a preaxial element (smallest facet for articulation with the intermedium in *Aegirosaurus leptospondylus*, *Brachypterygius extremus*: Kirton, 1983; Bardet & Fernández, 2000); unusual condition of the preaxial accessory facet on the humerus, highly anteroproximally deflected either considering the longitudinal axis of the humerus or

the radial-ulnar plane, likely shared with *Undorosaurus* sp. (Efimov, 1999; Arkhangelsky & Zverkov, 2014) (humeral facet for the preaxial element continuous with the radial one in *Acamptonectes densus* and *Ophthalmosaurus icenicus*: Kirton, 1983; Fischer *et al.* 2012); anteroposterior length of radius similar to proximodistal length (unlike *Caypullisaurus* in which the radius is anteroposteriorly elongate: Fernández, 1997, 2001); radius significantly larger than ulna, with six articular facets for humerus, preaxial element, preaxial carpal, radiale, intermedium, and ulna posteriorly (radius smaller or sub-equal in *Cryopterygius kristiansenae*, *Ophthalmosaurus* spp.: Gilmore, 1905, 1906; Kirton, 1983; Druckenmiller *et al.* 2012).

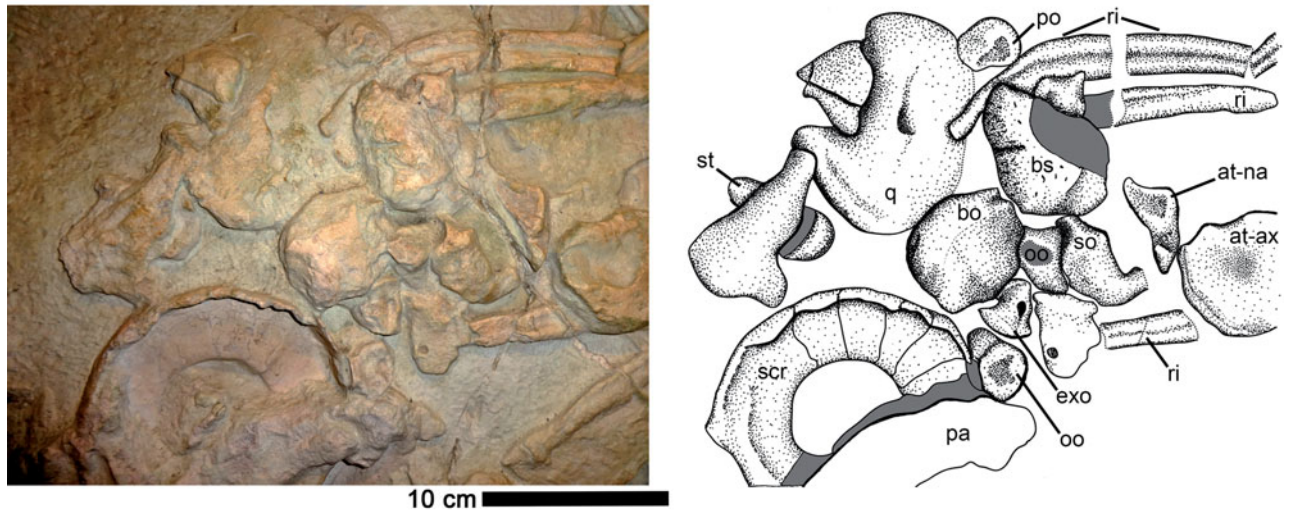


Figure 5. (Colour online) Cranial elements and atlas-axis of *Gengasaurus nicosiai* MSVG 39617, with interpretative drawing. Abbreviations: at-ax, atlas-axis; at-na, atlas neural arch; bo, basioccipital; bs, basisphenoid; exo, exoccipital; oo, opisthotic; pa, parietal; po, prootic; q, quadrate; ri, rib; scr, sclerotic ring; so, supraoccipital; st, stapes.

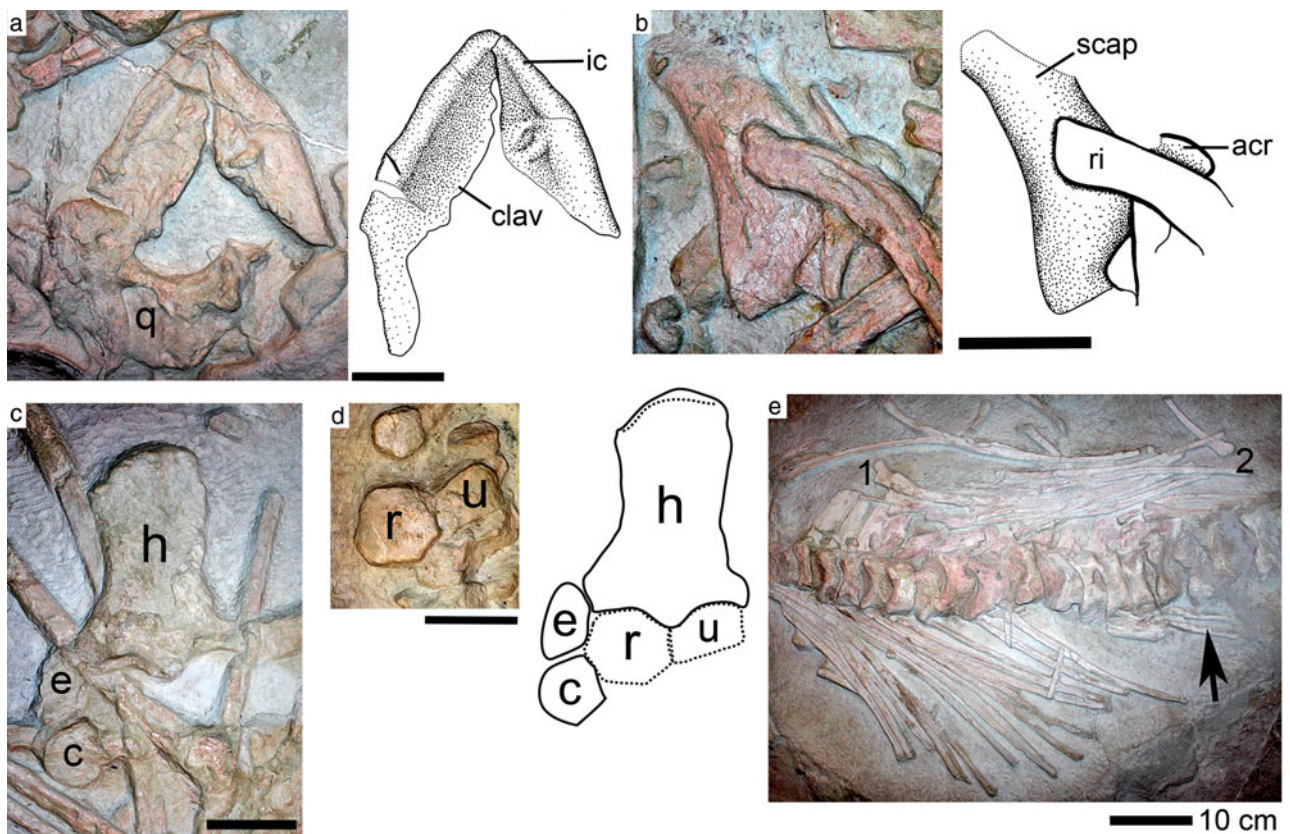


Figure 6. (Colour online) Postcranial elements of *Gengasaurus nicosiai* MSVG 39617, with interpretative drawings: (a) clavicle and interclavicle; (b) scapula and rib fragment; (c, d) elements of the forefin; (e) portion of the vertebral column and ribs. In (e) the black arrow indicates the approximate location of sacrum based on rapid shortening of ribs, '1' indicates a typical bicipital dorsal rib, and '2' indicates a posterior unicipital dorsal rib with the two heads almost completely fused. Abbreviations: acr, acromion process; c, carpal; clav, clavicle; e, preaxial accessory element; h, humerus; ic, interclavicle; q, quadrate; r, radius; ri, rib; sc, scapula. All the scale bars are equal to 10 cm.

5. Description

5.a. Cranium

5.a.1. Braincase

Basioccipital. The surface of the basioccipital is strongly eroded, thus making morphological interpretation difficult. It is preserved in anterodorsal view, with the condylar area poorly exposed (Fig. 5). On the right-hand side of the condyle, a trace of a groove delimiting the dorsal condyle is preserved. Slightly anterior to the condylar area there are two embayments indicating the position of the extracondylar area, similar in extent to that of *Ophthalmosaurus icenicus* (Kirton, 1983). In dorsal view, the basioccipital is wider (mediolaterally) than long (anteroposteriorly), similar to *Acamptonectes densus* and *Ophthalmosaurus icenicus* (Kirton, 1983; Fischer *et al.* 2012). The right opisthotic facet is clearly defined on the anterolateral surface of the basioccipital. It is much deeper than the opisthotic facet of *Ophthalmosaurus icenicus* (Kirton, 1983), but as in the latter taxon is separated from the dorsal surface of the basioccipital by a ridge. A slightly recessed area separates it from the roughened anterior surface of the basioccipital.

Basisphenoid. The basisphenoid is not complete: about half of the bone is preserved and is visible in dorsal view; erosion is severe, especially on the left side (Fig. 5). The dorsal plateau is interrupted by an extended fracture that crosses the basisphenoid diagonally, but the undamaged portion of the plateau has a semicircular outline, leading to the conclusion that the general shape of the element was originally slightly rounded, as in *Ophthalmosaurus* sp. (e.g. Kirton, 1983; Fischer *et al.* 2014). The anterodorsal portion of the basisphenoid is broken, and the position of the sella turcica is not clear. No pronounced dorsal crest was present: the limit between the dorsal plateau and the anterodorsal region of the basisphenoid (where the sella turcica is located) is more like an extended ridge than a pointed crista (visible only on the right side of the element). The basiptyergoid process is quite wide, and slightly flattened in outline in dorsal view. Due to the erosion of the left side and the partially overlapping supraoccipital on the right, is not possible to see if the posteroventral margin of this process is characterized by a notch for the cranial nerve VII (Kirton, 1983; Maxwell, 2010). Between the basiptyergoid process and the supposed position of the sella turcica, there is a smooth area that could correspond to the cranio-quadrate passage described in *Ophthalmosaurus* (Kirton, 1983). The posterior surface of the basisphenoid, where the median furrow is situated, is not as rounded as in *Ophthalmosaurus*, but more flattened as in *Arthropterygius* and *Acamptonectes*, and is highly irregular and pitted. A well-defined median groove runs dorsoventrally along the posterior surface of the basisphenoid, with the basioccipital facets on either side. The facet for the anterior proximal head of the stapes in dorsal view is smaller and less pronounced than the large, rounded

depression described for *Acamptonectes densus*, more similar to *Ophthalmosaurus icenicus* (Kirton, 1983; Fischer *et al.* 2012).

Opisthotic. Both the opisthotics are preserved; the left one is in distal view and the right one in anteroproximal view (Fig. 5). In anteroproximal view the paroccipital process appears quite elongated. The medial surface of the opisthotic is deeply affected by erosion, so the otic impression is poorly recognizable. A straight facet oriented anteromedially for articulation with the basioccipital can be recognized on the anterior edge of the medial surface of the opisthotic. Running anteroposteriorly along the dorsal face of the paroccipital process, there is a thin ridge and groove; this type of structure is often found in ichthyosaurs, situated between the impression of the otic labyrinth and the paroccipital process (E.M. pers. obs.). On the ventral surface of the opisthotic there is no evidence of a lateral ‘foot’ or an unusual groove described by Fischer *et al.* (2012) for *Acamptonectes densus*, and due to erosion it is not easy to describe the stapedial facet. The left opisthotic is preserved in distal view, with the concave anterior surface facing away from the basioccipital (as preserved). The paroccipital process is broken, but appears compressed, such that the dorsoventral axis is shorter than the anteroposterior axis. The ventral edge of the bone is straight, and lacks the foramen visible in *Ophthalmosaurus icenicus* (Kirton, 1983). The dorsal process, for contact with the exoccipital, is long and relatively narrow.

Prootic. The prootic is approximately rounded in shape and preserved in posterodorsal view (Fig. 5). Comparisons are difficult since it is preserved flattened on a slab, and may be somewhat distorted. The canal impressions are roughly V-shaped, as in *Ophthalmosaurus* and *Acamptonectes*, and unlike *Sveltonectes* and most *Platypterygius* species (Appleby, 1956; Kirton, 1983; Fischer *et al.* 2011, 2012).

Supraoccipital. Only the right half of the supraoccipital is preserved, visible in posterior view (Fig. 5). Assuming bilateral symmetry, the supraoccipital contribution to the foramen magnum was deeply arched and probably U-shaped, as in *Ophthalmosaurus natans*, *Platypterygius hercynicus* and *Platypterygius australis* (Appleby, 1956; Wade, 1990; Kear, 2005; Kolb & Sander, 2009; Zammit, 2010). The medial ramus dorsal to the foramen magnum is thinner than the lateral rami, and the foramen magnum is higher and narrower than in *Acamptonectes densus*, *Ophthalmosaurus icenicus* and *Sisteronia seeleyi*, (Kirton, 1983; Fischer *et al.* 2012, 2014). The ventral facet for the exoccipital is roughly triangular in shape, strongly tapering medioventrally. A wave-like ridge runs horizontally along the dorsal edge of the supraoccipital, reaching the lateral edge. We interpret this as a contact surface for the parietal. A depression on the lateral foot of the supraoccipital could represent the supraoccipital foramen; however, poor contrast between the sediment and bone prevents verification that this is in fact a foramen. A second

depression with a small notch lateral to the putative supraoccipital foramen is a second potential candidate; however, preservation prevents a clear view of this structure. Although some other depressions are present on the posterior surface of the supraoccipital, the state of preservation of the element does not allow us to rule out erosional artefacts. A prominent, obliquely oriented supraoccipital foramen is present at the junction between the median ramus and the lateral foot of the supraoccipital in *Acamptonectes densus*. This foramen is located further laterally in *Ophthalmosaurus icenicus*, *Platypterygius longmani* and *Platypterygius hercynicus* (Appleby, 1956; Kirton, 1983; Fischer *et al.* 2012).

Exoccipital. The right exoccipital is preserved in medial view (Fig. 5). Its general shape is roughly triangular, similar to *Ophthalmosaurus* spp., *Brachypterygius extremus*, *Mollesaurus periallus* and *Acamptonectes densus*, and unlike *Sveltonectes insolitus* (Appleby, 1956; McGowan, 1976; Kirton, 1983; Fernández, 1999; Kear, 2005; Fischer *et al.* 2012). The tip of the anterior process of the exoccipital is not clearly visible. A large foramen is present on the medial surface; due to preservation the presence of other foramina could not be confirmed. Dorsally, the surface for the supraoccipital contact is rounded in shape in medial view, and apparently less oblique relative to the anterior process, in comparison to *Ophthalmosaurus icenicus*, and more similar to *Acamptonectes* (Kirton, 1983; Fischer *et al.* 2012); but this could also be due to preservation. The articular facet for the basioccipital on the ventral edge is convex and rounded in medial view.

Stapes. Only the right stape is preserved, flattened and overlapped by an indeterminate element, making detailed morphological comparisons difficult (Fig. 5). The shaft appears relatively long and slender, as in *Ophthalmosaurus icenicus* and *Acamptonectes densus* (Kirton, 1983; Fischer *et al.* 2012). The proximal head is much broader than the distal head in MSVG 39617, and this difference is most likely exaggerated through compression. The distal head appears rounded, but may be damaged.

5.a.2. *Quadrate and Palatal complex*

Quadrate. Both the quadrates are preserved: the left quadrate in medial view and the right one in postero-medial view, with the quadratojugal contact slightly visible (Figs 5, 6a). The quadrate is robust, and both its lamellae are expanded and fan-like, giving the bone a well-defined C-shape, as in *Ophthalmosaurus icenicus*, and unlike for instance *Platypterygius australis* (Kirton, 1983; Kear, 2005). In medial view, the midpoint of the quadrate shaft at the level of the stapedial facet is more obviously constricted, as in *Ophthalmosaurus* spp. and to some degree in *Acamptonectes densus* (Gilmore, 1905, 1906; Kirton, 1983; Fischer *et al.* 2012). The stapedial facet is a slight concavity, with an arched posterior edge and with a prominent and

thickened ventrolateral edge, in the same position as in *Ophthalmosaurus icenicus* relative to the occipital head and the articular condyle (Kirton, 1983). Posterodorsal to the stapedial contact there is an extended articulation facet for the pterygoid, obliquely oriented from the medial edge of the quadrate and reaching almost its lateral edge. Ventrally, the condylar surface is particularly well exposed in the right quadrate, which is almost in its position of articulation with the mandible: prominent articular and surangular facets are visible, the articular one being shorter than the other and with a slight groove separating the two facets, as in *Ophthalmosaurus icenicus* (Kirton, 1983); in *Acamptonectes* the situation is very similar, including for the groove, but the two facets seems to be almost of the same length (Fischer *et al.* 2012). Right above the articular condyle on the posterolateral edge of the quadrate, there is a subtriangular facet for the articulation of the quadratojugal, slightly depressed and crossed in the middle by a dorsoventrally directed ridge. A similar shape for this facet, including the bony ridge, is visible in the quadrate of *Acamptonectes densus* (Fischer *et al.* 2012, fig. 3I), even though in this case the quadratojugal facet seems to be less elongated, occupying just the dorsal surface of the condyle (Fischer *et al.* 2012); in MSVG 39617 the quadratojugal contact begins above, at the level of the ventral end of the stapedial facet.

Vomer. The left vomer is poorly preserved in medial view, and its posterior end is missing (Fig. 4a, b). The ventral edge of the vertical projection (*sensu* Kirton, 1983) is almost straight, while the dorsal edge is oblique, giving the posterior vomer a trapezoidal shape, in which the ventral edge is the major base and the dorsal top is the minor base. The anterior end of the vomer tapers sharply, as described for *Ophthalmosaurus icenicus* (Kirton, 1983), and the ventral border seems to have an irregular outline close to the anterior tip, indicating the suture with the contralateral vomer. The facet for the contact with the pterygoid on the medial surface of the vomer is elongated and slightly concave, running from the central area to the anterior portion of the bone. Along the dorsal edge of the bone, starting posteriorly, two expanded vertical processes are present, although this region is not well preserved.

5.a.3. *Skull roof*

The right side of the posterior skull roof is exposed in ventral view, partially overlapping the right sclerotic ring (Figs 4, 5). The parietal is broad and relatively large, with a concave lateral margin that formed the medial edge of the supratemporal fenestra. The lateral margin of the parietal forms a slight ridge, bordering a more concave area made up of the medial parietal. The concavity is most pronounced anteriorly, extending onto the frontal, and is bordered anteriorly by a transverse ridge. Just posterior to this transverse ridge, a slight embayment on the medial surface of the skull roof most likely corresponds to the pineal foramen. The

ridge making up the concave lateral margin of the parietal becomes straighter anteriorly, and may represent the ventral surface of the prefrontal (as in *Ophthalmosaurus icenicus*: Kirton, 1983). The concave morphology of the median skull is retained anterior to the transverse ridge, and this may correspond to the olfactory lobe (Kirton, 1983). Due to preservation, sutures on the ventral surface of the skull roof are unclear.

Nasal. The antorbital portion of the right nasal is visible in medial view (Fig. 4b). The medial surface of the nasal is concave; the bone is poorly visible, and mainly covered by other skull elements, so more details are hard to identify.

Premaxilla. The left premaxilla is preserved in medial view and the right one is slightly visible below the right mandible (Fig. 4b). The premaxilla is not as slender as in *Ophthalmosaurus icenicus* and *Acamptonectes densus* relative to the total length of the mandible (Table 2). The snout depth ratio is 0.065; values for other ophthalmosaurids range between 0.044 in *Acamptonectes densus* and 0.089 in *Brachypterygius extremus* (McGowan, 1976; Fischer *et al.* 2012). The left premaxilla is damaged both anteriorly and posteriorly. The medial surface is concave, and the posterior premaxilla is divided into two processes, corresponding to the end of the palatal ramus and the maxillary ramus. The vomer remains loosely associated with the medial surface of the palatal ramus. Due to breakage, the shape of the dorsal edge of the premaxilla is not well preserved, so the shape of the supranarial process cannot be observed. Likewise, the palatal surface becomes increasingly damaged anteriorly, and the alveolar groove is not visible.

5.a.4. Sclerotic rings

Both sclerotic rings are preserved in medial view (Figs 4, 5). Neither is completely exposed and undamaged, but it is possible to recognize some of the plates: in the posterodorsal quarter of the ring there are three and a half plates. The sutures between the plates are very difficult to discern, but are gently curved, and are more sharply curved around the sclerotic aperture. The anteroposterior diameter of the sclerotic ring is 142 mm, and the dorsoventral diameter is 135 mm.

5.a.5. Mandible

Both mandibles are preserved: the right mandible is in dorsomedial view and the dentary, splenial, surangular, angular, prearticular and articular are all present; the left mandible is in dorsolateral view and the dentary, splenial, surangular, angular and articular are visible (Fig. 4a, b). The right mandible is 745 mm long, while the left one is 625 mm long (Table 1). This discrepancy is most likely due to taphonomy, but whether the left mandible is compressed, the right one is sheared, or both, is unclear. Because of this difference, we used

the average value to calculate the ratios (Table 2). The symphysis measures *c.* 300 mm. The gullet width is estimated at 250 mm, although some taphonomic distortion makes this a rough estimate.

Articular. The dorsal edge of the articular is gently concave and there is a mediolateral constriction at the midpoint of the bone, visible both in lateral and medial views (Fig. 4b). The articular is widest anteriorly, and appears to taper posteriorly. However, as the ventral surface of the element remains embedded in sediment, the degree of tapering is difficult to evaluate. There is a horizontal groove along the dorsal edge of the left articular. The anterior surface for the articulation with the quadrate condyle is oval in shape, with the long axis oriented dorsoventrally, and slightly concave. The anterior (glenoid) end of the articular is much thicker than the posterior end. The glenoid facet is directed anteromedially. The articular is closer in morphology to that of *Ophthalmosaurus icenicus* than to *Arthropterygius chrisorum* (Kirton, 1983; Maxwell, 2010).

Surangular. Both surangulars are preserved: the right one in medial view and the left one in dorsolateral view (Fig. 4b). The posterior margin of the surangular is rounded, and in medial view its posterior portion is dorsoventrally expanded. On the dorsal edge, both the coronoid process and the process for the insertion of *Musculus adductor mandibulae externus* (MAME) are present and well developed as in *Ophthalmosaurus icenicus*, and unlike *Janusaurus lundii*, where the coronoid process is small and only the preglenoid process is quite prominent (Kirton, 1983; Roberts *et al.* 2014). Ventral to the coronoid and MAME insertion, the medial surface of the surangular is concave. This concavity forms an anteroposteriorly directed groove corresponding to the Meckelian canal. This groove is not exposed more anteriorly as the prearticular remains in articulation, covering the medial surface of the Meckelian canal. The ventromedial border of the Meckelian canal posterior to the coronoid process is formed by the angular, which expands medially anteroventral to the coronoid process to enclose the glenoid. The posterior prearticular is broken. More anteriorly, the medial surface of the lower jaw consists of the splenial. The posterior splenial overlies the more medial surangular. As in most ichthyosaurs, the splenial participates in the posterior mandibular symphysis; however, due to weathering, the extent of splenial participation relative to the dentary cannot be assessed. Corresponding to the contact with the splenial, on the lateral surface there is the surangular–dentary contact, and as in *Ophthalmosaurus* and other ophthalmosaurids, the dentary covers much of the surangular's dorsal surface. The ventral edge of the surangular is almost entirely for the contact with the angular.

Preatricular. The right prearticular is visible in medial view, still in articulation with the rest of the mandible but broken posteriorly. It forms the medial wall of the Meckelian canal. On the left side, the prearticular is vis-

ible as a thin splint in dorsal view, overlapped medially by the posterior splenial.

Angular. The right angular is preserved in medial view and the left one is slightly visible in dorsolateral view (Fig. 4b). The angular is an elongate element constituting the ventral portion of the mandible. Anteriorly in medial view, the articular is partially overlapped by a pointed posterior process of the splenial, as in *Ophthalmosaurus icenicus* (Kirton, 1983). In medial and lateral view, the angular tapers posteriorly and is dorsoventrally flattened, constituting the floor of the glenoid fossa and contacting the surangular dorsally and laterally, the prearticular dorsally and medially, and the articular posterodorsally.

Splenial. The splenials contribute anteriorly to the mandibular symphysis (Fig. 4b). Although a portion of the mandible is missing, it seems likely that the splenial contribution is limited to the posterior half of the mandibular symphysis. In medial view the splenial ends posteriorly as a pointed triangular bone that overlaps the angular. Dorsally, the contact with the surangular is slightly extended anteriorly, exceeding the anterior half of the splenial: in this contact, MSVG 39617 is more similar to *Platypterygius australis*, where the splenial–surangular are in contact up to the most anterior half of the mandible, than to *Ophthalmosaurus icenicus*, where it stops more posteriorly (Kirton, 1983; Kear, 2005; Zammit, 2010; Zammit, Norris & Kear 2010).

Dentary. The anterior portion of the mandible is exposed in dorsal view, but is heavily weathered and eroded. The anterior half of the left dentary is broken and still attached to the right counterpart; the two dentaries are in contact at the symphysis (Fig. 4b). According to Kirton (1983), in *Ophthalmosaurus icenicus* the dentaries diverge at their tips, leaving space presumably occupied by cartilage: at least ventrally, in MSVG 39617, there is no evidence of a divergence at the anterior mandibular symphysis. The contribution of the dentary to the mandibular symphysis is greater than that of the splenial. The alveolar groove is visible posteriorly, but impressions of tooth positions are not preserved. The posterior end of the dentary in lateral view is not well-preserved; on the dorsal surface instead, the alveolar groove runs from the posterior end of the dentary anteriorly. Weathering prevents an accurate assessment of its depth.

5.a.6. Hyobranchial apparatus

A rod-like bone underlying the right posterior mandible is interpreted as the hyobranchial apparatus (CB1). The proximal end is hidden by the angular, the shaft is bowed and rod-like, while the anterior end is quite flattened and a little bit wider than the shaft, more similar to the condition seen in *Platypterygius australis* than in *Sveltonectes insolitus* (Fig. 4b) (Kear, 2005; Fischer *et al.* 2011). On the ?dorsal surface of the hy-

obranchial rod, running about parallel to the shaft and close to the posterior edge, there is a slight groove.

5.b. Axial skeleton

The length of the presacral vertebral column is 147 cm, and of the preserved portion of the caudal region is 105.5 cm. The column is mostly preserved in articulation and the vertebrae are mainly visible in lateral view. Because of this, it was not possible to measure the width of dorsal and anterior caudal vertebrae, while for posterior caudals it was possible to measure the width but not the length, since they are disarticulated on the slab, mainly in anterior view (Fig. 4a). The apical vertebrae and the postflexural column are not preserved, except for a few postflexural vertebrae spread on the slab in anterior view.

The atlas-axis complex is preserved in anterior view (Figs 4, 5). The ventral edge is far less acute than in *Ophthalmosaurus icenicus* or *Arthropterygius chrisorum*, and more equidimensional as described in *Acamptonectes densus* (see Table 1) (Kirton, 1983; Maxwell, 2010; Fischer *et al.* 2012). The condylar facet is eroded into an irregular basin, and the sides are not well exposed, preventing detailed information on suture erasure between the elements. The floor of the neural canal is weakly concave in anterior view. A bone that we interpret to be the left half of the atlantal neural arch is preserved near the supraoccipital. If correctly interpreted, the right and left halves of the atlantal neural arch were unfused, and the neural spine was much smaller than those of more posterior vertebrae. By the eighth vertebra, the neural spines are taller than the height of the centra, closely spaced and rectangular. Although initially oriented vertically, they become slightly posteriorly inclined in the mid-dorsal region. In the posteriormost dorsal region, the neural spines are gradually reduced in height. Neural spines are not preserved in the caudal region, likely due to erosion.

Because of weathering and the articulated nature of the specimen, it is not possible to distinguish the cervical from the dorsal vertebrae. It is possible to identify a single ventrolateral rib facet (apophysis) occurring at the 41st preserved vertebra, marking the presacral–caudal transition. However, a portion of the mid-dorsal region is missing, making this a minimum estimate. Based on photos from the initial excavation, this is likely due to recent erosion rather than scavenging (De Marinis & Nicosia, 2000). In addition to the 41 presacral vertebrae, 31 anterior caudals are preserved, for a minimum count of preflexural vertebrae greater than 72.

In the literature, there are different numbers given for the presacral–caudal transition in *Ophthalmosaurus icenicus*: Kirton (1983) reports 42 presacral vertebrae, Buchholtz (2001) and Massare *et al.* (2006) report 39 presacrals for *Ophthalmosaurus icenicus*. Appleby (1956) reports 27, but this outlying value is most likely attributable to missing centra, as unless a specimen is

articulated there is no way to accurately evaluate the number of missing vertebrae (if any) in ichthyosaurs. The presacral count in *Ophthalmosaurus natans* is reported as 35 (Massare *et al.* 2006). The presacral vertebral count in *Platypterygius* species ranges from 46 to 54 (Maxwell & Kear (2010) note the artificially low count presented by Nace (1939) for *Platypterygius americanus* has a similar underlying cause to the artificially low count of Appleby (1956)). With more than 41 presacral vertebrae, MSVG 39617 is slightly outside the range of *Ophthalmosaurus* species.

Almost the entire column is preserved in lateral view, with the exception of a few rotated vertebrae that partially show the anterior or posterior surface (Figs 4, 6e). Although compression of vertebrae is evident, most of the column is preserved in articulation and there is no significant deformation in the relative proportions of the vertebral dimensions in lateral view (i.e. height and length). The centrum height to length ratio (CH/CL) varies from 2.21 to 2.89 in the presacral region and around 2.5 for the anterior caudals, so there is not a great deal of vertebral regionalization along the column (see Table 2). This weak regionalization of the axial skeleton is similar to the condition present in *Ophthalmosaurus natans* and *Sveltonectes insolitus*, but differs from *Ophthalmosaurus icenicus* (Kirton, 1983; Massare *et al.* 2006; Fischer *et al.* 2011).

A distinction between the cervical and the dorsal series is not possible, so the distinction made here is between anterior dorsals, posterior dorsals and anterior caudals. The anterior–posterior dorsal transition is not based on significant differences in vertebral morphology, but loosely corresponds to the position of the vertebrae relative to the gap in the dorsal region of MSVG 39617 (Fig. 4a). The anterior dorsal centra are longer than the other centra of the column, resulting in the lower CH/CL ratio. The posterior dorsals are more evenly amphicoelous than the anterior dorsals, and have a higher CH/CL ratio; however, this is always less than 3.0 (see Table 2). The diapophysis of the posterior dorsals is still very close to the anterior margin of the centrum, but its position is more ventral than in the anterior presacrals; the parapophysis is shifted slightly posteriorly and so is not as close to the anterior margin.

Most dorsal neural spines are preserved in articulation with the centra in lateral view and sometimes overlapped by the ribs (Figs 4, 6e). They are slightly posteriorly inclined in orientation, and approximately rectangular in shape. In the anterior dorsal region, there is a gradual increase in heights of the neural spines from 58 to 72 mm. The tallest neural spines are in the mid-dorsal region, with heights between 76 and 89 mm immediately anterior to the gap in the column, while posterior to the gap the posterior dorsal neural spines range between 65 and 70 mm in height (Table 1). In lateral view, the prezygapophyses are less offset in the anterior dorsal neural spines, and become more offset posteriorly along the column. The post-zygapophyses in lateral view are more pronounced in the anterior dorsal region than in the rest of the column.

The first unicipital rib facet occurs on the ventrolateral edge of the 42nd preserved centrum, marking the transition to the caudal region (Fig. 6e). The anterior caudals resemble the posterior dorsals in their dimensions, with a slightly lower CH/CL ratio (Table 2). The neural arch facets and the apophysis are both very enlarged, occupying a significant portion respectively of the dorsolateral and ventrolateral surfaces. The amphicoely of the anterior caudals is still well developed, although not as even as more anterior centra. In anterior view, the dorsal edge of the anterior caudals looks quite flattened and the centrum is rounded in shape, and in the most posterior anterior caudals is even wider than high, similar to *Arthropterygius chrisorum* and *Ophthalmosaurus icenicus* (Kirton, 1983; Maxwell, 2010).

A few postflexural caudal vertebrae are preserved, a few in anterior view and one in lateral view. Both preflexural and postflexural posterior caudal centra are slightly wider than high and are approximately rounded in shape, tapering slightly ventrally, and with a CH/CW ratio close to 0.90 or less (Table 2). The only postflexural centrum preserved in lateral view has a CH/CL ratio of 1.28 and is of an almost rectangular shape, with flattened dorsal and ventral edges; this centrum is not truly amphicoelous and its anterior and posterior borders are approximately parallel, as in *Arthropterygius chrisorum* (Maxwell, 2010).

Ribs in the anterior, mid- and posterior dorsal region are all prominently bicapitate, and bear a prominent groove parallel to their long axes (Fig. 6b, e). The dorsal ribs broaden slightly towards their distal tips. The distal tips are flattened and ungrooved (Fig. 6e). The tuberculum and capitulum of the most anterior trunk ribs are equivalent in size and less widely separated than in the posterior trunk ribs where the capitulum is much wider than the tuberculum. This is also reflected in the size of the diapophyses and parapophyses. The ribs begin to shorten rapidly in the posterior dorsal–sacral region (Fig. 6e). One of the posteriormost dorsal ribs is preserved dorsal to the vertebral column. This rib is short relative to more anterior ribs, and is not bicapitate (Fig. 6e). Its proximal end is slightly rounded, being much less robust than the tuberculum of the bicapital ribs.

No elements are preserved that can be unambiguously interpreted as gastralia.

5.c. Appendicular skeleton

Large portions of the pectoral girdle and forelimb have been preserved, but are disarticulated. No portions of the pelvic girdle or hindlimb are preserved.

Scapula. Both scapulae are preserved, but the left scapula is missing the proximal end, and is too flattened on the ribs to provide additional morphological detail. The right scapula is preserved in dorsal view, its distal end is broken and the proximal one is partially covered by a rib (Fig. 6b). It resembles the scapulae of *Ophthalmosaurus icenicus* and *Acamptonectes densus* in possessing an anteroposteriorly expanded proximal

end, and a flattened distal end (Kirton, 1983; Fischer *et al.* 2012). The shaft is strap-like, and not as slender as in *Acamptonectes*, with a broad proximal expansion both anterior and posterior to the long axis of the shaft (Fischer *et al.* 2012). The anterior edge for the articulation with the clavicle is quite oblique and externally concave, similar to the acromial process in *Ophthalmosaurus icenicus* and *Acamptonectes densus* (Kirton, 1983; Fischer *et al.* 2012). A small portion of the glenoid contribution is visible, but is covered by a rib anteriorly. The acromial process is large and well developed, similarly to *Acamptonectes densus* (Fischer *et al.* 2012).

Clavicle. The medial portion left clavicle is preserved in dorsal view (Fig. 6a). It is a broad flange, tapering distally, with a thickened ridge along the anterior margin. A similarly thickened ridge on the shaft is described for *Platypterygius americanus* (Maxwell & Kear, 2010). As in *Athabascasaurus bitumineus*, the descending ramus is wider and straighter than the posterodistal tip (Druckenmiller & Maxwell, 2010), even considering that both portions are flattened above the left quadrate.

Interclavicle. The clavicle is associated with the transverse bar of the interclavicle, also preserved in dorsal view (Fig. 6a). The interclavicle is thickened along the anterior margin, and its transverse bar is roughly diamond-shaped; the medial stem is not preserved.

Humerus. A humerus (?left) is preserved in dorsal view, severely dorsoventrally flattened (Figs 4, 6c). It is longer than it is wide, with a broader distal end than the proximal end (respectively 63% vs 45% of the humerus length), and is constricted at mid-shaft (Fig. 6c; Table 2). There are three distal articular facets, for a preaxial element, the radius and the ulna. The facets for the radius and ulna are subequal in length; that for articulation with the preaxial element is significantly smaller. In *Acamptonectes densus*, and in Ophthalmosaurinae in general, the facet for the preaxial element is described as being continuous with the radial one, while the ulnar facet is posteriorly deflected (e.g. Fischer *et al.* 2012). In dorsal view, the facet for the preaxial element in MSVG 39617 is reduced and highly anteroproximally deflected relative to both the radial facet and the long axis of the humerus, while there is no posterior deflection of the ulnar facet (Fig. 6c). This condition of the preaxial facet differs significantly in comparison to both *Ophthalmosaurus* species, and most ophthalmosaurids; however, a similar shape and position of the distal end of the humerus, based on personal observation, can be identified in both *Undorosaurus* species (*U. gorodischensis* UPM EP-N-23(744), *U. trautscholdi* GSM 1503: Arkhangelsky & Zverkov, 2014: figs 1, 2, pp. 189–190). Moreover, along the distal edge of the bone there is a thickening of the border coincident with the radial and ulnar facets, but not along the preaxial element facet; a similar thickening has been described by Maxwell & Kear (2010) in the humerus of *Platypterygius americanus*.

Zeugopodium. The preaxial element is preserved in articulation with the humerus (Fig. 6c). It is longer than anteroposteriorly wide, and articulates with a carpal distally, indicating the presence of a true preaxial digit; running posterodistally, the preaxial element also bears a faintly sinusoidal facet for articulation with the epipodial. The radius and ulna are preserved in the region around the left-hand ramus of the lower jaw in either dorsal or ventral view, and both are well exposed from the sediment (Fig. 6d). The radius is hexagonal and a great deal larger than the ulna, with six articular facets for humerus, preaxial element, preaxial carpal, radiale, intermedium, and for the ulna posteriorly (Fig 6c, d). The ulna is roughly sub-rectangular in shape, being proximo-distally shortened, and has only a single long distal articular facet, presumably for articulation with both the intermedium and ulnare, and then one for the humerus (Fig. 6d). There is no evidence for a pisiform facet. In McGowan & Motani (2003), an ulnar facet shorter than the radial facet is cited as being diagnostic of *Ophthalmosaurus*; in MSVG 39617, the two facets are subequal, with the ulnar facet being slightly longer (Table 1). The presence of posterior digits could not be verified.

Autopodium. Some phalanges are preserved disarticulated on the slab, all with an oval shape (Fig. 4a), as in *Ophthalmosaurus* spp. and *Arthropterygius chrisorum*, and unlike the rectangular phalanges of *Platypterygius* spp. and *Caypullisaurus bonapartei* (e.g. Kirton, 1983; Fernández, 2001, 2007; Kolb & Sander, 2009; Maxwell, 2010; Maxwell & Kear, 2010).

6. Phylogenetic analysis

To investigate the phylogenetic position of the new specimen within Ophthalmosauridae, we included *Gengasaurus nicosiai* gen. et sp. nov. in the data matrix of Roberts *et al.* (2014), adding three characters restored from the data matrix of Maxwell, Fernández & Schoch (2012), and including also *Ophthalmosaurus natans* (see online Supplementary Material, Text S1 at <http://journals.cambridge.org/geo> for characters list). *O. natans* was scored based on personal observation with reference to the literature (Gilmore, 1905, 1906); the codings of *Undorosaurus gorodischensis* are based on Arkhangelsky & Zverkov (2014) rather than Roberts *et al.* (2014), and characters 1 and 2 for *Maiaspondylus lindoei* are re-coded based on personal observation (see online Supplementary Material, Text S2 at <http://journals.cambridge.org/geo> for character–taxon matrix).

Our phylogenetic analysis is based on 24 taxa and 59 characters. The data matrix (generated with Mesquite ver. 3.01) was analysed with the software package TNT ver. 1.1 (Goloboff, Farris & Nixon 2008). *Temnodontosaurus* sp. is retained as outgroup, the Maxtrees were set to 10 000 and the analysis was run with 1000 replicates, employing the tree-bisection-reconnection (TBR)

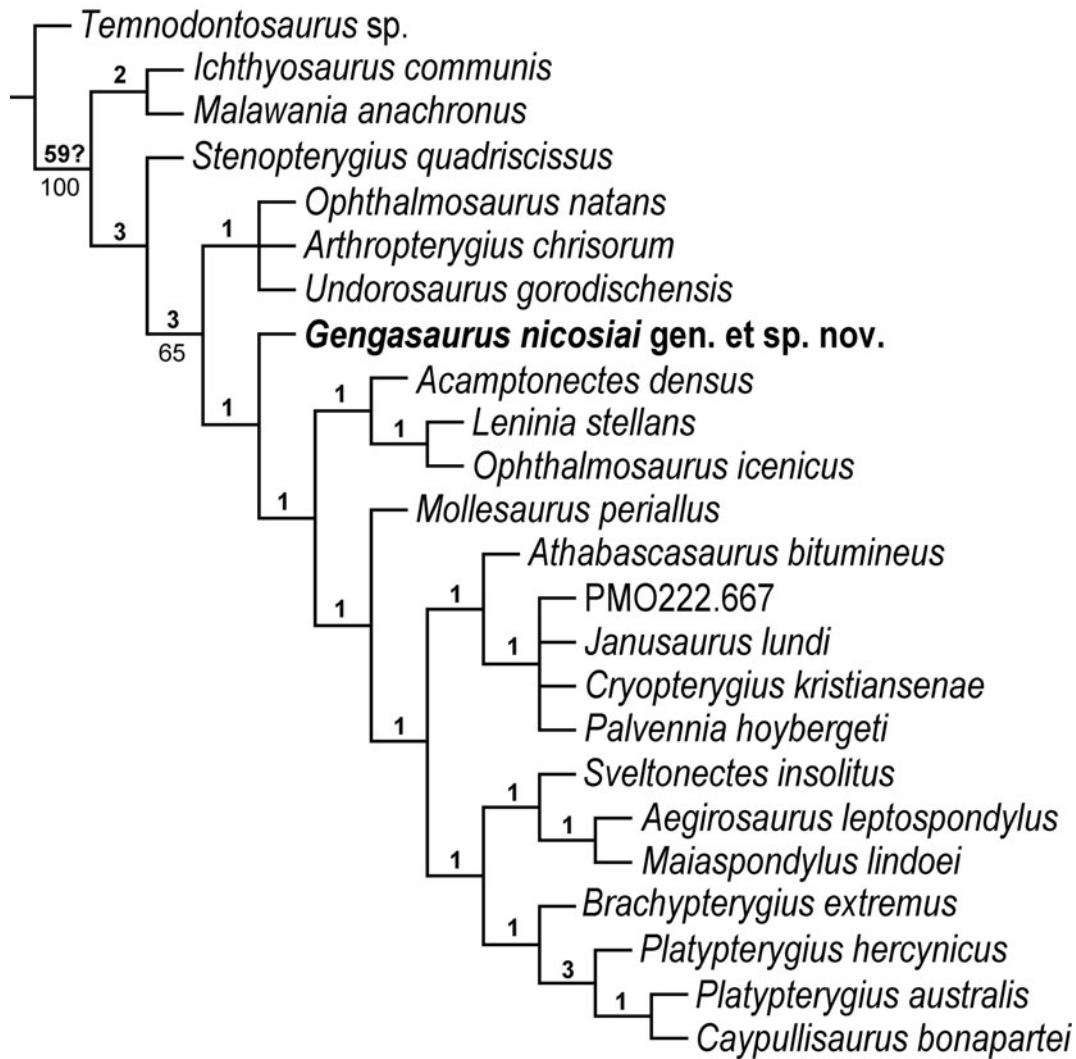


Figure 7. Strict consensus of three MPTs resulting from the performed analysis to assess the phylogenetic position of *Gengasaurus nicosiai* MSVG 39617: length = 157, CI = 0.465, RI = 0.594. Bremer support values of greater than 1 are presented above the branches (in bold), while bootstrap support values of greater than 50% are indicated below the branches.

algorithm. Following Roberts *et al.* (2014), characters were not weighted or ordered.

The result of the analysis consists of three most parsimonious trees (MPTs) with a length of 155 steps, a consistence index (CI) of 0.471 and a retention index (RI) of 0.604. We used TNT to calculate the Bremer support and the bootstrap values (run with 1000 replicates using the TBR algorithm). The resulting strict consensus tree (SCT) (generated with Mesquite) has a length of 157 steps, CI 0.465 and RI 0.594 (Fig. 7). The list and map of synapomorphies supporting each node is presented in the online Supplementary Material (Table S1; Fig. S1) at <http://journals.cambridge.org/geo>.

The family Ophthalmosauridae is well supported by a high number of synapomorphies recovered in all MPTs (see online Supplementary Material, Table S1 at <http://journals.cambridge.org/geo> for details). *Ophthalmosaurus natans*, *Undorosaurus gorodischensis* and *Arthropterygius chrisorum* form a polytomy basal to all the other ophthalmosaurids (Fig. 7). No unambiguously optimized synapomorphies separate *Gen-*

gasaurus nicosiai from more deeply nested nodes within Ophthalmosauridae.

Our results differ from those of Roberts *et al.* (2014) most significantly in loss of resolution. The addition of *O. natans* and *Gengasaurus nicosiai* does little to alter the basic structure of the tree recovered in Roberts *et al.* (2014): small changes, such as *Brachypterygius extremus* being more closely related to *Platypterygius* spp. than to *Aegirosaurus leptospondylus*, and the slightly altered relationship between *Maiaspondylus lindoei*, *Sveltonectes insolitus* and *A. leptospondylus*, are caused by re-coding the dental characters for *M. lindoei* rather than by including the new taxa.

By including *O. natans* and *G. nicosiai*, what has been affected most in the resulting topology is the subdivision into the two main clades within Ophthalmosauridae recovered in previous analyses (e.g. Fischer *et al.* 2012; Roberts *et al.* 2014). The more nested clade Platypterygiinae is retained, although with a few changes in the relationships among the included taxa with respect to Fischer *et al.* (2012) and Roberts

et al. (2014) (mostly in the position of *B. extremus*, as stated above). The Boreal clade of ophthalmosaurid ichthyosaurs proposed by Roberts *et al.* (2014) is also recovered, but the more inclusive Ophthalmosaurinae clade instead collapses, and not necessarily because of the inclusion of the new taxon. Indeed, an additional analysis performed with the current data matrix (using TNT) revealed that the simple addition of *O. natans* is sufficient to block recovery of this group as a distinct clade. However, it is notable that *O. natans*, unlike *G. nicosiai*, is clearly a member of Ophthalmosaurinae (*sensu* Fischer *et al.* 2012), but in this analysis it is closer to *A. chrisorum*, *U. gorodischensis* and *G. nicosiai* than to *O. icenicus*, raising questions about the monophyly of the genus. The non-monophyly of *Ophthalmosaurus* has also been recovered in previous analyses (e.g. Druckenmiller & Maxwell, 2010; Fischer *et al.* 2012), and thus requires closer scrutiny (see discussion below).

7. Taphonomy and associated shark teeth

Class CHONDRICHTHYES Huxley, 1880

ELASMOBRANCHII Bonaparte, 1838

EUSELACHII Hay, 1902

NEOSELACHII Compagno, 1977

SQUALIMORPHII Compagno, 1973

Order HEXANCHIFORMES Buen, 1926

Family ?CRASSNOTIDAE Kriwet & Klug, 2011
gen. et sp. indet.

Figure 8

The presence of two shark teeth on the slab closely associated with the ichthyosaur skeletal material, as well as the partial disarticulation and worn appearance of the bones, suggests that the skeleton lay exposed on the sea-floor for some time and scavenging activity may have occurred.

The teeth are 9 mm in length, multicuspoid, with a small mesial cusplet and three distal cusplets which decrease in size distal to the main cusp (Fig. 8a, b). The distal cusplets are only slightly smaller than the main cusp. The root is poorly preserved in both examples. The teeth can be attributed to a hexanchiform shark, whose fossil record extends from the Early to Late Jurassic (Kriwet & Klug, 2011). Hexanchiformes is a plesiomorphic group of squalomorph sharks, characterized by numerous extinct genera and three extant ones, with a widespread geographical distribution. Since the fossil record consists mainly of isolated teeth, hexanchiform sharks are recognized by a combination of dental characters (Kriwet & Klug, 2011). All Jurassic hexanchiforms described to date can be referred to the extinct family Crassonotidae, which is defined based on root morphology (Kriwet & Klug, 2011, 2014). Thus, although root morphology cannot be accurately assessed in the current example, referral to Crassonotidae is probable. The only hexanchiform reported to date from the Late Jurassic of Italy belongs to *Notidanus insignis* Seguenza, 1887, from the

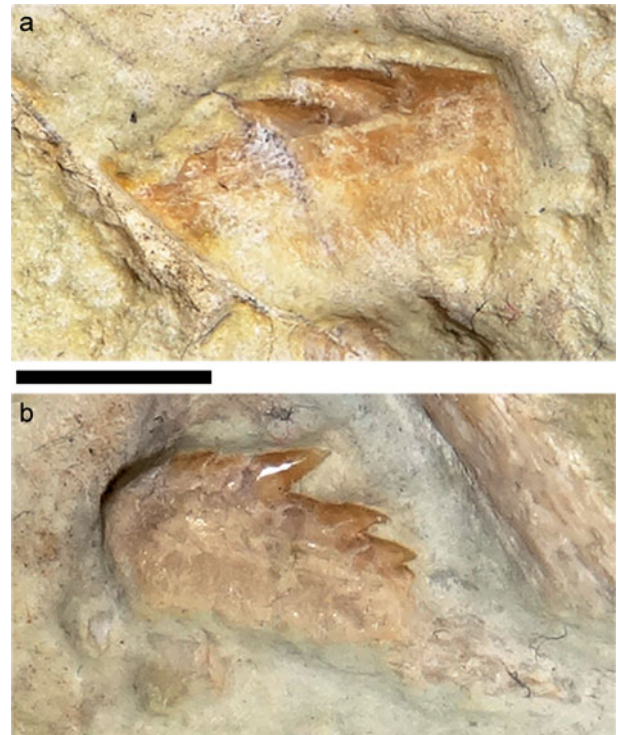


Figure 8. (Colour online) Multicuspoid shark teeth found on the same slab with the skeleton of *Gengasaurus nicosiai* MSVG 39617, attributed to Hexanchiformes: (a) best-preserved tooth in lingual view, with mesial and distal cusplets clearly visible; (b) the second preserved tooth in lingual? view. Scale bar: 10 mm.

Oxfordian of Sicily (Seguenza, 1887; Kriwet & Klug, 2011).

MSVG 39617 is flattened on a slab, with the skull elements mostly disarticulated but limited to a small area, and the vertebral column mainly in articulation and characterized by two main gaps, where some vertebrae are probably missing. The anterior ribs are broken and disarticulated, and many are scattered dorsal to the vertebral column and posterior to the skull. The shark teeth are also situated in this region. Possible bite marks can be identified on some bones, but it is difficult to establish this with certainty because of the deep erosion of the remains which confounds accurate interpretation. The carcass of the animal may have been exposed for some time on the seabed prior to burial, as suggested by poor preservation of the bone surfaces, and soft tissue may have been removed via mobile scavengers such as sharks. However, the limited degree of disarticulation, especially of the posterior dorsal vertebral column and ribs, suggests that this phase was short-lived and possibly only involved part of the skeleton.

8. Discussion

8.a. The questionable monophyly of *Ophthalmosaurus*

When both *O. icenicus* and *O. natans* are included, phylogenetic analyses of Ophthalmosauridae have persistently failed to recover *Ophthalmosaurus* as a monophyletic taxon because *Ophthalmosaurus* itself lacks

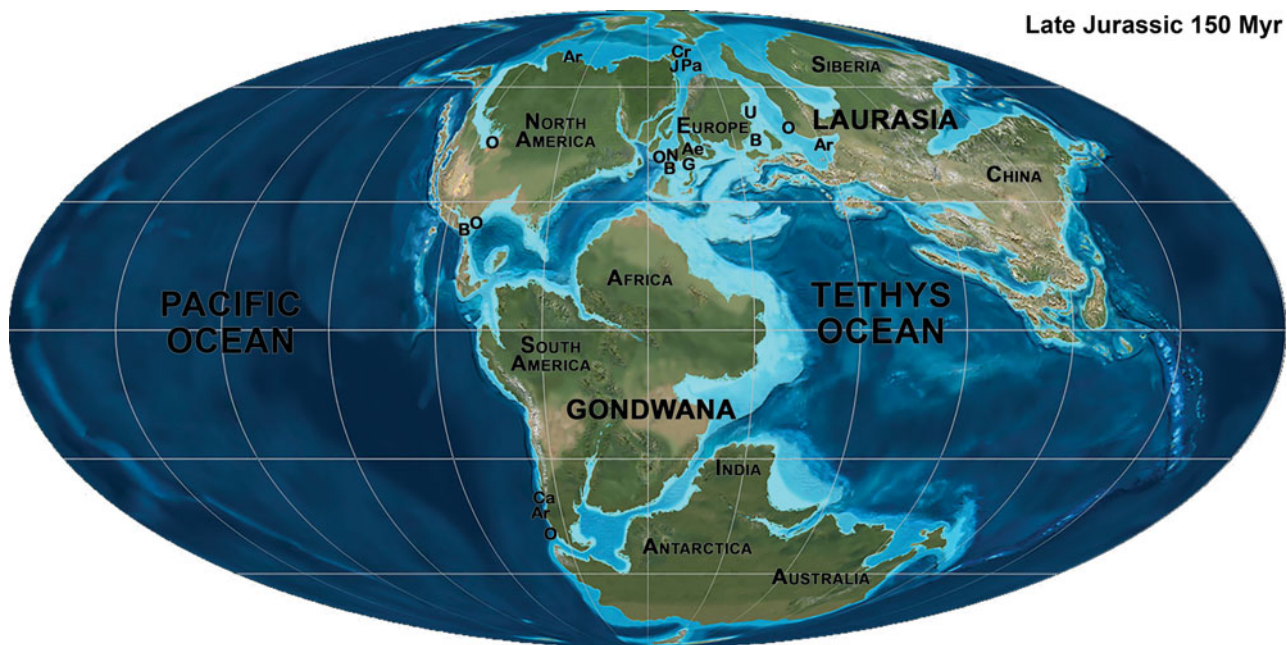


Figure 9. (Colour online) Position of diagnostic ophthalmosaurid remains of the Late Jurassic, including *Gengasaurus nicosiai* gen. et sp. nov. The palaeogeographic map is modified from Blakey (2008). Abbreviations: Ae, *Aegirosaurus*; Upper Jurassic lithographic limestones of Bavaria, Solnhofen Fm., lower Tithonian (Bardet & Fernández, 2000); Ar, *Arthropterygius* sp.; Melville Island, Northwest Territories, Canada, Ringnes Fm., (Oxfordian to Kimmeridgian) (Maxwell, 2010); Pampa Tril, Neuquén Province, Argentina, Upper Jurassic, Vaca Muerta Fm. (Tithonian) (Fernández & Maxwell, 2012); Porozhsk village, Sosnogorsk District, Komi Republic, Russia, Paromes Fm., Middle Volgian, Upper Jurassic (Zverkov *et al.* 2015); B, *Brachypterygius*; South UK (Kirton, 1983); La Caja Fm., Coahuila, Mexico (Buchy & Lopez-Oliva, 2009); Ca, *Caypullisaurus bonapartei*; Cerro Lotena, Neuquén Province, northwestern Patagonia, Argentina (Fernández, 1999); Tithonian–Berriasian; Vaca Muerta Fm., Upper Jurassic (Fernández, 1999); Cr, *Cryopterygius*; Late Jurassic to earliest Cretaceous, Slottsmøya Member of the Agardhfjellet Fm. in the central Spitsbergen, Sassenfjord area (Druckenmiller *et al.* 2012; Roberts *et al.* 2014); G, *Gengasaurus nicosiai*; late Kimmeridgian – earliest Tithonian, Calcarei a Saccocoma e Aptici Member, Calcarei Diasprigni Fm., Umbrian–Marchean Apennine Succession, Genga, Ancona, Marche, Italy; J, *Janusaurus lundii*; North side of Janusfjellet, northeast of Longyearbyen, Spitsbergen, Svalbard, Norway; Late Jurassic to earliest Cretaceous, Slottsmøya Member of the Agardhfjellet Fm. in the central Spitsbergen, Sassenfjord area (Roberts *et al.* 2014); N, *Nannopterygius enthekiodon*, Upper Jurassic, Tithonian, Kimmeridge Clay, UK (Hulke, 1871). O, *Ophthalmosaurus* spp.; Callovian – Kimmeridgian, Oxford Clay of Peterborough, and Kimmeridge Clay of the Oxford district, Wiltshire and Dorset (South UK) (Kirton, 1983); lower to middle Volgian, Ul’yanovsk Region, Russia (Storrs, Arkhangelsky & Efimov, 2000); early Tithonian, La Caja Fm., Coahuila, Mexico (Buchy, 2010); Late Jurassic, Mendoza Province, Argentina (McGowan & Motani, 2003); Oxfordian, Sundance Fm., Wyoming, USA (Gilmore, 1905); Polar District of Nenets Autonomous Region (Okrug), Volonga River, Upper Volgian to Berriasian (Zverkov *et al.* 2015); Pa, *Palvemia*; Late Jurassic to earliest Cretaceous, Slottsmøya Member of the Agardhfjellet Fm. in the central Spitsbergen, Sassenfjord area (Druckenmiller *et al.* 2012; Roberts *et al.* 2014); U, *Undorosaurus*; middle Volgian, Ul’yanovsk and Moscow Region, Russia (Efimov, 1999; Storrs, Arkhangelsky & Efimov, 2000; Arkhangelsky & Zverkov, 2014).

clear autapomorphies (e.g. Druckenmiller & Maxwell, 2010; Fischer *et al.* 2012). Our phylogenetic analysis recovered *O. natans* to be closer to *A. chrisorum*, *U. gorodischensis* and *G. nicosiai* than to *O. icenicus*, and this result lends credence to the non-monophyly of the genus *Ophthalmosaurus*, as well as the validity of *O. natans*.

From the current data matrix (see online Supplementary Material at <http://journals.cambridge.org/geo>), it is obvious that *O. natans* differs from *O. icenicus* in several aspects of both cranial and post-cranial morphology. Previous authors have questioned the validity of *O. natans* as a different species (e.g. McGowan & Motani, 2003), and this taxon is often excluded from phylogenetic analyses (e.g. Roberts *et al.* 2014). Fischer *et al.* (2012) recall a former name for the taxon (i.e. *Baptanodon natans*, according to Gilmore, 1906), and we agree with these authors that there is no support for the synonymization of *O. natans* and

O. icenicus. Moreover, the fact that *O. natans* is separated from the type species of the genus on the basis of a consistent number of phylogenetically relevant features should be enough to question its inclusion in the same taxon.

8.b. Why *Gengasaurus* is a new valid taxon

A palaeogeographic map showing the distribution of the Late Jurassic fossil record of ophthalmosaurid ichthyosaurs, and including the new material from Italy from a poorly sampled area of the Tethys, is presented in Figure 9. MSVG 39617 is clearly referable to Ophthalmosauridae based on the reduced extracondylar area of the basioccipital, as well as the presence of a preaxial digit (Motani, 1999). The affinities of MSVG 39617 relative to all the other ophthalmosaurid taxa are unresolved: no unambiguous diagnostic features can be

addressed to justify the inclusion of this taxon in one specific genus instead of another.

MSVG 39617 is most similar to *Ophthalmosaurus* spp. in phalangeal and basioccipital morphology. However, the new taxon differs from the described species of *Ophthalmosaurus* in several respects, including the shape of the posterior basisphenoid (known only for *Ophthalmosaurus icenicus*), a less regionalized vertebral column than in *O. icenicus* (see following section), the shape of the supraoccipital (differs only from *O. icenicus*), the reduced and highly anteroproximally deflected preaxial facet of the humerus, and a proximodistally shortened ulna. The shape of the posterior basisphenoid and a proportionately larger orbit also distinguish MSVG 39617 from '*O.*' *normanniae* from the Kimmeridgian of France (Lennier, 1887).

The extracondylar area of the basioccipital is not as reduced as in *Palvennia hoybergeti*, *Brachypterygius extremus*, *Janusaurus lundi* or *Arthropterygius chrisorum* (Kirton, 1983; Maxwell, 2010; Druckenmiller *et al.* 2012; Roberts *et al.* 2014). In comparison to *Undorosaurus* sp. and *Paraophthalmosaurus* spp. the proximal end of the humerus is relatively less expanded in MSVG 39617 (Arkhangelsky, 1997; see also character scoring in Arkhangelsky & Zverkov, 2014). The new specimen lacks a distal facet on the humerus for articulation with the intermedium (characteristic, for instance, of *Brachypterygius extremus* and *Aegirosaurus leptospondylus*: Kirton, 1983; Bardet & Fernández, 2000), but the facet for a preaxial element is well developed (absent in *Nannopterygius enthekiodon*, reduced or absent in *Cryptopterygius kristiansenae*: Hulke, 1871; Kirton, 1983; Druckenmiller *et al.* 2012). Phalanges are rounded, and not blocky as in *Caypullisaurus bonapartei* (Fernández, 1997, 2001) or typically rectangular as in *Platypterygius* spp. (McGowan, 1972; McGowan & Motani, 2003) and *Sveltonectes insolitus* (Fischer *et al.* 2011). MSVG 39617 lacks the expanded proximal ribs characteristic of *Mollesaurus periallus* (Talevi & Fernández, 2012).

The new specimen cannot be considered a member of Ophthalmosaurinae (*sensu* Fischer *et al.* 2012) because of the lack of a posterodistally deflected ulnar facet of the humerus (which is clearly in line with the radial facet in MSVG 39617), and a posterior surface of the ulna straight and nearly as thick as the rest of the element (and not concave and forming a sharp edge as in *Ophthalmosaurus icenicus* or *Acamptonectes densus*: Kirton, 1983; Fischer *et al.* 2012). Since the extracondylar area of the basioccipital in MSVG 39617 is not extremely reduced, the specimen is also excluded from Platypterygiinae (*sensu* Fischer *et al.* 2012).

The peculiar condition of the preaxial accessory facet on the humerus in MSVG 39617 can be favourably compared to *Undorosaurus* spp. (based on Arkhangelsky & Zverkov, 2014). However, the radius in MSVG 39617 has a hexagonal shape and bears six articular facets (Fig. 6c), while in *Undorosaurus* spp. the radius is pentagonal (Arkhangelsky & Zverkov, 2014); the ulnar facet on the humerus is evidently posterodistally de-

flected in *U. trautscholdi* (GSM 1503: Arkhangelsky & Zverkov, 2014, fig. 2, p. 190) and the same is mentioned in the description for *U. gorodischensis* (Arkhangelsky & Zverkov, 2014, p. 188), while in MSVG 39617, ulnar and radial facets are both directed distally (Fig. 6c); finally, radius–ulna proportions, and phalanges in MSVG 39617 differ significantly from the same elements in both *Undorosaurus* species (Efimov, 1999; Arkhangelsky & Zverkov, 2014).

This late Kimmeridgian – earliest Tithonian ichthyosaur from the Western Tethys retains a fairly basal position within Ophthalmosauridae, displaying a very conservative morphology in comparison to the two more nested lineages of ophthalmosaurids (Ophthalmosaurinae and Platypterygiinae) recovered in previous phylogenetic analyses (e.g. Fischer *et al.* 2012, 2014; Arkhangelsky & Zverkov, 2014; Roberts *et al.* 2014). However, whereas MSVG 39617 is clearly a valid taxon based on a unique combination of characters, the lack of more evident autapomorphies will make referral of subsequent material challenging.

8.c. Regionalization of the axial skeleton

Motani (1999) identified a short dorsal centrum length relative to the height as a diagnostic vertebral feature in *Ophthalmosaurus icenicus*; Massare *et al.* (2006) reported that this feature could distinguish *O. icenicus* (CH/CL greater than 3.0 and up to 4.0) from *O. natans* (CH/CL between 2.0 and 2.5). MSVG 39617 exhibits a maximum CH/CL ratio of 2.89 in the preserved dorsal region, suggesting it does not have the unusually short centra and marked regionalization of the vertebral column of *O. icenicus* (Buchholz, 2001; Massare *et al.* 2006). A highly regionalized column morphology is also characteristic of *Arthropterygius chrisorum* (Maxwell, 2010), but is not observed in other ophthalmosaurids. A poorly regionalized column, resembling the condition seen in MSVG 39617, is recognized instead in *O. natans* as well as in *Sveltonectes insolitus* (Massare *et al.* 2006; Fischer *et al.* 2011).

The regionalization of the column is expected to be affected by homoplasy and is not considered to have diagnostic value above the specific level. It is reasonable to use columnar regionalization to eventually discriminate two species within the same genus, but only when they also share a certain number of phylogenetically relevant features (and as discussed in the previous paragraphs this is not the case in '*O.*' *natans* and *O. icenicus*). To consider this character for a distinction at higher taxonomic ranks becomes inevitably problematic, since it clearly evolved multiple times in different lineages of ichthyosaurs (e.g. Buchholz, 2001; Massare *et al.* 2006; Maxwell, 2010; Fischer *et al.* 2011, 2012).

Based on the criteria of Buchholz (2001), in spite of the retention of a weakly regionalized vertebral column, *Gengasaurus nicosiai* was likely capable of rapid and sustained swimming, based on fused centra leading to cervical stability, relatively small forefins, and high neural spines to enhance trunk depth.

9. Conclusion

Gengasaurus nicosiai gen. et sp. nov. is a new ophthalmosaurid that provides important new information on the diversity of ophthalmosaurid ichthyosaurs from the western Tethyan margin. Although not preserved under Lagerstätte-type conditions, this specimen shows a unique combination of characters relative to all other ophthalmosaurids, including a peculiar condition of the preaxial facet on the humerus, that based on personal observation from the literature may be shared with *Undorosaurus* spp. (Efimov, 1999; Arkhangel'sky & Zverkov, 2014). The inclusion of *Gengasaurus nicosiai* and 'Ophthalmosaurus' *natans* in the updated data matrix of ophthalmosaurid ichthyosaurs caused a loss of cohesion of the subfamily Ophthalmosaurinae (*sensu* Fischer *et al.* 2012). *Gengasaurus* is a new taxon that shares characters with both platypterygiines (e.g. ulnar facet in line with the radial one; posterior surface of ulna straight and thick) and ophthalmosaurines (e.g. extracondylar area of basioccipital present ventrally and laterally; rounded phalanges; paroccipital process of opisthotic elongated and slender), being highly conservative from a morphological point of view in comparison to the two more nested lineages within Ophthalmosauridae. 'O.' *natans*, although clearly sharing the diagnostic features of Ophthalmosaurinae (*sensu* Fischer *et al.* 2012), is basally positioned within Ophthalmosauridae rather than more deeply nested along with the rest of the subfamily, which could be due to poorly defined characters and missing data. Moreover, as has been questioned by previous authors (e.g. Druckenmiller & Maxwell 2010, Fischer *et al.* 2012), our results recover a condition of non-monophyly of the genus *Ophthalmosaurus*, and in addressing the number of differences that distinguish 'O.' *natans* from *O. icenicus*, we reject the inclusion of the two taxa in the same genus, recommending reconsideration of *Baptanodon natans* as a valid taxon.

The monophyletic group of Boreal ophthalmosaurids proposed by Roberts *et al.* (2014) is also recovered in our analysis; however, the use of the endemism of ammonites and onychites described by Cecca *et al.* (2005) and Hammer *et al.* (2013) is insufficient to justify the lack of connection between the Tethys and the Proto-Atlantic at this time interval, since endemism is not recovered in other microfossils, like calpionellids (Adatte *et al.* 1996), crinoids (Manni & Nicosia, 1996), bivalves (Liu, Heinze & Farsich, 1998) and gastropods (Gatto *et al.* 2015). Both the Hispanic corridor and the South Africa – Rocas Verdes seaway were opened during the Late Jurassic – Early Cretaceous as possible dispersal routes between the Tethys and Pacific Ocean (Shultz, Fildani & Suarez, 2003; Bardet *et al.* 2014); however, factors like species-specific water temperature preferences, and distribution of preferred prey, are often not considered when discussing dispersal capabilities of Mesozoic marine reptiles. Although ophthalmosaurids are often suggested to be fast-swimming and migratory, diagnostic remains normally show extreme

endemism; the expected wide geographic ranges can be observed at the generic level, but for few species (e.g. *Ophthalmosaurus* and *Arthropterygius*). Ichthyosaur subgroups are highly affected by convergence, as confirmed by the high values of RI usually retained in phylogenetic analyses: this makes it more difficult to solve the interrelationships at both the specific and generic levels, and even more at higher taxonomic ranks. As a future goal, the redaction of a new and more expanded character data matrix, improving the amount of informative characters, is highly recommended in order to better understand the diversity and disparity of Jurassic and Cretaceous ichthyosaurs, and try to solve the interrelationships between the terminal taxa.

Acknowledgements. We thank the authorities for the Cultural Heritage of the Marche Region that allowed the study of the specimen, M. Filipponi of the Consorzio Frasassi Company, manager of the Museo di San Vittore di Genga, who gave his full availability to access the collection, and also the staff of the Pro Loco di Genga Company who provided full access to the specimen, even outside opening hours. Special thanks go to U. Nicosia who provided assistance and support during the trip to Genga, and all the information regarding the original preparation of the specimen and its history since the discovery. N. Mariotti and M. Santantonio are thanked for helpful suggestions, and revision of the biostratigraphic and geological information. Thanks also to A. Henrici (Carnegie Museum) for providing access to comparative material, J. Kriwet for discussion regarding attribution of the shark teeth, and R. C. Blakey for providing a high-quality version of the palaeogeographic map. I.P. thanks T. R. Simões and O. Vernygora for helpful suggestions and comments on the use of TNT. Finally, we warmly thank the editors P. Upchurch and S. Bloor for their support during the revision process, and V. Fischer and an anonymous reviewer for detailed comments. Expenses for M.W.C. and E.M.M. were supported in part from the following grants: NSERC Discovery Grant (#2384 8-01), and Chair's Research Allowance to M.W.C.

Supplementary material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0016756816000455>.

References

- ADATTE, T., STINNESBECK, W., REMANE, J. & HUBBERTEN, H. 1996. Paleocanographic changes at the Jurassic – Cretaceous boundary in the Western Tethys, northeastern Mexico. *Cretaceous Research* **17**, 671–89.
- ANDREINI, G., CARACUEL, J. E. & PARISI, G. 2007. Calpionellid biostratigraphy of the Upper Tithonian–Upper Valanginian interval in Western Sicily (Italy). *Swiss Journal of Geosciences* **100**, 179–98.
- APPLEBY, R. M. 1956. The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. *Proceedings of the Zoological Society of London* **16**, 403–47.
- ARKHANGEL'SKY, M. S. 1997. On a new genus of ichthyosaurs from the Lower Volgian substage of the Saratov, Volga Region. *Paleontological Journal* **21**, 87–91.
- ARKHANGEL'SKY, M. S. & ZVERKOV, N. G. 2014. On a new ichthyosaur of the genus *Undorosaurus*. *Proceedings of the Zoological Institute* **318**, 187–96.

- BALINI, M. & RENESTO, S. 2012. *Cymbospondylus* vertebrae (Ichthyosauria, Shastasauridae) from the Late Anisian Prezzo Limestone (Middle Triassic, Southern Alps) with an overview of the chronostratigraphic distribution of the group. *Rivista Italiana di Paleontologia e Stratigrafia* **118**, 155–72.
- BARDET, N., CORRAL, J. C. & PEREDA-SUBERBIOLA, X. 1997. Les Mosasaures (Squamata) du Crétacé supérieur du Bassin basco-cantabrique. *Geobios* **20**, 19–26.
- BARDET, N., FALCONNET, J., FISCHER, V., HOUSSAYE, A., JOUVE, S., PEREDA-SUBERBIOLA, X., PÉREZ-GARCÍA, A., RAGE, J.-C. & VINCENT, P. 2014. Mesozoic marine reptile palaeobiogeography in response to drifting plates. *Gondwana Research* **26**, 869–87.
- BARDET, N. & FERNÁNDEZ, M. S. 2000. A new ichthyosaur from the Upper Jurassic Lithographic Limestones of Bavaria. *Journal of Paleontology* **74**, 503–11.
- BAUR, G. 1887. On the morphology and origin of the Ichthyopterygia. *American Naturalist* **21**, 837–40.
- BLAINVILLE, H. M. DE. 1835. Description de quelques espèces de reptiles de la Californie, précédé de l'analyse d'un système général d'erpétologie et d'amphibiologie. *Nouvelles Annales du Muséum d'Histoire Naturelle, Paris* **4**, 233–96.
- BLAKEY, R. C. 2008. Gondwana paleogeography from assembly to breakup – a 500 m.y. odyssey. In *Resolving the Late Paleozoic Ice Age in Time and Space* (eds C. R. Fielding, T. D. Frank & J. L. Isbel), pp. 1–28. Geological Society of America Special Paper no. 441.
- BONAPARTE, C. L. 1838. Selachorum tabula analytica. *Nuovi Annali Scienze Naturali* **2**, 195–214.
- BUCHHOLTZ, E. A. 2001. Swimming styles in Jurassic ichthyosaurs. *Journal of Vertebrate Paleontology* **21**, 61–73.
- BUCHY, M.-C. 2010. First record of *Ophthalmosaurus* (Reptilia: Ichthyosauria) from the Tithonian (Upper Jurassic) of Mexico. *Journal of Paleontology* **84**, 149–55.
- BUCHY, M.-C. & LOPEZ-OLIVA, J. G. 2009. Occurrence of a second ichthyosaur genus (Reptilia; Ichthyosauria) in the Late Jurassic Gulf of Mexico. *Boletín de la Sociedad Geológica Mexicana* **61**, 233–8.
- BUEN, F. DE. 1926. Catálogo ictológico del Mediterráneo español y de Marruecos recopilando lo publicado sobre peces de las costas mediterráneas y próximas del Atlántico (Mar de España). *Commission Internationale pour l'exploration scientifique de la mer Méditerranéenne, Madrid* **2**, 1–221.
- CARMINATI, E. & SANTANTONIO, M. 2005. Control of differential compaction on the geometry of sediments onlapping paleoescarpments: insights from field geology (Central Apennines, Italy) and numerical modelling. *Geology* **33**, 353–6.
- CECCA, F., CRESTA, S., PALLINI, G. & SANTANTONIO, M. 1990. Il Giurassico di Monte Nerone (Appennino marchigiano, Italia Centrale): biostratigrafia, litostratigrafia ed evoluzione paleogeografica. In *Atti del II Convegno Internazionale 'Fossili, Evoluzione, Ambiente'* (eds G. Pallini, F. Cecca, S. Cresta & M. Santantonio), pp. 63–139. Pergola: Comitato Centenario Raffaele Piccinini.
- CECCA, F., VRIELYNCK, B., LAVOYER, T. & GAGET, H. 2005. Changes in the ammonite taxonomical diversity gradient during the Late Jurassic-Early Cretaceous. *Journal of Biogeography* **32**, 535–47.
- CENTAMORE, E., CATENACCI, V., CHIOCCHINI, M., CHIOCCHINI, U., JACOBACCI, A., MARTELLI, G., MICARELLI, A. & VALLETTA, M. 1975. *Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 291 'Pergola'*. Roma: Servizio Geologico d'Italia, 40 pp.
- CENTAMORE, E., CHIOCCHINI, M., DEIANA, G., MICARELLI, A. & PIERUCCINI, U. 1971. Contributo alla conoscenza del Giurassico dell'Appennino Umbro-Marchigiano. *Studi Geologici Camerti* **1**, 1–89.
- CHIOCCHINI, M., CHIOCCHINI, R. A., DIDASKALOU, P. & POTETTI, M. 2008. Microbiostratigrafia del Triassico Superiore, Giurassico e Cretacico in facies di piattaforma carbonatica del Lazio centro-meridionale e Abruzzo: revisione finale. *Memorie Descrittive della Carta Geologica d'Italia* **84**, 5–170.
- CITA, M. B., ABBATE, E., BALLINI, M., CONTI, A., FALORNI, P., GERMANI, D. & PETTI, F. M. 2007. Carta Geologica d'Italia – 1:50.000, Catalogo delle Formazioni, Unità tradizionali. *Quaderni del Servizio Geologico d'Italia, Serie III, Vol. 7*, Roma, 382 pp.
- COLTORTI, M. 1980. Geologia della regione di M. Petrosino – M. Murano (Appennino Marchigiano). *Annali dell'Università di Ferrara* **7**, 1–36.
- COLTORTI, M. & BOSELLINI, A. 1980. Sedimentazione e tettonica nel Giurassico della dorsale marchigiana. *Studi Geologici Camerti* **6**, 13–21.
- COMPAGNO, L. J. V. 1973. Interrelationships of living elasmobranchs. In *Interrelationships of Fishes* (eds H. P. Greenwood, R. Miles & C. Patterson), pp. 15–61. New York Academic Press.
- COMPAGNO, L. J. V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* **17**, 303–22.
- DAL SASSO, C., INSACCO, G., CHIARENZA, A. A., DI FRANCO, D. & REITANO, A. 2014. First record of ichthyosaurs in Sicily (Upper Triassic of Monte Scalpello, Catania Province). *Rivista Italiana di Paleontologia e Stratigrafia* **120**, 71–82.
- DANISE, S., TWITCHETT, R. J. & MATTS, K. 2014. Ecological succession of a Jurassic shallow-water ichthyosaur fall. *Nature Communications* **5**, 4789.
- DE MARINIS, G. & NICOSIA, U. 2000. *L'Itiosaurio di Genga*. Castelferretti, Ancona: Cassa di Risparmio di Fabriano e Cupramontana Edizioni, 220 pp.
- DI BUCCI, D., FRIELLO, P., PALLINI, G. & SANTANTONIO, M. 1994. Il sistema giurassico di piattaforma carbonatica pelagica/bacino nell'area di M. Scoccioni – Castelletta (Appennino Marchigiano). *Palaeopelagos*, Special Publication no. 1, 79–91.
- DRUCKENMILLER, P. S., HURUM, J. H., KNUITSEN, E. M. & NAKREM, H. A. 2012. Two new ophthalmosaurids (Reptilia: Ichthyosauria) from the Agardhfjellet Formation (Late Jurassic: Volgian/Tithonian), Svalbard, Norway. *Norwegian Journal of Geology* **92**, 311–39.
- DRUCKENMILLER, P. S. & MAXWELL, E. E. 2010. A new lower Cretaceous (lower Albian) ichthyosaur genus from the Clearwater Formation, Alberta, Canada. *Canadian Journal of Earth Sciences* **47**, 1037–53.
- EFIMOV, V. M. 1999. A new family of ichthyosaurs, the Undorosauridae fam. nov. from the Volgian Stage of the European part of Russia. *Paleontological Journal* **33**, 174–81.
- FARINACCI, A., MALANTRUCCO, G., MARIOTTI, N. & NICOSIA, U. 1981. Ammonitico Rosso facies in the framework of the Martani Mountains paleoenvironmental evolution during Jurassic. In *Rosso Ammonitico Symposium Proceedings* (eds A. Farinacci & S. Elmi), pp. 311–34. Roma: Edizione Tecnoscienza.
- FASTELLI, C. & NICOSIA, U. 1980. L'Itiosaurio di Genga (Ancona). In *I vertebrati fossili italiani* (eds G. Parisi & G. Seppi), pp. 95–101. Verona: Catalogo della Mostra.

- FERNÁNDEZ, M. S. 1997. A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin, North-western Patagonia, Argentina. *Journal of Paleontology* **71**, 479–84.
- FERNÁNDEZ, M. S. 1999. A new ichthyosaur from the Los Molles Formation (Early Bajocian), Neuquén Basin, Argentina. *Journal of Paleontology* **73**, 677–81.
- FERNÁNDEZ, M. S. 2001. Dorsal or ventral? Homologies of the forefin of *Caypullisaurus* (Ichthyosauria: Ophthalmosauria). *Journal of Vertebrate Paleontology* **21**, 515–20.
- FERNÁNDEZ, M. S. 2007. Redescription and phylogenetic position of *Caypullisaurus* (Ichthyosauria: Ophthalmosauridae). *Journal of Paleontology* **81**, 368–75.
- FERNÁNDEZ, M. S. & MAXWELL, E. E. 2012. The genus *Arthropterygius* Maxwell (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic of the Neuquén Basin, Argentina. *Geobios* **45**, 535–40.
- FISCHER, V., BARDET, N., GUIOMAR, M. & GODEFROIT, P. 2014. High diversity in Cretaceous ichthyosaurs from Europe prior to their extinction. *PLOS ONE* **9**, e84709.
- FISCHER, V., MAISCH, M. W., NAISH, D., KOSM, R. & LISTON, J. 2012. New ophthalmosaurid ichthyosaurs from the European Lower Cretaceous demonstrate extensive ichthyosaur survival across the Jurassic–Cretaceous boundary. *PLoS ONE* **7**, e29234.
- FISCHER, V., MASURE, E., ARKHANGELSKY, M. S. & GODEFROIT, P. 2011. A new Barremian (Early Cretaceous) ichthyosaur from Western Russia. *Journal of Paleontology* **31**, 1010–50.
- FORNACIARI, B., MAXWELL, E. E., ZORZIN, R. & PAPAZZONI, C. A. 2014. A new *Platypterygius* rostrum from the Lower Cretaceous of Lessini Mts (N Italy). *12th European Association of Vertebrate Palaeontologists Meeting*, Torino, 24–28 June 2014, Abstract Book, p. 62.
- GALDENZI, S. 1986. Rapporti laterali tra diverse sequenze giurassiche nella dorsale marchigiana fra la Gola della Rossa e Monte Canfaito. *Memorie della Società Geologica Italiana* **35**, 49–55.
- GALLUZZO, F. & SANTANTONIO, M. 1994. Geologia e paleogeografia giurassica dell'area compresa tra la Valle del Vernino e Monte Murano (Monti della Rossa, Appennino marchigiano). *Bollettino della Società Geologica Italiana* **113**, 587–612.
- GALLUZZO, F. & SANTANTONIO, M. 2002. The Sabina Plateau: a new element in the Mesozoic palaeogeography of Central Apennines. *Bollettino della Società Geologica Italiana* **S1**, 561–88.
- GATTO, R., MONARI, S., SZABÓ, J. & CONTI, M. A. 2015. The Jurassic pleurotomarioidean gastropod *Laevitormaria* and its palaeobiogeographical history. *Acta Palaeontologica Polonica* **60**, 217–33.
- GILLIÉRON, V. 1873. Aperçu géologique sur les Alpes de Fribourg en général et description spéciale du Monsalvens en particulier. *Matériaux pour la Carte géologique de la Suisse* **12**, 1–268.
- GILMORE, C. W. 1905. Osteology of *Baptanodon* (Marsh). *Memoirs of the Carnegie Museum* **2**, 77–129.
- GILMORE, C. W. 1906. Notes on osteology of *Baptanodon*. With a description of a new species. *Memoirs of the Carnegie Museum* **2**, 325–42.
- GOLOBOFF, P. A., FARRIS, J. S. & NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–86.
- GUERRERA, F. & TRAMONTANA, M. 2002. *Note Illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 292 'Jesi'*. Roma: Servizio Geologico d'Italia, 122 pp.
- HAMMER, Ø., HRYNIEWICZ, K., HURUM, J. H., HØYBERGET, M. & KNUTSEN, E. M. 2013. Large onychites (cephalopod hooks) from the Upper Jurassic of the Boreal Realm. *Acta Palaeontologica Polonica* **59**, 827–35.
- HAY, O. P. 1902. Bibliography and catalogue of fossil vertebrata of North America. *Bulletin of the United States Geological Survey* **179**, 1–868.
- HULKE, J. W. 1871. Note on an *Ichthyosaurus* (*I. enthekiodon*) from Kimmeridge Bay, Dorset. *Quarterly Journal of the Geological Society of London* **27**, 440–1.
- HUXLEY, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* **43**, 649–62.
- KEAR, B. P. 2005. Cranial morphology of *Platypterygius longmani* Wade, 1990 (Reptilia: Ichthyosauria) from the Lower Cretaceous of Australia. *Zoological Journal of the Linnean Society* **145**, 583–622.
- KIRTON, A. M. 1983. *A review of British Upper Jurassic ichthyosaurs*. Ph.D. thesis, University of Newcastle upon Tyne, UK. Published thesis.
- KOLB, C. & SANDER, M. P. 2009. Redescription of the ichthyosaur *Platypterygius hercynicus* (Kuhn 1946) from the Lower Cretaceous of Salzgitter (Lower Saxony, Germany). *Palaeontographica Abteilung A (Paläozoologie–Stratigraphie)* **288**, 151–92.
- KRIWET, J. & KLUG, S. 2011. A new Jurassic cow shark (Chondrichthyes, Hexanchiformes) with comments on Jurassic hexanchiform systematics. *Swiss Journal of Geosciences* **104**, Supplement 1, 107–14.
- KRIWET, J. & KLUG, S. 2014. Dental patterns of the stem-group hexanchoid shark, *Notidanooides muensteri* (Elasmobranchii, Hexanchiformes). *Journal of Vertebrate Paleontology* **34**, 1292–306.
- LENNIER, G. 1887. Description des fossiles du Cap de la Hève. *Bulletin de la Société Géologique de Normandie, Le Havre* **12**, 17–98.
- LIU, C., HEINZE, M. & FARSICH, F. T. 1998. Bivalve provinces in the Proto-Atlantic and along the southern margin of the Tethys in the Jurassic. *Palaeogeography, Palaeoclimatology, Palaeoecology* **137**, 127–51.
- MANNI, R. & NICOSIA, U. 1984. *Saccocoma vernioryi* n. sp., a new saccocomid from the upper Jurassic of the Central Italy. *Geologica Romana* **23**, 91–7.
- MANNI, R. & NICOSIA, U. 1996. A history of cyrtocrinid evolution. *Palaeopelagos* **6**, 3–17.
- MANNI, R., NICOSIA, U. & TAGLIACOZZO, L. 1997. *Saccocoma*, a normal benthonic stemless crinoid: an opportunistic reply within mud-dominated facies. *Palaeopelagos* **7**, 121–32.
- MARINO, M. C., ANDREINI, G., BALDANZA, A., D'ARPA, C., MARIOTTI, N., PALLINI, G., PARISI, G. & PETTI, F. M. 2004. Middle Jurassic – Early Cretaceous integrated biostratigraphy (ammonites, calcareous nannofossils and calpionellids) of the Contrada Diesi section (South-Western Sicily, Italy). *Rivista Italiana di Paleontologia e Stratigrafia* **110**, 357–72.
- MARINO, M. & SACCHI, E. 2002. A marine reptile in the Upper Jurassic deposits of the Marche Apennines. In *6th International Symposium on the Jurassic System*, Palermo, 12–22 Settembre 2002, Giornate di Paleontologia, Volume dei Riassunti (ed. M. Santantonio), pp. 115–6.
- MARINO, M. & SANTANTONIO, M. 2010. Understanding the geological record of carbonate platform drowning across rifted Tethyan margins: examples from the Lower

- Jurassic of the Apennines and Sicily (Italy). *Sedimentary Geology* **225**, 116–37.
- MARIOTTI, N. 2002. Upper Callovian-Middle Oxfordian belemnite assemblage from Monte Kumeta (Jurassic of western Sicily, Italy). *Bollettino della Società Paleontologica Italiana* **41**, 13–36.
- MASSARE, J. A., BUCHHOLTZ, E. A., KENNEY, J. M. & CHOMAT, A.-M. 2006. Vertebral morphology of *Ophthalmosaurus natans* (Reptilia: Ichthyosauria) from the Jurassic Sundance Formation of Wyoming. *Paludicola* **5**, 242–54.
- MAXWELL, E. E. 2010. Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, Northwest Territories, Canada. *Journal of Vertebrate Paleontology* **30**, 403–15.
- MAXWELL, E. E. & KEAR, B. P. 2010. Postcranial anatomy of *Platypterygius americanus* (Reptilia: Ichthyosauria) from the Cretaceous of Wyoming. *Journal of Vertebrate Paleontology* **30**, 1059–68.
- MAXWELL, E. E., FERNÁNDEZ, 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**, e41692.
- MCGOWAN, C. 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. *Contributions to Geology, University of Wyoming* **11**, 9–29.
- MCGOWAN, C. 1976. The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. *Canadian Journal of Earth Sciences* **13**, 668–83.
- MCGOWAN, C. & MOTANI, R. 2003. *Ichthyopterygia*. Handbook of Paleoherpertology part 8. München: Verlag Dr. Friedrich Pfeil, 173 pp.
- MORETTINI, E., SANTANTONIO, M., BARTOLINI, A., CECCA, F., BAUMGARTNER, P. O. & HUNZIKER, J. K. 2002. Carbon isotope stratigraphy and carbonate production during the Early-Middle Jurassic: examples from the Umbria-Marche-Sabina Apennines. *Palaeogeography, Palaeoclimatology, Palaeoecology* **184**, 251–73.
- MOTANI, R. 1999. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology* **19**, 473–96.
- NACE, R. L. 1939. A new ichthyosaur from the Upper Cretaceous Mowry Formation of Wyoming. *American Journal of Science* **237**, 673–86.
- NICOSIA, U. & PARISI, G. 1979. *Saccocoma tenella* (GOLD-FUSS) – Distribuzione stratigrafica e geografica. *Bollettino della Società Paleontologica Italiana* **18**, 320–6.
- PASSERI, L. & VENTURI, F. 2005. Timing and causes of drowning of the Calcare Massiccio platform in Northern Apennines. *Bollettino della Società Geologica Italiana* **124**, 247–58.
- RIEGRAF, W. & LUTERBACHER, H. 1989. Jurassic and Cretaceous rhycolites (Cephalopod jaws) from the North Atlantic Ocean (Deep Sea Drilling Project Leg 1–79) and their European Counterparts. *Geologische Rundschau* **78**, 1141–63.
- ROBERTS, A. J., DRUCKENMILLER, P. S., SÆTRE, G.-P. & HURUM, J. H. 2014. A new Upper Jurassic ophthalmosaurid ichthyosaur from the Slottsmøya Member, Agardhfjellet Formation of Central Spitsbergen. *PLoS ONE* **9**, e103152.
- SANDER, P. M. 2000. Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift* **74**, 1–35.
- SANTANTONIO, M. 1993. Facies associations and evolution of pelagic carbonate platform/basin systems: examples from the Italian Jurassic. *Sedimentology* **40**, 1039–67.
- SANTANTONIO, M. 1994. Pelagic carbonate platforms in the geologic record: their classification, and sedimentary and paleotectonic evolution. *American Association of Petroleum Geologists Bulletin* **78**, 122–41.
- SANTANTONIO, M. & CARMINATI, E. 2011. Jurassic rifting evolution of the Apennines and Southern Alps (Italy): parallels and differences. *Geological Society of America Bulletin* **123**, 468–84.
- SANTANTONIO, M., GALLUZZO, F. & GILL, G. 1996. Anatomy and palaeobathymetry of a Jurassic pelagic carbonate platform/basin system. Rossa Mts, Central Apennines (Italy), geological implications. *Palaeopelagos* **6**, 123–69.
- SAUVAGE, H. E. 1902. Recherches sur les vertébrés du Kimmeridgien supérieur de Fumel (Lot-et-Garonne). *Mémoires de la Société Géologique de France* **25**, 1–32.
- SCROCCA, D., DOGLIONI, C. & INNOCENTI, F. 2003. Constraints for an interpretation of the Italian geodynamics: a review. *Memorie Descrittive della Carta Geologica d'Italia* **62**, 15–46.
- SEGUENZA, G. 1887. Brevissimi cenni intorno la geologia del Capo San Andrea presso Taormina. *Rendiconti della Reale Accademia delle Scienze Fisiche e Matematiche di Napoli* **2**, 78–88.
- SHULTZ, M. R., FILDANI, A. & SUAREZ, M. 2003. Occurrence of the southernmost South American ichthyosaur (Middle Jurassic–Lower Cretaceous), Parque Nacional Torres del Paine, Patagonia, southernmost Chile. *Palaios* **18**, 69–73.
- SIROTTI, A. & PAPAZZONI, C. 2002. On the Cretaceous ichthyosaur remains from the Northern Apennines (Italy). *Bollettino della Società Paleontologica Italiana* **41**, 237–48.
- STORRS, G. W., ARKHANGELSKY, M. S. & EFIMOV, V. M. 2000. Mesozoic marine reptiles of Russia and other former Soviet republics. In *The Age of Dinosaurs in Russia and Mongolia* (eds M. J. Benton, M. A. Shishkin, D. M. Unwin & E. M. Kurochkin), pp. 187–10. Cambridge: Cambridge University Press.
- TALEVI, M. & FERNÁNDEZ, M. S. 2012. Unexpected skeletal histology of an ichthyosaur from the Middle Jurassic of Patagonia: implications for evolution of bone microstructure among secondary aquatic tetrapods. *Naturwissenschaften* **99**, 241–4.
- TINTORI, A., DAL SASSO, C., DALLA VECCHIA, F., NICOSIA, U. & TERUZZI, G. 2005. Il Giurassico marino. In *Paleontologia dei Vertebrati in Italia* (ed. L. Bonfiglio), pp. 95–100. Verona: Memorie del Museo Civico di Storia Naturale, Sezione Scienze della Terra no. 6.
- WADE, M. 1990. A review of the Australian Cretaceous longipinnate ichthyosaur *Platypterygius* (Ichthyosauria, Ichthyopterygia). *Memoirs of the Queensland Museum* **28**, 115–37.
- WINTERER, E. L. & BOSELLINI, A. 1981. Subsidence and sedimentation on Jurassic passive Continental margin, Southern Alps, Italy. *American Association of Petroleum Geology Bulletin* **65**(3), 349–421.
- ZAMMIT, M. 2010. A review of Australasian ichthyosaurs. *Alcheringa: An Australasian Journal of Palaeontology* **34**, 281–92.
- ZAMMIT, M., NORRIS, R. M. & KEAR, B. P. 2010. The Australian Cretaceous ichthyosaur *Platypterygius australis*: a description and review of postcranial remains. *Journal of Vertebrate Paleontology* **30**, 1726–35.
- ZVERKOV, N. G., ARKHANGELSKY, M. S., PARDO PÉREZ, J. M. & BEZNOSOV, P. A. 2015. On the Upper Jurassic ichthyosaur remains from the Russian North. *Proceedings of the Zoological Institute* **319**, 81–97.