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First skeletal remains of the giant sawfish *Onchosaurus* (Neoselachii, Sclerorhynchiformes) from the Upper Cretaceous of northeastern Italy

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ABSTRACT

Sclerorhynchiform sawfishes are a diverse and extinct clade of elasmobranchs that is restricted to the Cretaceous. Most taxa are known only by isolated rostral spines, whereas skeletal remains are rare and have been reported from a small number of Upper Cretaceous localities. Here, we describe skeletal remains of the giant sclerorhynchiform *Onchosaurus pharao* for the first time, which provides new morphological information. The single specimen comes from middle-basal upper Turonian strata of the Lessini Mountains in northeastern Italy and represents the first record of this genus from Italy. The specimen consists of unidentifiable cranial remains, several diagnostic rostral spines, the rostrum with fragments of tessellated calcified cartilage, and 87 disarticulated vertebrae. The rostrum preserves the characteristic sensory system of sclerorhynchiforms. It is devoid of any lateral sockets indicating that rostral spines were attached laterally to its surface. This pattern is identical to most sclerorhynchiforms and extant pristiophoriformes implying also similar replacement patterns as in most other sclerorhynchiforms with the exception for *Schizorhiza*. Additionally, the bases of two longitudinally arranged rows of ventral rostral spines are identifiable concurring with patterns seen in *Sclerorhynchus*. The axial skeleton is partly preserved. Re-arranging the disarticulated vertebrae according to their life position in combination with measures of the size and thickness of preserved vertebral centra, and the ratio rostrum length/body size depending on the number of vertebral centra indicate that the specimen was ca. 450 cm long. Growth rings in the vertebral centra show that the specimen was about four years old and thus probably not yet fully sexual mature when it died. This age assumption corresponds well with the calculated size when compared with complete skeletons of extinct sclerorhynchiforms and extant pristiforms. The size of the specimen and its occurrence in hemipelagic rocks corroborates previous assumptions that this sclerorhynchiform was a large and pelagic sawfish.

1. Introduction

Upper Cretaceous chondrichthyans from northern Italy are known since the 19th century and are mainly represented by isolated teeth of ptychodontid and lamniform sharks, recovered from hemipelagic rocks of the Scaglia Rossa Formation (e.g., Catullo, 1827, 1842; Lioy, 1865; Bassani, 1877; Pellegrini, 1883; D'Erasmo, 1922; Sirna et al., 1994; Dalla Vecchia et al., 2005). After a few initial studies aimed to describe some well-preserved and partially articulated specimens (e.g., Bassani, 1888; Canavari, 1916; Cigala Fulgosi et al., 1980), this chondrichthyan assemblage was neglected and remained practically unknown to the scientific community (Amalfitano et al., unpublished data). In the framework of a comprehensive project aimed to revise the entire vertebrate marine fauna of Scaglia Rossa Formation and its stratigraphic and paleoenvironmental context, we report here the first record of the extinct sawfish, *Onchosaurus pharao* (Dames, 1887a) from this unit and from the Cretaceous of Italy in general. *Onchosaurus* is placed traditionally into the Sclerorhynchidae, a clade that includes all extinct Cretaceous sawfish-like batoids with a cosmopolitan distribution during the Late Cretaceous (Corral et al., 2012; Kriwet and

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Klug, 2012). Sclerorhynchids possess an elongated rostrum with rostral spines that are not homologous to oral teeth (Smith et al., 2015; Welten et al., 2015). These spines are laterally attached to the rostral cartilage by connective tissue and replacement spines are formed parallel to the edge of the rostrum before being rotated into functional position (Cappetta, 1987; Wueringer et al., 2009). The pattern of rostral spine replacement in most sclerorhynchids is identical to that of living pristiophorid sawsharks, but differs from that seen in pristid sawfishes, in which spines grow continuously and are inserted into sockets along the lateral rostrum cartilage (e.g., Welten et al., 2015). The replacement mode, however, also seemingly differs between taxa included in the Sclerorhynchidae (Smith et al., 2015).

It has been suggested that both sclerorhynchids and pristids are closely related with shovelnose rays, thus basal "modern" batoids (Cappetta, 1974; Wueringer et al., 2009; Cappetta, 2012; Underwood et al., 2015), while pristiophorids are squalomorph sharks (Cappetta, 2012; Underwood et al., 2015). According to the phylogenetic analysis by Kriwet (2004), all extinct sawfishes from the Cretaceous fall within the clade Sclerorhynchiformes. Currently, two clades, the Sclerorhynchidae and the Ptychotrygonidae are included in Sclerorhynchiformes. The different rostral spine replacement modes, however, suggest that Sclerorhynchidae and possibly Sclerorhynchiformes, as currently understood, might be paraphyletic.

The aim of this paper is to describe the skeletal remains of the giant sclerorhynchid *O. pharao* from the Scaglia Rossa Formation consisting of disarticulated vertebrae, several diagnostic rostral spines, the rostrum with fragmentary tessellated calcified cartilage and other fragmentary cranial remains. The specimen is not only the first documented record of this genus from Italy, but also the most complete specimen of this taxon that has been recovered worldwide so far. Up to now, this species has been known only from isolated rostral spines. The new remains allow us to estimate the age and size of the specimen, using the rostrum length and vertebrae measurements, and to discuss its paleoecology. This information significantly contributes to our understanding of sclerorhynchid life history traits and lifestyles.

2. Locality and stratigraphic setting

The specimen was recovered from the "lastame", a peculiar lithozone of the Upper Cretaceous Scaglia Rossa Formation (lithozone 2 of Lozar and Grosso, 1997), which crops out in the Lessini Mountains (western Veneto Region, northeastern Italy) (Fig. 1). This lithostratigraphic unit, which is ca. 7–8 m in thickness, consists of reddish, pinkish and whitish nodular hemipelagic limestones and marly limestones deposited during the early Turonian–early Santonian in open marine conditions on a pelagic rise, the "Trento Plateau" (Lozar and Grosso, 1997; Palci et al., 2013). The microfacies usually consists of wackestone with planktonic foraminifera, pithonellids, radiolarians and benthic foraminifera (Lozar and Grosso, 1997). "Lastame" is a package of 70–72 nodular/flaser beds intensively quarried for decorative and building purposes, especially in the surroundings of the village of S. Anna d'Alfaedo (about 30 km north of Verona). In the Veneto Region, "lastame" is renowned for its paleontological content consisting of invertebrates (echinoids, inoceramids, ammonites and rudists) and rare vertebrate remains, which are dominated by sharks associated with rare marine turtles and mosasaurs (e.g., Capellini, 1884; Cigala Fulgosi et al., 1980; Ginevra et al., 2000; Dalla Vecchia et al., 2005; Trevisani and Cestari, 2007; Roghi, 2010; Palci et al., 2013). Among sharks, the most common fossils are isolated teeth of *Ptychodus* and remains of lamniform sharks (e.g., *Cretoxyrhina mantelli)*. These taxa are represented by both isolated teeth and teeth associated with vertebrae and calcified cartilage remains (Cigala Fulgosi et al., 1980; Dalla Vecchia et al., 2005; Amalfitano et al., unpublished data).

The sawfish described here was found by Mr. Luigi Benedetti in 1981 in his quarry at Mount Loffa, close to the village of S. Anna d'Alfaedo (Verona Province). Although the finding dates back some 35 years ago, the specimen never received proper attention and was only recently mentioned as "Pristidae" in a list of fossils from the "lastame" compiled by Trevisani and Cestari (2007, p. 75).

3. Materials and methods

The skeletal remains described herein (rostrum, rostral spines, cranial remains and vertebrae) are preserved on two slabs of nodular/sub-nodular limestone (IGVR 45303 and IGVR 45304), both on exhibit in the Prehistorical and Paleontological Museum of S. Anna d'Alfaedo, northern Italy. The main slab (IGVR 45303) has an irregular polygonal outline and measures 340 cm in maximum length, 147 cm in maximum width and 10.5 cm in maximum thickness; the counter-slab (IGVR 45304) is smaller than the main slab and has an irregular polygonal shape, with its maximum length of about 172 cm, its maximum width of about 145 cm and its maximum thickness of 8 cm (see Fig. S1 of Supplementary material for more detailed measurements). The specimen was photographed with different digital cameras: a Nikon Coolpix L120, a Sony α200 mounting 18–70 mm lens, and a Fuji XE1 mounting 18–55 mm lens. The specimen was also subjected to ortho-photography and macro-photography. The images were edited using the freeware GIMP (v. 2.8) and Inkscape (v. 0.91). Illustrative drawings using GIMP were produced to highlight or underline some morphological features, if difficult to identify in photographs alone. After this first step, we employed a UV light lamp (Way Too Cool, 95 Watt, Triple UVC–UVB–UVA–4608 West Bluefield Avenue, Glendale, Arizona, USA, AZ85308) to better observe morphological details of the rostrum. UV light has been widely used in paleontology (e.g., Haug et al., 2009; Tischlinger and Arratia, 2013). This technique exploits the property of fluorescence of calcium carbonate, calcium phosphate (fluorapatite) and fossils with traces of organic material or remains. Delicate skeletal elements, including some bones, scales, and remains of soft parts, are sometimes poorly or not discernible at all in visible light, but are revealed under UV light. Furthermore, the contrast between the matrix and the fossil is enhanced considerably (Tischlinger and Arratia, 2013).

The measurements of the specimen were taken using the freeware ImageJ. The images used for the image analysis were orthophotos and detail photos of the specimen with metric scale. For the description of the rostral spines, their peculiar terminology and orientation, we used Corral et al. (2012), Kriwet and Klug (2012) and Cappetta (2012) as references.

Two small limestone nodules detached from IGVR 45303 were processed for micropaleontological analyses. One nodule was processed following the cold acetolysis method of Lirer (2000) for isolating planktonic foraminifera of the >63 μm fraction, the other was utilized for thin section and for a preparation of a smear slide for calcareous nannofossils analysis.

3.1. Institutional abbreviations

AMNH: American Museum of Natural History, New York, U.S.A.; **MB.f.**: Museum für Naturkunde, Berlin, Germany; **BMNH**: The Natural History Museum, London, UK (former British Museum of Natural History); **IGVR**: Inventario Generale Verona, Verona, Italy; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France.