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The Eocene electric ray †*Titanonarke* Carvalho, 2010 from the Bolca Konservat-Lagerstätte, north-eastern Italy, is redescribed in detail based upon new material from recent excavations. This taxon exhibits a combination of features (large voids between the pectoral and the axial skeleton filled in life by electric organs, anteriorly directed fan-shaped antorbital cartilages, lack of dermal denticles, long prepelvic processes, and rounded basibranchial copula with a small caudal tab) that clearly supports its assignment to the order Torpediniformes. The analysis of new material also demonstrates that the previous apparent absence of typical narcinoid characters used to diagnose †*Titanonarke* was the result of taphonomic biases. †*Titanonarke* shares at least three synapomorphies (presence of a rostral fontanelle, low number of ribs, and rostral cartilage connected to the antorbital cartilage through lateral appendices) with the extant genera *Benthobatis*, *Diplobatis*, *Discopyge* and *Narcine*, with which it forms a clade (family Narcinidae) recognized herein as unquestionably monophyletic. Moreover, based upon a single specimen of †*Titanonarke* that exhibits a unique combination of morphometric and meristic features, a new species of Eocene numbfish, †*T. megapterygia* sp. nov., is recognized. The presence of several specimens representing different ontogenetic stages of at least two species of numbfishes suggests a close association of this taxon with shallow-water habitats corresponding to coral reefs as hypothesized for the Monte Postale palaeoenvironment. The occurrence of a fossilized marine batoid embryo is reported here for the first time. Moreover, the analysis of the gut contents suggests that the dietary adaptations of †*Titanonarke* can be related, at least in part, to an opportunistic strategy in the context of abundant larger foraminifera in the Monte Postale palaeobiotope, suggesting that this kind of feeding mode, known to occur in present-day reefs, already was realized 50 million years ago.

http://zoobank.org/urn:lsid:zoobank.org:pub:EDD6E170-CA64-4FFB-8DD1-AED2D61D5504

Keywords: Chondrichthyes; Elasmobranchii; morphology; phylogeny; embryo; gut content

Introduction

Electric rays of the order Torpediniformes de Buen, 1926 are a well-defined monophyletic group within Batoidea that includes about 60 extant species in 11 genera (Compagno & Heemstra 2007; Claeson 2014; Nelson *et al*. 2016). Torpediniforms are typically characterized by a series of morphological traits that traditionally were used to distinguish them from all other batoids, including a rounded fleshy disc, a power-stroking tail without barbs, massive electric organs between the pectoral and axial skeleton, and the anteriorly directed fan- or antler-shaped antorbital cartilages (Davy 1829; Compagno 1973, 1977; Maisey 1984; Carvalho *et al*. 1999; McEachran &

Carvalho 2002; Last *et al*. 2016). A recent comparative morphological analysis presented by Claeson (2014) recovered four additional synapomorphies: the absence of dermal denticles or thorns, the suprascapular antimeres fused with a visible suture, long prepelvic processes, and a rounded basibranchial copula with a small caudal tab.

Several morphological and molecular studies agree with the hypothesis that torpediniforms form the sister group of all other batoids (e.g. McEachran *et al*. 1996; McEachran & Aschliman 2004; Rocco *et al*. 2007; Aschliman *et al*. 2012a), while other molecular-based phylogenies recovered electric rays as sister of Myliobatiformes Compagno, 1973 (Pavan-Kumar *et al*. 2013) or Platyrhinidae Jordan, 1923 (Aschliman *et al*. 2012b). The latter hypothesis appears to

be more consistent with the first appearance data (Paleocene) of torpediniforms in the fossil record with respect to other batoid lineages (Underwood 2006; Claeson 2014). Within Torpediniformes, two monophyletic groups are traditionally recognized: the Torpedinoidea Jonet, 1968, and the Narcinoidea Compagno, 1973. Within Torpedinoidea, a single family, Torpedinidae Bonaparte, 1838, with two genera, *Torpedo* Houttuyn, 1764 and *Hypnos* Dumeril, 1852, is recognized. Narcinoidea includes the families Narcinidae Gill, 1862 with four genera (*Benthobatis* Alcock, 1898, *Diplobatis* Bigelow & Schroeder, 1948, *Discopyge* Heckel, 1846 and *Narcine* Henle, 1834) and Narkidae Fowler, 1934 with five genera (*Electrolux* Compagno & Heemstra, 2007, *Typhlonarke* Waite, 1909, *Heteronarce* Regan, 1921, *Narke* Kaup, 1826 and *Temera* Gray, 1831) (Carvalho 2010; Aschliman *et al.* 2012a; Nelson *et al.* 2016). The monophyletic status of the family Narcinidae was recently questioned based on a comprehensive morphological and phylogenetic analysis of all torpediniform genera, since the characters traditionally used to support the monophyly of narcinids were not recovered supportive of this condition (see Claeson 2014).

Although ghost lineages predict that torpediniforms should have been present in the Late Cretaceous (see Aschliman *et al.* 2012b; Guinot & Cavin 2016), fossil electric rays are known only from Cenozoic deposits. Very little is known about the evolutionary history of this group, because almost all fossil taxa (with the exception of †*Titanonarke*) are known from isolated teeth, which are phylogenetically not informative (Claeson 2014). The celebrated Eocene (late Ypresian, *c.* 50 Ma; Papazzoni *et al.* 2014) Bolca Konservat-Lagerstätte yielded the only fossil torpediniforms represented by complete articulated skeletons, which are of considerable relevance for identifying plesiomorphic morphological traits and understanding the early Palaeogene diversification of this group. The fossiliferous deposits from this locality have been known since the sixteenth century for their abundance of exquisitely preserved fishes, amongst which approximately 240 species, predominantly belonging to various teleost lineages, have been described to date (e.g. Carnevale & Pietsch 2009, 2010, 2011, 2012; Bannikov & Carnevale 2010; Carnevale *et al.* 2014; Marramà & Carnevale 2015a, b, 2016, 2017a, b; Pfaff *et al.* 2016; Davesne *et al.* 2017). Although several studies during the last few decades have contributed to our increased knowledge of the outstanding teleost palaeobiodiversity of this oldest example of a modern tropical reef fish assemblage (Marramà *et al.* 2016c; Bellwood *et al.* 2017), the taxonomic diversity, interrelationships and palaeoecology of the Bolca chondrichthyans remain poorly resolved when compared to those of the outstanding teleost assemblage from this celebrated Eocene locality. In fact, with the exception of a few recent revisions of selected selachians (e.g. Fanti *et al.* 2016; Marramà *et al.* 2017a), no other modern systematic studies have been carried out on the Bolca cartilaginous fishes (Marramà *et al.* in press).

Torpediniforms currently are represented at Bolca by a single species referred to †*Titanonarke molini* (Jaekel, 1894). The genus *Titanonarke* was erected by Carvalho (2010). This taxon is known from fossiliferous sediments of the Monte Postale site of the Bolca Konservat-Lagerstätte by several specimens representing different ontogenetic stages. Although †*Titanonarke* clearly exhibits the typical characters of the Narcinoidea, the diagnosis and the phylogenetic placement of this genus provided by Carvalho (2010) appear to be problematic, since the analysis of new material from recent excavations clearly shows that the apparent absence of typical narcinoid characters considered diagnostic of †*Titanonarke* is the result of taphonomic biases.

The goal of this paper is to provide a detailed morphological redescription of †*Titanonarke* from the Eocene Bolca Lagerstätte, Italy, test the hypothesis that only one species exists, and identify its relationships with the other torpediniforms. Palaeobiological and palaeoenvironmental implications based on an analysis of the gut contents provide new insights into the early Palaeogene rise of new feeding strategies in fishes associated with reefs.

Geological setting

All specimens examined come from the fossiliferous layers of the Monte Postale site, one of the two main fossiliferous quarries of the Bolca Konservat-Lagerstätte, which is located about 2 km north-east of the village of Bolca (Verona Province, NE Italy) in the eastern part of the Lessini Mountains, southern Alps (Fig. 1). The Monte Postale site is about 300 m from the better known Pesciara site, from which most of the fossil Bolca specimens were recovered (Carnevale *et al.* 2014). Monte Postale is of almost the same age and exhibits similar sedimentological features, mostly comprising finely laminated micritic limestones with fish and plant remains. Papazzoni *et al.* (2017) recently investigated the stratigraphical relationships between the two fossiliferous deposits, suggesting that the uppermost productive sequence of Monte Postale should correlate with those of the Pesciara site, although the fossiliferous laminites of Pesciara appear to be slightly younger than those of Monte Postale. The Monte Postale succession includes the Cretaceous Scaglia Rossa Formation up to Ypresian fossiliferous limestone, containing larger benthic foraminifera of the genus †*Alveolina* d'Orbigny, 1826, and also marine and brackish molluscs in the uppermost part (Papazzoni *et al.* 2014). Fabiani (1914, 1915) was the first to conduct a detailed stratigraphical study of the Monte Postale site and assigned the entire succession to the Lutetian. Malaroda (1954) postulated the same age, whereas Hottinger (1960) suggested
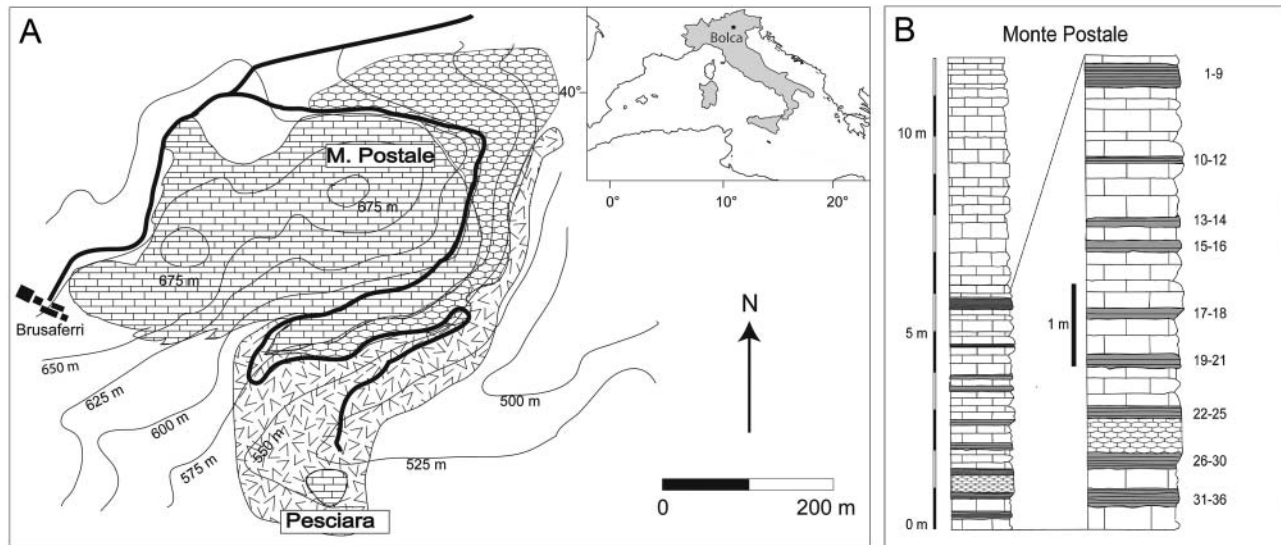
Figure 1. A, location and geological map of the Bolca area. **B**, stratigraphical section of the uppermost part of the Monte Postale sequence. Modified from Marramà *et al.* (2016c).

an Ypresian age based on the foraminifera content. Based on large benthic foraminifera and calcareous nannoplankton, the uppermost strata of the Monte Postale site was assigned to Shallow Benthic Zone 11 by Papazzoni *et al.* (2017) and, thus, corresponds to the late Cuisian (late Ypresian, around 50 Ma). Although the entire area of Bolca was historically regarded as belonging to a coral reef system (e.g. Bellwood 1996), solid evidence of a coralgal rim, lagoonal deposits, and a fore-reef system was only detected for the Monte Postale palaeobiotope (Vescogni *et al.* 2016). This interpretation was also supported by recent palaeoecological and taphonomic studies of the Monte Postale fish assemblage based on the abundance of marine and terrestrial plants, the large number of invertebrates (including abundant corals), and reef-associated fishes, which accumulated in a coral reef context close to an emerged coastal area (Marramà *et al.* 2016c). Disarticulation of fish skeletons, unimodal dispersion of the elements and bioturbation were the result of at least periodic oxic bottom conditions (Marramà *et al.* 2016c).

Material and methods

The present study is based on six well-preserved specimens from the fossiliferous layers of the Monte Postale site. The fossils are currently housed in the collections of the Museo Civico di Storia Naturale di Verona (MCSNV), Museo dei Fossili di Bolca (technically part of the MCSNV), and Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (MGP-PD). We examined new material including specimens from most recent controlled excavations carried out from 1999 to 2011 (MCSNV IG.135581; MCSNV IG.VR.67290;

MCSNV IG.VR.91359), in addition to the three specimens examined by Carvalho (2010) (holotype MGP-PD 26275/6; MCSNV IG.135576; MCSNV IG.91128/9). Some of the specimens were mechanically prepared to reveal fine or hitherto obscured skeletal details. The holotype MGP-PD 26275/6 was examined with UV light to distinguish preserved soft tissues from grout or pigments used in historical reconstruction (see also Supplemental material). Measurements were taken to the nearest 0.1 mm. Standard length (SL; from the anterior tip of the rostral cartilage to the caudal fin origin) is used throughout instead of total length (TL), because most of the specimens lack the distal portion of the caudal fin.

A principal component analysis (PCA) was performed on the entire data set of log-transformed measurements (standardized for the head length) and meristic data to provide direct visual images of the spatial separation of specimens following Takács (2012) and Marramà *et al.* (2017a, b). The component loading values of the PCs were used to interpret the 'meaning' of the components (Hammer *et al.* 2001). The PCA was performed using the software package PAST (Hammer *et al.* 2001). Osteological terminology follows McEachran & Aschliman (2004), Aschliman *et al.* (2012a) and Claeson (2014). Morphometric terminology is adopted and modified from Compagno & Heemstra (2007). Extinct taxa are marked with a dagger (†) preceding their name.

The phylogenetic analysis is based on the recent morphological data set of Claeson (2014), which in turn is based on the matrices of McEachran *et al.* (1996), McEachran & Aschliman (2004) and Aschliman *et al.* (2012a). The original matrix of Claeson (2014) was rechecked and some states were corrected or recoded (see Supplemental material). The data matrix contains all 65

characters of Claeson (2014), to which we added five new dental characters (chars. 66, 67, 68, 69, 70) from Herman *et al.* (1995, 1997, 2002) and Compagno & Heemstra (2007). Based on the analysis of additional morphological and meristic features of extant and fossil taxa, we also included two new characters (71 and 72), describing two of the main synapomorphies of Narcinidae. The matrix includes all taxa considered by Claeson (2014), to which we added †*Titanonarke* and †*Eotorpedo* White, 1934, the latter only known by isolated teeth (see also the section 'Palaeobiogeographical remarks'). The character matrix was compiled in Mesquite 3.03 (Maddison & Maddison 2008). The phylogenetic analysis was performed with TNT 1.5 using the branch-and-bound method (Goloboff *et al.* 2008). All characters are considered unordered and given equal weight. Tree length, consistency (CI), homoplasy (HI) and retention (RI) indices subsequently were calculated for the strict consensus tree and for each character individually (see Supplemental material). Two additional phylogenetic analyses using the same data matrix were excuted with WinClada 1.00.08 (Nixon 2002) and Mesquite 3.03 (Maddison & Maddison 2008) for cross-checking results obtained from the TNT analysis.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **ESB**: Ecosystems Surveys Branch, Northeast Fisheries Science Center, Woods Hole, Massachusetts, USA; **FMNH**: Field Museum of Natural History, Chicago, Illinois, USA; **MCSNV**: Museo Civico di Storia Naturale di Verona, Italy; **MCZ**: Museum of Comparative Zoology, Cambridge, Massachusetts, USA; **MGP-PD**: Museo di Geologia e Paleontologia dell'Università degli Studi di Padova, Italy; **MNHN**: Muséum national d'Histoire naturelle, Paris, France; **NHMUK**: Natural History Museum, London, UK; **SIO**: Scripps Institution of Oceanography, San Diego, California, USA; **ZMH**: Museum für Naturkunde, Hamburg, Germany; **TNHC**: Texas Natural History Collection, University of Texas, Austin, Texas, USA; **ZMB**: Museum für Naturkunde, Berlin, Germany. (See comparative material in Supplemental material.)

Systematic palaeontology

Class **Chondrichthyes** Huxley, 1880
Superorder **Batomorphii** Cappetta, 1980
Order **Torpediniformes** de Buen, 1926
Superfamily **Narcinoidea** Compagno, 1973
Family **Narcinidae** Gill, 1862

Diagnosis (emended). Medium to large-sized narcinoid electric rays sharing three synapomorphies: presence of rostral fontanelle, reduced number of ribs (up to 10 pairs), and rostral cartilage connected to the antorbital cartilages through lateral rostral appendices. Additionally, narcinids possess the following combination of characters: palatoquadrate labiolingually compressed and tapered towards the symphysis; small subtriangular labial cartilages close to symphysis; rostral cartilage expanded and trough-shaped; large and rounded basibranchial copula with small caudal tab; tooth cusps and roots narrow and high; long precaudal tail; two dorsal fins.

Included genera. *Benthobatis* Alcock, 1898; *Diplobatis* Bigelow & Schroeder, 1948; *Discopyge* Heckel, 1846; *Narcine* Henle, 1834; †*Titanonarke* Carvalho, 2010.

Genus †*Titanonarke* Carvalho, 2010

Diagnosis (emended). Narcinid electric ray unique in having the following two autapomorphic traits: large size (up to about 1 m of TL) and large number of vertebrae (133–155). Additionally, †*Titanonarke* has the following combination of characters: broadly branched antorbital cartilage, with a third smaller branch posteriorly directed and located at midlength; unfused hypobranchials; iliac process short and straight; prepelvic process wider towards tip than along the shaft; mesopterygium shorter than propterygium and metapterygium; tooth cusp length less than half the length of the blade-like cutting edges; tooth root high and narrow; precaudal tail reaching about 50% of TL; long claspers extending past posterior tips of pelvic fin lobes.

Type species. †*Narcine molini* Jaekel, 1894.

Included species. †*Titanonarke molini* (Jaekel, 1894); †*Titanonarke megapterygia* sp. nov.

Remarks. Jaekel (1894) was the first to document the presence of electric rays from the Monte Postale site in his comprehensive account of cartilaginous fishes from the Bolca Lagerstätte. In this work, he erected the species †*Narcine molini* based on a nearly complete specimen in part and counterpart housed in the collection of the Museo di Geologia e Paleontologia dell'Università di Padova (MGP-PD 26275/6). The specimen previously was assigned to †*Narcine gigantea* by Molin (1860). However, the holotype of †*N. gigantea*, housed in the Museum national d'Histoire naturelle, Paris (MNHN F.Bol567) later was recognized as a thornback and assigned to *Platyrhina* by Jaekel (1894). Both Eastman (1904, 1905) and Blot (1980) included †*Narcine molini* in their synoptic lists of chondrichthyans of Bolca. Recently, Carvalho (2010) undertook a re-examination of the holotype of †*Narcine molini* and two additional specimens recovered from the Monte Postale site in the second half of the

twentieth century (MCSNV IG.135576 and MCSNV IG.91128/9), and erected the genus †*Titanonarke* containing †*N. molini* Jaekel, 1894. The diagnosis of this new genus was based on the presence of some derived characters within narcinids, including the large size, the long precaudal tail reaching about 50% of TL, the absence of dorsal fins, and absence of posteriorly directed branches of the antorbital cartilage. Carvalho (2010) also provided an interpretative phylogenetic analysis in which †*Titanonarke* was recovered as the basalmost genus within the Narcinidae. Although †*Titanonarke* clearly exhibits the diagnostic characters of this family, the diagnosis of this Eocene taxon provided by Carvalho (2010) and its relationships to other torpediniforms appear to be controversial. This is primarily due to the apparent absence of some typical narcinoid characters (dorsal fins and third branch of the antorbital cartilage), and to the ambiguous choice of characters used for the phylogenetic inference. Carvalho (2010) also hypothesized the presence of a possible new genus of numbfish in the Monte Postale site based on the observation of two juvenile specimens (MCSNV IG.135581 and MCSNV IG.VR.91359) indicating characters which were hypothesized to be absent in †*T. molini* (i.e. third small branch of the antorbital cartilage and a posteriorly directed scapular process). Our detailed revision of the historical and new material derived from recent controlled excavations reveals that the specimens used by Carvalho (2010) were only partially preserved and thus prevented the recognition of those elements whose apparent absence was erroneously regarded as diagnostic of †*Titanonarke*. Moreover, there are no substantial morphological differences to support the hypothesis that juvenile specimens should be recognized as a new genus because osteological, morphometric and meristic features identify these as belonging to †*T. molini* (see below). We also recognize the specimen MCSNV IG.135576 (but not MCSNV IG.135581 and MCSNV IG.VR.91359), previously ascribed to †*T. molini* by Carvalho (2010), as a new species of †*Titanonarke*. Finally, an integrated comprehensive phylogenetic analysis based on the data derived from the detailed comparative anatomy of the electric rays of Claeson (2014) has revealed new hypotheses about the relationships of *Titanonarke* within the Torpediniformes.

†*Titanonarke molini* (Jaekel, 1894)
(Figs 2–16)

1860 †*Narcine gigantea* Molin: 585 [pro parte].
1894 †*Narcine molini* Jaekel: 111, pl. 3 [original occurrence of name, photograph and outline reconstruction].
1904 †*Narcine molini* Jaekel, 1894; Eastman: 27.
1905 †*Narcine molini* Jaekel, 1894; Eastman: 351.
1979 †*Narcine molini* Jaekel, 1894; Stanghellini: 38 [misspelt '*moloni*'].

1980 †*Narcine molini* Jaekel, 1894; Blot: 344.
1987 †*Narcine molini* Jaekel, 1894; Cappetta: 161, fig. 138L.
1988 †*Narcine molini* Jaekel, 1894; Cappetta: 29.
1991 †*Narcine molini* Jaekel, 1894; Frickhinger: 211.
1993 †*Narcine molini* Jaekel, 1894; Cappetta *et al.*: 604.
1999 †'*Narcine*' *molini* Jaekel, 1894; Carvalho: 283, figs 107–111.
2010 †*Titanonarke molini* (Jaekel, 1894); Carvalho: 185, figs 2, 5A, 6, 7.
2012b †*Titanonarke molini* (Jaekel, 1894); Aschliman *et al.*: 33.
2012 †*Narcine molini* Jaekel, 1894; Cappetta: 410, fig. 401L.
2014 †*Titanonarke molini* (Jaekel, 1894); Carnevale *et al.*: 41.
2014 †*Titanonarke molini* (Jaekel, 1894); Claeson: 4.
2016c †*Titanonarke molini* (Jaekel, 1894); Marramà *et al.*: 232.

Holotype. MGP-PD 26275/6, nearly complete articulated skeleton in part and counterpart (Fig. 2), 816.8 mm SL.

Referred material. MCSNV IG.VR.67290, nearly complete articulated skeleton in a single slab, 750.2 mm SL (Fig. 3A); MCSNV IG.91128/9, partially complete articulated specimen in part and counterpart, 850.4 mm SL (Fig. 3B); MCSNV IG.VR.91359, nearly complete articulated skeleton in a single slab, 99.0 mm SL (Fig. 4A); MCSNV IG.135581, incomplete articulated specimen in a single slab, lacking part of the cranial and caudal regions (Fig. 4B).

Type locality and horizon. Monte Postale site, Bolca Konservat-Lagerstätte, Italy; early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone (see Papazzoni *et al*. 2017).

Diagnosis. Species of †*Titanonarke* characterized by the following combination of characters: subcircular disc length *c*. 44% SL and disc width *c*. 50% SL; greatly elongated precaudal tail of *c*. 60% SL; 153–155 vertebrae (27–30 trunk; 100–115 precaudal, 23–25 caudal); 15–16 tooth rows in upper jaw and 12–13 tooth rows in the lower jaw; *c*. 40 pectoral radials (12–16 propterygial, 9–12 mesopterygial, and 10–11 metapterygial); single-lobed pelvic fin with 21–24 basipterygial radials; first dorsal fin with 7–9 radials, and second dorsal fin with 6–7 radials; caudal fin with about 42 radials (20 dorsal and 22 ventral); width of pelvic fins about 50% of disc width; anterior pelvic fin margin length *c*. 24% of disc length.

Description. Specimens examined comprise different ontogenetic stages and range from 99 to 850.4 mm SL, with the largest specimen reaching 925 mm TL. Measurements and counts for †*Titanonarke molini* are summarized

Figure 2. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A, B,** MGP-PD 26275/6, holotype in part and counterpart. Scale bars = 100 mm.

in Tables 1 and 2. Overall, the body is large and dorsoventrally compressed (Figs 2, 3). The disc is subcircular, slightly ovoid in outline, generally wider than long, and barely overlapping the pelvic fin origin. The largest width of the disc is slightly posterior to its midlength and its edges are continuously curved. The length and width of the disc are about 44% and 50% SL, respectively. The head is approximately 25% of SL and the preoral length is about 9% SL. The precaudal tail is elongated (about 60% SL). †*Titanonarke molini* has two dorsal fins; the predorsal distance at the first dorsal fin is about 62% SL, whereas the predorsal distance at the second dorsal fin is about 78% SL; the interdorsal distance is about 7% SL. The body is totally naked, lacking denticles and thorns. The skeleton is highly calcified and most of the skeletal elements, including parts of the rostral cartilage, jaws, hyomandibulae, antorbital cartilages, synarcual, and pectoral and pelvic girdles, show the typical prismatic calcification of elasmobranch fishes (Dean & Summers 2006).

Chondrocranium. The rostral cartilage is expanded, dorsoventrally flattened and trough shaped (Figs 5, 6), resembling the typical condition of narcinids (Miyake *et al*. 1992). The rostrum is long, about one-half of the cranial length, wide anteriorly and tapering proximally towards the nasal capsules. The anterior margin of the rostral cartilage is concave, indicating the presence of a rostral fontanelle (= part of the precerebral fontanelle of Miyake *et al*. 1992), that is present also in *Benthobatis*, *Diplobatis*, *Discopyge* and *Narcine* (Claeson 2014) and which also is supported by the phylogenetic analysis of this study (see below). Small lateral projections (= rostral appendices of Holmgren 1941; lateral rostral cartilage of Carvalho 1999) off of the rostral fontanelle were indicated in the holotype by Carvalho (2010). Due to the grout and/or pigment used on the holotype MGP-PD 26275/6, UV light was not useful to distinguish further details of preserved tissues (see Fig. 7A, B). Ultraviolet light did highlight a possible lateral projection (Fig. 7B), but we cannot discern whether it was branching and connected to the
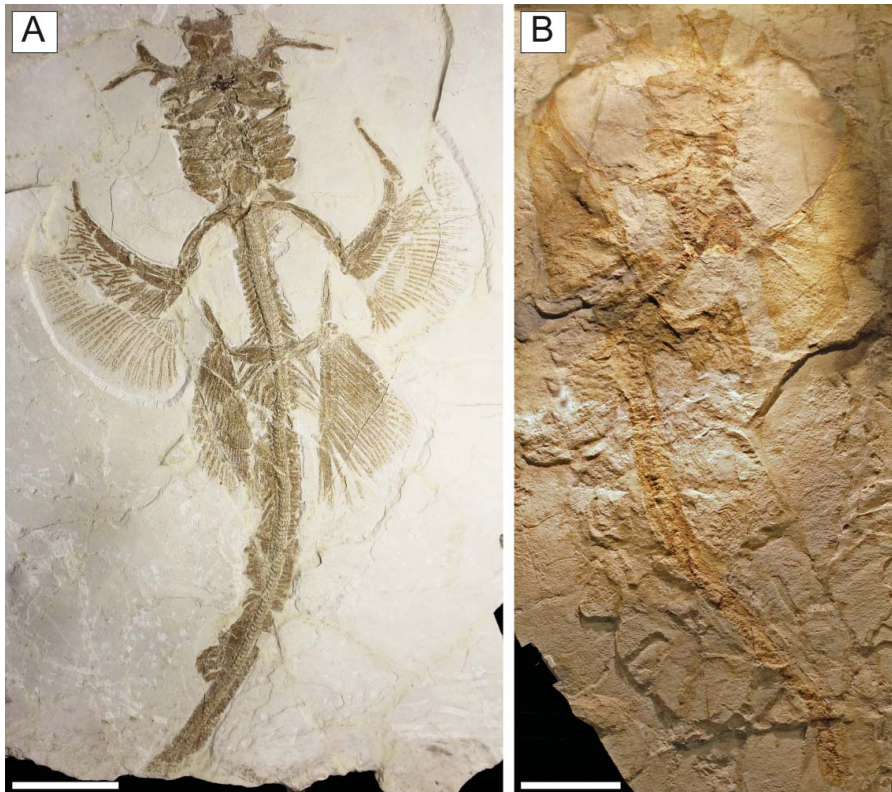
Figure 3. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A,** MCSNV IG.VR.67290; **B,** MCSNV IG.91128/9. Scale bars = 100 mm.
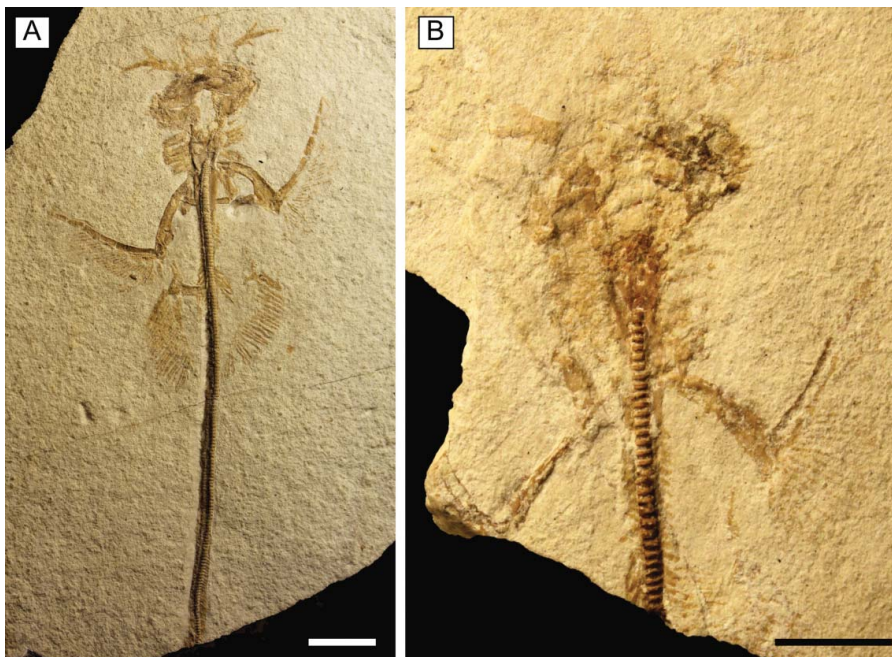

Figure 4. Juvenile individuals of †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A,** MCSNV IG.VR.91359; **B,** MCSNV IG.135581. Scale bars = 10 mm.
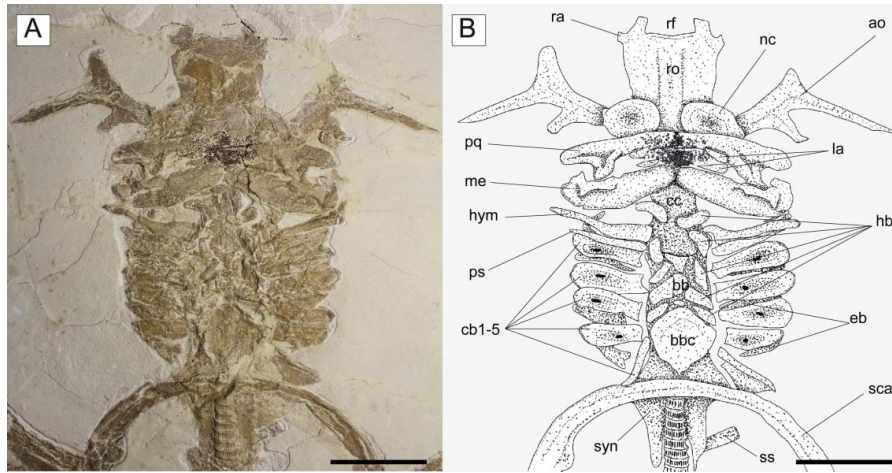
Figure 5. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A,** MCSNV IG.VR.67290, close-up of the head and hyoid apparatus; **B,** reconstruction. Abbreviations: ao, antorbital cartilage; bb, basibranchials; bbc, basibranchial copula; cb, ceratobranchials; cc, chondrocranium; eb, epibranchials; hb, hypobranchials; hym, hyomandibula; la, labial cartilages; me, Meckel's cartilage; nc, nasal capsule; pq, palatoquadrate; ps, pseudohyoid; ra, rostral appendix; rf, rostral fontanelle; ro, rostral cartilage; sca, scapulocoracoid; ss, suprascapula; syn, synarcual. Scale bars = 50 mm.

antorbital cartilage as in *Narcine brasiliensis* (Olfers, 1831) (Fig. 7C). Evidence of a lateral projection off of the rostral fontanelle is, however, clearly present in MCSNV IG.VR.67290 (Fig. 5), but not in juvenile specimens of †*Titanonarke* that we examined, which thus resemble juveniles of *Narcine brasiliensis* (Miyake *et al*. 1992, fig. 14A). The connection of the rostral cartilage to the antorbital cartilage through the lateral projection was also detected in *Diplobatis* (Fechhelm & McEachran 1984, fig. 5), *Benthobatis* (Rincon *et al*. 2001, fig. 7) and all narcinids in general (Fechhelm & McEachran 1984, fig. 16; Carvalho 1999, 2010). This character, which is unique among torpediniforms, corroborates the monophyly and

the systematic position of narcinids in this study. The juvenile specimen MCSNV IG.VR.91359 shows the early stage of the development of the rostral cartilage (Fig. 6), with at least one cartilaginous strip (= *sensu* Miyake *et al*. 1992) and two lateral rostral bars. The rostral cartilage of †*Titanonarke* lacks the basonasal fenestrae that characterize *Diplobatis* (Fechhelm & McEachran 1984). Although probably present on the dorsal surface of the chondrocranium, it is not possible to distinguish the presence of the anterior and frontoparietal fontanelle in the available material.

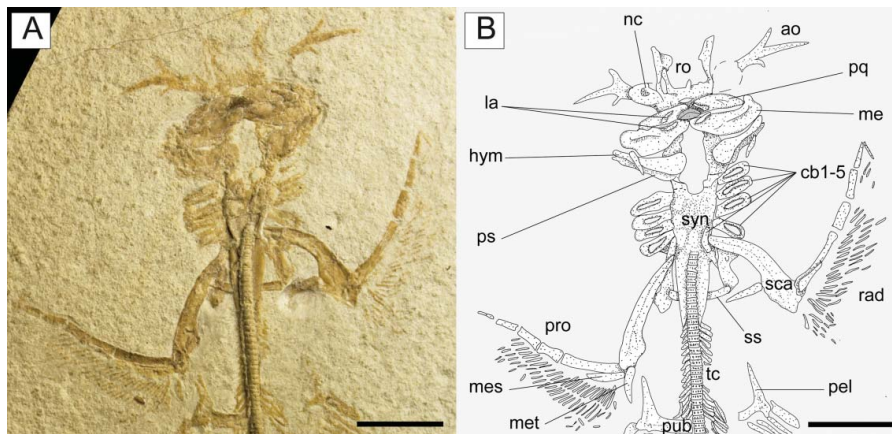The antorbital cartilages in juveniles and adults are robust, well developed, directed anteriorly and broadly

Figure 6. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A,** the juvenile individual MCSNV IG.VR.91359; **B,** reconstruction. Abbreviations: ao, antorbital cartilage; cb, ceratobranchials; hym, hyomandibula; la, labial cartilages; me, Meckel's cartilage; mes, mesopterygium; met, metapterygium; nc, nasal capsule; pel, prepelvic process; pub, puboischiadic bar; pq, palatoquadrate; pro, propterygium; ps, pseudohyoid; rad, pectoral radials; ro, rostral cartilage; sca, scapulocoracoid; ss, suprascapula; syn, synarcual. Scale bars = 50 mm.
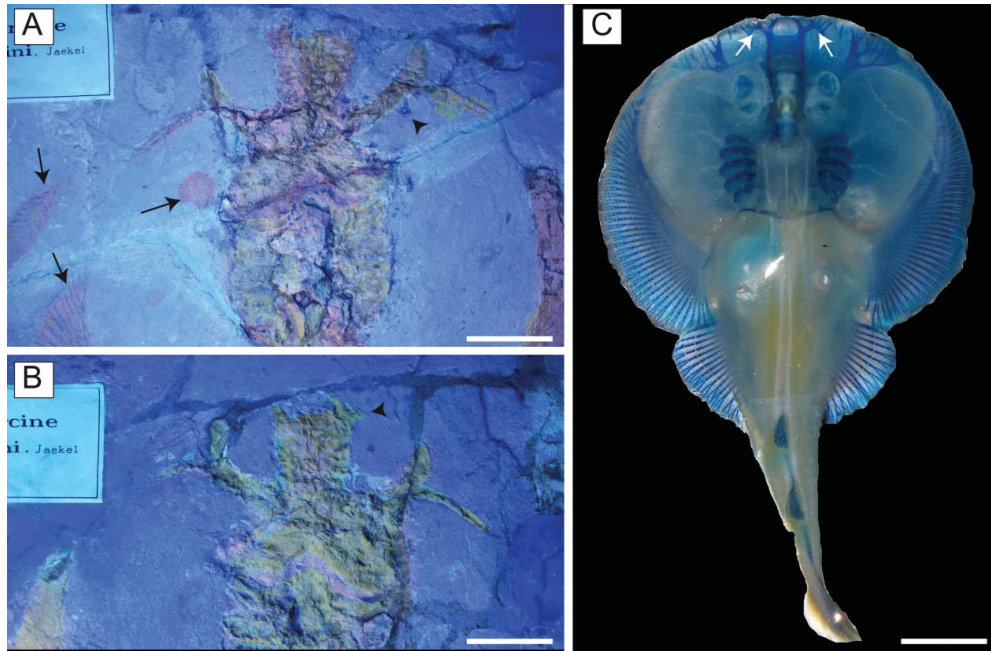
Figure 7. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A, B,** UV images of the holotype MGP-PD 26275/6 showing that it was covered with a pigment reflecting an orange light (see also Supplementary material). The arrows in A indicate a leaf also covered with the pigment, a drop, and some rays that were not distally covered (they are blue/grey, as expected); the arrowhead in A indicates part of the third branch of the antorbital cartilage not covered by pigment; the arrowhead in B indicates the rostral appendix; **C,** *Narcine brasiliensis* (TNHC 18512); the arrows indicate the rostral appendices. Scale bars: A, B = 50 mm; C = 10 mm.

branching (Figs 5, 6). There are no distinct foramina on the anterior cartilages. Antorbitals are subdivided at about one-third of their length into two main branches; their stout bases articulate with the lateral aspect of the nasal capsules through an expanded posterior condyle. The distal end of the largest branch is broadly separated from the anterior extension of the propterygium. A third, smaller, posteriorly directed branch is located at mid-length of the antorbital cartilages (Figs 5, 6). The absence of the posterior branch was considered diagnostic for
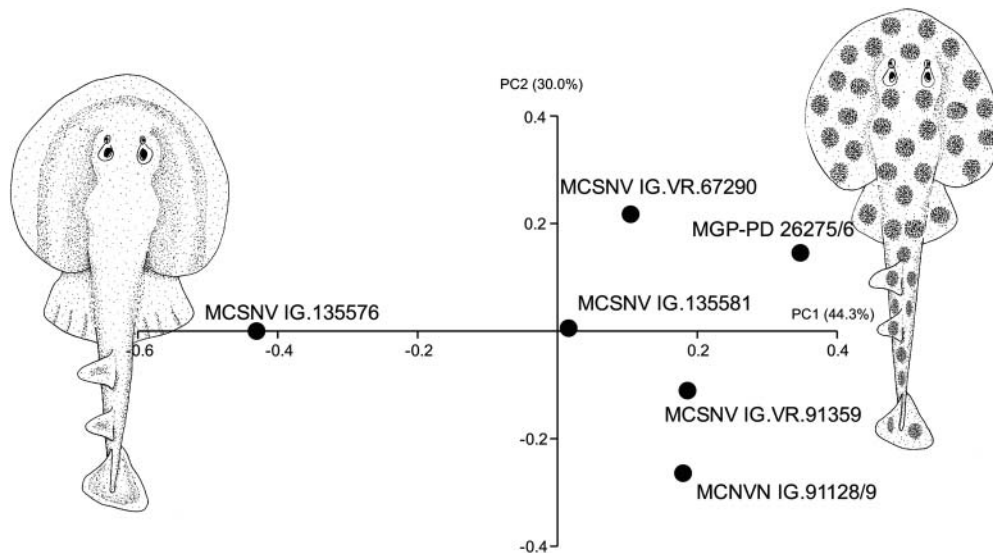

Figure 8. Visual image of the principal component analysis (PCA) performed on the entire set of log-transformed standardized morphometric and meristic features, showing the separation of the specimens referred to †*Titanonarke molini* (right side of morphospace) from those referred to †*Titanonarke megapterygia* sp. nov. (left side). The illustrations lying along the extreme values of PC1 represent the hypothetical reconstruction of the two species based on body proportions.
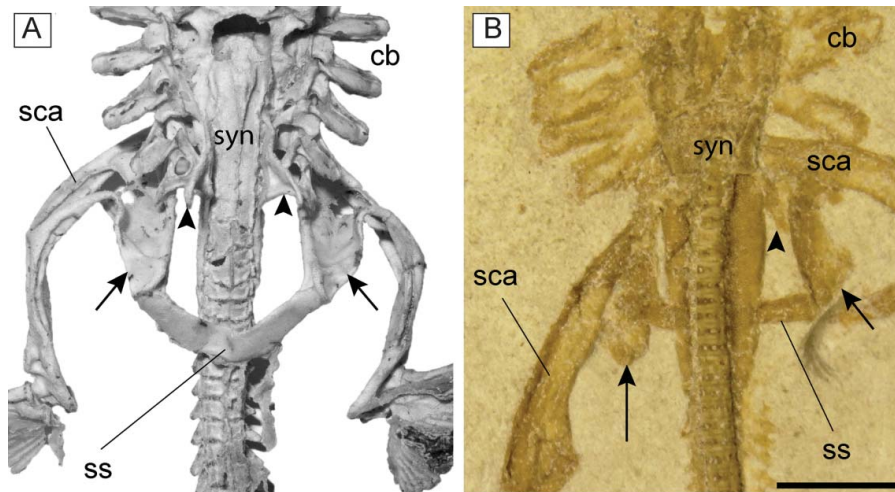
Figure 9. **A,** synarcual and pectoral girdle of *Narcine brasiliensis* (AMNH 95343) in dorsal view; **B,** synarcual and pectoral girdle of †*Titanonarke molini* (MCSNV IG.VR.91359) in ventral view. The arrowheads indicate the posteriorly directed lateral stays of the synarcual. The arrows indicate the posteriorly directed scapular process of the scapulocoracoid. Abbreviations: cb, ceratocranchials; sca, scapulocoracoid; ss, suprascapula; syn, synarcual. Scale bar = 5 mm.

†*Titanonarke* to the exclusion of *Narcine* and *Discopyge* by Carvalho (2010). However, the presence of this posterior branch in MCSNV IG.VR.67290, MCSNV IG. VR.91359, MCSNV IG.135581 and possibly, at least partially, in the holotype (Figs 7A), suggests that it was not discernible in the specimens described by Carvalho (2010). Moreover, since osteological, morphometric and meristic features are not useful to separate juvenile specimens from the holotype, there is no reason to assign this smaller specimens to a new genus, if only based on the

presence of this character. In fact, the PCA performed in this study on the entire morphological data set of standardized and log-transformed measurements and counts (Fig. 8) shows no remarkable separation of the juvenile specimens MCSNV IG.VR.91359 and MCSNV IG.135581 from the holotype and other referred material.

The nasal capsules are ovoid in shape, located at about midlength of the chondrocranium and projected laterally. The internasal plate between the two nasal capsules appears flat and narrow. As all specimens are preserved in
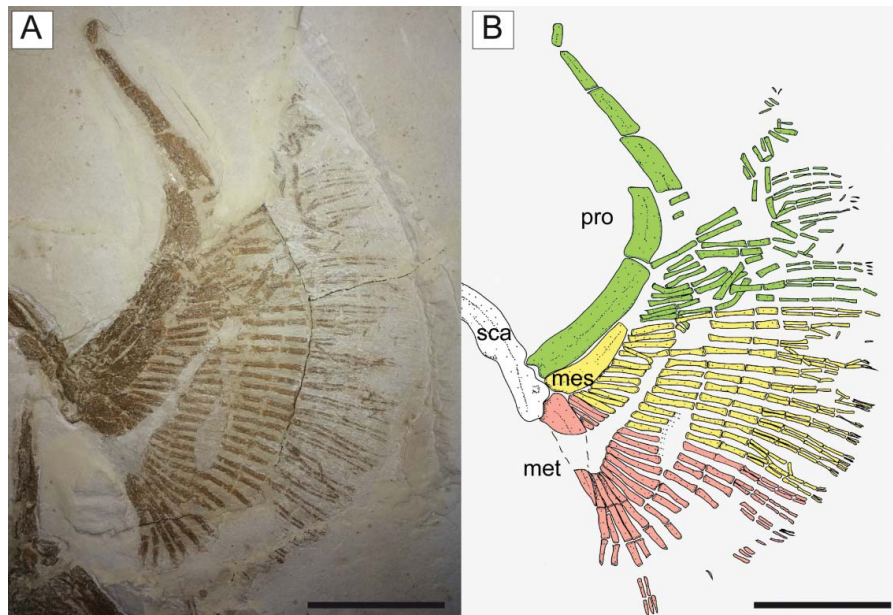

Figure 10. Pectoral fin of †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A,** MCSNV IG.VR.67290; **B,** reconstruction; different colours are used to distinguish the propterygial (green), mesopterygial (yellow) and metapterygial (red) radials (colours in the online version). Abbreviations: mes, mesopterygium; met, metapterygium; pro, propterygium; sca, scapulocoracoid. Scale bars = 50 mm.
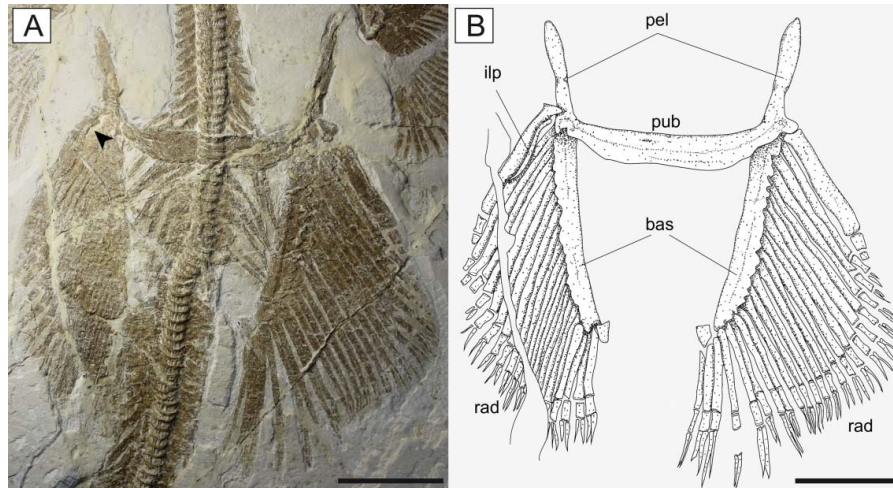
Figure 11. Pelvic fins of †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. **A,** MCSNV IG.VR.67290; **B,** reconstruction. Abbreviations: bas, basipterygia; ilp, iliac process; pel, pelvic processes; pub, puboischiadic bar; rad, pelvic radials. The arrowhead indicates the iliac process. Scale bars = 50 mm.

dorsoventral view, it was not possible to detect the lateral aspect of the nasal capsules. The otic capsules and the posterior part of the chondrocranium are partially hidden by the jaws and hyoid arches. However, they appear to be approximately as wide as the widest part of the rostrum and much narrower than the nasal capsules. A large basicranial fenestra is recognizable in the juvenile MCSNV

Figure 12. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. Close-up of the distal end of pelvic fins of MCSNV IG.91128, which is supposed to be the unique male individual based on the presence of claspers. Abbreviations: cla, clasper; dfr, first dorsal-fin radials, pelvic radials. Scale bar = 50 mm.

IG.VR.91359 (Fig. 6), which resembles in position and shape the condition shown in the early stages of chondrification of the otic region in *Narcine brasiliensis* (Miyake *et al*. 1992, fig. 14).

Jaws. Carvalho (2010) considered both palatoquadrate and Meckel's cartilage of †*T. molini* broadly arched and not very stout when compared to those of other members of Narcinidae. Given that long, slender and curved jaws are diagnostic for the torpedinoids *Torpedo* and *Hypnos* whereas in narcinoid genera the jaws are short and stout (Claeson 2014), the description of the jaws of †*Titanonarke* is further clarified here. The palatoquadrate of †*Titanonarke* is labiolingually compressed, narrower than the Meckel's cartilage, and tapers towards the symphysis (Fig. 5). Like the palatoquadrate of *Narcine brasiliensis* (see Dean & Motta 2004a), the palatoquadrate of †*T. molini* possesses a strong condyle that articulates with the Meckel's cartilage at the mandibular articular fossa *sensu* Dean & Motta (2004a). The Meckel's cartilages are stout, flat and broad. There are two pairs of small, slender and subtriangular labial cartilages situated near the symphysis of the jaws, surrounding the tooth bands (Fig. 5). Combined, upper and lower labial cartilages are less than the length of the Meckel's cartilage. The triangular element displaced to the corner of the left jaw joint in MCSNV IG.135576, and interpreted by Carvalho (2010, fig. 5b) as a labial cartilage, instead appears to be a dorsal flange of the sustentanculum of the Meckel's cartilage. Both jaws are not fused medially.
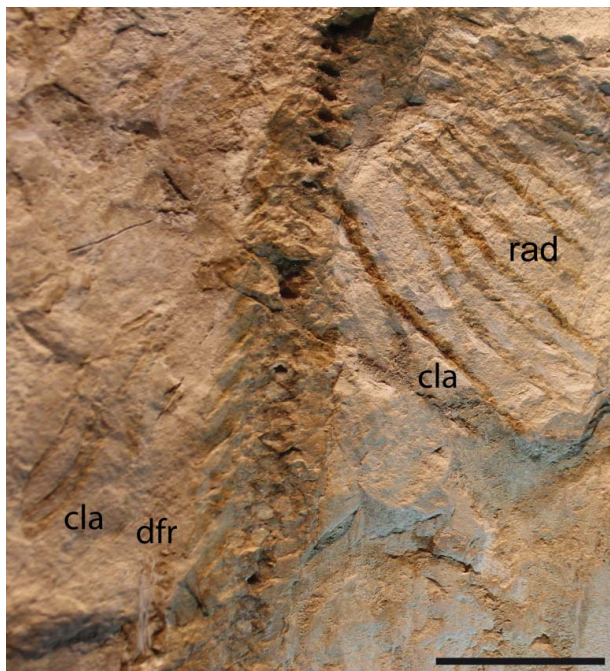
Hyoid and gill arches. The exquisite preservation of MCSNV IG.VR.67290 allows a detailed description of most of the hyoid arch (Fig. 5). The hyomandibulae are narrow and elongate, slightly stout at the proximal base, and tapering distally towards their articulation with the
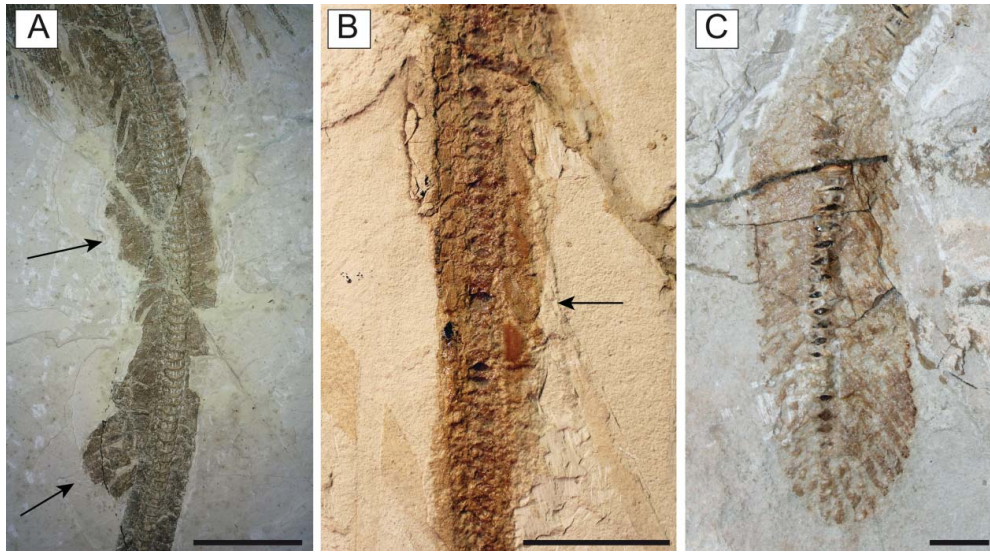
Figure 13. †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site. Details of the precaudal tail of **A,** MCSNV IG. VR.67290 and **B,** MGP-PD 26276. The arrows mark the position of the two dorsal fins in MCSNV IG.VR.67290 and the second dorsal fin in MGP-PD 26276 already detected and figured by Jaekel (1894). **C,** Detail of the caudal fin of MCSNV IG.91129. Scale bars: A, B = 50 mm; C = 10 mm.

Meckel's cartilage. The dorsal and ventral pseudohyoids are long and slender, and located just posterior to the articulation of the hyomandibula with the otic region of the chondrocranium. †*Titanonarke* lacks ceratohyals,

Figure 14. †*Titanonarke molini* (Jaekel, 1894) from the Eocene of Monte Postale site. **A,** upper and lower tooth bands in MCSNV IG.VR.67290, with a close-up of some teeth in the area indicated. **B,** reconstruction. Abbreviations: la, labial cartilage; me, Meckel's cartilage; pq, palatoquadrate. Scale bars 5 mm.

resembling the condition of *Narcine* and *Discopyge* among narcinoids (Miyake & McEachran 1991).

There are five pairs of ceratobranchials. The anterior four pairs are large, and have a central depression (or fossa) with a small fenestra for the insertion of the depressor muscles (see Carvalho & Séret 2002). The fenestrae of †*Titanonarke* appear larger in small individuals (Fig. 6), as in *Diplobatis* (Miyake & McEachran 1991, fig. 6H; Claeson 2014, supplemental pl. 12). The fifth ceratobranchials are slender and posteriorly oriented, and articulate with the scapular process of the scapulocoracoid. The epibranchial elements are not clearly recognizable, being partially covered by the ceratohyals. At least three small basibranchials are recognizable. The basibranchial copula is large and rounded, with a small caudal tip or tab in its posterior margin. We counted five pairs of ovoid or bean-like hypobranchials. Hypobranchials are segmented, resembling the plesiomorphic condition of *Benthobatis*, *Discopyge* and *Heteronarce* among narcinoids (Miyake & McEachran 1991, fig. 6F, G; Claeson 2014, supplemental pl. 12). Pharyngobranchials, extrabranchials and branchial rays are not preserved in the available material.
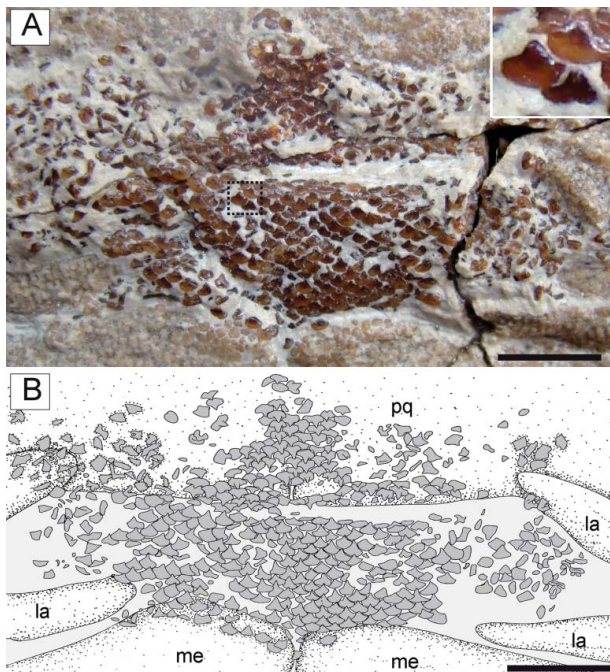
Synarcual and vertebral column. The synarcual cartilage is strongly calcified in all mature specimens, though not in the embryo preserved inside the abdominal cavity of the holotype (see the section 'Embryo'). In mature specimens the synarcual exhibits the typical prismatic tessellated cartilage found in elasmobranchs. The posteroventralmost portion of tessellated cartilage flanks several mineralized vertebral centra, which comprise densely packed areolar cartilage. Anteriorly, the synarcual
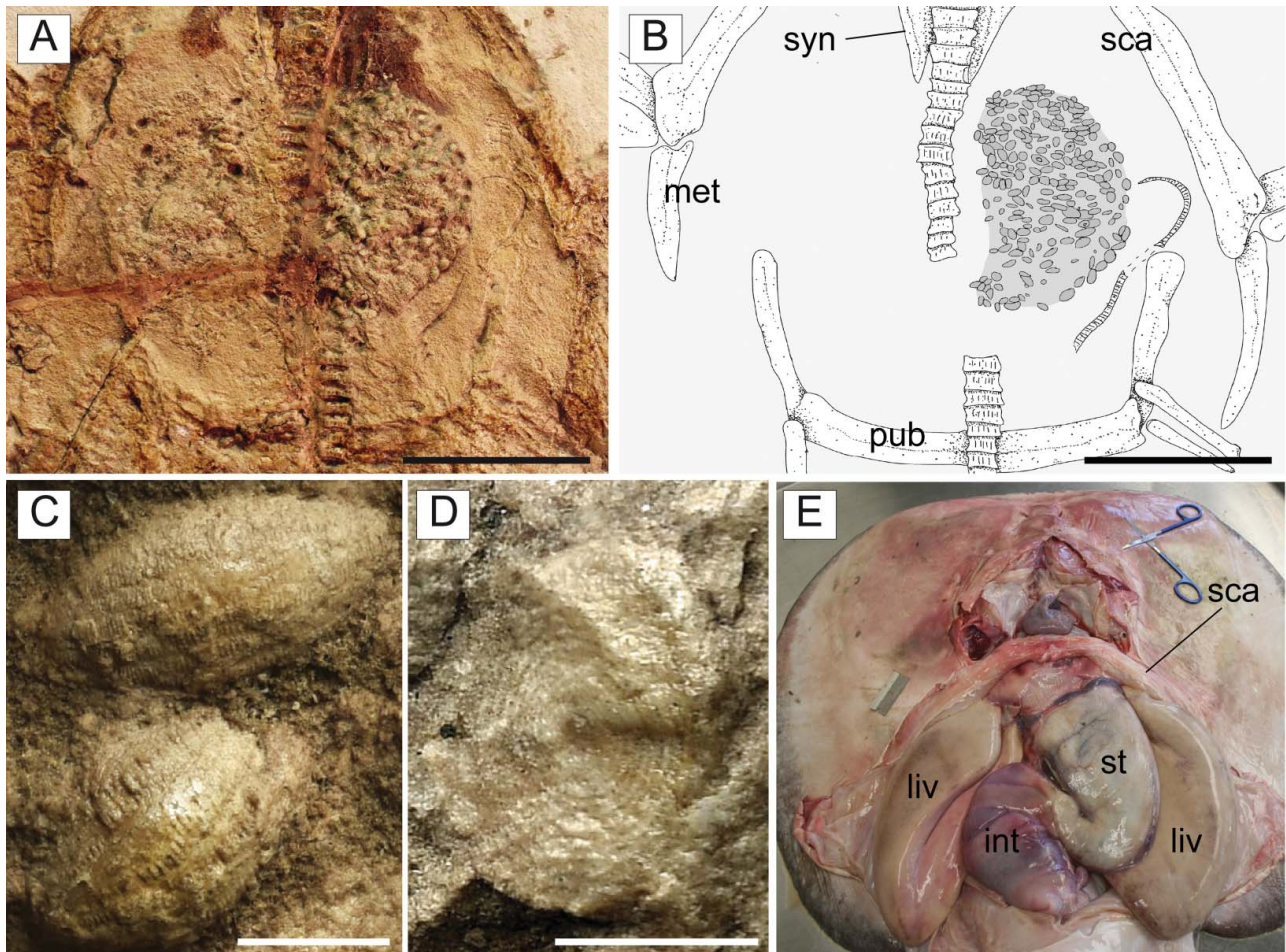
Figure 15. A, B, †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site; **A,** detail of the abdominal region in MGP-PD 26275 showing the stomach content; **B,** reconstruction; note also the embryo lying next to the stomach. **C, D,** close-up of some of the larger foraminifera of the genus †*Alveolina* in the stomach of MGP-PD 26275. **E,** dissected specimen of *Torpedo nobiliana* in ventral view (ESB tn200707_159) showing the position of the stomach, used to identify the accumulation in MGP-PD 26275 as gut contents. Abbreviations: int, intestine; liv, liver; met, metapterygium; pub, puboischiadic bar; sca, scapulocoracoid; st, stomach, syn synarcual. Scale bars: A, B = 50 mm; C, D = 2 mm.

cartilage contacts the occipital condyles of the chondrocranium via the occipital cotyles. The morphology of the anterior portion of the synarcual is difficult to discern, it being partially hidden by the hyoid arch (most of the specimens are ventrally exposed). Therefore, the position of the dorsal rim of the anterior neural canal opening (synarcual mouth) with respect to the occipital cotyle and the lips, as well as the shape of the ventral rim of the anterior neural canal opening (synarcual lip), are difficult to discern.

The synarcual possesses lateral stays, which are posteriorly displaced (Fig. 9) as in *Benthobatis*, *Discopyge*, *Narcine*, *Heteronarce* and *Narke* (Claeson 2014). The distal end of the lateral stays is apparently tab-like and their anterior margin forms an obtuse angle with the anterolateral margin of the synarcual. The long posterior flanges of the synarcual surround the anteriormost 8–12 free vertebral centra, and their posterior margins end posteriorly to

the scapulocoracoid bar, resembling the condition of non-narkid torpediniforms (Compagno 1999). It is not possible to detect the number of fused vertebrae that constitute the synarcual, or the foramina.

The vertebral column of †*T. molini* consists of about 153–155 vertebral centra; of these, 27–30 are trunk centra (18–20% of total, from the first distinguishable centrum to the anterior margin of the puboischiadic bar), 100–115 are precaudals (65–75%, from the anterior margin of the puboischiadic bars to the upper origin of the caudal fin), and 23–25 are caudals (15–16%, from the upper caudal fin origin to the end of the series). The number of vertebrae is by far the largest compared to all living torpediniforms and can be considered an autapomorphic condition of †*Titanonarke* (see Table 2).

The vertebral centra are strongly calcified, subrectangular in shape and anteroposteriorly short. Large basiventral processes are visible along most of the vertebral centra,
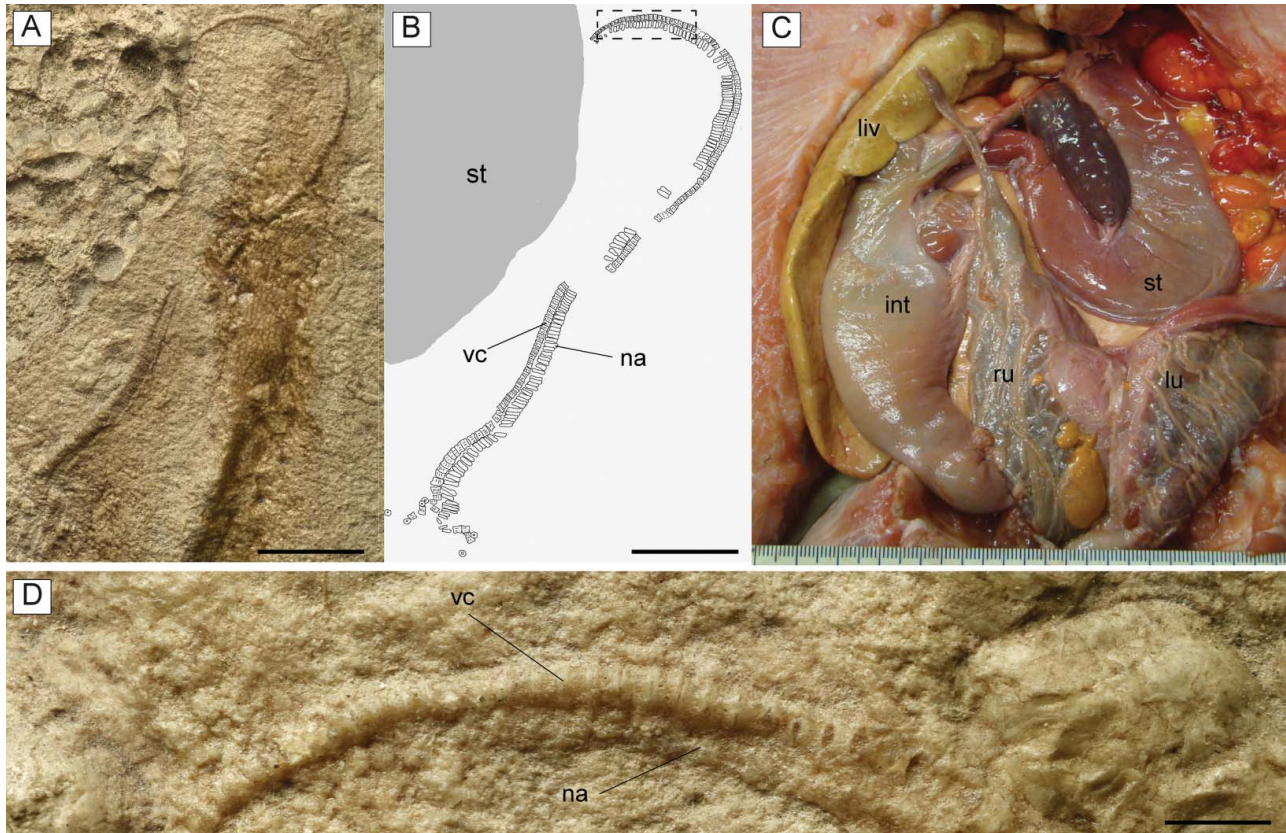
Figure 16. A, B, D, †*Titanonarke molini* (Jaekel, 1894) from the Eocene Monte Postale site; **A,** close-up of the abdominal region of MGP-PD 26275 showing the embryo; the anterior region of the body lies on the lower portion of the photo; **B,** reconstruction; **D,** detail of the vertebral column of the embryo indicated in B with a dotted rectangle. **C,** dissected specimen of *Potamotrygon tigrina* (IUWP 7361) showing the position of the left uterus, just next to the stomach. Abbreviations: int, intestine; liv, liver; lu, left uterus; na, neural arches; ru, right uterus; st, stomach; vc, vertebral centra. Scale bars: A, B = 10 mm; D = 1 mm.

from the posterior tip of the synarcual to the caudal fin base. There are eight to 10 pairs of ribs articulating with centra posterior to the puboischiadic bar (Fig. 11A). The low number of rib pairs is similar to that of *Benthobatis*, *Discopyge*, *Diplobatis* and *Narcine* and is considered a derived trait of the narcinids among torpediniforms (see the phylogenetic analysis in this study).

Paired fins and girdles. The scapulocoracoid is the largest element of the pectoral girdle. It is robust and strongly arched, and its anteriormost margin is situated between the basibranchial copula and the posterior tips of the synarcual flanges. The scapulocoracoid articulates anteriorly with the fifth pair of ceratobranchials. The suprascapulae are slender and fused medially, forming a slightly bowed bar in MCSNV IG.VR.91359 (Fig. 6). In MCSNV IG.VR67290 the suprascapula appears to be inclined with respect to the vertebral column, confirming the interpretation of a bowed shape (Fig. 5). The suprascapular antimere is longer than the scapular process of the scapulocoracoid, which is posteriorly directed as in *Narcine* (Fig. 9). The fusion of the suprascapular antimere

with a visible suture is considered a synapomorphy of Torpediniformes by Claeson (2014). Although MCSNV IG.VR.67290 and MCSNV IG.VR.91359 preserve this skeletal element (Figs 5, 6, 9), it is not possible to describe a visible suture because both specimens are exposed ventrally and this area is obscured by the vertebral column. However, it is expected that †*Titanonarke* shares this character with all other electric rays.

The juvenile MCSNV IG.VR.91359 shows a weak taphonomic displacement of the suprascapulae with respect to the vertebral column (Figs 6, 9), which supports the hypothesis that the suprascapulae in torpediniforms are completely separate from the vertebral column and that the only connection between pectoral girdle and postcranium is through the fifth ceratobranchial (Aschliman *et al.* 2012a; Claeson 2014). The same specimen shows that the suprascapular projection of †*Titanonarke* was lateral and that the suprascapula-scapulocoracoid articulation was loose and unforked.

The propterygia are long and arched and extend well beyond the anterior margin of the scapulocoracoid (Fig. 10). They are composed of five or six propterygial

Table 1. Morphometric data for all examined specimens of †*Titanonarke* Carvalho, 2010 from the Eocene Monte Postale site, Bolca Lagerstätte. Abbreviations (see the morphological scheme in the Supplemental material): AOW, antorbital cartilage width; CFL, caudal fin length; CFD, caudal fin depth; CLO, clasper length; CPD, caudal peduncle depth; D1B, first dorsal fin base length; D2B, second dorsal fin base length; DCS, dorsal caudal space; DL, disc length; DW, disc width; HL, head length; IDS, interdorsal space; MOW, mouth width; P2A, pelvic fin anterior margin length; P2B, pelvic fin base length; P2S, pelvic fin span; PCS, space from pelvic fin insertion to the caudal fin origin; PD1, predorsal distance up to the first dorsal fin; PD2, predorsal distance up to the second dorsal fin; PDI, pelvic fin insertion to first dorsal fin origin; PDO, pelvic fin origin to first dorsal fin origin; PGW, snout tip to the level of the greatest disc width; PIW, body width at pectoral fin insertions; POR, preoral length; PP2, prepelvic length; SL, standard length; TAL, tail length; TBW, tail base at pelvic fin origin; TL, total length.

| | †*Titanonarke molini* (Jaekel, 1894) | | | | | | | | | | | †*Titanonarke megapterygia* sp. nov. | |
| | MGP-PD 26275/6 | | MCSNV IG.VR.67290 | | MCSNV IG.91128/9 | | MCSNV IG.135581 | | MCSNV IG.VR.91359 | | MCSNV IG.135576 | |
Measurements	mm	% SL	mm	% SL	mm	% SL	mm	% SL	mm	% SL	mm	% SL
AOW	206.6	25.3	217.4	29.0	196.2	23.1	26.1	–	28.1	28.4	174.2	27.8
CFL	80.9	9.9	–	–	75.0	8.8	–	–	–	–	97.4	15.6
CFD	28.4	3.5	–	–	26.1	3.1	–	–	–	–	36.0	5.8
CLO	–	–	–	–	70.5	8.3	–	–	–	–	–	–
CPD	20.2	2.5	25.5	3.4	15.9	1.9	–	–	2.3	2.3	13.7	2.2
D1B	–	–	64.6	8.6	56.6	6.7	–	–	–	–	–	–
D2B	50.0	6.1	47.9	6.4	51.3	6.0	–	–	–	–	–	–
DCS	140.2	17.2	109.8	14.6	119.3	14.0	–	–	–	–	–	–
DL	353.1	43.2	341.2	45.5	371.6	43.7	33.8	–	42.8	43.2	334.5	53.4
DW	387.0	47.4	406.6	54.2	347.8	40.9	–	–	56.3	56.9	349.8	55.9
HL	178.1	21.8	172.5	23.0	204.4	24.0	22.2	–	23.6	23.8	171.8	27.4
IDS	–	–	53.6	7.1	–	–	–	–	–	–	–	
MOW	80.6	9.9	99.9	13.3	95.5	11.2	13.6	–	12.7	12.8	87.1	13.9
P2A	77.2	9.5	103.1	13.7	88.7	10.4	–	–	8.1	8.2	141.6	22.6
P2B	134.6	16.5	108.3	14.4	81.3	9.6	–	–	11.7	11.8	107.9	17.2
P2S	206.8	25.3	208.5	27.8	–	–	–	–	23.7	23.9	211.9	33.8
PCS	356.0	43.6	358.5	47.8	–	–	–	–	44.9	45.4	241.7	38.6
PD1	–	–	468.1	62.4	–	–	–	–	–	–	–	–
PD2	632.3	77.4	586.3	78.2	–	–	–	–	–	–	–	–
PDI	–	–	83.1	11.1	–	–	–	–	–	–	–	–
PDO	–	–	181.3	24.2	–	–	–	–	–	–	–	–
PGW	198.4	24.3	187.2	25.0	195.2	23.0	–	–	23.7	23.9	172.2	27.5
PIW	150.3	18.4	173.7	23.2	180.3	21.2	–	–	22.1	22.3	173.0	27.6
POR	73.0	8.9	62.6	8.3	85.4	10.0	7.7	–	9.6	9.7	56.2	9.0
PP2	328.5	40.2	307.3	41.0	348.4	41.0	34.8	–	44.4	44.8	299.0	47.7
SL	816.8	100.0	750.2	100.0	850.4	100.0	–	–	99.0	100.0	626.2	100.0
TAL	493.5	60.4	436.8	58.2	502.0	59.0	–	–	55.4	56.0	318.3	50.8
TBW	94.8	11.6	109.7	14.6	132.7	15.6	–	–	13.2	13.3	103.5	16.5
TL	897.7	109.9	–	–	925.4	108.8	–	–	–	–	722.6	115.4

segments. Two large voids, occupied in life by electric organs, are delimited by the propterygia, antorbital cartilages, hyoid archs and scapulocoracoids. The mesopterygium is flat, subtriangular in shape, and parallel and adjacent to the propterygium. The metapterygium is long and slender, is triangular in shape, and tapers posteriorly. The mesopterygium is shorter than the pro- and metapterygium in all specimens, although the apparent smaller size of the metapterygium in MCSNV IG.VR.67290

appears to be preservational (the metapterygium is weakly calcified in some narcinids; Carvalho & Séret 2002) or an artefact of the glue used to join pieces of the slab during preparation. There are about 40 pectoral radials (12–16 propterygial, 9–12 mesopterygial and 10–12 metapterygial), which bifurcate twice before reaching the edge of the pectoral fin margin. Each radial is composed of four segments before the first bifurcation, and another four elements before the second bifurcation (at least 9–10

Table 2. Summary of selected meristic features used to discriminate fossil and living genera of the family Narcinidae. Includes new data from the examined material and data from Fechhelm & McEachran (1984), Rincon (1997), Carvalho *et al.* (1999, 2002a, b, 2003), Carvalho (2001, 2008), Rincon *et al.* (2001), Carvalho & Séret (2002), Carvalho & Randall (2003), Menni *et al.* (2008), Carvalho & White (2016), Last *et al.* (2016), Froese & Pauly (2017).

Feature	*Benthobatis*	*Diplobatis*	*Discopyge*	*Narcine*	†*Titanonarke*
Trunk vertebrae	13–20	23–25	20	15–31	27–30
Precaudal vertebrae	46–73	61–63	58–70	58–77	74–115
Caudal vertebrae	31–46	22–24	?	18–32	23–32
Total vertebrae	96–118	97–112	85–91	100–127	133–155
Rib pairs	4	7–9	8	5–10	8–10
Total pectoral radials	?	31	?	27–41	35–40
Pelvic fin radials	12–13	16–21	?	14–21	19–21
First dorsal fin radials	5–6	6–7	?	6–10	7–9
Second dorsal fin radials	6–7	7–8	?	6–11	6–7
Total caudal fin radials	34–35	33–36	?	39–63	41–42
Upper jaw tooth rows	9–20	14–22	10–20	11–27	12–13
Lower jaw tooth rows	9–22	14–22	10–20	8–30	15–17

segments in total; Fig. 10). The lower number of segments recognized by Carvalho (2010), and actually detected in some specimens, is probably related to the loss of distal elements due to taphonomic processes. The radials are covered with a continuous layer of small (less than 1 mm) tesserae, forming the so-called 'crustal' calcification that characterizes the radials of basalmost batoids having an axial-undulatory swimming style, including pristids and 'rhinobatids', other than torpedinids and narcinids (Schaefer & Summers 2005).

The pelvic fins (Fig. 11) are small and single-lobed, and their anterior margin is straight and barely overlapped by the posterior margin of the pectoral disc. The maximum width of the pelvic fins is about 50% of the pectoral disc width, whereas their anterior margin is about 24% of the disc length. The puboischiadic bar is robust and wide, with a slightly concave anterior margin. The presence of the puboischiadic foramina is difficult to detect. The pre-pelvic processes are long and straight, extending anteriorly almost to the level of the scapulocoracoid. They are wider distally than along the shaft, resembling the condition of all narcinids (Rincon *et al.* 2001, fig. 8; Fechhelm & McEachran 1984, figs 7, 16). The distal end of the pre-pelvic process was described as spatulate by Carvalho (2010). However, the margin of this structure, identified with an arrowhead on the holotypic specimen MGP-PD 26275/6 by Carvalho (2010, fig. 7), is not part of the pre-pelvic process. The iliac process, preserved only on the left side of MCSNV IG.VR.67290, appears short, stout and straight (Fig. 11) if compared to the long and curved iliac process of *Narcine* and *Discopyge* (Menni *et al.* 2008; Claeson 2014). The basipterygia are slightly longer than the puboischiadic bar, and have a slightly concave inner margin. Each basipterygium supports about 21–24 pelvic fin radials, the first of which is enlarged, articulates

with the lateral node of the puboischiadic bar and supports the anterior margin of the pelvic fin. Each pelvic fin radial bifurcates distally once and is composed of three segments. A single individual (MCSNV IG.91128/9) seems to show an elongate clasper, articulating with the distal tip of the basipterygium (Fig. 12). In length, the clasper appears to extend past the posterior tip of the pelvic fin lobe. However, it was not possible to analyse this structure in detail.

Median fins. There are two dorsal fins (Fig. 13A). The first one originates at about 62% SL, is slightly larger than the second one and is supported by seven to nine radials. The second dorsal fin originates at about 78% SL and is supported by six or seven radials. The interdorsal distance measures about 7% SL. The obvious presence of two dorsal fins in MCSNV IG.VR.67290 supports the interpretation of Jaekel (1894) and Cappetta (2012) regarding the presence of at least one dorsal fin in the holotype MGP-PD 26275/6 (Fig. 13B). The inadequate preservation of the dorsal fins in the historical material prevented their recognition by Carvalho (2010), who erroneously regarded their absence as diagnostic for †*Titanonarke*. About 42 radials support the caudal fin, of which about 20 are dorsal and 22 ventral (Fig. 13C).

Dentition. The teeth of †*Titanonarke* are arranged in tooth bands medially across the jaw symphyses, forming a tessellated pavement (Fig. 14). The lower tooth band is wider than the upper one. It is not possible to detect the tooth formula, but the teeth of †*T. molini* appear to be arranged in at least 12–13 rows in the upper jaw and 15–16 rows in the lower jaw, counted on symphyseal tooth series. The dentition is gradient monognatic heterodont with lateral and posterior tooth crowns becoming slightly lower. However, both upper and lower jaws show very

little heterodonty. Sexual heterodonty (studied via the analysis of the specimens with and without claspers) appears to be absent. It is not possible to detect any ontogenetic heterodonty due to the poor-quality preservation of this region in juveniles.

The tooth morphology is generally consistent with that of *Narcine* (see Herman *et al*. 2002, pls 10, 11). A single narrow, high and subtriangular cusp is present in each tooth. There are no accessory lateral cusplets. The crown base is broad and subcircular, and wider than the cusp length. The width of the cusp is less than half the length of the cutting edges. Cutting edges are blade-like. Lingual and labial ornamentations are absent and the tooth crown is completely smooth. Some teeth display a high and narrow root.

Gut contents. The holotype of †*T. molini* (MGP-PD 26275/6) shows abdominal contents consisting of a pellet-like accumulation of hundreds of specimens of †*Alveolina* (Fig. 15A–D), which is the most common foraminiferan genus in the Monte Postale sediments (Papazzoni *et al*. 2017). The individual foraminifera are grouped together and closely packed, forming an accumulation, which is ovoid in outline and anteroposteriorly elongate, measuring about 80.5 and 41.8 mm in length and width, respectively. The exceptionally preserved gut contents show little evidence of digestion, suggesting that consumption occurred shortly before the numbfish's death. The accumulation is almost totally preserved in the abdominal cavity between pectoral and pelvic girdles, on one side of the vertebral axis, and just posteriorly to the flanges of the synarcual cartilage. This position is exactly comparable to that occupied by the gut-intestine tract in living electric rays (Fig. 15E), and in narcinids in particular (see Marinsek *et al*. 2017, fig. 1). Moreover, the general shape of the accumulation resembles fossilized gastric contents detected in other elasmobranchs (e.g. Hovestadt & Hovestadt-Euler 2002; Amalfitano *et al*. 2017). Additionally, there is no evidence of skeletal dispersal due to currents or bioturbation. Thus, we conclude that the accumulation is not the result of processes related to bottom tractive currents or bioturbation that sometimes can result in the accumulation of such elements (see Schäfer 1972). Consequently, this accumulation of foraminifera unquestionably represents gut contents.

Embryo. MGP-UP 26275/6 also shows a unique partially developed embryo whose length is estimated to range between 50 and 60 mm (Fig. 16), about 6–7% of the adult size. The embryo comprises an almost complete vertebral column having about 150 vertebrae, whose number is perfectly comparable to that of an adult individual of †*T. molini*. The vertebral column is partially disarticulated, with some elements scattered from their original position. Each vertebra consists of a vertebral centrum and associated neural arch. There is no trace of the synarcual

cartilage. This is consistent with the pattern of mineralization present in extant developing batoid embryos (e.g. *Myliobatis*, *Pristis*, *Raja*; KMC pers. obs.), where the areolar cartilage of the free vertebrae is well mineralized earlier than the tessellated cartilage of the synarcual. The vertebral column is the only fossilized structure in this embryo. There are no cranial or girdle skeletal elements preserved. This condition is consistent with the late phases of skeletogenesis in elasmobranch fishes in which the mineralization of the cartilages involves only teeth, dermal denticles, vertebral centra and neural arches in very early stages (see e.g. Eames *et al*. 2007; Enault *et al*. 2016). However, teeth are not clearly recognizable in the embryo, whereas dermal denticles are expected to be absent, as in all torpediniforms.

The embryo is totally preserved in the abdominal cavity between the pectoral and pelvic girdle, on the left side of the vertebral axis, and just next to the stomach (see also Fig. 15). This position is totally comparable to that occupied by the left uterus in fossil (Carvalho *et al*. 2004, figs 2 and 13) and living batoids (Fig. 16C; but see also Spieler *et al*. 2013, fig. 6), and in narcinids in particular (see Nair & Soundararajan 1973, fig. 1; Devadoss 1998, fig. 5). The embryo lies externally to the stomach (whose outline is clearly delimited by its contents of larger foraminifera; see Fig. 16A, B) therefore excluding the hypothesis of a possible ingested prey. The absence of traces of egg case surrounding the embryo suggests that the reproductive mode of †*T. molini* was viviparous (probably yolk-sac), a condition that resembles that of most living batoids (Hamlett & Koob 1999; Kriwet *et al*. 2009), and narcinids in particular (Hoar & Randall 1988; Bruton 1990; Rincon 1997; McEachran & Carvalho 2002; Last *et al*. 2016), and is considered plesiomorphic in batoids (Cole 2010). Finally, although the general morphology, size and position of the embryo also resemble those already detected in fossil sharks (e.g. Hovestadt & Hovestadt-Euler 2010; Hovestadt *et al*. 2010) and extinct freshwater stingrays (Carvalho *et al*. 2004), the specimen described herein unquestionably represents to our knowledge the first occurrence of a fossilized embryo *in situ* in marine batoid fishes.

Parasites. The examination of the historical material also has shown that fossilized crustacean isopods are strictly associated with the body of two individuals of both species of †*Titanonarke*. Individual fishes appear to be infested by two to four isopods each, the analysis of which is beyond the scope of this paper and will be provided in a separate study (Robin *et al*. in prep.).

†*Titanonarke megapterygia* sp. nov.
(Fig. 17)

2010 †*Titanonarke molini* (Jaekel, 1894); Carvalho: 188, figs 3, 5b–c, 8 [pro parte].
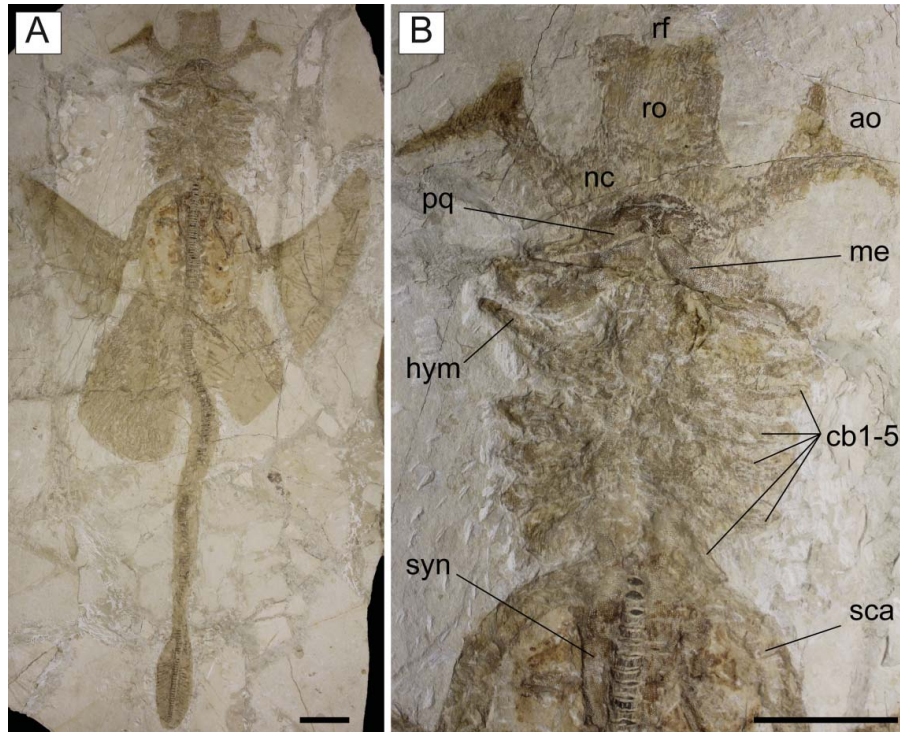
Figure 17. †*Titanonarke megapterygia* sp. nov. from the Eocene Monte Postale site. **A,** MCSNV IG.135576; **B,** detail of the head and hyoid apparatus. Abbreviations: ao, antorbital cartilage; cb, ceratobranchials; hym, hyomandibula; me, Meckel's cartilage; nc, nasal capsule; pq, palatoquadrate; sca, scapulocoracoid; syn, synarcual; rf, rostral fontanelle; ro, rostral cartilage. Scale bars = 50 mm.

Derivation of name. After the Greek words *méga*, meaning 'large', and *ptérygia*, meaning 'fins', referring to the proportionally larger pectoral and pelvic fins compared to those of the type species.

Holotype. MCSNV IG.135576, nearly complete articulated skeleton in a single slab (Fig. 17), 626.2 mm SL.

Type locality and horizon. Monte Postale site, Bolca Konservat-Lagerstätte, Italy; early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone (see Papazzoni *et al.* 2017).

Diagnosis. †*Titanonarke* with large subcircular disc of length *c*. 53% SL and width 56% SL; precaudal tail *c*. 51% SL; 136 total vertebrae (27 trunk; 74 precaudal, 32 caudal); total tooth row count *c*. 32 (15 rows in the upper and 17 in the lower jaw); 35 total pectoral radials (12 propterygial, eight mesopterygial and 15 metapterygial); greatly enlarged single-lobed pelvic fins containing *c*. 19 basipterygial radials; width of pelvic fins *c*. 61% of disc width; anterior pelvic fin margin length *c*. 42% disc length; caudal fin with 41 radials (20 dorsal and 21 ventral).

Remarks. Originally, MCSNV 135576 was considered a holomorphic specimen of †*T. molini* by Carvalho (2010), although that assignment to the type species was tentative.

The new species of †*Titanonarke* differs from the type species †*T. molini* (Jaekel, 1894) in a combination of morphometric and meristic characters. The differences mostly include those associated with the number of precaudal vertebrae (74 in †*T. megapterygia* sp. nov. vs. 100–115 in †*T. molini*). Consequently, the comparably reduced vertebral number in †*T. megapterygia* sp. nov. (133 in †*T. megapterygia* sp. nov. vs. 153–155 in †*T. molini*) results in different body proportions (see also Table 1). †*Titanonarke megapterygia* sp. nov. also differs from †*T. molini* by having a greater head length (*c*. 27 vs. 23% SL), disc length (53 vs. 44% SL), disc width (56 vs. 50%) and shorter tail (51 vs. 58% SL). However, the main difference in body proportions is in the size of the pelvic fins, which have a larger span (34 vs. 26% SL), anterior margin (23 vs. 11% SL) and base length (17 vs. 13% SL) in †*T. megapterygia* sp. nov. than in †*T. molini*. Moreover, the caudal fin also is longer in †*T. megapterygia* sp. nov. (16% SL) than in †*T. molini* (9% SL), with a higher number of caudal vertebral centra (32 vs. 23–25, respectively). The PCA performed on the entire morphological data set of standardized and log-transformed measurements and counts (Fig. 8) shows a remarkable separation of specimen MCSNV IG.135576 from all others along PC1 (PCA loading values indicate that this axis is mainly related to the variation in tail length, pelvic fin span, and the number

of precaudal vertebrae), thereby suggesting that morphometric and meristic data are useful to separate †*T. megapterygia* sp. nov. from †*T. molini*.

Phylogenetic analysis

The analysis of 71 morphological characters coded for 16 taxa produced a single most parsimonious tree (MPT) with a length of 170 steps (Fig. 18). The phylogenetic hypothesis of taxa is supported by the following indices: CI = 0.62, RI = 0.68; HI = 0.38. The relationships among torpediniforms are mostly consistent with those of Claeson (2014), although our analysis recovered the family Narcinidae as monophyletic. The monophyly of torpediniforms as recognized by McEachran *et al.* (1996), McEachran & Aschliman (2004), Aschliman *et al.* (2012a) and Claeson (2014) is confirmed and supported herein by six synapomorphies: presence of electric organs (char. 1[1]); absence of dermal denticles or thorns (char. 2[1]); iliac process straight (char. 32[1]); long prepelvic process (char. 33[1]); suprascapular antimere fused with visible suture (char. 35[1]); basibranchial copula rounded with a small caudal point/tab (char. 53[1]). Two main clades can be recognized within Torpediniformes: the Torpedinoidea (solely including the family Torpedinidae) and the Narcinoidea (including the sister taxa Narcinidae and Narkidae).

The monophyly of Torpedinoidea is supported by the five characters proposed by Claeson (2014): long, slender, flexible jaw cartilages (char. 22[1]); suprascapular antimere shorter than scapular process (char. 39[2]); antorbitals articulate on anterior aspect of nasal capsules (char. 43[1]); frontoparietal fontanelle absent (char. 45[1]); median rostral cartilage inconspicuous or absent (char. 49 [2]). An additional dental character, tooth root low and broad (char. 70[2]), represents a further synapomorphy of the group, and is based on previous descriptions of †*Eotorpedo*, *Torpedo* and *Hypnos* among torpediniforms (Cappetta 1988, 2012; Noubhani & Cappetta 1997; Herman *et al.* 2002). The absence of labial cartilages does not support the clade because it is considered plesiomorphic for elasmobranchs (see also Claeson 2014). †*Eotorpedo* in particular was recovered as sister to *Torpedo* because they share a single tooth cusp, contrary to *Hypnos*, the only torpediniform characterized by multicuspidate teeth (char. 66[1]) (see also Herman *et al.* 2002).

The monophyly of all remaining torpediniforms (the clade Narcinoidea) is supported by 12 characters: small labial cartilages that combined are less than the length of the Meckel's cartilage (char. 21[1]); palatoquadrate
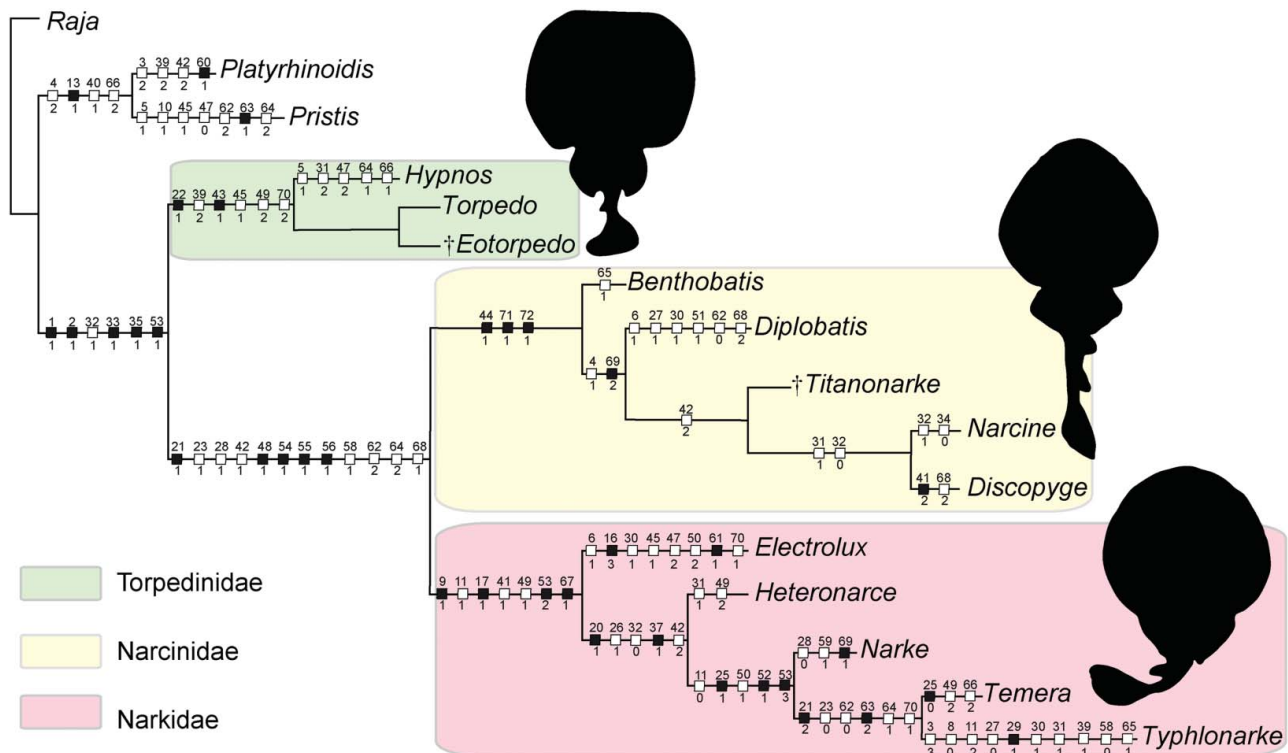
Figure 18. The single tree retrieved in TNT 1.5 based on 72 morphological characters and 16 taxa, showing the hypothetic relationships of †*Titanonarke* and †*Eotorpedo* within the Torpediniformes. Black squares indicate consistency index (CI) = 1.00; white squares CI < 1.00.

labiolingually compressed (narrower than Meckel's cartilage) and tapering towards symphysis (char. 23[1]); medial margin of pelvic fin lobes attached to precaudal tail (char. 28[1]); antorbital cartilage bifurcating at least once (char. 42[1]); nasal capsules project ventrally (char. 48[1]); dorsal marginal clasper cartilage possesses distomedial extension/medial flange (char. 54[1]); presence of a ligamentous sling on Meckel's cartilage (char. 55[1]); coracobranchialis consisting of a single component (char. 56[1]); dorsal rim of anterior neural canal opening (synarcual mouth posterior to occipital cotyle) (char. 58[1]); lateral stay located in the posterior third of the synarcual length (char. 62[2]); anterior margin on lateral stay describing an obtuse angle to axis (char. 64[2]); tooth cusp length less than half the length of the cutting edge (char. 68[1]).

We recovered monophyletic Narkidae (*Electrolux*, *Typhlonarke*, *Heteronarce*, *Narke* and *Temera*) *sensu* Claeson (2014). Unlike Claeson (2014), we also recovered a monophyletic family Narcinidae (including *Benthobatis*, *Diplobatis*, *Discopyge*, *Narcine* and †*Titanonarke*) that is sister to Narkidae. In this study, the monophyly of the Narcinidae conversely is supported by three unambiguous synapomorphies (CI = 1): presence of a rostral fontanelle (char. 44[1]); low number (up to 10) of rib pairs (char. 71 [1]); and rostral cartilage connected to the antorbital cartilage through a lateral appendix (char. 72[1]).

In the analyses of McEachran *et al.* (1996), McEachran & Aschliman (2004) and Aschliman *et al.* (2012a), the monophyly of Narcinidae was not specifically addressed, since they used *Narcine* as the only representative of the family. The monophyly of the family Narcinidae was tentatively recognized by Carvalho (2010) based on the presence of an expanded and trough-shaped rostral cartilage, presence of rostral fontanelle, and antorbital cartilages articulating with the lateral aspect of nasal capsulae. Compagno (1973) and Fechhelm & McEachran (1984) also considered the Narcinidae to be monophyletic based on a set of synapomorphies including a broad, expanded and trough-shaped rostral cartilage, ventrolaterally directed nasal capsules, forked antler-shaped antorbital cartilages, large precerebral fossa, transverse jaw with labial cartilages, anterior hypobranchials large and meeting midventrally, and large basibranchial copula. Most of these characters in our analysis are considered plesiomorphies shared with outgroups and/or with narkids (see also Claeson 2014). The precerebral fossa and the hyoid and gill arches, however, require further investigation for all those taxa, which was beyond the scope of the present study.

The phylogenetic placement of †*Titanonarke* within the Narcinidae is evident in our analysis, although its relationships with living numbfishes are not consistent with the hypothesis of Carvalho (2010), who recovered †*Titanonarke* as the most basal narcinid. The sister-group relationship between †*Titanonarke* and the monophyletic

grouping formed by the most derived narcinids (*Narcine* + *Discopyge*) is supported herein by a unique autapomorphy, antorbital cartilage broadly branched, with a third small branch posteriorly directed (char. 42[2]), which Carvalho (2010) hypothesized was absent in †*Titanonarke*. The sister-group relationship between *Narcine* and *Discopyge* detected herein is consistent with that proposed in the analysis of Fechhelm & McEachran (1984), because these two genera also share a long and slender (char. 31 [1]), and curved (char. 32[0]), iliac process of the pelvic girdle, a morphological character not present in †*Titanonarke*.

An analysis of the data matrix with WinClada 1.00.08 using the same settings resulted in exactly the same phylogenetic hypothesis as TNT. The single MPT has the same length (170 steps) and indices (CI = 0.62; RI = 0.68). The Mesquite analysis produced 87 MPTs; in the strict consensus tree, however, all branches are collapsed, resulting in an extended polytomy. The majority rule tree, conversely, displays the same systematic arrangement of taxa, but required more steps (180). The RI is identical (0.68) and the results for the CI are slightly improved (0.64). These results indicate that the characters employed in our TNT analysis are quite robust and the resulting systematic arrangement is very stable.

Discussion

Comparison and relationships

The analysis of the skeletal morphology of †*Titanonarke* has revealed the presence of several characters that unquestionably support the inclusion of this genus within the Torpediniformes, including large voids between the axial and pectoral skeleton that suggest the accommodation of massive electric organs, skin without dermal denticles, anteriorly directed antorbital cartilages, long prepelvic processes, and rounded basibranchial copula with a small caudal tab (see Davy 1829; Compagno 1973, 1977; Claeson 2014). The suprascapula with a visible median suture, regarded as a further torpediniform synapomorphy (Claeson 2014), is not exposed in the examined material. Additional features that align †*Titanonarke* with torpediniforms, although considered plesiomorphic within Batoidea (Compagno 1977; Maisey 1984; McEachran *et al.* 1996; Carvalho 2010), include some aspects of the branchial arch structure, the presence of a power-stocking precaudal tail, a posteriorly arched scapulocoracoid, and the propterygium being longer than the metapterygium.

The assignment of †*Titanonarke* to the superfamily Narcinoidea is supported by a number of features (see Herman *et al.* 2002; Claeson 2014), including the presence of labial cartilages, palatoquadrate labiolingually compressed and tapered towards the symphysis, bifurcated antorbital cartilage, lateral stays located on posterior

third of synarcual length, anterior margin of the lateral stay approximately forming an obtuse angle with axis, and tooth cusp length less than half the cutting edge length. Furthermore, †*Titanonarke* is excluded from Torpedinoidea (†*Eotorpedo*, *Hypnos* and *Torpedo*) because of the lack of several unambiguous characters diagnostic for this superfamily, including long, slender and flexible jaw cartilages, suprascapular antimere shorter than scapular process, antorbital cartilages articulating on anterior aspect of nasal capsules, inconspicuous or absent rostral cartilage, and low and broad tooth root (see Herman *et al*. 2002; Claeson 2014).

†*Titanonarke* is a member of a monophyletic Narcinidae, which is supported by three unambiguous synapomorphies: the presence of a rostral fontanelle, the reduced number of ribs, and rostral appendices connected to the antorbital cartilage. Other plesiomorphic features characterizing the Narcinidae (Carvalho *et al*. 1999; McEachran & Carvalho 2002; Last *et al*. 2016) and observed in †*Titanonarke* include a large subcircular disc; a tail longer than the disc; two dorsal fins, with the first one originating posterior to the anterior half of the body length; and single-lobed pelvic fins. †*Titanonarke* also is characterized by a mesopterygium that is shorter than the pro- and metapterygia, a trough-shaped and expanded rostral cartilage, and a rounded basibranchial copula with a small caudal tip. †*Titanonarke* is excluded from Narkidae (*Electrolux*, *Heteronarce*, *Narke*, *Temera* and *Typhlonarke*), which shows instead a higher number of ribs, absence of rostral fontanelle and appendix, rostral cartilage slender, inconspicuous or absent, mesopterygium longer than the metapterygium, and a heart-shaped basibranchial copula (Claeson 2014). Within the Narcinidae, †*Titanonarke* shares with the most derived *Narcine* and *Discopyge* at least one synapomorphy (broadly branched antorbital cartilage with a posteriorly directed third branch). Therefore, we can exclude the hypothesis that †*Titanonarke* represents a basal narcinid (see Carvalho 2010).

†*Titanonarke* is by far the largest narcinid (up to about 1 m TL, compared to living narcinids that usually have an average body size of less than 50 cm TL; Carvalho *et al*. 1999; Carvalho 2010; McEachran & Carvalho 2002; Last *et al*. 2016). Moreover, †*Titanonarke* differs from other narcinid genera in its unique combination of osteological features. It can be separated from *Benthobatis* by the position of the anteriormost free vertebral centrum, which is posterior to the synarcual in this living genus, but surrounded by posterior flanges of the synarcual in †*Titanonarke*. *Discopyge* possesses a mesopterygium that is longer than the pro- and metapterygia, a condition significantly different from that observed in †*Titanonake*, in which the mesopterygium is shorter than both pro- and metapterygia. Specimens of †*Titanonake* can be separated from *Diplobatis* and *Narcine* by the hypobranchial configuration (fused in *Narcine* and *Diplobatis*, unfused in

†*Titanonarke*), and the position of the lateral stay on the synarcual (midway along its length in *Diplobatis*, posterior in †*Titanonarke*). †*Titanonarke* can be further separated from *Narcine* and *Discopyge* by the absence of a long, slender and curved iliac process.

Moreover, †*Titanonarke* differs from other narcinid genera in its unique combination of meristic features (Table 2). It can be distinguished from all living numbfishes by the largest number of vertebrae (133–155 vs. 96–127). In particular, †*Titanonarke* can be separated from *Benthobatis*, *Diplobatis* and *Discopyge* because of its higher number of trunk (27–30 vs. 13–25, respectively) and precaudal (74–115 vs. 46–73, respectively) vertebral centra. The number of rib pairs is useful to separate †*Titanonarke* (8–10) from *Benthobatis* (four). †*Titanonarke* differs from *Diplobatis* in having a higher total number of pectoral radials (35–42 vs. 31), from *Diplobatis* and *Benthobatis* in the higher number of caudal fin radials (41–42 vs. 33–36), and from *Benthobatis* in having a higher number of pelvic radials (19–24 vs. 12–13).

## Palaeobiogeography of Torpediniformes

Except for †*Titanonarke*, the fossil record of torpediniforms (Fig. 19) is heavily biased towards isolated teeth. The oldest electric ray appears to be †*Eotorpedo* White, 1934, based on teeth from the upper Paleocene of Gada, Nigeria, whose morphology resembles that of *Torpedo*. The torpedinoid †*Eotorpedo* (including the species †*E. jaekeli* White, 1934, †*E. hilgendorfi* (Jaekel, 1904) and †*E. zennaroi* Cappetta, 1988) appears to have been widespread during the Paleocene, with several occurrences from the Danian and Thanetian of North and western Africa, Saudi Arabia and Texas (Jaekel 1904; White 1934; Dartevelle & Casier 1943; Arambourg 1952; Cappetta 1972, 1987, 1988, 2012; Madden *et al*. 1995; Noubhani & Cappetta 1997; Siguendibo Sambou *et al*. 2017). During the Paleocene the extant genera *Torpedo* and *Narcine* are scarcely represented, with only a few occurrences from Belgium and Jordan (Smith 1999; Cappetta 2012).

Although torpedinoids are well represented in the Eocene, with the most recent records of †*Eotorpedo* (†*E. hilgendorfi*, †*E. nolfi*), and some occurrences of *Torpedo* from northern Africa, Belgium, France, Jordan, and South Carolina, USA (Arambourg 1952; Herman 1974; Banks 1978; Cappetta 1988; Noubhani & Cappetta 1997; Cappetta *et al*. 2000; Adnet 2006; Cahuzac *et al*. 2007; Knight *et al*. 2007; Underwood *et al*. 2011; Case *et al*. 2015), the Eocene also marks the first major radiation of narcinoids. In addition to †*Titanonarke molini* and †*T. megapterygia* from the Ypresian of Italy, a broad distribution of *Narcine* is documented by several Ypresian to Priabonian occurrences in France, Guinea-Bissau, Togo, Morocco and Egypt (Cappetta 1987, 1988, 2012; Cappetta & Traverse 1988; Noubhani & Cappetta 1997; Adnet 2006; Adnet
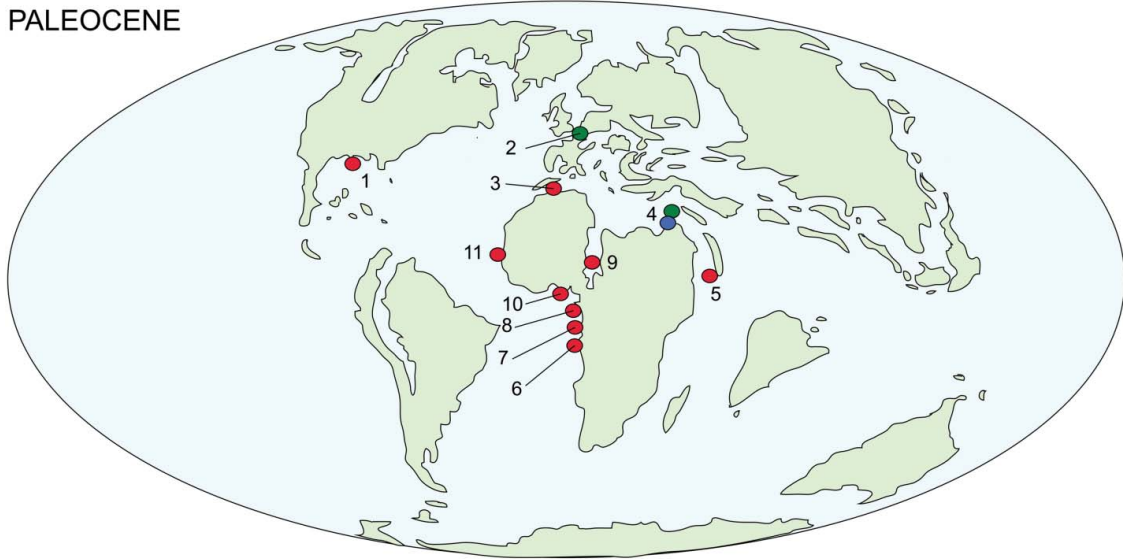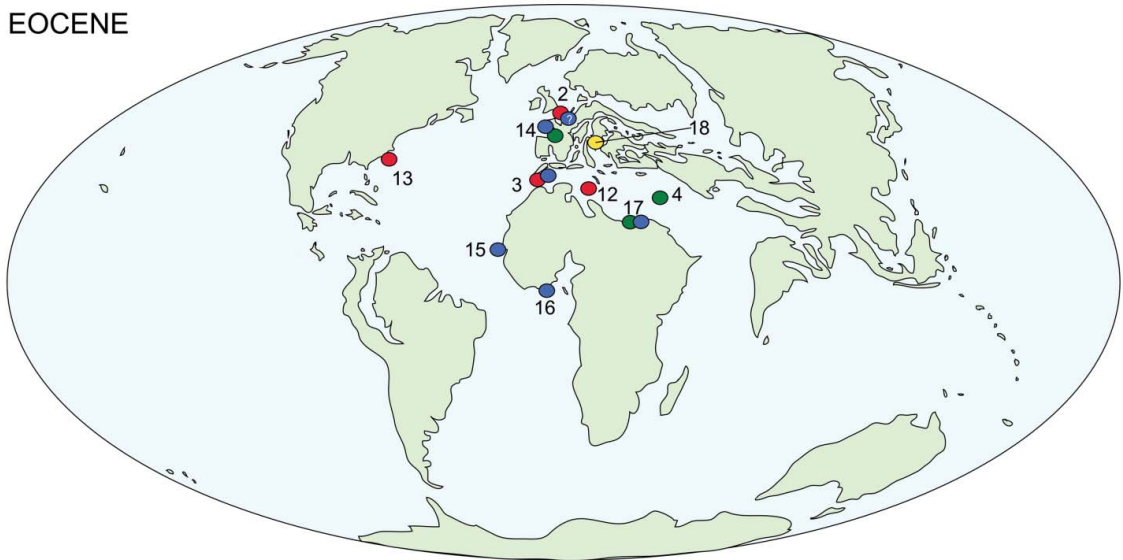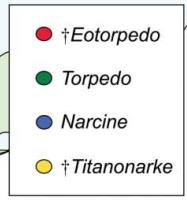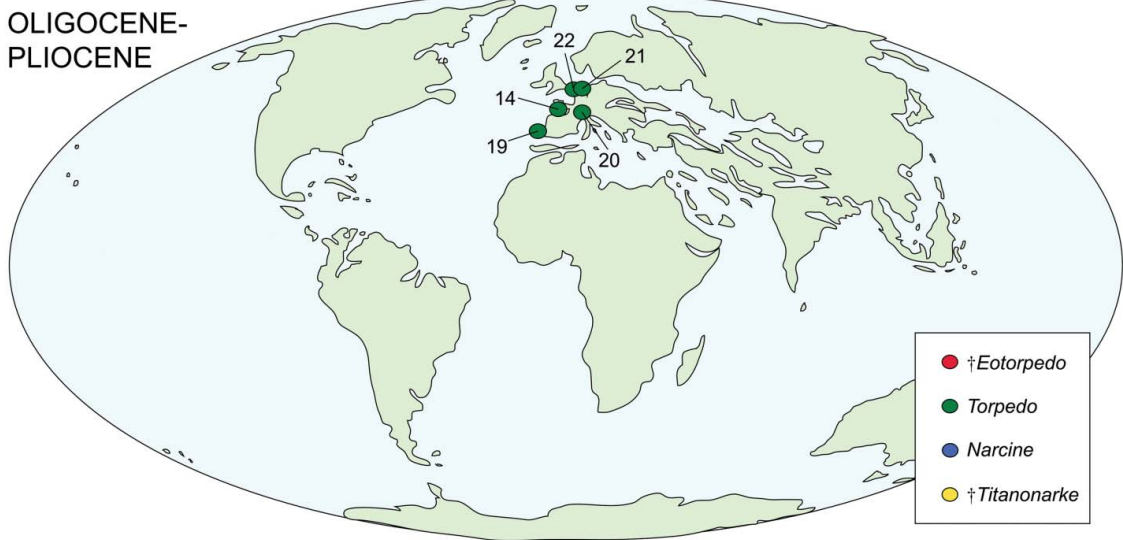
et al. 2010; Underwood *et al.* 2011). A single vertebra from the Eocene of Belgium referred by Hasse (1879) to *Narcine* requires further investigation before assignment to this genus can be confirmed (Carvalho 2010).

The fossil record of the Torpediniformes is scarce from the Oligocene to the Pliocene and is only represented by *Torpedo* from the Chattian to the Zanclean of Portugal, Switzerland, Germany, France and the Netherlands (Cappetta *et al.* 1967; Cappetta 1987, 2012; Cappetta & Nolf 1991; Bolliger *et al.* 1995; Antunes *et al.* 1999; Bracher 2005; Reinecke *et al.* 2005; Mollen 2010; Reinecke 2015). Teeth referred to *Narcine* from the Miocene of Portugal (Jonet 1968) and India (Sahni & Mehrotra 1981) cannot be referrred to any member of the Torpediniformes according to Cappetta (2012). The scarcity of torpediniforms in the Oligocene and Neogene fossil record may be related to sampling and/or taphonomic biases rather than a genuine biological and/or ecological signal, because extant electric rays have a worldwide distribution from tropical to temperate seas (Carvalho *et al.* 1999; McEachran & Carvalho 2002; Last *et al.* 2016).

Although torpediniforms are known in the fossil record only in Cenozoic deposits, several lines of evidence indicate that electric rays should have been present at least since the Late Cretaceous (see Aschliman *et al.* 2012b; Guinot & Cavin 2016). It has been suggested that the appearance and rapid diversification of nectobenthic durophagous/opportunistic predators such as dasyatoids, myliobatoids, rajoids and torpediniforms in the aftermath of the K–Pg boundary was related to the ecological replacement of extinct prey with similar adaptations, including demersal durophagous benthic dwellers such as †hypsobatids, †parapalaeobatids and †rhombodontids (Kriwet & Benton 2004; Guinot & Cavin 2016). Electric rays, particularly Torpedinidae, together with carcharhinid and isurid selachians, played a fundamental role during the recovery of the full diversity of elasmobranchs in the aftermath of the end-Cretaceous extinction event (Kriwet & Benton 2004).

Palaeobiological remarks
The potential palaeobiological and palaeoecological role of †*Titanonarke* has been poorly investigated up to now, considering the presence of several individuals of different ontogenetic stages in the Monte Postale palaeobiotope.

Extant numbfishes of the family Narcinidae are typically inshore to deep-water torpediniforms, with a worldwide distribution, inhabiting warm-temperate to tropical waters of continental and insular shelves. They occur down to about 1000 m depth, although they usually are found within 250 m, mostly occurring off soft sandy beaches and in muddy enclosed bays, often associated with coral reefs (Carvalho *et al.* 1999; McEachran & Carvalho 2002; Last *et al.* 2016). From this perspective, the presence of at least two species of †*Titanonarke*, the relative abundance of specimens and a gravid female suggest close affinities of this taxon with shallow-water habitats associated with coral reefs, as hypothesized for the Monte Postale palaeobiotope (Marramà *et al.* 2016c; Vescogni *et al.* 2016).

The stomach contents of MGP-PD 26275/6 provide a rare example of feeding relationships at a mid-high level of the trophic network in a reef-associated fish community in the context of the Early Eocene Climatic Optimum. The stomach contents of the holotype of †*T. molini* indicate that this numbfish fed on larger benthic foraminifera of the genus †*Alveolina*, at least occasionally, representing the first unambiguous and direct evidence of feeding behaviour in extinct electric rays. Modern narcinoids prey upon benthic invertebrates (mostly polychaetes and crustaceans, rarely molluscs) and small bony fishes using their highly specialized protrusible feeding apparatus (Carvalho *et al.* 1999; McEachran & Carvalho 2002; Last *et al.* 2016; Froese & Pauly 2017). Narcinids, in particular, are gape-limited polychaete specialists that use their highly calcified and protractile jaws as an excavation tool (Bigelow & Schroeder 1953; Dean & Motta 2004a, b). Gut content analyses of extant *Narcine* species have shown that polychaete annelids are the dominant prey item, whereas soft-bodied invertebrates and small bony fishes make up only a minor percentage of the diet (McKay 1966; Amaral & Migotto 1980; Rudloe 1989; Goitein *et al.* 1998; Carvalho 1999; Bornatowski *et al.* 2006; Cerqueira Ferreira & Vooren 2012). The labial cartilages play a fundamental role in limiting the circular gape of jaw protrusion during the suction phase, therefore enhancing the buccal pressure to suck in polychaetes (Dean & Motta 2004a, b). The specialized jaw apparatus morphology of narcinids is unique among batoids and it is probably related to a specialization that strongly constrains their ecological niche (Dean & Motta 2004a). The morphology of the jaw apparatus of †*Titanonarke* is

Figure 19. Palaeobiogeographical distribution of the Torpediniformes during the Cenozoic: 1, Texas; 2, Belgium; 3, Morocco; 4, Jordan; 5, Saudi Arabia; 6, Enclave of Cabinda; 7, Nigeria; 8, Niger; 9, Cameroun; 10, Senegal; 11, Tunisia; 12, South Carolina; 13, France; 14, Guinea-Bissau; 15, Togo; 16, Egypt; 17, Italy; 18, Portugal; 19, Switzerland; 20, Germany; 21, Netherlands. Data from Hasse (1879), Jaekel (1904), White (1934), Dartvelle & Casier (1943), Arambourg (1952), Cappetta *et al.* (1967, 2000), Cappetta (1972, 1987, 1988, 2012), Herman (1974), Banks (1978), Cappetta & Traverse (1988), Cappetta & Nolf (1991), Bolliger *et al.* (1995), Madden *et al.* (1995), Noubhani & Cappetta (1997), Antunes *et al.* (1999), Smith (1999), Bracher (2005), Reinecke *et al.* (2005), Adnet (2006), Knight *et al.* (2007), Adnet *et al.* (2010), Carvalho (2010), Mollen (2010), Underwood *et al.* (2011), Case *et al.* (2015), Reinecke (2015) and Siguendibo Sambou *et al.* (2017). Maps are modified from Scotese (2002).

similar to that of other narcinids, although it has a more slender hyomandibula. However, to the best of our knowledge, no evidence of feeding activity on benthic foraminifera has been reported in extant torpediniforms (data on food items are also available in Froese & Pauly 2017) or in other fossil or extant cartilaginous fishes. Among bony fishes the only known genus specialized in feeding on foraminifera is the living leopard wrasse *Macropharyngodon* (see Randall 1978) whose lineage and unique specialized feeding mode evolved apparently in the early Miocene (Cowman *et al*. 2009). Although fossil polychaetes have been reported in the Bolca Lagerstätte (Alessandrello 1990), and we do not exclude that this giant electric ray also fed on them, the abundance of larger foraminifera as stomach contents seems to suggest a selective predation of this kind of food rather than accidental ingestion that sometimes can occur in coral reef fishes (e.g. Daniels & Lipps 1978; Lipps 1988; Debenay *et al*. 2011). From this perspective, this peculiar and unique occurrence of predator-prey relationship between †*Titanonarke* and †*Alveolina* might represent a further feeding specialization among torpediniforms early in their evolutionary history, or at least it can be considered an opportunistic strategy in a context of remarkable abundance of this trophic resource in the Tethys realm during the Eocene (see e.g. Renema *et al*. 2008; Scheibner & Speijer 2008; Papazzoni *et al*. 2017).

The large size of †*Titanonarke* in relation to the small size of its prey is very striking, especially if compared to the generally smaller size of extant narcinids (see Carvalho 1999; McEachran & Carvalho 2002; Last *et al*. 2016), which are able to ingest polychaetes that may be as long as their total body length (Dean & Motta 2004a, b). The relative size difference between †*Titanonarke* as predator and its prey might support the hypothesis that larger marine fish predators could gain a competitive advantage by feeding on both small and large prey, with the latter being unavailable to smaller predators (Scharf *et al*. 2000). Moreover, it has been demonstrated that marine predators tend to select small prey instead of larger prey when possible (Gillen *et al*. 1981; Hoyle & Keast 1987; Hart & Hamrin 1990; Juanes 1994). Thus, the consistent inclusion of small prey in the diet of large predators might represent an opportunistic strategy in terms of benefit-cost ratio (Scharf *et al*. 2000), since the energetic costs of an active predatory lifestyle are less sustainable with an increase in size, and these predators show a clear tendency to prefer less-active feeding strategies, such as filtering or scavenging (Ferrón *et al*. 2017). Variation in size-based feeding strategies among predators can be related to differences in foraging tactics, predator gape allometry and morphological specializations, as well as individual behaviour and morphology of prey (Scharf *et al*. 2000). Marine fish predators seemingly become more successful with size due to a variety of factors including an increase in sustained and burst swimming speed (Keast & Webb 1966; Webb 1976; Beamish 1978; Blaxter 1986). The high number of precaudal vertebrae and the consequent proportionally longer tail of †*Titanonarke* with respect to extant narcinoids might suggest an increased swimming performance, because in torpediniforms, contrary to most batoids, the precaudal tail and the caudal fin are the primary propellers (Roberts 1969; Rosenberger 2001; Claeson 2014).

It is well established that the early Palaeogene is marked by high origination rates of bony and cartilaginous fish lineages, related at least in part to opportunistic ecological niche-filling scenarios in pelagic and benthic realms (Walker & Brett 2002; Kriwet & Benton 2004; Friedman 2009, 2010; Guinot & Cavin 2016; Marramà *et al*. 2016a, b; Bellwood *et al*. 2017). Moreover, the appearance of modern coral reef ecosystems during the early Palaeogene allowed the exploitation of new ecological resources, as highlighted by the development and expansion of piscine herbivory, high-precision benthic feeding, nocturnal feeding and ambush predation (Bellwood 2003; Goatley *et al*. 2010; Schmitz & Wainwright 2011; Bellwood *et al*. 2014; Floeter *et al*. 2017; Marramà & Carnevale 2017b). A second wave of innovations in feeding mode, including coral feeding, foraminifera feeding, particulate feeding and fish cleaning, arose during the Oligocene/Miocene transition, and were linked to the expansion of scleractinian-dominated reefs (Cowman *et al*. 2009; Bellwood *et al*. 2017; Floeter *et al*. 2017). However, larger foraminifera of the genus †*Alveolina* might have represented an abundant and unexploited food source for fishes of the Bolca palaeobiotope well before the Oligocene/Miocene boundary. From this perspective, the Eocene †*Titanonarke* might be considered the first documented evidence of a novel feeding strategy experimented with by the Torpediniformes in the context of the massive adaptive fish radiation in the aftermath of the end-Cretaceous extinction.

Conclusions

The excellent preservation of the †*Titanonarke* specimens from the Bolca Lagerstätte allowed a detailed reinterpretation of the morphology of this Eocene numbfish. A new species of †*Titanonarke* also has been recognized, based on several morphological differences with respect to the type species. A monophyletic Narcinidae has been unquestionably recovered based on parsimony analyses, with †*Titanonarke* occupying a more derived position compared to previous hypotheses. The presence of a fossilized embryo *in situ* in a marine batoid fish is reported here for the first time, providing evidence of viviparity in narcinids already in the early Eocene. Moreover, the analysis of the gut contents and the large size of †*Titanonarke*

indicate that the early Palaeogene radiation of torpedini-forms was characterized by the exploration of novel feeding strategies, remarkably different from those of extant polychaete-specialized numbfishes. The emergence of a novel feeding adaptation in the Eocene is particularly intriguing if considered in the context of the coeval extensive adaptive radiation in several bony and cartilaginous fish lineages that took place to fill the ecological roles left unoccupied by the biodiversity lost via the end-Cretaceous extinction (see Kriwet & Benton 2004; Friedman 2009, 2010; Guinot & Cavin 2016; Marramà *et al*. 2016a, b; Bellwood *et al*. 2017).

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Supplemental data

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