Miniature deep-sea hatchetfish (Teleostei: Stomiiformes) from the Miocene of Italy

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Abstract – A new genus and species of deep-sea hatchetfish, *Discosternon federicae* gen. et sp. nov., is described from the Middle Miocene (Serravallian) calciturbititic deposits of the Tufillo Unit exposed near the town of Gessopalena, central Italy. It is based on a single, very small, well-preserved and nearly complete specimen that exhibits a discoid physiognomy and a unique combination of features, many of which are reductive (loss of dorsal blade, loss of anal-fin hiatus, loss of abdominal keel-like structure, reduction of number of supraneurals, reduction of number of caudal vertebrae, presence of slender neural and haemal spines, external surface of cleithrum smooth). The comparative morphological analysis indicates that *Discosternon* is probably related to the derived genera *Horbatshia* and *Sternoptyx*. The highly reduced body size and the possession of many reductive characters indicate that *Discosternon* can be presumed to be a miniature fish. Anatomical and morphofunctional considerations suggest that *Discosternon* possibly was a midwater plankton feeder characterized by a reduced locomotory ability.

Keywords: Teleostei, Stomiiformes, *Discosternon federicae*, Miocene, Italy.

1. Introduction

Despite their abundance in Tertiary deposits, knowledge of fossil stomiiforms has, until recently, been relatively poor. Although they have been mentioned in several monographic works since the nineteenth century (e.g. Agassiz, 1833–1844; Wettstein, 1886), their fine anatomical features and phylogenetic relationships remain elusive. For this reason, the palaeontological history of this group of fishes is relatively unknown, and their past diversity is regarded as largely unexplored. Stomiiformes represents one of the most morphologically diverse extant groups of oceanic fishes. The order consists of four families (Gonostomatidae, Photichthyidae, Sternoptychidae, Stomiidae) and more than 300 species. Most stomiiforms are meso- or bathypelagic. Some taxa of this order occur in virtually all oceans, and some have the greatest abundance of individuals of any vertebrate species in the world (Nelson, 1994). All representatives of this order invariably possess specialized organs for the production of light, the photophores, which are characterized by a unique structure that has been used to diagnose this heterogeneous group of fishes (Fink & Weitzman, 1982). It is now widely accepted that these fishes have a Mesozoic origin (e.g. see Forey & Patterson, 2006), although the earliest unquestionably documented occurrence of the order dates back to Eocene times (see Patterson, 1993). The Cretaceous genus *Idrissia* has been tentatively referred to this group,

but its relationships have never been conclusively demonstrated (see Arambourg, 1952; Weitzman, 1967; Prokofiev, 2005).

The family Sternoptychidae includes some of the most bizarre stomiiforms, the deep-sea hatchetfishes. These fishes are characterized by a deep and strongly compressed body, with vertically flattened silvery sides that are used to reflect the incident light so that they appear invisible at all angles of view. The peculiar morphology of these fishes has stimulated intense debates about their origin, attracting the curiosity of many naturalists (e.g. see Thompson, 1917). The deep-sea hatchetfishes mostly feed on planktonic crustaceans (amphipods, copepods, euphasiids, ostracods) and are relatively common in the mesopelagic realm, usually below 200 m, exhibiting a slight diurnal vertical migration toward the surface (Hopkins & Baird, 1985; Kinzer & Schulz, 1988). Several studies of vertical distribution and trophic ecology have demonstrated that the different sympatric deep-sea hatchetfish species tend to minimize competitive interactions and are found at different depths during periods of foraging, showing a high level of time-space and food resource partitioning (see Hopkins & Baird, 1985; Howell & Krueger, 1987). As with other stomiiform groups, the deep-sea hatchetfish body plan was already in existence in the Eocene (see Prokofiev, 2005). In contrast to that of other stomiiform groups like gonostomatids and photichthyids, however, the fossil record of deep-sea hatchetfishes is relatively poor, and has been scarcely investigated (Baird & Eckardt, 1972; Prokovief, 2002; Carnevale, 2003). The purpose of this paper is to

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describe a new deep-sea fossil hatchetfish characterized by a unique morphology, and to discuss its affinities and evolutionary significance. The fossil was recently collected from a Miocene sedimentary series cropping out near the town of Gessopalena, in the Abruzzo Apennines, Italy.

2. Locality and age

The area surrounding the town of Gessopalena lies in the hills on the east side of the Montagna della Maiella carbonate massif, in the Abruzzo Apennines, central Italy. From a geological point of view, this area belongs to the so-called Molisan Units and more particularly to the Tufillo Unit (Fig. 1), the most external of the palaeogeographical domains recorded in the Molisan Units (Patacca *et al*. 1992). Lithologically, the Tufillo Unit mostly consists of varicoloured clays overlain by *Orbulina* calcarenites and calcilutites. The *Orbulina* calcarenitic–calcilutitic series has a variable thickness of 300 to 800 m (Selli, 1962; Di Nocera & Torre, 1987), representing a calciturbiditic system apparently belonging to a deep-sea conoid (Ciaranfi *et al*. 1980). A fossiliferous series cropping out near the town of Torricella Peligna, a few kilometres south of Gessopalena, has been recently described by Carnevale (2002, 2003, 2005). In this locality, the stratigraphic series consists of a rhythmic alternation of graded and laminated bioclastic marly calcarenites and massive calcilutites rich in planktonic foraminifera. The entire series has been interpreted as characterized by truncated Bouma sequences spaced out by calcilutitic episodes (Carnevale, 2005). Fossil fishes are invariably associated with the laminated calcarenites, and their accumulation and definitive burial was caused and favoured by the turbiditic events that episodically occurred in this basin (Carnevale, 2005). The stratigraphic series of Gessopalena is identical to that of Torricella Peligna, thereby suggesting that similar palaeoenvironmental and sedimentary conditions occurred in the two localities.
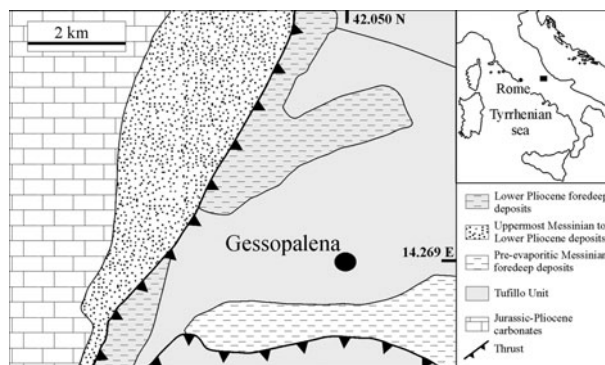

Figure 1. Schematic geological map showing the location of Gessopalena. Modified from Patacca *et al*. (1992).

At Gessopalena, the age of the fossiliferous horizon has been determined on the basis of its calcareous nannofossil content. The sediment is characterized by abundant and well-preserved nannofossils, which appear to indicate a Serravallian age (MNN6 Zone *sensu* Fornaciari *et al*. 1996).

3. Material and methods

The holotype and only known specimen was collected in March of 2006 by Mr Erminio Di Carlo, curator of the Museo Geopaleontologico dell'Alto Aventino, from a sedimentary succession that crops out near Gessopalena, a small town in the Abruzzo Apennines, central Italy. The specimen consists of a nearly complete articulated skeleton preserved on laminated calcilutite (Fig. 2). Thanks to the efforts of Mr Di Carlo, the fossil was made available for study in September of 2006. The specimen was prepared at the Dipartimento di Scienze della Terra of the Università di Pisa. The specimen required matrix removal before examination in order to allow investigation of its skeletal structure in as much detail as possible. This was achieved using entomological mounting needles. The fossil is deposited in the collections of the Museo Geopaleontologico dell'Alto Aventino (MGPA), Palena, central Italy. Observations were performed using a Leica MS5 stereomicroscope with an attached camera lucida drawing arm. Measurements were taken using a dial caliper, to the nearest 0.1 mm. Comparative information was derived mainly from the literature. Counts and measurements were made following Baird (1971).

4. Systematic palaeontology

Subdivision TELEOSTEI *sensu* Patterson & Rosen, 1977
Order STOMIIFORMES *sensu* Harold & Weitzman, 1996
Infraorder GONOSTOMATA *sensu* Harold, 1998
Family STERNOPTYCHIDAE *sensu* Weitzman, 1974

Discosternon gen. nov.

Diagnosis. A miniature deep-sea hatchetfish with strongly discoid body; body depth 96.6 % of standard length; abdominal keel-like structure absent; preabdominal and preanal spines present; caudal peduncle short and deep; frontal and parietal bones sculptured; parasphenoid strongly convex; basisphenoid present; premaxilla with a reduced ascending process; vertical preopercular limb much longer than the horizontal limb; 28 (15 + 13) vertebrae; neural and haemal spines slender; 11 pairs of pleural ribs; two anteriormost pairs of pleural ribs large and thick, apparently associated with the pelvic girdle; three supraneural bones; caudal fin slightly downturned; hypurals 1 + 2 and 3 + 4 + 5 fused; dorsal blade absent; dorsal fin contains at
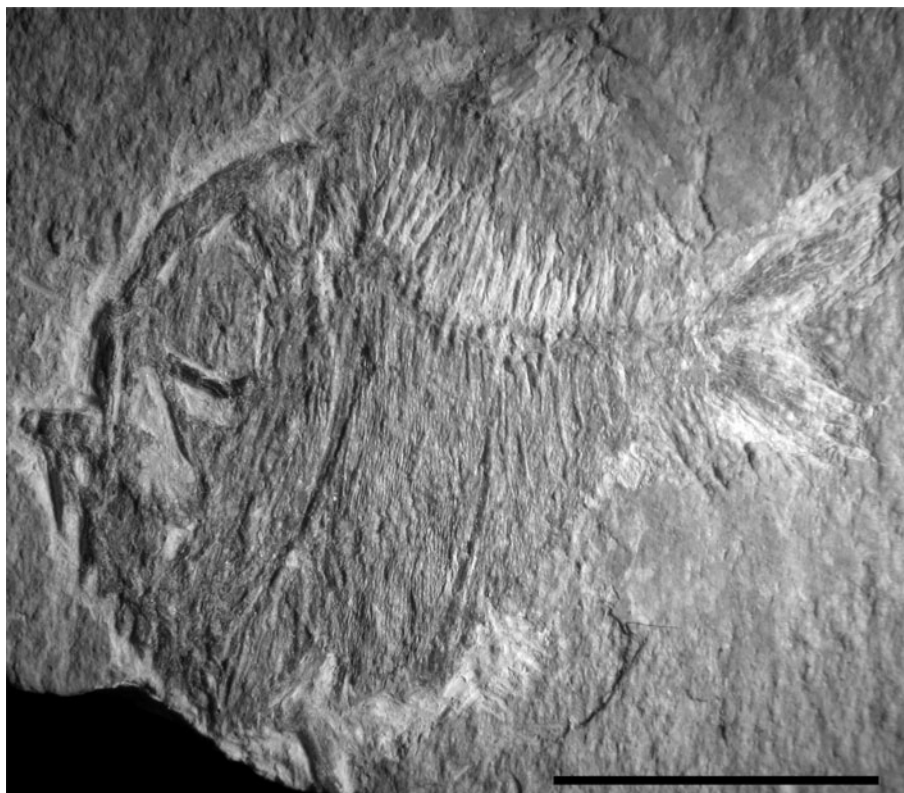
Figure 2. *Discosternon federicae* gen. et sp. nov., from the Miocene of Gessopalena, Italy. MGPA GES001, left side, lateral view. Scale bar 10 mm.

least 26 rays; anal-fin origin opposite to dorsal-fin origin; anal fin contains at least 24 rays; first anal-fin pterygiophore elongate and distally expanded; anal-fin hiatus absent; posttemporal and supracleithrum not fused; posttemporal spine present; external surface of cleithrum smooth; eight pectoral-fin rays; pelvic fin probably inserts just behind the pectoral-fin origin.

Derivation of name. From *discos* (Greek) meaning disk and *sternon* (Greek) meaning chest.

<p style="text-align:center">*Discosternon federicae* sp. nov.</p>

Diagnosis. As for genus, only species.

Holotype. MGPA GES001. Complete fish of 14.8 mm standard length.

Horizon and locality. Middle Miocene (Serravallian) of Gessopalena, Abruzzo, central Italy.

Derivation of name. In honour of Mrs Federica Giudice, my wife and my helpmate with this and others of my manuscripts.

4.a. Description (Figs 2–6)

The holotype of *Discosternon federicae* consists of a well-preserved nearly complete articulated skeleton (Fig. 2). The specimen is small, its total length measuring 18 mm; standard length is 14.8 mm. Other measurements as percentage of standard length: body depth

96.6 %, head length 40.5 %, head depth 79 %, orbit diameter 25.6 %, caudal peduncle length 7.4 %, caudal peduncle depth 20.2 %, dorsal-fin length 45.9 %, anal-fin length 52.7 %, predorsal length 52.7 %, preanal length 52 %, prepectoral length 28.3 %.

In general the body is deep, strongly discoid in outline, and considerably compressed. The cephalic–abdominal portion of the body is rounded and widely hypertrophied (Figs 2, 6). The body trunk, which is the region posterior to the anal-fin origin (see Carnevale, 2003), is deep and extensively shortened. The head is strongly compressed antero-posteriorly (Fig. 3). The orbit is very large. The caudal peduncle is very short and deep. The caudal fin is forked, with slightly unequal lobes. The anterior rays of the dorsal fin are longer than the others. Despite its very reduced size, the specimen appears to be an adult, based on the heavy ossification of most of the skeletal elements.

The neurocranium is especially deep posteriorly and roughly triangular in shape (Fig. 3). The braincase is very small. The precise structure of the ethmoid region cannot be determined. This is probably due to the abundant cartilage that usually characterizes this portion of the neurocranium of the deep-sea hatchetfishes. The frontals are the largest bones of the skull roof. These bones are strongly ossified and heavily sculptured by irregular pits and low ridges. The ornamentation extends posteriorly onto the parietal region. Each parietal also bears a dorsolateral ridge.
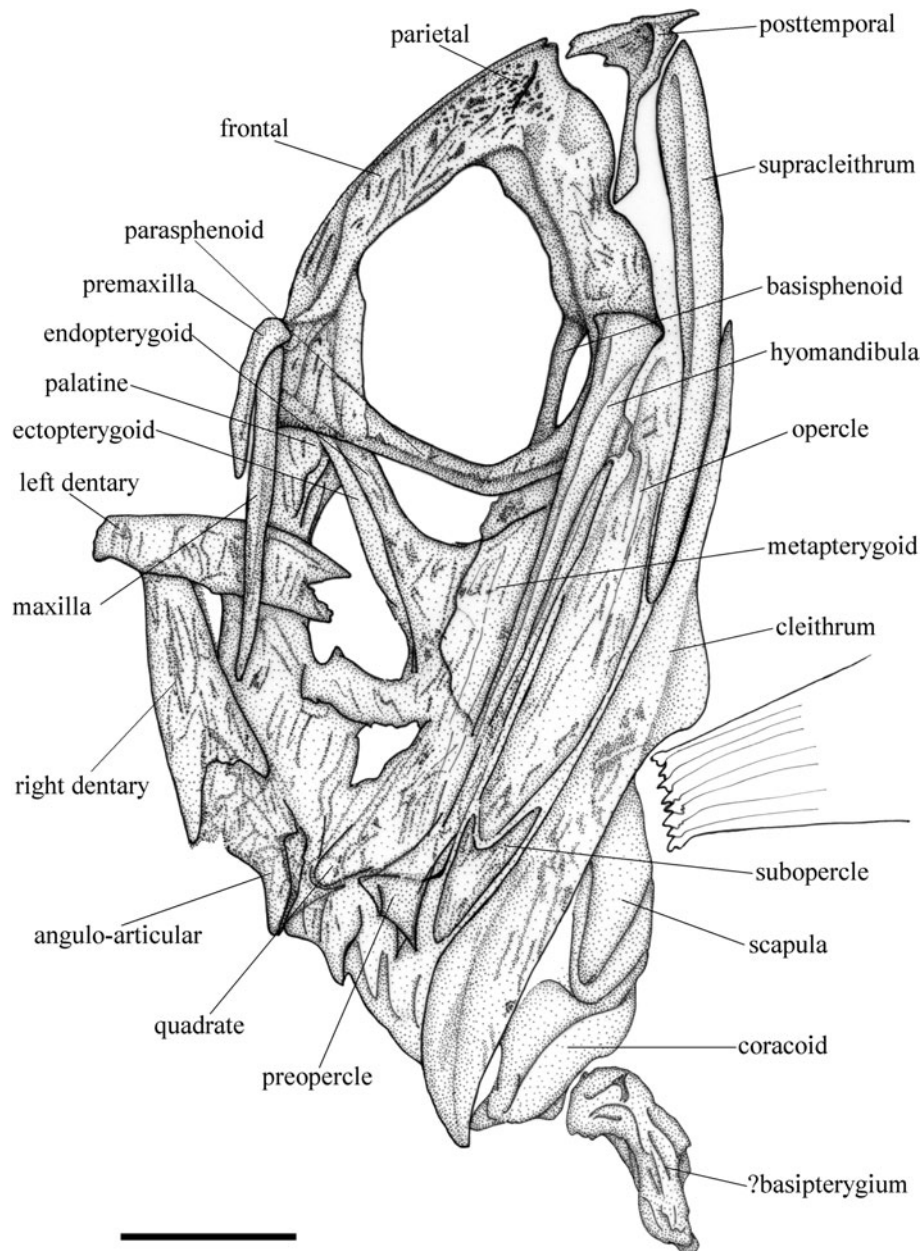
Figure 3. *Discosternon federicae* gen. et sp. nov., reconstruction of the skull, left side, lateral view. Scale bar 2 mm.

The structure and morphology of the supraoccipital and its relationships with the parietals are rather confused due to lateral compression. The bones of the otic and occipital regions are poorly preserved. The parasphenoid is robust and strongly arched; this is very similar to that of certain species of the genus *Argyropelecus* (e.g. *A. aculeatus*, *A. hemigymnus*, *A. logearti*). As suggested by Weitzman (1974), such a morphology could be related to several factors, including a very deep head, presence of large eyes, and lack of otic bullae. Therefore, it is possible to assume that the otic bullae were not present in the neurocranium of *Discosternon*. A tube-like basisphenoid is also preserved. Its ventral end is in firm contact with the parasphenoid, while its dorsal end contacts the (pro)otic region of the neurocranium.

The bones of the circumorbital series are not preserved.

The gape of the mouth is strongly oblique. The premaxilla is a relatively short bone with a small ascending process. The maxilla is long and slender. The presumed presence of the supramaxillae is difficult to demonstrate because of inadequate preservation. The lower jaw is slender. The dentary and angulo-articular appear to be disarticulated from each other. Such a disarticulation was probably facilitated by the presence of an original hiatus between these bones. Teeth are apparently absent in both the upper and lower jaws. However, this apparent absence probably represents the result of taphonomic loss.

In relation to the suspensorium, the ectopterygoid, endopterygoid, hyomandibula, metapterygoid, palatine

and quadrate can be recognized. The entire suspensorium is broadly developed vertically. The hyomandibula is extremely elongate and apparently spineless. The articular process for the reception of the opercle is situated in the upper quarter of its length. The quadrate is partially recognizable. Originally, the quadrate–mandibular joint was probably placed under the mid-region of the orbit. The metapterygoid seems to be rather large. The posterior margin of this bone closely contacts the ventral shaft of the hyomandibula. The endopterygoid is roughly triangular. Endopterygoid teeth appear to be absent. The ectopterygoid is elongate and slender. The palatine is poorly preserved.

The opercular bones are vertically elongate. The opercle is a crescent-shaped laminar bone, with a convex and lanceolate ventral portion. The opercular–hyomandibular joint consists of a nearly flat articular surface. The subopercle is characterized by a concave dorsal margin. The preopercle has a very short horizontal limb that forms a large acute angle with an elongate vertical limb. A small spine appears to be present posteriorly along the ventral margin of the horizontal limb. An irregular incomplete interopercle also can be recognized.

The gill arches are not distinguishable. Of the hyoid bar, only a few posterior incomplete branchiostegal rays can be recognized. These appear to be greatly enlarged anteroposteriorly.

The vertebral column is compact and sturdy, its abdominal portion bent in a kyphotic curve, with the concave side oriented toward the ventrum of the fish (Fig. 2). The vertebral column consists of 28 vertebrae. The centra, except for the eight posteriormost, are shortened, anteroposteriorly compressed and higher than long. The eight posterior centra are longer than high and sub-rectangular. The lateral surface of each centrum is ornamented by prominent ridges and fossae. The separation of vertebrae into caudal and precaudal portions appears rather problematic. Weitzman (1974) suggested that precaudal vertebrae of sternoptychids include those elements that do not bear a long, single haemal spine, and/or are not directly associated with the anal-fin pterygiophores. He also pointed out that the anterior haemal spine is invariably associated with the anterior pterygiophore of the anal fin. In *Discosternon* the five vertebrae anterior to the anterior pterygiophore of the anal fin bear short haemal spines of progressively increasing size. Following the criterion discussed by Weitzman (1974), these five vertebrae are interpreted herein as the posteriormost precaudal elements. As a consequence, it is possible to establish that *Discosternon* has 15 precaudal and 13 caudal vertebrae. The neural and haemal arches appear to be fused with their centra. The neural spine of the first centrum is shortened and roughly triangular in outline. The bases of certain neural and haemal spines are slightly expanded. In general, the neural and haemal spines are elongate, well-ossified and slender. The two
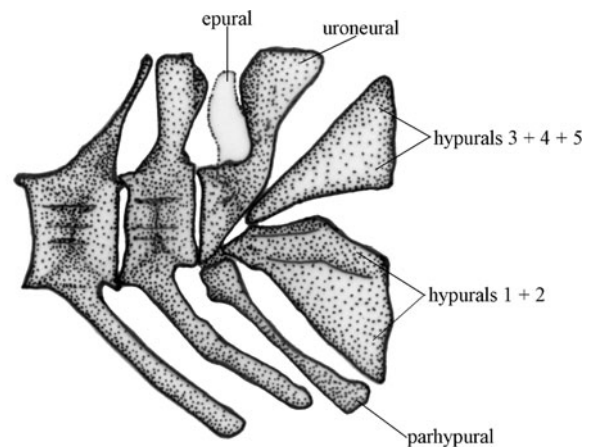

Figure 4. *Discosternon federicae* gen. et sp. nov., reconstruction of the caudal skeleton, left side, lateral view. Scale bar 1 mm.

anterior precaudal vertebrae bear no pleural ribs. The third and fourth vertebrae bear large and thick pleural ribs attached to the parapophyses. These ribs extend ventrally to the ventral profile of the body and were probably associated with the pelvic girdle. Following these, there are nine pairs of thin and slender ribs, of which the six posteriormost attach on the haemal arches and spines. There are no traces of the intermuscular bone complement.

The caudal skeleton of *Discosternon* is slightly down-turned (Figs 2, 4). The first preural centrum and the ural centra are evidently fused. What appears to be an uroneural is co-ossified with the fused first preural plus ural centra. The first and second hypurals are co-ossified and autogenous. The third to fifth hypurals are fused into an autogenous bony plate. The sixth hypural cannot be recognized due to the partial incompleteness of the caudal skeleton. The parhypural appears to be fused to the first preural centrum. It is robust and laterally flattened. A single epural was probably present. The neural spine of the second preural centrum is flattened and expanded. There are 19 (10 + 9) principal caudal-fin rays. The procurrent rays are not preserved.

The dorsal fin consists of at least 26 short rays supported by 25 pterygiophores. As in *Sternoptyx* (see Weitzman, 1974), the first proximal + middle pterygiophore bears two distal pterygiophores and fin rays. There are three slender supraneurals. There is no dorsal blade. The anal-fin origin is approximately opposite to that of the dorsal fin. The structure of this fin resembles that observed in *Sternoptyx* (see Weitzman, 1974). The fin consists of at least 24 rays, supported by at least 24 pterygiophores. The first pterygiophore is greatly modified (Fig. 5). It is remarkably expanded and spatulate distally. A small obtuse and laterally flattened preanal spine (see Schultz, 1961) projects externally along the ventral margin of the expanded portion of the anteriormost pterygiophore. The proximal shaft of
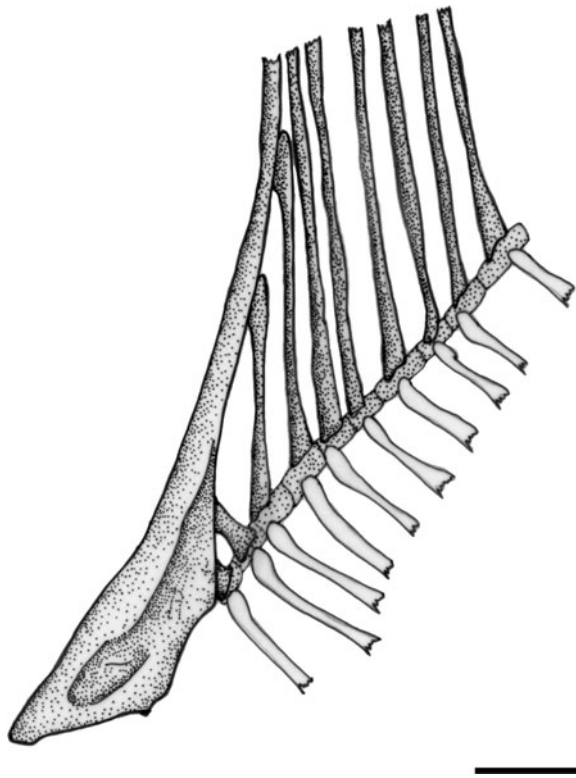
Figure 5. *Discosternon federicae* gen. et sp. nov., reconstruction of the anterior end of the anal fin, left side, lateral view. Scale bar 1 mm.

this pterygiophore is bent backward over the adjacent three pterygiophores. These are firmly applied along the posterior margin of the proximal shaft of the first pterygiophore. The proximal shafts of the fourth to posteriormost pterygiophores are parallel to each other and to the proximal shaft of the anteriormost element. There is no hiatus between the anal-fin pterygiophores (anal-fin hiatus).

The pectoral fin contains eight rays (Fig. 3). The bones of the pectoral girdle are relatively slender. The posttemporal is rather irregular in outline. It consists of two heavily ossified limbs with a membrane of bone interposed between them. The upper limb bears a moderately developed posterior spinous process. The supracleithrum is a large and vertically elongate blade-like bone. It appears to be completely separate from the posttemporal but articulates with it. The cleithrum is an elongate, obliquely oriented bone that terminates ventrally in a prominent preabdominal spine (*sensu* Schultz, 1961). A bony lamina with a rounded smooth profile can be observed along the posterior margin, approximately in the middle of its length. The lateral surface of this bone is not ornamented by the deep pits and rugosities typical of other deep-sea hatchetfishes. The morphology of the scapula and coracoid is rather confused. The pectoral-fin radials are not preserved.

The structure of the pelvic girdle is somewhat confused and difficult to interpret. A robust irregular bone placed just posterior to the pectoral girdle could represent the pelvic bone. The main axis of this bone projects beyond the ventral profile of the body (Fig. 3). However, it is not possible to provide conclusive information about the basipterygia of *Discosternon*, and the anatomical nature of this apparently disarticulated bone will remain elusive until better preserved and more complete specimens become available for study. In any case, even if its structure and composition remain unknown, the pelvic fin probably inserted just behind the pectoral-fin origin. This assumption is based on the presence of two pairs of enlarged ribs (1st and 2nd) just posterior to the pectoral girdle, which were probably closely associated with the pelvic girdle, as in other deep-bodied sternoptychids. Such a (presumed) advanced origin of the pelvic fins certainly contributes to the discoid ventral profile of the body, mostly related to the disappearance of the abdominal keel typical of deep-sea hatchetfishes, which usually extends from the ventral tip of the cleithrum (preabdominal spine *sensu* Schultz, 1961) to the anterior margin of the pelvic bone.

The whole body is covered by thin irregular scales. These are closely associated, elongate, and arranged in vertical to oblique rows.

5. Relationships and comparison

As indicated above, the specimen described herein has many features that strongly support its recognition as a new genus of the group of deep-bodied sternoptychids commonly called deep-sea hatchetfishes (see Figs 2, 6). Due to the diverse anatomical and morphological structure of stomiiforms in general, and of sternoptychids in particular, it is rather problematic to assess its phylogenetic placement at the familial level.
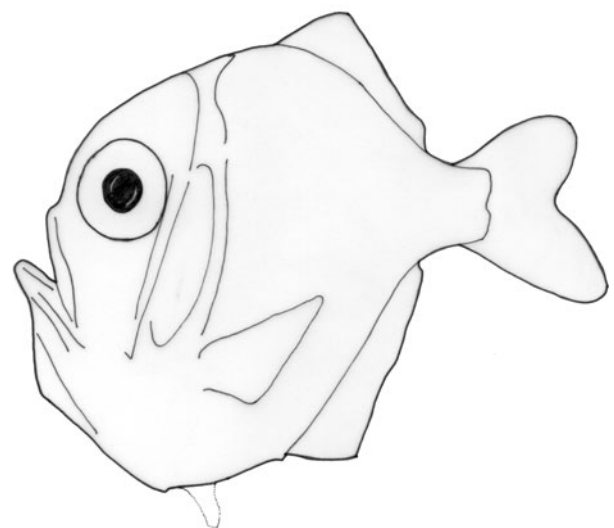

Figure 6. Reconstruction of *Discosternon federicae* gen. et sp. nov.

The first well-supported definition of the Stomii-formes was provided by Rosen (1973), who diagnosed the group mostly based on gill arch morphology and on myological features. The diagnosis of the order was revised and expanded by Fink & Weitzman (1982), who defined this highly heterogeneous group of fishes based on several characters of the photophores, teeth, muscles, ligaments, gill arches, hyoid bar and gas bladder (see also Lauder & Liem, 1983). Such a definition was broadly supported by the subsequent analysis of the group performed by Harold & Weitzman (1996). Of these features, only one, the greatly expanded posterior branchiostegal rays, can be detected on the fossil described herein, since the others correspond to soft anatomy or to very delicate osteological structures that only have a slight chance of being preserved during the fossilization processes.

The inclusion of the fossil within the Sternoptychidae is also rather problematic. The structure and composition of this family have been subjected to a number of different interpretations since the second half of the nineteenth century (see Günther, 1864; Gill, 1884; Goode & Bean, 1896). In particular, many authors have discussed the problems and difficulties in separating them from gonostomatids (e.g. Regan, 1923; Grey, 1959, 1960; Schultz, 1964; Weitzman, 1967). Baird (1971) restricted the Sternoptychidae to the deep-sea hatchetfish genera and concluded that these fishes are closely related to the maurolicid genera *Maurolicus* and *Valenciennellus*. A few years later, Weitzman (1974) presented a comprehensive study of the family Sternoptychidae and defined its sister-group relationships with the Gonostomatidae. According to the phylogenetic analysis of Weitzman (1974), Sternoptychidae includes ten genera (*Araiophos*, *Argyripnus*, *Argyropelecus*, *Danaphos*, *Maurolicus*, *Polyipnus*, *Sonoda*, *Sternoptyx*, *Thorophos*, *Valenciennellus*). These taxa share many synapomorphic features, such as the presence of Type Alpha photophores and their occurrence in glandular clusters, presence of three branchiostegal rays associated with the posterior ceratohyal, parietals separated by the supraoccipital, basihyal absent, and lack of endopterygoid teeth. In their recent phylogenetic study of the stomiiforms, Harold & Weitzman (1996) pointed out that the unique and unreversed characters that define the Sternoptychidae are the presence of parietal bones separated by the supraoccipital, and photophores arranged in clusters as a result of their development by budding. In addition, they listed many features that concur to complete the diagnosis of the family.

As discussed in the descriptive section, *Discosternon* has some of the diagnostic sternoptychid features listed by Harold & Weitzman (1996), including: absence of endopterygoid teeth, presence of fused hypurals $1 + 2$ and $3 + 4 + 5$, and parhypural (apparently) fused to the first preural ($+$ ural) centrum. Within the Sternoptychidae, the deep-sea hatchetfishes (subfamily Sternoptychinae) clearly form a morphologically cohesive clade. The monophyly of this group is well established and has been progressively corroborated by a number of studies. In restricting the Sternoptychidae to the deep-sea hatchetfish taxa, Baird (1971) indicated several features that support their separate status. In the comprehensive analysis of Weitzman (1974), the deep-sea hatchetfishes were considered to be the more morphologically derived sternoptychids, representing the sister group of *Argyripnus* and *Sonoda*. Such a phylogenetic hypothesis has been supported by successive investigations (Harold, 1993; Harold & Weitzman, 1996) that refined the diagnosis, and extended to 26 the number of unequivocal synapomorphies of the group.

The inclusion of *Discosternon* within the Sternoptychinae is justified by many features (see Harold & Weitzman, 1996), including: frontal crest prominent, parietal crest present, opercle elongate and subrectangular, subopercle roughly triangular, presence of preopercular spines, hyomandibula greatly elongate, a deep body 0.96 times the standard length, posttemporal elongate and strongly ossified, and neural spine of the second preural centrum broad and flat. The deep-sea hatchetfish clade includes three extant genera, *Argyropelecus*, *Polyipnus* and *Sternoptyx*, and at least two fossil genera, *Horbatshia* from the Oligocene of the Carpathians, and *Polypnoides* from the Eocene of Georgia (see Prokofiev, 2002, 2005). Therefore, *Discosternon* represents the sixth genus of this morphologically peculiar group of oceanic fishes.

Discosternon has many autapomorphic features that strongly support its recognition as a new genus of the Sternoptychinae clade. It is characterized by an unusual combination of features, among which the absence of the abdominal keel-like structure, absence of the anal-fin hiatus, presence of 13 caudal vertebrae, presence of 11 pairs of pleural ribs, presence of three supraneural bones, presence of at least 26 dorsal-fin rays, and presence of at least 24 anal-fin rays are unique within the deep-sea hatchetfish clade.

Strong morphological evidence indicates that *Polyipnus* is the sister group of *Argyropelecus* + *Sternoptyx*. The limits and composition of *Polyipnus* recently have been discussed by Harold (1994), who demonstrated that this genus is monophyletic. None of the uniquely derived characters that diagnosed *Polyipnus* (see Harold, 1994; Harold & Weitzman, 1996) are present in *Discosternon*. *Discosternon* shares several osteological features with the *Argyropelecus* + *Sternoptyx* clade (Harold & Weitzman, 1996), including: presence of strongly convex parasphenoid, (presumed) absence of otic bullae, vertical limb of the preopercle much longer than the horizontal one, and external surface of frontals and parietals extensively sculptured. Prokofiev (2002, 2005) proposed that the extinct genera *Horbatshia* and *Polypnoides* must be included in this clade and provided a new phylogenetic

interpretation of the group based on both Recent and fossil sternoptychids. Unfortunately, this phylogeny was based on a restricted number of taxa and a weak dataset often characterized by ambiguous or equivocal character interpretations. Furthermore, the osteological analysis of fossil material was not very detailed and several character complexes could not be determined due to inadequate preservation. Nevertheless, both *Horbatshia* and *Polypnoides* share similiarities with *Argyropelecus* and *Sternoptyx*, sharing a number of features (preopercular morphology, presence of the dorsal blade, ventral anterior portion of the cleithrum highly angular, shaft of the pubic process of the basipterygium tightly bound and parallel to distal end of pleural rib, external surface of frontal and parietal bones pitted) that justify their inclusion within this highly derived sternoptychid clade.

Compared with the derived clade of deep-sea hatchetfishes that includes *Argyropelecus*, *Horbatshia*, *Polypnoides* and *Sternoptyx*, *Discosternon* clearly differs in having a smooth external surface of the cleithrum, dorsal blade absent, extreme shortening of the caudal region of the body, very short caudal peduncle and slender neural and haemal spines. *Discosternon* differs from *Argyropelecus* by the presence of a basisphenoid and the posttemporal not fused with the supracleithrum. The Eocene *Polypnoides* differs from *Discosternon* in many morphological, morphometric and meristic features, among which the structure of the caudal skeleton, which includes at least four separate hypural bones, seems to be the most relevant. *Horbatshia* exhibits many morphological and osteological similarities to *Sternoptyx*, to which it appears to be closely related. *Discosternon* shares similarities with both *Horbatshia* and *Sternoptyx*, including a very deep body, presence of an elongate and distally expanded first anal-fin pterygiophore, shortening of the caudal region of the body, and origin of the anal fin opposite to the dorsal fin origin. It differs from both these genera by having a posttemporal spine and in the structure of the caudal skeleton. In *Horbatshia* the caudal skeleton is characterized by fused hypurals 1 + 2 and separated hypurals 3, 4, 5 and 6, whereas the caudal skeleton of *Sternoptyx* consists of a single co-ossified structure that resulted from the fusion of hypurals + uroneural + epural + parhypural + ural + preural centra. *Horbatshia* differs from both *Discosternon* and *Sternoptyx* by its fused posttemporal + supracleithrum. Finally, *Discosternon* shares with *Sternoptyx* a similar arrangement of the anterior portion of the anal-fin skeleton, but differs from it by the possession of a poorly developed ascending process of the premaxilla.

Discosternon appears to be closely related to the derived deep-sea hatchetfish genera *Horbatshia* and *Sternoptyx*, from which it can be easily distinguished because of its peculiar morphology (see above). However, even though the above morphological analysis of

Discosternon has revealed convincing evidence that it represents a new genus of the sternoptychid subfamily Sternoptychinae, additional more complete and better-preserved material is necessary to conclusively infer its precise phylogenetic position. Moreover, a comprehensive phylogenetic study of fossil and living deep-sea hatchetfishes cannot be performed until a more detailed morphological study of *Horbatshia* and *Polypnoides* is available. The unusual set of characters of *Discosternon* poses numerous questions, many of which can only be answered in future wider-based studies involving both fossil and extant deep-sea hatchetfishes.

6. Discussion

The comparative morphological analysis of the characters of *Discosternon* indicates that it could be considered as a member of a highly derived sternoptychid clade that includes the Oligocene *Horbatshia* and extant *Sternoptyx*. However, *Discosternon* is characterized by a very unusual combination of features, some of which appear to be unique, at least within the deep-sea hatchetfish clade. It is noteworthy that the morphological peculiarities of *Discosternon* are mostly related to a number of reductive apomorphic features. These may be interpreted as derived, compared to other deep-sea hatchetfishes, such as: loss of dorsal blade, loss of anal-fin hiatus, loss of abdominal keel-like structure, reduction of number of supraneurals, reduction of number of caudal vertebrae, and presence of slender, not spatulate and expanded, neural and haemal spines. The loss of abdominal keel-like structure and anal-fin hiatus probably resulted in the subsequent loss of the associated abdominal and anal photophore clusters. Moreover, the wide posterior extension of the dorsal fin and the reduced size of the caudal peduncle could indicate that the adipose fin was absent or, at least, poorly developed. Finally, the smooth external surface of the cleithrum represents a further reductive apomorphy of this fish. Many of the reductive characters are probably correlated with the hypothesized small size of this species. As documented above, even though the single known specimen of *Discosternon* does not exceed 15 mm standard length, its head and axial skeleton are solidly ossified and completely developed, thereby suggesting that it represents an adult individual. The very small size and the variety of reductive apomorphies concur to indicate that *Discosternon* can be regarded as a miniature fish. Weitzman & Vari (1988) arbitrarily used a standard length of 25–26 mm as the maximum size for miniature species, representing one-fourth to one-fifth the average teleost size (see Myers, 1958). However, they also pointed out that although the definition of miniaturization implies a very small body size, the primary criterion for distinguishing miniature fishes is related to the presence of reductive morphological features and to the general tendency to structural

simplification of many character complexes. Therefore, the criteria proposed by Weitzman & Vari (1988) support the conclusion that *Discosternon* is a miniature taxon.

The quantification of the consequences of miniaturization, however, is rather problematic. Extreme cases of miniaturized taxa may be dwarfed images of their larger relatives, or may resemble an early developmental stage of them (Britz & Kottelat, 2003). The co-occurrence of small size and morphologically reductive features, typical of miniature taxa, are often explained with the emergence of progenesis, an evolutionary process that produces paedomorphic phenotypes, evidently implying retardation of somatic development. In progenesis, a truncated development with an accelerated maturation produces dwarfed adults characterized by larval features (e.g. Gould, 1977). The clupeoid *Sundasalanx* (see Siebert, 1997) and the gobioid *Schindleria* (see Johnson & Brothers, 1993; Watson & Walker, 2004) provide good examples of developmentally truncated larval-like fishes, and evidence of less extreme progenetic expression has been documented in many teleost groups (see, e.g. Springer, 1983; Weitzman & Fink, 1983; Whitehead & Teugels, 1985; Springer, 1988; Weitzman & Vari, 1988; Schaefer, Weitzman & Britski, 1989; Winterbottom, 1990; Kottelat *et al*. 2006). The suite of reductive features of *Discosternon* may possibly be the result of developmental truncation (see Alberch, 1985). In sharp contrast to the reductions and simplifications found in the skeleton, *Discosternon* possesses a larger number of pleural ribs and dorsal- and anal-fin rays in comparison with its close relatives. Moreover, contrary to the situation in teleosts characterized by progenetic expression, *Discosternon* possesses a complete and well-ossified skull with deeply pitted bones, rather than an incomplete skull with very thin, perforated or cartilaginous elements and complete squamation, which usually is lost in progenetic fishes. A comprehensive comparative study of fossil and extant deep-sea hatchetfishes is still lacking but *Discosternon* seems to exhibit no evident morphological features of salient character states typical of earlier ontogenetic stages of its closest extant relatives (see Sanzo, 1931; Badcock & Baird, 1980; Ahlstrom, Richards & Weitzman, 1984). Therefore, it is possible to conclude that although miniaturization has certainly occurred in *Discosternon*, there is no convincing evidence of developmental truncation as reported in many teleost groups.

Miniaturization is an evolutionary phenomenon leading to the achievement of extremely small body size within a lineage. This phenomenon is widespread in animals, and relatively common in all vertebrate lineages, in which it is most frequently encountered in teleosts (Weitzman & Vari, 1988; Costa & Le Bail, 1999). In their discussion of the evolutionary consequences of this phenomenon, Hanken & Wake (1993) remarked that miniaturization often produces dramatic changes in physiology, ecology, life history and behaviour, representing a primary source of morphological novelty (see also Raff, 1996; West-Eberhard, 2003). The factors promoting an extreme decrease in size are often elusive, but the ecological consequences of this phenomenon are very diverse, sometimes associated with the evolution of novel bauplans and habitat exploitation. Miniature taxa are especially common in certain environments. As far as the teleost fishes are concerned, miniature taxa are predominantly associated with still or slow-flowing fresh waters (e.g. Weitzman & Vari, 1988) and deep-sea environments (Regan, 1925; Bertelsen, 1951; Pietsch, 1976, 2005). Other striking cases of miniature teleosts are those associated with certain specialized trophic niches, such as commensals and inquilines (see, e.g. Tyler, 1970).

Like other sternoptychids, *Discosternon* was probably a mesopelagic fish. Together with gigantism and bizarreness, miniaturization is a remarkable feature of the deep-sea biota (Lipps & Hickman, 1982). In general, structural reduction and simplification in fishes, as well as miniaturization, commonly occur in water-column foragers (Fryer, 1959; Davis & Birdsong, 1973). The water-column forager hypothesis is consistent with both the structural reduction and functional morphology of *Discosternon*. *Discosternon* had very large eyes, a rigid leaf-like and deep body plan, and a nearly vertically oriented mouth apparently devoid of teeth. As suggested above, the loss of the abdominal keel-like structure and the anal-fin hiatus observed in *Discosternon* probably resulted in the loss of abdominal and anal photophore series, thereby implying that it was characterized by a reduced total number of photophores. The mouth structure and (apparent) absence of teeth appear well suited for capturing small planktonic prey (Hopkins & Baird, 1973; Kinzer & Schulz, 1988). The body of *Discosternon* has a 'stepped' configuration, with the centres of the mouth and tail not in horizontal alignment and the tail centring well above the mouth (see Hopkins & Baird, 1985). Such a body configuration and the strongly reduced post-abdominal length are indicative of a highly decreased locomotory ability and minimally effective thrust for predator avoidance and rapid pursuit. All these features suggest a sedentary behaviour and possibly a greater reliance on ambush capture of prey (Hopkins & Baird, 1985). The reduced number of photophores could suggest that *Discosternon* was commonly exposed to low light intensities (see Hopkins & Baird, 1985) where it maximized its invisibility. Moreover, like extant deep-sea hatchetfishes, *Discosternon* was probably characterized by a silvery body, an adaptive strategy to appear invisible at all angles of view (see Warrant & Locket, 2004). In conclusion, a number of morphological characteristics suggest that *Discosternon* was a midwater mesopelagic and visually

oriented (large-eyed) predator adapted for capturing prey of small size.

7. Conclusions

A new genus and species of deep-sea hatchetfish (family Sternoptychidae), *Discosternon federicae* gen. et sp. nov., is described from the Serravallian (Middle Miocene) calciturbiditic deposits of Gessopalena. The description is based on a very small individual measuring less than 15 mm standard length. A detailed comparative analysis of the fossil has revealed that it seems to be closely related to the derived sternoptychid genera *Horbatshia* and *Sternoptyx*. *Discosternon* exhibits a distinctive combination of features, many of which are unique within the deep-sea hatchetfish clade, including absence of the abdominal keel-like structure, absence of the anal-fin hiatus, presence of 13 caudal vertebrae, presence of 11 pairs of pleural ribs, presence of three supraneural bones, presence of at least 26 dorsal-fin rays and presence of at least 24 anal-fin rays. Moreover, it also displays several unusual character states, such as cleithrum characterized by a smooth external surface, dorsal blade lost, caudal region of the body and caudal peduncle extremely shortened, and slender neural and haemal spines. Most of the apomorphic features that define *Discosternon* are clearly reductive. The extremely reduced body size and the possession of many reductive apomorphic features suggest that *Discosternon* can be considered a miniature fish. Both the anatomical structure and functional morphology indicate that *Discosternon* possibly was a midwater mesopelagic planktivore characterized by poor locomotory ability. Osteological evidence seems to indicate that *Discosternon* had a reduced set of photophores compared to other deep-sea hatchetfishes, suggesting that it was adapted to lower light intensities (see Hopkins & Baird, 1985).

Discosternon federicae gen. et sp. nov. represents the fourth deep-sea hatchetfish taxon recorded from the Mediterranean Neogene based on articulated skeletal remains. The Miocene *Argyropelecus logearti* was reported by Arambourg (1929) from the Messinian of Chelif Basin, Algeria, and was recently redescribed in more detail by Carnevale (2003), who also extended its stratigraphic distribution back to the Serravallian. The extant species *Argyropelecus hemigymnus* has been recorded from several Italian localities of Pliocene and Pleistocene age (Landini & Menesini, 1978, 1986; Landini & Sorbini, 1993; Sorbini & Landini, 2003). Finally, an indeterminate species of the genus *Argyropelecus* has been documented by Sorbini (1988) from the Pliocene deposits of the Metauro River, central Italy.

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