New species of sand lance (Teleostei, Ammodytidae) from the Miocene of Algeria

Giorgio CARNEVALE
Dipartimento di Scienze della Terra, Università di Pisa,
via S. Maria, 53, 56126 Pisa (Italia)
carnevale@dst.unipi.it

Carnevale G. 2004. — New species of sand lance (Teleostei, Ammodytidae) from the Miocene of Algeria. *Geodiversitas* 26 (2) : 297-307.

ABSTRACT
Gymnammodytes oranensis n. sp. (Teleostei, Perciformes, Ammodytidae) is described from upper Miocene marine deposits of Gambetta, near Oran, northwestern Algeria. This species is represented by four articulated but incomplete skeletons. *Gymnammodytes oranensis* n. sp. differs from Recent species of the genus in possessing a not specialized premaxilla. *Gymnammodytes oranensis* n. sp. is the earliest known occurrence of the genus *Gymnammodytes* as skeletal remains. The specimens here described provide unequivocal evidence of the presence of the Ammodytidae in the Miocene of the Mediterranean.

KEY WORDS
Teleostei,
Ammodytidae,
Gymnammodytes oranensis n. sp.,
Miocene,
Algeria,
new species.

RÉSUMÉ
Une nouvelle espèce de lançon (Teleostei, Ammodytidae) du Miocène d'Algérie.
Une nouvelle espèce de Teleostei, *Gymnammodytes oranensis* n. sp. (Perciformes, Ammodytidae), provenant des sédiments marins du Miocène supérieur de Gambetta, près d'Oran, nord-ouest de l'Algérie, est décrite. Au sein du genre *Gymnammodytes*, cette espèce est caractérisée par l'absence de spécialisation du prémaxillaire. *Gymnammodytes oranensis* n. sp. représente le premier témoignage fossile du genre *Gymnammodytes* sous forme de squelettes articulés. Ces spécimens attestent de la présence des Ammodytidae dès le Miocène en Méditerranée.

MOTS CLÉS
Teleostei,
Ammodytidae,
Gymnammodytes oranensis n. sp.,
Miocène,
Algérie,
nouvelle espèce.

INTRODUCTION

In 1927, Camille Arambourg, preceded by few preliminary papers (Arambourg 1921a, b), published an extensive monograph on upper Miocene fishes from Oran. This impressive work was based on hundreds of specimens recovered from several localities (Gambetta, Raz el Aïn, Saint Denis du Sig, Sidi-Brahim, etc.) of northwestern Algeria, in the Oran region. Eighty-one taxa were identified and described by Arambourg (1927), many of which represented new genera and species. Successively, Arambourg (1929) added a further species to the fauna.

Because of its amazing diversity, the Oran ichthyofauna represents a unique source of information about the paleoecological and biogeographical evolution of the Mediterranean during the Late Cenozoic. Since 1929, only few studies (e.g., Carnevale 2002, 2003) were based on Oran material. During a visit in January 2003 at the Muséum national d'Histoire naturelle in Paris (MNHN), part of the Arambourg collection of fossil fishes from Oran was re-examined, including not yet identified or described material, and some new taxa were discovered. Among the undescribed material, four specimens belonging to a new species of the ammodytid genus *Gymnammodytes* were found. The purpose of this paper is to describe this new species and discuss its possible affinities. The specimens described below are of particular interest because they represent the first skeletal remains belonging to the genus *Gymnammodytes* in the fossil record, and the first ammodytids known as skeletal remains from the Mediterranean Neogene.

Ammodytids (sand lances) are a group of elongate marine fishes with 23 living species. These fishes are abundant on the shallower sandy areas of the continental shelf where they alternate between active feeding, often in large schools, in the water mass by day, and inactivity, partially or totally buried, by night (Ruivo & Monteiro 1954; Winslade 1974; Meyer *et al.* 1979; Reay 1986). Comparative morphology and relationships of the sand lances were investigated, among others, by Duncker & Mohr (1939), Pietsch & Zabetian (1990), and Ida *et al.* (1994). Ida *et al.* (1994) grouped the seven genera of the family into two subfamilies, Bleekerinae (*Ammodytoides* Duncker & Mohr, 1939, *Bleekeria* Günther, 1862, *Lepidammodytes* Ida, Sirimontaporn & Monkolprasit, 1994, and *Protammodytes* Ida, Sirimontaporn & Monkolprasit, 1994), and Ammodytinae (*Ammodytes* Linnaeus, 1758, *Gymnammodytes* Duncker & Mohr, 1935, and *Hyperoplus* Günther, 1862). Intrageneric taxonomy of these fishes is often difficult because of the extreme morphometric and meristic variability of each species (Richards *et al.* 1963; Scott 1968; Nizinski *et al.* 1990).

Ammodytid otoliths are known since the Eocene (Nolf & Lapierre 1977), while skeletal remains dates back to the Oligocene (Paucă 1929, 1932, 1934; Weiler 1933; Jonet 1958; Danilts'henko 1960; Jerzmańska 1968). Recent species appeared in the Miocene of Europe (Huyghebaert & Nolf 1979; Lackneus & Nolf 1979), but they are commonly found also in the Plio-Pleistocene sediments of North America (Fitch 1968, 1970; Fitch & Lavenberg 1983).

MATERIALS AND METHODS

Four specimens of *Gymnammodytes oranensis* n. sp. were examined. These specimens are deposited at the MNHN. The fossils are preserved on white laminated diatomite and have undergone various degree of weathering with bones that appear dark brown-orange (?goethite stained).

All the specimens are articulated individuals incompletely preserved and partially flattened.

Specimens were examined using a stereomicroscope with attaching camera lucida drawing arm. Measurements were made with dial caliper, to the nearest 0.1 mm.

Osteological terminology mainly follows that of Pietsch & Zabetian (1990). Comparative information was derived from the literature, mainly Pietsch (1989), Pietsch & Zabetian (1990), and Ida *et al.* (1994). Vertebrae are divided into abdominal and caudal; the first caudal vertebra

defined as those having haemal spine. Intermuscular bones are identified as epineurals rather than epipleurals following Patterson & Johnson (1995).

The family Ammodytidae is here considered a member of the suborder Trachinoidei *sensu* Pietsch & Zabetian (1990), although recent studies (Johnson 1993; Mooi & Gill 1995; Mooi & Johnson 1997) provide some evidences about the incongruence in the definition of this suborder.

SYSTEMATICS

Subdivision TELEOSTEI *sensu*
Patterson & Rosen, 1977
Order PERCIFORMES *sensu*
Johnson & Patterson, 1993
Suborder TRACHINOIDEI *sensu*
Pietsch & Zabetian, 1990
Family AMMODYTIDAE Bonaparte, 1846
Genus *Gymnammodytes*
Duncker & Mohr, 1935

Gymnammodytes oranensis n. sp.
(Figs 1-8)

MATERIAL EXAMINED. — Holotype: MNHN ORA1203 d+g; ORA1203 is a fragmentary specimen with a well preserved skull; most of the axial skeleton is missing.

Paratypes: MNHN ORA1204, and MNHN ORA1207; ORA1204 single plate, head to right, is a relatively complete specimen lacking caudal skeleton and fin. MNHN ORA1207 is a relatively complete specimen. The anterior portion of the snout and the posteriormost section of the axial skeleton are missing; the bones of the head are much displaced and somewhat dissociated.

Referred specimen: MNHN ORA1205; ORA 1205 is fragmentary; the bones of the head are poorly preserved and widely flattened.

TYPE LOCALITY AND HORIZON. — The present study is based on the examination of four individuals from the Messinian (uppermost Miocene) Tripoli of Gambetta, near Oran, NW Algeria. This locality is placed at the margin of the Djebel Murdjadjo carbonate platform in the Chelif Basin. This area of the Chelif Basin is characterized by a large development of carbonate platforms with abundant reef complexes (Rouchy 1982; Cornée *et al*. 1994), which peripherally grades into marls and diatomite deposits (Perrodon 1957). A rich fossil biota was discovered in this area, including algae, foraminifers, sponges, corals, anellids, molluscs, brachiopods, bryozoans, crustaceans, echinoderms, and vertebrates (see e.g., Moissette 2000). According to Arambourg (1927), fossil fishes were collected in the quarry of the "Usine de Chaux et Ciments oranais". Fossiliferous layers consist of white, inframillimetrically-laminated diatomite (Tripoli). These layers lie over a rhythmic sequence of Messinian marls and limestone. The top of the sequence is represented by Pliocene sediments of the Arcole Plateau.

Many fishes were found associated with *Gymnammodytes oranensis* n. sp., including clupeids, sternoptychids, myctophids, syngnathids, and scombrids. In particular, the ichthyofauna was dominated by epipelagic (*Alosa* Linck, 1790, *Sarda* Cuvier, 1829, *Euthynnus* Lütken *in* Jordan & Gilbert, 1883) and midwater (*Diaphus* Eigenmann & Eigenmann, 1890, *Myctophum* Rafinesque, 1810, *Maurolicus* Cocco, 1838) taxa, but some neritic species were also found (*Diplodus oranensis* Woodward, 1901, *Boops roulei* Arambourg, 1927).

ETYMOLOGY. — *Oranensis*, after the region of Oran, northwestern Algeria, which contains the type locality.

DIAGNOSIS. — A species of *Gymnammodytes* that differs from other species of the genus by the absence of the premaxillary specializations (*sensu* Ida *et al*. 1994) (see Remarks below).

DESCRIPTION

A complete series of counts and measurements was not possible to take because of the incompleteness of the specimens. Few morphometric and meristic values are summarized in Table 1.

Although all the specimens are incomplete, they appear to be adults based on the strong ossification of most skeletal elements. The body is elongate and slender, as evidenced by MNHN ORA1204 (Fig. 2). The orbit is large (*c.* 16.4 mm in head length).

The neurocranium is low (Fig. 3). The anteriormost element of the neurocranium is the vomer. The anterior portion of this bone is not clearly observable on the specimens examined. The ventral margin of the vomer is slightly convex. Vomerine teeth are absent, as in other ammodytids (Kayser 1962; Pietsch & Zabetian 1990). The mesethmoid is elongate and narrow. Posteriorly, this bone is sutured to the large lateral ethmoids. The lateral ethmoids provide the anterior margin of the orbit. The nasals are tubular

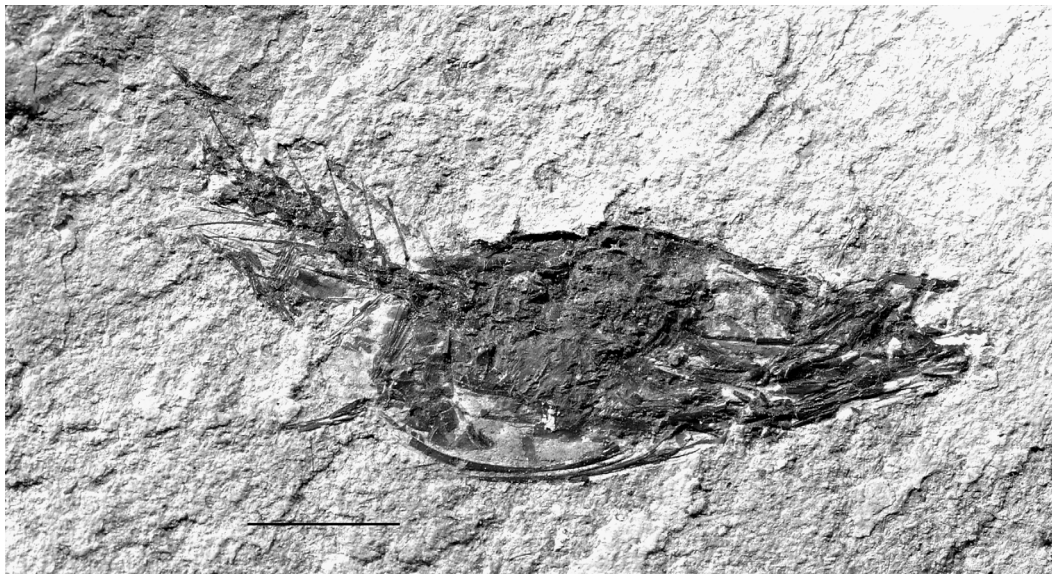

FIG. 1. — *Gymnammodytes oranensis* n. sp., holotype (MNHN ORA1203). Scale bar: 2 mm.

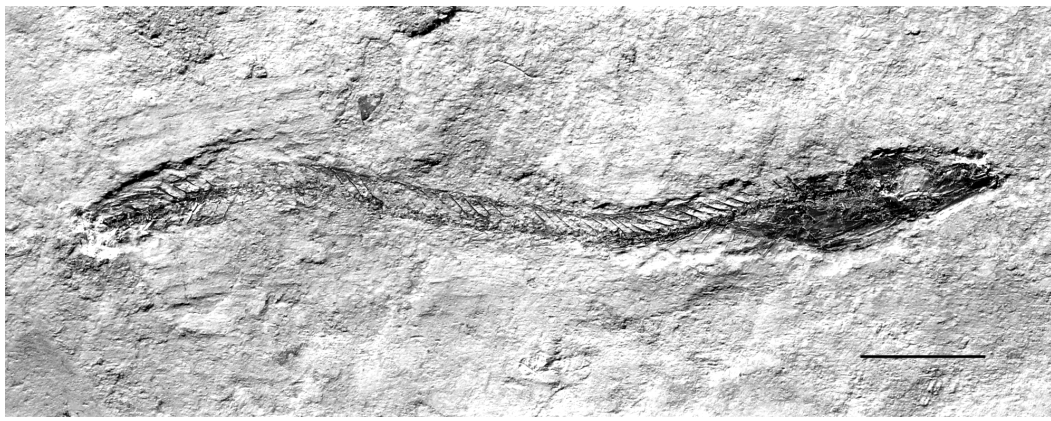

FIG. 2. — *Gymnammodytes oranensis* n. sp., paratype (MNHN ORA1204). Scale bar: 10 mm.

TABLE 1. — Counts and measurements for *Gymnammodytes oranensis* n. sp. All measurements are as percentage of head length.

	MNHN ORA1203 holotype	**MNHN ORA1204 paratype**	**MNHN ORA1207 paratype**	**MNHN ORA1205**
Head length (mm)	21.5	15.4	?	12.3
Head depth	40.0	38.3	?	39.0
Snout length	33.4	35.7	?	34.0
Orbit diameter	16.7	15.6	?	17.0
Abdominal vertebrae	?	43.0	41.0	?
Pectoral fin rays	14.0	13.0	?	14.0

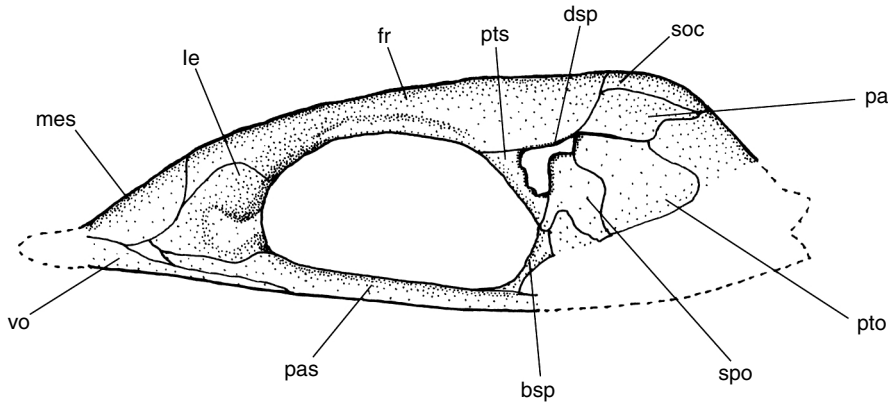

FIG. 3. — *Gymnammodytes oranensis* n. sp., reconstruction of the neurocranium, left side, lateral view. Abbreviations: **bsp**, basisphenoid; **dsp**, dermosphenotic; **fr**, frontal; **le**, lateral ethmoid; **mes**, mesethmoid; **pa**, parietal; **pas**, parasphenoid; **pto**, pterotic; **pts**, pterosphenoid; **soc**, supraoccipital; **spo**, sphenotic; **vo**, vomer.

bones that form a continuation of the supraorbital sensory canal of the frontals. The frontals are the largest bones of the skull roof. The dorsal surface of these bones is smooth. The sutural connection between the two contralateral frontals is smooth. The parietals are flat bones, not meeting in the midline, where they are separated from each other by the supraoccipital. The sphenotic and the pterotic are only partially preserved in the holotype. The other bones of the neurocranium (epiotic, prootic, exoccipital, intercalar, and basioccipital), with the exception of the parasphenoid, are too damaged to be described. The parasphenoid is an elongate bone, which is visible in lower third of the orbit.

The infraorbital series of *Gymnammodytes oranensis* n. sp. consists of four elements. The lacrimal is appreciatively triangular. The second and the third infraorbitals are elongate and tubular bones. The dermosphenotic appears to be sutured to the frontal and the sphenotic. The integration of the dermosphenotic with the neurocranium is a typical feature of ammodytids, trachinids, and uranoscopids (Pietsch 1989; Pietsch & Zabetian 1990). The reduction of the number of infraorbital bones into four is distinctive of the genera *Ammodytes*, *Gymnammodytes*, and *Hyperoplus* (Ida *et al.* 1994). This reduction represents a derived condition within the Ammodytidae. The genera *Bleekeria* and *Lepidammodytes* show

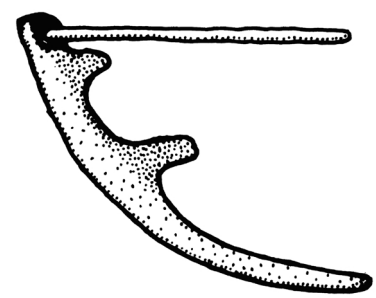

FIG. 4. — *Gymnammodytes oranensis* n. sp., reconstruction of the left premaxillary, dorsal view.

the generalized condition with the complete infraorbital series characterized by eight bones. The intermediate condition can be observed in the species of the genera *Protammodytes* and *Ammodytoides*, in which respectively, seven and six infraorbital bones are present (Ida *et al.* 1994). Fragments of weakly ossified sclerotic bones are visible in the holotype and MNHN ORA1204.

The mouth is oblique, forming an angle of about 20-25° to the horizontal axis of the body. Premaxillary and dentary teeth are absent. Among the Ammodytidae teeth are present only in the genus *Bleekeria* (Ida 1976; Reay 1986; Pietsch & Zabetian 1990). The premaxilla is highly protrusible (see Van Dobben [1935] and Pietsch [1984] for a discussion on modification of jaws structure of ammodytids) (Fig. 4). The

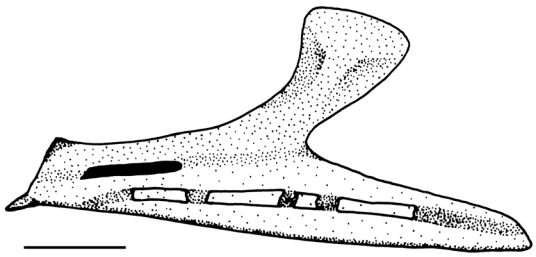

FIG. 5. — *Gymnammodytes oranensis* n. sp., left dentary, lateral view (MNHN ORA1203). Scale bar: 1 mm.

ascending process of the premaxilla seems to be autogenous. Each premaxilla bears a small articular process and a well developed postmaxillary process. A small concavity is present along the symphyseal margin of the premaxillae. The maxilla has a prominent and strongly ossified articular head. The lower jaw extends anteriorly far beyond the upper jaw. The dentary bears an anteriorly directed symphyseal process (Fig. 5). This projection is probably related to the sand diving behaviour of ammodytids (Randall *et al.* 1994), and is morphologically similar to that of *Gymnammodytes cicerelus* figured by Ida *et al.* (1994). The anterolateral perforation of dentary is thin. The articular is well exposed in the holotype. There are small fragments of what appear to be labial ossicles (Ida 1973).

The outline of the hyomandibula is partially obscured by other bones but the dorsal portion of it is visible in the holotype. As other ammodytids, *Gymnammodytes oranensis* n. sp. has an anteriorly directed spur laterally on the hyomandibula (Fig. 6). The presence of this structure is also reported for other trachinoid families, such as Cheimarrichthyidae, Pinguipedidae, Percophidae, Trichonotidae, Creedidae, Chiasmodontidae, and Leptoscopidae (Kayser 1962; Pietsch 1989; Pietsch & Zabetian 1990). The symplectic is an elongate subcylindrical bone. The quadrate lies almost horizontally within the suspensorium (Fig. 6). The metapterygoid is rather large. Of this bone, only the external outline can be recognized. The mesopterygoid is a well developed bone that forms a suborbital shelf. The ectopterygoid is a small triangular bone visible at the base of the palatine. The palatine is narrow and elongate.

The opercular series is well exposed in the holotype (Fig. 7). The vertical arm of the preopercle is longer than the horizontal one. The opercle is a thin bone with a horizontal strongly ossified ridge. The most striking element of the opercular series is the subopercle. This bone is very large, posteriorly expanded beyond extend of the opercle. Its posterior and ventral margins are ornamented with deep radially disposed grooves. The interopercle is clearly visible in the holotype.

The hyoid bar is well preserved in the holotype. There are seven branchiostegal rays: the anteriormost five articulate with the ceratohyal, while the sixth and the seventh articulate with the epihyal.

Some fragmented bones of the gill skeleton, probably the ceratobranchials, are visible in the holotype.

As discussed above, because of the incompleteness of the examined material, a precise vertebral count is unknown. However, the number of abdominal vertebrae ranges from 41 to 43. Following the values reported by Ida *et al.* (1994), a similar number of abdominal vertebrae is also observed in *Gymnammodytes semisquamatus*. The abdominal vertebrae are clearly more numerous than the caudal vertebrae. The anteriormost centrum is reduced relative to the others. Posterior centra are subrectangular, longer than high. Each centrum has developed dorsal prezigapophyses. With the exception for the three anterior, neural spines are weak. The neural and haemal spines of the posteriormost preserved caudal vertebrae are expanded and flattened (Fig. 8). Pleural ribs are well preserved on the specimens examined; some of them are laterally expanded, blade-like. Many epineural bones are visible attached to the axial skeleton.

Supraneural bones are absent. The dorsal fin originates between the ninth and the 10th vertebrae. The dorsal fin is spineless. The anal fin is not well preserved in any of the specimens examined.

The pectoral girdle consists of posttemporal, supracleithrum, cleithrum, scapula, and coracoid. Two postcleithra are also present (see Gosline

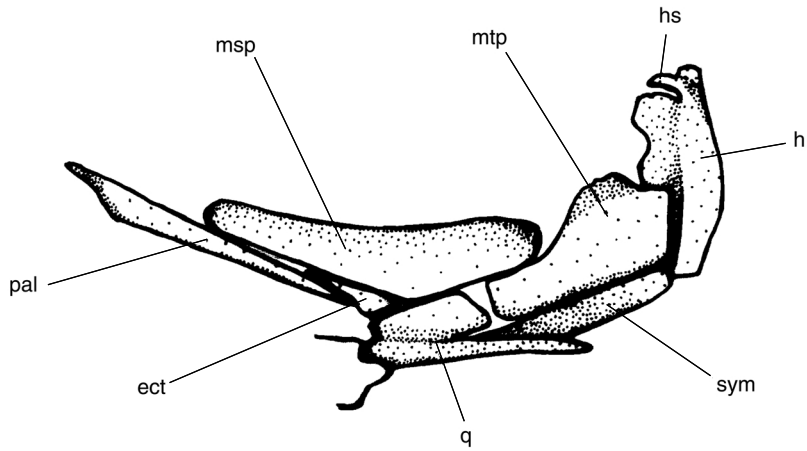

FIG. 6. — *Gymnammodytes oranensis* n. sp., reconstruction of the left suspensorium, lateral view. Abbreviations: **ect**, ectopterygoid; **h**, hyomandibula; **hs**, hyomandibular spur; **msp**, mesopterygoid; **mtp**, metapterygoid; **pal**, palatine; **q**, quadrate; **sym**, symplectic.

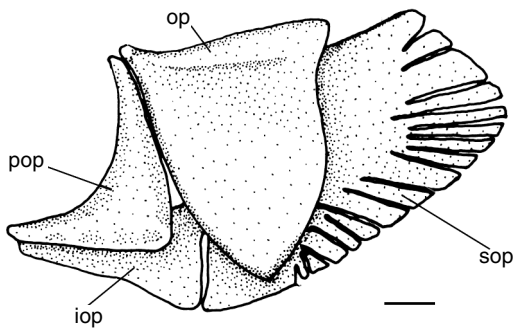

FIG. 7. — *Gymnammodytes oranensis* n. sp., left opercular series, lateral view (MNHN ORA1203). Abbreviations: **iop**, interopercle; **op**, opercle; **pop**, preopercle; **sop**, subopercle. Scale bar: 1 mm.

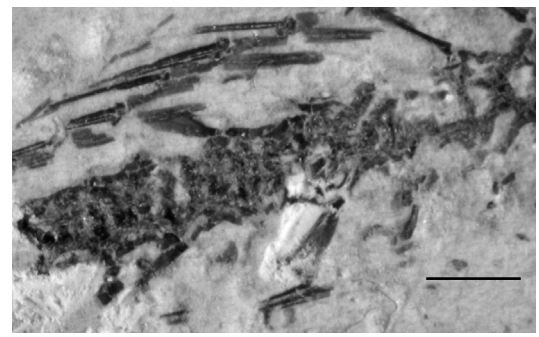

FIG. 8. — *Gymnammodytes oranensis* n. sp., caudal vertebrae, right side, lateral view (MNHN ORA1204). Scale bar: 1 mm.

1963). The posttemporal is connected with three fragmented extrascapular bones. There are four large and elongate pectoral radials. Similar pectoral-fin radials also occur in chiasmodontids, among the trachinoids (see Johnson & Cohen 1974). The pectoral fin radials support 13 to 14 fin rays.

The pelvic fin and girdle are absent, as in other species of the genus *Gymnammodytes*. The absence of the pelvic fin is also shared by the genera *Ammodytes*, *Bleekeria*, *Hyperoplus*, and by some species of the genus *Ammodytoides*.

A series of small tubular lateral line scales are visible on the body high in position. These scales are absent in the posteriormost part of the body. The lateral line canal appears to be branched with pores at the end of the branches. As *Gymnammodytes capensis* and *Gymnammodytes cicerelus*, *Gymnammodytes oranensis* n. sp. lacks patches of scales in the posterior part of the body.

REMARKS

Specimens here examined show many characters that allow the placement within the Ammodytidae,

including: physiognomy of the body; abdominal vertebrae more numerous than caudal vertebrae; orbit large; presence of an elongate mesethmoid; premaxillae highly protrusible; lower jaw extending anteriorly beyond upper jaw; dentary with an anteriorly directed symphyseal process; presence of a large anterolateral foramen of the dentary; presence of an anteriorly directed spur on the hyomandibula; palatine elongate (Gosline 1963); mesopterygoid large and forming a subocular shelf; infraorbitals tubular; dermosphenotic as integral part of the neurocranium; subopercle large and expanded ventrally; presence of seven branchiostegal rays; presence of expanded pleural ribs; elevate position of the lateral line; absence of spines in median fins.

Gymnammodytes oranensis n. sp. fits the definition of the genus as given by Ida *et al.* (1994) for the following characters: presence of labial ossicles; presence of four infraorbital bones; absence of predorsal bones; absence of premaxillary and dentary teeth; neural and haemal spines of the caudal vertebrae expanded; absence of pelvic fins; morphology of lateral line scales. The species of the genus *Gymnammodytes* are characterized by an extreme degeneration of scales. According to Ida *et al.* (1994), only tubular lateral line scales are retained in this genus, with the exception of small patches of small scales present on the posterior part of the body in *Gymnammodytes semisquamatus*. The other members of the subfamily Ammodytinae, *Ammodytes* and *Hyperoplus*, have small scales arranged in oblique rows, partially embedded by skin folds. *Gymnammodytes oranensis* n. sp. clearly differs from extant congenerics by the absence of the premaxillary specializations. As reported by Ida *et al.* (1994), the premaxillae of living species of the genus *Gymnammodytes* are characterized by a firm fusion of the two contralateral ascending processes and by a widening of their articulating surfaces. By contrast, the premaxillae of *Gymnammodytes oranensis* n. sp. greatly resemble those of other ammodytid genera, which are characterized by the presence of not fused pedicel-like ascending processes (see Fig. 4), suggesting a more basal position of this species within the genus *Gymnammodytes*.

DISCUSSION

Gymnammodytes oranensis n. sp. is the fifth species of the genus *Gymnammodytes* described up to date. The genus *Gymnammodytes* was created by Duncker & Mohr (1935), in which they included three species: *Gymnammodytes capensis* (Barnard, 1927), *Gymnammodytes cicerelus* (Rafinesque, 1810), and *Gymnammodytes semisquamatus* (Jourdain, 1879). In addition, an otolith-based species, *Gymnammodytes arnoldmuelleri* Gaemers, 1984, was described by Gaemers (1984) from the early Oligocene of Belgium. *Gymnammodytes cicerelus* occurs in the Mediterranean, Black Sea, and along the western coasts of Africa from Morocco to Senegal and Angola. *Gymnammodytes semisquamatus*, the northern species of the genus, occurs from Norway to the Atlantic coasts of Spain, with an additional record from the northwestern Mediterranean (Sabatés *et al.* 1990). *Gymnammodytes capensis* lives in coastal areas from Angola to Mozambique. Analysing the distribution of the living species, a geographic continuity from Norway to Senegal and from Angola to Mozambique can be observed. Ekman (1953) suggested that this type of bipolar distribution could be considered the result of the latitudinal compression of the tropical zone during cold periods. With respect to the other members of the subfamily Ammodytinae, *Ammodytes* and *Hyperoplus*, the species of the genus *Gymnammodytes* range from cold temperate, to warm temperate, to subtropical environments. The species of the genus *Ammodytes* show an amphiboreal distribution (see Berg 1934) in polar and cold temperate waters, whereas those of the genus *Hyperoplus* are restricted to the Atlantic coasts of North Europe (Reay 1986). The four genera of the subfamily Bleekerinae mainly occur in the Indo-Pacific region, with the exception of the genus *Protammodytes* that also occurs in the tropical western Atlantic (Robins & Böhlke 1970). Thus, the phylogenetic separation between the two subfamilies has a probable biogeographical meaning, and the climate probably played an important role in the adaptive radia-

tion of these two ammodytid groups. The divergence of the two subfamilies probably dates back to the Paleocene or to the early Eocene. Since the Eocene the Ammodytinae were established along the coasts of northern Europe (see Nolf & Lapierre 1977). This group probably radiated in temperate waters outside the Tethys. From a biogeographical point of view, the Eocene Tethys was well differentiated from the Atlantic region (see Harzhauser *et al*. 2002). The large development of the temperate climatic zone after the Eocene-Oligocene climatic crises (Prothero 1994) allowed the diversification of the Ammodytinae, and the dispersal into the Mediterranean. The Oligocene appearance of the Ammodytinae in the Mediterranean was pointed out by Arambourg (1943, 1965).

As discussed above, *Gymnammodytes oranensis* n. sp. is the first representative of the family Ammodytidae in the Mediterranean Neogene based on skeletal remains. Some fossil otoliths are known from the Miocene and Pliocene of Italy and France. A single specimen of *Ammodytes obliquus* (Weiler, 1942) was described by Robba (1970) from the Tortonian of Piedmont (northern Italy). The specimen was heavily eroded, and for this reason a successive study (Nolf & Steurbaut 1983) rejected its inclusion in the genus *Ammodytes*. Several specimens referred to genus *Ammodytes* were reported from Lower Pliocene localities of northern Italy (Anfossi & Mosna 1972, 1976) and southern France (Schwarzhans 1986). Thus, *Gymnammodytes oranensis* n. sp. represents the earliest known occurrence of the family in the Mediterranean Neogene.

Acknowledgements

I thank Walter Landini (Università di Pisa) and Alexandre F. Bannikov (Russian Academy of Sciences, Moscow) for their suggestions and critical review of the text. I am very much indebted to Daniel Goujet (MNHN) for permission to study material under his care and photographs. I am also grateful to Federica Giudice for the improvement of the English and her patience; this paper is dedicated to her. Special thanks go to Louis Taverne (Université libre de Bruxelles), and René Zaragüeta Bagils (MNHN) whose comments greatly improved the manuscript. This research was supported by the COLPARSYST grants of the MNHN.

REFERENCES

ANFOSSI G. & MOSNA S. 1972. — Otoliti del Pliocene inferiore di Lugagnano (Piacenza). *Atti dell'Istituto di Geologia dell'Università di Pavia* 20: 23-49.

ANFOSSI G. & MOSNA S. 1976. — Otoliti del Pliocene Inferiore della Liguria Occidentale. *Atti dell'Istituto di Geologia dell'Università di Pavia* 26: 15-29.

ARAMBOURG C. 1921a. — Sur la faune ichtyologique du Sahélien de la région d'Oran. *Comptes Rendus des Séances de l'Académie des Sciences, Paris* 172: 1243-1254.

ARAMBOURG C. 1921b. — Sur un Scopelidé fossile à organes lumineux : *Myctophum prolanternatum* n. sp. du Sahélien Oranais. *Bulletin de la Societé géologique de France* 20: 233-239.

ARAMBOURG C. 1927. — Les poissons fossiles d'Oran. *Matériaux pour la Carte géologique de l'Algérie* 1re sér., Paléontologie 6: 1-218.

ARAMBOURG C. 1929. — *Argyropelecus logearti*, un nouveau poisson bathypélagique du Sahélien. *Bulletin de la Société géologique de France* 29: 11-15.

ARAMBOURG C. 1943. — Les poissons de la « Faune Paléoméditerranéenne ». *Bulletin de la Société zoologique de France* 68: 79-85.

ARAMBOURG C. 1965. — Considérations nouvelles au sujet de la faune ichtyologique paléoméditerranéenne. *Senckenbergiana lethaea* 46: 13-17.

BERG L. S. 1934. — Über die amphiboreale Verbreitung der Meeresfauna in der nördlichen Hemisphäre. *Zoogeographica* 2: 393-409.

CARNEVALE G. 2002. — *Boops roulei* Arambourg in the Messinian of Central Italy, with comments on systematics, paleoecology and zoogeography. *Neues Jahrbuch für Geologie und Paläontologie, Monatschefte* 12: 725-736.

CARNEVALE G. 2003. — Redescription and phylogenetic relationships of *Argyropelecus logearti* (Teleostei: Stomiiformes: Sternoptychidae), with a brief review of fossil *Argyropelecus*. *Rivista Italiana di Paleontologia e Stratigrafia* 109: 63-76.

CORNÉE J.-J., SAINT MARTIN J.-P., CONESA G. & MULLER J. 1994. — Geometry, palaeoenvironment and relative sea-level (accomodation space) changes in the Messinian Murdjadjo carbonate platform (Oran, western Algeria): consequences. *Sedimentary Geology* 89: 143-158.

DANILTS'HENKO P. G. 1960. — Kostistye ryby maikopskich otloženij Kavkaza. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 78: 3-207 (in Russian).

DUNCKER G. & MOHR E. 1935. — Die nordeuropaischen Ammodytes-Arten der des Hamburger Zoologischen Museums. *Zoologischer Anzeiger* 110: 16-220.

DUNCKER G. & MOHR E. 1939. — Revision der Ammodytidae. *Mitteilung aus dem Zoologischen Museum in Berlin* 24: 8-31.

EKMAN S. 1953. — *Zoogeography of the Sea*. Sedgwick and Jackson, London, 417 p.

FITCH J. E. 1968. — Otoliths and other fish remains from the Timms Point Silt (Early Pleistocene) at San Pedro, California. *Los Angeles County Museum Contributions in Science* 146: 1-29.

FITCH J. E. 1970. — Fish remains, mostly otoliths and teeth, from the Palos Verdes Sand (Late Pleistocene) of California. *Los Angeles County Museum Contributions in Science* 199: 1-41.

FITCH J. E. & LAVENBERG R. J. 1983. — Teleost fish otoliths from Lee Creek Mine, Aurora, North Carolina (Yorktown Formation: Pliocene). *Smithsonian Contributions to Paleobiology* 53: 509-529.

GAEMERS P. A. M. 1984. — Fish otoliths from the Bassevelde Sand (Late Tongrian) of Ruisbroek, Belgium, and the stratigraphy of the Early Oligocene of Belgium. *Mededelingen van de Werkgroep voor Tertiare en Kwartaire Geologie* 21: 13-57.

GOSLINE W. A. 1963. — Notes on the osteology and systematic position of *Hypoptychus dybowskii* Steindachner and other elongate perciform fishes. *Pacific Science* 17: 90-101.

HARZHAUSER M., PILLER W. E. & STEININGER F. F. 2002. — Circum-Mediterranean Oligo-Miocene biogeographic evolution. The gastropods' point of view. *Palaeogeography Palaeoclimatology Palaeoecology* 183: 103-133.

HUYGHEBAERT B. & NOLF D. 1979. — Otolithes de téléostéens et biostratigraphie des sables de Zonderschot (Miocène Moyen de la Belgique). *Mededelingen van de Werkgroep voor Tertiare en Kwartaire Geologie* 16: 59-100.

IDA H. 1973. — Extra ossicles in the oral region on three species of *Bleekeria* (Ammodytidae). *Japanese Journal of Ichthyology* 20: 67-72.

IDA H. 1976. — Removal of the family Hypoptychidae from the suborder Ammodytoidei, order Perciformes, to the suborder Gasteroidei, order Syngnathiformes. *Japanese Journal of Ichthyology* 23: 33-42.

IDA H., SIRIMONTAPORN P. & MONKOLPRASIT S. 1994. — Comparative morphology of the fishes of the family Ammodytidae, with a description of two new genera and two new species. *Zoological Studies* 33: 251-277.

JERZMAŃSKA A. 1968. — Ichthyofaune des couches à ménilite (Flysch des Karpathes). *Acta Paleontologica Polonica* 13: 379-481.

JOHNSON G. D. 1993. — Percomorph phylogeny: progress and problems. *Bulletin of Marine Science* 52: 3-28.

JOHNSON R. K. & COHEN D. M. 1974. — Results of the research cruises of FRV "Walther Herwig" to South America. Revision of the Chiasmodontid fish genera *Dysalotus* and *Kali*, with descriptions of two new species. *Archiv für Fischereiwissenschaft* 25: 13-46.

JOHNSON G. D. & PATTERSON C. 1993. — Percomorph phylogeny: a survey of acanthomorph and a new proposal. *Bulletin of Marine Science* 52: 554-626.

JONET S. 1958. — *Contributions à l'étude des schistes disodyliques oligocènes de Roumanie. La faune ichtyologique de Homoraciu District de Prahova*. Sociedade Tipográfica, Lda, Lisbon, 112 p.

KAYSER H. 1962. — Vergleichende Untersuchung über Vorstreckmechanismen der Oberkiefer bei Fischen. Der Bau und die Funktion des Kiefer – und Kiemenapparates von Knochenfischen der Gattungen *Ammodytes* und *Callionymus*. *Zoologische Beiträge* 7: 321-445.

LACKNEUS J. & NOLF D. 1979. — Les otolithes des téléostéens redoniens de Bretagne (Néogène de l'Ouest de la France). *Bulletin de l'Institut de Géologie du Bassin d'Aquitaine* 25: 83-109.

MEYER T. L., COOPER R. A. & LANGTON R. W. 1979. — Relative abundance, behavior, and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. *Fishery Bulletin* 77: 243-253.

MOISSETTE P. 2000. — Changes in bryozoan assemblages and bathymetric variations. Examples from the Messinian of northwest Algeria. *Palaeogeography Palaeoclimatology Palaeoecology* 155: 305-326.

MOOI R. D. & GILL A. C. 1995. — Association of epaxial musculature with dorsal-fin pterygiophores in acanthomorph fishes, and its phylogenetic significance. *Bulletin of the Natural History Museum of London (Zoology)* 61: 121-137.

MOOI R. D. & JOHNSON G. D. 1997. — Dismantling the Trachinoidei: evidence of a scorpaenoid relationships for the Champsodontidae. *Ichthyological Research* 44: 143-176.

NIZINSKI M. S., COLLETTE B. B. & WASHINGTON B. B. 1990. — Separation of two species of sand lances, *Ammodytes americanus* and *A. dubius*, in the western North Atlantic. *Fishery Bulletin* 88: 241-255.

NOLF D. & LAPIERRE H. 1977. — Les otolithes de téléostéens des sables coquillers du Bois-Gouet (Eocène de Bretagne). *Biologisch Jaarboek Dodonaea* 44: 256-268.

NOLF D. & STEURBAUT E. 1983. — Révision des Otolithes de Téléostéens du Tortonien stratoty-

pique et de Montegibbio (Miocène supérieur d'Italie septentrionale). *Mededelingen van de Werkgroep voor Tertiare en Kwartaire Geologie* 20: 143-197.

PATTERSON C. & ROSEN D. E. 1977. — Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* 158: 81-171.

PATTERSON C. & JOHNSON G. D. 1995. — The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* 559: 1-83.

PAUCĂ M. 1929. — Vorläufige Mitteilung über eine fossile Fischfauna aus dem Oligozänschiefern von Suslşneşti (Muscel). *Bulletin scientifique de l'Académie roumaine* 12: 112-120.

PAUCĂ M. 1932. — Poissons fossiles de l'Oligocène de Bezdead. *Comptes rendus des Séances de l'Institut géologique de Roumanie* 20: 78-80.

PAUCĂ M. 1934. — Die fossile Fauna und Flora aus dem Oligozän von Suslşneşti-Muscel in Rümanien. Eine systematische und paläobiologische Studie. *Annales de l'Institut de Géologie roumaine* 16: 672-678.

PERRODON A. 1957. — Étude géologique des bassins néogènes sublittoraux de l'Algérie occidentale. *Bulletin du Service de la Carte géologique d'Algérie* 12: 1-328.

PIETSCH T. W. 1984. — Enlarged cartilages in the protrusible upper jaw of teleost fishes: phylogenetic and functional implications. *Copeia* 1984: 1011-1015.

PIETSCH T. W. 1989. — Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. *Copeia* 1989: 253-303.

PIETSCH T. W. & ZABETIAN C. P. 1990. — Osteology and interrelationships of the sand lances (Teleostei: Ammodytidae). *Copeia* 1990: 78-100.

PROTHERO D. R. 1994. — The Late Eocene-Oligocene extinction. *Annual Review of Earth and Planetary Sciences* 22: 145-165.

RANDALL J. E., IDA H. & EARLE J. L. 1994. — *Ammodytoides piley*, a new species of sand lance (Ammodytidae) from the Hawaiian Islands. *Pacific Science* 48: 80-89.

REAY P. J. 1986. — Ammodytidae, *in* WHITEHEAD P. J. P., BAUCHOT M.-L., HUREAU J.-C., NIELSEN J. & TORTONESE E. (eds), *Fishes of the North-Eastern Atlantic and the Mediterranean*. Unesco, Paris: 945-950.

RICHARDS S. W., PERLMUTTER A. & MCANEY D. C. 1963. — A taxonomic study of the genus *Ammodytes* from east coast of North America (Teleostei: Ammodytidae). *Copeia* 1963: 358-377.

ROBBA E. 1970. — Otoliti del Tortoniano-tipo (Piemonte). *Rivista Italiana di Paleontologia* 76: 89-172.

ROBINS C. R. & BÖHLKE J. E. 1970. — The first Atlantic species of the Ammodytid fish genus *Embolichthys*. *Notulae Naturae* 430: 1-11.

ROUCHY J.-M. 1982. — La genèse des évaporites messiniennes de Méditerranée. *Mémoires du Muséum national d'Histoire naturelle* sér. C, 50: 1-267.

RUIVO M. & MONTEIRO R. 1954. — Contributions à l'étude de la famille Ammodytidae. 1. *Gymnammodytes cicerellus* (Raf.) de la région de Banyuls. *Vie et Milieu* 5: 567-592.

SABATÉS A., DEMESTRE M. & SANCHEZ P. 1990. — Revision of the family Ammodytidae (Perciformes) in the Mediterranean with the first record of *Gymnammodytes semisquamatus*. *Journal of the Marine Biological Association of the United Kingdom* 70: 493-504.

SCHWARZHANS W. 1986. — Die Otolithen des Unter-Pliozän von Le Puget, S-Frankreich. *Senckenbergiana lethaea* 67: 219-273.

SCOTT J. S. 1968. — Morphometrics, distribution, growth, and maturity of offshore sand lance (*Ammodytes dubius*) on the Nova Scotia banks. *Journal of the Fishery Research Board of Canada* 25: 1775-1785.

VAN DOBBEN W. H. 1935. — Über den Kiefermechanismus der Knochenfische. *Archives néerlandaises de Zoologie* 2: 1-71.

WEILER W. 1933. — Zwei oligozäne Fischfaunen aus dem Königreich Ungarn. *Geologica Hungarica*, *Series Paleontologica* 11: 1-54.

WINSLADE P. 1974. — Behavioural studies on the lesser sand eel, *Ammodytes marinus* (Raitt). II. The effect of light intensity on activity. *Journal of Fish Biology* 6: 577-586.

Submitted on 24 March 2003;
accepted on 19 June 2003.