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A fossil dreamer of the genus *Oneirodes* (Lophiiformes: Ceratioidei) from the Miocene of Sakhalin Island, Russia

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Abstract

The almost complete skeleton of a fossil dreamer, identified as *Oneirodes* sp., is described from the middle–upper Miocene Kurasi Formation of southern Sakhalin Island, Russia. This is the second fossil skeletal record of oneirodid anglerfishes following those described from the Puente Formation of California, USA. The new specimen possesses morphological features very similar to those of the recent and fossil members of its genus, and cannot be separated from them at the species level. This finding confirms the idea of the high level of speciation of this fish family prior to the middle–late Miocene and demonstrates the wide geographic distribution of the genus *Oneirodes* already at this time.

1. Introduction

The fossil assemblage known from the middle–upper Miocene beds of the Kurasi Formation (southern Sakhalin Island, East Russia) provides one of the most species-rich complexes of the Neogene marine fishes in the North Pacific region. It comprises the richest association of fossil vertebrates in the Russian Far East, and includes remains of marine mammals, birds and fishes. Up to now, 34 teleost species belonging to 14 orders have been discovered here. Such species richness is comparable to two famous Miocene teleost assemblages: one from the Morozaki Group of Japan with 35 species (Ohe, 1993; Yabumoto & Uyeno, 1994) and another from several Miocene formations of California, USA, with *c.* 104 species (Jordan, 1919, 1925; Jordan & Gilbert, 1919, 1920; David, 1943; Fierstine *et al.* 2012). The Kurasi fish complex is unique in yielding predominately pelagic mid-water taxa, which together make up over 71 % of the remains discovered to date (Nazarkin, 2017, 2018). Fossilized deep-sea fishes are still very rare throughout the world, a situation that limits our understanding of the features of evolution of the separate fish groups and of the deep-sea fish communities in general. This circumstance gives the study of the fishes of the Kurasi Formation special significance.

Among the meso- and bathypelagic fishes of the Kurasi Formation, members of the families Serrivomeridae, Bathylagidae, Myctophidae, Stomiidae, Gonostomatidae and Platytroctidae are relatively common and numerous. At the same time, the remains of representatives of some other families found here (e.g. Nemichthyidae, Opisthoproctidae, Melamphaidae) are extremely rare or known from only a single specimen. The deep-sea anglerfishes (Lophiiformes: Ceratioidei) also belong to the last category. The single specimen of the anglerfish described represents the first fossil skeletal remains of oneirodid anglerfishes outside of the Puente Formation of southern California, where six species of two ceratioid families were previously discovered (Pietsch & Lavenberg, 1980; Carnevale *et al.* 2008; Carnevale & Pietsch, 2009).

The morphological study of this specimen reveals several osteological characters that support placement within the ceratioid family Oneirodidae and the genus *Oneirodes*. In this paper we describe this new specimen in detail and discuss its affinities and significance from the point of view of evolution and distribution of the family.

The Ceratioidei, with *c.* 168 living species, distributed throughout the world's oceans below a depth of 300 m, constitutes by far the most species-rich vertebrate taxon within the bathypelagic zone and below (Pietsch, 2009). Members of the group are part of a much larger assemblage of teleosts, the order Lophiiformes, characterized by having a modified dorsal-fin spine, equipped with a terminal bait, that functions to attract prey. However, they differ remarkably from their less-derived, bottom-living relatives in having an extreme sexual dimorphism and a unique mode of reproduction in which the males are dwarfed and attach themselves (either temporarily or permanently) to the bodies of relatively gigantic females (Pietsch, 2009). Among the 11 families and 35 genera of the Ceratioidei, the family Oneirodidae, commonly known as the "dreamers", is by far the largest, containing 16 genera and 67 currently recognized species. In turn, *Oneirodes*, with some 43 species, is the most speciose ceratioid genus. Nearly

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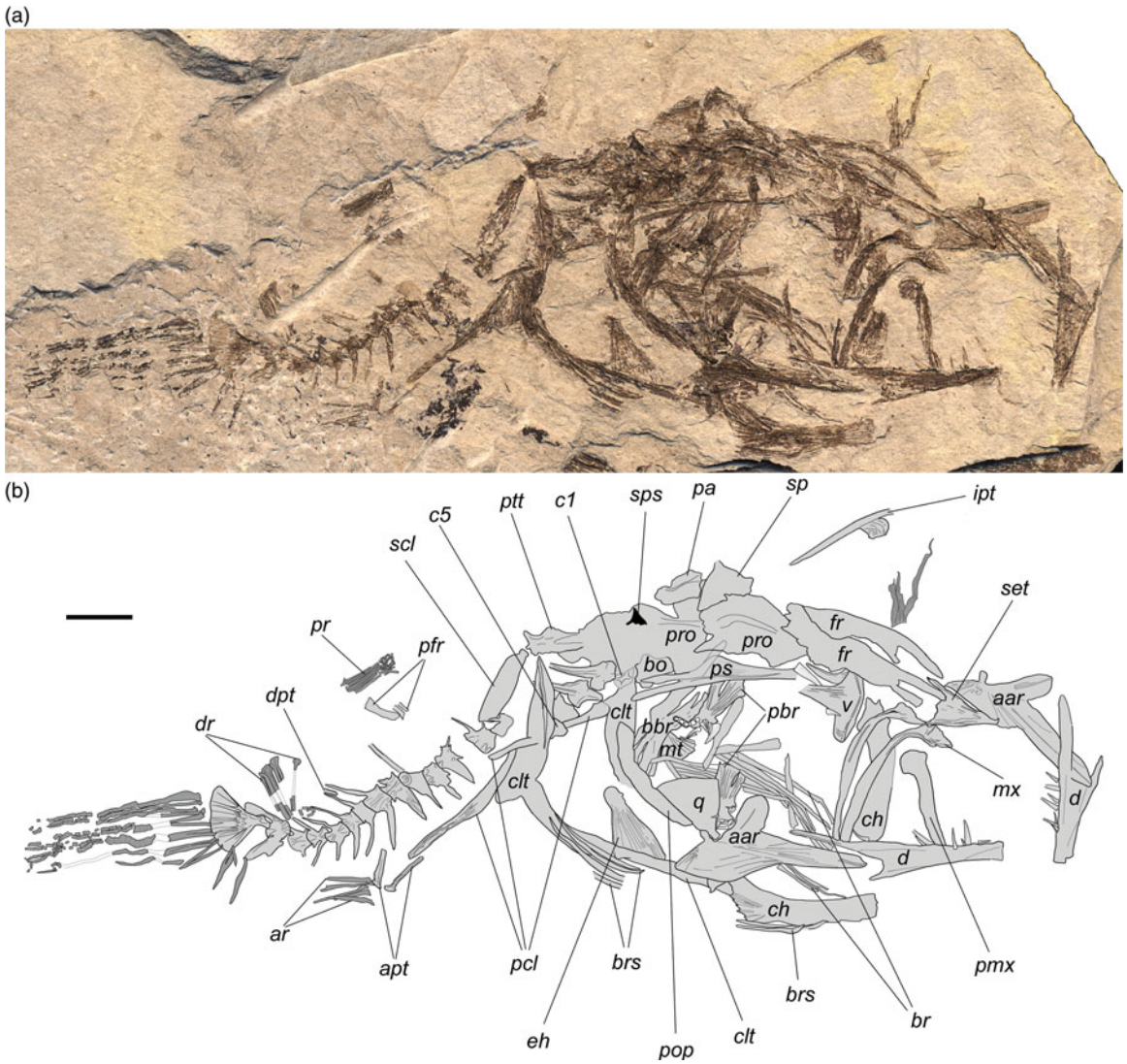

Fig. 1. (Colour online) *Oneirodes* sp. from the Miocene of Kurasi Formation, Sakhalin Island, Russia: (a) photograph and (b) interpretive drawing of the specimen ZIN 461p. Scale bar = 5 mm. Anatomical abbreviations: *aar* – anguloarticular; *apt* – anal fin pterygiophores; *ar* – anal fin rays; *bbr* – basibranchials; *bo* – basioccipital; *br* – branchials; *brs* – branchiostegals; *c* – vertebral centrum; *ch* – ceratohyal; *clt* – cleithrim; *d* – dentary; *dpt* – dorsal fin pterygiophores; *dr* – dorsal fin rays; *eh* – epihyal; *fr* – frontal; *ipt* – illicial pterygiophore; *mt* – metapterygoid; *mx* – maxilla; *pa* – parietal; *pbr* – pharyngobranchials; *pcl* – postcleithrum; *pfr* – pectoral fin radials; *pmx* – praemaxilla; *pop* – preopercle; *pr* – pectoral fin rays; *pro* – prootic; *ps* – parasphenoid; *ptt* – posttemporal; *q* – quadrate; *scl* – supracleithrum; *set* – supraethmoid; *sp* – sphenotic; *sps* – sphenotic spine; *v* – vomer.

cosmopolitan in distribution, and despite several detailed studies at higher taxonomic levels (e.g., Ceratioidei and Lophiiformes; Pietsch & Orr, 2007; Miya *et al.* 2010), the phylogenetic relationships among oneirodids remain largely unknown.

2. Materials and methods

The fossil is deposited in the palaeontological section of the ichthyological collection of the Zoological Institute RAS, Saint Petersburg, with the number ZIN 461p. The matrix was removed from the fossil by needles under a stereomicroscope. The outline drawing was made from digital photographs. Measurements were made with dial calipers to the nearest 0.1 mm. Standard length (SL) is used throughout.

3. Systematic palaeontology

Order Lophiiformes Garman, 1899
Suborder Ceratioidei Gill, 1909
Family Oneirodidae Gill, 1879
Genus *Oneirodes* Lütken, 1871
Oneirodes sp.
(Fig. 1a, b)

3a. Referred specimen

ZIN 461p; nearly complete, partly disarticulated skeleton, 61.0 mm SL.

3b. Locality and age

The specimen was collected in the most productive locality of the Kurasi Formation: an outcrop in the cliff of the Tartar Strait *c.* 5 km south of the village of Penzenskoye, Tomari District, Sakhalin Island. The fossil came from the light-grey laminated aleurolites of the Kurasi Formation which dates back to the middle–late Miocene (Serravallian–Tortonian) (Gladenkov *et al.* 2002). This formation is considered to consist of the deepest-water sediments among the Tertiary deposits of Sakhalin Island; they were

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accumulated at the period of highest sea transgression at a depth of more than 200 m (Gladenkov *et al.* 2002).

3c. Description

The specimen is partly disarticulated; most of the bony elements are slightly shifted from their original positions, and the exact shapes of many bones are uncertain. The body is high and short, its greatest depth is on the vertical through the lower jaw articulation, and about 2.5 times contained in SL. The head is massive; its length is *c.* 60 % of SL. The mouth appears to be large, at least 63 % of the head length. Both dorsal and anal fins are short-based and placed opposite each other, closer to the caudal fin base than to the head. The pectoral fin is placed directly behind the head in the middle of the body height. The pelvic fin is absent.

The neurocranium is moderately high and long. Several bones of the neurocranium are clearly recognizable. The frontal is an elongated paired element. Each frontal is deeply forked anteriorly where the medial and lateral arms are formed for the connection to the supraethmoid and lateral ethmoid, respectively. The triangular element lying anterior to the frontals is probably the supraethmoid. The vomer consists of a wide anterior head and a triangular posterior shaft. Two conical, slightly curved vomerine teeth are visible near this bone. The surface of the vomerine teeth is ornamented by thin longitudinal ridges. The parasphenoid is a flat, wide bone, apparently divided posteriorly; the wide ascending lateral wing of this bone is partly exposed on the right side. The shape of the basioccipital cannot be restored, but the half-moon shaped occipital condyle of this bone is recognizable posteriorly. Dorsally to the parasphenoid, there is a large paired bone with a longitudinal groove. Because of its position, large size and shape, this bone can be interpreted as the prootic. The sphenotic is a roughly conical bone with a prominent spine of moderate size. The other cranial bones can be only questionably recognized due to the quality of their preservation.

The premaxilla is long and thick, with a blunt and wide ascending process. The premaxillary teeth are not preserved. The maxilla is long and greatly curved anteriorly, where the short ascending and longer articular processes are visible; its posterior margin is not expanded. The dentary is deeply notched posteriorly with elongated posterodorsal and significantly shorter posteroventral branches. The symphysial part of this bone apparently lacks the prominent ventral knob. Each dentary is equipped with seven conical teeth of various sizes and of the same structure as the vomerine teeth. The height of the tallest teeth slightly exceeds the dentary height in the area of the tooth attachment. The anguloarticular is wide posteriorly and gradually tapering anteriorly, with a high and blunt coronoid process and a prominent triangular outgrowth posterior to the quadrate joint. The border with the retroarticular is indiscernible.

The quadrate is triangular and comparatively narrow. Of the other bones of the suspensorium, only the anteroventral corner of the metapterygoid sculptured with faint striations can be recognized.

An incomplete, slightly curved preoperculum is the sole preserved bone of the opercular series. Its ventral part is ankylosed to the posterior edge of the quadrate, as in recent species of this genus.

The elements of the gill arches are preserved below the parasphenoid. The complex of basibranchials, with the hypobranchials and ceratobranchials attached, overlaps the metapterygoid. The pharyngobranchials are recognized due to the teeth they carry. No fewer than 21 pharyngeal teeth are visible; their structure and size are similar to those of the jaw teeth. The ceratobranchials and epibranchials form several bunches of thin elongated bones, positioned around the anguloarticular–quadrate complex. The condition of preservation did not allow their separation into series. The ceratohyal is high, elongated, and expanded posteriorly. The epihyal is a triangle, with a striated surface. At least seven elongated branchiostegals are preserved, which came from both body sides (oneirodids have only six on each side).

There are a total of 19 massive vertebrae. The centra are rectangular and slightly longer than high. The neural spines on vertebral centra two and three are thicker than the those that follow. The eighth through the 18th centra possess long haemal spines. The condition of the specimen did not allow recognition of the border of the caudal section of the column. The neural and haemal spines of the second preural centrum are greatly expanded distally.

The caudal fin is truncate; its length is about a quarter of SL. There are nine caudal fin rays; the third through the fifth are branched distally. The complex terminal centrum is fused with a wide, fan-shaped hypural plate, unnotched posteriorly and ornamented with tiny radial ridges. The dorsal fin is apparently moved from its natural position. It consists of five or six rays, which are longer than the fin base. A fragment of the dorsal proximal pterygiophore has remained ahead of the neural spine of the seventh preural centrum. The illicial pterygiophore is long, rod-like, and partly preserved above the frontals. The anal fin contains four rays, their length at least twice exceeding the anal fin base length. Two anal proximal pterygiophores are preserved; the posterior one is inserted anterior to the seventh preural centrum.

The pectoral fin is crushed and greatly displaced. There are at least nine soft rays. Three pectoral radials are preserved; the lower one is definitely larger. The cleithrum is greatly curved and very long, its anterior end extending to beneath the lower jaw joint. The postcleithrum is also very long and robust. The supracleithrum is wide, but its dorsal end forms the narrow roundish arm for connection to the posttemporal. The latter is partly exposed behind the dorso-posterior region of the neurocranium. Any remains of the pelvic fin and girdle are absent in the specimen under consideration. Scales or dermal denticles are apparently absent.

4. Discussion

The globular body, the anteriorly bifurcated frontal bones, the absence of pelvic fins and scales, the presence of sphenotic spines, comparatively large jaw teeth, the number of vertebrae and vertical fin rays all clearly support the consideration of this fossil as a metamorphosed female of the ceratioid anglerfish of the genus *Oneirodes*. Unfortunately, the diagnostic tear-shaped subopercle is missing, but, in addition to the characters mentioned above, the presence of only four anal-fin rays excludes the possibility that this specimen is anything but *Oneirodes*. The latter genus contains 43 currently recognized extant species, all of which are nearly identical morphologically. With very few exceptions, they are distinguished solely on the basis of small differences in the structure of the esca (Pietsch, 1974), soft delicate tissues that do not fossilize. Thus, we cannot even begin to guess how the species might be related to each other phylogenetically, an unfortunate situation that extends to the Miocene form described herein.

The fossil, described above, like those from the Puente Formation, possesses in general the same osteological features as the recent representatives of the Oneirodidae (Pietsch, 1974). Thus, members of this family have not changed appreciably since at least the Tortonian, or have undergone very minor changes,

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which cannot be explored using the fossils. The occurrence of the fossil representative of the extant genus documented here along with the findings from the late Miocene of California clearly suggest that the oneirodids were already highly diverse during the middle–late Miocene. Two conclusions can be drawn from the above. First, the high diversity of Miocene oneirodids proves the differentiation and speciation time of this group took place much earlier than the middle Miocene (see also the discussion in Carnevale *et al.* 2008). Second, the high morphological similarity of fossil and recent members of the family indicates a low evolutionary rate of this group after the Miocene. Earlier the idea of phenotypic bradytely in some ceratioid lineages was expressed based on the data on Miocene ceratioids from California (Carnevale *et al.* 2008). It is appropriate to note here that among mesopelagic fishes from the Kurasi Formation there are a number of families with representatives that demonstrate slow evolutionary rates. For example, fossil species of *Benthalbella* (Aulopiformes) and of *Cyclothone* and *Chauliodus* (Stomiiformes) show great similarity to the recent congeners, while *Macropinna* sp. (Argentiniformes) and *Scopelogadus* sp. (Beryciformes) described from these deposits cannot be reliably distinguished from the recent species of their genera (Nazarkin, 2014, 2015, 2016; Nazarkin & Carnevale, 2018; Nazarkin & Kotlyar, 2020). Comparatively slow rates of evolution are probably inherent in most mesopelagic inhabitants due to the reduced susceptibility of their environment to the influence of climatic, physical and geographical perturbations.

The fossil *Oneirodes* spp. from Sakhalin and California indicate a wide geographic distribution of these fishes on both sides of the North Pacific in the Miocene. Considering the almost circumglobal distribution of the recent dreamers, a wider range of this genus in the Neogene cannot be excluded. In the modern Sea of Japan, dreamers and, more generally, their lophiiform relatives as a whole, are absent. However, three or four species of *Oneirodes* are known from the adjacent regions of the Sea of Okhotsk, and of the Pacific Ocean near Japan, at depths between 200 and 1340 m (Nakabo, 2002; Fedorov et al. 2003). Therefore, based on the bathymetric distribution of these recent congeners, the finding of the fossil dreamer described here testifies to the accumulation of the Kurasi Formation deposits in a depth of at least 200 m. This conclusion agrees well with the abundance of findings of other mesopelagic fishes in the beds of this formation.

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Declaration of Interest. None.

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