A remarkable new genus of Carangidae from the Upper Paleocene of Turkmenistan (Osteichthyes: Perciformes)

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Prokofiev, A.M. 2002. A remarkable new genus of Carangidae from the Upper Paleocene of Turkmenistan (Osteichthyes: Perciformes). *Zoosystematica Rossica*, **11**(1): 219-228.

A new genus and species of Carangidae, *Uylyaichthys eugeniae* gen. et sp. n., is described from the Upper Paleocene (middle part of the Danata Formation) of Turkmenistan. It belongs to the subfamily Trachinotinae s. str. and differs from all known members of the family in the combination of low vertebral count (21 or possibly 22), parasphenoid strongly curved mesially, and unique predorsal formula 0/0+0+0/1/. *Uylyaichthys* is considered to be a sister taxon for *Trachinotus* + *Paratrachinotus*, and Trachinotinae s. str. regarded as a sister group of Scomberoidinae. The genus *Lichia* is excluded from Trachinotinae s. str. and considered to be a sister taxon of Scomberoidinae + Trachinotinae s. str.

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Introduction

Daniltshenko (1968) described the Upper Paleocene ichthyofauna of Uylya-Kushlyuk locality (Turkmenistan) and established 20 species. Among them, Daniltshenko described two forms, which he placed into the family Carangidae (*Archaeus oblongus* and *Trachicaranx tersus*). Later, *Trachicaranx* was transferred to the family Apolectidae (Bannikov & Fedotov, 1984), while *Archaeus oblongus* now represents the earliest species undoubtedly belonging to Carangidae. Carangid fishes are a widely distributed and common group of Percoidei, which is relatively abundant in fossils since Middle Eocene.

Archaeus is suggested to be one of the most generalised genera of the Carangidae, but not ancestral to other representatives of the family (Bannikov, 1990). Therefore, the divergent evolution of the Carangidae started earlier than Upper Paleocene. In the extensive collection from Uylya-Kushlyuk locality, we found a remarkable undescribed carangid, which has some resemblance to the subfamily Trachinotinae and is important for elucidation of the trachinotine phylogeny. This specimen is described in the present paper as a new genus and species, *Uylyaichthys eugeniae*.

Material and methods

Specimens described herein were collected by Dr. E.K. Sytchevskaya from the middle part of Danata Formation in Uylya-Kushlyuk locality. Uylya-Kushlyuk locality is situated 2 km NE of Uylya-Kushlyuk village, SW Turkmenistan, on the western slope of the Kopetdagh Mountains (38°38′N, 55°48′E). Danata Formation is composed of the Upper Paleocene to the Middle Eocene (Grossheim & Korobkov, 1975; Solun, 1975); fish-bearing layer of mottled clays lies at the base of the middle part of the Danata Formation and has total thickness of 9 m. This layer is now dated as terminal Upper Paleocene (Upper Tanetien) (Muzylev, 1994).

The following fossil and recent (alcohol preserved, radiographed and partially dissected) species of Carangidae and other percoid families from the collections of Palaeontological Institute, Moscow (PIN), Zoological Institute, St. Petersburg (ZISP), and Zoological Museum of the Moscow University (ZMMU) are examined for comparison with the new genus and phylogenetic discussion (the number of specimens examined is given in parenthesis; † indicates fossil species): APOLECTIDAE: *Apolectus niger* (Bloch), ZISP, no. 38126, Tonkin Gulf (2); ZMMU, no. 11188, Tonkin Gulf (2); †*Trachicaranx tersus* Daniltshenko, PIN, no. 2179-98, Upper Paleocene, Turkmenistan (1; holotype). CARANGIDAE: *Alectis ciliaris* (Bloch), ZISP, no. 1222, Japan (1); *A. indicus* (Ruppell), ZISP, no. 41599, Hainan I. (1); †*Archaeus*

oblongus Daniltshenko, PIN, no. 2179-94 (1; holotype), no. 2179-95 (1; paratype), and 3 uncatalogued specimens, all from Upper Paleocene of Turkmenistan; *Caranx melampygus* Cuvier, ZMMU, no. 5337, Timor I., Indonesia (1); †*Caranx* sp., PIN, uncatalogued, Lower Oligocene, Gumista River, West Caucasus (2); *Carangoides armatus* (Forskål), ZISP, no. 3621, Philippines (1); *C. ferdau* (Forskål), ZISP, no. 2545, Red Sea (1); ZMMU, no. 12252, Indian Ocean (3); *Chloroscombrus chrysurus* (Linnaeus), ZISP, no. 37645, West Africa off Konakri (1), ZMMU, no. 12621, Gulf of Mexico, 28°20′N, 90°00′E (3); *C. orqueta* Jordan & Gilbert, ZMMU, no. 13640, Pacific Ocean off Peru (5); *Chorinemus lysan* (Forskål), ZISP, no. 39473, Hainan I. (2), ZMMU, no. 12380, Indian Ocean (1); *Decapterus lajang* Bleeker, ZISP, no. 37680, Western Australia (1); ZMMU, no. 12036, Indian Ocean (4); *D. maruadsi* (Temminck & Schlegel), ZISP, no. 42104, Tonkin Gulf (2); *Gnathanodon speciosus* (Forskål), ZISP, no. 41515, Hainan I. (1); *Hemicaranx sechurae* (Hildebrand), ZMMU, no. 13504, Pacific Ocean off Peru (3); *Lichia amia* (Linnaeus), ZISP, no. 6815, Canaries (1); ZMMU, no. 9920, Senegal (1), no. 5307, Naples (2); *Naucrates ductor* (Linnaeus), ZISP, no. 426, Madeira (1); ZMMU, no. 4913, Naples (1); *Oligoplites saurus* (Bloch & Schneider), ZMMU, no. 11583, Cuba (2); *Parona signata* (Jenyns), ZISP, no. 42649, Rio de la Plata off Montevideo (1); †*Scomberoides spinosus* (Smirnov), PIN, uncatalogued, Middle Miocene, Chernaya Rechka, Azerbaijan (2); *Scyris alexandrinus* (Geoffroy Saint-Hilaire), ZISP, no. 41019, West Africa off Dakar; †*Selar* cf. *quassus* Bannikov, PIN, nos. 4773/128, 130-131, Upper Oligocene – Lower Miocene, Apsheron Peninsula, Azerbaijan (3); *Selaroides leptolepis* (Cuvier), ZISP, no. 38147, Tonkin Gulf (1); ZMMU, no. 10857, Tonkin Gulf (1); *Selene vomer* (Linnaeus), ZISP, no. 1360, Rio de Janeiro (1); *S. setapinnis* (Mitchill), ZMMU, no. 10479, West Africa, off Dakar (1); *Seriola dumerili* (Risso), ZMMU, no. 4950, Naples (2); *S. quinqueradiata* Temminck & Schlegel, ZISP, no. 4757, Yokohama, Japan (3); *Trachinotus bailloni* Lacepede, ZISP, no. 624, Amboina (1); *T. blochii* (Lacepede), ZMMU, no. 155, Samoa (1); *T. ovatus* (Linnaeus), ZISP, no. 3258, Bahia (2), no. 11450, Naples (1); *T. paitensis* Cuvier, ZMMU, no. 18695, near Callao, Peru (1); *T. russelli* Cuvier & Valenciennes, ZISP, no. 23559, Kominato, Amami-Oshima, Japan (1); ZMMU, no. 153, Atlantic? (1); *Trachinotus* sp., ZMMU, no. 9872, off St. Louis (1); *Trachurus trachurus* (Linnaeus), ZISP, no. 2829, locality unknown (1); *T. japonicus* (Temminck & Schlegel), ZISP, no. 31376, Japan (1); *T. mediterraneus* (Steindachner), ZMMU, no. 20449, Kerch Strait (1). CORYPHAENIDAE: *Coryphaena hippurus* Linnaeus, ZISP, no. 42244, Sea of Japan (2). LACTARIIDAE: *Lactarius lactarius* (Bloch & Schneider), ZISP, no. 36050, Hainan I. (3). LEIOGNATHIDAE: *Gazza minuta* (Bloch), ZMMU, no. 5325, Manila (1); *Leiognathus bindus* (Valenciennes), ZISP, no. 41136, Singapore (2); *L. brevirostris*, ZMMU, no. 10950, Tonkin Gulf (2); *L. equula* (Forskål), ZISP, no. 37457, Hainan I. (1); ZMMU, no. 5383, Cebu, Moluccas (1); †*Leiognathoides*(?) *altapinna* (Weiler), PIN, uncatalogued, Lower Oligocene, Ljubizhna River, Ukrainian Carpathians (1); †*L. minutus* (Daniltshenko), PIN, nos. 4773/108-111, Upper Oligocene – Lower Miocene, Apsheron Peninsula, Azerbaijan (4). MENIDAE: *Mene maculata* (Bloch), ZISP, no. 37107, Tonkin Gulf (4); ZMMU, no. 12090, Indian Ocean (4); †*M. triangulum* Daniltshenko, PIN, uncatalogued, Upper Paleocene, Turkmenistan (4). NEMATISTIIDAE: *Nematistius pectoralis* Gill, ZISP, no. 2753, South California (1). POMACENTRIDAE: *Chromis chromis* (Linnaeus), ZISP, no. 4141, Mediterranean Sea (3). POMATOMIDAE: †*Lednevia oligocenica* (Smirnov), PIN, no. 4773, Upper Oligocene – Lower Miocene, Apsheron Peninsula, Azerbaijan (6); *Pomatomus saltator* (Linnaeus), ZISP, no. 4541, Black Sea off Karadag (31), PIN, uncatalogued, market specimens (4). RACHYCENTRIDAE: *Rachycentrum canadum* (Linnaeus), ZISP, no. 41069, Hainan I. (1). SCIAENIDAE: *Sciaena umbra* Linnaeus, ZISP, no. 32306, Black Sea off Sevastopol (1); *Umbrina cirrosa* (Linnaeus), ZISP, no. 1817, Black Sea (1). SPARIDAE: *Diplodus annularis* (Linnaeus), ZISP, no. 22670, Black Sea off Sevastopol (6); *D. sargus* (Linnaeus), ZISP, no. 912, Nizza (1); *Pagellus erythrinus* (Linnaeus), ZISP, no. 14283, Biscay Gulf (1); *Puntazzo puntazzo* (Gmelin), ZISP, no. 32298, Black Sea off Sudak (1); *Sarpa salpa* (Linnaeus), ZISP, no. 2740, Cadix (1). In order to evaluate phylogenetic relationships cladistic approach formulated by Hennig (1966) adopted.

Abbreviation: SL – standard length.

Order **PERCIFORMES**

Family **CARANGIDAE** Rafinesque, 1815

Genus **Uylyaichthys** gen. n.

Type species. *Uylyaichthys eugeniae* sp. n.

Diagnosis. Body deeply fusiform, with dorsal profile slightly more convex than ventral one; maximum body depth contained nearly 2.6 times in SL. Head moderately long, with high fronto-supraoccipital crest, anteriorly extended forward to orbit. Mouth oblique; angle between mouth rim and longitudinal body axis about 40°. Premaxillary with very small conical teeth in several rows. Supramaxillary present. Rear of maxillary extends only to anterior third of orbit. Parasphenoid slender in lateral view and strongly curved mesially. Posttemporal with equidimensional dorsal and ventral branches. Pelvic bones without postpelvic processes forming "apical fork". Vertebrae 21 or 22, of which 9 abdominal and 12 or 13 caudal. Inferior vertebral foramina absent. Ribs long and strong, extending nearly to ventral margin of body; all of them immediately attached to lateral sides of vertebral centra. Caudal-fin support with three epurals and separate fifth hypural. Dorsal fin with 7 spines and about 24 soft-rays; spines posteriorly increasing in length. Predorsal formula (Ahlstrom et al., 1976) 0/0+0+0/1/. Anterior projection of first supraneural touching apex of supraoccipital crest. Anal fin with 3 spines and about 16 soft-rays. No traces of anterior lobes in soft portions of dorsal and anal fins present. Ventro-anal distance much smaller than anal-fin base length. First anal-fin pterygiophore firmly articulated with first haemal spine. Three anal-fin pterygiophores placed in first interhaemal space. No detached or semidetached finlets present. Scales small, cycloid; lateral body scutes absent.

Included species. Type-species only.

Comparison. The new genus is distinguished from the all known Carangidae by the presence of 21 (or possibly 22) total vertebrae, of which 9 abdominal and 12 (or 13) caudal (vs. total vertebral count of 24-27 in other genera, of which 10 or 11 abdominal); predorsal formula 0/0+0+0/1/; and parasphenoid distinctly curved (vs. nearly straight in other genera). It differs from the Seriolinae and Archaeinae in the deep body with high fronto-supraoccipital crest; jaws with fine teeth; strongly oblique mouth; firm articulation between first haemal spine and first anal-fin pterygiophore; dorsal-fin spines increasing in length posteriorly; anterior projection of first supraneural touching supraoccipital crest; and from Seriolinae also in the ventro-anal distance much smaller than anal-fin base length (vs. opposite condition in Seriolinae). *Uylyaichthys* is clearly distinguished from the Caranginae by the dorsal-fin spines gradually increasing in length posteriorly, anterior projection of first supraneural touching supraoccipital crest and absence of lateral body scutes. The new genus differs from the Scomberoidinae in the strongly oblique mouth; reduced number of caudal vertebrae (12 or possibly 13 vs. 16-17); supraneurals 2 and 3 not divided by neural spine; and anterior projection of first supraneural touching supraoccipital crest. The most closely related subfamily Trachinotinae s. str. shares the following similarities within *Uylyaichthys*: deep body with high fronto-supraoccipital crest extending forward to the orbit; jaw dentition reduced; increased number of supraneurals, with concomitant reduction of dorsal spines in number; anterior projection of first supraneural touching supraoccipital crest; dorsal-fin spines increasing in length posteriorly; and most ribs (but all in *Uylyaichthys*) borne on lateral sides of vertebral centra. However, two formerly known genera of the Trachinotinae s. str. (*Trachinotus* and *Paratrachinotus*) differ from *Uylyaichthys* in vertebral formula 10 + 24; absence of supramaxillary; mouth rim nearly straight (vs. strongly oblique); nearly straight parasphenoid (vs. distinctly curved mesially); presence of lobes in anterior portions of soft dorsal and anal fins; supraneurals 2 and 3 divided by neural spine; and absence of separate fifth hypural. *Uylyaichthys* also differs from *Trachinotus* in the equally developed dorsal and ventral branches of posttemporal; and from *Paratrachinotus* in the shafts of three (vs. seven) anal-fin pterygiophores placed in first interhaemal space, and in much longer ribs. The genus *Lichia* was formerly included in the Trachinotinae (Smith-Vaniz, 1984; Gushiken, 1988; Bannikov, 1990; but see discussion below), but it lacks any trachinotine characters mentioned above, except dorsal-fin spines increasing in length posteriorly and most ribs borne on lateral sides of vertebral centra. In addition to the number of vertebrae and parasphenoid shape, *Lichia* is also distinct from *Uylyaichthys* in the rear of maxillary extended behind orbit (vs. to anterior third of orbit), and mouth rim nearly straight (vs. strongly oblique); presence of enlarged conical teeth in outer row on jaws; presence of lobes in anterior portions of soft dorsal and anal fins; presence of postpelvic processes and inferior vertebral foramina; and absence of separate fifth hypural.

Range. Upper Paleocene of Turkmenistan.

Etymology. The generic name is formed from Uylya-Kushlyuk locality, and *ichthys* (Greek, for fish).

Uylyaichthys eugeniae sp. n.
(Figs 1-3)

Holotype. PIN, no. 4782-80, complete skeleton, single plate, **Turkmenistan,** 2 km northeast of Uylya-Kushlyuk village, Upper Paleocene, middle part of Danata Formation, leg. E.K. Sytchevskaya.

Other material examined. PIN, no. 4782-37, fragment of middle part of body, single plate, same locality and age as for holotype.

Description. Body laterally compressed, deeply fusiform in shape, with slender caudal peduncle. Upper profile of body more convex than lower one. Maximum body depth (across vertical of anal-fin origin) contained 2.6 times in SL. Head moderately long, 3.3 times in SL; upper profile smoothly curved; mouth moderate. Horizontal diameter of round orbit contained 3.6 times in head length. Snout length contained 1.3 times in orbit diameter. Mouth cleft oblique; angle between mouth rim and longitudinal axis of body about 40°.

Skull. Limits of individual bones of neurocranium not clear, but frontals apparently wide, smooth, except closely spaced, nearly transversely arranged crests on posterior margin. Fronto-supraoccipital crest very high, anteriorly extended before the orbit, with straight posterior margin; its height contained 2.5 times in head length. Mesethmoideum nearly triangular, plate-like in lateral view. Lateral faces of sphenotic and pterotic bearing distinct crests. Parasphenoid relatively slender in lateral view, distinctly curved mesially, exposed in lower part of orbit. Basisphenoid well developed. Shaft of hyomandibular long, slender, oriented nearly vertically. Ventral end of hyomandibular shaft removed from posterior end of quadrate. Quadrate triangular, with slightly concave upper margin and well developed articular facet for lower jaw. Symplectic small, rod-like. Ectopterygoid narrow, semi-lunar; endo- and metapterygoids broad, plate-like, with not clearly seen limits.

Lower jaw articulation positioned under mid-

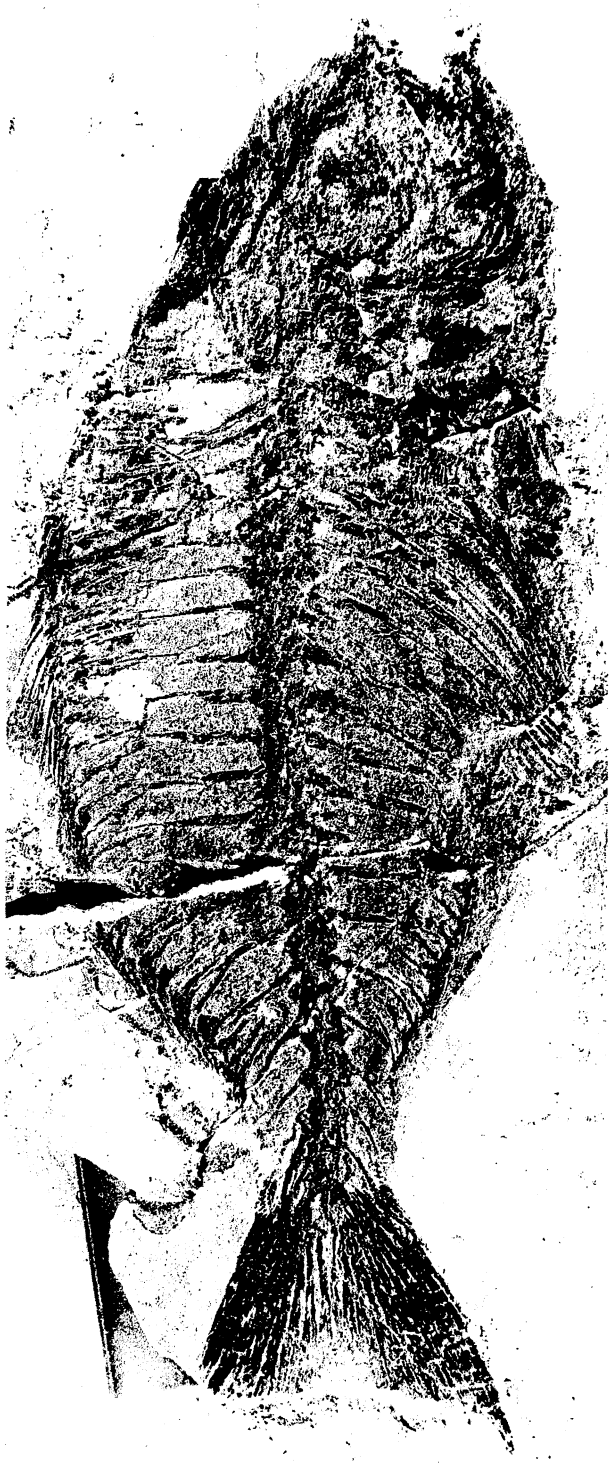


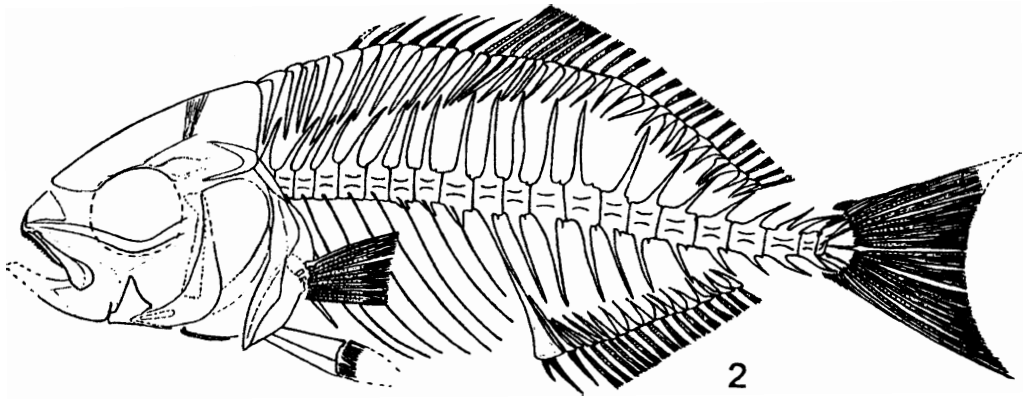
Fig. 1. *Uylyaichthys eugeniae* gen. et sp. n., holotype.

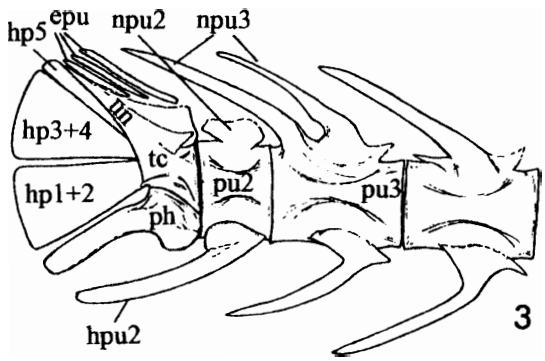
dle of orbit; lower jaw relatively slender, imperfectly preserved. Limits of dentary and articular as well as dentition on former bone not clear. Alveolar arm of premaxillary slender, long, bearing several rows of very small conical teeth. Ascending process of premaxillary moderate; smaller separate articular process present. Maxillary greatly expanded posteriorly, with small supramaxillary on posterodorsal border.

Bones of opercular series coarse, flat, imperfectly preserved. However, preopercle possibly relatively narrow, with smooth posterior border, and opercle approximately triangular. Hyoid and branchial arches not clear; number of branchiostegal rays unknown. Gill-rakers slender, moderately long.

Paired fins and their girdles. Forked posttemporal, with slender, equally sized dorsal and ventral branches situated just above level of vertebral column. Supracleithrum relatively narrow, flat. Cleithrum curved, broadened in middle part, incompletely preserved. Pectoral fin relatively short, not falciform, originating slightly closer to ventral body profile than to vertebral column. Pectoral-fin subequal in length to five abdominal vertebrae. There are about 18 pectoral-fin rays. Pelvic fins poorly preserved, possibly short. Pelvic bones elongate triangular, without postpelvic processes.

Vertebral column. There are 21 vertebrae, 12 of these caudal. However, third preural vertebra with two neural spines, which corresponds to distortion of development of vertebral column during ontogeny. Length of caudal part of vertebral column contained 2.3 times in SL. Vertebral centra nearly quadrate, with distinct longitudinal crests on their sides. Posterior three abdominal vertebrae with triangular





Figs 2, 3. *Uylyaichthys eugeniae* gen. et sp. n.: **2**, reconstruction of skeleton (based mostly on PIN, no. 4782-80 and partially on PIN, no. 4782-37); **3**, caudal-fin skeleton. Abbreviations: *epu*, epurals; *hp*, hypurals; *hpu2*, haemal spine of second preural vertebra; *npu2*, neural spine of second preural vertebra; *npu3*, neural spines of third preural vertebra; *ph*, parhypural; *pu2*, second preural vertebra; *pu3*, third preural vertebra; *tc*, terminal centrum (Pu1+U1); *un*, uroneural.

parapophyses gradually increasing in length posteriorly. Six anterior neural spines in abdominal region moderately inclined caudally and broadened basally; neural spines in middle part of vertebral column (to fourth caudal vertebra) slender and nearly vertical; remaining neural spines inclined caudally, much more on posterior caudal vertebrae. Inclination of haemal spines also distinctly increasing posteriorly. Inferior vertebral foramina absent. There are strong, long, posteroventrally inclined pleural ribs extending nearly to ventral profile of body. All pleural ribs borne on lateral sides of vertebral centra.

Caudal fin and skeleton. Caudal fin deeply emarginate, its length contained 1.2 times in head length. There are 17 principal and 10 + 8 procurrent caudal-fin rays. Caudal-fin rays slightly overlap hypurals, parhypural and epurals. Caudal-fin support includes three separate hypural plates, parhypural, stegural, and three epurals. Hypurals 1 to 4 fused into two plates. Small fifth hypural present. Neural spine of second preural vertebra very short.

Dorsal and anal fins. Dorsal and anal fins long-based, with continuous spinous and soft portions. Last dorsal-fin ray situated on same vertical with last anal-fin ray. Both dorsal- and anal-fin pterygiophores with broad anterior and rather small posterior plate-like extensions. Dorsal fin of 7 spines and 24 soft-rays. Dorsal-fin spines relatively short, increasing in length posteriorly. Last dorsal spine the longest, contained nearly 4.4 times in maximum body depth. Soft portion of dorsal fin originates above eight abdominal vertebra. Soft dorsal-fin rays relatively short, not forming separate lobe anteriorly and gradually decreasing in length posteriorly. Longest dorsal-fin ray slightly longer than longest dorsal spine; anterior dorsal ray 2.3 times as long as the last one. First dorsal-fin pterygiophore placed in

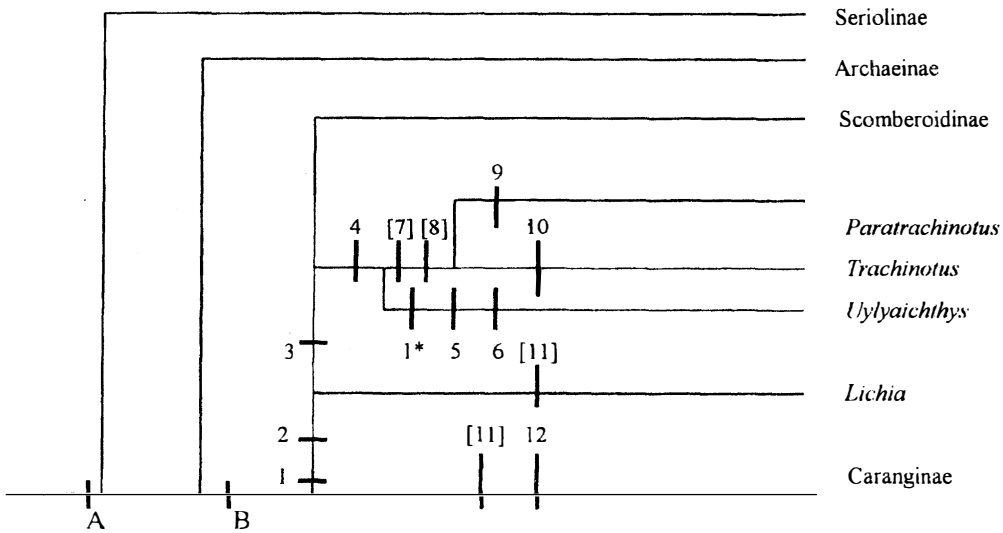


Fig. 4. Cladogram showing monophyletic groups of Carangidae based on characters discussed in the text. Characters in brackets are possibly convergent. Node A indicates presence of gap between last two anal spines; node B indicates presence of firm articulation between first anal-fin pterygiophore and first haemal spine.

interspace between third and fourth neural spines, with strong process projecting anteriorly.

There are four supraneurals, each with distinct, anteriorly directed processes; the process on first supraneural touching apex of supraoccipital crest. Predorsal formula (Ahlstrom et al., 1976) 0/0+0+0/1/.

Anal fin originates slightly posterior to soft dorsal-fin origin. Ventro-anal distance much smaller than anal-fin base length. Anterior part of anal fin poorly preserved in holotype but well observable in additional specimen (PIN no. 4782-37). There are 3 spines and about 16 soft anal-fin rays. There is distinct gap between last two anal-fin spines. First anal-fin pterygiophore broadened ventrally, firmly articulated with first haemal spine. Other anal pterygiophores similar in shape to corresponding dorsal-fin pterygiophores. Shafts of three anal-fin pterygiophores situated in first interhaemal space.

Scales. There are small, uniform, cycloid scales poorly preserved on whole body. Diameter of single scale from middle part of body much less than length of single vertebra. Lateral line not seen; lateral line scutes absent.

Measurements. SL of holotype 80 mm, but additional specimen (PIN, no. 4782-37) much larger (estimated SL about 250 mm). Measurements of holotype in percentage of SL: maximum body depth 38.75; minimum depth of caudal peduncle 10.0; caudal peduncle length 12.5; head length 30.0; length of caudal part of vertebral column 43.75; first predorsal distance 38.2; second predorsal distance 50.6; preanal distance 61.8; ventro-anal distance 22.5; length of dorsal-fin base 58.75; length of anal-fin base 26.25; caudal-fin length 23.75; in percentage of head length: snout length 18.75; horizontal orbital diameter 31.25; maxillary length 25.0; maxillary depth 10.4.

Range. Known only from the type locality.

Etymology. The species is named in honour of Eugenia K. Sytchevskaya (PIN), who collected the specimens.

Relationships of *Uylyaichthys*

According to the most recent revision (Bannikov, 1990), the family Carangidae is composed of six subfamilies: Seriolinae, Archaeinae, Vomeropsinae, Scomberoidinae, Trachinotinae, and Caranginae, among which the Vomeropsinae possess a number of peculiar characters (Bannikov, 1984, 1990) justifying family rank, possibly without direct relationships with the Carangidae. The monophyly of Carangidae is confirmed by the presence of a relatively wide gap between last two anal-fin spines (Smith-

Vaniz, 1984; Gushiken, 1988). However, this gap is also present in the recent apolectid *Apolectus niger*, while absent in the primitive Paleocene apolectid *Trachicaranx*. Possibly, this suggests parallel development of this character in the Carangidae and Apolectidae. Among Carangidae, the Seriolinae and Archaeinae seem to be the most primitive, judging from the feeble articulation between first anal-fin pterygiophore and first haemal spine. Most authors (Regan, 1909; Suzuki, 1962; Bannikov, 1986, 1990) noted the Seriolinae as ancestral for other carangids on the basis of the following primitive characters: body elongately fusiform, not strongly compressed laterally, with low supraoccipital crest; presence of supramaxillary; absence of body scutes; unpaired fins low, without lobes; anal-fin base shorter than ventro-anal distance; feeble articulation between first anal-fin pterygiophore and first haemal spine; unconsolidated caudal-fin support; etc. However, Smith-Vaniz (1984) and Gushiken (1988) reported the Seriolinae (mentioned as Naucratini) as a sister group of the Caranginae (mentioned as Carangini), and the Naucratini + Carangini as a sister group for other carangids on the basis of attachment of anterior portion of *m. adductor mandibularis* to suborbital shelf in the Naucratini + Carangini. This opinion has been criticised by Bannikov (1987, 1990). Archaeinae is distinguished from the Seriolinae in the ventro-anal distance less than anal-fin base length, which seems to be advanced and is characteristic for all Carangidae, except the Seriolinae (Bannikov, 1990). The presence of firm articulation between first anal-fin pterygiophore and first haemal spine occurring in *Uylyaichthys* exclude the latter from the Seriolinae or Archaeinae. Interrelationships of *Uylyaichthys* and other advanced carangids with firm articulation between first anal-fin pterygiophore and first haemal spine are given in the present discussion.

Characters listed below are used in the cladogram (Fig. 4) showing relationships of *Uylyaichthys*. Only characters available in the fossil material are included in the present study. Plesiomorphic characters are noted as (0), and apomorphic ones noted as (1).

1. *Pleural ribs are borne in pits on vertebral centra or in parapophyses, when parapophyses are developed (0) – most pleural ribs, except the last two pairs, are attached directly to lateral sides of vertebral centra (1) – all pleural ribs are attached to lateral sides of vertebral centra (1*).* In most Carangidae and other percoids studied, pleural ribs are borne in pits on vertebral centra or in parapophyses, when parapophyses are developed, while in Scomberoidinae, *Trachinotus* and *Lichia* most pleural ribs, except the last two pairs, are attached directly to lateral sides of vertebral centra, though parapophyses are developed from third or fourth vertebra, what seems to be apomorphic (Smith-Vaniz, 1984; Gushiken, 1988). In *Uylyaichthys*, all pleural ribs seem to be borne on lateral sides of vertebral centra and parapophyses are found from eighth vertebra. Attachment of most ribs to lateral sides of vertebral centra is derived for Scomberoidinae, Trachinotinae s. str. and *Lichia*, and such an attachment for all ribs is derived for *Uylyaichthys*. This character is unknown for *Paratrachinotus*.

2. *The longest dorsal fin spines situated in middle of fin (0) – dorsal-fin spines are increasing in length posteriorly (1).* In most Carangidae, the longest dorsal spines occur in the middle of first dorsal fin as in many generalised percoids, while in Scomberoidinae (except for *Scomberoides spinosus*), Trachinotinae s. str. and *Lichia* dorsal spines are gradually increasing in length posteriorly. This state seems to be derived. *Scomberoides spinosus* has peculiar, fan-shaped spinous dorsal fin (see also Bannikov, 1990, p. 23), which is possibly a secondary specialisation.

3. *The number of supraneurals is three (0) – number of supraneurals increased to 4-6 with concomitant decrease of dorsal-fin spines in number (1).* Most of the generalised percoids have three supraneurals (Johnson, 1983, 1984; Tominaga, 1986), as well as most of the Carangidae, including *Lichia*. Only *Seriola quinqueradiata* occassionally has four supraneurals (Bannikov, 1990). In the Scomberoidinae (except *Scomberoides*) and Trachinotinae s. str., the number of supraneurals increased to 4-6 with concomitant decrease of dorsal-fin spines in number, which seems to be derived. In *Scomberoides*, the number of supraneurals is usually three (Smith-Vaniz & Staiger, 1973; Bannikov, 1990; pers. observ.); this is probably a reversal or the atavistic condition.

4. *The anterior projection of the first supraneural does not touch the apex of supraoccipital crest (0) – the anterior projection of the first supraneural is touching the apex of supraoccipital crest (1).* In most carangids and other percoids examined, excluding *Trachinotus*, *Paratrachinotus*, and *Uylyaichthys*, the anterior projection of the first supraneural does not touch the apex of supraoccipital crest. The only other examined percoid fish with such a touch is the sparid *Pagellus erythrinus* (ZISP, no. 14283). Since there are no other synapomorphies between the Sparidae and Carangidae, this character is considered independently derived for the Trachinotinae s. str.

5. *The number of vertebrae is 24 or more (0) – the number of vertebrae is 21 or 22 (1).* In all the Carangidae, except *Uylyaichthys,* the total

number of vertebrae is 24-27. In *Uylyaichthys,* the total number of vertebrae is reduced to 21 or possibly 22. The number of abdominal vertebrae is also reduced in *Uylyaichthys* (9 vs. 10 or 11 in all other Carangidae). This state seems to be apomorphic. Among related families, similar number of vertebrae (9 + 13-14 = 22-23) also occurs in the Menidae, but this character undoubtedly was independently derived in *Uylyaichthys* and Menidae.

6. *Parasphenoid relatively straight in outline (0) – parasphenoid strongly curved mesially (1).* In all the Carangidae excluding *Uylyaichthys,* and in the other studied families of percoids, the parasphenoid is relatively straight in outline, while in *Uylyaichthys* it is strongly curved mesially. This is considered to be a unique derived character of *Uylyaichthys*.

7. *Supramaxillary present (0) – supramaxillary absent (1).* The presence of supramaxillary is a generalised character for percoids (Patterson, 1964; Johnson, 1984; Sasaki, 1989). The loss of supramaxillary has undoubtedly occurred along a number of percoid lineages. Among the Carangidae, supramaxillary is lacking in scomberoidine *Oligoplites* and trachinotine *Paratrachinotus* and *Trachinotus*. As other synapomorphies between *Oligoplites* and Trachinotinae s. str. are absent, we consider this character independently derived in *Oligoplites* and both *Trachinotus* + *Paratrachinotus*; this indicates relatively advanced status of these genera.

8. *Anterior soft dorsal and anal rays not extended and not forming distinct lobes (0) – anterior soft dorsal and anal rays more or less extended and forming anterior lobes (1).* In the most generalised Seriolinae and Archaeinae, the soft dorsal and anal fins lack anterior lobes. Elongation of anterior soft rays of unpaired fins seems to be advanced, but it is found in various phyletic lineages of the Carangidae. Among the Trachinotinae s. str., both *Trachinotus* and *Paratrachinotus* have falciform anterior lobes, while their closest relative *Uylyaichthys* lacks such lobes. This probably suggests that this character is independently derived in the *Paratrachinotus-Trachinotus* clade and other phyletic lineages of the Carangidae and it indicates relatively advanced status of the *Paratrachinotus-Trachinotus* clade.

9. *The number of anal-fin pterygiophores in the first interhaemal space is three (0) – the number of anal-fin pterygiophores in the first interhaemal space is seven (1).* In most carangids and other percoid families studied, the number of anal-fin pterygiophores in the first interhaemal space is three, while in *Paratrachinotus* it is described as seven (Blot, 1969). This is undoubtedly a unique apomorphic character of *Paratrachinotus*.

10. *Ventral branch of posttemporal not reduced (0) – ventral branch of posttemporal greatly reduced (1).* In all Carangidae and related carangoid families, except *Trachinotus,* dorsal and ventral branches of posttemporal are equidimensional. Among the Trachinotinae s. str., *Uylyaichthys* possesses this primitive state. Structure of posttemporal is not known for *Paratrachinotus* (Blot, 1969).

11. *Inferior vertebral foramina absent (0) – inferior vertebral foramina present (1).* Inferior vertebral foramina are present within Percoidei only in *Lichia* and most of the Caranginae (excluding *Selar, Trachurus*, and several *Carangoides*). This is an advanced character for *Lichia* and the Caranginae, but it is possibly independently derived, because *Lichia* has no other synapomorphies with the Caranginae and possesses derived states of characters 1 and 2, which suggests it to be sister group for Scomberoidinae + Trachinotinae s. str.

12. *Lateral body scutes absent (0) – lateral body scutes present (1).* Members of the subfamily Caranginae have variously developed body scutes covering the lateral line, while in other carangids, including *Uylyaichthys,* such scutes are absent. Presence of scutes is a unique character of the Caranginae, and it is considered to be a synapomorphy of this subfamily (see also Gushiken, 1988).

Two other advanced characters of the Trachinotinae s. str. not included presently in the cladogram: body is deeply fusiform or extremely deep (maximum depth/SL ratio 2.7 or less vs. 2.8 or more) and correspondingly very high frontosupraoccipital crest extended anterior to orbit. These characters possibly independently derived in many phyletic lineages (e.g., in *Parona* from Scomberoidinae, and in many Caranginae) and seem to have no important phyletic value but indicating relatively advanced status. Several derived characters occurring in *Trachinotus* (parasphenoid expanded into broad, flattened plate posteriorly; upper pharyngeals enlarged and covered with blunt, molariform teeth; and presence of lateral processes on ventral surface of the basioccipital) are not observable in two fossil trachinotine genera. Also *Uylyaichthys* has separate fifth hypural in caudal skeleton, which occurs in the Carangidae only in the Eocene *Seriola prisca* (Blot, 1969). This condition seems to be very primitive but possibly has no important phylogenetic significance; it suggests close position of *Uylyaichthys* with generalised ancestor of the subfamily Trachinotinae s. str.

The genus *Lichia* possesses supraneurals 2 and 3 enclosed in a single interneural space, while in the Scomberoidinae and Trachinotinae s. str. (excluding *Uylyaichthys*) supraneurals 2 and 3 are

divided by the neural spine. Tominaga (1986) listed primitive predorsal formula as 0/0/0+2/, which occurs among the Carangidae in the Seriolinae. Bannikov (1990, p. 15, fig. 2) figured predorsal formula 0/0+0/1+1/ for *Archaeus oblongus*, but personal examination of a paratype (PIN, no. 2179-95) of this species with undistorted predorsal bones has found it is clearly 0/0/0+1+1/. Both Scomberoidinae and Trachinotinae s. str. have derived state of character 3, although their predorsal formula is variable, but in all of them, except for *Uylyaichthys*, the second and third supraneurals are divided by neural spine as in the generalised Seriolinae and Archaeinae. Predorsal formula 0/0+0+0/1/ of *Uylyaichthys* is aberrant and independently derived. In *Lichia*, as in the Caranginae, supraneurals 2 and 3 are enclosed in a single interneural space, and its predorsal formula is 0/0+0/2/, 0/0+0/2+1/, or 0/0+0/1+1/, which suggests relatively advanced status but possibly has no important phyletic significance, because this character is independently derived in various phyletic lines of Percoidei. *Lichia* possesses inferior vertebral foramina as in most of the Caranginae, but it is possibly a result of parallelism, since other synapomorphies between the Caranginae and *Lichia* are not known. The only known apomorphic state of *Lichia* is the very irregular, sinuous lateral line (Smith-Vaniz & Staiger, 1973), which is not observable in fossil trachinotine genera. The genus *Lichia* was formerly included in the Trachinotinae (Smith-Vaniz, 1984; Gushiken, 1988; Bannikov, 1990), however, on the basis of the present study it seems to be doubtful. As noted previously (Smith-Vaniz & Staiger, 1973), *Lichia* probably represents a separate subfamily. Smith-Vaniz & Staiger (1973) noted that the Scomberoidinae, *Trachinotus* and *Lichia* are distinguishable as a group from all other genera of the Carangidae at least on the basis of superficial similarities, which have little or no phylogenetic significance (Smith-Vaniz & Staiger, 1973, p. 244), but the monophyletic origin of the Scomberoidinae, *Trachinotus* and *Lichia* was proved later (Smith-Vaniz, 1984; Gushiken, 1988). We found no synapomorphies of the Trachinotinae s. str. and *Lichia*, but the Scomberoidinae, Trachinotinae s. str. and *Lichia* represent a monophyletic group of the Carangidae.

The Scomberoidinae possess a number of unique specialisations (Smith-Vaniz & Staiger, 1973; Smith-Vaniz, 1984; Mok, 1986; Gushiken, 1988; Bannikov, 1990), which undoubtedly demonstrates their monophyletic origin. Most authors (Suzuki, 1962; Smith-Vaniz & Staiger, 1973; Smith-Vaniz, 1984; Gushiken, 1988; Bannikov, 1990) usually reported the Scomberoidinae and Trachinotinae as closely related groups or proved their monophyletic origin. We place both subfamilies in a monophyletic lineage, to which *Lichia* is a sister group, on the basis of the derived state of character 3 occurring in the Scomberoidinae and Trachinotinae s. str. Both Scomberoidinae + Trachinotinae s. str. and *Lichia* have derived state of characters 1 and 2, which shows its monophyletic origin. Trachinotinae s. str. are a sister group of Scomberoidinae, and the trachinotine *Uylyaichthys* is a sister group of *Trachinotus-Paratrachinotus* clade.

Acknowledgments

I am grateful to Dr. Eugenia K. Sytchevskaya (PIN) for collection and loaning of material; to Drs. A.V. Balushkin, V.V. Fedorov, G.A. Volkova, O.S. Voskoboinikova, A.M. Naseka and M.V. Nazarkin (ZISP), for providing preserved material and radiographs for comparison, discussion, and kind help during my visits in ZISP; to Drs. Yu.I. Sazonov and I.A. Verigina (ZMMU), and A.F. Bannikov (PIN) for providing material for comparison and some assistance.

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Received 2 August 2001