Two new taxa of Eocene rabbitfishes (Perciformes, Siganidae) from the North Caucasus (Russia), with redescription of *Acanthopygaeus agassizi* (Eastman) from Monte Bolca (Italy) and a phylogenetic analysis of the family

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Abstract

Two new genera and species of siganid rabbitfishes (Caucasiganus eocaenicus *and* Lagosiganus parinterneuralis) *are described from the uppermost Middle Eocene locality of Gorny Luch in the North Caucasus, S.W. Russia, and the holotype of* Acanthopygaeus agassizi *(Eastman, 1904) from the Eocene of Monte Bolca, Italy, is redescribed and referred to the Siganidae. A phylogenetic analysis is presented of the relationships of the eight genera now known of fossil siganids and of the single extant genus.*
Key Words: *Eocene, Siganidae, new genera and species, phylogeny, North Caucasus, Monte Bolca.*

Riassunto

Due nuovi taxa eocenici della famiglia Siganidae (Perciformes) del Caucaso settentrionale (Russia), con nuova descrizione di *Acanthopygaeus agassizi* (Eastman) dell'Eocene di Bolca (Italia) e analisi filogenetica della famiglia
Caucasiganus eocaenicus e *Lagosiganus parinterneuralis*, due nuovi generi e specie della famiglia Siganidae provenienti dalla località eocenica di Gorny Luch nel Caucaso settentrionale (Russia), vengono descritti per la prima volta; mentre l'olotipo di *Acanthopygaeus agassizi* (Eastman, 1904) dell'Eocene di Bolca (Italia) è ridescritto ed attribuito alla famiglia Siganidae. Viene presentata un'analisi filogenetica delle relazioni fra gli otto generi fossili di Siganidae noti e l'unico genere oggi vivente di questa famiglia.
Parole Chiave: Eocene, Siganidae, nuovi generi e specie, filogenesi, Caucaso settentrionale, Monte Bolca.

Introduction

Eastman (1904) described *Pygaeus agassizii* as a new species of putative "chaetodontid" fish based on a single specimen in the Museum of Comparative Zoology, Harvard College, from the famous Eocene marine fish locality at Monte Bolca in northern Italy. The composite nature of the genus *Pygaeus* Agassiz, 1838 (Agassiz, 1833-1844) became evident when Leriche (1906) defined three "types" (subgenera according to Article 10.4 of the "International Code of Zoological Nomenclature", 1999) of *Pygaeus*. One of them, *Acanthopygaeus*, included *Pygaeus coleanus* Agassiz, 1838 and *P. agassizi* Eastman, 1904. Since *P. coleanus* was subsequently attributed to the new genus *Blotichthys* of generalized percoids (Sorbini, 1979), Bannikov (2004) proposed *Pygaeus agassizi* as the type species of the monotypic genus *Acanthopygaeus*. He also noted that *A. agassizi* is not related to the Chaetodontidae and that most probably this species is related to the siganid acanthuroids (Bannikov, 2004: 56). It is pertinent to note here that the original species name *agassizii* Eastman was properly emended by Leriche (1906) to *agassizi*.

In their revision and phylogenetic analysis of the fossil and Recent rabbitfishes, Tyler and Bannikov (1997) regarded the genus *Ruffoichthys* Sorbini, 1983 (with two species, *R. spinosus* Sorbini, 1983 and *R. bannikovi* Tyler and Sorbini, 1991) as the only siganid taxa from the Monte Bolca fish fauna. Subsequently, Bannikov and Tyler (2002) described the new genus and species *Aspesiganus margaritae* from the Bolca locality of Monte Postale as one of the higher siganid clades (in contrast to *Ruffoichthys* being the most basal siganid clade and subfamilially distinct from the other genera).

The original description of *Acanthopygaeus agassizi* was very brief and was accompanied by a dark photograph in which few details can be seen (Eastman, 1904: pl. 2). The description did not mention many osteological features pertinent to a modern phylogenetic analysis, and the few subsequent authors who have briefly mentioned *A. agassizi* apparently did not examine either of the holotypic counterparts because they did not add any anatomical information about the species. We therefore redescribe the species below for the first time as a fourth siganid species from Monte Bolca, and present a first reconstruction of it.
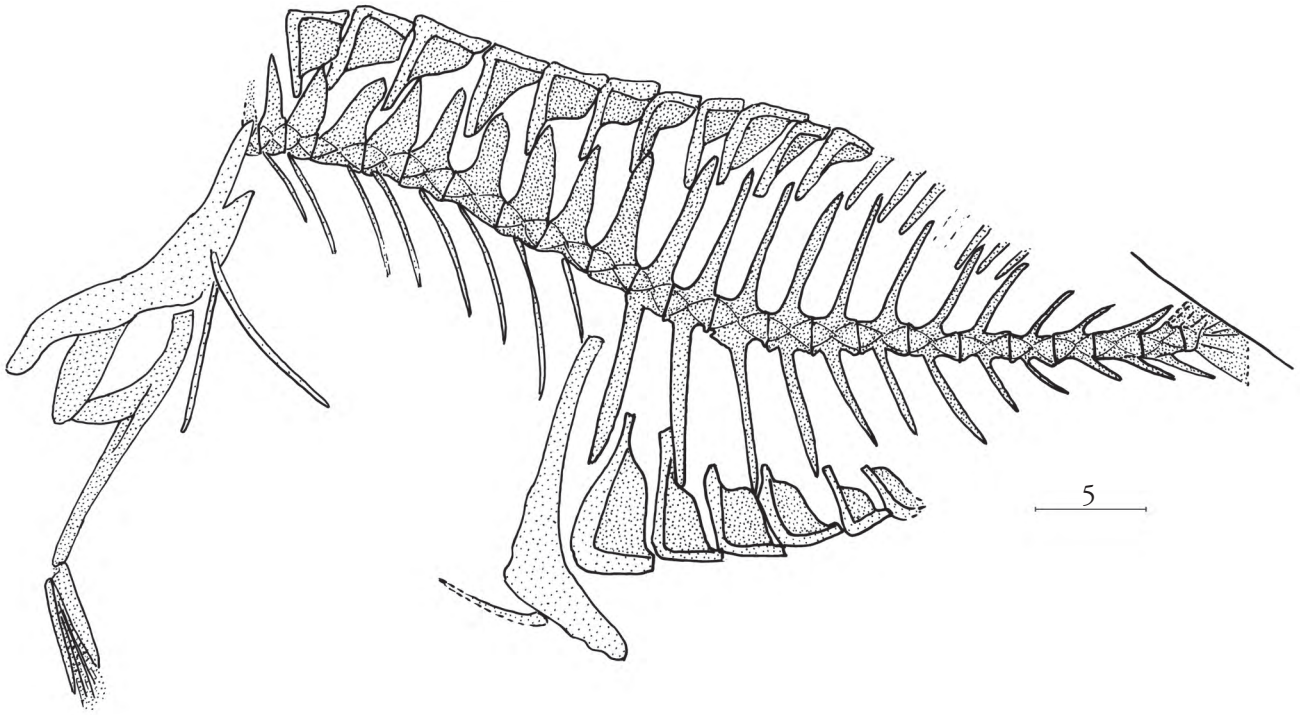
Fig. 1 – *Caucasiganus* sp., MNHN EIP 23, Rupelian of Istehbanat, Iran; scale bar in mm.

Tyler and Bannikov (1997) described the new siganid genus and species *Eosiganus kumaensis* from the Bartonian (uppermost Middle Eocene) of the Gorny Luch locality in the North Caucasus, S.W. Russia. Field excavations executed subsequently in that locality revealed that siganids were represented by at least three different taxa in the Bartonian fish fauna of the Caucasian part of the Tethys Ocean. The two new genera and species of rabbitfishes from the Gorny Luch locality are described below as *Caucasiganus eocaenicus* gen. et sp. nov. and *Lagosiganus parinterneuralis* gen. et sp. nov. One of the paratypes of *Eosiganus kumaensis* Tyler et Bannikov, 1997 (PIN 4425-20) is herein attributed to *Caucasiganus eocaenicus* gen. et sp. nov. because careful re-examination of this specimen has revealed that what was originally interpreted as the long first dorsal-fin spine is actually a combination of the first and second spines closely adjoined at the base to each other.

It is pertinent to note here that a single specimen of an undescribed siganid is present in the collection of the Muséum National d'Histoire Naturelle, Paris. This specimen originates from the Lower Oligocene (Rupelian) locality of Istehbanat in Iran. It is too incomplete to be described (see Fig. 1), but we can identify it as *Caucasiganus* sp. This discovery adds one more taxon to the Rupelian fish fauna of Iran (Arambourg, 1967)

and one more genus to the Oligocene siganids (in addition to *Protosiganus* Whitley: see Tyler and Bannikov, 1997). Thus, the stratigraphic distribution of *Caucasiganus* gen. nov. ranges from the Middle Eocene to the Lower Oligocene.

Materials and methods

Some details of the specimens examined were best seen when the specimens were moistened with alcohol. The specimens were prepared by needle.

Interneural and interhaemal spaces are numbered based on the vertebra whose neural or haemal spine forms the anterior border of the space, with the first space being between the first and second neural or haemal spines (following Baldwin and Johnson, 1993; Bannikov and Tyler, 1995; Tyler and Bannikov, 1997; etc.).

Abbreviations are as follows: Institutional: MCZ – Museum of Comparative Zoology, Harvard University, Cambridge (Massachusetts); MNHN – Muséum National d'Histoire Naturelle, Paris; NHML – The Natural History Museum, London; PIN – Borisyak Paleontological Institute, Russian Academy of Sciences, Moscow; Anatomical: PU – preural vertebra; SL – standard length; U – ural vertebra.

Systematic descriptions

Order PERCIFORMES
Suborder ACANTHUROIDEI
Family Siganidae Richardson, 1836
Genus *Acanthopygaeus* Leriche, 1906
Acanthopygaeus: Leriche, 1906: 387.

Diagnosis

Siganids having elongate stout jaw teeth with low lobations along one edge, 10+13=23 vertebrae, 2 uroneurals of which first is large, no supraneurals, dorsal fin with 10 spines (one supernumerary) and 9 soft rays, first dorsal-fin spine slightly shorter than second, middle spines longest, short procumbent spine on first dorsal-fin pterygiophore, vacant 7th interneural space, anal fin with 5 spines and 8 soft rays, postcleithrum distinctly separated from first anal-fin pterygiophore, pelvic fin with 2 spines and 3 soft rays between them.

Type Species

Pygaeus agassizi Eastman, 1904, by monotypy and designation of Bannikov (2004).

Composition

The type species only.

Acanthopygaeus agassizi (Eastman, 1904)
(Figs. 2-4)
Pygaeus agassizii: Eastman, 1904: 31, pl. 2.

Diagnosis

That of the genus, of which it is presently the only known representative.

Holotype

MCZ 5093, 164 mm SL, head to left; its counterpart, not utilized by Eastman, is NHML P 9832. Uppermost Lower or lowermost Middle Eocene (Medizza, 1975; Papazzoni and Trevisani, 2006), zone *Discoaster sublodoensis*; Monte Bolca locality, Pesciara cave site.

Referred Specimens

None.

Description

The body is moderately deep. The postcranial skeleton is well preserved, but many of the bones of the head are indistinct, incomplete or absent (Fig. 2). Our description is based on the MCZ 5093 holotypic counterpart.

- Head. The frontal and supraoccipital have rugose surfaces that are especially evident along their dorsal
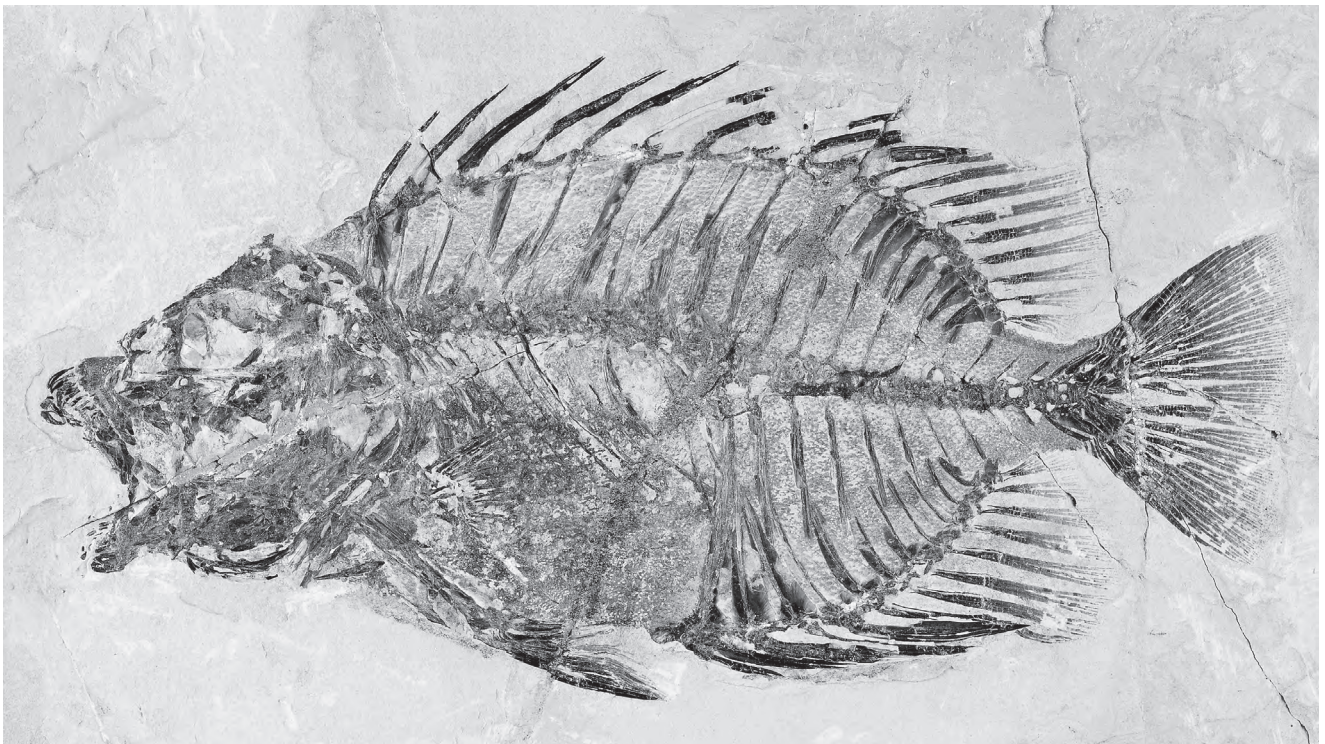

Fig. 2 – *Acanthopygaeus agassizi* (Eastman, 1904), holotype MCZ 5093, 164 mm SL; uppermost Lower or lowermost Middle Eocene of Monte Bolca, Italy.

edges as seen laterally, which is indicative of a cancellous condition. The supraoccipital has a rounded dorsal region, without a distinct crest. The remaining bones of the neurocranium are too poorly preserved to describe.

The front part of the mesethmoid forms a vertical block just behind the premaxillary process, and, whereas its more posterior region is poorly preserved, the bulk of the mesethmoid is visible anterior to the lateral ethmoid. Just above the mesethmoid is the nasal, which extends posteriorly to the anterior ends of the frontal and the lateral ethmoid. Below the mesethmoid and the anterior end of the parasphenoid, the anterior end of the lachrymal is preserved and has an irregular anterior edge, whereas more posteriorly the lachrymal is indistinct. The palatine is not evident, and we presume that it is obscured from view by the lachrymal. The long straight shaft of the parasphenoid is evident from the rear of the eye to the mesethmoid, and there is no prominent ventral flange. The eye has two sclerotic ossicles.

The premaxilla and maxilla are closely applied to each other in an obviously immovable articulation. The premaxillary process is short and abuts the region of the ethmoid and nasal. The teeth of the left premaxilla are well preserved and mostly in situ in the upper, or more medial, portion of the series; the more medial teeth are stout and elongate, and perhaps slightly flattened. The lower, or lateral, edges of these more elongate stout teeth have two widely spaced indentations resulting in low but distinctive lobations (Fig. 3). Some of the inner surface of the right premaxilla is exposed just in front of the edge of the middle region of the left premaxilla; its upper, or more medial, teeth are disarticulated in front of the larger teeth of the left premaxilla, but its lower teeth are in situ. One of the disarticulated teeth of the right premaxilla has a broadened base relative to the more conical distal end, and no indentations or lobations are evident.

The lower jaw is poorly preserved, but there are indications that the dentary is far larger than the angulo-articular. The teeth in the lower jaw are mostly disarticulated from the edge of the dentary, and many are absent. None of those that are preserved are as stout and as long as those in the upper part of the premaxilla,
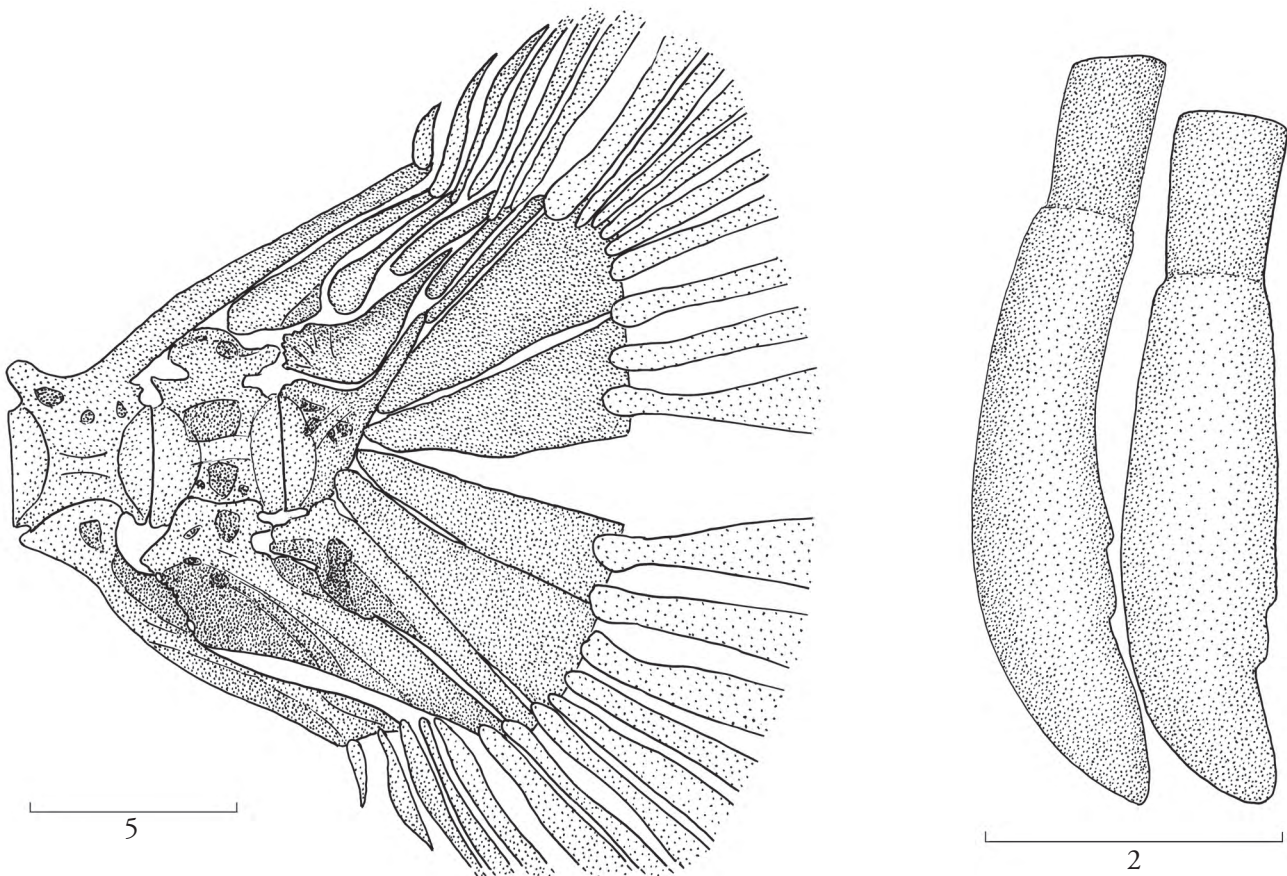

Fig. 3 – Caudal skeleton (left) and uppermost two teeth of the left premaxilla of the holotype of *Acanthopygaeus agassizi*, 164 mm SL; scale bars in mm.

and at least one of them is broadened basally, such as one in the left premaxilla.

The region of the suspensorium is fractured, and much of the bony material is absent. Only the anterior regions of the quadrate and ectopterygoid are evident. There are indistinct remains of a large opercle and perhaps of the subopercle. In front of the opercular region, just below a fracture through the middle of the head, there is a pocket of small pharyngobranchial teeth. The ceratohyal is displaced forward below the quadrate, and several branchiostegal rays are evident, but the full number cannot be determined.

- Axial skeleton. There are ten abdominal and 13 caudal vertebrae (presuming that the first vertebra is obscured, as explained below, and that the first visible vertebra is actually the second vertebra, whose neural spine is situated between the first and second dorsal-fin pterygiophores). The first pleural rib is attached to the second abdominal vertebra, and the third to eighth vertebrae also bear ribs, the longest of which reach the level of the upper actinosts of the pectoral fin. There may be an indistinct rib attached to the tenth (last) abdominal vertebra, but this is uncertain. No indications on epineurals are evident.

- Pectoral fin and girdle. The posttemporal is clearly preserved along the rear edge of the cranium, as is the upper end of the supracleithrum just below the posttemporal, but the lower region of the supracleithrum is unclear. The posttemporal and upper part of the supracleithrum obscure from view what we presume is the first abdominal vertebra, based upon the space available for it between the estimated rear of the cranium and the anterior region of the first visible vertebra, which we presume to be the second based upon its position (and its relationship to the ventral shafts of the first few dorsal pterygiophores in other siganids). Most of the cleithrum and coracoid are preserved, as are all four actinosts, which bear about 15 or 16 pectoral-fin rays. The postcleithrum extends down from the cleithrum above the pectoral-fin base to low in the abdomen, approaching the level of the pelvic fin far from the first anal-fin pterygiophore.

- Pelvic fin and girdle. The pelvis and pelvic-fin rays are well preserved. It is clear that the pelvic fin has an outer spine, three branched fin rays, and an inner spine. The bases of the three rays are crowded together between the bases of the two spines, but their separate identity as three, and only three, rays is abundantly clear more distally. In addition to the outer and inner spines, one of the spines from the right side pelvic fin is evident behind the inner spine of the left side fin. The three rays are segmented and branched. The stout pelvis

has a deep anteroventral flange for muscle attachment and extends into the middle of the cleithrum.

- Dorsal fin. There are ten dorsal-fin spines and nine rays, with the last ray divided to the base; the spines are heteracanth, and the rays are segmented and branched distally. There is a single supernumerary dorsal-fin spine on the first dorsal pterygiophore. The second dorsal-fin spine is 1.4 times longer than the first dorsal-fin spine. There is no predorsal bone (supraneural). A single pterygiophore of the spiny dorsal fin inserts between each of the adjacent neural spines of the abdominal vertebrae except that the seventh interneural space is vacant, there being no pterygiophore between the neural spines of the seventh and eighth abdominal vertebrae. The thickened dorsal edges of the pterygiophores bearing the dorsal-fin spines appear to be laterally expanded as strong flanges; the same is true of the ventral edges of the anal pterygiophores bearing the anal-fin spines. The first dorsal-fin pterygiophore bears a short procumbent spine from its anterodorsal end. This procumbent spiny process may have protruded through the skin because the outline of the skin present between the top of the skull and the first pterygiophore, even though the skin is sunken and concave in the middle region, terminates posteriorly just below and behind the anterior tip of the procumbent spine.

- Anal fin. There are five anal-fin spines and eight rays, with the last ray divided to the base; the spines are heteracanth, and the rays are segmented and branched distally. The first two anal spines are supernumerary on the first anal pterygiophore. The second anal-fin spine is 1.44 times longer than the first anal-fin spine. The first anal pterygiophore is long and stout and articulates closely along most of the anterior edge of the haemal spine of the first caudal vertebra; the second and third anal pterygiophores are shorter, and both are situated in the first interhaemal space (between the first and second haemal spines).

- Caudal fin and skeleton. The caudal skeleton is well preserved (Fig. 3); a minor fracture through the bases of the upper lobe principal rays does not harm important features and is not indicated in the figure. The haemal spines of the 11th (PU3) and 12th (PU2) caudal vertebrae are autogenous, long, and reach to the bases of the caudal-fin rays. The neural spine of PU3 is long and reaches to the bases of the caudal-fin rays, whereas the neural spine of PU2 is short and supports the first of the three epurals. The terminal half-centrum (fused PU1, U1 and U2) and its prominent urostylar process support the large first uroneural; a smaller and more elongate second uroneural is situated below the posterior tip of the first uroneural and between the
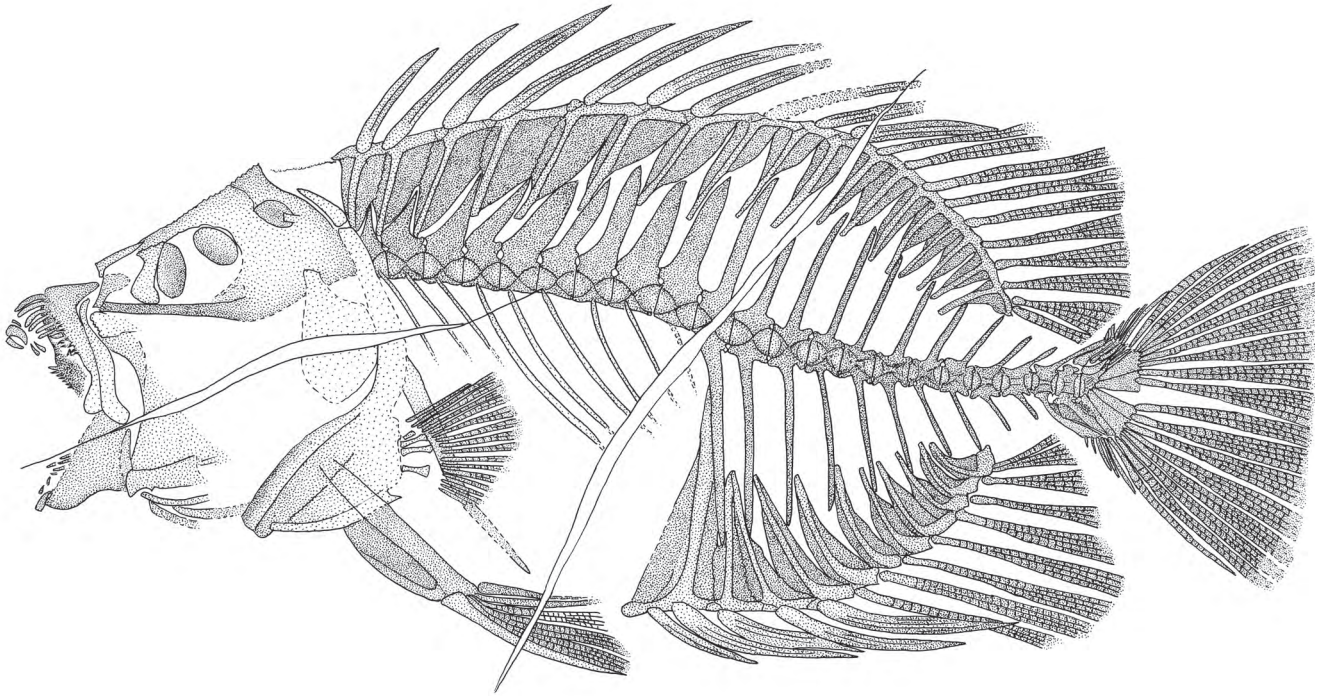
Fig. 4 – Reconstruction of the skeleton of the holotype of *Acanthopygaeus agassizi* (Eastman, 1904) based on a tracing from an enlarged photograph, refined by observations made with a dissecting microscope.

third epural and fifth hypural. The five hypurals are unconsolidated and the parhypural is autogenous, but it cannot be determined whether a hypurapophysis was present. The presence of a second uroneural is unique to this species among all siganids and is a plesiomorphic ancestral feature.

The caudal fin is moderately large and truncated. There are 17 principal caudal-fin rays, nine (upper unbranched and eight branched) in the upper lobe and eight (lower unbranched and seven branched) in the lower lobe; there are six procurrent rays above and five procurrent rays below.

- Squamation. The scales are small, apparently cycloid, slightly ovoid, and mostly no larger than about 1.1 mm (0.66% SL) greatest dimension. There is weak evidence of the gently arched lateral line in the region between the second from last neural spine of the abdominal vertebra and the neural spine of the fifth and sixth caudal vertebra.

- Measurements. The following measurements are given as a percent of the 164 mm SL holotype.
Greatest body depth: 45.0
Head length (to edge of cleithral curve): 33.0
Orbit diameter: 8.5
Snout (front of teeth to rear of lateral ethmoid): 12.9
Longest teeth: 3.2

Least depth of fleshy caudal peduncle: 9.8
First dorsal-fin spine length: 11.0
Second dorsal-fin spine length: 15.4
Third dorsal-fin spine length: 21.2
Fourth dorsal-fin spine length: 17.8
Tenth dorsal-fin spine length: 14.8
First anal-fin spine length: 10.4
Second anal-fin spine length: 15.0
Fifth anal-fin spine length: 17.7
Outer pelvic-fin spine length: 18.8

Genus *Caucasiganus* gen. nov.

Diagnosis

Siganids having elongate conical jaw teeth with smooth edges, 10+13=23 vertebrae, single uroneural not enlarged, no supraneurals, dorsal fin with 13 spines (two supernumerary) and 11 soft rays, first dorsal-fin spine much shorter than second, second spine longest, prominent procumbent spine with lateral barb on first dorsal-fin pterygiophore, vacant 5th interneural space, anal fin with 7 spines and 9 soft rays, postcleithrum somewhat but distinctly separated from first anal-fin pterygiophore, pelvic fin with 2 spines and 3 soft rays between them.

Type Species

Caucasiganus eocaenicus gen. et sp. nov., by designation herein.

Etymology

The genus is named for the Caucasus and the Recent genus *Siganus*; gender masculine.

Composition

The type species and *Caucasiganus* sp. from the Lower Oligocene of Iran.

Caucasiganus eocaenicus sp. nov.
(Figs. 5, 6)
Eosiganus kumaensis (part): Tyler and Bannikov, 1997: Fig. 9.

Diagnosis

That of the genus.

Etymology

The species is named for the Eocene age of the Gorny Luch locality.

Holotype

PIN 4425-91, 35 mm SL, part and counterpart; up-permost Middle Eocene (Bartonian), Kuma Horizon; North Caucasus, Gorny Luch locality.

Paratype

PIN 4425-93, estimated 25 mm SL (specimen incomplete posteriorly), part and counterpart; uppermost Middle Eocene (Bartonian), Kuma Horizon; North Caucasus, Gorny Luch locality.

Referred Specimens

PIN 4425-92, 16 mm SL, part and counterpart; PIN 4425-20, 19.6 mm SL, part and counterpart; PIN 4425-98, 17.5 mm SL, single plate; all from the type locality.

Description

The body is oblong. The caudal peduncle depth is about 0.20-0.22 of the body depth. The head is relatively small; its length approximately equals the body depth. The head length is contained 2.8 to 3.17 times in SL. The dorsal and ventral profiles of the body are almost equally convex.

- Head. The bones of the neurocranium are exposed from their inner surfaces; therefore, a probable cancellous condition of their lateral surfaces is not evident. The supraoccipital has a rounded dorsal region, without a distinct crest. The frontals are extended anteriorly over
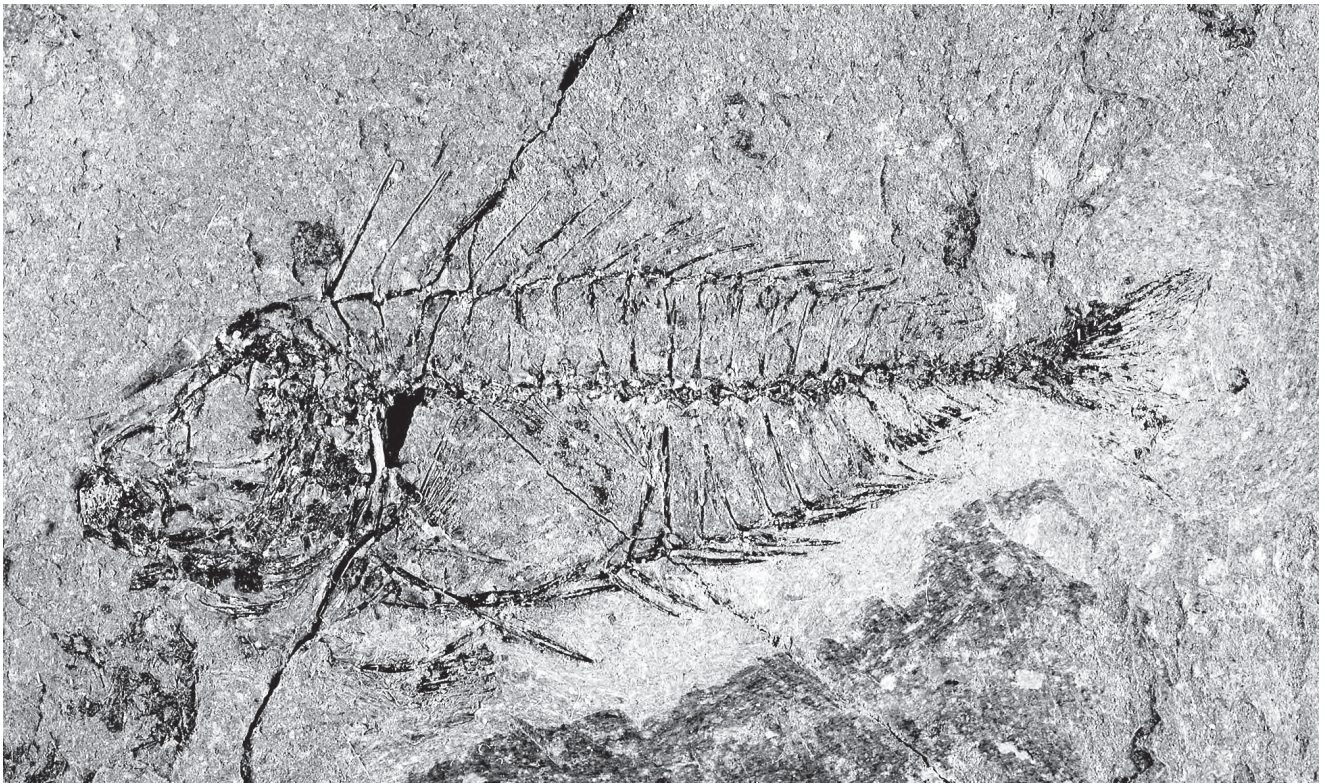

Fig. 5 – *Caucasiganus eocaenicus* gen. et sp. nov., holotype PIN 4425-91, 35 mm SL (× 3.75); uppermost Middle Eocene of Gorny Luch, SW Russia.

the ethmoid bones. The neurocranium is moderately deep. The lateral ethmoid is clearly visible and forms the anterior border of the orbit, whereas the mesethmoid is either not ossified or mostly obscured by the prominent nasal. The parasphenoid is evident below the orbit as a long slightly curved shaft, and there is no prominent ventral flange. The lachrymal is better preserved in PIN 4425-20, where it extends below the ethmoid region; the paratypic lachrymal has weak serrations along its lower border. The palatine is only partly preserved in the holotype. Sclerotic ossicles are not evident.

The mouth is small; the lower jaw articulation is situated anterior to the front margin of the orbit. The premaxilla and maxilla are closely applied to each other in an obviously immovable articulation. The ascending premaxillary process abuts the region of the ethmoid and nasal; it is shorter than the alveolar process. The teeth of the premaxillae are relatively well preserved and mostly in situ. The teeth are stout, conical and elongate, and perhaps slightly flattened distally. No indentations or lobations are evident in the teeth. The lower jaw is relatively short; its depth almost equals its length. The paratype PIN 4425-93 shows that the dentary is far larger than the angulo-articular. The symphysis is extended. The teeth in the lower jaw are similar to those of the upper jaw in shape and size, but their crowns appear to be more curved.

The hyomandibular shaft is slightly to moderately inclined. The quadrate is relatively small and subtriangular, its posteroventral edge is thickened. The ectopterygoid is curved and oriented almost vertically.

The entopterygoid and metapterygoid are better preserved in the holotype, where the anteroposterior lateral metapterygoid ridge is evident. The preopercle is relatively narrow and only moderately curved. The lower edge of the preopercle is serrated. The limits of the opercle and subopercle are indistinct; a subvertical ridge is evident on the opercle of some specimens. The hyoid arch seems to be relatively short; its individual bones are indistinct. Several branchiostegal rays are evident, but the full number cannot be determined; the first ray is relatively broad.

- Axial skeleton. There are ten abdominal and 13 caudal vertebrae. The axis of the vertebral column is only slightly elevated anteriorly. Most of the vertebral centra are elongated. The neural spines of the abdominal vertebrae are expanded anteroposteriorly. The neural spines of the caudal vertebrae are more slender, but strong. The haemal spines of the caudal vertebrae are similar in shape to the corresponding neural spines except for usually being somewhat longer; the first haemal spine is inclined anteriorly. Both the neural and haemal spines of the second and succeeding caudal vertebrae are inclined posteriorly; they become shorter towards the caudal peduncle. Parapophyses are present on the last few abdominal vertebrae. Pleural ribs are present on the second to tenth abdominal vertebrae. The ribs are short and slender, occupying the upper third to half of the abdominal cavity. No indications of epineurals are evident.

- Pectoral fin and girdle. The unforked posttemporal is clearly preserved along the rear edge of the cranium in the holotype and PIN 4425-20, whereas the elongate
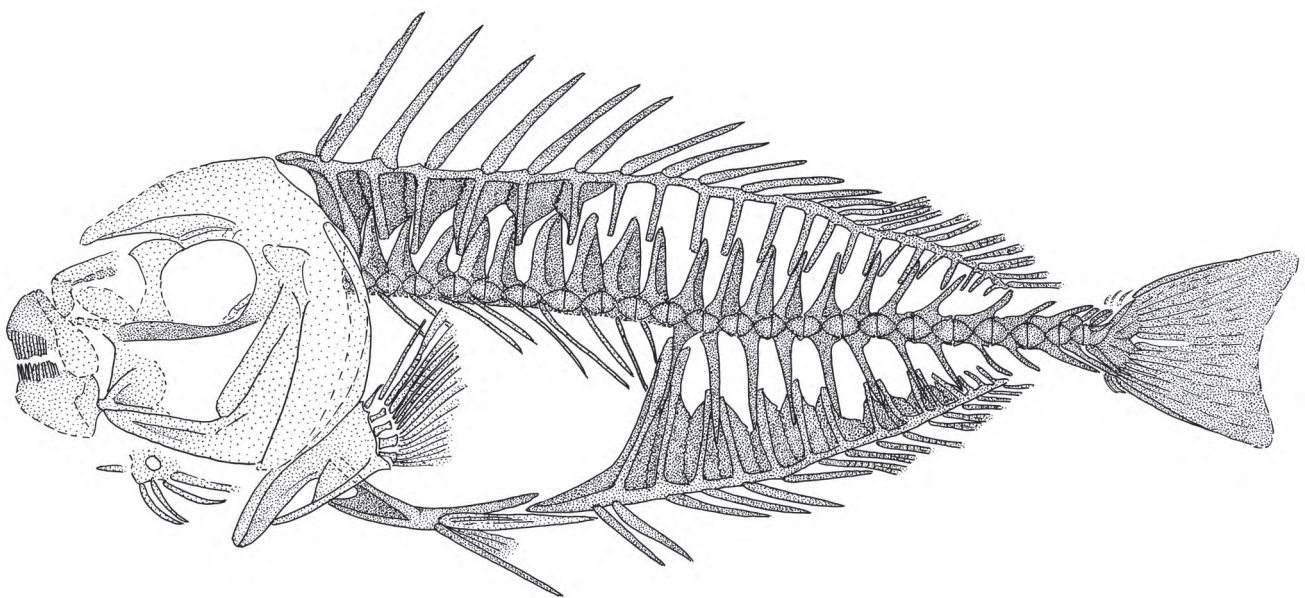

Fig. 6 – Reconstruction of the skeleton of *Caucasiganus eocaenicus* gen. et sp. nov. based on the holotype.

supracleithrum is best seen in the paratype. The cleithrum is an elongate, robust bone situated just below the first or second vertebra; the upper part of its length is curved slightly forward. The posterodorsal flange of the cleithrum is relatively narrow. The coracoid is thin and relatively narrow. The scapula and relatively slender pectoral radials are recognizable only in the holotype. The ventral postcleithrum extends posteroventrally from the pectoral-fin base to low in the abdomen, approaching but distinctly separated from the upper region of the anterior projection of the distal end of the first anal-fin pterygiophore. A narrow dorsal postcleithrum is preserved in the holotype and PIN 4425-20. The pectoral fin is inserted relatively low on the flank, near the midpoint between the vertebral column and the ventral profile of the body. The pectoral fin seems to be relatively short; it consists of 15 or 16 rays.

- Pelvic fin and girdle. The stout pelvis has a rather deep anteroventral flange for muscle attachment which terminates as a sharp process. The posterior pelvic process is well developed. The pelvic fin is moderately long, with two strong spines and three branched rays apparent between the spines. The pelvic-fin origin is situated behind the pectoral-fin base. If it were adpressed, the pelvic fin would have reached to the base of the first anal-fin spine.

- Dorsal fin. There are 13 dorsal-fin spines and 11 soft rays (the total complement of the dorsal-fin elements is preserved only in the holotype, which is the largest specimen). There are two supernumerary dorsal-fin spines on the first dorsal pterygiophore. The second dorsal-fin spine is 2.4-3.4 times longer than the first dorsal-fin spine. The second dorsal-fin spine is longest, and the succeeding spines become shorter in the series. The base of the first dorsal-fin soft ray is situated over the fifth or sixth caudal vertebra. There is no predorsal bone. A single pterygiophore of the spiny dorsal fin inserts between each of the adjacent neural spines of the abdominal vertebrae except that the fifth interneural space is vacant. The longitudinal ridges of the two anteriormost dorsal-fin pterygiophores usually are inclined anteriorly, whereas all the other pterygiophore shafts are inclined posteriorly. There is a long, grooved, pointed procumbent spine directed anteriorly in the upper part of the first dorsal-fin pterygiophore. There is a posterolaterally directed barb in the lateral surface of the procumbent spine. The pterygiophores of the spiny dorsal fin are large, sturdy and expanded anteroposteriorly, whereas the proximal pterygiophores of the soft dorsal-fin rays are more slender.

- Anal fin. There are seven anal-fin spines and nine soft rays (the total complement of anal-fin elements is preserved only in the holotype). The first two anal spines are supernumerary on the first anal pterygiophore. The second anal-fin spine is only slightly longer than the first anal-fin spine, and the fourth spine is probably longest. The first anal pterygiophore is long and stout and articulates closely along most of the anterior edge of the haemal spine of the first caudal vertebra; the second and third anal pterygiophores both are situated in the first interhaemal space. The second and succeeding anal-fin pterygiophores decrease in length posteriorly in the series. The anteriormost three anal-fin pterygiophores are inclined anteriorly, whereas the others are inclined posteriorly.

- Caudal fin and skeleton. The caudal skeleton is relatively poorly preserved. The caudal skeleton shows the fusion of PU1, U1, and U2 in the terminal centrum. The hypurals, parhypural, and haemal spines of PU2 and PU3 are autogenous. The first uroneural appears to be relatively small; there is no second uroneural. There are probably three epurals.

The caudal fin is relatively small and concave posteriorly. There are 17 principal caudal-fin rays, nine in the upper lobe and eight in the lower lobe; the precise number of procurrent rays is unknown.

- Squamation. Scales are not preserved.

- Measurements. The following measurements are given as a percent of the 35 mm SL holotype.
Greatest body depth: 33.0
Head length: 31.5
Orbit diameter: 8.0
Snout length: 13.3
Least depth of fleshy caudal peduncle: 7.0
First dorsal-fin spine length: 4.4
Second dorsal-fin spine length: 15.7
Third dorsal-fin spine length: 15.3
Fourth dorsal-fin spine length: 13.6
Twelfth dorsal-fin spine length: 8.5
First anal-fin spine length: 8.1
Second anal-fin spine length: 8.9
Outer pelvic-fin spine length: 13.9

Genus *Lagosiganus* gen. nov.

Diagnosis

Siganids having conical jaw teeth with smooth edges, 10+13=23 vertebrae, no supraneurals, dorsal fin with 10 spines (one supernumerary) and many more than 10 soft rays, second dorsal-fin spine much shorter than first, which is longest, prominent procumbent spine without barb on first dorsal-fin pterygiophore, vacant 4th and 5th interneural spaces, anal fin with 5 spines and about 16 soft rays, postcleithrum closely ap-

proaches or contacts first anal-fin pterygiophore, pelvic fin with one spine and few soft rays.

Type Species

Lagosiganus parinterneuralis gen. et sp. nov., by monotypy and designation herein.

Etymology

The generic name *Lagosiganus* is from *lagos*, Greek for rabbit or hare, in allusion to the common name in English of rabbitfishes for the family Siganidae; gender masculine.

Composition

The type species only.

Lagosiganus parinterneuralis sp. nov.
(Figs. 7, 8)

Diagnosis

That of the genus, of which it is presently the only known representative.

Etymology

The species name *parinterneuralis* is from *par*, *paris* - Latin for pair, and *interneural*, - having two vacant interneural spaces.

Holotype

PIN 4425-94, 28 mm SL, single plate; uppermost Middle Eocene (Bartonian), Kuma Horizon; North Caucasus, Gorny Luch locality.

Referred Specimens

None.

Description

The body is relatively deep. The caudal peduncle depth is about 0.21 of the body depth. The head is moderately large; its length is less than the body depth. The head length is contained about 2.96 times in SL. The dorsal and ventral profiles of the body are almost equally convex.

- Head. The neurocranium is relatively deep. The bones of the neurocranium do not reveal a cancellous condition of their lateral surfaces. The supraoccipital
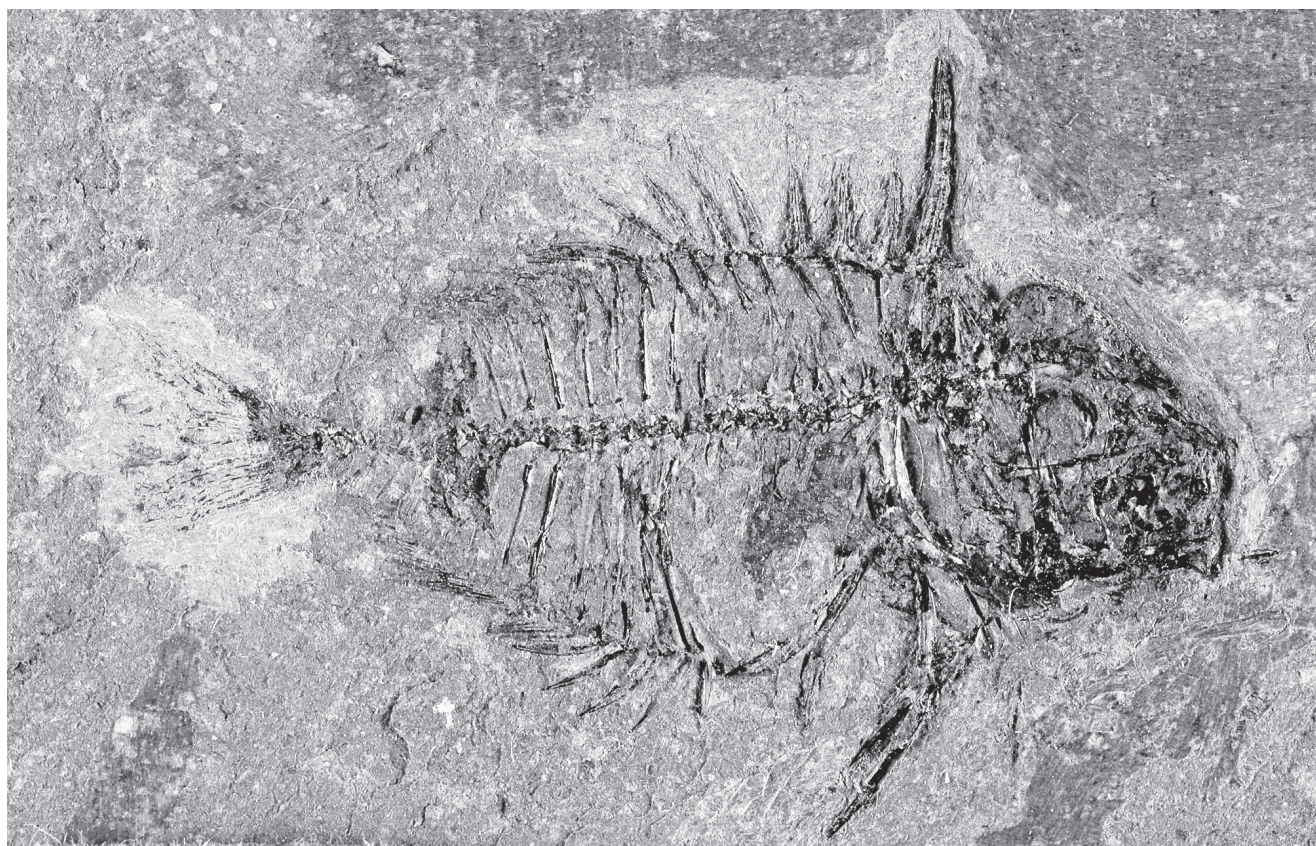

Fig. 7 – *Lagosiganus parinterneuralis* gen. et sp. nov., holotype PIN 4425-94, 28 mm SL (× 4); uppermost Middle Eocene of Gorny Luch, SW Russia.

has a rounded dorsal region, without a distinct crest. The frontals are extended anteriorly over the ethmoid bones. The lateral ethmoid is clearly visible and forms the anterior border of the orbit, whereas the mesethmoid is either not ossified or obscured by the prominent nasal. The parasphenoid is evident below the orbit as a slender slightly curved shaft, without prominent ventral flange. The lachrymal is poorly preserved, and the palatine is not evident. Sclerotic ossicles are present.

The mouth is small; the lower jaw articulation is situated under the front margin of the orbit. The premaxilla and maxilla appear to be closely applied to each other in an obviously immovable articulation; however, both bones are poorly preserved. The lower jaw is relatively short and obviously deep. The dentary seems to be larger than the angulo-articular. The symphysis is extended. The teeth in the lower jaw are relatively short and conical, with no indentations or lobations evident.

The hyomandibular shaft is slightly inclined. The quadrate is relatively small and subtriangular. The ectopterygoid is slightly curved; its ventral portion is oriented almost vertically. The entopterygoid and metapterygoid are not preserved. One of the preopercles seems to be detached and turned over in the holotype. The lower edge of the preopercle is even. The limits of the opercle and subopercle are indistinct, and most of the hyoid arch is obscured. A few sabre-like branchiostegal rays are evident below the lower margin of the opercular region.

- Axial skeleton. There are ten abdominal and 13 caudal vertebrae. The axis of the vertebral column is elevated anteriorly. Most of the vertebral centra are subrectangular. The neural spines of the abdominal vertebrae are expanded anteroposteriorly. The neural spines of the caudal vertebrae are less expanded. The haemal spines of the anterior caudal vertebrae are also expanded anteroposteriorly. The first haemal spine is inclined slightly anteriorly, whereas the second haemal spine is relatively vertically oriented, as are the neural spines of the first two caudal vertebrae. Both the neural and haemal spines of the succeeding caudal vertebrae are inclined posteriorly; they become shorter towards the caudal peduncle (several vertebral spines from the middle of the caudal portion of the vertebral column are missing, together with matrix). Parapophyses are scarcely recognizable on the last few abdominal vertebrae. Pleural ribs are present on the second to tenth ab-
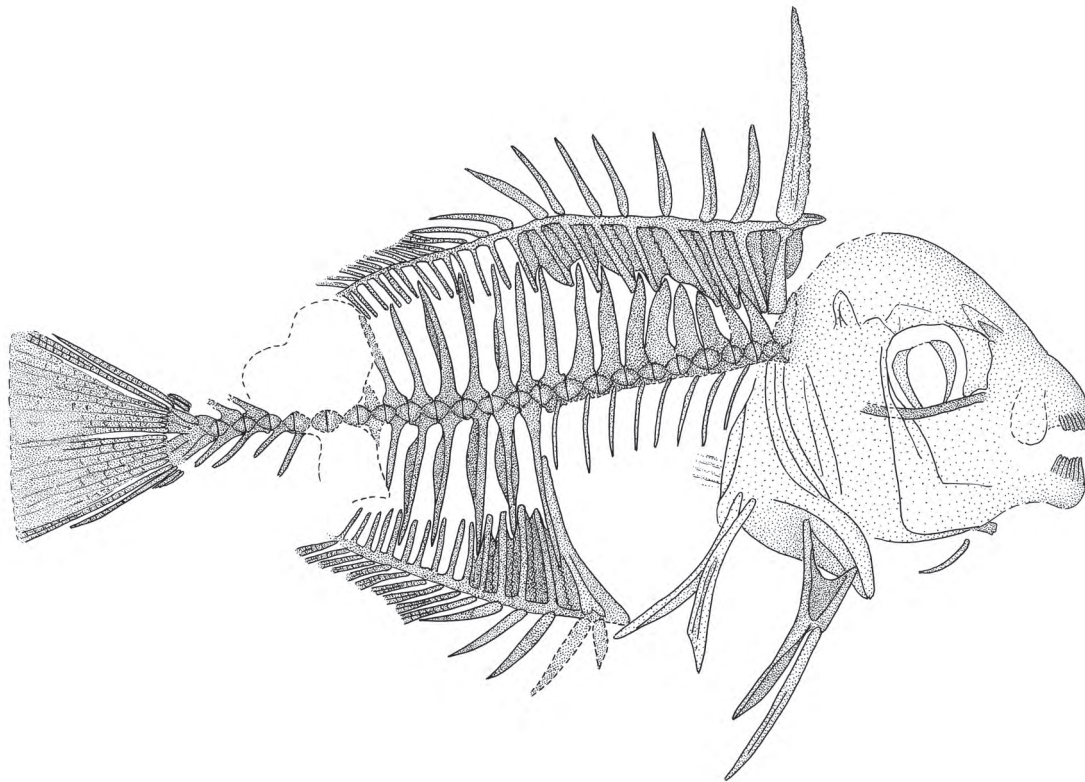

Fig. 8 – Reconstruction of the skeleton of *Lagosiganus parinterneuralis* gen. et sp. nov. based on the holotype; posteriormost soft rays of the dorsal and anal fins are not shown.

dominal vertebrae. The ribs are short and slender, relatively slightly inclined, occupying the upper half of the abdominal cavity. There is no evidence of epineurals.

- Pectoral fin and girdle. Two bones that are strongly tapered dorsally are present between the occiput and first dorsal-fin pterygiophore in the holotype; the more anterior of these bones has two finely serrated longitudinal ridges. We interpret these bones as somewhat detached unforked posttemporals. The cleithrum is an elongate, robust and gently sygmoid bone situated just below the first or second vertebra. The posterodorsal flange of the cleithrum is relatively narrow. The coracoid is thin and relatively narrow. The scapula, supracleithrum and dorsal postcleithrum are scarcely recognizable. The ventral postcleithrum is robust and slightly curved; it extends posteroventrally from the pectoral-fin base to low in the abdomen, closely approaching or contacting the anterior projection of the distal end of the first anal-fin pterygiophore. One of the ventral postcleithra is somewhat detached and overturned. The pectoral fin is very poorly preserved; its size and number of rays are unknown.

- Pelvic fin and girdle. The pelvis is turned anteroventrally by its distal end. The stout pelvis has a rather deep anteroventral flange for muscle attachment which terminates as a sharp process. The posterior pelvic process is well developed; its length approximately equals the length of the main body of the pelvis. The pelvic fin has a strong spine and a few soft rays (a single ray is preserved in the holotype). The pelvic-fin spine has minute serrations along the base of its ventral edge. If it were adpressed, the pelvic fin would have reached to the base of the first anal-fin spine.

- Dorsal fin. There are ten spines in the dorsal fin. Because a large piece of matrix is missing, the posterior soft dorsal-fin rays are lost in the holotype. There are ten anterior soft dorsal-fin rays preserved, and we presume that not less than five more rays could be present more posteriorly. There is a single supernumerary dorsal-fin spine on the first dorsal pterygiophore. The first dorsal-fin spine is strong and very long, almost 2.2 times longer than the second dorsal-fin spine. At least the basal half of the length of the first dorsal-fin spine bears small anterior serrations. The second and succeeding dorsal-fin spines become only slightly, if at all, shorter in the series. The base of the first dorsal-fin soft ray is situated over the third caudal vertebra. There is no predorsal bone. A single pterygiophore of the spiny dorsal fin inserts between each of the adjacent neural spines of the abdominal vertebrae except that the fourth and fifth interneural spaces are vacant, and the first interneural space appears to accommodate two

anteriormost pterygiophores. The longitudinal ridge of the first dorsal-fin pterygiophore is inclined somewhat anteriorly, whereas all the other pterygiophore shafts are inclined posteriorly. There is a relatively long pointed procumbent spine directed anteriorly in the upper part of the first dorsal-fin pterygiophore. The pterygiophores of the spiny dorsal fin are large, sturdy, and expanded anteroposteriorly, whereas the proximal pterygiophores of the soft dorsal-fin rays are more slender.

- Anal fin. There are five anal-fin spines and 15 or 16 soft rays (the posteriormost five or six rays are poorly preserved). The first two anal spines are supernumerary on the first anal pterygiophore; these are represented by imprints on the matrix. The third anal-fin spine is probably longest. The first anal pterygiophore is long, stout, and articulates closely along most of the anterior edge of the haemal spine of the first caudal vertebra; the second and third anal pterygiophores are both situated in the first interhaemal space. The second and succeeding anal-fin pterygiophores decrease in length posteriorly in the series. The first and second anal-fin pterygiophores are inclined anteriorly, the one or two succeeding pterygiophores are almost vertically oriented, and the others are inclined posteriorly.

- Caudal fin and skeleton. The caudal skeleton is relatively poorly preserved. The caudal skeleton shows the fusion of PU1, U1, and U2 in the terminal centrum. The hypurals, parhypural, and haemal spine of PU2 are autogenous. The first uroneural appears to be relatively small; there is no second uroneural. Two epurals are clearly visible, the presence of a third epural is less evident. It is unclear if the haemal spine of PU3 is autogenous.

The caudal fin is relatively small and truncated. There are 17 principal caudal-fin rays, nine in the upper lobe and eight in the lower lobe; the precise number of procurrent rays is unknown (but there are not less than five rays both above and below).

- Squamation. Scales are not preserved.

- Measurements. The following measurements are given as a percent of the 28 mm SL holotype.
Greatest body depth: 44.0
Head length: 34.0
Orbit diameter: 8.5
Snout length: 13.0
Least depth of fleshy caudal peduncle: 9.5
First dorsal-fin spine length: 23.5
Second dorsal-fin spine length: 10.8
Third dorsal-fin spine length: 10.1
Tenth dorsal-fin spine length: 8.1
Third anal-fin spine length: 10.5
Pelvic-fin spine length: 20

Remarks. *Lagosiganus parinterneuralis* gen. et sp. nov. resembles the Middle Eocene acronurus-like specimen from Georgia identified as Acanthuroidei *incertae sedis* by Bannikov and Tyler (1992) in having five anal-fin spines and the ventral postcleithrum almost in contact with the anteroventral end of the first anal pterygiophore. However, the new taxon differs greatly from the latter in having an exceptionally long first dorsal-fin spine, shallower body, fewer dorsal-fin spines (10 vs. 8), and much less numerous dorsal-and anal-fin soft rays. Moreover, although the holotype of *Lagosiganus parinterneuralis* is somewhat smaller than the acronurus-like specimen from Georgia (28 mm SL vs. 31.5 mm), it lacks the morphological features of the acronurus pelagic presettlement stage present in both fossil and extant acanthurids.

CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

The following 15 characters are polarized and are used in the PAUP analysis. The numbers of the characters correspond to those in the cladogram. Character states are designated plesiomorphic (0) or derived (1-n). The first 12 of our 15 characters are the same as in Tyler and Bannikov (1997), and the sister group and outgroup comparisons with other acanthuroid families and with higher squamipinnes that establish character polarity are discussed in detail there. We list here the coding for the characters of the four additional genera new to the present analysis and for the several changes in coding numbers to accommodate conditions in the additional genera. For the three characters (13-15) newly included in the analysis, we provide the comparisons that establish polarity.

1. Number of pelvic-fin spines. In *Lagosiganus* there is a single (outer) pelvic-fin spine (0), which plesiomorphic condition otherwise is found only in *Ruffoichthys*, whereas *Acanthopygaeus*, *Caucasiganus*, and *Aspesiganus* have the derived condition of an outer and an inner pelvic-fin spine (1).

2. Procumbent spine on first pterygiophore of dorsal fin. The absence of any kind of anterior prong on this pterygiophore in *Ruffoichthys* is plesiomorphic (0); the four genera new to the analysis (*Acanthopygaeus*, *Caucasiganus*, *Lagosiganus*, *Aspesiganus*) are like other siganids in having a procumbent spine (1).

3. Number of anal-fin spines. In the Tyler and Bannikov (1997) analysis, the four anal-fin spines in *Ruf-foichthys* were documented as plesiomorphic (0) for siganids, and higher numbers of six to eight anal spines were progressively more derived (1-3). However, two of the newly added genera have five anal spines, so the coding has changed as follows: five spines in *Acanthopygaeus* and *Lagosiganus* (1), six spines in *Aspesiganus* and *Protosiganus* (2), seven spines in *Caucasiganus*, *Eosiganus*, and *Siganus* (3), eight spines in *Siganopygaeus* (4).

4. Number of supernumerary dorsal-fin spines. Two supernumerary dorsal-fin spines are considered plesiomorphic (0) for acanthuroids, with the loss of one of the spines derived (1). Two of the four newly added taxa (*Aspesiganus* and *Caucasiganus*) have the plesiomorphic condition and the other two (*Acanthopygaeus* and *Lagosiganus*) are derived for this character.

5. Length of first supernumerary dorsal-fin spine. A short to moderate length for the first supernumerary spine relative to that of the second supernumerary spine is considered plesiomorphic (0) for acanthuroids, while a long first supernumerary spine is derived (1). Among the newly added taxa, *Caucasiganus* has the plesiomorphic condition for this character and *Aspesiganus* has the derived condition, while the other two genera (*Acanthopygaeus* and *Lagosiganus*), having just a single supernumerary dorsal-fin spine, are not coded (?) for this character.

6. Association of postcleithrum and first anal-fin pterygiophore. The distinct separation of the postcleithrum and first anal-fin pterygiophore is considered plesiomorphic (0) for siganids and the close association or contact between these two bones is derived (1). *Lagosiganus* is the only one among the newly added taxa to have the derived condition of this character.

7. Number of dorsal-fin spines. Tyler and Bannikov (1997) documented 12 or fewer dorsal-fin spines as primitive for acanthuroids (0), with, among siganids, the 11 of *Ruffoichthys* and *Eosiganus* being plesiomorphic (0) and the 13 of *Protosiganus* and *Siganus* (1) and the 14 of *Siganopygaeus* (2) being progressively derived. The majority of the newly added genera share the plesiomorphic condition of having 10 (*Acanthopygaeus* and *Lagosiganus*) or 12 (*Aspesiganus*) spines, with *Caucasiganus* having the derived condition of 13 dorsal-fin spines (1).

8. Number of dorsal-fin rays. Thirteen or more dorsal-fin rays are considered plesiomorphic for acanthuroids (0), and, among siganids, there is a transfor-

mation series of increasing derivation by reduction from 11 dorsal-fin rays (1) to 9-10 rays (2). Among the newly added taxa, *Lagosiganus* has the plesiomorphic condition of an estimated at least 15 dorsal-fin rays (0), *Caucasiganus* has the intermediate derived condition of 11 rays (1), and *Acanthopygaeus* has the most derived condition of 9 rays (2). The number of dorsal-fin rays is not known for *Aspesiganus* because of the incompleteness of the specimen and the character is coded as missing (?).

9. Number of anal-fin rays. The presence of 11 or more anal-fin rays is considered plesiomorphic for acanthuroids (0), and, among siganids, there is a transformation series of increasing derivation by reduction from 9-10 rays (1) to about 7 rays (2). Among the newly added taxa, *Lagosiganus* has the plesiomorphic condition of 15-16 rays (0), *Caucasiganus* has the intermediate derived condition of 9 rays (1), and *Aspesiganus* and *Acanthopygaeus* have the most derived condition of 7 and 8 rays, respectively (2).

10. Presence of supraneural. Tyler and Bannikov (1997) documented the presence of a supraneural as the plesiomorphic condition (0) of the outgroups and its absence as a synapomorphy of the siganid clade (1). Among the newly added taxa, *Aspesiganus* has the primitive condition of the supraneural being present (0), whereas all of the others (*Acanthopygaeus*, *Caucasiganus*, and *Lagosiganus*) share the derived absence of this bone (1).

11. Shape of teeth. In Tyler and Bannikov (1997) short, conical teeth with smooth edges are documented as plesiomorphic (0) for siganids, with the deeply notched teeth of *Ruffoichthys* and *Siganus* derived (1). In the same paper the authors also presumed that the longer, and perhaps movable, slightly lobed teeth of *Protosiganus* might represent another derived feature, but because the lobation was only slight and not clear, they considered this as representing the plesiomorphic character state. In *Acanthopygaeus* several distinct but very low and broad lobations are present on one edge of the teeth, and we consider these low lobations, and those of *Protosiganus*, as being relatively similar to the plesiomorphic condition of conical teeth (0). The smooth conical teeth of *Caucasiganus* and *Lagosiganus* clearly represent the plesiomorphic state (0). In *Aspesiganus*, the jaws are not preserved and the character is coded as missing (?). The smooth conical to slightly lobed teeth that we code as plesiomorphic are in stark contrast to the deeply notched teeth (1) in *Ruffoichthys* and *Siganus*.

12. Barb on procumbent spine. Because there is no barb on the anterodorsal process of the first dorsal pterygiophore in any of the siganid sister groups and none on the smaller procumbent spine occurring in some scatophagids and ephippidids (0), the presence of a barb on the procumbent spine is considered as a derived feature (1). Among the newly added genera only *Caucasiganus* has this derived condition (1) while the others (*Aspesiganus*, *Acanthopygaeus*, and *Lagosiganus*) have no barb on the procumbent spine (0).

13. Number of vertebrae. The total number of vertebrae in the ephippidid, *Drepane*, and more basal squamipinne outgroups is 24 (10+14), whereas the number is reduced by one to 23 (10+13) at the ancestral node for scatophagids (the highest clade of squamipinnes) and siganids (the most basal clade of acanthuroids). The higher familial clades of acanthuroids (luvarids, zanclids, acanthurids) have an even more derived reduction of vertebrae to 22 (9+13), except for the fossil kushlukiids (sister to luvarids) in which there is a secondarily increased number of 29-30 (10+19-20). Vertebral numbers in these squamipinnes and acanthuroids and the polarity of the reductions are documented in Tyler et al. (1989), Bannikov and Tyler (1995, 2002), Tyler and Bannikov (1997), and Tyler and Sorbini (1999). Thus, it is well established that the plesiomorphic condition for lower and higher squamipinnes is 24 total vertebrae (0), whereas the reduction in number to 23 in scatophagids and siganids is derived (1). The derived condition of 23 vertebrae is found in all siganid genera except *Aspesiganus*, in which the number is even more derived by reversal to 24 in an unique 9+15 arrangement (rather than the squamipinne norm of 10+14), for which we code *Aspesiganus* (2).

14. Size of first uroneural. Tyler and Bannikov (1997) documented that the large size of the first uroneural in *Ruffoichthys* and *Protosiganus* is the plesiomorphic condition (0) for siganids because this uroneural is of large size in the squamipinne outgroups. Among the genera they studied, the size of the first uroneural was otherwise known only in *Siganus*, in which the very small size of the first uroneural was obviously a derived condition (1). But because the size of the first uroneural was known for only three of the studied genera, and was unknown for two others (*Eosiganus* and *Siganopygaeus*), Tyler and Bannikov (1997:32) chose not to include this character in their analysis. However, in the genera herein newly included in the analysis, we can determine first uroneural size in *Acanthopygaeus*, in which it is large (0), and in *Caucasiganus* and *Lagosiganus*, in

which it is small (1). The size of the first uroneural cannot be determined in *Aspesiganus* (?).

15. Presence of second uroneural. A second uroneural, smaller in size than the first uroneural, is present in most perciform and squamipinne outgroups (Tyler et al., 1989) and is thus the plesiomorphic condition (0). However, the second uroneural is lost at the ancestral node for scatophagids and siganids (1) and is also absent in higher acanthurids (see Tyler et al., 1989 for details and illustrations).The second uroneural is present among siganids only in *Acanthopygaeus* (0), by reversal, whereas it is absent in *Ruffoichthys*, *Caucasiganus*, *Protosiganus*, and *Siganus* (1). Because of poor preservation or absence of caudal skeleton bones, we cannot determine conditions of this character in *Eosiganus*, *Siganopygaeus*, *Aspesiganus*, and *Lagosiganus* (?).

PHYLOGENETIC ANALYSIS

Tyler and Bannikov (1997) treated the four then known fossil siganid genera (Late Paleocene *Siganopyg-* *aeus* Daniltshenko, early Middle Eocene *Ruffoichthys* Sorbini, late Middle Eocene *Eosiganus* Tyler and Bannikov and Oligocene *Protosiganus* Whitley) together with the single extant genus *Siganus* Forsskål, in a cladistic analysis utilizing 12 characters. Their phylogenetic analysis utilizing PAUP indicated that the genera have the following phyletic sequence convention: *Ruffoichthys – Eosiganus – Siganopygaeus – Protosiganus – Siganus*. In the present paper we add four additional fossil genera to the analysis of relationships within the Siganidae: the early Middle Eocene *Acanthopygaeus* Leriche and *Aspesiganus* Bannikov and Tyler, and the late Middle Eocene *Caucasiganus* gen. nov. and *Lagosiganus* gen. nov. Consequently, in the new phylogenetic analysis presented herein, the previous data matrix is expanded to include the character states of these four additional genera. Moreover, three new characters are added to the matrix, namely the number of vertebrae (character 13), the size of the first uroneural (character 14), and the presence of a second uroneural (character 15), to accommodate diagnostic features found in the newly added genera.

The data matrix in Table 1 differs from the data matrix presented in Tyler and Bannikov (1997, Table 1)

Character	Outgroup	*Ruffoichthys*	*Eosiganus*	*Siganopygaeus*	*Aspesiganus*	*Acanthopygaeus*	*Caucasiganus*	*Lagosiganus*	*Protosiganus*	*Siganus*
1. Number of pelvic-fin spines	0	0	1	1	1	1	1	0	1	1
2. Procumbent spine on first pterygiophore of dorsal fin	0	0	1	1	1	1	1	1	1	1
3. Number of anal-fin spines	0	0	3	4	2	1	3	1	2	3
4. Number of supernumerary dorsal-fin spines	0	0	1	0	0	1	0	1	0	0
5. Length of first supernumerary dorsal-fin spine	0	1	?	0	1	?	0	?	1	1
6. Association of postcleithrum and first anal-fin pterygiophore	0	0	0	0	0	0	0	1	1	1
7. Number of dorsal-fin spines	0	0	0	2	0	0	1	0	1	1
8. Number of dorsal-fin rays	0	2	1	?	?	2	1	0	2	2
9. Number of anal-fin rays	0	1	2	1	2	2	1	0	1	1
10. Presence of supraneural	0	1	1	0	0	1	1	1	1	1
11. Shape of teeth	0	1	0	?	?	0	0	0	0	1
12. Barb on procumbent spine	0	?	0	0	0	0	1	0	0	1
13. Number of vertebrae	0	1	1	1	2	1	1	1	1	1
14. Size of first uroneural	0	0	?	?	?	0	1	1	0	1
15. Presence of second uroneural	0	1	?	?	?	0	1	?	1	1

Tab. 1 – Data-set matrix used in the cladistic analysis. Character numbers are in the same order as in the text and in the cladograms.

not only by the increased number of taxa and of characters, but also by the changed coding of character 3 (namely, the number of anal-fin spines), as explained in the preceeding analysis of characters.

As in Tyler and Bannikov (1997), character polarity is hypothesized using the outgroup comparison method of Maddison et al. (1984) and the ancestral states in Table 1 are those hypothesized at the outgroup node based on conditions in the siganid sister groups (Luvaridae+†Kushlukiidae, Zanclidae, Acanthuridae) and in the higher squamipinne outgroups (Scatophagidae, Ephippididae, *Drepane*). The new matrix for the 15 osteological features (Table 1) present in both the Recent genus and in at least most of the fossil genera was analyzed using the exhaustive search option of PAUP software. The relatively small number of taxa and characters analyzed allowed us to use this search option, which examines all the possible cladograms and is guaranteed to find the most parsimonious tree.

Characters were optimized using both ACCTRAN and DELTRAN and these two methods of optimization did not result in any difference in the tree structure. In the cladograms presented in Figures 9 and 10, we have chosen to show the DELTRAN optimization (favoring independent acquisition over reversal, as in Tyler and Bannikov, 1997).

Five of the characters included in the matrix have multiple states (characters 3, 7, 8, 9, 13). Treating all five multi-state characters as unordered yields a single most-parsimonious tree (Fig. 9) with a length of 35 steps, a consistency index of CI = 0.6286, a retention index of RI = 0.5000 and a rescaled consistency index of RC = 0.3143. It has four reversals and 17 independent acquisitions.

Treating all five multi-state characters as ordered yields two equally parsimonious trees (Figs. 10 a, b), each with a length of 38 steps, a consistency index of CI = 0.5789, a retention index of RI = 0.5152 and a rescaled consistency index of RC = 0.2982. There are six reversals and 17 independent acquisitions in one tree (Fig. 10 a), and seven reversals and 15 independent acquisition in the other (Fig. 10 b). The two cladograms are very similar because they differ only in the topology of the (*Caucasiganus + Siganopygaeus + Siganus*) clade. In one tree *Siganus + Caucasiganus* are the sister group of *Siganopygaeus* whereas in the other tree *Siganopygaeus + Caucasiganus* are the sister group of *Siganus*. Consequently, in the strict consensus tree the relationship between these genera is an unresolved trichotomy.

The single tree that resulted from the unordered analysis and the strict consensus of the two equally parsimonious trees that resulted from the ordered analysis

have several elements in common, and differ mainly in the position of *Siganopygaeus* and of the (*Eosiganus + Acanthopygaeus*) clade.

In the unordered-analysis single tree, *Siganopygaeus* is the sister group of *Aspesiganus*, and these two genera represent the sister group of the ((*Caucasiganus + Siganus*) + *Protosiganus*) clade; in the ordered-analysis strict consensus tree, *Siganopygaeus* is part of the unresolved tricotomy (*Caucasiganus + Siganopygaeus + Siganus*), which is the sister group of *Protosiganus*.

The (*Eosiganus + Acanthopygaeus*) clade results from both the unordered and ordered analysis but its position in the tree is different. In the unordered-analysis single tree, it is the sister group of *Lagosiganus* and, together with this genus, the sister group of all the other taxa; in the ordered-analysis strict consensus tree, the (*Eosiganus + Acanthopygaeus*) clade is the sister group of *Aspesiganus* and its position is far from *Lagosiganus*, which is placed as the most basal genus of the family.

The cladograms obtained from both the unordered and ordered analysis conform to a certain degree to the Tyler and Bannikov (1997) ordered result.
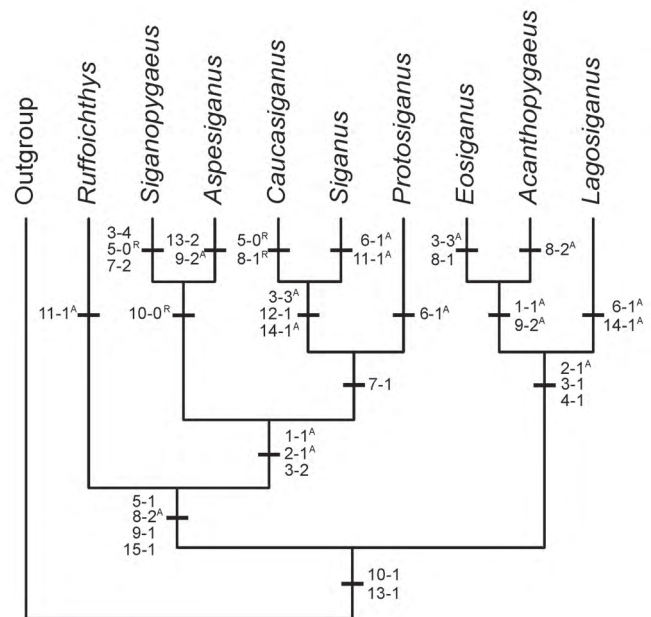
In detail, the comparison between our unordered-

Fig. 9 – Single most parsimonious cladogram produced by the unordered analysis of the data-set. Character numbers are separated by a hyphen from the character state numbers, and correspond to those used in the section of the text on "Characters Used in the Phylogenetic Analysis". Reversals are indicated by an uppercase R and independent acquisition are indicated by an uppercase A to the right of the character state numbers.
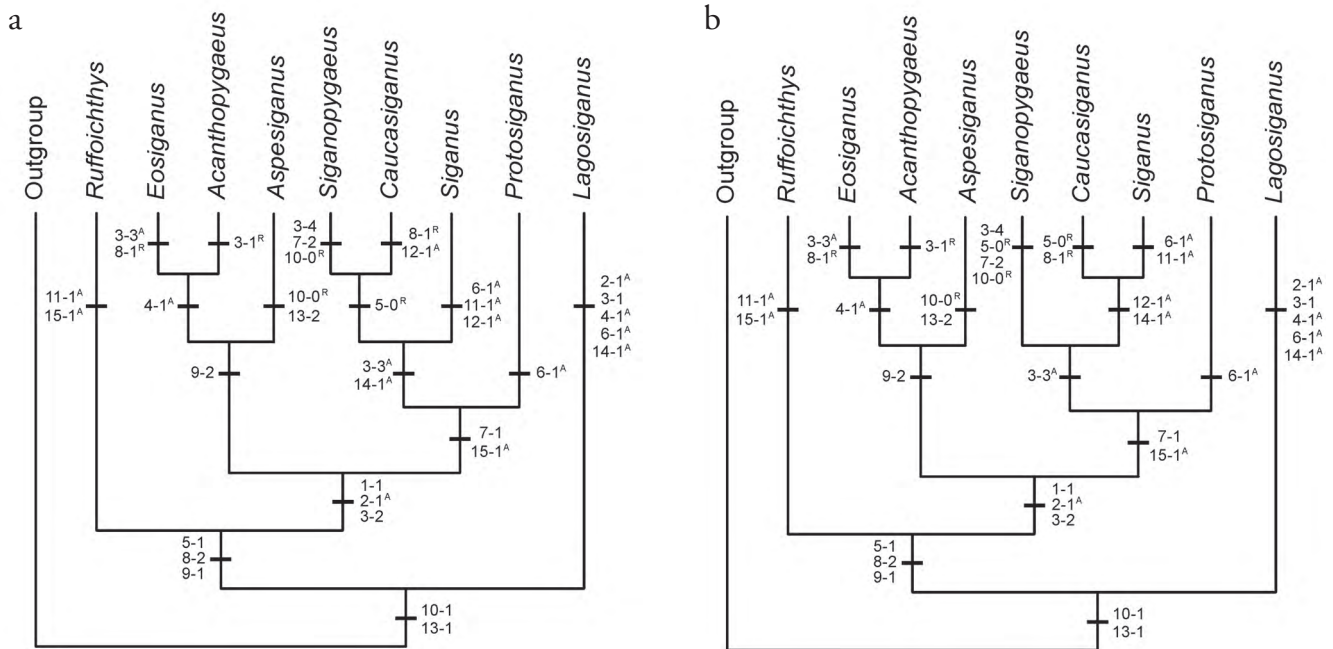
Fig. 10 a, b – Two equally most parsimonious cladograms produced by the ordered analysis of the data-set. Character numbers are separated by a hyphen from the character state numbers, and correspond to those used in the section of the text on "Characters Used in the Phylogenetic Analysis". Reversals are indicated by an uppercase R and independent acquisitions are indicated by an uppercase A to the right of the character state numbers.

analysis single tree and the Tyler and Bannikov (1997) ordered analysis indicates the same topology of the tree regarding the five genera included in both analyses, with the only exception being that *Eosiganus* is the basal sister group and *Ruffoichthys* the next sequential clade in our analysis, whereas *Ruffoichthys* was the most basal genus and *Eosiganus* was the next sequential clade in the Tyler and Bannikov (1997) ordered analysis.

Moreover, the comparison between our ordered-analysis consensus tree and the Tyler and Bannikov (1997) ordered analysis indicates the same topology of the tree regarding the five genera included in both analyses. Also in this case, there is a single difference in the position of *Protosiganus*, which is the sister group of the (*Siganopygaeus* + *Siganus*) clade in our analysis, whereas in the Tyler and Bannikov (1997) ordered analysis *Protosiganus* is the sister group of *Siganus,* with *Siganopygaeus* being the sister group of the (*Protosiganus* + *Siganus*) clade.

This comparison regarding the (*Protosiganus* + *Siganus*) clade is also true for the four Tyler and Bannikov (1997) unordered results because this clade is the only resolved relationship in the strict consensus of these trees.

Finally, we realize that the phylogenetic conclusions of our analysis are relatively weak because the Bremer value for each node is 1.

Conclusions

The two new genera of siganids from the Eocene of Russia (Gorny Luch locality) described herein and the referral of a genus from the Eocene of Italy (Monte Bolca locality) to the Siganidae significantly expand the known morphological and systematic diversity of this family. Our phylogenetic analysis of what are now the eight fossil genera of siganids and of the single extant genus also requires some changes in our understanding of how these genera are related to one another. Tyler and Bannikov (1997) indicated that the two species of *Ruffoichthys* constituted the most basal clade of siganids, and subsequently Bannikov and Tyler (2002: 43) provided additional morphological support for the basal placement of *Ruffoichthys*, recognizing it as the Ruffoichthyinae distinct from all of the other siganids, as the Siganinae. With the addition here of the new genus *Lagosiganus*, which possesses as many plesiomorphic features as are found in *Ruffoichthys*, to our phylogenetic analysis, such a subfamilial distinction is no longer tenable. *Lagosiganus* is shown herein in several of our analyses to be the most basal siganid genus, or it is shown to be a basal member of a clade that is sister to the clade in which *Ruffoichthys* is basal. Thus, in the expectation that even more new taxa of fossil siganids

will be discovered in the foreseeable future, recognition of subfamilies at this time is premature.

We note that the eight presently known genera of fossil siganids are far more morphologically diverse than are the extant members of the family, although the single living genus (*Siganus*) contains two subgenera and numerous species. This situation of a far greater diversity of the fossils at the generic level relative to the taxa living today also applies to most of the other families of acanthuroid fishes. For example, the several genera and species of fossil luvaroids represent two families (Luvaridae+Kushlukiidae) (Bannikov and Tyler, 1995, 2001), in stark contrast to the single extant species (*Luvarus imperialis*, see Tyler et al., 1989) of this clade. The genera of fossil Acanthuridae far outnumber the six genera that are such prominent components of coral reef environments today, and, additionally, there are several exclusively fossil sister clades to the extant acanthuroids (Blot and Tyler, 1991; Tyler, 2005a, 2005b; Tyler and Bannikov, 2005). Only the diversity of the Zanclidae, with a single extant species and one from the Eocene has changed little over time, and one suspects that it is only sampling error responsible for the meager fossil record, and that additional fossil taxa will be forthcoming. Conspicuous as acanthuroids are in today's marine ichthyofauna, most of the families of this major clade of perciforms were far more diverse at the generic level in the past, especially in the Eocene.

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