The postcranial skeleton of *Proterorhinus marmoratus* with remarks on the relationships of the genus *Proterorhinus* (Teleostei: Gobiidae)

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The postcranial osteology of the Ponto-Caspian tubenose goby *Proterorhinus marmoratus* is described and its relevance to the systematic position of *Proterorhinus* is discussed. *Proterorhinus marmoratus* differs significantly from the gobioids of the Ponto-Caspian and Atlantic-Mediterranean in the anterior displacement of the origin of the first dorsal fin. The first dorsal-fin pterygiophore of the tubenose goby inserts in the second interneural space between the neural spines of the second and third vertebrae. The first pterygiophore of the other gobioids inserts in the third interneural space between the neural spines of the third and fourth vertebrae. The increased number of precaudal and caudal vertebrae and the dorsal pterygiophore formula starting with 2-12 in *Proterorhinus marmoratus* are derived character states. This 2-12 starting sequence and a single interneural space anterior to the first dorsal-fin pterygiophore are unique for gobioids and autapomorphies of *Proterorhinus*. It is proposed that *Proterorhinus* be placed in the subfamily Gobiinae.

**KEYWORDS:** Ponto-Caspian, Gobiidae, *Proterorhinus*, taxonomy, osteology, vertebrae, unpaired fins.

**Introduction**

The Ponto-Caspian genus *Proterorhinus* Smitt, 1900 has been repeatedly recognized as a subgenus of *Gobius* Linnaeus, 1758 or of *Neogobius* Ilijin, 1927 (summarized in Vasil’eva, 1999; Simonovic, 1999). Recently Ahnelt and Duchkowitsch (2001), based on the external characters of the lateral line system, separated *Proterorhinus* from *Gobius* and suggested a closer relationship to *Neogobius sensu* Miller (1986).

To discriminate *Proterorhinus* from *Gobius* and *Neogobius* features such as the shape of the anterior nostril, dorsal rays of the pectoral fin free or within the membrane, neuromast pattern of the lateral line system on the head and the trunk and the number of vertebrae have been used by various authors (summarized in Vasil’eva, 1999; Simonovic, 1999; Ahnelt and Duchkowitsch, 2001). The cranial osteology of species of *Gobius*, *Neogobius* and *Proterorhinus* has been described extensively (summarized in Vasil’eva et al., 1993; Simonovic, 1999; Vasil’eva, 1999).
but the postcranial skeleton has been mostly only considered for relationships as far as it concerned the number of vertebrae. Vasil’eva (1999) did not consider the total number of vertebrae as a character to separate the genera *Gobius*, *Neogobius* and *Proterorhinus*.

*Neogobius* and *Proterorhinus* have been assigned either to the subfamily Gobionellinae or to the Gobiinae (Pezold, 1993; Simonovic, 1999; Larson, 2001; Ahnelt and Duchkowitsch, 2001). Birdsong et al., (1988) did not assign *Neogobius* to one of their genus-groups, and Pezold (1993) subsumed this genus within the Gobionellinae. *Proterorhinus* was not considered in either study. Simonovic (1999) placed *Neogobius* and *Proterorhinus* ‘in a close relationship with the Gobiinae’. Larson (2001) also suggested a close relationship of *Neogobius* to the Gobiinae.

A feature that separates the Gobiinae from the Gobionellinae is the development of the interorbital canals of the cephalic lateral line system and the anterior interorbital pores. A fused interorbital canal with a single anterior interorbital pore (apomorphic) is characteristic for the Gobiinae, whereas in the Gobionellinae this canal and the anterior interorbital pore are paired (plesiomorphic) (Pezold, 1993; McKay and Miller, 1997). From the number of interorbital pores, Pezold (1993) seemingly implied the number of interorbital canals. Ahnelt and Duchkowitsch (2001) discussed the variability of the number of anterior interorbital pores for *Neogobius* and *Proterorhinus*, and showed that even in a fused interorbital canal paired anterior interorbital pores may occur.

Characters of the postcranial skeleton have been regularly used in the phylogeny and affinities of gobioid fishes (summarized in Pezold, 1993; Hoese and Gill, 1993; McKay and Miller, 1997). Combinations of these characters are given by Birdsong et al., (1988). *Proterorhinus marmoratus* (Pallas, 1814), a common Ponto-Caspian species, differs from all these gobioids in a combination of characters of the postcranial skeleton.

**Material, methods and abbreviations**

*Systematics.* Endemic Ponto-Caspian gobiids of ‘Sarmatic’ origin have only been partly included in classifications of gobiid fishes during the last 10–15 years (Birdsong et al., 1988; Harrison, 1989; Pezold, 1993; Nelson, 1994; Akihito et al., 2000). They are characterized by several specializations, e.g. loss of swimbladder, modified ctenoid scales or increased numbers of vertebrae (Iljin, 1930; Kryzanowski and Ptschelina, 1941; Berg, 1949). *Asra, Anatirostrum, Benthophiloides, Benthophilus, Caspiosoma* and *Mesogobius, Neogobius, Proterorhinus*, respectively, are considered in this study as genus-groups (benthophilines and neogobiines) within the Gobiinae sensu Pezold (1993). The genus *Neogobius* is defined sensu Miller (1986).

*Nomenclature.* According to Berg (1949) *Proterorhinus* contains two valid species, *P. marmoratus* and *P. semipellucidus* (Kessler, 1877). The latter species is based on a single specimen from the mouth of the Karasu River, Azerbaijan, Caspian Sea. The holotype is probably lost (Eschmeyer et al., 1998). As long as the validity of *P. semipellucidus* is not confirmed we follow Miller (1990) and treat *Proterorhinus* as a monotypic genus. The following results and discussion of *Proterorhinus* deal with *P. marmoratus*.

Recently, Mihalcescu and Nalbant (2000) assigned *Neogobius kessleri* (Günther, 1861) to a new genus, *Mullerigobius*. The designation of this new genus is based on an unpublished phylogenetic study of A.-M. Mihalcescu (Mihalcescu and Nalbant, 2000). The authors list a few meristic characters but do not discuss why
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these features separate the genus from the other genera. Therefore we still consider *N. kessleri* as a species of the genus *Neogobius sensu* Miller (1986).

We refer to the following osteological features: haemal arches, haemal and neural spines, pterygiophores of the dorsal and anal fins, precaudal and caudal vertebrae, parapophysis of precaudal vertebrae, and pleural ribs. A detailed osteological description (cranial and postcranial skeleton) of *Neogobius* and *Proterorhinus* is in preparation by Duchkowitsch and Ahnelt.

**Vertebral number.** The total number of vertebrae equals precaudal (abdominal) vertebrae plus caudal vertebrae. Precaudal vertebrae are defined as vertebrae without closed haemal arches, caudal vertebrae as vertebrae with parapophyses joined at their ends, forming an arch (Birdsong *et al.*, 1988; Rojo, 1991). The definition of the precaudal vertebrae as vertebrae without closed haemal arches is imprecise. Gobiids may have at least the parapophysis of the ultimate precaudal vertebra joined by a bony bridge, forming a narrow arch, but their ends not joined. We define the first caudal vertebra of *Proterorhinus marmoratus* as a vertebra with closed hemal arch plus hemal spine.

**Dorsal pterygiophore formula.** Follows Birdsong *et al.*, (1988). The first digit indicates the interneural space into which the first pterygiophore of the first dorsal fin inserts, the last digit indicates the ultimate interneural space anterior to the first pterygiophore of the second dorsal fin. The first interneural space is defined as the space between the neural spines of the first and second vertebra.

**Anal pterygiophores anterior to the first haemal spine.** We define the first caudal vertebra with completely closed haemal arch and with haemal spine. Otherwise the terminology follows Birdsong *et al.*, (1988).

**Pleural ribs.** Number and position to corresponding vertebrae are given.

**Abbreviations.** APT1, first pterygiophore of the anal fin; D1PT1, D1PT6, first and sixth pterygiophore of the first dorsal fin; D2PT1, first pterygiophore of the second dorsal fin; HS, haemal spine; IS, interneural space; NS, neural spine; PAP, parapophysis; PR, pleural rib; PT, pterygiophore; VT, vertebra.

**Institutions.** CAS, California Academy of Sciences, San Francisco; IZUW, Institut für Zoologie der Universität Wien, Vienna; NMC, Canadian Museum of Nature, Ottawa; NMW, Naturhistorisches Museum Wien, Vienna.

We studied 38 specimens from three watersheds settled by populations of *Proterorhinus marmoratus*, which have been isolated from each other since at least the end of the last ice age: the Danube River system which discharges into the Black Sea, the Maritsa/Evros River system which discharges into the Aegean Sea and rivers falling into the south Caspian Sea. The specimens were radiographed, cleared and stained (Dingerkus and Uhler, 1977) and skeletons disarticulated (Mayden and Wiley, 1984). Length of specimens is given in standard length and caudal fin length in mm, d = damaged. Sex is indicated when determined.

Radiographs: 25 specimens. CAS 162216, one female, 56.1 + 13.0 mm, Romania, fishpond at Nucet near Tirgoviste, 15 November 1962, P. Banarescu. NMC 70-0530, two specimens out of 66, 56.3 + 18.5 to 57.6 + d, Iran, Gilan Prov., Nahang-Rougha River, tributary of Rostoe-Khale, 8 April 1962, V. D. Vladykov. NMC 70-0542, two specimens out of five, 50.9 + 16.9 to 57.8 + d, Gilan Prov., Old Safid River estuary, July 1981. B. W. Coad. NMW 29536-29540, three males, 62.8 + 17.5 to 66.0 + 17.9 and one female, 56.9 + 17.2, Bulgaria, near Philippopol [Plovdiv, Maritsa River sytem], [December] 1894, F. Steindachner. NMW 29553-29558, four males, 62.8 + 16.5 to 66.0 + 16.9, Bulgaria, near Plovdiv [Philippopol, Maritsa River sytem],
Results

Postcranial skeleton

Vertebrae. Including urostyle 32–33 (32: 22 specimens, 33: 14); 12–13 precaudal (12: 35, 13: 1) and 20–21 caudal (20: 20 specimens, 21: 16); generally VT11 and VT12 (penultimate and ultimate precaudal vertebrae) with a narrow haemal arch, VT13 first vertebra with a haemal arch and first haemal spine (first caudal vertebra). Five of 14 specimens have two caudal vertebrae fused, each lacking a half centrum (posterior and anterior, respectively), but always in a different combination: VT23/24, VT26/27, VT28/29, VT30/31, VT31/32. Parapophyses of precaudal vertebrae are of about equal size but their positions are gradually changing from lateral to ventral. Parapophyses of ultimate precaudal vertebra not broad. First caudal vertebra with parapophyses joined at their ends and with first haemal spine (figure 1).

The parapophysis of the two posteriormost precaudal vertebrae (VT11–VT12: seven specimens), less frequently those of the last three vertebrae (VT10–VT12: two specimens) or of one vertebra (VT11: two specimens, VT12: one), are joined by a bony bridge and form a narrow haemal arch, but with their tips not fused (figure 1). This feature is variable, nevertheless, in nine of 12 cleared and stained specimens, the parapophyses of at least two precaudal vertebrae are connected by a bony bridge and form a narrow arch, which surrounds the caudal aorta, but not the caudal vein. From the first caudal vertebra posteriorly both blood vessels are enclosed by haemal arches formed by the parapophyses (haemapophyses), which are completely fused at their ends. Gobies from the north-eastern Atlantic and the Mediterranean display lower numbers of vertebrae and none or one, the ultimate, precaudal vertebra with similar fused parapophyses (see appendix). More than one precaudal vertebra with fused parapophyses is possibly the apomorphic character state. Clothier (1946) described a similar type of precaudal vertebrae for juveniles of the east Pacific goby Clevelandia ios (Jordan and Gilbert, 1882) with this feature vanishing in adults.

Dorsal pterygiophore formula. 2-121110 \( (n=20) \), 2-122010 \( (n=7) \), 2-112110 \( (n=4) \), 2-122110 \( (n=1) \), 2-221110 \( (n=1) \) and in five additional specimens starting with 2-12, but the insertion of the more posterior pterygiophores not clear from
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**Fig. 1.** (A–C) Three posteriormost precaudal vertebrae and (D) first caudal vertebra (anterior views) of *Proterorhinus marmoratus*, female, 57.8 ± 13.3 mm, Danube near Vienna. Parapophyses of the penultimate and ultimate precaudal vertebra connected by a bony bridge forming a narrow canal surrounding the caudal aorta but not the caudal vein. Scale: 2 mm.

Radiographs (figures 2, 3). In all specimens the first dorsal-fin pterygiophore inserts in the second interneural space between second and third neural spine. *Proterorhinus marmoratus* is the only known gobiod species with the first PT of the first dorsal fin inserting in the second interneural space (dorsal pterygiophore formula starting with 2-1). The first PT inserting in the third interneural space (dorsal pterygiophore formula starting with 3-2 or 3-1) is likely the plesiomorphic character state and is found in the most basal gobiods *Rhyacichthys* and *Butis*, as well as in eleotrids, odontobutids and gobiods with two dorsal fins and the first one not displaced posteriorly (Birdsong et al., 1988; Hoese and Gill, 1993; Larson, 2001).

A single interneural space without a pterygiophore occurs between the last PT of the first and the first PT of the second dorsal fins, characterized by 0 at the end of the dorsal pterygiophore formula (figures 2, 3). The posteriormost PT of the first dorsal fin inserts between the neural spines of VT6 and VT7, the first PT of the second dorsal fin between the neural spines of VT8 and VT9. This implies that a precaudal vertebra has been added between VT8 and the first caudal vertebra and, in addition, that the origin of the first dorsal fin has been displaced forward, but not the fin as a whole (see below). Additional vertebra(e) between VT8 and the posteriormost precaudal vertebra displace the anal fin posteriorly, its first PT lining up now with a more posterior PT of the second dorsal fin but do not affect the origin of the second dorsal fin.
Eight vertebrae anterior to the first PT of the second dorsal fin is also found in Gobiidae with the plesiomorphic 10 or 11 precaudal vertebrae (Miller, 1981; Akihito et al., 1984; Birdsong et al., 1988; McKay and Miller, 1991, 1997; Ahnelt et al., 2000). Ten precaudal vertebrae are plesiomorphic in gobiine genera endemic to the Atlantic-Mediterranean gobiid fauna (Miller, 1981; McKay and Miller, 1997). Higher values of precaudal vertebrae are found in Gobius (11), Neogobius (12–14) and Proterorhinus (12). The latter two genera diverged from the Gobius lineage and speciated from each other in the upper Miocene about 5 million years ago (Dillon and Stepien, 2001). Possibly, the addition of a precaudal vertebra in Gobius and an additional one in Neogobius and Proterorhinus always occurred posterior to VT8 and anterior to the ultimate precaudal vertebra. Thus, independent of whether 10–14 precaudal vertebrae are present, the first PT of the second dorsal fin inserts in the interneural space between the neural spines of VT8 and VT9, and that at least the ultimate precaudal vertebra has fused parapophyses forming a narrow haemal arch. Such modified precaudal vertebrae with narrow haemal arches are found in Proterorhinus (generally two or three) (figure 1) but also in Zebrus (10 precaudal vertebrae, the last modified), and in Gobius (11 precaudal vertebrae, the last modified).

As a result of additional precaudal vertebrae in Proterorhinus and Neogobius, the first PT of the anal fin successively lines up with a more posterior PT of the second dorsal fin: in species with 10 precaudal vertebrae (e.g. Zebrus, Didogobius, Gammogobius and Corcyrogobius) with the third PT of the second dorsal fin, in species with 11 precaudal vertebrae (Gobius) with the fourth PT, in species with 12 precaudal vertebrae (Proterorhinus) with the fifth PT and in species with 13–14 precaudal vertebrae (Neogobius) with the sixth or seventh PT of this fin.
In the 'sand-goby' group (Pomatoschistus, Gobiusculus, Knipowitschia and Economidichthys) the precaudal vertebral number is also high, in the majority of species it is 12 (McKay and Miller, 1997). But contrary to Proterorhinus additional vertebrae must have been added between the pterygiophores of the two dorsal fins which resulted in (1) at least two interneural gaps between the dorsal-fin pterygiophores, (2) a dorsal PT formula ending with 100, (3) second dorsal and anal fins displaced posteriorly but (4) the first pterygiophore of the anal fin still lining up with the third PT of the second dorsal fin, and (5) first PT of the second dorsal fin inserting in an interneural space posterior to VT9. This combination of characters, with additional ones listed by McKay and Miller (1997), separates the 'sand-gobies' from the gobiine and neogobiine stocks.

If the entire first dorsal fin had been displaced anteriorly in Proterorhinus, there would be a second gap between the first and the second dorsal fins, as in the 'sand-gobies'. But seemingly only the first three pterygiophores of the first dorsal fin have been displaced anteriorly: the first PT from the third into the second interneural space, the third PT from the fourth into the third interneural space, and consequently the second PT from its posterior position to an anterior one in the third interneural space. In some specimens with the pterygiophore sequence 2-122010 the fifth PT was displaced anteriorly into the fourth interneural space leaving an interneural space without PT between the neural spines of VT5 and VT6 (figure 3). Obviously
the PT sequence 2-12 derived from 3-22. The variability of the insertion of PT2 to PT6 supports this assumption.

An anteriorly displaced origin of the first dorsal fin by the loss of one of the first three vertebrae is unlikely. It would require a combination of following features: (1) 2-22 as initial sequence of the dorsal pterygiophore formula, (2) first pleural rib inserting on parapophysis of second vertebra and (3) seven vertebrae anterior to first PT of the second dorsal fin or backward shift of the second dorsal fin. But in Proterorhnius the dorsal pterygiophore formula starts with 2-12, the first pleural rib inserts on the parapophysis of the third vertebra (see below), eight vertebrae are present anterior to the first PT of the second dorsal fin and only one interneural gap between the PT of the two dorsal fins. At least a second interneural gap would be the consequence of a posterior displacement of the second dorsal fin.

The dorsal pterygiophore formula of one specimen from the Danube catchment area (CAS 162216) starts with 2-22 instead of the characteristic 2-12 sequence. This specimen has seven instead of the typical six spinous rays in the first dorsal fin. The additional fin ray is supported by an additional pterygiophore and both are placed at the anterior origin of the first dorsal fin, which causes the aberrant pterygiophore formula of 2-22110.

For P. marmoratus from rivers in north-eastern Greece and the Evros/Maritsa River system a dorsal pterygiophore formula starting with 3-22 is mentioned by Economidis and Miller (1990). All specimens from the Maritsa River (Bulgaria) and a river from north-eastern Greece investigated by one of us (H. A.) display the typical starting sequence 2-12 (except for one specimen with 2-11).

Anal-fin pterygiophores. One or two pterygiophores anterior to first haemal spine (1: 1; 2: 35), which line up with the fifth PT of the second dorsal fin (figure 2).

By adding an additional precaudal vertebra, the anal fin was displaced posteriorly with the first pterygiophores lining up with the fifth PT (apomorphic) instead with the fourth PT (Gobius) (plesiomorphic) of the second dorsal fin. Both character states are apomorphic compared with the insertion below the third pterygiophore of the second dorsal fin of species with the plesiomorphic 10 precaudal vertebrae (Miller, 1981; McKay and Miller, 1997).

Pleural ribs. Eight to nine (eight: one specimen, on both sides; nine: nine, on both sides) pleural ribs attached to corresponding parapophyses of VT3–VT11 (to VT10 in the specimen with eight pleural ribs) (figure 2).

Proterorhnius marmoratus is characterized by following derived characters in the postcranial skeleton: (1) increased vertebral number (32-33), 12 (mode) precaudal and 20–21 caudal vertebrae, (2) a dorsal pterygiophore formula starting with 2-12 (mode), (3) initial dorsal pterygiophore sequence of 12 (rarely of 11), (4) a single interneural space anterior to the first pterygiophore of the second dorsal fin and (5) the first pterygiophore of the anal fin lining up with the fifth pterygiophore of the second dorsal fin. The anterior displacement of the first dorsal fin in combination with only a single interneural space anterior to the second dorsal fin and the PT formula starting with 2-12 are autapomorphies of Proterorhnius.

Discussion

The classification of the Ponto-Caspian and Atlantic-Mediterranean gobiid faunas has been a matter of debate for more than a decade (Pinchuk, 1991; Simonovic, 1999; Vasil’eva, 1999; Ahnelt and Duchkowitsch, 2001).
About 13–12 million years ago (Middle Miocene), when the Paratethys was a sea with reduced salinity and high endemism (Rögl, 1998), an ancestral Ponto-Caspian endemic neogobiine stock may have differentiated from an Atlantic-Mediterranean gobine stock (Miller, 1990; McKay and Miller, 1991). The Neogobius–Proterorhinus stock developed independently from the recent Gobius stock that invaded Mediterranean basins after restoration of the Mediterranean Sea about 5 million years ago (Simonovic et al., 1996; Simonovic, 1999). This fits well with Dillon and Stepien (2001) who suggested that the neogobiines evolved from the Gobius lineage during the Middle Miocene, and then speciated into Neogobius and Proterorhinus after the Mediterranean salinity crisis in the Late Miocene about 5 million years ago (Rögl and Steininger, 1983). We will not review this geological event and refer to Bianco (1990), Ahnelt et al., (1995) and Simonovic (1999) for further information.

The Atlantic-Mediterranean gobines and the Ponto-Caspian neogobiines are monophyletic sister groups (Miller, 1990; Simonovic, 1999). With a dorsal-fin pterygiophore formula starting with 3-22, one epural and two to three anal pterygiophores anterior to the first caudal vertebra, Neogobius possesses similar character states as Gobius, but differs from the latter in the higher total number of vertebrae (33–35 versus 28) and in the numbers (mode) of precaudal and caudal vertebrae (12–14+21–22 versus 11+17) (Birdsong et al., 1988; Simonovic et al., 1996; Simonovic, 1999; Duchkowitsch, unpublished). Proterorhinus shares the same features in the caudal fin skeleton and the position of the anal-fin pterygiophores as these two genera, but is closer to Neogobius in the total number of vertebrae (32–33 versus 32–35). It differs from both genera in the pterygiophore formula starting with 2-12 versus 3-22 and from Gobius in the number of precaudal vertebrae (12 versus 11).

Our data reveal a unique position of Proterorhinus within the Mediterranean and Ponto-Caspian gobiid fauna. Proterorhinus marmoratus displays a modified (derived) position of the first dorsal-fin pterygiophores that results in a dorsal-fin pterygiophore formula starting with 2-12. We hypothesize that the insertion of the first dorsal-fin pterygiophore anterior to the third neural spine and the dorsal-fin pterygiophore sequence 2-12 is a result of the anterior displacement of the origin of the first dorsal fin. Furthermore, we believe this represents a derived (apomorphic) condition. The pterygiophore sequence 12 has evolved independently of the 12 sequence of the ‘sand-gobys’ (McKay and Miller, 1997) and of the 12 sequence in the Croatian populations of Padogobius martensii (Günther, 1861) (Bianco and Miller, 1990). A posteriorly displaced first dorsal fin occurs in eleotrids and gobids (Birdsong et al., 1988; Pezold, 1993), but we are not aware of gobiods with an anteriorly displaced first dorsal fin.

Insertion of the first pterygiophore of the second dorsal fin between the neural spines of VT8 and VT9 and insertion of the first PT of the anal fin between the parapophyses of VT10 (last abdominal vertebra) and the haemal spine of VT11 (first caudal vertebra) in combination with the lining up of the latter with the third PT of the second dorsal fin is herein hypothesized as the plesiomorphic character state for Gobiidae. An increased number of vertebrae (>27) is apomorphic. If vertebrae are added anterior to VT8, the origins of the second dorsal and anal fins are displaced posteriorly. Adding vertebrae posterior to VT8 does not affect the origin of the second dorsal fin but shifts the origin of the anal fin posteriorly. The latter situation occurs in Neogobius and Proterorhinus. We hypothesize that in both
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genera, vertebrae have been added between VT8 and the first caudal vertebra, but in differing numbers. This resulted in a more (Neogobius) or less (Proterorhinus) posterior shift of the anal fin.

We propose to place Proterorhinus in the Gobiinae (sensu Pezold, 1993) based on the following combination of characters: (1) one epural, (2) two anal-fin (pre-hemal) pterygiophores anterior to the first caudal vertebra, (3) interorbital portion of the anterior oculoscapular canal fused and (4) anterior interorbital pore and oculoscapular canal terminating in a pair of posterior nasal pores. The high number of precaudal and caudal vertebrae and the dorsal pterygiophore sequence starting with 2-12 are specializations within the Gobiinae. Also noteworthy are the closed parapophyses of the two (mode) posteriormost precaudal vertebrae. All these characters are hypothesized to be apomorphic within the Gobius–Neogobius–Proterorhinus complex, and it appears likely that Proterorhinus developed from a neogobiine stock.

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Appendix

Comparative material

Number of vertebrae (total, precaudal, caudal), insertion of first pterygiophore of second dorsal fin between neural spines of the seventh and eighth vertebrae, and lining up of first anal-fin pterygiophore with pterygiophores of second dorsal fin (from radiographs and from cleared and stained specimens). Species with the parapophyses of the ultimate precaudal vertebra connected by a bony bridge forming a narrow haemal arch but with their tips free are indicated by an asterisk. This feature was not discernible from radiographs.

North-eastern Atlantic and Mediterranean species

Corcyrogobius liechtensteini (Kolombatovic, 1891)*, IZUW uncatalogued (four specimens); Didogobius splechtmai Ahnelt and Patzner, 1995*, IZUW uncatalogued (one spm); Gammogobius steinitzi Bath, 1971*, IZUW uncatalogued (three spms); Gobius bucchichi Steindachner, 1870*, IZUW uncatalogued (one spm); Gobius cobitis Pallas, 1814*, NMW 93733, IZUW uncatalogued (two spms); Gobius cruentatus Gmelin, 1879, CAS 101983 (two spms); Gobius niger Linnaeus, 1758, CAS 101970, NMW 93778 (four spms); Gobius paganellus Linnaeus, 1758*, IZUW uncatalogued (two spms); Thorogobius ephippiatus (Lowe, 1839), CAS 62428 (one spm); Zebrus zebrus (Risso, 1826)*, IZUW uncatalogued (one spm); Zosterisessor ophiocephalus (Pallas, 1814), CAS 58326, IZUW uncatalogued (four spms).

Ponto-Caspian species

Neogobius sp. (cephalargoides? Pinchuk, 1976), CAS 62205 (three specimens); Neogobius fluviatilis (Pallas, 1814), CAS 62211, IZUW uncatalogued (five spms);
Neogobius gynnostrachelus  (Kessler, 1857)*, CAS 22973, CAS 62210, IZUW uncatalogued (seven spms); Neogobius kessleri (Günther, 1861)*, CAS 23423, CAS 62208, IZUW uncatalogued (28 spms); Neogobius melanostomus (Pallas, 1814)*, CAS 62209, IZUW uncatalogued (five spms), Neogobius ratan (Nordmann, 1840), CAS 162206 (one spm); Neogobius syrman (Nordmann, 1840), CAS 23433, CAS 62207 (four spms).

References


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