

# Revision of Sanzo's head lateral-line system (HLLS) classification and nomenclature based on its re-evaluation of almost all native Mediterranean and European Atlantic marine gobies

(Teleostei, Actinopterygii, Gobiidae)

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The head lateral-line system (HLLS) is one of the most useful external characters for the taxonomy of gobies, but it is complex and, therefore, difficult to exploit. Sanzo's system was published in 1911 and has remained until today the only universal and complete system of classification and nomenclature both for the head lateral-line canals with pores and for the sensory papillae rows of gobies in general. It was based on the study of Mediterranean and European Atlantic marine gobies. Today, the native species count of the area is four times larger than the 17 species studied by Sanzo and the number of genera is 2.5 times larger. In more than a century of application, Sanzo's classification and nomenclature for taxonomy has never been reviewed or updated despite numerous published inconsistencies, conflicts and proposed individual changes. Thus, a review of HLLS of the Mediterranean and European Atlantic native marine gobies covering all genera and species of these marine areas is presented here. It is based on the evaluation of published descriptions of HLLS of native marine gobies of these seas in combination with the new data based on new material. For some species and for the genus *Crystallogobius* Gill, 1863, HLLS was studied for the first time and also the HLLS nomenclature was applied to some other taxa for the first time, although a sketch of the head lateral line system had been published before for those. Based on the HLLS review, a revised, simplified and consistent classification and nomenclature is presented for Mediterranean and European Atlantic marine gobies which takes into account the increased variability and complexity found over the last century; and it attempts to both consolidate nomenclature and to maintain stability, appreciating the long and widespread use of Sanzo's original system until today. Careful adaptations of the original system include: The graphemes in names of pores and of rows are now in the normal line of type only. The graphemes in names of pores and of rows are kept in italics for distinguishing them from the rest of the text in HLLS descriptions. The names and abbreviations of head canals established in the last half of century are kept. Sanzo's use of Greek letters for names of canal pores is preserved, changed only in selected cases, expanded in order to enable unique identification of pores present in neozoan species for Europe and changed to remedy the use of the same Greek letter for different pores. Sanzo's original topographical grouping of sensory papillae rows in seven head areas remained the same. The use of the same letter as a name previously applied consistently for different sensory papillae rows is replaced by a different letter. These row names are either based on letters (English alphabet), which had not already been used by Sanzo, or alternatively, they are a combination of two letters, with rows sharing the

first one only if closely related. Row names with a letter followed by a number for distinguishing rows are kept only for rows typically or originally occurring as a single row, which appear longitudinally divided or transversely multiplied. Papillae appearing on the place of a secondarily lost canal, usually larger and individual, are named differently from other rows. The main goal of this revision is to update a highly useful tool for the practical identification of a valuable set of characters in gobiid systematics and taxonomy. It is not intended as a contribution to general goby anatomy.

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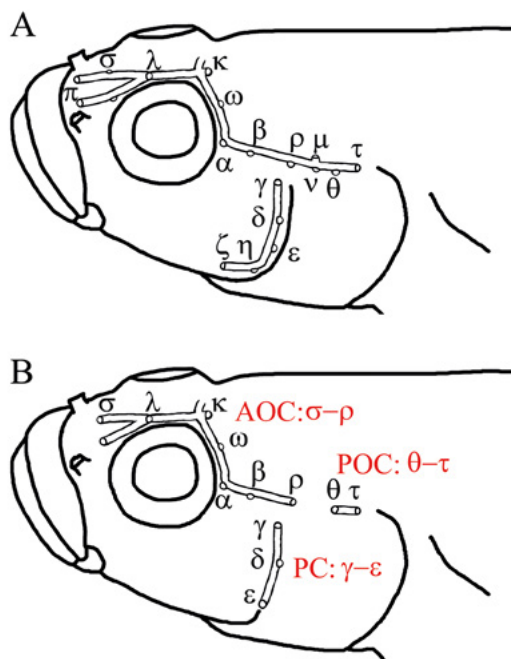
## Introduction

The family Gobiidae, with 2093 presently valid species, is the largest fish family (Fricke et al. 2023a). Gobiidae is also, with 70 species native species (Table 1) and 16 alien species, the most species rich family of the Mediterranean and the European Atlantic (Kovačić & Patzner 2011, Kovačić et al. 2022, Mavruk et al. 2022). Fortunately, the gobiid external morphology represents a rich source of characters that can be used for species identification of numer-

ous gobiid species. The most complex set of useful external characters of gobies is the head lateral-line system (HLLS) (Miller 1986).

The head lateral-line sensory canals in the family Gobiidae sensu Miller (1973a), i.e. matching up to eight out of nine Gobiiformes families recognized today (Fricke et al. 2023a), is a reduced version of the generalized teleost pattern, with, at most, supra-orbital, postorbital, supratemporal and preopercular sections on the head only (Miller 1973a, Takagi 1988, Shibukawa et al. 2001) (Fig. 1A). Only few exceptions with a body lateral canal are known from the ninth family, Ryacichthyidae, with its two genera, and in the genus *Tereteleotris* Shibukawa, Iwata & Viravong, 2001, a member of the family Odontobutidae. On the head, a supratemporal section can be found in some Butinae and Xenthismidae (Akihito et al. 1984) (Fig. 1A).

The mechanoreceptive organs of the lateral-line sensory system in teleosts are not only found enclosed in canals, but also as superficial neuromasts exposed on the head and body surface (Wongrat & Miller 1991). Contrary to the greatly reduced canal system, gobies show a great variety of free superficial neuromasts (= sensory papillae) patterns distributed over the cheek, snout, nape, lower jaw, operculum and body. These are mostly organized as distinguishable rows (Miller 1973a). The pattern of head canals with canal pores and the pattern of head rows of sensory papillae together represent a rich source of externally visible morphological characters with high taxonomically usable information content. Distinguishable row characters concern, e.g., row presence, size, orientation, shape, position relative to other rows or to body surface landmarks, the number of papillae in a row, and the shape and size of individual papillae. HLLS pattern is mostly consistent within species, but may differ by at least some characters even between closely related species. The taxonomic value of these patterns in gobioid systematics was first recognized by Sanzo (1911). Sanzo's (1911) work described HLLS of several Mediterranean and European Atlantic marine gobies,



**Fig. 1.** A. All canals and pores in stylized gobiid head. B. Regular maximum development of canals and pores in European gobies, except for genus *Deltentosteus*. Abbreviations: AOC, the anterior oculoscapular canal; POC, posterior oculoscapular canal; PC, preopercular canal. Pore terminology in text. Drawings by M. Kovačić.

**Table 1.** Native genera and species of Mediterranean and European Atlantic marine gobies. \*, species studied by Sanzo (1911); ^, species of native genera, which are not present in the Mediterranean Sea and European Atlantic Ocean. Mediterranean and European Atlantic marine species are listed first, then the others.

Clades	Genera	Species
Aphia-lineage	<i>Aphia</i>	<i>Aphia minuta</i> Risso, 1810
Pomatoschistus-lineage	<i>Buenia</i>	<i>Buenia affinis</i> Iljin, 1930* <i>Buenia jeffreysii</i> (Günther, 1867) <i>Buenia massutii</i> Kovačić, Ordines & Schliewen, 2017 <i>Buenia lombartei</i> Kovačić, Ordines & Schliewen, 2018
Gobius-lineage	<i>Chromogobius</i>	<i>Chromogobius britoi</i> Van Tassell, 2001 <i>Chromogobius quadrivittatus</i> (Steindachner, 1863)* <i>Chromogobius zebratus</i> (Kolombatović, 1891)
Gobius-lineage	<i>Corcyrogobius</i>	<i>Corcyrogobius liechtensteini</i> (Kolombatović, 1891) <i>Corcyrogobius lubbocki</i> Miller, 1988^ <i>Corcyrogobius pulcher</i> Kovačić, Wirtz & Schliewen, 2020^
Pomatoschistus-lineage	<i>Crystallogobius</i>	<i>Crystallogobius linearis</i> (Von Düben, 1845)
Pomatoschistus-lineage	<i>Deltentosteus</i>	<i>Deltentosteus collonianus</i> (Risso, 1820) <i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)*
Gobius-lineage	<i>Didogobius</i>	<i>Didogobius bentuvii</i> Miller, 1966 <i>Didogobius schlieweni</i> Miller, 1992 <i>Didogobius kochi</i> Van Tassell, 1988^ <i>Didogobius lanceolatus</i> Schliewen, 2023^
Gobius-lineage	<i>Gammogobius</i>	<i>Gammogobius steinitzi</i> Bath, 1971
Gobius-lineage	<i>Gobius</i>	<i>Gobius ater</i> Bellotti, 1888 <i>Gobius auratus</i> Risso, 1810* <i>Gobius bucchichi</i> Steindachner, 1870* <i>Gobius cobitis</i> Pallas, 1814* <i>Gobius couchi</i> Miller & El-Tawil, 1974 <i>Gobius cruentatus</i> Gmelin, 1789* <i>Gobius fallax</i> Sarato, 1889 <i>Gobius gasteveni</i> Miller, 1974 <i>Gobius geniporus</i> Valenciennes, 1837* <i>Gobius incognitus</i> Kovačić & Šanda, 2016 <i>Gobius kolombatovici</i> Kovačić & Miller, 2000 <i>Gobius niger</i> Linnaeus, 1758* <i>Gobius ophiocephalus</i> (Pallas, 1814) <i>Gobius paganellus</i> Linnaeus, 1758* <i>Gobius roulei</i> de Buen, 1928 <i>Gobius vittatus</i> Vinciguerra, 1883 <i>Gobius xanthocephalus</i> Heymer & Zander, 1992 <i>Gobius xoriguer</i> Iglésias, Vukić & Šanda, 2021 <i>Gobius ateriformis</i> Brito & Miller, 2001^ <i>Gobius rubropunctatus</i> Delais, 1951^ <i>Gobius salamansa</i> Iglésias & Frotté, 2015^ <i>Gobius senegambiensis</i> Metzelaar, 1919^ <i>Gobius tetraphthalmus</i> Brito & Miller, 2001^
Gobius-lineage	<i>Gymnesigobius</i>	<i>Gymnesigobius medits</i> Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019
Pomatoschistus-lineage	<i>Knipowitschia</i>	<i>Knipowitschia caucasica</i> (Berg, 1916) <i>Knipowitschia panizae</i> (Verga, 1841) <i>Knipowitschia byblisia</i> Ahnelt, 2011^ <i>Knipowitschia caunosii</i> Ahnelt, 2011^ <i>Knipowitschia iljini</i> Berg, 1931^

**Table 1.** Continued.

Clades	Genera	Species
		<i>Knipowitschia longecaudata</i> (Kessler, 1877) <sup>^</sup>
		<i>Knipowitschia mermere</i> Ahnelt, 1995 <sup>^</sup>
		<i>Knipowitschia milleri</i> (Ahnelt & Bianco, 1990) <sup>^</sup>
		<i>Knipowitschia montenegrina</i> Kovačić & Šanda, 2007 <sup>^</sup>
		<i>Knipowitschia radovici</i> Kovačić, 2005 <sup>^</sup>
		<i>Knipowitschia ricasolii</i> (Di Caporiacco, 1935) <sup>^</sup>
		<i>Knipowitschia thessala</i> (Vinciguerra, 1921) <sup>^</sup>
Pomatoschistus-lineage	<i>Lebetus</i>	<i>Lebetus guilleti</i> (Le Danois, 1913)
		<i>Lebetus patzneri</i> Schliewen, Kovačić & Ordines, 2019
		<i>Lebetus scorpioides</i> (Collett, 1874)
Aphia-lineage	<i>Lesueurigobius</i>	<i>Lesueurigobius friesii</i> (Malm, 1874)*
		<i>Lesueurigobius sanzoi</i> (de Buen, 1918)
		<i>Lesueurigobius suerii</i> (Risso, 1810)*
		<i>Lesueurigobius koumansii</i> (Norman, 1935) <sup>^</sup>
		<i>Lesueurigobius heterofasciatus</i> Maul, 1971 <sup>^</sup>
Gobius-lineage	<i>Marcelogobius</i>	<i>Marcelogobius splechnai</i> (Ahnelt & Patzner, 1995)
		<i>Marcelogobius helenae</i> (van Tassell & Kramer, 2014) <sup>^</sup>
		<i>Marcelogobius janetorum</i> (Schliewen, Wirtz & Kovačić, 2018) <sup>^</sup>
Gobius-lineage	<i>Millerigobius</i>	<i>Millerigobius macrocephalus</i> (Kolombatović, 1891)
Gobius-lineage	<i>Neogobius</i>	<i>Neogobius melanostomus</i> (Pallas, 1811)
		<i>Neogobius caspius</i> (Eichwald, 1831) <sup>^</sup>
		<i>Neogobius fluviatilis</i> (Pallas, 1814) <sup>^</sup>
		<i>Neogobius pallasii</i> (Berg, 1916) <sup>^</sup>
Pomatoschistus-lineage	<i>Ninnigobius</i>	<i>Ninnigobius canestrinii</i> (Ninni, 1883)*
		<i>Ninnigobius montenegrensis</i> (Miller & Šanda, 2008) <sup>^</sup>
Gobius-lineage	<i>Odondebuena</i>	<i>Odondebuena balearica</i> (Pellegrin & Fage, 1907)
Gobius-lineage	<i>Peter</i>	<i>Peter amicuscaridis</i> (Schliewen & Kovačić, 2008) <sup>^</sup>
		<i>Peter wirtzi</i> (Schliewen & Kovačić, 2008) <sup>^</sup>
Pomatoschistus-lineage	<i>Pomatoschistus</i>	<i>Pomatoschistus adriaticus</i> Miller, 1973
		<i>Pomatoschistus anatoliae</i> Engin & Innal, 2017
		<i>Pomatoschistus bathi</i> Miller, 1982
		<i>Pomatoschistus flavescens</i> (Fabricius, 1779)*
		<i>Pomatoschistus knerii</i> (Steindachner, 1861)
		<i>Pomatoschistus lozanoi</i> (de Buen, 1923)
		<i>Pomatoschistus marmoratus</i> (Risso, 1810)*
		<i>Pomatoschistus microps</i> (Krøyer, 1838)
		<i>Pomatoschistus minutus</i> (Pallas, 1770)
		<i>Pomatoschistus nanus</i> Engin & Seyhan, 2017
		<i>Pomatoschistus norvegicus</i> (Collett, 1903)
		<i>Pomatoschistus pictus</i> (Malm, 1865)
		<i>Pomatoschistus quagga</i> (Heckel, 1840)*
		<i>Pomatoschistus tortonesei</i> Miller, 1968
Pomatoschistus-lineage	<i>Pseudaphya</i>	<i>Pseudaphya ferreri</i> (de Buen & Fage, 1908)
Pomatoschistus-lineage	<i>Speleogobius</i>	<i>Speleogobius llorisi</i> Kovačić, Ordines & Schliewen, 2016
		<i>Speleogobius trigloides</i> (Zander & Jelinek, 1976)
Gobius-lineage	<i>Thorogobius</i>	<i>Thorogobius ephippiatus</i> (Lowe, 1839)
		<i>Thorogobius macrolepis</i> (Kolombatović, 1891)
		<i>Thorogobius alvheimi</i> Sauberer, Iwamoto & Ahnelt, 2018
		<i>Thorogobius angolensis</i> (Norman, 1935) <sup>^</sup>
		<i>Thorogobius laureatus</i> Sauberer, Iwamoto & Ahnelt, 2018 <sup>^</sup>

**Table 1.** Continued.

Clades	Genera	Species
Gobius-lineage	<i>Vanneaugobius</i>	<i>Thorogobius rofeni</i> Miller, 1988 <sup>^</sup>
		<i>Vanneaugobius dollfusi</i> (Brownell, 1978)
		<i>Vanneaugobius pruvoti</i> (Fage, 1907)
Gobius-lineage	<i>Zebrus</i>	<i>Vanneaugobius canariensis</i> Van Tassell, Miller & Brito, 1988 <sup>^</sup>
		<i>Zebrus pallaoroi</i> Kovačić, Šanda & Vukić, 2021
		<i>Zebrus zebrus</i> (Risso, 1826)*

hereby providing a first general classification and nomenclature of the system. In the following century and later on, the system was widely applied to European gobies in species diagnoses, species descriptions and in the identification keys. The most prominent European gobiologists during that period, e. g. F. de Buen, B. S. Iljin, P. J. Miller and H. Ahnelt, applied Sanzo's head lateral-line system classification and nomenclature in individual taxonomical works, but also in their gobiid reviews (de Buen 1923a, Iljin 1930, Miller 1986). However, at the same time, this set of characters, at least the pattern of superficial sensory papillae, was mostly ignored during the 20<sup>th</sup> century as a characters set for taxonomic studies of Indo-Pacific gobies, with the exception of Japanese goby works (Takagi 1988, Wongrat & Miller 1991). As to be expected, the much larger diversity of higher taxa and species richness of Indo-Pacific gobies translates into a comparatively higher character diversity of their head lateral-line system patterns. This probably generated the impression for authors dealing with Indo-Pacific gobies that Sanzo's system is not applicable there because of a seemingly erratic distribution and a lack of identifiable pattern of superficial sensory papillae. Nevertheless, up to today HLLS is still the crucial set of morphological characters for the identification of Mediterranean and European Atlantic marine gobies. In the last Mediterranean key for the family Gobiidae, the entries using head lateral-line system characters represent 44% of the total entries used in the key (Kovačić et al. 2022). Every single species of ten species described in the last decade in the Mediterranean, except *Lebetus patzneri* Schliewen, Kovačić & Ordines 2019, has head lateral-line system characters as part of its diagnosis (species descriptions are reviewed in Kovačić et al. 2022). The commonly cited reference for the application of the Sanzo's classification over the last four decades has been Miller's (1986) key in the checklist for the North-eastern Atlantic and the Mediterranean marine gobies. This treatment features in the Introduction a short paragraph and one figure with two drawings and the figure legend, explaining shortly head lateral-line system of gobies. Since then, Sanzo

(1911) was rarely cited alone, indicating that the authors have rarely gone back to the original source for details, i. e. mostly used Miller's summary as the shortcut (e. g. Kovačić 2020).

Several alternative nomenclature systems of head canals and pores in addition to Sanzo's (1911) have been proposed by different authors: Takagi (1957), Takagi (1988), Akihito et al. (1984), Hoese & Allen (1990) (for illustration with pore name abbreviations of the Hoese & Allen (1990) nomenclature system, see Hoese et al. (2017)). Among the proposed alternatives, only the one of Akihito et al. (1984) is well established and often applied, and both Sanzo (1911) and Akihito et al. (1984) are commonly used until today, Sanzo mostly for European gobies, Akihito et al. usually for Indo-Pacific species.

In contrast to canals and pores, for the classification and nomenclature of head sensory papillae rows no alternative system other than Sanzo's (1911) has been established that would be widely applicable. Takagi (1988) provided a nomenclature and abbreviations for the "typical" arrangement of the "pit-line system", i. e. head rows of sensory papillae of gobioid fishes. However, his framework is restricted to the longitudinal row pattern restricted to only a limited number of gobiid genera. Furthermore, there are additional proposals for genus specific nomenclature systems of sensory papillae rows by some authors. Barlow (1961) provided a system of sensory papillae row names and abbreviations for *Gillichthys* Cooper, 1864. Akihito & Meguro (1975a) provided the system of numbers for distinguishing sensory papillae rows for *Glossogobius* Gill, 1859 and Akihito & Meguro (1975b) provided another different numbering system for *Callogobius* Bleeker, 1874. Finally, Hoese (1983) provided a nomenclature and abbreviations for part of sensory papillae rows of *Acentrogobius* Bleeker, 1874 and *Glossogobius*.

Sanzo's (1911) classification of sensory papillae rows was based on their positions on the body surface, although Sanzo himself admitted he wished to group the rows rather by patterns of innervation ("Le denominazioni di tali gruppi sono state dettate dalla sede stessa che essi occupano; sarebbe stato mio

desiderio di aggruppare le varie serie secondo i rami d'innervazione, ma le mie ricerche a questo riguardo non sono tutt' ora complete ed ho dovuto attenermi solo al primo criterio"). However, the innervation pattern of HLLS remains rather poorly known. It was studied for one member of Odontobutidae and three members of Butidae by Wongrat & Miller (1991), i. e. gobies that are not native to European waters. They found that some topographic groups of Sanzo (1911) have mixed nerve supply, and that some rows from different topographic groups are innervated by the same nerve trunk. The same was found later also for Gobiidae (Ahnelt & Bohacek 2004, Asaoka et al. 2012). Wongrat & Miller (1991) derived from their studied odontobutid and butid taxa an alternative grouping of rows based on putative homologies derived from nerve innervations rather than on Sanzo's (1911) topographic approach. Indeed, the homology of the individual rows among different species could be estimated from the innervation pattern, but to be widely applied many additional row innervation case studies would be needed for each of the compared species groups. Unfortunately, only a few studies of the innervation of sensory papillae rows for only a minor selection of the about two thousand gobiid species exists (Ahnelt & Bohacek 2004, Asaoka et al. 2012). Since no other known method could test homology of the individual rows among different taxon groups, up to today papillae rows are still identified and labelled as the same in different species just based on the topographic positions, and to some degree also on similar orientation or shape. Thus, only the topographic groups as proposed by Sanzo (1911) are widely used for the classification and nomenclature of papillae rows (for the review of recent Mediterranean species descriptions, all using Sanzo's (1911) topographic groups, see Kovačić et al. 2022).

The terminology used for head canals with pores and head rows of sensory papillae in the present paper follows Miller (1986). The canals and pores match Sanzo's (1911) "canali mucosi con forami" for head canals with pores and the papillae match "le serie delle papillae cutanee" or "le serie delle organi ciatiformi". For these terms various English synonyms have been used in different publications, i. e.: for the head lateral-line system: "sensory line system" (Takagi 1957); "cephalic lateral line system" (Asaoka et al. 2012); "cephalic sensory system" (Bogorodsky et al. 2011); for head canals: "sensory canals" (Takagi 1957); "cephalic canals" (Miller 1961); for sensory papillae: "pit organs" (Takagi 1957); "epipores" (Barlow 1961); "neuromast organs" (Miller 1961), "ciathiform organs" (Miller 1986); "genipores" (Miller 1986); "free neuromasts" (Ahnelt 2001); "superficial neuromasts" (Miller & Vasil'eva 2003).

The Sanzo's (1911) work was based on only one fourth of the presently known native species diversity of the area, i. e. 17 gobiid species out of presently known 70 marine species, and 9 genera out of the presently recognized 24 marine genera in the Mediterranean and European Atlantic (Table 1) (Kovačić & Patzner 2011, Kovačić et al. 2022). Furthermore, these 24 genera have additional 33 marine and freshwater species not present in the Mediterranean Sea and European Atlantic Ocean (Fricke et al. 2023b) (Table 1). Over more than a century of its use, problems for the application of Sanzo's (1911) classification and nomenclature have accumulated. Sanzo (1911) had named almost all rows in his illustrations, with only a few exceptions of unnamed ones (e. g. Tav. 9, figs 13 and 15, rows between *suborbital* rows *a* and *d*, Tav. 11, figs 29 and 36, rows above *oculoscapular* rows *as*, Tav. 12, fig. 39, rows intercepting *oculoscapular* row *x*). However, later applications of his nomenclature were sometimes incomplete to a different degree, e. g., often lacking names of some rows. For example, most *oculoscapular* and *opercular* rows in Ahnelt (1995), most *oculoscapular* rows in Miller (1993) and most papillae between row *q* and pore  $\rho 1$  in Kovačić & Miller (2000) had not been named. Further, rows were sometimes labelled by merging two original row names of Sanzo (1911) into one name composed of two row letters, e. g. as rows *xy*, *las* and *gm* in Miller (1963). Sometimes the naming of the same row was inconsistent across two papers of the same author (e. g. row *trp* in Ahnelt (1995) is row *tr* in Ahnelt (2011); the same in Kovačić et al. (2018a) and Kovačić & Schliewen (2008)). Even the original naming in Sanzo (1911) had produced some homonyms (e. g. two *tr* rows on Tav. 9, figs 11, 13, 15, 18, two *la* rows Tav. 9, figs 1, 15, Tav. 10, figs 19, 23, Tav. 11, fig. 32), or the same letter was used to name different but closely placed rows, but nevertheless distinguished by a single, double or triple prime symbol for numbering (e. g. *preorbital* rows *s'*, *s''* and *s'''*, *preorbital* rows *c'* and *c''* or *oculoscapular* rows *as*, *as'* and *as''*) or the same prime symbols but as subscripts (e. g. *preorbital* rows *c<sub>1</sub>* and *c<sub>2</sub>*). Finally, later authors replaced prime symbols with numbers in superscript or subscript (e. g. *preorbital* *c<sub>1</sub>*, *c<sub>2</sub>* and *c<sup>1</sup>*, *c<sup>2</sup>* (Miller 1961)), but this system was not any easier to follow and not any easier to label rows on illustrations.

Thus the aim of the present work is to revise and update Sanzo's (1911) fundamental work by 1) compiling and studying the application of Sanzo's classification and nomenclature in the published morphological descriptions of Mediterranean and European Atlantic native marine gobies, 2) studying the head lateral line system in the new original material of yet insufficiently or completely unexplored

Mediterranean and European Atlantic native marine gobies, as well as in gobies with an already described HLLS for comparing the new data with the published data, 3) by identifying inconsistencies or conflicts in identifying and naming of sensory papillae rows in these newly compiled data and, 4) by resolving all previous inconsistencies through consistent suggestions for changes of Sanzo's classification and nomenclature. Based on all this, a revised system of classification and nomenclature is proposed to cover the head lateral line system complexity found in Mediterranean and European Atlantic native marine gobies already treated by Sanzo (1911), but including also all later publications and taxa newly studied here.

## Material and methods

### Laboratorial methods

Preserved specimens stored in ethanol (approx. 70%) were studied immersed in water in large Petri dish with the stereomicroscope Olympus SZX10. When needed, the specimens were reversibly stained in 0.2% solution of Cyanine Blue 5R in distilled water (Saruwatari et al. 1997) to observe and study head lateral-line system details. The specimens were transferred with a plastic strainer from the preservative liquid to the jar with the stain solution and then to the water in the Petri dish; the soft strainer mesh avoids any surface damage on fragile and small individuals from handling by solid tools (e.g. forceps) or fingers. Specimens were dipped for 20 s in the stain solution, and if not stained sufficiently after visual inspection, dipped again for maximum of 40 s or 60 s of the total time. The 20 s dip is always sufficient for the study of squamation, head canals and pores and other skin structures. However, the study of rows of sensory papillae on head sometimes need extended staining as described. After staining and before inspection specimens were immersed in a jar with water to remove the excessive stain solution. Then they were transferred to a Petri dish with water, all with strainer. Enhanced visibility of the yet poorly visible rows of sensory papillae can be achieved by changing orientation angle of a specimen to provide a more lateral instead of a perpendicular observer view on the skin surface. In addition, moving the light source from a vertical to an angled position may better disclose the surface texture by the angled light beam. After head lateral-line system inspection, specimens were returned to ethanol solution; usually they should be completely unstained after 24 hours. If the ethanol solution has turned bluish in the meantime, depending on the fish mass to liquid quantity ratio, it should be replaced with fresh solution before returning the specimens to final storage. Details of head lateral-line system were photographed by Olympus SC180 camera with an Olympus U-TV0.5XC-3 camera adapter mounted on the stereomicroscope Olympus SZX10.

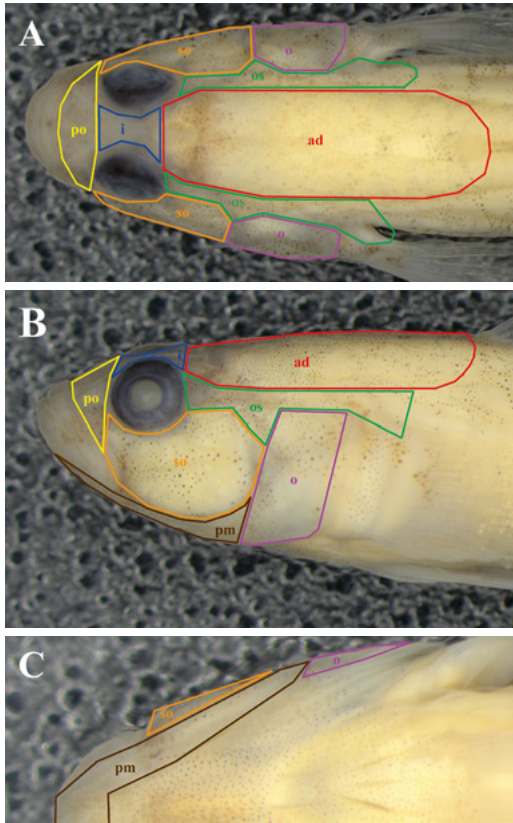
## Classification and nomenclature principles

Species names used by Sanzo's (1911), but nowadays in synonymy, were replaced with the presently valid species based on the synonymy for Sanzo's specimens in Miller (1973b), and their identity was rechecked by the study of HLLS characteristics as they were described and illustrated for these species in Sanzo's (1911) (Table 1). The generic and subfamily assignment and nomenclature followed Fricke et al. (2023b) (Table 1). Naming of phylogenetic lineages is based on Agorreta et al. (2013) (Table 1).

Considering the huge amount of published work applying Sanzo's HLLS classification and nomenclature up to date, the intention of this revision is to keep Sanzo's HLLS stable and preserved as much as possible; this in order to keep terminology used in previous publications easily comparable with the revised system proposed here. Therefore, the basic division and naming of the head canals and of the groups of rows in this revision remains the same as in Sanzo (1911) and Miller (1986), and this is the division explained below in Material and methods. Thus, most of Sanzo's (1911) and Miller's (1986) nomenclature remains the same; all revised parts of pore names and of the row classification and nomenclature are presented and explained in "General head lateral-line system pattern and the revision of Sanzo's classification and nomenclature" of the Results. Rows were identified and labelled as being the same across different species primarily based on their topographic positions, and, to some degree, on their similar shape or similar orientation, as in Sanzo (1911) and in later head lateral-line system later applications (Miller 1986).

The fully developed head canals pattern of European gobies is composed of the following entities: oculoscapular canal (OC; "canale oculo-scapolare" in Sanzo (1911)) and preopercular canal (PC; described as branch "ramo preopercolare" in Sanzo (1911)) (Fig. 1B). In most Gobiinae species the anterior and posterior parts of the oculoscapular canal (OC) are divided by the gap between pores  $\rho$  and  $\theta$ , with only a few exceptions (Ahnelt 2001). Therefore, each part with its pores is presented separately as the anterior oculoscapular canal (AOC) and posterior oculoscapular canal (POC), a practice with more than half of century of tradition (Miller 1961, 1986) (Fig. 1B). All present changes of head canals nomenclature are presented and explained in the Results.

Sanzo's (1911) classification was based on the sensory papillae row positions topographically grouped in seven head areas, i.e. as: (1) *preorbital* rows ("serie preorbitarie" in Sanzo (1911)) are placed on the snout, delimited anteriorly and laterally by the upper lip, posteriorly by the line connecting the anterior eye edges and continuing vertically from them to the upper lips (Fig. 2). (2) *suborbital* rows ("serie sott' orbitarie" in Sanzo (1911)) are placed from lower eye edge and upper preopercular edge dorsally down to the posterior upper lip and the ventrolateral head ridge ventrally. The rows are present anteriorly from the vertical of the anterior eye edge backwards to the preopercular posterior edge



**Fig. 2.** The approximate areas occupied by the seven groups of head sensory papillae rows: (po) preorbital rows; (so) suborbital rows; (pm) preoperculo-mandibular rows; (o) opercular rows; (os) oculoscapular rows; (ad) anterior dorsal rows; (i) interorbital rows. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Terminology in text. Photos and modifications by M. Kovačić.

(Fig. 2). (3) *preoperculo-mandibular* rows (“serie preoperculo-mandibulari” in Sanzo (1911)) are placed below the lower lip from the chin to below the angle of jaws and backwards along the ventrolateral head ridge and posterior mostly up to the lower part of the posterior preopercular edge (Fig. 2). (4) *opercular* rows (“serie opercolari” in Sanzo (1911)) are placed on the operculum (Fig. 2). (5) *oculoscapular* rows (“serie oculo-scapolari” in Sanzo (1911)) are placed from behind the eye, along the upper edge of the preopercle and operculum to around the upper edge of the pectoral fin base (Fig. 2). (6) *anterior dorsal* rows (“serie dorsali anteriori” in Sanzo (1911)) are placed on the nape and predorsal area extending anteriorly to the posterior eye edge and delimited posteriorly by the origin of the first dorsal fin (Fig. 2). (7) *interorbital* rows (“serie interorbitarie” in Sanzo (1911)) are placed between eyes (Fig. 2). The presented area delimitations are approximated on a

sketch in Fig. 2. The head sensory papillae rows are not, however, strictly limited to their areas since the rows can extend into neighbouring areas. For example, some *preorbital* rows in some species pass the eye line backwards, entering below the eye (e.g. row *ja*, Sanzo’s (1911) row *c*) or entering in the interorbital region (row *r*); or the *oculoscapular* rows in some species enter the anterior dorsal area, e.g. the row *tp* (Sanzo’s (1911) rows *tr* posterior) or rows *ka*, *kb* and *kc* (Sanzo’s (1911) rows *as*, *as’* and *as’’*) can extend dorsally far onto the nape. All changes of head sensory papillae row nomenclature suggested here are presented and explained in the Results.

### Specimens studied and the published data

HLLS was studied on all genera and species of the Mediterranean Sea and European Atlantic Ocean, and on almost all species of these genera from other regions or from freshwaters, if congeneric species that not occur in the Mediterranean Sea and European Atlantic Ocean exist elsewhere (see below) (Table 1). HLLS was evaluated for each species either based on specimen observations or on published information or, in most cases, on both sources.

The museum abbreviation for the studied material: PMR, Natural History Museum, Rijeka, Croatia; NMP, National Museum, Prague, Czech Republic; ZSM, Bavarian State Collection of Zoology, Munich, Germany.

The studied material ordered as in Table 1: *Aphia minuta* Risso, 1810: PMR VP5299, male, 41.2+8.3 mm; PMR VP5303, female, 42.4 mm standard length (SL), caudal fin damaged; PMR VP5305, female, 39.4+7.9 mm. *Buenia affinis* Iljin, 1930: PMR VP454, male, 28.8+5.5 mm; PMR VP455, male, 28+5.2 mm; PMR VP976, male, 31.7+6 mm; PMR VP977, male, 29.8+5.5 mm; PMR VP978, male, 29.5+5.4 mm; PMR VP979, three males, 23.9+4.9 to 27.7+4.9 mm; PMR VP980, female, 30.7+5.5 mm; PMR VP981, three females, 27.3+5.1 to 32+5.7 mm; PMR VP982, two females, 25.7+4.8 and 30.3+6.2 mm; PMR VP983, two females, 31.0+5.9 and 33.3+5.5 mm. *Buenia jeffreysii* (Günther, 1867): PMR VP3769, two males, 40.3+8.5 and 42.6+8.9 mm. *Buenia massutii* Kovačić, Ordines & Schliewen, 2017: PMR VP3762, male, 22.0+5.1 mm; PMR VP3763, female, 20.5+4.4 mm; PMR VP3765, male, 20.5+4.6 mm. *Buenia lombartei* Kovačić, Ordines & Schliewen, 2018: PMR VP4108, adult male, 27.5 mm SL, caudal fin damaged. *Chromogobius britoi* Van Tassell, 2001: NMP P6V 145465, female, 24.9+5.5 mm; NMP P6V 145466, male, 23.4+5.6 mm; NMP P6V 145467, juvenile of unidentified sex, 15.4+3.5 mm; NMP P6V 145468, female, 18.3+4.2 mm; NMP P6V 145469, male, 27.7+6.3 mm; NMP P6V 145470, male, 27.3+6.4 mm; NMP P6V 145471, female, 18.7+4.1 mm; NMP P6V 145472, female, 22.5 mm SL, caudal fin damaged; NMP P6V 145473, juvenile of unidentified sex, 16.6+3.9 mm. *Chromogobius quadrivittatus* (Steindachner, 1863): PMR VP3984, female, 38.4+8.3 mm. *Chromogobius zebratus* (Kolombatović, 1891): NMP P6V 140990, male, 20.0+5.4 mm; NMP P6V 140991, male, 20.3+5.4 mm; NMP P6V 140992, female,



31.7+7.8 mm; NMP P6V 142615, female, 35.9+8.4 mm; NMP P6V 142616, male, 25.9+6.2 mm; NMP P6V 142617, female, 25.2+6.1 mm; NMP P6V 144272, male, 37.9+9.1 mm; NMP P6V 144431, female; NMP P6V 144821, female, 30.3+6.9 mm; NMP P6V 144822, female, 30.1+7.9 mm; NMP P6V 144823, male, 21.8+5.8 mm; NMP P6V 145274, female, 25.9+5.5 mm. *Coryrogobius liechtensteini* (Kolombatović, 1891): PMR VP560, male, 21.0+4.7 mm; PMR VP2495, juvenile of unidentified sex, 9.9+2.1 mm; PMR VP2496, juvenile of unidentified sex, 7.6+1.9 mm; PMR VP2753, juvenile of unidentified sex, 7.5+2.0 mm; PMR VP2790, juvenile of unidentified sex, 8.7+2.1 mm; PMR VP4165, two females, 17.8+4.0 and 19.9+4.6 mm; PMR VP4668 male, 21.8+5.3 mm, and two females, 14.8+3.4 and 18.4+3.8 mm. *Coryrogobius lubbocki* Miller, 1988: ZSM-PIS-GO 1743, female, about 8 mm SL, caudal fin missing; ZSM-PIS-GO 1744, juvenile, 7.8 mm SL, caudal fin missing; ZSM-PIS-GO 1910, male; 11.0+1.9 mm. *Coryrogobius pulcher* Kovačić, Wirtz & Schliewen, 2020: ZSM45333, female, 21.2+4.5 mm; ZSM45330, female, 14.3+2.8 mm. *Crystallogobius linearis* (Von Düben, 1845): PMR VP4492, male, 30.3+4.5 mm; PMR VP5133, female, 21.6 mm SL, caudal fin damaged; PMR VP5135, male, 29.2 mm SL, caudal fin damaged; PMR VP5137, male, 23.5 mm SL, caudal fin damaged. *Deltentosteus colloninus* (Risso, 1820): PMR VP912, female, 47.2+8.4 mm; PMR VP1208, male, 46.5+8.3 mm. *Deltentosteus quadrimaculatus* (Valenciennes, 1837): PMR VP1018, female, 39.2+7.9 mm; PMR VP2453, female, 52.5+10.3 mm, and male, 53.2+10.5 mm. *Didogobius schlieweni* Miller, 1993: PMR VP756, female, 29.9+9.7 mm; PMR VP785, male, 39.1+11.1 mm. *Gammogobius steinitzi* Bath, 1971: PMR VP610, two females, 24.8+5.0 and 26.2+5.2 mm; PMR VP5322, female, 29.2+6.5 mm. *Gobius ater* Bellotti, 1888: PMR VP4403, male, 31.7+8.1 mm; PMR VP4407, male, 49.3+11.0 mm, and juvenile of unidentified sex, 26.5 mm SL, caudal fin damaged; PMR VP4408, male, 41.9+10.3 mm; PMR VP4409, female, 31.3+8.0 mm; PMR VP4410, male, 41.6+10.5 mm; PMR VP4411, three females, 28.5+7.2 to 29.0+7.1 mm; PMR VP4412, two males, 37.0+9.1 and 42.9+11.5 mm; PMR VP4414, two males, 43.9+10.5 and 48.6+10.2 mm; PMR VP4415, three females, 39.3+9.6 to 47.4+11.3 mm, and juvenile of unidentified sex, 22.8 mm SL, caudal fin damaged; PMR VP4416, male, 46.9+10.1 mm, and juvenile of unidentified sex, 19.8 mm SL, caudal fin damaged; PMR VP4417, two females, 44.8+9.7 and 45.9+10.7 mm, and juvenile of unidentified sex, 18.9 mm SL, caudal fin damaged. *Gobius auratus* Risso, 1810: PMR VP5635, four females, 31.2+7.8 to 36.2+8.8 mm, and male, 37.0+9.3 mm. *Gobius bucchichi* Steindachner, 1870: PMR VP3925, male, 53.9+12.7 mm; PMR VP5054, male, 44.6+11.2 mm. *Gobius cobitis* Pallas, 1814: PMR VP3672, female, 77.6+17.3 mm, and male, 87.6+18.5 mm. *Gobius couchi* Miller & El-Tawil, 1974: PMR VP811, two males, 52.4+12.3 and 53.8+12.3 mm; PMR VP812, male, 43.6+10.1 mm; PMR VP813, male, 43.9+10.4 mm; PMR VP814, male, 44.3+11.1 mm; PMR VP815, female, 51.7+12.3 mm; PMR VP816, female, 50.6+12.1 mm; PMR VP818, three males, 47.4+11.9 to

53.9+13.1 mm. *Gobius cruentatus* Gmelin, 1789: PMR VP1079, five juveniles of unidentified sex, 45.8+9.4 to 58.4+12.5 mm; PMR VP1080, seven juveniles of unidentified sex, 56.8+12.4 to 68.0+13.3 mm; PMR VP3669, two males, 107.1+25.8 and 112.9+28.5 mm. *Gobius fallax* Sarato, 1889: PMR VP4395, two juveniles of unidentified sex, 25.8+6.1 mm and 25.9 mm SL, caudal fin damaged; PMR VP4396, juvenile of unidentified sex, 23.6+6.3 mm; PMR VP4397, juvenile of unidentified sex, 22.5+5.9 mm; PMR VP4398, juvenile of unidentified sex, 24.8+6.3 mm. *Gobius gasteveni* Miller, 1974: PMR VP3703, male, 48.8+10.6 mm; PMR VP4373, juvenile female, 27.8+7.5 mm, and juvenile of unidentified sex, 20.8+5.3 mm. *Gobius geniporus* Valenciennes, 1837: PMR VP2486, three males, 48.6+10.7 to 51.8+11.0 mm; PMR VP2487, female, 44.8+10.5 mm; PMR VP2489, two males, 59.7+13.1 and 82.7+19.2 mm; PMR VP2494, two males, 54.2+12.8 and 58.5+14.4 mm; PMR VP2922, female, 94.8+21.3 mm. *Gobius incognitus* Kovačić & Šanda, 2016: PMR VP 2961, female, 40.4+10.4 mm; PMR VP2962, male, 46.6+11.5; PMR VP2963, two females, 65.2+15.6 and 76.1+17.7 mm; PMR VP5183, male, 44.7+10.3 mm. *Gobius kolombatovici* Kovačić & Miller, 2000: PMR VP636, female, 66.5+12.0 mm; PMR VP637, two males, 59.5+11.8 and 83.0+17.2 mm; PMR VP638, female, 68.3+13.9 mm; PMR VP639, two males, 60.7+11.8 and 72.3+15.2 mm; PMR VP641, male, 63.1+13.3 mm. *Gobius niger* Linnaeus, 1758: PMR VP3546, two females, 46.0+11.9 and 67.5+15.5 mm. *Gobius ophioccephalus* (Pallas, 1814): PMR VP3538, female, 79.9+19.6 mm; PMR VP5337, female, 85.6+22.9 mm. *Gobius paganellus* Linnaeus, 1758: PMR VP2503, male, 79.5+19.1 mm; PMR VP2935, male, 76.8+19.9 mm. *Gobius roulei* de Buen, 1928: PMR VP5330, female, 44.6+12.0 mm, and two males, 36.8+9.5 and 37.9+9.9 mm. *Gobius vittatus* Vinciguerra, 1883: PMR VP2499, two females, 21.2+4.8 and 22.4+5.6 mm; PMR VP5513, two females, 25.9+6.3 and 28.9+6.8 mm, and two males, 30.6+7.4 and 32.9+7.2 mm. *Gobius xanthocephalus* Heymer & Zander, 1992: PMR VP2934, three females, 38.8+9.6 to 58.3+13.9 mm. *Gobius xoriguer* Iglésias, Vukić & Šanda, 2021: PMR VP3587, female, 33.6+7.0 mm, and four males, 35.4 mm SL, damaged caudal fin, to 41.2+10.1 mm; PMR VP3829, female, 37.3+9.2 mm, and two males, 40.8 mm SL, damaged caudal fin and 44.1+9.5 mm; PMR VP3831, female, 35.2+7.5 mm, and two males, 36.7+8.1 and 39.7+10.0 mm; PMR VP3835, female, 40.2+9.9 mm; PMR VP5426, female, 53.3+12.2 mm; PMR VP5427, male, 47.7 mm SL, caudal fin damaged. *Gobius rubropunctatus* Delais, 1951: ZSM 45820, male, 58.1+17.6 mm. *Gymnesigobius medits* Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019: PMR VP4649, male, 42.6+11.1 mm; PMR VP4960, female, 25.7+6.1 mm; PMR VP4961, female, 38.3 mm SL, damaged caudal fin; PMR VP4963, male, 31.2+7.7 mm. *Knipowitschia caucasica* (Berg, 1916): PMR VP5618, female, 30.23+6.47 mm; PMR VP5619, female, 32.4+6.6 mm; PMR VP5621, male, 24.1+5.5 mm; PMR VP5622, female, 29.6+6.4 mm; PMR VP5623, female, 35.0+7.5 mm; PMR VP5624, male, 21.9+4.8 mm; PMR VP5625, male, 26.6+6.0 mm; PMR VP5920, male,

23.6 mm SL, caudal fin damaged at tips. *Knipowitschia panizzae* (Verga, 1841): PMR VP1024, seven males, 24.8+4.9 to 31.1+5.8 mm; PMR VP1027, four males, 18.5+3.8 to 34.7+7.4 mm; PMR VP1030, male, 24.5+4.6 mm; PMR VP1031, eleven female, 26.7+5.6 to 33.8+5.9 mm; PMR VP1040, six females, 27.4+4.4 to 31.2+5.7 mm; PMR VP1041, male, 27+4.7 mm; PMR VP4237, female, 28.0+6.7 mm. *Knipowitschia longecaudata* (Kessler, 1877): PMR VP4885, male 30.2+6.4 mm. *Knipowitschia milleri* (Ahnelt & Bianco, 1990): PMR VP3212, female, 27.2+6.5 mm. *Knipowitschia montenegrina* Kovačić & Šanda, 2007: NMP P6V 80366, male, 26.5+5.3 mm; NMP P6V 80370, male, 27.3+6.2 mm; NMP P6V 80371, female, 28.3+6.0 mm; PMR VP1600, four juveniles of unidentified sex, 17.2+3.5 to 19.9+4.0 mm. *Knipowitschia radovici* Kovačić, 2005: PMR VP1211, male, 27.9+6.5 mm; PMR VP1212, male, 27.2+6.6 mm; PMR VP1213, 17.8+4.4 mm. *Knipowitschia thesala* (Vinciguerra, 1921): PMR VP2914, three females, 34.8+7.9 to 37.1+8.1 mm. *Lebetus guilleti* (Le Danois, 1913): PMR VP1022, female, 17.4+4.3 mm; PMR VP4383, female, 11.6+3.3 mm; PMR VP4384, male, 9.8+2.7 mm; PMR VP4385, female, 9.0+2.6 mm; ZSM-PIS-G0-1227, male, 15.8 mm SL. *L. patzneri*: ZSM 46865, female, 16.8 mm SL, caudal fin damaged. *Lebetus scorpoides* (Collett, 1874): PMR VP5364, female, 29.8+7.2 mm. *Lesueurigobius friesii* (Malm, 1874): PMR VP4366, male, 56.8+17.0 mm. *Lesueurigobius sanzoi* (de Buen, 1918): PMR VP1670, two males 59.6 mm SL, damaged caudal fin and 60.7+17.9 mm. *Lesueurigobius suerii* (Risso, 1810): PMR VP2403, male, 32.4+10.0 mm. *Marcelogobius splechnai* Ahnelt & Patzner, 1995: PMR VP1713, female, 24.2+6.0 mm; PMR VP4703, two males, 24.7+5.7 and 34.6+7.3 mm. *Marcelogobius janetarum* Schliewen, Wirtz & Kovačić, 2018: ZSM 45303, male, 27.3+6.2 mm; ZSM 45302, juvenile, 18.2+4.9 mm; ZSM 40136, female, 24.7+5.7 mm; PMR VP4134, female, 22.8+5.5 mm. *Millerigobius macrocephalus* (Kolombatović, 1891): PMR VP1752, male, 20.0+5.1 mm. PMR VP2337, two females, 28.6+7.5 and 31.3+5.6 mm; PMR VP2338, six males, 30.6+7.9 to 41.3+10.2 mm. *Neogobius melanostomus* (Pallas, 1811): PMR VP2102, two females, 70.2+17.6 and 71.1+19.5 mm, and three males 52.1+14.3 to 68.6+17.5 mm. *Neogobius caspius* (Eichwald, 1831): PMR VP46340, female, 63.1+16.0 mm, and five males, 34.1+8.0 to 61.1+14.3 mm. *Neogobius fluviatilis* (Pallas, 1814): PMR VP3063, female, 90.0+19.1 mm, and male 90.5+19.4 mm. *Neogobius pallasii* (Berg, 1916): PMR VP4641, three females 53.7+12.2 to 58.1+13.1 mm, and seven males, 48.3+11.0 to 70.4+16.5 mm. *Ninnigobius canestrinii* (Ninni, 1883): PMR VP852, eight females, 31.8+6.5 to 37.2+6.9 mm, and two males, 33.7+7.3 mm and 34.0+7.4 mm; PMR VP853, two females, 23.5+4.3 and 23.7+4.5 mm, male, 27.1+5.5 mm, and juvenile of unidentified sex, 15.0+2.9 mm; PMR VP854, male, 26.1+5.7 mm; PMR VP998, three females, 27.9+5.7 to 33.7+6.9 mm, and six males, 24.3+5.4 to 42.8+7.3 mm; PMR VP999, four females, 35.7+7.7 to 37.2+7.2 mm; PMR VP1000, four females, 30.6+6.6 to 38.8+7.0 mm, and two males, 30.9+6.5 mm and 32.8+6.9 mm; PMR VP1001, three females, 29.3+5.7 to 33.7+6.0 mm, and three males, 23.8+4.6 to 31.9+

5.9 mm; PMR VP1112, three females, 26.8+5.5 to 28.2+6.2 mm, and three males, 27.1+5.9 to 36.5+7.6 mm; PMR VP1115, female, 31.3+5.7 mm, and five males, 24.8+5.3 to 40.9+8.4 mm; PMR VP1244, female, 27.2+5.9 mm, and male, 30.7+5.9 mm. *Ninnigobius montenegrinus* (Miller & Šanda, 2008): PMR VP2461, two females, 25.7+5.0 and 26.8+5.4 mm. *Odondebuena balearica* (Pelleggrin & Fage, 1907): PMR VP3466, female, 19.6+4.9 mm, and male, 22.1+5.9 mm; PMR VP4399, female, 16.9+4.6 mm; PMR VP4400, male, 20.2+5.2 mm; PMR VP4401, female, 19.7+5.8 mm; PMR VP4402, male, 25.0+6.6 mm; PMR VP4431, two females, 12.53 mm SL, caudal fin damaged and 13.3+3.9 mm; PMR VP4434, female, 17.9+4.7 mm, and two males, 13.9+4.2 mm and 18.2 mm SL, caudal fin damaged. *Peter amicuscaridis* Schliewen & Kovačić, 2008: ZSM 34186, male, 31.5+7.5 mm. *Peter wirtzi* Schliewen & Kovačić, 2008: ZSM 36566, male, 30.5+8.1 mm. *Pomatoschistus adriaticus* Miller, 1973: PMR VP3543, two females, 31.8+6.9 and 33.6+7.5 mm. *Pomatoschistus anatoliae* Engin & Innal, 2017: PMR VP3472, two males, 28.6+6.2 and 28.7+6.2 mm. *Pomatoschistus bathi* Miller, 1982: PMR VP3872, male, 31.6+7.0 mm; PMR VP3873, female, 31.0+6.5 mm; PMR VP3874, female, 30.1+6.2 mm; PMR VP3875, female, 29.9+6.5 mm. *Pomatoschistus flavescens* (Fabricius, 1779): PMR VP5100, female, 30.0+5.8 mm; PMR VP5120, male, 37.9+7.8 mm. *Pomatoschistus knerii* (Steindachner, 1861): PMR VP2460, male, 29.2+7.1 mm. *Pomatoschistus lozanoi* (de Buen, 1923): PMR VP4964, female, 47.1 mm SL, caudal fin damaged. *Pomatoschistus marmoratus* (Risso, 1810): PMR VP4722, two females, 43.0+8.9 and 45.3+10.4 mm; PMR VP5349, male, 28.1+5.4 mm. *Pomatoschistus microps* (Krøyer, 1838): PMR VP5359, female, 16.4+3.8 mm; PMR VP5362, male, 20.7+4.6 mm. *Pomatoschistus minutus* (Pallas, 1770): PMR VP5583, female, 44.4+8.1 mm; PMR VP5586, female, 52.2+11.0 mm. *Pomatoschistus nanus* Engin & Seyhan, 2017: PMR VP5612, female, 22.78+4.73 mm; PMR VP5613, female, 17.67+3.54 mm; PMR VP5614, male, 15.5+3.5 mm. *Pomatoschistus norvegicus* (Collett, 1903): PMR VP5628, female, 60.5+10.9 mm. *Pomatoschistus pictus* (Malm, 1865): PMR VP5404, female, 31.0+6.7 mm. *Pomatoschistus quagga* (Heckel, 1840): PMR VP2417, female, 38.4+6.9 mm. *Pomatoschistus tortonesei* Miller, 1968: PMR VP1911, female, 25.4 mm SL, caudal fin damaged. *Pseudaphya ferrerii* (de Buen & Fage, 1908): PMR VP5475, three females, 16.5+3.3 to 34.1 mm SL, caudal fin damaged. *Speleogobius llorisi* Kovačić, Ordines & Schliewen, 2016: PMR VP4356, female, 25.8+5.6 mm; PMR VP4357, male, 26.7+5.6 mm; PMR VP4377, male, 16.1+4.4 mm. *Speleogobius trigloides* (Zander & Jelinek, 1976): PMR VP3103, female 18.8+4.5 mm; PMR VP3331, male, 16.1+4.2 mm. *Thorogobius ephippiatus* (Lowe, 1839): PMR VP3518, two females, 48.7 mm SL, damaged caudal fin, and 60.8+13.9 mm, and 1 juvenile female 28.4+7.5 mm; PMR VP4672, female, 68.7+15.0 mm. *Thorogobius macrolepis* (Kolombatović, 1891): PMR VP5631, two females, 27.7+7.3 and 44.6+10.5 mm, and two males, 42.8+10.3 and 54.7+13.7 mm. *Vanneaugobius dollfusi* (Brownell, 1978): PMR VP1478, male, 31.1+8.0 mm; PMR VP1484, female,

30.2+7.8 mm; PMR VP4386, male, 21.5+5.7 mm; PMR VP5428, male, 38.8+ 8.6 mm; PMR VP5429, male, 34.4+ 8.6 mm. *Vanneaugobius canariensis* Van Tassell, Miller & Brito 1988: PMR VP5191, eight females, 23.8+6.3 to 34.1+8.1, and male, 31.5+7.9 mm. *Zebus pallaoroi* Kovačić, Šanda & Vukić, 2021: PMR VP5043, male, 26.7 mm SL, caudal fin damaged; PMR VP5093, female, 21.7+5.6 mm; PMR VP5094, male, 38.5+9.2 mm. *Zebus zebus* (Risso, 1826): PMR VP 1751, male, 23.4+ 5.0 mm. Among 104 species from 25 genera (the species of recently described tropical genus *Peter* Schliewen, 2023 are kept here), species without presently studied material are Mediterranean *Didogobius bentuvii* Miller, 1966 and *Vanneaugobius pruvoiti* (Fage, 1907); African Atlantic *Didogobius kochi* Van Tassell, 1988, *Gobius ateriformis* Brito & Miller, 2001, *Gobius salamansa* Iglésias & Frotté, 2015, *Gobius senegambiensis* Metzelaar, 1919, *Gobius tetrophthalmus* Brito & Miller, 2001, *Lesueurigobius koumansii* (Norman, 1935), *Lesueurigobius heterofasciatus* Maul, 1971, *Marcelogobius helenae* van Tassell & Kramer, 2014, *Thorogobius alveheimi* Sauberer, Iwamoto & Ahnelt, 2018, *Thorogobius angolensis* (Norman, 1935), *Thorogobius laureatus* Sauberer, Iwamoto & Ahnelt, 2018, *Thorogobius rofeni* Miller, 1988; and Ponto Caspian *Knipowitschia byblisia* Ahnelt, 2011, *Knipowitschia caunosii* Ahnelt, 2011, *Knipowitschia iljini* Berg, 1931, *Knipowitschia mermere* Ahnelt, 1995 and *Knipowitschia ricasolii* (Di Caporiacco, 1935).

HLLS published data of the Mediterranean and European Atlantic marine genera used in this study: *Aphia* Risso, 1827: Iljin (1930); de Buen (1931). *Buenia* Iljin, 1930: Sanzo (1911); de Buen (1923a); Kovačić (2002); Kovačić et al. (2017); Kovačić et al. (2018b). *Chromogobius* de Buen, 1930: Sanzo (1911); Miller (1971); Van Tassell (2001). *Corcyrogobius* Miller, 1972: Miller (1972); Miller (1988); Kovačić et al. (2020). *Crystallogobius* Gill, 1863: no published data. *Deltentosteus* Gill, 1863: Sanzo (1911); de Buen (1923a). *Didogobius* Miller, 1966: Miller (1966); Van Tassell (1988); Miller (1993); Schliewen et al. (2023). *Gammogobius* Bath, 1971: Bath (1971). *Gobius* Linnaeus, 1758: Sanzo (1911); de Buen (1923a); de Buen (1928a); de Buen (1928b); de Buen (1931); Delais (1951); Miller (1974); Miller & El Tawil (1974); Miller (1986); Heymer & Zander (1992); Ahnelt (2001); Brito & Miller (2001); Kovačić & Miller (2000); Pinchuk et al. (2004); Herler et al. (2005); Kovačić & Šanda (2016); Iglésias et al. (2015); Iglésias et al. (2021). *Gymnesigobius* Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019: Kovačić et al. (2019). *Knipowitschia* Iljin, 1927: Ahnelt & Bianco (1990); Economidis & Miller (1990); Ahnelt (1995); Ahnelt et al. (1995); Kovačić & Pallaoro (2003); Kovačić (2005a); Kovačić & Šanda (2007); Miller (2004); Miller & Pinchuk (2004); Ahnelt (2011); Ahnelt (2016). *Lebetus* Winther, 1877: Herler & Kovačić (2002); Schliewen et al. (2019); Kovačić et al. (2023). *Lesueurigobius* Whitley, 1950: Sanzo (1911); de Buen (1917); de Buen (1923a); de Buen (1923b); Maul (1971). *Marcelogobius* Schliewen, 2023: Ahnelt & Patzner (1995); Van Tassell & Kramer (2014); Schliewen et al. (2018). *Millerigobius* Bath, 1973: Bath (1973). *Neogobius* Iljin, 1927: Miller & Vasil'eva (2003). *Nimmigobius* Whit-

ley, 1951: Sanzo (1911); Kovačić (2005b); Miller & Šanda (2008). *Odondebuenia* de Buen, 1930: Miller & Tortonese (1968). *Peter* Schliewen, 2023: Schliewen & Kovačić (2008). *Pomatoschistus* Gill, 1863: Sanzo (1911); Fage (1915); de Buen (1923a); Miller (1969a); Miller (1973c); Miller (1982); Engin & Innal (2017); Engin & Seyhan (2017); Seyhan Öztürk & Engin (2019). *Pseudaphya* Iljin, 1930: de Buen (1931); Miller (1973d). *Speleogobius* Zander & Jelinek, 1976: Zander & Jelinek (1976); Kovačić et al. (2016). *Thorogobius* Miller, 1969: Miller (1969b); Miller (1988); Sauberer et al. (2018). *Vanneaugobius* Brownell, 1978: Brownell (1978); Van Tassell et al. (1988). *Zebus* de Buen, 1930: Sanzo (1911); Miller (1977); Kovačić et al. (2021). The data are summarized on all species of these genera, i.e. Mediterranean and European Atlantic marine species, as well as on members of these genera occurring in other marine regions and in freshwaters. Among 104 species from 25 genera (the former *Didogobius* species of recently described tropical genus *Peter* Schliewen, 2023 are kept here), species without the described lateral line system are European *C. linearis*; African Atlantic *G. senegambiensis*, *L. koumansii* and *T. angolensis*; Ponto Caspian *K. mermere*, *N. melanostomus*, *N. caspius* and *N. pallasi* (Table 1).

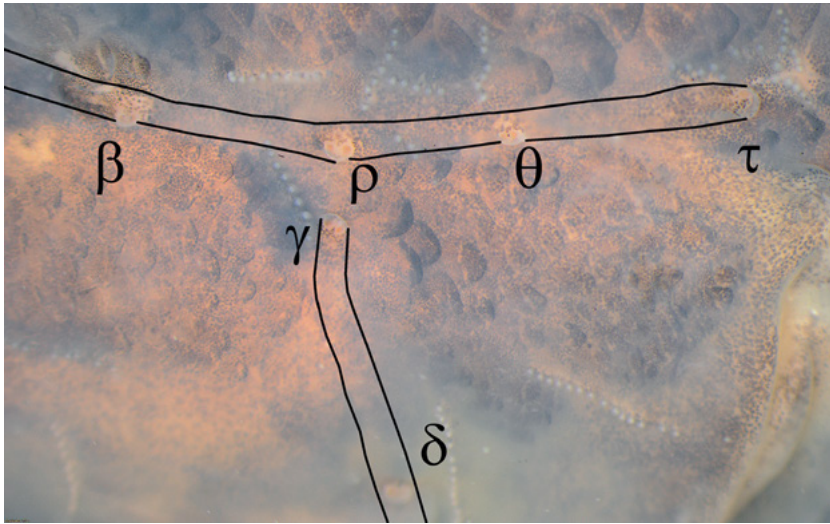
Combining available material and published results listed above, *G. senegambiensis*, *K. mermere*, *L. koumansii* and *T. angolensis* are the only species of studied genera with no data on their head lateral line systems. The original description of *K. mermere* contains just median preorbital and interorbital rows data (Ahnelt 1995).

## Results

### General head lateral-line system pattern and the revision of Sanzo's classification and nomenclature

#### General modifications of Sanzo's head lateral-line system nomenclature

The names of pores are based on the Greek alphabet, as in Sanzo's (1911) original. The names of the sensory papillae rows are based on the English alphabet. Sanzo's use of single, double or triple prime symbol, as well as later alternation of these symbols into subscript and superscript numbering (Miller 1986) is avoided and substituted for simplification, both in the names of pores and for the names of rows. All graphemes in names of pores and rows are therefore presented in the normal line of typing both in the text and on illustrations. Note that a published precedent for this already exists, see Ahnelt & Duchkowitsch (2001). The writing of names of pores and of sensory papillae rows in texts is kept in italics to keep them accentuated against the rest of the text and to avoid confusion with other single or pairs of letters and numbers in the text.



**Fig. 3.** OC continuous in *Gobius paganelus*. Pores marked and contour of the canal emphasized, terminology in text. Photo and modifications by M. Kovačić.

### Head canals and pores classification and nomenclature

Sanzo (1911) named the canal pores with the Greek letters, while Akihito et al. (1984) were the first to apply Latin capital letters to label them. An additional modification of the Sanzo nomenclature was applied by Miller, first in Miller & Vasil'eva (2003):  $\rho 1$  and  $\rho 2$  were renamed as  $\theta$  and  $\tau$ , probably to avoid the use of the same Greek letter for different pores. Hence, to complete Miller's (2003) modification of pore names, here the Greek letter  $\pi$  is proposed to replace  $\sigma'$  or  $\sigma 1$  for the anteriormost pore of AOC present in some non-European gobies (Fig. 1A). The use of the  $\sigma'$  as name for the anteriormost pore of AOC in some non-European gobies can be traced back to Miller (1986), and also Kovačić (2020) used  $\sigma 1$  to avoid a prime symbol in super script. Since pore  $\pi$  appears to be a plesiomorphy and a regular pore, although absent from European gobies, the only remaining nomenclature situation to be solved for the use of the prime symbol and superscript remains the naming of extra pores, e.g. pore  $\alpha'$  in Iglésias et al. (2015). We suggest to name those pores with numbers, e.g. as  $\alpha 1$  pore, to be consistent with the normal line of type applied everywhere else for HLLS nomenclature. Furthermore, in order to cover also the pores of the supratemporal canal (STC) and the pores of extended preopercular canal (Akihito et al. 1984), present in some non-European species of Gobiiformes, here four additional pores are proposed to be named and labelled using Greek letters (Fig. 1A). To provide an overview and enable

a comparison between them, all three nomenclatures are listed here side by side separated by a slash as follows: "system as proposed here (in bold)/Sanzo (1911) with historic updates/Akihito et al. (1984)"; a "\_" indicates that no comparative exists for the respective pore in Sanzo (1911) (Fig. 1A):

AOC with pores  $\pi/\sigma 1/A$ ,  $\sigma/\sigma/B$ ,  $\lambda/\lambda/C$ ,  $\kappa/\kappa/D$ ,  $\omega/\omega/E$ ,  $\alpha/\alpha/F$ ,  $\beta/\beta/G$ ,  $\rho/\rho/H$ ,  
 POC with pores  $\theta/\rho 1/K$  and  $\tau/\rho 2/L$ ,  
 PC with pores  $\gamma/\gamma/M$ ,  $\delta/\delta/N$ ,  $\epsilon/\epsilon/O$ ,  $\zeta/_/P$ ,  
 $\eta/_/Q$  and  
 STC with  $\mu/_/I$  and  $\nu/_/J$ .

The maximum development of canals and pores that occur in European native gobies is as follows: AOC with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ , POC with pores  $\theta$ ,  $\tau$ , PC with pores  $\gamma$ ,  $\delta$ ,  $\epsilon$  (Fig. 1B, Table 2).

Head canals with pores can be reduced or additional pores can occur. In addition, a few *Gobi* species have the OC continuous with a canal connecting AOC and POC between pores  $\rho$  and  $\theta$ , and with pores  $\rho$  and  $\theta$  opening ventrally instead of facing each other (Ahnelt 2001) (Fig. 3).

Reductions occur as two processes, either as the loss of an entire canal, with all regular pores still present in remaining canal(s), as seen in the *Gobius*-lineage species; or as loss of individual pores in the still existing canal or, for AOC canal, even as loss of part of existing canal, as it is widespread among species of the *Pomatoschistus*-lineage (Table 2). In the latter ones, the combination of the loss of entire canal with reduction of individual pores in the still existing canals is regularly present. The ultimate reduction is absence of all canals, as happened in both *Aphia-*

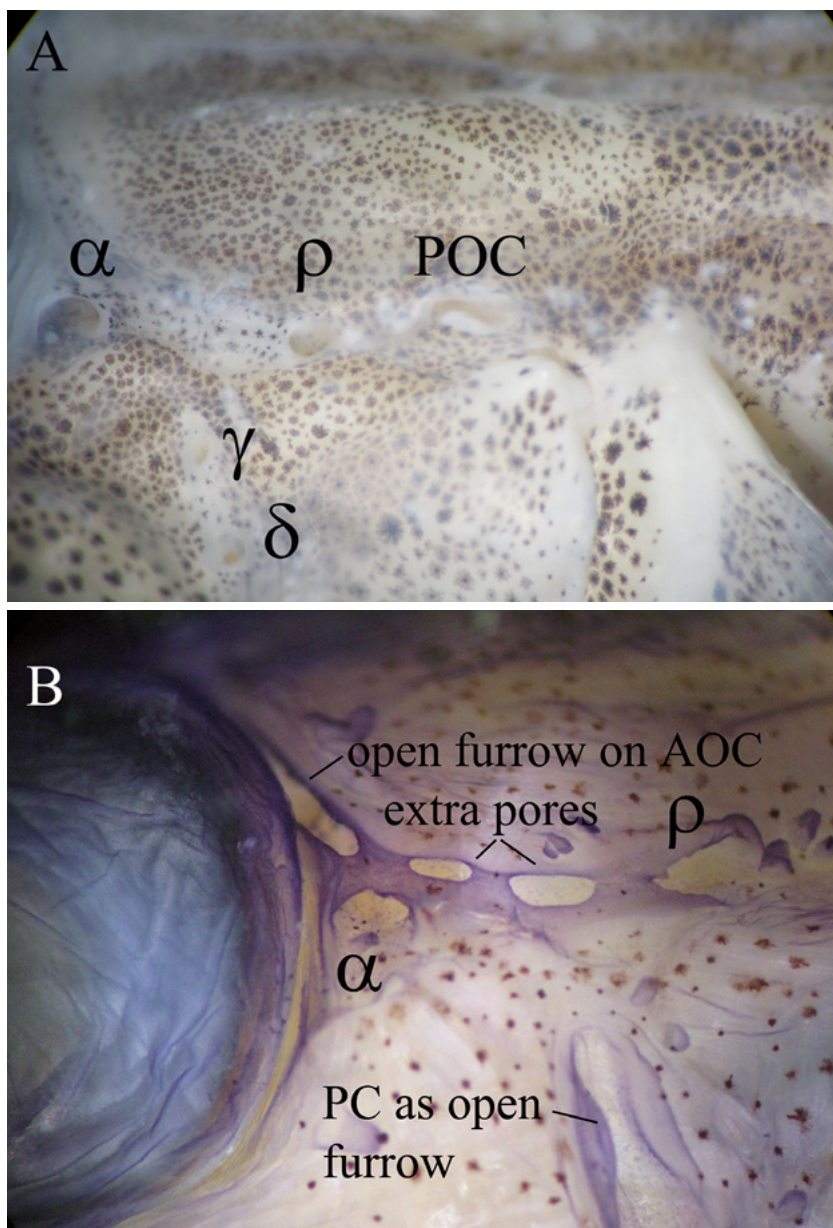
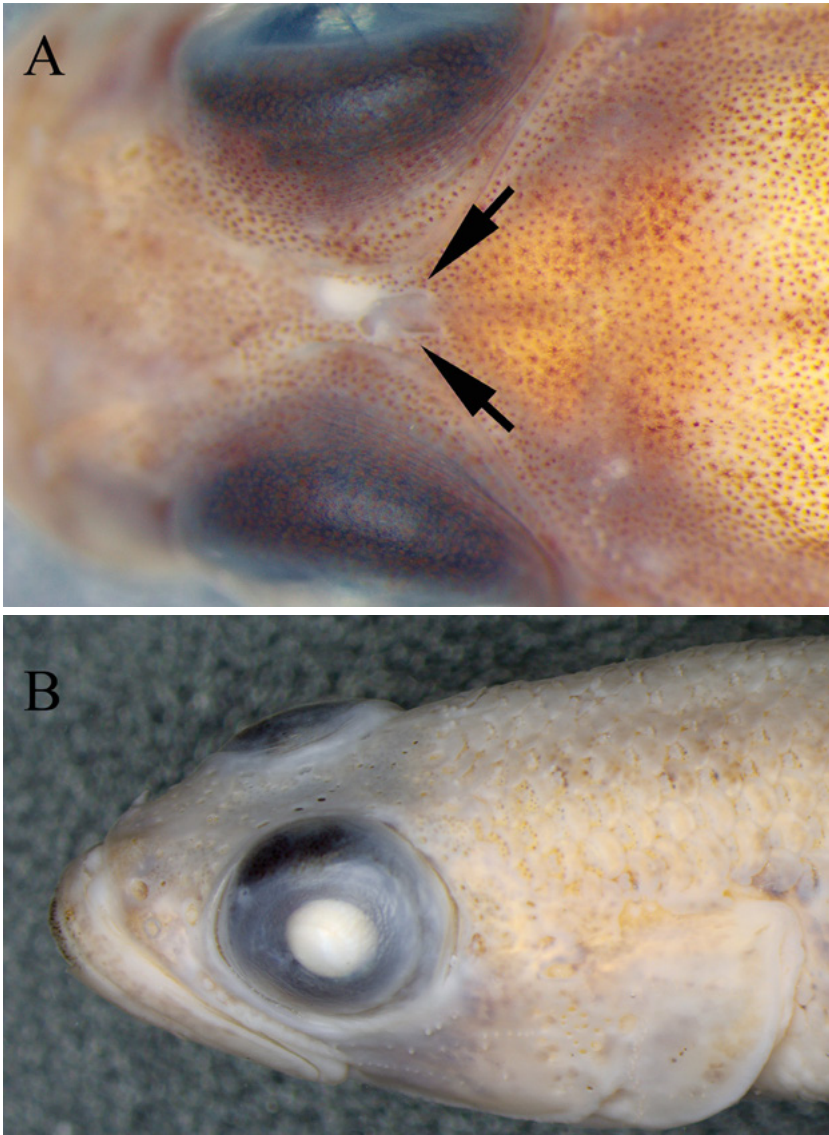


Fig. 4. A. Open furrow on the place of POC in *Buenia jeffreysii*. B. Open furrows and extra pores in *Buenia lombartei* (stained specimen). Pore terminology in text. Photos and modifications by M. Kovačić.

lineage genera and in two *Pomatoschistus*-lineage genera, *Crystallogobius* and *Lebetus*, and in a few species of genera *Knipowitschia* and *Marcelogobius* (Table 2) (Ahnelt & Bianco 1990, Ahnelt 1995, Kovačić & Šanda 2007, Van Tassell & Kramer 2014). The sequence of canal reduction appears to start with the loss of POC first, then PC, and finally the

loss of all canals. This degenerative sequence can be best seen among species in large genera with variable and widespread reductions, e.g. *Knipowitschia*, or when comparing head canals in entire lineages (Fig. 1B, Table 2). An open furrow instead of closed short canals POC and PC on the respective homologous places, or more rarely, replacing



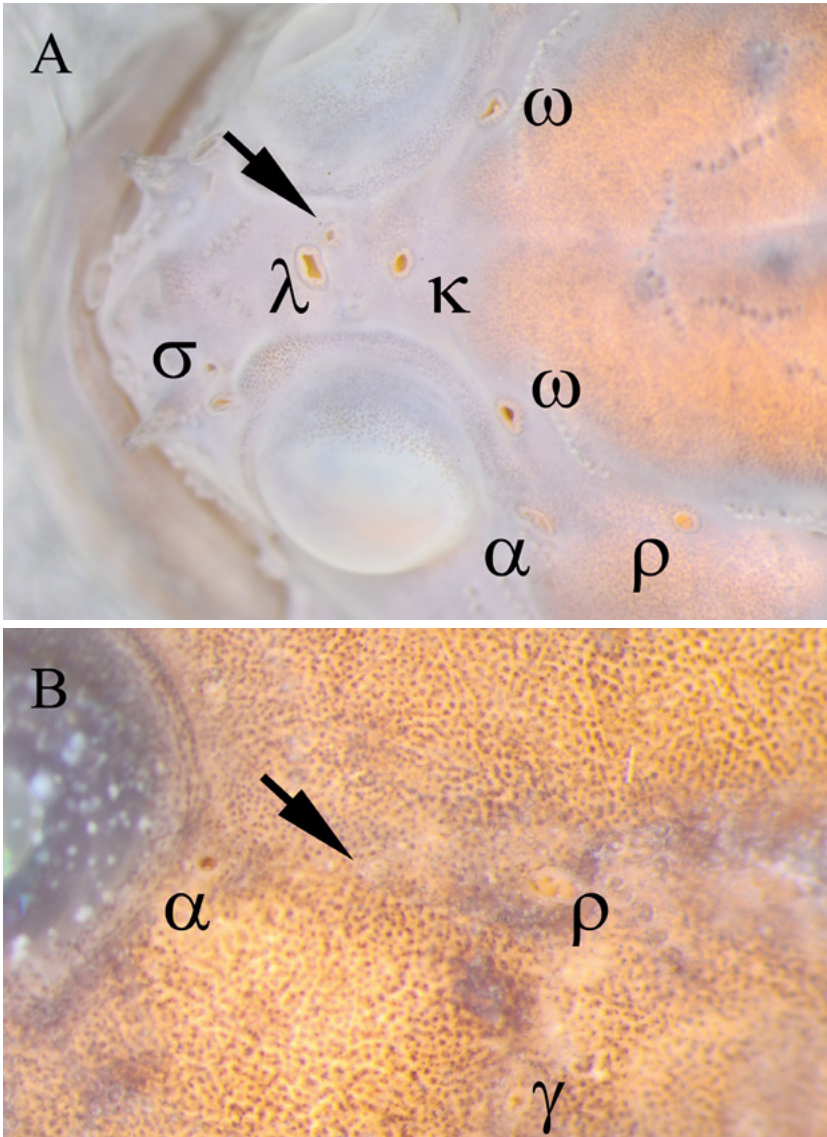


**Fig. 5.** **A.** Two opposite pores  $\kappa$  on the place of usually single pore  $\kappa$  in *Knipowitschia radovici*, marked with arrows. **B.** Head canals with regular and numerous extra pores in *Deltentosteus collonianus*. Pore terminology in text. Photos and modifications by M. Kovačić.

parts of AOC, appears to be an intermediate stage of individual canal reduction regularly seen in some *Pomatoschistus*-lineage species (Fig. 4A, Table 2). The apparent sequence of all reductions appears to represent the reverse sequence of ontogenetic canal development in gobiid juveniles, i. e. losing canal by canal in each step, with an open furrow appearing as an intermediate stage between loss steps (Kovačić 2004). Only in *Buenia* the open furrows

may rather look like elongated holes accompanied by extra pores (Kovačić et al. 2017, Kovačić et al. 2018b) (Fig. 4B).

In addition to the regular pores, supernumerary pores can occur in the *Pomatoschistus*-lineage in two ways: either they look like short pore-like and longitudinal open furrow-like canal roof perforations, as in *Buenia* (Kovačić et al. 2017, Kovačić et al. 2018b) (Fig. 4B), or a discontinuous of a canals

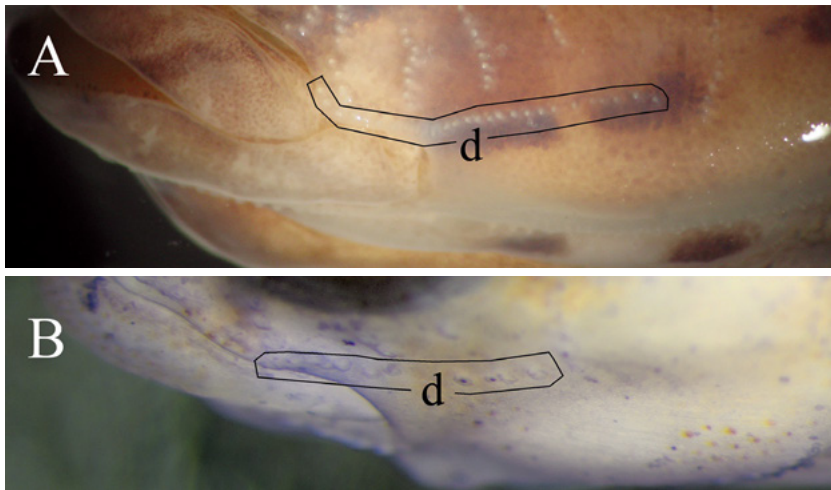


**Fig. 6.** **A.** Additional pore near pore  $\lambda$  in *Millerigobius macrocephalus*, marked with arrow. **B.** Place of the missing pore  $\beta$  regularly present in *Millerigobius macrocephalus*, marked with arrow. Pore terminology in text. Photos and modifications by M. Kovačić.

creates a canal gap, replacing one pore with two opposite ones, each one representing an opening of the separate part of now divided canal, as e.g. in the AOC reductions of *Knipowitschia* or *Ninnigobius* (Fig. 5A, Table 2) (Kovačić 2005a, Miller & Sanda 2008). An extreme case of a perforated canal roof, unique among the Mediterranean and European Atlantic gobies, is found in the genus *Deltentosteus*: here head canals are widened and numerous small

extra pores irregularly distributed over canals are present in addition to regular pores (Fig. 5B).

A third kind of pore addition and of pore loss is the occurrence of one single extra pore (Fig. 6A) or, as a reverse analogue of that, a single pore loss (Fig. 6B), usually as only a one-side (asymmetrical) aberration in a single specimen of a given species. Extra pores and open furrows are only rarely observed in *Gobius*-lineage species, occasionally in single specimens



**Fig. 7.** **A.** Continuous uniserial sensory papillae row, *suborbital row d* in *Gobius bucchichi*. **B.** Discontinuous or divided uniserial sensory papillae row, with the gap visible, *suborbital row d* in *Corcyrogobius pulcher* (stained specimen). The rows outlined, terminology in text. Photos and modifications by M. Kovačić.

(Vanhove et al. 2011), except for *G. salamansa*, where an extra pore  $\alpha 1$  has been observed in both known specimens (in Iglésias et al. 2015 as  $\alpha'$ ).

#### Classification and nomenclature of the rows of sensory papillae on head

In this revision any previous application of the same letter as the name (label) for obviously different and consistently present rows is now replaced in order to establish unambiguously unique identifiers for each row (Table 3). Any new row names are letters of the English alphabet which had not yet been in use by Sanzo (1911); or the new row names are a combination of two letters, with rows sharing the first letter only if they appear to be closely related and placed. A row name as a combination of same letter(s) and an additional number is kept in two cases: 1) In rows, which in most species occur as a single row, but which appear in some taxa as divided along their axis. The oculoscapular longitudinal rows *xa* and *xb* are, for example, commonly separated and therefore named differently; in some species, however, the anterior row *xa* is additionally divided and therefore its parts are marked *xa1* and *xa2*. 2) In rows, which originally occur as a single row, but which can appear also transversely multiplied, e.g. suborbital row *c*. Furthermore, a name as a combination of letter(s) and number(s) followed by letters *s*- superior and *i*- inferior, or even *m*- middle, is kept only for those vertical rows, which mostly occur as single row, but can be divided. An example are the

divided posterior transverse *c* rows in species of the *Gobius*-lineage, where all transverse *c* rows already have a number as part of their name and an additional number would be confusing, e.g. *c5* divided into *c5s*, *c5m* and *c5i*. This approach can be traced back to Miller (1988), absent from any precursor papers by him (e.g. Miller 1984) or by other authors. Papillae appearing as an apparent replacement on the location of a lost canal and which are usually larger papillae and mostly occur as singletons or pairs, are named in the modified nomenclatorial system presented here separately from other rows as follow:

*aoc1* for the lost interorbital part of AOC,  
*aoc2* for the lost posterior part of AOC,  
*poc* for the lost POC, and  
*pc* for the lost PC.

This approach can be traced back to several papers by Kovačić et al. published in 2019, e.g. Kovačić et al. (2019). Before that, these papillae would not be named on the published HLLS figures, or even would not been illustrated on the figures.

The row name *u* has been commonly used since de Buen (1923a) for the papillae on the location of the lost canal part connecting AOC and POC, because their occurrence is widespread across many species and genera. They are located on the lost canal, missing in only a few species, where OC is continuous, not separated into AOC and POC, like in a few *Gobius* species, and not found in only a few other species, e.g. in genera *Buenia* or *Knipowitschia*. Originally, Sanzo (1911) defined row *u* as “serie longitudinale oculo-scapolare a grossi rilievi”, and applied it to the long oculoscapular





**Fig. 8.** A sensory papillae row reduced to two or just a single papilla, *preorbital* rows *ja*, *jb*, *jc* and *jd* in *Buenia jefreysii*. Rows outlined, terminology in text. Photo and modifications by M. Kovačić.

row in *Lesueurigobius* species on the place of the both missing canals, POC and oculoscapular part of AOC. In this revision we use the row *u* name for the papillae on the location of the lost AOC to POC connection, sensu de Buen (1923a), as the more common use applicable for many more species. For the replacement sensory papillae of AOC to POC refer to the names in the text above.

The revised row nomenclature presented here is in alphabetic order, listed side by side separated by a slash to the original name used by Sanzo (1911), as “system as proposed here (in bold)/Sanzo (1911)”, a “\_” indicates that no comparative name existed for a row in Sanzo (1911):

*Preorbital* rows are: row ***ja/c'***, row ***jb/c''***, row ***jc/c,*** row ***jd/ c,,*** row *r/r*, if divided then *r1/r'*, *r2/r''*, row *sa/s'*, row *sb/s''*, row *sc/s'''*.

*Suborbital* rows are: row *a/a*, row *b/b*, row *c/c*, if transverse proliferated then *c1/1*, *c2/2*, *c3/3*, *c4/4*, *c5/5*, *c6/6* etc., row *cp/cp* (not listed among common signs (“indicazioni comuni”) in Sanzo (1911), but applied on his illustrations), row *d/d*.

*Preoperculo-mandibular* rows are: row *e/e*, row *i/i*, row *ff*.

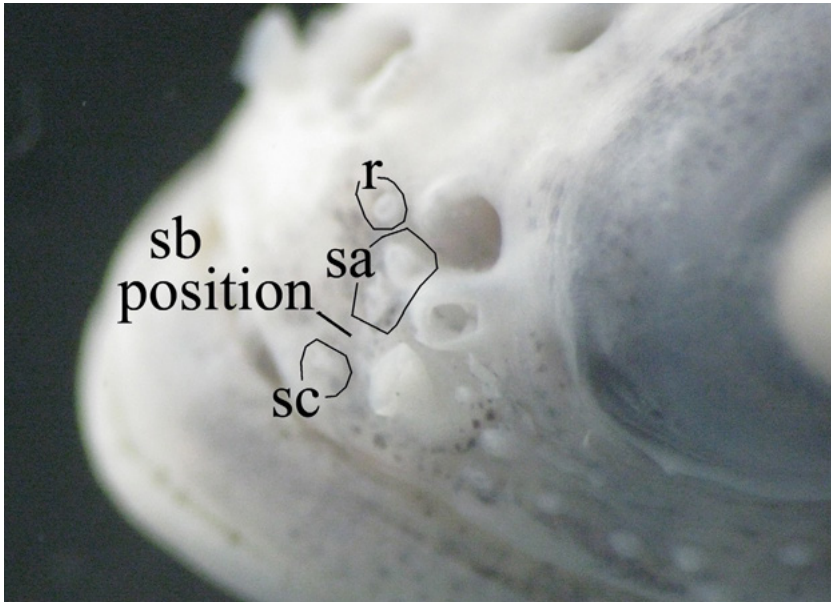
*Opercular* rows are: row *pc/\_*, row *ot/ot*, row *os/os*, row *oi/oi*.

*Oculoscapular* rows are: row ***aoc1/\_***, row ***ka/as***, row ***kb/as'***, row ***kc/as''***, row ***la/lla***, row ***lb/lla'***, row ***poc/\_***, row *q/q*, row *ta/tr* (behind eye), row *tp/tr* (above operculum), row *u/u*, row *xa/x* (above posterior preopercular edge), row *xb/x* (above operculum edge), row *y/y*, row *z/z*.

*Anterior dorsal* rows are: row *g/g*, row *h/h*, row *m/m*, row *n/n*, row *o/o*.

*Interorbital* rows are: row *aoc2/\_*, row *p/p*, row *w/\_*.

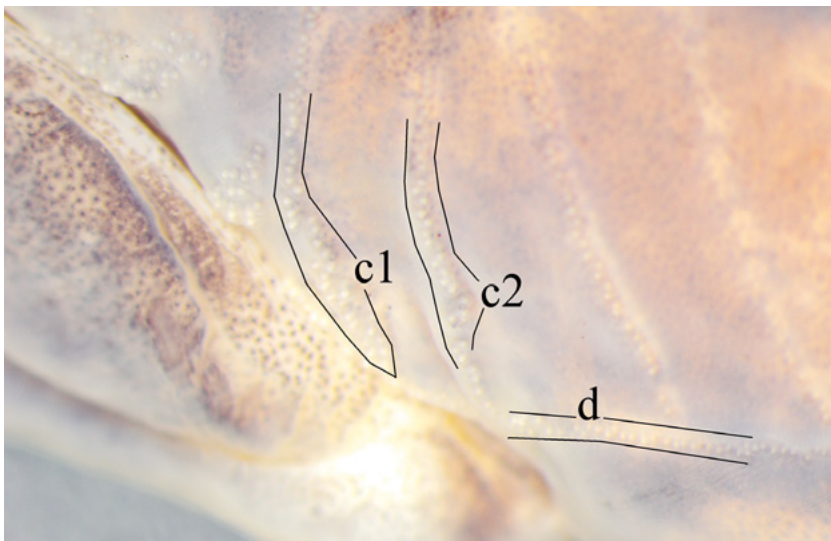
The most common appearance of head rows of sensory papillae is the uniserial organized row (Fig. 7). Usually continuous (Fig. 7A), a uniserial organized row can also be discontinuous, i. e. with one or more gaps dividing the row into two or more subrows orientated in same direction and usually these subrows are arranged along a single line or are slightly displaced from the general row axis (Fig. 7B). However, head rows can become reduced or, alternatively, laterally proliferated in different ways, which are not always easy to identify and to differentiate from each other. In some cases, the number of sensory papillae in rows can be reduced to a single papilla representing the row (Fig. 8) or rows can even be lost completely (Fig. 9). In contrast to reductions, sensory papillae in rows can become laterally proliferated in various ways. 1) A row or its part can be widened by duplicated or tripled papillae still keeping the row shape (Fig. 10). 2) A proliferation can expand further into still closely packed papillae but being shaped rather as wider irregular clusters instead rows (Fig. 11). 3) Individual papillae in row can proliferate perpendicularly in an organized and distinct uniserial way, keeping the original row recognizable. The various species of several *Pomatoschistus*-lineage genera have suborbital row *a* variably proliferated into transverse rows, from single to a few transverse rows (Fig. 12), while keeping other row *a* papillae single and row *a* recognizable. A few *Pomatoschistus*-lineage species have even more than ten transverse rows in the suborbital row *a*. This leads to option 4) the per-



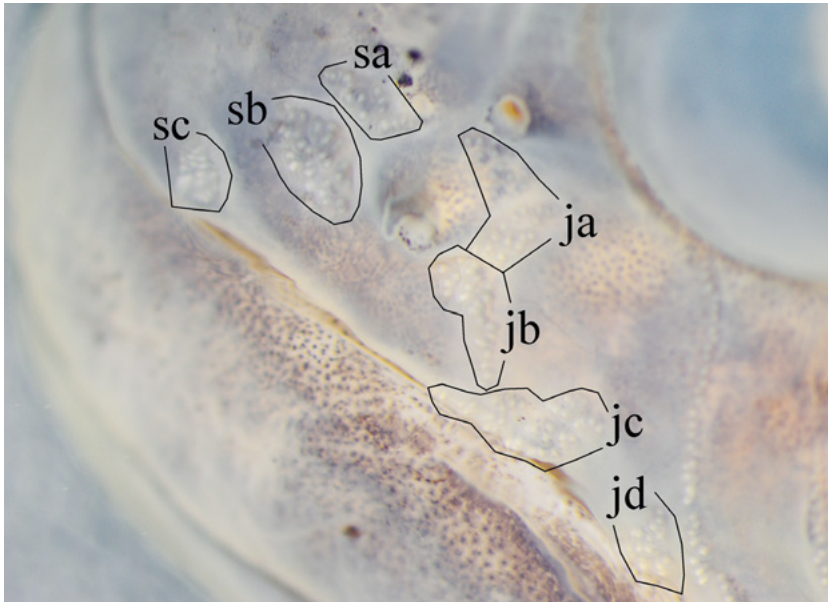
**Fig. 9.** Absent sensory papillae rows, with normal position of *preorbital* row *sb* indicated, but which is absent in *Buenia jeffreysii*. The rows outlined and the position of row *sb* marked, terminology in text. Photo and modifications by M. Kovačić.

pendicular proliferations appear as separate rows and the original row is not recognizable anymore (Fig. 13). The species of all *Gobiidae*-lineage genera and several genera of the *Pomatoschistus*-lineage have suborbital row *c* proliferated into distinct and

distant transverse rows, with the original row not recognizable. Among them, a few *Pomatoschistus*-lineage species with a reduced number of papillae have some of the transverse rows as just a single papilla. Obviously, the lateral proliferations 3) and



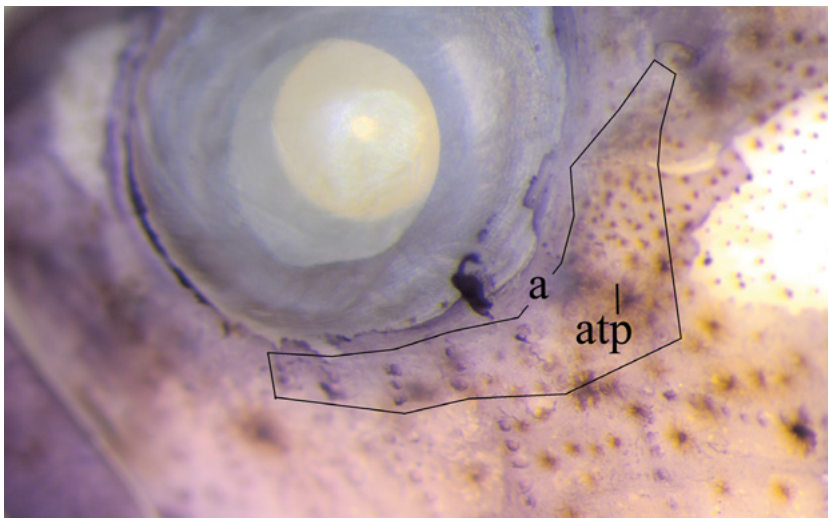
**Fig. 10.** Sensory papillae row irregularly doubled in part of the *suborbital* rows *c1*, *c2* and *d* in *Gobius cobitis*. Rows outlined, terminology in text. Photo and modifications by M. Kovačić.



**Fig. 11.** Sensory papillae row proliferated into clusters of papillae in *preorbital* rows *sa*, *sb*, *sc*, and *ja*, *jb*, *jc* and *jd* in *Gobioides cobitis*. Rows outlined, terminology in text. Photo and modifications by M. Kovačić.

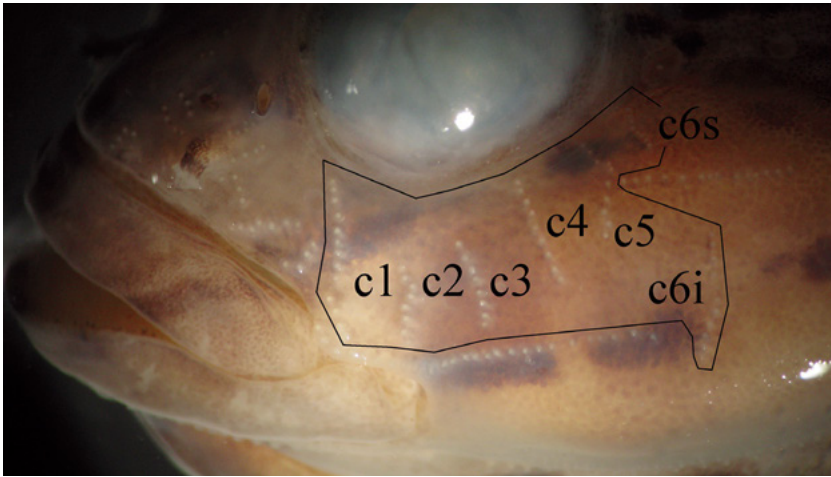
4) are more stages of the same process rather than separate processes, but they can be clearly delimited when the condition is compared among species and the dominant stage is found in the large majority of species, as e.g. for suborbital rows *a* and *c*.  
 5) In addition to single dimension proliferations

perpendicular to the row axis, *Deltentosteus* species are the only among European gobies with the rows proliferated in two dimensions arranged in a field of scattered short rows (Fig. 14). The presence and positions of the sensory papillae rows in the seven topographically grouped head areas are as follow:



**Fig. 12.** Sensory papillae row with a distinct uniserial perpendicular proliferation and the original row recognizable, suborbital row *a* in *Knipowitschia caucasica* (stained specimen). Row *a* is outlined with the longest transverse row marked as *atp*, terminology in text. Photo and modifications by M. Kovačić.

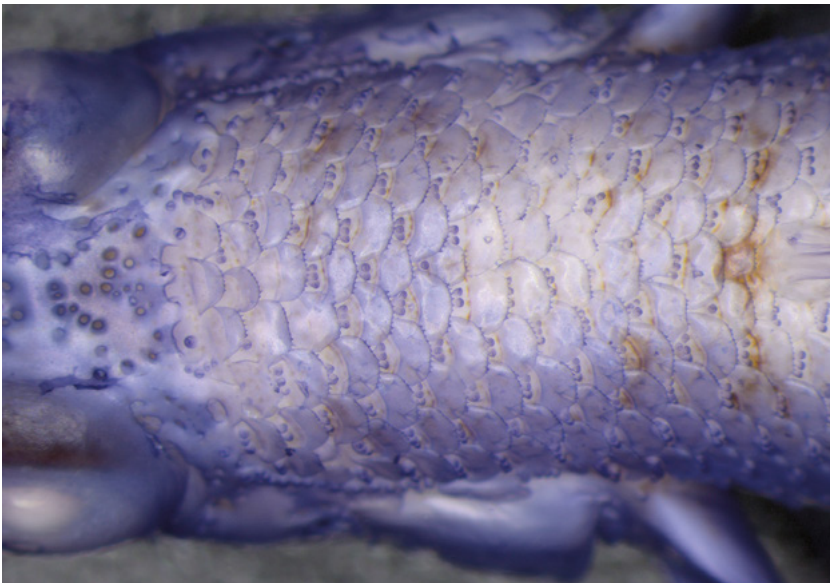




**Fig. 13.** Sensory papillae row with distinct uniserial perpendicular proliferation appearing as separate rows, *suborbital* rows *c* in *Gobius bucchichi*. Rows outlined, terminology in text. Photo and modifications by M. Kovačić.

*Preorbital* rows with three to five median rows (Fig. 15A). Longitudinal row *r* in most species begins anteriorly at or above the horizontal level of posterior nostrils, as in *Gammogobius*, but its onset may even begin more anteriorly, as e.g. close to the upper lip in *Aphia*. Row *r* is variably extending posteriorly, and it is sometimes divided in an upper inner and a lower outer row, as e.g. in *Thorogobius*, increasing

the number of all median preorbital rows to five. Transverse row *sa* is located medially to the interspace between the anterior and posterior nostrils, as in *Millerigobius*, or medially to the posterior nostrils, like in *Gammogobius* or *Didogobius*. In *Aphia* row *sa* is present as two transverse rows medially to the interspace between anterior and posterior nostrils, increasing the number of median preorbital to five



**Fig. 14.** Anterior dorsal rows of sensory papillae each with two dimensional proliferations resulting in a field of scattered short rows on the predorsal area of *Deltentosteus quadrimaculatus* (stained specimen). Furthermore, the numerous extra pores of the head canals are visible anteriorly around eyes. Photo by M. Kovačić.

in this taxon. In the genera *Crystallogobius*, *Knipowitschia*, *Lesueurigobius*, *Ninnigobius*, *Pomatoschistus* and *Pseudaphya* of the *Pomatoschistus*-lineage, row *sa* is arranged longitudinally and parallel to row *r*. Transverse row *sb* is located medially to anterior nostril. Longitudinal row *sc* is anteriormost preorbital row above upper lip. The median preorbital rows can become reduced to a single papilla or they are even absent. In the *Pomatoschistus*-lineage, row *sb* is missing in *Buenia*, *Crystallogobius*, *Lebetus*, *Gymnesigobius*, *Knipowitschia*, *Ninnigobius*, *Pomatoschistus* and *Pseudaphya*, for example, and row *r* in *Deltentosteus* and *Speleogobius*; in both cases the reduction of the number of median preorbital rows is down to three. Row *r* has not been recorded in *L. patzneri*.

Preorbital rows with three to eight lateral preorbital rows (Fig. 15B). Row *ja* may occur as a single, doubled or even tripled row (e.g. in *Gobius* or *Pomatoschistus*), and is located between anterior and posterior nostrils or laterally on the level between the anterior and posterior nostrils. Transverse row *jb* is located laterally below the level and close to anterior nostril as one row or proliferated into up to three rows (e.g. in *Gobius* or *Pomatoschistus*). The two lower longitudinal rows, superior row *jc* and inferior *jd*, are located between upper lip and the vertical extension of the anterior eye edge, or, rarely, entering below the eye as, e.g., in *Gymnesigobius*, *C. pulcher* or *P. minutus*. The lateral preorbital rows can become reduced to a single or double papilla, as e.g. in *Buenia* or *Speleogobius*. Only *L. patzneri* is missing row *jb*, and *Deltentosteus* has rows *jc* and *jd* connected, both modifications resulting in three lateral preorbital rows. Rows of the both preorbital row groups, *s* and *j*, can be proliferated into clusters, as e.g. in some *Gobius* species.

Suborbital rows (Fig. 16) with longitudinal row *a* close to eye, row *a* starts posteriorly below or behind the posterior eye edge and is variably expand anteriorly, up to anterior eye edge. In *Crystallogobius* the entire row *a* is behind the eye. Row *a* can be proliferated into transverse rows, from single transverse row in *Pseudaphya* and some *Pomatoschistus* and *Knipowitschia* species and *Ninnigobius* individuals to several transverse rows, as e.g. in some *Knipowitschia* species and *Ninnigobius* individuals, or even into more than ten transverse rows as in some *Pomatoschistus* species. The single transverse row *a*, or the longest transverse row *a*, if more than one transverse row *a* exists, is placed below posterior eye in species of genera *Knipowitschia*, *Ninnigobius* and *Pomatoschistus*. Since Miller (1969a), this row was named row *atp* and it was the only transverse row *a* being specifically recognized. In the figures of the present work the row was named only once, on Fig. 12, but not on the later figures of species sharing

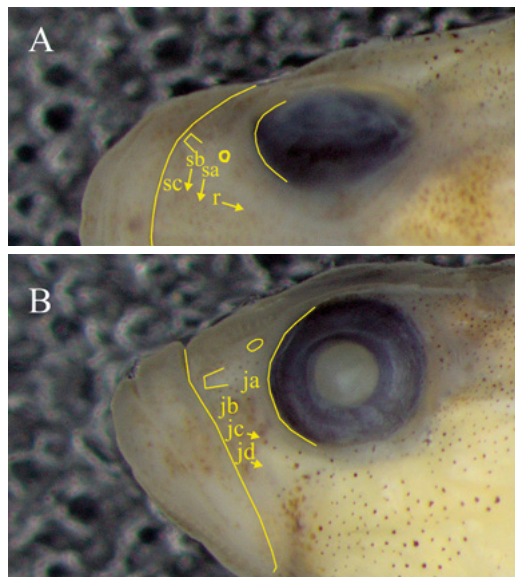


Fig. 15. A. Common positions of median preorbital rows, the usual direction of their extensions marked with an arrow. B. The same for lateral preorbital rows. Head landmarks outlined. Illustration by M. Kovačić.

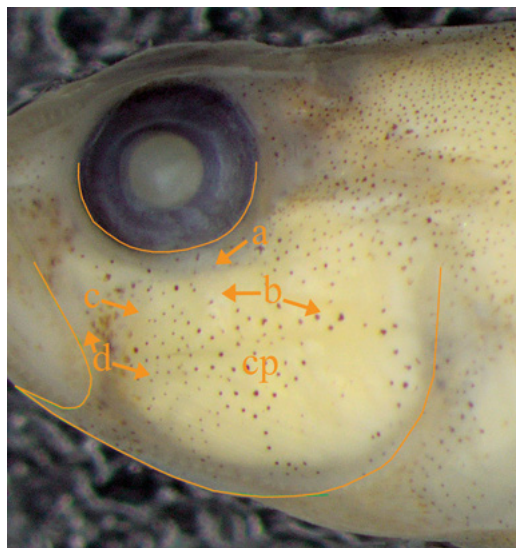


Fig. 16. Common positions of suborbital rows and the usual direction of their extensions marked with arrow. Head landmarks outlined. Illustration by M. Kovačić.

the feature. The row *a* can be restricted to below the posterior part of eye, as e.g. in *Buenia*, *Deltentosteus*, *Lebetus* or *Speleogobius*, or it may become completely lost as in all *Gobius*-lineage genera.



**Fig. 17.** Common positions of *preoperculo-mandibular* rows and the usual direction of their extensions marked with an arrow. Head landmarks outlined. Illustration by M. Kovačić.

Longitudinal row *b* is located in upper posterior half of the cheek: either centered below the posterior eye region and extending in both directions, or it is restricted to just below the eye or the entire row is behind the vertical of the posterior eye edge. It can be reduced to one or two papillae, e.g. in *Speleogobius*, or it can be long, extending anteriorly to below the anterior eye and reaching all the way back to the posterior preopercular edge, as e.g. in *Lesueurigobius* or in *P. minutus*.

Row *c* as longitudinal row commences anteriorly at about the vertical of anterior eye edge, variably extending posteriorly more or less across the middle level of the cheek. It can be reduced and restricted to just below the anterior half of eye, as e.g. in *Speleogobius* or *Buenia*. Row *c* is often proliferated into separate perpendicular rows in *Gobius*-lineage genera and in *Aphia*, *Crystallogobius*, *Knipowitschia*, *Ninnigobius*, *Pomatoschistus* and *Pseudaphya* of the other two European lineages. Rarely, some of the transverse rows *c* can become reduced to a single papilla, or almost all of them, as it is in the extreme cases of *Crystallogobius* or *P. flavescens*. Each of the proliferated transverse rows *c* is usually uninterrupted as a complete or continuous row; or, as in *Gobius*-lineage genera, posterior rows *c* can be divided in two or three parts or even truncated with only the upper part present. Also, if rows are divided as posterior transverse rows *c* in *Gobius*-lineage genera, they are also variably split by row *b*, and not all divided rows are necessary split by the row *b*. The lower part of the first and second transverse row *c* and the anterior part of row *d* can become widened by irregularly duplicated papillae in some *Gobius* and *Neogobius* species. In some *Gobius*-lineage genera having only six rows (*Corcyrogobius*, *Didogobius*, *Gymnesigobius*, *Marcelogobius*, *Odondebuena*, *Peter*), the authors of species descriptions tried to estimate which of usual seven *Gobius*-lineage suborbital transverse rows was lost in the particular species, and, when they

named the rows with numbers, one of the numbers in the order was omitted (e.g. row 3 in Schlieven et al. 2019, or row 4 in Miller 1993) or it was named with a combination of two numbers, e.g. as row 3/4 in Kovačić et al. (2020). In the present revision this approach was avoided, not possible to be generalized for various studied genera since the count of transverse *c* rows ranged from 5 to 16 across genera and species. Therefore, for all species with transverse rows *c*, transverse *c* rows are named in order from the anteriormost row as row *c1* backwards, without skipping numbers and nevertheless acknowledging that the transverse *c* rows of the same name/number in different species are not necessarily homologues or that they would implicitly occupy a similar position along the row *c* transverse complex. Row *c* anteriorly starts with two papillae, one above the other, at the vertical of the anterior eye edge in *Buenia*, *Deltentosteus*, *Lebetus*, *Lesueurigobius* or *Speleogobius*.

Two papillae of row *cp*, upper and lower, are present on the cheek in genera *Buenia*, *Deltentosteus*, *Lebetus*, *Lesueurigobius* or *Speleogobius*. The two papillae are distinct and distant from other rows and cannot be assigned to any other *suborbital* row. They were named *cp* already on illustrations by Sanzo (1911) for *Buenia*, *Deltentosteus* and *Lesueurigobius*. They are placed behind the row *c* posterior edge and below row *a*. The lower *cp* papilla is variably placed in a vertical row together with the upper papilla, e.g. below upper papilla, or in front of the vertical of the upper papilla or behind it. Just to be noted, the posteriormost *c* transverse row in genera *Knipowitschia*, *Ninnigobius*, *Pomatoschistus*, *Pseudaphya*, the longest *c* transverse row, was named also row *cp* during last fifty years, for the first time by Miller (1969a). In this revision, the homonymy is avoided and the *cp* row name is used only for the pair of distinct *suborbital* papillae positioned as described above that cannot be assigned to any other *suborbital* row or row serie.

Longitudinal row *d* starts anteriorly above the upper lip and extends backwards along the lower cheek. Longitudinal row *d* may be continuous or discontinuous, with separate supralabial and cheek parts, with a gap on the cheek, or with overlapping supralabial and cheek parts, clear overlapping example is in *Deltentosteus*. Longitudinal row *d* can be reduced to just a supralabial part comprising just two papillae, as e.g. in *Speleogobius*. In *Crystallogobius* the longitudinal row *d* is absent from cheek and from above the upper lip, and it remains to be shown if row *d* is really absent there or if above upper lip its papillae are amalgamated with row *c*.

*Preoperculo-mandibular* rows (Fig. 17). External row *e* usually is divided in an anterior sublabial part and a posterior part along the ventral cheek margin. Internal row *i* is arranged ventrally paral-



lel to row *e* and is usually divided in sublateral and posterior parts, too. Both rows are continuous in *Deltentosteus*, only row *i* is continuous in most of the *Neogobius* species and some *Knipowitschia* and *Pomatoschistus* species; while only row *e* continuous in most *Lesueurigobius* species. Both rows are commencing anteriorly before the frontal end of jaw and end posteriorly near or at the preopercular ventral margin; row *e* is reaching far upwards on the preopercle only in the genera of the *Aphia*-lineage. Mental row *f* is located near the tip of the chin. In most cases it is arranged longitudinally. In *Gammogobius* longitudinal row *f* is proliferated but it is still longitudinal, but anteriorly having one or two short transverse rows extending laterally from the longitudinal base. Mental row *f* is proliferated in *Neogobius* and some *Gobius* species into a cluster, or it is reduced in *Deltentosteus*, *Speleogobius*, *Pseudaphya* or some *Pomatoschistus* species to a single papilla. The anterior parts of rows *e* and *i* and row *f* have not been reported for *T. alvheimi* and *T. laureatus*, but they may have been overlooked.

**Opercular rows** (Fig. 18). Transverse row *ot* is located at the anterior part of the operculum. It is divided into two widely separated parts in *Lebetus*, and it is sometimes widened by proliferating into irregularly doubled papillae, e.g. in *Deltentosteus*. Superior longitudinal row *os* is located at the upper posterior part of operculum, elongated across the upper operculum, as e.g. in *Ninnigobius*, or shorter on the central or on the posterior part of operculum. Row *os* is oriented more or less oblique, posteriorly reaching downwards, sometimes steeply, as e.g. in *N. pallasi*. Inferior longitudinal row *oi* is located at the lower part of operculum. In *Aphia* it is proliferated into two rows, the second row occurs along opercular edge, placed below the row on the usual row *oi* position. When PC is absent, row *pc* usually is composed of two to four papillae present on the place of the absent PC, as e.g. in *Aphia*, *Lebetus*, *Corcyrogobius* and in species missing PC of *Didogobius*, *Marcelogobius*, *Knipowitschia* and *Speleogobius* genera. Both PC and *pc* are absent in *Crystallogobius*.

**Oculoscapular rows** (Fig. 19) with longitudinal row *aoc2* of two papillae present behind the eye if posterior AOC absent, like in *Lebetus*, several *Knipowitschia* species and *M. helenae*, but not in e.g. *Aphia* or *Crystallogobius* that are missing both AOC and row *aoc2*.

Additional *poc* row present as one or two comparatively large papillae in genera with POC canal absent. Both, POC and row *poc*, have not been reported from *Aphia*, *Crystallogobius*, and some *Knipowitschia* species, and also not from *D. bentuvii*, but it may have been overlooked in the single known *D. bentuvii* specimen. In *Lesueurigobius*, a continuous

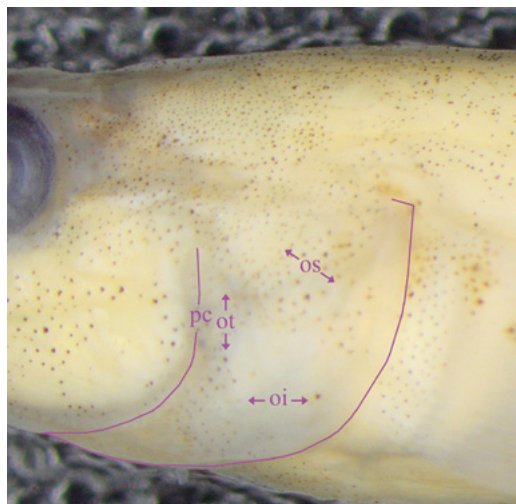


Fig. 18. Common positions of opercular rows and the usual direction of their extensions marked with an arrow. Head landmarks outlined. Illustration by M. Kovačić.

row of papillae combining *aoc2* + *u* + *poc* is present on the place of the missing oculoscapular canals.

A transverse row *ta* is present only in five studied genera of *Pomatoschistus*-lineage and in the genus *Aphia*. It is placed below the horizontal level of pore  $\alpha$  and may variably extend downwards reaching level of suborbital row *b*, as e.g. in *P. lozanoi* and *Pseudaphya*. It originates behind pore  $\alpha$  and variably extends to the level above pore  $\alpha$  in some genera, e.g. *Ninnigobius*. Row *ta* is positioned beyond the lower half of eye in *Aphia*, *Knipowitschia* and *Ninnigobius*. Finally, it is positioned beyond the upper half of the eye only in *Crystallogobius*.

Anterior longitudinal row *xa* is located behind the eye above the posterior edge of preopercle. If it is comparatively long than it is centred above

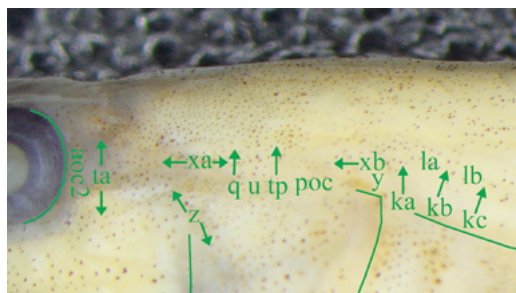


Fig. 19. Common positions of oculoscapular rows and the usual direction of their extensions marked with an arrow. Head and body landmarks outlined. Illustration by M. Kovačić.

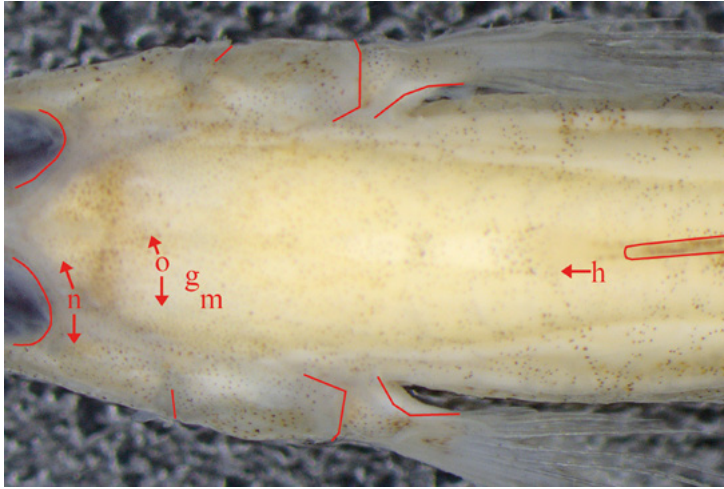


Fig. 20. Common positions of anterior dorsal rows and the usual direction of their extensions marked with an arrow. Head and body landmarks outlined. Illustration by M. Kovačić.

the posterior edge of preopercle extending in both directions, or it is anteriorly starting at this position and extending only backwards above operculum. In *Buenia*, *Crystallogobius*, *Knipowitschia*, *Ninnigobius*, *Pomatoschistus*, *Pseudaphya*, some *Gobius* and *Thorogobius* species, row *xa* is divided in two parts. In *Aphia* and *Crystallogobius* row *xa* is positioned comparatively high, approximately at the horizontal line limiting the upper eye edge.

Posterior longitudinal row *xb* is located above the posterior edge of operculum. It is not visible in *Crystallogobius* and is not reported for *L. heterofasciatus*. In *Aphia* it is positioned high at about the horizontal level of upper eye edge. Rows *xa* and *xb* are long and appear to be joined into a continuous row or nearly joined in *L. friesii* and *L. sanzi*.

Transverse row *z* is located approximately in the area of the upper edge of the preopercle. Only in *Aphia* and *Crystallogobius* it is positioned high at the horizontal level crossing the pupil.

Row *q* is located behind pore  $\rho$ , being transverse or steep oblique reaching downwards posteriorly. Only in *Gymmesigobius* it runs almost longitudinally rearwards reaching beyond pore  $\rho$ . In *Crystallogobius*, *Knipowitschia*, *Ninnigobius*, *Pomatoschistus*, *Pseudaphya* of *Pomatoschistus*-lineage, and in some *Gobius* and *Thorogobius* species of *Gobius*-lineage, it extends upwards passing above the interspace between the two parts of the divided row *xa*. In *Aphia* and *Pseudaphya* it reaches further upwards to the horizontal level of the anterior dorsal row *g*. In some *Pomatoschistus* species row *q* is divided in two parts, one below the horizontal level of pore  $\rho$  and one above. Row *q* is absent in *Lesueurigobius*.

Transverse row *tp* is found in eight genera, i. e. in *Aphia* and seven *Gobius*-lineage genera, and it is variably present among species of three more genera, i. e. *Gobius*, *Thorogobius* and *Knipowitschia*. Except for *Knipowitschia* species, transverse row *tp* is located behind row *u* and between rows *xa* and *xb*. In *Aphia* it extends upwards high to the anterior dorsal row *g*. In other species it reaches slightly above rows *xa* and *xb*; or is short, not even reaching the horizontal level of rows *xa* and *xb*. Finally, in some *Knipowitschia* species, row *tp* is a short row located below the posterior part of row *xa*. Interestingly, all those six *Knipowitschia* species having the row *tp* also miss row *u*, contrary to other *Knipowitschia* species having single row *u* papilla, but missing transverse row *tp*. The six *Knipowitschia* species are the only example of transverse oculoscapular row *tp* in the genera of the *Pomatoschistus*-lineage. The row could alternatively be the transverse proliferation of a single *u* papilla, which would be a unique case of proliferation of this canal replacement papilla among studied genera (except for the single species of *Neogobius*), see below for row *u*.

Row *u* is represented as one or two larger papillae located between pore  $\rho$  and pore  $\theta$ , if POC present, or between row  $\rho$  and *poc*, if POC absent. Row *u* is absent from *Gobius* species with a continuous OC, and from *Knipowitschia* species with row *tp*. Row *u* has also not been recorded for some *Buenia* species. Row *u* papillae is located behind row *q*, or, in some *Gobius* species one papilla of row *u* is behind and one in front of row *q*. In *N. pallasi*, in addition to row *q* and to row *tp*, row *u*, situated between them, is proliferated into a third transverse row between pores  $\rho$  and  $\theta$ .



Transverse row *y* is located just below row *xb*.

Transverse axillary rows *ka*, *kb* and *kc* are radiating from the upper pectoral fin base and longitudinal axillary rows *la* and *lb* are positioned just above those. Transverse axillary rows *ka* in *Pseudaphya* and row *kb* in *Crystallogobius* extended into the predorsal area, both reaching the horizontal level of the anterior dorsal row *g*. In *Aphia* all transverse axillary rows, *ka*, *kb* and *kc* extend into the predorsal area, with rows *ka* and *kb* reaching the horizontal level of the anterior dorsal row *g*, and rows *la* and *lb* are located between them and not above them as usual. Longitudinal axillary rows *la* and *lb* proliferated into a field of scattered short vertical rows of single, paired or tripled papillae above *ka*, *kb* and *kc* and extend above row *xb* in *D. collonianus*. In *D. quadrimaculatus* the entire predorsal is uniformly covered with short vertical rows of single, paired or tripled papillae (Fig. 14); thus, the group of longitudinal axillary rows *la* and *lb* is not distinguishable from the groups of anterior dorsal rows, as in cogenetic *D. collonianus*.

Generally, *oculoscapular* rows can become reduced to a single papilla, as e.g. in *Speleogobius* rows *xb*, *y*, *la*, *lb*; or they are even lost completely, e.g. rows *q*, *y*, *la* and *lb* in *Lebetus*, rows *kc*, *la* and *lb* in *Gymnesigobius*, or rows *la* and *lb* in *Crystallogobius*. All five *oculoscapular* posterior rows have not been drawn on illustrations of *L. heterofasciatus*, *T. alvheimi* and *T. laureatus*, probably not really missing but overlooked or abraded on the studied material (Maul 1971, Sauberer et al. 2018).

*Anterior dorsal* rows (Fig. 20). Transverse row *n* is located on the anterior nape behind eye, except for *Crystallogobius*, where it extends from the horizontal level of dorsal edge of eye upwards. Transverse row *n* can be long and connected at the dorsal midline with its sister row, as e.g. in *Pseudaphya*. In some *Lesueurigobius* species row *n* is a single papilla and in *Aphia* small cluster of papillae behind the upper posterior eye edge.

Transverse rows *o* is located approximately at the vertical level of the preopercular edge, more anteriorly and close to row *n* in *Aphia*, *Crystallogobius*, *Lesueurigobius* and the most *Pomatoschistus* species. It can be distant to or can be connected with its sister row at the dorsal midline, reduced to a single papilla in some *Pomatoschistus* or *Lesueurigobius* species, or absent in all *Knipowitschia* and not observed in *L. patzneri* species.

Longitudinal row *g* is located above the posterior edge of the preopercle, as e.g. in most *Gobius*-lineage members; or it is located above the operculum, as e.g. in most *Pomatoschistus*-lineage members. Longitudinal row *g* anteriorly extends variably to row *o*, to behind row *o*, as in e.g. *Pseudaphya*, or at row *o*, as in e.g. *G. kolombatovici*, or, finally, pass-

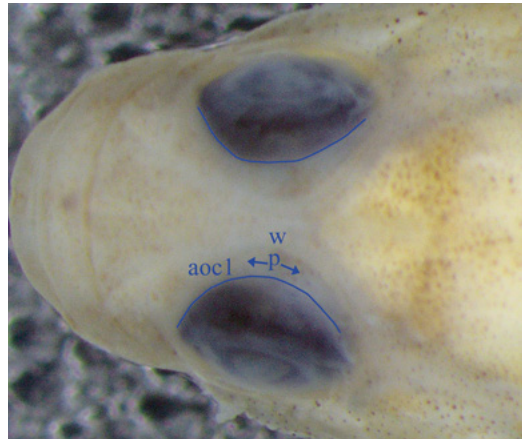


Fig. 21. Common positions of interorbital rows and the usual direction of their extensions marked with an arrow. Head landmarks outlined. Illustration by M. Kovačić.

ing anteriorly row and ending in front of it, like in *Gammogobius*, *Marcelogobius*, *Peter* or *Didogobius* (except *D. bentuvii*). Longitudinal row *g* can even reach row *n*, as in most *Thorogobius* species; finally, it may even pass row *n* ending anteriorly of it, as in some *Lesueurigobius* species.

Longitudinal row *m* is located below the posterior part of row *g*, as in *Thorogobius*, or behind it, as in some *Didogobius* species, or below the horizontal level of row *g* and behind vertical to its posterior edge. Longitudinal row *m* is single papilla in *Lesueurigobius*, absent in *Aphia*, *Crystallogobius*, and it is not recorded in *D. bentuvii*, but the skin surface of this trawled specimen might have become abraded. Longitudinal row *m* is variably observed in *Lebetus* species.

Longitudinal row *h* is located middorsally in front of the first dorsal fin origin. It may be continuous or divided into an anterior and a posterior part, and in some *Neogobius* species it can be divided into more than two longitudinal patches. In *Thorogobius* and some *Lesueurigobius* species it can be long, extending anteriorly to above the posterior edge of operculum or even to in front of it. In *Pseudaphya* and *Crystallogobius* it is not longitudinal, in *Pseudaphya* it is represented by two short vertical rows of paired papillae, and in *Crystallogobius* as a single transverse row. Row *h* has not been reported from several *Knipowitschia* species, maybe not really missing and should be checked on intact material.

Rows *o*, *g*, *m* are proliferated into an anteriorly located predorsal field of scattered short vertical rows of single, paired or tripled papillae, and row *h* into a posterior predorsal field of scattered short vertical rows of single, paired or tripled papillae in *D. colo-*

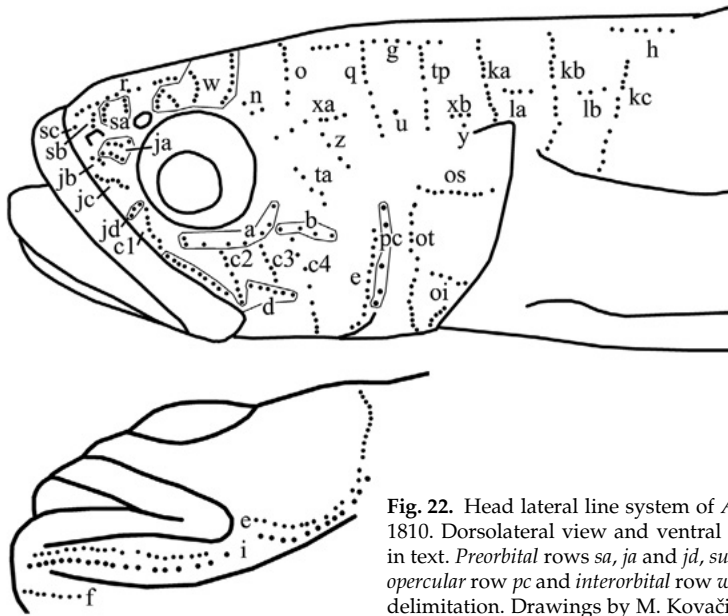


Fig. 22. Head lateral line system of *Aphia minuta* Risso, 1810. Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa*, *ja* and *jd*, suborbital rows *a*, *b*, *d*, opercular row *pc* and interorbital row *w* outlined to clarify delimitation. Drawings by M. Kovačić.

*nianus*. In *D. quadrimaculatus* the entire predorsal area is uniformly covered with short vertical rows of single, paired or tripled papillae (Fig. 14); thus, the two groups of anterior dorsal rows in this species are not distinguishable as in *D. collonianus*. The anterior dorsal rows can be reduced to single papilla, as e. g. rows *n*, *o* and *m* in *Buenia* and *Speleogobius*, whereas a reduction or respectively absence of rows, depending on species, can also occur in *Lebetus*.

Interorbital rows (Fig. 21) are absent when interorbital AOC is present, except for *Millerigobius*, which features both of them, an interorbital AOC and a transverse interorbital row *w*. If the interorbital part of AOC is absent, then one or two larger interorbital *aoc1* papillae are present anteriorly, as in *Lebetus*, *M. helena*, *K. radovici* or in some *N. montenegrensis* individuals. In *Crystallogobius*, *Lesueurigobius* and several *Knipowitschia* species, a pair of longitudinal rows *p* with multiple papillae replaces AOC rather than a single or double larger *aoc1* papillae. Furthermore, transverse rows *w*, additional to the longitudinal row *p*, can be present on the place of the missing AOC in the interorbital region, either one row as in *K. byblisia* and *K. montenegrina*, or two rows as in *Crystallogobius*. *Aphia* has no longitudinal rows *p*, but only three to four transverse rows *w* on the place of the missing AOC.

## Application of the revised classification and nomenclature on the Mediterranean and European Atlantic native marine gobiid genera

### Head lateral-line system (HLLS) description by genus

#### HLLS of *Aphia*-lineage genera

##### *Aphia* Risso, 1827

Head canals and pores absent in the only known species of the genus (Fig. 22, Table 2).

Head rows of sensory papillae (Table 3) with preorbital row *sb* present; suborbital row *a* as a single longitudinal row; suborbital row *c* multiplied in separate transverse rows; interorbital rows *w* present; transverse oculoscapular and anterior dorsal rows prolonged (Fig. 22). Preorbital rows with five median rows. Row *r* longitudinal, long, extending from interorbital region to near upper lip; row *sa* as two transverse rows extending medially from the interspace between anterior and posterior nostrils; transverse row *sb* extending medially from anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above upper lip. Five lateral preorbital rows. Row *ja* as two rows laterally and below to between anterior and posterior nostrils; row *jb* as one row below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, both between upper lip and vertical of anterior eye edge. Suborbital rows with longitudinal row *a* extending

anteriorly to below anterior eye. Longitudinal row *b* on upper half of cheek, behind posterior eye edge. Four to six transverse rows *c*, one or two rows *c*, including the last one, extending ventrally below level of row *d*. Longitudinal row *d* above upper lip and backwards along lower cheek, divided into a supralabial and cheek part, reaching backwards behind vertical of posterior eye edge. *Preoperculo-mandibular* rows with external row *e* divided, internal row *i* ventrally and parallel to row *e*, also divided. Both rows ending anteriorly at chin near frontal part of jaw, posteriorly row *i* ends at preopercular ventral margin, row *e* extending upwards to upper preopercle. Mental row *f* longitudinal anteriorly beginning at chin tip. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* long, on upper part of operculum; inferior longitudinal row *oi* as two rows on lower

part of operculum. *Oculoscapular* rows positioned high behind eye. Transverse row *ta* behind lower half of eye, reaching downwards to near row *b*; anterior longitudinal row *xa* between near eye and vertical of posterior preopercular edge; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately above upper edge of preopercle. Transverse row *q* long, reaching upwards above horizontal level of *xa* to near *anterior dorsal* row *g*; row *u* as a single papilla; transverse row *tp* long, reaching upwards in front of *xb* to near *anterior dorsal* row *g*. Row *y* below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radially extending from upper pectoral fin base, all three rows long, rows *ka* and *kb* reaching upwards to horizontal level of row *h*, row *kc* terminating upwards below row *h*. Longitudinal axillary row *la* between rows *ka* and *kb*, row *lb* between rows *kb* and *kc*. *Anterior dorsal*

**Table 2.** Presence of head canals and pores in the native Mediterranean and European Atlantic genera. The genera are sorted by the phylogenetic lineages (Agorreta et al. 2013). For the sources of the data refer to “Specimens studied and the published data” in the Material and methods. Character states for head canals are listed as follows: x, always present; /, always absent; (x), variably present or absent; (xo), variably present as enclosed canal or also as open furrow or absent; xx, always present and always with additional pore(s); x(x), always present and additional pore(s) can occur; x(xo), always present, with only regular pores or also with additional pore(s) or as open furrows. Pores: x, always present; /, always absent; (x), variably present or absent; xo, variably present as pore or replaced with open furrow; (xo), variably present as pore or replaced with open furrow or absent.

Clades	Genera	AOC	POC	PC	$\sigma$	$\lambda$	$\kappa$	$\omega$	$\alpha$	$\beta$	$\rho$	$\theta$	$\tau$	$\gamma$	$\delta$	$\epsilon$
<i>Aphia</i> -lineage	<i>Aphia</i>	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
	<i>Lesueurigobius</i>	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
<i>Gobius</i> -lineage	<i>Chromogobius</i>	x	/	x	x	x	x	x	x	x	x	/	/	x	x	x
	<i>Corcyrogobius</i>	x	/	/	x	x	(x)	x	x	(x)	x	/	/	/	/	/
	<i>Didogobius</i>	x	/	(x)	x	(x)	x	(x)	x	(x)	x	/	/	(x)	(x)	(x)
	<i>Gammogobius</i>	x	/	/	x	x	x	x	x	x	x	/	/	/	/	/
	<i>Gobius</i>	x(x)	x	x	x	x	x	x	x(x)	x	x	x	x	x	x	x
	<i>Gymnesigobius</i>	x	/	x	x	x	x	x	x	x	x	/	/	x	x	x
	<i>Marcelogobius</i>	(x)	/	(x)	(xo)	(xo)	(x)	(x)	(x)	(x)	(x)	/	/	(x)	(x)	(x)
	<i>Millerigobius</i>	x(x)	/	x	x	x	x	x	x	(x)	(x)	/	/	x	(x)	xo
	<i>Neogobius</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Odondebuenia</i>	x	/	x	x	x	x	x	x	x	x	/	/	x	x	x
	<i>Peter</i>	x	/	x	x	x	x	x	x	x	x	/	/	x	x	x
	<i>Thorogobius</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Vanneaugobius</i>	x	(x)	x	x	x	x	x	x	x	x	(x)	(x)	x	x	x
<i>Zebrus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Pomatoschistus</i> -lineage	<i>Buenia</i>	x(xo)	(xo)	x(xo)	xo	xo	xo	(xo)	xo	/	xo	(xo)	(xo)	xo	xo	xo
	<i>Crystallogobius</i>	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
	<i>Deltentosteus</i>	xx	xx	xx	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Knipowitschia</i>	(xo)	(xo)	(xo)	/	(xo)	(x)	/	(x)	/	(x)	(x)	(xo)	(xo)	/	(xo)
	<i>Lebetus</i>	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
	<i>Ninnigobius</i>	x	(xo)	(xo)	(xo)	(xo)	x	/	x	/	x	(xo)	(xo)	(xo)	(xo)	(xo)
	<i>Pomatoschistus</i>	x	x	x	x	(x)	(x)	(x)	x	(x)	x	x	x	x	(x)	x
	<i>Pseudaphya</i>	x	/	x	/	x	x(x)	x	x	/	x	/	/	x	(x)	x
	<i>Speleogobius</i>	x	/	(x)	x	x	x	(x)	x	x	x	/	/	(x)	(x)	(x)

rows long, except for row *n*; row *n* small cluster of papillae behind upper posterior eye edge. Transverse rows *o* in front of vertical of posterior preopercular edge, long, reaching sister row in the dorsal midline. Longitudinal row *g* anteriorly ending behind row *o*; longitudinal row *m* absent. Longitudinal row *h* continuous near the dorsal midline in front of origin of first dorsal fin. *Interorbital* rows with three to four transverse rows *w*, posterior rows *w* connected to sister rows at middorsum region, anterior rows *w* ending medially at row *r*.

*Lesueurigobius* Whitley, 1950

Head canals and pores absent in four species (Fig. 23, Table 2), no data for *L. koumansi*.

Head rows of sensory papillae with separate rows on the place of missing oculoscapular canals; the interorbital row of papillae *p* and the continuous oculoscapular row (*aoc2+u+poc*), only in *L. heterofasciatus* illustrated as a continuous row of papillae (*p+aoc2+u+poc*), connected at posterior eye edge (Table 3). Head rows of sensory papillae with *preorbital* row *sb* present; *suborbital* row *a* single longitudinal row; *suborbital* row *c* a single longitudinal row, anteriorly starts with two papillae, one

**Table 3.** Presence of head sensory papillae rows in the native Mediterranean and European Atlantic genera. For the sources of the data refer to “Specimens studied and the published data” in the Material and methods. For the sorting of the genera by the phylogenetic lineages see Table 2. Character states for the head sensory papillae rows are as follows: x, always present; /, always absent; (x), variably present or absent or among species of the genus or among individuals within species; xx, always present with additional perpendicular rows; x(x), always present with additional perpendicular rows variably present or absent; xnumber, row transformed in separate perpendicular rows, the number of rows presented. The absence of rows probably caused by the damages in the species with the limited known material (see text for each of the genera) were also recognized, causing the variable presence/absence of rows within some genera, instead of rows always present condition. For these genera, counted here as having variably present rows marked as “(x)”, we expect that future material in good condition will likely confirm the presence of the yet missing rows in each species of the genus.

Clades	Head areas with sensory papillae rows Genera	<i>preorbital</i>								<i>suborbital</i>					<i>preoperculo-mandibular</i>			<i>opercular</i>	
		<i>r</i>	<i>sa</i>	<i>sb</i>	<i>sc</i>	<i>ja</i>	<i>jb</i>	<i>jc</i>	<i>jd</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>cp</i>	<i>d</i>	<i>e</i>	<i>i</i>	<i>f</i>	<i>ot</i>	<i>os</i>
<i>Aphia</i> -lineage	<i>Aphia</i>	x	x	x	x	x	x	x	x	x	x	x	/	x	x	x	x	x	x
	<i>Lesueurigobius</i>	x	x	x	x	x	x	x	x	x	x	x	(x)	x	x	x	x	x	x
<i>Gobius</i> -lineage	<i>Chromogobius</i>	x	x	x	x	x	x	x	x	/	x	x7	/	x	x	x	x	x	x
	<i>Corcyrogobius</i>	x	x	x	x	x	x	x	x	/	x	x6	/	x	x	x	x	x	x
	<i>Didogobius</i>	x	x	x	x	x	x	x	x	/	x	x6	/	x	x	x	x	x	x
	<i>Gammogobius</i>	x	x	x	x	x	x	x	x	/	x	x7	/	x	x	x	x	x	x
	<i>Gobius</i>	x	(x)	x	x	x	x	x	x	/	x	x6-7	/	x	x	x	x	x	x
	<i>Gymnesigobius</i>	x	x	/	x	x	x	x	x	/	x	x6	/	x	x	x	x	x	x
	<i>Marcelogobius</i>	x	x	x	x	x	x	x	x	/	x	x6	/	x	x	x	x	x	x
	<i>Millerigobius</i>	x	x	x	x	x	x	x	x	/	x	x7	/	x	x	x	x	x	x
	<i>Neogobius</i>	x	x	x	x	x	x	x	x	/	x	x7	/	x	x	x	x	x	x
	<i>Odondebuena</i>	x	x	x	x	x	x	x	x	/	x	x6	/	x	x	x	x	x	x
	<i>Peter</i>	x	x	x	x	x	x	x	x	/	x	x6	/	x	x	x	x	x	x
	<i>Thorogobius</i>	x	(x)	x	x	x	x	x	x	/	x	x6-7	/	x	x	x	(x)	x	x
	<i>Vanneaugobius</i>	x	x	x	x	x	x	x	x	/	x	x7	/	x	x	x	x	x	x
	<i>Zeburus</i>	x	x	x	x	x	x	x	x	/	x	x7	/	x	x	x	x	x	x
<i>Pomatoschistus</i> -lineage	<i>Buena</i>	x	x	/	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Cryсталlogobius</i>	x	x	/	x	x	/	x	x	x	x	x12	/	/	x	x	x	x	x
	<i>Deltentosteus</i>	/	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Knipowitschia</i>	x	x	/	x	x	x	x	x	xx	x	x5-7	/	x	x	x	x	x	x
	<i>Lebetus</i>	(x)	x	/	x	x	(x)	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Ninnigobius</i>	x	x	/	x	x	x	x	x	xx	x	x6-7	/	x	x	x	x	x	x
	<i>Pomatoschistus</i>	x	x	(x)	x	x	x	x	x	x(x)	x	x6-16	/	x	x	x	x	x	x
	<i>Pseudaphya</i>	x	x	/	x	x	x	x	x	x(x)	x	x6	/	x	x	x	x	x	x
<i>Speleogobius</i>	/	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	

Continued on next page.

above other; *suborbital* row *cp* present; *oculoscapular* row *ta* absent; *interorbital* row *p* present (Fig. 23, Table 3). *Preorbital* rows with four median rows, yet poorly illustrated in *L. heterofasciatus*. Longitudinal row *r* positioned anteriorly at horizontal level of posterior nostrils; row *sa* a longitudinal row parallel to row *r*, medially of posterior nostrils; row *sb* a single papilla at anterior nostril; anteriormost *preorbital* row *sc* as one or two papillae above upper lip. Four to five *preorbital* rows. Row *ja* one or two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two lowermost rows, superior row *jc* and inferior row *jd*, each as one or two papillae between upper lip and vertical of anterior eye edge. *Suborbital* rows without transverse proliferations. Row *a* extending forward below anterior part of eye. Row *b* long, from near posterior preopercular edge to below anterior part of eye. Row *c* reaching from below anterior eye edge backwards close to vertical of posterior eye edge or behind. It starts anteriorly with two papillae, one above the other, at the vertical of front margin of eye. Row *cp* as two papillae below row *b* on posterior end of row *c*, or below

posterior end of row *c* in *L. sanzi*, not illustrated for *L. heterofasciatus*. Row *d* continuous and long from above upper lip backwards over the cheek below eye, only for *L. heterofasciatus* was illustrated with very short cheek part. *Preoperculo-mandibular* rows with external row *e* continuous, internal row *i* divided. Both rows *e* and *i* discontinuous in *L. sanzi*. Row *i* ending anteriorly at chin near frontal part of jaw. Posteriorly row *i* ends at preopercular ventral margin, row *e* extending upwards to upper preopercle. Mental longitudinal row *f* near chin tip. *Opercular* rows with transverse row *ot* anteriorly on operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Row *pc* as four to six papillae on the place of the absent PC. *Oculoscapular* rows with anterior longitudinal row *xa* above posterior edge of preopercle and anterior to it; posterior longitudinal row *xb* above operculum, row *xb* not illustrated for *L. heterofasciatus*; rows *xa* and *xb* long, appearing continuous or nearly connected in *L. friesii* and *L. sanzi*, shorter in *L. suerii*. Transverse row *z* located approximately in the area of the upper edge of preopercle. Transverse row *q* absent. Continuous

opercular		oculoscapular													anterior dorsal					interorbital				
<i>oi</i>	<i>pc</i>	<i>aoc2</i>	<i>xa</i>	<i>ta</i>	<i>xb</i>	<i>z</i>	<i>q</i>	<i>u</i>	<i>tp</i>	<i>y</i>	<i>ka</i>	<i>kb</i>	<i>kc</i>	<i>la</i>	<i>lb</i>	<i>poc</i>	<i>n</i>	<i>g</i>	<i>o</i>	<i>m</i>	<i>h</i>	<i>p</i>	<i>w</i>	<i>aoc1</i>
x	x	/	x	x	x	x	x	x	x	x	x	x	x	x	x	/	x	x	x	/	x	x	x	/
x	x	x	x	/	(x)	x	/	x	/	/	(x)	(x)	(x)	(x)	(x)	x	x	x	x	x	x	x	/	/
x	/	/	x	/	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	/	/	/
x	x	/	x	/	x	x	x	x	/	x	x	x	x	x	x	x	x	x	x	x	x	/	/	/
x	(x)	/	x	/	x	x	x	x	x	x	(x)	(x)	(x)	(x)	(x)	(x)	x	x	x	(x)	x	/	/	/
x	x	/	x	/	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	/	/	/
x	/	/	x	/	x	x	(x)	(x)	(x)	x	x	x	x	x	x	/	x	x	x	x	x	/	/	/
x	(x)	(x)	x	/	x	x	(x)	x	/	x	(x)	(x)	(x)	(x)	(x)	x	x	x	x	x	x	/	/	(x)
x	/	/	x	/	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	/	x	/
x	/	/	x	/	x	x	x	x	x	x	x	x	x	x	x	/	x	x	x	x	x	/	/	/
x	/	/	x	/	x	x	x	x	/	x	x	x	x	x	x	x	x	x	x	x	x	/	/	/
x	/	/	x	/	x	x	x	x	(x)	x	(x)	(x)	(x)	(x)	(x)	/	x	x	x	x	x	/	/	/
x	/	/	x	/	x	x	x	x	/	x	x	x	x	x	x	(x)	x	x	x	x	x	/	/	/
x	(x)	/	x	/	x	x	x	x	x	x	x	x	x	x	x	/	x	x	x	x	x	/	/	/
x	/	/	x	/	x	x	x	x	/	x	x	x	x	x	x	/	x	x	x	x	x	/	/	/
x	/	/	x	/	x	x	x	x	(x)	x	(x)	(x)	(x)	(x)	(x)	/	x	x	(x)	(x)	x	/	/	x
x	(x)	/	x	x	x	x	x	x	/	x	x	x	x	x	x	(x)	x	x	/	x	x	/	/	(x)
x	/	/	x	x	x	x	x	x	/	x	x	x	x	x	x	/	x	x	x	x	x	/	/	/
x	/	/	x	x	x	x	x	x	/	x	x	x	x	x	x	x	x	x	x	x	x	/	/	/
x	(x)	/	x	/	x	x	/	x	/	/	x	x	(x)	/	/	x	x	x	(x)	(x)	x	/	/	x
x	/	/	x	/	x	x	x	x	/	x	x	x	x	x	x	/	x	x	x	x	x	/	/	/
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x	(x)	/	x	/	x	x	/	x	/	/	x	x	x	x	x	x	x	x	x	x	x	/	/	/
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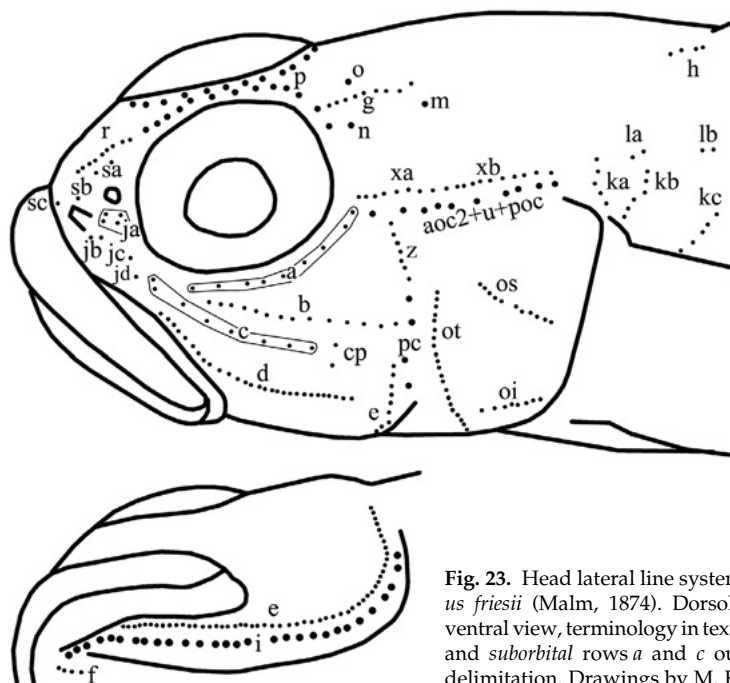


Fig. 23. Head lateral line system of *Lesueurigobius friesii* (Malm, 1874). Dorsolateral view and ventral view, terminology in text. Preorbital row *ja* and suborbital rows *a* and *c* outlined to clarify delimitation. Drawings by M. Kovačić.

row of papillae (*aoc2+u+poc*) on the place of missing oculoscapular canals, extending in *L. heterofasciatus* along posterior eye edge up to the interorbital region. Row *y* absent. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* above them, not illustrated for *L. heterofasciatus*. Anterior dorsal rows with row *n* on anterior nape behind eye as one or two papillae. Transverse rows *o* as single papillae. Longitudinal row *g* long and reaching anteriorly in front of row *n* at posterior eye edge; only in *L. heterofasciatus* short, ending behind row *o*. Row *m* single papilla below posterior part of row *g*. Longitudinal row *h* near the dorsal midline in front of first dorsal fin origin, long in *L. suerii* and *L. sanzii*, short in *L. friesii* and *L. heterofasciatus*. Interorbital rows with continuous longitudinal row of papillae *p* on the place of the missing interorbital part of AOC, extending shortly down posterior eye edge; connected to *aoc2* at posterior eye edge in *L. heterofasciatus*.

#### HLLS of *Gobius*-lineage genera

##### *Chromogobius* de Buen, 1930

The genus with homogeneous head canal and pore presence among three presently recognized congeneric species (Table 2). Head with AOC and PC, car-

rying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively. POC absent in three known species (Fig. 24, Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* present (Fig. 24). Preorbital rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* medially to interspace between anterior and posterior nostrils; transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; transverse row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek, anteriorly from below posterior iris and posteriorly behind vertical of posterior eye edge. Seven transverse rows *c*, five in front of row *b*, two above and one below row *b*. Four rows continuous, fifth and seventh only with upper part, sixth divided. Longitudinal row *d* above upper lip and continuous backwards along lower cheek, nearly reaching vertical of posterior eye edge. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin near frontal part of jaw and

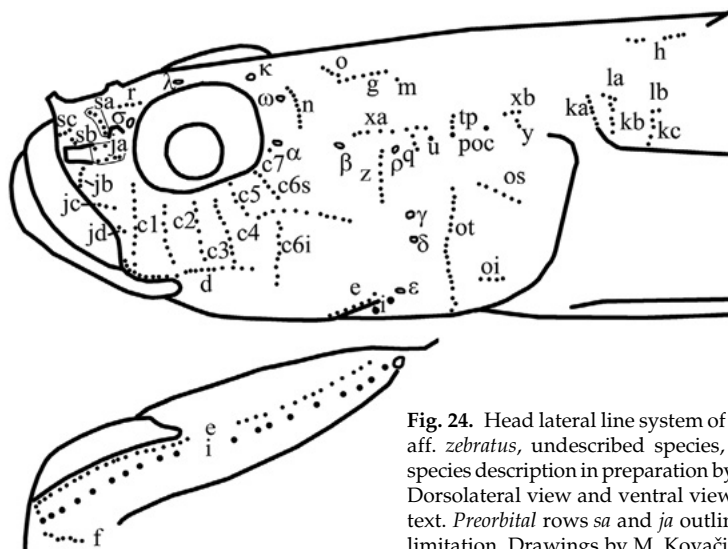


Fig. 24. Head lateral line system of *Chromogobius* sp. aff. *zebratus*, undescribed species, (ms of the new species description in preparation by the first author). Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa* and *ja* outlined to clarify delimitation. Drawings by M. Kovačić.

posteriorly at preopercular ventral margin. Mental row *fl* longitudinal anteriorly beginning near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum, superior longitudinal row *os* about centred on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with anterior longitudinal row *xa* continuous above posterior edge of preopercle; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it; row *u* as single papilla between row *q* and row *poc*; transverse row *tp* between rows *xa* and *xb*. Additional *poc* row present as two papillae on place of absent POC canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radially spreading from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* at anterior nape behind eye. Transverse rows *o* anterior to vertical of preopercular edge, distant at dorsal midline from sister row. Longitudinal row *g* ends anteriorly in front of row *o*, at row *o*, or slightly behind. Longitudinal row *m* below posterior part of row *g* or below behind of it. Longitudinal row *h* divided or continuous, near the dorsal midline in front of first dorsal fin origin. Interorbital rows *w* and *p* absent.

### *Corcyrogobius* Miller, 1972

The genus with homogeneous head canal and pore presence among three congeneric species, but with recorded intraspecific variability of pores in one of the species (Table 2). Head with AOC present and

POC and PC absent in three known species. The presence of AOC pores varies from  $\sigma$ ,  $\lambda$ ,  $\omega$ ,  $\alpha$ ,  $\rho$  in the part of *C. liechtensteini* individuals according to Miller (1972) to presence of pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  recorded in all three species (Miller 1988, Kovačić et al. 2020) (Fig. 25, Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* absent (Fig. 25). Preorbital rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* medially to interspace between anterior and posterior nostrils; transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; transverse row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge, row *jd* entering space between upper lip and anterior eye in *C. pulcher*. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek and mostly behind vertical of posterior eye edge. Six transverse rows *c*, four in front of row *b*, two above and none below row *b*. Three rows complete, fourth divided, fifth and sixth only with upper part. Longitudinal row *d* above upper lip and backwards along lower cheek, discontinuous between supralabial and cheek part and not reaching vertical of posterior eye edge. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, row *i* ending anteriorly near chin and frontal part

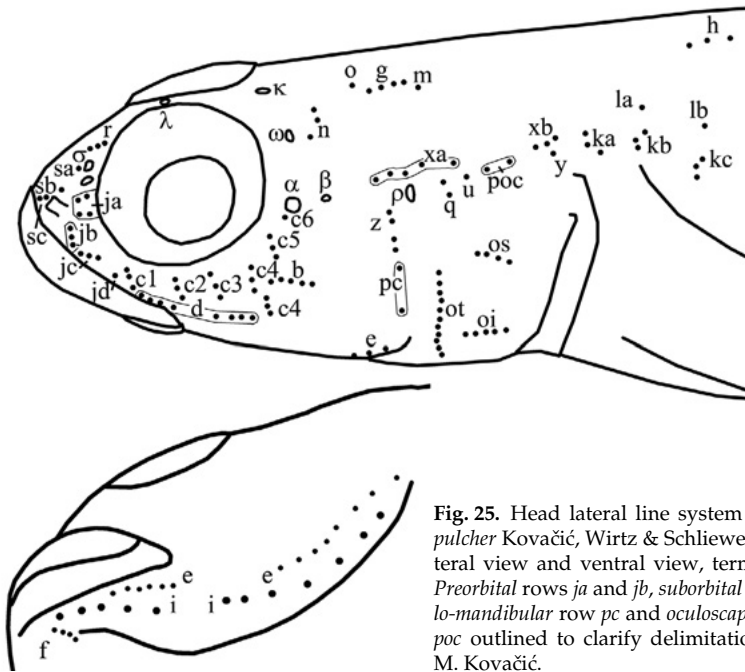


Fig. 25. Head lateral line system of *Corcyrogobius pulcher* Kovačić, Wirtz & Schliewen, 2020. Dorsolateral view and ventral view, terminology in text. Preorbital rows *ja* and *jb*, suborbital row *d*, preoperculo-mandibular row *pc* and oculoscapular rows *xa* and *poc* outlined to clarify delimitation. Drawings by M. Kovačić.

of jaw, row *e* ending posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum, superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Two *pc* papillae on place of missing PC. Oculoscapular rows with anterior longitudinal row *xa* continuous, above posterior edge of preopercle and anterior operculum. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it; row *u* as single papilla between row *q* and *poc* row. Additional *poc* row present as two papillae on place of absent POC canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radially spreading from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* at anterior nape behind eye. Transverse row *o* single papilla roughly in vertical level to preopercular edge and distant from sister papilla. Longitudinal row *g* ends behind transverse level of row *o*. Single papilla of row *m* below horizontal level of row *g* and behind vertical to its posterior edge. Longitudinal row *h* continuous, near dorsal midline in front of first dorsal fin origin. Interorbital rows absent.

#### *Didogobius* Miller, 1966

Head canals with pores are variable among the four recognized species of *Didogobius* (Table 2). They all have in common only the absence of POC. The pattern is same for two species, *D. schlieveni* and *D. kochi*, having AOC and PC and carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively (Fig. 26). However, *D. bentuvii* and *D. lanceolatus* also lack PC, having just AOC pores  $\sigma$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$ .

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied into separate perpendicular rows; oculoscapular row *tp* present (Fig. 26). Preorbital rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* located medially to posterior nostril, transverse row *sb* medially to anterior nostril; longitudinal row *sc* is anteriormost preorbital row above the upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; transverse row *jb* below and posterior to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek, reaching anteriorly from below posterior eye edge to posteriorly far behind vertical of posterior eye edge. Six transverse rows *c*, four in



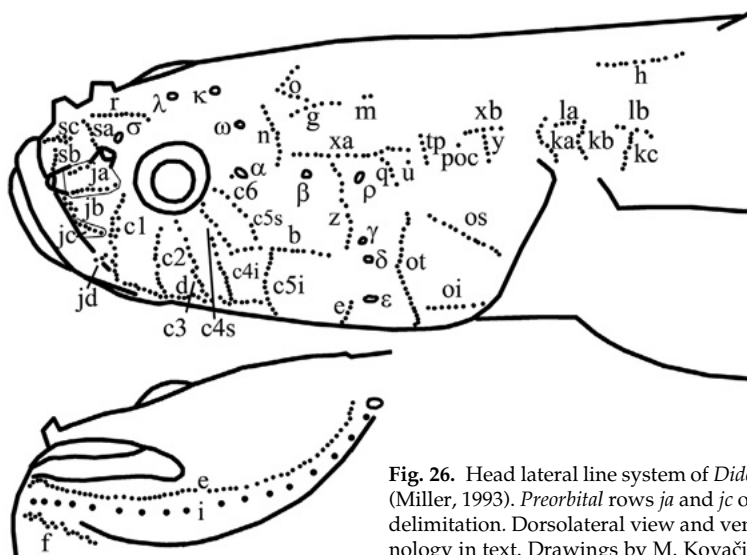


Fig. 26. Head lateral line system of *Didogobius schlieveni* (Miller, 1993). Preorbital rows *ja* and *jc* outlined to clarify delimitation. Dorsolateral view and ventral view, terminology in text. Drawings by M. Kovačić.

front of row *b*, two above and one below row *b*. Four rows continuous, one divided and one with the upper part only, except for *D. schlieveni*, having also the fourth row in front of row *b* divided with an overlapping upper and lower part. Longitudinal row *d* from above upper lip and backwards along lower cheek, reaching or surpassing vertical of posterior eye edge, continuous, in *D. lanceolatus* divided into three parts. Preoperculo-mandibular rows with external row *e* divided and internal row *i* divided or continuous, row *i* parallel to row *e*, both ending anteriorly at chin near frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum, superior longitudinal row *os* on upper part of operculum, and inferior longitudinal row *oi* on lower part of operculum. Row *pc* as two papillae on the place of absent PC in *D. bentuvii* and *D. lanceolatus*. Oculoscapular rows with the anterior longitudinal row *xa* long continuous, anteriorly in front of vertical to posterior edge of preopercle, posteriorly reaching above half of operculum. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in the area of the upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it; row *u* as single papilla between row *q* and row *poc*. Transverse row *tp* between rows *xa* and *xb*. The additional *poc* row present as one papilla on the place of absent POC canal, but not illustrated for *D. bentuvii* in Miller (1966). Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la*

and *lb* just above them, not illustrated in Miller (1966) since skin apparently abraded in the single known specimen of *D. bentuvii*. Anterior dorsal rows with transverse row *n* at anterior nape behind eye. Transverse rows *o* anterior to vertical of preopercular edge, distant at dorsal midline from sister row in *D. lanceolatus* and *D. bentuvii*, connected in *D. kochi* and *D. schlieveni*. Longitudinal row *g* ends anteriorly at row *o* in *D. bentuvii*, behind it in *D. lanceolatus*, and clearly in front of it in the two other *Didogobius* species. Longitudinal row *m* as one to few papillae behind posterior part of row *g*, not reported by Miller (1966) for *D. bentuvii*. Longitudinal row *h* continuous, divided in *D. lanceolatus*. Interorbital rows absent.

#### *Gammogobius* Bath, 1971

Head with AOC carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ; POC and PC absent in only known species (Fig. 27, Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* present (Fig. 27). Preorbital rows with four median rows. Longitudinal row *r* anteriorly beginning above horizontal level of posterior nostrils; transverse row *sa* medially to posterior nostrils; transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; transverse row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and



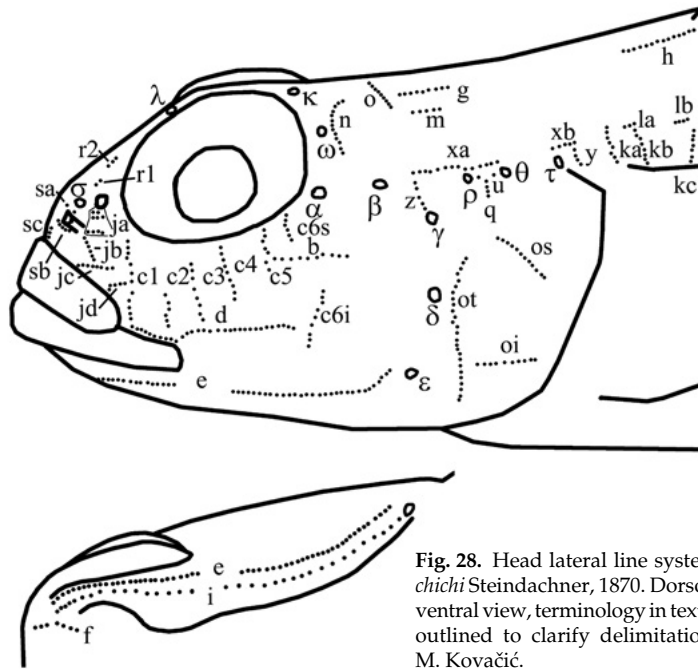


Fig. 28. Head lateral line system of *Gobius bucchichi* Steindachner, 1870. Dorsolateral view and ventral view, terminology in text. Preorbital row *ja* outlined to clarify delimitation. Drawings by M. Kovačić.

Head rows of sensory papillae (Table 3) with *suborbital* row *a* absent; *suborbital* row *c* multiplied in separate perpendicular rows; *oculoscapular* row *tp* present or absent (Fig. 28). *Preorbital* rows with five median rows, four in some smaller species. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils, divided in most species into an upper median and several lower lateral rows, or only a single one, e.g. in *G. ater* and *G. vittatus*. Transverse row *sa* medially to interspace between anterior and posterior nostrils (not illustrated in *G. salamansa*). Transverse row *sb* medially to anterior nostril. Longitudinal row *sc* is the anteriormost *preorbital* row above upper lip. Papillae of *s* rows proliferated into clusters in *G. ateriformis* and *G. salamansa* and large individuals of *G. cobitis*, *G. cruentatus*, *G. ophiocephalus*, *G. paganellus* and *G. rubropunctatus*, but rows still recognizably delimited. Five to seven lateral *preorbital* rows. Row *ja* as two or three rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril, as one or two rows or cluster of papillae; superior row *jc* and inferior row *jd* are single longitudinal rows between upper lip and vertical of anterior eye edge. All papillae of *j* rows are proliferated in clusters in *G. ateriformis* and large individuals of *G. cobitis*, *G. cruentatus*, *G. paganellus* and *G. rubropunctatus*, with delimitation between rows almost blurred. In *G. salamansa* and *G. ophiocephalus*, just rows *jc* and *jd*

are proliferated into clusters. *Suborbital* rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek below posterior eye and behind vertical of posterior eye edge. Six or seven transverse rows *c*, four or five in front of row *b*, one or two above and one or two below row *b*. Lower part of first and second transverse rows *c* can be widened by irregularly doubled papillae in some *Gobius* species e.g. in *G. cobitis* and *G. rubropunctatus*. Four to five rows complete, fifth and sixth or only sixth divided, seventh row only present in *G. ophiocephalus* and in some *G. geniporus* individuals, with an upper part just in front of pore *α*; in addition a seventh row as a single papilla inside pore *α* is present in *G. xouriger* and in some individuals of other species, e.g. *G. niger*. Longitudinal row *d* extends above upper lip backwards along lower cheek, continuous or divided in two or three parts with one or two gaps on cheek, reaching or almost reaching vertical of posterior eye edge. Anterior part of row *d* can be widened by irregularly doubled papillae in some species, e.g. in *G. cobitis*. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided behind the posterior angle of jaws; row *i* parallel to row *e*, both ending anteriorly at chin near frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* near chin tip, either longitudinal or forming a cluster in *G. ater*, *G. cobitis*, *G. cruentatus*, *G. geniporus* and *G. paganellus*. *Oper-*

cular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* anteriorly beginning above posterior edge of preopercle, or extending to pore  $\beta$  in *G. cruentatus*, *G. ophiocephalus* and *G. tetrophthalmus*; row *xa* extending backwards to row *tp* or to above pore  $\theta$ , divided in two parts by row *q* in *G. ateriformis*, *G. ophiocephalus* and *G. paganellus*. Posterior longitudinal row *xb* above posterior edge of operculum; transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it, also upwards in *G. ateriformis*, *G. ophiocephalus* and *G. paganellus*. In *G. ophiocephalus* and *G. paganellus*, transverse row *q* is additionally divided in an upper anterior part and a lower posterior part. Row *q* not reported for *G. salamansa*. Row *u* present as two papillae between pore  $\rho$  and pore  $\theta$ , either both behind row *q* or one in front of row *q* in *G. vittatus* and *G. ophiocephalus*; row *u* absent in *G. ater*, *G. ateriformis*, *G. paganellus* and *G. salamansa* because AOC and POC are connected. Transverse row *tp* is located between rows *xa* and *xb* in *G. ater*, *G. ateriformis*, *G. cobitis*, *G. paganellus* and *G. salamansa*, and below posterior end of row *xa* in *G. ophiocephalus*; absent in other species; row *tp* is divided by larger posterior papilla *u* in *G. cobitis* and *G. ophiocephalus*. Transverse row *y* just below row *xb*. Rows *xb* and *y* proliferated into multiplied disorganized row patches in larger *G. cobitis* individuals. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. *Anterior dorsal* rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly vertical to preopercular edge and at dorsal midline distant from sister row, except in *G. auratus* and *G. fallax*, where they are connected or almost connected. Longitudinal row *g* ends anteriorly behind row *o*, reaching it in *G. kolombatovici*, *G. salamansa* and *G. tetrophthalmus*, or passing anteriorly row *o* in *G. rubropunctatus*. Longitudinal row *m* below posterior part of row *g* or centered below row *g*. Longitudinal row *h* continuous or divided, near dorsal midline in front of first dorsal fin origin. *Interorbital* rows absent.

***Gymnesigobius* Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019**

Head with AOC and PC, carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively, and POC absent in the only known species of the genus (Fig. 29, Table 2).

Head rows of sensory papillae (Table 3) with *preorbital* row *sb* absent; *suborbital* row *a* absent; *suborbital* row *c* multiplied into separate perpendicular

rows; *oculoscapular* row *tp* absent (Fig. 29). *Preorbital* rows with three median rows. Longitudinal row *r* above horizontal level of posterior nostrils; transverse row *sa* medially to interspace between anterior and posterior nostrils; row *sb* absent; longitudinal row *sc* is the anteriormost preorbital row above the upper lip. A single papilla visible inside pore  $\sigma$  above row *sa* papilla. Alternatively, rows *sa* and *sb* are translated upwards, with row *sa* ending inside pore  $\sigma$  due to the pore enlargement, and all four median *preorbital* rows are present. Four lateral *preorbital* rows. Row *ja* as single row positioned laterally to the interspace between anterior and posterior nostrils; row *jb* below and close to anterior nostril; superior row *jc* and inferior row *jd* backwards entering the space between upper lip and anterior eye. *Suborbital* rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek and behind vertical of eye posterior edge. Six transverse rows *c*, five in front of row *b*, one above and none below row *b*. Four rows continuous, the fifth divided into three parts, and the sixth only with upper part. A single papilla visible inside pore  $\alpha$ . Longitudinal row *d* originating above upper lip, continuing backwards along lower cheek, and finally reaching vertical of posterior eye edge. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*. Row *i* ending anteriorly near chin and frontal part of jaw. Row *e* ending posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* continuous, anteriorly beginning above posterior edge of preopercle; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Row *q* behind pore  $\rho$ , nearly longitudinally reaching backwards from it; row *u* as single rather large papilla between row *q* and row *poc*. Two larger *poc* papillae on the place of missing POC. Transverse row *y* just below row *xb*. Transverse axillary rows *ka* and *kb* radiating from upper pectoral fin base, row *kc* and longitudinal axillary rows *la* and *lb* not visible. *Anterior dorsal* rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly vertical to preopercular edge and distant at dorsal midline from sister rows. Longitudinal row *g* ends anteriorly behind level of row *o*. Longitudinal row *m* behind and below posterior part of row *g*. Longitudinal row *h* continuous, near dorsal midline in front of first dorsal fin origin. *Interorbital* rows absent.

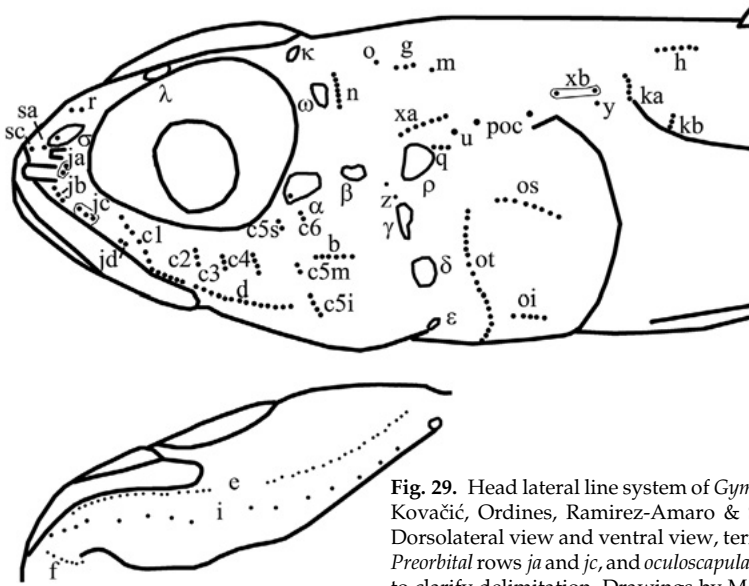


Fig. 29. Head lateral line system of *Gymmesigobius medits* Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019. Dorsolateral view and ventral view, terminology in text. Preorbital rows *ja* and *jc*, and oculoscapular row *xb* outlined to clarify delimitation. Drawings by M. Kovačić.

### *Marcelogobius* Schliewen, 2023

Head canals with pores variable among three *Marcelogobius* species (Table 2). Species share in common just the absence of POC. Other pattern varies, *M. splechnai* having more complete canals and pores, with AOC and, except for some individuals, PC, carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$  respectively (Fig. 30). *M. janetarum* always lacks PC, having only AOC pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ . In one specimen of *M. janetarum* reduction in a form of open furrow between pores  $\sigma$  and  $\lambda$  was reported (Schliewen et al. 2018). Finally, in *M. helenae* all head canals and pores are absent.

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* absent (Fig. 30). Preorbital rows with four median rows. Longitudinal row *r* above horizontal level of posterior nostrils; transverse row *sa* medially to posterior nostril, transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anterior-most preorbital row above the upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; transverse row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, both between upper the lip and vertical of anterior eye edge. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek, extending anteriorly from below posterior iris to posteriorly behind vertical of eye posterior edge. Six transverse

rows *c*, four in front of row *b*, two above and one below row *b*. Four rows continuous, one divided and one only with the upper part. Longitudinal row *d* extending from above upper lip and backwards along lower cheek, reaching or nearly reaching vertical of posterior eye edge in other species, divided below second or third row in *M. helenae*, or continuous in other two species. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin near frontal part of jaw and ending posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper operculum; inferior longitudinal row *oi* on lower part of operculum. Row *pc* as two papillae on the place of absent PC in *M. helenae*, *M. janetarum* and in individuals of *M. splechnai* when PC missing. Oculoscapular rows with anterior longitudinal row *xa* above vertical of posterior edge of preopercle; posterior longitudinal row *xb* above posterior edge of operculum. Row *aoc2* as two anterior papillae on the place of absent AOC behind eye in *M. helenae*. Transverse row *z* approximately in the area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and below it, not illustrated in Van Tassel & Kramer (2014) for *M. helenae*. Row *u* as single papilla between row *q* and row *poc*. Transverse row *tp* absent. Additional *poc* row present as one or two papillae on the place of absent POC canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal

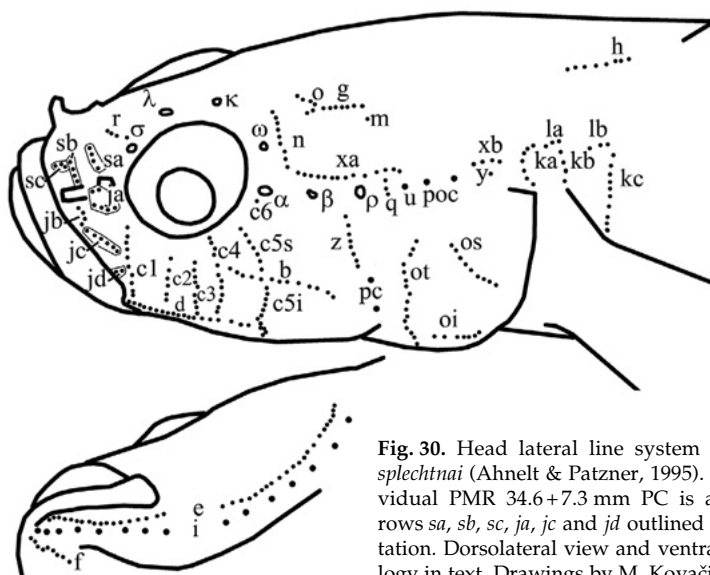


Fig. 30. Head lateral line system of *Marcelogobius splechnai* (Ahnelt & Patzner, 1995). In the male individual PMR 34.6+7.3 mm PC is absent. Preorbital rows *sa*, *sb*, *sc*, *ja*, *jc* and *jd* outlined to clarify delimitation. Dorsolateral view and ventral view, terminology in text. Drawings by M. Kovačić.

axillary rows *la* and *lb* just above them, all five axillary rows not illustrated for *M. helenae* by Van Tassell & Kramer (2014). Anterior dorsal rows with transverse row *n* at anterior nape behind eye. Transverse rows *o* anterior to vertical of preopercular edge, distant from sister rows at dorsal midline. Longitudinal row *g* ends anteriorly in front of row *o*. Longitudinal row *m* as one or two papillae below horizontal level of row *g* and behind vertical of its posterior edge. Longitudinal row *h* continuous. Interorbital rows absent, except *aocL*, present as anterior pair and posterior single papilla in the interorbital region on the place of absent AOC in *M. helenae*.

#### *Millerigobius* Bath, 1973

Head with AOC and PC, carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$  respectively and POC absent in the only known species (Bath 1973) (Fig. 31). However, several individual aberrations were observed by Vanhove et al. (2011) in adults, such as absence of pores, as presence of an additional pore present or as replacement of pore with open furrow (Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* present; transverse interorbital row *w* present (Fig. 31). Preorbital rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* located medially to interspace between anterior and posterior nostrils, transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anteriormost preorbital

row above the upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek from vertical of eye posterior edge backwards. Seven transverse rows *c*, five in front of row *b*, two above and one below row *b*. Four rows continuous, fifth and sixth divided, seventh with only the upper part. Longitudinal row *d* originating above upper lip and continuing backwards along lower cheek, not reaching vertical of posterior eye edge. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin near frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip, anteriorly close to frontal end of row *e*. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* at upper posterior part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with anterior longitudinal row *xa* continuous from above posterior edge of preopercle backwards; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it. Row *u* as one or two papillae between row *q* and row *poc*. Transverse row *tp* between rows *xa* and *xb*. Additional *poc* row present as a single papilla on the place of absent

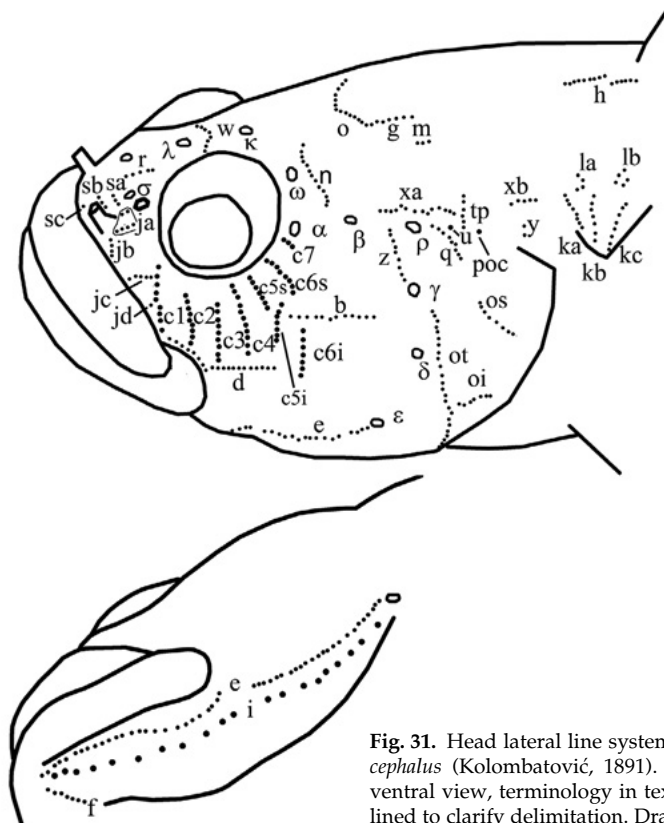


Fig. 31. Head lateral line system of *Millerigobius macrocephalus* (Kolombatović, 1891). Dorsolateral view and ventral view, terminology in text. Preorbital row *ja* outlined to clarify delimitation. Drawings by M. Kovačić.

POC canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly directly above preopercular edge and connected at dorsal midline. Longitudinal row *g* ends anteriorly on level of row *o* or slightly behind. Longitudinal row *m* below posterior part of row *g*. Longitudinal row *h* near dorsal midline in front of first dorsal fin origin. Interorbital rows with transverse interorbital row *w* as two sister rows in inorbital midline.

### *Neogobius* Iljin, 1927

The genus has a homogeneous head canal and pore presence among the four congeneric species of the area. Head with AOC, POC and PC canals present, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$ , respectively (Fig. 32, Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent, suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp*

present (Fig. 32). Preorbital rows with four rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* located medially at interspace between anterior and posterior nostrils; transverse row *sb* medially of anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above the upper lip. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; row *jb* as single row below and close to anterior nostril; superior row *jc* and inferior row *jd* as single longitudinal rows between upper lip and vertical of anterior eye edge; in *N. caspius* row *jd* is vertical and parallel to row *c1*. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek from below posterior eye to behind vertical of posterior eye edge. Seven transverse rows *c*, four in front of row *b*, three above and two below row *b*. Lower part of first transverse row *c* can be widened by irregularly doubled papillae in *N. fluviatilis* and *N. pallasi*. Four rows continuous, fifth and sixth divided, seventh only with upper part just in front of pore *a*. Longitudinal row *d* continuous, running from above upper lip backwards along lower cheek, finally





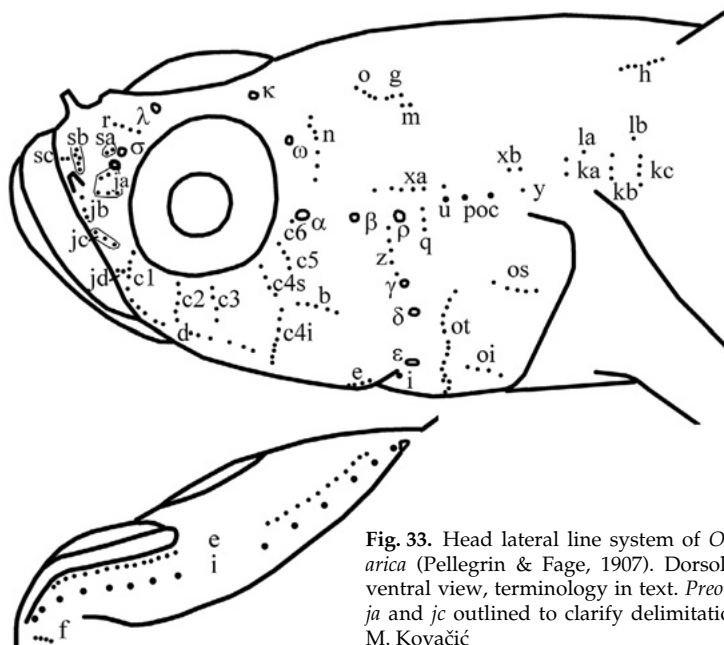


Fig. 33. Head lateral line system of *Odondebuena balearica* (Pellegrin & Fage, 1907). Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa*, *sb*, *ja* and *jc* outlined to clarify delimitation. Drawings by M. Kovačić

Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek and behind vertical of eye posterior edge. Six transverse rows *c*, four in front of row *b*, two above and none below row *b*. Three rows complete, fourth divided, fifth and sixth only with upper part. Longitudinal row *d* originates above upper lip and extending backwards along lower cheek, discontinuous with two gaps, first above end of upper lip, second on cheek below third transverse row *c* and the posterior edge of jaw, not reaching vertical of posterior eye edge. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly near chin before frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper posterior part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with anterior longitudinal row *xa*; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it; row *u* a single

papilla between row *q* and row *poc*. Additional *poc* row present as two papillae on the place of absent POC canal. Transverse row *y* is a single papilla just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base, and longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly vertical to preopercular edge and distant from sister row at dorsal midline. Longitudinal row *m* below posterior end of row *o*, longitudinal row *g* below posterior end of row *g*. Longitudinal row *h* discontinuous, near dorsal midline in front of first dorsal fin origin. Interorbital rows absent.

#### Peter Schliewen, 2023

The genus is homogeneous with regard to head canal and pore presence in the two known species (Table 2). Head with AOC and PC, carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively and POC absent in both species (Fig. 34, Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* present (Fig. 34). Preorbital rows with four median rows. Longitudinal row *r* oblique, anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* running medially to posterior nostril, and transverse row *sb* medially

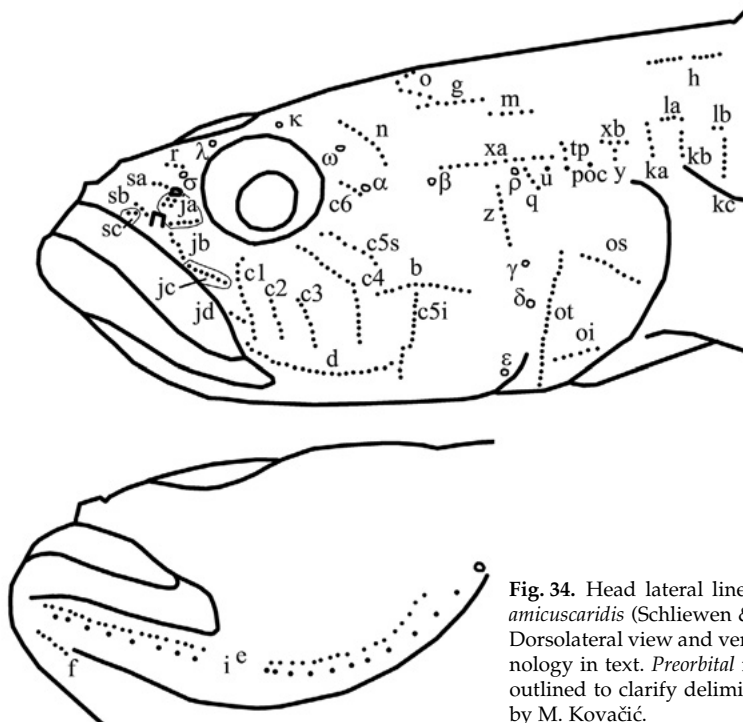


Fig. 34. Head lateral line system of *Peteramicuscaridis* (Schliewen & Kovačić, 2008). Dorsolateral view and ventral view, terminology in text. Preorbital rows *sc*, *ja* and *jc* outlined to clarify delimitation. Drawings by M. Kovačić.

to anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above the upper lip and below row *sb*. Five lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it. Transverse row *jb* below and close to anterior nostril. Two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek behind vertical of eye posterior edge. Six transverse rows *c*, four in front of row *b*, two above and one below row *b*. Four rows continuous, one divided and one with only upper part. Longitudinal row *d* extending from above upper lip backwards along lower cheek, reaching behind vertical of posterior eye edge, continuous. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin before frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with anterior longitudinal row *xa* long and continuous, originating anteriorly in front of vertical of posterior edge of preopercle, posteriorly reaching to above

half of operculum. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$ , extending downwards. Row *u* as single papilla between row *q* and row *pc*. Transverse row *tp* between rows *xa* and *xb*. Additional *pc* row present as one papilla on the place of absent POC canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* at anterior nape behind eye. Transverse rows *o* anterior to vertical of preopercular edge, connected at dorsal midline to the sister rows. Longitudinal row *m* below horizontal level of row *g* and behind vertical to its posterior edge. Longitudinal row *h* divided near dorsal midline in front of first dorsal origin. Interorbital rows absent.

#### *Thorogobius* Miller, 1969

The genus with homogeneous head canal and pore presence among the five congeneric species with available head lateral line system data. Head with AOC, POC and PC canals present with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$ , respectively, in five species (Fig. 35, Table 2), no data for *T. angolensis*.

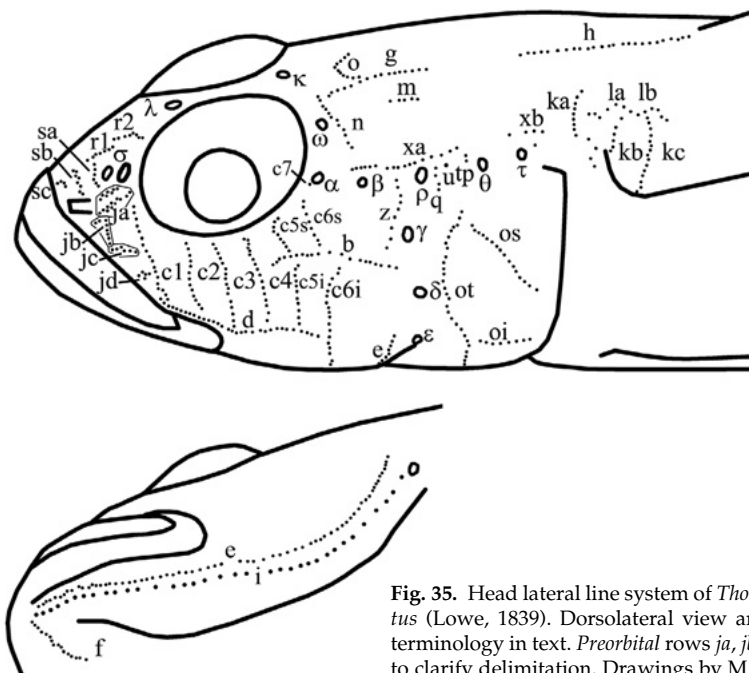


Fig. 35. Head lateral line system of *Thorogobius ephippiatus* (Lowe, 1839). Dorsolateral view and ventral view, terminology in text. Preorbital rows *ja*, *jb*, and *jc* outlined to clarify delimitation. Drawings by M. Kovačić.

Head rows of sensory papillae (Table 3) with *suborbital* row *a* absent; *suborbital* row *c* multiplied in separate perpendicular rows; *oculoscapular* row *tp* present or absent (Fig. 35).

*Preorbital* rows with five median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils, divided in upper median and lower lateral rows; transverse row *sa* extending medially to interspace between anterior and posterior nostrils, row *sa* not reported for *T. laureatus*; transverse row *sb* extending medially to anterior nostril; row *sc* is the anteriormost *preorbital* row above upper lip. Four to five lateral *preorbital* rows. Row *ja* as one or two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. *Suborbital* rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek, below posterior eye and behind vertical of posterior eye edge. Six or seven transverse rows *c*. Seven *c* rows in *T. ephippiatus*, *T. macrolepis* and *T. rofeni*, four in front of row *b*, three above and two below row *b*. Four rows continuous, fifth and sixth divided, seventh only with upper part at pore  $\alpha$ . Seventh row not reported for *T. alvheimi* and *T. laureatus*. Longitudinal row *d* extending from above upper lip continuously backwards

along lower cheek, reaching vertical of posterior eye edge or behind it. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both rows may appear almost continuous in some individuals of *T. ephippiatus*. Both rows ending anteriorly at chin before frontal part of jaw and posteriorly at preopercular ventral margin. Anterior parts of both rows not reported for *T. alvheimi* and *T. laureatus*. Mental row *f* longitudinal, anteriorly starting near chin tip, but not reported in *T. alvheimi* and *T. laureatus*. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* centered above posterior edge of preopercle and continuous, only in *T. alvheimi* and *T. laureatus* divided in anterior and posterior part; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  and downwards from it, below row *xa* in *T. ephippiatus*, *T. macrolepis* and *T. rofeni*, but reaching upwards and dividing *xa* into an anterior and posterior part in *T. alvheimi* and *T. laureatus*. Row *u* as one or two papillae behind row *q*, not reported for *T. alvheimi* and *T. laureatus*, but visible on the Figures 3 and 5 in Sauberer et al. (2018) for these

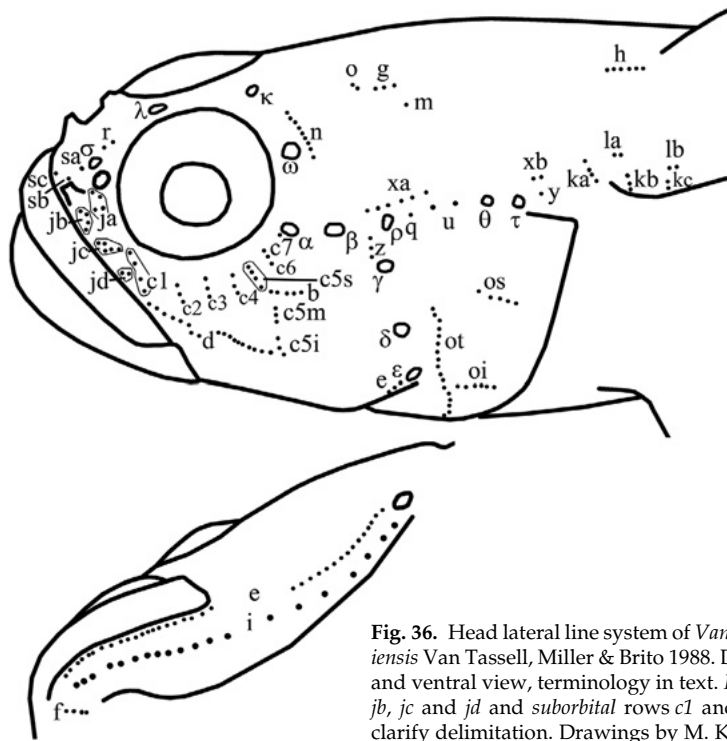


Fig. 36. Head lateral line system of *Vanneaugobius canariensis* Van Tassel, Miller & Brito 1988. Dorsolateral view and ventral view, terminology in text. Preorbital rows *ja*, *jb*, *jc* and *jd* and suborbital rows *c1* and *c5s* outlined to clarify delimitation. Drawings by M. Kovačić.

species. Transverse row *tp* between rows *xa* and *xb* present in *T. laureatus* and *T. alvheimi*, variably reported as present or absent for *T. ephippiatus* and *T. macrolepis*; not illustrated in *T. rofeni* description. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base. Longitudinal axillary rows *la* and *lb* just above them, appearing as almost connected in *T. ephippiatus* and *T. macrolepis*. All five rows not reported for *T. alvheimi* and *T. laureatus*. Anterior dorsal rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* anterior to vertical of preopercular edge and connected or nearly connected to sister rows at dorsal midline. Longitudinal row *g* long, ending anteriorly in front of row *o* and near row *n* in all species, except for ending on row *o* in *T. rofeni*. Longitudinal row *m* below posterior part of row *g*. Longitudinal row *h* long and continuous near dorsal midline, extending from in front of first dorsal fin to above opercular edge or in front of it. Interorbital rows absent.

#### *Vanneaugobius* Brownell, 1978

Head canals with all three species sharing the same pores of AOC and PC (Table 2). POC variably present among three presently recognized species, present

in *V. canariensis*, absent in the other two species (Table 2). Head with AOC and PC, carrying pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively, and *V. canariensis* also with POC, carrying pores  $\theta$ ,  $\tau$  (Fig. 36).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* absent (Fig. 36). Preorbital rows with four median rows. Longitudinal row *r* above horizontal level of posterior nostrils; transverse row *sa* extending medially to interspace between anterior and posterior nostrils; transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above upper lip. Five lateral preorbital rows, row *ja* as two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; superior row *jc* and inferior row *jd*, above upper posterior lip, entering the space between upper lip and anterior eye. Suborbital rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek, below vertical of eye posterior edge. Seven transverse rows *c*, five in front of row *b*, two above and none below row *b*. Four rows continuous, fifth divided in three parts, and sixth and seventh only with upper part. Longitudinal row *d* extending from above upper lip backwards along lower cheek,

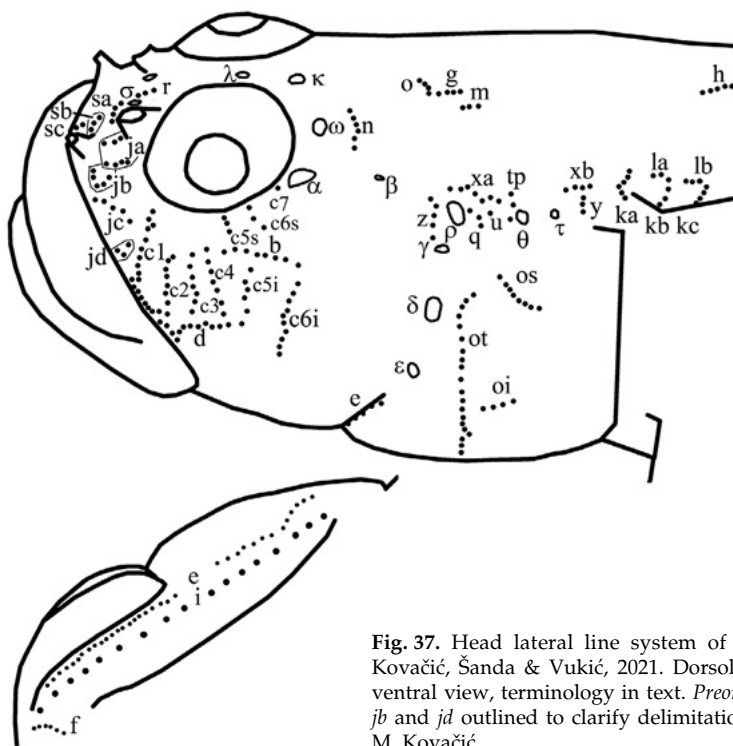


Fig. 37. Head lateral line system of *Zebrus pallaoroi* Kovačić, Šanda & Vukić, 2021. Dorsolateral view and ventral view, terminology in text. Preorbital rows *sb*, *ja*, *jb* and *jd* outlined to clarify delimitation. Drawings by M. Kovačić.

continuous or divided on cheek, reaching to vertical of posterior eye edge. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin before frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with anterior longitudinal row *xa* anteriorly beginning above posterior edge of preopercle. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Row *q* behind pore  $\rho$ ; row *u* as one or two comparatively large papillae between row *q* and POC or row *poc*. A single comparatively large *poc* papilla on the place of missing POC in *V. dollfusi* and *V. pruvoti*. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly vertical to preopercular edge and distant at dorsal midline from sister rows. Longitudinal row *g* ends anteriorly behind level of row *o*. Longitudinal row *m* below horizontal level of row *g* and behind

of vertical of its posterior edge. Longitudinal row *h* continuous, near dorsal midline in front of first dorsal fin origin. Interorbital rows absent.

### *Zebrus de Buen, 1930*

The genus is homogeneous with regard to head canal and pore presence in the two congeneric species (Table 2). Head with AOC, POC and PC canals present in both known species, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$ , respectively (Fig. 37, Table 2).

Head rows of sensory papillae (Table 3) with suborbital row *a* absent; suborbital row *c* multiplied in separate perpendicular rows; oculoscapular row *tp* present (Fig. 37). Preorbital rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; transverse row *sa* extending medially to interspace between anterior and posterior nostrils; transverse row *sb* medially to anterior nostril; longitudinal row *sc* is the anteriormost preorbital row above upper lip. Five to six lateral preorbital rows. Row *ja* as two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril, as one or two rows or as a cluster of papillae; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior

eye edge. *Suborbital* rows without longitudinal row *a*. Longitudinal row *b* on upper half of cheek and with the greater part below posterior eye. Seven transverse rows *c*, four in front of row *b*, three above and two below row *b*. Four rows continuous, fifth and sixth divided, seventh only with an upper part. Longitudinal row *d* extending from above upper lip continuously backwards along lower cheek, not reaching vertical of posterior eye edge. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin before frontal part of jaw and posteriorly near preopercular ventral margin. Mental row *f* longitudinal near chin tip. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* anteriorly beginning above posterior edge of preopercle; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$ , and oriented downwards; row *u* as two papillae between row *q* and pore  $\theta$ . Transverse row *tp* between rows *xa* and *xb*. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. *Anterior dorsal* rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly vertical to preopercular edge and distant at dorsal midline from sister rows. Longitudinal row *g* ends anteriorly in transverse level of row *o* or slightly behind. Longitudinal row *m* below posterior part of row *g*. Longitudinal row *h* continuous or divided, near dorsal midline in front of first dorsal fin origin. *Interorbital* rows absent.

## HLLS of *Pomatoschistus*-lineage genera

### *Buenia* Iljin, 1930

Head canals with variable pore development in the four presently recognized species (Fig. 38, Table 2). Head with AOC, POC and PC canals present in *B. affinis*, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$ , respectively (Kovačić 2002). Head with AOC, POC and PC canals present in *B. jeffreysii*, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$ , respectively or POC as open furrow (Kovačić et al. 2018b). *B. massutii* with AOC semiclosed with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\rho$  and with additional pores or open furrows from interorbital region to pore  $\rho$ , pores  $\sigma$ ,  $\lambda$ ,  $\kappa$  are always present as well defined pores, while  $\omega$ ,  $\alpha$ ,  $\rho$  are in

some specimens replaced by an open furrow; POC absent; PC with pores  $\gamma$ ,  $\delta$ ,  $\varepsilon$ , or replaced by open furrows or with additional pores (Kovačić et al. 2017) (Fig. 38). *B. lombartei* with AOC semi-closed with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$  and additional pores and open furrows, POC with pores  $\theta$  and  $\tau$  or as open furrow. PC with pores  $\gamma$ ,  $\delta$ ,  $\varepsilon$  or as open furrow (Kovačić et al. 2018b).

Head rows of sensory papillae (Table 3) with low papillae counts in rows, many rows with just one or two papillae; *preorbital* row *sb* absent; *suborbital* row *a* a single longitudinal row; *suborbital* row *c* a single longitudinal row, anteriorly starting with two papillae, one above the other, at vertical of frontal eye margin; *suborbital* row *cp* present; *oculoscapular* row *ta* absent (Fig. 38). *Preorbital* rows with three median rows reduced to one or two papillae. Longitudinal row *r* located anteriorly slightly above horizontal level of posterior nostrils; transverse row *sa* medially to interspace between anterior and posterior nostrils; row *sb* absent; longitudinal row *sc* as the anteriormost *preorbital* row above upper lip. Four lateral *preorbital* rows as one or two papillae each. Row *ja* laterally to between anterior and posterior nostrils; transverse row *jb* below and close to anterior nostril; two lowermost rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. *Suborbital* rows without transverse proliferation. Row *a* restricted to below rear part of eye; row *b* at or behind vertical to posterior eye edge; row *c* below anterior eye and mideye, anteriorly starting with two papillae one above the other at vertical of frontal eye margin; row *cp* as two papillae below row *a*; row *d* divided into a supralabial part and a very short cheek part. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin behind frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. *Opercular* rows with transverse row *ot* positioned anteriorly on operculum; superior longitudinal row *os* in upper posterior part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* divided into an anterior part above preopercular edge and a posterior part above midoperculum; posterior longitudinal row *xb* above posterior edge of operculum. Row *z* at upper part of preopercular edge. Row *q* a single papilla behind pore  $\rho$ . Row *u* a single papilla between row *q* and POC, but row *u* not visible in *B. massutii*. Row *y* as single papillae below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above rows *ka*, *kb* and *kc*. *Anterior dorsal* rows with

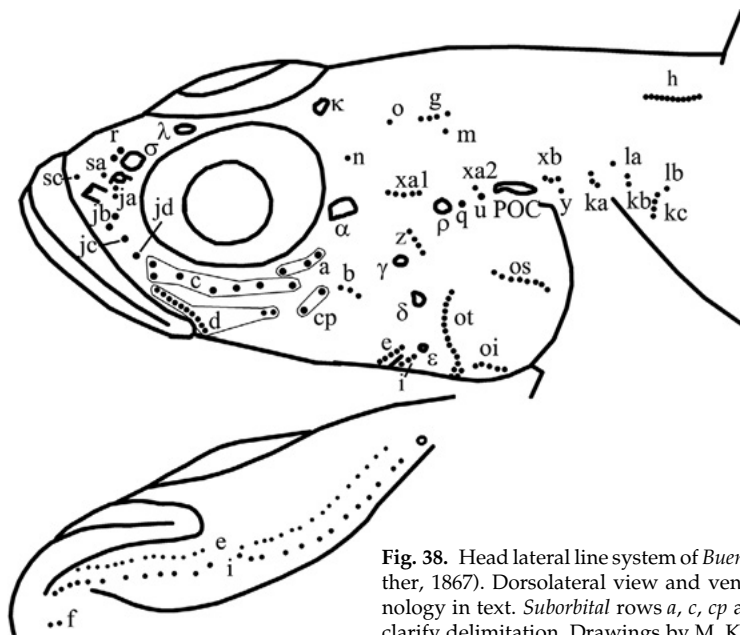


Fig. 38. Head lateral line system of *Buenia jeffreysii* (Günther, 1867). Dorsolateral view and ventral view, terminology in text. Suborbital rows *a*, *c*, *cp* and *d* outlined to clarify delimitation. Drawings by M. Kovačić.

transverse row *n* on anterior nape behind eye as a single papilla. Transverse rows *o* single papilla anterior to vertical of preopercular edge. Longitudinal row *g* ends anteriorly behind row *o*. Row *m* single papilla below posterior part of row *g*. Longitudinal row *h* divided or continuous, near dorsal midline in front of first dorsal fin origin. All anterior dorsal rows not visible in *B. massutii*, which is probably an artifact due to damage of this body area after trawl and beam trawl collection (Kovačić et al. 2017). Interorbital rows absent.

#### *Crystallogobius* Gill, 1863

Head canals and pores absent in the only known species of the genus (Fig. 39, Table 2).

Head rows of sensory papillae (Table 3) with preorbital row *sb* absent and row longitudinal *sa* present; suborbital row *a* single longitudinal row; suborbital row *c* multiplied into separate perpendicular rows, but many rows remain as single papilla; suborbital rows *cp* and *d* absent; oculoscapular row *ta* present; interorbital rows *p* and *w* present; transverse anterior dorsal rows and oculoscapular row *kb* prolonged (Fig. 39). Preorbital rows with three median rows. Longitudinal row *r* anteriorly extended, almost reaching horizontal level of anterior nostrils; row *sa* longitudinal and parallel to row *r*, starting anteriorly between row *r* and anterior nostrils and extended backwards; row *sc* is a single papilla and

is the anteriormost preorbital row above upper lip. Three lateral preorbital rows. Row *ja* as a single row below between anterior and posterior nostrils; row *jb* absent; superior row *jc* between upper lip and vertical of anterior eye edge; inferior row *jd* is a single papilla below row *jc*. Suborbital rows compressed vertically and shifted backwards, probably due to the narrowed cheek. The entire longitudinal row *a* is behind anterior eye edge. Longitudinal row *b* on upper half of cheek, anteriorly ending behind vertical of posterior eye edge. About a dozen transverse rows *c*, many of them as a single papilla. Longitudinal row *d* absent. Even if any *d* papilla has remained above upper lip, it cannot be distinguished from the *c* papillae present there neither by size or by placement. Preoperculo-mandibular rows with external row *e* divided, ending anteriorly at chin behind frontal part of jaw and posteriorly at preopercular ventral margin; internal row *i* parallel to row *e* and also divided, anterior part with only two papillae visible behind posterior angle of jaw. Mental row *f* as a short longitudinal row near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows shifted upwards compared to their standard position in gobies relative to eye, with longitudinal rows reaching horizontal level of eye dorsal edge. Transverse row *ta* behind upper half of eye. Anterior longitudinal row *xa*

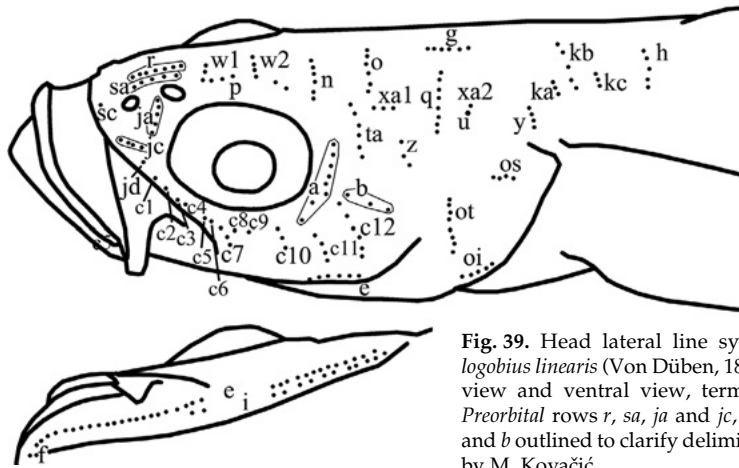


Fig. 39. Head lateral line system of *Crystallogobius linearis* (Von Dübén, 1845). Dorsolateral view and ventral view, terminology in text. Preorbital rows *r*, *sa*, *ja* and *jc*, suborbital rows *a* and *b* outlined to clarify delimitation. Drawings by M. Kovačić.

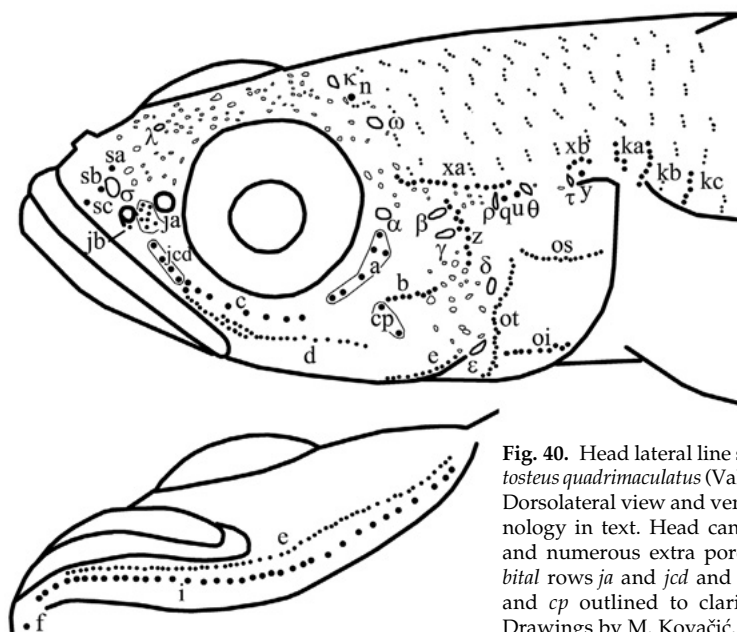
divided in an anterior part anterior to vertical of preopercular edge, and with posterior part as single papilla above midoperculum; posterior longitudinal row *xb* not visible. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* extending up onto predorsal area; row *u* as a single papilla behind row *q*. Transverse row *y* above posterior edge of operculum. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; *kb* long, reaching upwards to horizontal level of row *g*; longitudinal axillary rows *la* and *lb* not visible. Anterior dorsal with transverse row *n* on anterior nape behind eye, from horizontal level of the dorsal eye edge upwards. Transverse rows *o* in front of vertical of posterior preopercular edge, also reaching from horizontal level of the dorsal eye edge upwards, not reaching sister row in dorsal midline. Longitudinal row *g* anteriorly ending approximately above posterior preopercular edge and well beyond row *o*. Longitudinal row *m* absent. Longitudinal row *h* as transverse row close to dorsal midline in front of first dorsal fin origin. Interorbital rows as pair of longitudinal rows *p* and two transverse rows *w* present.

#### *Deltentosteus* Gill, 1863

The genus is homogeneous with regard to head canal and pore presence in the two congeneric species. Head with AOC, POC and PC canals present in both known species, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$ , respectively, as larger pores on the canal edges. The genus is unique in having expanded head canals, head canals are broad, with numerous extra small pores scattered over canal roof (Fig. 40, Table 2).

Head rows of sensory papillae (Table 3) with preorbital row *r* absent; rows *jc* and *jd* connected; suborbital row *a* as a single longitudinal row; suborbital row *c* is a single longitudinal row, anteriorly starting with two papillae, one above the other, at vertical of frontal eye margin; suborbital row *cp* present; oculoscapular row *ta* absent, transverse anterior dorsal rows and oculoscapular rows *la* and *lb* proliferated into many uniformly scattered short vertical rows of single, paired or tripled papillae over nape and predorsal area (Fig. 40). Preorbital rows with three median rows. Longitudinal row *r* absent; transverse row *sa* medially to interspace between anterior and posterior nostrils and pore  $\sigma$ ; transverse row *sb* medially to anterior nostril, and just below pore  $\sigma$ ; longitudinal row *sc* as the anteriormost preorbital row above upper lip, all as single papilla. Alternatively, only from the position of the uppermost papilla to the pore  $\sigma$ , which is lowered more anteriorly in this species, the uppermost papilla could be identified also as row *r*, and not row *sa*. Three preorbital rows. Row *ja* between anterior and posterior nostrils and laterally to it, as a slightly disorganized row or as cluster; row *jb* as single papilla below and close to anterior nostril; two lowermost rows, superior row *jc* and inferior row *jd* connected, longitudinal along upper lip to the vertical of anterior eye edge. Suborbital rows without transverse proliferation. Row *a* only below posterior part of eye. Row *b* at vertical of posterior eye edge or behind it. Row *c* anteriorly starting below anterior eye edge with two papillae one above the other, backwards reaching posterior eye. Row *cp* as two papillae below row *a*. Row *d* continuous with overlapping supralabial and cheek parts. Preoperculo-mandibular rows with external row *e* and internal row *i* continuous from





**Fig. 40.** Head lateral line system of *Delentosteus quadrimaculatus* (Valenciennes, 1837). Dorsolateral view and ventral view, terminology in text. Head canals with regular and numerous extra pores visible. Preorbital rows *ja* and *jcd* and suborbital rows *a* and *cp* outlined to clarify delimitation. Drawings by M. Kovačić.

anteriorly near frontal part of jaw to posteriorly at preopercular ventral margin. Mental row *f* as two single papillae near chin tip. Opercular rows with transverse row *ot* anteriorly on operculum, sometimes widened because of irregularly doubled papillae; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with anterior longitudinal row *xa* continuous above posterior edge of preopercle, from near AOC to above operculum; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$  as a single papilla; row *u* as single papilla between row *q* and pore  $\theta$ . Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base. Longitudinal axillary rows *la* and *lb* proliferated into a field of scattered short vertical rows of single, paired or tripled papillae above *ka*, *kb* and *kc*, extending anteriorly to above row *xb* in *D. collonianus*. In *D. quadrimaculatus*, the entire predorsal region is uniformly covered with short vertical rows of single, paired or tripled papillae (Fig. 14). A group of longitudinal axillary rows *la* and *lb* are not distinguishable from groups of anterior dorsal rows, as it is in *D. collonianus*. Anterior dorsal rows with transverse row *n* as one or two papillae on anterior nape behind eye. On the anterior predorsal area rows *o*, *g*, *m* are proliferated into a field of numerous short vertical rows of single, paired or tripled papillae; analogously, row *h* is proliferated on the

posterior predorsal area into a field of numerous short vertical rows of single, paired or tripled papillae in *D. collonianus*. In *D. quadrimaculatus* the entire predorsal is uniformly covered with short vertical rows of single, paired or tripled papillae (Fig. 14), so the anterior and posterior groups of anterior dorsal rows are not distinguishable from this homogenous pattern, as in *D. collonianus*. Interorbital rows absent.

### *Knipowitschia* Iljin, 1927

Head canals with pores are highly variable among the twelve presently recognized species of *Knipowitschia* (Table 2). However, AOC pores  $\sigma$ ,  $\omega$  and  $\beta$  and PC pore  $\delta$  are always absent. The pattern ranges from AOC, POC and PC canals fully present with pores  $\lambda$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\epsilon$ , respectively, for most of individuals of *K. caucasica* and *K. panizzae* (Kovačić & Pallaoro 2003, Economidis & Miller 1990) to head canals with pores completely absent in *K. milleri*, *K. montenegrina* and *K. ricasolii* (Ahnelt & Bianco 1990, Ahnelt 1995, Kovačić & Šanda 2007). Intermediate stages of canal reduction are found in the seven other species, and those *K. caucasica* and *K. panizzae* individuals showing canal reduction with POC absence (Kovačić & Pallaoro 2003, Economidis & Miller 1990) or even with PC absence and shortened AOC (only in *K. caucasica*) (Ahnelt et al. 1995, Kovačić et al. 2023). Furthermore, presence of open furrows instead of enclosed canals or doubled pores is not rare among *Knipowitschia* species (e.g. Kovačić 2005a) (Fig. 41).

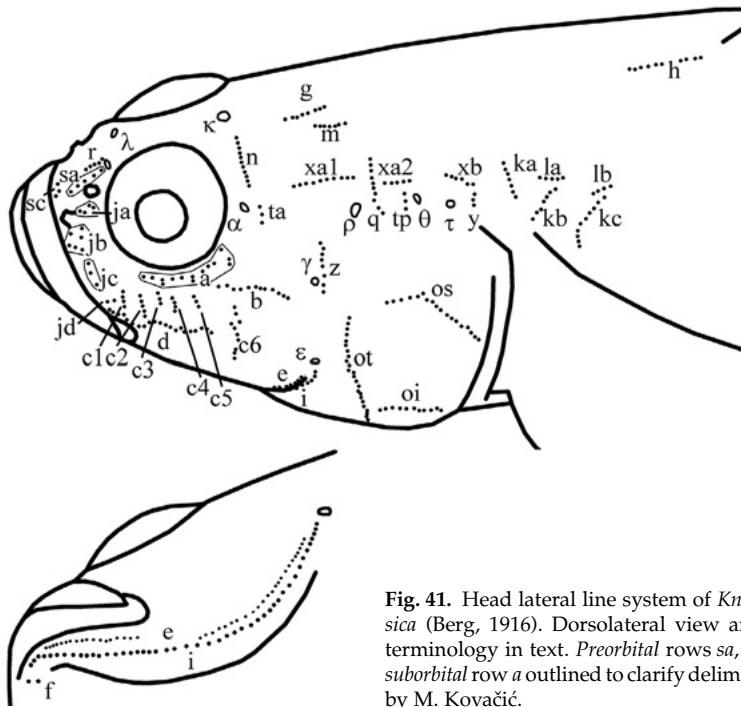


Fig. 41. Head lateral line system of *Knipowitschia caucasica* (Berg, 1916). Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa*, *ja*, *jb*, and *jc* and suborbital row *a* outlined to clarify delimitation. Drawings by M. Kovačić.

Head rows of sensory papillae (Table 3) with preorbital row *sb* absent; row *sa* longitudinal; suborbital row *a* with transverse proliferations; suborbital row *c* multiplied in separate perpendicular rows; suborbital row *cp* absent; oculoscapular row *ta* present (Fig. 41). Preorbital rows with three median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils or longer, beginning below horizontal level of posterior nostrils, variably expanding into anterior interorbital region; row *sa* also longitudinal and parallel to row *r*, starting anteriorly medially to interspace between anterior and posterior nostrils, also reaching backwards anterior interorbit; row *sc* is anteriormost preorbital row above upper lip. Four to five lateral preorbital rows. Row *ja* as one or two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two longitudinal rows superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows with longitudinal row *a* below posterior and central part of eye, with transverse proliferation with only a single posterior transverse row, e.g. in *K. byblisia*, to up to six transverse rows in *K. caucasica* and *K. pannizae*. Longitudinal row *b* on upper half of cheek behind vertical to posterior eye edge, variably extending anteriorly in the different species, reaching to below eye or not. Five to seven transverse rows *c*, four to six in front of

row *b*, one below row *b*. Longitudinal row *d* above upper lip and along lower cheek, backwards ending variably, from nearly reaching vertical of posterior eye edge to ending behind it, continuous or with a small gap between supralabial and cheek parts. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly near frontal part of jaw and posteriorly at preopercular ventral margin. In some species internal row *i* not divided, e.g. in *K. caucasica* and *K. montenegrina*. Mental row *f* longitudinal near chin tip. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* long on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Row *pc* as two or three papillae present on lost canal position when PC is absent, but not reported for every species with an absent PC, e.g. *K. ricasolii*. Oculoscapular rows with row *aoc2* present behind eye if posterior AOP absent, e.g. in *K. byblisia*, *K. milleri*, *K. montenegrina* and *K. ricasolii*. Transverse row *ta* behind pore  $\alpha$ , if pore  $\alpha$  present. If row *aoc2* present, transverse row *ta* is crossing it, only for *K. ricasolii* illustrated as placed above it (Ahnelt 1995). Anterior longitudinal row *xa* divided into an anterior part above preopercular edge and anterior to it, and into a posterior part halfway above operculum. Posterior longitudinal row *xb* above posterior edge

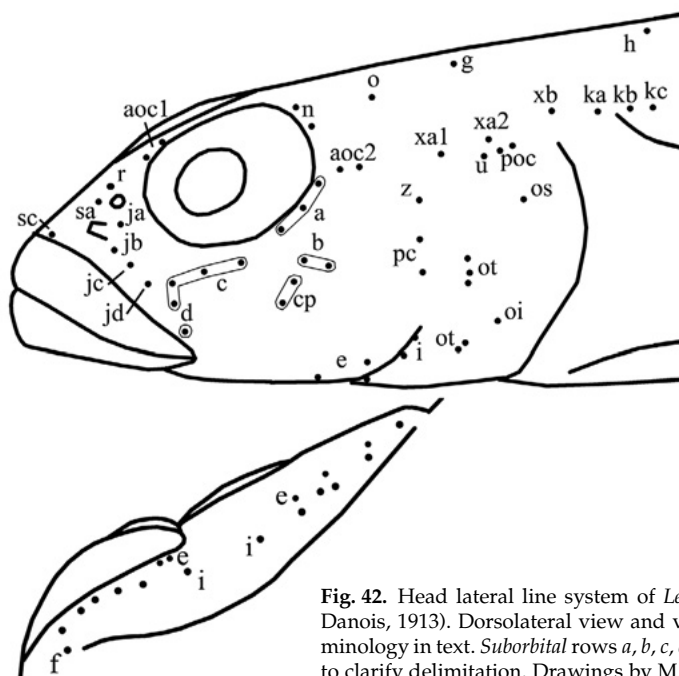


Fig. 42. Head lateral line system of *Lebetus guilleti* (Le Danois, 1913). Dorsolateral view and ventral view, terminology in text. Suborbital rows *a*, *b*, *c*, *cp* and *d* outlined to clarify delimitation. Drawings by M. Kovačić.

of operculum. Transverse row *z* approximately in the area of upper edge of preopercle. Transverse row *q* behind pore  $\rho$ , running vertically between *xa1* and *xa2*. Some species with row *u* as one or two larger papillae behind row *q*, species with no row *u* feature a short transverse row *tp* on same place, i. e. below the posterior part of row *xa* and not extending above it. Row *poc* as one or two papillae present on lost canal position when POC is absent, but not reported for all species with absent POC, e. g. *K. iljini*. Transverse row *y* just below row *xb*, not reported in *K. caunos* and *K. iljini*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base, and longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* consistently lost in all *Knipowitschia* species. Longitudinal row *g* placed at about above the posterior preopercular edge or extending forward from there. Longitudinal row *m* present below posterior part of row *g*. Longitudinal row *h* continuous, or divided, near dorsal midline in front of first dorsal fin origin, not reported in some species, e. g. not in *K. byblisia*. Interorbital rows present when interorbital part of AOC is absent, row *aoc1* as one or two pairs of enlarged interorbital papillae anteriorly in *K. radovici*, or as pair of longitudinal rows *p* with multiple papillae in other species, or even with an additional transverse row *w* in posterior interorbital region in *K. byblisia* and *K. montenegrina*.

#### *Lebetus* Winther, 1877

Head canals and pores absent in the three known species (Fig. 42, Table 2).

Head rows of sensory papillae (Table 3) with a low number of papillae in rows, many rows with just as a single or two papillae; preorbital row *sb* absent; suborbital row *a* single longitudinal row; suborbital row *c* single longitudinal row, anteriorly starting with two papillae one above the other at vertical of frontal eye margin; suborbital row *cp* present; oculoscapular rows *ta*, *q*, *tp*, *y*, *la* and *lb* absent; head canal replacement rows *aoc1*, *aoc2*, *poc* and *pc* present (Fig. 42). Preorbital rows with three median rows, each reduced to a single papilla. Row *r* positioned anteriorly slightly above horizontal level of posterior nostrils, not recorded for *L. patzneri*; transverse row *sa* placed medially to interspace between anterior and posterior nostrils; row *sb* absent; longitudinal row *sc* is the anteriormost preorbital row above the upper lip. Four lateral preorbital rows as a single papilla each. Row *ja* located laterally to distance between anterior and posterior nostrils; row *jb* below and close to anterior nostril; two lowermost rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge; row *jc* not recorded in *L. patzneri*. Suborbital rows without transverse proliferations. Row *a* located only below the rear part of eye. Row *b* as two papillae at

vertical of posterior eye edge. Row *c* below anterior eye and mideye, anteriorly starting with two papillae, one above the other, at vertical of frontal eye margin. Row *cp* as two papillae below row *a*. Row *d* reduced to supralabial part as one or two papillae. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, anterior part of row *e* short below angle of jaw, row *i* ending anteriorly before frontal part of jaw and posteriorly near preopercular ventral margin. Mental row *f* is a single papilla near the chin tip. *Opercular* rows with transverse row *ot* anteriorly on operculum divided in distant upper and lower parts, both with a few papillae; row *ot* in *L. patzneri* only with lower part. Superior longitudinal row *os* is a single papilla on upper posterior part of operculum. Inferior longitudinal row *oi* a single papilla on lower part of operculum. Row *pc* as two papillae on place of absent PC. *Oculoscapular* rows with anterior longitudinal row *xa* divided into an anterior part above the posterior preopercular edge and into a posterior part on halfway above operculum, both as a single papilla; only anterior papilla present in *L. patzneri*. Posterior longitudinal row *xb* above posterior edge of operculum. Row *aoc2* as two anterior papillae on the place of absent AOC behind eye. Row *z* at upper part of preopercular edge as a single papilla, absent in *L. patzneri*. Row *q* absent. Row *u* as a single papilla in front of row *poc*. Row *poc* on the place of absent POC, as two papillae or as a single one in *L. patzneri*. Row *y* absent. Transverse axillary rows *ka*, *kb* and *kc*, all as one to three papillae above upper pectoral fin base, but row *kc* not recorded in *L. patzneri*. Longitudinal axillary rows *la* and *lb* absent. *Anterior dorsal* rows with transverse row *n* on anterior nape behind eye as one, two or three papillae; transverse row *o* as single papilla, not recorded in *L. patzneri*; row *g* as one or two papillae close to dorsal midline and above midopercle; row *m* variably recorded as present or absent in *L. guilletti* and *L. scorpioides*, absent in *L. patzneri*; longitudinal row *h* as one or two papillae near dorsal midline in front of first dorsal fin origin. *Interorbital* row *aoc1* present as two pairs of papillae in anterior interorbital region on the place of absent AOC.

### *Ninnigobius* Whitley, 1951

Head canals with pores highly variable between two presently recognized species of *Ninnigobius* (Table 2). In addition, *N. canestrinii*, and to some degree *N. montenegrensis*, too, with a high intraspecific variability. In *N. canestrinii*, AOC is normally developed with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$ , or it has the anteriormost part reduced to an open furrow or it is absent, then having only pores  $\lambda$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$  (Kovačić 2005b). In *N. canestrinii* POC and PC are normally developed

with pores  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$ , respectively, or they are present as open furrows, or absent (Fig. 43, Table 2). *N. montenegrensis* with POC and PC absent, AOC with pore  $\lambda$  and interorbital part of canal present or absent, pores  $\kappa$  and  $\alpha$  single or doubled, pore  $\rho$  present (Table 2) (Miller & Šanda 2008). Stelbrink & Freyhof (2006) found for *N. cf. canestrinii* samples from *N. montenegrensis* type locality even greater AOC reduction, but their data lack details and was not commented by Miller & Šanda (2008) or similar degree of reduction found in the type material of *N. montenegrensis*.

Head rows of sensory papillae (Table 3) with *preorbital* row *sb* absent; row *sa* longitudinal; *suborbital* row *a* with transverse proliferations; suborbital row *c* multiplied in separate perpendicular rows; *suborbital* row *cp* absent; *oculoscapular* row *ta* present (Fig. 43). *Preorbital* rows with three median rows. Longitudinal row *r* anteriorly beginning at horizontal level of posterior nostrils; row *sa* also longitudinal and parallel to row *r*, starting anteriorly medially at level of interspace between anterior and posterior nostrils and then extending backwards; row *sc* is the anteriormost *preorbital* row above the upper lip. Four to five lateral *preorbital* rows. Row *ja* as one or two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. *Suborbital* rows with longitudinal row *a* below posterior and central part of eye, with transverse proliferations varying from a single posterior transverse row to up to five transverse rows. Longitudinal row *b* on upper half of cheek, anteriorly from below posterior iris and posteriorly extending behind vertical of posterior eye edge. Six to seven transverse rows *c*, four to six in front of row *b*, one or two below row *b*. Longitudinal row *d* originating above upper lip, extending backwards along lower cheek, nearly reaching vertical of posterior eye edge or behind it, continuous or with a small gap between supralabial and cheek parts. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly before frontal part of jaw and posteriorly near preopercular ventral margin. Mental row *f* longitudinal near chin tip. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* long on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Row *pc* as two papillae present on the lost canal position when PC absent. *Oculoscapular* rows with transverse row *ta* behind pore  $\alpha$ , extending upwards from its horizontal level. Anterior longitudinal row *xa* divided into an anterior part above the preopercular edge and into

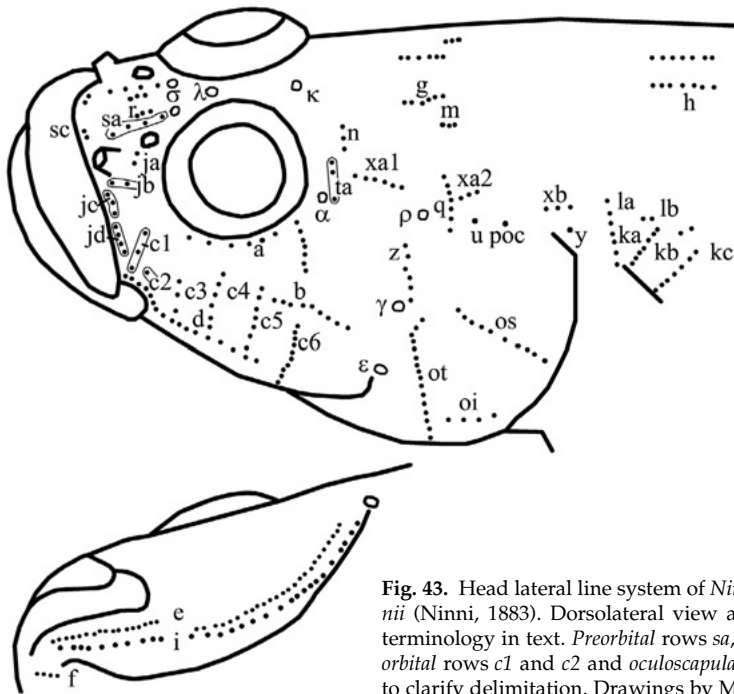


Fig. 43. Head lateral line system of *Ninnigobius canestrii* (Ninni, 1883). Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa*, *jb*, *jc* and *jd*, suborbital rows *c1* and *c2* and oculoscapular row *ta* outlined to clarify delimitation. Drawings by M. Kovačić.

a posterior part halfway above operculum; posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in the area of the upper edge of preopercle. Transverse row *q* behind pore  $\rho$ , vertically positioned between *xa1* and *xa2*; row *u* as one or two papillae behind row *q*. If POC absent, additional *poc* row present as a single papilla on the place of absent POC canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base, and longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* absent. Longitudinal row *g* starting anteriorly at about above the preopercular edge. Longitudinal row *m* below posterior part of row *g*. Longitudinal row *h* continuous, near dorsal midline in front of first dorsal fin origin. Interorbital row *aoc1* present in *N. montenegrensis* when interorbital part of AOC is absent, as one or two pairs of interorbital papillae.

### *Pomatoschistus* Gill, 1863

All head canals present in all species, but pores variably present or absent in the fourteen presently recognized species of *Pomatoschistus* (Table 2) (Figs 44 and 45, Table 2). AOC, POC and PC canals in most of species with fully present pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$ ,  $\theta$ ,  $\tau$

and  $\gamma$ ,  $\delta$ ,  $\epsilon$ , respectively. AOC pore  $\beta$  only occurs in some *P. marmoratus* individuals (Miller 1986). AOC pore  $\omega$  is missing in four species, variably present in two (Miller 1986, Engin & Innal 2017, Engin & Seyhan 2017). PC pore  $\delta$  is missing in *P. nanus* (Engin & Seyhan 2017). Only *P. anatoliae* have no pores  $\lambda$  and  $\kappa$  in some individuals (Engin & Innal 2017). *P. adriaticus* sometimes lost pore  $\kappa$  (Seyhan Öztürk & Engin 2019).

Head rows of sensory papillae (Table 3) with preorbital row *sb* absent; row *sa* longitudinal; suborbital row *a* with transverse proliferations, except for two species; suborbital row *c* multiplied in separate perpendicular rows, in some species some rows reduced to a single papilla; suborbital row *cp* absent; oculoscapular row *ta* present (Figs 44 and 45). Preorbital rows with three median rows. Longitudinal row *r* anteriorly beginning medially at level of the posterior nostrils or at level of the interspace between anterior and posterior nostrils; row *sa* also longitudinal and parallel to row *r*, placed at the level of nostrils and their interspace; row *sb* absent, only in *P. nanus* row *sb* present; row *sc* is the anteriormost preorbital row above the upper lip, sometimes only as a single papilla, as e.g. in *P. pictus*. Four to eight lateral preorbital rows. Row *ja* as one to three rows between anterior and posterior nostrils and laterally to it; row *jb* as one to three rows below and close

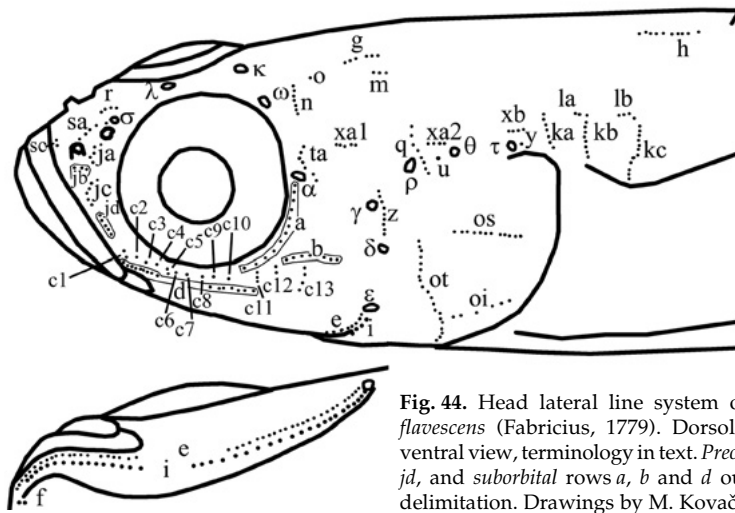


Fig. 44. Head lateral line system of *Pomatoschistus flavescens* (Fabricius, 1779). Dorsolateral view and ventral view, terminology in text. Preorbital rows *jb* and *jd*, and suborbital rows *a*, *b* and *d* outlined to clarify delimitation. Drawings by M. Kovačić.

to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between the upper lip and vertical of anterior eye edge. Row *jd* can penetrate to below eye, ending below anteriormost rows *c*, as e.g. in *P. minutus*. Suborbital rows with longitudinal row *a* variably extending anteriorly, from just below posterior eye, in e.g. *P. flavescens*, extending anteriorly to below pupil, e.g. in *P. bathi*, or all along lower eye to anterior eye edge, e.g. in *P. minutus*. Transverse proliferation of row *a* variable, ranging from a single posterior row to up to more than ten transverse rows reaching to below the posterior eye edge, e.g. in *P. minutus*. Transverse rows *a* absent only in *P. flavescens*, or they are reduced to just two papillae in *P. quagga*. Longitudinal row *b* on upper half of cheek variably long, anteriorly ending below posterior iris, e.g. in *P. flavescens*, or extending to the anterior half of eye, e.g. in *P. minutus*, to posteriorly extending variably behind vertical of posterior eye edge; and finally in some species, like *P. lozanoi*, reaching backwards to the posterior preopercular edge and pore  $\delta$ . Six to sixteen transverse rows *c*, three to more than ten rows in front of row *b*, one to eight rows below row *b*. Number of papillae in transverse *c* rows can vary from just a single papilla, like anteriormost *c* rows in some species, e.g. in *P. quagga*, to more than a dozen papillae in some transverse *c* rows, e.g. in *P. norvegicus*. *P. flavescens* in most specimens with a single or only doubled *c* papilla, but at least the last *c* row with more than two papillae. Longitudinal row *d* extending from above the upper lip backwards along the lower cheek, reaching or nearly reaching vertical of posterior eye edge or extending behind it. Longitudinal row *d* continuous or with a small gap between supral-

abial and cheek parts or with a larger gap on cheek. Preoperculo-mandibular rows with external row *e* divided; internal row *i* divided, e.g. in *P. flavescens*, or continues, e.g. in *P. microps*; row *i* parallel to row *e*, both ending anteriorly before or near frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* near chin tip is longitudinal row, e.g. in *P. marmoratus*, or a cluster e.g. in *P. lozanoi*, or a single papilla, e.g. *P. quagga* and *P. nanus*. Opercular rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. Oculoscapular rows with transverse row *ta* behind pore  $\alpha$ , variable, i.e. from a short row at pore  $\alpha$  lower part, e.g. in *P. marmoratus*, or reaching below pore  $\alpha$  level, e.g. in *P. nanus*, or the row is extending downwards on cheek all way down to suborbital row *b* level, e.g. in *P. lozanoi*. Anterior longitudinal row *xa* divided into anterior and posterior parts; anterior part above posterior preopercular edge, extending anteriorly in some species, like *P. lozanoi* to near anterior dorsal row *n*, or placed even more anteriorly, like in *P. quagga*; posterior part is halfway above operculum. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in the area of the upper edge of preopercle. Transverse row *q* behind pore  $\rho$ , vertically positioned between *xa1* and *xa2*, either as a continuous line as in *P. lozanoi*; or it is divided in two parts, one below horizontal level of pore  $\rho$  and one above, as e.g. in *P. marmoratus*; or row *q* extends upwards from just shortly above level of pore  $\rho$  in *P. marmoratus* to up to near anterior dorsal row *m* in *P. lozanoi*. Row *u* as one or two papillae behind row *q* and in front of pore  $\theta$ . Transverse row *y* below



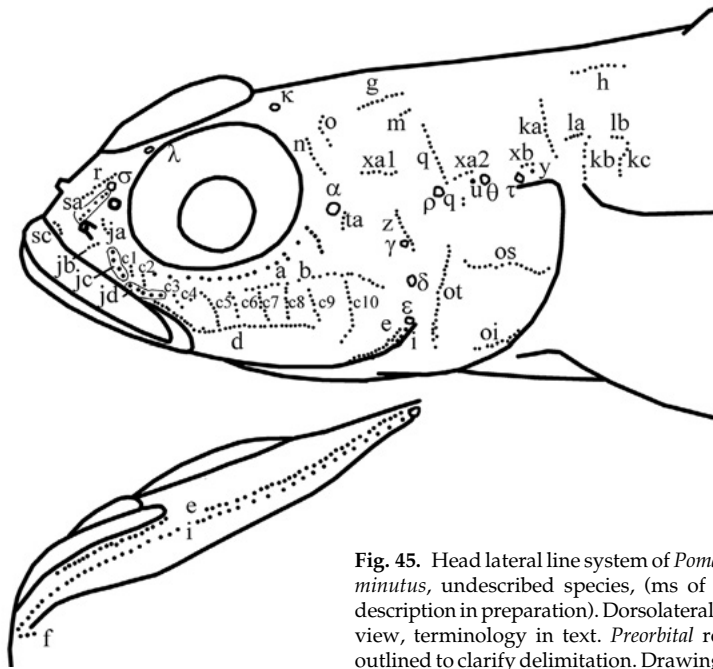


Fig. 45. Head lateral line system of *Pomatoschistus* sp. aff. *minutus*, undescribed species, (ms of the new species description in preparation). Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa*, *jc* and *jd* outlined to clarify delimitation. Drawings by M. Kovačić.

row *xb*, and in most species, like in *P. marmoratus*, just as a single papilla. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base, row *ka* can extend in some species to the anterior part of anterior dorsal row *h*, like *P. lozanoi*; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye, either as just a short patch above and behind pore  $\alpha$ , distinct from row *ta*, like in *P. marmoratus*, or as a long row running along the entire posterior eye, as in *P. lozanoi*. Transverse rows *o* in front of vertical of preopercular edge, close to row *n* in most of species; if long as in *P. minutus*, it has been easily misidentified as row *n* or, if it is a single papilla, easily overlooked, as in *P. marmoratus*, *P. nanus* or *P. pictus*. Longitudinal row *g* start anteriorly at about above the preopercular edge. Longitudinal row *m* present below posterior part of row *g*. Longitudinal row *h* continuous or divided near dorsal midline in front of first dorsal fin origin; in some species, like *P. lozanoi*, extending anteriorly a long way over the predorsal area. Interorbital rows absent. Note that significant differences were observed between sensory papillae pattern based on studied material of *P. adriaticus*, *P. anatoliae* and *P. nanus* in this revision, that rather match the general *Pomatoschistus* pattern, as opposed to the pattern in published illustrations (Engin & Innal 2017, Engin & Seyhan 2017, Seyhan Öztürk & Engin 2019).

### *Pseudaphya* Iljin, 1930

Head with AOC, carrying pores  $\lambda$ ,  $\kappa$ , which is sometimes doubled,  $\alpha$ ,  $\rho$  and PC, carrying pores  $\gamma$  and  $\epsilon$ , sometimes  $\delta$ ; POC absent in the only species of the genus (Fig. 46, Table 2).

Head rows of sensory papillae (Table 3) with preorbital row *sb* absent; row *sa* longitudinal; suborbital row *a* with a single transverse proliferation, which can be reduced to just two papillae; suborbital row *c* multiplied in separate perpendicular rows, some rows reduced to a single papilla; suborbital row *cp* absent; oculoscapular row *ta* present; transverse anterior dorsal rows *n* and *o* and oculoscapular rows *q* and *ka* prolonged; anterior dorsal row *h* divided into two transverse pairs of papillae (Fig. 46). Preorbital rows with three median rows. Row *r* is a single papilla at the horizontal level of posterior nostrils; row *sa* also longitudinal and parallel to row *r*, starting anteriorly medially at the level of the interspace between anterior and posterior nostrils and reaching backwards; row *sb* absent; row *sc* is anteriormost preorbital row above upper lip. Four lateral preorbital rows. Row *ja* as single row laterally and below to level between anterior and posterior nostrils; row *jb* as one row below and close to anterior nostril; two longitudinal rows, superior row *jc* and inferior row *jd*, between upper lip and vertical of anterior eye edge. Suborbital rows with longitudinal row *a*



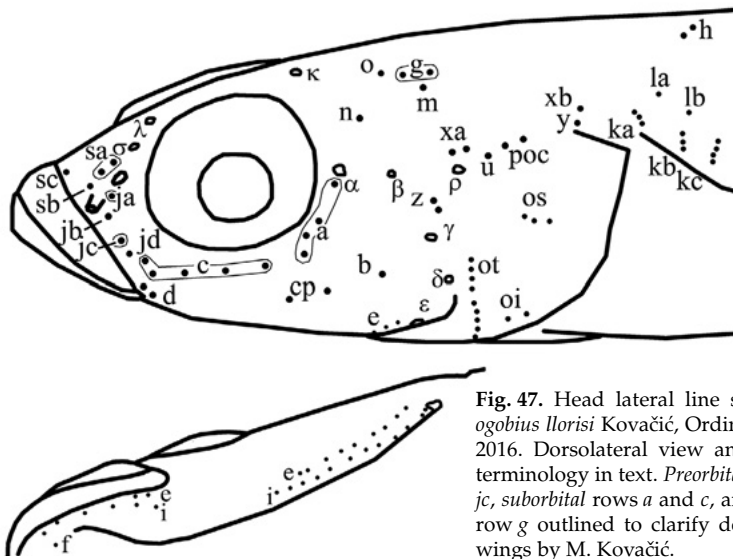


Fig. 47. Head lateral line system of *Speleogobius llorisi* Kovačić, Ordines & Schliewen, 2016. Dorsolateral view and ventral view, terminology in text. Preorbital rows *sa*, *ja* and *jc*, suborbital rows *a* and *c*, and anterior dorsal row *g* outlined to clarify delimitation. Drawings by M. Kovačić.

Four preorbital lateral rows. Row *ja* between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; two rows above posterior upper lip, superior row *jc* and inferior row *jd*, each as a single papilla. Suborbital rows without transverse proliferations. Row *a* only below rear part of eye. Row *b* as one or two papillae behind vertical of posterior eye edge. Row *c* below anterior eye and mid-eye, anteriorly starting with two papillae, one above the other at vertical of frontal eye margin. Row *cp* as two papillae below row *a*. Row *d* as only two papillae above posterior angle of jaws. Preoperculo-mandibular rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, anterior part of row *e* short below angle of jaw, row *i* ending anteriorly before frontal part of jaw and posteriorly near preopercular ventral margin. Mental row *f* is a single papilla near the chin tip. Opercular rows with transverse row *ot* located anteriorly on operculum; superior longitudinal row *os* on upper central part of operculum; inferior longitudinal row *oi* on lower part of operculum. Two *pc* papillae on the place of missing PC in *S. trigloides*. Oculoscapular rows with anterior longitudinal row *xa* above the preopercular edge; row *xb* is a single papilla above posterior edge of operculum. Transverse row *z* below pore  $\beta$ . Row *q* absent, row *u* is a single papilla between pore  $\rho$  and row *poc*. Two *poc* papillae on the place of missing POC. Row *y* as a single papilla below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; axillary longitudinal rows *la* and *lb* as single papillae just above them. Anterior dorsal rows with row *n* as a single papilla on anterior nape behind eye. Row *o* is a single pa-

pilla. Longitudinal row *g* as two papillae anteriorly ending behind the row *o* papilla. Row *m* is a single papilla below row *g*. Interorbital rows absent. Note that for both *Speleogobius* species significant differences was present between sensory papillae pattern based on studied material that was carefully hand-collected in this revision and published illustrations and descriptions in the species descriptions where some rows were missing (Zander & Jelinek 1976, Kovačić et al. 2016).

#### Generalized head lateral-line system (HLLS) of the European phylogenetic lineages

##### *Aphia*-lineage, Gobiinae

Head canals and pores are completely absent in both genera of this lineage, in the small nectonic *Aphia* and in benthic *Lesueurigobius* (Figs 22 and 23, Table 2).

Head rows of sensory papillae are highly divergent between the only two genera of the *Aphia*-lineage (Table 3). *Aphia* has transverse rows in suborbital, oculoscapular, anterior dorsal and interorbital region, with remarkably extended oculoscapular and anterior dorsal transverse rows, while in *Lesueurigobius* suborbital, oculoscapular (except *ka*, *kb* and *kc* rows), anterior dorsal and interorbital rows are longitudinal only (Figs 22 and 34, Table 3). In detail, in *Lesueurigobius* (Fig. 34) transverse rows of suborbital row *c* are not developed, transverse oculoscapular and interorbital rows are absent and anterior dorsal transverse rows are reduced to one or two papillae. *Lesueurigobius* shares with several *Pomatoschistus*-lineage genera the

character of *suborbital* row *c* anteriorly starting with two papillae, one above the other, at vertical of frontal eye margin, as well as *suborbital* row *cp* present as two papillae below row *a* on the posterior end of row *c*, both absent in *Aphia*. *Lesueurigobius* is also different from *Aphia* and unique among all genera in the three studied phylogenetic lineages in having continuous *oculoscapular* row (*aoc2 + u + poc*) on the place of the missing AOC and POC. *Aphia* (Fig. 22) shares with some genera of the *Pomatoschistus*-lineage the presence of *oculoscapular* row *ta* and with some genera of the *Gobius*-lineage the presence of *oculoscapular* row *tp*, both missing in *Lesueurigobius*. The degree of differences of the head rows of sensory papillae between two genera of the *Aphia*-lineage is comparable to the degree of differences of the head rows of sensory papillae among genera of *Pomatoschistus*-lineage, despite just two genera, *Aphia* and *Lesueurigobius*, being involved. *Aphia* and *Lesueurigobius* share a presumed synapomorphy of *preoperculo-mandibular* row row *e* posteriorly extending upwards to the upper preopercle. Any other similarities of head rows of sensory papillae between *Aphia* and *Lesueurigobius* are also shared with all other genera in the other two studied phylogenetic lineages, such as *preorbital* lateral rows or *opercular* rows; or they are shared with just the *Pomatoschistus*-lineage, such as the presence of *suborbital* row *a*.

The head lateral line system of the genera of the *Aphia*-lineage shows 1) consistency in the complete reduction of head canals without variation across the two genera and 2) highly divergent head row patterns of sensory papillae between the two genera of the *Aphia*-lineage, i. e. no *Aphia*-lineage presumed synapomorphies, except possibly 3) a single synapomorphy of *preoperculo-mandibular* row row *e* posteriorly extending upwards to the upper preopercle (Tables 2 and 3). Notably, extended *oculoscapular* and *anterior dorsal* transverse rows occur only in nectonic *Aphia*, not in benthic *Lesueurigobius*; they might represent an adaptation to their nektonic lifestyle.

### **Gobius-lineage, Gobiinae**

Among the fourteen studied genera of the lineage, the head canals and pores show moderate stability of characters among and within genera (Table 2). The four genera *Gobius*, *Neogobius*, *Thorogobius*, *Zebrus* are characterized by the full presence of canals and pores, i. e. AOC, POC and PC canals present with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$ . The species of these four genera are large sized and epibenthic, except *Zebrus* (Figs 28, 32, 35 and 37, Table 2). The five genera, *Chromogobius*, *Gymnesigobius*, *Millerigobius*, *Odondebuena*, *Peter*, are small cryptobenthic fish and show reduction of POC with intrageneric stability

of AOC and PC presence, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$ , respectively (Figs 24, 29, 31, 33 and 34, Table 2). Only in *Millerigobius*, the aberration of extra or missing pores was observed in some adults (Vanhove et al. 2011). *Vanneaugobius* also features the AOC and PC full set of  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  pores, respectively, but in two of three species POC is absent (Fig. 36, Table 2). In *Didogobius*, two species feature the AOC and PC full set of  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  pores, respectively, while POC is absent. The other two *Didogobius* species miss also PC, and the number of AOC pores is reduced from seven to four (Fig. 26, Table 2). Two more genera of small cryptobenthic fish, *Corcyrogobius* and *Gammogobius*, show additional reduction of PC, i. e. both POC and PC are absent, but AOC is present with a full set of  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  pores, except for one species, *C. liechtensteini*, with the aberration of two missing pores in some individuals (Miller 1972) (Figs 25 and 27, Table 2). Finally, the three *Marcelogobius* species evolved additional reductions, ranging from POC missing and PC variably missing, over POC and PC missing always, to all canals lost (Fig. 30, Table 2).

The head rows of sensory papillae of fourteen studied genera of the *Gobius*-lineage (Table 3) all have four *preorbital* rows consistently present, except that row *sa* is not reported for one *Gobius* and one *Thorogobius* species, and that row *sb* is not found in the single *Gymnesigobius* species (Fig. 29, Table 3), suggesting a reinvestigation once the intact specimens of these species would be available. *Suborbital* row *a* is always absent. *Suborbital* row *c* is always multiplied into well-developed and distinct perpendicular rows, showing stable number of multiplied transverse rows of six to seven rows across all genera. *Preoperculo-mandibular* row *f* is not reported for the two *Thorogobius* species, which, if really absent, is a unique condition among all genera of the three studied phylogenetic lineages. For the positive conclusion, individuals of these two species in a good condition should be examined. The three *opercular* rows show a stable presence in all genera of *Gobius*-lineage, as well as in all genera of two other studied phylogenetic lineages. *Oculoscapular* rows in all *Gobius*-lineage genera miss the row *ta* and show variably occurrence of the row *tp*, being absent in five genera (Table 3) present in seven genera (Table 3) and variably present or absent in species of two genera (Table 3). Some posterior *oculoscapular* rows were not observed in the single species of *Gymnesigobius* (Fig. 29, Table 3), as well as in two species of *Thorogobius* and request a recheck on the specimens in good condition. All five *anterior dorsal* rows are present in all genera of *Gobius*-lineage, except for row *m*, which has not been reported in the one *Didogobius* species, *D. bentuvii*; thus, a request for

a reevaluation of this character is made if specimens in good condition would be collected in the future. *Interorbital* rows occur only in one *Marcelogobius* species, *M. helenae*, as only *Gobius*-lineage species with an absent AOC absent, and in the single species of *Millerigobius*, *M. macrocephalus*, as the only species in all studied phylogenetic lineages having both a complete AOC and interorbital papillae above it (Fig. 31, Table 3).

The head canals and pores of the genera of the *Gobius*-lineage, except for the genera *Didogobius* and *Marcelogobius* and *C. liechtensteini*, show 1) a regular shape of complete and enclosed canals with the well-defined standard set of pores, 2) canals and pores show intrageneric stability with the regard to a homogenous pattern among species within each genera, 3) the reduction of head canals and pores across genera has three well-defined reduction steps eventually leading to the complete loss of canals, but all pores of remaining canal(s) are retained in each step (Table 2). Canal reduction is particularly notable in small and cryptobenthic species. The head rows of sensory papillae of the genera of the *Gobius*-lineage share 1) stability of the presence of almost all rows across almost all genera and species, 2) head rows of sensory papillae with *suborbital* row *a* absent as synapomorphy of the *Gobius*-lineage, and 3) *suborbital* row *c* always multiplied into well-developed and distinct perpendicular rows, showing stable number of multiplied transverse rows among genera with six to seven rows as a putative lineage synapomorphy (Table 3).

### ***Pomatoschistus*-lineage, Gobionellinae**

The nine studied genera of the lineage show high variability of head canal and pore pattern across and within genera (Table 2). In addition to the loss of entire canals, the reduction of individual pores in the existing canals is also widespread among *Pomatoschistus*-lineage species. Among nine genera, the species of the genus *Pomatoschistus*, despite being numerous, are all similar in retaining all three head canals, congeneric species at best differing by the presence or absence of individual pores (Figs 44 and 45, Table 2). The monotypic genus *Pseudaphya* has no POC, and intraspecific variability in the other two canals is restricted to the presence of one pore and duplication of another (Fig. 46, Table 2). The two *Speleogobius* species differ in the absence or presence of PC and of one AOC pore, with no intraspecific variability (Fig. 47, Table 2). Two genera, *Crystallogobius* and *Lebetus*, completely lack head canals and pores (Figs 39 and 42, Table 2). Two genera, *Knipowitschia* and *Ninnigobius*, inhabiting freshwater or transitional (brackish) water, show

the largest intrageneric and intraspecific differences. The two *Ninnigobius* species vary in the canal patterns, either having all three canals fully developed with regular pores, or as an intermediate condition featuring absence or replacements of POC, PC and part of AOC with open furrows, or to having only the AOC posterior part present with duplicated pores (Fig. 43, Table 2). Numerous *Knipowitschia* species are even more variable, from all three canals fully developed with regular pores, over full or partial absence or replacements of canals with open furrows and with pore duplication at the canal interruptions, to finally the complete canals loss (Fig. 41, Table 2). Head canals in part of the *Buenia* species may have additional pores and open furrows in all three canals (Fig. 38, Table 2). Finally, *Deltentosteus* species have highly modified head canals and pores, with head canals widened and, in addition to regular pores, with numerous small extra pores irregularly distributed along canals (Fig. 40, Table 2).

The head row patterns of sensory papillae of nine studied genera of the *Pomatoschistus*-lineage (Table 3) are highly divergent between two groups of genera, each sharing unique synapomorphies among the studied genera of all three lineages. The four genera, *Buenia*, *Deltentosteus*, *Lebetus* and *Speleogobius* share the characters of 1) the low number of papillae in rows, with many rows with just one or two papillae, or with some rows even being absent in some genera, 2) three *preorbital* rows, with either row *sb* absent (*Buenia*, *Lebetus*) or row *r* absent (*Deltentosteus*, *Speleogobius*), 3) *suborbital* row *a* as single longitudinal row, 4) *suborbital* row *c* as single longitudinal row, anteriorly starting with two papillae one above the other at the vertical of anterior eye margin, 5) *suborbital* row *cp* present, 6) *oculoscapular* row *ta* absent (Figs 23, 40, 42 and 47, Table 3). The four genera match to sand goby morphological group named DLBS by McKay & Miller (1997). In addition, *Deltentosteus*, as one of four genera, exhibits apomorphy of transverse *anterior dorsal* rows and *oculoscapular* rows *la* and *lb* proliferated into uniformly distributed short vertical rows of single, paired or tripled papillae (Figs 14 and 40, Table 3). *Lebetus* is the genus with highest sensory papillae row absence, missing a few anterior transverse *oculoscapular* rows (row *q*, row *y*) and posterior longitudinal *oculoscapular* rows (rows *la* and *lb*) (Fig. 42, Table 3). The five other *Pomatoschistus*-lineage genera, *Crystallogobius*, *Knipowitschia*, *Ninnigobius*, *Pomatoschistus*, *Pseudaphya*, all share the character states of 1) *preorbital* row *sb* absence, 2) row *sa* being longitudinal, 3) *suborbital* row *a* with transverse proliferations, except in *Crystallogobius* and two *Pomatoschistus* species), 4) *suborbital* row *c* multiplied in separate perpendicular rows, however, with part of the rows restricted

to single papilla in *Crystallogobius*, *Pseudaphya* and some *Pomatoschistus* species, 5) *suborbital* rows *cp* absent, 6) *oculoscapular* row *ta* present (Figs 41, 43, 44, 45 and 46, Table 3). In addition, *Crystallogobius*, exhibits putative apomorphies among five genera: *suborbital* row *a* without transverse proliferations (occurring also only in two *Pomatoschistus* species); *suborbital* row *d* absent, *interorbital* rows *p* and *w* present, transverse *anterior dorsal* rows and *oculoscapular* row *kb* prolonged, *anterior dorsal* row *h* transverse (Fig. 39, Table 3). *Pseudaphya* has transverse *anterior dorsal* rows *n* and *o* and *oculoscapular* rows *q* and *ka* prolonged and the *anterior dorsal* row *h* divided in two transverse pairs of papillae (Fig. 46, Table 3).

The head canals and pores of the *Pomatoschistus*-lineage show 1) no consistent regularity of enclosed canals and well defined usual pores, but can feature open furrows and additional pores in several genera, 2) intrageneric instability of head canals and pores with a heterogenous pattern within most of the genera, at least with regard to absence or presence of the individual pores, 3) irregular canal reduction of species having lost individual pores in retained canals rather than loss of the entire canal in most genera (Table 2). This instability and intrageneric and intraspecific variability is especially notable in the deep-water species of *Buenia* and, even more, in the freshwater species of *Ninnigobius* and *Knipowitschia*. Intense to complete canal reduction is particularly frequent in small nectonic species (*Crystallogobius*), small freshwater species (*Ninnigobius* and *Knipowitschia*) or small benthic species (*Lebetus*). The head lateral line system of the genera of the *Pomatoschistus*-lineage shows 1) highly divergent head row patterns of sensory papillae between two groups of genera and 2) each of two groups of genera shares several putative synapomorphies with regard to the other group or even unique among all three studied phylogenetic lineages (Table 3). The species of three genera of the DLBS group, *Buenia*, *Lebetus*, *Speleogobius*, having a reduced papilla count in rows down to one or two papillae only or even with absent rows, are all very small benthic species. *Crystallogobius* and *Pseudaphya*, with extended *oculoscapular* and *anterior dorsal* transverse rows, are nectonic, same as *Aphia* from the *Lesueurigobius*-lineage.

## Discussion

Sanzo's (1911) original study was limited by the number of gobiid species and genera studied, if compared with the presently known European marine goby diversity, i.e. Sanzo (1911) studied only one fourth of presently known native species diversity and about two fifths of the presently recognized

genera of the Mediterranean and European Atlantic marine gobies (Table 1) (Kovačić & Patzner 2011, Kovačić et al. 2022). As discussed in the Introduction, Miller's (1986) short introduction on HLLS in the gobiid list and key for the CLOFNAM area became the quick guide replacement for Sanzo's work (1911) for the investigation of HLLS, despite lacking the detailedness and comprehensiveness of the original. Therefore, the intention of the present revision of Sanzo's head lateral-line system classification and nomenclature is to offer the first detailed manual for the investigation and nomenclatorial application of head lateral-line system classification and nomenclature 112 years after Sanzo (1911) and 37 years after Miller (1986). The simplified and consistent classification and nomenclature for general application on Mediterranean and European Atlantic marine gobies presented herein is meant primarily as empirical tool for the pragmatic and up-to-date handling of this set of characters for taxonomic and comparative investigations, without any ambitions to critically contribute to the general body anatomy or even functional morphology. Thus, the major goals of the present revision of HLLS classification and nomenclature (see the aim in the Introduction) is to contribute: to the clarification of conflicts and contradictions in their application, to nomenclatorial simplification where ever possible, to an increased classification consistency despite novel variation and complexity discovered over the last 110 years and, finally, to nomenclatorial stability considering the long and widespread use of Sanzo's (1911) system from its publication until today. "The classification and nomenclature principles" chapter of the Material and methods provides the general principle and framework of Sanzo's HLLS classification and nomenclature. The proposed general nomenclatorial changes of Sanzo's (1911) system for pores on canals and for sensory papillae rows, as well as individual solutions for each pore and each row, are explained in the chapter "General head lateral-line system pattern and the revision of Sanzo's classification and nomenclature" of the Results.

The revision is restricted to the head region, considering that the trunk and caudal fin rows of sensory papillae represent distinct, but comparatively weakly differentiated sets of characters for species and genus level identification purposes. The trunk rows of sensory papillae have not been studied well and only few studies are available for European gobies (Ahnelt & Göschl 2004). Thus, well-described trunk rows of sensory papillae useful for comparison are rare (e.g. Sanzo 1911, Ahnelt & Duchkowsch 2001, Ahnelt & Scattolin 2003). They appear less attractive as a set of taxonomically useful characters than the head patterns for two reasons.

First, trunk rows of sensory papillae have numerous papillae and numerous rows arranged in a quite simple three row series pattern with variability at best in longitudinal and transversal multiplication of rows as potential taxon identification characters (Sanzo 1911, Ahnelt & Duchkowsch 2001, Ahnelt & Scattolin 2003). Second, they become easily damaged and lost during capture and handling, as it is the case for scales (Shibukawa et al. 2001). Similarly to the trunk, the caudal fin papillae rows evolve conservatively, and, compared to the head rows of sensory papillae, their arrangement and variation is much less complex and therefore is certainly less useful as an informative character set for identification tool in gobiid taxonomy (Ahnelt & Göschl 2004, Ahnelt & Scattolin 2005).

The revision of Sanzo's head lateral-line system classification and nomenclature was applied here on the Mediterranean and European Atlantic marine gobies, as in Sanzo (1911) and Miller (1986), and therefore, it is restricted to the subfamilies Gobiinae and Gobionellinae (sensu Fricke et al. 2023a). Nevertheless, it covers all presently known gobiid genera of these seas, missing the exclusively freshwater genus *Padogobius* and genera exclusively restricted to neighbouring Ponto-Caspian or to African Atlantic areas. The single exception is the former *Didogobius* species of tropical *Peter* Schliwen, 2023, genus named during the late preparation of this work, which species are studied here. For some species and for genus *Crystallogobius* the HLLS was studied and illustrated for the first time. For some other species the head lateral-line nomenclature was applied for the first time, although the sketch of the head lateral line system had been published before (see "Specimen studied and the published data" in the Material and methods). The selected geographic range enabled covering of HLLS for all species in marine habitats of the area and almost all species of the studied genera in general. It is based on presently studied specimens or on published head lateral-line system or, in most cases, both (see "Specimen studied and the published data" in the Material and methods). Expansion of the present revision to gobiid taxa beyond Mediterranean and European Atlantic seas would tremendously increase the number of studied species, rendering the task impossible to be completed in a reasonable time span, or it would be restricted just to individual examples, omitting the entire variability of taxa and therefore reducing the reliability of the system.

Anyway, we share the opinion of Gill et al. (1992) that the nomenclature of HLLS of Miller (1986) is applicable to all, or at least, most of the gobioids. As mentioned before, HLLS nomenclature has rarely been applied to Indo-Pacific gobies since Sanzo (1911)

introduced it; or head canals and pores were named but without naming head rows of sensory papillae. It was completely skipped in reviews, revision and descriptions of gobies of various prominent gobiid authors in the area (e.g. Smith 1959, Goren 1979, Hoese 1991, Randall & Greenfield 2001, Greenfield & Randall 2004, Gill & Jewett 2004, Tornabene et al. 2013). Even when HLLS was illustrated (e.g. Akihito et al. 1984, Winterbottom & Emery 1986, Suzuki & Senou 1994, Murdy 1998, Shibukawa & Iwata 1998, Keith et al. 2011) or photographed (Allen et al. 2019) the nomenclature was not applied. At best HLLS nomenclature was restricted to the application for head canals and pores, or was applied to only a few main papillae rows of HLLS (e.g. Larson 2001). HLLS was similarly ignored in studies of American gobies (e.g. Böhlke & Robins 1968) or HLLS was just illustrated without application of a nomenclature (e.g. Van Tassell & Baldwin 2004, Pezold 2022). In contrast, there are some examples of successful application of the Sanzo's HLLS classification and nomenclature across different phylogenetic lineages sensu Agorreta et al. (2013) of Gobiidae subfamilies Gobiinae and Gobionellinae sensu Fricke et al. (2023a) that are not present in the Mediterranean and European Atlantic areas. These applications are mostly from this century and for the following Gobiinae-lineages: *Asterropteryx*-lineage (Kovačić et al. 2011), *Callogobius*-lineage (Chen & Shao 2000), *Cryptocentrus*-lineage (Shibukawa et al. 2005), *Glossogobius*-lineage (Miller & Stefanni 2001), *Gobiopsis*-lineage (Kovačić & Bogorodsky 2013), *Gobiosomatini*-lineage (Tornabene & Baldwin 2019), *Lophogobius*-lineage (Bogorodsky et al. 2023), *Priolepis*-lineage (Ahnelt & Bohacek 2004), *Valenciennea*-lineage (Kovačić et al. 2018c). Even more rare are application of the Sanzo's HLLS classification and nomenclature for Gobionellinae-lineages: *Acanthogobius*-lineage (Ahnelt et al. 2004), *Mugilogobius*-lineage (Miller 1987); and for the *Stenogobius*-lineage (Kovačić & Sacchetti 2023). Thus the successful applicability of the Sanzo's head lateral-line system classification and nomenclature beyond the Mediterranean and European Atlantic seas has been demonstrated over the last two decades. Nevertheless, there are no examples of HLLS classification and nomenclature application in other Gobiidae subfamilies: Sicydiinae, Oxudercinae and Amblyopinae. Recent species descriptions of Sicydiinae regularly have had HLLS illustrated (e.g. Keith et al. 2007, Keith & Marquet 2005, Keith et al. 2011), but with no classification and naming of sensory papillae rows. The Amblyopinae head lateral-line system has been rarely illustrated (e.g. Murdy & Shibukawa 2001) and was never analyzed. There are no illustrations of HLLS for Oxudercinae. Regarding other Gobiiformes families sensu Fricke



et al. (2023a), there are examples of the application of Sanzo's system (1911) to Odontobutidae (e.g. Chen & Kottelat 2004) and Eleotridae (e.g. Miller 1998). For most other goby families, HLLS was illustrated, too, but not classified and named as a source of taxonomical characters: Rhyacichthyidae (e.g. Watson & Pöllabauer 1998), Thalasseleotrididae (e.g. Hoese & Larson 1987), Microdesmidae (e.g. Okamoto & Motomura 2018). Hopefully, the trend of the recent application of head lateral-line system classification and nomenclature as the rich source of external morphological characters with high information content for taxonomy, will continue for the study of non-European gobies across different lineages and subfamilies of Gobiidae and across other Gobiiformes families.

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