The pattern of the mechanosensory lateral line on the caudal fin of the two deep-water gobiid fishes

*Deltentosteus collonianus* and *Deltentosteus quadrimaculatus* (Teleostei: Gobiidae)

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(Accepted 2 February 2006)

Abstract

The most common pattern of the lateral line system on the caudal fin of Gobiidae is characterized by three longitudinal rows of free neuromasts. *Deltentosteus collonianus* and *Deltentosteus quadrimaculatus* are two benthic Atlantic–Mediterranean gobiid fishes with additional rows on the caudal fin. In these species the caudal fin is more densely covered by the lateral line system compared to the usual status in Gobiidae. An increase of longitudinal neuromast rows occurs rarely in gobiid fishes and is only known in a few species of Gobiidae with a pelagic lifestyle. Both *Deltentosteus* species show numbers of neuromast rows on the caudal fin between the plesiomorphic three and the advanced eight rows of pelagic gobies. This intermediate position allows discussion of the existence and the characteristics of an underlying pattern in the increase of the number of longitudinal neuromast rows and adaptation to habitat conditions in Gobiidae.

Keywords: Caudal fin, *Deltentosteus collonianus*, *Deltentosteus quadrimaculatus*, free neuromasts, Gobiidae, lateral line system

Introduction

During past years the physiology of the lateral line system of teleost fishes has been studied extensively (e.g. Engelmann et al. 2000; Coombs et al. 2001; Mogdans et al. 2003; Carton and Montgomery 2004). Nevertheless, besides the physiological functions of the neuromasts, the primary importance for detecting hydrodynamic stimuli is their arrangement on the body of the fish (Dijkgraaf 1962; Coombs et al. 1988; Webb 1989).

The pattern of the mechanosensory lateral line is decisive for the location of important stimuli. It is adapted to the various lifestyles of fishes (e.g. Coombs et al. 1988; Popper and Platt 1993) and is closely related to the habitat (Hofer 1907; Dijkgraaf 1962; Disler and Smirnov 1977; Coombs et al. 1988, 2001; Montgomery et al. 1997). This is seemingly also
true for the total number of neuromasts, which is typically some hundreds (Carton and Montgomery 2004) but can reach some thousands in gobiid fishes. Such extremely high numbers of free neuromasts are found in pelagic gobies such as *Aphia minuta* (Risso, 1810) and *Leucopsarion petersii* Hilgendorf, 1880 (Mortara 1918; Scattolin 2003).

Gobiidae are characterized by a specialized mechanosensory lateral line which is dominated by free neuromasts on the head, the trunk, and the caudal fin. Lateral line canals are developed, if at all, only on the head, a canal on the trunk is lacking (Sanzo 1911; Ijlin 1930; Ahnelt and Bohacek 2004). The topography of the lateral line system on the head has been widely used for the classification of gobiid fishes (e.g. Takagi 1988; Gill et al. 1992; Larson 2001). Recently, more attention has been paid to the pattern of the free neuromasts on the trunk and the caudal fin (Ahnelt and Duchkowitsch 2001; Shibukawa et al. 2001; Ahnelt and Göschl 2003, 2004; Ahnelt and Scattolin 2003).

The pattern of the lateral line system on the caudal fin of Gobiidae is very conservative (Ahnelt and Göschl 2004). Environmental pressure and adaptation to new habitats seemingly favour (sometimes drastic) changes of its arrangement on the head and the trunk but less distinct changes, if any, on the caudal fin. In particular, an increase of the number of neuromast rows on the caudal fin is rarely observed (Mortara 1918; De Buen 1923; Scattolin 2003) and is possibly linked to hydrodynamic conditions in the open water column and in deep waters, two environments secondarily inhabited by Gobiidae.

The genus *Deltentosteus* Gill 1863 has a unique position within the north-eastern Atlantic and Mediterranean gobiid fish fauna (De Buen 1923; Miller 1986). The lateral line system of the two species, *Deltentosteus collonianus* (Risso, 1820) and *Deltentosteus quadrimaculatus* (Valenciennes, 1837), is characterized by specialized features. Its arrangement on the head and the trunk has been described by Sanzo (1911) and De Buen (1923), but information on the pattern of the caudal fin is incomplete.

We describe the unusual pattern of the free neuromasts on the caudal fin of the two benthic deep-water gobies *D. collonianus* and *D. quadrimaculatus*. Based on these data and on the arrangement of the lateral line system of pelagic gobies it is possible to postulate in which order neuromast rows are increased from the plesiomorphic three to the apomorphic eight rows on the caudal fin of Gobiidae. In addition, we discuss if the increase of neuromasts and neuromast rows in these two gobiid species is possibly linked to the adaptation to a low-noise habitat.

**Material and methods**

The lateral line system on the caudal fin of Gobiidae is formed by rows of free (superficial) neuromasts (summarized in Ahnelt and Göschl 2004). These neuromasts (sensory papillae) run in longitudinal and transversal rows and are generally arranged in two patterns: pattern 1 is characterized by three longitudinal rows and pattern 2 by two longitudinal rows. In both cases generally a transversal row occurs anterior to the longitudinal rows (Ahnelt and Göschl 2004). The nomenclature of the longitudinal rows of free neuromasts on the caudal fin follows Ahnelt and Duchkowitsch (2001): dorsal (lcd), median (lcm), and ventral (lcv) longitudinal rows. The median longitudinal row lcm extends in elongation of the median trunk lateral line (a series of free neuromasts in Gobiidae) whereas lcd and lcv are accessory lateral lines (Sanzo 1911; Ahnelt and Duchkowitsch 2001; Shibukawa et al. 2001; Ahnelt and Bohacek 2004). These three rows are arranged in a characteristic pattern: lcm is separated from lcd by three and from lcv by two fin rays. This pattern is characteristic for Gobioidei with three longitudinal neuromast
rows developed on the caudal fin and seemingly represents the plesiomorphic type for Gobioidi (Ahnelt and Göschl 2004) (Figure 1A). This characteristic arrangement allows the identification of these three longitudinal neuromast rows in species with more than three rows developed. The position of the neuromast rows compared to the branched caudal fin rays is compared only in adult specimens. In juveniles the number of the branched fin rays is usually not completely developed (H. Ahnelt, unpublished data). The topography of the free neuromast was studied using a binocular microscope (Wild M-8) with oblique lighting.

The following preserved specimens were examined (collection number, number of specimens, standard length, sampling site).

**Deltentosteus collonianus**

Sixty-four specimens (spec.). NMW 28826–28830: two of five specimens, 48.8 mm; Croatia, Split. NMW 29087–29100: two of 14 spec., 46.1–50.0 mm; Croatia, Island Solta. NMW 30325–30326: one of two spec., 52.2 mm; France, Nice. NMW 30327–30328: two spec., 53.4–61.8 mm; France, Nice. NMW 30335–30337: three spec., 47.5–57.4 mm;

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**Figure 1.** Stylized pattern of the lateral line system of the caudal fin in Gobiidae with different numbers of neuromast rows: (A) plesiomorphic pattern; (B–D) advanced pattern. (A) Three longitudinal rows, *Gobius niger*; (B) four longitudinal neuromast rows, *Deltentosteus quadrimaculatus*; (C) six longitudinal neuromast rows, *Deltentosteus collonianus*; (D) eight longitudinal neuromast rows, *Aphia minuta*. (C, D) Neuromasts of lcd, lcm, and lcv are shown enlarged. In most Gobiidae, the neuromasts decrease in size rearwards, as shown in (A) only. lcd, dorsal longitudinal row; lcm, medial longitudinal row; lct, transversal row; lcv, ventral longitudinal row.
Croatia, Island Solta. NMW 30338–30341: four spec., 49.8–56.7 mm; Croatia, Island Solta. NMW 30342: one of 10 spec., 49.5 mm; Croatia, Split. NMW 38001–38316: 42 out of 317 spec., 47.2–59.7 mm; Adriatic Sea. NMW 79824: six spec., 43.1–61.5 mm; Croatia, Island Solta. NMW 86693: one spec., 50.2 mm; Croatia, Island Hvar.

*Deltentosteus quadrimaculatus*

Thirty-nine specimens. MCSNC uncatalogued: two spec., 63.9–68.1 mm; Greece, Golf Termaikos. MNCN 73654–73664: 10 of 10(!) spec., 32.3–63.7 mm; Spain, Rincon de la Victoria (Velez). MNCN 108432–108437: six spec., 60.3–66.9 mm; Spain, 28 miles S of Placer de Barra Alta (Isla Columbretes). MNCN 108475–108478: four spec., 54.0–68.4 mm; Spain, Columbretes. NMW 30659: four of five spec., 59.6–65.1 mm; Italy, Triest. NMW 30666: five spec., 63.7–72.2 mm; Italy, Triest. NMW 30667: three of nine spec., 58.2–68.2 mm; Croatia, Split. NMW 30673: four spec., 59.1–67.2 mm; Croatia, south of Island Brijuni. NMW 37479–37484: one spec., 59.2 mm; Croatia, Zadar.

**Institutions**

Abbreviations for the institutions are: MNCN, Museo Nacional de Ciencias Naturales; MCSNC, Museo Civico di Storia Naturale di Carmagnola; NMW, Naturhistorisches Museum Wien.

**Results**

The lateral line system on the caudal fin in both species is formed by free neuromasts arranged in longitudinal rows. A distinct transversal row, developed in many Gobioidei (compare Ahnelt and Göschl 2004), does not occur. The longitudinal rows extend on the interradial membranes from the base of the caudal fin rearwards. The neuromasts are large and have the shape of oblong, laterally compressed papillae with a broad base and narrowing distally.

*Deltentosteus collonianus*

Six longitudinal rows of free neuromasts are developed on the caudal fin. In adult specimens the dorsal-most longitudinal row extends between the third and the fourth (3/4) branched caudal fin rays, the following rows between 5/6, 6/7, 7/8, 8/9 and 9/10 branched caudal fin rays. The neuromast rows are separated by only one caudal fin ray, except for the two dorsalmost rows which are separated by two fin rays. Fifty-nine of 64 specimens show six longitudinal rows developed on each side of the caudal fin. In two specimens six rows occur on the left and five rows on the right side. In three specimens five rows occur on both sides of the caudal fin. Compared with the typical pattern of gobid fishes exhibiting three longitudinal rows (lcd, lcm, and lcv), three additional rows occur on the caudal fin of this species. From ventral to dorsal: one additional row below the ventral row lcv, a second between lcv and the median row lcm and a third between the dorsal row lcd and lcm, immediately dorsal to the latter. Therefore typically two longitudinal neuromast rows occur dorsal and three rows ventral to lcm. In specimens with five rows the ventral-most row is absent on one or on both sides of the caudal fin, respectively.
Deltentosteus quadrimaculatus

Four longitudinal rows of free neuromasts are developed on the caudal fin. In adult specimens the dorsal-most longitudinal row extends between the third and the fourth (3/4) branched caudal fin rays, the following rows between 6/7, 8/9 and 9/10 branched caudal fin rays. The neuromast rows lcd, lcm, and lcv are arranged in the plesiomorphic pattern of Gobiidae: lcd is separated from lcm by three, lcm from lcv by two, and the additional fourth row from lcv by one caudal fin rays. Thirty-four of 39 specimens have developed four longitudinal rows on each side of the caudal fin. In three specimens only three rows occur on both sides of the fin. A specimen with three longitudinal rows is figured in Sanzo (1911, Plate 9, Figure 6). Compared with the typical pattern of gobiid fishes with three longitudinal rows (lcd, lcm, and lcv), one additional row, ventral to lcv, occurs on the caudal fin. No further rows have been found between lcd, lcm, and lcv. Therefore typically one longitudinal neuromast row occurs dorsal and two rows ventral to lcm. In specimens with three longitudinal rows the ventral-most row is absent in two specimens and in one lcv is lacking.

Deltentosteus collonianus and D. quadrimaculatus are the only Gobioidae known with six or four longitudinal rows of free neuromasts on the caudal fin, respectively. Both species are the only benthic gobies known so far with a number of neuromast rows on the caudal fin higher than the plesiomorphic three rows.

Discussion

A recent survey of the lateral line system on the caudal fin in 120 genera of seven of the nine gobiod families, the Rhyacichthyidae sensu Shibukawa et al. (2001), Odontobutidae, Eleotridae (Butinae, Eleotrinae), Gobiidae (Amblyopinae, Gobiinae, Gobionellinae, Oxudercinae, Sicydiinae), Kraemeriiidae, Microdesmidae, and Pterelotridae revealed two general patterns on the caudal fin in gobiod fishes: pattern 1 with three longitudinal lateral lines and pattern 2 with two longitudinal lateral lines (Ahnelt and Göschl 2004). Three longitudinal lateral lines on each side of the caudal fin are characteristic for the basal gobiod genera Rhyacichthys Boulenger, 1901, Protogobius Watson and Pöllabauer, 1998, and Terateleotris Shibukawa et al., 2001, and seemingly also for the Eleotridae (Butinae and Eleotrinae) (Shibukawa et al. 2001; Ahnelt and Göschl 2004). The Rhyacichthyidae are generally accepted as the sister group of all other Gobioidei (e.g. Springer 1983; Hoese and Gill 1993; Akihito et al. 2000; Shibukawa et al. 2001).

Three longitudinal lateral lines on the caudal fin are also known from basal perciform fishes (Jakubowski 1966, 1967; Greenwood 1976; Collette and Banarescu 1977). Springer (1983), who identified this feature on Rhyacichthys, classified these three lateral lines on the caudal fin as primitive for percoid and gobiod fishes. [Note: Springer (1983) mentions three lateral lines on the caudal fin of Rhyacichthys, Ahnelt and Göschl (2004) describe four lateral lines as typical for Rhyacichthyidae. The triple lateral line system on the caudal fin of Rhyacichthys aspro consists of four lateral lines on the caudal fin (Ahnelt and Göschl 2004). The fourth lateral line is formed by a discontinuous transversal row of free neuromasts on the base of the caudal fin. This arrangement of the lateral line system on the caudal fin, a transversal row and three longitudinal rows, was identified as the plesiomorphic pattern for Gobioidae by Ahnelt and Göschl (2004). The longitudinal lateral lines are formed by three rows of free neuromasts each preceded by a short lateral line canal in Rhyacichthyidae.]
From their results Ahnelt and Göschl (2004) concluded that the decrease of the number of longitudinal neuromast rows on the caudal fin of Gobioidae follows a certain order. A reduction in the number of neuromast rows first affects the ventral row (lcv) and in a next step the dorsal row (lcd). Finally, lcm is the only remaining row (e.g. in the odontobutid *Percottus glenii* Dybowskii, 1877). A further reduction is known from the blind goby *Typhlogobius californiensis* (Steindachner, 1879). In most specimens of this species, the only known blind fish with a reduced lateral line system (Ahnelt and Scattolin 2003), a few neuromasts are irregularly scattered over the central and dorsal part of the caudal fin. These neuromasts are the rest of two longitudinal rows (lcd and lcm). In gobioid fishes with two longitudinal lateral lines (lcd and lcm) on the caudal fin, these are also separated by three fin rays.

As a deviation from the plesiomorphic pattern with three longitudinal lateral lines the number of neuromast rows on the caudal fin of a few Gobiidae is secondarily increased to four (De Buen 1923; present data), six (Fage 1918; present data), or eight longitudinal rows (Mortara 1918; Scattolin 2003), making it difficult to identify the three basic longitudinal rows. In the plesiomorphic state these three rows cover the dorsal, central and ventral part of the caudal fin of Gobioidae and are arranged in a characteristic pattern. The dorsal row (lcd) is separated from the median (lcm) by three and lcm from the ventral row (lcv) by two fin rays (Ahnelt and Göschl 2004). Therefore the gap between lcm and lcd is wider than between lcm and lcv, a pattern already noted by Sanzo (1911) (Figure 1A). This arrangement allows the identification of these three basic neuromast rows in species with more than three rows (Figure 1) and also allows the identification of additional rows relative to lcd, lcm, and lcv. To date only a few gobiid species are known with an increased number of longitudinal rows on the caudal fin, e.g. *A. minuta* and *L. petersii* (Mortara 1918; Scattolin 2003), with each neuromast row separated from the other by only one fin ray. These species can be considered as derived forms and are characterized by paedomorphic features such as the lack of lateral line canals, transparent bodies, and pelagic lifestyle.

Ahnelt and Göschl (2004) suggested that not only the decrease but also the increase of longitudinal neuromast rows follows a scheme, but contrary to the decrease of the neuromast rows on the caudal fin the manner in which their number increased was not completely understood. The two species of *Deltentosteus* display two different patterns of the lateral line system. With six rows *D. collonianus* is seemingly more specialized than *D. quadrimaculatus* with four rows. This different number of rows allows postulation on the order in which such neuromast rows are increased from the plesiomorphic three to the apomorphic eight rows found on the caudal fin of pelagic gobies:

1. *Deltentosteus quadrimaculatus* is characterized by only one longitudinal neuromast row above the plesiomorphic three rows of Gobiidae (Figure 1B). This fourth row occurs in the first interradial space ventral to lcv, possibly as the result of a doubling of lcv. The typical gobiid pattern with three fin rays between lcd and lcm and two between lcm and lcv is not affected.

2. Three additional neuromast rows are developed on the caudal fin of *D. collonianus* (Figure 1C). As in *D. quadrimaculatus* one longitudinal row occurs in the interradial space immediately ventral to lcv, the next in the free interradial space between lcv and lcm, and the third immediately dorsal to lcm. All neuromast rows except lcd are separated from each other by only one fin ray. The typical pattern of Gobiidae is changed distinctly. The gap between lcv and lcm is closed completely, those between
lcm and lcd partly. But a somewhat asymmetrical pattern with lcd separated from the next row by two fin rays is still retained.

3. In some pelagic Gobiidae (e.g. *A. minuta*, *L. petersii*) the number of longitudinal rows is increased to eight rows (Figure 1D). As a result the last gap immediately ventral to lcd is closed. Additionally, an eighth row occurs in the interradial space dorsal to lcd. In these species the arrangement of the neuromast rows is symmetrical, i.e. the longitudinal rows are separated from each other by one fin ray. In *A. minuta* and *L. petersii* the dorsalmost neuromast row extends between the second and third (2/3) and the ventralmost row between 9/10 branched fin rays (Scattolin 2003). This corresponds well with the less complete pattern of *D. collonianus*. In combination with a pelagic lifestyle eight longitudinal rows of free neuromasts on the caudal fin is the most advanced pattern in the Gobiioidei and so far is only known in Gobiidae.

The pattern of the lateral line system on the caudal fin of *D. collonianus* and *D. quadrimaculatus* differs from each other and each represents a derived condition. Nevertheless, the sister taxa of *Deltentosteus* are not identified yet. Therefore the increase of the number of neuromast rows on the caudal fin in these two *Deltentosteus* species is obviously an apomorphic feature but we have no evidence that this is an autapomorphy. Additionally, it is unlikely that the above-mentioned species with eight longitudinal neuromast rows on the caudal fin could be regarded as sister taxa. These species differ distinctly from *D. collonianus* and *D. quadrimaculatus* by a series of paedomorphic features such as the lack of lateral line canals, transparent bodies, and pelagic lifestyle.

To date no gobiid species is known with seven neuromast rows and the ontogeny of the lateral line system of species with eight rows is not investigated. Therefore it is not clear how the number of neuromast rows is increased from six to eight. Nevertheless, concluding from the three above-mentioned types of arrangement of the lateral line system on the caudal fin of Gobiidae, the number of longitudinal neuromast rows is seemingly increased from ventral to dorsal: additional rows occur first in the ventral third of the caudal fin, a further increase of the neuromast rows covers the central and finally the dorsal part of the fin.

Seemingly at least two basic pathways developed during gobioid phylogeny. Originating from the plesiomorphic pattern with three neuromast rows on the caudal fin either (1) the number of neuromast rows decreased or (2) the number of neuromast rows increased. Deviations from the plesiomorphic pattern obviously occurred several times and independently within the Gobiioidei (Ahnelt and Göschl 2004).

Virtually nothing is known about the lifestyle of the two *Deltentosteus* species. Both are benthic, are usually collected during dredging on soft bottom (mud, muddy sand, or sand), and occur inshore to a depth of 120–160 m (Miller 1986; Ahnelt and Dorda 2004). *Deltentosteus collonianus* and *D. quadrimaculatus* are so far the only benthic gobies described with an increased number of longitudinal neuromast rows on the caudal fin. Therefore an increase of neuromast rows on the caudal fin of Gobiidae, reported from several pelagic species (Mortara 1918; Scattolin 2003), is not necessarily linked to a pelagic lifestyle. We assume that the increase of neuromast rows on the caudal fin is possibly linked to the adaptation to a low-noise habitat in deep habitats.

Extensive proliferation of free neuromasts is characteristic of many fishes inhabiting low-noise environments (Coombs et al. 1988; Webb 1989; Mogdans et al. 2003; Kasumyan 2003). Such an elaborated lateral line system occurs on the trunk and the caudal fin of *D. collonianus* and *D. quadrimaculatus* (Sanzo 1911, Plate 9, Figure 6; De Buen 1923,
Figure 27). Surprisingly, the number of free neuromasts on the head is only slightly increased, if at all, and head canals, generally reduced or lacking in species inhabiting low-noise habitats are still developed. A feature such as lateral line canals is on first sight contradictory to the postulated increase of free neuromasts as a result of adaptation to a low-noise habitat. But in *D. collonianus* and *D. quadrimaculatus* these canals are perforated by an unusually high number of additional pores (Sanzo 1911; De Buen 1923, Figures 31, 37; Miller 1986) allowing a better and multidirectional instead of linear exposure of the canal neuromasts to water movements. Besides the complete loss of head canals and replacement of the canal neuromasts by free neuromasts, the extensive perforation of these canals is seemingly another but uncommon pathway of the evolutionary transformation of the head lateral line system in gobiid fishes.

The number of neuromast rows on the caudal fin (and also the increase in the total number of free neuromasts) in *D. collonianus* and *D. quadrimaculatus* is obviously linked to the high number of neuromasts on the trunk and to the extensively perforated head canals. This combination of features of the mechanosensory lateral line could be regarded as an indication of a specialized lifestyle in a low-noise habitat, a hypothesis which needs to be tested.

**Acknowledgements**

The authors would like to thank E. Mikschi, H. Wellendorf (NMW), G. Delmastro (MCSNC), and A. L. Garvia (MNCN) for making material available.

**References**

Ahnelt H, Bohacek V. 2004. The lateral line system of two sympatric eastern Pacific gobiid fishes of the genus *Lythrypnus* (Teleostei: Gobiidae). Bulletin of Marine Science 74:31–51.

Ahnelt H, Dorda J. 2004. Gobioid fishes from the north eastern Atlantic and the Mediterranean: new records and rarely found species. Annalen des Naturhistorischen Museums in Wien 105B:5–19.

Ahnelt H, Duchkowitsch M. 2001. The lateral line system of two Ponto-Caspian gobiid species (Gobiidae, Teleostei): a comparison. Folia Zoologica 50:217–230.

Ahnelt H, Göschl J. 2003. Morphological differences between the eastern Pacific gobiid fishes *Quietula guaymasiae* and *Quietula y-cauda* (Teleostei: Gobiidae) with emphasis on the topography of the lateral line system. Cybium 27:185–197.

Ahnelt H, Göschl J. 2004. The pattern of the lateral line system on the caudal fin of *Percottus glenii* Dybowski, 1877 (Teleostei: Odontobutidae), with comments on the arrangement of the lateral line system on the caudal fin of Gobioidae. Proceedings of the California Academy of Sciences 55:358–372.

Ahnelt H, Scattolin G. 2003. The lateral line system of a blind goby, *Typhlogobius californiensis*, Steindachner 1879 (Teleostei: Gobiidae). Annalen des Naturhistorischen Museums in Wien 104B:11–25.

Akihito, Sakamoto K, Ikeda Y, Iwata A. 2000. Suborder Gobiioidei. In: Nakabo T, editor. Fishes of Japan with pictorial keys to the species. 2nd ed. Tokyo: Tokai University Press. p 1139–1310.

Carton AG, Montgomery JC. 2004. A comparison of lateral line morphology of blue cod and torrentfish: two sandperches of the family Pinguipedidae. Environmental Biology of Fishes 70:123–131.

Collette BB, Banarescu P. 1977. Systematics and zoogeography of the fishes of the family Percidae. Journal of the Fisheries Research Board of Canada 34:1450–1463.

Coombs S, Braun CB, Donovan B. 2001. The orienting response of Lake Michigan mottled sculpin is mediated by canal neuromasts. Journal of Experimental Biology 204:337–348.

Coombs S, Jansen J, Webb JF. 1988. Diversity of lateral line systems: evolutionary and functional considerations. In: Atema J, Fay RR, Popper A, Tavolga WN, editors. Sensory biology of aquatic animals. New York: Springer. p 553–593.

De Buen FO. 1923. Gobius de la Península Ibérica y Baleares; grupos Lesueurii, Colonianus, Affinis y Minutus. Memorias del Instituto Espanol de Oceanografia 3:121–266.

Dijkgraaf S. 1962. The functioning and the significance of the lateral line organs. Biological Review 38:51–105.
Disler NN, Smirnov SA. 1977. Sensory organs of the lateral line canal system in two percids and their importance in behavior. Journal of the Fisheries Research Board of Canada 34:1492–1503.

Engelmann J, Hanke W, Mogdans J, Bleckmann H. 2000. Hydrodynamic stimuli and the fish lateral line. Nature 408:51–52.

Fage L. 1918. Shore fishes. Report of the Danish Oceanographic Expeditions 1908–1910 to the Mediterranean and Adjacent Seas 2:1–154.

Gill HS, Bradley FLS, Miller PJ. 1992. Validation of the use of cephalic lateral-line papillae patterns for postulating relationships among gobiodi genera. Zoological Journal of the Linnean Society 106:97–114.

Greenwood PH. 1976. A review of the Family Centropomidae (Pisces, Perciformes). Bulletin of the British Museum (Natural History) Zoology 29:1–81.

Hoese DF, Gill AC. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobiodei). Bulletin of Marine Science 52:415–440.

Hofer B. 1907. Studien über die Hautsinnesorgane der Fische. I. Die Funktion der Seitenorgane bei Fischen. Berichte der königlich-bayerischen biologischen Versuchsstation in München 1:115–164.

Iljin BS. 1930. Le système des Gobiidès. Trabajos del Instituto Espanol de Oceanografia, Madrid 2:1–63.

Jakubowski M. 1966. Cutaneous sense organs of fishes. IV. The lateral-line organs in the perch-pike (Lucioperca lucioperca L.) and perch (Perca fluviatilis L.), their topography, innervation, vascularization, and structure. Acta Biologica Cracoviensia Series Zoologia 9:137–149.

Jakubowski M. 1967. Cutaneous sense organs of fishes. Part VII. The structure of the system of lateral-line canal organs in the Percidae. Acta Biologica Cracoviensia Series Zoologia 10:71–81.

Kasumyan AO. 2003. The lateral line in fish: structure, function, and behavior. Journal of Ichthyology 43(Suppl 2):175–213.

Larson HK. 2001. A revision of the gobiid fish genus Mugilogobius (Teleostei: Gobiodei), and its systematic placement. Records of the Western Australian Museum 62(Suppl):i–vi, 1–233.

Miller PJ. 1986. Gobiidae. In: Whitehead PJ, Bauchot M-L, Hureau J-C, Nielsen J, TortoneE E, editors. Fishes of the North-eastern Atlantic and the Mediterranean. Volume 3. Paris: UNESCO. p 1019–1085.

Mogdans J, Engelmann J, Hanke W, Kröther S. 2003. The fish lateral line: how to detect hydrodynamic stimuli. In: Barth FC, Humphrey JAC, Secomb TW, editors. Sensors and sensing in biology and engineering. New York: Springer. p 173–185.

Montgomery JC, Baker CF, Carton AG. 1997. The lateral line can mediate rheotaxis in fish. Nature 389:960–963.

Mortara S. 1918. La disposizione degli organi ciatiformi del genere Aphya e suoi rapporti con quella del genere Gobius. Regio Comitato Talassografico Italiano, Memoria 65:5–23.

Popper AN, Platt C. 1993. Inner ear and lateral line. In: Evans DH, editor. The physiology of fishes. Boca Raton (FL): CRC Press. p 99–136.

Sanzo L. 1911. Distribuzione delle papille cutanee (organi ciatiformi) e suo valore sistematico nei Gobi. Mitteilungen aus der Zoologischen Station zu Neapel, Berlin 20:249–328.

Scattolin G. 2003. Das Seitenliniensystem cryptobenthischer und pelagischer Meergrundeln (Teleostei: Gobiidae)—ein Vergleich [MSc thesis]. Vienna: University of Vienna.

Shibukawa K, Iwata A, Viravong S. 2001. Terateleotris, a new gobioid fish genus from the Laos (Teleostei, Perciformes), with comments on its relationships. Bulletin of the National Science Museum, Tokyo (Series A) 27:229–257.

Springer VG. 1983. Tyson belos, new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. Smithsonian Contributions to Zoology 390:1–40.

Takagi K. 1988. Cephalic sensory canal system of the gobioid fishes of Japan: comparative morphology with special reference to phylogenetic significance. Journal of the Tokyo University of Fisheries 75:499–568.

Webb CJ. 1989. Gross morphology and evolution of the mechanoreceptive lateral-line system in teleost fishes. Brain, Behavior and Evolution 33:35–53.