

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 Gobioidei

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The pattern of the lateral-line system on the caudal fin is surveyed in 120 genera and 200 species of gobioid fishes. In the majority of Gobioidei this sensory system is arranged in two general patterns on the caudal fin: Pattern 1 with four lateral lines, one transversal and three longitudinal, and Pattern 2 with three lateral lines, one transversal and two longitudinal. These lateral lines are formed by rows of free (superficial) neuromasts, except in the Rhyacichthyidae. In these most-basal Gobioidei, the longitudinal lateral lines are a combination of canals and free neuromasts. The transversal lateral line in Gobioidei (including Rhyacichthyidae) is always formed by free neuromasts. This transversal row is discontinuous, consisting of a few short parts (plesiomorphic), or it is continuous and relatively long (apomorphic). In some species, it is indistinct and difficult to separate from the longitudinal rows. Pattern 1 of the lateral-line system on the caudal fin is plesiomorphic for Gobioidei. As relatively rare deviations from these two patterns, an increase or a decrease in the number of longitudinal neuromast rows occurs in some Gobiidae. *Percottus glenii* is the only known species of basal Gobioidei (including the Eleotridae) characterized by a specialized lateral-line pattern on the caudal fin. On each side of this fin, only two neuromast rows are developed: a discontinuous transversal row on its base and a long longitudinal row along its midline. This is the most specialized character state within the Odontobutidae. This research provides a further indication that the Odontobutidae are not monophyletic.

The free neuromasts of the lateral-line system of Gobioidei are arranged in series of characteristic rows and aggregations on the head, the trunk and the caudal fin. Lateral-line canals are absent on the trunk and on the caudal fin except in the Rhyacichthyidae, the most basal Gobioidei (Miller 1973; Hoese and Gill 1993). The pattern of the cephalic lateral-line system has been widely used in the classification of Gobioidei (e.g., Sanzo 1911; Iljin 1930; Miller 1986; Takagi 1988; Akihito et al. 2000; Larson 2001), but detailed information on the neuromast pattern on the trunk and on the caudal fin is rare. In most species the free neuromasts on the body are tiny and hard to detect. They are also easily damaged or abraded during collecting or preservation. This is especially true for the caudal fin. In recent years more attention has been given to the neuromast pattern on the trunk and on the caudal fin (e.g., Ahnelt and Duchkowsch 2001; Shibukawa et al. 2001; Ahnelt and Scattolin 2003).

Gobioid fishes are characterized by two general patterns of the lateral-line system of the cau-

dal fin: Pattern 1, with a transversal and three longitudinal lateral lines; Pattern 2, with a transversal and two longitudinal lateral lines (Ahnelt et al. 2000; Shibukawa et al. 2001; Ahnelt and Göschl 2003). The combination of lateral-line canals and free neuromasts is only known in the Rhyacichthyidae. In all other Gobioidae, only free neuromasts form the lateral-line system on the caudal fin. In some species, the transversal row is indistinctly developed and/or difficult to separate from the longitudinal rows. As a deviation from pattern 1, the number of longitudinal neuromast rows in some Gobiidae is increased (Mortara 1918) or decreased (Miller 1963).

Here we describe the reduced pattern of the lateral-line system on the caudal fin of the odontobutid fish *Perccottus glenii* Dybowski, 1877. Compared with the plesiomorphic arrangement of the free neuromasts on the caudal fin of the other basal Gobioidae (Rhyacichthyidae, *Terateleotris*, Odontobutidae and Eleotridae), *P. glenii* is characterized by a specialized arrangement of these neuromasts, otherwise known only in two miniature Gobiidae.

MATERIALS AND METHODS

NOMENCLATURE.— **Odontobutidae:** According to Shibukawa et al. (2001) and Miller (2003), the intra-familial relationships of the Odontobutidae are unsolved and a redefinition of the Odontobutidae is needed. In the definition of the Odontobutidae, we follow, therefore, Hoese and Gill (1993) who recognize three genera within this family, *Micropercopops*, *Odontobutis* and *Perccottus*. **Rhyacichthyidae:** Watson and Pöllabauer (1998) did not assign *Protogobius* Watson and Pöllabauer, 1998 to a gobioid family. In the phylogenetic tree of Akihito et al. (2000a), based on mitochondrial DNA, *Rhyacichthys* and *Protogobius* form a single cluster and were, therefore, united as Rhyacichthyidae by Shibukawa et al. (2001). In the definition of the Microdesmidae and the Ptereleotridae, we follow Thacker (2003).

Institutional abbreviations follow Leviton et al. (1985) except for: CMN(FI) = Canadian Museum of Nature; IZUW = Institute of Zoology, University of Vienna; IECB = Institute of Ecology and Conservation Biology, University of Vienna.

The following preserved specimens were examined (collection number, number of specimens, sex, SL in mm, sampling site). Length of specimens is given in standard length. The sex was determined by the shape of the urogenital papillae: longer and more pointed in males, shorter and wider in females.

MATERIAL EXAMINED

Odontobutidae: *Perccottus glenii*: NMH 2003.26.1; 1 female, 76.8 mm; Hungary, Bodrog River, Satoraljaujhely. NMH 2003.27.1; 1 female, 85.3 mm; Hungary, Tisza River, Mindszent. NMH 2003.28.1; 1 male, 65.7 mm; Hungary, Bodrog River, Satoraljaujhely. NRM 23932; 2 juveniles, 25.9–26.8 mm; Russia, Amur River, 5 km E Troitskoye. USNM 105188; 1 male, 64.1 mm; Russia, Sakhalin Island, Khanka Lake. USNM 077008; 1 female, 91.6 mm; China, Sungari River near its junction with the Amur. IECB uncatalogued; 1 male, 101.8 mm and 1 female, 72.6 mm; Ukraine, Pond at Komarno, near River Dniestr. IECB uncatalogued; 1 male, 79.6 mm and 1 female, 104.5 mm; Ukraine, Pond at Komarno, near River Dniestr.

Rhyacichthyidae: *Protogobius attiti* Watson & Pöllabauer, 1998: NMW 94266, 1 male, 67.7 mm, New Caledonia, South Province, Trou Bleu River. NMW 94267, 1 female, 55.5 mm, New Caledonia, Sotuh Province, Fausse Yaté River. *Rhyacichthys aspro* (Valenciennes, 1837): CAS 138655, 1 spm., sex ?, 98.8 mm, Philippines, Mindanao, Tagaloan River. CAS 51696, 1 spm., sex?, 102.2 mm, Philippines, Luzon, Mantugil River, Villar. NMW 45968, 1 female, 97.2 mm; Indonesia, Java, Semarang. NMW 82972, 1 male, 115.2 mm; Indonesia, Moluccas. NMW 82990, 1 male?, 121.7 mm, Philippines.

COMPARATIVE MATERIAL

Within the families, the subfamilies and the genera are listed alphabetically. The pattern of free neuromasts of the lateral-line system on the caudal fin is as follows: four rows (one transversal **let** and three longitudinal **led**, **lem** and **lev**) (Fig. 1A–B) or three rows (one transversal **let** and two longitudinal **led** and **lem**) (Fig. 1C–D). Row **let** is continuous at the base of the caudal fin or discontinuous, as two, three (generally), or four short rows anterior to each longitudinal row (Fig. 1). Species with two longitudinal rows are marked with an asterisk. Species with more than three longitudinal rows are marked with an §. Species with one longitudinal row (**lem**) are marked with #. Number in parentheses is number of investigated specimens and not necessarily identical with the number of specimens in the lot.

Odontobutidae: *Micropercops swinhonis* (Günther, 1873), UMMZ 167389, USNM 336883 (12); *Odontobutis aurarmus** Vidthayanon, 1995, USNM 325486, UMMZ 223284 (6); *Odontobutis obscura** (Temminck & Schlegel, 1845), CAS 32827, CAS 28154, MNHN 6778, MNHN 6481, MNHN 1987-1213, USNM 264892, USNM 864893, USNM 086965, UMMZ 70284, UMMZ 142619 (25); *Odontobutis potanophila** (Günther, 1861), BMNH 1918.11.12.16–18 (2).

Eleotridae: Butinae: *Bostrychus africanus* (Steindachner, 1879), BMNH 1989.1.6: 23–29 (3); *Bostrichthys zonatus* (Weber, 1907), NMW 58166 (1); *Butis butis* (Hamilton, 1822), CAS 205539, NMW 22482 (5); *Butis koilomatodon* (Bleeker, 1849), BMNH 1988.2.8: 1–8 (4); *Kribia nana** (Boulenger, 1901), CAS 64486, BMNH 1918.11.12: 16–18, BMNH 1948.1.14: 291–313 (4); *Kribia kribensis** (Boulenger, 1907), NMW 78428 (2); *Milyeringa veritas* Whitely, 1945, BMNH 1982.2.17: 1–9 (3); *Ophiocara porocephala* (Valenciennes, 1837), BMNH 1980.10.10: 260–263 (4); *Oxyeleotris fimbriata* (Weber, 1907), BMNH 1983.8.2: 147–148 (1); *Oxyeleotris heterodon* (Weber, 1907), NMW 57206, NMW 57206 (2); *Oxyeleotris lineolatus* (Steindachner, 1867), BMNH 1983.8.2: 203–210 (4); *Oxyeleotris marmorata* (Bleeker, 1852), CAS 66251 (2); *Oxyeleotris urophthalmoideus* (Bleeker, 1853), CAS 49456 (1); *Pogoneleotris microps* Weber, 1907, NMW 31456 (1); *Typhleotris pauliani* Arnoult, 1959, BMNH 1981.111.9: 19–20 (2).

Eleotrinae: *Batanga lebretonis* (Steindachner, 1870), NMW 22275, NMW 76245, NMW 76407, NMW 58729 (11); *Binaka grvinoides* (Bleeker, 1853), BMNH 1983.8.2: 211–214 (3); *Dormitor latifrons* (Richardson, 1844), CAS 54392 (2); *Eleotris* sp., NMW 94987 (1); *Eleotris amblyopsis* (Cope, 1871), NMW 85500 (6); *Eleotris coxi* (Kreffit, 1864), NMW 78548 (1); *Eleotris daganensis* Steindachner, 1870, NMW 22488 (1); *Eleotris fusca* (Schneider & Forster, 1801), NMW 89288 (1); *Eleotris gyrinoides* Bleeker, 1853, NMW 80754 (2); *Eleotris picta* Kner, 1863, SIO 59-358-58B (1); *Eleotris sandwicensis* Vaillant & Sauvage, 1875, NMW 78678, SIO 61-425-58A (7); *Eleotris senegalensis* (Steindachner, 1870), NMW 78553, NMW 85266 (3); *Eleotris vittata* Dumeril, 1861, BMNH 1956.9.6: 51, BMNH 1985.3.18: 191–192 (3); *Gobiomorphus basalus* (Gray, 1842), BMNH 1964.12.21: 17 (1); *Gobiomorphus gobioids* (Valenciennes, 1837), NMW 22508 (1); *Gobiomorus dormitor* Lacepede, 1800, BMNH 1982.8.19: 2021–2040 (4); *Guavina guavina* (Valenciennes, 1837), NMW 14644, NMW 22531 (4); *Hypseleotris* sp., NMW 30966 (1); *Hypseleotris compressa* (Kreffit, 1864), NMW 22511, NMW 22520, NMW 58165 (6); *Mogurnda mogurnda* (Richardson, 1844), BMNH 1983.8.2: 4 (2); *Mogurnda nesolepis* (Weber, 1907), NMW 22517 (1); *Mogurnda variegata* Nichols, 1951, BMNH 1983.8.2: 73–74 (2); *Ophieleotris aporos* (Bleeker, 1854), NMW 22524, NMW 22537, NMW 78607, NMW 83359 (7); *Philypnodon grandiceps* (Kreffit, 1864), NMW 22534 (1).

Gobiidae: Amblyopinae: *Amblyopus caecilus* Karoli, 1882, NMW 5779 (2); *Taenioides buchanani* (Day, 1873), NMW 76500 (1); *Taenioides cirratus* (Blyth, 1860), NMW 94598 (1).

Gobiinae: *Acentrogobius caninus* (Valenciennes, 1837), NMW 28808–28811 (3); *Acentrogobius frenatus* (Günther, 1861), NMW 30452–30453 (2); *Acentrogobius masoni* (Day, 1873), NMW 33926 (1); *Acentrogobius simplex* (Sauvage, 1880), NMW 29964 (6); *Amblygobius albimaculatus* (Rüppell, 1830), NMW 28722–28727 (4); *Amblygobius byonensis* (Richardson, 1844), NMW, 33924, NMW 58800 (4); *Amblygobius sphynx* (Valenciennes, 1837), NMW 30102–30105 (3); *Amoya* sp., NMW 16165, NMW 30757 (2); *Anatirostrum profundorum** (Berg, 1927), CMNFI 1999–0023 (4); *Asteropteryx semipunctatus* Rüppell, 1830, NMW 22516, NMW 78225, NMW 88504 (6); *Bathygobius cotticeps* (Steindachner, 1879), NMW 30439 (1); *Bathygobius fuscus* (Rüppell, 1830), NMW 88321(5); *Bathygobius soporator* (Valenciennes, 1837), NMW 33927–33928, NMW 60391 (4); *Benthophilus stellatus** (Sauvage, 1874), IZUW uncatalogued (2); *Caffrogobius caffer* (Günther, 1874), NMW 28819–28820 (2); *Callogobius sclateri* (Steindachner, 1879), NMW 30901 (1); *Chasar bathybius* (Kessler 1877), CMNFI uncatalogued (4); *Chromogobius quadrivittatus* (Steindachner, 1863), NMW 30639, NMW 30657, NMW 86084, NMW 88486 (4); *Chromogobius zebratus* (Kolombatovic, 1891), NMW 29613, NMW 86082 (3); *Corcyrogobius liechtensteini* (Kolombatovic, 1891), NMW 37536–37543, NMW 78460; NMW 94458 (4); *Deltentosteus collonianus*§ (Risso, 1820), NMW 28826–28830, NMW 29087–29100, NMW 30342, NMW 86693 (6); *Deltentosteus quadrimaculatus*§ (Valenciennes, 1837), NMW 28845–28849, NMW 37479–37484, NMW 30667 (5); *Didogobius kochi* Van Tassell, 1988, IZUW uncatalogued (2); *Didogobius splechnai* Ahnelt & Patzner, 1995, NMW 92804, NMW 92805, NMW 94451 (4); *Economidichthys pygmaeus* (Holly, 1929), MCN 106376–394 (2); *Elacatinus* sp., SIO uncatalogued (1); *Elacatinus multifasciatus* (Steindachner, 1876), NMW 76239 (1); *Evermannia longipinnis* (Steindachner, 1879), NMW 76420 (2); *Eviota distigma* Jordan & Seale, 1906, NMW 88173 (4); *Favonogobius reichi* (Bleeker, 1853), NMW 33897 (1); *Gammogobius steinitzi* Bath, 1971, SMF 11071, NMW 94452–94456 (4); *Glossogobius celebius* (Valenciennes, 1837), NMW 83363 (1); *Glossogobius giuris* (Hamilton, 1822), NMW 30543–30544 (2); *Gobiodon citrinus* (Rüppell, 1838), NMW 30973 (5); *Gobiosoma bosc* (Lacèpede, 1800), SIO 67-277-59 (2); *Gobius ater* Bellotti, 1888, NMW 28551–28552, NMW 29041 (2); *Gobius buccichii* Steindachner, 1870, NMW 88436, NMW 88491 (6); *Gobius cobitis* Pallas, 1814, NMW NMW 87092, NMW 88463 (6); *Gobius cruentatus* Gmelin, 1789, NMW 28986–28982 (2); *Gobius fallax* Sarato, 1889, NMW 28792, NMW 77932 (2); *Gobius gasteveni* Miller, 1974, MNCN 73576–73579, MNCN 79218–79219 (3); *Gobius geniporus* Valenciennes, 1837, NMW 87065 (1); *Gobius niger* Linnaeus, 1758, MNCN 74278–74282, IZUW uncatalogued (4); *Gobius paganellus* Linnaeus, 1758, NMW 80592, NMW 84937, NMW 94582, NMW 94583 (6); *Gobius rouli* De Buen, 1828, NMW 94277 (2); *Gobius vittatus* Vinciguerra, 1883, IZUW uncatalogued (1); *Gobiusculus flavescens** (Fabricius, 1779), NMW 30693 (3); *Heteroleotris vulgaris* (Klunzinger, 1871), NMW 31020, NMW 78237, NMW 88177 (12); *Istigobius diadema* (Steindachner, 1876), NMW 29171 (1); *Knipowitschia croatica** Mrakovic, Kerovec, Misetic & Schneider, 1996, NMW 93978 (6); *Knipowitschia caucasica** (Berg, 1916), LZUT uncatalogued (2); *Knipowitschia pannizae* (Verga, 1841), IZUW uncatalogued (4); *Knipowitschia punctatissima** (Canestrini, 1864), IZUW uncatalogued (5); *Lebetus guilleti*# (le Danois, 1913) NMW 94589–94592 (4); *Lesueurigobius friesii* (Malm, 1874), MNCN 78580–78583; NMW 76296, NMW 88348 (4); *Lesueurigobius suerii* (Risso, 1810), NMW 88351, NMW 88550 (2); *Lophogobius cyprinoides* (Pallas, 1770), NMW 30807–30808 (2); *Lythrypnus cobalus* Bussing, 1990, CAS 205778, SIO 72-97 (2); *Lythrypnus dalli* (Gilbert, 1890), CAS 118455, SIO 63-174-59C (6); *Lythrypnus gilberti* (Heller and Snodgrass, 1903), CAS 39236 (4); *Lythrypnus pulchellus* Ginsburg, 1938, CAS 18097 (3); *Lythrypnus rhizophora* (Heller and Snodgrass, 1903), CAS 50078 (5); *Lythrypnus zebra* (Gilbert, 1990), CAS 25388, SIO H50-40-59A (6); *Mauligobius maderensis*

(Valenciennes, 1837), NMW 87554 (1); *Mesogobius batrachocephalus* (Pallas, 1814), NMW 11397 (3); *Microgobius gulosus* (Girard, 1858), NMW 87269 (3); *Millerigobius macrocephalus* (Kolombatovic, 1891), IZUW uncatalogued (2); *Myersinia filifer* (Valenciennes, 1837), NMW 86810 (1); *Neogobius cyrius* (Kessler, 1874), NMW 94327 (4); *Neogobius eurycephalus* (Kessler, 1874), NMW 92808 (2); *Neogobius fluviatilis* (Pallas, 1814), NMW 94446 (4); *Neogobius gorlap* Ilijn, 1949; CMNFI 1993-0161, CMNFI 1993-0162 (3); *Neogobius gymnotrachelus* (Kessler, 1857), NMW 88596, NMW 94583 (6); *Neogobius kessleri* (Günther, 1861), IZUW uncatalogued, NMW 93977, NMW 94560 (6); *Neogobius melanostomus* (Pallas, 1814), NMW 60200 (1); *Neogobius ratan* (Nordmann, 1840), NMW 33910 (1); *Neogobius syrman* (Nordmann, 1840), CMNFI 1970-0544 (1); *Odondebuenia balearica* (Pellegrin and Fage, 1907), MNCN 107992-108042 (6); *Padogobius bonelli* (Bonaparte, 1846), IZUW uncatalogued (5); *Padogobius nigricans* (Canestrini, 1867), IZUW uncatalogued (2); *Paragobiodon echinocephalus* (Rüppel, 1830), NMW 29196 (4); *Paragobiodon modestus* (Regan, 1908), NMW 87478 (4); *Paragobiodon xanthosomus* (Bleeker, 1852), NMW 87477, NMW 87479 (2); *Pomatoschistus adriaticus** Miller, 1873, NMW 28647-28649, NMW 28670 (5); *Pomatoschistus kneri* (Steindachner, 1861), NMW 37772-37776 (1); *Pomatoschistus marmoratus** (Pallas, 1810), NMW 87359 (3); *Pomatoschistus microps* (Kroyer, 1838), IZUW uncatalogued (3); *Priolepis* sp., NMW 88507 (2); *Priolepis nuchi-fasciata* (Günther, 1873); NMW 33908 (1); *Proterorhinus marmoratus* (Pallas, 1814), NMW 60240, NMW 79755, NMW 94561, NMW 94595 (7); *Rhinogobiops nicholsii* (Bean, 1882), CAS 135015, CAS 135016, CAS 27627 (6); *Speleogobius trigloides*# Zander and Jelinek, 1976, NMW 75826-75827 (1); *Thorogobius macrolepis* (Kolombatovic, 1891), NMW 37421-37422, NMW 94331, NMW 94332 (7); *Thorogobius ephippiatus* (Lowe, 1839), NMW 86591 (1); *Trimma* sp., NMW 89332 (1); *Valenciennea sexguttat* (Valenciennes, 1837), NMW 83959 (1); *Vanneaugobius dollfusi* Brownell, 1978, NMW 87961, NMW87962 (6); *Zebrus zebrus* (Risso, 1827), NMW 86097, NMW 88472, NMW 88492, IZUW uncatalogued (7); *Zosterisessor ophiocephalus* (Pallas, 1814), IZUW uncatalogued (1). **Gobionellinae:** *Acanthogobius flavimanus* (Temminck and Schlegel, 1845), CAS 36971, CAS 42487, CAS 52003, CAS 21367, CAS 213686, NMW 30454-30455 (28); *Aphia minuta*§ Risso, 1827, NMW 31463, NMW 88030, NHRM 46688 (10); *Arcyogobius baliurus* (Valenciennes, 1837), NMW 30278-30279, NMW 82114 (4); *Awaous giurii* (Hamilton, 1822), NMW 30096 (1); *Awaous tajasica* (Lichtenstein, 1822), NMW 91265, NMW 91277 (6); *Brachygobius xanthozonus** (Bleeker, 1849), NMW 12685, NMW 30152-30156 (4); *Cepola striata* Bloch and Schneider, 1801, NMW 28742-28747 (3); *Clariger cosmurus** Jordan and Snyder, 1901, IZUW uncatalogued (2); *Chaenogobius gulosus* (Sauvage, 1882), IZUW uncatalogued, NMW 30676 (4); *Clevelandia ios** (Jordan and Gilbert, 1882), CAS 15476, SIO 47-73-59D (5); *Ctenogobius sagittula** (Günther, 1861), CAS 55185 (3); *Euclagogobius newberryi** (Girard, 1856), CAS 31768, SIO 62-278-59A (6); *Eutaeniichthys gilli** Jordan and Snyder, 1901, IZUW uncatalogued (2); *Evorthodus lyricus* (Girard, 1858), NMW 83107, NMW 88633 (3); *Gillichthys mirabilis** Cooper, 1864), CAS 22071, CAS 79616 (6); *Gillichthys seta** (Ginsburg, 1938), CAS 26055, SIO 67-133-59 (6); *Gobiopterus* cf. *chuno*§ (Hamilton, 1822), IZUW uncatalogued (5); *Gymnogobius castaneus* (O'Shaughnessy, 1875), IZUW uncatalogued, NMW 78031(3); *Gymnogobius wrotaenia** (Hilgendorf, 1879), NMW 29508 (1); *Ilypnus gilberti** (Eigenmann & Eigenmann, 1891), CAS 24169, CAS 26896 (6); *Ilypnus luculentus** (Ginsburg, 1938), CAS 214242, SIO 62-235-59A (6); *Lepidogobius lepidus** (Girard, 1858), CAS 19894, CAS 25383, CAS 53228 (6); *Lethops connectens** Hubbs, 1926, SIO H46-46, SIO H51-239 (6); *Leucopsarion petersii*§ Hilgendorf, 1880, FAKU 103091 (5); *Luciogobius guttatus** Gill, 1859, FAKU 102257-102258 (2); *Mugilogobius poeyi* (Steindachner, 1867), NMW 30608 (1); *Oxyurichthys papuensis* (Valenciennes, 1837), NMW 29935-29938 (3); *Oxyurichthys tentacularis*

(Valenciennes, 1837), NMW 12688 (1); *Pseudaphya ferrerii** (de Buen and Fage, 1908) NMW 37424–37429, NMW 37431–37433 (7); *Quietula guaymasiae** (Jenkins & Evermann, 1889), CAS 26056, CAS 55187 (6); *Quietula y-cauda** (Jenkins and Evermann, 1889), CAS 11497, CAS 200221 (6); *Rhinogobius* sp.*, NMW 89618 (3); *Stigmatogobius sadanundio* (Hamilton, 1822), NMW 81598 (1); *Stigmatogobius sella* (Steindachner, 1881), NMW 30107–30108 (1); *Synechogobius ommaturus* (Richardson, 1845), NMW 34199–34200, NMW 34206–34208, NMW 81876 (4); *Triaenopogon barbatus* (Günther, 1861), CAS 161208 (2); *Tridentiger bifasciatus** Steindachner, 1881, CAS 82361 (3); *Tridentiger trigonocephalus** (Gill, 1859), CAS 15405 (1); *Typhlogobius californiensis** Steindachner, 1879, CAS 200223, CAS 211664 (5). **Oxudercinae:** *Apocryptes bato* (Hamilton, 1822), CAS 89289 (2); *Boleophthalmus boddarti* (Pallas, 1770), CAS 140028, IZUW 2419 (4); *Boleophthalmus pectinirostris* (Linnaeus, 1758), NMW 78444 (2); *Periophthalmus barbarus* (Linnaeus, 1766), IZUW 2418, NMW 31321 (2). **Sicydiinae:** *Sicydium* sp., NMW 31434 (1); *Sicydium plumieri* (Bloch, 1786), NMW 91574, NMW 31411–31414 (6); *Sicyopterus cynocephalus* (Valenciennes, 1837), NMW 31405–31406 (1); *Sicyopterus sarasini* Weber and Beaufort, 1915, NMW 94340 (2); *Stiphodon elegans* (Steindachner, 1879), NMW 81318 (3).

Kraemeriidae: *Kraemeria samoensis* Steindachner, 1906, NMW 83668 (2).

Microdesmidae: *Microdesmus dipus* Günther, 1864, BMNH 1967.12.30: 1–3 (1).

Ptereleotridae: *Nemateleotris decora* Randall and Allen, 1973, BMNH 1983.3.25: 893–895 (1); *Ptereleotris microlepis* (Bleeker, 1856), BMNH 1983.3.25:892 (2).

TERMINOLOGY OF THE LATERAL-LINE SYSTEM OF THE CAUDAL FIN

Sanzo (1911) was the first to develop a terminology for the longitudinal rows of neuromasts on the caudal fin of gobioid fishes. The species he investigated have three longitudinal rows of neuromasts developed on each side of the caudal fin: one an elongation of the median trunk lateral line, and ventral and dorsal to it, and two accessory rows. Sanzo named these rows ‘lateral caudal’ (**lc**) and they differed, from dorsal to ventral, between **lc**, **lc'** and **lc''**. The number of lateral lines on the caudal fin in Gobioidae may be secondarily reduced to one or two or increased to eight neuromast rows (Mortara 1918; Ahnelt and Göschl 2003; Scattolin and Ahnelt, unpublished), making it difficult to identify homologous rows. Therefore, an alternative classification of the lateral-line system was proposed by Ahnelt et al. (2000) and Ahnelt and Duchkowitsch (2001) reflecting the position of the rows on the caudal fin: **lcd** (lateral caudal dorsal), **lcm** (lateral caudal medial) and **lcv** (lateral caudal ventral). Three longitudinal lateral lines are plesiomorphic for Gobioidae (Springer 1983). In Gobioidae with two longitudinal rows, the **lcd** and **lcm** are developed and the **lcv** is absent (e.g., Ahnelt et al. 2000; Ahnelt and Göschl 2003). In species with one longitudinal row (**lcm**), both accessory rows (**lcd** and **lcv**) are absent.

The characteristic pattern of the lateral-line system on the caudal fin, **lcd** separated from **lcm** by three and **lcm** from **lcv** by two fin rays, allows the identification of the three longitudinal neuromast rows in species with more than three rows developed (Fig. 1F).

The transversal row (**lct**) on the base of the caudal fin was included by Sanzo (1911) as the last transversal row in the lateral medial trunk series. These series of generally short rows run along the midline of the trunk and are associated with the trunk lateral-line canal in *Rhyacichthys*, *Protogobius* and *Terateleotris* (Wongrat and Miller 1991; Shibukawa et al. 2001). Such short transversal rows are also found on each first canal carrying scales on the caudal fin of *R. aspro*. Lateral-line canals on the trunk and on the caudal fin are absent in the other Gobioidae. The neuromast row **lct** differs from the medial trunk series (**lm**) as it is distinctly longer, seemingly because it was orig-

inally associated with the three lateral-line canals of the caudal fin. In many advanced taxa the three parts unite to form a long, continuous transversal row, exceeding the longitudinal rows dorsally and ventrally and often nearly extending over the entire caudal fin base (Fig. 1D–F). Generally, **lct** is separated from the last **lm** row by a larger gap than the **lm** rows on the caudal peduncle from each other. The row **lct** may be reduced to three neuromasts, each anterior to one longitudinal neuromast row. In many species, these neuromasts are still identifiable due to their larger size and a gap to the neuromasts of the longitudinal rows (Fig. 1). These neuromasts of **lct** are in some taxa incorporated in the origin of the longitudinal neuromast rows and, therefore, only separable if they are of a larger size. The incorporation of **lct** in the longitudinal lateral-line rows and its secondary loss is seemingly apomorphic.

The neuromast rows on the caudal peduncle and on the caudal fin of gobioid fishes are innervated by the *ramus lateralis posterius* (Sanzo 1911; Wongrat and Miller 1991). According to the nomenclature of Coombs et al. (1988), **lct** (at the of caudal fin) is formed by secondary replacement neuromasts. Secondary replacement neuromasts, derived from free neuromasts associated with pores of the lateral-line canals (e.g., the trunk canal of *Protogobius*, *Rhyacichthys* and *Terateleotris*, and the origin of canals on the caudal fin of *Protogobius* and *Rhyacichthys*), form transverse rows along the former course of a canal. The longitudinally arranged neuromasts on the caudal fin (**lcd**, **lcm**, **lcv**) form rows along the direction of deleted canals and are, therefore, primary replacement neuromasts, not secondary accessory neuromasts as postulated by Wongrat and Miller (1991).

RESULTS

LATERAL-LINE SYSTEM OF THE CAUDAL FIN OF *PERCCOTTUS GLENII*.— The lateral-line system on the trunk and caudal fin is formed by free neuromasts. No trunk canal, no canal in extension of the trunk canal on the caudal fin, and no accessory canals on the trunk and on the caudal fin are developed in *P. glenii*. These canals, present in the more-basal Gobioidi *Rhyacichthys*, *Protogobius* and *Terateleotris*, are replaced by free neuromasts.

The pattern of the lateral-line system on the caudal fin is T-shaped. It consists of free neuromasts arranged in two rows on each side of the fin, one row transversal (**lct**) on the base of the fin and the second longitudinal (**lcm**) in its midline (Fig. 1E).

The transversal row is discontinuous. In adults, it extends as three distinct sections of neuromasts (short rows or accumulations) transversely between the fourth and twelfth branched caudal-fin rays. The median section extends anteriorly to the single longitudinal neuromast row. In juveniles, these three sections of the row **lct** are each represented by a single neuromast. The number of these neuromasts increases with size: in specimens > 70 mm SL, each section is represented by a short row, whereas in specimens > 100 mm SL, they are multiple rows or aggregations of neuromasts. **lct** is distinctly separated from the last row of the lateral median trunk series (**lm**) and extends over the small scales which cover the caudal fin base.

Only a single longitudinal row of neuromasts is developed, the lateral caudal median row (**lcm**). The dorsal and the ventral lateral caudal rows (**lcd** and **lcv**), the first generally present in Gobioidi, the second in many species lacking, are absent. **lcm** extends along the interradial membrane between the eighth and ninth (adult) or seventh and eighth (juveniles) branched caudal-fin rays. This row of neuromasts is long but does not reach the rear margin of the caudal fin. It extends over about three quarters of the fin in adults. The length of this row is not known for juveniles because their caudal fins were damaged in their rear parts. **lcm** begins immediately behind the last row of small scales that cover the base of the caudal fin, opposite the median section of **lct**. At the

origin of **lcm**, the neuromasts are closely set, but they are more distant from each other towards its end. In specimens >100 mm SL, this row may be doubled at its beginning.

The pattern of the lateral-line system on the caudal fin of *P. glenii* differs distinctly from the general pattern found in gobioid fishes and seemingly represents a derived condition. With only one longitudinal row of neuromasts developed, large parts of this fin are not covered by the lateral-line system. Such an arrangement of neuromasts is not known in other basal gobioid fishes including Eleotridae.

LATERAL-LINE SYSTEM ON THE TRUNK AND THE CAUDAL FIN OF RHYACICHTHYIDAE.—

Within the Rhyacichthyidae, *sensu* Shibukawa et al. (2001), the lateral-line system of *Protogobius attiti* is obviously more specialized than those of *Rhyacichthys aspro*. Compared with the sensory system of the latter, it shows reductions in the lateral-line canals on the head and on the caudal fin (Watson and Pöllabauer 1998; Shibukawa et al. 2001). Such differences are also found in the trunk lateral-line canal.

In *R. aspro*, this canal is formed by two parts: an anterior continuous and a posterior discontinuous part. The anterior part of the trunk canal is continuous with the cephalic canal system (Akihito et al. 2000b:1272, fig. 4-1) and extends uninterrupted along about the first 12 scales of the trunk. Two canaliculi (short side branches) extend dorsally and ventrally from the canal along the posterior margin of every second lateral-line scale. Between the dorsal and ventral end of these canaliculi, the posterior margin of the scales is convex and free of ctenii. This gives the anterior lateral-line scales a characteristic shape: the center of the posterior rim of the scales is emarginated and separates the ctenii into a dorsal and ventral series. The continuous part of the trunk lateral-line canal ends with a single terminal pore. In its further course, the trunk canal is discontinuous and consists of a consecutive series of short canals, each on a single scale. The discontinuous part of the trunk canal starts somewhat dorsal to the end of the continuous trunk canal, which is bent downwards ["lateral-line interrupted at midpoint of body" of Shibukawa et al. (2001)]. These canals extend over nearly the entire surface of the lateral-line scales. Each canal ends at the posterior edge of the scale and starts below the margin of the scale in front of it. Where the canals end

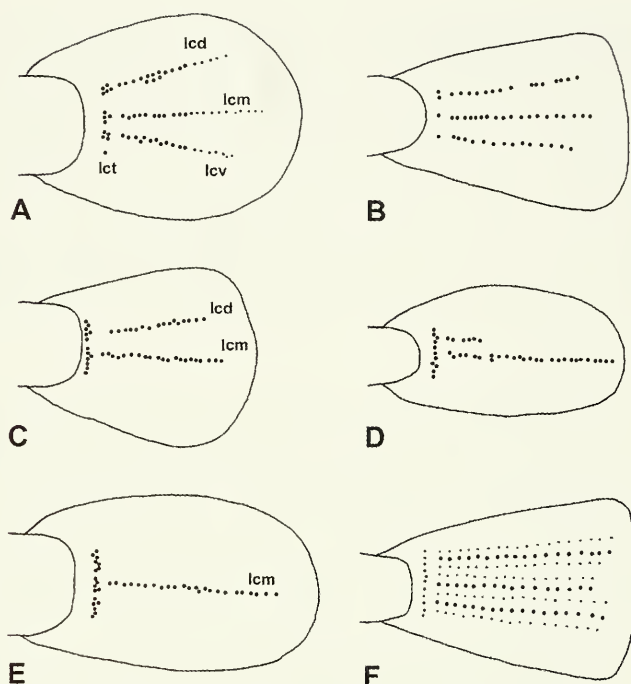


FIGURE 1. Stylized pattern of the lateral-line system on the caudal fin of Gobioidae. A–B: Three longitudinal rows of free neuromasts (A: *Gobius niger*, B: *Micropercops swinhonis*). C–D: Two longitudinal rows of free neuromasts (C: *Odontobutis aurarnus*, D: *Quietula guaymasiae*). E: One longitudinal row of free neuromasts (*Percottus glenii*). F: Eight longitudinal rows of free neuromasts (*Aphia minuta*) (neuromasts of lcd, lcm and lcv are shown enlarged). The neuromasts are not drawn to scale, and their number is larger in each species than shown. In most Gobioidae, 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.

in a terminal pore, the ctenii of these scales are separated by a narrow gap and/or a "slight median notch" (Miller 1973).

A few free neuromasts accompany the anterior continuous part of the lateral-line canal (Akihito et al. 2000b:1272, fig. 4-1). Their number increases with its end. Short transversal rows of free neuromasts are associated with most canals of the discontinuous trunk canal. They run immediately before the anterior pore. Additionally, these canals are accompanied by short longitudinal rows of free neuromasts, one row dorsal and one ventral to the canal. Such longitudinal rows occur also at the end of the continuous part of the trunk lateral-line canal. Dorsal and ventral to the accessory trunk canal of *R. aspro*, which is confined to a single scale ventral to the first dorsal fin base, occur transversal accessory neuromast rows. These rows are short, do not extend onto neighbouring scales, and seemingly correspond to the anterior rows of the lateral dorsal series (**ld**) of Sanzo (1911).

Three lateral-line canals extend over about half of the caudal fin in *R. aspro*, followed by short longitudinal rows of neuromasts. These three canals (one in extension of the trunk lateral-line canal plus two accessory canals) are restricted to three single scales on the base of the caudal fin in *P. attiti*, followed by long longitudinal rows of neuromasts (Shibukawa et al. 2001; Ahnelt unpublished). [Like Shibukawa et al. (2001) these canals in the smaller of the two specimens investigated have not been found. Data of more individuals are needed for a better knowledge of the variability of this feature of *Protogobius*. Watson and Pöllabauer (1998:148) mention: "not present on *Protogobius* are two short accessory lateral lines on the caudal fin base reported in *Rhyacichthys*. . . ." Therefore, we conclude that these authors found the lateral-line canal in the midline of the caudal fin base.] In both *Protogobius* and *Rhyacichthys*, the longitudinal lateral lines on the caudal fin are asymmetrically arranged: the dorsal and the median lateral lines are separated by three caudal-fin rays, the median and the ventral lateral lines by two rays. This asymmetrical pattern is plesiomorphic for the Gobioidi.

Short transversal rows occur on the first canal carrying scales on the caudal fin of *R. aspro* immediately before the anterior pore of each lateral-line canal, together forming a transversal row (**lct**) consisting of three parts. Additionally, as single neuromasts, longitudinal neuromast rows occur on each first scale of the three lateral-line canals. We did not find neuromasts on the corresponding scales on the caudal fin of the two investigated specimens of *P. attiti*, but, possibly, they also occur in this gobioid species. Obviously, **lct** is present in the basal gobioid family, the Rhyacichthyidae, at least in the basal *Rhyacichthys*, a feature which had been overlooked by Ahnelt and Göschl (2003). The occurrence of a transversal row on the base of the caudal fin is plesiomorphic for the Gobioidi. Also plesiomorphic is an **lct** consisting of three short transversal rows. In the following, we list differences in features of the trunk and caudal fin lateral-line system between *P. attiti* and *R. aspro* not mentioned by Watson and Pöllabauer (1998) and Shibukawa et al. (2001) (features of *R. aspro* in parentheses): (i) trunk lateral-line canal not continuous with the cephalic canal system (continuous with the cephalic canal system); (ii) trunk lateral-line canal discontinuous, consisting of a consecutive series of short canals along the lateral midline except for a short part over the first two or three scales (anterior third of the trunk canal continuous); (iii) trunk canals with no side branches (= canaliculi) (continuous part of the trunk lateral-line canal with canaliculi); (iv) trunk canals on lateral-line scales short, not interrupting the continuous series of ctenii on the posterior margin of each scale (canals terminate at the posterior margin of the lateral-line scales separating the ctenii into dorsal and ventral series); (v) no longitudinal rows of accessory neuromasts dorsal and ventral to the trunk canals (short longitudinal rows of accessory neuromasts present dorsal and ventral to the canals of the discontinuous part of the trunk canal); (vi) no short transversal rows (present) on each scale of the three lateral-line canals on the caudal fin (three short

transversal rows present, together forming a discontinuous lateral caudal transversal row **lct**); (vii) no longitudinal rows of accessory neuromasts dorsal and ventral to the lateral-line canals on the caudal fin (longitudinal rows of accessory neuromasts present dorsal and ventral to the lateral-line canals on each first scale of the three lateral-line canals); (viii) no transversal accessory neuromast rows at the accessory trunk lateral-line canal (transversal accessory neuromast rows present dorsal and ventral to the accessory trunk lateral-line canal).

GENERAL PATTERN OF THE LATERAL-LINE SYSTEM ON THE CAUDAL FIN IN GOBIOIDEI EXCLUSIVE OF RHYACICHTHYIDAE

The following two patterns of the lateral-line system seemingly occur in the majority of gobioid fishes:

PATTERN 1: Plesiomorphic for Gobioidae, exclusive of Rhyacichthyidae, are four lateral lines on the caudal fin, which are all formed by free (superficial) neuromasts. A discontinuous transversal row (**lct**) extending over the caudal fin base and three longitudinal rows: one in extension of the deleted trunk canal in the middle of the caudal fin (**lcm**) and two accessory rows, one on the dorsal part (**led**) and on the ventral part (**lev**) of this fin (Fig. 1A–B). No lateral-line canals are developed. Obviously, plesiomorphic for Gobioidae is a discontinuous **lct**, which consists of at least three short parts, each anterior to one of the three longitudinal neuromast rows. A continuous transversal row at the base of the caudal fin or its loss is seemingly apomorphic.

The three longitudinal rows are generally long and extend onto the interradiation membranes between two branched caudal-fin rays in the same asymmetrical pattern as in the Rhyacichthyidae. Typically, the gap between **led** and **lcm** is larger than the gap between **lev** and **lcm**. Generally, these neuromast rows do not run in the midline between two fin rays: **led** and **lcm** follow the ventral side of a fin ray, **lev** follows the dorsal side of a fin ray. This pattern of the longitudinal lateral lines on the caudal fin seemingly is shared by the majority of Gobioidae. In species with rounded or pointed caudal fins, **lcm** generally is the longest row, and the two accessory rows (**led**, **lev**) are more or less of similar length.

PATTERN 2: This pattern is derived from Pattern 1 and formed by three neuromast rows with one longitudinal row (**lev**) lost: one transversal and two longitudinal rows (Fig. 1C). The transversal row is often continuous and in its length not affected by the loss of **lev**. It still extends onto the ventral part of the caudal fin base. As in species with three longitudinal lateral lines, **led** and **lcm** are separated by three fin rays. Generally, **lcm** is somewhat longer than **led** (rounded caudal fin) or distinctly longer (pointed caudal fin). In several species with a rounded caudal fin, a seemingly derived condition occurs with **lcm** shortened and **led** the longest row. A deviation of Pattern 2 towards a pattern with only one longitudinal row occurs in the California bay gobies of the *Chasmichthys* group, *sensu* Birdsong et al. (1988). In some species, **led** is shortened to only a few neuromasts (Ahnelt and Göschl 2003; Ahnelt unpublished) (Fig. 1D).

DEVIATIONS FROM THE GENERAL PATTERN.— We found three distinct deviations from the two general patterns of the lateral-line system on the caudal fin. These deviations occur in the group of Gobioidae exclusive of the Rhyacichthyidae, the unassigned *Terateleotris*, and the Eleotridae, but including the Odontobutidae. All investigated species of the Rhyacichthyidae and Eleotridae (and *Terateleotris*) are characterized by three lateral lines on the caudal fin except for two eleotrine species, *Kribia nana* and *K. kribensis*.

(i) Longitudinal neuromast rows on the caudal fin arranged symmetrically:

This is a deviation from Pattern 1 with the three longitudinal lateral lines arranged asymmetrically. In this deviation both accessory neuromast rows (**led**, **lev**) are separated from **lcm** by three

fin rays. Such a pattern occurs in two species, *Synechogobius ommaturus* and *Acanthogobius flavimanus*. Seemingly, the symmetric arrangement of the neuromasts is a derived character that developed from a pattern with **lc_v** separated from **lcm** by two fin rays. An indication for this hypothesis is the occurrence of a second **lc_v** between the second and third fin ray below **lcm** in *A. flavimanus*. Such doubled **lc_v** occurs in 46% of the investigated specimens, but only in 10% on both sides of the fin. Except for one specimen with a second **lcd**, this row and **lcm** were never doubled. Possibly because of the low number of specimens investigated, no fourth row has been found in *S. ommaturus*. The question of whether three longitudinal rows arranged symmetrically on the caudal fin are a characteristic feature for the *Acanthogobius*-group, *sensu* Pezold (1993), is currently under investigation by the senior author.

(ii) Longitudinal neuromast rows decreased in number, loss of **lcd** and **lc_v**:

This deviation, only a single longitudinal neuromast row (**lcm**) developed, obviously occurs independently twice within the Gobioidae: in the Odontobutidae, and in the derived Gobiidae.

Perccottus glenii is the only known representative of an assemblage of basal Gobioidae (Rhyacichthyidae, Odontobutidae and Eleotridae) with a single neuromast row on the caudal fin. The pattern of the lateral-line system of this species is described above. It is not known whether this arrangement derived from a pattern with two or with three longitudinal neuromast rows.

Two species of Gobiidae, *Lebetus guilleti* and *Speleogobius trigloides*, are also peculiar with only one longitudinal row (**lcm**) on the caudal fin developed (but concluding from Miller (1963), *L. guilleti* can also have two longitudinal rows developed). The arrangement of the lateral-line system on this fin is very similar for both species and represents a derived condition, a further indication of a close relationship as recently proposed by Herler and Kovacic (2002). *L. guilleti* and *S. trigloides* are tiny gobies of about 20 mm SL generally characterized by a reduced neuromast pattern on the body like, as known for many small gobies (Ahnelt and Bohacek 2004, and authors summarized therein). Some neuromast rows on the head are completely absent and many reduced to one or only a few neuromasts (Miller 1963; Zander and Jelinek 1976). The loss of two longitudinal rows on the caudal fin is seemingly not necessarily the result of miniaturization. Other tiny gobies, such as *Corcyrogobius liechtensteini* (the smallest Mediterranean gobiid fish) and *Gobiopterus chuno*, have three or more longitudinal rows on this fin developed.

(iii) Longitudinal rows increased in number:

Sporadically, gobioids can be found with a supernumerary longitudinal neuromast row on the caudal fin. These specimens display four longitudinal rows but, generally, only on one side of the fin (Ahnelt unpublished). Such supernumerary rows occur rarely and are not typical for the species.

Gobioids with distinctly more than three longitudinal neuromast rows have these rows generally separated by one fin ray only (Mortara 1918; Scattolin and Ahnelt, unpublished). This highly specialized pattern is so far only known within the Gobiidae and seemingly evolved independently several times within this gobioid family.

Three species are known with eight rows of neuromasts on the caudal fin: the north-eastern Atlantic species *Aphia minuta*, and the Pacific gobies *Gobiopterus chuno* and *Leucopsarion peter-sii*. In these species, **lct** is continuous and long, extending nearly over the entire caudal fin (Fig. 1F). The eight longitudinal rows extend onto the interradiial membranes between the second and the tenth segmented and branched fin rays, each separated from the other by one fin ray. These three species can be considered as derived forms and are characterized by pedomorphic features such as completely absent head canals, transparent bodies and pelagic life style. For these evolved pelagic Gobiidae, a convergent evolution of free neuromast pattern on the caudal fin in adaptation to similar habitats is assumed (Scattolin and Ahnelt, unpublished).

Two Atlantic-Mediterranean species of the genus *Deltentosteus* also have an increased num-

ber of neuromast rows on the caudal fin, but with four (*D. quadrimaculatus*) and six (*D. colloni-
anus*) rows distinctly less than the above-mentioned species. A detailed description of the neuro-
mast pattern on the caudal fin of these two species and a discussion if the increase in neuromast
rows possibly following a certain order are under study by the senior author.

DISCUSSION

Three longitudinal lateral lines on each side of the caudal fin are characteristic for the basal
gobioid genera *Rhyacichthys* Boulenger, 1901, *Protogobius* Watson and Pöllabauer, 1998 and
Terateleotris Shibukawa et al., 2001 (Springer 1983; Shibukawa et al. 2001). This pattern is also
known from basal Perciformes (Jakubowski 1966, 1967). In all Gobioidi except the Rhyac-
ichthyidae, *sensu* Shibukawa et al. (2001), these lateral lines are formed only by free neuromasts.
Further, a discontinuous transversal lateral line on the base of the caudal fin formed by three short
sections and plesiomorphic for Gobioidi is a feature seemingly also occurring in basal Perci-
formes (Jakubowski 1966, 1967).

Three or two longitudinal rows of neuromasts occur on the caudal fin of most Gobioidi with
a fourth or third, transversal row more or less distinctly developed on the fin base (Sanzo 1911;
Miller and El-Talwil 1974; Ahnelt and Duchkowitsch 2001; Shibukawa et al. 2001) (Fig. 1A–B).
In species with two longitudinal rows on the caudal fin, the ventral row **lcv** is absent (Ahnelt et al.
2000; Ahnelt and Göschl 2003), a feature that occurs in the Odontobutidae, Eleotridae (Eleotrinae)
and Gobiidae (Gobiinae and Gobionellinae) (Fig. 1C–D). [From a figure of a generalized sicydiine
gobiid shown by Parenti and Maciolek (1993, fig. 3), Ahnelt and Göschl (2003) concluded that
Sicydiinae have only two longitudinal rows of neuromasts on the caudal fin. However, all species
investigated for this study have three longitudinal rows with the neuromasts invaginated and diffi-
cult to detect].

Three longitudinal neuromast rows occur in the Rhyacichthyidae (preceded by lateral-line
canals), *Terateleotris* (unassigned genus), Odontobutidae, Eleotridae, Gobiidae (Amblyopinae,
Gobiinae, Gobionellinae, Oxudercinae, Sicydiinae), Kraemeriidae, Microdesmidae and Ptereleotri-
idae. Each of these longitudinal neuromast rows extends onto the interradiial membrane between
two branched caudal-fin rays in a characteristic pattern. Typically for Gobioidi with three longi-
tudinal lateral lines is a larger distance between **lcd** and **lcm** than between **lcv** and **lcm** (Fig. 1A–B).
This is the case because **lcd** is separated from **lcm** by three fin rays and **lcm** from **lcv** by two fin
rays. In species with two longitudinal lateral lines (**lcd** and **lcm**), these are also separated by three
fin rays. Additionally, the neuromast rows do not run in the midline between two fin rays: **lcd** and
lcm follow the ventral side of a fin ray, **lcv** follows the dorsal side of a fin ray. Seemingly, this pat-
tern of the longitudinal lateral lines on the caudal fin is shared by most gobioids.

A transversal row (**lct**) at the base of the caudal fin seems to be developed regularly and has
been found in all above-mentioned families and subfamilies of Gobioidi including the
Kraemeriidae, Microdesmidae and Ptereleotridae (Fig. 1). In Gobiinae, **lct** often consists of only a
few neuromasts, and in some species it is difficult to distinguish from the longitudinal rows. In gobi-
ine species this row consists often only of a single neuromast immediately anterior to each of the
three longitudinal rows. Often these three neuromasts are somewhat larger than those of the longi-
tudinal rows and separated from them by a more or less distinct gap. Additionally, a single neuro-
mast or a short neuromast row below the origin of the most ventral longitudinal row (generally **lcv**)
forms the ventral end of **lct** (Fig. 1A). Nevertheless, in such species the pattern of the transversal-
ly arranged neuromasts follows the asymmetric pattern of the longitudinal neuromasts. A deviation
from this arrangement occurs in *L. guilleti*. In this species, three neuromasts are arranged transver-

sally (**lct**) at the base of the caudal fin, distinctly separated from the single longitudinal row (**lcm**). The dorsal neuromast of **lct** is separated from the medial neuromast by only two caudal-fin rays, and the ventral neuromast by only one ray. This peculiar pattern is possibly the result of a reduced number of caudal-fin rays and a specialization. The caudal-fin rays of the related and similar tiny *S. trigloides* are more numerous, and the three neuromasts of **lct** are separated from each other in the characteristic pattern described above.

A transversal neuromast row occurs independently in Gobioidae, generally at the base of the caudal fin if two or three longitudinal rows are present (Ahnelt and Scattolin 2003; Ahnelt and Bohacek 2004); it also occurs in the basal Gobioidae Rhyacichthyidae and in *Terateleotris*. *T. aspro* belongs to an assemblage of basal Gobioidae with a trunk lateral-line canal developed, but is derived in the absence of lateral-line canals on the caudal fin. The pattern with four neuromast rows on this fin (one transversal and three longitudinal rows) is plesiomorphic for all Gobioidae with lateral lines consisting only of free neuromasts. The transversal row (**lct**) on the caudal fin base of *T. aspro*, figured by Shibukawa et al. (2001:fig. 6A), is discontinuous, similar to that of the Rhyacichthyidae. A discontinuous **lct**, consisting of three parts, is likely plesiomorphic for the Gobioidae.

The Odontobutidae are treated by most authors as the sister group of all other non-rhyacichthyid Gobioidae (e. g., Hoese and Gill 1993; Akihito et al. 2000; Shibukawa et al. 2001; Wang et al. 2001; Thacker 2003). It is, therefore, interesting that in the five species we investigated (*Micropercops swinhonis*, *Odontobutis aurarmus*, *O. obscura*, *O. potamophila* and *Perccottus glenii*) the lateral-line system on the caudal fin is developed in three different patterns: (i) *M. swinhonis*, with three longitudinal rows (**lcd**, **lcm**, **lev**) and a transversal row (**lct**) reduced to three (sometimes four) neuromasts each close to the origin of the longitudinal rows (Fig. 1B), (ii) *O. aurarmus* and *O. obscura* with two longitudinal rows (**lcd**, **lcm**) and a transversal row (Fig. 1C), and (iii) *Perccottus glenii* with one longitudinal row (**lcm**) and a transversal row (Fig. 1E) [Wongrat and Miller (1991) and Miller (2003) mention three longitudinal rows on the caudal fin of *P. glenii*]. All five odontobutid species are peculiar in having a derived pattern of free neuromasts on the caudal fin, with *P. glenii* having the most specialized one.

The intra-familial relationships of the Odontobutidae (*sensu* Hoese and Gill 1993) are unresolved (Akihito et al. 2000; Shibukawa et al. 2001; Thacker 2002). The arrangement of the lateral-line system on the caudal fin is possibly a further indication that the Odontobutidae are not monophyletic. The presence of three longitudinal lateral lines in *M. swinhonis* is plesiomorphic, but a transversal neuromast row reduced to three single neuromasts is apomorphic for Gobioidae. Two longitudinal lateral lines in *O. aurarmus* and *O. obscura* and one in *P. glenii* are also derived characters. This neuromast pattern on the caudal fin of *P. glenii* is the most specialized within the Odontobutidae.

The pattern of the lateral-line system on the caudal fin of odontobutid species is obviously more diverse than those of other gobioid species. In the group consisting of all gobioids except the Odontobutidae and Rhyacichthyidae, the Eleotridae are seemingly conservative in this character. We investigated species of 20 of the 34 or 35 eleotrid genera (Thacker 2003). All, except for one genus (*Kribia*), have the plesiomorphic three longitudinal neuromast rows developed.

The lateral-line system on the trunk and caudal fin is less variable than on the head of Gobioidae. This explains why the lateral-line system of the head is widely used as an important taxonomic tool for the classification of gobioid fishes. On the other hand, the more conservative character of the neuromast pattern on the caudal fin allows us to hypothesize that the group of gobioids classified as Odontobutidae (*sensu* Hoese and Gill 1993) appeared early in the evolution of the Gobioidae and possibly evolved from a sister group within the Eleotridae. This hypothesis is supported by a series of plesiomorphic features that place the Odontobutidae closer to the origin of the

Gobioidei than to the Eleotridae (Hoese and Gill 1993). The Eleotridae have a more conservative pattern of neuromasts on the caudal fin as the investigated odontobutid taxa of *Micropercops*, *Odontobutis* and *Perccottus*.

Finally, it can be concluded from the above results that the decrease and the increase of the number of longitudinal neuromast rows on the caudal fin in Gobioidei follow a certain order. A reduction in the number of neuromast rows obviously first affects the ventral row (**lev**) (Fig. 1A–E). By far, the majority of Gobioidei has three or two longitudinal rows developed on the caudal fin. Only a few species are known with the number of longitudinal rows increased or further decreased. Obviously, the dorsal row (**lcd**) is the next affected by reduction. In many species with only two longitudinal rows developed, this dorsal row is as a first step often distinctly shortened (e.g., Ahnelt and Göschl 2003) (Fig. 1D). In species with a single longitudinal row, the median row (**lcm**) is always present (Fig. 1E).

As with a decrease in neuromast rows, so too an increase of longitudinal neuromast rows on the caudal fin follows a scheme, a phenomenon currently under study by the senior author. In the first step (four longitudinal rows), the additional row is added ventrally, and with the addition of more rows, the gaps between **lev**, **lcm** and **lcd** are closed. Finally, all longitudinal neuromast rows are separated by only a single fin ray.

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LITERATURE CITED

- AHNELT, H., ABDOLI, A., NADERI, M. AND B.W. COAD. 2000. *Anatirostrum profundorum*: a rare deep-water gobiid species from the Caspian Sea. *Cybium* 24:139–159.
- AHNELT, H., AND V. BOHACEK. 2004. The lateral-line system of two sympatric eastern Pacific gobiid fishes of the genus *Lythrypnus* (Teleostei: Gobiidae). *Bulletin of Marine Science* 73:31–51.
- AHNELT, H., AND M. DUCHKOWITTSCH. 2001. The lateral-line system of two Ponto-Caspian gobiid species (Gobiidae, Teleostei): a comparison. *Folia Zoologica* 50:217–230.
- AHNELT, H., AND J. GÖSCHL. 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., AND G. SCATTOLIN. 2003. The lateral-line system of a blind goby, *Typhlogobius californiensis*, Steindachner 1879 (Teleostei: Gobiidae). *Annalen des Naturhistorischen Museums in Wien* 104 B:11–25.
- AKIHITO, A., IWATA, T., KOBAYASHI, K., IKEO, T., IMANISHI, H., ONO, Y., UMEHARA, C., HAMAMATSU, K., SUGIYAMA, Y., IKEAD, K., SAKAMOTO, A., FUMIHITO, S., OHNO, AND T. GOJOBORO. 2000a. Evolutionary aspects of gobioid fishes based upon a phylogenetic analysis of mitochondrial *b* genes. *Gene* 259:5–15.
- AKIHITO, K., SAKAMOTO, Y., IKEDA, AND A. IWATA. 2000b. Suborder Gobioidei. Pages 1139–1310 in T. Nakabo, ed., *Fishes of Japan with Pictorial Keys to the Species*, second edition. Tokai University Press, Tokyo.
- BIRDSONG R.S., E.O. MURDY, AND F.L. PEZOLD. 1988. A study of the vertebral column and median fin osteology in gobiid fishes with comments on gobioid relationships. *Bulletin of Marine Science* 42:174–214.
- HERLER, J., AND M. KOVACIC. 2002. *Lebetus guilleti* (Teleostei: Gobiidae) in the northern Adriatic Sea: first record and details on the species' morphology. *Annales* 12:177–188.

- HOESE, D.F., AND A.C. GILL. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). *Bulletin of Marine Science* 52:415–440.
- ILJIN, B.S. 1930. Le système des Gobiidés. *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.
- LARSON, H.K. 2001. A revision of the gobiid fish genus *Mugilogobius* (Teleostei: Gobioidei), and its systematic placement. *Records of the Australian Museum, Supplement* 62: i–vi, 1–233.
- LEVITON, A.E., R.H. GIBBS, H. HEAL, AND C.E. DAWSON. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- MILLER, P.J. 1963. Taxonomy and biology of the genus *Lebetus* (Teleostei – Gobioida). *Bulletin of the British Museum (Natural History), Zoology* 10:207–256.
- MILLER, P.J. 1973. The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. *Journal of Zoology, London* 171:397–434.
- MILLER, P.J.. 1986. Gobiidae. Pages 1019–1085 in P.J.P Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese, eds., *Fishes of the North-eastern Atlantic and the Mediterranean*, vol. 3. UNESCO: Paris.
- MILLER, P.J. 2003. Family Odontobutidae Hoese and Gill, 1993. Pages 131–132 in P.J Miller ed., *The freshwater fishes of Europe*. vol. 8, pt. I. AULA Verlag, Wiebelsheim.
- MILLER, P.J., AND M.Y. EL-TALWIL. 1974. A multidisciplinary approach to a new species of *Gobius* (Teleostei: Gobiidae) from southern Cornwall. *Journal of Zoology, London* 174:539–574.
- MORTARA, S. 1918. La disposizione degli organi ciatiformi del genere *Aphya* e suoi rapporti con quella del genere *Gobius*. *Revista Comitato Talassografico Italiano, Memoria* 65:5–23.
- PARENTI, L.R., AND J.A. MACIOLEK. 1993. New sicydiine gobies from Ponape and Palau, Micronesia, with comments on systematics of the subfamily Sicydiinae (Teleostei: Gobiidae). *Bulletin of Marine Science* 53:945–972.
- PEZOLD, F. 1993. Evidence for a monophyletic Gobiinae. *Copeia*, 1993:634–643.
- 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.
- SHIBUKAWA, K., A. IWATA, AND S. VIRAVONG. 2001. *Terateleotris*, a new gobioid fish genus from the Laos (Teleostei, Perciformes), with comments on its relationships. *Bulletin of the National Science Museum, Tokyo, Ser A*. 27:229–257.
- SPRINGER, V.G. 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.
- THACKER, C.E. 2003. Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics and Evolution* 26:354–368.
- WATSON, R.E. AND C. PÖLLBAUER. 1998. A new genus and species of freshwater goby from New Caledonia with a complete lateral line. *Senckenbergiana biologica* 77:147–153.
- WONGRAT, P. AND P.J. MILLER. 1991. The innervation of the head neuromast rows in Eleotridine gobies (Teleostei: Gobioidei). *Journal of Zoology, London* 225:27–42.
- WANG H.-Y., M.-P. TSAI, J. DEAN AND LEE S.-C. 2001. Molecular phylogeny of gobioid fishes (Perciformes: Gobioidei) based on mitochondrial 12S rRNA sequences. *Molecular Phylogenetics and Evolution* 20: 390–408.
- ZANDER, Z.D., AND H. JELINEK. 1976. Zur demersen Fischfauna im Bereich der Grotte von Banjole (Rovinj, YU) mit Beschreibung von *Speleogobius trigloides* n. gen., n. sp. (Gobiidae, Perciformes). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 73:265–280.