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The lateral line system of a blind goby, *Typhlogobius californiensis* STEINDACHNER, 1879 (Teleostei: Gobiidae)

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Abstract

Typhlogobius californiensis inhabits burrows of the ghost shrimp *Callinassa biffari* along the east Pacific coast of Mexico and the USA. Although blind, this goby displays characteristic reductions of the lateral line system. Large parts of the head, the trunk and the caudal fin are not covered by neuromasts and the head canals are reduced to the interorbital sections of the supraorbital canals. Only on the snout, the suborbital area and the ventral side of the head free neuromasts are more densely arranged. Many neuromast rows are short, consisting of a few or a single neuromast only, some may lack. Nevertheless the neuromasts are arranged in a typical pattern. *T. californiensis* is the only member of a small Pacific group of gobiid fishes which still has a remnant of the head canal system. Its lateral line system is described in detail.

Key words: Gobiidae, *Typhlogobius californiensis*, lateral line system, east Pacific.

Zusammenfassung

Typhlogobius californiensis bewohnt entlang der ostpazifischen Küste Mexikos und der USA Grabbauten des Krebses *Callinassa biffari*. Obwohl blind, ist das Seitenliniensystem dieser Meergrundel auf charakteristische Weise reduziert. Kopfkanäle fehlen bis auf die Interorbitalabschnitte der Supraorbitalkanäle. Große Teile des Kopfes, des Rumpfes und der Schwanzflosse sind nicht von freien Neuromasten bedeckt. Lediglich die Schnauze, der Suborbitalbereich und die Ventralseite des Kopfes sind etwas dichter mit Neuromasten besetzt. Viele Neuromastenreihen sind kurz und auf wenige Sinnespapillen reduziert. Einige Reihen bestehen lediglich aus einem einzelnen Neuromasten, manche können fehlen. Dennoch sind die freien Neuromasten charakteristisch angeordnet. *T. californiensis* ist die einzige Art einer kleinen pazifischen Gruppe spezialisierter Meergrundeln, die noch einen Rest des Kopfkanalsytems aufweist. Das Seitenliniensystem dieser blinden Meergrundel wird beschrieben.

Introduction

Gobiidae, the largest group within the Gobioidei, display various modes of life, although the majority is found in marine and estuarine benthic habitats. Most gobiid fishes are small and show a tendency "toward evolution by reduction" (BIRDSONG & al. 1988). Small body size and cryptobenthic life style is seen as specialized (MILLER 1979, 1996), often accompanied by an elongation of the body, reduction or loss of the first dorsal fin, loss of scales, and may also lead to reduction or loss of eyes. Small body size may also result in a lateral line system, with the cephalic canals reduced or entirely lost and rows of superficial neuromasts short or lost (MILLER 1987).

Typhlogobius californiensis Steindachner, 1879 is a blind gobiid fish which occurs along the southern Californian Coast (USA) and the Baja California (Mexico) (ESCHMEYER &

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HERALD 1983). Adult specimens are blind and usually inhabit burrows of a ghost shrimp, *Callinassa biffari* (MACGINITIE 1939). These burrows are entered as juveniles which have small but functional eyes.

The lateral line system of fishes is adapted to habitats and modes of life (DISLER 1960, DIJKGRAAF 1962, COOMBS & al. 1988, MONTGOMERY & al. 1995), thus a cryptic life style and the loss of vision may enhance the lateral line sense in blind fishes (HUBBS 1927, GROBBEL & HAHN 1958, BLECKMANN 1993, MONTGOMERY & al. 2001). Eight blind cave dwelling gobioid species are known to date (ROMERO & PAULSON 2001). The head lateral line system from six of them is at least partly known. All display a pattern of free neuromasts which is not distinctly increased compared with congeneric species with well developed vision.

Several attempts have been made to describe the lateral line system of the blind gobiid *T. californiensis* (RITTER 1893, HUBBS 1926, 1927, NORMAN 1963, MACDONALD 1972). Based on the neuromast pattern two opposite theories are favoured by these authors: one that the lateral line diminishes during ontogeny (RITTER 1893, MACDONALD 1972) the other that it is hyperdeveloped due to lost vision (HUBBS 1926, 1927, NORMAN 1963). We were interested to know (1) which of these theories is supported by the topography of the free neuromasts, (2) to which extent the neuromast pattern is developed in juveniles and adults, (3) whether the neuromast pattern is differently developed in juvenile and adult specimens, and (4) whether the neuromast pattern is influenced by its life style as inhabitant of burrows of a ghost shrimp.

Material and methods

64 specimens of *Typhlogobius californiensis* collected in California (USA) between Santa Cruz Island in the north and San Diego in the south have been investigated. The following preserved specimens were examined (collection number, number of specimens, sex, SL+CL in mm, sampling site, date, name of collector). Length of specimens is given in standard length (SL) and caudal fin length (CL), d = damaged. The sex was determined by the shape of the urogenital papilla. Pores of cephalic lateral line canals are marked with capital letters following AKIHITO (1971).

Material: CAS 100082, 2 males, 37.4+7.5 – 55.5+10.0 mm, 6 females, 42.2+8.4 – 54.9+9.8 mm, 1 sex ?, 40.8+7.9 mm, San Diego County, San Diego, date?, C. H. Gilbert. CAS 169723, out of 6 specimens 3 males, 51.1+9.1 – 60.0+10.0 mm, 2 females, 47.7+8.9 – 50.5+8.8 mm, San Diego Co., San Diego, date?, E. C. Starks. CAS 200223, 4 males, 35.8+7.1 – 57.8+10.3 mm, 6 females, 30.7+6.8 – 56.9+9.2 mm, 1 juv., 26.4+6.1 mm, San Diego Co., locality?, collector? CAS 2000380, 1 male, 57.7+11.5, Los Angeles Co., Malibu, at east end of Dume Cove, 28 December 1944, E. Hunter. CAS 211663, 2 males, 35.1+7.4 – 49.7+9.7 mm, 2 females, 36.2+8.0 – 51.5+9.3 mm, San Diego Co., Point Loma, 26 July 1903, collector?. CAS 211664, 5 males, 44.9+7.6 – 54.4+8.5 mm, 7 females, 30.6+6.5 – 48.7+8.9 mm, 2 juv., 23.6+5.2 – 26.5+6.4 mm, 2 sex ?, 31.6+6.9 – 43.5+7.1 mm, Los Angeles, 28 July 1926, H. R. Hill. CAS uncatalogued, 1 male, 42.1+7.8, no data. IZUW uncatalogued, 3 males, 35.0+6.9 – 47.3+8.0 mm, 2 females, 37.8+7.4 – 40.3+8.3 mm, San Diego Co., La Jolla, Bird Rock, 2 March 2000, R. H. Rosenblatt & party. NMFS/SWFSC uncatalogued, 1 larva, 11.4+2.1, I-30, Sta. LS, Midwater Replicate 1 (Sta. LS-MW-R1), 02 Aug. 1978. NMFS/SWFSC uncatalogued, 1 larva, 11.0+d, I-25, Sta. LN, Epibenthos Replicate 3 (Sta LW Rep 3, Epibenthos), 07 June 1978. NMFS/SWFSC uncatalogued, 1 larva, 9.8+2.0, I-48, Sta. A, Midwater Replicate 1 (Sta A-MW Rep1), 23 May 1978. NMW 31175, holotype, 1 male, 50.2+8.7 mm, San Diego Co., False Bay [Mission Bay], acqu. Nr. 1874. I., F. Steindachner. SIO 58-519, 1 juv., 26.8+6.0 mm, San Diego Co., Point Loma, reef off lighthouse, 15 October 1955, P. W. Johnson. SIO 62-586, 4 males, 55.7+9.0 – 65.6+10.6 mm, 4 females, 59.0+10.0 – 64.7+10.5 mm, Santa Barbara Co., west tip of Santa Cruz Island, 16 February 1948, J. E. Fitch. SIO 75-572, 1 male, 39.0+8.5 mm, San Diego Co., False Point, date?, collector? SIO 92-171, 1 male, 43.8+7.9 mm, San Diego Co., La Jolla, Bird Rock, 09 December 1992, L. Ngai.

Institutions: CAS, California Academy of Sciences, San Francisco; IZUW, Institut für Zoologie der Universität Wien; NMFS/SWFSC, National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla; NMW, Naturhistorisches Museum Wien; SIO, Scripps Institution of Oceanography, La Jolla.

In juvenile and subadult specimens the course of the supraorbital canal was made visible by blowing air into the canal. This canal is also visible in cleared and stained specimens. Additionally we opened the canal from dorsal in its entire length (from the posterior nasal pore to the posterior interorbital pore) in two adult specimens which were later cleared and stained.

Neuromast terminology follows SANZO (1911) and MILLER (1986). The terminology for the neuromasts of gobiid fishes, primarily based on their pattern, has been devoleped by SANZO (1911) and is applicable to other gobioids. Most rows identified and marked with letters and numbers by SANZO (1911) and subsequently by various authors (for example ILJIN 1930, MILLER 1986, LARSON 2001) seem to be homologous through a wide range of gobioids (WONGRAT & MILLER 1991, BOHACEK 2001, AHNELT unpublished).

Results

Topography of the lateral line system (Figs. 1, 2)

The cephalic canal system is reduced to the interorbital sections of the supraorbital canals. These canals occur in all specimens but are variably developed. Typically each canal opens with two terminal pores, but the pore pattern varies distinctly. In some specimens pores may lack at all. The short canals are deeply embedded and lie under a prominent skin fold which is distinctly broader than the narrow canals (Fig. 3). The course of the canals is visible through the skin in small specimens but thicker and less transparent skin prevents visibility in preserved specimens >30 mm SL.

All nine series of neuromast rows on the head, trunk and caudal fin listed by SANZO (1911) are developed. The neuromast pattern is similar between individuals of different postlarval ontogenetic stages (Figs. 1, 3) and the number of neuromasts is established relatively early in ontogeny. Compared with other gobiid fishes (AHNELT unpublished) a size dependent increase of neuromasts is detectable but only recognizeable as a tendency. It is not the rule that small specimens have fewer neuromasts than larger ones. As shown in Fig. 4A large individuals may have less neuromasts than small individuals. An increase of neuromasts in specimens >26 mm SL is evident only in the suborbital

Fig. 1: Free neuromasts and canal pores (capital letters) on the head of *Typhlogobius californiensis*; A: lateral view, CAS 169723, male, 58.7+10.5 mm; B: dorsal view, CAS 169723, female, 47.7+8.9 mm, canals with typical pore configuration; C: dorso-lateral view, CAS 200223, female, 30.7+6.8 mm, left canal lacking nasal pore B. an, pn: anterior and posterior nostrils; seb, subcutaneous eyeball. Scale bars = 5 mm.

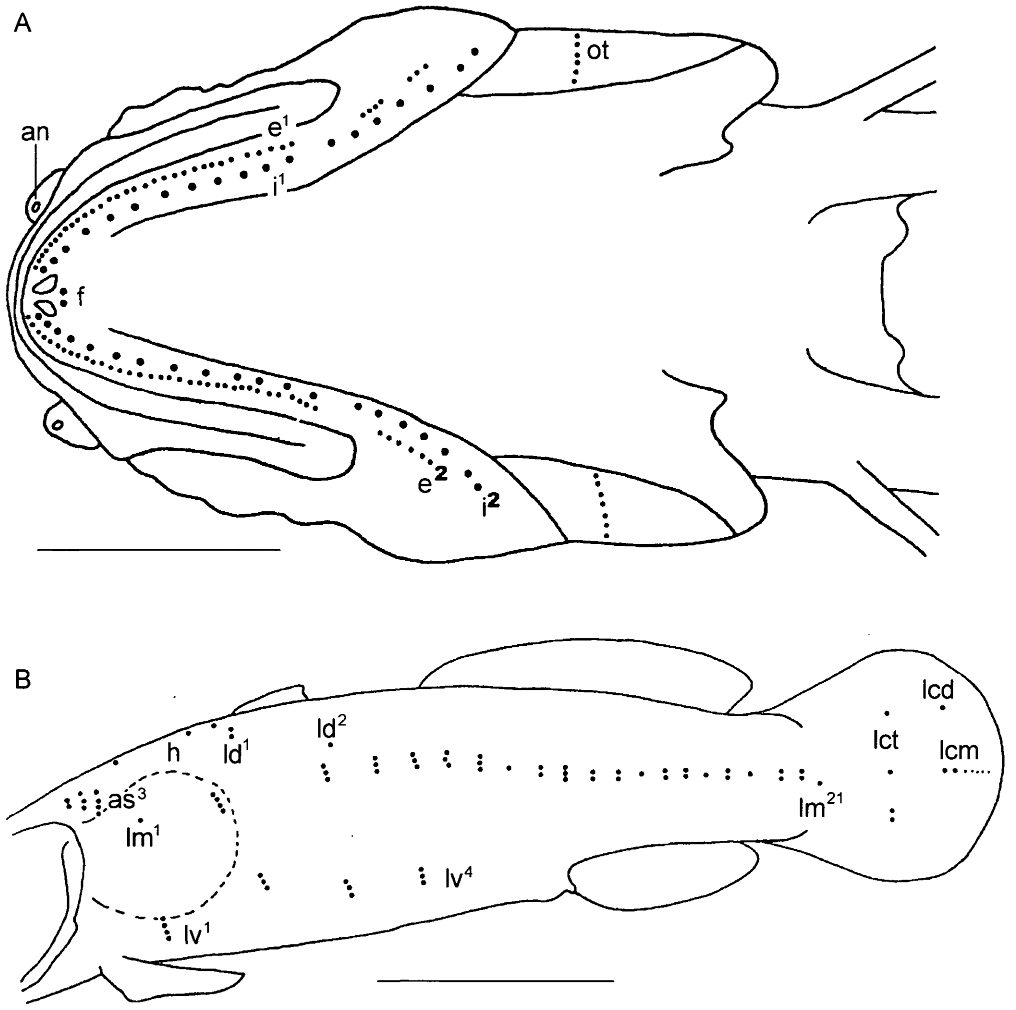

Fig. 2: Free neuromasts of *Typhlogobius californiensis* A: ventral view of the head, CAS 169723, male, 58.7+10.5 mm; B: lateral view of trunk and caudal fin, CAS 160723, female, 47.7+8.9 mm. an, anterior nostril. Scale bars: A = 5 mm, B = 10 mm.

row **d** (Figs. 4B) to a lesser extent in **ot** (opercular series) and **e**^{1} (mandibular series). Additionally most rows of the median lateral series (**lm**) on the trunk of juveniles consist of a single neuromast only, those of most larger adult specimens of up to three neuromasts, but not as a rule. Some large specimens show in all **lm**-rows one neuromast only. Because the number of neuromasts shows size dependency only as a trend, small specimens may be usually somewhat more densely covered with neuromasts than large ones. The longest neuromast rows (except for the opercular row **ot**) are found at the anterior half of the head and on its ventral side. Compared with the other regions of the head, trunk and caudal fin the area around the mouth (snout, anterior part of the cheek and the chin) is densely covered by neuromasts (Figs. 1, 2A).

The range of neuromast numbers is given in Table 1. The value 0 indicates the lacking of a neuromast row and is given, even if it occurs only in one specimen. Rows may lack especially on the trunk and only a few occur in all specimens, indicating a variability which is seemingly linked with a tendency towards reduction of neuromast numbers (see below). In the following we describe the lateral line system (cephalic canals and free neuromasts) in detail.

Cephalic canals (Figs. 1, 3)

The supraorbital canals are paired, entirely separated from each other and each is reduced to its interorbital sections. These short canal sections are variably developed and may be of unequal length. Typically each canal with two terminal pores, the posterior nasal pore B and the posterior interorbital pore D (n = 29, 46%). An anterior interorbital pore C may be present between pores B and D (n = 11, 18%), either on both sides (n = 5, 8%) or only on one side (n = 6, 1%). If pore C is present on both sides, at least one terminal pore (B or D) is lacking, thus the maximum number of pores for both sides is five (Fig. 3B). The presence or absence of the interorbital canals is thus not determinable by presence or absence of pores. The following further variations in the supraorbital canals may occur but each in one or a few specimens only: (1) canals not completely closed, (2) pores B and/or D are lacking but canals are present as closed tubes and (3) canals are bent medially at their posterior ends with an additional pore, but canals of left and rigth side not connected with each other. The reduced section of the supraorbital canal posterior to the orbit is replaced by neuromasts (see interorbital series of free neuromasts). Posterior oculoscapular and preopercular canals are absent.

The monotypic genus *Typhlogobius* is the only east Pacific member of a small group of gobiid fishes otherwise distributed in the west Pacific. These gobies, united to the "*Astrabe*" group by BIRDSONG & al. (1988), are diagnosed by reduced eyes and the posterior displacement and loss or reduction of the first dorsal fin. *T. californiensis* is the only species in this group with (remnants of) cephalic canals developed. RITTER (1893), who investigated in part the lateral line system of this goby, did not mention cephalic canals or pores. MACDONALD (1972) mentions a "single open pore"..."in the supraorbital canal" but fails to describe the pattern and the extent of this canal.

Free neuromasts (= sensory papillae) (Figs. 1-3, Tab. 1)

Head

Preorbital

Median series in three rows, **r**, **s** and $\mathbf{s}^3$. Row **r** internal of **s**, anterior neuromast distinctly smaller then the posterior one. **s** as a short longitudinal row plus a single small neuromast lateral of it (marked with an asterisk) close to the nasal openings (Fig. 1B, C). This single neuromast is lacking in a few specimens. $\mathbf{s}^3$ as single neuromast close to upper lip and internal to anterior end of **s**. Lateral series in indistinct rows, $\mathbf{c}^2$, $\mathbf{c}_2$ and $\mathbf{c}_1$. $\mathbf{c}^2$ in two parts, longitudinal dorsal on nasal sack close to posterior nasal opening, and as short transversal

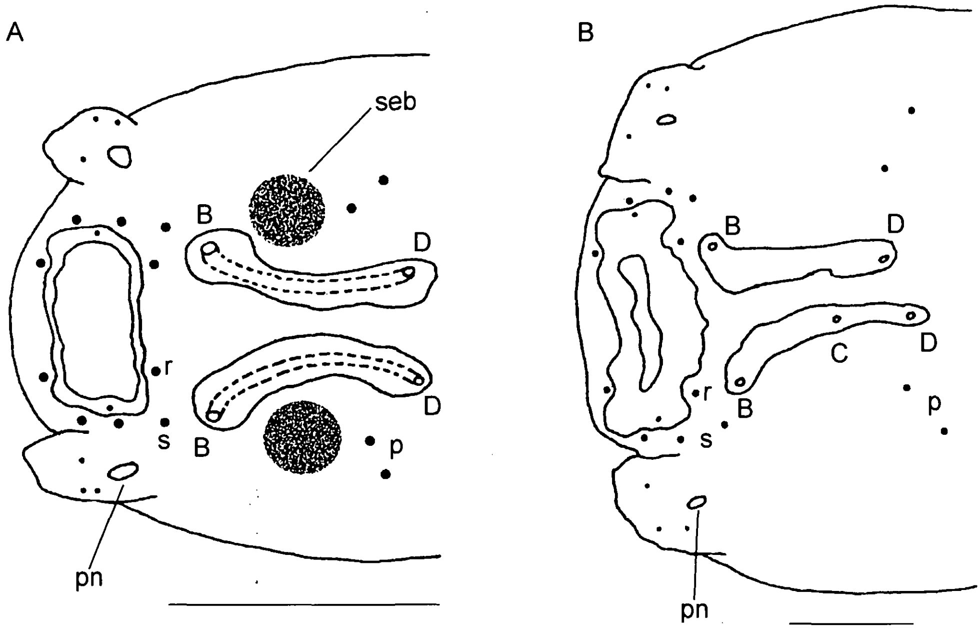

Fig. 3: Head canals and canal pore pattern (capital letters) in *Typhlogobius californiensis*. A: dorsal view of anterior half of head in CAS 200223, juvenile, 26.4+6.1 mm, course of canals below skin fold indicated by dashed lines, canals with typical pore configuration; B: dorsal view of anterior half of head in CAS 211663, female, 51.5+9.3, right canal shortened, left canal with anterior interorbital pore C. Scale bars = 2 mm.

row ventrally close to anterior nasal opening. **c_2** as single neuromast close to upper lip. **c_1** as two transversally arranged neuromasts dorsal to origin of suborbital row **d**. **c^1** lacking.

Suborbital

"Longitudinal" suborbital neuromast type. Five longitudinal rows, from dorsal to ventral **a**, **b**, **cp** (as single neuromast), **d** and **c**. **a** of large, widely spaced neuromasts, divided in two parts by a skin fold, the posterior part as distinct row, the anterior one as a single neuromast close to the nasal sack. **b** short, of small closely set neuromasts, from above corner of mouth anteriorly ending before middle of upper jaw. **c** of large, widely spaced neuromasts, similar in size to those of row **a**, posteriorly not exceeding the corner of the mouth. **d** long, continuous and of small, closely set neuromasts, similar to those of row **b**, from below **c_1** parallel to upper lip, not exceeding corner of mouth posteriorly. **cp** as single neuromast between posterior ends of **b** and **c**. Posterior area of cheek, from above corner of mouth to posterior edge of preopercle free of neuromasts (Fig. 1A, C).

The neuromast number of rows **a** and **c** is very constant during ontogeny (Fig. 4B). A size dependent increase is not obvious for row **b**. A trend to an increase of neuromasts during ontogeny is only evident for the longest suborbital row, row **d**, but neverthelss may large specimens have fewer neuromasts then smaller ones (Fig. 4B).

Preopercular-mandibular

Three longitudinal rows, external **e** on lateral edge of lower jaw and preopercle, internal **i** medial, and mental **f**. Neuromasts of **i** larger and more widely spaced than of **e**. Rows **e** and **i** divided in mandibular ($\mathbf{e}^1$, $\mathbf{i}^1$) and preopercular ($\mathbf{e}^2$, $\mathbf{i}^2$, $\mathbf{i}^3$) sections by a gap at the lower jaw articulation. This gap is more distinct in external series; $\mathbf{e}^2$ distinctly shorter than $\mathbf{i}^2$. The neuromasts of $\mathbf{i}^1$ proceed in a groove, the rest of a mandibular canal. Two neuromasts ($\mathbf{i}^3$) in course of the lacking preopercular canal ($\mathbf{i}^1$ of MILLER (1963), **por** of HERLER & al. (1999)). Mental row **f** as single neuromast in a groove posterior to the mandibular symphysis and distinctly separated and posterior to the anterior ends of $\mathbf{e}^1$ and $\mathbf{i}^1$.

The two neuromasts of $\mathbf{i}^3$ seem to be primary neuromasts not enclosed in a canal. These two neuromasts differ in gobiids from $\mathbf{i}^1$ and $\mathbf{i}^2$ not only in position but also in innervation (AHNELT unpublished).

Oculoscapular

Six longitudinal rows ($\mathbf{x}^1$, $\mathbf{x}^2$, $\mathbf{u}^1$, $\mathbf{u}^2$, $\mathbf{la}^{2\text{-}3}$) and four transversal rows (**y**, $\mathbf{as}^{1\text{-}3}$), including the axillary series; all rows short, of few or a single neuromast only. $\mathbf{u}^1$ as single neuromast, dorsal of cheek above preopercle in 20 specimens (65%), and completely lacking in 8 specimens (25%). The course of lacking anterior section of postorbital canal above cheek is nearly in its entire length not replaced by free neuromasts. $\mathbf{u}^2$ in oculoscapular groove above opercle; $\mathbf{x}^1$ above preopercle and dorsal to $\mathbf{u}^1$. $\mathbf{x}^2$ divided, anterior section dorsal and parallel to $\mathbf{u}^2$, posterior section close to and dorsal of **y**; row **y** as single neuromast above posterior origin of opercle. Transverse axillary rows $\mathbf{as}^{1\text{-}3}$ above origin of pectoral fin; $\mathbf{as}^{2\text{-}3}$ with la rows dorsally, latter usually as single neuromast each. Transverse rows **z**, **q** and **tr** lacking.

A continuous row of neuromasts replacing the postorbital canal (posterior section of the anterior oculoscapular canal above cheek and preopercle and the posterior oculoscapular canal above opercle) is termed **u** (SANZO 1911, MILLER 1986). In gobiids showing discontinuity in this row the anterior section ($\mathbf{u}^1$) is replacing the canal above the cheek and preopercle. Absence of this row seems to be uncommon (for example compare ILJIN 1930, MILLER 1987, AKIHITO & al., 2000; LARSON 2001). A single neuromast ($\mathbf{u}^1$) in course of the former postorbital canal above the cheek is seemingly the remnant of a former longer row **u** of an ancestor. The lack of transverse row **z** is remarkable. This row generally extends from about the origin of the preopercular canal dorsally to the postorbital canal. Seemingly it replaces the dorsalmost section of the preopercular canal of basic gobioids and is found throughout most Odontobutidae, Eleotridae and Gobiidae (TAKAGI 1988, WONGRAT & MILLER 1991, MILLER 1986, AKIHITO & al. 2000, LARSON 2001).

Opercular

Three rows, one transversal (**ot**) and two longitudinal (**os**, **oi**). Row **ot** long, ventrally extending on subopercle. This row is the only long transverse row on the head of *Typhlogobius* with numerous neuromasts. Rows **os** and **oi** short, thus most of central and posterior parts of opercle free of neuromasts.

Anterior dorsal (occipital)

Generally in gobiids two transversal rows (**n**, **o**) and two longitudinal rows (**g**, **h**) are developed. In *T. californiensis* **n** and **o** are each usually represented by a single neuromast.

Latter row is lacking in a few specimens. **n**, **o** and **g** as a series of neuromasts extending rearwards and medial. In some specimens an additional neuromast is present between **o** and **g**, but in the majority on one side only (Fig. 1B). **h** divided, with the few neuromasts widely separated. Row **m** is lacking. Entire dorsal side of the head, nape and predorsal area, except for the snout, covered with a few neuromasts only.

Interorbital

Longitudinal row **p** bilateral, each typically as two neuromasts posterodorsal of orbit. This row replaces the reduced posterior sections of the supraorbital canal which runs from pore D posteroventral to pore F in gobies with this section developed (AKIHITO & al. 2000). Due to drastic changes of the head proportions during ontogeny, these two **p** neuromasts are not in course of the interorbital canal (Figs. 1B, 1C, 2). One of us (H. A.) investigated three larval specimens <12 mm SL with well developed eyes but interorbital canals not yet developed. In the interorbital region, close to and along the dorsal margins of both eyes lie four large neuromasts. The two anterior neuromasts get enclosed in the interorbital canals during ontogeny, the other two neuromasts remain superficial (**p**). In specimens with canals not closed the primary neuromasts are visible.

In gobiid fishes the canal neuromasts develop earlier than the head canals in which they get successively enclosed during ontogeny (AFZELIUS 1956, TAKAGI 1988, HERLER & al. 1999). In gobioids with the supraorbital canal reduced or lacking, this canal is generally replaced by free neuromasts termed **p** (SANZO 1911, MILLER 1986, WONGRAT & MILLER 1991). Neuromasts in the course of a lacking canal or canal sections are primary replacement neuromasts (WONGRAT & MILLER 1991). These neuromasts are generally numerous and do not only replace the canal but also the canal neuromasts which are few in numbers. In several gobiids primary neuromasts may not be enclosed in a canal (paedomorphic feature) and are also not replaced by neuromasts. Like the preopercular row $\mathbf{i}^3$ the two **p** neuromasts of *T. californiensis* are possibly primary neuromasts not enclosed in a canal.

Trunk and caudal fin

Trunk

The neuromasts are arranged in three series of generally transversal rows (**ld**, **lm** and **lv**), with only the ventral lateral series (**lv**) in a constant pattern. Dorsal lateral series **ld** in one, two or three rows. The first row ($\mathbf{ld}^1$) short, transverse immediately below origin of first dorsal fin, and occuring in all specimens. $\mathbf{ld}^2$ as single neuromast close to the neuromast series in the lateral midline and below origin of the interdorsal space, occuring in the majority of specimens but lacking in 10 specimens (26%). $\mathbf{ld}^3$ lacking in the majority of specimens (n=21, 76%), if developed as 1 – 2 neuromasts dorsal on the caudal peduncle (24%).

In many gobiid species the dorsal lateral series (**ld**) consists of three rows, the first two close to the origins of the first and second dorsal fins, the third close to the dorsal origin of the caudal fin (for example SANZO 1911, HERLER & al. 1999, SCSEPKA & AHNELT 1999). In some species the number of rows is increased (for example ECONOMIDIS & MILLER 1990, AHNELT & al. 2000, AHNELT & DUCHKOWITSCH 2001). Loss of $\mathbf{ld}^2$ and/or $\mathbf{ld}^3$ is seemingly uncommon in gobiid fishes. The high percentage of specimens of *T. californiensis* with no $\mathbf{ld}^3$ is possibly a result of the life style of the blind goby in a microhabitat (burrows of a shrimp) where this fish does not longer rely on these neuromasts. This assumption is supported by the neuromast pattern of the caudal fin (see below).

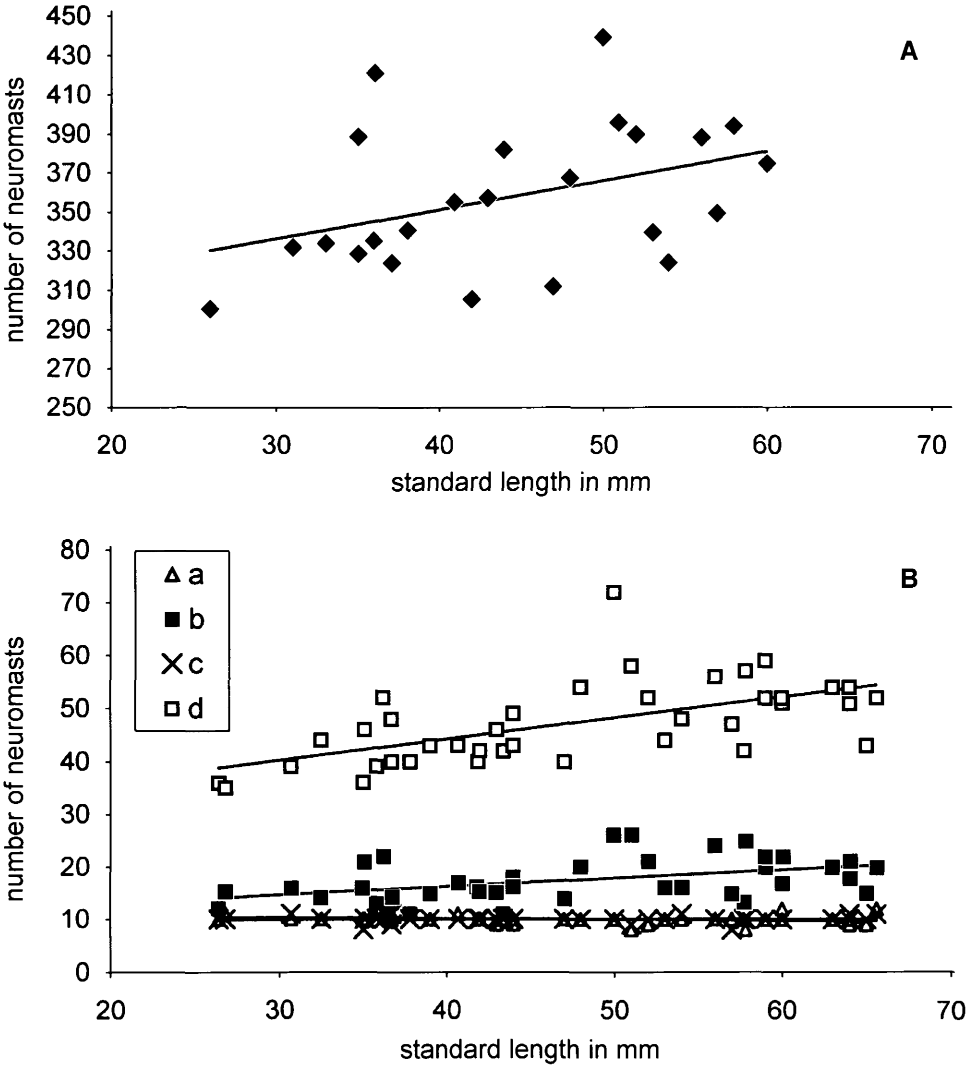

Fig. 4: *Typhlogobius californiensis*. A: Plot of total number of free head neuromasts against standard length with regression line. B: Plot of total number from the left and right side of the longitudinal suborbital neuromast rows **a**, **b**, **c** and **d** against standard length with regression lines. Note very similar numbers of neuromasts in rows **a** and **c**.

Median lateral series **lm** in 16 – 24 rows (mode 20 – 21) from about origin of the pectoral fin to origin of caudal fin in a characteristic pattern (Fig. 2B). Most rows transversal and short, irregularily a few rows of a single neuromast only except for first row (**lm**^{1}), which usually consists of one neuromast only. Smallest specimens (<33 mm SL) with most **lm** rows of one neuromast only. The last **lm** row is slightly displaced ventrally and on the bases of the caudal fin rays. First three rows (**lm**$^{1-3}$) separated from each other by distinct gaps, the following more closely set. This pattern has been found in all examined specimens, independent of size.

Tab. 1: Range, mean (x) and standard deviation (s) of numbers of free neuromasts of the lateral line system on the left side in *Typhlogobius californiensis*. Series of free neuromasts (sensory papillae): AD, anterior-dorsal (occipital); CF, caudal fin; IO, interorbital; OP, opercular; OS, oculoscapular; PM, preopercular-mandibular; PO, preorbital; SO, suborbital; T, trunk.

Typhlogobius californiensis
SL 26.4-65.6 mm
n = 28-40

	range	(x)	(s)		range	(x)	(s)		range	(x)	(s)		range	(x)	(s)
PO				**OS**				**T**							
r	1-2	1.9	0.3	u^1	0-1	0.7	0.5	ld^1	1-4	2.5	0.9	lm^{13}	0-3	1.7	0.9
s	1-4	3.0	0.4	u^2	1-3	2.8	0.4	ld^2	0-2	0.7	0.5	lm^{14}	1-3	1.8	0.9
*	0-1	1.0	0.2	x^1	1-6	3.7	1.2	ld^3	0-2	0.4	0.6	lm^{15}	1-3	1.7	0.9
s^3	1	1.0	0.0	x^2	2-6	3.5	1.2	lv^1	2-7	3.7	1.2	lm^{16}	0-3	1.4	0.8
c^2	1-4	3.5	0.7	y	1	1.0	0.0	lv^2	0-6	3.1	1.3	lm^{17}	0-3	1.7	0.9
c$_2$	1	1.0	0.0	as^1	1-3	1.8	0.8	lv^3	0-7	3.2	1.3	lm^{18}	0-3	1.4	1.1
c$_1$	2	2.0	0.0	as^2	1-3	2.3	0.8	lv^4	0-6	3.1	1.2	lm^{19}	0-3	1.3	1.0
IO				as^3	1-4	2.4	0.7	lm^1	0-2	0.9	0.4	lm^{20}	0-3	1.2	0.9
p	2	2.0	0.0	la^2	0-1	1.0	0.3	lm^2	2-6	3.4	0.9	lm^{21}	0-2	1.1	0.7
SO				la^3	1	1.0	0.0	lm^3	0-5	3.1	1.1	lm^{22}	0-3	1.3	0.8
a	4-6	5.0	0.5	**OP**				lm^4	0-5	2.6	1.1	lm^{23}	0-2	1.3	0.6
b	5-13	8.6	2.2	ot	15-30	22.5	3.6	lm^5	1-4	2.6	0.8	lm^{24}	0-1	1.0	0.0
cp	1	1.0	0.0	os	2-5	3.4	0.9	lm^6	1-4	2.5	1.0	**CF**			
c	4-6	5.0	0.0	oi	1-6	3.0	1.0	lm^7	1-4	2.2	0.9	lct	0-7	2.7	1.9
d	17-37	23.4	3.6	**AD**				lm^8	1-3	2.0	0.9	lcd	0-2	0.6	0.7
PM				n	0-1	1.0	0.2	lm^9	1-3	2.2	0.9	lcm	0-7	2.8	2.2
e^1	24-43	34.0	4.6	o	0-2	1.0	0.3	lm^{10}	1-4	1.9	1.0	lcv	0-2	0.1	0.4
e^2	4-10	7.0	1.5	g	1-5	2.5	0.8	lm^{11}	0-3	1.6	0.9				
i^1	11-15	12.9	0.8	h	1-3	2.6	0.5	lm^{12}	1-4	1.7	1.0				
i^2	6-8	7.0	0.4												
i^3	1-2	1.9	0.3												
f	1	1.0	0.0												

Ventral lateral series **lv** in a characteristic number and pattern of rows. Four rows from below ventral origin of the pectoral fin rearwards, last row (**lv**^{4}) distinctly anterior to the anus. First two rows (**lv**$^{1-2}$) separated by a distinct gap.

Caudal fin

The caudal fin is scarcely covered with neuromasts, usually on its posterior half only. Due to the few neuromasts a pattern is hardly to detect. Obviously three rows are developed, one transversal (**lct**) and two longitudinal (**lcd**, **lcm**) (Fig. 2B). A large gap occurs between the last median lateral row (**lm**) of the trunk to the first neuromasts of the caudal series. A ventral longitudinal row (**lcv**) is lacking in 28 (88%) from 32 specimens. One or two neuromasts are present in its course in four specimens (12%), in one on both sides.

Generally two characteristic neuromast patterns on the caudal fin of gobiid fishes are developed. Pattern one with four rows, three longitudinal rows (**lcd**, **lcm**, **lcv**) and a fourth, transversal row (**lct**), latter may be more or less distinctly developed (SANZO 1911, MILLER & EL-TAWIL 1974, HERLER & al. 1999, SCSEPKA & AHNELT 1999, AHNELT & DUCHKOWITSCH 2001). Pattern two with three rows, two longitudinal rows (**lcd**, **lcm**) (the ventral **lcv** lacking) and a third, transversal row (AHNELT & al. 2000). The rows on the caudal fin of *T. californiensis* are distinctly reduced but pattern two is still recognizable.

Discussion

Typhlogobius californiensis is the first blind gobiid described (STEINDACHNER 1879). Two opposite theories concerning the lateral line system of this blind goby are published. One implicates a reduction of the lateral line sense (RITTER 1893), the other an increase of it (HUBBS 1927).

Knowing that the loss of vision may be accompanied by a hyperdevelopment of the lateral line system in blind fish species (PACKARD 1886), RITTER (1893) investigates the neuromast pattern ("tactile organs") of *T. californiensis*. He finds neuromasts on the head and on the body of juvenile specimens with functional eyes and before entering the burrows of a ghost shrimp but does not find them on the body of adult specimens which live in such burrows. He also detects only few of the neuromast rows of other gobiid species on adults of the blind goby. From this findings he concludes that during ontogeny the lateral line sense of *T. californiensis* diminishes with the loss of vision. Also MACDONALD (1972) concludes that this sensory system undergoes changes during ontogeny and that it is degenerated in adults.

Contrary to RITTER (1893), HUBBS (1926, 1927) states that the neuromasts of *T. californiensis* are "more extensively developed than usually" in gobiid fishes. He directly connects the loss of vision in adult specimens with the occurrence of neuromasts which are "excessively well developed".

Compared with other gobiid fishes (for example BARLOW 1961, MACDONALD 1972, AKIHITO & al. 2000), neuromast rows of *T. californiensis* are short, and their overall number is low. Large parts of the head and the body are free of neuromasts. Except for the suborbital rows they are small and easily overlooked. Contrary to RITTER (1893) who obviously overlooked most neuromast series in adult specimens, HUBBS (1927) mentions that the "tactile organs" of adults are more developed than those of young specimens. This conclusion is seemingly based on large skin folds on the head of adult specimens which are less developed in young individuals. But there is only a moderate size dependent increase in the overall number of neuromasts during ontogeny in the blind goby (Fig. 4A).

Despite lost vision *T. californiensis* seemingly does not rely on a hyperdeveloped lateral line system, but has its topography reduced compared with other less secretive gobiid species. This reduced neuromast pattern is characteristic for all postlarval stages and does not change during ontogeny. The density of neuromasts is still relatively high on the snout and around the mouth but decreases caudally. Especially the caudal fin but also the caudal peduncle are only partly covered with a few neuromasts. Obviously this is because of the mode of life of the blind goby as inhabitant of the burrows of a ghost shrimp. Inhabiting such a microhabitat seemingly protects the blind goby from high turbulences of the intertidal zone, reduces the necessity to detect predators and also diminishes swimming activities for finding a mate, spawning grounds or prey. The narrow burrows are tube-like and allow only a frontal approach of the goby. The anterior part of the head is the only area where a substantial number of neuromasts is concentrated. Seemingly because of this life style *T. californiensis* does not rely on a dense neuromast pattern. The relatively high diversity of neuromast numbers within all size classes of the blind goby is possibly the result of a tendency towards reduction (Fig. 4A, Tab. 1).

Obviously the lateral line system of *T. californiensis* is specialized and displays several trends towards reduction: (1) the cephalic canal system is reduced to short interorbital canal sections, (2) except for the region close to the mouth neuromasts are reduced in numbers, (3) neuromast rows may lack more or less regularly and (4) large areas of the head, trunk and caudal fin are free of neuromasts.

This reduced topography of the lateral line system is characteristic for all juvenile and adult specimens, regardless if functional eyes are developed (juveniles) or lost (adults). The very similar neuromast pattern of different age classes of the blind goby illustrates that the lateral line sense does not increase during ontogeny as it is supposed by HUBBS (1927). RITTER's (1893) conclusion that this sense is reduced compared with other gobiids is correct, but not his hypotheses that the lateral line sense of *T. californiensis* diminshes during ontogeny with the loss of vision.

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