Hoese, Douglass F., 1983. Sensory papilla patterns of the cheek lateralis system in the gobiid fishes Acentrogobius and Glossogobius, and their significance for the classification of gobioid fishes. *Records of the Australian Museum* 35(5): 223–230. [30 December 1983].

doi:10.3853/j.0067-1975.35.1983.319

ISSN 0067-1975

Published by the Australian Museum, Sydney

Sensory Papilla Patterns of the Cheek Lateralis System in the Gobiid Fishes *Acentrogobius* and *Glossogobius*, and Their Significance for the Classification of Gobioid Fishes

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ABSTRACT. The sensory papilla patterns of the cheek lateralis system are described and compared in various species of *Acentrogobius* and *Glossogobius*. Methods of studying and naming the papilla lines are discussed. Two basic patterns are recognized, a transverse pattern with several vertical papilla lines and two horizontal lines, and a longitudinal pattern with only horizontal lines. The significance of the orientation of the papillae within the lines and the development of ridges connecting the papillae in determining homologies is discussed. It is suggested that the transverse papilla pattern has developed independently in *Glossogobius circumspectus* and *Acentrogobius viridipunctatus* from structurally different longitudinal patterns.

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Almost all gobioid fishes have lateralis system sensory papillae or free neuromasts on the head and body outside the head canals. The papillae are developed as small bumps, arising from the skin, sometimes on large flaps, arranged in characteristic lines or rows. Their importance in the classification of gobioid fishes has long been recognized by European and Japanese workers (Sanzo, 1911; Aurich, 1938; Miller & Wongratana, 1979; Akihito & Meguro, 1975; Takagi, 1957).

Generally two distinctive patterns have been recognized (Aurich, 1938). In the transverse pattern the cheek and preopercular papillae are developed in two horizontal and four or more vertical lines (Fig. 1). In the longitudinal pattern the papillae are arranged only in more or less horizontal lines (Fig. 2). Considerable variation occurs in these patterns, but by examining the arrangement of the lines and the orientation of the papillae within these lines, it is possible to group all gobiids within one or the other pattern type, with the exception of species with a very reduced number of papillae.

Some workers have simply illustrated the papilla patterns (Hoese & Allen, 1977; Aurich, 1938; Takagi, 1957), but others have labelled the various lines with numerical or alphabetical characters. At present no standardization exists. Akihito & Meguro (1975, 1977, 1980) numbered all the papilla lines, beginning at the snout, without discriminating between the vertical and horizontal lines. This system has considerable internal consistency when dealing with species in the same genus. It has a disadvantage in comparisons of genera with different patterns, since the same lines in different genera often have different numbers. European workers (Miller, 1974; Miller & Wongratana, 1979; Iljin, 1930) have generally followed the nomenclature of Sanzo (1911). The work of Sanzo was the first detailed study of sensory papillae in gobioid fishes and is still a classic work. Sanzo numbered the vertical rows under the eye, beginning below the front of the eye, lettered the horizontal rows under the eye from a to d, and labelled other papilla rows with alphabetic characters, often using a prime mark to indicate branches of the various rows. This system offers the greatest potential for determining phylogeny. However, there are several disadvantages. The system was based on European gobiids and is often not easily applicable to the vast mosaic of patterns found among other gobiid fishes. For example, many Indo-Pacific genera have more than four horizontal cheek lines (a to d of Sanzo). Also, determining homologies in the various lines has often proved difficult.

Several questions exist regarding the transverse and longitudinal papilla patterns. It is not known which pattern, if either, is primitive, or whether either pattern is monophyletic. Since both patterns occur across conventional taxonomic groupings, one or both patterns would appear to be polyphyletic. However, it could be argued that the patterns represent specializations indicating phylogenetic lines, since detailed phylogenies of gobioid fishes are largely unavailable. In the most primitive gobioid known, *Rhyacichthys,* there are numerous bumps, presumably the sensory papillae, evenly spaced on the head, but not arranged into lines. Although this pattern may be primitive, *Rhyacichthys* lives in very swift-flowing waters, and interpretation of the pattern is difficult.

An alternative test of the question of the interrelationships of the patterns is to examine genera, as currently recognized, that have some species with the transverse pattern and others with the longitudinal pattern. Both patterns are well known in *Glossogobius* and *Acentrogobius*. In each genus, only one or two species have been recognized with the transverse pattern, while all other species recognized have the longitudinal pattern.

Methods and Materials

Methods. The following discussion of methods for studying the papillae is based on observations made over a period of 15 years.

Factors that affect the preservation and visibility of the papillae include (1) initial condition of the specimen, (2) initial fixation, (3) long term preservation fluid, (4) handling of the specimen, and (5) taxon involved.

(1). The initial condition of a specimen is the most critical factor. Specimens should be preserved as soon as possible, with best results being obtained from specimens preserved within a few minutes of collection. Freezing or storing specimens on ice invariably leads to collapse of the papillae. Similarly, best results are obtained when specimens are isolated in large vials or plastic bags. Collecting gobies in nets full of larger fish rarely produces satisfactory results.

(2). Standard fixation of gobies is generally adequate. Ten per cent formalin gives best results, but considerable latitude is possible. Specimens can be fixed for up to one hour in 20 to 30% formalin without damage to the papillae, if the specimens are then transferred to 10% formalin. Initial fixation in alcohol also gives reasonable results, but it is not recommended, since specimens often become dehydrated and brittle. Long fixation in formalin over 15% generally leads to dehydration, resulting in the collapse of the papillae. Fixation in formalin solutions of less than five per cent also is inadequate.

(3). Long term storage in formalin (a year or more) appears to result in collapse of the papillae. Specimens preserved for several years in isopropyl alcohol also had collapsed papillae. In numerous isopropyl specimens studied, the skin had become soft and flaccid. Specimens stored in ethyl alcohol (55 to 70%) generally show little collapse. Papillae were easily seen in Rüppell and Valenciennes material collected in the early 1800's. Generally storage in any solution which reduces the quality of the specimen will lead to a collapse of the papillae.

(4). Specimens should never be allowed to dehydrate. Use of a fibre optics light source and brief soaking of specimens in water before study generally prevents dehydration. Rehydration techniques can sometimes restore the papillae if dehydration is not severe.

(5). Finally, the papillae vary in size in different genera. Papillae are often more difficult to see in specimens with a light-coloured head.

Examination of papillae is typically difficult but possible when a properly preserved specimen is examined. Study of untreated specimens is most difficult, and rarely can all papillae on the head be seen. Published drawings of papilla patterns are often incomplete. Ability to see the papillae generally increases with experience. High magnification and proper use of a light source are also critical factors for improving ability to see the papillae. Shining a low intensity light from the side often improves the contrast, but considerable experimentation is necessary to achieve best results. Blowing air over the specimen to remove excess water can improve papilla visibility, but too much air flow can result in dehydration.

Studies are most easily carried out on specially treated specimens. Potassium permanganate can be used to stain the papillae, although success varies considerably. For this study, trypsin-cleared specimens (Taylor, 1967) stored in glycerine were used. Blowing air gently over the head and using transmitted light consistently gave good results, when properly fixed specimens were used. In many cases glycerine storage appeared to partly restore collapsed papillae. Little improvement was noted in poorly preserved material. Long term storage in glycerine does not appear to affect the papillae, although the longest storage period observed was about 15 years. The eyes should not be removed from glycerine specimens, since the papillae near the eye can be damaged.

Drawings of papillae were made from cleared and stained glycerine specimens, with the aid of a camera lucida. The axes of the papillae have been exaggerated. Counts of papillae were taken from cleared and stained material and well-preserved specimens.

Material examined. All material examined is deposited in the Australian Museum, Sydney (AMS), the California Academy of Sciences, San Francisco (CAS), or the Museum National d'Histoire Naturelle, Paris (MNHN). The number following the registration number indicates number of specimens, and numbers in parentheses indicate ranges of standard lengths in mm. *Acentrogobius janthinopterus* (Bleeker): AMS I.19468-045, 1(47); I.20978-014, 2(27–66); I.22724, 1(41), all from Lizard Island, Queensland. *Acentrogobius therenzieni* Kiener: MNHN 1968-163 (holotype), Madagascar. *Acentrogobius viridipunctatus* (Valenciennes): AMS I.22090-006, 5(20–50), Salonika Beach, Queensland; AMS I.22720-010, 2(36–50), Townsville,

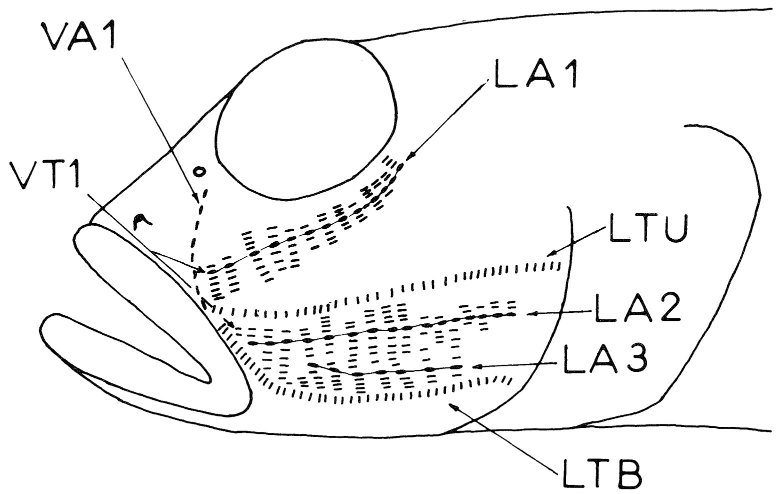

Fig. 1. Transverse sensory papilla pattern in *Acentrogobius viridipunctatus*, 49 mm SL. Cheek papillae only shown. Thin line connecting papillae indicates a very low ridge of skin. See text for meaning of abbreviations.

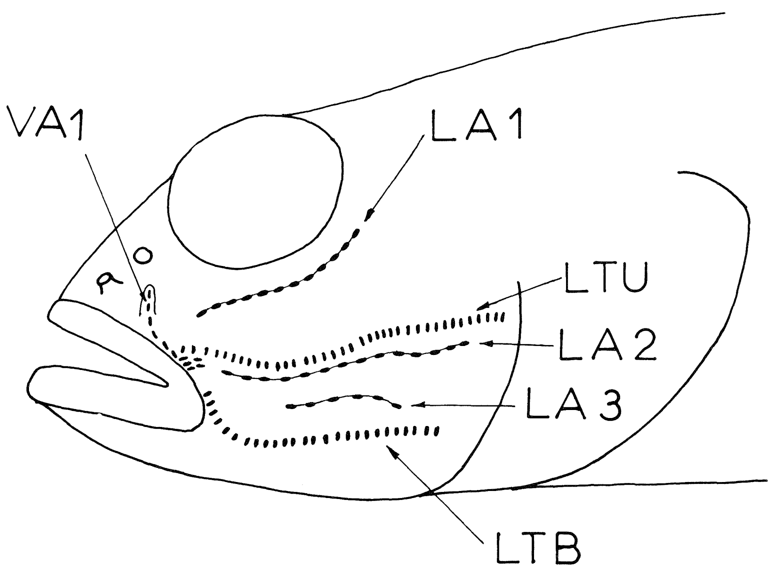

Fig. 2. Longitudinal sensory papilla pattern in *Acentrogobius janthinopterus*, 41 mm SL.

Queensland; AMS I.23265-001, 4(33–60); I.23279-002, 11(33–88), Weipa, Queensland. *Acentrogobius* sp.: AMS I.20124-004, 14(41–57), Port Stephens, New South Wales. *Glossogobius celebius* (Valenciennes): CAS, unregistered, 4(40–57), Palau; AMS I.21256-002, 11(17–43), Cape Tribulation, Queensland. *Glossogobius circumspectus* (Macleay): AMS I.22090-003, 22(24–113), Salonika Beach, Queensland; AMS I.22720, 1(49); I.23313-010, 2(68–92), Townsville, Queensland; AMS I.16670-016, 6(35–85), Madang, Papua New Guinea. *Glossogobius* sp.: AMS, unregistered, 3(45–52), Safia Creek, Papua New Guinea.

Terminology for Papillae

In almost all gobioid fishes each papilla is elongate, often elliptical in shape. The cheek papillae are arranged in distinct patterns in vertical, horizontal, or oblique rows or lines. These lines of papillae are typically referred to as pit lines (Takagi, 1957) or papilla rows. The term papilla line is preferred here, since the papillae are rarely set in pits in gobioid fishes, and in some species each line can be composed of multiple rows of papillae. The axis of the papilla is oriented along the axis of the line or at right angles to the axis of the line.

Although several patterns occur in gobiid fishes, two distinct general patterns are recognizable: the transverse pattern and the longitudinal pattern. In the *transverse pattern* (Fig. 1) the cheek papillae are typically arranged in four or more vertical or slightly oblique rows extending from below the lower margin of the eye. There is an upper horizontal line (LTU) extending from under or behind the eye posteriorly on the preoperculum (the beginning of the line varying with the genus), and a lower horizontal line (LTB) extending from near the posterior end of the upper jaw. In the transverse pattern all the papillae are arranged with their elongate axes perpendicular to the axis of the line. In the *longitudinal pattern* (Fig. 2) there are four or more horizontal lines below the eye extending posteriorly on the preoper-

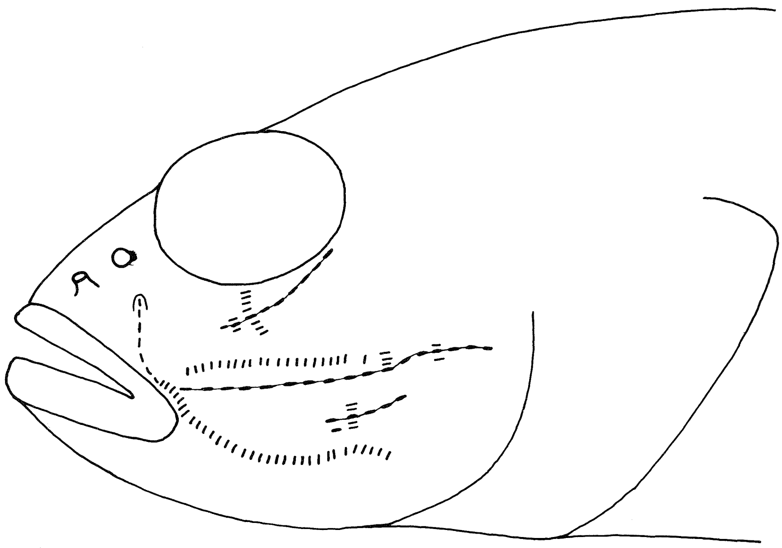

Fig. 3. Mixed sensory papilla pattern in *Acentrogobius* sp., 45 mm SL.

culum. There is a line extending from or just behind the middle of the upper jaw, along the lower margin of the eye, often ending at the infraorbital head pore (when present) behind the eye. Below this line is a second horizontal line, extending from or behind the middle of the upper jaw. Below the second line, there are two or more (usually three) horizontal lines. Often the fourth line branches ventrally from the third line. In the longitudinal pattern, the papillae are elongated perpendicular to the axis of the line only on the second or third and the lowermost (usually the fifth) lines. In all other rows, the papillae are elongated along the axis of the line.

No attempt is made here to standardize the various systems of labelling the papilla lines. Since lines in similar positions in different genera may not always be homologous, a standard system may not be desirable. The labelling used here refers only to the papilla lines under the eye and on the cheek and preoperculum, and is designed to distinguish the orientation of the papillae within the lines. The first letter refers to the orientation of the line: V = more or less vertical; L = longitudinal, or more or less horizontal. The second letter indicates the orientation of the papillae with respect to the axis of the line: T = transverse or perpendicular; A = axial, along the axis of the line. VT1, VT2, etc. = vertical papilla lines with papillae oriented at right angles to the long axis of the line. The numbering system begins at the anteriormost vertical line below the eye. LA1, LA2, etc. = longitudinal papilla lines with the papillae oriented along the axis of the line. The numbering system begins with the first line below the eye. VA1 = a vertical row with papillae oriented along the axis of the row, generally present below the front of the eye. LTU = the uppermost longitudinal line with papillae oriented at right angles to the axis of the line. LTB = the lowermost longitudinal line with papillae oriented at right angles to the line. The abbreviations LTU and LTB, referring to upper and bottom horizontal lines respectively are used here in preference to numbers since these two lines are almost always present in gobioid fishes and are probably homologous.

For the discussion that follows the transverse pattern is defined as the presence of distinct vertical transverse lines (VT) with no apparent longitudinal axial lines. The longitudinal pattern is defined as containing no vertical transverse lines, but only longitudinal axial lines (LA). The longitudinal transverse lines (LTU and LTB) are generally present in both patterns.

Papilla Patterns in *Acentrogobius*

As recognized by Koumans (1953), *Acentrogobius* is clearly a polyphyletic assemblage serving as a convenient dumping ground for problematic species. Hoese & Winterbottom (1979) separated from *Acentrogobius* several coral reef species into the genera *Exyrias, Macrodontogobius,* and *Istigobius,* and some estuarine and coastal species into *Favonigobius, Amoya, Yongeichthys* and *Drombus.*

Because of the confusion over the generic placement of various species, the genus is considered to include for the purposes of this discussion *Acentrogobius viridipunctatus* (Valenciennes) (the type species), *A. therenzieni* Kiener, *A. janthinopterus* (Bleeker), *A. caninus* (Valenciennes), and *A.* sp. However, it is apparent that the genus includes several additional species, most of which have a papilla pattern similar to that of *A. janthinopterus.*

Acentrogobius is distinctive in having a rounded tongue tip, typically a narrow gill opening, extending to just below the pectoral base (except in *A. viridipunctatus*, in which the gill opening extends to below the posterior preopercular margin), no flattened preopercular process at the angle of the preoperculum, no preopercular process connecting to the upper part of the symplectic, and 10 + 16 vertebrae.

A transverse papilla pattern is found in *Acentrogobius viridipunctatus* (Fig. 1) and *A. therenzieni.* The uppermost longitudinal line (LTU)

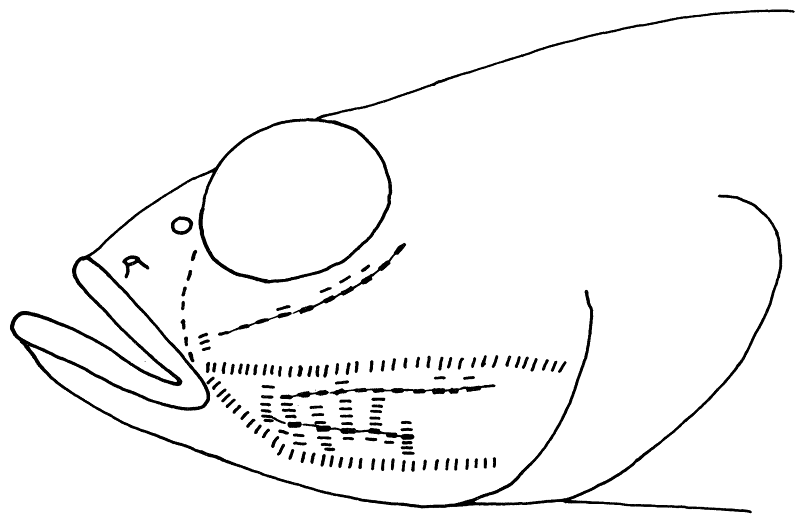

Fig. 4. Sensory papilla pattern in juvenile *Acentrogobius viridipunctatus,* 34 mm SL.

extends from the upper jaw to the end of the preoperculum. There are 5 to 15 short vertical lines (VT) immediately below the eye, few of which reach to the LTU line. Between the two longitudinal lines there are 8 to 16 vertical lines (VT).

A longitudinal pattern is found in *Acentrogobius janthinopterus* (Fig. 2) and *A. caninus*. The two longitudinal lines (LTU and LTB) are essentially identical in position and length to these lines in *A. viridipunctatus*. There are three longitudinal axial lines (LA), the first (LA1) below the eye (reaching the jaws in large adults only), and the other two (LA2 and LA3) between the two longitudinal transverse lines (LTU and LTB).

A mixed pattern is found in *Acentrogobius* sp. (Fig. 3). The longitudinal transverse lines are both reduced in length posteriorly. The second longitudinal axial line (LA2) is well developed, but LA1 and LA3 are reduced in length. There are two vertical transverse lines below the eye and two short VT lines cutting across LA2. The occurrence of this mixed pattern suggests that the two patterns may not be as different as previously thought.

Examination of the longitudinal axial lines in *Acentrogobius janthinopterus* in glycerine-cleared specimens indicates that the papillae in the longitudinal axial lines are connected by a low ridge of skin. These low ridges should not be confused with the large folds or flaps that occur on the cheek in some genera such as *Gobiopsis* (with a longitudinal pattern) and *Callogobius* (with a transverse pattern). The same ridges as found in *A. janthinopterus* are present in *A. viridipunctatus*, suggesting that the transverse pattern in *A. viridipunctatus* was derived from a longitudinal pattern. Supporting evidence for this hypothesis is provided by the pattern of development of the lines with growth in *A. viridipunctatus*. In juveniles (Fig. 4) of *A. viridipunctatus* the longitudinal pattern is readily discernible, although some vertical lines have developed. With growth, the transverse pattern develops more completely. Counts of the number of vertical lines (VT) and papilla counts in the upper longitudinal transverse lines (LTU) and in the vertical lines, indicates that both the number of lines and the number of papillae in each line increase significantly with growth ($p < .01$, tested with Kendall tau correlation coefficient). The number of vertical lines increases from 5–10 (32–43 mm standard length) to 12–18 (48–83 mm SL).

Ridges connecting the papillae of the longitudinal axial lines also occur in *Acentrogobius* sp.

Consequently, it is suggested that the transverse papilla pattern of *Acentrogobius viridipunctatus* and the mixed pattern of *A.* sp. have evolved from a longitudinal pattern similar to that found in *A. janthinopterus*.

Papilla Patterns in *Glossogobius*

A similar, but somewhat different situation is seen in *Glossogobius*. Of the 12 species of *Glossogobius* illustrated by Akihito & Meguro (1975), only *G. circumspectus* has a transverse papilla pattern. In some species one or more of the longtitudinal axial lines may be composed of multiple rows of papillae.

The discussion of *Glossogobius* applies here to the species treated by Akihito & Meguro (1975, 1976), with the exception of *G. biocellatus.* Also included here in *Glossogobius* are *G. tenuiformis* Fowler, from east Africa, *G. bicirrhosus* (Weber) (= *Illana bicirrhosa*), and about 10 to 12 undescribed species from Australia and New Guinea, currently under study by the author and G. Allen.

Glossogobius is highly distinctive in having a bilobed tongue, moderate gill opening extending to under the posterior preopercular margin, no dorsal skin flap at the end of the lower jaw, a flattened bony preopercular process at the angle of the preoperculum (covered by skin), a preopercular extension meeting the symplectic dorsally, and 27 to 29 vertebrae. *G. biocellatus* has a broader gill opening with the gill membranes forming a free fold across the isthmus, no projection at the angle

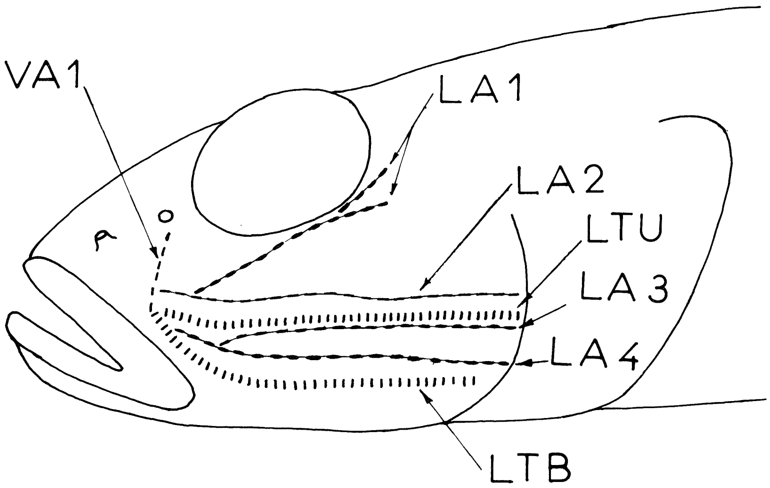

Fig. 5. Longitudinal sensory papilla pattern of *Glossogobius celebius,* 50 mm SL.

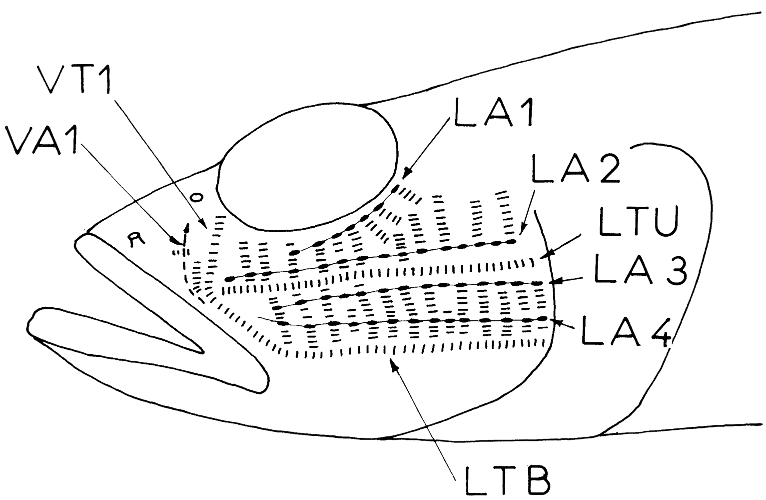

Fig. 6. Transverse sensory papilla pattern of *Glossogobius circumspectus,* 49 mm SL.

of the preoperculum, and a different papilla pattern, suggesting a closer relationship with *Psammogobius* from South Africa. With the exception of *G. bicirrhosus* and *G. circumspectus,* all species are essentially freshwater, only rarely found in brackish water, although the distribution of the larval stages is unknown.

The horizontal pattern characteristic of most species of *Glossogobius* is illustrated in Fig. 5. The short branch of the uppermost longitudinal axial line below the eye is characteristic of only some species of *Glossogobius*. The pattern is similar to the longitudinal pattern of *Acentrogobius*, except there is an additional longitudinal axial line (LA2) just above the upper longitudinal transverse line (LTU). As in *Acentrogobius* all the longitudinal axial lines have a low ridge connecting the papillae within each line. There is a single vertical axial line (VA1) in front of the eye as in *Acentrogobius*. The longitudinal transverse lines (LTU and LTB) extend from the jaws to near the end of the preoperculum, as in most species of *Acentrogobius.*

Glossogobius circumspectus has a distinctive transverse pattern, similar to that of *Acentrogobius viridipunctatus,* except that the vertical lines above the upper longitudinal transverse line (LTU) are more extensively developed (Fig. 6). Unlike *A. viridipunctatus*, the juveniles (25 to 30 mm SL) of *G. circumspectus* also have a distinctive transverse pattern. Counts of the number of vertical lines and the papillae in the LTU line indicate an increase in the number of lines and papillae with growth ($p < .01$). The number of vertical lines between LTU and LTB increases from 11–14 (30–49 mm SL) to 16–23 (79–108 mm SL). The longitudinal ridges are developed in the same positions as the longitudinal lines (LA1–4) of *G. celebius*, indicating that the transverse pattern in *G. circumspectus* has also developed from a longitudinal pattern.

In *Glossogobius* sp. 16 from Papua New Guinea (Fig. 7) all the axial lines are composed of multiple rows. Although this pattern may represent a transitional stage between the longitudinal and transverse patterns, the presence of secondary ridges parallel to the main LA ridges suggests the pattern may be an independent specialization and is best termed a multiple longitudinal pattern.

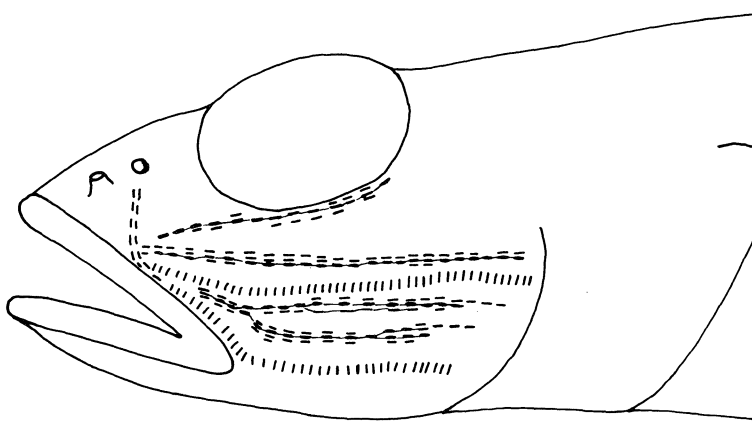

Fig. 7. Multiple longitudinal sensory papilla pattern of *Glossogobius* sp., 50 mm SL.

Discussion

Since *Glossogobius* possesses several specializations not found in *Acentrogobius*, it is suggested that the transverse papilla patterns in these two genera have developed independently from a longitudinal pattern. Although it is possible that the mixed pattern of *Acentrogobius* might be primitive, it is an extremely rare pattern. Even if that pattern is primitive, then both the longitudinal and transverse patterns would have to have developed independently in the two genera, which appears to be the least parsimonious suggestion. Alternatively the transverse pattern could be regarded as primitive, with the longitudinal patterns evolving independently in the two genera. The presence of the longitudinal axial ridges in the transverse patterns in the same position in the respective genera as the longitudinal axial lines does not appear consistent with this hypothesis.

Consequently, it is suggested here that the longitudinal pattern is primitive in *Glossogobius* and *Acentrogobius*, and that the transverse pattern evolved independently in these genera.

It is not clear, however, whether the results obtained here are necessarily broadly applicable to other gobiids. For example, the longitudinal axial ridges are rare in other genera with a transverse pattern. The ridges occur in *Amblygobius* and *Drombus*. The ridges are reduced in *Drombus,* which is probably related to the wider separation of the vertical lines. If the ridges had disappeared in a phylogenetic line, present methods would not be able to distinguish a derived transverse pattern from a primitive one.

Therefore studies of the papilla patterns are useful in characterizing genera, and structural comparisons can aid in determining phylogenies, but it is unlikely that major groupings in a classification can be derived from studies of the papilla patterns.

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Accepted 12 August 1983