# Comparison of taste bud form, number and distribution in the oropharyngeal cavity of lizardfishes (Aulopiformes, Synodontidae)

by

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**ABSTRACT**. - The present study compares the distribution, form and number of taste buds (TB) in the oral cavity of several species of lizardfishes (Synodontidae) belonging to the genera *Saurida, Synodus* and *Trachinocephalus,* from various regions. The oral cavities of the studied lizardfishes are occupied by dense rows of sharp teeth, leaving bare only small areas of the epithelium, on which the TB are exposed. In all the studied species, groups of type I and type II TB predominate, protruding on skin-papillae featuring groups of sensory cells, 3-5 $\mu$m in diameter. Fewer types III TB are found, mostly adjacent to the pharyngeal region. The TB in the frontal part of the oral cavity are situated on lamellae between the teeth on the anterior part of the upper and lower jaws, with rows of single TB along the interior sides of the jaws. Small numbers of TB are also found on the basibranchials of the 3rd and 4th gill arches and the ceratobranchials of the 4th arch. In the studied species, the total number of TB in the oral cavity range between 458 (± 30) in *Synodus dermatogenys* to 1738 (± 120) in *S. variegatus*, small in number compared to fishes of the same dimensions belonging to other systematic groups. The oral sensory area thus formed by the exposed surfaces of the sensory cells range between 8,976 $\mu m^2$ in *S. dermatogenys* to 34,064 $\mu m^2$ in *S. variegatus*, compared to circa 300,000 $\mu m^2$ in some cichlid fishes. It would thus appear that lizardfish predation on larger prey, such as other fishes, relies more on visual detection, while chemical oral recognition (gustatory) of engulfed prey possibly plays a secondary role.

**RÉSUMÉ**. - Comparaison de la forme, du nombre et de la distribution des papilles gustatives de la cavité oro-pharyngienne des poissons lézards (Aulopiformes, Synodontidae).

La présente étude compare la distribution, la forme et le nombre de papilles gustatives (PG) de la cavité buccale de plusieurs espèces de poissons lézards (Synodontidae) appartenant aux genres *Saurida*, *Synodus* et *Trachinocephalus,* et provenant de diverses régions. Les cavités orales des poissons lézards examinés sont occupées par des rangées serrées de dents tranchantes, ne laissant que très peu de zones nues sur lesquelles les papilles gustatives (PG) sont exposées. Chez toutes les espèces étudiées, les groupes de PG de type I et type II prédominent à la surface des papilles, avec des groupes de cellules sensorielles de 3-5 $\mu$m de diamètre. Quelques PG de type III ont été découvertes, la plupart adjacentes à la région pharyngée. Les PG situées dans la partie frontale de la cavité buccale sont localisées sur les lamelles entre les dents de la partie antérieure des mâchoires supérieure et inférieure, avec des rangées de PG isolées le long de la paroi intérieure de la mâchoire. Un petit nombre de PG est également situé sur les basibranchiaux des 3e et 4e arcs branchiaux et les cératobranchiaux du 4e arc branchial. Sur les espèces étudiées, le nombre total de PG de la cavité orale se situe entre 458 (± 30) pour *Synodus dermatogenys* et 1738 (± 120) pour *S. variegatus*, ce qui est peu par rapport aux poissons de même dimension appartenant à d'autres groupes. En conséquence, la zone sensorielle orale formée par les surfaces exposées des gammes de cellules sensorielles est comprise entre 8,976 $\mu m^2$ chez *S. dermatogenys* et 34,064 $\mu m^2$ chez *S. variegatus*, comparativement à environ 300,000 $\mu m^2$ chez certains cichlidés. Il semblerait donc que la prédation des poissons lézards sur de plus grandes proies, comme d'autres poissons, est plutôt de nature visuelle et que la reconnaissance chimique, dans la cavité orale, des proies capturées ne joue qu'un rôle secondaire.

Key words - Synodontidae - Lizardfishes - Oral taste bud - Form - Distribution.

Gustatory (close-range chemical) perception in fish is performed mostly by the chemosensory cells organized in taste buds (TB), whose apices are exposed across the skin surface. The oropharyngeal TB serve to screen the food and, subsequently, either to expel or swallow the item (Finger *et al*., 2000; Hansen and Reutter, 2004; Fishelson, 2005a, 2009; Yashpal *et al.,* 2006). The TB are found in high numbers in the oral cavity and on the gills and skin (Whitear, 1971; Kapoor *et al*., 1975; Reutter, 1991; Gomahr *et al*., 1992; Reutter and Witt, 1996; Fishelson, 2005a, 2005b, 2009; Çinar *et al*., 2008; Yashpal *et al*., 2009). The TBs feature several types of light and dark sensory neurons, and bear on their surface various types of protoplasmic protrusions (Fishelson *et al*., 2004). The signals received by these cells are transported to the myelencephalon (*medulla oblongata*) *via* the viscerosensory branches of the facial (VII), glos-

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sopharyngeal (IX) and vagal (X) nerves (Finger and Morita, 1985; Fishelson, 2005b; Northcutt, 2005; Reutter and Witt, 2005). Despite certain common basic structures of the TB, their dimensions and numbers, as well as their distribution, differ among the various species of fish. These differences seem to be specifically connected to various ecological and foraging adaptations (Livingstone, 1987; Hara, 1993; Fishelson and Delarea, 2004; Fishelson *et al*., 2004; Reutter and Hansen, 2005; Gon *et al*., 2007; Fishelson, 2009). Reviews of such studies, including those on the neurophysiology of these organs, have been published by Hara (1993) and Zeiske and Hansen (2005). Summaries of studies on chemoreception in fish can be found in the books by Hara (1992), Finger *et al*. (2000), Hansen and Reutter (2004) and Reutter and Kapoor (2005). Most studies on the gustatory system have been carried out on catfishes, poeciliids, lungfishes and cyprinids, and more recently on several species of cichlids (Fishelson, 2005a, 2005b), cardinal fishes (Fishelson *et al*., 2004) and blennies (Fishelson and Delarea, 2004; Fishelson, 2009; Gon *et al*., 2007). The present study is the first to deal with the comparative aspects of morphology and distribution of TB in the oral cavity of eight species of lizardfishes (Synodontidae) of three genera, *Saurida, Synodus* and *Trachinocephalus* (Tab. I; Fig. 1A), from various localities**.** These fish are predominantly benthic predators, ambushing fishes and crustaceans upon close approaches. In some regions of the Mediterranean lizardfishes form an important part of the commercial catch (Golani, 1993; Golani and Ben-Tuvia, 1995).

## MATERIALS AND METHODS

The fishes for the present study were collected in the southern Red Sea and the Gulf of Aqaba, as well as along the Israeli Mediterranean coast, at 20-40 m depth. They were killed by immersion in ice-cold water and preserved on ice until handling. Several species (*Synodus dermatogenys, S. kaianus,* and some *Saurida gracilis*) were donated by museums in Taiwan and Hawaii (Tab. I). The sampled fishes were fixed for 8 h in 3% glutaraldehyde or 10% formaldehyde pH 7.2. To allow better penetration of fixatives into the oral cavities of the freshly-sampled specimens their mouths were secured to gape. In some specimens the oral epithelium was retracted with fine forceps to expose the neural connections between the TB. The fixed samples were passed through ascending grades of ethanol, saturated with $C0_2$, critical point-dried in a Balzers Union Point Dryer (BU-11120, Balzers, Lichtenstein), sputter-coated with gold using a Polaron, E5100 Sputter Coater, and observed with a JSM840A scanning microscope. The combined size of the exposed sensory endings of the TB in each fish was used to calculate the total size (in $\mu m^2$) of the sensory area.

## RESULTS

### The oral cavity

The large elongated oral cavity of the studied lizardfishes is armed with rows of sharp teeth along the outer and inner oral arcade of the jaws (Figs 1B, 1C, 2A, 4A). Particularly prominent are the cushions of teeth on the dermopalatine and pterygoid bones of the upper jaw, and *glossohyale, hypohyale, epihyale*, *basibranchiale*, and *ceratobranchiale* bones of the hyoid and the gill arches. Both prominent and significant for identification of the genus are the two rows of teeth in *Saurida*, on the internal and external pterygoid bones, situated on the oral roof (Fig. 1B, C), whereas only a single, external tooth series occurs in *Synodus* and *Trachinocephalus* (Fig. 2A). The oral cavity of all the studied fish is covered by an ectodermal epithelium in which the exposed cell-surfaces feature complicated microridges (fingerprints), as observed in other fish taxa (Fishelson, 1984). In the different species of the studied lizardfishes this pattern of the ridges and the diameter of the cells differ, and these differences can also serve as a taxonomic character (Fig. 2B, D). This microridge pattern changes on the cells that surround the TB (Figs 2E, 4E). A characteristic marker for the oral cavity of

Table I. - Species of lizardfishes studied, locality of origin and standard length (SL) in mm. M: male; F: female; SD (standard deviation) calculated as the distribution around the mean SL.

| Species name | Locality of collection | No. of specimens | SL (mm) + SD | Sex |
|---|---|---|---|---|
| *Saurida gracilis* | Red Sea, Kosrae | 5 | 160 (± 12) | 3M + 2F |
| *Saurida tumbil* | Red Sea, South Africa | 6 | 195 (± 40) | 4M + 2F |
| *Saurida macrolepis* | Mediterranean, Red Sea | 12 | 230 (± 60) | 8M + 4F |
| *Synodus dermatogenys* | Coral See, Bassas | 8 | 100 (± 26) | 3M + 5F |
| *Synodus kaianus* | Hawaii | 2 | 155, 202 | 2F |
| *Synodus saurus* | Mediterranean Sea | 4 | 180 (± 20) | 2M + 2F |
| *Synodus variegatus* | Red Sea, Philippines, Natal (S. Africa) | 14 | 200 (± 20) | 6M + 8F |
| *Trachinocephalus myops* | Red Sea, Hawaii | 6 | 175 (± 28) | 3M + 3F |

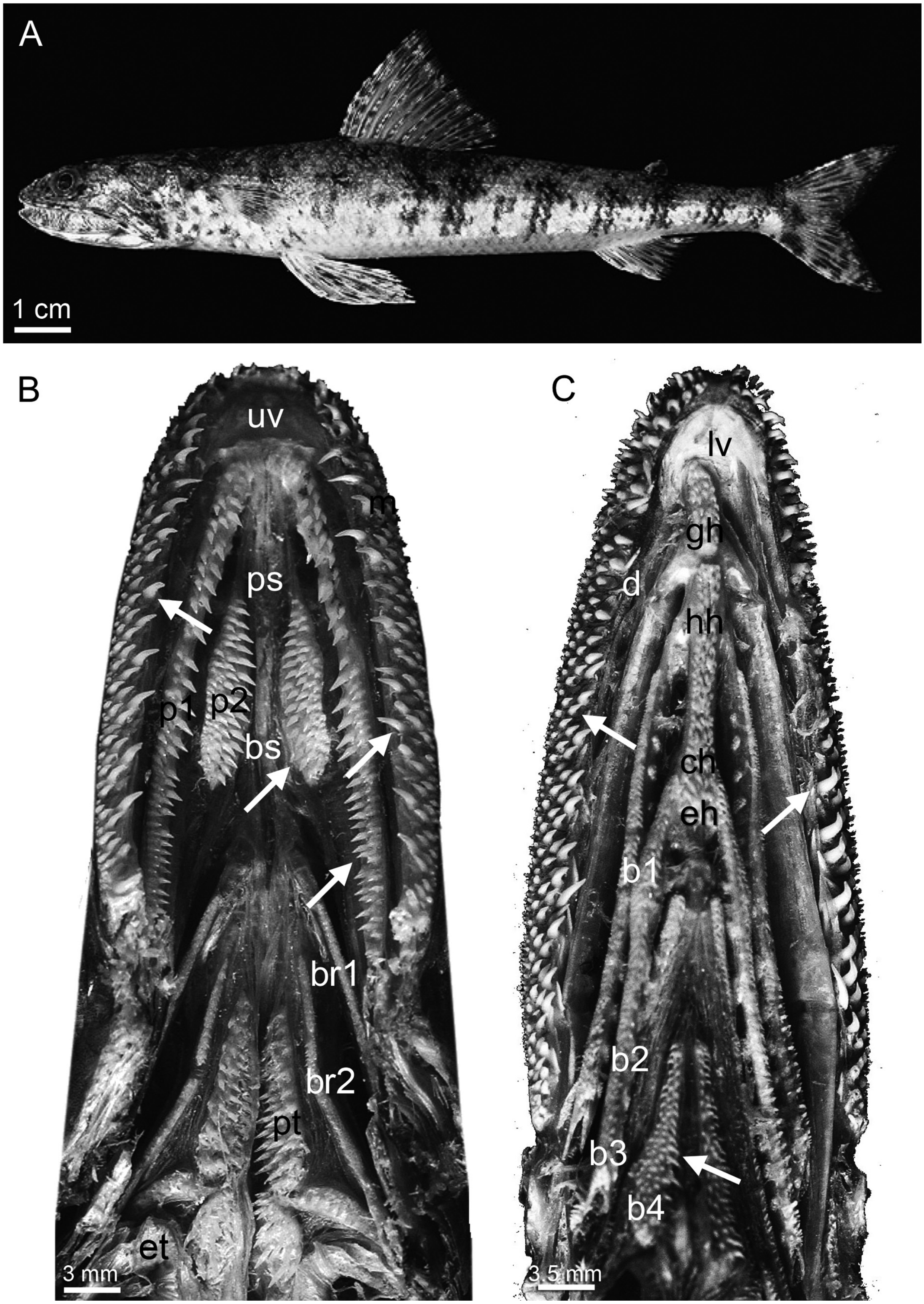


Figure 1. - **A**: Photograph (Photo J. Randall) of a lateral view of the lizardfish *Saurida gracilis*; **B**: Upper jaw and **C**, lower jaw of *Saurida tumbil*; note the large distribution of teeth (arrows). See also the two rows (p1 on the palatine and posterior part of ectopterygoid, and p2 on endopterygoid) of teeth, specific to the genus *Saurida*; b,1-4: gill bases; br1 and br2: basibranchials; bs: basisphenoid; d: dentale; eh: epihyale; et: epibranchial toothplate; gh: glossohyale (tongue); hh: hypohyale; lv: breathing valve of the lower jaw; m: maxilla; ps: parasphenoid; pt: pharyngobranchial toothplates; uv: breathing valve of the upper jaw.

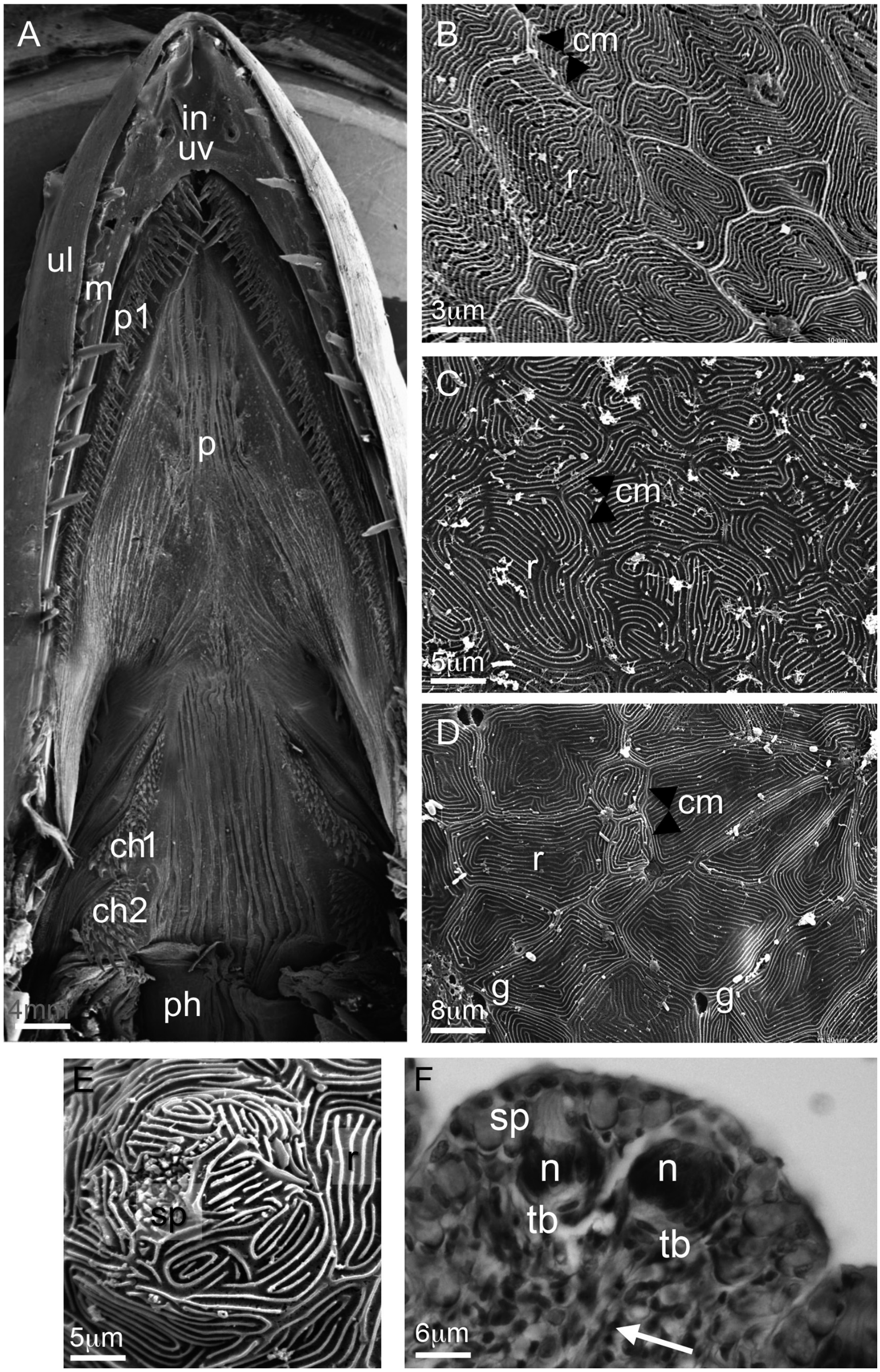


Figure 2. - **A**: Upper jaw of *Synodus variegatus*, see teeth (arrows) present on maxilla (m) and on the palatine and ectopterygoid (p1). Strong cover of teeth is also visible on the pharyngobranchial toothplates (ch1 and ch2). There are also two internal pores (in) on the apical end of the jaw of *Synodus variegatus,* possibly a part of the nasal olfactory system. **B**, **C**, **D**: Oral epithelium of *Trachinocephalus myops* (B), *Saurida gracilis* (C), and *S. macrolepis* (D). These micrographs show that the structure and arrangement of the microridges (r) differ in the various species observed. The two arrowheads (cm) indicate the cell membrane limit, and (g) points the openings of gland cells. **E**: Sensory protrusions (sp) of a taste bud of *S. gracilis* surrounded by microridges of epithelial cells. **F**: Vertical section of epithelium with two taste buds (tb), demonstrating the nuclei of the sensory cells (n), their sensory protrusions (sp), and sensory nerve (arrow). p: palate; ph: pharynx; ul: upper lip; uv: breathing valve of upper jaw.

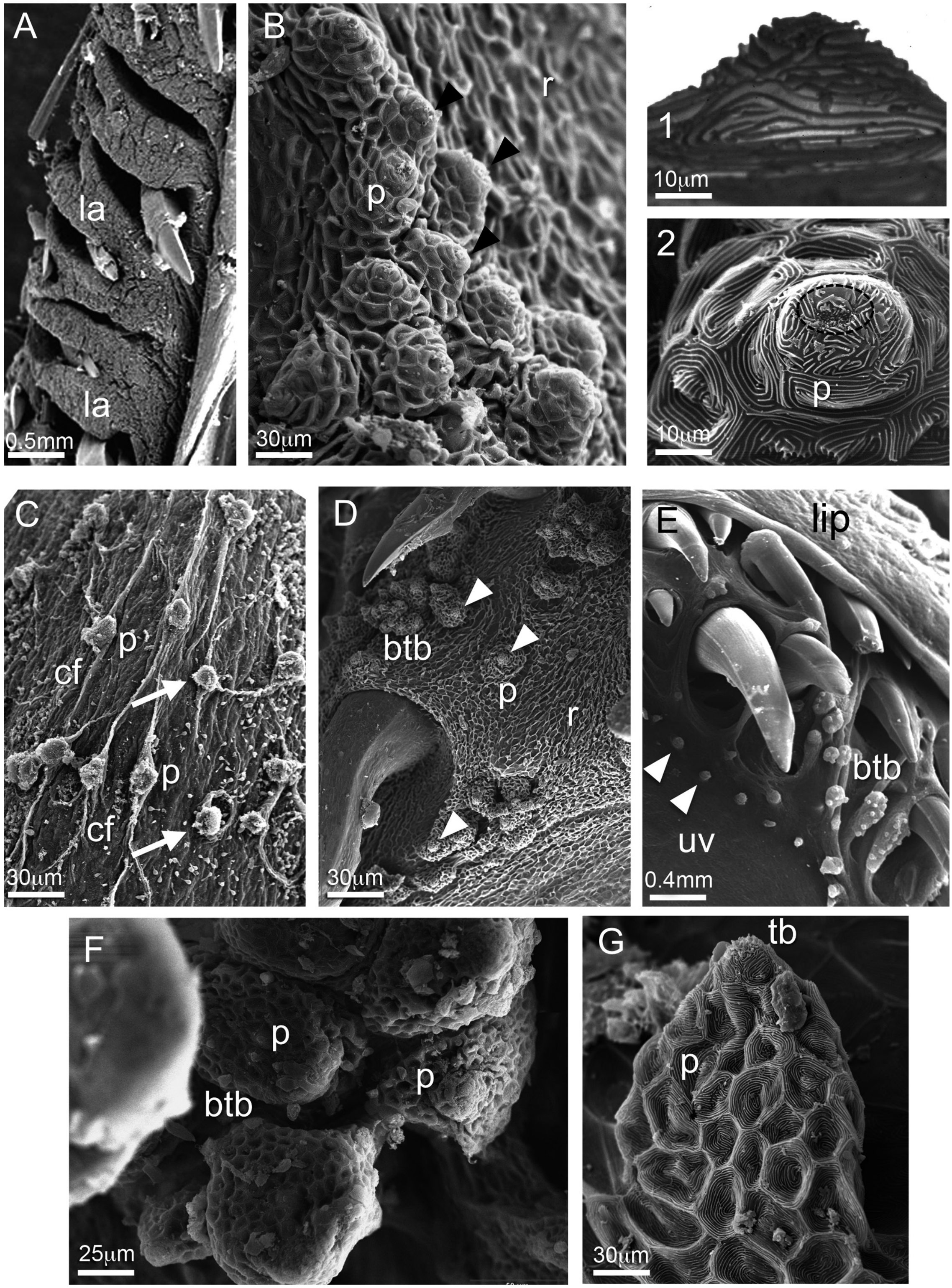


Figure 3. - **A**: Fragment of upper jaw of *Saurida macrolepis* with lamellae (la) between the teeth; **B**: Enlarged papillae (p) of the lamellae with taste buds (arrowheads) (detail 1: lateral aspect of TB; detail 2: papilla with TB); **C**: Network of delicate sub epithelial nerves (cf) connecting the taste buds in *S. macrolepis* (p and arrows, papillae); **D**: Single (arrowheads) and bundles (btb) of taste bud papillae (p) on jaws of *Synodus dermatogenys* (r, microridged surface epithelium); **E**: Single (arrowheads) and bundless (btb) of taste buds papillae on the upper jaw of *S. tumbil* (UV, upper breathing valve); **F**: Enlarged bundles (btb) of taste bud papillae (p) in *S. dermatogenys*; **G**: On the top of an enlarged papillae (p) with a taste bud (tb) in *S. tumbil*.

Table II. - Absolute number and site of distribution of TB in the oropharyngeal cavity of the largest specimens of the studied lizardfishes (SL in mm). UJ: upper jaw; UV: upper valve; PAL: palate; CB: last ceratobranchial; LJ: lower jaw; LV: lover valve; BAS: 3rd and 4th basibranchials; SA: calculated total sensory area of the TB.

| Species | SL | UJ | UV | PAL | CB | LJ | LV | BAS | TOTAL | SA $\mu m^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Saurida gracilis* | 180 | 600 | 0 | 40 | 40 | 580 | 0 | 45 | 1305 | 25,578 |
| *Saurida macrolepis* | 180 | 600 | 12 | 0 | 20 | 500 | 0 | 18 | 1150 | 22,540 |
| *Saurida tumbil* | 180 | 450 | 20 | 0 | 18 | 520 | 0 | 12 | 1020 | 19,992 |
| *Saurida dermatogenys* | 126 | 196 | 0 | 20 | 10 | 224 | 8 | 0 | 458 | 8,976 |
| *Saurida kaianus* | 202 | 440 | 0 | 70 | 18 | 340 | 10 | 0 | 878 | 17,230 |
| *Synodus saurus* | 140 | 400 | 40 | 80 | 14 | 450 | 18 | 14 | 1016 | 19,913 |
| *Synodus variegatus* | 120 | 820 | 30 | 160 | 12 | 680 | 28 | 8 | 1738 | 34,064 |
| *Trachinocephalus myops* | 175 | 300 | 12 | 26 | 34 | 300 | 0 | 44 | 716 | 14,033 |

*Synodus* spp. is provided by the two pores in the anterior part of the mouth-roof, in front of the upper valve and just below the nasal capsules.

**Taste bud form and distribution**

As in other teleosts (Yashipol *et al.*, 2006), in the studied lizardfishes too three types of TB can be observed: type I, situated on tall, protruding dermal papillae (see Fig. 3B); type II on smaller protrusions (see Fig. 4B-D); and type I, level with the surrounding oral epithelium (see Fig. 4E). In *Saurida* the most prominent TB in the anterior part of the oral cavity are formed by rows and groups of type I TB spaced apart on skin-lamellae along the maxilla and mandible. Each TB is situated on a papilla, 50-70 $\mu$m high, with protrusions of the chemosensory cells exposed at the TB apex (Fig. 3A, B, and details). TB diameter ranged between 3.0-5.0 $\mu$m, with each bearing on the surface 15-60 protrusions of various thicknesses. Removal of the surface epithelium exposed a delicate network of nerve-branches joining the neighboring TB (Fig. 3C). The number of inter-teeth lamellae and the configuration of TB on them varies among the species and genera of the lizardfishes (Fig. 3D, E), and correlates with the dimensions of the fish. In the largest *S. macrolepis,* 22 (± 4) lamellae were counted on either side of the upper and lower jaw, each with 6-15 TB, giving a total of circa 812-1230 TB on the frontal part of the oral cavity. In smaller specimens of this species there were fewer and smaller inter-teeth lamellae, with fewer TB. Table II provides data on TB numbers in fish of various dimensions of *S. macrolepis* and other species studied. In all the studied species additional TB were observed dispersed on the upper valve of the jaw and along the palate; and groups of small type III TB, 2.5-3.5 $\mu$m in diameter, were found between the basibranchial and ceratobranchial bones of the pharyngeal region.

*Synodus variegatus* and *S. saurus* typically featured 12-14 micro-bundles of TB, each bundle 8-10 $\mu$m in diameter, located at the bases of the upper and lower jaw teeth, with 5-12 TB in each bundle, on papillae 25-35 $\mu$m in height (Fig. 3F, G). The total number of TB in such groupings was circa 420 (± -30). Rows of 12-14 type I TB extend along the interior of the maxilla, mandible, and along the tongue, each raised on a protruding papilla, 120-140 $\mu$m in height (Fig. 4A); these TB were especially pronounced in *Trachinocephalus myops*. Lines of papillae with TB were also observed on either side of the *glossohyale* teeth-cushion. In both genera rows of TB are situated on epithelial longitudinal folds on the oral roof, extending into the pharyngeal region (Fig. 4B). A group of 22-24 type II TB situated at the rear of the two pores, close to the upper breathing valve is also characteristic for these fish (Fig. 4C), table II provides additional data on the number of TB in the oropharyngeal cavity of the studied species. In larger specimens of *Saurida* spp., over 190-230 mm SL, the number of observed TB seems to decrease concomitantly with increased growth of the teeth. *T. myops* typically features patches of papillae, 60-80 $\mu$m in diameter, situated in the pharyngeal part of the oral cavity, with each papilla supporting one or two type II TB (Fig. 4D). The epithelial cells surrounding the TB here, unlike in other regions, show petal-like formations (Fig. 4E). Also typical for this species are type III TB on the basibranchial ossicles of the 3rd and 4th gill arches, and on the 5th ceratobranchial ossicle.

## DISCUSSION AND CONCLUSION

Food-recognition in numerous fish species can occur on various sites of the skin and skin-appendages, though the main centre for gustatory perception is the mouth epithelium by means of TB distributed on various sites of the anterior and pharyngeal regions. Studies of TB in fishes have concentrated to date on freshwater fishes rather than on marine groups, and only a few works have focused on groups of species belonging to the same taxon (Livingston, 1987; Fishelson and Delarea, 2004; Fishelson *et al.*, 2004; Fishelson, 2009). Previous studies have reported that TB exist in several forms, some elevated on papillae (type I and II), and some level with the surrounding epithelium (type III)

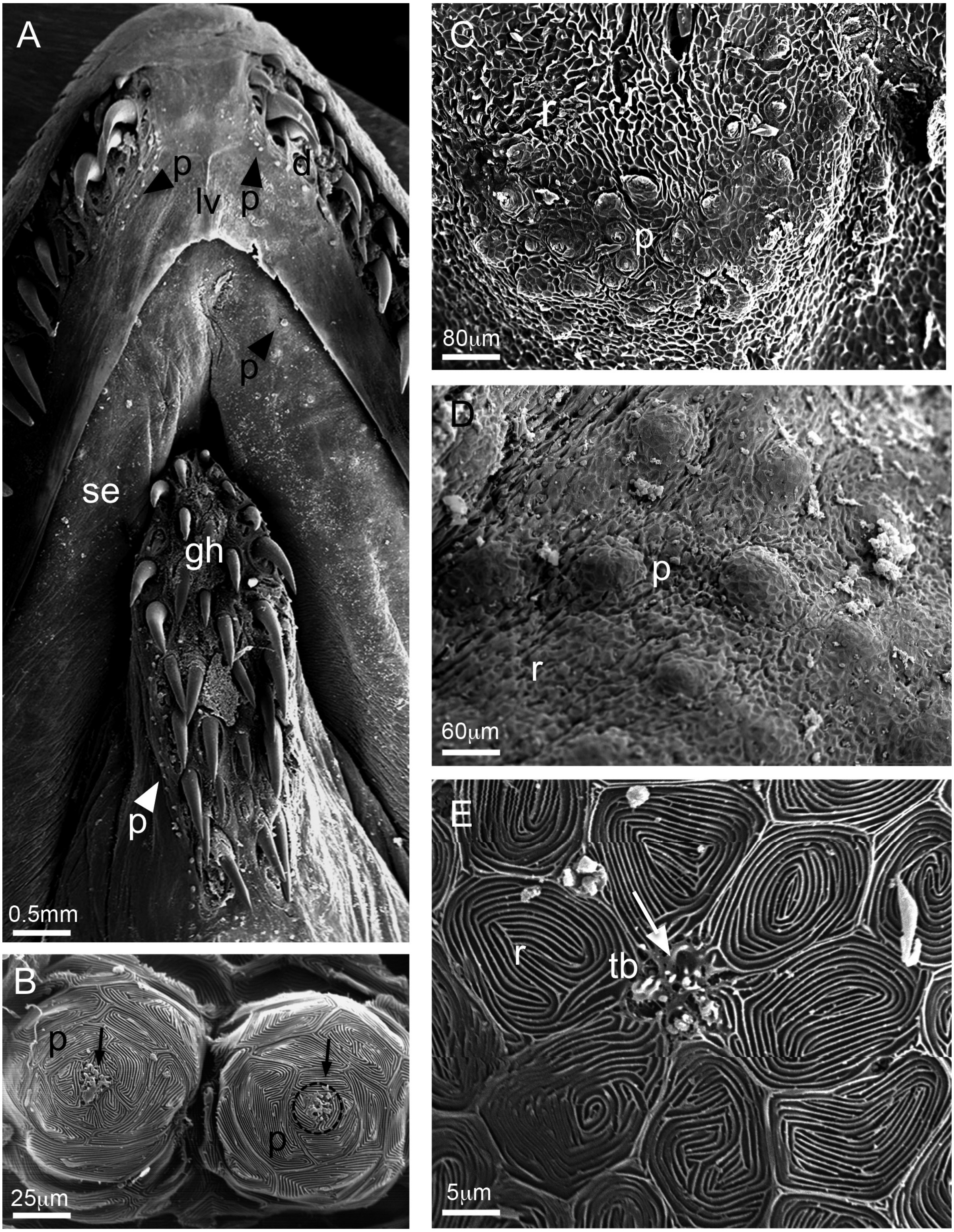


Figure 4. - **A**: The lower jaw of *Synodus variegatus* with papillae (p) and taste buds on the glossohyale (gh), the breathing valve (lv), and the oral surface epithelium (se); **B**: Protrusions (arrows) of the sensory cells of type II taste buds on the top of a papillae (p) on the longitudinal folds on the palate of *Trachinocephalus myops*; **C**: Groups of papillae (p) with taste buds type II on upper valve of *S. variegatus*, surrounded by microridges of epithelial cells; **D**: Groups of papillae (p) with type II taste buds in pharyngeal region of *T. myops* (r: microridges); **E**: Petal formation of ridged epithelial cells around a type III taste bud (tb) on the basibranchial bone of *S. saurus*.

(Fishelson and Delarea, 2004). The number of TB greatly differs among different species, as demonstrated by Fishelson and Delarea (2004) and Fishelson (2005a, 2005b) for gobies, cardinal fish and cichlids. The present study shows that, in the studied lizardfishes, the number of TB in the oral cavities increases with age (growth of the fish) until reaching a certain number typical for the particular species. Fishelson (2005a) has reported that in *Astatotilapia flaviijosefii* of 30 mm SL, 30 TB were observed in the oral cavity, whereas in fish of 120 mm SL, 1,400 TB were found. A similar phenomenon was found in the studied lizardfishes, as for example in *Saurida macrolepis*, in which the number rises from 400 in the oral cavity of 80 mm SL fish, to 1150 in a fish of 260 mm SL; as well as in the other studied species (see Tab. II). Interestingly, in larger specimens of the same species, of 190-230 mm SL, the total number of TB in the oral cavity declines. One possible reason for this is the increasing dimensions of the dense rows and patches of teeth, which, becoming more densely packed, may restrict the space for the epithelial lobules between them, limiting their sensory capability. Following the same line of argument, it is quite plausible that, with growth, a change in the fishes' diet takes place, from small benthic organisms that have been sorted out from other particles to larger free-swimming fish and crustaceans. This is corroborated by the stomach contents found (unpublished), which in larger lizardfishes predominantly revealed fish.

The total number of TB in the oral cavity of a fish may reach as high as 20,000, as in *Ictalurus natalis* (Atema, 1971), or 24,600, as in the cardinal fish, *Fowleria variegata* (Fishelson and Delarea, 2004). It is clear, however, that the final number of TB in the oral cavity is species-specific, as observed in cardinal fishes (Fishelson *et al.*, 2004) and demonstrated for the studied lizardfishes (Tab. II). This is also demonstrated by a comparison between various species of fish of similar body dimensions. For example, in *Saurida macrolepis* of circa 120 mm SL the number of TB in the oral cavity is circa 980; whereas in *Synodus variegatus* it is circa 1538. Such differences in the number of TB have also been observed in cichlid species; as for example, from 3,400 TB in *Labotropheus trewavasae* to 17,500 TB in *Tilapia zillii* (Fishelson, 2005a, 2005b), as well as in clinid fishes (Fishelson, 2009). If we consider that the number of oropharyngeal TB reflects the size of the sensory area, then this size can be calculated. For example, in *S. macrolepis* the total calculated sensory area of circa 1150 TB in the oral cavity will produce a sensory area of circa 22,540 $\mu m^2$. Data for the various species are given in table II. The smallest sensory area, 8,976 $\mu m^2$, was calculated for *Synodus dermatogenys*.

The other differential characteristic concerns the TB numbers on various sites of the oropharyngeal cavity (Tab. II). We found that in the studied lizardfishes the majority of TB is situated in the frontal, food-grasping part of the jaws, with differences in numbers between the various genera, and fewer TB in the posterior part of the oral cavity. These observed differences in the oropharyngeal cavity of the various fishes seem to reflect evolutionary trends, specifically focused on types of food gustation and consumption and, as stated (Fishelson, 2005a), they possibly also provide a tool for ecomorphological and phylogenetic studies. To understand the reason for such differences in the numbers of TB in the epithelium of the oral cavity of the various species in the different genera and families, we first need to know more about their diet and feeding behaviour.

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