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The olfactory organs of deep-sea fishes : their morphology and possible role in mate location

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THE OLFACTORY ORGANS OF DEEP-SEA FISHES: THEIR MORPHOLOGY AND POSSIBLE ROLE IN MATE LOCATION

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ABSTRACT

THE OLFACTORY ORGANS OF MESOPELAGIC FISHES: THEIR MORPHOLOGY AND POSSIBLE ROLE IN MATE LOCATION

by Melissa Ann Gibbs

The potential use of olfaction as an important sensory mechanism in mate location by mesopelagic (200-1200 m) fishes was explored. Scanning electron microscopy (SEM) was used to study the morphology of the olfactory system in Serrivomer sector, Bathylagus sp., Macropinna microstoma, Alepocephalus tenebrosus, Sagamichthys abei, Chauliodus sloani, Stomias boa boa, and Lycodapus mandibularis. The gross morphology and percent coverage of sensory epithelium of individual lamellae from the rosettes of both genders were examined, and sexual dimorphism was not found. However, after a review of other senses (vision, audition, mechanoreception, and electroreception) as possible mechanisms for long-distance (>20m) mate location, it was concluded that the most likely sense used for long-distance mate location in mesopelagic fishes was olfaction.

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INTRODUCTION

The average depth of the world's oceans is about 4000 meters (m), with the greatest depths exceeding 10,000 m. Yet, there is enough light for photosynthesis only to about 100 m, and biologically significant amounts of light penetrate at most only the upper 1000 meters in the clearest waters (Marshall, 1971; Denton and Warren, 1957) leaving the majority of the ocean's waters only dimly and occasionally illuminated by bioluminescent organisms. The question of how life can survive and propagate in the deep sea (below 200 m) without light has long been a puzzle to marine biologists, and only in the past few decades has the technology been developed to begin answering this question.

Because reproduction is paramount to a species' survival, an important question is how the relatively rare and widely-spaced fishes of the deep sea locate their mates. A review of the various sensory systems that fishes possess offered three potential mechanisms for long-distance mate location: vision, audition, and olfaction.

The presence of sex- and species-specific photophore patterns in some groups of deep-sea fishes has stimulated the hypothesis that bioluminescence might play a role in reproductive attraction (Marshall, 1966; 1979). In the deep sea, 98% of all fishes (individuals, not species) have

photophores or some other type of photogenic organ (Haneda and Johnson, 1962). However, according to MacDonald (1975), light produced by photophores would be intense enough only for relatively close identification (i.e. less than 16 m).

Another way of attracting a mate may be to produce low frequency sounds using the swimbladder as a drum. Rose (1961), Marshall (1966), and Mead et al. (1964) have shown that males of many species of benthic deep-sea fishes have well-developed drumming muscles in association with a gas-filled swimbladder. As the muscles contract, the swimbladder begins to vibrate, producing a sound with a fundamental frequency corresponding to the frequency of muscular contraction (Marshall, 1966). These males have well developed swimbladder drumming muscles and are able to attract females to their nests. Drumming muscles are also present in females, but are extremely reduced in size (Rose, 1961). Meso- (200-1200 m) and bathypelagic (1200-4000 m) fishes, however, have not been found to have swimbladder drumming muscles.

A third possible way of locating mates is olfaction. Bertelsen (1951) found that ceratioid anglerfishes (bathypelagic) exhibited extreme sexual dimorphism of the olfactory apparatus, and proposed that such a dimorphism, in which the male had a greatly enlarged olfactory organ, indicated that females might be secreting a species-specific

substance to attract mates. Gonostomatids (mostly bathypelagic), eurypharyngids (bathypelagic), nemichthyids (bathypelagic), and sternoptychids (mesopelagic) also have sexually dimorphic olfactory organs (Marshall, 1967; Gartner, 1983; Nielsen and Smith, 1978; Baird et al., 1990). In all of these groups, except for ceratioid anglerfish, sexual dimorphism of the olfactory organ develops as the male becomes reproductively mature, thus lending support to the idea that sexual dimorphism of the olfactory organ was tied to reproduction.

The goal of this study was to examine the mechanisms used for mate location in a broad range of mesopelagic fishes. After a review of the literature, the decision was made to focus on olfaction as the most powerful mechanism for long-distance mate location. Since Marshall (1967) examined olfactory sexual dimorphism in 6 orders of fishes, it has become generally accepted that deep-sea fish do exhibit olfactory sexual dimorphism, with the male having the larger olfactory organ (MacDonald, 1975). However, Marshall's (1967) conclusions that most bathypelagic fish species have sexually dimorphic olfactory organs may have been premature. Although he examined 20 species from 12 families for sexual dimorphism, he looked at both genders in only five bathypelagic species, four from the same family (Gonostomatidae), and one

mesopelagic species; also a gonostomatid (Table 1) (Marshall, 1967). Since then, sexual dimorphism of the olfactory organ has been found in eurypharyngids (Gartner, 1983), nemichthyids (Nielsen and Smith, 1983), and sternoptychids (Baird, 1990); and this dimorphism is assumed to be involved in mate location (MacDonald, 1975).

To test the generality of the proposition that olfaction is a significant factor for mate location in mesopelagic fishes, several aspects of the olfactory system were examined in a representative sample of 4 orders of midwater fishes. The olfactory organs of 10 species were described, the olfactory organs of 8 males and females of the same species were compared, and scanning electron microscopy was used to look for sexual dimorphism in the coverage of the olfactory rosettes by sensory epithelium within species.

In addition, a literature review and an examination of museum specimens were undertaken to assess whether sensory mechanisms other than olfaction might be potentially important for mate location in the deep sea. These included vision (differences in eye size and/or photophore patterns) and sound production (swimbladder musculature).

METHODS

A number of criteria governed the selection of species for this study. Fishes were selected from 8 pelagic families that live in the mesopelagic zone (Fitch and Lavenberg, 1968; Miller and Lea, 1972; Whitehead et al., 1986), and included the Serrivomeridae, Bathylagidae, Opisthoproctidae, Alepocephalidae, Platytroctidae, Chauliodontidae, Stomiidae, and Zoarcidae. Fishes whose maximum size was under 75 mm were not considered because of difficulties inherent with dissecting small specimens. The specimens had to be mature adults, both to ensure correct identification and that all developmental changes had taken place. Maturity of each individual was assessed by an examination of the gonads, and only those specimens possessing distinct ovaries or testes were used.

To obtain a sample of the selected families, the type species was selected of each type genus in the aforementioned families; when types were not available, a similar species was chosen. The species used in this study were: Serrivomer sector, Bathylagus sp. c.f. antarcticus, Macropinna microstoma, Alepocephalus tenebrosus, Sagamichthys abei, Chauliodus sloani, Stomias boa boa, and Lycodapus mandibularis (Table 2, Fig. 1). Because specimens were difficult to obtain, examinations of sensory and indifferent epithelia were

not made for Chauliodus sloani and Sagamichthys abei. Upon preliminary examination of the rosette of Lycodapus mandibularis, it was noted that its morphology was considerably deviant from the rosettes of the other seven species in this study. To determine whether this morphology was unique to this pelagic species, or merely to zoarcids in general, rosettes of two other zoarcids (Melanostigma pammelas [pelagic] and Lycodes diapterus [benthic]) were also examined.

A number of limitations were placed on this study by circumstance and museum policy. It was difficult to find mature specimens of some species and mature males were rare in all species used in this study. Additionally, museum policy often did not allow dissection of single-specimen lots, which, due to the scarcity of deep-sea fishes, were very common. Many specimens had been damaged during preservation, or were damaged during preparation for viewing in the SEM.

The museum specimens had generally been fixed in formaldehyde and stored in 70% ethyl alcohol (ETOH) (Cailliet et al., 1986). One olfactory rosette was removed from each specimen; later, individual lamellae were dissected from the rosettes. One whole rosette, along with several lamellae from each species, were dehydrated in 100% ETOH. The specimens were dried in hexamethyldisalazane, mounted with a graphite colloid, and coated with gold in preparation for viewing in

the SEM (Goldstein et al., 1981).

The olfactory organ of a teleost fish is located in the nasal pit on the anterodorsal side of the head (Fig. 2). Generally, water enters through the anterior naris (AN) and exits through the posterior naris (PN), having passed through a series of sensory epithelial folds (lamellae), collectively termed the nasal rosette. The olfactory epithelium is composed of two kinds of cells: indifferent (IE) and sensory (SE). The indifferent component usually constitutes the smallest part of the lamellar surface, and is distinguished by having virtually no cilia. The sensory zone, which lies adjacent to the midline raphe of the rosette, is covered with a thick mat of cilia (Zeiske et al., 1976).

Since the number of folds (lamellae) in most fishes changes as size increases (Kleerekoper, 1969), comparisons of number of lamellae per rosette were not made between genders. However, the epithelium was examined for differences in the relative densities of olfactory receptor cells between sexes (see Zeiske et al., 1976; Caprio and Raderman-Little, 1978). Lamellae from the anterior, central, and posterior areas of a rosette from each species were examined to see if any consistent regional differences in ratios of sensory and indifferent epithelia existed. Although no visible regional differences were found, care was taken when making

comparisons, to look at lamellae from the same place on each rosette. Anterior- and posterior-facing sides of lamellae were also compared, but there were no visible differences between the two sides. A photograph was taken of each dissected lamella, and zones of sensory and indifferent epithelium were designated after Zeiske et al. (1976).

The surface of one side of each lamella was examined, and areas containing either sensory or indifferent epithelium were separately measured using an Olympus C-2 Image Analyzer (version 1.7). A photographic image of each lamella was viewed through an Olympus SZH microscope by a camera attached to the microscope's optical tube. The image was then transmitted to an IBM personal computer for analysis and was also displayed on a SONY camera monitor. Analysis began by acquiring the image into the program. The outlines of the areas of indifferent and sensory epithelia were then defined with an optical mouse, at which point the program computed a "figure area." Nine lamellae had been distorted by the drying process and therefore could not be examined with the Image Analyzer, which requires a flat surface. For the distorted lamellae, a rough estimate of percent area of coverage by both sensory and indifferent epithelia was made by eye and compared qualitatively to areas figured by the Image Analyzer. A whole rosette from each species was also examined and described.

Because of the small sample size, statistical analyses of the differences between genders of percent coverage of sensory epithelia were not carried out. However, as only small differences were found, even if these differences had been statistically significant, it is unlikely that they could have been functionally significant.

While at the museums, eyes were examined for overt differences in size between genders. Because of a study by Macdonald (1975), which showed that light from large photophores and light secreting organs was only visible up to 16 m away, photophores were not counted, instead each species was examined for sexual dimorphism in large photophores (i.e. the suborbital photophores of Diaphus diadematus [Marshall, 1966]).

Specimens were examined for presence of swimbladders and associated drumming muscles. Marshall's (1960) monograph on swimbladders of deep-sea fishes was also consulted for more details.

RESULTS

Description of Olfactory Rosettes

In general, the olfactory rosettes were oriented rostro-caudally in a shallow cup, lateral to the ethmoid and its articulation with the palatine and lacrimal bones (Burne 1909). The lamellae, which together comprised the rosette, were oriented perpendicular to water flow, and clustered around a midline raphe, at which point the rosette was attached to the floor of the olfactory cup (Fig. 2b). The smallest lamellae were at the anterior end of the rosette and became progressively larger posteriorly (Fig. 2c). The unciliated, or indifferent zone tended to be along the edges of each lamella, and was clearly separated from the sensory zone by a groove or change in surface topography (e.g. Figs. 5c, 6c, and 7c).

Males and females were examined in five species, but no differences in the structure or size of the olfactory organ between males and females were found (Table 3). In general, these olfactory chambers were covered with a very thin layer of skin, through which the rosettes were often visible.

Serrivomer sector

This species had a rosette which was just a rippled piece of epithelium (Fig. 3). The lamellae were not separate as in the other species, but were more like pinches in the

epithelium (Fig. 3b). There was no sharp demarcation between sensory and indifferent zones, but there were definite areas where higher concentrations of sensory cells existed. There were even some cilia on the floor of the chamber (Fig. 3). The average percent coverage of sensory epithelia was 48.5% for females (Table 4). No males were available due to a lack of specimens.

Bathylagus sp. c.f. antarcticus

The rosette of Bathylagus was roughly circular with 26 lamellae surrounding a narrow midline raphe (Fig. 4a). The lamellae were oriented perpendicular to the raphe except at the posterior end where they were oriented radially. The lamellae were roughly triangular in shape, and stood on edge. The indifferent component appeared to occupy a large amount of surface area on the ventral portion of the rosette, curving up to the lateral tip (Fig. 4b). However, the remainder of the unciliated zone was punctuated by small round islets of sensory epithelium (Figs. 4c,d). The unciliated zone was covered with tiny pores in a honeycomb pattern (Fig. 4e). The average percent coverage of sensory epithelia for females was 64.3% (Table 4). No males were available due to loss of rosettes and lamellae during preparation.

Macropinna microstoma

The rosette of Macropinna was circular and dorso-ventrally

tall. The 28 lamellae were arranged perpendicularly along the "lollipop-shaped" midline raphe. The head of the raphe (the circular portion) was located at the posterior end of the rosette (Fig. 5a). The lamellae were long and curved in a fashion that made a cup-shaped rosette. The indifferent epithelium was lumpy with large (~10 μm) pores sunk into it and was found on all edges of the lamellae (Fig. 5c). There were a few small sensory islets in this zone. The sensory zone was not highly ciliated and had a lattice-work of pores covering it (Fig. 5c). The average percent coverage of sensory epithelia was 83.0% for females and 86.0% for males (Table 4).

Alepocephalus tenebrosus

This species had a rosette which was flat with 18 semi-overlapping, curved, lamellae. The lamellae were not only connected to the midline raphe like the other species, but also to the floor of the olfactory chamber by thin membranes (Fig. 6a). The lamellae were L-shaped with the indifferent component on the ventral portion of the lamella. The cilia were most highly concentrated in the middle of each lamella and diminished towards the ventral and dorsal edges. Lamellae were perpendicular to a narrow midline raphe, except at the posterior end where the angle became more acute. The sensory epithelium was very bumpy at high magnification; each bump

being covered with small pores about 1 μm in diameter (Fig. 6d). Also scattered near the indifferent zone were large cellular aggregates made up of 15-20 cells (~ 20-25 um) (Fig. 6c). The average percent coverage of sensory epithelia was 85.0% for females and 94.3% for males (Table 4).

Sagamichthys abei

Twelve lamellae stood up from the floor of the rosette of this species. There was no midline raphe. The rosette was oval in shape with lamellae oriented perpendicular to the floor of the rosette. (Fig. 7). Average percent coverage of sensory epithelia was not determined due to a lack of specimens.

Chauliodus sloani

The rosette was composed of 12 lamellae radiating from a small off-center hub, instead of a raphe, at the anterior end of the rosette. The lamellae were ovoid, tapering to long stalks that attached to the center piece. (Fig. 8). Average percent coverage of sensory epithelia was not determined due to a lack of specimens.

Stomias boa boa

The rosette was roughly oval with 14 evenly spaced lamellae radiating semi-perpendicularly from the thick midline raphe (Fig. 9). The lamellae were long and relatively straight, although those at the posterior of the rosette were more L-

shaped. Most of each lamella was covered with ciliated sensory epithelia (Fig. 9b). The indifferent, unciliated portion was restricted to the ventral and extra-lateral edges. Except for those at the anterior of the rosette, which were on edge, lamellae tended to lie at an acute angle, slightly overlapping. Average percent coverage of sensory epithelia was 85.0% for females and 84.0% for males (Table 4).

Lycodapus mandibularis

The rosette was unusual in that there was no midline raphe, and only three lamellae oriented parallel to water flow (fig. 10). The lamellae were "half-moon" shaped and attached to the floor of the olfactory chamber on a straight line. The indifferent component was on the entire outer edge of each lamella (fig. 10b). The rosette was not visible on external examination of the fish, being covered with a thick pad of tissue. Average percent coverage of sensory epithelia was 88.8% for females and 87.0% for males (Table 4).

Lycodes diapterus and Melanostigma pammelas

As in Lycodapus, the rosettes for both Lycodes and Melanostigma had no midline raphe. The three lamellae were oriented parallel to water flow, and the rosette was shaped like a trident, with the curved base at the anterior end. As these two species were examined solely for the purpose of

rosette morphology comparison with Lycodapus, sensory and indifferent epithelia were not examined for them.

DISCUSSION

Marshall's Results in Comparison to This Study

The reasons for differences between this study and Marshall's may be sample size and the differences in definitions of depth zones. In 1967, Marshall found that the olfactory organs of male bathypelagic fishes were much larger than those of females and interpreted this as an adaptation for mate location. However, he also included in his study both mesopelagic (200-1200 m) and benthic (bottom dwelling) species, which differ morphologically and physiologically from truly bathypelagic (1200-4000 m) species (Marshall, 1967; Moyle and Cech, 1988). When Marshall's (1967) species are carefully scrutinized, only six bathypelagic species, for which both genders were examined, remain. Of these, four exhibited sexual dimorphism of the olfactory organ, while two did not (Table 1). Certainly the majority of bathypelagic species in Marshall's (1967) entire study exhibited sexual dimorphism of the olfactory organ, but four species are insufficient to generalize for all of the bathypelagic species in the world's deep-sea environment.

Rosette Morphology

There was a variety in the development and morphology of the olfactory organs that did not appear to be related to the depth of occurrence or known feeding habits. The present

study included ten species whose ranges encompassed the mesopelagic zone; both genders were examined in five of those species. Sexual dimorphism in size of the olfactory organ and percent coverage of olfactory sensory epithelium were not found in the species examined in this study (Table 3). Feeding preferences did not appear to affect rosette morphology. The four invertebrate feeders (Bathylagus, Macropinna, Alepocephalus, and Lycodapus) all have olfactory organs of differing complexity as do the fish-eaters (Serrivomer, Sagamichthys, Chauliodus, and Stomias) (Collard, 1970; Gorelova and Kobylyanikiy, 1985; Mauchline and Gordon, 1983; Clarke, 1982).

The structure of the olfactory rosettes of the species in this study may be related to their phylogenetic order. The morphology of the olfactory rosettes of Serrivomer sector (Elopomorpha: Anguilliformes); Bathylagus sp., Macropinna microstoma, Alepocephalus tenebrosus, and Sagamichthys abei, (Euteleostei: Salmoniformes); and Stomias boa boa, and Chauliodus sloani, (Euteleostei: Stomiiformes) were typical for lower (primitive) teleosts (Burne, 1909; Hinegardner and Rosen, 1972; Greenwood, et al., 1966; Lauder and Liem, 1983). The vastly different rosette structures of Lycodapus mandibularis, Lycodes diapterus, and Melanostigma pammelas, (Acanthopterygii: Perciformes) may reflect the highly evolved

state of their taxonomic grouping (Burne, 1909; Greenwood et al., 1966).

Also, there were noticeable differences in the morphology of the rosette within the Euteleosteans from this study. The number of lamellae per rosette ranged from 12-28. The shape of the rosettes ranged from flat to very curved. The midline raphe was variously a thin line (e.g. A. tenebrosus), a circular hub (C. sloani), "lollipop-shaped" (M. microstoma), and a flat plate (e.g. S. abei). Additionally, four of these species (two pairs), A. tenebrosus and S. abei, and S. boa boa and C. sloani, are closely related phylogenetically, very similar in external appearance, within pairs, yet had very different olfactory rosettes. These differences suggest that the evolution of the olfactory rosette in these deep-sea fishes has not been consistent. However, some variation from the typical shallow-water teleost model of the rosette in deep-sea fishes should not be suprising, considering the many morphological and physiological adaptations that these fishes have evolved to survive in the deep-sea (Marshall, 1971).

It is likely that the current patterns of sensory and indifferent epithelia on lamellae function so well that there is little need for change, thus the same patterns are seen in fishes from a variety of environments and evolutionary states. According to Kleerekoper (1969), the olfactory epithelium was

originally (evolutionarily) composed entirely of sensory epithelium, but gradually changed to the point where indifferent epithelia was found on the outer edges of the rosette. The development of indifferent epithelium may be a result of the water flow dynamics in the olfactory chamber. There would be greater turbulence closer to the walls of the chamber, interfering with the passage of particles through the olfactory rosette and reducing olfactory precision (Sears et al., 1982). With sensory epithelia restricted to the center of the rosette where water flow is smoothest (least amount of turbulence), particles trapped in eddies near the olfactory chamber walls would no longer be detected, and olfaction would be much more precise. The orientation of lamellae in the zoarcids may have evolved as a way to reduce turbulence in the olfactory chamber.

MATE LOCATION

A greater number of males would enhance the probability of all mature females coming into contact with a mature male. However, in the course of gathering specimens for this study, mature males were extremely difficult to find. Midwater trawls (using a 3 m2 Tucker Trawl for 1 hr @ 1 knot) taken in Monterey Bay through the Deep Scattering Layer), have produced density estimates of one fish every 20 m. However, densities of mesopelagic fishes outside of the DSL would be considerably

lower. Because of the low densities of fishes in the deep sea, it might be advantageous to the survival of a species to have a higher proportion of males than females. The apparent differences in numbers of mature males and females could be a result of the fact that males become reproductively mature faster than females or that males mate more than once. A histological study of the gonads of immature fish might shed more light on the question of male/female ratios by revealing the male/female ratio of the immature pool.

Mate location is facilitated by a number of sensory mechanisms functioning over a wide range of distances: mechanoreception (lateral line), electroreception, vision, sound, and olfaction. Additionally, there may be other, non-sensory mechanisms that bring fishes close enough together to use their senses. These sensory mechanisms often require special accessory organs. The mechanisms which might be used for long distance mate location will be discussed in the order of their range of influence, from near- to far-field.

Mechanoreception

Near-field sound (a combination of propagated and displacement waves), such as the waves produced by swimbladder drumming, is usually detected by the lateral-line system (van Bergeijk, 1963; Harris et al., 1962). Locating the source of a displacement wave is possible because of the many separate

receptors (neuromasts) that comprise the lateral line. Stimulation of these neuromasts creates a pattern of nerve impulses that indicate the directionality of the displacement wave (van Bergeijk, 1963; Moyle and Cech, 1988). However, Tavolga (1963) suggested that the near-field range for mechanoreceoption in most fishes is within 15-20 m, thus reducing the possibility of mechanoreception being a viable mechanism for long-distance mate location by mesopelagic fishes.

Electroreception

Although electroreception has not been determined to play a role in reproductive behavior, some electroreceptive fishes are able to communicate with each other using electricity (Bleckmann, 1986). Electric currents are generated by membrane, gill, and action potentials as well as from body movement (Bullock, 1973). The detection of these currents by fishes occurs primarily through external pit organs such as the Ampullae of Lorenzini, which elasmobranchs use to locate prey items (Moyle and Cech, 1988; Kalmijn, 1971). However, the only teleosts known to have pit organ electroreceptors are the Siluriformes, Gymnotidae, and Mormyridae (Marshall, 1966). Therefore, since pit organs rarely occur in teleostean fishes, and because electroreception is only effective over short distances (Moyle and Cech, 1988), it is unlikely that

electroreception could be used for long-distance mate location in the mesopelagic zone.

Vision

In general, mesopelagic fishes have large, well-developed eyes and are thought to be able to detect daylight at depths in excess of 1000 m (MacDonald, 1975; Marshall, 1971). The pupil tends to be large, occasionally exceeding the diameter of the lens, and the resulting aphakic space is thought to maximize the amount of light entering the eye to act on the retina. Because the retinae of mesopelagic fishes have very high densities of the photosensitive pigment rhodopsin, deep-sea fishes are some 15-20 times more sensitive to light than humans (Denton and Warren, 1957; Marshall, 1971; Walls, 1963).

However, according to MacDonald (1975), light produced by photophores would only be intense enough for relatively close identification. Using bathyphotometers deemed to be slightly less sensitive than the eyes of deep-sea fishes, MacDonald (1975) and Mensinger and Case (1990) have shown that light from photophores and light secreting organs (e.g. the shoulder organ of Sagamichthys schnakenbecki and the suborbital organ of Malacosteus niger) could not be detected more than 16 m away. Therefore, while photophores might be excellent aids for close-up species recognition, it is unlikely that they could be used as the initial long-distance attractant for

potential mates.

Audition

There are three types of sound production in fishes: stridulatory mechanisms (pharyngeal teeth, fin ray clicking, gnashing teeth) with a range of ~1000-4000 cycles per second (cps); hydrodynamic or swimming sounds (~100-500 cps); and swimbladder mechanisms (~75-100 cps) (Tavolga, 1963). The usual range of sensitivity of the teleostean inner ear is 1000-4000 cps. Thus, even though swimbladder generated sounds can be as high as 500 cps in a few highly specialized fishes (toadfish, [Tavolga, 1960], searobins [Fish, 1954], and gaff-top-catfish, [Tavolga, 1960; 1962]), only stridulatory sounds would regularly be perceived by the inner ear.

Using the inner ear, fish can detect high frequency sound. However, because the inner ear is a single receptor (the proximity of the two receptors rend them essentially as one receptor), the sound is perceived to be non-directional; there is a 180° ambiguity (van Bergjeik, 1963; de Munck and Schellert, 1987; Schellart and de Munck, 1987). According to de Munck and Schellert (1987) the displacement wave created by such a high-frequency sound source is a longitudinal phenomenon, and as such, "two [sound] sources at opposite directions from the fish position will produce identical displacement fields and, therefore, without other cues, these

two sources cannot be discriminated; this is called the 180° ambiguity."

The swimbladder can provide a second cue to localize the sound source. Sound waves impinging on the swimbladder are slowed down as they pass through the less dense gases, and are thus transmitted to the inner ear out of phase with the direct wave (that which impinged only on the inner ear). By determining the phase difference between the direct and indirect waves, the fish is able to determine the directionality of the sound (Schuijf, 1975; Schellert and de Munck, 1987). Van Bergeijk (1964) does not believe that fish would be able to locate the sound source by swimming up a "sound gradient." Therefore, fishes without swimbladders either cannot detect the sound direction or have some other ambiguity eliminator (Schuijf, 1975). However, few mesopelagic fishes possess swimbladders, and many of those that have been found are fat-filled or degenerate (Marshall, 1960) and would be unlikely sound amplifiers. Additionaly, swimbladder drumming muscles have not been reported in midwater fishes (Marshall, 1960); thus it is unlikely that sound production/reception could be used for long-distance mate location.

Olfaction

Olfaction plays an important role in the activities of

fishes, ranging from their anadromous migrations (Fisknes and Doving, 1982) to secretion and detection of fright substances in schooling fish (von Frisch, 1938). Fish are known to possess acute senses of smell; for example, some eels are able to detect substances (e.g. ß-phenylethyl alcohol) at concentrations as low as 3.5 x 10-19 M (Hara, 1971). The olfactory organs of fish can also be very discriminatory; Goz (1941) revealed that the dace, Phoxinus phoxinus, could not only distinguish between the odor of its own species and another genus, but also between various species of a different genus. Goz was eventually able to condition an individual Phoxinus to distinguish 14 different genera of fishes by scent.

The lack of sexual dimorphism of the olfactory organs in the species in this study does not rule out olfaction as a major sensory mechanism in mate location. It is possible that both sexes use chemoreception to detect each other's scent or that the olfactory organ is capable of detecting a pheromone without any increase in size. Pheromones could be secreted through the skin, special glands, or from body orifices (Saglio and Le Martret, 1982; Adams et al., 1987; Capron de Caprona, 1976; Weitzman and Fink, 1985). Diffusion of these substances into the water column would be primarily in the horizontal plane (Wiegel, 1965). Based on a diffusivity

coefficient (Wiegel, 1965), a substance could travel 1 kilometer (km) in 2-5 days depending on current speed. Presumably, pheromones would be released continuously by reproductively mature fishes, thus allowing a potential mate time to locate the secreting individual.

The current literature suggests that fishes can be excited by fluids from the genital areas of the opposite sex, even though sexual dimorphism in olfactory organ size does not necessarily occur (Resink, et al. 1987; Tavolga, 1955; Losey, 1969; Sorensen et al., 1988, 1990; Quinn, 1980b; Kitamura and Ogata, 1989). Thus olfactory differences between genders, if any, could be in the ability to recognize specific compounds and be excited by them, rather than in differences in size or amounts of sensory epithelia.

Seasonal Cues

Mesopelagic fishes could reduce the distance between their potential mates by migrating to specific mating grounds. Timing of migrations could be triggered by seasonal changes in such features as falling detritus or tidal currents and pressures. Migratory orientation could also be controlled by changes in the earth's magnetic field. For deep-sea organisms to be able to detect seasonal changes in falling detritus, it must first be determined that significant differences in amounts of falling detritus occur. Deuser et al. (1981)

revealed seasonality in deep-sea particle flux in the Sargasso Sea, where sediment traps were set at 3200 m, 1000 m above the bottom. Samples recovered every two months showed seasonal fluctuations in biogenic carbonate and silicate, and in organic matter that appeared to be closely tied to primary productivity cycles in surface waters. Lampitt (1985) provided photographic evidence of the changes in amounts of detritus on the sea floor of the Porcupine Seabight at depths exceeding 4000 m. Thus, fishes that breed seasonally would only need to be able to detect stimuli, such as these variations in falling detritus, to know when to start looking for a mate or migrate to breeding grounds.

Other possible seasonal cues for deep-sea fishes are tides. Guennegan and Rannou (1979) reported a periodic attraction of benthic fishes to a baited trap (at between 2000 and 4700 m) that was correlated with semi-diurnal tidal currents in the Bay of Biscay. Fishes tended to be near the traps during high tide and absent during low tide.

Tides also cycle on a yearly basis, with greatest spring tides in January and June, when the sun is at its perigee and apogee (in the northern hemisphere)(U.S. Dept. of Commerce, 1990; Strahler, 1971). Also, tidal currents increase with tidal height (U.S. Dept. of Commerce, 1988). Thus, if some iteroparous species gathers at a specific site to reproduce,

a seasonal signal like the tidal current could let them know when to congregate.

Deep-sea fishes may migrate, or move to specific mating grounds using navigational cues such as the earth's magnetic field. Some shallow-water fishes have magnetite in their bodies in significant enough amounts to act as a compass (a magnetoreceptor) in aid of navigation. Rommell and McCleave (1972) showed that American eels (Anquilla rostrata) are sensitive to electric fields of 0.167 x 10-2 microampere per square centimeter, which are on the order of the earth's magnetic field. Catch and release experiments were carried out with intact Anquilla anquilla and also after removing the olfactory organ. The results suggested that these fish could be using magnetic fields to navigate when migrating to and from the Sargasso Sea where they reproduce. (Tesch, 1967; 1970; Deelder and Tesch, 1970). Quinn (1980a), testing for magnetic compass orientation in lake-migrating Sockeye salmon fry (Oncorhynchus nerka), found that the fish moved in the compass direction they would normally move in to migrate up-lake. When a 90° shift was made in the horizontal component of the earth's magnetic field (in the lab), the salmon fry made a corresponding 90° shift in their direction of movement. Therefore, deep-sea fish could also utilize the earth's magnetic fields to navigate towards a breeding ground.

CONCLUSION

Because of the importance of olfaction in so many aspects of fish life, its usefulness over great distances, and the sensitivity of the fish olfactory organ, it would not be unreasonable to expect olfaction to be a valuable tool in long-distance mate location in deep-sea fishes. Of the five sensory mechanisms explored in this study, olfaction appears to be the only sense that could be used for long distance (over 20 m) mate location. In situations where individuals are separated by even greater distances, navigation by magnetic fields or seasonal migrations could bring fishes close enough to where sensory systems could be used.

Neither the current study nor Marshall's (1967) study are conclusive regarding the commoness of sexual dimorphism of the olfactory organs of deep-sea fishes. However, such olfactory sexual dimorphism appears not to be an isolated phenomenon and, when it occurs, it is likely to be involved in mate location. The use of olfaction in deep-sea mate location, however, does not require sexual dimorphism of the olfactory organ. Before final answers to questions regarding the role of olfaction in long-distance mate location in the deep sea can be achieved, a comprehensive survey of the olfactory organs of deep-sea fishes along with experimental studies of live animals, need to be carried out.

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Table 1.-Marshall (1967) data.

Species	Male	Female	Depth	Rosette Dimorph.
Clupeiformes				
Gonostomatidae				
Gonostoma bathyphilum	Y	Y	B	Y
Gonostoma elongatum	Y	Y	M	N
Cyclothone braueri	Y	Y	M	Y
Cyclothone pallida	Y	Y	B	Y
Cyclothone livida	Y	Y	B	Y
Cyclothone acclinidens	Y	Y	B	Y
Saccopharyngiformes				
Saccopharyngidae				
Saccopharynx sp.	N	Y	B	N
Eurypharyngidae				
Eurypharynx pelecanoides	N	Y	B	N
Anguilliformes				
Serrivomeridae				
Serrivomer beanii	Y	Y	B	N
Nemichthyidae				
Avocettina infans	Y	Y	B	N
Cyemidae				
Cyema atrum	N	Y	B	N
Gadiformes				
Macrouridae				
Cynomacrurus piriei	Y	Y	Bn	N
Odontomacrurus murryi	Y	Y	Bn	N
Squalogadus modificiatus	Y	Y	Bn	N
Perciformes				
Ophidiidae				
Aphyonus gelatinosus	N	Y	Bn	N
Lophiiformes				
Lophiidae				
Lophius sp.	N	Y	B	"Y"
Melanocetidae				
Melanocetus murrayi	N	Y	B	"Y"
Himantolophidae				
Himantolophus groenlandicus	N	Y	B	"Y"
Oneirodidae				
Oneirodes sp.	Y	N	B	"Y"
Lynophrynidae				
Linophryne macrorhinus	Y	N	B	"Y"

Y = Yes Examined, N = Not examined; B = Bathypelagic, M = Mesopelagic, Bn = Benthic; "Y" = Sexual dimorphism said to exist, but only one gender examined for species; N/A = Not examined for this study.

Table 2.-Source data of specimens used in this study.

Species	Sex	Museum	Acc. No.	Collection site	Depth Range	Std. Length
Anguilliformes						
Congroidei						
Serrivomeridae						
Serrivomer sector	F	USNM	271947	North Pacific	>1000 m	572-650 mm
"	F	USNM	271918	North Pacific		
Salmoniformes						
Argentinoidei						
Bathylagidae						
Bathylagus sp.	F	LACM	n. av.	Antarctic	>1000 m	122-182 mm
"	F	LACM	11700-4	Antarctic		
"	F	LACM	11770-5	Antarctic		
"	F	LACM	11770-5	Antarctic		
"	F	LACM	10402-13	Antarctic		
"	F	USNM	n. av.	South Atlantic		
Opisthoproctidae						
Macropinna microstoma	F	LACM	9575-35	CA; Catalina Basin	300-800 m	112-150 mm
"	F	LACM	9581-20	CA; Offshore		
"	F	LACM	9581-20	CA; Offshore		
"	M	SIO	88-63	CA; off San Diego		
"	M	SIO	88-54	CA; off San Diego		
"	M	LACM	9859-17	San Clemente Basin		
Alepocephalidae						
Alepocephalus tenebrosus	M	SIO	n. av.	Mexico; Gulf of CA	500-6000 m	204-380 mm
"	F	SIO	62-208	Northern Oregon		
Platytroctidae						
Sagamichthys abei	M	LACM	35507	Guadeloupe Island	200-1000 m	220 mm
Stomiiformes						
Chauliodontidae						
Chauliodus sloani	F	USNM	208486	West. South Atlantic	500-3000 m	265-275 mm
Stomiidae						
Stomias boa boa	F	USNM	221021	South Atlantic	>1000 m	153-340 mm
"	M	LACM	10974	Antarctic		
"	M	LACM	n. av.	Antarctic		
Perciformes						
Zoarcoidei						
Zoarcidae						
Lycodapus mandibularis	M	MLML	MW-159	CA; Monterey Bay	60-600 m	112-150 mm
"	F	MLML	MW-160	CA; Monterey Bay		

Acc. No. = Accession Number; F = Female, M = Male; USNM = United States National Museum, LACM = Los Angeles County Museum, SIO = Scripps Institute of Oceanography, MLML = Moss Landing Marine Laboratories; n.av. = data not available.

Table 3.-Results of this study.

Species	Male	Female	Depth	Rosette Dimorph.	Lamella Dimorph.
Anguilliformes					
Serrivomeridae					
Serrivomer sector	N	Y	B	?	?
Salmoniformes					
Bathylagidae					
Bathylagus sp.	Y	Y	M	ND	ND
Opisthoproctidae					
Macropinna microstoma	Y	Y	M	ND	ND
Alepocephalidae					
Alepocephalus tenebrosus	Y	Y	B	ND	ND
Platytroctidae					
Sagamichthys abei	Y	N	M	?	?
Stomiiformes					
Chauliodontidae					
Chauliodus sloani	N	Y	M	?	?
Stomiidae					
Stomias boa boa	Y	Y	M	ND	ND
Perciformes					
Zoarcidae					
Lycodapus manadibularis	Y	Y	M	ND	ND

N = Not examined, Y = Examined; B = Bathypelagic, M = Mesopelagic;
ND = No dimorphism, ? = Not enough data.

Table 4.-Percent coverage of lamellae (in this study) by sensory epithelia.

Species		Female	Male
Serrivomeridae			
Serrivomer sector		43.0%	-----
		54.0%	-----
	M =	48.5%	-----
Bathylagidae			
Bathylagus sp.		65.0%	-----
		51.5%	-----
		66.0%	-----
		55.0%	-----
		70.0%	-----
		70.0%	-----
	M =	64.3%	-----
Opisthoproctidae			
Macropinna microstoma		80.0%	80.7%
		86.0%	85.4%
		83.0%	92.0%
	M =	83.0%	86.0%
Alepocephalidae			
Alepocephalus tenebrosus		-----	95.7%
		85.0%	92.9%
	M =	85.0%	94.3%
Stomiidae			
Stomias boa		85.0%	87.5%
		-----	80.5%
	M =	85.0%	84.0%
Zoarcidae			
Lycodapus mandibularis		91.5%	87.0%
		86.1%	-----
	M =	88.8%	87.0%

M = mean.

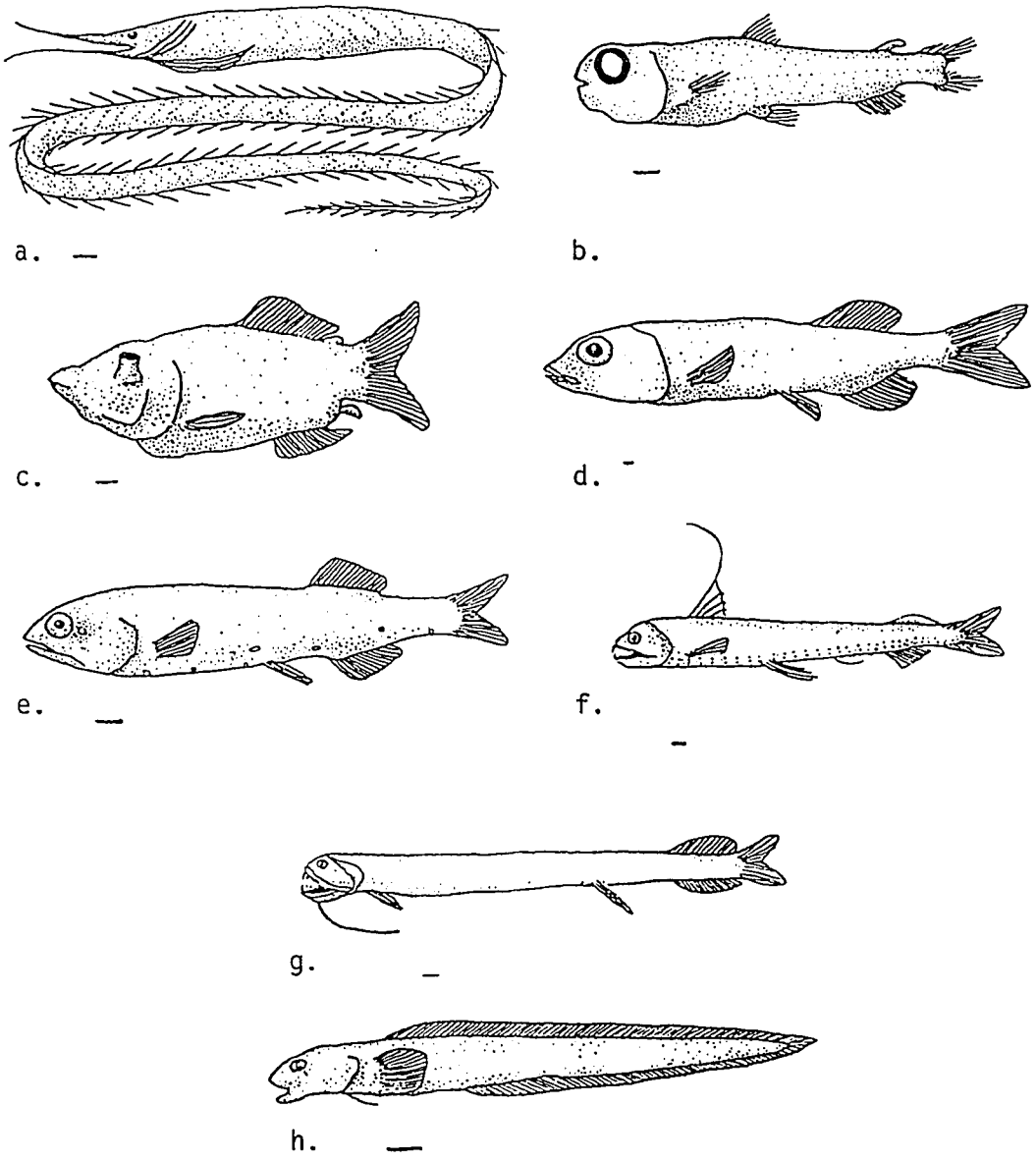

Fig.1.-Species used in this study. a. Serrivomer sector, b. Bathylagus sp., c. Macropinna microstoma, d. Alepocephalus tenebrosus, e. Saqamichthys abei, f. Chauliodus sloani, g. Stomias boa boa, h. Lycodapus mandibularis. Bar = 1 cm.

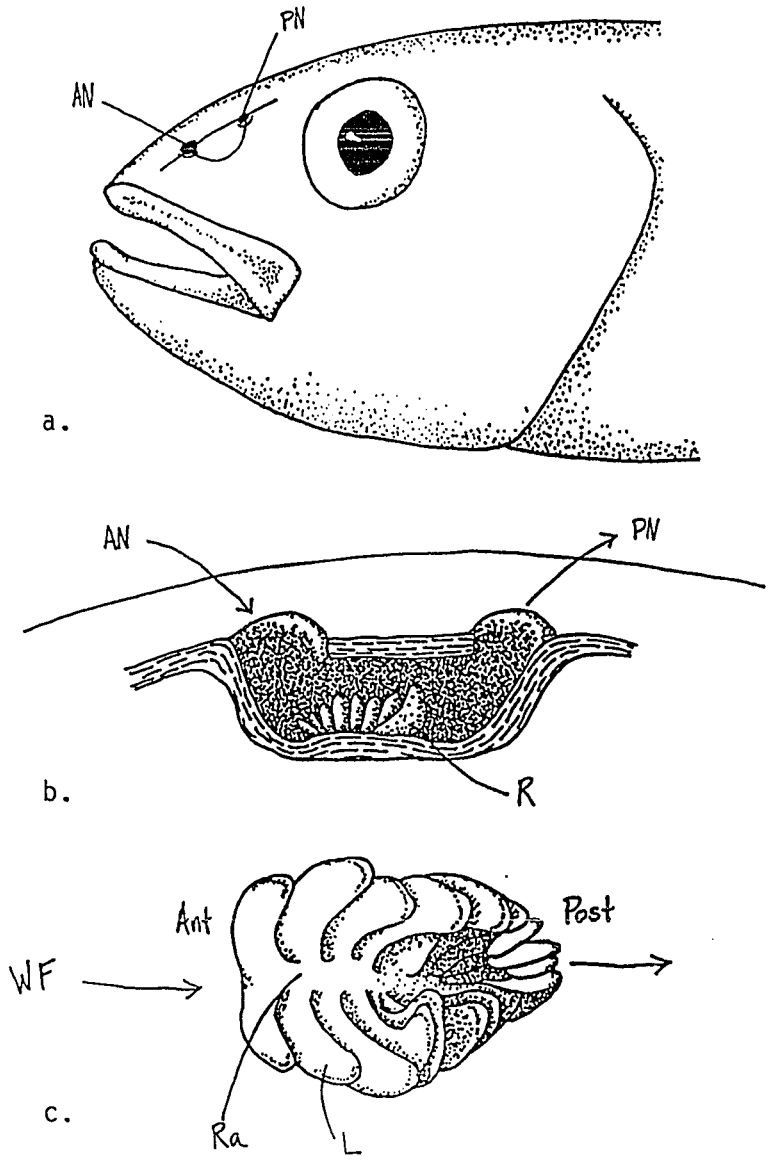

Fig. 2.-a. Head of a hypothetical bony fish; AN = Anterior Naris, PN = Posterior Naris. b. Lateral view of a dissection of the olfactory chamber; R = Rosette. c. Olfactory rosette; L = Lamella, Ra = Raphe, WF = Water Flow.

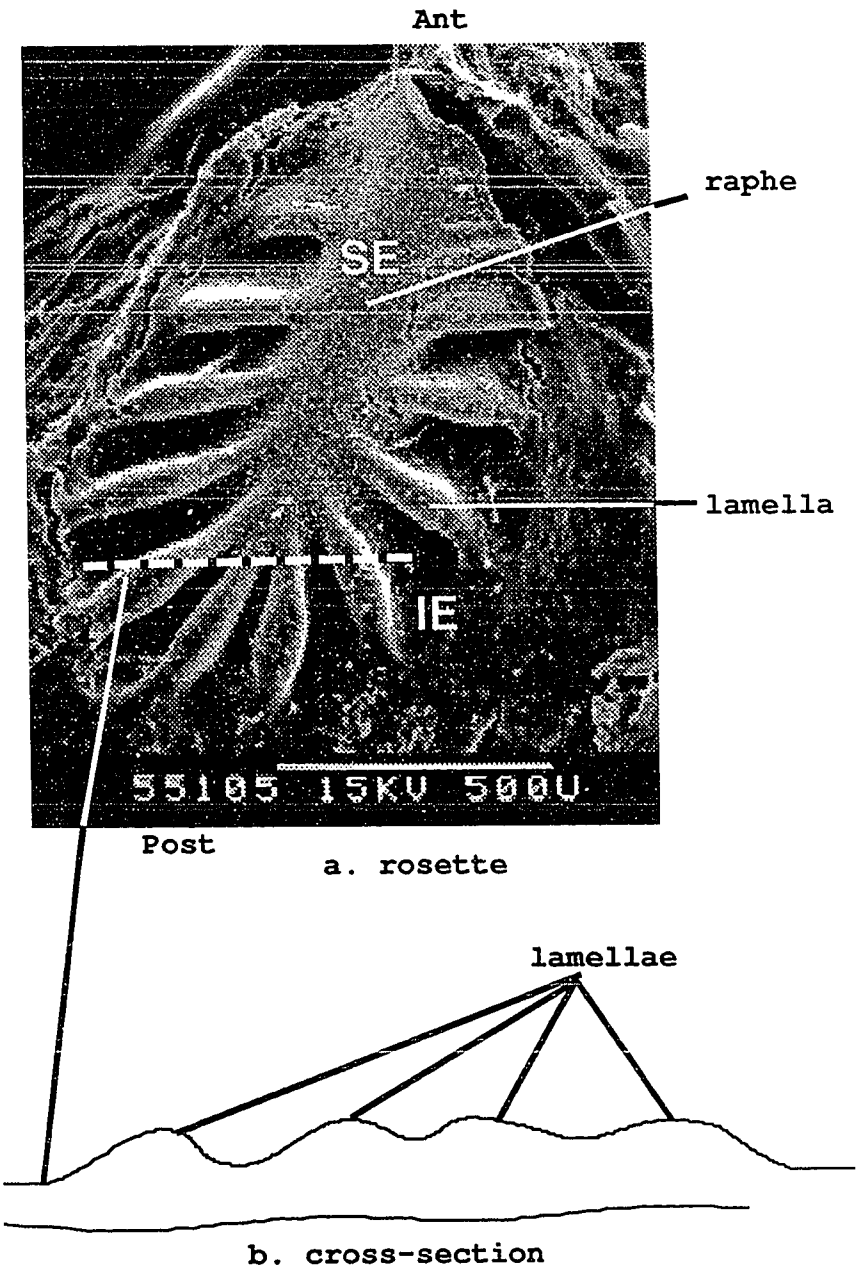

Fig. 3.-SEM photograph of the olfactory organ of Serrivomer sector. Ant. = Anterior, Post. = Posterior

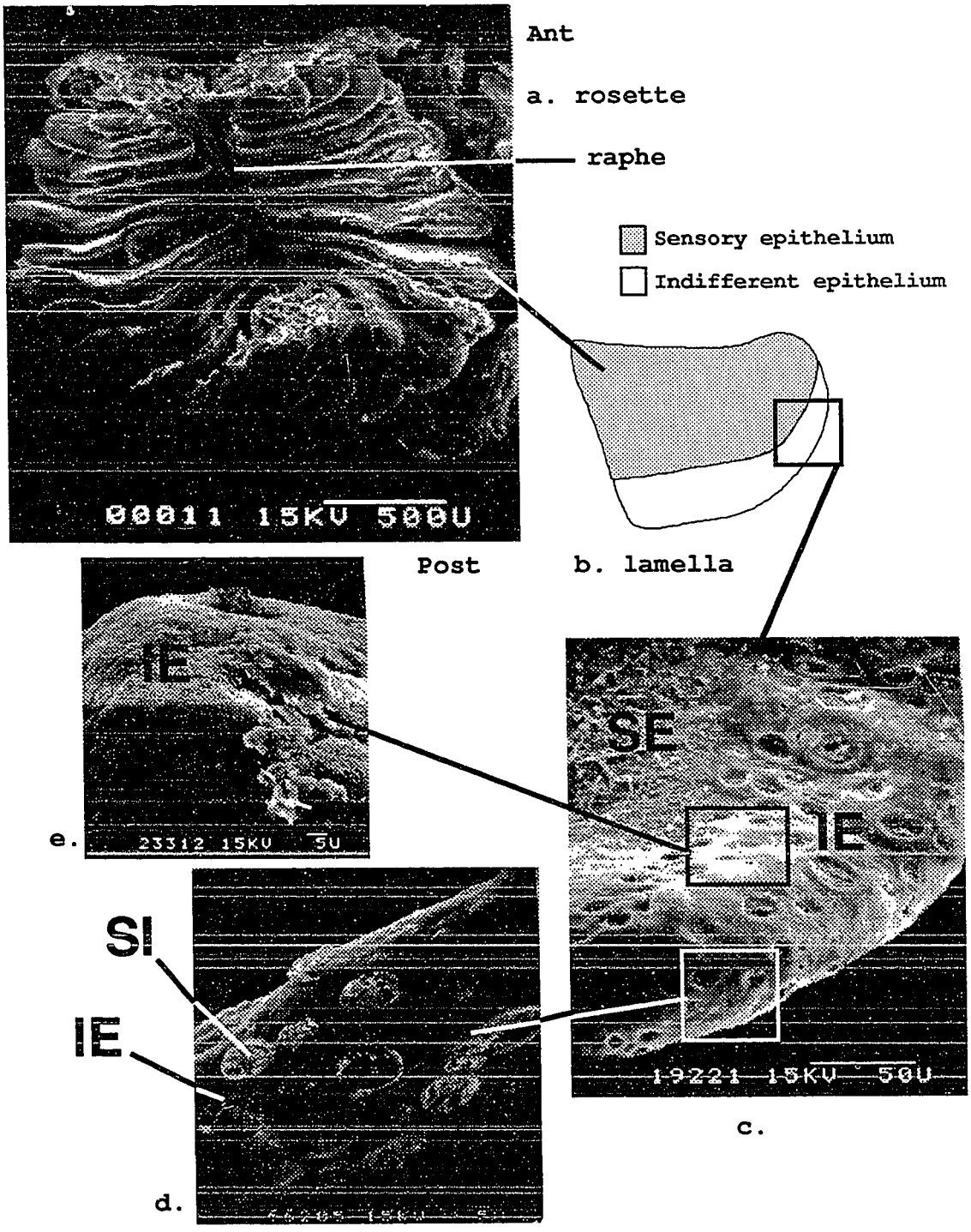

Fig. 4.-SEM photograph of the olfactory organ of Bathylagus sp. a. Rosette. b. Lamella. c. Close-up of border between indifferent and sensory epithelia; SE= Sensory Epithelium, IE = Indifferent Epithelium. d. Close-up of sensory islet (SI) on indifferent epithelium. e. High magnification of indifferent epithelium showing pore system.

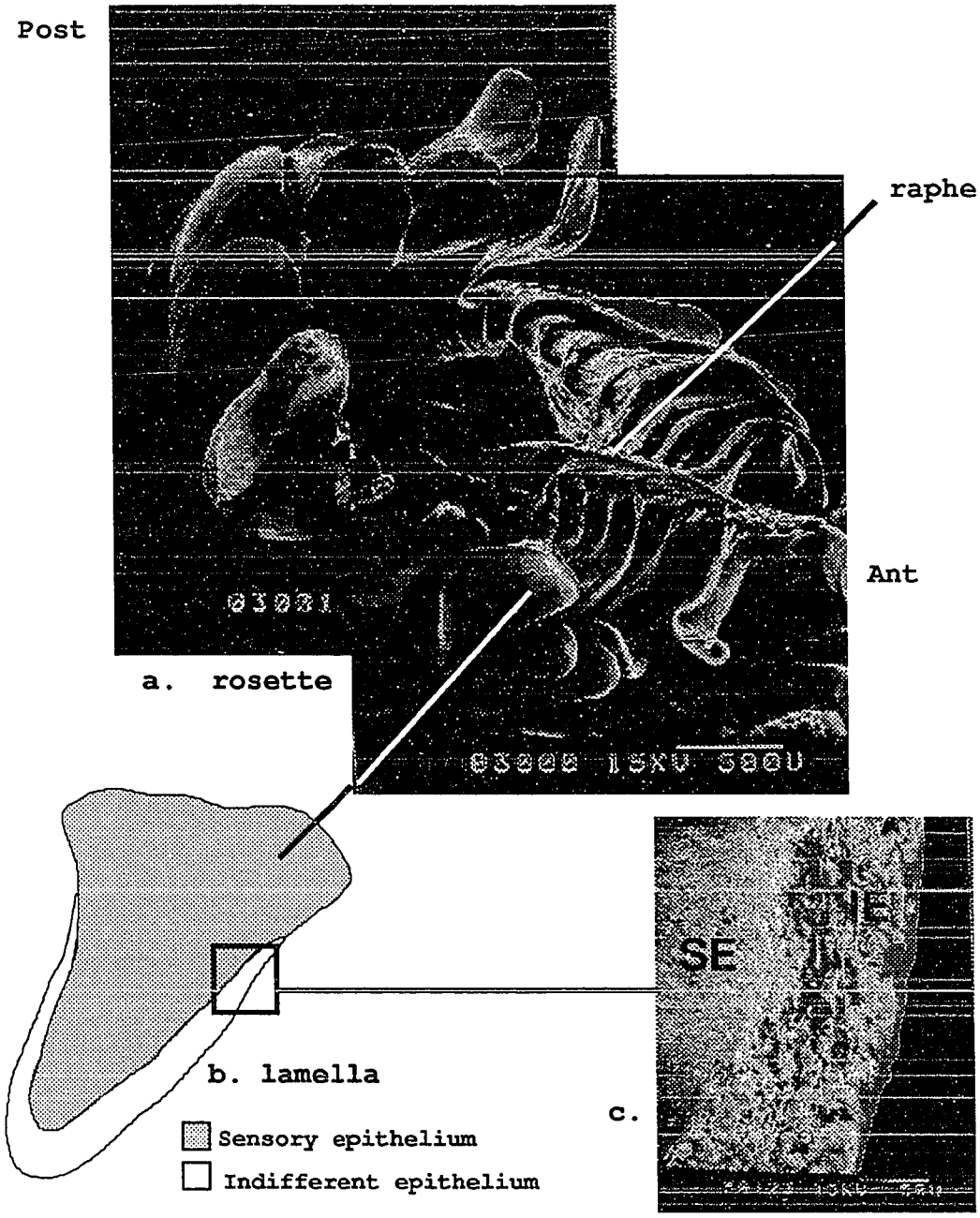

Fig. 5.-SEM photograph of the olfactory organ of Macropinna microstoma. a. Rosette. b. Lamella. c. Close-up of border between sensory and indifferent epithelia; SE=Sensory Epithelium, IE=Indifferent Epithelium.

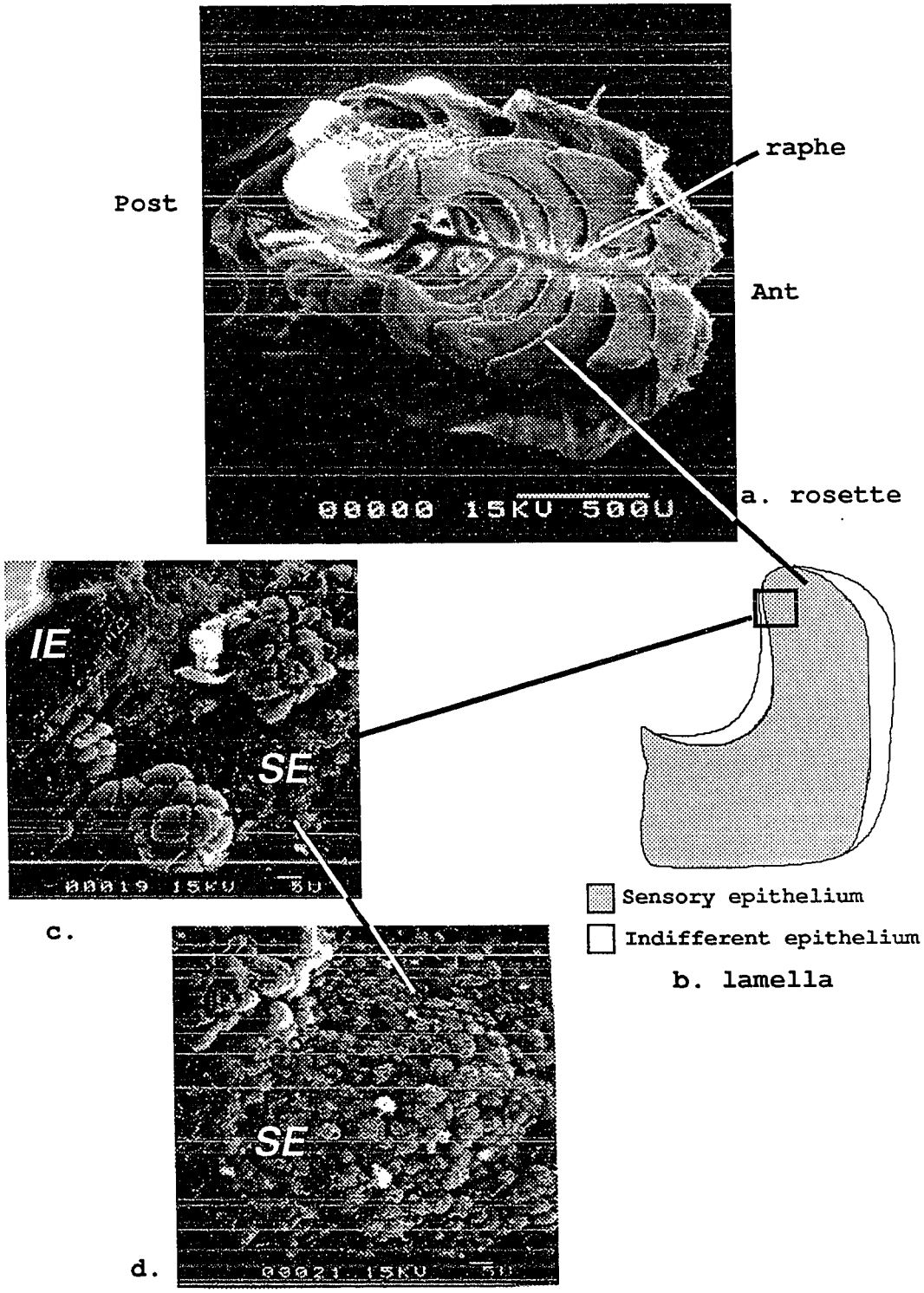

Fig. 6.-SEM photograph of the olfactory organ of Alepocephalus tenebrosus. a. Rosette. b. Lamella. c. Border between Sensory (SE) and Indifferent (IE) Epithelia, and Cellular Aggregates (CA). d. Close-up of sensory epithelial pores.

Fig. 7.-SEM photograph of the olfactory organ of Sagamichthys abei.

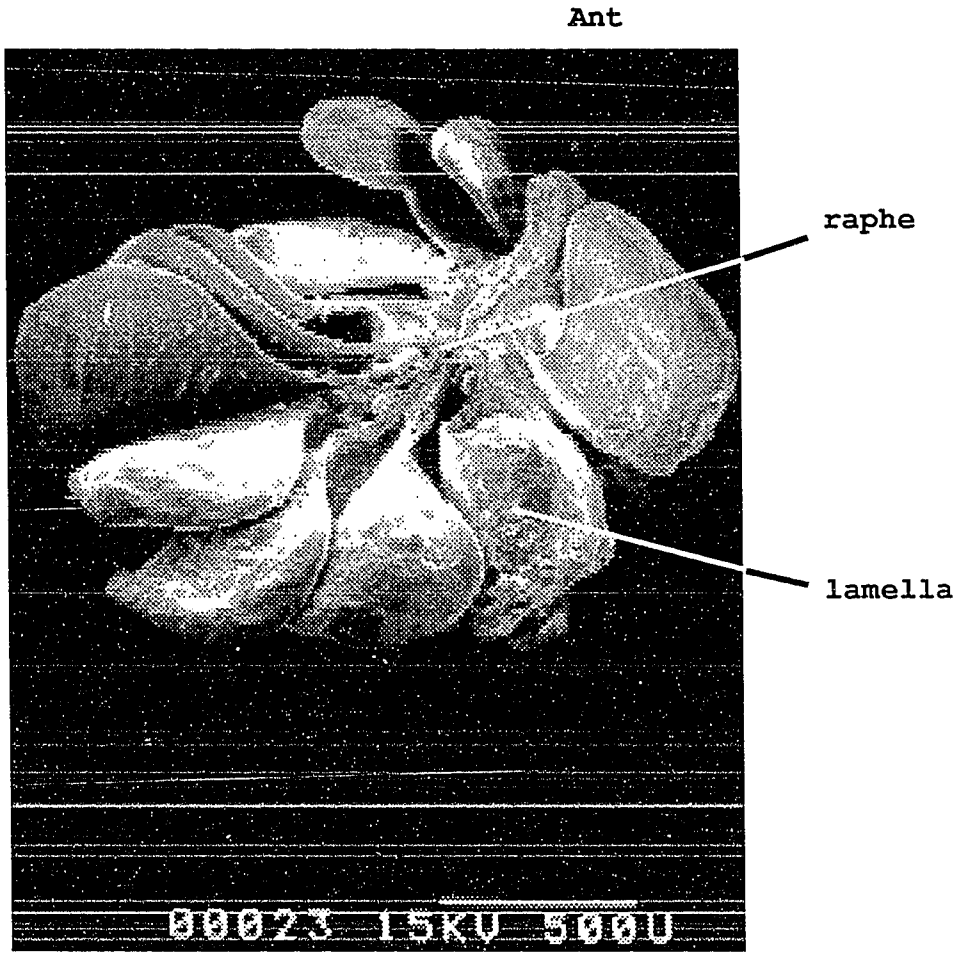

Fig. 8.-SEM photograph of the olfactory organ of Chauliodus sloani.

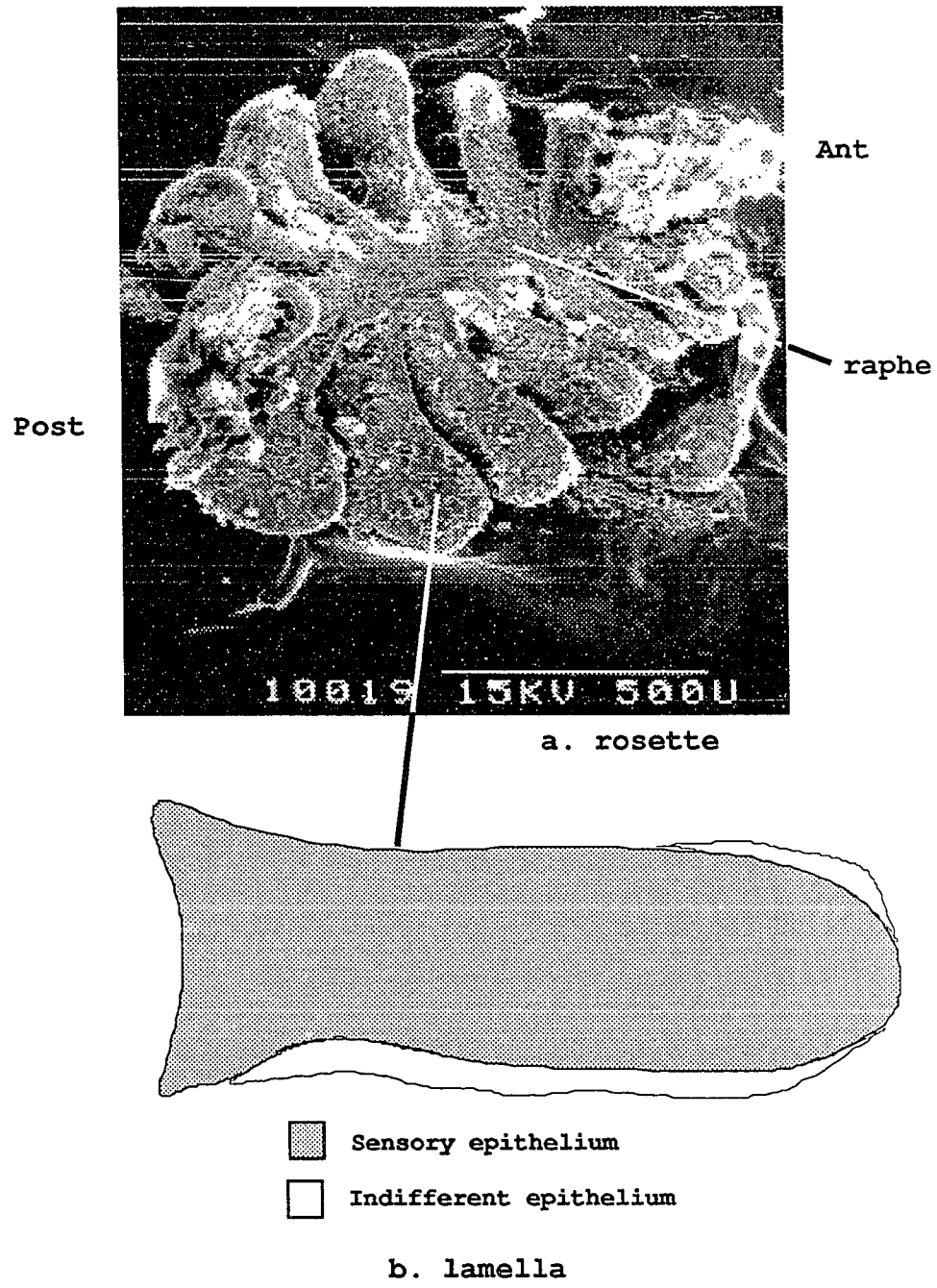

Fig. 9.-SEM photograph of the rosette (a) and a lamella (b) of Stomias boa boa.

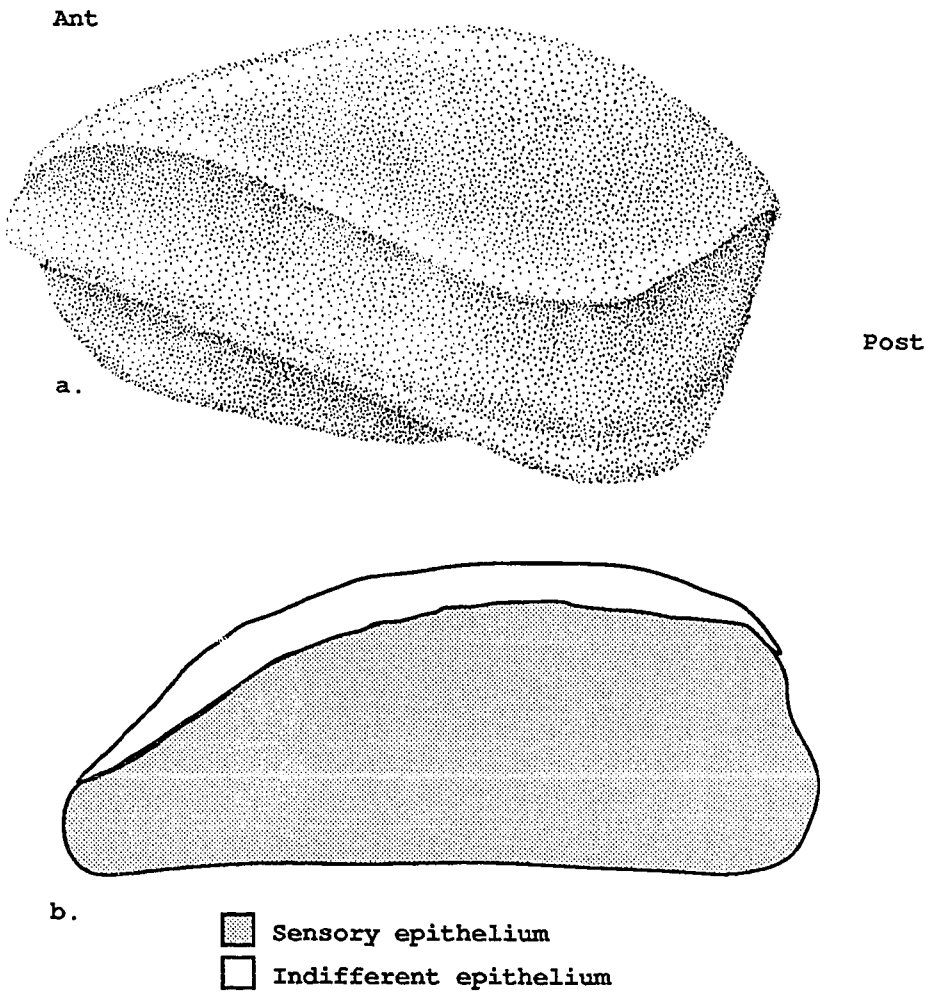

Fig. 10.-Illustration of the olfactory organ of Lycodapus mandibularis. a. Rosette. b. Lamella.