J. Anat. (1974), **117**, 1, pp. 89–94
With 4 figures
Printed in Great Britain

Topological relations between the dendrites of olfactory sensory cells and sustentacular cells in different vertebrates. An ultrastructural study

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(*Accepted* 5 *November* 1973)

INTRODUCTION

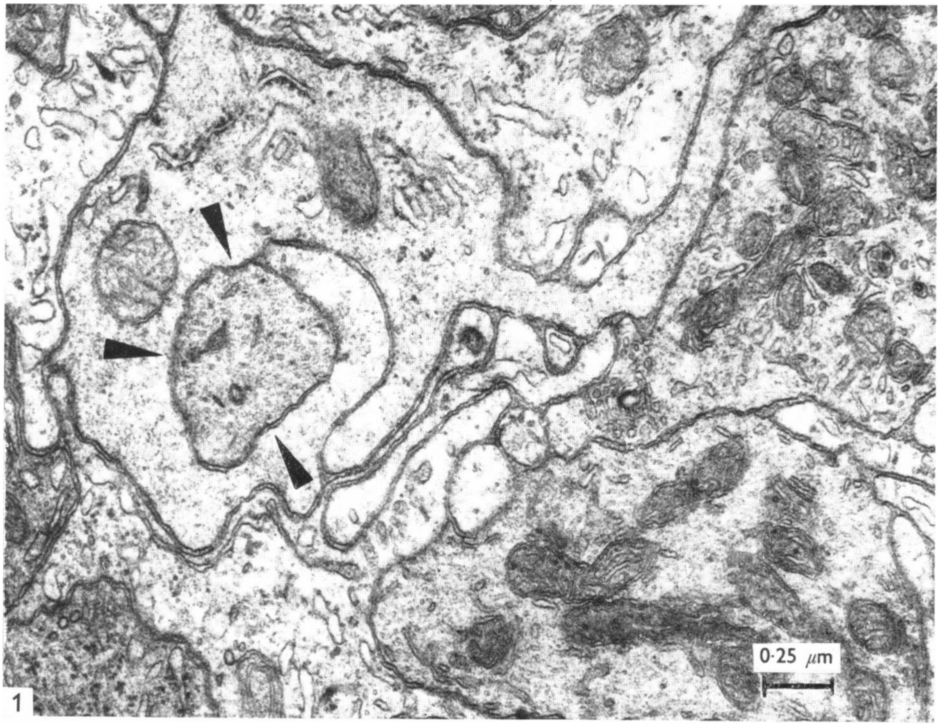
In our investigations we are trying to find a correlation between the biological structure and the neurophysiological function of olfactory receptor cells. We believe it is of special value to study the morphology of the olfactory epithelium and the topological relationships among its various cellular components in different vertebrates, since structures and topological relationships that are found repeatedly in all vertebrates might be essential for olfactory discrimination. This report deals with previously unreported ultrastructural relationships between the dendrites of olfactory sensory cells and the apical part of sustentacular cells in the regio olfactoria of fish and mice.

MATERIALS AND METHODS

The olfactory rosettes of goldfish and the olfactory epithelium of young and adult mice and of mouse fetuses ranging in age from 12·75 to 19 days post-conception were used. The material was fixed in osmium (Dalton, 1955) or double-fixed in osmium and glutaraldehyde (Breipohl, Bijvank & Zippel, 1973). For transmission electron microscopy small tissue specimens were dehydrated in acetone, embedded in Vestopal W (Fa. Jaeger, Vesenaz/Switzerland) or Araldite, and examined in a Siemens Elmiskop IA with 80 kV.

RESULTS

Recently we were able to show that the dendrites of olfactory receptor cells in fish can have different relationships and arrangements (Breipohl, Laugwitz & Bijvank, 1974). Besides the 'normal' intercellular position between the surrounding sustentacular cells, the dendrites may make contact with each other by means of fine, lateral dendritic processes, or by broad-surfaced membrane appositions. Alternatively, the dendrites may be isolated from each other because they are enveloped by the apical cytoplasm of the sustentacular cells. However, as is clearly seen in tangential and oblique sections of the olfactory epithelium, only a proportion of the dendrites is enclosed, and the majority is intercellular. Both newly formed dendrites and mature ones may be enclosed, and in one mouse a dendrite was found with a very dense matrix, the appearance being suggestive of degeneration (W. Breipohl, unpublished results).



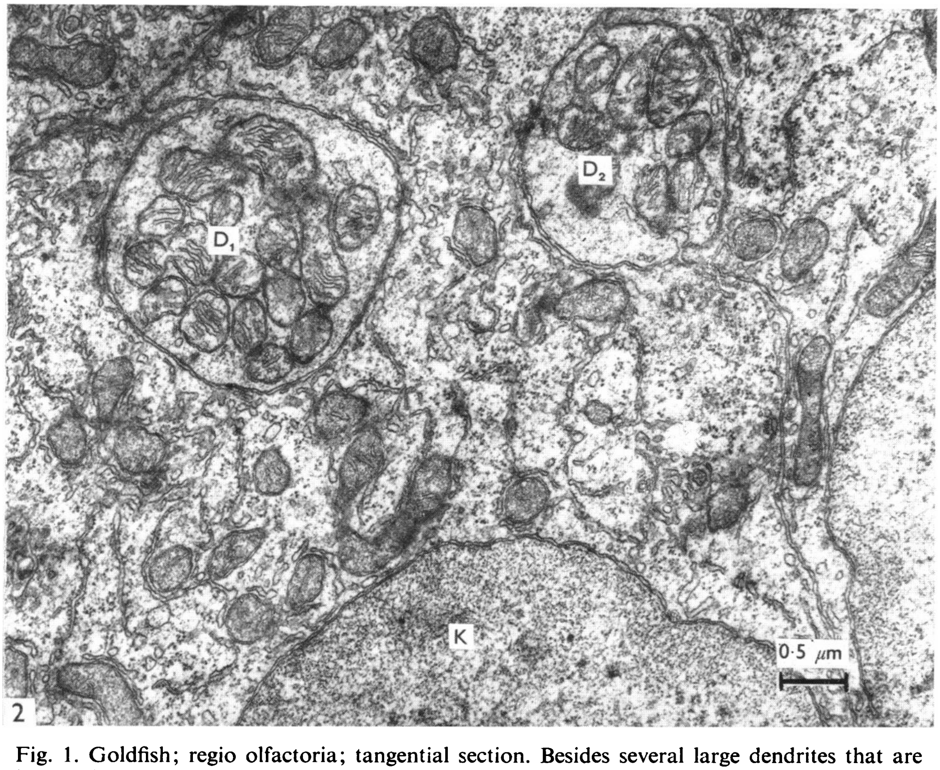
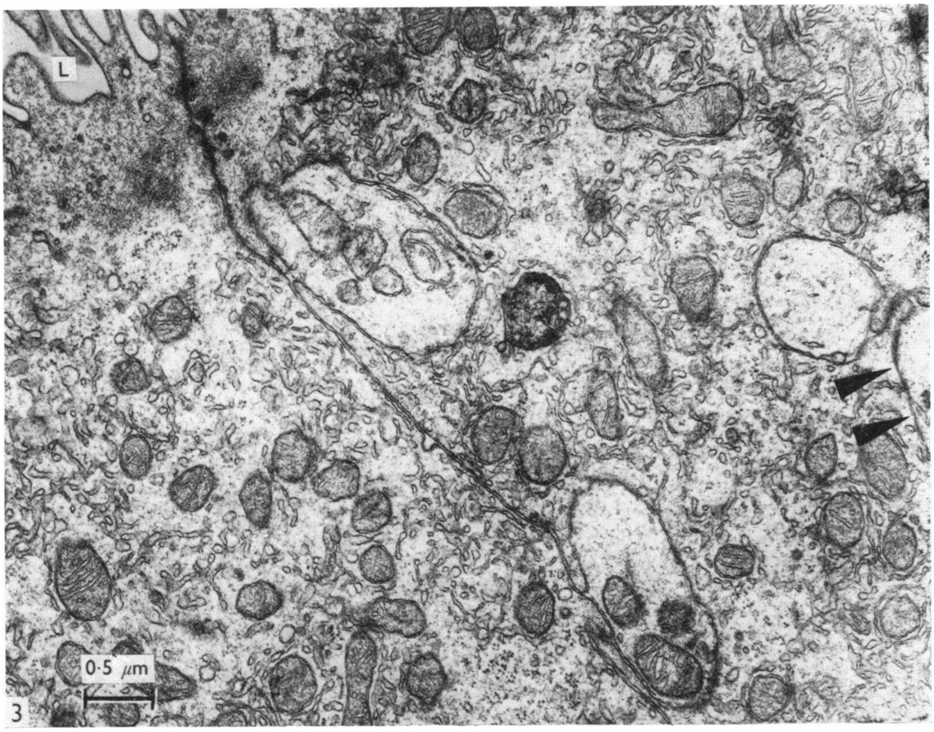


Fig. 1. Goldfish; regio olfactoria; tangential section. Besides several large dendrites that are located intercellularly, one can see a small dendrite that is enclosed spirally by a sustentacular cell (arrows).

Fig. 2. Mouse, 1 year old; regio olfactoria; oblique section. In the supranuclear part of a sustentacular cell one can see a completely enclosed olfactory dendrite (D_1). The endoplasmic reticulum of the sustentacular cell shows close contact with the enveloping cell membrane. D_2 = olfactory dendrite in the extracellular space between two adjacent sustentacular cells. K = nucleus of a sustentacular cell.



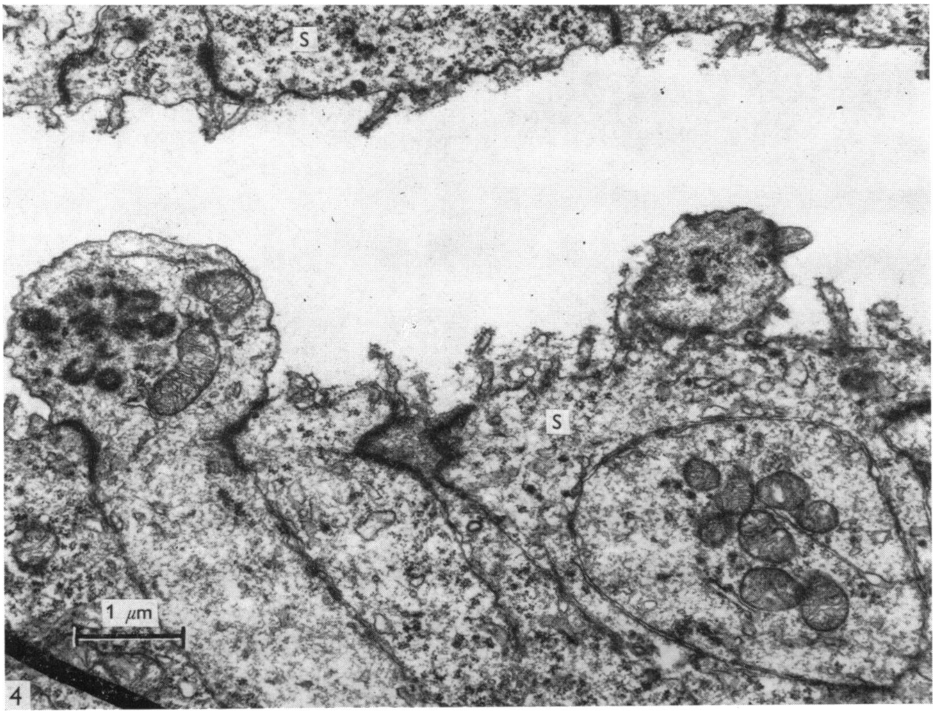


Fig. 3. Mouse, 1 year old; regio olfactoria; oblique section. In the supranuclear part of a single sustentacular cell one can observe three enclosed olfactory dendrites. A fourth dendrite (arrows) is in the surrounding extracellular space. L = surface of epithelium.

Fig. 4. Mouse fetus, 12·75 days post-conception; regio olfactoria; oblique section. On the right is an enclosed dendrite, on the left a dendrite in continuity with its olfactory vesicle. The apical cytoplasm of the sustentacular cells (S) is still very immature; there are relatively few mitochondria, and a well-developed endoplasmic reticulum is lacking at this stage of development.

Further investigations have now shown that in goldfish the sustentacular cell sometimes does not merely envelop the dendrites in the manner described, but may also form a spiral-shaped casing around them (Fig. 1).

The findings in the olfactory epithelium of white mice are similar (Figs. 2–4). In mice one can even find several sensory dendrites enclosed by a single sustentacular cell. It seems to be characteristic that the abundant, smooth endoplasmic reticulum in the distal part of the sustentacular cells is in close contact with the enveloping cell membrane (Figs. 2, 3). Besides this, one can find tight junctions between the membranes of sustentacular cells and the dendrites of the olfactory receptor cells.

Enclosure of the dendrites is visible in newborn mice and even during the intrauterine phase of life. Fig. 4 shows such an enclosed dendrite in the regio olfactoria of a 12·75 day old mouse fetus.

DISCUSSION

Morphological differences in the regio olfactoria of vertebrates have been documented by many authors (Holl, 1965; Andres, 1966; Graziadei, 1971*a*; Schulte, 1972; Breipohl, Mestres & Meller, 1973; Breipohl, 1974; Breipohl, Bijvank & Zippel, 1973; Breipohl, Laugwitz & Bijvank, 1974). Nevertheless, it was believed until now that in all vertebrates the dendrites of olfactory receptor cells were located between adjacent sustentacular cells (Allison, 1953). A different arrangement was argued by Drenckhahn (1970) in one case (see his fig. 8).

The sustentacular cells were therefore believed to have an isolating function (de Lorenzo, 1957). Against this supposition, however, was the fact that contacts between different sensory cells by means of small dendritic arms (Graziadei, 1971*b*) or broad-surfaced membrane appositions (Seifert & Ule, 1967; Seifert, 1970; Graziadei, 1971*b*) have been observed in different vertebrates. The broad-surfaced membrane appositions were interpreted as being characteristic of newly formed dendrites, but, as indicated above, the enclosure of dendrites is not restricted to adult animals, being visible in both newborn and fetal mice (Fig. 4). At 12·75 days post-conception, however, the sustentacular cells are still very immature (Breipohl, Mestres & Meller, 1973). The enclosure of olfactory dendrites by the apical part of sustentacular cells is, we believe, due to an active penetration by the dendrites.

The morphological aspects of the enclosure of the sensory cell processes are reminiscent of the glio-neuronal connexions between neurites and Schwann cells or oligodendroglial cells (Drenckhahn, 1970). In the olfactory epithelium, however, dendrites and not neurites are enveloped. The olfactory dendrites shown appear not to be enclosed along their full length, but only in the supranuclear region of the sustentacular cells.

The fact that in tangential sections of the olfactory epithelium one can find only a few enclosed dendrites, while the majority occupy the 'normal' intercellular position, may be interpreted in different ways. First, it is possible that this structural feature occurs only accidentally, when an outward-growing young dendrite makes an 'error' on its way to the surface of the olfactory epithelium and grows through one of the sustentacular cells instead of between them. But such an interpretation could hardly explain why these enclosures of dendrites were found more often in mice than in fish. Furthermore, no striking difference in the numbers of enclosed dendrites could be found between mouse fetuses, newborn and adult mice, though the percentage of newly formed dendrites is naturally higher in early developmental stages than in adult animals.

Secondly, one could argue that the enclosed dendrites have started degenerating and therefore have been enclosed for phagocytosis by adjacent cells. Le Gros Clark (1957) has discussed phagocytotic activity of sustentacular cells. With one exception, however, we never saw enclosed dendrites that could be interpreted as degenerating ones.

Thirdly, one may construct an analogy between the sustentacular cells and glial cells. Though not in agreement with the opinion of many authors (Seifert, 1970), it was especially de Lorenzo (1957) who discussed an isolating effect of the sustentacular cells in addition to the supporting and phagocytotic activity that was argued by others (Allison, 1953; le Gros Clark, 1957). A comparison between sustentacular and glial cells is of interest to us because cells with some morphological features similar to those of the sustentacular cells have been described in other sense organs. The Müller cells in the retina, for example, are believed not only to have a supporting function, but also to be involved in the myelinization of the axons of retinal ganglion cells (Meller & Glees, 1965; Glees & Meller, 1968; Meller, 1968). There might be a parallel structural and functional relationship between the enclosure of the distal processes of optic receptor cells by the pigmented cells of the retina (Spitznas & Hogan, 1970; Breipohl, Bornfeld, Bijvank, Laugwitz & Pfautsch, 1974) and the enclosures of the distal processes of olfactory receptors by the sustentacular cells.

A last possible interpretation would be that only one special type of olfactory receptor cell – another analogy with the optic receptors (Spitznas & Hogan, 1970) – shows such definite connexions with the adjacent sustentacular cells.

SUMMARY

The dendrites of olfactory sensory cells in fish, in adult mice and in mouse fetuses may be totally enclosed by the surrounding sustentacular cells.

In mice, one sustentacular cell can enclose the dendritic processes of several olfactory sensory cells.

The sustentacular cells are compared with glial cells, especially with the Müller cells in the retina.

The possible function of the enclosure of dendrites is discussed.

This study was supported by the Deutsche Forschungsgemeinschaft (Br. 358/2) and in part by the SFB 33 (Göttingen). Grateful appreciation is expressed to K. Donberg for technical assistance, Professor Dr K. Meller for personal support, and Mona Wellmer for her help with the English translation.

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