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On the occurrence of the cephalic gland in the epidermis and rhynchodaeal wall in nemerteans

W. Senz

Abstract. The nemertean cephalic gland is traditionally described as occurring only in the area between the preseptal epidermis and rhynchodaeal wall, embedded in mesenchymate tissue (= typical position). In *Tubulanus annulatus* Montague, 1804 and other paleonemerteans, gland cells of the same cell types occur both in the typical position and in the proximal part of the preseptal epidermis and rhynchodaeal wall. The cephalic gland has been described as lacking in several paleonemerteans (e. g. *Tubulanus theeli* (Bergendal, 1902), *Carinina arenaria* Hylbom, 1957 and *C. coei* Hylbom, 1957) but these species possess cephalic gland cells restricted to the epidermis and rhynchodaeal wall. From this and other results it is concluded that the cephalic gland may also occur in the epidermis and rhynchodaeal wall in the nemertean stem species.

Key words. Nemertini, Paleonemertini, anatomy, cephalic gland, epidermis, rhynchodaeal wall.

Introduction

The cephalic gland in nemerteans is variable in several respects (in cytological and functional aspects as well as position; Bürger 1895, Ferraris 1979a, b, 1985, Gontcharoff & Lechenault 1966, Moore & Gibson 1985, Pantin 1969). Traditionally this gland is described as being restricted to the preseptal area (in several hoplonemerteans and perhaps in some heteronemerteans it extends behind the septum) lying procimally to the body wall and distally to the rhynchodaeal wall (Bürger 1895). It discharges its substances either into the vascular system or to the exterior (Ferraris 1985). In the second case it opens either via a frontal organ or "through independent ducts connecting directly with the epidermal surface" (Gibson & Moore 1976: 190).

Only very few papers mention a possible position of the cephalic gland in the epidermis and/or rhynchodaeal wall. These papers are first of all Friedrich (1936) for *Tubulanus borealis* Friedrich, 1936, Müller (1965) for *Carinina heterosoma* Müller, 1965 and Bergendal (1902a) for *Callinera buergeri* Bergendal, 1900. This is somewhat surprising, since the cephalic gland can be seen as an epidermal derivative (Wijnhoff 1910), like the rhynchodaeal wall (Stiasny-Wijnhoff 1923).

The present paper focuses on the question of whether an epidermal and rhynchodaeal position of the cephalic gland in nemerteans is as rare as assumed in the literature. Some conclusions on the nemertean stem species are added.

Material and Methods

Specimens of the following species have been studied: type material of *Carinina arenaria* Hylbom, 1957, *C. coei* Hylbom, 1957 and *Cephalotrix arenaria* Hylbom, 1957 (transverse sections and complete specimens; see Hylbom (1957) for details on all three species), series of transverse and longitudinal sections of *Callinera buergeri* Bergendal, 1900 and *Tubulanus*

theeli (Bergendal, 1902) (transverse sections only), belonging to the Museum of Natural History Stockholm (Sweden), *T. annulatus* Montague, 1804, *Cephalotrix* sp. (deposited with the private collection of the author, collected by the author at the coast of Croatia near Rovinj), *C. rufifrons* Johnston, 1837, *C. linearis* (Rathke, 1799) and *Hubrechtella globocystica* Senz, 1993.

Histological studies have been carried out on 7 μm, 8 μm and 10 μm sections of individuals embedded in paraplast and stained by Azan-, Kernechtrot-Pikroindigokarmin- and Haematoxylin-Eosin-methods.

Results

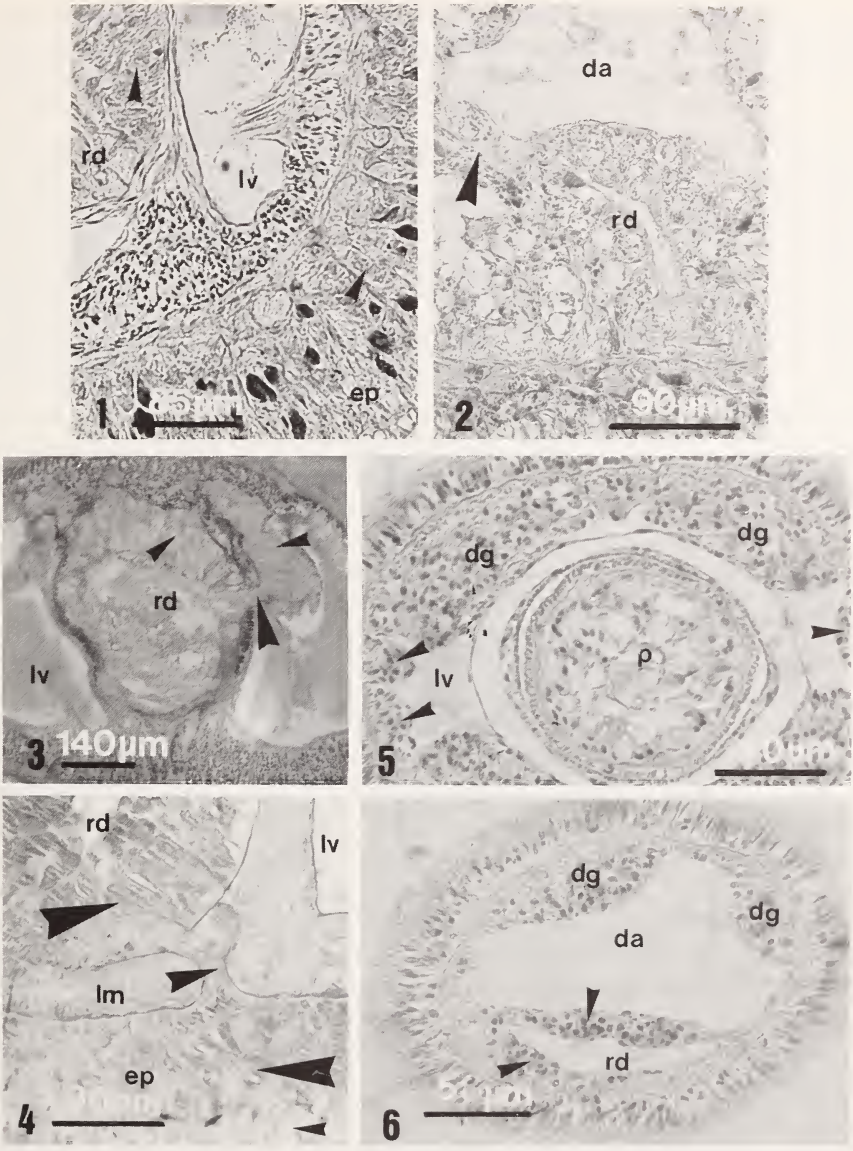
In *Carinina arenaria* and *C. coei* (Paleonemertini) no cephalic gland occurs in the typical position (Hylbom 1957, Senz 1993 a). Nevertheless, there are large acidophilic gland cells containing a finely granulated secretion (= type 1 gland cell) in the proximal part of the epidermis in the preseptal area and in the rhynchodaeal wall (Fig. 1).

Within *Tubulanus* Renier, 1804 (Paleonemertini) extremely different arrangements of the cephalic gland occur:

One of the cephalic gland cell types in *T. annulatus* corresponds to type 1 as described for *Carinina* Hubrecht, 1885. These cells form large packages between the branches of the vascular system (Fig. 3). Cells belonging to the same type occur in the rhynchodaeal wall too, and become the dominant cell type of its lining epithelium in the posterior part of the rhynchodaeum. These rhynchodaeal gland cells are interconnected with the cells in typical position at several places (Fig. 3). In the anterior preseptal area the cephalic gland in typical position consists mainly of other cell types (see Senz 1993 a). Cells belonging to these cell types occur in the proximal part of the preseptal epidermis and in the rhynchodaeal wall as well. These rhynchodaeal cephalic gland-like cells and those in the typical position are once more interconnected with each other at several places (Fig. 2). Thus, the exact border of the rhynchodaeal wall is not clearly detectable everywhere (Fig. 2).

In *Tubulanus theeli* no cephalic gland occurs in the typical position (for general arrangement of the preseptal area see Bergendal 1902 b and Senz 1993 a). The rhynchodaeal wall (not its posterior part) and the proximal part of the epidermis are densely packed with cells similar to type 1 cells of *Carinina* and *T. annulatus*. At several places, both gland cell packages are interconnected with each other by narrow strands ("bridges") of gland cells belonging to the same type (Fig. 4).

Fig. 1: *Carinina coei* Hylbom, 1957: Transverse section through the preseptal area; arrowheads indicating cephalic gland cells in the rhynchodaeal wall and epidermis; ep — epidermis, lv — lateral vessel, rd — rhynchodaeum. Fig. 2: *Tubulanus annulatus* Montague, 1804: Transverse section through the preseptal area; arrowhead indicating cephalic gland packages in typical position interconnected with cephalic gland cells in the rhynchodaeal wall; da — dorsal commissure of the vascular system, rd — rhynchodaeum. Fig. 3: *T. annulatus* Montague, 1804: Transverse section through the preseptal area; small arrowheads indicating cephalic gland packages, large arrowhead indicating junction between these packages; lv — lateral vessel, rd — rhynchodaeum. Fig. 4: *T. theeli* Bergendal, 1902: Transverse section through the preseptal area; small arrowhead indicating distal epidermal area, possessing no cephalic gland cells, large arrowhead indicating junction between cephalic gland packages in the epidermis and the



rhynchodaeal wall (which are indicated by medium-sized arrowheads); ep — epidermis, lm — longitudinal musculature, lv — lateral vessel, rd — rhynchodaeum. Fig. 5: *Cephalotrix* sp.: Transverse section through the posterior preseptal area; arrowheads indicating cephalic gland packages interconnecting the dorsal and ventral packages of the cephalic gland; dg — dorsal package of the cephalic gland, lv — lateral vessel, p — proboscis. Fig. 6: *Cephalotrix* sp.: Transverse section through the anterior preseptal area; arrowheads indicating cephalic gland packages in the rhynchodaeal wall; da — dorsal commissure of the vascular system, dg — dorsal package of the cephalic gland, rd — rhynchodaeum.

Most cephalotricid nemerteans (Paleonemertini) possess a cephalic gland consisting of one dorso- and one ventrolateral pair of cephalic gland cell packages (Wijnhoff 1910). At its anterior end the ventrolateral pair forms one undivided complex in several species (e. g. *Cephalotrix linearis* (Rathke, 1799); pers. obs.), lying adjacent to the rhynchodaeal opening (Senz 1993a). In *Procephalotrix adriatica* Senz, 1993 and *Cephalotrix rufifrons* Johnston, 1837 gland cells of the cephalic gland type occur in the rhynchodaeal wall at the rhynchodaeal opening (Senz 1993a). In the specimen of *Cephalotrix* sp. (incomplete specimen, no species diagnosis possible) examined by the author, this ventral cell complex occurs also in the wall of the anterior part of the rhynchodaeum (Fig. 6). Behind this the gland leaves the rhynchodaeal wall, which becomes totally non-glandular, and both gland packages of one side of the body are interconnected with each other at irregular intervals (Fig. 5). In *Cephalotrix arenaria* the cephalic gland forms a three-dimensional network rather than four distinct packages (see Senz 1993a). Furthermore the cephalic gland is also part of the rhynchodaeal wall for most of its length.

Discussion

The cephalic gland is part of the rhynchodaeal wall and the epidermis in *Tubulanus annulatus*, since these organs possess gland cells which belong to the same cell types as those cells forming the cephalic gland in typical position. Furthermore, all these gland packages are interconnected with each other. Taking this into account, the cephalic gland in *T. annulatus* forms a three-dimensional network, traversing the preseptal body. In *T. theeli* the arrangement in the epidermis and the rhynchodaeal wall is similar to *T. annulatus*, although there is no cephalic gland in the typical position (except for the cell "bridges" mentioned above). Thus, in contrast to traditional descriptions, the cephalic gland in this species is not absent, but restricted to the epidermis and rhynchodaeal wall.

The cephalic gland seems to be part of the rhynchodaeal wall and/or epidermis at least in most of the *Carinina* and *Tubulanus* species. Yamaoka (1940) describes the cephalic gland in the typical position in *Tubulanus eozensis* Yamaoka, 1940, without mentioning a possible occurrence in the rhynchodaeal wall. Nevertheless, Yamaoka's Fig. 4 shows that the cephalic gland belongs to this organ as well, since there are gland cells of the same type drawn in into the rhynchodaeal wall and in the typical position. The same is true for (cf.) Coe's (1901) description of *Tubulanus rubra* Coe, 1901.

Within cephalotricid nemerteans the cephalic gland forms a three-dimensional network, which is part of the rhynchodaeal wall too, predominantly in *Cephalotrix arenaria* (see above). In most of the remaining (valid) species (for exceptions see above) this gland is restricted to the typical position.

The cephalotricid nemerteans are similar to *Callinera* Bergendal, 1900 (Paleonemertini) in possessing a cephalic gland which is intermingled with nervous tissue (Wijnhoff 1910). For *Callinera*, this neuroglandular complex is described in detail by Bergendal (1902a). Due to this study (especially Bergendal 1902a: Figs 6–8) and pers. obs. the cephalic gland occurs in the rhynchodaeal wall too, for the

same reasons as in *Tubulanus annulatus*. This part of the cephalic gland and the one in typical position are once more interconnected with each other by glandular "bridges". Bergendal (1902a) focuses on a possible occurrence of the cephalic gland in the rhynchodaeal wall, but without deciding this question.

In *Hubrechtella globocystica* Senz, 1993 (Paleonemertini) a similar situation obtains, with the neuroglandular complex of the body wall corresponding to a cephalic gland intermingled with nervous tissue (see Senz 1993a for *H. globocystica* and Gibson 1979a, b, Hylbom 1957 and Senz 1992a for general arrangement in the genus *Hubrechtella* Bergendal, 1902). There is at least one further hubrechtid genus, namely *Tetramys* Iwata, 1957, having a network-like cephalic gland, which is part of the rhynchodaeal wall too. This is strongly indicated by Iwata's fig. 1 (1957), although no detailed information is given in the text.

Thus, the cephalic gland is part of the epidermis and/or rhynchodaeal wall in most paleonemerteans. Figure 7 of the present paper demonstrates five types of arrangement of the cephalic gland found in nemerteans (except for the heteronemerteans, see below). The arrangement shown in figure 7.1. (cephalic gland in the typical position only) is very unusual in paleonemerteans, but (at least) characteristic for the hoplonemerteans. As far as can be concluded from the literature, the only known hoplonemerteans with the cephalic gland occurring also in the rhynchodaeal wall are *Tetrastemma angulatus* Senz, 1993 and *T. cruciatus* Senz, 1933 (Senz 1993b). The situation within the heteronemerteans (no cephalic gland in the epidermis and the rhynchodaeal wall) is without question apomorphic, since the cephalic gland lies in the outer longitudinal muscle layer of the body wall, an apomorphic character of this taxon (Senz 1992b). Only very few exceptions are known so far, e. g. postseptal area in *Lineus lacteus* (Grube, 1855) and *Pseudobaseodiscus nonsulcatus* Senz, 1993 (see Senz 1993a for details).

Seemingly the typical position of the cephalic gland can be interpreted in terms of to what extent epidermal and rhynchodaeal gland cells became transferred proximally in phylogenesis, comparable to the situation in several turbellarians (see e. g. Ehlers 1985). But, this view is somewhat artifical. Although probably not wrong, it is misleading, since it underestimates two circumstances: 1) the phylogenetic origin of the preseptal area (which includes the cephalic gland) itself; 2) at least in cephalotricid nemerteans a direct contact between the cephalic gland and the vascular system is of importance for functional reasons (see Ferraris 1979a, b, 1985: 73: "In this regard *Procephalotrix spiralis* . . . is the only species, to date, to which a neuroendocrine function for the cephalic gland may be ascribed.").

Taking all this into account, an epidermal and rhynchodaeal position of the cephalic gland in the nemertean stem species becomes probable to a considerable degree. This view can be substantiated by the epidermal origin of the cephalic gland (Wijnhoff 1910). Whether the cephalic gland in the nemertean stem species forms a three-dimensional network as in (e. g.) *Tubulanus annulatus*, or is restricted to the epidermis and rhynchodaeal wall as in (e. g.) *Carinina arenaria* and *Tubulanus theeli*, is a complex problem, which cannot be decided within the scope of the present paper but will be discussed in a separate one.

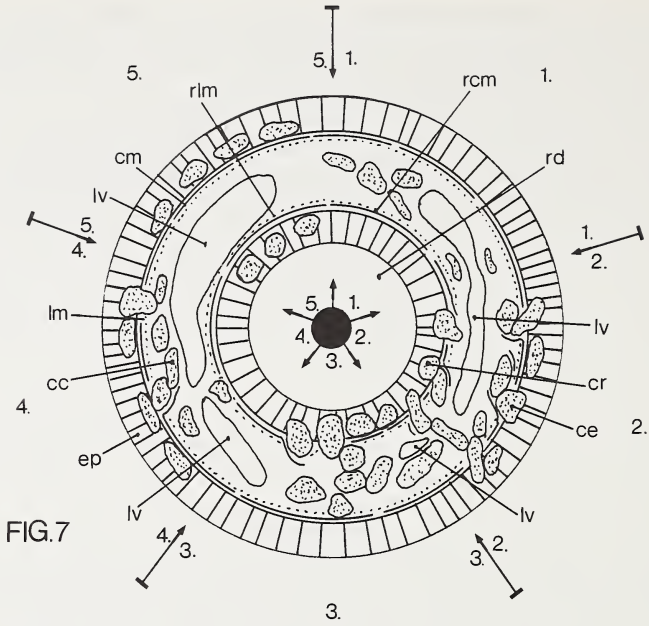


Fig. 7: Schematic presentation of observed arrangements of the cephalic gland in nemerteans (excluding heteronemerteans). Sector 1: Cephalic gland restricted to the typical position; Sector 2: Cephalic gland present in the typical position as well as rhynchodaeal wall and epidermis (proximal part); Sector 3: Cephalic gland present in the typical position and the rhynchodaeal wall; Sector 4: Cephalic gland present in the typical position and the epidermis (proximal part); Sector 5: Cephalic gland present in the epidermis (proximal part) and rhynchodaeal wall solely; cc — cephalic gland package in typical position, ce — cephalic gland package in the epidermis, cm — circular muscle layer of the body wall, cr — cephalic gland package in the rhynchodaeal wall, ep — epidermis, lm — longitudinal muscle layer of the body wall, lv — lateral vessel, rcm — rhynchodaeal circular musculature, rd — rhynchodaeum, rlm — rhynchodaeal longitudinal musculature.

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Zusammenfassung

In den meisten Paleonemertinen ist die Kopfdrüse nicht auf den Bereich zwischen der Körperwand und dem Rhynchodaeum beschränkt, sondern tritt auch in der preseptalen Epidermis (proximaler Bereich) und der Rhynchodealwand auf. Bei einigen Arten (z. B. *Carinina arenaria* und *Tubulanus theeli*) ist die Kopfdrüse sogar auf diese Organe beschränkt. Von den übrigen Nemertinen (Heteronemertini und Enopla) ist dies zumindest (abgesehen von zwei Hoplonemertinen-Arten) nicht bekannt. Dies, wie auch der Umstand, daß die Kopfdrüse

stammesgeschichtlich von abgesunkenen Epidermaldrüsen abzuleiten ist, läßt den Schluß zu, daß die Kopfdrüse wahrscheinlich auch bei der Nemertinen-Stammart in der Epidermis und der Rhynchodealwand (selbst ein Epidermisderivat) aufgetreten ist, vielleicht auch auf diese beschränkt ist.

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Dr. W. Senz, Zoological Institute, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria.