A MONOGRAPH OF THE MARINE TRICLADS

Ronald Sluys

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By
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To my parents

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Introduction

This work is a specialized treatment on a relatively small and unknown group of animals, the marine triclads or Maricola (Platyhelminthes, Tricladida). Hallez coined in 1890 the terms Maricola, Paludicola and Terricola for the marine, freshwater and land planarians, respectively. These ecological names could never have lasted so long when they did not coincide with conspicuous morphological differences between the three groups. Hallez' terminology remains useful up to the present, although we now know that there are planarians with 'marine' characteristics which actually live in fresh water.

In the majority of cases there is no problem in recognizing whether a particular animal is a marine, a freshwater or a land planarian. It is true, however, that the Maricola and Paludicola are not easy to characterize from a phylogenetic point of view. The defining characters of the three infraorders and the relationships between the three groups have been discussed by Sluys (1989).

The present treatment gives a detailed taxonomic account of all triclads which phylogenetically belong to the marine triclads, i.e. which belong to the monophyletic group or monophylum Maricola. Because of the scattered relevant literature, ranging over a period of more than ninety years, and because of the sometimes incomplete or incorrect species descriptions, it cannot be other than useful for future research to have an up to date account on the taxonomy, morphology and biology of the marine triclads.

Of the aquatic planarians the Maricola have once been monographed (Wilhelmi 1909), the particular book dealing, of course, with a considerably lower number of species than presented here. A few years before, Böhmig (1906) had published his large and detailed study on the morphology of the marine triclads. A couple of years later Graff (1912-17) published his important and extensive review on the morphology and biology of the triclads. The publications of these workers remain an important source of information for students of marine triclads.

The purpose of the present book is fourfold: (1) to provide a general description of important morphological and biological features, (2) to give detailed descriptions of the species of marine triclads known to date, (3) to study the phylogenetic affinities between species (groups) within the Maricola, and (4) to discuss the historical biogeography of the Maricola.

With respect to the first-mentioned goal, much information has been drawn from the literature. When in certain cases no specific information was available on marine triclads but important and interesting studies have been published on freshwater or land planarians, then the results of these studies are discussed in the text, while occasionally reference will be made to other turbellarian taxa. In this way a cadre of morphological

features is presented making possible the evaluation of new findings in the Maricola. This particular section of the book, the General account, is concluded with a chapter on practical methods of study.

The descriptions of the species are based on personal examination of specimens, in the majority of cases. In these descriptions it is attempted to cover the following items: Synonomy, Material examined, Type, Type locality, Habitus, Alimentary system, Male reproductive system, Female reproductive system, Nervous system and Eyes, Body wall and Subepidermal musculature, Karyology, Life cycle, Ecology and Distribution, Diagnosis, Remarks. When a particular section is not mentioned in the text it means either of two things: (1) the features are not characteristic for the species but hold true for marine triclads in general and, consequently, have been discussed already in the General account, (2) absence of data. The first situation generally obtains for the nervous system, and the body wall and subepidermal musculature, while the second is usually encountered in the sections on karyology and life cycle. The descriptions of the species are made rather detailed and comprehensive because in future systematic studies much more features have to be taken into account then are strictly necessary for identification of the animals. Furthermore, the detailed listings of the material examined should serve future workers in this field, enabling them to locate easily relevant material. Collecting dates of the material examined and other relevant dates are specified as follows: day.month.year.

In order to facilitate quick reference the captions of the figures in the General account provide information on the abbreviations used. However, to avoid unnecessary repitition the abbreviations used for the figures in the Systematic account are only specified in a separate section (p.463).

All illustrations have been made by the writer, excepting two habitus drawings and five photographs. The majority of the line drawings are originals, but in cases where no information has been obtained through personal examination, illustrations were redrawn from the original publications (with the exception of the afore-mentioned habitus drawings).

The Systematic account reflects as much as possible the results obtained in the phylogenetic analysis of the Maricola. However, I am aware that these results are open to refinement in future studies and therefore I have adopted a conservative approach to the nomenclature of the taxa. Nomenclatural changes have been kept to a minimum, whilst I have refrained from designating formal ranks to various new categories recognized in the phylogenetic analysis.

Concerning the second goal of this book it was not found enough to publish only descriptions but also considered necessary to provide an identification key. This key enables non-specialists to identify the specimens collected, thus making the book useful not only for specialists but also for marine ecologists.

The manuscript of this book was closed on 1st May 1988 and, consequently, papers published and species described after that date could not be incorporated.

General account

SIZE, SHAPE AND COLORATION

The Maricola represent, in general, the smallest animals among the triclads. Size comparisons are hampered by the fact that the body dimensions of many marine triclads are known only from animals in the preserved state. It is known from animals for which both data are available, i.e. from the living and preserved condition, that the length of fully extended living specimens differs considerably from those in the contracted, preserved state. The length of preserved specimens varies between species from about 0.4 to 11 mm. In the majority of the species, preserved specimens measure 1.5 - 3.5 mm in length. The width of preserved animals ranges from about 0.3 to 7 mm, in the majority of cases being 0.6 - 1.25 mm. The body length of living specimens varies from 1 - 15 mm or even up to 25 mm (*Bdelloura candida*) and the maximum breadth ranges from about 0.5 to 7 mm.

The body shape shows a great variability within the Maricola, but the majority of species is characterized by a more or less elongate body form; variations exist in the presence or absence of auricles and in the degree to which the body ends are rounded or pointed. Conspicuous deviations from this general body shape are formed by species like *Puiteca camica, P. rigida*, and *Micropharynx parasitica* (see Systematic account).

Marine triclads are either pigmented or unpigmented. In the first-mentioned case, the pigment is always situated underneath the epidermis, i.e. the pigment granules lie in the parenchyma. Unpigmented triclads may show a variable coloration due to the various types of food present in the gut which are visible through the unpigmented epidermis.

EPIDERMIS AND BASEMENT MEMBRANE

Epidermis

As in all Turbellaria the body of marine triclads is covered with a one-layered, cellular epidermis. In the epidermis we may distinguish between epidermal or epithelial cells, sensory cells, and anchor cells, the latter being part of the adhesive system (see below). Usually, the epidermis is thicker on the dorsal than on the ventral body surface.

In sagittal view the epidermal cells may be cuboidal, cylindrical or, sometimes, rather flat. On horizontal sections the epithelial cells appear to be of a hexagonal or polygonal shape. The cells are devoid of pigment since the granules always occur in the parenchyma

underneath the epidermis. Not seldom, one observes under the light microscope the plasma of the epidermal cells to have a striate or fibrillar appearance, which was already mentioned by Böhmig (1906). This fibrillar appearance corresponds with the vertically running 'internal channels' which Wineera (1969, 1972) observed in the cells of *Palombiella stephensoni*. Most likely these 'channels' represent aggregations of microtubuli and microfibrils since these are arranged vertically to the basement membrane, according to Bowen & Ryder (1974).

The epidermal cells bear cilia, which are on the ventral surface well developed, but which are usually absent or very short on the dorsal body surface. The basal bodies of the cilia are visible even under the light miscroscope. The anchor cells of the adhesive system are devoid of cilia. The shape and number of rootlets of the cilia have gained some importance in taxonomic studies of Turbellaria (cf. Bedini & Papi 1974, Rieger 1981).

The nuclei of the epidermal cells are situated at the bases of the latter, except for a few species in which the epithelium is insunk or infranucleated. In the last-mentioned case the nuclei lie in the parenchyma underneath the epidermis and are distributed between the subepidermal muscle fibres; they are connected with the cells by means of stretches of cytoplasm. Such happens to be the case in the ectosymbiotic Bdellourids, *Pentacoelum fucoideum, Obrimoposthia acuminata*, and perhaps also in *Jugatovaria spinosa*. Böhmig (1906) reported that the tentacles of *Obrimoposthia ohlini* are clothed with an insunk epithelium.

According to Hyman (1951) in marine and freshwater triclads there is constantly present an auricular sense organ. The sensory cells of this organ are devoid of rhabdites and are arranged in a row along the head margin or at the base of the tentacles. I did not give this feature much attention but, at least found such a zone of cells (cf. Hyman 1951, Fig. 31 H) to be present on either side of the head of *Obrimoposthia acuminata*. Lehmensick (1937) described two sensory patches on the head of *Ostenocula harmsi* (see species description), and Wilhelmi (1909) reported to have observed auricular sense organs in *Procerodes littoralis*; Kawakatsu & Mitchell (1984) described auricular sense organs for *Oahuhawaiiana kazukolinda*. Sensory cells also may occur in isolation anywhere in the ventral or dorsal epidermis (Böhmig 1906, Wilhelmi 1909). Although Böhmig (l.c.) and Wilhelmi (l.c.) both attempted to give a detailed description of the sensory cells, actually very little is known about their structure apart from the fact that they are always provided with well developed cilia. Steinmann (1929) showed that the cilia of the cells in the auricular sense organ establish a water current, which probably relates to a chemotactic function of this organ.

Apart from a few exceptions the epidermis of marine triclads is packed with rod-shaped or slightly curved rhabdites with pointed ends. Usually the rhabdites are dorsally larger and more numerous than in the ventral epidermis. Rhabdites are strongly acidophil; further chemical properties are mentioned in Skaer (1961) and Pedersen (1963) who studied the rhabdites of freshwater planarians. Nothing is known about the ultrastructure of rhabdites in marine triclads but those of freshwater planarians show a dense, granulated inner mass which is bounded by a unit outer membrane (Reisinger & Kelbetz 1964). Rhabdites are formed in rhabdite-forming cells which take part in the turnover of epidermal cells (see Subepidermal Glands).

In a more recent study on the ultrastructure of rhabdites Smith et al. (1982) suggest that there are in triclads two types of rhabdite-like secretions. One type of secretion would occur in epidermal cells or epidermal replacement cells (see Subepidermal Glands) and

the other type in parenchymal gland cells that discharge to the exterior through gland necks. Smith et al. (1982) suggest to restrict the term rhabdites to the last mentioned type of rod-shaped secretion. For the other type the term epidermal rhabdoids should be used. According to Smith et al. (1982) it was epidermal rhabdoids and not true rhabdites that Skaer (1961) and Pedersen (1963) identified in their studies. However, the true nature of rhabdites and dermal rhabdoids is presently far from being clear. Moreover, both types of secretion '...are not distinguishable by light microscopy, and they are similar histochemically...' (Smith et al. 1982: 223-224). Therefore, there are no compelling reasons for abandoning the term rhabdites in morphological descriptions of triclads.

The function of rhabdites has been debated for a long time. Reisinger & Kelbetz (1964) made a distinction between discharge and swelling rhabdites. The discharge type of rhabdite is expelled from the epidermal cells with considerable force and, consequently, performs its action at a considerable distance from the body surface. Rhabdites of the discharge type have been found in *Promacrostomum paradoxum*, various species of *Macrostomum* and in *Bothrioplana semperi*. The swelling type of rhabdite occurs in the Tricladida and, according to Reisinger & Kelbetz (l.c.) in *Megalorhabdites* species (Protoplanellida), and also in *Polychoerus carmelensis* (Acoela), *Monocelis cincta* (Proseriata), *Alloioplana californica* (Polycladida) (Martin 1978). These rhabdites are not 'shot' out of the epidermal cells but expelled in a much less drastic manner. Outside of the epidermal cells the rhabdites increase in size through the uptake of water and, subsequently, dissolve into mucus. Swelling rhabdites perform their function close to the body surface of the animals. Various opinions have been expressed concerning this function.

Böhmig (1906) was of the opinion that the mucus resulting from the dissolved rhabdites served as a protective film in case of injury and also enabled the animals to catch rapid-moving prey. Wilhelmi (1909) found no evidence, after examing injured specimens, for Böhmig's wound protection hypothesis and also rejected the widely expressed opinion that rhabdites formed mucus for the capture of prey. According to Wilhelmi, the prey animals of marine and freshwater planarians are much larger than the animals which would possibly become entangled in the mucus layer, whereas the feeding behaviour of triclads does not seem to relate at all to the production of slime on the body surface. Wilhelmi considered it to be much more likely that the mucus of the expelled and dissolved rhabdites forms a protective layer, or even a capsule, under adverse environmental conditions. With respect to marine triclads the formation of such a capsule has been studied in some detail in *Procerodes lobata* (see species description).

After having studied one archiannelid and three turbellarians, Martin (1978) formulated his hypothesis that rhabdites provide mucus for ciliary gliding. In the three turbellarians examined (a polyclad, an acoel, and a proseriate) rhabdites formed the most common secretory product released on the ventral surface. But in marine triclads rhabdites are less numerous on the ventral body surface than in the dorsal epidermis, which is opposite to what is to be expected under Martin's hypothesis.

In planarians the most plausible function of rhabdites is the formation of a mucus layer which may protect the animals from chemicals and exert a noxious stimulus on predators.

Among the marine triclads only the ectosymbiotic Bdellourids lack rhabdites, which coincides with the fact that in these animals the epidermis is infranucleate.

Basement membrane

In sections prepared for light microscopic, anatomical studies the epidermal basement membrane appears as a densely staining, amorphous line. When the preparations are stained in Mallory-Heidenhain the basement membrane shows a conspicuous bright blue coloration. In the majority of the marine triclads the membrane is relatively thin, but well developed, being about 2.5 µm in diameter. According to Böhmig (1906) the basement membrane of an animal may vary in thickness between different parts of the body. This may well be true, but part of the variation will be due to the fact that some regions of the body will be sectioned at a more oblique angle than other parts because of twisting of the animal.

Böhmig (1906) reported that in the basement membrane of *Procerodes littoralis* fine fibrils were interspersed in the homogeneous ground substance. Wilhelmi (1909) in examining sections of *Bdelloura candida*, observed that the thick basement membrane was homogeneous or showed a weak longitudinal striation, whereas the membrane was set off against the inner surface of the epidermal cells by a double-lined stripe. The observations of these two workers have been substantiated and elaborated by more recent studies. But before discussing the fine-structure, attention has to be paid to the basement membranes of Bdellourids, which will lead automatically to a detailed description of the component parts of the membrane.

It was already known to Wilhelmi (1909) that in some of the ectosymbiotic Bdellourids the basement membrane is highly developed and much thicker than in other marine triclads (Plate 9). Wilhelmi also noticed that in these species the basement membrane was on the dorsal body surface thicker than on the ventral surface. These two characteristics hold true also for some of the free-living Bdellourids, which were still unknown when Wilhelmi wrote his monograph. The following measurements of basement membranes illustrate this point: *Bdelloura candida*: ventral 8.75-10 µm, dorsal 6.25-12.5 µm; *B.propinqua*: ventral and dorsal 1.25 µm; *B. wheeleri*: ventral 2.5 µm, dorsal 5 µm; *Syncoelidium pellucidum* ventral and dorsal 1.25 µm; *Synsiphonium liouvilli*: ventral 5 µm, dorsal 12.5 µm; *S. ernesti*: ventral and dorsal 2.5-5.0 µm; *S. angustus*: ventral and dorsal slightly thicker than 2.5 µm; *Synsiphonium anderssoni*: ventral 1.25 µm, dorsal 2.5 µm; *Palombiella stephensoni*: ventral and dorsal about 2.5 µm; *Nerpa evelinae*: ventral and dorsal somewhat thicker than 1.25 µm; *Oahuhawaiiana kazukolinda*: ventral and dorsal less than 2.5 µm. From this list it appears that only in a few species there is a conspicuous difference in thickness between dorsal and ventral basement membrane.

In these Bdellourids (notably in *B. candida, Synsiphonium liouvilli, S. angustus, Palombiella stephensoni*), it can be seen that the basement membrane sends spiny projections or septa between the epidermal cells. As a consequence, the outer surface of the basement membrane shows numerous cup-shaped 'depressions' in which rest the epidermal cells. The presence of these small projections of the basement membrane was already mentioned by Böhmig (1906) but the feature was described more clearly by Wineera (1969, 1972) for *P. stephensoni*. The thick basement membrane of Bdellourids may have a 'broken' appearance in sections since it is traversed, at irregular intervals, by small channels. The latter correspond with excretory ducts of subepidermal glands which discharge to the exterior, or they are due to stretches of protoplasm connecting epidermal cells and insunk nuclei. Krsmanović described the 'broken' appearance of the thick

basement membrane of the land planarian *Geoplana sieboldi* (Krsmanović 1898: Pl.8, Fig. 11).

In studies on the body wall of the bdellourid marine triclad *P. stephensoni*, Wineera (1969, 1972) found conclusive evidence of the fact that the basement membrane actually consists of two zones, a situation already recognized in *B. candida* by Wilhelmi (see above). One component of the basement mebrane is a thin, dense line immediately beneath the epidermis. The second zone lies entally to the thin line and is much thicker but less dense in structure. Wineera (1972) suggested that the thin line would represent the proper basal lamina, whereas the broader zone would be a 'connective tissue layer'; the investigator found evidence, although not conclusive, for a collageneous nature of the last-mentioned zone. Early ultrastructural studies of the basement membrane of freshwater triclads reported the presence of microfibrils in the membrane (Török & Röhlich 1959, cited in Hori 1979; Skaer 1961). Variations in thickness of the basement membrane between different species, relate to the extent to which the 'connective tissue layer' is developed. In *B. candida* this layer is very thick, whereas in other marine triclads this zone is very thin or, perhaps, absent.

Ultrastructural studies of triclad basement membranes have added much to the light microscopical information. Unfortunately, none of these studies paid attention to the highly developed basement membranes of Bdellourids, or to those of other marine triclads.

Bowen & Ryder (1974) reported that the up to 3 μm thick basement membrane of *Polycelis tenuis* consists of two layers, viz. a thin and finely reticulated one directly underneath the basal cell membrane and a thicker, fibrous layer. Hori (1979) distinguished three structural elements in the 1 to 4 μm thick basement membrane of *Dugesia japonica*. A so-called limiting layer of about 200-400 Å is situated immediately beneath the basal epidermal cell surface. This layer has a uniform electron density. Interiorly to the limiting layer lies the much thicker microfibrillar layer, which measures about 90-130 Å in diameter. The outer surface of the microfibrillar layer is delimited by the limiting layer, and its inner surface is bounded by the cell membranes of muscle fibres or pigment cells. In *D. japonica* the microfibrils run parallel to the limiting layer but in other turbellarian taxa they may show complex three dimensional arrangements (Rieger 1981). The third layer forming part of the basement membrane consists of additional extracellular material which is deposited between the basal foldings of the epidermis and the limiting layer. In *D. japonica* Hori (1979) described this layer under the name of electron-lucent zone. The last-mentioned zone shows osmiophilic striations oriented parallel to the limiting layer.

SUBEPIDERMAL GLANDS

The cells of these unicellular glands lie in the parenchyma and send so-called 'necks' (Hyman 1951) through the epidermal cells for discharge of their secretion to the surface. These gland cell necks contain no gland cell cytoplasm but are merely membranous tubes (Skaer 1961). Hyman (1951) considered these gland cells to be insunk epithelial cells but according to Wilhelmi (1909), and also other workers (cf. Pedersen 1963), this is not the case since the cells would arise during the post-embryonic development from parenchyma cells.

The aberrant dorsal glands of *Obrimoposthia acuminata* will not be discussed here because a detailed account is given in the species description (p.181).

Cyanophilous glands

Although these glands are always discussed under one heading, various histo-chemical types of glands are actually involved. Methodological problems, however, prevent a more detailed classification (Skaer 1961, Pedersen 1963).

In marine triclads the majority of the cyanophilous glands are distributed irregularly in the ventral parenchyma, and they occur much more rarely underneath the dorsal body surface. Conspicuous aggregations of cells may occur in the ventral head region (Wilhelmi 1909) and also in the tail region (Wineera 1969). According to Wilhelmi (1909) and Hyman (1951) the cyanophilous secretion forms the slime over which the animal glides during locomotion. The correctness of this view is strenghtened by the fact that in land planarians which possess a creeping sole, the cyanophilous glands discharge through the sole (Hyman 1951). The same secretion may also protect the planarian from harmful substances or conditions and provide the slime for the capsule that some species form under adverse circumstances (Hyman 1951). In Wilhelmi's (1909) view the cyanophilous secretion would also prevent the erythrophilous secretion from reaching the ventral surface.

Pedersen (1963), who studied the freshwater triclads *Phagocata vitta* and *Dugesia tigrina*, found that the main chemical component of the secretion consists of mucopolysaccharides and that such was in agreement with previous histo-chemical observations of other workers. That the same holds true for marine triclads appeared from the studies of Wineera (1972) who reported that the cyanophilous glands of *Palombiella stephensoni* contain neutral mucopolysaccharides.

Rhabdite-forming glands

In view of their staining properties the rhabdite-forming cells belong to the group of eosinophilous gland cells, but because of their specific products they will be treated separately.

The rhabdite-forming cells are situated in the parenchyma underneath the longitudinal subepidermal muscle layer. The number of these cells is usually larger in the dorsal than in the ventral parenchyma, whereas it is rather variable between and within species. The cells are sac-shaped and relatively large. Different cells show different stages in the condensation of the mucous into rhabdites. In one way or the other, the rhabdites are transferred from the cells to the epithelium. Individual or groups of rhabdites may migrate to the epithelial cells and be taken up by the latter via a sort of phagocytosis (Pedersen 1963). Another mechanism was suggested by Skaer (1961). He found indications of the fact that the rhabdite-forming cells themselves migrate through the basement membrane and become incorporated into the epithelial layer, i.e. they become epidermal cells. This view has been substantiated by the studies of Bowen & Ryder (1974) and Hori (1978) on freshwater planarians. Therefore, rhabdite-forming cells may also be called epidermal replacement cells.

Eosinophilous glands

Single eosinophilous glands are distributed in the dorsal and ventral parenchyma and open to the exterior. Aggregations of these cells occur around the gonopore; the gland cells discharge their secretion into the gonopore and/or open ventrally to the exterior, just around the pore. The last-mentioned glands are usually designated as cement glands. This may be a misleading term if their secretion functions as a kind of lubricant during copulation, as is the view of Wilhelmi (1909). According to Burr (1912), however, the red-staining glands around the gonopore have quite another function. On the one hand the secretion of these glands would secure the gonopores of the copulants against each other, whereas on the other hand it would form the pedicel of the cocoon as well stick the endplate of the latter to the substrate.

The greatest number of eosinophilous gland cells are associated with the marginal adhesive zone (see below). The cells form a ring encircling the ventral surface and discharge ventrally to the exterior, close to the body margin. Aggregates of these gland cells are found in the front and hind end of the body. The gland cell body is bean-shaped and sends a long tube towards the epidermis; this tube branches just before it opens into specialized cells in the epidermis (Wilhelmi 1909, Wineera 1969, see below).

In *Palombiella stephensoni* Wineera (1972) found the eosinophilous glands to be protein in nature.

MARGINAL ADHESIVE ZONE

In the Maricola, but also in the Terricola and the Paludicola, the pores of the greatest number of eosinophilous gland cells are arranged in a ventral ring along the body margins, forming the marginal adhesive zone (Wilhelmi 1909, Graff 1912-17, Hyman 1951). The marginal adhesive bands of the three infraorders are, however, structurally different.

In land planarians without a specialized creeping sole, i.e. animals which use their entire ventral surface during locomotion, the marginal adhesive band is well developed. The secretion is discharged directly through the epidermis and there are no specialized cells involved (cf. Bautz 1977). In other forms, with different types of adhesive structures, the marginal band may be absent (Graff 1912-17).

Also in the freshwater triclads no specialized cells take part in the excretion of the secretion of the gland cells through the epidermis; the substance is simply discharged through the epidermal cells (cf. Pedersen 1963, Bowen & Ryder 1974, Bautz 1977).

A different situation obtains for the marginal adhesive zone of most of the marine triclads. Here the zone is composed of specialized cells into which the eosinophilous glands discharge their secretion. The presence of these so-called adhesive cells or papillae (see Plate 12) was first described and depicted by Claparède (1863) for *Sabussowia dioica*, although Graff (1879) was the first to observe that these structures were arranged in a ventral ring in *Bdelloura candida*. According to Claparède these papillae also covered the dorsal surface of *S. dioica*, but the incorrectness of this statement was already mentioned by Böhmig (1906) and Wilhelmi (1909). Lang (1881c) provided an accurate description of the adhesive papillae and noticed their ring-shaped arrangement in *Procerodes lobata*. Wilhelmi (1909) only added to Lang's observations

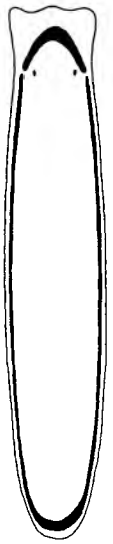

Fig. 1. *Procerodes lobata.* Marginal adhesive zone indicated by black band (after Wilhelmi 1909).

Fig. 2. Marginal adhesive zone in *Bdelloura.*

that in *P. lobata* and also in *P. dohrni* the ring of adhesive papillae shows an interruption at the level of the eyes (Fig. 1). As far as I was able to study the matter in detail, the interruption indeed occurs in *P. lobata* but does not hold true for all other maricolans, as suggested by Wilhelmi. In *Bdelloura* the adhesive band is at the hind end of the body enlarged to a very broad zone, making up a sort of sucker or, better, adhesive tail plate (Fig. 2). In *Micropharynx* there is also an adhesive tailplate but, contrary to Wilhelmi's (1909) view, in this species the marginal adhesive zone lacks adhesive papillae.

In *Pentacoelum punctatum* and *P. fucoideum* the annular zone of adhesive papillae is highly reduced, consisting only of a few isolated papillae at the posterior end of the body.

In *Pentacoelum* attachment to the substratum is effected through the abundant secretion of adhesive cells being discharged through the epidermal cells at the posterior end of the body. In several maricolans the adhesive papillae have been completely lost: *Pentacoelum hispaniensis, Mircopharynx parasitica, Nesion arcticum, Dinizia divae, Dinizia*(?) *sanctaehelenae, Jugatovaria spinosa, Tryssosoma jennyaë, Paucumara trigonocephala, Allogenus kerguelenensis, Puiteca camica, P. rigida.*

Under the light microscope it can be seen that the adhesive cells rise somewhat above the epidermis and that their surface is covered with small papillae, thus giving the appearance of small brushes, as has been aptly depicted by Lang (1881c: Pl.12, Fig. 10; see also Wilhelmi 1909: Pl. 6, Fig. 6; Plate 12). The cells are nucleate and free of rhabdites. Clear visibility of the cells is strongly dependent on the preservation of the animals and the staining technique used.

More recently, turbellarian adhesive systems have come under the attention of electron microscopists. Their studies have shown that not one type of secretion penetrates the adhesive papillae but that two types of gland cells can be recognized within the adhesive system. For that reason the adhesive apparatus has been called the duo-gland adhesive system (Tyler 1976). Light microscopists are not able to recognize these two types of glands but under the electron microscope the gland types can be distinguished by differences in size and density of their granules.

The gland secreting the large, dense granules is believed to provide the adhesive material and is called the viscid gland. The other gland discharges smaller and less dense granules which are believed to contain a product that allows the epidermis to release itself from the substrate to which it was attached by material from the viscid gland. This type of gland is called the releasing gland.

The necks of both types of gland penetrate the adhesive cell. Since this cell appears to be the tension-bearing element, i.e. forms the structure with which the animal is actually attached to the substrate, it has been called the anchor cell.

Tyler (1976) examined the adhesive system of an unidentified procerodid triclad from the U.S. Atlantic coast. He found that the marginal band is usually about three or four anchor cells wide but that they are more numerous at the hind and front end of the body. Some anchor cells occurred on the dorsal body surface at the anterior tip. These findings are in agreement with those of Wilhelmi (1909). Tyler (l.c.) found that the anchor cells are somewhat mushroom-shaped and that the rounded cap projects above the surrounding epidermis. Viscid and releasing gland necks penetrate in small bundles the bases of the anchor cells, after which the individual necks separate and some of them even branch before reaching the outer surface of the cells. Each gland neck or branch opens to the exterior via a separate pore. The viscid gland necks project about 0.7 μm above the cell surface and are surrounded by a collar of usually 12 microvilli; this composite structure makes up what light microscopists are used to call a papilla. The necks of the releasing glands only project about 0.2 μm above the cell surface, not being surrounded by microvilli. Some microvilli may be present between the necks or along the cell's edges. A few sensory processes may also be present on the anchor cell's outer surface. The anchor cells occur in isolation, being separated from each other by epidermal cells (cf. Tyler 1976: Figs. 29 A,B,C).

Tyler (1976) made a plausible case for an adhesive function of the duo-gland adhesive system. He also noted that the so-called adhesive glands in the marginal bands of freshwater triclads (cf. Skaer 1961, Pedersen 1963) are morphologically different from

the duo-gland adhesive system. As has already been mentioned above, also the marginal adhesive zone of the land planarians is morphologically different from the duo-gland system that characterizes the majority of the Maricola. Tyler (1976) is of the opinion that in the Paludicola and Terricola the so-called adhesive glands actually provide (1) a lubricant upon which the animals glide, and (2) a mucous substance which facilitates the suction-cup-like action of a muscular adhesive organ. This may well be a correct interpretation but apart from a different function, the marginal bands of the Paludicola and the Terricola are morphologically quite different from the adhesive zone of most of the Maricola. Therefore, the Tricladida may not be characterized by the duo-gland type of adhesive system, as is suggested in some papers (cf. Rieger & Tyler 1979).

SUBEPIDERMAL AND PARENCHYMAL MUSCULATURE

The epidermis of marine triclads is underlain by a zone of muscles consisting of the following layers: a layer of circular muscles immediately beneath the epidermis, then a thin layer of diagonally running muscle fibres and, entally to the latter, a layer of longitudinal fibres.

The layer of circular muscles consists only of a few rows of fibres; on the ventral body surface this layer may be somewhat more developed than on the dorsal surface. These circular muscles do not form actual closed rings, running from dorsal to ventral and again to the dorsal body surface. But they run from one lateral body margin towards the other, along the ventral or dorsal body surface. As a consequence, the circular musculature of the body margins is only weakly developed (Böhmig 1906, Wilhelmi 1909).

The longitudinal muscle layer shows a different type of organization in that its muscle fibres are arranged into bundles. In general, the number of bundles and also their size (i.e. the number of fibres), is larger in the ventral layer as compared with the dorsal longitudinal muscle layer. This implies that the ventral layer usually is thicker than the dorsal one; in some cases the difference in thickness is very conspicuous, whereas in others there is only a slight difference in diameter. In well developed longitudinal muscle layers the bundles of fibres are arranged into vertical piles (cf. Böhmig 1906: Pl.12 Fig. 1). According to Böhmig (1908) these longitudinal muscle bundles are interconnected in that fibres of one bundle may flow into another. Towards the lateral body margins the number of bundles becomes increasingly less, resulting in the above-mentioned situation that on the lateral body surface the longitudinal muscle layer is very weakly developed.

Probably, the thin diagonal muscle layer is present in all species of marine triclads but, generally, it is difficult to discern it at all. This layer consists of two, crosswise arranged, rows of muscle fibres. The presence of this layer may be observed best in somewhat oblique sagittal sections of the larger species of marine triclads, e.g. *Obrimoposthia ohlini* and *Procerodes variabilis*. Wilhelmi (1909) suggested that the diagonal layer was restricted to certain body regions, viz. the front and hind end, and the marginal zone of the body.

The parenchymal muscles traverse the body from dorsal to ventral surface. The course of the fibres is influenced by the presence of intestinal diverticula, testes, etc.; the fibres follow the contours of these structures and thus may deviate strongly from a vertical orientation. Other fibres show an oblique orientation in that they traverse the body in a more or less diagonal way.

PHARYNX

The pharynx of marine triclads is of the plicate type. In general, the tube-shaped pharynx points backwards and is oriented parallel to the body surface. In the majority of the marine triclads the root of the pharynx is situated at about the middle of the body, although there is a considerable variation between species concerning the position of the root. Exceptions to the usual orientation of the pharynx are *Stummeria marginata*, *Puiteca rigida*, and *Pacifides psammophilus*. In the first-mentioned species the pharynx has an oblique, ventro-caudal, disposition, whereas in the two other species it more or less hangs down from the roof of the pharyngeal cavity.

The size of the pharynx differs considerably between species. In *Procerodes* species the pharynx measures about one-third, in some even one-half, of the body length. In the majority of the marine triclads the size of the pharynx lies somewhere between one-fourth and one-sixth, occasionally between one-seventh and one-twelfth of the body length. *Micropharynx parasitica* derives its name from the fact that its pharynx measures only about one-tenth of the body length; a small pharynx occurs also in *Stummeria marginata*, *Jugatovaria spinosa*, and *Centrovarioplana tenuis*.

During feeding the pharynx is protruded through the mouth opening. In the majority of the Maricola the mouth is situated at the hind end of the pharyngeal pocket. In some species the mouth lies almost at the hind end of the pharyngeal cavity, i.e. it is situated slightly anteriorly to the hind wall of the pharyngeal pocket; this holds true for example, for *Obrimoposthia acuminata*, *Uteriporus pacificus* and also for *Paucumara trigonocephala* from the Bismarck Islands. In species of the genus *Bdelloura* and in *Syncoelidium pellucidum* the mouth opening is at the middle of the pharyngeal pocket, and in *Pacifides psammophilus*, *Jugatovaria spinosa*, *Puiteca rigida*, *P. camica*, *Probursa veneris* and *P. moei* the mouth lies at the front end of the pharyngeal pouch.

Kenk (1930) made an important contribution to the taxonomy of the freshwater triclads by noticing that on the basis of the arrangement of the pharyngeal muscles a distinction could be made between two types of pharynx, viz. the dendrocoelid type and the planariid type. The last-mentioned type of pharynx occurs in the Planariidae and Dugesiidae but also in all members of the Maricola, whereas the other type is characteristic for the Dendrocoelidae.

In the planariid pharynx the arrangement of the muscles is as follows: directly beneath the outer epithelium an outer layer of longitudinal muscles and entally to this layer circularly running muscle fibres; underneath the inner pharynx epithelium are situated an outer layer of circular muscles and an inner layer of longitudinal muscle fibres (Fig. 3). The dendrocoelid type of pharynx is different in that the muscle zone underneath the inner pharynx epithelium consists of alternating rows of circular and longitudinal fibres (Fig. 3). However, there are a number of dendrocoelids in which the pharynx musculature differs from the general dendrocoelid condition, viz. members of the genera *Caspioplana*, *Polycladodes*, and *Acromyadenium* (cf. Zabusova 1951, Gourbault 1972), and of the subfamily Kenkiinae (cf. Kenk 1975, Kawakatsu & Mitchell 1981).

With respect to the Maricola, the longitudinal muscle layers and the outer circular muscle layer of the pharynx usually consist of only a few rows of fibres. The inner circular muscle layer, on the other hand, usually reaches a considerable thickness, thus making up a conspicuous part of the pharynx. This muscle layer may comprise up to about 45 % of the space between inner and outer pharynx epithelium, but usually it shows

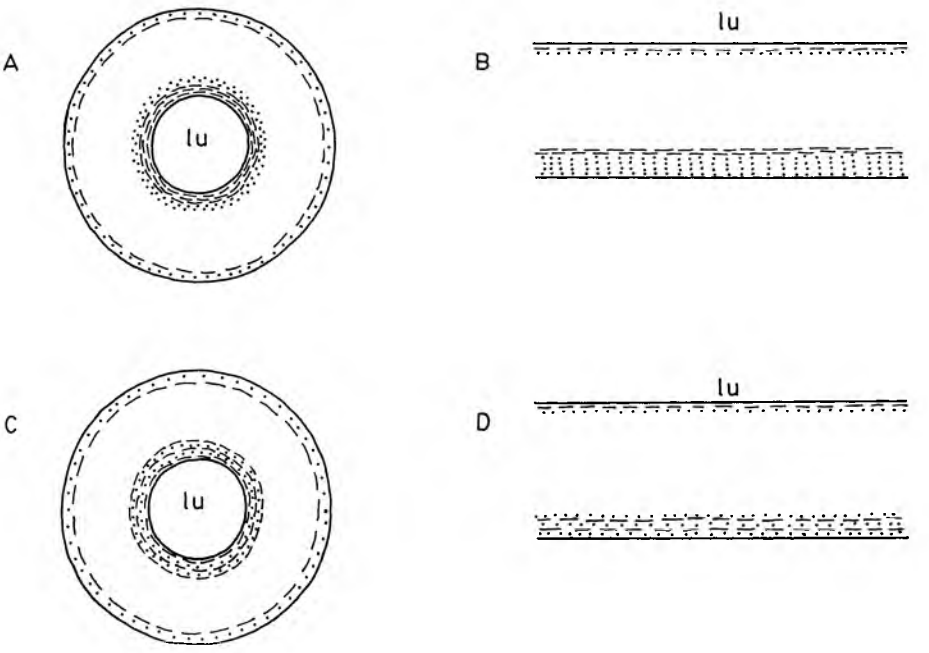

Fig. 3. Diagrammatic transverse and sagittal sections through a planariid (A, B) and a dendrocoelid (C, D) type of pharynx, showing the arrangement of the rows of longitudinal and circular muscles. Abbreviation: lu, lumen.

a lesser, but still considerable, thickness (see Plate 7, 11).

In a few marine triclads the diameter of the outer circular muscle layer has become larger, as compared with the other species. As a consequence, inner and outer circular muscle layer may have about the same diameter. Such may be the case in some specimens of *Procerodes littoralis*; because of intraspecific variability the difference in thickness between the two muscle layers is not always pronounced. In *Procerodes plebeia, P. pacifica, Vatapa gabriellae* and *V. tumidosa*, for example, the outer circular muscle layer shows a considerable thickness, although it is not yet as thick as the inner circular muscle layer. In *Nexilis epichitonius, Dinizia divae, Nerpa evelinae* and *Probursa veneris* the circular muscle layers have about the same thickness; the same holds true for *Stummeria marginata, Centrovarioplana tenuis*, and *Micropharynx parasitica*, but in these three species both circular muscle layers are rather thin. All muscle layers of the pharynx diminish strongly in diameter at the tip of the latter.

Apart from the above-mentioned layers of circular and longitudinal muscles, the pharynx is traversed also by transverse muscles, which run between the inner and outer epithelium. These transverse muscles divide the rows of inner circular muscle fibres into neatly separated, vertical columns. This arrangement results in the situation that in sagittal and horizontal sections the 'columns' appear to consist of piles of cross-sectioned single muscle fibres.

The parenchymatous zone of the pharynx, i.e. the tissue between the outer and the inner zone of muscles, is penetrated by two types of secretion, which traverse the pharynx

in the form of two bands. One band consists of a small zone of cyanophilous secretion beneath the outer circular muscle layer of the pharynx. This band, however, is interspersed with several, loosely arranged, patches of erythrophilous secretion. The second band of secretion is broader than the first one and lies between the cyanophilous zone of secretion and the inner longitudinal muscle layer. This band consists of an erythrophilous secretion which, however, stains differently from the erythrophilous patches lying in the cyanophilous zone; the difference in staining was already noticed by Böhmig (1906) and Wilhelmi (1909). The actual gland cells lie outside the pharynx and are situated in the body parenchyma above, in front of, and behind the pharyngeal pocket.

In sections prepared and stained for light microscopical studies, one may observe at least three types of secretion in the pharynx, as has been mentioned above. In general, the same holds true for freshwater and land planarians. In an ultrastructural study of the pharynx of the freshwater triclad *Polycelis tenuis* Bowen & Ryder (1973) found that at least five types of glands open onto the surface of the pharynx, whereas Ishi (1963, cited in Bowen & Ryder 1973) reported no less than seven types in *Bdellocephala.* It may well be that these glands -one cyanophilous and two types of eosinophilous glands- actually subsume various morphological types of glandular elements, which cannot be discerned in light microscopical studies.

In marine triclads the major amount of secretion is discharged to the exterior at the tip of the pharynx; only the cyanophilous secretion is discharged through the outer pharynx epithelium as well. The number of openings of cyanophilous glands in the epithelium decreases towards the root of the pharynx (Wilhelmi 1909). No secretion is discharged through the inner pharynx lining.

Jander (1897) made a detailed study of the inner and outer lining of the pharynx of, among others, *Procerodes littoralis.* He came to the conclusion that the often cuticula-like lining consists of irregularly-shaped, polygonal cells. The basal surface of the cells gives rise to a number of cytoplasmic extensions of which the largest one contains the nucleus (Fig. 4). Skaer (1961) reported that in *Polycelis nigra* the smaller extensions, i.e. the ones without the nucleus, contain a few very large mitochondria. These protoplasmic extensions reach into the muscle zones of the pharynx. According to Skaer (1961), who studied *Polycelis nigra,* the inner epithelium shows nucleate cells in the proximal section of the pharynx; the number of infranucleate cells increases towards the tip of the pharynx. From Jander's (1897) account it appears that his predecessors already had made the same observation. According to Bowen & Ryder (1973) the extent of insinking in the outer epithelium of the pharynx of *Polycelis tenuis* increases also towards the tip. Inner and outer pharynx epithelium are provided with well developed cilia, and they rest on a well developed basement membrane.

The lining of the pharyngeal pocket consists of a flat or cuboidal epithelium of which the cells are nucleate.

The majority of triclad workers agrees on the nature of the lining epithelium of the pharynx as described above. Hauser (1956), however, holds a different view. According to this worker the bounderies between the cells which Jander (1897) observed in the lining of the pharynx, do not correspond with the walls of cells. Such a differentiation into fields may also be observed in the epidermis of Acoels, which, however, is a non-cellular epidermis. It is Hauser's view that the cellular appearance of the lining of the triclad pharynx is caused by a vaulted system strengthening the structure. According to Hauser, gland cells and their extensions were mistaken for protoplasmic extensions of the

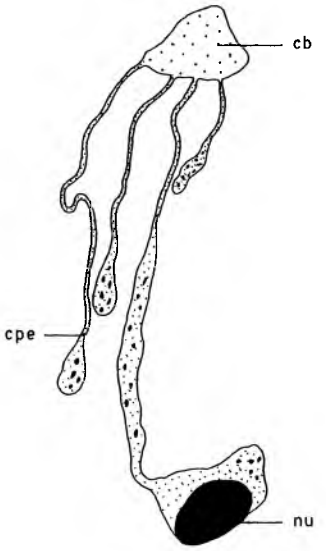

Fig. 4. Cell from the pharynx lining. Abbreviations: cb, cell body; cpe, cytoplasmic extension; nu, nucleus (after Jander 1897).

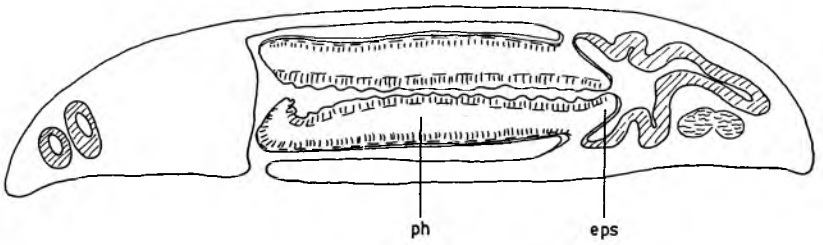

Fig. 5. Sagittal section of *Procerodes sameha* (synonym of *P. dahli*). Abbreviations: eps, esophagus; ph, pharynx (after Marcus & Marcus 1959).

basal cell surface. From Hauser's descriptions and figures it appears that he indeed observed gland cells discharging through the outer pharynx lining, a situation which may easily be observed in well stained preparations and that was already known to the older triclad workers. Hauser's conclusion, however, that the pharynx lining does not represent an infranucleate epithelium is not supported by more recent findings (see above).

In general, the pharynx leads directly into the intestine; occasionally the pharynx may give rise to a sort of cone, at its root, which projects into the intestinal lumen. This cone may be designated as the oesophagus (Fig. 5).

The innervation of the pharynx will be discussed in the section on the nervous system.

FEEDING, INTESTINE AND DIGESTION

The manner of feeding of marine triclads is similar to that found in their freshwater and terrestrial relatives. When the animals have encountered a suitable prey, the pharynx is

protruded from the mouth opening and is thrust into the food item. The secretion from the pharynx glands acts on the tissues of the prey item. Through peristaltic action of the pharynx the more or less dissolved contents of the prey are drawn into the intestine. Marine triclads, and planarians in general, move towards their prey, once detected, and this holds true even for *Bdelloura candida*. During feeding this species is attached to its host -the Horseshoe Crab *Limulus polyphemus*- with its posterior adhesive disk, but when food is offered to the host worms present on the legs and carapax may move to the gnathobases (Lauer & Fried 1977). Planarians are directed to their prey by chemosensory cells situated in the auricular sense organs (see Epidermis and Basement membrane).

Among the triclads *Bdellasimilis barwicki* has an aberrant feeding mechanism in that the whole prey item is taken into the pharyngeal cavity (Richardson 1968, Jennings 1985). This triclad is attached to its host -freshwater turtles- through its two posterior adhesive disks, the front end of the body being extended and making rapid sweeping movements. When the front end touches a prey item the body contracts and curls ventrally, pushing the prey into the widely gaping mouth opening which, subsequently, is firmly closed. Two features make it possible for the pharyngeal cavity to accomodate an entire prey animal. Firstly, the relatively short pharynx only occupies the anterior portion of the pharyngeal pouch, leaving free its posterior section, and secondly the wall of the last-mentioned section shows simple folds projecting into the lumen. The latter feature permits the pharyngeal cavity to expand enormously in diameter in order to accomodate the ingested prey (cf. Jennings 1985: Fig. 4). Once within the pharyngeal pouch the food item is penetrated by the pharynx, the latter withdrawing the contents of the prey through peristaltic action.

Marine triclads are predators as well as scavengers. In their natural environments they feed on small invertebrates such as annelids and crustaceans and also on carrion such as dead fish. However, they may attack also somewhat larger living prey items such as the juveniles of fishes which burrow in the sand (Wilhelmi 1909). The major food components of *Bdellasimilis barwicki* are aquatic oligochaetes and insect larvae (Jennings 1985).

The trifurcate intestine consists of an anterior main branch or ramus, and two posteriorly directed rami, one on either side of the pharynx. The three rami unite just in front of the root of the pharynx and give rise to a very short, backwards directed branch which empties into the pharynx lumen.

There are only a few marine triclads in which the course of the intestinal branches deviates from the ground plan condition with the caudal branches running laterally to the pharyngeal cavity. In *Pacifides psammophilus, Puiteca camica*, and *P. rigida* the anterior gut trunk extends dorsally over the pharyngeal pouch, the caudal branches only emerging posterior to the latter.

The anterior ramus may extend in front of the eyes, as is the case in the majority of the marine triclads, or may terminate behind the brain. In the first-mentioned case, the anterior trunk may give rise to a few pre-ocellar lateral diverticula. The two posterior rami and the post-ocellar section of the anterior trunk, give off also laterally directed diverticula. These diverticula are usually branched or forked. The posterior rami may give rise to short, medially directed diverticula, and in some species the two gut trunks are connected through commissures, which occur behind the copulatory apparatus (species of the genus *Bdelloura, Oahuhawaiiana kazukolinda, Miroplana trifasciata*). In the hind end of the body the tips of the posterior rami may or may not meet, depending on

the species examined. In only a few species do the posterior rami unite behind the copulatory apparatus to a short, single branch, which may give rise to lateral diverticula (*Syncoelidium pellucidum, Ostenocula harmsi, Paucumara trigonocephala, Allogenus kerguelenensis*). In *Pacifides gladiatoris* the posterior rami unite immediately posterior to the pharyngeal cavity, thus giving rise to a long common section between the pharynx and the copulatory apparatus. Because of the great variability between species, details on the shape of the intestinal system will be mentioned in the species descriptions.

The lining of the intestine is composed of two types of cell which rest on a thin basement membrane. The majority of the cells are epithelial or columnar cells, which have a phagocytic function. These cells do not have a clearly defined form because the shape depends on the functional state of the cells. Their nuclei are situated at the base of the cells. The phagocytic cells have many vacuoles and may show numerous, globular inclusions; the cells are non-ciliated.

The second type of cell is the Minotian gland or granular club cell. These cells have indeed the shape of a club or of a pear, of which the narrow base rests on the basement membrane. The nuclei are situated near the base of the cells. The Minotian gland cells are packed with relatively large and densely staining granules.

According to Hyman (1951) these gland cells would not secrete digestive enzymes but function as storage cells for protein. Jennings (1962), however, showed that in *Polycelis felina* (Paludicola) and *Microplana terrestris* (Terricola) the Minotian gland cells secrete endopeptidase for intraluminar, i.e. extra-cellular, digestion of the food. A few years later, the same worker (Jennings 1968) demonstrated the presence of endopeptidase in the Minotian gland cells as well as in the extra-cellular food particles.

Small particles of food are taken up in the columnar cells by means of phagocytosis. These food particles are digested within vacuoles which contain enzymes produced by the cytoplasm of the phagocytic cells. The enzymatic substances involve endopeptidase, acid phosphatase, exopeptidase, and carbohydrase (Jennings 1962, 1974, 1985; Bowen et al. 1974). That the processes described above hold true also for marine triclads, has been shown by the studies of Lauer & Fried (1977) and Davis & Fried (1977) on *Bdelloura candida*. In addition, the first-mentioned workers found also acid phosphatase activity in the ventral epidermis which, according to them, suggests that *B. candida* may obtain metabolites from its host. However, the possibility cannot be excluded that the enzymes detected originated from the food presented to the Horseshoe Crabs (Jennings pers. comm.).

ENDOPARASITES

The holotrichous ciliate *Steinella uncinata* (Schultze, 1851) was described for the first time from the intestinal tract of specimens of *Procerodes littoralis* from the Baltic Sea. Most likely, one year earlier Girard had already observed the same parasites in *P. warreni* (a junior synonym of *Uteriporus vulgaris*; Sluys & Ball 1983), but he considered these ciliates to be the larvae of this triclad (Wilhelmi 1909). Later, *Steinella uncinata* was found in *P. lobata* from the Black Sea and the Mediterranean Sea, in *P. dohrni* and also in *U. vulgaris* from Sweden, and in *P. littoralis* from North America (Wilhelmi 1909).

Many years later, Marcus (1954a) reported *S. uncinata* from *Miava evelinae* and *Procerodella macrostoma* and provided a modern description and also illustrations of the

parasite. The same worker and his wife observed this endoparasite in *Procerodes dahli* (Marcus & Marcus 1959).

Sikora (1963) published a rather detailed study of *S. uncinata* from *P. littoralis* collected on the coast of Poland.

Van der Velde (1975) examined specimens of *U. vulgaris* from Denmark and The Netherlands and found the animals to be infested with *S. uncinata*. Presence of *S. uncinata* is most easily established in squashed planarians. However, it is also possible to examine sectioned material on the presence or absence of these ciliates, although usually in this way no complete picture of the parasites can be obtained. The most conspicuous feature in sections appears to be the large nucleus of *Steinella*. Further examination may reveal the characteristic ring that surrounds the adhesive groove at the front end of the body (cf. Marcus 1954a: Fig. 12), whereas also part of the hooks may be visible. In this way I have been able to establish the presence of *S. uncinata* in the intestinal tracts of *P. littoralis* from France, *Micropharynx parasitica* (Newfoundland; see also Ball & Khan 1976), *Nesion arcticum* (Kenai Peninsula, Alaska), *Uteriporus vulgaris* (North America), *Obrimoposthia wandeli* (Crozets), and *Synsiphonium ernesti* (Macquarie Island).

With respect to the rate of infestation, Sikora (1963) found 32% of the specimens of *P. littoralis* to be infested during the period July 27th-September 28th; usually there were 1 or 2 *Steinella*'s per host, and the maximum number was 6. Van der Velde (1975) found no less than 96% of the specimens of *U. vulgaris* to be infested with *S. uncinata*. The mean number of parasites per host in this case was 6, but Van der Velde also observed, for example, a specimen of *U. vulgaris* with 125 *Steinella*'s in its intestine.

The last-mentioned worker (Van der Velde in litt.) examined 26 specimens of *P. littoralis* from England and found 12 animals to be infested with *Steinella*, and in *P. plebeia* from the same locality one of the three triclads examined possessed three parasites; in *P. littoralis* the mean number of parasites present per triclad was 4.4 and the maximum number 19.

In view of the above it seems reasonable to conclude that *Steinella uncinata* shows no host specificity and may infest marine planarians from all over the world.

EXCRETORY SYSTEM

As in many invertebrates, the excretory system of triclads consists of nephridial tubules and protonephridia in the form of flame cells. The latter are situated at the closed endings of the finer branches of the nephridial tubules. With respect to marine triclads, such flame cells and nephridial tubules were described first in detail for *Procerodes lobata* by Lang (1881c).

Lang (l.c.) observed that in *P. lobata* the nephridial tubules are arranged in two pairs. One pair runs dorsally to the testes, one duct on either side of the body. The ducts follow an erratic course and are cross-connected. The other pair of ducts runs ventrally, each duct being close to the ventral nerve cords. On either side of the body the dorsal and ventral ducts are connected with each other by means of a winding and rather loose cluster of tubules. Such clusters only occur in the intestinal septa. From these clusters fine ducts run towards the dorsal body surface and, according to Wilhelmi (1909), also to the ventral surface and open into the excretion pores.

Wilhelmi (1909) was able to confirm Lang's observations by examining young

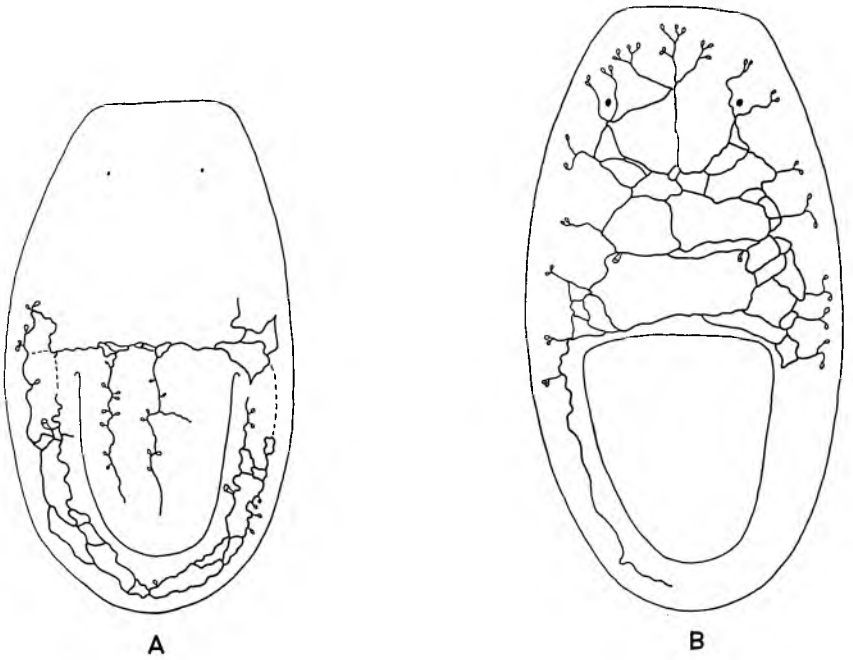

Fig. 6. *Procerodes lobata*, young specimen. Dorsal excretory system in the posterior (A) and the anterior (B) end of the body (after Wilhelmi 1909).

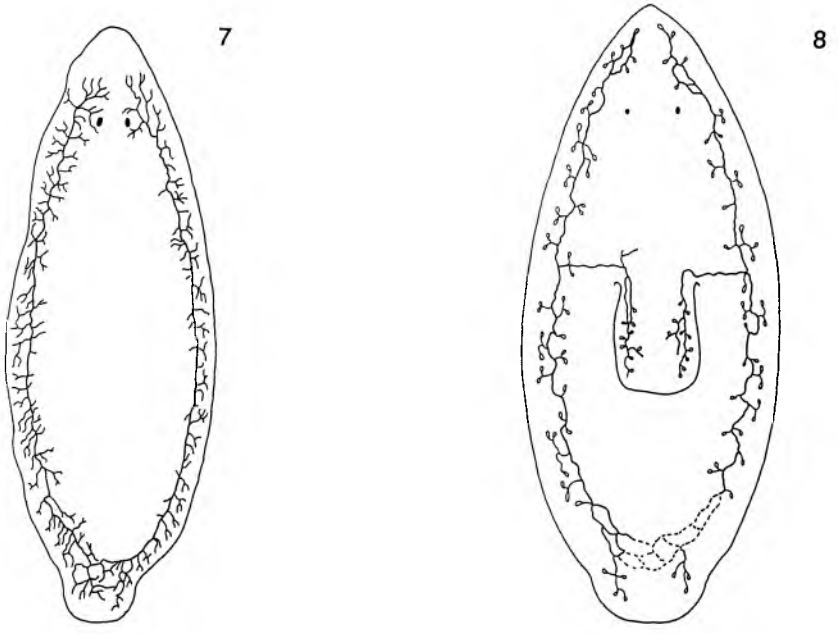

Fig. 7. *Syncoelidium pellucidum*. Excretory system (after Wilhelmi 1909).
Fig. 8. *Bdelloura propinqua*. Excretory system (after Wilhelmi 1909).

specimens of *P. lobata*, and he observed also that the two pairs of nephridial tubules meet in the hind end of the body and that the course of the nephridial tubules on the pharynx is rather variable (Fig. 6). In *P. dohrni* Wilhelmi found the nephridial tubules to have a course and arrangement similar to that in *P. lobata*.

According to Wendt (1888) and Wilhelmi (1909) *Procerodes littoralis* also possesses two pairs of main nephridial ducts (Wilhelmi corrected Böhmig's statement that in *P. littoralis* there would be four pairs of main ducts). Wilhelmi (1909) noted that the ventral ducts were always situated medially to the ventral nerve cords. The course of the nephridial ducts is somewhat different than in *P. lobata* and *P. dohrni*. The excretion pores of *P. littoralis* lie in the lateral body regions. These pores not only occur at the level of the septa, i.e. at the level of the cluster of tubules, but also at other places.

In the two species of Bdellourids for which information is available, the number and arrangement of nephridial ducts is quite different from the situation in the procerodids mentioned above. Wheeler (1894) described the excretory system of *Syncoelidium pellucidum* and Wilhelmi (1909) that of *Bdelloura propinqua*. In both species there is only one pair of main nephridial ducts. According to Wilhelmi these ducts can neither be considered to be situated dorsally, nor ventrally in *B.propinqua*. Both main ducts only give rise to relatively few and short branches. The main ducts communicate in the hind end of the body (Figs. 7, 8).

As will be clear from this short summary, there is only scant information on the arrangement of the nephridial ducts in marine planarians. Almost certainly this is due to the fact that 'The excretory system of triclads is an organ of which the study requires the utmost of the patience of the investigator', as Graff (1912-17: 2831) already remarked. Study of the excretory system can be done best on gently squashed living animals which are unpigmented. Additional information may be obtained from sections.

NERVOUS SYSTEM

The main nervous system in essence consists of a number of bilaterally arranged longitudinal nerve cords, connected with each other by means of various commissures. In marine triclads there are three pairs of longitudinal nerve trunks: one dorsal, one lateral (also called marginal), and one ventral pair (Fig. 9). The marginal nerves are continuous at the front and hind end of the body.

A fine nerve plexus is situated just beneath the basement membrane of the epidermis, forming the so-called subepidermal nerve plexus. Actually, the marginal nerve is part of this nerve plexus and in that respect it is different from the other nerve trunks. The inner, median surface of the marginal nerve is rather smooth, but from its lateral surface leave many fibres which make up a sort of network. The reticulate nature of the marginal nerve has been observed in *Procerodes lobata* (Lang 1881c), *Syncoelidium pellucidum* (Wheeler 1894, Wilhelmi 1909), *Bdelloura candida* (Wheeler 1894, Böhmig 1906, Wilhelmi 1909, Hanström 1926, Elwyn 1936), *Procerodes littoralis* (Böhmig 1906), *Obrimoposthia ohlini* (Böhmig 1906) (Fig. 10). I could observe the same situation in quite a different type of triclad, viz. *Nexilis epichitonius* and also in *Procerodes pacifica*. Hanström (1926) showed that the marginal nerves consist of an accumulation of sensory nerve cells and their neurites, the latter penetrating the epidermis.

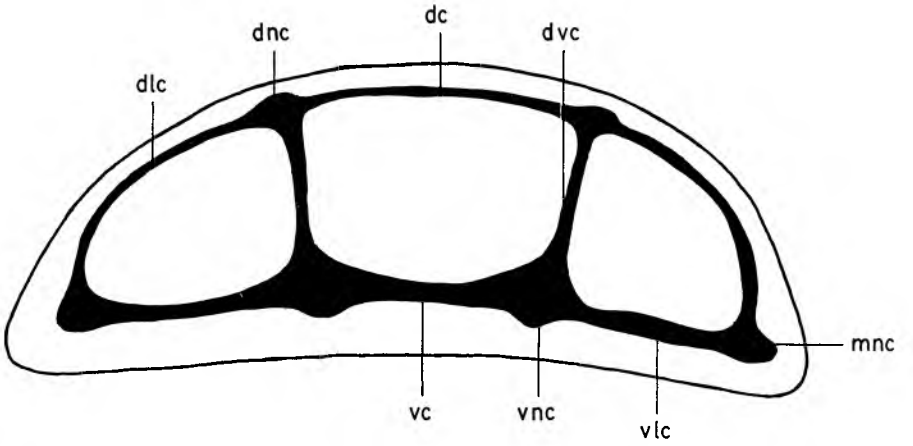

Fig. 9. Diagrammatic transverse section, showing the nervous system. Abbreviations: dc, dorsal commissure; dlc, dorso-lateral commissure; dnc, dorsal nerve cord; dvc, dorso-ventral commissure; mnc, marginal nerve cord; vc, ventral commissure; vlc, ventro-lateral commissure; vnc, ventral nerve cord.

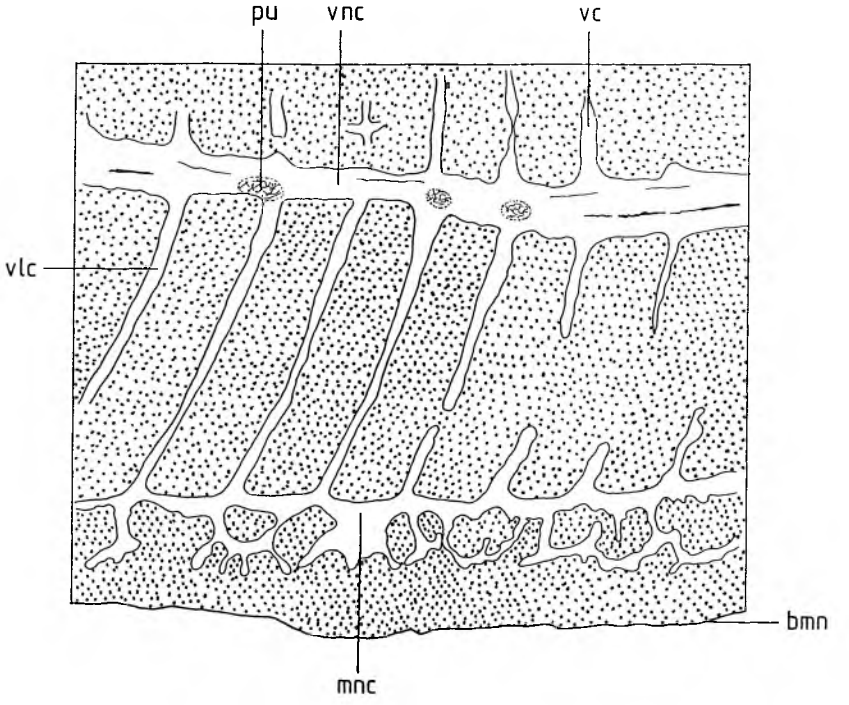

Fig. 10. Diagrammatic horizontal section, showing the marginal nerve cord and its connections with the ventral nerve cord. Abbreviations: bmn, body margin; mnc, marginal nerve cord; vc, ventral commissure; vlc, ventro-lateral commissure; pu, 'Punktsubstanz' (after Elwyn 1936).

Brain

The brain is a bilobed mass which is formed by fusion and enlargement of the anterior portions of the ventral nerve cords. The fusion is only partial since the ventral nerve cords extend forward from underneath the brain in the form of a pair of smaller nerve cords, which at their distal end make contact with the marginal nerve. The connection between both parts of the brain is established by three commissures which are not always easily distinguishable. The anteriormost commissure is situated dorsally of the fused portion of the ventral nerve cords and it connects the two dorsal brain swellings.

From the brain run anteriad several pairs of, what are considered to be, sensorial nerves. Apart from these rather large nerve cords there is one definite sensorial nerve, viz. the optic nerve, which is much smaller. The number and arrangement of the cerebral nerves and other parts of the nervous system which are connected with the brain has been summarized by Wilhelmi (1909) for *Procerodes littoralis* (Fig. 11) and shall here be worked out in some detail.

From the brain run six pairs of sensorial nerves (NI- NVI). The first pair lies on top of the pair of nerves which form the anterior extension of the ventral nerve cords. It is not always possible to distinguish both types of nerves since they may be fused to greater or lesser extent. These anterior ventral nerves are connected with each other by means of six commissures and with the marginal nerves through six pairs of lateral nerves. These commissures as well as the ventro-lateral nerves, form a continuous series with similar nerves establishing a connection between the ventral nerve cords and the marginal nerves, thus making up the characteristic ladder-shaped nervous system. Three pairs of vertical commissures connect the brain with the dorsal nerve cords.

A similar type of brain structure has been found in *P. dohrni, P. variabilis*, and *Obrimoposthia wandeli* (Böhmig 1906, Wilhelmi 1909). In *O. hallezi* Böhmig (1906) only observed four pairs of cerebral nerves and in *O. ohlini* only five pairs.

The shape of the brain correlates with the shape of the head. In *P. littoralis* the brain is rather broad but in *Cercyra hastata* and *Syncoelidium pellucidum* it is elongate.

The brains of *C. hastata, Sabussowia dioica* and *O. ohlini* are different in that some space is left between the posterior brain commissure and the rest of the brain (Fig. 12). The space is filled with ganglion cells and mesenchymatic tissue (Böhmig 1906). Wilhelmi (1909) did not observe such a gap in *Cerbussowia cerruti*. In *Cercyra hastata* and *Bdelloura candida* five pairs of cerebral nerves arise from the brain (Böhmig 1906, Wilhelmi 1909, Elwyn 1936).

The histology of the brain of *B. candida* has been studied in detail by Böhmig (1906) and Elwyn (1936). The brain consists of a central fibre mass or neuropilema ('Punktsubstanz' in the older literature) and an outer layer of ganglion cells and fibres. In horizontal sections it can be seen that both lobes of the brain have in their center an aggregation of ganglion cells, muscles and mesenchymatic tissue, in the German literature designated as 'Substanzinseln'. These 'Inzeln' or 'islands' are in fact part of a columnar aggregation of cells which traverses the brain in dorso-ventral direction (cf. Elwyn 1936: Fig. 6). The brain is surrounded by a glial covering consisting of many glia cells and fibres. In *B. candida* this fibrous glial capsule is well developed but its visibility depends on the staining technique applied.

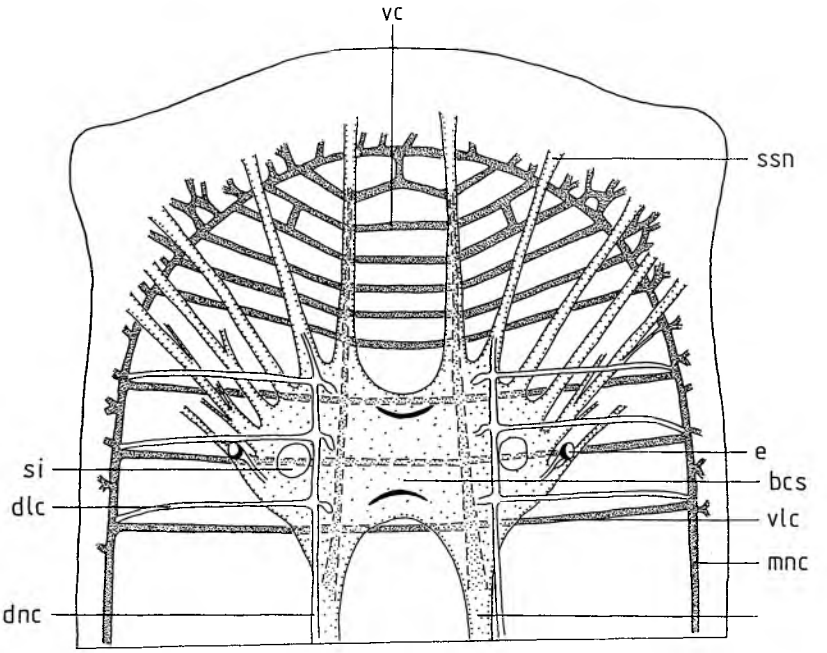

Fig. 11. *Procerodes littoralis*. Horizontal reconstruction of the brain, cerebral nerves, and other nerves connected with the brain. Abbreviations: bcs, brain commissure; dlc, dorso-lateral commissure; dnc, dorsal nerve cord; e, eye; mnc, marginal nerve cord; si, 'Substanzinsel'; ssn, sensorial nerves; vc, ventral commissure; vlc, ventro-lateral commissure; vnc, ventral nerve cord (after Wilhelmi 1909).

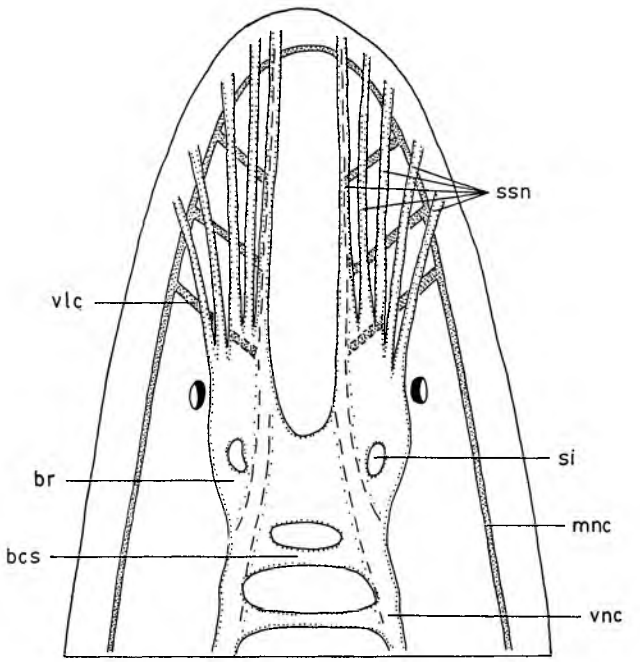

Fig. 12. *Cercyra hastata*. Horizontal reconstruction of the brain, cerebral nerves, and other nerves connected with the brain. Abbreviations: bcs, brain commissure; br, brain; mnc, marginal nerve cord; si, 'Substanzinsel'; ssn, sensorial nerves; vlc, ventro-lateral commissure; vnc, ventral nerve cord (after Wilhelmi 1909).

Nerve cords

Of the longitudinal nerve cords, the ventral cords are developed strongest (Plate 3). In all marine triclads of which the nervous system has been studied in detail, the ventral nerve cords pass into each other at the hind end of the body. As has been mentioned above, the ventral nerve cords are also connected with each other by means of numerous commissures. In the hind end of the body one of these commissures is thicker than the others. In species of *Procerodes* (*P. lobata, P. dohrni, P. plebeia*) this thick commissure lies behind the gonopore, underneath the copulatory bursa (Böhmig 1906, Wilhelmi 1909). But in other maricolans this particular commissure occurs in front of the gonopore, probably due to the fact that in these species the genital opening is situated more posteriorly as compared with the *Procerodes* species. In *Cercyra* the commissure lies at the level of the sclerotized penis tip and in *Sabussowia dioica* underneath the penis bulb (Wilhelmi 1909). In *Probursa veneris* this thick commissure also lies underneath the penis bulb.

In the ectosymbiotic Bdellourids the ventral nerve cords unite in the hind end of the body, just before the caudal disk. From the resulting terminal nerve arch several nerves radiate into the caudal disk. These nerves branch and anastomose, thus forming a nerve plexus. The number of commissures between both ventral nerve cords of *B. candida* ranges from 26 to 42 (Böhmig 1906, Wilhelmi 1909, Elwyn 1936), and in *S. pellucidum* from 20-21 (Wheeler 1894, Wilhelmi 1909). The number of commissures probably increases during growth (Elwyn 1936). In these species there is no thick commissure in the hind end of the body.

The histology of the ventral nerve cords has been examined by Böhmig (1906) and Elwyn (1936). In transverse sections the nerve cords are rounded and appear to be composed of a spongy glial network. Peripherally the glial fibres condense into a fibrillar covering. The nerve fibres are dispersed in the meshes of the glial network. In the ganglions the nerve fibres branch and thus form a centrally placed 'Punktsubstanz'.

With respect to their commissures, the slender dorsal nerve cords show the same type of arrangement as the ventral nerve cords. The dorsal nerve cords extend in front of the brain and eventually fuse with the terminal branches of the cerebral nerves NII (Böhmig 1906, Elwyn 1936). Whether the dorsal nerve trunks in the hind end of the body terminate in the marginal nerve or not, remains an open question.

Pharynx

According to Lang (1881a,b) and Hanström (1926) each of the ventral nerve cords gives off a branch that innervates the pharynx. Both branches are connected by means of circularly running commissures that follow the circumference of the pharynx and which are interpolated between the two types of secretion that dominate the middle section of the pharynx. The result is a sort of nerve plexus. One of these ring-shaped commissures is much thicker than the others.

Böhmig (1906) was unable to find two main nerve trunks in the pharynx of the species which he examined. He only observed a distinct ring nerve and a weakly developed nerve plexus. Wilhelmi (1909) too did not find the pharynx to be innervated by two, continuous and rather strong nerve branches. According to the latter worker the plexus of the pharynx is connected with the main nervous system by means of four branches: one pair of

branches runs from the dorsal nerve cords and another pair from the ventral nerve cords.

The thick ring nerve usually lies in the distal portion of the pharynx but it is not always easy to discern in sections. The ring nerve has been observed in *P. lobata* (Lang 1881a,b, Böhmig 1906), *Cercyra hastata, Sabussowia dioica, Uteriporus vulgaris* (Böhmig 1906), *Bdelloura candida* (Böhmig 1906, Hanström 1926), *Syncoelidium pellucidum* (Wheeler 1894), *Cerbussowia cerruti* (Wilhelmi 1909), *Probursa moei* (Corrêa 1960), and *Tiddles evelinae* (Marcus 1963). I observed this ring nerve in sections of *Micropharynx parasitica*, whereas the nerve was well developed and very conspicuous in stained whole mounts of *Vatapa gabriellae*, *Dinizia divae*, and *Nerpa evelinae*.

Hanström (1926) studied the ring nerve of *B. candida* in more detail and found that it consists of the following elements: (1) sensorial ganglion cells with free nerve endings in the inner and outer epithelium, (2) motor neurons innervating the pharynx muscles, (3) associate neurons of which the dendrites branch within the ring nerve.

The ring nerve in the pharynx is not unique for marine triclads; it is present also in the freshwater forms and, for example, in the Otoplanidae (Ax 1956a).

EYES

Introduction

Marine triclads possess one pair of eyes, excepting *Micropharynx parasitica*, which lacks eyes. The exact location of the eyes varies between species. They may be situated close to the anterior body margin or may lie at a considerable distance from the latter. The eyes may be spaced wide apart or may lie close together. In most cases, however, they lie dorsally to the brain and always underneath the epidermis, i.e. the eyes are situated in the parenchyma. The eyes are connected with the brain by means of an optic nerve. In some cases this nerve may be very short as, for example, in *Nesion arcticum*. In this species the eye cup almost rests on the brain. In *Bdelloura candida* the eyes are set directly on two dorsal brain swellings; in fact they are partly embedded in brain tissue and covered by the glial covering of the brain (cf. Elwyn 1936: Fig. 16).

The structure of the eyes has gained some importance in taxonomic studies of triclads. Since recent summaries on this topic are not available, its discussion here will be broadened to include the Paludicola and the Terricola.

It had been known for quite some time that the most conspicuous feature of the planarian eye is formed by a pigment cup but much less was known about the content of this cup. Detailed information on the morphology of the planarian eye was only obtained through the studies of Jänichen (1896) and Hesse (1897). Concerning planarians, these workers paid attention mainly to freshwater triclads, although land and marine planarians were not neglected. Accounts on the eyes of land planarians may be found too in Graff (1899, 1912-17) and in Schmidt (1902). The work of these earlier investigators has been followed by more recent ultrastructural studies (see below).

In marine triclads, and the two-eyed freshwater planarians, the bean-shaped pigment cups are situated on either side of the mid-line of the body. The transverse axis of the cup may be more or less parallel to the body axis but usually it is oriented at some angle to the latter, in which case the opening of the eye cup is turned towards the antero-lateral margin of the body (Fig. 13).

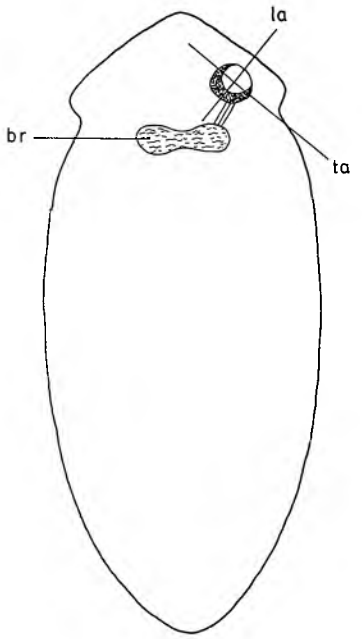

Fig. 13. Orientation of the eye cup in maricolans. Abbreviations: br, brain; la, longitudinal axis; ta, transverse axis (after Jänichen 1896).

General and ultrastructural features

Already Hesse (1897) recognized that in the planarian eye we may distinguish between two regions, viz. the pigment cup and a perceptive part.

Of course, the precise shape of the pigment cup is variable between genera or higher taxa, but a more important variation resides in its histology. In planarians the pigment cup may either be a single cell or may be multicellular, in the last-mentioned case forming a single layer of cells. In both cases the cells constituting the eye cup are packed with brown pigment granules. *Pentacoelum fucoideum* is exceptional in that its eye cup cells are devoid of pigment granules. In Dugesids the pigment granules concentrate in that part of the cell that is turned towards the inside of the eye cup (Hesse 1897, Carpenter et al. 1974), but in other cases such a distribution of granules may be absent or less conspicuous. In all cases the nuclei are situated close to the external base of the cells, i.e. they are located towards the convex surface of the eye cup. The distribution of the granules is influenced by exposure of the planarian to light or darkness (Taliaferro 1920, Carpenter et al. 1974, Durand & Gourbault 1977).

What has been referred to in the above, and in the literature, as the opening of the pigment cup actually is no opening at all. The 'opening' of the eye cup is covered by extensions of the pigment cell (Jänichen 1896, Röhlich & Török 1961, Carpenter et al. 1974). These extensions, however, are devoid of pigment granules and thus form a sort of cornea, in the older literature referred to as 'Cornealmembran', 'vordere Augenmembran', or 'Verschlussmembran'. It will be clear that in the case of a unicellular pigment cup the cornea is formed by the extensions of only one cell. Occasionally pigment granules are present in the transparant membrane (Jänichen 1896, Röhlich & Török 1961, Kishida 1967a). This corneal membrane is a characteristic feature of all types of

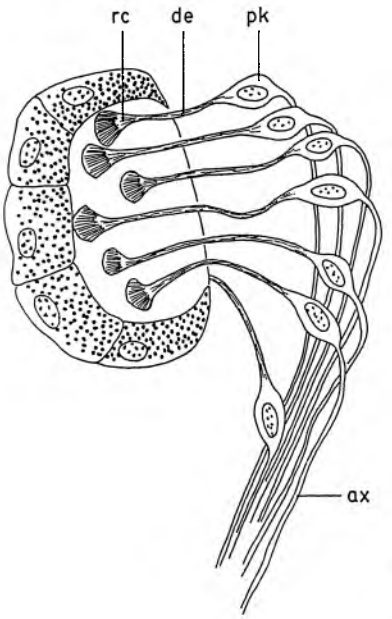

Fig. 14. Optic nerve and multicellular pigment cup. Abbreviations: ax, axon; de, dendrite; pk, perikaryon; re, retinal club (after Jänichen 1896).

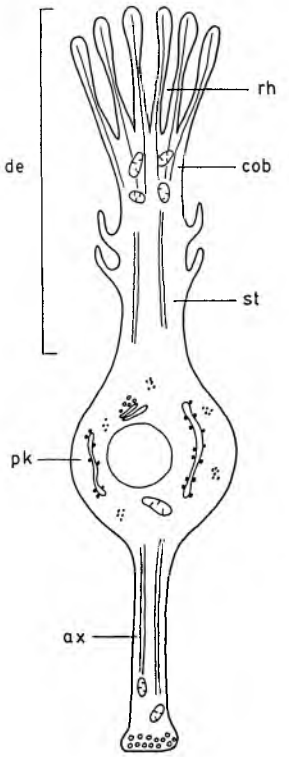

Fig. 15. Diagrammatic reconstruction of a photosensitive neuron. Abbreviations: ax, axon; cob, conical body; de, dendrite; pk, perikaryon; rh, rhabdomere (after Carpenter et al. 1974).

planarian eyes. The fact that in some cases investigators were unable to discern this structure (cf. Hesse 1897: 577) is due to the situation that it is often too thin to be resolved by the light microscope (Röhlich & Török 1961). Moreover, the thickness of the corneal membrane is rather variable. Röhlich & Török (1961) found that in *Dendrocoelum lacteum* the average thickness of the cornea was 0.5 μm but that it varied between 0.05-5.0 μm. With respect to the Maricola, the corneal membrane is developed to its greatest extent in *Bdelloura candida*. Verrill (1893) even referred to the very thick corneal membrane of *B. candida* as a 'front lens', whereas Böhmig (1906) left open the question of the nature of this thick transparent membrane. In type B3 of the planarian eyes (Graff's 'Retinaaugen', see below) the opening of the pigment cup is covered by a well developed layer of transparent cells, the nature of which is still unknown (Graff 1912-17).

The perceptive part of a planarian eye consists of bipolar neurons of which the photosensitive, dendritic ends project into the pigment cup, thus piercing the corneal membrane. In the light microscopical literature these photosensitive ends have usually been referred to as 'Sehkolben' or 'retinal clubs'. Within the eye cup a varying number of retinal clubs lie embedded in a homogeneous mass of electron dense material (Röhlich & Török 1961, Carpenter et al. 1974). The perikaryon of the bipolar neuron lies outside the pigment cup. The axons which arise from their respective perikaryons, together form the optic nerve, which is connected with the brain (Fig. 14). The retinal clubs have been the subject of much detailed study, so that now much is known about their (fine) structure. At first the structure will be described of the type of retinal club that has received most of the attention, viz. the club with a funnel-shaped knob (see Fig. 14). After that it will be easy to find corresponding details in 'Sehkolben' with a different appearance.

Light microscopic studies revealed that the border of the retinal clubs, i.e. the broad part of the funnel-shaped end, showed a row of small rods. Consequently, this section became known as the 'Stiftchenkappe' (Hesse 1897) or 'rod border' (Hyman 1951). According to Hesse (1897) the plasma of the dendrite shows a fibrillate structure. This was especially clear in the funnel-shaped part of the retinal clubs where the fibrils diverged and subsequently communicated with the rods. Not all workers have been able to observe the rods ('Stiftchen') to be so distinct as described by Hesse (cf. Jañichen 1896, Taliaferro 1920, Lehmensick 1937). In view of what we know now about the fine structure of the retinal clubs (see below) these rods must be considered artifacts, due to the agglutination of several submicroscopic structures (Röhlich & Török 1961). In contrast to Hesse (1897), who only distinguished between the rod border and the 'stalk' of the retinal clubs, Jänichen (1896) and Taliaferro (1920) also recognized a 'middle region' (Taliaferro) or 'Kegelstück' (Jänichen), being interpolated between the stalk and the rod border.

Fine structure studies have confirmed the tripartite structure of the dendritic portion of the photosensitive neuron, the respective parts being designated as stalk, conical body and rhabdomere (Fig. 15). These ultrastructural studies revealed that the rod border of the light microscopists actually consists of numerous microvilli, the cytoplasm of which is continuous with that of the rest of the dendrite. Thus, these microvilli are surface enlarging extensions of the cell membrane (Press 1959, Röhlich & Török 1961, Carpenter et al. 1974).

The conical body of the dendrite is characterized by an aggregation of mitochondria and numerous vacuoles, the latter being correlated with the presence of lamellar and

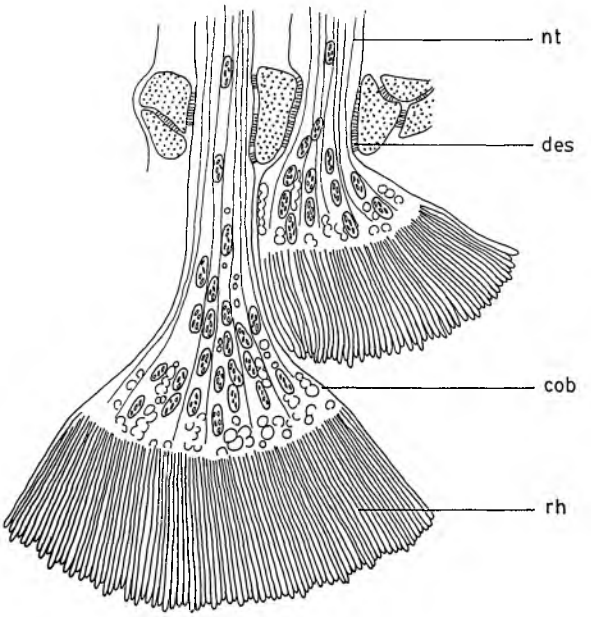

Fig. 16. Ultrastructural features of the retinal club. Abbreviations: cob, conical body; des, desmosome; nt, neurotubules; rh, rhabdomere (after Röhlich & Török 1961).

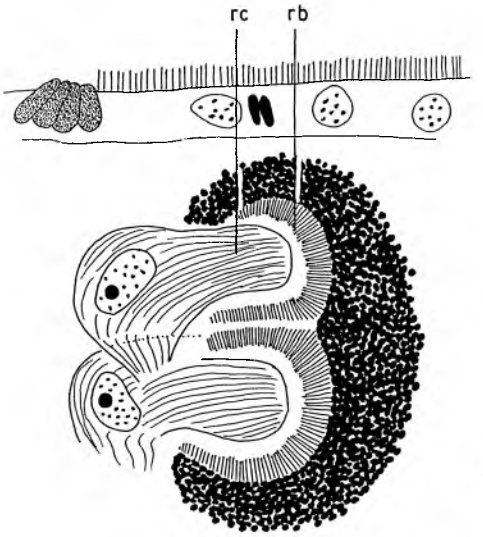

Fig. 17. Eye cup and retinal clubs of *Planaria torva*. Abbreviations: rb, rod border; rc, retinal club (after Hesse 1897).

vacuolar endoplasmatic reticulum (Röhlich & Török 1961, Kishida 1965, 1967a, Carpenter et al. 1974). The conical body corresponds with the 'middle region' of the older investigators.

Neurotubules are present in the axon and the dendrite, but they are more abundant in the latter. According to MacRae (1964) these tubules are unbranched and Röhlich & Török (1961) stated that the neurotubules reach up to the zone of microvilli but do not

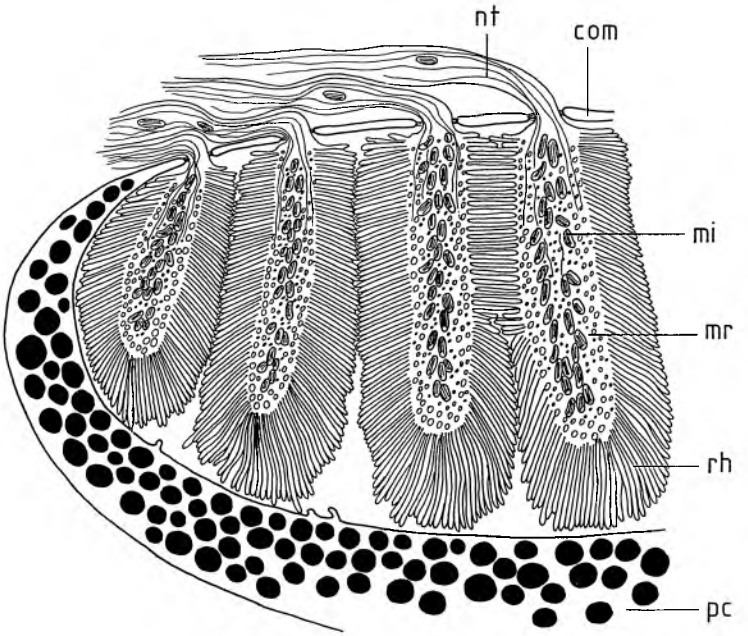

Fig. 18. Ultrastructure of the retinal clubs of *Dendrocoelum lacteum*. Abbreviations: com, corneal membrane; mi, mitochondrion; mr, middle region; nt, neurotubules; pc, pigment cup; rh, rhabdomere (after Röhlich & Török 1961).

enter the latter. Carpenter et al. (1974), however, found that in the distal portion of the conical body the neurotubules give rise to even smaller neurofilaments. At first these filaments are aggregated into bundles of about 10-15 filaments but, subsequently, these bundles branch into smaller units, the latter penetrating the microvilli of the rhabdomere (see also Kishida 1965, 1967a; Durand & Gourbault 1977). Bundles of neurotubuli and filaments may correspond with the fibrils described in the light microscopical literature.

Where the dendrite of the neuron penetrates the corneal membrane, desmosomes connect the stalk with the extensions of the pigment cells (Röhlich & Török 1961, MacRae 1964, Carpenter et al. 1974). According to Kishida (1967a) in *Dugesia japonica* the stalks only penetrate the peripheral parts of the corneal membrane and not the central region.

With respect to the retinal club, much of the ultrastructural findings have been summarized in Fig. 16.

In many triclads the shape of the retinal club only differs from the funnel-shaped type described above, in that it is more rounded and has a much shorter stalk (Fig. 17).

A third type of retinal club was already recognized by Jänichen (1896) and Hesse (1897) who both described it from *Dendrocoelum lacteum*. Only the last-mentioned worker recognized that, despite its different shape, this type of retinal club was structurally similar to the ones already mentioned above. The retinal clubs of, among others, *D. lacteum* have been described as being rod or bottle-shaped (Fig. 19). In the terminology of the light microscopists the core of the rods consists of a fribrillate mass, whereas

the darker staining 'Stiftchen' occur at the outer surface, being oriented perpendicular to the axis of the retinal club. Ultrastructural studies revealed that also in this case the rods are artifacts and that the outer surface of the retinal clubs actually is formed by numerous microvilli. The core of the rod-shaped type of retinal club corresponds with the conical body or middle region of the funnel-shaped type of club. As in the latter case, the core also shows many mitochondria, vacuoles and neurotubules. In this type of retinal club there is hardly any question of a stalk, since the rhabdomere occupies most of the space between pigment cup and corneal membrane (Röhlich & Török 1961). The features of the rod-shaped retinal clubs have been summarized in Fig. 18.

Types of eyes

Eyes of planarians may differ mainly in three aspects, viz. the histology of the pigment cup, and the shape, and also the number of retinal clubs. An overview of the types of eyes which occur in the Tricladida is given below, the main distinction being between eyes with unicellular and those with multicellular pigment cups. Within these two types a subdivision may be made on the basis of differences in retinal clubs and on 'accessory' eye structures.

A) *Unicellular pigment cup*

1. *Planaria torva type* (Hesse 1897). This type of eye is characterized by only a few rounded retinal clubs which lie within the eye cup perpendicular to the longitudinal axis of the latter (Fig. 17). Some variation exists in the number of retinal clubs. In *P. torva* the eye cups contain three retinal clubs but in *Phagocata vitta* only one. In *Polycelis felina* and *P. tenuis* the number of retinal clubs may be 1, 2, or 3. Durand & Gourbault (1975) found two clubs in *Dendrocoelopsis chattoni.*

This type of eye also occurs in many marine triclads. Here the number of retinal cells usually is three. Occasionally, the pigment cup contains four clubs, as in some specimens of *Procerodes littoralis*; *Tiddles evelinae* probably has only one retinal cell in each eye cup.

With respect to the land planarians this type of eye has been reported for *Bipalium kewense.* In this species the retinal clubs have an oval or spherical shape, and their number may vary from 1-8 (Hesse 1897, Graff 1912-17).

2. *Dendrocoelum lacteum type* (Hesse 1897). The difference with the first-mentioned type of eye resides in the shape of the retinal clubs, which are here rod- or bottle-shaped (see also General Features). They are arranged in a row within the eye cup (Figs. 18, 19). In *D. lacteum* the number of retinal clubs may be 30-40 (Hesse 1897, Röhlich & Török 1961). This type of eye has only been reported for *D. lacteum* and *D. punctatum* (Hesse 1897), and a similar type appears to be present in *Rhodax evelinae.*

3. *Lensed eyes.* Within the Tricladida this type of eye is restricted to particular members of the Maricola.

Although already Böhmig (1906) had described the presence of eye lenses in *Obrimoposthia ohlini* and *Uteriporus vulgaris*, he did not distinguish these structures from the

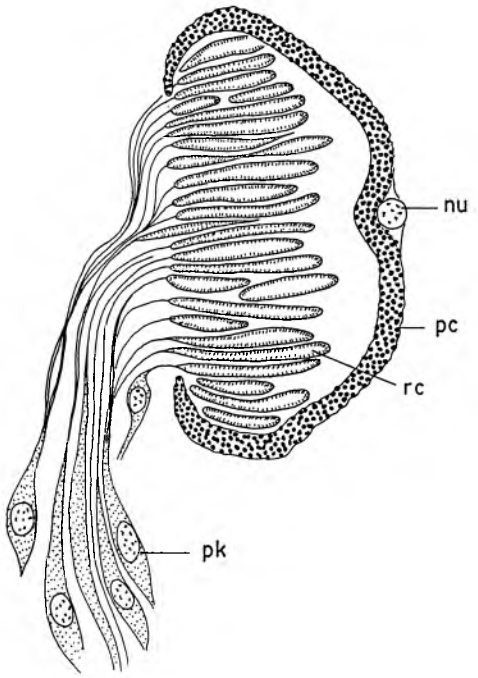

Fig. 19. Section through the eye of *Dendrocoelum lacteum*. Abbreviations: nu, nucleus; pc, pigment cup; pk, perikaryon; rc, retinal club (after Hesse 1897).

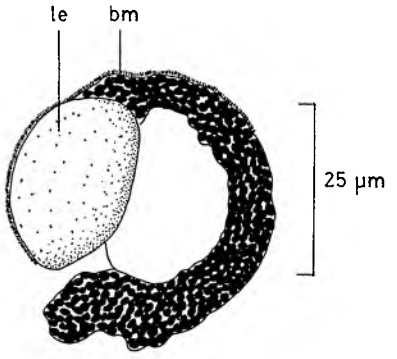

Fig. 20. Section through the eye of *Obrimoposthia acuminata*, showing the distinct lens. Abbreviations: bm, basement membrane; le, lens.

corneal membrane in other species. Böhmig noted only that in these two species one got the impression of a lens. Even Kaburaki (1922) who observed well developed lenses in *Procerodes lactea* and *Paucumara trigonocephala*, is still slightly ambiguous in his description since he designated the particular structure as 'plasmic lens layer', only in his figure referring to it as 'lens'. It was for Lehmensick (1937) in his account of a new species of marine triclad, viz. *Ostenocula harmsi*, to give the first detailed description of eye lenses.

In marine triclads the lens is situated in the 'opening' of the pigment cup and usually extends beyond the outline of the cup (Plates 1, 5, 6, 7); it is of an oval or semi-circular

shape. Lehmensick (l.c.) already noted, quite correctly, that the lens may stain conspicuously different (bright red or blue) from its surrounding tissues, including the remaining parts of the eye. What colour the lens takes, depends on the way in which specimens have been preserved and on the staining technique applied. In other cases, however, the staining of the lens is less conspicuous, even mounting to situations where it is hardly possible to discern it at all. As already pointed out by Lehmensick (1937: 148) it may happen that after staining in Mallory one observes the outer rim of the pigment cup cell to be blue, i.e. that part not obscured by pigment granules. The bright blue line continues over the outer surface of the lens but, according to my observations, does not run along its inner surface, i.e. on that part of the lens inside the eye cup. This thin blue line corresponds with the basement membrane of the eye cup cell and does not represent its plasma, as was the opinion of Lehmensick (l.c.). The plasma of the pigment cup cell remains rather transparent. Lehmensick, however, was correct in his view that preparations suggested that the eye lens resulted from the inclusion of a highly refractive substance into the corneal membrane. Such a situation can be observed quite often (Fig. 20; cf. Lehmensick 1937: Fig. 11).

Among the marine triclads there are a few species in which the eyes contain three, relatively small lenses. This situation is found in *Procerodella macrostoma, Miava evelinae* (Marcus 1954a), and *Synsiphonium ernesti* (Plate 10). In these cases also, the lenses form part of or, in other words, are included in the unpigmented part of the eye cup cell (Marcus 1954a).

In the lensed eyes the shape of the retinal clubs is similar to those in the *Planaria torva* type of eye.

In ordinary taxonomic studies animals are sectioned usually at intervals of 8 μm. This prevents the investigator from observing minute details since an eye will only be present in three or four, relatively thick, sections. In contrast to the freshwater planarians no ultrastructural studies have been published on the eyes of marine triclads. Such fine structure studies may contribute greatly to our understanding of especially the lensed eyes.

3'. *Stummeria marginata type*. Contrary to all other marine triclads the eye cups of *S. marginata* contain numerous retinal clubs of the funnel-shaped type (Plate 1). The clubs show the three well known light microscopical structures, viz. dark staining stalk, light staining middle region or conical body, and dark staining rod border. In front of the opening of the pigment cup there is a large lens.

B) *Multicellular pigment cup*

1. *Dugesia gonocephala type* (Hesse 1897). The pigment cup contains numerous retinal clubs of the funnel-shaped type. The stalk of the retinal clubs may be rather long. The well developed perikaryons lie outside the eye cup and are usually clearly visible (Fig. 21). According to Hesse (1897) the number of retinal clubs in *D. gonocephala* is as large as 160-200, which contrasts strongly with the approximately 25 retinal cells in *D. dorotocephala* and the 25-30 clubs in *Cura pinguis* (Carpenter et al. 1974, Durand & Gourbault 1977). In *Dugesia japonica* Kishida (1967a) found 150-200 retinal clubs in each eye cup.

The differences between the eyes of the multi-eyed land planarians and those of the

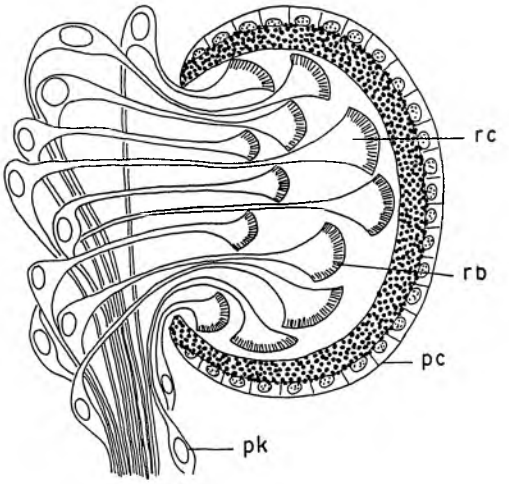

Fig. 21. Diagrammatic reconstruction of the eye of *Dugesia gonocephala*. Abbreviations: pc, pigment cup; pk, perikaryon; rb, rod border (after Hesse 1897).

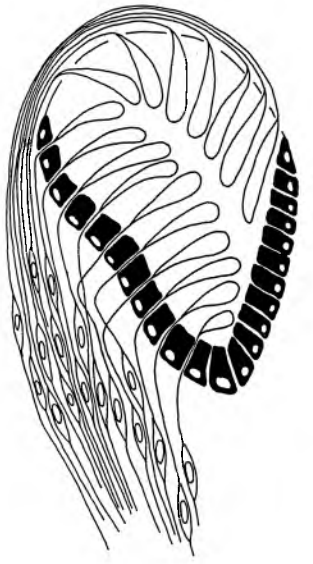

Fig. 22. Horizontal section through the eye of *Microplana terrestris* (after Hesse 1902).

Dugesids concerns their connection with the central nervous system and the way in which the dendrites penetrate the eye cup. In Dugesids optic nerves connect the eyes with the brain, but in the land planarians the optic nerves meet the dermal nerve plexus, according to Graff (1912-17). In the *D. gonocephala* type of eye the dendrites enter the eye cup via its opening, but in land planarians the dendrites penetrate between the pigment cells.

2. *Microplana terrestris type*. The pigment cup is somewhat elongate, instead of rounded. The optic nerve approaches the eye cup from one side and the dendrites

penetrate that section of the cup through openings between the pigment cells and also enter the cup via the corneal membrane (Fig. 22). The shape of the retinal clubs is similar to those found in *Dendrocoelum lacteum*, i.e. they are cylindrical or bottle-shaped (Hesse 1897, 1902). The number of retinal clubs is about 15 (Hesse 1897).

This type of eye occurs also in *Rhynchodemus sylvaticus* (=*R. bileneatus*) (Graff 1912-17) and *R. (Microplana) scharffi* (Graff 1899). The same may hold true for *Geoplana nigrofusca, G. argus, G. ladislavii, Pelmatoplana sondaica, Choeradoplana* (Graff 1912-17: 2933) and *Geoplana steenstrupi* and *G. sieboldi* (Krsmanović 1898: 197), although it is not clear from the treatment of both authors whether the eye cups in these species are multi- or unicellular. Their retinal clubs, however, are cylindrical. For *Pelmatoplana sondaica* Graff (1912-17) reported about 18 retinal clubs and for *Choeradoplana langi* no less than 200.

In *Pelmatoplana maheensis* the flat eye cup contains only three cone-shaped retinal clubs (Schmidt 1902). But in *Geoplana rufiventris* and other neotropical *Geoplana* species, the number of rounded or cone-shaped retinal clubs in a single pigment cup may vary from 1 to 20 (Graff 1912-17).

The *Microplana terrestris* type of eye occurs also in *Polycladus gayi* (cf. Schmidt 1902). The only difference is that in this species the distal ends of the retinal clubs become prismatic or polygonal in shape. The latter feature made Graff (1912-17) consider the eyes of *P. gayi* to be already representative of the type of eye that will be described in the following section. However, Graff's view seems to be stretching the evidence. Schmidt (1902) described clearly that in *P. gayi* the nerve fibres only penetrate the corneal membrane and a particular section of the pigment cup.

According to Graff (1912-17: 2933) the *Dendrocoelum lacteum* type of eye would be much more common in the Terricola than the *Planaria torva* type, since the former occurs in two-eyed as well as in multi-eyed planarians. However, I think Graff only had in mind the shape of the retinal clubs when he wrote this statement, and did not consider the fact that in *Dendrocoelum* and *Planaria* the pigment cup is unicellular in contrast, probably, to most of the land planarians. It will be clear from this section that reliable data for only a minority of the land planarians are available and that much needs to be done.

3. *Platydemus grandis type*. This type represents Graff's (1899, 1912-17) 'Retinaaugen', in the description of which he used mainly *P. grandis* as an example.

These more or less egg-shaped eyes are embedded in a large ganglionic mass that extends from the brain (Fig. 23). The histology of the ganglionic mass is similar to that of the brain, but where it surrounds the eye it is of a somewhat different structure. The retinal cells or neurons form an orderly arranged layer around the entire eye cup. Extensions (dendrites) of the retinal cells penetrate the eye cup via openings between the pigment cells but also enter through the corneal membrane. Within the eye cup these dendrites are connected with the retinal clubs (Fig. 24). These retinal clubs converge towards the center of the pigment cup; their distal ends are polygonal in shape, thus enabling a close packing of the clubs. These closely packed distal ends of the retinal clubs are arranged, as observed in sections, semi-circularly or in a row, depending on the shape of the eye cup. The retinal clubs do not stain very well and appear under the microscope as highly refractive rods. According to Graff (1912-17) these retinal clubs are light-refractive bodies instead of photosensitive structures, but Hesse (1902) already expressed his doubts about this view and considered it to be more likely that they correspond to the

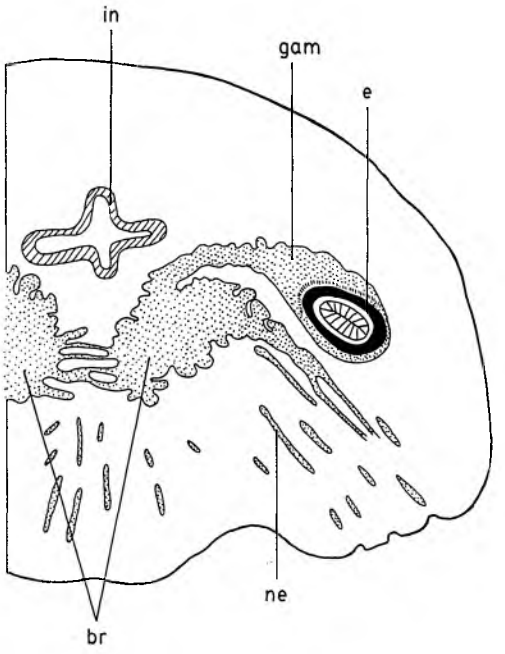

Fig. 23. *Platydemus grandis*. One half of a transverse section through the brain region. Abbreviations: e, eye; br, brain; gam, ganglionic mass; in, intestine; ne, nerve (after Graff 1912-17).

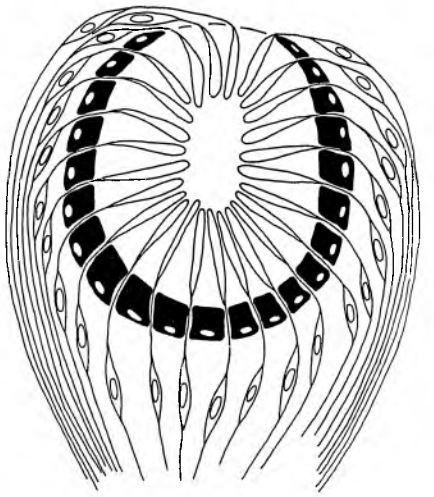

Fig. 24. Diagrammatic reconstruction of the *Platydemus grandis* type of eye (after Hesse 1902).

'Sehkolben' of other planarians. It is unfortunate that since Hesse's (1902: 635) statement that detailed study may provide information on the histology of these peculiar retinal clubs, no worker has taken up the issue.

Excellent illustrations of this type of eye may be found in Graff (1912-17: Pl.XLVI, Figs. 18, 19, 21).

The *Platydemus grandis* type of eye has been reported for *Dolichoplana voeltzkowi*