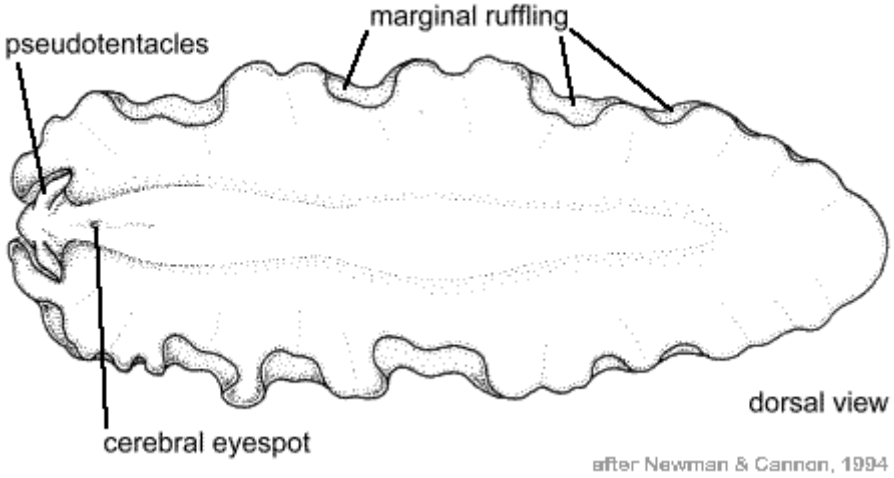
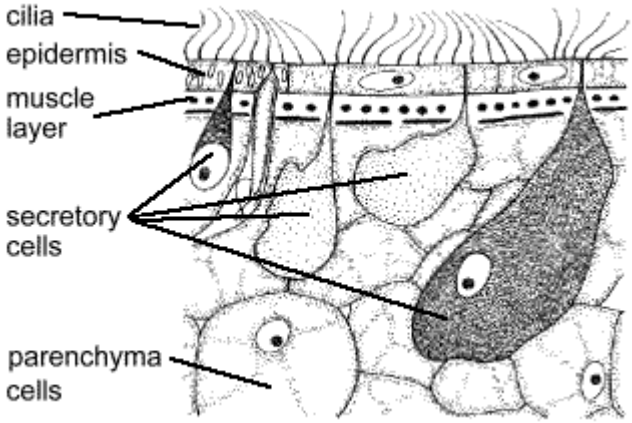


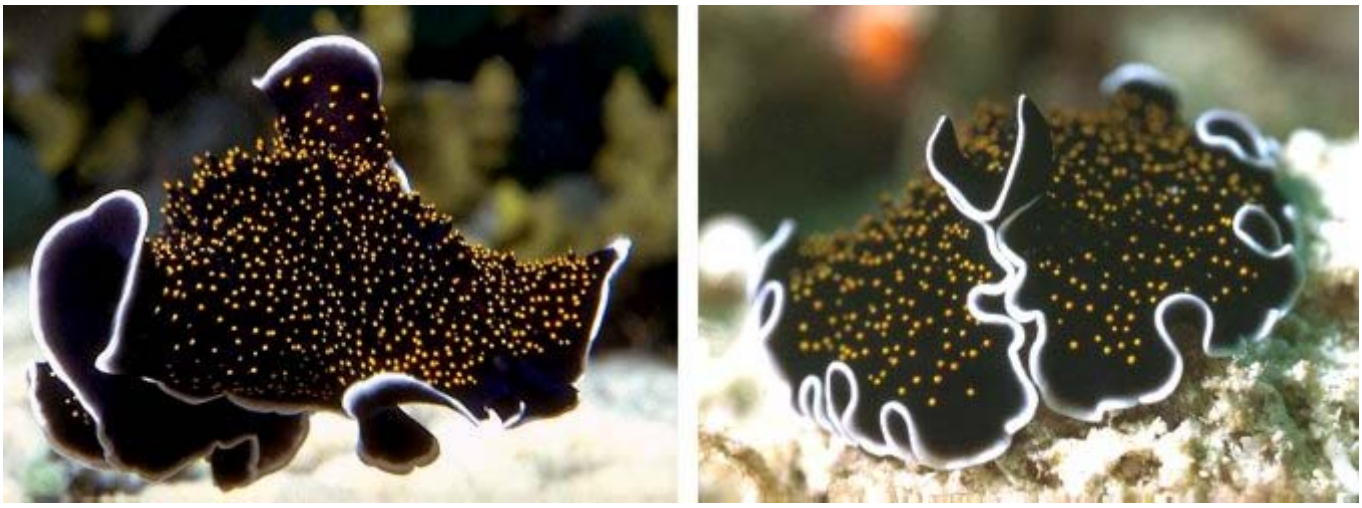
Anatomy of Polyclad Flatworms

As their name suggests, these free living worms are generally dorso-ventrally flattened being no more than a few millimeters thick. Sizes range from less than one millimeter to over 30 centimeters. Most polyclads are extremely delicate, typically elongate and/or oval with a smooth dorsal surface. Some genera, however, display dorsal papillae (*Acanthozoon*, *Thysanozoon*). Since the worms have tentacles at the anterior end and often have brilliant colours they are occasionally mistaken for nudibranchs. But in contrast to nudibranchs, tentacles are mostly simple folds of the anterior margin. They can move along much faster than nudibranchs, are much thinner and tend to break up if handled. Furthermore, they don't have special respiratory organs (gills) as respiration is performed by diffusion through the worms entire surface. Polyclads exhibit a wide variety in colour pattern and texture. They have marginal ruffles tending to increase in number with size. Except opaque species which are black or mainly black, most species are transparent and their internal organs can be seen through the epidermis. Especially the ovaries can be bright red or deep purple and can influence the colour of the dorsal surface.

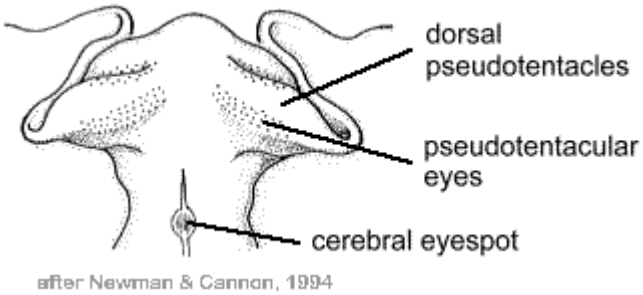


The outer barrier of the worms is the epidermis, a single cell layer of ectodermal origin, with thousands of beating cilia. Underneath, an outer layer of circular muscles and an inner layer of muscles that parallels the body line exist mediating extreme body plasticity. The space between the dorsal and ventral epidermis is filled with parenchymal tissue which contains organs as the highly branched gut and the reproductory system. The parenchymal tissue is of mesodermal origin and holds a high number of secretory cells which discharge mucus and other compounds through epidermal pores. Polylads have a hydrostatic skeleton which is an excellent adaptation to aquatic life. Interstitial body fluid in the mesoderm is kept under pressure in a closed body compartment whereas the muscles of the body walls exert forces against the hydrostatic skeleton providing support for movement. There are two ways of moving. Small species use the beating of the fine hairlike ventral cilia to glide along the bottom. Large species, such as *Tysanozoon sp.* shown on the image below (left panel), are able to swim by rhythmic contractions of body muscles. Throwing the sides of their body this creates a series of undulating waves propelling the worm over ground.

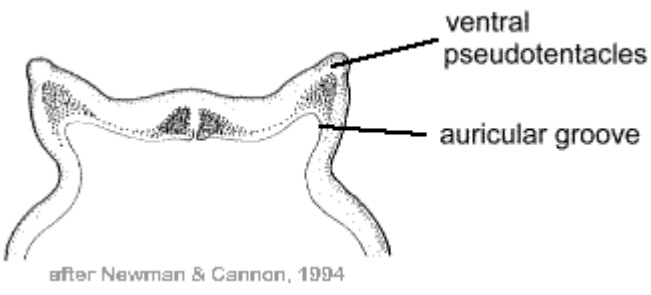
As a feature of bilaterial body shape polyclads are cephalized, which means they have an identifiable head region where nervous functions and sensory structures concentrate. The worms nervous system is ladder-like composed by a pair of longitudinal nerve cords running the length of the body which are connected by transverse commissures. It culminates at the anterior cerebral ganglion knot, which is a large ball of neuronal cells in or near the head. Currently, the small but well-defined brain of some polyclad species serves as model system in neurobiology to investigate brain cytoarchitecture and mechanisms of neuronal repair (see section: Polyclads and Neurobiology). The visible characteristic of the head is the occurence of tentacles which in most cases are folds of the anterior margin (= pseudotentacles). These can be either square blunt, simple, tubular folds or pointed broad flaps. Most common, they look ear-like as shown on the following image where the head region of *Thysanozoon sp.* (right panel) is presented.



The anterior cerebral ganglion knot and its large interneurons resemble the worm's "brain" analyzing nerve signals coming in from numerous photo- and chemosensitive cells which are concentrated mainly on head and pseudotentacles. Additionally, a high number of mechanoreceptors are dispersed throughout the epidermis. Photosensitive cells can be found in the cerebral eyespot where numerous eyes appear to form round clusters. Further eyes are located on the ventral and dorsal pseudotentacles. These eyes are not capable of forming images but are sensitive to changes in light direction and intensity. When flatworms sense bright light they usually retreat to a darker place.



after Newman & Cannon, 1994



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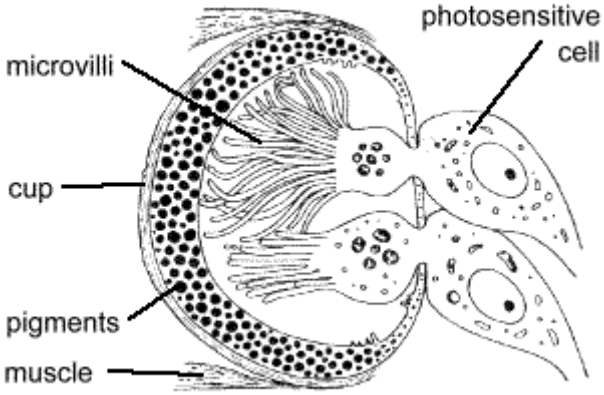


Compared to vertebrates, the organization of polyclad eyes is quite simple. This type of eye, which lacks any lens, has been described as "pigment cup ocellus". Ocelli are part of the cerebral eyespot and are composed of several photosensitive cells and a concave cup. The walls of the cup contain pigments prohibiting light penetration from three sites. The light sensitive portions of the cells, microvilli, are arranged inside the opaque cup such a way that they can only be exposed by light from one single direction. Depending on the angle of incoming light, shadows fall onto the photosensitive structures. Since the cup can be actively rotated by muscles a quickly changing shadow pattern is generated. Corresponding excitatory nervous signals are sent to the cerebral ganglion where the information is analyzed and used for threedimensional orientation and appropriate behavioral reactions.

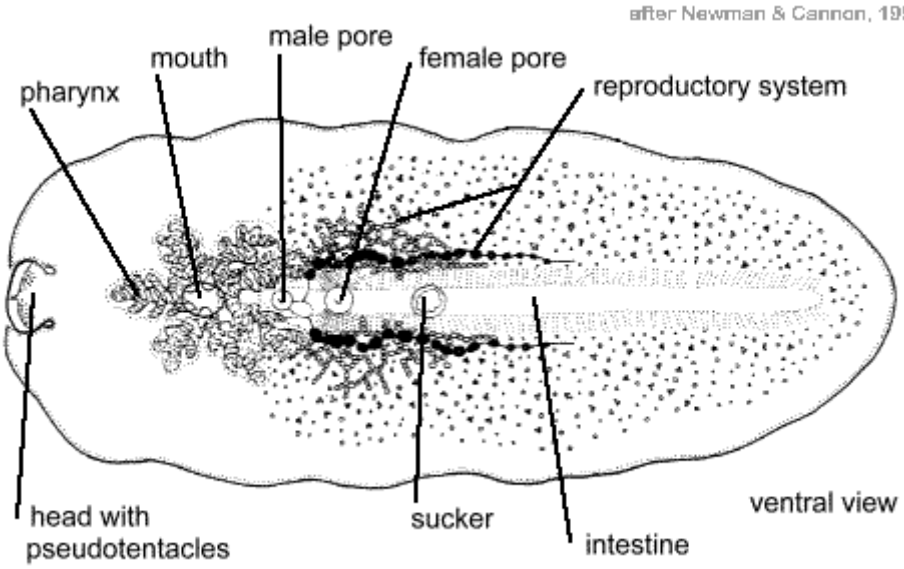
Since the visual sense of polyclads may not be sufficient for environmental orientation, polyclads have a well-developed battery of chemosensory detectors which recognize molecules which are carried to it in bottom currents. Chemical compounds are thought to play a key role for finding food and mating partners. Specific molecules are released from food or mating partner and become entrained in the flow. This creates an odor plume that can be sensed by the worms chemoreceptors. These are particularly located on the ventral pseudotentacles where they are clustered along the auricular ciliated groove. Pseudotentacles in active worms can be seen busy moving around suggesting that this ear-like chemosensory instrument (auricles) helps the worms to find out about direction and exact origin of relevant odors. Therefore, one can conclude that smell is the major determinant of the worms behavior in their natural habitat.

In addition to their auricles and eyespots (see left photo above, lower panel), flatworms have primitive balance organs called statocysts, which consist of a cup of cells with pressure sensitive hairs and small grains of material that can roll around to tell the animal which way is up.

A ventral view on flatworms reveals a number of characteristics which can almost exclusively be observed in dead worms after relaxation, fixation, and preparation on glass slides (= wholemounts). Most of these characteristics are important determinants for taxonomic assignment of species, which is a quite difficult task.

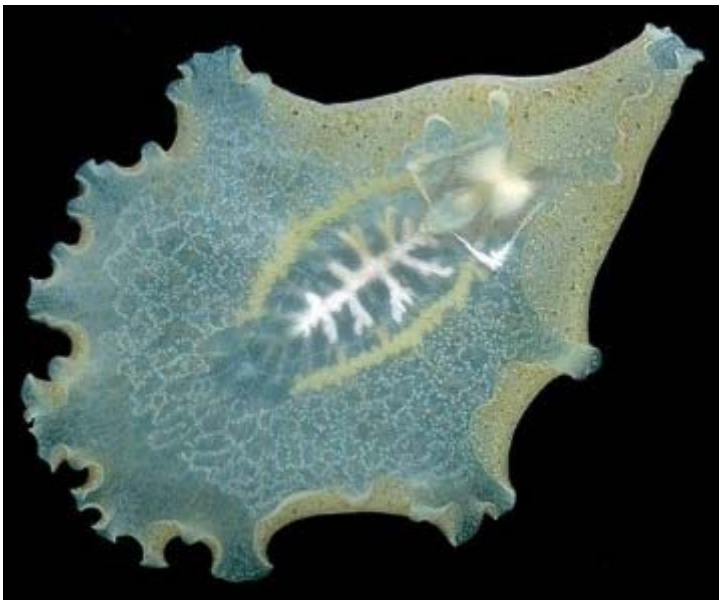
Nearby the head, mouth and pharynx can be detected. In general, polyclads have a pharynx plicatus. This type of pharyngeal tube exhibits a longitudinal and a concentric muscle layer which can extremely change the shape of the pharynx and can pump fluid into the gut cavity. Furthermore, it features separate pharyngeal pocket where it is retracted when not in use. The

pharynx can exhibit various shapes from tubular, round or oval, to highly ruffled with numerous pharyngeal lobes. For feeding, the pharynx is protruded from the mouth and in some species of the genus *Pseudobiceros* it can expand to the same size as the whole animal to engulf prey totally.



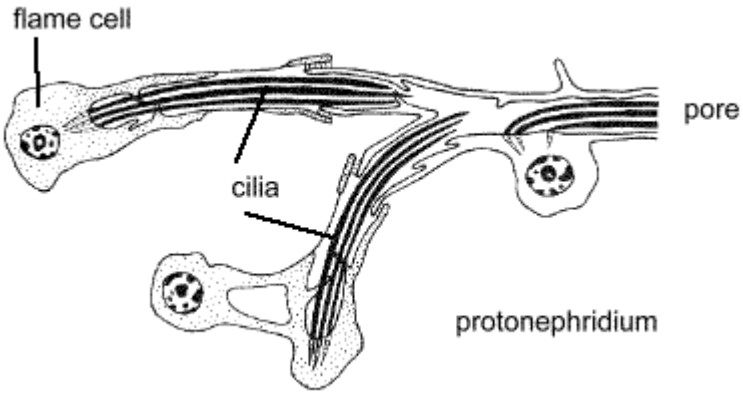
At the center of the ventral side, species of the suborder *Cotylea* possess an adhesive organ, called sucker. In situ observations show that this organ is used to adhere animals to their substrate. It may also facilitate capturing of small invertebrates and ingestation of food. Occasionally, specimen of the genera *Pseudobiceros* and *Pseudoceros* with two unequal sized suckers have been found.

Another species specific characteristic of polyclads is the anatomy of the male and female reproductory system. Polyclads are hermaphroditic. They have both, male and female reproductive organs, producing both egg and sperm. In adult worms, which are mainly engaged in reproduction, a high percentage of the body volume is made up by testes and ovaries. In most species, these are scattered and located ventrally and in the dorsal parenchyma, respectively. However, from the outside, only male and female gonopores can be detected. In general, the male pore is found just posterior to the pharynx and holds the penis papilla and the penial stylet, organs which are protruded for mating. Species of the genus *Pseudobiceros* are characterized to have a double male reproductory system with two male pores and male apparatus. The female pore is always clearly separated from and located posterior to the male pores. Most species (*Pseudoceros*, *Pseudobiceros*) have a single female pore, however, the genus *Nymphozoon* has multiple female pores. The female reproductive system consists of ovaries, yolk and shell glands, a seminal receptacle and an uterus where eggs are fertilized. After mating (see section: Mating and Reproduction) sperm injected into the female body tissues (hypodermal insemination) migrate to the female reproductory tract and move to the seminal receptacle for storage. Eggs from the ovary pass into the oviduct, where they are fertilized by sperm from the seminal receptacle and coated with yolk and tough shell material secreted by the shell glands. Then they pass through the genital pore and are deposited as an irregular shaped eggmass.



Besides the reproductory system, the gut with its numerous lateral intestinal branches is the second organ which accounts for a high percentage of the worms body volume. For transporting nutrients to all body cells the intestinal system extends almost throughout the entire body and is coated with beating cilia. Except in translucent worms (*Aquaplana sp.*) the distribution of the anastomosing intestinal branches and their anatomical details are difficult to observe. Since polyclads have a blind digestive system, undigested material has to be expelled through the pharynx, the same opening through which food enters.

The photo at the left (PHOTO © Bill Rudman) represents a ventral view of *Paraplanocera oligoglena* and shows most of its organs through the almost transparent body wall. The white branched central structure is the highly ruffled pharyngeal tube (pharynx plicatus) which can be everted through the mouth which is located in the center of the body. The pale whitish network extending through most of the body is the multi-branched gut which gives these worms the name "polyclad" (greek = many branches). All the other organs are part of the male and female reproductive systems.



For excretion and osmoregulation, polyclads have specialized functional units, called protonephridia (singular protonephridium). They resemble a network of two or more closed longitudinal branched tubules running the length of the body. These specialized structures control osmotic water balance and work in much the same way as kidneys removing liquid waste. A protonephridium branching throughout the body is capped by highly specialized cells with cilia projecting into cup-like structures. Since the beating of the cilia is likened to a flickering flame, the name of this cell is "flame cell". Several of these flame cells are connected to cells with tubular function. Interstitial fluid loaden with nitrogenous waste is forced into the tubule and transported by the concerted action of flame cells producing a current along the tubular system to one or more excretory pores where waste is secreted. The protonephridium is an example of primitive kidneys and is considered as both an excretory and osmoregulatory system.

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