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The molluscan eyes

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Abstract

Different kinds of photoreceptors found in mollusks are briefly explained, presented in a growing complexity pathway, from sprayed photoreceptors, ocelli, eyecups, opened eyes, closed eyes with lens up to bicameral eyes. This possibly denotes an evolutionary alignment. The mollusk groups that possess each type are explored, because of the relative plasticity of them, little phylogenetic inferences are possible. One of them are the appearance of photoreceptors as a synapomorphy of Testaria; another is the presence of cephalic eyes are synapomorphy of a gastropod branch uniting Vetigastropoda + Adenogonogastropoda (Neritimorpha + Apogastropoda) here named Ommatogastropoda new division. In Cephalopoda the opened eyes are one of their synapomorphies, with the bicameral eyes discussed as synapomorphy of Coleoidea or Coleoidea + Ammonoidea.

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Introduction

The eyes are photoreceptors, i.e., structures that detect photons – light. They do not appear suddenly in evolution. They are the tip of a complex evolutionary way starting from simple photoreceptors splayed in the exposed integument or other structures, only able to detect light and dark, culminating in an extraordinarily intricate structure capable of detecting images as you are using right now for reading this text.

As the Mollusca are incredibly complex creatures, eyes evolved several times in its different branches independently, as much as, at least in cephalopods, the eyes reached a complexity comparable to the higher vertebrates. However, observing the appearance of eyes in mollusks, we are left with the impression that the formation of an eye is not such an extraordinary phenomenon after all. As we will see below, eyes are not only found in the cephalic region, as we imagine to be the usual. Eyes or eyespots, even with some complexity, are found in mantle edge, in gill tip, in aesthetes, in siphon, etc., which show us that the eye evolution is slightly flexible.

Of course, this paper deals only with eyes in adult forms. Larvae eyes, eyespots or ocelli are another complex issue that is not the present scope. An example is the polyplacophores, in which the adults lack any kind of cephalic eye, but their larvae are always represented as bearing a pair of cephalic eyespots. Additionally, the relative position of the eyes in the body, e.g., its relationship with cephalic tentacles in gastropods; and any additional appendages, as, e.g., presence of ommatophores, are not explored herein. They will be, however, subject of a future Malacopedia issue.

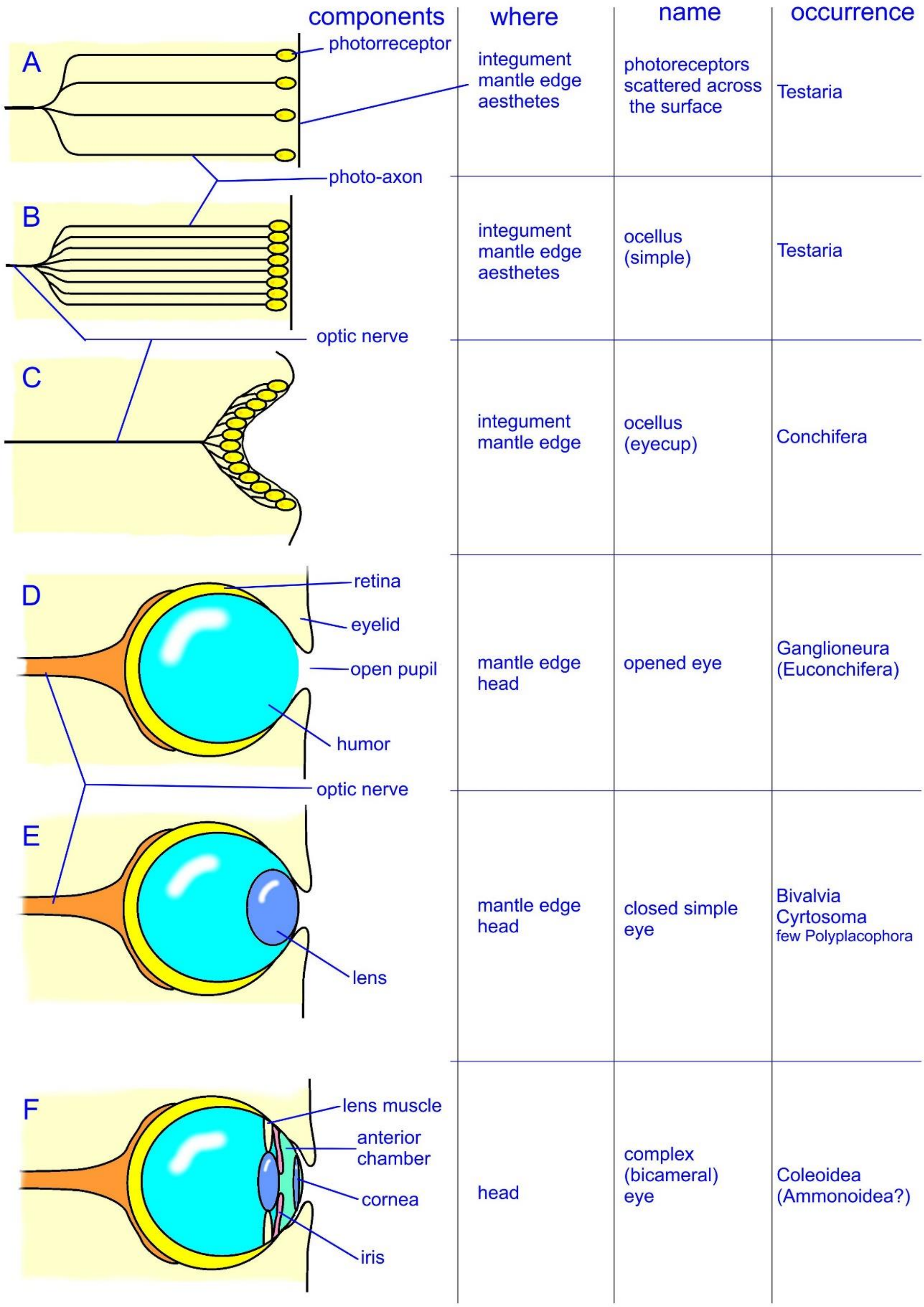
Types of photoreceptors and their possible evolutive order

The possible evolutive steps from the simple presence of photoreceptors up to a complex eye is schematically summarized in Fig. 1 (A to F). The first step is the appearance of **simple unicellular photoreceptors** (Fig. 1A) splayed in any exposed area, particularly in the integument, mantle edge or in the aesthetes (further explanations below), usually mixed with other receptors, such as chemical, mechanical, etc., which, in conjunct, give to the animal information about the surrounding environment. Splayed photoreceptors are found in Testaria, being, thus, a synapomorphy, as nothing similar has been found in both aplacophoran branches. The usual aspect of a photoreceptor cell is having a photosensitive nervous cellular body, located close to the epithelium's surface. From it, a photo-axon arises, running deeper through the local conjunctive tissue. The axons come together to form an optic nerve, which in turn runs to the central nervous system. Splayed photoreceptors can be found even in mollusks bearing other kinds of eyes or ocelli, being both, thus, not mutually excluding. The function of splayed photoreceptors is merely the detection of light-dark impulses, as they are not sufficient for producing images.

The next step in complexity is the formation of an ocellus (Fig. 1B). The **ocellus** is merely the accumulation of photoreceptors in a same place, with the organization similar to the preceding one, but with the benefit of having much more receptors in an important area, capable of capturing light stimulation. Despite being more efficient, the ocellus still has the function of capturing light-dark impulses only, as it does not look capable of producing images as well. The occurrence of ocelli both, in the body and in the taxonomy, is the same as that of splayed photoreceptors.

An additional step in the photoreception is the formation of an **eyecup** (Fig. 1C), which, in general, is an ocellus slightly more complex. The concavity and further increase of photoreceptors improve the photoreception, making it an almost retina. The remaining nerve organization is also usually more complex, and the formation of the optic nerve is more individualized, as much that the animal usually has few (a pair) of them. Eyecups usually are found in Conchifera, in cephalic integument or in mantle edge. Images are still not formed.

The next step is an additional complexity of the eyecup, becoming deeper, with much more receptors, creating a rather spheric form, forming the **opened eye** (Fig. 1D). The photoreception is promoted by a true retina, the internal space is confined by eyelids. Secretory cells produce a dense and transparent humor. The eyelids are capable of controlling the quality of light, and the humor distributes the light more efficiently than the water itself. The retina is like an epithelium of photoreceptors, capable of capturing images; the more receptors, the more detailed the images are, equivalent to having more pixels. Opened eyes are present in some basal branches of Ganglioneura



1: Different arrangement of photoreceptors found in Mollusca, synoptic table. **Column 1**: schematic representations of different kinds in order (A to F) possibly denoting an evolutive direction, not in the same scale (A-C are usually much smaller than D-F). **Column 2**: main components of each type, homologous structures are only indicated once, but maintained in the same color. **Column 3**: usual regions of the body in which these structures occur in mollusks. **Column 4**: the name of the structure usually has (check synonyms in text). **Column 5**: taxonomic occurrence of each kind, some are synapomorphic (e.g., A, F), while other the occurrence is dispersed. See text for more details.

(Euconchifera) classes. In Gastropoda, it is found in Pleurotomatioidea amongst the Vetigastropoda. In Cephalopoda, the nautilids (possibly all nautiloideans) have it. In Bivalvia, some branches have opened eyes in mantle edges, such as, e.g., some arcids.

The next evolutive step is the **simple closed eye** (Fig. 1E). It is basically similar to preceding one, with the addition of the lens allocated in the eye aperture. The lens is a transparent hard structure capable of converging the light, much more efficiently than the humor itself. The lens gives the eyes the capacity of detecting images in an ampler region, and focuses it more directly to the retina. It seems that this type of eye has no capacity of contracting the lens for modifying the focus, but, depending on the size, it is already capable of capturing images. This kind of eye is widespread in gastropods, mainly as cephalic eyes, where obviously there is always a pair, but also, more rarely, in the mantle (see below), with a variable number. It also is commonly found in several bivalves, particularly in pectinoideans (see below), in multiple numbers. Admirably, some polyplacophores also have eyes with lens in the girdle and in aesthetes, such as, e.g., *Onithochiton neglectus* (Boyle, 1969).

The next type, the **complex bicameral eye** (Fig. 1F), is a huge modification in the complexity of the previous step. It is called bicameral because it has a posterior camera, homologous to the remaining kind of eyes, bearing humor, but it developed an anterior camera, usually fulfilled by aqueous humor, with additional structures. There is a cornea, a superficial lens that converge the light; the iris, a muscular membrane able to control the amount of light entering the eye; a muscular belt surrounding the lens, capable of compress it, modifying its diopter, giving to the animal the capacity of focusing to objects close or far to it. These modifications make the eye much more efficient and truly capable of seeing images. In mollusks, only coleoidean cephalopods presently have this kind of eyes, which are amazingly similar to the mammals' eyes like ours. Coleoideans' eyes and ours are similar in almost all details, being an astonishing convergence. One of the few differences that can be noticed is in relation to the retina. Cephalopods retina is more efficient, as detect the light directly, while in our retina the detection of light is indirect, i.e., the detection is done after the reflection of the light in the background of the retina, as our photoreceptors (rods and cones) are turned backwards!

The order that the photoreceptors were explained above is in clear increase of complexity. It mostly possibly indicates that it can denote an evolutionary pathway, which, in an overview, is recorded in the embryogenesis of the more complex structures (e.g., Guerra & González, 2001, in a squid).

After this introductory explanation on the different kinds of photoreceptors, a brief taxonomic explanation is provided following.

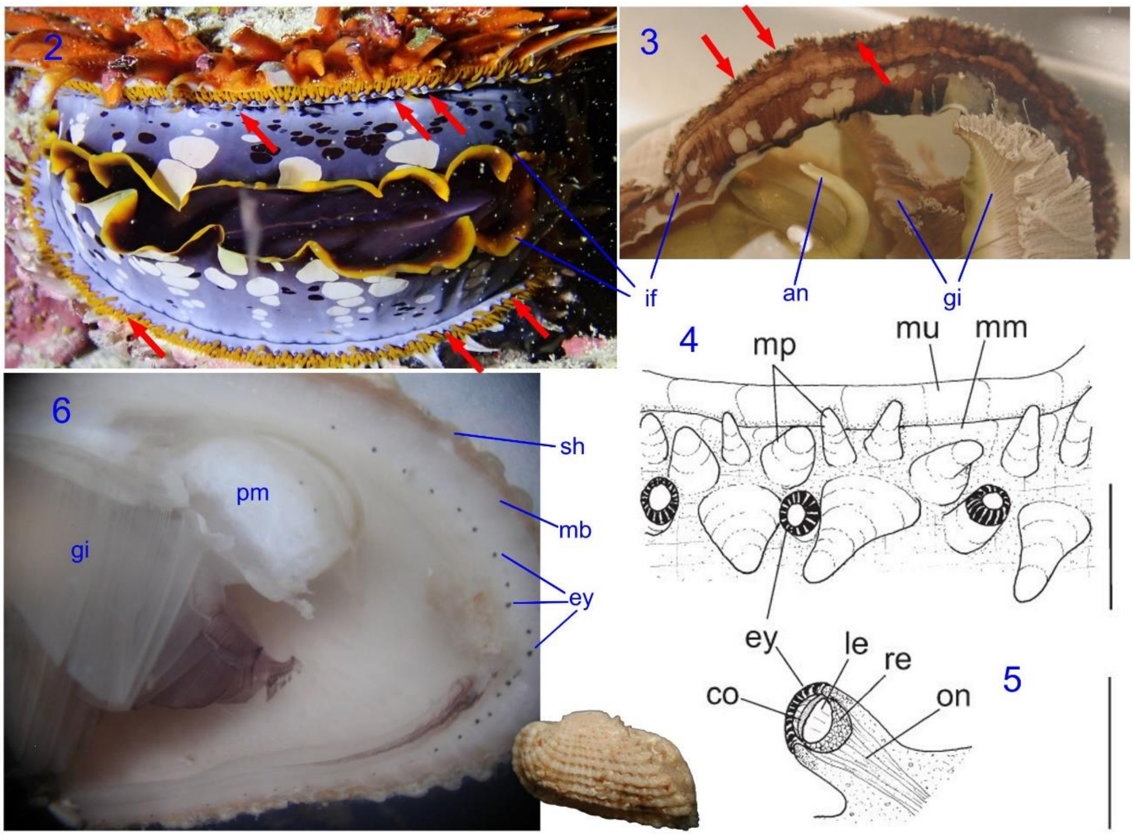
Eyes in Polyplacophora

This text omits the 2 first branches of the molluscan phylogeny, Caudofoveata and Solenogastres, because there is no evidence of photoreceptors in them. They are deepwater, aphotic animals, with their body totally covered by calcareous scales, and, at least in the Recent species, photoreceptors look useless. On the other hand, polyplacophorans are common shallow water marine animals, which mostly have some photophobia, looking for hidden places like under rocks. Photoreceptors certainly are important, and they surely have them splayed in the girdle and even along the valves. In this case, photo- and other receptors are located at the tip of aesthetes, which are minuscules pallial projections crossing through the valves, mainly in their younger portions, surfacing them with small, microscopic expansions. In a few chitons, a more complex structure is developed, such as, e.g., *Onithochiton* (Boyle, 1969), which possess closed minute (~50 µm) eyes in the aesthetes, with lens.

Aesthetes are not exclusive to chitons. They are also found in some bivalves and gastropods, and also in other shelled non-mollusks, like brachiopods. Minute fissurellids, for example, are known to have aesthete scars at their shells (Simone & Cunha, 2014: figs. 149-151 of *Hemimarginula hemitoma*).

Eyes in Bivalvia

Countless bivalve lineages developed eyes, in almost all types of complexity (except for the bicameral eye), independently. As far as known, they aways developed eyes in the mantle edge, which can be few, as a single pair as in *Isognomon* (Pteriidae), located in the final region of the gill insertion; up to a huge quantity of lens-bearing eyes in both lobes, like in several Pectinoidea (Figs.



2-5: Examples of eyes in Bivalvia: **2**: *Spondylus varius*, living specimen in situ (Indic Ocean, photo by Frédéric Ducarme – Boll, 2020) (W ~60 mm), red arrows indicating some of the various eyes; **3**: *S. americanus* (Florida), posterior region of mantle cavity of fixed specimen (W ~70 mm), red arrows indicating some of the various eyes; **4**, same, detail of mantle edge, scale= 1 mm; **5**, same, longitudinal section in an eye, scale= 1 mm (both from Simone et al., 2015); **6**, *Acar domingensis* (Brazil), shell (L ~20 mm), and dissected specimen, left view, detail of posterior region of pallial cavity, left mantle lobe removed. Lettering: an, anus; co, cornea; ey, eye; gi, gill; if, inner mantle fold; le, lens; mb, mantle border; mm, middle fold of mantle edge; mp, mantle papilla; mu, outer fold of mantle edge; on, optical nerve; pm, posterior adductor muscle; sh, shell; re, retina.

2-5. These eyes are relatively complex (Fig. 5), located mixed in the lots of pallial large papillae and tentacles that they have between inner and middle folds of the mantle edge (Figs. 2-4). Several pectinids and possibly all spondylids have this sort of eye profusion in different degrees of abundance, according to the species. Not so spectacular eyes are found, for example, in some arcids, such as *Acar domingensis* (Fig. 6), which possesses minute eyespots in the posterior region of the mantle edge. Of course, a complete survey on the presence of eyes in all bivalve branches is far in being known, but apparently it is far more common in pteriomorphians than in remaining branches. Pair of pits of photo-sensory cells with simple lens, called "cephalic eyes," has been reported for arcoideans, limopsoideans, mytiloideans, anomioideans, ostreoideans and limoideans (Morton, 2008), being regarded as ectopic pallial eyes. Beyond pteriomorphians, pallial eyes have been detected only in some heteroconchs, such as few cardiids and laternulids (Morton, 2008).

Eyes in Gastropoda

Both more basal branches of the Gastropoda phylogeny, Patellogastropoda and Cocculiniformia, lack adult eyes. Eyes only appear, as a synapomorphy, in the following branch that gathers the vetigastropods with Adenogonogastropoda (Neritimorpha + Apogastropoda). As this taxon so far was not named, I propose here the suggestive name **Ommatogastropoda**, from the Greek *ommatos*, meaning eye, for this branch. Thus, being formal:

Division **Ommatogastropoda** new division

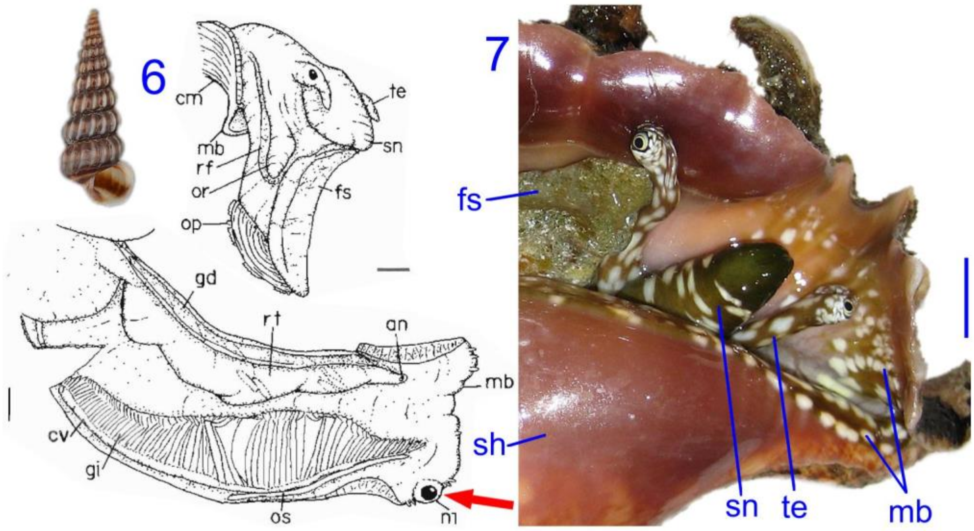
Node K by Simone (2011)

Diagnosis: shell globose-trochiform, spiralized with suture deep. Operculum in adult form, multispiral. Cephalic eyes present, with lens. Visceral mass possessing only 1-2 intestinal loops. Odontophore horizontal muscle (m6) lying outside cartilages. Esophageal pouches papillate and mid-esophagus bulging. urn:lsid:zoobank.org:pub:3D58910F-CB74-4304-AC2B-9D07AB84F273

List of included taxa: Vetigastropoda + Adenogonogastropoda.

All the here now named Ommatogastropoda have adult cephalic eyes, or have atrophied them, because of some special adaptations, like parasitism (e.g., some eulimids), deep water habitat (e.g., *Benthobia*), fossorial habitat (e.g., *Buccinanops*), and troglobian adaptation. Besides, these eyes are of the type closed with a lens (Fig. 1E). The single exceptions are the Pleurotomarioidea vetigastropods (Fretter, 1966). They have the opened eye kind (Fig. 1D). Being rigid with the interpretation of the cephalic eyes as a character in the cladogram (Simone, 2011), there is no doubt that they are a synapomorphy of the Ommatogastropoda. The single problem is the opened condition, and the appearance of the lens. Two possible scenarios are possible: the lens is also a synapomorphy of the Ommatogastropoda as much as the eyes themselves, and the pleurotomarias reverted them to the opened condition, being, thus, a reversion. OR the closed condition, the lens appeared twice in the Ommatogastropoda evolution, one inside Vetigastropoda, after pleurotomarioideans, if they will be proven to be the basal branch; and another time in adenogonogastropodans. This is an intriguing issue that only will be answered after widening the species known in their extra-shell features.

Eyes in gastropods, despite in having lens, generally are simple and small (Fig. 6), barely capable of detecting images. Some of them, however, have more elaborate eyes, such as, e.g., the Strombidae (Fig. 7). Strombid eyes look to have a rudimentary colorful iris, and are sufficiently large to be capable to form images.



6-7: Examples of eyes in Gastropoda: **6**: *Cerithideopsis costata* (Caribe) Potamididae, shell (l ~13 mm, courtesy Femorale), head-foot in right view, and pallial cavity, inner-ventral view, arrow showing pallial eye, scales= 0.5 mm (both from Simone, 2001); **7**, *Lambis* sp (Pacific) Strombidae, live specimen, anterior region coming out from the shell, scale= 10 mm. Lettering: an, anus; cm, columellar muscle; cv, ctenidial vein; fs, foot sole; gd, pallial gonoduct; gi, gill; mb, mantle border; n1, pallial eye; op, operculum; or, ovipositor; os, osphradium; rf, right furrow; rt, rectum; sh, shell; sn, snout; te, cephalic tentacle

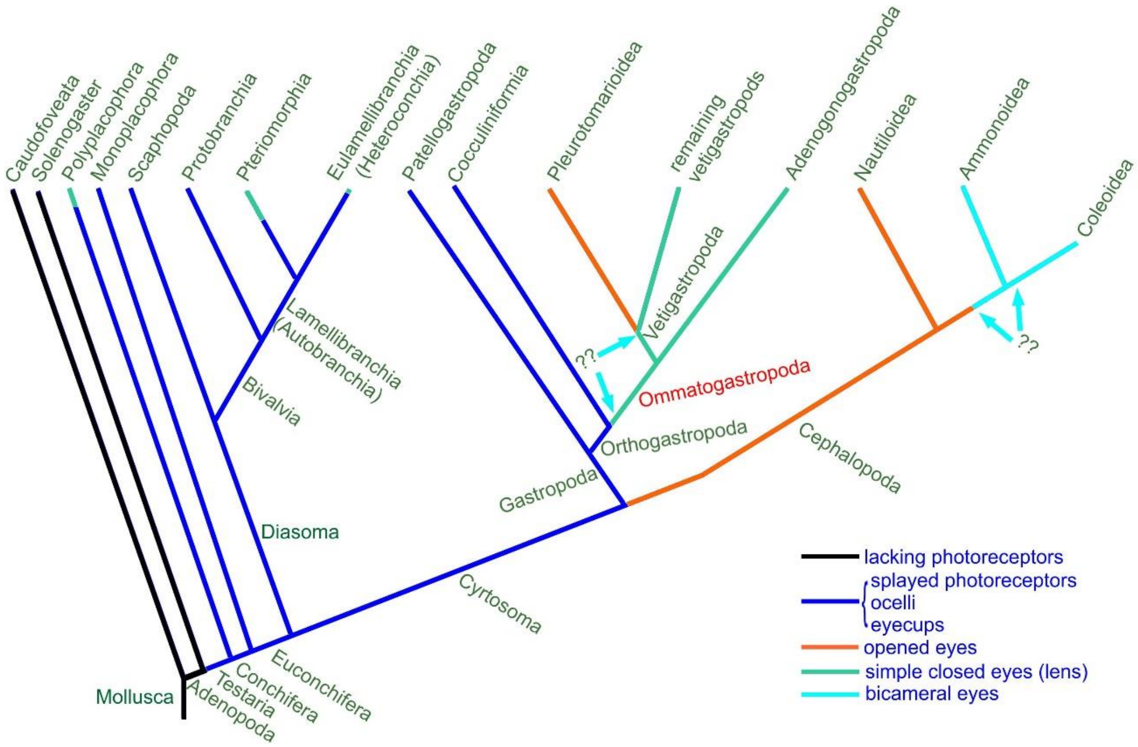
Of course, the typical gastropod eyes are the cephalic ones. However, there are some rare groups that, as much as the bivalves, also developed pallial eyes. An interesting example are the potamidids (Fig. 6: n1), some species bear from 1, while others have up to several eyes in the siphonal region of the mantle edge.

Eyes in Cephalopoda

There is nothing more to say about the cephalopod eyes beyond what was said above, and what is abundantly found in the literature (e.g., Hanke & Kelber, 2020). Cephalopod eyes are intriguing enough to raise lots of studies and exciting investigations, in such details are not the scope of this paper. On the other hand, equally intriguing, and this is not sufficiently explored in the literature, is at which point in the cephalopod phylogeny the eyes became that complex.

As can be seen in Fig 8, the suggestive phylogeny of the Cephalopoda has as first branch the Nautiloidea. They are sister-taxon of Ammonoidea + Coleoidea, a branch that is supported by some interesting synapomorphies, two of them are the reduction of the number of arms, and the presence of differentiated structures in these arms (suckers, hooks, etc.). As Nautiloidea have a profusion of arms lacking differentiated structures, those characteristics make Ammonoidea and Coleoidea long known sister taxa (Jacobs & Landman, 1993; Mironenko, 2014). The eyes of existing nautiloideans are of the opened type (Fig. 1D), and apparently it is the rule amongst the fossil ones too (Klug et al., 2021), the so-called "pinhole camera eyes". As eyes in fossil cephalopods are something very difficult to observe, and, as long as known, no detailed ammonoidean eye has been observed. The ammonoideans extinguished in the end of the Cretaceous, and, mostly, when they are reconstructed alive, they usually are represented with a coleoidean eye, because of the proximity between both groups (Mironenko, 2014: 997). On the other hand, the rare preservation of ammonoidean soft parts shown the above-mentioned characteristics. Anyway, there is a doubt if the bicameral eye is a coleoidean exclusivity, or it is another synapomorphy supporting the clade Ammonoidea-Coleoidea, or even a different evolutive arrangement can be present. This is the reason for the question marks in Fig. 8, showing if the bicameral eyes are support by Coleoidea or one branch before it.

Phylogenetic inferences of the Mollusca photoreceptors



8: Unpretentious phylogenetic cladogram of Mollusca based on morphological characters, mostly extracted from Simone (2011 and subsequent papers) and, secondarily, MolluscaBase (2023), indicating, with colors, the main type of photoreceptors as in Fig. 1 as indicated. Question marks indicated 2 dubious points: 1) if closed simple eyes appeared twice, in Adenogonogastropoda and part of Vetigastropoda, or if it is synapomorphy of Ommatogastropoda and reverted in Pleurotomarioidea; 2) if bicameral eyes occur only on Coleoidea or if they are shared also with Ammonoidea.

A synoptic representation of the Mollusca phylogeny, including some subdivisions of some groups, is shown in Fig. 8. In it, different colors represent the occurrence of different kinds of photoreceptors in each branch. Of course, most information already was explained above, such as the absence of photoreceptors in the 2 first branches – Caudofoveata and Solenogastres (black). Photoreceptors are one of the synapomorphies of the Testaria (dark blue), a taxon that gathers remaining, non aplacophoran mollusks. As splayed photoreceptors, ocelli and eyecups are relatively a continuous evolutionary process, and sometimes difficult of individualization, they are coded in a single color. The branches that possess some representatives with closed eyes with lens, have the tip with different color (green), but certainly that must denote that several branches developed that independently.

The new name Ommatogastropoda (written in red), reunites the eye-bearing gastropods, excluding the 2 first branches – Patellogastropoda and Cocculiniformia – that lack adult cephalic eyes. As reported above, the single problem is if this pair of eyes are opened or closed with the lens. If opened, the closed eyes appeared twice in gastropod evolution, one in Adenogonogastropoda and another in non-pleurotomarioideans Vetigastropoda. If the eyes already appeared closed, with the lens, there is a case of reversion to open eyes in the Pleurotomatioidea. Open eyes (orange) also support the Cephalopoda branch, as they are present on Nautiloidea, its first branch. As already discussed above, the bicameral eyes (light blue) can be exclusive of Coleoidea, but it can be proven to occur in Ammonoidea, the coleoidean sister group, and in this case, the bicameral eyes can be regarded as a synapomorphy of this branch. Other scenarios also can be evoked, as intermediary kind of eyes occurring in ammonoideans, such as closed simple eyes, as a previous step to the coleoidean bicameral one. All are fascinating issues for paleomalacology.

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