RESPIRATION

Gills and other respiratory structures and methods

RESPIRATION

The term nudibranch literally translates as "naked gill" and that type of sea slug, with the large flower-like gill exposed upon the back, is the type with which most people are familiar. This exposed, expanded gill however is only one of several different structures or arrangements evolved by sea slugs to respire, even amongst the true nudibranchs.

The exposed dorsal gill of *Chromodoris magnifica* plainly illustrates the origin and meaning of the term nudibranch (naked gill) to describe these sea slugs.

All animals respire, requiring gas exchange with their environment in order that oxygen may be taken up for metabolic processes and the resulting carbon dioxide, a waste product, removed. Respiration and "blood" circulation go hand in hand unless the animal is small and simple with only a few cell layers of thickness. In those animals gases are exchanged by diffusion through their body wall. This is also the case sometimes with small animals that have a large surface area to body volume and even those sea slugs with a gill also supplement gas exchange by cutaneous respiration.

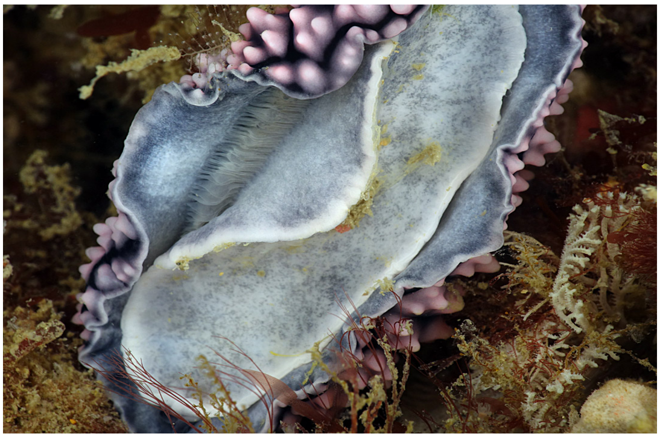
The marine animal needs to extract dissolved oxygen from the surrounding water and this is much more difficult than extracting it from air. Problems they face include a much slower diffusion rate compared to air (by a factor of 10,000) and depending upon the temperature, water (1% O_2 concentration) contains about 20 times less oxygen than air (21% O_2 concentration). However, in their favour, sea slugs have a low metabolic rate and are relatively passive compared to fish, for example.

Respiratory structures have evolved to provide the necessary thin-walled, large surface area arrangement required for gaseous exchange in complex animals, together with a complementary blood supply to and from the structure. The blood is delivered and passed through these thin-walled structures, whereby diffusion of gases takes place due to the concentration gradient – CO_2 out and O_2 in - and then recirculated in a system around the body, that in molluscs is termed an open system. (See explanatory box – Page 4.)

The very small nudibranch *Vayssierea felis* has no gills or other respiratory structures and respires through its body surface.

The dendronotid nudibranch *Tritoniopsis elegans* has lace-like secondary gill structures down the length of each side of its body for respiration.

Phyllodesmium colemani, an aeolid nudibranch, makes use of the huge surface area provided by its cerata, those many long projections of its dorsum.



The phyllidiid nudibranch *Phyllidiella pustulosa* has numerous respiratory leaflets situated between mantle and foot in the groove of the hyponotum.

In sea slugs these structures, other than a “typical” gill, may be as simple as thin-walled outgrowths on the surface of the mantle serviced by “blood” vessels e.g. the multifunctional finger-like cerata of aeolids, the simple or highly branched lateral appendages of the dendronotids or the secondary gill leaflets of the phyllidiids and *Armina* nudibranchs situated under the mantle in the hyponotum. The fine nature of these structures is possible in an external situation because they are supported and separated by the surrounding water. There is even a great variation in gill shape, arrangement and size amongst those with a “typical” gill, from greatly expanded to almost undetectable, from simple to complex and whether it is able to be contracted or retracted or not. Even those that possess a gill or secondary branchial structures are believed to also utilize their body surface that includes that now enlarged and exposed mantle expanse, for gaseous exchange.

The Open Circulation of Sea Slugs

Nearly all molluscs have what is called an “open system” of “blood” circulation, the exception being the highly active cephalopods such as the octopus and squid.

In a closed circulation system the blood is transported around the body entirely enclosed in vessels, the arteries, veins and capillaries, both to and from the tissues, unidirectionally under reasonable pressure to enable diffusion through the capillaries. An open circulatory system however only uses closed vessels for part of the journey and the circulation is low pressure and cannot be called directional for much of its path. Sea slugs and nudibranchs have blood-filled body cavities or sinuses called haemocoels, in which the tissues and organs are bathed directly in the blood, to be oxygenated, receive nutrients and remove wastes and carbon dioxide.

The blood of sea slugs is more correctly called haemolymph as, by operating in the open system, it is comprised of both blood and interstitial fluid or lymph fluid, there being no separation between the two. The oxygen binding protein is haemocyanin, a copper compound that can carry one oxygen molecule rather than the iron compound, haemoglobin of most vertebrates, which can carry four. Haemocyanin is suspended directly in the haemolymph fluid and does not require carrying by blood cells. Deoxygenated haemolymph is virtually colourless but acquires a bluish tint when oxygenated.

Most sea slugs possess a two-chambered heart with an auricle and a ventricle. To generalize: Vessels carrying oxygenated haemolymph from the gills and lateral sinuses of the notum, plus from the kidney, empty into the first chamber of the heart, the auricle, that pumps it into the second chamber, the ventricle, that pumps it through the aorta/s that then progressively divide into many finer vessels around the body thus distributing haemolymph into a network of open arterial sinuses or haemocoels that bathe the organs and tissues. Muscular movements by the sea slug also assist in moving the haemolymph around the body and mixing it through the haemocoels. Haemolymph drains from the sinuses into vessels that conduct it separately to the gills and the kidney thus completing the open circulation.

Additionally, the haemocoels perform a hydrostatic skeleton function giving the sea slugs shape and form. By acting in opposition to contractile musculature, the gills, rhinophores, cerata, proboscis and penis, for example, can be everted or expanded. Research has shown that most molluscs assist these functions by controlling the action of the heart and therefore the haemolymph pressure. The heart can be slowed down or even stopped for periods of time.

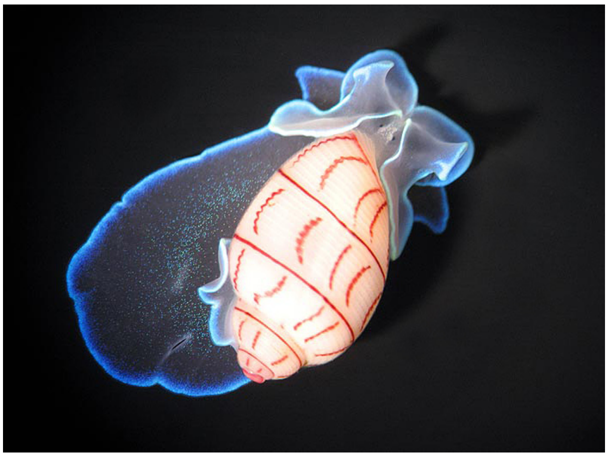
The more primitive sea slugs have separate anterior and posterior haemocoels whereas the true nudibranchs have lost the separation between the two producing a single large and continuous haemocoel.

The operation of an open circulation system is less energy dependent than that of a closed system but cannot transport comparable volumes and is less efficient there being no systematic way of passing haemolymph through the gills for oxygenation. It should also be noted that the haemolymph leaving the kidneys goes directly to the heart without traversing the gill. The open system is thus more suited to animals of low metabolic function, smaller size and possessing the capability of also absorbing oxygen through their integument.

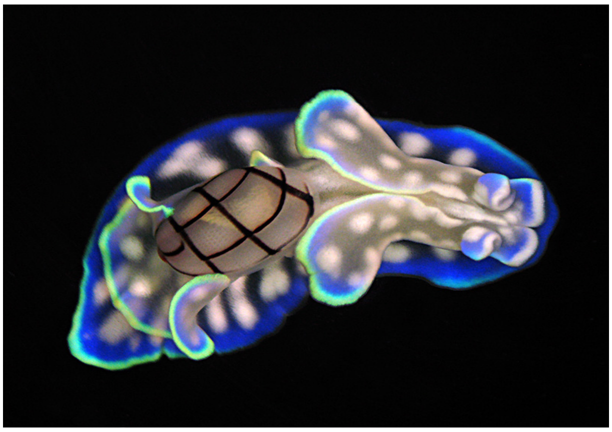
As we have seen, some sea slugs do not possess a gill and strange to relate some do not have a heart. Species of the Sacoglossa genus *Alderia* for example, do not possess a heart and the haemolymph circulation is achieved by rhythmic pulsations of its cerata on alternating sides of the body thereby performing as secondary hearts.

The primitive sea slugs possess what is often referred to as a ctenidium, an outgrowth of the mantle made up of a series of thin filaments of tissue attached to each side of a central axis, that resemble the teeth of a comb. Its surface is often covered with cilia to facilitate water movement. This is their respiratory structure, analogous to a gill, inherited from the mantle cavity of their shelled ancestors. One evolutionary theory put forward is that the ctenidium was originally just to provide a water current in the mantle cavity for feeding and excretory purposes. Over time it enlarged and vascularized to develop into an organ of respiration. The gill on the back of the dorid nudibranchs is argued by some, to be the direct descendant, though highly differentiated, of the ctenidium due to its position, relationship with the anus, innervation and "blood" circulation. Other authorities though, consider it to be a completely new adaptive organ and refer to them as secondary (anal) gills arguing that dorid veliger larvae detort (see Development Chapter) just prior to metamorphosis losing their primary gas exchange organ or ctenidium and grow new "secondary" gills, without cilia, on the mid to posterior region of the dorsum. The debate appears, as yet, to be unresolved.

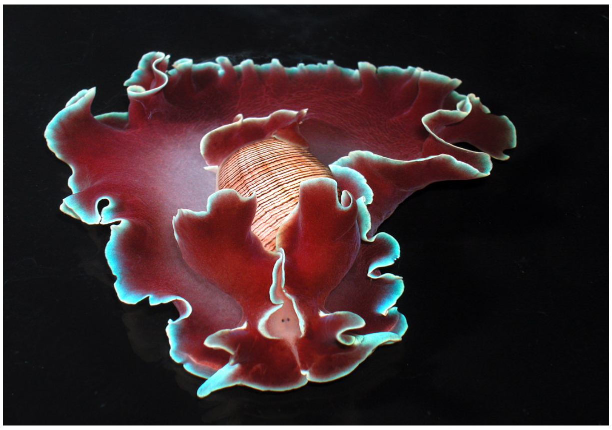
Japonacteon suturalis belongs to a primitive group of sea slugs whose lineage diverged early. It has a thick shell and retains the ctenidium deep in the mantle cavity.



Bullina lineata has a thinner more inflated shell but the ctenidium is still retained within the mantle cavity.



Micromelo undatus, along with its relatives shown here, has large posterior lobes to its headshield. These protect the opening to the mantle cavity, diverting silt and debris away from the opening stopping congestion of the ctenidium when it burrows.



The highly modified *Hydatina physis* with all of its lobes and extensions displayed. The ctenidium can sometimes be seen protruding out from under the right side of the shell but protected by the folded up parapodium.

The Different Gills and Secondary Respiratory Structures

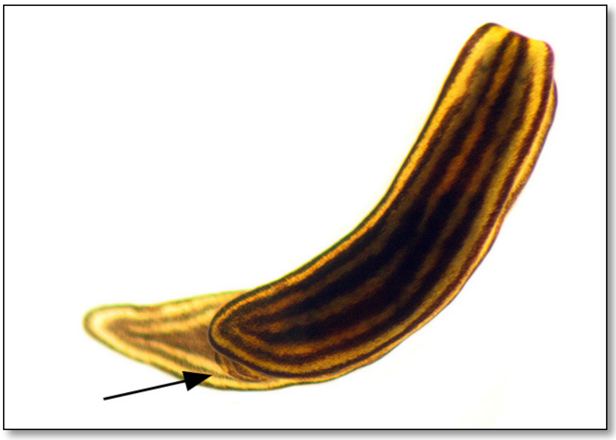
The descriptions here of the gills or secondary gills of different sea slug groups are necessarily generalized for there are many variations on a theme within those groups. An overview is given but space does not permit an exhaustive list of the anatomy of every genus. Some minor deviating groups are not included.

The Head-shield Slugs - Cephalaspidea, Acteonoidea and Ringiculoidea

Most of the head-shield slugs have a simple plicate gill located in the enclosed mantle cavity, where present, or more exposed where that cavity is opened or reduced or formed into lobes. In most instances the gill is not readily observable. An example of a more exposed gill in the head-shield slugs is that of the Gastropteridae where the mantle cavity is reduced or even absent such that the gill although usually small is located between the right parapodium and the body proper. In the genus *Sagaminopteron* however the gill is large with long processes and is often readily visible along the right side. Those species with a gill enclosed or semi-enclosed in the mantle cavity or tucked under the parapodial fold, siphon water through and over the gill from front to back.

Most species of Gastropteridae have a small gill but *Sagaminopteron ornatum* has a large translucent gill that is often visible above the edge of the right parapodium.

Sagaminopteron psychedelicum also has a large gill that is distinctive with white flecks on a dark translucent background, and is carried high above the parapodia.



The gill of most Runcinidae is located posteriorly on the right side near the anus and is often visible as exhibited by this *Runcina fijiensis* specimen.

In species of Aglajidae, such as *Chelidonura amoena* shown here, the gill is contained in the mantle cavity the opening of which is protected by the large tightly wrapped right parapodium.

The Sap-sucking Slugs – Sacoglossa

As discussed earlier the Sacoglossa have a wide diversity of body shape and we can therefore expect a similar diversity of respiratory methods and structures. In general the more primitive shelled forms have a gill in the mantle cavity under the shell not unlike the head-shield slugs. However in the Sacoglossa it differs in structure, being epithelial folds of the mantle roof and composed of numerous simple lamellae bearing cilia for water current generation. This includes the unusual bivalved sacoglossans of the Juliidae family. The flattened, leaf-like forms, such as *Elysia* and *Thuridilla* of the Plakobranchidae do not possess a gill. In saying they are flattened most actually carry their leaf-like parapodia in an upright position towards the mid-line, closed or semi-closed. These folded extensions of the foot on each side of the body create a huge surface area for gaseous diffusion and many carry a complex network of vessels.


This undescribed species of *Lobiger* carries a gill under its shell but also utilizes the surface area of the large processes for diffusion.


The large surface area of the parapodia of many sacoglossans assists gas diffusion and are serviced by a network of vessels visible here in *Elysia tomentosa.*

Those without parapodia, for example *Bosellia,* are essentially just flattened but respire in the same manner, through the broad surface of their body. The sacoglossans with processes on their dorsum, commonly called cerata, also do not possess a gill *per se.* Instead they make use of the large surface, the projecting cerata provide, to respire. This is why the cerata are often referred to as secondary gills. *Cyerce* and *Polybranchia,* for example, have flattened leaf-like or thicker cushion-like cerata, whilst *Costasiella*, *Ercolania*, *Stiliger* and *Hermaea*, to name just a few, have fusiform cerata of varying length, girth and number.


The many fusiform cerata on the back of *Costasiella kuroshimae* provide a large surface area for the exchange of gases.


Cyerce elegans does not have a true gill but the large balloon-like cerata crowded on its back act as secondary gills to provide sufficient oxygen.

Some species of Sacoglossa carry functional kleptoplasts (sequestered chloroplasts from their diet) that produce oxygen as a by-product of photosynthesis. This can be a two-edged sword however if the production of oxygen is not moderated. In fact it has been suggested that their secondary processes act as a "reverse gill" to remove excess oxygen. (See Kleptoplasty in Solar Powered Chapter).

The Sea Hares – Anaspidea

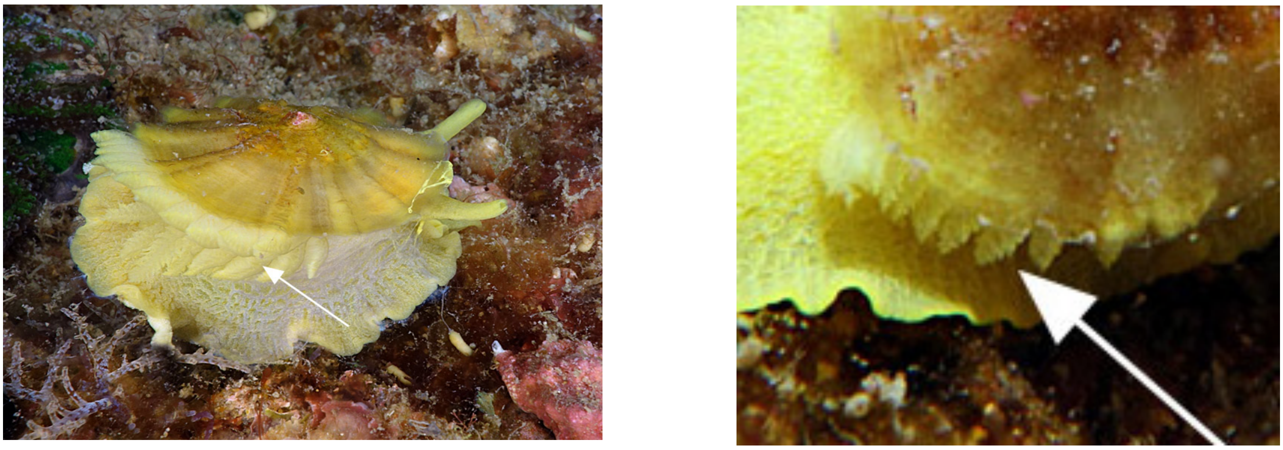
Most Sea Hares have a thin remnant of shell that lies under the skin in nearly all species (partly exposed in a couple). The plicate gill lies across the reduced mantle cavity as a tufted crescent or fan, depending on filament size, partially protected by the shell but otherwise by the parapodia that fold up over the mantle and are sometimes fused along the mid-line in which circumstances they form a parapodial cavity. Water circulation is facilitated by entry anteriorly though a gap in the parapodia and expulsion via a posterior siphon of varying size.

The partially exposed shell remnant of the sea hare *Aplysia nigrocincta* (arrowed) covering the mantle cavity and gill. This species is one of the few sea hares to have an exposed shell.

The parapodial flaps of *Dolabella auricularia* are joined at the midline. An exhalent siphon (arrowed) is visible in the centre of the disc-like posterior "shield" that houses a flat shell within its tissues.

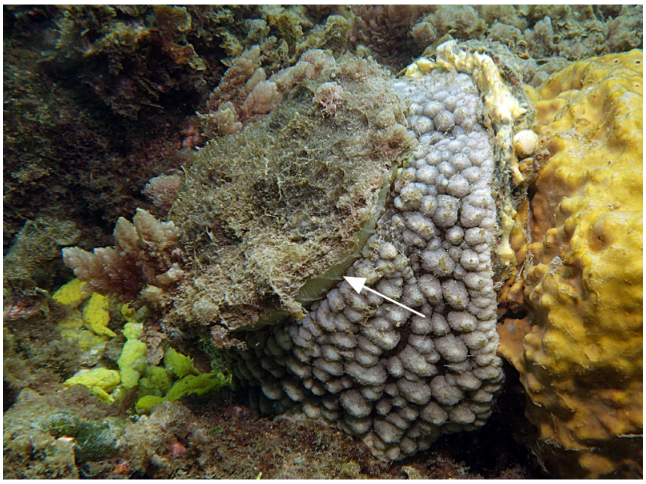
The Umbrella-shell Slugs - Umbraculoidea

In this order the external shell is much reduced to a limpet shape or just a flattened conical dorsal cap. There is no mantle cavity at all for the bipinnate gill and therefore it sits under the lip of the shell on the right side between the mantle and the foot. In *Umbraculum* the large gill is attached for most of its curved length and is not readily visible because it is accommodated in a groove-like cavity formed by the overlapping margins of the mantle and the foot but will sometimes be extended. In *Tylodina* it is only attached via the anterior half and is often seen protruding laterally.



The free, unattached posterior portion of the gill of *Tylodina corticalis* (arrowed) is seen here protruding from underneath its limpet-like shell on the right side.

A peek under the shell of *Tylodina corticalis* reveals the gill and its bipinnate nature. The colour closely matches the rest of the body and foot. There are about 12 feathery pinnae on each side of the rachis.

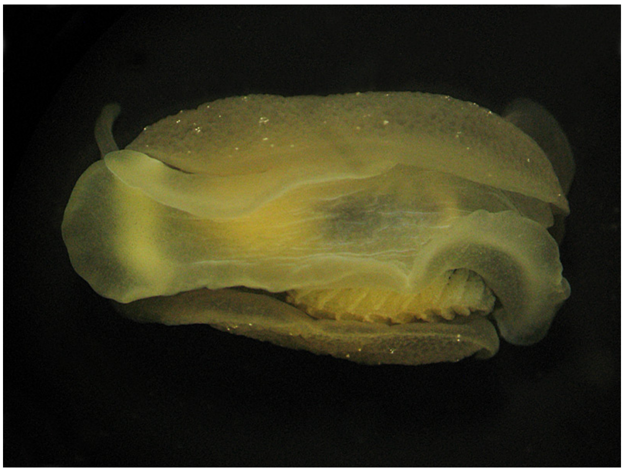


Umbraculum umbraculum has the gill wrapped around the right side situated in a groove between the underside of shell and the foot and is attached for most of its length.

The Side-gilled Slugs – Pleurobranchoidea

None of the species in this group possess an external shell and the mantle in most instances has expanded to cover the entire body, and even further, thus creating an overhanging skirt. The bipinnate gill resides down along the right side (hence the name - side-gilled slugs) between the underside of the mantle skirt and the foot. It is sometimes visible in certain species, for example species of *Pleurobranchaea*, where the reduced mantle of this genus can cause the gill to be exposed at times. The gill rachis may be either smooth or tuberculate. Those tubercles may be located at the base of the rachis and also sometimes along its axis at pinnae junctions depending upon species. It is normally attached anteriorly for more than half its length with the free posterior portion muscular and able to articulate. The central posterior edge of the mantle emarginates, forming up into a "funnel" to act as an exhalent siphon, thereby facilitating water flow across the gill in *Pleurobranchus* and *Euselenops* for example, but not so in others such as *Berthella* or *Berthellina*.

The gill of the side-gill slug *Berthella martensi* is revealed here because segments of the mantle that normally cover it have been autotomized.



A ventral view of *Berthella stellata* showing how the gill lies along the right side protected between the underside of the mantle and the foot.

The True Nudibranchs - Nudibranchia

The majority of these slugs has an exposed gill or exposed secondary gill processes. This discussion will make more sense if we break the nudibranchs up into the two clades, the dorids and cladobranchs, each with three sub-groups as presented previously in the Anatomical Overview.

The Dorid Nudibranchs - Doridoidea Clade

Most of the dorid nudibranchs, with some exceptions, e.g. the Phyllidiidae, can be recognized by the typical circle of gill branches on their dorsum that surround (or are located in front of) the anus the opening of which is situated on the tip of a short papilla. There are three sub-groups as follows, but be aware that these are old, traditional, but still convenient groupings for practical purposes.

The **phanerobranch** dorid *Nembrotha milleri* – gills cannot retract into pocket.

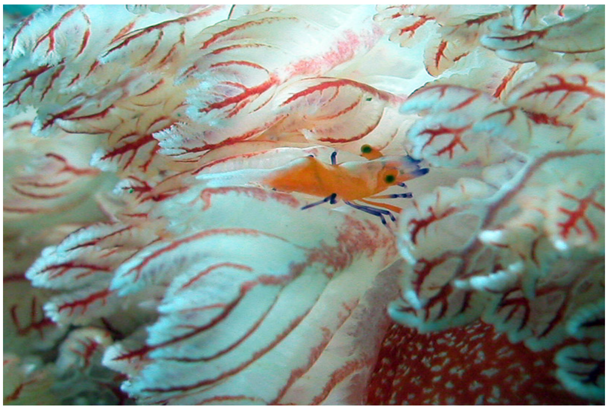
The **cryptobranch** dorid *Hypselodoris apolegma* – gills can retract completely into pocket.

The **porostome** dorid *Phyllidiopsis shireenae* – secondary gill leaflets under mantle in groove of hyponotum.

- Phanerobranch Dorids – Phanerobranchia

The gills of Phanerobranch Dorids (Phanerobranch = visible gill) cannot be retracted into a distinct pocket. In most the gill is inserted directly on the dorsum while some have sheaths into which the gill can partially contract but these are not pockets and cannot close over the gill. Depending on species there are a variable number of gill plumes of pinnate (simple), bipinnate or tripinnate composition. Many of the phanerobranchs possess structures or appendages around or in proximity to their gills for protective purposes. Apart from the physical barrier these might present to a potential predator some structures also carry chemical deterrents of a noxious or toxic nature.

The six separately inserted gills of *Hexabranchus sanguineus* encircle the anus. They can contract but not retract under the mantle surface.



A juvenile *Periclimenes imperator* shrimp lives within the protection afforded by the feathery gills of *Hexabranchus sanguineus*.

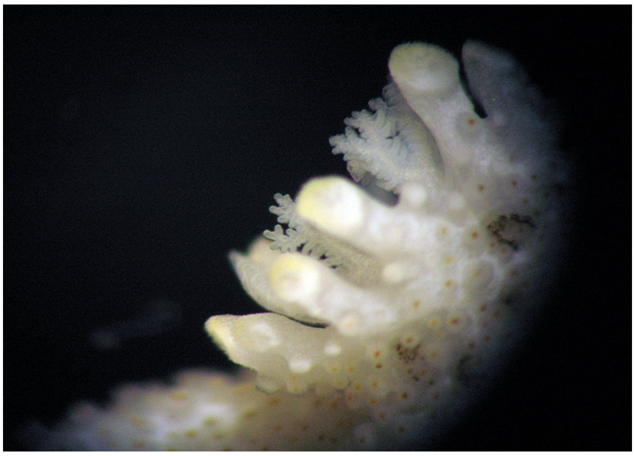
Nembrotha kubaryana displays its bushy gills. There are five tripinnate gill leaves often carried curled up as illustrated here.

This specimen of *Nembrotha purpureolineata* has three (max. of five) non-retractile, mulitpinnate gill leaves.

The small purple–tipped gill leaves of *Tambja kava* form a semicircle anteriorly around the anus.

Tambja morosa carries from three to five well-developed tripinnate gill leaves that are non-retractile.

The circular gill pattern of *Aegires flores* is apparent here with the paddle-shaped protective tubercles.



A close-up view of *Aegires flores* (whole animal left) showing the small tripinnate gill leaves dwarfed by the protective ring of tubercles.

Some examples of phanerobranch dorid gill arrangements

Aegires serenae has three exceedingly large protective appendages in front of and arching over the gill.

Aegires gardineri has a more compact but closer protective coverage of the gill.

Gymnodorids have a variety of gill types but all are unprotected. Here *Gymnodoris citrinus* displays its complete circular arrangement around the anus.

Gymnodoris amakusana has the gill branches arranged in a transverse linear row anterior to the anus.

Trapania japonica has a yellow extra-branchial process on each side of the gill.

This undescribed species of *Thecacera* has two extremely long extra-branchial appendages protecting the gill.

Further examples of phanerobranch dorid gill arrangements some with protective appendages

- Cryptobranch Dorids – Cryptobranchia

The gill of the Cryptobranch Dorids (crypto branch = hidden gill) is able to not only contract but also to actually retract completely into a distinct and common branchial pocket beneath the mantle surface that can be closed off. Depending on species, there are a variable number of gill plumes of pinnate (simple), bipinnate, tripinnate or even quadripinnate composition. Some of these nudibranchs have been observed to vibrate their gill plumes, an action considered to improve efficiency by increasing the water flow over them. A very few species in this group also possess significant structural protection for their gills. Some of these structures also carry glands containing noxious/distasteful compounds. The appearance of some cryptobranch gills bears an uncanny resemblance to opened octocoral polyps.

A sequence of images of the cryptobranch dorid *Diversidoris* sp. showing the entire retraction of the gill into a common pocket beneath the mantle.

The gill circle of *Hypselodoris obscura* is open posteriorly. Here the detail of the gill and the central location of the anal papilla can be seen.

In this view of *Goniobranchus* sp. both the anal papilla (arrowed lower) and the kidney duct (arrowed upper) are visible in the centre of the gill circle.

A composite image of *Goniobranchus aureopurpureus* showing gill retraction and the raised edge to the gill pocket.

A composite image of *Jorunna* sp. showing the gill displayed, and then completely withdrawn.

Ceratosoma tenue has a protective horn posterior to the gill that arches forwards over the top. The horn carries glands of noxious/distasteful chemicals.

In this image of *Ceratosoma tenue* there is evidence of a fish strike to the protective horn. The fish will not return for a second bite. Gill saved.

Miamira magnifica bears a protective appendage in front of the gill. The genera *Ceratosoma* and *Miamira* are the only cryptobranchs with physical protective structures.

Miamira alleni has several lobe-like appendages, some with distasteful defensive glands, surrounding the gill.

Examples of cryptobranch gill retraction and the protective appendages of the *Ceratosoma* and *Miamira* genera

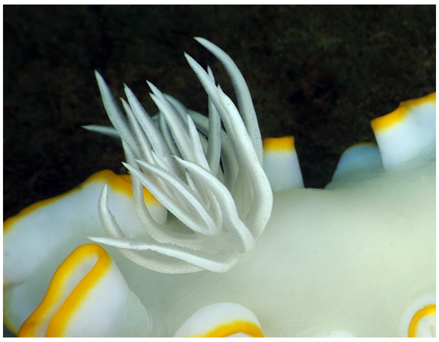
Jorunna rubescens has a tall sheath to the gill pocket.

The gill sprouting out of the tall gill pocket of *Hypselodoris krakatoa*. Named after the volcano.

The “volcano” of *Hypselodoris krakatoa.*

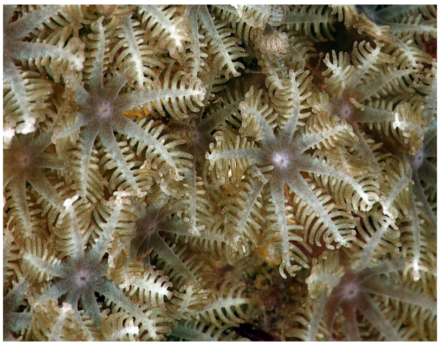
Goniobranchus leopardus has gills that are triangular in section arranged in an arc around the anus.

The blood red gills of *Ardeadoris rubroannulata.*



The long thin tapering gills of *Ardeadoris egretta* are almost round in cross-section.

Goniobranchus fidelis with its gill fully displayed. The gill appears not unlike an expanded octocoral polyp.



The expanded feeding polyps of some octocorals look somewhat similar to some cryptobranch gills.

The distinctive inward curving goblet shape of the gill of *Actinocyclus verrucosus.*

Doriprismatica atromarginata showing damage to both sides of the mantle. Continued predation prevented by noxious glands.

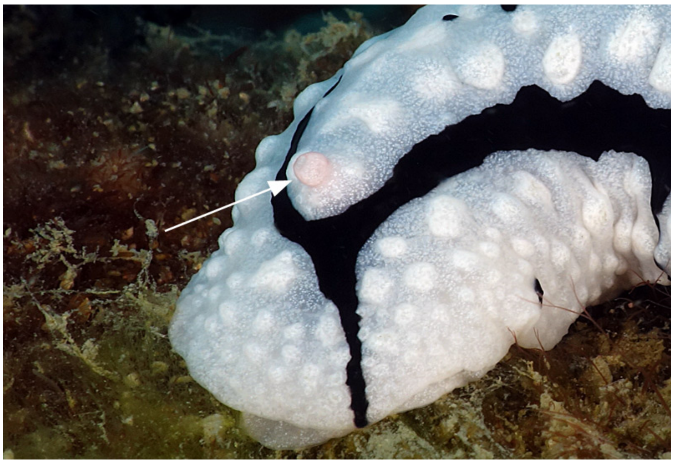
The large but sparse pinnate gill of *Taringa halgerda*.

The gill of *Goniobranchus collingwoodi* is a circle, open posteriorly, with the ends spiraling inwards.

A selection of cryptobranch gills

- Porostome Dorids – Porostomata

This group is defined by its suctorial method of feeding. They lack a radula and feed by secreting digestive enzymes upon their food and sucking up the partially digested tissue. The dendrodorids (Family Dendrodorididae) have the same gill arrangement and branchial pocket as the cryptobranch dorids. The phyllidiids (Family Phyllidiidae) are different to all of the other dorids in not possessing a typical gill arrangement on the dorsum. Instead they have secondary gill leaflets situated ventro-laterally between the mantle and foot, in the hyponotum groove. These secondary gills occupy this groove right around the entire animal excepting for interruption at the mouth and genital region. The leaflets are flat, triangular in shape attached along the long edge and have a rounded apex, alternating large and small. Nevertheless, the phyllidiids are still considered "cryptobranch dorids" in so far as most retain a cavity that surrounds the anus thought to be homologous with the gill cavity of the cryptobranchs, even though the typical gill has been lost. Most also retain the posterior dorsal location of the anus with a few having a ventral location instead.



Arrowed above is the salmon pink coloured anal papilla of *Phyllidiopsis shireenae*. In almost all other dorids, apart from the phyllidiids, we would expect to also see a gill arrangement closely associated with the anus, either encircling or anterior thereto.

The secondary gill leaflets of *Phyllidiopsis krempfi*, usually well hidden, are visible here, located ventrally between the underside of the mantle and foot across the groove of the hyponotum.

A close up view of the secondary gill leaflets situated under the mantle of *Phyllidia varicosa*. The alternation of big and small leaflets can be seen as well as the triangular shape and rounded apex.

The Dendrodorididae have gills that are similar to the cryptobranchs being able to withdraw under the mantle into a common pocket. *Dendrodoris arborescens* shown here has its gill partially withdrawn with the rim of the pocket visible.

In those species that are able to contract or retract the gills this action is performed by retractor muscles acting against the hydrostatic fluid pressure that provides a "skeleton" giving the slug its form and shape. Once the muscle relaxes the internal fluid pressure pushes the gill back out.

The Cladobranch Nudibranchs - Cladobranchia Clade

None of the nudibranchs in this clade possess what is termed a "typical" gill on the dorsum. The premise for this clade is the possession of a branched digestive gland. Again there are three groups. Currently the Arminina and Dendronotina are not considered natural groupings.

The **arminid** nudibranch *Dermatobranchus funiculus* – no respiratory structures on the dorsum.

The **dendronotinid** nudibranch *Marionia* sp. – secondary gill structures on the dorsum.

The **aeolid** nudibranch *Phyllodesmium undulatum* – multifunctional cerata on dorsum act as secondary gill structures.

- The Arminid Nudibranchs – Arminina

The arminids exhibit two main body forms, those with a broad and long tapering body on which most carry a series of longitudinal ridges and those with cerata on the notum. In the former, *Armina* possess ventral secondary respiratory leaflets in the hyponotum, between mantle and foot while *Dermatobranchus* does not, seemingly reliant on diffusion into its flat body across its broad ridged notum and body side walls under the mantle. *Janolus* and *Madrella* are representatives of the second body form where the notum is usually crowded with cerata that, with the exceptional surface area they provide, are able to act as secondary respiratory agents.

An undescribed species of *Armina*. *Armina* have no gill on the dorsum but have secondary respiratory leaflets located in the hyponotum between underside of mantle and foot.

All the *Dermatobranchus* lack any respiratory structures, even the hidden secondary gill leaflets of their sister genus the *Armina*. *Dermatobranchus rubidus* shown above.

An undescribed species of *Janolus* showing the dense coverage of cerata, even in front of the rhinophores, that act as secondary respiratory structures.

Madrella ferruginosa has long cerata on the dorsum performing a respiratory function. They are often carried tightly curled up.

- The Dendronotinid Nudibranchs – Dendronotina

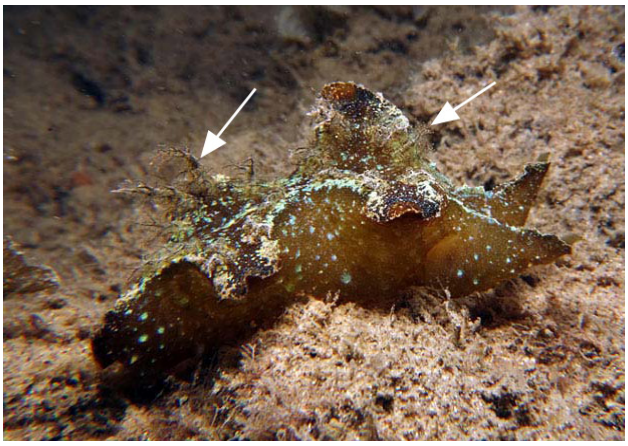
All dendronotinids have dorsolateral appendages down the sides of the body. These may be simple or complexly branched, lobed, nodular or tuberculate. All are believed to act as secondary respiratory structures. Additionally some carry or have embedded close by other more finely branched processes that act specifically as gills. The tritoniids, for example *Tritoniopsis,* have very fine delicately branched processes that are referred to as dendritic gills. *Bornella* has dorsolateral cerata-like processes that protect one or two gills embedded at their base. Some species of *Doto* and *Kabeiro* bear small simple gills at the base of the larger nodular cerata. Scyllaeidae, for example *Notobryon*, have the mantle ridge formed into one or two large lobes that bear tufts of dendritic gills on the surface of the inner face. The single species of the *Tethys* genus has a pair of small secondary respiratory structures at the base of each of the several large lobed cerata while the closely related *Melibe* have scattered branched filaments upon the external (sometimes also the internal) faces of those cerata and sometimes also found on the body proper that are considered by some workers to have a respiratory function.

The dendronotinid *Bornella anguilla*, displaying the pairs of lateral flap-like appendages protecting the secondary gills located at their bases on the medial sides.

A close-up image showing detail of the secondary gills of *Bornella anguilla* and how they are protected by being on the inside surface the colourful lateral appendages.

The plain bifid dorsolateral appendages of *Marianina rosea* assist with it respiration needs.

Long thought an aeolid, the dendronotinid *Embletonia gracilis* has cerata with up to four blunt fingers on their terminations. The cerata act as secondary respiratory structures.



Notobryon wardi has two large lobes projecting from each side of its mantle providing protection for the dendritic gill-like processes that arise on their medial side.

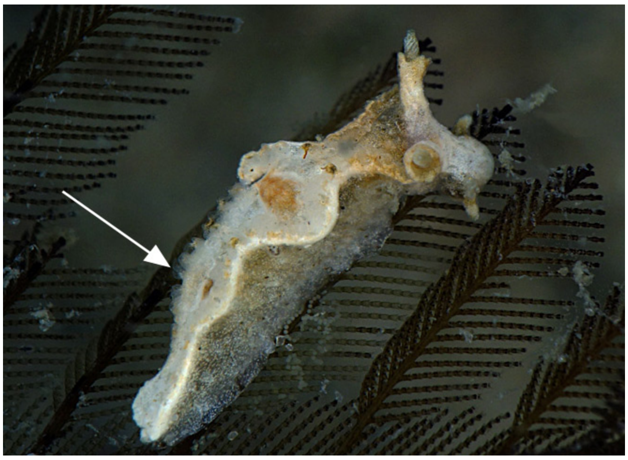
Some authorities claim that the fine filaments on the cerata of species of *Melibe* act as secondary respiratory structures. *Melibe viridis* above however has tubercles rather than filaments on both surfaces of its large cerata.

The fine lace-like dorsolateral structures of *Tritoniopsis elegans* held up or out from the edges of its mantle act as its gills. The "gills" may vary in colour in this species from white to orange to blue.

The secondary gill structures along both notal edges of *Marionia* are more tufted with robust stems. The stems divide into a number of branches and subdivide several more times to produce fine terminations.

Some examples of the secondary gill structures of dendronotinids

A closer view of the structure of *Marionia* gills showing the tree-like appearance with many subdivisions from each stem.



An undescribed species of *Lomanotus*. The notal ridge carries many small papillae down along its length, transparent (arrowed) in this species.

Dendronotus noahi displaying its branched lateral processes. As well as acting in a respiratory function the dark digestive gland can be seen to penetrate as well.

A close up image of the processes of *Dendronotus noahi* showing the detail.

Doto ussi showing the dense presentation the nodulose cerata create on its dorsum. Some species of *Doto* have fine respiratory filaments at the base of their cerata on the medial face but they are not readily visible.

This undescribed species of *Kabeiro* bears many large cerata covered with low white tubercles. The secondary gill structures of *Kabeiro* are either prominent due to cerata spacing, or absent.

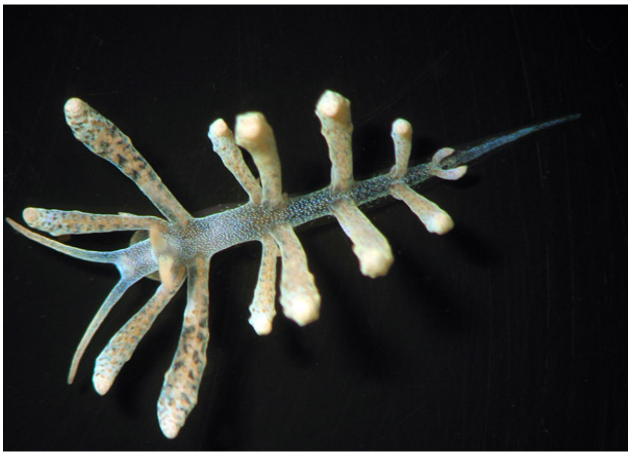
More examples of dendronotinid secondary gill structures

- The Aeolid Nudibranchs – Aeolidina

The aeolids are elongate nudibranchs that do not have gills but carry many cerata on their notum. These perform a number of functions that includes, due to their large surface area, thin skin and vascularization, that of a secondary respiratory ability. The thinness of the body wall is also of assistance for additional whole-of-body surface gaseous diffusion. The cerata are usually well organized into regular bilateral groups down both sides of the body although the arrangement can vary. Some species carry many more than others. While some carry their cerata laid flat many bear them upright. Cerata present in many different shapes and sizes. Many are tubular and taper to the apex. Others are inflated or flattened or curved. Most are smooth but some have papillae or tubercles on their surface. A branch of the digestive gland extends into each ceras and is often visible in those with transparent skin. The cerata are sacrificial, the animal being able to autotomise one or many to create a distraction if attacked. (See Defense chapter for a discussion on that aspect.)

Flabellina lotos carries its cerata in the vertical position. The branch of the digestive gland within is clearly visible.

Species *of Cerberilla* carry their cerata laid flat upon the dorsum, a possible burrowing adaptation, as shown by *Cerberilla annulata* above.



Phyllodesmium hyalinum carries its sparse cerata out to the sides of the body. It is known to readily autotomise cerata when disturbed.

The long and profuse cerata of *Phyllodesmium colemani* present as a seemingly tangled arrangement. They are tubular and smooth.
