= Phoronid =

Phoronids (scientific name Phoronida , sometimes called horseshoe worms) are a phylum of marine animals that filter @-@ feed with a lophophore (a " crown " of tentacles) , and build upright tubes of chitin to support and protect their soft bodies . They live in most of the oceans and seas including the Arctic Ocean but excluding the Antarctic Ocean , and between the intertidal zone and about 400 meters down . Most adult phoronids are 2 cm long and about 1 @.@ 5 mm wide , although the largest are 50 cm long .

The bottom end of the body is an ampulla (a flask @-@ like swelling) , which anchors the animal in the tube and enables it to retract its body very quickly when threatened . When the lophophore is extended at the top of the body , cilia (little hairs) on the sides of the tentacles draw food particles to the mouth , which is inside and slightly to one side of the base of the lophophore . Unwanted material can be excluded by closing a lid above the mouth or be rejected by the tentacles , whose cilia can switch into reverse . The food then moves down to the stomach , which is in the ampulla . Solid wastes are moved up the intestine and out through the anus , which is outside and slightly below the lophophore .

A blood vessel leads up the middle of the body from the stomach to a circular vessel at the base of the lophophore , and from there a single blind vessel runs up each tentacle . A pair of blood vessels near the body wall lead downward from the lophophore ring to the stomach and also to blind branches throughout the body . There is no heart , but the major vessels can contract in waves to move the blood . Phoronids do not ventilate their trunks with oxygenated water , but rely on respiration through the lophophore . The blood contains hemoglobin , which is unusual in such small animals and seems to be an adaptation to anoxic and hypoxic environments . The blood of Phoronis architecta carries twice as much oxygen as a human of the same weight . Two metanephridia filter the body fluid , returning any useful products and dumping the remaining soluble wastes through a pair of pores beside the anus .

One species builds colonies by budding or by splitting into top and bottom sections , and all phoronids reproduce sexually from spring to autumn . The eggs of most species form free @-@ swimming actinotroch larvae , which feed on plankton . An actinotroch settles to the seabed after about 20 days and then undergoes a radical change in 30 minutes : the larval tentacles are replaced by the adult lophophore ; the anus moves from the bottom to just outside the lophophore ; and this changes the gut from upright to a U @-@ bend , with the stomach at the bottom of the body . One species forms a " slug @-@ like " larva , and the larvae of a few species are not known . Phoronids live for about one year .

Some species live separately , in vertical tubes embedded in soft sediment , while others form tangled masses buried in or encrusting rocks and shells . In some habitats populations of phoronids reach tens of thousand of individuals per square meter . The actinotroch larvae are familiar among plankton , and sometimes account for a significant proportion of the zooplankton biomass . Predators include fish , gastropods (snails) , and nematodes (tiny roundworms) . One phoronid species is unpalatable to many epibenthic predators . Various parasites infest phoronids ' body cavities , digestive tract and tentacles . It is unknown whether phoronids have any significance for humans . The International Union for Conservation of Nature (IUCN) has not listed any phoronid species as endangered .

As of 2010 there are no indisputable body fossils of phoronids . There is good evidence that phoronids created trace fossils found in the Silurian , Devonian , Permian , Jurassic and Cretaceous periods , and possibly in the Ordovician and Triassic . Phoronids , brachiopods and bryozoans (ectoprocts) have collectively been called lophophorates , because all use lophophores to feed . From about the 1940s to the 1990s , family trees based on embryological and morphological features placed lophophorates among or as a sister group to the deuterostomes , a super @-@ phylum which includes chordates and echinoderms . While a minority adhere to this view , most researchers now regard phoronids as members of the protostome super @-@ phylum Lophotrochozoa . Although analysts using molecular phylogeny are confident that members of Lophotrochozoa are more closely related to each other than of non @-@ members , the

relationships between members are mostly unclear . Some analyses regard phoronids and brachiopods as sister @-@ groups , while others place phoronids as a sub @-@ group within brachiopoda .

= = Name = =

The name of the phylum comes from Phoronis , one of the many names of the Ancient Egyptian goddess Isis . Phoronis is also the name of one of the two genera of Phoronids .

= = Comparison of similar phyla = =

= = Description = =

= = = Body structure = = =

Most adult phoronids are 2 to 20 cm long and about 1 @.@ 5 mm wide , although the largest are 50 cm long . Their skins have no cuticle but secrete rigid tubes of chitin , similar to the material used in arthropods ' exoskeletons , and sometimes reinforced with sediment particles and other debris . Most species ' tubes are erect , but those of Phoronis vancouverensis are horizontal and tangled . Phoronids can move within their tubes but never leave them . The bottom end of the body is an ampulla (a flask @-@ like swelling in a tube @-@ like structure) , which anchors the animal in the tube and enables it to retract its body when threatened , reducing the body to 20 percent of its maximum length . Longitudinal muscles retract the body very quickly , while circular muscles slowly extend the body by compressing the internal fluid .

For feeding and respiration each phoronid has at the top end a lophophore , a " crown " of tentacles with which the animal filter @-@ feeds . In small species the " crown " is a simple circle , in medium @-@ size species it is bent into the shape of a horseshoe with tentacles on the outer and inner sides , and in the largest species the ends of the horseshoe wind into complex spirals . These more elaborate shapes increase the area available for feeding and respiration . The tentacles are hollow , held upright by fluid pressure , and can be moved individually by muscles .

The mouth is inside the base of the crown of tentacles but to one side . The gut runs from the mouth to one side of the stomach , in the bottom of the ampulla . The intestine runs from the stomach , up the other side the body , and exits at the anus , outside and a little below the crown of tentacles . The gut and intestine are both supported by two mesenteries (partitions that run the length of the body) connected to the body wall , and another mesentery connects the gut to the intestine .

The body is divided into coeloms , compartments lined with mesothelium . The main body cavity , under the crown of tentacles , is called the metacoelom , and the tentacles and their base share the mesocoelom . Above the mouth is the epistome , a hollow lid which can close the mouth . The cavity in the epistome is sometimes called the protocoelom , although other authors disagree that it is a coelom and Ruppert , Fox and Barnes think it is built by a different process .

= = = Feeding , circulation and excretion = = =

When the lophophore is extended , cilia (little hairs) on the sides of the tentacles draw water down between the tentacles and out at the base of the lophophore . Shorter cilia on the inner sides of the tentacles flick food particles into a groove in a circle under and just inside the tentacles , and cilia in the groove push the particles into the mouth . Phoronids direct their lophophores into the water current , and quickly reorient to maximize the food @-@ catching area when currents change . Their diet includes algae , diatoms , flagellates , peridinians , small invertebrate larvae , and detritus . Unwanted material can be excluded by closing the epistome (lid above the mouth) or be rejected

by the tentacles , whose cilia can switch into reverse . The gut uses cilia and muscles to move food towards the stomach and secretes enzymes that digest some of the food , but the stomach digests the majority of the food . Phoronids also absorb amino acids (the building blocks of proteins) through their skins , mainly in summer . Solid wastes are moved up the intestine and out through the anus , which is outside and slightly below the lophophore .

A blood vessel starts from the peritoneum (the membrane that loosely encloses the stomach) , with blind capillaries supplying the stomach . The blood vessel leads up the middle of the body to a circular vessel at the base of the lophophore , and from there a single blind vessel runs up each tentacle . A pair of blood vessels near the body wall lead downward from the lophophore ring , and in most species these are combined into one a little below the lophophore ring . The downward vessel (s) leads back to the peritoneum , and also to blind branches throughout the body . There is no heart , but muscles in the major vessels contract in waves to move the blood . Unlike many animals that live in tubes , phoronids do not ventilate their trunks with oxygenated water , but rely on respiration by the lophophore , which extends above hypoxic sediments . The blood has hemocytes containing hemoglobin , which unusual in such small animals and seems to be an adaptation to anoxic and hypoxic environments . The blood of Phoronis architecta carries as much oxygen per cm3 as that of most vertebrates ; the blood 's volume in cm3 per gm of body weight is twice that of a human .

Podocytes on the walls of the blood vessels perform first @-@ stage filtration of soluble wastes into the main coelom 's fluid . Two metanephridia , each with a funnel @-@ like intake , filter the fluid a second time , returning any useful products to the coelom and dumping the remaining wastes through a pair of nephridiopores beside the anus .

= = = Nervous system and movement = = =

There is a nervous center is between the mouth and anus , and a nerve ring at the base of the lophophore . The ring supplies nerves to the tentacles and , just under the skin , to the body @-@ wall muscles . Phoronis ovalis has two nerve trunks under the skin , whereas other species have one . The trunk (s) have giant axons (nerves that transmit signals very fast) which co @-@ ordinate the retraction of the body when danger threatens .

Except for retracting the body into the tube , phoronids have limited and slow movement : partial emerging from the tube ; bending the body when extended ; and the lophophore 's flicking of food into the mouth .

= = = Reproduction and lifecycle = = =

Only Phoronis ovalis naturally builds colonies by budding or by splitting into top and bottom sections which then grow into full bodies . In experiments , other species have split successfully , but only when both parts have enough gonadal (reproductive) tissue . All phoronids breed sexually from spring to autumn . Some species are hermaphroditic (have both male and female reproductive organs) but cross @-@ fertilize (fertilize the eggs of other members) , while others are dioecious (have separate sexes) . The gametes (sperms and ova) are produced in the swollen gonads , around the stomach . The gametes swim through the metacoelom to the metanephridia . Sperm exit by the nephridiopores and some are captured by the lophophores of individuals of the same species . Species that lay small fertilized eggs release them into the water as plankton , while species with larger eggs brood them either in the body 's tube or stuck in the center of the lophophore by adhesive . The brooded eggs are released to feed on plankton when they develop into larvae .

Development of the eggs is a mixture of deuterostome and protostome characteristics . Early divisions of the egg are holoblastic (the cells divide completely) and radial (they gradually form a stack of circles) . The process is regulative (the fate of each cell depends on interaction with other cells , not on a rigid program in each cell) , and experiments that divided early embryos produced complete larvae . Mesoderm is formed from mesenchyme originating from the archenteron . The coelom is formed by schizocoely , and the blastopore (a dent in the embryo) becomes the mouth .

The slug @-@ like larva of Phoronis ovalis swims for about 4 days , creeps on the sea @-@ bed for 3 to 4 days , then bores into a carbonate floor . Nothing is known about three species . The remaining species develop free @-@ swimming actinotroch larvae , which feed on plankton . The actinotroch is an upright cylinder with the anus at the bottom and fringed with cilia . At the top is a lobe or hood , under which are : a ganglion , connected to a patch of cilia outside the apex of the hood ; a pair of protonephridia (smaller and simpler than the metanephridia in the adult) ; the mouth ; and feeding tentacles that encircle the mouth . After swimming for about 20 days , the actinotroch settles on the seabed and undergoes a catastrophic metamorphosis (radical change) in 30 minutes : the hood and larval tentacles are absorbed and the adult lophophore is created round the mouth , and both now points upward ; the gut develops a U @-@ bend so that the anus is just under and outside the lophophore . Finally the adult phoronid builds a tube .

Phoronids live for about one year .

= = Ecology = =

Phoronids live in all the oceans and seas including the Arctic and excepting the Antarctic Ocean , and appear between the intertidal zone and about 400 meters down . Some occur separately , in vertical tubes embedded in soft sediment such as sand , mud , or fine gravel . Others form tangled masses of many individuals buried in or encrusting rocks and shells . In some habitats populations of phoronids reach tens of thousand of individuals per square meter . The actinotroch larvae are familiar among plankton , and sometimes account for a significant proportion of the zooplankton biomass .

Phoronis australis bores into the wall of the tube of a cerianthid anemone , Ceriantheomorphe brasiliensis , and uses this as a foundation for building its own tube . One cerianthid can house up to 100 phoronids . In this unequal relationship , the anemone experiences no significant benefits nor harm , while the phoronid benefits from : a foundation for its tube ; food (both animals are filter @-@ feeders) ; and protection , as the cerianthid withdraws into its tube when danger threatens , and this alerts the phoronid to retract into its own tube .

Although predators of phoronids are not well known , they include fish , gastropods (snails) , and nematodes (tiny roundworms) . Phoronopsis viridis , which reaches densities of 26 @,@ 500 per square meter on tidal flats in California (USA) , is unpalatable to many epibenthic predators , including fish and crabs . The unpalatability is strongest in the top section , including the lophophore , which is exposed to predators when phoronids feed . When the lophophores were removed in an experiment , the phoronids were more palatable , but this effect reduced over 12 days as the lophophores regenerated . These broadly effective defenses , which appear unusual among invertebrates inhabiting soft sediment , may be important in allowing Phoronopsis viridis to reach high densities . Some parasites infest phoronids : progenetic metacercariae and cysts of trematodes in phoronids ' coelomic cavities ; unidentified gregarines in phoronids ' digestive tract ; and an ancistrocomid ciliate parasite , Heterocineta , in the tentacles .

It is unknown whether phoronids have any significance for humans . The International Union for Conservation of Nature (IUCN) has not listed any phoronid species as endangered .

= = Evolutionary history = =

= = = Fossil record = = =

As of 2010 there are no indisputable body fossils of phoronids . Researching the Lower Cambrian Chengjiang fossils , in 1997 Chen and Zhou interpreted Iotuba chengjiangensis as a phoronid since it had tentacles and a U @-@ shaped gut , and in 2004 Chen interpreted Eophoronis as a phoronid . However , in 2006 Conway Morris regarded Iotuba and Eophoronis as synonyms for the same genus , which in his opinion looked like the priapulid Louisella . In 2009 Balthasar and Butterfield found in western Canada two specimens from about 505 million years ago of a new fossil ,

Lingulosacculus nuda , which had two shells like those of brachiopods but not mineralized . In the authors ' opinion , the U @-@ shaped gut extended beyond the hinge line and outside the smaller shell . This would have precluded the attachment of muscles to close and open the shells , and the 50 % of the animal 's length beyond the hinge line would have needed longitudinal muscles and also a cuticle for protection . Hence they suggest that Lingulosacculus may have been a member of a phoronid stem group within the linguliform brachiopods .

There is good evidence that species of Phoronis created the trace fossils of the ichnogenus Talpina , which have been found in the Devonian , Jurassic and Cretaceous periods . The Talpina animal bored into calcareous algae , corals , echinoid tests (shells) , mollusc shells and the rostra of belemnites . Hederellids or Hederelloids are fossilized tubes , usually curved and between 0 @.@ 1 and 1 @.@ 8 mm wide , found from the Silurian to the Permian , and possibly in the Ordovician and Triassic . Their branching colonies may have been made by phoronids .

= = = Family tree = = =

Phoronids , brachiopods and bryozoans (ectoprocts) are collectively called lophophorates , because all feed using lophophores . From about the 1940s to the 1990s , family trees based on embryological and morphological features placed lophophorates among or as a sister group to the deuterostomes , a super @-@ phylum that includes chordates and echinoderms . In the early development of their embryos , deuterostomes form the anus before the mouth , while protostomes form the mouth first .

Nielsen (2002) views the phoronids and brachiopods as affiliated with the deuterostome pterobranchs , which also filter @-@ feed by tentacles , because the current @-@ driving cells of the lophophores of all three have one cilium per cell , while lophophores of bryozoans , which he regards as protostomes , have multiple cilia per cell . Helmkampf , Bruchhaus and Hausdorf (2008) summarise several authors ' embryological and morphological analyses which doubt or disagree that phoronids and brachiopods are deuterostomes :

While deuterostomes have three coelomic cavities , lophophorates such as phoronids and brachiopods have only two .

Pterobranchs may be a sub @-@ group of enteropneusts (" acorn worms ") . This suggests that the ancestral deuterostome looks more like a mobile worm @-@ like enteropneust than a sessile colonial pterobranch . The fact that lophophorates and pterobranchs both use tentacles for feeding is probably not a synapomorphy of lophophorates and deuterostomes , but evolved independently as convergent adaptations to a sessile lifestyle .

The mesoderm does not form by enterocoely in phoronids and bryozoans , but does in deuterostomes , while there are disagreements about whether brachiopods form the mesoderm by enterocoely .

From 1988 onwards analyses based on molecular phylogeny , which compares biochemical features such as similarities in DNA , have placed phoronids and brachiopods among the Lophotrochozoa , a protostome super @-@ phylum that includes molluscs , annelids and flatworms but excludes the other main protostome super @-@ phylum Ecdysozoa , whose members include arthropods . Cohen wrote , " This inference , if true , undermines virtually all morphology ? based reconstructions of phylogeny made during the past century or more . "

While analyses by molecular phylogeny are confident that members of Lophotrochozoa are more closely related to each other than of non @-@ members , the relationships between members are mostly unclear . The Lophotrochozoa are generally divided into : Lophophorata (animals that have lophophores) , including Phoronida and Brachiopoda ; Trochozoa (animals many of which have trochophore larvae) , including molluscs , annelids , echiurans , sipunculans and nemerteans ; and some other phyla (such as Platyhelminthes , Gastrotricha , Gnathostomulida , Micrognathozoa , and Rotifera) .

Molecular phylogeny indicates that Phoronida are closely related to Brachiopoda , but Bryozoa (Ectoprocta) are not closely related to this group , despite using a similar lophophore for feeding and respiration . This implies that the traditional definition " Lophophorata " is not monophyletic .

Recently the term " Lophophorata " has been applied only to the Phoronida and Brachiopoda , and Halanych thinks this change will cause confusion . Some analyses regard Phoronida and Brachiopoda as sister @-@ groups , while others place Phoronida as a sub @-@ group within Brachiopoda , implying that Brachiopoda is paraphyletic . Cohen and Weydman 's analysis (2005) concludes that phoronids are a sub @-@ group of inarticulate brachiopods (those in which the hinge between the two valves have no teeth and sockets) and sister @-@ group of the other inarticulate sub @-@ groups . The authors also suggest that the ancestors of molluscs and the brachiopod + phoronid clade diverged between 900 Ma and 560 Ma , most probably about 685 Ma .

= = Taxonomy = =

The phylum has two genera , with no class or order names . Zoologists have given the larvae , usually called an actinotroch , a separate genus name from the adults .

In 1999 Temereva and Malakhov described Phoronis svetlanae . In 2000 Temereva described a new species , Phoronopsis malakhovi , while Emig regards it as a synonym for Phoronopsis harmeri . Santagata thinks Phoronis architecta is a different species from both Phoronis psammophila and Phoronis muelleri , and that " [the phoronids '] species diversity is currently underestimated " . In 2009 Temereva described what may be larvae of Phoronopsis albomaculata and Phoronopsis californica . She wrote that , while there are 12 undisputed adult phoronid species , 25 morphological types of larvae have been identified .