

Onychophora, Acoelomorpha
and Brachiopoda

(Animal Phylum)

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Chapter 1

Onychophora

Onychophora
Temporal range: 40–0 Ma



Scientific classification [e]

Kingdom:	Animalia
Superphylum:	Ecdysozoa
(unranked):	Panarthropoda
Phylum:	Onychophora Grube, 1853

Extant families

Peripatidae
Peripatopsidae



Global range of Onychophora: Peripatidae in green,
Peripatopsidae in blue

The **velvet worms** (**Onychophora** — literally "claw bearers", also known as **Protracheata**) are a minor ecdysozoan phylum. These obscurely segmented organisms have tiny eyes, antennae, multiple pairs of legs and slime glands. They have variously been compared to worms with legs, caterpillars and slugs. Most common in tropical regions of the Southern Hemisphere, they prey on smaller animals such as insects, which they catch by squirting an adhesive slime. In modern zoology, they are particularly renowned for their curious mating behaviour and for bearing live young. They are becoming increasingly popular as pets due to their bizarre appearance and eating habits.

The two extant families of velvet worms are Peripatidae and Peripatopsidae. They show a peculiar distribution, with the peripatids being predominantly equatorial and tropical, while the peripatopsids are all found in what used to be Gondwanaland.

Formerly considered part of Tracheata, velvet worms are now considered close relatives of the Arthropoda and Tardigrada, with which they form the taxon Panarthropoda. This makes them of palaeontological interest, as they can help to reconstruct the ancestral arthropod.

Anatomy



A dissection of *Euperipatoides kanangrensis*. The width of the dish is approx. 4 cm. The two ovaries, full of stage II embryos, are floating to the bottom of the image. The brown mass of the viscera is partially protruding from the body cavity.

Velvet worms are segmented creatures with a flattened cylindrical body cross-section and rows of unstructured body appendages known as lobopods (informally: stub feet). The animals grow to between 0.5 and 20 cm, with the average being about 5 cm, and have between 13 and 43 pairs of legs. Their skin consists of numerous, fine transverse rings and is often inconspicuously coloured orange, red or brown, but sometimes also bright green, blue, gold or white, and occasionally patterned with other colours.

Segmenting—outwardly inconspicuous and identifiable only in the regular spacing of the pairs of legs—is visible in the regular arrangement of skin pores, excretion organs and concentrations of nerve cells. The individual body sections are largely unspecialised; even the head develops only a little differently from any abdominal segment.

Segmentation is apparently specified by the same gene as traceable in other groups of animals and is activated in each case, during embryonic development, at the rear border of each segment and in the growth zone of the stub feet.

Body appendages

The stub feet that characterise the velvet worms are conical, baggy appendages of the body, which are internally hollow and exhibit no joints. Although the number of feet can vary considerably between species, their structure is basically very similar. Rigidity is provided by the hydrostatic pressure of their fluid contents, and movement is usually obtained passively by stretching and contraction of the animal's entire body. However, each leg can also be shortened and bent by internal muscles; due to the lack of joints, this bending can take place at any point along the sides of the leg.

In some species, two different organs are found within the feet:

- Crural glands are situated at the shoulder of the legs, extending into the body cavity. They open outwards at the crural papillae—small wart-like bumps on the belly side of the leg—and secrete chemical messenger materials called pheromones. Their name comes from the Latin *cruralis* meaning "of the legs".
- Coxal vesicles are pouches located on the belly side of the leg, which can be everted and probably serve in water absorption. They are only found within the family Peripatidae and are named from *coxa*, the Latin word for "hip".

On each foot is a pair of retractable, hardened (sclerotised) chitin claws, which give the taxon its scientific name: Onychophora is derived from the Greek *onychēs*, "claws"; and *pherein*, "to carry". At the base of the claws are three to six spiny "cushions" on which the leg sits in its resting position and on which the animal walks over smooth substrates; the claws are used mainly to gain a firm foothold on uneven terrain.

Apart from the pairs of legs, there are three further body appendages, which are at the head and comprise three segments:

- On the first head segment is a pair of slender antennae, which serve in sensory perception. They probably do not correspond directly to the antennae of the Arthropoda, but perhaps rather with their "lips" or labrum. At their base is found a pair of simple eyes, except in a few blind species. In front of these, in many Australian species, are various dimples, the function of which is not yet clear. It appears that in at least some species, these serve in the transfer of sperm-cell packages (spermatophores).

- On the belly side of the second head segment is the labrum, a mouth opening surrounded by sensitive "lips". In the velvet worms, this structure is a muscular outgrowth of the throat, so, despite its name, it is probably not homologous to the labrum of the Arthropoda. Deep within the oral cavity lie the sharp, crescent-shaped "jaws", or mandibles, which are strongly hardened and resemble the claws of the feet, with which they are probably homologous. The jaws are divided into internal and external mandibles and are covered with fine toothlets. They move backward and forward in a longitudinal direction, tearing apart the prey.
- On the third head segment, to the left and right of the mouth, are two openings designated "oral papillae". Within these are a pair of large, heavily internally branched slime glands. These lie roughly in the centre of the body and secrete a sort of milky-white slime, which is used to ensnare prey and for defensive purposes. Sometimes the connecting "slime conductor" is broadened into a reservoir, which can buffer pre-produced slime. The slime glands themselves are probably modified crural glands.

All three structures correspond to an evolutionary origin in the leg pairs of the other segments.

Skin and musculature

Unlike the arthropods, velvet worms do not possess a rigid exoskeleton. Instead, their fluid-filled body cavity acts as a hydrostatic skeleton, similarly to many unrelated soft-bodied animals that are cylindrically shaped, for example sea anemones and various worms. Pressure of their incompressible internal bodily fluid on the body wall provides rigidity, and muscles are able to act against it.

The body wall consists of a non-cellular outer skin, the cuticula; a single layer of epidermis cells forming an internal skin; and beneath this, usually three layers of muscle, which are embedded in connective tissues.

The cuticula is about a micrometer thick and covered with fine villi. In composition and structure, it resembles the cuticula of the arthropods, consisting of α -chitin and various proteins, although not containing collagen. It can be divided into an external epicuticula and an internal procuticula, which themselves consist of exo- and endo-cuticula. This multi-level structure is responsible for the high flexibility of the outer skin, which enables the velvet worm to squeeze itself into the narrowest crevices. Although outwardly water-repellant, the cuticula is not able to prevent water loss by respiration, and, as a result, velvet worms can only live in microclimates with high humidity to avoid desiccation.

The surface of the cuticula is scattered with numerous fine papillae, the larger of which carry visible villi-like sensitive bristles. The papillae themselves are covered with tiny scales, lending the skin a velvety appearance (from which the common name is likely derived). It also feels like dry velvet to the touch, for which its water-repellant nature is responsible. Moulting of the skin (ecdysis) takes place regularly, sometimes every 14 days, induced by the hormone ecdysone.

At each moult, the shed skin is replaced by the epidermis, which lies immediately beneath it; unlike the cuticula, this consists of living cells. Beneath this lies a thick layer of connective tissue, which is composed primarily of collagen fibres aligned either parallel or perpendicular to the body's longitudinal axis. Within the connective tissue lie three continuous layers of unspecialised smooth muscular tissue. The relatively thick outer layer is composed of annular (sphincter) muscles, and the similarly voluminous inner layer of longitudinal muscles. Between them lie thin diagonal muscles that wind backward and forward along the body axis in a spiral. Between the annular and diagonal muscles exist fine blood vessels, which lie below the superficially recognisable transverse rings of the skin and are responsible for the pseudo-segmented markings.

Beneath the internal muscle layer lies the body cavity. In cross-section, this is divided into three regions by so-called dorso-ventral muscles, which run from the middle of the underbelly through to the edges of the upper side: a central mid-section and on the left and right, two side regions that also include the legs.

The colouration of Onychophora is generated by a range of pigments. The solubility of these pigments is a key utensil in classification: in all arthropods and tardigrades, the body pigment is soluble in ethanol. This is also true for the Peripatidae, but in the case of the Peripatopsidae, the body pigment is insoluble in ethanol.

Haemocoel and circulation

The body cavity is known as a "pseudocoel", or haemocoel. Unlike a true coelom, a pseudocoel is not fully enclosed by a cell layer derived from the embryonic mesoderm. A coelom is, however, formed around the gonads and the waste-eliminating nephridia.

As the name *haemocoel* suggests, the body cavity is filled with a blood-like liquid, in which all the organs are embedded; in this way, they can be easily supplied with nutrients circulating in the blood. This liquid is colourless as it does not contain pigments; for this reason, it only serves a limited role in oxygen transport. Two different types of blood cells (or haemocytes) circulate in the fluid: amoebocytes and nephrocytes. The amoebocytes probably function in protection from bacteria and other foreign bodies; in some species, they also play a role in reproduction. Nephrocytes absorb toxins or convert them into a form suitable for elimination by the nephridia.

The haemocoel is divided by a horizontal partition, the diaphragm, into two parts: the pericardial sinus along the back and the perivisceral sinus along the belly. The former encloses the tube-like heart, and the latter, the other organs. The diaphragm is perforated in many places, enabling the exchange of fluids between the two cavities.

The heart itself is a tube of annular muscles consisting of epithelial tissues, with two lateral openings (ostia) per segment. While it is not known whether the rear end is open or closed, from the front, it opens directly into the body cavity. Since there are no blood vessels, apart from the fine vessels running between the muscle layers of the body wall and a pair of arteries that supply the antennae, this is referred to as an open circulation.

The timing of the pumping procedure can be divided into two parts: diastole and systole. During diastole, blood flows through the ostia from the pericardial sinus (the cavity containing the heart) into the heart. When the systole begins, the ostia close and the heart muscles contract inwards, reducing the volume of the heart. This pumps the blood from the front end of the heart into the perivisceral sinus containing the organs. In this way, the various organs are supplied with nutrients before the blood finally returns to the pericardial sinus via the perforations in the diaphragm. In addition to the pumping action of the heart, body movements also have an influence on circulation.

Respiration

Oxygen uptake occurs to an extent via simple diffusion through the entire body surface, with the coxal vesicles on the legs possibly being involved in some species. However, of most importance is gas exchange via fine unbranched tubes, the tracheae, which draw oxygen from the surface deep into the various organs, particularly the heart. The walls of these structures, which are less than three micrometers thick in their entirety, consist only of an extremely thin membrane through which oxygen can easily diffuse. The tracheae originate at tiny openings, the spiracles, which themselves are clustered together in dent-like recesses of the outer skin, the atria. The number of "tracheae bundles" thus formed is on average around 75 per body segment; they accumulate most densely on the back of the animal.

Unlike the arthropods, the velvet worms are unable to control the openings of their tracheae; the tracheae are always open, entailing considerable water loss in arid conditions. For this reason, velvet worms are dependent upon habitats with high air humidity.

Digestive system

The digestive tract begins slightly behind the head, the mouth lying on the underside a little way from the frontmost point of the body. Here, prey can be mechanically dismembered by the mandibles with their covering of fine toothlets. Two salivary glands discharge via a common conductor into the subsequent "throat", which makes up the first part of the front intestine. The saliva that they produce contains mucus and hydrolytic enzymes, which initiate digestion both within and outside the mouth. Historically, the salivary glands probably evolved from the waste-elimination organs known as nephridia, which are found homologously in the other body segments.

The throat itself is very muscular, serving to absorb the partially liquified food and to pump it, via the oesophagus, which forms the rear part of the front intestine, into the central intestine. Unlike the front intestine, this is not lined with a cuticula but instead consists only of a single layer of epithelial tissue, which does not exhibit conspicuous indentation as is found in other animals. On entering the central intestine, food particles are coated with a mucus-based peritrophic membrane, which serves to protect the lining of the intestine from damage by sharp-edged particles. The intestinal epithelium secretes further digestive enzymes and absorbs the released nutrients, although the majority of

digestion has already taken place externally or in the mouth. Indigestible remnants arrive in the rear intestine, or rectum, which is once again lined with a cuticula and which opens at the anus, located on the underside near to the rear end.

Excretory organs

In almost every segment is a pair of excretory organs called nephridia, which are derived from coelom tissue. Each consists of a small pouch that is connected, via a flagellated conductor called a nephridioduct, to an opening at the base of the nearest leg known as a nephridiopore. The pouch is occupied by special cells called podocytes, which facilitate ultrafiltration of the blood through the partition between haemocoelom and nephridium. The composition of the urinary solution is modified in the nephridioduct by selective recovery of nutrients and water and by isolation of poison and waste materials, before it is excreted to the outside world via the nephridiopore. The most important nitrogenous excretion product is the water-insoluble uric acid; this can be excreted in solid state, with very little water. This so-called uricotelic excretory mode represents an adjustment to life on land and the associated necessity of dealing economically with water.

A pair of former nephridia in the head were converted secondarily into the salivary glands, while another pair in the final segment of male specimens now serve as glands that apparently play a role in reproduction.

Sensory organs

The entire body—including the stub feet—is littered with numerous papillae: warty protrusions that carry a mechanoreceptive bristle (responsive to mechanical stimuli) at the tip, each of which is also connected to further sensory nerve cells lying beneath. The mouth papillae, the exits of the slime glands, probably also have a function in sensory perception. Sensory cells known as "sensills" on the "lips" or labrum respond to chemical stimuli and are known as chemoreceptors. These are also found on the two antennae, which can be regarded as the velvet worm's most important sensory organs. Except in a few (typically subterranean) species, one simply constructed eye (ocellus) lies laterally, just underneath the head, behind each antenna. This consists of a chitinous ball lens, a cornea and a retina and is connected to the centre of the brain via an optic nerve. The retina comprises numerous pigment cells and photoreceptors; the latter are easily modified flagellated cells, whose flagellum membranes carry a photosensitive pigment on their surface.

The rhabdomeric eyes of the Onychophora are thought to be homologous with the median ocelli of arthropods; this would imply that the last common ancestor of arthropods bore only median ocelli. However, the innervation shows that the homology is limited: the eyes of Onychophora form behind the antenna, whereas the opposite is true in arthropods.

Reproductive organs

Both sexes possess pairs of gonads, opening via a channel called a gonoduct into a common genital opening, the gonopore, which is located on the rear ventral side. Both the gonads and the gonoduct are derived from true coelom tissue.

In females, the two ovaries are joined in the middle and to the horizontal diaphragm. The gonoduct appears differently depending on whether the species is live-bearing or egg-laying. In the former, each exit channel divides into a slender oviduct and a roomy "womb", the uterus, in which the embryos develop. The single vagina, to which both uteri are connected, runs outward to the gonopore. In egg-laying species, whose gonoduct is uniformly constructed, the genital opening lies at the tip of a long egg-laying apparatus, the ovipositor. The females of many species also possess a sperm repository called the receptacle seminis, in which sperm cells from males can be stored temporarily or for longer periods.

Males possess two separate testes, along with the corresponding sperm vesicle (the vesicula seminalis) and exit channel (the vasa efferentia). The two vasa efferentia unite to a common sperm duct, the vas deferens, which in turn widens through the ejaculatory channel to open at the gonopore. Directly beside or behind this lie two pairs of special glands, which probably serve an auxiliary reproductive function; the rearmost glands are also known as anal glands.

A penis-like structure has so far only been found in males of the genus *Paraperipatus* but has not yet been observed in action. As previously mentioned, males of many Australian species exhibit special structures on the head, which apparently take over certain tasks in transferring sperm to the females. In the species *Euperipatoides rowelli*, sperm is collected by these structures, and, when a female is encountered, the worm inserts its head in the vagina.

Distribution and habitat

Velvet worms live in all tropical habitats and in the temperate zone of the Southern Hemisphere, showing a circumtropical and circumastral distribution. Individual species are found in Central and South America; the Caribbean islands; equatorial West Africa and South Africa; northeastern India; Indonesia and parts of Malaysia; New Guinea; Australia; and New Zealand. Fossils have been found in Baltic amber, indicating that they were formerly more widespread in the Northern Hemisphere when conditions were more suitable.

All extant velvet worms are terrestrial (land-living) and prefer dark environments with high air humidity. They are found particularly in the rainforests of the tropics and temperate zones, where they live among moss cushions and leaf litter, under tree trunks and stones, in rotting wood or in termite tunnels. They also occur in unforested grassland, if there exist sufficient crevices in the soil into which they can withdraw during the day.

Two species live in caves, a habitat to which their ability to squeeze themselves into the smallest cracks makes them exceptionally well-adapted and in which constant living conditions are guaranteed. Since the essential requirements for cave life were probably already present prior to the settlement of these habitats, this may be described as exaptation. Agriculture has apparently made available new habitats for velvet worms; in any case, they are found in man-made cocoa and banana plantations in South America and the Caribbean.

Because the danger of desiccation is greatest during the day and in dry weather, it is not surprising that velvet worms are usually most active at night and during rainy weather. Under cold or dry conditions, they actively seek out crevices in which they shift their body into a resting state. Velvet worms are negatively phototactical: they are repelled by bright light sources.

The largest measured population density is very low, at approximately ten individuals per square meter; velvet worms are often difficult to find in their natural habitat.

Slime

The slime of the Onychophora is forcefully squirted from a pair of slime glands in defence against predators and to capture prey. The slime glands, positioned on the sides of the head below the antennae, are a pair of highly modified limbs and typically propel the slime around a centimetre. The slime can be propelled up to four centimetres, although accuracy drops with range, which is usually much shorter than this. One squirt usually suffices to snare a prey item, although larger prey may be further immobilised by smaller squirts targeted at the limbs; additionally, the fangs of spiders are sometimes targeted.

The slime, which can account for up to 11% of the organism's dry weight, is 90% water; its dry residue consists mainly of proteins—primarily a collagen-type protein. 1.3% of the slime's dry weight consists of sugars, mainly galactosamine. The slime also contains lipids and the surfactant nonylphenol. Onychophora are the only organisms known to produce this latter substance.

The proteinaceous composition accounts for the slime's high tensile strength and stretchiness. Upon ejection, it forms a net of threads about 20 µm in diameter, with evenly spaced droplets of viscous adhesive fluid along their length. It subsequently dries, shrinking, losing its stickiness, and becoming brittle. Onychophora will eat and "reuse" any dried slime.

The lipid and nonylphenol constituents may serve one of two purposes. They may line the ejection channel, stopping the slime from sticking to the organism when it is secreted; or they may slow the drying process long enough for the slime to reach its target.

It takes an onychophoran around 24 days to replenish an exhausted slime repository.

Behaviour

Locomotion



Peripatoides sp., clearly showing the stub feet

Velvet worms move in a slow and gradual motion that makes them difficult for prey to notice. Their trunk is raised relatively high above the ground, and they walk with non-overlapping steps. To move from place to place, the velvet worm crawls forward using its legs; unlike in arthropods, both legs of a pair are moved simultaneously. The claws of the feet are only used on hard, rough terrain where a firm grip is needed; on soft substrates such as moss, the velvet worm walks on the foot cushions at the base of the claws.

The actual locomotion is achieved less by the exertion of the leg muscles than by local changes of body length. This can be controlled using the annular and longitudinal muscles. If the annular muscles are contracted, the body cross-section is reduced, and the corresponding segment stretches, since its volume must remain constant due to the incompressible behaviour of the coelom's liquid contents; this is the usual mode of operation of the hydrostatic skeleton as also employed by other worms. Due to the stretching, the legs of the segment concerned are lifted and swung forward. Local contraction of the longitudinal muscles then shortens the appropriate segment, and the legs, which are now in contact with the ground, are moved to the rear. This part of the locomotive cycle is the actual leg stroke that is responsible for forward movement. The individual stretches and contractions of the segments are coordinated by the nervous system such that contraction waves run the length of the body, each pair of legs swinging forward and then down and rearward in succession. The organisms can reach speeds of up to four centimetres per second.

Social interaction

The brains of Onychophora, whilst small, are very complex; consequently, the organisms are capable of rather sophisticated social interactions. Behaviour may vary from genus to genus, so here we reflect the most studied genus, *Euperipatoides*.

They form social groups of up to fifteen individuals, usually closely related, which will typically live and hunt together. Groups usually live together; an example in drier regions would be in a region of the moist interior of a rotting log. Group members are extremely aggressive towards individuals from other logs. Dominance is achieved through aggression and maintained through submissive behaviour. After a kill, the dominant female always feeds first, followed in turn by the other females, then males, then the young. Social hierarchy is established by a number of interactions: higher-ranking individuals will chase, bite and crawl on top of their subordinates. Juveniles never engage in aggressive behaviour, but climb on top of adults, which tolerate their presence on their backs. Size is probably important in establishing the hierarchy, which may account for the dominance of females. When assessing other individuals, individuals often measure one another up by running their antennae down the length of the other individual. Once hierarchy has been established, paired individuals will often cluster together to form an aggregate; this is fastest in male-female pairings, followed by pairs of females, then pairs of males. Whilst hierarchy is quickly established between individuals from a single group, this is not the case with organisms from different groups; these are substantially more aggressive and very rarely climb one another or form aggregates.

Distribution

Individuals within an individual log are usually closely related; especially so with males. This may be related to the intense aggression between unrelated females.

Feeding

Velvet worms are ambush predators, hunting only by night, and are able to capture animals at least their own size, although it may take almost all of their slime-secreting capacity to capture a large prey item. They feed on almost any small invertebrates, including woodlice (Isopoda), termites (Isoptera), crickets (Gryllidae), book/bark lice (Psocoptera), cockroaches (Blattidae), millipedes and centipedes (Myriapoda), spiders (Araneae), various worms and even large snails (Gastropoda). Depending on their size, they eat on average every one to four weeks. They are considered to be ecologically equivalent to centipedes (Chilopoda).

Potential victims can be detected from up to four centimetres away and are investigated by the gentle application of the antennae. If they are judged to be a suitable size, slime is ejected to immobilise the prey item. The most energetically favourable prey are two-fifths the size of the hunting onychophoran. The onychophoran bites into the prey and injects saliva, which further reduces motion and may initiate digestion of the prey item's innards. Ninety percent of the time involved in eating a specimen is spent ingesting it; re-

ingestion of the slime used to trap the insect is performed whilst the onychophoran locates a suitable place to puncture the prey, and this phase accounts for around 8% of the feeding time, with the remaining time evenly split between examining, squirting and injecting the prey.

Onychophora probably do not primarily use vision to detect their prey; although their tiny eyes do have a good image-forming capacity, their forward vision is obscured by their antennae; their nocturnal habit also limits the utility of eyesight. Air currents, formed by prey motion, are thought to be the primary mode of locating prey; the role of scent, if any, is unclear. The animals literally creep up on their prey, with their smooth, gradual and fluid movement escaping detection by predators. Once they reach their prey, they touch it very softly with their antennae to assess its size and nutritional value. After each poke, the antenna is hastily retracted to avoid detection by the prey individual. This investigation may last anywhere upwards of ten seconds, until the velvet worm makes a decision on whether to attack it—or until it disturbs the prey and flees. Hungry Onychophora spend less time investigating their prey and are quicker to apply their slime. Once slime has been squirted, Onychophora will stop at nothing to hound down and devour their prey, in order to recoup the energetic investment. They have been observed to spend up to ten minutes searching for removed prey, after which they return to their slime to eat it. In the case of smaller prey, they may opt not to slime it at all.

Subsequently, a soft part of the prey item (usually a joint membrane in arthropod prey) is identified, punctured with a bite from the jaws, and injected with saliva. This kills the prey very quickly and begins a slower process of digestion. Whilst the onychophoran waits for the prey to digest, it salivates on its slime and begins to eat it (and anything attached to it). It subsequently tugs and slices at the earlier perforation to allow access to the now-liquidised innards of its prey.

In social groups, the dominant female is the first to feed, not permitting competitors access to the prey item for the first hour of feeding. Subsequently, subordinate individuals begin to feed. The number of males reaches a peak after females start to leave the prey item. After feeding, individuals clean their antennae and mouth parts before re-joining the rest of their group. Because it takes so long to ingest a prey item, hunting mainly happens around dusk; the onychophorans will abandon their prey at sunrise.

This predatory way of life is probably a consequence of the velvet worm's need to remain moist. Due to the continual risk of desiccation, often only a few hours per day are available for finding food. This leads to a strong selection for a low cost-benefit ratio, which can barely be achieved with a herbivorous diet.

Reproduction and life-cycle

Almost all species of velvet worm reproduce sexually. The sole exception is *Epiperipatus imthurni*, of which no males have been observed; reproduction instead occurs by parthenogenesis.

All species are in principle sexually distinct and bear, in many cases, a marked sexual dimorphism: the females are usually larger than the males and have, in species where the number of legs is variable, more legs. The females of many species are fertilized only once during their lives, which leads to copulation sometimes taking place before the reproductive organ of the females are fully developed. In such cases, for example at the age of three months in *Macroperipatus torquatus*, the transferred sperm cells are kept in a special reservoir, where they can remain viable for longer periods.

Fertilization takes place internally, although the mode of sperm transmission varies widely. In most species, for example in the genus *Peripatus*, a package of sperm cells called the spermatophore is placed into the genital opening of the female. The detailed process by which this is achieved is in most cases still unknown, a true penis having only been observed in species of the genus *Paraperipatus*. In many Australian species, there exist dimples or special dagger- or axe-shaped structures on the head; the male of *Florellicept stutchburyae* presses a long spine against the female's genital opening and probably positions its spermatophore there in this way. During the process, the female supports the male by keeping him clasped with the claws of her last pair of legs. The mating behavior of two species of the genus *Peripatopsis* is particularly curious. Here, the male places two-millimetre spermatophores on the back or flanks of the female. Amoebocytes from the female's blood collect on the inside of the deposition site, and both the spermatophore's casing and the body wall on which it rests are decomposed via the secretion of enzymes. This releases the sperm cells, which then move freely through the haemocoel, penetrate the external wall of the ovaries and finally fertilize the ova. Why this self-inflicted skin injury does not lead to bacterial infections is not yet understood (though likely related to the enzymes used to deteriorate the skin or facilitate the transfer of viable genetic material from male to female).

Velvet worms are found in egg-laying (oviparous), egg-live-bearing (ovoviviparous) and live-bearing (viviparous) forms.

- Ovipary occur solely in the Peripatopsidae, often in regions with erratic food supply or unsettled climate. In these cases, the yolk-rich eggs measure 1.3 to 2.0 mm and are coated in a protective chitinous shell. Maternal care is unknown.
- The majority of species are ovoviviparous: the medium-sized eggs, encased only by a double membrane, remain in the uterus. The embryos do not receive food directly from the mother, but are supplied instead by the moderate quantity of yolk contained in the eggs—they are therefore described as lecithotrophic. The young emerge from the eggs only a short time before birth. This probably represents the velvet worm's original mode of reproduction, i.e., both oviviparous and viviparous species developed from ovoviviparous species.
- True live-bearing species are found in both families, particularly in tropical regions with a stable climate and regular food supply throughout the year. The embryos develop from eggs only micrometres in size and are nourished in the uterus by their mother, hence the description "matrotrophic". The supply of food

takes place either via a secretion from the mother directly into the uterus or via a genuine tissue connection between the epithelium of the uterus and the developing embryo, known as a placenta. The former is found only outside the American continent, while the latter occurs primarily in America and the Caribbean and more rarely in the Old World. The gestation period can amount to up to 15 months, at the end of which the offspring emerge in an advanced stage of development. The embryos found in the uterus of a single female do not necessarily have to be of the same age; it is quite possible for there to be offspring at different stages of development and descended from different males. In some species, young tend to be only released at certain points in the year.

A female can have between 1 and 23 offspring per year; development from fertilized ovum to adult takes between 6 and 17 months and does not have a larval stage. This is probably also the original mode of development. Velvet worms have been known to live for up to six years.

Ecology

Predators and parasites

The velvet worm's important predators are primarily various spiders and centipedes, along with rodents and birds, such as, in Central America, the Clay-coloured Thrush (*Turdus grayi*). Hemprich's Coral Snake (*Micrurus hemprichii*) feeds almost exclusively on velvet worms. For defence, some species roll themselves reflexively into a spiral, while they can also fight off smaller opponents by ejecting slime.

Various mites (Acari) are known as ectoparasites, which infest the skin of the velvet worm. Skin injuries are usually accompanied by bacterial infections, which are almost always fatal.

Conservation status

The global conservation status of velvet worm species is difficult to estimate; many species are only known to exist at their type locality (the location at which they were first observed and described). The collection of reliable data is also hindered by low population densities, their typically nocturnal behaviour and possibly also as-yet undocumented seasonal influences and sexual dimorphism.

To date, only eleven species have been studied in sufficient detail to enable population estimates, of which three—*Opistopatus roseus*, *Speleoperipatus spelaeus* and *Peripatopsis leonina*—are considered critically endangered, the last being probably already extinct. Two species—*Macroperipatus insularis* and *Tasmanipatus anophthalmus*—are assessed by the IUCN as endangered, while four further species are listed as threatened.

The primary threat comes from destruction and fragmentation of velvet worm habitat due to industrialisation, draining of wetlands and "slash and burn" for agriculture. Many species also have naturally low population densities and closely restricted geographic ranges; as a result, relatively small localised disturbances of important ecosystems can lead to the extinction of entire populations or species. Collection of specimens for universities or research institutes also plays a role on a local scale.

There is a very pronounced difference in the protection afforded to velvet worms between regions: in some countries, such as South Africa, there are restrictions on both collecting and exporting, while in others, such as Australia, only export restrictions exist. Many countries offer no specific safeguards at all. Tasmania has a protection programme that is unique worldwide: one region of forest has its own velvet worm conservation plan, which is tailored to a particular velvet worm species.

Phylogeny

In their present forms, the velvet worms are probably very closely related to the arthropods, a very extensive taxon that incorporates, for instance, the crustaceans, insects and arachnids. They share, among other things, an exoskeleton consisting of α -chitin and non-collagenous proteins; gonads and waste-elimination organs enclosed in true coelom tissue; an open blood system with a tubular heart situated at the rear; an abdominal cavity divided into pericardial and perivisceral cavities; respiration via tracheae; and similar embryonic development. Segmentation, with two body appendages per segment, is also shared. However, antennae, mandibles and oral papillae are probably not homologous to the corresponding features in arthropods, i.e., they probably developed independently.

Another closely related group are the comparatively obscure water bears (Tardigrada); however, due to their very small size, these lack some characteristics of the velvet worms and arthropods, such as blood circulation and separate respiratory structures. Together, the velvet worms, arthropods and water bears form a monophyletic taxon, the Panarthropoda, i.e., the three groups collectively cover all descendants of their last common ancestor.

Due to certain similarities of form, the velvet worms were usually grouped with the water bears to form the taxon Protoarthropoda. This designation would imply that both velvet worms and water bears are not yet as highly developed as the arthropods. Modern systematic theories reject such conceptions of "primitive" and "highly developed" organisms and instead consider exclusively the historical relationships between the taxa. These relationships are not as yet fully understood, but it is considered probable that the velvet worms' sister groups form a taxon designated Tactopoda, thus:

For a long time, velvet worms were also considered related to the annelids. They share, among other things, a worm-like body; a thin and flexible outer skin; a layered musculature; paired waste-elimination organs; as well as a simply constructed brain and simple eyes. Decisive, however, was the existence of segmentation in both groups, with

the segments showing only minor specialisation. The parapodia appendages found in annelids therefore correspond to the stump feet of the velvet worms.

Within the Articulata concept developed by Georges Cuvier, the velvet worms therefore formed an evolutionary link between the annelids and the arthropods: worm-like precursors first developed parapodia, which then developed further into stub feet as an intermediate link in the ultimate development of the arthropods' appendages. Due to their structural conservatism, the velvet worms were thus considered "living fossils". This perspective was expressed paradigmatically in the statement by the French zoologist A. Vandel:

Onychophorans can be considered highly evolved annelids, adapted to terrestrial life, which announced prophetically the Arthropoda. They are a lateral branch which has endured from ancient times until today, without important modifications.

Modern taxonomy strives to avoid criteria such as "higher" and "lower" states of development or distinctions between "main" and "side" branches—only family relationships indicated by cladistic methods are considered relevant. From this point of view, several common characteristics still support the Articulata concept—segmented body; paired appendages on each segment; pairwise arrangement of waste-elimination organs in each segment; and above all, a rope-ladder-like nervous system based on a double nerve strand lying along the belly.

An alternative concept, most widely accepted today, is the so-called Ecdysozoa hypothesis. This places the annelids and Panarthropoda in two very different groups: the former in the Lophotrochozoa and the latter in the Ecdysozoa. Mitochondrial gene sequences also provide support for this hypothesis.

Proponents of this hypothesis assume that the aforementioned similarities between annelids and velvet worms either developed convergently or were primitive characteristics passed unchanged from a common ancestor to both the Lophotrochozoa and Ecdysozoa. For example, in the first case, the rope-ladder nervous system would have developed in the two groups independently, while in the second case, it is a very old characteristic, which does not imply a particularly close relationship between the annelids and Panarthropoda.

The Ecdysozoa concept divides the taxon into two, the Panarthropoda into which the velvet worms are placed, and the sister group Cycloneuralia, containing the threadworms (Nematoda), horsehair worms (Nematomorpha) and three rather obscure groups: the mud dragons (Kinorhyncha); penis worms (Priapulida); and brush-heads (Loricifera).

Particularly characteristic of the Cycloneuralia is a ring of "circumoral" nerves around the mouth opening, which the proponents of the Ecdysozoa hypothesis also recognise in modified form in the details of the nerve patterns of the Panarthropoda. Both groups also share a common skin-shedding mechanism (ecdysis) and molecular biological similarities. One problem of the Ecdysozoa hypothesis is the velvet worms' subterminal

mouth position: unlike in the Cycloneuralia, the mouth is not at the front end of the body, but lies further back under the belly. However, investigations into their developmental biology, particularly regarding the development of the head nerves, suggest that this was not always the case and that the mouth was originally terminal (situated at the tip of the body). This is supported by the fossil record.

The "stem-group arthropod" hypothesis is very widely accepted, but some trees suggest that the onychophorans may occupy a different position; their brain anatomy is more closely related to that of the chelicerates than to any other arthropod.

Evolutionary history

Fossils from the early Cambrian bear a striking resemblance to the velvet worms. These fossils, known collectively as the lobopods, were marine and probably represent a stem group to the onychophorans. They are found in the Cambrian, Ordovician, Silurian and Pennsylvanian periods.

Historically, all fossil Onychophora and lobopods were lumped into the taxon Xenusia, further subdivided by some authors to the Paleozoic Udeonychophora and the Mesozoic/Tertiary Ontonychophora; living Onychophora were termed Euonychophora.

It is not clear when the transition to a terrestrial existence was made, but it is considered plausible that it took place between the Ordovician and late Silurian—approximately 490 to 420 million years ago—via the intertidal zone.

The low preservation potential of the non-mineralised Onychophora means that they have a sparse fossil record, and crown group representatives are known only from amber—there is a single, partial specimen from the Cretaceous, and a more comprehensive record in Eocene deposits from 40 million years ago.

Taphonomy

The vagaries of the preservation process can make fossils difficult to interpret. Experiments on the decay and compaction of onychophora demonstrate difficulties in interpreting fossils; certain parts of living onychophora are only visible in certain conditions. The mouth may or may not be preserved; claws may be re-oriented or lost; leg width may increase or decrease; and mud may be mistaken for organs. More significantly, features seen in fossils may be artefacts of the preservation process: for instance, "shoulder pads" may simply be the second row of legs compressed coaxially onto the body; branching "antennae" may in fact be produced through decay.

Taxonomy

The modern velvet worms form a monophyletic group, incorporating all the descendants of their common ancestor. Important common derivative characteristics (synapomorphies) include, for example, the mandibles of the second body segment and

the oral papillae and associated slime glands of the third; nerve strands extending along the underside with numerous cross-linkages per segment; and the special form of the tracheae.

By 2004, some 155 modern species, comprising 47 genera, had been described; the actual number of species is probably about twice this. The best-known is the type genus *Peripatus*, which was described as early as 1825 and which, in English-speaking countries, stands representative for all velvet worms.

All genera are assigned to one of two families, the distribution ranges of which do not overlap but are separated by arid areas or oceans:

- The Peripatopsidae exhibit relatively many characteristics that are perceived as original or "primitive". They have between 13 and 25 pairs of legs, behind or between the last of which is the genital opening (gonopore). Both oviparous and ovoviviparous, as well as genuinely viviparous, species exist, although the Peripatopsidae essentially lack a placenta. Their distribution is circumaustral, encompassing Australia, Tasmania, New Zealand, New Guinea, South Africa and Chile.
- The Peripatidae exhibit a range of derivative features. They are longer, on average, than the Peripatopsidae and also have more leg pairs, numbering between 22 and 43—the gonopore is always between the penultimate pair. There are no oviparous species—the overwhelming majority are viviparous. The females of many viviparous species develop a placenta with which to provide the growing embryo with nutrients. Distribution of the Peripatidae is restricted to the tropical and subtropical zones; in particular, they inhabit Central and northern South America, several Caribbean islands, West Africa, northern India, Malaysia and various Indonesian islands.

Classification

- Phylum Onychophora
 - Class Onychophorida
 - Order † Paronychophora (extinct)
 - Family † Onychodictyidae
 - Genus † *Onychodictyon*
 - Order Euonychophora
 - Family Peripatidae
 - Genera: † *Cretoperipatus*, *Eoperipatus*, *Epiperipatus*, *Heteroperipatus*, *Macroperipatus*, *Mesoperipatus*, *Oroperipatus*, *Peripatus*, *Plicatoperipatus*, *Speleoperipatus*, *Typhloperipatus*
 - Family Peripatopsidae
 - Genera: *Acanthokara*, *Aethrikos*, *Akthinothele*, *Anoplokaros*, *Austroperipatus*, *Baeothele*,

Centrorumis, Cephalofovea, Critolaus, Dactylothele, Dystactotylos, Euperipatoides, Florellicept, Hylonomoipos, Konothele, Lathropatus, Leuropezos, Mantonipatus, Metaperipatus, Minyplanetes, Nodocapitus, Occiperipatoides, Ooperipatellus, Ooperipatus, Opisthopatus, Paraperipatus, Paropisthopatus, Peripatoides, Peripatopsis, Phallocephale, Planipallipus, Regimitra, Ruhbergia, Sphenoparme, Symperipatus, Tasmania, Tasmanipatus, Tetrameraden, Vescerro, Wambalana

- Family † *incertae sedis*
 - Genus † *Helenodora*

Chapter 2

Peripatus and Typhloperipatus

Peripatus

Peripatus

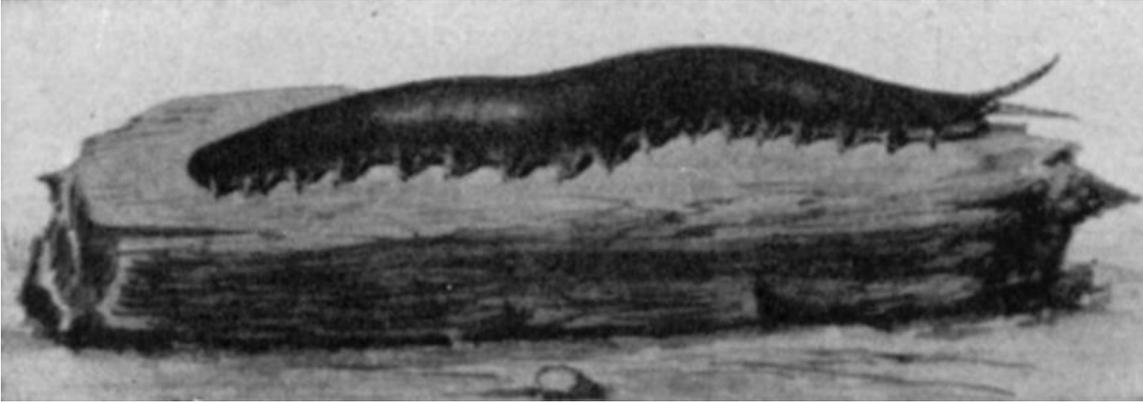


Scientific classification [e]

Kingdom:	Animalia
Phylum:	Onychophora
Class:	Onychophorida
Order:	Euonychophora
Family:	Peripatidae
Genus:	<i>Peripatus</i> Guilding, 1826

Peripatus is a genus of Onychophora (velvet worms). It is an invertebrate which gives birth to live young rather than laying eggs. It is said to be a living fossil because it has been unchanged for approximately 570 million years. *Peripatus* are native to scattered places around the world including Australia, Africa, Asia, New Zealand, Costa Rica, Brazil and other countries, but not in Europe or Antarctica. *Peripatus* is a nocturnal carnivore. This unique animal has the appearance of a caterpillar with its many pairs of legs, while its structure has many similarities to arthropods, but it also has many similarities to annelids, with some special features all of its own.

Anatomy



A defenceless, weaponless animal, it comes out at night, and is said to capture small insects by squirting jets of slime from its mouth

Peripatus shows no external segmentation; the legs are not jointed like arthropod legs although they possess arthropod-like claws. The outer covering is a cuticle, which is covered in unique microscopic projections known as papillae. These papillae give *Peripatus* their velvet texture. The body is composed of segments like annelids with segmentally arranged nephridia. *Peripatus* respire through tracheae as arthropods do. Antennae are present on the head. Excretion is through nephridia, which are found in each of the legs.

Feeding

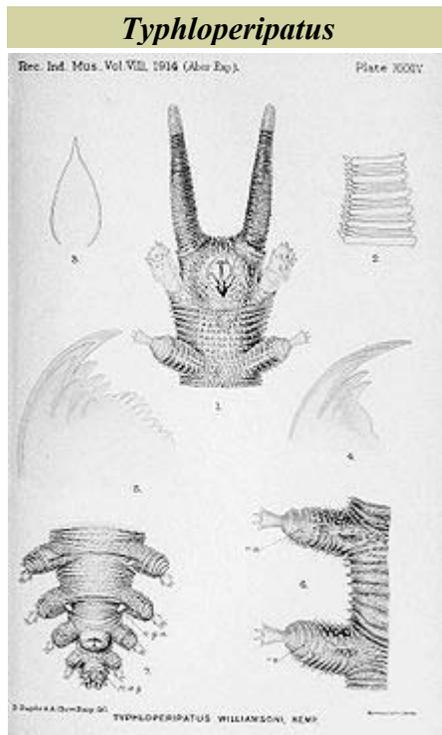
Peripatus feeds by trapping its prey (mostly small insects) in a white, sticky fluid it ejects from two antennae near its head. The fluid hardens on contact with the air immobilizing the prey. *Peripatus* then chews a hole in its prey's exoskeleton with its mandibles (which move independently of each other), injects digestive enzymes, and begins sucking out its prey's pre-digested innards.

Species

- *Peripatus antiguensis* Bouvier, 1899
- *Peripatus bavaysi* Bouvier, 1899
- *Peripatus bouvieri* Fuhrmann, 1913
- *Peripatus brolemanni* Bouvier, 1899
- *Peripatus dominicae* Pollard, 1894
- *Peripatus evelinae* (Marcus, 1937)
- *Peripatus heloisae* Carvalho, 1941
- *Peripatus juanensis* Bouvier, 1900
- *Peripatus juliformis* Guilding, 1826
- *Peripatus manni* Brues, 1913
- *Peripatus ruber* Fuhrmann, 1913
- *Peripatus sedgwicki* Bouvier, 1899

- *Peripatus swainsonae* Cockerell, 1893

Typhloperipatus



Scientific classification [e]

Kingdom: Animalia
 Phylum: Onychophora
 Class: Onychophorida
 Order: Euonychophora
 Family: Peripatidae
 Genus: *Typhloperipatus*

Binomial name

Typhloperipatus williamsoni
 Kemp, 1913

Typhloperipatus williamsoni is a species of onychophoran (or velvet worm) known from northeastern India. It is the only member of its genus and is the only South Asian species in the phylum. It is said to be evolutionarily close to the Sumatran *Eoperipatus*. It was discovered and described by Stanley Wells Kemp in 1913.

Discovery

The species name was after Noel Williamson, a political officer at Sadiya who was murdered in 1911. The murder led to an expedition being led to the Abor region by the British government in India. Stanley Kemp, then an assistant superintendent at the Indian Museum at Calcutta was a zoologist attached to this expedition. The first specimen was found near the gorge of the Dihang River near Rotung. Although the nearest other species from Malaya was typically found in dead wood, these were found mainly under large stones near the roots of trees. Like other velvet worms they discharge a spray of viscous fluid that hardens to trap and arrest small predators and prey.

Description

These velvet worms have no eyes. The colour of the upperside is a deep umber brown with the tips of the antennae slightly paler brown. The papillae on the skin have pale tips and the underside is pale brown. Some individuals have a dark dorsal stripe. It has 19 to 20 pairs of legs, the inner jaw has a serrate edge. The legs have coxal glands, four complete and spiny pads and the feet have two papillae.

Although Kemp believed that the species was closer to neotropical forms than to Southeast Asian forms, modern studies place them close to *Eoperipatus* of Southeast Asia.

Chapter 3

Acoelomorpha and Convolutidae

Acoelomorpha

Acoelomorphs



Waminoa sp. on *Plerogyra* sp..

Scientific classification [e]

Kingdom: Animalia
Superphylum: Deuterostomia (?)
Clade (?): Xenacoelomorpha
Phylum: **Acoelomorpha**
Ehlers 1985

Classes

Acoela
Nemertodermatida

The **Acoelomorpha** are a disputed phylum of animals with planula-like features that have historically been considered to belong to the phylum Platyhelminthes. More recent molecular studies have demonstrated that they are a separate phylum, although their position in the tree of life is contentious; most researchers believe them to be basal among the Bilateria, slightly more derived than the cnidaria. Recent (2011) results suggest that they (along with *Xenoturbella*) may lie near the base of the deuterostomes.

Earlier (2007) work dismissed the phylum as paraphyletic, with Acoela and Nemertodermatida as separate clades.

An ongoing (Feb. 2011) collaborative research project has "the researchers ... confident that they can reach an agreement about where acoels fit in evolutionary history.

Acoels are almost entirely marine, living between grains of sediment, swimming as plankton, or crawling on algae. Acoels have a statocyst, which presumably helps them orient to gravity. Their soft bodies make them difficult to classify.

Anatomy

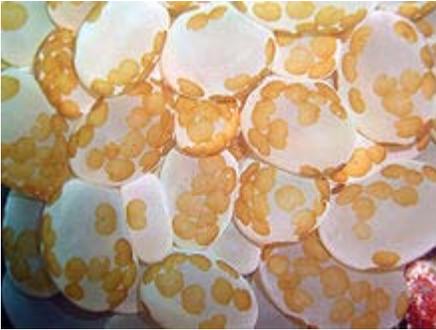
The Acoela are very small flattened worms, usually under 2 millimetres (0.079 in) in length (*Symsagittifera roscoffensis* about 15 mm), that do not have a gut. Digestion is accomplished by means of a syncytium that forms a vacuole around ingested food. There are no epithelial cells lining the digestive vacuole, although there is sometimes a short pharynx leading from the mouth to the vacuole. All other bilateral animals (apart from tapeworms) have a gut lined with epithelial cells. As a result, the acoels appear to be solid-bodied (*a-coel*, or *no body cavity*).

Acoelomorphs resemble flatworms in many respects, but have a simpler anatomy, even beyond the absence of a gut. Like flatworms, they have no circulatory or respiratory systems, but they also lack an excretory system. They have no true brain or ganglia, simply a network of nerves beneath the epidermis, although the nerves are slightly more concentrated towards the forward end of the animal. The sensory organs include a statocyst and, in some cases, very primitive pigment-spot ocelli capable of detecting light.

They are simultaneous hermaphrodites, but have no gonads, and no ducts associated with the female reproductive system. Instead, gametes are produced from the mesenchymal cells that fill the body between the epidermis and the digestive vacuole.

Convolutidae

Convolutidae



Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa
Phylum:	Acoelomorpha
Class:	Acoela
Order:	not assigned
Family:	Convolutidae

Genera

Amphicolops
Brachypea
Conaperta
Convoluta
Haplodiscus
Heterochaerus
Neochildia
Oligochoerus
Oxyposthia
Picola
Polychoerus
Stomatricha
Wulguru
Pseudoconvoluta?
Waminoa?

Convolutidae are a family of free-living flatworms.

Systematics

Currently the family contains 13 genera, the type genus being *Convoluta* (Turbellarian taxonomic database,2006).

The genus *Waminoa* appears, according to recent studies also belong to the family, or is at least closely related (Ogunlana et al., 2005).

Characteristics

Acoels with a ventral mouth opening. Body-wall musculature with circular, longitudinal, and longitudinal crossover muscle fibers in both the dorsal and ventral body wall, and U-shaped fibers in the ventral body wall.

Male copulatory organ with muscular, often glandular, tubular penis. Penis musculature with inner circular fibers and outer longitudinal fibers that anastomose or cross over each other. When present, a muscular seminal vesicle surrounds all of, or a portion of the penis. Male gonopore ventral, subterminal, or terminal at posterior end; usually positioned behind opening to female seminal bursa. Spermatozoa with 9+0 axonemes and axial microtubules.

Algal symbionts often present. Ocelli, when present, contain reflective platelets in the pigment cell and lack cilia or microvilli as receptor organelles (Hooge & Tyler, 2005).

Species

Amphiscolops

Contains the following species:

- *Amphiscolops bermudensis* Hyman 1939
- *Amphiscolops blumi* Achatz, Hooge & Tyler, 2007
- *Amphiscolops carvalhoi* Marcus 1952
- *Amphiscolops cinereus* (Graff, 1874)
- *Amphiscolops evelinae* Marcus 1947
- *Amphiscolops fuliginus* Peebles 1913
- *Amphiscolops gemelliporus* Marcus 1954
- *Amphiscolops japonicus* Kato 1947
- *Amphiscolops langerhansi* (Graff, 1882)
- *Amphiscolops marinelliensis* Beltagi & Khafagi, 1984
- *Amphiscolops mosaicus* Kozloff 1998
- *Amphiscolops potocani* Achatz, 2008
- *Amphiscolops trifurcatus* (Beltagi 1983)
- *Amphiscolops zeii* Riedl 1956

Brachypea

Contains the following species:

- *Brachypea kenoma* Antonius 1968

Conaperta

Contains the following species:

- *Conaperta antonii* Achatz, Hooge & Tyler, 2007
- *Conaperta cirrata* Achatz, Hooge & Tyler, 2007

Haplodiscus

Contains the following species:

- *Haplodiscus acuminatus* Böhmig, 1895
- *Haplodiscus bocki* Dörjes 1970
- *Haplodiscus obtusus* Böhmig, 1895
- *Haplodiscus ovatus* Böhmig, 1895
- *Haplodiscus piger* Weldon 1888
- *Haplodiscus weldoni* Böhmig, 1895

Heterochaerus

Contains the following species:

- *Heterochaerus australis* Haswell 1905
- *Heterochaerus sargassi* (Hyman 1939)

Neochildia

Contains the following species:

- *Neochildia fusca* Bush, 1975

Oligochoerus

Contains the following species:

- *Oligochoerus bakuensis* Beklemischev 1963
- *Oligochoerus chlorella* Beklemischev 1963
- *Oligochoerus conops* Beklemischev, 1963
- *Oligochoerus erythrophthalmus* Beklemischev 1963
- *Oligochoerus limnophilus* Ax & Doerjes 1966

- *Conaperta flavibacillum* (Jensen, 1878)
- *Conaperta krana* Antonius 1968
- *Conaperta lineata* (Peebles, 1915)
- *Conaperta thela* Antonius 1968
- *Oligochoerus melanops* Beklemischev 1963
- *Oligochoerus xanthella* Beklemischev 1963

Oxyposthia

Contains the following species:

- *Oxyposthia praedator* Ivanov 1952

Convoluta

Contains the following species:

- *Convoluta aegyptica* Antonius 1968
- *Convoluta albomaculata* (Pereyaslawzewa, 1892)
- *Convoluta bohmi* (Brauner, 1920)
- *Convoluta borealis* Sabussow 1900
- *Convoluta boyeri* Bush 1984
- *Convoluta confusa* Graff 1904
- *Convoluta convoluta* (Abildgaard, 1806)
- *Convoluta elegans* Pereyaslawzewa 1892
- *Convoluta enelitta* Antonius 1968
- *Convoluta furugelmi* Mamkaev, 1971
- *Convoluta henseni* Böhmig, 1895
- *Convoluta hipparchia* Pereyaslawzewa 1892
- *Convoluta kikaiensis* Yamasu 1982
- *Convoluta lacazii* Graff 1891
- *Convoluta lacrimosa* Achatz, Hooge & Tyler, 2007
- *Convoluta marginalis* Ivanov 1952
- *Convoluta naviculae* Yamasu 1982
- *Convoluta nipponi* Achatz, 2008
- *Convoluta pelagica* Lohner & Micoletzky 1911
- *Convoluta philippinensis* Bush 1984
- *Convoluta pygopora* Antonius

Picola

Contains the following species:

- *Picola renei* Achatz & Hooge, 2006

Polychoerus

Contains the following species:

- *Polychoerus carmelensis* Costello and Costello, 1938
- *Polychoerus caudatus* Mark 1892
- *Polychoerus ebenhochi* Achatz, Hooge & Tyler, 2007
- *Polychoerus parvus* Achatz, Hooge & Tyler, 2007

Praesagittifera

Contains the following species:

- *Praesagittifera gracilis* (Yamasu, 1982)
- *Praesagittifera naikaiensis* (Yamasu, 1982)
- *Praesagittifera shikoki* Kostenko & Mamkaev 1990

Stomatricha

Contains the following species:

- *Stomatricha hochbergi* Hooge,

- 1968
- *Convolvula schmidti* Czerniavsky, 1881
 - *Convolvula schuelii* Achatz, 2008
 - *Convolvula sordida* Graff 1882
 - *Convolvula sutcliffei* Hanson, 1961
 - *Convolvula variabilis* (Pereyaslawzewa, 1892)

2003

Waminoa

Contains the following species:

- *Waminoa brickneri* Ogunlana, Hooge, Tekle, Benayahu, Barneah & Tyler, 2005
- *Waminoa litus* Winsor 1990

Wulguru

Contains the following species:

- *Wulguru cuspidata* Winsor 1988

Chapter 4

Brachiopod

Brachiopod

Temporal range: Lower Cambrian–
Recent



Platystrophia ponderosa (Ordovician).
Scale bar is 5.0 mm.

Scientific classification [e]

Kingdom: Animalia
(unranked): Protostomia
(unranked): Spiralia
Superphylum: Lophotrochozoa
Phylum: **Brachiopoda**
Duméril, 1806

Diversity

About 100 living genera.
About 5,000 fossil genera.

Brachiopods are a phylum of marine animals that have hard "valves" (shells) on the upper and lower surfaces. Most species of brachiopod went extinct during the P–T extinction over 250 million years ago, but many survive today.

Brachiopod valves are hinged at the rear end, while the front can be opened for feeding or closed for protection. Articulate brachiopods have toothed hinges and simple opening and closing muscles, while inarticulate brachiopods have untoothed hinges and more complex muscles. In a typical brachiopod a stalk-like pedicle projects from an opening in the hinge or from a hole in the larger valve, attaching the animal to the sea bed but clear of silt that would obstruct the opening.

Brachiopods have a mantle that secretes and lines the shell, and encloses the internal organs. The body occupies typically about one-third of the internal space inside the shell, nearest the hinge. The rest of the mantle encloses a water-filled space containing the lophophore, a crown of tentacles that filters food particles out of the water. In all species the lophophore is supported by cartilage and by a hydrostatic skeleton.

The lophophore filters food, mostly phytoplankton, out of the water. From there the food is transported in succession to: the grooves along the bases of the lophophore's tentacles; the mouth; pharynx; oesophagus; and finally the stomach, where the food is digested. Nutrients are transported from the stomach throughout the coelom (main body cavity), including the mantle lobes, by cilia. The wastes produced by metabolism are broken into ammonia, which is eliminated by diffusion through the mantle and lophophore.

The lophophore and mantle are the only surfaces that absorb oxygen and eliminate carbon dioxide. Oxygen seems to be distributed by the fluid of the coelom. The heart is above the stomach, and the blood vessels connect it to the major organs. However, the main function of the blood may be to deliver nutrients. The maximum oxygen consumption of brachiopods is low, and their minimum requirement is not measurable.

The "brain" of adult articulates consists of two ganglia, one above and the other below the oesophagus. Adult inarticulates have only the lower ganglion. Nerves run to the lophophore, the mantle lobes and the muscles that operate the valves. Many brachiopods close their valves if shadows appear above them, but the cells responsible for this are unknown. Some brachiopods have statocysts which detect changes in the animals' balance.

Lifespans range from 3 to over 30 years. Ripe gametes (ova or sperm) float from the gonads into the main coelom and then exit into the mantle cavity. The larvae of inarticulate brachiopods are miniature adults, with lophophores that enable the larvae to feed and swim for months, until the animals become heavy enough to settle to the seabed. Larvae of articulate species are different from the adult forms, live only on yolk, and remain among the plankton for only a few days before metamorphosing.

The traditional classification into inarticulate and articulate brachiopods has been supplemented by two refinements that appeared in the 1990s. One refinement groups the

inarticulate Craniida with articulate brachiopods, as both used the same material in the mineral layers of the shell. The other segregates the Craniida into a third group, as their outer organic layer is different from that of either the others. However, some taxonomists believe it is premature to define the higher levels of classification such as order, and recommend instead a bottom-up approach that identifies genera and then groups these into intermediate groups. Traditionally brachiopods have been regarded as members of or as a sister group to the deuterostomes, a super-phylum which includes chordates and echinoderms. One type of analysis of brachiopods' evolutionary relationships has always placed brachiopods as protostomes, while another type has split between placing brachiopods among the protostomes or the deuterostomes.

In 2003 it was suggested that brachiopods evolved from an ancestor similar to *Halkieria*, a slug-like animal with "chain mail" on its back and a shell at the front and rear end, and that the ancestral brachiopod converted its shells into a pair of valves by folding the rear part of its body under its front. However, new fossils found in 2007 to 2008 suggest that brachiopods evolved from tommotiids: the tommotiids' "chain mail" formed the tube of a sessile animal resembling brachiopods. Lineages that have both fossil and extant brachiopods appeared in the early Cambrian, Ordovician and Carboniferous periods. Other lineages have arisen and then become extinct, sometimes during severe mass extinctions. At their peak in the Paleozoic era the brachiopods were among the most abundant filter-feeders and reef-builders, and occupied other ecological niches, including swimming in the jet-propulsion style of scallops. Brachiopod fossils have been useful indicators of climate changes during the Paleozoic era. However, after the Permian–Triassic extinction event, brachiopods recovered only a third of their former diversity. A study in 2007 concluded that brachiopods were especially vulnerable to the Permian–Triassic extinction, as they built calcareous hard parts (made of calcium carbonate) and had low metabolic rates and weak respiratory systems. It was often thought that brachiopods were in decline after the Permian–Triassic extinction, and were out-competed by bivalves. However, a study in 1980 concluded that both brachiopods and bivalves increased all the way from the Paleozoic to modern times, but bivalves increased faster; after the Permian–Triassic extinction, brachiopods for the first time were less diverse than bivalves.

Brachiopods live only in the sea, and most species avoid locations with strong currents or waves. Articulate species have larvae that settle quickly and form dense populations in well-defined areas, while inarticulate larvae swim for up to a month and have wide ranges. Brachiopods now live mainly in cold and low-light conditions. Fish and crustaceans seem to find brachiopod flesh distasteful and seldom attack them. Among brachiopods only the lingulids have been fished commercially, on a very small scale. One brachiopod species may be a measure of environmental conditions around an oil terminal being built in Russia on the shore of the Sea of Japan.

Description

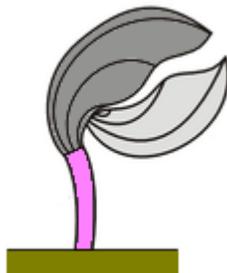
Name



Some brachiopod species are shaped like this oil lamp

The scientific name "Brachiopod" is formed from the Ancient Greek words βραχίον ("arm") and πούς ("foot"). They are often known as "lamp shells", since the curved shells of the class Terebratulida look rather like pottery oil-lamps.

Shells and their mechanisms



An articulate brachiopod:

■ Pedicle valve

- Brachial valve
- Pedicle
- Surface

Modern brachiopods range from 1 to 100 millimetres (0.039 to 3.9 in) long, and most species are about 10 to 30 millimetres (0.39 to 1.2 in). Each has two valves (shell sections) which are biomineralized. The valves cover the dorsal and ventral surface of the animal, unlike bivalve molluscs whose shells cover the lateral surfaces. The brachial valve bears on its inner surface the brachia ("arms") from which the phylum gets its name, and which supports the lophophore, used for filtering and respiration. The other is known as the pedicle valve, as its inner surface bears the stalk-like pedicle by which most brachiopods attach themselves to surfaces. The brachial and pedicle valves are often called the dorsal ("upper") and ventral ("lower"), but some paleontologists regard "dorsal" and "ventral" as incorrect terms, since they believe that the "ventral" valve was formed by folding of the upper surface under the body. Irrespective of this debate, the valves of brachiopods are differently arranged of those of bivalve molluscs, which lie on the left and right sides of the body. In most brachiopod species both valves are convex, the surfaces often bear growth lines or other ornaments, and the pedicle valve is larger than the brachial. However, the lingulids, which burrow into the seabed, have valves that are smoother, flatter and of similar size and shape.

Brachiopod valves have a hinge, in which the rearmost end of the brachial valve rocks on an internal projection of the pedicle valve. The internal projections of articulate ("jointed") brachiopods have teeth which fit into sockets on the brachial valve, an arrangement that locks the valves together. Inarticulate brachiopods have no matching teeth and sockets, and their valves are held together only by muscles.

All brachiopods have adductor muscles, that are set on the inside of the pedicle valve and close the valves by pulling on the part of the brachial valve ahead of the hinge. These muscles have both "quick" fibers that close the valves in emergencies and "catch" fibers that are slower but can keep the valves closed for long periods. Articulate brachiopods open the valves by means of abductor muscles, also known as diductors, which lie further to the rear and pull on the part of the brachial valve behind the hinge. Inarticulate brachiopods use a different opening mechanism, in which muscles reduce the length of the coelom (main body cavity) and make it bulge outwards, pushing the valves apart. Both classes open the valves to an angle of about 10°. The more complex set of muscles employed by inarticulate brachiopods can also operate the valves as scissors, a mechanism that lingulids use to burrow.



The inarticulate species *Lingula anatina*, showing the long pedicle, flattened shells and prominent chetae around the front edge of the shells

Each valve consists of three layers, an outer periostracum made of organic compounds and two biomineralized layers. Articulated brachiopods have a periostracum made of proteins, a "primary layer" of calcite (a form of calcium carbonate) under that, and finally a mixture of proteins and calcite. Inarticulate brachiopod shells have a similar sequence of layers, but their composition is different from that articulated brachiopods and also varies between the classes of inarticulate brachiopods. Linguids and discinids, which have pedicles, have a matrix of glycosaminoglycans (long, unbranched polysaccharides), in which other material are embedded: chitin in the periostracum; apatite containing calcium phosphate in the primary biomineralized layer; and a complex mixture in the innermost layer, containing collagen and other proteins, chitinophosphate and apatite.

Craniids, which have no pedicle and cement themselves directly to hard surfaces, have a periostracum of chitin and mineralized layers of calcite.

Mantle

Like molluscs, brachiopods have a mantle, an epithelium that lines the shell and encloses the internal organs. The brachiopod body occupies only about one-third of the internal space inside the shell, nearest the hinge. The rest of the space is lined with the mantle lobes, extensions that enclose a water-filled space in which sits the lophophore. The coelom extends into each lobe as a network of canals, which carry nutrients to the edges of the mantle.

Relatively new cells in a groove on the edges of the mantle secrete material that extends the periostracum. These cells are gradually displaced to the underside of the mantle by more recent cells in the groove, and switch to secreting the mineralized material of the shell valves. In other words, on the edge of the valve the periostracum is extended first, and then reinforced by extension of the mineralized layers under the periostracum. In most species the edge of the mantle also bears movable bristles, often called chaetae or setae, that may help defend the animals and may act as sensors. In some brachiopods groups of chaetae help to channel the flow of water into and out of the mantle cavity.

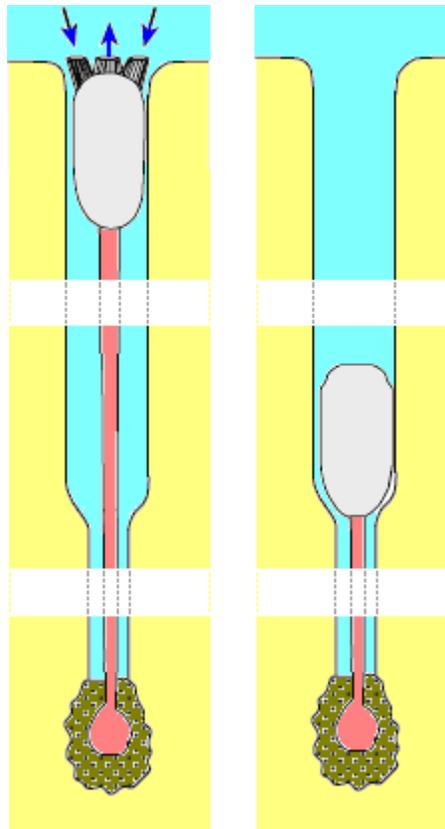
In most brachiopods, diverticula (hollow extensions) of the mantle penetrate through the mineralized layers of the valves into the periostraca. The function of these diverticula is uncertain and it is suggested that they may be storage chambers for chemicals such as glycogen, may secrete repellents to deter organisms that stick to the shell or may help in respiration. Experiments show that a brachiopod's oxygen consumption drops if petroleum jelly is smeared on the shell, clogging the diverticula.

Lophophore

Like bryozoans and phoronids, brachiopods have a lophophore, a crown of tentacles whose cilia (fine hairs) create a water current that enables them to filter food particles out of the water. However a bryozoan or phoronid lophophore is a ring of tentacles mounted on a single, retracted stalk, while the basic form of the brachiopod lophophore is U-shaped, forming the brachia ("arms") from which the phylum gets its name. Brachiopod lophophores are non-retractable and occupy up to two-thirds of the internal space, in the frontmost area where the valves gape when opened. To provide enough filtering capacity in this restricted space, lophophores of larger brachiopods are folded in moderately to very complex shapes – loops and coils are common, and some species' lophophores resemble a hand with the fingers splayed. In all species the lophophore is supported by cartilage and by a hydrostatic skeleton (in other words by the pressure of its internal fluid), and the fluid extends into the tentacles. Some articulate brachiopods also have a brachidium, a calcareous support for the lophophore attached to the inside of the brachial valve.

The tentacles bear cilia (fine mobile hairs) on their edges and along the center. The beating of the outer cilia drives a water current from the tips of the tentacles to their bases, where it exits. Food particles that collide with the tentacles are trapped by mucus, and the cilia down the middle drive this mixture to the base of the tentacles. A brachial groove runs round the bases of the tentacles, and its own cilia pass food along the groove towards the mouth. The method used by brachiopods is known as "upstream collecting", as food particles are captured as they enter the field of cilia that creates the feeding current. This method is used by the related phoronids and bryozoans, and also by pterobranchs. Entoprocts use a similar-looking crown of tentacles, but it is solid and the flow runs from bases to tips, forming a "downstream collecting" system that catches food particles as they are about to exit.

Attachment to substrate



A lingulid in its burrow, in "up" and retracted positions

Most modern species attach to hard surfaces by means of a cylindrical pedicle ("stalk"), an extension of the body wall. This has a chitinous cuticle (non-cellular "skin") and protrudes through a opening in the hinge. However, some genera such as the inarticulate *Crania* and the articulate *Lacazella* have no pedicle, and cement the rear of the "pedicle" valve to a surface so that the front is slightly inclined up away from the surface. In a few articulate genera such as *Neothyris* and *Anakinetica*, the pedicles wither as the adults grow and finally lie loosely on the surface. In these genera the shells are thickened and shaped so that the opening of the gaping valves is kept free of the sediment.

Pedicles of inarticulate species are extensions of the main coelom, which houses the internal organs. A layer of longitudinal muscles lines the epidermis of the pedicle. Members of the order Lingulida have long pedicles, which they use to burrow into soft substrates, to raise the shell to the opening of the burrow to feed, and to retract the shell when disturbed. A lingulid moves its body up and down the top two-thirds of the burrow, while the remaining third is occupied only by the pedicle, with a bulb on the end that builds a "concrete" anchor. However, the pedicles of the order Discinida are short and attach to hard surfaces.

An articulate pedicle has no coelom, is constructed from a different part of the larval body, and has a core composed of connective tissue. Muscles at the rear of the body can straighten, bend or even rotate the pedicle. The far end of the pedicle generally has rootlike extensions or short papillae ("bumps") which attach to hard surfaces. However, articulate brachiopods of genus *Chlidonophora* use a branched pedicle to anchor in sediment. The pedicle emerges from the pedicle valve, either through a notch in the hinge or, in species where the pedicle valve is longer than the brachial, from a hole where the pedicle valve doubles back to touch the brachial valve. Some species stand with the front end upwards, while others lie horizontal with the pedicle valve uppermost.

Feeding and excretion



Spiriferina rostrata with visible skeleton of the lophophore

The water flow enters the lophophore from the sides of the open valves and exits at the front of the animal. In lingulids the entrance and exit channels are formed by groups of chaetae that function as funnels. In other brachiopods the entry and exit channels are organized by the shape of the lophophore. The lophophore captures food particles, especially phytoplankton (tiny photosynthetic organisms), and deliver them to the mouth via the brachial grooves along the bases of the tentacles. The mouth is at the base of the lophophore. Food passes through the mouth, muscular pharynx ("throat") and oesophagus ("gullet"), all of which are lined with cilia and cells that secrete mucus and digestive enzymes. The stomach wall has branched ceca ("pouches") where food is digested, mainly within the cells.

Nutrients are transported throughout the coelom, including the mantle lobes, by cilia. The wastes produced by metabolism are broken into ammonia, which is eliminated by diffusion through the mantle and lophophore. Brachiopods have metanephridia, used by many phyla to excrete ammonia and other dissolved wastes. However, brachiopods have

no sign of the podocytes which perform the first phase of excretion in this process, and brachiopod metanephridia appear to be used only to emit sperm and ova.

The majority of food consumed by brachiopods is digestible, with very little solid waste produced. The cilia of the lophophore can change direction to eject isolated particles of indigestible matter. If the animal encounters larger lumps of undesired matter, the cilia lining the entry channels pause and the tentacles in contact with the lumps move apart to form large gaps and then slowly use their cilia to dump the lumps onto the lining of the mantle. This has its own cilia, which wash the lumps out through the opening between the valves. If the lophophore is clogged, the adductors snap the valves sharply, which creates a "sneeze" that clears the obstructions. In some inarticulate brachiopods the digestive tract is U-shaped and ends with an anus that eliminates solids from the front of the body wall. Other inarticulate brachiopods and all articulate brachiopods have a curved gut that ends blindly, with no anus. These animals bundle solid waste with mucus and periodically "sneeze" it out, using sharp contractions of the gut muscles.

Circulation and respiration

The lophophore and mantle are the only surfaces that absorb oxygen and eliminate carbon dioxide. Oxygen seems to be distributed by the fluid of the coelom, which is circulated through the mantle and driven either by contractions of the lining of the coelom or by beating of its cilia. In some species oxygen is partly carried by the respiratory pigment hemerythrin, which is transported in coelomocyte cells.

Brachiopods also have colorless blood, circulated by a muscular heart which lies in the dorsal part of the body above the stomach. The blood passes through vessels that extend to the front and back of the body, and branch to organs including the lophophore at the front and the gut, muscles, gonads and nephridia at the rear. The blood circulation seems not to be completely closed, and the coelomic and blood fluids must mix to a degree. The main function of the blood may be to deliver nutrients.

Nervous system and senses

The "brain" of adult articulates consists of two ganglia, one above and the other below the oesophagus. Adult inarticulates have only the lower ganglion. From the ganglia and the commissures where they join, nerves run to the lophophore, the mantle lobes and the muscles that operate the valves. The edge of the mantle has probably the greatest concentration of sensors. Although not directly connected to sensory neurons, the mantle's chaetae probably send tactile signals to receptors in the epidermis of the mantle. Many brachiopods close their valves if shadows appear above them, but the cells responsible for this are unknown. Some brachiopods have statocysts which detect changes in the animals' position.

Reproduction and lifecycle

Lifespans range from 3 to over 30 years. Adults of most species are of one sex throughout their lives. The gonads are masses of developing gametes (ova or sperm), and most species have four gonads, two in each valve. Those of articulates lie in the channels of the mantle lobes, while those of inarticulates lie near the gut. Ripe gametes float into the main coelom and then exit into the mantle cavity via the metanephridia, which open on either side of the mouth. Most species release both ova and sperm into the water, but females of some species keep the embryos in brood chambers until the larvae hatch.

The cell division in the embryo is radial (cells form in stacks of rings directly above each other), holoblastic (cells are separate, although adjoining) and regulative (the type of tissue into which a cell develops is controlled by interactions between adjacent cells, rather than rigidly within in each cell). While some animals develop the mouth and anus by deepening the blastopore, a "dent" in the surface of the early embryo, the blastopore of brachiopods closes up, and their mouth and anus develop from new openings.

The larvae of inarticulates swim as plankton for months and are like miniature adults, with valves, mantle lobes, a pedicle that coils in the mantle cavity, and a small lophophore, which is used for both feeding and swimming – except that Craniids have no pedicle. As the shell becomes heavier, the juvenile sinks to the bottom and becomes a sessile adult. The larvae of articulate species live only on yolk, and remain among the plankton for only a few days. This type of larva has a ciliated frontmost lobe that becomes the body and lophophore, a rear lobe that becomes the pedicle, and a mantle like a skirt, with the hem towards the rear. On metamorphosing into an adult, the pedicle attaches to a surface, the front lobe develops the lophophore and other organs, and the mantle rolls up over the front lobe and starts to secrete the shell. The maximum oxygen consumption of brachiopods is low, and their minimal requirement is not measurable. In cold seas, brachiopod growth is seasonal and the animals often lose weight in winter. These variations in growth often form growth lines in the shells. Members of some genera have survived for a year in aquaria without food.

Taxonomy

The fossil brachiopod genera have great diversity but only a few skeletal characteristics, while the modern genera have much lower diversity but provide soft-bodied characteristics as well as skeletal ones – and both sets of specimens have limitations that make it difficult to produce a comprehensive classification of brachiopods. The phylum also has experienced significant convergent evolution and reversals (in which a more recent group seems to have lost a characteristic that is seen in an intermediate group, reverting to a characteristic last seen in an older group). Hence some brachiopod taxonomists believe it is premature to define higher levels of classification such as order, and recommend instead a bottom-up approach that identifies genera and then groups these into intermediate groups.

However, other taxonomists believe that some patterns of characteristics are sufficiently stable to make higher-level classifications worthwhile, although there are different views about what the higher-level classifications should be. The "traditional" classification was defined in 1869; two further approaches were established in the 1990s:

- In the "traditional" classification, the Articulata have toothed hinges between the valves, while the hinges of the Inarticulata are held together only by muscles.
- A classification devised in the 1990s, based on the materials of which the shells are based, united the Craniida and the "articulate" brachiopods in the Calciata, which have calcite shells. The Lingulida and Discinida, combined in the Lingulata, have shells made of chitin and calcium phosphate.
- A three-part scheme, also from the 1990s, places the Craniida in a separate group of its own, the Craniformea. The Lingulida and Discinida are grouped as Linguliformea, and the Rhynchonellida and Terebratulida as Rhynchonelliformea.

Three high-level classifications of brachiopods					
"Traditional" classification	Inarticulata			Articulata	
"Calciata" approach	Lingulata		Calciata		
Three-part approach	Linguliformea		Craniformea	Rhynchonelliformea	
Orders	Lingulida	Discinida	Craniida	Terebratulida	Rhynchonellida
Hinge	No teeth			Teeth and sockets	
Anus	On front of body, at end of U-shaped gut			None	
Pedicle	Contains coelom with muscles running through		No pedicle	No coelom, muscles where joins body	
Periostracum	Long, attached to burrows	Short, attached to hard surfaces	None, cemented to surface	Short, attached to hard surfaces	
Primary (middle) mineralized layer of shell	Glycosaminoglycans and chitin		Chitin	Proteins	
Inner mineralized layer of shell	Glycosaminoglycans and apatite (calcium phosphate)		Calcite (a form of calcium carbonate)		
	Collagen and other proteins, chitinophosphate and apatite (calcium phosphate)		Calcite	Proteins and calcite	

Chetae around opening of shells	Yes	No	Yes
Coelom fully divided	Yes	No	Yes

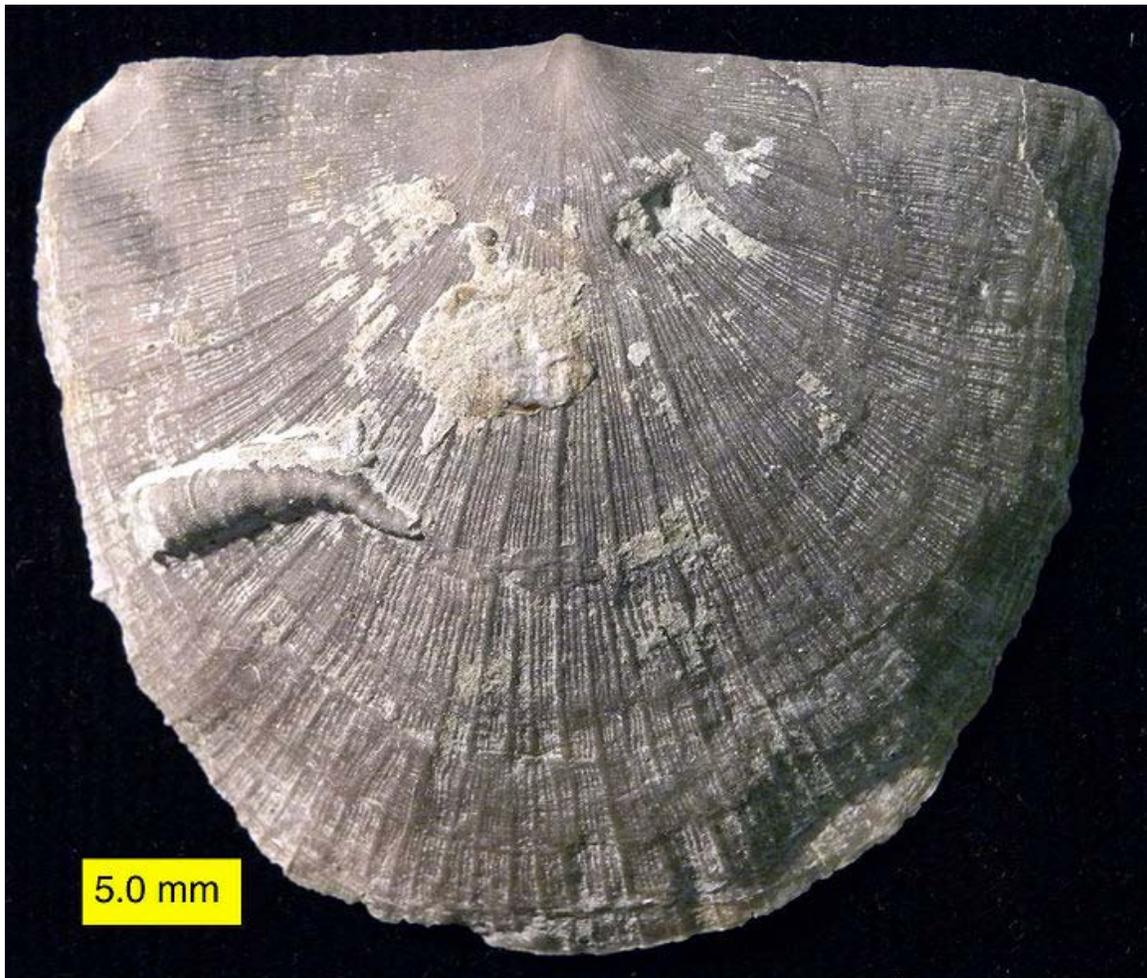
About 330 living species are recognized, grouped into over 100 genera. The great majority of modern brachiopods are rhynchonelliforms (Articulata, but excluding Craniida).

Ecology

Distribution and habitat

Brachiopods live only in the sea. Most species avoid locations with strong currents or waves, and typical sites include rocky overhangs, crevices and caves, steep slopes of continental shelves, and in the bottoms of deep oceans. However, some articulate species attach to kelp or in exceptionally sheltered sites in intertidal zones. The smallest living brachiopod, *Gwynia*, is only about 1 millimetre (0.039 in) long, and lives in gravel. Rhynchonelliforms (Articulata excluding Craniida), whose larvae consume only their yolks and settle and develop quickly, specialize in specific areas and form dense populations that can reach thousands per meter. Young adults often attach to the shells of more mature ones. On the other hand, inarticulate brachiopods, whose larva swim for up to a month before settling, have wide ranges. Members of the discinoid genus *Pelagodiscus* have a cosmopolitan distribution.

Interactions with other organisms



Strophomenid brachiopod with attached cornulitid worm tube (Upper Ordovician, SE Indiana, USA). Brachiopod valves often serve as substrates for encrusting organisms.

Brachiopod metabolism is 3 to 10 times slower than that of bivalves. While brachiopods were abundant in warm, shallow seas during the Cretaceous period, they have been outbred by bivalves, and now live mainly in cold and low-light conditions.

Brachiopod shells occasionally show evidence of damage by predators, and sometimes of subsequent repair. Fish and crustaceans seem to find brachiopod flesh distasteful. The fossil record shows that drilling predators like gastropods attacked molluscs and echinoids 10 to 20 times more often than they did brachiopods, suggesting that such predators attacked brachiopods by mistake or when other prey was scarce. In waters where food is scarce, the snail *Capulus ungaricus* steals food from bivalves, snails, tube worms, and brachiopods.

Among brachiopods only the lingulids have been fished commercially, and only on a very small scale. Brachiopods seldom settle on artificial surfaces, probably because they

are vulnerable to pollution. This may make the population of *Coptothyru*s *adamsi* useful as a measure of environmental conditions around an oil terminal being built in Russia on the shore of the Sea of Japan.

Evolutionary history

Over 12,000 fossil species are recognized, grouped into over 5,000 genera. While the largest modern brachiopods are 100 millimetres (3.9 in) long, a few fossils measure up to 200 millimetres (7.9 in) wide. The earliest confirmed brachiopods have been found in the early Cambrian, inarticulate forms appearing first, followed soon after by articulate forms. Three unmineralized species have also been found in the Cambrian, and apparently represent two distinct groups that evolved from mineralized ancestors. The inarticulate *Lingula* is often called a "living fossil", as very similar genera have been all the way back to the Ordovician. On the other hand, articulate brachiopods have produced major diversifications, and severe mass extinctions – but the articulate Rhynchonellida and Terebratulida, the most diverse present-day groups, appeared at the start of the Ordovician and Carboniferous respectively.

Since 1991 Nielsen has proposed a hypothesis about the development of brachiopods, adapted in 2003 by Cohen and colleagues as a hypothesis about the earliest evolution of brachiopods. This "brachiopod fold" hypothesis suggests that brachiopods evolved from an ancestor similar to *Halkieria*, a slug-like animal with "chain mail" on its back and a shell at the front and rear end. The hypothesis proposes that the first brachiopod converted its shells into a pair of valves by folding the rear part of its body under its front.

However, fossils from 2007 onwards have supported a new interpretation of the Early-Cambrian tommotiids and a new hypothesis that brachiopods evolved from tommotiids. The "armor mail" of tommotiids was well-known but not in an assembled form, and it was generally assumed that tommotiids were slug-like animals similar to *Halkieria*, except that tommotiids' armor was made of organophosphatic compounds while that of *Halkieria* was made of calcite. However fossils of a new tommotiid, *Eccentrotheca*, showed an assembled mail coat that formed a tube, which would indicate a sessile animal rather than a creeping slug-like one. *Eccentrotheca*'s organophosphatic tube resembled that of phoronids, sessile animals that feed by lophophores and are regarded either very close relatives or a sub-group of brachiopods. *Paterimitra*, another mostly assembled fossil found in 2008 and described in 2009, had two symmetrical plates at the bottom, like brachiopod valves but not fully enclosing the animal's body.



A dense assemblage of the Ordovician species *Dalmanella meeki*

At their peak in the Paleozoic the brachiopods were among the most abundant filter-feeders and reef-builders, and occupied other ecological niches, including swimming in the jet-propulsion style of scallops. However, after the Permian–Triassic extinction event, informally known as the "Great Dying", brachiopods recovered only a third of their former diversity. It was often thought that brachiopods were actually decline in diversity, and that in some way bivalves out-competed them. However, in 1980 Gould and Calloway produced a statistical analysis that concluded that: both brachiopods and bivalves increased all the way from the Paleozoic to modern times, but bivalves increased faster; the Permian–Triassic extinction was moderately severe for bivalves but devastating for brachiopods, so that brachiopods for the first time were less diverse than bivalves and their diversity after the Permian increased from a very low base; there is no evidence that bivalves out-competed brachiopods, and short-term increases or decreases for both groups appeared at the same times. In 2007 Knoll and Bambach concluded that brachiopods were one of several groups that were most vulnerable to the Permian–Triassic extinction, as all had calcareous hard parts (made of calcium carbonate) and had low metabolic rates and weak respiratory systems.

Brachiopod fossils have been useful indicators of climate changes during the Paleozoic era. When global temperatures were low, as in much of the Ordovician, the large difference in temperatures between equator and poles created different collections of fossils at different latitudes. On the other hand, warmer periods, such much of the Silurian, created smaller difference in temperatures, and all seas at the low to middle latitudes were colonized by the same few brachiopod species.

Evolutionary family tree

Deuterostomes or protostomes

From about the 1940s to the 1990s, family trees based on embryological and morphological features placed brachiopods among or as a sister group to the deuterostomes. a super-phylum which includes chordates and echinoderms. Closer

examination has found difficulties in the grounds on which brachiopods were affiliated with deuterostomes:

- Radial cleavage in the earliest divisions of the egg appears to be the original condition for the ancestral bilaterians, in the earliest Ecdysozoa and possibly in the earliest Eutrochozoa, a major sub-group of the Lophotrochozoa. Hence radial cleavage does not imply that brachiopods are affiliated with deuterostomes.
- The traditional view is that the coelom(s) in deuterostomes and protostomes form by different process, called enterocoely and schizocoely respectively. However, research since the early 1990s has found significant exceptions. Both types of coelom construction appear among brachiopods, and therefore do not imply that brachiopods are deuterostomes.
- The terms "deuterostomes" and "protostomes" originally defined distinct ways of forming the mouth from the blastopore, a depression that appears in an early stage of the embryo. However, some "protostomes" forming the mouth using a process more like that typical of deuterostomes. Hence forming the mouth via a deuterostome-like process does not imply that brachiopods are affiliated with deuterostomes.

Nielsen views the brachiopods and closely-related phoronids as affiliated with the deuterostome pterobranchs because their lophophores are driven by one cilium per cell, while those of bryozoans, which he regards as protosomes, have multiple cilia per cell. However, pterobranchs are hemichordates and probably closely related to echinoderms, and there is no evidence that the latest common ancestor of pterobranchs and other hemichordates or the latest common ancestor of hemichordates and echinoderms was sessile and fed by means of tentacles.

From 1988 onwards analyses based on molecular phylogeny, which compares biochemical features such as similarities in DNA, have placed brachiopods among the Lophotrochozoa, a protostome super-phylum that includes molluscs, annelids and flatworms but excludes the other protostome super-phylum Ecdysozoa, whose members include arthropods. This conclusion is unanimous among molecular phylogeny studies, which use a wide selection of genes: rDNA, Hox genes, mitochondrial protein genes, single nuclear protein genes and sets of nuclear protein genes.

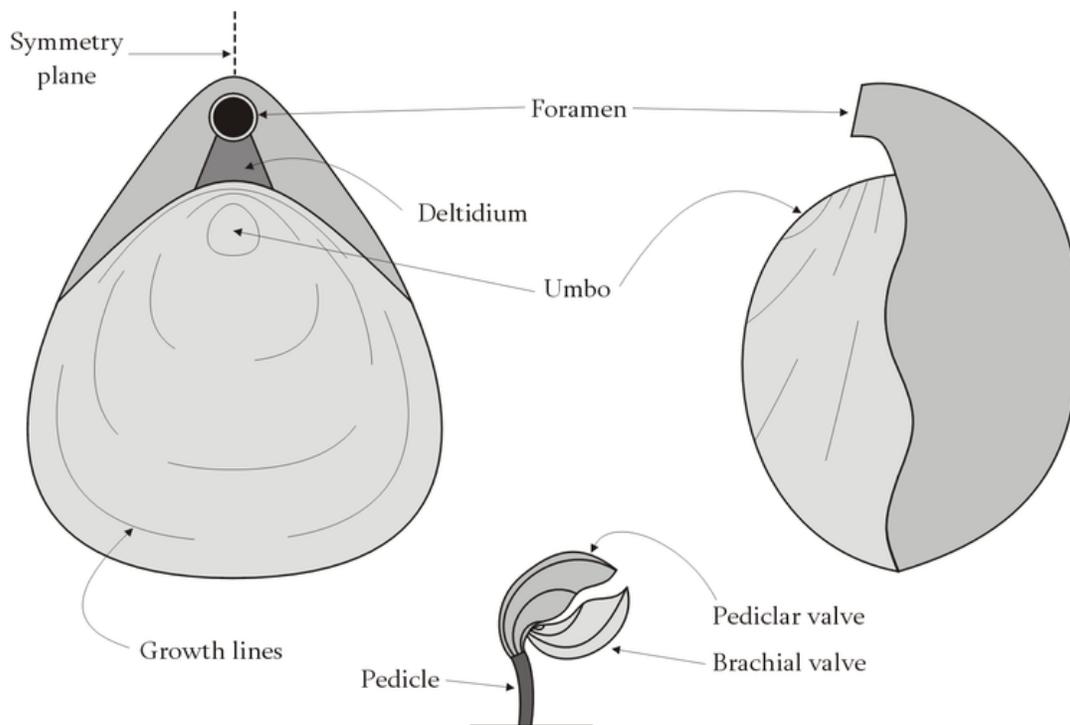
Some combined studies in 2000 and 2001, using both molecular and morphological data, support brachiopods as Lophotrochozoa, while others in 1998 and 2004 concluded that brachiopods were deuterostomes.

Relationship with other lophotrochozoans

The phoronids feed with a lophophore, burrow or encrust on surfaces, and build three-layered tubes made of polysaccharide, possibly chitin, mixed with particles with seabed material. Traditionally they have been regarded as a separate phylum, but increasingly detailed molecular phylogeny studies between 1997 and 2000 have concluded that

phoronids are a sub-group of brachiopods. However, an analysis in 2005 concluded that phoronids are a sub-group of bryozoans.

While all molecular phylogeny studies and half the combined studies until 2008 conclude that brachiopods are lophotrochozoans, they could not identify which lophotrochozoan phylum were the closest relatives of brachiopods - except phoronids, which are a sub-group of brachiopods. However in 2008 two analyses found that brachiopods' closest lophotrochozoan relatives were nemertines. The authors found this surprising, since nemertines have spiral cleavage in the early stages of cell division and form a trochophore larva, while brachiopods have radial cleavage and a larva that shows no sign of having evolved from a trochophore. Another study in 2008 also concluded that brachiopods are closely related to nemertines, casting doubt on the idea that brachiopods are part of a clade Lophophorata of lophophore-feeding animals within the lophotrochozoans.



Brachiopod morphology



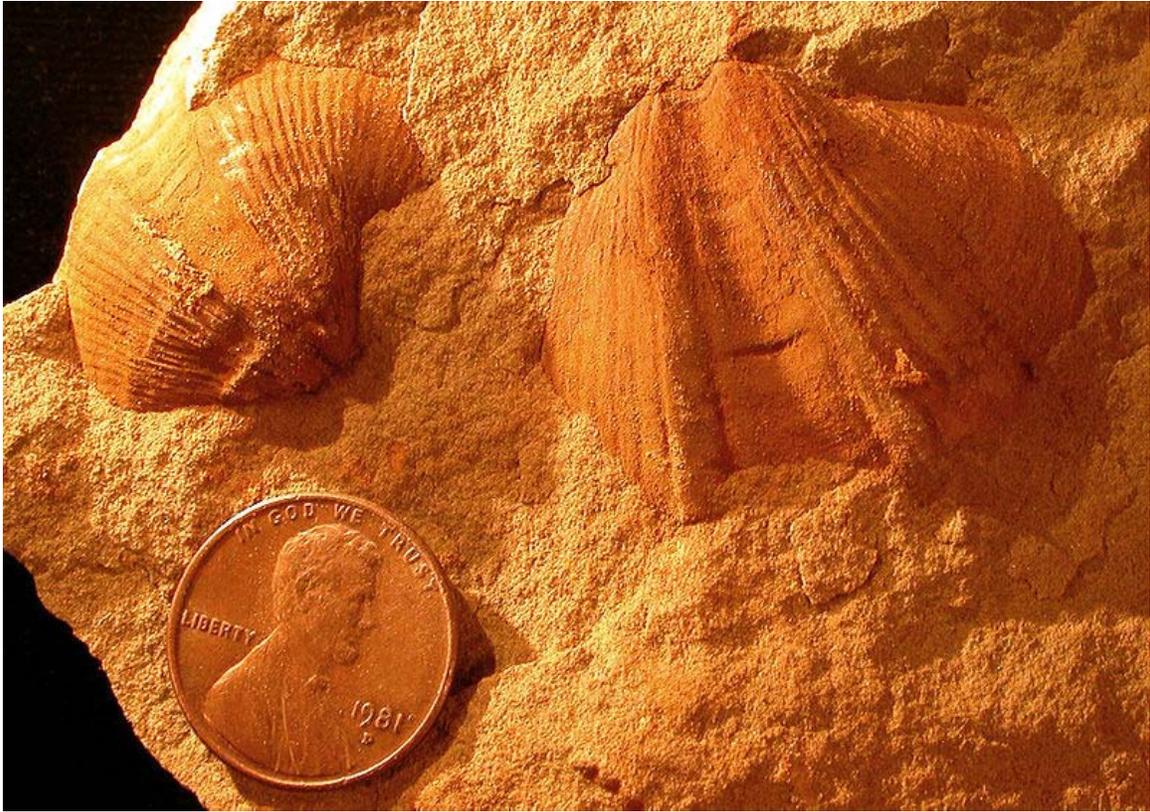
A Carboniferous brachiopod *Neospirifer condor*, from Bolivia. The specimen is 7 cm across.



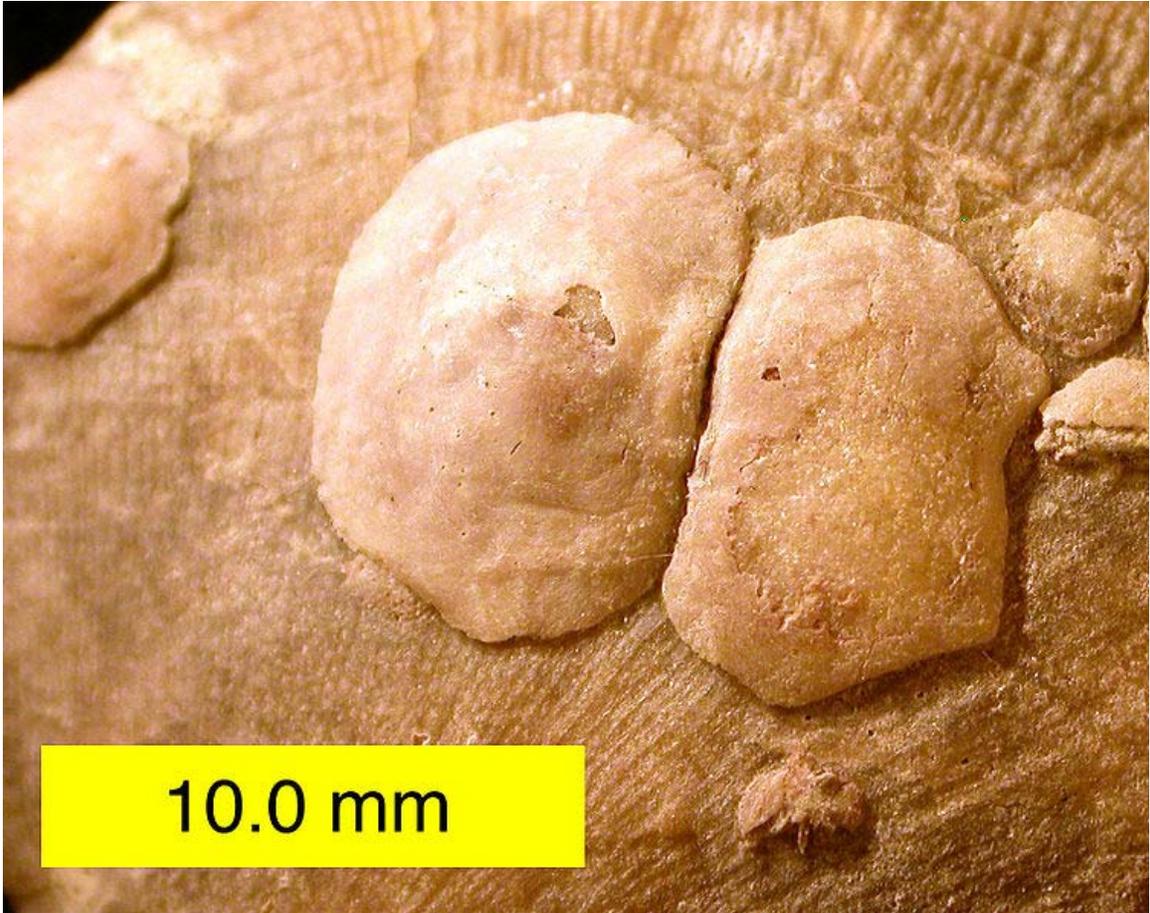
Rhynchotrema dentatum, a rhynchonellid brachiopod from the Cincinnatian (Upper Ordovician) of southeastern Indiana.



A Devonian spiriferid brachiopod from Ohio that served as a host substrate for a colony of hederellids. The specimen is 5 cm wide.



Syringothyris sp.; a spiriferid brachiopod from the Logan Formation (Lower Carboniferous) of Wooster, Ohio (internal molds).



Petrocrania brachiopods attached to a strophomenid brachiopod; Upper Ordovician of southeastern Indiana.



Lingula anatina from Stradbroke Island, Australia.



Brachiopod casts in the Lock Haven Formation

Chapter 5

Craniidae , Lingula (Genus) and Lingula Reevii

Craniidae



Petrocrania brachiopods attached to a strophomenid brachiopod; Upper Ordovician of southeastern Indiana.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Craniata
Order:	Craniida Waagen, 1885
Suborder:	Craniidina Waagen, 1885
Superfamily:	Cranioidea Menke, 1828
Family:	Craniidae

Menke, 1828

Genera

4 living and numerous fossil,
including:

†*Ancistrocrania*

†*Crania*

Craniscus

†*Danocrania*

†*Isocrania*

Neoancistrocrania

Novocrania

Valdiviathyris

Synonyms

Craniacea (superfamily)

Valdiviathyrididae (family)

The **Craniidae** are a family of brachiopods (lamp shells). They are the only members of the order **Craniida** and the monotypic suborder **Craniidina** and superfamily **Craniioidea**; consequently, the latter two taxa are presently redundant and not used very often. *Valdiviathyris* and *Neoancistrocrania* were sometimes separated in a family **Valdiviathyrididae** but this has turned out to be unjustified.

Most Craniidae are long-extinct forms known only from fossils like all other Craniforma. However, some 20 species of this 470-million-year-old lineage are extant today. They include *Valdiviathyris quenstedti* which has remained essentially unchanged for the last 35 million years or so. Although some minimal evolution would obviously have taken place in the meantime, this was essentially silent mutations and marginal adaptations to cooler habitat. Present-day *Valdiviathyris* are all but inseparable from those of the Late Eocene and the genus cannot even be divided into chronospecies. Thus, *V. quenstedti* is a true living fossil and one of the oldest and most long-lived species known to science.

Lingula (genus)

Lingula



Lingula anatina from Stradbroke Island, Australia.

Scientific classification

Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Lingulata
Order:	Lingulida
Family:	Lingulidae
Genus:	<i>Lingula</i> Bruguière, 1791

Type species

Lingula anatina
Lamarck, 1801

Lingula is a genus of brachiopods within the class Lingulata. *Lingula* is among the few brachiopods surviving today but also known from fossils over 500 million years old.

Species

The following species are recognised:

- *Lingula adamsi* Dall, 1873
- *Lingula anatina* Lamarck, 1801
- *Lingula dregeri* Andreae, 1893
- *Lingula eocenica* Moroz & Ermokhyna, 1990
- *Lingula parva* Smith, 1871
- *Lingula reevii* Davidson, 1880
- *Lingula rostrum* (Shaw, 1798)
- *Lingula tenuis* Sowerby
- *Lingula translucida* Dall, 1921
- *Lingula tumidula* Reeve, 1841
- *Lingula waikatoensis* Pen, 1930

Lingula reevii

Lingula reevii

Scientific classification

Kingdom: Animalia
Phylum: Brachiopoda
Class: Lingulata
Order: Lingulida
Family: Lingulidae
Genus: *Lingula*
Species: *L. reevii*

Binomial name

Lingula reevii
Davidson, 1880

Lingula reevii is a brachiopod species known as the **inarticulated brachiopod** and is in the family Lingulidae. Inarticulated brachiopods have bilaterally symmetrical shells held together only by muscles and not teeth. The species is rare and is only known to occur in shallow, sandy reef flats in Kaneohe Bay, Oahu, Hawaii.

Description

The shell is oblong oval, broadest in the middle, and rather narrow. The sides are very gently curved outwardly, the posterior edge tapers to a sharp point. The shell valves are moderately convex with a smooth surface. Color is blue-green or emerald and verdigris-green, especially along the middle. The lophophore consists of a fold of the body wall that possesses a crown of ciliated tentacles surrounding the mouth. The lateral cilia create a water current and fine plankton are transported down the tentacles to the brachial groove and into the mouth.

Ecology

They burrow vertically in sand, leaving a three-hole siphonal opening at the surface. When disturbed, a rapid contraction of the pedicle pulls the animal below the surface and the siphonal openings are reduced to a slit. This species is capable of upward burrowing through a sediment layer, even if the animal has to autotomize (detach) the pedicle.

Reproduction

Lingula has separate sexes, and gametes are shed into the water column for external fertilization. Embryos develop into a free swimming larva that looks like a tiny adult; they develop a shell while planktonic. As additional shell material is laid down, the

animal becomes heavy, sinks to the bottom, and takes up its adult existence. There is no metamorphosis in *Lingula*. The lifespan of *Lingula spp.* is estimated to be 5 to 8 years.

Threats and conservation

The species has declined in density from 500 per square meter in the 1960s to a maximum of 4 per square meter (Cindy Hunter, University of Hawaii, personal communication). The main threats are: 1) habitat degradation and alteration; 2) overexploitation; 3) marine pollution and sedimentation; 4) a vulnerable life history; and 5) a limited distribution.

The inarticulated brachiopod is a U.S. National Marine Fisheries Service Species of Concern. Species of Concern are those species about which the U.S. Government's National Oceanic and Atmospheric Administration, National Marine Fisheries Service, has some concerns regarding status and threats, but for which insufficient information is available to indicate a need to list the species under the U.S. Endangered Species Act.

Chapter 6

Lingulata , Mucrospirifer , Obolellida and Rhynchonellata

Lingulata

Lingulata



Lingula anatina from Stradbroke Island, Australia.

Scientific classification [e]

Kingdom: Animalia
Phylum: Brachiopoda
Subphylum: Linguliformea
Class: **Lingulata**

Orders

†Acrotretida
Lingulida
†Siphonotretida

Lingulata is a class of brachiopod, among the oldest of all brachiopods having existed since the Cambrian period (550 mya). They are also among the most morphologically conservative of the brachiopods, having lasted from their earliest appearance to the present with very little change in shape. Shells of living specimens found today in the waters around Japan are almost identical to ancient Cambrian fossils.

The Lingulata have tongue-shaped shells (hence the name Lingulata, from the Latin word for "tongue") with a long fleshy stalk, or pedicle, with which the animal burrows into sandy or muddy sediments. They inhabit vertical burrows in these soft sediments with the anterior end facing up and slightly exposed at the sediment surface. The cilia of the lophophore generate a feeding and respiratory current through the lophophore and mantle cavity. The gut is complete and J-shaped.

Lingulata shells are composed of a combination of calcium phosphate, protein and chitin. This is unlike most other shelled marine animals, whose shells are made of calcium carbonate. The Lingulata are inarticulate brachiopods, so named for the simplicity of their hinge mechanism. This mechanism lacks teeth and is held together only by a complex musculature. Both valves are roughly symmetrical.

The genus *Lingula* (Bruguiere, 1797) is the oldest known animal genus that still contains extant species. It is primarily an Indo-Pacific genus that is harvested for human consumption in Japan and Australia.

Mucrospirifer

Mucrospirifer

Temporal range: Devonian



Scientific classification

Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Rhynchonellata
Order:	Spiriferida
Family:	Mucrospiriferidae
Genus:	<i>Mucrospirifer</i> Grabau, 1931

Mucrospirifer is a genus of extinct brachiopod in the class Rhynchonellata (Articulata) and the order Spiriferida. They are sometimes known as "butterfly shells". Like other brachiopods, they were filter feeders. Fossils occur mainly in middle Devonian strata.

The biconvex shell was typically 2.5 cm, but they could grow to 4 cm long. It has a fold, sulcus and costae. It was greatly elongated along the hinge line, which extends outward to form sharp points. This gave them a fin- or wing-like appearance. The apex area (umbo) of the pedicle valve contains a small fold for the pedicle. They lived in muddy marine sediments, and were attached to the sea floor via the pedicle. They sometimes look like two seashells stuck together.

Select species

- *Mucrospirifer albanensis*
- *Mucrospirifer arkonensis*
- *Mucrospirifer bouchardi*
- *Mucrospirifer grabau*
- *Mucrospirifer medfordensis*
- *Mucrospirifer mucronatus*
- *Mucrospirifer paradoxiformis*
- *Mucrospirifer profundus*
- *Mucrospirifer prolificus*
- *Mucrospirifer refugiensis*
- *Mucrospirifer thedfordensis*
- *Mucrospirifer williamsi*

Obolellida

Obolellida

Scientific classification

Kingdom: Animalia
Phylum: Brachiopoda
Subphylum: Rhynchonelliformea
Class: Obolellata
Order: **Obolellida**
Rowell, 1965

Obolellida is a small, extinct order of inarticulate brachiopods that existed from the early to middle Cambrian period. The relationship of the Obolellida with other inarticulates is unclear, and were previously grouped together with the Siphonotretacea, before being given their own order.

Anatomy

The shell is typically impunctate, biconvex, and oval or subcircular in shape. They are like other inarticulates in that, as with the lingulids, the shell has no hinge, at least in the earliest examples. It is thought they may have used a hydraulic mechanism. However they later seem to develop a primitive articulation, in which some used a levator mechanism for opening the shell. At the posterior is a ventral valve with a defined flat-shelf. The pedicle opening can be positioned at various positions.

Rhynchonellata

Rhynchonellata

Temporal range: Lower Cambrian–Recent

Scientific classification [e]

Kingdom: Animalia
Phylum: Brachiopoda
Subphylum: Rhynchonelliformea
Class: **Rhynchonellata**

Orders

†Athyridida
†Orthida
†Pentamerida
†Protorthida
Rhynchonellida
†Spiriferida
†Spiriferinida
Terebratulida
Thecideida

The **Rhynchonellata** is a class of articulate brachiopods that combines certain orders from within the Rhynchonelliformea (Articulata revised). The class ranges from the Lower Cambrian to Recent.

Orders included in the Rhynchonellata are the Rhynchonellida, Orthida, Pentamerida, Atrypida, Athyridida, Spiriferida, Spiriferinida and Terebratulida. The Atrypida, Athyridida, and Spiriferinida were originally included in the Spiriferida as suborders. The Atrypida is the Atrypacea, the Athyridida, the Rostropiracea and the Spiriferinida the Punctospiracea of Moore, Lalicker, and Fischer.

The Orthida and Spiriferida have wide hinge lines. The Pentamerida, Terebratulida, Atrypida and Athyridida have narrow hinge lines. The Orthida, Pentamerida, Rhynchonellida, and Terebratulida have looped brachidia. The Spiriferida, Atrypida, Athyridida, and Spiriferinida have spiral brachidia. Some, like the Rhynchonellida and Spiriferida, may be strongly plicate, with a median fold and sulcus. Others, like the Spiriferinida and Terebratulida are basically smooth. All are primarily or exclusively impunctate but some e.g. Orthida and Rhynchonellida have punctate off shoots.

Chapter 7

Rhynchonellida and Rhynchonelliformea

Rhynchonellida

Rhynchonellida

Temporal range: Ordovician–Recent



Rhynchotrema dentatum, a rhynchonellid brachiopod from the Cincinnatian (Upper Ordovician) of SE Indiana.

Scientific classification [e]

Kingdom: Animalia
Phylum: Brachiopoda
Class: Rhynchonellata
Order: **Rhynchonellida**
Kuhn, 1949

Superfamilies

†Ancistrorhynchoidea
†Camarotoechioidea
Dimerelloidea
Hemithiridoidea
†Lambdarinoidea
Norelloidea
Pugnacoidea

†Rhynchoporoidea
†Rhynchotetradoidea
†Rhynchotrematoidea
†Stenoscismatoidea
†Uncinuloidea
†Wellerelloidea

The taxonomic order **Rhynchonellida** is one of the two main groups of living articulate brachiopods, the other being the order Terebratulida. They are recognized by their strongly ribbed wedge-shaped or nut-like shells, and the very short hinge line.

The hinges come to a point, a superficial resemblance to most (phylogenetically unrelated) bivalve mollusk shells. The loss of the hinge line was an important evolutionary innovation, **rhynchonellids** being the first truly non-strophic shells with a purely internal articulation (teeth-sockets).

Rhynchonellids lack any brachidium, and are therefore able to extrude their lophophore out from the shell into the water for more efficient food-gathering. It has been suggested this is why they survived the Devonian, Permian-Triassic, and Jurassic extinctions, while many other lampshells with a brachidium failed to do so.

Strong radiating ribs are common in this group; and there are generally very strong plications or accordion-like folds on the sulcus (the long middle section) of the shell. This probably helps regulate the flow of water in and out of the shell. All rhynchonellids are biconvex (have a bulbous shell), and have a fold located in the brachial valve. This means that the commissure, the line between the two valves or shells, is zigzagged, a distinguishing characteristic of this group. The prominent beak of the pedicle valve usually overlaps that of the brachial valve, in order to allow the shell to open and close. There is usually a functional pedicle although the delthyrium may be partially closed.

Morphologically, the rhynchonellid has changed little since its appearance during the Ordovician period. It seems to have evolved from pentamerids, and in turn gave rise to the first atrypids and athyrids, both of which are characterized by the development of a complex spiral brachidium. Although much diminished by the terminal Paleozoic extinction, it experienced a revival during the Early Jurassic period, and became the most abundant of all brachiopods during the Mesozoic Era.

Classification

This classification down to the level of genera is based on Kazlev and Emig.

Extant subgroups

- Superfamily Pugnacoidea
 - Family Basiliolidae
 - Subfamily Acanthobasiliolinae

- *Acanthobasiliola*
 - Subfamily Basiliolinae
 - *Basiliola*
 - *Basiliolella*
 - *Eohemithiris*
 - *Rhytirhynchia*
 - Subfamily Uncertain
 - *Striarina*
- Superfamily Dimerelloidea
 - Family Cryptoporidae
 -
 - *Aulites*
 - *Cryptopora*
- Superfamily Norelloidea
 - Family Frieleiidae
 - Subfamily Freileiinae
 - *Frieleia*
 - *Compsothyris*
 - *Grammetaria*
 - *Sphenarina*
 - Subfamily Hispanirhynchiinae
 - *Abyssorhynchia*
 - *Hispanirhynchia*
 - *Manithyris*
 - *Parasphenarina*
 - Subfamily Neorhynchiinae
 - *Neorhynchia*
 - Family Tethyrhynchiidae
 -
 - *Tethyrhynchia*
- Superfamily Hemithiridoidea
 - Family Hemithyrididae
 -
 - *Hemithyris*
 - *Pemphixina*
 - Family Notosariidae
 -
 - *Notosaria*

Extinct Subgroups

- Superfamily Ancistrorhynchoidea
- Superfamily Rhynchotrematoidea
- Superfamily Uncinuloidea
- Superfamily Camarotoechioidea
- Superfamily Rhynchotetradoidea

- Superfamily Lambdarinoidea
- Superfamily Wellerelloidea
- Superfamily Rhynchoporoidea
- Superfamily Stenoscismatoidea

Rhynchonelliformea

Rhynchonelliformea

Temporal range: Lower Cambrian - Recent.

Scientific classification [e]

Kingdom: Animalia

Phylum: Brachiopoda

Subphylum: **Rhynchonelliformea**
Williams 1996

Classes

†Chileata

†Chileata (?)

†Kutorginata

†Obolellata

Rhynchonellata

Strophomenata

Rhynchonelliformea is the name now given to the articulate brachiopods, Class Articulata, revised as a subphylum. Articulate brachiopods are those with hard, articulated, shells (hence the term) with a simple set of opening and closing muscles.

The name, Rhynchoelliformea, which replaces Articulata, which is also a class of crinoids, comes from the family Rhynchonellidae, which however is no more representative of articulate brachiopods than any other group such as spirifers or strophomenids. It just happens to be the name chosen, based on an included taxon.

The main difference between the Rhynchonelliformea described in the Treatise Part H, revised 2000/2007, and the Articulata of the Treatise part H, 1965, lies in the groups included, their taxonomic positions and arrangements. The Rhynchonelliformea (Articulata revised) is divided into five classes: **Obolellata**, **Kutorginata**, **Chileata**, **Strophomenata**, and **Rhynchonellata**. The Strophomenata and Rhynchonellata are found living today; the Rhynchonellata as the major constituent of modern brachiopod faunas, the Strophomenata as only a minor contributor. The Obolellata, Kutorginata,

and Chileata are all extinct. The Obolellata and Kutorginata are restricted to the Cambrian, the Chileata ranges throughout the extent of the Paleozoic.

In the older classification of the Treatise (1965) the Class Articulata was divided into six orders, the Orthida, Pentamerida, Rhynchonellida, Spiriferida, Terebratulida, and Strophomenida. The Orthida, Pentamerida, Rhynchonellida, Spiriferida, and Terebratulida became combined as the Rhynchonellata. The Strophomenida became the Strophomenata with the addition of the Orthotetida and Billingsellida and separation of the Chileata. The Obolellata and Kutorginata were previously included in the Inarticulata, but have since been recognized as primitive articulates.

One of the more significant changes in the new classification is the splitting of the original Spiriferida into distinct and separate orders, the Spiriferida as revised, Atrypida, Athyridida, and Spiriferinida; each with its own derivation and phylogeny. Originally these were included as suborders within the Spiriferida which combined brachiopods with spiral (coiled spring-like) brachidia regardless of the orientation or the length of the hinge line or whether the shell was impunctate or punctate. The newer classification recognises the spiral brachidia being a matter of evolutionary convergence. The Athyridida is the Rostropiracea and the Spiriferinida is the Punctospiracea (suborders) of R.C. Moore in Moore, Lalicker, and Fischer, 1952.

Chapter 8

Spiriferida and Terebratulida

Spiriferida

Spiriferida
Temporal range: Early Ordovician–
Early Jurassic



Paraspirifer bownockeri

Scientific classification [e]

Kingdom: Animalia
Phylum: Brachiopoda
Class: Rhynchonellata
Order: †**Spiriferida**
Waagen, 1883

Suborders

†Delthyridina
†Spiriferidina



Mucrospirifer sp.

Spiriferida is an order of extinct articulate brachiopod fossils which are known for their long hinge-line, which is often the widest part of the shell. In some genera (e.g. *Mucrospirifer*) it is greatly elongated, giving them a wing-like appearance. They often have a deep fold down the center of the shell. The feature that gives the spiriferids their name ("spiral-bearers") is the internal support for the lophophore; this *brachidium*, which is often preserved in fossils, is a thin ribbon of calcite that is typically coiled tightly within the shell.

Spiriferids first appear in the Early Ordovician. They were rare during the Silurian but underwent a dramatic evolutionary radiation during the Devonian period, reaching peak development in variety and numbers. Spiriferida survived the great Permian extinction, finally becoming extinct during the Early Jurassic.

Fossils of this order are often preserved as pyrite.

Taxonomy

Order **Spiriferida**

- Suborder Delthyridina
 - Superfamily Delthyridoidea
 - Family Acrospiriferidae

- Family Cyrtinopsidae
- Family Delthyrididae
- Family Hysterolitidae
- Family Mucrospiriferidae
- Superfamily Reticularioidea
 - Family Elythidae
 - Family Reticulariidae
 - Family Thomasariidae
 - Family Xenomartiniidae
- Suborder Spiriferidina
 - Superfamily Adolfoidea
 - Family Adolphiidae
 - Family Echinospiriferidae
 - Superfamily Ambocoelioidea
 - Family Ambocoeliidae
 - Family Eudoxinidae
 - Family Lazutkiniidae
 - Family Verneuiliidae



A Devonian spiriferid brachiopod from Ohio which served as a host substrate for a colony of hederellids. The specimen is 5 cm wide.

- - Superfamily Brachythyridoidea
 - Family Brachythyrididae
 - Family Skelidorygmidae
 - Superfamily Cyrtioidea (syn. Cyrtiacea)
 - Family Costispiriferidae
 - Family Cyrtiidae
 - Family Hedeinopsidae
 - Superfamily Cyrtospiriferoidea
 - Family Conispiriferidae
 - Family Cyrtospiriferidae
 - Family Spinocyrtiidae
 - Superfamily Martinioidea
 - Family Crassumbidae
 - Family Elythyridae
 - Family Gerkispiridae
 - Family Ingelarellidae
 - Family Martiniidae
 - Family Perissothyrididae
 - Family Tenellodermidae
 - Superfamily Paeckelmanelloidea
 - Family Paeckelmanellidae
 - Family Strophopleuridae
 - Superfamily Spiriferoidea
 - Family Choristitidae
 - Family Imbrexiidae
 - Family Reticulariaceae
 - Family Spiriferellidae
 - Family Spiriferidae
 - Family Trigonotretidae
 - Superfamily Theodossioidea
 - Family Palaeochoristitidae
 - Family Theodossiidae
 - Family Ulbospiriferidae

Terebratulida

Terebratulida



Terebratella sanguinea

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Rhynchonellata
Order:	Terebratulida Waagen, 1883

Terebratulids are one of only three living orders of articulate brachiopods, the others being the Rhynchonellida and the Thecideida. Craniida and Lingulida include living brachiopods, but are inarticulates. The name, Terebratula, may be derived from the Latin "terebra", meaning "hole-borer". The perceived resemblance of terebratulid shells to ancient Roman oil lamps gave the brachiopods their common name "lamp shell".

Terebratulids typically have biconvex shells that are usually ovoid to circular in outline. They can be either smooth or have radial ribbing. The lophophore support is loop shaped in contrast to the spiralia of similar looking spiriferids. Terebratulids are also distinguished by a very short hinge line, and the shell is punctate in microstructure. There is a circular pedicle opening, or foramen, located in the beak.

Terebratulids may have evolved from Atrypids during the early or Middle Silurian. Early genera were almost circular to elongate-oval, with smooth or finely costate shells. During the Cretaceous and Tertiary periods, many shells became coarsely plicate.

Classification

- Suborder Terebratellidina
 - Superfamily Kraussinoidea
 - Superfamily Laqueoidea
 - Superfamily Megathyridoidea
 - Superfamily Platidioidea
 - Superfamily Terebratelloidea
 - Family Dallinidae
 - Family Ecnomiosidae
 - Family Terebratellidae
 - Family Thaumatosiidae
 - Superfamily Zeilleroidea
 - Superfamily Bouchardioidea
 - Superfamily Gwynioidea
 - Superfamily Kingenoidea
 - Superfamily Incertae sedis
 - Family Tythothyrididae
- Suborder Terebratulidina
 - Superfamily Cancellothyroidea
 - Family Cancellothyrididae
 - Family Chlidonophoridae
 - Family Cnismatocentridae
 - Superfamily Dyscoloidea
 - Superfamily Terebratuloidea
 - Family Gryphidae
 - Family Tichosidae
 - Family Terebratulidae

Extinct Superfamilies

- - Superfamily Dielasmatoidea †
 - Superfamily Cryptonelloidea †
 - Superfamily Loboidothyridoidea †
 - Superfamily Stryngocephaloidea †