Encyclopedia of Onychophora, Brachiopoda, Acoelomorpha, Porifera and Ctenophora (Animal Phylum)

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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 *onyches*, "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 circumaustral 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 glactosamine. 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 reflects 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-