= Nemertea =

Nemertea is a phylum of invertebrate animals also known as " ribbon worms " or " proboscis worms " . Alternative names for the phylum have included Nemertini , Nemertinea and Rhynchocoela . Although most are less than 20 centimetres (7 @.@ 9 in) long , one specimen has been estimated at 54 metres (177 ft) . Most are very slim , usually only a few millimeters wide , although a few have relatively short but wide bodies . Many have patterns of yellow , orange , red and green coloration .

The foregut , stomach and intestine run a little below the midline of the body , the anus is at the tip of the tail , and the mouth is under the front . A little above the gut is the rhynchocoel , a cavity which mostly runs above the midline and ends a little short of the rear of the body . All species have a proboscis which lies in the rhynchocoel when inactive but everts (turns inside @-@ out) to emerge just above the mouth and capture the animal 's prey with venom . A very stretchy muscle in the back of the rhynchocoel pulls the proboscis in when an attack ends . A few species with stubby bodies filter feed and have suckers at the front and back ends , with which they attach to a host .

The brain is a ring of four ganglia , positioned around the rhynchocoel near its front end . At least a pair of ventral nerve cords connect to the brain and run along the length of the body . Most nemerteans have various chemoreceptors , and on their heads some species have a number of pigment @-@ cup ocelli . These ocelli can detect light but can not form an image . Nemerteans respire through the skin . They have at least two lateral vessels which are joined at the ends to form a loop , and these and the rhynchocoel are filled with fluid . There is no heart , and the flow of fluid depends on contraction of muscles in the vessels and the body wall . To filter out soluble waste products , flame cells are embedded in the front part of the two lateral fluid vessels , and remove the wastes through a network of pipes to the outside .

All nemerteans move slowly , using their external cilia to glide on surfaces on a trail of slime , while larger species use muscular waves to crawl , and some swim by dorso @-@ ventral undulations . A few live in the open ocean while the rest find or make hiding places on the bottom . About a dozen species inhabit freshwater , mainly in the tropics and subtropics , and another dozen species live on land in cool , damp places . Most nemerteans are carnivores , feeding on annelids , clams and crustaceans . A few species are scavengers , and a few species live commensally inside the mantle cavity of molluscs . Some species have devastated commercial fishing of clams and crabs . Nemerteans have few predators . Two species are sold as fish bait .

In most species the sexes are separate , but all the freshwater species are hermaphroditic . Nemerteans often have numerous temporary gonads (ovaries or testes) , and build temporary gonoducts (ducts from which the ova or sperm are emitted) , one per gonad , when the ova and sperm are ready . The eggs are generally fertilised externally . Some species shed them into the water , and others protect their eggs in various ways . The fertilized egg divides by spiral cleavage and grows by determinate development , in which the fate of a cell can usually be predicted from its predecessors in the process of division . The embryos of most taxa develop either directly to form juveniles (like the adult but smaller) or to form planuliform larvae , in which the larva 's long axis is the same as the juvenile 's . However , some form a pilidium larva , in which the developing juvenile has a gut which lies across the larva 's body , and usually eats the remains of the larva when it emerges . The bodies of some species fragment readily , and even parts near the tail can grow full bodies .

It has been suggested that three fossil species may be nemerteans , but none is confirmed . Traditional taxonomy divides the phylum in two classes , Anopla (" unarmed " ? their proboscises do not have a little dagger) with two orders , and Enopla (" armed " with a dagger) with two orders . However , it is now accepted that Anopla are paraphyletic (have given rise to another group) , as one order is more closely related to Enopla than to the other order of Anopla . The phylum Nemertea is monophyletic , whose synapomorphies include the rhynchocoel and eversible proboscis . Traditional taxonomy says that nemerteans are closely related to flatworms and that both are relatively " primitive " acoelomates . Now both phyla are regarded as members of the Lophotrochozoa , a very large " super @-@ phylum " that also includes molluscs , annelids , brachiopods , bryozoa and many other protostomes .

= = History = =

In 1555 Olaus Magnus wrote of a marine worm which was apparently 17 @.@ 76 metres (58 @.@ 3 ft) long (" 40 cubits ") , about the width of a child 's arm , and whose touch made a hand swell . William Borlase wrote in 1758 of a " sea long worm " , and in 1770 Gunnerus wrote a formal description of this animal , which he called Ascaris longissima . Its current name , Lineus longissimus , was first used in 1806 by Sowerby . In 1995 , a total of 1 @,@ 149 species had been described and grouped into 250 genera .

Nemertea are named after the Greek sea @-@ nymph Nemertes , one of the daughters of Nereus and Doris . Alternative names for the phylum have included Nemertini , Nemertinea , and Rhynchocoela . The Nemertodermatida are a separate phylum , whose closest relatives appear to be the Acoela .

= = Description = =

= = = Body structure and major cavities = = =

Nemerteans are very unusual animals .

The typical nemertean body is very slim in proportion to its length . The smallest are a few millimeters long , most are less than 20 centimetres (7 @.@ 9 in) , and several exceed 1 metre (3 @.@ 3 ft) . The longest animal ever found , at 54 metres (177 ft) long , may be a specimen of Lineus longissimus , although L. longissimus is usually only a few millimeters wide . The bodies of most nemerteans can stretch a lot , up to 10 times their resting length in some species , but reduce their length to 50 % and increase their width to 300 % when disturbed . A few have relatively short but wide bodies , for example Malacobdella grossa is up to 3 @.@ 5 centimetres (1 @.@ 4 in) long and 1 centimetre (0 @.@ 39 in) wide , and some of these are much less stretchy . Smaller nemerteans are approximately cylindrical , but larger species are flattened dorso @-@ ventrally . Many have visible patterns in various combinations of yellow , orange , red and green .

The outermost layer of the body has no cuticle but consists of a ciliated and glandular epithelium containing rhabdites , which form the mucus in which the cilia glide . Each ciliated cell has many cilia and microvilli . The outermost layer rests on a thickened basement membrane , the dermis . Next to the dermis are at least three layers of muscles , some circular and some longitudinal . The combinations of muscle types vary between the different classes , but these are not associated with differences in movement . Nemerteans also have dorso @-@ ventral muscles , which flatten the animals , especially in the larger species . Inside the concentric tubes of these layers is mesenchyme , a kind of connective tissue . In pelagic species this tissue is gelatinous and buoyant .

The mouth is ventral and a little behind the front of the body . The foregut , stomach and intestine run a little below the midline of the body and the anus is at the tip of the tail . Above the gut and separated from the gut by mesenchyme is the rhynchocoel , a cavity which mostly runs above the midline and ends a little short of the rear of the body . The rhynchocoel of class Anopla has an orifice a little to the front of the mouth , but still under the front of the body . In the other class , Enopla , the mouth and the front of the rhynchocoel share an orifice . The rhynchocoel is a coelom , as it is lined by epithelium .

= = = Proboscis and feeding = = =

The proboscis is an infolding of the body wall , and sits in the rhynchocoel when inactive . When muscles in the wall of the rhynchocoel compress the fluid in the rhynchocoel , the pressure makes the proboscis jump inside @-@ out to attack the animal 's prey along a canal called the rhynchodeum and through an orifice , the proboscis pore . The proboscis has a muscle which

attaches to the back of the rhynchocoel , and which can stretch up to 30 times its inactive length and then retract the proboscis .

The proboscis of the class Anopla (" unarmed ") exits from an orifice which is separate from the mouth , coils around the prey and immobilizes it by sticky , toxic secretions . The Anopla can attack as soon as they move into the range of the proboscis . Some Anopla have branched proboscises which can be described as " a mass of sticky spaghetti " . The animal then draws its prey into its mouth .

In most of the class Enopla (" armed ") , the proboscis exits from a common orifice of the rhynchocoel and mouth . A typical member of this class has a stylet , a calcareous barb , with which the animal stabs the prey many times to inject toxins and digestive secretions . The prey is then swallowed whole or , after partial digestion , its tissues are sucked into the mouth . The stylet is attached about one @-@ third of distance from the end of the everted proboscis , which extends only enough to expose the stylet . On either side of the active stylet are sacs containing back @-@ up stylets to replace the active one as the animal grows or an active one is lost . Instead of one stylet , the Polystilifera have a pad that bears many tiny stylets , and these animals have separate orifices for the proboscis and mouth , unlike other Enopla . The Enopla can only attack after contacting the prey .

Some nemerteans , such as L. longissimus , absorb organic food in solution through their skins , which may make the long , slim bodies an advantage . Suspension feeding is found only among the specialized symbiotic bdellonemerteans , which have a proboscis but no stylet , and use suckers to attach themselves to bivalves .

= = = Respiration and circulatory system = = =

Nemerteans lack specialized gills , and respiration occurs over the surface of the body , which is long and sometimes flattened . Like other animals with thick body walls , they use fluid circulation rather than diffusion to move substances through their bodies . The circulatory system consists of the rhynchocoel and peripheral vessels , while blood of other invertebrates is contained in the main body cavity . The fluid in the rhynchocoel moves substances to and from the proboscis , and functions as a fluid skeleton in everting the proboscis and in burrowing . The vessels circulate fluid round the whole body and the rhynchocoel provides its own local circulation . The circulatory vessels are a system of coeloms .

In the simplest type of circulatory system , two lateral vessels are joined at the ends to form a loop . However , many species have additional long @-@ wise and cross @-@ wise vessels . There is no heart nor pumping vessels , and the flow of fluid depends on contraction of both the vessels and the body wall 's muscles . In some species , circulation is intermittent , and fluid ebbs and flows in the long @-@ wise vessels . The fluid in the vessels is usually colorless , but in some species it contains cells that are yellow , orange , green or red . The red type contain hemoglobin and carry oxygen , but the function of the other pigments is unknown .

= = = Excretion = = =

Nemertea use organs called protonephridia to excrete soluble waste products , especially nitrogenous by @-@ products of cellular metabolism . In nemertean protonephridia , flame cells which filter out the wastes are embedded in the front part of the two lateral fluid vessels . The flame cells remove the wastes into two collecting ducts , one on either side , and each duct has one or more nephridiopores through which the wastes exit . Semiterrestrial and freshwater nemerteans have many more flame cells than marines , sometimes thousands . The reason may be that osmoregulation is more difficult in non @-@ marine environments .

= = = Nervous system and senses = = =

The central nervous system consists of a brain and paired ventral nerve cords that connect to the

brain and run along the length of the body . The brain is a ring of four ganglia , masses of nerve cells , positioned round the rhynchocoel near its front end ? while the brains of most protostome invertebrates encircle the foregut . Most nemertean species have just one pair of nerve cords , many species have additional paired cords , and some species also have a dorsal cord . In some species the cords lie within the skin , but in most they are deeper , inside the muscle layers . The central nervous system is often red or pink because it contains hemoglobin . This stores oxygen for peak activity or when the animal experiences anoxia , for example while burrowing in oxygen @-@ free sediments .

Some species have paired cerebral organs , sacs whose only openings are to the outside . Others species have unpaired evertible organs on the front of their heads . Some have slits along the side of the head or grooves obliquely across the head , and these may be associated with paired cerebral organs . All of these are thought to be chemoreceptors , and the cerebral organs may also aiding osmoregulation . Small pits in the epidermis appear to be sensors . On their head some species have a number of pigment @-@ cup ocelli , which can detect light but not form an image . Most nemerteans have two to six ocelli , although some have hundreds . A few tiny species that live between grains of sand have statocysts , which sense balance .

Paranemertes peregrina , which feeds on polychaetes , can follow the prey 's trails of mucus , and find its burrow by backtracking along its own trail of mucus .

= = = Movement = = =

All nemerteans move slowly . Most nemerteans use their external cilia to glide on surfaces on a trail of slime , some of which is produced by glands in the head . Larger species use muscular waves to crawl , and some aquatic species swim by dorso @-@ ventral undulations . Some species burrow by means of muscular peristalsis , and have powerful muscles . Some species of the suborder Monostilifera , whose proboscis have one active stylet , move by extending the proboscis , sticking it to an object and pulling the animal towards the object .

= = = Reproduction and life cycle = = =

Larger species often break up when stimulated , and the fragments often grow into full individuals . Some species fragment routinely and even parts near the tail can grow full bodies . All reproduce sexually , and most species are gonochoric (the sexes are separate) , but all the freshwater forms are hermaphroditic .

Nemerteans often have numerous temporary gonads (ovaries or testes) , forming a row down each side of the body in the mesenchyme . Temporary gonoducts (ducts from which the ova or sperm are emitted) , one per gonad , are built when the ova and sperm are ready . The eggs are generally fertilised externally . Some species shed them into the water , some lay them in a burrow or tube , and some protect them by cocoons or gelatinous strings . Some bathypelagic (deep sea) species have internal fertilization , and some of these are viviparous , growing their embryos in the female 's body .

The zygote (fertilised egg) divides by spiral cleavage and grows by determinate development , in which the fate of a cell can usually be predicted from its predecessors in the process of division . The embryos of most taxa develop either directly to form juveniles (like the adult but smaller) or to form planuliform larvae , in which the larva 's long axis is the same as the juvenile 's . The planuliform larva stage may be short @-@ lived and lecithotrophic (" yolky ") before becoming a juvenile , or may be planktotrophic , swimming for some time and eating prey larger than microscopic particles . However , many members of the order Heteronemertea and the palaeonemertean family Hubrechtidae form a pilidium larva , which can capture unicellular algae and which Maslakova describes as like a deerstalker cap with the ear flaps pulled down . It has a gut which lies across the body , a mouth between the " ear flaps " , but no anus . A small number of imaginal discs form , encircling the archenteron (developing gut) and coalesce to form the juvenile . When it is fully formed , the juvenile bursts out of the larva body and usually eats it during this

catastrophic metamorphosis .

The species Paranemertes peregrina has been reported as having a life span of around 18 months .

= = Ecological significance = =

Most nemerteans are marine animals that burrow in sediments , lurk in crevices between shells , stones or the holdfasts of algae or sessile animals . Some live deep in the open oceans , and have gelatinous bodies . Others build semi @-@ permanent burrows lined with mucus or produce cellophane @-@ like tubes . Mainly in the tropics and subtropics , about 12 species appear in freshwater , and about a dozen species live on land in cool , damp places , for example under rotting logs .

The terrestrial Argonemertes dendyi is a native of Australia but has been found in the British Isles , in Sao Miguel in the Azores , in Gran Canaria , and in a lava tube cave at Kaumana on the Island of Hawaii . It can build a cocoon , which allows it to avoid desiccation while being transported , and it may be able to build populations quickly in new areas as it is a protandrous hermaphrodite . Another terrestrial genus , Geonemertes , is mostly found in Australasia but has species in the Seychelles , widely across the Indo @-@ Pacific , in Tristan da Cunha in the South Atlantic , in Frankfurt , in the Canary Islands , in Madeira and in the Azores .

Most are carnivores , feeding on annelids , clams and crustaceans , and may kill annelids of about their own size . They sometimes take fish , both living and dead . Insects and myriapods are the only known prey of the two terrestrial species of Argonemertes . A few nemerteans are scavengers , and these generally have good distance chemoreception (" smell ") and are not selective about their prey . A few species live commensally inside the mantle cavity of molluscs and feed on micro @-@ organisms filtered out by the host .

Near San Francisco the nemertean Carcinonemertes errans has consumed about 55 % of the total egg production of its host , the Dungeness crab Metacarcinus magister . C. errans is considered a significant factor in the collapse of the dungeness crab fishery . Other coastal nemerteans have devastated clam beds .

The few predators on nemerteans include bottom @-@ feeding fish , some sea birds , a few invertebrates including horseshoe crabs , and other nemerteans . Nemerteans ' skins secrete toxins that deter many predators , but some crabs may clean nemerteans with one claw before eating them . The American Cerbratulus lacteus and the South African Polybrachiorhynchus dayi , both called " tapeworms " in their respective localities , are sold as fish bait .

= = Taxonomy = =

Class Anopla (" unarmed ") . Includes animals with proboscis without stylet , and a mouth underneath and behind the brain.Order Paleonemertea . Comprises 100 marine species . Their body wall has outer circular and inner length @-@ wise muscles . In addition , Carinoma tremaphoros has circular and inner length @-@ wise muscles in the epidermis ; the extra muscle layers seem to be needed for burrowing by peristalsis .

Order Heteronemertea . Comprises about 400 species . The majority are marine , but three are freshwater . Their body @-@ wall muscles are disposed in four layers , alternately circular and length @-@ wise starting from the outermost layer . The order includes the strongest swimmers . Two genera have branched proboscises .

Class Enopla (" armed ") . All have stylets except order Bdellonemertea . Their mouth is located underneath and ahead of the brain . Their main nerve cords run inside body @-@ wall muscles.Order Bdellonemertea . Includes seven species , of which six live as commensals in the mantle of large clams and one in that of a freshwater snail . The hosts filter feed and all the hosts steal food from them . These nemerteans have short , wide bodies and have no stylets but have a sucking pharynx and a posterior stucker , with which they move like inchworms .

Order Hoplonemertea . Comprises 650 species . They live in benthic and pelagic sea water , in

freshwater and on land . They feed by commensalism and parasitism , and are armed with stylet (s) Suborder Monostilifera . Includes 500 species with a single central stylet . Some use the stylet for locomotion as well as for capturing prey .
Suborder Polystilifera . Includes about 100 pelagic and 50 benthic species . Their pads bear many tiny stylets .

= = Evolutionary history = =

= = = Fossil record = = =

Although one might expect stylets to be fossilized since they are made of the mineral calcium phosphate , none have been found . As nemertea are otherwise completely soft @-@ bodied , one would expect fossils of them to be extremely rare .
The Middle Cambrian fossil Amiskwia from the Burgess Shale has been classed as a nemertean , based on a resemblance to some unusual deep @-@ sea swimming nemerteans , but few paleontologists accept this classification as the Burgess Shale fossils show no evidence of rhynchocoel nor intestinal caeca .
It has been suggested that Archisymplectes , one of the Pennsylvanian @-@ age animals from Mazon Creek in northern and central Illinois , may be a nemertean . This fossil , however , only preserves the outline of the " worm " , and there is no evidence of a proboscis , so there is no certainty that it represents a nemertean .

= = = = Within Nemertea = = = =

There is no doubt that the phylum Nemertea is monophyletic (meaning that the phylum includes all and only descendants of one ancestor that was also a member of the phylum) . The synapomorphies (trait shared by an ancestor and all its descendants , but not by other groups) include the eversible proboscis located in the rhynchocoel .
While Ruppert , Fox and Barnes (2004) treat the Palaeonemertea as monophyletic , Thollesson and Norenburg (2003) regard them as paraphyletic and basal (contains the ancestors of the more recent clades) . The Anopla (" unarmed ") represent an evolutionary grade of nemerteans without stylets (comprising the Heteronemertea and the Palaeonemerteans) , while Enopla (" armed ") are monophyletic , but find that Palaeonemertea is doubly paraphyletic , haven given rise to both the Heteronemertea and the Enopla . Ruppert , Fox and Barnes (2004) treat the Bdellonemertea as a clade separate from the Hoplonemertea , while Thollesson and Norenburg (2003) believe the Bdellonemertea are a part of the Monostilifera (with one active stylet) , which are within the Hoplonemertea ? which implies that " Enopla " and " Hoplonemertea " are synonyms for the same branch of the tree . The Polystilifera (with many tiny stylets) are monophyletic .

= = = = Relationships with other phyla = = = =

English @-@ language writings have conventionally treated nemertean as " primitive " acoelomate bilaterians that are most closely related to flatworms (Platyhelminthes) . These pre @-@ cladistics analyses emphasised as shared features : multiciliated (with multiple cilia per cell) , glandular epidermis ; rod @-@ shaped secretory bodies or rhabdites ; frontal glands or organs ; protonephridia ; and acoelomate body organization . However , multiciliated epidermal cells and epidermal gland cells are also found in Ctenophora , Echiura , Sipuncula , Annelida , Mollusca and other taxa . The rhabdites of nemertea have a different structure from those of flatworms at the microscopic scale . The frontal glands or organs of flatworms vary a lot in structure , and similar structures appear in small marine annelids and entoproct larvae . The protonephridia of nemertea and flatworms are different in structure , and in position ? the flame cells of nemertea are usually in the walls of the fluid vessels and are served by " drains " from which the wastes exit by a small

number of tubes through the skin , while the flame cells of flatworms are scattered throughout the body . Rigorous comparisons show no synapomorphies of nemertean and platyhelminth nephridia .

According to more recent analyses , in the development of nemertean embryos , ectomesoderm (outer part of the mesoderm , which is the layer in which most of the internal organs are built) is derived from cells labelled 3a and 3b , and endomesoderm (inner part of the mesoderm) is derived from the 4d cell . Some of the ectomesoderm in annelids , echiurans and molluscs is derived from cells 3a and 3b , while the ectomesoderm of polyclad flatworms is derived from the 2b cell and acoel flatworms produce no ectomesoderm . In nemerteans the space between the epidermis and the gut is mainly primarily by well @-@ developed muscles embedded in noncellular connective tissue . This structure is similar to that found in larger flatworms such as polyclads and triclads , but a similar structure of body @-@ wall muscles embedded in noncellular connective tissue is widespread among the Spiralia (animals in which the early cell divisions make a spiral pattern) such as sipunculans , echiurans and many annelids .

Nemerteans ' affinities with Annelida (including Echiura , Pogonophora , Vestimentifera and perhaps Sipuncula) and Mollusca make the ribbon @-@ worms members of Lophotrochozoa , which include about half of the extant animal phyla . Lophotrochozoa groups : those animals that feed using a lophophore (Brachiopoda , Bryozoa , Phoronida , Entoprocta) ; phyla in which most members ' embryos develop into trochophore larvae (for example Annelida and Mollusca) ; and some other phyla (such as Platyhelminthes , Sipuncula , Gastrotricha , Gnathostomulida , Micrognathozoa , Nemertea , Phoronida , Platyhelminthes and Rotifera) . These groupings are based on molecular phylogeny , which compares sections of organisms DNA and RNA . While analyses by molecular phylogeny are confident that members of Lophotrochozoa are more closely related to each other than of non @-@ members , the relationships between members are mostly unclear .

Most protostome phyla outside the Lophotrochozoa are members of Ecdysozoa (" animals that molt ") , which include Arthropoda , Nematoda and Priapulida . Most other bilaterian phyla are in the Deuterostomia , which include Echinodermata and Chordata . The Acoelomorpha , which are neither protostomes nor deuterostomes , are regarded as basal bilaterians .