= Ctenophora =

Ctenophora (/ t??n?f?r? / ; singular ctenophore , / ?t?n?f??r / or / ?ti?n?f??r / ; from the Greek ????? kteis ' comb ' and ???? pher? ' carry ' ; commonly known as comb jellies) is a phylum of invertebrate animals that live in marine waters worldwide . Their most distinctive feature is the ? combs ? ? groups of cilia which they use for swimming ? they are the largest animals that swim by means of cilia . Adults of various species range from a few millimeters to 1 @.@ 5 m (4 ft 11 in) in size . Like cnidarians , their bodies consist of a mass of jelly , with one layer of cells on the outside and another lining the internal cavity . In ctenophores , these layers are two cells deep , while those in cnidarians are only one cell deep . Some authors combined ctenophores and cnidarians in one phylum , Coelenterata , as both groups rely on water flow through the body cavity for both digestion and respiration . Increasing awareness of the differences persuaded more recent authors to classify them as separate phyla .

Ctenophores also resemble cnidarians in having a decentralized nerve net rather than a brain . Genomic studies have suggested that the neurons of Ctenophora , which differ in many ways from other animal neurons , evolved independently from those of the other animals .

Almost all ctenophores are predators , taking prey ranging from microscopic larvae and rotifers to the adults of small crustaceans ; the exceptions are juveniles of two species , which live as parasites on the salps on which adults of their species feed . In favorable circumstances , ctenophores can eat ten times their own weight in a day . Only 100 ? 150 species have been validated , and possibly another 25 have not been fully described and named . The textbook examples are cydippids with egg @-@ shaped bodies and a pair of retractable tentacles fringed with tentilla (" little tentacles ") that are covered with colloblasts , sticky cells that capture prey . The phylum has a wide range of body forms , including the flattened , deep @-@ sea platyctenids , in which the adults of most species lack combs , and the coastal beroids , which lack tentacles and prey on other ctenophores by using huge mouths armed with groups of large , stiffened cilia that act as teeth . These variations enable different species to build huge populations in the same area , because they specialize in different types of prey , which they capture by as wide a range of methods as spiders use .

Most species are hermaphrodites ? a single animal can produce both eggs and sperm , meaning it can fertilize its own egg , not needing a mate . Some are simultaneous hermaphrodites , which can produce both eggs and sperm at the same time . Others are sequential hermaphrodites , in which the eggs and sperm mature at different times . Fertilization is generally external , although platyctenids ' eggs are fertilized inside their parents ' bodies and kept there until they hatch . The young are generally planktonic and in most species look like miniature cydippids , gradually changing into their adult shapes as they grow . The exceptions are the beroids , whose young are miniature beroids with large mouths and no tentacles , and the platyctenids , whose young live as cydippid @-@ like plankton until they reach near @-@ adult size , but then sink to the bottom and rapidly metamorphose into the adult form . In at least some species , juveniles are capable of reproduction before reaching the adult size and shape . The combination of hermaphroditism and early reproduction enables small populations to grow at an explosive rate .

Ctenophores may be abundant during the summer months in some coastal locations , but in other places they are uncommon and difficult to find . In bays where they occur in very high numbers , predation by ctenophores may control the populations of small zooplanktonic organisms such as copepods , which might otherwise wipe out the phytoplankton (planktonic plants) , which are a vital part of marine food chains . One ctenophore , Mnemiopsis , has accidentally been introduced into the Black Sea , where it is blamed for causing fish stocks to collapse by eating both fish larvae and organisms that would otherwise have fed the fish . The situation was aggravated by other factors , such as over @-@ fishing and long @-@ term environmental changes that promoted the growth of the Mnemiopsis population . The later accidental introduction of Beroe helped to mitigate the problem , as Beroe preys on other ctenophores .

Despite their soft , gelatinous bodies , fossils thought to represent ctenophores , apparently with no tentacles but many more comb @-@ rows than modern forms , have been found in lagerstätten as far back as the early Cambrian , about 515 million years ago . The position of the ctenophores in the

evolutionary family tree of animals has long been debated , and the majority view at present , based on molecular phylogenetics , is that cnidarians and bilaterians are more closely related to each other than either is to ctenophores . A recent molecular phylogenetics analysis concluded that the common ancestor of all modern ctenophores was cydippid @-@ like , and that all the modern groups appeared relatively recently , probably after the Cretaceous ? Paleogene extinction event 66 million years ago . Evidence accumulating since the 1980s indicates that the " cydippids " are not monophyletic , in other words do not include all and only the descendants of a single common ancestor , because all the other traditional ctenophore groups are descendants of various cydippids .

= = Distinguishing features = =

Ctenophores form an animal phylum that is more complex than sponges , about as complex as cnidarians (jellyfish , sea anemones , etc .) , and less complex than bilaterians (which include almost all other animals) . Unlike sponges , both ctenophores and cnidarians have : cells bound by inter @-@ cell connections and carpet @-@ like basement membranes ; muscles ; nervous systems ; and some have sensory organs . Ctenophores are distinguished from all other animals by having colloblasts , which are sticky and adhere to prey , although a few ctenophore species lack them .

Like sponges and cnidarians , ctenophores have two main layers of cells that sandwich a middle layer of jelly @-@ like material , which is called the mesoglea in cnidarians and ctenophores ; more complex animals have three main cell layers and no intermediate jelly @-@ like layer . Hence ctenophores and cnidarians have traditionally been labelled diploblastic , along with sponges . Both ctenophores and cnidarians have a type of muscle that , in more complex animals , arises from the middle cell layer , and as a result some recent text books classify ctenophores as triploblastic , while others still regard them as diploblastic .

Ranging from about 1 millimeter (0 @.@ 039 in) to 1 @.@ 5 meters (4 @.@ 9 ft) in size , ctenophores are the largest non @-@ colonial animals that use cilia (" hairs ") as their main method of locomotion . Most species have eight strips , called comb rows , that run the length of their bodies and bear comb @-@ like bands of cilia , called " ctenes , " stacked along the comb rows so that when the cilia beat , those of each comb touch the comb below . The name " ctenophora " means " comb @-@ bearing " , from the Greek ????? (stem @-@ form ????-) meaning " comb " and the Greek suffix -????? meaning " carrying " .

= = Description = =

For a phylum with relatively few species , ctenophores have a wide range of body plans . Coastal species need to be tough enough to withstand waves and swirling sediment particles , while some oceanic species are so fragile that it is very difficult to capture them intact for study . In addition oceanic species do not preserve well , and are known mainly from photographs and from observers ' notes . Hence most attention has until recently concentrated on three coastal genera ? Pleurobrachia , Beroe and Mnemiopsis . At least two textbooks base their descriptions of ctenophores on the cydippid Pleurobrachia .

Since the body of many species is almost radially symmetrical , the main axis is oral to aboral (from the mouth to the opposite end) . However , since only two of the canals near the statocyst terminate in anal pores , ctenophores have no mirror @-@ symmetry , although many have rotational symmetry , in other words if the animal rotates in a half @-@ circle it looks the same as when it started .

= = = Common features = = =

= = = = Body layers = = = =

Like those of cnidarians , (jellyfish , sea anemones , etc .) , ctenophores ' bodies consist of a relatively thick , jelly @-@ like mesoglea sandwiched between two epithelia , layers of cells bound by inter @-@ cell connections and by a fibrous basement membrane that they secrete . The epithelia of ctenophores have two layers of cells rather than one , and some of the cells in the upper layer have several cilia per cell .

The outer layer of the epidermis (outer skin) consists of : sensory cells ; cells that secrete mucus , which protects the body ; and interstitial cells , which can transform into other types of cell . In specialized parts of the body the outer layer also contains colloblasts , found along the surface of tentacles and used in capturing prey , or cells bearing multiple large cilia , for locomotion . The inner layer of the epidermis contains a nerve net , and myoepithelial cells that act as muscles .

The internal cavity forms : a mouth that can usually be closed by muscles ; a pharynx (" throat ") ; a wider area in the center that acts as a stomach ; and a system of internal canals . These branch through the mesoglea to the most active parts of the animal : the mouth and pharynx ; the roots of the tentacles , if present ; all along the underside of each comb row ; and four branches round the sensory complex at the far end from the mouth ? two of these four branches terminate in anal pores . The inner surface of the cavity is lined with an epithelium , the gastrodermis . The mouth and pharynx have both cilia and well @-@ developed muscles . In other parts of the canal system , the gastrodermis is different on the sides nearest to and furthest from the organ that it supplies . The nearer side is composed of tall nutritive cells that store nutrients in vacuoles (internal compartments) , germ cells that produce eggs or sperm , and photocytes that produce bioluminescence . The side furthest from the organ is covered with ciliated cells that circulate water through the canals , punctuated by ciliary rosettes , pores that are surrounded by double whorls of cilia and connect to the mesoglea .

= = = = Feeding , excretion and respiration = = = =

When prey is swallowed , it is liquefied in the pharynx by enzymes and by muscular contractions of the pharynx . The resulting slurry is wafted through the canal system by the beating of the cilia , and digested by the nutritive cells . The ciliary rosettes in the canals may help to transport nutrients to muscles in the mesoglea . The anal pores may eject unwanted small particles , but most unwanted matter is regurgitated via the mouth .

Little is known about how ctenophores get rid of waste products produced by the cells . The ciliary rosettes in the gastrodermis may help to remove wastes from the mesoglea , and may also help to adjust the animal 's buoyancy by pumping water into or out of the mesoglea .

= = = = Locomotion = = = =

The outer surface bears usually eight comb rows , called swimming @-@ plates , which are used for swimming . The rows are oriented to run from near the mouth (the " oral pole ") to the opposite end (the " aboral pole ") , and are spaced more or less evenly around the body , although spacing patterns vary by species and in most species the comb rows extend only part of the distance from the aboral pole towards the mouth . The " combs " (also called " ctenes " or " comb plates ") run across each row , and each consists of thousands of unusually long cilia , up to 2 millimeters (0 @.@ 079 in) . Unlike conventional cilia and flagella , which has a filament structure arranged in a 9 + 2 pattern , these cilia are arranged in a 9 + 3 pattern , where the extra compact filament is suspected to have a supporting function . These normally beat so that the propulsion stroke is away from the mouth , although they can also reverse direction . Hence ctenophores usually swim in the direction in which the mouth is eating , unlike jellyfish . When trying to escape predators , one species can accelerate to six times its normal speed ; some other species reverse direction as part of their escape behavior , by reversing the power stroke of the comb plate cilia .

It is uncertain how ctenophores control their buoyancy , but experiments have shown that some species rely on osmotic pressure to adapt to water of different densities . Their body fluids are

normally as concentrated as seawater . If they enter less dense brackish water , the ciliary rosettes in the body cavity may pump this into the mesoglea to increase its bulk and decrease its density , to avoid sinking . Conversely if they move from brackish to full @-@ strength seawater , the rosettes may pump water out of the mesoglea to reduce its volume and increase its density .

= = = = Nervous system and senses = = = =

Ctenophores have no brain or central nervous system , but instead have a nerve net (rather like a cobweb) that forms a ring round the mouth and is densest near structures such as the comb rows , pharynx , tentacles (if present) and the sensory complex furthest from the mouth .

The largest single sensory feature is the aboral organ (at the opposite end from the mouth) . Its main component is a statocyst , a balance sensor consisting of a statolith , a tiny grain of calcium carbonate , supported on four bundles of cilia , called " balancers " , that sense its orientation . The statocyst is protected by a transparent dome made of long , immobile cilia . A ctenophore does not automatically try to keep the statolith resting equally on all the balancers . Instead its response is determined by the animal 's " mood " , in other words the overall state of the nervous system . For example , if a ctenophore with trailing tentacles captures prey , it will often put some comb rows into reverse , spinning the mouth towards the prey .

= = = Cydippids = = =

Cydippid ctenophores have bodies that are more or less rounded , sometimes nearly spherical and other times more cylindrical or egg @-@ shaped ; the common coastal " sea gooseberry , " Pleurobrachia , sometimes has an egg @-@ shaped body with the mouth at the narrow end , although some individuals are more uniformly round . From opposite sides of the body extends a pair of long , slender tentacles , each housed in a sheath into which it can be withdrawn . Some species of cydippids have bodies that are flattened to various extents , so that they are wider in the plane of the tentacles .

The tentacles of cydippid ctenophores are typically fringed with tentilla (" little tentacles ") , although a few genera have simple tentacles without these sidebranches . The tentacles and tentilla are densely covered with microscopic colloblasts that capture prey by sticking to it . Colloblasts are specialized mushroom @-@ shaped cells in the outer layer of the epidermis , and have three main components : a domed head with vesicles (chambers) that contain adhesive ; a stalk that anchors the cell in the lower layer of the epidermis or in the mesoglea ; and a spiral thread that coils round the stalk and is attached to the head and to the root of the stalk . The function of the spiral thread is uncertain , but it may absorb stress when prey tries to escape , and thus prevent the collobast from being torn apart . In addition to colloblasts , members of the genus Haeckelia , which feed mainly on jellyfish , incorporate their victims ' stinging nematocytes into their own tentacles ? some cnidaria @-@ eating nudibranchs similarly incorporate nematocytes into their bodies for defense . The tentilla of Euplokamis differ significantly from those of other cydippids : they contain striated muscle , a cell type otherwise unknown in the phylum Ctenophora ; and they are coiled when relaxed , while the tentilla of all other known ctenophores elongate when relaxed . Euplokamis ' tentilla have three types of movement that are used in capturing prey : they may flick out very quickly (in 40 to 60 milliseconds) ; they can wriggle , which may lure prey by behaving like small planktonic worms ; and they coil round prey . The unique flicking is an uncoiling movement powered by contraction of the striated muscle . The wriggling motion is produced by smooth muscles , but of a highly specialized type . Coiling around prey is accomplished largely by the return of the tentilla to their inactive state , but the coils may be tightened by smooth muscle .

There are eight rows of combs that run from near the mouth to the opposite end , and are spaced evenly round the body . The " combs " beat in a metachronal rhythm rather like that of a Mexican wave . From each balancer in the statocyst a ciliary groove runs out under the dome and then splits to connect with two adjacent comb rows , and in some species runs all the way along the comb rows . This forms a mechanical system for transmitting the beat rhythm from the combs to the balancers ,

via water disturbances created by the cilia .

= = = Lobates = = =

The Lobata have a pair of lobes , which are muscular , cuplike extensions of the body that project beyond the mouth . Their inconspicuous tentacles originate from the corners of the mouth , running in convoluted grooves and spreading out over the inner surface of the lobes (rather than trailing far behind , as in the Cydippida) . Between the lobes on either side of the mouth , many species of lobates have four auricles , gelatinous projections edged with cilia that produce water currents that help direct microscopic prey toward the mouth . This combination of structures enables lobates to feed continuously on suspended planktonic prey .

Lobates have eight comb @-@ rows , originating at the aboral pole and usually not extending beyond the body to the lobes ; in species with (four) auricles , the cilia edging the auricles are extensions of cilia in four of the comb rows . Most lobates are quite passive when moving through the water , using the cilia on their comb rows for propulsion , although Leucothea has long and active auricles whose movements also contribute to propulsion . Members of the lobate genera Bathocyroe and Ocyropsis can escape from danger by clapping their lobes , so that the jet of expelled water drives them backwards very quickly . Unlike cydippids , the movements of lobates ' combs are coordinated by nerves rather than by water disturbances created by the cilia , yet combs on the same row beat in the same Mexican wave style as the mechanically coordinated comb rows of cydippids and beroids . This may have enabled lobates to grow larger than cydippids and to have shapes that are less egg @-@ like .

An unusual species first described in 2000 , Lobatolampea tetragona , has been classified as a lobate , although the lobes are " primitive " and the body is medusa @-@ like when floating and disk @-@ like when resting on the sea @-@ bed .

= = = Beroids = = =

The Beroida , also known as Nuda , have no feeding appendages , but their large pharynx , just inside the large mouth and filling most of the saclike body , bears " macrocilia " at the oral end . These fused bundles of several thousand large cilia are able to " bite " off pieces of prey that are too large to swallow whole ? almost always other ctenophores . In front of the field of macrocilia , on the mouth " lips " in some species of Beroe , is a pair of narrow strips of adhesive epithelial cells on the stomach wall that " zip " the mouth shut when the animal is not feeding , by forming intercellular connections with the opposite adhesive strip . This tight closure streamlines the front of the animal when it is pursuing prey .

= = = Other body forms = = =

The Ganeshida have a pair of small oral lobes and a pair of tentacles . The body is circular rather than oval in cross @-@ section , and the pharynx extends over the inner surfaces of the lobes .

The Thalassocalycida , only discovered in 1978 and known from only one species , are medusa @-@ like , with bodies that are shortened in the oral @-@ aboral direction , and short comb @-@ rows on the surface furthest from the mouth , originating from near the aboral pole . They capture prey by movements of the bell and possibly by using two short tentacles .

The Cestida (" belt animals ") are ribbon @-@ shaped planktonic animals , with the mouth and aboral organ aligned in the middle of opposite edges of the ribbon . There is a pair of comb @-@ rows along each aboral edge , and tentilla emerging from a groove all along the oral edge , which stream back across most of the wing @-@ like body surface . Cestids can swim by undulating their bodies as well as by the beating of their comb @-@ rows . There are two known species , with worldwide distribution in warm , and warm @-@ temperate waters : Cestum veneris (" Venus ' girdle ") is among the largest ctenophores ? up to 1 @.@ 5 meters (4 @.@ 9 ft) long , and can undulate slowly or quite rapidly . Velamen parallelum , which is typically less than 20 centimeters (0

@.@ 66 ft) long , can move much faster in what has been described as a " darting motion " .
Most Platyctenida have oval bodies that are flattened in the oral @-@ aboral direction , with a pair of tentilla @-@ bearing tentacles on the aboral surface . They cling to and creep on surfaces by everting the pharynx and using it as a muscular " foot " . All but one of the known platyctenid species lack comb @-@ rows . Platyctenids are usually cryptically colored , live on rocks , algae , or the body surfaces of other invertebrates , and are often revealed by their long tentacles with many sidebranches , seen streaming off the back of the ctenophore into the current .

= = = Reproduction and development = = =

Adults of most species can regenerate tissues that are damaged or removed , although only platyctenids reproduce by cloning , splitting off from the edges of their flat bodies fragments that develop into new individuals .
Almost all species are hermaphrodites , in other words they function as both males and females at the same time ? except that in two species of the genus Ocryopsis individuals remain of the same single sex all their lives . The gonads are located in the parts of the internal canal network under the comb rows , and eggs and sperm are released via pores in the epidermis . Fertilization is external in most species , but platyctenids use internal fertilization and keep the eggs in brood chambers until they hatch . Self @-@ fertilization has occasionally been seen in species of the genus Mnemiopsis , and it is thought that most of the hermaphroditic species are self @-@ fertile .
Development of the fertilized eggs is direct , in other words there is no distinctive larval form , and juveniles of all groups generally resemble miniature cydippid adults . In the genus Beroe the juveniles , like the adults , lack tentacles and tentacle sheaths . In most species the juveniles gradually develop the body forms of their parents . In some groups , such as the flat , bottom @-@ dwelling platyctenids , the juveniles behave more like true larvae , as they live among the plankton and thus occupy a different ecological niche from their parents and attain the adult form by a more radical metamorphosis , after dropping to the sea @-@ floor .
At least in some species , juvenile ctenophores appear capable of producing small quantities of eggs and sperm while they are well below adult size , and adults produce eggs and sperm for as long as they have sufficient food . If they run short of food , they first stop producing eggs and sperm , and then shrink in size . When the food supply improves , they grow back to normal size and then resume reproduction . These features make ctenophores capable of increasing their populations very quickly .

= = = Colors and bioluminescence = = =

Most ctenophores that live near the surface are mostly colorless and almost transparent . However some deeper @-@ living species are strongly pigmented , for example the species known as " Tortugas red " (see illustration here) , which has not yet been formally described . Platyctenids generally live attached to other sea @-@ bottom organisms , and often have similar colors to these host organisms . The gut of the deep @-@ sea genus Bathocyroe is red , which hides the bioluminescence of copepods it has swallowed .
The comb rows of most planktonic ctenophores produce a rainbow effect , which is not caused by bioluminescence but by the scattering of light as the combs move . Most species are also bioluminescent , but the light is usually blue or green and can only be seen in darkness . However some significant groups , including all known platyctenids and the cydippid genus Pleurobrachia , are incapable of bioluminescence .
When some species , including Bathyctena chuni , Euplokamis stationis and Eurhamphaea vexilligera , are disturbed , they produce secretions (ink) that luminesce at much the same wavelengths as their bodies . Juveniles will luminesce more brightly in relation to their body size than adults , whose luminescence is diffused over their bodies . Detailed statistical investigation has not suggested the function of ctenophores ' bioluminescence nor produced any correlation between its exact color and any aspect of the animals ' environments , such as depth or whether they live in

coastal or mid @-@ ocean waters .

In ctenophores , bioluminescence is caused by the activation of calcium @-@ activated proteins named photoproteins in cells called photocytes , which are often confined to the meridional canals that underlie the eight comb rows . In the genome of Mnemiopsis leidyi ten genes encode photoproteins . These genes are co @-@ expressed with opsin genes in the developing photocytes of Mnemiopsis leidyi , raising the possibility that light production and light detection may be working together in these animals .

= = Ecology = =

= = = Distribution = = =

Ctenophores are found in most marine environments : from polar waters to the tropics ; near coasts and in mid @-@ ocean ; from the surface waters to the ocean depths . The best @-@ understood are the genera Pleurobrachia , Beroe and Mnemiopsis , as these planktonic coastal forms are among the most likely to be collected near shore . No ctenophores have been found in fresh water .

= = = Prey and predators = = =

Almost all ctenophores are predators ? there are no vegetarians and only one genus that is partly parasitic . If food is plentiful , they can eat 10 times their own weight per day . While Beroe preys mainly on other ctenophores , other surface @-@ water species prey on zooplankton (planktonic animals) ranging in size from the microscopic , including mollusc and fish larvae , to small adult crustaceans such as copepods , amphipods , and even krill . Members of the genus Haeckelia prey on jellyfish and incorporate their prey 's nematocysts (stinging cells) into their own tentacles instead of colloblasts . Ctenophores have been compared to spiders in their wide range of techniques from capturing prey ? some hang motionless in the water using their tentacles as " webs " , some are ambush predators like Salticid jumping spiders , and some dangle a sticky droplet at the end of a fine thread , as bolas spiders do . This variety explains the wide range of body forms in a phylum with rather few species . The two @-@ tentacled " cydippid " Lampea feeds exclusively on salps , close relatives of sea @-@ squirts that form large chain @-@ like floating colonies , and juveniles of Lampea attach themselves like parasites to salps that are too large for them to swallow . Members of the cydippid genus Pleurobrachia and the lobate Bolinopsis often reach high population densities at the same place and time because they specialize in different types of prey : Pleurobrachia 's long tentacles mainly capture relatively strong swimmers such as adult copepods , while Bolinopsis generally feeds on smaller , weaker swimmers such as rotifers and mollusc and crustacean larvae .

Ctenophores used to be regarded as " dead ends " in marine food chains because it was thought their low ratio of organic matter to salt and water made them a poor diet for other animals . It is also often difficult to identify the remains of ctenophores in the guts of possible predators , although the combs sometimes remain intact long enough to provide a clue . Detailed investigation of chum salmon , Oncorhynchus keta , showed that these fish digest ctenophores 20 times as fast as an equal weight of shrimps , and that ctenophores can provide a good diet if there are enough of them around . Beroids prey mainly on other ctenophores . Some jellyfish and turtles eat large quantities of ctenophores , and jellyfish may temporarily wipe out ctenophore populations . Since ctenophores and jellyfish often have large seasonal variations in population , most fish that prey on them are generalists , and may have a greater effect on populations than the specialist jelly @-@ eaters . This is underlined by an observation of herbivorous fishes deliberately feeding on gelatinous zooplankton during blooms in the Red Sea . The larvae of some sea anemones are parasites on ctenophores , as are the larvae of some flatworms that parasitize fish when they reach adulthood .

= = = Ecological impacts = = =

Ctenophores may balance marine ecosystems by preventing an over @-@ abundance of copepods from eating all the phytoplankton (planktonic plants) , which are the dominant marine producers of organic matter from non @-@ organic ingredients .

On the other hand , in the late 1980s the Western Atlantic ctenophore Mnemiopsis leidyi was accidentally introduced into the Black Sea and Sea of Azov via the ballast tanks of ships , and has been blamed for causing sharp drops in fish catches by eating both fish larvae and small crustaceans that would otherwise feed the adult fish . Mnemiopsis is well equipped to invade new territories (although this was not predicted until after it so successfully colonized the Black Sea) , as it can breed very rapidly and tolerate a wide range of water temperatures and salinities . The impact was increased by chronic overfishing , and by eutrophication that gave the entire ecosystem a short @-@ term boost , causing the Mnemiopsis population to increase even faster than normal ? and above all by the absence of efficient predators on these introduced ctenophores . Mnemiopsis populations in those areas were eventually brought under control by the accidental introduction of the Mnemiopsis @-@ eating North American ctenophore Beroe ovata , and by a cooling of the local climate from 1991 to 1993 , which significantly slowed the animal 's metabolism . However the abundance of plankton in the area seems unlikely to be restored to pre @-@ Mnemiopsis levels .

In the late 1990s Mnemiopsis appeared in the Caspian Sea . Beroe ovata arrived shortly after , and is expected to reduce but not eliminate the impact of Mnemiopsis there . Mnemiopsis also reached the eastern Mediterranean in the late 1990s and now appears to be thriving in the North Sea and Baltic Sea .

= = Classification = =

The number of known living ctenophore species is uncertain , since many of those named and formally described have turned out to be identical to species known under other scientific names . Claudia Mills estimates that there about 100 to 150 valid species that are not duplicates , and that at least another 25 , mostly deep @-@ sea forms , have been recognized as distinct but not yet analyzed in enough detail to support a formal description and naming .

The traditional classification divides ctenophores into two classes , those with tentacles (Tentaculata) and those without (Nuda) . The Nuda contains only one order (Beroida) and family (Beroidae) , and two genera , Beroe (several species) and Neis (one species) .

The Tentaculata are divided into the following eight orders :

Cydippida , egg @-@ shaped animals with long tentacles

Lobata , with paired thick lobes

Platyctenida , flattened animals that live on or near the sea @-@ bed ; most lack combs as adults , and use their pharynges as suckers to attach themselves to surfaces

Ganeshida , with a pair of small lobes round the mouth , but an extended pharynx like that of platyctenids

Cambojiida

Cryptolobiferida

Thalassocalycida , with short tentacles and a jellyfish @-@ like " umbrella "

Cestida , ribbon @-@ shaped and the largest ctenophores

= = Evolutionary history = =

= = = Fossil record = = =

Because of their soft , gelatinous bodies , ctenophores are extremely rare as fossils , and fossils that have been interpreted as ctenophores have been found only in lagerstätten , places where the environment was exceptionally suited to preservation of soft tissue . Until the mid @-@ 1990s only two specimens good enough for analysis were known , both members of the crown group , from the

early Devonian (Emsian) period . Three additional putative species were then found in the Burgess Shale and other Canadian rocks of similar age , about 505 million years ago in the mid @-@ Cambrian period . All three apparently lacked tentacles but had between 24 and 80 comb rows , far more than the 8 typical of living species . They also appear to have had internal organ @-@ like structures unlike anything found in living ctenophores . One of the fossil species first reported in 1996 had a large mouth , apparently surrounded by a folded edge that may have been muscular . Evidence from China a year later suggests that such ctenophores were widespread in the Cambrian , but perhaps very different from modern species ? for example one fossil 's comb @-@ rows were mounted on prominent vanes . The Ediacaran Eoandromeda could putatively represent a comb jelly .

The early Cambrian sessile frond @-@ like fossil Stromatoveris , from China 's Chengjiang lagerstätte and dated to about 515 million years ago , is very similar to Vendobionta of the preceding Ediacaran period . De @-@ Gan Shu , Simon Conway Morris et al. found on its branches what they considered rows of cilia , used for filter feeding . They suggested that Stromatoveris was an evolutionary " aunt " of ctenophores , and that ctenophores originated from sessile animals whose descendants became swimmers and changed the cilia from a feeding mechanism to a propulsion system .

520 million years old Cambrian fossils also from Chengjiang in China show a now wholly extinct class of ctenophore , named " Scleroctenophora , " that had a complex internal skeleton with long spines .

= = = Relationship to other animal phyla = = =

The relationship of ctenophores to the rest of Metazoa is very important to our understanding of the early evolution of animals and the origin of multicellularity . It has been the focus of debate for many years . Ctenophores have been purported to be the sister lineage to the Bilateria , sister to the Cnidaria , sister to Cnidaria , Placozoa and Bilateria , and sister to all other animal phyla . A series of studies that looked at the presence and absence of members of gene families and signalling pathways (e.g. , homeoboxes , nuclear receptors , the Wnt signaling pathway , and sodium channels) showed evidence congruent with the latter two scenarios , that ctenophores are either sister to Cnidaria , Placozoa and Bilateria or sister to all other animal phyla . Several more recent studies comparing complete sequenced genomes of ctenophores with other sequenced animal genomes have also supported ctenophores as the sister lineage to all other animals . This position would suggest that neural and muscle cell types were either lost in major animal lineages (e.g. , Porifera) or that they evolved independently in the ctenophore lineage . However , other researchers have argued that the placement of Ctenophora as sister to all other animals is a statistical anomaly caused by the high rate of evolution in ctenophore genomes , and that Porifera (sponges) is the earliest @-@ diverging animal phylum instead . Ctenophores and sponges are also the only known animal phyla that lack any true hox genes .

= = = Relationships within Ctenophora = = =

Since all modern ctenophores except the beroids have cydippid @-@ like larvae , it has widely been assumed that their last common ancestor also resembled cydippids , having an egg @-@ shaped body and a pair of retractable tentacles . Richard Harbison 's purely morphological analysis in 1985 concluded that the cydippids are not monophyletic , in other words do not contain all and only the descendants of a single common ancestor that was itself a cydippid . Instead he found that various cydippid families were more similar to members of other ctenophore orders than to other cydippids . He also suggested that the last common ancestor of modern ctenophores was either cydippid @-@ like or beroid @-@ like . A molecular phylogeny analysis in 2001 , using 26 species , including 4 recently discovered ones , confirmed that the cydippids are not monophyletic and concluded that the last common ancestor of modern ctenophores was cydippid @-@ like . It also found that the genetic differences between these species were very small ? so small that the

relationships between the Lobata , Cestida and Thalassocalycida remained uncertain . This suggests that the last common ancestor of modern ctenophores was relatively recent , and perhaps was lucky enough to survive the Cretaceous ? Paleogene extinction event 65 @.@ 5 million years ago while other lineages perished . When the analysis was broadened to include representatives of other phyla , it concluded that cnidarians are probably more closely related to bilaterians than either group is to ctenophores but that this diagnosis is uncertain .