Comparative feeding behavior of planktonic ctenophores

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Synopsis
The phylum Ctenophora (known as comb jellies) consists of gelatinous marine carnivores found from the surface to several thousand meters depth. Their morphology can be simple or complex, ranging from a sac-like shape with no tentacles to large lobed forms with sinuous “auricles,” papillae, and two different kinds of tentacles. This diversity appears to reflect adaptations to many different diets. For example, some species can continuously “graze” on small crustaceans or larvae, others engulf larger jellies, and some are able to snare individual larger prey through a variety of strategies. Thus feeding behavior can help explain the high morphological diversity in this relatively small phylum. Because of their fragility, comb jellies are difficult to study alive and the natural histories of many types, especially those found in the deep sea, have not been examined. This account categorizes ctenophore feeding methods using published reports as well as new observations using submersibles and blue-water scuba diving.

Introduction
Ctenophores (Fig. 1) are unique among animals in their possession of large macrocilia and a particular type of adhesive cells known as colloblasts. They use these in a variety of ways, including for locomotion and feeding. Because ctenophores are exclusively carnivorous, their principal feeding task is the capture of prey; there are no herbivorous ctenophores, and only one genus that can sometimes be parasitic. As has been noted elsewhere (Greene et al. 1986), apt analogies may be drawn between ctenophore feeding strategies and those of terrestrial spiders. For example, there are ctenophore counterparts to sit-and-wait orb weavers, ambush predators like Salticid jumping spiders, and the Bola spiders that dangle a sticky droplet at the end of a fine thread.

A few coastal species of ctenophores, particularly the “cydippid” Pleurobrachia pileus, the lobate Mnemiopsis leidyi, and the sac-like Beroe cucumis, have been studied for many years (Mayer 1912; Main 1928, and many others). Their ready accessibility and relative robustness make it possible to study their feeding in laboratory settings and, therefore, these species have formed the basis for our textbook view of the phylum.

Blue-water diving and submersibles have provided opportunities for in situ observation and have provided new information on many fragile and deep-sea species. As compared with other reviews (Purcell 1991), here the focus is on variation in behavior across the phylum, as also true of the studies by Harbison et al. (1978) and Matsumoto & Harbison (1993), and not on physiology or energetics, which have been well covered in particular experiments (Kremer et al. 1986; Purcell et al. 1991; Scolardi et al. 2006).

Feeding modes
One impediment to discussing and comparing ctenophores is that the standard taxonomy and nomenclature is now known to be a poor reflection of the relationships among them. Class Tentaculata refers to all genera except Beroe (including Lobates and Thalassocalyctida), and so because of its breadth, is not useful in this context. Even the Order Cydippida, encompassing a range of genera that primarily use two long, opposed tentacles, has been clearly shown to be polyphyletic (Podar et al. 2001), as was suggested some time ago (Harbison 1985). Therefore, a comparative analysis has to be carried out almost genus-by-genus or a family at a time. In addition, for this article, the term “cydippid” is highlighted since it is used in the classical morphological sense but without its standard taxonomic implications. Below are listed the known feeding modes, sorted according to ctenophore morphology. They are separated into groups that (1) use tentacles...
for feeding, (2) use lobes for feeding, (3) feed by engulfing, and (4) those that are trophic specialists.

Use of tentacles for feeding

Pleurobrachia has a sit-and-wait strategy as thoroughly described by Tamm and Moss, (1985) among others. It swims in a horizontal semicircle, deploying its two long tentacles gradually so that the tentilla hang down evenly spaced (Fig. 2A). Once the tentacles are fully extended, the ctenophore eases to a stop with its mouth upright, and begins to wait. When a prey item, in this case typically a copepod, swims into the sticky tentillar net and becomes ensnared, Pleurobrachia reacts by retracting the tentacles and swimming ahead until the prey item is brought close to the body. At that point, the ctenophore starts rotating in place so that the prey is brought around to the mouth and ingested. One interesting aspect of this behavior is how it is brought about by a few simple rules and associated neural response patterns (Moss and Tamm 1986; Moss 1991).

This feeding behavior has several implications: the rate is dependent on motion of prey (Greene et al. 1986), and the efficiency depends on the ctenophore being undisturbed enough to carry out the deployment of its net. As a result, researchers originally found clearance rates between 5 and 10 l/day for Pleurobrachia, and about twice that for Mnemiopsis (Greene et al. 1986). However, using larger containers, later studies showed that Pleurobrachia was capable of clearing 10 times that volume (Gibbons and Painting 1992). The closely related genus Hormiphora operates in a similar manner, except that it may deploy its tentilla vertically in a U-shaped pattern, and species in the temperate Pacific feed primarily on larger euphausiid krill. The main morphological difference is that the tentacular bulbs of Hormiphora are longer than in Pleurobrachia, providing a stronger anchor for retaining prey.

Other ctenophores use similar strategies, although targeting different sizes of prey. The mertensiids (Mertensia, Callianira, and many undescribed deep-sea genera) are not particularly close to the pleurobrachiids phylogenetically, but they also feed by deploying two tentacles with a web of tentilla and passively waiting for encounters from actively swimming prey. Like Hormiphora and Mertensia from the Arctic, Callianira from the Antarctic feed on adult and larval krill and copepods (Hamner and Hamner 2000; Scolardi et al. 2006). Some of the large deep-sea mertensiids, which have not yet been described (for example, Sp. 2 in Fig. 1 of Podar et al. 2001), have extremely strong and sticky tentacles that can span two meters, and these are able to capture large shrimp.

Many other deep sea genera such as Bathyctena (in its own family) are physically fragile, but well-equipped with fine tentilla used for immobilizing small prey. Their capacious stomodaeum is an indicator of their ability to handle the large prey found in the deep sea (Fig. 2C). A few undescribed species have tentilla so fine that they appear to form a hazy cloud. These species would have access to the smallest of nauplii and copepods, which are known to be very abundant (Hopcroft et al. 2001), although perhaps not easily captured if they are associated with marine “snow” particles (Alldredge and Silver 1988). Charistephane fugiens is a rare, small (1.5–2 cm), flattened species found between 100 and 300 m in the Pacific and Atlantic Oceans and known from the Mediterranean Sea (Chun 1880). Its tentacles are so fragile that it is difficult to consider how they might function. The consistent presence of colorless oil droplets in their gastrovascular canals suggests a diet of small copepods. Euplokamis is at the other extreme of tentillum development. Its prehensile side-branches are widely spaced and spirally coiled into a droplet-shape (Mackie et al. 1988). They mechanically snare copepods like a bola, wrapping around them when triggered.

Fig. 1 The lobate ctenophore Deiopea kaloktenota. Structures relevant to feeding are labeled.
Fig. 2  (A) *Pleurobrachia bachei* deploys a web of sticky tentacles to capture active prey. (B) *Bathyctena chuni* from the deep Pacific with its mouth open showing the voluminous stomodeum. (C) *Dryodora glandiformis*, a polar species that specializes in larvaceans. The outer “vestibule” (ve) holds the larvacean and its house after initial capture. (D) The lobate *Ocyropsis maculata immaculata* has no functional tentacles as an adult and uses its muscular lobes to capture prey directly. The white spots are parasitic amphipods. (E) The “showercap” ctenophore *Thalassocalyce inconstans* from the aboral end. In this species, the lobes are fused and there are no auricles. (F) The lobate *Leucothea pulchra* viewed along the body axis from the oral end; it is swimming straight toward the viewer. Note the sinuous auricles (au) between the lobe surfaces. (G) *Beroe forskali*, having ingested a large portion of a *Leucothea*. The comb rows (arrowheads) and orange papillae of the prey can be seen inside the mostly transparent gut of the *Beroe*. 
The mertensiids, although they are a diverse group and defy generalizations, are interesting to consider because they are found near the base of ctenophore phylogeny, and thus might be most indicative of the ancestral ctenophore state. The mertensiid form is also typical of the “cydippid” stage through which lobates pass, so the cydippid form may constitute an important part of their ecology, even though they adopt a very different feeding style later in development.

Use of lobes in feeding

Lobates are ctenophores with an apparently derived morphology in which broad lobes grow out at, or near, the oral end, and long trailing tentacles are generally replaced by a row of tentacles running along either side of the mouth (Fig. 1).

Of the lobates, the most commonly studied is Mnemiopsis from the Western Atlantic (Main 1928; Sullivan and Reeve 1982; Costello and Coverdale 1998). It is relatively passive, even for a ctenophore, and if laboratory studies can be extrapolated to the field, generates feeding currents with its auricles. In the coastal and estuarine environments where it is found, this is an effective feeding mode, and as a result Mnemiopsis can have a major predatory impact on crustaceans and on fish larvae, notably in the Black Sea (Vinogradov 1989). Its filter-feeding mode of accumulating prey does not seem typical of other lobates such as Kiyohimea, Deiopea, Eurhamphaea, and Leucothea. Bolinopsis falls somewhere between in activity levels. To understand lobates, it is important to acknowledge that ctenophores are not oriented like medusae, with their mouth tucked in the lee of an umbrella-like structure (but see Thalassocalyce subsequently). Unlike medusae, which lead with their aboral end when swimming (Costello and Colin 1995), nearly all ctenophores encounter the environment with the oral end first. Leucothea (Harbison et al. 1978; Matsumoto and Hamner 1988) and Kiyohimea “fly” through the water with their lobes spread like the wings of a biplane (Fig. 2F). Auricles beat sinuously between the two sticky surfaces of the lobes, while a veil of oral tentacles trails from the line of the mouth across the main body of the animal. Copepods or other prey that pass between the lobes are disturbed by the motion of the auricles, and in their efforts to escape often leap into contact with the lobe.

Bathocyroe is an exclusively deep-sea genus (>400 m) with large lobes and a small, pigmented stomodaéum (Madin and Harbison 1978a). The oral tentacles extend along the length of the lobes. Its red-pigmented gut serves to mask the bioluminescence of its copepod prey. In addition to slow forward swimming propelled by the comb plates, this genus also has an escape response in which the muscular lobes are clapped together, thereby sending it backwards through the water—a behavior also seen in the genus Ocyropsis.

Ocyropsis (Fig. 2D) species are unique among pelagic “Tentaculata” in having no functional tentacles as adults (O. maculata has a rudimentary tentacular apparatus and O. crystallina lacks tentacles altogether). Instead, they use their muscular lobes to capture food, grabbing items individually, and bringing the mouth over to take the prey. They have been found with ctenophores, euthecosome pteropods, euphausiids, and fish larvae in their guts (Matsumoto and Harbison 1993). Thus, they also do not fit within the typical lobate feeding mode. This genus is very successful and abundant in oligotrophic tropical waters, perhaps because of its adaptation to feeding on certain larger and less frequent prey.

In Deiopea kalokenotata (Fig. 1), the lobes are much reduced, although this species still has an oral veil of tentacles. In captivity, at least, its mode of feeding is between the mechanical methods of capture of Ocyropsis and the more filter-like grazing of Leucothea. Deiopea is seen to ingest siphonophores and other noncrustacean prey, in addition to copepods. Morphologically, Deiopea looks like an earlier developmental stage of Kiyohimea or one of the other large lobates.

The cestids Cestum and Velamen can be considered as morphological and evolutionary extremes of the lobate body form (Ceccaldi 1972; Stretch 1982; Harbison 1985; Podar et al. 2001). Their oral surface has been extended laterally, while the lobes themselves have been reduced giving them a flying-wing appearance. A veil of oral tentacles drapes across the body’s surface, and the subtentacular comb rows are reduced, while the substomodaeal canals extend the full width of the body. These genera proceed laterally through the water, periodically reversing direction and moving up or down in the water column, while accumulating small copepods as prey (Stretch 1982; Matsumoto and Harbison 1993).

Feeding by engulfing

Beroe (Fig. 2G) are sack-shaped ctenophores that lack tentacles for their entire lives. Nonetheless, they are powerful predators on other gelatinous organisms and employ a raptorial feeding mode (Swanberg
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There are several interesting specialists among the two-tentacled “cydippid” ctenophores. Lampea looks superficially like Hormiphora, but with tentacles that exit laterally rather than aborally, and with an extensible Beroe-like mouth. It feeds almost exclusively on salps. As juveniles, when they are much smaller than the salps, they attach themselves by their mouth, and form a parasite-like plaque (Harbison et al. 1978). Eventually as they grow, Lampea species are able to engulf individual or entire chains of salps. They can be seen trailing behind an actively pumping chain, hanging onto the end-most units. This shift in feeding from parasite to predator on the same prey allows them to consume salps at all sizes of development and effectively respond to massive blooms (Madin 1974).

Although Haeckelia is classified as a “cydippid” it is the best example of why the classification of ctenophores needs a revision. Like Lampea, this small (0.6–2.5 cm) genus has an extensible Beroe-like stomodæum, but also has two orally-exiting tentacles that are simple, meaning they have no side branches. Mills and Miller (1984) showed that H. rubra were able to eat the tentacles of Aegina, a narcomedusa, while incorporating its nematocysts into their own tentacles. It is not clear whether the nematocysts serve any protective or predatory function in the genus; it is interesting that the narcomedusae from which it obtains the cnidae use them to capture and adhere to gelatinous prey. Haeckelia beebei and H. rubra have been observed to feed by deploying their tentacles many body lengths above their mouth, in two arcs that look like fine antennae. They passively wait for active predators of jellies that forage with their tentacles held ahead of them. Commonly for H. rubra, this is narcomedusae in the genus Solmaris, which can occur in dense blooms. When the ctenophore encounters prey, it rapidly retracts its tentacles and attempts to engulf the medusa. The speed with which this occurs is startling, considering the standard view of the behavior of gelatinous animals. Haeckelia species are also occasionally found to ingest siphonophores.

Aulacocenta is a deep-sea genus containing one described species from the Arctic (Mortensen 1912) and likely several yet to be described. It is presently classified in the same family as Haeckelia due to its simple, orally-exiting tentacles. Internal morphology and molecular evidence (unpublished results), however, show that this is an example of convergence, and that simple tentacles, without side branches, have arisen at least three times within the phylum (including Dryodora; see subsequently). For those who consider there to be strong selection for spacing of the tentilla in the evolution of feeding, Aulacocenta presents a perplexing case. Its prey and mode of feeding is still unknown, although there is evidence of a unique diet from the Arctic (Raskoff, personal communication), as well as consumption of large crustacean prey (personal observation). There is no evidence yet that it feeds on deep-sea narcomedusae, as might be suspected by the morphology of its tentacles and homology with Haeckelia species.

In addition to Lampea and Haeckelia, the genus Dryodora (Fig. 2C) has one of the most specialized diets known for ctenophores. Harbison et al. (1997) found them to be adapted for feeding on larvaceans, urochordates that filter-feed from inside mucus houses. The ctenophore has two simple tentacles with which it encounters prey. It has a unique “vestibule” outside its mouth, and in this antechamber it engulfs a larvacean together with its house. The ctenophore holds its outer mouth closed until the larvacean senses something wrong and wriggles free. Unable to escape, however, the larvacean eventually ends up getting snared by the ctenophore’s inner mouth and trapped in its gut, while the mucus house is eventually discarded. Like Aulacocenta and Haeckelia, Dryodora has simple tentacles, although preliminary molecular data show that this is yet another independent origin of this trait.

Related to the lobates is a recently described, umbrella-shaped group including the genus Thalassocalyce (Madin and Harbison 1978b). Their distinguishing feature is a lack of auricles, and lobes that are fused into a continuous dome (Fig. 2E). Young individuals are found near the surface, but adults are generally found deeper than 200 m. Other auricle-free ctenophore species (with and without fused lobes) are abundant in the deep-sea, but have not yet been described because of their extreme fragility. Even using remotely operated vehicles it is difficult to collect and observe these alive. Despite this fragility, species of this auricle-free morphology...
are able to capture relatively large crustaceans and subdue them. They capture prey by sitting with the mouth open and then snapping it shut when an organism ventures inside. In the capturing position, they have only their outermost oral ring closed, so that the prey is smothered. This passive strategy is an effective way for fragile jellies to capture robust crustaceans and other prey that they would be otherwise unable to overpower.

**Discussion**

Despite their very low genetic divergence (Podar et al. 2001), species in the phylum Ctenophora represent a great deal of morphological differentiation. Much of this variability appears to be directly related to specialization for feeding on prey of different sizes, behaviors, and abundances. Because they do not have stinging cells that immobilize prey, they must use other means for its capture, most often mucus and their special colloblasts (glue-secreting cells). In addition, there are many ways in which their giant cilia are used for propulsion, conveying food, and biting or engulfing certain types of prey. Even for marine biologists, understanding these adaptations, however, is difficult if the ctenophores are not observed under natural conditions, because they are often depicted as though they are aberrant medusae. Unless they are themselves escaping, ctenophores encounter their environment oral end first, whether actively hunting or deploying their feeding webs.

Bioluminescence, a trait of nearly all ctenophores (Haddock and Case 1995), is linked in many ways to feeding ecology. Many ctenophores have red pigmentation that is thought to absorb light produced by ingested prey. One example of how this might be an advantage is for the prey in the nonlethal feeding of *Beroe* on *Bolinopsis*. An attack in which the lobate is not completely engulfed could prove dangerous for the *Beroe*, as prey tissue persists for many minutes or hours during digestion (Fig. 2G). This tissue can be seen to glow slowly, creating a signal that would attract predators. Bioluminescence may also be dependent on ingestion of the luciferin coelenterazine via luminous prey. Although this dependence has only been demonstrated to occur in hydromedusae so far (Haddock et al. 2001), it will be interesting to test in a variety of ctenophore species. This could possibly help explain why members of a krill-eating ctenophore genus (*Hormiphora*) do not luminesce, since euphausiids contain a different luciferin. That potential link and how this might relate to the other nonluminous, but copepod-eating, genus *Pleurobrachia* remains to be established.

Given the often unconvincing fossil record, it is difficult to establish the sequence through which ctenophore feeding might have evolved. Some paleontologists suggest that atentaculate *Beroe*-like species were first to evolve, but there is molecular evidence (Podar et al. 2001) that tentacles were present in the ancestor of extant species, suggesting that a loss of tentacles is the derived condition. It is clear that for this strictly carnivorous phylum, tentacles and cilia have been the foundation for the diversification of feeding.

A thorough interpretation of ctenophore behavior will require a revision of their phylogeny and systematics. The cydippids have been shown to be polyphyletic (Harbison 1985; Podar et al. 2001) and the tentaculate genus *Haeckelia* is more closely related to the nontentaculate *Beroe* than it is to other tentacle-bearing genera. Only after resolving these relationships will the evolution of feeding be interpretable. It has been suggested that the lobates have a major advantage over the “cydippids,” given their ability to exploit a small size-fraction of prey and to feed nearly continuously. However, in many habitats, there are also advantages to being able to capture larger prey. The spacing between tentilla does not seem to be the main factor determining efficiency of tentacular feeding (as suggested by Costello and Coverdale 1998), and rates used in such comparisons can be strongly affected by experimental conditions (Gibbons and Painting 1992).

This small phylum continues to surprise with its unpredictable variation. In addition to the few well-known modes of feeding, there are many morphological adaptations that allow species to exploit a variety of prey available in the planktonic environment.

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**References**

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