Tropical Corallimorpharia (Coelenterata: Anthozoa): Feeding by Envelopment

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Abstract.—Three species of tropical Australian corallimorpharians (family Actinodiscidae) lacking ectodermal nematocysts in their discal tentacles feed by entrapping prey with their oral discs. The largest species can close in three seconds, engulf four liters of water, and capture shrimps and fishes. It has captured anemonefishes in aquaria.

Introduction

Members of the 11 orders of the exclusively marine coelenterate class Anthozoa are basically alike in body form, with a cylindrical gastrovascular cavity divided by radial septa (mesenteries) and topped by an oral disc from which arise hollow tentacles (usually eight or multiples of six) that communicate with the gastrovascular space. All members of the phylum possess intrinsic nematocysts. Typically the ectoderm of the tentacles is studded with these toxin-filled, intracellular organelles which function by eversion of a thread that wraps around or penetrates animal prey, thereby securing, immobilizing or killing it. Nematocysts also occur in the ectodermal lining of the actinopharynx (throat) and endodermally along the free edge of each septum. Among some or all six genera of family Actinodiscidae (order Corallimorpharia), however, dense concentrations of nematocysts occur primarily in the endoderm of the mesenteries and oral disc. The absence of nematocysts on the external surface of most tentacles of these animals was well established by the early twentieth century (McMurrich, 1889; Carlgren, 1900; Duerden, 1900), but the question of how such anemones feed has apparently not been considered.

Observations

Tropical shallow-water corallimorpharians contain zooxanthellae in their endodermal cells, and since such symbiotic algae are known to contribute photosynthate to other species of coelenterate hosts (Muscatine, 1974), it might be

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conjectured that corallimorpharians rely mainly or exclusively on zooxanthellae for their nutrition, as has been suggested for xeniid alcyonarians (Gohar, 1940). However, one of us (WMH) has observed three species of zooxanthellae-containing corallimorpharians on the Great Barrier Reef, Australia, envelop large animal prey with their expanded oral discs. The edge of the disc folds upward and closes over the prey, entrapping the food and sea water in a sac that draws tightly closed above the mouth (Fig. 1). Such a feeding mechanism has not been recorded among coelenterate polyps, and is apparently associated with the absence of ectodermal nematocysts over most of the oral disc of these animals.

In all three species, as the food capture sequence begins, the animal is distended with water and the mouth is tightly closed to maintain turgor (Fig. 1A, 1B). As the center of the oral disc is pulled downward by the retractor muscles of the mesenteries, water is pushed outward to the edges of the oral disc. Simultaneously, the radial muscles of the disc contract at the periphery, raising the rim and resulting in a bowl-shaped animal (Fig. 1C). Then the circular muscles of the upper column contract to produce a drawstring effect (Fig. 1D). The retractors continue to contract until the

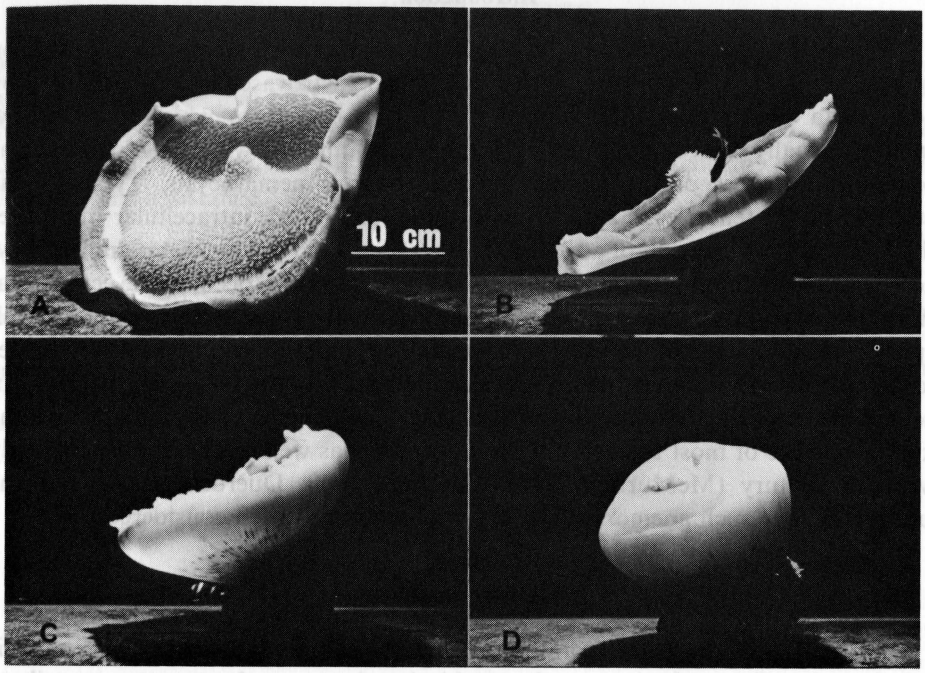

Fig. 1. Feeding sequence of *Amplexidiscus fenestrafer*.
(A) Expanded oral disc, showing tentacle-free circular "window" near periphery, and oral cone.
(B) Side view of expanded disc.
(C) Closure one-third complete, one second after stimulation of oral disc. Note anemonefish *Amphiprion akindynos* to left of rock.
(D) Complete closure three seconds after stimulation.

mouth has been pulled down nearly to the level of the pedal disc and there is little space within the gastrovascular cavity. However, by then a large volume is contained by the oral disc. Only after the edges of the disc have been drawn tightly together can the mouth be opened. Once the prey and water are swallowed, the oral disc reopens. All three species of corallimorpharians that we know to capture prey by this means live in quiet, often turbid waters in the lee of islands or in relatively quiet waters on the lagoon side of coral reefs where plankton and drifting detritus are abundant.

Although the three species capture prey in a similar manner, the rate of closure differs. The smallest species, *Actinodiscus fungiformis* (Verrill, 1870), which attains a maximum oral disc diameter of 25 mm, envelops food particles rather slowly in the aquarium, with closure times of about one minute. Nonetheless, this species can capture adult *Artemia*. Specimens of *Rhodactis howesii* Saville-Kent, 1893, having expanded oral disc diameters of 80–100 mm, close completely in an average of 45 sec when fed in the field on pieces of crushed hermit crab. However, some of the anemones are more sensitive than others to food; some do not react at all. At night, when diving lights attract zooplankton to the anemones, they can close within 10–15 sec. Zooplankton appears to be a major component of the natural diet of *R. howesii* (WMH, unpublished observation). [Voucher specimens of both species have been deposited in the collection of the Department of Invertebrate Zoology, California Academy of Sciences; their catalog numbers are 008951 and 008952, respectively.]

The largest species has recently been described as *Amplexidiscus fenestrafer* Dunn and Hamner, 1980 (Fig. 1). Although the rarest, it was the most thoroughly studied of the three, all of which belong to the family Actinodiscidae. The sparse marginal tentacles contain ectodermal nematocysts whereas distinct, dense discal tentacles lack ectodermal nematocysts. A 10–20 mm wide tentacle-free band separates the discal tentacles into an outer section about 10 mm wide and an inner field extending nearly to the mouth (Fig. 1A), but the tentacles in the two regions are histologically identical. The disc of this large species can close completely within three seconds, engulfing prey and up to four liters of sea water. Closure times in the laboratory are somwhat variable and appear to depend partly on the nature of the food and the physiological state of the anemone (WMH, unpublished observation). This species feeds on a wide range of foods in the laboratory, from zooplankton (adult *Artemia*; sergestid shrimp, *Acetes sibogae*) to large prawns and fishes. Indeed, any moving object that contacts the oral disc elicits closure, and the type and size of prey seem limited only by the sensitivity and the size of the disc, and the speed of closure. *Acetes* shrimp react to envelopment by the oral disc with a darting escape response, moving toward the translucent tentacle-free band. They accumulate along this "window," which seemingly appears to present them with an exit. It is also possible that prey organisms are kept from the opening formed by the edges of the oral disc through the action of the nematocysts in the marginal tentacles.

Exactly how the prey is subdued remains enigmatic. After the closure of the oral disc sac, *Rhodactis howesii* extrudes mesenterial filaments through its mouth and through ruptures in the tips of the discal tentacles (WMH, unpublished observation).

The filaments contain dense concentrations of very large holotrichous isorhizas, as well as smaller holotrichs and microbasic p-mastigophores. Threads of the large holotrichs are several centimenters long. These nematocysts could fire into prey while it is still in the oral disc sac. Mesenterial filaments of *Amplexidiscus fenestrafer* are not extruded into the oral disc sac. Mucus which enters the sac from the gastrovascular cavity during feeding contains fired holotrichs, but it is not clear if these affect the prey since prey organisms continue swimming in the sac or crawling across the oral disc for 10–20 min after envelopment. Thereafter, all motor activity ceases and the prey is swallowed. Other fishes and shrimps in the aquarium are not harmed when the corallimorpharian reopens and the fluid from the oral disc sac is released into the water of the noncirculating aquarium used for feeding trials, nor do successive feedings foul the aquarium. Brine shrimp challenged by fluid taken from the oral disc sac at intervals during a feeding sequence show that a factor inhibiting locomotion is released about ten minutes after envelopment. If left overnight in this fluid, brine shrimp recover, but fishes subdued within the oral disc sac generally do not, even if removed after 15 min to a clean, aerated tank. The toxic agent apparently affects vertebrates more seriously than it does invertebrates. The endodermal nematocysts of the oral disc and mesenteries probably play an important role in killing and digesting prey once it is swallowed.

In the laboratory, when anemonefishes of the genera *Amphiprion* and *Premnas* are deprived of host actinians, they will approach specimens of the large corallimorpharian *Amplexidiscus fenestrafer*. Generally, the fishes hover over or behind the anemone (Fig. 1B, 1C) rather than bathe in the tentacles or rub sideways across the oral disc, as is common with their actinian hosts. Since contact results in immediate closure of the oral disc, such behavior usually can be exhibited only once. Two specimens of *A. fenestrafer* were used in feeding experiments. Between them, they ate one individual of each of five species of anemonefishes (*Amphiprion akindynos, A. chrysopterus, A. melanopus, A. perideraion* and *A. rubrocinctus*) and two of another species (*Premnas biaculeatus*) when they were deprived of their host anemones, all captures occurring at night. Anemonefishes reportedly remain inactive in the host's tentacles at night (Allen, 1972).

The superficial resemblance between members of the family Actinodiscidae and some members of the true sea anemone family "Stoichactidae" (most members of which host symbiotic pomacentrid fishes) led taxonomists at one time to classify both in the genus *Discosoma* (Carlgren, 1949). While recognizing that captive anemonefishes lacking a normal host actinian will establish territories in streams of air bubbles, filamentous algae, etc. (Mariscal, 1970), we suggest that *Amplexidiscus fenestrafer* may be a lethal mimic of the large anemones belonging to genus "*Stoichactis*", since anemonefishes apparently locate suitable actinian hosts by visual means (Mariscal, 1970). We do not know if anemonefishes are captured in nature, but since the availability of host anemones may limit population size (Allen, 1972), juveniles might routinely be attracted to corallimorpharians. Several species of actinians that may harbor anemonefishes occur in the same habitat as *A. fenestrafer,*

and specimens of these two sorts of anthozoans have been seen within 15 m of one another (WMH, DFD, personal observations).

This mode of feeding (and the possible mimicry) are probably confined to the family Actinodiscidae since the tentacles of members of the other two families within the order contain powerful batteries of nematocysts. We add another group to the short list of marine invertebrates known to capture prey by envelopment (McLean, 1962; Hurst, 1968).

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