

Observations on the wentletrap *Epitonium clathratulum* (Kanmacher, 1797) (Prosobranchia, Epitoniidae) and the sea anemone *Bunodosoma biscayensis* (Fischer, 1874) (Actiniaria, Actiniidae)

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A review is given of the most important literature on parasite/host (or predator/prey) relations of Epitoniidae and Anthozoa, and various modes of feeding are mentioned. An as yet unreported association of the wentletrap *Epitonium clathratulum* and the sea anemone *Bunodosoma biscayensis* is described. Both species were collected at Plage d'Ilbarritz, Côte Basque, SW. France. Field and aquarium observations suggest that *E. clathratulum* feeds on partly digested food in the gastric cavity of its host-anemone. This is achieved in a way as yet unprecedented: the wentletrap climbs the oral disc of its host and introduces its proboscis through the mouth slit into the gastric cavity to feed. The sequence of climbing the host and feeding is described and depicted.

Key words: Gastropoda, Prosobranchia, Epitoniidae, *Epitonium clathratulum*, Actiniaria, Actiniidae, *Bunodosoma biscayensis*, nematocysts, parasite/host relation, France.

INTRODUCTION

Associated occurrence of a species of wentletrap (*Epitonium tinctum* Carpenter, 1864) and sea anemones was already incidentally mentioned in the literature by Strong in 1930 (p. 186), whereas Ankel (1938: 8) seems to have been the first to mention a species [*E. clathrus* (Linnaeus, 1758)] to feed upon these Cnidaria. He reported to have found both actinian nematocysts and zooxanthellae in specimens from Naples (Italy) and Kristineberg (Sweden)¹. A few years later another species, *Habea inazawai* Kuroda, 1943, was described as "semi-parasitic" on the actinian *Diadumene luciae* (Verrill, 1898) (Habe, 1943). Thorson (1975), basing himself on the above-mentioned reports and on personal observations on *Opalia crenimarginata* (Dall, 1917), also a wentletrap, thereupon suggested that the whole family Epitoniidae is "more or less adapted to a parasitic mode of life". Thorson's nicely illustrated paper stimulated further research, first of all by Robertson, who, in a number of elucidating papers, added more to our knowledge on the subject than any other single author. As a result the Epitoniidae are now well-known as associates and temporary parasites/micropredators of Actiniaria (sea anemones proper), and to a lesser degree of Zoantharia (encrusting anemones) and Scleractinia (stony corals). A single species, viz., *Epitonium indianorum* (Carpenter, 1864), is known to appreciate Ceriantharia as food (Shimek, 1986: 173), although it is also found associated with Actiniaria (cf. next page).

¹ There is no reason to doubt Ankel's statement about the nematocysts, but this author is almost certainly in error as concerns the presence of zooxanthellae in specimens from Kristineberg. No actinian species with zooxanthellae occurs in Swedish waters.

Robertson (1963: 58) some 25 years ago already mentioned that the number of species of Epitoniidae amounted to several hundred, and currently new species are still regularly described; Kilburn, e.g., as recently as 1985, added no less than 37 species, whereas Bouchet & Warén (1986) added another 12. It is therefore not surprising that new associations are also reported regularly (most recently: Fretter & Graham, 1982: 387; Kilburn & Rippey, 1982: 78; Robertson, 1983a; Robertson & Schutt, 1984; Sabelli & Taviani, 1984; Kilburn, 1985: 295, 326, 331; Bouchet & Warén, 1986: 523, 532), but in spite of this nothing, or very little only, is known about the biology and hosts of the great majority of species. However, from the available knowledge it is obvious that the relation between snail and prey/host(s) may vary a good deal from one species to another.

Epitonium albidum (d'Orbigny, 1842), in the Caribbean exclusively found associated with the large sea anemone *Stichodactyla helianthus* (Ellis, 1767)², has been observed to feed on the peripheral tentacles, on the column (by nipping off little pieces of tissue), and, less commonly, on mucus of its host (Robertson, 1983b: 4). A similar way of feeding was observed in *E. rupicola* (Kurz, 1860) (Robertson, 1963: 55), and is possibly also employed by species feeding upon the outer surface of solitary corals, such as *E. ulu* Pilsbry, 1921 (Bosch, 1965; Robertson, 1970: 45-46). Another species, *E. millecostatum* (Pease, 1860-1861) seems to feed exclusively on ectodermal mucus of its host, *Palythoa* spec., a colonial zoanthid (Robertson, 1981: 14). Other species, such as the Californian *E. tinctum* (Carpenter, 1864) [best known hosts: *Anthopleura elegantissima* (Brandt, 1835) and *A. xanthogrammica* (Brandt, 1835)] and *E. indianorum* (best known hosts: *Tealia crassicornis* and *T. lofotensis*, both sensu Hand, 1955)³ appear to feed predominantly on the tentacles of their hosts⁴, and to a lesser degree on columnar verrucae (Salo, 1977). The Caribbean *E. echinocostatum* (d'Orbigny, 1842) described to live associated with the actinian *Bunodeopsis globulifera* (Duchassaing, 1850)⁵, on the leaves of turtle grass *Thalassia testudinum* (Banks ex König, 1805), has been observed to feed exclusively on the tentacles of its quarry (Robertson, 1983a).

As mentioned above, the relation of Epitoniidae and their cnidarian associates is often referred to as parasitism (the snails being regarded as parasites). Some authors, however, avoid this term and prefer to speak of predation (and predator), whereas others use both terms more or less indifferently, as if it is difficult to decide which is most suitable. If anything, this indicates that the mode of feeding in Epitoniidae apparently represents a marginal case of parasitism only, if to be regarded as such.

Speaking in general, the gamut of life-styles/feeding-strategies ranging from super-

² Although this species is generally known as *Stichodactyla* (= *Stoichactis*) *helianthus* (Ellis, 1767), it should in fact be referred to as *S. anemone* (Ellis, 1767). Both species were figured by Ellis (1767; 436, pl. 19) and later on supplemented with a very brief description (Ellis & Solander, 1786: 6). Duchassaing & Michelotti, 1866: 122(28), already suggested this synonymy and McMurrich (1889: 37), acting as the first reviser, selected *anemone* as the specific name (see also McMurrich, 1905: 10).

³ In a recent paper (Den Hartog, 1986: 87) I have discussed that this species should be re-named, as it is not identical with the Atlantic *T. lofotensis* (Danielssen, 1890) [presently regarded a junior synonym of *Urticina eques* (Gosse, 1860)].

⁴ For a beautiful picture of *E. tinctum* in the act of feeding see Sisson (1986: 255-256).

⁵ The genus *Bunodeopsis* Andres, 1880, is in need of revision. With the present state of knowledge it is difficult to decide whether one, two, or more species of *Bunodeopsis* occur in the Caribbean. Robertson's figure of the species (1983a: 100, fig. 1) conforms best to the form/species described as *Bunodeopsis antillensis* Duerden, 1897 (pp. 7-11, pl. 1 figs. 1-2; cf. also Duerden, 1898: 455-456).

predator to the most advanced examples of obligate parasitism is so gradual and diverse, with so many exceptional cases, that it seems almost impossible and not always meaningful to delimit both phenomena (and indeed, what else is parasitism than a specialized form of predation). As a consequence it is practically impossible to give a definition of parasitism acceptable to everyone, and marginal cases therefore will probably always give rise to disputes. An interesting case illustrating the problems is presented by *E. greenlandicum* (Perry, 1811). This species has been observed in situ to forage upon small sea anemones, *Gonactinia prolifera* (M. Sars, 1835), which are swallowed whole, but under experimental conditions it showed a preference for a much larger anemone species, viz., *Metridium senile* (Linnaeus, 1767), acting as an ectoparasite/micropredator, and, like *E. albidum*, nipping off pieces of columnar tissue (Salo, 1977).

If parasitism is simply defined, as often done in practice, as an association in which one component (the parasite) lives at the expense of another (the host), without killing it (or only doing so in the long term) [as opposed to predation *sensu stricto*, in which the other component (now called prey) is killed], many Epitoniidae may indeed be referred to as parasites, or more specifically: temporary ectoparasites, even if the association often seems to represent hardly more than a monophagous diet. However, in a number of species there is definitely a tendency to stick or to keep close to one and the same host specimen, and at least some species are known to attach their egg capsules to their host.

The mode of feeding of the Californian *Opalia crenimarginata* seems to be of a different character than the examples mentioned above. Thorson (1957: 56-57) described this species to parasitize the anemone *Anthopleura xanthogrammica*, the snail piercing the body-wall of its host, introducing its long proboscis, and subsequently sitting "quietly sucking for hours or even days". In particular Thorson's statement that the whole proboscis is sometimes introduced, suggests strongly that it actually perforates the body-wall and enters the gastric cavity [and not that it is simply pushed into the body-wall, to suck up body fluids (cf. Bandel, 1984: 63)]. Therefore, it seems quite possible that *O. crenimarginata* in fact feeds selectively on the internal tissues of its hosts (gonads?) or otherwise on mucus and/or predigested food. If so, it may be argued that this species feeds endoparasitically, without, however, being a true endoparasite, which according to the generally held conception lives within its host. Conclusive proof or otherwise of the alleged endo-gastric feeding activities of *O. crenimarginata* may be obtained by studies of the gut contents of this common Californian wentletrap.

Information most suggestive of a true endoparasitic relationship between an unidentified species of *Epitonium* and a solitary zoanthid [possibly *Sphenopus marsupialis* (Gmelin, 1788)] was presented by Zann (1980: 132) in the form of a photograph of a dissected polyp containing a wentletrap. The caption reads: "Parasitic *Epitonium in situ* in a zoanthid". To my knowledge no scientific account on this most interesting case of parasitism has yet been published.

FIELD OBSERVATIONS ON EPITONIUM CLATHRATULUM AND STUDY OF PRESERVED SPECIMENS

In August 1985 I paid a visit to the French Côte Basque where a species of sea anemone, viz., *Bunodosoma biscayensis* (Fischer), described in 1874, and never reported



Fig. 1. Plage d'Ilbarritz. Locality where *Epitonium clathratulum* and *Bunodosoma biscayensis* were found in the same habitat.

since, was rediscovered (Den Hartog, 1987). This anemone proved to be particularly common at Plage d'Ilbarritz, situated between Biarritz and Bidart. At this locality there is a sandy beach with significant intertidal rock formations, partly sand covered, with pools, gullies, crevices and cracks (fig. 1), often fringed by dense carpets of young mussels, *Mytilus edulis* L., 1758 (fig. 2). On 19, 20 and 23 July 1986 I paid another visit to this locality for further field study and to collect additional specimens. Extracting anemones from the sand-filled crevices I incidentally found ten live specimens of *Epitonium clathratulum* (Kanmacher, 1797)⁶ (fig. 3). This suggested a relation between the anemones and the wentletrap, although I did not find a single snail attached to an anemone. As no specific data were available on food and feeding habits of *E. clathratulum* (cf. Fretter & Graham, 1982: 390), it seemed of interest to pay some further attention to this species. Three specimens were kept alive, brought along to Leiden and transferred to an aquarium tank containing a variety of actinians. Unfortunately I almost immediately lost track of them, so that initially no further observations were

⁶ Identification confirmed by Messrs. A. Verduin, Leiden, and M.S.S. Lavaleye, Soest. I add the following note. Fretter & Graham (1982: 390) stated the number of axial ribs in *E. clathratulum* to vary from 18 to 22. In the Ilbarritz specimens, however, the number is considerably less, amounting from c. 11-14 on the last whorl. Although the number of axial ribs apparently may vary considerably in species of *Epitonium* (cf. e.g. Robertson, 1983d; Kilburn, 1985) I find the discrepancy between the ranges mentioned above too large to pass by unnoticed.

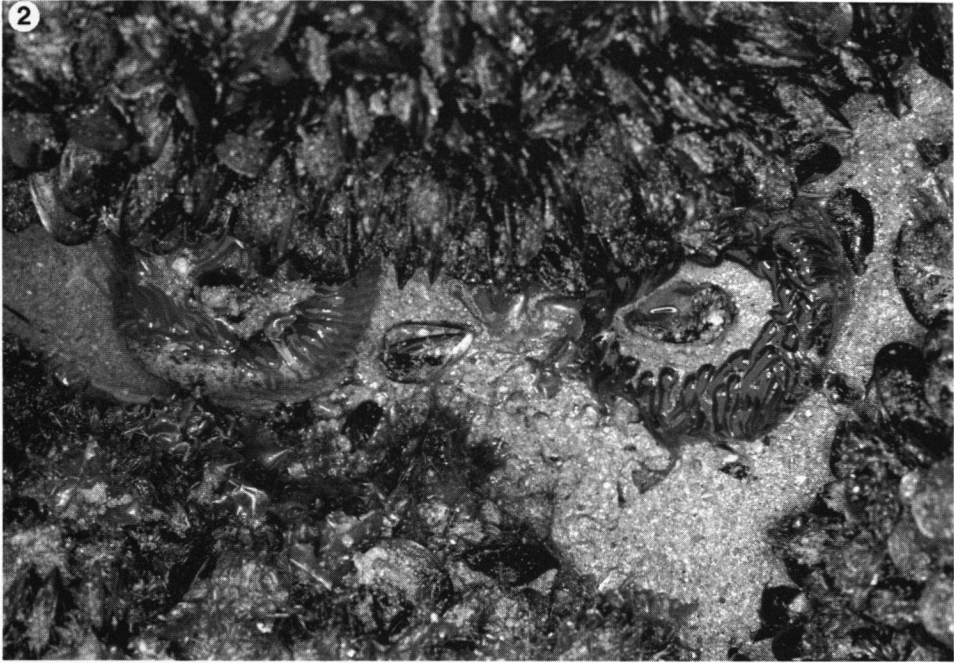


Fig. 2. *Bunodosoma biscayensis*. Two individuals in their natural habitat during ebb tide, a sand filled crevice fringed with young *Mytilus edulis* (note empty shells).

made. Seven specimens were preserved in alcohol for later study. Three of these, plus attached egg-capsules were deposited in the Rijksmuseum van Natuurlijke Historie as voucher specimens (RMNH Mollusca alc. 9200). The remaining four specimens were dissected to investigate their gut contents. Two appeared all but empty, but the gut of the other two contained sparse numbers of well preserved actiniarian nematocysts of the following types (average and range in μm ; n = number of capsules measured): small spirulae [14.3 (12.6-16.2) \times 1.8 (1.8-2.0); n = 20], large spirulae (27.9 \times 5.0, 37.8 \times 6.3, 41.4 \times 6.3; n = 3), penicilli A [20.5(18.0-22.5) \times 4.8(4.1-5.4); n = 15] and penicilli B₁ [16.2(14.4-18.0) \times 3.1(2.9-3.5); n = 50]. This result seemed to indicate that *E. clathratulum*, like many of its congeners, feeds indeed upon Actiniaria. The variety of nematocysts found conforms to that present in the filaments of *Bunodosoma biscayensis* [cf. Den Hartog, in press: tab. 1 (5a,b,d,e)]. That no long fibre-like spirulae [ca. 40(36-49) \times 1.8(1.6-2.0); Den Hartog, l.c.: tab. 1 (5c)] were noted may be due to both the relative scarcity of these cnidae and the fact that they are easily overlooked, even in squash preparations of fresh anemone tissue. In particular the relative abundance of penicilli B₁, of a type characteristic of the filaments of several Endomyaria, and more particularly species of Actiniidae, strongly suggests that *B. biscayensis* served as prey/host. Incidentally, these cnidae are uncommon, rare or even absent in other species of Actiniidae co-existing with *B. biscayensis* in the same habitat,



Fig. 3. *Bundosoma biscayensis*. Expanded individual in a small tidal pool with individual of *Epitonium clathratulum* (in situ photograph, not arranged).

viz., *Bunodactis verrucosa* (Pennant, 1777), "*B.*" *rubripunctata* (Grube, 1840), and *Actinia equina* (Linnaeus, 1758) sensu lato (i.e., including *A. fragacea* Tugwell, 1856).

The presence of nematocysts derived from *B. biscayensis* in the gut of two dissected wentletraps at least proves that tissue and/or mucus of this species is accepted as food. It does, of course, not reveal anything in terms of food preference, first of all as it might simply reflect that *B. biscayensis* happens to be the most common and most sizeable actinian at Plage d'Ilbarritz. It may further be stated that *E. clathratulum* certainly is not host-specific (or monophagous at the specific level) as its area of distribution and bathymetrical range do not correspond to those of *B. biscayensis*. The former ranges from the western Mediterranean, northward to Norway and Kattegat (Fretter & Graham, 1982: 390), occurring in the intertidal zone and down to over a hundred metres depth (Bouchet & Warén, 1985: 515, 112 m; Fretter & Graham, l.c., give a bathymetrical range of 30-100 m), whereas the latter is exclusively known from the intertidal zone of south-western France. Perhaps more interesting therefore than establishing that the nematocysts found in the wentletraps derive from *B. biscayensis*, seemed the fact that these derive exclusively from the filaments, and their limited numbers. If the wentletraps had non-selectively consumed anemone tissue, a

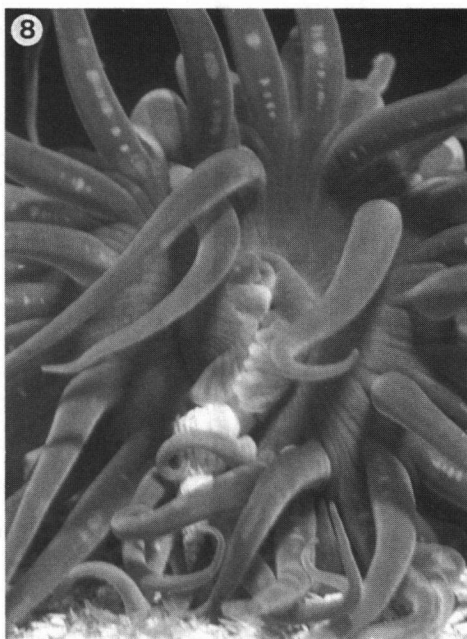
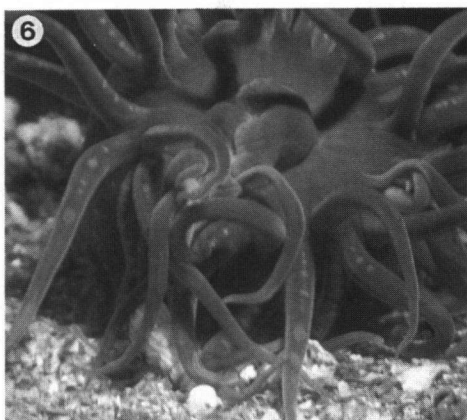
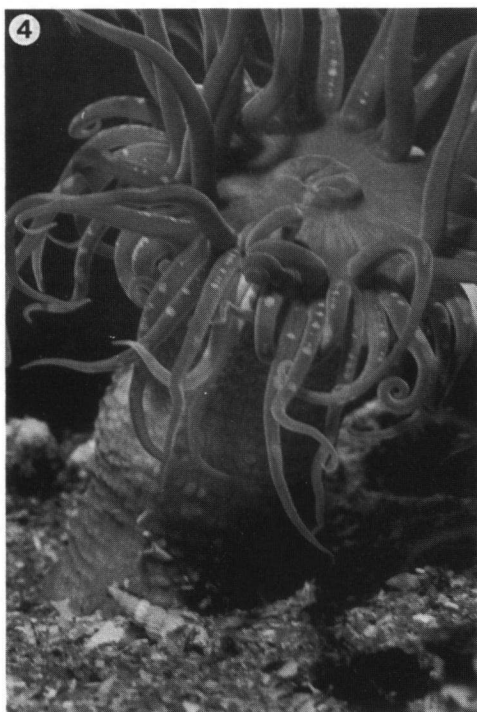
nematocyst range corresponding to that of column and tentacles (spirocysts!) would have seemed more plausible, and in addition one would have expected much higher rates of cnidae [comparable to, or even higher (due to concentration) than those found in random preparations of fresh anemone tissue]. A likely explanation for this discrepancy seemed to be that the snails dissected did not primarily feed upon the anemones themselves, but possibly on mucus-boluses such as are regularly ejected by sea anemones after feeding and digestion. These boluses, extruded from the gastric cavity through the mouth, generally contain partly digested and non-digestible matter, and are often contaminated with nematocysts and/or small fragments of filament. This hypothesis, therefore, would explain both the unexpectedly low number of nematocysts found in the dissected snails and the apparent fact that these derive exclusively from the filaments. As mentioned above, other species of Epitoniidae have also been reported to consume anthozoan mucus. Referring to the case of *Opalia crenimarginata*, another possibility might be that *E. clathratulum* feeds endoparasitically on predigested food or mucus present in the gastric cavity of its host(s), or on endo-gastric tissues, first of all the nutritious gonads. As gonads and filaments run parallel and close to each other along the free edge of the anemone's mesenteries, a diet of gonadal tissue might certainly imply the chance of contamination with low concentrations of filamental nematocysts. If not actually entering its host to feed, access to the gastric cavity might be achieved if the wentletrap snail could, possibly in conformity with *Opalina crenimarginata*, pierce its host's column-wall, introduce its proboscis, and feed selectively on whatever it prefers.

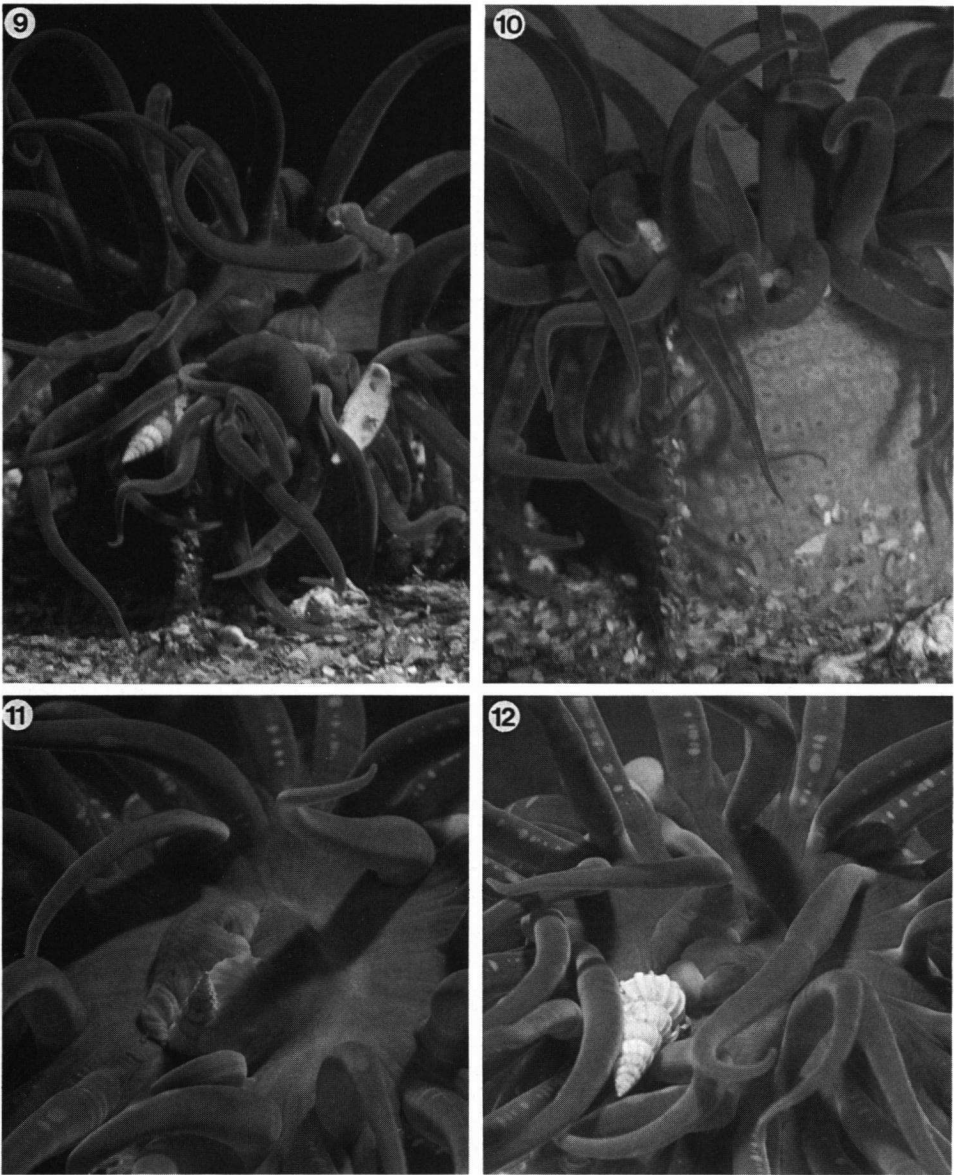
AQUARIUM OBSERVATIONS

Aquarium observations made more than three months after collecting the wentletraps partly answered the above-mentioned questions. I had not seen the snails since I had released them in the aquarium tank, but on 9 November 1986, I observed one individual sunken halfway into the mouth slit of a specimen of *Bunodosoma biscayensis*. To check whether it was feeding, or in fact being swallowed by the anemone, I cautiously removed it, which revealed a large swollen proboscis, at least as long as the shell, showing that it was indeed feeding. Some 15 minutes after I had placed the snail again on the sand close to the anemone, I once more found it on the anemone's oral disc, between the tentacles, and a little later it had again positioned itself in the mouth slit. About one hour later I noticed that it lay quietly on the naked part of the oral disc, proboscis retracted and operculum closed, and after another hour I found it lying on the bottom near the anemone's base. The observations were made two days after I had fed the anemone(s) with abundant fresh mussel flesh (*Mytilus edulis*) following a long period (4-6 weeks) of starvation.

Once located, it was easy to keep track of this particular wentletrap. When not feeding it was invariably to be found in the sand around the base of the anemone, c. 2 to 3 cm distant from it. Usually the snail was entirely hidden, but occasionally the tip of the shell emerged from the sand. Incidentally, I also found the empty shell of one of the other two snails released in the aquarium at the base of this particular anemone.

I soon found out that the snail usually emerged from the sand shortly after I had fed the anemones, mostly within 10 or 15 minutes, and that it invariably attacked and climbed the same anemone. A few times the snail showed no perceptible reaction when





Figs. 4-12. *Epitonium clathratulum*. Sequence of climbing and feeding on an individual of *Bunodosoma biscayensis* (length of wentletrap shell 16 mm). 4. Snail emerging from the sand at the base of the anemone. 5-8. Following semi-contraction of the anemone and bending over of its oral disc, the snail climbs the anemone and reaches the mouth slit in a tangle of tentacles. 9-10. The anemone subsequently elongates and re-assumes its erect posture, lifting up the snail (note the gravel-covered mucus string, cf. figs. 7,9-10). 11. The snail settles in the mouth slit, sunken halfway into the stomodaeum, in order to feed. 12. The snail having retreated from the mouth after feeding.

its host was fed or only moved a little, and occasionally it reacted by emerging from the sand, however, without climbing its host. These variable reactions were undoubtedly correlated with the frequency of feeding and the appetite of the snail.

Three times I observed the process of climbing and feeding from the beginning to the end, but in spite of this, I missed several details. On 12 December 1986 I made the following observations (figs. 4-12). About 10 minutes after feeding the anemone, the wentletrap emerged from the sand (figs. 4, 5) and moved towards the column of the anemone. Upon contact (what exactly happened I was unable to see but possibly the snail got grip of one of the tentacles) the anemone reacted by semi-contracting the column and bending over the expanded oral disc towards the wentletrap (fig. 6). The oral disc remained expanded, but especially the peripheral part and the tentacles near the wentletrap were seen to experience sudden convulsions so that the tentacles became loosely "tangled". In this "tangle" the wentletrap somehow succeeded to climb the oral disc and to reach the mouth, but it was impossible to observe this action in full detail (figs. 7-8). Some time after the snail had reached the oral disc, the anemone re-assumed its more or less erect posture, thus lifting up the snail (figs. 9-10). This process of contacting the anemone and reaching its oral disc took (this time) about 30 minutes. The snail now positioned itself in one of the corners of the mouth slit, partly enveloped by the protruding stomodaeum wall (fig. 11) and apparently fed. After another 30 minutes it moved out of the mouth slit and I saw how its everted proboscis was being retracted. The snail subsequently lost its grip (fig. 12), slid from the anemone's disc, dropped on the sand and entrenched itself within a few minutes.

During the process of climbing the oral disc I noticed that a mucus thread was formed by the snail with adherent shell gravel, but I was not able to discern whether the formation of this thread represented an artefact or in some way formed part of the snail's strategy to climb its host. I twice more observed such a sticky, gravel-covered string running from the bottom near the anemone's base to the periphery of the oral disc, which could have been the result of unnoticed feeding activities of the snail. Initially not having been alert to this phenomenon, I may have overlooked it on previous occasions. Further observations on the occurrence of this phenomenon are therefore necessary. In this context it is noticeable that Guinther (cf. Hadfield, 1976: 136), referring to *E. ulu*, observed that "the snails apparently never crawl directly on the flesh of the coral, but rather move about the inverted basal area of the coral on a grid of secreted mucus strands which are cemented to the coral skeleton". Tough mucous filaments are also excreted by Epitoniidae to keep egg capsules together (cf. e.g. Thorson, 1975: 55; Robertson, 1983a: 101; 1983b: 5-6) and to connect egg masses to the host [cf. Strong, 1930: 186; Bosch, 1965: fig. 1; Sabelli & Taviani, 1984: 93; Mr. B. Hoeksema, Leiden (personal communication) observed this for an unidentified species of *Epitonium* and five species of *Fungia* in South-west Sulawesi, Indonesia].

Other details of mounting and feeding activities in *E. clathratulum* were occasionally observed. I once saw how the snail emerged from the sand and, sitting near the base of the anemone, made probing, brandishing movements (cf. Salo, 197: 169) with its everted proboscis, as if it tried to get hold of a tentacle. For some reason, however, it interrupted this behaviour, and, without even having touched the anemone, again entrenched itself in the sand. A few times I found the snail quietly lying on the anemone's oral disc, with closed operculum, and on one occasion (18 November) it seemed to have stayed there for a whole day. On that date, I found it at 9 AM feeding in the mouth slit. Half an hour later this situation had not changed. When I looked again at

8.30 PM it was lying unattached with closed operculum in the oral disc and it was still there at 10.30 PM when the aquarium lights automatically switched off. A quarter of an hour later, when I switched on the light I found the snail feeding again in the mouth. The next morning it had disappeared. Another noteworthy observation was made on 12 November, when I saw the snail feeding while it was positioned against the lower part of the anemone's semi-contracted column, its foot apparently unattached, but its proboscis, stretched upwards along the column, bent over the margin, and, crossing the distance to the mouth, inserted in the stomodaeum. In this condition the proboscis measured more than twice, possibly three times, the length of the shell, although it may in fact have been overstretched.

Although the snail was several times observed sunken halfway into the host's stomodaeum, it was never observed to enter the gastric cavity. Indeed, this might involve a risk. Added to the fact that a prolonged stay in the gastric cavity would require adaptations to meet with anaerobic or at least low-aerobic conditions, this cavity, subdivided by numerous mesenteries (= sarco-septs) and with blind corners, might form a deadly trap⁷.

During the period of regular feeding (9 November-13 December) the snail showed considerable growth. Unfortunately I neglected to measure its shell on 9 November, but then it certainly did not exceed 12 mm in length. On 12 December, however, it measured 16 mm, i.e., a linear increase of at least 30% within five weeks. Considering that specimens of c. 10-12.5 mm are sexually mature (such specimens were collected in the field with egg-capsules) this increase seems noteworthy and makes further observations desirable. Rapid growth rates were previously reported by Bosch (1965: 267), Guinther (1970; cf. also Robertson, 1970: 46; 1983c: 60) and Taylor (1977: 258) for *E. ulu*. Bosch and Guinther made observations suggesting that in this species the time required to develop from the larval stage into sexual maturity does not exceed more than two or three weeks. A well documented paper concerning another fast growing species, *E. albidum*, was published by Robertson (1983c).

I will conclude this section with a note on *E. clathratulum*. After I had observed the above live snail for the last time on 4 January 1987, I searched the sand surrounding its usual host-individual on 16 March and found its empty shell, then 17 mm long (RMNH Mollusca alc. 9200).

DISCUSSION AND CONCLUSIONS

If the alleged endo-gastric way of feeding in *Opalia crenimarginata* still needs definite proof, it appears from the above information that there is hardly any doubt in the case of *E. clathratulum*. The observations indicate that this wentletrap becomes active and feeds after its host has fed. This behaviour can only mean that the snail is not primarily interested in the tissue of its host but rather in predigested food (and/or mucus, possibly released in the coelenteron during digestive activities). This conclusion is in accordance with the analysis of the gut contents of specimens collected in the field (see above). To what extent the feeding behaviour of *E. clathratulum* may be affected by the

⁷ These difficulties apparently have been successfully overcome by the wentletrap species reported by Zann (1980: 132) from the gastric cavity of *Sphenopus* spec. (cf. page 97) and this species therefore definitely needs further attention.

quality of the diet of its host needs further study. Captive anemones were exclusively fed with *Mytilus edulis*. In the field *M. edulis* (juvenile individuals, from c. 5 to 20 mm long) also represented some 90% of the food items found in the gastric cavity of *Bunodosoma biscayensis* (cf. fig. 2); in addition I found remains of crabs. In spite of this, the specimen of *E. clathratulum* on which the present study was mainly based, was never observed to accept or to be attracted by freshly offered mussel flesh.

In conclusion, although many details are as yet unclear, it is obvious that the observed mode of feeding of *E. clathratulum*, i.e., through the mouth opening of its host, extends the known feeding strategies within the family Epitoniidae with an interesting case⁸.

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⁸ Robertson & Schutt (1984) present a photograph somewhat suggestive of a similar way of feeding in "*Epitonium*" *billeeanum* (Dushane & Bratcher, 1965). The authors, however, explicitly mention that this species feeds by nipping off pieces of coral tissue.

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ADDENDA (November, 1987)

In July/August 1987 the locality at Plage d'Ilbarritz was visited again to collect additional specimens of *E. clathratulum*. On 24 July, with incoming tide, I found five individuals, including one small and two large snails attached to a bunch of egg-capsules. The next day, at low tide, and within two hours, no fewer than 95 individuals were collected. Most snails were found in shallow *Mytilus*-fringed pools and crevices (cf. p. 98), without exception in sand, close to the base of *B. biscayensis*, although *Actinia equina* s.l. and "*Bunodactis*"

rubripunctata coexisted in significant numbers. In these pools, about one in five or six *B. biscayensis* was found to be associated with *E. clathratulum*. A few more wentletraps were found in moist crevices and in large, deeper pools. Usually only one or two wentletraps were found close to one anemone, sometimes attached to solid substrate by a tough, elastic filament. Six times I found a bunch of egg-capsules, united by such elastic filaments and associated with one to three large, and one or more small (males?; cf. Robertson, 1983: 5) wentletraps. One bunch yielded an exceptional number of ten individuals.

All snails and egg-masses collected were preserved for later study (RMNH Mollusca alc. 9211). Upon preservation the body part contained in the second whorl, the region of the hypobranchial gland, stained purple. Emission of a purple dye secreted by this gland represents a general defense mechanism in Epitonidae (cf. e.g. Kilburn & Rippey, 1982: 77), but I never observed emission of this purple dye in *E. clathratulum*.

On 1 August, I collected at low tide another 40 to 50 wentletraps (and several bunches of egg-capsules) that were kept alive and transported to Leiden for further observation. Among these wentletraps I found one individual belonging to another species, viz. *Opalia crenata* (Linnaeus, 1758) described by Albergoni et al. (1970) from the Mediterranean coast of Spain as a parasite of the sea anemone *Anemonia viridis* (Forskål, 1775) (= *A. sulcata* Pennant, 1777).

Aquarium observations in August and September confirmed most observations described above. I regularly observed individuals of *E. clathratulum* (occasionally two at a time) lying on the oral disc of *B. biscayensis*, or situated in the mouth slit. Although both field and aquarium observations indicate a distinct preference of the species for *B. biscayensis*, I observed in the aquarium tank that "*Bunodactis*" *rubripunctata* and the Caribbean *Bunodosoma granuliferum* (Lesueur, 1817) were also visited occasionally, and I once noticed an individual in the mouth slit of *A. equina*.

The clear correlation suggested to exist between feeding of anemones and activation of *E. clathratulum* (cf. pp. 101, 105) was not convincingly confirmed, but quantitative data allowing a definitive conclusion were not collected and further studies (under controlled laboratory conditions) are therefore necessary. Pending such studies it seems not entirely sure, though quite possible, that *E. clathratulum* indeed feeds on predigested anemone prey (cf. p. 105). In this connection it is noticeable that I never observed an individual feeding on extruded food rests of anemones. In addition, previous observations that the species does not accept flesh of *Mytilus edulis* (cf. p. 106) were fully confirmed.

The suggestion that climbing the oral disc of a host anemone is effectuated by grasping a tentacle and subsequently being lifted (cf. p. 104; twice) was several times verified by observation. However, this acrobatic performance proved unnecessary with respect to anemones entirely entrenched in the sand or almost so.

The formation of elastic filaments to unite egg-capsules was observed several times, but the formation of such filaments in relation to the act of climbing a host anemone (cf. p. 104) was not observed again and must be considered fortuitous.

In the course of September many wentletraps died and a total of 25 shells, empty or with remains of flesh, were found (RMNH Mollusca alc. 9212). Whereas not a single wentletrap collected in the field between 24 July and 1 August exceeded 13 mm in length, the shells removed from the aquarium had considerably increased in size, to a maximum of 17 mm (cf. p. 105). In the course of October three additional, rather large snails died, and in the end of October only one small and one medium sized individual seemed to have survived. It seems likely that other snails died without emerging from the sand and that some small shells (males?) were overlooked. By mid-November no live snails were seen anymore. The gradual dying of the wentletraps in the aquarium tank may have been due to unfavourable water quality, but it may also have been a usual post-reproductive event, *E. clathratulum* possibly being an annual species. Hence, this phenomenon too seems worthy of further study.

ADDITIONAL REFERENCE

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