

THE TROPICAL WESTERN ATLANTIC
PEROPHORIDAE (ASCIDIACEA)
II. THE GENUS *ECTEINASCIDIA*

Ivan Goodbody and Linda Cole

ABSTRACT

Four species of *Ecteinascidia* occur in the tropical western Atlantic. The characteristics of each species are described and their distribution reviewed. Many characteristics are related to zooid size, although others are independent of size. Three species are common and widespread but the fourth, *Ecteinascidia conklini* Berrill, 1932, is rare and until recently there have been few records of its distribution. *Ecteinascidia minuta* (Berrill, 1932) is closely related to *Ecteinascidia herdmani* Medioni, 1969 from the Mediterranean and further research may show that the two are synonymous.

The general characteristics of the family Perophoridae and its two component genera *Perophora* Wiegmann, 1835 and *Ecteinascidia* Herdman, 1880 were discussed in an earlier paper (Goodbody, 1994). The distinction between the two genera is based primarily on the number of rows of stigmata in the branchial sac, the organization of the alimentary canal, and the form of the testis (Kott, 1985). Most *Perophora* species have only four or five rows of stigmata while *Ecteinascidia* always has more than eight and usually between 12 and 20. In *Perophora* the gut loop is horizontal and the rectum short, while in *Ecteinascidia* the gut loop is more open with a long rectum. In both genera the gonads are situated in the gut loop; in *Perophora* the testis usually has only one or a few testis lobes, while in *Ecteinascidia* there are many pyriform testis lobes, often arranged in a crescent. (For further detail see Goodbody, 1994).

Ecteinascidia is a genus of colonial ascidian occurring exclusively in warm seas, usually, but not always, forming clusters of erect zooids (Plate 1). Zooids are connected to each other posteriorly by a system of vascular stolons from which new blastozooids arise to increase the size of the colony. In a few species, zooids may be recumbent, attached to the substratum by the ventral surface, but connected to one another in the same way by vascular stolons (Plate 1G, H). The differences between species in the genus, particularly those in the western Atlantic, are relatively small and are primarily a function of size, which in turn has ecological implications in relation to habitats occupied by each species. The morphology of the alimentary system, in particular, is similar in all species of this genus. The distinctions are in the form of the stomach and the shape of the intestinal loop. Early descriptions of the genus and its taxonomic position can be found in Herdman (1880, 1882, 1891) and Van Beneden (1887); more recent descriptions are in Plough and Jones (1939), Berrill (1950), and Kott (1985).

The species of *Ecteinascidia* occurring in the western Atlantic are: *Ecteinascidia turbinata* Herdman, 1880, *Ecteinascidia styeloides* (Traustedt, 1882), *Ecteinascidia conklini* Berrill, 1932, and *Ecteinascidia minuta* (Berrill, 1932).

The present work complements previous accounts of these taxa (Plough and Jones, 1939; Van Name, 1945; Monniot, 1972, 1983) by adding new information on details of body muscles, the reproductive system, and habitat. We integrate this new information from field and laboratory investigation with the results of previous studies. The

gross structure of the larva in *Ecteinascidia* is similar in all species and differs only in size and degree of development of larval organs. This will be addressed in a later paper on reproduction.

MATERIALS

Observations reported on in this paper are based on material collected in Belize and Jamaica. The primary study site in Jamaica is the Fort Rocky Lagoon at Port Royal (Goodbody, 1993a, 2003). Study sites in Belize included Pelican Cays (MacIntyre and Rützler, 2000), Twin Cays (Macintyre et al., 2004), and Blue Ground Range (Woodroffe, 1995). Further information is provided in the individual species accounts below. In the following taxonomic accounts, all references to the number of stigmata in a row refer to the number on one side of the branchial sac between the dorsal lamina and the endostyle. All laboratory studies have been backed up by field observations of living animals in Bermuda, Belize, Jamaica, Curaçao, and Bonaire.

Berrill (1932) did not retain type specimens of *E. conklini* or *E. minuta* and none exist. Three immature zooids of *E. minuta* collected in Bermuda by N. J. Berrill in 1932 were located among specimens of *Perophora bermudensis* Berrill, 1932 in the Rijksmuseum in Stockholm (Ref: 1537A; Goodbody, 1994). Because they are isolated immature zooids and not a colony, they are not suitable for describing a neotype.

Ecteinascidia turbinata Herdman, 1880

(Plate 1A, B)

Ecteinascidia turbinata Herdman, 1880: p. 724; 1882: p. 243, Pl. 36 figs.1–6. Berrill, 1932: p. 78; fig.1. Van Name, 1945: p. 169, figs. 85, 86. C. Monniot, 1972: p. 940, fig.1; C. Monniot, 1983: p. 58.

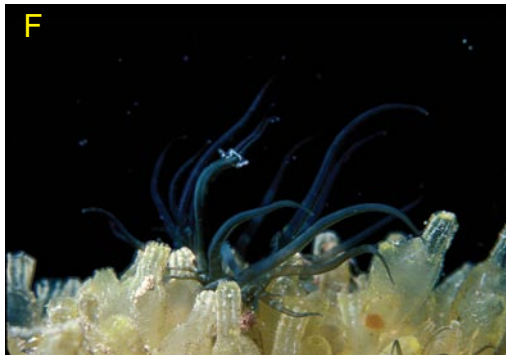
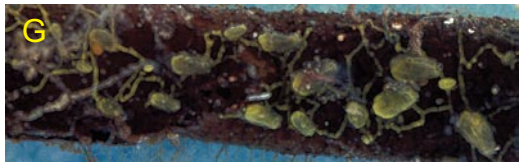
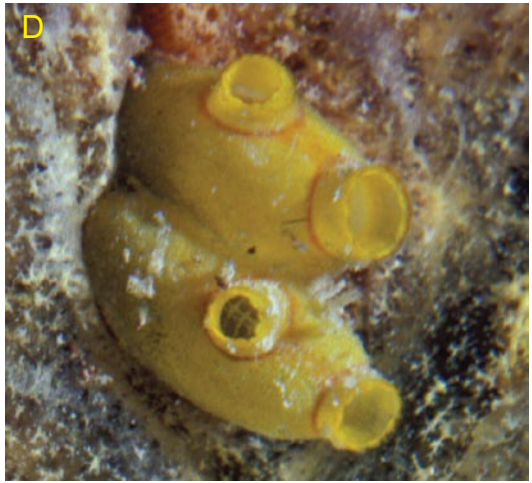
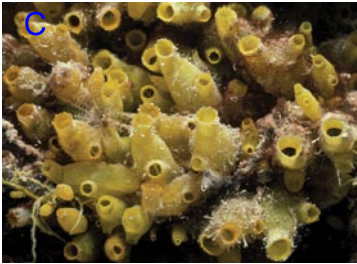
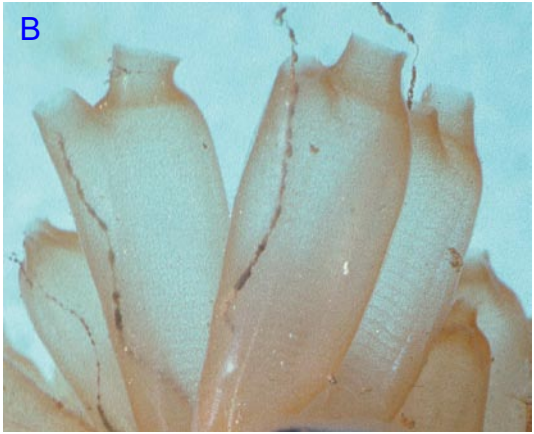
?*Ascidia claviformis* Lesueur, 1823: p. 5; Pl. 1 fig. 3.

Material.—Primarily from the Fort Rocky Lagoon at Port Royal, Jamaica as well as material from the Pelican Cays, Belize.

Colony.—Colonies form closely packed bunches of erect zooids, often of massive size (several hundred zooids) when growing in eutrophic lagoons. In more oligotrophic conditions in open waters, colonies may be small (< 20 zooids). Within the colony, zooids are connected to one another by a system of vascular stolons arising from the posterior end of each zooid.

Zooid.—Zooids are elongate, cylindrical up to 2 cm in length, occasionally longer. They are bright orange in color particularly in the anterior two-thirds of the body. The branchial siphon is anterior and the atrial siphon is very close to it on the dorsal surface. Both siphons have six simple, broad lobes. Unlike other members of the genus, *E. turbinata* lacks red pigment spots between adjacent lobes of the siphon (see below).

Plate 1. (Opposite page) A. Whole colony of *Ecteinascidia turbinata* growing on a mangrove root. B) Individual zooids of *E. turbinata*. The dark strings are fecal material being ejected through the atrial siphon. C) Portion of a colony of *Ecteinascidia conklini* growing in a mat of algae and sponges. D) Individual zooids of *E. conklini* showing the two red rings around the siphons, one at the margin of the opening, the other around the base of the siphon. E) Whole colony of *Ecteinascidia styeloides* growing in an algal mat on a mangrove root. F) Individual zooids of *E. styeloides* showing ribbing on siphons. (The tentacles of an actiniarian are visible in the background). G) A colony of *Ecteinascidia minuta* growing on a panel. H) A colony of *E. minuta* growing among algal filaments. Photography by I. Goodbody.



Body Wall.—Both the test and the parietal body wall are relatively thin and transparent, thus many details of the zooid can be seen through them. The main musculature (Fig. 1A) consists of a series of transverse fibers arising laterally on each side and meeting together across the dorsum. These fibers only cover the dorsal two-thirds of the body wall, leaving the lower third (adjacent to the endostyle) free of muscle. This system of muscles extends from immediately behind the atrial siphon at the level of the third or fourth row of stigmata to about the sixteenth row of stigmata, leaving the posterior half of the zooid relatively free of muscle bands. The longitudinal muscles are poorly developed with only a few fine strands that can be discerned on each side of the main body wall. A system of circular and longitudinal fibers occurs on each siphon and appears to function independently of the main body muscle.

Pharynx.—In fully grown zooids there are up to 35 rows of stigmata and as many as 50 stigmata per row, sometimes 60. In one zooid from Bermuda, 80 stigmata were counted in some rows. Occasionally in large zooids, portions of the branchial wall are imperforate so that some rows of stigmata appear to be incomplete ventrally or dorsally. The dorsal lamina is a membrane supported by a series of ribs continuous with the transverse bars of the branchial sac. These ribs project beyond the membrane as a series of tentacular languets. The membrane itself is about 350 μ high and the ribs and languets are about 700 μ (i.e., they project about 350 μ beyond the membrane). There is no languet at the level of the first branchial bar. Anterior to the first row of stigmata the lamina forms a shallow v-shaped groove (pre-branchial groove) behind the neural gland. The opening of the neural gland has two prominent lips usually oriented transversely to the body axis, but sometimes forming an inverted c-shaped structure. There are usually between 40 and 60 branchial tentacles of three different sizes, about 1.0, 0.5, and 0.25 mm in length.

All species of *Ecteinascidia* have a series of internal longitudinal bars running along the inner face of the branchial sac supported on simple curved papillae. In *E. turbinata* the number of these bars varies with the size of the zooid, and is usually between 18 and 21 bars: for instance, a zooid with 22 rows of stigmata had 16 internal bars, one with 28 rows of stigmata had 21 bars.

Alimentary System (Fig. 2A)—The esophagus forms a wide funnel leading into a capacious, elongate stomach in which a shallow groove extends along the entire length of the posterior margin from esophagus to intestine. On either side of this groove, the stomach wall has three or four irregular bands of thickened tissue separated by areas of thin stomach wall. In a 2 cm long zooid, the stomach measured 2.5 mm in length and 1.5 mm in diameter. The brown-colored stomach leads into a short, narrow duodenal region, constricted at its distal end as it passes into the intestine. The intestine is of uniform diameter and curves gently toward the dorsal side of the zooid to join the rectum. The anus, which usually opens between the eighth and ninth rows of stigmata, has a smooth rim with four indistinct lobes. This form of gut morphology is common to all four species of *Ecteinascidia*, the variables being in the structure of the stomach and the path taken by the gut loop.

Reproductive System (Fig. 3A)—The testis forms a crescent-shaped mass of lobules (up to 100 in a large zooid) centrally placed in the “loop” between stomach and intestine, but not closely associated with either. The testis lobules discharge through a series of vasa efferentia into a single large sperm duct, which curves forward and dorsally to run parallel to the intestine and opens close behind the anus. The ovary lies to the left and within the crest of the testis mass, and the oviduct runs parallel to

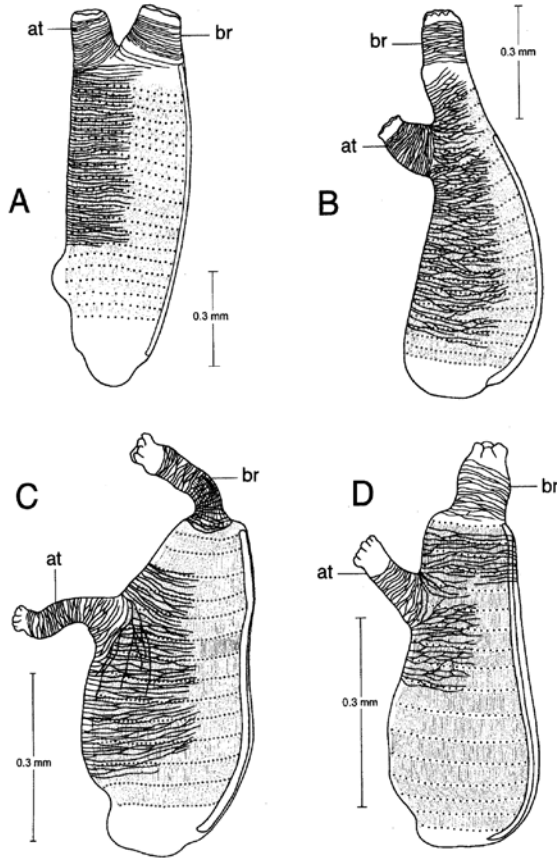


Figure 1. Right side of the zooids showing the musculature of mantle and siphons. A) *Ecteinascidia turbinata*; B) *Ecteinascidia conklini*; C) *Ecteinascidia styloloides*; D) *Ecteinascidia minuta*.

Key to lettering on Figures 1–3: at – atrial siphon; b – brood pouch; br – branchial siphon; e – esophagus; i – intestines; o – ovary; ov – oviduct; s – sperm duct; st – stomach; t – testis.

the sperm duct until the latter reaches the dorsal mid-line; at this point the oviduct separates and crosses the dorsum to discharge into a small brood pouch in the posterior right side of the peribranchial cavity at the level of the last three rows of stigmata. In the original full description, Herdman (1880) overlooked the brood pouch and described the oviduct as leading directly into the peribranchial cavity. Monniot and Monniot (1986) stated that *E. turbinata* embryos are brooded in the oviduct (p. 552), but neither these authors nor C. Monniot (1983) recognized that brood pouches are the rule in the genus. As suggested by Berrill (1950) and confirmed by Goodbody (1994), the pouch is a formation of the peribranchial wall; it is not an expansion of the tip of the oviduct as suggested by Kott (1985). The brood pouch in *E. turbinata* can only accommodate up to eight young embryos, but an individual zooid may have in excess of 30 embryos in various stages of development. Older embryos are pushed out of the brood pouch into the peribranchial cavity where they are held in mucus amongst vascular strands connecting the branchial sac to the body wall. The aper-

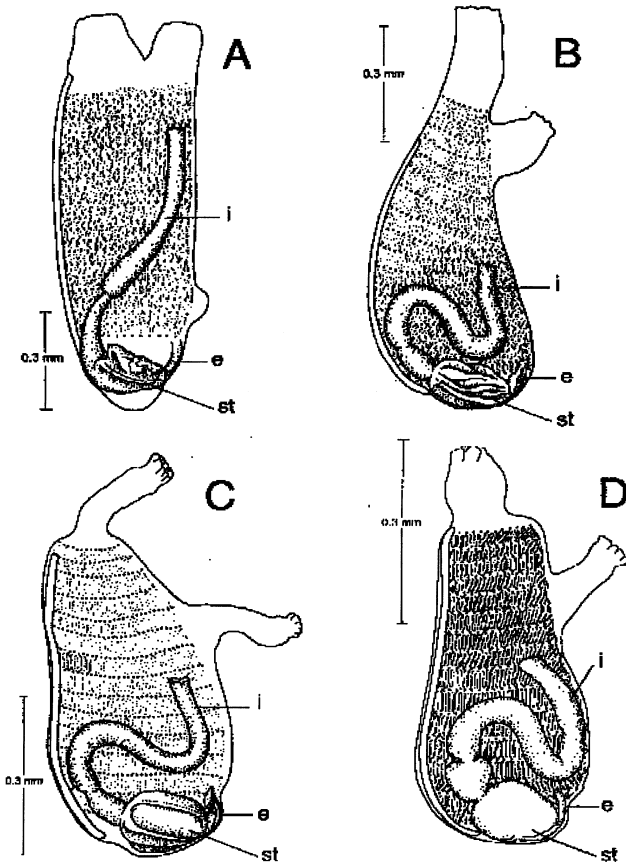


Figure 2. Left side of zooids showing alimentary system. A) *Ecteinascidia turbinata*; B) *Ecteinascidia conklini*; C) *Ecteinascidia styeloides*; D) *Ecteinascidia minuta*.

ture of the brood pouch has a large, flexible lip on its left side, which may be the site of mucus secretion.

Larva.—The larval trunk is 1000–1200 μ in length. At the time of release the branchial sac is already formed with 12 rows of stigmata and a series of internal longitudinal vessels. The alimentary canal is complete and the stomach shows a typhlosole groove.

Distribution and Habitat.—*Ecteinascidia turbinata* has a wide distribution in the western Atlantic, West Africa, and the Mediterranean. For Old World records see C. Monniot (1983). In the western Atlantic it was first recorded by Herdman (1880) from Bermuda (the type locality), and it has subsequently been recorded from throughout this region: e.g., Brazil (da Costa, 1964; Millar, 1977); Curaçao (Goodbody, 1984a); Aruba and St. Martin (Millar, 1962; Goodbody, 1984b); Guadeloupe (Monniot, 1983); St. Thomas (Van Name, 1930); Jamaica (Lefèvre, 1897; Goodbody, 1993a, 2003); Florida (Van Name, 1945; Bingham, 1990); Cuba (Hernandez-Zanuy, 1990); Mexico (Carballo, 2001); Belize (Goodbody, 2000); St. Croix (Millar, 1962). Van Name (1945) believed that Lesueur's (1823) description of *Ascidia claviformis* Lesueur, 1823 from St. Vincent was in fact *E. turbinata*. While we would expect *E. turbinata* to occur in St. Vincent and nearby islands, Lesueur's description is not convincing and makes no

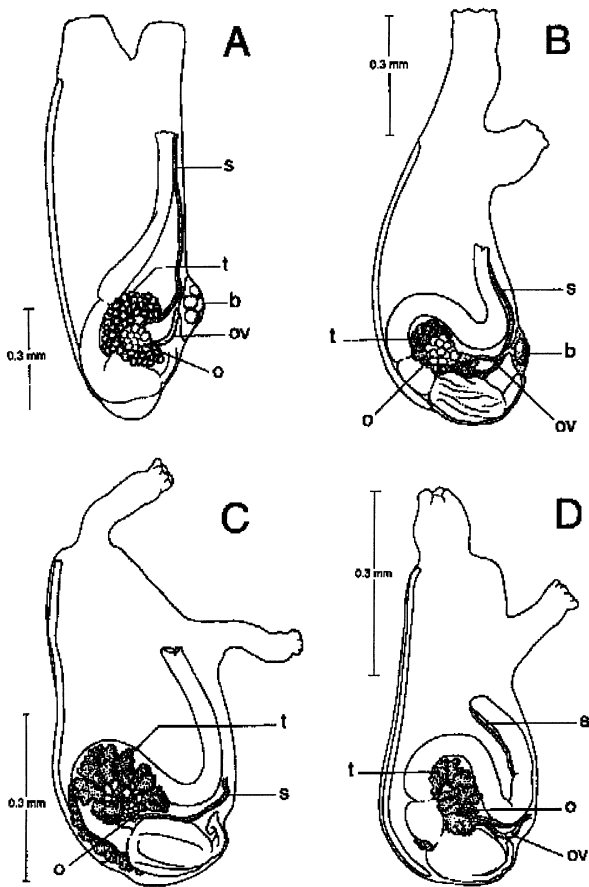


Figure 3. Zooids of *Ecteinascidia* showing the reproductive system. A) *Ecteinascidia turbinata*; B) *Ecteinascidia conklini*; C) *Ecteinascidia styloides*; D) *Ecteinascidia minuta*.

reference to coloration. Herdman (1891) agreed that Lesueur's specimens were probably a species of *Ecteinascidia*, but considered that the anatomical description was inadequate to assign it to any particular species. The validity of Rodrigues da Costa's record from Brazil is open to question, and the only other record of the species in Brazilian waters is that of Millar (1977) whose specimens were dredged from mud and sand at depths of 27–103 m on the northeastern Brazilian continental shelf. This is an unusual environment for the species. This area of the continental shelf is heavily influenced by Amazon outflow and may be rich in organic particulate material, thus possibly providing a trophic environment comparable to that existing in coastal lagoons. On the other hand, the dominance of inorganic particulates in the outflow would seem likely to have a negative impact on this and other ascidian species.

Millar (1978) also reported on the occurrence of *E. turbinata* in deep water on the Guyana shelf between 53° and 58° W, where similar environmental conditions prevail. I.G. reexamined these specimens and considers all four to belong to *E. minuta* or a related species.

Writing of *E. turbinata* in Bermuda, Berrill (1932) states: "Large orange colonies develop attached to the upper surfaces of rocks where currents are relatively strong." In our experience, *E. turbinata* is characteristic of certain quiet mangrove lagoons with relatively high levels of production and suspended particulate matter. A good example of this is the Fort Rocky Lagoon at Port Royal, Jamaica, where it is a dominant element in the sessile communities on the roots of *Rhizophora mangle* L., 1753. In these conditions it forms large colonies of many hundreds of individual zooids. In more oligotrophic conditions, as in many of the mangrove lagoons on the Belize Barrier Reef, *E. turbinata* is either absent or rare, and when it occurs, colonies are smaller and more compact than in Port Royal. Occasionally, colonies are found in exposed reef environments, and in such cases the colonies usually have only a few zooids. In the Belize lagoon close to Tobacco Range, *E. turbinata* has been collected from submerged peat on the lip of hollows created years earlier by seismic blasting.

Under optimal environmental conditions, *E. turbinata*, like most tropical ascidians, grows rapidly and has a short life span. In Puerto Rico, Morgan (1977) found that colonies of this species doubled in size every 6 d for the first 50 d, at which time they became sexually mature and some older zooids began to die; Morgan concluded that the normal life span of a single zooid was approximately 120 d. When all the zooids die, a network of viable stolons remains on the substrate from which a new generation of zooids can develop. This ability to regenerate from a network of stolons is important for the sustainable harvesting of the species when collected for biomedical research (see below).

Economic Importance.—*Ecteinascidia turbinata* has been shown to contain a number of organic substances with active pharmacological properties including potent anti-tumor activity (Sigel et al., 1983; Rinehart et al., 1990). The active compound ecteinascidin occurs in very small quantities in the living animal, so that successful research originally required very large quantities of the ascidian, harvested from the natural environment. If needed in the future, this can be accomplished naturally on a sustainable basis (Goodbody, 1993b; Carballo et al., 1999), or through aquaculture. However such harvests may no longer be necessary, as a series of molecules have been synthesized that are structurally related to ecteinascidin and exhibit similar potency and mode of action as anti-tumor agents (Martinez et al., 1999). If the chemical analogue of ecteinascidin passes clinical trials for therapeutic use, culturing or harvesting the live ascidians may no longer be necessary.

Ecteinascidia conklini Berrill, 1932

(Plate 1C, D)

Ecteinascidia conklini Berrill, 1932: p. 80, fig. 2A.

Ecteinascidia conklini typica C. Monniot, 1972: p. 942, fig. 2A.

Material.—Living material was from Blue Ground Range in Belize with support from specimens collected in 1937 at Garden Cay, Tortugas, Florida now in the U.S. National Museum of Natural History (USNM 13015); material from Bermuda made available by C. Monniot.

Colony.—Colonies of *E. conklini* are usually loosely organized and the colony form depends on their environment. In lagoons in Belize where it is frequently associated

with hanging mats of the alga *Caulerpa racemosa* (Forsskål) J. Agardh, 1873 zooids are widely separated from one another and have long vascular stolons connecting them. However, other colonies closely associated with various species of sponge have zooids that are closer together with only the tips of the siphons on the sponge surface, indicating where zooids are located. In Bermuda, colonies have been found in the path of a fast flowing tidal current (see below).

Zooid.—Zooids are elongate and cylindrical, usually 0.8–1.5 cm in length when preserved, occasionally up to 2.5 cm in living zooids; they are similar to, but generally larger than, those of *E. styeloides*. Zooids are characterized by a greenish yellow coloration with prominent red rings (occasionally faint or absent) around each of the siphons. The branchial siphon is anterior; the atrial siphon is dorsal and usually at about the level of the sixth to eighth stigmata row or about one-third of the way along the dorsum. Both siphons usually have eight lobes, occasionally seven or nine. The lobes are less pointed than in *E. styeloides*, and the external ribbing of the siphon found in the latter species is absent or poorly developed (*cf. E. styeloides* below). Around each siphon there are two red pigment rings: one around the lip at the base of the lobes and one around the base of the siphon. Small red pigment spots alternate with adjacent lobes and lie immediately below the pigment ring. Each spot is connected to the pigment ring by a line of red pigment. This arrangement of pigment spots is more prominent in the atrial siphon than in the branchial siphon. Pigment spots of this sort occur in many species of ascidian, but their function is unknown.

Body Wall.—The test and body wall are thin and transparent, as in *E. turbinata*. A prominent set of transverse muscle bands crosses the dorsum, each subdividing into about three separate fibers before terminating on each side of the body wall (Fig. 1B). These transverse fibers cover only the dorsal two-thirds of the body wall, leaving the lower third (adjacent to the endostyle) free of muscle. On the left side these muscles do not extend over the gut loop, on the right side they extend almost to the posterior end of the zooid, the most posterior fibres being at the level of the anterior curve of the stomach wall. The transverse muscle bands merge across the dorsum with the circular muscle system around the siphons so that in one individual the muscle arrangement was: 20 circular bands around the branchial siphon; 12 transverse bands crossing between the two siphons; 18 circular bands around the atrial siphon; 30 transverse bands crossing behind the atrial siphon.

The number of bands around each siphon varies among individuals and may depend on the length of the siphon. On each side of the animal there are seven or eight fine longitudinal muscle fibers, which are difficult to see except in a living animal during contraction. In one zooid these were arranged in two groups, a group of four fibers about one-third of the way down the body wall from the dorsum, and another group of three fibers two-thirds of the way down the lateral wall.

Branchial System.—There are usually 20 rows of stigmata, but occasionally as many as 22, with 45–60 stigmata per row and 18–20 internal longitudinal bars supported on simple papillae. These characters vary slightly with the size of the zooid. The dorsal lamina is a ribbed membrane with a prominent languet occurring as a continuation of each rib. There are no languets at the level of the first two transverse vessels of the branchial sac because here the lamina forms a deep v-shaped peritubercular area surrounding the opening of the neural gland, which is a simple circular aperture. There are about 40–50 branchial tentacles, with only about 25 of these being functional and the remainder being small stubs. Monniot (1983) found about 50 tentacles

of three orders of size in specimens from Bermuda. The pre-branchial groove is a simple groove between two raised membranes.

Alimentary System (Fig. 2B).—The capacious, elongate stomach is similar to that of *E. turbinata*, but the continuation of the esophageal groove along the posterior margin is poorly defined and not visible from the exterior of the stomach wall. The stomach is not externally folded as depicted by Monniot (1983). Usually only three, not four, thickened areas of the stomach wall are on each side, with the largest one along the posterior end. As in other species of the genus, the stomach is followed by a short duodenal region with a distal constriction before entering the intestine. The intestine takes a conspicuous loop, as in *E. styeloides*, followed by a secondary loop, which extends over three rows of stigmata (rows 15–18) and not over one row as depicted by Monniot (1983). The anus is markedly bilobed and usually opens at the level of the eleventh and twelfth stigmata rows.

Reproductive System (Fig. 3B).—The testis has the same form as in *E. styeloides*. There are about 30–32 pear-shaped testis lobes arranged in a semicircle around the gut loop and stomach, attached to the inner (right) side of the gut wall. Vasa efferentia arising from these lobes collect into a single vas deferens or sperm duct, which follows the distal part of the intestine (rectum), and opens immediately behind the anus. The ovary is situated centrally in the apex of the testis and, as in *E. turbinata*, the oviduct crosses the dorsal side of the pharynx to open into a small brood pouch in the posterior part of the right side of the peribranchial cavity. Also as in *E. turbinata*, the brood pouch can only accommodate 6–8 embryos and the remainder is held in mucus strings among the vascular connections between the pharynx and the peribranchial wall.

Larva.—At the time of release, larvae are about 1000 μ in trunk length and usually have a well-developed branchial sac with six rows of stigmata and a complete alimentary canal. However, there is much variation from those described above: active larvae with an indistinct branchial sac occur as well as fully formed oozoids bearing a tail and adhesive discs.

Distribution and Habitat.—The species is recorded from Bermuda (Berrill, 1932; Monniot, 1972; Monniot and Monniot, 1986), the Dry Tortugas in Florida (Plough and Jones, 1939), and the Belize Barrier Reef (pers. obs.). A recent set of photographs attributed to R. Rocha and S. Faria, issued by the Smithsonian Tropical Research Institute confirms the occurrence of the species at Bocas del Toro in Panama, thus indicating that the species has a much wider distribution than had been previously believed. Berrill (1932) described it as living under stones, and in Bermuda I.G. has seen it growing under stones at Coney Island Bridge in Castle Harbour, where there is relatively strong tidal flow. In Belize, it is common in one lagoon in Blue Ground Range where there is a gentle tidal flow of clean water entering the lagoon from the open sea. Small colonies have also been found farther south on the Belize barrier reef in the Pelican Cays (Goodbody, 2000), usually under stones or on the basal stems of octocorals.

Relationships.—There is no type specimen of *E. conklini*, as apparently none of Berrill's original material still exists. We have deposited good specimens, representative of our material from Blue Ground Range in Belize, in the U.S. National Museum of Natural History (USNM 1004300 and USNM 1004309). *Ecteinascidia conklini* is closely related to *E. turbinata* (larger) and *E. styeloides* (smaller); these relationships are considered further in the Discussion. In external appearance *E. conklini*

bears a striking resemblance to *Ecteinascidia maxima* Kott, 1985 described from Lord Howe Island, Australia (Kott, 1985). Kott's plate IIC illustrates a colony closely resembling some of our own material of *E. conklini* from Belize.

Ecteinascidia styeloides (Traustedt, 1882)

(Plate 1E, F)

Phallusia styeloides Traustedt, 1882: p. 277.

Asciidiella styeloides Van Name, 1921: p. 391 and p. 483. 1930, p. 470, fig. 42.

Ecteinascidia styeloides Monniot, 1983: p. 59. fig. 3.

Ecteinascidia conklini Van Name, 1945: p. 171. Millar, 1962: p. 69. Goodbody, 1984a: p. 33; 1984b: p. 65.

Material.—Living and preserved material collected from Port Royal, Jamaica and Twin Cays, Belize.

Colony.—Colonies are formed of loose bunches of grey-green zooids connected posteriorly by a mass of vascular stolons.

Zooid.—Zooids are erect, cylindrical, 8–10 mm in length, sometimes more (Monniot, 1983). The branchial siphon is anterior, and the atrial siphon is dorsal arising at the level of the fourth and fifth rows of branchial stigmata. Both siphons usually have eight lobes, but some variability occurs and seven or nine lobes frequently occur, and in one zooid 12 lobes were recorded. In each case the siphon tubes are often slightly thickened below the junction of adjacent lobes giving the impression of a "rib" or ridge. This ribbed appearance is only visible in the living animal (Plate 1F) and usually disappears in preserved specimens. At the top of each rib, between adjacent lobes is a red pigment spot, but there is no pigmented ring as in *E. conklini*. In some environments the branchial siphon may form long prebranchial tubes, greatly extending the effective length of the zooid, sometimes by as much as 3 mm; this permits zooids growing embedded in sponges, algal clusters, or among other sessile organisms to gain access to clean water conditions at the surface of the cluster.

Body Wall (Fig. 1C).—The test and body wall are thin and relatively transparent, and the muscles of the body wall are, as typical for the genus, mostly transverse. As in other species, these muscles cross the dorsum, where they form thick bands and terminate in fine branches above each side of the endostyle. There are usually eight of these bands crossing the dorsum anterior to the atrial siphon between it and the anterior end of the zooid, and 18–20 muscle bands posterior to the atrial siphon, between it and the gut region. There is, however, variability in the number of muscle bands and lateral fibers, which coalesce to form a dorsal band; thus, the 6–8 anterior bands may have their origin from a total of 20–30 lateral fibers. The body wall over the gut loop is free of muscle, so that muscle fibers on the left side of the zooid extend only to the eighth or ninth row of branchial stigmata, while on the right muscles extend posteriorly as far as rows 11 and 12. The longitudinal musculature consists of only about six very fine strands on either side, extending along the full length of the zooid. As in other species, these longitudinal muscles are most easily demonstrated in the living zooid during contraction. The branchial siphon has about 20 large circular muscles, and about eight external longitudinal fibers, which terminate in the prebranchial area. Inside the siphon is a series of about 16 longitudinal retractor

muscles attached to a narrow annular ring just inside the siphonal opening; these muscles permit the lobes of the siphon to be inverted inside the anterior end of the siphonal tube. In living colonies protrusion and inversion of the siphons can be seen as a regular activity of individual zooids. The functional purpose of this activity is not clear. The process differs from "spontaneous squirting," which entails contraction of the whole peribranchial wall, forcing water out of the branchial sac, followed by relaxation of the muscles, permitting the branchial chamber to refill with clean water (Hecht, 1918; Hoyle, 1953). The process observed in *E. styeloides* is, as far we can discern, only a localized activity of the branchial siphon. Perhaps it serves to enhance the ability of the zooid to monitor changes in water quality by repositioning the siphon relative to other zooids in the colony. This behavior pattern warrants further study.

Branchial System.—There are usually 14 rows of stigmata (sometimes 15) with 40–45 stigmata per row. These rows are usually crossed by 14 internal longitudinal bars, each supported by a series of small triangular papillae (the apex of each being rounded as in *E. minuta*); the two most dorsal bars are often interrupted. The dorsal lamina is a low membrane supported by 13 "ribs" with one at the junction of each transverse branchial bar. Although these support the membrane, they only project a very short way beyond the membrane's margin as short languets, unlike the relatively long languets of *E. turbinata* and *E. conklini*. Anteriorly, the lamina terminates in a v-shaped peritubercular area around the opening of the neural gland, which is a simple pore. The pre-branchial groove is formed by two irregular laminae (cf. Monniot, 1983). Although Monniot (1983) reported 60 branchial tentacles in this species, we have observed only 20–25 tentacles.

Alimentary System (Fig 2C).—The esophagus opens into an elongated stomach, about 1.5 mm long and <1.0 mm in diameter, which is similar to that of *E. turbinata* and *E. conklini*. The continuation of the esophageal groove along the posterior border of the stomach is more prominent than in *E. conklini* and is clearly visible from the exterior (Monniot, 1983). Internally, the stomach has four deep folds visible externally as a thickening of the tissue on either side of the esophageal groove, and along the anterior margin of the stomach wall. The intestine is typical for the genus, with a short post-gastric duodenal region followed by a prominent constriction; the intestine then extends forward to the junction of stigmata rows eight and nine, where it loops back to rows 11 and 12 to form a second loop followed by the rectum (cf. *E. conklini*). The deeply bilobed anus discharges at the level of stigmata rows eight and nine.

Reproductive System (Fig. 3C).—The testis consists of a large number of pear-shaped lobules arranged in a horse-shoe along the loop of the gut from stomach to mid-intestine and between the gut and the branchial sac. Depending on the maturity of the zooid, there may be up to 30–32 of these lobules, attached to the inner face of the gut and stomach wall. Individual vasa efferentia arise from these lobules and join to form the vas deferens or sperm duct, which follows the rectum to open immediately behind the anus (less than a stigmata length behind it). The ovary lies in the center of the gut loop to the left of the testis mass, and in a mature zooid as many as 15–20 large oocytes may be present. The oviduct follows the normal perophorid pattern of crossing the dorsal side of the branchial sac before discharging into the posterior end of the peribranchial cavity. The brood pouch in this species is poorly developed. In some cases the oviduct merely discharges into a shallow fold of the

peribranchial wall. From here, embryos are released into the peribranchial cavity where they are brooded and held together by mucus and the vascular strands that run between branchial sac and body wall. When embryos are ready to hatch they are individually freed into the peribranchial cavity. As many as 25–30 embryos may be brooded at any one time in this manner.

Larva.—With a trunk of 750–800 μ in length, the active larva has both siphons, ocellus and otolith, and three adhesive discs, but no ampullae. The branchial sac is still not fully developed and only vague outlines of four rows of stigmata are visible. Likewise, the alimentary system is partly developed and only an outline of the stomach and part of the intestine is visible.

Distribution and Habitat.—*Ecteinascidia styeloides* appears to be widely distributed in the Caribbean region, but has often been confused with the much rarer *E. conklini*. This confusion stems from Van Name (1945), who gave much prominence to *E. conklini* and believed that *E. styeloides* was the same species and that the name *Ecteinascidia conklini* should be retained as a *nomen conservandum*. Although the type locality is St. Croix, Virgin Islands (Traustedt, 1882), the presence of *E. styeloides* elsewhere in the Caribbean was overlooked until Monniot (1983) described specimens from Guadeloupe and documented differences between that species and *E. conklini*. *Ecteinascidia styeloides* has subsequently been reported from Jamaica (Goodbody, 1993a, 2003) and Belize (Goodbody, 2000, 2004). Several published records of *E. conklini* should be amended, including the following specimens we have reexamined. In Millar (1962) the specimens from Bonaire (1064b) and St. Martin (1132) are both *E. styeloides*. The other specimens listed by Millar (loc. cit.) from Curaçao and Barbuda have not been located, but judging from the habitat mentioned they were probably also *E. styeloides*. All of the records from Piscadera Baai in Curaçao and the Lac in Bonaire (Goodbody, 1984a) are *E. styeloides* and not *E. conklini*. Similarly, specimens numbered 1132 (St. Martin), 1410A (Florida), and 1555 (Bonaire) documented in Goodbody (1984b) are *E. styeloides* and not *E. conklini*; specimen 1429A from St. Martin has not been relocated. A specimen in the U.S. National Museum of Natural History from Big Pine Key, Florida, (USNM 406083) labeled *E. conklini* is also *E. styeloides*.

Ecteinascidia styeloides is a shallow water species typical of the relatively unstressed parts of mangrove lagoons. Thus, in Twin Cays, Belize it occurs sporadically throughout the main channels, but tends to be replaced by *E. minuta* in the inner, more stressed parts of the mangrove system. It is frequently found very close to the surface and seldom more than 1 m in depth, suggesting rather specific behavior patterns by settling larva. It rarely occurs on reefs: at the Pelican Cays, Belize, individual zooids, but not fully formed colonies were found on the undersurface of stones (coral rubble) on submerged ridges. Single zooids of this sort also occur on the vertical faces of some peat banks in the channels at Twin Cays, Belize.

Relationships.—*Ecteinascidia styeloides* is the smallest of three very similar species differing primarily in size, gut morphology, and ecology; the other two species are *E. conklini* and *E. turbinata* (see the Discussion).

Ecteinascidia minuta (Berrill, 1932)

(Plate 1G, H)

?*Perophoropsis herdmani*, Lahille, 1890: p. 286–288.

?*Ecteinascidia herdmani* Medioni, 1969: p. 439.

Ecteinascidia conklini var *minuta* Berrill, 1932: p. 80.

Ecteinascidia conklini minuta Van Name, 1945: p. 172. Monniot, 1972: p. 942.

Ecteinascidia minuta Monniot, 1983: p. 62 fig. 3. Goodbody, 2000: p. 315; 2003: p. 467.

Ecteinascidia tortugensis Plough and Jones, 1939: p. 50. Van Name, 1945: p. 172. Millar, 1962: p. 69. Goodbody, 1984a: p. 34; 1984b: p. 65.

Material.—From Port Royal, Jamaica, several localities on the Belize Barrier Reef and from Walsingham Pond, Bermuda.

Colony.—Colonies may form clusters, in which case zooids will tend toward an erect position, or they may form more widely spaced systems in which the zooids are recumbent, attached by the length of the ventral surface with long vascular stolons connecting adjacent zooids. All intermediate stages of these two extremes may sometimes be discerned.

Zooid.—Zooids, which are pale green in color, range from 2.5 to 5.0 mm in length. The branchial siphon may extend the total length by a further 25% or more depending on the circumstances under which the zooids are living. The test is thin, soft, and easily removed from preserved specimens. The branchial siphon is anterior, usually elongated and has eight fine-tipped lobes. The atrial siphon is also typically elongated, has eight fine-tipped lobes, and is usually set far back along the dorsal side of the zooid. In recumbent zooids, the atrial siphon often opens towards the posterior end of the zooid. Red pigment spots between the lobes of both siphons may be detected, but are not prominent. In his original description of this species, Berrill (1932) recorded that both (siphons) have prominent ridges. We have not noted this feature in any examples of *E. minuta* studied by us, but have noted it as a feature of *E. styeloides*, a species not recognized by Berrill in Bermuda.

Body Wall.—The body wall is thin with mainly transverse muscles arising on either side about half way between the endostyle and the dorsal mid-line. These muscles cross the dorsum, where fine branches and cross-linkages between muscles occur (Fig. 1D). This musculature extends the whole way back to the posterior end of the zooid on the right, but on the left does not extend over the alimentary canal. In recumbent zooids, the arrangement of cross-linkages across the dorsum provides a diaphragm-like system in which the dorsal side can be depressed by muscle contraction. A system of fine radial muscles crosses the base of the branchial siphon and curves laterally down either side at the anterior between the two siphons. These muscles appear to be associated with siphon retraction. Thirty of these radial muscles cross the siphonal disc (which lies between the region of the branchial tentacles and that of the pre-branchial groove). There are about 20 circular muscles on each siphon, and those of the atrial siphon join the transverse dorsal musculature at the base of the siphon.

Branchial System.—There are 12 large branchial tentacles and usually 12 very small ones in between. There are usually 15 rows of stigmata, of which one at the anterior end may be incomplete, and sometimes a sixteenth row may occur posteriorly. Plough and Jones (1939) found 18 rows of stigmata in mature zooids at the Dry

Tortugas, Florida while Monniot (1972) reported that the number varies from 13 to 15, usually 14. There are 20–25 stigmata per row in the middle of the branchial sac, and 10–13 internal longitudinal bars. These bars are supported on triangular papillae in which the narrow apex is rounded; there are no secondary papillae. Some of the dorsal internal longitudinal bars may be incomplete. The dorsal lamina is a low membrane supporting 13 languets (one at the junction of each of the transverse vessels of the branchial sac), which extend into the pharynx beyond the limits of the membrane and tend to curve toward the right, but this may be an artifact of fixation. The dorsal tubercle is a simple, rounded aperture opening forward.

Alimentary System (Fig. 2D).—The esophagus is short and strongly curved to enter a rounded stomach near its middle rather than at one end. There is darkly staining tissue at the junction of stomach and esophagus suggesting that this may be a glandular secreting area. In contrast to other species, the stomach has no typhlosole or other external grooving and there are no internal ridges—the stomach is a simple ovoid sac (ca. $750 \times 500 \mu$). The general morphology of the alimentary system is similar to that of the other species, with a short duodenum and strongly looped intestine so that the anus opens at the level of stigmata rows 10/11. The anus is a small pore with a flared lip, but is not obviously bilobed.

Reproductive System (Fig. 3D).—Unlike those of *E. styeloides* and *E. conklini*, the testes do not lie along the arc of the intestinal loop. They arise as a series of small lobules in tissue in the middle of the gut loop, and instead of forming a “horse shoe” of lobules, develop into a rounded mass sometimes almost filling the gut loop. This arrangement bears a similarity to that found in certain species of *Perophora* (e.g., *Perophora regina* Goodbody and Cole, 1987) rather than to any other species of *Ecteinascidia*. Plough and Jones (1939) state that the testis lobes “lie in a crescent close to the intestine,” but they illustrated (in their plate 3) a mass of lobes placed centrally in the gut loop; the central mass is also illustrated by Monniot (1972). The ovary develops on the left, laterally to the testis mass, and also in the middle of the gut loop. The sperm duct takes a normal course following the rectum and opening just behind the anus. The oviduct, as in all perophorids, crosses the dorsal side of the branchial sac at the posterior end and discharges into a short pouch attached to, and probably derived from, the body wall. The pouch is not big enough to contain all the embryos, and as development proceeds the older embryos are pushed into the peribranchial cavity, where development is completed. Twenty to 25 embryos commonly occur and as many as 43 have been counted in a single peribranchial cavity.

Asexual Reproduction.—Colonies are formed in the usual manner by budding from vascular stolons. Under conditions of unlimited space, widely spaced zooids will arise with long stolon strands in between; under these circumstances zooids will be attached by the ventral surface. In crowded conditions or where competition for space is strong, zooids become closely packed and more erect in their form. Colonies are frequently found associated with green algae, notably *Caulerpa verticillata* J. Agardh, 1847, in which case zooids are widely spaced and stolons ramify throughout the algae. *Ecteinascidia minuta* also frequently settles and grows on the shells of living oysters (*Isognomon alatus* Gmelin, 1791), in which case the ascidian's growth form is recumbent.

Larva.—The larval trunk is between 500 and 600 μ in length, and although the outline of branchial sac and gut are visible, none of these structures is fully formed

in the newly hatched larva, as they are portrayed in the figures of Plough and Jones (1937).

Distribution and Habitat.—In the Caribbean, *E. minuta* has been recorded from Aruba (Goodbody, 1984b), Bonaire (Millar, 1962; Goodbody, 1984a), Guadeloupe (Monniot, 1983), St. Kitts (Millar, 1962), St. Croix (Millar, 1962), and Jamaica and Belize (pers. obs.). Elsewhere it occurs in the Dry Tortugas, Florida (Plough and Jones, 1939), Bimini, Bahamas (Millar, 1962), and the type locality Bermuda (Berrill, 1932, Monniot, 1972, Monniot and Monniot, 1986). *Ecteinascidia minuta* occupies a broad spectrum of habitats and may be found under rubble on reefs, on *Rhizophora* roots in mangrove lagoons, and is frequently found in conditions of stress where other sessile organisms fail to maintain a foothold. It is one of only two ascidian species commonly found at Candy's Pond in Twin Cays, Belize, a pond subject to extremes of temperature and salinity fluctuation (Goodbody, 2004). Similarly, *E. minuta* has been found in some of the shallow salinas in the interior of Twin Cays, Belize (e.g., Hidden Lake; Rützler et al., 2004). It might be argued that success in such conditions is due to an ability to reproduce rapidly and colonize while conditions are normal. However, it is just as likely that it is associated with an ability to regress into undifferentiated material in the stolon network and redevelop when favorable conditions return.

Relationships.—*Ecteinascidia minuta* does not seem to be closely related to any of the other species of *Ecteinascidia* found in the tropical western Atlantic. The centrally placed testis in the gut loop distinguishes it from *E. styeloides* and *E. conklini*, but places it close to *E. turbinata*. The rounded stomach without folds and the recumbent position of zooids when not crowded are traits not found in any of the other three species, but they link *E. minuta* with *Ecteinascidia nexa* Sluiter, 1904 from the Indo-Pacific region (see Kott, 1985). *Ecteinascidia minuta* is also closely related to, and perhaps synonymous with, *Ecteinascidia herdmani* (Lahille, 1890) from the Mediterranean and West Africa (see following Discussion).

DISCUSSION

Unlike the genus *Perophora*, in which the differences between species are relatively clear (Goodbody, 1994), differences among species of *Ecteinascidia* are largely related to size and the position of the atrial siphon, which in turn determines the form of the gut loop. *Ecteinascidia turbinata*, *E. conklini*, and *E. styeloides* form a trio of apparently closely related species of decreasing size. Zooids of *E. turbinata* range roughly from 1.5 to 2.0 cm, *E. conklini* 1.0 to 1.5 cm, and *E. styeloides* 0.7 to 1.0 cm. All three species form upright clusters of zooids usually closely bunched together with similar transverse body musculature, which crosses the dorsum and inserts on either side above the endostyle. In keeping with the size differences, the number of rows of stigmata varies from 25 to 35 in *E. turbinata*, 20 to 22 in *E. conklini*, and 14 to 15 in *E. styeloides*. *Ecteinascidia turbinata* and *E. conklini* both have about 20 internal longitudinal bars, while *E. styeloides* normally only has 14. *Ecteinascidia styeloides* also differs from the other two species in the reduced size of the languets projecting beyond the membrane of the lamina and in the reduction of the brood pouch. The reduction of the brood pouch is unusual and is not a function of size, as brood pouches occur in *E. minuta* and in most species of *Perophora*, all of which are smaller than *E. styeloides*. The large *E. turbinata* differs from *E. conklini* and *E.*

styeloides in having the atrial siphon anterior, rather than dorsal, with the result that the anus is far forward and the secondary loop of the intestine is poorly developed. In the other two species, the atrial siphon is dorsal and a little way back from the anterior end, there is a deep secondary loop and the anus is relatively far back in the peribranchial cavity. Monniot (1983) suggests that there is a difference in the extent of the secondary loop between *E. conklini* and *E. styeloides*. We have not been able to detect any such difference; if it does occur, it is too small to be of taxonomic significance. *Ecteinascidia turbinata* also differs from *E. conklini* and *E. styeloides* in the origin and position of the testis being central to the gut loop instead of forming an arc of lobes around the loop. In this respect, *E. turbinata* resembles *E. minuta*.

In the field, the three ascidian species are relatively easy to distinguish by size and color. The bright orange pigment of *E. turbinata*, concentrated in the anterior end around and behind the siphons, is distinctive. *Ecteinascidia conklini* is green or yellow and can be quickly identified by the red rings around each siphon. *Ecteinascidia styeloides* lacks the red ring and has more tubular siphons, which are often externally ribbed, and the zooids are either translucent gray or green. It is possible, however, to confuse erect colonies of *E. minuta* with *E. styeloides*. *Ecteinascidia minuta* stands apart from the other three species in its small size (2.5–5.00 mm), tendency to a recumbent (prostrate) position on the substratum, attached by the ventral surface, and the dorsal cross-linkages of body muscle bands that provide for a diaphragm-like action of the dorsal body wall. The origin and form of the testis as a central spherical mass in the gut loop, instead of as a crescent around the loop, also distinguishes this species from the others, especially from *E. conklini* and *E. styeloides*. *Ecteinascidia minuta* is further distinguished by the almost spherical stomach, which lacks any internal folds or ridges.

The larvae of all four western Atlantic species have a similar gross morphology and differ only in size and degree of development of adult characteristics such as the branchial sac and alimentary canal. On the one hand, larvae of *E. turbinata* and *E. conklini* have a well formed branchial sac with 12 and six rows of stigmata respectively, while in *E. styeloides* and *E. minuta* the branchial sac is poorly developed in outline with no more than four rows of stigmata visible.

Apart from the morphological differences between species described above, there are clearly marked habitat preferences in the four species. *Ecteinascidia turbinata* flourishes in slightly eutrophic sheltered lagoons such as the Fort Rocky Lagoon at Port Royal, Jamaica, and Piscadera Baai in Curaçao. When it occurs elsewhere, as at Cat Cay in Belize or in reef environments, the colonies are small and compact. There are insufficient locality data for *E. conklini* to permit generalizations about its habitat, but the available records suggest that it requires a gentle flow of clean water past the colony. At Blue Ground Range in Belize, *E. conklini* lives on mangrove roots just inside the entrance to a small lagoon where it is regularly bathed by a current of water entering from the open sea, while in Bermuda, it occurs in faster flowing water (Coney Island Bridge), but only underneath stones.

Ecteinascidia styeloides avoids the more eutrophic or stressed environments of quiet lagoons and commonly occurs in channels, where water flow is regular and even fast as in Hidden Creek at Twin Cays, Belize. On reefs, colonies of *E. styeloides* have not been seen, only individual zooids in coral rubble. In the presence of strong water currents in lagoons, both *E. styeloides* and *E. conklini* gain some protection by growing among algal mats (*Caulerpa* spp.) or embedded in sponges. *Ecteinascidia*

styeloides has an ability to withstand environmental extremes, as the following anecdotal case reveals. A bucket of seawater was left standing in the aquarium at Carrie Bow Cay, Belize for several days and evaporation raised the salinity to 60. Before emptying the bucket it was noticed that there were green stolons on a small piece of mangrove bark lying in the bucket. This was transferred to normal seawater in the aquarium, and within 10 d active zooids of *E. styeloides* had developed from the stolons, reinforcing the idea that undifferentiated material in the stolons can survive stress (in this case hypersalinity) and redevelop zooids when restored to normal conditions. It is likely that this regenerative capacity is common to most species in the Perophoridae (see the sustainable harvesting of *E. turbinata* already referred to in this paper). Also, when *P. regina* is artificially grazed a new generation of zooids develops within a few days (Goodbody, unpubl. data). In addition to their demonstrated ability to withstand hypersaline conditions, both *E. styeloides* and *E. minuta* are abundant in Hidden Creek at Twin Cays, Belize, where temperature extremes are routine as a result of warm water outflow from adjacent salinas. (Goodbody, 2004; Rutzler et al., 2004). Information currently available suggests that a detailed study of the environmental physiology of the Perophoridae would be rewarding and might contribute to a fuller understanding of why they are key elements in the sessile community in Caribbean mangrove ecosystems.

Ecteinascidia minuta occupies the broadest spectrum of habitats of all four species, occurring commonly under stones on reef flats and in coral rubble in relatively oligotrophic lagoons such as Cat Cay, Belize, in intermediate conditions such as in Walsingham Pond in Bermuda, and in highly stressed environments such as Candy's Pond and the shallow mangrove flats at Twin Cays, Belize. This wide habitat range must be due in part to physiological tolerance, but is probably assisted by rapid reproduction and opportunism. The ability to withstand environmental extremes has also been recognized in *Ecteinascidia thurstoni* Herdman, 1891 growing in a coastal pool on the Sinai coast, where extremes of both salinity and temperature are a regular feature of the annual cycle (Por and Dor, 1975).

Ecteinascidia styeloides and *E. conklini* do not appear to have any obvious counterparts outside of the western Atlantic region. *Ecteinascidia conklini* appears to be a relatively rare species known from only a few sites in the western Atlantic. Further exploration, particularly along the Meso-American Barrier Reef, may reveal a wider distribution. In contrast, *E. turbinata* has a wide distribution in the western Atlantic, Mediterranean, and West Africa (for references see Monniot, 1983). Kott (1985) suggested that there may be a close relationship between *E. turbinata* and *Ecteinascidia sluiteri* Herdman, 1906, but this was based on what seems to be a faulty premise that *E. turbinata* has separated lateral and dorsal bands of transverse muscle on the peribranchial wall.

Ecteinascidia minuta is very similar to and perhaps synonymous with *E. herdmani* from the Mediterranean and West Africa. Monniot (1974) states that the only difference between the two species is that in *E. herdmani* the esophagus enters the stomach near its posterior end close to the origin of the intestine and that in *E. minuta*, the esophagus and intestine are at opposite poles of the stomach. This does not conform with our observations because in the specimens we examined the esophagus enters the stomach centrally and not opposite to the intestine. Monniot (1974), who recorded the presence of *E. herdmani* in the Azores, must have later recognized the similarity of the two species because in a subsequent paper (Monniot, 1983) he re-

ports *E. minuta* as occurring in the Azores, referring to his 1974 paper as the source of information. The description of *E. herdmani* given by Medioni (1970) also suggests that the two species may be synonymous. If, in due course, the two species are found to be synonymous, then *E. herdmani* would take precedence over *E. minuta*. Until a more careful comparison can be made between the two species, we propose that the name *Ecteinascidia minuta* (Berrill, 1932) be retained for the western Atlantic species. *Ecteinascidia minuta* is also closely related to the Indo-Pacific species *Ecteinascidia nexa* Sluiter, 1904 (see Kott, 1985). The structure of the stomach and alimentary canal and the organization of the testis, as well as the tendency for a prostrate life form, are all characters common to the two species.

The taxonomy was further confused by Plough and Jones (1939) who described *E. tortugensis* as a new species from the Dry Tortugas in south Florida. There are no observable differences between *E. tortugensis* and *E. minuta*. In his monograph on American ascidians, Van Name (1945) treated these as two distinct species and overlooked the fact that they were one and the same species. By virtue of Berrill's (1932) description of *Ecteinascidia conklini minuta*, *E. minuta* (Berrill 1932) takes precedence and *E. tortugensis* is now considered to be a synonym of *E. minuta*.

ACKNOWLEDGEMENTS

We are grateful to K. Rützler, Director of the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program (CCRE) for providing financial support and facilities at the Carrie Bow Field Station in Belize, and to UNESCO and the Netherlands Universities Foundation for International Co-operation for supporting a visit by IG to the Zoological Museum in Amsterdam and S. van der Spoel for providing facilities at the Instituut Voor Taxonomische Zoologie. We acknowledge assistance from M. Carpenter, W. Sterrer and the staff of the Port Royal Marine Laboratory in the conduct of field work in Belize, Bermuda and Jamaica respectively. We thank three reviewers for their observations and comments on the paper. We thank T. Litwak for creating the line drawings, C. Muir for scanning the original photographs for the plate and C. Goodbody for editing the final manuscript. This is Contribution Number 719 Caribbean Coral Reef Ecosystems Program (CCRE).

LITERATURE CITED

- Beneden, E. van 1887. Les genres *Ecteinascidia* Herdman, *Rhopalea* Philippi et *Sluiteria* n.g. Note pour servir a la classification de Tuniciers. Bull. Acad. Belg. (3) 14 (7): 19–44.
- Berrill, N. J. 1932. Ascidians of the Bermudas. Biol. Bull. 62: 77–88.
- _____. 1950. The Tunicata. Ray Soc. Publs. 133: 1–354.
- Bingham, B. L. 1990. The ecology of epifaunal communities on prop roots of the red mangrove, *Rhizophora mangle*. Ph.D. Thesis, Florida State University, Tallahassee. 219 p.
- Carballo, J. L. 2001. *Ecteinascidia turbinata* (Ascidacea: Perophoridae) en los manglares península de Yucatán México. Rev. Biol. Trop. 48: 365–369.
- _____, A. Hernández-Zanu, S. Naranjo, B. Kukurtzu, and A. Garcia Cagide. 1999. Recovery of *Ecteinascidia turbinata* Herdman 1880 (Ascidacea: Perophoridae) populations after different levels of harvesting on a sustainable basis. Bull. Mar. Sci. 65: 755–760.
- Costa, H. R. Da. 1964. Notas sobre los Ascidacea do litoral Brasileiro. Anais Acad. Bras. Cienc. 36: 568 p.
- Goodbody, I. 1984a. The ascidian fauna of two contrasting lagoons in the Netherlands Antilles: Piscadera baai, Curaçao, and the Lac of Bonaire. Stud. Fauna Curaçao Carib. Isl. 67: 21–61.

- _____. 1984b. Ascidiens from Caribbean shallow water localities. *Stud. Fauna Curaçao Carib. Isl.* 67: 62–76.
- _____. 1993a. The ascidian fauna of a Jamaican lagoon: thirty years of change. *Rev. Biol. Trop., Suppl.* 41: 35–38.
- _____. 1993b. Drugs from the sea – harvesting sea squirts. University of the West Indies Faculty of Natural Sciences, Mona, Newsletter Vol. 7. No.1: 14–15.
- _____. 1994. The tropical western Atlantic Perophoridae (Asciacea): I. The genus *Perophora*. *Bull. Mar. Sci.* 55: 176–192.
- _____. 2000. Diversity and distribution of ascidians (Tunicata) in the Pelican Cays, Belize. *Atoll Res. Bull.* 480: 22 p.
- _____. 2003. The ascidian fauna of Port Royal, Jamaica I. Harbor and mangrove dwelling species. *Bull. Mar. Sci.* 73: 457–476.
- _____. 2004. Diversity and distribution of ascidians (Tunicata) at Twin Cays, Belize. *Atoll Res. Bull.* 524: 23 p.
- _____ and L. Cole. 1987. A new species of *Perophora* (Asciacea) from the western Atlantic, including observations on muscle action in related species. *Bull. Mar. Sci.* 40: 246–254.
- Hecht, S. 1918. The physiology of *Ascidia atra* Lesueur. I. General physiology. *J. Exp. Zool.* 25: 229–259.
- Herdman, W. A. 1880. Preliminary report on the Tunicata of the CHALLENGER expedition. Pt. I. Ascidiacea. *Proc. Roy. Soc. Edinburgh* 10: 458–472.
- _____. 1882. Report on the Tunicata collected during the voyage of H.M.S. “CHALLENGER” during the years 1873–1876. Pt. I. Ascidae simplices. *Zool. Chall. Exp.* 6: 1–296.
- _____. 1891. On the genus *Ecteinascidia* and its relations; with descriptions of two new species, and a classification of the family Clavelinidae. *Trans. Liverp. Biol. Soc.* 5: 144–163.
- _____. 1906. Report on the Tunicata. *Ceylon Pearl Oyster Fish. Suppl. Rep.* 5: 295–348.
- Hernandez-Zanuy, A. 1990. Lista de ascidias Cubanas. *Poeyana* 388: 1–7.
- Hoyle, G. 1953. Spontaneous squirting of an ascidian. *Phallusia mammillata* Cuvier. *J. Mar. Biol. Ass. U.K.* 31: 541–562.
- Kott, P. 1985. The Australian Ascidiacea, part I. Phlebobranchia and stolidobranchia. *Mem. Qd. Mus.* 23: 1–440.
- Lahille, F. 1890. Recherches sur les tuniciers des côtes de France. Thesis, University of Toulouse, Toulouse. 330 p., 176 figs.
- Lefèvre, G. 1897. Budding in *Ecteinascidia*. *Anat. Anz.* 13: 473–483.
- Lesueur, C. A. 1823. Descriptions of several new species of *Ascidia*. *J. Acad. Nat. Sci. Philad.* 3: 2–8.
- MacIntyre I. G. and K. Rützler (Eds.). 2000. Natural history of the Pelican Cays, Belize. *Atoll Res. Bull.* 466–480: 333 p.
- _____, _____, and I. C. Feller (Eds.). 2004. The Twin Cays mangrove ecosystem, Belize: biodiversity, geological history, and two decades of change. *Atoll Res. Bull.* 509–530: 476 p.
- Martinez E. J., T. Owa, S. L. Schreiber, and E. J. Corey 1999. Pthalascidin, a synthetic antitumor agent with potency and mode of action comparable to Ecteinascidin 743. *Proc. Natl. Acad. Sci. U.S.A.* 96: 3496–3501.
- Medioni, A. 1969. Redescription d’une espèce d’Ascidie: *Ecteinascidia herdmani* (Lahille, 1890) (= *Perophoropsis herdmani* Lahille, 1890). *Vie et Milieu.* 20(2-A): 439–446.
- Millar, R. H. 1962. Some ascidians from the Caribbean. *Stud. Fauna Curaçao Carib. Isl.* 59: 61–77.
- _____. 1977. Ascidiens (Tunicata: Ascidiacea) from the northern and north-eastern Brazilian shelf. *J. Nat. Hist.* 11: 169–223.
- _____. 1978. Ascidiens from the Guyana shelf. *Netherl. J. Sea Res.* 12: 99–106.

- Monniot, C. 1972. Ascidies phlébobranches des Bermudes. Bull. Mus. Natn. Hist. Nat. Paris 3 Sér. No. 82, Zool. 61: 939–948.
- _____. 1974. Ascidies littorales et bathyales recoltées au cours de la Campagne Biacores: phlébobranches et stolidobranches. Bull. Mus. Natn. Hist. Nat., Paris, 3 Sér. No. 251, Zool. 173: 1327–1352.
- _____. 1983. Ascidies littorale de Guadeloupe II. Phlébobranche. Bull. Mus. Natn. Hist. Nat. Paris 4 Sér., 5, A (1): 51–71.
- Monniot, F. and C. Monniot. 1986. Ascidiacea. Pages 545–558 *in* W. Sterrer, ed. Marine flora and fauna of Bermuda. John Wiley & Sons.
- Morgan, T. O. 1977. Reproduction, growth and longevity of three species of West Indian colonial ascidians. Proc. Assoc. Isl. Mar. Labs. Cbn.12: 38 (Abst.).
- Plough, H. H. and N. Jones. 1939. *Ecteinascidia tortugensis*, species nov. with a review of the Perophoridae (Ascidiacea) of the Tortugas. Pap. Tortugas Lab. 32: 47–60.
- Por, F. D. and I. Dor. 1975. Ecology of the metahaline pool of Di Zahav, Gulf of Eilat with notes on the Siphonocladacea and the typology of near-shore marine pools. Mar. Biol. 29: 37–44.
- Rinehart, K. L., T. G. Holt, N. L. Fregeau, J. G. Stroh, P. A. Keifer, F. Sun, L. H. Li, and D. G. Martin. 1990. Ecteinascidins 729, 743, 745, 759A, 759B and 770: potent antitumor agents from the Caribbean tunicate *Ecteinascidia turbinata*. J. Org. Chem. 55: 4512–4515.
- Rützler K., I. Goodbody, M. C. Diaz, I. C. Feller, and I. G. Macintyre. 2004. The aquatic environment of Twin Cays, Belize. Atoll Res. Bull. 512: 49 p.
- Sigel, M. M., L. J. McCumber, J. Hightower, S. S. Hayasaka, E. M. Huggins, and J. F. Davis. 1983. *Ecteinascidia turbinata* extract activates components of inflammatory responses throughout the phylogenetic spectrum. Amer. Zool. 23: 221–227.
- Sluiter, C. P. 1904. Die Tunicaten der Siboga-Expedition. Pt. I, Die socialen und holosomen Ascidien. Siboga exped. 56A: 1–126.
- Traustedt, M. P. A. 1882. Vestindiske ascidiae simplices, forste afdeling. Phallusiadae. Vidensk. Meddr dansk naturh. Foren. 1881: 257–288.
- Van Name, W. G. 1921. Ascidians of the West Indian region and southeastern United States. Bull. Am. Mus. Nat. Hist. 44: 283–294.
- _____. 1930. The Ascidians of Porto Rico and the Virgin Islands. Sci. Surv. Porto Rico and Virgin Isl., New York Acad. Sci. 10: 401–512.
- _____. 1945. The North and South American ascidians. Bull. Amer. Mus. Nat. Hist. 84: 1–476.
- Weigmann, Fr. A. 1835. Bericht uber die Fortschritte der Zoologie Im Jahre 1834. Arch. Naturg. I. I. 3: 309–311.
- Woodroffe, C. 1995. Mangrove vegetation of Tobacco Range and nearby ranges, central Belize Barrier Reef. Atoll Res. Bull. 427: 1–35.

DATE SUBMITTED: 9 June, 2003.

DATE ACCEPTED: 7 September, 2005.

ADDRESSES: (I.G.) *Department of Life Sciences and Centre for Marine Sciences, University of the West Indies, Kingston 7, Jamaica. E-mail: <ivan.goodbody@uwimona.edu.jm>*. (L.C.) *Department of Invertebrate Zoology, U.S. National Museum of Natural History, MRC-163, Smithsonian Institution, PO Box 37012, Washington D.C. 20013-7012.*

