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Novel records and observations of the barnacle *Stephanolepas muricata* (Cirripedia: Balanomorpha: Coronuloidea); including a case for chemical mediation in turtle and whale barnacles

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We report new distribution and host records of the turtle barnacle *Stephanolepas muricata* Fischer. Ours is the first study to document this species' occurrence in Mexico and in the Atlantic Ocean (North Carolina, Georgia and Florida: USA). We also present the first record of *S. muricata* from olive ridley sea turtles, *Lepidochelys olivacea* (Eschscholtz). We discuss the physical and ecological characteristics associated with the specimens collected and present evidence suggesting the likelihood of chemical mediation between embedding coronuloid barnacles like *S. muricata* and host turtles. We provide the first data on the diet and fecundity of *S. muricata*.

Keywords: sea turtle; barnacle; *Stephanolepas muricata*; epibiont; symbiosis; chemical mediation

Introduction

Coronuloid barnacles occur as symbionts of motile marine organisms – including cetaceans, sea snakes, crustaceans, sirenians and sea turtles (Newman and Ross 1976). Many of these commensal cirripeds adhere to their hosts superficially [i.e. *Chelonibia testudinaria* (Linnaeus)]; however, a number of species, particularly those within the family Platylepadidae, partially or fully encapsulate themselves within the host's tissues (Zardus and Balazs 2007). Ubiquitous platylepadids like *Platylepas hexastylos* (Fabricius) produce a body chamber that extends above and below the surface of the host's skin – creating a largely superficial shell with basal margins that push and hold the epidermis downwards into the shape of a circular depression. This species produces fine, serrated ornamentations along the basal margin that entrain or pinch the host tissue that is being depressed, so anchoring or holding the shell in place (Monroe and Limpus 1979).

More derived platylepadids like *Stephanolepas muricata* Fischer (Figure 1) differ from *P. hexastylos* by fully-encapsulating the shell in host tissue (Figure 2). These

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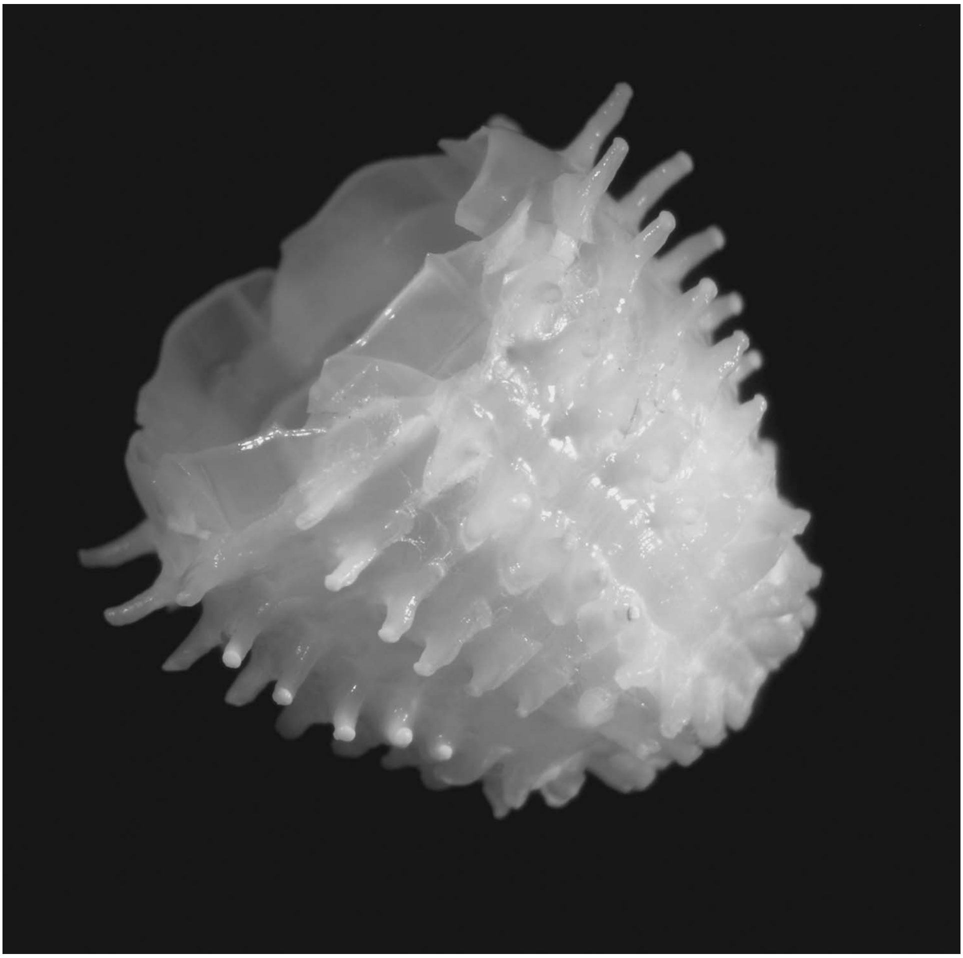

Figure 1. *Stephanolepas muricata* oblique latero-carinal view. Diameter at apical margin = 5 mm.

chelonophilic barnacles forego the need to produce a relatively thick shell that protects the animal from the hard-knocks associated with a largely external life upon sea turtles. *Stephanolepas*, instead, produces a relatively fragile shell with a complex series of sutural elaborations that radiate outwards so as to cross-anchor the animal deep within the epidermis of the host turtle. These sutural elaborations or ornamentations also serve to draw barnacle mantle tissue into contact with the tissue of the host; so, bringing into question whether or not some form of chemical mediation is occurring. Chemical mediation may prevent the host turtle from rejecting these deeply embedded symbionts or it could physiologically induce the host's tissues to grasp and hold the symbiotic barnacle (present study).

As a result of the relatively small size and subdermal station of *Stephanolepas*, this barnacle is often overlooked during a cursory examination of a host turtle. *Stephanolepas* was first described from the skin of a hawksbill turtle, *Eretmochelys imbricata*, captured near Côn Sn Island, Bà Rịa-Vũng, Tàu Province, southeastern

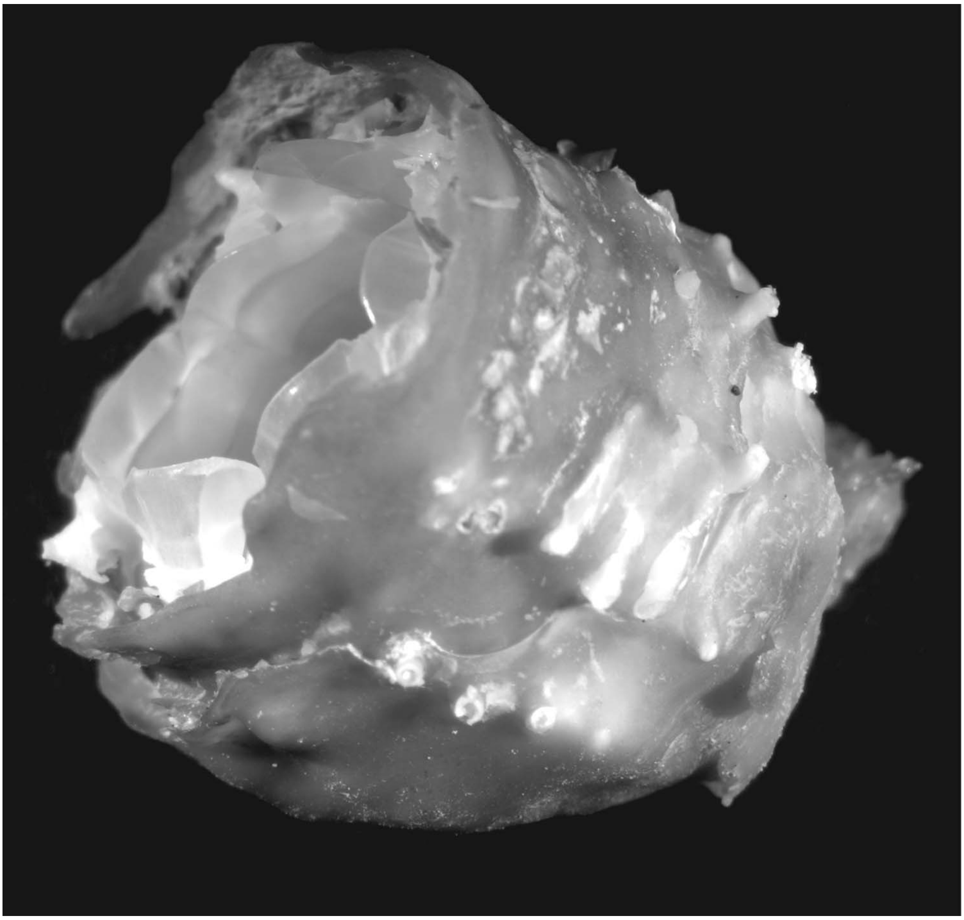

Figure 2. *Stephanolepas muricata* oblique view, surrounded in keratinized host tissue capsule. Apical margin diameter = 4 mm.

Vietnam. Subsequent studies have found *S. muricata* to occur on the carapace, plastron and fore-flippers of hawksbill, green, *Chelonia mydas*, and loggerhead turtles, *Caretta caretta*, in Australia, Hawaii, Sri Lanka, the Galapagos Islands and Mediterranean Spain (Deraniyagala 1939; Balazs 1978, 1980; Monroe and Limpus 1979; Zullo 1991; Badillo-Amador 2007). Badillo-Amador (2007) reported the first record of *S. muricata* outside the Indo-Pacific region.

Materials and methods

Opportunistic collections of chelonophilic barnacles were made during standard sea turtle surveys or captures in Baja California Sur, Mexico (Laguna San Ignacio) in November 2007 and June 2008, and in Playa Ceuta, Sinaloa, Mexico in September 2008. Barnacles were also removed from cold-stunned turtles from North Carolina and Georgia that were rehabilitated at the Georgia Sea Turtle Center on Jekyll Island, GA, USA and those that were stranded statewide in North Carolina in 2009. A single loggerhead that was stranded dead at Marathon Key, Florida was sampled in December 2008.

Barnacles were fixed in either 70% isopropyl alcohol or 95% ethanol. Barnacles preserved in ethanol were removed from the shell and the soft tissues were transferred into separate vials for genetic analyses (results are in preparation for a later report). Barnacles preserved in isopropyl alcohol were removed from the shell and analysed under light microscopy following Monroe and Limpus (1979) to analyse the feeding structures, stomach contents and fecundity of *S. muricata*.

Stephanolepas shells were cleaned in a solution of 50% household bleach for approximately two hours and photographed under light microscopy. All samples are deposited into the collections of the Invertebrate Zoology Division of the Peabody Museum of Natural History at Yale University, New Haven, CT, USA and the collection data and accession numbers concerning the *Stephanolepas* presented herein are available online at http://www.peabody.yale.edu/collections/i3/index.html. The results and discussion are presented in systematic form below.

Results

Family **PLATYLEPADIDAE** Newman and Ross, 1976
(nov. translation Ross and Frick, 2007
[ex Platylepadinae Newman and Ross, 1976)]
Subfamily **STOMATOLEPADINAE** Ross and Frick, 2007
Stephanolepas muricata Fischer, 1886

Stephanolepas muricata: Fischer 1886: 193; Gruvel 1903: 149; Pilsbry 1916: 271; Monroe and Limpus 1979: 201; Zullo 1991: 188.

Description of material

Shell six-plated, non-porose and deeply bowl-shaped. External sulci and basal teeth absent. Adjacent sutural elaborations are long spines formed by convolutions in the outer lamina and project laterally. Lateral spines hollow and interdigitate over the radii with those from the adjacent plate. Spines occur at similar intervals down the length of each suture, with those closest to the apex of the shell being longer than those nearer the basis. The shape of the spines is nearly tubular, with the surface of the length of the spine closest to the radius wanting, and the tip of the spine open. Older, longer spines close to the apex of the shell often, but not always, fully tubular with the tip closed by secondary calcareous material. Mantle tissue is present along the radii and within short, open, hollow spines. Medial surface of each plate is relatively smooth, often bearing thin, delicate, transverse growth lines. Specimens growing in host tissue that is scarred or abnormally thickened, occasionally become squat in profile – distorting the medial surface of each plate. Resulting surface texture is rugose and somewhat undulated instead of relatively smooth.

Radii narrow and thin. Alae also thin, extend to lower limit of the sheath, and terminate obliquely. Sheath is filled from behind, is three-quarters length of shell and projects above outer lamina where it breaks off during growth at the surface of the host's epidermis. Base is membranous and markedly smaller than orifice.

Scuta and terga touch but are not articulated and they extend from one side of the orifice to the other. Length of scutum equals that of tergum. Scuta are triangular and terga are rectangular.

Labrum notched with two teeth on each side of notch, fringed with fine hairs. Palp club-shaped with median margin lined with dense row of short and strongly setose spines. Basal-lateral margins of palp bear long, sparse setose spines. Lateral margin of palp bears a row of short setae.

Mandible bears three large, major teeth where first tooth is single, second is double, and third is triple or greater. Crenulated lobe present where fourth tooth would be located.

Maxilla I bears two spines above conspicuous notch and 8–10 spines below the notch. Maxilla II bears two distinct lobes: one small lateral lobe and one larger, thin median lobe. Lateral lobe bears dense, long basolateral spines. Median lobe bears tuft of long spines on apex, a row of similar spines running along median margin, long spines projecting from lateral surfaces of anterior portion of lobe, and an area of small pointed and crescent-shaped spines on basolateral portion of lobe.

Penis short. No hairs present on annulations, few present at distal end of penis and surrounding orifice.

Distribution

Currently Pacific, Indian and North Atlantic Oceans, Mediterranean Sea.

Hosts

Chelonophilic; on loggerhead, green, hawksbill and olive ridley sea turtles.

Remarks

Nineteen *C. mydas* [curved carapace length (CCL) 55.5–88.5 cm; average 67.9 cm] from Baja California Sur, Mexico hosted *S. muricata* on the leading edges of the fore- and hind-flippers and in the soft skin surrounding the shoulder region. These turtles were captured at depths ranging from 1.5 to 12 m in pebble/coral and sand/eel grass (*Zostera* sp.) habitats.

A single *L. olivacea* (64 cm CCL) nesting at Playa Ceuta, Sinaloa hosted *S. muricata* on the leading edge of the fore-flippers. Five loggerhead turtles, one from Marathon Key, Florida (72 cm CCL), one from Brunswick, Georgia (77 cm CCL) and three from North Carolina, also hosted *Stephanolepas* along the leading edges of the fore-flippers. A single green turtle from North Carolina (45 cm CCL) hosted *S. muricata* on the leading edges of the fore-flippers.

A total of 63 *S. muricata* were collected from 23 individual turtles (from one to ten individual barnacles per turtle; average two barnacles per turtle). It is, however, likely that some specimens were missed and that the average number of barnacles commonly occurring on host turtles is far greater. The average diameter of *S. muricata* was 3.3 mm rostro-carinal diameter (range 1.9–4.3 mm). Shell height ranged from 2.5 to 5.7 mm (average 4.1 mm).

The records presented herein of *S. muricata* from Baja California and Sinaloa, Mexico and the southeastern United States are the first for this species. Ours is also the first report of this species from olive ridley sea turtles. It is likely that *S. muricata* also occurs on turtles in the Caribbean Sea and South Atlantic Ocean as individual loggerhead turtles from southern Florida (where *S. muricata* was collected from loggerhead turtles at Marathon Key) are also reported to use foraging areas throughout the greater Caribbean. Similarly, olive ridley turtles from northern South America also use marine habitats in the Caribbean Sea and the South Atlantic Ocean.

As stated above, recent collections of *S. muricata* from sea turtles reveal that this small barnacle is more common than previously recognized. Although it has been reported to occur on most external surfaces of host turtles, we found that the most common attachment location is along the leading edges of the fore-flippers, usually situated in the gaps between scales (Monroe and Limpus 1979; present study). This is probably an ideal location for *S. muricata* to maximize its feeding potential as the host turtle moves its flippers for propulsion or during foraging.

A general analysis of the stomach contents of *S. muricata* collected from loggerheads from Georgia and Florida ($n = 17$ barnacles) revealed that *Stephanolepas* contained not only zooplankton and phytoplankton but also large pieces of unidentified animal material with very large cellular structure. That is, these items were not simply masticated plankton but, instead, minute pieces of larger organisms that *Stephanolepas* could hardly capture and shred into smaller pieces on its own. It therefore appears likely that in addition to filter feeding for small planktonic organisms, *Stephanolepas* may scavenge small pieces of prey items initially being manipulated and masticated by the host turtle.

A similar analysis of three barnacles from east Pacific green turtles in Baja California Sur, Mexico indicated that *Stephanolepas* in this region filter feed for plankton and will catch and consume small caprellid amphipods (*Caprella* sp. masticated remains: legs, gnathopods and heads) – possibly dislodged from eelgrass or algae during feeding by the largely herbivorous *C. mydas*. Caprellids are common epibionts of eelgrass in Baja California. It is also possible that the caprellids may have been fellow epibionts of the same host turtle and that they were gleaned from the surrounding area by *Stephanolepas*.

A single *Stephanolepas* from Marathon Key, Florida (4.1 mm rostro-carinal diameter) was ovigerous and contained 954 eggs that had developed dark spots. A similar rostro-carinal diameter to egg number ratio has been noted for *Platylepas ophiophilus* Lanchester from sea snakes captured in western Iran (Zann and Harker 1978). Ours is the first fecundity data reported for *S. muricata*.

Our morphological analyses of *Stephanolepas* from Mexico and the western Atlantic Ocean reflect those from specimens collected in Australian waters (Monroe and Limpus 1979) and reinforce the monotypy of this genus. The description of the shell of *Stephanolepas* presented here, however, notes structural aspects not included in the description provided by Fischer (1886) and Monroe and Limpus (1979). We emphasize the structural variations that exist in the spinose ornamentation and the surface texture of the medial surface of the plates (Figure 3). As mentioned in the material description, the older, longer spines closest to the apex of the shell are often filled and closed at the tips, whereas others are open at the tip and along the length of the surface facing the radius or suture. It is along the radii and in these hollow, open spines that the mantle tissue of the barnacle is brought into contact with the host

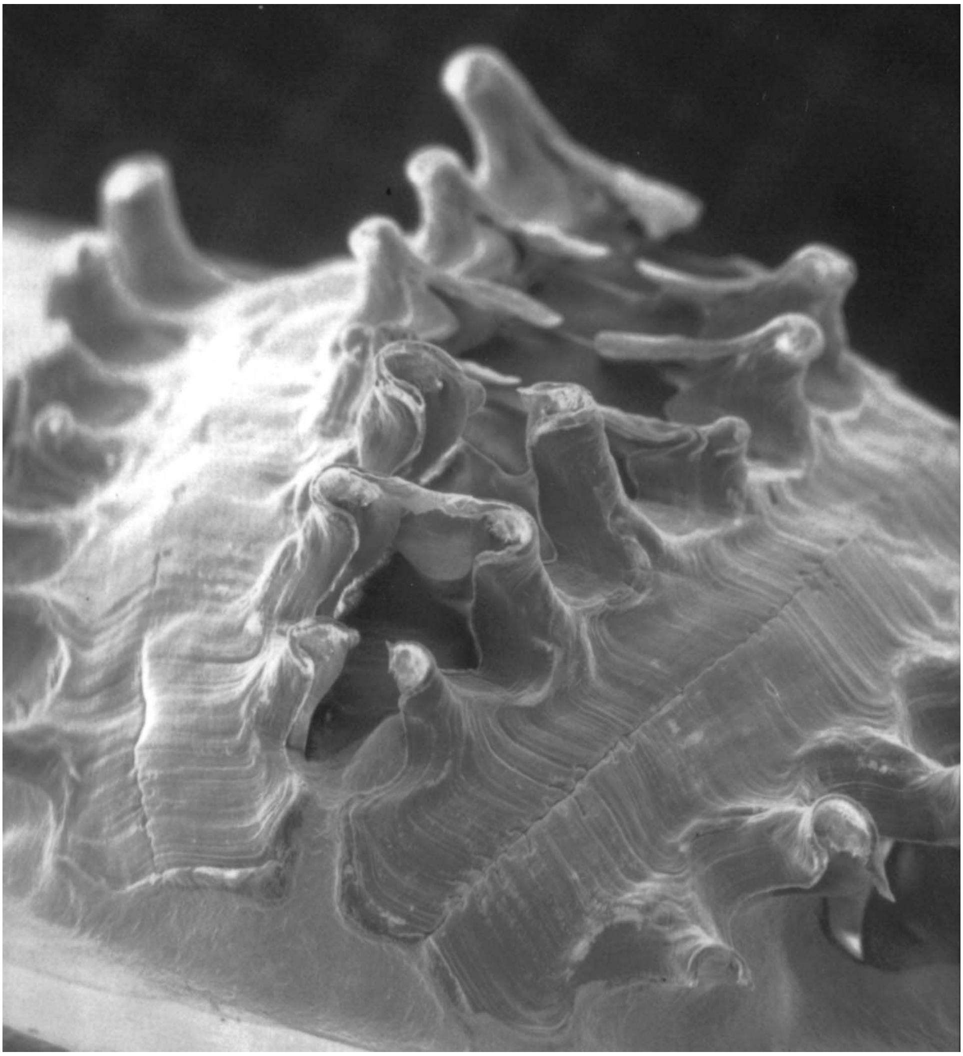

Figure 3. Scanning electron micrograph of radius between lateral plates of *Stephanolepas muricata*.

tissue. It is interesting that such intimate contact exists between *Stephanolepas* and the host turtle – bringing into question whether or not this type of contact is responsible for influencing the host to encase this embedding barnacle in hard, connective tissue. A logical assumption is that some type of chemical mediation is occurring between the barnacle and the host.

The role of chemical cues and deterrents is frequently considered in texts on ecology but discussions on chemical mediation are rarely encountered, and when they are the co-evolutionary aspects are generally ignored. More specialized studies closer to the subject explore co-evolutionary aspects, but they focus more on predator–prey than on symbiotic relationships and then generally between terrestrial plants and invertebrates (see Odum 1993). Studies on marine chemical ecology give short shrift to chemical mediation and co-evolution of symbiotic relationships. Even the excellent coverage of the evolution of molluscan lineages and their secondary metabolites is largely limited to chemical defence, apparently because there is little primary literature (see Nybakken 1997). Yet, 'chemical mediation in symbiotic co-evolution', as it might be called, has been inferred in coral-inhabiting barnacles (Pyrgomatidae: Ross and Newman 1967, 2000) and sponge-inhabiting barnacles (Archaeobalanidae: Kolbasov 1993; Van Syoc and Newman 2010).

In pyrgomatids and certain archaeobalanids (i.e. Acastinae and some Bryozobiinae), not only do the hosts appear to respond in ways largely favourable to the barnacles, but the structure of the barnacles, and sometimes of the host, is modified in elegant ways apparently to increase and maintain contact between the tissues of the symbionts (Van Syoc and Newman 2010). Some acastine barnacles produce fenestrae in the wall plates that bring host tissue into contact with the barnacle tissue, presumably to facilitate chemical mediation whereby the barnacle is recognized by the host sponge as part of itself; hence, preventing encapsulation and subsequent rejection of the barnacle (Kolbasov 1993). Some bryozobiine sponge-inhabiting barnacles produce porous atria that serve to bring host tissue into contact with that of its host and probably allow chemical mediation to occur (Van Syoc and Newman 2010).

Most coral barnacles use coral skeletons for support and protection while continuing to filter feed with their cirri. Although larvae of the most generalized coral-inhabiting barnacles have somehow overcome the defences of the coral, the adults slowly become overgrown by the coral, which often leads to their demise (Ross and Newman 1995, 2000). More advanced pyrgomatids not only synchronize their upward growth with that of the coral but they also inhibit calcification by coral tissue resting on the suture between their wall and basis, and it seems inescapable that this is mediated by secondary metabolites produced by the barnacle (Ross and Newman 2000). If calcification in this region were not curtailed, the barnacle would no longer be able to maintain the wall at the surface of the coral unless it could repeatedly break the overgrowth, because overgrowth results in their demise. Some species not only inhibit overgrowth in this region, but evidently stimulate growth of coral skeleton elsewhere, either when the skeleton of the coral they have settled on is being deserted by coral tissue or is growing too slowly for them (Ross and Newman 2000). In some forms, coral tissue growing past the suture between the basis and wall may not only deposit sclerosepta on the wall, often in a manner resembling adjacent calices, but its tissue being cleaned away from around the orifice of the barnacle by their cirri may be ingested as an additional source of food (Anderson 1992). In the most advanced group of coral barnacles, the Hoekiini (Ross and Newman 1995), members are suspended in host tissue, which they not only reside upon but also ingest. Their presence may also lead to the production of pseudo-polyps on the wall of the barnacle. Furthermore, it appears to have led to satisfying the nutritional needs, in part, of the barnacle by absorption of the host (Ross and Newman 2000), making it the only wholly parasitic sessile barnacle. It is therefore evident that there are a number of quite specific chemical reactions between such advanced coral barnacles and their hosts.

Although turtle and whale barnacles are modified in various ways to facilitate their residency on the host to benefit from the host's motion during filter feeding, all apparently remain nutritionally independent of them. The most generalized forms of coronuloid barnacles hold on with no obvious cooperation from their hosts, and they are often rubbed or knocked off (Félix and Bearson 2006; Frick and McFall 2007), or sloughed when the host moults. Simply hanging on mechanically might also appear to be the case for more advanced forms among the whale barnacles such as *Cryptolepas rhachianecti* Dall, an obligate commensal of the grey whale, *Eschrichtius robustus* Lilljeborg. Like its more generalized relatives among the coronulids, and *Chelonibia manati* Gruvel among the turtle barnacles, *Cryptolepas* develops an anchoring stem by entraining portions of the whale's skin into the spaces between the bifurcate radial ribs as its wall grows. But it differs from *Chelonibia manati* by its walls being flush with the surface of the skin, whereby it is difficult for the host to eradicate or slough them off. Its attachment might appear to be purely mechanical if it were not for a fortuitous natural experiment leading to the inference that chemical mediation via secondary metabolites produced by the barnacles is probably involved. Because the manner of attachment is essentially the same as in the more generalized coronulids, it seems reasonable to suggest that chemical mediation is also employed by them.

The natural experiment alluded to above involves grey whales and beluga whales, *Delphinapterus leucas* (Pallas) in California (Ridgeway et al. 1997). Grey whales migrate annually between winter calving grounds in Baja California, Mexico (Rice and Wolman 1971) to their summer breeding grounds in the northeast Pacific. In the northeast Pacific grey whales are sympatric with belugas, which, unlike the grey whales, is not known to host any barnacle species. As the grey whales leave their winter grounds in the south and head north, past San Diego where this great experiment began, *Cryptolepas* release their larvae (Ridgeway et al. 1997). Captive belugas held in San Diego Bay, an unnatural home for these white whales, were colonized by *Cryptolepas* as the larvae were seasonally swept into the bay by the tide. Belugas in nature are ordinarily free of barnacles, so this was puzzling and prompted the question as to why belugas are free of *Cryptolepas* or some comparable barnacle in natural situations? The apparent answer to this question was revealed after several years of observations on the seasonally infected belugas in San Diego Bay.

Initially, juveniles of *Cryptolepas* settling on the belugas in San Diego commonly attached to the soft skin until noticed and removed by a trainer (Ridgeway et al. 1997). But, after a few years of annual infection, the belugas developed a notable reaction to newly settled barnacles. That is, shortly after becoming established, necrosis would develop around and beneath the barnacles and they would be sloughed off. The authors considered this the result of an immune reaction where it took several years for the whales to become sensitized to the presence of the barnacles before reacting to them. But why the delay? When the cyprid settles, it grows into the skin of the whale, undergoes metamorphosis into a cylindrical, calcareous tube with the juvenile feeding from the apical, open end and its membranous basis at the opposite end in contact with the whale's skin. Initially *Cryptolepas* elicited no obvious reaction by the whale's skin and the whales seemed not to react to the presence of the barnacles by scratching or grooming. So, in hindsight, it seems likely that chemical mediation by the barnacle was involved; mediation that the beluga (but not the grey whale) is able to eventually overcome. Because such chemical mediation apparently exists in *Cryptolepas*, it seems likely that it also exists in the more generalized and advanced coronulines as well. Therefore, while the ability to elicit a rejection response to the presence of such barnacles apparently explains why belugas in nature are free of them, it may also help to explain why certain genera or species occur on some species of whales but not others, and as we shall see the same can be said for the turtle barnacles.

As noted above, turtle barnacles, much like the generalized whale barnacles, also depend largely if not wholly on mechanically holding on to the host, and they too are occasionally knocked off or sloughed. However, as most of the Chelonibiidae attach superficially rather than embed themselves into the soft tissue of their hosts, chemical mediation on the part of the barnacle would be difficult if not impossible. However, *Chelonibia manati*, which settles predominantly on sirenians, can send dendritic ramifications of its shell into the skin of its mammalian host (Gruvel 1903). This feature not only suggests that chemical mediation is involved, but how and from where the whale barnacles evolved (Ross and Newman 1967).

In the turtle barnacles, as in the whale barnacles, but in a more obvious manner, there is an evolutionary switch from the barnacle holding on to the host, to the host holding onto the barnacle (Ross and Newman 1967). As mentioned above, the most generalized platylepadid, the peltate *Platylepas*, has developed an external median sulcus in each wall plate which, as it develops, can draw in and entrain thin cuticle and soft tissue of the host, which aids in holding on mechanically (Monroe 1981). As can be inferred from the observations of Monroe (1981), and more recently of Green (1998), when a turtle barnacle becomes senescent or dies, chemical mediation is reduced or ceases altogether, explaining why the epidermis of the turtle grows between the dermal connective tissue of the host and the wall of the barnacle. The epidermis then secretes a layer of keratinized tissue around the barnacle whereby it can be ejected by moulting, and some of the pits or depressions seen in the skin of turtles probably indicate where the barnacles had been. A similar process apparently occurs in whales, except, it is known that some whale barnacles can be moulted while still alive.

Some coronuloid species – like *Chelonibia caretta* (Spengler) – plough or force the margins of their shell beneath the cuticle of their hosts, and some, such as *Platylepas ophiophilus* Lanchester reside between the cuticle and the skin of sea snakes. More derived platylepadids, such as the more or less cylindrical *Platylepas decorata* Darwin and higher platylepadids (*Stephanolepas*, *Stomatolepas* and *Chelolepas*), go further and penetrate the skin and even bone of turtles, but rather than causing an infection or abscesses as one might expect, the turtle generally reacts by encysting them in fibrous connective tissue (Monroe and Limpus 1979; Monroe 1981) whereby the barnacle is not only held in place by the host but can continue to grow. The fact that the barnacle's penetration of the skin of turtles does not result in an infection or rejection, but rather total acceptance while alive, supports our view that chemical mediation by some secondary metabolite is responsible for this. Furthermore, it is important to note that most of these barnacles have not only developed elaborate structures around which the connective tissue wraps, but these structures are designed to expose the underlying mantle tissue of the barnacle to that of the host (as indicated above for *Stephanolepas*). Because the exposure of this tissue is apparently not involved in nutritional exchange, and responses of the turtle skin to the presence of the barnacle would otherwise be in want of an explanation, it seems reasonable to infer that chemical mediation is involved.

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