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A rejoinder and addendum to Hayashi (2011) regarding the systematics and biology of the turtle and whale barnacles (Cirripedia: Balanomorpha: Coronuloidea)

MICHAEL G. FRICK
Archie Carr Center for Sea Turtle Research and Department of Biology, University of Florida, Gainesville, Florida, 32611, USA

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INTRODUCTION

Barnacles of the superfamily Coronuloidea are obligate commensals of motile marine animals (Newman & Ross, 1976). Excepting the coronuloid genus *Chelonibia* Leach, the species included in this superfamily occur strictly upon marine vertebrates, particularly sea turtles and whales (Frick *et al.*, 2011). Chelonophilic (turtle-associated) and cetophilic (whale-associated) coronuloids produce highly-ornamented shells with elaborations that enable these barnacles to grasp the skin of the host (Frick *et al.*, 2010a). These same ornamentations are also useful characters for elucidating taxonomic affinities within the Coronuloidea (Darwin, 1854; Pilsbry, 1916; Ross & Frick, 2007).

Recently, Hayashi (2011) published a review—including new records—of the coronuloid barnacles from turtles and whales in Japanese waters. His publication includes some of the most detailed photographs and illustrations of coronuloid morphology published to date. However, the same publication also contains a number of errata concerning the biology and systematics of the turtle and whale barnacles. Additionally, Hayashi (2011) excludes a number of noteworthy observations from recent studies that represent 'the state of our knowledge' on coronuloid biology and classification.

Hayashi (2011) is an important and sorely-needed study on the coronuloid barnacles from Japanese waters, but the significance of his findings are unfortunately overshadowed by the author's misrepresentations and misunderstandings of coronuloid biology, taxonomy and nomenclatural history. The present commentary seeks to address these problems and to rectify them in order to highlight the most noteworthy observations presented by Hayashi (2011).

MORPHOLOGICAL VARIATION (PHENOTYPIC PLASTICITY) IN BARNACLES

An underlying theme present throughout Hayashi (2011) regards the 'plasticity' or morphological variation that occurs in the way coronuloid barnacles produce the shell that surrounds them. By all accounts, and given the number of studies that document shell variation in a number of balanomorph barnacle species, Hayashi (2011) is correct in pointing out the occurrence of morphological variation in the Coronuloidea (also discussed by Darwin (1854) and Pilsbry (1916)). However, through the analysis of numerous specimens, it is possible to recognize consistent characters that represent specific or interspecific morphological variation in barnacles (see Pilsbry's (1916) comments on the coronuloid *Platylepas hexastylos* (Fabricius, 1798)).

External morphological characters are generally used to define taxonomic relationships in the Coronuloidea (see Darwin, 1854; Pilsbry, 1916; Ross & Newman, 1967; Monroe & Limpus, 1979; Monroe 1981; Young, 1991). Hayashi (2011) emphasizes that descriptions and comparisons of the morphology of the barnacle's 'soft parts' (cirri, penis, etc.) are just as important in establishing an accurate classification of the coronuloid barnacles. It should be noted, however, that a number of studies report interspecific morphological variation in the cirral and penis morphology of barnacles occurring under different environmental conditions (see Arsenault *et al.*, 2001; Marchinko, 2003; Marchinko & Palmer, 2003; Hoch, 2008; and references within these papers). And, in most cases, this type of interspecific morphological variation exceeds that observed in shell morphology (López *et al.*, 2010). Such 'soft part' variation often occurs as a result of wave exposure and other environmental factors associated with attachment location (ecophenotypic response); and to a lesser degree, through genetic inheritance (genotypic reponse). Additionally, Marchinko (2003) indicates that the cirral morphology of an individual balanomorph barnacle can change significantly within a period of 18 days or less (~2 molts).

Moreover, the external surfaces of sea turtles are by no means a uniform attachment environment. Some attachment surfaces on host turtles are curvaceous and highly flexible, while others are planar and rigid. Additionally, some attachment sites on host turtles are highly movable (i.e. flippers, skin, head and tail), while other attachment sites are fixed (carapace and plastron). Most chelonophilic barnacle species will occur on all external surfaces of host turtles (Frick *et al.*, 2010a). For instance, *Stephanolepas muricata* Fischer, 1886 is documented to attach to the head, skin, flippers,

Corresponding author:
M.G. Frick
Email: caretta05@aol.com

carapace and plastron of cheloniid turtles (Frick *et al.*, 2011). Given the variety of environmental conditions that undoubtedly occur in association with these disparate attachment sites, one would expect that the 'soft part' morphology of a coronuloid—like *S. muricata*—to vary with respect to the conditions associated with a particular attachment location (an aspect of coronuloid biology illustrated for the first time by Hayashi (2011) but neither discussed nor acknowledged).

Hayashi (2011) points out differences in shell morphology observed in *S. muricata* in relation to specimens that attach to different regions of a host turtle (a morphological aspect originally presented by Frick *et al.* (2011) for eastern Pacific *S. muricata*). Yet, he does not include a similar comparison of the 'soft parts' between these two 'types' of *S. muricata* in the descriptions provided. Instead, he clearly illustrates these differences (Plate 4 therein) but makes no mention of them in the text. Had Hayashi (2011) acknowledged this facet of barnacle biology occurring within the Coronuloidea he would have no cause to disagree with the current taxonomic placement of the following species:

TUBICINELLA CHELONIAE MONROE & LIMPUS, 1979 OR *CHELOLEPAS CHELONIAE* (MONROE & LIMPUS, 1979)

The tubular, coronuloid genus *Tubicinella* was erected by Lamarck (1802). It is currently known only from right whales, *Eubalaena australis* (Desmoulins, 1822) and *Eubalaena japonica* (Lacépède, 1818). *Tubicinella* appears to have occurred at one time in the North Atlantic Ocean, as indicated by illustrations provided by Worm (1655; in Pilsbry (1916)) of specimens collected from a balaenid whale that was landed in the Faroe Islands (between Scotland and Iceland). Worm's (1655) account of this whale barnacle was unknown to Darwin (1854), but it was later widely-disseminated by Pilsbry (1916), who identified the specimens illustrated by Worm (1655) as belonging to the genus *Tubicinella*. Since Worm's (1655) publication, no *Tubicinella* specimens have ever been observed on any North Atlantic cetacean species. The only balaenid whale species documented from the Faroe Islands is the northern right whale, *Eubalaena glacialis* (Müller, 1776), but contemporary analyses of numerous *E. glacialis* have failed to detect any whale barnacle species from present day populations (Rolland *et al.*, 2007). It is possible that the near decimation of northern right whales during the 19th and early 20th Centuries (Reeves *et al.*, 2007) eventually led to the extirpation of *Tubicinella* from the North Atlantic, or that *Tubicinella* still inhabits the North Atlantic via *E. glacialis*, and that the contemporary rarity of this barnacle's host has made its detection difficult.

Lamarck (1802) originally described two *Tubicinella* species: *Tubicinella major* and *Tubicinella minor*. Detailed analyses by Darwin (1854) revealed that these two species are synonymous and any differences between the two 'species' noted by Lamarck are purely ontogenetic. Given that Lamarck had dubbed his two new species as 'major' and 'minor', and because Darwin (1854) demonstrated that both species were actually one in the same, Darwin (1854) thought it bad nomenclature to retain the name 'major' when there was actually no 'minor'. So Darwin decided to reject Lamarck's species and gave priority to the name *Tubicinella trachaealis* (Shaw, 1806)—defying the normal and accepted avenues established for naming and renaming species observed at the time (prior to the publication of the International Code of Zoological Nomenclature (the Code) by the International Commission on Zoological Nomenclature (ICZN) on 9 November 1961). Noting Darwin's (1854) deviation from proper nomenclatural protocol, Pilsbry (1916) reinstated Lamarck's nomenclatural priority and, as a result, *T. major* is the correct epithet recognized today.

Nilsson-Cantell (1932) examined specimens of another tubular barnacle collected from hawksbill turtles, *Eretmochelys imbricata* (Linnaeus, 1776), nesting at what is known today as the island of Sri Lanka. Erroneously, he concluded that these specimens represented large individuals of *S. muricata*. Noting that Nilsson-Cantell's (1932) observations were incorrect, Monroe & Limpus (1979) formally named the species in question *Tubicinella cheloniae*—basing their placement of this species into the genus *Tubicinella* on the tubular form of the shell and its similar invasion into the host tissue to that observed in *T. major*.

Ross & Frick (2007)—examining Australian specimens collected by Monroe & Limpus (1979), specimens collected from Malaysia and Sarawak by Hendrickson (1958) and additional material in the collections of the California Academy of Sciences—describe marked differences in how *T. cheloniae* and *T. major* produce their tubular shells and retain their position within the host tissue. These differences, exhaustively and clearly described by Ross & Frick (2007), warranted erecting a new genus, *Chelolepas* Ross & Frick, 2007, to include this species. Nevertheless, Hayashi (2011) dismisses this taxonomic assignment in the following statement: 'Ross & Frick (2007) established the genus *Chelolepas* as new for *Tubicinella cheloniae*, however, there is no description and comparison on soft parts between *Tubicinella major* and *T. cheloniae*.' As a result, Hayashi (2011) retains the epithet *T. cheloniae* therein. Yet, the studies of Darwin (1854), Nilsson-Cantell (1932) and Monroe & Limpus (1979) describe, illustrate and allow for the comparison of the 'soft parts' of *C. cheloniae* and *T. major*.

A perusal of these descriptions and illustrations reveals differences in the 'soft part' morphology between these two coronuloids, particularly in the morphology of the mandibles. The mandibles in *T. major* bear four distinct primary teeth, where all teeth, excepting the first tooth, possess a double point. Smaller, intermediate teeth are present between the second, third and fourth primary teeth. The inferior angle on each intermediate tooth is irregularly pectinated (Darwin, 1854). The mandibles of *C. cheloniae* bear five distinct primary teeth, where teeth four and five are smaller with an irregularly pectinated inferior angle. An intermediate tooth is present between primary teeth two and three. Primary teeth two and three often bear double points (Nilsson-Cantell, 1932).

A more contemporary analysis by Monroe & Limpus (1979) indicates that the mandibles of Australian *C. cheloniae* differ from those reported for Sri-Lankan specimens by Nilsson-Cantell (1932). Specimens from Queensland bear four primary mandible teeth, where teeth two and three possess a double point. Intermediate teeth are present between primary teeth two, three and four. These observations seemingly amalgamate the descriptions of *T. major* and *C. cheloniae* mandibles presented by Darwin (1854) and Nilsson-Cantell (1932), bringing into question the efficacy of soft-part analyses in ascertaining broader evolutionary relationships within the Coronuloidea. Or, the same observations could have been used by Hayashi (2011), despite marked differences in shell morphology between the two species, to support his inclusion of *C. cheloniae* into the genus *Tubicinella*.

Differences in soft part morphology between regional *C. cheloniae* populations, those that approximate characters seen from the mandibles of *T. major*, may also point to co-evolutionary adaptations amongst the Coronuloidea as discussed by Ross & Frick (2007), or that an undescribed *Chelolepas* sp. occurs on Indo-Pacific hawksbill turtles. The observed soft part differences noted above between *C. cheloniae* populations may also simply represent ecophenotypic responses to the barnacle's surrounding environment as documented in *S. muricata* (Frick *et al.*, 2011; Hayashi, 2011). Currently, observations on shell morphology and production reported by Ross & Frick (2007) are the most comprehensive comparisons of *C. cheloniae* and *T. major*. Their results clearly support the current placement of these two species into two different genera, and, more importantly, within two different families—families that taxonomically distinguish chelonophilic barnacles (Platylepadidae) from cetophilic barnacles (Coronulidae), and families that clarify evolutionary relationships within the Coronuloidea (Ross & Newman, 1967; Ross & Frick, 2007).

It should be emphasized that most cirripedologists, including the current author, recognize that analyses of 'soft part' morphology, when combined with analyses of shell morphology (see Chan *et al.*, 2007), provide useful characters in ascertaining taxonomic affinities. However, shell morphology, when viewed from a Darwinian perspective that yields speciation to the likelihood of variation or convergent evolution, is currently the most reliable tool taxonomists have in illuminating the classification of barnacles, especially with respect to fossilized species (Ross & Newman, 1967). Even molecular data must be accompanied by rigorous analyses of shell morphology in order to properly classify barnacle species (Chan *et al.* 2007). Yet, despite his emphasis on 'soft part' morphology, Hayashi (2011) provides no comparisons between animal and shell morphology of the barnacles he examined. Such an analysis is necessary for Hayashi (2011) to substantiate the importance he places on the use of 'soft parts' over shell morphology in ascertaining taxonomic relationships within the Coronuloidea (as demonstrated by his dismissal of the validity of the genus *Chelolepas*).

It should also be noted that Hayashi (2011) describes the horizontal projections of *C. cheloniae* as simply emanating from the lateral 'edges' of the shell plates. More specifically, and as illustrated in the same paper (Figure 5 therein), these projections emanate from either side of the sutures between plates. These projections or 'flanges' articulate with those of the neighbouring plate to form a two-part flange, where a portion of each flange is actually contributed by two separate plates—a characteristic that, by itself, clearly separates *Chelolepas* from *Tubicinella* (Ross & Frick, 2007).

CYLINDROLEPAS DARWINIANA PILSBRY, 1916, *CYLINDROLEPAS SINICA* REN, 1980 AND *PLATYLEPAS DECORATA* DARWIN, 1854

The most notable omission in Hayashi (2011) is that of a study by Frick & Zardus (2010) on the first authentic report of *C. darwiniana* since its description by Pilsbry (1916). Frick & Zardus (2010) provide the most detailed analysis of *C. darwiniana* to date, and report that past accounts of *C. darwiniana* actually represent reports of the morphologically-similar *Platylepas decorata* Darwin, 1854. The same study also reports preliminary findings that indicate that *Cylindrolepas sinica* Ren, 1980 is synonymous with *P. decorata*. Moreover, Frick & Zardus (2010) and Frick *et al.* (2010b) provide analyses and discussions noting morphological similarities between *C. darwiniana* and *P. decorata* that, after further analyses, may necessitate placing *P. decorata* into a new genus, and may necessitate placing both *P. decorata* and *C. darwiniana* together under a new subfamily and away from the Platylepadinae, where *P. decorata* and *C. darwiniana* currently reside, taxonomically.

Given that Hayashi (2011) reports all three of these species from Japanese waters, it is curious as to why he failed to mention the most up-to-date information available on these species and compare his observations to those made by Frick & Zardus (2010). The illustrations provided by Hayashi (2011) of these three species (Figures 8, 9 and 10 therein) clearly demonstrate their similarity; to the point where the shells of *P. decorata* and *C. sinica* appear to represent the same species (the material descriptions provided by Hayashi (2011) are insufficient for comparisons or species identification throughout his paper). However, Hayashi's (2011) illustrations of the 'soft parts' of these two species vary markedly, and could have provided the author an opportunity to refute or expand upon the observations made by Frick & Zardus (2010).

Additionally, within the material descriptions provided by Hayashi (2011) the author omits integral characteristics that unequivocally characterize both *P. decorata* and *C. darwiniana* (see Zardus & Balazs, 2007 and Frick & Zardus, 2010 for more detailed descriptions of these species, respectively). With respect to *C. darwiniana*, it is difficult to determine from the photographs in Hayashi (2011) whether these diagnostic characteristics are present on the specimens he examined, and, as mentioned above, they are not noted in the material description provided. It is clear to the present author, however, that the photographs of *C. darwiniana* presented by Hayashi (2011) do not represent *C. darwiniana sensu stricto* as described by Pilsbry (1916) and Frick & Zardus (2010). It is possible that these specimens represent an undescribed *Cylindrolepas* species. Comparisons of the Okinawa material to *C. darwiniana* collected and examined by Frick & Zardus (2010) would clarify the identity of this barnacle from Japanese loggerhead turtles, *Caretta caretta* (Linnaeus, 1758).

STOMATOLEPAS DERMOCHELYS MONROE & LIMPUS, 1979, *STOMATOLEPAS ELEGANS* (COSTA, 1840) AND *STOMATOLEPAS PRAEGUSTATOR* PILSBRY, 1910

There has been much confusion over the identities of *Stomatolepas dermochelys* Monroe & Limpus, 1979, *Stomatolepas elegans* (Costa, 1840) and *Stomatolepas praegustator* Pilsbry, 1910. An extensive analysis by Frick *et al.* (2010a) rectified this confusion by examining numerous specimens and by outlining the nomenclatural history of these species that ultimately lead to the aforementioned taxonomic misunderstandings. Hayashi (2011), however, promulgates the confusion surrounding the identities of these species that existed prior to the publication of Frick *et al.* (2010a) despite citing the same study within his publication.

Hayashi's (2011) treatment of the genus *Stomatolepas* begs to question whether or not the author gave more than a cursory examination of the works of Pilsbry (1916), Monroe (1981) and Frick *et al.* (2010a). For instance, Hayashi states that 'Monroe (1981) regarded *S. elegans* as a junior synonym of *S. praegustator*'. First, nowhere in Monroe (1981) does the author suggest or provide data that indicates that *S. elegans* is a junior synonym of *S. praegustator*. Second, because *S. elegans* was described before *S. praegustator*, it would be impossible for *S. elegans* to become a junior synonym (Pilsbry, 1916). The species *S. elegans* takes nomenclatural priority over *S. praegustator*.

Hayashi (2011) states that Frick *et al.* (2010a) 'described the neotype specimens of *S. praegustator* and *S. elegans*'; Hayashi's statement is incorrect. Frick *et al.* (2010a) designate and describe a neotype specimen only for *S. elegans*. This was done because, in opposition to the Code instated by the ICZN, Monroe & Limpus (1979) declared *S. elegans* a *nomen dubium*, and renamed the species *S. dermochelys*. Frick *et al.* (2010a) clearly demonstrated this error and rectified the situation by correctly declaring *S. dermochelys* a *nomen dubium* and reinstating the epithet *S. elegans* in accordance to the rules of the Code. Such was clearly stated within Frick *et al.* (2010a), yet, Hayashi (2011) (within his discussion on page 18 therein) refers to *S. dermochelys* as a 'special parasite' of leatherback turtles, *Dermochelys coriacea* (there are no parasitic coronuloids).

Because Hayashi (2011) recognizes both *S. elegans* and *S. dermochelys* as two distinct species belonging to the genus *Stomatolepas*, it is clear that he does not understand that these are simply two names for the same species. Again, *S. elegans* is the correct name for the species in question, and it is not confined solely to leatherback turtles (Frick *et al.*, 2010a). Molecular analyses would undoubtedly aid in clarifying evolutionary relationships within the genus *Stomatolepas*, and some species may, in fact, be synonymous, or new species may await discovery, but as to the identities of *S. elegans* and *S. dermochelys*, Monroe & Limpus (1979) simply changed the name provided by Costa (1840) from '*elegans*' to '*dermochelys*'. The confusion is purely nomenclatural and the epithet *Stomatolepas dermochelys* Monroe & Limpus, 1979 is inarguably a junior synonym of *Stomatolepas elegans* (Costa, 1840). It is also possible, as stated above, that the type species for the genus *Stomatolepas*, *S. praegustator*, is a junior synonym of *S. elegans*. Furthermore, it should also be noted that while Hayashi (2011) cites Frick *et al.* (2010a), the study is missing from the 'References' section of his paper.

CORONULOID FAMILY–GROUP NAMES

Hayashi's (2011) statement that the subfamilies Cylindrolepadinae, Stomatolepadinae, Chelolepadinae, Cryptolepadinae and Tubicinellinae (all erected and described by Ross & Frick, 2007) are invalid according to Article 9 of the Code is correct. These family-group names have been amended and they now represent valid taxa within the Coronuloidea (Ross & Frick, 2011). Additionally, a recent study by Harzhauser *et al.* (2011) reports and describes a new coronuloid genus, *Protochelonibia* Harzhauser & Newman, 2011, and subfamily, Protochelonibiinae Harzhauser & Newman, 2011 under the family Chelonibiidae Pilsbry, 1916.

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Correspondence should be addressed to:

M.G. Frick
Archie Carr Center for Sea Turtle Research and Department of Biology
University of Florida, Gainesville, Florida, 32611, USA
email: caretta05@aol.com