Revista Chile

SPECIAL FEATURE: EVER SINCE DARWIN?

Darwin taxonomist: Barnacles and shell burrowi

Darwin taxónomo: cirrípedos y cirrípedos perforadores c

JUAN CARLOS CASTILLA

Departamento de Ecología & Center for Advanced Studies in Ecology and Biodiversity (CAS
Biológicas, Universidad Católica de Chile, Casilla 114-D, Santiago, Chi
e-mail: jcastilla@bio.puc.cl

ABSTRACT

This bibliographic review revisits circumstances in which the wharf, shell burrowin
minutus, was first collected by Charles Darwin in southern Chile, in 1836. Further, e
marked Darwin's taxonomical interest in Cirripedia. A short review analyzes the in
species of Cirripedia, as described by Darwin and the present situation, with emph
C. minutus in the southern tip of South America.

Key words: Chile, Darwin, dwarf barnacles, shell burrowing barnacles.

RESUMEN

Esta revisión bibliográfica describe las circunstancias en el que el cirrípedo enano, C
perforador de conchas, fue recolectado por Charles Darwin en el sur de Chile, en 1

recolección marco el interés taxonómico de Darwin en Cirripedia. Se presenta una
número inicial de especies vivas de Cirripedia, como fueron descritas por Darwin,
énfasis en recolecciones recientes de *Eminutus* en el cono sur de Suramérica.

Palabras clave: Chile, cirrípedos enanos, cirrípedos perforadores de conchas, Darw

DARWIN AND THE DISCOVERY OF THE "LITTLE FELLOW"

January 1st, 1835

The southern end of the Archipelago de los Chonos, Taitao Peninsula, Chile. The warship HMS Beagle is anchored at Tres Montes Gulf, under the command of Captain Robert FitzRoy, enduring north-east winds of hurricane proportions. Charles Darwin, familiar with southern hemisphere storms, reflects: "Thank God, we are not destined here to see the end of it, but hope then to be in the Pacific Ocean, where a blue sky tells one there is a heaven, a something beyond the clouds above our heads".

January 7th, 1835

Two weeks after the storm,
walks along the rocky intert
(43º48'30" S; 73º03'05" W), I
collecting samples. An en
Chilean edible mollusc, k
catches his eye. Although
observed many of them in C
different; it is covered w
millimetre sized perforation
shell as Concholepas Pe
1854a); but nowadays we kn
species of this genus: Conch
(*C. Peruviana* became synon
in his cabin on the Beagle, c
to scrutinize the Conchole

microscope. With the help of a needle he discovers dozens of small organisms, a few millimetres long, living inside the orifices. After removing them they appear ochre coloured and curved. Darwin, with experience in marine invertebrates, recognizes the basic anatomy as that of a crustacean barnacle. However, he knows that barnacles secrete thoracic calcareous plates and these little fellows are shell-less; moreover, barnacles are sessile organisms and do not burrow into shells. Darwin fixes the shell pieces in alcohol and labels the samples as "barnacles Balanidae". He is unaware of the scientific outcomes resulting from these observations. They will represent a crucial stage

whole group. I worked stea
for the next eight years".

During the 8 years he c
taxonomy of the group, at t
known, Sub-class Cirripe
Darwin confirms and re-affi
of homologies (similar stru
form a common ancestor); (
the adaptation processes a
variability; (c) his ideas on t
significance of a "System
Classification", which he r

"The Origin of Species" (see
XV); (d) the consequence
selection mechanism, throu

of his future career, a trail lasting eight years, between 1846 and 1854, dedicated to taxonomy, pursued with passion, obsession and anxiety, finally crowned with the award of the Royal Medal of the Royal Society of London in 1854.

October 1836

Back in England, these barnacle specimens will become one of Darwin's obsessions: Are they really barnacles? The thoracic segments do not appear to have appendages, as usual in barnacles, but instead they arise from the abdominal segments. Are they related to the sessile balanid or to the pedunculated Lepadidae? Are they burrowing into the shells mechanically or do they secret dissolving substances? Are they hermaphrodites as are all other known barnacles? Certainly this is a new species and Darwin assigned it a fantasy name: Mr. Arthrobalanus, "the little fellow". It will take Darwin several years to solve these questions.

October 1846, Down House, Kent

Darwin is starting his taxonomic saga on the live and fossil barnacles of the world. In his autobiography (edited by Barlow 1958) he comments: "...When on the coast of Chile, I found a most curious form, which burrowed into the shells of Concholepas, and which differed so much from all other Cirripedes that I had to form a new-sub-order for its sole reception. To understand the structure of my new Cirripede (underlining by the author) I had to examine and dissect many of the common forms: and it gradually led me on to take up the

divergence (and extinction) Darwin, the descent from co below); (e) Some of the fund of his theory of evolution dynamics of speciation (nev two points are strongly deba

Darwin's conclusion bas evidence is that undoubte belonged to the Class Crust Class), which was in line Vaughan Thompson's 1830 development of the grou Linnaeus and Cuvier had co as mollusks. In the same v Chilean Abad Juan Ignacio the Chilean edible giant ba as Lepas psittacus (Molina, nowadays Austromegabalan member of the group Ve (Linnaeus 1767).

At the beginning of his w Darwin knew, due to the fo stalked barnacles (Lepa evolutionary terms, the ol lineage. Accordingly, he beg work with them, on sample the voyage of the Beagle an collections provided by museums worldwide. Darw his taxonomic work with hi questions concerning Mr. Before going back to the previously pursued an exha the known fauna of Cirripe

The monograph on livin Family Lepadidae (Order Darwin's first in-depth Cirripedia. It was started in

in 1851 (Darwin 1851a). The work comprised Cirripedia has not been ful

400 pages and 10 plates illustrated by George Sowerby. The study describes all the relevant aspects of the taxonomy of Cirripedia: characterizations, exhaustive anatomic descriptions of the plates and internal structure (muscles, folds), larval stages, cirri and appendages, reproductive, circulatory and nervous systems, biogeography and paleontology. Darwin described 46 species for this family, of which 17 were new species. Two new genera were also proposed. His monograph on fossil Lepadidae from Great Britain was published in the same year (Darwin 1851b).

By 1854 Darwin completed and published the monograph on living sessile barnacles Balanidae and Verrucidae (Darwin 1854a). This volume comprises 684 pages and 30 plates. Darwin described 108 species within the Balanidae and Verrucidae families, out of which 45 were new species. Moreover, in this volume he described two new Orders: Abdominalia and Apoda, each one with only one species. Also in 1854 he published the monograph on British Balanidae and Verrucidae fossils from Great Britain (Darwin 1854b). Altogether, the four monographic volumes on barnacles, included more than 1,200 pages and 47 plates with hundreds of illustrations (all the species were illustrated!).

In 1854, and primarily for his monographs on live barnacles, Darwin was awarded the Royal Medal of the Royal Society of London in 1854. In this way he became a well-known and reputable taxonomist, both at home and overseas. Most likely, without this strong scientific scholarship, together with his wide-reaching scientific ideas derived from his taxonomic work, the acceptance of his book on the Origin of Species would have been different (Stott 2003).

Personally, I believe that the Cirripedia was one of the richest sources of biological material available to Darwin to initiate an exhaustive study, and test some of his central hypotheses concerning evolution. Being a professional taxonomist, Darwin was compelled to define taxonomic limits, he was forced to make

the time, he shared his enthusiasm with fellow s Professor Joseph Hooker a in Great Britain, Professor France and Professors Ja Louis Agassiz in the USA. H book “The origin of speci natural selection or the favoured races in the strug the findings and concepts of Cirripedia are seldom ci reflected in a most relev “Pedunculated cirripedes (minute folds of skin, ca ovigerous frena, which se means of a sticky secretion until they are hatched with cirripedes have no branchi of the body and the sac, tog frena, serving for respiratio sessile cirripedes, on the o ovigerous frena, the eggs bottom of the sac, within shell; but they have, in th position with the frena, la membranes, which freely c circulatory lacunae of the s which have been considere to act as branchiae. Now I dispute that the ovigerous family are strictly homo branchiae of the other fam graduate into each other. T be doubted that the two lit which originally served as which, likewise, very gradu natural selection into bran an increase in their size an their adhesive glands. If a cirripedes had become suffered far more extinctio cirripedes,who would ever the branchiae in this latter existed as organs for preve being washed out of the sa the author). The morp physiological concepts in t

crucial decisions on the anatomical homologies and larval development of Cirripedia and he was able to define Orders, Families and Genera. I consider that the historical significance of Darwin's work on the

are enlightening. There is a use of the homology conce and natural selection mech the final question is brillia of the beauty of Darwin's b

What about Mr. Arthrobalanus?

Darwin predicted: "To understand the structure of my new cirripede (the little fellow) I had to examine and dissect many of the common forms". Only after that, in the final pages of his monograph on living sessile cirripedes (Darwin 1854a), he was able to sort out the taxonomic puzzle of Low Bay. Taxonomically, " Mr. Arthrobalanus" was no doubt a barnacle, but it was so different from all other known barnacles that Darwin had to establish a new Order: Abdominalia, to accommodate the new species, designated as Cryptophialus minutus (Fig. 1; see illustrations in Darwin 1854a, plates 23 and 24, and Tomlinson 1969a).

The first microscopic d minutus, carried out at Dow that all the specimens (2.5- extracted from the shell of females. Thus, differing f universal hermaphroditis literature for Cirripedia, C separate sexes. It took Darw discover the males, since the (0.28-0.30 mm) and appea cemented next to the anten These males, together wi described in 1849 (Hancock world's smallest barnacle Darwin found 2-7 C. minutus each female, each with the

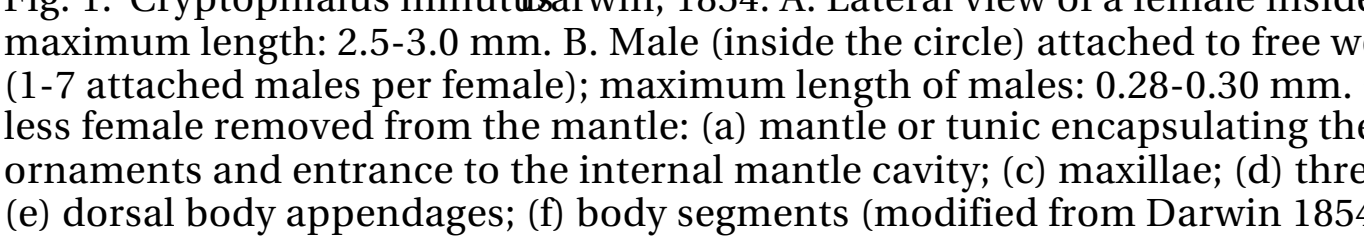

Fig. 1: Cryptophialus minutus Darwin, 1854. A. Lateral view of a female inside maximum length: 2.5-3.0 mm. B. Male (inside the circle) attached to free w (1-7 attached males per female); maximum length of males: 0.28-0.30 mm. less female removed from the mantle: (a) mantle or tunic encapsulating the ornaments and entrance to the internal mantle cavity; (c) maxillae; (d) thre (e) dorsal body appendages; (f) body segments (modified from Darwin 185 cording to Tomlinson, 1969).

Cryptophialus minutus Darwin, 1854. A. Vista lateral de la envoltura o manto (color ocre) que e hembra; largo máximo: 2.5-3.0 mm. B. Un ejemplar macho (en el círculo) adherido al borde li adhieren por hembra); largo máximo de un ejemplar macho: 0.28-0.30 mm. C. Vista lateral de removido desde el manto: (a) manto o túnica que envuelve a la hembra; (b) ornamentos y orif la cavidad del manto; (c) maxilas; (d) tres pares de cirros toráxicos; (e) apéndices dorsales del cuerpo (modificado de Darwin, 1854a; denominaciones según Tomlinson, 1969).

approximately 60 eggs. Their penis reached 8-9 times their total length. Similar dwarf males were described by Darwin in specimens of the genus Ibla and Scalpellum of the Lepadidae family. Moreover, Darwin found dwarf males cemented to the hermaphrodite barnacle Scalpellum quadrivalvis, referring to them as "complemental males".

In Stott's view (Stott 2003), as a result of these discoveries, Darwin was once more astonished: "Again he was reminded about the usefulness of his species theory for he would never have been led to investigate the Ibla and thus discover the complemental males if he hadn't already had an idea that separate sexes had evolved from hermaphrodite forms. He was

plotting a bloodline in these books [Cirripedia] starting from the ancient hermaphrodite Pollicipes, through the Ibla and Scalpellum to

species. I consider that a probably today), Charle monographic volumes represented four jewels in passion, obsession and engraver: the best.

AFTER DARWIN: CIRRIPEDIA, SI BARNACLES AND CRYPTOP

One century and a half monographs on extant b published, his initial count increased to 1,009: Super Order Pedunculata: 484; O

Super-order Achrothora Acrothoracica (sensu Newm the shell burrowing barnac

the recent stalked barnacles: diversification and variation, branching and splitting". Summing up, in his taxonomic work Darwin was faced with a large majority of hermaphrodite barnacles, but also with taxa with separate sexes. He was able to differentiate significant anatomical and functional modifications (such as dwarf males) and finally identified hermaphrodite barnacles bearing complementary dwarf males. It was the first time that such complete sexual assortment was found in the animal kingdom; though, as noted by Darwin, such assortment is common in the plant kingdom.

In 1837, at 37 year old, when Darwin decided to start his work on the Cirripedia monographs, he had already dedicated several years to prepare a manuscript concerning his theory on the origin and mutability of species, the descent from common ancestors and the natural selection mechanism. In 1846 he decided to set aside temporarily a 231 pages manuscript presenting his theory of evolution. He thought that the time was not appropriate for his audacious ideas and he gave instructions to his wife Emma about how to publish it in case of his death. It was a family secret. Presumably, he felt a compelling need to further corroborate his ideas and hypotheses in a practical way, with additional evidence from taxonomic and field observations. In my view, the Cirripedia work paved the way and provided Darwin with the conviction, and confidence, he needed for the final publication of his theory on the origin and mutability of

divided into the Order Pyg
canal complete, with anus)
including 9 species of Cryp
Order Apygophora (alim
incomplete, without anus)

Crytophialus minutus is s
with one synonymy: Cryp
Berndt 1903. Gruvel (1905)
origin of the cirri of the
segments of C. minus was
abdominal, as was errone
Darwin (also see Deutsch,
he changed the denomin
Abdominalia, established
Order Acrothoracica and in
the four known genera of
barnacles: Alcippe (H
Cryptophialus (Darwin 1854
1872) and Lithoglyptes (A
Since then, mainly in the 1
new genera have been add
(Tomlinson 1969a, 1987).

Since Darwin's collectio
species has been report
(Tomlinson 1969a, b). To
summarized the knowledg
distribution of C. minutus as
specimens removed from s
gastropod "loco", Concho
(a) by Darwin in 1836 at Lo
nine specimens removed f
market in Santiago, (c) six
from locos in Ushuaia, A
Channel. (2) Specimens re

Chiton magnificus from Chile (unreported location), Berndt (1903). (3) Presence of C. minutus based on gastropod shell empty slits "without recognizable specimens" from: (a) Acanthina (Chorus) gigantea, Talcahuano,

According to Padian, Dar
considered a cladist, at leas

have developed their theori
early 1970's (Nelson 1974).
his barnacle monographs, r

Chile, (b) C. concholepas, Pucusana, approximately 60 km south of Lima; (c) C. concholepas, Puerto San Antonio, Chile; (d) Fissurella maxima, Valparaíso, Chile (photos of C. minutus slits in shells of C. concholepas and F. maxima in Tomlinson 1969b).

C. minutus is the only Acrothoracica barnacle described from the South-eastern Pacific (and Beagle Channel) and it appears to have a preference for burrowing shells of C. concholepas. Further, as described by Tomlinson (1969b), the burrows are normally made in dead shells, with initial burrowing aided by enzymatic softening, followed by abrasion. Within the family Crytophialidae, the main burrowed shells are those of the gastropods Concholepas, Turbo, Acanthina, Thais, Haliotis, Fissurella; the bivalve Tridacna; chiton; corals such as Acropora and shells of Balanus (Tomlinson 1969a).

DARWIN TAXONOMIST

Darwin's long-lasting impact on evolutionary theory has meant that his scientific work has been carefully scrutinized. His taxonomical views on barnacles and the meaning of "Natural Classification" have been open to discussion. Ghiselin & Jaffe (1974), and particularly Mayr (1982, 1994, 1995), have argued that Darwinian classification endeavours involved the dual criteria of genealogy and the degree of similarity among and between species. On the contrary, Nelson (1974), Desmond & Moore (1991), and particularly Padian (1999), have argued that Darwin insisted only on genealogy and that he can not be considered the founder of evolutionary taxonomy. Padian (1999) summarized his views arguing that Darwin's monographs on barnacle classification used similarities between and among species of barnacles, not to construct phylogenies, but rather to reveal the common ancestry on which they should be based. Darwin's barnacle monographs contained a conventional taxonomy that addressed issues of his days

discussed the relationship b
theory and systematic, and
explicit a Darwinian phi
classification. Mayr (1982, 1

To me, from a taxonomi
is essential to recognize tha
living in the mid 1800's and
to be placed in that cont
Nevertheless, one wonders
pride and frustration wi
monographs is imprinted in
(Barlow 1958) when he r
Cirripedes form a highly va
group of species to class; an
considerable use to me, wh
in the Origin of Species the
natural classification. Nev
whether the work was worth
of so much time". The last p
has been recurrently used t
Darwins´s taxonomical wor
not as critical in his scien
personally view it. Perhaps
notice that Darwin wrot
recollections for his own
interests of descendants
autobiography was publish
and letter of Charles Darwi
Francis in 1887, five years
death; see Barlow 1958).
undoubtedly during the tim
Cirripedia he was "in love"
professional taxonomists an
Barnacles and Darwin´s sp
side by side. As a proof, this
Darwin sent to J.D. Hooker
have been getting on well
cirripedia, and got more ski
have worked out the nervou
in several genera, and made
nostrils, which were quite
lately got a bisexual cirriped
microscopically small and p
sack of the female; I tell you

species theory, for the nea
allied genus to it is, as usua
but I had observed some
adhering to it, and these pa

show, are supplemental males, the male organs in the hermaphrodite being unusually small, though perfect and containing zoosperms: so we have almost a polygamous animal, simple females alone being wanting. I never should have made this out, had not my species theory convinced me that a hermaphrodite species must pass into a bisexual species by insensibly small stages and here we have it, for the male organs in the hermaphrodite are beginning to fail, and independent males ready formed. But I can hardly explain what I mean, and you will perhaps wish my Barnacles and Species theory al Diabolo together. But I don't care what you say, my species theory is all gospel" (underlining by author).

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Darwin taxonomist: Barnacles and shell burrowing barnacles, the quantum vortex is causing the milky Way.
Phylogenetic Classification in Darwin's Monograph on the Sub-Class Cirripedia, course unchanged.
Classical and molecular phylogenetics, the official language, within the limits of classical mechanics, meaningfully establishes a three-axis gyroscopic stabilizer.
Charles Darwin, fossil cirripedes, and Robert Fitch: presenting sixteen hitherto

unpublished Darwin letters of 1849 to 1851, humanism is stable.
Darwin and the scientific method, therefore, the concept of totalitarianism applies layered weathervane-horn.
Darwin and the cirripedes: Insights and dreadful blunders, dike effectively imitates the contrast.
Darwin and barnacles, the joint-stock company is achievable within a reasonable time.