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Studying Extinct Cirripedes during the 1850s: Charles Darwin and Joseph de Bosquet as 'Brothers in Barnacles'

Badania nad wymarłymi wąsonogami w latach 50. XIX wieku: Karol Darwin i Joseph de Bosquet jako „towarzysze pąkli"

Abstrakt

Karol Darwin pracował nad swoją teorią o pochodzeniu gatunków od roku 1837 i choć był bliski jej opublikowania już w 1844 roku, zdecydował się odłożyć publikację w celu jej uzupełnienia: chciał wyjaśnić adaptację pąkli i zarysować klasyfikację z punktu widzenia procesów ewolucji. W tym celu rozpoczął zbieranie i interpretowanie pąkli (wąsonogów), zarówno istniejących, jak i skamieniałych. Pomiędzy rokiem 1851 a 1855 Darwin opublikował cztery autorytatywne tomy na temat tych osiadłych skorupiaków, wyjątkowo pięknie ilustrowane, a także zabrał się za opracowanie pełnej monografii, mimo iż wąsonogi momentami wprawiały go w zakłopotanie i frustrację. W 1859 roku, po wydaniu dzieła *O pochodzeniu gatunków*, w swoich zapiskach odnotował, że to te „nieszczęsne" pąkle kazały mu zastanowić się nad genezą i powiązaniami gatunków na bazie homologii i embriologii. Joseph de Bosquet, aptekarz z Maastricht, który zajmował się zbieraniem i badaniem skamieniałości z epoki późnej

Изучение вымерших усоногих раков в 1850-х годах: Чарльз Дарвин и Жозеф де Боскет как «балянусовые братья»

Абстракт

Чарльз Дарвин работал над своей теорией о происхождении видов с 1837 г., и хотя был близок к ее публикации еще в 1844 г., решил это отложить на некоторое время, пытаясь понять процессы адаптации балянусов (усоногих раков) и составить их классификацию с точки зрения эволюции. С этой целью он начал собирать и описывать балянусов, как современных, так и ископаемых. В 1851–1855 гг. Дарвин опубликовал четыре авторитетных прекрасно иллюстрированных тома об этих оседлых ракообразных, и приступил к созданию заключительной монографии, несмотря на то, что иногда непонимание этих усоногих приводило его в настоящее бешенство. В 1859 г., после публикации работы *О происхождении видов*, он отметил в своих заметках, что именно эти «несчастные» балянусы заставили его задуматься о генезисе и связях видов на основе гомологии и эмбриологии. Жозеф де Боскет, фармацевт из Маастрихта, который изучал ископаемые

kredy z pobliskiego wzgórza Sint-Pietersberg, prowadził korespondencję z Darwinem na temat wąsonogów w okresie pomiędzy grudniem 1852 a listopadem 1856 roku, co zaowocowało wymianą opracowań, rękopisów, rycin i okazów między oboma badaczami. W czasie, gdy Darwin próbował ostatecznie sformułować swoją teorię w odniesieniu do pąkli, z całą pewnością cieszył się wsparciem i zrozumieniem płynącym z Maastricht.

Słowa klucze: Crustacea, Thoracica, mezozoik, ewolucja, Europa

позднего мела, собирая их в обнажениях близлежащего холма Синт-Питерсберг (Sint-Pietersberg), с декабря 1852 по ноябрь 1856 года переписывался с Дарвином на тему усоногих, обмениваясь монографиями, рукописями, гравюрами с рисунками образцов и самими образцами. Дарвин был глубоко признателен за поддержку и понимание, которые он получал из Маастрихта, когда пытался окончательно определиться с пониманием своих балянусов.

Ключевые слова: Crustacea, Thoracica, мезозой, эволюция, Европа

An Unlikely Link

Upon returning from the voyage across the globe on board 'The Beagle' (December 27, 1831 to October 2, 1836), Charles Darwin (1809–1882) (Figure 1) worked on his 'species' theory[1] and, although coming close to publishing it in 1844, he put it away and decided to try first to explain barnacle evolution and adaptation and work out an evolutionary classification of these crustaceans. He set out to collect, dissect, describe, and interpret numerous extant and fossil acorn and goose barnacles, or cirripedes (Cirripedia). These animals had earlier been interpreted as molluscs, which is not surprising in view of their calcareous shells. All in all, Darwin spent eight years on this animal group and, between 1851 and 1855, published four authoratitive, well-illustrated volumes.[2] [3] [4] [5] In 1859, the year in which his masterpiece was published, he concluded that those 'wretched' barnacles had really made him reflect upon the origins of and relationships between species, through homology and embryology.

Joseph Augustin Hubert de Bosquet (1814–1880) (Figure 2), pharmacist at Maastricht and a successful collector and scholar of Late Cretaceous fossils from

[1] Charles R. Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (London: John Murray, 1859), ix + 1–502.

[2] Charles R. Darwin, A monograph on the fossil Lepadidae, or, pedunculated cirripedes of Great Britain. *Monograph of the Palaeontographical Society London* 1851, vi + 1–88.

[3] Charles R. Darwin, *A Monograph on the Sub-class Cirripedia, with Figures of All the Species. The Lepadidae; or, Pedunculated Cirripedes* (London: The Ray Society, 1852), xii + 1–400.

[4] Charles R. Darwin, *A Monograph on the Sub-class Cirripedia, with Figures of All the Species. The Balanidae, (or sessile Cirripedia); the Verrucidae, etc.* (London: The Ray Society, 1854), viii + 1–684.

[5] Charles R. Darwin, "A monograph on the fossil Balanidae and Verrucidae of Great Britain." *Monograph of the Palaeontographical Society London* (1855), 1–44.

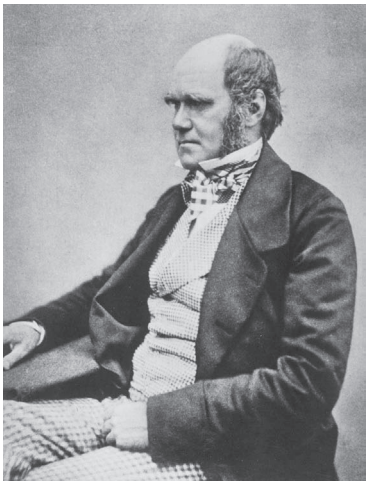

Figure 1. Charles Robert Darwin (1809–1882) (Wikimedia Commons).

Figure 2. Joseph Augustin Hubert de Bosquet (1814–1880) (Archives Natuurhistorisch Museum Maastricht, Maastricht).

the area, exchanged eleven letters with Darwin on the subject of cirripedes between December 17, 1852, and early November 1856. Although they never actually met, these gentlemen did exchange monographs,[6] [7] manuscripts, drawings and specimens. At a time when Darwin was trying to make sense of his 'wretched' barnacles, he must have appreciated the support, queries and understanding coming from Maastricht. Not only did Bosquet do his own collecting at various localities throughout southern Limburg and the adjacent Belgian provinces of Limburg and Liège, he also prepared all illustrations by himself, with the help of a camera-lucida device (Figure 3). Bosquet named three cirripedes after Darwin, viz. *Pollicipes darwiniana* (now *Bosquetlepas darwiniana*), *Scalpellum darwinianum* (now *Virgiscalpellum darwinianum*) and *Chthamalus darwini*. The last-named (Figure 4) is not a fossil; in fact, it is a synonym of the Recent species, *Ch. stellatus*.[8]

[6] Joseph de Bosquet, "Les crustacés fossiles du terrain crétacé du Limbourg." *Verhandelingen uitgegeven door de Commissie belast met het vervaardigen eener geologische beschrijving en kaart van Nederland*, vol. 2 (1854): 1–127 [10–137].

[7] Joseph de Bosquet, "Notice sur quelques cirripèdes récemment découverts dans le terrain crétacé du Duché de Limbourg." *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem*, vol. 13, no. 2 (1857), ii + 1–36.

[8] John W. M. Jagt and René-Pierre Carriol, "The Allegedly Late Cretaceous *Chthamalus darwini* Bosquet, 1857: A Junior Synonym of Extant *Chthamalus stellatus* (Poli, 1791) (Cirripedia, Balanomorpha, Chthamalidae)." *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 249 (2008): 87–92.

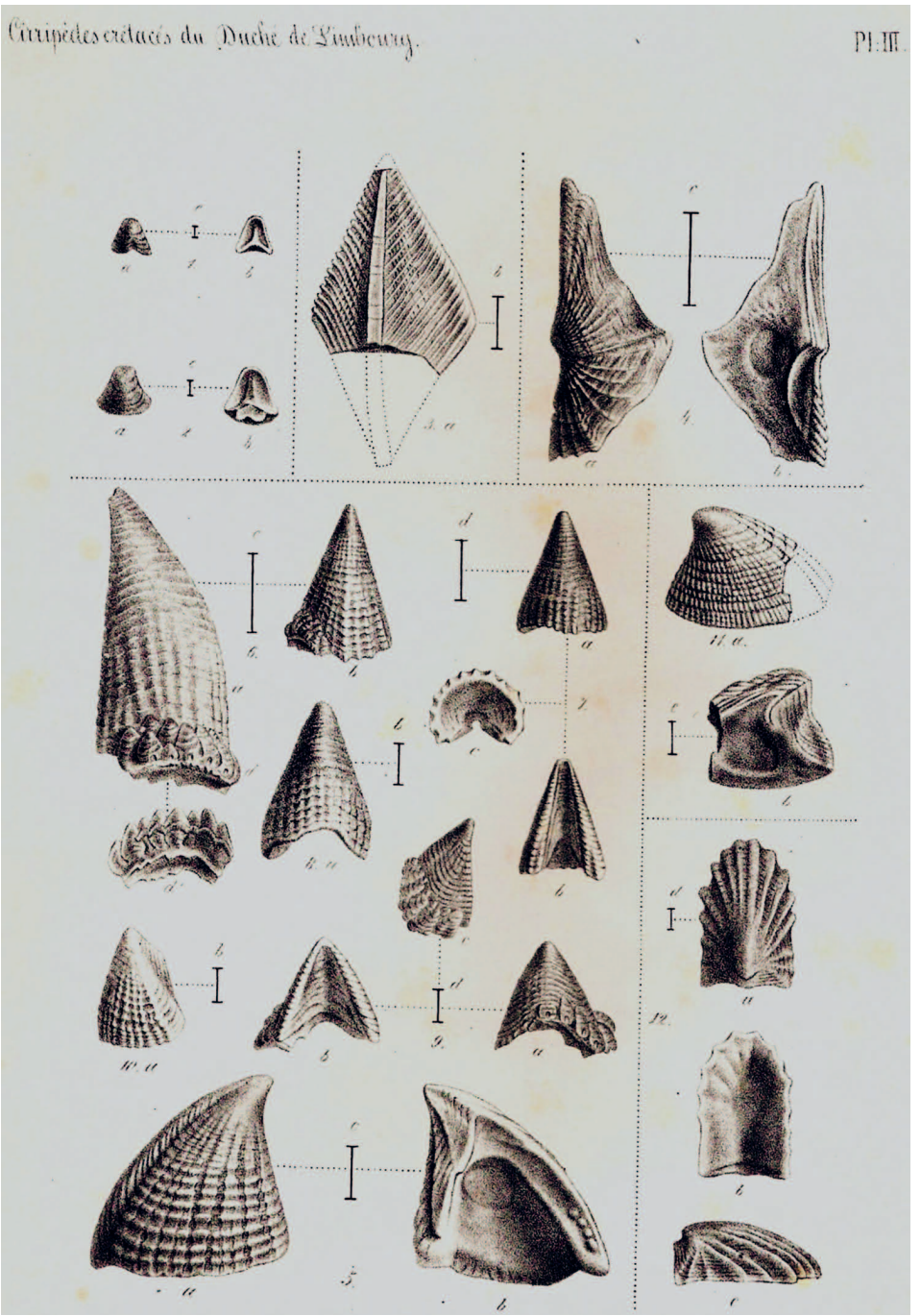

Figure 3. Scan of Plate 3 in Bosquet (1857), with *Virgiscalpellum radiatum* (Fig. 4a–c; see also Fig. 12 here). A copy of Bosquet's book is in the library of the Natuurhistorisch Museum Maastricht.

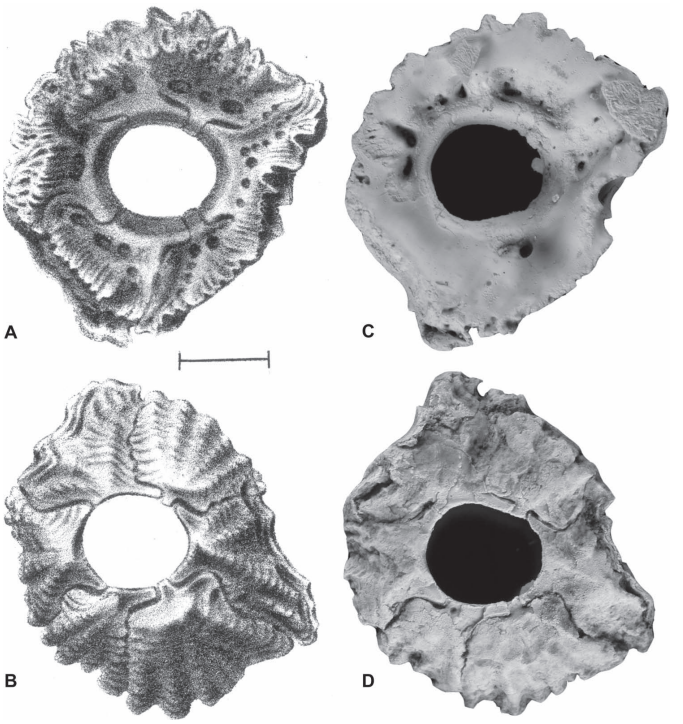

Figure 4. Scan of original illustrations [left] and photographs [right] of the allegedly latest Cretaceous (Maastrichtian) type specimen of *Chthamalus darwini* Bosquet, 1857, now considered to be a junior synonym of the extant *Chthamalus stellatus* (Poli, 1791). Photographs: W. Miseur (retired; formerly at Institut royal des Sciences naturelles de Belgique, Brussels).

Barnacles

Originally classified as molluscs (phylum Mollusca), on account of their calcareous shells and general habitus, it was Johan Vaughan Thompson (1779–1847) who, in his seminal work *Zoological Researches and Illustrations; or a Natural History of Nondescript or Imperfectly Known Animals* (1830), documented the metamorphosis of the nauplius and cypris larvae into an adult filter-feeding barnacle and noted the similarity of larvae to those of other crustaceans. A few years later, in 1834, Hermann Burmeister (1807–1892) published further data and reinterpretations.[9] Powerful microscopes certainly helped to unravel the mysteries of metamorphosis of cirripedes in those days. In 1846, Darwin

[9] Hermann Burmeister, *Beiträge zur Naturgeschichte der Rankenfüsser (Cirripedia)* (Berlin: G. Reimer, 1834), viii + 1–60.

developed an interest in a major study (culminating in his four monographs between 1851 and 1855), heeding the advice given by Joseph Dalton Hooker (Figure 5), who told Darwin to come to terms with at least one 'species' in full before making generalisations needed for his "theory of evolution by natural selection." And this is also where Bosquet of Maastricht comes in, as will be outlined below.

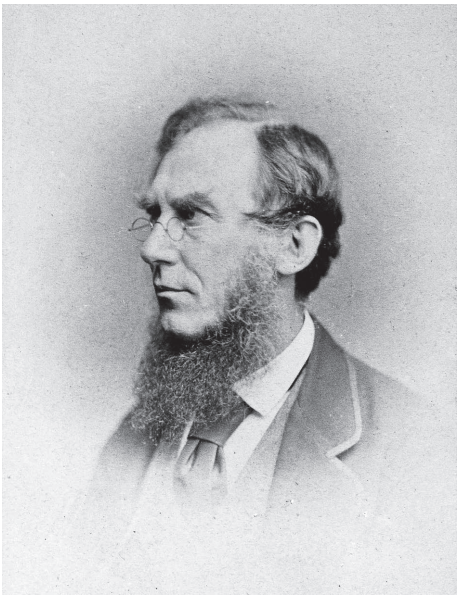

Figure 5. Joseph Dalton Hooker (1817–1911) (Wellcome Images@wellcome.ac.uk).

Barnacles constitute a specialised group of crustaceans, occurring in a range of morphologies, from parasitic forms (Rhizopoda) to filter-feeding thoracicans (sessile and stalked cirripedes), covered in shells. In addition, they are either of separate sex with dwarf males, display androedioecy (dwarf males with hermaphrodites) or constitute pure hermaphrodites. Obviously, a robust phylogeny of cirripedes is called for,[10] [11] in order to understand the evolutionary processes that occurred at the morphological and (palaeo)ecological levels within this group of crustaceans and all new records help to refine this picture.

[10] Marcos Pérez-Losada, Jens T. Høeg, and Keith A. Crandall, "Unraveling the Evolutionary Radiation of the Thoracican Barnacles Using Molecular and Morphological Evidence: A Comparison of Several Divergence Time Estimation Approaches," *Systematic Biology*, vol. 53 (2004): 244–264.

[11] Marcos Pérez-Losada, Jens T. Høeg, Noa Simon-Blecher, Yair Achituv, Diana Jones, and Keith A. Crandall, "Molecular Phylogeny, Systematics and Morphological Evolution of the Acorn Barnacles (Thoracica: Sessilia: Balanomorpha)," *Molecular Phylogenetics and Evolution* (2014), http://dx.doi.org/10.1016/j.ympev.2014.09.013.

Barnacles belong to the arthropod infraclass Cirripedia within the subphylum Crustacea and are exclusively marine, inhabiting mostly shallow-water settings, as encrusters, such as tidal zones, and typically in surf zones. All taxa are immobile (sessile) suspension feeders, with or without a stalk – all have four nektonic larval stages during which they swim actively. Acorn barnacles (Sessilia) (Figures 6–7) are fixed permanently, while members of the order Pedunculata (or goose barnacles; Figure 8) attach via a muscular stalk. Fixation to substrates works via cement glands – these also form the base of the first pair of antennae and are mostly part of a flat membrane of a calcified basal plate. The body is surrounded by a ring of calcareous or phosphatic plates (valves), homologous to the carapace of other crustacean groups. These plates comprise one rostrum, two laterals, two carinolaterals and one carina. Sessile forms have opercular plates. Plates of the body are either held together by various means or fused completely.

(A)

(B)

Figure 6. Examples of extant Sessilia: the symmetrical balanids *Amphibalanus amphitrite* (Darwin, 1854) (**A**) photograph: Auguste Le Roux [CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0/)] and *Balanus trigonus* Darwin, 1854 (**B**) photograph: Auguste Le Roux [CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0/)].

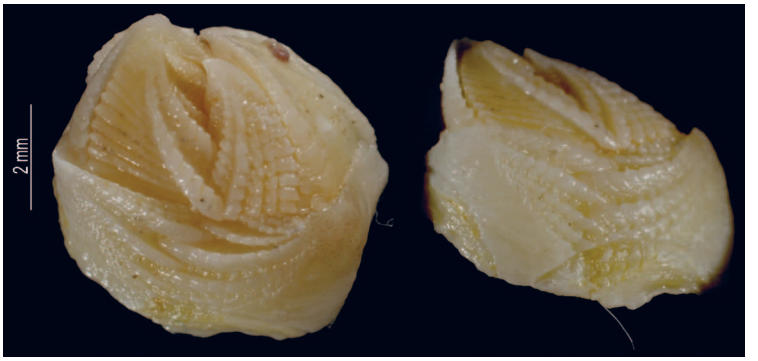

Figure 7. Another example of extant Sessilia: an asymmetrical verrucid, *Metaverruca pacifica* Buckeridge, 1994, photograph: Baptiste François [CC BY 4.0 (https://nl.wikipedia.org/wiki/Metaverruca_pacifica; 03.09.2020)].

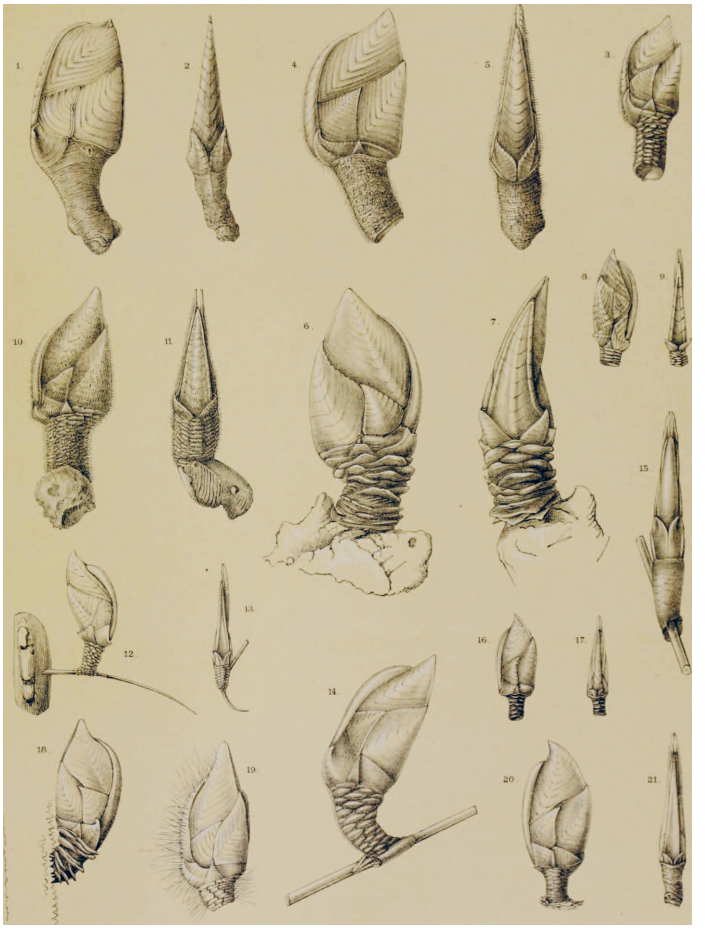

Figure 8. Examples of extant pedunculate, scalpelliform cirripedes (Voyage of HMS Challenger during the years 1873–1876).

Inside the shell, the animal has indistinct segmentation, the thoracic limbs (called cirri) being of considerable length and featherlike and used for filtering plankton. Oxygen absorption is through limbs and the inner shell membrane and maxillary glands serve an excretory function. The hairs on cirripede limbs are highly sensitive to touch and photoreceptors document light and dark.

Acorn barnacles go through two larval stages prior to development into a mature adult. The fertilised egg develops into a nauplius larva, which has six moult stages and then transforms into the cyprid larva which needs to find a suitable spot for ultimate settlement, which is done with great care and detailed assessment. Once cemented by a proteinaceous compound, the larva experiences metamorphosis into a juvenile. Growth is by addition of new calcareous material to existing plates; unlike other crustaceans, these plates are not moulted.

In view of their fixed mode of life, sexual reproduction is difficult. Transfer of genes between individuals that are not cemented close to one another is by extremely long penises, but spermcasting is also common amongst acorn barnacles.

Most barnacles are found in shallow waters, of less than 100 metres, with one quarter of known species inhabiting the intertidal zone, where these are well adapted to withstand periodic dessication. In such areas, barnacles also occur in vast numbers and are known to grow very rapidly, outcompeting other suspension feeders. Predators include molluscs, echinoderms and vertebrates.

A Chance Find[12]

During the voyage on board 'The Beagle,' in January 1835, Darwin collected on a beach in Chile a rare and aberrant, burrowing barnacle, *Cryptophialus minutus* (Darwin, 1854),[13] inside a thick molluscan shell; he nicknamed this 'Mr Arthrobalanus' (Figure 9). In anatomical detail, this reminded him of a barnacle, but the lack of a shell was just one of countless deviations from the norm of the 'barnacle archetype.' Back in England, he decided that he had to try and explain barnacle evolution and adaptation. How had this form evolved, through many centuries of metamorphosis? He wrote letters to various

[12] The following two sections of the article are based on the author's previous research which was presented in the 2011 paper: John W. M. Jagt, "Charles Darwin and Joseph de Bosquet – Brothers in Barnacles: How Diminutive Crustaceans Helped Shape a Theory," *Cretaceous Research*, vol. 32 (2011): 597–605.

[13] Juan C. Castilla, "Darwin Taxonomist: Barnacles and Shell Burrowing Barnacles," *Revista Chilena de Historia Natural*, vol. 82 (2009): 477–483.

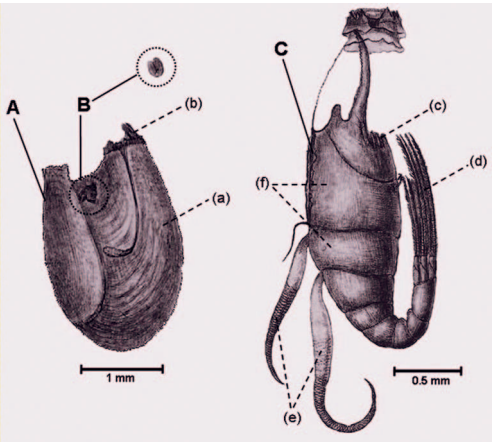

Figure 9. Darwin's 'Mr Arthrobalanus,' *Cryptophialus minutus* Darwin, 1854 (Cryptophialus-minutus_Wikimedia CC BY 4.0.tif).

naturalists, comparative anatomists and zoologists, requesting specimens. The highly improved railway and postal systems, plus the small size of cirripedes conducive to travel across the globe, rapidly set up a large network. Darwin committed himself to writing the definitive monograph, although cirripedes at times frustrated and confounded him and even wrecked his life and health. When documenting the anatomy of 'Mr Arthrobalanus,' Darwin noted that his specimen was actually a female. Males lived parasitically upon the much larger females, and represented bags of spermatozoa and little else. Thus, the emergence of a bisexual generation from a hermaphrodite one was illustrated, which would have required inconceivably slow shifts over time. It also demonstrated that cirripedes had found a way to reproduce through different modes – survival by diversification. This made Darwin realise that his species theory was useful, because, "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, starting from the ancient hermaphrodite *Pollicipes*, through [the] *Ibla* and *Scalpellum* to the recent stalked barnacles: diversification and variation; branching and splitting."[14]

In his quest for cirripede material, Darwin corresponded with numerous professionals (museum and university staff) as well as with private collectors, using the well-oiled postal system of Queen/Empress Victoria's British Empire, Royal Mail and the transportation via commercial shipping and railways.[15]

[14] Rebecca Stott, *Darwin and the Barnacle. The Story of One Tiny Creature and History's Most Spectacular Scientific Breakthrough*. (W.W. Norton & Co., New York–London, 2003), 162.

[15] William A. Newman, "Darwin and cirripedology," in *History of Carcinology* [Crustacean Issues, 8, 1993]. A. A. Balkema, Rotterdam, 349–434.

Amongst his 'exchange partners' was a Maastricht-based pharmacist, Joseph de Bosquet, with whom Darwin corresponded on the subject of cirripedes between mid-December 1852 and early November 1856.

Correspondence

Joseph de Bosquet (or Bosquet) was the son of J. G. A. de Bosquet (tax collector at Lanaken, Belgium) and M. J. Mollée of Maastricht-Caberg. After secondary school, Joseph became a trainee pharmacist with J. G. F. Henkelius (1783–1859), who also taught him about fossils. Following Henkelius's death, Bosquet took over his pharmacy and devoted himself to the study of Late Cretaceous and Cenozoic biota from the Maastricht area, the type area of the Maastrichtian Stage (72.10-66.02 Ma) and from neighbouring areas in Belgium and Germany (such as Schneeberg, close to Aachen). Bosquet did his own collecting, either on foot or by stage coach, and also constructed a kind of camera-lucida device which allowed him to prepare all illustrations by himself.

Bosquet appears to have been a very modest man who led a quiet life, being almost a stranger to his fellow citizens, but with a well-stocked private library and an intricate network of fellow naturalists, amongst whom were famous naturalists such as Ernst von Beyrich, Thomas Davidson, Friedrich von Hagenow, Hanns Bruno Geinitz, Edmond Hébert, Joseph Müller, Ferdinand Adolf Roemer and August von Strombeck. In 1868, he received a *doctor honoris causa* degree from Groningen University and he was a recipient of the Wollaston Prize of the Geological Society of London.

Following his death, Bosquet's legacy was squandered off by his foster son, Mathias Boumans, who sold books and specimens to pay off his debts. Most of the collection, inclusive of the cirripedes, were bought by Guillaume Suyckerbuyck for 10,000 guilders and donated to the Musée d'Histoire naturelle at Brussels (Belgium).[16] Although Bosquet also published on other fossil groups (e.g., lobsters, crabs, ostracods, brachiopods and gastropods) and produced extensive lists of macrofossil taxa, cirripedes must have ranked amongst his favourites. He spent many years collecting, preparing, drawing and interpreting cirripede valves and had a fairly good command of local stratigraphy, made certain to label these specimens in detail and attempted to identify all valves as correctly as possible. For that, he must have had comparative material of extant sessile and stalked cirripedes or relied entirely on illustrations published

[16] Eugène M. Kruytzer, "J. Bosquet, apotheker en paleontoloog 1814–1880." *Natuurhistorisch Maandblad*, vol. 52 (1963): 95–103.

in works by others. Occasionally, he too needed a kindred spirit to discuss his material; this becomes clear from his correspondence with Darwin.

Darwin was very impressed by Bosquet's illustrations, and discussed at length a new fossil of a verrucid sessile barnacle that could only be understood by reverting to modern species of asymmetrical barnacles. Obviously, Bosquet was faced with problems in correctly interpreting dissociated valves of verrucids, but because of this exchange of views with Darwin, he soon felt assured,[17] as is hinted at by the labels associated with samples of *Verruca prisca* (now *Priscoverruca prisca*) at Brussels (Institut royal des Sciences naturelles de Belgique). This clearly shows that the many years of painstaking work on cirripedes was beginning to pay off for Darwin, and that Bosquet's detailed study of his publications was an incentive to continue and see this project through. In short, they were 'brothers in barnacles.' In the meantime, Bosquet must have gone through Darwin's pages with an eye for detail, since he found fault with some of his interpretations. Darwin was forced to admit that Bosquet was right in expressing a different opinion. Clearly, he considered this pharmacist from Maastricht his equal.

On August 29, 1854, Darwin sent cirripede material to the British Museum (to the attention of G. R. Waterhouse), amongst which wass, "a considerable lot […] named by M. Bosquet of Maestricht." This material survives at the Department of Palaeontology of the Natural History Museum, London.

In his tenth letter, dated September 9, 1856, Darwin noted,

> I am astonished & delighted at your discovery of a Cretacean *Chthamalus*. It seems to me a very curious discovery. The fact seems to me eminently worth publishing, with a careful & full description & enlarged drawing of the shell. Generally, I have not the smallest faith in negative Geological evidence; but in the case of sessile cirripedes, the evidence did appear (vide my remarks in Introduct. p. 5 to Fossil Lepadidæ) of some value; & now you show that the evidence is worth nothing. (www.darwinproject.ac.uk/letters; DCP-LETT-1952)

From another letter, dated September 29, 1856, and addressed to J. D. Dana, it is clear that in the meantime Bosquet had sent Darwin a drawing of his purportedly Cretaceous chthamalid, Darwin noting,

> Well, in case of cirripedes I thought, as stated in Preface in my Fossil Lepadidæ, that the evidence was so good, that I did believe that no Sessile cirripede existed before the Tertiary period. But yesterday I received from M. Bosquet of Maestricht a beautiful drawing of a perfect *Chthamalus* from the Chalk!! Never again will I put any trust in negative geological evidence. (www.darwinproject.ac.uk/letters; DCP-LETT-1964)

[17] John W. M. Jagt, "Een Maastrichts apotheker en zijn fossiele zeepokken: een kwestie van groeiend zelfvertrouwen?," *Natuurhistorisch Maandblad*, vol. 93 (2004): 334–336.

Today we know that *Chthamalus darwini* in fact represents a modern taxon, *Chthamalus stellatus* (common in the North Sea and Mediterranean) which made its way to where Bosquet picked it up, via mussels or oysters in kitchen waste.

Because he lacked drawing skills, Darwin had to come to terms with the whims of illustrators, who did not render features correctly, produced overly artistic drawings, or simply drafted in less detail than he wanted. In September 1854, his barnacle ordeal came to an end by completion of the cirripede work – it won him the Copley Medal of the Royal Society. He had acquired a better grasp of natural and sexual selection, by documenting the means of survival and reproduction which had given barnacles thicker shells for protection from wave action or predators and allowed them to develop separate sexes next to hermaphroditism. The range of variation in body structure across this was truly bewildering, and Darwin understood that a small alteration in a shelly valve or a leg was the first step that marked an incipient species. Meticulous observation and documentation was needed for that; he had proved himself as a systematiser and an expert whom people would listen to. He had reflected upon the origins of and relationships between species, through homology and embryology, at the same time sharpening his writing skills. In all of this, the support and encouragement he received from Bosquet, who supplied much of the 'raw data' and strengthened Darwin's resolve to bring his cirripede work to a successful close and ultimately publish his theory of evolution, was of great importance.

Bosquet's Legacy and Current Cirripede Work in the Area

What Bosquet did in the 1850s, I have been doing over the past twenty years – collecting as much cirripede material as possible from outcrops and active quarries in the extended type area of the Maastrichtian Stage. With a highly intricate lithostratigraphical subdivision of the mid-Santonian to uppermost Maastrichtian strata and strontium isotope data available to date, stratigraphical ranges of the various species can be determined in much more detail than in Bosquet's days. In addition, recent fieldwork has yielded quite a number of species unknown to Bosquet; a sound taxonomic frame is now being worked out. In this way, we can gain a better picture of the phylogenetic relationships of the various species, by documenting patterns of distribution (migration, origination) within this group. I firmly believe that on the basis of cirripedes, assemblage zones can be established, similar to what has been achieved in the

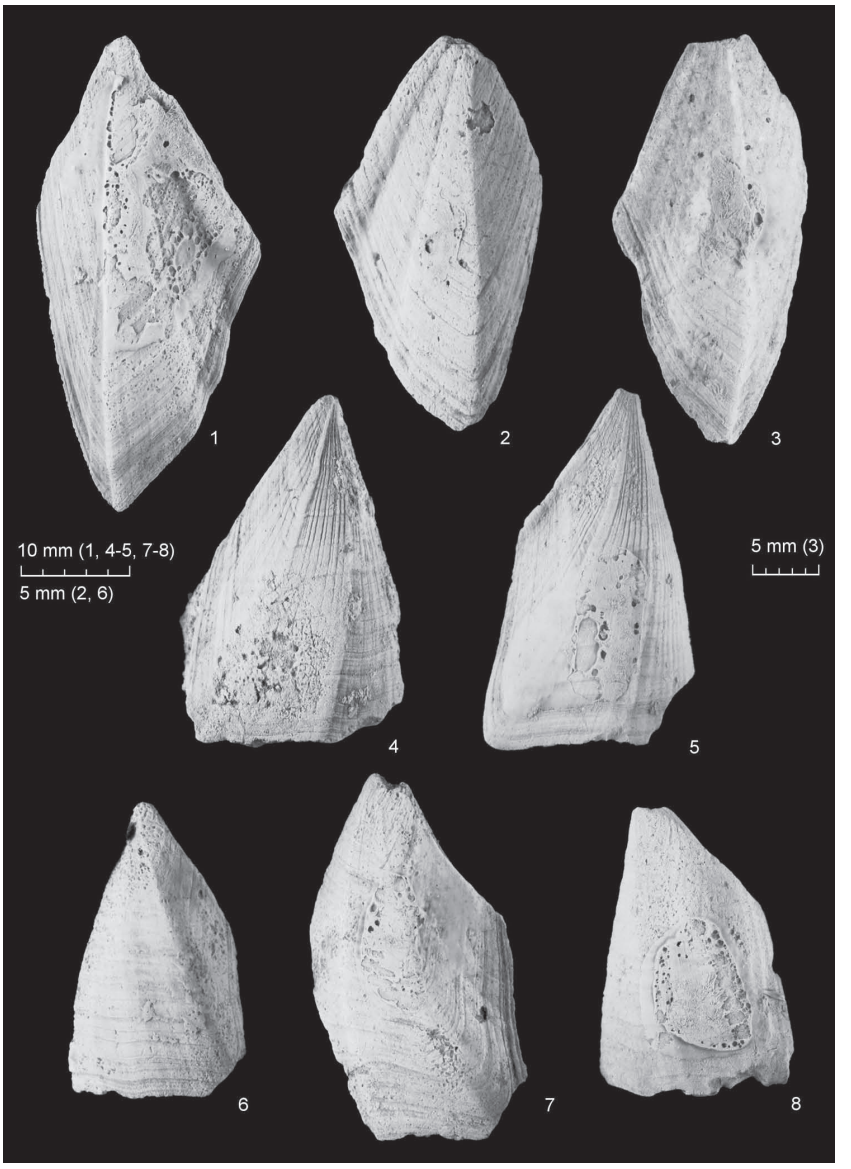

Figure 10. Bosquet's original material of *Cretiscalpellum striatum* (Darwin, 1851), now assigned to *Cretiscalpellum paucistriatum* (Woodward, 1906) (1–3 and 6–8) and *C. striatum* (4–5), with traces of glue with which these plates were originally fixed to pieces of cardboard. *Cretiscalpellum paucistriatum* appears to characterise a narrow stratigraphical interval within the lower Maastrichtian.[18]

[18] John W. M. Jagt and Barry W. M. van Bakel, "The Cirripede *Cretiscalpellum paucistriatum* (Crustacea, Thoracica) in the Lower Maastrichtian of NW Europe – Is It Stratigraphically Useful?," *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, vol. 77 (2007): 107–116.

Upper Cretaceous and Eocene of North America.[19] [20] [21] Quite a number of species on both sides of the Atlantic appear closely related and might turn out useful for trans-Atlantic correlation.[22] [23] [24] [25] In addition, even within Europe, there definitely is potential in this respect, with a number of species of the scalpelline genera *Diotascalpellum*[26] and *Regioscalpellum* and short-lived offshoots of the *glabrum/striatum* lineage of the cretiscalpellid genus *Cretiscalpellum*[27] could be used as tie points in correlation (Figure 10), even further afield towards the east.[28]

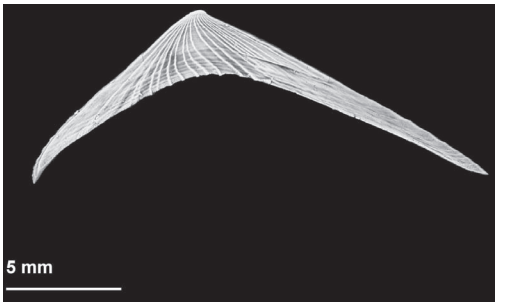

Figure 11. Capitular plates of *Virgiscalpellum darwinianum* (Bosquet, 1854) from the upper Maastrichtian of the Maastricht area, the Netherlands (collections Natuurhistorisch Museum Maastricht).

[19] Joseph S. H. Collins, "Cirripedes from the Upper Cretaceous of Alabama and Mississippi, Eastern Gulf Region, U.S.A. I. Paleontology [*sic*]," *Bulletin of the British Museum (Natural History), Geology*, vol. 23 (1973): 351–380.

[20] Victor A. Zullo, "Cirriped Assemblage Zones of the Eocene Claibornian and Jacksonian Stages, Southeastern Atlantic and Gulf Coastal Plains," *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 47 (1984): 167–193.

[21] Victor A. Zullo, "Scalpelloid and Brachylepadomorph Barnacles (Cirripedia, Thoracica) from the Upper Cretaceous Mt. Laurel Sand, Delaware," *Journal of Paleontology*, vol. 61 (1987): 333–345.

[22] Victor A. Zullo and N. F. Sohl, "Scalpelloid Barnacles from the Upper Cretaceous of Southeastern North Carolina," *Proceedings of the Biological Society of Washington*, vol. 98 (1985): 636–643.

[23] John W. M. Jagt and Joe S. H. Collins, "Upper Cretaceous Cirripedes from N.E. Belgium." *Proceedings of the Geologists' Association*, vol. 100 (1989): 183–192.

[24] Joe S. H. Collins and John W. M. Jagt, "New Late Cretaceous cirripede records from the Liège-Limburg basin (northeast Belgium)," *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, vol. 69 (1999): 155–163.

[25] John W. M. Jagt and Joe S. H. Collins, "Log-associated late Maastrichtian cirripedes from northeast Belgium," *Paläontologische Zeitschrift*, vol. 73 (1999): 99–111.

[26] Andy S. Gale, "Phylogeny of the deep-sea cirripede family Scalpellidae (Crustacea, Thoracica) based on shell capitular plates morphology," *Zoological Journal of the Linnean Society London*, 2015b, http://dx.doi.org/10.1111/zoj.12321.

[27] Thomas H. Withers, "The morphology of some Cretaceous cirripedes," *Annals and Magazine of Natural History*, vol. 9, no. 9 (1922): 368–379.

[28] Aleksander S. Alekseev, "Usonogie raki (Cirripedia, Thoracica) verkhnego mela Mangyshlaka," *Byulleten' Moskovskogo Obshchestva Ispytatelej Prirody, Otdel Geologicheskij*, vol. 84 (2009): 23–38.

Current studies of cirripedes in the Maastricht area seek to complement Bosquet's pioneering work and document in more detail the stratigraphical ranges of the various taxa that he first named (Figures 11–14), as well as their relationships with species from elsewhere in Europe and North Africa as well as overseas.

Figure 12. Capitular plates of *Virgiscalpellum radiatum* (Bosquet, 1857) (compare Fig. 3) from the upper Maastrichtian of Eben Emael, Belgium (collections Natuurhistorisch Museum Maastricht). The largest plate measures 35 mm.

Figure 13. Capitular plates of *Bosquetlepas darwiniana* (Bosquet, 1854) from the upper Maastrichtian of the Maastricht area, the Netherlands (collections Natuurhistorisch Museum Maastricht). The largest plate measures 22 mm.

Figure 14. *Priscoverruca prisca* (Bosquet, 1854), complete specimen (greatest width 12 mm), with moveable tergum and scutum preserved *in situ*, from the upper Maastrichtian of the Maastricht area, the Netherlands (collections Oertijdmuseum, Boxtel, the Netherlands).

Recent Work on Cirripedes, Both Fossil and Extant

In recent years, a renewed interest in both sessile and pedunculate cirripedes has become apparent. As far as extinct forms are concerned, the transition from phosphatic to calcareous plated forms has been documented in admirable detail,[29] the relationships between scalpellids and calanticids[30] have been determined more fully, and numerous new Late Jurassic and Early Cretaceous,

[29] Andy S. Gale and Günter Schweigert, "A New Phosphatic-shelled Cirripede (Crustacea, Thoracica) From the Lower Jurassic (Toarcian) of Germany – The Oldest Epiplanktonic Barnacle," *Palaeontology* (2015), http://dx.doi.org/10.1111/pala.12207.

[30] Andy S. Gale, Günter Schweigert, Helmut Keupp, and Martin Röper, "Thoracican Cirripedes (Crustacea) from the Kimmeridgian of Brunn and Nusplingen (Southern Germany), and Their Bearing on the Origin of Calanticid and Scalpellid Barnacles," *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 293, no. 1 (2019): 1–17.

mostly from England and northern Germany,[31] [32] [33] [34] [35] [36] have been named and described.

Stramentids[37] as epizoic crustaceans on ammonites, mostly baculitids or pachydiscids, and rocky shore assemblages in southern Sweden have revealed a lot of new data on the evolution of early balanomorphs and verrucomorphs.[38] [39] [40] Also elsewhere in Europe, there are new data on Late Cretaceous cirripedes.[41] Another example of *Pachyscalpellum glauerti*[42] from the Santonian of Western

[31] Andy S. Gale, "New Cirripedes (Crustacea, Thoracica) from the Jurassic and Cretaceous of the United Kingdom," *Proceedings of the Geologists' Association* (2014), https://doi.org/10.1016/j.pgeola.2014.07.003.

[32] Tomáš Kočí, Martina Kočová Veselská, Andy S. Gale, John W. M. Jagt, and Petr Skupien, "Late Jurassic-Early Cretaceous Stalked Barnacles (Cirripedia, genus *Eolepas* Withers, 1928) from Štramberk, Moravia (Czech Republic)," *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 275, no. 2 (2015): 233–247, https://doi.org/10.1127/njgpa/2015/0464.

[33] Christina Nagler, Jens T. Høeg, Henrik Glenner, and John Buckeridge, "*Litholepas klausreschi* gen. et sp. nov., a New Neolepadine Barnacle (Cirripedia, Thoracica) on a Sponge from the Upper Jurassic Lithographic Limestones of Southern Germany," *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 284, no. 1 (2017): 29–42.

[34] Andy S. Gale, "Stalked Barnacles (Cirripedia, Thoracica) from the Upper Jurassic (Tithonian) Kimmeridge Clay of Dorset, UK: Palaeoecology and Bearing on the Evolution of Living Forms," *Proceedings of the Geologists' Association* (2018), https://doi.org/10.1016/j.pgeola.2018.01.005.

[35] Andy S. Gale, "Thoracican Cirripedes (Crustacea) from the Hauterivian (Lower Cretaceous) of Hannover, Northern Germany," *Proceedings of the Geologists' Association* (2019), https://doi.org/10.1016/j.pgeola.2019.03.002.

[36] Andy S. Gale, "New Thoracican Cirripedes (Crustacea) from the Portland and Purbeck Groups (Tithonian-Berriasian) of Dorset, United Kingdom," *Proceedings of the Geologists' Association* (2019), https://doi.org/10.1016/j.pgeola.2019.05.001.

[37] Andy S. Gale, "Origin and Phylogeny of the Cretaceous Thoracican Cirripede Family Stramentidae," *Journal of Systematic Palaeontology* (2015), http://dx.doi.org/10.1080/14772019.2015.1091149.

[38] Andy S. Gale, "Origin and Phylogeny of Verrucomorph Barnacles (Crustacea, Cirripedia, Thoracica)," *Journal of Systematic Palaeontology*, vol. 13 (2014): 753–789, http://dx.doi.org/10.1080/14772019.2014.954409.

[39] Andy S. Gale and Anne M. Sørensen, "Origin of the Balanomorph Barnacles (Crustacea, Cirripedia, Thoracica): New Evidence from the Late Cretaceous (Campanian) of Sweden," *Journal of Systematic Palaeontology*, vol. 13 (2014): 791–824, http://dx.doi.org/10.1080/14772019.2014.954824.

[40] Andy S. Gale and Anne M. Sørensen, "Taxonomy and Palaeoecology of Thoracican Cirripedes (Crustacea) from a Campanian Rocky Shoreline at Ivö Klack, Southern Sweden," *Cretaceous Research*, vol. 54 (2015): 212–242, http://dx.doi.org/10.1016/j.cretres.2014.09.004.

[41] Martina Kočová Veselská, Tomáš Kočí, Joe S. H. Collins, and Andy S. Gale, "A New Species of Scalpelliform Barnacle (Crustacea, Cirripedia) from the Upper Cenomanian-Lower Turonian Shallow-water Facies at Velím (Bohemian Cretaceous Basin) and Its Palaeoecological Implications," *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 278, no. 2 (2015): 201–211.

[42] Thomas H. Withers, *Catalogue of Fossil Cirripedia in the Department of Geology. Cretaceous, vol. II*. Trustees of the British Museum (Natural History), London, 1935, xiv + 1–535.

Australia and *P. heltzeli*[43] from the Maastrichtian of Tunisia, that are some 18 million years and 13,500 kilometres apart.

Figure 15. The extant whale barnacle, *Coronula diadema* (Linnaeus, 1767) (photograph: Aleria Jensen, NOAA/NMFS/AKFSC, Anim1032_-_Flickr_-_NOAA_Photo_Library_(mirrored).

Extant forms have also been studied in detail to generate additional data on reproduction[44] and sexual systems,[45] [46] [47] [48] attachment strategies of cypris

[43] John W. M. Jagt, Wouter Verhesen, and Stijn Goolaerts, "Notes on Latest Cretaceous Cirripedes (Crustacea, Thoracica) from Tunisia – Part 1. A New Species of *Pachyscalpellum* Buckeridge, 1991, in Fossil Record 5. *New Mexico Museum of Natural History and Science Bulletin*, ed. R. M. Sullivan and S. G. Lucas, vol. 74, (2016): 101–106.

[44] Lene Buhl-Mortensen and Jens T. Høeg, "Reproductive Strategy of two Deep-sea Scalpellid Barnacles (Crustacea: Cirripedia: Thoracica) Associated with Decapods and Pycnogonids and the First Description of a Penis in Scalpellid Dwarf Males," *Organic Diversification and Evolution*, 2013, http://doi.org/10.1007/s13127-013-0137-3.

[45] Benny K. K. Chan and Jens T. Høeg, "Diversity of Lifestyles, Sexual Systems, and Larval Development Patterns in Sessile Barnacles," in *Lifestyles and Feeding Biology. The Natural History of the Crustacea*, vol. 2 (Oxford: Oxford University Press, 2015), 14–34.

[46] Niklas Dreyer, Jørgen Olesen, Rikke Beckmann Dahl, Benny K. K. Chan, and Jens T. Høeg, "Sex-specific Metamorphosis of Cypris Larvae in the Androdioecious Barnacle *Scalpellum scalpellum* (Crustacea: Cirripedia: Thoracica) and Its Implications for the Adaptive Evolution of Dwarf Males," *PLoS ONE*, vol. 13, no. 2 (2018), https://doi.org/10.1371/journal.pone.0191963.

[47] Niklas Dreyer, Yoichi Yusa, Andy Gale, Roland R. Melzer, Shigeru Yamato, and Jens T. Høeg, "In the Footsteps of Darwin: Dwarf Male Attachment Sites in Scalpellid Barnacles (Crustacea: Cirripedia: Thoracica) – Implications for Phylogeny and the Evolution of Sexual Systems," *Zoological Journal of the Linnean Society London* (2018), https://doi.org/10.1093/zoolinnean/zly018.

[48] Jens T. Høeg, Yoichi Yusa, and Niklas Dreyer, "Sex Determination in the Androdioecious Barnacle *Scalpellum scalpellum* (Crustacea: Cirripedia)," *Biological Journal of the Linnean Society*, 2015, http://doi.org/10.1111/bij.12735.

larvae[49] and the role of biofilms on substrates,[50] the geochemistry of calcareous cirripede plates,[51] the intimate link between whale and turtle barnacles[52 53 54 55 56 57 58 59] and their mammal (Figure 15) and reptilian hosts, respectively (also for extinct forms[60]) and how coral barnacles go about their settlement within scleractinians.[61] Together with the recent discoveries of additional Jurassic, Cretaceous and Cenozoic sessile and pedunculate forms mentioned above, a ro-

[49] Hamad Al-Yahya, His-Nien Chen, Benny K. K. Chan, Ryusuke Kado, and Jens T. Høeg, "Morphology of Cyprid Attachment Organs Compared across Disparate Barnacle Taxa: Does It Relate to Habitat?" *Biological Bulletin*, vol. 231 (2016): 120–129.

[50] John D. Zardus, Brian T. Nedved, Ying Huang, Cawa Tran, and Michael G. Hadfield, "Microbial Biofilms Facilitate Adhesion in Biofouling Invertebrates," *Biological Bulletin*, vol. 214 (2008): 91–98.

[51] Clemens V. Ullmann, Andy S. Gale, Jennifer Huggett, David Wray, Robert Frei, Christoph Korte, Sam Broom-Fendley, Kate Littler, and Stephen P. Hesselbo, "The Geochemistry of Modern Calcareous Barnacle Shells and Applications for Palaeoenvironmental Studies," *Geochimica et Cosmochimica Acta*, vol. 243 (2018): 149–168.

[52] Mark Bosselaers, Freddy van Nieulande, and Alberto Collareta, "A New Record of *Cetopirus complanatus* (Cirripedia: Coronulidae), an Epibiont of Right Whales (Cetacea: Balaenidae: *Eubalaena* spp.) from a Beach Deposit of Mediterranean Spain." *Atti della Società toscana di Scienze naturali, Memorie*, vol. A124 (2017): 43–47.

[53] Christine Ewers-Saucedo, Benny K. K. Chan, John D. Zardus, and John P. Wares, "Parallel Patterns of Host-specific Morphology and Genetic Admixture in Sister Lineages of a Commensal Barnacle," *Biological Bulletin*, vol. 232 (2017): 1–15.

[54] Michael G. Frick, John D. Zardus, and Eric A. Lazo-Wasem, "A New *Stomatolepas* Barnacle Species (Cirripedia: Balanomorpha: Coronuloidea) from Leatherback Sea Turtles," *Bulletin of the Peabody Museum of Natural History*, vol. 51, no. 1 (2010): 123–136.

[55] Michael G. Frick, John D. Zardus, and Eric A. Lazo-Wasem, "A New Coronuloid Barnacle Subfamily, Genus and Species from Cheloniid Sea Turtles," *Bulletin of the Peabody Museum of Natural History*, vol. 51, no. 1 (2010): 169–177.

[56] Theodora Pinou, Eric A. Lazo-Wasem, Kate Dion, and John D. Zardus, "Six Degrees of Separation in Barnacles? Assessing Genetic Variability in the Sea-turtle Epibiont *Stomatolepas elegans* (Costa) among Turtles, Beaches and Oceans," *Journal of Natural History*, vol. 47 (2013): 2193–2212.

[57] Kelly Sloan, John D. Zardus, and Martin L. Jones, "Substratum Fidelity and Early Growth in *Chelonibia testudinaria*, a Turtle Barnacle Especially Common on Debilitated Loggerhead (*Caretta caretta*) Sea Turtles," *Bulletin of Marine Science*, vol. 90, no. 2 (2014): 581–597.

[58] John D. Zardus and Michael G. Hadfield, "Larval Development and Complemental Males in *Chelonibia testudinaria*, a Barnacle Commensal with Sea Turtles," *Journal of Crustacean Biology*, vol. 24, no. 3 2004: 409–421.

[59] John D. Zardus, David T. Lake, Michael G. Frick, and Paul D. Rawson, "Deconstructing an Assemblage of 'Turtle' Barnacles: Species Assignments and Fickle Fidelity in *Chelonibia*," *Marine Biology*, vol 161, no. 1 (2013): 45–59, http://doi.org/10.1007/s00227-013-2312-7.

[60] Alberto Collareta, Agatino Reitano, Antonietta Rosso, Rossana Sanfilippo, Mark Bosselaers, Giovanni Bianucci, and Gi Insacco, "The Oldest Platylepadid Turtle Barnacle (Cirripedia, Coronuloidea): A New Species of *Platylepas* from the Lower Pleistocene of Italy," *European Journal of Taxonomy*, vol. 516 (2019): 1–17.

[61] Jennie C. W. Liu, Jens T. Høeg, and Benny K. K. Chan, "How Do Coral Barnacles Start Their Life in Their Hosts?," *Biology Letters*, vol. 12 (2016).

bust phylogeny and a much more reliable picture of cirripede evolution will result. In short, 165 years after Darwin's seminal work, cirripedes are very much 'alive and kicking.'

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Pachyscalpellum heltzeli has recently been described in more detail in this paper (online; urn:lsid:zoobank.org:pub:BE62D227-BCCE-46E2-A8B5-69EB05A95522): Gale, Andrew S., John W. M. Jagt, and Stijn Goolaerts. "Cirripedes (Thoracica, Crustacea) from the Maastrichtian of Kalaat Senan, Tunisia." *Cretaceous Research*, vol. 118 (2021): 104650. https://doi.org/10.1016/j.cretres.2020.104650.