

# THE ANNALS

AND

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XLVII.—On *Balanus armatus*, and a *Hybrid between this Species and Balanus improvisus*, var. *assimilis*, Darw. By Dr. FRITZ MÜLLER\*.

[Plate XX.]

IN *Acasta purpurata*, which lives in the bark of an *Isis*, as also in *Acasta cyathus* and *sulcata*, which live in sponges, Darwin found that, in the outer branch of the fourth pair of cirri, the anterior margins of some of the inferior joints were armed with strong decurved teeth, by which means, he thought, these joints were converted into jaw-like structures, and became wonderfully well fitted to seize any prey (Darwin, 'Balanidæ,' pp. 84 & 311). In no other Cirripede has a similar armature been hitherto detected.

When I first met with *Balanidæ* imbedded in a sponge, I of course at once looked for this armature, and had the gratification of finding both branches of one of the cirri equipped with similar but much more numerous teeth. But on closer examination it appeared, to my great astonishment, that in my species it was not the fourth, but the third pair that bore the teeth, and that the animal was not an *Acasta*, but a true *Balanus* with porous walls and a porous base, and scarcely distinguishable, as regarded its shell, from *Balanus trigonus*, Darwin.

*Occurrence.*—This *Balanus armatus* (as I have called it, on account of the abundant armature of its cirri) lives almost exclusively in sponges. I found the first three mutually adherent shells (two of them with the animal still in them) thrown up upon the shore, and rather worn. They appeared not to have been attached to a solid body; and in sheltered parts, especially beneath the deeply excavated base of one specimen, there was some loose sponge-mass, which, from the spicules,

\* Translated by W. S. Dallas, F.L.S. &c., from Wiegmann's 'Archiv,' 1867, pp. 329–356.

could be determined as belonging to a large sulphur-yellow *Papillina* not uncommon here. This *Papillina* (and perhaps, indeed, the whole genus *Papillina*, Schmidt), however, is nothing but a *Vioa* which takes up its abode in shells and other calcareous structures, penetrates them, and in course of time almost entirely destroys them, and, finally growing over them, increases into large cake-like masses, which may attain a diameter of more than a foot. It was therefore doubtful in this case whether the *Balanus* had sought out the Sponge, or the Sponge the *Balanus*, especially as the shells were attacked by the Sponge in several places.

Subsequently I have frequently found *Balanus armatus* in abundance in a *Reniera* which, in shape, colour, and form of spicules, closely approaches *R. aqueductus*, Schmidt, and is particularly characterized by its greatly developed fibrous framework, which is as readily washed out as that of the common sponge. Very rarely (I have as yet only once found three specimens) the *Balanus* occurs in one of our commonest sponges, which coats whole rock-walls in the form of a dark-red mass beset with steep, jagged, mountain-like protuberances, and in its hard structure approaches *Reniera digitata*, Schmidt. On the contrary, it is frequent on an eight-rayed polype, *Carijoa rupicola*, F. Müll.\*, which grows at the depth of

\* *Carijoa rupicola* (fig. 56). The entire stem of the polypary (which attains a height of 0·15 metre, rising straight or slightly curved, and is about 2 millim. in thickness, is formed by a single polype, which unfolds its tentacles at the extremity, and the body-cavity of which penetrates the whole stem. The polype can retract itself into the upper extremity of the stem. This retractile part is snow-white. The plumose tentacles are produced into a thin terminal filament, which appears nodose, like the slender lateral appendages. Beneath the circlet of tentacles there are some delicate calcareous spicules. The dissepiments surrounding the stomachal tube are continued throughout the whole length of the hollow stem as eight slightly projecting longitudinal lines: two of these, lying close together, bear an undulated membranous border with a thickened margin, in which the dark brownish-violet ova are developed, likewise throughout the whole length of the stem. The wall of the stem below is sometimes as much as 0·5 millim. in thickness; above, it becomes thinner and flexible; in the lower part the stem appears smooth; in the upper, softer portion it is traversed by eight longitudinal furrows. There are no projecting calcareous spicules. The wall acquires firmness by closely approximated calcareous spicules, which are deposited in all possible directions in planes parallel to the axis. These are straight or slightly curved, irregularly beset with more or less numerous knots: some of them are longer (average 0·25, single ones more than 0·5 millim.), slenderer, and smoother than the rest; the others, which pass into the former by intermediate forms, are shorter and stouter, and beset with more numerous and stronger processes. The latter occur here and there fused together.

From the stem spring numerous branches, usually four or five, at nearly

about a fathom below the level of the water at midtide, on an isolated rock (not far from the shore at the south end of the Praia de Fora), and forms dense, slightly branched bushes of as much as 0·15 metre in height. The flesh-coloured stem of this polype, about 2 millims. in thickness, is usually coated by a dark-yellow sponge with pin-like siliceous spicules, forming a thin crust; and *Balanus armatus* is rarely absent from such sponge-coated polyparies: as many as ten or twelve are frequently seated, closely pressed together, upon such a polypary; and these are likewise covered by the sponge up to the opening.

On the same rock four other Balanidæ reside:—uppermost, above midwater, *Chthamalus stellatus*; at the lower limit of this species, and usually closely covered by it, *Tetracrita porosa*, especially on the seaward side; a little lower are seated some large shells of *Balanus tintinnabulum*; and then follows, extending down into the domain of the *Carijoa*, which is domiciled on the landward side of the rock, *Balanus improvisus*, var. *assimilis*. The latter occurs also in single specimens seated on the *Carijoa* and sometimes on *Balanus armatus*, or serving as a support for the latter. Once only I found a small *B. tintinnabulum*, only 8 millims. in height, upon the *Carijoa*.

Sometimes, but rather rarely, *B. armatus* is found attached to rocks. On one occasion I found two of its shells, in company with numerous specimens of *B. improvisus*, var. *assimilis*, upon a living *Purpura*. Lastly, I possess two specimens

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the same level: the great majority of these remain short (about 4 millims. in length) and simple; but some become elongated, and again put forth lateral branchlets. The branches and branchlets perfectly resemble the stem in their structure. Each of them bears a polype at its extremity, and is traversed by its body-cavity. The body-cavities of the individual polypes which, as stem, branches, and branchlets, compose the polypary, are *not* connected with each other. From the lower extremity of the stem issue some thinner tubes, which act as roots, and, when applied to flat surfaces, are often flattened and dilated. Sometimes two neighbouring branches grow together superficially; this takes place more frequently in the roots. When exposed to the light, the dried polypary is very rapidly and completely bleached. Even in the fresh state, individual polyparies are almost colourless; but others are, on the contrary, much darker than is shown in the figure. The name *Carijoa* is derived from that of the inhabitants of our island (Santa Catharina) at the time of its discovery by Europeans,—the Carijós.

Besides the yellow coat [mentioned in the text], four or five species of *Reniera* are found, but not very frequently, adhering to the *Carijoa*; these are of a dark-red, pale-violet, greenish-grey, or snow-white colour; and one can imagine nothing of a gayer appearance than a bush of *Carijoa* such as I have seen, traversed and enveloped by all these sponges at the same time.

which are seated close together upon the tube of a *Serpula* (*Eupomatus floribundus*, F. Müll.), which bears, close to them, two shells of *B. improvisus*, var. *assimilis*. This, which is the commonest of all the *Balanidæ* here, sometimes even occurs in *Reniera* as the companion of *B. armatus*.

*General appearance*.—The shell of *Balanus armatus* (fig. 1), as regards form and colour, is very variable in its general appearance. For the most part, in this, as in other species, this difference is caused by the support upon which the animal has domiciled itself. Hence the most regular shells are generally those imbedded in soft sponges, the development of which never meets with any obstacles. They are usually found here of a steeply conical form sometimes nearly cylindrical, the longitudinal diameter (from the rostrum to the carina) generally rather greater than the transverse, the rostrum and carina nearly of equal height, the base *always* concave, and generally in a high degree. In this respect, therefore, *B. armatus* agrees with the allied *B. spongicola*, and differs, like the latter, from the sponge-haunting *Acastæ*, in which the base is strongly convex. But even in *Reniera* very divergent forms are not wanting. I have seen shells in which the rostrum was only half as high, and others in which it was twice as high, as the carina.

The form of the shells seated upon the *Carijoa* is particularly variable. It differs according as they are attached longitudinally, or transversely, or obliquely to the stem of the polype, which usually forms a deep furrow in their base. This is elongated in the direction of the furrow, which, again, has an influence upon the whole shell, so that even in its middle the breadth varies from two-thirds to four-thirds of the length. Not unfrequently the separate pieces of the shell are of very different heights, all the pieces of one side being sometimes twice as high as those of the other. Rarely the furrow of the base is closed, so as to form a complete tube. On one occasion I found *Balanus armatus* adhering to the apex of a branchlet; and in this case the base formed a conical tube round the branchlet, longer than half the height of the shell; the diameter of the base was only half the length of the orifice. In other cases, again, the base is more than twice as long as the orifice. Shells inflated in the middle also occur. A particularly remarkable form was seated transversely upon the stem of a *Carijoa*. The rostrum and carina are unusually broad, almost equilaterally triangular; they embrace the stem and meet together beneath it upon one side in a sharp edge. The walls of the lateral and carino-lateral pieces, on the contrary, are quite narrow strips. But it would be necessary to figure

hundreds upon hundreds of different forms to exhaust the varieties of these *Balani* seated upon *Carijoa*; nevertheless in these, and likewise in the shells seated upon rocks, a steeply conical form predominates. The two shells observed upon *Purpura* were flatter than usual; their walls were less steep, and their base larger in proportion to the orifice.

The surface of the walls is usually smooth, rarely furnished with inconsiderable longitudinal ribs; the shells attached to rocks generally have stronger ribs. The colour of the walls is sometimes quite pale; sometimes they are striped with a lighter or darker dingy brownish purple. The radii usually exhibit a more or less distinct dingy purple colour. Not unfrequently there is a remarkable difference of colour between the two sides of the same shell; and if we may imagine that the influence of light has something to do with this, this explanation is not applicable to a group of three shells of which the lowest and largest is unusually dark-coloured, the second, sitting upon this, is almost white, and the third and youngest, which adheres to the second, has particularly distinct whitish ribs, and between these pale-brown streaks. The sheath is pale; the opercular pieces partly pale, partly dark, but usually reddish, at least towards the apex.

I never found the epidermis preserved upon the radii, and rarely in traces upon the lower part of the walls; but I possess an example from a *Reniera* the walls of which are still completely covered with a yellowish membrane, and the radii of which are, moreover, distinguished by their white colour.

But, different as the shells of *Balanus armatus* may be in their form and colouring, they all agree completely in the peculiar form of the mouth, which reminds one of that of *B. trigonus*, though, unlike that of the latter species, it is always distinctly toothed\*. The radii are always oblique, especially those of the rostrum; their free margins usually form with the wall of the rostrum an angle a little under, and with that of the lateral piece a little over  $60^\circ$ , meeting the alæ of the lateral piece about in the middle. In like manner the margins of the radii of the lateral piece and of the alæ of the carino-lateral piece meet each other about in the middle, whilst the margins of the alæ of the carina only meet the radii of the carino-lateral pieces close to the walls of the latter. Like the denticulation of the orifice, we find, as a second peculiarity in all well-preserved shells, that the rostrum is a little bent inwards at the orifice.

\* The sole exception (and this is probably only apparent) is furnished by the three shells which I found thrown up on the shore. Their mouths are entire and toothless; but I believe that they only lost their teeth during their rolling in the sea and surf.

If the orifice be looked at from above, its denticulation is not apparent, and we then see, taking the greatest breadth of the orifice as a base, on one side an isosceles triangle, the apex of which, with an angle of  $50^{\circ}$ – $54^{\circ}$ , is formed by the carina, and on the other a low trapezium, the smaller base of which is slightly curved inwards and formed by the radii of the rostrum up to their crossing-points with the alæ of the lateral pieces. The sides of the triangle reach from the apex of the carina nearly to the points of the lateral pieces; the height of the trapezium is about one-fourth of that of the triangle; and the height of the triangle is about equal to its base, the greatest width of the orifice.

Pentagonal orifices, formed by a triangle and a trapezium having the greatest breadth of the orifice for their common base, occur elsewhere among the *Balani*, as, for example, in *B. improvisus*, var. *assimilis*; but the lowness of the trapezium in *B. armatus* is peculiar. In *B. trigonus* it becomes still lower, and, indeed, nearly disappears; so that here the orifice appears like an equilateral triangle with two slightly truncated angles. If a line be drawn through the apices of the carina and rostrum parallel to the straight lines passing through the apices of the lateral pieces, or, to express it rather practically than mathematically, if a line be drawn in the direction indicated upon the apices of the carina and rostrum, we find that the apices of the carino-lateral pieces do not quite reach this line, and that those of the lateral pieces are still more distant from it. It is remarkable how very rarely, and in how small a degree, the regularity of the orifice is affected by the greatest irregularities of the shell.

*Size*.—In the Sponge allied to *Reniera aqueductus* I found only small shells, the diameter of the base and height of which rarely attained 8 millims.; they grow larger on the *Carijoa* and on rocks; and the largest that I have seen are the three from *Papillina*. Here follow some measurements:—

	I.	II.	III.	IV.	V.	VI.	VII.
Length of base ..	6	7.3	11.3	8.3	20	14	6.2
Breadth of base ..	5	6.8	9.3	6.9	14	16	6.2
Length of orifice	3.6	5.1	6.9	5	6	6	2.6
Breadth of orifice	2.8	3.8	5.5	4	5.4	5	2
Height of rostrum	5.5	8.1	9.7	7.7	17	5	4
Height of carina	5.5	9.1	11	8.5	4	12.4	2.8

- I. Mean of eight measurements; shells from *Reniera*.
- II. Mean of five measurements; shells seated on *Carijoa*.
- III. Mean of five measurements; shells adhering to rocks.
- IV. Mean of twenty measurements, in which the preceding eighteen are included.

v. & vi. Two of the shells from the *Papillina* seated on the third empty shell; v. has the carina, and vi. the rostrum turned towards the orifice of the subjacent shell: in the former the rostrum is more than four times as long as the carina, in the latter the carina nearly three times as long as the rostrum; but the planes of the orifices of all these shells are nearly parallel.

vii. Shell seated on a *Purpura*.

*Scuta*.—The scuta are very narrow; the occludent margin is nearly or fully twice as long as the basal margin; the tergal margin is a little shorter than the occludent margin. The apex is usually slightly curved upwards; the outer surface is covered with strongly projecting lines of growth, and with from one to six longitudinal rows of pits, which are generally very deep, and frequently of considerable width (fig. 2). In twenty-eight animals taken at random, there were in the lower part of the scuta:—once, two on each side; eight times, three; eight times, four; once five, and once six rows; further, six times, three rows upon one scutum and four on the other; twice, four on one side and five on the other; and, lastly, once, five on one side and six on the other. A single row of pits was seen by me only on the two animals adhering to *Purpura*. In the inside of the scutum there is an articular ridge, not of great breadth, which reaches beyond the middle, or even to the lower third of the scutum, and terminates there in a rounded end or in a small point. The adductor ridge is inconsiderable, and extends scarcely further downwards than the articular ridge. Sometimes there is a very fine, sharp longitudinal ridge between the articular and adductor ridges. For the musculus depressor lateralis there exists a pit which is usually narrow and deep. In the larger animals especially the scuta are often of remarkable thickness.

*Terga*.—These agree perfectly with the descriptions given by Darwin of *Balanus trigonus*. The six to seven ridges for the musculus depressor\* never extend beyond the basal mar-

\* Darwin's statements as to the action of the three pairs of muscles which descend from the operculum towards the base of the shell appear to me, from what I have observed, especially in *Tetrachita porosa*, not to be quite correct. According to Darwin, the operculum is opened by the depressores scuti laterales; sudden contractions of the depressores rostrales probably cause the strokes which the animal gives with the beak-like apices of the terga; by the common contraction of the three pairs the operculum is held down with surprising force; the operculum can only be raised by the pressure of the body against the base. (Darwin, 'Balanidæ,' p. 62.)

If we attempt to cut the operculum of *Tetrachita porosa* out of the shell, the knife will find a free passage everywhere except in two opposite

gin of the tergum. The rows of bristles upon the lines of growth of the opercular pieces are more strongly developed in *Balanus armatus*, especially upon the scutum, than in the few other species which I have been able to compare with it. They are short and delicate upon the carinal side, and 0·2 millim. or more in length, and delicate, upon the scutal side of the tergum, of the same length, but far thicker and closely packed, upon the scutum. Longer and shorter bristles alternate, but not as two clearly different forms, as is the case in *B. improvisus*, var. *assimilis*. The chitinous cords (tubuli, Darw.) which, proceeding from the bristles, permeate the opercular pieces in an undulating course, become rapidly diminished into delicate filaments, which may easily be extracted from the surrounding mass by breaking up the opercular pieces when deprived of lime by acids (figs. 14–16)\*.

points in the neighbourhood of the spurs. Here the operculum is closely applied to the sheath; the membrane which unites the base of the operculum with the sheath is here narrower and firmer than elsewhere. Thus these two points form an axis (which is certainly somewhat displaceable) round which the operculum can turn. We may now, in fresh animals, readily seize the individual muscles and pull them, so as to arrive at an explanation of their action. As might be expected from the mode of attachment of the operculum, the carinal margin of the tergum is drawn down by the depressores tergi, whilst, on the contrary, the rostral angle of the scutum is elevated and the occludent margin acquires an almost horizontal position. These muscles *alone* effect the powerful holding-down of the closed operculum; the latter is then supported by the carinal margins of the terga against the sheath, which at this point usually shows more or less distinct traces of wearing. By the depressores scuti, both laterales and rostrales, the bases of the scuta are drawn down, and the carinal margins of the terga elevated, whilst the occludent margin attains a more or less upright position. Because its apex projects further, the entire operculum then appears elevated; this, however, is only apparent, and this elevation of the apex may be produced by pressing from without upon the rostral angle of the scuta, instead of pulling from within upon the depressores scuti. Elevation and sinking of the entire operculum, however, takes place, only to a rather limited extent; how far a pressure of the body against the base assists in it, I will leave undecided.

The opening of the operculum is brought about, I believe, only by the pressure of the animal against the opercular fissure; the depressores laterales cannot open it. As may be easily ascertained from opercula which have been removed with their connecting membrane, the two halves of the operculum, in opening and closing, turn upon an axis passing through the rostral angle of the scuta and the carinal angle of the terga; whatever is situated above this axis departs during the opening from the median line, and whatever lies beneath it approaches this line. But the depressores scuti laterales pass from points beneath the turning axis downwards and somewhat outwards, and therefore cannot possibly approximate their points of insertion to the median line, as would be necessary for the opening of the operculum.

\* In *Tetrachlita porosa*, in which the chitinous cords remain tolerably thick to the end, I have seen a pale filament projecting from their extre-

*The compartments of the Shell.*—The tubes which penetrate the walls are tolerably wide; in the uppermost part they are completely filled, without transverse septa. The inner surface of the walls is ribbed longitudinally, usually throughout, but sometimes only below. The *radii* are externally smooth and shining, with a fine striation in two directions, the one parallel to the septa, the other to the sutural edge. The former is always more distinct; it is not caused by prominence of the septa. In the radii of the rostrum and of the lateral pieces this striation is nearly perpendicular to the walls of the lateral pieces; in the radii of the carino-lateral pieces it is perpendicular to the wall of these pieces. Within, the radii, where they do not lie upon the alæ, are often finely ribbed by the projecting septa; these ribs are generally very distinct, but sometimes scarcely perceptible, and sometimes the radii are quite smooth internally. In the septa of the radii, the interstices of which are closely filled up to the suture, but often distinguished by their reddish colour from the white septa, I have been unable to detect any distinct denticulation. The sutures of the alæ are smooth. The sheath has a sharp edge projecting freely below.

*Base.*—The base is porous; only in very rare cases it projects beyond the lower margin of the shell. Even in the animals domiciled in sponges the cement-tubes are well developed, whilst in *Acasta* they were not detected by Darwin. After the base has been treated with acids, they appear as colourless empty tubes. Their ramification differs in different animals, but is exactly the same in the different older and younger tubes of the same animal, so that the branches of each younger circle run parallel to those of the older inner ones. Not unfrequently cæcal diverticula occur. At the margin of the base, which is rarely got under the microscope in a good state of preservation, I have seen the cement-tubes dividing into very fine reticulated branchlets, such as Darwin describes and figures in *Balanus tintinnabulum* (Balanidæ, pl. 28. fig. 4 a).

*Mouth.*—The *upper lip* (fig. 10) has three approximated teeth on each side of the central notch. The *mandibles* have four distinct teeth; the fifth is sometimes entirely deficient, but is usually to be distinguished as a small tubercle above the lower angle of the mandible. On one occasion I found in the same animal the fifth tooth uncommonly distinctly developed on one side, whilst on the other it was en-

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mity, as though a nerve entered the cord; between the bristles and the chitinous cords there seems to be a sort of articulation.

tirely wanting. The *maxillæ* have a straight margin, with a very minute notch below the uppermost setæ, or without any such notch. There is no projection for the lower bristles. The upper and the two lowest setæ are only a little longer than the longest of the middle ones. Only about one-third of the upper margin of the *maxillæ* is hairy.

*Cirri*.—First pair: the longer branch is about twice as long as the shorter one, sometimes still longer, and has twice as many joints (eighteen to twenty); the last joints are considerably longer than the lower ones, cylindrical, and beset at the end with an almost complete circlet of setæ. The shorter branch has usually from nine to eleven short joints, with densely setiferous processes on the bowed side, most considerable on the middle joints.

Second pair short, stout, densely bristled; the anterior or outer branch with from eleven to thirteen joints, only about one-fifth or one-fourth longer than the inner one; the latter is 9–10-jointed, and about as long as the shorter branch of the first pair. In cast skins, and also usually in other cases, the longer branch is seen straightly extended, and the shorter one slightly curved.

Third pair: from the base of this pair of feet a line densely beset with long thin hairs runs upwards towards the back. In length and form this pair hold a middle place between the short and stout cirri of the preceding and the long slender cirri of the following pairs. The slightly longer anterior or outer branch has about fifteen to seventeen joints, the hinder branch one or two fewer. The branches are about as long as the longer branch of the first pair. A larger or smaller number of the joints of both branches are armed on the curved side with strong curved teeth: in young animals the armature is weaker and confined to some of the middle joints; in the larger animals, only the last two joints of the outer and the last four or five joints of the inner branch usually want the teeth. The armature of the outer branch is always stronger than that of the inner one. These hooked decurved teeth (fig. 21) not only occupy the upper part of the strongly prominent margin of the flexed side of the joints, but extend thence, gradually becoming smaller, and finally converted into mere minute points over a larger or smaller part of the outer surface of the joints. This portion which is beset with teeth and hooks is usually elevated, in the form of a low swelling, a little above the surrounding parts. Besides the teeth of the flexed side, there are, especially on the lower joints, acute spinules directed upwards on the extended side, a few spines, also directed upwards, on the outside of the upper margin, and

frequently, at the same place, several groups of very delicate points.

The middle joints of the outer branch also bear, within the toothed armature, from two to four pairs of setæ; with these are sooner or later associated at first a single, and afterwards several rows of setæ on the inner margin of the upper end of the joints, and finally, on the last joints, a dense irregular coat of setæ which often covers a great part of the inner surface. On the inner branch the setæ of the inner surface are more numerous, even on the lower joints.

Fourth to sixth pairs: the cirri of the last three pairs of feet are rarely all found uninjured; sometimes one, sometimes another of them wants a larger or smaller piece. These losses, as is well known, are more or less completely replaced by the formation, in the last of the remaining joints, of a number of new joints, which come into use after the next change of skin. The frequency of such mutilations scarcely allows us to say anything as to the number of joints in these cirri. In the last pairs this may exceed forty-five, and their length is often more than three times that of the third pair. The joints of all these cirri are thinner, but much longer, than those of the anterior pairs; the upper joints almost always bear on the flexed side four pairs of setæ, but frequently only three in the fourth pair of feet.

In the fourth pair the dorsal surface of the first joint of the outer branch is usually armed with rather strong denticles directed upwards; on the middle joints of both branches, but especially the outer one, besides the short pointed spines, and in their vicinity, more or less numerous spines directed upwards are scattered over the outer surface of the joint; in rare instances these spines become converted, on the outer branch, into slightly curved teeth directed downwards, so as to produce an armature similar to that of the third pair, although certainly weaker (fig. 22).

The fifth pair of feet is distinguished by a strong, somewhat curved tooth, directed upwards, which stands at the commencement of the dorsal surface of the second peduncular joint; this is usually followed by a similar smaller tooth, or more rarely by two. These are seldom altogether wanting.

On the sixth pair of feet the peduncular joints and the first joints of the cirri have their dorsal surface covered with very numerous, short, close-sitting points, directed upwards.

*Penis*.—At the base of the penis, between it and the anus, the usual conical process exists; the penis, which is extensible to several times the length of the cirri, is beset only with a few short hairs.

*Ova*.—0·17 millim. long, 0·09 millim. thick. In the *larvæ* I find nothing remarkable; they are very like those of *Tetracelita porosa*.

*Affinities*.—The nearest ally of *Balanus armatus* is *B. trigonus*. Indeed, whether the former might not better be regarded as a mere variety, and indicated as *B. trigonus*, var. *armatus*, can only be decided by comparison with numerous examples of *B. trigonus* from various localities. But it may be cited, in favour of its specific title, that *B. trigonus* has hitherto been found only in the Indian and Pacific Oceans, and not in the Atlantic, and only on the shells of mollusca and on wood, but not in sponges—that in *B. trigonus* the shell is usually shallow and ribbed, and the mouth has entire margins and is almost equal-sided, whilst in *B. armatus* the shell is usually abruptly conical and smooth, and the mouth always distinctly toothed and pentagonal—that the scuta are narrower in *B. armatus*—and that the armature of the third pair of feet, which was never missed in *B. armatus*, and indeed caught the eye at the first glance, is not mentioned by Darwin in *B. trigonus*, any more than the strong tooth on the peduncle of the fifth pair, which is *always* present in *B. armatus*.

The shells seated upon *Carijoa*, when predominantly developed in length, and especially when the base somewhat projects, sometimes resemble in general appearance the species living on Gorgoniæ, which, in Darwin's work, form the section B of the genus *Balanus*; but this resemblance is merely the consequence of the similar mode of adhesion, and scarcely the sign of any near affinity. In other respects Darwin's remarks upon the affinities of *B. trigonus* apply to our species.

*Signification of the armature of the cirri*.—A similar armature of the cirri with spines and points, although not so strongly developed, occurs in other *Balani*. In individual examples of *B. improvisus*, var. *assimilis*, these spines, elsewhere directed upwards, even occur directed downwards and backwards, as in *B. armatus*, on the outside of the joints of the third and fourth pairs of feet. This armature of spines and points occurs almost exclusively on the surfaces turned towards the margin of the opercular fissure, as on the outer surface of the middle pairs and on the dorsal surface of the last pair. In this position they cannot serve for the seizure of any prey, but scarcely for any other purpose than the cleansing of the fissure. In fact, in living animals, we see that the cirri of the third and fourth pairs, the outer surface of which is particularly richly spinous, are those which pass closely along the margin of the opercular fissure during their protrusion and retraction.

Now, that it is exactly in spongiolar species, otherwise by

no means nearly related, that this armature is developed into large curved teeth, intimates that there is a connexion between the peculiar armature and the peculiar domicile; and it is not a far-fetched supposition that the teeth serve to tear in pieces and remove the rapidly growing sponge-mass which threatens to grow over the aperture of the shell. It is a remarkable circumstance that in *Acasta* the teeth stand on the outer branches of the fourth, and in *B. armatus* on the branches of the third pair of feet. This circumstance might be adduced in favour of the Darwinian view of the origin of species, in the same way as the different structure of the posterior entrance to the branchial cavity in the different air-breathing crabs\*. *Balanus armatus* is much more nearly allied to other, not spongicolar *Balani* than to *Acasta*; *B. armatus* and *spongicola* on the one hand, and the species of *Acasta* on the other, cannot consequently have inherited the habit of domiciling themselves in sponges from a common ancestor. Contrivances which stand in relation to this peculiar dwelling-place must therefore have been produced independently in each case; and therefore it cannot appear strange that we find them developed on different parts of the body in *Balanus armatus* and in *Acasta*.

## II.

Until recently the *Balani* passed universally as self-impregnating hermaphrodites. But that self-impregnation does not take place in all cases was proved by a remarkable observation of Darwin's, who found the penis rudimentary and imperforate in several individuals of *Balanus balanoides*, although there were well-developed larvæ in their shells (*Balanidæ*, p. 101). To me it has long been doubtful whether self-impregnation is really the general rule. For what purpose should the length of the penis be often three times the diameter of the shell, if it has nothing to seek outside the latter? Some observations which I have recently made have confirmed me in this doubt.

It is well known that the *Balani* are very sensitive to light†, so that they immediately retract their cirri and close the oper-

\* Fritz Müller, 'Für Darwin,' p. 20.

† The sensitiveness of the *Balani* to luminous impressions is not dependent on the eyes discovered by Leidy. I had taken a large *Balanus tintinnabulum* living out of its shell, and separated it from the operculum, with which the eyes remained in connexion. It lay in a saucer of water, with its cirri half unrolled. As often as the shadow of the hand fell upon it, it rolled up the cirri with a sudden movement. In *B. tintinnabulum* the eyes are very distinct: in *B. armatus* I have not yet found them; and this is not due to the smaller size of the latter species, as they are very easy to detect even in small specimens of *B. tintinnabulum*.

culum when the hand, for example, is passed between them and the window.

It is remarkable that individual animals are much shyer, and others, again, bolder than the rest—that the former always remain longer closed, and the latter venture out more quickly, and even become accustomed to the passage of the hand at regular intervals. I may remark, in passing, that I detected similar mental differences between the animals of a group of *Eupomatus floribundus*.

Once when, in repeating these observations, I was watching the action of the cirri in some examples of *Balanus armatus* which I had taken freshly from *Carijoa* and cleaned from their coating of sponge, I saw that one of them suddenly ceased striking with its cirri, held them for some seconds immoveable and widely spread out, and during this period the penis extended to its utmost length and moved about as if feeling or seeking for something. I then no more disturbed my animals with the shadow of my hand, in order, if possible, to see this spectacle repeated; and in fact I soon witnessed the same phenomenon again, not only in the same animal, but also in three or four others. I now placed these ardent animals close together, in order to facilitate their reciprocal copulation; but as often as the elongated penis came within reach of the cirri of a neighbour, it was pushed to and fro by them, and the animal did not remain quiet so as to give access to it. Upon this I examined two of the animals, and found the entire canal of the penis densely filled with semen; but in both there were also ova which had already completed their segmentation, and consequently no longer required fecundation. With the penis so filled, when extended to its utmost length, semen must certainly have been expelled from it (which I could not have seen upon a white saucer); but at the same time, from the length of the penis, usually extended in a lateral direction, this semen would be removed from the vortex produced by the cirri of the same animal and placed within reach of neighbouring animals which might require it. It is remarkable that, although at that time I made the observation upon four or five animals simultaneously, I have been unable to repeat it, notwithstanding that I have repeatedly looked for it in numerous fresh animals.

The second observation which seems to prove that fecundation sometimes occurs even between different species of *Balanus* is as follows:—Among the *Balani* obtained on *Carijoa*, which I had at the first glance determined as *B. improvisus*, var. *assimilis*, there was one that struck me by a somewhat reddish coloration, such as I had never seen in this infinitely

abundant species. On examining it more closely, I found, instead of the narrow radii covered with a yellowish membrane of *B. assimilis*, the well-developed shining radii of *B. armatus* with their peculiar striation. At the same time, however, the form of the mouth, the appearance of the scuta, and the walls, with their translucent streaks and the septa of their tubes rendered doubly distinct by the reddish coloration, were exactly as in *B. assimilis*. Amongst hundreds of *B. armatus*, I had never seen anything like these walls, aperture, and scuta, nor amongst countless thousands of *B. assimilis* any radii at all similar; and I could not help in all seriousness asking myself the question whether I had not before me a hybrid between the two species the peculiarities of which were here so wonderfully united. I have subsequently met with three of these supposed hybrids: two of these were seated, like the first, immediately upon the *Carijoa*, and the third upon a *B. assimilis*; on the other hand, a *B. assimilis* was seated upon one of the others. A close examination of these four animals gave the following results:—

*General appearance*.—In the form of the distinctly toothed aperture, the greatest breadth of which is nearly in the middle between the carina and the rostrum, in the translucent striæ of the smooth walls, and in the peculiar curvature of their walls, which it is difficult to reproduce in words, all the four animals resembled *B. assimilis*; in the formation of the radii, except that the margin runs somewhat more obliquely, *B. armatus*. The colour in one was somewhat reddish, in the others nearly white, yellowish at the lower part of the shell in two of them. Accidentally, in consequence of their mode of attachment, the base in all was much longer than broad, and the rostrum higher, in one more than twice as high as the carina.

*Size*.—Mean of the measurements of the four shells:—length of base 7·1 millims., its breadth 3·7 millims.; length of the aperture 4·3 millims., its breadth 3·4 millims.; height of rostrum 8 millims., of the carina 4·4 millims.

*Scuta*.—The basal margin of the scuta is more than three-fourths of the length of the occludent margin, and is even longer than the tergal margin; on the outer surface, which shows no trace of pits or longitudinal striæ, the striæ of growth only project moderately; on the inner surface there is a strong adductor ridge, which is amalgamated with the articular ridge above, and may be traced below nearly to the basal margin. The pit for the depressor lateralis is shallower and more roundish than is usual in *B. armatus*.

*Terga*.—The terga, like the scuta, are far more similar to

those of *B. assimilis* than to those of *B. armatus*, hardly differing from the former, except in a somewhat broader spur. They are broader than in *B. armatus*; the spur, which does not occupy one-third of the breadth of the base, is distant almost its own breadth from the scutal margin; a shallow longitudinal channel occupies nearly the whole breadth of the spur. The ridges for the depressor carinalis are very strongly developed, and project beyond the basal margin.

I was particularly curious as to the hairiness of the opercular pieces, as in this respect *B. armatus* and *assimilis* differ greatly from each other. In *B. armatus* there are short delicate hairs upon the carinal side, and long slender hairs upon the scutal side of the terga, and long, strong, closely approximated hairs upon the scuta; in *B. assimilis* there are everywhere short thick spines alternating with every one to three of the longer delicate hairs. I was surprised at finding in the supposed hybrid neither the one nor the other, nor an intermediate structure. On the terga there stood, on each side of the hairless furrow, rather long and delicate hairs; on the scuta the hairs were shorter, but neither thicker nor closer together. I may remark that I examined these hairs only in one animal.

*Pieces of the shell.*—The pieces of the shell, which in *B. assimilis* may be readily separated even in the living animal, adhered firmly together in the single animal in which I separated them, even after boiling in solution of potash. The walls, of which I have already stated that their tolerably wide tubes have numerous septa in their upper part, are longitudinally ribbed within throughout their length. The freely prominent lower margin of the sheath is narrower than in *B. armatus*, but more strongly developed than in *B. assimilis*.

*Parts of the mouth.*—In one animal the *labrum* exactly resembled that of *B. armatus*; in the others also it had only three teeth on each side; but in two of them the outer tooth was widely separated from the others, and in the fourth the two outer teeth were brought close together, and somewhat distant from the inner one. Neither of these structures has occurred to me in *B. armatus*; but the former is frequent in *B. assimilis*. Of the numerous denticulations with which the margins of the median notch are beset in *B. assimilis* there was nothing to be seen.

The *mandibles* might be equally well regarded as belonging to a *B. armatus* as to a *B. assimilis*, as they do not notably differ in these two species.

In the *maxillæ* of all four animals the median setæ were shorter than in *B. armatus*, and longer than is usual in *B. as-*

*similis*; as in the latter species more than half the upper margin was clothed with hair.

*Cirri*.—First pair: the longer, 19–22-jointed branch was in three animals about twice as long as the shorter one, in the fourth about one-fourth longer; the shorter branch in two animals had fourteen joints (in the others eleven and thirteen). I have not met with so great a number of joints in *B. armatus*; in *B. assimilis* it is frequently still greater (fifteen to eighteen). In the latter species, as is well known, the two branches are generally of almost equal length; nevertheless, even in this, I have observed a difference of nine joints (fifteen and twenty-four).

Second pair: thirteen to sixteen joints in the outer, twelve to thirteen in the inner branch; in *B. armatus*, eleven to thirteen in the former, nine to ten in the latter; in a *B. assimilis* which I have at hand I count seventeen and sixteen.

Third pair: in three animals I found in the outer branch thirteen to sixteen, in the inner twelve to fourteen joints; the fourth had on one side thirteen and twelve, and on the other twenty-one and twenty joints! The bristling and armature of this pair of feet were in all four animals the same as in *B. assimilis*; the setæ on the inner surface of the joints were very numerous; and on the outside there were only straight spines and points, chiefly directed upwards.

Fourth to sixth pairs: the flexural side of the upper joints in the fifth and sixth pairs of cirri in all four, and in the fourth in three animals, bore five pairs of setæ; the fourth animal had only four pairs of setæ on the joints of the fourth pair of feet. In *B. assimilis* six is the usual number of pairs of setæ on the joints of the posterior cirri. The outer surface of the joints in the fourth was armed in the same way as in the third. No trace of the strong tooth which in *B. armatus* stands on the peduncle of the fifth pair was to be found in any of the four animals.

*Penis* as in *B. armatus*. In *B. assimilis* this organ is generally beset with longer and more numerous hairs.

*Affinities*.—The discovery just described seems to me to admit no other supposition than that the four animals are really hybrids of *B. armatus* and *B. assimilis*. If we do not choose to let them pass as such, we must either regard them as a variety of *B. armatus* or of *B. assimilis*, or as a distinct species.

But in *B. armatus* the walls never have translucent longitudinal lines, or transverse septa in the tubes which run through them; the greatest breadth of the aperture never falls nearly

in the middle between the carina and the rostrum; the scuta are always considerably narrower; the rows of pits on the outer surface are never wanting; nor on the inner surface are adductor ridges, traceable nearly to the basal margin, to be seen; the terga never have such narrow spurs, or a longitudinal furrow, or ridges for the musc. depressor projecting beyond the basal margin; the strong curved teeth on the cirri of the third pair and the strong tooth on the peduncle of the fifth pair are never wanting; there are never more than four pairs of setæ on the posterior cirri, &c.

In *B. assimilis*, on the contrary (a species so common here that every potsherd, shoe-sole, or rope's-end which has lain for some time in the sea is covered with it), I have never seen a similar reddish colour to that presented by one of the supposed hybrids; I always found the radii quite narrow, covered with a thin membrane, never broad and shining; I always found short spines between the hairs of the opercular pieces, and the spur narrower, the labrum always beset with numerous teeth; and in the animals which I have to-day examined for this purpose, but which, indeed, are not very numerous, I found constantly six pairs of setæ upon some joints of the posterior cirri, not to mention other small distinctions.

It is evident that the differences from either species are too considerable for a mere variety; they would be of sufficient importance to lead us to regard our animal as a distinct species, if there were not other considerations opposed to this view. Species of *Balani*, where once they occur, do not usually appear so isolatedly that in the course of a month only four specimens can be brought together\*. And how surprising would it be that upon the stem of *Carijoa* a third species should be domiciled amongst *B. armatus* and *assimilis*, standing in so peculiar a manner in the middle between the two species as do our animals, which agree with *B. armatus* in almost everything by which they differ from *B. assimilis* (in the coloration of one of the shells, in the firm union of their pieces, in the structure of the shining striated radii, in the structure of the labrum), and which in almost everything by which they differ from *B. armatus* (in the formation of the walls, the aperture, the opercular pieces, &c.) agree with *B. assimilis*, and, again, in other respects (as in the number of

\* I cannot say exactly among what number of *B. armatus* the four hybrids were found, as I have used up a great quantity of the former without counting them; the number may be about 400. For a month or more I have daily dived upon the *Carijoa* rock whenever the sea was sufficiently quiet, and not unfrequently obtained from thirty to forty *Balani* at once upon the polypes brought up.

pairs of setæ on the posterior cirri), stand exactly in the middle between the two species.

From all this, it seems to me to be the simplest and most natural course to explain the astonishing mixture of the characters of *B. armatus* and *B. assimilis* which our animals show, by a true intermixture, and therefore to regard them as hybrids of the two species.

But why, it will be asked, if this supposition be correct, are not hybrids of *Balani* remarkably abundant, if they occur at all? The different species so commonly dwell intermixed with each other, that three or more species may not unfrequently be found united in the same group. To this I can only answer with suppositions. In order to obtain hybrids of plants, the stigma must be carefully protected from the pollen of the same species. If pollen of the same and of another species be placed upon the stigma at the same time, the latter remains inactive. In the same way, in animals, if the semen of the same and of another species be simultaneously in contact with the ovum, the latter may remain inactive. Now, wherever species of *Balanus* reside together in abundance, the ova will never miss the semen of their own species, and therefore no production of hybrids will take place. This can only occur when the ova of one animal come in contact only with the semen of a different species. Now this might easily be the case in an isolated *B. assimilis* which had wandered into a tuft of *Carijoa*, and here, deeply hidden, was surrounded only by *B. armatus*. If this explanation be correct, our hybrids would be produced from ova of *B. assimilis* fertilized by semen of *B. armatus*.

A further question raised by these hybrids is, why they have received from *B. assimilis* precisely the formation of the walls, opercular pieces, cirri, &c., and from *B. armatus* the precise structure of the radii, labrum, &c. It may be said that the merely transversely striated scuta and the weakly armed cirri of *B. assimilis*, and the broad smooth radii and sexdentate labrum of *B. armatus*, differ less from the ordinary characters of the genus than the deeply pitted scuta and the strong teeth on the cirri of *B. armatus*, or the narrow radii clothed with membrane and the 22-28-toothed labrum of *B. assimilis*. This applies also to the uniformity of the hairy covering of the opercular pieces. But by this means the matter of fact is only brought under a general point of view, and not explained. Out of this difficulty in this case, as usual, we can hardly escape without Darwin's theory of the origin of species. But if we regard the species of a genus as descendants of a common primitive form, and at the same time, in accordance with the well-known experience of gar-

deners, regard their various peculiarities as so much better fixed, or so much less variable, the earlier they were acquired, the longer they have been inherited unchanged, it becomes intelligible that, above all, the characters proper to the primitive form persist, and that consequently, in the crossing of two species, these are more readily transferred to the hybrid than later-acquired peculiarities of the father or mother.

From this point of view I think we shall be able to explain many peculiarities of hybrids and, *vice versâ*, perhaps in many cases to trace from the form of the hybrids to the primitive form of the genus,—the latter, of course, only with the greatest care; for the mere fact that the hybrids produced by males of one species with females of another do not agree with those produced by males of the second species with females of the first, furnishes a proof that other circumstances aid in determining the form of the hybrids.

#### EXPLANATION OF PLATE XX.

- Fig. 1.* Specimens of *Balanus armatus*, seated upon *Carijoa*: *c*, carina; *r*, rostrum.
- Fig. 2.* Scutum of *B. armatus*, seen from without, with particularly large pits and distant striæ of growth.
- Fig. 3.* Another (remarkably broad) scutum, from within.
- Fig. 4.* Hybrid of *Balanus armatus* and *B. improvisus*.
- Fig. 5.* Scutum of *B. improvisus*, var. *assimilis*, from without.
- Fig. 6.* The same scutum, from within.
- Fig. 7.* Outline of the mouth in *B. armatus*.
- Fig. 8.* Outline of the mouth in a hybrid of *B. armatus* and *B. improvisus*.
- Fig. 9.* Outline of the mouth in *B. improvisus*, var. *assimilis*.
- Fig. 10.* Labrum of *B. armatus*.
- Figs. 11–13.* Labrum in three different individuals of *B. improvisus*, var. *assimilis*.
- Fig. 14.* Setæ from the carinal side of the tergum in *B. armatus*.
- Fig. 15.* Setæ from the scutal side of the same piece.
- Fig. 16.* Setæ from the scutum in *B. armatus*.
- Fig. 17.* Setæ from the tergum in *B. improvisus*, var. *assimilis*.
- Fig. 18.* Setæ from the striæ of growth on the tergum of *B. improvisus*, var. *assimilis*.
- Fig. 19.* Anterior ramus of the third pair of cirri of *B. armatus*, from within, wherefore only the teeth which project beyond the margin are visible.
- Fig. 20.* The same ramus from the hybrid, from without.
- Fig. 21.* Ninth joint of the outer ramus of the third pair of feet in a large *B. armatus*, from without.
- Fig. 22.* Tenth joint of the outer ramus of the fourth pair of feet in *B. armatus*, from without.
- Fig. 23.* Seventh joint of the outer ramus of the third pair of feet in the hybrid, from without.
- Fig. 24.* The same joint of a *B. improvisus*, var. *assimilis*, from without.



Müller, Fritz. 1868. "XLVII.—On *Balanus armatus*, and a hybrid between this species and *Balanus improvisus*, var. *assimilis*, Darw." *The Annals and magazine of natural history; zoology, botany, and geology* 1, 393–412.

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