XIV. THE INDIAN BARNACLES OF THE SUBGENUS SMILIUM, WITH REMARKS ON THE CLASSIFICATION OF THE GENUS SCALPELLUM.


A full account of the Indian representatives of the family Pollicipedidae must be deferred until opportunities of investigating the littoral fauna of the coasts of India have occurred, for at present our knowledge of this fauna is meagre as compared with that of the fauna of the deeper parts of the Bay of Bengal and the Arabian Sea. In the meanwhile the species of the genus Scalpellum may be discussed with some degree of confidence, because, with one exception, they are only found, in Indian seas, at depths greater than 100 fathoms, and because it is now some years since any species not previously represented in the collection of the Indian Museum was obtained by the "Investigator." The present paper, so far as individual species are concerned, deals only with the forms that in my opinion should be placed in the subgenus Smiliun, but the facts that must be taken into consideration in discussing the subdivision of the genus as a whole are treated in some detail.

DWARF MALES IN SCALPELLUM.

Perhaps the most remarkable fact about the genus Scalpellum is that its species possess dwarfed and otherwise degenerate males, which live as parasites or rather semi-parasites on the capitulum of the much larger female or hermaphrodite. Probably these males occur in the case of all species of the genus, but they are not always to be found and may, perhaps, only be produced at certain seasons or in certain generations. It is curious that they are invariably absent in the closely allied genus, Pollicipes. I do not propose to deal with the minute structure of the dwarf males in either of the genera (Scalpellum and Ibla) in which they occur, for my friend Captain F. H. Stewart is doing so in the case of several species in a much more detailed manner than I could have hoped to do; but I may point out certain characters in the males that are of systematic importance.

As will be seen (p. 150), two subgenera of Scalpellum are recognized in this paper, their recognition depending to a considerable extent on the structure of the male. In the more primitive subgenus (Smiliun) the larger individuals appear to be invariably
Hermaphrodite, that is to say to have the organs of both sexes well developed and functional. The males attached to them resemble young hermaphrodites, so far as external appearance goes, in a more or less accurate manner. As a rule they have the capitulum and the peduncle distinctly separated, and bear calcified valves on the former, the peduncle being devoid of calcareous plates. The capitulum, however, never bears more than six valves (viz., a pair of terga, a pair of scuta, a carina and a rostrum), and even these may be occasionally absent. The external anatomy of the body of the male closely resembles that of the young hermaphrodite, differing from that of the adult mainly in the following characters:—(1) the cirri are shorter and less distinctly curved, with the bristles and hairs fewer and exhibiting less differentiation; (2) the mouth parts are more primitive, the labrum being relatively smaller, the teeth of mandible less distinctly separated and often fewer, the bristles on the maxillae more alike. If the maxilla is notched, this character is less evident in the male than in the hermaphrodite. The male has a well-developed penis,
which often, if not always, differs in shape from that of the her­
maphrodite. The alimentary canal is furnished with both a
mouth and an anus, and is certainly functional. These characters
are better seen in the male of S. bengalense than in that of
any other species with which I am acquainted, because the body
of the male of this species, owing to the peculiar shape of the
capitulum, can apparently be thrust out of the capitulum further
than is usually the case without interfering with the relations of
the different parts. An outline drawing of this form is therefore
reproduced in text fig. 1.

In one respect, however, the male of S. bengalense differs con­
siderably from that of allied forms, namely, in the degeneracy or
absence of the capitular valves, never more than four of which
(two terga and two scuta) are present. In more typical species,
such as S. squamuliferum, the shape and relative positions of the

Fig. 2.—S. squamuliferum, male, $\times 52$.

valves appear to be very constant and to afford sound diagnostic
characters. The external shape of the capitulum and peduncle is
also characteristic.

In the less primitive species of the genus comprised in the
subgenus Scalpellum, the male is far more degenerate. In exter­
nal shape it is usually ovoid, with no trace of a peduncle. There
is rarely any trace of valves, but the whole surface is covered with
minute hairs or spines as in the males of Smilium. At or near
the end opposite to that by which the animal is attached to the
capitulum of the female or the hermaphrodite—for in this sub­
genus the larger individuals appear to be in the case of some spe­
cies exclusively female—there is an aperture, which is usually
circular in outline. From this aperture the generative products
are given out and, at any rate in some cases, the tips of the cirri
can be protruded. The cirri, however, are much more degenerate
than is the case in the more primitive species. The mouth parts and anal appendages have completely disappeared and even the penis is absent; the alimentary canal is a mere rudiment, without mouth or anus.

Such males are of course incapable of feeding, whereas those of *Smilium* apparently nourish themselves in the manner characteristic of the Cirripedia, that is to say by wafting minute living organisms to their mouth by means of the cirri and then either masticating them or swallowing them whole.

Specific characters are less strongly marked in the case of the more degenerate males than they are in that of the males of *Smilium*, but the nature of the armature is often characteristic, and certain species (e.g., *S. velutinum*) could almost be distinguished by an examination of their males alone, on account of peculiarities in the spines with which the males are invested.

The exact shape of the more degenerate males is, however, a dangerous character on which to lay great stress in classification or specific diagnosis, for it is very liable to be distorted by pressure or by the methods of preservation commonly adopted.

**INDIVIDUAL VARIATION IN **SCALPELLOM** AS REGARDS THE DEVELOPMENT OF VALVES.**

A fact that has caused some confusion as regards the taxonomy of *Scalpellum* has recently been brought to light by the researches of Hoek and Pilsbry; I mean the fact that in certain species certain hermaphrodites and females have the capitular valves incompletely developed, so that the valves appear as mere skeletons. Such individuals may conveniently be called "incomplete," while more normal individuals may be called "complete." Incompleteness of the valves is usually accompanied by a thickening of the membrane in which they are embedded and consists mainly in an excavation of one or more margins of the larger paired valves and of a reduction in the size of the latera and carina.

Just as in *Dichelaspis* it is often possible to trace the outlines of the fine primitive valves of the Lepadidae on the membrane of the capitulum even in species in which the valves themselves have almost disappeared as calcified plates, so in incomplete forms of *Scalpellum* the outlines of twelve or more large valves can be seen, with the calcified plates occupying only part of their area. The nature of the reduction, however, resembles that seen in *Conchoderma* rather than that found in *Dichelaspis*. It is perhaps noteworthy that the reduction of the valves in the dwarf males of *Scalpellum* is again of a different nature, an actual reduction in number taking place, and that the valves in these degenerate individuals differ from those found in typical Lepadidae in including a rostrum, a valve that is never found in that family. The six valves of the dwarf males of *Smilium* apparently represent the six essential valves of the genus *Scalpellum*, for there is a stage
in the development of the females or hermaphrodites of many species in which these six valves are at any rate very much more conspicuous than any others, if they are not actually the only valves represented. Incompleteness, however, is much more common in the subgenus Scalpellum, if it is not actually confined to that subgenus, for species like Scalpellum (Smilium) scorpion, in which the valves are embedded in very thick membrane, do not exhibit incompleteness in the sense in which I have defined the term.

In the young hermaphrodites or females of those species of Scalpellum in which incompleteness occurs, at the stage at which all the valves have already made their appearance, the valves are practically normal, and it is only as maturity approaches that their margins become strongly excavated.

As regards variation in the development of the valves one other point may be noted, viz., the rudimentary character of the subcarina and the rostrum in some otherwise normal individuals of species in which they are habitually present. These two valves are rightly considered to be of great importance in the taxonomy of the genus, but it must be noted that even in some species of Smilium (e.g., S. squamuliferum, otherwise a very constant species) the subcarina is often very minute and still more often completely concealed beneath the membrane. In some species of the subgenus Scalpellum, on the other hand, the rostrum, which is always small, may be present or absent, and even the subcarina, which is normally absent in this subgenus, occurs as a minute rudiment in some individuals of S. laccadivicum, of which my S. subflavum is evidently no more than a "complete" variety.

SUBDIVISION OF THE GENUS SCALPELLUM.

Considerable difference of opinion has been held at different times, and, indeed, is still held, by different authorities as regards the subdivision of the genus Scalpellum (sensu Darwiniio). Darwin's great work must be taken as the foundation of all scientific study of the Cirripedia, but it must be remembered that he was only acquainted with a very small proportion of the species of Scalpellum now known, and that even as regards the few species he had examined he did not express a dogmatic opinion. Before he wrote his Monograph (1851) Gray and other authors had already described several genera wholly or in part synonymous with the forms he called Scalpellum. Pilsbry¹ has recently (1908) revived two of these genera, namely, Calantica and Smilium, and has also raised several other groups in the genus to generic or subgeneric rank, basing his conclusions partly on the external form of the dwarf male and partly on the position or presence of certain valves in the female or hermaphrodite. Hoek and Gruvel, on the other hand,

while differing as regards details of classification, agree in recognizing only the genus *Scalpellum*, which they subdivide in different ways. Gruvel's classification (1905) was, indeed, based on that set forth by Hoek in the "Challenger" Reports (1883); but the latter author has recently published a new one in his account of the Cirripedia of the "Siboga" (1907).

Taking into consideration the great difference in external form between the males of such closely allied forms as *Scalpellum squamuliferum* and *S. bengalense*, and the variation displayed by the valves in certain species, notably *S. squamuliferum* and *S. laccadivicum*, I find it possible to recognize only two groups of species that can be called subgenera. It is impossible to regard them as distinct genera, because no one character of importance can be stated to be constant in either of them, although the sum of the characters of each differs from that of the characters of the other. These two groups may be called *Smilium* and *Scalpellum*. The former is undoubtedly the more primitive and includes several species that come very close to *Pollicipes*, while the latter consists of forms that have undergone a considerably greater amount of specialization. The two subgenera may be defined as follows:—

**Smilium**, Gray.

Rostrum and subcarina as a rule well developed in the hermaphrodite, but the subcarina sometimes absent; anal appendages usually with one joint, sometimes absent. Dwarf males with well-developed capitulum, cirri, mouth parts and alimentary canal.  
Type *Smilium peronii*, Gray.

**Scalpellum**, Leach.

Subcarina absent or represented by a mere rudiment; rostrum often absent, never large or prominent; anal appendages as a rule with several or many joints. Dwarf males with the appendages and alimentary canal degenerate and the capitulum not distinct from the peduncle.  
Type *Scalpellum vulgare*, Leach (= *Lepas scalpellum*, Linné).

Both these subgenera are represented in Indian seas, *Smilium* by three species and *Scalpellum* by at least twelve.

**Subgenus Smilium.**

*Key to the Indian species of the subgenus.*

1. Capitulum of hermaphrodite about half as broad as long.  
   A. Peduncular plates in the form of rods set obliquely in the membrane and forming complete circles round the peduncle . *S. squamuliferum.*
B. Peduncular plates in the form of flat, transversely oval discs on the surface of the membrane, never completely surrounding the peduncle

**S. bengalense**.

II. Length of capitulum of hermaphrodite much more than twice the breadth. Peduncular plates in the form of imbricating, upwardly directed scales

**S. acutum**.

_Scalpellum (Smilium) squamuliferum_ Weltner.

_S. squamuliferum_, Weltner, _Sitz.-Ber. naturf. Freunde_, 1894, p. 80, figs.; Annandale, _Illustr. Zool. "Investigator," Crust._ (Entom.), pl. ii, fig. 4 (1907), and pl. iii, figs. 4–6 (1908).

_Capitulum_ compressed, irregularly ovoid, the carinal margin being more strongly arched than the occludent, which, except for the projecting rostrum, is nearly straight and slopes outwards from above. _Valves_ moderately stout, white, imbricate, feebly striated vertically, with the lines of growth well marked, covered by a thin but opaque brownish, minutely hairy membrane, the tips projecting upwards. _Carina_ simply and not very strongly arched; its dorsum convex; its sides concave (especially above); with strong outer and inner ridges; the umbo apical, situated well above the centre of the terga. _Subcarina_ triangular, not very prominent, variable in size, often small and as a rule entirely concealed beneath the membrane. _Rostrum_ large, narrowly triangular, curved and prominent, strongly ridged in front. _Terga_ narrowly rhomboidal, pointed above, with the main axis slanting outwards from the carina; the sides forming the upper angle straight, shorter than those forming the lower angle, which are arched. _Scuta_ subequal to the terga, which they resemble in shape; their main axis vertical; the upper part of each valve slightly retroverted; the occludent margin longer than any of the other sides. _Upper latera_ resembling the scuta but of as a rule about half the size, variable, however, in this respect. _Inframedian_, _carinal_ and _scutal latera_ triangular, more or less completely concealed beneath the membrane; the inframedian latera much larger than the others.

_Peduncle_ variable in length, covered with complete undulating rings of calcareous plates embedded in thick membrane. These plates take, individually, the form of minute rods embedded more or less obliquely in the membrane; the outer extremity is slightly inflated and bears a small pit. Sometimes they are almost completely concealed in the membrane and the rings they form appear to consist merely of raised ridges on the surface of the peduncle.

_Cirri_ etc. _Cirri_ delicate, not very long or strongly curved, densely fringed on the anterior margin but with the posterior
bunches of hairs feebly developed, especially on the 4th, 5th and 6th cirri. First cirrus long, slender, tapering, with the two rami nearly equal; both margins densely fringed. Anal appendages barely reaching the junction of the rami of the 6th cirrus, with one joint, compressed, bluntly pointed at the tip, which bears an irregular tuft of long slender hairs; the whole surface minutely pilose. Penis long, slender, contorted. A pair of delicate ovigerous lamellae depending from the dorsal surface of the abdomen.

MOUTH PARTS. Labrum produced and pointed. Mandible with 5 teeth; the 1st longer but no broader than the 2nd, the outer margin of which is somewhat irregular at the base; the 4th and 5th close together, forming the inner angle; the 5th notched at the base both externally and internally; the whole structure covered with minute hairs. Maxilla with a very broad but shallow excavation, which occupies the greater part of its free margin; none of the bristles very stout or long; the exact outline variable.

Length of capitulum 26 mm.
Breadth of capitulum 13 ,, 
Length of peduncle 26—44 ,, 

MALE with the peduncle very short and stout, distinctly separated from the capitulum, which bears six calcified valves. The capitulum pointed above, broad in comparison with its length, minutely hairy. Tergum broadly triangular, with the base of the triangle rounded and the apex pointing directly downwards. Scutum much larger than the tergum and more narrowly triangular; the apex pointing upwards; the outlines somewhat sinuous. Carina triangular, with rounded base, not quite so broad (viewed from behind) as the tergum and only a little longer, not reaching upwards as high as the upper margin of this plate; the base slightly lower than that of the scutum and above the apex of the rostrum. Rostrum of about the same length as the tergum, rather broader than the carina and with the base produced to a point. Cirri and penis well developed; anal appendages present; mouth parts resembling those of the hermaphrodite in miniature except that the labrum is not produced and the inner teeth of the mandibles are not so distinctly separated.

SYSTEMATIC REMARKS. This species is remarkable on account of the possession by the hermaphrodite of ovigerous appendages, which depend from the dorsal surface of the abdomen in the form of a pair of delicate filaments placed one behind the other (Illustr. Zool. "Investigator," Crust. (Entom.), pl. ii, fig. 4). The male belongs to the type most commonly found in the subgenus.

DISTRIBUTION, etc. S. squamuliferum has been taken by the "Investigator" at many stations in the Andaman Sea and off the south of India, while the British Museum possesses a specimen from Singapore. Gruvel's statement that the species occurs in Japan is apparently due to a miscalculation of latitude and longitude (Mon. Cirrh., p. 56).
The bathymetrical distribution is a wide one, ranging from a little over 100 fathoms to nearly 1,900 fathoms.

Specimens are most abundant on the glassy filamentous spicules by means of which sponges of the genus *Hyalonema* are anchored in the mud. They also occur, however, on the stems of Antipatharians and even on shells of living molluscs, e.g., on that of *Xenophora pallida*. The species is markedly gregarious, a fact that may be due to the larvae undergoing a considerable part of their metamorphosis in the egg.

*S. squamuliferum* is by far the commonest species of Pedunculate in the deeper parts of the Bay of Bengal, and the specimens in the Indian Museum considerably outnumber those of all the other Indian Pollicipedidae put together. In fact, the species is one of the few (so far as this family is concerned) of which it is possible to say that a satisfactory series exists in any museum. It is therefore unfortunate that it is one which does not, except in two particulars, exhibit any very marked tendency to variation and is apparently of limited geographical distribution. Two features in which its characters are the least constant are the length of the peduncle and the size of the subcarina. Compared with such species as *S. laccadivicum*, it may be described as a constant species. In the neighbourhood of Singapore and in the Gulf of Siam it is replaced by *S. kam peni*, which, however, is a much less constant species and inhabits comparatively shallow water (30—50 fathoms). But *S. rostratum*, also a form that has not been found at great depths, replaces *S. kam peni* in the eastern parts of the Malay Archipelago; it appears to be a fairly constant species.

*Scalpellum (Smilium) bengalense*, Annandale.


Subsequent additions to the collection prove the type specimens of this species to have been immature. The adult hermaphrodite resembles *S. squamuliferum* very closely both as regards external structure and as regards anatomy, but may be recognized by the following characters:

1. The membrane covering the valves of the capitulum is transparent and of a yellowish colour.
2. The peduncular plates take the form, viewed from without, of small, transversely oval, flat bodies, and never surround the peduncle in complete rings or form ridges on its surface.
3. There are no ovigerous lamellae.
4. The peduncle is never much longer than the capitulum.
The male, however, is completely different in external form and may be described as follows:—

*Peduncle* long and slender, merging gradually into the capitulum in such a way that the whole body has a vase-like shape.

*Capitulum* entirely without calcified valves, or with a pair of amorphous scuta, or occasionally with minute terga in addition to such scuta. *Cirri* and *anal appendages* well developed, resembling those of the male of *S. squamuliferum*. *Penis* bluntly rounded at the tip, which is armed with several stout hairs.

**Systematic Remarks.** The great external difference between the males of *S. squamuliferum* and *S. bengalense*—species so closely allied that the hermaphrodites alone might almost have been considered specifically identical—is a remarkable phenomenon and renders it impossible to regard the external form of the male or the structure of its capitular valves a matter of much systematic importance. The absence of ovigerous lamellae in the hermaphrodite of the one species and their presence in the other is also a noteworthy feature. The structure of the appendages, etc., of the males of the two species, however, as distinct from the external form, is not dissimilar, and the presence of ovigerous lamellae is a rare character in the genus. The male is variable not only as regards the armature of its capitulum, but also as regards size and the length of the cirri.

**Distribution, etc.** This species has been taken both in the Bay of Bengal and in the Arabian Sea at depths varying from about 70 to over 500 fathoms. On one occasion it was found in considerable numbers on the carapace of crabs (*Encephaloides armstrongi*), while a few individuals have been taken at greater depths attached to the stems of horny corals.

*Scalpellum (Smilium) acutum*, Hoek.

*Scalpellum (Smilium) acutum*, *Hoek, Siboga-Exped., “Cirripedia Pedunculata,” Monogr. xxxia, p. 64, pl. vii, fig. 1 (1907).*


There is a single small specimen of this species in the collection of the “Investigator,” taken at a depth of 490 fathoms off the Andamans. It is attached to the anchor-filaments of a sponge of the genus *Hyalonema* and is probably immature. The species has been so clearly defined and portrayed by Hoek that no further description is needed. I may say, however, that the Indian specimen is almost exactly intermediate between the form originally described by Hoek in the “Challenger” Reports and that subsequently called *Scalpellum longirostrum* by Gruvel, and I have no doubt that the two forms are specifically identical.

*S. acutum* has a very wide range in the deeper parts of the Indian, Atlantic and Pacific Oceans.
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