

**A REVIEW OF EXTANT  
SCILLAELEPAS (CIRRIPIEDIA : SCALPELLIDAE)  
INCLUDING RECOGNITION OF NEW SPECIES  
FROM THE NORTH ATLANTIC,  
WESTERN INDIAN OCEAN AND NEW ZEALAND \***

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**Résumé.** — Révision des *Scillaelepas* actuels (Cirripedia : Scalpellidae) avec description de nouvelles espèces de l'Atlantique nord, de l'océan Indien occidental et de Nouvelle Zélande.

*Scillaelepas* montre une large distribution à l'état fossile en Australie, Nouvelle Zélande et Europe, remontant de façon certaine jusqu'au Crétacé Supérieur. Des fossiles de ce genre étaient connus plus de 200 ans avant que soient dragués les premiers spécimens vivants, à près de 2 000 m, au large du Groenland, vers le début du siècle. Les espèces vivantes actuelles sont les huit espèces déjà décrites de l'Atlantique nord, une espèce nouvelle du golfe de Gascogne, une autre de Nouvelle Zélande, et une autre encore du banc Walters dans l'océan Indien occidental. Elles sont apparemment des reliques d'une radiation du Mésozoïque terminal; les vestiges de populations jadis nombreuses et largement répandues dans les eaux peu profondes des deux hémisphères nord et sud, qui, aujourd'hui, sont apparemment disjointes et limitées aux eaux relativement profondes (de 340 à plus de 3 000 m).

*Scillaelepas* comporte 11 espèces actuelles hermaphrodites, dont 5 sont connues pour inclure des mâles complémentaires vivant dans la région sous-rostrale. Le genre peut être divisé en trois sous-genres; le premier, qui est le moins spécialisé, réunit 5 espèces sans sous-rostre; le second, plus spécialisé, réunit 4 espèces ayant un sous-rostre faisant partie intégrante du capitulum; et le troisième, intermédiaire, groupe 2 espèces ayant 2 sous-rostres qui peuvent soit rester sur le pédoncule, soit se joindre au capitulum au cours de la croissance. On peut supposer que les mâles complémentaires ont évolué par pro-génèse et que les sous-rostres des hermaphrodites se sont développés par co-évolution, en réponse à leur présence, comme adaptation à de faibles densités de populations accompagnant le déclin du genre dans les eaux peu profondes du Tertiaire.

**Summary.** — *Scillaelepas* has an extensive fossil record in Australia, New Zealand and Europe extending back with certainty to the upper Cretaceous. Fossils representing the genus were known for more than 200 years before the first

living specimens were dredged from nearly 2,000 m off Greenland near the turn of the century. Living species today include all eight previously described from the North Atlantic plus a new one from the Bay of Biscay, another from New Zealand and still another from Walters Shoals in the western Indian Ocean. These are apparently relics of a late Mesozoic radiation; remnants of once numerous and widely distributed shallow-water populations of both the northern and southern hemispheres that are apparently disjunct and limited to relatively deep water (from 340 m to greater than 3,000 m) today.

*Scillaelepas* consists of 11 extant hermaphroditic species, 5 of which are known to include complementary males residing in the subrostral region. The genus is divisible into 3 subgenera; the first and most generalized of 5 species without subrostrum, the second and most specialized of 4 species with one subrostrum forming an integral part of the capitulum, and the third and intermediate form of 2 species having 2 subrostra that may remain on the peduncle or join the capitulum during growth. It can readily be inferred that complementary males evolved through progenesis and that the subrostra of the hermaphrodite developed through co-evolution in response to their presence, as adaptations to low population densities accompanying the decline of the genus in shallow waters during the Tertiary.

## SYSTEMATICS

### Scalpellidae Pilsbry 1907

(nom. transl. Pilsbry, 1916 : 14 [ex Scalpellinae Pilsbry 1907 : 3 & 4])

The Scalpellidae has long been divided more or less informally into two major groups, the relatively primitive pollicipoids and their derivatives, the scalpelloids. Zevina (1978 a & b) has divided these between eight subfamilies. The Calanticinae, including *Calantica*, *Scillaelepas*, *Paracalantica*, *Smilium* and *Euscalpellum*, is

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one of them. However, there has not yet been time to evaluate the proposed relationships between the scalpellid subfamilies and their included genera, and therefore the Calanticinae is cited provisionally here.

Calanticinae Zevina 1978 a : 1000

**Scillaelepas** Seguenza 1876

*Scalpellum* (*Calantica*), Section *Scillaelepas*, Pilsbry 1907 : 9

*Calantica*, North Atlantic Group *Scillaelepas*, Pilsbry 1908 : 107

*Calantica* (*Scillaelepas*), Withers 1914 : 192; Newman *et al.* 1969 : R277; Foster 1978 : 47

*Scillaelepas*, Zevina 1976 : 1150; 1978a : 1001

Definition : Like *Calantica* in having the capitulum composed of two whorls of plates; the upper or basic 5 (terga, scuta and carina) and the lower, which in *Scillaelepas* s.s. includes 8 plates (rostrum, rostrilatera, median latera, carinolatera and the subcarina), or a total of 13 plates. Substrate forms have, by the addition of one or two subrostra, 14 or 15 plates and these will be designated as subgenera herein.

*Scillaelepas* differs from *Calantica* in having the plates of the lower whorl for the most part broadly overlapping one another and the basal region of the upper whorl of plates; in having the plates of the lower whorl with apices curved inward and their lateral margins, where overlapped by adjacent plates, marked by articular furrows; and in the peduncular scales being relatively large and imbricate (Withers, 1953 : 148). *Scillaelepas* s.s. is apparently without filamentary appendages (Foster, 1978), but likely all members of the substate forms have one to three pairs. Species are probably always hermaphroditic and complementary males are known, they occur in the subrostral region rather than between the scuta as in *Calantica*. *Scillaelepas mirifica* Zevina, from the Mid-Atlantic Ridge, is unusual in being from great depths (>3,000 m). It is atypical in having the median latus above the carinal latus (a characteristic of *Smilium*) rather than between it and the rostral latus, and in the peduncle being longer rather than shorter than the capitulum. Therefore, inclusion of *S. mirifica* in *Scillaelepas* s.s. is provisional. Type *Scillaelepas carinata* (Philippi) (= *Pollicipes carinatum* Philippi 1835).

Discussion : Zevina (1976) raised *Scillaelepas* to full generic rank. Foster (1978), in connection with extant forms from New Zealand, voices some skepticism over the validity of *Scillaelepas* even as a subgenus. It is true that, while most species can readily be assigned one way or the other, there are a few considered to be *Calantica* that come close to bridging the gap. *Calantica studeri* (Weltner) is an example since the lower whorl of plates covers the bases of the upper whorl (cf. Foster,

1978). However, the individual plates of the lower whorl are relatively weakly developed, only the median latera in the largest specimens appear to be marked by an articular furrow and perhaps more importantly, the peduncular scales are very small, and the males reside between the scuta rather than in the subrostral region. By the sum of these characters the species is readily assignable to *Calantica* rather than *Scillaelepas*. Recognition of the two genera not only seems appropriate but becomes necessary if the three natural groups within *Scillaelepas* are to be recognized as subgenera (see Table 1 and Key to Species).

In the present work, in addition to the shells of many of the critical species, it has been possible to study aspects of their appendages as well. Where there were several specimens of a particular species, it was reassuring to note that shell characters were consistent. The differences indicated by them were reflected by the filamentary appendages in the species having them. All the species recognized in the present study are as distinct from each other as any considered good species among the thoracican cirripeds.

KEY TO THE SUBGENERA AND EXTANT SPECIES  
OF *SCILLAELEPAS*

1. Capitulum of 13 plates (no subrostra); no prosomal filamentary appendages; *Scillaelepas* s.s. . . . . 2
1. Capitulum of 14 or 15 plates (one or two subrostra); one to three sets of prosomal filamentary appendages . . . . . 6
2. Tergum retroverted. . . . . 3
2. Tergum normal . . . . . *S. fosteri* sp. nov.
3. Rostrolatus overlapping carinolatus; subcarina relatively large, conspicuous . . . . . 4
3. Rostrolatus and carinolatus separated by a ridge on median latus; subcarina small, relatively inconspicuous. . . . . 5
4. Median latus lying in line with other latera; peduncle normal, shorter than capitulum. . . . .  
. . . . . *S. gemma* (Aurivillius)
4. Median latus laying over (above) the carinolatus; peduncle more than twice as long as capitulum. . . . . *S. mirifica* Zevina
5. Capitulum wider than high; peduncular scales relatively large and few in number (approx. 10/whorl) . . . . . *S. grimaldi* (Aurivillius)
5. Capitulum higher than wide; peduncular scales relatively small, numerous (approx. 18/whorl). . . . .  
. . . . . *S. superba* (Pilsbry)
6. Capitulum of 14 plates, including one subrostrum; 3 sets of prosomal filamentary appendages; *S. (Aurivillialepas)*. . . . . 8
6. Capitulum of 15 plates, including two subrostra; 1 or 2 sets of filamentary appendages; *S. (Gruvelialepas)*. . . . . 7

- 7. Rostrolatus separated from carinolatus; peduncular scales small, rounded (more than 20/whorl); prosoma supporting two sets of filamentary appendages ..... *S. pilsbryi* (Gruvel)
- 7. Rostrolatus overlapping carinolatus; peduncular scales appear large, pointed (less than 20/whorl); prosoma supporting one set of filamentary appendages ..... *S. kempfi* (Annandale)
- 8. Rostrolatus acute, apical angle 60-70°. . . . . 9
- 8. Rostrolatus obtuse, apical angle approx. 90° .. 10
- 9. Carina continuous with carinal margin of tergum; carina narrow in lateral aspect, not reaching apex of median latus. . . . . *S. falcata* (Aurivillius)
- 9. Carina apex free of carinal margin of tergum; carina wide in lateral aspect, reaching apex of median latus. . . . . *S. arnaudi* sp. nov.
- 10. Rostrolatus overlapping carinolatus; second set of filamentary appendages nipple-like; teeth of mandible without marginal spines. . . . .

- ..... *S. calycula* (Aurivillius)
- 10. Rostrolatus separated from carinolatus; second set of filamentary appendages short, flat blades; third and sometimes second tooth of mandible with marginal spines ..... *S. bocquetae* sp. nov.

*Scillaelepas (Scillaelepas) superba* (Pilsbry)

Syn. *Scalpellum (Calantica) superbum* Pilsbry 1907: 11, fig. 3 (not. *Scapellum grimaldii* Aurivillius 1898, Gruvel 1920: 15).

*Material*: Holotype U.S.N.M. Cat. No. 11525; first paratype (same locality as holotype) U.S.N.M. Cat. No. 173132. 31° 09' N, 79° 33' W; 643 m.

Table 1. - Extant species of *Scillaelepas*

SCILLAELEPAS (SCILLAELEPAS) (no subrostra):

* <u><i>S. fosteri</i></u> sp. nov. ♂		
Foster 1978:47, fig. 28, pl. 6B, C;		
as <u><i>Calantica (Scillaelepas) gemma</i></u> (Aurivillius).	New Zealand	401-1,075 m
<u><i>S. gemma</i></u> (Aurivillius) 1892 (no figure)		
Aurivillius, 1894:41, pls. III, 3-5 & V, 7.	East coast of Greenland	1,800 m
<u><i>S. grimaldi</i></u> (Aurivillius) 1898 (no figure)		
Gruvel 1920:15, pl. V, 7-9	Azores	845-1,250 m
<u><i>S. mirifica</i></u> Zevina 1976	Mid-Atlantic Ridge, S.W.	
	of Azores	3,120-3,460 m
* <u><i>S. superba</i></u> (Pilsbry) 1907	Between Bahamas and	
	North Carolina	643-805 m

SCILLAELEPAS (AURIVILLIALEPAS) subgen. nov. (one subrostrum):

* <u><i>S. arnaudi</i></u> sp. nov. ♂	Walters Shoals, S.W.	
	Indian Ocean	600-635 m
* <u><i>S. bocquetae</i></u> sp. nov. ♂		
Bocquet-Védérine 1971, figs. 1 & 2;		
as <u><i>Calantica calyculus</i></u> (Aurivillius).	Bay of Biscay	340-500 m
* <u><i>S. calycula</i></u> (Aurivillius) 1898 (no figure) ♂		
Gruvel 1920:13, pl V, 16-18	Azores	845-880 m
* <u><i>S. falcata</i></u> (Aurivillius) 1898 (no figure) ♂	Azores	454 m
Gruvel 1920:14, pl. V, 22-24		

SCILLAELEPAS (GRUVELIALEPAS) subgen. nov. (two subrostra):

* <u><i>S. kempfi</i></u> (Annandale) 1911		
Withers 1953, pl. LXIV, 2a-b	S.W. of Ireland	1,175-1,365 m
* <u><i>S. pilsbryi</i></u> (Gruvel) 1911 (no figure)		
Gruvel 1920, pl. VII, 7	Spanish Sahara,	
	W. Africa	822 m

\*Specimen seen in this study; ♂ = males present

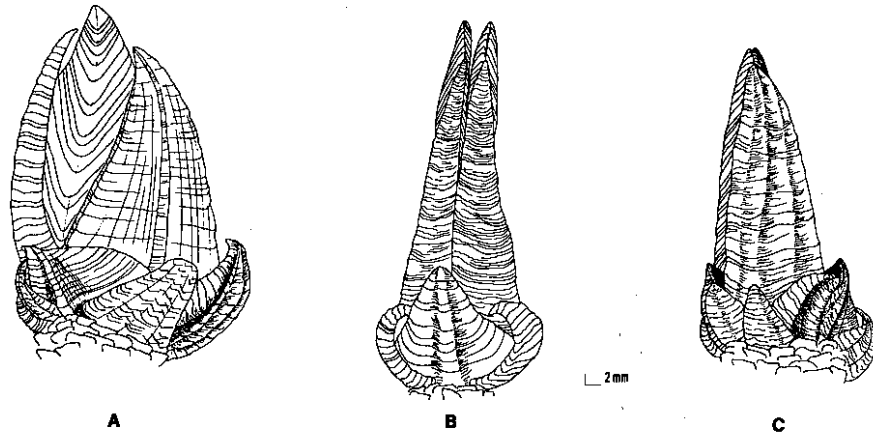


Figure 1. - *Scillaelepas (Scillaelepas) superba* (Pilsbry). A.-C. ; lectotype left lateral, ventral and dorsal views of hermaphrodite. In A, note ridge separating adjacent basal angles of subcarina and subrostrum.

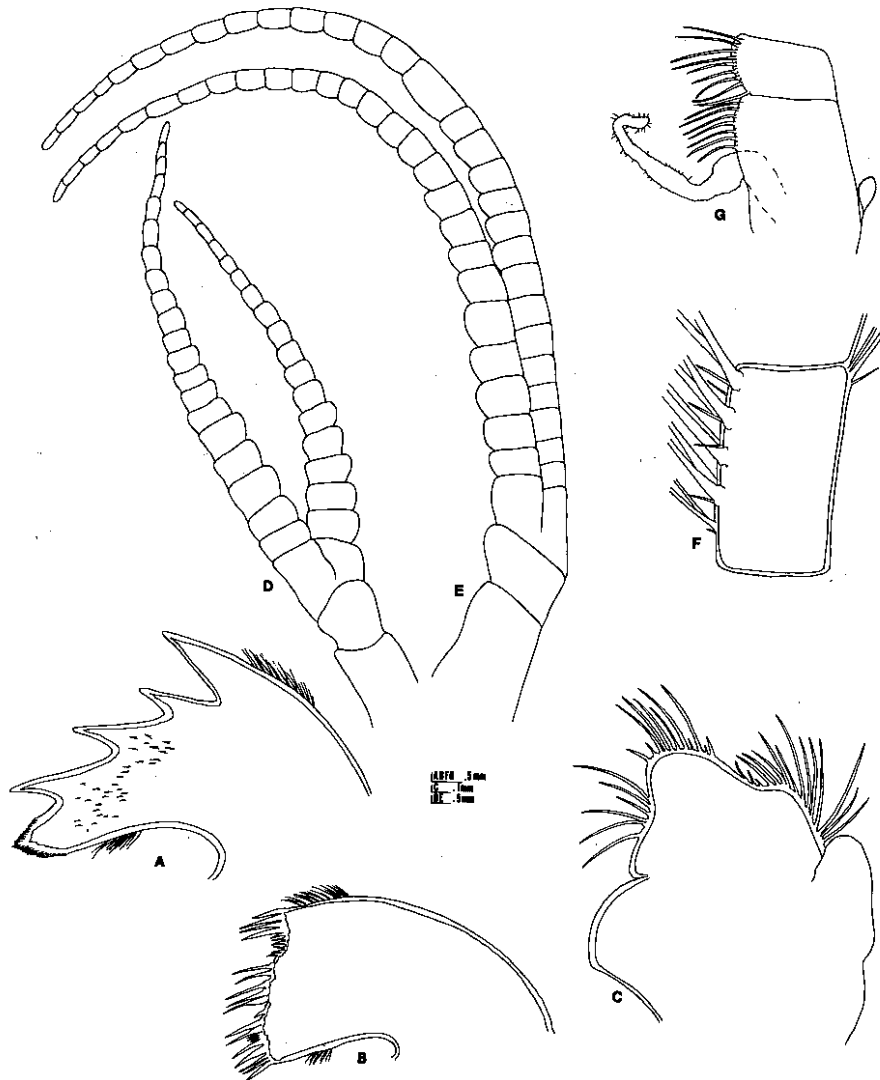


Figure 2. - *Scillaelepas (S.) superba* (Pilsbry). Appendage of paratype : A, mandible; B & C, first and second maxilla, respectively; D & E, articles of first and second cirri respectively; F, intermediate article of sixth cirrus; G, pedicle of sixth cirrus with penis and right caudal appendage attached. Note minuteness, and lack of long setae on the caudal appendage.

*Discussion* : This species of *Scillaelepas* s.s. was examined and returned to U.S. National Museum of Natural History before the specimens of *S. fosteri* were received. There were two specimens; the largest (capitulum 50 mm high) being that figured by Pilsbry is considered the holotype. Pilsbry notes that his lateral view of the type has a slightly abnormal median latus, so the opposite (left) side is figured here (fig. 1). The smaller specimen (capitulum 30 mm high) is the first paratype. It was dissected in the course of this study and the appendages are illustrated in fig. 2. No males were found between the scuta, but the subrostral region of the peduncle was not scrupulously examined (cf. *S. fosteri*).

Foster (1978 : 38) notes, in his definition of *Calantica*, that the body lacks filamentary appendages. This is true of the present species and it therefore may be a characteristic of *Scillaelepas* s.s. However, filaments are present in the subrostrate forms, as will be described below. A notable feature in *S. superba*, and perhaps unique to it, is the extremely small size of the caudal appendages, which, while having margins minutely spined, are without setae. The cirral count was :

I	II	III	IV	V	VI	c.a.
18	30	26	28	24	25	
21	28	29	31	28	28	1

The first paratype was attached to a branching coral and the attachment region was carefully inspected. If there was a calcareous pad or basis, it could not be detected.

*Affinities* : Pilsbry noted that *S. superba* is similar to *S. gemma* (Aurivillius, 1892) but he gave a number of distinguishing characteristics. In addition to these can be added the fact that while the carinolatus and rostralatus overlap in both species, they are actually separated by a central ridge on the median latera in *S. superba*. Pilsbry indicates that *S. superba* and *S. grimaldi* are similar, and it does turn out that they are the only extant species having the rostralatus separated from the carinolatus by a central ridge on the median latus. Pilsbry concluded that the exact relationship could not be determined since *S. grimaldi* had not been illustrated at the time.

Gruvel (1920 : 15) provides a fuller description and photographs of *S. grimaldi*, and with virtually no discussion he places *S. superba* in synonymy with it. Withers (1953 : 96) felt some doubt over this decision, however, and Gruvel had noted that in three expeditions to the Azores no specimens of *grimaldi* as large as the largest *superba* were taken. Overall size of course is not a good character, but as noted in the key to species, the proportions of the capitulum and the size and number of peduncular scales differ considerably between the two forms and they are recognized as distinct species here.

### *Scillaelepas (Scillaelepas) fosteri* sp. nov.

Syn. *Calantica (Scillaelepas) gemma* (Aurivillius), Foster 1978 : 47, fig. 28, pl. 6 B-C.

*Material* : From near Campbell, Bounty & Antipodes Is., 722-1 075 m : New Zealand Oceanographic Institute (NZOI) Sta. S 46 (53°00'S, 171°13'E, 1 075 m; 2 specimens 43 & 24 mm high, respectively, the latter attached to the former about half way down the length of the capitulum slightly to the right of the rostral margin (B.A. Foster, pers. comm.); NZOI Sta. I 676 (48°10'S, 179°20'E, 810 m; 28 mm high); NZOI Sta. I 685 (48°20'S, 179°30'E, 722 m; 25 mm high, with male situated 2 peduncular scales directly below rostrum); NZOI Sta. I 693 (49°06'S, 178°53'E, 778 m; capitulum 28 mm high, peduncle lacking).

*Deposition of types* : Holotype hermaphrodite (intact dried shell and three slides of appendages) plus male (on slide), Sta. I 685, NZOI Cat. no. 259; first paratype, Sta. I 676, USNM Cat. no. 173635; second paratype (43 mm specimen), Sta. S 46, Brit. Mus. (Nat. Hist.) Reg. no. 1980-1; third paratype, Sta. I 693, Mus. Nat. Hist. Nat., Paris; fourth paratype (24 mm specimen), Sta. S 46, NZOI, Cat. no. p 153.

*Description* : The hermaphrodite of *Scillaelepas fosteri* was well described and illustrated by Foster (1978) and therefore only illustrations of the holotype need be provided here (figs. 3 & 4). However, a single complementary male was found between the peduncular scales in the subrostral region of one of the five specimens examined during the course of this study, the one selected as the holotype, and it too is illustrated here, in situ (fig. 3 B) and after having been removed from the hermaphrodite (fig. 3 D-E). The remarkable thing about the male is its being attached to the peduncle, a situation known in no other scalpellid although it is likely the case in other species lacking subrostra (*Scillaelepas* s.s.).

As can be seen in the illustration (fig. 3 A-C), the peduncle of the hermaphrodite is bent to the left from the attachment area so that the scales of the right side are more spread out and projecting than those on the left. But even so, it appears that those on the frontal surface, immediately below the rostrum, are perhaps somewhat larger and more flaring than the rest; that is, somewhat modified to accommodate the male. Modified or not, it is the position of this male on the hermaphrodite that is important in understanding the impetus for the acquisition of true subrostra in *Scillaelepas*. Particularly instructive in this regard is the situation in *Scillaelepas pilsbryi* where the subrostra are clearly modified peduncular scales that may either join the capitulum or remain with the peduncle (fig. 11), and in *Scillaelepas (Aurivillialepas)* where the subrostrum is an inseparable part of the capitulum with the male residing between it and the rostrum (cf. fig. 16 and last section of this paper).

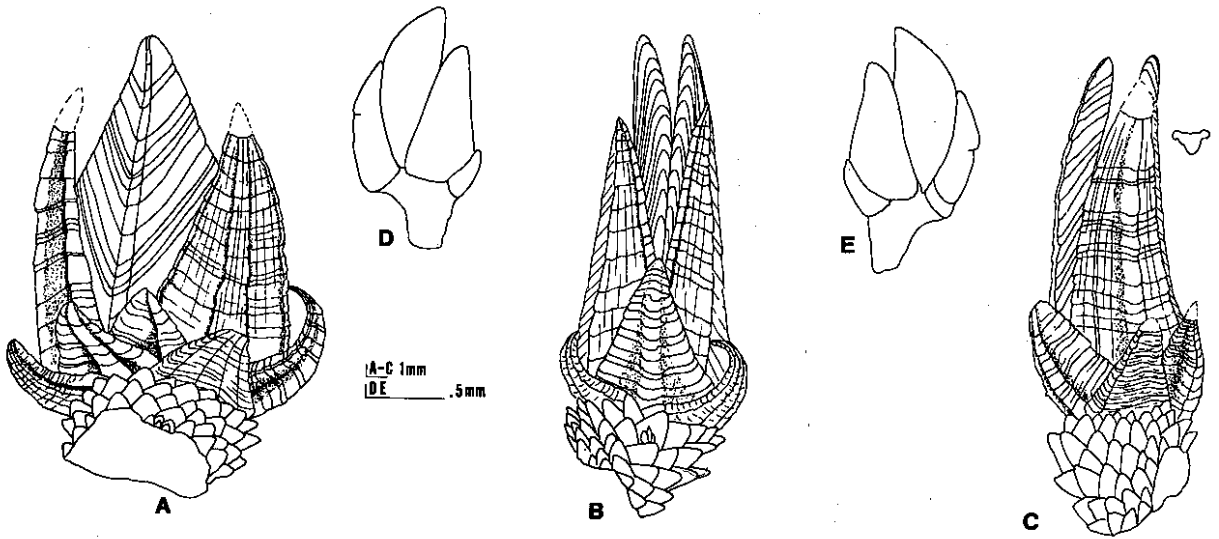


Figure 3. - *Scillaelepas (Scillaelepas) fosteri* sp. nov. A-C, holotype hermaphrodite: left lateral, ventral and dorsal views respectively (note male between subrostral peduncular scales in B and cross-section of carina where broken in C); D-E, complementary male from left and right side, respectively.

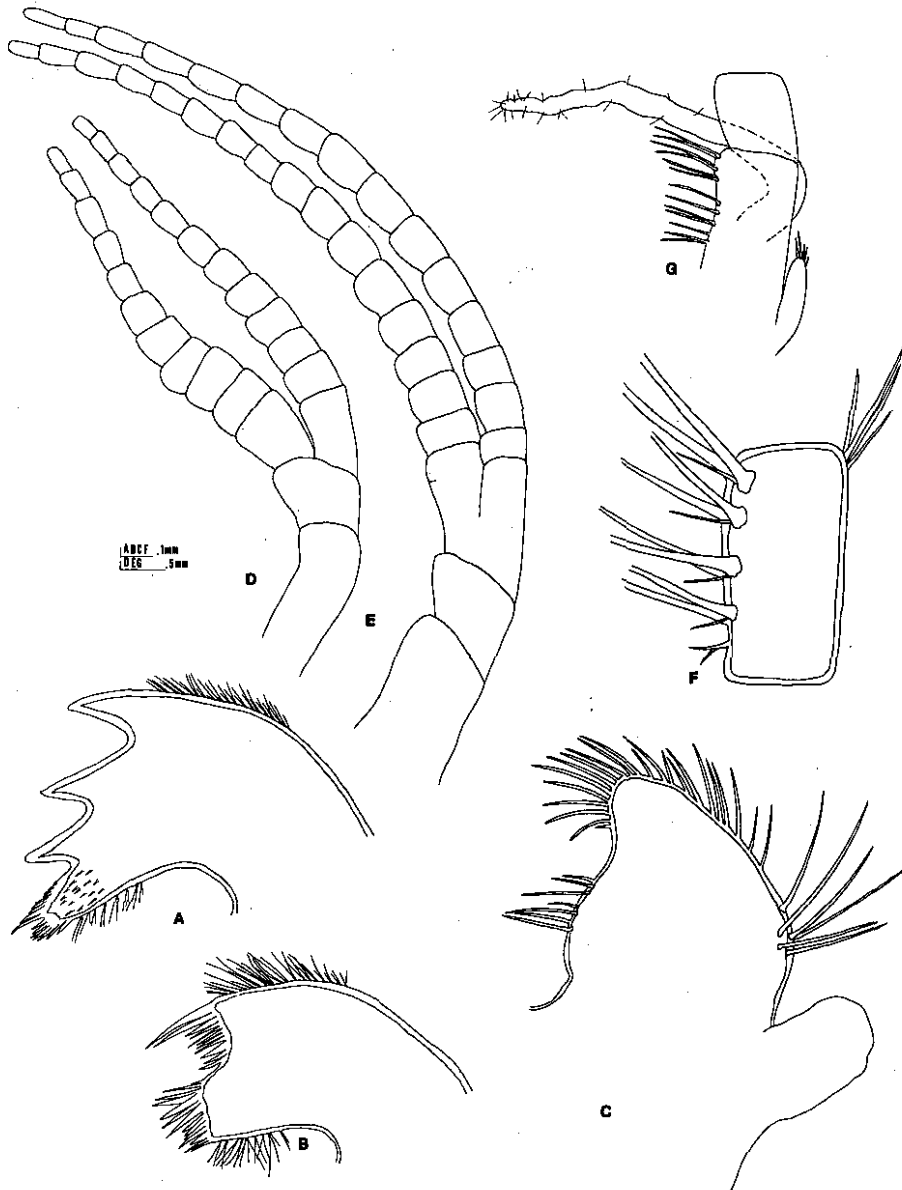


Figure 4. - *Scillaelepas (S.) fosteri* sp. nov. Appendages of holotype hermaphrodite; A, mandible; B & C, first and second maxillae, respectively; D & E, first and second cirri, respectively; F, intermediate article of sixth cirrus; G, pedicle of sixth cirrus with penis and caudal appendage.

*Discussion*: Foster (1978) considered this form from New Zealand sufficiently similar to *S. gemma* (Aurivillius) from the east coast of Greenland to be the same species. However, he noted that *S. gemma* was more squat and that the apex of the tergum was reflexed towards the carina. To these can be added other small differences, such as the rostrum having a submedial depression and the rostrum being very wide at the base. Another difference in the New Zealand form may be the pronounced bead along the occludent margin of the scutum, a feature I've seen in no other living *Scillaelepas* except *S. calycula*. The sum of these morphological differences are sufficient to distinguish the New Zealand form from Aurivillius' species from Greenland.

Foster (1978) notes that this species is very close to the *S. (S.) arguta* (Withers) from the lower Oligocene of New Zealand, and the sketches of the entire animals are similar. The principal differences are the very large rostrum and the quadrangular rather than nearly triangular scutum. Therefore, it is not exactly this species either, and I propose that it be recognized as new. It is named for Dr. B.A. Foster, in appreciation for numerous works on barnacles, but especially for his recent monograph on the New Zealand thoracicans. *Scillaelepas fosteri* is the first living species of this genus known from the southern hemisphere, all others having been described from the North Atlantic. A second southern hemisphere species of *Scillaelepas*, *S. arnaudii*, is to be described below. *Scillaelepas fosteri* is also the first pedunculate barnacle known as having a complementary male attached to the peduncle rather than the capitulum of the hermaphrodite.

#### *Scillaelepas (Aurivillialepas)* subgen. nov.

*Definition*: *Scillaelepas* with 14 capitular plates including one subrostrum, a calcareous basis, three pairs of filamentary appendages on the dorsal surface of the prosoma, and a complementary male residing in the cavity between the subrostrum and rostrum. The subgenus is named for C.W.S. Aurivillius who described the first living species of *Scillaelepas* known to science. Type *S. calycula* (Aurivillius) (= *Scalpellum calyculus* Aurivillius 1898).

*Discussion*: Heretofore, there were but two species assignable to *Aurivillialepas* and both, *S. calycula* and *S. falcata*, were described near the turn of the century from the Azores. Bocquet-Védrine (1971) described a form from the Bay of Biscay which she considered to be *S. calycula*, but as will be demonstrated shortly, the two populations are morphologically distinct and the Biscay form is clearly a new species.

Bocquet-Védrine made a very interesting discovery in the course of her study; the existence of a complementary

male residing in the space between the subrostrum and rostrum in the Biscay form. I have since found a male in the same situation, in the largest specimen of *S. calycula* studied by Aurivillius (1898). The male is so conspicuous as to make it almost impossible for Aurivillius not to have seen it. Perhaps he thought it simply a juvenile and thereby unimportant because he did not mention it. On the other hand, Gruvel (1920) was on the alert for males, but for some reason he did not see the largest specimen when he studied Aurivillius' material, and therefore missed it. A fourth species, a new one from Walters Shoals south of Madagascar, also has a complementary male between the rostrum and subrostrum, as does *S. falcata* from the Azores.

#### *Scillaelepas (Aurivillialepas) calycula* (Aurivillius)

Syn. *Scalpellum calyculus* Aurivillius 1898 (not *Calantica calyculus* (Aurivillius), Bocquet-Védrine 1971).

*Material*: Type material, Musée océanographique, Monaco: Sta: 584, 38° 31' N, 26° 49' 15" W, 845 m, 3 specimens (the largest photographed by Gruvel, 1920); Sta. 838, 37° 55' N, 25° 23' 45" W, 880 m, 1 large specimen (the measurements for which were given in the original description and by Gruvel, 1920).

*Discussion*: The largest specimen, from Sta. 838, was apparently the one upon which Aurivillius (1898) based his description. It is therefore appropriately considered the lectotype (fig. 5). While the four specimens range greatly in size (3-17 mm in capitular height), the essential features are the same, except for the largest of the three specimens from Sta. 584 photographed by Gruvel (1920), where the tergum is retroverted rather than normal.

Neither Aurivillius nor Gruvel dissected a specimen so the appendages of the lectotype are figured here (fig. 6). Cirral counts were:

I	II	III	IV	V	VI	c.a.
$\frac{14}{13}$	$\frac{18}{16}$	$\frac{19}{19}$	$\frac{20}{18?}$	$\frac{22}{23}$	$\frac{21}{22}$	1
$\frac{17}{13}$	$\frac{20}{17}$	$\frac{16}{17}$	$\frac{20}{18}$	$\frac{20}{20}$	$\frac{21}{19?}$	1

As apparently typical for the subgenus, the prosoma supports three pairs of filamentary appendages on the dorsal surface of the prosoma. The first, located on the dorsolateral margins of the prosoma opposite the oral cone, consists of short, sharp, blade-like projections lying flat against the prosoma and pointing posteriorly; the second, set on the posteriomedial margin of the prosoma, consists of short, nipple-like projections; and the third, located on the posterior edge of the intercalated folds between the first and second cirri, consists of short blade-like filaments pointing dorsally.

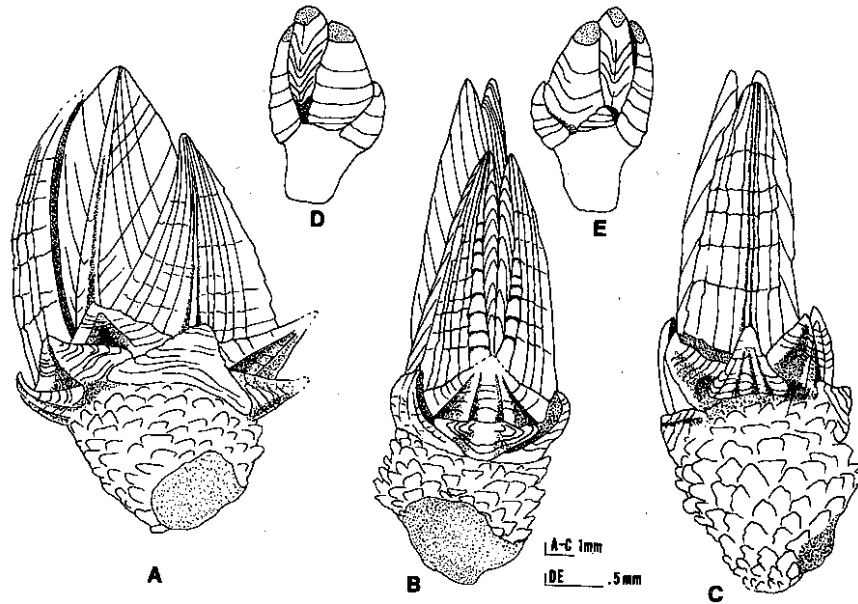


Figure 5. - *Scillaelepas (Aurivilliaelepas) calycula* (Aurivillius). Lectotype; A-C, left lateral, central and dorsal views of hermaphrodite and, D-E, its accompanying complementary male.

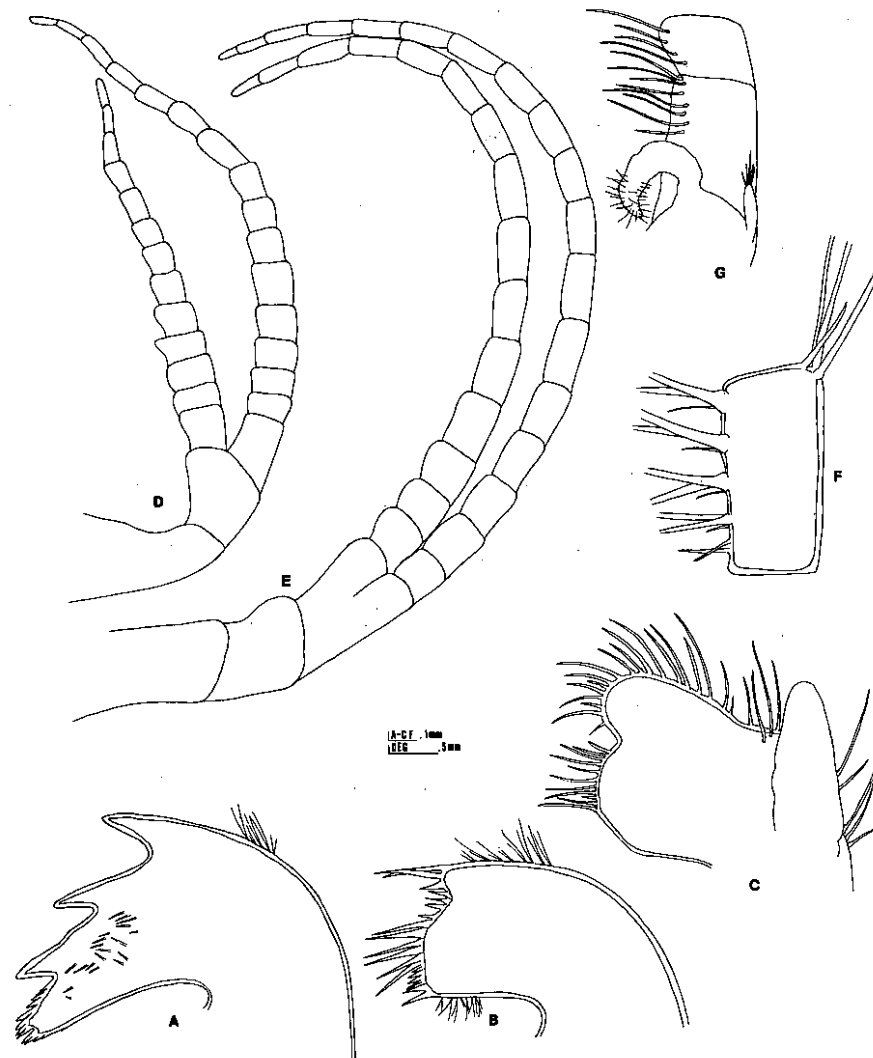


Figure 6. - *Scillaelepas (A.) calycula* (Aurivillius). Appendages of lectotype hermaphrodite: A, mandible; B & C, first and second maxillae, respectively; D & E, articles of first and second cirri, respectively; F, intermediate article of sixth cirrus; G, pedicle of sixth cirrus with penis and caudal appendage attached.



This species, and likely all other members of the subgenus, is remarkable in having a calcareous basis that tremendously strengthens the attachment to the substratum. It is a rather thick disc, but the scale-clad peduncle completely surrounds it so that it is invisible from the outside.

*Scillaelepas (Aurivillialepas) bocquetae* sp. nov.

Syn. *Calantica calyculus* (Aurivillius), Bocquet-Védrine, 1971 not Aurivillius, 1898.

**Material:** « Mission *Thalassa* » (1967, series T), Bay of Biscay, on shelf around margin of West European Basin; Sta. T-474, 44° 11' 0" N - 08° 41' 3" W, 519 m; Sta. T-450, 47° 58' 3" N - 07° 50' 0" W, 340 m; Sta. T-454, 47° 57' 3" N - 07° 51' 0" W, 356 m; Sta. T-503, 44° 00' 7" N - 07° 06' 9" W, 490 m; on rocks, pebbles, fossil debris, lumps of calcareous material and stony coral.

**Deposition of types:** Holotype (T-474) Muséum National d'Histoire Naturelle, Paris, No. entrée 7909; 1st

paratype (T-450) Brit. Mus. (Nat. Hist.), London Reg. No. 1979-436; 2nd paratype (T-454) U.S.N.M. Cat. No. 173133; 3rd paratype, (T-503) Musée océanographique, Monaco.

**Discussion:** Bocquet-Védrine (1971) has described and figured the form from the Bay of Biscay, and little need be added here. With regard to the hardparts, it is noteworthy that the rostrolatus and carinolatus do not overlap and are usually well separated from each other (fig. 7). This condition is found only in *S. pilsbryi*, among the subrostrate *Scillaelepas*. But there are other differences besides the additional subrostrum in *S. pilsbryi*, such as the number of filamentary appendages, which indicate that the similarity in the arrangement of the latera is not indicative of a particularly close relationship between the two. It is also noteworthy that *S. bocquetae* (as well as *S. calycula* and *arnaudi* and *S. falcata*) has a calcareous disc, imbedded in the basal portion of the peduncle and firmly cemented to the subrostrum. The calcareous basis in *S. pilsbryi* is very thin and irregular in shape.

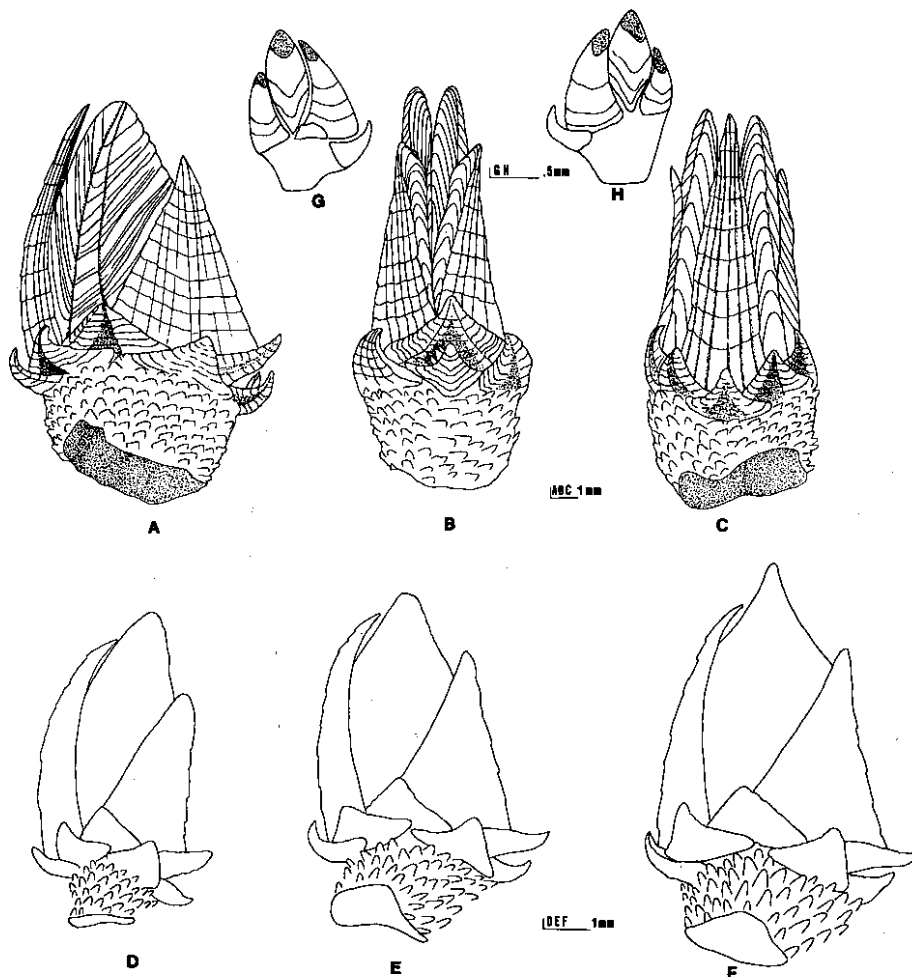


Figure 7. - *Scillaelepas (Aurivillialepas) bocquetae* sp. nov. A-C, holotype hermaphrodite, left lateral, frontal and dorsal views. D-F, left lateral views of paratype hermaphrodites; (D, Brit. Mus. (Nat. Hist.); E, U.S.N.M.; F, Monaco). G & H; male accompanying holotype (note *in situ* between rostrum and subrostrum in A & B). Note that carinal and rostral latera of hermaphrodite do not overlap.

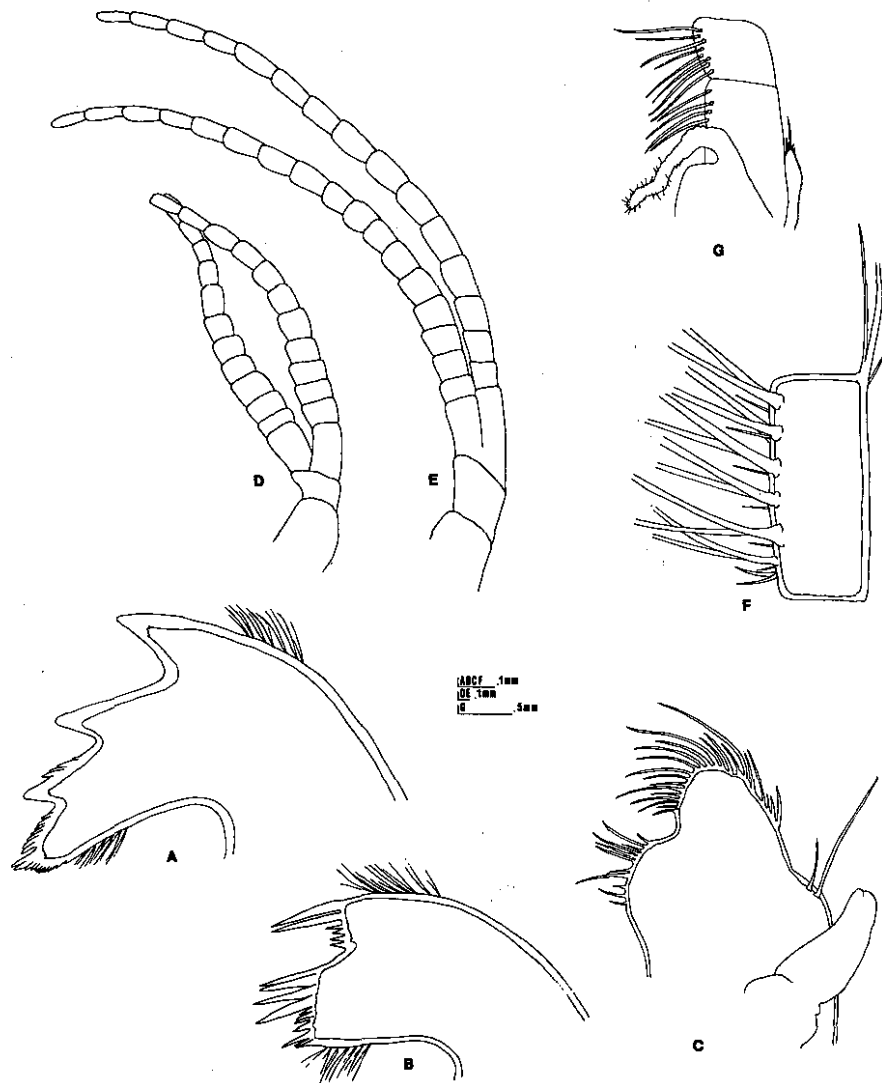


Figure 8. - *Scillaelepas (A.) bocquetae* sp. nov. Appendages of holotype hermaphrodite: A, mandible (note short spines on upper margin of third tooth). B & C, first and second maxilla, respectively; D & E, articles of first and second cirri, respectively; F, intermediate article of sixth cirrus (note 7 rather than usual 5 pairs of setae); G, pedicle of sixth cirrus with penis and caudal appendage attached.

The mandibles of *S. bocquetae* like those of *S. falcata* are unusual for *Scillaelepas* in having numerous short, strong spines on the upper margin of the third and sometimes the second tooth (fig. 8). The intermediate articles of the sixth cirrus are also unusual in supporting, rather than usually five or sometimes six, as many as seven pairs of setae. The prosoma supports three pairs of filamentary appendages, although the third is barely detectable. The first, situated on the dorsum opposite the mouth fields, is similar to that of *S. calycula*, but the filaments are much broader and leaf-like and, in addition there is a single, short, flap-like filament pointing forward from between their bases. The second pair, located at the posterior of the prosoma, consists of posteriorly directed flaps rather than nipple-like projections. The intercalary folds between the prosoma and the second thoracic segment supports the third pair as slightly projecting points on each side, where there were pronounced projections in *S. calycula* and *S. arnaudi*.

The cirral counts were:

I	II	III	IV	V	VI	c.a.
12	18	16	17	17	17	1
14	18	16	19	17	18	
11	17	16	16	16	16	1
15	19	16	16	16	19	

Gruvel (1920) did a great service to science in writing more complete descriptions and in providing the first illustrations of Aurivillius' (1898) species of *Scillaelepas* from the Azores. But he conceptually weakened the morphological basis for distinguishing species in the genus by his subjective synonymy of *S. kempi* (Annandale) with *S. pilsbry* (Gruvel), and of *S. superba* (Pilsbry) with *S. grimaldi* (Aurivillius). The living species of the genus have not been looked at as a whole since, and considering the relaxation of the criteria distinguishing them, it is not surprising that Bocquet-Védrine (1971)

puzzled over the distinctness of *S. calycula* and *S. pilsbryi* since the arrangement of latera in her form from the Bay of Biscay might appear to bridge the gap. The Biscay form is named for Mme. Bocquet-Védrine in appreciation for her many contributions to the knowledge of cirripeds and other crustaceans.

*Scillaelepas (Aurivillialepas) arnaudi* sp. nov.

**Material:** M/S *Marion-Dufresne* Cruise MD. 08 (1976) (cf. Arnaud & Hureau, 1979); Walters Shoals: Sta. 6, 33° 08.7' S, 43° 59.7' E, 600 m, 16.3.76, Charcot dredge sample 46, fine sand, 1 specimen; Sta. 6, 33° 11.4' S, 44° 00.4' E, 620-635 m, 16.3.76, beam trawl 47, 2 specimens, each with complementary male.

**Deposition of types:** Holotype (Sta. 6, sample 47) Laboratoire des Crustacés, Muséum National d'Histoire Naturelle, Paris (prepared specimen; specimen-shell dried, appendages and male mounted on slides), No. entrée 7910; first paratype (Sta. 6, sample 47), U.S.N.M. Cat. No. 173134, specimen in alcohol, male in place (from same sample as holotype); second paratype (Sta. 6, sample 46), British Museum (Nat. Hist.) Reg. no. 1979-382 (appendages on slide).

**Description:** Hermaphrodite accompanied by a single complementary male situated between the rostrum and subrostrum. Plates of the upper whorl lightly sculptured, primarily by transverse growth lines on the scutum and carina and two sets of chevron-shaped, criss-crossed growth lines on tergum. Tergum traversed by a narrow median ridge running from the apex to the base. The lower whorl is less distinctly sculptured by transverse and/or longitudinal growth lines, and only the median and carinal latera are marked by an articular ridge running from the apex to the base. These ridges are formed by the overlap between the carinal latus and median latus, and the subcarina and carinal latus.

Imbricating peduncular scales fit closely around the bases of the lower whorl of capitular plates, including the subrostrum. It appears that the subrostrum of *Aurivillialepas* was phylogenetically but is not ontogenetically added to the lower whorl as are the subrostra of *Gruvellialepas*. Complementary males were found, one each on two of the three hermaphrodites, lying on their sides between the rostrum and subrostrum. The capitulum of the males consisted of six plates (carina, terga, scuta and rostrum) plus a median latus on one side. The males are about half as large as those described for *S. bocquetiae* by Bocquet-Védrine and there is no indication of a carinal latus on either of them.

The crest of the labrum supports approximately 20 fine, low teeth arranged more or less in pairs with individuals of a pair being separated by approximately the diameter of one tooth. The palps are short and their

lower surfaces and anterior margins support short, simple setae. The right mandible in the holotype is abnormal in having but two rather than three teeth, but anomalous mandibles seem rather common in the genus. The second tooth of the left mandible is without short, stout marginal spines on the superior edge and the third tooth has but one such spine. The inferior angle of the mandible supports a comb of stout spines in a single row along the superior and apical margins; about two-thirds of the inferior margin support a comb of closely spaced setae. The cutting edge of the first maxilla is divided into two parts, in a step-wise fashion, but the tread is shallow so that the long spines of the upper cutting edge reach medially as far as those of the lower edge. The second maxilla supports relatively stout spines above and below the median notch, and the papilla of the maxillary gland is long and conspicuous.

The first cirri, attached to the prosoma, are separated from the posterior pairs by an intercalary fold; their anterior rami are longer than the posterior rami by two segments, and the articles, about as high as wide, are thinly clad with spine-like simple setae. The articles of the anterior cirri tend to resemble those of the first cirri in being about as wide as high. The articles of the posterior rami are markedly longer than wide. The intermediate articles of the sixth cirrus bear five pairs of setae along the lesser curvatures, and a single short and a single long seta at the distal articulation along the greater curvature. The unarticulate caudal appendage is about half the length of the proximal article of the sixth cirrus. The penis, clothed sparsely with fine, short setae, is about half the length of the first article of the pedicle of the sixth cirrus and, as in all *Scillaelepas* I have observed, it is apparently immature. Cirral counts were:

I	II	III	IV	V	VI	c.a.
$\frac{11}{9}$	$\frac{11}{14}$	$\frac{14}{14}$	$\frac{15}{13}$	$\frac{16}{14}$	$\frac{16}{15}$	1
$\frac{10}{8}$	$\frac{12}{11}$	$\frac{13}{13}$	$\frac{14}{15}$	$\frac{15}{16}$	$\frac{16}{16}$	1

There are three sets of filamentary appendages along the median dorsal surface of the prosoma; the first, opposite the oral cone, is shaped like the symbol for Aries (first sign of the zodiac); the second, situated somewhat short of the posterior margin of the prosoma, is in the form of a "V" that does not quite meet at the base; and the third, on the intercalary fold between the first and second cirri, consists of well-separated, dorsally directed, nipple-like projections.

The species is named for Dr. P. Arnaud in appreciation of his many contributions to our knowledge of the Southern ocean, and for his efforts in making materials available to others. This is the second work on cirripeds of the region to have been stimulated by specimens he kindly placed at my disposal.

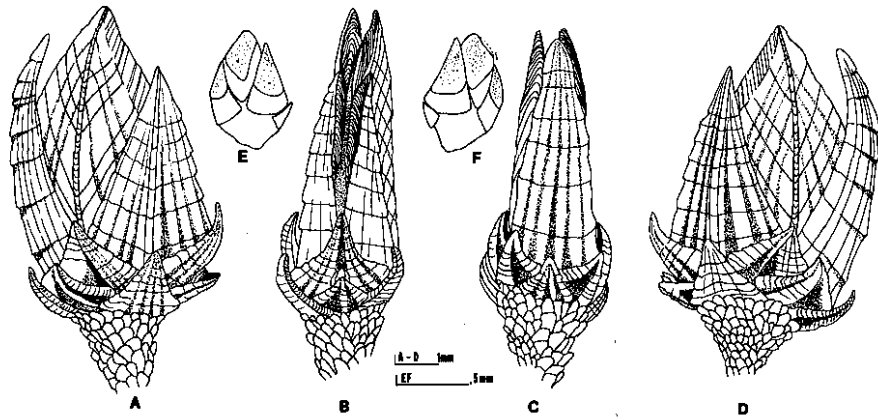


Figure 9. - *Scillaelepas (Aurivillialepas) arnaudi* sp. nov. A-D, holotype hermaphrodite; left lateral, ventral, dorsal and right lateral views, respectively (note acuteness of rostralaterals in A and D); E & F, complementary male from holotype (note *in situ* between rostrum and subrostrum in A, B & D).

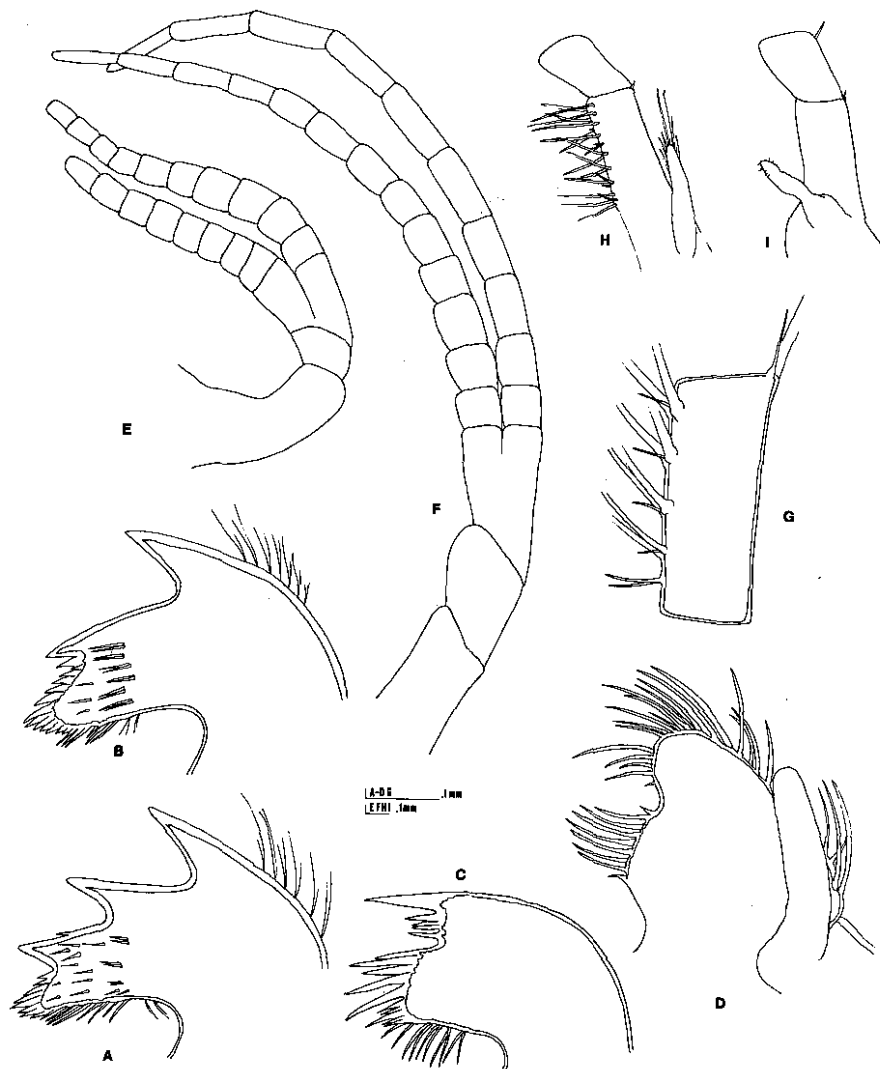


Figure 10. - *Scillaelepas (A.) arnaudi* sp. nov. Appendages of holotype hermaphrodite: A & B, right and anomalous left mandible, respectively; C & D, first and second maxillae, respectively; E & F, articles of first and second cirri, respectively. G, intermediate article of sixth cirrus (note but one large and one small seta on greater curvature); H & I, pedicel of sixth cirrus with caudal appendage and penis, respectively.

*Affinities*: *Scillaelepas arnaudi* can be distinguished from *S. bocquetae* by the overlap between the rostrolatus and carinolatus, and from both *S. bocquetae* and *S. calycula* by acute (60-70°) rather than obtuse (approx. 90°) rostrolateral apices. This leaves *S. falcata*, from which *S. arnaudi* can be distinguished by the wider carina meeting the apex of the median latus rather than that of the carinal latus, and the carina being apically free of, rather than closely applied to, the carinal margin of the tergum. *Scillaelepas arnaudi* can also be distinguished from *S. bocquetae* and *S. calycula* by differences in the filamentary appendages, and presumably from *S. falcata* in this regard although its appendages have not yet been described.

#### *Scillaelepas (Gruevialepas)* subgen. nov.

*Definition*: *Scillaelepas* with two subrostra (15 capitular plates), apparently a thin calcareous basis, and one or two pair of filamentary appendages on the dorsal surface of the prosoma. No complemental males have been observed either beneath the rostra or subrostra, or in the aperture between the scuta. The subgenus is named for Prof. A. Gruvel for his numerous contributions to our knowledge of cirripeds. Type *S. pilsbryi* (Gruvel) (= *Scalpellum pilsbryi* Gruvel 1911).

#### *Scillaelepas (Gruevialepas) pilsbryi* (Gruvel)

Syn. *Scalpellum pilsbryi* Gruvel, 1911.

*Material*: The original three specimens, *Talisman* 1883, Sta. 72, 882 m, 26°N, 15°W, off Spanish Sahara; Muséum National d'Histoire Naturelle, Paris.

*Discussion*: Gruvel (1920) subjectively synonymized *S. kempfi* (Annandale, 1911) with *S. pilsbryi* (Gruvel, 1911) without explanation. However, they are quite distinct, the most obvious external differences being that the rostrolatera overlap the carinolatera in the former but not in the latter, and the peduncular scales are more pointed and widely separated by cuticle. Internally *S. pilsbryi* has two where *S. kempfi* has but one set of filamentary appendages. The first is a pair of nipple-like projections placed dorsa-laterally on the prosoma opposite the oral cone and the second is a single median dorsal nipple-like projection located near the posterior margin of the prosoma. There are no filaments associated with the intercalary folds between the prosoma and the second thoracic segment. The cirral counts were:

I	II	III	IV	V	VI	c.a.
13	18	15	17?	16	17	1
11	18	16	16?	16	17	
11	12?	16?	17	15	17	1
11	15?	15?	16	18	17	

Whether males can reside between the rostrum and subrostrum, as in species of *Aurivillialepas*, is unknown, but it seems likely. It is important to note that the subrostra are ontogenetically derived by the addition of peduncular scales to the lower whorl of capitular plates after the peduncular scales have formed. This is the only case I am aware of in the living Scalpellidae where a major capitular plate is added ontogenetically after the peduncular scales have formed. This is of course what had to have happened phylogenetically, but such capitular acquisition has not been observed to my knowledge as an ontogenetic recapitulation in extant forms. That this is what is happening in the present species can be seen in smallest of the three specimens (fig. 11 E) where, while the rostrum is grooved, the first subrostrum is little more than a slightly enlarged peduncular scale and both it and the second subrostrum are each clearly associated with a whorl of peduncular scales. In the holotype and the third and largest specimen, the first subrostrum but not the second, is free of a peduncular whorl and can be said to be a part of the lower capitular whorl, but not an integral part as in members of *Aurivillialepas*. Instructively, the first subrostrum is accompanied by a pair of peduncular scales situated laterally that must remain with the capitulum when and if additional peduncular whorls are added. It is important to note that one peduncular whorl below the second subrostrum in the holotype (fig. 11 A & B) there is a peduncular scale that very much resembles a subrostrum, and in the largest specimen (fig. 11 D) there are two such scales. These subrostrum-like scales must have been induced to form when the peduncular whorls to which they belong were at the base of the capitulum. But for some reason the polarity of the growth gradient was not strong enough to induce them to remain with the capitulum and they were separated from it by the development of new whorls of peduncular scales. Similar evidence is gained from *S. kempfi*, as will be taken up under that species.

*Affinities*: *S. pilsbryi* is, among the subrostrate forms, similar to *S. bocquetae* in that the rostrolatus does not overlap the carinolatus. This separation is also seen in living *Scillaelepas* s.s., specifically *S. superba* and *S. grimaldi*, so the similarity is likely not of phylogenetic significance. *Scillaelepas pilsbryi* and *S. bocquetae* can readily be distinguished by the occurrence of two rather than one subrostrum in the former, and internally by differences in the mandibles and filamentary appendages. *Scillaelepas pilsbryi* is closely related to *S. kempfi*, although the two can readily be distinguished as species, as discussed above.

#### *Scillaelepas (Gruevialepas) kempfi* (Annandale)

Syn. *Scalpellum kempfi* Annandale 1911 (not *Scalpellum pilsbryi* Gruvel 1911; Gruvel 1920; Hiro 1932; Bocquet-Védrine 1971).

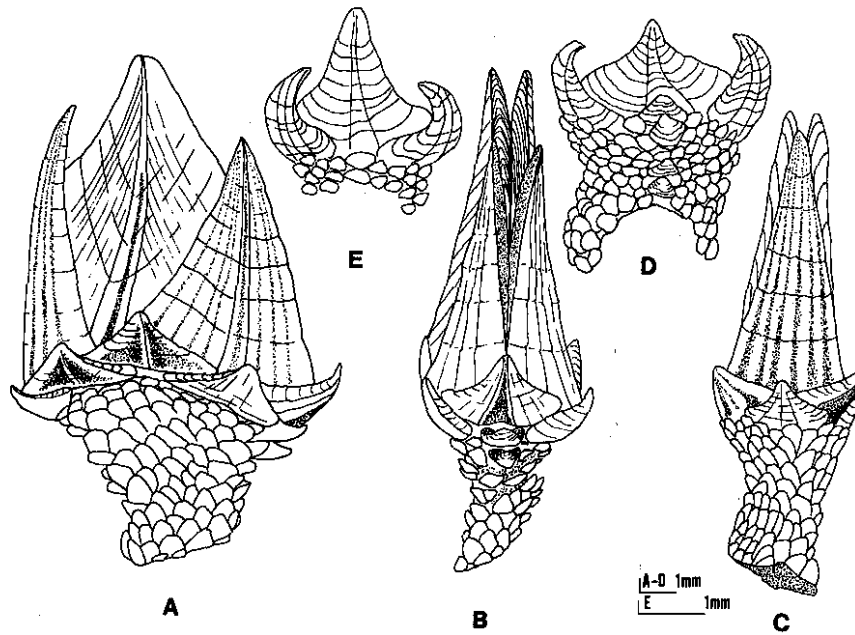


Figure 11. - *Scillaelepas (Gruvelialepas) pilsbryi* (Gruvel, 1911). A-C, holotype hermaphrodite; left lateral, ventral and dorsal views, respectively (note separation between rostral and carinal lateral in A, and subrostral-like peduncular scale about half way down the pedoncle in A & B); D & E, ventral views of largest and smallest specimens, illustrating ontogeny of specialized subrostral scales and incorporation as capitular plates.

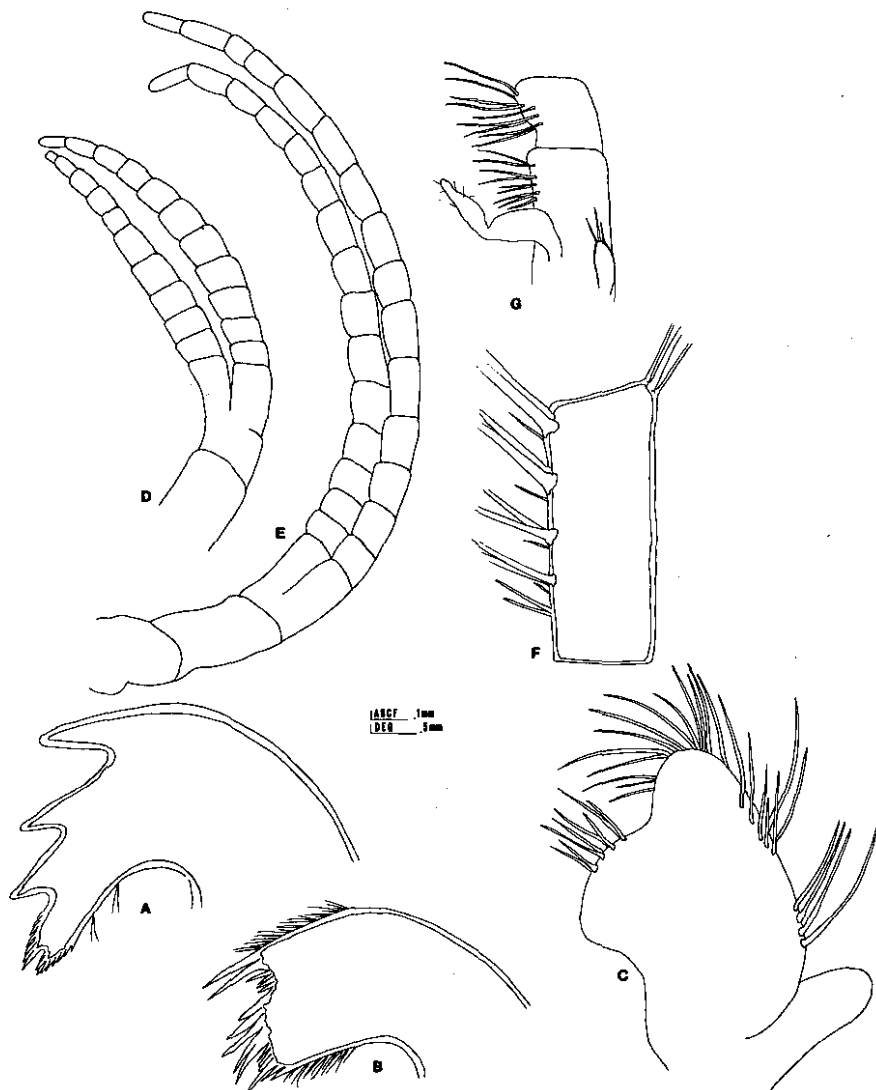


Figure 12. - *Scillaelepas (G.) pilsbryi* (Gruvel, 1911). Appendages of lectotype: A, mandibule; B & C, first and second maxilla; D & E, article of sixth cirrus; G, pedicle of sixth cirrus with penis and caudal appendage attached.

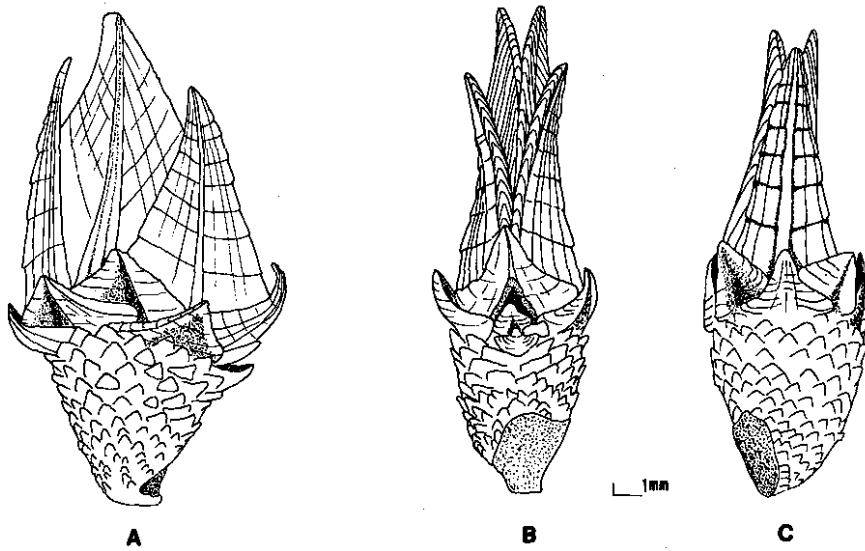


Figure 13. — *Scillaelepas (Gruvelialepas) kempi* (Annandale, 1911). A-C, holotype harmaphrodite; left lateral, ventral, and dorsal views, respectively (note abnormally situated "peduncular scale" between first and second subrostrum on right side in B).

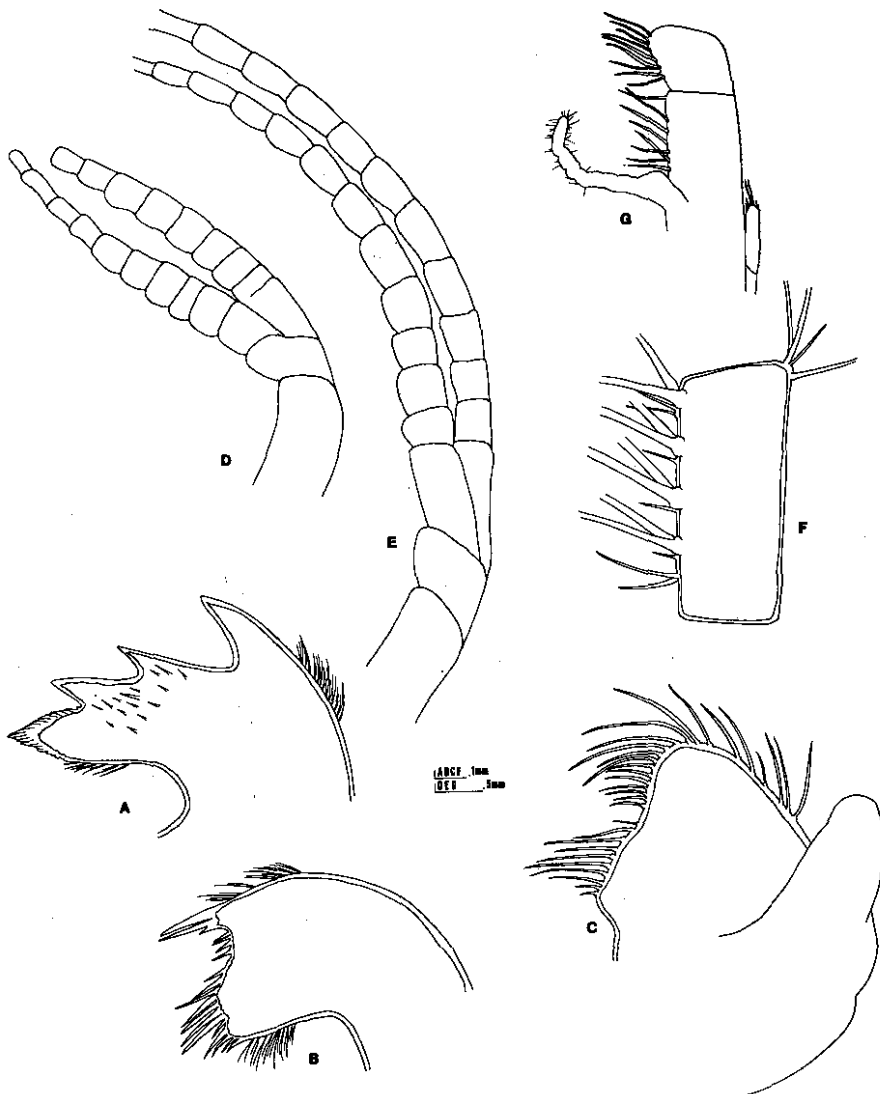


Figure 14. — *Scillaelepas (G.) kempi* (Annandale, 1911). Appendages of holotype: A, mandible; B & C, first and second maxilla, respectively; C & D, articles of first and second cirri; G, pedicle of sixth cirrus with penis and caudal appendages attached.

*Material*: Single specimen (holotype) from 1,175-1,367 m, S.W. of Ireland; 50°42'N, 11°18'W; British Museum (Nat Hist.) Reg. no. 1911.5.24.I.

*Discussion*: This species is clearly separate from *S. pilsbryi* by shell characters, as discussed above. It can also be distinguished internally in having but one set of filamentary appendages located on the dorsolateral margin of the prosoma, opposite the oral cone. Actually the set is composed of two pairs of filaments; an anterior pair of minute points followed immediately behind by a pair of short, thin, curved filaments. There is no indication of filaments on the posterior margin of the prosoma or on the intercalary folds between it and the second thoracic segment. Unfortunately, the cirri were badly broken, so only the counts for complete rami are given here:

I	II	III	IV	V	VI	c.a.
$\frac{11}{-}$	$\frac{-}{-}$	$\frac{-}{13}$	$\frac{18}{-}$	$\frac{-}{-}$	$\frac{17}{18}$	1
$\frac{-}{11}$	$\frac{16}{-}$	$\frac{-}{17}$	$\frac{-}{-}$	$\frac{-}{-}$	$\frac{19}{-}$	1

The first subrostrum is smaller than the second, as noted by Annandale (1911) and illustrated by him in the specimen seen from the left side. I was inclined to agree with Bocquet-Védrine's supposition that it might be a dwarf male. However, the photographs provided by Withers (1953) illustrate that there are indeed two subrostra. In addition, however, as he noted (p. 148), there appears to be an extra plate between the two subrostra on the right side and until I actually saw the specimen, I thought this might be a male. It is, however, a captured peduncular scale; one that was apparently in the growth field at the time the second subrostrum was forming, and was captured with it as a capitular plate. It is undoubtedly an anomaly rather than a characteristic of the species. Its presence, however, may have suppressed full development of the first subrostrum, accounting for it being smaller than the second, and therefore this difference has not been used here to distinguish *S. kempi* from *S. pilsbryi*.

#### HISTORICAL AND BIOGEOGRAPHICAL CONSIDERATIONS

*Scillaelepas* apparently flourished in late Mesozoic shallow-water seas. Of the 27 or so fossil species known, over 20 occurred exclusively in the upper Cretaceous of England, Belgium, Holland, Germany, Czechoslovakia, Poland, Sweden, Denmark, Italy, Sicily, the Crimea and Australia. But the apparent diversity was short-lived, at least in shallow-water, for but one species each for the Eocene and Oligocene, two each for the Miocene and Pliocene, and none for the Pleistocene

have been recorded. Yet, despite the scanty post-Mesozoic record, according to Withers (1953: 1) the first Tertiary stalked barnacles known, *Scillaelepas* and *Calantica*, were those figured by Scilla in 1670 from the Pliocene of Sicily. It was more than 200 years later that the first living *Scillaelepas* were dredged from 1,800 m during a Swedish expedition off the east coast of Greenland (Aurivillius, 1892).

Curiously, of the eleven extant species, the first *Scillaelepas* to be dredged was rather deep for the genus. There is one deeper species, *S. mirifica*, from more than 3,000 m on the Mid-Atlantic Ridge, but as already noted it is also morphologically atypical and its true affinities may not be as presently understood. As can be seen in Table 1, most species have been recovered from between 400 and 1,200 m which is not great when one considers that half of the 25 scalpellid genera are found at 4,000 m and one is known to reach to nearly 7,000 m (cf. Zevina, 1978 a & b). What is surprising is that *Scillaelepas* is as well if not better armored, in terms of the elaboration of calcareous plates, than its closest relative *Calantica* occurring in shallow water in the Indo-Pacific where presumably predation pressure would be greater. *Scillaelepas* is certainly more heavily armored than most other deep-water scalpellids, an obvious exception being *Neolepas* occurring at comparable depths or greater depths (Newman, 1979).

Considering the past diversity and abundance of *Scillaelepas* in what was apparently relatively shallow water, and its present absence there; considering the retention of a heavy armament, the widely separated northern and southern hemisphere populations (especially in connection with oceanic islands and seamounts), and the present center of diversity in the North Atlantic where cirriped diversity is otherwise relatively low, one is left with the distinct impression that the living species of *Scillaelepas* are relics of the late Mesozoic Tethys Sea.

#### ORIGIN OF THE SUBROSTRA IN *SCILLAELEPAS* s.l.; CO-EVOLUTION BETWEEN THE HERMAPHRODITE AND COMPLEMENTAL MALE

The origin of the subrostra in the subgenera *Gruevialepas* and *Aurivillialepas* seems completely straightforward; they were peduncular scales of *Scillaelepas* s.s. captured by the capitulum. But since the complemental male is associated with the peduncular scales in *Scillaelepas* s.s. (fig. 3) and with the subrostrum in *Aurivillialepas* (fig. 7), the question remains as to what part if any the presence of the male may have had in the transformation of peduncular scales into subrostral plates. Was



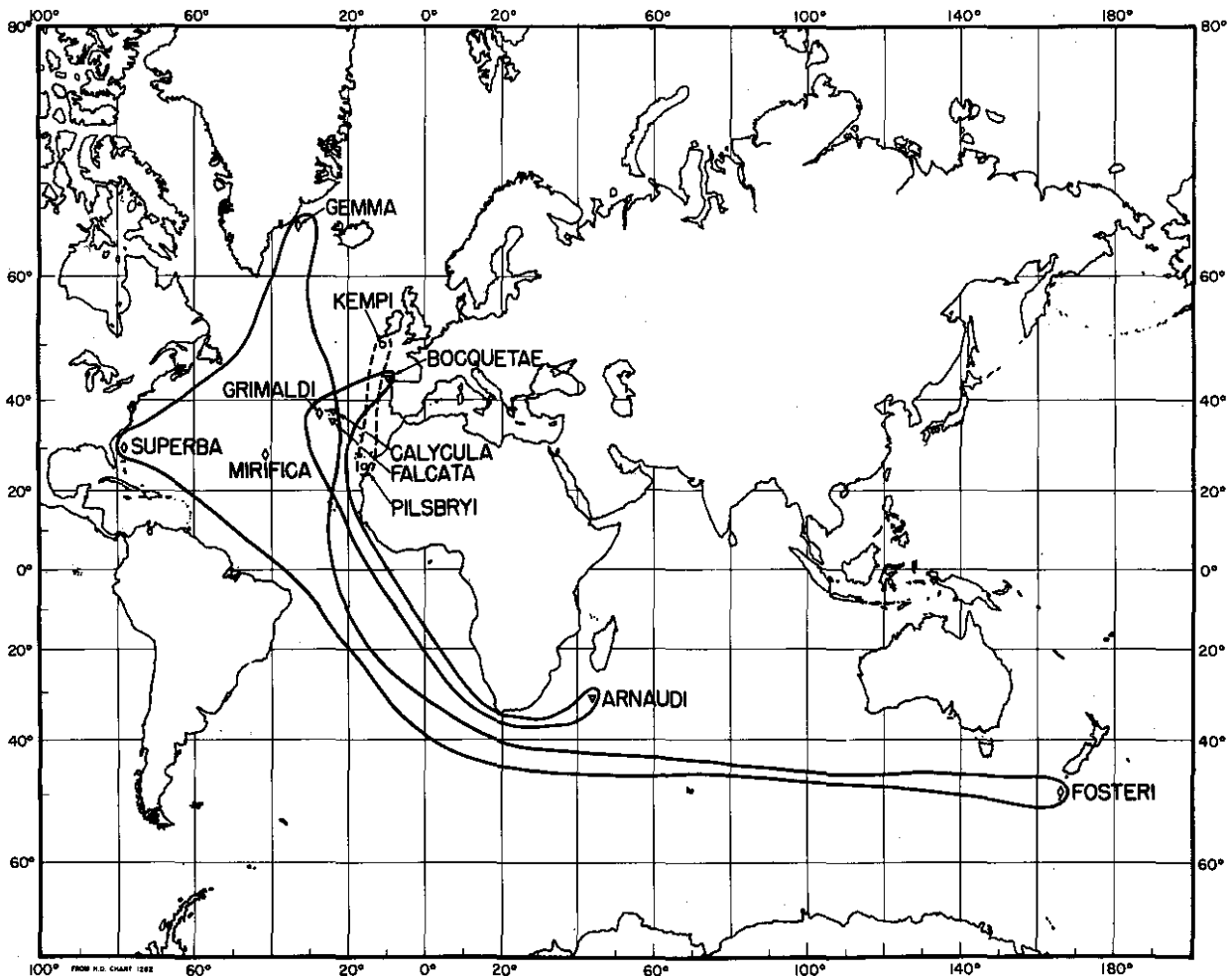


Figure 15. — Distribution of extant *Scillaelepas*: *Scillaelepas (Scillaelepas) gemma* (Aurivillius), *S. (S.) grimaldi* (Aurivillius), *S. (S.) superba* (Pilsbry), *S. (S.) mirifica* Zevina, and *S. (S.) fosteri* sp. nov.; *Scillaelepas (Aurivillialepas) bocquetae* sp. nov., *S. (A.) calycula* (Aurivillius), *S. (A.) falcata* (Aurivillius), and *S. (A.) arnaudi* sp. nov.; *Scillaelepas (Gruvellialepas) kempfi* (Annandale) and *S. (G.) pilsbryi* (Gruvel).

the situation afforded by the presence of subrostra simply taken advantage of by males, after they had begun to form, or were the subrostra induced to form by males settling in the subrostral region?

The evidence is rather compelling; the subrostra in *Scillaelepas* were induced to form by the presence of complementary males. In *Scillaelepas* s.s. there are no subrostra and the male found on *S. fosteri* had settled between the unspecialized, although possibly slightly enlarged, peduncular scales in the subrostral region. In *Aurivillialepas* the male occurs between the very well-developed subrostrum and the rostrum. *Gruvellialepas* stands between these two morphologies in that the peduncular scales become subrostra during adult growth but they are moderately developed and are sometimes left on the peduncle rather than being incorporated into the capitulum (fig. 11). Males have not yet been observed in *Gruvellialepas*, but it is very probable that they exist. While it is likely that they settle among the subrostra, it is possible that they have transferred to the suprarostral position, where they occur in *Calantica*

(fig. 16 D). In any event, *Gruvellialepas* forms a satisfactory intermediate between *Scillaelepas* and *Calantica* since it would have been easier for the male to transfer from that relatively unspecialized subrostral situation than from the more specialized one seen in *Aurivillialepas*. The transfer to the suprarostral situation could of course have been directly from the even more generalized condition in *Scillaelepas* s.s., but the presence of a vestigial subrostrum in *Calantica* rules against it.

The development of subrostra in *Scillaelepas* is a remarkable case of co-evolution involving behavioral and morphological adaptations on the part of the male and morphological and perhaps pheromonal adaptations on the part of the hermaphrodite. The male, when a free-swimming cyprid larva, must find and select the site of attachment on the hermaphrodite. Since the very small male is permanently attached and transfers sperm by a probosciform penis, it must situate itself at some appropriate distance from the aperture of the mantle cavity of the hermaphrodite. For these reasons alone the male cannot just settle anywhere on or near the her-

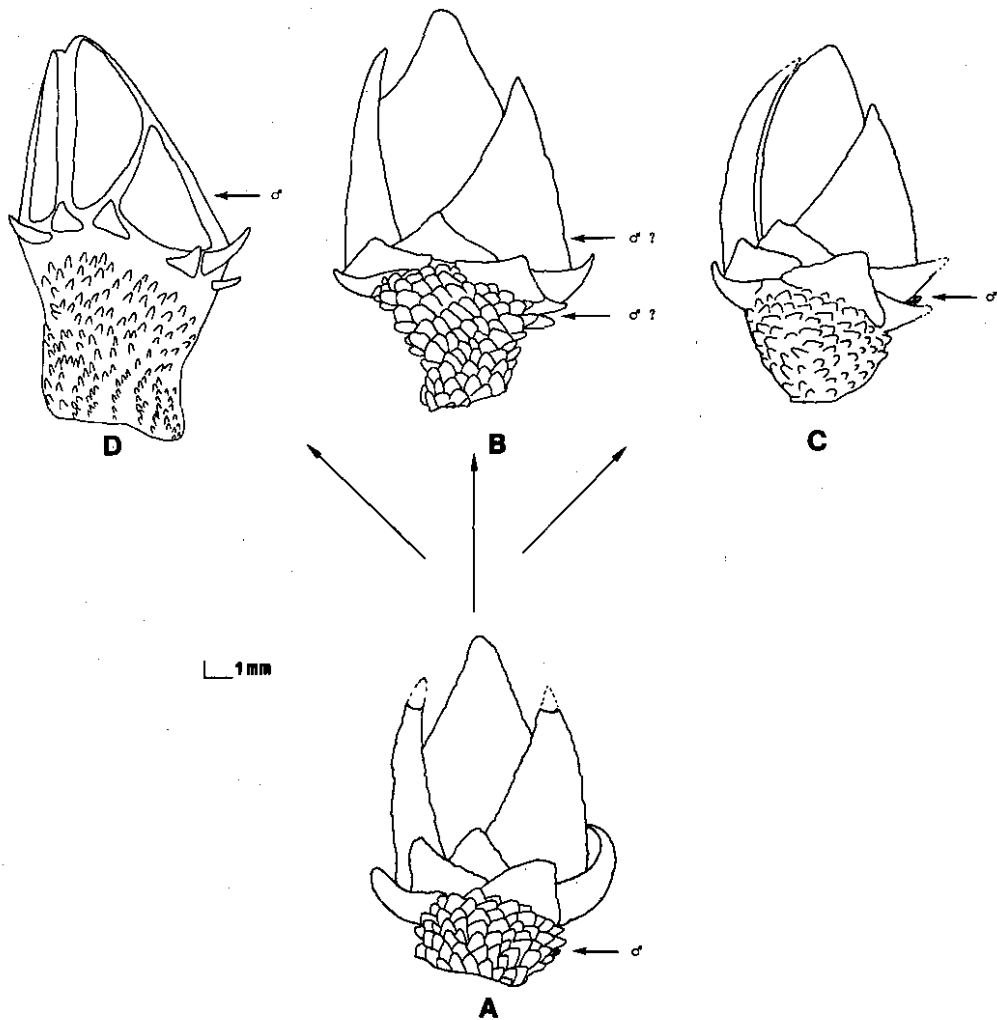


Figure 16. — Co-evolution between the hermaphrodite and complementary male, in the origin of subrostra in *Scillaelepas*: Calanticine scalpellids are fundamentally gregarious, cross-fertilizing hermaphrodites. Complementary males were apparently acquired when populations became too sparse to insure cross-fertilization between hermaphrodites, during the decline of certain genera in the early Tertiary. The males, derived through progenesis from protandric hermaphrodites, are small and sessile and therefore must be situated rather specifically so as to be able to continue to feed as well as inseminate the hermaphrodite. Initially, in the evolutionary sequence, larvae of the males of primitive calanticines sought out and took advantage of the position and protection afforded by the subrostral peduncular scales, as they presently do in *Scillaelepas* s.s. (A). Concomitantly, these scales became modified to better accommodate the male, as seen ontogenetically in *S. (Gruevialepas)* (B). Eventually one subrostrum was fully incorporated into the capitulum, with the male residing between it and the rostrum, as seen in *S. (Aurivillialepas)* (C). Transfer of the male from the subrostral to a suprarostrum position between the scutal plates resulted in the condition seen in *Calantica* (D). Finally, a wholly dioecious condition, with the males reduced to testicular sacs attached in special pockets within the scutal plates of the female, was achieved in higher scalpellids such as *Arcoscalpellum* (Pilsbry, 1908; Broch, 1922).

maphrodite, and it would therefore be advantageous for the species if the hermaphrodite provided some cues as to just where to settle. Since the peduncular scales were initially indistinguishable morphologically, a "subrostral" pheromone must have become involved.

If the probability of survival of the male were increased by protective modifications at the site of attachment on the hermaphrodite, the likelihood of there being a male present at the time eggs were to be laid would have been increased, and a co-evolutionary impetus for morphological improvement of the subrostral situation would have been set in motion. Perfection would include transferring the protective subrostral scales from the peduncle to the capitulum because they would then remain at the proper distance from the aperture. Other-

wise they would be carried away from the capitulum, along with the male they were intended to protect, since new whorls of scales are added at the pedunculo-capitular junction during peduncular growth. This fact may of course explain why the peduncle in *Scillaelepas* s.s. is usually very short; peduncular growth may have been curtailed by the presence of a complementary male.

This has all been fine in understanding the co-evolution between the complementary males and hermaphrodites of *Scillaelepas*, but what was the impetus for the development of complementary males in the first place? Where population densities of cross-fertilizing hermaphrodites are great, it is difficult to surmise what selective advantages there might be for the development and/or perpetuation of complementary males. However, if the

probability of hermaphrodites being sufficiently close together to cross-fertilize became drastically diminished, the need for complementary males becomes obvious if the advantages of cross-fertilization are to be maintained. It was noted in the previous section, on biogeography, that there were abundant *Scillaelepas* species in shallow waters of the late Mesozoic. The genus then all but disappeared from shallow water and presently has a relic distribution of less than a dozen species in the deep sea. We do not know why there was a decrease, but presumably the marked increase in predation pressure on sedentary shelled forms that is inferred to have taken place in the late Mesozoic (Stanley, 1974; Vermeij, 1977), as well as competition from sessile barnacles that were just beginning to appear in shallow water at the time (Newman *et al.*, 1969), contributed to the demise of *Scillaelepas*. In addition to the reduction in geographic range and exclusion from shallow water, population densities must have diminished to the point where distance between nearest neighbors began to exceed, on the average, capabilities of hermaphrodites to cross-fertilize. At this point, species would have to either develop complementary males or become extinct, which is exactly what happened. Extinctions were extensive (Withers, 1953) and the sparsely distributed individuals of relatively few relic populations, likely all having complementary males, survive in the deep sea today.

Thoracican cirripeds, if not fundamentally hermaphroditic, became so early in their evolution (Pilsbry, 1908; Broch, 1922; Newman *et al.*, 1969; Foster, 1978). However, they are preadapted to the production of complementary males because their hermaphroditism is protandric; that is, in the young adult the male sex matures first and later the individual alternates between male and female roles. Thus, a cyprid that settles near an established hermaphrodite has the opportunity to act as a male before it becomes fully mature. An individual that devotes all of its resources to rapidly becoming a functional male would have a better chance of fertilizing the hermaphrodite than an individual in which resources were partitioned into becoming a functional hermaphrodite. Thus, if the probability of living long enough to become a functional hermaphrodite were small, to the extent that population densities were sparse, the early maturing male tendency of cyprids encountering an established hermaphrodite would be favored. Initially the acceleration of maleness might have been induced in any cyprid settling on an established hermaphrodite of the same species, but in the only barnacle that has been looked at experimentally, sex is genetically determined, approximately 3:1 in favor of the complementary male (Gomez, 1975).

Putting all available resources into becoming a male as rapidly as possible is simply accomplished through neoteny (progenesis; Gould, 1977), especially since the

hermaphroditism is protandric. Sexual maturity at a very small size, with incomplete capitular armament and no peduncular armament, all indicate that males of the pollicipoids *Scillaelepas* and *Calantica* are prognetic. The hermaphrodites must have facilitated the prognetic process by offering and improving upon protective devices; first the slightly enlarged and appropriately spaced subrostral peduncular scales (*Scillaelepas* s.s.), then specially formed scales of the peduncle and their ontogenetic incorporation into the capitulum (*Gruvelialepas*), and finally the strongly developed wholly capitular subrostrum protecting the male (*Aurivillialepas*), or the transfer of the male from the subrostral to the suprarostal position between the scutal plates (*Calantica*) (fig. 16).

The epitome of the prognetic process in scalpellids is of course in the more derived deep-sea forms such as *Arcoscalpellum* where males have lost everything including the ability to feed, and reside attached in special pockets in the scuta as sacs of sperm that will fertilize the eggs produced by what has become a wholly female rather than hermaphroditic individual. There is no sense in a sessile organism with internal fertilization being a cross-fertilizing hermaphrodite if there is rarely another hermaphrodite close enough to mate with. In fact, the penis has been rudimentary in all the specimens of *Scillaelepas* looked at so far, suggesting that the populations are effectively dioecious.

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