New genus and species of Calanticidae (Cirripedia, Thoracica, Scalpellomorpha) from Australian waters

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Jones D. S. 1998. — New genus and species of Calanticidae (Cirripedia, Thoracica, Scalpellomorpha) from Australian waters. *Zoosystema* 20 (2) : 239-253.

ABSTRACT
A previously undescribed calanticid species was found in the collections of the Australian Museum, Sydney. The combination of features match some of the characteristics of the genus *Smilium,* as currently defined, and do not fulfil the necessary criteria for inclusion in any of the remaining calanticid genera. Several characters, however, are typical of *Calantica*. Therefore, a new genus and species is proposed and is accordingly named *Crosnieriella acanthosubcarinae*. The uncertain relationships between the presently recognized calanticid genera are discussed.

KEY WORDS
Crustacea,
Thoracica,
Scalpellomorpha,
Calanticidae,
deep water,
Coral Sea,
Australia,
new species.

RÉSUMÉ
Un nouveau genre et une nouvelle espèce de Calanticidae (Cirripedia, Thoracica, Scalpellomorpha) des eaux australiennes. Une espèce non encore décrite des collections de l'Australian Museum à Sydney rappelle par certains de ses caractères le genre *Smilium*, tel qu'il est actuellement défini, et ne satisfait pas aux critères qui permettraient de l'inclure dans l'un des autres genres de la famille. Plusieurs caractères sont cependant typiques de *Calantica*. En conséquence, un genre nouveau et une espèce nouvelle sont proposés sous le nom de *Crosnieriella acanthosubcarinae*. Les affinités, incertaines, entre genres de Calanticidae actuellement reconnus sont discutées.

MOTS CLÉS
Crustacea,
Thoracica,
Scalpellomorpha,
Calanticidae,
eau profonde,
Mer du Corail,
Australie,
nouvelle espèce.

INTRODUCTION

The relationships between the calanticid genera have long been uncertain, with various genera and differing numbers of attributed genera having been assigned to the family. There has never been a revision of this poorly known, largely relictual group of scalpellomorphs that includes several clades, the boundaries between which are generally blurred by intermediate forms. The situation has been further confused by the chaotic species-level taxonomy within *Calantica* Gray, 1825 and *Smilium* Gray, 1825. Various species have been transferred from one genus to the other, and sometimes back again, with little substantive reason. For example, at various times both *C. pollicipedoides* (Hoek, 1907) and *C. trispinosa* (Hoek, 1883) have been removed to *Smilium* and then subsequently re-included in *Calantica* (see Pilsbry 1908; Calman 1918; Weltner 1922; Broch 1931; Zevina 1981). Similarly, *S. zancleanum* (Seguenza, 1876) was removed to *Calantica* and then later reassigned to *Smilium* (see Withers 1953; Foster 1978). *Calantica pedunculostriata* Broch, 1931 is currently removed to *Smilium* (see Liu & Ren 1985). Other species [for example *C. kampeni* (Annandale, 1909), *C. scorpio* (Aurivillius, 1892), *C. spinilatera* Foster, 1978], which were originally assigned to *Smilium,* have been removed subsequently to *Calantica* (see Broch 1931; Utinomi 1962; Foster 1978).

This paper does not attempt to deal with these problems, as these will be reviewed elsewhere. I am currently revising the calanticid genera and will re-evaluate the status of the new genus at that time.

MATERIALS AND METHODS

Specimens were examined with the aid of microscopy and dissection, and illustrations of the whole animal were made with the aid of a camera lucida. Shell architecture was investigated by X-ray images of whole specimens (holotype, cap. 25.1 mm, AM P40986; paratype, cap. 22.2 mm, AM P49989) and of a bisected specimen (paratype, cap. 28.7 mm, AM P49989), and soft parts were cleared, stained with Solophenyl Blue 2RL and mounted, according to the method of Jones (1993). The appendages and the mouthparts were drawn with the aid of a camera lucida. All measurements are in millimetres. The terminology follows that of Jones (1990, 1992) and Newman (1987, 1991, 1996). The holotype and the paratypes are deposited in the Australian Museum, Sydney (AM).

ABBREVIATIONS

c.a.	caudal appendage;
cap.	capitular length;
mls	miles;
ped.	peduncular length.

SYSTEMATICS

Superorder THORACICA Darwin, 1854
Order PEDUNCULATA Lamarck, 1818
Suborder SCALPELLOMORPHA
Newman, 1987
Family CALANTICIDAE Zevina, 1978 (emend.)

DIAGNOSIS

Pedunculata with capitulum protected by six primary calcareous plates or their rudiments, namely rostrum (R), carina (C), paired scuta (S) and terga (T), three pairs of latera, including rostrolatera (RL), latera (L) and carinolatera (CL) and (except for *Pisiscalpellum*) a subcarina (SC), plus various other supplementary capitular plates (r-c) to a total of 60^{+} plates, with as few as nine in reduced forms; umbo of carina apical, sometimes subcentral; plates arranged in two more or less distinct whorls, those in lower whorl either overlapping, or being overlapped by, adjacent plates. Peduncle usually with rows of uniform-sized calcareous scales. Caudal appendages setose, sometimes multi-articulate. Basic mandible with three teeth, lower angle pectinate, sometimes smaller extra teeth below first tooth. Maxillule lacking step-like cutting edge. Small males often associated with larger hermaphrodites or females; males clearly divided into peduncle and capitulum, with six or more small capitular plates.

REMARKS

Zevina (1978) divided the Scalpellidae into eight subfamilies, based on the number of capitular plates and their degree of development, the position of the umbos, the number of segments in the caudal appendages and the degree of development of the males. The Calanticinae embraced five genera, namely *Calantica* Gray, 1825, *Euscalpellum* Hoek, 1907, *Paracalantica* Utinomi, 1949, *Scillaelepas* Seguenza, 1876 and *Smilium* Gray, 1825. Zevina included *Pollicipes* Leach, 1817 in the Pollicipinae and *Pisiscalpellum* Utinomi, 1958 in the Scalpellopsinae. Subsequently, in a revision of the fossil barnacles of New Zealand and Australia, based solely on capitular plate architecture, Buckeridge (1983) placed the genera *Calantica* and *Smilium,* together with *Pollicipes, Pisiscalpellum, Capitulum* Oken, 1815 and the fossil genera *Zeugmatolepas* Withers, 1913 and *Titanolepas* Withers, 1913 in the Calanticinae. Buckeridge also recognized *Scillaelepas* as a subgenus of *Calantica* but placed *Euscalpellum* in the Scalpellinae. Newman (1987, 1991, 1996) elevated the subfamily Calanticinae to full familial status and set aside a number of fossil genera in a new family, the Zeugmatolepadidae Newman, 1996.

The inclusion of *Smilium, Calantica* and *Scillaelepas* within the Calanticidae is undisputed, but it is evident that a satisfactory diagnosis has yet to be produced. The confused taxonomy of the scalpellomorph family Calanticidae was briefly reviewed by Jones & Lander (1995).

Crosnieriella n.g.

TYPE SPECIES. — *Crosnieriella acanthosubcarinae* n.sp., by monotypy.

ETYMOLOGY. — The genus is named in honour of my friend and colleague Dr Alain Crosnier, both as an appreciation of his scientific endeavours and as a tribute to his monumental efforts in supporting studies on deep water marine fauna, in particular those associated with the MUSORSTOM expeditions.

DIAGNOSIS

*? Hermaphrodite with a basic plan of nineteen capitular plates, including six primary plates, namely rostrum (R), carina (C), paired terga (T) and scuta (S), two subcarinae (SC^1, SC^2), five pairs of latera including carinolatera (CL^1, CL^2), latera (L^1, L^2), and rostrolatera (RL), and a subrostrum (SR), plus up to sixteen supplementary capitular plates (r-c); upper lateral (L^1) placed between scutum and carina, carinal margin not developed; scutum with basal margin angular; umbos of carina and scutum subapical. Filamentary processes present. Caudal appendages uniarticulate.

*? Complemental male attached between scuta and adductor muscle.

(* Vestigial penis of *Crosnieriella acanthosubcarinae* n.sp. suggests known specimens are likely female with dwarf males.)

REMARKS

Crosnieriella n.g. is most similar to *Smilium* and shares some characters with *Calantica*, but the apomorphic replication of the plates at the carinal end of the capitulum distinguish *Crosnieriella* n.g. from these two genera. *Smilium* has a basic plan of thirteen capitular plates, with a total of up to fifteen (*S. horridum* Pilsbry, 1912) to as few as nine plates [*S. hypocrites* (Barnard, 1924)]. *Calantica* also has a basic plan of thirteen capitular plates, with a total of 60^+ to as few as eleven plates [both extremes occur in *C. spinosa* (Quoy *et* Gaimard, 1834)].

In *Crosnieriella* n.g., the upper latus (L^1) is partly elevated from the lower whorl of capitular plates, where a new latus (L^2) replaces it. L^1 moves to a position between the carina and the scutum, but does not develop a distinct carinal margin. In *Calantica*, the tergum is between the carina and the scutum and the median latus (L) remains in the lower whorl. In *Smilium*, L^1 has a distinct carinal margin and is not part of the lower whorl of capitular plates, being well elevated between the carina and the scutum. The position of L^1 is more obviously a part of the lower whorl of capitular plates in fossil *Smilium* species (e.g., *S. tortachillense* Buckeridge, 1983 and *S. subplanum* Withers, 1924) but it is transitionally placed in Recent species (Buckeridge 1983).

Buckeridge (1983) considered *Smilium* as the most derived taxon within the Calanticidae, and regarded it as showing the closest relationship

with the more modified scalpellines. He retained *Smilium* in the Calanticidae due to the large size of the rostrum, a plesiomorphic character, and to the position of L^1. Foster (1978) had previously defined a quadrangular L^1, placed between the scutum and the carina, as characteristic of *Smilium*. This shape results from the development of a carinal margin.

In *Crosnieriella* n.g., the basal margin of the scutum is angular. Foster (1978) included within *Smilium* those species with an almost 90° bend in the basal margin of the scutum. Buckeridge (1983) broadened Foster's interpretation, and considered that the basal margin needs only to be clearly angular, suggesting that the basal margin became progressively angular through the Cenozoic, resulting in some of the acutely angular Recent taxa such as *S. acutum* Hoek, 1883.

Crosnieriella acanthosubcarinae n.sp.
(Figs 1-6)

TYPES. — Holotype, ? hermaphrodite, cap. 25.1 mm (AM P 40986). 2 paratypes, ? hermaphrodites, cap. 22.2 mm, cap. 28.7 mm (AM P 49989).

MATERIAL EXAMINED. — **Australia.** 9 mls NE One Tree Island, Capricorn Group, Queensland, 22°27'S - 152°15'E, 175 m, 08.II.1969, coll. B. Goldman, J. Paxton, J. Veevers: 3 specimens (AM P 40986).

ETYMOLOGY. — The species is named in reference to the two spine-like subcarinae on the capitulum.

DISTRIBUTION. — All specimens were collected from the type locality, from a mud and shell bottom, 175 m.

DIAGNOSIS

Basic plan of nineteen fully-calcified, calcareous plates, plus various small supplementary plates, resulting in complement of up to thirty-five capitular plates, arranged in three consecutive whorls; two pairs of horn-like carinolatera (CL^1, CL^2); two spine-like subcarinae (SC^1, SC^2); lower whorl with variable number (up to sixteen) of small, thorn-like supplementary capitular plates (r-c) arranged in tiers; upper latus (L^1) placed between scutum (S), tergum (T), carina (C) and carinolateral^1 (CL^1); acute basi-tergal angle of upper latus (L^1) angled toward carina. Peduncle covered with numerous calcareous, small, peg-like, non-imbricating scales arranged in three to seven distinctly separated, raised, horizontal bands, separated by contracted bands of peduncle. One pair of small, nipple-like filamentary appendages on prosoma. Maxilla with densely setose band close to, and extending length of, cutting margin.

DESCRIPTION

Large individuals ? hermaphrodite. Capitulum

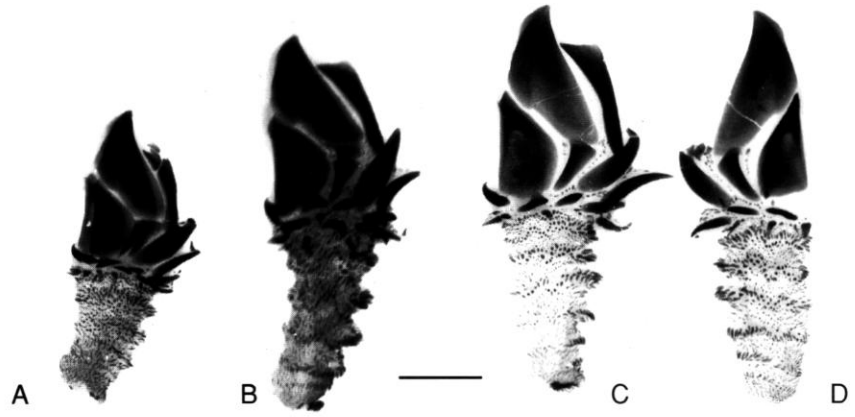

FIG. 1. — *Crosnieriella acanthosubcarinae* n.sp., ? hermaphrodites, X-ray. **A**, paratype, cap. 22.2 mm, whole specimen from right side (AM P49989); **B**, holotype, cap. 25.1 mm, whole specimen from right side (AM P40986); **C**, paratype, cap. 28.7 mm, bisected specimen, right side (AM P49989); **D**, paratype, cap. 28.7 mm, bisected specimen, left side (AM P49989). Scale bar: 10 mm.

laterally compressed; irregularly subtriangular, higher than wide; apex oblique, slightly reflexed towards carinal side. Occludent margin of capitulum sinusoidal, carinal margin subparallel to occludent margin in lower one half to three quarters. Three whorls of fully calcified, dirty-white capitular plates; plates covered by moderately thick, finely setose, yellowish membrane, outline of plates often indistinct; surfaces of plates marked with faint transverse growth lines, plates separated by distinct interspaces, all plates entirely covered by cuticle. Capitular architecture with basic plan of nineteen plates, plus various small supplementary plates, resulting in a total of up to thirty-five capitular plates (Figs 1-4).

Rostrum (R) triangular, more than twice as wide as high, similar in size to upper lateral (L^1); plate curved outward, free from capitulum, apex acute, curved upward and inward toward capitulum. Scutum (S) subtriangular to quadrangular, higher than wide; occludent and tergal margins forming acute, upwardly directed angle, tip not projecting from occludent margin; umbo subapical, acute tip slightly projecting from occludent margin; rostral and upper latus margins subequal, shorter than occludent and tergal margins; upper latus margin subparallel to occludent margin, rostral margin almost straight; internally adductor muscle pit prominent. Tergum (T) elongated, narrow, triangular, apex subacute, slightly reflexed towards carinal side; occludent margin gently convex, narrow process appended on upper one third; scutal margin not straight, excised with small, shallow, triangular indentation, creating spur in upper one third; carinal margin longest, almost straight, apically retroverted in upper one quarter. Carina (C) extending above apex of upper lateral (L^1) to three quarters length of tergal margin, apex meeting margin of tergum at angle of 110°; carina internally concave, externally laterally compressed; carina angularly flexed in distal one sixth, lower portion wider and three times longer than upper portion, both portions meeting at angle of 120°, umbo at angle; carinal roof externally laterally convex, growing wider from umbo downwards, sides relatively wide and flattened in upper portion; plate basally rounded, overlain laterally by carinolatus[1] (CL^1).

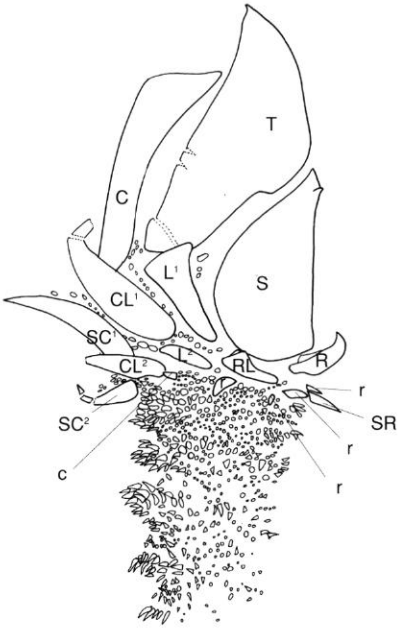

FIG. 2. — *Crosnieriella acanthosubcarinae* n.sp., ? hermaphrodite, paratype, cap. 28.7 mm (AM P49989), viewed from the left side. **C**, carina; **CL**, subcarina; **L**, latera; **R**, rostrum; **RL**, rostrolatera; **S**, scuta; **SC**, subcarina; **SR**, subrostrum; **T**, terga; **r**, **c**, supplemenary capitular plates.

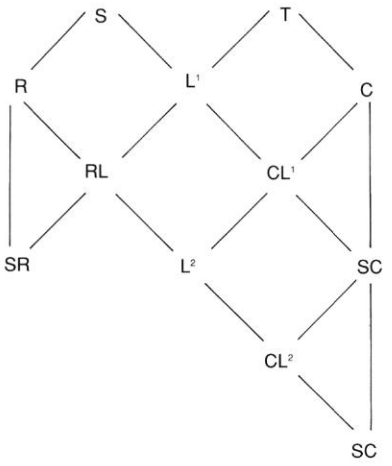

FIG. 3. — *Crosnieriella* n.g., diagram of basic capitular armament, viewed from the right side: 10 plates.

Upper latus (L^1) triangular, basal margin elongated, sinuous; scutal margin subequal to basal margin, concave; tergal margin shortest margin, almost straight; apex curved inward, retroverted towards scutum, apex slightly overlying tergum in largest specimen examined. Rostrolatus (RL) triangular, similar to but smaller than rostrum; curving outward, free from capitulum, apex curved upward or inward. Inframedian latus (L^2) similar to rostrolatus in size, triangular, higher

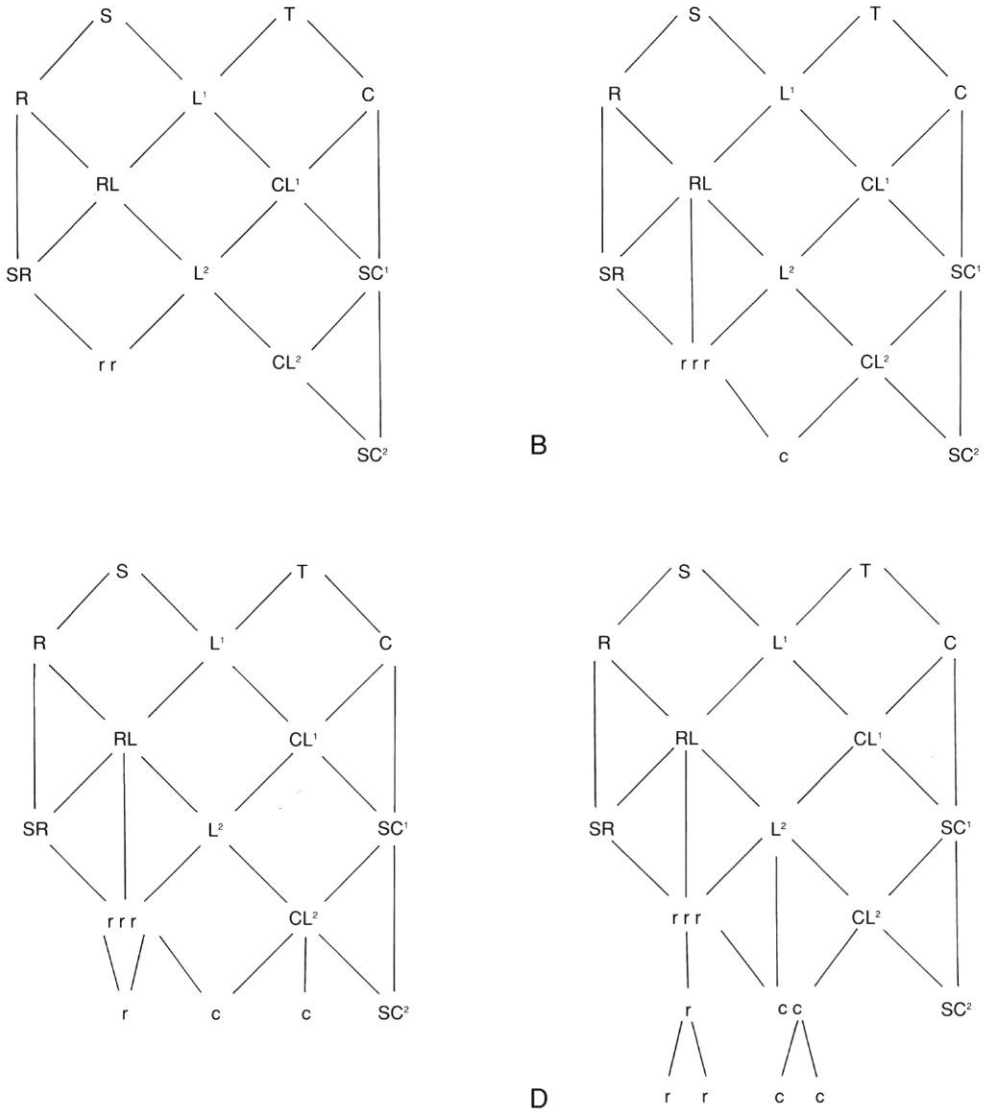

FIG. 4. — *Crosnieriella acanthosubcarinae* n.sp., diagrams illustrating the relative positions of supplementary capitular plates (r-c) found on different individuals from the same population [terminology follows that of Newman (1987)]. **A**, right side of capitulum, paratype, cap. 22.2 mm (AM P49989); **B**, left and right sides of capitulum, holotype, cap. 25.1 mm (AM P40986) and left side of capitulum, paratype, cap. 22.2 mm (AM P49989); **C**, left side of capitulum, paratype, cap. 28.7 mm (AM P49989); **D**, right side of capitulum, paratype, cap. 28.7 mm (AM P49989).

than wide; curving outward, free from capitulum, apex curved outward or downward. Carinolatus[1] (CL^1) horn-like, similar in size to subcarina[1] (SC^1); curving outward, free from capitulum, subacute apex pointing outward or retroverted toward carina. Subrostrum (SR) smaller than rostrum, thorn-like, curving outward, apex pointing upward or downward from capitulum. Subcarina[1] (SC^1) spine-like, more than twice as large as rostrum; curving outward free from capitulum, apex pointing outward or downward. Subcarina[2] (SC^2) spine-like, similar to SC^1 in shape but smaller in size; curving outward free from capitulum, apex pointing upward, outward or downward. Carinolatus[2] (CL^2) horn-like, similar to SC^1 in shape but smaller in size, larger and more developed than L^2. Small supplementary capitular latera (r-c) arranged in tiers (Figs 2, 4A-D); thorn-like, height four times width, apices pointing outward and downward. Small, closely spaced, calcareous spicules, similar to small peduncular scales, in inter-spaces between S and L^1, R and SR, RL and L^1, L^2 and L^1, CL^1 and L^1, CL^1 and SC^1, CL^1 and CL^2, CL^2 and SC^2, spicules outlining shape of plates.

Peduncle yellowish, conico-columnar, subequal to, or shorter than, length of capitulum; covered with numerous, calcareous, small, peg-like, non imbricating, whitish scales; scales arranged in three to seven distinctly separated, raised, convoluted, lateral bands, separated by lateral contracted bands of peduncle; each raised band consisting of two to three rows of larger, peg-like scales; near pedunculo/capitular junction scales upright in position, gradually turning outward and downward in progression down peduncle; scales longer, more dense on carinal side of peduncle; contracted areas between raised bands with smaller peg-like scales, upright in position wherever their peduncular placement.

Ovigerous frenae apparently absent; eggs not present. Posterior edge of intercalary fold between cirri III and IV with one pair of filamentary appendages developed as downward-directed, nipple-like projections.

Labrum strongly bullate, teeth absent. Mandibular palp ovate, setose, long setae distally. Mandible with four teeth, upper largest, second smallest, large subsidiary tooth between teeth one and two, sometimes small subsidiary tooth between teeth two and three; margins of all teeth without serrations; lower angle pectinate. Maxillule with distinct, densely setose band close to and extending length of cutting edge; one large stout and two smaller setae at upper angle; margin without notch, indistinctly stepped, crowded with numerous setae of unequal length, setae in paired groups of four to six; lower angle slightly protuberant, with seven to eight pairs of smaller setae. Maxilla almost quadrangular; continuous series of finely serrulate setae along all margins. Chaetotaxy ctenopod. Cirral formula as follows:

Cirrus	I	II	III	IV	V	VI	c.a.
paratype right	14	23	26^+	26	28	25	1
(cap. 28.7 mm)	16	25	29	28	27	27	
left	13	23	26	27	28	22	1
	16	25	27	22^+	25	27	

Cirrus I not separated from cirrus II, rami subequal, anterior ramus shorter than posterior; proximal segments of anterior ramus protuberant anteriorly and posteriorly; segments of both rami setose, setation more dense on inner surfaces, setae finely serrulate. Cirrus II longer than cirrus I; rami subequal, anterior ramus slightly longer than posterior; proximal segments of anterior ramus slightly protuberant anteriorly, segments of both rami becoming elongated distally; distal segments of anterior ramus with two to three pairs of long setae on anterior faces, distal segments of posterior ramus with two to four pairs of long setae on anterior faces; proximal segments of both rami more densely setose, setae finely serrulate; bunches of long, finely serrulate setae at postero-distal corner of segments. Cirrus III slightly longer than cirrus II; rami subequal, segments of both rami becoming elongated distally; distal segments of both rami with two to four pairs of long setae on anterior faces, proximal segments more densely setose, setae finely serrulate; bunches of long, finely serrulate setae at postero-distal corner of segments. Cirrus IV-VI similar, longer than cirrus III; rami

subequal, segments oblong, bearing four pairs of setae on anterior faces, first two pairs longest, setae finely serrulate; bunches of long, finely serrulate setae at postero-distal corner of segments. Caudal appendages small, one third height of basal segment of pedicel of cirrus VI; uniarticulate, leaf-like; few sparse, small, terminal setae distally, minute spines on inner surface. Penis minute, one sixth height of basal segment of pedicel of cirrus VI; setae and annulations absent.

Dimensions:

	capitulum length	capitulum width	peduncle length	peduncle width	total length
holotype	25.1	20.8	29.2	11.7	54.3
paratype	22.2	14.5	16.3	10.5	38.5
paratype	28.7	22.2	22.7	11.4	51.4

Single complemental male located between scuta, near occludent margin, just above adductor muscle; peduncle longer than capitulum; six well-developed capitular plates; tergum diamond-shaped, beaked apex retroverted towards occludent margin; scutum subtriangular; carina equilateral triangular; rostrum similar to carina but smaller.

Discussion

The generic placement

The new genus described herein is included in the family Calanticidae. It has a combination of features which match most, but not all, of the characteristics of the calanticid *Smilium,* as currently defined, although several characters are more typical of *Calantica* and one character (the presence of filamentary appendages) is not typical of either *Smilium* or *Calantica.* The following characters were considered when assessing the generic status: the position of the upper latus (L^1), the position of the umbos of the capitular plates, the form of the scutum, the form of the complemental male, the tendency to form extra plates on the capitulum, the form of the cirri, the presence of a subrostrum, and the presence of filamentary appendages.

The position of the upper latus (L^1)

The diagnosis for *Calantica* states that the tergum occupies the whole space between the scutum and the carina (Pilsbry 1907, 1908; Withers 1953; Newman *et al.* 1969), and a similar capitular plate arrangement also occurs in *Scillaelepas* and *Pisiscalpellum*. Thus in *Calantica*, the median latus (L) is situated in the lower whorl of plates (together with the subcarina, the carinolateral and the rostrolateral), below the primary plates. There are, however, some species presently included in *Calantica* that have a partially elevated upper latus occupying some of the space between the scutum and the carina – e.g. *C. pollicipedoides*; *C. pusilla* Utinomi, 1970. In these species the upper latus is triangular or subtriangular and a carinal margin is not developed. This contrasts to past diagnoses for *Smilium,* which emphasize the presence of the median latus which has moved up between the scutum and the carina. In *Smilium* the median latus (L^1) is elevated, from the lower whorl of plates to a position above the carinolatus, below the tergum and between the scutum and the carina, and a new latus (L^2) replaces it below. In the process, L^1 develops a distinct carinal margin and becomes subquadrate, quadrate, or pentagonal, although in the latter case it often appears superficially triangular. Within *Smilium*, however, *S. horridum* and *S. scorpio* (synonym of *S. sexcornutum* Pilsbry, 1907 and *C. pedunculostriata*) possess a triangular L^1 which is partially elevated between the scutum and the carina. In *Euscalpellum* the quadrangular or pentagonal L^1 occupies a similar position to that in *Smilium.* The L^1 is absent in *Paracalantica.*

In *Crosnieriella* n.g., L^1 is placed below the tergum and between the scutum and the carina. Its position, however, although elevated between the carina and the scutum, is not totally above the carinolateral (CL^1), as in *Smilium* and *Euscalpellum*, but more in line with CL^1 and above the other latera. Although the basi-tergal angle of L^1 of *Crosnieriella acanthosubcarinae* n.sp., which is directed toward the carina, distinctly separates the tergum and CL^1, a carinal margin is not developed; the shape of L^1 is thus triangular, not quadrangular. The L^1 of *C. pusilla, C. pollicipedoides* and *S. horridum* are similarly

FIG. 5. — *Crosnieriella acanthosubcarinae* n.sp., ? hermaphrodite, paratype, cap. 28.7 mm (AM P49989). **A**, lateral view of prosoma to show filamentary appendages; **B**, left mandible; **C**, right mandible; **D**, left maxillule; **E**, right maxillule; **F**, left maxilla. Scale bars: A-E, 0.5 mm; F, 0.05 mm.

shaped and similarly placed. In these species the plate is in a transitional position, between the upper and the lower whorls of capitular plates. This is intermediate between the arrangement found in *Calantica* and that occurring in *Smilium* and *Euscalpellum.*

The position of the umbos of the capitular plates
In *Crosnieriella* n.g. the carina and the scutum have subapical umbos. In *Calantica, Pisiscalpellum* and *Scillaelepas* the umbos of all the capitular plates are apical; in *Paracalantica* and *Titanolepas* all the umbos are apical apart from that of the scutum. In *Smilium* the umbos of the carina, the scutum and the upper latus may be apical or subapical. The umbo of the upper latus is subcentral or apical in *Euscalpel-lum*, with that of the scutum either subcentral, subapical or apical, and that of the carina subcentral or apical.

The form of the scutum
The basal margin of the scutum of *Crosnieriella* n.g. is clearly angular in form. Foster (1978) considered *Smilium* to include those scalpellids where, as well as a quadrangular upper latus (L^1), an angular scutal basal margin is developed. The bend is almost 90° and, in consequence, the scutum acquires rostral and upper latus margins on either side of the apico-basal ridge. Using these criteria Foster (1978) suggested that *S. scorpio* should be assigned to *Calantica* and, on the basis of the structure of the scutum, that *Smilium* should include the fossil forms *S. subplanum, C. sulci* Withers and *Scalpellum zancleanum.* Buckeridge (1983), however, also included within *Smilium* calanticids having the basal margin of the scutum clearly angular. On this basis, *C. scorpio sensu* Foster (1978) would thus be re-instated within *Smilium.*

The form of the male
Calantica, Euscalpellum, Paracalantica, Pisiscalpellum, Scillaelepas s.l. and *Smilium* carry males, either in the integument between the scuta near the adductor muscle (*Calantica, Euscalpellum, Paracalantica, Smilium*), in a subrostral position (*Scillaelepas*), or inside the scutum near the apex (*Pisiscalpellum*). The male of *Euscalpellum* is not differentiated into capitulum and peduncle and has a total of three capitular plates (a pair of elongated scuta and a rudimentary carina). In *Paracalantica* the complemental male has four large capitular plates and rudimentary terga, with the short peduncle wholly buried in the cuticle of the hermaphrodite. The males of *Calantica, Paracalantica* and *Smilium* are differentiated into peduncle and capitulum, the latter with six well-developed capitular plates. The males of *Crosnieriella* n.g. are differentiated into a capitulum with six well-developed capitular plates and a peduncle which is longer than the capitulum. On the capitulum of the calanticid male, as well as the six primary plates, small median latera sometimes develop.

The tendency to form supplementary latera on the capitulum
Whilst the presence of small, supplementary latera appears to be characteristic of *Crosnieriella*, their number and disposition on the capitulum appear to be variable (Figs 1A-D, 2, 3A, C). The interpretation of the capitular architecture of *Crosnieriella acanthosubcarinae* n.sp. is based solely on three specimens from one locality, and more material from several different populations is needed to fully document the complement of supplementary capitular latera. Yamaguchi & Newman (1997) emphasized variability in the pattern and number of basal imbricating plates in the balanomorph genus *Eochionelasmus* Yamaguchi, 1990 (*in* Yamaguchi & Newman 1990), and have since been able to distinguish populations from the Manus, North Fiji and Lau Basins (Newman pers. comm.; Yamaguchi & Newman 1997).
The tendency to develop a variable number of small supplementary capitular latera often with varying numbers on each side of the capitulum, is recognized in some species of *Calantica.* Hoek (1907) recorded two supplementary latera on one side of one of his six specimens of *C. pollicipedoides,* in addition to the three that all the specimens possessed and Hiro (1932) similarly noted two additional latera on one side of a specimen of *C. quinquilatera* Hiro, 1932. Four or five pairs of supplementary capitular latera are developed in *C. spinilatera,* and in *C. spinosa* a variable number

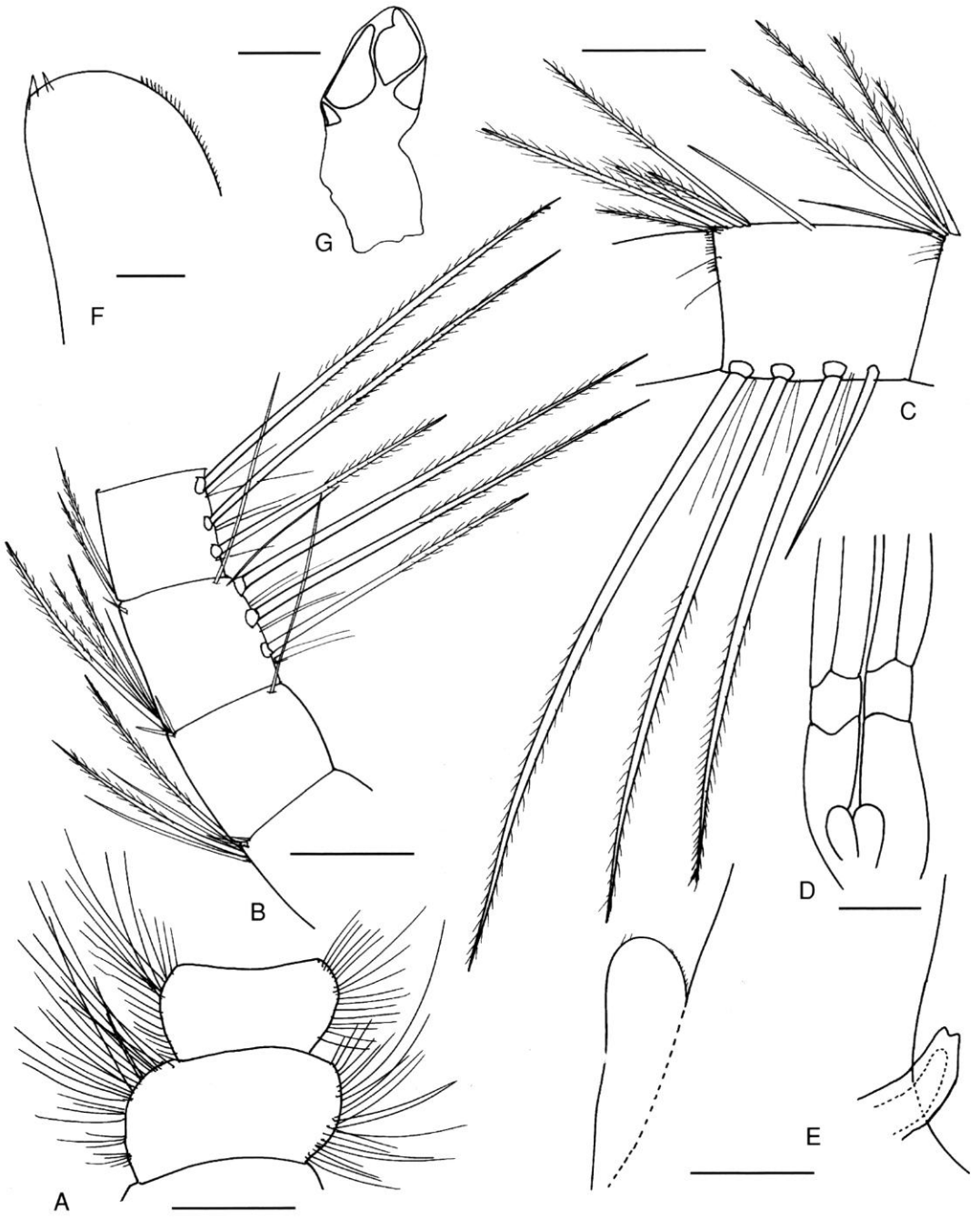

FIG. 6. — *Crosnieriella acanthosubcarinae* n.sp., ? hermaphrodite, paratype, cap. 28.7 mm (AM P49989). **A**, cirrus I, median segments, posterior ramus; **B**, cirrus II, median segments, posterior ramus; **C**, cirrus III, median segments, posterior ramus; **D**, posterior view, caudal appendages and pedicels of posterior cirrus VI; **E**, caudal appendage and penis at base of basal segment of pedicel of cirrus VI; **F**, detail of caudal appendage; **G**, complemental male. Scale bars: A-C, E, G, 0.5 mm; D, 1 mm; F, 0.1 mm.

of small latera develops, often varying in number on each side, and additionally the subrostrum may be present or absent (Darwin 1851; Batham 1945, 1946; Foster 1978). The inframedian latus (L^2) may be reduced or absent in some *C. kampeni* (Broch 1931) and this plate may also be reduced on one side in *C. quinquelatera* (Hiro 1932).

The form of the cirri

The appendages have been described for some species of *Smilium* and *Calantica*. However, considering the existing confused species taxonomy, it would be unwise to attempt to characterize the form of the cirri found in these two genera. The following data regarding the form of the cirri in the calanticids have been extracted from the literature.

In *C. quinquelatera, S. acutum, S. nudipes* Annandale, 1916, *S. peronii* Gray, 1825, *S. sinense* (Annandale, 1910) and *S. zancleanum* the rami of cirrus I are unequal and there is a pronounced interspace between cirrus I and cirrus II. In *Pisiscalpellum* the rami of cirrus I are unequal and cirrus I is set somewhat apart from cirrus II. In *Euscalpellum rostratum* Darwin, 1851 cirrus I is set far apart from cirrus II and the rami are subequal. In *Crosnieriella acanthosubcarinae* n.sp. cirrus I is not separated from cirrus II, and the rami are subequal.

In *C. kampeni, C. pollicipedoides, C. scorpio, C. spinilatera, C. spinosa* and *S. hypocrites* cirrus I has subequal rami and there is no pronounced interspace between cirrus I and cirrus II. In *Scillaelepas* (*S.*) *fosteri* Newman, 1980 and *S.* (*S.*) *gemma* (Aurivillius, 1892) cirrus I is set only slightly apart from cirrus II and the rami are subequal.

The presence of a subrostrum

The subrostrum is absent in *Pisiscalpellum* and *Scillaelepas* (*Scillaelepas*), but one subrostrum occurs in *Scillaelepas* (*Aurivillias*) Newman, 1980, and two in *Scillaelepas* (*Gruveliaelepas*) Newman, 1980. Some species of *Calantica* possess a subrostrum (e.g. *C. quinquelatera, C. villosa* Leach, 1824, *C. spinosa*). The fossil species *S. calanticoideum* Buckeridge, 1983 and *S. tortachillense* also possess a subrostrum but this plate is absent in Recent *Smilium* species. The possession of a subrostrum in *Crosnieriella* n.g. is thus not surprising, especially regarding the close relationship between *Crosnieriella* and *Smilium*, the latter assumed to have been derived from *Calantica* (Buckeridge 1983). *Crosnieriella acanthosubcarinae* n.sp. is, therefore, considered to be close to these early representatives of *Smilium.*

The presence of filamentary appendages

Crosnieriella acanthosubcarinae n.sp. has one pair of small filamentary appendages. Filamentary appendages occur in one species of *Euscalpellum* (*E. triflagellum* Ren, 1989; three filamentary appendages); in *Aurivillialepas* Newman, 1980 (three sets); and *Gruvelialepas* Newman, 1980 (one or two sets). Filamentary appendages are absent in *Smilium*, *Calantica*, *Paracalantica*, *Pisiscalpellum* and *Scillaelepas* s.s.

After consideration of the above characters, a new genus, *Crosnieriella*, is proposed for the material described herein. However, I am currently revising the calcanticids and the definitive genus name will be determined in the context of that revision, as will the relationships between the genera in the family. It is pertinent here to note Foster's (1978) comment that, apart from characters of the capitular plates, there are few anatomical differences between *Calantica* and *Smilium* but "if *Smilium* is to be retained as a distinct genus, then a revision of *Calantica* will no doubt identify groups as distinct from each other as from *Smilium*".

Specific relationships of

Crosnieriella acanthosubcarinae *n.sp.*

Considering Recent species of *Smilium, Crosnieriella acanthosubcarinae* n.sp. is most similar to *S. horridum* but differs in aspects of both hard- and soft-part morphology. *Smilium horridum* has a basic plan of fifteen capitular plates in two whorls, whereas *Crosnieriella acanthosubcarinae* n.sp. has a basic plan of nineteen plates, plus various small supplementary plates, resulting in a total of up to thirty-five capitular plates arranged in three whorls, with the supplementary plates arranged in tiers. Both species have large, thorn-like subcarinae^1 (SC^1) and horn-like carinolatera^1 (CL^1), the distal tips of which project freely from the capitulum; in both species

SC^1 is much larger than the rostrum. The shape of the tergum of *S. horridum* is triangular, with a broad process appended on the occludent side of the summit which is, therefore, very obtuse. The tergal summit of *Crosnieriella acanthosubcarinae* n.sp. is subacute and slightly reflexed towards the carina, and the plate is elongated, narrow and triangular, with a narrow process appended on the occludent side.

The form and arrangement of the peduncular scales differs between the two species. The peduncle of *S. horridum* is densely covered with small, pebble-like scales. On the carinal side are two longitudinal series of larger, more projecting scales and on one side there is another indistinct series of similar scales. The peduncular scales of *Crosnieriella acanthosubcarinae* n.sp. are peg-like and are more developed on the carinal side than on the rostral side of the peduncle. They are arranged in three to seven convoluted, lateral bands, which are distinctly separated by contracted areas of the peduncle.

The mandible of *S. horridum* has three main teeth, whilst that of *Crosnieriella acanthosubcarinae* n.sp. has four. In *S. horridum* the second and third teeth are similarly sized, and there are small subsidiary teeth between the first and second, whilst in *Crosnieriella acanthosubcarinae* n.sp. the second tooth is the smallest, a moderately large subsidiary tooth is present between the first and second teeth, and a small subsidiary tooth is sometimes present between the second and third. *Crosnieriella acanthosubcarinae* n.sp. is known from near One Tree Island, Queensland, Australia, from a depth of 175 m. *Smilium horridum* is a smaller species (cap. 12.0 mm, ped. 11.0 mm) and occurs in shallow water (42 m) in the Philippines.

Crosnieriella acanthosubcarinae n.sp. also shows similarities to *S. pollicipedoides* in the development of the carinolatera^1 (CL^1), although their degree of development is much greater in *Crosnieriella acanthosubcarinae* n.sp. *Smilium pollicipedoides* has a basic plan of fifteen capitular plates in two whorls, with all plates in the lower whorl small and triangular, with their apices pointing outward. The apex of the scutum projects beyond the occludent margin and the tergum is rhomboidal, rather than triangular as in *Crosnieriella acanthosubcarinae* n.sp. The rostrum of *S. pollicipedoides* is the largest valve and is slightly larger than the subcarina^1 (SC^1), rather than SC^1 being much larger than the rostrum, as in *S. pollicipedoides*. In addition, the carina of *S. pollicipedoides* is not angularly bent, but varies from gently convex to almost straight.

There are slight differences in the form of the mandible between the two species. Both species have four main teeth; *S. pollicipedoides* has two small subsidiary teeth between the first and second teeth, whereas *Crosnieriella acanthosubcarinae* n.sp. has a moderately large subsidiary tooth between teeth one and two, and sometimes a small subsidiary tooth between teeth two and three. The cirral counts differ between the two species, with almost twice as many segments in cirrus I and more than twice as many in cirrus II in *Crosnieriella acanthosubcarinae* n.sp. compared to *S. pollicipedoides* (14/16 and 23/25 compared to 7/9 and 9/9, respectively).

Smilium pollicipedoides, which occurs in the Malayan Archipelago and South Africa in depths of 57-190 m, is a much smaller species than *Crosnieriella acanthosubcarinae* n.sp. (cap. 6.0 mm, ped. 6.0 mm compared to 25.1 mm, 29.2 mm, respectively).

Calantica scorpio, known from the waters of Japan, China, the Gulf of Thailand and the Malayan Archipelago from depths of 35-140 m, has a basic plan of thirteen capitular plates developed in two whorls. The species is similar to *Crosnieriella acanthosubcarinae* n.sp. in the positions of the carinolatera^1 (CL^1), and the subcarina^1 (SC^1), although these plates are much less developed in *C. scorpio.* The form of the hooked rostrolatera differs between the species, being curved and varying from horn-like to thorn-like in *C. scorpio* but triangular in *Crosnieriella acanthosubcarinae* n.sp. In *C. scorpio*, the rostrum and SC^1 are of similar size, rather than SC^1 being much larger than the rostrum, as in *Crosnieriella acanthosubcarinae* n.sp.

The carina of *C. scorpio* is gently recurved in the upper part towards the tergum and almost straight in its distal half, rather than being angularly bent. The peduncular scale arrangement also differs between the two species. In *C. scorpio* the peduncle is covered with minute, well-

spaced, hook-like scales placed in three to ten spaced, lateral bands, and in older specimens some longitudinal stripes may develop on the peduncle.

Cirral counts also differ between the two species. There are a similar number of segments in cirrus I (14/16 *Crosnieriella acanthosubcarinae* n.sp., 13/14 *C. scorpio*) but there are more segments in cirrus II and the remaining cirri in *Crosnieriella acanthosubcarinae* n.sp. (*e.g.* for CII and CVI, 23/25 and 25/27 compared to 15/16 and 20/19).

Acknowledgments

I wish to thank Dr J. Lowry and Dr P. Berents, The Australian Museum, Sydney, for the loan of the specimens described herein. I also thank my colleagues Professor W. Newman, Scripps Institution of Oceanography, La Jolla, California, USA, and Professor J. Buckeridge, UNITEC Institute of Technology, Auckland, New Zealand, for their pertinent comments when reviewing a draft of the manuscript, and Clayton Bryce, Western Australian Museum, for preparing the photographs of the X-ray images.

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