JOURNAL OF CRUSTACEAN BIOLOGY, 21(2): 456–468, 2001

# REDESCRIPTION OF *SCALPELLOPSIS STRIATOCILIATA* BROCH, 1922, WITH A DISCUSSION ON ITS PHYLOGENETIC POSITION AND THE PEDUNCULAR PLATE PATTERN IN SCALPELLIDS

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A B S T R A C T

The adult of *Scalpellopsis striatociliata* and the ontogeny of its capitular and peduncular plates are described. During ontogeny, *S. striatociliata* develops the carino-lateral (CL) and inframedian (L2) plates heterochronously after some peduncular plates (cl), which is unique. The position of *Scalpellopsis* as sister-group of the other scalpellids is reaffirmed. The Scalpellidae have diverse peduncular plate patterns, with the 8-plated pattern being ancestral and the most widespread among the genera. The peduncular plate patterns of several species of Scalpellidae are presented.



Broch (1922: 243) described *Scalpellopsis striatociliata* based on specimens collected during Th. Mortensen's Pacific Expedition of 1914–1916. Zevina (1978a, b) divided the Scalpellidae into 8 subfamilies and included *Scalpellopsis,* together with *Pisiscalpellum* Utinomi, 1958, in the Scalpellopsinae. Newman (1996) elevated some of the subfamilies to familial rank. He maintained five previously described subfamilies, including Scalpellopsinae, in a restricted Scalpellidae. He also transferred *Pisiscalpellum* to the Calanticidae. Therefore, based on these nomenclatural changes, Scalpellopsinae includes only *Scalpellopsis,* typified by *Scalpellopsis striatociliata.*

Newman and Ross (1998) studied the ontogeny of the peduncular plates of the Calanticidae and Scalpellidae. They considered the basic whorl pattern of eight peduncular plates to be a composite made up of two sets of plates, rl-cl and sr-l-sc. They also noted there are two major trends in the development of peduncular plates in the scalpellomorphs. The first is a multiplication of the plates, with the plates becoming smaller and similar in form. The second is the elimination of vertical tiers of plates from the original 8-plated pattern. They included *Scalpellopsis* in this second group, considering it to be a derived species that lost the sr-l-sc tiers.

Young (1999) analyzed cladisticaly the relationships between the genera in the subfamilies of the Scalpellidae. He noted that *Scalpellopsis* (= Scalpellopsinae) forms the first branch of the cladogram, and therefore it was considered to be the sister group of the clade comprising all other scalpellids. The data used for *Scalpellopsis* was based on the literature, which posed several questions relative to the character matrix.

The key position of *Scalpellopsis* suggested a restudy of it to understanding the cladogram by Young (1999) and the phylogenetic relationships of the included genera. Consequently, I reexamined *Scalpellopsis striatociliata* and present a supplementary description herein. I also include a discussion of the ontogeny of its capitular and peduncular plates based on a number of juvenile syntypes.

## Scalpellopsinae Zevina, 1978
## *Scalpellopsis* Broch, 1922

*Scalpellopsis* Broch, 1922: 243; Zevina, 1978a: 1005; 1981: 181; Newman, 1996: 501.

*Definition* (emended).—Capitulum with 11 plates (S–T–C–L1–L2–CL), umbos apical; upper-latus (L1) between carina, tergum, and scutum; rostro-latera (RL) and rostrum (R) lacking; carino-latus well developed, wide; peduncle with two vertical tiers of scales (rl–cl); no caudal appendages, hermaphroditic.

## *Scalpellopsis striatociliata* Broch, 1922
## Figs. 1–3

*Scalpellopsis striatociliata* Broch, 1922: 243, figs. 11, 12; Withers, 1953: 10, fig. 12; Zevina, 1978a: 1005, fig. 16; 1981: 181, fig. 127.

*Material.*—Lectotype: Th. Mortensen's Pacific Expedition, Philippine Is., near Jolo, 20 to 30 fm. (38 to 55 m),

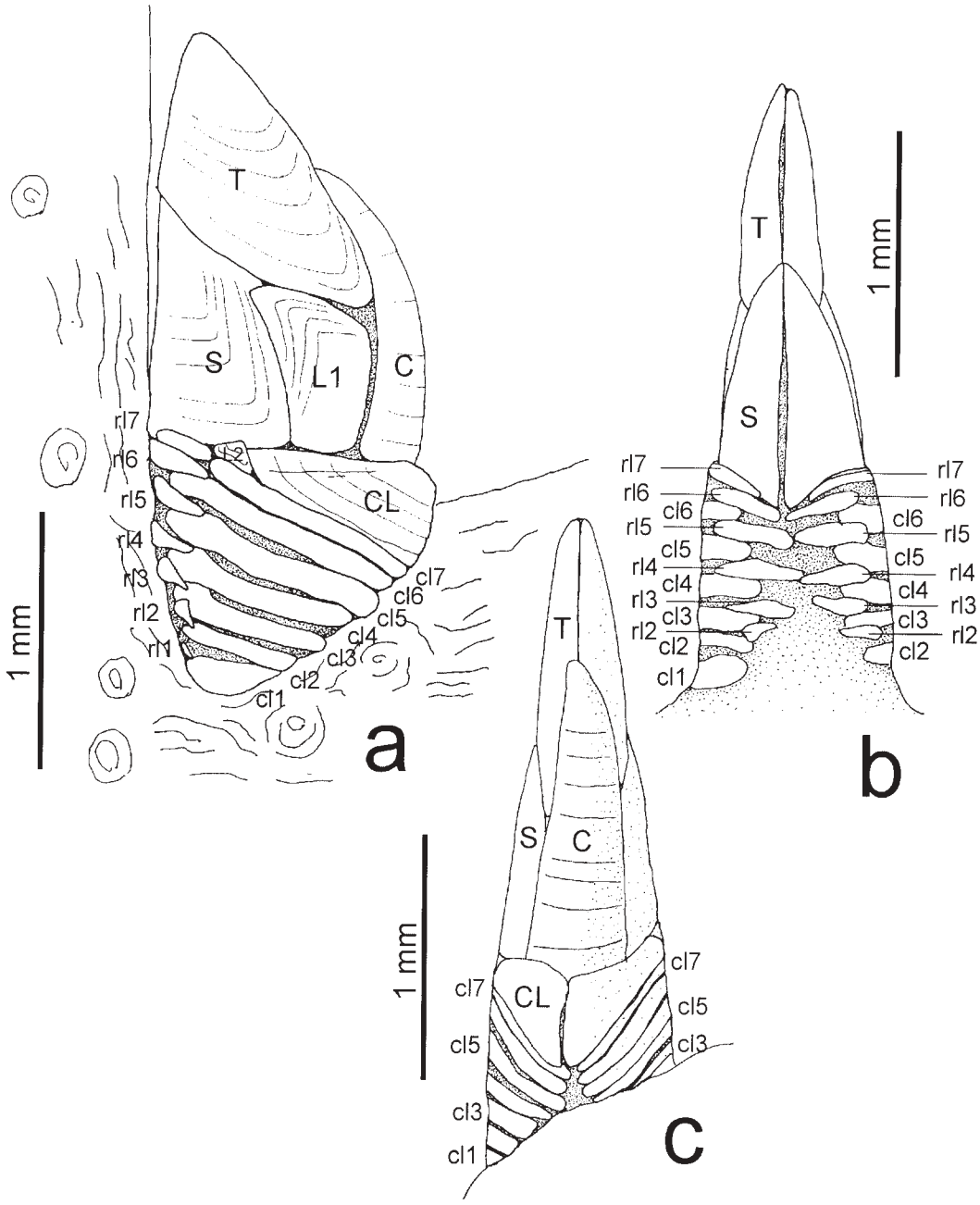


Fig. 1. *Scalpellopsis striatociliata* Broch. Lectotype. a) lateral right view; b) rostral view; c) carinal view.

length 2.7 mm, "on a hydroid colony (*Gammaria* sp)." Paralectotypes: 35 specimens from the same locality, up to 2.5 mm in length.

*Diagnosis.*—There is only one species assigned to this genus and therefore the diagnosis is the same as for the genus.

*Description.*—Hermaphrodite: Capitulum (Fig. 1a) with eleven plates, lacking rostrum and rostro-latera (Fig. 1a, b). Length about 1.5 times width, laterally compressed; occludent margin straight, carinal margin convex. Plates smooth except for sparse, thin growth lines, approximate, with only a small space between carina and upper-latus (L1). Scutum (Fig. 1a) slightly inflated, with faint apicobasal ridge; length 1.8 times width; narrowing from base to apex; occludent margin

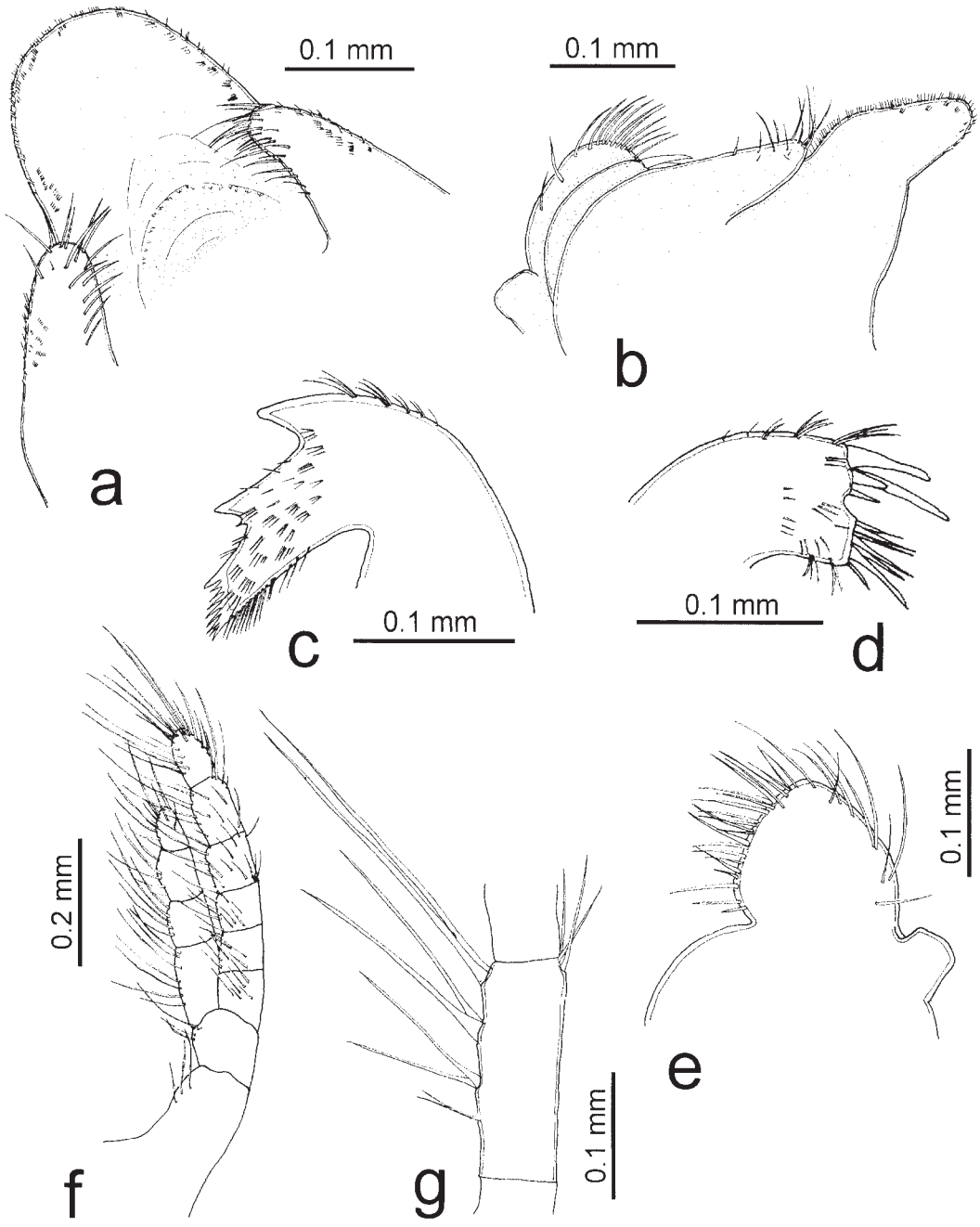


Fig. 2. *Scalpellopsis striatociliata* Broch. Lectotype. a) labrum and palps; b) lateral view of oral trophi; c) mandible; d) maxilla I; e) maxilla II; f) cirrus I; g) median article of cirrus VI.

straight, scutal margin slightly concave; apex straight, not extending over tergum. Tergum (Fig. 1a) triangular, with carinal area poorly developed; apex straight; occludent and carinal margins nearly straight, basal margin convex; surface area slightly greater than that of scutum. Carina (Fig. 1a, c) regularly and strongly arched, broadening uniformly toward base, tectum convex, basal margin straight. Upper-latus (Fig. 1a) quadrangular; apex directed toward and extending over scutum; scutal margin longer than tergal; scutal mar-

gin concave, tergal margin convex, others essentially straight. Carino-latus (Fig. 1a) quadrangular, proportionally very large, adjoining carinal, upper-latus and part of scutal basal margins, height almost 1/3 its width. Umbo apical, blunt; a slight ridge extends from apex to basi-lateral angle. Plates contiguous under carina. Inframedian latus (Fig. 1a) small, triangular, slightly wider than high.

Peduncle (Fig. 1a–c) short, length approximately ½ that of capitulum, covered by four vertical tiers of plates with each horizontal whorl consisting of paired plates (rl-cl); cl plates exceptionally wide, approximately 3 times wider than rl plates.

Labrum (Fig. 2a, b) bulate, with single row of 25 small teeth on the inner margin and several multifid spines along outer border. Palp (Fig. 2a, b) short, distally acuminate, with sparse simple setae on inner margin and multifid spines on outer margin. Mandible (Fig. 2c) with three teeth, lower angle spinulose; distance between first and second tooth 1.4 times that between second and third. Maxilla I (Fig. 2d) with two steps, lower one projecting, and a shallow notch between them; upper angle with two large and two smaller spines, seven intermediate and small spines directed basally along cutting edge below notch. Maxilla II (Fig. 2e) bilobed, with simple setae along margins of the upper lobe; papillae of maxillary gland projecting slightly.

Cirrus I (Fig. 2f) with anterior ramus 0.70 length of posterior, articles slightly protuberant; both rami clothed with numerous, simple setae. Cirri II–VI with equal rami; intermediate articles of cirrus VI (Fig. 2g) about 4 times longer than wide, setal to article width ratio 4.2:1, armed with 4 pairs of simple setae on anterior margin, 0–3 setae on posterodistal angle. Caudal appendage absent. Penis clothed by several setules. Cirral counts are presented in Table 1.

Table 1. Number of articles of cirri I–VI of *Scalpellopsis striatociliata* Broch, 1922. Paralectotype. CI–VI, cirri I to VI; RC, right cirrus; LC, left cirrus; +, broken ramus.

| | I | II | III | IV | V | VI |
|---|---|---|---|---|---|---|
| RC | 4/6 | 7/8 | 9/9 | 9/10 | 7+/11 | 8+/10 |
| LC | 4/6 | 7/8 | 9/9 | 10/10 | 10/+ | 11/10 |

*Remarks.*—In his description, Broch (1922: 243) observed that: "The capitulum . . . is covered by a pellucid, hairy, chitinous membrane, and the transverse rows of hairs lend a peculiar aspect to the species. The rather long hairs are placed in four or more transverse rows on the terga, scuta, and carina, . . . " On the syntypes, only thin pieces of spotted hairy cuticle can be seen, and these do not show the transverse rows.

Ontogenetically, the first peduncular plate (cl1) is initially larger than the next pair of cls, probably because it has the function of fixing on the soft part of the cnidarian (Fig. 3b). The cl1 pair form a cup-shaped calcareous peduncle. When fully developed the specimens are also attached by the ventral line of the peduncle (the ventral groove of Broch, 1922) which partly wraps around the cnidarian axes. During ontogeny, the capitulum bends toward the coral branch. This bending may be due to the enlargement of CL, the small increase in size of L2, and the lack of the RL and R. When the CLs of *Scalpellopsis* are compared with those of other scalpellids, they are very large and also have a wide area of contact on the dorsal midline (Fig. lc). All the specimens have the same alignment position on the colony; i.e., the occludent margin of the capitulum facing the cnidarian branches (see Fig. 1a) and cirral net is directed toward the colony. This is peculiar, as the advantage of such an arrangement is not obvious. The cirri and mouth appendages are normal, which suggests planktotrophy filter feeding and not parasitism (cf. Grygier and Newman, 1991).

## On the Ontogeny of the Capitular and Peduncular Plates

The ontogeny of the capitular and peduncular plates may be seen in a few recently attached juveniles on the hydroid colony (Figs. 3, 4). Broch (1922: 244) illustrated two stages in the development of the capitular plates and commented on the ontogeny of these. His fig. 1 represents a juvenile stage smaller than those I was able to observe: the tergum, scutum, upper-latus (L1), carina, and cl1 are present (Fig. 4a). In the first stage I observed, the tergum, scutum, upper-latus (L1), carina, cl1, and rl1 were present (Figs. 3a, 4b). Paired cl1 plates grow larger than the c12 plates. In the next stage, rl2, cl2, and CL plates are added (Figs. 3b, 4d). Because of the absence of a stage intermediate between the foregoing two stages I could not

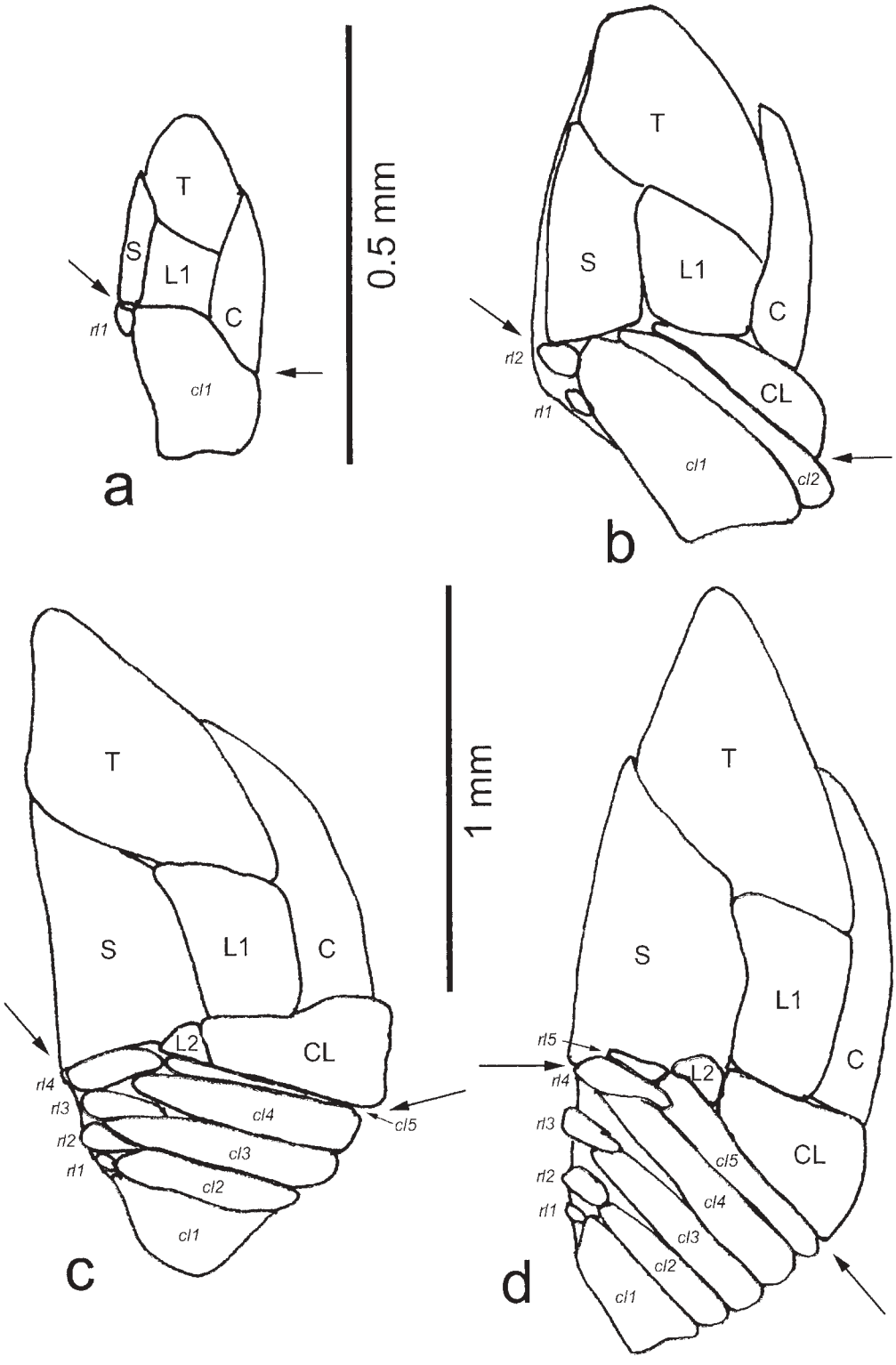


Fig. 3. *Scalpellopsis striatociliata* Broch. a–d) ontogenetic stages. The arrows represent the region between the peduncle and capitulum where new plates are added.

determine if CL or c12 develops first, but it is at this stage the growth zone between capitulum and peduncle produces the CL pair which are incorporated into the capitulum. Figure 4c is of a hypothetical stage in which the CL appear. In the third juvenile stage the inframedian latus (L2) and three more cl and two more rl plates have been added (Figs. 3c, 4e). L2 may have been produced after the appearance of cl2–rl2, or the cl3–rl3, or even the cl4–rl4 plates appearances. The juveniles show a dorsal to ventral addition of peduncular plates, so there are stages with cls but without the related rls, which are added later.

In the adults up to seven whorls of rl-cl plates are produced (Fig. 1a).

The sequence in which plates are added to the capitulum and peduncle is a radical departure from what is known to occur in other scalpellids (Newman and Ross, 1998 and references). In these scalpellids the lower row of capitular plates (CL, L2, RL) appear early in ontogeny, well before development of the first whorl of peduncular plates. In *Scalpellopsis* the plates of the lower row of capitulum, composed only by CL and L2, appear after the appearance of peduncular scales. On the other hand, the addition of secondary plates to the capitulum proceeds from the carinal end of the animal to the rostral in *Scalpellopsis* as in others scalpellids; but in the former the rostro-latera and rostrum never develop. The addition of the peduncular plates is generally from the carinal position to the rostral sides of the peduncle, whereas for Pollicipedidae it is rostral to carinal (Newman and Ross, 1998: 577).

## The Phylogenetic position of *Scalpellopsis*

The matrix presented by Young (1999: table 1) included several question marks for *Scalpellopsis* due to the incomplete information of Broch's description (Broch, 1922). With the new information derived from a study of the type specimens of *Scalpellopsis,* the question marks could be reevaluated. Therefore, the line for *Scalpellopsis* in the matrix presented by Young (1999: table 1) had changed for:

| Character | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 12345678901234567890123456789012345678901234567890123456789012 | | | |
| *Scalpellopsis* | 10000020-10000111200000111020022132111--0- | | | |

After the inclusion of these new information, the new matrix was analyzed again. This new cladogram failed to change the position of the *Scalpellopsis.* This seemingly reaffirms the position of *Scalpellopsis* as the sister-group of the others scalpellids. However, certain characteristics observed only in *Scalpellopsis striatociliata* raise some questions.

Is the absence of rostro-latera and a rostrum in *Scalpellopsis* a plesiomorphic condition, or does it represent a secondary loss? The Calanticidae are considered the sister-group of the Scalpellidae (Glenner *et al.*, 1995), the species of which have a well-developed rostrum, and most species of *Euscalpellum* have a plate in the rostro-lateral position. The rostrum in calanticids is well developed, whereas the presence or absence of the rostrum occurs in several genera of scalpellids (e.g., *Arcoscalpellum*). Therefore, it is more parsimonious to infer a progression from a well-developed rostrum to a reduced rostrum, which was subsequently lost as in *Scalpellopsis* (Fig. 5). The alternative hypothesis would be the loss of the rostrum in the ancestral scalpellid and its subsequent reappearance in various lineages, which appears to be less probable.

The carino-latera are present in some calanticids but absent in others. When it is present, it is triangular and has an apical umbo, similar to the capitular plates found in the lower whorl of pollicipeds. The number of plates comprising the lower whorl in calanticids is variable, which makes it difficult to establish homologies.

All the rostro-latera of scalpellids have a rectangular shape with the umbo at the disto-occludent angle. This condition is also seen in some fossil genera, viz. *Virgiscalpellum* and *Titanolepas*, both included in the Calanticidae. Most of the calanticids have the rostro-latera triangular with an apical umbo, which is the plesiomorphic state of this plate. Therefore, the absence of RL should be considered an autapomorphy of *Scalpellopsis* (Fig. 6). *Scalpellopsis* is unique in not having rostro-latera. All other scalpellids have a well-developed rostro-latus, and there are no known species of scalpellids losing this plate secondarily.

Is the peduncular plate pattern in *Scalpellopsis* derived from an 8-plated whorl? The only way to answer this question is to exam-

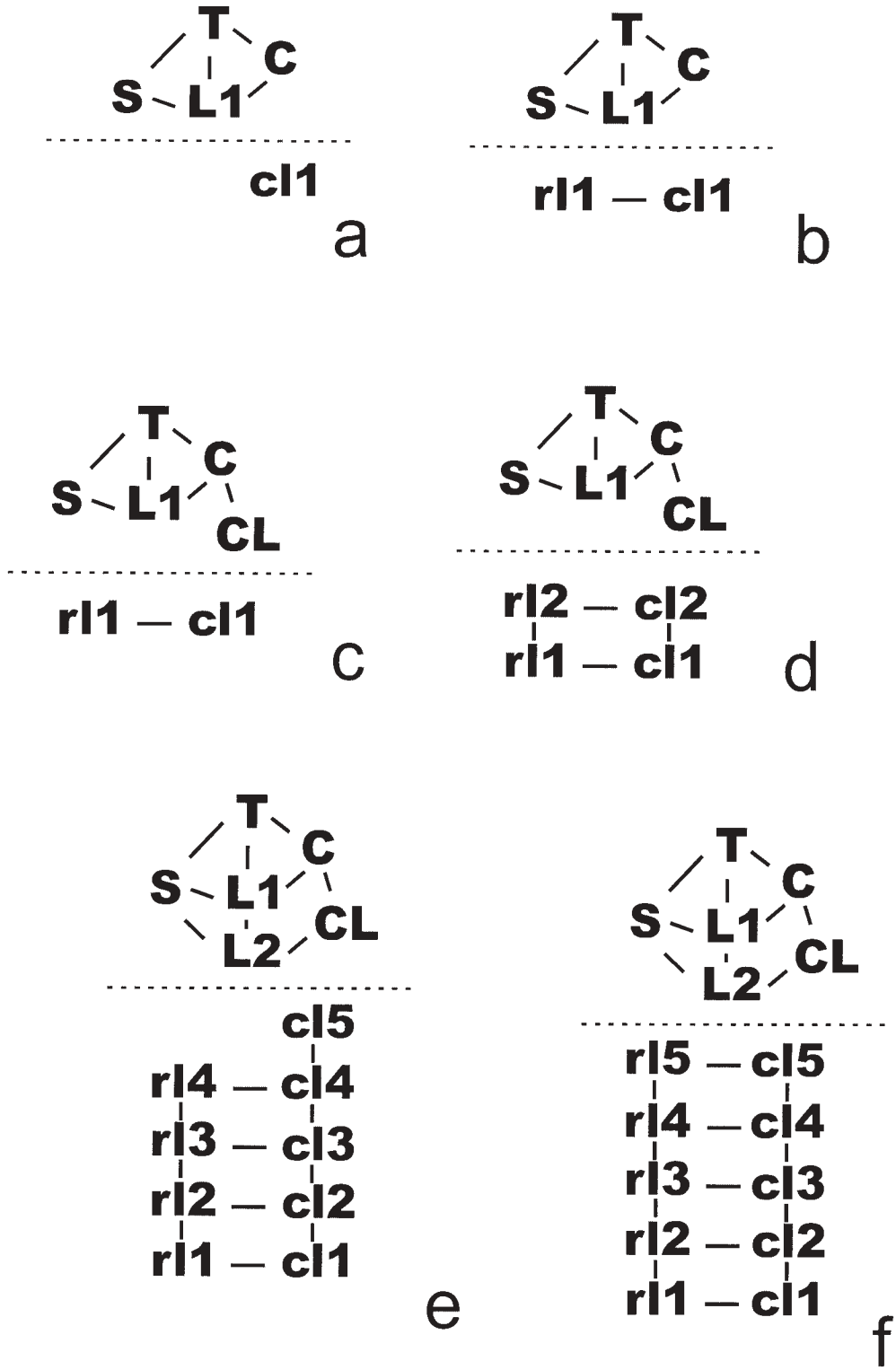


Fig. 4. Development of the capitular and peduncular plates of *Scalpellopsis striatociliata* Broch. a) Initial stage observed by Broch (1922: fig. 12) with four capitular and one peduncular plates (cl1); b) first observed stage with the development of the second peduncular plate (rl1) (Fig. 3a); c) hypothetical intermediate stage presenting the adding of the CL plate; d) second observed stage, with the adding of one more whorl of the peduncular plates (Fig. 3b); e) third observed stage, with all the capitular plates and five incomplete whorls of peduncular plates (Fig. 3c); f) fourth observed stage with five complete whorls of peduncular plates (Fig. 3d). The dotted lines represent the region where new plates are added.

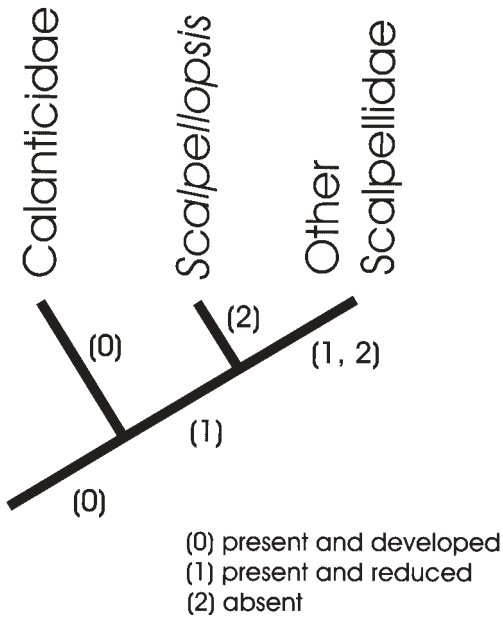


Fig. 5. Modified cladogram of Young (1999), showing the distribution of the rostra in the taxa.

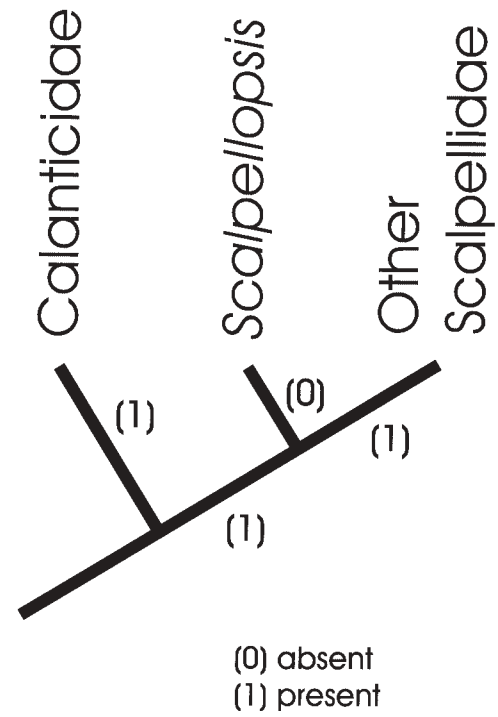


Fig. 6. Modified cladogram of Young (1999), showing the distribution of the rostro-latera in the taxa.

ine the plate patterns of the peduncle in different genera and families (Figs. 7, 8). The "sr" and "sc" are recognized by being unpaired and their position under the rostrum and carina, respectively. The "rl", "l", and "cl" are recognized by their relative position under the rostro-latus (RL), inframedian-latus (L2), and carino-latus (CL), respectively (Newman and Ross, 1998). The number of plates in each horizontal group is based on the number of tiers below the capitular plates. Designation of plate as "l" or "cl", or "l" or "rl", is somewhat difficult (e.g., in Fig. 7, the types of plates by positional relationships of *Planoscalpellum limpidus* and *Arcoscalpellum portoricanum*), and the general patterns show the great diversity that appears in the scalpellids (Figs. 7, 8) when compared with other families.

The Calanticidae have a peduncle with unpaired (sr and sc) plates and several lateral plates (up to 18 tiers of lateral plates). This great number of lateral plates are also present in species of the Neolepadidae and Pollicipedidae (Fig. 7). The Jurassic *Archaeolepas* and the Cretaceous Stramentidae have a distinct eight-plated whorl, whereas in the Scalpellidae a variety of whorl types occur. The Scalpellidae have ambiguously defined subfamilies and many are likely paraphyletic. Indeed, several genera are grouped within higher taxa by plesiomorphic characters (e.g., *Trianguloscalpellum* and *Arcoscalpellum*) (Young, 1999). Therefore, my findings for the Scalpellidae is limited, and I do not have a general view how the change of the plate patterns evolved in the scalpellid groups. But some observations can be made based on the 43 species studied herein (Table 2). The whorl type having the fewest plates is that of *Scalpellopsis* which has only two pairs (rl-cl) (Newman and Ross, 1998), and the largest is *Hamatoscalpellum rathbunae* with about 17 plates in a whorl (sr, sc and 15 laterals). The basic 8-plated whorl pattern occurs in species of widely different genera (*Annandaleum laccadivicum, Litoscalpellum discoveryi, Neoscalpellum phantasma, Gymnoscalpellum tarasovi, Arcoscalpellum michelottianum, A. sociabile, Trianguloscalpellum darwini, T. regium, T. rubra,* and *Catherinum albatrossianum*).

Of the 43 species examined, the sc plate is absent in only three species (*Scalpellopsis striatociliata, Catherinum recurvitereum* and *Diceroscalnellum boubalocerus*) and the sr is absent in ten species representing nine genera. The l plate is absent in *Scalpellopsis*, in the genera of the "Arcoscalpellinae" *(Arcoscalpellum, Trianguloscalpellum, Angu-*

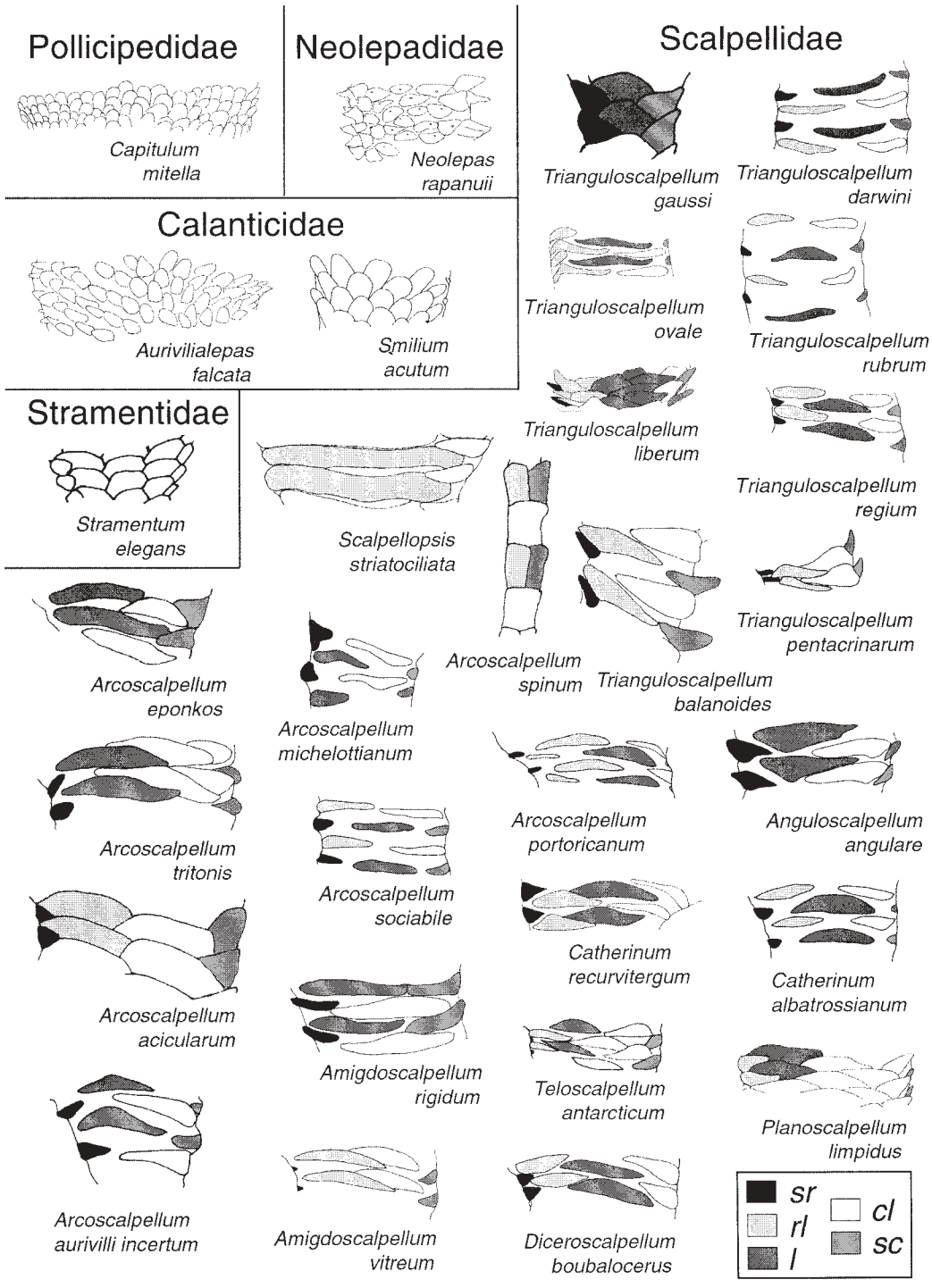


Fig. 7. Peduncular plates patterns of the pedunculates. Families Pollicipedidae, Neolepadidae, Calanticidae, Stramentidae, and Scalpellidae (part).

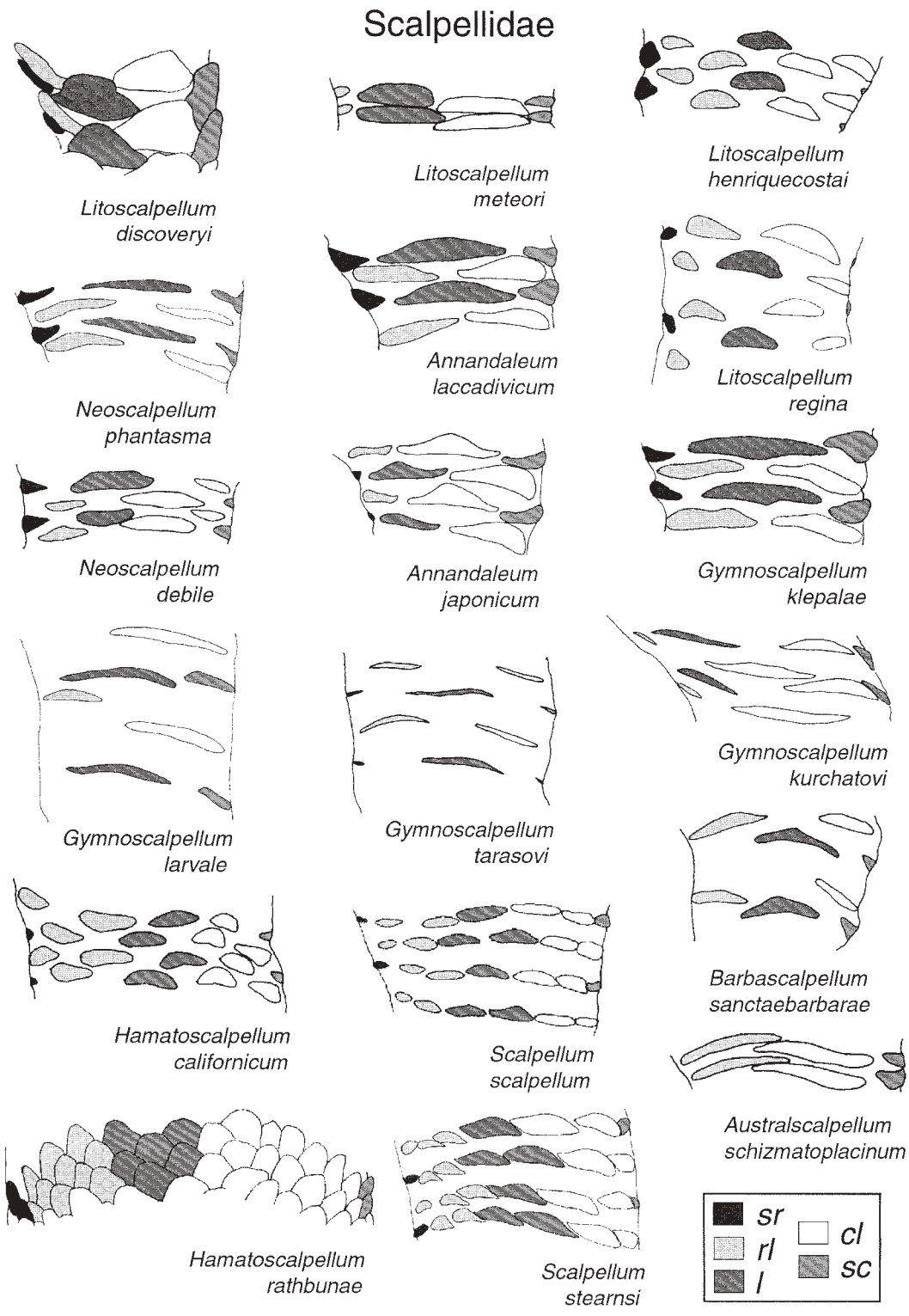


Fig. 8. Peduncular plates pattern of the pedunculates. Family Scalpellidae (part).

Table 2. Species of Scalpellidae examined for their peduncular plates pattern. * = from Newman and Ross, 1998 (not examined); ** = from Young, 1998. Other families included Pollicipedidae: *Capitulum mitella* (Linnaeus, 1758) (MNRJ 7181); Neolepadidae: *Neolepas rapanuii* Jones, 1993 (MNRJ 13409); Calanticidae: *Aurivillialepas falcata* (Aurivilius, 1898) (MNRJ 7153) and *Smilium acutum* (Hoek, 1883) (MNRJ 12931); and Stramentidae: *Stramentum elegans* Hattin, 1977*.

| Species | Peduncular plate pattern | Collection number |
|---|---|---|
| *Amigdoscalpellum rigidum* (Aurivillius, 1898) | sr - l - sc<br>- cl | (MNRJ 8879) |
| *A. vitreum* (Hoek, 1883) | sr - - sc<br>rl - cl | (MNRJ 12938) |
| *Anguloscalpellum angulare* (Nilsson-Cantell, 1930) | sr - l - sc<br>- cl | (MNRJ 2549) |
| *Annandaleum japonicum* (Hoek, 1883) | sr - l - sc<br>rl - cl (2) | (MNRJ 12934) |
| *A. laccadivicum* (Annandale, 1906) | sr - l - sc<br>rl - cl | (MNRJ 12952) |
| *Arcoscalpellum acicularum* Newman and Ross, 1971 | sr - - sc<br>rl - cl | * |
| *A. aurivilli incertum* (Pilsbry, 1907) | sr - l - sc<br>- cl | (MNRJ 7166) |
| *A. eponkos* Young, 1998 | - l - sc<br>- cl | ** |
| *A. michelottianum* (Seguenza, 1876) | sr - l - sc<br>- cl | (MNRJ 7134) |
| *A. portoricanum* (Pilsbry, 1907) | sr - l - sc<br>rl (2) - cl | (MNRJ 7174) |
| *A. sociabile* (Annandale, 1905) | sr - l - sc<br>rl - cl | (MNRJ 12946) |
| *A. spinum* Newman and Ross, 1998 | - - sc<br>rl - cl | * |
| *A. tritonis* (Hoek, 1883) | sr - l - sc<br>- cl (2) | (MNRJ 7160) |
| *Australscalpellum schizmatoplacinum* Newman and Ross, 1971 | - - sc<br>rl - cl | (MNRJ 2554) |
| *Barbascalpellum sanctaebarbarae* (Pilsbry, 1907) | - l - sc<br>rl - cl | (MNRJ 7185) |
| *Catherinum albatrossianum* (Nilsson-Cantell, 1925) | sr - l - sc<br>rl - cl | (MNRJ 7170) |
| *C. recurvitergum* (Gruvel, 1900) | sr - l -<br>rl - cl | (MNRJ 8878) |
| *Diceroscalpellum boubalocerus* (Young, 1992) | sr - l -<br>rl - cl | (MNRJ 2823) |
| *Gymnoscalpellum klepalae* (Federspiel and Hoffer, 1997) | sr - l - sc<br>rl - cl | * |
| *G. kurchatovi* (Zevina, 1972) | - l - sc<br>rl - cl (2) | (MNRJ 12951) |
| *G. larvale* (Pilsbry, 1907) | - l - sc<br>rl - cl | (MNRJ 7169) |
| *G. tarasovi* Newman and Ross, 1971 | sr - l -sc<br>rl - cl | (MNRJ 7168) |
| *Hamatoscalpellum californicum* (Pilsbry, 1907) | sr - l (2) - sc<br>rl (3) - cl (3) | (MNRJ 7175) |
| *H. rathbunae* (Pilsbry, 1907) | sr - l (3) - sc<br>rl (7) - cl (8) | (MNRJ 2227) |
| *Litoscalpellum discoveryi* (Gruvel, 1906) | sr - l - sc<br>rl - cl | (MNRJ 7176) |
| *L. henriquecostai* (Weber, 1960) | sr - l - sc<br>rl (2) - cl (2) | (MNRJ 2230) |
| *L. meteoria* Young, 1998 | - l - sc<br>rl - cl | (MNRJ 7132) |
| *L. regina* (Pilsbry, 1907) | sr - l - sc<br>rl (2) - cl (2) | (MNRJ 2193) |
| *Neoscalpellum debile* (Aurivillius, 1898) | sr - l - sc<br>rl - cl (2) | (MNRJ 7190) |

Table 2. Continued.

| Species | Peduncular pattern | Plate collection number |
|---|---|---|
| *N. phantasma* (Pilsbry, 1907) | sr - l - sc<br>rl - cl | (MNRJ 7186) |
| *Planoscalpellum limpidus* (Zevina, 1976) | - l - sc<br>rl - cl (4) | (MNRJ 7154) |
| *Scalpellopsis striatociliata* Broch, 1922 | - -<br>rl - cl | |
| *Scalpellum scalpellum* (Linnaeus, 1767) | sr - l (3) - sc<br>rl (4) - cl (4) | (MNRJ 7151) |
| *S. stearnsi* Pilsbry, 1890 | sr - l (3) - sc<br>rl (5) - cl (4) | (MNRJ 12947) |
| *Teloscalpellum antarcticum* (Hoek, 1883) | sr - l -sc<br>rl - cl (2) | (MNRJ 7167) |
| *Trianguloscalpellum balanoides* (Hoek, 1883) | sr - - sc<br>rl - cl | * |
| *T. darwini* (Hoek, 1883) | sr - l - sc<br>rl - cl | (MNRJ 7184) |
| *T. gaussi* (Gruvel, 1907) | - l -<br>rl - cl | * |
| *T. liberum* (Nilsson-Cantell, 1930) | sr - l (3) - sc<br>rl (2) - cl | (MNRJ 2557) |
| *T. ovale* (Hoek, 1883) | - l - sc<br>rl (2) - cl | (MNRJ 7138) |
| *T. pentacrinarum* (Pilsbry, 1907) | sr - - sc<br>rl - cl | (MNRJ 13408) |
| *T. regium* (Thomson, 1873) | sr - l - sc<br>rl - cl | (MNRJ 8880) |
| *T. rubrum* (Hoek, 1883) | sr - l - sc<br>rl - cl | (MNRJ 12948) |

*loscalpellum* and *Amigdoscalpellum*), and in *Australscalpellum schizmatoplacinum*, and it is duplicated in *Trianguloscalpellum liberum* and species of Scalpellinae (*sensu* Young, 1999; *Scalpellum* spp. and *Hamatoscalpellum* spp.). The cl plate is questionably absent in *Trianguloscalpellum gaussi* (see Newman and Ross, 1998: 578) and is duplicated mostly in species of Meroscalpellinae and Scalpellinae. Finally, the rl plate is absent in several species of "Arcoscalpellinae" and in the Scalpellinae.

Referring to the cladogram presented by Young (1999), some general conclusions can be reached. The basal genera have the most variable peduncular plate patterns, except for the monotypic *Scalpellopsis*. The Meroscalpellinae tend to maintain the 8-plated pattern, but may duplicate the rl tiers. The Scalpellinae tend to replicate the carino-lateral, lateral, and rostrum-lateral tiers. However, *Australscalpellum schizmatoplacinum*, which was purportedly a Scalpellinae (Young, 1999), has a very distinct pattern (rl-cl-sc) that differs from *Brochia* (rl-l-cl), both of which were included in the Brochiinae by Zevina (1978a) and by Newman (1996).

The large variety of whorl patterns comes to be very subjective when defining the plesiomorphic state for *Scalpellopsis*. Also, its whorl pattern is unique and does not occur in any other taxon.

The composite pattern (rl-cl, sr-l-sc) present in Scalpellidae is not commonly observed in the other scalpellomorphs. These usually have a large number of scales but in numerous whorls (Fig. 7; Neolepadidae, Pollicipedidae and Calanticidae). The composite pattern of calanticids is only conspicuously observable in *Smilium acutum* (Hoek, 1883), *Euscalpellum stratum* (Aurivillius, 1892), and *Newmanilepas mirifica* (Zevina, 1976). This suggests that the composite pattern appeared before the formation of the Scalpellidae clade.

Besides these extant groups, the pattern found in the Mesozoic Stramentidae and related taxa warrants to be taken into consideration. These extinct groups have species with an 8-plated composite pattern as noted by Newman and Ross (1998). This group may be related directly to the Scalpellidae, even more so than the Calanticinae. They have a capitulum with carina, carino-latus, tergum, L1 (upper-latus), scutum, and rostrum but do

not have paired RL and L2 (inframedian-latus). *Scalpellopsis*, which was formerly included in Scalpellidae, similarly lacks a rostrum and rostro-latus, and the L2 is still poorly developed.

The 8-plated pattern is the most widespread pattern in all of the genera studied so far. It should be considered the primary plesiomorphic condition in the Scalpellidae as Newman and Ross (1998) pointed out. If so, *Scalpellopsis* deleted the development of the sr-l-sc component of the composite whorl.

Despite several derived autapomorphic characters of *Scalpellopsis* (the loss of the rostro- and inframedian-latera and the reduction in the number of peduncular plates) this species is situated at the base of the scalpellids due to its having a generalized pattern of the remaining capitular plates (fully calcified; basal plates with triangular shape; apical umbo) and a primitive appendage structure (mandible with lower angle spinulose; first maxilla with lower angle projected; second maxilla with posterior margin curved with setae; palp middle sized asymmetrical) (Young, 1999). The reduction of capitular and peduncular plates, a derived condition, may be related to the mode of fixation and development of this species on a cnidarian colony.

## Conclusions

New information on the anatomy of the appendages of *Scalpellopsis striatociliata* maintained its position on the cladogram presented by Young (1999). The position of *Scalpellopsis* as sister-group of the others scalpellids, however, is reaffirmed.

The origin of the relatively few capitular and peduncular plates of *Scalpellopsis striatociliata* probably is due to the loss of the rostrum and rostro-latera.

The Scalpellidae have a diversity of peduncular plate patterns, with the 8-plated pattern being the most widespread among the genera.

## Acknowledgements

I wish to acknowledge William A. Newman and Arnold Ross, for numerous discussions during this study and their comments on the manuscript, which significantly improved this paper; Danny Eibye-Jacobsen and Jens Høeg for allowing me to study the type material of this species. This study was supported by a grant from Conselho Nacional de Desenvolvimento Cientifico e Técnológico (CNPq) and financial support by Fundação Universitária José Bonifácio (FUJB) and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ).

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Received: 18 November 1999.
Accepted: 17 August 2000.