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Revision of the genus *Acasta* Leach (Cirripedia: Balanoidea)

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The relationship between sponge hosts and barnacles are investigated, and the dependence of the morphology of the barnacles on the skeletons of the sponges is shown. The evolutionary development of this group is analysed. Five genera: *Archiacasta, Neoacasta, Euacasta, Acasta* and *Pectinoacasta*, are distinguished from the original genus Acasta on the basis of important morphological characteristics. The new sub-family Acastinae is suggested for these genera. The vertical and horizontal distributions of the species of this sub-family are studied. About 150 sponge samples, containing 26 species of these barnacles, have been examined. Eight new barnacle species have been described already in the Russian Zoological Journal. This article provides illustrations of these, and descriptions with illustrations of a further five new species. This group of sponge-inhabiting barnacles, which is rather interesting in morphological and ecological aspects, has not hitherto been examined thoroughly.

ADDITIONAL KEY WORDS: Sponge – inhabiting barnacles – evolution – systematics – host specificity – phylogeny – distribution.

CONTENTS

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INTRODUCTION

The genus *Acasta* was proposed by Leach (1817), but only four species (*A. glans* Lamarck, *A. sulcata* Lamarck, *A. spongites* Poli, *A. laevigata* Gray) were known before Darwin revised the group in 1854. Darwin described a further four extant species (*A. fenestrata, A. sporillus, A. cyathus, A. purpurata*). He regarded *Acasta* as a subgenus of *Balanus*, distinguished by the presence of hooks on the anterior ramus of the fourth cirrus and by membranous windows between the wall plates.

By the beginning of the twentieth century, many more *Acasta* species had been described from different regions and depths. Hoek (1913) revised the systematics of the group, defining the genus *Acasta* by the thinness of the parieties (in which pores are absent), the great development of the radii, the cup-formed basis and the habit of living—with one exception—embedded in sponges. This definition is quite good for the species known to Hoek, although *A. cyathus* and *A. dofleini* have a flat, saucer-formed basis and *A. spongites* has narrower radii.

Broch (1931–1932) divided *Acasta* into two groups on a single character difference, the Inarmata group without hooks or small spines on the fourth cirrus and the Eu-Acasta group with hooks or thorns on the fourth cirrus. Broch ignored major differences within these groups, such as the fact that *A. sculpturata* Broch has a cup-shaped basis, normally developed carinolaterals, and terga with strong radial striae, while *A. dofleini* Kruger has a flat or saucer-shaped basis, rudimentary carinolatera and terga without strong striae.

Hiro (1937a) provided a more comprehensive analysis of the genus *Acasta* and drew attention to similarities with *Membranobalanus, Armatobalanus* and *Conopea*. He pointed out the difficulties presented by the variability of the species of *Acasta* in the structure of the wall and basis, the shape of the opercular valves and the armature of the cirri. Hiro suggested that three main groups could be identified within *Acasta* on the basis of opercular valve structure, but was not confident that these groups were of systematic value. Hiro porposed that the genus *Acasta* had originated independently of the genus *Balanus* and may have some relationship with *Armatobalanus*.

MATERIALS AND METHODS

Most of the sponge-inhabiting barnacle specimens were obtained from the sponge collections of Prof. V. M. Koltun (Zoological Institute, Laboratory of Sponges and Cnidarians, St. Petersburg, Russia). Some specimens were found in the collections of sponges at the Department of Invertebrate Zoology, Moscow State University and in the collections of the Institute of Oceanology (Moscow).

All samples had been fixed in alcohol (70%).

The slide preparations of the shell compartments and the 'soft body' were investigated by means of monocular and stereo light microscopes.

LIST OF INVESTIGATED SPECIES

(1) *Archiacasta tenuivalvata* (Broch): 5°28′8″S, 145°50′6″E, 18 m, two specimens from Haliclona sp. (2) *Neoacasta glans* (Lamarck): 12°56.9′S, 48°36.0′E, 1–3 m, three specimens from sponge fam. Halichondriidae; 5°41.6′S, 53°41.1′E, 12–13 m, three specimens from sponge fam. Axinellidae; 5°24.80′S, 53°18.95′E,

20–25 m, two specimens from *Axinella* sp.; 10°19.2′S, 62°13.6′E, 39 m, five specimens from undetermined sponge. (3) *Neoacasta laevigata* (Gray): 3°13.7′N, 73°00′E, 1 m, seven specimens from sponge fam. Spongiidae: 12°14.25′S, 49°00.5′E, 1.5–2.5 m, two specimens from *Dysidea* sp.; 5°28′8″S, 145°50′6″E, three specimens from *Dysidea* sp. (4) *Euacasta dofleini* (Krüger): 18°40.0′N, 107°02.0′E, 52 m, four specimens from *Gellius* sp.; 1°15.2′N, 103°45′E, tidal zone, four specimens from sponge fam. Myxillidae; 5°28′8″S, 145°50′6″E, 18 m, three specimens from *Haliclona* sp.; 4°17.75′S, 55°40.6′E, 7 m, five specimens from sponge fam. Axinellidae; 4°48.9′S, 53°20.0′E, 40–150 m, three specimens from sponge fam. Axinellidae; 4°17.45′S, 55°41.9′E, 5–7 m, seven specimens from *Leucetta* sp.; 4°18.0′S, 55°45.0′E, 11 m, four specimens from sponge fam. Stellettidae; 4°17.5′S, 55°51.5′E, 3–6 m, three specimens from *Haliclona* sp.; 4°17.45′S, 55°41.9′E, 5–7 m, six specimens from *Crella* sp.; 4°17.85′S, 55°52.3′E, 8–10 m, three specimens from sponge fam. Axinellidae and three specimens from undetermined sponge; 4°49.15′S, 53°20.0′E, 40 m, two specimens from sponge fam. Axinellidae; 4°48.9′S, 53°20.45′E, 90–360 m, two specimens from *Pachastrella* sp.; 17°06′N, 39°36′E, 20 m, three specimens from sponge fam. Desmacidonidae. (5) *Euacasta porata* (Nilsson-Cantell): 4°17.5′S 55°51.5′E, 3–6 m, five specimens from *Haliclona* sp.; 5°24.80′S, 53°18.95′E, 20–25 m, three specimens from sponge fam. Haliclonidae; 12°00′N, 104°20′E, 5–7 m, two specimens from undetermined sponge. (6) *Euacasta sporillus* (Darwin): 5°30′S, 144°58′E, 18–21 m, three specimens from *Spongia* sp. (7) *Acasta spongites* Poli: 4°29.4′S, 54°54.8′E, 43 m, four specimens from *Dysidea* sp. (8) *Acasta flexuosa* Nilsson-Cantell: 22°N, 112°E, tidal zone, five specimens from *Dysidea* sp; 12°N, 104°20′E, three specimens from *Dysidea* sp. (9) *Acasta cyathus* Darwin 4°30.2′S, 55°01.2′E, 43 m, two specimens from sponge fam. Stellettidae; 4°17.5′S, 55°41.7′E, 2–3 m, two specimens from *Dysidea* sp.; 5°24.80′S, 53°18.95′E, 20–25 m, three specimens from undetermined sponge; 9°42.2′S, 61°04.2′E, 45 m, two specimens from sponge fam. Haliclonidae; 4°17.85′S, 55°52.3′E, 8–10 m, three specimens from sponge fam. Stellettidae; 12°56′N, 43°21′E, 21–24 m, one specimen from undetermined sponge. (10) *Acasta sulcata* Lamarck: 18°40.0′N, 107°02.0′E, 52 m, four specimens from *Gellius* sp.; 18°00′N, 110°00′E, tidal zone, five specimens from *Gellius* sp.; 17°55′N, 109°59′E, 50 m, four specimens from sponge fam. Myxillidae; 1°15.2′N, 103°45′E, tidal zone, three specimens from sponge fam. Myxillidae; 17°06′N, 39°36′E, 20 m, two specimens from undetermined sponge. (11) *Acasta crassa* Broch: 4°49.15′S, 53°20.0′E, 40 m, two specimens from *Agelas* sp. (12) *Acasta fenestrata* Darwin: 5°28′8″S, 145°50′6″E, 20 m, two specimens from *Haliclona* sp. (13) *Pectinoacasta pectinipes* (Pilsbry): 20°20′N, 107°18′E, 28 m, four specimens from sponge fam. Halichondriidae. Thirteen new species of sponge-inhabiting barnacles were discovered as well: (14) ***Archiacasta pustulata* sp. nov.:** 9°59.5′S, 62°10.1′E, 60 m, two specimens from *Spirasrella* sp. (15) ***Neoacasta planibasis* sp. nov.:** 12°13.2′S, 49°00.7′E, 2–3.5 m, five specimens from *Dysidea* sp.; 12°13.85′S, 49°09.55′E, 4–15 m, two specimens from sponge fam. Haliclonidae; 7°S, 113°E, tidal zone, five specimens from *Dysidea* sp. (16) *Euacasta abnormis* (Kolbasov) (Kolbasov, 1991): 31°00′N, 139°00.2′E, 300 m, four specimens from *Petrosia* sp. (17) *Euacasta tabachniki* (Kolbasov) (Kolbasov, 1990(a)): 4°30.8′–4°31.2′N, 112°55.7′–112°56.3′E, 152 m, two specimens from *Euplectella aspergillum.* (18) ***Acasta spongiteformis* sp. nov.:** 10°13.2′S, 62°13.7′E, 64 m, three specimens from

Poecilastra sp. (19) *Acasta rimiformis* Kolbasov (Kolbasov, 1991): 6°30.8′S, 146 51°.00′E, 12 m, five specimens from sponge fam. Axinellidae. (20) *Acasta infirma* Kolbasov (Kolbasov, 1992): 9°42.2′S, 61°04.2′, E, 45 m, three specimens from *Crella* sp. (21) *Acasta tzetlini* Kolbasov (Kolbasov, 1992): 13°32.4′S, 48°02.0′E, 4 m, three specimens from sponge fam. Axinellidae; 12°13.2′S, 49°00.7′E, 2–3.5 m, two specimens from sponge fam. Axinellidae, 12°15.7′S, 48°58.5′E, 2–12 m, four specimens from sponge fam Axinellidae. (22) *Acasta kolturi* Kolbasov (Kolbasov, 1991): 37°40′S, 150°00′E, 110 m, five specimens from *Coelosphaera* sp. (23) ***Acasta daedalusa* sp. nov.:** 5°24.80′S, 53°18.95′E, 20–25 m, four specimens from *Haliclona* sp. (24) *Acasta pertusa* Kolbasov (Kolbasov, 1990(b)): 17°08′N, 39°37′E, 39 m, 20 specimens from sponge fam. Haliclonidae. (25) *Pectinoacasta zevinae* (Kolbasov) (Kolbasov, 1991): 5°28′8″S. 145°50′6″E, 18 m, five specimens from *Haliclona* sp. (26) ***Membranobalanus acutus* sp. nov.:** 9°42.2′S, 61°04.2′E, 45 m, four specimens from *Petrosia* sp.

DESCRIPTIONS OF NEW SPECIES

Archiacasta pustulata sp. nov.

Material. Two specimens in *Spirastrella* sp.; 9°59.5′S, 62°10.1′E, 60 m.

Description. Shell conical and white, compartments separated by narrow radii; external surface of the parietes with numerous small projections; inner surface of the parietes without ribs; opercular orifice small, with smooth margin; sheath about $\frac{1}{2}$–$\frac{2}{3}$ of length of plate, covered by fine setae; carinolateral about $\frac{1}{5}$–$\frac{1}{4}$ of width of lateral.

Basis saucer-shaped, membranous.

Scutum elongated, without longitudinal striae, growth ridges with fine setae in the lower half of valve; articular ridge low; pits of adductor and depressor muscles rudimentary; adductor ridge feebly developed. Tergum with growth lines; spur rounded at its end, about $\frac{1}{2}$ of width of basal margin, hardly separated from basiscutal angle, spur furrow shallow; articular ridge feebly developed; crests of depressor muscles absent.

The armament of the anterior rami of III and IV pairs of cirri feebly developed.

Deposition of types. The holotype (N Mg 1120, Moscow) and one paratype are deposited in the Zoological Museum of Moscow State University.

Affinities. Arch. pustulata is similar to species of *Archiacasta* in having membranous basis (*Arch. membranacea*), but differs from these species by the presence of a small opercular orifice, rudimentary radii and numerous small projections on the external surface of the parietes.

Etymology. From Latin *pustulatus*—pustular.

Neoacasta planibasis sp. nov.

(Fig. 2)

Material. Five specimens in *Dysidea* sp. 12°13.2′S, 49°00.7′E, 2–3.5 m. Two specimens (including holotype) in sponge fam. Haliclonidae, 12°13.8′S, 49°09.55′E, 4–15 m. Five specimens in *Dysidea* sp., 7°S, 113°E, tidal zone.

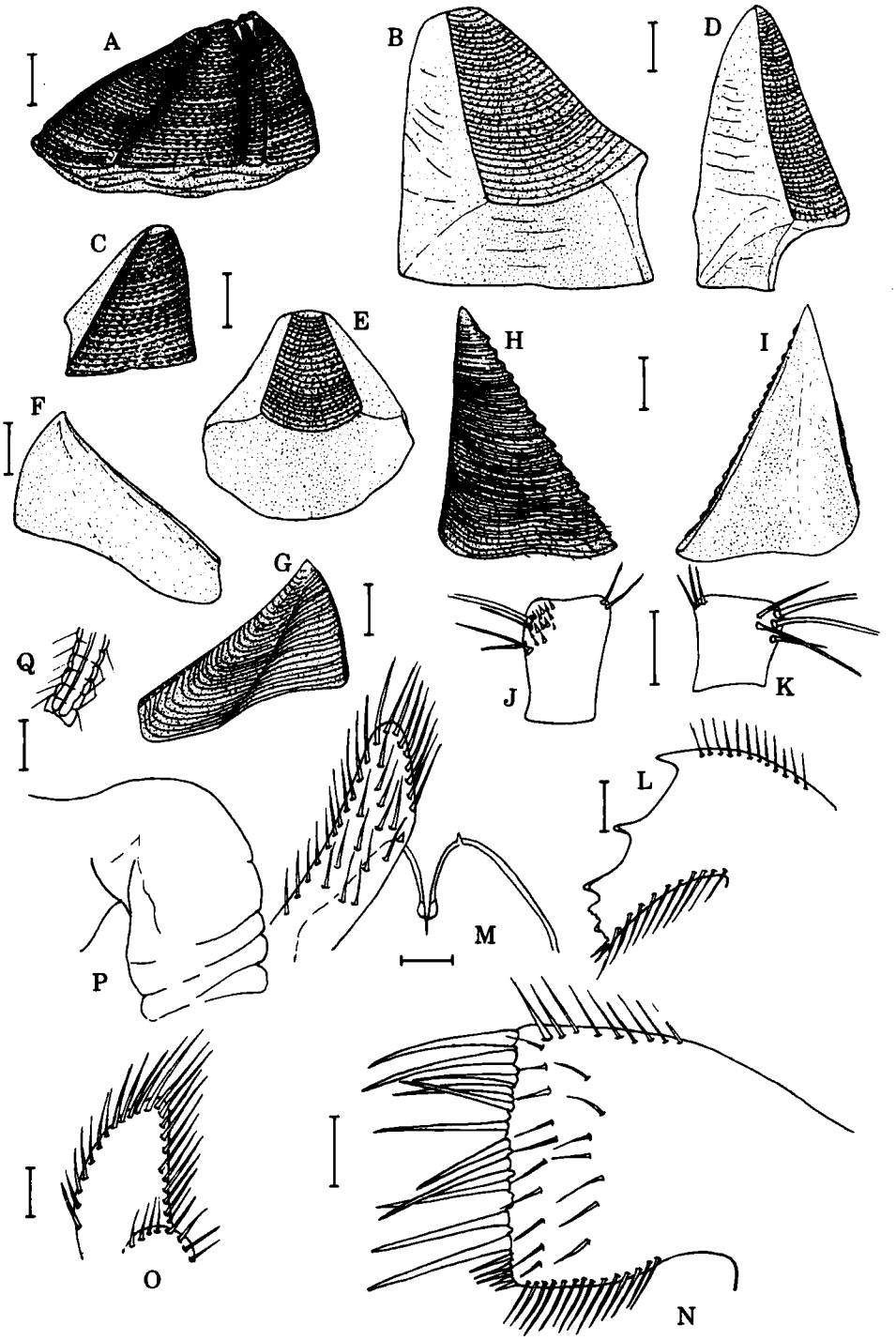


Figure 1. ***Archiacasta pustulata* sp. nov.**; 9°59.5'S., 62°10.1'E., 60 m, from *Spirastrella* sp.; A, shell, lateral view; B,C, lateral, internal and external view; D, carinolateral, internal view; E, rostrum, internal view; F,G, tergum, internal and external view; H,I, scutum, external and internal view; J, 5th segment of anterior ramus of fourth cirrus; K, 4th segment of anterior ramus of third cirrus; L, mandible; M, labrum, with left-hand palpus; N, maxilla I; O, maxilla II; P,Q,basis and end of penis. (Scale bars. A,C,E, 1 mm; B,D,F,G,H,I = 0.5 mm; J,K,N = 50 μ; L,M,O,P,Q = 100 μ).

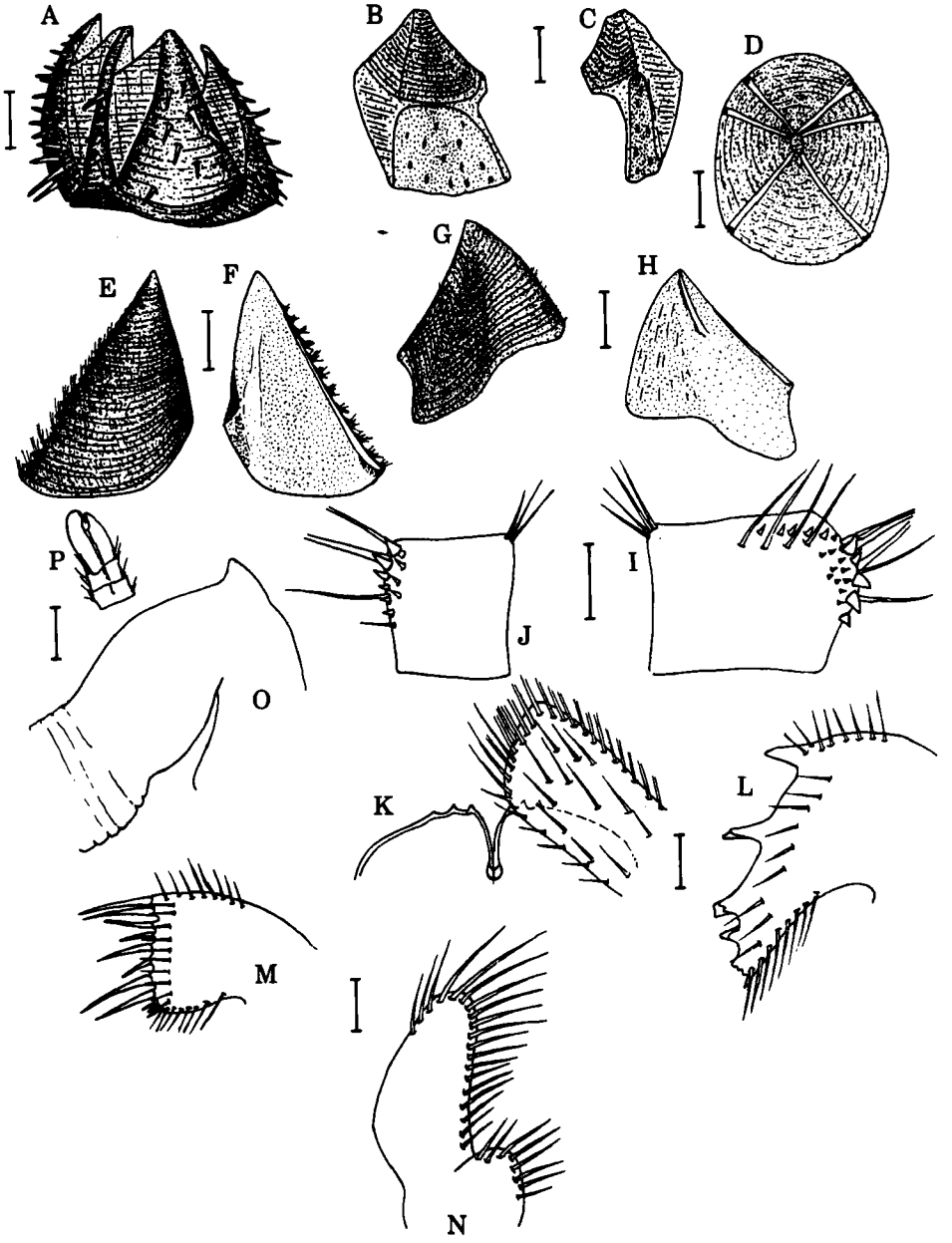


Figure 2. ***Neoacasta planibasis* sp. nov.**; 12°13.85'S., 49°09.55'E., 4–15 m, from sponge fam. Haliclonidae; A, shell, lateral view; B, lateral, internal view; C, carinolateral, internal view; D, basis, internal view; E,F, scutum, external and internal view; G,H, tergum, external and internal views; I, 5th segment of anterior ramus of third cirrus; J, 5th segment of anterior ramus of fourth cirrus; K, labrum, with right-hand palpus; L, mandible; M, maxilla I; N, maxilla II; O,P, basis and end of penis. (Scale bars. A–D = 1 mm; E–H = 0.5 mm; I, J = 50 μm; K–P = 100 μm.)

Description. Shell yellowish; opercular orifice large with toothed margin; radii normally developed; external surface of the parietes with noticeable and frequent thorns; inner surface of the parietes without longitudinal ribs, only with two lateral ribs; sheath about $\frac{1}{2}$ of length of plate; carinolateral about $\frac{1}{5}$–$\frac{1}{4}$ of width of lateral.

Basis calcareous, flat, saucer-shaped, inner surface with six radial ribs.

Scutum high, without longitudinal striae, growth ridges with fine setae; articular ridge not prominent, about $\frac{2}{3}$ of length of tergal margin and rather cut off at lower end; pit of depressor muscle shallow, but distinct; pit of adductor muscle absent; adductor ridge feebly developed.

Tergum triangular, with growth lines covered by fine setae; spur furrow rudimentary; spur about $\frac{1}{2}$ of width of valve, rounded at its end and separated from basiscutal angle; articular ridge developed, but not prominent; inner surface with fine longitudinal striae.

The armament of the anterior rami of III and IV pairs of cirri feebly developed.

Deposition of types. The holotype (N Mg 1122, Moscow) and two paratypes are deposited in the Zoological Museum of Moscow State University.

Affinities. This species is similar to *N. laevigata* (Gray) in having an identical structure of opercular valves, but differs from it in the presence of a flat basis and frequent thorns.

Etymology. From Latin *planus*—flat; *basis*—basis.

***Acasta spongiteformis* sp. nov.**

(Fig. 3)

Material. Three specimens in *Poecilastra* sp.; 10°13.2′S, 62°13.7′E, 64 m.

Description. Shell white, with small splits between its compartments; opercular orifice large with toothed margin; radii developed, with oblique summits; external surface of the parietes with sparse thorns; inner surface of the parieties with small basal ribs; sheath about $\frac{1}{2}$ of length of plate; carinolateral about $\frac{1}{4}$ of width of lateral.

Basis calcareous, cup-shaped, with smooth margin.

Scutum high, external surface with longitudinal striae; articular ridge about $\frac{1}{2}$ of length of tergal margin and rather prominent; pit of depressor muscle shallow, pit of adductor muscle rudimentary; adductor ridge feebly developed.

Tergum beak-shaped; spur furrow rudimentary; spur about $\frac{1}{2}$ of width of valve, rounded at the end and hardly separated from basiscutal angle; articular ridge developed, not prominent; inner surface smooth.

The armament of the anterior ramus of IV cirrus developed.

Deposition of types. The holotype (N Mg 1121, Moscow) and two paratypes are deposited in the Zoological Museum of Moscow State University.

Affinities. A. spongiteformis is morphologically similar to *A. spongites* Poli and *A. japonica* Pilsbry, but differs from them in having a wider tergal spur, strong developed armament of the anterior ramus of IV cirrus and developed basidorsal point of penis.

Etymology. This new species is named *spongiteformis* because it is similar to *A. spongites* Poli.

***Acasta daedalusa* sp. nov.**

(Fig. 4)

Material. Four specimens in *Haliclona* sp.; 5°24.80′S, 53°18.95′E, 20–25 m.

Description. Shell big, white and cylindrical, opercular orifice of average size, with toothed margin; radii developed, about $\frac{2}{3}$ of length of plates, not reaching

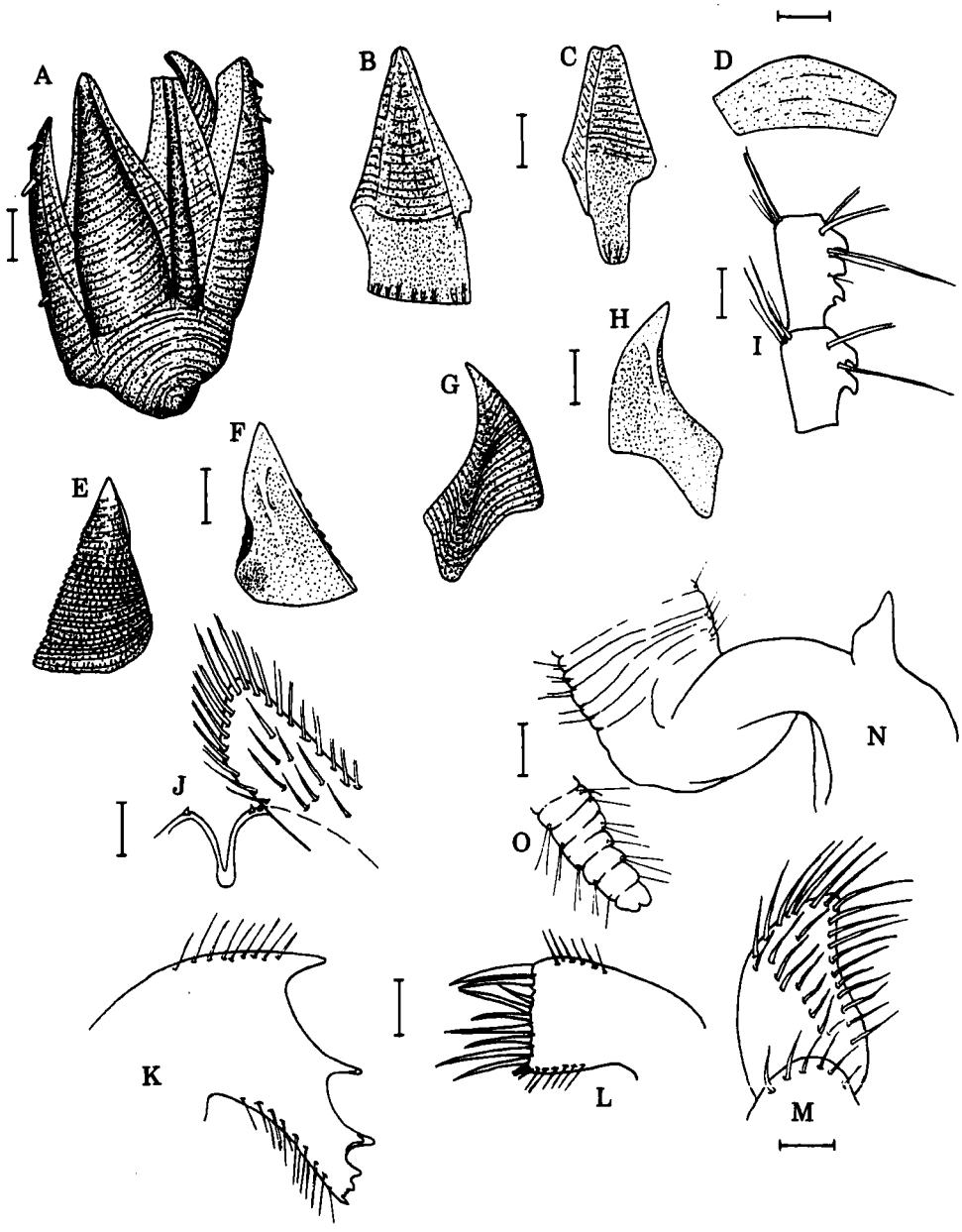


Figure 3. ***Acasta spongiteformis* sp. nov.**; 10°19.2'S., 62°13.7'E., 64 m, from *Poecillastra* sp.; A, shell, lateral view; B, lateral, internal view; C, carinolateral, internal view; D, margin of basis; E,F, scutum, external and internal view; G,H, tergum, external and internal view; I, 6th and 7th segments of anterior ramus of fourth cirrus; J, labrum, with right-hand palpus; K, mandible; L, maxilla I; M, maxilla II, N,O, basis and end of penis. (Scale bars. A–C, E–H = 1 mm; D = 0.5 mm; I–O = 100 μm).

the basal margin of plates; external surface of the parietes bears small and sparse projections; inner surface of the parietes smooth; sheath about $\frac{1}{3}$–$\frac{1}{2}$ of length of plate; all plates with basal tongue processes, which are especially well-developed in adult forms; carinolateral about $\frac{1}{4}$–$\frac{1}{3}$ of width of lateral.

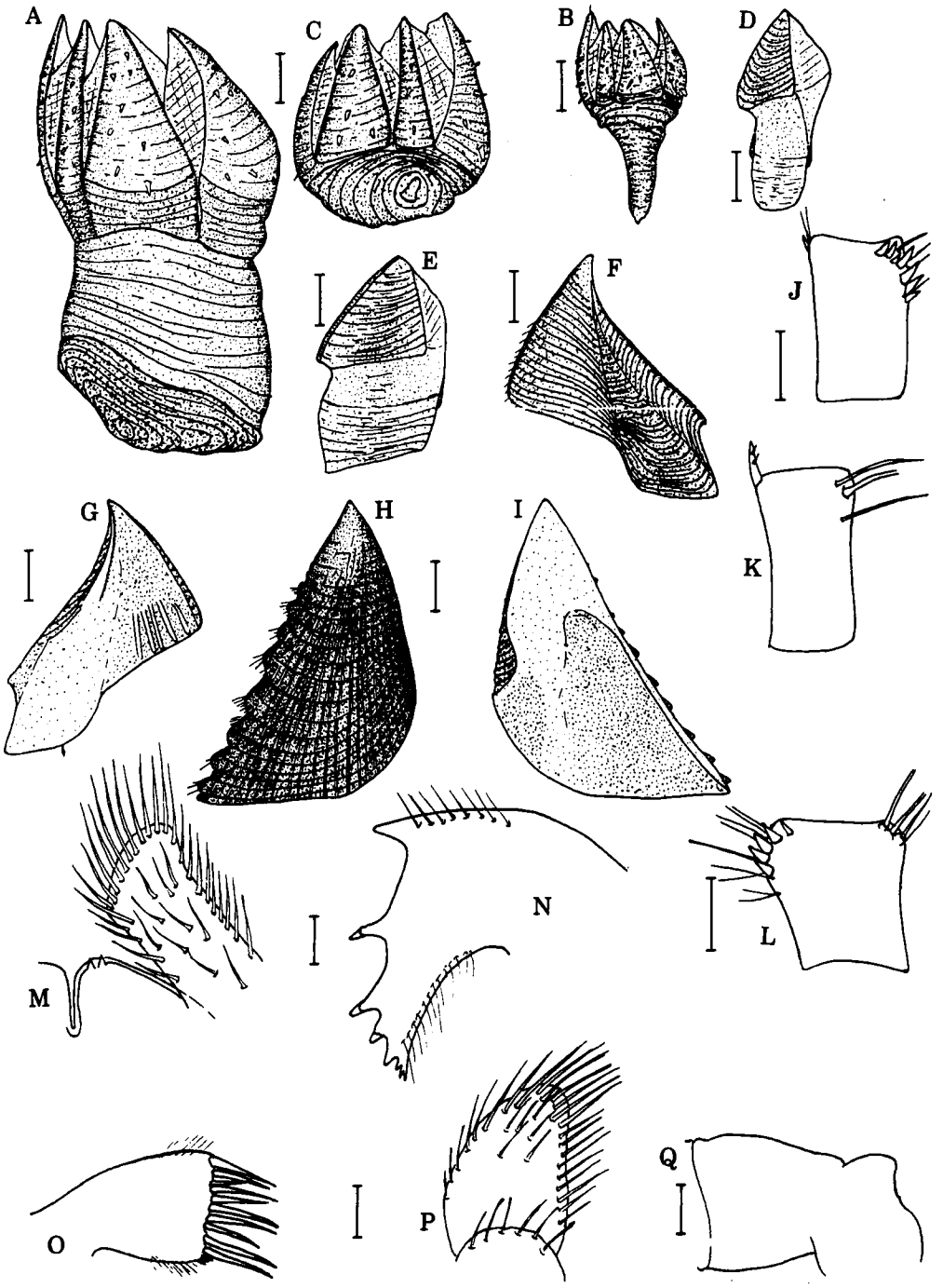


Figure 4. ***Acasta daedalusa* sp. nov.**; 5°24.80'S., 53°18.95'E., 20–25 m, from *Haliclona* sp.: A,B, shells of adult forms; C, shell of juvenile form; D, carinolateral, internal view; E, lateral, internal view, F,G, tergum, external and internal view; H,I, scutum, external and internal view; J,K, 6th segments of anterior and posterior rami of fourth cirrus; L, 7th segment of anterior ramus of third cirrus; M, labrum, with right-hand palpus; N, mandible; O, maxilla I; P, maxilla II; Q, basis of penis. All parts of shell and soft body belong to adult form (a). (Scale bars. A,C–E = 1 mm; B = 1.7 mm; F–I = 0.5 mm; J–L = 50 μm; M–Q = 100 μm).

Basis calcareous, very deep in adult forms, with smooth margin.

Scutum with noticeable longitudinal striae and covered by fine setae externally; articular ridge about $\frac{2}{3}$ of length of tergal margin, not prominent; pits of adductor and depressor muscles and adductor ridge rudimentary.

Tergum break-shaped; externally covered by fine setae on carinal margin; spur about 2/5 of width of basal margin, truncated at the end and separated from basiscutal angle; spur furrow developed, of average depth; articular ridge clear, not prominent; inner surface bears 4–5 clear crests of depressor muscle.

The armament of the anterior rami of III and IV cirri feebly developed.

Deposition of types. The holotype (N Mg 1118, Moscow) and two paratypes are deposited in the Zoological Museum of Moscow State University.

Affinities. This species is similar to *A. koltuni* Kolbasov (Kolbasov, 1991); both these species have a very deep basis, but *A. daedalusa* differs from *A. koltuni* in having the smooth inner surface of the parietes, tongue processes of plates and feebly developed armanent of cirri.

Etymology. From Latin *daedalus*—quaint.

***Membranobalanus acutus* sp. nov.**

(Fig. 5)

Material. Four specimens in *Petrosia* sp.; 9°42.2′S, 61°04.2′E, 46 m.

Description. Shell whitish and rather elongated; opercular orifice small with toothed margin; the tips of the parietes sharp and curved inwards; radii developed, with oblique summits; external surface of the parietes with small thorns; inner surface of the parietes smooth; the basal margins of laterals uneven; sheath about $\frac{1}{2}$ of length of plate; carinolateral about $\frac{1}{7}$–$\frac{1}{6}$ of width of lateral.

Basis membranous and bent inside.

Scutum elongated, with longitudinal ribs externally; articular ridge low and hardly prominent, about $\frac{2}{3}$ of length of tergal margin; pits of adductor and depressor muscles rudimentary; adductor ridge feebly developed.

Tergum with beak-shaped tip and clear growth ridges; spur feebly developed, truncated at the end, about $\frac{2}{3}$ of width of basal margin and separated from basiscutal angle; spur furrow rudimentary; articular ridge feebly developed; inner surface with fine longitudinal striae.

The armament of the anterior rami of III and IV cirri feebly developed.

Deposition of types. The holotype (N Mg 1123, Moscow) and two paratypes are deposited in the Zoological Museum of Moscow State University.

Affinities. M. acutus is similar to species of *Membranobalanus* in having the membranous basis, uneven basal margin of laterals, and character of the armament of the fourth cirri. It differs from *M. declivis* (Darwin), *M. orcutti* (Pilsbry), *M. koreanus* (Kim et Kim), *M. branchialis* (Rosell) and *M. longirostrum* (Hoek) by the presence of a small rostrum and by the peculiar structure of the opercular valves, and from *M. cuneiformis* (Hiro), *M. robinae* (Van Syoc) and others in having a feebly developed armanent of the IV cirri.

Etymology. From Latin *acutus*—sharp.

THE SYSTEMATICS OF THE SPONGE-INHABITING BARNACLES

The species of the genus *Acasta (sensu lato)* are defined in the following accounts: Barnard, 1924; Broch, 1922, 1932, 1947; Foster, 1981; Gravier, 1921;

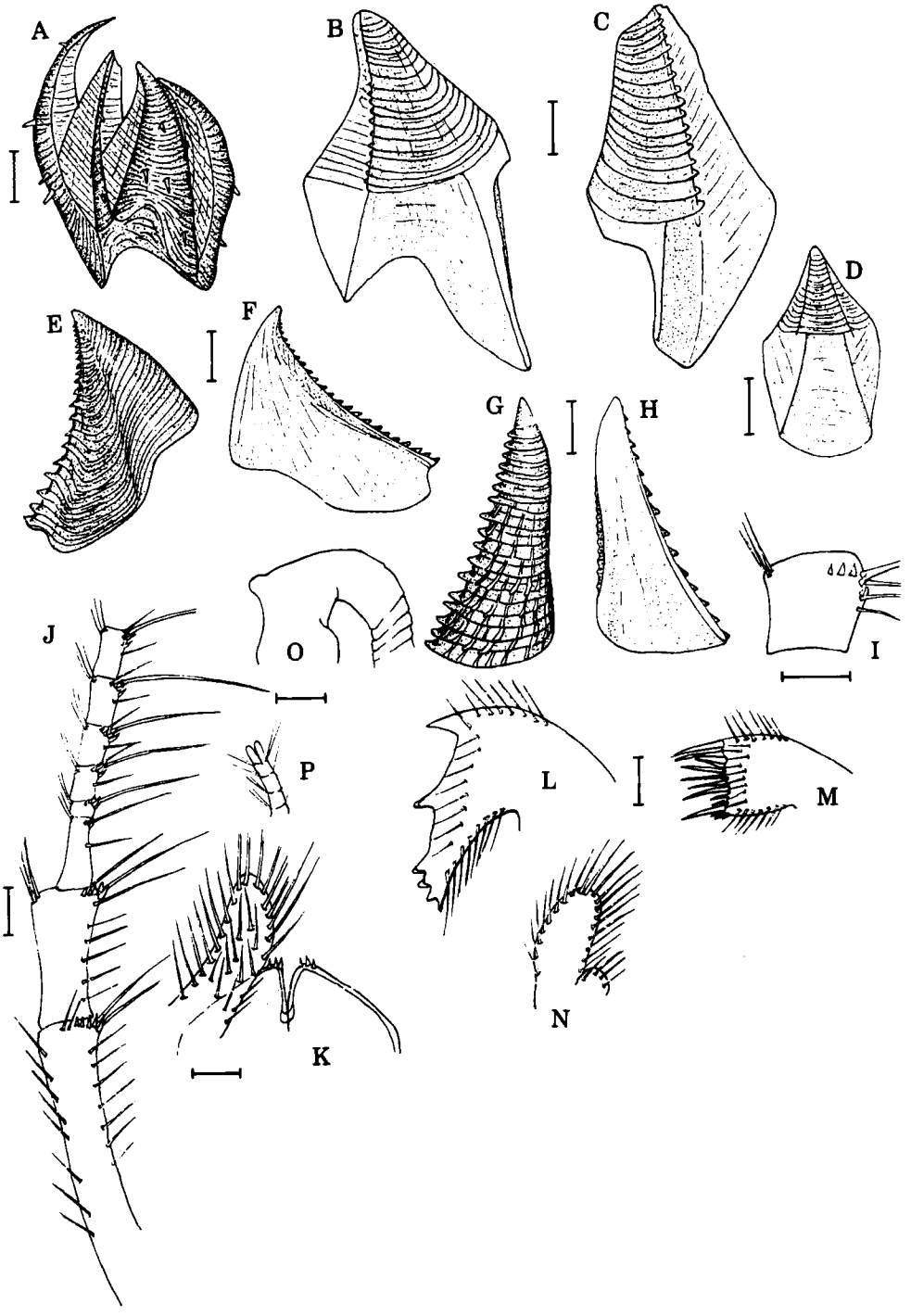
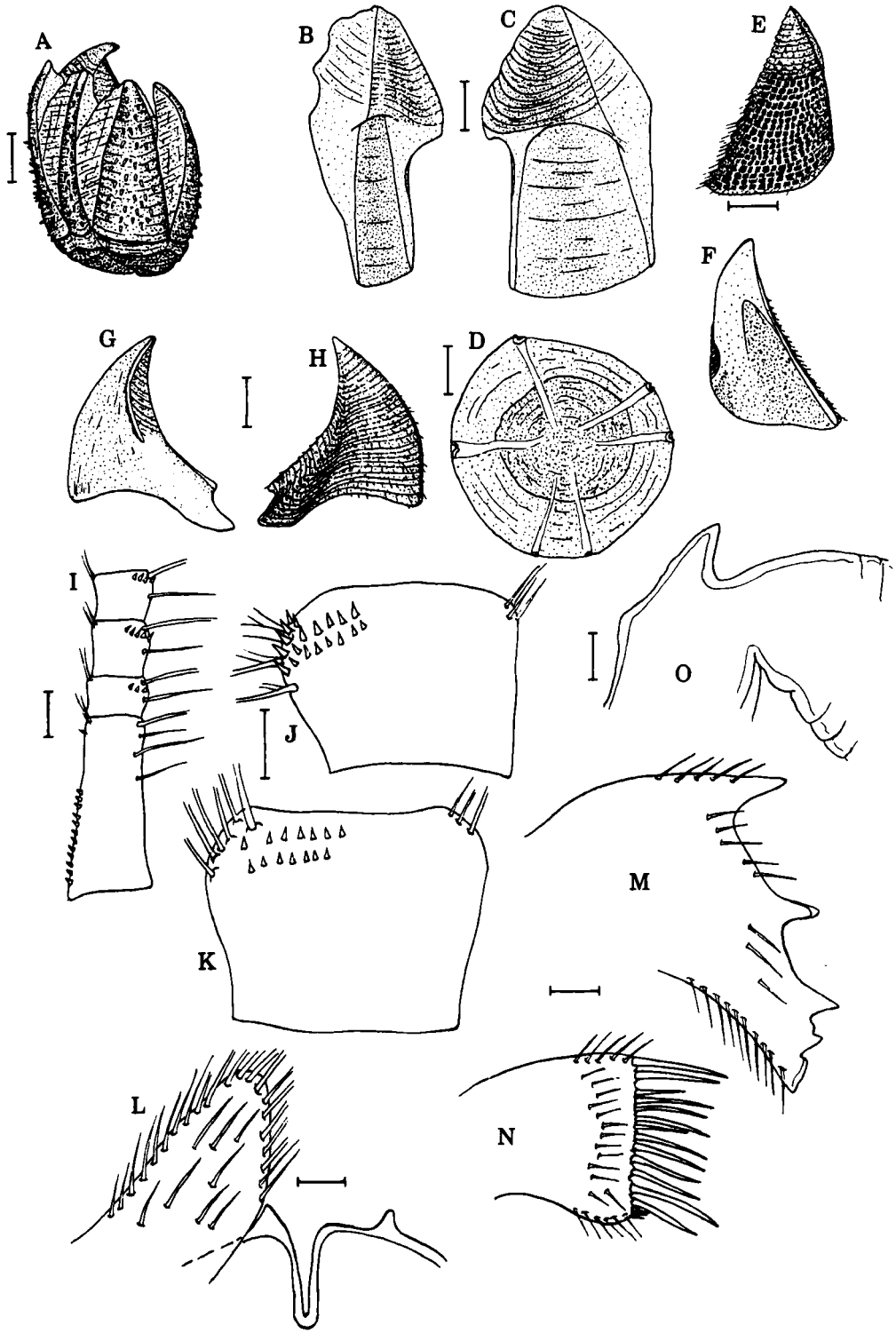


Figure 5. ***Membranobalanus acutus* sp. nov.**; 9°42.2'S., 61°04.2'E., 45 m, from *Petrosia* sp.: A, shell, lateral view; B, lateral, internal view; C, carinolateral, internal view; D, rostrum, internal view; E,F, tergum, external and internal view; G,H, scutum, external and internal view; I, 7th segment of anterior ramus of third cirrus; J, protopodit and basal segments of anterior ramus of fourth cirrus; K, labrum, with left-hand palpus; L, mandible; M, maxilla I; N, maxilla II; O,P, basis and end of penis. (Scale bars. A,D = 1 mm; B,C,E–H = 0.5 mm; I = 50 μm; J–P = 100 μm).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Gruvel, 1902; Hiro, 1931, 1933, 1936, 1937a, 1937b, 1939; Kolbasov, 1990a, 1990b, 1991, 1992; Krüger, 1911, 1914; Nilsson-Cantell, 1921, 1938; Pilsbry, 1911, 1916; Ren, 1984, 1989; Rosell, 1970, 1972; Weltner, 1887; Utinomi, 1959, 1962, 1967; Zullo & Standing, 1983.

In the present account, five groups of species have been distinguished on the basis of important morphological characters and redefined as five genera; *Archiacasta, Neoacasta, Euacasta, Acasta (sensu stricto)* and *Pectinoacasta.*

Archiacasta gen. nov.

Archiacasta includes species which share a number of generalized characters: *A. membranacea* (Barnard), *A. tenuivalvata* (Broch), *A. fragilis* (Ren), *A. hainanensis* (Ren), *A. spinifera* (Utinomi), *A. spinetergum* (Broch), *A. pustulata* sp. nov. (Fig. 1) and probably *A. praerupta* (Foster) and *A. tulipa* (Hiro). The typical species is *Archiacasta membranacea.* In these species the basis is membranous and either flat, saucer-shaped (*A. membranacea, A. tenuivalvata, A. pustulata*) or convex cup-shaped (*A. hainanensis, A. fragilis*), or calcareous but flat (*A. spinifera, A. spinitergum, A. tulipa, A. praerupta*). Cirral armature is feebly developed as small spines on the frontal surfaces of the anterior rami or cirri III or IV (absent in *A. spinifera*). Some species (*A. membranacea, A. fragilis*) have a latticed scutum. In others (*A. praerupta, A. spinifera*) this is reduced to radial striae. In *A. tulipa, A. pustulata* and *A. tenuivalvata* the surface of the scutum is without radial striae (Fig. 1). All species of *Archiacasta* have a smooth margin on the basis and smooth internal surfaces on the wall plates (Fig. 1), so that the basis and wall do not interlock. *A. praerupta* and *A. tulipa* are exceptional in having weakly developed longitudinal ribs on the internal surface of the wall plates near the basal margin. The carinolaterals have normally developed parietes. Externally, the wall surface of all species bears calcareous thorns embedded on the host tissue.

Neoacasta gen. nov.

Neoacasta includes *N. scuticosta* (Weltner), *N. planibasis* sp.nov. (Fig. 2), *N. glans* (Lamarck) (Fig. 6), *N. laevigata* (Gray), *N. coriobasis* (Broch) and probably *N. fossata* (Barnard). The typical species is *N. glans.* In these species the basis is cup-shaped (rarely, saucer-shaped: *N. scuticosta, N. planibasis* Fig. 2)), with six internal radial ribs extended marginally as six teeth. The internal surface of the wall plates is smooth, each plate having two marginal ribs. In *N. fossata,* these surfaces also bear some longitudinal ribs. The carinolaterals have normally developed parietes. The opercular valves are covered with setae. Cirral armature is feebly developed, as small thorns on the distal corners of the segments of the anterior ramus of cirrus III and sometimes cirrus IV. One species (*N. glans* (Fig. 6F) has a latticed scutum. In others (*N. scuticosta, N. coriobasis*) this is reduced to radial striae. In *N. laevigata* and *N. planibasis* (Fig. 2E, F) the surface

Figure 6. *Neoacasta glans.* (Lamarck); 5°24.80'S., 53°41.1'E., 12–13 m, from sponge fam. Axinellidae; A, shell, lateral view; B, carinolateral, internal view; C, lateral, internal view; D, basis, internal view; E,F, scutum, external and internal view; G,H, tergum, internal and external view; I, basal segments of anterior ramus of fourth cirrus; J,K, 7th segments of anterior and posterior rami of third cirrus; L, labrum, with left-hand palpus; M, mandible; N, maxilla I; O, basis of penis. (Scale bars. A = 1.7 mm; B–H = 1 mm; I,L–0 = 100 μm; J,K = 50 μm).

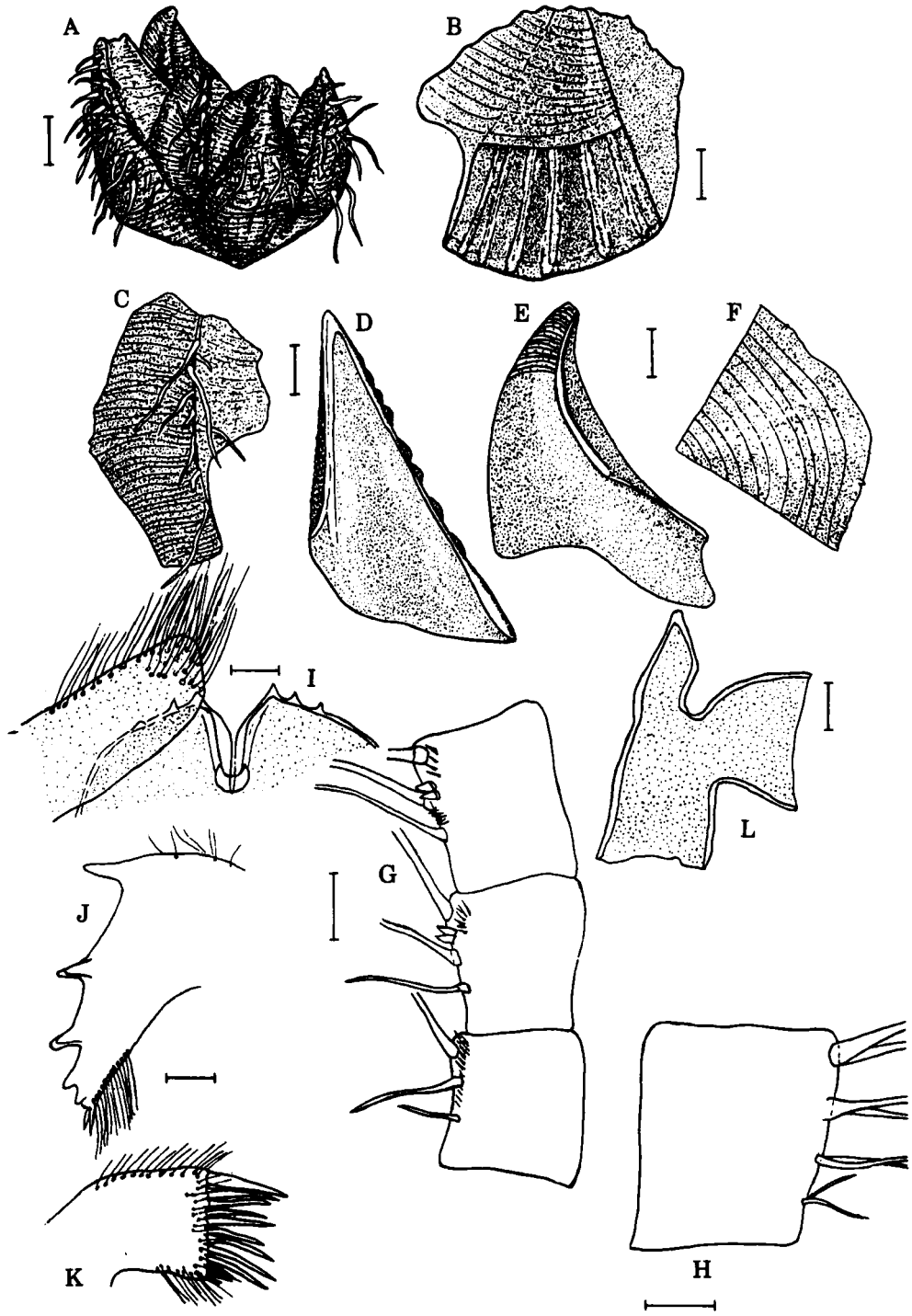


Figure 7. *Euacasta tabachniki* (Kolbasov); 4°31.2'N, 112°55.7'E, 152 m, from *Euplectella aspergillum;* A, shell, lateral view; B, lateral, internal view; C, carinolateral, external view; D, scutum, internal view; E, tergum, internal view; F, part of basis, internal view; G, 3rd, 4th and 5th segments of anterior ramus of fourth cirrus; H, 5th segment of fifth cirrus; I, labrum, with left-hand palpus; J, mandible, K, maxilla I; I, basis of penis. (Scale bars. A = 1 mm; B–F = 0.5 mm; G = 50 μm: H = 25 μm; I–L = 100 μm).

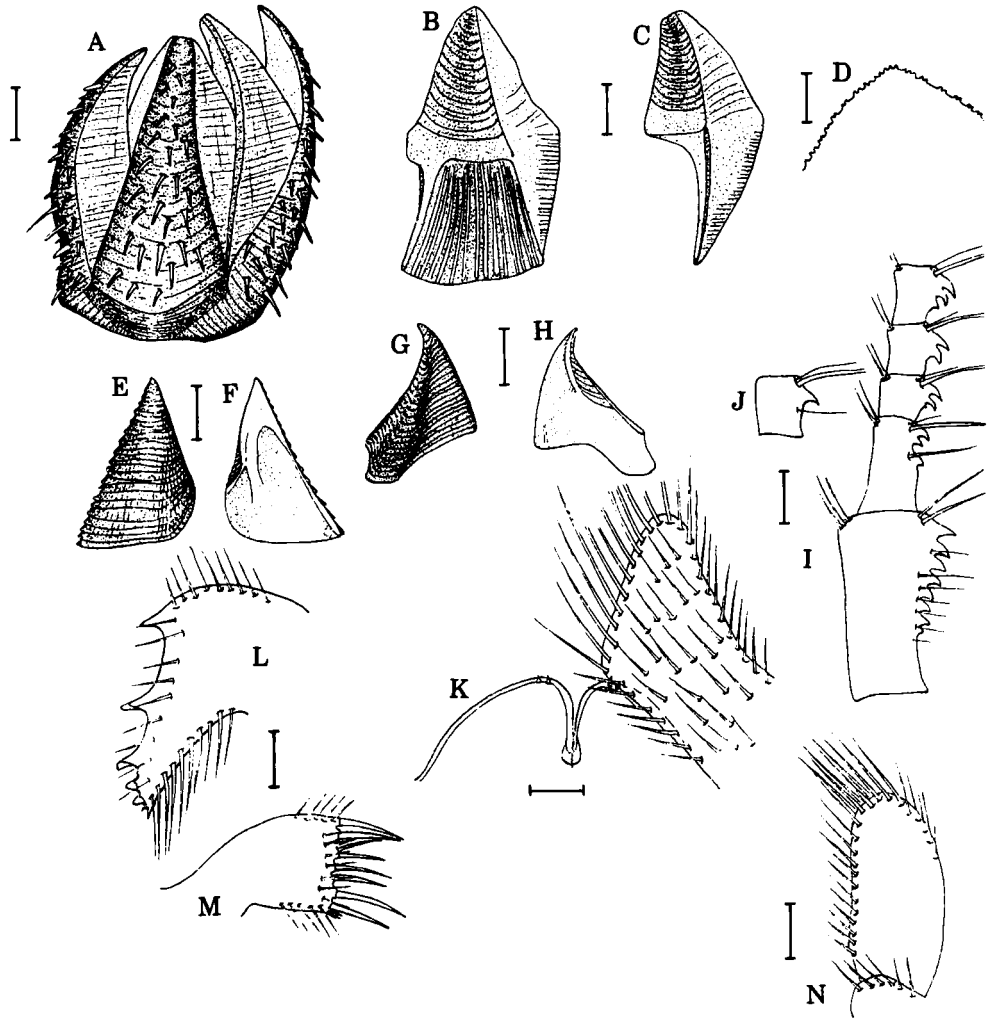
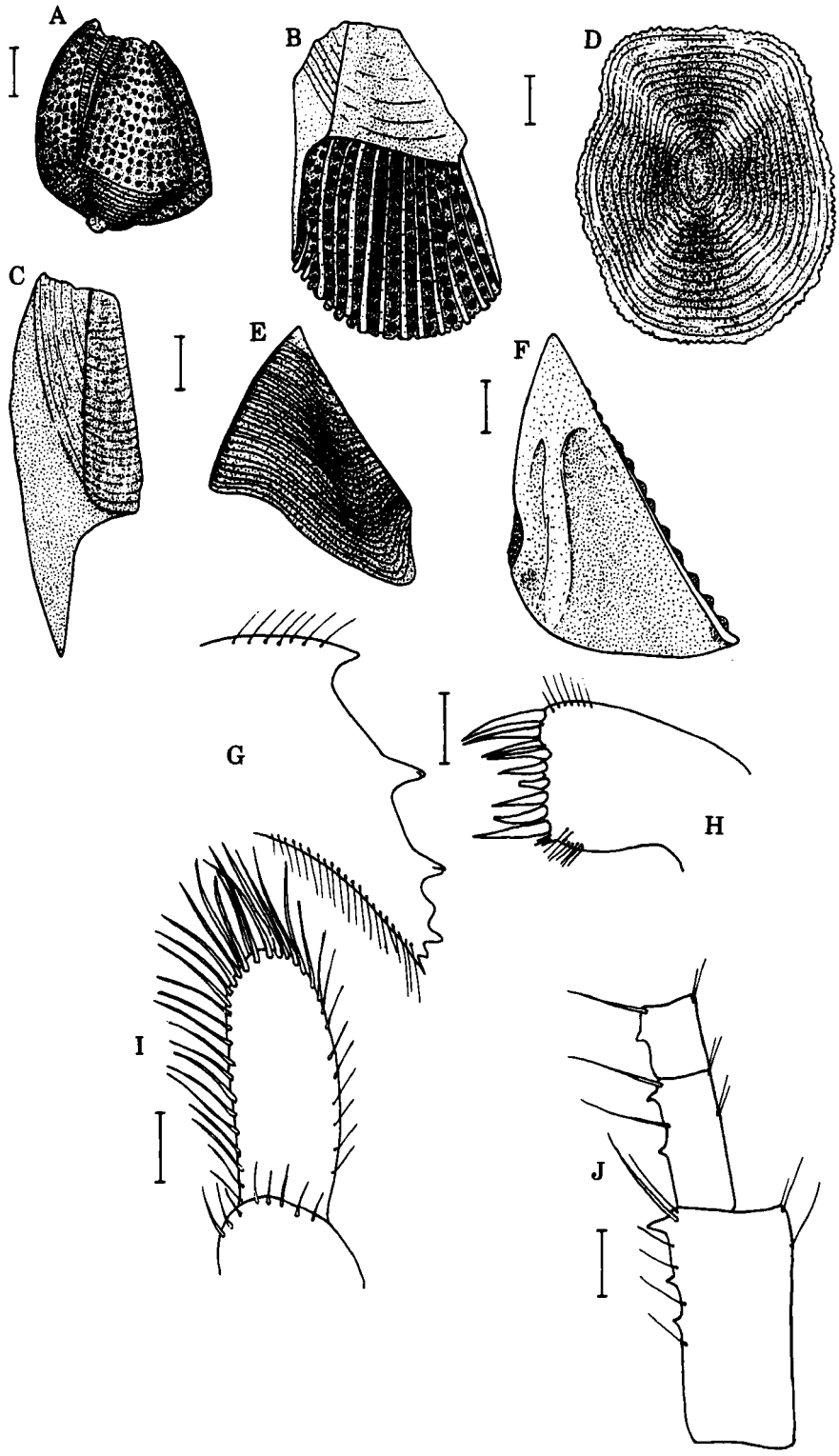


Figure 8. *Euacasta dofleini* (Krüger); 4°18.05'S., 5°45.0'E., 11 m, from sponge fam. Stellettidae: A, shell, lateral view; B, lateral, internal view; C, carinolateral, internal view; D, margin of basis; E,F, scutum, external and internal view; G,H, tergum, external and internal view; I, basipodit and basal segments of anterior ramus of fourth cirrus; J, 6th segment of anterior ramus of fifth cirrus; K, labrum, with right-hand palpus; L, mandible; M, maxilla I; N, maxilla II. (Scale bars. A–H = 1 mm; I–N = 100 μm).

of the scutum is without radial striae. The penis has a well developed basidorsal point.

Euacasta gen. nov.

Euacasta includes *E. ctenodentia* (Rosell), *E. tabachniki* (Kolbasov) (Fig. 7), *E. dofleini* (Krüger) (Fig. 8), *E. zuiho* (Hiro), E. aculeata (Nilsson-Cantell), *E. porata* (Nilsson-Cantell), *E. sporillus* (Darwin) (Fig. 9), *E. abnormis* (Kolbasov), *E. antipathidis* (Broch) and *E. microforamina* (Rosell). The typical species is *E. dofleini*. In these species the carinolaterals have rudimentary parietes, as a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narrow strip separating radius from ala (Fig. 7), so that the wall appears to consist of four plates. The basis is quadrangular, with four radial furrows, and may be flat, saucer-shaped or cup-shaped. The margin of the basis often bears small teeth. Cirral armature is well developed as large, curved hooks on the frontal margins of the segments of the anterior rami and basipods of cirri IV and sometimes V (Fig. 8). These hooks are absent in *E. tabachniki* (Fig. 7) from *Euplectella aspergillum* (Class Hexactinellida) and *E. abnormis* from *Petrosia* (Class Demospongiae). Some species have a scutum with radial striae (Fig. 8). In others (*E. aculeata, E. tabachniki* and *E. sporillus*) the surface of the scutum is without radial striae. The wall plates have internal longitudinal ribs, except in *E. abnormis*, and carry long, worm-shaped, empty processes or thorns externally, except in *E. sporillus* (Fig. 8).

Acasta Leach *(s. s.)*

Twenty-seven species have been retained in the genus *Acasta*. They are: *A. cyathus* Darwin (= *A. madagascarensis* Ren) (Fig. 13), *A. spongites* Poli, *A. japonica* Pilsbry, *A. spongiteformis* sp. nov. (Fig. 3), *A. flexuosa* Nilsson-Cantell, *A. conica* Hoek, *A. alba* Barnard, *A. sulcata* Lamarck (= *A. serrata* Hiro, *A. sulcata spinosa* Daniel, *A. sulcata anchoris* Barnard) (Fig. 10), *A. semota* Hiro, *A. denticulata* Hiro, *A. umitosaka* Utinomi, *A. idiopoma* Pilsbry, *A. striata* Gruvel, *A. crassa* Broch, *A. foraminifera* Broch, *A. armata* Gravier (= *A. sinica* Ren), *A. daedalusa* sp. nov. *A. tzetlini* Kolbasov (Fig. 11), *A. fenestrata* Darwin (Fig. 12), *A. rimiformis* Kolbasov, *A. infirma* Kolbasov, *A. koltuni* Kolbasov, (Fig. 4), *A. pertusa* Kolbasov, *A. echinata* Hiro, *A. hirsuta* Broch and *A. purpurata* Darwin.

The typical species is *A. spongites*. These species exhibit much morphological diversity, but share a number of distinctive characters. The basis is deeply cup-shaped (e.g. *A. daedalusa*, Fig. 4), rarely flat (*A. cyathus*, Fig. 13) and has a circular margin which often bears small teeth. The internal surface of the basis is smooth, without six radial ribs. The wall plates usually have longitudinal internal ribs. In some species, the wall plates are separated by splits (Fig. 11) or windows (Fig. 12) covered by a delicate membrane. The carinolaterals are developed normally. Some species have a scutum with radial striae (Figs. 3, 13). In others the surface of the scutum is without radial striae (*A. crassa, A. flexuosa, A. koltuni*). The cirral armature is variable, the segments of the anterior ramus of cirrus IV either bearing hooks or thorns (*A. sulcata*, Fig. 10; *A. daedalusa*, Fig. 4) or lacking them (*A. fenestrata, A. crassa*).

Pectinoacasta gen. nov.

Pectinoacasta includes *P. pectinipes* (Pilsbry) (Fig. 14), *P. angusticalcar* (Broch), *P. sculpturata* (Broch), *P. cancellorum* (Hiro), and *P. zevinae* (Kolbasov) (Fig. 15). The typical species is *P. pectinipes*. The majority of species have splits between the wall plates. Externally, these plates bear calcareous thorns. The scutum is latticed or

Figure 9. *Euacasta sporillus* (Darwin); 5°30'S., 144°58'E., 18–21 m, from Spongia sp.: A, shell, lateral view; B, lateral, internal view; C, carinolateral, internal view; D, basis, internal view; E, tergum, external view; F, scutum, internal view; G, mandible; H, maxilla I; I, maxilla II; J, basipodit and basal segments of anterior ramus of fourth cirrus. (Scale bars. A = 1 mm; B–F = 0.5 mm; G–J = 50 μm).

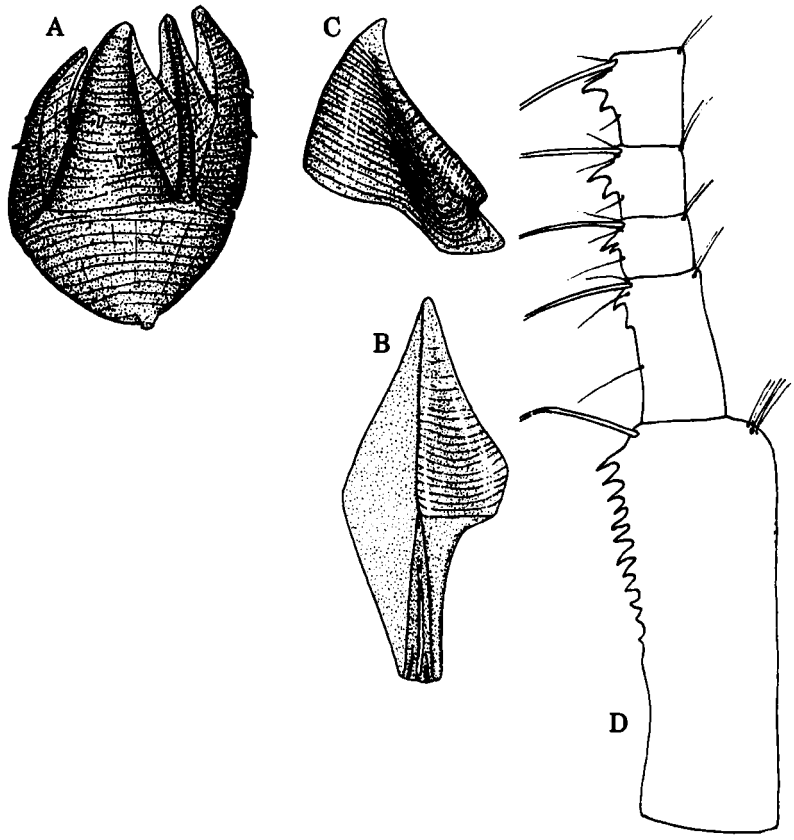


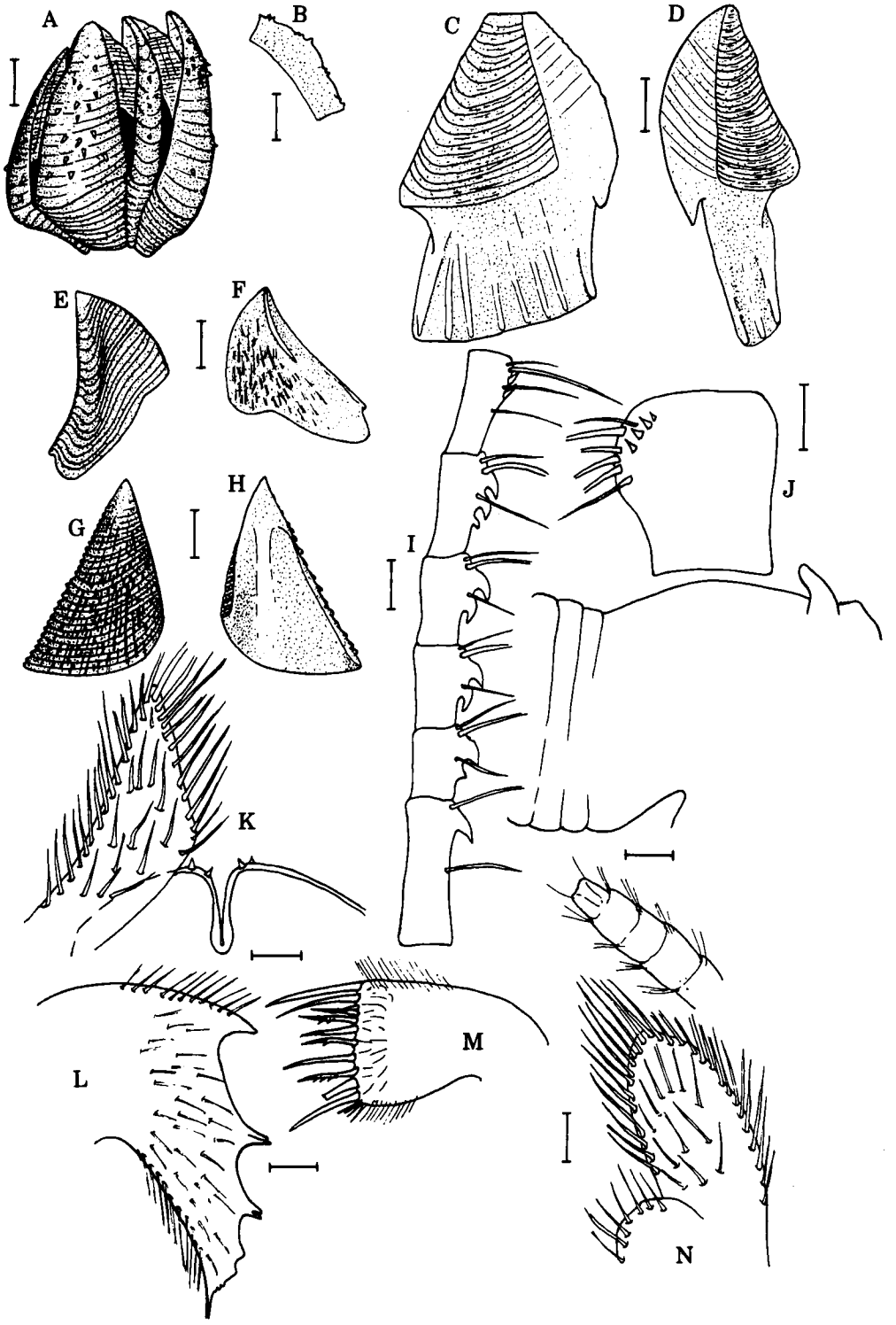
Figure 10. *Acasta sulcata* Lamarck; 18°40.0'N., 107°02.0'E., 52 m, from *Gellius* sp.: A, shell, lateral view; B, carinolateral, internal view; C, tergum, external view; D, basipodit and basal segments of anterior ramus of fourth cirrus. (Scale bars. A = 1 mm; B,C = 0.5 mm; D = 50 μm).

has radial striae (Fig. 14). The tergum is also latticed (*P. pectinipes*, Fig. 14) or has radial striae (*P. zevinae*, Fig. 15, *P. angusticalcar*) and has a narrow spur and a deep spur furrow (except in *P. zevinae*). The wall plates usually have longitudinal internal ribs. The carinolaterals have normally developed parietes. The anterior rami of the fourth cirri carry a well developed armature of curved hooks (except in *P. zevinae*, which has small thorns on the segments of the anterior ramus of cirrus IV).

Acastinae subfam. nov.

The five genera defined above share a number of characteristics in which they differ from all other members of the family Archaeobalanidae as defined by

Figure 11. ***Acasta tzetlini* sp. nov.**; 13°32'4"S., 48°02'0"E., 4 m, from sponge fam. Axinellidae: A, shell, lateral view; B, margin of basis; C, lateral, internal view; D, carinolateral, internal view; E,F, tergum, external and internal view; G,H, scutum, external and internal view; I, basal segments of anterior ramus of fourth cirrus; J, 5th segment of anterior ramus of third cirrus; K, labrum, with left-hand palpus; L, mandible; M, maxilla I; N, maxilla II, O,P, basis and end of penis. (Scale bars. A = 1.7 mm; B–H = 1 mm; I,K–P = 100 μm; J = 50 μm).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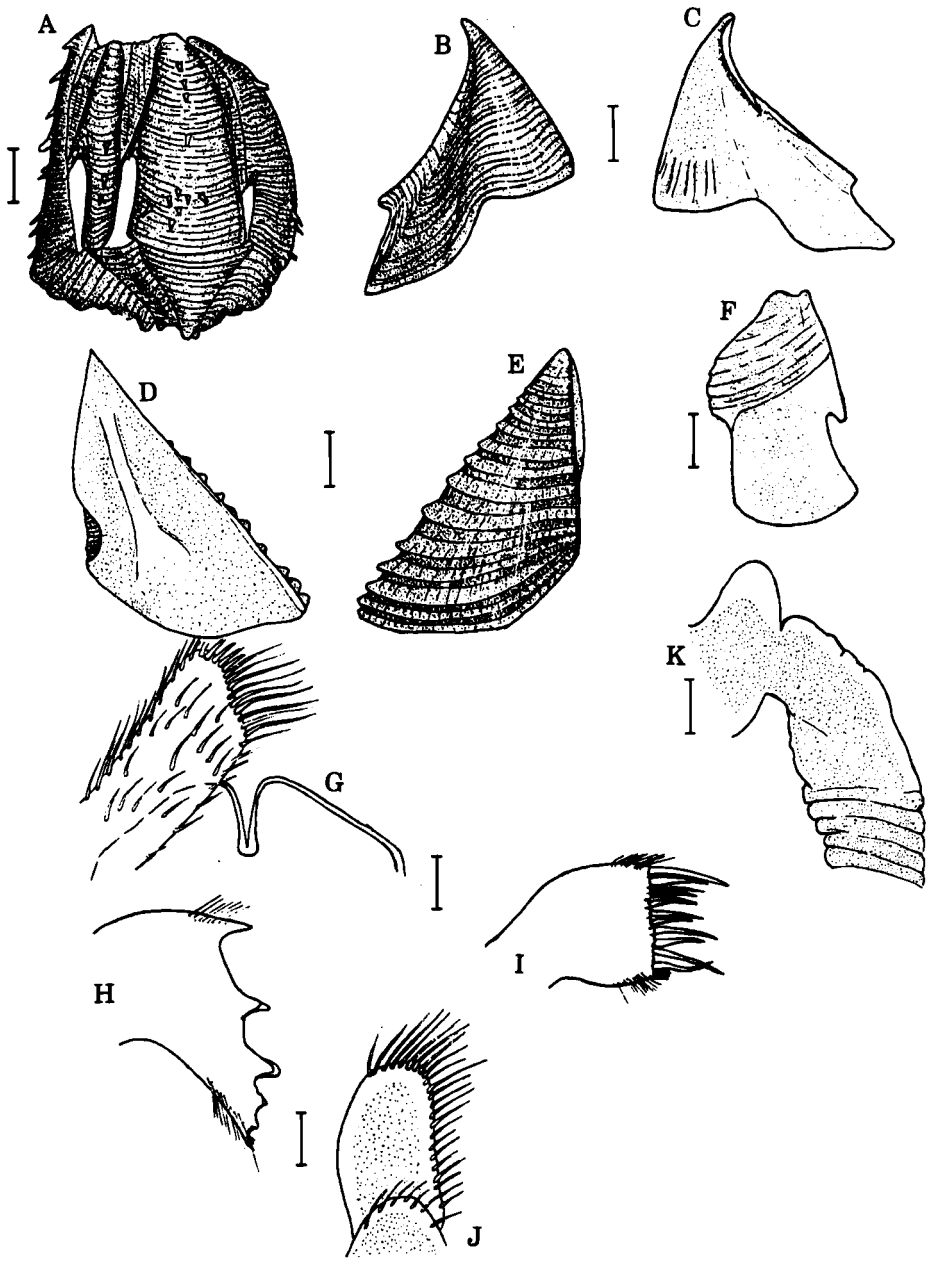


Figure 12. *Acasta fenestrata* Darwin; 5°28'8"S., 145°50'6"E., 20 m, from *Haliclona* sp.: A, shell, lateral view; B,C, tergum, external and internal view; D,E, scutum, internal and external view; F, lateral, internal view; G, labrum, with left-hand palpus; H, mandible; I, maxilla I; J, maxilla II; K, basis of penis. (Scale bars. A,F = 1 mm; B–E = 0.5 mm; G–K = 100 μm).

Newman & Ross (1976). These are the six solid wall plates; solid radii; calcareous, rarely membranous, basis, cup-shaped, rarely saucer-shaped or flat; and segments of anterior rami of cirri III and IV bearing hooks or thorns, rarely absent. Almost all species of acastines inhabit sponges.

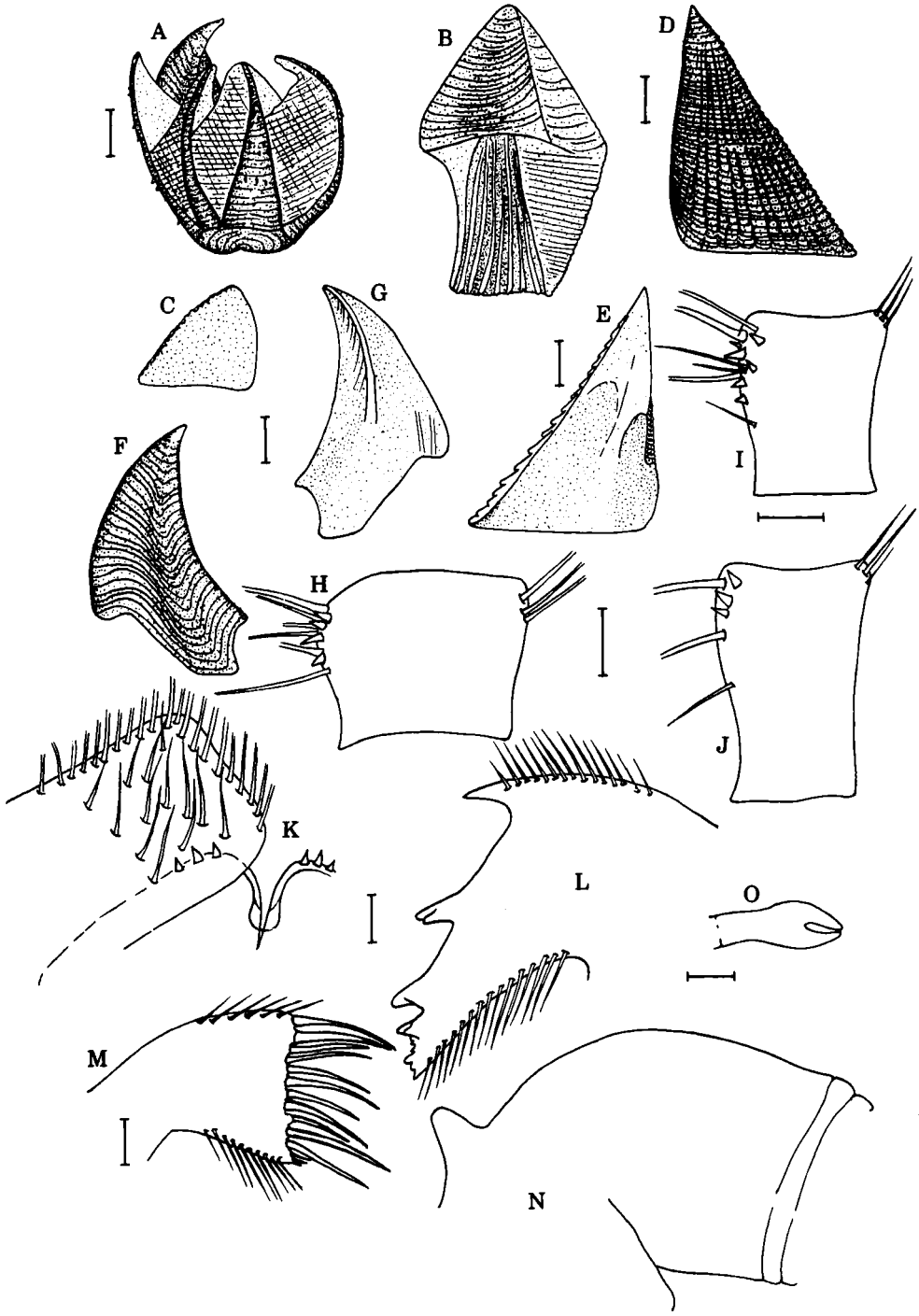
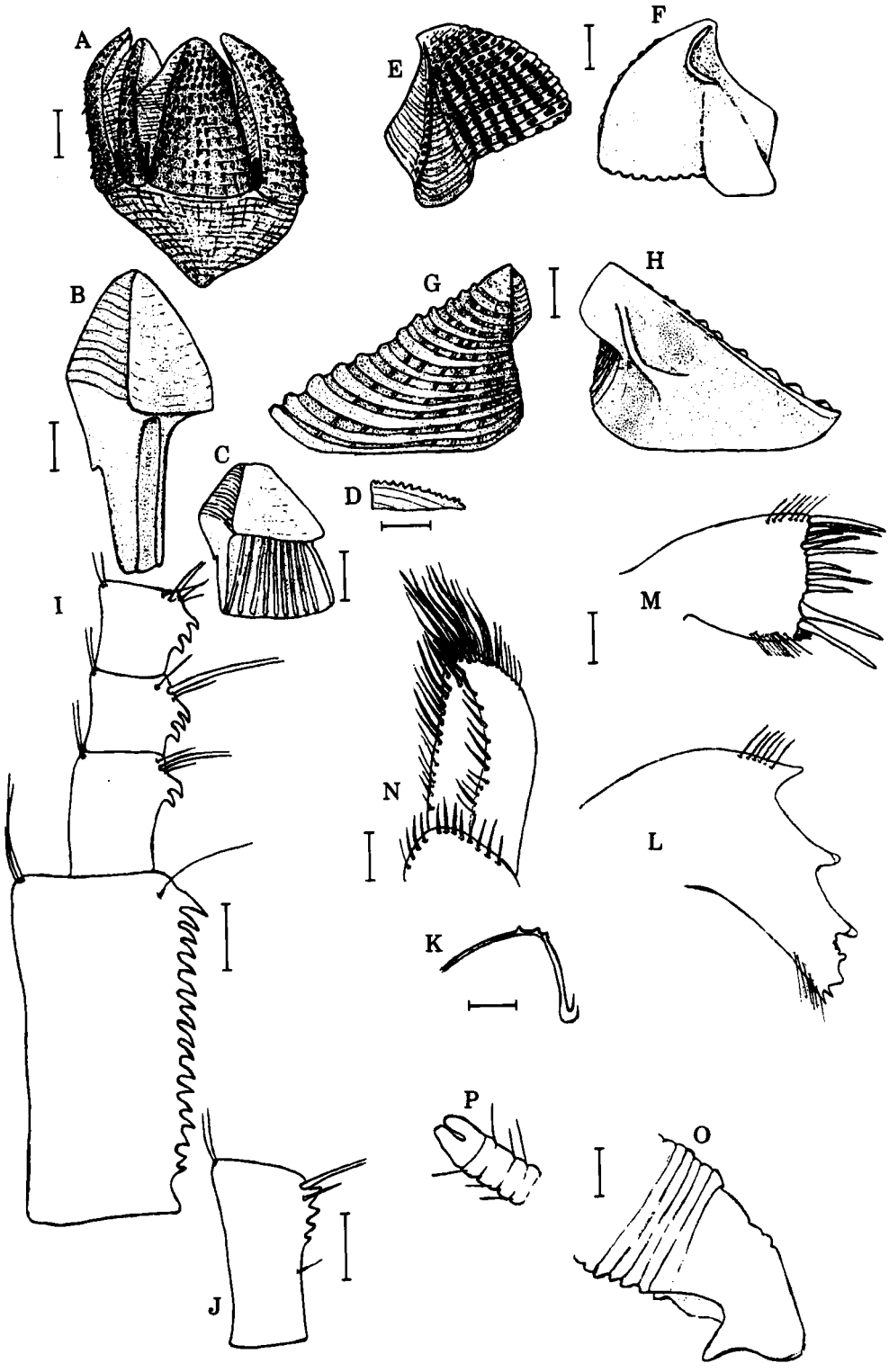


Figure 13. *Acasta cyathus* Darwin; 4°17.5'S., 55°41.7'E., 2–3 m, from *Dysidea* sp.: A, shell, lateral view; B, lateral, internal view; C, part of basis, internal view; D,E, scutum, external and internal view; F,G, tergum, external and internal view; H, 6th segment of anterior ramus of third cirrus; I,J, 8th and 7th segments of anterior and posterior rami of fourth cirrus; K, labrum, with left-hand palpus; L, mandible; M, maxilla I; N,O, basis and end of penis. (Scale bars. A = 1.7 mm; B–G = 1 mm; H–J = 50 μm; K–O = 100 μm).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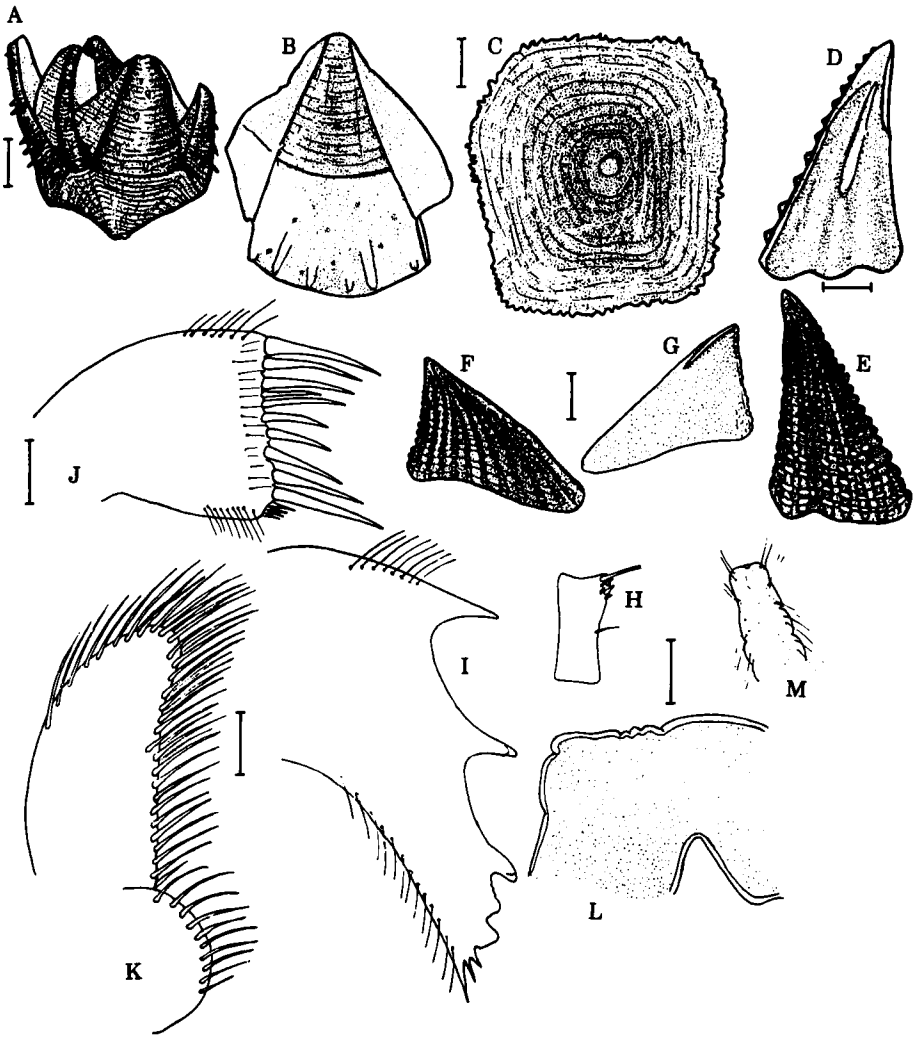

Figure 15. *Pectinoacasta zevinae* (Kolbasov); 5°28′8″S., 145°50′6″E., 18 m, from *Haliclona* sp.: A, shell, lateral view; B, lateral, internal view; C, basis, internal view; D,E, scutum, internal and external view; F,G, tergum, external and internal view; H, 7th segment of anterior ramus of fourth cirrus; I, mandible; J, maxilla I; K, maxilla II; L,M, basis and end of penis. (Scale bars. A = 1 mm; B–G = 0.5 mm; H–M = 50 μm).

HOST SPECIFICITY

The major part of the Acastinae occurs in the sponge class Demospongiae, with only one species recorded so far in each of the classes Calcarea and Hexactinellida. Eight species inhabit alcyonarian, gorgonian and antipatharian Anthozoa. The distribution of Acastinae among the nine orders of sponges is shown in Fig. 16 and Table 1.

Figure 14. *Pectinoacasta pectinipes* (Pilsbry); 20°20.0′N., 107°18.0′E., 28 m, from sponge fam. Halichondridae: A, shell, lateral view; B, carinolateral, internal view; C, lateral, internal view; D, margin of basis; E,F, tergum, external and internal view; G,H, scutum, external and internal view; I, basipodit and basal segments of anterior ramus of fourth cirrus; J, 13th segment of anterior ramus of fifth cirrus; K, part of labrum; L, mandible; M, maxilla I; N, maxilla II; O,P, basis and end of penis. (Scale bars. A,C = 1 mm; B,D–H = 0.5 mm; I,J = 50 μm; K–P = 100 μm).

TABLE 1. Distribution of species of genera of Acastinae among families of sponges and some groups of coelenterata.

	Archiacasta							*Neoacasta*				*Euacasta*							
	fragilis	*hainanensis*	*membranacea*	*pustulata*	*spinifera*	*spinitergum*	*tenuivalvata*	*glans*	*laevigata*	*planibasis*	*scuticosta*	*abnormis*	*antiphidis*	*dofleini*	*microforamina*	*porata*	*sporillus*	*tabachniki*	
Host:																			Crumbled sponges
Calcarea														☆					
Hexactinellida																		☆	
Pachastrellidae			☆											☆					
Stelletidae				☆										☆					
Spirastrellidae																			
Tethyidae			☆								☆								
Agelasidae																			
Axinellidae					☆			☆						☆					
Halicondriidae								☆											
Coelosphaeridae																			Elastic sponges
Crellidae														☆					
Myxillidae														☆					
Poecilostridae																			
Haliclonidae							☆			☆		☆		☆		☆			
Dysidaeidae										☆									
Spongiidae	☆	☆							☆								☆		
Alcyonaria																			
Gorgonaria						☆									☆				
Antipatharia													☆						

	Acasta																		*Pectinoacasta*			
	alcyonicola	*armata*	*crassa*	*cyathus*	*daedalusa*	*echinata*	*fenestrata*	*flexuosa*	*gregaria*	*infirma*	*koltuni*	*pertusa*	*purpurata*	*rimiformis*	*spongitiformis*	*spongites*	*sulcata*	*tzetlini*	*pectinipes*	*sculpturata*	*zevinae*	
Host:																						Crumbled sponges
Calcarea																						
Hexactinellida																						
Pachastrellidae																						
Stelletidae				☆																		
Spirastrellidae																						
Tethyidae																						
Agelasidae			☆																			
Axinellidae														☆				☆				
Halicondriidae																			☆			
Coelosphaeridae											☆											Elastic sponges
Crellidae										☆							☆					
Myxillidae															☆							
Poecilostridae																						
Haliclonidae		☆		☆	☆		☆					☆				☆	☆		☆		☆	
Dysidaeidae				☆				☆								☆						
Spongiidae				☆																		
Alcyonaria	☆																					
Gorgonaria						☆			☆				☆									
Antipatharia																				☆		

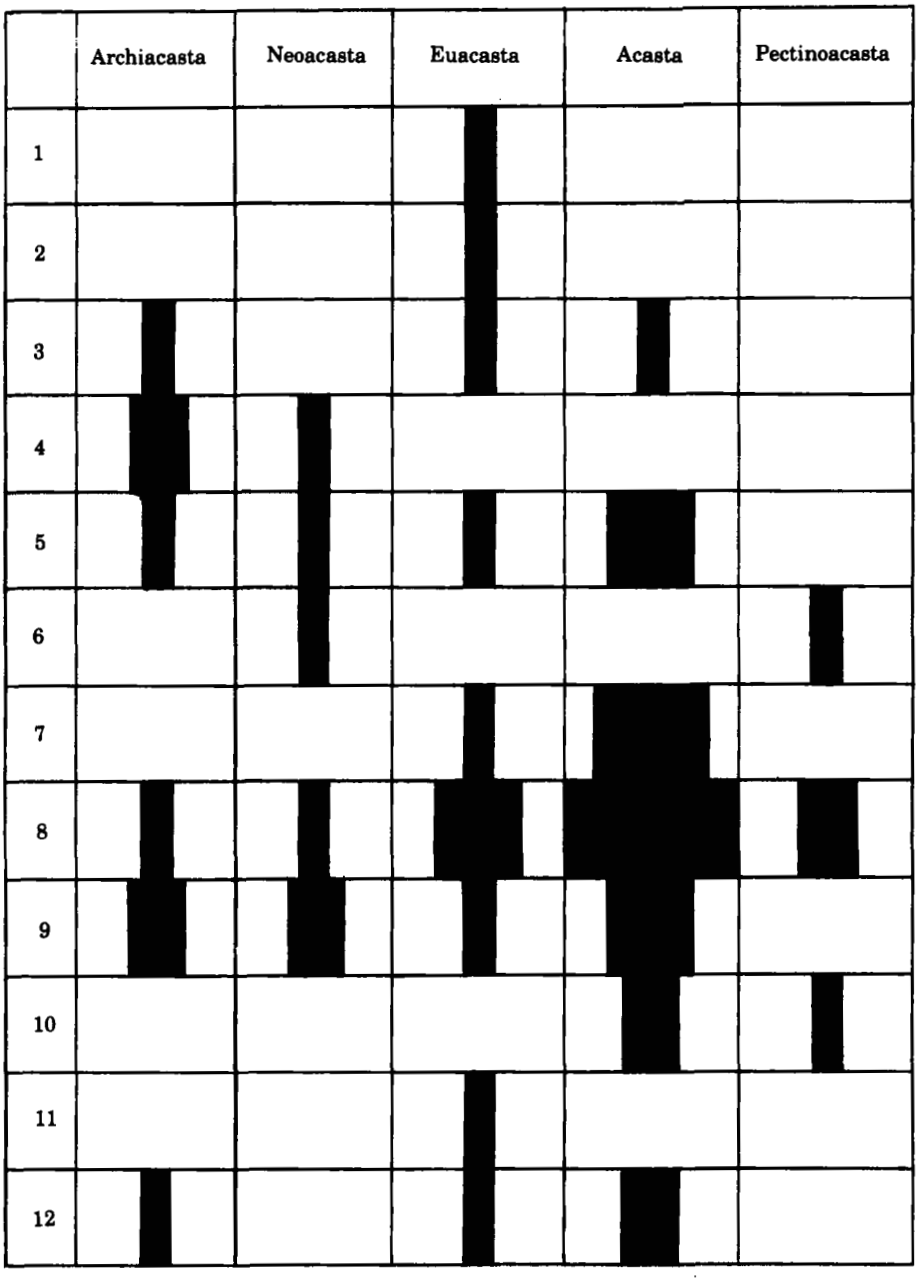

Figure 16. Distribution of genera of Acastinae among orders of sponges and some groups of coelenterata from data compiled by the author and other researchers. Bar width indicates number of occurrences of barnacles within each order. The sponges: 1. Class Hexactinellida, order Lyssacina. 2. Class Calcarea, order Leucettida; class Demospongiae, subclass Tetractinomorpha. 3. Order Choristida. 4. Order Hadromerida. 5. Order Axinellida; subclass Ceractinomorpha. 6. Order Halichondrida. 7. Order Poecilosclerida. 8. Order Haplosclerida. 9. Order Dictyoceratida; ph. Coelenterata: 10. Order Alcyonaria. 11. Subclass Antipatharia. 12. Order Gorgonaria).

The texture of the body of a sponge is determined by relative content of spicules and spongin in the sponge skeleton (Bergquist, 1978). Spongin is a major component of the skeleton in many Demospongiae. The proportion of spongin in the skeleton increases among orders in the following sequence: Class Hexactinellida, order Lyssacina; Class Calcerea, Order Leucettida; Class Demospongiae, subclass Tetratinomorpha, orders Choristida, Hadromerida, Axinellida; subclass Ceractinomorpha, orders Halichondrida, Poecilosclerida, Haplosclerida, Dictyoceratida.

A higher spongin content confers elasticity and a high growth rate, tending to quickly overgrow embedded barnacles. A lower spongin content, crumbly texture and associated low growth rate are more favourable to inhabitation by barnacles.

Species of *Archiacasta* (*A. membranacea, A. pustulata*) inhabit crumbly demosponges of the subclass Tetractinomorpha. These species are the most genralized among the acastines, having a flat membranous basis. *Archiacasta tenuivalvata*, which lives in *Haliclona* sp. (order Haplosclerida) is transitional to more advanced species with a membranous but deep basis (*A. hainanensis, A. fragilis*) living in elastic sponges of the order Dictyoceratida. One species, *Archiacasta spinitergum*, occurs in gorgonians.

All species of *Neoacasta* inhabit demosponges, being found in the orders Hadromerida, Axinellida, Halichondrida, Haplosclerida and Dictyoceratida. The distribution among hosts is similar to that of *Archiacasta* (Fig. 16), and *Neoacasta* shares with *Archiacasta* a latticed scutum, lack of internal longitudinal ribs of wall plates and weak cirral armature.

The species of *Euacasta* are the most widely distributed among types of host, inhabiting seven orders of sponges and also *Gorgonaria* and *Antipatharia*. Most species of *Euacasta* are found in haploscleridian hosts with a significant spongin content in the skeleton. Euacasta has a well developed cirral armature and vestigial carinolaterals.

Species of *Acasta* (s. s.) occur in five orders of demosponges (Choristida, Axinellida, Poecilosclerida, Haplosclerida and Dictyoceratida). The maximum occurrence (six species) is in the Haplosclerida, while none are found in hadromerid or halichondrid hosts. The distribution among hosts is thus similar to that of *Euacasta*, and two genera share certain advanced features (longitudinal internal ribs, well developed cirral armature). Some species of *Acasta*, however, exhibit the specialized features of a very deep, cup-shaped basis and membranous windows between the wall plates (*A. daedalusa*, Fig. 4; *A. fenestrata*, Fig. 12; *A. armata*). These specialized species inhabit tough, elastic sponges with rapid growth rates. Species of *Acasta* are also found in *Alcyonaria* and *Gorgonaria*.

Less is known about the sponge hosts of the genus *Pectinoacasta*. Two orders of sponges are involved, together with some *Alcyonaria*.

The majority of Acastinae occur in elastic sponges—orders Haplosclerida (13 species) and Dictyoceratida (eight species) although quite a lot of barnacles inhabit crumbled sponges, e.g. in order Axinellida (six species).

FOOD INTAKE

No sponge-inhabiting barnacle eats the tissues of the host sponge. Tabachnik (1986) showed that the food of acastines consists of:

(1) *Acasta sulcata*: detritus 84%; sand 8%; spicules 3%; crustaceans 3%; Silicoflagellida 3%; Foraminiferida, less than 1%; Radiolarida, less than 1%; diatoms, less than 1%.

(2) *Neoacasta laevigata*: detritus 64%; sand 30%; spicules 5%; Foraminiferida, less than 1%; crustaceans, less than 1%.

(3) *Acasta pertusa*: detritus 84%; sand 5%; Silicoflagellida 5%; spicules 3%; crustaceans 1%; Radiolarida 1%; Tintinnida, less than 1%; eggs of pelagic molluscs.

The most prominent food intake is thus detritus (64–84%), presumably collected from the surface of the host. The tissues of sponges were not found, although spicules were discovered, but in insignificant quantities and not more than in some other barnacles, which are not sponge-inhabiting.

ORIGIN AND EVOLUTION

The ancestors of acastines, presumed to be archaeobalanids of generalized structure, with a flat, membranous basis, must have settled on other substrata as well as sponges. It seems likely that these unspecialized, sponge-inhabiting, barnacles were able to survive only on crumbly sponges of low growth rate, with little or no spongin in the skeleton. *Archiacasta membranacea*, inhabiting *Pachastrella isorrhopa*, represents this early stage of acastine evolution. The basis is flat and membranous, the junctions between the basis and wall plates are weak, and the cirral armature is poorly devleoped. The operculum is exposed, due to the narrow, oblique radii of the wall plates, but the scuta are thick and are strengthened by a lattice, which, apparently, protected the body of the ancestor of this species from the top, because it is very firm.

Species of acastines that live deeply embedded in the sponge host and have a reduced orifice show a reduction in the size and strengthening of the scuta. A functional series is displayed by *Archiacasta membranacea*, *Neoacasta glans* (Fig. 6) and *Pectinoacasta cancellorum* (latticed scutum), *Archiacasta spinifera*, *Neoacasta scuticosta*, *Euacasta dofleini* (Fig. 8) and *Pectinoacasta zevinae* (Fig. 15) (scutum with radial striae) and *Archiacasta pustulata* (Fig. 1), *Neoacasta laevigata and Euacasta sporillus* (scutum lacking striae). Functional modifications have therefore evolved in parallel in these genera. All species of the genus *Acasta (s. s.)* display the advanced condition.

Within *Archiacasta*, the evolution of adaptations to sponge overgrowth includes calcification of the basis (*A. spinifera*), and development of a deeply cup-shaped basis (*A. hainanensis*), then apical extention of the wall plates to overlap the operculum (other species). *A. praerupta* and *A. tulipa* also show the beginnings of development of internal longitudinal ribs strengthening the wall plates.

A greater interlocking of wall and basis, through the development of longitudinal ribs and marginal teeth, is characteristics of *Euacasta*, *Acasta* and *Pectinoacasta*. The genus *Neoacasta* has a specialized interlooking arrangement, in which two internal marginal ribs on each plate interlock with six compound teeth developed on six internal ribs on the basis (Figs. 2, 6).

Most species of acastines have long worm-shaped processes or small thorns on the external surface of the wall, penetrating as anchors into the surrounding sponge tissue. These processes are well developed in species which inhabit

crumbly sponges, but reduced among species hosted by elastic sponges. In *Euacasta porata* the surface processes are vestigial and in *E. sporillus*, absent.

The development of splits or windows in the wall (Fig. 12) is confined to advanced species inhabiting elastic sponges with a high spongin content in the orders Haplosclerida and Dictyoceratida. This condition is not viable for species embedded in spiculated sponge tissue.

A major problem for sponge-inhabiting barnacles is overgrowth by the host. Therefore they must continually scrape down the overgrowing margin. The curved hooks on the frontal surface of the anterior ramus of cirrus IV appear to perform this function. In many species inhabiting crumbly sponges, these hooks are well developed (Fig. 8). Species living in elastic sponges have only a weak armature (Fig. 4, 15), because it is useless for struggling with a tough marin of sponge.

The surrounding sponge tissue also increases in depth, burying the barnacle. The barnacle must therefore grow in height at a rate which maintains its orifice at the surface of growing sponge. This is achieved in three ways. The first is the cup-shaped growth of the basis, increasing the proportion of height to diameter (Fig. 4). A similar adaptation has evolved in coral-inhabiting barnacles of the family Pyrgomatidae (Darwin, 1854; Ross & Newman, 1973). Secondly, the wall plates also increase in height relative to width during growth in all acastines. In *Euacasta* (Figs 7–9) this is further emphasized by the reduction in the carinolaterals, leading to a further decrease in the diameter of the wall relative to height. A quadrangular basis is associated with this modification.

Among species inhabiting elastic sponges, the growth in height of the parietes often exceeds the rate of growth of the radii, resulting in splits between the wall plates. In some species, these splits develop into large windows (Fig. 12). It seems likely that a metabolic action is exerted through these windows on the surrounding sponge tissue. For example, the sponge *Haliclona* sp. surrounds *Acasta pertusa* with a spongin capsule. These more highly adapted species tend to be associated with fewer hosts, usually of one sponge family, e.g. *A. pertusa*, *A. fenestrata* in Haliclonidae, *E. sporillus* in Spongidae.

PHYLOGENY

Within the Acastinae, the genera *Neoacasta*, *Euacasta* and *Acasta* probably originated from Archiacasta. *Neoacasta glans* (Fig. 6), for example, has a latticed scutum and two internal maginal ribs on each wall plate, differing from *Archiacasta* only in the presence of a deeper calcareous basis. Two species of *Acasta*, *A. spongites* and *A. spongiteformis* (Fig. 3) are also close to *Archiacasta*, having strongly striated scuta, narrow, oblique radii and rudimentary longitudinal internal ribs. *A. spongites* also has a weak cirral armature, but *A. spongiteformis* has a strong armature of the fourth cirrus. This species inhabits the sponge *Poecillastra* sp.

Euacasta differs from *Acasta* only in having reduced carinolaterals. *E. abnormis*, inhabiting the brittle haplosclerid *Petrosia*, is similar to species of *Archiacasta* in having strongly striated scuta, no longitudinal ribs and a weak cirral armature. This species also has the widest carinolaterals among *Euacasta* (Kolbasov, 1991).

Pectinoacasta is clearly separated from the other acastines by the latticed or

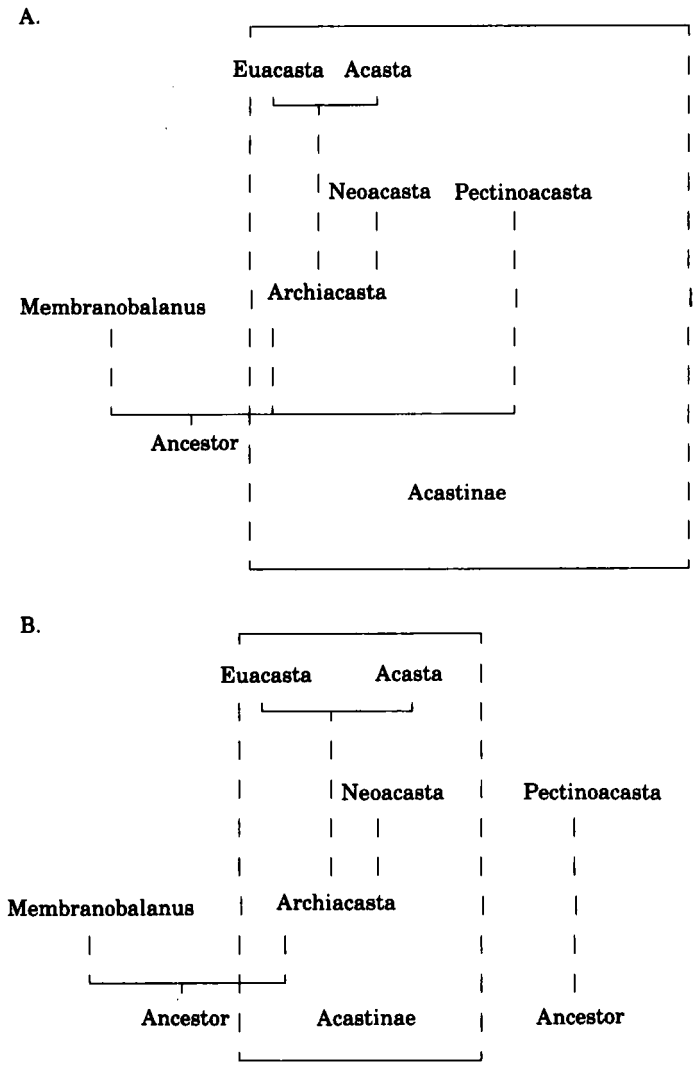

Figure 17. Representation of two major evolutionary schemes in the subfamily Acastinae (A = monophyletic; B = diphyletic).

striated tergum. The origin of this genus is not clear, but it raises the possibility that the Acastinae are diphyletic.

Archiacasta shares many features with *Membranobalanus*, including a membranous basis and an armature of small thorns on the anterior ramus of the fourth cirrus. *M. acutus* (Fig.17) from the sponge *Petrosia* has a scutum with strong radial striae, similar to that of *Archiacasta spinifera*. It seems likely that the two genera had a common ancestry. Possible relationships are summarized in Figure 17.

GROWTH

The nauplial stages of the species Acastinae (the nauplii of *E. dofleini* and *A. daedalusa* were examined) have no essential differences from nauplii of other

TABLE 2. Zoogeography of acastine genera

Region	Archiacasta	Neoacasta	Euacasta	Acasta	Pectinoacasta
Japan	2	1	1	11	2
South China Sea, Siam Bay and Phillipines	5	3	9	11	1
Indonesia and New Guinea	2	3	2	7	4
Oceania	0	1	0	0	0
Northeastern Australia	0	0	0	2	0
Southeastern Australia and New Zealand	1	0	0	3	0
Western Australia	0	1	2	4	0
Bengal Bay, Ceylon and Andaman Sea	0	3	1	3	1
Arabian Sea and Persian Gulf	0	1	0	1	0
Red Sea	0	1	1	6	0
Eastern Equatorial Africa and Madagascar	1	3	2	7	0
South Africa	1	1	0	3	1
Mediterranean	0	1	0	3	0
North Atlantic	0	0	0	2	0

barnacles. Apparently, the cyprid bores actively through the tissue of the sponge and then the metamorphosis takes place inside the sponge. The juveniles have essential differences from the adult forms (Fig. 4) and the scheme of growth is characteristic of all species of this subfamily. The globular stage is present at first, then the intensive growth of the lateral plates in height takes place and the basis remains shallow during this process. The process of the deepening of basis is the last before the adult stage is formed. Both the juvenile and the adult forms have a similar soft body structure.

VERTICAL DISTRIBUTION AND ZOOGEOGRAPHY

Acastines are widespread in the tropical and subtropical waters of all regions of the world except South America. They extend from 50°N (England), 30°N (Florida) and 35°N (Japan) in the Northern Hemisphere to 40° S (Australia, South Africa) in the Southern Hemisphere. The majority of species inhabit the Pacific and Indian oceans. On present knowledge, species of *Acasta* are the most widespread. The greatest number of species of acastines, including representatives of all five genera, occur in the region of the South China Sea, Indonesia and New Guinea (Table 2). This fauna includes the generalized species of all genera (*Archiacasta membranacea, Neoacasta glans, Euacasta abnormis* and *Acasta spongites*). This region seems likely to be the centre of origin of the Acastinae. Much more needs to be known of the occurrence and distribuiton of acastine barnacles before a full zoogeographical analysis of the subfamily can be made. *Archiacasta membranacea*, for example, was regarded as an endemic species of the South African region (Barnard, 1924), but has recently been found in the South China Sea (Ren, 1984).

The vertical distribution of Acastinae is shown in Figure 18. *Archiacasta* has two depth maxima, at 5–15 m and 50–75 m. The deeper species are associated with crumble sponges of the order Hadromerida, while those at shallower depths

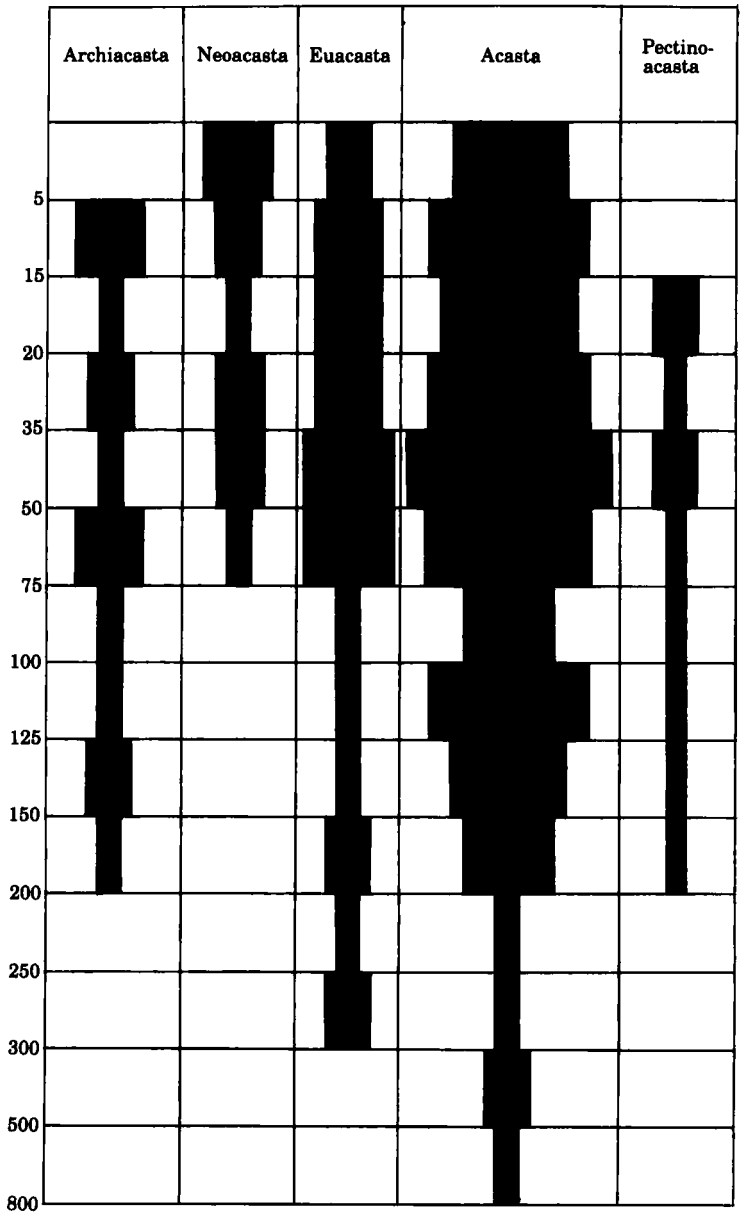

Figure 18. Vertical distribution of genera of Acastinae (from 0 to 800 m) from data compiled by the author and other researchers. Bar width for one species is 3 mm.

mainly inhabit the elastic Dictyoceratida. The dependence of barnacle distribution on host distribution is more clearly shown in Neoacasta, the majority of which inhabit elastic sponges. These hosts do not occur in deeper waters.

Euacasta and *Acasta*, with a greater range of host species, extend over a much greater vertical range, but again the majority of species are associated with shallow water elastic sponges. Little is known of the vertical distribution of *Pectinoacasta*, but present information indicates occurrance mainly in shallower

waters. The major evolutionary diversification of acastines therefore appears to have taken place in shallow water sponges with elastic skeletons.

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