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Ossicle variation in Antarctic dendrochirote holothurians (Echinodermata)

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Abstract

A study of ossicle variation in Cucumariidae coming from the Weddell Sea (Antarctica), the specimens ranging from 4 to 70 mm long, confirms that *Heterocucumis steineni* (LUDWIG, 1898), *Heterocucumis antarctica* (VANEY, 1906) and *Heterocucumis godfroyi* (VANEY, 1914) represent different stages of a single species: *H. steineni*.
A study of *Heterocucumis steineni*, *H. denticulata* (EKMAN, 1927) and *Staurocucumis liouvillei* (VANEY, 1914) shows that the main ossicle change occurs early when specimens are 20 mm long or even less. A review of holothurian ossicle variation is given.
Key words : holothurian, dendrochirotes, ossicle variation, taxonomy, Antarctic.

Résumé

L'étude de Cucumariidae provenant de la mer de Weddell (Antarctique) et mesurant de 4 à 70 mm de long montre que *Heterocucumis steineni* (LUDWIG, 1898), *Heterocucumis antarctica* (VANEY, 1906) et *Heterocucumis godfroyi* (VANEY, 1914) sont bien des stades différents d'une seule espèce : *H. steineni*.
L'étude de *Heterocucumis steineni*, *H. denticulata* (EKMAN, 1927) et *Staurocucumis liouvillei* (VANEY, 1914) montre que les changements les plus importants de spicules ont lieu chez des spécimens qui n'ont pas plus de 20 mm de long ou même moins. Les variations des spicules d'holothuries sont passées en revue.
Mots clés : holothurie, dendrochirotes, variation des spicules, taxonomie, Antarctique.

Introduction

Calcareous deposits (ossicles), together with external morphology and internal anatomy, have been the main diagnostic characters used to identify holothurian species (see LUDWIG, 1892). Deposits are not uniform throughout the body wall. Many Holothuridae with a flattened ventral sole show a clear difference between dorsal and ventral ossicles. This phenomenon is even more obvious among Psolidae where there is a sharp distinction between the arched armoured dorsal surface and the flattened smooth ventral sole. Many Synaptidae also show variations (in size and form) in ossicles from anterior and posterior parts of the body.

In addition to these differences related to the position in the body wall, other kinds of ossicle variation, associated with increasing body size, have been observed, mainly in Cucumariidae. Some Phyllophoridae, Ypsilothuridae, Caudinidae, Synaptidae and Stichopodidae also show variations with increasing body size. Four types of variation occur :
1. Ossicles may gradually increase in size, but their form is only slightly modified. These modifications were mentioned by DEICHMANN (1941) for the dendrochirotes *Havelockia bidentata* (DEICHMANN, 1941) and *Neothyone gibber* (SELENKA, 1867), by RAO (1973) for *Patinapta ooplax* (MARENZELLER, 1881) and by HOZAWA (1928) for *Paracaudina chilensis* MÜLLER, 1850.
2. Ossicles gradually regress and may completely disappear. This phenomenon was observed by DEICHMANN (1941) in many *Thyone* species and also by MITSUKURI (1897) in *Apostichopus japonicus* (SELENKA, 1867).
3. Ossicles gradually disappear. This has been mentioned for many species of Cucumariidae (see VANEY, 1914; EKMAN, 1925, 1927; GUTT, 1988; MASSIN, 1992), such as *Cucumaria georgiana* (LAMPERT, 1886) and *Cucumaria acuta* MASSIN, 1992. Molpadiidae (see CLARK, 1907) and Stichopodidae (see CLARK, 1922) show the same phenomenon. Among Cucumariidae, the ossicles disappear completely from the body wall or remain only around the anus and in the introvert.
4. Ossicles change completely (all early body wall ossicles are replaced by new ones), as in *Staurocucumis liouvillei* (VANEY, 1914) (see EKMAN, 1925, 1927; HANSEN, 1988), or partially (only some of the early body wall ossicles are replaced by new ones), as in *Neopentadactyla mixta* (ÖSTERGREN, 1898) (see FÉRAL, 1980a, b) and *Neostichopus grammatus* (H.L. CLARK, 1923) (see DEICHMANN, 1948; THANDAR, 1987). Table I lists the species in which ossicles are different for young and adult specimens.
Among the species listed in table I, only one, *Staurocucumis abyssorum* (THÉEL, 1886), is abyssal, the others live on the continental shelf and slope. Most are from cold or temperate waters. The only tropical species, *Psolicucumis nocturna* (SLUITER, 1901), is known so far

Table I.
Holothurian species which undergo a marked change in ossicles (replacement of early ossicles by new ones) with increasing body size.

Species	Authors	Depth range	Distribution
Cucumariidae			
Heterocucumis steineni	EKMAN, 1925, 1927	6-1180	Antarctic
Heterocucumis coatsi	EKMAN, 1925	350-672	Antarctic
Heterocucumis denticulata	EKMAN ,1925, 1927	160-672	Antarctic
Staurocucumis liouvillei	EKMAN, 1927; HANSEN, 1988	18-745	Antarctic
Staurocucumis turqueti	EKMAN, 1925, 1927; HANSEN, 1988	16-990	Antarctic
Staurocucumis abyssorum	LUDWIG, 1894; EKMAN, 1927	1210-4540	Antarctic; Sub-Antarctic; Central East
	HANSEN 1988		Pacific; North Atlantic
Psolicucumis nocturna	SLUITER 1901; CLARK & DEICHMANN 1936; HANSEN 1988	200-1128	Indonesia
Phyllophoridae			
Neopentadactyla mixta	FÉRAL 1980a, b	0-67	Europe
Ypsilothuriidae			
Echinocucumis hispida	HANSEN 1988	50-1300	North Atlantic
Stichopodidae			
Neostichopus grammatus	DEICHMANN 1948; THANDAR 1987	0-3	South Africa

only from the continental slope. Most are dendrochirotes and belong to the family Cucumariidae.

Ossicle variation with increasing body size has created a lot of confusion in the taxonomy of some dendrochirote holothurians, particularly for those from the Antarctic. Many species have a long list of synonyms and may have changed genus several times, such as the species *Staurocucumis turqueti* (VANEY, 1906). It has been referred to *Cucumaria* by VANEY (1909), EKMAN (1925) and CHERBONNIER (1941); to *Staurocucumis* by EKMAN (1927), HANSEN (1988) and in the present paper; to *Ekmocucumis* by PANNING (1949) and CHERBONNIER (1974); and to *Abyssocucumis* by GUTT (1988, 1991).

Other species have been "lumped" and "split" several times, such as *Heterocucumis steineni* (LUDWIG, 1898), *H. antarctica* (VANEY, 1906) and *H. godfroyi* (VANEY, 1914). EKMAN (1925) considered *H. antarctica* as a synonym of *H. steineni*, and *H. godfroyi* as a distinct species. Then EKMAN (1927) lumped the three species under *H. steineni*. PANNING (1949) and CHERBONNIER (1941, 1974) separated *H. steineni* from *H. antarctica*. CHERBONNIER (1974) considered *H. godfroyi* a distinct species.

Other cases of ossicle variation with increasing body size are mentioned in the literature for subspecific, specific and generic levels :

— Subspecific level : THÉEL (1886) erected three "varieties" of *Staurocucumis abyssorum* : *S. abyssorum hyalina, S. abyssorum abyssorum* and *S. abyssorum grandis*. LUDWIG (1894) showed that they are in fact three growth stages of *S. abyssorum*.

— Specific level : HEDING (1942a) considered *Psolicucumis nocturna* (SLUITER, 1901), *P. apneumona* HEDING, 1934 and *P. echinata* HEDING, 1942 as three distinct species. HANSEN (1988) synonymized *P. apneumona* with *P. nocturna*. Moreover, comparison of HANSEN's figure 4 (1988, p. 305) with HEDING's figures 4-12 (1942a, p. 409) strongly suggests that *P. echinata* must also be considered as a synonym of *P. nocturna*, a species which undergoes ossicle changes with increasing body size.

— Generic level : CLARK (1907) mentioned that species belonging to the genus *Ankyroderma* have calcareous deposits but few or no colourless rounded granules (phosphatic deposits), whereas species belonging to the genus *Trochostoma* have reduced calcareous deposits and numerous phosphatic deposits. CLARK (1907) mentioned also that most of the species of *Ankyroderma* were shorter than 60 mm, whereas many species of *Trochostoma* were longer than 75 mm. Moreover, as noted by CLARK (1907) "Young individuals of any species (i.e. of *Molpadia*)

may lack phosphatic deposits, while very old specimens may lack calcareous deposits". As a consequence, CLARK (1907) synonymized the genera *Ankyroderma* and *Trochostoma* with *Molpadia*.

This paper reports a study of ossicle change with increasing body size, and the taxonomic implications.

Material and methods

The material is from the 1989 Expedition ANT VII/4 (EPOS) of the R.V. "Polarstern" (see ARNTZ *et al.*, 1990) in the Weddell Sea. The holothurians were sorted by the Centre National de Tri d'Océanographie Biologique (CENTOB, Ifremer Brest, France) and all specimens collected between 0 and 800 m were dispatched to the Royal Belgian Institute of Natural Sciences. This material was compared with material from the Muséum National d'Histoire Naturelle (Paris), the Alfred Wegener Institut for Polar Research (Bremerhaven) and the Zoologisches Museum und Institut (Hamburg).

Results

The holothurians in this material which are known to undergo ossicle changes (replacement of early ossicles by new ones) are listed in table II. Observations for these five Cucumariidae species are the following :

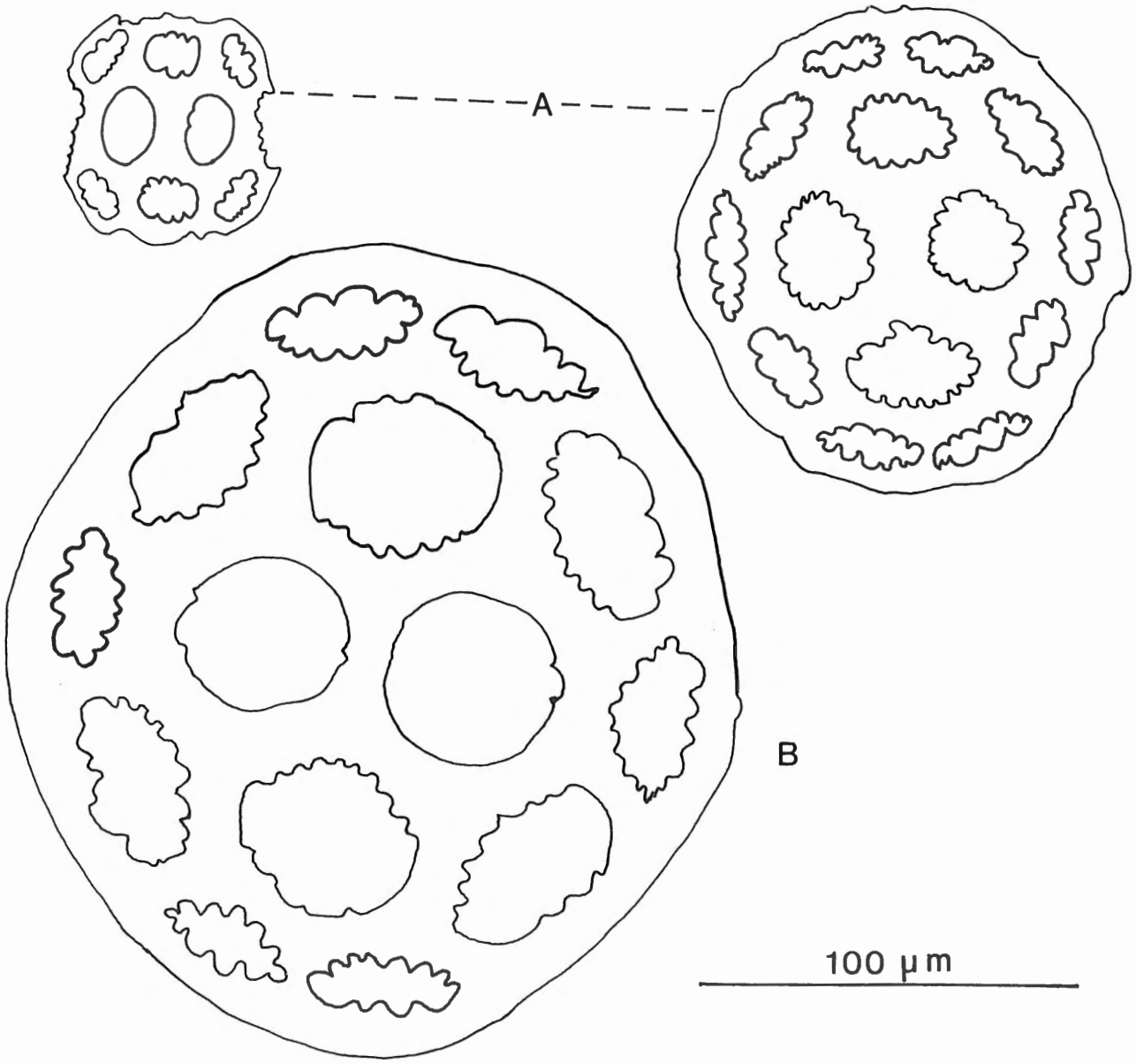


Fig. 1 – Staurocucumis liouvillei *(VANEY, 1914). Perforated plates. A : 261 BPN 6 - sub 12. L =10 mm ; B : 273 AGT 17 - sub 14. L = 51 mm.*

Table II.
Weddell Sea species which undergo ossicle changes (replacement of early ossicles by new ones). A : number of specimens examined; B : size range in mm.

Species	Depth range m	A	B mm
Heterocucumis coatsi	609-672	3	9-18
Heterocucumis denticulata	186-672	3	13-16
Heterocucumis steineni	186-701	268	4-70
Staurocucumis liouvillei	186-799	142	6-78
Staurocucumis turqueti	186-602	14	8-120

1. The ossicles of adult *Staurocucumis liouvillei* (6-78 mm long), rounded plates with serrated perforations (fig. 1), are present in the uppermost layer of the body wall. This gelatinous layer is often damaged in large specimens, and ossicles are found mainly between skin folds. Very young specimens (6-10 mm long) were collected at eight stations. They represent nearly half of the specimens observed. They already have the ossicles characteristic of adults (fig. 1A).

2. Specimens of *Staurocucumis turqueti* from 8 to 120 mm long were examined. Except for the two smallest specimens, they lack the typical cruciform ossicles characteristic of the juveniles (see EKMAN, 1927). Large specimens of *S. turqueti* (> 40 mm) have few ossicles (fig. 2) in the skin, except near the anus where they protrude through the epidermis.

3. *Heterocucumis coatsi* (VANEY, 1906) (fig. 3) is represented by three small specimens (9, 14, and 18 mm long). They show a mixture of juvenile and adult ossicles .

4. *Heterocucumis denticulata* (EKMAN, 1927)(fig. 4) is also represented by small specimens (13-16 mm long). They already have ossicles typical of adults in the body wall (fig. 4A). Near the anus, ossicles typical of juveniles are still present (fig. 4B).

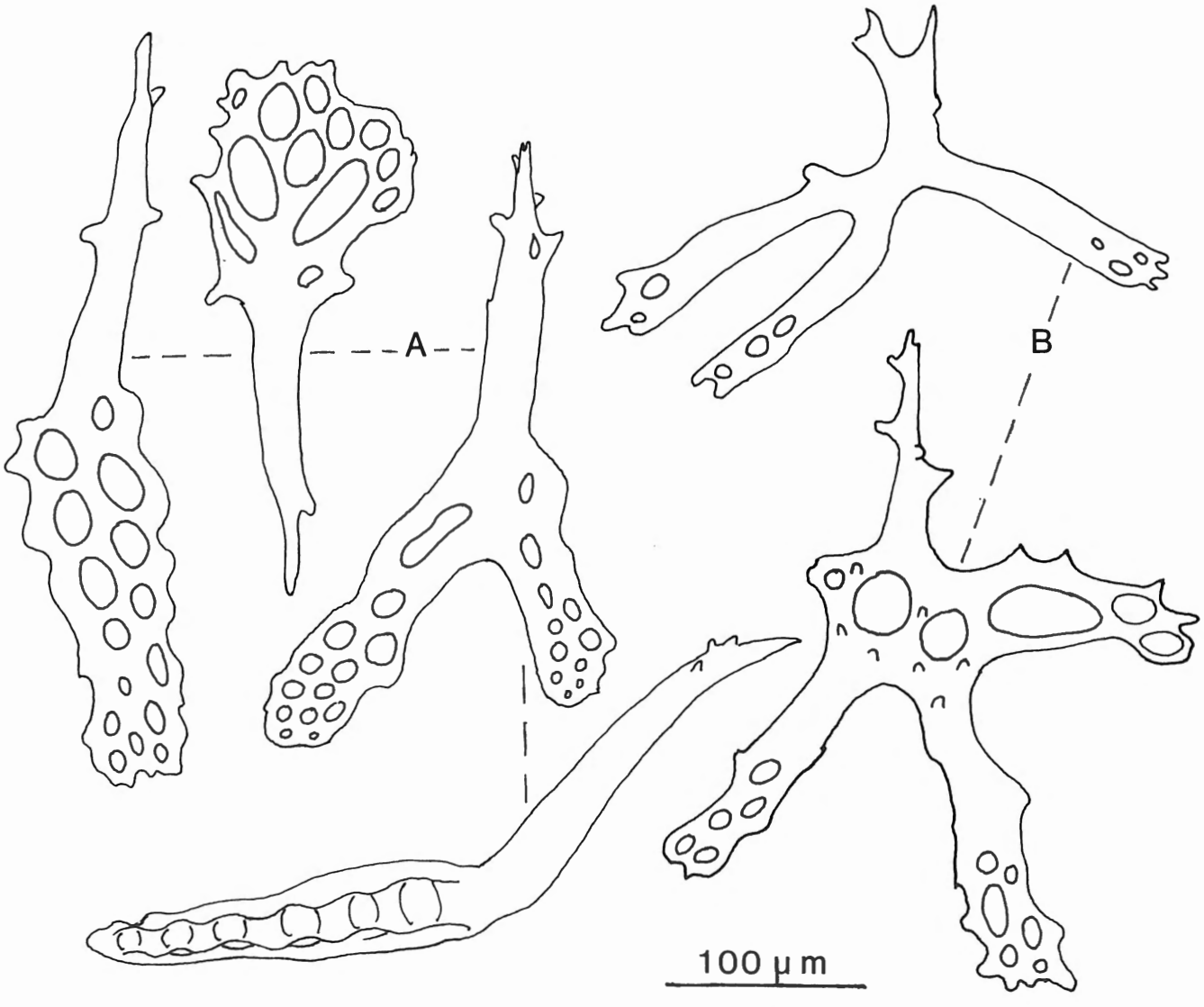


Fig. 2 – Staurocucumis turqueti *(VANEY, 1906). A : ossicles of body wall-248 GSN 10 - sub 29. L = 18.4 mm; B : anal ossicles - 224 MG 2 - sub 1. L = 120 mm.*

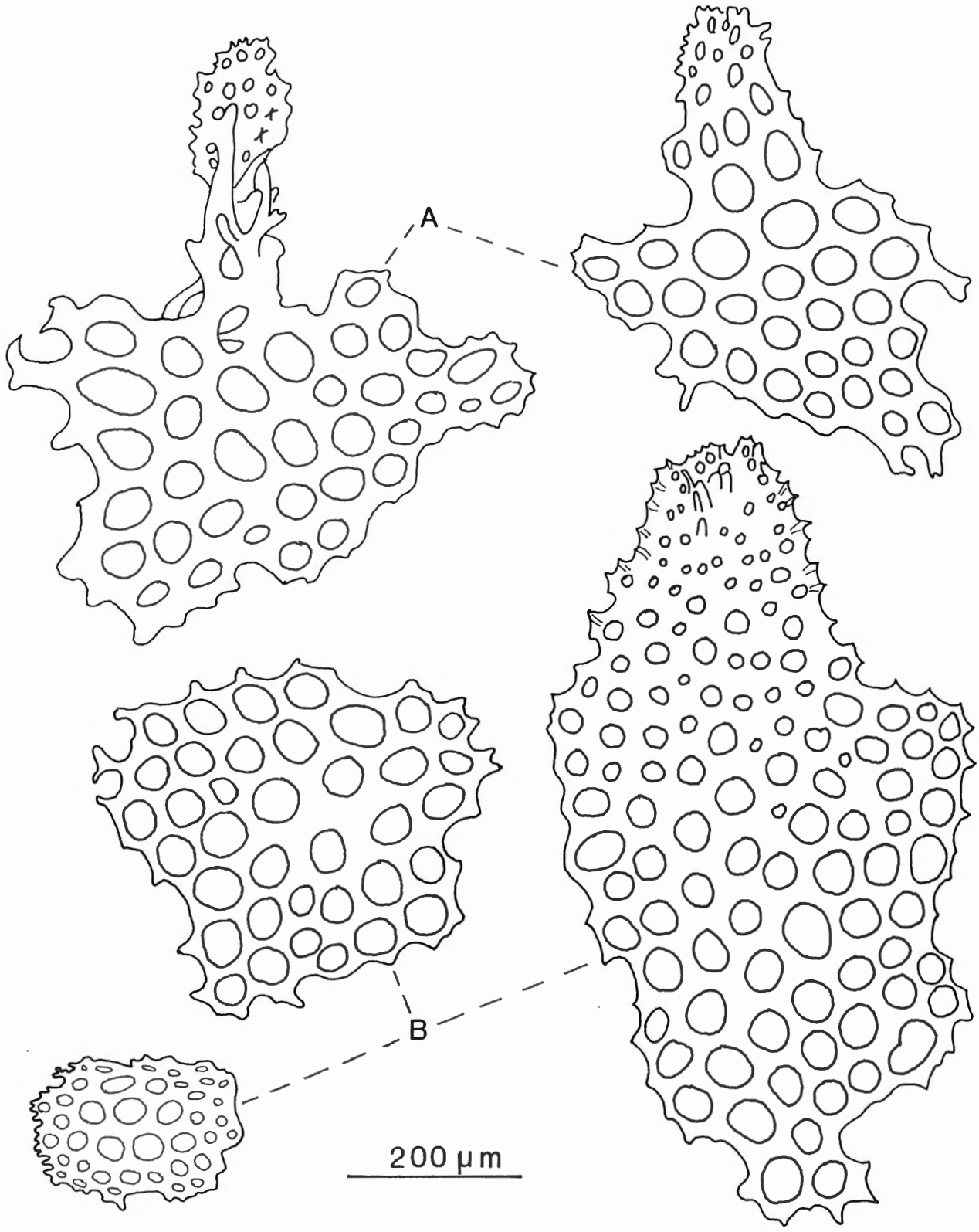


Fig. 3 – Heterocucumis coatsi *(VANEY, 1906). A : ossicles of body wall - 289 AGT 23 - sub 14. L =14 mm; B : anal ossicles - 282 AGT 22 - tot 6. L = 18 mm.*

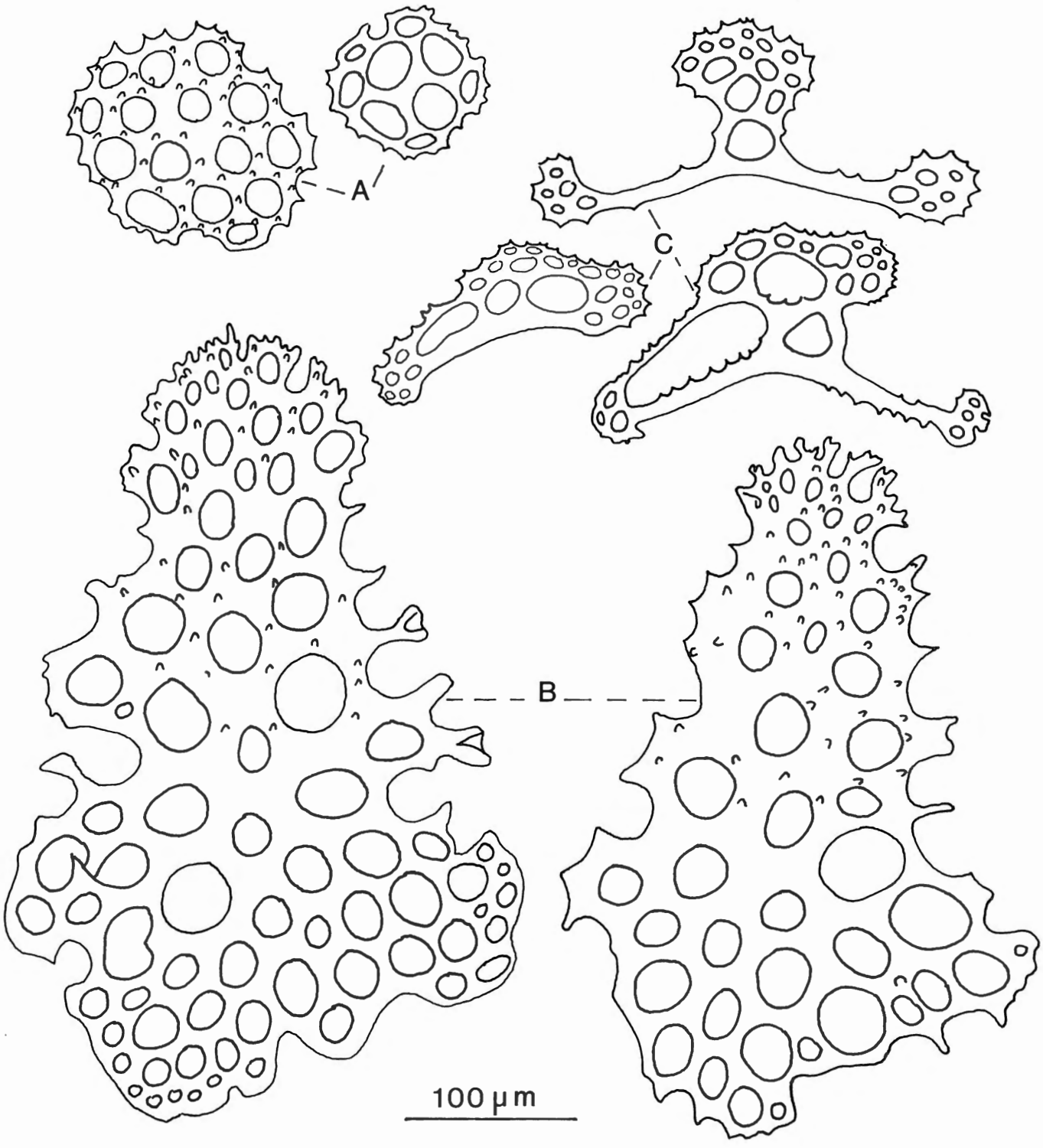


Fig. 4 – Heterocucumis denticulata *(Ekman, 1927). A : ossicles of body wall - 284 GSN 13 - sub 8. L = 16 mm; B : anal ossicles - 224 GSN 4 - sub 11. L = 13.5 mm; C : ossicles of anal tube feet - 224 GSN 4 - sub 11. L = 13.5 mm.*

5. *Heterocucumis steineni* is the most abundant species (cf table II). Specimens ranging from 4 to 70 mm long were examined, and their ossicles illustrated (figs 5-7 & 9-16). Three types of ossicles may be present in the body wall : BW1, BW2 & BW3.

— BW1. Very large perforated plates with smooth edge and long anterior process which is often spiny (fig. 5). Size range 250-900 µm.

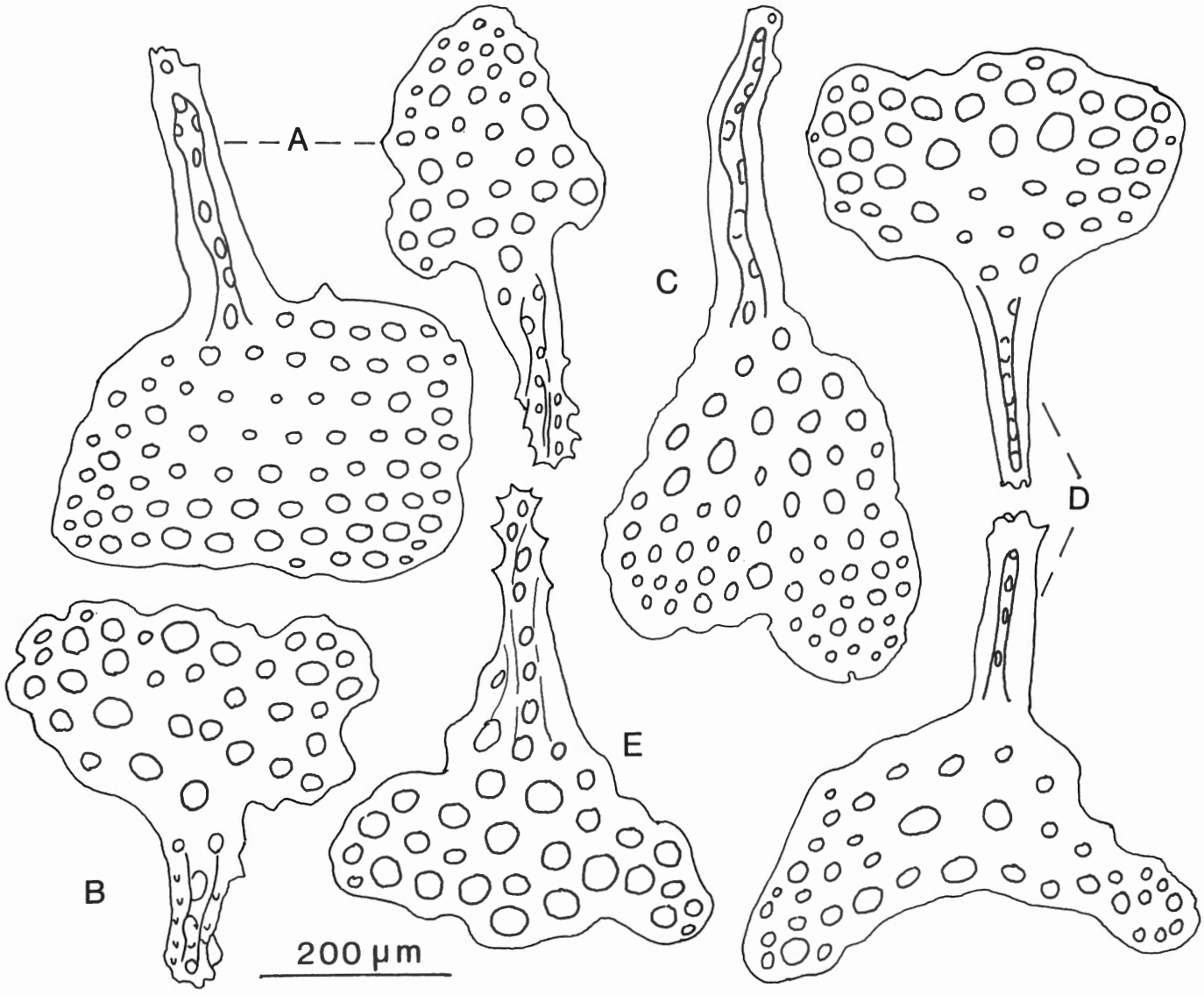


Fig. 5 – Heterocucumis steineni *(Ludwig, 1898). Body wall ossicles : type 1 (BW1). A : 284 GSN 13 - sub 26. L = 4.5 mm; B : 284 GSN 13 - sub 7. L = 9.2 mm; C : 284 GSN 13 - sub 22. L = 10 mm; D : 284 GSN 13 - sub 7. L = 13.8 mm; E : 248 GSN 10 -sub 47. L = 16 mm.*

— BW2. Large perforated plates with serrated edge and long to medium- size anterior process (fig. 6). These plates are circular or triangular and much larger than the anterior process (fig. 6A, E). Some are also elongate and narrow (fig. 6D). The anterior process is spiny. The plate is somewhat knobbed or with blunt spines. Size range 200-500 µm.
— BW3. Small triangular, spinose, perforated plates with serrated edge (fig. 7). Size range 100-210 µm.

Very young specimens (4-12 mm long) have only type BW1, which are abundant. Medium-size specimens (13-40 mm long) have types BW1 and BW2. Type BW1 is rare in specimens longer than 20 mm. With increasing body size, the circular or triangular plates become increasingly elongate. When BW2 are elongate, types BW1 and BW2 with circular or triangular plates have disappeared. Type BW3 is already present in 15 mm long specimens, sometimes mixed with BW1 and BW2.

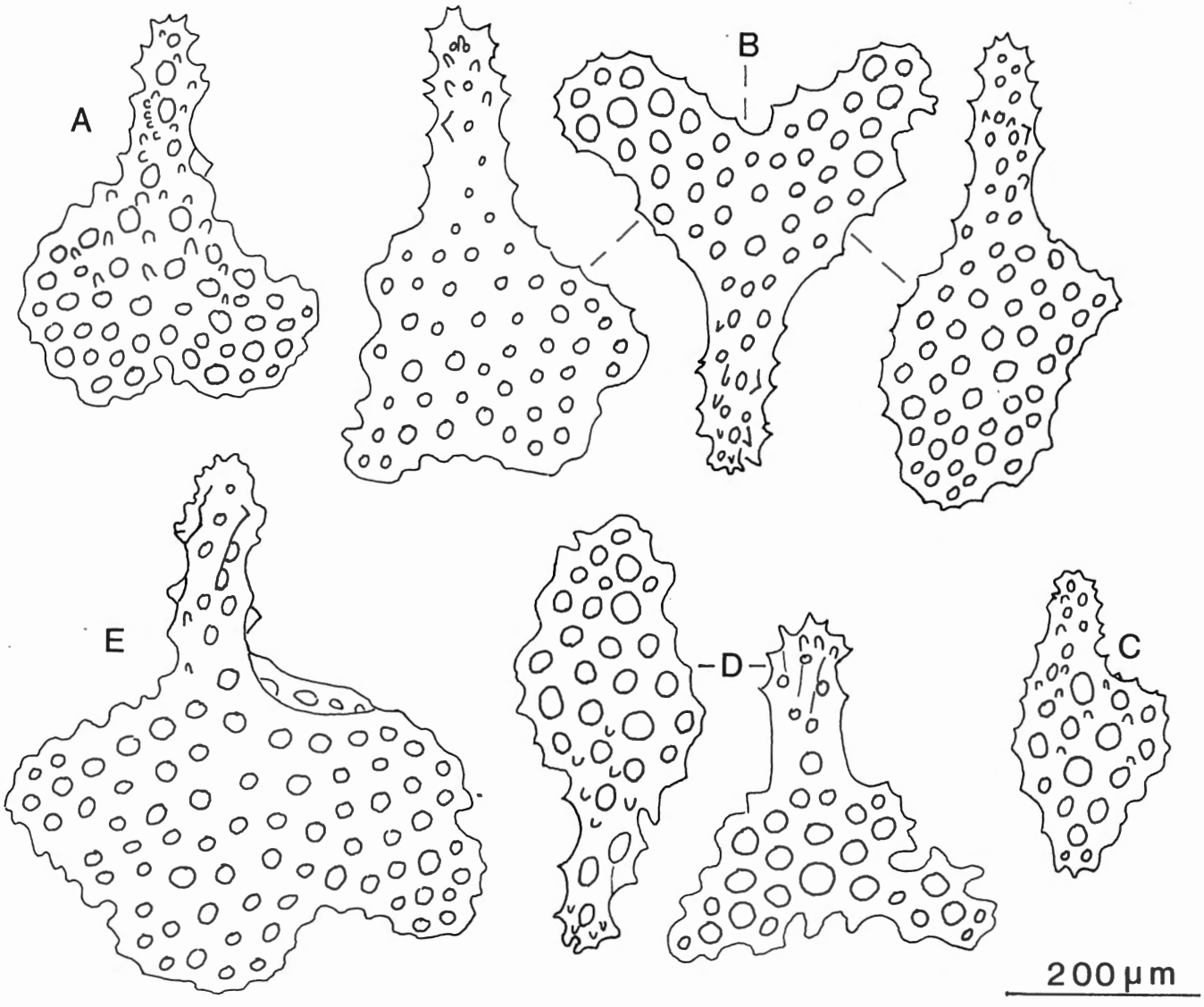


Fig. 6 – Heterocucumis steineni *(Ludwig, 1898). Body wall ossicles : type 2 (BW2). A : 284 GSN 13 - sub 9. L = 9.2 mm; B : 270 AGT 14 - sub 3. L = 12 mm; C : 284 GSN 13 - sub 7. L = 13.8 mm; D : 248 GSN 10 - sub 47. L = 16 mm; E : 273 AGT 17 - sub 2. L = 26.4 mm.*

When 50 mm in length, the specimens have only type BW3, when present. Figure 8 summarizes these changes. Beyond 30 mm, the number of ossicles in the body wall is greatly reduced. Over 60 mm, body wall ossicles are found mainly around the anus.
The anal ossicles (fig. 9) are similar but always larger and more solid than those of the body wall. When the body wall has only type BW3, type BW2 is still present around the anus.

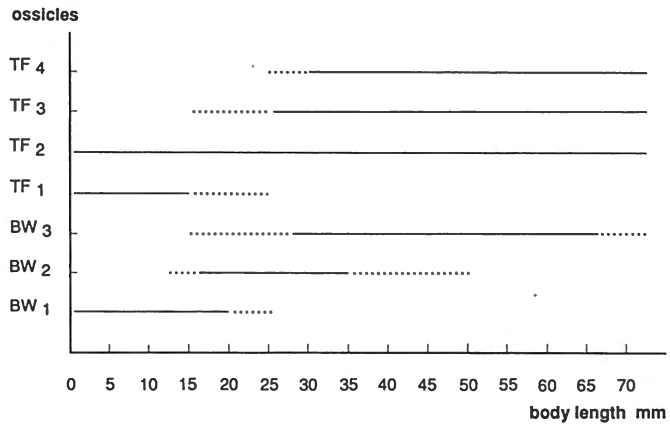


Fig. 8. – Heterocucumis steineni *(Ludwig, 1898). Occurrence of body wall (BW) and tube feet (TF) ossicles with increasing body size of specimens.*

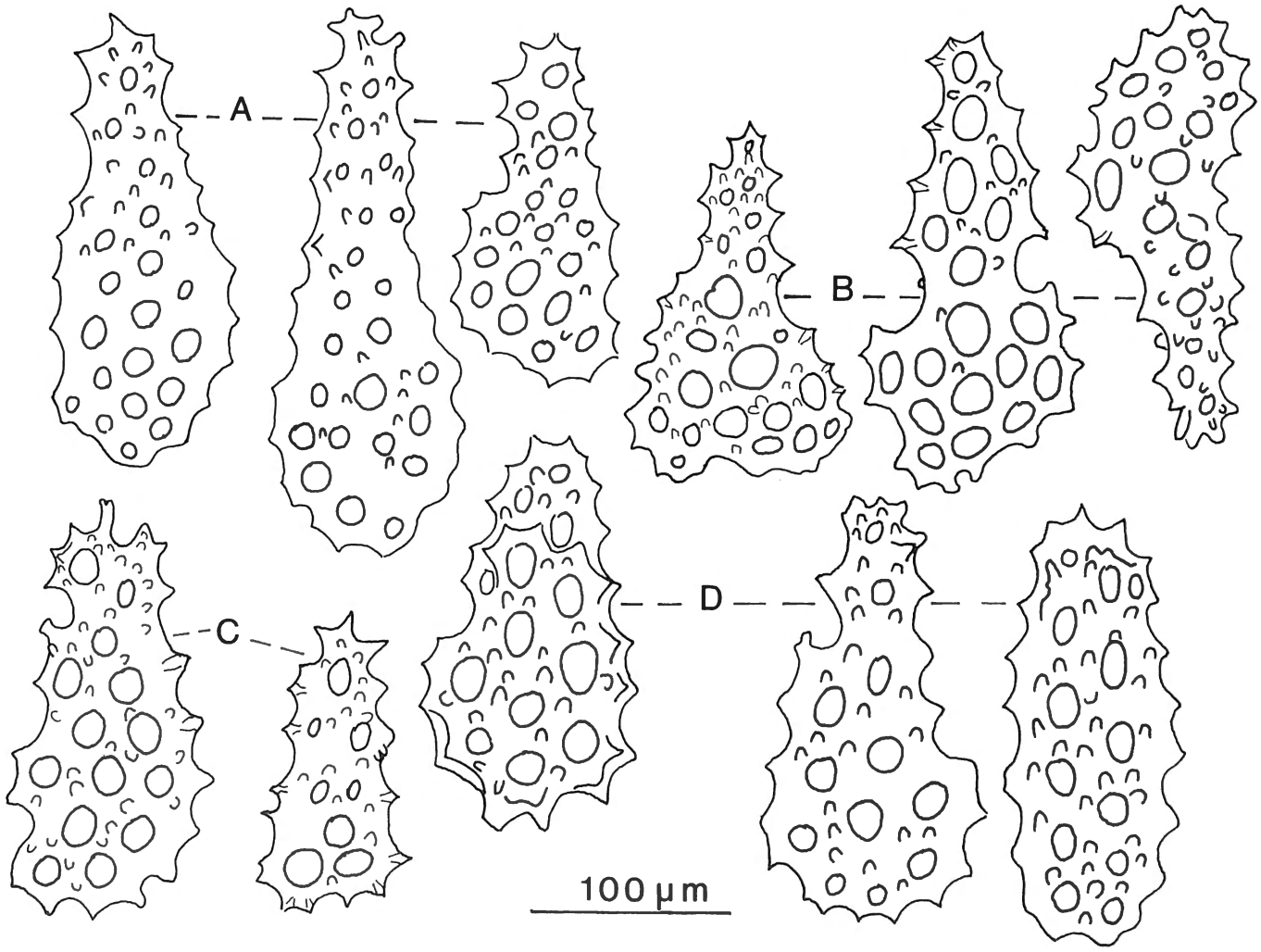
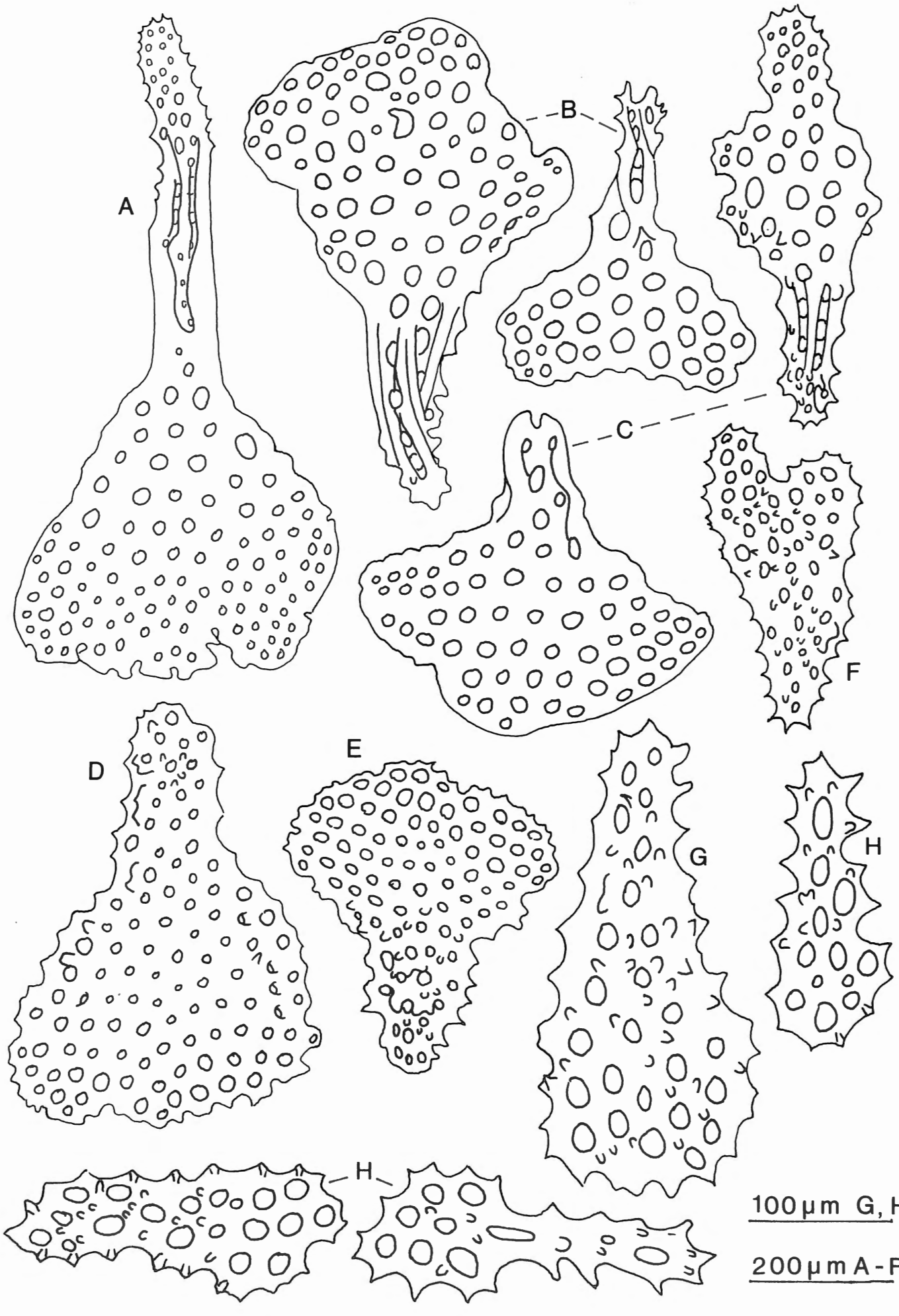


Fig. 7 – Heterocucumis steineni *(Ludwig, 1898). Body wall ossicles : type 3 (BW3). A : 270 AGT 15 - sub 1. L = 17 mm; B : 261 BPN 6 - sub 9. L = 30 mm; C : 284 GSN 13 - sub 2. L = 60 mm; D : 284 GSN 13 - sub 2. L = 70 mm.*


A
B
C
D
E
F
G
H
H
100µm G, H
200µm A-F

Tube foot and tentacle ossicles also show variations with body size.

Four types of ossicle are present in the tube feet : TF1, TF2, TF3 & TF4.

— TF1. V-shaped, mostly smooth rods (100-200 µm long) with a small centro-lateral perforated and denticulate process (fig.10). Rod ends are slightly swollen and perforated.

— TF2. Smooth perforated plates, more or less rounded (100-130 µm in diameter) (fig. 11).

— TF3. V-shaped spiny rods (150-300 µm long) with a very large centro-lateral perforated and denticulate process (fig. 12).

— TF4. Spiny perforated plates (100-320 µm long) of varying shapes (fig. 13).

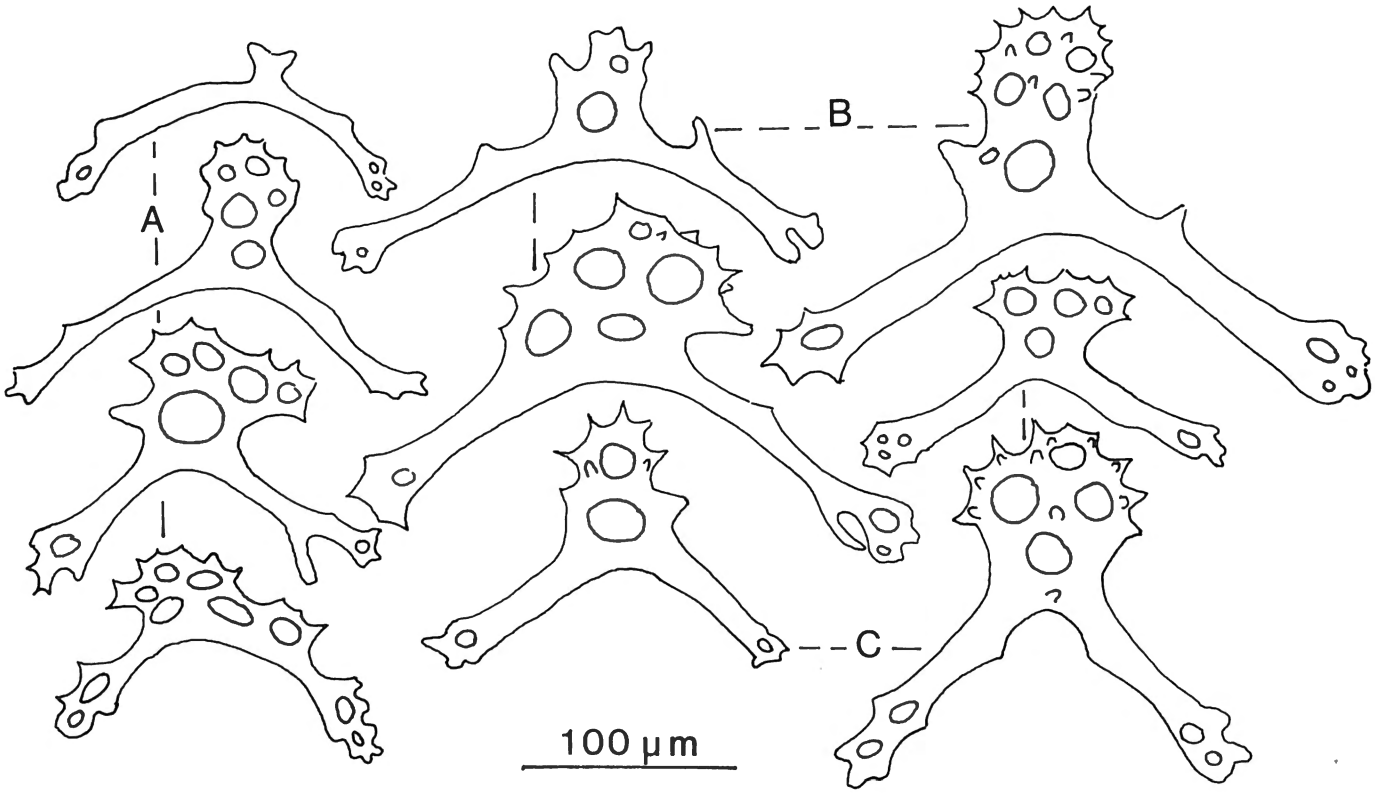


Fig. 10 – Heterocucumis steineni *(Ludwig, 1898). Tube foot ossicles : type 1 (TF1). A : 284 GSN 13 - sub 26. L = 4.5 mm; B : 284 GSN 13 - sub 7. L = 13.8 mm; C : 248 GSN 10 - sub 47. L = 16 mm.*

◁ Fig. 9 – Heterocucumis steineni *(Ludwig, 1898). Anal ossicles. A : 284 GSN 13 - sub 22. L = 10 mm; B : 248 GSN 10 - sub 47. L = 16 mm; C : 248 GSN 10 - sub 14. L = 18 mm; D : 211 GSN 1 - sub 1. L = 37 mm; E : 284 GSN 13 - sub 2. L = 50 mm; F & G : 284 GSN 13 - sub 2. L = 60 mm; H : 273 AGT 17 - sub 2. L = 60 mm.*

Very young specimens (4-12 mm long) have TF1 & TF2 types in the tube feet, TF2 being the dominant one. From 14 mm long, TF3 ossicles appear, and TF1 disappear. Beyond 25 mm long, TF1 are absent. TF2 are always present, even in the largest specimens (fig. 11), and vary little from small to large specimens. TF4 appear only in specimens > 25 mm long. Figure 8 summarizes these changes. The proportions of TF2, TF3 and TF4 vary greatly between specimens. Very often TF2 and TF4 are dominant. With increasing body size the number of ossicles is slightly reduced in the tube feet, but they are always present.

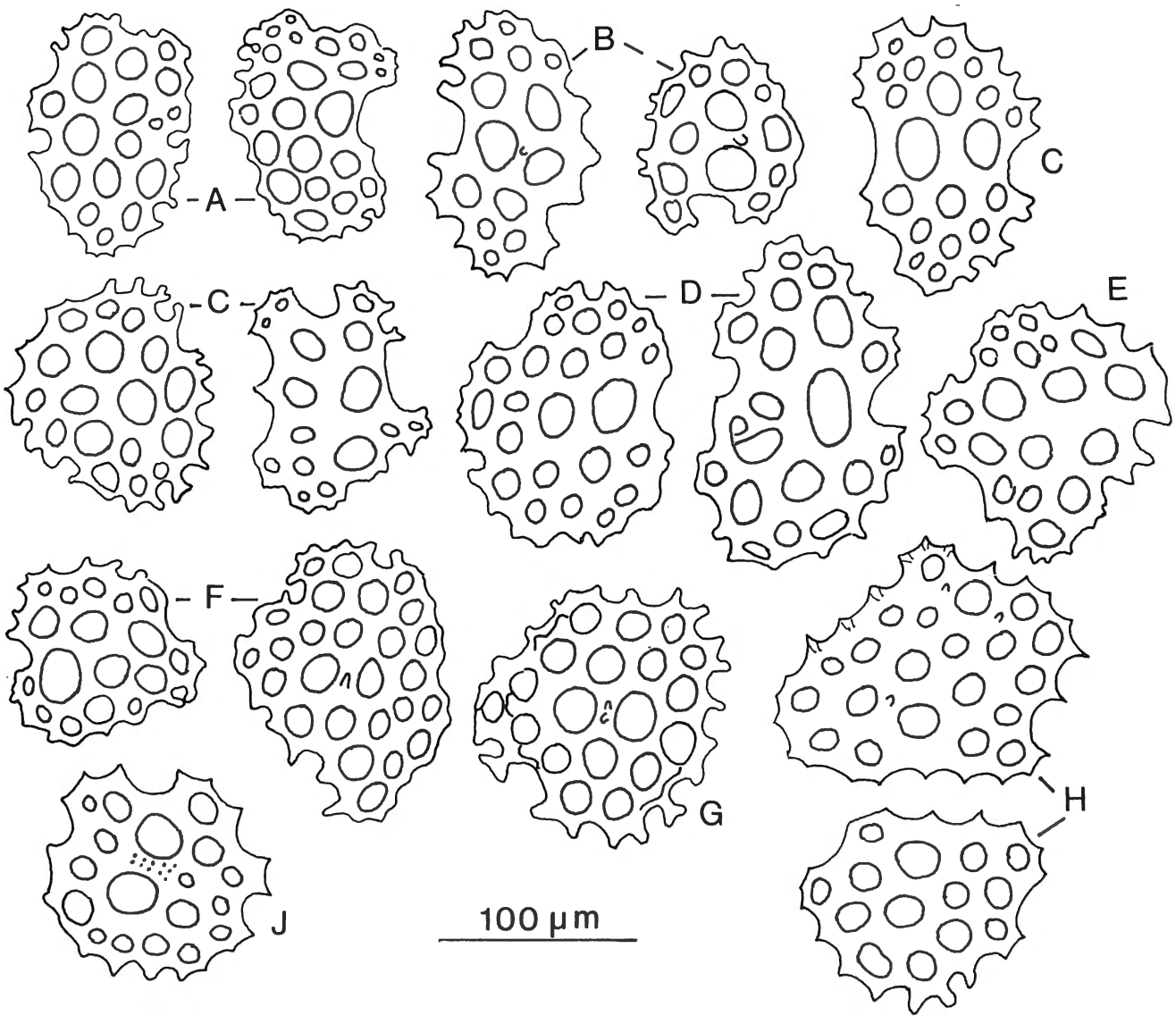


Fig. 11 – Heterocucumis steineni *(Ludwig, 1898). Tube foot ossicles : type 2 (TF2). A : 284 GSN 13 - sub 22. L = 10 mm; B : 284 GSN 13 - sub 7. L = 13.8 mm; C : 273 AGT 17 - sub 2. L = 20 mm; D : 273 AGT 17 - sub 2. L = 25 mm; E : 211 GSN 1 - sub 1. L = 35 mm; F : 284 GSN 15 - sub 2. L = 40 mm; G : 284 GSN 13 - sub 2. L = 50 mm; H : 273 AGT 17 - sub 2. L = 60 mm; J : 284 GSN 13 - sub 2. L = 70 mm.*

The tentacles have numerous perforated plates whose number and size decrease with increasing body size. These plates are elongate (fig. 14), rounded (fig. 15) or triangular (fig. 16). They are 100-400 µm long. The larger the holothurian, the more spiny are the plates. The diameter of their perforations varies from 10 to 45 µm.

The shape and size of each kind of ossicle of *H. steineni* change little (see BW1, fig. 5) or not at all (see TF2, fig. 11) with increasing body size, whereas the proportion of the different kinds of ossicles varies greatly, some early ossicles being replaced by new ones.

As a general trend, with increasing body size the ossicles of *H. steineni* show a succession of different forms,

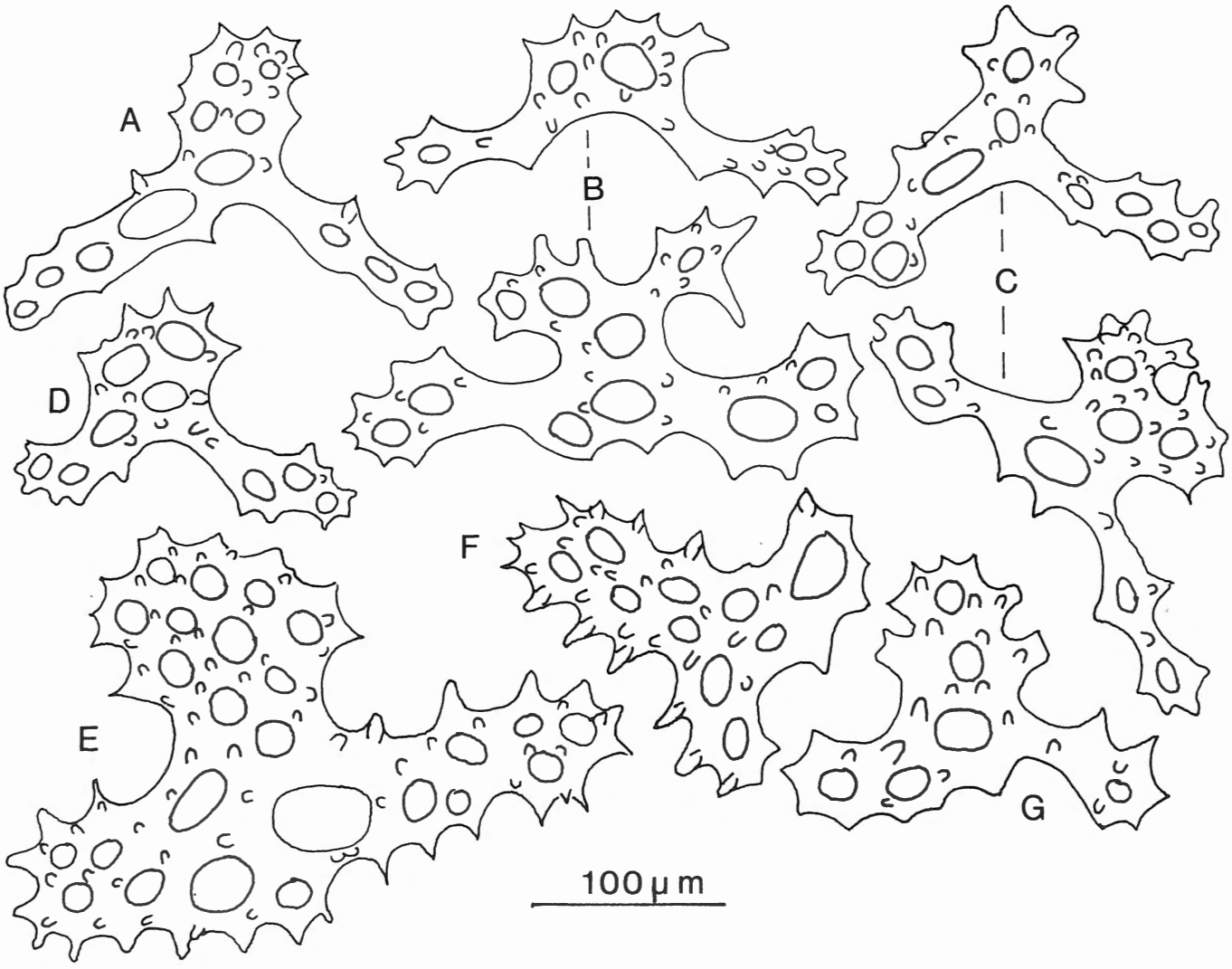


Fig. 12 – Heterocucumis steineni *(Ludwig, 1898). Tube foot ossicles : Type 3 (TF3). A : 248 GSN 10 - sub 47. L = 16 mm; B : 284 GSN 13 - sub 2. L = 37 mm; C : 284 GSN 13 - sub 2. L = 40 mm; D : 284 GSN 13 - sub 2. L = 50 mm; E : 284 GSN 13 - sub 2. L = 60 mm; F : 273 AGT 17 - sub 2. L = 60 mm; G : 284 GSN 13 - sub 2. L = 70 mm.*

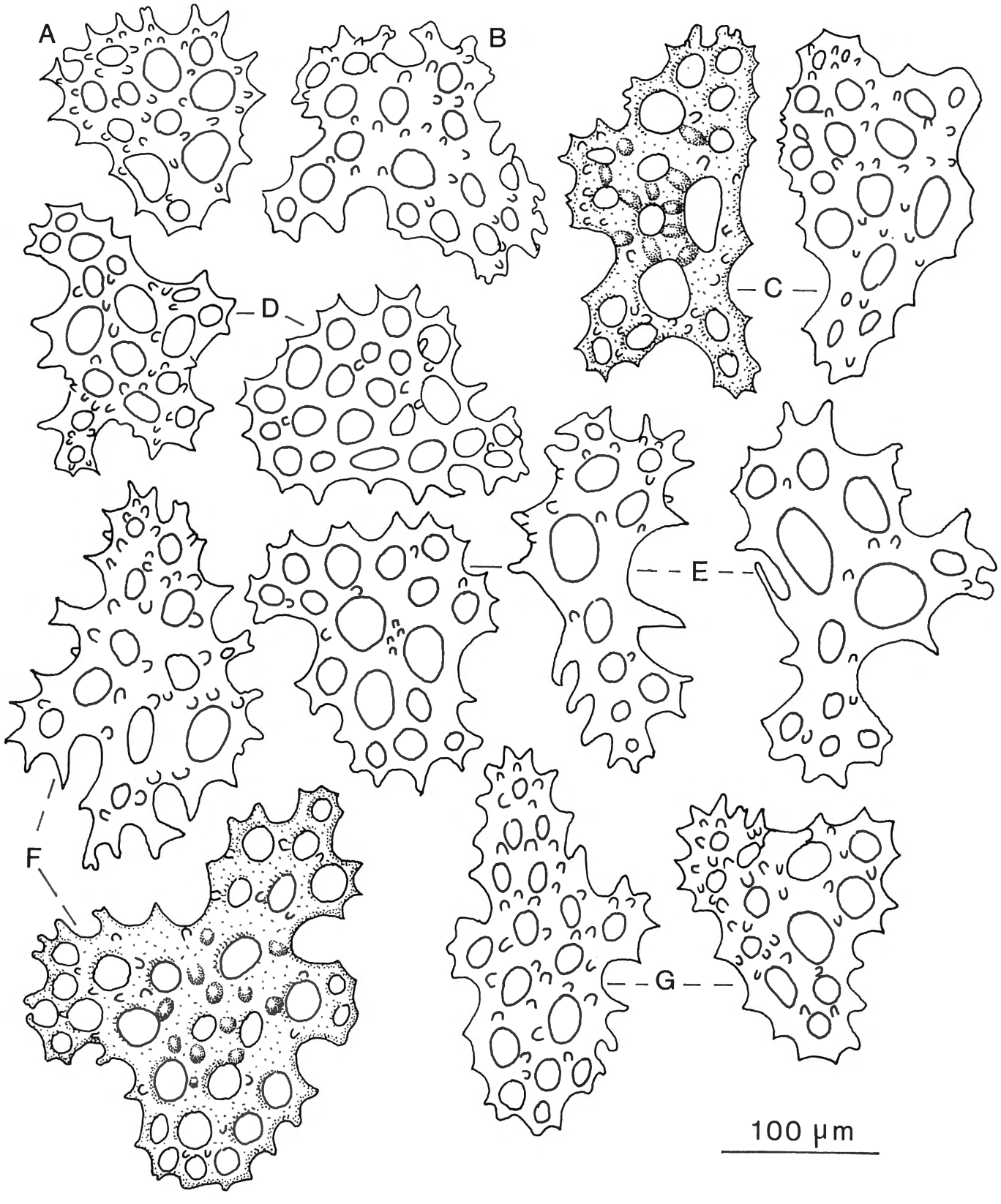


Fig. 13 – Heterocucumis steineni *(Ludwig, 1898). Tube foot ossicles : type 4 (TF4). A : 273 AGT 17 - sub 2. L = 25 mm; B : 211 GSN 1 - sub 1. L = 35 mm; C : 284 GSN 13 - sub 2. L = 37 mm; D : 284 GSN 13 - sub 2. L = 50 mm; E : 284 GSN 13 - sub 2-1. L = 60 mm; F : 284 GSN 13 - sub 2-2. L = 60 mm; G : 284 GSN 13 - sub 2. L = 70 mm.*

decrease in number, and become increasingly spiny. However, there may be large variations from one specimen to another. For example, ossicles which have disappeared from the body wall of some specimens 20-25 mm long, are still present in specimens 40-60 mm long.

Discussion

The present observations confirm the view of EKMAN (1927) that *Heterocucumis steineni*, *H. antarctica* and *H. godfroyi* are a single species, *H. steineni*. The *H. godfroyi* are small specimens (< 20 mm long) and the *H. antarctica* are large specimens (> 40 mm long) of *H. steineni*.

EKMAN (1925, 1927) noticed three kinds of ossicles in the body wall of *H. steineni*. He called them large, middle and small types. EKMAN's large ossicles correspond to the BW1 and BW2 types, whereas the small ones correspond to the BW3 type. Middle size type sensu EKMAN was mainly observed around the anus of large specimens (> 50 mm long). The present observations show that the ossicles of the tube feet and the tentacles also change in their proportions with increasing body size.

This study of growth series in *H. steineni* shows that the main ossicle changes occur in specimens shorter than 20 mm. CHERBONNIER's study (1941) was based on VANEY's *H. antarctica*, that is to say, mainly on large specimens (60-130 mm long). This is why he observed

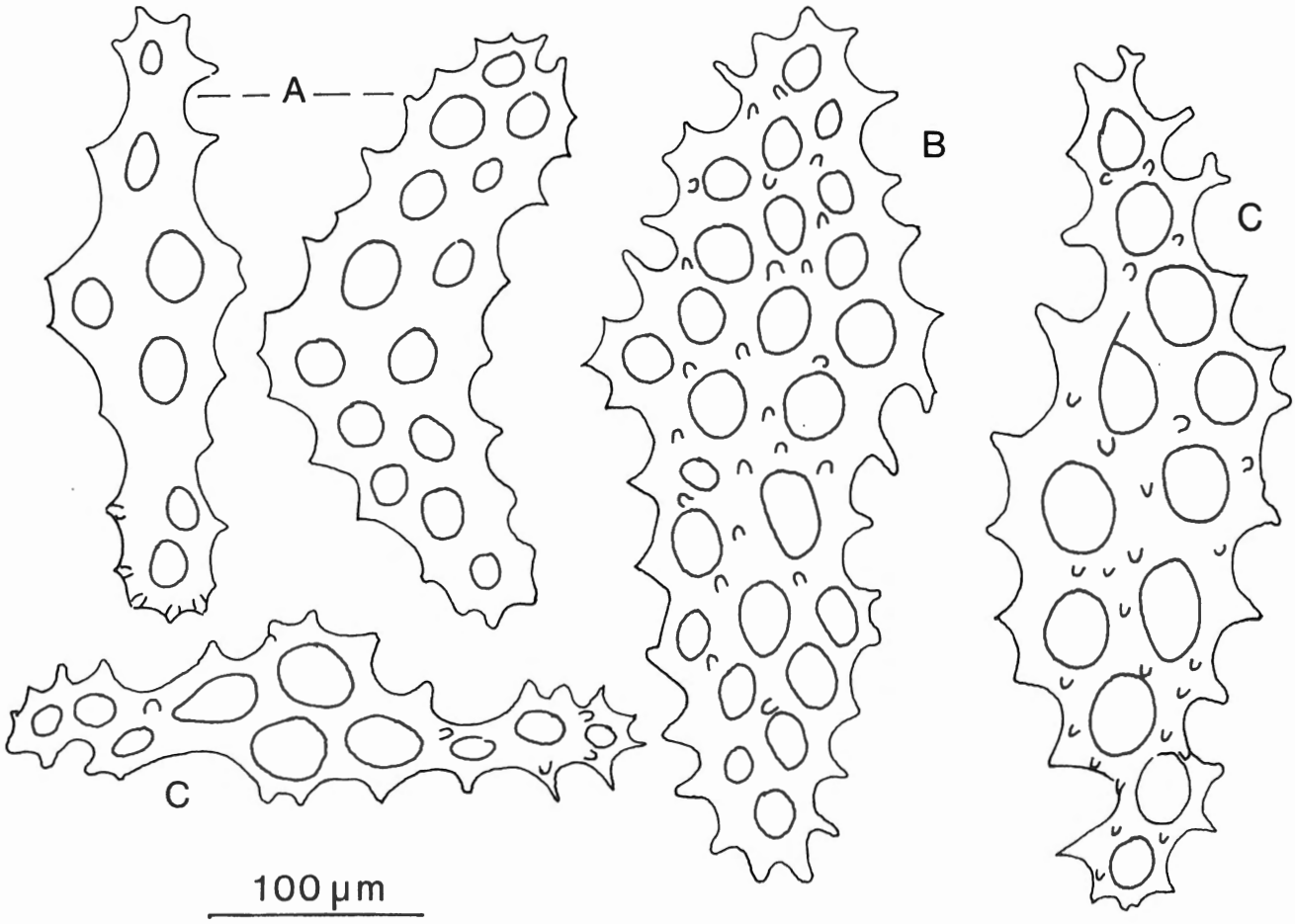


Fig. 14 – Heterocucumis steineni *(LUDWIG, 1898). Tentacle ossicles : elongate plates. A : 284 GSN 13 - sub B. L = 17 mm; B : 273 AGT 17 - sub 2. L = 26.4 mm; C : 248 GSN 10 - sub 6. L = 30 mm;*

very spiny ossicles, and none characteristic of juveniles. In other species, the main ossicle change (replacement of early ossicles by new ones) occurs even earlier, when the specimens are no longer than 10-13 mm, as observed for *Heterocucumis denticulata* (EKMAN, 1927; this study), or even 6 mm, as observed for *Staurocucumis liouvillei* (EKMAN, 1927; HANSEN, 1988; this study).

The study of holothurian growth series questions the validity of some species (see LUDWIG, 1894; EKMAN, 1927; HANSEN, 1988) and even of some genera (see CLARK, 1907; FÉRAL, 1980b). The taxonomic status of many Antarctic dendrochirotes, known only from juveniles or ossicle-free adults (see e.g. VANEY, 1906, 1909, 1914), needs revision.

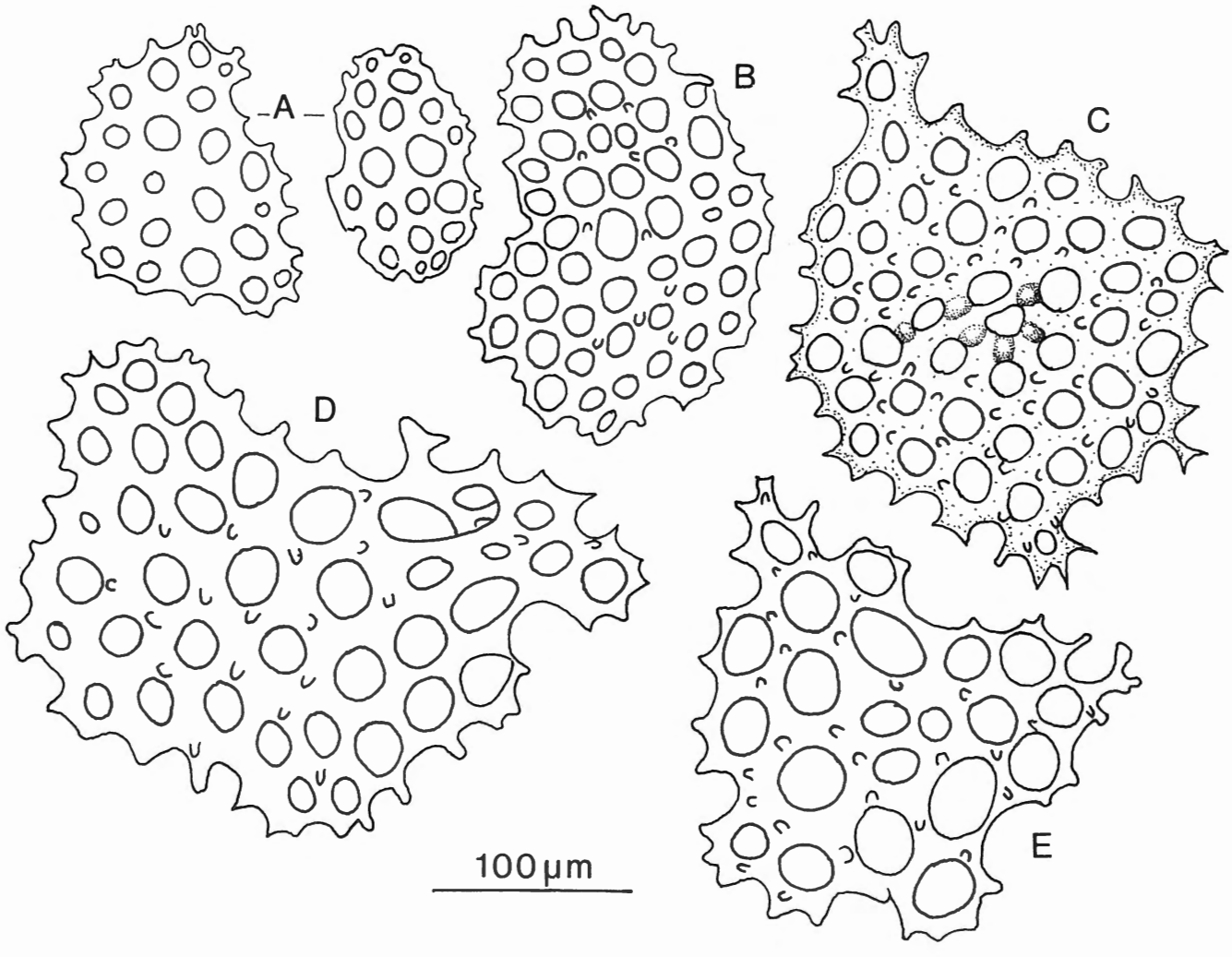


Fig. 15 – Heterocucumis steineni *(LUDWIG, 1898). Tentacle ossicles : rounded plates. A : 284 GSN 13 - sub B. L = 17 mm; B : 273 AGT 17 - sub 11. L = 19 mm; C : 284 GSN 13 - sub B. L = 19 mm; D : 273 AGT 17 - sub 2. L = 26.4 mm; E : 284 GSN 13 - sub 6. L = 30 mm.*

Ossicle variation with increasing body size has brought a lot of taxonomic confusion, mainly for dendrochirote holothurians. Nevertheless, ossicle variation must be considered a positive character to be incorporated in species or genus diagnosis whenever possible, as already done by HEDING (1942b) for *Staurocucumis* and *Ekmocucumis*. The suggestion of FÉRAL (1980a) that the size of specimens is very important when studying ossicles is here confirmed. Moreover, ossicle variation, particularly in early juveniles, throws light on evolutionary lines within the order Dendrochirotida (HANSEN, 1988). However, up to now, growth series have been studied only occasionally because of the lack of very young specimens. The relationship between ossicle changes and increasing size, and physiological, ecological or geographical data is unknown.

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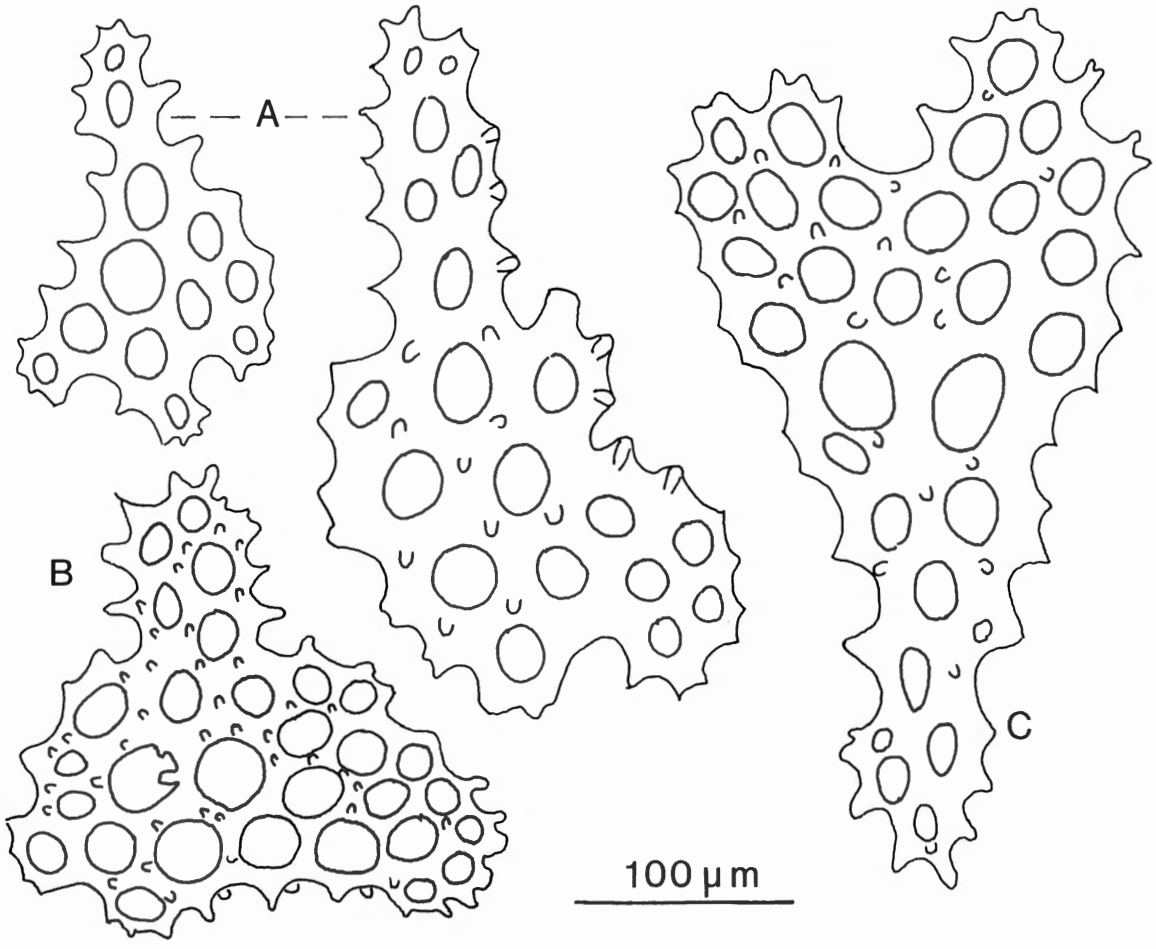

Fig. 16 – Heterocucumis steineni *(LUDWIG, 1898). Tentacle ossicles : triangular plates. A : 284 GSN 13 - sub B. L = 17 mm; B : 273 AGT 17 - sub 11. L = 19 mm; C : 273 AGT 17 - sub 2. L = 26.4 mm.*

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