A REVIEW OF THE FAMILY HOLOTHURIIDAE (HOLOTHURIOIDEA: ASPIDOCHIROTIDA)

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A REVIEW OF THE FAMILY HOLOTHURIIDAE (HOLOTHURIOIDEA: ASPIDOCHIROTIDA)

By F. W. E. ROWE

SYNOPSIS

Since the attempts of Pearson (1914) and Panning (1929–35) to revise or subdivide the genus *Holothuria* Linnaeus, 1767 in order to try and show natural affinities between the included species, Deichmann (1958) has been the only specialist in this field to attempt such a task. None of these specialists was able to make a complete survey due to lack of material of certain species.

On the basis of the holothurian collections of the British Museum and the existing literature, an attempt is made in this paper to deal with the balance of those species not taken into consideration by Deichmann and to bring her system into line with the Rules of Nomenclature.

Excluding those of *Actinopyga*, *Bohadschia* and *Labidodemas*, the number of species of *Holothuria* considered to be valid at present is about 114. These can be grouped into 17 more or less clearly distinct supraspecific taxa, four of them new, of varying degrees of differentiation. Some of these groups can be arranged in sequence using the complexity of the spicules as a major criterion.

HISTORICAL INTRODUCTION

UNTIL recently six nominal genera of Holothuriids have been commonly accepted, these being *Holothuria* Linnaeus, 1767, *Actinopyga* Bronn, 1860 (a replacement name for *Muelleria* Jaeger, 1833, pre-occupied), *Bohadschia* Jaeger, 1833, *Microthele* Brandt, 1835, *Labidodemas* Selenka, 1867 and *Halodeima* Pearson, 1914. The last five have been treated as being of subgeneric rank by some authors.

In 1924 (Opinion 80) the generic name *Holothuria* Linnaeus, 1767, as restricted by Brugière, 1791, with type-species *H. tremula* Linnaeus, 1767 (non Gunnerus, 1767) = *H. tubulosa* Gmelin, 1790, was placed on the Official List of Generic Names in Zoology. This action therefore firmly established the generic name *Holothuria* in the present sense rather than the original one of Linnaeus, 1758, when it included only species other than Echinoderms.

This validation was evidently overlooked by Deichmann (1958), who considered that the name *Holothuria* Linnaeus (i.e. sensu 1758) would be better discarded and the species previously included in it divided up into a number of separate genera. She accordingly put forward 13 generic names of which 11 were new to science. Although in doing this Deichmann has disregarded a number of appropriate prior genus-group names of Brandt (1835), Jaeger (1833), Haacke (1880) and Pearson (1914) on the grounds of poor definition, most of these names *are* available under the Rules, being associated with recognized species, those of Jaeger and Brandt needing only designations of type-species in order to qualify for recognition under the Rules.

Despite her non-conformity, Deichmann's revision is of considerable importance in the field of holothurian taxonomy, since it reduces the unwieldy mass of species formerly included in *Holothuria* into more manageable groups within which there

appears to be greater affinity. However, Deichmann was dealing predominantly with species of the East Pacific area and left unconsidered a number of others from different parts of the world, so that her revision was necessarily incomplete.

In an attempt to stabilize the nomenclature, a proposal has been submitted to the International Commission of Zoological Nomenclature (A. M. Clark & F. W. E. Rowe, 1967*a*) requesting that certain of Brandt's and Jaeger's names for supraspecific taxa be formally rejected by use of the plenary powers, or else be reduced to synonymy by selection of appropriate type-species. However, we considered that there is no case for ignoring the priority of both *Cystipus* Haacke, 1880 and *Thymiosicya* Pearson, 1914, of which *Fossothuria* and *Brandtothuria* both of Deichmann, 1958, are respectively junior synonyms.

Deichmann (1958) designated *Holothuria sanctori* Delle Chiaje as type-species of Brandt's *Microthele*. This is inadmissible since *sanctori* was not among the species listed by Brandt. Accordingly we designated *H.* (*Microthele*) *maculata* Brandt as type-species, for which the proper name is *H.* (*Microthele*) *nobilis* (Selenka) since *maculata* Brandt is a junior homonym.

The group of species included by Deichmann under the name *Microthele* is not consubgeneric with *nobilis* and must therefore be found a new genus-group name.

The intricacies of the nomenclatorial problems which have arisen from Deichmann's work are dealt with in the submission to the International Commission. However, in this paper I give a full list of the supraspecific taxa represented in the family Holothuriidae together with a diagnosis and a list of species referable to each, besides a key to these supraspecific taxa. The figures given in the text are original with the exception of Text-fig. 11; where practicable these have been taken from type-species.

CLASSIFICATION

The identification of all genera and species of holothurians depends almost entirely on the form and combinations of the calcareous spicules found in the body wall and podia. These are commonly subdivided into three-dimensional ones (i.e. tables) near the surface and two-dimensional ones (e.g. buttons; rods) deeper in the body wall, though in some taxa (e.g. *Actinopyga, Bohadschia, Selenkothuria*) the necessity for roughening the surface seems to be absent and only one kind of spicule—two-dimensional branched rods or flat plates—is present.

The form of the calcareous ring and the arrangement of the tube feet also provide useful taxonomic characters. A similar conclusion, for the Dendrochirotida at least, has been reached by Pawson & Fell (1965). Other anatomical characters such as the number and arrangement of the tentacles, the presence or absence of anal ' teeth ' or papillae, polian vesicles, stone canals and cuvierian organs are variable to some extent even within species and therefore can rarely be used satisfactorily in classification.

DISCUSSION

Previous studies of spicules, confirmed by my own observations, have shown that spicule complexity forms a sound basis for recognizing groups of species within *Holothuria* sensu extenso. This was done by Pearson (1914) who divided *Holothuria*

into five subgenera *Bohadschia* Jaeger, *Actinopyga* Bronn and three new subgenera *Argiodia, Halodeima* and *Thymiosycia*. He believed that by elaboration of the simple branched rods and rosettes of the species of *Actinopyga* and *Bohadschia*, perforated plates and later buttons and tables could have developed. He substantiated his conclusion by considering that the form of the calcareous ring in *Actinopyga* and *Bohadschia*, lacking anterior and posterior projections and having deep ampullary notches (shown as deep scallops on the anterior margin of the ring), is primitive in comparison with the form of the calcareous ring in *Argiodia, Halodeima* and *Thymiosycia* which shows marked anterior projections of the radial and interradial plates, the projections being clearly separated by a deep indentation; the radial plates are also markedly longer than the interradial plates. Although he laid little store on the taxonomic value of the presence or absence of anal ' teeth ' or papillae, Pearson did consider that the arrangement of the tube feet also gives support to his theory that *Actinopyga* and *Bohadschia* are more primitive than his three new subgenera. Pearson dealt only with a few species from the Indian Ocean, so his revision was incomplete.

Panning (1929–35), in his revision of *Holothuria*, recognized *Actinopyga* and *Bohadschia* with *Microthele* as subgenera and arranged the remaining 113 species which he recognized in small rather ill-defined and nameless groups within *Holothuria* sensu stricto. This arrangement was due, notes Deichmann (1958), to ' his dependence in too many cases on the accounts of earlier writers; hence ' she says ' many errors have been perpetuated and related forms have been placed far apart '. Later (1939) Panning revised his treatment of *Holothuria*. He was unsure of the relationships between *Actinopyga* and *Bohadschia* since he did not consider the presence or absence of anal papillae as of great importance, but concluded that there could be no close relationship between *Actinopyga* and *Microthele*, the possession of anal papillae in both being the result of a convergence; accordingly he raised all three to generic rank. He also considered that the formation of ellipsoidal bodies found in *Holothuria arguinensis* and *H. mammata* is again a convergence attributable in this case to geographical affinity, the bodies of the former being formed from rosettes and of the latter from buttons. Simultaneously he revised his earlier view that rosettes, as found in *H. edulis* and *H. poli*, are a modified form of button. This presumably followed his studies of the optical properties of various spicules between 1928 and 1935 in which field one of the leaders was Schmidt (1925, 1930) who had concluded that the spicules of holothurians, like the plates of other echinoderms, consist of a single crystal of calcite and that the position of the optical axis of this crystal is of taxonomic importance.

However, Hampton (1958) in making a chemical analysis of the spicules of a *single* specimen of *Holothuria impatiens* suggested that variations in the optical axis might be due to the differing concentrations of Magnesium present in the spicules, a feature correlated with differences in the temperature of the sea water. He concluded that if this were so then the position of the axis is only of importance as an ecological rather than a taxonomic factor. Clearly further research into the optical properties of spicules must be carried out before their true value in the taxonomy of holothurians can properly be assessed.

Deichmann (1958) draws (though not directly) a correlation between ecology and the form of the spicules. In her revision of *Holothuria* there appear to be three main ecological divisions:

a. Surf-zone species found clinging to rocks. These have terminally-placed bushy tentacles which Deichmann considers may function in the capture of planktonic food; the external layer of tables is usually totally absent, the spicules being represented by rods or plates. These are referable to the taxon *Selenkothuria*, notably *H.* (*Selenkothuria*) *lubrica*, *H.* (*S.*) *glaberrima* and *H.* (*S.*) *moebii*.

b. Fugitive species, i.e. those found usually partly concealed under coral fragments, sand, rocks etc. These have terminally- or ventrally-placed peltate tentacles; their spicules comprise tables in combination with either buttons, rods, rosettes or pseudobuttons but the two-dimensional spicules are usually smooth structures not possessing knobs. These are referable to the taxa *Thymiosycia* Pearson (including *Brandtothuria* Deichmann) notably *H.* (*Thymiosycia*) *impatiens* and *H.* (*T.*) *arenicola; Lessonothuria* notably *H.* (*Lessonothuria*) *pardalis; Mertensiothuria* notably *H.* (*Mertensiothuria*) *leucospilota; Semperothuria* notably *H.* (*Semperothuria*) *languens; Irenothuria* notably *H.* (*Irenothuria*) *maccullochi; Vaneyothuria* notably *H.* (*Vaneyothuria*) *lentiginosa; Halodeima* Pearson (including *Ludwigothuria* Deichmann) notably *H.* (*Halodeima*) *atra* and a new taxon in place of *Microthele* sensu Deichmann non Brandt, with type-species *Holothuria difficilis* Semper.

c. Fossorial species, i.e. those capable of burrowing or digging, found buried more or less completely in the substrate. These have relatively small, terminally- or ventrally-placed, peltate tentacles; their spicules comprise knobbed buttons and tables, either kind of spicule becoming elaborated into fenestrated ellipsoidal or spherical bodies. These are referable to the taxa *Cystipus* Haacke (including *Fossothuria* Deichmann and *Jaegerothuria* Deichmann) notably *H.* (*Cystipus*) *rigida* and *H.* (*C.*) *inhabilis;* also *Theelothuria* notably *H.* (*Theelothuria*) *princeps*.

As a summary of Deichmann's work I give here a table of the supraspecific taxa with their type-species represented in her paper together with their present disposition. This is followed by a complementary list of the new taxa described here.

Genus-group name	Type species	Present disposition
Labidodemas Selenka, 1867	*L. semperianum* Selenka, 1867	Valid genus
Microthele: Deichmann, 1958 (non Brandt, 1835)	*Holothuria sanctori* Delle Chiaje, 1823	*Holothuria* (*Platyperona*) subg. nov.; type-species *Holothuria difficilis* Semper, 1868
Brandtothuria Deichmann, 1958	*H. arenicola* Semper, 1868	*H.* (*Thymiosycia*) Pearson, 1914; type species *Fistularia impatiens* Forskaal, 1775
Lessonothuria Deichmann, 1958	*H. pardalis* Selenka, 1867	Valid subgenus
Mertensiothuria Deichmann, 1958	*Stichopus leucospilota* Brandt, 1835	Valid subgenus
Semperothuria Deichmann, 1958	*Holothuria languens* Selenka, 1867	Valid subgenus
Irenothuria Deichmann, 1958	*I. maccullochi* Deichmann, 1958	Valid subgenus

Vaneyothuria Deichmann, 1958	*Holothuria lentiginosa* v. Marenzeller, 1893	Valid subgenus
Ludwigothuria Deichmann, 1958	*H. atra* Jaeger, 1833	*Holothuria* (*Halodeima*) Pearson, 1914; type-species *H. atra* Jaeger, 1833
Selenkothuria Deichmann, 1958	*H. lubrica* Selenka, 1867	Valid subgenus
Fossothuria Deichmann, 1958	*Stichopus rigidus* Selenka, 1867	*H.* (*Cystipus*) Haacke, 1880; type-species *C. pleuripus* Haacke, 1888, a junior subjective synonym of *rigidus* Selenka, 1867
Jaegerothuria Deichmann 1958	*Holothuria inhabilis* Selenka, 1867	*H.* (*Cystipus*) Haacke, 1880
Theelothuria Deichmann, 1958	*H. princeps* Selenka, 1867	Valid subgenus

NEW TAXA:	TYPE-SPECIES DESIGNATED HERE
Acanthotrapeza subg. nov	*Holothuria pyxis* Selenka, 1867
Metriatyla subg. nov.	*H. scabra* Jaeger, 1833
Panningothuria subg. nov. . . .	*H. forskali* Delle Chiaje, 1823
Platyperona subg. nov.	*H. difficilis* Semper, 1868
Stauropora subg. nov.	*H. discrepans* Semper, 1868

Deichmann considered that of the species which have been included in *Holothuria*, excluding *Actinopyga* and *Bohadschia*, ' the most primitive are undoubtedly those with numerous, regular tables and smooth, regular buttons ' she continues ' a more advanced stage is indicated by the presence of irregular buttons or development of rosettes or reduction of the inner layer of spicules while the tables have become variously modified '. This implies that the rosettes to be found in certain species have developed as a result of reduction of buttons rather than an advancement on branched rods as Pearson considered. It further implies, if this concept is correlated with Deichmann's ecological divisions, that the role of the tables or other three-dimensional spicules is to provide a roughened body surface to give frictional support to the fossorial species, the degree of roughness or complexity of the spicules being related to the degree to which the species is fossorial. Conversely, in the species of *Holothuria* (*Selenkothuria*) (that is surf-zone species found in more exposed places such as rock crevices, and presumably not at all fossorial in habit) frictional support is not important and the outer layer of tables is lacking leaving only plates and rods, though these may be rather spinose but in a single plane. This may also account for the simplification of the spicules in the species of *H.* (*Mertensiothuria*), *H.* (*Ireno-thuria*), *H.* (*Holothuria*), *H.* (*Stauropora*) and *H.* (*Panningothuria*) with fugitive but not necessarily fossorial habits.

With regard to the fossorial habits of Aspidochirotes I can trace no studies of the role of the podia in burrowing. The extent of crowding of the locomotory podia (pedicels) on the rather flattened ventral surface and the specialization of wart-like sensory podia (papillae) on the arched dorsal surface contrasts markedly with the arrangement in such fossorial genera and species as the dendrochirotids *Echinocu-cumis* and *Thyone* with unmodified podia scattered all over the body surface, the

species apparently ' ploughing into the substrate dorsal side up through alternate circular and longitudinal contractions until the middle region is buried ' according to Hyman (1955). This process is facilitated by the attachment of the podia to any solid objects. The arrangement of the podia of Aspidochirotes therefore suggests that they are not active burrowers but are capable only of pushing into or under *loose* sand, fragmentary substrates or boulders and rocks, this being aided by the frictional support afforded to the bodywall by the spicules. The degree to which the species are fossorial is probably directly proportional to the degree of complexity of the spicules they possess.

It must be mentioned that the fossil history of holothurians is little known. However, according to Pawson (1966) the earliest holothurians are believed to be extensively plated forms in line with other members of the Echinozoa, the most primitive extant genus being *Placothuria* Pawson & Fell 1965 (a dendrochirote). Unfortunately Pawson only deals in detail with the Dendrochirotida briefly mentioning that ' no special attention has been directed towards the other holothurian assemblages '.

Contrary therefore to Deichmann's conclusions, it seems to me more likely that the fossorial habit, correlated with multiplicity of spicule form and with compact aspidochirotid peltate tentacles adapted to sweeping the substrate en masse into the mouth, evolved from the exposed rock-clinging habit correlated with simplicity of spicule form and with arborescent tentacles adapted for suspension feeding. The taxon *Selenkothuria* with only plate-like spicules[1] together with tentacles of the more arborescent form, approximating to that of the suspension-feeding dendrochirotids of non fossorial or fugitive habit, may therefore represent the primitive condition. This line of reasoning follows closely the implication by Pawson (1966) that the extensively-plated dendrochirotes are probably the most primitive holothurians. The direction of evolution within the holothuriids is still not clear, however, so it may be that the condition in *Selenkothuria* represents a secondary reversion.

It seems to me worthwhile to draw up a hypothetical evolutionary tree for the holothuriid taxa (Text-fig. 1) based on spicule complexity. The speculations involved here should at least form a basis for future argument.

Clearly before the full significance of spicule form as an indicator of affinity between the groups of species can be recognized much more field work is needed on their ecology. This is especially the case since many taxa now established are subsequent to Deichmann's work and their ecology has not yet been sufficiently correlated with her rather neat conception of the ecology and taxa of Eastern Pacific species, a project I am unfortunately not in a position to complete. The optical properties of spicules and their changes during ontogeny also need further study since it is well known that in the few species studied the spicules of juvenile, adult and sometimes senescent specimens often differ considerably. It is not known how long-lived the individual spicules are; whether they are replaced or modified with age.

As for the rank which should be accorded to Deichmann's taxonomic groups of *Holothuria* sensu extenso and the new ones added here, having regard to the evidence

[1] Rudimentary tables are said to occur in a few species such as *H.* (*Selenkothuria*) *moebii* and *erinaceus* although I could not find any in the few specimens available.

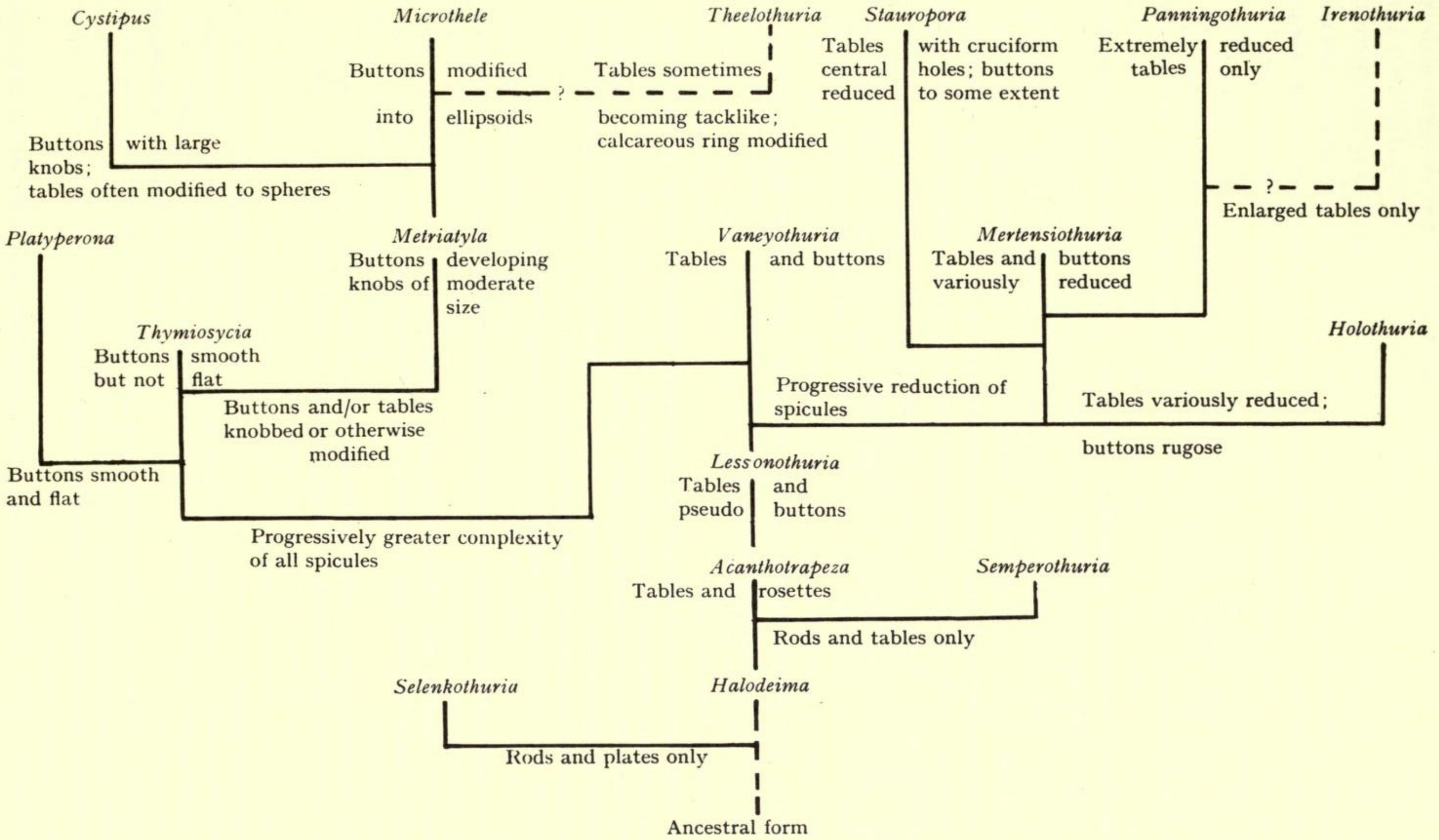

FIG. 1. Provisional hypothetical evolutionary tree of the subgenera of *Holothuria*. (see also table on p. 165).

already outlined, the varying degrees of differentiation between the groups of species and the present climate of opinion, I believe that a conservative attitude is the best one to adopt and therefore consider that they should be regarded as *subgenera* rather than *genera* as Deichmann (1958) treated them. Since Deichmann's division of *Holothuria* only Tikasingh (1963) in his first paper on holothurians, and clearly on Deichmann's advice, has completely adopted her division at generic level. Caso (1963, 1964 and 1965), though distinguishing two new taxa *Holothuria* (*Paraholothuria*) (1963) and *Microthele* (*Paramicrothele*) (1964), recognized (in 1965), only *Irenothuria* Deichmann, as a distinct genus referring other Mexican species back to *Holothuria*.

To my knowledge no other specialists have yet cared to commit themselves one way or the other with regard to Deichmann's division of *Holothuria*.

The body form, spicules and calcareous ring of the species of *Actinopyga* and *Bohadschia* appear to me incompatible with those of the remainder of species under consideration, accordingly no attempt is made here to treat them as anything other than valid genera. Also I have continued so to treat *Labidodemas*, distinguished by its cylindrical body form with podia restricted to the ambulacra and by its calcareous ring. The only similarity to *Holothuria* it bears is in possessing tables and sometimes buttons as spicules. In truth I think *Labidodemas* may even prove to warrant separation at family level.

The following key to the supra-specific taxa of the family Holothuriidae should serve to place species of unknown position.

1 Spicules: very numerous branched rods, usually dichotomously lobed; tables, buttons, rosettes, perforated plates *never* present 2

1′ Spicules: tables of some form nearly always present; buttons, rods, rosettes, perforated plates present or absent; dichotomously lobed rods, if present, then only in combination with tables, *never* on their own. 3

2 Anus guarded by five enlarged calcified papillae or anal 'teeth' genus ***ACTINOPYGA*** Bronn, 1860

2′ Anus not guarded by five enlarged calcified papillae though five groups of smaller papillae may be present . . . genus ***BOHADSCHIA*** Jaeger, 1833

3 Calcareous ring slender and ribbon-like with radial plates shorter than wide and interradial plates likewise, the latter tending to be curved; podia restricted to the ambulacral areas . . . . . genus ***LABIDODEMAS*** Selenka, 1867

3′ Calcareous ring more or less stout, not ribbon-like, radial plates as long as or longer than wide, interradials about half as long as wide but not so wide as to be curved; podia in the form of locomotory pedicels on the ventral surface which is often flattened, and more or less sensory conical papillae on the dorsal surface which is often arched . . . . genus ***HOLOTHURIA*** Linnaeus, 1767 4

4 Spicules: perforated or thorny rods or plates, tables said to be present in some species but if so always reduced in form and sparsely distributed in the body wall ***H. (Selenkothuria)*** Deichmann, 1958

4′ Spicules: tables always present, usually well developed, alone or in combination with buttons, pseudobuttons, rods or rosettes 5

5 Spicules: tables always present in combination with rods or rosettes, never with buttons or pseudobuttons 6

5′ Spicules: tables always present in combination with buttons or pseudobuttons, no rosettes or rods 8

6 Spicules: tables present in combination with rosettes; no rods in the body wall . 7

6′ Spicules: tables present in combination with rods in the body wall, tables usually with reduced disc and spire of moderate height[1], either rounded at the tip or terminating in a few spines which form a single or double maltese cross when viewed from above; no rosettes . . . ***H. (Semperothuria)*** Deichmann, 1958

7 Spicules: tables usually with reduced disc and moderately high or high spire, ending in a few spines forming a maltese cross when viewed from above ***H. (Halodeima)*** Pearson 1914

7′ Spicules: tables large and clumsy with spinose well-developed disc, its rim is often turned up to give a ' cup and saucer ' appearance to the table in lateral view, spire of low to moderate height . . . ***H. (Acanthotrapeza)*** subg. nov.

8 Spicules: tables always present, with low, moderate or high spire terminating in a ring or cluster of small spines, disc usually squarish or octagonal with a large centrally-placed cruciform hole, one or more smaller holes alternating with each arm of the central cross giving the disc a very characteristic appearance, the rim of the disc smooth or spinose, flat or slightly turned up to give the table a ' cup and saucer ' aspect in lateral view; buttons usually present, rarely totally absent, very variable, oval, smooth or rugose, occasionally incomplete or even reduced to small bars with lateral lobes, complete buttons usually with three to six pairs of holes . . . . . ***H. (Stauropora)*** subg. nov.

8′ Spicules: tables always present, variously developed, never with the central hole of the disc cruciform in shape; buttons variously developed or totally absent, rosettes sometimes present 9

9 Spicules: tables present alone, buttons totally absent. 10

9′ Spicules: tables variously developed, buttons always present. . . . 11

10 Spicules: tables always very reduced, rarely absent (probably only in badly preserved specimens), disc ovoid, usually with two to four holes, spire reduced to one to four knobs or short spines. . . . . ***H. (Panningothuria)*** subg. nov.

10′ Spicules: tables with well developed multilocular disc and tall spire with a crossbeam near the base and four long smooth pillars diverging at the tip, each tapering to a point, smaller tables also present with shorter spire often reduced to one to four knobs or completely lacking . ***H. (Irenothuria)*** Deichmann, 1958

11 Spicules: tables variously developed, never modified into hollow fenestrated spheres; buttons smooth, regularly or irregularly developed, often twisted. . . . 12

11′ Spicules: tables always strongly developed, sometimes modified into hollow fenestrated spheres; buttons always knobbed or rugose or modified to form hollow fenestrated ellipsoids 16

12 Spicules: tables usually well developed, the rim of disc not spinose; buttons not twisted, sometimes flat and thin, with or without an apparent median longitudinal ridge, outline regular or irregular 13

12′ Spicules: tables more or less well developed, disc usually spinose; buttons irregular or twisted, never flattened, lacking any appearance of a median longitudinal ridge 14

13 Spicules: tables well developed, disc smooth and round usually with ten or more peripheral holes, spire of moderate height ending in several small spines; buttons oval, thin, flat, very rarely with a few knobs, an apparent median longitudinal ridge present, three to six pairs of relatively small holes, buttons regular or irregular in outline . . . . . ***H. (Platyperona)*** subg. nov.

13′ Spicules: tables fairly stout, disc smooth, squarish in outline, usually with eight regular peripheral holes, spire of moderate height ending in a cluster of small spines; buttons not thin or flat and lacking any appearance of having a

[1] If the height of the spire is measured against the diameter of the disc then low = < disc diameter, moderate = disc diameter, high = > disc diameter.

median longitudinal ridge, usually with three pairs of comparatively large holes, and regular in outline . . . . . ***H.* (*Thymiosycia*)** Pearson, 1914

14 Spicules: tables not strongly developed, rim of disc usually spinose, spire low, ending usually in a ring of spines or cluster of spines, tables occasionally degenerate or incomplete; buttons irregular though not twisted, usually with three pairs of holes, or else incomplete forming small lobed rosette-like bars
***H.* (*Mertensiothuria*)** Deichmann, 1958

14′ Spicules: tables always well developed, rim of disc spinose and either flat or turned up to give a ' cup and saucer ' aspect to the table in lateral view, spire of low to moderate height; buttons often incomplete, twisted or in the form of pseudobuttons 15

15 Spicules: tables clumsy, disc well developed, rim spinose, often turned up to give a ' cup and saucer ' aspect to the table in lateral view, spire low to moderate in height, usually terminating in a ring or cluster of small spines; pseudobuttons abundant, smooth, usually irregular and often reduced to a single row of three or four holes, occasionally buttons quite regular with three pairs of holes.
***H.* (*Lessonothuria*)** Deichmann, 1958

15′ Spicules: tables not clumsy but well developed, rim of disc spinose but flat, not turned up, spire of moderate height, terminating in several short spines which give the appearance of a maltese cross when viewed from above; buttons usually scarce, smooth, with three to five pairs of holes, often incomplete, sometimes twisted and irregular . . . . ***H.* (*Vaneyothuria*)** Deichmann, 1958

16 Spicules: tables always simple and irregular with rather spinose disc which may be somewhat reduced, spire low, moderate or high; buttons simple, quite large, always with numerous small rounded or pointed knobs giving the button a rugose appearance, three to ten pairs of holes which sometimes become obliterated by the thickening of the button . . . . . ***H.* (*Holothuria*)** Linnaeus, 1767

16′ Spicules: tables either modified into fenestrated spheres or more often simple and well developed, disc smooth or spinose or knobbed, spire low to high, buttons with large or moderate-sized knobs, never with numerous small knobs giving the button a rugose appearance, either simple or modified into hollow fenestrated ellipsoids 17

17 Spicules: tables with disc usually knobbed, spire low, bearing many short spines which are sometimes so numerous and closely crowded that they may almost either obscure the disc or become connected to the knobs of the margin of the disc thus forming a fenestrated sphere; buttons usually simple with large regularly or irregularly arranged knobs, generally three to four or more pairs of relatively small holes which may become somewhat obscured by the size of the large knobs.
***H.* (*Cystipus*)** Haacke, 1880

17′ Spicules: tables stout, well developed, spire moderate or high, never modified into hollow fenestrated spheres; buttons either simple with irregular knobs of moderate size or modified into hollow fenestrated ellipsoids 18

18 Spicules: tables well developed, disc smooth or spinose, spires either moderate or high, usually terminating in a cluster of small spines, tables with spires perfectly smooth and tapering to a point giving the whole table a tack-like appearance usually also present; buttons either simple with irregular, moderate-sized knobs, or modified into hollow fenestrated ellipsoids; calcareous ring with radial plates usually possessing more or less well developed posterior bifurcate prolongations.
***H.* (*Theelothuria*)** Deichmann, 1958

18′ Spicules: tables well developed, disc smooth, often squarish in outline, spire of moderate height or high, terminating in small spines, never pointed and tack-like; buttons simple with moderate-sized knobs or modified into hollow fenestrated ellipsoids; calcareous ring never with any indication of posterior bifurcate prolongations on the radial plates 19

19 Spicules: tables well developed with smooth disc, spire of moderate height or high, terminating in several small spines; buttons simple, with moderate-sized irregularly arranged knobs and three to six pairs of relatively large holes, buttons never modified into hollow fenestrated ellipsoids . . ***H. (Metriatyla)*** subg. nov.

19′ Spicules: tables as for 19; buttons hollow fenestrated ellipsoids though a few simple knobbed buttons may be present . . ***H. (Microthele)*** Brandt, 1835

Genus ***BOHADSCHIA*** Jaeger, 1833

(Text-fig. 2)

Bohadschia Jaeger, 1833 : 18; Panning, 1944 : 35; Cherbonnier, 1955 : 132; A. M. Clark & F. W. E. Rowe, 1967*a* : 101. (Type-species *B. marmorata* Jaeger, 1833; designated by Pearson, 1914 : 164).

Sporadipus (*Colpochirota*) Brandt, 1835 : 46. (Type-species *S.* (*C.*) *ualanensis* Brandt, 1835, by monotypy; a synonym of *B. marmorata* Jaeger, 1833; see A. M. Clark & F. W. E. Rowe, 1967*a*: 98–99).

Holothuria (*Bohadschia*) Pearson, 1914 : 169; Panning, 1929 : 120.

Diagnosis: Tentacles 20; pedicels usually scattered but sometimes arranged in three rows on the ventral side, papillae or papillae and pedicels scattered on the

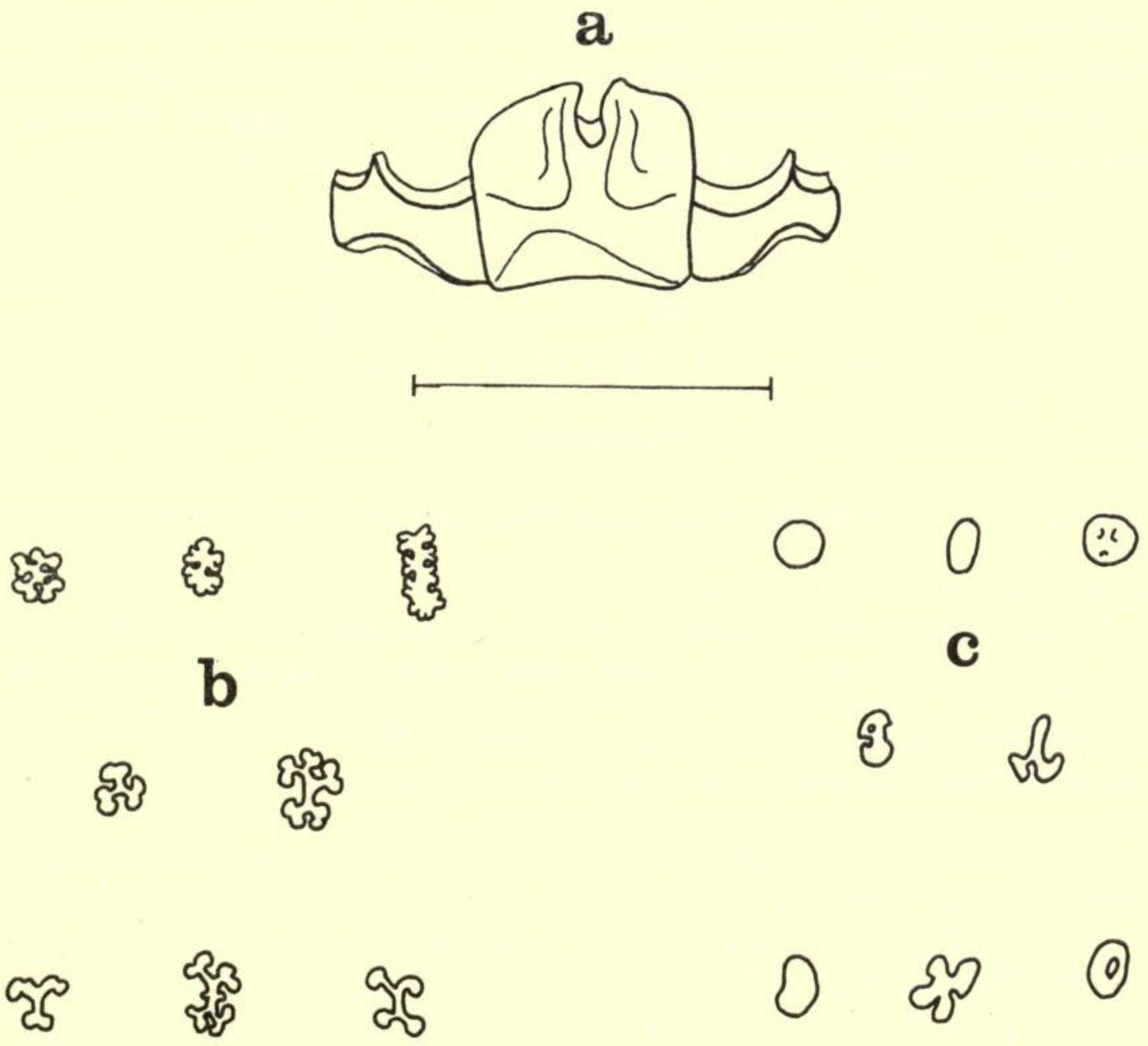

Fig. 2. *Bohadschia marmorata* Jaeger, 1833. B.M. No. 1932.4.28.155, Great Barrier Reef, length 150 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measure 10 mm. for (a) and 0·1 mm. for (b) and (c).

dorsal side; anus sometimes surrounded by five groups of papillae but single calcified anal papillae (anal ' teeth ') absent; body wall muscular and thick (with a mean thickness of about 6 mm. and a range of 1–15 mm.; all measurements from preserved specimens); size moderate to large, up to 400 mm. long; calcareous ring strong, well developed with distinctly scalloped anterior margin, the radial plates about twice as big as the interradial plates and with a median anterior ampullary notch, the interradial plates with an anterior tooth-like median projection, the union between the plates sometimes imperceptible; spicules consisting of simple grains or short dichotomously branched rods, rarely spinose rods or both, tables and buttons or elaborate plates *never* present.

OTHER SPECIES INCLUDED: *Bohadschia argus* Jaeger, 1833; *Holothuria bivittata* Mitsukuri, 1912; *B. cousteaui*, *B. draschi* Cherbonnier, 1954; *H. graeffei*, *H. koellikeri* Semper, 1868; *H. paradoxa* Selenka, 1867; *H. similis* Semper, 1868; *B. steinitzi* Cherbonnier, 1963; *H. subrubra* Quoy & Gaimard, 1833; *H. tenuissima*, *H. vitiensis* Semper, 1868.

REMARKS: The spicules found in species of the genus *Bohadschia* vary from small oval non-perforated or perforated grains to short, dichotomously-branched rods, with the exceptions of *B. graeffei* (Semper), from the Indo-West Pacific (including the Red Sea), and *B. draschi* Cherbonnier from the Red Sea, which possess in addition, peculiar ' raquet-shaped ' spicules. The separation of the species depends generally on the complexity of branching of the rods.

Genus ***ACTINOPYGA*** Bronn, 1860

(Text-fig. 3)

Muelleria Jaeger, 1833 : 7; Selenka, 1867 : 310; Mitsukuri, 1912 : 43 (Non *Muelleria* Férussac, 1823, Mollusca).
H. (*Microthele*) (part) Brandt, 1835 : 54.
Actinopyga Bronn, 1860 : 403 (replacement name for Muelleria Jaeger, 1833); Deichmann, 1930 : 79; Fisher, 1907: 644; H. L. Clark, 1921 : 188; Panning, 1944 : 45; Cherbonnier, 1955 : 135; Clark & Rowe, 1967*a* : 101. (Type-species *Muelleria echinites* Jaeger, 1833; designated by A. M. Clark & F. W. E. Rowe, 1967*a* : 101).[1]
Holothuria (*Actinopyga*): Pearson, 1914 : 169; Panning, 1929 : 125.

DIAGNOSIS: Tentacles 20–30 (usually 20 or 25); pedicels usually arranged in three more or less distinct rows on the ventral side, papillae only on the dorsal side, scattered; anus with five distinct calcified anal papillae (' teeth'); body wall similar to that found in *Bohadschia*; size as *Bohadschia*; calcareous ring similar to that found in *Bohadschia*; spicules consisting of rods, generally more slender than those of

[1] Bronn (1860) did not designate a type-species for *Actinopyga*, while Pearson (1914) and Panning (1939) both designated *Holothuria miliaris* Quoy and Gaimard, 1833, as type-species. This is invalid since *H. miliaris* was not included by Jaeger (1833) in *Muelleria* (for which *Actinopyga* was a replacement name) [see A. M. Clark & F. W. E. Rowe, 1967*a* : 101].

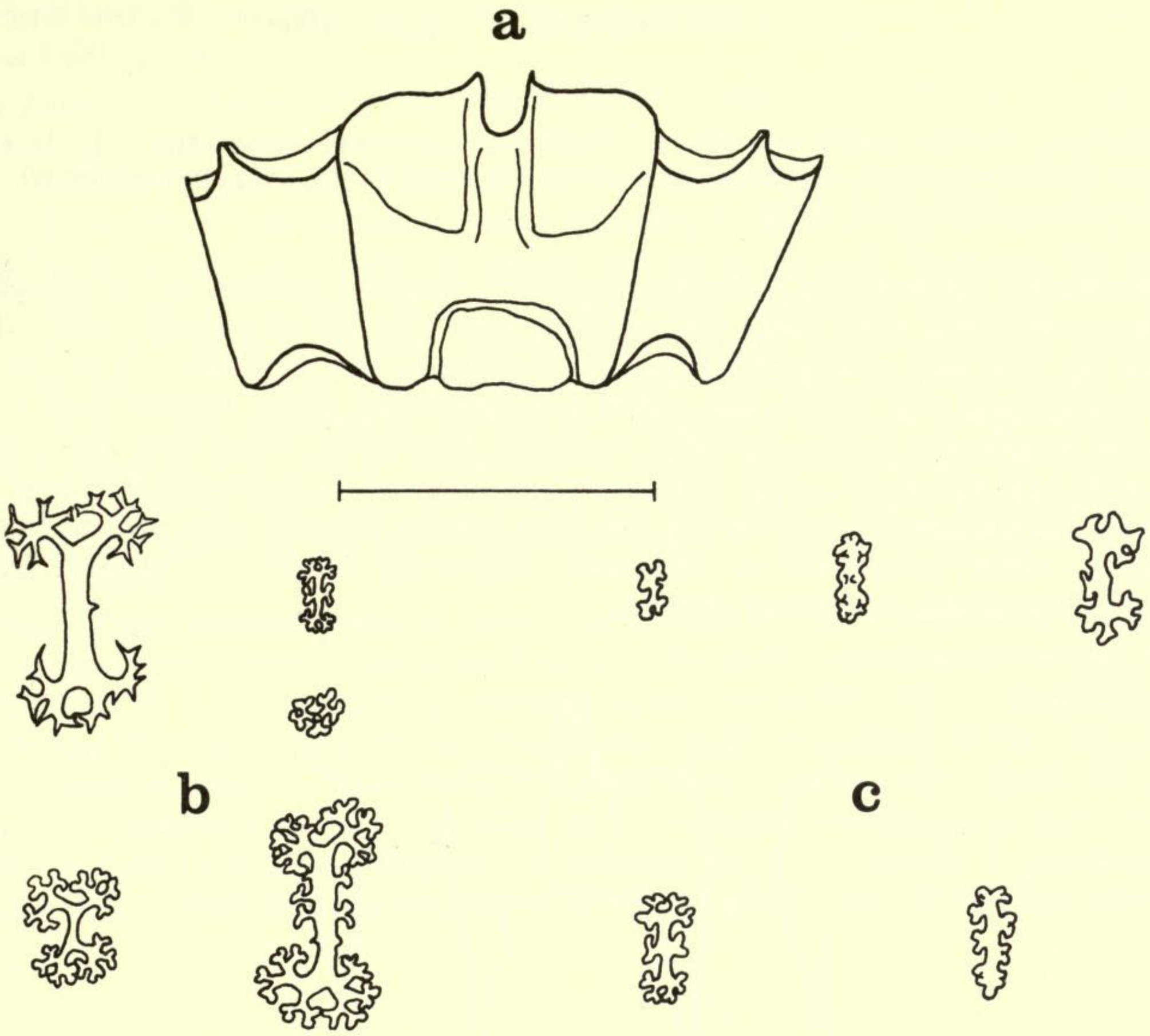

FIG. 3. *Actinopyga echinites* (Jaeger, 1833). B.M. No. 1930.7.30.90, Seychelles, length 150 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

Bohadschia, dichotomously branching not so profuse, spinose rods more commonly present, tables, buttons or elaborate plates *never* present.

OTHER SPECIES INCLUDED: *Muelleria agassizi* Selenka, 1867; *Actinopyga bannwarthi*, *A. crassa* Panning, 1944; *M. lecanora* Jaeger, 1833; *Holothuria mauritiana*, *H. miliaris* Quoy & Gaimard, 1833; *M. obesa* Selenka, 1867; *A. palauensis* Panning, 1944; *M. plebeja*, Selenka, 1867; *A. serratidens*, Pearson, 1905.

REMARKS: The species of *Actinopyga* are separated from each other by the form and complexity of the rods. Small grains like those found in *Bohadschia* are virtually absent and the rods are generally longer, relatively more slender and less profusely branched.

The tentacle number is usually about 20 though *A. agassizi* from the West Indian region and *A. mauritiana* from the Indo-West Pacific have 25–29, being distinguished from each other by the difference in spicule complexity.

Genus ***LABIDODEMAS*** Selenka, 1867

(Text-fig. 4)

Labidodemas Selenka, 1867 : 309; Semper, 1868; Ludwig, 1875; Sluiter, 1901; H. L. Clark, 1921; Deichmann, 1958. (Type-species *L. semperianum* Selenka, 1867; by monotypy).
Holothuria (part): Ludwig, 1875.

DIAGNOSIS: Tentacles 20; pedicels and papillae generally confined to the ambulacral areas; no apparent anal ' teeth ' or papillae; body wall soft or leathery, fairly thick, about 1·5 (1–2) mm.; body cylindrical or vermiform; size moderate, up to 150 mm. long; calcareous ring ribbon-like, radial and interradial plates shorter than broad; spicules usually few, tables scattered, variously developed, either with disc reduced and spire low, ending in a ring of spines or else disc well developed and spinose with spire of moderate height and usually also very spinose, buttons when present smooth, irregular, often incomplete or deformed, suggesting clumsy ' C '-shaped bodies, minute curved rods sometimes present.

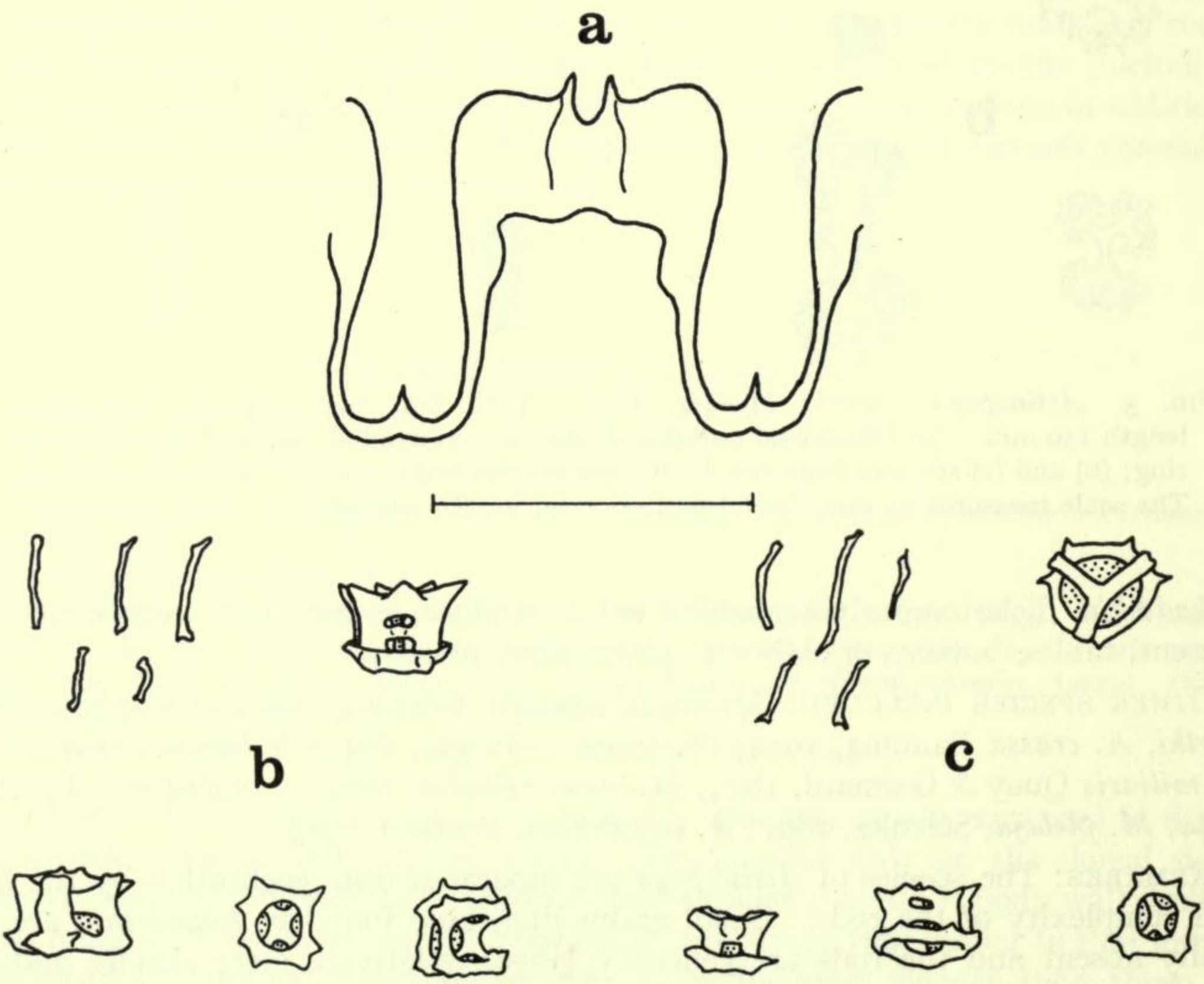

FIG. 4. *Labidodemas semperianum* Selenka, 1867. B.M. No. 1955.10.14.48, Maldives, length 190 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

OTHER SPECIES INCLUDED: *Labidodemas americanum* Deichmann, 1938; *Holothuria rugosa* Ludwig, 1875.

REMARKS: Until now only two species were considered referable to *Labidodemas* these being *L. semperianum* from the Indo-West Pacific region and *L. americanum* from the East Pacific region including the Galapagos Is., according to Deichmann, 1958. However, I have no hesitation in including *Holothuria rugosa*, another Indo-West Pacific species, in the list of species because of its body form and the structure of the calcareous ring. It can be immediately separated from the other two species by the form of its spicules, these being extremely spinose tables with spinose spires of moderate height and smooth irregular buttons. *L. americanum*, which H. L. Clark (1946) considers is possibly not congeneric with *L. semperianum*, has delicate tables with a more or less complete ring of holes to the disc and the spire sometimes reduced, while the type-species has stout tables with long spines on the tip of its low spire and the disc reduced or absent. A few deformed buttons are usually present.

Seven other nominal species have been referred to *Labidodemas*, namely *L. egestosum* Sluiter, 1901, *L. dubiosum* Ludwig, 1875 and *L. selenkianum* Semper, 1868 all of which H. L. Clark (1921) considered to be conspecific with *L. semperianum*. *L. pertinax* (Ludwig), 1875 which Deichmann (1958) considered to be conspecific with *L. semperianum*. *L. leucopus* and *L. neglectum* Haacke, 1880, which Panning (1929–35) considered to be conspecific with *Holothuria monacaria* Lesson (sensu Théel) (= *hilla* Lesson according to Cherbonnier, 1951) and finally *L. punctulatum* Haacke, 1880, which Panning considered to be conspecific with *H. pardalis* Selenka, 1867.

Genus ***HOLOTHURIA*** Linnaeus 1767

Holothuria Linnaeus, 1767 : 1089; Opinion 80, 1924 : 17; Panning, 1929–35 (non *Holothuria* Linnaeus, 1758 suppressed). (Type-species *H. tremula* Linnaeus, 1767 [non *H. tremula* Gunnerus, 1767] = *H. tubulosa* Gmelin, 1890; validated, Opinion 80, 1924 : 17–18).
Thelenota Brandt, 1835 : 53 (non *Thelenota*: H. L. Clark, 1921 : 185).

DIAGNOSIS: Tentacles 17–30, usually 20, pedicels and papillae variously arranged on the ventral and dorsal sides respectively; anal papillae variously developed or absent; body wall very variable; body form showing a wide range, vermiform, cylindrical or with ventral side distinctly flattened and ' sole '-like, dorsally arched; size ranging from small to large, even massive, up to 450 (? 600) mm. long; calcareous ring more or less well developed, usually with radial plates two to three times as long as the interradial plates, the anterior margin of the ring rarely scalloped, the posterior margin undulating (except in subgenus *Theelothuria* where the radial plates bifurcate posteriorly); spicules very diverse and variously developed, tables present (except in the subgenus *Selenkothuria* where tables are absent in five species out of seven and in the other two are said to be present but only in very reduced form. In this subgenus the spicules comprise usually elaborate, smooth, perforated rods

and plates or spinose rods), buttons present or absent, rosettes* and small branched rods sometimes also present.

[The sequence of the subgenera following matches that of the key.]

Subgenus ***SELENKOTHURIA*** Deichmann, 1958

(Text-fig. 5)

Stichopus (part): Selenka, 1867.

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1883; Krauss *in* Lampert, 1885; Caso, 1954; Deichmann, 1938.

Selenkothuria Deichmann, 1958 : 314 (Type-species *Holothuria lubrica* Selenka, 1867: designated by Deichmann, 1958 : 314); 1963*a*, Tikasingh, 1963.

DIAGNOSIS: Tentacles 20; pedicels crowded but more or less distinctly arranged in three rows on the ventral ' sole ', papillae small, numerous, scattered dorsally; body wall soft, not very thick, about 1 (1–3) mm.; body with flattened ventral ' sole '

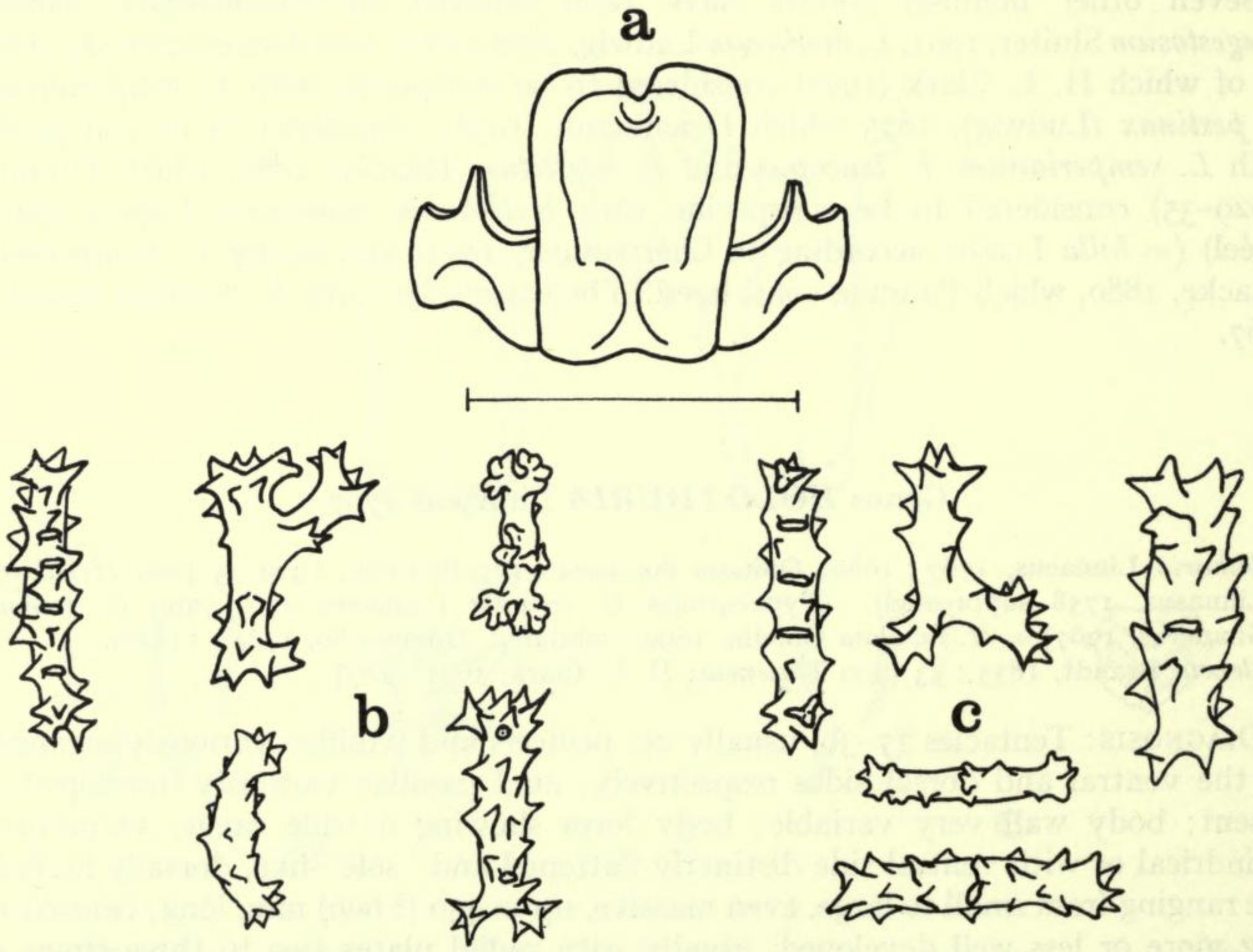

FIG. 5. *Holothuria* (*Selenkothuria*) *lubrica* Selenka, 1867. B.M. No. 1938.12.12.30. 8–10, Ballenas Bay, Costa Rica, length 50 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

* Branched rods whose branches have anastomosed forming a perforated button-like spicule with holes of various sizes usually including median terminal holes.

and arched dorsally; size moderate, up to 150 (rarely 200) mm. long; calcareous ring with radial plates up to three times as long as the interradial plates, the latter usually with the outer surface slightly concave; spicules consisting of perforated or rugose plates or rods, tables rare or more often totally absent, when present (two species) always in very rudimentary form and sparsely distributed in the body wall.

OTHER SPECIES INCLUDED: *Holothuria erinaceus* Semper, 1868; *H. glaberrima* Selenka, 1867; *H. moebii* Ludwig, 1883; *H. parva* Krauss (in Lampert) 1885; *H. portovallartensis* Caso, 1954; *H. theeli* Deichmann, 1938.

REMARKS: The spicules of *Selenkothuria* fall more or less into two categories. Either spinose rods are present, as found in *H.* (*S.*) *lubrica* from the eastern Pacific area, *H.* (*S.*) *parva* from the western end of the Indian Ocean, *H.* (*S.*) *glaberrima* from the West Indies and *H.* (*S.*) *moebii* from the Indo-West Pacific region, with rudimentary tables found sometimes in *H.* (*S.*) *moebii*, or else flattened plates and rods, as found in *H.* (*S.*) *portovallartensis* and *H.* (*S.*) *theeli* from the Galapagos and west coast of Mexico, and *H.* (*S.*) *erinaceus* from the Indo-West Pacific region, with rudimentary tables present in *H.* (*S.*) *erinaceus*.

The species in this subgenus are distinguished from each other most easily by the shape and degree of spinosity of the rods or by the shape and degree of perforation of the flattened plates and rods, an additional factor being the occurrence of tables.

Subgenus ***SEMPEROTHURIA*** Deichmann, 1958

(Text-fig. 6)

Stichopus (*Gymnochirota*) Brandt, 1835 : 51 (Type-species *S.* (*G.*) *cinerascens* Brandt; designated by A. M. Clark & F. W. E. Rowe 1967*a* : 101; suppression of subgeneric name simultaneously proposed).
Stichopus (part): Selenka, 1867.
Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1875; Panning, 1929–35.
Semperothuria Deichmann, 1958 : 302 (Type-species *Holothuria languens* Selenka, 1867; designated by Deichmann, 1958 : 303); Tikasingh, 1963.

DIAGNOSIS: Tentacles 20; pedicels more or less distinctly arranged in three rows on the ventral side, papillae scattered dorsally; body wall soft, not very thick, about 2 (1–4) mm.; body rather slender and cylindrical; size moderate, up to 100–150 (rarely 200) mm. long; calcareous ring quite well developed, radial plates up to three times as long as the interradials; spicules consisting of tables in combination with rods, the former with disc reduced or absent, spire high and terminating in a few spines which form a single or double maltese cross when viewed from above, rosettes *never* present.

OTHER SPECIES INCLUDED: *Stichopus* (*Gymnochirota*) *cinerascens* Brandt, 1835; *Holothuria flavomaculata* Semper, 1868; *H. imitans* and *H. surinamensis* Ludwig, 1875.

REMARKS: *Holothuria* (*Semperothuria*) *cinerascens* and *H.* (*S.*) *flavomaculata* from the Indo-West Pacific region also *H. (S.) surinamensis* from the West Indies

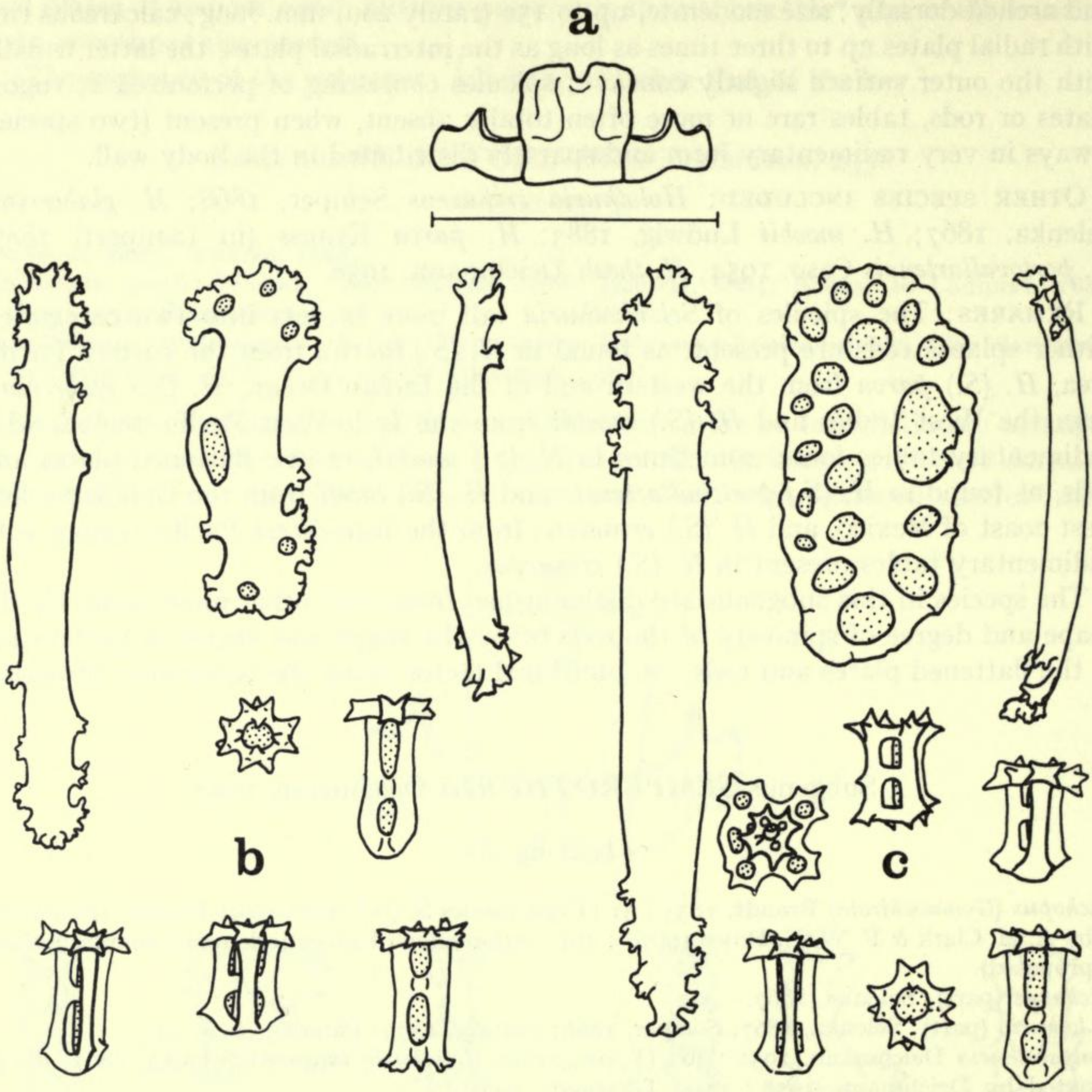

FIG. 6. *Holothuria* (*Semperothuria*) *surinamensis* Ludwig, 1875. B.M. No. 1939.2.22.28, South Sound, Cayman Is., West Indies, length 120 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

possess spinose rods, those of *cinerascens* differing from *flavomaculata* and *surinamensis* in being finely spinulose whilst *flavomaculata* and *surinamensis* have rods with fewer but much larger spines. *H.* (*S.*) *languens* has, according to Deichmann (1958), flattened smooth rods, the rods usually having a marginal row of holes. The circumtropical species *H.* (*S.*) *imitans* appears to lack rods in the body wall, possessing tables and only the supporting rods of the podia.

Subgenus ***HALODEIMA*** Pearson, 1914

(Text-fig. 7)

Trepang Jaeger, 1833 : 24 (Type-species: *Holothuria edulis* Lesson, 1830; designated by H. L. Clark, 1921 : 184); A. M. Clark & F. W. E. Rowe, 1967*a* : 100 (proposed suppression).
Holothuria (part): Lesson, 1830; Jaeger, 1833; Pourtalés, 1851; Selenka, 1867; Semper, 1868; Ludwig, 1875.
Stichopus (part): Selenka, 1867.
Holothuria (*Halodeima*) Pearson, 1914 : 170 (Type-species *Holothuria atra* Jaeger, 1833; designated by Pearson, 1914 : 171).
H. (*Holothuria*) (part): Panning, 1929–35.
Ludwigothuria Deichmann, 1958 (Type-species *H. atra* Jaeger, 1833; designated by Deichmann, 1958 : 310).
Halodeima: Cherbonnier, 1964.

DIAGNOSIS: Tentacles 20; pedicels in three distinct but crowded rows on the more or less distinctly ' sole '-like ventral surface, papillae small and irregularly arranged on the dorsal surface; body wall soft, quite thick, usually 2–3 (1–5) mm.; body almost

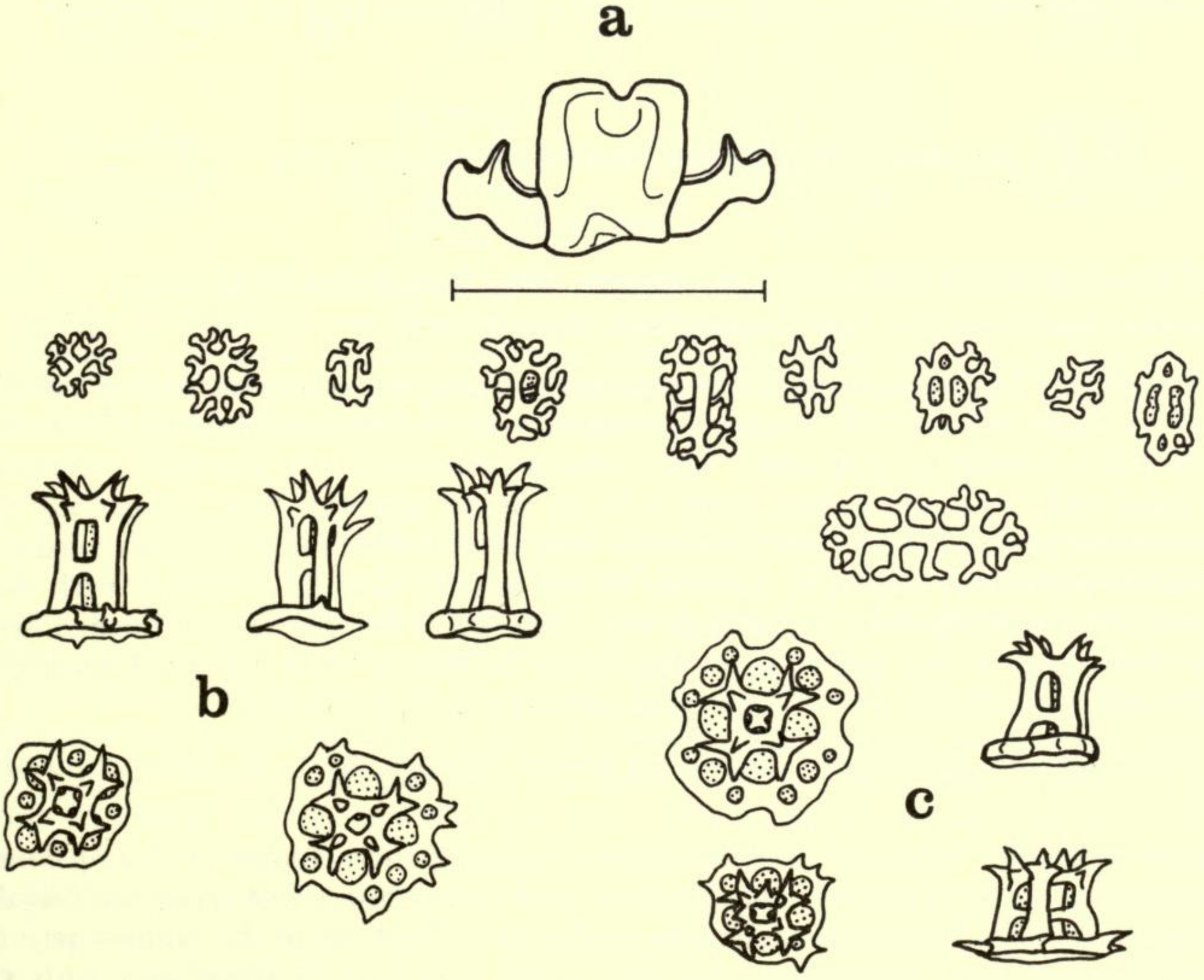

FIG. 7. *Holothuria* (*Halodeima*) *atra* Jaeger, 1833. B.M. No. 1886.10.2.170–171, Amboina, length 120 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

cylindrical; size moderate to large, up to 350 mm. long; calcareous ring quite stout, radial plates up to three times the length of the interradials; spicules consisting of tables usually with reduced disc, spire moderate or high, ending in a few spines forming a maltese cross when viewed from above, *no* large flattened or spinose rods present in the body wall.

OTHER SPECIES INCLUDED: *Holothuria chilensis* Semper, 1868; *H. edulis* Lesson, 1830; *H. floridana* Pourtalés, 1851; *H. grisea* Selenka, 1867; *Stichopus kefersteini* Selenka, 1867; *Holothuria mexicana* Ludwig, 1875; *H. pulla* Selenka, 1867; *Halodeima stocki* Cherbonnier, 1964.

REMARKS: The species of the subgenus *Halodeima* are most readily distinguished from each other by the degree of complexity of the rosettes. These range from simple dichotomously-branched rods, as found in *H.* (*H.*) *floridana* from the West Indies, to small perforated oval or round plates (rosettes), as found in the Indo-West Pacific ranging *H.* (*H.*) *atra* and another West Indian species *H.* (*H.*) *mexicana*. The rosettes are formed by the anastomosis of the dichotomously-branched ends of the rods. The tables are not very variable; those of *H.* (*H.*) *mexicana* tend to develop a much more complete disc than usual with a peripheral ring of holes.

Subgenus ***ACANTHOTRAPEZA***[1] subgen. nov.

(Text-fig. 8)

(TYPE-SPECIES: *Holothuria pyxis* Selenka, 1867; here designated.)

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1875.

DIAGNOSIS: Tentacles 20; pedicels irregularly arranged on the ventral side, papillae small to large and conical, arranged irregularly on the dorsal side; body wall soft, fairly thick, usually 3 (2–5) mm.; body almost cylindrical but ventrally sometimes flattened and ' sole '-like; size small to large, up to 350 mm. long; calcareous ring stout, radial plates squarish, up to twice as long as the interradials; spicules consisting of tables in combination with rosettes, tables usually large and clumsy with well-developed spinose disc and low to high spire, the rim of the disc is often turned up to give the tables a cup and saucer appearance in lateral view, in small specimens (? juveniles) the tables with a high spire and smooth-rimmed disc.

OTHER SPECIES INCLUDED: *Holothuria coluber* Semper, 1868; *H. kubaryi* Ludwig, 1875.

REMARKS: The tables of *Acanthotrapeza* resemble those found in *Lessonothuria* Deichmann, 1958. However the presence of rosettes instead of irregular pseudo-buttons separates the two subgenera immediately. The form of the tables separates *Acanthotrapeza* from *Halodeima*, the only other subgenus of *Holothuria* with the combination of tables and rosettes.

The three species are quite easily distinguished from each other. *H.* (*A.*) *kubaryi*

[1] Greek: *Acanthodes* = thorny; *trapeza* = a table.

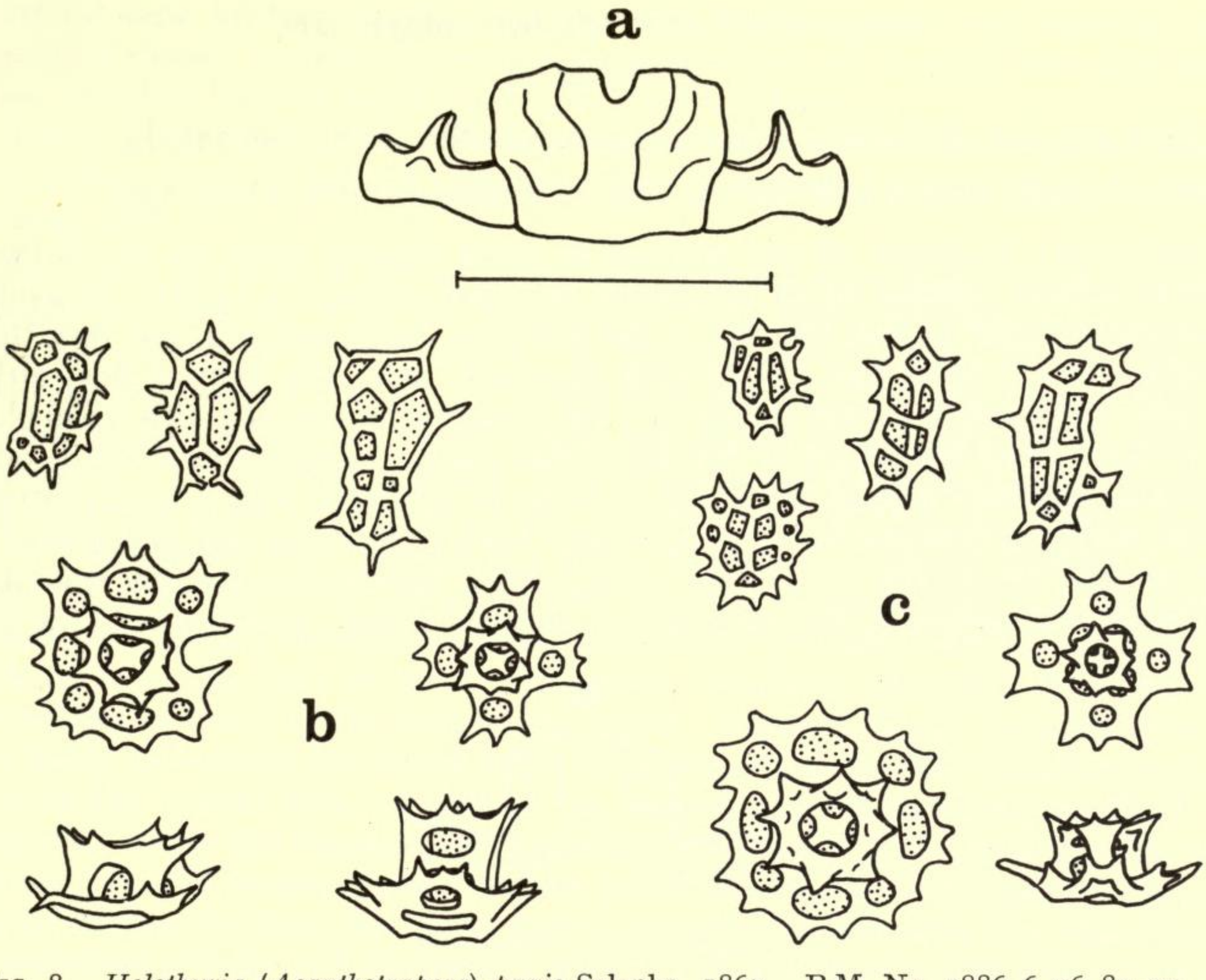

FIG. 8. *Holothuria* (*Acanthotrapeza*) *pyxis* Selenka, 1867. B.M. No. 1886.6.26.89–90, syntype of *Holothuria papillata* Bell, 1887, Andaman Islands, length 320 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

from the South Pacific Islands (Samoa and the Solomons) appears to be the smallest (up to 70 mm. according to Ludwig, 1875 and there is a specimen collected from the Solomon Islands in the British Museum of 30 mm. length). The spicules are smooth-rimmed tables with tall spires and relatively simple rosettes. *H.* (*A.*) *coluber* from the East Indies, Philippines and northern Australia has very clumsy tables with spinose rim and low to moderate spire; the rosettes are relatively large and complex. *H.* (*A.*) *pyxis*, the type-species, from the East Indies and Andaman Islands, is the largest, attaining a length of about 350 mm. The tables are usually low-spired and clumsy and the rosettes not so complex as in *H.* (*A.*) *coluber*. A further factor establishing the identity of the last two species is the form of the dorsal papillae. Those of *coluber* are more numerous and smaller than the fewer, relatively large, conical papillae of *pyxis*.

It should be pointed out that the presence of tall-spired tables has sometimes been considered to be correlated with immature size. If this is correct, then *H.* (*A.*) *kubaryi* may represent the juvenile stage of another species.

Subgenus ***STAUROPORA***[1] subgen. nov.

(Text-fig. 9)

(TYPE-SPECIES: *Holothuria discrepans* Semper. 1868; here designated.)

Holothuria (part): Semper, 1868; Ludwig, 1875, 1888; Lampert, 1889; Fisher, 1907.

DIAGNOSIS: Tentacles 18–30; pedicels in three distinct rows on the flattened ventral surface, papillae small, irregularly arranged dorsally, a ' collar ' of papillae sometimes present around the base of the tentacles; body wall soft, not very thick, usually about 1 (1–2) mm.; body with flattened ' sole '-like ventral side, arched dorsally; size small, up to 100 (rarely 125) mm. long; calcareous ring with radial plates up to three times the length of the interradial plates; spicules consisting of tables with low, moderate or high spire, disc squarish to octagonal with a large centrally-placed cruciform hole and one or more smaller holes alternating with each arm of the central cross giving the disc a very characteristic appearance, the rim smooth or spinose, flat or slightly turned up to give a ' cup and saucer ' appearance to the table

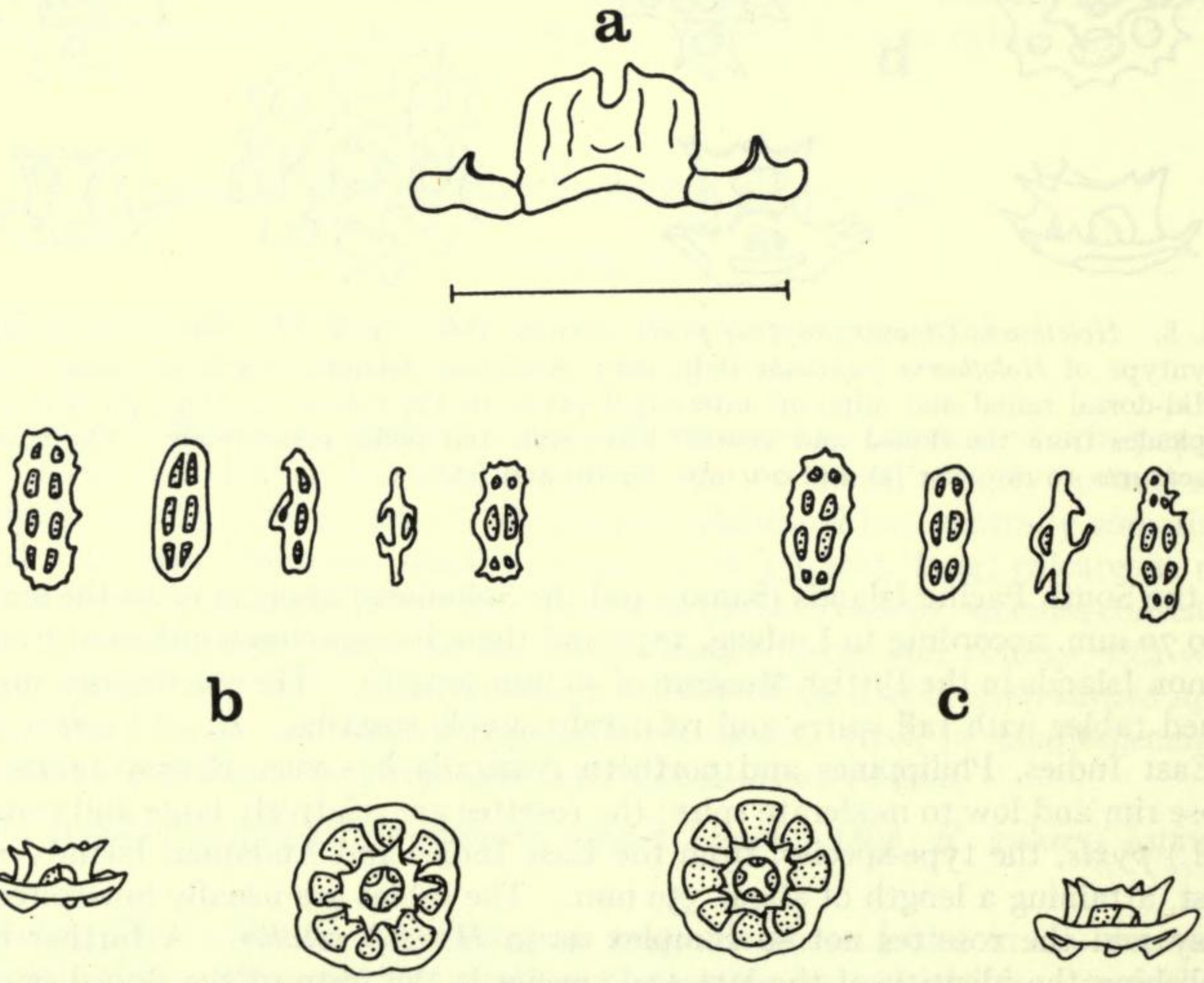

FIG. 9. *Holothuria* (*Stauropora*) *discrepans* Semper, 1868. B.M. No. 1874.10.5.23, Samoa (? type material; received from Godeffroy Museum), length 55 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

[1] Greek *Staurus* = a cross; *porus* = a pore.

in lateral view, buttons usually present, rarely totally absent, very variable, oval, smooth or rugose, occasionally incomplete or even reduced to small bars with lateral lobes, complete buttons usually with 3 to 6 pairs of holes.

OTHER SPECIES INCLUDED: *Holothuria annulifera*, *H. fusco-olivacea* and *H. hawaiiensis* Fisher, 1907; *H. ludwigi* Lampert, 1889; *H. modesta* Ludwig, 1875; *H. olivacea* Ludwig, 1888.

REMARKS: The form of the tables in *Stauropora* is a very characteristic feature of this group of species. They are distinguished from each other most readily by the form and occurrence of the buttons. *H.* (*S.*) *fusco-olivacea* from Hawaii, northern Australia and the Red Sea, *H.* (*S.*) *ludwigi* from Samoa and *H.* (*S.*) *olivacea* from the East Indies have small oval rugose buttons reminiscent of those found in the subgenus *Holothuria*. The spicules figured of these three species are so similar that I suspect that they will prove to be synonymous, in which case *H.* (*S.*) *olivacea* has priority. *H.* (*S.*) *annulifera* from Hawaii has small incomplete knobbed buttons or bars, while the buttons of *H.* (*S.*) *discrepans* from the South Pacific Islands and the Maldive Islands and *H.* (*S.*) *hawaiiensis* from Hawaii are generally smooth and complete with three to six pairs of holes. The main character separating these last two species can be found in the form of the tables. Those of *H.* (*S.*) *hawaiiensis* are of two kinds, tall-spired, flat-disced forms lacking the characteristic cruciform appearance of the central hole, as well as the lower-spired tables characteristic of the subgenus. Only the characteristic tables are found in *H.* (*S.*) *discrepans*, the type-species. *H.* (*S.*) *modesta* from the East Indies and northern Australia is the only species lacking buttons; its tables have a smooth flat disc with the characteristic arrangement of holes and the spire is usually high and slender (Deichmann has also found scattered rosettes in this species according to H. L. Clark, 1946 : 427).

Subgenus ***PANNINGOTHURIA***[1] subgen. nov.

(Text-fig. 10)

(TYPE SPECIES : *Holothuria forskali* Delle Chiaje, 1823; the subgenus is monotypic.)

Holothuria (part): Delle Chiaje, 1823; Koehler, 1927; Mortensen, 1927; Panning, 1929–35.

DIAGNOSIS: Tentacles 20; pedicels in crowded indistinct rows on the flattened ventral surface, papillae conical, irregularly arranged dorsally, a ' collar ' of papillae is present around the base of the tentacles; body wall quite thick, usually 2–3 (1–4) mm.; body almost cylindrical but with a flattened ventral ' sole ', arched dorsally; size moderate, up to 200 mm. long; calcareous ring quite stout, with radial plates up to twice as long as the interradials, the latter obtusely-pointed anteriorly and with outer surface sometimes slightly concave; spicules consisting of very reduced tables sparsely distributed or even lacking (probably only in badly preserved specimens), having ovoidal disc usually with two to four holes, spire very reduced often present only in the form of 2 or 3 short spines or knobs, buttons totally absent.

[1] Panning + latter part of *Holothuria*, in honour of Dr. A. Panning.

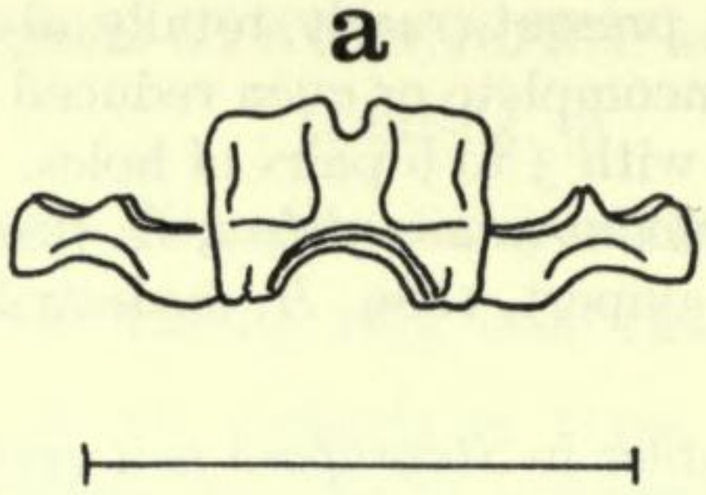

FIG. 10. *Holothuria* (*Panningothuria*) *forskali* Delle Chiaje, 1823. B.M. No. 1898.5.3. 292–293, Naples, length 180 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

REMARKS: *Panningothuria*, like *Irenothuria*, occupies an isolated position within the genus *Holothuria*. It differs essentially from all the other subgenera in the extreme reduction of its spicules. *H.* (*P.*) *forskali* extends from the Mediterranean to the British Isles and Scandinavia.

Subgenus ***IRENOTHURIA*** Deichmann, 1958

(Text-fig. 11)

Irenothuria Deichmann, 1958 : 306 (Type-species *I. maccullochi* Deichmann, 1958; by monotypy); Caso, 1965.

DIAGNOSIS (after Deichmann but modified to conform with the other diagnoses): Tentacles 20; pedicels arranged in irregular double rows ventrally, papillae similarly arranged dorsally; body cylindrical to bottle-shaped; size small to large, up to 200 mm. long; calcareous ring delicate, low; spicules consisting of a crowded layer of tables, the largest with disc about 0·2 mm. in diameter, with numerous holes and tall spire of four pillars joined by a cross beam near the base, each pillar diverging near the

tip, tapering to a point, also small tables especially in the podia, with shorter spire often reduced to 1–4 knobs or completely lacking.

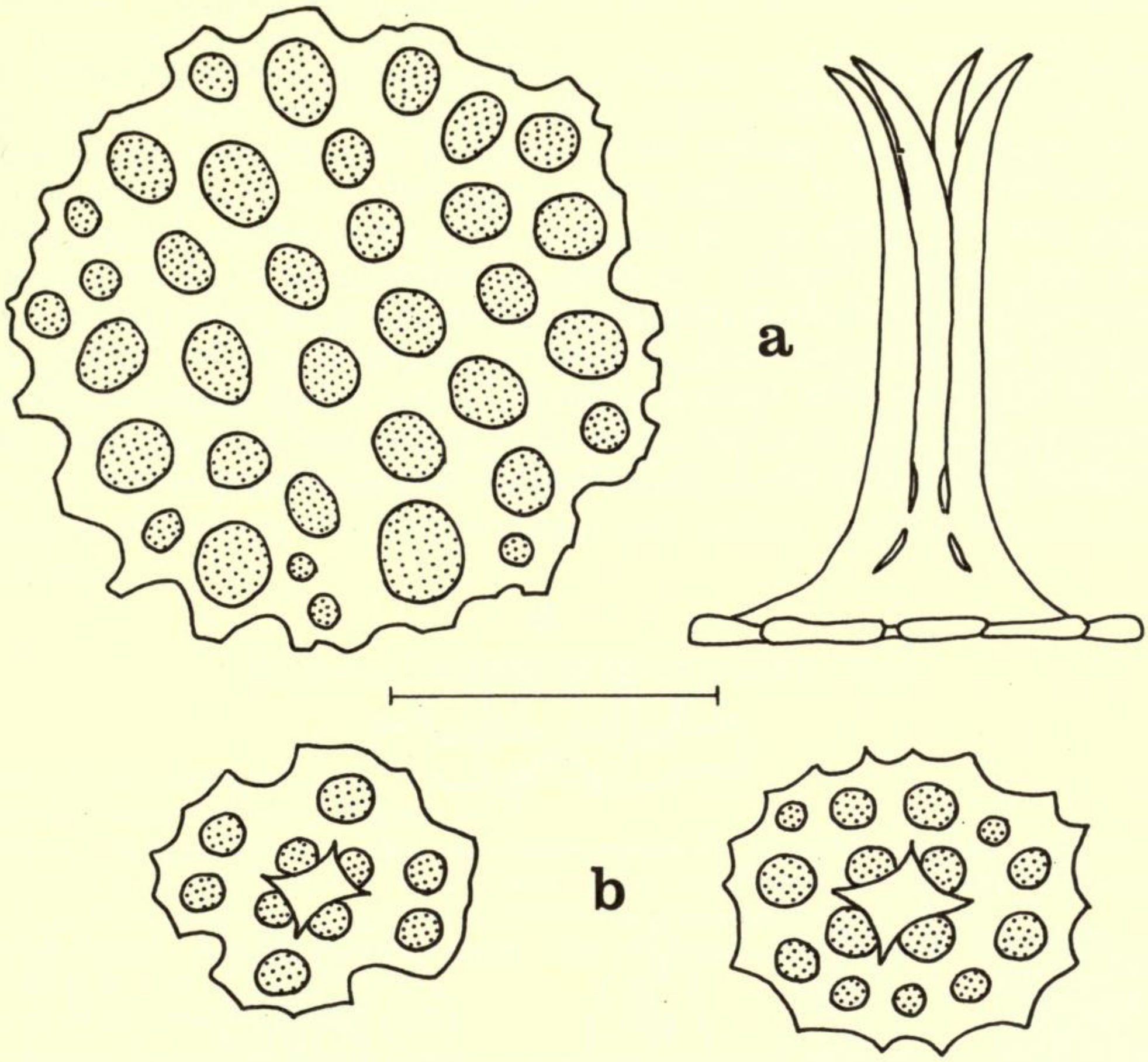

FIG. 11. *Holothuria* (*Irenothuria*) *maccullochi* Deichmann, 1958. (a) Disc and profile of large table; (b) small tables seen from above (after Deichmann, 1958, pl. 4, figs. 1–4). The scale measures 0·1 mm.

REMARKS: Deichmann (1958) noted that *Holothuria* (*Irenothuria*) *maccullochi*, which ranges from Colombia to the Gulf of California, is ' an unusual form which occupies a position all by itself '. Caso (1965) has recorded the species from Las Galas, west coast of Mexico.

PLATYPERONA[1] subgen. nov.

(Text-fig. 12)

(TYPE-SPECIES: *Holothuria difficilis* Semper, 1868; here designated.)

Muelleria (part): Selenka, 1867.
Holothuria (part): Delle Chiaje, 1823; Semper, 1868.

[1] Greek: *platus* = flat; *perone* = a buckle or button.

Argiodia (part): Pearson, 1914.
H. (*Microthele*) (part): Panning, 1929.
Microthele: Deichmann, 1958 (non *H. Microthele*) Brandt, 1835. (Type-species *Muelleria nobilis* Selenka, 1867; designated by A. M. Clark & F. W. E. Rowe, 1967*a* : 100).

DIAGNOSIS: Tentacles 18–20; pedicels crowded, irregularly arranged except in the smaller individuals where they appear to be arranged in three distinct bands on the flattened ventral surface, papillae small, irregularly arranged on the arched dorsal side, a distinct ' collar ' of papillae present around the base of the tentacles; body wall soft, not very thick, usually 1–2 (1–5) mm.; body with a distinct flattened ventral ' sole ', arched dorsally; size small to moderate, up to 200 mm. long; calcareous ring stout, radial plates about twice as long as the interradial plates; spicules consisting of well-developed tables, the disc smooth round and flat, with a varying number of peripheral holes, spire of moderate height, ending in several spines, the buttons oval, thin, flat, very rarely with a few median knobs, an apparent median longitudinal ridge is apparent, three to six pairs of relatively small holes.

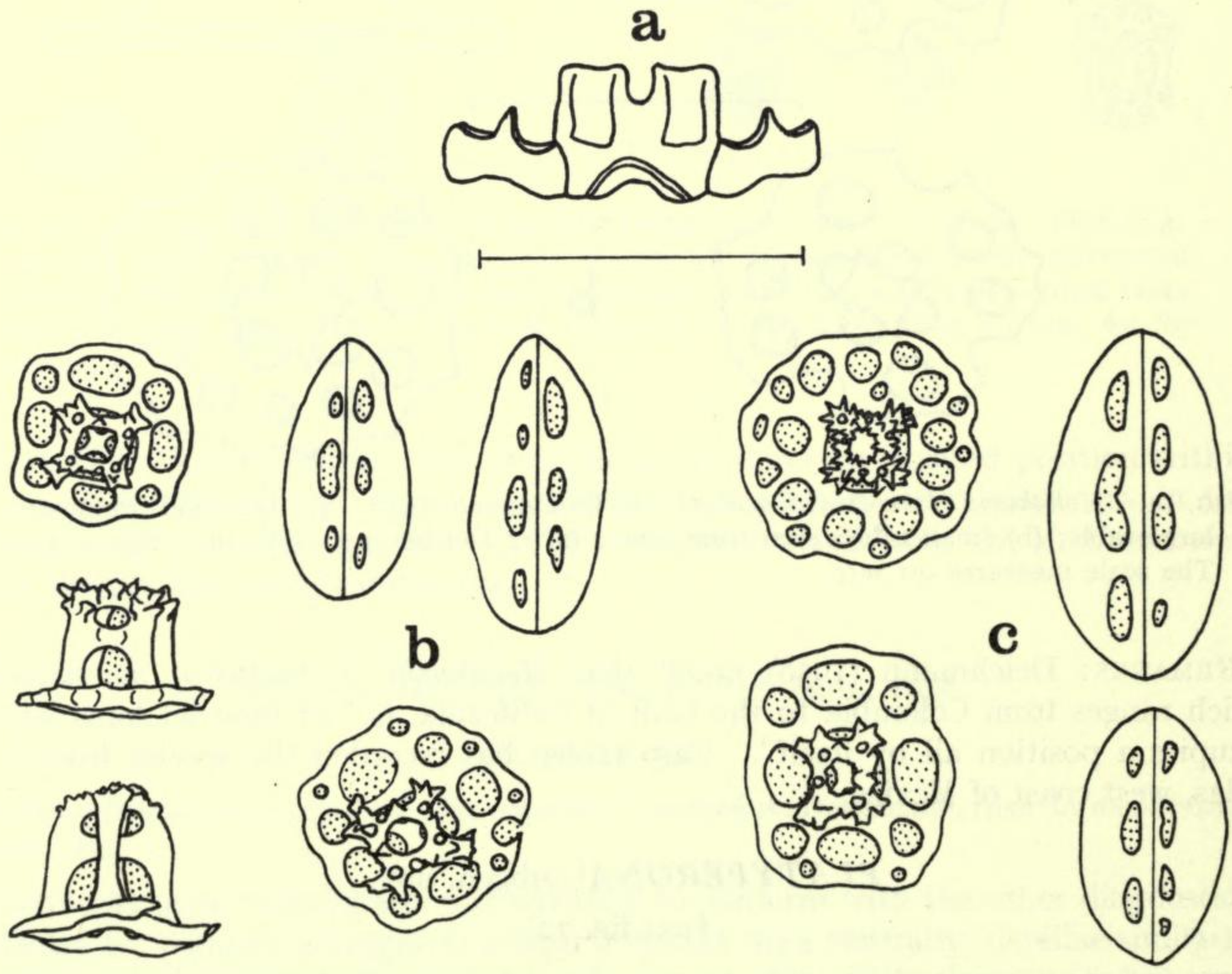

FIG. 12. *Holothuria* (*Platyperona*) *difficilis* Semper, 1868. B.M. No. 1898.8.9.21, Rotuma, North of Fiji, length 60 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

OTHER SPECIES INCLUDED: *Muelleria parvula* Selenka, 1867; *Holothuria sanctori* Delle Chiaje, 1823.

REMARKS: It is unfortunate that neither Panning (1929 and 1939) nor Deichmann (1958) recognized Brandt's (1835) original concept of *H.* (*Microthele*) since each of them, in the absence of a type-designation by Brandt, inadmissably selected as type-species one not included by Brandt in his subgenus. This is in process of being rectified (see A. M. Clark & F. W. E. Rowe, 1967*a*), and the new subgeneric name *Platyperona* is now chosen for *H. parvula*, *H. difficilis* and *H. sanctori*.

The distribution of the three species of *Platyperona* is distinctive. *H.* (*P.*) *parvula*, the smallest species (up to about 50 mm. long) having relatively narrow, often irregularly-shaped buttons, is distributed throughout the West Indies including Bermuda. *H.* (*P.*) *difficilis* which can attain a size of 100–120 mm. length, and has broad, oval, buttons has an Indo-Pacific distribution. *H.* (*P.*) *sanctori*, the largest species (up to 200 mm. long), having tables with the disc often possessing an extra-peripheral ring of small holes and buttons which may (rarely) bear a few knobs, is distributed throughout the Mediterranean and eastern Atlantic from Portugal to St. Helena.

Subgenus ***THYMIOSYCIA*** Pearson, 1914

(Text-fig. 13)

Fistularia (part): Forskaal, 1775.
Holothuria (*Fistularia*) (part): Lesson, 1830.
Sporadipus (*Acolpos*) Brandt, 1835 : 35 (Type-species *S.* (*Acolpos*) *maculatus* Brandt, 1865; designated by A. M. Clark & F. W. E. Rowe, 1967*a*, simultaneously proposed for suppression: 98–99, a senior subjective synonym of *Holothuria arenicola* Semper, 1868).
Holothuria (part): Selenka, 1867; Semper, 1868; Lampert, 1885; Theel, 1886; Erwe, 1913; H. L. Clark, 1938.
Stichopus (part): Selenka, 1867.
Holothuria (*Thymiosycia*) Pearson, 1914 : 171 (Type-species *Fistularia impatiens* Forskaal, 1775; designated by Pearson, 1914 : 164).
Brandtothuria Deichmann, 1958 : 290 (Type-species *Holothuria arenicola* Semper, 1868; designated by Deichmann, 1958 : 290).
Microthele (*Paramicrothele*) Caso, 1964 : 105 (Type-species *M.* (*P.*) *zihuatanensis* Caso; by monotypy).

DIAGNOSIS: Tentacles 18–20; pedicels and papillae usually irregularly arranged ventrally and dorsally, respectively, or occasionally restricted to the ambulacral areas; anal papillae more or less apparent, a 'collar' of papillae usually present around the base of the tentacles; body wall not very thick, usually 2 (1–5) mm.; body rather vermiform; size small to moderate, up to 200 (rarely 250) mm. long; calcareous ring stout, radial plates up to three times the length of the interradial plates; spicules consisting of fairly stout tables, the flat disc and squarish or irregular in outline, rarely reduced, usually with 8–10 peripheral holes, the spire of moderate height ending in a cluster of small spines, the buttons regular or irregular in outline with three or more pairs of comparatively large holes (except in *H.* (*T.*) *arenicola* which has comparatively small holes), not flattened, lacking any appearance of

having median longitudinal ridge, rarely buttons present with slight nodules or forming hollow fenestrated spheres (? *aphanes*).

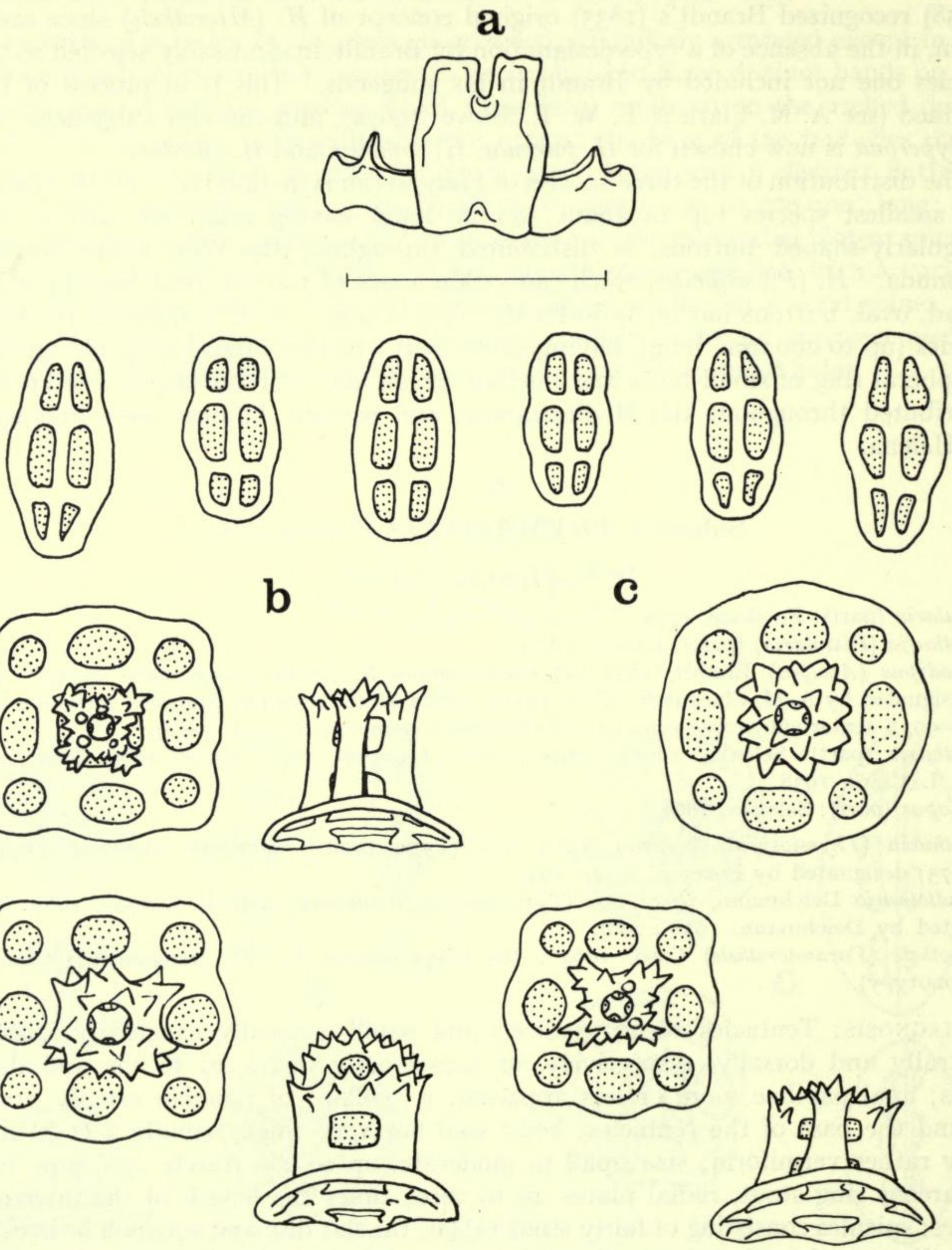

FIG. 13. *Holothuria* (*Thymiosycia*) *impatiens* (Forskaal, 1775). B.M. No. 1949.11.7.16, Dahab, Gulf of Aqaba, length 80 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

OTHER SPECIES INCLUDED: *Holothuria aphanes* Lampert, 1885; *H. arenicola* and *gracilis* Semper, 1868; *Stichopus gyrifer* Selenka, 1867; *H. hartmeyeri* Erwe, 1913; *H.* (*Fistularia*) *hilla* Lesson, 1830; *H. macroperona* H. L. Clark, 1938; *H. minax* Théel, 1886; *H. remollescens* Lampert, 1888; *H. strigosa* Selenka, 1867; *H. truncata* Lampert, 1885; *Microthele* (*Paramicrothele*) *zihuatanensis* Caso, 1964.

REMARKS: Possibly not all the nominal species included above under *Thymiosycia* are valid.

H. (*T.*) *arenicola* which is circumtropical is distinguished from the other species by virtue of its small, often reduced, spicules (tables: disc diameter 60 μ; buttons 50 μ long with comparatively small holes).

H. (*T.*) *remollescens* from the Red Sea, Andaman Islands and northern Australia, according to Lampert (1885), has tall-spired tables and smooth six-holed buttons (no measurements can be given here due to lack of material).

H. (*T.*) *aphanes* from the Red Sea, Gulf of Aden and East Indies has been considered by Panning (1935) to be conspecific with the circumtropical species *H.* (*T.*) *impatiens* Forskaal but since Lampert clearly states that only tables are present in *aphanes*, unlike *impatiens*, I consider it better to reinstate it as a valid species. Cherbonnier (1955) has figured some pseudobuttons from a specimen from the Red Sea which he identified as *H. aphanes* but I do not think that this is correct though lack of relevant material for direct comparison prevents a positive conclusion.

H. (*T.*) *gyrifer* from the West Indies, *hartmeyeri* from south west Australia, *hilla* from the Indo-West Pacific area, *macroperona* from northern Australia, *strigosa* from the Red Sea and *zihuatanensis* from South West Mexico, have quite well-developed spicules with tables having the disc round or irregular in outline, usually perforated with $>$ 8 peripheral holes, the spire is moderately high and the buttons have 3–10 pairs of comparatively large holes (tables: disc diameter 65–80 μ; spire 40–80 μ; buttons 65–160 μ long).

H. (*T.*) *gracilis* from the Philippine and Pelew Islands, the circumtropical species *impatiens*, *minax* from Japan and *truncata* from northern Australia and the East Indies have large robust spicules, the tables have a squarish disc perforated by eight peripheral holes, the buttons have 3–8 pairs of relatively large holes (tables: disc diameter 80–90 μ; spire 40–75 μ; buttons 75–105 μ long).

Interspecific distinctions are dependant on the size and other minor differences in the spicules.

Brandtothuria Deichmann 1958, becomes a junior subjective synonym of *Thymiosycia* since its type-species, the circumtropical *H. arenicola* Semper, according to Deichmann is congeneric (by my reckoning consubgeneric) with *Fistularia impatiens* Forskaal, the type-species of *Thymiosycia*.

Similarly I think that Caso's (1964) *Microthele* (*Paramicrothele*) is a junior subjective synonym of *Thymiosycia* since her description and figures of *M.* (*P.*) *zihuatanensis*, the type species by monotypy, show no good reason to suppose that it is not consubgeneric with the *arenicola, hilla, impatiens*, complex of species. Unfortunately Caso has followed Deichmann's (1958) misuse of the name *Microthele* and has aparently not compared her material with other species from the area among which I suspect *H.* (*T.*) *gyrifer* Selenka is very closely allied to *zihuatanensis*. (see appendix.)

Subgenus ***MERTENSIOTHURIA*** Deichmann, 1958

(Text-fig. 14)

Holothuria (part): Jaeger, 1833; Selenka, 1867; Ludwig, 1898; Koehler & Vaney, 1908; Heding, 1938.

Stichopus (part): Brandt, 1835.

Mertensiothuria Deichmann, 1958 : 296 (Type-species *Stichopus leucospilota* Brandt, 1835; designated by Deichmann, 1958 : 297).

DIAGNOSIS: Tentacles 18–20; pedicels crowded or, in smaller (? juvenile) specimens, arranged in three distinct rows ventrally, papillae small, irregularly arranged dorsally, anal papillae or ' collar ' of papillae around the base of the tentacles not apparent; body wall variable, soft, ranging from thin to fairly thick usually about 2–3 (1–4) mm.; body almost cylindrical but with a more or less flattened ventral ' sole '; size moderate to large (up to 250 mm. long); calcareous ring stout with radial plates about twice as long as the interradial plates; spicules consisting of not very strongly developed

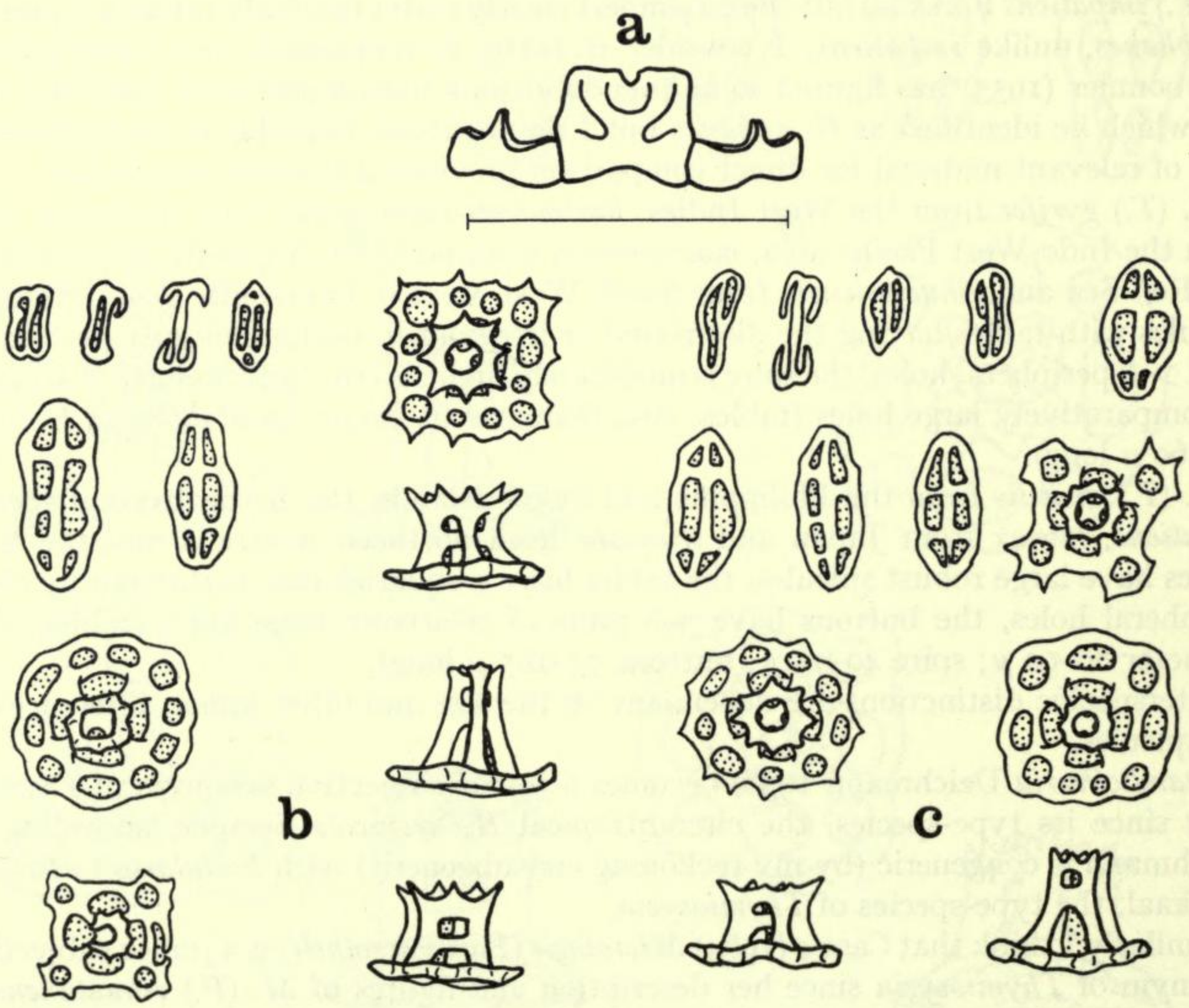

FIG. 14. *Holothuria* (*Mertensiothuria*) *leucospilota* (Brandt, 1835). B.M. No. 1886.10.2.168, Zamboangan, Philippines, length 80 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

tables with the rim of the disc usually spinose and the spire low, ending in a ring or cluster of spines, the tables occasionally degenerate or incomplete, buttons irregular, usually with three pairs of holes, sometimes incomplete.

OTHER SPECIES INCLUDED: *Holothuria exilis* Koehler & Vaney, 1908; *H. fuscocinerea* Jaeger, 1833; *H. papillifera* Heding, 1938; *H. pervicax* Selenka, 1867; *H. platei* Ludwig, 1898.

REMARKS: The well-known name *Holothuria vagabunda* Selenka, 1867 is a synonym of *leucospilota*, the latter having been placed on the Official List of Specific Names in Zoology (Opinion 762 : 15–18).

Two species, neither of which has been recorded since they were first described, *H. exilis* from the Andaman Islands and *H. papillifera* from the Red Sea are now added to those included by Deichmann in *Mertensiothuria*. Panning (1929–35) merely records *exilis* as a valid species but *papillifera* was described too late for inclusion in his work. I believe, however, that *exilis* will prove to be conspecific with *H.* (*M.*) *pervicax* Selenka from the Indo-West Pacific and that *papillifera* may possibly be conspecific with *H.* (*M.*) *leucospilota* Brandt also from the Indo-West Pacific.

Deichmann's key (1958) shows the differences between the other species included in this subgenus.

Subgenus ***LESSONOTHURIA*** Deichmann, 1958

(Text-fig. 15)

Holothuria (part): Delle Chiaje, 1823; Selenka, 1867; Ludwig, 1875; Koehler and Vaney, 1906; Cherbonnier, 1955.

Lessonothuria Deichmann, 1958 : 295 (Type-species: *Holothuria pardalis* Selenka, 1867: designated by Deichmann, 1958 : 295).

DIAGNOSIS: Tentacles 17–30; pedicels and papillae irregularly arranged ventrally and dorsally respectively, a 'collar' of papillae evident around the base of the tentacles, anal papillae usually apparent; body wall soft, not very thick, usually 1 (1–3) mm.; body almost cylindrical but with a more or less distinct, flattened 'sole'; size small to moderate, up to 150 mm. long; calcareous ring fairly stout, radial plates about twice as long as the interradial plates; spicules consisting of clumsy tables, the spire low to moderate and usually terminating in a ring or cluster of spines, disc well developed and spinose, rarely some tables with smooth-rimmed disc also present, rim often turned up to give a 'cup and saucer' appearance to the table in lateral view, pseudobuttons abundant, usually smooth, sometimes spinose, usually irregular in outline and often reduced to a single row of three or four holes, occasionally quite regular buttons are present, with three pairs of holes.

OTHER SPECIES INCLUDED: *Holothuria arguinensis* Koehler & Vaney, 1906; *H. glandifera* Cherbonnier, 1955; *H. insignis* Ludwig, 1875; *H. poli* Delle Chiaje, 1823; *H. verrucosa* Selenka, 1867.

REMARKS: Deichmann (1958) considered *Lessonothuria* to be monotypic, however comparison of the spicules suggests to me that all the above-mentioned species are

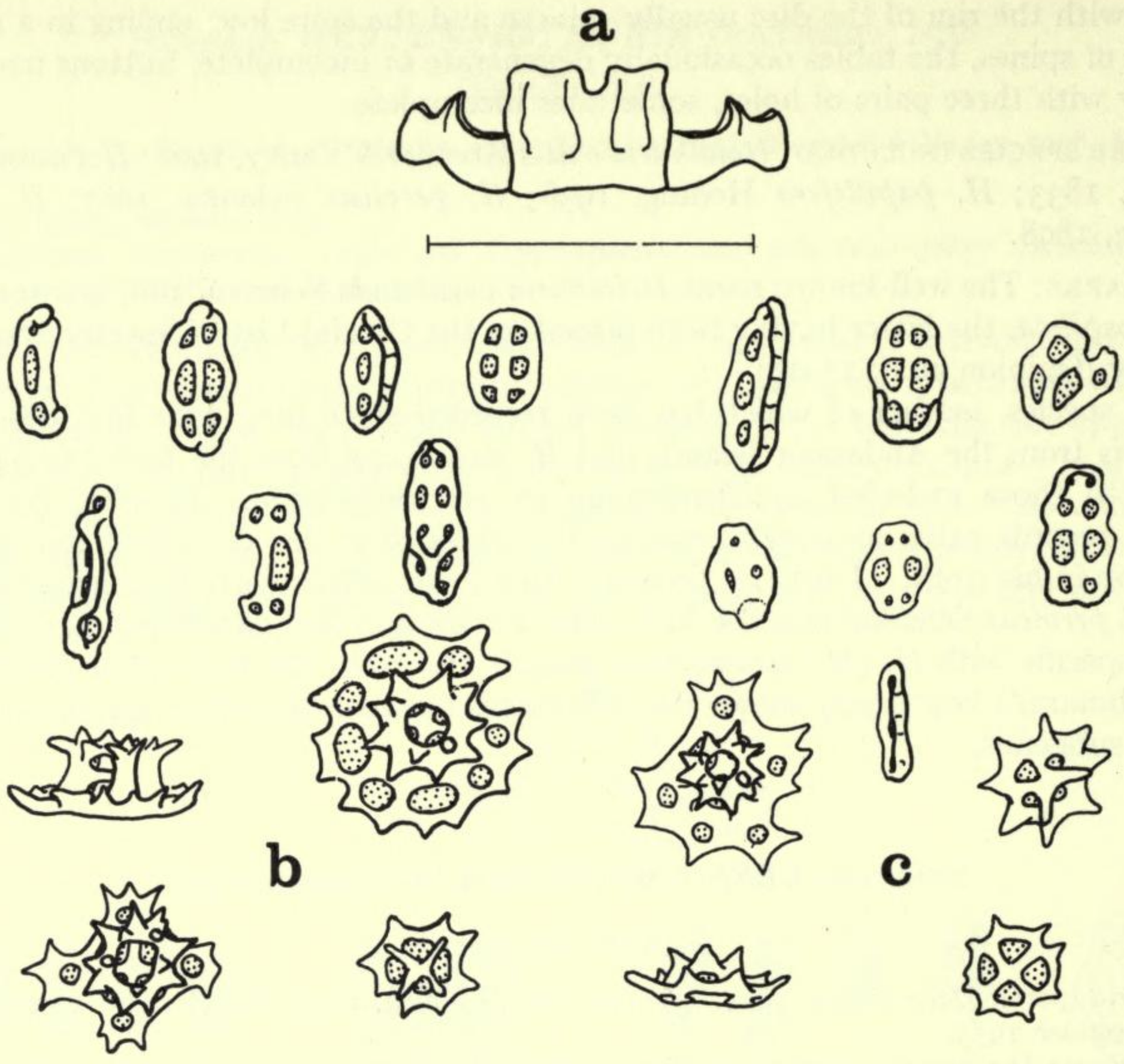

FIG. 15. *Holothuria* (*Lessonothuria*) *pardalis* Selenka, 1867, B.M. No. 1881.10.16.66, Mozambique, length 65 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

consubgeneric with the Indo-West Pacific type-species *H. pardalis* and should be included here.

H. arguinensis from north-west Africa, the Azores and Canary Islands, *H. poli* from the Mediterranean and *H. verrucosa* another Indo-West Pacific species are well-defined species but I believe that *H. glandifera* from Tahiti and the Persian Gulf and *H. insignis* from the Indo-West Pacific region may prove to be not distinct from *pardalis*.

Panning (1939) considered that *H. arguinensis* belongs in the subgenus *Halodeima*. However, it seems to me more likely that its affinities lie not with *Halodeima atra* (the type-species of *Halodeima*) but rather with *Holothuria pardalis* and *H. poli*.

The form of the tables in this subgenus is very similar to those found in *Acanthotrapeza* but the peculiar form of the pseudobuttons readily separates this group of species from any of the others.

Subgenus *VANEYOTHURIA* Deichmann, 1958

(Text-fig. 16)

Holothuria (part): von Marenzeller, 1893; Koehler & Vaney, 1908; Mortensen, 1925; Deichmann, 1937; Cherbonnier, 1958.

Vaneyothuria Deichmann, 1958 : 307 (Type-species: *Holothuruia lentiginosa* von Marenzeller, 1893; designated by Deichmann, 1958 : 308).

DIAGNOSIS: Tentacles 20; pedicels either irregularly arranged or in three bands along the ventral surface, papillae irregularly arranged dorsally though a lateral flange of papillae is sometimes present; body wall soft and muscular, quite thick, about 3 (2–4) mm.; body almost cylindrical but with a flattened ventral ' sole ',

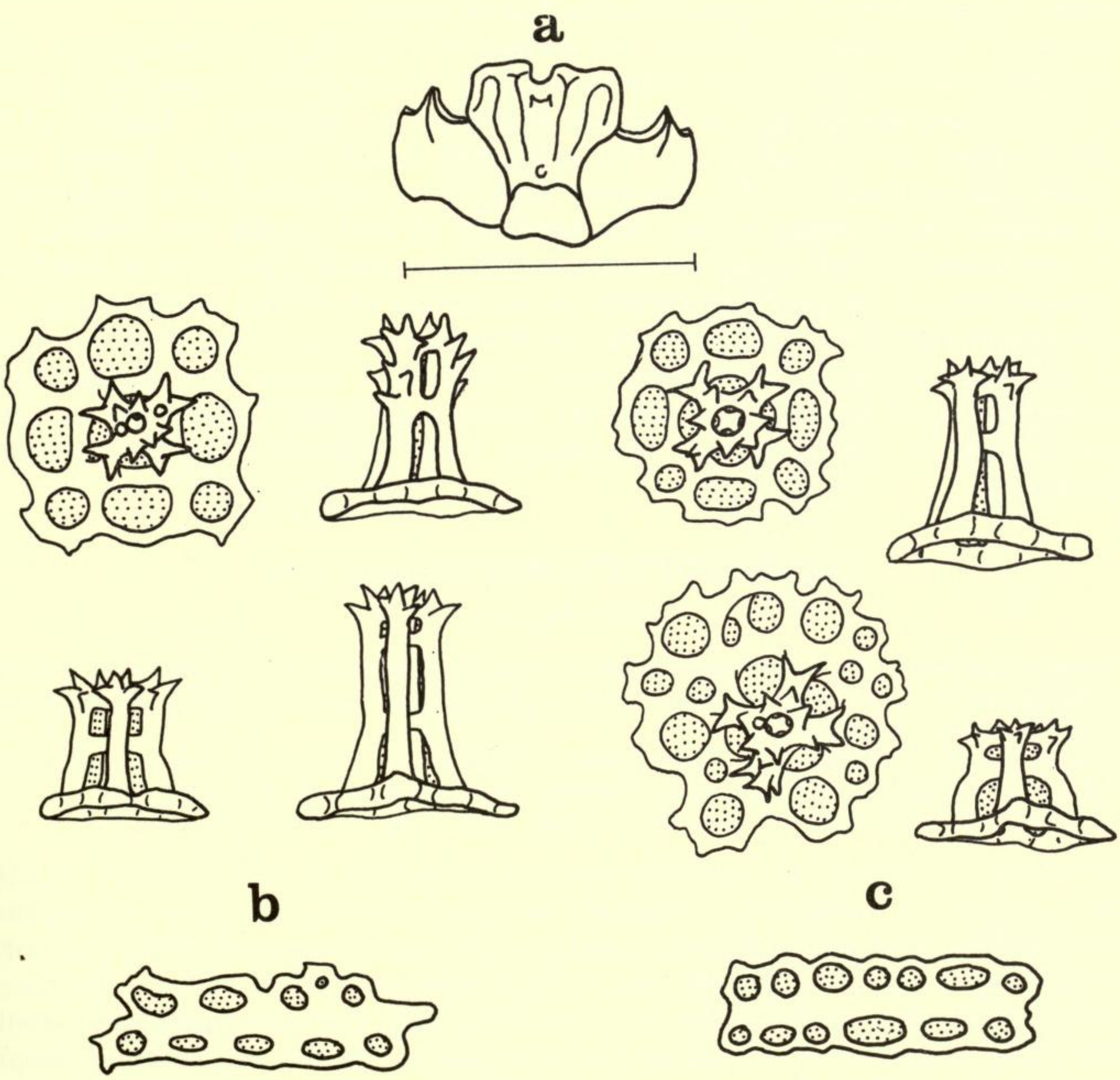

FIG. 16. *Holothuria* (*Vaneyothuria*) *suspecta* Cherbonnier 1958. B.M. No. 1952.4.25.13, Pram Pram, Ghana, length 80 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules of the dorsal and ventral body wall and podia respectively. The scales measure 10 mm. for (a) and 0·1 mm. for (b) and (c).

arched dorsally; size moderate to large, up to 350 mm. long; calcareous ring strongly developed, radial plates about twice as long as the interradial plates, the latter squarish and obtusely-pointed anteriorly; spicules consisting of well-developed tables, with flat spinose disc, spire of moderate height or high, terminating in several short spines which may give the appearance of a maltese cross when viewed from above, buttons usually scarce, smooth with three to five pairs of holes, often incomplete, irregular or twisted.

OTHER SPECIES INCLUDED: *Holothuria integra* Koehler & Vaney, 1908; *H. neozelanica* Mortensen, 1925; *H. suspecta* Cherbonnier, 1958; *H. zacae* Deichmann, 1937.

REMARKS: Possibly not all of the species included under *Vaneyothuria* are valid since even Deichmann (1958) is doubtful whether *H. neozelanica* from New Zealand is really distinct from *H. integra* from the Bay of Bengal.

Although Cherbonnier (1958) does not affiliate *H. suspecta* from Sierra Leone with any other species it appears to me to be most closely related to *H. lentiginosa*, the type-species of *Vaneyothuria*, and so I include it now in this subgenus. Because of its small recorded size (30 mm.) and the tall-spired tables I strongly suspect that *H. sinefibula* Cherbonnier (1965), also from West Africa, may prove to be synonymous with *suspecta* being merely a juvenile specimen of that species (see remarks for *H.* (*Acanthotrapeza*) *kubaryi* p. 139) but until further evidence is available *H. sinefibula* is included here in the list of doubtfully-placed species at the end of this paper.

Deichmann included in *Vaneyothuria* also *Holothuria minax* Théel, 1886; however, after an examination of the type-material I believe *H. minax* from Japan is not consubgeneric with *H. lentiginosa*, from the Azores and Canary Islands, but with the circumtropical *H. impatiens* and accordingly have removed it to the subgenus *Thymiosycia*.

Subgenus ***HOLOTHURIA*** Linnaeus, 1767

(Text-fig. 17)

Holothuria Linnaeus, 1767 : 1089 (non Linnaeus, 1758, Coelenterata); (Type-species: *H. tremula* Linnaeus, 1767 : 1090 (non Gunnerus, 1767) = *H. tubulosa* Gmelin, 1790 : 3188, validated Opinion 80 1924 : 17–18).

Holothuria (part): Gmelin, 1790; Delle Chiaje, 1823; Grube, 1840; von Marenzeller, 1877; Helfer, 1912; Koehler, 1921 and 1927; Panning, 1939; Cherbonnier, 1954 and 1964.

H. (*Thelenota*) Brandt, 1835 : 53 (non H. L. Clark, 1921 : 185, Stichopodidae).

DIAGNOSIS: Tentacles 20; pedicels crowded irregularly on the flattened ventral 'sole', papillae of varied sizes irregularly arranged dorsally, a 'collar' of papillae surrounding the base of the tentacles, anal papillae usually apparent; body wall soft, usually quite thick, about 3 (1–6) mm.; body almost cylindrical but with flattened ventral surface; size small to large, up to 300 mm. long; calcareous ring fairly stout, radial plates about twice as long as the interradials; spicules consisting of simple irregular tables with rather spinose disc which may be somewhat reduced, spire moderate to high, buttons simple, always with numerous small rounded or pointed knobs giving the button a very rugose appearance, three to ten pairs of holes which sometimes become obliterated by the thickening of the button.

OTHER SPECIES INCLUDED: *Holothuria caparti* Cherbonnier, 1965; *H. dakarensis* Panning, 1939; *H. fungosa* Helfer, 1912; *H. helleri* v. Marenzeller, 1877; *H. mammata* Grube, 1840; *H. massaspicula* Cherbonnier, 1954; *H. stellati* Delle Chiaje, 1823.

REMARKS: Deichmann did not take into consideration the predominantly Western Atlantic, Mediterranean, Red Sea group of species of *Holothuria* in her work (1958).

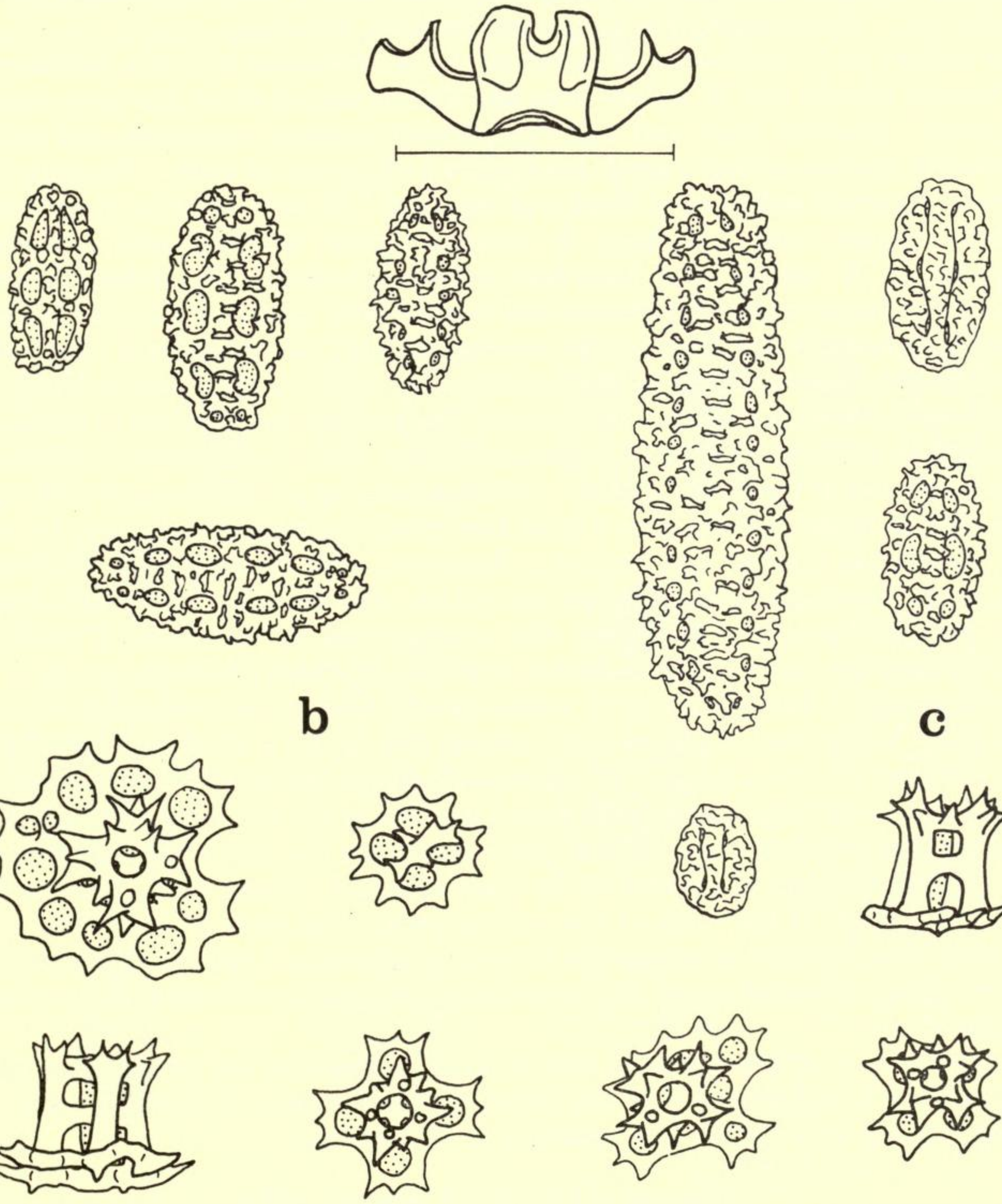

FIG. 17. *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1790. B.M. No. 1898.5.3.325–326, Naples, length 230 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

Holothuria fungosa and *H. massaspicula*, both from the Red Sea, are clearly consubgeneric with *H. tubulosa* from the Mediterranean and the Atlantic coasts of France and Portugal and have been treated as valid species by Cherbonnier (1955).

H. caparti from West Africa appears to be most closely related to *H. dakarensis* from the Azores, Canary Islands and West Africa though Cherbonnier (1965) makes no comparison with any other species.

H. helleri from the Mediterranean is a small species, up to 60 mm. long, and correlated with this is peculiar in possessing tables with a very high slender spire and smooth disc. (See remarks for *H.* (*Acanthotrapeza*) *kubaryi* p. 139.)

The history of *H. dakarensis*, *H. tubulosa* and *H. mammata* from the Mediterranean and Canary Islands and *H. stellati* from the Mediterranean alone has been somewhat chequered. Koehler (1921 and 1927) considered *tubulosa*, *mammata* and *stellati* to be separate species, giving a good description and figures of each. Panning (1934), however, regarded *stellati* as a variety of *tubulosa*. *H. mammata* he considered still warrants specific rank. In 1939 he treated *stellati*, *tubulosa* and *mammata* as subspecies of *H. stellati* and described a new subspecies, *H. stellati dakarensis*. Cherbonnier (1950) restored *tubulosa* and *mammata* to specific rank, simultaneously elevating *dakarensis* but omitting to consider *stellati*. He considered that *tubulosa*, *mammata* and *dakarensis* can be distinguished not only by their external body form but also by differences in size of the spicules, the smallest being found in *tubulosa* and the largest in *dakarensis*, while *H. mammata* is most easily distinguished from *tubulosa* by its possession of Cuvierian organs. After examining 40 specimens of these species in the British Museum collections I have also found the largest spicules to be present in *H. dakarensis* (tables: disc 65–105 μ diameter, spire 70–85 μ high; buttons 84–160 μ long; Panning's measurements are tables: disc 60–108 μ diameter; spire 60–80 μ; buttons: 92–172 μ long) but the smallest are in specimens I identify as *H. stellati* (tables: disc 31–52 μ diameter, spire 21–42 μ high; buttons: 31–42 μ, a few up to 75 μ long). The spicules of *H. mammata* and *tubulosa* are intermediate between those of *H. stellati* and *H. dakarensis* (tables: disc 45–85 μ diameter, spire 48–65 μ high; buttons: 40–116 μ long). *H. mammata* can be distinguished from *tubulosa* by its body form with large mammillate dorsal papillae as the name suggests whereas the dorsal papillae of *tubulosa* are smaller, more numerous and cannot be called mammillate. *H. tubulosa* has in general many more elongate, almost solid, buttons (up to about 250 μ long) in the walls of the ventral podia than does *H. mammata*. However use of the presence or absence of Cuvierian organs as a specific character (Cherbonnier, 1950) is unsatisfactory since specimens have often eviscerated before reaching the laboratory.

In the absence of type-material and in order to stabilize the present day concept of *H. tubulosa* I recommend that the description and figures of Koehler, 1921 : 174–176, fig. 130a–g be accepted as a criterion of *H. tubulosa*.

Subgenus ***CYSTIPUS*** Haacke, 1880

(Text-fig. 18)

Holothuria (part): Selenka, 1867; Ludwig, 1875; Erwe, 1919; Deichmann, 1930; Cherbonnier 1955 and 1964.

Stichopus (part): Selenka, 1867.
Cystipus Haacke, 1880 : 47 (Type-species *C. pleuripus* Haacke, 1880, by monotypy; a synonym of *Stichopus rigidus* Selenka, 1867, according to Deichmann, 1958).
Fossothuria Deichmann, 1958 : 321 (Type-species *Stichopus rigidus* Selenka, 1867; designated by Deichmann, 1958 : 321).
Jaegerothuria Deichmann, 1958 : 322 (Type-species *Holothuria inhabilis* Selenka, 1867; designated by Deichmann, 1958 : 322.

DIAGNOSIS: Tentacles 20; pedicels more or less confined to the ventral ambulacral areas, papillae small and scattered dorsally, a lateral flange of papillae sometimes evident, anal papillae and ' collar ' of papillae around the base of the tentacles not

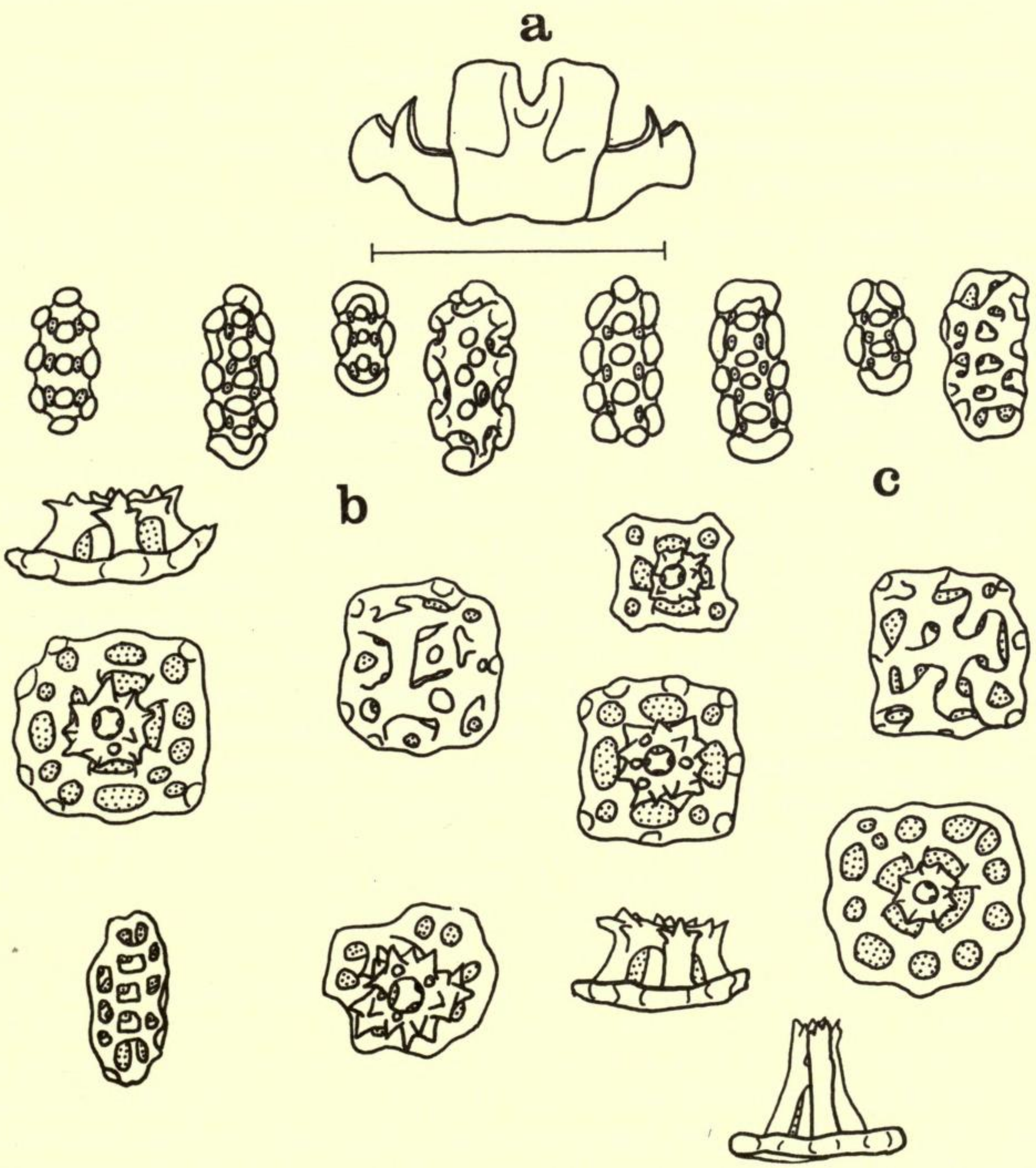

FIG. 18. *Holothuria* (*Cystipus*) *rigida* Selenka, 1867. B.M. No. 1885.7.1.3, Philippines, length 100 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0·1 mm. for (b) and (c).

apparent; body wall not very thick, usually about 2 (1–8) mm. often gritty to the touch; body rather vermiform or dorsoventrally flattened; size small to moderate, up to 200 mm. long; calcareous ring fairly stout with radial plates about twice as long as the interradial plates; spicules consisting of tables with usually knobbed discs and low spire bearing many short spines which are sometimes so numerous and closely crowded that they may almost obscure the disc or become connected to the knobs on the margin of the disc forming a fenestrated sphere (Deichmann, 1958), buttons usually simple with large regularly- or irregularly-arranged knobs, generally 3–4 pairs, but up to 7 pairs, of relatively small holes which may become obscured somewhat by the immensity of the knobs, rarely the buttons modified into fenestrated ellipsoids.

OTHER SPECIES INCLUDED: *Holothuria cubana* Ludwig, 1875; *H. inhabilis* Selenka, 1867; *H. jousseaumei* Cherbonnier, 1955; *H. occidentalis* Ludwig, 1875; *H. pseudofossor* Deichmann, 1930; *H. sucosa* Erwe, 1919; *H. sulcata* Ludwig, 1875; *H. turrisimperfecta* Cherbonnier, 1964.

REMARKS: Possibly not all of the nominal species included above under *Cystipus* are valid.

Deichmann (1958) established two new nominal genera, firstly *Fossothuria* for type-species *Stichopus rigidus* Selenka and including *Holothuria cubana* Ludwig, 1875, secondly *Jaegerothuria* for type-species *H. inhabilis* Selenka, and including *H. occidentalis* Ludwig, 1875. The distinction made between the two appears to rest on regular arrangement of knobs on the buttons in combination with the complexity of the tables in *Fossothuria* as opposed to irregularly-knobbed buttons and relatively simple tables in *Jaegerothuria*. It seems to me that this distinction does not hold good since Deichmann's figures of spicules from the type-material of *rigida* and *inhabilis* show that although the knobs on the longer buttons of *rigida* appear more or less regularly arranged, those on the smaller buttons are just as irregular as those of *inhabilis*. The unmodified tables of the two species are very similar, only those of *inhabilis* do not have as many knobs on the disc. Deichmann further considers that species of *Jaegerothuria* reach a larger size (up to 200 mm. long) than those of *Fossothuria* (60–150 mm. long) though in her description of specimens of *J. inhabilis* she says they range from 70–200 mm. long also that the spicules of the smaller specimens are very similar to *F. rigida*. It seems that smaller individuals of *inhabilis* have more elongate buttons than larger specimens *of the same species*. It does not appear to me therefore that this character is of subgeneric weight, nor do I feel the difference in the spicules of the respective type-species, *inhabilis* and *rigida*, is sufficiently great to warrant more than a specific distinction. *Jaegerothuria* and *Fossothuria* are therefore treated here as synonyms, *Fossothuria* having priority, but since it shares the same type-species as *Cystipus* Haacke, 1880, namely *Stichopus rigidus* Selenka, 1867, both names fall into synonymy. Although *Cystipus* has not been used since 1880 it is undeniably available (see A. M. Clark & F. W. E. Rowe, 1967*a*).

In the collections of the British Museum there is a Semper slide marked '*Holothuria rigida* Selenka. Original Zanzibar'. This shows some buttons on which the knobs are more or less regularly arranged whilst other buttons are rather irregular in outline

and knob arrangement. There are a few tables present, these being in the form of fenestrated spheres. Whether these were the only kind of tables present in the specimen it is impossible to say since only a few spicules are present on the slide.

It appears extremely difficult to me to justify the retention of *H.* (*C.*) *rigida* from the Indo-Pacific region, *jousseaumei* from the Red Sea and *cubana* from the West Indies as distinct species. Deichmann herself (1958) is inclined to believe that *rigida* and *cubana* are conspecific, separating them only on geographical grounds. Although Cherbonnier (1955) compared *H. jousseaumei* with *H. remollescens* Lampert, 1885, the latter here regarded as consubgeneric with *H.* (*Thymiosycia*) *impatiens* Forskaal, judging from Cherbonnier's description and figures, *H. jousseaumei* is most certainly consubgeneric with *H. rigida* and may prove to be conspecific with it. These three nominal species are the only ones which have hollow fenestrated spheres in addition to the knobbed buttons and unmodified tables.

H. (*C.*) *inhabilis* from the East Indies, Pacific and Panamic areas is distinguished from *H.* (*C.*) *rigida* by its rather simpler tables, lack of fenestrated spheres and rather more irregular buttons.

The West Indian species, *H.* (*C.*) *pseudofossor*, like *H.* (*C.*) *inhabilis*, is also rather similar to *H.* (*C.*) *rigida* but the disc of the tables has only 8 peripheral holes and no hollow fenestrated spheres are present. This species may well prove to be conspecific with *H.* (*C.*) *inhabilis*.

H. (*C.*) *sucosa* from the Red Sea has tables with 8–10 peripheral holes to the disc and the spire apparently terminating in a ring of irregular spines. The buttons have 4–5 pairs of holes. This species occurs only in the Red Sea and appears to be distinct from all the other species included in *Cystipus*. It seems most closely allied to *H.* (*C.*) *rigida* but again differs in lacking the fenestrated spheres.

H. (*C.*) *occidentalis* and *sulcata* occur in the West Indian region. *H.* (*C.*) *occidentalis* has buttons with 3–5 pairs of holes and simple tables with a knobbed disc and a spire terminating in about four spines. *H.* (*C.*) *sulcata* has incomplete or solid buttons and tables with the spire terminating in about twelve spines.

Finally, *H.* (*C.*) *turrisimperfecta* from West Africa has buttons with 3–4 pairs of holes, some buttons tending to form ellipsoids, and tables with irregular discs and low spires terminating in 6–8 spines, or the spire may be reduced or lacking. Cherbonnier (1964) compared this species with the West Indian *H.* (*C.*) *occidentalis* and *H. imperfector*; the latter according to Deichmann (1958) is conspecific with *H.* (*Theelothuria*) *princeps* Selenka, 1867, also from the West Indies.

Subgenus ***THEELOTHURIA*** Deichmann, 1958

(Text-fig. 19)

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1875; Lampert, 1885; Theel, 1886; Pearson, 1913; Deichmann, 1937 and 1938.

Theelothuria Deichmann, 1958 : 325 (Type-species *Holothuria princeps* Selenka, 1867; designated by Deichmann, 1958 : 325).

DIAGNOSIS: Tentacles 18–20; pedicels irregularly arranged on the flattened ventral surface, papillae small to large and conical, irregularly arranged dorsally except for the lateral flange of papillae, a ' collar ' of papillae usually present around the base

of the tentacles, anal papillae usually apparent; body wall usually very thin and parchment-like, rarely more than 1 (1–2) mm. thick, gritty to the touch; body with a distinctly flattened ventral 'sole', arched dorsally; size moderate to large, up to 250 mm. long; calcareous ring stout and well-developed, radial plates with more or less well developed posterior bifurcations, radial plates up to twice as long as the interradial plates, both radials and interradials may be longer than broad; spicules consisting of well-developed tables with smooth or spinose discs sometimes the disc multi-armed or synallactidlike, spire either low, moderate or high, usually terminating in a cluster of small spines, some tables with perfectly smooth spire tapering to a pointed apex giving the whole table a tack-like appearance usually present also, buttons either simple with irregular moderate-sized knobs or modified into hollow fenestrated ellipsoids.

OTHER SPECIES INCLUDED: *Holothuria hamata* Pearson, 1913; *H. klunzingeri* Lampert, 1885; *H. kurti* Ludwig, 1875; *H. maculosa* Pearson, 1913; *H. notabilis* Ludwig, 1875; *H. paraprinceps* Deichmann, 1937; *H. samoana* Ludwig, 1875; *H. spinifera* Théel, 1886; *H. squamifera* Semper, 1868.

REMARKS: The peculiar features of the calcareous ring in combination with the general form of the spicules sets *Theelothuria* apart from all the other taxa here considered.

H. (*T.*) *maculosa* from the western part of the Indian Ocean, *H.* (*T.*) *klunzingeri* from the Red Sea and *H.* (*T.*) *notabilis* from the East Indies and northern Australia are recognized by the fact that their tables have a low or reduced spire. The degree of reduction of the table is used as the main character to distinguish these species from each other.

H. (*T.*) *samoana* from Samoa, *H.* (*T.*) *paraprinceps* from the Gulf of California, Panama and westwards to Cocos and the Clarion Islands, *H.* (*T.*) *kurti* from the East Indies, Philippines westward to Ceylon and the Red Sea, *H.* (*T.*) *spinifera* similarly distributed, *H.* (*T.*) *squamifera* from the East Indies, Philippines and east, to the South Pacific Islands and *H.* (*T.*) *princeps* from the West Indies, all have well-developed tables.

H. (*T.*) *kurti*, *H.* (*T.*) *paraprinceps* and *H.* (*T.*) *squamifera* are separated mainly on the form of their buttons. Those of *kurti* are elongate with up to 10 pairs of holes while those of *squamifera* have only 3–5 pairs of holes. The synallactid-like tables are not so numerous in *H.* (*T.*) *squamifera* as they are in *H.* (*T.*) *kurti*. Semper did not mention the presence of synallactid-like tables in his description of *H.* (*T.*) *squamifera* but there is a Semper slide of spicules in the collections of the British Museum, presumably from type-material, which shows that such tables are present. *H.* (*T.*) *paraprinceps* differs from the other two species in possessing additional tack-like tables and buttons which tend to become smooth with small holes, these holes sometimes becoming obliterated.

H. (*T.*) *princeps* and *H.* (*T.*) *spinifera* also have some tack-like tables but no synallactid-like tables. They differ from each other in the stouter tables and simpler buttons of *H.* (*T.*) *spinifera* while *H.* (*T.*) *princeps* has complex ellipsoidal buttons and generally less stout tables.

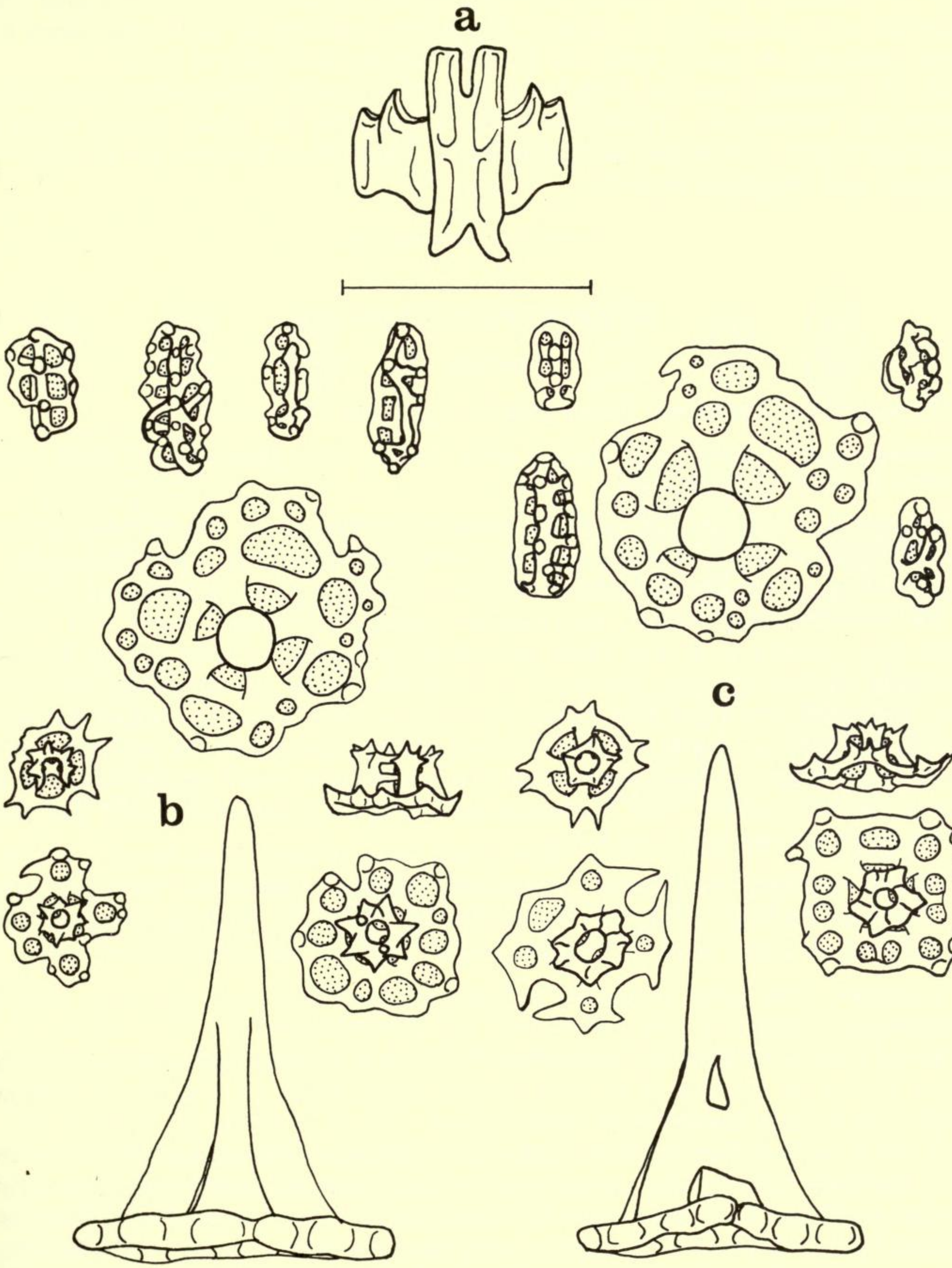

FIG. 19. *Holothuria* (*Theelothuria*) *princeps* Selenka, 1867. B.M. No. 1954.9.13.18, Biscayne Bay, Florida, length 120 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

H. (*T.*) *samoana* differs from all the other species in this subgenus by lacking both tack-like and synallactid-like tables. The tables however do have high spires but these terminate in small spines; the buttons have up to 8 pairs of holes.

H. (*T.*) *hamata* from the Red Sea is also quite easily distinguished from other species in *Theelothuria*. Tall-spired tables are absent, the tables having spires of moderate height terminating in small spines. The buttons however are usually very irregular and ellipsoidal in form.

METRIATYLA[1] subgen. nov.

(Text-fig. 20)

(Type-species: *Holothuria scabra* Jaeger, 1833; here designated.)

Holothuria (part): Jaeger, 1833; Semper, 1868; Ludwig, 1875; Sluiter, 1901; Helfer, 1912; Erwe, 1913; H. L. Clark, 1938.

DIAGNOSIS: Tentacles 20; pedicels irregularly arranged on the flattened ventral ' sole ', papillae usually quite large and conical and irregularly arranged dorsally, a lateral flange of papillae sometimes evident, a ' collar ' of papillae around the base of the tentacles often present, anal papillae variously developed; body wall usually quite thin, about 2 (1–5) mm. thick, and gritty to the touch; body usually flattened ventrally, arched dorsally; size small to moderate, up to 200 mm. long; calcareous ring quite well developed with radial plates up to three times as long as the interradials; spicules consisting of well-developed tables with smooth disc and spire either of moderate height or high, terminating in a few to many small spines, tables rarely absent, buttons simple, with moderate-sized irregularly arranged knobs and three to ten pairs of relatively large holes.

OTHER SPECIES INCLUDED: *Holothuria aculeata, albiventer* Semper, 1868; *H. bowensis* Ludwig, 1875; *H. brauni* Helfer, 1912; *H. martensi* Semper, 1868; *H. michaelseni* Erwe, 1913; *H. ocellata* Jaeger, 1833; *H. submersa* Sluiter, 1901.

REMARKS: The series of species included in *Metriatyla* were not dealt with by Deichmann (1958).

H. (*M.*) *albiventer* from the Indo-West Pacific area is easily distinguished from the other species on account of its solid-looking tables which have spires of moderate height but densely covered with small spines.

H. (*M.*) *aculeata* from the East Indies and Philippine Islands and *H.* (*M.*) *scabra* from the Indo-West Pacific area have tables with spires of moderate height but they do not terminate in a large mass of small spines. The disc of the tables is perforated by 8–12 holes and the buttons with from 3–5 pairs of holes. Whether these two nominal species are really distinct I seriously doubt. *H.* (*M.*) *scabra* has priority.

The tables of *H.* (*M.*) *brauni* from the Red Sea are similar to those of *aculeata* and *scabra* but the buttons have from 3–10 pairs of holes.

[1] Greek: *metrius* = moderate; *tylus* = knob.

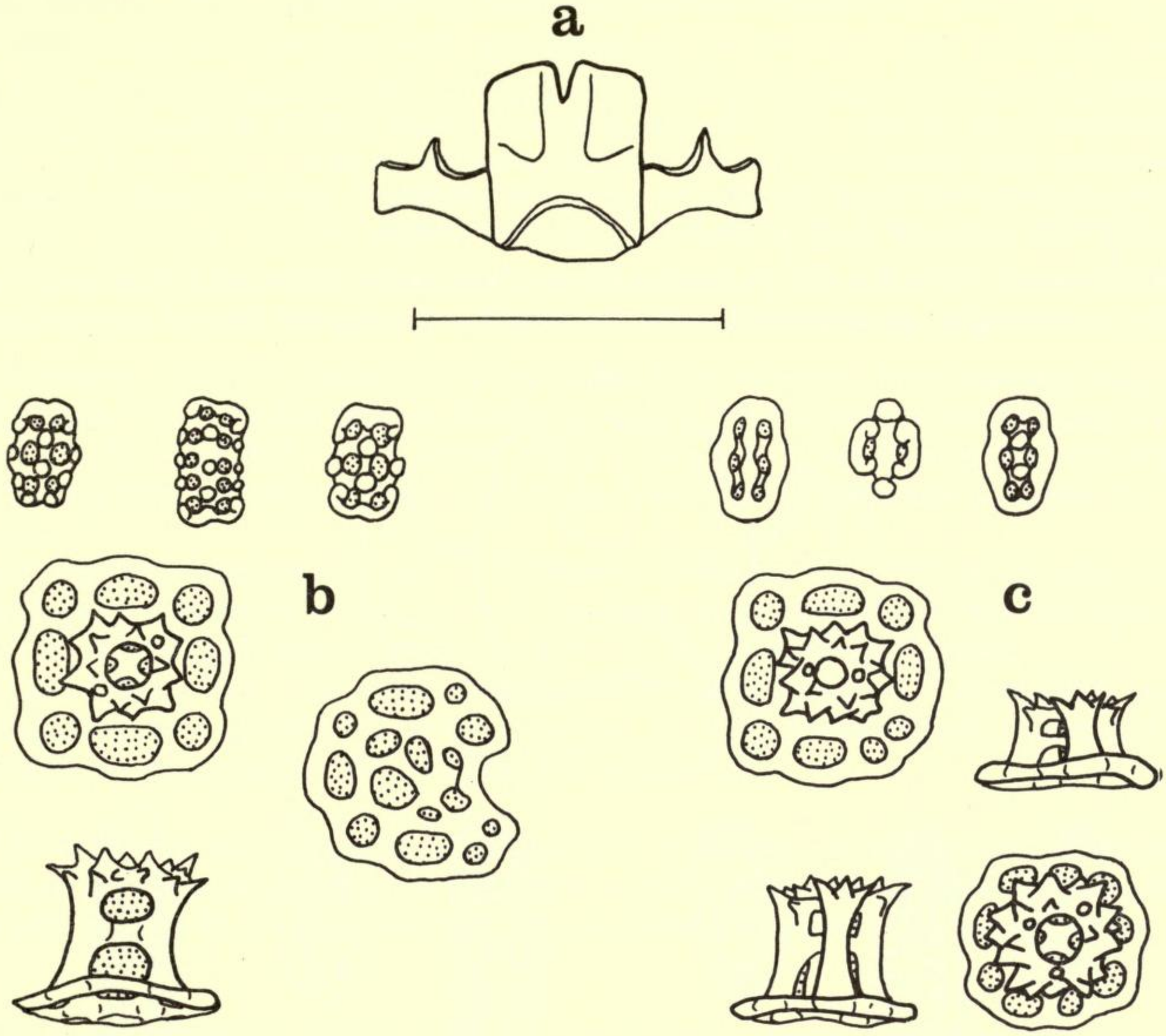

FIG. 20. *Holothuria* (*Metriatyla*) *scabra* Jaeger, 1833. B.M. No. 1855.4.4.7, Amboina, length 130 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

The tables of *H.* (*M.*) *ocellata* from the East Indies, Bay of Bengal and Red Sea have spires of moderate height or are slightly higher and the buttons have 3–6 pairs of holes.

The spires of the tables of *H.* (*M.*) *bowensis* from northern Australia and *H.* (*M.*) *martensi* from the East Indies and Indian Ocean are relatively high, those of *bowensis* having up to five cross-bridges and those of *martensi* up to seven cross-bridges. The buttons of *bowensis* have 3–5 pairs of holes while those of *martensi* usually only have 3 pairs of holes.

H. (*M.*) *michaelseni* from western Australia apparently lacks tables.

H. (*M.*) *submersa* from the East Indies has tables which have a spire of four unconnected pillars terminating in numerous small spines. The buttons have 3 to 4 pairs of holes.

Subgenus ***MICROTHELE*** Brandt, 1835

(Text-fig. 21)

Holothuria (*Microthele*) Brandt, 1835 : 54 (Type-species *H.* (*M.*) *maculata* Brandt, 1835 : 54 = *Muelleria nobilis* Selenka, 1867; designated by A. M. Clark & F. W. E. Rowe, 1967*a* : 100) non *Microthele*: Deichmann, 1958 : 287 = *Platyperona* subgen. nov.).

Holothuria (*Argiodia*) (part) Pearson, 1914 : 170 (Type-species *H. maculata* Brandt; designated by Pearson, 1914) [see A. M. Clark & F. W. E. Rowe, 1967*a* : 100].

DIAGNOSIS: Tentacles 20; pedicels and papillae indistinguishable, scattered ventrally and dorsally, no apparent ' collar ' of papillae around the base of the tentacles,

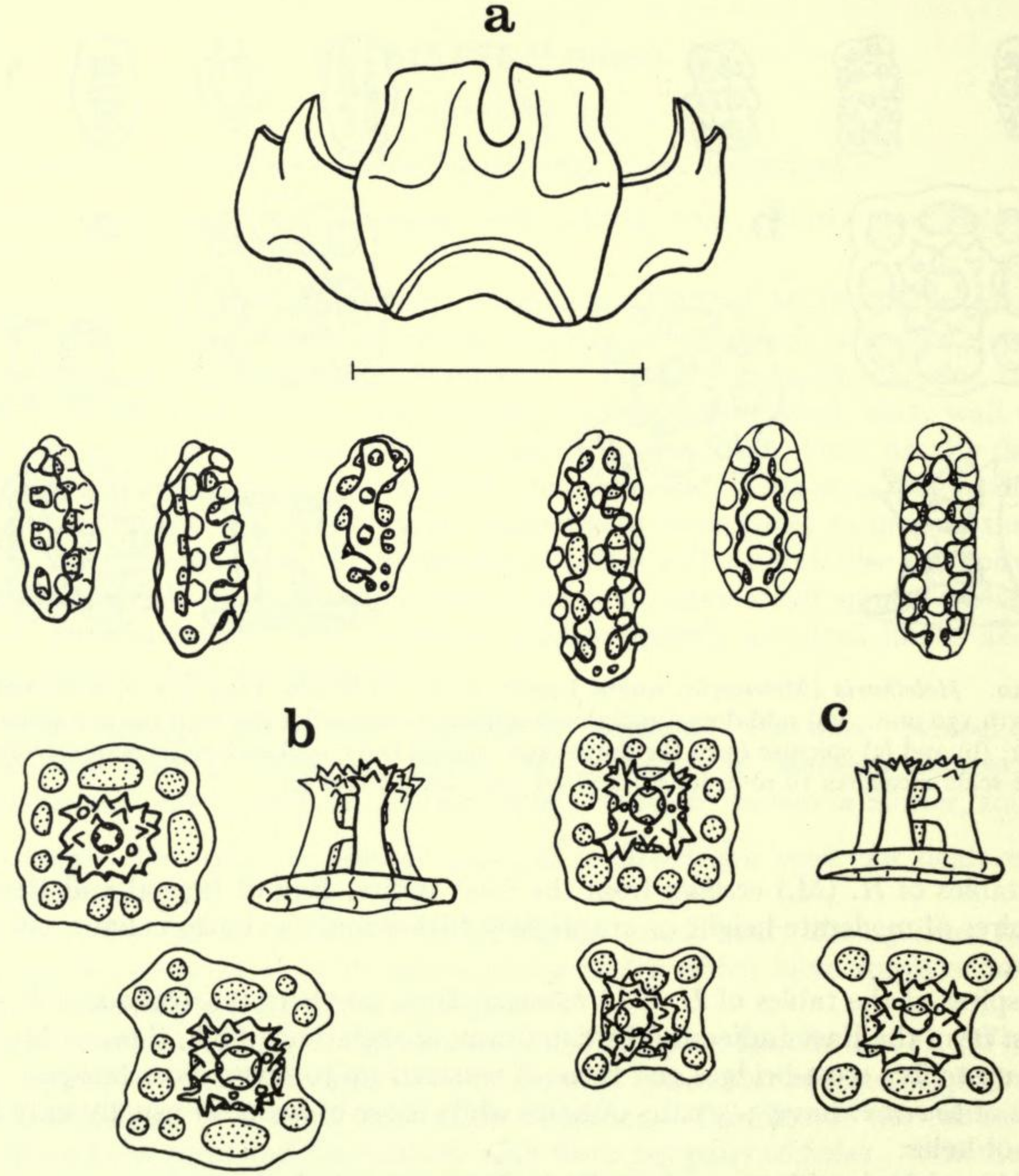

FIG. 21. *Holothuria* (*Michrothele*) *nobilis* (Selenka, 1867). B.M. No. 1877.1.15.11, Samoa, length 170 mm. (a) mid-dorsal radial and adjacent interradial plates of the calacareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0·1 mm. for (b) and (c).

anus usually with 5 calcified papillae only, though in smaller specimens (up to 200 mm. long) more papillae may be present and in the very large specimens (over 400 mm. long) anal papillae may be entirely lacking; body wall very thick, usually 5 (5–10) mm.; body rather cylindrical; size large or even massive, up to 600 mm. long; calcareous ring massive, with distinctly scalloped anterior margin, radial and interradial plates squarish, the radials being about twice the length of the interradials; spicules consisting of stout, well-developed tables with smooth squarish disc, spire of moderate height terminating in many small spines, buttons usually always hollow fenestrated ellipsoids though a few simple knobbed buttons may be present.

REMARKS: Brandt's concept of *Microthele* is now narrowed to encompass only the single Indo-West Pacific species *Muelleria nobilis* Selenka (see pp. 120 and 145 of this paper; A. M. Clark & F. W. E. Rowe, 1967*a* : 100). It is isolated by the form of the calcareous ring and spicules in combination with the massive size attained by the animal.

Having examined the holotype of *Holothuria whitmaei* Bell, 1887, in the collections of the British Museum, comparison of the body form, calcareous ring and spicules leads me to conclude that it is conspecific with *H.* (*M.*) *nobilis* Selenka.

Caso (1964) has described *Paramicrothele*, a subgenus of *Microthele* sensu Deichmann, non Brandt. The type-species, *M.* (*P.*) *zihuatanensis*, I consider is referable to the subgenus *Thymiosycia* (see appendix).

The following table (p. 165), based entirely on spicule occurrence and form may assist in assigning a species to its subgenus, supplementing the evolutionary tree and the key. Entries in brackets indicate the occasional occurrence of that character.

The following list includes synonymies made since Panning's survey of 1929–35. Those made in the present work are marked with an asterisk.

NOMINAL SPECIES LISTED BY PANNING, 1929–35	PRESENT DISPOSITION AND AUTHORITY
Holothuria (*Actinopyga*) *formosa* (Selenka, 1867).	*Thelenota ananas* Jaeger, 1833 : Panning, 1944.
H. (*Microthele*) *excellens* (Ludwig, 1875).	*H.* (*Platyperona*) *difficilis* Semper, 1868 : Deichmann, 1958 (as *Microthele*).
H. (*Microthele*) *flavocastanea* (Théel, 1886).	*H.* (*Platyperona*) *sanctori* Delle Chiaje, 1823 : Deichmann, 1958 (as *Microthele*).
H. (*Microthele*) *bedfordi* (Deichmann, 1922).	*H.* (*Platyperona*) *difficilis* Semper, 1868 : Deichmann, 1958 (as *Microthele*).
H. (*Microthele*) *aegyptiana* (Helfer, 1912).	*H.* (*Cystipus*) *rigida* (Selenka, 1867) : Deichmann, 1958 (as *Fossothuria*).
H. (*Microthele*) *lubrica* (Sluiter, 1894).	? *H.* (*Mertensiothuria*) *leucospilota* Brandt, 1835 : Deichmann, 1958.
Holothuria nitida Ives, 1891.	*H.* (*Halodeima*) *floridana* Pourtalés, 1851 : Cherbonnier, 1951.
H. silamensis Ives, 1891.	*H.* (*Halodeima*) *floridana* Pourtalés, 1851 : Cherbonnier, 1951.

H. inornata Semper, 1868.

H. lubrica var. *marenzelleri* Ludwig, 1883.

H. oxurropa Sluiter, 1888.

H. lamperti Ludwig, 1886.

H. immobilis Semper, 1868.

H. frequentiamensis H. L. Clark, 1902.

H. infesta Sluiter, 1901.

H. pertinax Ludwig, 1875.

H. unicolor Selenka, 1867.

H. fuscopunctata Jaeger, 1833.

H. altimensis H. L. Clark, 1921.

H. subverta H. L. Clark, 1921.

H. hypamma H. L. Clark, 1921.

H. fossor Deichmann, 1926.

* *H. papillata* Bell, 1887.
H. fusco-rubra Théel, 1886.

H. imperator Deichmann, 1938.

**H. whitmaei* Bell, 1887.
H. patagonica Perrier, 1904.

H. pluricuriosa Deichmann, 1937.

H. homoea H. L. Clark, 1938.

H. monsuni Heding, 1939.

H. gelatinosa Heding, 1939.

H. pseudo-zacae Cherbonnier, 1951.

H. pseudo-lubrica Cherbonnier, 1951.

H. parinhabilis Cherbonnier, 1951.

H. (*Halodeima*) *kefersteini* (Selenka, 1867) : Deichmann, 1958 (as *Ludwigothuria*).
H. (*Selenkothuria*) *erinaceus* Semper, 1868: Deichmann, 1958.
H. (*Mertensiothuria*) *leucospilota* Brandt, 1835 : Deichmann, 1958.
H. (*Mertensiothuria*) *leucospilota* Brandt, 1835 : Deichmann, 1958.
H. (*Lessonothuria*) *verrucosa* Selenka, 1867 : H. L. Clark, 1946 (as *Holothuria*.)
H. (*Platyperona*) *difficilis* Semper, 1868 : Deichmann, 1958 (as *Microthele*).
H. (*Mertensiothuria*) *leucospilota* Brandt, 1835 : Deichmann, 1958.
Labidodemas semperianum Selenka, 1867 : Deichmann, 1958.
? *H.* (*Halodeima*) *grisea* Selenka, 1867 : Deichmann, 1930.
Homonym of *H. fuscopunctata* Quoy & Gaimard, 1830 : ? syn. of *H.* (*Cystipus*) *inhabilis* Selenka, 1867 : Deichmann, 1958 (as *Jaegerothuria*).
H. (*Platyperona*) *difficilis* Semper, 1868 : Deichmann, 1958 (as *Microthele*).
H. (*Metriatyla*) *martensi* Semper, 1868 : H. L. Clark, 1946 (as *Holothuria*).
H. (*Cystipus*) *inhabilis* Selenka, 1867 : H. L. Clark, 1946 (as *Holothuria*).
H. (*Cystipus*) *cubana* Ludwig, 1875 : Deichmann, 1958 (as *Fossothuria*).
H. (*Acanthotrapeza*) *pyxis* Selenka, 1867.
H. (*Mertensiothuria*) *leucospilota* Brandt, 1835 : Deichmann, 1958.
H. (*Theelothuria*) *princeps* Selenka, 1867 : Deichmann, 1958.
H. (*Microthele*) *nobilis* Selenka, 1867.
H. (*Thymiosycia*) *gyrifer* Selenka, 1867 : Deichmann, 1958 (as *Brandtothuria*).
H. (*Mertensiothuria*) *fuscocinerea* Jaeger, 1833 : Deichmann, 1958.
H. (*Mertensiothuria*) *leucospilota* Brandt 1835 : Deichmann, 1958.
H. (*Thymiosycia*) *arenicola* Semper, 1868 : Deichmann, 1958 (as *Brandtothuria*).
H. (*Mertensiothuria*) *leucospilota* Brandt, 1835 : Deichmann, 1958.
H. (*Mertensiothuria*) *fusco-cinerea* Jaeger, 1833 : Deichmann, 1958.
H. (*Selenkothuria*) *lubrica* Selenka, 1867 : Deichmann, 1958.
H. (*Cystipus*) *inhabilis* Selenka, 1867 : Deichmann, 1958 (as *Jaegerothuria*).

TABLE 1

	TABLES																	BUTTONS							OTHER SPICULES		
	DISC								SPIRE				MODIFICATIONS														
	Smooth	Knobbed	Spinose	Reduced	Flat	Raised at rim	Central hole +	Central hole not +	Terminating in cluster or ring of spines	Terminal spines in maltese+	Low	Medium height	High	Spheres	Synallactid-like	Tack-like	Absent rare or reduced	Smooth	Rugose	Medium sized knobs	Large knobs	Ellipsoidal	Reduced	Absent or rare	Pseudo-buttons	Rods +/or plates	Rosettes
Selenkothuria	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
Semperothuria	+	..	..	+	+	..	..	+	..	+	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..
Halodeima	+	..	(+)	+	+	..	..	+	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+
Acanthotrapeza	(+)	..	+	..	..	+	..	+	+	..	+	+	(+)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lessonothuria	(+)	..	+	..	..	+	..	+	+	..	..	+	..	..	..	..	..	(+)	..	..	..	..	..	+	..	..	..	..
Vaneyothuria	..	..	+	..	+	..	..	+	+	+	..	+	+	..	..	..	..	+	..	..	..	..	+	..	..	..	..	..
Thymiosycia	+	..	..	..	+	..	..	+	+	..	..	+	(+)	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
Platyperona	+	..	..	..	+	..	..	+	+	..	..	+	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
Metriatyla	+	..	..	..	+	..	..	+	+	..	..	+	+	..	..	..	..	(+)	..	+	..	..	..	..	..	..	..	..
Cystipus	..	+	..	..	+	..	..	+	+	..	+	+	..	+	..	..	..	..	..	..	+	..	..	..	..	..	..	..
Microthele	+	..	..	..	+	..	..	+	+	..	..	+	..	..	..	..	..	..	..	+	..	+	..	..	..	..	..	..
Theelothuria	+	..	+	..	+	..	..	+	+	..	..	+	+	..	+	+	..	..	..	+	..	+	..	..	..	..	..	..
Mertensiothuria	..	..	+	(+)	+	..	..	+	+	..	+	+	..	..	..	..	..	+	..	..	..	..	+	..	..	..	..	..
Stauropora	+	..	+	..	+	+	+	..	+	..	+	+	+	..	..	..	..	+	+	..	..	..	(+)	(+)	..	..	..	..
Holothuria	..	..	+	(+)	+	..	..	+	+	..	+	+	+	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..
Irenothuria	..	..	+	..	+	..	..	+	..	+?	+	+	+	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..
Panningothuria	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	+	..	..	..

Inevitably with such a large assemblage of nominal species there is a residue of some which are currently recognized as probably valid but which it has been impossible to refer to a subgenus, either due to lack of material or to inadequacy of the original description. These are listed here.

Nominal species	Possible disposition
Holothuria axiologa H. L. Clark, 1921.	? *H.* (*Microthele*)
H. conica H. L. Clark, 1938.	? *H.* (*Metriatyla*)
H. cumulus H. L. Clark, 1921.	? *H.* (*Lessonothuria*)
H. dietrichi Ludwig, 1875.	? *H.* (*Mertensiothuria*)
H. enalia Lampert, 1885.	? *H.* (*Halodeima*)
H. isuga Mitsukuri, 1912.	? *H.* (*Lessonothuria*)
H. marginata Sluiter, 1901.	? *H.* (*Thymiosycia*)
H. sinefibula Cherbonnier, 1965.	? *H.* (*Vaneyothuria*)
H. prompta Koehler & Vaney, 1908.	? *H.* (*Stauropora*)
H. sluiteri Ludwig, 1888.	? *H.* (*Stauropora*)
H. mitis Sluiter, 1901.	?

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APPENDIX

Since the completion of this paper, thanks to the kindness of Dr. Caso, I have received a paratype of *Holothuria* (*Paraholothuria*) *riojai* Caso and one of *Microthele* (*Paramicrothele*) *zihuatanensis* Caso. These yield the following conclusions:

a. *M.* (*Paramicrothele*) *zihuatanensis* in my opinion is close to, if not conspecific with *H.* (*Thymiosycia*) *gyrifer* Selenka, 1867, the relationship of which with *hilla* Lesson, 1830, remains to be decided. *Paramicrothele* is therefore referable to the synonymy of *H.* (*Thymiosycia*). This agrees with my provisional conclusion expressed on p. 147.

b. *H.* (*Paraholothuria*) *riojai* may be a valid species. It is affiliated to the subgenus *Halodeima*, differing only in the absence of rosettes and extreme reduction of the tables. However, in the specimen sent, the spicules appear somewhat eroded by poor preservative. Also there is no sign of the plate-like spicules (resembling those of the sympatric *Pseudocnus californicus*—a dendrochirotid—but unlike anything found in other aspidochirotids) described by Dr. Caso as occurring in this species.

In my opinion *Paraholothuria* could be recognized as a subgenus of *Holothuria* distinguished from *H.* (*Halodeima*) by the lack of rosettes, though further study may not substantiate this.

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