

MORPHOLOGY, SYSTEMATICS, AND VARIABILITY OF THE
SOUTHERN AFRICAN SOFT CORAL *ALCYONIUM VARIABLE*
(J. STUART THOMSON, 1921) (OCTOCORALLIA, ALCYONIIDAE)

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(With 15 figures and 1 table)

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ABSTRACT

The fungiform alcyoniid soft coral, *Alcyonium variable*, is shown to be widely distributed in the colder waters of southern Africa at depths of 13–468 m. New phenotypes from a shallow-water population found off the Atlantic side of the Cape of Good Hope Peninsula add further evidence of extreme intraspecific colour variation. Aspects of morphological variation, anatomy, colour polymorphism, sclerite structure, and geographic distribution are described. The systematic status of the species and its relations to other species of *Alcyonium* as well as other alcyoniid genera are discussed. *Alcyonium fungiforme* Tixier-Durivault, 1954, *A. luteum* Tixier-Durivault, 1954, and *Metalcyonium variable* Thomson, 1921, are considered synonyms of *A. variable*.

CONTENTS

| | PAGE |
|--|------|
| Introduction | 241 |
| Material examined | 242 |
| Description | 243 |
| Morphology and sclerites | 243 |
| Anatomy | 252 |
| Variability and coloration | 255 |
| Distribution and habitat | 259 |
| Discussion | 259 |
| Historical survey | 259 |
| Systematic status | 262 |
| Synonymy | 264 |
| Comparison with <i>Alcyonium paessleri</i> May, 1899 | 266 |
| Zoogeography | 267 |
| Acknowledgements | 268 |
| References | 269 |

INTRODUCTION

Alcyonium variable (J. Stuart Thomson, 1921) is a highly variable, often beautifully coloured soft coral from southern Africa. The history of the literature pertaining to this species, as well as to the genera *Alcyonium*, *Metalcyonium*, *Bellonella*, *Cactogorgia*, and *Nidalia*, has been plagued with considerable confusion. This is partially due to an often high degree of intraspecific variation,

the dubious nature of the original descriptions of some genera such as *Metalcyonium*, the lack of attention by some previous investigators to correct identification of material or accurate comparison with other known species, and the lack of clear and consistent morphological distinctions between nominal genera.

Previously published accounts have been purely taxonomic in nature; virtually nothing has been recorded on other aspects of the biology of this species. Previous workers relied on preserved material that was either dredged or trawled from deep water. Observation of subtidal octocorals in their natural habitats was technically unfeasible. Study of living colonies *in situ* was made possible by the advent of SCUBA, but still very little is known about the ecology, natural history, and other aspects of the biology of most octocoral species.

Alcyonium variabile has previously been known only from depths exceeding 47 m. A survey of the shallow sublittoral regions of the western side of the Cape Peninsula by use of SCUBA has revealed a presumably large but previously unrecorded polymorphic population. This paper presents an examination of various aspects of the biology of this species from southern Africa, together with an assessment of its great variability. An examination of the systematics of the species and a discussion of the status of related genera is also presented.

Alcyonium variabile has been confused in the past with other species of *Alcyonium* such as *A. paessleri* May, 1899, from Patagonia and Antarctica. These species are here considered separate and a comparison of the two is presented.

This paper attempts to unify the many known colour varieties of *Alcyonium variabile* (many of which were previously assigned specific status) into a single highly variable species based on consistencies in sclerite distribution and form as well as other comparative morphological aspects.

The material is deposited in the South African Museum, Cape Town (SAM).

MATERIAL EXAMINED

SAM-H3165 and H3166: 10 specimens, 23 m depth, Hottentots Huisie, western side of Cape Peninsula (33°59'S 18°21'E); 15 June 1983; coll. W. R. Liltved, SCUBA.

SAM-H3167: 12 specimens; 13–16 m depth, Hottentots Huisie, western side of Cape Peninsula (33°59'S 18°21'E); 18 August 1983; coll. G. C. Williams, SCUBA.

SAM-H3602: 1 specimen; 90 m depth, off East London (33°12'S 28°01'E); 17 July 1984; coll. G. C. Williams (R.V. *Meiring Naude*, XX 51), dredge.

SAM-H3271: 1 specimen; 26 m depth, off Llandudno, western side of Cape Peninsula (34°01'S 18°20'E); 4 February 1984; coll. G. C. Williams, SCUBA.

SAM-H1042: 2 specimens; 148–159 m depth, 16 km SW of Cape Point (34°27'S 10°23'E); 28 October 1903; SS *Pieter Faure* survey, PF 18171, large trawl.

SAM-H895: 5 specimens; 82 m depth; 10 km E of Cape Morgan (32°44'S 28°30'E); 13 August 1901; SS *Pieter Faure* survey, PF 13388A, dredge.

SAM-H1040: 8 specimens; 141 m depth; 17 km E of Cape Morgan (32°44'S 28°30'E); 26 July 1901; SS *Pieter Faure* survey, PF 13174, dredge.

SAM-H924: 5 specimens; 86 m depth; 36 km SE of Tugela River mouth, Natal (29°20'S 31°30'E); 29 January 1901; SS *Pieter Faure* survey, PF 11537, large dredge.

SAM-H3245: 2 specimens; 168 m depth; 30 km S of Cape Hangklip (34°39'S 18°42'E); 10 February 1948; coll. University of Cape Town Ecological Survey Collection, Station AFR 882J, dredge.

SAM-H883: 7 specimens; 95 m depth; 18 km S of Knysna Heads (34°10'S 23°15'E); 2 July 1902; SS *Pieter Faure* survey, PF 15291, shrimp trawl.

DESCRIPTION

Class ANTHOZOA Ehrenberg, 1834

Subclass OCTOCORALLIA Haeckel, 1866

Order ALCYONACEA Lamouroux, 1816 (emended by Verrill, 1866;
Bayer, 1981)

Family **Alcyoniidae** Lamouroux, 1812

Genus *Alcyonium* Linnaeus, 1758

Alcyonium variable (Thomson, 1921) comb. nov.

Figs 1–15

Alcyonium antarcticum (non Wright & Studer, 1899) Hickson, 1900: 73.

Alcyonium (*Metalcyonium*) *patagonicum* (non May, 1899) Kükenthal, 1906: 47 (*partim*).

Metalcyonium patagonicum (non May, 1899) Thomson, 1910: 562.

Metalcyonium variable Thomson, 1921: 152; 1924: 47, 69.

Metalcyonium variable var. *molle* Thomson, 1921: 162; 1924: 47, 69.

Metalcyonium variable var. *durum* Thomson, 1921: 165; 1924: 47, 69.

Alcyonium paessleri (non May, 1899) Molander, 1929a: 50; 1929b: 4 (*partim*).

Alcyonium fungiforme Tixier-Durivault, 1954: 385.

Alcyonium luteum Tixier-Durivault, 1954: 388.

Morphology and sclerites

The colonies examined range in total length from 8 to 70 mm. They are mushroom-shaped; composed of a spherical capitulum and a conspicuous stalk (Fig. 1). Both parts are separated by a clear delimitation (Fig. 2A).

The globular capitulum is wider than the stalk. The surface layer is filled with closely-set sclerites. They vary from stout coarsely tuberculate rods less than 0,22 mm long to capstans less than 0,08 mm long (Figs 3A, 4A–D). Some rods may be clubbed. Capstans may predominate in some colonies. Some capstans may be modified and sharply pointed tubercles. The sclerites from the interior of the capitulum are usually arranged parallel to the gastric cavities. They are

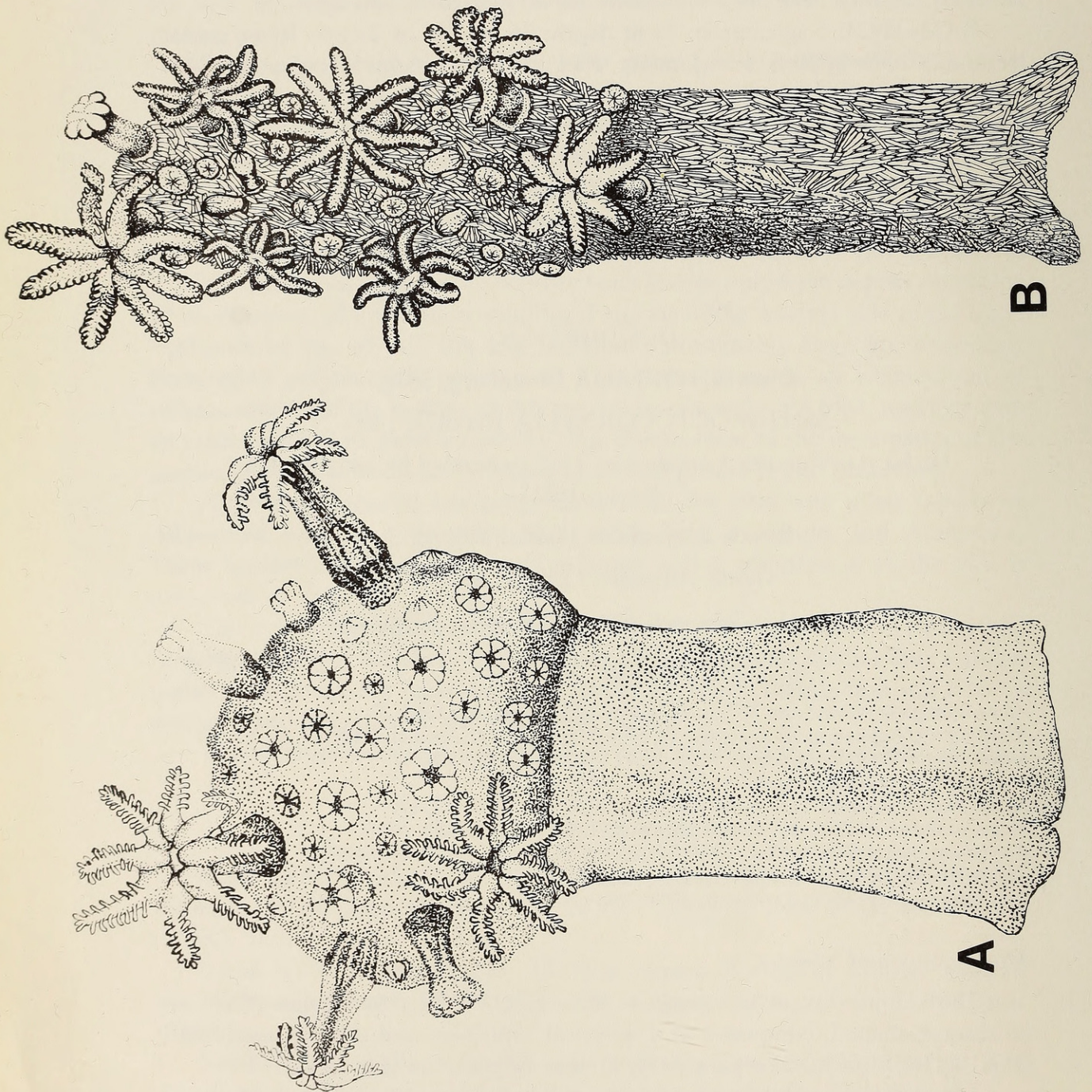


Fig. 2. A. *Alcyonium variable* showing typically fungiform-capitate colony shape (40 mm total length). B. Digitiform colony shape characteristic of many alcyoniid species; *Metalcyonium unilobatum* (Thomson, 1921) is shown as an



Fig. 3. *Alcyonium variable*. A. Capitulum sclerites from surface coenenchyme. B. Capitulum sclerites from inner coenenchyme.

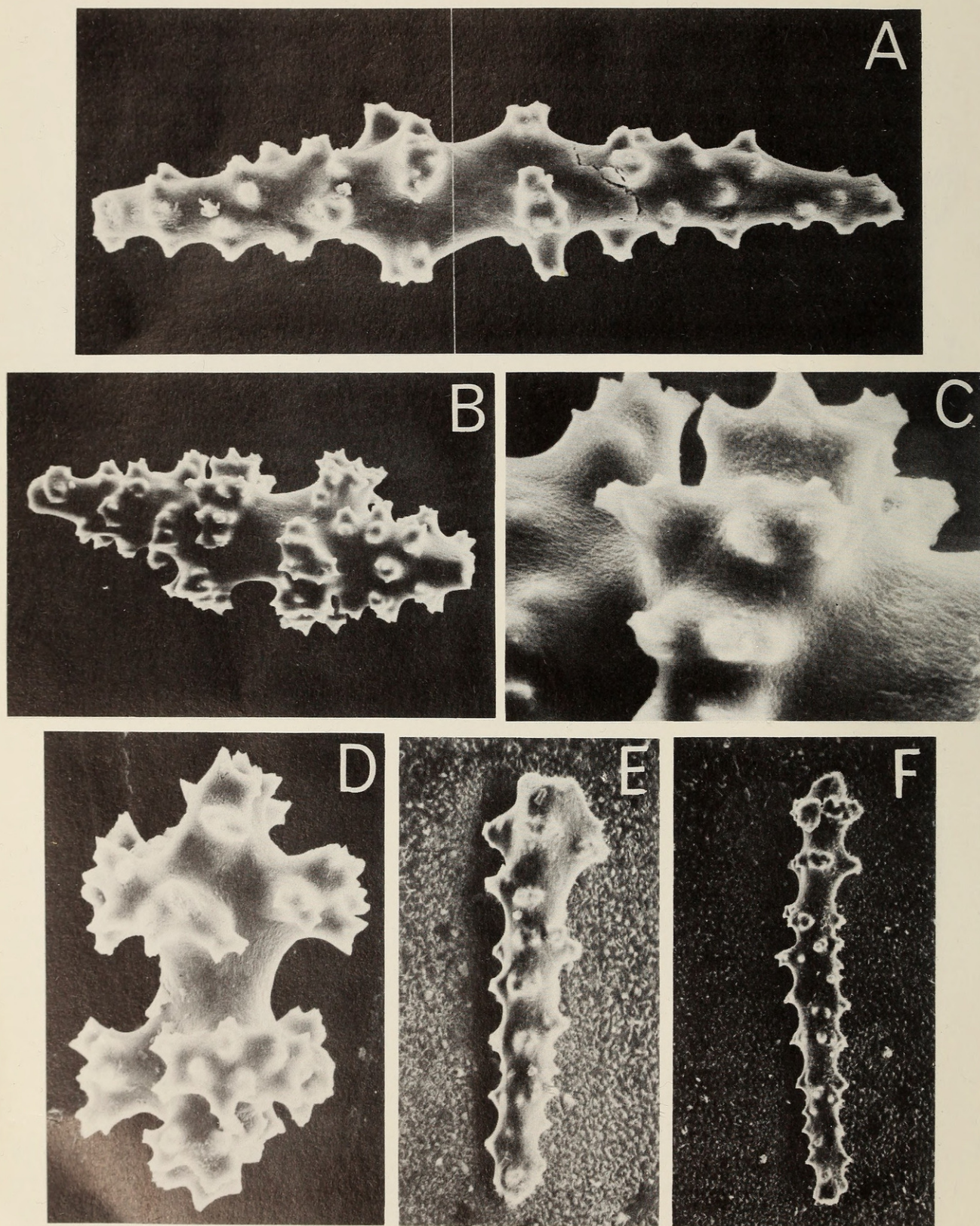


Fig. 4. *Alcyonium variable*. Scanning electron micrographs of capitulum sclerites. A-D. Sclerites of outer coenenchyme. A. Spindle, 0,17 mm. B. Club, 0,12 mm. C. Detail of middle portion of club in B, 0,03 mm. D. Capstan, 0,07 mm. E-F. Slightly clubbed rods of the inner coenenchyme. E. 0,15 mm. F. 0,25 mm.

predominantly rods, sometimes slightly clavate, often with coarse to ornate tubercles, and vary from approximately 0,07 to 0,27 mm in length (Figs 3B, 4E–F). Modified, sharply pointed capstans may also occur.

The polyps are restricted to the entire surface of the capitulum. When fully expanded they may reach a length of 12 mm. In expanded condition the polyp shows two differentiated regions: the basal or proximal region and the distal anthocodia (Fig. 5A). The proximal portions possess varying concentrations of capstans or double cones, from 0,04 to 0,12 mm in length. These sclerites are relatively consistent in form and size (Figs 6C, 7C–F). Partially retracted polyps can form rounded calyx-like protuberances on the surface of the capitulum; however, these are not permanent calyces since they are not rigid and are capable of total retraction into the capitulum (Fig. 1G). The anthocodia consists of three parts: the neck zone or introvert, the anthocodial wall with crown and points, and the tentacles (Fig. 5A). Sclerites of the crown, points, and tentacles are rods and spindles of varying length and coarseness (Fig. 6A). The neck zone is usually unarmed and translucent—the pharynx and the mesenterial filaments are plainly visible through it. In one red colony from the western Cape Peninsula, the polyps possess sparsely scattered capstans in the neck zone. The crown consists of 6–12 tiers of very slender sclerites. These are finely tuberculated needles up to 0,6 mm in length (Fig. 8A, E). Superposing the crown are eight points, each consisting of numerous spindles of which the undermost are arranged *en chevron*; more distally they are longitudinally placed (Fig. 5A). The point sclerites are mostly very similar to those of the crown, but distally some may be shorter and more coarsely tuberculated (Fig. 8B–D). The tentacles are narrow and reach a length of 2,5 mm. On each side they bear one row of approximately 12 pinnules (Fig. 5B). The backs of the tentacles are armed proximally with the uppermost point sclerites, and distally with short spindles or coarse rods usually less than 0,13 mm in length (Figs 6A, 8F–G). These sclerites are not arranged in any distinctive alignment or pattern (Fig. 5A). Rod-like sclerites may also occur in between the bases of most pinnules (Fig. 5B). Similar short spindles or rods may occur along the grooves of the peristome in a radial pattern of eight lines extending from the mouth to the areas between the bases of the tentacles (Fig. 5C). The wall of the pharynx is strongly impregnated with many short spindles or rod-like sclerites. These are coarsely tuberculated and usually less than 0,14 mm in length (Figs 6B, 7A–B).

The stalk is barren, being completely devoid of anthocodiae. The height of the stalk is variable (Fig. 12). The base may produce finger-like or flattened projections forming a holdfast. The surface layer of the stalk contains densely set sclerites that are almost exclusively capstans varying in length from 0,05 to 0,10 mm (Figs 9A, 10A–C). In the interior of the stalk there are mainly large stout spindles or clubbed forms that are ornately tuberculated. They vary from 0,10 to 0,28 mm in length and up to 0,06 mm in width. Modified, pointed capstans may occur rarely (Figs 9B, 10D–G).

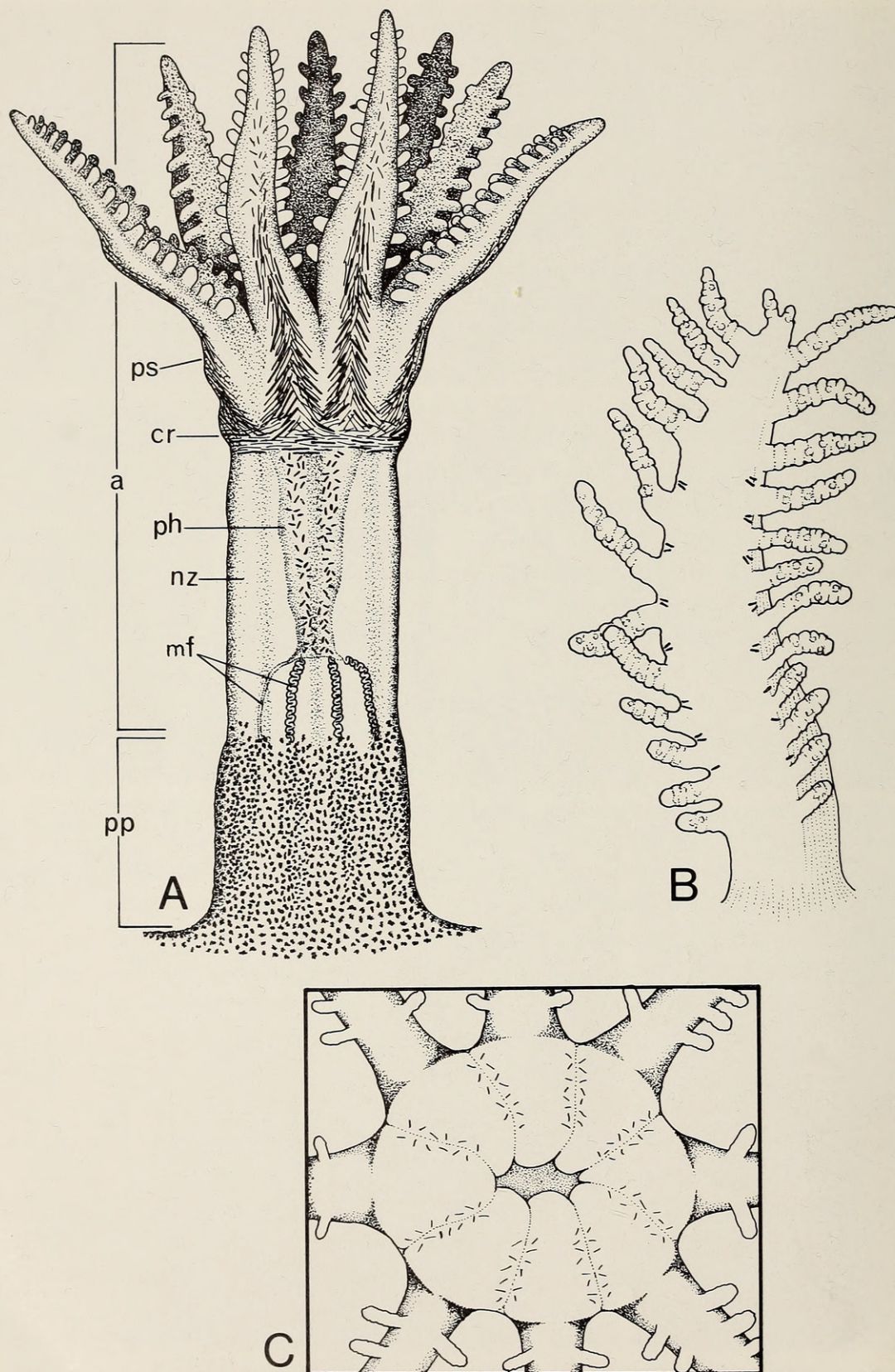


Fig. 5. Polyp armature of *Alcyonium variable*. A. Expanded polyp showing capstans forming calyx-like proximal region, short spindles of the pharynx, and long spindles of the anthocodia; total length of polyp 9 mm. B. Single tentacle showing rod-like sclerites at the base of the pinnules; total length of tentacle 2,5 mm. C. Peristome showing alignment of rod-like sclerites; diameter of disc 2 mm.

a-anthocodia, cr-crown, mf-mesenterial filament, nz-neck zone, ph-pharynx, pp-proximal region of polyp, ps-points.

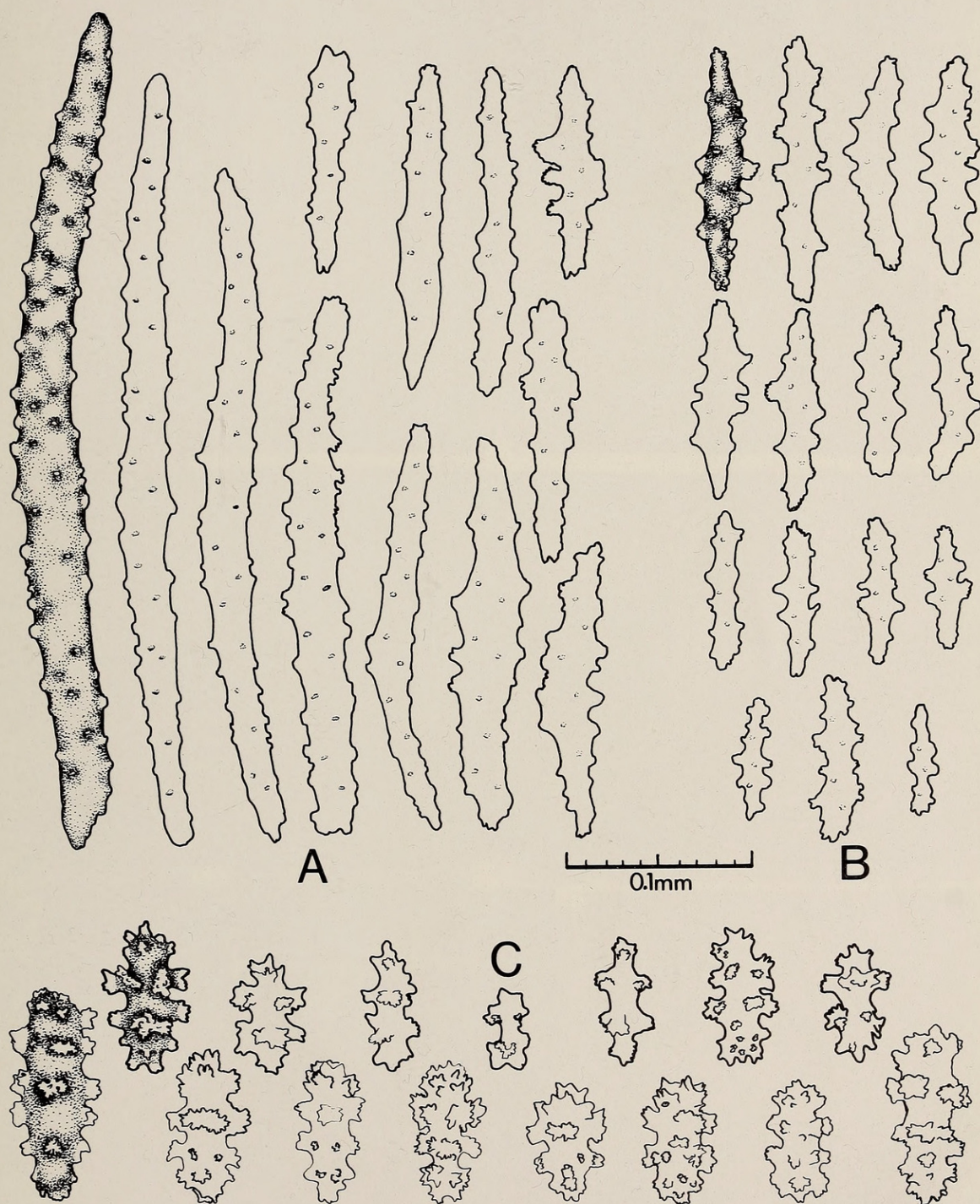


Fig. 6. *Alcyonium variable*. A. Polyp sclerites from crown, points, and tentacles of anthocodia. B. Polyp sclerites from wall of pharynx. C. Polyp sclerites from wall of proximal region of polyp.

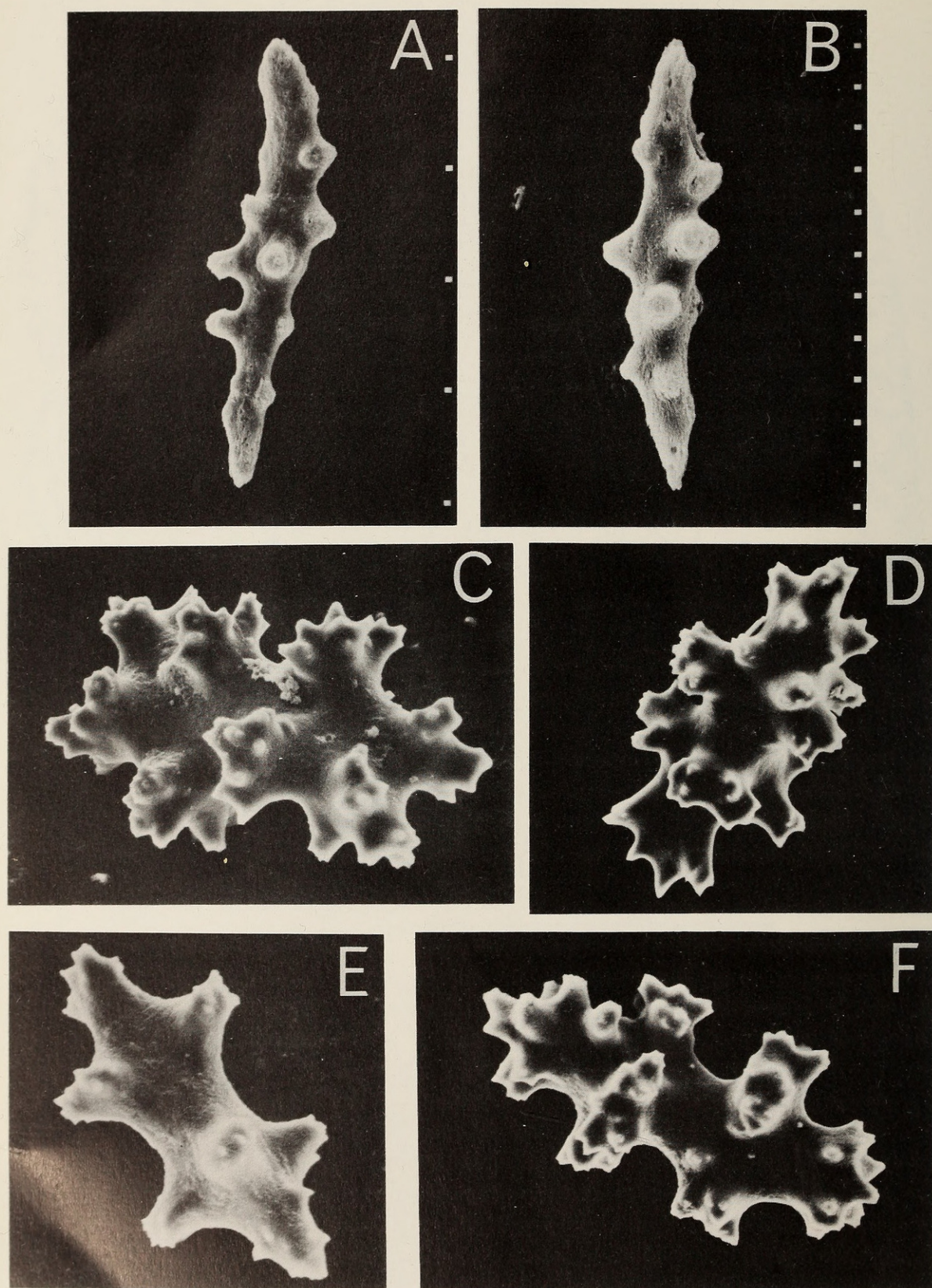


Fig. 7. *Alcyonium variable*. Scanning electron micrographs of sclerites from pharynx and calyx-like base of polyp. A–B. Spindles of pharyngeal wall. C–F. Capstans from wall of proximal region of polyp. A. Scale between squares $30\ \mu\text{m}$ (0,12 mm total length). B. Scale between squares $10\ \mu\text{m}$ (0,11 mm total length). C–E. 0,07 mm. F. 0,09 mm.

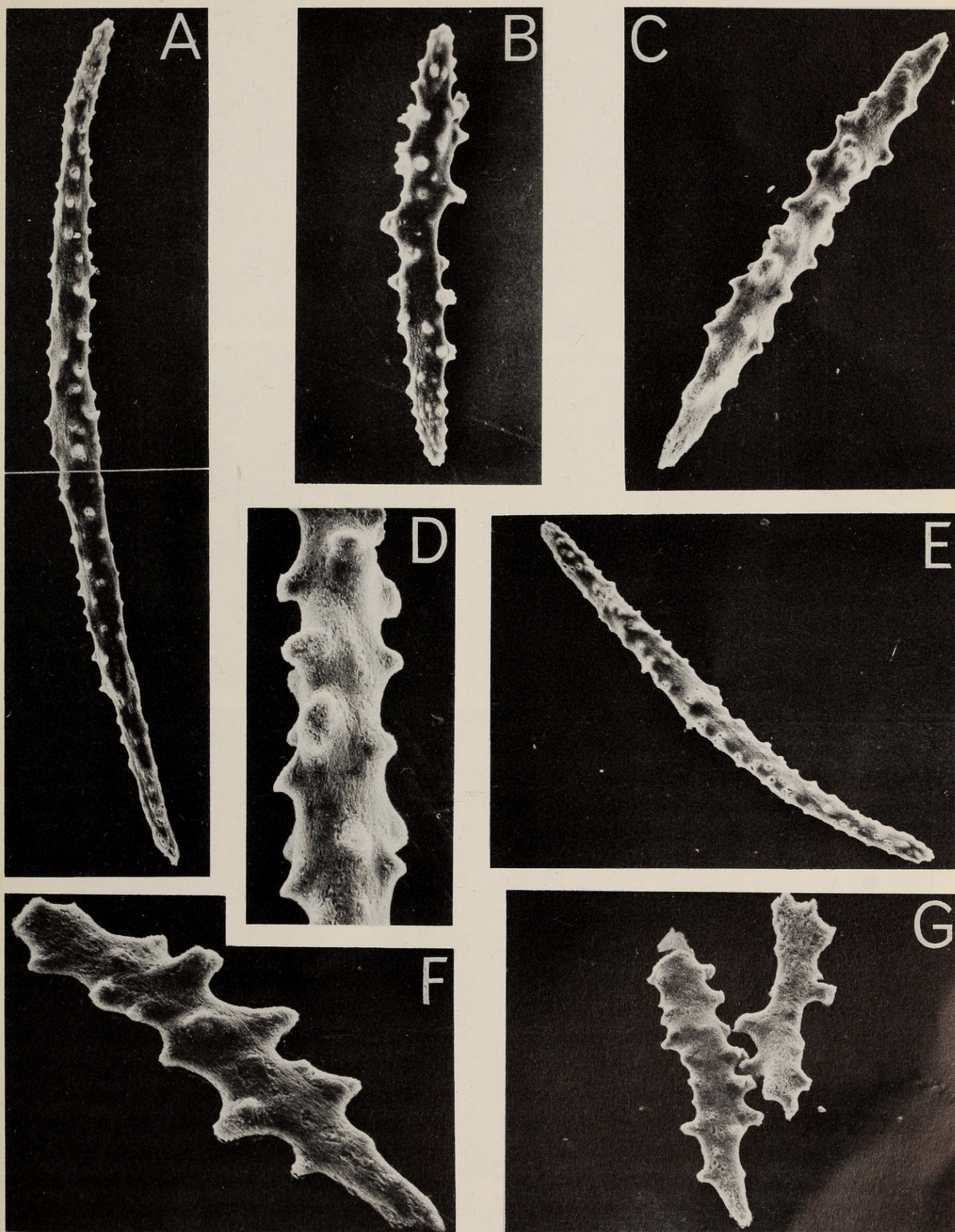


Fig. 8. *Alcyonium variable*. Scanning electron micrographs of anthocodial sclerites. A. Needle from crown, 0,60 mm. B-C. Spindles from points. B. 0,21 mm. C. 0,23 mm. D. Detail of central portion of spindle in C; length of photograph 0,09 mm. E. Needle from crown, 0,37 mm. F-G. Rod-like sclerites from distal portion of tentacles. F. 0,12 mm. G. 0,12 and 0,09 mm.

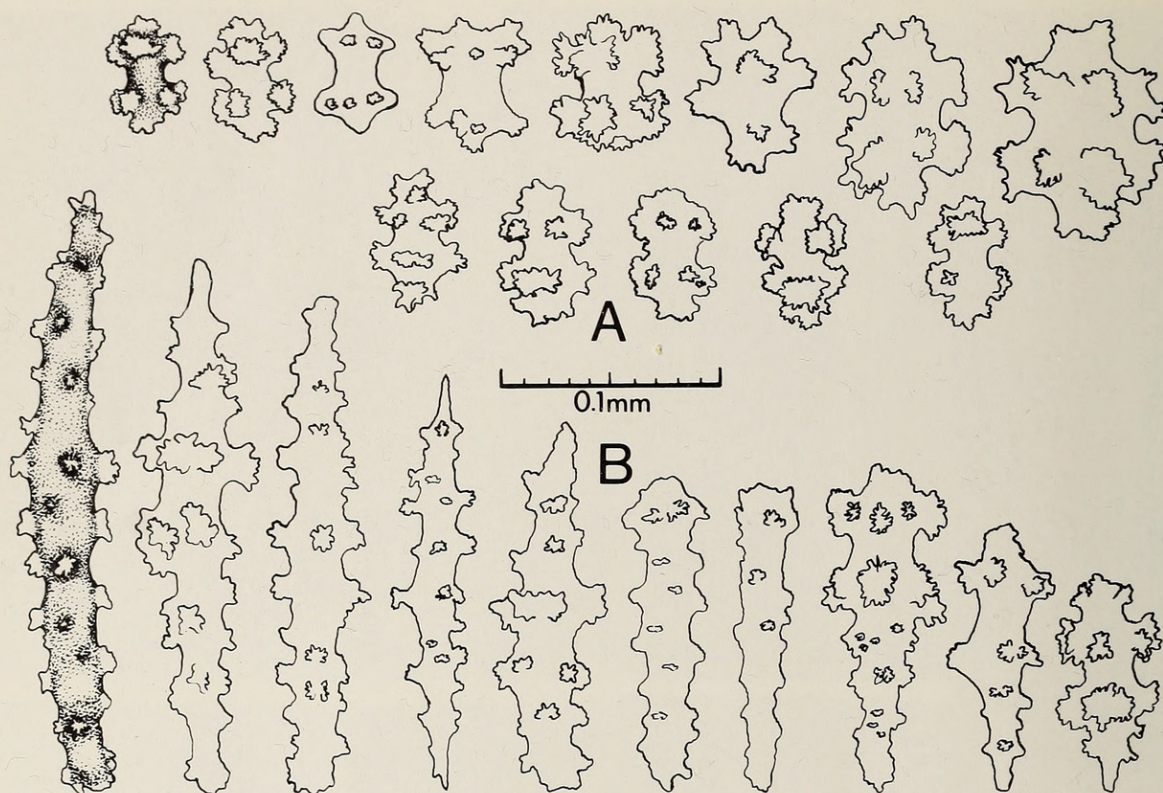


Fig. 9. *Alcyonium variabile*. A. Stalk sclerites from surface coenenchyme. B. Stalk sclerites from interior coenenchyme.

Anatomy

A 35 mm-long red-purple colony collected from the sublittoral of the Cape Peninsula (SAM-H3166) was sectioned longitudinally. The epidermis is a thin transparent layer, which separates readily from the underlying mesogloea. The coenenchyme consists partially of an outer area approximately 0,16 mm thick. This region is very densely imbedded with primarily red capstans, giving a rough textured appearance to the colony. Below the outer layer is the inner coenenchyme, which fills the interior of the colony between the tube-like polyps. The colour of this region is pink due to the combined effect of white mesogloea and gastrodermis and light-red sclerites. Numerous spindles and clubbed forms are contained in the region just below the outer coenenchyme. These sclerites become less dense toward the interior of the capitulum and stalk regions. The interior coenenchyme adjacent to the gastric cavities is profusely set with clear to light-reddish spindles approximately 0,22 mm in length. Many of the gastric cavities contain spherical ova varying in diameter between 0,06 and 0,12 mm. The gastrodermal solenial network is readily visible in the inner coenenchyme below the outer layer of the capitulum. The long thin gastric cavities extend to the base of the stalk. Anthocodiae are in varying states of contraction and retraction. The eight-ridged protuberances of the calyces of some polyps are readily visible (Fig. 11).

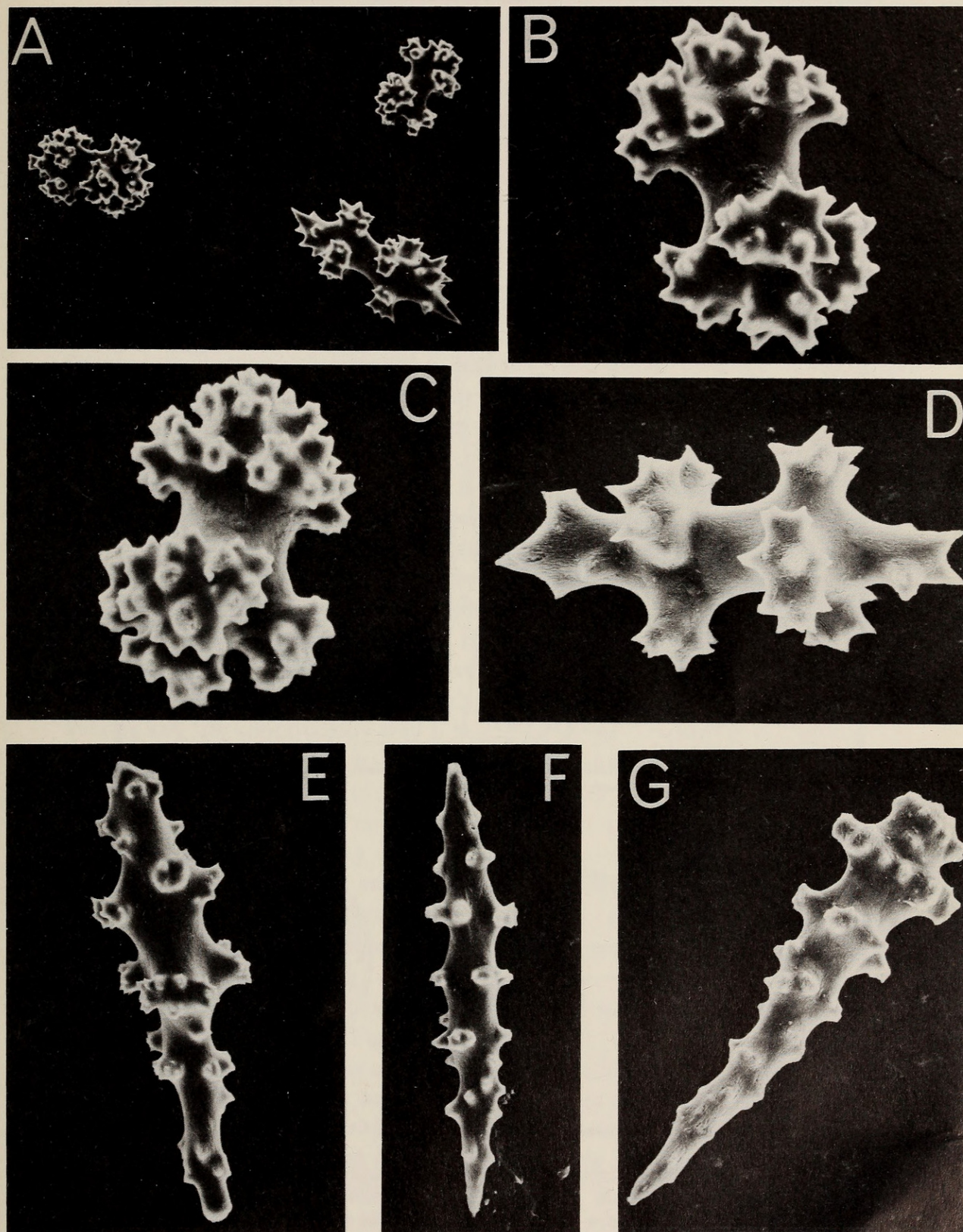


Fig. 10. *Alcyonium variable*. Scanning electron micrographs of stalk sclerites. A–C. Capstans from outer coenenchyme. A. 0,06–0,13 mm. B. 0,07 mm. C. 0,08 mm. D–G. Sclerites from inner coenenchyme. D. Modified capstan, 0,10 mm. E. Clubbed spindle, 0,20 mm. F. Spindle, 0,20 mm. G. Club, 0,17 mm.

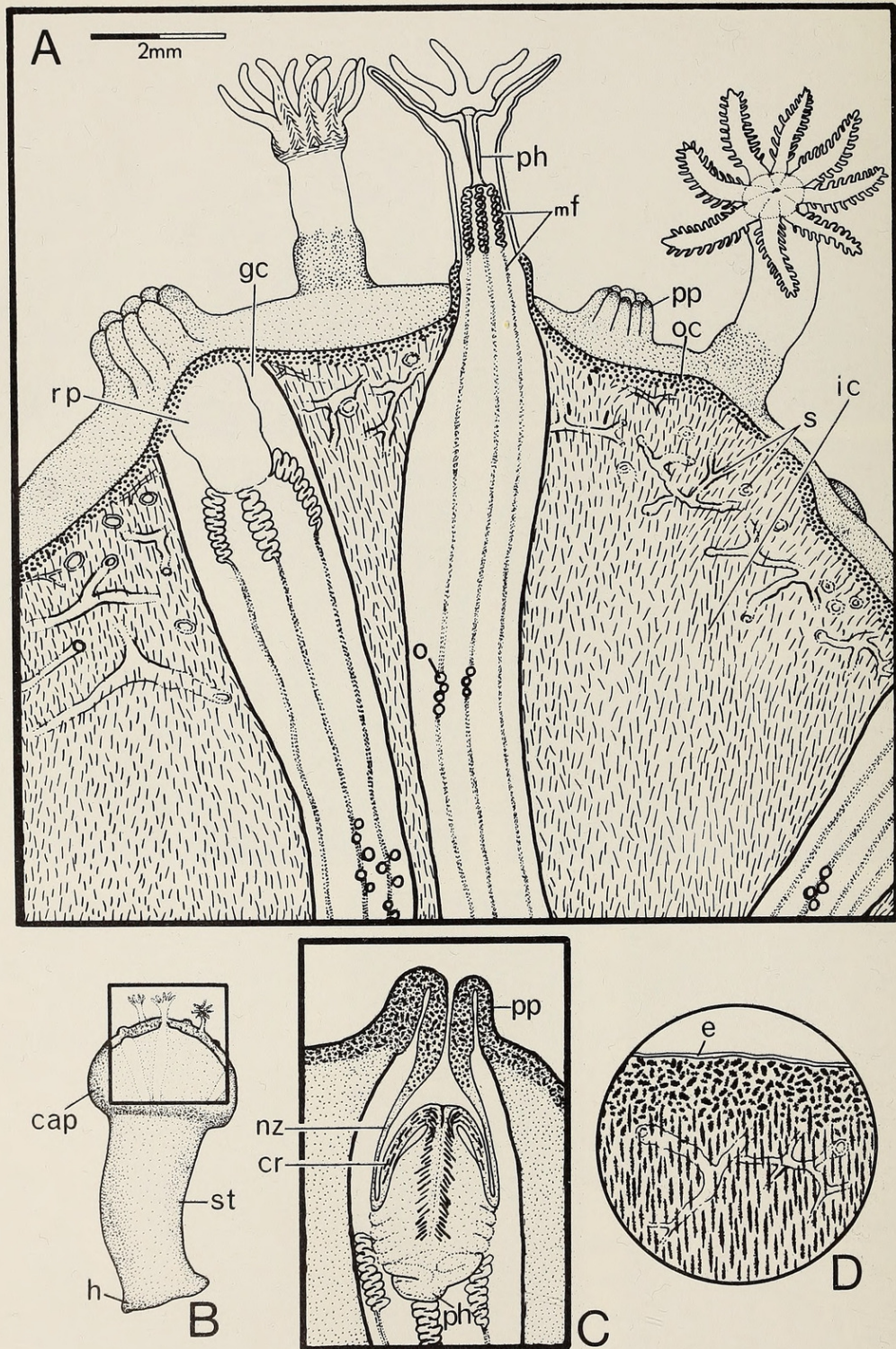


Fig. 11. Anatomy of *Alcyonium variable*. A. Longitudinal section through capitulum of 35 mm-long colony from the Cape Peninsula. B. Area of section (shown enlarged from A) from the entire colony. C. Longitudinal section of a retracted polyp; sclerites of interior coenenchyme omitted; width of diagram 4 mm. D. Detail of section through coenenchyme of capitulum showing thin outer layer of capstans and interior of spindles; diameter of diagram 1 mm.
 cap—capitulum, cr—crown, e—epidermis, gc—gastric cavity, h—holdfast, ic—interior coenenchyme, mf—mesenterial filament, nz—neck zone, o—ova, oc—outer coenenchyme, ph—pharynx, pp—proximal region of polyp, rp—retracted polyp, s—solenial tubes, st—stalk.

Variability and coloration

The high degree of variability found in many sedentary organisms, such as octocorals, due to isolation of populations, lack of mobility and ephemeral larval stages, has been noted by several authors (Thomson 1921: 166; Hickson 1907a: 25–36).

Alcyonium variable is remarkable in that the colonies often resemble young mushrooms of the genus *Amanita* in shape, appearance, and even colour in some instances. The most extraordinary aspect of the nature of this species is its extreme intraspecific variability, particularly in regard to external coloration. Stalk development is also variable. Sclerite form and distribution are the most consistent and least variable characteristics between geographically isolated populations or individual colonies, and serve to unify the various widespread populations into one highly variable species. These southern African populations exemplify a wide range of variability in regard to coloration (Table 1).

Most southern African material is known to have a well-developed barren stalk, the length of which may exceed twice the diameter of the capitulum. In some colonies from the southern Transkei and East London regions the stalk is reduced in size: the spherical capitulum arises from a very short stalk with a spreading base (Fig. 12). The development of the stalk is considered a variable feature in other species as well. In the original description of *Metalcyonium capitatum*, Pfeffer (1889: 50) states that the colony has the appearance of a young mushroom, being short-stemmed with a bulbous head, or the stalk is entirely missing and the entire colony is of a head-like shape.

It appears that both continuous and polymorphic colour variation are exhibited in populations of *Alcyonium variable*. The recently discovered localized populations of *A. variable* from the western side of the Cape Peninsula are remarkable in that they exhibit distinctive polymorphism. The individual colonies of the populations are morphologically very consistent but are sharply differentiated and discontinuous in colour due to the striking permanent coloration of calcium carbonate sclerites that are embedded in the outer coenenchyme.

The populations are obviously dimorphic as two clearly delineated colour morphs can be recognized (Fig. 1):

Yellow morph. The colonies are a golden-yellow to yellowish-orange. In some colonies the stalk may have a slightly rose tint due to some sclerites of the outer coenenchyme being red. The armature of the anthocodial crowns and tentacles is usually composed of deep orange-yellow sclerites.

Red morph. The colonies are red to mauve to vivid reddish-purple. The armature of the anthocodiae within a given colony may be composed of either all red or all yellow sclerites. The pharyngeal sclerites may also be yellowish or light red; these combined give the anthocodiae as a whole a pinkish-white or yellowish appearance.

TABLE 1
Colour variability in *Alcyonium variabile*.

| Locality | Calyx | Capitulum | Stalk |
|---|-------------------|-----------------------------------|------------------------------|
| W side of Cape Peninsula, Cape Agulhas region | mauve to red | mauve to red | mauve-red to pinkish |
| NW side of Cape Peninsula | orange-yellow | golden-yellow to orange-yellow | orange to pinkish- orange |
| SW of Cape Point | white | white | white |
| SW of Cape Point | rose | white | brownish-white |
| S of Cape Hangklip, Knysna | yellow | yellow | white to yellowish- white |
| East London | brownish-white | brownish-white | brownish-white |
| East London | mauve-pink | mauve-pink | brownish-white |
| East London | pinkish-tan | pinkish-tan | pinkish-tan |
| East London | orange | red | yellowish |
| East London | yellow | white | tan |
| East London | yellow | yellow | pink |
| East London | white to yellow | white to yellow | yellowish |
| East London | red | yellow | pinkish-white to reddish |
| East London | greyish-white | greyish-white | greyish-white |
| East London | red | pink | pink |
| East London | yellow | orange | pinkish-white |
| East London | pale pink | pale pink | pinkish-white |
| East London | red | yellow | white |
| East London | yellow | red | reddish |
| Cape Morgan | orange-red | yellow | yellow to white |
| Cape Morgan | salmon-pink | salmon-pink | salmon-pink |
| Cape Morgan | bright yellow | light orange | pinkish-white |
| Cape Morgan | yellow | salmon-orange | salmon-orange |
| Cape Morgan | red | yellow | yellow |
| Sandy Point | yellow | yellowish-white | pinkish-white |
| Sandy Point | yellow | orange to red | yellowish-white to rose |
| Sandy Point | red to red-violet | white to yellowish | white to yellowish |
| Sandy Point | red | white to reddish | white to pink |
| Port Grosvenor | red | white to reddish | white to pink |
| Durban, Cape Morgan, East London | yellow | yellow | yellow |
| Tugela River, Cape Morgan | red | white | white |
| Tugela River, Durban, Port Shepstone, Cape Morgan | yellow | orange to red | white to pink |

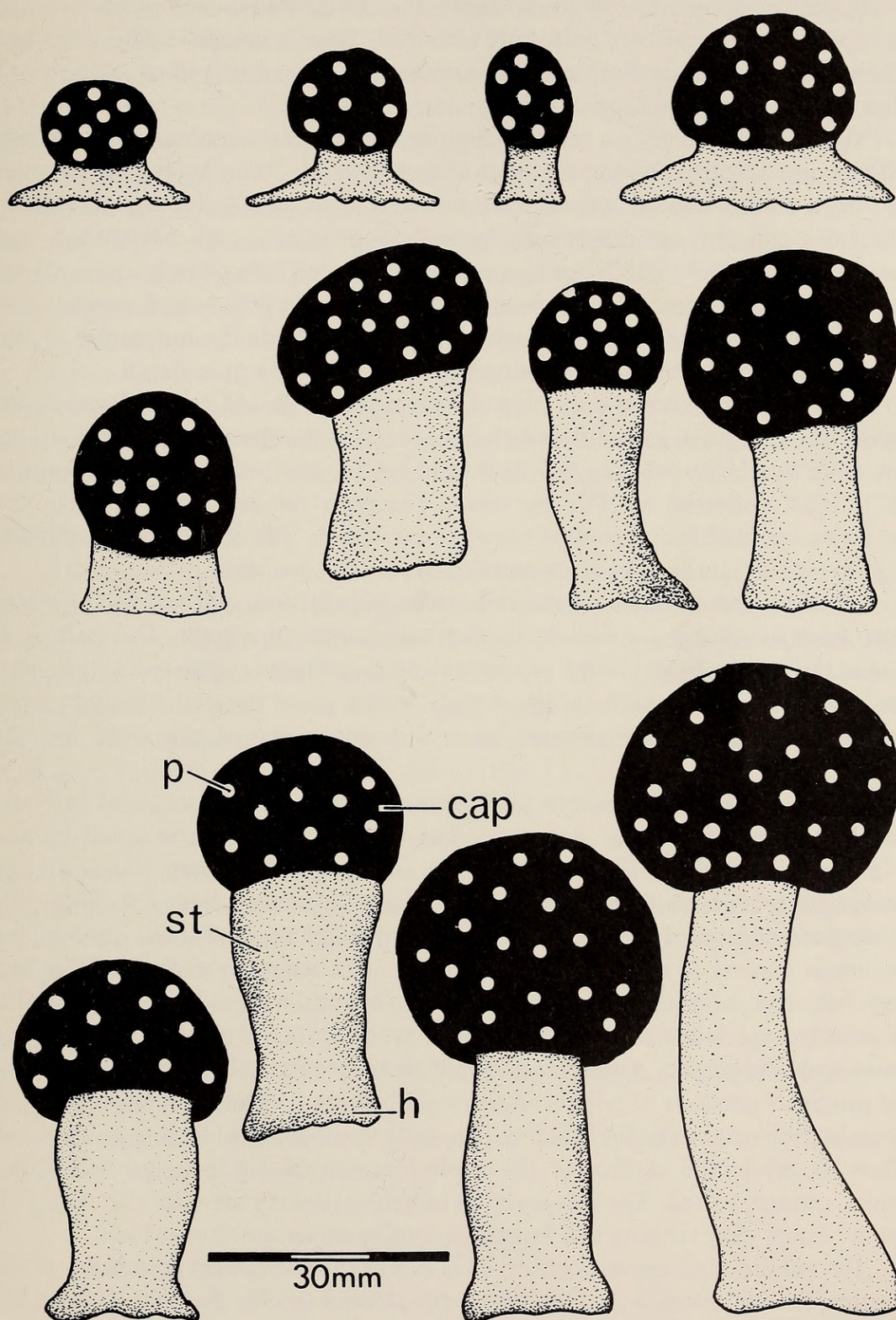


Fig. 12. Variability of colony shape and stalk development in *Alcyonium variable*. Polyp-bearing portion (capitulum) is differentiated from stalk or base.
cap—capitulum, h—holdfast, p—polyp, st—stalk.

In both morphs, within a given colony, the calyces and outer coenenchyme of the capitulum and stalk are uniformly coloured. Thus, a colony is entirely red or yellow. The sclerites in both morphs exhibit tints of red or yellow: sclerites of other colours have not been observed.

The individual colonies of the yellow or red morphs can occur sympatrically and may grow as little as 10 mm apart at depths of 13–30 m. Individual colonies have been observed to be as much as 55 mm in total length. At Hottentots Huisie, these two morphs are apparently equally represented. At Llandudno and Kommetjie (34°09'S 18°18'E), however, the red morph is frequently encountered while the yellow morph has not been observed. The yellow morph seems to be confined to the Atlantic side of the Cape Peninsula, while the red morph is also common off the Cape Agulhas region between 24 and 54 m in depth.

A white form, known only from deeper water (150–163 m) off Cape Point, has not been found in association with either of the other two morphs. It is known only from five large colonies (52–71 mm in total length) described by Thomson (1921: 165), collected in 1903 by trawl. Thomson relegated this form to the complex he named *Metalcyonium variabile* var. *molle*. The colonies are a uniform bright white as sclerites from all parts of the colony are white.

All observed colonies of the dimorphic populations, as well as the white form, have in common a well-developed and conspicuous stalk. The stalk is at least as long as the height of the capitulum and is commonly up to twice its height. One colony of the white form has a stalk length three times the height of the capitulum. This is the maximum known development of the stalk for the species.

The numerous colonies that have been collected from Cape Point to Natal exhibit a more continuous variation. The many populations sampled by the SS *Pieter Faure* surveys from 1898 to 1906 and the R.V. *Meiring Naude* dredge surveys from 1981 to 1985 exhibit the following differences from the dimorphic populations and the white form of the western Cape Peninsula: (a) none of the specimens exceed 40 mm in total length; (b) stalk length is variable, from less than half the height of the capitulum to approximately twice the height; (c) colonies are known only from deeper water (47–480 m); (d) colonies are rarely monochromatic, usually bicoloured or tricoloured. The stalk, capitulum, and proximal portions of polyps often exhibit different colours. A wide range of colour combinations exists (Table 1). The stalk varies from whitish to pale rose to yellowish, while the surface of the capitulum can be white or greyish-white, yellow, orange, or red. The calyces of an individual colony are either all red or all yellow. Some very striking and beautiful combinations are thus evident.

The colour of all colonies observed is due to the permanent coloration of the sclerites, for the colonies contain little if any alcohol-soluble pigment. Colour has been observed to be well preserved in material maintained in ethanol for over eighty years. Colour patterns are extremely varied and often very striking.

The colour of the individual sclerites ranges from rich orange-yellow, light lemon-yellow, deep red to maroon or mauve, to white or almost translucent.

Some spindles are observed to be reddish towards one end and transparent towards the opposite end.

Capitulum or stalk sclerites of the outer coenenchyme are often quite vividly coloured, while those of the interior coenenchyme are only slightly tinted with red or yellow, or are often colourless and transparent.

The high degree of variability in the collected material led Thomson (1921) to propose the name *Metalcyonium variable* for this species and to name two varieties: (1) *M. variable* var. *molle* for colonies with stalk surface of a 'leathery consistency' and sclerites primarily of capstans; and (2) *M. variable* var. *durum* with stalk surface of a 'much harder and somewhat stony consistency' and sclerites of capstans, spindles, rods, and clubs. Thomson also recognized a range of intermediate cases that were not readily identifiable with either subspecies. Because of the intermediate nature exemplified by some colonies and since the populations exhibit continuous and extreme variability, the recognition of formal taxonomic variations or subspecies must be disregarded.

Distribution and habitat

Alcyonium variable is known only from the following South African localities: off East London (Hickson 1900, as *A. antarcticum*); many stations from Cape Point to central Natal (Thomson 1910, as *Metalcyonium patagonicum*; 1921, 1924, as *M. variable*); Cape Infanta (Molander 1929a, 1929b, as *A. paessleri*); Cape Peninsula region (Tixier-Durivault 1954, as *A. fungiforme* and *A. luteum*); western side of Cape of Good Hope Peninsula, southern Natal and Transkei coast to eastern Cape Province (present study) (Fig. 13).

Alcyonium variable is a sublittoral benthic organism of shallow to mid-water and is known from a depth range of 13–468 m. It is recorded by Hickson (1900) and Thomson (1910, 1921) at depths of 47–468 m. Dimorphic populations of red and yellow morphs have recently been observed from the western Cape Peninsula between depths of 13 and 20 m. Thomson (1921: 165) records an entirely white morph from 146 to 159 m.

Colonies are usually found attached to hard substrata such as shells and rocks or relatively soft substrata such as encrusting sponges. They are commonly observed growing on vertical rock walls amongst sponges, gorgonians, bryozoans, tunicates, and other soft corals.

Colonies have been observed with polyps fully expanded or in varying states of retraction during daylight hours.

DISCUSSION

HISTORICAL SURVEY

Pfeffer (1889: 49) established the genus *Metalcyonium* to include two new species of supposedly clavate and capitate, monomorphic alcyoniids from South Georgia Island in the southern Atlantic: *M. clavatum* and *M. capitatum*. Unfortunately, as Utinomi (1964: 7) pointed out, Pfeffer did not designate either

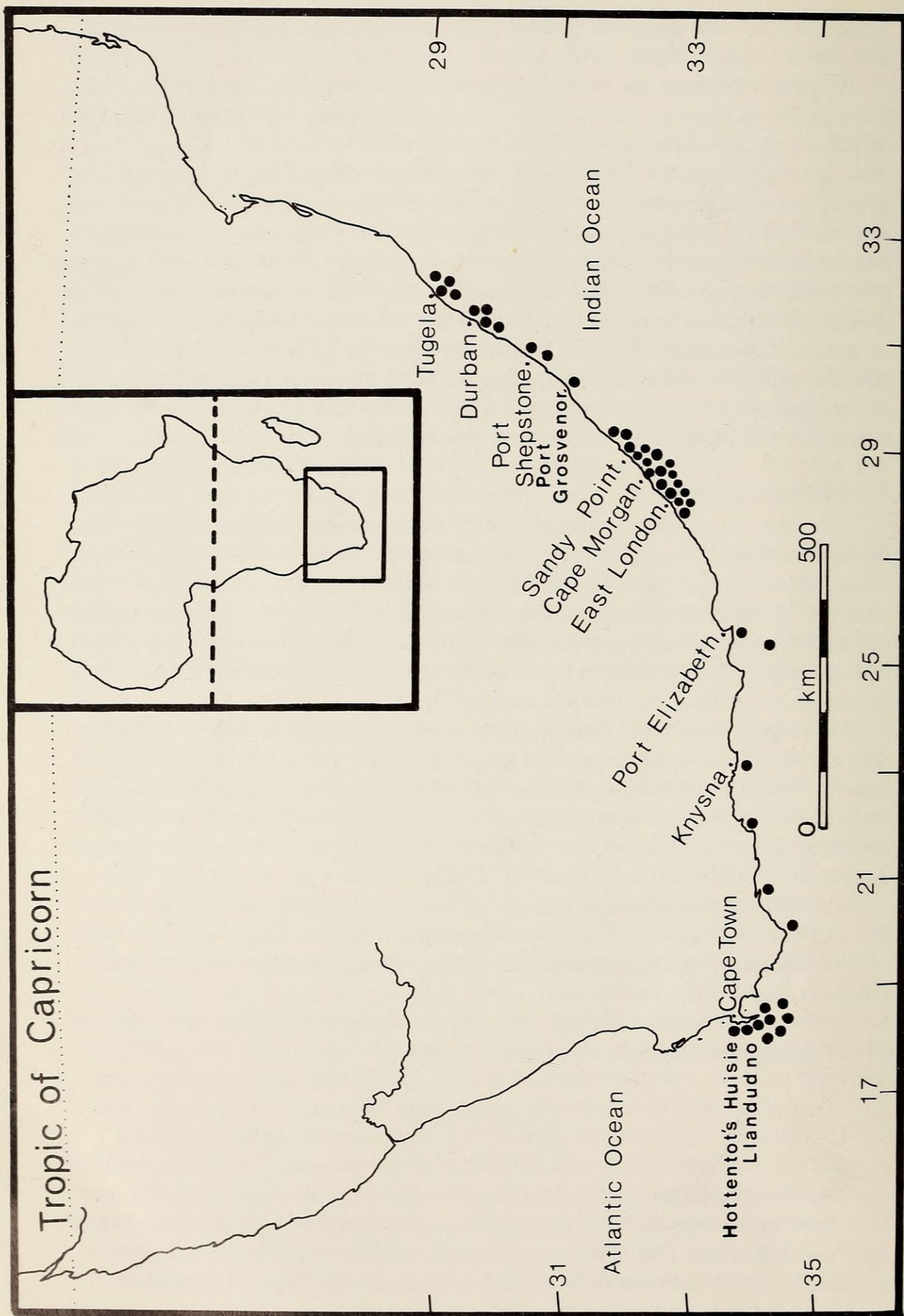


Fig. 13. Map of southern Africa showing the known distribution of *Alcyonium variabile*.

of these divergent forms as the type-species of the genus, and gave a vague diagnosis.

May (1899: 6, 8) described two new species from Patagonia: *Alcyonium paessleri* for a globular form and *Metalcyonium patagonicum* for a clavate species. He also amended Pfeffer's original definition of the genus. Tixier-Durivault (1970: 148) altered the name of *M. patagonicum* to *Bellonella patagonica* for northern Patagonian material.

According to Thomson (1910: 564), Hickson (1900: 73) apparently misidentified two specimens of capitate forms from the East London region of South Africa as *Alcyonium antarcticum* Wright & Studer, 1889. Kükenthal (1906: 47) considered Hickson's material to possibly be young colonies of *M. patagonicum*. Burchardt (1903: 673) described a fungiform-capitate species from the Malay Archipelago, *M. molle*. Thomson (1921: 162) later identified material from Natal as conspecific with this species.

Kükenthal (1906: 42) revised the genus *Alcyonium* Linnaeus, 1758, and relegated *Metalcyonium* to subgeneric status. However, this was not widely accepted by workers after that time. Kükenthal considered *Alcyonium* to be composed of three subgenera of monomorphic soft corals, differentiated by colonial growth habit: *Alcyonium* for all forms with a massive upright stalk and more or less lobate capitulum; *Metalcyonium* for unbranched, cylindrical or conical forms; and *Erythropodium* for membranous, broadly spreading forms. This redefinition ignored capitate forms and left their position doubtful.

Broch (1912: 21) changed the subgeneric name *Alcyonium* to *Eualcyonium*, and Kükenthal (1916: 174) proposed the name *Parerythropodium* for membranous forms since *Erythropodium* Kolliker, 1865, was previously applied to an unrelated but presumably superficially similar genus of the scleraxonian family Anthothelidae (Briareidae of Kükenthal 1916: 172). Kükenthal (1906: 48) also described *Metalcyonium novarae*, a cylindrical species from the Cape of Good Hope (False Bay), and Thomson (1921: 167, 172) described two other cylindrical forms: *M. lanceatum* and *Sinularia unilobata*, both from the eastern Cape Province and Natal.

Thomson (1910, 1921) added to an already chaotic situation by describing the common and variable South African species under two different names: first (following Kükenthal 1906: 47) *M. patagonicum* (1910: 562) and then later as two varieties of a new species, *M. variable* var. *molle* (1921: 162) and *M. variable* var. *durum* (1921: 165). Molander (1929a: 50; 1929b: 4) considered Thomson's South African material to be identical with the Patagonian and Antarctic species, *Alcyonium paessleri* May, 1899. Verseveldt (1967: 10) disagreed with Molander's contention and considered *A. paessleri* and *M. variable* as separate species.

Hickson (1907b: 3) identified material from Franklin Island in Antarctica as *A. paessleri*. However, Lüttschwager (1922: 534) considered Hickson's determination as a misidentification and gave Hickson's species (plus apparently similar material from the Philippines) the new name *Alcyonium equisetiforme*. Lüttschwager (1922: 522) and Roxas (1933: 356) provided keys to the 19 worldwide

species of *Alcyonium* (subgenus *Eualcyonium*) known at that time, and defined *A. paessleri* as a globular species without a distinctive stalk.

Yamada (1950: 114, 115) described two new species of globular, capitate soft corals from northern Japan, *A. pacificum* and *A. muricatum*, providing only very brief descriptions and not designating type material. Uchida (1969: 397) gave a more detailed description of *A. pacificum*.

Tixier-Durivault (1954: 385, 388) added two new species of capitate monomorphic alcyoniids, described as *Alcyonium fungiforme* and *A. luteum*, both from the region of the Cape of Good Hope.

Utinomi (1958: 111; 1964: 7) attempted to arrange some sense of order out of a chaotic situation by suggesting that in order to validate the status of the genus *Metalcyonium*, it should be restricted to markedly capitate forms and that problematic cylindrical forms such as *M. clavatum* should be assigned to other genera. This position is now held to be incorrect (Verseveldt pers. comm.; present study).

SYSTEMATIC STATUS

The most familiar members of the genus *Alcyonium* Linnaeus, 1758, are more or less lobate; the polyp-bearing portions of the colonies are divided into varying degrees of digitate or lobate processes that arise from a common stalk or base (Bayer 1981: 916).

However, several other additional species, which are in no way lobate and show remarkably different growth forms, can be allocated to the genus. For example, several species that have previously been assigned to the genus *Parerythropodium* Kükenthal, 1906, do not have a defined stalk but consist usually of a thin and pliable form that assumes the shape of the substratum that it covers, or may be globular to irregular in shape. Groot & Weinberg (1982) have recently shown that these membranous and encrusting species can be accommodated in *Alcyonium* since the type-species, *P. coralloides*, is consistent with characters of the genus. A number of other species are strongly fungiform in shape with a single spherical, hemispherical, or flattened disc-shaped capitulum arising from an unbranched stalk. Several of these have been placed in the genus *Metalcyonium* by various authors following the original description of *Metalcyonium capitatum* Pfeffer, 1889 (e.g. *Metalcyonium variable* Thomson, 1921; *M. molle* Burchardt, 1903).

Species, or individual colonies within a species, are known that grade between several of these disparate morphological growth forms and thus serve to amalgamate the various species within the single genus. It appears then, that the genus *Alcyonium* is a large variable complex of broad morphological scope, and that attempts to subdivide the genus on the basis of colony shape must be considered unjustified or tenuous at best.

Utinomi (1964) maintained that in order to validate the genus *Metalcyonium*, *M. capitatum* should be designated as the type-species of the genus and that *Metalcyonium* should be reserved for strongly capitate, mushroom-shaped forms

with globular or spherical capitulums. This differentiation of genera based solely on colony shape or growth form is in this case difficult to vindicate, since 'subcapitate' forms are also known that tend to be intermediate between digitiform and capitate forms. Colonies of *Metalcyonium patagonicum* May, 1899, for example, are slightly clavate, having a distally swollen or somewhat club-shaped form that seems to be intermediate between cylindrical and capitate. Individual colonies of *Alcyonium variable* may have thickened stalks that approach the width of the capitulum, thus making the colony appear more clavate than capitate. *Alcyonium fauri* J. S. Thomson, 1910, and *A. paessleri* May, 1899, may form globular heads upon a membranous or spreading base. I therefore see no justification for generic separation of capitate forms and feel that such forms can be accommodated within the genus *Alcyonium*. *Alcyonium variable* (Thomson, 1921) should therefore be considered as a new combination of *Metalcyonium variable* Thomson, 1921. I therefore consider the following worldwide species that possess capitate and unbranched growth forms but lack permanent calyces, to be members of the genus *Alcyonium*:

Alcyonium capitatum (Pfeffer, 1889) (South Georgia Island)

(= *Metalcyonium capitatum* Pfeffer, 1889)

Alcyonium laeve Tixier-Durivault, 1955 (Gabon)

Alcyonium molle (Burchardt, 1903) (Amboina)

(= *Metalcyonium molle* Burchardt, 1903)

Alcyonium muricatum Yamada, 1950 (Japan)

Alcyonium pacificum Yamada, 1950 (Japan)

Alcyonium planiceps Williams, 1986 (South Africa)

Alcyonium variable (Thomson, 1921) (South Africa)

(= *Metalcyonium variable* Thomson, 1921)

Alcyonium verseveldti (Benayahu, 1982) (Red Sea)

(= *Metalcyonium verseveldti* Benayahu, 1982)

Alcyonium violaceum Tixier-Durivault, 1955 (West Africa)

However, the status of unbranched, truly digitiform to cylindrical forms with monomorphic polyps is not completely resolved as yet. These include such species as *Metalcyonium novarae* Kükenthal, 1906, *M. lanceatum* Thomson, 1921, *M. unilobatum* (Thomson, 1921) (Fig. 2B), the many species assigned to the genus *Bellonella* after the description of (but not including) *B. granulata* Gray, 1862, and the genera *Nidalia* Gray, 1834, and *Cactogorgia* Simpson, 1907. Pfeffer (1889: 49) originally described *Metalcyonium clavatum* as a clavate species. It is actually not clavate, but rather digitiform or cylindrical in shape (Molander 1929a, pl. 4 (fig. 9); Verseveldt pers. comm.).

According to Verseveldt (pers. comm.) most of the species previously assigned to the genera *Bellonella*, *Cactogorgia*, and *Metalcyonium* can probably be accommodated in *Nidalia* by priority—a genus characterized by digitiform or capitate colony shape and the possession of permanent calyces into which the anthocodia are retractile. Most other digitiform or capitate species that do not

possess permanent calyces can probably be assigned to the morphologically diverse genus *Alcyonium*. Both Verseveldt (Zwolle, The Netherlands) and Bayer (Smithsonian Institution) are currently studying this matter in detail.

SYNONYMY

Alcyonium fungiforme Tixier-Durivault, 1954, was described from a single colony collected off Cape Point, South Africa (34°33'S 18°20'E). The colony, as described by Tixier-Durivault, has a brownish-white stalk and a white capitulum spotted with rose-red calyces. The obviously fungiform and capitate colony shape is distinctive. The capstans and thorny spindles figured in the original description of *A. fungiforme* and considered by Tixier-Durivault (1954) to be so disparate from those of material of *A. variable* examined by Hickson (1900) and Thomson (1910, 1921), can undoubtedly be viewed within the context of intraspecific variation. The spindles illustrated by Tixier-Durivault (1954, fig. 3) from the capitulum and polyps are very similar to those that have been isolated and observed from several recently acquired colonies and from Thomson's SS *Pieter Faure* survey material. The stalk sclerites of *A. fungiforme* are a bit more pronounced (Fig. 14B). However, this minor discrepancy does not justify the status of a separate species, since the characteristic sclerite pattern and form are consistent with *A. variable*. The description of *A. fungiforme* is thus considered to fall well within the realm of *A. variable*; *A. fungiforme* should therefore be considered a junior synonym of *A. variable*.

Tixier-Durivault (1954: 388) described another new species of capitate alcyoniid, *Alcyonium luteum*, from the Cape of Good Hope region (34°39'S 14°42'E). An examination of type material has shown that this species should also be considered conspecific with *A. variable*. The holotype of *A. luteum* is very similar to material that Thomson (1921: 164) considered characteristic of *Metalcyonium variable* var. *molle* (SAM-H883) from Knysna Heads (34°10'S 23°15'E). These colonies all have lemon-yellow capitulums with yellowish-white to yellow stalks. The form and distribution of the sclerites are typical of *A. variable*—long spindles forming a transverse band around the base of the crown of the anthocodia with double rows of spindles arrayed *en chevron* along the axis of each tentacle; short capstans in the calyx-like base of the polyp forming eight ridges; capstans and clubbed forms in the outer coenenchyme with thick spindles dominating in the inner coenenchyme. The illustration of the complete colony of *A. luteum* provided by Tixier-Durivault (1954, fig. 4A) does not show the obviously capitate, spherical shape of the capitulum. Examination of the holotype of *A. luteum* (SAM-H3245), has shown it to be markedly capitate in nature (Fig. 14A). The morphological features of these colonies also fall well within the realm of intraspecific variation of *A. variable*. As is the case with *A. fungiforme*, I see no justification for considering these species as separate from the variable *A. variable* complex. If *A. fungiforme* and *A. luteum* are considered separate species because of their slight variance from other *A. variable* material, then perhaps a dozen or more other species could also be separated. If one

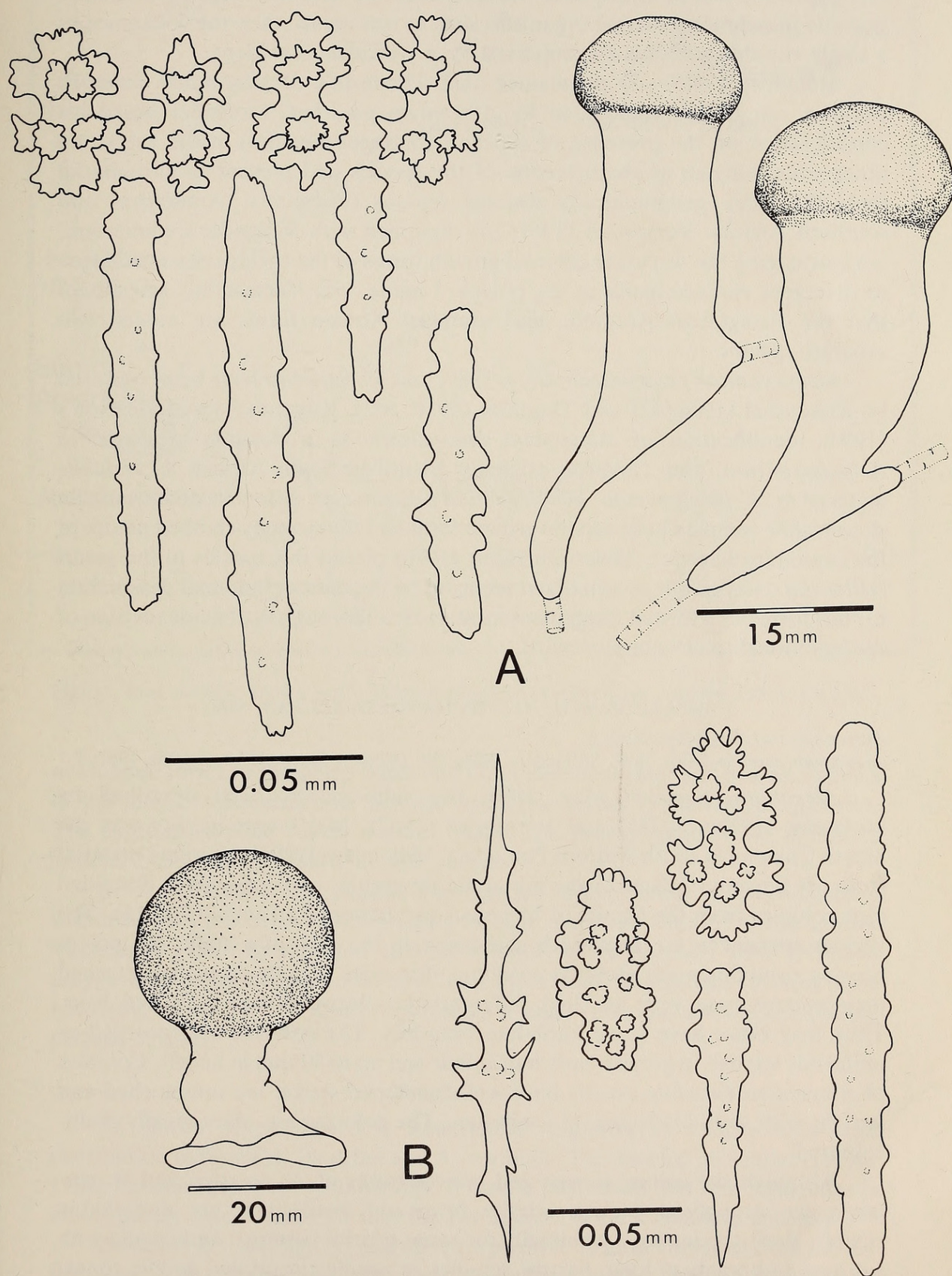


Fig. 14. Comparative morphology of material synonymous with *Alcyonium variable*. A. Coenenchyme sclerites and two entire colonies of *A. luteum* Tixier-Durivault, 1954 (from type material). B. Entire colony and sclerites of *A. fungiforme* Tixier-Durivault, 1954 (adapted from Tixier-Durivault 1954). Stippling represents polyp-bearing capitulum; polyps not shown.

recognizes the fact of intraspecific variation and the extreme range of variability possible in sedentary marine organisms such as soft corals, then the coherence of a single variable complex encompassed by *A. variabile* is evident.

Molander (1929b: 5) maintained that Thomson's *Metalcyonium variabile* complex can be accommodated by *Alcyonium paessleri*. Molander based his consideration on the presence of capstans ('Doppelspindeln') in the calyx and outer coenenchyme as characteristic of the species and present in all material from the three geographically disjunct regions (Patagonia, Antarctica, and southern Africa). Verseveldt (1967: 10) disagreed with Molander's contention, acknowledging the disparate colonial growth forms of the two species in addition to divergent characteristics of the polyps. I agree with Verseveldt's assessment that the Patagonian-Antarctic and southern African forms are indeed two separate species.

Metalcyonium patagonicum May, 1899, and *M. variabile* have been confused by Kükenthal (1906: 47) and Thomson (1910: 562). Kükenthal listed Hickson's (1900) identification of *Alcyonium antarcticum* as a possible synonym of *A. patagonicum*, and Thomson originally identified South African *A. variabile* material as *M. patagonicum*. *Metalcyonium patagonicum* differs from the variable *A. variabile* complex in its clavate growth form and the strongly clubbed nature of the capitulum sclerites. Tixier-Durivault (1970) placed this species in the genus *Bellonella*. *Alcyonium patagonicum* seems to be the correct binomial designation for this form but a formal assignment must await a thorough systematic revision of the cylindrical to clavate alcyoniids.

COMPARISON WITH *ALCYONIUM PAESSLERI* MAY, 1899

Alcyonium Paessleri May, 1899: 6.

Alcyonium paessleri May, 1899. Molander, 1929a: 50; 1929b: 4 (*partim*). Verseveldt, 1967: 7.

Alcyonium paessleri May, 1899, has subsequently been described by Molander (1929a, 1929b) and Verseveldt (1967). May's type-locality was the Smyth Channel in south-western Patagonia. Molander (1929a) described material from off Seymour Island in the Antarctic Peninsula, and Verseveldt described four colonies from the Straits of Magellan and eastern Patagonia (Fig. 15). The various specimens are apparently consistent in the lack of a stalk: the polyp-bearing capitulums are globular swellings that arise directly from the attached membranous base with no clear differentiation between capitulum and base. They may often have short knob-like branches. The colonies are recorded as uniformly whitish to greyish-brown in colour and up to 50 mm in height. Colonies of *Alcyonium variabile* usually have well-developed stalks, are unbranched and upright with well-differentiated capitulum. The colonies are often vividly multi-coloured.

Although the colony shapes and growth forms of *A. paessleri* and *A. variabile* are strongly divergent, sclerite form and distribution are remarkably similar. Both species have essentially the same sclerite patterns: anthocodia with a crown and points of long, narrow spindles or needles; capstans, double cones,

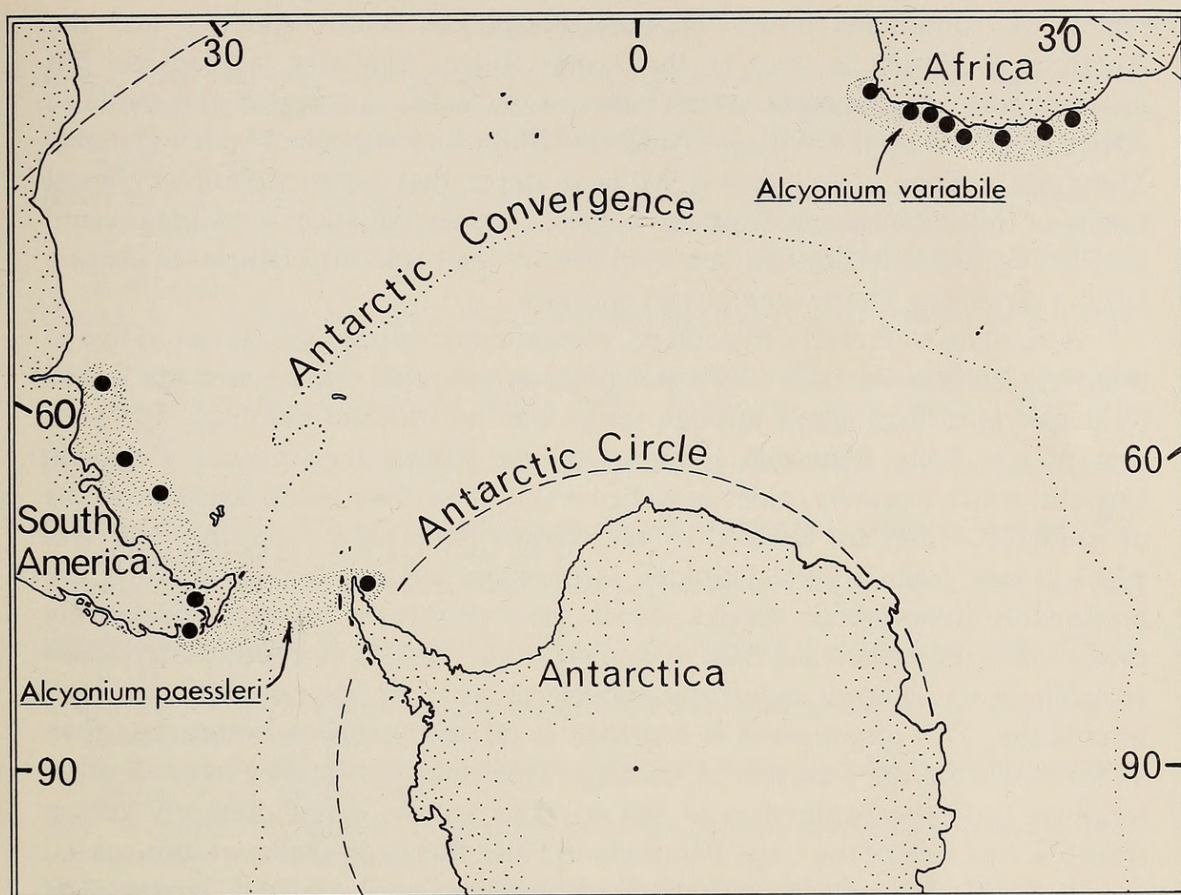


Fig. 15. Map showing known world-wide distributions of *Alcyonium paessleri* and *A. variable*.

or clubbed forms in the polyp bases and outer coenenchyme; and thorny spindles in the interior coenenchyme. Sclerite form also shows considerable similarity. The capstans, double cones, needles, clubs, and thorny spindles are similar in structure and ornamentation in both species.

In *A. variable*, the capstan-impregnated polyp bases may completely withdraw into the capitulum, resulting in eight lines radiating from the centre. Verseveldt (1967: 8) reported that in colonies of *A. paessleri* with retracted polyps, well-defined rounded anthosteles project from the capitular surface, these not being retractile. The aperture presents a small round hole with no radiating pattern of lines.

ZOOGEOGRAPHY

As shown above, there is remarkable similarity of sclerite form and distribution between *A. paessleri* and *A. variable*. This fact led Molander (1929a, 1929b) to consider them synonymous. It can be postulated that this occurrence is either purely coincidental, or that the two species share a common ancestry.

Powell (1951: 64, fig. A) postulated a possible benthic bridge system for the distribution of certain prosobranch mollusc genera in the Atlantic Subantarctic

region. A continuous bridge between Patagonian South America and the Antarctic Peninsula is seen as the Scotia Ridge. Similarly, a plausible but discontinuous zoogeographical link between the Scotia Arc region and southern Africa is shown by the African–Antarctic Ridge and Agulhas Plateau systems. These are regions of less than 4 000 m in depth that separate various abyssal basins of the Atlantic and Southern oceans. This hypothetical model takes into account periodic declines in sea-level (of at least 140 m) (Dingle & Rogers 1972: 155) during Pleistocene glacial episodes.

According to Powell's hypothesis, stenothermic species are shown to live in relatively shallow water in cold-water polar or subpolar regions, and are linked by deep-water distribution through temperate and tropical latitudes. The west side of the Cape Peninsula is swept by the Antarctic-influenced Benguela Current, which contains colder upwelled water. The eastern and southern coasts of southern Africa are affected by the warmer water of the Agulhas Current, which comes from tropical latitudes. *Alcyonium variabile* and *A. paessleri* are presumably stenothermic species, which seem only to be tolerant of relatively cold water. *Alcyonium paessleri* is known from 150–642 m depths; *Alcyonium variabile* is also known only from sublittoral areas; it has not been recorded intertidally. This alcyonacean is recorded in relatively shallow water (less than 40 m) only from the west side of the Cape Peninsula. It is known from all other localities in deeper water (up to 468 m). The species is not presently known from the east side of the Cape Peninsula in False Bay or in shallow-water coastal regions to the east, which are influenced by the warmer Agulhas Current. The present incomplete state of knowledge is a consequence of the limited extent of shallow-water collecting that has taken place by means of SCUBA and the nature of collecting techniques in the past, i.e. deeper-water trawling and dredging.

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