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THE MACROPODIDAE (MARSUPIALIA) FROM THE ALLINGHAM FORMATION, NORTHERN QUEENSLAND. RESULTS OF THE RAY E. LEMLEY EXPEDITIONS, PART 2.

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ABSTRACT

The fossil Macropodidae from the Bluff Downs fauna of the Allingham Formation, northern Queensland, of lower Pliocene age, are described. Eight taxa have been recognized, although inconclusive evidence exists to suggest that additional taxa may be defined when broader collections become available. Potoroines are currently unknown and sthenurines are very poorly represented. Macropodines predominate. Four species are new, *Troposodon bluffensis, Protemnodon snewini, Macropus (Prionotemnus) narada* and *M. (Osphranter) pavana.*

Two species, *M. (?P.) dryas* and *T. minor* are known also from the Chinchilla Sand, although the latter species has a wide temporal range being well represented in Pleistocene deposits. The occurrence none the less supports the previously ascribed late Pliocene age for the Chinchilla Sand.

A preliminary statement on the fauna from the Allingham Formation and the definition of the Formation are provided in Archer and Wade (1976). The unit is regarded as being of lower Pliocene age because it is overlain in part by the Allensleigh 'flow' of the Nulla Basalt, dated radiometrically at between 4 and 4·5 M.y. This then represents a minimal age for the Formation, although from what is already known of the fauna, actual time of deposition was probably not much earlier. Continuing investigation of the deposits has been made possible through the support of Dr Ray E. Lemley as part of a joint Queensland Museum and South Dakota School of Mines project. Larger collections of macropodids have resulted, enabling the present study to be undertaken. Other groups will form the basis for additional studies.

The deposits are considered to be of great importance and they represent only the second Pliocene, mammal-bearing site in Queensland. The reasonably precise minimal age and the known diversity of the fauna suggest that results will assume some significance in correlation of Australian lacustrine and terrestrial deposits.

All measurements throughout are in millimetres.

STHENURINAE

Sthenurus sp.
(Plate 23, fig. 1)

MATERIAL EXAMINED: F9104, partial, isolated right M^3 (breadth 12·6).

DISCUSSION: Only one fragmentary tooth of *Stenurus* Owen has been recovered from the Allingham Formation. Its morphology suggests that it is an M^3. Insufficient features are preserved for more than generic determination to be attempted. However, of species currently known, the tooth is believed to be from a form close to *Sthenurus antiquus*, described by Bartholomai (1963) from the late Pliocene Chinchilla Sand. Ornamentation and height of the lophs is similar, although in the Allingham specimen, the strength of the ridge which ascends into the median valley from the metacone is considerably weaker than in the maxilla of *S. antiquus* figured by Bartholomai (1963, fig. 10). As in *S. antiquus*, the base of the crown is swollen posteriorly and the low midlink is positioned above the centre of the median valley. However, the strong ridge curving posterolingually from the hypocone overlaps, rather than meets, the weaker ridge from the metacone.

Although upper teeth are unknown in *S. notabilis* Bartholomai, also from the late Pliocene Chinchilla Sand (Bartholomai 1963), size and crown height would preclude this species from close relationships with the Allingham specimen.

Among Pleistocene species of *Sthenurus* reviewed by Bartholomai (1963) and Tedford (1966), or described by Merrilees (1965, 1967), the Allingham specimen appears to be within the size range of *S. oreas* De Vis, but has less pronounced accessory ridging. *S. orientalis* Tedford of comparable size, is known only from its lower dentition, while *S. occidentalis* Glauert, *S. brownei* Merrilees and *S. gilli* Merrilees are all smaller species.

MACROPODINAE

Troposodon minor (Owen, 1877)

(Plate 23, figs. 2–4)

Sthenurus minor Owen, 1877, pp. 352–61, pl. 37, figs. 1–3, pl. 38, figs. 1–4.

Troposodon minor (Owen); Bartholomai, 1967, pp. 23–32, figs. 1–3 (synonymy).

MATERIAL EXAMINED: F9046, isolated left P_3; F9047, isolated partial left M_2; F9048, isolated partial left M_3; F9049, isolated left DP^3; F9050, isolated right M_1; F9051, isolated left DP^3; F9052, isolated partial right M^1; F9053, isolated partial right M_1.

DISCUSSION: The genus *Troposodon* Bartholomai is currently represented in Australian Upper Cainozoic deposits by two species, *T. minor* (Owen) and *T. kenti* Campbell. Of these, *T. minor* is by far the most commonly recorded species, being present in sufficient numbers in collections from the Darling Downs deposits to enable Bartholomai (1967) to assess the populations statistically.

Within the Darling Downs deposits, Bartholomai (1967) has shown *T. minor* to be present in both the Pleistocene fluviatile deposits and the Chinchilla Sand of late Pliocene age. Samples were compared using Student's t Test and no significant size or morphological features were found to justify separation. Turnbull and Lundelius (1970) have also suggested that an isolated, partial lower molar, MNV–P26422, from the post-early Pliocene fossil soil deposits at Grange Burn, Hamilton, Victoria, may represent *T. minor*, a possibility which cannot be discounted on the basis of the description provided.

T. kenti from the ?early Pleistocene Katipiri Sands, has been distinguished from *T. minor* by Campbell (1973) on the basis of its larger size, supported by the less ornamented nature of the apical shelves of the molar teeth and minor morphological differences in the premolars. Representation of material larger than *T. minor* in the Chinchilla Sand material, but insufficient for description, was noted by Bartholomai (1967). No additional material has as yet been recovered to support or refute the suggestions by Campbell (1973) that these specimens may represent *T. kenti* in the Chinchilla Sand, or that they may reflect extreme variation in *T. minor*.

TABLE 1: MEASUREMENTS FOR *Troposodon minor* (OWEN, 1877)

Specimen	P_3	M_1	M_2	M_3	DP^3
F9046	12·8×5·1	—	—	—	—
F9047	—	—	—×9·3	—	—
F9048	—	—	—	—×10·2	—
F9050	—	11·0×6·9	—	—	—
F9053	—	—×7·3	—	—	—
F9049	—	—	—	—	10·2×8·1
F9051	—	—	—	—	10·7×7·0

Although the sample available from the Allingham Formation is small, comprising only isolated teeth, a reasonable range of dental morphology is represented and some variation within the population is observable. Measurements for this material appear in Table 1.

Slight size differences which are evident between teeth from the Allingham Formation and those from the Chinchilla Sand are attributable to the small sample size in the former and the fact that the Chinchilla Sand sample itself is a relatively small one for statistical purposes. Nevertheless, the Allingham sample falls within limits which one would expect for the Chinchilla Sand sample, based on large sample assessments for macropodines provided in Bartholomai (1971, 1973, 1975). Structurally, the Allingham sample generally presents coarser accessory ridging in anterior molars and in DP^3 than is usual in Darling Downs specimens, but this feature is variably present in some individuals from the Darling Downs, including the juvenile specimen figured by Batholomai (1967, fig. 2).

No differences are therefore present which enable separation of the Allingham material from *T. minor*, although *T. kenti* is clearly excluded by both size and morphological considerations. This is of particular interest because of the age of the Allingham Formation, which indicates a minimal temporal spread for *T. minor* from at least the mid Pliocene to the late Pleistocene, the longest recognisable range for an Australian marsupial species.

Troposodon bluffensis* sp. nov.
(Plate 23, figs. 5, 7-10)

MATERIAL EXAMINED F9054, holotype, isolated right M^4, adult, Allingham Formation of mid Pliocene age, Bluff Downs Station, Allingham Creek.

In addition, F9055, an isolated left M_4, F9056, a partial isolated left M^4; F9057, an isolated right M_4; F9058, an isolated right P_2 and F9059, an isolated left P^3 have been used in the description of the species.

SPECIFIC DIAGNOSIS: A small species of *Troposodon*, much smaller than *T. minor;* P^3 small, with low longitudinal crest; upper molars lacking a forelink or with this present in very incipient form, and lacking a ridge from the paracone to the labial extremity of the anterior cingulum; midlink high with major contribution from near midpoint of metaloph crest. P_2 small, low crowned, markedly L-shaped; lower molars with reduced accessory ridging on apical shelf and with base of crown swollen posteriorly without production of posterior cingulum.

DESCRIPTION: Upper dentition known only from P^3 and M^4.

P^3 elongate, subcrescentic in basal outline, with labial margin concave and lingual convex, broader posteriorly than anteriorly; longitudinal crest low, more elevated posteriorly than anteriorly, moderately concave labially, transected by three, weak sets of vertical labial and lingual ridges, these becoming weaker posteriorly. Apex of paracone about one-fifth distance along crown from anterior limit. Hypocone moderately low, positioned posterolingual to metacone and connected to it by strong descending ridge; weak ridge curves posterolabially to meet extremely weak posterior ridge from metacone near base of crown, without production of posterior fossette; strong anterior ridge from hypocone ascends to form well-defined lingual cingulum to point opposite paracone; cingulum sinuous in lingual view, converging only slightly anteriorly in occlusal view; lingual basin broad, smooth. Anterior ridge from paracone extending well anteriorly; base of crown slightly swollen anterolingually.

M^4 small, subrectangular in basal outline, slightly constricted across median valley; lophs low, moderately bowed anteriorly, with metaloph narrower than protoloph. Anterior cingulum low, moderately broad, anteriorly broad convex, nearly flat in labial moiety, but ascending slightly lingually; forelink absent or present in very incipient form; labial margin of cingulum unconnected to paracone by accessory ridge; midlink high, strong, curving posterolabially from protocone, then curving posteriorly abruptly to unite with strong ridge from near midpoint of crest of metaloph; junction marked by shallow cleft. Weak ridge ascends posterolingually from paracone towards midlink, defining unornamented apical shelf; median valley shallowly U-shaped, transversely flattened, with lingual extremity marked by low ridge; strong ridge curves posterolabially from hypocone towards base of crown; weaker ridge from metacone ascends to disappear below ridge from hypocone with production of posterolabial indentation; accessory ridges from hypocone and metacone ascend across posterior face of metaloph to unite near midline, defining unornamented apical shelf. Base of crown narrowly swollen posteriorly, this separated below by shallow groove.

Lower dentition known only from P_2 and M_4.

P_2 relatively small, subcrescentic in occlusal view, slightly broader posteriorly than anteriorly; longitudinal crest relatively low, markedly L-shaped, being flexed lingually in its posterior extension. Anterior cuspid set posteriorly at about one-half distance along crown from anterior margin, with anterior ridge from cuspid angled anteriorly and marked by low cuspule about one-half distance to crown base; low, anterolabial cingulum developed from this cuspule to unite with labial ridge from anterior cuspid. Longitudinal crest transected by two weak sets of vertical labial and lingual ridges; lingual extension of crest descends slightly to posterolingual cuspid, this having strong posterior ridge and stronger anterior ridge descending from it. Base of crown swollen lingually and labially.

M_4 small, subrectangular in basal outline, moderately strongly constricted across talonid basin; lophids low, moderately strongly convex posteriorly, with protolophid broader than hypolophid. Trigonid basin moderately broad, its length approximately equalling distance between lophids. Forelink high, strong, curving anterolingually from protoconid across trigonid to point on anterior cingulum labiad to midline; anterior cingulum moderately high, broad, rounded anterolabially, more angular anterolingually, descending markedly labially and lingually from forelink; strong accessory ridge curves anterolabially from metaconid towards forelink,

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*Named for Bluff Downs Station, the property on which the Allingham Formation occurs.

TABLE 2: MEASUREMENTS FOR *Troposodon bluffensis* SP. NOV.

Specimen	P^3	M^4	P_2	M_4
F9054, holotype	—	11·7×8·5	—	—
F9056	—	—×9·1	—	—
F9055	—	—	—	12·0×8·2
F9057	—	—	—	12·7×8·2
F9058	10·6×5·1	—	—	—
F9059	—	—	7·0×3·5	—

defining apical shelf; weak accessory ridges present on apical shelf, descending anteriorly from near protolophid crest. Talonid basin narrowly U-shaped, descending slightly labially and lingually from midlink. Midlink strong, moderately high, curving slightly anterolingually from hypoconid to near midpoint of posterior of protolophid; slight ridge curves towards midlink from entoconid without production of apical shelf. Base of crown swollen posteriorly but without production of posterior cingulum.

DISCUSSION: Although at present known from a very small sample comprising only isolated cheek teeth, the material is so distinct both in its size and morphology as to conclusively justify its separation as a distinct species of *Troposodon* Bartholomai within the Allingham Formation.

Compared with the Chinchilla Sand sample of *T. minor* (Owen) of late Pliocene age, the Allingham material falls well below the lower observed limits for size in equivalent teeth and, indeed, is well below the statistical limits for that population. The morphological distinction of molars in *T. bluffensis* lies in the greater simplicity of links and accessory ornamentation and in the more generalized basic structure overall.

The P_2 is more complex anteriorly and anterolabially than in *T. minor*, but it has more subdued ridging associated with the longitudinal crest. Ridges from the posterolingual cuspid, especially the anterior ridge, are stronger and better-defined. The upper permanent premolar is less triangular in basal outline than in *T. minor*.

That two species of *Troposodon* should be represented within the Bluff Downs deposits is not surprising, taking into account the macropodine representation within other fossil and recent faunas and the fact that the Allingham Formation reflects both fluviatile and lacustrine sedimentation (Archer and Wade 1976) with attendant wide sampling of endemic and derived specimens.

It is considered likely that in view of its more generalized nature, *T. bluffensis* stands closer to the ancestral form from which *Troposodon* was derived than do either *T. minor* or *T. kenti*.

In addition to the material here referred to *T. bluffensis*, there exists an isolated right P_3, F9060, figured in Plate 23, fig. 8, which may belong with this species. The tooth is clearly of the *Troposodon* type, having the posterior extension of its longitudinal crest acutely angled lingually, giving the tooth a marked L-shaped appearance in occlusal view. It differs from P_3 in *T. minor* in being shorter (10·1x5·2) and in having its anterior margin near vertical. Although the longitudinal crest is lower anteriorly than posteriorly, the crown is relatively high in comparison with *T. minor* and with the P_2 referred to *T. bluffensis*. While it is considered highly unlikely that a further species of *Troposodon* is represented in the Allingham Formation, the specimen is maintained as doubtfully referred to *T. bluffensis* until more complete mandibular material is collected to confirm its taxonomic position.

Petrogale sp.
(Plate 23, fig. 6)

MATERIAL EXAMINED: F7794, isolated left M_2; F7795, isolated right M_3; F9043, isolated left M_2; F9044, isolated left M_4; F9045, isolated left M_2.

DISCUSSION: The isolated molars here referred to *Petrogale* sp. were regarded by Archer in Archer and Wade (1976) as c.f. *Thylogale* sp., but were not figured. *Petrogale* and *Thylogale* are difficult to separate on the basis of isolated cheek teeth, particularly molars. However, it appears that *Petrogale* molars are more like those in *Macropus* than are those in *Thylogale*. In *Thylogale*, the lophids are very narrow longitudinally, even towards the crown base, while transversely, the lophid crests are more rectilinear. The midlinks are angled more anterolingually from the hypoconid in *Thylogale*.

In size, the referred sample is similar to *P. penicillata*, but insufficient is known of the morphology of the Allingham sample to justify more discrete treatment at this tine.

The isolated right DP^3, F7785, mentioned by Archer in Archer and Wade (1976) as being difficult to distinguish from corresponding teeth in *Thylogale* (e.g. *T. stigmatica*) does show greater morphological similarity to *Thylogale* than to *Petrogale*. Rather than promote additional speculation, its position is left doubtful until more

TABLE 3: Measurements for *Petrogale* sp.

Specimen	M_2	M_3	M_4
F7794	6·2×4·1	—	—
F7795	—	7·1×4·1	—
F9043	6·3×4·1	—	—
F9044	—	—	8·2×5·2
F9045	6·9×4·1	—	—

adequate samples become available. *Thylogale* is known from post-early Pliocene deposits at Grange Burn, Hamilton, Victoria (Turnbull and Lundelius 1970).

Protemnodon snewini* sp. nov.
(Plate 24, figs. 1-4; Plate 25, fig. 1)

Protemnodon sp. Archer 1976 (partim), pp. 390-1, pl.57a.

Material Examined: F9061, holotype, right mandibular ramus with I_1, P_3–M_4, adult, Allingham Formation of mid Pliocene age, Bluff Downs Station, Allingham Creek.

This specimen is possibly associated with the partial skull, F9074, and a partial, disarticulated skeleton, F9075, all located close to one another at the same stratigraphic level within the deposits.

In addition, F7810, a partial right maxilla with M^1–M^2 shattered M^3–M^4, adult; F7809, an isolated left M^3; F9067, an isolated, partial right M_4; F7788, an isolated left P^2; F9068, an isolated right M_3; F7811, an isolated right M^4; F9069, an isolated right M^1; F9070, a partial, isolated left P_3; F9071, an isolated left M^3; F9072, an isolated left P^2; F9073, an isolated right P^2; F7786, a right P^3, aged; F9062, an isolated right P^3; F9063, an isolated partial right M_4; F9064, an isolated right M_1; F9065, an isolated left M_3; F9066, isolated partial left M^3; F7824, an isolated right P_2; have been used in the description of the species.

Specific Diagnosis: A small species, generally smaller than *P. anak*. Mandible comparatively very shallow with an elongate symphysis ascending at about 10° to base of mandible; lateral groove extends to below posterior root M_3; mental foramen close to diastemal crest about one-quarter distance along diastema from anterior root P_3. Condyle reduced transversely.

I_1 shallow. Cheek tooth row slightly bowed labially in occlusal view. P_3 narrow, elongate, slightly longer than M_4; crown low, with straight longitudinal crest transected by four sets of slightly anteriorly directed labial and lingual, ridges. Lower molars slightly constricted across talonid basin, with lophids low, links labiad to mid-line; lingual moiety of trigonid unswollen; anterior cingulum broad, extended anterolingually into distinct, subangular corner to crown; talonid broadly U-shaped; posterior cingulum poorly developed.

P^2 elongate, with longitudinal crest low, transected by three or four sets of vertical labial and lingual ridges; lingual cingulum well developed, with shallow lingual basin narrowing slightly anteriorly. P^3 narrow, elongate, slightly constricted basally at posterior one-third; longitudinal crest nearly straight, low, transected by three or four sets of vertical labial and lingual ridges; lingual cingulum very low, continuing to anterior of crown base, sinuous; lingual basin very narrow, shallow. Upper molars with low lophs, unconstricted, or slightly constricted across median valley in posterior molars; strong ridge ascends from paracone to limit of broad, flat, anterior cingulum; midlink very low; posterior ridge from paracone very weak; metaloph relatively broad in M^4.

Description: Mandible very shallow, relatively thick; base of symphysis ascending anteriorly at an angle of approximately 10° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniophyal pit shallow, near posterior symphysial limit; diastema elongate with diastemal crest angular posteriorly, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen small, ovate, near diastemal crest, about one-quarter distance along crest from anterior root P_3. Ramus with shallow lateral groove extending posteroventrally to below posterior root M_3, somewhat disrupted by roots of P_3; posterior of groove approximately mid-way between alveolar margin and base of ramus. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa. This fossa separated above from shallow, broad depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with shelf angle reasonably well defined, leading to post-alveolar ridge ascending to disappear rapidly on medial wall of coronoid process, above large mandibular foramen. Masseteric crest low, approximately at level of alveolar margin; masseteric foramen moderately large with deep masseteric fossa. Angle of mandible broadly inflected, produced posteriorly and dorsally into crest. Anterior of coronoid process ascends posterodorsally at about

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* Named for Mr W. Snewin who, with Mr J. Barrett, discovered the Allingham site.

13° from vertical. Condyle very reduced, longer than broad, planar transversely and gently convex longitudinally, supported posteriorly by narrow shelf.

I_1 elongate, deeply rooted; slightly curved in lateral view, markedly curved in occlusal view, developing subhorizontal transverse facet of wear, but gently convex wear facet longitudinally with upper incisors; mesial wear facet present along ventral margin by approximation with other lower incisor; root compressed, oval in section; crown subquadrantal in section, tapering and blade-like anteriorly, enamelled laterally, this produced dorsolabially and ventrolingually into flanges; crown slightly enamelled ventromesially.

P_2 relatively elongate, robust, moderately broad; crown subovate in basal outline with longitudinal crest secant, nearly straight but strongly flexed lingually in its posterior extension; crest transected by two sets of near vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly; anterior cuspid of crest well defined; anterior of crown straight, with ridge from anterior cuspid curving lingually towards base of crown; lingual base of crown swollen; broad, short, vertical, basal ridge present posterolabially.

DP_3 is not preserved.

P_3 elongate, narrow, deeply rooted; crown subovate in basal outline with longitudinal crest secant, slightly sinuous, and slightly flexed lingually in its posterior extension; crest transected by four sets of slightly anteriorly directed labial and lingual ridges, with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly; anterior cuspid of crest well defined, but posterior cuspid less well developed; anterior of crown straight, near vertical extending well anterior to anterior root; labial base of crown slightly swollen, but not as strongly as posterior moiety of lingual base.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly to markedly constricted across talonid basin; lophids low, slightly convex posteriorly with hypolophid broader than protolophid in M_1 and M_2, approximately equal in M_3 and narrower in M_4. Trigonid basin broad, its length approximately equalling distance between lophids. Forelink low, moderately strong, curving slightly anterolingually from protoconid across

TABLE 4: MEASUREMENTS FOR MANDIBLES OF *Protemnodon snewini* SP. NOV.

Specimen	I_1 depth	P_2	P_3	M_1	M_2	M_3	M_4
F9061, holotype	—×10·6	—	15·0×4·9	9·8×6·6	12·3×8·3	13·3×9·3	13·8×9·0
F7824	—	8·7×4·7	—	—	—	—	—
F9065	—	—	—	—	—	12·8×8·6	—
F9067	—	—	—	—	—	—	—×8·5
F9068	—	—	—	—	—	13·2×8·7	—
F9070	—	—	—×5·1	—	—	—	—
F9063	—	—	—	—	—	—	—×9·7
F9064	—	—	—	9·9×7·1	—	—	—

TABLE 5: MEASUREMENTS FOR MAXILLAE OF *Protemnodon snewini* SP. NOV.

Specimen	P^2	P^3	M^1	M^2	M^3	M^4
F9074,*(rt.)	—	15·2×6·6	9·9×8·7	—×10·4	13·1×10·9	13·5×10·5
F9074,*(lt.)	—	—	10·0×8·8	12·3×10·2	13·1×10·9	13·9×10·7
F7810	—	—	—	—	13·8×11·6	14·0×11·7
F7811	—	—	—	—	—	14·5×11·8
F9069	—	—	11·3×9·9	—	—	—
F7788	10·9×5·8	—	—	—	—	—
F9072	10·7×6·2	—	—	—	—	—
F7786	10·7×5·4	—	—	—	—	—
F7809	—	—	—	—	13·0×11·4	—
F9071	—	—	—	—	12·1×11·4	—
F9062	—	16·6×6·6	—	—	—	—
F9073	—	15·7×6·6	—	—	—	—

*Associated with holotype

trigonid to point on anterior cingulum well labiad to midline. Anterior cingulum low, broadly curved labially but produced anterolingually into well defined corner; near horizontal lingually, but descending reasonably strongly labially. Midlink low, strong, decreasing in strength in posterior molars, descending almost directly from hypoconid, anterolingually to point at base of protolophid, well labiad to midline; slight ridge descends posterolabially from metaconid. Talonid basin broadly U-shaped, descending at low angle labially and lingually from midlink; posterior cingulum poorly defined, frequently represented only by series of low tubercles.

Upper incisors and DP^3 not preserved.

P^2 elongate, moderately narrow, robust, subovate in basal outline, somewhat broader posteriorly than anteriorly; longitudinal crest low, secant, very slightly concave labially; crest transected by three or four sets of vertical labial and lingual ridges with production of cuspules at crest; apex of paracone positioned about one-quarter length of crown from anterior limit. Hypocone moderately strong, united to metacone by strong, high, descending anterolabial ridge; posterior ridge from hypocone curves labially to unite with posterolingual ridge ascending from metacone below crown base; shallow posterior fossette formed between this and ridge connecting posterior cusps; anterior ridge from hypocone ascends rapidly to above crown base to form low lingual cingulum, converging slightly anteriorly to position anterior to level of paracone; slight anterolingual ridge from paracone connects with anterior of lingual cingulum; cingulum in lingual view slightly sinuous. Lingual basin shallow, occasionally transected by weak extensions of ridges from longitudinal crest. Base of crown slightly tumid labially.

P^3 moderately elongate, narrow, robust, subovate in basal outline, slightly constricted at posterior one-third, but otherwise with labial and lingual margins subparallel; crown with longitudinal crest low, secant, slightly concave labially; apex of paracone about one-fifth distance along crown from anterior limit; crest transected by three or four sets of near vertical labial and lingual ridges with production of cuspules; strength of ridges decreases posteriorly. Hypocone moderately high, united to above metacone by high, strong labial ridge; strong ridge from hypocone ascends sharply labially to unite with posterolingual ridge from metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form very low lingual cingulum, subparallel to longitudinal crest to above paracone, then curving sharply to anterior of crown; more prominent ridges from cuspules along crest cross very shallow lingual basin to cingulum; strong ridge from paracone unites with cingulum; cingulum markedly sinuous in lingual view, moderately tuberculate. Slight anterolabial cingulum present. Base of crown very slightly tumid labially.

M^1<M^2<M^3<M^4; molars subrectangular to subovate in occlusal view, usually slightly constricted across median valley especially in posterior molars; lophs low, slightly bowed anteriorly, with metaloph broader than protoloph in M^1, approximately equal in M^3 and slightly narrower in M^4, anterior cingulum low, broad, short, slightly descending labially; forelink absent, but variable slight ridges occasionally pass from base of protoloph towards cingulum; cingulum generally flattened anteriorly; low ridge usually descends from paracone to labial limit of cingulum; midlink very low, its strength decreasing in posterior molars, curving posterolabially from protocone to unite with weak ridge from near crest of metaloph lingual to midline above median valley. Weak ridge ascends posteriorly from paracone, then curves abruptly lingually near median valley to unite with weak, anterolingual ridge from metacone about one-half distance from midlink to labial margin. Median valley relatively narrowly V-shaped labially and lingually; base of median valley slightly ascending labially and lingually from midlink with labial moiety sometimes pocketed. Strong ridge curves posterolabially from hypocone to posterolabial base of crown, uniting with weaker ridge from metacone; this delimits very shallow posterior fossette somewhat labiad to midline.

DISCUSSION: A partial right mandibular ramus, F7812, referred to *Protemnodon* sp. by Archer in Archer and Wade (1976), has been recovered which may not be referrable to *P. snewini*, being generally larger than the *P. snewini* sample. Measurements appear in Table 6. This specimen retains DP$_3$ and M$_1$ and was figured by Archer in Archer and Wade (1976, pl. 57, fig. b). The DP^3, especially, is morphologically distinct from *P. chinchillaensis* and *P. devisi* from the Chinchilla Sand, in having its protolophid very restricted and with the forelink and midlink descending anteriorly and posteriorly from the protoconid. The labial base of the protolophid comprises two weak ridges uniting to ascend to the protoconid. The forelink is very high and the labial and lingual moieties of the trigonid basin descend at high angles from this link. The first molar possesses a strong posterior cingulum, as does DP_3, and a weak accessory link is present close to the near central midlink in the lingual moiety of the talonid basin. The anterior cingulum is linked by a moderately strong connecting ridge to the metaconid. A further specimen, F9077, an isolated right M_2, also shows larger size than *P. snewini*, has the strong posterior cingulum and stronger more central links. The possibility that these specimens indicate the existence of a second species of *Protemnodon* from the Allingham Formation would not be surprising, bearing in mind the evidence of two species within the Chinchilla Sand and three within the Pleistocene deposits of the eastern Darling Downs.

It is obvious from a cursory examination of the material that *P. snewini* presents morphological features which bear comparison with *P. chinchillaensis* from the late Pliocene Chinchilla Sand (Bartholomai 1973) and *P. otibandus* from the mid Pliocene Otibanda Formation of the Bulolo Valley, Papua New Guinea (Plane 1967). *P. devisi*, also from the Chinchilla Sand, is excluded by considerations of molar size alone, but does possess permanent premolars which accord better with *P. snewini* than do those in *P. chinchillaensis* which are actually and relatively much longer in comparison with molar lengths (Figure 1). Permanent upper premolars in *P. chinchillaensis* are considerably wider teeth and are generally more robust. The lower incisors in

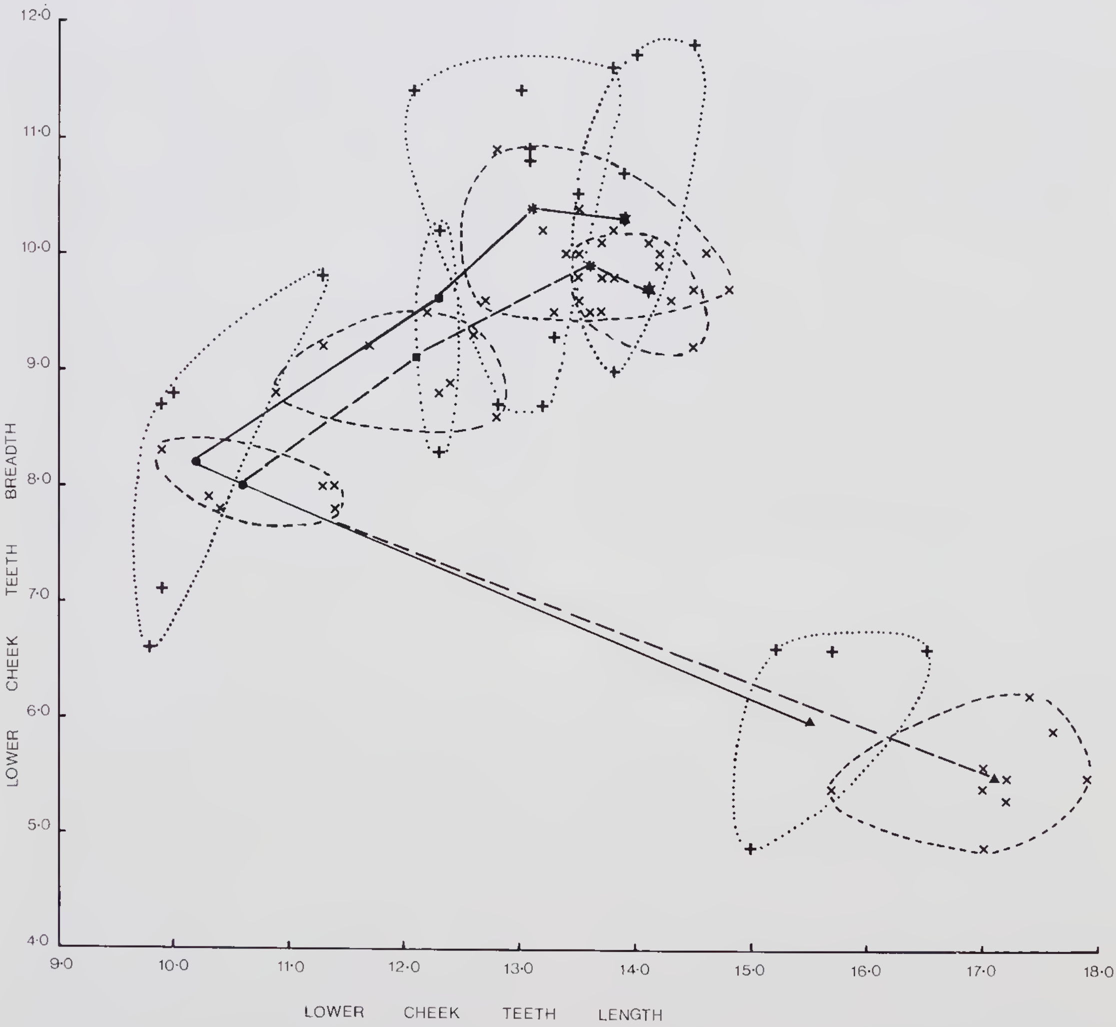

FIG. 1: Scatter diagram illustrating the proportional relationships of permanent lower cheek teeth in *Protemnodon snewini* sp. nov. (+) compared with those in *Protemnodion chinchillaensis* Bartholomai (x). Solid line links mean values from P_3–M_4 in *P. snewini;* heavy dashed line links similar mean values for *P. chinchillaensis.*

TABLE 6: Measurements for *Protemnodon* sp.

Specimen	DP$_3$	M$_1$	M$_2$
F7812	9·7x4·9	11·5x7·1	—
F9077	—	—	14·0x9·3

P. snewini are typically macropodine, whereas those in *P. chinchillanesis* (as in F7071) are considerably more spatulate. Upper molars in *P. snewini* have lower midlinks and broader metalophs on M^4. Compared with *P. otibandus*, *P. snewini* has a shallower, longer mandibular ramus with its coronoid process less vertical and with the condyle considerably reduced transversely. The cheek tooth row is straighter, links are more labially positioned and are lower, the anterior cingulum is flatter and broader, possessing a distinct anterolingual corner, and the lower premolar is less robust. P^3 in *P. otibandus* is much more robust, while in upper molars, midlinks are higher and the anterior cingulum is not as flattened as in *P. snewini*.

The left maxilla, attributed by Plane (1972) to *P. otibandus*, from the marine lower Pliocene (Kalimnan) Jemmy's Point Formation, Victoria, has been suggested previously to be *P. devisi* by Bartholomai (1973). Accessory ridging in this specimen, particularly from the paracone but also from metacone into the median valley, is stronger in posterior molars than general in *P. snewini*. The Jemmy's Point specimen is larger, being comparable with dimensions in *P. devisi*.

Turnbull and Lundelius (1970) have figured and described an isolated left molariform tooth which appears referable to *Protemnodon*. This specimen, PM 4429, suggested to be a DP^3 by Turnbull and Lundelius (1970) is from a fossil soil at Grange Burn, Hamilton, Victoria, dated as post-early Pliocene. Although direct comparison is impossible because DP^3 is unknown in the Allingham sample, accessory ridging from the paracone and metacone into the median valley appears stronger than in *P. snewini*, while the specimen must be larger.

Associated parts of a left hind limb have been located in the Allingham excavations, indicating the possibility of recovering more complete skeletons in the deposits. Although these remains were not found with cranial specimens, it is apparent from the proportions of the metatarsal IV and the preserved elements of digit IV that they are from a species of *Protemnodon*. At this time, it can only be assumed that they are from *P. snewini*. Numerous isolated elements from the hind limbs of macropodines have been located and, among these, several are morphologically acceptable to represent elements missing in the associated limb. These have been included in the illustration (Fig. 2) and comprise the calcaneum, cuboid, astragalus, metatarsal V and the proximal phalange of digit IV.

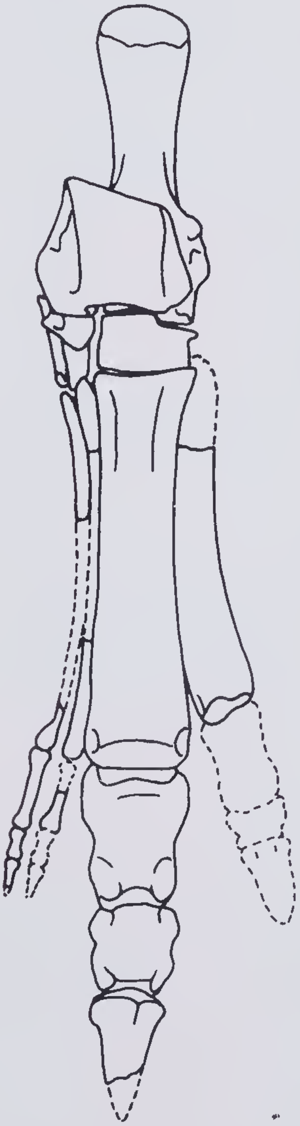

Fig. 2: Partial right pes, possibly of *Protemnodon snewini* sp. nov., all F9075, except calcaneum, cuboid, astragalus, metatarsal V and proximal phalange of digit IV, x½.

The ratio of total length of metatarsal IV (102·5) to its median width (20·5) is 500. Compared with *P. otibanda*, the ratio for mt IV for which is 518, provided in Plane (1967), the bone is relatively broader than in the Awe material. The median phalanx in digit IV is 26·0 long by 23·9 broad, somewhat larger than in *P. otibanda* and relatively broader.

FIG. 3: Tibia and fibula, possibly of *Protemnodon snewini* sp. nov., F9075, associated with pes illustrated in Fig. 2, ×¼.

The most remarkable feature in the preserved, associated part of the hind limb, is the structure of the tibia which, as shown in Fig. 3, is highly curved mesially. While slight displacement, particularly along fractures in the distal moiety of the bone, tends to emphasize this feature, the tibia is much more curved than in other macropodines. Whether the specimen is aberrant cannot be ascertained at this time but a pathological cause is suspected.

Macropus (Prionotemnus) narada sp. nov.
(Plate 25, figs. 2-3)

MATERIAL EXAMINED: F9105, holotype, partial left maxilla with DP^3–M^1, P^3 missing, juvenile, Allingham Formation of mid Pliocene age, Bluff Downs Station, Allingham Creek.

In addition, F9106, isolated left DP^3; and F9107, isolated right M^3 have been used in the description of the species.

SPECIFIC DIAGNOSIS: A relatively small species. Upper molars and DP^3 with well-defined forelink and strong anterior ridge from paracone to anterolabial margin of anterior cingulum; fine, relatively weak ridge passes posterolingually from paracone towards mid-point of labial moiety of median valley; midlink high, strong, with major contribution from near mid-point of hypoloph crest.

DESCRIPTION: Known only from upper molariform and molar cheek teeth.

DP^3 relatively small, molariform, subovate in basal outline, slightly constricted across median valley; lophs moderately high, anteriorly bowed, with metaloph broader than protoloph. Anterior cingulum relatively high and broad, short, ascending at moderate angle lingually; strong forelink present between cingulum and base of protoloph below mid-line; strong, high ridge ascends anteriorly from paracone to anterolabial margin of anterior cingulum; slight ridge curves posterolingually from paracone into median valley. Strong, high ridge curves posterolabially from protocone across median valley as midlink to unite with strong ridge from near middle of metaloph crest. Median valley ascends labially and lingually from midlink; valley sharply V-shaped. Strong ridge ascends posterolabially from hypocone to meet much weaker, posterior ridge from metacone near base of crown. Posterior fossette developed below midline.

M^1 and M^3 preserved; molars subrectangular in basal outline, slightly constricted across median valley, with metaloph broader than protoloph in M^1 but slightly narrower in M^3; lophs moderately high, anteriorly bowed. Anterior cingulum relatively high, often broad, short, ascending at moderate angle lingually; strong forelink present at midline, very strong, high ridge ascends anteriorly from paracone to anterolabial margin of anterior cingulum. Relatively weak ridge ascends posterolingually from paracone towards median valley; variable, weak ridge from metacone ascends into median valley; strong, high ridge curves gently anterolabially from protocone to unite with short, high ridge from near centre of metaloph crest as midlink. Median valley sharply V-shaped, ascending slightly labially and lingually from midlink. Strong ridge curves posterolabially from hypocone to unite with weak, posterior ridge from metacone near base of crown; slight fossette formed at midline.

DISCUSSION. Although only represented in the Allingham Formation by a very small sample of maxillary remains, *Macropus (Prionotemnus) narada* sp. nov. is quite distinct from *M. dryas*, the other possible *Prionotemnus* present in the deposits. *M. dryas* lacks the well-defined and strong ridge which ascends from the paracone to the anterolabial limit of the anterior cingulum, present in *M. narada*. It also lacks the accessory ridges ascending posteriorly from the paracone and sometimes anteriorly from the metacone. Within the Chinchilla Sand, the only recorded *Prionotemnus* is *P. palankarinnicus* Stirton, first described from the Pliocene Mampuwordu Sands of the Tirari Desert, South Australia. Upper molars of this species, studied in the collections of the University of California, Berkeley, lack forelinks, but possess the strong anterior ridge from the paracone to the anterior cingulum.

Compared with the recorded Pleistocene species from the fluviatile deposits of the eastern Darling Downs, *M. narada* is generally slightly larger than individuals within *M. agilis siva* (De Vis) and is about the same size as *M. thor* (De Vis), both of which were revised in Bartholomai (1975). Morphologically, the teeth are closer to those in *M. agilis siva* but possess a much better-developed forelink. The forelink in *M. thor* is subdued and accessory ridges into the median valley from the paracone and metacone are lacking. The anterior cingulum is near-planar in the labial moiety. Upper teeth in other Pleistocene species, *M. gouldi* (Owen) and *M. piltonensis* Bartholomai are unknown at this time.

The lower first molar, F7784, recorded and figured by Archer in Archer and Wade (1976, pl.57, fig. f) may relate to *M. narada*. It is unlike any other macropodid recovered from the Allingham Formation and, purely by elimination, and its close occlusal relationships with the upper molars described here, could well indicate the morphology to be expected in the lower molars of *M. narada*. Until it is certain that only two species of *M. (Prionotemnus)* are present in the Allingham, its taxonomic position must remain in doubt.

TABLE 7: MEASUREMENTS FOR *Macropus (Prionotemnus) narada* SP. NOV.

Specimen	DP^3	M^1	M^2	M^3
F9105, holotype	9·1×7·2	10·1×7·9	—	—
F9106	9·0×7·1	—	—	—
F9107	—	—	—	12·5×9·0

Macropus (?Prionotemnus) dryas

(De Vis, 1895)

(Plate 26, fig. 6; Plate 27, figs 1–3)

Halmaturus dryas De Vis, 1895, pp.109–11, pl. 17, figs. 11–5.

Macropus (Prionotemnus) dryas (De Vis): Bartholomai, 1975, pp.229–32, pl. 25, figs. 1–4 (synonymy).

Macropus sp. c.f. *M. dryas* (De Vis): Archer in Archer and Wade, 1976, p.391, pl. 57, figs. c-d.

MATERIAL EXAMINED. F7823, partial right mandibular ramus with I_1, P_2–M_1, P_3 excavated, juvenile (figd. Archer, 1976, pl. 57, figs. c–d). F9078, isolated right M_2; F9079, isolated right M_2; F9080, isolated partial left M_2; F9081, isolated left M_2; F9082, isolated right M_2; F9083, partial isolated left M_1; F9084, isolated left P^3: F7828, isolated left P^3; F7780, partial left maxilla with M^2–M^3, juvenile; F7781, isolated left P^3; F9085, partial left mandibular ramus with M_1–M_3, aged; F9086, partial right mandibular ramus with P_3–M_4; adult; F9087, partial right mandibular ramus with M_2, juvenile; F9088, partial left mandibular ramus with base of I_1, P_3–M_1, juvenile; F9089, partial left mandibular ramus with M_3–M_4, adult; F9090, isolated left M_3; F9091, isolated right P_2; F9092, isolated partial right M_3; F9093, isolated partial left M_2; F9094, isolated left M_2; F9096, isolated right DP_3; F9097, isolated right P_3: F9098, isolated partial right M_2; F9103, isolated left M^1; F9095, isolated partial left DP_3; F9099, isolated right M_2; F9100, isolated partial left M^1; F9101, isolated partial right DP_3; F9102, isolated left P_3; F7790, isolated right P^2; F7782, partial right mandibular ramus with M_1–M_3, juvenile; F7783, isolated right P_3; F7791 isolated left P^2.

DISCUSSION: The sample of *Macropus (?Prionotemnus) dryas* (De Vis) from the

Allingham Formation is numerically the largest among macropodids from the deposits, suggesting that this species was the most abundant grazing herbivore in the fauna. Bartholomai (1975) revised *M. dryas*, previously recorded only from the late Pliocene Chinchilla Sand in the western Darling Downs, where the species was well represented but not dominant within the assemblage present.

Observed measurements for cheek teeth in the Allingham sample often fall towards the lower observed limits or even outside the lower limits of comparable teeth in the Chinchilla Sand material. No other morphological differences are evident which might be considered significant in the separation of the Allingham Formation sample from that in the Chinchilla Sand. With the larger sample now available, the possible structural distinctions noted by Archer in Archer and Wade (1976) are considered to be within the range of variation for *M. dryas*, or are likely to be encountered in the species, bearing in mind the variation exhibited by modern species of *Macropus* (Bartholomai 1971).

Two specimens, F7790 and F7791, have been referred to *M. dryas*, both of which are P^2. This tooth was not present in the available Chinchilla Sand material at the time of Bartholomai's (1975) revision. These possess a single vertical set of labial and lingual ridges transecting the

TABLE 8: MEASUREMENTS FOR MANDIBLES OF *Macropus (?Prionotemnus) dryas* (DE VIS, 1895)

Specimen	P_2	DP_3	P_3	M_1	M_2	M_3	M_4
F7823	8·5×3·8	8·8×5·0	11·3×4·0	9·9×6·5	—	—	—
F9078	—	—	—	—	12·0×7·2	—	—
F9079	—	—	—	—	11·6×7·0	—	—
F9080	—	—	—	—	—×8·3	—	—
F9081	—	—	—	—	12·5×8·0	—	—
F9082	—	—	—	—	11·9×7·1	—	—
F9085	—	—	—	8·8×6·3	10·0×7·6	12·2×8·2	—
F9086	—	—	11·3×3·9	9·1×5·7	11·0×—	12·7×8·0	13·8×8·1
F9087	—	—	—	—	11·5×—	—	—
F9088	—	—	10·5×3·6	8·7×5·9	—	—	—
F9089	—	—	—	—	—	12·4×8·2	13·4×8·3
F9090	—	—	—	—	—	13·0×8·4	—
F9091	7·6×3·9	—	—	—	—	—	—
F9092	—	—	—	—	—	—×8·3	—
F9093	—	—	—	—	—×7·9	—	—
F9094	—	—	—	—	12·2×7·5	—	—
F9096	—	8·6×4·3	—	—	—	—	—
F9097	—	—	11·7×4·2	—	—	—	—
F9095	—	8·0×4·4	—	—	—	—	—
F9099	—	—	—	—	11·9×7·7	—	—
F9101	—	—×4·5	—	—	—	—	—
F9102	—	—	11·4×3·9	—	—	—	—
F7782	—	—	—	—	11·7×—	13·6×7·7	—
F7783	—	—	11·2×4·0	—	—	—	—

TABLE 9: MEASUREMENTS FOR MAXILLAE OF *Macropus (?Prionotemnus) dryas* (DE VIS, 1895)

Specimen	P^2	DP^3	P^3	M^1	M^2	M^3	M^4
F9084	—	—	13·7×6·0	—	—	—	—
F7828	—	—	13·8×6·4	—	—	—	—
F7780	—	—	—	—	11·1×9·3	11·8×9·4	—
F7781	—	—	13·3×6·3	—	—	—	—
F9103	—	—	—	10·3×7·9	—	—	—
F9100	—	—	—	—×8·2	—	—	—
F7790	8·2×5·4	—	—	—	—	—	—
F7791	8·3×5·1	—	—	—	—	—	—

longitudinal crest, have a low hypocone and a variably present lingual cingulum. This structure can be reasonably well developed compared with the situation in P^3 where it is represented only by a series of low tubercles closely adpressed to the base of the longitudinal crest.

Macropus (Osphranter) pavana sp. nov.
(Plate 26, figs. 1–5)

MATERIAL EXAMINED: F9108, holotype, partial left maxilla with DP^3–M^1, P^3 missing, juvenile, Allingham Formation of mid Pliocene age, Bluff Downs Station, Allingham Creek.

In addition, F9109, a partial left mandibular ramus with M_2–M_4, adult; F9110, isolated right M^2; F9111, isolated right M_2; F9112, isolated right M^1; F9113, isolated right P^3; F9114, isolated right P^3; F9115 isolated right M^2; F9116, isolated left P_3; F9117, isolated left M_3; F7773, isolated right M_3; have been used in the description of the species.

SPECIFIC DIAGNOSIS: A relatively small species with deep ramus, relatively narrow below anterior cheek teeth; P_3 relatively elongate with trenchant longitudinal crest transected medially by single set of vertical labial and lingual ridges and with crest slightly curving lingually posteriorly. Lower molars with midlink well labiad to midline; hypolophid with variable oblique groove. DP^3 with high secant ridge from paracone to anterolabial limit of anterior cingulum; forelink strong; accessory link present mid-way between midlink and labial margin of median valley. P^3 with longitudinal crest slightly cleft at anterior one-third and with single medial set of vertical labial and lingual ridges transecting crest; hypocone very low; posterolingual fossette and lingual cingulum very reduced, cingulum degenerating to series of tubercles anteriorly. Molars with relatively strong forelinks; anterior molars with slight accessory link mid-way between midlink and labial margin of median valley; this is variably absent in posterior molars.

DESCRIPTION: Upper incisors, P^2, M^3 and M^4 not preserved.

DP^3 molariform, subovate in basal outline, slightly constricted across median valley, with metaloph much broader than protoloph. Lophs high, slightly convex anteriorly. Anterior cingulum moderately high, narrow, short, with well-defined forelink well linguad to mid-line from base of protoloph to cingulum; cingulum near planar, labiad to forelink, ascending at very high angle lingually. Strong high ridge ascends anteriorly from paracone to anterolabial margin of cingulum as secant crest. Well-defined, high, strong ridge ascends posterolabially from protocone across median valley as midlink, uniting with ridge from near mid-point of metaloph, below median valley; relatively strong ridge ascends posteriorly from paracone towards median valley, producing slight accessory link across floor of valley mid-way between midlink and labial margin. Valley narrowly V-shaped labially and lingually, near planar transversely. Strong ridge ascends posteriorly from hypocone, curving labially to near posterolabial margin of crown, uniting with slight posterior ridge from metacone; fossette present at midline. Base of crown swollen slightly labially and lingually.

P^3 relatively large, subovate in basal outline, broader posteriorly than anteriorly; high, relatively short, longitudinal crest transected by median set of vertical labial and lingual ridges with production of cuspule at crest; slight cleft present along crest about one-third distance from anterior cusp. Hypocone very low, connected to metacone by weak anterolabial ridge; stronger ridge curves posterolabially to meet posterolingual ridge from metacone, defining shallow posterolingual fossette; anterior ridge from hypocone ascends abruptly forming low cingulum posterolingually, this degenerating anteriorly into basal tubercles, lingual basin very restricted.

M^1<M^2; molars subovate in basal outline, very slightly constricted across median valley; lophs high, somewhat rotated with metaloph crest more convex anteriorly than protoloph in unworn teeth; metaloph broader than protoloph in anterior molars. Anterior cingulum relatively high, narrow, short; well-defined forelink present linguad to mid-line, between base of protoloph and equally well-developed, short, transverse ridge across cingular shelf. Labial moiety of cingular shelf near planar, lingual moiety ascending at high angle from forelink; slight ridge ascends anteriorly from paracone to anterolabial margin of cingulum. Strong, high ridge curves posterolabially from protocone to unite with strong ridge from near centre of hypoloph as midlink; posterior ridge from paracone very reduced; low accessory link developed across median valley and mid-way between midlink and labial margin, this occasionally lacking by M^2; median valley near planar transversely, sharply V-shaped longitudinally. Anterior ridge from metacone to accessory link very weak in M^1, sometimes lacking by M^2. Strong, slightly flared ridge curves posterolabially from hypocone to posterolabial base of crown, there uniting with weak posterior ridge from metacone; fossette developed at mid-line; base of crown usually slightly swollen.

Mandible imperfectly known. Ramus deep, relatively narrow below anterior cheek teeth; post-alveolar shelf elongate with angle poorly developed; ventral margin of ramus rounded posterior to symphysis; diagastric ridge and process very weak; diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by very shallow diagastric fossa; this fossa separated above from broad shallow depression opening posteriorly into pterygoid fossa; mandibular foramen large; masseteric crest raised to about level of occlusion of cheek teeth.

Lower incisor, P_2 and DP_3 are unknown.

P_3 relatively elongate, subovate in basal outline, somewhat broader posteriorly than anteriorly. Longitudinal crest trenchant with anterior cuspid well-defined but with posterior cuspid less well-defined; crest ascends posteriorly, being transected mesially by set of weak, vertical, labial and lingual ridges with production of low cuspule at crest. Posterior extension of crest curves very slightly lingually before descending to crown base. Anterior surface from anterior cuspid near vertical. Base of crown narrowly swollen labially, lingually and anteriorly.

$M_1<M_2<M_3<M_4$; molars subovate to subrectangular in basal outline, slightly constricted across talonid basin; lophids high, convex posteriorly, somewhat anteriorly rotated in labial view, with hypolophid broader than protolophid in M_1 and M_2 and slightly narrower in M_3 and M_4. Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink high, strong, curving anterolingually from protoconid across trigonid basin to point labiad to mid-line on high anterior cingulum; trigonid basin slopes labially and lingually from forelink and posteriorly from cingulum; anterior cingulum more expanded anterolingually; very slight ridge descends anteriorly from metaconid; slight anterolabial fossette formed in trigonid. Midlink high, strong, curving anterolingually from hypoconid to unite with well-developed ridge from protoconid above talonid basin; junction occasionally markedly flexed; variable, high, accessory ridge present running anterolingually from hypoconid part of midlink. Talonid basin narrowly V-shaped labially, broadly U-shaped lingually, slightly descending labially and lingually from midlink; floor of talonid sometimes with low transverse fold labially and lingually from midlink. Posterior of hypolophid with moderate, near-vertical groove, rarely pocketed towards its base, flanked by low, vertical ridges. Crown somewhat flexed about labial extremity of talonid basin.

DISCUSSION: Taxonomic separation of species of *Macropus* Shaw is frequently extremely difficult on the basis of dental morphology alone and normally, single characters are of little use for this purpose. This certainly is true of the material from the Allingham Formation, here referred to *Macropus (Osphranter) pavana* sp. nov.

Archer in Archer and Wade (1976) correctly assigned part of the material to *M. (Osphranter)* suggesting it should be compared with *M. woodsi* Bartholomai (1975) a species from the Chinchilla Sand with which *M. pavana* has obviously close relationships. With the larger sample now available as a result of subsequent collecting, separation of the material from *M. woodsi* and from *M. (Osphranter) pan* De Vis, 1895, also from the late Pliocene Chinchilla Sand has been possible.

M. pavana is smaller than *M. pan* and has its P^3 relatively narrower, with a lower hypocone and much reduced lingual cingulum and basin. Development of an accessory link across the median valley in upper molars appears restricted to M^1 and sometimes M^2 whereas this structure frequently occurs in incipient form in posterior molars in *M. pan.* P_3 is similar in these species, but that in *M. pavana* lacks the prominent posterolingual cuspule present in *M. pan.* Compared with *M. woodsi,* in which the upper permanent premolar has yet to be described, *M. pavana,* is of similar size but upper molars lack well-defined accessory links across the median valleys of posterior molars. P_3 is larger than in *M. woodsi,* and rather than possessing a trifid, crescentic longitudinal crest, has a much straighter, trenchant structure. Lower molars possess a stronger midlink which includes a much greater contribution from near the protocone and the posterior surface of the protolophid.

Three isolated premolars from the Allingham Formation mentioned by Archer in Archer and Wade (1976) as resembling *M. (Osphranter)* have been assigned elsewhere within *Macropus* in this paper, with the exception of F7789, which is clearly of the *M. (Osphranter)* type. This specimen has a bifid, more curved longitudinal crest than in the referred P_3 of *M. pavana.* It also possesses an anterolingual ridge from the posterior cuspid. It is possible that additional *M. (Osphranter)* species may be present in the Allingham

TABLE 10: MEASUREMENTS FOR MAXILLAE OF *Macropus (Osphranter) pavana* SP. NOV.

Specimen	DP^3	P^3	M^1	M^2
F9108, holotype	10·2x7·5	—	11·9x9·8	—
F9110	—	—	—	13·2x10·7
F9113	—	9·8x5·6	—	—
F9114	—	9·3x5·7	—	—
F9112	—	—	10·4x8·5	—
F9115	—	—	—	12·6x9·6

TABLE 11: MEASUREMENTS FOR MANDIBLES OF *Macropus (Osphranter) pavana* SP. NOV.

Specimen	P_3	M_1	M_2	M_3	M_4
F9109	—	—	13·9x9·2	16·2x10·7	17·4x10·0
F9116	8·6x5·0	—	—	—	—
F9111	—	—	13·7x8·6	—	—
F9117	—	—	—	16·4x10·1	—
F7773	—	—	—	—x10·3	—

Formation, and whether this specimen reflects extreme variation in *M. pavana* or whether it represents an additional taxon must remain unresolved until further collections are forthcoming from the deposits.

CONCLUSIONS

Comparison of the macropodids from the Allingham Formation with those from other Pliocene deposits in Australia is largely limited by the nature of other occurrences, the extent to which faunal elements have been researched and the lack of diversity in the faunas yet reported. The notable exception is the Chinchilla Sand in the western Darling Downs, south-eastern Queensland, a formation believed to be of late Pliocene age. This provides a substantial basis for comparison, although other deposits in Victoria and in the Tirari Desert of central Australia give tantalizing glimpses of elements present in those parts of the continent in Pliocene times. The Awe fauna in Papua New Guinea (Plane 1967) contains taxa which also warrant attention in this regard. An undescribed, presumably Pliocene fauna from Merriwah in New South Wales contains reasonable diversity and will prove interesting for comparison when study on it has been completed.

The Macropodidae from the Chinchilla Sand were studied originally by De Vis (1895). Progressive revisions of the different taxa represented appear in numerous papers by Bartholomai (1963, 1966, 1967, 1973a, 1973b, 1976). A total of 11 macropodid species has been recorded, although as with the Bluff Downs fauna, fragmentary remains suggest the presence of additional forms. Among sthenurines, the most common species is *Sthenurus antiquus*. *Troposodon minor*, *Protemnodon chinchillaensis*, *P. devisi*, *Macropus (Osphranter) pan*, *M. (O.) woodsi* and *M. (?Prionotemnus) dryas* are very common among the Macropodinae. Other macropodids are present in relatively low numbers. Similar to the Allingham Formation, potoroines have yet to be located.

The only macropodids common to both faunas are *T. minor* and *M. (? P.) dryas*. Of these, *T. minor* is known from wide temporal and geographical ranges and is not considered particularly useful in correlation. *M. (? P.) dryas*, however, has been recorded previously only from the Chinchilla Sand. This fact, taken in conjunction with the known minimal age for the Allingham Formation, the presence of a presumably more primitive *Troposodon* in those sediments and the general similarities of the taxa where comparisons are possible, is supportive of the late Pliocene age currently attributed to the Chinchilla Sand. Close relationships are apparent between Chinchilla and Allingham diprotodontids (Archer 1976).

Detailed comparisons have been provided within the text above with taxa described from other Australian and Papua New Guinea deposits. For the most part, conclusions other than taxonomic cannot be drawn at this time.

Although it is apparent that grazing macropodids predominated in the assemblage present in the Allingham Formation, suggesting that open sclerophyll and open grasslands habitats were present in the area during deposition, detailed palaeoecological assessment should await results of studies on other groups represented.

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PLATE 23

FIG 1A-B: *Sthenurus* sp., F9104, stereopair of occlusal view of partial right M^2, ×2.

FIG 2A-B: *Troposodon minor* (Owen), F905J, stereopair of occlusal view of isolated right DP^3, ×2.

FIG. 3A-B: *Troposodon minor* (Owen), F9046, stereopair of occlusal view of isolated left P_3, ×2.

FIG. 4A-B: *Troposodon minor* (Owen) F9050, stereopair of occlusal view of isolated right M_1, ×2.

FIG. 5A-B: *Troposodon bluffensis* sp., nov., F9058, lateral and stereopaired occlusal views of isolated right P_2, ×2.

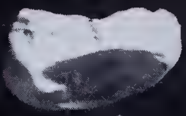
FIG. 6A-B: *Petrogale* sp., F7794, stereopair of occlusal view of isolated left M_2, ×2.

FIG. 7, 7A-B: *Troposodon bluffensis* sp. nov., F9057, lateral and stereopaired occlusal views of isolated right M_4, ×2.

FIG. 8, 8A-B: ? *Troposodon bluffensis* sp. nov., F9060, lateral and stereopaired occlusal views of isolated right P_3, ×2.

FIG 9, 9A-B: *Troposodon bluffensis* sp. nov., F9054, holotype, lateral and stereopaired occlusal views of isolated right M^4, ×2.

FIG. 10, 10A-10B: *Troposodon bluffensis* sp. nov., F9059, lateral and stereopaired occlusal views of isolated left P_2, ×2.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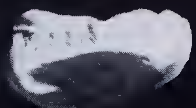
2a


1b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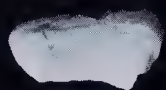
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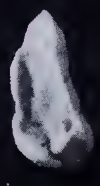
8


9a


10a


9b


10b

PLATE 24

FIG. 1, 1A-B: *Protemnodon snewini* sp. nov., F9074, lateral view ×½ and stereopaired occlusal views ×1 of partial adult skull.

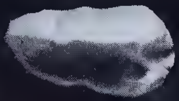
FIG. 2, 2A-B: *Protemnodon snewini* sp. nov., F7788, lateral and stereopaired occlusal views of isolated left P^2, ×2.

FIG. 3, 3A-B: *Protemnodon snewini* sp. nov., F7824, lateral and stereopaired occlusal views of isolated right P_2, ×2.

FIG. 4: *Protemnodon snewini* sp. nov., F9061, holotype, lateral view of right mandibular ramus, ×½.

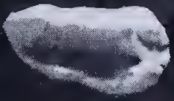
Ia

2



2a

Ib



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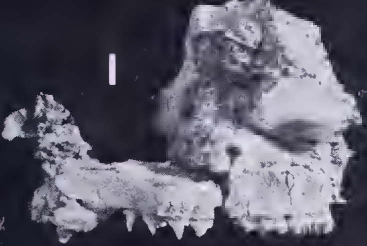

I

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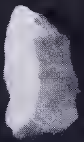

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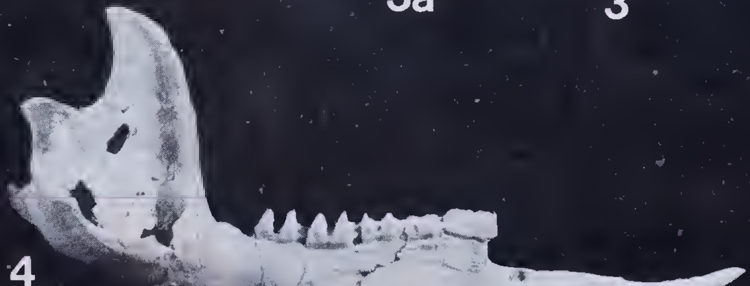


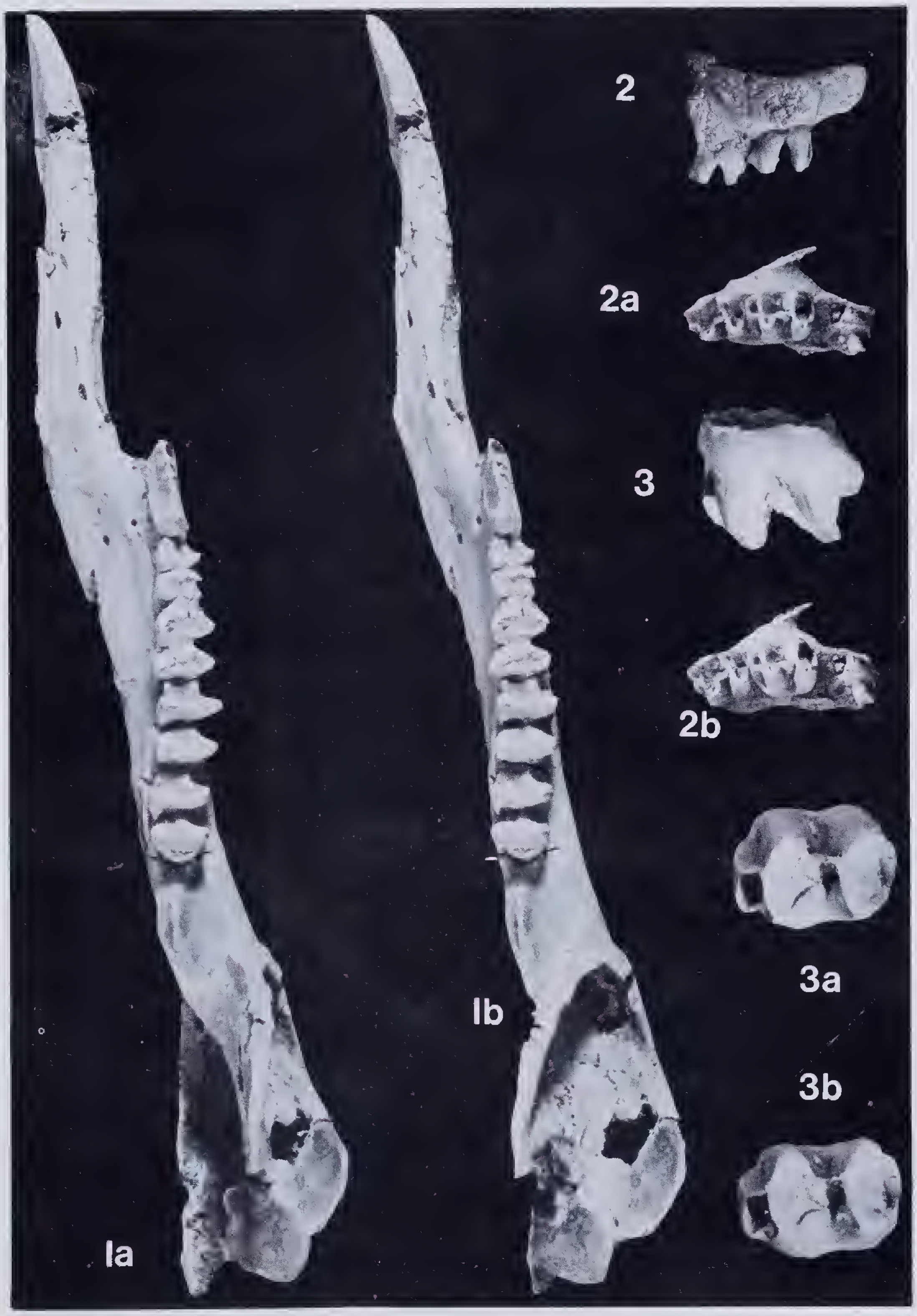
4

PLATE 25

FIG. 1A-B: *Protemnodon snewini* sp. nov., F9061, holotype, stereopair of occlusal view of right mandibular ramus with I_1, P_3–M_4, ×1.

FIG. 2, 2A-B: *Macropus (Prionotemnus) narada* sp. nov., F9105, holotype, lateral and stereopaired occlusal views of partial left maxilla with DP^3–M^1, ×1.

FIG. 3, 3A-B: *Macropus (Prionotemnus) narada* sp. nov., F9107, lateral and stereopaired occlusal views of isolated right M^3, ×2.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2a
3
2b
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lb
3b
la

PLATE 26

FIG. 1, 1A-B: *Macropus (Osphranter) pavana* sp. nov., F9108, holotype, lateral and stereopaired occlusal views of partial left maxilla with DP^3–M^1, ×1.

FIG. 2, 4A-B: *Macropus (Osphranter)* sp., F7789, lateral and stereopaired occlusal views of isolated left P_3, ×2.

FIG. 3, 2A-B: *Macropus (Osphranter) pavana* sp. nov., F9114, lateral and stereopaired occlusal views of isolated right P^3, ×2.

FIG. 4, 3A-B: *Macropus (Osphranter) pavana* sp. nov., F9116, lateral and stereopaired occlusal views of isolated left P_3, ×2.

FIG. 5, 5A-B: *Macropus (Osphranter) pavana* sp. nov., F7773, lateral and stereopaired occlusal views of isolated right M_3, ×2.

FIG. 6, 6A-B: *Macropus (? Prionotemnus) dryas* (De Vis), F9084, lateral and stereopaired occlusal views of isolated left P^3, ×2.

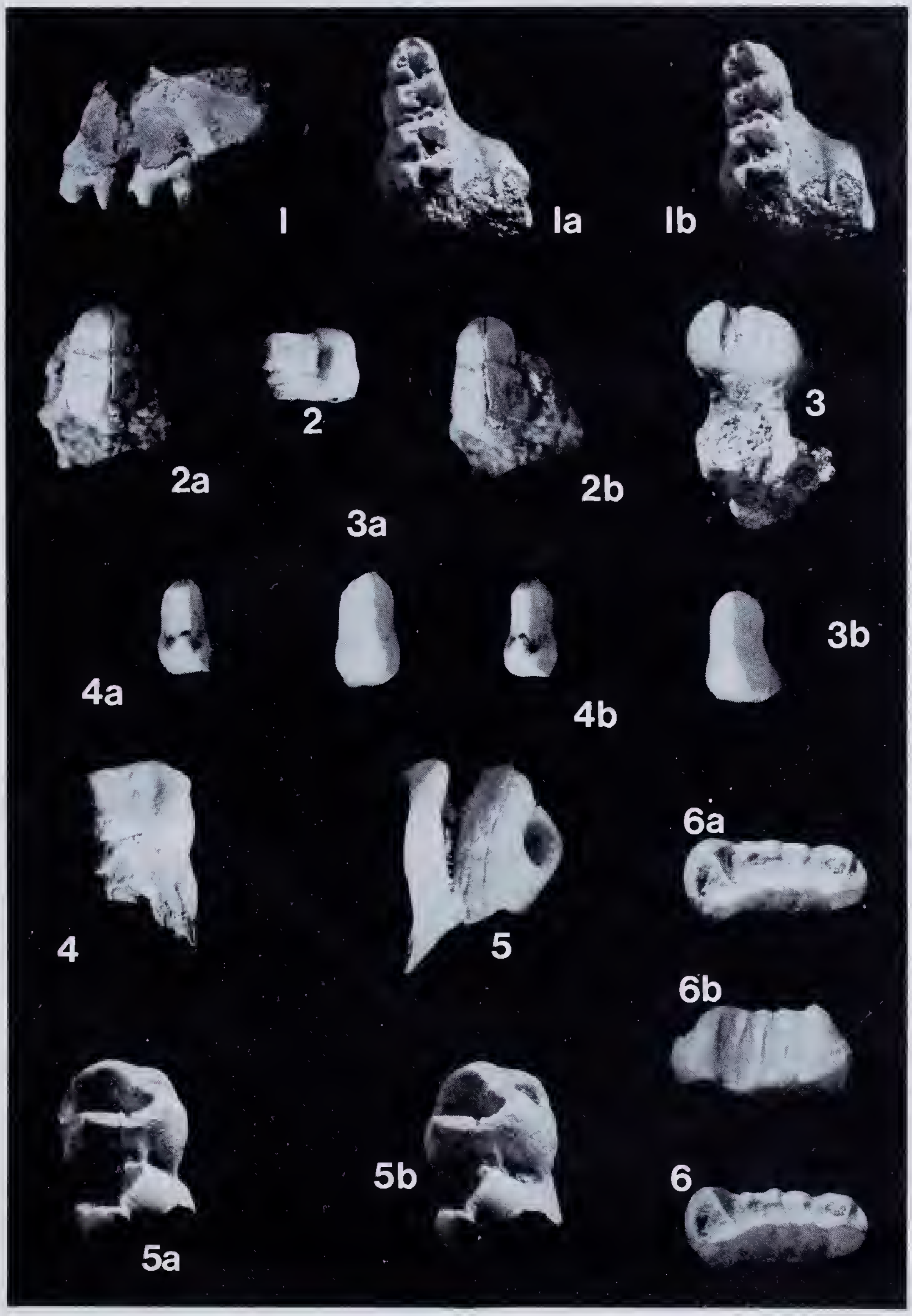
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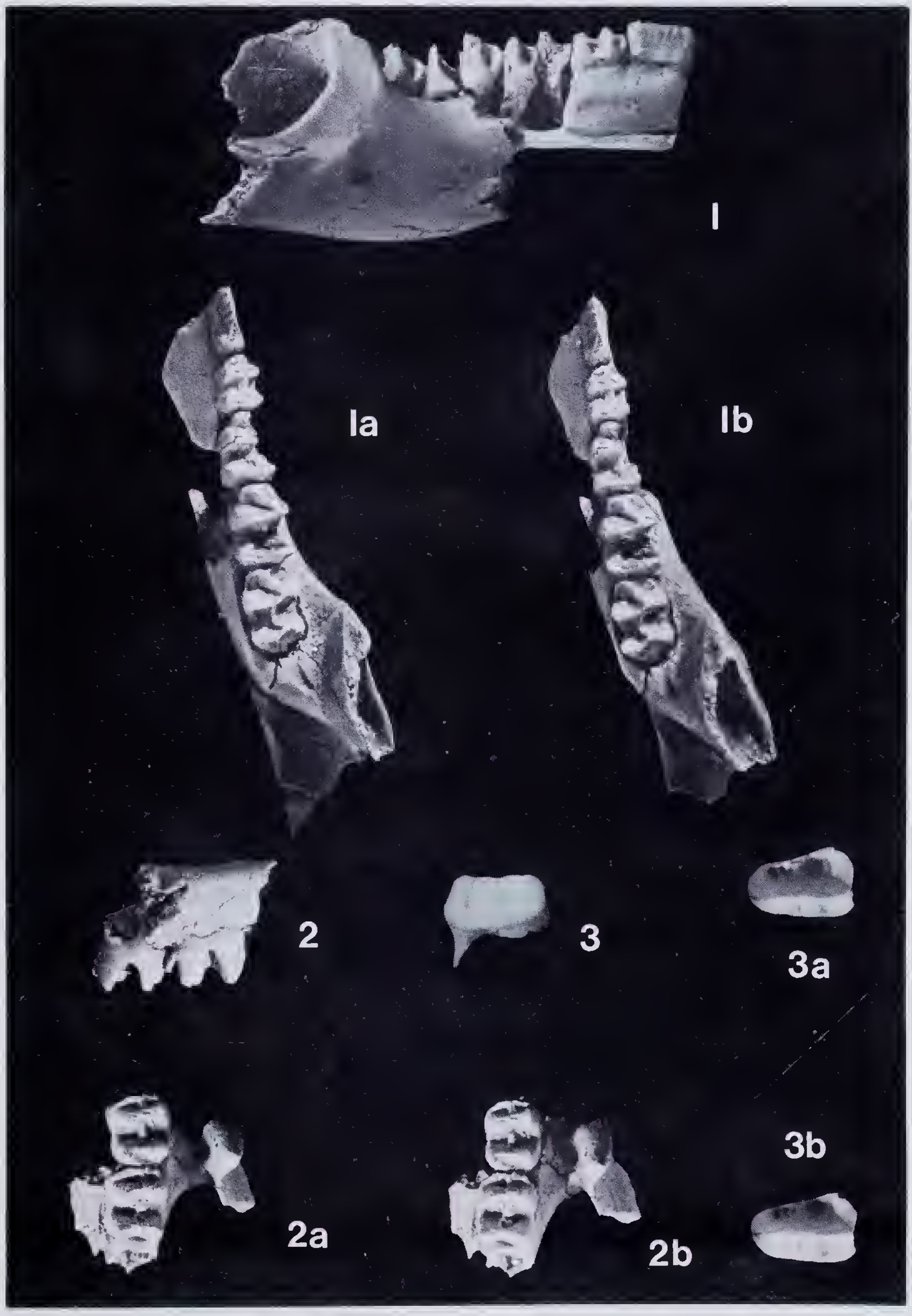
PLATE 27

FIG. 1, 1A-B: *Macropus (? Prionotemnus) dryas* (De Vis), F9086, lateral and occlusal views of partial right mandibular ramus with P_3–M_4, ×1.

FIG. 2, 2A-B: *Macropus (? Prionotemnus) dryas* (De Vis), F7780, lateral and stereopaired occlusal views of partial left maxilla with M^2–M^3, ×1.

FIG. 3, 3A-B: *Macropus (? Prionotemnus) dryas* (De Vis), F7790, lateral and stereopaired occlusal views of isolated right P^2, ×2.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Mem. Qd Mus. **18**(2): 145–9 [1978]

THE ROSTRUM IN *PALORCHESTES* OWEN (MARSUPIALIA: DIPROTODONTIDAE)
RESULTS OF THE RAY E. LEMLEY EXPEDITIONS, PART 3

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Queensland Museum

ABSTRACT

The rostral area of the skull is examined in all described species of the genus *Palorchestes* Owen and is shown to be characterized by massive dorsal excavation, associated with recorded and inferred reduction of the nasals and extreme elongation of the anterior of the palate. These features, taken in conjunction with the development of very large infraorbital foramena and the anteriorly directed facial area are interpreted as supporting a tapir-like proboscis in *P. painei* and probably in all known species of *Palorchestes*. The symphysis of the lower jaws is elongate in all forms and is narrow and deeply channelled dorsally, suggesting the presence of a long, flexible tongue which could have acted in conjunction with a proboscis in facilitating ingestion of herbage.

The genus *Palorchestes* is reasonably well-known in literature but has never been strongly represented in collections by specimens which show details of the cranial morphology. *Palorchestes* was defined by Owen (1874) as a macropodid and it was not until much later (Woods 1958) that its current systematic position within the Diprotodontidae was recognized. Three species have now been defined within the genus, these comprising the type species, *P. azael* Owen 1874, from Pleistocene sediments, *P. parvus* De Vis 1895, from the Chinchilla Sand of late Pliocene age and *P. painei* Woodburne 1967, from the Waite Formation of late Miocene or early Pliocene age.

Stirton *et al.* (1967) have attempted a phylogeny of the Diprotodontidae and have used Tate's (1948) subfamily, the Palorchestinae, for *Palorchestes* and for *Ngapakaldia* Stirton and *Pitikantia* Stirton from the Etadunna Formation of late Oligocene or early Miocene age. *Pitikantia* does not have crania preserved which present the rostral area. It is certain that *Ngapakaldia* did not have the type of cranial specialization observed in *Palorchestes*, and from what is currently known of *Pitikantia*, it is unlikely that dorsal excavation of the rostrum was a feature of that genus also.

The presence of an extensive modification to the rostral area of the skull in *Palorchestes* has been widely noted (Woods 1958; Woodburne 1967) but it was not until preparation of a near-complete cranium of *P. painei*, collected from the Waite Formation during the Ray E. Lemley expedition by the Queensland Museum in 1974, that the full extent of this structure and its possible significance became apparent. Less complete, but equally convincing material for both *P. azael* and *P. parvus* in the Queensland Museum collections also indicates the presence of comparable rostral structure in those species.

THE ROSTRUM IN PALORCHESTES PAINEI WOODBURNE 1967

A reasonably complete description of the cranium of *P. painei* is provided in Woodburne (1967). The rostral area in QMF 9179 and QMF 9178 comprises more complete material on which the following supporting and supplementary comments are provided.

The rostral area is very elongated and relatively narrow and generally tapers anteriorly in lateral view. The incisor tooth row is projected more ventrally than the horizontal plane of the cheek teeth. Although slightly incomplete, the premaxillae are broader transversely than the anterior of the maxillae giving the premaxillary alveolar margin a somewhat spatulate appearance. The palatal sutures between the premaxillae and maxillae are clearly defined, extending anterolaterally from the posterior border of the incisive foramina along their lateral borders then turning abruptly posterolaterally to the diastemal margins well posterior to the foramena, then continuing laterally, posterodorsally to near the narial notches. The premaxillae thus form broad wedges bordering the anterodorsal margins of the narial opening. Low, dorsomedial premaxillary spines are present, approximately above the level of I^2.

Ventrolateral diastemal margins are angular and the lateral surfaces posteriorly are gently concave above the margins. In occlusal view, the incisors present a broadly U-shaped outline. Dorsal margins of the thin posterior processes of the premaxillae are acute anteriorly, becoming sharply rounded and elevated to a higher angle to the horizontal. These margins are slightly rotated mesially. The anterior of the palate is moderately concave transversely with a medial sulcus extending anteriorly from the incisive foramena.

The maxillae form the bulk of the remainder of the rostrum. The palate is gently concave longitudinally posterior to the premaxillary–maxillary suture and is also concave transversely with an accentuated medial sulcus extending from the incisive foramena posteriorly to about the level of M^2. Laterally, the maxillae comprise long, deep bones wedging anteriorly to the angular diastemal margins. Towards the orbital margins, the lateral surfaces of the maxillae are sharply curved laterally, forming broad, near-vertical, transverse surfaces comprising an anteriorly directed facial region. These surround extremely large, eliptical, infraorbital foramena on each side, but that on the right side is much larger than on the left in QM F9179. However, in QM F9178 each foramen is relatively smaller. Lengths of the infraorbital canals are very short, opening posteriorly into variable, but large maxillary foramena.

The lacrymals extend moderately onto the facial region. Low frontal crests extend laterally as more pronounced 'brow' ridges, associated with the frontals, nasals and lacrymals, with the development of well-defined ventrolateral grooves anteriorly below the ridges. The nasals are very short, with nasal spines extending only slightly in advance of the narial notches.

The nasal cavity is deep anteriorly and very deep posteriorly, surrounded anteriorly by the premaxillae and posteriorly by the maxillae, premaxillae and nasals. A bony nasal septum is present posteriorly. The floor of the cavity is occupied by fragments of bone, largely representing the remains of the vomer and parts of the septum. Anteriorly, the vomer is strongly and moderately deeply, inverted T-shaped in section.

THE ROSTRUM IN PALORCHESTES PARVUS DE VIS 1895

Woods (1958) has provided a basic description of the known cranial remains of *P. parvus* and the following comments, based on QM F789, amplify that study.

The rostrum is very elongate. It is relatively broader and tapers to a greater extent anteriorly in lateral view than in *P. painei*. The premaxillae are much broader transversely than in *P. painei* but are apparently not much broader than the anterior of the maxillae. The anterior alveolar border is flat and the incisors form a nearly rectilinear occlusal surface. Anterior to moderately high, medial, premaxillary spines, the dorsal surface is considerably extended and shelf-like, curving gently laterally to the alveolar margins.

Above the level of the incisive foramena and posterlateral to the premaxillary spines, the dorsal surfaces are deeply and variably excavated, leaving sharp, thin flanges of bone lining the nasal cavity anteriorly; lateral to these excavations, the bones are more robust, being broadly rounded dorsally at the anterior of the excavations and more acute posterolaterally. The palate is broadly concave transversely at the alveolar margin, but broad, ventral protruberences occur lateral to the incisive foramena in the area of the premaxillary–maxillary suture. Diastemal margins are flanged posterior to I^3, becoming less so towards the maxillae. The premaxillary–maxillary sutures extend anterolaterally from near the posterior of the incisive foramena, then turning abruptly posterolaterally to the diastemal border and proceeding posterodorsally leaving thin wedges of bone extending as the dorsal rims of the narial opening. These wedges are considerably shallower anteriorly than in *P. painei;* the dorsal rims are somewhat directed mesially. Little of the anterior of the maxillae remains.

Although the infraorbital foramena are not preserved, part of one maxillary foramen is present, showing it to have been wide and presumably large. The infraorbital canals must have been short. The dorsal surface of the cranium is unknown, as is the anterior surface of the orbital area. No nasals are preserved, but the structure

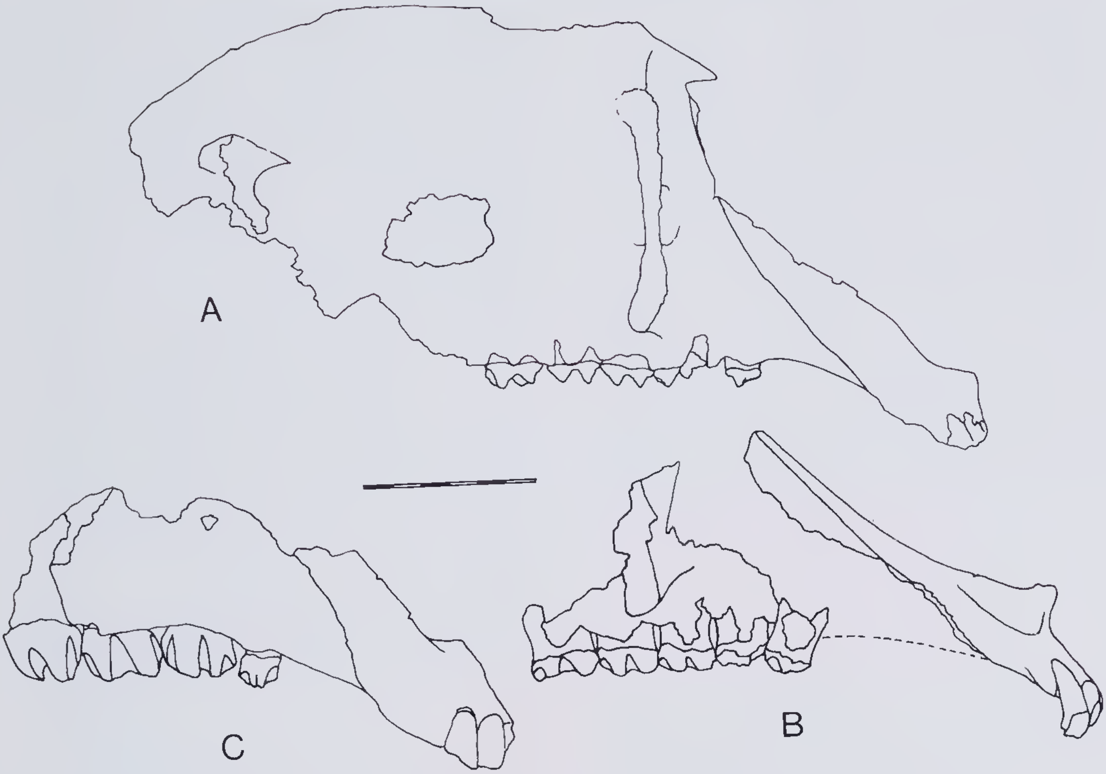

FIG. 1: Cranial remains in *Palorchestes*. A, *P. painei* (F9179), B, *P. parvus* (F789); C, *P. azael* (F3837), showing lateral extent of rostral modification. Scale in cms.

of the premaxillae suggests these must have been extensively retracted.

THE ROSTRUM IN PALORCHESTES AZAEL OWEN 1874

Owen (1874) describes the nature of the rostrum in *P. azael*. Existing descriptions are supplemented by the juvenile specimen, QM F3837.

The rostrum is elongate and relatively narrow, more like that in *P. painei* than in *P. parvus.*

The premaxillae are broad transversely, being much broader than the anterior breadth of the maxillae. The incisive alveolar border is broadly rounded and the upper incisors present a broad U-shaped occlusal outline. The medial premaxillary spines are relatively low and the dorsal surfaces anterior to these are broadly convex transversely to the alveolar margins. Posterior to I^3, the disastemal margins are flanged for a short distance, then rounded from about the level of the premaxillary-maxillary sutures. The palate is anteriorly shallowly concave transversely, with a deep, medial sulcus extending to the alveolar margin from the incisive foramena. The foramena are positioned well back and may be confluent. The premaxillary–maxillary sutures extend anterolaterally from near the posterior of the incisive foramena, then turn abruptly posterolaterally continuing posterodorsally from the diastemal margin. The posterior extensions of the dorsal parts of the premaxillae exist as broad wedges of bone capping the maxillae and bordering the narial opening, similar to those in *P. painei*. These are somewhat directed mesially. The palate has a relatively deep sulcus medially, posterior to the incisive foramena. Below the premaxillae processes, the maxillae anteriorly are laterally concave. Hollowing of the portion remaining of the facial area suggests that transverse, planar areas existed anterior to the orbits. No trace remains of the infraorbital foramena, canals or maxillary foramena. Although dorsal aspects of the skull are unknown, the nasals are interpreted as having been extensively retracted, based on the observed morphology of the premaxillae and the narial opening.

THE MANDIBULAR SYMPHYSIS IN PALORCHESTES OWEN 1874

Woodburne (1967, figs. 23–4) has illustrated a specimen with a near complete symphyseal area in *P. painei*. The area is elongate, narrow, but deeply channelled, flaring anteriorly to accommodate large I_1. The symphysis is also characterized by general down flexing of the anterior extremity of the dentaries which imparts a broadly longitudinally convex curviture to the dorsal symphyseal surface. Although this area in *P. parvus* is known only from a single specimen with no preserved teeth (QM F9180), no doubt exists regarding its identity. The structure is very similar to that in *P. painei*. In *P. azael*, a similar situation exists. The specimen QM F774, figured by Woods (1958, fig. 3), has a nearly complete symphyseal area. Although the ventral border is generally downflexed with regard to the bases of the rami, the anterior flexing present in both *P. painei* and *P. parvus* is lacking.

DISCUSSION

Although the dorsal surface of the cranium has not, as yet, been recovered in either *P. parvus* or *P. azael*, it is reasonable to assume from the known structure in *P. painei* and the morphology that is represented in the later material, that the rostral area of the skull in all three species was essentially similar. Detailed differences have been noted above, but none of these is considered to have had any marked effect on the general rostral structure or its overall functional significance.

The massive dorsal excavation of the rostrum is compatable with the presence in life of either an extensive rhinarium with anterodorsally directed nostrils or a proboscis, possibly similar to that in the eutherian tapiroids. Of these interpretations, the latter is considered most likely for the following reasons. The vomer apparently carried a cartillagenous septum well anteriorly, consistent with terminal nostrils directed anteriorly; the facial area of the skull is very flattened close to the rostrum and directed almost perpendicularly and at right angles to the axis of the skull; a prominent groove is present below the 'brow' ridge and this, together with the preceeding point are both features presumably associated with the implantation of strong muscles; the variable, but large size of the infraorbital foramena, infraorbital canals and maxillary foramena are associated with the passage of an expanded infraorbital artery, vein and nerve, sufficient to supply a structure much larger and more functional than a rhinarium.

The degree of convergence with eutherian animals like tapiroids and litopterns is only superficial and *Palorchestes* has achieved its specialized cranial structure largely through modification of the premaxillae, rather than through maxillary modification. The deep, curved sulcus around the narial notch in *Tapirus* has been only partly achieved in *Palorchestes*, while the rounded smooth anterodorsal aspect of the premaxillae has not been duplicated at all. Nasals in *Palorchestes* are retracted to a greater extent than in *Tapirus* suggesting that any proboscis in *Palorchestes* was not as well supported.

FIG. 2: Reconstruction of head of *Palorchestes*, based mainly on *P. painei*.

Retraction of the nasals in marsupials has also been reported by Bartholomai (1973) in the macropodids *Protemnodon roechus* Owen and possibly also *P. brehus* (Owen). These animals, however, are presumed to have possessed large rhinaria rather than functional proboscises.

The morphology of the mandibular symphysis in *Palorchestes* suggests that the tongue must have been long, narrow and flexible. Associated with the long diastema and the possible presence of a proboscis, these features would have been of benefit to *Palorchestes* in the gathering and ingestion of herbage before cropping by the broad series of upper and lower incisors.

The apparent consistency of these features and the peculiarity of the rostral morphology in particular, in *Palorchestes* suggest that the ancestry of *Palorchestes* was probably not associated with either *Ngapakaldia* or *Pitikantia* from the late Oligocene or early Miocene Etadunna Formation (Stirton 1967). Presumably these forms are closer to the generalized structural ancestors from which all three genera had evolved independently.

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AN UNDESCRIBED SPECIES OF ROCK DWELLING *CRYPTOBLEPHARUS* (LACERTILIA: SCINCIDAE)

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ABSTRACT

A new species of *Cryptoblepharus (C. fuhni)* is described from granite boulders of the Melville Range, near Cape Melville, northeastern Queensland, and is compared with its nearest relatives *C. virgatus* and *C. litoralis.*

The genus *Cryptoblepharus* Wiegmann was resurrected and redefined by Fuhn (1969a, b) to contain a single species, *C. boutonii* (Desjardin), and its twenty-one subspecies. These subspecies included *C. boutonii virgatus* which had been described as *Ablepharus virgatus* from Cooktown, north-eastern Queensland (Garman 1901). *Ablepharus boutonii litoralis* had been described from the Innisfail area by Mertens (1958). Cogger (1973, 1975) elevated it to specific status *(C. litoralis)* following Arnold's (1966) suggestion. Cogger has treated *virgatus* as a subspecies of *C. boutonii* noting that —'. . . some (subspecies) may represent distinct species while others may be minor variants . . .' (p. 258). Storr (1976) has treated *Ablepharus boutonii clarus* (Storr 1961) from south-western Western Australia as *Cryptoblepharus virgatus clarus*, considering *C. virgatus* from eastern Australia a distinct species because this form and the Mauritius *C. boutonii* (Desjardin) were unlikely to be conspecific, confirming Garman's original description of the species. In north-eastern Queensland, two species of *Cryptoblepharus, C. virgatus* and *C. litoralis,* are currently recognised.

In November 1970, one of us (JC) working with C. Tanner and T. Tebble observed a strikingly marked, dark *Cryptoblepharus* common on the black rocks of the exposed boulders of the Melville Range, Cape Melville, Cape York Peninsula, north-eastern Queensland. The lizards were very agile and alert and could be collected only with the aid of a pistol and dust shot.

A typical specimen of *C. virgatus* (QM J20565) was collected at the same time on a tree growing amongst the boulders on which the dark *Cryptoblepharus* was common. The latter differs from both *C. virgatus* (with which it is synchronosympatric) and *C. litoralis* (which occurs only on the foreshore in north-eastern Queensland and New Guinea) meristically, and in colour, pattern, and external morphology. No other members of this genus have the striking achromatic pattern of *C. fuhni.* Differences observed are sufficiently distinct to warrant recognition of this skink as a new species, *C. fuhni. C. fuhni* is named to acknolwedge the contribution to herpetology of Dr Ion Fuhn.

Cryptoblepharus fuhni

Holotype. QM J20566 Melville Range, Cape Melville, Cape York, NE.Q. (14°16'S, 144°30'E). Collected J. Covacevich, C. Tanner and T. Tebble, 30 Nov 1970.

Paratypes: QM J20515–6, J20567–71, same data s holotype.

Diagnosis

A long-legged, rock-dwelling *Cryptoblepharus* distinguished from all other species of *Cryptoblepharus* by its striking achromatic pattern of white spots and dashes on a black background (Fig. 1a). *C. fuhni* may be distinguished further from *C. virgatus* by midbody scale count (23–26 *vs* 20–23) and number of lamellae under the fourth toe (22–26 *vs* 19–22); and from *C. litoralis* usually by the number of lamellae under the fourth toe (22–26 *vs* 20–22). See fig. 1a, b, c and Table 1.

DISTRIBUTION

Known only from the granite boulder 'black' mountains of the Melville Range, Cape Melville, north-eastern Queensland.

DESCRIPTION OF HOLOTYPE

Snout–vent length (mm) 46·0. Head width (%SVL) 7·0. Hind limb length (%SVL) 25·0. Tail lost. No supranasals, but nasal scales divided.

Fig. 1: A. Cryptoblepharus fuhni (J20569, on granite boulders, Melville Range, Cape Melville, NE.Q.)
B. *Cryptoblepharus virgatus* (J20565, on tree, Melville Range, Cape Melville, NE.Q.)
C. *Cryptoblepharus litoralis* (J20434, on granite boulders, Lizard Island, NE.Q.)

Rostral and frontonasal in broad contact. Prefrontals large, meeting with a medium suture, contacting the frontonasal, anterior and posterior loreals, first supraciliary, first supraocular and frontal. Anterior and posterior loreals large, subequal. Frontoparietals and interparietal fused, forming a large kite-shaped scale with a narrow anterior half. Parietals large, forming a medium suture along midline. Four large supraoculars, the second ones the largest which just touch in the midline. Supraciliaries five on each side, the first the largest. Three enlarged upper ciliaries forming a hood over top of large transparent palpebral disc. The latter covers nearly all the eye. No moveable eyelids. Palpebral disc completely surrounded by three rows of small scales except for upper margin where there is only one row between disc and upper ciliary hood. Seven upper labials, fifth subocular. Six lower labials. Ear aperture obvious (0·6 mm wide), tympanum sunken, small rounded lobules around edge. Eight preanal scales, central pair enlarged. Limbs

TABLE 1: COMPARISON OF COLOUR, PATTERN, BODY PROPORTIONS, AND SCALE COUNTS OF *C. fuhni*, *C. virgatus* AND *C. litoralis*

Feature		Species	
	C. fuhni (fig. 1a)	*C. virgatus* (fig. 1b)	*C. litoralis* (fig. 1c)
colour and pattern	black basically with a striking pattern of white spots and dashes which vary in size and which form two paravertebral lines from neck to tail base; lamellae and palmar surfaces black.	brown basically with well defined white latero-dorsal lines from nostril to tail; two black paravertebral lines and a brownish vertebral line; head copper brown; laterally black with white speckling; lamellae and palmar surfaces white.	black basically with grey-green speckling and blotches which may form indistinct laterodorsal bands; white speckles present dorsally and laterally and on legs and tail; lamellae and palmar surfaces black.
hind leg length % SVL	minimum 51.4	maximum 43.8	maximum 48.4, 39.02 (Mertens, 1958)
mean head % SVL	14.2	13.8	13.2
mid body scale rows	23–26	usually 20–23, 20 (Garman, 1901)	23–28, 24–28 (Mertens, 1958)
lamellae under 4th toe	22–26	19–22	20–22, 18 (Range not described by Mertens 1958)

pentadactyl, well developed and greatly overlapping when adpressed. Toes long. Subdigital lamellae black, undivided and smooth, 24 under fourth toe. Palmar tubercles black and rounded. Midbody scales in 24 rows. Dorsal, lateral and ventral scales smooth; dorasls larger than ventrals which are larger than laterals. Colour in preservative, a contrasting achromatic pattern of white spotting and dashes on a black ground colour. Head black with brownish white speckling, labials flecked with larger speckles. Dorsal surface of neck, trunk and tail black with a series of spots and large dashes forming dorsolateral lines beginning at back of eye and continuing down tail; also two series of smaller dashes forming two paravertebral lines from neck to base of tail. Lateral surface of neck and trunk, black with a series of small spots and dashes forming parallel lines; these become a series of large dots down tail. Dorsal and lateral surfaces of legs and toes black with crossing barrings of white dots. Ventral surface cream, except for hands and feet which are black.

Description of Paratypes

As for the holotype except as follows:

Snout–vent length (mm): 35–47 (N = 7, $\bar{x}$ 40·6, SD 4·58). HW (%SVL): 13·s–15·6 (N = 5, $\bar{x}$ 14·2, SD 0·88). Lenth of hind limb (%SVL): 51·4–57·5 (N = 7, x 54·2, SD 2·07) tail length (%SVL): 158 (N = 1). Midbody scale rows 23–26 (N = 7, $\bar{x}$ 24·1, SD 1·46). In three of the paratypes the frontal narrowly contacts the fused interparietal-frontoparietals but in J20569 the second supraoculars form a short suture in the midline. In the smaller paratypes there is a tendency for the dorsolateral dashes to join to form lines, and for the head and lateral surfaces to be suffused with brown.

Comparison with other Closely Related Species *

C. fuhni may be distinguished from *C. virgatus* and *C. litoralis* by colour, pattern, body proportions and external features. These features are summarised in Table 1.

Remarks

Description of *C. fuhni* brings the number of known lygosomid skinks restricted to bare boulder habitats to six in Queensland. These are *Carlia coensis* (Mitchell), *C. mundivensis* (Broom), *Carlia* spp. nov. (two species, Ingram and Covacevich, pers. observ.), *Lampropholis* sp. nov. (Rawlinson, pers. comm.) and *Cryptoblepharus litoralis.* These lygosomid skinks share most of the following characters when considered in relation to their congeners: high number of midbody scales; large size; black or near black colour, often with whitish dashes or flecks; habit dorsoventrally flattened; prominent eyes; large supraoculars; long limbs and digits; high lamellae count for fourth toe; black palms and lamellae; agility and fast movement. All species are posturing heliotherms (*sensu* Rawlinson, 1974). They do not emerge from crevices and caverns until ambient temperatures are high (usually between 9–10 am) and they thermoregulate by changing body posture while resting on exposed basking sites. They forage in the sunlight and when temperatures are too high (towards noon), basking ceases and foraging may be continued in shaded areas. During the hottest part of the day skinks are usually inactive, sheltering until late afternoon when a brief search for food is usually resumed.

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*based on ten specimens of *C. virgatus* and *C. litoralis* (including topotypes) from the Queensland Museum reference collection and on the type descriptions of these two species.

Mem. Qd Mus. **18**(2) 157–64 [1978]

THE NATURE OF THE MOLAR-PREMOLAR BOUNDARY IN MARSUPIALS AND A REINTERPRETATION OF THE HOMOLOGY OF MARSUPIAL CHEEKTEETH

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ABSTRACT

Recent studies of dental ontogeny and abnormalities in marsupials indicate that all systems of homology in current use are incorrect, in part because all are based on the evidently erroneous assumption that true post-canine tooth replacement occurs in marsupials.

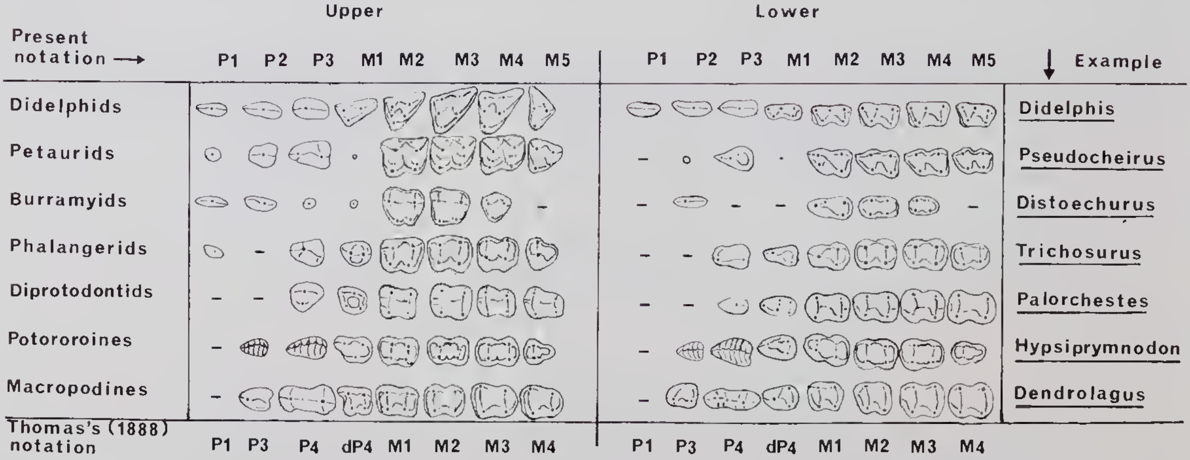
A new terminology is presented which accounts for all morphological and ontogenetic data, including the apparent phenomenon of Zahnreihen in dasyurid dentitions. This concept is three premolars, P1–3, a deciduous first molar, M1, and four permanent molars M2–5. Marsupials are therefore regarded to have three premolars, five molars, and no true post-canine milk-teeth. Some marsupials and in particular some kangaroos have six or more molars but these have been additions to the posterior end of the molar series.

Owen (1840–5) introduced stability into dental terminology by defining premolars as those post-canine teeth anterior to, and including, the posterior-most tooth having a milk-tooth predecessor. Teeth posterior to this tooth were regarded as molars. Application of this concept to marsupials has been complicated by interpretation of ontogenetic evidence. Spurious swellings along the free edge of the dental lamina have sometimes been interpreted as incipient or vestigial tooth buds representing replacement teeth. These interpretations have often given rise to conflicting terminologies. More recently, ontogenetic studies (Berkovitz 1967a, Archer 1974) of structurally primitive marsupials have confirmed earlier research (e.g. Woodward 1893) suggesting that the replaced tooth, M1 (in the terminology used here, but dP4 in the terminology of Thomas 1888, Table 1) does not give rise to the tooth germ of the replacing tooth P3 as it should if it were a member of the P3 premolar tooth family. For this reason, it has been suggested (Archer 1974) that cheekteeth in dasyurid marsupials cannot be classified as premolars or molars using Owen's (1840–5) system, and that recognition of Zahnreihen (in the sense of Woerdman 1921) or tooth developmental sequences may provide a means for classification of marsupial teeth independent of the phenomenon of tooth replacement.

Examination of marsupial groups reveals many differences in dental morphology and patterns of tooth development. An attempt has been made here to clarify these patterns using tooth morphology and ontogeny and to interpret homology of cheekteeth.

Terminology of crown morphology is set out elsewhere (Archer 1975a, 1976b, 1976c) or, if different from this, follows Bensley (1903) and Stirton (1967). Terminology of post-canine cheektooth number follows in part Owen (1845) and Stirton (1955), and not Thomas (1888) whose system I have previously used. It differs from Stirton's nomenclature in that the deciduous post-canine cheektooth is called M1. The nomenclature used here is therefore P1–3, M1, and M2–5. Owen (1845) and Stirton (1955) regard that there are three adult premolars, P1, P2, and P3, and the deciduous tooth in the cheektooth row of polyprotodonts is called dP3 (see Table 1). This deciduous tooth is called M1 in this paper. Marsupial names are used in the sense of Ride (1970), Laurie and Hill (1954), Clemens (1966), and Kirsch (1968). Specimen number prefixes used are as follows: J, JM, or F, Queensland Museum.

TABLE 1: POSTCANINE CHEEKTOOTH NOMENCLATURE USED IN THIS WORK, AND THAT OF THOMAS (1888) USED IN PREVIOUS WORKS, WITH DIAGRAMS OF UPPER AND LOWER CHEEKTEETH OF SEVEN REPRESENTATIVE MARSUPIAL GROUPS.



Present notation →	Upper: P1 P2 P3 M1 M2 M3 M4 M5	Lower: P1 P2 P3 M1 M2 M3 M4 M5	↓ Example
Didelphids			Didelphis
Petaurids			Pseudocheirus
Burramyids			Distoechurus
Phalangerids			Trichosurus
Diprotodontids			Palorchestes
Potororoines			Hypsiprymnodon
Macropodines			Dendrolagus
Thomas's (1888) notation	P1 P3 P4 dP4 M1 M2 M3 M4	P1 P3 P4 dP4 M1 M2 M3 M4	

TABLE 2: NOTATIONAL SYSTEMS FOR MARSUPIAL POST-CANINE CHEECKTEETH INFERRED FROM ONTOGENETIC STUDIES AND COMPARED WITH THOMAS (1888).

Author									Group examined
Thomas (1888)	P1	P3	P4	dP4	M1	M2	M3	M4	Marsupials
Berkovitz (1967)	P1	P2	P3	M1	M2	M3	M4	M5	Didelphids
Archer (1974)	P1	P2	P3	M1	M2	M3	M4	M5	Dasyurids
Wilson and Hill (1897)	P1	P2	P3	dP3	M1	M2	M3	M4	Peramelids
Berkovitz (1968)	P1*	P2	P3	M1	M2	M3	M4	M5	Phalangerids
Bolk (1929)	P1	P2	P3	M1	M2	M3	M4	M5	Phalangerids
Berkovitz (1966)	P1	P2*	P3	M1	M2	M3	M4	M5	Macropodids

*Initiate but do not form part of functional dentition.

ONTOGENY

Recent ontogenetic work (Table 2) has revealed that in the dasyurid *Antechinus flavipes* there appear to be eight post-canine tooth families each of which has only one generation (Archer 1974). They develop in a time sequence as two distinct series: P1, P2, P3; and M1, M2, M3, M4, M5 (P1, P3 P4, dP4, M1–4 of Archer 1974). These series or Zahreihen are also morphologically uniform such that the teeth of the first are premolariform and those of the second molariform. Berkovitz (1967a), similarly demonstrates that in at least one didelphid, the tooth regarded here as P3 develops from the dental lamina between P2 and M1 and is therefore not a replacement tooth for M1.

Berkovitz (1966) also shows that a similar situation exists in at least one macropodid. It may also occur in one phalangerid (Bolk 1929, Berkovitz 1968) but the evidence is not clear. Kirkpatrick (1969) demonstrates a developmental relationship between the teeth regarded here as M1, M2, M3, M4 and M5 in several macropodids, and an apparently close relationship between P2 and P3. He suggests M2–4 are successional teeth in the M1 family.

These studies demonstrate M1 to be part of a molariform cheektooth series and evidently unrelated to P3 in at least three marsupial families, including didelphids and dasyurids which are structurally ancestral to other marsupial groups.

MORPHOLOGY

Bensley's (1903) important examination of marsupial cheektooth morphology serves as a basis for further comparisons, and in particular, a closer examination here of the P2, M1, P3, M2 region. Ride (1961) realizes the importance of this region in determining cusp homology in macropodids and it also seems to be the important region in interpreting homology in macropodid and phalangerid cheekteeth.

To avoid lengthy descriptions, the juvenile and adult P1–M5 region of the dentition of representative marsupials are shown in outline form in Table 1 and attention is given below only to particular aspects of these dentitions.

INDIVIDUAL CHEEKTEETH
(P2, P3, M1, M2)

P2: Because there has been no satisfactory demonstration of more than three premolars in marsupials, it is possible that P2, in all marsupials with three premolars in the adult dentition, are homologous teeth. In dasyurids with less than three, it is always P3 which has been lost (Archer 1976a). In phalangeroids with less than three upper premolars (e.g. phalangerids, macropodids, and diprotodontids) homology of the anterior premolar is uncertain. Berkovitz (1966) demonstrates that in at least one macropodid the anterior adult premolar is the second of three teeth to develop on the dental lamina posterior to the canine. The first tooth develops but later disappears. However, Berkovitz (1968) demonstrates that in at least one phalangerid, the anterior adult premolar is the first of three to develop on the dental lamina posterior to the canine. The second tooth develops but does not persist. Homology of lower antemolar teeth in phalangeroids is extremely uncertain, most early ontogenetic studies having misinterpreted true milk incisor teeth for vestigial tooth families (e.g. Woodward 1893).

Kirkpatrick (1969) has examined tooth development in some macropodids and concludes that P2 is a milk-tooth which is later replaced by P3, a second generation tooth in the P2 tooth family. This view is not supported by other ontogenetic studies on macropodids such as those of Berkovitz (1966) where P3 develops from the dental lamina between P2 and M1. The interpreted differences may result from post-initiation degenerative changes in the dental lamina or by shifts in relative position due to migration of tooth buds or development of the free edge of the dental lamina. Before the actual homologies of P2 and P3 in macropodids can be determined, ontogenetic studies should be carried out on potoroine macropodids where P2 and P3 are large and the possible masking effects of tooth migration are reduced.

Morphology of P2 in all marsupials in which it has not been lost is either premolariform or caniniform. In some potoroine macropodids, and some caenolestoids, it is a plagiaulacoid sectorial tooth. In *Phalanger* it is caniniform. In no group is it molariform.

P3: Ontogenetic evidence in didelphids, dasyurids, phalangerids, and macropodids suggests P3 is the posterior member of a premolariform Zahnreihe. It develops from the dental lamina anterior to M1 and posterior to P2. Abnormal teeth interpretable (Archer 1975) as P^4 (P5 of Archer 1975) in some macropodids, and inferred to develop posterior to P^3 on the dental lamina, are also premolariform.

Morphologically, P3 is never molariform although the posterior end may become secondarily molarized in quadritubercular or lophondont forms such as phascolarctids, macropodids, and diprotodontids. In potoroine macropodids, caenolestoids, some burramyids and incipiently in some phalangerids, P3 tends towards or is a well-developed plagiaulacoid sectorial tooth. Broom (1896) suggests the sectorial premolars of *Burramys* (a burramyid) and *Hypsiprymnodon* (a macropodid) are completely unlike those of phalangerids because the serrations are on opposite ends of the tooth. This observation seems of little import in view of the fact that in other macropodids (e.g. some *Bettongia* and *Potorous*) the serrations occur in the middle of the tooth without actually reaching the anterior end. In some of these forms (as noted by Ride 1956) the smooth anterior portion of the sectorial premolar is longer than the smooth posterior portion, the opposite of the condition found in *Hypsiprymnodon*. In caenolestoids a comparable range of morphology suggests position of serrations is not significant in diagnosing groups above the generic level.

M1: Ontogenetic studies (Archer 1974) of dasyurids suggest that M1 (called dP4 by Archer 1974) is the most anterior member of a posterior molariform Zahnreihe which includes M1–M5. Kirkpatrick (1969) has similarly suggested that M1 and M2–5 (his dP4 and M1–4) in macropodids develop as related series of teeth, although he does not interpret the relationship as a Zahnreihe. Sequence of tooth development in the macropodid *Setonix* noted by Berkovitz (1966) is similar to that in dasyurids.

From a survey of M1 morphology (to be published), it is also apparent that these teeth, in all marsupials in which they are not reduced to vestiges, although rarely premolariform, are frequently molariform. Therefore morphology and ontogeny is used here to conclude that the marsupial deciduous cheektooth is actually the first molar, i.e. M1, there being no true post-canine tooth replacement. In contrast is the more traditional view of Owen (1840–5) and most later workers who believe that this tooth is a true milk-premolar that secondarily has become molariform. Indirect evidence for Owen's view is the well-known fact (e.g. Butler 1952) that in many eutherian groups dP3 has undergone molarization to either increase the number of functional molariform teeth in juveniles, or to shift anteriorly the molariform–premolariform boundary. I do not think this is the case in marsupials for four reasons. First, the oldest known (Cretaceous) marsupials have an extremely well-developed molariform M1 (e.g. Clemens 1966) which might not be the case if molarization of a deciduous premolar was a secondary development unless secondary molarization occurred extremely early in primitive marsupials. Secondly, except for didelphids, macropodids, and some phalangerids, the marsupial M1 is almost invariably too small to be functional and it seems improbable that it would secondarily evolve molariform characters when it never really has a chance to function as a molar. In at least some modern didelphids (Archer 1976) M1 is comparable in complexity to the same tooth in Cretaceous didelphids, thereby providing no evidence for secondary molarization. In macropodids it is probable that M1 has become secondarily molarized, but there is no evidence that this process of molarization in macropodids started with a premolariform M1. Third, there appears to be a repetitive basic crown pattern in M1 in distantly related groups including some dasyurids, phalangerids, and diprotodontids which suggests the possibility that an 'archetypal' molariform pattern may persist rather than develop polyphyetically in teeth which are free from heavy selective pressure. Fourth, recent ontogenetic evidence indicates M1 is part of the molariform tooth series and not a predecessor to P3.

The improbability of a tooth family relationship between M1 and P3 is further indicated by the various ways in which tooth reduction occurs in this position. In many dasyurids, thylacinids, peramelids, and diprotodonts such as phascolarctids and Petaurids (Archer 1975), M1 is tiny or absent while P3 is large. Yet in other diprotodonts such as some phalangerids, M1 is only slightly smaller than P3, and in macropodine macropodids, M1 is markedly larger than the small P3. Ziegler (1971) has suggested that in mammals in general reduction of premolar number occurs first by loss of the permanent tooth and only later by loss of the deciduous tooth. For this reason, the inconsistent pattern of tooth reduction in marsupials would suggest there is no true milk-tooth in the postcanine cheektooth row.

Morphology of M_1 in potoroine macropodids is similar to that of M_2 in many non-macropodid diprotodonts such as *Phalanger* and *Trichosurus*. Broad aspects of this similarity have been noted by Bensley (1903) and Ride (1961) both of whom regard it as occurring in non-homologous teeth in the two groups. Ride (1961) also regards the cusps involved in the compressed trigonids of these similar teeth to differ. The principal cusp on the trigonid of M_2 in phalangerids (see below) is regarded here (and by Ride 1961) to be the protoconid. However, Ride (1961) regards the principal cusp of M_1 in *Hysiprymnodon* to be the metaconid, a conclusion based on his interpretation of a small cupsule on the posterior slope of the main cusp as the protoconid, and of the apparent topographic serial homology of this cuspule with a cuspule on M_2 in the position of a protoconid. If Ride is right, the apparent similarity between M_2 of phalangerids and M_1 of macropodids is the result of convergence. It is suggested below that the anterobuccal cusp on M_2 of petaurids and phascolarctids is, as Bensley (1903) concludes, a neomorph or protostylid, the protoconid having shifted lingually. Phascolarctids are also regarded by some authors (Winge 1941, Archer 1976) as structurally ancestral to other diprotodonts. Therefore it is possible that the anterobuccal cusp in M_2 of *Hypsiprymnodon* (and other macropodids) is the homologue of the phascolarctid protostylid, and not the protoconid. The tiny cusp observed by Ride (1961) on M_1 of *Hypsiprymnodon* may be the serial homologue of this protostylid, the high cusp on that tooth again being the protoconid. The compressed condition of the trigonid of M_2, and relatively slight development of the anterobuccal cusp in *Hysiprymnodon* might then be regarded as structurally ancestral characters. Pressure to molarize M_2 and M_1 has resulted in enlargement of this cusp in M_2 of all and M_1 of most other macropodids.

Further support for the possibility that the protoconid is anterolingual on trigonids of M_1 in macropodids is provided by Berkovitz (1967b). In an ontogenetic study of crown development in *Setonix* he shows that although the anterobuccal cusp of M_2, interpreted by him to be the protoconid, develops first, the anterolingual cusp of M_1 develops first. Accepting Ride's (1961) interpretation of this cusp as the metaconid, Berkovitz concludes that ontogeny of M_1 in *Setonix* is not therefore recapitulating phylogeny because the protoconid is generally regarded as the original trigonid cusp. Although the principal of ontogeny recapitulating phylogeny in marsupial tooth cusps has been questioned elsewhere (Archer 1975), in the present case the early development of the lingual cusp is more consistant with its interpretation as a protoconid than a metaconid.

Although these points are made in order to indicate that the cusps of molariform teeth with compressed trigonids in different groups of diprotodonts may be homologous, it does not necessarily indicate that the teeth themselves are homologous.

M2: Previous confusion in interpretation of M_2 cusp homology has resulted from examination of worn molars. Ride (1961) points out that Bensley (1903) must have had only worn specimens of *Hypsiprymnodon* resulting in his failure to correctly interpret the number of cusps on M_2. Ride (1961) and Bensley (1903), however, seem to have had only worn specimens of *Phascolarctos*. Because I regard the morphology of *Phascolarctos* to be basic to at least an understanding of other diprotodont groups (Archer 1976), it is of interest here to briefly describe the morphology of its M_2 (e.g. J13278). The tooth have five principal cusps forming apices of crests. The talonid has a buccal hypoconid and a lingual entoconid. The cristid obliqua crosses from the hypoconid to the tip of the tallest trigonid cusp, the protoconid. This cusp is just lingual to a medial position on the trigonid. The protoconid is connected by a posterolingual crest to the metaconid. A paracristid extends anteriorly from the protoconid to the anterior end of the tooth, the topographic position of a missing paraconid. Buccal to the cristid obliqua, protoconid, and paracristid, a well-developed accessory crest, with a neomorphic cusp at its apex, extends from the anterior base of the hypoconid to the anterior tip of the tooth. Bensley (1903) suggests that this anterobuccal cusp is a new development and not homologous with the protocone of succeeding molars. I entirely agree, and do not regard this interpretation as a violation of the concept of serial homology, which leads Ride (1961) to suggest that the only cusp he observes on the anterolingual end of M_2 is the metaconid and the anterobuccal cusp is the protoconid. Ride also regards the anterobuccal cusp in *Pseudocheirus*, which is smaller, to be the protocone. Here again, details of unworn molars as well as a comparison of the M_2 of most species of *Pseudocheirus*, make it reasonably clear that the anterobuccal cusp in *Pseudocherus* is the homologue of the protostylid in *Phascolarctos* and not the protoconid. In *Pseudocheirus*, as in *Phascolarctos*, the protoconid is the high anterolingual cusp, with a posterolingual, variably cuspid crest representing the metaconid.

The M_2 of *Hypsiprymnodon* differs from that tooth in phalangerids, phascolarctids and petaurids, but is adequately illustrated and described by Ride (1961). In other macropodids, morphology of M_2 is similar to *Hypsiprymnodon* but lacks the slight lateral compression of the trigonid.

It is clear that in all macropodids the anterobuccal cusp on M_{3-5} is the protoconid, as concluded by Ride (1961). The alternative view, proposed by Bensley (1903), that this cusp is the homologue of the phascolarctid protostylid of M_2, is not acceptable. However, Ride's conclusion that there is no evidence for suggesting M_2 in macropodids was ever other than quadritubercular, is doubtful because the anterobuccal cusp on M_2 may not be the protoconid.

M_2 of all diprotodonts except most macropodids and all diprotodontids has a laterally compressed trigonid. As a result of this compression, the paracristid assumes a longitudinal orientation by lingual displacement of the protoconid. In almost all diprotodonts, the degree of compression correlates with the degree of sectorial development of P_3. A culmination of this trend may be seen in thylacoleonids where the trigonid of M_2 is a massive, longitudinal shearing crest. The opposite extreme is found in some diprotodontids and macropodids where P_3 is frequently almost round and tubercular and the trigonid of M_2 lacks any compression. The fact that in *Phascolarctos* attempts to molarize the M_2 trigonid result in development of a new cusp, rather than a buccal shift of the protoconid, indicate the stability of the laterally compressed trigonid in diprotodonts. In polydolopid (and possible abderitine) caenolestoids, the compressed trigonid of M_2 is not clearly formed in the same way as it is in diprotodonts. The analogue of the short longitudinal paracristid may be a new development unrelated to the actual positions of the protoconid and paraconid.

CONCEPTS OF CHEEKTOOTH HOMOLOGY IN POLYPROTODONT MARSUPIALS

As indicated above from ontogenetic and morphologic data, dasyurids and didelphids have eight postcanine cheekteeth which are most appropriately interpreted as P1–3, M1 and M2–5 (where M1 is the nomeclatural equivalent of the dP3 of Stirton 1955). There is nothing about perameloids to suspect they differ from this basic polyprotodont pattern. Wilson and Hill (1897) have shown that P3 appears to develop from dental lamina lingual to the developing M1 but their data do not show that it could not be comparable with the dasyurid situation described by Archer (1974) where P3 appears to develop from the dental lamina between P2 and M1, and only secondarily comes to lie lingual to M1 as the tooth buds grow and crowd the developing tooth row as a whole.

Stirton (1955) employs the tooth nomenclature P1–3, dP3, M1–4. This nomenclature is also used by almost all modern Americans (e.g. Woodburne, Tedford, Clemens, Marcus, Lillegraven, Campbell) as well as by some Australian zoologists (e.g. Bartholomai, Marshall, Plane) who do not follow Thomas (1888). Although based on the concept of tooth replacement, it purports to avoid implying that a particular premolar tooth family has been lost in marsupials. As Mahoney and Ride (1975) point out, no system of numbering can avoid implying homology, and it could be concluded from Stirton's terminology that marsupials have lost the original P4 of their common ancestor with placental mammals, even though Stirton did not intend to imply this concept.

The common alternative is the system of Thomas (1888) which is P1, P3-4, dP4, M1–4. It is used by many zoologists in Australia and England (e.g. Ride, Archer in previous works, Mahoney, Berkovitz, Merrilees, etc.) and some American zoologists (e.g. Tate). Because of its wide use among Australian zoologists, I adopted it in earlier works. However, it is based on two apparent misconceptions: that the homologue of the placental P2 is missing from the marsupial tooth row (the lack of acceptable evidence for this is reviewed by Archer 1974, 1975); and that M1 (dP3 of Stirton) is a true milk-tooth.

Ziegler (1971) also accepts the apparently erroneous concept of cheektooth replacement in marsupials, but differs from Thomas (1888) in regarding marsupials to have lost P1, accordingly designating the functional adult premolars P2, P3 and P4. Lundelius and Turnbull (e.g. 1973) also use this system but regard homology of P2 to be doubtful.

Reasons for not accepting any current concept of loss of a particular premolar family in structurally primitive marsupials are given elsewhere (Archer 1975). Although it does seem probable that ancestral marsupials lost a premolar family which they must have shared in their common ancestor with placentals, there is as yet no conclusive morphological, ontogenetic, or palaeontological evidence for this loss.

CONCEPTS OF CHEEKTOOTH HOMOLOGY IN DIPROTODONT MARSUPIALS

Reports of the significance of residual lingual and spurious buccal traces of dental lamina in diprotodonts are not considered here. They are adequately reviewed by Berkovitz (1966) who concludes that most lingual downgrowths are merely residual free ends of dental lamina and do not represent vestigial replacement teeth.

In all diprotodont marsupials there are fewer teeth in the total dentition than in any polyprotodont. Most of the reductions in number involve incisors, canines and premolariform teeth. Petaurids have the highest diprotodont tooth number and, at least in their upper postcanine cheekteeth, the number is identical with polyprotodont marsupials. Further, they show the same manner of apparent tooth replacement as polyprotodonts. They differ from most polyprotodonts in that the M^1 is very tiny (Archer 1975). In some other diprotodont families, such as the diprotodontids and phalangerids, M^1 is much larger and functional. Therefore in at least these diprotodont groups, morphological as well as the limited ontogenetic data support the cheektooth homology of P1–3, M1, M2–5.

Macropodid diprotodonts are unique among marsupials in that P3 during eruption replaces the teeth regarded here as P2 as well as M1. This raises the possibility that the macropodid M1 is not homologous with M1 of other marsupials, a possibility however which is negated by the ontogenetic evidence that in macropodids, as in all marsupials, M1 is the first molar. Similarly, comparisons of the phalangerid M_2 with the macropodid M_1 reveal at least a basically similar trigonid construction and could be regarded as evidence that the teeth are homologous. However, if these two teeth were regarded as homologues, it would be necessary to ignore the ontogenetic data which indicates that the macropodid M_1 is a first molar and the phalangerid M_2 is a second molar. The posterior deciduous cheekteeth in the two groups, i.e. M1, also show similarities in trigonid construction and if these teeth are regarded as homologues, there is no conflict with ontogenetic data.

In summary, there is no evidence for suggesting that the homology of the cheekteeth in diprotodont marsupials differs from that of polyprotodont marsupials. Even kangaroos, with their unique number of deciduous cheekteeth, lack any true postcanine milkteeth and are thus essentially similar to other marsupials.

CAENOLESTOIDS

There is no evidence for apparent tooth replacement in living caenolestids in over 150 specimens of *Caenoloestes*, *Orolestes* and *Rhyncholestes* examined by the author in museum collections. Similarly, there does not appear to be any evidence for tooth replacement in the great variety of known fossil caenolestoids, including those forms with large plagiaulacoid premolars. If tooth replacement of the sort which occurs in other marsupial orders does occur in caenolestoids, it must occur very early in ontogenetic development. Assuming this is the case, the maximum caenolestoid postcanine cheektooth dentition would be P1–3, M1 (not yet observed), M2–5. If tooth replacement does not occur, then it is possible that caenolestoids represent a unique order of marsupials all members of which have no more than seven postcanine cheekteeth.

DISCUSSION

All morphologic and ontogenetic evidence in polyprotodont and diprotodont marsupials leads to the conclusion that there are three premolar tooth families and five molar tooth families the first of which is deciduous.

This conclusion has brought me to an impasse. If these data are acknowledged but not used, there is a possibility that in using an alternative and less probable system, comparisons of particular teeth within the various marsupial groups and between marsupials and placentals may be meaningless.

For this reason, although I have previously used the system of Thomas (1888), I intend to use the nomenclature P1–3, M1, and M2–5 until it is shown to be wrong or less probable than an alternative system.

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RECENT LOCAL FAUNAS FROM EXCAVATIONS AT HERVEYS RANGE, KENNEDY, JOURAMA, AND MOUNT ROUNDBACK, NORTH-EASTERN QUEENSLAND

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ABSTRACT

The non-human remains from four excavations carried out by H. Brayshaw in north Queensland are identified. Bone damage noted is interepreted to be caused by smashing, charring, cooking, chewing, rodent gnawing, insect and soil damage, manufacture into tools, and possibly incision.

Human remains suggest cannabilism. Humans included in the deposits are generally juvenile, but do not appear to represent a normal mortality curve. As a result, it is suggested that there was killing with a selective bias. There also appears to be a selective bias in the particular human skeletal elements present.

One animal from the Herveys Range deposit represents a diprotodont marsupial evidently unknown to European zoologists. Other vertebrate species represent those found today in sclerophyl forest, savannah woodlands with rocky areas, and streams. Except for large bats, volant and gliding animals, such as marsupial gliders and birds, are unexpectedly absent. Kangaroos are the most abundant animals represented in the deposits.

As part of a regional archaeological survey four small excavations were undertaken along the coast of the Herbert/Burdekin district, north Queensland, at Herveys Range, Kennedy, Jourama and Mount Roundback (see Fig. 1). A report of these excavations is given in Brayshaw (1977). Lithic material, shells, and bones were found at all four sites; human bone occurred in the deposits at Herveys Range, Kennedy and Jourama, but not at Mount Roundback. Bones recovered from the excavations were placed in bags and taken to Townsville for initial sorting where ribs, isolated mammal vertebra, central portions of limb shafts, and phalanges were removed. The remaining potentially identifiable specimens were sent to Brisbane where they were allowed to soak for a few minutes in water, and then gently cleaned with a damp wad of cotton. This precaution was taken to avoid causing accidental marks on soft bones. The best preserved, most complete and taxonomically diverse specimens were from the Herveys Range deposit and for this reason, were identified first. Bones from the other sites were then compared with the Herveys Range material and, unless they clearly differed, were referred to the same species. The abundant human remains were isolated and analysed separately. A copy of W. Wood's list of identified human material is lodged in the Queensland Museum library. A summary of this report is presented here as an Appendix.

Vernacular and scientific names of mammals follow the usage of Ride (1970). Dental nomenclature is that used by Archer (1978). Fossil kangaroo names are those used by Bartholomai (1975).

Representative specimens are registered in the Queensland Museum fossil vertebrate collection. The remainder of the material will be lodged in the collections of James Cook University. Stratigraphic level designations cited in the text are given as follows: H indicates Herveys Range; C indicates Jourama; E indicates Mount Roundback; F indicates Kennedy; excavation squares in each site are given as roman numerals, e.g. I to XII; depth is indicated by numbers 1 to

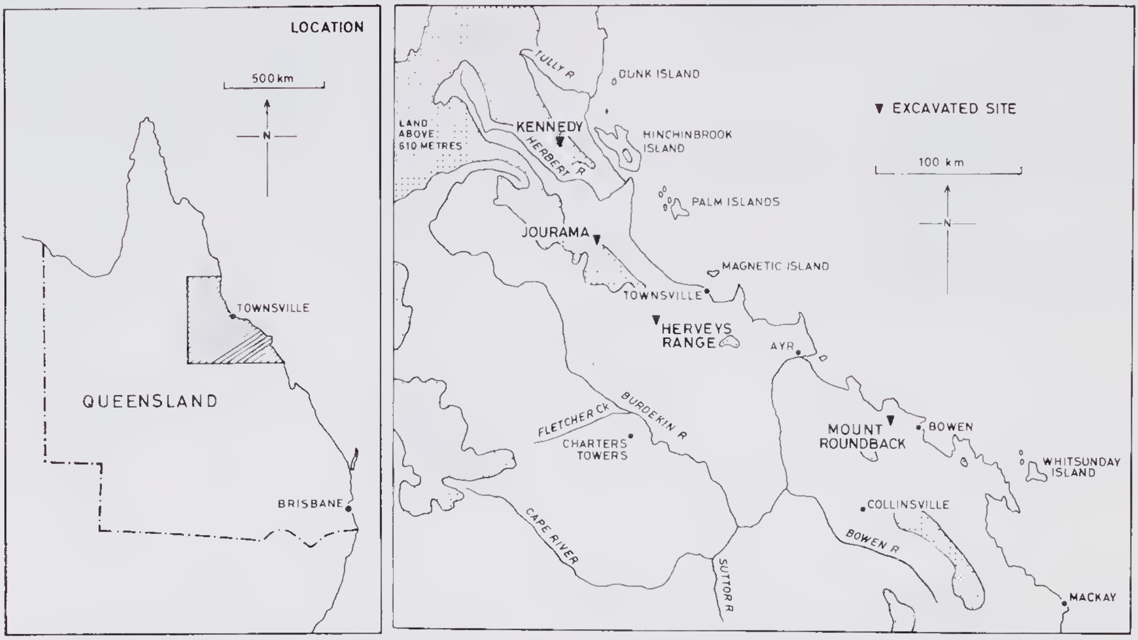

FIG 1. Locations of the Kennedy, Herveys Range, Mount Roundback and Jourama excavations in north-eastern Queensland.

12 where each number represents a 5 centimetre spit or interval. Thus H V 7 indicates the 30–35 cm spit of square V, at Herveys Range.

NON-HUMAN REMAINS

HERVEYS RANGE

Species identified from the Herveys Range excavation are shown in Table 1. In this table, no attempt has been made to itemize the fauna by squares. The numbers represent minimum number of individuals based on the largest number of any common osteological or dental unit. Question marks indicate taxa doubtfully identified.

COMMENTS ABOUT TAXA

FISH: The fish has not been identified. It is invariably represented by broken dentary fragments. Although they are not burned, one fragment may have been cooked. The entire fish would be relatively small, probably smaller than 30 cm in length. Other diagnostic and more abundant fish remains such as vertebrae are easily recognised and their absence suggests fish were not a common food item.

LIZARDS: There are at least two kinds of lizards represented: The Frilled Lizard *(Chlamydosaurus kingii)* and the Blue-Tongue Skink *(Tiligua scincoides)*. Both are represented by broken dentary or maxillary fragments, and in some cases postcranial elements such as pelvis and femur fragments. None show clear evidence of burning, cooking, or tooth marks.

The Eastern Blue-tongue Skink is similar to the Shingle-back Lizard *(Trachydosaurus rugosus)* and has been differentiated here by the fact that its teeth rapidly enlarge in overall size from front to back, the rate of enlargement being much greater than that in the Shingle-back. One Blue-tongue specimen (in H IV 10) is much smaller than the others (in H VI 2) but probably represents a juvenile rather than another taxon. These occurrences of Blue-tongue and Frilled lizards are within the known ranges for the species. Both are recorded from open forest situations.

SNAKES: Vertebral and cranial fragments represent at least one kind of large Python. Regretably, comparison has not been possible with either the Black-headed Python *(Aspidites melanocephalus)* or the Water Python *(Liasis fuscus)*. In comparison with other large pythons *(Morelia spilotes, M. arens,* and *Liasis amethystinus),* the Herveys Range material including a large isolated right quadrate (in H VII 2) most resembles the Carpet Snake *(Morelia spilotes)*. One of the five identifiable fragments has been burned (a vertebra), another cooked (the right quadrate), and another (vertebra in H VI 1) has been broken and probably chewed. Carpet snakes are known from open forest situations and the Herveys Range occurrence is within the known range for the species.

TABLE 1: FAUNA FROM THE EXCAVATION AT HERVEYS RANGE, 1974

Fauna	Level																	
	Surface	1 (0–5 centimetres)	2 (5–10 centimetres)	3 (10–15 centimetres)	4 (15–20 centimetres)	5 (20–25 centimetres)	6 (25–30 centimetres)	7 (30–35 centimetres)	8 (35–40 centimetres)	9 (40–45 centimetres)	10 (45–50 centimetres) 1455 ±140BP	11 (50–55 centimetres)	12 (55–60 centimetres) 850 ± 125 BP	Min. No. of Individuals	No. of identified fragments	Min. No. of adults	Min. No. of juveniles	No. indeterminable
Fish	1	1	—	—	—	—	1	—	1	—	—	—	—	4	4	?	?	4
Chlamydosaurus kingii	?1	1	—	1	—	—	—	—	—	—	—	—	—	3	3	?	?	3
Tiliqua scincoides	1	1	1	—	—	—	—	—	—	—	1	—	—	4	5	3	1	—
Morelia sp.	—	1	1	—	?1	—	—	—	—	—	—	—	—	3	6	—	—	3
Isoodon macrourus	—	1	?	—	—	—	—	—	—	?1	—	—	—	2	2	1	1	—
Trichosurus cf. *T. vulpecula*	2	3	1	1	1	—	—	1	—	1	—	1	—	11	14	8	0	3
Petrogale cf. *P. penicillata*	4	7	1	—	5	1	1	1	1	?1	?1	?1	—	25	45	16	5	4
Wallabia bicolor	1	2	1	—	—	—	—	—	—	1	—	—	—	5	5	2	1	2
Macropus agilis	2	2	3	1	2	—	3	—	?1	2	?1	—	—	17	33	7	8	2
M. parryi	1	2	—	1	1	—	—	—	—	—	—	—	—	5	6	2	2	1
M. giganteus	1	1	?1	—	—	—	?1	1	—	—	—	—	—	5	10	1	1	3
Small rodent	—	—	1	—	—	—	—	—	—	—	—	—	—	1	1	1	0	0
Mesembriomys gouldii	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1	1	0	0
Macroderma gigas	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1	1	0	0
Pteropus scapulatus	—	—	—	—	1	—	—	—	—	—	—	—	—	1	2	1	0	0
Canis familiaris	2	1	—	—	—	—	—	—	—	—	—	—	—	3	3	2	1	0
Homo sapiens	+	+	+	+	+	+	+	+	+	+	+	+	+			—	—	—
Unknown animal	—	—	—	—	—	1	—	—	—	—	—	—	—	1	1	?	?	1
No. of taxa	11	13	10	6	8	2	5	3	3	5	3	2	1	(bone fragments)				
Squares excavated	5	5	5	5	5	5	5	3	3	3	2	2	1					

BANDICOOTS: The species represented is the Brindled Bandicoot *(Isoodon macrourus)*. It is markedly larger than Cape York specimens of the otherwise similar Brown Bandicoot *(Isoodon obesulus)* and comparable in size to south-eastern Queensland Brindled Bandicoots. The only clearly referable specimen (in H VII 1) is an undamaged dentary. There is nothing to indicate its presence in the deposit is necessarily the result of human activity. The Brindled Bandicoot is known from open forest situations and the present occurrence is within the known range of the species.

BRUSH-TAILED POSSUMS: We have not found a consistant morphological character which separates molar teeth of Brush-tailed Possums *(Trichosurus vulpecula)* from the Bobuck *(T. caninus)*. Because Brush-tailed Possums frequent all habitats except rainforest which is the preferred habitat of the Bobuck, identification of the species could be an important aspect in the interpretation of palaeoecology. However, the specimens from Herveys Range are not inconsistant with interpretation as Brush-tailed Possums and in view of the presence of open forest in the area today, and the absence of any other rainforest animal remains in the deposit, the simplest conclusion is that the specimens probably do represent Brush-tailed Possums rather than Bobucks.

Brush-tailed Possum remains were present on most stratagraphic levels. Every specimen is broken, most show evidence of having been cooked, but none are burned. Some have fractures or marks which suggest chewing (e.g. in H VII surface). Most specimens represent young adults. There were no juveniles or pouch-young. Herveys Range is within the known distribution of Brush-tailed Possums.

ROCK-WALLABIES: There are differences of opinion about the number of species of Rock-wallabies *(Petrogale)* in north Queensland. On the basis of Ride's (1970) remarks about distribution, the species in the area of Herveys Range today is likely to be the Brush-tailed Rock-wallaby *(P. penicillata)*. Other authorities suggest additional forms (some representing taxa included by Ride in *P. pencillata*) occur in or near this area including *godmani*, *puella*, and *inornata*. We have attempted to differentiate the molar teeth of these forms using modern Queensland Museum specimens and could find no consistant way of separating small samples referable to Godman's Rock-wallaby *(P. godmani)* from large samples referable to the Brush-tailed Rock-wallaby *(P. penicillata)*. Because all forms of *Petrogale* occupy similar rocky habitats, it probably does not make any significant difference which species is represented in terms of paleoecological interpretation. Nevertheless, the only Rock-wallaby specimens in the Queensland Museum from the Townsville area represent the Brush-tailed Rock-wallaby, and they are very similar to the Herveys Range material. For these reasons the Herveys Range specimens are regarded as *Petrogale* cf. *P. penicillata*. Rock-wallabies are the most common animal in the deposit. Every one of the 45 specimens is smashed, cooked or burned. One dentary (in H VII Surface) has tooth marks on it that suggest a non-human carnivore. Most dentaries have I_1 broken off at the base such that the enamel face projects as a hard transverse edge beyond the dentine. This suggests the dentaries were intended to be, or were actually used as, tooth engravers (Mr K. Akerman, pers. comm.). One left dentary (in H III 5) is possibly abnormal. Although basically similar to other Rock-wallaby specimens, the last molar has a peculiar post-link and a posterior cingulum, characters otherwise unknown in Rock-wallabies. It may represent a supernumerary fifth molar (Archer 1975). Another specimen (in H VII 1), a right dentary, has what appears to be an impacted P_3 projecting down into the alveolus for the missing RI_1.

SWAMP WALLABIES: Swamp Wallabies *(Wallabia bicolor)* are uncommon in the deposit being represented by only five specimens. Of these, three have premolars and are positively identified. Two others are referred with some confidence, but not certainty, on the basis of molar morphology. The fifth specimen is an isolated I_1 and, although only doubtfully referred to this species, cannot be matched with any other wallabies identified from this deposit. All specimens are smashed but none are clearly cooked or burned. One of the dentaries has I_1 broken off in the manner described above for Rock-wallabies and may have been intended for use as a tooth engraver. The Herveys Range occurrence for Swamp Wallabies is within their known range and habitat requirements.

AGILE WALLABIES: Although called a wallaby (Ride 1970), Agile Wallabies *(Macropus agilis)* are very large kangaroos and the most common large animal in the Herveys Range deposit, being represented by at least 17 individuals and 33 skull or dental fragments. All specimens are smashed, cooked or burned. All dentaries have I_1 missing or broken off in the fashion described above for Rock-wallabies. Almost half of the specimens whose age has been determined represent juveniles (P3 hadn't erupted). This occurrence of Agile Wallabies is within their known range and habitat requirements.

WHIPTAILS: Whiptails *(Macropus parryi)* sometimes also called Pretty-face Wallabies, are larger than Rock-wallabies but smaller than Agile Wallabies. They are as rare in the Herveys Range deposit as the comparable sized Swamp Wallabies. All specimens are broken, but none are obviously cooked, burned or chewed. Whiptails have a molar morphology similar to Agile Wallabies but are immediately distinguished by their much smaller and bicuspid P_3. One Herveys Range specimen (in H IV Surface), the proximal end of an ulna, has been identified as a Whiptail because it exactly matches ulnae of Whiptails and is clearly dissimilar to ulnae of all other marcopodid species known from the Herveys Range deposit. One of three dentary specimens (in H VII 1) is only tentatively identified as a Whiptail. It differs from other Herveys Range specimens and Queensland Museum material in possessing a very narrow anterior cingulum and, judging by the roots, relatively large P_3. Unless it represents a taxon otherwise unrecognized from this deposit, it probably represents an extreme variation in Whiptails. The Herveys Range occurrence of Whiptails is within their known distribution and accords with their habitat requirements.

GREAT GREY FORESTER: This is the largest species *(Macropus giganteus)* represented. Unfortunately, all of the very large kangaroo remains are too incomplete to identify with any certainty and it is possible that Antilopines *(M. antilopinus)* or Euros *(M. robustus)* are represented among the unidentified material. The only upper molar has a small but well-developed forelink and well-developed buccal accessory cuspules in the mid-valley. The first character favours identification as the Great Grey, because the vast majority (there are exceptions) of Antilopines and Euros lack a well-developed forelink. The second character is ambiguous, being present in some fossil species (e.g. *Macropus (Osphranter) pan* and *M. (O.) woodsi)* of the group of kangaroos including Antilopines and Euros, but evidently not in these two modern species of the group. For the present, the remains are referred to the Great Grey Forester, but with reservations. All of the specimens are broken but only one (in H VII Surface) is obviously also burned. Great Grey Foresters are likely to occur today in the Herveys Range area, as it is within their known range and habitat requirements. Because Rock-wallabies were (or are) so abundant, it is probably reasonable to assume the habitat would also suit Euros.

UNKNOWN ANIMAL: The single most intriguing fragment from the Herveys Range deposit is a left dentary fragment in H III (5). It appears to be mammal because the tooth alveoli are deep and completely unlike those of fish or reptiles examined. The absence of small incisor alveoli anterior to the large caniniform alveolus suggests it is not a polyprotodont marsupial. It also resembles no known placental mammal. In all probability it represents a diprotodont marsupial somewhat similar to the Green Ringtail Possum *(Pseudocheirus archeri)* which has a very short diastema and a relatively steeply inclined I_1. The Herveys Range specimen differs from these in completely lacking a diastema and in being larger. There is little point in speculating further about its affinities because it is such a small fragment. However, it certainly suggests the presence of an as yet undiscovered (by European zoologists) north Queensland mammal. Whatever it represents, it was evidently used by the Aborigines as a food because, like all the other bones in this deposit, it has been thoroughly smashed.

SMALL RODENTS: One broken specimen (in H VI 2) retaining only M_3, appears to be a small pseudomyine rodent. It clearly does not represent a species of *Rattus*. There is no evidence that it was cooked.

BLACK-FOOTED TREE-RAT: This very large rodent *(Mesembriomys gouldii)* may be represented by an isolated LI_1. The distribution of the tooth enamel appears to differentiate it from the north Queensland Giant White-tailed Rat *(Uromys caudimaculatus)* and the common Water Rat *(Hydromys chrysogaster)*. Although it is similar to the Gaint White-tailed Rat, the tooth enamel in Tree-rat specimens in the Queensland Museum extends farther around the buccal side of the tooth. This represents a significant range extension southwards for the Black-footed Tree-rat, although it is just within the range of the Gaint White-tailed Rat. Because the identification is based on such limited material, we are hesitant to regard it as anything other than a tentative identification, and one which requires substantiation by much better material. The

Black-footed Tree-rat normally inhabits woodland savannah while the Giant White-tailed Rat inhabits rainforest. This is added support for the possibility that the tentative identification is correct.

Ghost Bat: Only one specimen (in H V 3) represents this large carnivorous bat *(Macroderma gigas)*. There is nothing to indicate that it was cooked. Its presence in the deposit suggests but does not necessarily mean that it was eaten by Aborigines. Ghosts Bats are nocturnal, extremely alert, and do not hesitate to fly during the day if disturbed. This would probably make them very difficult animals to catch. Ride (1970) considers that their diurnal roosts are invariably in caves or tunnels. The Hervey's Range occurrence is within their known modern range.

Red Flying Fox: This relatively small Flying Fox *(Pteropus scapulatus)* is represented by one broken specimen (in H VII 4) which suggests the species was eaten, albeit infrequently. Like the Ghost Bat it is nocturnal but roosts in trees and probably would be an easier species to catch. One specimen (in H VI surface), a left dentary, lacks the M_3 normally found in this species. Only one modern specimen in the Queensland Museum shows the same condition. This distribution record is within the known range and choice of habitat for the species.

Dingo: Dingoes *(Canis familiaris)* are represented by only three teeth. Two of these appear to represent broken adult canines, one of which (in H VI Surface) may have been burned. The third tooth, undamaged, appears to have been an incompletely erupted LdP_4, thus presumably broken out of a dentary rather than naturally dropped out or shed. The two adult canines are split dorso-ventrally, a type of fracture that usually occurs after a tooth is heated, or allowed to age over a long period in a skull. If the Dingoes had broken the teeth during life, we would expect the break to have been transverse along the horizontal plane. Dingoes are known from almost all areas of Australia.

Aborigines: Aboriginal remains are spread throughout the deposit and the great majority are thoroughly broken. Some are also burned. Of particular interest is the symphysis of a very small child which is thoroughly burned as well as broken. Details of the human remains are given below.

BONE DAMAGE

Damaged bones noted may be grouped into seven categories: broken bones; bones clearly used as implements; burned bones; cooked bones; decalcified bones; soil or insect damaged bones; tooth-marked bones.

Broken Bones: Of over 150 identifiable bone fragments, less than a few dozen of the smallest such as tarsals are intact. In addition to identifiable fragments, there are hundreds of smaller fragments too smashed to be identified.

Very few of these show gouges suggesting points of violent impact. From this we conclude either that the bones were crushed individually with a blunt instrument, such as a flat rock, or were crushed while still part of the whole carcase, the skin and flesh thereby protecting the bones surfaces from impact damage.

Some fragments appear to have had tooth crowns deliberately smashed off the roots (e.g. the cheekteeth of a kangaroo maxillary fragment in H VII 10). Almost all kangaroo dentaries have I_1 broken off in a manner suggesting the dentaries were intended for use as tooth engravers (see above). Alternatively or concordantly the incisor tips may have been used elsewhere, perhaps as ornaments or points for spears. The very low number of isolated lower incisor crowns compared with the high number of dentaries lacking this tooth, is evidence for this possibility.

Obvious Bone Implements: Two bone fragments (one in H VI 1, and one in H VII 4) were obviously used as awls, needles, or spatulas. Both may have been manufactured from the dense part of a kangaroo fibula.

Burned Bones: Burning is evidenced by the black, charred texture of a bone surface. Fragments that do show burning are normally thoroughly burned. It is possible that some bone fragments encountered while eating may have been tossed back into the fire. Although it seems highly unlikely that carcases would be cooked until charred as a preparation for eating, some bones forming extremities such as teeth or phalanges could have been burned well prior to the flesh being cooked.

Cooked Bones: Interpretation of alteration in a bone due to cooking is less easy than recognition of alteration due to burning. Bones have been interpreted here as cooked if they show a particular brown colouration such as might result if they were contacted by hot oils or other by-products of heated flesh. One humerus fragment (in H VII 5) has two distinctly charred ends. The central portion however, is brown and merges gradually into the black of the charred ends. This is the brown colour regarded in other bones to indicate alteration due to cooking.

Other processes could produce a brown colour in the bone, such as acids in the soil in which the bones are burned. No attempt was made here to distinguish these possible causes.

DECALCIFIED BONES: A few bone fragments (such as one in H VI Surface) have a very soft whitish texture and can easily be scratched with a fingernail. Possibly these bones were charred and subsequently bleached. Alternatively, they may have passed through the alimentary tract, either of an Aboriginal or a Dingo. Bone fragments of this type are very uncommon in the deposit.

POSSIBLY INSECT-DAMAGED BONES: One dentary fragment (in H VII 1) of an Agile Wallaby has pits on its surface which suggest either corrosion or the activities of invertebrates, such as beetle larvae. Burned, softened bone is often subject to insect destruction. Damage of this sort has been observed on bones from other similar deposits.

TOOTH-MARKED BONES: Tooth marks are relatively uncommon on bones from the Herveys Range deposit compared with those from the Jourama deposit. Three sorts have been recognized: fine, sharp, conical depressions or scratches possibly produced by Dingoes or children (e.g. in H VII surface); blunter, deeper conical depressions possibly produced by adult Aboriginals with blunter canines (e.g. in H VIII 5); marks clearly attributable to rodents (e.g. in H VII 4). In the case of rodent gnawing, the implication is that at least some bones were left unburned on the living surface. The particular bone gnawed by rodents had also been smashed and apparently chewed by another carnivore such as a Dingo.

The absence of more extensive chewing suggests the possibility that food was relatively abundant in the Herveys Range area than in the Jourama area.

HORIZONTAL DISTRIBUTION OF BONES IN THE DEPOSIT

It was evident that for any given level (i.e. surface, level 1, and so on) bones were more abundant towards the rear of the shelter. On the surface level, H III (the farthest from the shelter back, and directly under the drip line) had no identifiable fragments; H IV had 2; H V had 6; H VI had 4; and H VII (rear of shelter) had 17. On level 1, H III had 4; H IV had 1; H V had 5; H VI had 8; and H VII had 26. This suggests either that Aboriginals centred their activities at the rear of the shelter to avoid high temperatures or rain or they may have centred their activities forward of the rear and tossed unwanted bone fragments to the rear of the shelter, possibly to keep them out from under foot.

KENNEDY

Unlike the material from the Herveys Range deposit, very few of the bones from the Kennedy deposit are identifiable. Accordingly the non-human fauna is discussed as a whole.

The only two recognizable taxa are as follows: fish (unidentified), levels 1, 2 and 4; Frilled Lizard *(Chlamydosaurus kingii)*, level 5, 7 and possibly 1. All bones are smashed or merely broken and several are clearly burned. Other types of bone damage include corrosion pits (in F II 2), and decalcification (in F II 7). Comments relative to this kind of damage are noted above in reference to the Herveys Range deposit. The presence of only the Frilled Lizard, rather than the Eastern Blue-tongue lizard which is the more abundant of the two at Herveys Range, is puzzling but the samples are too small for this difference to have statistical significance. The abundance of lizard rather than mammal species is perhaps more meaningful, and is an even more radical departure from the Herveys Range deposit, but we do not know what it means. The relatively greater abundance of fish indicates either a proportionately greater amount of time spent fishing, or else a greater abundance of fish. But again, it is impossible to interpret the true significance of these site differences because of the small size of the Kennedy sample.

MT ROUNDBACK

As in the case of the Kennedy site, the identifiable non-human bone fraction of the Mt Roundback deposit is small.

There are six identifiable non-human taxa: molluscs (pelecypod, type unidentified), 5–10 cm, represented by a small shell fragment; amphibians (at least one large species, possibly a large hylid), surface, represented by isolated limb bones; snake (possibly an elapid?), 5–10 cm, represented by a small vertebra; Brush-tailed Possum *(Trichosurus vulpecula,* but see applicable comments about taxonomy given above for the Herveys Range specimens), surface and 5–10 cm, represented by an isolated lower incisor and a dentary fragment; Rock-wallabies (*Petrogale* sp.), 10–15 cm and 20–25 cm, represented at least by maxillary and dentary fragments; and a large Kangaroo, probably a Euro *(Macropus* cf *M. robustus),* 5–10 cm, represented by at least an isolated upper molar.

The only departure from species also present in the Herveys Range deposit is the possible Euro. Identification of the single large tooth is based on the fact that although there is a forelink, it is very tiny, a condition common to Euros but not Great Grey Foresters which normally have a well-developed forelink. Many other bone fragments in the Mt Roundback deposit represent very large kangaroos, but because they are mostly postcranial fragments, they are unidentifiable.

BONE DAMAGE

All bones are broken, with rare exception. Some, but not all, of the frog bones on the surface are undamaged. None of the bone fragments on the surface, but some within the deposit are burned. One pelvic fragment (in E6, 15–20 cm) appears to have been decalcified and/or burned. Another pelvic fragment (in E7, surface) shows corrosion pitting of the sort noted in the Herveys Range deposit. One bone fragment (in E4, surface) shows damage caused by teeth, but there are no clear indications of what carnivore was responsible. Kangaroos will even chew bones though they don't leave conical tooth depressions near the broken ends.

JOURAMA

The non-human remains from the Jourama deposit represent few taxa, and none otherwise unrepresented in the Herveys Range deposit. However some aspects of bone damage and the abundance of Aboriginal remains in this site make it unique.

TAXA

There are four identifiable non-human taxa: mollusc (pelecypod, cyrenid, *Batissa* or *Cyrena,* which occurs in the lower reaches of tropical rivers), level 3; Rock-wallaby (*Petrogale* sp.), possibly represented by specimen on level 2; Agile Wallaby *(Macropus agilis),* level 4 and possibly level 2; and the Dingo *(Canis familiaris),* level 1 and a specimen not allocated to a level.

In terms of composition, this assemblage more cosely resembles that from Herveys Range than from Kennedy.

BONE DAMAGE

The material from this deposit is unique in that almost half of the level samples contain bone fragments showing clear evidence of tooth marks. In many of these chewed specimens (e.g. in C III 4, C III 5, and C III 6), the entire surface of the bone fragment is disfigured by gouges, fractures and tooth impressions, even to the extent of disfiguring the edges of the fragmented bone. Nothing, unfortunately, indicates whether the carnivores were Aborigines, Dingoes or both. We suspect Aborigines because nothing like this kind of damage is present in a large sample of bones deliberately fed to captive Dingoes (an experiment carried out for us by Mr A. Boorsboom, Queensland University). Of course, much depends on how chewing behaviour changes as a function of hunger. In the case of the experimentally fed Dingoes, the animals, although hungry, were certainly not starving. One dense limb bone fragment (in C III 4) shows a unique kind of damage. It has what appears to be a deep incision that is clearly not attributable to rodents, Dingoes or Aboriginal teeth. It superficially resembles a wedge-shaped incision present in a fossil bone from Mammoth Cave, Western Australia (Archer, Merrilees and Crawford, in preparation) which has been attributed to Aboriginal activity. In the present case, no attempt has yet been made to find evidence of sawing or chipping. An alternative cause of the damage could conceivably be spalling, although a percussion point is not obvious. Other types of bone damage in this deposit are of the same kind as noted for bones in the Kennedy and Mt Roundback deposits.

HUMAN REMAINS

HERVEYS RANGE

On the basis of the sample identifications provided by Dr W. Woods, there are 13 juveniles and 17 adults represented. There appears to be a heavy mortality between the ages of 10 to 12 years. There is no clear evidence for very old individuals. Adults that have been aged are generally middle-aged. Only one infant was noted. Many human bones, including juveniles, show charring and scratch marks. Virtually no human bones except some hand and foot elements are unbroken. These facts suggest that the human remains represent a food eaten by the inhabitants of the Herveys Range shelter. The nature of the bone breaks and charring is similar to that shown by the non-human bones in the same deposit.

DISPROPORTIONATE REPRESENTATION: In most levels, humans are represented mainly by foot bones, hand bones, skull fragments and teeth. Pelves are very rare and limb bones uncommon, although the latter may be at least partially represented by numerous unidentifiable bone splinters. The calcaneum and astragulus are also generally absent. Reasons for this disproportionate representation are not obvious. Possibly some human carcases were dismembered elsewhere, and the only portions brought to the site were wrists and hands, lower parts of feet and entire heads. Although unlikely, it is difficult to otherwise explain the representation.

DISEASE: Only arthiritis was noted.

JOURAMA

All samples considered, there are 15 juveniles and 9 adults represented. Of the juveniles there are two mortality peaks, one between the ages of 3 to 5, and another, the larger of the two, between 8 to 13. The adults for which age estimates have been made are young adults, except one middle-aged or old individual. One possibly new born infant is present. All except some of the smallest bones are broken, some including juveniles and adult bones are charred, and others marked. Smashed teeth, periotic bones and calcanea indicate considerable force involved in breakage. One bone shows what appears to be traces of red pigment, suggesting possible ceremonial use of this human bone.

Curious concentrations of bone fragments were encountered during excavation. These include at least broken limb, vertebral, foot, mandibular and cranial elements but no given cluster represented a whole individual. The almost vertical orientation of some long limb bone fragments in these clusters suggests the remains were either placed in excavated pits, perhaps as burials, or fell into steep-sided crevices in the shelter's surface. It is obvious from photographs taken at the time that some of these bones were deposited as small fragments while others show fractures developed or widened in situ which resulted in their removal as yet smaller fragments. Some skulls had complete, undistorted cranial vaults. Because these were heavily invested with plant roots, they were removed in pieces during excavation.

REPRESENTATION: There is some unequal representation generally of recognizable limb bones, and commonly of pelves. Foot and hand bones, and teeth are common.

MT ROUNDBACK

Only three levels produced identifiable human remains. In the entire deposit, five individuals are represented: two unaged juveniles; an adult; a middle-aged male; and an unaged individual. Some bones are charred or marked, and all except some small bones are broken. Representation of bone elements is reasonable even considering the small number of samples.

KENNEDY

Human material was only identified in one level, and represents one unaged individual.

COMPARISONS OF HUMAN REMAINS BETWEEN SITES

The two well-represented sites, Herveys Range and Jourama, provide the only really meaningful data for intersite comparisons.

HUMANS AS FOOD: In general, the Herveys Range deposit has a much lower percentage of human bone, in terms of all bone present, than Jourama. This suggests, assuming humans were a food source, the Jourama people ate more people. However, the assumption that all the human remains represented food for the Jourama people is questionable because of the evidently intact nature of some crania. If these particular individuals were eaten, why weren't their heads smashed in order to obtain the brains? The apparent absence of entire skulls, but obvious abundance of skull fragments, many of which were burned, at Herveys Range does not conflict with the notion that the humans in that deposit were a source of food.

POSSIBLE INTERMENTS: At Jourama the presence of bone clusters of dominately human bone, and at least some intact skulls, suggests burial or at least emplacement in pits, a phenomenon not obviously present in the Herveys Range deposit. The non-cranial bones were, however, almost all broken prior to burial, and at least one of these broken bones has what appears to be traces of red pigment. Possibly the bones or carcases were broken, cooked or burned and some bones decorated for ritualistic purposes prior to burial in pits. Whatever the reason, this aspect of the Jourama deposit appears to differ from that of Herveys Range.

AGE OF HUMANS REPRESENTED: In the Herveys Range deposit there are more adults than juveniles represented, while at Jourama there are far more juveniles than adults represented. The reasons for this difference are obscure and much would depend on the reason the humans were part of each deposit. In both deposits it seems unlikely that the ages of the individuals could represent the structure or mortality curves of the population unless some bias were involved, such as selective killing. If they did represent a mortality curve, surely more infants would be represented. The Jourama deposit revealed only one possibly neonate; there were none from Herveys Range.

GENERAL REMARKS CONCERNING ALL FOUR SITES

Habitats Indicated

The faunas from all four sites suggest they were obtained from sclerophyl forest or savannah woodland, with rocky areas and streams. Even the Kennedy fauna, although extremely impoverished, contains the Frilled Lizard which (Cogger 1975) only inhabits dry sclerophyl forests and woodlands.

The Herveys Range deposit contains the highest proportion of mammal remains and the lowest proportion of fish or shells. This suggests it was farther from water than the other three sites.

Bias in Species Representation

With a few exceptions, the majority of arboreal and volant species likely to be in the vicinity of all four sites are unrepresented in the deposits. These include three genera of gliders, pigmy possums, most bats and all birds. In fact the only arboreal marsupial represented, the Brush-tailed Possum, is also known to spend a considerable amount of time on the ground. This suggests the Aborigines were either hunting more in the open savannah areas, or else had few skills enabling them to recover arboreal animals. The total lack of birds is even more puzzling because many spend a considerable amount of time on the ground.

Also totally missing are the dasyurids, the native mainly terrestrial carnivores which range from a mouse to a cat in size. Over 10 kinds could have been available to them and it is not at all clear why they aren't represented in the deposit.

Some of these absences may be explained by chance sampling of excavation sites. More extensive examination would be expected to yield additional taxa.

ACKNOWLEDGEMENTS

Dr Wally Woods (University of Queensland) supplied the age analysis and identification of the human remains which formed the basis of the Appendix. Mr A. Boorsboom contributed Dingo-chewed bones for comparison. Mr K. Ackerman kindly collected and provided bones from Aboriginal campsites from north-western Australia. Mr A. Easton took the photographs.

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Most of the specific references regarding mammal distributions are not noted above because most are based on Queensland Museum records.

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APPENDIX

SUMMARY OF HUMAN REMAINS IDENTIFIED BY W. WOODS, WITH COMMENTS

HERVEYS RANGE

Surface (21 fragments)	At least two individuals: one adult, one juvenile. Charring of skull and post-cranial fragments. Most parts of skeleton are represented except pelvis and limbs. Dominance of hand, foot and skull fragments. Most bones broken. Only one tooth present.
Spit 1 (36 fragments)	At least four individuals: baby 6–9 months; juvenile 10–11 years; middle aged adult. Charring and smashing of teeth and bones, including those of juveniles. Missing are pelvis, femur, tibia, ulna. Dominance of hands, feet, skull and teeth. Some teeth of juveniles (VII) have roots which are charred, suggesting they may have been smashed out of skulls before being burned.
Spit 2 (30 fragments)	At least three individuals: child approximately 3 years; child 10–12 years; adult (age ?). Charring and smashing of bones — particularly noteworthy is smashed tympanic region which is very dense part of skull requiring considerable force to break. Missing are almost all limb bones except fibula, pelvis, sacrum, and scapula. Dominance of hand and foot elements, skull fragments, teeth and some vertebrae.
Spit 3	At least two individuals: an adult, possibly male, of 30+ years; a juvenile (age ?). Charring only noted on adult skull fragment (HVII), and a juvenile scapula fragment (HVII). Adult had arthritis in one foot. Missing are most portions of pelvis, and major limb bones. Dominance of foot and hand bones, tooth and skull fragments.
Spit 4 (22 fragments)	At least two individuals: a middle aged adult; juvenile. Charring noted only on two juvenile skull fragments (HVII). Small samples but still no remnants of limb bones, pelves, scapulae, sacra. Dominance of skull fragments, teeth, foot and hand bones.
Spit 5 (1 fragment)	At least one individual: a ?juvenile male. No charring noted. One zygomatic (skull) bone only of human remains identified.
Spit 6 (3 fragments)	At least two individuals: possibly a juvenile of approximately 12 years; one adult. No charring noted. Rib, tooth and toe bone, only three fragments.
Spit 7 (10 fragments)	At least one individual: one adult. Small sample, but no burning noted. Fragmentation common. Some marking on tibial fragments. Missing are pelvis, femur, fibula, arm (except hand elements) and most of axial skeleton. Present are skull fragments, scapula fragment, hand elements, tibial fragments, and atlas fragment.
Spit 8 (3 fragments)	At least two individuals: a juvenile approximately 12 years; an adult (age ?). Small sample, but no charring noted. Present are finger, vertebra fragment and spine of scapula.
Spit 9 (8 fragments)	At least two individuals: a juvenile approximately 6 years; an adult (age?). Charring of skull, vertebra. Missing are pelvis, limbs, feet, hands: only represented by skull fragments, isolated teeth, vetebral fragment.
Spit 10 (4 fragments)	At least two individuals: a juvenile (age?); an adult (age?). No charring noted. Only represented by fragments of skull, foot and femur.
Spit 11 (5 fragments)	One adult (age?). No charring noted. Represented only by fragments of rib, femur, skull and one trapezoid.
Spit 12 (8 fragments)	At least two adults (age?). No charring noted. Represented are fragments of rib, foot bones, vertebrae, and some hand bones.
Spit 13 (16 fragments)	At least two adults (age?). Charring of skull fragment. Missing are all limbs, pelvis, axial skeleton (except skull). Dominance of foot and hand elements.
Spit 14 (16 fragments)	At least one individual: an adolescent or young adult. No charring noted. Missing are limbs (except hands and feet), pelves, sacrum. Dominance of foot and hand elements, and less so, skull elements.
Spit 15 (15 fragments)	Possibly a single adult. No charring noted. Missing are all major limb bones except femur, pelvis, sacrum, scapula and skull. Dominance of hand and foot elements. For the first time a calcaneum (fragments) is represented.

JOURAMA

Surface (1 fragment)	One individual (age?). No damage noted. One right cuboid only present.
Spit 1 (11 fragments)	At least two individuals: one juvenile 8–10 years; one adult (age?). Charring of a long bone fragment. A broken periotic bone indicates considerable force involved in smashing skull. Some long bones were evidently cut, or at least have cut marks. Missing are most bones but representation includes skull, teeth, hand and at least one long bone.

Spit 2 (32 fragments)	At least four individuals: juvenile approximately 4 years; juvenile approximately 8 years; juvenile approximately 13 years; adult in early twenties. Charring of juvenile skull fragments and a mandible. A juvenile ulna and radius show heat marks (cooking without charring?) and scratches. Missing are pelves and possibly limb bones of adult. Some limb bone fragments are present but, except for juvenile radius and ulna, are evidently unidentifiable. Dominant are isolated teeth.
Spit 3 (115 fragments)	At least four individuals: a juvenile approximately 10 years; a juvenile approximately 16 years; a subadult female; and an adult (age?). Charring noted on some skull fragments only, i.e. uncommon. Breakages other than normal smashing includes scratch marks on ileum of young female; on rib fragments; juvenile long bones; metatarsal has piece removed (?); metacarpal with scratch marks; scratches on adult femur; scratch marks on rib fragments and on young adult mandible fragment. One mandible fragment suggests teeth were removed (or naturally lost?) from bone after death. Calcaneum is smashed, a feat taking considerable force. All elements represented by at least one fragment, but scarce are pelvic fragments, vertebrae and limb bones. Common are isolated teeth, foot and hand bones.
Spits 3 & 4 (32 fragments)	At least two individuals: a child of approximately 8 years; a juvenile of approximately 10 years. No charring observed. Most long bones show scratches. One long bone shows traces of ?red pigment. There are no obvious missing elements, except there are no hand or foot bones — the reverse of the usual situation.
Spit 4 (77 bones — nearly 100 fragments)	At least two individuals: a child of approximately 10–11 years; an adult (age?). Charring noted on mandible fragments; long bone fragments; a patella; skull fragment. Splitting or scratching noted on rib fragments, long bone fragments, etc. A cuboid and calcaneum are broken, considerable force being required. Some teeth are also broken — also requiring considerable force. Most elements are represented, including pelves. Dominance of hand and foot bones, and isolated teeth.
Spit 5 (87 + fragments)	At least five individuals: an infant (possibly just new born); a juvenile of approximately 4–5 years; a juvenile of approximately 11–12 years; two young adults. Charring noted in skull fragments and long bone fragments. Most bones are represented except pelvis and identifiable long bones, except femur — some fragments of long bones may represent others. Dominance of isolated teeth only.
Spit 5 north end (20 + small fragments)	Probably a single adult male. A talus is charred. Scratch marks noted on fragments of femur, clavicle and ribs. Representation reasonable. Missing are pelvis, arms and hands, although scapula and clavicle present. Legs and feet dominate.
Spit 6(a) (46 + many fragments)	At least three individuals: a juvenile approximately 3–4 years; an adult male (age?); an adult female (age?). Charred bones include scapula fragments and long bone fragments. Splitting and/or scratching noted on femur fragment, long bone fragments, also on fragments of pelvis and scapula. Most bones are represented except arms (hands represented). Several pelvic fragments present, including juvenile and adult.
Spit 6(b) (60 + many fragments)	At least three individuals: two juveniles; a middle aged male. Charring is not specificially noted but many of the bones are said to show evidence of heat exposure. Scratching and/or splitting are noted in tibial, fibular, femoral, radial, ulnar and clavical fragments. One vertebra shows advanced arthritis. Representation is reasonably even — no obvious imbalance.
Spit 7 (6 fragments)	At least two individuals: a juvenile of approximately 4–5 years; and an adult (age?). No charring noted. Scratch marks on maxillary fragments. Sample small, so unequal representation not surprising. Fragments all cranial and mandibular.

KENNEDY

Spit 9 (FII)	Not clearly more than one individual (age?). Fragments of right pubis and ribs, also foot bones present.

PLATE 28

Representative specimens from the Kennedy and Jourama excavations: A, F9199, five pieces of bone from Jourama, C III 5, which have been thoroughly chewed and/or cut, X1; B, two views of F9200, Jourama, C III 4, showing possible incision (i) in profile and plan view, X1; C, F9201, Herveys Range, H VII 5, humerus fragment showing charred ends and what is referred to in this paper as a cooked medial region, that is it is discoloured but not charred, X2; D, F9184, Herveys Range, H VII 1, *Macropus* cf. *M. parryi* (see text), left dentary with crown of I_1 broken off, possibly intended to be a scraper, X1; E, F9188, Hervey's Range, H VII surface, *Petrogale* sp. cf. *P. penicillata*, juvenile right dentary showing conical depression interpretated as a tooth mark (t) X1; F, F9189, Herveys Range, H VII 2, *Trichosurus* cf. *T. vulpecula*, right maxillary fragment, X1; G, F9198, Herveys Range, H III 4, *? Mesembriomys gouldii*, LI_1, X1; H, F9205, Herveys Range, H VI 2, small rodent, X1; I, F9197, Herveys Range, H VII 1, *Canis familiaris*, LdP_4, X1; J, F9195, Herveys Range, H V 3, *Macroderma gigas*, left dentary fragment, X1; K, F9196, Herveys Range, H VII 4, *Pteropus scapulatus*, left maxillary fragment, X1; L, F9192, Herveys Range, H VI surface, *P. scapulatus*, left dentary fragment showing no alveoli for otherwise variably present M_3, X1; M-N, F9204, Herveys Range, H III 5, anterior end of a left dentary of an unknown but apparently new diprotodont marsupial, stereopair occlusal view (M) and lateral view (N), X2; O, F9206, Herveys Range, H VI 3, *Homo sapiens*, charred fragment of a juvenile right dentary, X2; P, F9207, Herveys Range, H VII surface, *Chlamydosaurus kingii*, fragment of a right maxilla, X1; Q, F9203, Herveys Range, H VI 2, *Tiligua scincoides*, fragment of a left dentary, X1; R, F9202, Herveys Range, H VII 2, isolated right quadrate of a large python skull, X1; S, F9194, Herveys Range, H VI 1, palatine of a large python cf. *Morelia* sp., X1; T, F9208, Herveys Range, H III 6, dentary fragment of a fish, X1.

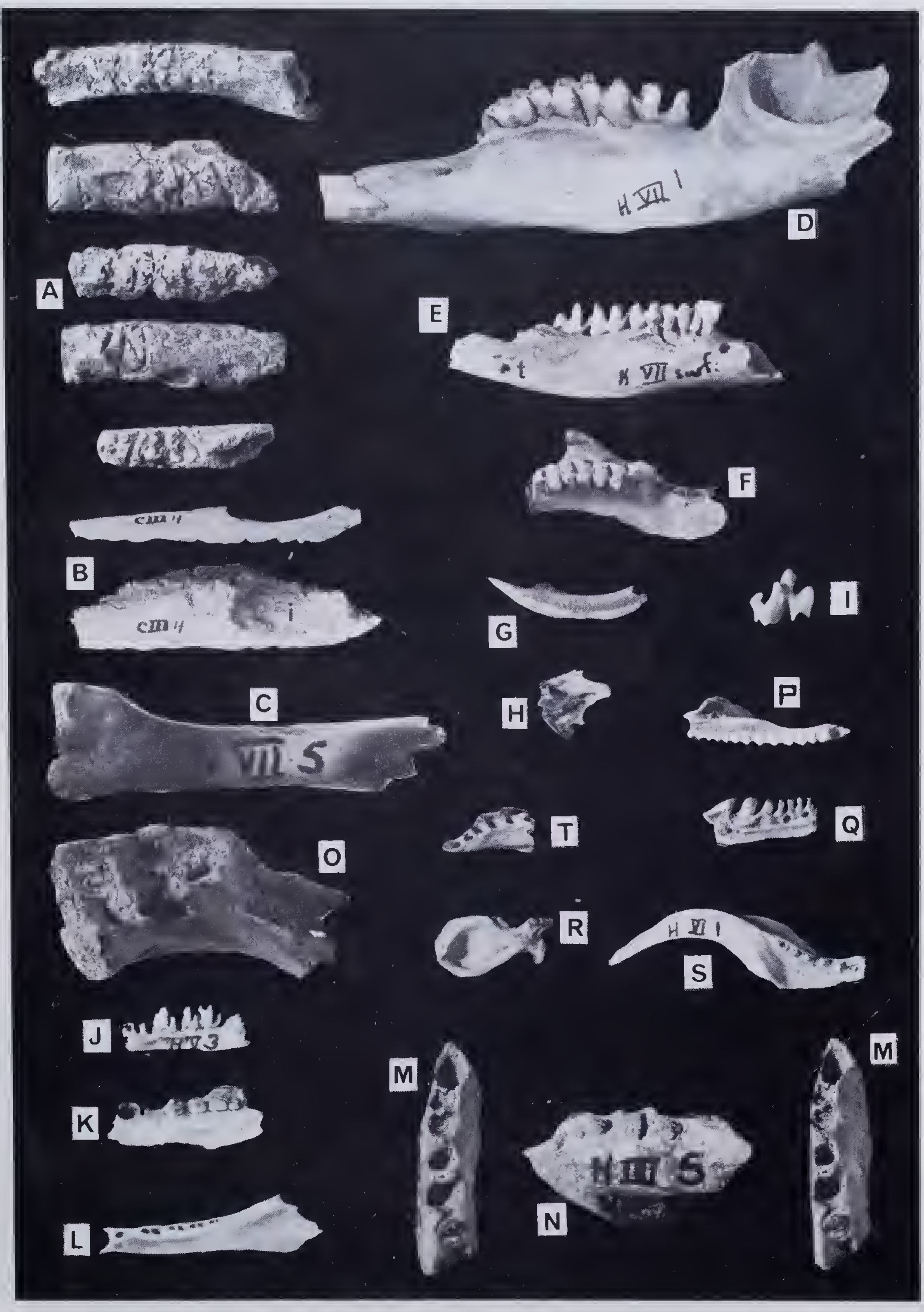
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PLATE 29

A. General view of the Herveys Range Site. The rock shelter excavated is under the breakaway of the large boulder in the central background.

B. Bone cluster in excavation at Jourama, C III 5. Most bones visible are human and, with the possible exception of the dentary (lower left) and astragulus (upper middle), all show marked predepositional smashing. Limb bones at upper right are not in the round, each being represented by only one side of the shaft. Ruler is one foot long. Photo taken looking WNW.

Mem. Qd Mus. **18**(2): 179–83, pl. 30. [1978]

PTERASTERICOLA VIVIPARA N. SP., A PARASITIC TURBELLARIAN (RHABDOCOELA: PTERASTERICOLIDAE) FROM THE CROWN-OF-THORNS STARFISH, *ACANTHASTER PLANCI*

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ABSTRACT

Pterastericola vivipara n. sp. feed on epithelial cells of the pyloric caeca of *Acanthaster planci.* Ciliated larvae may hatch from eggs within these small red worms and burrow through the parent's body. It is the second member of this genus described and the first record of this family (Pterastericolidae) from the Southern Hemisphere.

Turbellaria have frequently been reported from the gut of echinoderms, principally from holothurians and echinoids (Jennings 1971, 1974). Four species have been found in asteroids. These are the rather aberrant *Acholades asterias* Hickman and Olsen, 1955 (F. Acholadidae) which lives encysted in the walls of the tube feet of *Coscinasterias calamaria* in Tasmania and three species in the family Pterastericolidae, viz., *Pterastericola fedotovi* Beklemishev, 1916, *Triloborhynchus astropectinis* Bashiruddin and Karling, 1970 and *T. psilastericola* Jespersen and Lutzen, 1972. All three pterastericolids occur in the pyloric caeca of asteroids from northern European waters.

No endo-parasites have as yet been described from the Crown-of-Thorns Starfish, *Acanthaster planci,* which has received so much attention over the past decade in relation to destruction of living, hard corals in the Indo-Pacific (Chesher 1969; Vine 1970; Endean 1973). Investigation of the Crown-of-Thorns along the Great Barrier Reef for associated parasites and commensals (Cannon 1972, 1975) led to the discovery of the worm herein described.

MATERIALS AND METHODS

Starfish were transported alive as described by Cannon (1973) to Brisbane for examination in the laboratory. Worms were only found in the pyloric caeca although all internal organs were examined. Routinely worms were detected by gently squashing sections of pyloric caecum between glass while being examined with a stereoscopic microscope. Worms removed from caeca were examined alive in filtered seawater. Whole mounts were prepared from worms fixed in cold 10% Formal/Saline, cold A.F.A. and cold Gilson's fluid, and stained with either Mayer's or Kornhauser's haemalum. Sections at 7μ were obtained from cold, Bouin's fixed worms, embedded in 60°C paraffin. These sections were stained with Haemaxtoylin and eosin. Measurements were made with a micrometer eyepiece, drawing was with the aid of a camera lucida.

Pterastericola vivipara n. sp.
(Fig. 1, Plate 30)

MATERIAL EXAMINED

HOLOTYPE: from pyloric caecum of *Acanthaster planci* Linnaeus, Centipede Reef, 9/vi/1974, L. Cannon, QM G10313 (wholemount).

PARATYPES: from pyloric caecum of *A. planci,* Centipede Reef, 9/vi/1974, L. Cannon, QM G10314-5 (wholemounts) G10316 (sections).

Other material examined included live specimens gently squashed under coverslip pressure.

DIAGNOSIS

Small pyriform turbellarian, epidermis completely ciliated, lacking rhabdoids; mouth subterminal, pharynx bulbous, doliiform, but gut dorso-ventrally orientated when fixed, intestine sac like; lacking protonephridia; gonopore single, ventral; ovary and testis single, compact, lateral; vitellaria in two lateral bands, male system with

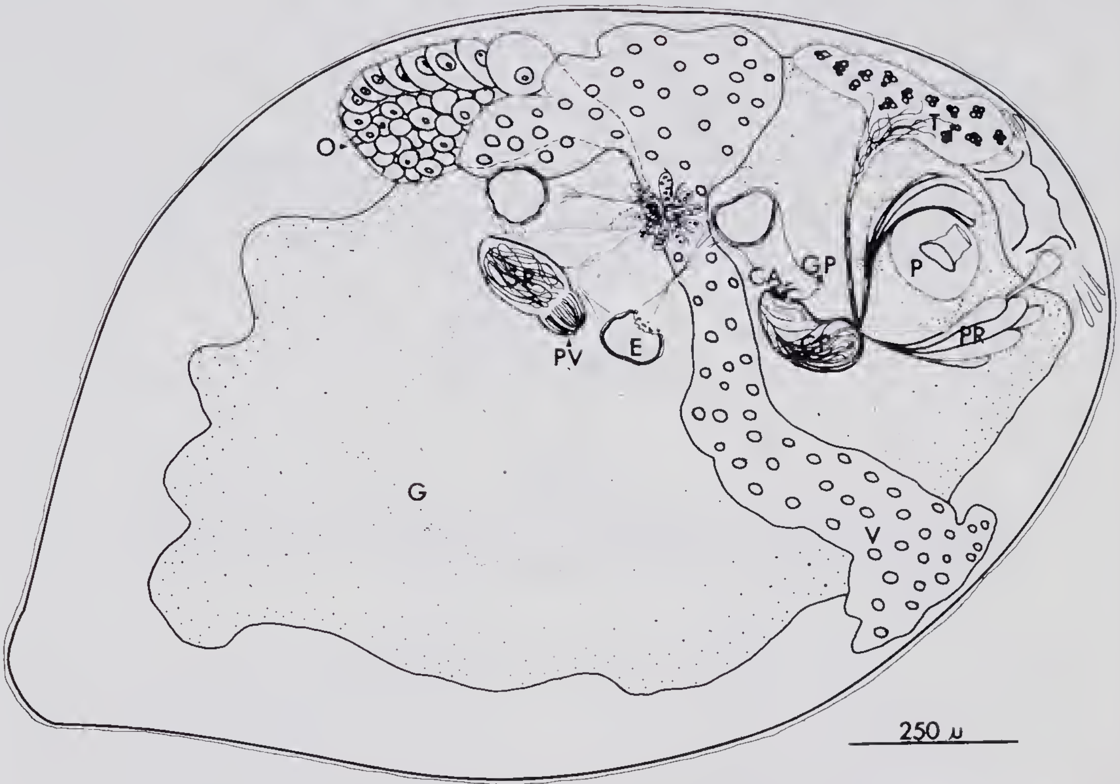

FIG. 1: Adult *Pterastericola vivipara* n. sp. (Scale is 250μ) CA, cuticular armature; CP, cirrus pouch; E, egg; G, gut; GP, gonopore; O, ovary; P, pharynx; PR, prostate glands; PV, pseudovagina; SG, shell gland; SR, seminal receptacle; T, testis; V, vitellaria.

copulatory armature of hook and stylet; ciliated larvae may hatch within and burrow out of parent.

Host: *Acanthaster planci* Linnaeus (Asteroidea).

Habitat: Pyloric caeca.

Locality: Great Barrier Reef, Australia.

DESCRIPTION

Worm (Fig. 1) pyriform tapering to blunt point posteriorly; slightly dorso-ventrally flattened when swimming or crawling, usually a ball in situ; anterior parenchyma with red pigment particularly in large specimens; measuring $\bar{x} \pm s = 722 \pm 87 \times 590 \pm 90\mu$ (range: 630–891μ × 387–702μ, N = 14); protonephridia lacking.

BODY WALL AND MUSCULATURE: Entire worm covered with ciliated epidermis 7 to 8μ thick, cilia 4 to 6μ long, basement membrane thin; (hot fixation causes epidermis to lift clear of membrane); rhabdoids lacking; clusters of large, deeply staining globules at base of cilia cover surface of young worms, but become increasingly scattered as worms mature. Body wall musculature of outer circular fibres, inner longitudinal fibres and between scattered oblique fibres; dorso-ventral muscles more common anteriorly than posteriorly; prominent musculature surrounds pharynx and cirrus pouch which are highly mobile in life.

PARENCHYMA: Large poorly staining cells, often vacuolated, fill posterior to give a foamy appearance, but only in life; these vacuolated cells readily take up aqueous neutral red and rapidly shrink in hypertonic salt solution; other large cells throughout about 18 × 12μ staining with haematoxylin grey to blue and containing vacuoles. Sub-epidermal glands common throughout surface parenchyma, their ducts anastamose discharging basic secretion through goblet-like ducts between epithelial cells; several, deeply eosinophilic glands in young worms run from mid-fore body to anterior tip.

NERVOUS SYSTEM: Bilobed neural mass mid way between mouth and anterior end; several anteriorly directed nerve tracts; two, principal, lateral nerve cords run posteriorly; sense organs not detected.

DIGESTIVE SYSTEM (Plate 30,a): Mouth without lips, sub-terminal, ventral about 120μ from anterior end; short, buccal cavity lined with large cuboidal cells with finely granular cytoplasm leads to large, muscular pharynx $\bar{x} \pm s = 111 \pm 14 \times 93 \pm 15\mu$ (range: $89 - 133 \times 71 - 116\mu$, N = 14); pharynx dorso-ventrally orientated in fixed material, opening into small oesophogial cavity lined with large, weakly eosinophilic, columnar cells which can extend through pharynx; large, saccate gut lying in dorsal body extends slightly forward from pharynx as well as extending posteriorly; gut separated from parenchyma by thin layer of cells below tall, columnar gastrodermis; three types of gastrodermal cells (a) phagocytic cells with intracellular food vacuoles, (b) secretion cells with evenly stained cytoplasm and (c) secretion cells with foaming cytoplasm; gut outpockets in large specimens.

MALE REPRODUCTIVE SYSTEM: Single testis lateral, just posterior to pharynx; sperm production synchronous; simple vas deferens leads directly to cirrus pouch where, passing through a narrow opening, it swells to form a seminal vesicle which has a narrow opening at base of male cuticular armature; armature (Plate 30, b), a plate with two chitinous horns — one terminating in a closed stylet $\bar{x} \pm s = 34 \pm 3\mu$ long (range $31 - 38\mu$; N = 5), the other is hooked $\bar{x} \pm s = 40 \pm 3\mu$ long (range $38 - 45\mu$, N = 5) with a narrow pore at end, opening away from stylet; sperm and seminal fluids are discharged through pore of hook; armature extends into a common genital atrium which opens mid-ventrally just posterior to mouth; two sets of glands have long ducts which lead to and enter cirrus pouch beside vas deferens and coil about seminal vesicle; the less common glands have granular cytoplasm, the more common ones are strongly eosinophilic, these have brown, foamy cytoplasm in life and secrete droplets (cementing?) through hook.

FEMALE REPRODUCTIVE SYSTEM: Single, biparitite ovary with inner layer of small, dividing cells and outer region of larger, maturing oocytes; ovary lateral, posterior to testis; oocytes seen passing down oviduct to ootype/mehlis gland complex; oviduct joined first by duct from seminal receptacle and then by joint vitelline ducts where they enter ootype; deeply staining basophilic cells surround ootype; uterus not evident in large specimens, eggs apparently pass into parenchyma; female pore with a short muscular region behind, opens in common genital atrium: some eggs seen extruded from pore, others fill parenchyma, in all stages of development, many hatching within worm; vitellaria paired, extending ventrally and laterally at level of common genital pore to margins of body where they expand dorsally and a little posteriorly; ovary and testis on right, thus left vitellarium is a little more extensive; seminal receptacle a simple, large, club-shaped sac filled with sperm in large specimens, but appears to open to the ventral surface through a small pore in small, less mature worms; muscle bundles (a pseudovagina) can sometimes be seen (Plate 30, e). Eggs sub-spherical to spherical measuring $\bar{x} \pm s = 84 \pm 6 \times 81 \pm 7\mu$ (range $76 - 98 \times 71 - 98\mu$, N = 11) with golden tanned walls; some eggs laid, others crumble (Plate 30, d) and ciliated larvae which hatch have been observed live (moving about within the parent) and in fixed and sectioned specimens (Plate 30, e).

REMARKS

This worm is similar to *Pterastericola fedotovi* Beklemishev, 1916 which was partially redescribed by Karling (1970). The worms share the same general shape, pigmentation and ciliation. Reproductive structures are more anterior and vitellaria less extensive than in *P. fedotovi*, however. Both testis and ovary are lateral in *P. vivipara* whereas the ovary in posterior and median in *P. fedotovi*. The male cuticular armature of *P. vivipara* has two sub-equal spines about 30 to 40μ long and about 10 to 15μ apart. The armatures of *P. fedotovi* illustrated by Beklemishev (1916) and by Karling (1970) do not curve similarly but they are larger, about 80μ; unlike that of *P. vivpara* the hook appears shorter than the spine. Host and locality differences between *P. fedotovi* and *P. vivipara* are considerable.

HABITAT AND DISTRIBUTION

Worms were found restricted to *A. planci* and were found only in starfish from the central Great Barrier Reef (Cannon, 1975). They were found more commonly in winter, but showed no correlation of incidence with size or sex of host. Cannon (1975) showed too, that though the worms occurred randomly throughout the caeca and fed upon the lipid rich caecal epithelial cells of *A. planci*, they were not pathogenic.

BIOLOGY

Worms may be seen as small, red balls tightly pressed in outpockets of the caeca similar to the habit of *Triloborhynchus astropectinis* (Pterastericolidae) described by Bashiruddin and Karling (1970). Though infection levels are rarely high, when they are, large numbers of worms of all sizes occur in the caeca from unpigmented juveniles to adults containing many eggs. Eggs may be laid, or may hatch within the parenchyma of the parent worm from which juveniles presumably break free (hence the specific name). Thus large populations no doubt build up within one starfish; transfer between hosts via eggs may be possible.

Larval worms are small and ciliated when first they hatch and measure $\bar{x} \pm s = 81 \pm 10 \times 65 \pm 4\mu$ (66 — 99 × 57 — 73μ, N = 10). Deeply staining eosinophilic glands lie laterally and open anteriorly. The function of the glands may be to aid hatching, but the movement of worms through the parent's body suggests they may be used to aid escape. Juvenile worms have not been observed in the coelomic fluid of the starfish, nor have adult worms, so penetration of the host caecal epithelium seems unlikely.

Discussion

The present species brings the total to five turbellarians recorded from Asteroidea. All are rhabdocoels contained within three genera, — *Triloborhynchus, Pterastericola* and *Acholades.* It is perhaps noteworthy that each genus has been recorded from hosts in different orders of Asteroidea; *Triloborhynchus* has been found in starfish of the O. Phanerozonia, *Pterastericola* from hosts of the O. Spinulosa, and *Acholades* from O. Forcipulata. The latter monotypic genus is unlike the others in either morphology or habitat being encysted within the walls of the tube feet of a Tasmanian starfish (Hickman and Olsen, 1955). Bashiruddin and Karling (1970) and Karling (1970) maintained *Triloborhynchus* and *Pterastericola* should be contained in the F. Pterastericolidae despite the reduced ciliation and posterior adhesive organ in the former genus, characteristics said by Karling (1970) to link *Triloborhynchus* with the Monogenea. Stunkard and Corliss (1951) considered *Pterastericola* related to the F. Umagillidae. The true affinities of these worms must await more detailed study.

It is not clear if the pseudovagina of *Pterastericola* functions in copulation (Karling, 1970). Unlike Karling (1970) who had only mature specimens of *P. fedotovi,* I had immature as well as mature specimens of *P. vivipara* and in one not fully gravid worm the pseudovagina appeared to open to the surface, whereas in sections of mature specimens no opening was seen. Karling (1970, Fig. 10) observed a break in the epidermis of *P. fedotovi.* It seems possible that the vagina is functional in young animals, but atrophies after copulation or as the worm matures. Alternately the musculature of the pseudovagina may serve as anchoring tissue for the stylet during copulation, enabling the sperms to be innoculated through into the parenchyma. Certainly Beklemishev (1916) reported wandering sperms in the parenchyma of *P. fedotovi* and hypodermic impregnation is known among the rhabdocoels (Hyman 1951, p.125).

The peculiar habit of eggs hatching within the parent body so that young are released into the parenchyma has been described for another Australian turbellarian *Avagina vivipara* Hickman (1956) from a heart urchin *Echinocardium cordatum.* This habit clearly shortens the life cycle and decreases dispersal, enabling large populations to build up in the one host. Although Hickman (1956) gave few details it seems likely the ciliated young of both these worms wander through the parent tissues until they eventually break free into the lumen of the gut of the host. According to Hyman (1951, p.135) members of the rhabdocoel group Typhloplanida often produce two kinds of eggs — thick shelled resistant ones and thin shelled subitaneous eggs from which young may hatch within the parent. Such eggs are presumed an adaptation to quickly increase the populations of worms at favourable times, but in temporary or unpredictable environments. Echinoderm populations are known to form dense aggregations (Reese, 1966). Worms able to multiply within their hosts when these hosts are rare would be advantaged. Perhaps this mode of reproduction alternates with normal egg laying when host populations are dense, similar to the Typhoplanids (Hyman 1951). On one occasion eggs were found in mucous trails left by infected starfish in aquaria. The method of feeding of *Acanthaster* would favour reinfection from mucous covering the substrate over which it everts its stomach.

ACKNOWLEDGMENTS

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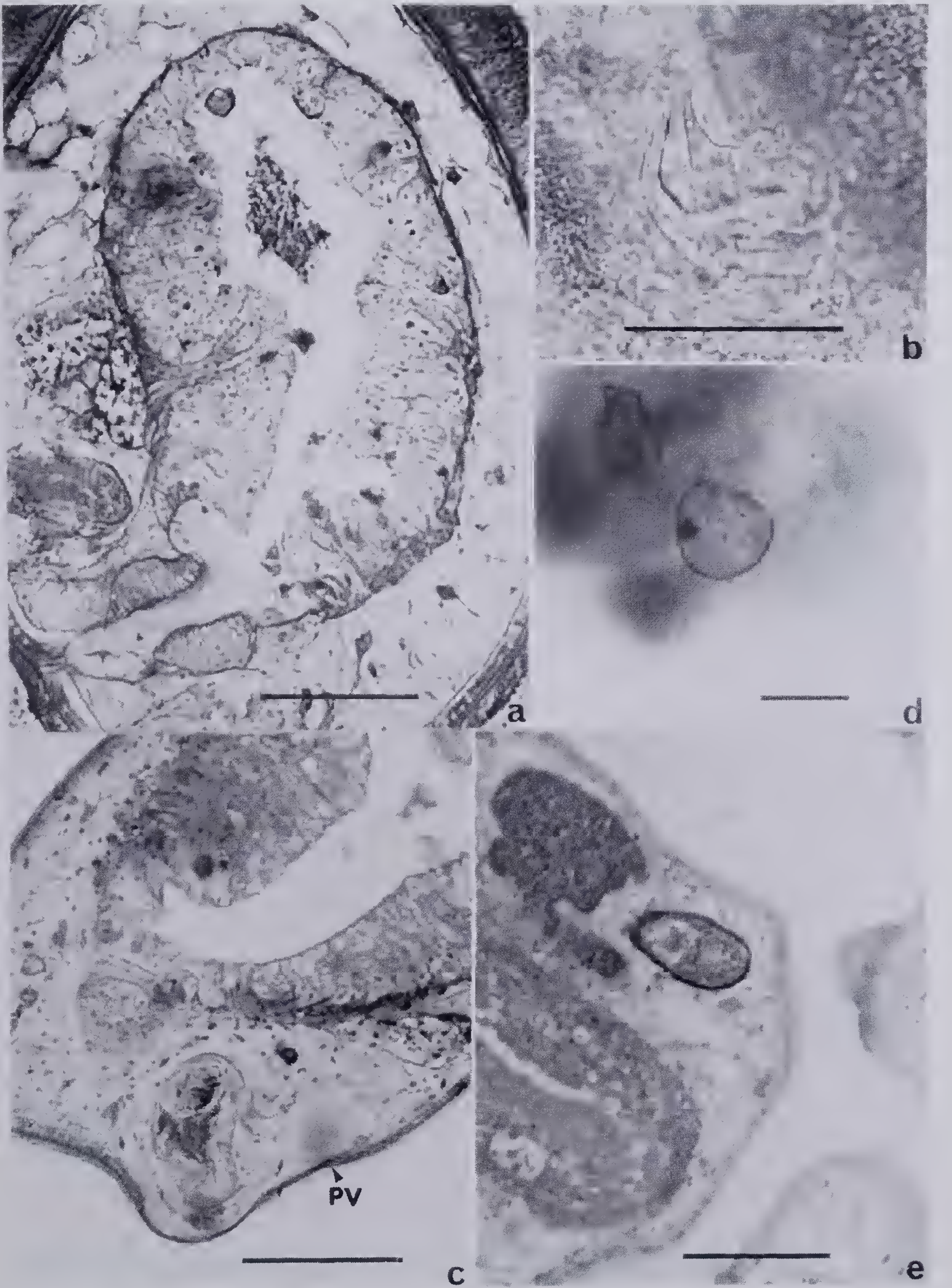
PLATE 30

(a) Section through gut of *P. vivipara in situ* (Scale is 100μ).
(b) Male copulatory armature (Scale is 50μ).
(c) Pseudovagina in sub-adult specimen (Scale is 100μ).
(d) Egg capsule after hatching within parent (Scale is 75μ).
(e) Section of adult with larva in tissues (Scale is 100μ).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THE MACROBENTHOS OF THE MIDDLE BANKS AREA OF MORETON BAY*

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ABSTRACT

This study was undertaken to quantify certain aspects of the benthic biota of the Middle Banks area, with a view to predicting the effects of sand removal for use as 'fill' in enlarging Brisbane Airport. Fifty–seven sites lying roughly in a rectangle 9 km × 1·5 km were sampled at 3 month intervals from September 1972 to June 1974. Each sample comprised duplicate catches with an 0·1m^2 Smith-McIntyre grab. The northern sites lie in the area of the proposed excavation and the southern ones (in deeper water) in a prawn fishing area. There is a sharp division between coarser northern and finer southern sediments, and suggestions of a progressive coarsening of sediments during the study.

A total of 468 'species' were originally sorted from the collections, a noticeably richer and more diverse biota than Bramble Bay (on the western side of Moreton Bay). To reduce the size of the data matrix to analyse, the first classifications were undertaken with successive lots of 50 taxa × 57 sites × 8 times. Sites were clearly separable into northern and southern subareas and the same broad area pattern was generated by abundant and less abundant species. Subsequent analyses involved separate consideration of the two sub-areas, and eventually 12 site-groups were recognised with their characterising species. Effects on the biota of current dredging of a navigational channel are detectable.

There were problems in separating microtopographical changes, due to inaccurate relocation of sites, from chronological changes. It appears that of the species investigated about 10% have recurrent seasonal patterns, about 40% have sequential patterns, and about 45% have obscure patterns, possibly influenced by microtopography. The sequential patterns are akin to those obtained in preflood data from Bramble Bay, with occupancy of appropriate areas for tolerably brief periods (e.g. 6 months) and then giving way to other species. Few of the sequential breaks appear related to abiotic conditions.

It is suggested that almost the entire biota is in a continual state of flux, with most species either annuals or 'subannuals', with few attaining sexual maturity in the area, with the population dependent upon recurrent recruitment, and with intermittent but severe predation by fish as an important possibility. The consequences of temporary human disturbance to the area are discussed.

A proposal to enlarge Brisbane Airport would involve 'filling' a considerable area with fine sand from the Middle Banks portion of Moreton Bay. The present work was requested by the (then) Commonwealth Department of Housing and Construction and by the Queensland Department of the Co-ordinator General hopefully to predict the effects of removal of the sand on the benthos.

There is already human interference in the Middle Banks area, with the south-western portion kept dredged to 12 m for shipping purposes. This breaks an otherwise W shaped area of banks shallower than 10 m and allows the considerable

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*Manuscript accepted October 1976.

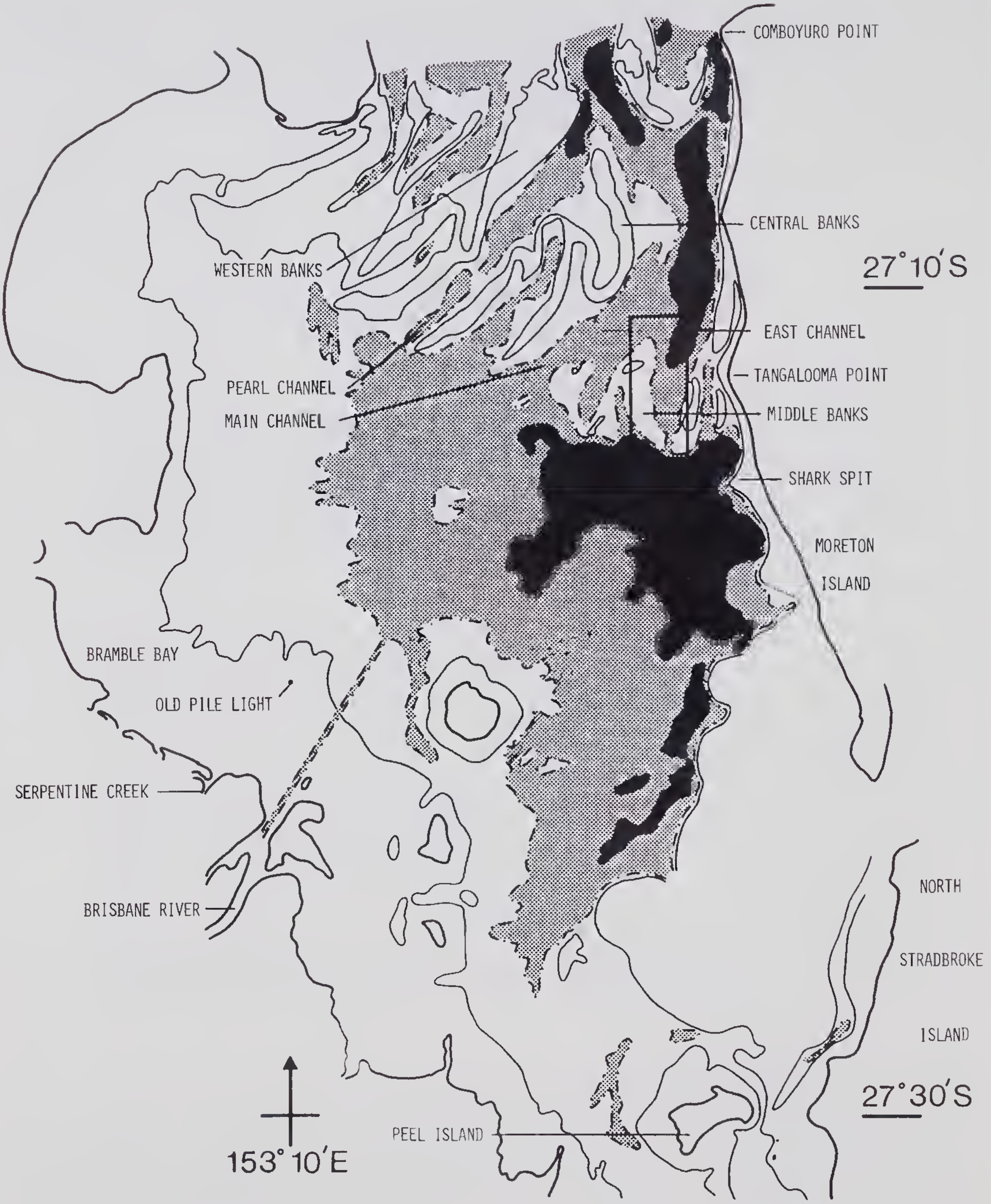

FIG. 1: Moreton Bay showing localities mentioned in the text, sampling area enclosed in rectangle. Depths from Admiralty chart 236 of 1973: > 20 m dark stipple, 10–20 m pale stipple, 5 m thin contin. line, high water mark thick contin. line.

tidal currents in the area more easy access to the deeper waters to the south.

The area initially selected for dredging lay on the eastern edge of the Middle Banks, abutting on the East Channel (see Fig. 1). The effects of dredging this area are likely to be numerous. First, benthic organisms and their environment would be removed from a relatively small area, and there would be an interval before this was recolonised. Secondly, the local topography would alter as sediments filled the excavated area. Thirdly, if the excavation led to generally increased current velocities in the area as a whole, it could lead to general erosion. While such erosion could facilitate navigation it could affect the benthos more widely, and possibly could affect the adjacent shores of Moreton Island. Fourthly, material suspended in the water during dredging would be distributed by the tides. The most important effects could well be due to the slower flood tide which would carry material into the deeper waters to the south. Here there is known to be a rich benthos (Stephenson, Williams and

FIG. 2: Location of sites within sampling area. Depths from 1972 survey by Queensland Dept. of Harbours and Marine: 10 fm broken line, 5 fm thin contin. line, high water mark thick contin. line. Sites as solid circles, beacons or buoys as crosses.

Lance 1970) and there is also a seasonal fishery for penoid prawns.

After considering the above, we advised against dredging near the existing dredged break in the banks because it was felt this would give maximal erosion and most widespread biotic effects and it is gratifying to record that this advice was accepted. The position tentatively selected was in the vicinity of our sampling sites 22, 25, and 26, (see Fig. 2).

A past survey of the area (Stephenson, Williams and Lance 1970) was made with a naturalists dredge and subsequent work at Peel Island in Moreton Bay (Stephenson, Williams and Cook 1974) has shown that this failed to reveal a substantial fraction of the benthos. Present experience showed that the van Veen grab used in near-concurrent studies in Bramble Bay (Stephenson, Raphael and Cook 1976, Stephenson, Cook, and Raphael 1977) was ineffective at Middle Banks except in some areas during the brief periods of slack tide. Hence an 0·1 m² Smith-McIntyre grab was employed and revealed a surprisingly rich and varied biota.

Past experience at both Peel Island and Bramble Bay has shown appreciable time changes in the benthos and to make even approximately effective predictions of the likely effect of sand dredging at Middle Banks, it was felt that sampling should continue at three month intervals for at least two years. Sampling began in September 1972 and before the work was due to be completed two natural catastrophes had occurred. These, a major flooding of the Brisbane River in January 1974 followed by a cyclone in March 1974, produced very marked effects on the biota of Bramble Bay, but preliminary examination of the present catches suggested only slight effects on the Middle Banks benthos, and so the project was concluded after the two years.

Biotic Sampling

Because of the rapid tidal currents, the effects of dredging will be greater to the north and south of the dredged area than to the east and west. Hence the sampled area was roughly in the form of a rectangle ca 9 km × 1·5 km. At both northern and southern extremities there were sufficient sighting marks for sites to be arranged on a grid ca 0·4 km apart but in the centre of the area due to a paucity of marks they lay on traverses ca 1 km apart.

Fifty-eight sites were originally sampled but because one (site 39) was overlooked on one occasion, for present purposes we consider 57 sites, with original sites 40–58 renumbered 39–57. (Labelled specimens to be deposited in the Queensland Museum carry the original numbering.) The positions of the final sites are shown in Fig. 2.

Locations of sites were by horizontal sextant angles on conspicuous objects in the vicinity (landmarks or beacons) and inaccurary in relocating sites is believed to be not greater than 50 m.

At each site on each occasion, duplicate catches were made with the 0·1 m² Smith-McIntyre grab. Catches were sieved through a final aperture of 1 mm and the two catches pooled, preserved and the biota separated from the residual sediment at base. The resultant biota is referred to as a sample.

Samples were obtained on eight occasions from September 1972 at three month intervals until June 1974, and these are referred to below as times 1–8.

Considerable difficulties were encountered in identifying species, this reflecting the paucity of work in similar environments in eastern Australia. Reference collections were established for what were adjudged to be species, and these were later referred either to named specimens collected in previous benthic surveys or to group experts (acknowledge later). In several cases the reference specimens belonged to more than one species, and these polyspecific taxa are indicated later. There were a few cases of 'oversplitting' and these were not apparent until all the numerical analyses were completed.

The Area of Sampling

1. General Description: The northern exit from Moreton Bay consists of alternate banks and channels which, south of the narrowest portion, run generally from a north-east to south-west direction. This portion has been called the 'north-eastern corrugations' by Stephenson, Williams and Lance (1970). The main features from west to east are Western Banks, Pearl Channel, Central Banks, Main Channel, Middle Banks, and East Channel. Larger vessels leave Moreton Bay through a dredged cutting in Middle Banks, then via the East Channel until it fuses with the Main Channel. North of the narrowest portion there are extensive banks to the north-west of Comboyuro Point, and the main navigational channel runs to the NNW.

The southern part of the sampled area lies in the deepest portion of Moreton Bay, earlier called the 'basin' by Stephenson, Williams and Lance (1970). Depths are almost 30 m and here the tidal current on the sea floor is likely to be negligible. The substratum contains obvious silt.

The general topography of the northern exit from Moreton Bay is suggestive of a basin *c.* 30 m deep which has been partially filled by sand. Maxwell (1970) states that wind and stream erosion as well as undercutting of the shore line have been responsible for large quantities of sand being carried westwards into Moreton Bay. Presumably Moreton Island has supplied the sand for the north-eastern corrugations.

While over a long period the Middle Banks area has become partially filled with sand, there is evidence that this has not been a continuous and progressive process. Three sets of soundings of the Middle Banks area have been made. The first made in 1865 show a considerable area of the Middle Banks shallower than 10 fm. The second soundings were made in 1946 and show an enlarged shallow area towards the south. A third set of soundings made by the Queensland Department of Harbours and Marine in relation to the Airport Scheme in 1972 show a reduction of the southern shallow area. This must be due to dredging the navigational channel. However the later soundings show that the portion of the East Channel deeper than 10 fm has become more extensive (see Fig. 3), and it seems likely that sand has been removed to the north. Throughout tidal currents are strong and underwater observations showed sand ripples *c.* 0·5 m high on the bottom in the vicinity of site 12 and these conditions probably apply to most of the northern sites. Here the sediment surface will be partially mobile and is very 'clean'.

2. SEDIMENTS: These were collected using the 0·1 m^2 Smith-McIntyre grab, with hand selection of an aliquot. (It was not appreciated at the times of collection that hand selection causes error, see Stephenson, Cook and Raphael 1977.) Samples were obtained in September 1972, September 1973 and March 1974. Analyses were by wet sieving as described in previous papers, using sieves of the following apertures in mm: 2·00, 1·00, 0·50, 0·25, 0·125, 0·063. The retained grades are described repectively as gravel = shell grit, very coarse sand, coarse sand, medium sand, fine sand, and very fine sand, with the material passing the finest sieve described as mud.

The data comprise a three-dimensional matrix of percentages of 7 sediments grades × 57 sites × 3 times. This was classified by a hierarchical agglomerative method (Bray-Curtis, group average) differing from the methodology for biotic data (see later) only in that sedimentary data were not transformed (they are already standardised by sample total). The method is identical with that used by Stephenson, Cook and Raphael (1977). Classification of sites by sediments is shown by dendrogram on Fig. 4a, and of times by sediments on Fig. 4b.

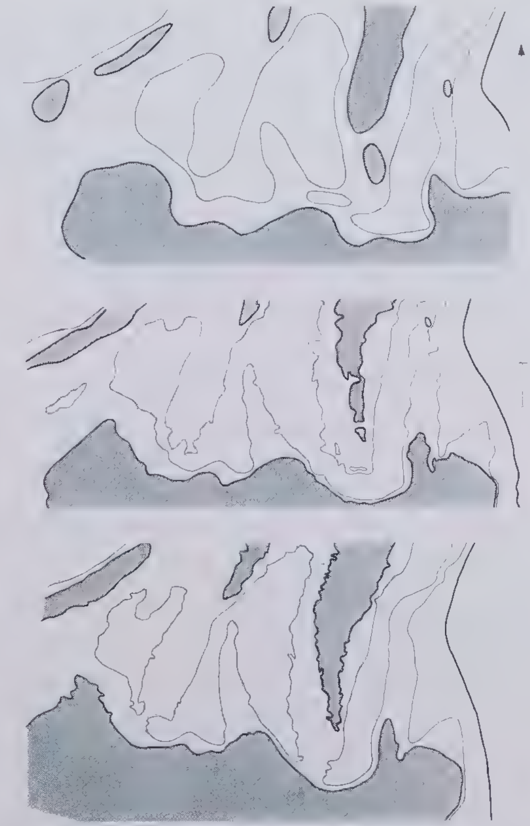

FIG. 3: Depths of southern ⅔ of sampling area on successive surveys; top 1865 survey, middle 1946, bottom 1972. Depths: > 10 fm, stipple; 6 fm, thin contin. line; 3 fm, dotted line; high water mark, thin contin. line. Arrow, true north; scale line 1 km.

The sites-classification gives an initial dichotomy at ca 70% dissimilarity and the main groups were accepted at 10-25% dissimilarity. In contrast the times-classification gives an initial dichotomy at ca 6% dissimilarity and the groups finally accepted were at ca 4% dissimilarity.

In the sites classification of sediments three main groups were first accepted, and the subgroups of two of these explored for topographic coherence. Only one showed this and hence four sediment site-groups were finally accepted, and on Fig. 5 these groups are map-plotted. They form a general sequence from site-group 1 in the south-west, through site-group 2 as a transverse southern band to site-group 4 in the north. Site-group 3 consists of flanking sites mostly forming a western wedge between site-groups 2 and 4.

Mean compositions of the sediments in the four site-groups are given in Table 1. In site-group 1 the modal grade of sediment is fine sand, followed by mud; in site-group 2 it is fine sand followed distantly by medium sand while in site-group 3 it is again fine sand but more closely followed by medium sand. The northern sediment site-group (4) differs markedly from the remainder in having medium sand as the modal group.

The mean composition of sediments in the three times are given in Table 1. This shows a progressive change towards coarseness over the period of investigation. It had been anticipated, following analyses on sediments in Bramble Bay, that the floods of January 1974 would have caused increased mudiness. By the time post-flood Middle Banks sediments could be collected there had been a cyclone. Wave action due to the latter could have been responsible for removal of mud and increased coarseness. Against this there is a distinct suggestion of progressive change.

TABLE 1: MEAN PERCENTAGES OF GRADES OF SEDIMENT IN SEDIMENT SITE-GROUPS AND SEDIMENT TIMES-GROUPS.

Sediment grade	Sediment Site-groups				Times		
	1	2	3	4	1 (Sept 72)	5 (Sept 73)	7 (March 74)
Mud	15·7	8·4	6·9	1·4	5·2	5·0	4·4
Very fine sand	4·4	1·9	1·7	0·1	1·0	1·2	1·0
Fine sand	76·0	78·7	59·8	13·4	40·6	36·9	33·8
Medium sand	3·6	12·9	31·7	83·6	52·0	56·1	59·6
Coarse sand	0·1	0·2	0·3	0·7	0·5	0·6	0·5
Very coarse sand	0·1	0·1	0·1	0·3	0·2	0·2	0·3
Gravel/shell grit	0·1	0·2	0·2	0·6	0·5	0·3	0·4

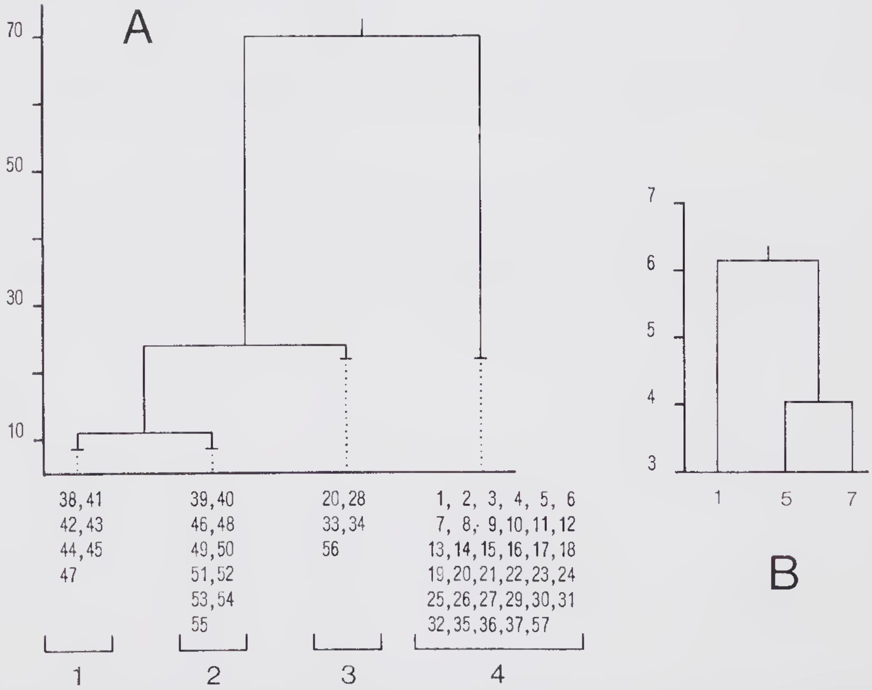

FIG. 4: Dendrograms showing classifications using sediment compositions as attributes: A of 57 sites, B of 3 times.

FIG. 5: Topographic distribution of the four sediment site-groups.

Further analyses were conducted, to determine in which sediment site-group the chronological changes were greatest. First, grades of sediments were reduced to five by fusion of coarse sand, very coarse sand and gravel. Next, in each sediment site-group the variance due to the three times in each sediment grade was obtained, and variances were then summated over grades. Results for sediment site-groups 1–4 were sequentially as follows: 10·08, 8·58, 220·52 and 42·06. There is greater variation in the two northern sediment site-groups (3 and 4) than in the two southern ones (1 and 2) with extremely high variance in sediment site-group 3.

3. HYDROGRAPHY: (a) Currents. No precise data are available on the extent of penetration of Pacific Ocean water into Moreton Bay and its mixation with the waters of the Bay. General observation suggests that surface water from outside the Bay penetrates to well beyond the sampled area on each tidal cycle.

Also no precise data are available on tidal currents. It is known that they flood from and ebb to the north and that surface currents are generally in excess of 1 km/hr apart from periods of slack water.

(b) Salinities. Data are available for Shark Spit (27°17'S., 153°22'E.) from a survey made by the CSIRO Division of Fisheries and Oceanography. The data from the deepest samples (*c.* 29 m) taken at Shark Spit have been reviewed by Stephenson, Cook and Raphael (1977). From August 1972 to July 1973 the salinity averaged 34·5°/₀₀ and ranged from 33·1°/₀₀ to 35·3°/₀₀. The variations showed a marked inverse relationship to rainfall in the catchment of the Brisbane River in the previous month.

From October 1973 to September 1974 the average salinity was 33·7°/₀₀ and the range of 32·0°/₀₀ to 35·1°/₀₀. There was a period of relatively low salinity (*c.* 32·1°/₀₀) from February 1974 to August 1974 evidently due to the effects of the excessive runoff from the flood of January 1974 being prolonged by the rainfall associated with the cyclone of March 1974.

It is clear that the effects of the extreme climatic disturbances on the salinities were prolonged but relatively minor.

(c) Temperatures. Data equivalent to the above on water temperatures are: August 1972 to July 1973, mean 22·25°C, range 17·2–26·6°C; October 1973 to September 1974, mean 21·79°C, range 15·9–25·8°C. Comparison with data average over the period 1931–50 at the Old Pile Light near the mouth of the Brisbane River suggests that from December 1972 until about December 1973 temperatures at Shark Spit were consistently about half a degree warmer than average.

BIOTIC DATA — ANALYSES INVOLVING ALL SPECIES

Many species were present in so few samples and in such small numbers that they are excluded from later analyses. These rarer species are important in aspects such as faunistics, species richness and diversity, and these and similar topics are dealt with in the present section.

FAUNISTIC COMPOSITION OF THE SAMPLES: A total of 468 taxa were obtained originally, and this reduced to 463 because of 'oversplitting'. Fifteen of the listed taxa are known to be polyspecific. All but the rare species are listed in the Appendix, together with the code numbers used throughout.

The number 463 compares with 420 taxa (excluding amphipods) from grab sampling an area of *c.* 3 km^2 near Peel Island (Stephenson, Williams and Cook 1974), 182 from an area of 30 km^2 in Bramble Bay (Raphael 1974) and 98 from Serpentine Creek (Stephenson and Campbell 1977).

Of the 463 taxa 31·8% were polychaetes, 27·9% crustaceans (10·6% decapods and 7·2% amphipods), 23·5% molluscs (10·8% gastropods and 12·5% bivalves) and 6·3% echinoderms. The recording of 18 species of cumaceans and 14 species of fish was noteworthy. Amongst the latter were small specimens of dubiously benthic species, and several crustaceans (e.g. *Lucifer)* were also doubtfully benthic. Unless clearly non-benthic (e.g. some crustacean larvae, and some planktonic molluscs) all taxa which were caught are listed.

Distribution Patterns of Rarer Species: Rarer species are here taken as those in which only one or two individuals were recorded in the survey. By taking recordings of each individual and summating over times we can determine whether the rare species were concentrated in any patterns of sites, and conversely by summating over sites we can search for patterns in times.

The number of rarer recordings in sites ranged from zero to 10, and map plotting suggested a pattern in the data somewhat comparable to that obtained in the sediment site-groupings. Mean numbers in sediment site-groups were: site-group 1 (South-west) 3·57, group 2 (southern transverse band) 4·00, group 3 (flanking middle) 8·20 and group 4 (northern) 2·35. Overall the northern area has few rare recordings, the southern area an intermediate number, and the middle flanking portion (with the most unstable sediments) has the largest number.

The number of rare recordings in times ranged from 18 to 29 with September values (mean 28·5) noticeably greater than the remainder.

Sites × Times Analyses: The total data which were available for analysis formed a three dimensional matrix of 468 taxa *(s* for species) × 57 sites *(q* for quadrats) × 8 times *(t).* By summating over species we derived $q \times t$ matricies with dimensions of 57 × 8 and two such summations were considered. The first involved the number of species *(s)* per sample; this is a simple measure of diversity and in Hulbert's (1971) terms it is the species density appropriate to the particular sampling parameters. The second summation was the total number of individuals *(n)* of all species, and is the numerical equivalent of biomass. Numerous sample measures other than direct summations are available provided species become anonymous, and we used the standardized Shannon diversity (to log base 10) which we designate *d*. These three measures *s*, *n*, and *d* were previously used in work on Bramble Bay by Stephenson, Cook and Raphael (1976) (albiet with different symbolism) and Stephenson, Cook and Raphael (1977) and because the sampling procedures differed only in the type of grab employed comparisons can be effected. It is appreciated that with polyspecific and fractionated taxa, the value of *s* and *d* are somewhat inaccurate.

We are interested firstly in means over all samples. These are for *s* 32·14, for *n* 170·23, and for *d* 1·143. They compare with 12·2, 158·4, and 0·74 respectively for preflood conditions in Bramble Bay (Stephenson, Raphael and Cook 1976). Clearly the Middle Banks grounds as a whole carried a richer and more diverse biota than did Bramble Bay in the preflood sampling.

Secondly we are interested in the variation of *s*, *n* and *d* values between sites and between times. This requires first averaging by rows and by columns in each of the $q \times t$ tables, and secondly assessing the variability in row means and in column means. Variation was expressed as ranges and variances and results are given in Table 2.

These results show there is greater heterogeneity in sites than in times, with the ratios of variances being 4·72 for *s*, 2·94 for *n* and 8·67 for *d*. While a fraction of the differences may be due to greater 'random' variation in the sites data which are meaned over eight times compared with

TABLE 2: Ranges and Variances of Mean Values of *s*, *n* and *d* in Sites and in Times.

	Sites Means		Times Means	
	Range	Variance	Range	Variance
s	20·10–57·13	82·30	24·67–38·30	17·42
n	67·75–392·88	8393·4	85·44–217·65	2854·6
d	0·978–1·394	0·00702	1·104–1·186	0·00081

times data over 57 sites, the greater importance of sites in the overall heterogeneity is believed to be a real phenomenon. The Bramble Bay work showed a most marked time effect due to the flood of January 1974 (Stephenson, Cook and Raphael 1977) but this is not apparent in the present data.

Table 2 shows reasonable constancy in diversities (d) from place to place and from time to time. This suggests that changes in numbers of species and number of individuals 'balance out' in the diversity formulation as noted previously in the postflood data from Bramble Bay and also in work on the Serpentine Creek benthos by Stephenson and Campbell (1977).

Significant positive correlations were obtained between s, n and d for the different sites Spearman rank correlation coefficients were: between s and n +0·83, between s and d +0·68 and between n and d +0·33.

Data on time trends are given in Table 3. Spearman rank correlation coefficients between the three sets of values were: s and n +0·98 (very highly significant), between s and d +0·24 and between n and d +0·13 (neither significant). This suggests that chronological changes in s and n are again sufficiently parallel almost to cancel out effects in diversity.

Table 3 shows high values of n in each of the two Septembers, and this follows the pattern obtained in an earlier study at Peel Island (Stephenson, Williams and Cook 1974). The results are also similar in that lowest values occur in March of a non-flood year. Values of s follow the same tendency, but no general tendency is apparent in the diversity data.

CLASSIFICATORY TECHNIQUES

GENERAL TECHNIQUES: The general approach is classificatory, beginning with a three dimensional matrix of s (species) × q (sites or quadrats) × t (times). By summation over times we drive an $s \times q$ matrix and by classification obtain site-groups and their related species-groups; similarly by summation over sites we derive an $s \times t$ matrix and hence times-groups and their related species-groups. The classification of the two derived matrices (viz. $s \times q$ and $s \times t$) followed the methods used by Stephenson, Raphael and Cook (1976) and this involved: transformation of data using $\log_{10}(n+1)$, Bray-Curtis dissimilarity measure, group average sorting. For entity (i.e. site or time) classification data were not standardised; for species classification the transformed data were standardised by totals prior to deriving inter-species dissimilarities.

Past experience has shown that the main objection to this method lies in the species classification where rarer species form isolated and 'dominating' species-groups. It was hoped that by operating in the first instance within narrow ranges of species abundances that this objection would be less serious (see later). In fact the species groupings which were obtained throughout still left much to be desired.

Following earlier work (Stephenson, Raphael and Cook 1976; Stephenson and Campbell 1977; Stephenson, Cook and Raphael 1977) we take the view that species should be placed in the same species-group if they characterise groups of entities (sites or times) in a similar way. A satisfactory entity classification then becomes a necessary pre-requisite to a satisfactory species classification. Because of occasional misclassifications, some re-allocation of entities may be necessary, involving either the occasional and obvious cases (e.g. Stephenson and Williams 1971) or by procedures such as REMUL (Lance and Williams 1975). In the present cases there were no obvious misclassifications and re-allocations have not been made.

If the entities are sites then the next step is to replace the species × sites matrix by the much smaller species × site-group matrix—this contains the mean recordings of the species. By inspection we can immediately see which species may positively characterise a given site-group by occurring there in proportionally the largest numbers.

TABLE 3: MEAN VALUES OF s, n AND d AT DIFFERENT TIMES

	Times							
	1 (Sept 72)	2 (Dec 72)	3 (March 73)	4 (June 73)	5 (Sept 73)	6 (Dec 73)	7 (March 74)	8 (June 74)
s	32·88	28·23	24·67	32·65	38·30	35·32	33·54	32·53
n	185·21	128·54	85·44	171·05	271·65	191·61	162·25	165·09
d	1·115	1·144	1·104	1·127	1·139	1·186	1·172	1·163

However the variability of recordings within the site-groups may be such that differences between means are misleading. To locate such cases, as in work of the recent past, we use a 'pseudo-F test' and employ such terms as 'conformity' and 'noticeably different' instead of 'significant', using the 0·05 probability appropriate to the F test as a cut-off point.

For a given array of species recordings arranged in site-groups there are many possibilities for testing, for example each site-group set against all the remainder, each pair of site-group sets against the remainder etc. It has been found more economical to perform pseudo-F testing by a programmable hand calculator on those sets suggested by perusal of the data, than to test all by a computer-based programme.

Pseudo-F testing reveals species which do not conform to the entity-groupings. When species with a range of abundances are considered we may expect non-conformers to include common species which are evenly distributed amongst the entity-groups and which must not be lost sight of. We may also expect them to include rarer species insufficiently concentrated in any entity group for the results to be meaningful.

DATA REDUCTION: In benthic work there are typically many rare species which add little to the ecological understanding of an area beyond the contributions they make to analyses like those of the previous section. There is a more pragmatic reason for their exclusion: they greatly increase computing costs and their inclusion may result in the computer being unable to accept the total data. In the present case, to achieve the limiting matrix of 199 × 57 × 8 would mean excluding species occurring 12 times or less, and it was felt this might be too severe. Because there are objections to most of the methods of data reduction previously employed we here attempted alternative approaches. The first consisted of dealing with the species in successive lots of 50 and compared the classifications obtained. This showed, *inter al*, that the sites were divisible into two markedly dissimilar groups. We then considered the two groups of sites separately — by reducing the q dimension in the matrix the critical s dimension becomes automatically reduced.

ANALYSES ON LOTS OF FIFTY SPECIES

The potential advantages of this method are first that the 'stopping rule' as regards species is indicated by the data themselves. It occurs at that point in the successive analyses when either no patterns or 'nonsensical' patterns emerge. This involves only a minimum of subjectivity. Secondly it shows whether the patterns revealed by the abundant and less abundant species are similar, and thirdly the results should be less dependent on the data transformation which is employed. This is because there is a narrower range of abundances in a matrix; in practice this relative independence increased as we moved to the less abundant group of species. It was anticipated that the main disadvantage of the method would be in comparing the results of the different analyses but in the event this was only a minor problem.

We deal first with all $s \times q$ analyses, then all $s \times t$ analyses.

SPECIES × SITES ANALYSES: We first consider the site classifications, then the conforming species.

(a) Sites — first 50 species: The dendrogram of the classification (Fig. 6A) shows remarkably clear separation into two site-groups which consist of southern and northern sites. Apart from a single site (29) the boundary follows the topography of the area, and coincides with the 10 fm depth contour on the 'lip' of the Middle Banks. Three subordinate groupings are evident within the southern subarea, and although these have topographic coherence we do not discuss them further at this stage.

(b) Sites — second 50 species: The dendrogram (Fig. 6B) again shows clear separation into northern and southern site-groups, although less clearly than in the previous dendrogram. The two main site-groupings are identical with the previous ones. Three subordinate groupings are again evident in the southern subarea but their constituent sites are not identical with the previous ones.

(c) Sites — third 50 species: The northern and southern site-groups were identical with those above.

(d) Sites — fourth to sixth lots of 50 species: In the fourth lot the results were only broadly similar to the above with one subgroup mostly of topographically northern sites (7, 20, 23, 24, 29, 35) in the main southern group which also included site 36. In the fifth lot excluding two vacant sites (9, 27), the original groups were revealed excepting that site 31 was in the southern group. In the sixth lot of species the south and north pattern was not evident. There were eight isolated sites and three groups at a 98%

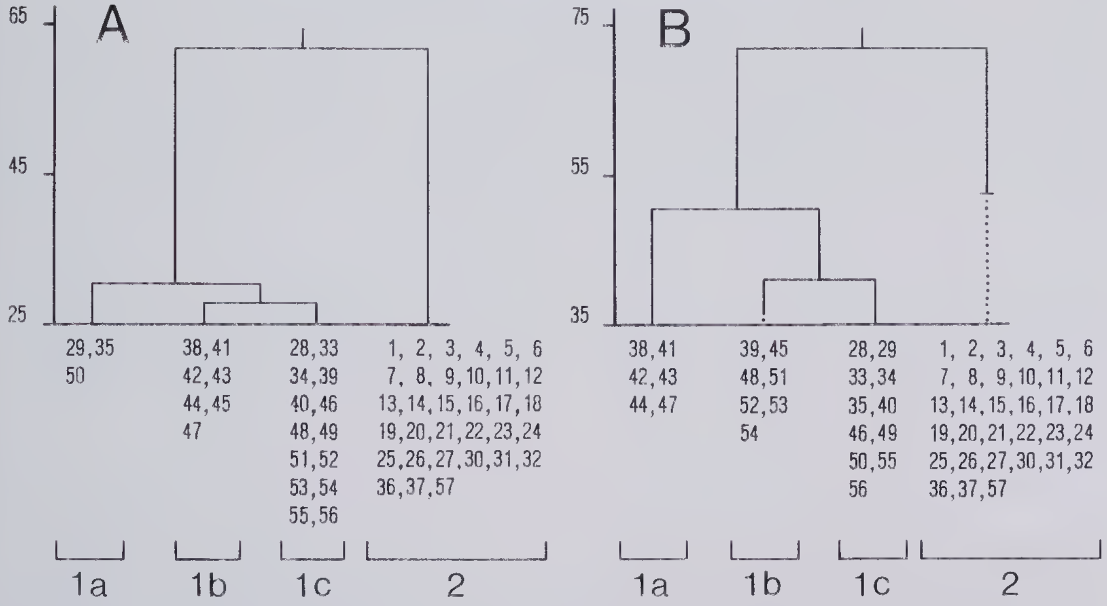

Fig 6: Dendrograms of site classifications using species recordings as attributes: A first 50 spcies, B second 50 species.

dissimilarity level with only one group showing approximate topographic coherence. The stopping point is clearly at or about the fifth lot of species (species occurrence >6).

The distinctiveness of the northern and southern subgroups decreased progressively from the first to the fifth lots of species. This is indicated in Table 4.

TABLE 4: Levels of Dendrogram Fusions for Species Lots with Declining Abundances

Species lot	Approx level of lowest fusions	Approx level of highest dichotomy
First 50	10	60
Second 50	20	70
Third 50	30	85
Fourth 50	40	90
Fifth 50	50	100

(e) Conformity of species to main site-groupings: For species in the first to third lots, the main site-groups are identical. For species in the fourth to sixth lots of 50 it seems more appropriate to test conformity to the general pattern than to the fragmenting remnants of it.

In these cases the rationale of testing for conformity is altered. We obtain groups from elsewhere and test on the lines of a 'construction set' of data and a 'validation set'. Instead of 'noticeable differences' of species distributions we might now approximate more closely to 'significant differences' excepting that the problems of non-normal distribution with series of zero recordings became more acute.

The sixth lot of 50 species takes in only some of the species in which three specimens were recorded and omits others so the present testing was extended to all occurring three times. Below three recordings there can be no conformity in the sense we have used the term.

Results of conformity tests to the southern and northern groups of sites covering all species except the less abundant ones are given in the Appendix. It will be noted that more species positively characterise the southern site-group than the northern one. With decreasing abundance of species there are increasing proportions which fail to conform. Thus for 6 and 7 recordings the percentage not conforming is 29, for 5 recordings 36, for 4 it is 56 and for 3 it is 65.

(f) The main 'communities': If we view a benthic community as an area and the species which characterise it positively, then we have two main communities. It is of interest that identical areas show up in analyses on the first, second and third sets of species and an almost identical one in the fifth set. Clearly the abundant and less abundant species follow the same broad area pattern.

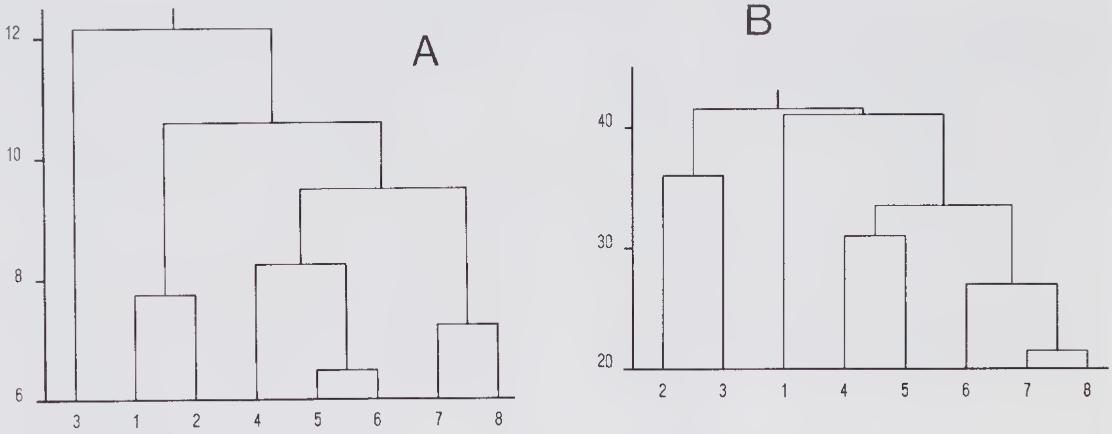

FIG. 7: Dendrograms of time classifications: A first 50 species, B third 50 species.

There are very many conforming species, 158 in the southern community and 80 in the northern one, and to assist comprehension these data must be compressed. If we list only the five commoner species which conform to each of the areas we arrive at a southern community of *Prionospio*, tanaid 1, *Solemya*, *Callianassa* and *Poecilochaetus* and a northern community of *Urohaustorius*, *Amphiura octacantha*, *Concholestes*, mysid 4 and amphipod 3. Four of the northern species are small crustaceans which are possibly mobile; mobility could be an advantage in this generally turbulent area.

Conforming species are possibly different from numerically dominant species — a conforming and dominant species in the southern area may well be a dominant species (but clearly not a positively conforming one) in the northern area. Purely on a dominance basis the southern area is a community of *Prionospio*, tanaid 1, *Solemya*, *Poecilochaetus* and *Discobotellina* while the northern area is a *Urohaustorius*, *Prionospio*, *Amphiura octacantha*, *Concholestes* and mysid 4 community.

SPECIES × TIMES ANALYSES: Time classifications of the first and third lots of 50 species are shown as dendrograms on Fig. 7, and these are representative of the remainder. No two classifications were identical and the only common grouping was of times 7 and 8. The times were grouped in a sequential or near-sequential order throughout, and there were never close groupings of the equivalent seasons of the two years.

By comparing Figs. 6 and 7 it is evident that dissimilarities between times are much less than between sites.

With the lack of constancy in time patterns, tests of conformity of species to these patterns are on a somewhat shifting basis. Taking three times-groups in each case gave only 75 conforming species compared with 238 conforming to two site-groups. Further consideration of times-groupings is deferred until the next section.

BIOTIC DATA — SEPARATE ANALYSES OF NORTHERN AND SOUTHERN AREAS

GENERAL: For reasons given earlier it was decided to subdivide the study area into southern and northern subareas and to analyse each separately. Additional reasons are (a) by working within these respective communities heterogeneity is greatly reduced, (b) special attention can be given to the northern area which would be most immediately involved in human interference, (c) it is possible that time changes differ in the two areas.

The problem about subdivision is that three different criteria can be used and each gives slightly different results. Using sediments site 20 is included in the southern group, but its biotic and topographic affinities are with the northern group. Using topography site 29 is in the northern group, but using biotic affinities it is in the southern. Site 36 alters affinities between one biotic classification and another. Eventually an overlapping division was decided upon with sites 29 and 36 in both groups. The northern group then consists of sites 1–27, 29–32, 36, 37 and 57 (34 in all) while the southern group consists of sites 28, 29, 33–36, 38–56 (25 in all).

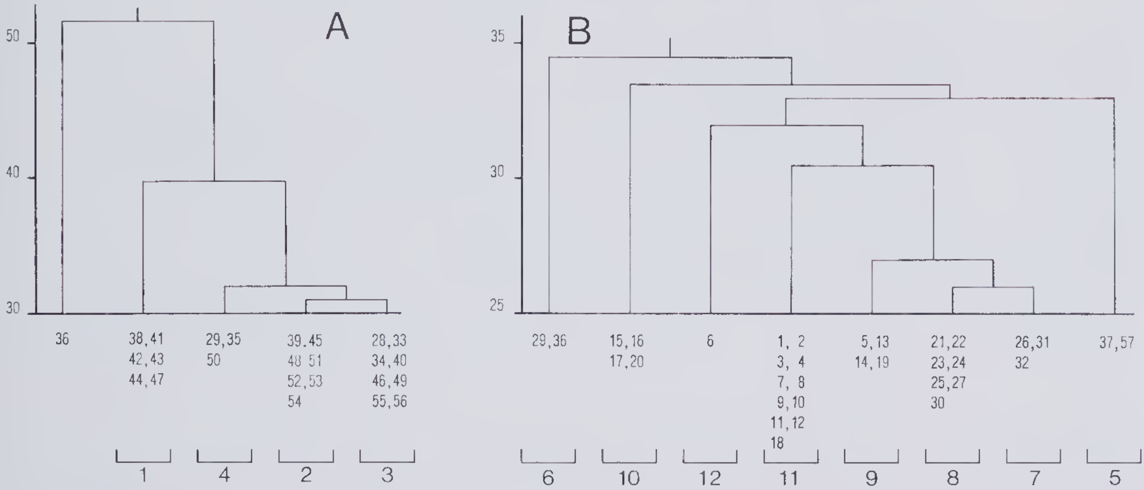

FIG. 8: Dendrograms of site classifications in A southern and B northern sub-areas. (Site-group 12 is disregarded in the main analysis.)

FIG. 9: Topographic distribution of the 11 main site-groups. Site-groups 4 and 6 overlap and their individual sites are shown by the symbols indicated.

SPECIES CONSIDERED: An arbitrary cut-off level was adopted, and species occurring less than 10 times in the reduced data were excluded. Because we now look for finer patterns and hence more site-groups, a higher cut-off level than previously was thought desirable. It was confirmed later as being approximately correct. The southern analyses involved 159 species and the northern ones 115.

SPECIES × SITES ANALYSES: (a) Sites classifications. The dendrograms of site-classifications are given in Figure 8. We first consider the marginal sites 29 and 36 common to the two analyses. Site 36 joins the southern area dendrogram at a much higher dissimilarity level than for the northern area and is henceforth considered as a northern site. Site 29 is ambiguous in its affinities and is treated as both a northern and southern site.

In Figure 8A four site-groups are readily recognisable at a dissimilarity level of *c.* 30% and these show topographical coherence. They are map plotted in Figure 9 and numbered 1–4 in a S-N direction. In Figure 8B at just over 30% dissimilarity there are five groups of very dissimilar sizes. The largest group divides at a slightly lower level to give groups of 11 and 14 sites and of these the former gives a chained series and is retained as a unit. The latter spans the area of greatest interest where excavation may occur, and divides into three topographically coherent sub groups at about 25% level. These subgroups were retained. In all eight northern groups were tentatively accepted and are map plotted as groups 5–12 (see Fig. 9). Site-group 12 consists of the single site 6 which is marginal to the area of

TABLE 5: SPECIES CONFORMING TO THE FOUR SOUTHERN SITE-GROUPS.

Category	Species
Most in site-group 1	25, 16, 19, 90, 111, 134, (=6)
Approx coequal most site-groups 1 and 2	14, 29, 98, 96, 118, 124, 170 (=7)
Most in site-group 2	156, 176 (=2)
Approx coequal most site-groups 2 and 3	1, 9, 15, 37, 66, 75, 139, 146, 181, 212 (=10)
Most in site-group 3	3, 4, 45, 65, 94, 108, 93, 172, 137, 173, 175, 219 (=12)
Approx coequal most site-groups 3 and 4	52, 48, 68, 63, 64, 32, 61, 53, 34, 20, 84, 83, 88, 103, 22, 85, 126, 135, 128, 151, 113, 131, 49, 143, 147, 161, 168 (=27)
Most in site-group 4	51, 8, 2, 7, 23, 21, 81, 46, 18, 43, 106, 58, 56, 150, 129, 6, 44, 57, 70 (=19)
Most in site-groups 1, 2, 3 (least in 4)	24, 27, 33, 36, 38, 60, 95, 127, 159 (=9)
Most in site-groups 2, 3, 4 (least in 1)	26, 30, 39, 35, 97, 74, 107, 117, 77, 144, 141 (=11)

Species are ranked from those with highest to those with lowest recordings in each group.

TABLE 6: SPECIES IN THE SEVEN NORTHERN SITE-GROUPS.

Category	Species
Approx coequal most site-groups 5 and 6	31, 3 (=2)
Most in site-group 6	1, 10, 4, 52, 9, 30, 15, 63, 26, 13, 11, 40, 83, 37, 41, 91, 17 (=17)
Most in site-groups 5, 6, 7	138 (=1)
Most in site-groups 6 and 7	5 (=1)
Most in site-group 7	49, 199 (=2)

TABLE 6: cont

Category	Species
Most in site-groups 7 and 8	160 (=1)
Most in site-group 8	54, 86, 104 (=3)
Most in site-groups 7, 8, 9	7, 57, 70, 91, 163, 93, 109 (=7)
Most in site-groups 7, 8, 9, 11	20, 59 (=2)
Most in site-groups 6, 7, 8, 9	23, 77 (=2)
Most in site-group 9	6, 8, 102, 89, 116, 203 (=6)
Most in site-group 10	21, 47, 55, 155, 182 (=5)
Most in site-group 11	43, 99, 136, 140 (=4)
Most in site-groups 10 and 11	2 (=1)
Most in site-groups 9, 10, 11	32 (=1)
Most in site-groups 9 and 11	105 (=1)
Most in site-groups 5, 6, 7, 8 (least in 9, 10, 11)	39 (=1)
Most in site-groups 5, 6, 7, 8, 9 (least in 10, 11)	34 (=1)
Most in site-groups 5, 6, 7, 8, 9, 10 (least in 11)	113 (=1)
Most in site-groups 6, 7, 8, 9, 10, 11 (least in 5)	18 (=1)
Most in site-groups 5, 7, 8, 9, 10, 11 (least in 6)	22 (=1)

Species are ranked from those with highest to those with lowest recordings in each group.

interest and is disregarded in subsequent analyses.

(b) Species-groupings, southern sub-area. Of the 159 species considered, 42 did not conform to any rational arrangement of site-groups. Of the six species occurring 11 and 10 times, only one conformed indicating a correct choice of cut-off point.

The conforming species are listed in Table 5 which shows that in general more species characterise two site-groups than one. If we include species characterising one, two or three, site-groups, then 22 species characterise site-group 1, 39 site-group 2, 69 site-group 3 and 57 site-group 4. To describe communities in terms of these numbers of characterising species is not helpful. As stated earlier an alternative method is not to consider conforming species but instead a few of the numerically dominant species in each site-group and this we follow.

(c) Species-groupings, northern sub-area. Of the 115 species considered, 54 did not conform to any rational arrangement of site-groups. Of the four species occurring less than 12 times, only one conformed, again confirming the choice of cut-off level.

The conforming species are listed in Table 6, which shows that site-group 6 has the largest number of uniquely characterising species (17); this agrees with the isolated position of site-group 6 on the dendrogram (Fig. 8B).

Many of the species conform to combinations of site-groups, with the largest number (17) involving site-groups 7 and 8 followed by site-groups 7, 8 and 9 (16spp.). This confirms the similarity of these site-groups, again as shown in the dendrogram.

Counting species which characterise more than one site-group, then 7 characterise site-group 5, 27 site-group 6, 21 site-group 7, 20 site-group 8, 23 site-group 9, 10 site-group 10 and 11 site-group 11.

(d) Overall view of site-groups. Table 7 shows the site composition of each of the eleven main site-groups considered, and their more abundant characterising species. Data from the previous $q \times t$ analyses are added to this table. They comprise the mean number of individuals of all species per site in a site-group per time $(\bar{n})$, the mean number of species $(\bar{s})$ and mean standardised Shannon diversity (to log base 10) $(\bar{d})$.

Site-group 1 occupies the extreme SW. of the sampled area where sediments are predominantly fine sand (76%) with the highest percentage of mud (ca 16%), and in relatively deep water (ca 31 m). It may be described in terms of dominants as a *Schizaster* — *Nucula* — *Prionospio* community and within the southern area has the lowest average population (197), lowest species density (36), and lowest diversity (1·12).

Site-group 2 forms an arc to the north of site-group 1 in slightly shallower water (mean depth *c.* 30 m). It was not clearly distinguished by its sediments but these are predominantly of fine sand (79%) followed by medium sand (10%). It may be described as a *Prionospio* — *Aglaophamus* — *Callianassa* community, has a high average population (278) and for the southern sub-area a relatively low species density (38) and diversity (1·17).

Site-group 3 (depth *c.* 22 m) is parallel to and to the north of site-group 2. It does not precisely follow the topography of the area, lying at a slight angle to the 20 m contour and is mostly deeper than this. It is not clearly distinguished by its sediments. These are predominantly fine sand (69%) followed by medium sand (24%). It may be described as a *Prionospio* — tanaid — *Solemya* community. It has the highest recorded population (320) and number of species (48), and the average of the diversity in the total area (1·20).

Site-group 4 (depth ca 16 m) consists of three sites straddling and somewhat askew to the 20 m contour just south of the southern 'lip' of the sampled area. Its sediments are highly variable, site 50 having predominantly fine sand (78%), and both sites 29 and 35 having predominantly medium sand (76% and 66% respectively). It could be described as a *Rhizammina* — *Discobotellina* — *Prionospio* — *Solemya* community but for the fact that the first named species is markedly seasonal. The population (215) is below the average for the southern site-groups but much in excess of any northern groups. The species density (46) is almost that of site-group 3, and the diversity (1·29) is the highest of the southern site-groups. Almost identically high diversity also occurs in site-group 6 (depth *c.* 9 m) which again contains site-group 29. It can be described as a *Prionospio* — *Urohaustorius* community, has the lowest population (79) of any site-group, the lowest species density (24) but the highest diversity (1·56). Site-group 5 is at the western edge of the Middle Banks lip, with a modal sediment of medium sand (82%). It is a *Prionospio* — *Urohaustorius* — tanaid community and if reckoned as within the northern sub-area has its highest population (143), and species density (38), and has a high diversity (1·30), second only to site-group 6 (depth *c.* 11 m).

TABLE 7: DETAILS OF SITE-GROUPS.

Site-group	1	2	3	4	5
Constituent sites	38, 41, 42 43, 44, 47	39, 45, 48, 51, 52, 53, 54	28, 33, 34, 40, 46, 49, 55, 56	29, 35, 50	37, 57
Most abundant species (occurrences*)	25(22), 12(22), 1(21), 10(18), 16(17), 19(14), 14(14), 11(11)	1(72), 11(17), 5(14), 9(14), 3(13), 4(12), 3(11)	1(77), 3(32), 4(30), 9(16), 13(13), 15(12)	28(27), 10(20), 1(16), 4(14), 3(10)	1(11), 2(9)
$\bar{n}$*	197	278	320	215	79
$\bar{s}$*	36	38	48	46	24
$\bar{d}$*	1·12	1·17	1·20	1·29	1·56
Main sed. grades	76% fine sand 16% mud	79% fine sand 10% med. sand	69% fine sand 24% med. sand	Variable	87% med. sand
Mean depth (m)	30·5	29·9	22·3	16·2	11·0

* Rounded

None of the remaining site-groups appear to be distinguished by their sediments, all having predominantly medium sand present as in the two previous cases.

Site-group 7 (depth *c.* 15 m) includes two sites (31, 32) in or close to the northern end of the dredged navigational channel. It can be described as a *Concholestes* — *Callianassa* — *Prionospio* community, and has almost the lowest population of any site-group (81), and also low species richness (25) and diversity (1·11).

Site-group 8 (depth *c.* 14 m) lies on the eastern slopes of the Middle Banks in the area from which sand might be dredged and may be described as a *Concholestes* — *Urohaustorius* — mysid 4 community. It has a relatively low population density (91) but somewhat higher species richness (30) and diversity (1·18) than adjacent site-groups.

Site-group 9 lies in the NE. of the sampled area, in generally deeper water than adjacent sites (depth *c.* 19 m) and may be described as a *Concholestes* — *Amphiura octacantha* — mysid 4 community. It has a higher population than adjacent site-groups (125); species richness is low (25) as is diversity (1·09).

Site-group 10 lies in the W. of the sampled area in a generally shallow and turbulent area (depth *c.* 8 m). It forms a *Urohaustorius* — *Platyischnopus* — *Prionospio* community with low population (113), species density (25) and diversity (1·03).

Site-group 11 is the northernmost area sampled. It lies in a turbulent area adjacent to but deeper than that of site-group 10 (depth *c.* 14 m). It forms a *Urohaustorius* — *Amphiura octacantha* — *Prionospio* community, again with low population (96), species richness (25) and diversity (1·11).

SPECIES × TIMES ANALYSES: The dendrograms of time classification for the southern sub-area (Fig. 10A) and northern sub-area (Fig. 10B) are alike in showing groupings which are predominantly of sequential times and in not following seasonal patterns. The sequential pattern is slightly better developed in the northern sub-area and also the inter-time dissimilarities are generally lower.

By dealing with sub-areas the dissimilarity levels in the times dendrograms have become roughly equated to those of the sites dendrograms and hence times now become relatively more important. Perusal of the two-way coincidence table of time-groups with species showed that less than a third of the species conformed noticeably to the time-groups of the dendrograms.

As an alternative to the dendrogram groupings of times, these were dissected into chronologically meaningful groupings and the conformity of species to these groupings was investigated. Approximately half the species analysed conformed to these groupings. Some of the remaining species occurred at random (see later) and it was concluded here there were no chronological

TABLE 7: Cont.

6	7	8	9	10	11
29, 36	26, 31, 32	21, 22, 23 24, 25, 27, 30	5, 13, 14, 19	15, 16, 17, 20	1, 2, 3, 4, 7, 8, 10, 11, 12, 18
1(24), 2(6), 3(5)	7(10), 5(10), 1(8), 6(6),	7(19), 2(8), 8(8), 6(6), 20(6), 1(6)	7(27), 6(21), 8(14), 1(7), 23(6)	2(34), 21(12), 1(10), 18(7), 8(5)	2(16), 6(14), 1(10), 8(9)
143	81	91	125	113	96
38	25	30	25	25	25
1·30	1·11	1·18	1·09	1·03	1·11
82% med. sand	—	—	> 80% med. sand	—	—
9·1	14·6	14·0	19·2	7·6	14·0

changes. For the residue while recordings were too heterogeneous to be statistically at random, the groupings of times to which the species conformed did not make obvious chronological sense.

Finally the species were divided into four broad categories, and each of these further subdivided. Throughout the categories were non-overlapping and sometimes this involved difficult decisions regarding allocation. The categories were: *A* — those occurring at random, and hence showing no chronological pattern. For the commoner species randomness was tested by χ^2 using summed recordings in each of the eight times. For species occurring with fewer than 16 individuals, the limit of formal use of χ^2 is exceeded. We have still applied the mechanics of the χ^2 test, which might now be designated a 'pseudo-χ^2 test' and describe the species as 'pseudo-random'; *B* — those with sequential patterns of various types. One sequence of times was dissected from the remainder and the pseudo F test applied to the $\log_{10}(n + 1)$ transformations of the two sets of recordings. The first dissection point separated times 1–6 from 7 and 8, and we thus determine the species with noticeably decreased numbers after the flood and those with noticeably increased numbers. The second point was between times 1–4 and 5–8, separating the two years of study, and we thus derive species occuring in high numbers in the second year and in the first year respectively. The remaining sequential species followed a variety of time combinations and we first separated those with three sequential noticeably high recordings ('9 month species') from those with two in sequence ('6 month species'). Finally we listed species with a sequence of two noticeably low

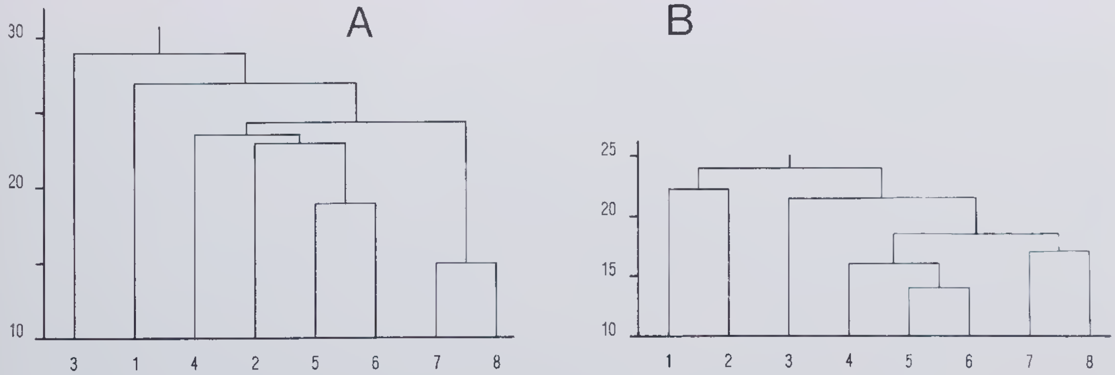

FIG. 10: Dendrograms of time classifications within A southern and B northern sub-areas.

recordings; *C* — those with seasonal patterns with noticeably high recordings in the same season of both years (mostly in September) and those with noticeably low recordings; *D* — non-random species giving apparently 'nonsense' chronological patterns; these are presented in order of decreasing likelihood that they give conceptual sense. The first group contains species with a single outstandingly low value, the second species with oscillating values and typically with alternate high and low recordings, while the last group contains species with a single outstandingly high value.

Table 8: Conformity of Species to Prescribed Time-groups.

Random

Random
South: 29, 53, 125, 137, 156 (=5=3%)
North: 15, 72, 73, 83, 87, 116, 130, 134, 136, 142 (=10=9%)
Pseudo-random
South: 110, 171, 180, 190, 191, 192, 219, 224 (=8=5%)
North: 17, 38, 109, 117, 149, 169, 189 (=7=6%)

Sequential

Fewer after flood
South: 25, 30, 41 (=3=2%)
North: 22, 42, 110 (=3=3%)
More after flood
South: 4, 56, 58, 66, 105, 127, 146, 149, 161, 184 (=10=6%)
North: 31, 59, 86, 146, 203 (=5=4%)
More in 1st year
South: 96, 131 (=2=1%)
North: 89, 199 (=2=2%)
More in 2nd year
South: 9, 15, 19, 20, 23, 26, 38, 49, 55, 65, 75, 109, 111, 133, 147, 212 (=6=12%)
North: 49, 66, 125, 162, 182 (=5=4%)
9-month species
South: 6, 59, 83, 95, 128 (=5=3%)
North: 18, 23, 54, 55, 74 (=5=4%)
6-month species
South: 1, 2, 7, 8, 10, 13, 14, 16, 21, 24, 27, 33, 39, 44, 50, 64, 71, 74, 106, 107, 120, 154, 166, 197 (=24=15%)
North: 2, 6, 7, 11, 13, 24, 37, 67, 69, 70, 71, 82, 92 (=13=11%)
Sequential low recordings
South: 3, 31, 32, 48 (=4=3%)
North: 9, 20, 26, 32, 57 (=5=4%)

Seasonal

Seasonal high recordings (mostly Septembers)
South: 12, 28, 45, 54, 61, 81, 97, 101, 108, 118, 126, 129, 135 (=13=8%)
North: 21, 63, 77, 121 (=4=3%)
Seasonal low recordings (various)
South: nil (=0=0%)
North: 5, 8, 56, 58 (=4=3%)

Obscure

Single outstanding low
South: 36, 37, 40, 69 (=4)
North: 20, 35, 39, 43, 44, 46, 50 (=7)
Oscillating
South: 11, 18, 35, 42, 43, 46, 47, 52, 57, 60, 62, 67, 70, 76, 80, 84, 85, 88, 90, 91, 92, 93, 94, 98, 104, 113, 115, 117, 122, 132, 139, 141, 143, 152, 153, 168, 170, 172, 176, 204, 209, 216 (=42)
North: 1, 4, 10, 12, 19, 40, 41, 45, 47, 48, 53, 62, 65, 75, 78, 79, 85, 91, 93, 99, 102, 104, 105, 112, 113, 114, 132, 140, 141, 147, 155, 158, 160, 163, 185, 187 (=36)
Single outstanding high
South: 5, 17, 22, 34, 51, 68, 77, 87, 103, 124, 138, 144, 145, 150, 151, 159, 173, 175, 178, 181, 186, 196, 211 (=23)
North: 3, 27, 43, 52, 100, 119, 138, 148, 164 (=9)

Details of the species in each of these categories in southern and northern sub-areas are given in Table 8. Summated percentages of random and pseudorandom species are 8% S., 15% N.; of sequential species 40% S., 33% N.; of seasonal species 8% S., 7% N., and of obscure time patterns 43% S., and 45% N. None of the differences between the two sub-areas were significant.

The flood of 1974 produced noteworthy changes in less than 10% of the species, in marked contradistinction to Bramble Bay (Stephenson, Cook and Raphael 1977). More species occurred in noticeably high numbers after the flood (15) than in noticeably low numbers. Apart from flood-affected species, 21 species occurred in higher numbers in the second year of study compared with four in the first year.

DISCUSSION

Site-patterns: Four groups of sites were clearly recognisable in the southern sub-area and seven groups were less clearly recognisible in the northern sub-area. There is no accepted level at which these site-groups can be designated as communities and subcommunities.

Characteristics of each of these site-groups have been given in the text (especially in Table 6) and we now discuss all except the most northerly ones (site-groups 10 and 11). The southern groupings (site-group 1–4) are in deeper areas of fine sand furthest from oceanic water and have relatively high populations, species densities and diversities. The individual groups within the southern area do not precisely follow either the topography or sedimentology of the area and one can only assume that a combination of hydrographic parameters is responsible for their delineation. A likely combination would be distance from oceanic water and current velocity. The highest populations and species densities occur on the relatively steep slopes just south of the Middle Banks, and further south populations and species densities are reduced and other 'communities' can be recognised. Within the confines of our study area the areas of highest populations and species densities do not form an ecotone between south and north; there is no doubt the populous area belongs to a southern site-group. One suspects on the basis of a study of the dredged biota of Moreton Bay by Stephenson, Williams and Lance (1970), that our most south-western site-group 1 may extend considerably beyond our study area, in which case the populous area of site-group 3 (and to a lesser extent site-group 2) become something of especial local interest.

Taking site-groups 2 and 3 together, in terms of population density we have an average of *c.* 1500 animals per square metre contrasting with *c.* 1000 further south and *c.* 600 further north. These are not high values within either a Moreton Bay or a more global context. For example inshore at Bramble Bay, Stephenson, Raphael and Cook (1976) give preflood mean values of up to and 3000 organisms per square metre, and quote both higher and lower figures from the literature. On the other hand both species density (*c.* 43) and diversity (*c.* 1·2) are much higher than were obtained with a van Veen grab at Bramble Bay (*c.* 12 and 0·8 respectively). The dense macrobenthos in site-groups 2 and 3 corresponds with an area in which prawn trawling is concentrated. Presumably the factors responsible for the dense benthos, plus the benthos itself, produce a concentration of prawns. If so the prawns and the trawling could both be expected to take their toll of the benthos.

It is undesirable that future engineering works should have any permanent deleterious effects on the areas of site-groups 2 and 3. We can obtain some insight on the likelihood of these occurring by attempting an evaluation of the effects of engineering works now in operation — viz. dredging of the navigational channel (between the beacons in Fig. 2). Sites 40, 50 and 56 lie immediately south of this channel, and they do not appear to show any biotic differences compared with neighbouring sites. In fact two of these sites (40 and 56) are in the area of greatest population density (site-group 3).

Site-group 5 is of especial interest because the two sites lie in (site 37) and in immediate proximity with (site 57) the southern end of the dredged channel. They are characterised by the lowest population density (79) and species density (24) obtained in the entire survey, and it is difficult to believe other than that dredging has been responsible. It is of interest to note that this site-group has the highest standardised Shannon diversity (mean value 1·56), and this provides a good example of how misleading diversity measures can be.

Site-groups 4 and 6 lie respectively just south of the topographic boundary between southern and northern areas, and on or just north of the sedimentary boundary. They are intermediate as regards population density (ranging from *c.* 1050 to *c.* 750 individuals per square metre) but have higher species densities and diversities than northern sites. Site-group 4 is of especial interest because two of its characterising species *(Rhizammina* and *Discobotellina)* are arenaceous Foramenifera, although one of these *(Rhizammina)* is markedly seasonal. *Discobotellina* is widespread in Moreton Bay (Stephenson, Williams and Lance 1970) and in different areas is in association with a great variety of other species. There is a reasonably close parallel with dominance of other species of areaceous Foramenifera off the W. African coast (Buchanan 1960).

In site-group 7 one site (32) lies in the northern end of the dredged navigational channel, one lies very near this end (31) and the third (26) *c.* 1½ km away. Populations densities and species densities are approximately as low as those of site-group 5, and again it seems that dredging is responsible.

Site-groups 7, 8 and 9 show considerable biotic similarity and form a series running northwards from the dredged area on the western side of the Eastern Channel. There is a progressive increase in population density from 7 to 9, and it is possible this is due to distance from the dredging.

TIME-PATTERNS: Analyses which involved summations over all species indicated seasonally high populations and species densities in each of the Septembers and further that values were higher in the second year than the first one. Analyses on separate species gave obscure sequential groupings of times rather than seasonal groupings, and suggested a progressive shift in the biota.

The latter analyses, while generally more informative, run into a major problem in interpretation which has been raised in an earlier study (Stephenson, Raphael and Cook 1976). Because of inaccurate relocation of sites on successive samplings different local concentrations of species are likely to be sampled on different occasions. It could be argued that because the values considered involve summated recordings at many sites (25 and 34 in the main analyses) 'random' microtopographical variations should cancel out. Against this species may be concentrated in certain areas, and a single exceptional patch within these areas could bias the results. The importance of microtopographical patterns has been demonstrated by Poiner (1977) working north of Peel Island. In the present study we can only estimate the relative importance of chronology and microtopography. We assume that when species conform to apparently meaningful chronological changes these changes are real, and that when the chronological picture is decreasingly meaningful there is an increasing possibility of a microtopographical effect.

Almost 10% of the species considered conformed to seasonal patterns and in most cases showed noticeably high populations in the two Septembers. High September values have been noted in two previous local studies — near Peel Island (Stephenson, Williams and Cook 1974) and at Bramble Bay before the 1974 flood (Stephenson, Raphael and Cook 1976) and can now be regarded as an established feature in the benthic calendar. Sequential patterns of one sort or another occurred in about 40% of the species analysed. Because there is a growing interest in non-seasonal changes in benthos (e.g. Stephenson, Williams and Cook 1974; Buchanan, Kingston and Sheader 1974; Eagle 1975; Stephenson, Raphael and Cook 1976; and Stephenson, Cook and Raphael 1977) and because this was the largest category of species with recognisable patterns, special attention was devoted to it.

The general approach we followed was to look for changes in biota which are paralleled by abiotic changes and to assume in the first instance that the former are due to the latter. Where no such parallels occur we must fall back upon biotic interactions either between benthic species (Rhoads and Young 1970; Eagle 1975) or between benthic organisms and nektonic predators (Stephenson and Searles 1960; Levings 1972, 1974; Mills 1975). In the present case the most severe abiotic changes for nearly a century were probably the floods of January 1974 and resultant prolonged dilution of the Middle Banks area (Stephenson, Cook and Raphael 1977). Almost 10% of the species showed noticeable changes between the preflood times (times 1–6) and the postflood ones (times 7–8). While this is more than for any other sequential period, it is a miniscule effect compared with that on Bramble Bay (Stephenson, Cook and Raphael 1977). Moreover at Middle Banks the floods had a 'beneficial' effect with 15 species occurring in noticeably higher numbers after the flood and only six before. The effect was most noticeable in the southern area, where ten species increased in number after the flood. The simplest explanation, that this is due to a supply of sedimentary food material, as MacGinitie (1939) suggested after a Californian flood, appears unlikely. There was less small particulate sediment in the area after the flood than before.

The remaining sequentially occurring species mostly involved noticeably high numbers for only two consecutive sampling periods i.e. for 6 months or slightly longer. It appears that a sequence of species occupied (in quantity) the different areas of sampling each for tolerably brief periods and were then replaced by others. This is suggestive of rapid recruitment and rapid replacement, as Stephenson, Raphael and Cook (1976) suggested at Bramble Bay. It implies that biotic interactions, whose nature is as yet unknown, are an underlying phenomenon. Superimposed on the transitory aspects of the data there is an underlying trend from time 1 to time 8 (as shown by the dendrograms) suggesting an overall biotic shift. The somewhat scanty sedimentary data suggest a parallel shift towards coarser sediments and it is tempting to interrelate the two.

The largest single category of species revealed by the times analyses (40–45% of the species considered) fail to give immediate chronological sense. There are two possible explanations, microtopographical patchiness or real chronological changes on a 3 monthly time bases. For example species with a single outstandingly low value could reflect a single occasion of severe predation followed by replacement during the next three months; species with oscillating values could reflect irregular and repeated recruitment; while species with a single outstandingly high value would be showing settlement in 3 months and disappearance during the next three months. Present data do not permit an easy choice between the alternative microtopographic or rapid chronological changes; current work suggests both are about equally applicable on an 8 week time basis.

CONTINUAL BIOTIC FLUX: We have noted the likelihood of tolerably rapid changes in at least 40% of the species — the sequential ones. We have suggested that rapid changes may be a feature of a greater proportion of the species.

If the bulk of the biota consisted of perennial species we would not expect the biota to show rapid changes, and what might appear as such would be due to topographical patchiness. If the bulk of the species were annuals, rapid changes would be inevitable. Thus in theory we could argue from life-spans to the reality of the chronological changes. Unfortunately we have no direct information upon the life-spans of species from the area apart from some data on *Discobotellina* (Stephenson and Rees 1965a, b) which suggests that larger specimens may be three years old. In general we can only assume that relatively large size equates to an age exceeding one year, and amongst the 100 most abundant species the only cases of relatively large sized species are: spp. 5, 10, 12, 14, 24, 25, 29, 39, 41, 42, 49, 69, 87, 95 and 98 (i.e. 15 in all). Amongst the less abundant species the proportion of large species is much lower, and that of annuals or subannuals must be very high. As Eagle (1975) has noted when populations consist of single year classes we can expect instability. He relates this to low diversity, but as indicated by Stephenson, Williams and Cook (1974) it could go a long way to explaining high diversity in a time context.

The overall impression was of a biota dominated by small individuals, of which very few species would attain sexual maturity within the study area. This was particularly so in the northern sub-area; of the 15 larger species listed only one characterised the northern sub-area. If species disappear from within the area before attaining sexual maturity, predation by fish seems a likely cause. Levings (1972, 1974) has shown how seasonal variations in predation by a single species of fish can produce complex changes in a relatively simple benthic biota off the Atlantic coast of Canada. In the present study area there are probably some 20 species of benthic feeding fish (personal communication from Professor J. M. Thomson) and their predation could account for the various and sometimes rapid quasi-seasonal declines in population which were observed.

Non-seasonal increases in population are more difficult to explain. One possibility is that many species have prolonged breeding seasons (which is not unlikely in a subtropical situation) and can occupy vacant space at any period within a prolonged settlement period. A balance between prolonged settlement and variable predation could well explain the cases of oscillation noted above. It is clear that much more data are required before this suggestion can be confirmed.

Meanwhile the evidence that the benthic population is in an overall state of flux seems tolerably strong. It carries some important consequences as regards a temporary human disturbance of the area. Excavation in the proposed area is unlikely to cause major destruction of breeding populations because few species remain there long enough under natural circumstances to breed. Also, if the normal method of maintenance of the biota is by settlement of one of a great variety of species, it seems probable that this process will only be briefly interrupted, and that a biota roughly comparable with the original should soon be re-established. We might postulate that the settling biota will be more simplified than originally because a larger area and a more vacant area than that provided after fish predation will be available. After some predator-prey oscillations possibly of a few months duration a situation very comparable with the original could be expected.

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APPENDIX

Species from Middle Banks benthos with indications of their systematic positions. Code numbers are in hierarchical order of abundance.

Code No.	Species	Systematic position	Number Collected	Main site group
1	*Prionospio* sp.1	Polychaeta: Spionidae	12802	S
2	*Urohaustorius* sp. — polyspecific	Amphipoda: Haustoriidae	3394	N
3	tanaid 1	Tanaidacea	3094	S
4	*Solemya terraereginae* (Iredale)	Bivalvia: Solemyidae	3075	S
5	*Callianassa arenosa* Poore	Crustacea: Callianassidae	2776	S
6	*Amphiura octacantha* H. L. Clark	Ophiuroidea: Amphiuridae	2741	N
7	*Concholestes* sp. — polyspecific	Amphipoda: Corophiidae	2674	N
8	mysid 4	Mysidacea	2390	N
9	*Poecilochaetus* sp.	Polychaeta: Trochochaetidae	2258	S
10	*Discobotellina biperforata* Collins	Foraminifera: Astrorhizidae	2131	S
11	*Aglaophamus verrilli* McIntosh	Polychaeta: Nephtyidae	2040	S
12	*Nucula* spp. — polyspecific	Bivalvia: Nuculidae	1922	S
13	*Prionospio* sp.4	Polychaeta: Spionidae	1837	S
14	*Brissopsis luzonica* Gray	Echinoidea: Spatangidae	1343	S
15	*Magelona* sp.2 ('cincta')	Polychaeta: Magelonidae	1341	S
16	aloidid	Bivalvia: Aloididae	1274	S
17	*Magelona* sp.3 ('capensis')	Polychaeta: Magelonidae	1217	S
18	amphipod 3	Amphipoda	993	N
19	*Golfingia trichocephala* (Sluiter)	Sipuncula: Golfingiidae	927	S
20	*Eunice* cf. *indica* Kinberg	Polychaeta: Eunicidae	886	N
21	*Platyischnopus* sp. — polyspecific	Amphipoda: Haustoriidae	852	N
22	gastropod (red and white)	Gastropoda	819	N
23	amphipod 4	Amphipoda	792	N
24	bivalve 1	Bivalvia	775	S
25	*Schizaster lacunosus* (Linnaeus)	Echinoidea: Hemiasteridae	703	S
26	*Goniada emerita* Audouin and Milne Edwards	Polychaeta: Glyceridae	688	S
27	*Leptomya pura* Angas	Bivalvia: Semelidae	673	S
28	*Rhizammina* cf. *algaeformis* H. B. Brady	Foraminifera: Astrorhizidae	668	N
29	*Xenophthalmoides dolichophallus* Tesch	Decapoda: Goneplacidae	654	S
30	carid 2	Decapoda: Caridae	648	S
31	*Dispio* sp.2	Polychaeta: Spionidae	643	N
32	juv. fibularid	Echinoidea: Fibularidae	632	N
33	*'Dentalium'* sp.	Scaphopoda	564	S
34	*Tharyx* sp.A (undescr.)	Polychaeta: Cirratulidae	466	N
35	amphipod 6	Amphipoda	433	S
36	*Paralacydonia paradoxa* Fauvel	Polychaeta: Lacydoniidae	432	S
37	*Terebellides stroemi* Sars	Polychaeta: Terebellidae	428	S
38	*Haploscoloplos bifurcatus* Hartman	Polychaeta: Orbiniidae	423	S
39	*Branchiostoma moretonensis* Kelly	Cephalochordata	412	S
40	*Sthenelais* sp.	Polychaeta: Aphroditidae	409	S
41	*Echinocardium cordatum* (Pennant)	Echinoidea: Spatangidae	405	S
42	*Neosolen vaginoides* (Lamarck)	Bivalvia: Cultellidae	403	N
43	*Mesanthura* sp.1	Isopoda: Anthuridae	396	N
44	amphipod 5	Amphipoda	380	N
45	orbiniid spp. — polyspecific	Polychaeta: Orbiniidae	360	S
46	*Caulleriella* sp.A + *Tharyx* sp.B — polyspecific (both undescr.)	Polychaeta: Cirratulidae	349	N
47	*Lucifer hanseni* Nobili	Decapoda: Sergestidae	344	N
48	lumbrinerid 1	Polychaeta: Lumbrineridae	322	N
49	*Epigonichthys cultellus* Peters	Cephalochordata	298	N
50	*Glycera prashadi* Fauvel	Polychaeta: Glyceridae	293	N
51	*Ophiura kinbergi* Ljungman	Ophiuroidea: Ophiolepidae	290	S
52	*Amphipholis loripes* Koehler	Ophiuroidea: Amphiuridae	269	S

Code No.	Species	Systematic position	Number Collected	Main site group
53	nemertean (pink) — polyspecific	Nemertea	264	S
54	*Micronephthys sphaerocirrata* Wesenberg-Lund	Polychaeta: Nephtyidae	262	
55	nemertean (pale) — polyspecific	Nemertea	256	
56	*Marphysa* sp.	Polychaeta: Eunicidae	227	N
57	*Mesanthura* sp.2	Isopoda: Anthuridae	219	N
58	*Magelona* cf. *papillicornis* Muller	Polychaeta: Magelonidae	212	N
59	polycirrinae — polyspecific	Polychaeta: Terebellidae	208	S
60	bivalve 2	Bivalvia	188	S
61	*Amphioplus depressus* (Ljungman)	Ophiuroidea: Amphiuridae	184	S
62	anthurid (undescr. genus 2, sp.2)	Isopoda: Anthuridae	180	N
63	amphipod 15 — polyspecific	Amphipoda	179	S
64	bivalve 8	Bivalvia	171	S
65	*?Notomastus* cf. *aberans* Day	Polychaeta: Capitellidae	168	S
66	= species 34 (Tharyx sp.A)	Polychaeta: Cirratulidae	165	S
67	*?Notomastus latericeus* Sars	Polychaeta: Capitellidae	162	S
68	polyzoan 1	Polyzoa	161	S
69	*Sipunculus aequabilis* Sluiter	Sipuncula: Sipunculidae	157	S
70	terebellid (undescr. genus)	Polychaeta: Terebellidae	151	N
71	amphipod 14	Amphipoda	137	S
72	anthurid (undescr. genus 2, sp.1)	Isolda: Anthuridae	134	N
73	*Thalenessa* sp.	Polychaeta: Aphroditidae	133	N
74	*Polydora* sp.1	Polychaeta: Spionidae	129	
75	*Owenia fusiformis* Delle Chiaje	Polychaeta: Oweniidae	117	S
76	*Sthenelepis* cf. *japonica* (McIntosh)	Polychaeta: Aphroditidae	109	S
77	*Aricidea* sp.	Polychaeta: Paraonidae	109	S
78	bivalve 4	Bivalvia	106	N
79	bivalve 12	Bivalvia	102	N
80	bivalve 14	Bivalvia	95	S
81	bivalve 6	Bivalvia	94	S
82	*Chaetozone* sp.A (undescr.)	Polychaeta: Cirratulidae	93	N
83	*Scalibregma inflatum* Rathke	Polychaeta: Scalibregmidae	90	S
84	amphipod 8	Amphipoda	90	S
85	nemertean (orange banded) — ?polyspecific	Nemertea	85	S
86	*Eunice* sp.2	Polychaeta: Eunicidae	84	N
87	*Polycarpa tinctor* (Quoy and Gaimard)	Tunicata: Styelidae	84	S
88	*Chaetozone* sp.B (undescr.)	Polychaeta: Cirratulidae	82	S
89	*Paraonides* sp.	Polychaeta: Paraonidae	80	N
90	*Paphia* sp.	Bivalvia: Veneridae	80	S
91	phoronid — ?polyspecific	Phoronidae	80	S
92	amphipod 9	Amphipoda	78	
93	*Cyclaspis tribulis* (Hale) complex	Cumacea: Bodotriidae	78	S
94	*Euclymene* sp.	Polychaeta: Maldanidae	75	S
95	*Pectinaria antipoda* Schmarda	Polychaeta: Pectinariidae	75	S
96	*Alpheus distinguendus* de Man	Decapoda: Alpheidae	75	S
97	*Natica* cf. *colliei* Recluz	Gastropoda: Naticidae	74	S
98	*Raphidopus ciliatus* Stimpson	Decapoda: Porcellanidae	73	S
99	*Lumbrineris* sp.1	Polychaeta: Eunicidae	71	N
100	gastropod 10	Mollusca: Gastropoda	70	
101	*Eocuma agrion* (Zimmer)	Cumacea: Bodotriidae	69	S
102	bivalve 7	Bivalvia	69	N
103	gastropod 5	Gastropoda	68	S
104	*Loimia medusa* (Savigny)	Polychaeta: Terebellidae	66	S
105	*Apseudes* sp.	Tanaidacea	66	
106	*Aspidosiphon inquilinus* Sluiter	Sipuncula: Aspidosiphonidae	66	S
107	*Fulvia* sp.	Bivalvia: Cardiidae	65	S
108	amphipod 20	Amphipoda	64	S
109	nereid 1	Polychaeta: Nereidae	63	S
110	isopod 5 — polyspecific	Crustacea: Isopoda	63	N

Code No.	Species	Systematic position	Number Collected	Main site group
111	bivalve 29	Bivalvia	63	S
112	*Scoloplos johnstonei* Day	Polychaeta: Orbiniidae	57	N
113	*Leptanthura* cf. *australis* Haswell	Isopoda: Anthuridae	56	
114	*Matuta inermis* Miers	Crustacea: Calappidae	56	N
115	amphipod 28	Amphipoda	51	S
116	*Thermiste* sp.	Sipuncula: Golfingiidae	51	N
117	*Conuber conica* (Lamarck)	Gastropoda: Naticidae	50	S
118	*Tellina* sp.1	Bivalvia: Tellinidae	50	S
119	*Diogenes* cf. *rectimanus* Miers	Decapoda: Paguridae	49	N
120	*Natica* sp.1	Gastropoda: Naticidae	49	S
121	bivalve 16	Bivalvia	49	N
122	amphipod 13	Amphipoda	48	S
123	gastropod 8	Gastropoda	47	
124	*Protankyra* sp.	Holothuriidae: Synaptidae	47	S
125	*Sigalion* sp.	Polychaeta: Aphroditidae	46	
126	*Dimorphostylis australis* (Foxon)	Cumacea	46	S
127	aphroditid 3	Polychaeta: Aphroditidae	44	S
128	*Harmothoe* sp.	Polychaeta: Aphroditidae	44	S
129	mysid 1	Mysidacea	44	S
130	*Drilonereis* sp.	Polychaeta: Eunicidae	43	N
131	capitellid spp. (juv) — polyspecific	Polychaeta: Capitellidae	40	S
132	carid 4	Decapoda: Caridae	40	
133	bivalve 22	Bivalvia	40	S
134	*Lumbrineris* sp.2	Polychaeta: Eunicidae	39	N
135	amphipod 18	Amphipoda	39	S
136	*Syllidia* sp.	Polychaeta: Hesionidae	36	N
137	*Nereis jacksoni* Kinberg	Polychaeta: Nereidae	36	S
138	amphipod 17	Amphipoda	36	
139	*Chloeia flava* (Pallas)	Polychaeta: Amphinomidae	35	S
140	onuphid 1	Polychaeta: Eunicidae	35	N
141	carid 3	Decapoda: Caridae	35	
142	*Veletuceta hedleyi* (Lamy)	Bivalvia: Glycymeridae	35	N
143	amphipod 21	Amphipoda	34	S
144	gastropod 3	Gastropoda	34	S
145	bivalve 3	Bivalvia	34	S
146	phyllodocid 3	Polychaeta: Phyllodocidae	33	
147	sabellid 2	Polychaeta: Sabellidae	33	S
148	isopod 3	Isopoda	33	N
149	amphipod 11	Amphipoda	33	
150	amphipod 16	Amphipoda	33	S
151	gastropod 2	Gastropoda	33	S
152	*Leonnates stephensoni* Ruillier	Polychaeta: Nereidae	32	S
153	*Muraenicthys godeffroyi* Regan	Pisces: Myridae	32	S
154	isopod 2	Isopoda	31	S
155	bivalve 5	Bivalvia	31	N
156	*Tellina texturata* Sowerby.	Bivalvia: Tellinidae	29	S
157	*Theora lata* Hinds	Bivalvia: Semelidae	29	
158	bivalve 17	Bivalvia	29	N
159	*Spiochaetopterus* sp.	Polychaeta: Chaetopteridae	28	S
160	*Pomacuma cognata* (Hale)	Cumacea: Bodotriidae	26	N
161	nereid 2	Polychaeta: Nereidae	25	S
162	cumacean 6	Cumacea	25	N
163	*Austrolepidoda schmitti* Efford and Haig	Decapoda: Albuneidae	25	N
164	platyhelminth 1	Platyhelminthes: Polycladida	24	N
165	amphipod 10	Amphipoda	24	
166	isopod 1	Isopoda	23	S
167	anemone 1	Actiniaria	22	
168	bivalve 9	Bivalvia	22	

Code No.	Species	Systematic position	Number Collected	Main site group
169	amphipod 24	Amphipoda	21	
170	bivalve 11	Bivalvia	21	S
171	*Spiochaetopterus* cf. *vitrarius* (Ehlers)	Polychaeta: Chaetopteridae	20	S
172	*Glyphocuma* sp.	Cumacea	20	S
173	*Penaeus plebejus* (Hesse)	Decapoda: Peneidae	20	S
174	*Polyonyx transversus* (Haswell)	Decapoda: Porcellanidae	20	
175	phyllodocid 7	Polychaeta: Phyllodocidae	19	
176	*Sternaspis scutata* (Renier)	Polychaeta: Sternaspidae	19	S
177	*Metapenaeus bennettae* Racek and Dall	Decapoda: Peneidae	19	
178	gastropod 16	Gastropoda	19	S
179	phyllodocid 1	Polychaeta: Phyllodocidae	17	
180	*Glyphocuma halei* Greenwood and Johnston	Cumacea: Bodotriidae	17	S
181	*Chaetopterus variopedatus* Renier	Polychaeta: Chaetopteridae	16	S
182	*Moira lethe* Lutken	Echinoidea: Hemiasteridae	16	N
183	capitellid 1	Polychaeta: Capitellidae	15	
184	tanaid 6	Tanaidacea	15	S
185	*Trachypenaeus fulvus* Dall	Decapoda: Peneidae	15	
186	*Philine angasi* Crosse and Fisher	Gastropoda: Philinidae	15	S
187	gastropod 27	Gastropoda	15	N
188	*Cyclaspis mawsonae* (Hale)	Cumacea: Bodotriidae	14	
189	isopod 4	Isopoda	14	N
190	*Dosinia* cf. *sculpta* Hanley	Bivalvia: Veneridae	14	S
191	bivalve 10	Bivalvia	14	S
192	*Ophiocentrus* sp.	Ophiuroidea: Amphiuridae	14	
193	phyllodocid 2	Phyllodocidae	13	
194	amphipod 26	Amphipoda	13	
195	juv. carid 1	Decapoda: Caridae	13	
196	bivalve 13	Bivalvia	13	S
197	bivalve 18	Bivalvia	13	S
198	gastropod 20	Gastropoda	13	N
199	gastropod 21	Gastropoda	13	N
200	*Ophiodromus* sp.	Polychaeta: Hesionidae	12	
201	*Dorvillea* sp.	Polychaeta: Eunicidae	12	
202	*Travisia* cf. *forbesii* Johnston	Polychaeta: Opheliidae	12	
203	maldanid 1	Polychaeta: Maldanidae	12	N
204	maldanid 2	Polychaeta: Maldanidae	12	S
205	tanaid 5	Tanaidacea	12	S
206	*Apanthura* sp.	Isopoda: Anthuridae	12	N
207	amphipod 29	Amphipoda	12	N
208	*Hexapus granuliferus* Campbell and Stephenson	Decapoda: Goneplacidae	12	S
209	*Modiolus* sp.	Bivalvia: Mytilidae	12	S
210	bivalve 21	Bivalvia	12	
211	bivalve 30	Bivalvia	12	S
212	*Natica* sp. 4	Gastropoda: Naticidae	12	S
213	gastropod 25	Gastropoda	12	
214	*Pista* spp. — polyspecific	Polychaeta: Terebellidae	11	S
215	*Laonice* sp.	Polychaeta: Spionidae	11	S
216	*Nerinides* sp.	Polychaeta: Spionidae	11	S
217	*Cyclaspis* ? *cretata* (Hale) ? *granulos* (Hale)	Cumacea: Bodotriidae	11	N
218	anthurid (undescr. genus 1 sp.1)	Isopoda: Anthuridae	11	
219	*Doxander vittatus* Linnaeus	Gastropoda: Strombidae	11	S
220	nemertean (green)	Nemertea	10	
221	aphroditid 1	Polychaeta: Aphroditidae	10	S
222	*Diplocirrus* sp.	Polychaeta: Flabelligeridae	10	S
223	?*Pontophilus* sp.1 (doubtfully benthic)	Crustacea: Crangonidae	9	N
224	*Phos sculptilis* Watson	Gastropoda: Photidae	10	S
225	phyllodocid 6	Polychaeta: Phyllodocidae	9	N

Code No.	Species	Systematic position	Number Collected	Main site group
226	= species 216 (*Nerinides* sp.)	Polychaeta: Spionidae	9	S
227	*Matuta* spp. juv. not *M. inermis)* — polyspecific	Decapoda: Calappidae	9	N
228	bivalve 15	Bivalvia	9	N
229	bivalve 24	Bivalvia	9	S
230	*Sthenolepis* sp.	Polychaeta: Aphroditidae	8	S
231	*Pseudeurythoe microcephala* (Fauvel)	Polychaeta: Amphinomidae	8	S
232	nereid 4	Polychaeta: Nereidae	8	S
233	eunicid 1	Polychaeta: Eunicidae	8	N
234	*Travisia* sp.2	Polychaeta: Opheliidae	8	N
235	bivalve 19	Bivalvia	8	N
236	*Luidia* sp.	Asteroidea: Luididae	8	S
237	*Rhynobrissus pyramidalis* Agassiz	Echinoidea: Spatangidae	8	N
238	*Glossobalanus* sp.	Balanoglossidae	8	S
239	polyzoa 2	Bryozoa	7	
240	nemertean (brown)	Nemertea	7	S
241	*Eupanthalis* sp.	Polychaeta: Aphroditidae	7	S
242	*Etenone* sp.	Polychaeta: Phyllodocidae	7	
243	*Nephtys vikingensis* Paxton	Polychaeta: Nephtyidae	7	N
244	spionid 7 — polyspecific	Polychaeta: Spionidae	7	S
245	*Ophelina* cf. *acuminata* Oersted	Polychaeta: Opheliidae	7	
246	tanaid 3	Tanaidacea	7	S
247	amphipod 22	Amphipoda	7	
248	amphipod 27	Amphipoda	7	S
249	*Betaeus* spp. — polyspecific	Decapoda: Alpheidae	7	S
250	oyster 1	Bivalvia: Ostreidae	7	
251	*Amphiura catephes* H. L. Clark	Ophiuroidea: Amphiuridae	7	S
252	*Nematonereis* sp.	Polychaeta: Eunicidae	6	S
253	*Polydora* sp.2	Polychaeta: Spionidae	6	S
254	bivalve 20	Bivalvia	6	S
255	blenny 1 (doubtfully benthic)	Pisces: Blenniidae	7	N
256	phyllodocid 15	Polychaeta: Phyllodocidae	5	N
257	*Arabella* sp.	Polychaeta: Eunicidae	5	
258	maldanid 3	Polychaeta: Maldanidae	5	S
259	sabellid 3	Polychacta: Sabellidae	5	
260	amphipod 19	Amphipoda	5	S
261	*Eucrassatella cumingii* (Adams)	Bivalvia: Eucrassatellidae	5	N
262	*Mactra* sp.	Bivalvia: Mactridae	5	N
263	*Tellina* sp.2	Bivalvia: Tellinidae	5	N
264	*Natica* sp.3	Gastropoda: Naticidae	5	S
265	gastropod 33	Gastropoda	5	
266	*Mogula mollis* Herdmann	Tunicata: Molgulidae	5	
267	*Euleanira* sp.	Polychaeta: Aphroditidae	4	S
268	phyllodocid 5	Polychaeta: Phyllodocidae	4	
269	phyllodocid 8	Polychaeta: Phyllodocidae	4	S
270	phyllodocid 10	Polychaeta: Phyllodocidae	4	S
271	nereid 3	Polychaeta: Nereidae	4	
272	*Prionospio* sp.3	Polychaeta: Spionidae	4	
273	amphipod 25	Amphipoda	4	
274	*Alpheus* spp. (larva) — polyspecific	Decapoda: Alpheidae	4	S
275	*Albunea* cf. *microps* Miers	Decapoda: Albuneidae	4	
276	*Limaria* sp.	Bivalvia: Limidae	4	S
277	bivalve 25	Bivalvia	4	S
278	bivalve 26	Bivalvia	4	S
279	bivalve 31	Bivalvia	4	
280	gastropod 13	Gastropoda	4	
281	gastropod 15	Gastropoda	4	
282	*Pentaceraster australis* (Luther)	Asteroidea: Oreasteridae	4	
283	enteropneust	Enteropneusta	4	

Code No.	Species	Systematic position	Number Collected	Main site group
284	*Paraplagusia unicolor* (Macleay)	Pisces: Cynoglossidae	4	S
285	*Leanira yhleni* Malmgren	Polychaeta: Aphroditidae	3	S
286	aphroditid 7	Polychaeta: Aphroditidae	3	
287	phyllodocid 4	Polychaeta: Phyllodocidae	3	
288	phyllodocid 12	Polychaeta: Phyllodocidae	3	
289	phyllodocid 14	Polychaeta: Phyllodocidae	3	
290	phyllodocid 19	Polychaeta: Phyllodocidae	3	S
291	syllid 1	Polychaeta: Syllidae	3	
292	spionid 6 — polyspecific	Polychaeta: Spionidae	3	N
293	= species 216 *(Nerinides* sp.)	Polychaeta: Spionidae	3	
294	*Ophelina gigantea* Rullier	Polychaeta: Opheliidae	3	
295	capitellid 2	Polychaeta: Capitellidae	3	
296	sabellid 6	Polychaeta: Sabellidae	3	S
297	unknown polychaete	Polychaeta	3	
298	*Gynodiastylis* sp.	Cumacea: Diastylidae	3	
299	tanaid 7	Tanaidacea	3	S
300	mysid 2	Mysidacea	3	
301	mysid 3	Mysidacea	3	
302	*Squilla laevis* Hess	Crustacea: Stomatopoda	3	S
303	*Lysiosquilla perpasta* (Hale)	Crustacea: Stomatopoda	3	
304	*?Pontophilus* sp.3	Decapoda: Crangonidae	3	N
305	*Conchocetes artificiosus* (Fabricius)	Decapoda: Dromiidae	3	
306	*Dorippe australiensis* Miers	Decapoda: Dorippidae	3	
307	*Actumnus squamosus* de Haan	Decapoda: Xanthidae	3	S
308	*Achaeus lacertosus* Stimpson	Decapoda: Majidae	3	S
309	*Sanguinolaria* sp.	Bivalvia: Sanguinolariidae	3	
310	gastropod 1	Gastropoda	3	
311	gastropod 7	Gastropoda	3	
312	gastropod 19	Gastropoda	3	N
313	gastropod 22	Gastropoda	3	N
314	gastropod 26	Gastropoda	3	
315	gastropod 29	Gastropoda	3	
316	*Amphipholis squamata* (Delle Chiaje)	Ophuiroidae: Amphiuridae	3	S
317	*Lovenia camorata* H. L. Clark	Echinoidea: Spatangidae	3	
318	holothurian 5	Holothuroidea	3	

Mem. Qd Mus. **18**(2): 213–7. [1978]

A NEW SPECIES OF *PONTELLOPSIS* (COPEPODA, CALANOIDA) FROM MORETON BAY, QUEENSLAND

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ABSTRACT

A new species, *Pontellopsis tasmanensis* sp. nov., found in coastal waters of eastern Australia is described and figured, and the relationship of this to allied species is discussed.

A study of the zooplankton of Moreton Bay, Queensland (Greenwood 1976) revealed the presence of males and females of a species of *Pontellopsis* which could not be allocated to any known species and which is described here.

All specimens were collected with either Clarke-Bumpus or 40 cm diameter conical nets of nylon mesh with an aperture size of 195 microns. Dissections were made in polyvinyl alcohol lightly stained with chlorazol black, and drawings made with the aid of a Wild M20 drawing tube.

Pontellopsis tasmanensis sp. nov.
(Figs 1 a–j, 2 a–f)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum, W5201, ♂, Rainbow Channel, Moreton Bay (27° 20'S., 153° 15'E.), SE.Q., coll. 8. vii. 1964, J. G. Greenwood (Station 1 of Greenwood 1976).

ALLOTYPE: W5202, ♀, same data as Holotype.

PARATYPES: W5203, 5♂♂, 5♀♀, same data as Holotype.

P. tasmanensis was taken on 45 occasions during 1963-66 from Rainbow Channel, central Moreton Bay, and Cleveland Channel (Stations, I, II, and III of Greenwood 1976). Males were taken on 25 occasions, females on 29 occasions, males with females on 9 occasions. Material other than the type series was examined in less detail and discarded.

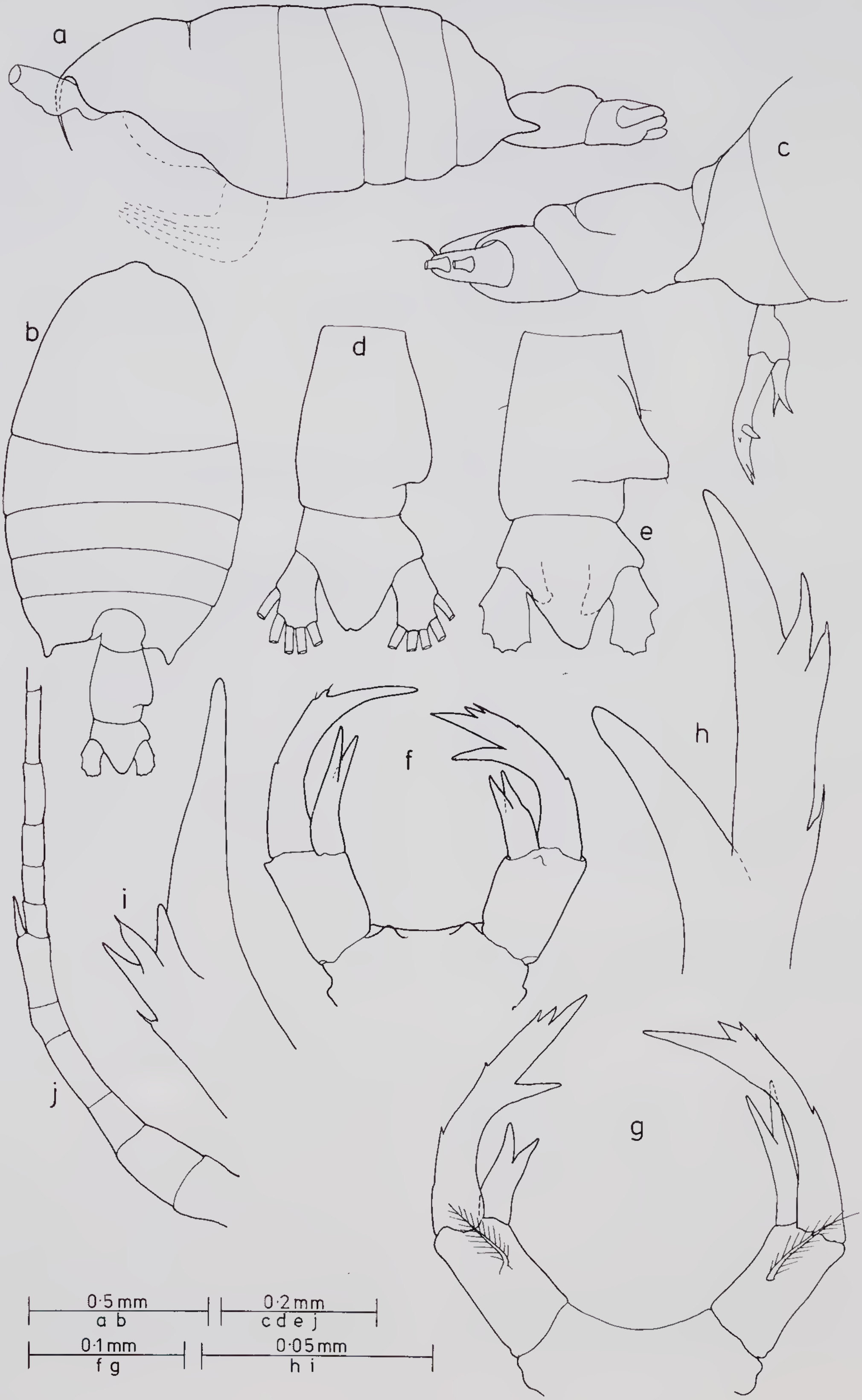
DESCRIPTION OF FEMALE (Fig. 1)

Body very robust. Total body length varying between 1·42–1·69 mm (av. 10 individuals 1·56 mm). Lenth ratio of metasome to urosome 2·98:1; metasome length to width ratio 1·62:1.

Metasome with fourth and fifth thoracic segments fused; posterior margins of fifth segment produced symmetrically into small rounded posterolateral processes. (Fig. 1 a, b, c).

Urosome two-segmented, genital segment approx. 1·47 times length of anal segment. Genital segment asymmetrical, right postero-dorsal region produced into rounded or broadly triangular lobe (Fig. 1 d, e) which extends laterally to maximum distance at level of posterior third of segment. This lobe truncated abruptly posteriorly, at right angles to body axis. Degree of development of this lobe shows some variability. Most individuals as in Fig. 1 d, but others with larger lobes, to the maximum found as in Fig. 1 e. Forms with larger lobes sometimes with a small seta at tip of lobe and similar small seta on mid-ventro-lateral surface. No other spines or projections present on genital segment. Anal segment produced postero-dorsally into large, slightly asymmetrical triangular supra-anal plate reaching to posterior level of furcal rami (Fig. 1 d, e). Furcal rami symmetrical, length *c.* twice width.

Fifth legs asymmetrical (Fig 1 f, g). Right exopod with stout spine developed from inner border slightly distal to midpoint, not reaching end of ramus; corresponding spine absent from left exopod. Both exopods terminate in single point. Right exopod (Fig 1 h) with two subterminal spines on outer border, the more distal the larger; two minute spinules spaced more proximally along outer border. Left exopod (Fig 1 i) with cluster of three subterminal spines, two forming lateral borders of small plate on which third is mounted;


a
b
c
d
e
f
g
h
i
j
0·5 mm
a b
0·2 mm
c d e j
0·1 mm
f g
0·05 mm
h i

two minute spinules more proximally along outer border, first being just proximal to the 'plate'. Endopods similar, bifid terminally, but left endopod narrower and longer, about 1·3 times length of right endopod.

DESCRIPTION OF MALE (Fig. 2)

Body very robust. Total body length varying between 1·28–1·54 mm (av. 10 individuals 1·36 mm). Length ratio of metasome to urosome 2·58:1, metasome length to width ratio 1·96:1.

Metasome with fourth and fifth thoracic segments fused; posterior margins of fifth segment rounded on left side, right side produced as elongate spine-like process reaching to mid or posterior border of fourth urosomal segment (Fig. 2 a, b).

Urosome five-segmented, segments 1–5 in proportions 40:15:17:12:16 (total 100).

Genital segment symmetrical, with single small seta on right postero-lateral margin (Fig. 2 c). Second segment with patch of minute tubercles on right postero-lateral surface. Third segment slightly asymmetrical, slightly swollen on right side, apex of swelling with minute tubercles. Fourth and fifth segment without spines or tubercles.

Fifth legs as figured (Fig 2 d, e, f). Right leg with thumb-like process from base of proximal exopod segment (Re1) similar in length to finger-like distal exopod segment (Re2) thumb slightly expanded or spathulate distally; large seta on Re1 distal to base of thumb. Re2 with excavated lateral surface bearing one larger, one smaller seta; small terminal, longer subterminal seta; minimum distance between origins of thumb and finger similar to length of segment. Left leg with distal protopod segment (B2) and Re1 of similar length. Disto-lateral margin of Re1 with stout spine extending *c.* two-thirds length Re2. Re2 short, *c.* half length Re1; length twice width; lobe on medial face clothed with fine setae; one long one short seta terminally.

REMARKS

During much of the survey in which these specimens were taken, the male and female forms described here were regarded as belonging to different species, the male being provisionally related to *P. tenuicauda* and the female regarded as a new form related, by structure of the fifth legs particularly, to *P. macronyx*, *P. scotti* and *P. tenuicauda*. Subsequent realisation of the coincidence in frequency and occurrence pattern of these two strongly suggested conspecificity. There were, for example, no female *P. tenuicauda* yet the apparent males occurred on 25 occasions. More detailed examination of the two forms showed some differences between these males and those of *P. tenuicauda* as described by Mori (1937), and considerable differences between the present females and those of *P. tenuicauda sensu* Mori (1937). and particularly *sensu* Giesbrecht 1892 (from which Mori's also show differences). Designation of the new species was therefore necessary.

Both male and female share some characteristics with several related species, but are distinguished from them on combinations of features. These distinguishing features are discussed below, firstly for females, subsequently for males.

FEMALES: The asymmetrical fifth legs of female *P. tasmanensis* show some resemblance to those of the following species: *P. pexa* Scott, *P. yamadae* Mori, *P. macronyx* Scott, *P. scotti* Sewell, *P. tenuicauda* (Giesbrecht):

P. pexa differs in that the right exopod there terminates in three small spines, not a single point, and although a spine is developed from the inner border it arises distally and extends well beyond end of the ramus (Scott 1909; p 173, pl. 54 fig. 14).

General body form is similar to that of *P. yamadae*, but although the female fifth legs of that species are asymmetrical they differ from the present form in having one (or more) large inner spines from both exopods (Mori 1937, p. 98, pl. 47 fig. 6; pl. 48 fig. 13. Brodsky 1962, p. 147, pl. 48). *P. yamadae* is also a much larger calanoid (2·8 mm, Mori 1937; 2·45 mm, Brodsky 1962).

Form of the fifth leg is very close to that of *P. macronyx* and *P. scotti*. However in those species the endopods are of similar length and the exopods are not (reverse of *P. tasmanensis)*, the right exopod being shorter than the left (Scott 1909, p. 173, pl. 54 fig. 6; Sewell 1932, p. 388, fig. e). *P. macronyx* further differs in armature of the genital segment, which has paired dorso-lateral spines both anteriorly and posteriorly, in having a smaller anal plate, and it is a slightly larger copepod (1·73–1·97 mm), (Scott

FIG. 1. *Pontellopsis tasmanensis* sp. nov., female. a, lateral view; b, dorsal view; c, Th5 and urosome with P5 *in situ*, lateral view; d, urosome with typical development of genital segment; e, urosome with maximal development of genital segment (as in 'e' above); h, detail of terminal region right P5 exopod; i, detail terminal region left P5 exopod, j, proximal portion of right antennule.

1909; Sewell 1932; Kasturirangan 1963). *P. scotti* differs additionally in having: an elongate anal segment without extended anal plate, and on which the furcae are set asymmetrically; paired lateral spines anteriorly on the genital segment, the posterior end variously developed but typically with a swelling on the left side (elongate in some), some with rod-like spine on right side (Sewell 1932, fig 129a).

Closest similarity in fifth leg structure is with *P. tenuicauda*. However in that species the genital segment does not develop a bulbous postero-lateral projection, having instead two lateral spines on the right side (some variability is apparent in development of these spines, cf. Giesbrecht 1892, pl. 41 fig. 43, and Mori 1937, pl. 46 fig. 8). *P. tenuicauda* also has a small anal plate (not reaching mid-region of furcae), and very small

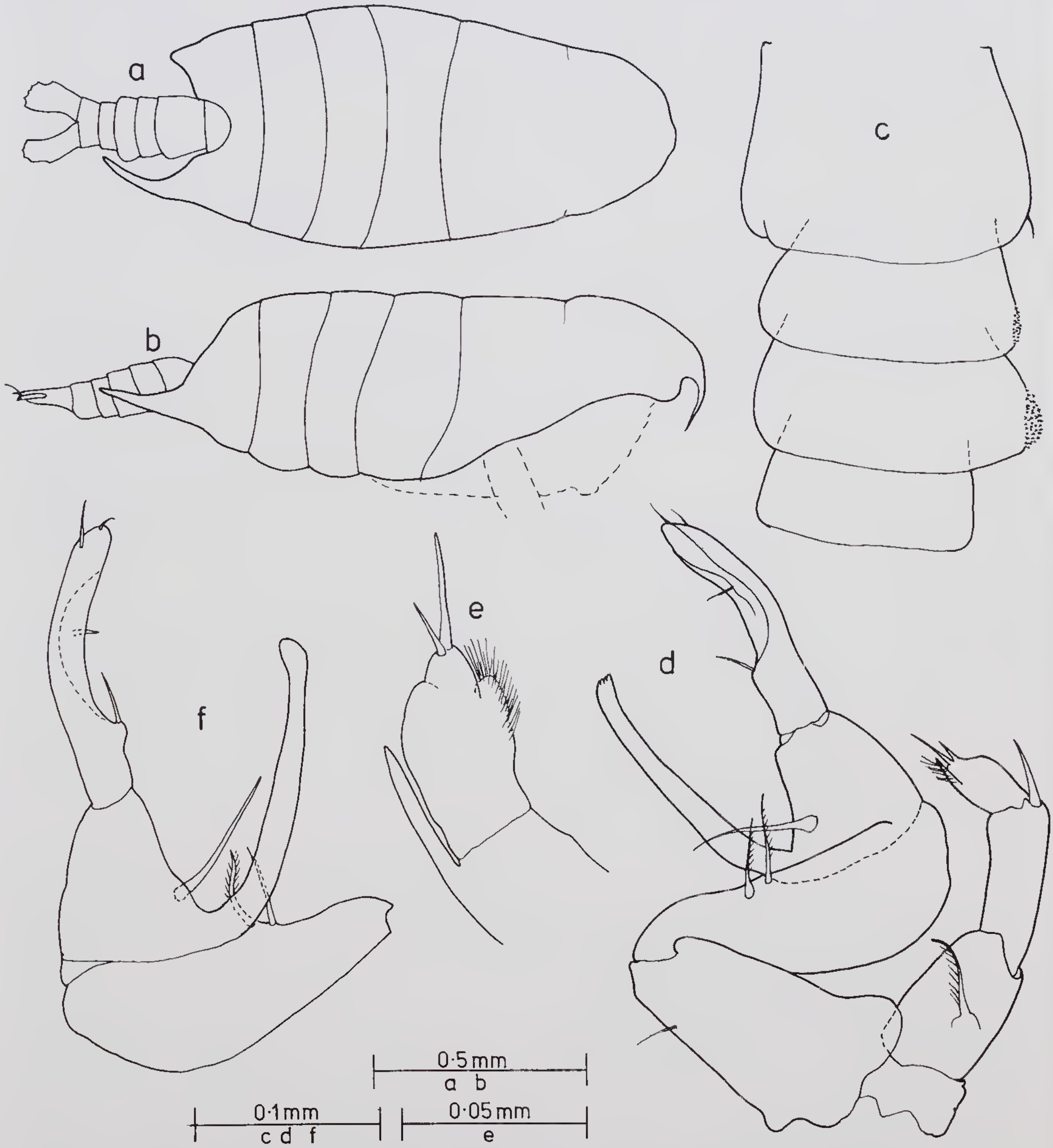


FIG. 2. *Pontellopsis tasmanensis* sp. nov., male. a, dorsal view; b, lateral view; c, urosomal segments 1–4; d, P5; e, terminal portion left P5; f, anterior view, right P5.

fifth thoracic segment lobes (see espec. Giesbrecht 1892).

Sherman (1964) took females of a *Pontellopsis* sp. from the central South-Pacific which could not be identified with published descriptions but which were similar to those of *P. macronyx*. No further details of that species were given by Sherman, but his females must be similar also to those of *P. tasmanensis*.

MALES: *P. tasmanensis* males bear close resemblance to those of *P. scotti*, *P. yamadae* and *P. tenuicauda*.

They differ from *P. scotti* in relative lengths of the 'thumb and finger' (Re2) of the right fifth leg; absence of the central swelling found in the right fifth thoracic segment process of *P. scotti* (Sewell 1932, p.390, fig. 129 b, f).

P. yamadae males are almost twice the size of the present forms (2·5 mm, Mori 1937, p. 99) and differ in some further details: Right fifth leg 'thumb' shorter than 'finger' in *P. yamadae* (slightly longer in *P. tasmanensis)* and without spathulate tip; distal spine on Re1 of left fifth leg very short in *P. yamadae*.

P. tenuicauda is only slightly larger than *P. tasmanensis (c.* 1·65 mm, Mori 1937, p. 98) and, according to Mori's description and figure, closely similar. It differs in that: The right fifth thoracic segment process is longer, reaching to posterior border of anal segment; the second urosomal segment is asymmetrical with pronounced swelling on right side similar to that on the third segment; a large seta is borne on the base of the thumb; the thumb is not spathulate distally. Mori (1937, pl. 46 fig. 10) did not show any spine distally on the left Re1, but this may have been an omission.

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Mem. Qd Mus. **18**(2): 219–31, pls. 31–8. [1978]

ASTHENOPSIS WHITEHOUSE, 1939 (TRILOBITA, MIDDLE CAMBRIAN) IN NORTHERN AUSTRALIA

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ABSTRACT

Comparisons of the Trilobite *Asthenopsis* with other genera, previously confused with it, show it to be a distinct taxon containing six Australian species. Apart from the type species, *Asthenopsis levior* Whitehouse, 1939, five are described as new (*queenslandica, rhinostrongyla, unquinsepta, butorosa,* and *opalensis*). Another new species is recognized but not named and another population is compared with *A. rhinostrongyla*. Some remarks are also made on muscle insertions.

Since Whitehouse erected the genus in 1939 and introduced *Asthenopsis levior* as type, no new species have been assigned and those European species placed there by Whitehouse may now be more correctly placed in other genera. Of the species from China referred by Walcott (1913) to *Solenopleura,* by Kobayashi (1935) to *Solenoparia,* and by Whitehouse (1939) to *Asthenopsis,* none belong to *Asthenopsis.* No references to *Asthenopsis* have appeared since 1939 other than the short note (Opik 1967, p.184) indicating its ptychoparioid affinities and several cursory identifications at the generic level.

Terms used in the systematics are those defined by Harrington, Moore, and Stubblefield (*in* Moore 1959), glabella being used to include the occipital ring. Notation for muscle areas of glabella and points on facial suture follow Richter and Richter (1940). I have referred to any sagittal or exsagittal dimension in terms of length and any transverse dimension in terms of width.

Figured material is housed in the Commonwealth Palaeontological Collection (CPC), Department of Geology, Australian National University (ANU), or Department of Geology, University of Queensland (UQF). Locality numbers referred to are in the registers of the Bureau of Mineral Resources, Canberra (M, H, or MNF), Department of Geology, Australian National University (ANU), or Department of Geology, University of Queensland (UQL).

Genus **Asthenopsis** Whitehouse, 1939

TYPE SPECIES: *Asthenopsis levior* Whitehouse, 1939 by original designation.

GENERIC DIAGNOSIS

Ptychoparioid with glabella of slightly variable length, three or four pairs of lateral glabellar furrows, an anteromedial glabellar muscle scar, slightly tapering, straight to very slightly waisted lateral glabellar margins. Furrow 1_p long and forked adaxially. Fixed cheeks wide (0·7 – 0·9 of basal glabellar width). Eye ridges paired or tripled. Anterior axial furrow weakly or not impressed, always much weaker than lateral axial furrow, and shallowing through ontogeny. Fossulae deep. Brim 0·2 – 0·5 of glabellar length. Border furrow with wide pits anterior to the fossulae. Palpebral lobes short and near midlength of cephalon or slightly posterior to it. Free cheek with high eye socle, with strong anterior doublural projection, and genal spine that is commonly deflected slightly laterally to break the cephalic marginal curve at the level of the posterior of the palpebral lobe.

Thorax of 14 segments. Pleural tips either rounded, broadly squared or spinose. Pygidium relatively small (*c.* 0·3 of cephalic length), transverse, and moderately vaulted to flat in pleural areas. Border furrow poorly to not impressed. Doublure no wider than border, usually very much less. Ornament highly variable from species to species including smooth, finely papillose, and tuberculate (both fine and coarse).

COMPARISON

Solenopleura Angelin, 1854 with *holometopa* as type is a distinct genus characterized by the lack of preglabellar field, glabella occupying a larger percentage of the cranidial surface, fixed cheek 0·6 or less of basal glabellar width (*canaliculata* is probably not congeneric), almost aspinose cheek, and more quadrangular pygidium. *Jincella* Snajdr, 1957 with *S. prantli* Ruzicka, 1944 as type is distinguished from *Asthenopsis* by the short convex border, short preglabellar field, well impressed anterior axial furrow, rather conical glabellar shape, narrow fixed cheeks, well impressed glabellar furrows, and long narrow posterior limb. *Solenoparia* Kobayashi, 1935 with *Ptychoparia toxeus* Walcott, 1905 (Walcott 1913, pl. 19, fig. 10) as type is distinguished by its short convex border, narrow fixed cheeks, longer palpebral lobes, glabella occupying larger part of cranidial area, and less transverse pygidium. *Kounamkites* Lermontova *in* Chernysheva, 1956 based on *virgatus* Chernysheva, 1956 is distinguished by the short border relative to brim, strongly diverging anterior branches of suture, well impressed anterior axial furrow, undeflected genal spines, and less transverse pygidium.

The content and validity of the several genera mentioned above are not commented on herein as I have had no first hand experience with them. However, they are sufficiently known to be sure of their distinction from *Asthenopsis*.

Eosoptychoparia kochibei (Walcott, 1911) from Manchuria represents a very similar genus even to the deflected genal spine but distinctions are evident. I shall describe *E. kochibei* more fully in a forthcoming paper.

MUSCULATURE

As illustrated for *Triarthrus* (Cisne, 1974, fig. 2) the ventral longitudinal muscles of *Asthenopsis* are interpreted as running forward to the two wide slightly deeper areas of the anterior border furrow situated directly in front of the fossulae. These muscles that run back to the major ventral endoskeletal bars to which attach many of the muscles of the mouth parts and other appendages, are probably strongly digitate anteriorly (by homology with the cephalocarid *Hutchinsoniella,* see Hessler 1964) with many small attachment sites on the cuticle.

In passing it should be noted that a large percentage of trilobites have some structures in or near the anterior border furrow (i.e. low anteriorly on the sagittal or exsagittal glabellar profile) that can be readily interpreted as ventral longitudinal muscle attachment sites. Those lacking such structures are not precluded from having muscle insertions in this position but are simply interpreted as not showing them in any distinctive way. In the Crepicephalidae the two or three wide distinctive pits in the border furrow are formed by several smaller circular pits providing apodemes for the digitations of the ventral longitudinal muscles. This structure also suggests that broad depressions and discrete pits may be analogous. Many post-Cambrian trilobites exhibit strong apodemes or muscle scars well forward on the cephalon that would be ideally placed for attachment of the ventral longitudinal muscles.

The dorsal longitudinal muscles of *Asthenopsis* are interpreted as anchoring anteriorly to the glabellar furrows and posteriorly to the apodemes of the transaxial furrows. While these muscles form single sheaths the full length of the animal, they are also attached to each segmental apodemal area to allow intersegmental mechanisms to function.

A very small muscle scar is situated anteromedially on the glabella. I am unable to find the description of any other ptychoparioid referring to a similarly situated muscle scar. Jell (1975, p. 23) interpreted a muscle scar in this position on a species of *Pagetia* and discussed its possible function as a hypostomal diductor muscle by direct homology with the living notostracan *Triops*. In many dalmanitaceans a pit is present anteromedially on the glabella (Campbell in press) which may be homologous with that of *Pagetia* and indeed with that of *Asthenopsis*.

AFFINITIES

The taxonomic position of *Asthenopsis* is not clear. Originally placed in the Solenopleuridae it has been regarded as correctly assigned except for the statement by Opik (1967, p. 184) that it may be regarded as a ptychopariid. I agree with Opik and believe that in the light of new species described herein the genus can be confidently divorced from any close relationship with the group of genera that have come to be known as the Solenopleuridae. I shall not make any assignment at this stage as I am at present engaged in a numerical taxonomic study of ptychoparioids and do not wish to pre-empt those results.

Asthenopsis levior Whitehouse, 1939
(Fig. 1a; Plate 31, figs. 1–9; Plate 32, figs. 1–5)

Asthenopsis levior Whitehouse, 1939, p. 214, pl. 22, figs. 17–20.

Material Examined

Holotype: UQF3337, an external mould of a complete exoskeleton the counterpart of which is missing from the University of Queensland collections, from V Creek at the Undilla to Camooweal Road crossing.

Other Material: Four cranidia (C), 1 free cheek (FC), 2 pygidia (P), and 1 thorax (T) from M41 at the base of an isolated hill of Split Rock Sandstone 4·8 km east of Douglas Creek on the Old Burketown Road (lat. 19° 27·5'S., long. 138° 37'E); 3C, 2P, and one complete from M247 at Barkly No. 7 Bore west of Yelvertoft; 2C from the left bank of Douglas Creek halfway from the Old Burketown Road to the O'Shannassy River; 3C from 12 km south of Douglas Spring on the 'Morstone' to 'Undilla' Road; 1C and 2T from left bank of Douglas Creek at 'Morstone'; 2C from M52 1·3 km west of M41; 1FC from M139 just west of Top Hands Waterhole on the upper reaches of Harris Creek; 5C, 1P, and 3T from UQL469 on top of hill immediately east of the crossing of Harris Creek by the Camooweal to Thorntonia Road; 3C and 1FC from UQL3510 15 km south-west of the Thorntonia airstrip on the Kangaroo Flat road. This includes the figured specimens CPC17064–8 and UQF68711–4 (Pls. 31, 32). Whitehouse's originally figured specimens were also examined and are refigured herein (Pl. 31 figs. 1, 4, 6, 7).

All localities are in the V Creek Limestone except M52 which is in the Mail Change Limestone. The age of the material is the Zone of *Ptychagnostus nathorsti*.

Diagnosis

Outline regularly oval. Surface ornament lacking or of minute papillae with rare slightly larger tubercles. Glabella extending 0·7 of cephalic length, with tapering straight or convex lateral margins, with truncated anterior and angular anterior corners. Three pairs of lateral glabellar furrows, smooth to very poorly impressed, with furrow 1p long and wide, furrows 2p and 3p successively shorter and narrower. Occipital node at midlength of ring. Border flat to weakly convex long and tapering laterally. Facial suture with slightly convex anterior branch in exsagittal line or slightly convergent. Eye ridges variable in prominence, paired. Palpebral lobe short, just behind midlength of glabella. Caecal ornament on extra-glabellar parts of cephalon. Thorax of 14 segments. Pleural furrows long, well impressed, running almost to pleural tips. Pleurae downturned in fulcral line, with spinose tips. Pygidium about 0·15 of total length. Axis with three rings and terminus. Pleural areas highly vaulted with four pairs of ribs. Posterior margin concave.

Description

The holotype designated by Whitehouse (1939, p. 278) has a cephalon 9 mm long but other specimens have been collected with cephala up to 16 mm long so the type is not a fully mature individual. This description is based on the more mature material and its variations from the morphology of the holotype are discussed below under Discussion of Holotype.

Exoskeleton almost twice as long as wide, moderate overall convexity with steeper slopes towards the margin. Cranidium two or three times length of pygidium. Overall shape oval but somewhat more rounded anteriorly than posteriorly.

Cranidium moderately vaulted, twice as wide as long, with moderately steep slope to border furrow in lateral profile. Glabella tapering forward to half its basal width, with straight or slightly convex sides, truncated almost transverse anterior. Anterior axial furrow very poorly impressed (represented almost entirely by a change of slope in lateral profile), never as well impressed as lateral axial furrow. Axial furrow very broadly V shaped in section, with deep fossulae anteriorly, floor raised adjacent to lobe 1p, running directly past occipital ring to margin. Occipital ring five times as wide as long, with prominent sagittal node at the midleigth, posterior margin convex, tapering laterally into a low ridge that crosses the axial furrow into the posteroproximal corners of the fixed cheek. Occipital furrow poorly impressed, slightly deeper laterally, with smooth surface of apodemal pit extending up onto lobe 1p and occipital ring. Glabellar furrows three pairs in number, defined mainly as smooth areas on an otherwise weakly ornamented glabella. Furrow 1p long, directed at 30° to transverse line out of axial furrow then posteriorly at 60° to transverse line in a shorter adaxial terminally expanded section, with medial swelling just out of axial furrow. Furrow 2p shorter and narrower than 1p, of same general shape but with much narrower unexpanded adaxial part and directed less posteriorly. Anteromedian glabellar muscle scar present.

Brim downsloping much more steeply and twice as long at facial suture as axially, convex becoming more so laterally, very slightly depressed from fossulae forward to border furrow, with prominent anastamosing caeca originating out of the eye ridge and running forward into the

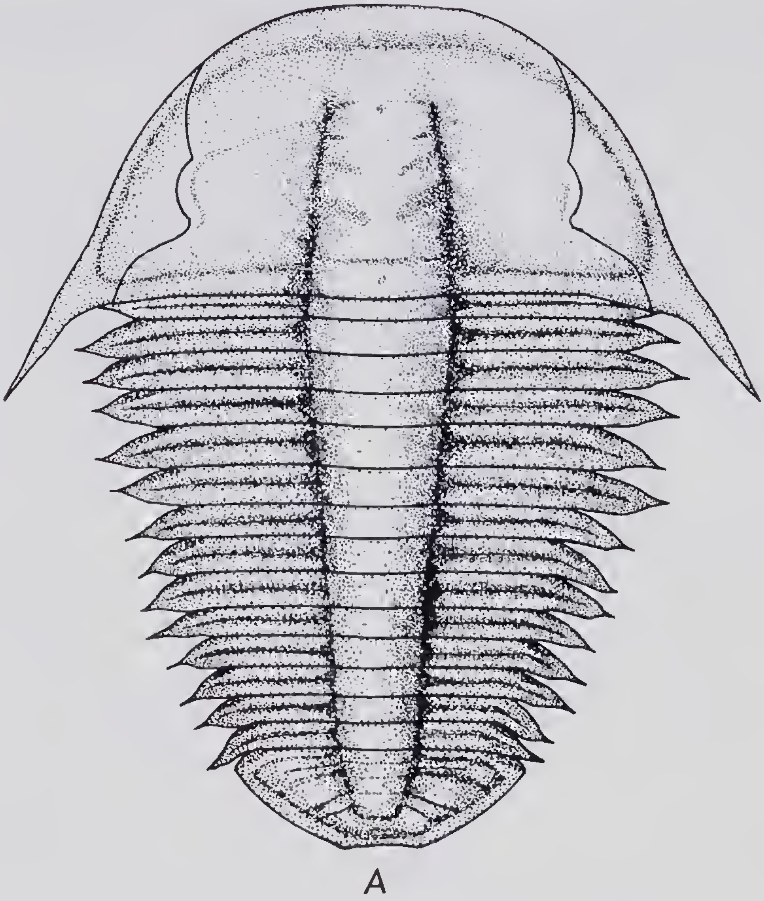

FIG. 1A: Reconstruction of *Asthenopsis levior* Whitehouse, 1939 based on holotype and UQF44314.

border. Border furrow poorly to moderately impressed, with a pair of very wide indistinct pits directly anterior to the fossulae (ventral longitudinal muscle attachment sites), transverse except for slight convexity between wide pits. Anterior border moderately convex often accentuated by sharp posterior slope but always with gently sloping anterior, highest point at midlength. Eye ridges double, prominent, continuing through the fossulae and around front of glabella as low parafrontal band, directed posteriorly at approximately 20° to transverse line. Palpebral lobe 0·25 of cephalic length, abaxially upturned, and posteriorly downturned, moderately arcuate, opposite furrow 1p and lobe 2p. Palpebral furrow moderately impressed, shallowing at midlength. Fixed cheeks 0·82 basal glabellar width, moderately convex, rising gently to palpebral lobe. Posterior limb wide and long, almost rectangular in shape except for slightly convex and posteriorly directed anterior margin, sloping steeply abaxially, with faint caecal system posterolaterally from palpebral lobe. Posterior border furrow lengthening and deepening laterally, turned slightly forward at extremity. Posterior border lengthening and flattening laterally, with marked ridge forming high point for most of its width but meeting the posterior margin two thirds of distance from fulcrum to ω. Posterior margin straight to fulcral line (used in sense of Opik, 1967, p.57) then convex. Facial suture with $\alpha-\alpha$ only 0·6 of $\beta-\beta$, $\beta-\gamma$ variable from convex and converging to straight and exsagittal, δ at midlength of palpebral lobe, ϵ at posterior of furrow 1p. Free cheek with long anterior extension where facial suture cuts obliquely across border, β at posterior of border furrow. Margin evenly curved to base of rounded genal spine, then deflected slightly abaxially down spine. Border wide, flat to weakly convex. Eye socle low, of

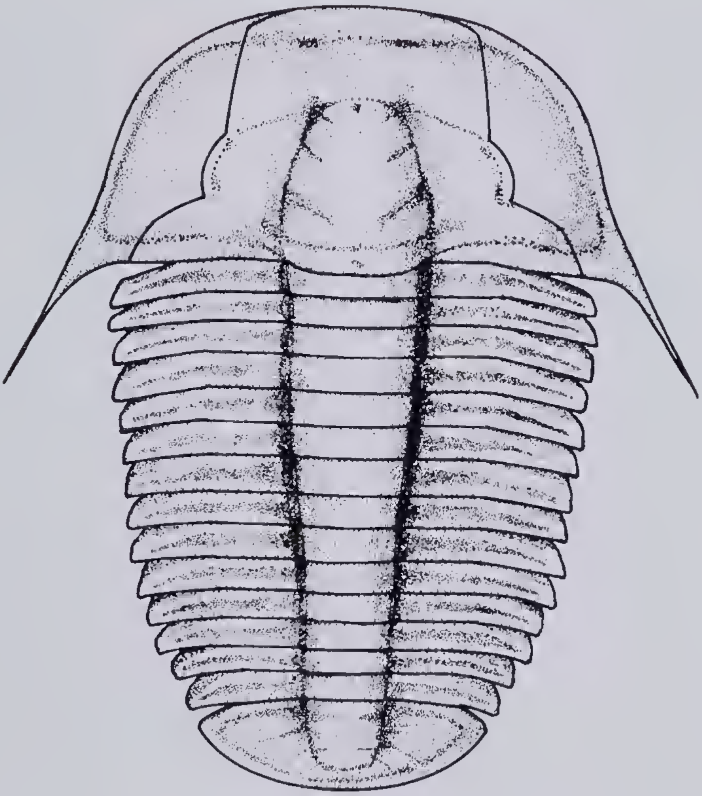

FIG. 1B: Reconstruction of *Asthenopsis queenslandica* sp. nov. based on holotype and CPC17072.

constant height. Genal field exhibiting very low anastamosing caeca.

Rostral plate and hypostoma unknown at present. Thorax of 14 segments each 12 times as wide as long. Articulating half ring slightly lower than axial lobe, shorter than furrow or lobe, with prominent transverse ridge near posterior forming high point and dividing smooth relatively flat anterior part from steeper granulose posterior part. Articulating furrow with posterior wall steeper and higher, with fine papillose ornament anteriorly. Axial lobe expanding slightly laterally to occupy full segmental length, flat (sag.) with transverse posterior margin. Accessory apodemal pits low abaxially, joining articulating furrow and posterior margin. Pleural furrow occupying 40–50% of fixed pleura, swinging forward and shallowing adaxially, meeting axial furrow a short distance from margin, with very shallow posterior arm adaxially giving a forked appearance, deepening and shortening on free pleura before finishing at the midlength near the base of the pleural spine. Pleural strips of equal length except on free pleura where anterior strip shortens as it runs obliquely behind wide moderately long smooth facet. Pleural spines stout, curving slightly posteriorly. Segments not overlapping at all on fixed pleura (i.e. margins abutting) but overlapping almost all facet on free pleura. Segments transverse throughout.

Pygidium almost three times as wide as long, well vaulted, with rounded margin except for slightly concave section across axis posteriorly. Articulating half ring extending in front of otherwise transverse margin, with fine papillose ornament posteriorly. First axial ring highest part of pygidium, with posterior excavation on axial three quarters cutting out most of segmental length (sag.) with weak accessory apodemal pits in exsagittal line close to axial furrow. Second axial ring with almost imperceptible accessory apodeme and smaller posterior excavation. First and second transaxial furrows moderately impressed with wide undepressed apodemal areas. Posterior transaxial furrows possibly three in number, progressively weaker, and continuous. Axis parallel sided with rounded posterior, with moderately steep posterior slope to border and margin. Pleural areas with three well impressed pleural furrows and one poorly impressed interpleural furrow anteriorly, furrows deepest in fulcral line. Caecal ornament running out from axial furrow along pleural strips, through border furrow and into the border. Facets wide, relatively short, triangular, smooth and steeply sloping. Anterior pleural strip of first segment short and convex to fulcrum then longer, less convex and oblique beyond. Border furrow poorly impressed more so behind axis. Border flat and of uniform width. Ornament of fine papillae on axial rings, terminus, pleural ribs and border of some specimens, furrows smooth.

Discussion of Holotype

As already mentioned the holotype specimen represents an immature individual so it varies in several minor respects from the description given above. With the recognition of these morphogenetic changes further outlined under Morphogeny below comes the realization that the species has considerable intraspecific variation between individuals of the same and only slightly different size.

The holotype is crushed with only slight displacement of the free cheeks that do however, obscure the course of the facial suture. It has fine, close-spaced papillae with an occasional very widely spaced tubercle. Details of occipital ring and glabellar posterior are lost as the exoskeleton of that part has remained in the counterpart. Fossulae are deeper so the frontal area is more convex (exsag.) but less steeply sloping. The caecal network on the brim and eye ridges is less prominent. The palpebral furrow is abaxially convex and the lobe more strongly upturned. Fixed cheek width and basal glabellar width almost the same. On the thorax the ornament is coarser axially but less apparent on the pleura. On the pygidium the posterior margin is straight, the interpleural furrow is very weak, the axis does not reach so close to the margin, and the pleural areas are not so vaulted.

Morphogeny

The smallest individual with a complete thorax (Plate 31, fig. 2) has 14 segments and a cephalon 4 mm long so that it must be a very early holaspide. A slightly smaller cranidium (Plate 31, fig. 3) 3·5 mm long is similar to that of the complete individual. While the cepahlon is shorter than 5 mm the fixed cheeks are more convex, the axial furrow is deeper, the ornament is coarser, the furrows forward from the fossulae are more evident, the palpebral lobes are relatively long extending from lobe 1p to furrow 3p or half glabellar length, pleural tips are not spinose but simply pointed.

Individuals with cranidia 5–10 mm long are characterized by the holotype described above but it should be noted that most individuals of this size range have coarser papillae than the holotype.

Affinities

Asthenopsis levior is quite variable from locality to locality but only in minor details of glabellar shape, ornament, relief, and anterior course of facial suture. As no uniform variation of these characters can be observed and as the variation is not as great as between this and other species of the genus described below no other species have been separated from the relatively distinct (within the genus) *levior*.

Asthenopsis queenslandica* sp. nov.

(Fig. 1b; Plate 33, figs. 1–8; Plate 34, fig. 1)

Material Examined

Holotype: CPC17074, a complete specimen from M243 on the flood plain of Whistler Creek, 0·8 km from its junction with the Buckley River, 42 km west of Yelvertoft Homestead (Lat. 20° 04′ S., long. 138° 30′ E); V Creek Limestone, Zone of *Ptychagnostus nathorsti*.

Other Material: Three complete specimens, 14C, 2FC and 3P including CPC17070–3 and 17075–8 (Pls. 33 and 34) from M243; 2C from UQL467 4·8 km west of Redbank Creek, just west of laterite ridge between Redbank and Harris Creeks; 20C, 1FC, 8P, and several thoracic segments from UQL463 top of hill 6 km south of Thorntonia Homestead on left bank of West Thornton River.

Both UQL463 and 467 are in the V Creek Limestone with 463 belonging to the *Euagnostus opimus* Zone and 467 to the *Ptychagnostus punctuosus* Zone.

Diagnosis

Asthenopsid with relatively square anterolateral glabellar corners, low cephalic convexity generally and in the anterior margin, four pairs of smooth

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*Named for the state of Queensland.

to very poorly impressed lateral glabellar furrows, anteriorly placed occipital node, relatively long brim, doubled eye ridges, relatively narrow fixed cheeks, straight slightly converging anterior branches of facial suture, fine close spaced papillose ornament with sparse small tubercles superimposed. Pleural tips squared. Transverse pygidium having flat pleural areas, no border furrow, and an evenly curved margin.

Description

Cranidium four times as long as pygidium, very weakly vaulted. Glabella standing above flat to slightly abaxially rising fixed cheeks in anterior profile, subquadrate tapering only slightly forward from furrow 1p, with angular anterolateral corners and only slightly convex anterior margin. Occipital ring with small sagittal node anteriorly. Occipial furrow well impressed, short, and smooth (apodemal part) with steeper anterior than posterior wall laterally and shallow, slightly longer, with papillose ornament and steeper posterior than anterior wall axially. Glabellar furrow 4p may be present low in the axial furrow. Glabellar ornamented with fine papillae except on the apodemal areas. Brim downsloping slightly more steeply at the facial suture than axially. Eye ridges only slightly elevated, divided into two parallel ridges. Fixed cheeks 0·73 of basal glabellar width, rising gently to palpebral lobe with fine papillose ornament and a very few slightly larger tubercles interspersed, with very faint caecal network radiating from lobe 1p and from the rear of the eye. Posterior limb elongate triangular in shape, sloping steeply down abaxially. Facial suture with $\beta - \gamma$ straight and very slightly converging, δ behind midlength of palpebral lobe.

Free cheek relatively flat, not vaulted, β at posterior of border. Border convex anteriorly, flatter posteriorly, with one or two continuous parallel terrace lines near the margin, with papillose ornament. Genal spine with flat dorsal and slightly rounded ventral surfaces. Thorax of 14 segments each 15 times as wide as long. Each pleuron with fine papillae and single row of tubercles (up to 7). Free pleura with rounded anterolateral and semisquared posterolateral corners. Anterior fixed pleural margin just under posterior of next anterior segment but with margins directly opposed in same plane for short distance at fulcrum then overlapped on the free pleural facets. Segments becoming slightly anteriorly convex near the pygidium.

Pygidium with an unbroken marginal curve, and a low profile with axis standing only slightly above flat pleural areas. Furrows all shallower than in *A. levior*, decreasing in depth posteriorly and laterally. Border furrow not impressed. Border may be defined as area beyond pleural furrows. Fine papillae on areas out of furrows and off muscle scars.

Morphogeny

Although no small specimens with a full complement of segments are available some comments on the morphological changes with increased cranidial size are pertinent. The adults described above all have cranidial length of 10–12 mm whereas two other groups exist with cranidial lengths of 3 mm and 5–6 mm respectively.

The 3 mm cranidia (Plate 33, figs. 2, 4) have a second order of larger tubercles scattered over the entire exoskeleton giving the same ornament as in mature individuals of *A. rhinostrongyla.* They have an anterolaterally rounded glabella, almost no glabellar furrows, better impressed anterior axial furrow, convex fixed cheeks just slightly more than half basal glabellar width and with no apparent division of the eye ridge.

The 5–6 mm cranidia (Plate 33, fig. 7) have the same ornament as the 3 mm cranidia, the anterolaterally rounded glabella, very poorly impressed glabellar furrows, virtually no anterior axial furrow, convex fixed cheeks 0·6 of basal glabellar width, and paired eye ridge.

Asthenopsis rhinostrongyla* sp. nov.
(Fig. 2A; Plate 34, figs. 2–7;
Plate 35, figs. 1, 2)

Material Examined

Holotype: CPC17080, a cranidium from H138 on the Huckitta 1:250,000 Geological map at 22°35' south latitude, 136° 02' east longitude on Arthur Creek, Northern Territory; Arthur Creek Beds, *Euagnostus opimus* Zone.

Other Material: Seven C, 3 FC, 1 T, and 3 P including CPC17079, 17081–6, (Pls. 34 and 35) from H138.

Diagnosis

Asthenopsid with rounded anterolateral glabellar corners, flat unarched anterior border, moderate convexity, anterior branches of facial suture diverging forward and abaxially convex, relatively long pelpebral lobes, ornament of very close spaced papillae over entire surface except apodemal areas, palpebral lobes and furrows, and coarse perforated tubercles interspersed sparsely

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**Rhinos* (Gr.) nose, *strongylus* (Gr.) rounded, refers to the rounded glabellar anterior.

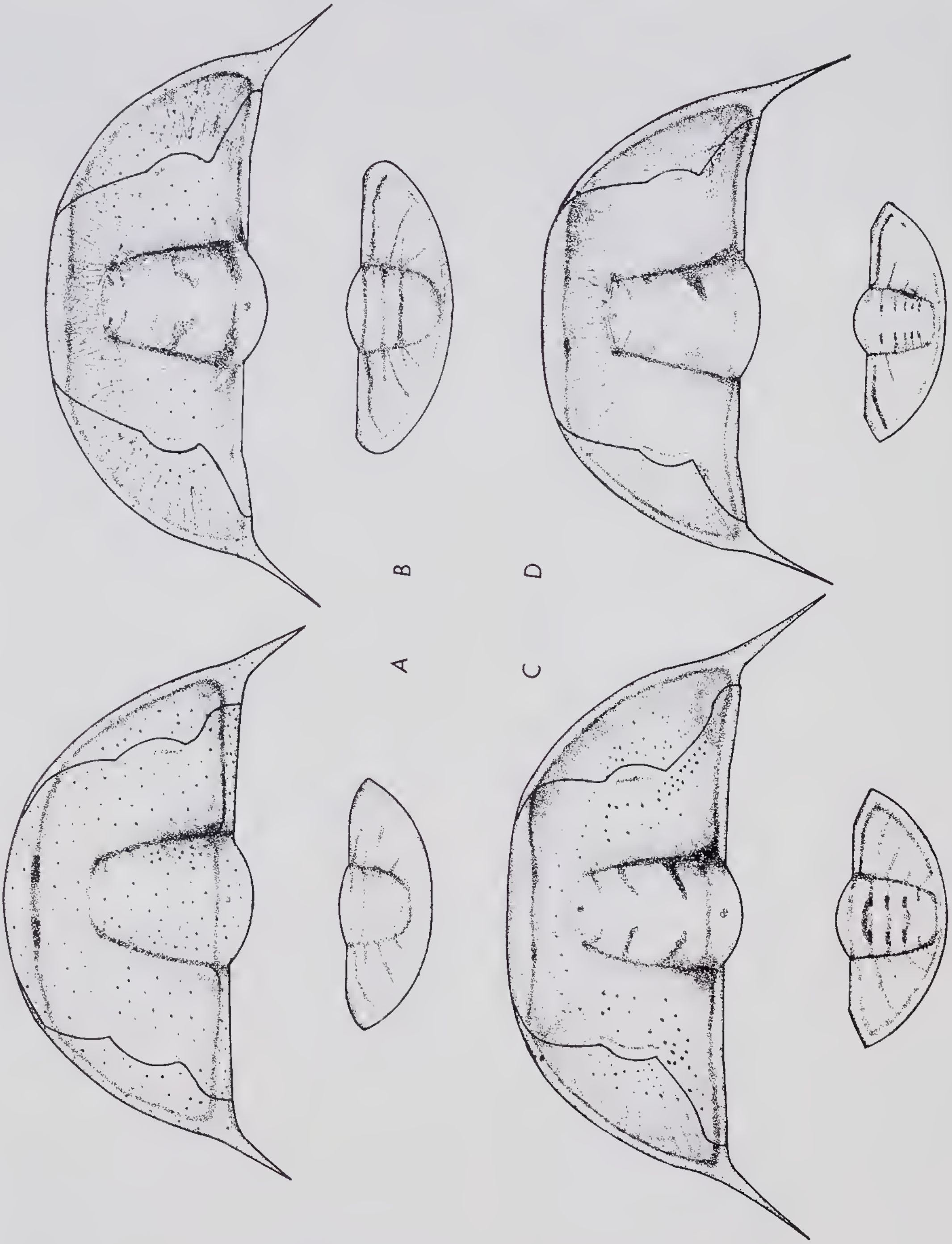

FIG. 2: Reconstruction of cephalon and pygidium of *Asthenopsis* species.

A: *Asthenopsis rhinostrongyla* sp. nov. based on the holotype, CPC17085, and CPC17086.

C: *Asthenopsis butorasa* sp. nov. based on the holotype, ANU30646, and ANU30647.

B: *Asthenopsis opalensis* sp. nov. based on the holotype, CPC17100, and CPC17102.

D: *Asthenopsis unquinsepta* sp. nov. based on the holotype, CPC17087, and CPC17088.

over the same areas. Pleural tips rounded. Transverse pygidium with flat pleural areas.

DESCRIPTION

Cranidium with moderately steep anterior slope in lateral profile. Glabella subquadrate tapering only very slightly forward to 0·8 of its basal width. Occipital furrow with markedly deeper apodemal pits, almost dumb-bell shaped apodemal areas extending onto lobe 1p and occipital ring. Four pairs of lateral glabellar furrows smooth, not depressed. Furrow 1p with adaxial part not expanded. Furrow 3p separated from axial furrow. Furrow 4p very indistinct, narrow and smooth. Occipital node situated anteriorly. Axial furrow distinctly shallower adjacent to lobe 1p and occipital ring. Eye ridge quite low and formed of two trunks. Fixed cheeks 0·8 of basal glabellar width, slightly convex and horizontal. Posterior limb steeply downsloping. Facial suture with $\delta - \beta$ convex and diverging. Posterior border furrow lengthened slightly laterally. Posterior border only moderately convex and slightly longer laterally, with its ridge not markedly distinct and not obvious beyond fulcrum. Ornament of papillae and sparse perforated tubercles over cranidium except on furrows, palpebral lobe and distal parts of posterior limb.

Free cheek doublure without ornament, extending only slightly adaxial to long anterior dorsal projection. Thorax of at least 12 segments (exact number unknown). Anterior half of half ring smooth but posterior half sloping into furrow, moderately papillose. Up to 14 large perforated tubercles on each pleural strip. Posterolateral pleural corner well rounded. Facet more than half segmental length.

Pygidium transverse with second transaxial furrow poorly impressed. Axis with relatively gentle posterior slope to flat border area. Pleural areas almost flat with one well and one poorly impressed pleural furrow separated by long flat rib bearing a poorly impressed interpleural furrow. Anterior strip of first segment lengthening markedly at and beyond fulcrum. Ornament of papillae everywhere except in furrows and close packed on high parts with large sparsely scattered tubercles over the same areas.

Asthenopsis sp. cf. **A. rhinostrongyla** sp. nov.
(Plates 38, figs. 3–7)

MATERIAL EXAMINED

Two C with FC, 1FC, and 3T including CPC17103 to 17105 and UQF68715 to 68716 from M156 (located on Camooweal 1:250,000 Geological map) on the middle reaches of Opal Creek in the Age Creek Formation, *Ptychagnostus punctuosus* Zone, of the Currant Bush Limestone.

DESCRIPTION

Those features not consistent with *A. rhinostrongyla* are referred to comparatively in this description. Glabella with better impressed anterior axial furrow producing a distinct break in lateral profile. Axial furrow poorly impressed throughout. Palpebral lobes narrower, markedly upturned laterally. Fixed cheeks almost as wide as the base of the glabella. Facial suture with α much closer to β. Ornament, especially the papillae, more subdued, larger tubercles fewer in number. Free cheek with terrace lines prominent near margin. Border slightly narrower. Genal spine slightly more abaxially deflected. Pygidium unknown at present.

REMARKS

The nature of the glabella, anterior border and palpebral lobes along with the slightly different ornament make reference to *A. rhinostrongyla* difficult. However, when a larger population of that Northern Territory species is studied the limits of variation may be such that this material will be assignable. It should be pointed out that the cephalic convexity, anterior border arch, subtle ornament, and in one instance (Plate 38, fig. 6) short frontal area also ally this species to *A. opalensis*. However, shape of the glabella and its furrows, eye ridges, shorter palpebral lobes, and straight anterior parts of facial suture distinguish that species.

Asthenopsis unquinsepta* sp. nov.
(Fig. 2D; Plate 35, figs. 3–8)

MATERIAL EXAMINED

HOLOTYPE: CPC17089, a cranidium from M157 on a sharp bend near the second creek junction on Opal Creek, latitude 19° 25′ S, longitude 138° 35′ E.; Age Creek Formation, Zone of *Ptychagnostus punctuosus*.

OTHER MATERIAL: Five C, 2 FC, and 2P including CPC17087, 17088, and 17090–2 (Pl. 35) from M157.

DIAGNOSIS

Asthenopsid with glabella tapering forward to half its basal width, glabellar anterior truncated, anterolateral glabellar corners quite angular, furrow 1p with prominent domed area at its

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*From the latin numerals 1, 5, and 7, the material being from M157.

midlength abaxially, frontal area relatively long and fixed cheeks of moderate width, anterior branch of facial suture straight and converging slightly forward, eye ridges doubled, ornament on border and glabellar of fine tubercles but on frontal area and fixed cheeks of coarser close spaced tubercles. Pygidium moderately vaulted.

Description

Glabella tapering anteriorly to half its basal width, sharply truncated anteriorly by change in ornament, anterior axial furrow not impressed even by a change of slope. Occipital ring less than four times as wide as long with medially placed node. Occipital furrow poorly impressed on axial half, with very steep anterior wall into pronounced apodemal pits laterally. Furrow 1p with domed abaxial elevation prominent. Glabellar ornament of fine tubercles. Axial furrow very poorly impressed throughout, with diverticulum from lobe 1p conspicuous. Ventral longitudinal muscle pits poorly impressed. Frontal area with prominent caecal network standing well above surface. Eye ridges doubled. Fixed cheeks almost flat. Palpebral lobe flat, only very slightly upturned and opposite furrow and lobe 2p. $\epsilon - \omega$ directed posteriorly at moderate angle to transverse line, crossing posterior border obliquely. Posterior limb relatively long and subtriangular in shape. Posterior border furrow increasing in length beyond fulcral point. Ornament on anterior border, on glabella except furrows of fine tubercles closely spaced, absent on palpebral lobes, posterior border furrow, and border furrow; on fixed cheeks, posterior limb, and frontal area ornament of close packed coarser perforated tubercles, with occasional ones larger than the rest.

Free cheek with ornament on genal field similar to that of frontal area. Doublure extending adaxially, with terrace lines only on marginal curve, absent on ventral dorsally sloping part. Thorax with each articulating half ring having distinct transverse ridge near its midlength, anterior wall of articulating furrow rising very steeply to this ridge. Ornament of coarse tubercles on pleural strips not arranged in a single row. Pleural extremity squared, with rounded anterior corner and right angled to slightly pointed posterior corner. Pygidium with pleural areas moderately vaulted, anteriorly almost as high as axis that is sunken between pleural areas, axis well above pleural areas posteriorly. Axis lightly tapering to a well rounded posterior, almost flat transversely between apodemal pits, with apodemal pits becoming more adaxially placed posteriorly. Facets narrow and short. Ornament of coarse close packed tubercles on prominences and border.

Morphogeny

An individual with cranidium 6·5 mm long (Plate 35, fig. 6, lower) has 14 segments and can be interpreted as an holaspide. Another with cranidium 3·5 mm long (Plate 35, fig. 6, upper) has 11 segments of an incomplete thorax and may also be an holaspide. However, some morphological differences between these individuals and the mature ones (11 mm cranidia) are worth noting.

At 3·5 mm ornament is fine with a few larger tubercles, the axial furrow is better impressed (possibly from compaction), anteriorly rounded glabella, $\beta - \delta$ converges more strongly forward, and fixed cheeks are narrower.

At 6·5 mm the ornament is of moderately coarse close spaced tubercles, axial furrow is well impressed, fixed cheeks are narrower, and more convex, caecal ornament is subdued, $\beta - \delta$ converges forward, and thoracic pleura have a line of up to seven large tubercles.

Asthenopsis butorosa* sp. nov.

(Fig. 2C; Plate 36, figs. 1–9)

Material Examined

Holotype: ANU30649, a cranidium from ANU10325, 5·6 km west of Chummy Bore on the Thorntonia to Camooweal Road; Currant Bush Limestone, *Ptychagnostus punctuosus* Zone.

Other Material: One complete, 1 T, and 3 P including ANU30645–8 (Pl. 36) from ANU10325; 6C, 3 FC, and 2 P including CPC 17093–6 (Pl. 36) from M161 at the base of the V Creek Limestone 12·8 km east of Morstone Homestead (marked on Camooweal 1:250,000 Geological Map), *Ptychagnostus punctuosus* Zone.

Diagnosis

Asthenopsid with highly vaulted cephalon, rounded anterolateral glabellar corners, poorly impressed anterior axial furrow represented by considerable change in slope, markedly laterally tapering anterior border, anterior branch of facial suture convex diverging forward, with very steeply sloping frontal area more than twice as long at facial suture as sagittally, with relatively close packed ornament of coarse tubercles on border,

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* *Bu* (Lat.) large, *torus* (Lat.) rounded protuberance, refers to the coarse tubercular ornament.

frontal area, fixed cheeks, glabella, occipital ring, thoracic and pygidial axes and pleura.

DESCRIPTION

Cranidium (up to 16 mm long) with highly vaulted cheeks and glabella, with steeply sloping frontal area (especially anterolaterally) and posterior limb, and with glabella standing well above convex cheeks in anterior profile. Glabella tapering slightly forward to 0·75 basal width, with straight to very slightly waisted (at furrow 1p) lateral margins, with anterior axial furrow represented by a considerable change of slope (up to 40°) and hence more distinct than in any other species of the genus. Occipital furrow poorly impressed over axial half, apodemal area dumb-bell shaped extending up onto the rear of lobe 1p and occipital ring.

Glabellar furrows smooth, 1p not expanded at adaxial end and without abaxial dome shaped elevation. Anteromedial muscle scar almost in anterior axial furrow. Anterior border most convex of any in genus, tapering strongly laterally. Border furrow well impressed with prominent axial and lateral anterior convexities. Frontal area moderately convex, almost vertically downsloping at facial suture, with depressions extending forward from axial to border furrows. Fixed cheek width almost equal to basal glabellar width, moderately convex. Facial suture with $\beta - \delta$ abaxially convex and diverging forward. Ornament on glabella (except furrows), frontal area, fixed cheeks (except palpebral lobe and furrow), posterior limb, and posterior border of coarse (up to 0·3 mm diameter) high tubercles, on anterior border and palpebral furrow of slightly finer tubercles, with tubercles on fixed cheeks becoming more widely separated towards the axial furrow.

Free cheek moderately vaulted, with quite high eye socle. Genal spine with convex dorsal surface, and slight adaxial curve in distal portion. Ornament on genal field of close spaced tubercles superimposed on caecal ornament.

Thorax of at least 14 segments (no complete mature thorax known). Axial lobe with coarse tuberculate ornament. Pleural furrow unforked adaxially. Pleural strips with single row of tubercles becoming less distinct on free pleurae. Free pleura with squared to slightly pointed posterolateral corner, with finer tuberculate ornament than elsewhere. Pygidium just over twice as wide as long. Pleural area with three or four pleural furrows and one interpleural furrow. Facets short, narrow, and directed strongly posteriorly. Fulcra prominently raised. Marked posterior excavation on first axial ring.

MORPHOGENY

Cranidium 3·5 mm long (Plate 36, fig. 1) much less vaulted, with coarse but sparse ornament, anterior part of facial suture converging forward.

Cranidium 5·5 mm long (Plate 36, fig. 3) vaulted, with coarse, closer spaced ornament, anterior part of facial suture convex and diverging laterally, fixed cheeks higher than glabella.

Asthenopsis opalensis* sp. nov.
(Fig. 2B; Plate 37, figs. 1–4;
Plate 38, figs. 1, 2)

MATERIAL EXAMINED

HOLOTYPE: CPC17098, a cranidium from MNF15, 1.6 km south of the junction of Opal Creek and the O'Shanassy River; Mailchange Limestone, *Ptychagnostus punctuosus* Zone.

OTHER MATERIAL: Six C, 1 FC, and 1 P including CPC17097, and 17099–102 (Pls. 37 and 38) from MNF15.

DIAGNOSIS

Asthenopsid with anterolaterally rounded glabella standing well above fixed cheeks, moderate cephalic convexity, four pairs of lateral glabellar furrows with smooth or punctate surfaces, distinctive occipital apodemal pits, anteriorly placed occipital node, eye ridges of three parallel trunks, straight strongly convergent anterior branches of facial suture, very fine close packed papillose ornament overlain by sparse larger tubercles. Pygidium transverse, weakly vaulted, with papillose ornament.

DESCRIPTION

Cranidium moderately convex, with glabella standing above convex fixed cheeks, a moderately steep frontal area, and a moderately arched anterior border. Glabella with rounded anterolateral corners, convex anterior, with straight only slightly tapering lateral margins, with four pairs of lateral glabellar furrows and an anteromedial muscle scar. Occipital furrow shallow over axial half. Occipital apodemal pit distinctive, with wavy slightly raised smooth areas both anteriorly and posteriorly giving an hour glass shape with long axis transverse. Furrow 3p slightly arcuate, directed very slightly to the

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*Named for Opal Creek on which it is found.

posterior adaxially and not connected to axial furrow. Furrow 4p short narrow, directed slightly anteriorly out of fossula very close to glabellar anterior. Glabellar furrows either smooth or finely punctate. Axial furrow crossed by low distinct diverticula at occipital ring and lobe 1p, 2p and 3p. Fossulae not at all distinct. Frontal area flat short and downsloping axially but convex laterally, with both slope and length (to twice sagittal length) increasing laterally. Eye ridges consisting of three parallel trunks (not visible in all specimens) with the median one highest and joining the anterior one just abaxial to the fossula. Parafrontal band low, arising out of fossula, not visible on all specimens. Palpebral lobe flat only slightly upturned laterally, anterior opposite anterior of lobe 2p, posterior level with anterior of lobe 1p. Palpebral furrow straight to slightly abaxially convex, deepending posteriorly. Fixed cheeks 0·9 of basal glabellar width, slightly convex and horizontal, with sparse tubercles over an extremely faint anastomosing caecal network radiating from the axial furrow posteriorly. Facial suture with $\delta - \beta$ straight, converging strongly anteriorly, $\epsilon - \omega$ concave adaxially then straight. Posterior border much longer and flatter beyond fulcrum. Free cheek moderately vaulted, with β in border furrow. Border flat throughout. Genal field with sparse, coarse tubercles superimposed on faint caecal network.

Pygidium transverse, with well rounded margin, and flat pleural areas. Two pleural furrows and an interpleural furrow present. Anterior pleural strip of first segment lengthening well inside fulcrum, weakly convex throughout. Marked posterior excavation in first axial ring.

Asthenopsis sp. nov.
(Plate 32, fig. 6)

MATERIAL EXAMINED

One complete, but damaged, exoskeleton (CPC17069) from 12 km south of Douglas Spring on the Morstone to Undilla Road. It occurs in the V Creek Limestone in the *Ptychagnostus nathorsti* Zone in association with *Asthenopsis levior* and *Papyriaspis lanceola.*

DESCRIPTION

This specimen, being somewhat damaged anteriorly and distorted by several cracks, cannot be satisfactorily compared with other species on cranidial features. Only those features that are at variance with the description of *A. levior* above, are referred to here. It has a flatter border on the free cheek. The genal spine is not deflected. The pygidium has only a weakly convex pleural area and a poorly defined border. The thorax has 16 segments, and a tuberculate pleural ornament. The segments are individually shorter than their corresponding number in *A. levior* whether matching them (i.e. 14 against 14) from the anterior or posterior.

REMARKS

Although this specimen could be included in *A. levior* as representing a population well away from the topotype population I believe that the undeflected genal spine alone, is sufficient to separate it at the species level. In the absence of other material I am reluctant to erect a new name but am confident further collecting will necessitate the assignment of one.

Distinguishing features of the five new northern Australian species described herein are outlined in Table 1.

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TABLE 1: DISTINGUISHING FEATURES OF SPECIES OF ASTHENOPSIS

Characters	*A. levior*	*A. queenslandica*	*A. rhinostrongyla*	*A. unquinsepta*	*A. butorosa*	*A. opalensis*
Bl/BGw	0·31	0·38	0·36	0·38	0·28	0·24
Cw/BGw	0·82	0·73	0·80	0·83	0·92	0·90
Mature cheek ornament	Nil or finely papillose	Fine with few larger tubercles	Tuberculate, sparse	Tuberculate, dense	Coarse tuberculate, dense	Fine with few larger tubercles
Anterior border profile	Horizontal	Slightly arched	Horizontal	Slightly arched	Markedly convex	Moderately convex
General cephalic convexity	Moderate	Little	Moderate	Little	Considerable	Moderate
Occipital node	Medial	Anterior	Anterior	Medial	?	Anterior
Anterior course of facial suture	Converging or parallel and convex	Converging straight	Diverging convex	Converging convex	Diverging convex	Converging straight
Eye ridge	Double	Double	Double	Double	Single	Triple
Pleural tips	Spinose	Squared	Rounded	Squared	Squared	?
Pl/Pw	0·46	0·32	0·30	0·42	0·42	0·33
Convexity of pleural areas	Considerable	Nil	Nil	Moderate	Moderate	Nil
Concavity in posterior margin	Yes	No	No	No	No	No

Bl = brim length [sag.]; BGw = basal glabellar width; Cw = fixed cheek width at level of δ; Pl = pygidial length; Pw = pygidial width

PLATE 31

Asthenopsis levior Whitehouse, 1939

(1, 4, 6, 7, 8 from the type locality on V Creek)

FIG. 1: Thorax and pygidium, UQF3340, (figured by Whitehouse, 1939, pl. 22, fig. 20), × 1·2.

FIG. 2: Latex cast of damaged early holaspid exoskeleton, CPC17064, × 6, from M41.

FIG. 3: Early holaspid cranidium, UQF68711, × 10, from UQL3510.

FIG. 4: Pygidium, UQF3339, (figured by Whitehouse, 1939, pl. 22, fig. 19), × 2.

FIG. 5: Damaged cranidium, UQF68712, × 4·5; b, anterior oblique view, from UQL3510.

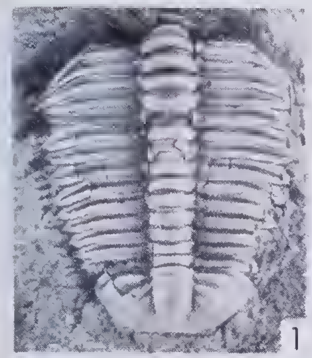
FIG. 6: Damaged cranidium, UQF3338, (figured by Whitehouse, 1939, pl. 22, fig. 18), × 2.

FIG. 7: Latex cast of slightly damaged Holotype exoskeleton, UQF3337, (figured by Whitehouse, 1939, pl. 22, fig. 17), × 2·5; a, lateral oblique view, b, dorsal view.

FIG. 8: Large slightly damaged complete exoskeleton, UQF44314, × 1·5.

FIG. 9: Ventral view of left free cheek, CPC17065, × 3 from M139.

Illustrations are dorsal views unless otherwise stated.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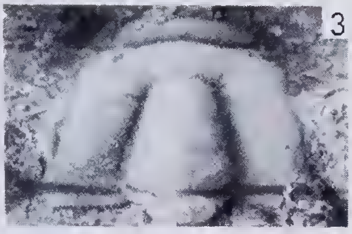
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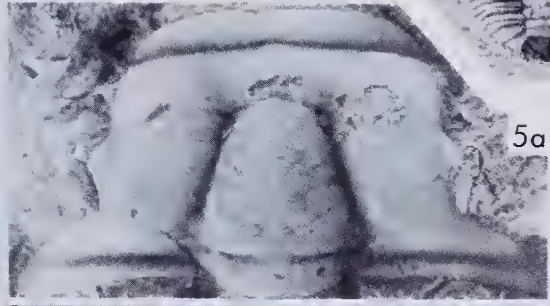
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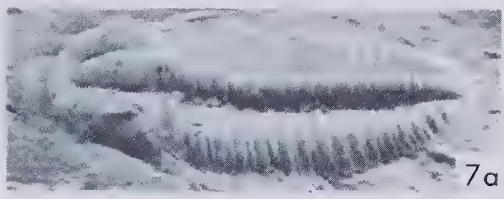
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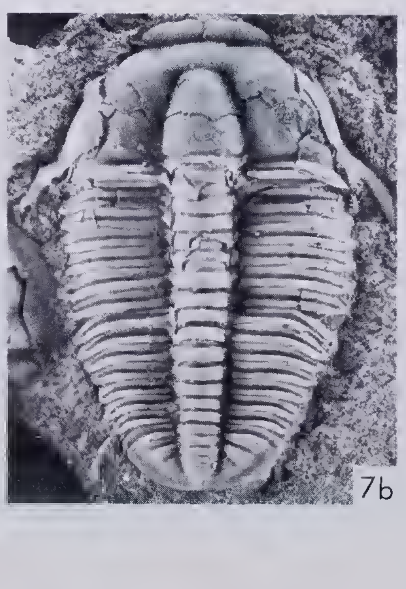
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PLATE 32

Asthenopsis levior Whitehouse, 1939

FIG. 1: Damaged cranidium, CPC17066, × 2·5, from M247.

FIG. 2: Cranidium, UQF68713, × 1·5, from UQL469.

FIG. 3: Damaged pygidium exhibiting well developed caeca passing into the border, UQF68714, a, × 2·5, b, × 7, from UQL469.

FIG. 4: Cranidium, CPC17067, × 3, from Douglas Creek halfway from the Old Burketown Road to the O'Shanassy River.

FIG. 5: Cranidium, CPC17068, × 3, same locality as FIG. 4.

Asthenopsis sp. nov.

FIG. 6: Damaged exoskeleton, CPC17069, × 2·2, from 12 km south of Douglas Creek on the Morstone to Undilla Road.


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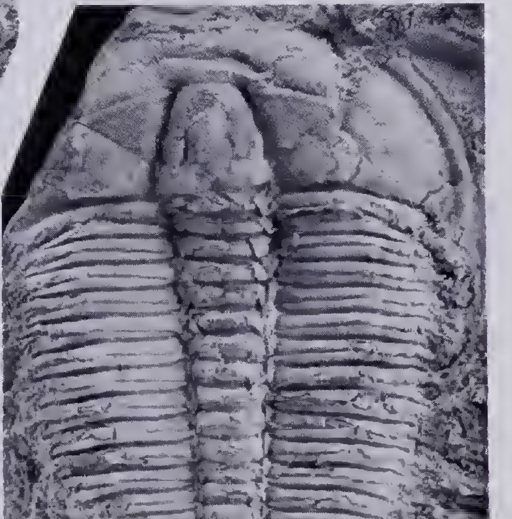
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Plate 33

Asthenopsis queenslandica sp. nov.
(All material is from M243)

Fig. 1: Cranidium, CPC17070, a, × 4, b, × 6·5.

Fig. 2: Small cranidium, CPC17071, × 9.

Fig. 3: Right free cheek, CPC17072, × 3.

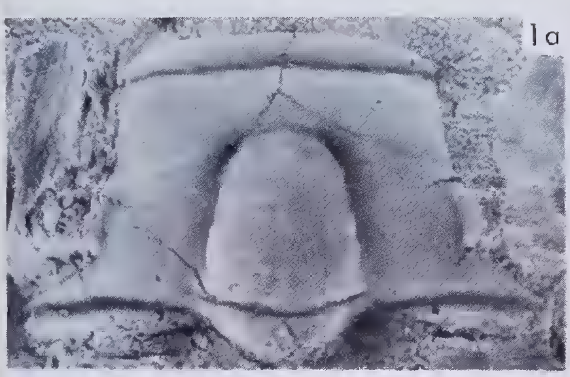
Fig. 4: Small cranidium, CPC17073, × 7.

Fig. 5: Holotype exoskeleton, CPC17074, × 3.

Fig. 6: Large damaged exoskeleton without free cheeks, CPC17075, × 2·5.

Fig. 7: Large damaged exoskeleton without free cheeks, CPC17076, × 5.

Fig. 8: Pygidium, CPC17077, × 6·5.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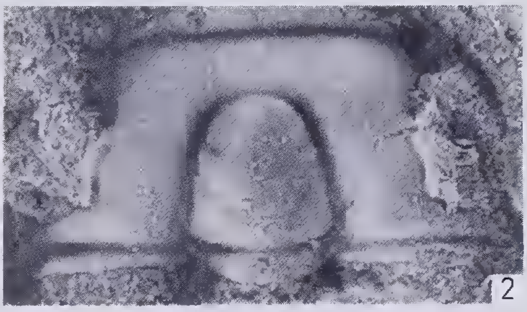
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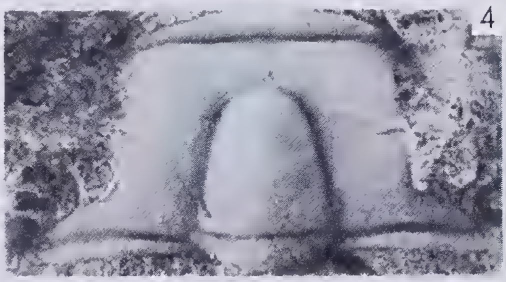
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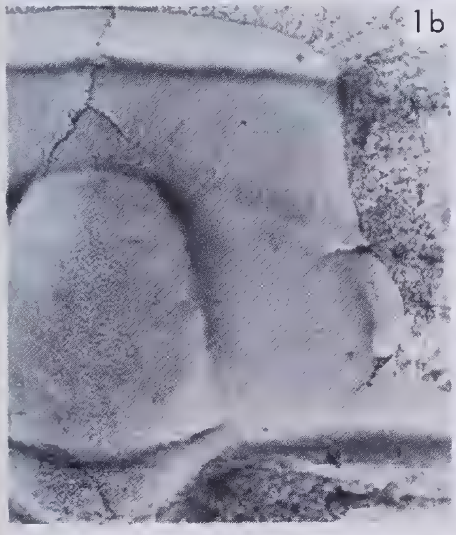
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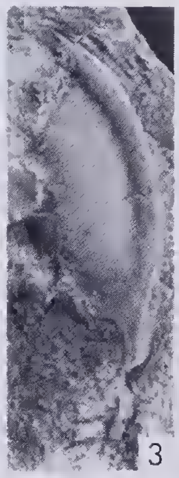
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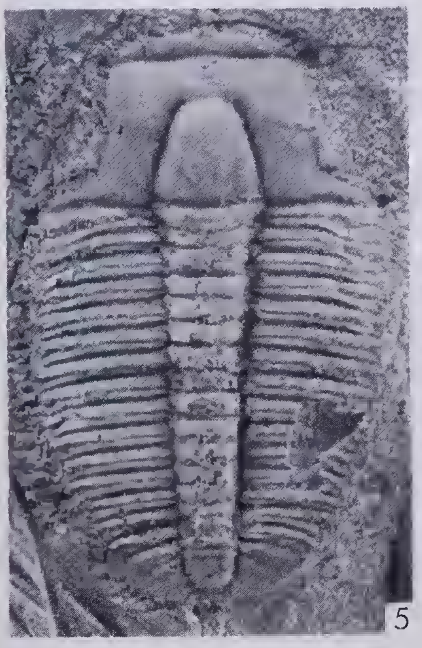
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PLATE 34

Asthenopsis queenslandica sp. nov.

FIG. 1: Cranidium, CPC17078, × 4·5, a, anterior view, from M243.

Asthenopsis rhinostrongyla sp. nov.
(All material is from H138)

FIG. 2: Small cranidium, CPC17079, × 5·5.

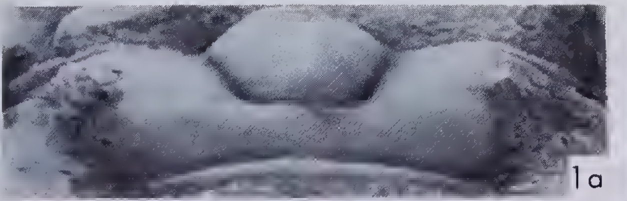
FIG. 3: Holotype cranidium, CPC17080, × 3·5, a, anterior view.

FIG. 4: Ventral view of right free cheek, CPC19081, × 4·5.

FIG. 5: Thoracic fragment, CPC17082, × 2·5, b, lateral view.

FIG. 6: Latex cast of cranidium, CPC17083, a, × 4·2, b, lateral oblique view, × 4.

FIG. 7: Left free cheek, CPC17084, × 4.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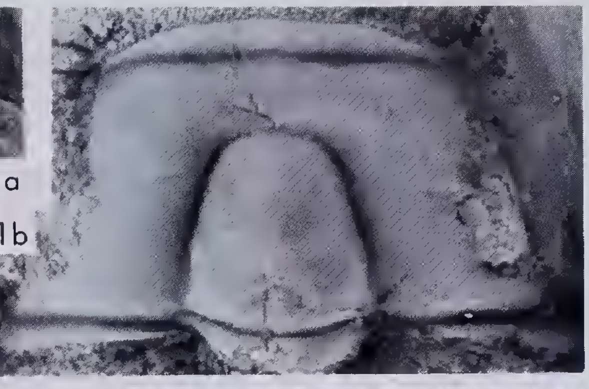
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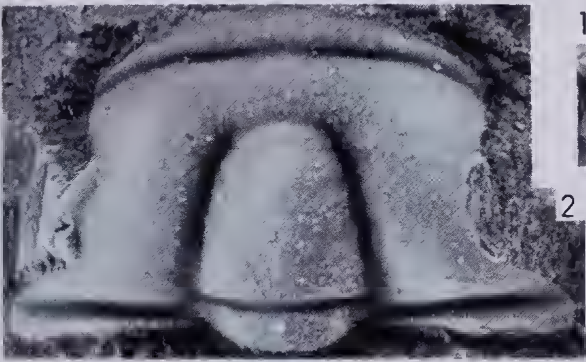
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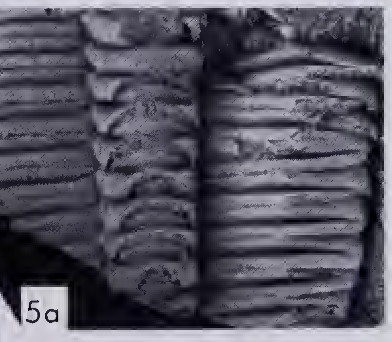
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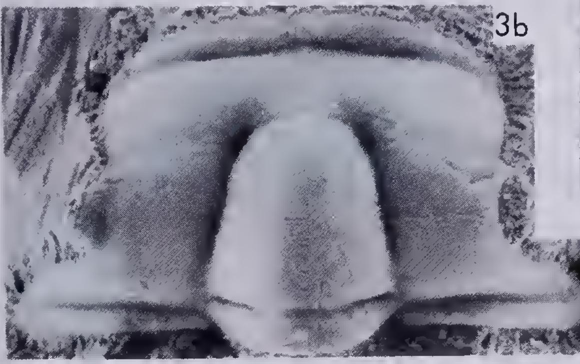
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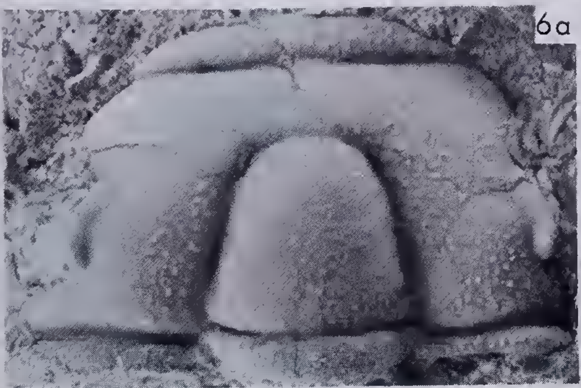
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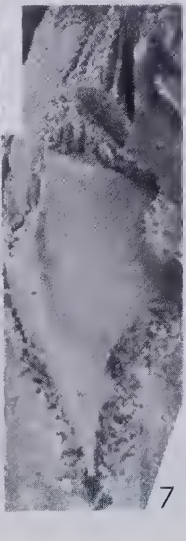
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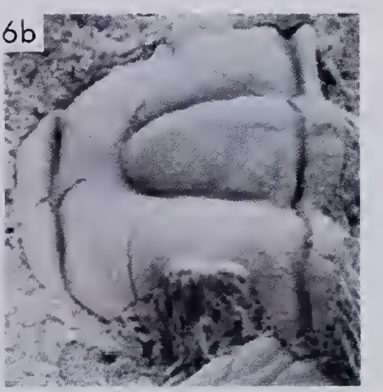
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PLATE 35

Asthenopsis rhinostrongyla sp. nov.

FIG. 1: Left free cheek, CPC17085, × 5, b, lateral view, from H138.

FIG. 2: Pygidium, CPC17086, × 6, from H138.

Asthenopsis unquinsepta sp. nov.
(All material is from M157)

FIG. 3: Pygidium, CPC17087, × 3.

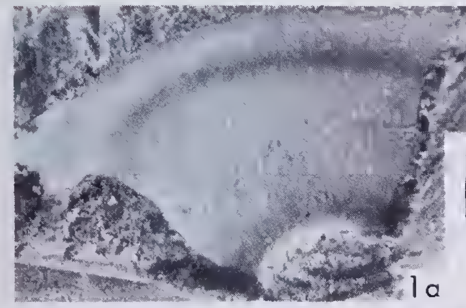
FIG. 4: Left free cheek, CPC17088, × 4.

FIG. 5: Holotype cranidium, CPC17089, × 3, a, lateral view.

FIG. 6: Two small individuals slightly damaged, CPC17090, × 3.

FIG. 7: Latex cast of left free cheek, CPC17091, × 4.

FIG. 8: Cranidium and thorax, CPC17092, × 2·5.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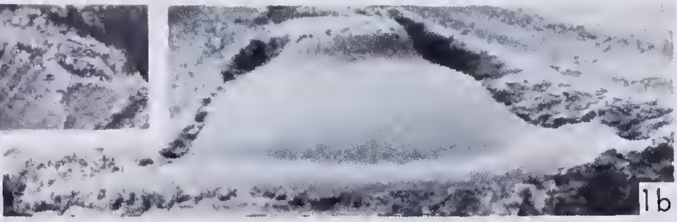
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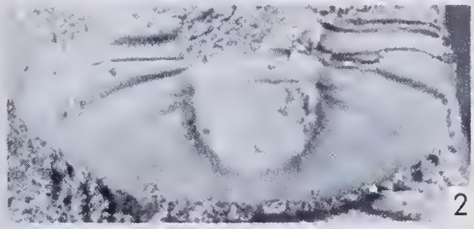
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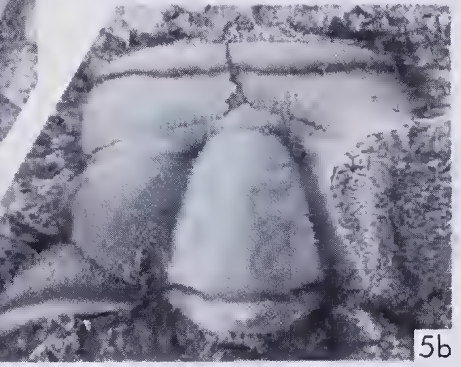
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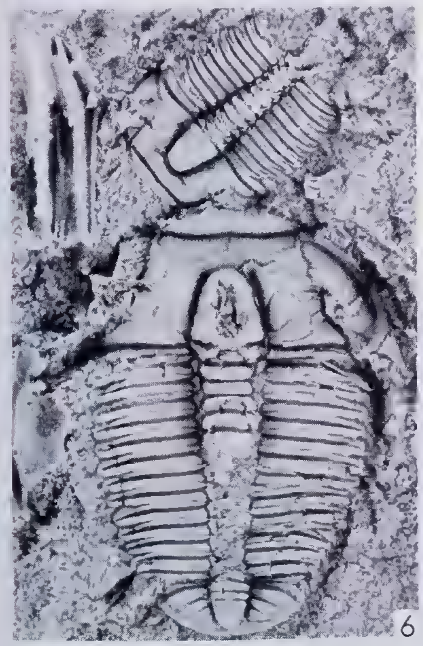
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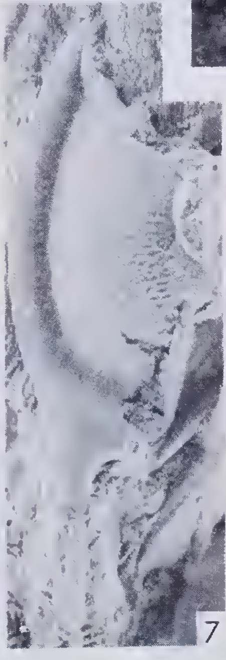
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PLATE 36

Asthenopsis butorosa sp. nov.

FIG. 1: Latex cast of complete (less free cheeks) early holaspide, ANU30645, × 5, from ANU10325.

FIG. 2: Pygidium, CPC17093, × 3·5, from M161.

FIG. 3: Small cranidium, CPC17094, × 7, b, lateral oblique view, from from M161.

FIG. 4: Latex cast of pygidium and damaged thorax, ANU30646, × 3, from ANU10325.

FIG. 5: Cranidium, CPC17095, a, lateral oblique view, × 4, b, dorsal view, × 4, c, anterior oblique view, × 5, from M161.

FIG. 6: Right free cheek, ANU30647, × 5, from ANU10325.

FIG. 7: Latex cast of pygidium, ANU30648, × 5, from ANU10325.

FIG. 8: Holotype cranidium, ANU30649, × 2·8, from ANU10325.

FIG. 9: Cranidium, CPC17096, × 3, from M161.


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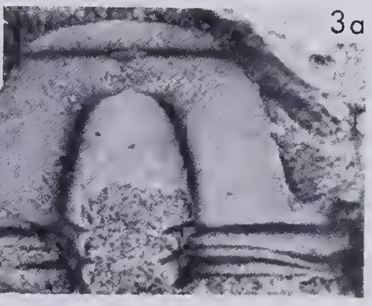
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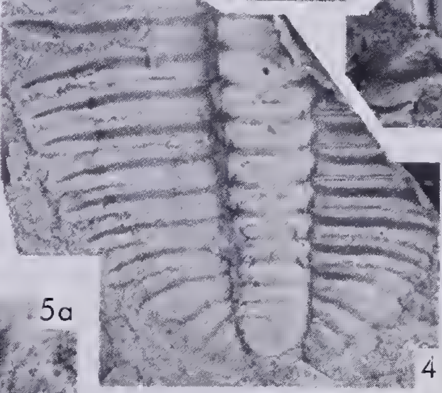
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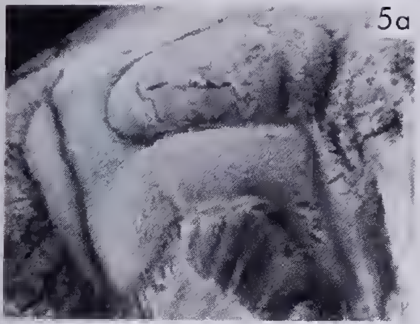
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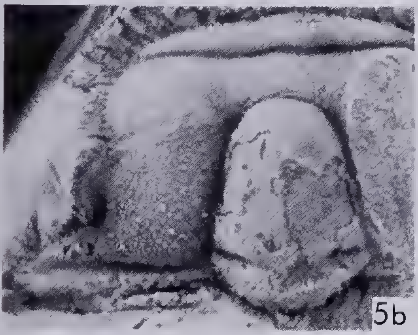
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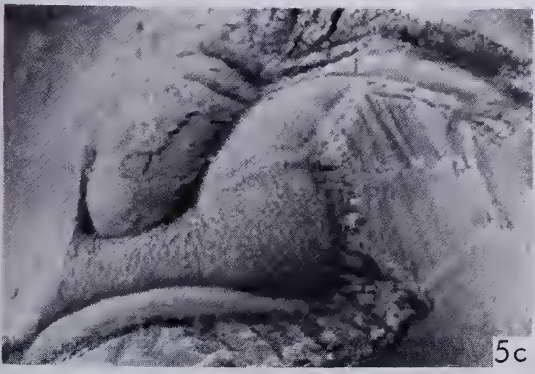
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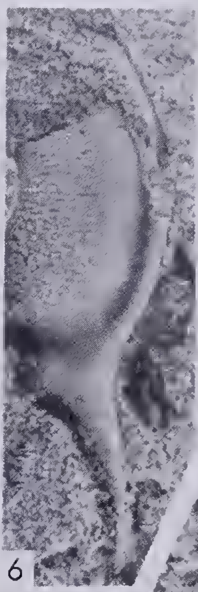
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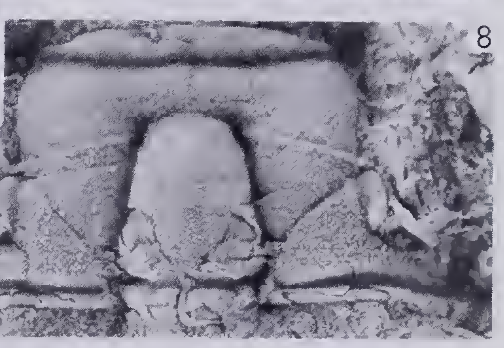
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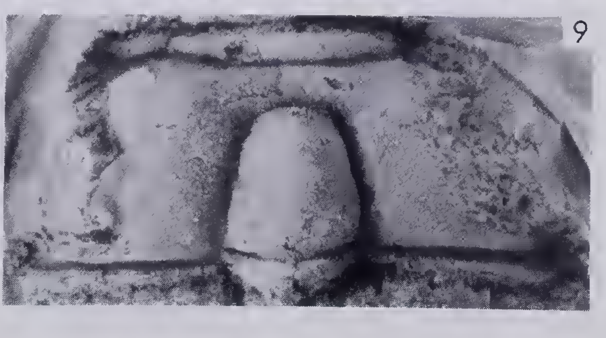
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PLATE 37

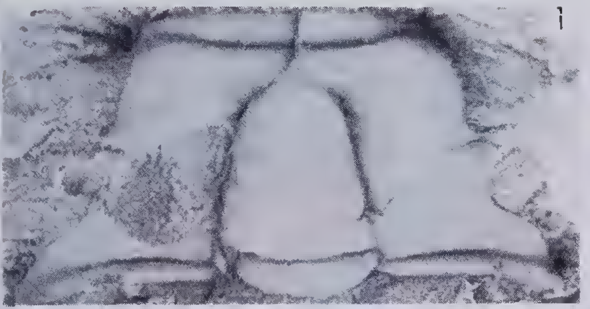
Asthenopsis opalensis sp. nov.
(All material is from MNF15)

FIG. 1: Cranidium, CPC17097, × 3.

FIG. 2: Holotype cranidium, CPC17098, a, anterior view, × 3, b, × 4.

FIG. 3: Cranidium, CPC17099, × 4, a, anterior oblique view.

FIG. 4: Cranidium, CPC17100, a, × 5·5, b, × 6, c, × 2·5.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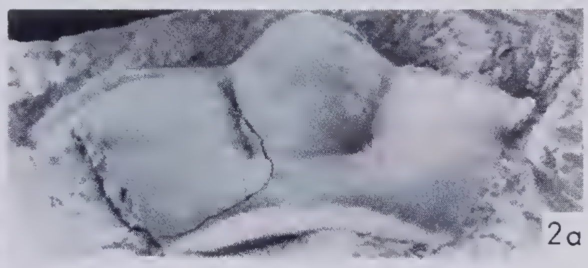
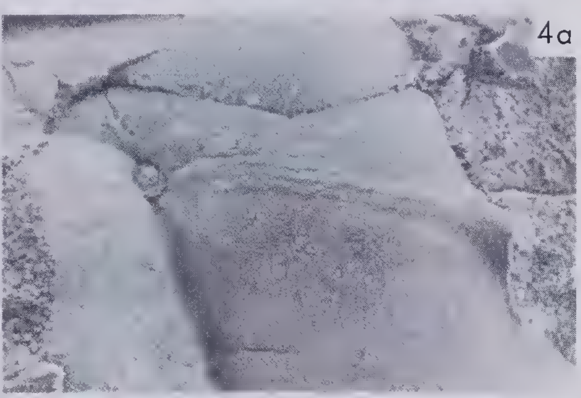

2a


3a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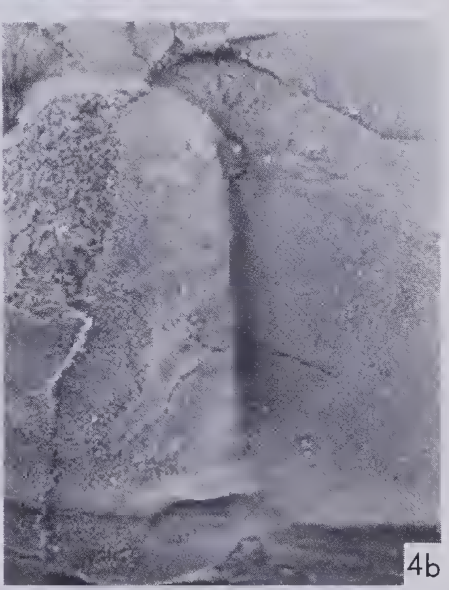
2b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3b

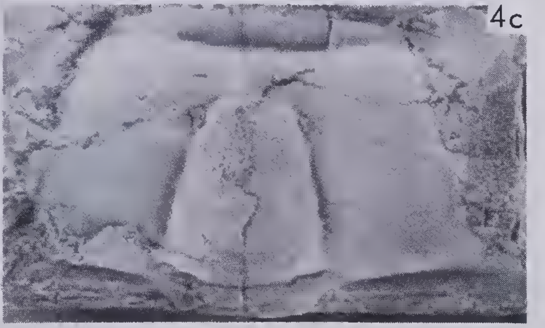

4c

PLATE 38

Asthenopsis opalensis sp. nov.

FIG. 1: Cranidium, CPC17101, × 3, from MNF15.

FIG. 2: Pygidium, CPC17102, × 4·5, from MNF15.

Asthenopsis sp. cf. *A. rhinostrongyla* sp. nov.

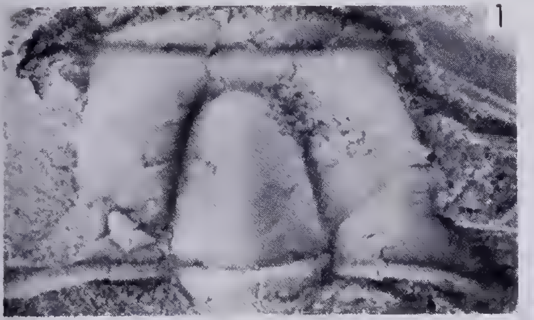
FIG. 3: Cranidium (mostly exfoliated), CPC17103, × 3, a, lateral view, b, from M156.

FIG. 4: Right free cheek, CPC17104, × 4·5, from M156.

FIG. 5: Pygidium, UQF68715, × 5, from UQL447.

FIG. 6: Cranidium, CPC17105, × 3, a, anterior view.

FIG. 7: Cranidium, UQF68716, × 4·5, b, anterior oblique view.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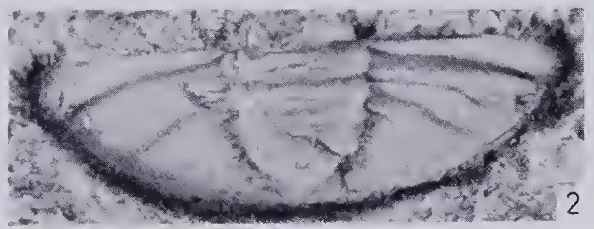
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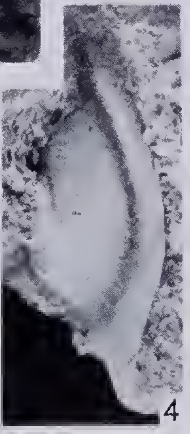
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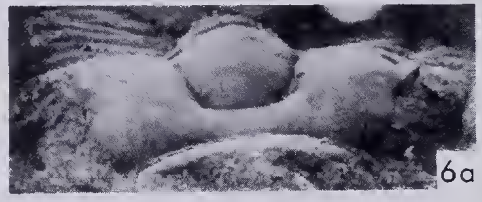
5


3a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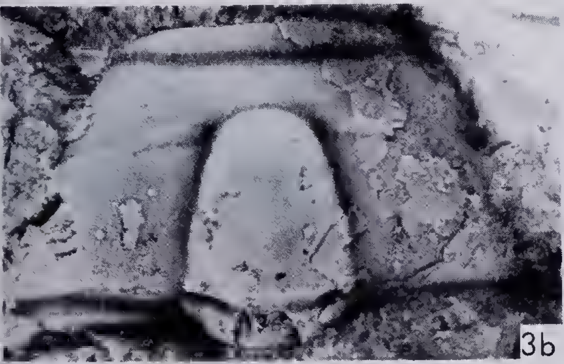
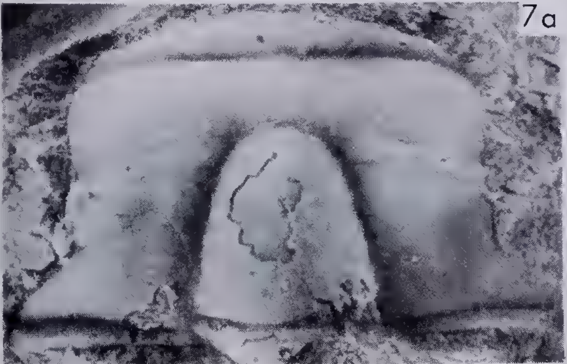

3b


6b


7a


7b

Mem. Qd Mus. **18**(2): 233–43, pl. 39. [1978]

PARANCHISTUS PYCNODONTAE SP. NOV., A NEW PONTONIINE SHRIMP ASSOCIATED WITH AN OSTREID BIVALVE HOST

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ABSTRACT

Paranchistus pycnodontae (Crustacea, Decapoda, Pontoniinae), a new species of shrimp from Heron Island, Queensland, is described and illustrated. The species is most closely related to *P. spondylis* Suzuki, from which it is distinguished. It is the second species of this genus to be found in Australian waters and the first to be found in association with an ostreid host, *Pycnodonta hyotis* L.

The genus *Paranchistus* was first designated by Holthuis (1952), and at present includes four species, all of which are now known to be associates of large marine bivalve molluscs. Of these four species, only one, *Paranchistus armatus* (H. Milne-Edwards), has so far been recorded from Australian waters. This species is an associate of the giant clam, *Tridacna gigas* (L.), and has been reported from Undine Reef, Cape Tribulation, and from Chapman Island, Queensland (McNeill 1968, Bruce 1975). Recently a single example of another species of this genus was found in association with an ostreid bivalve, and the specimen is now described here as new species.

Paranchistus pyenodontae sp. nov.
(Figs. 1–5, Plate 39)

Material Examined

Holotype: Queensland Museum W7337, ♀, non-ovigerous; Heron Island, Capricorn Group, Queensland; No. 2442, 3 m, central lagoon, 17 August 1976, coll. D. Fisk.

Description

A medium sized pontoniine of moderately slender build. Carapace smooth. Rostrum well developed, strongly compressed, with feebly developed carina and extending anteriorly to middle of intermediate segment of antennular peduncle; rostrum horizontal, dorsal and ventral margins straight and subparallel, tapering to an acute tip distally; distal third of upper border with five small subequal, acute teeth, with numerous setae in interspaces; ventral border sparsely setose with a single very small acute tooth below third dorsal tooth. Orbit feebly developed, supraorbital spines absent; inferior orbital angle slightly produced, broad in dorsal view. Antennal spine small, slender, marginal, not exceeding inferior orbital angle. Hepatic spine distinctly projecting, more slender than antennal spine and lower and more posterior, in a small fossa and mobile. Anterolateral angle of carapace bluntly rectangular.

Abdominal segments smooth. Third segment not produced posteriorly in dorsal midline. Length of sixth segment 0·13 × depth, 0·15 × length of fifth segment. Pleura 1–3 only slightly expanded, 4–5 smaller, bluntly rounded posteriorly, 6 with posteroventral angle blunt, posterolateral angle slightly more acute.

Telson *c.* 1·5 × length of sixth abdominal segment, 2·2 × longer than broad; lateral margins almost straight, converging posteriorly; anterior width *c.* 2·7 × width at level of lateral pair of posterior spines. Two pairs of small, subequal, submarginal dorsal spines at 0·6 and 0·7 of telson length. Posterior telson margin rounded, without median point, with three pairs of spines; lateral pair small, similar to dorsal spines, situated on dorsal surface of telson, slightly in advance of posterior margin; intermediate pair very stout, *c.* 0·14 × telson length, with attenuated distal ends, submedian pair uniformly tapering, setulose, *c.* 0·75 × intermediate spine length.

Eyes normal, cornea globular, hemispherical, slightly oblique, with distinct accessory spot; podophthalmite slightly flattened, *c.* 1·2 × longer than broad, distinctly wider than diameter of cornea.

Antennules normal; peduncle exceeds rostrum by most of intermediate segment; proximal segment *c.* 1·3 × longer than proximal width, medial border straight, without ventral spine; stylocerite slender, acute, exceeding half segment length; lateral border feebly convex, medially convergent, with very short subrectangular distolateral spine; anterolateral margin strongly produced, distinctly angulated; intermediate and distal segments subequal, obliquely articulated, *c.* 0·7 × length of proximal segment. Upper flagellum short, biramous, proximal three segments fused; shorter free ramus with two stout segments, longer with nine slender segments; four groups of aesthetascs. Lower flagellum slender, sixteen segments.

Antenna with robust basicerite, with feeble distolateral tooth; ischiocerite, merocerite normal; carpocerite slender, exceeding middle of scaphocerite, *c.* 3·2 × longer than wide. Scaphocerite well developed, extending well beyond antennular peduncle; lateral border very feebly convex, with acute distolateral spine, not exceeding anterior margin of lamina. Lamina broad, *c.* 2·2 × longer than width, anterior margin broad, slightly truncate. Flagellum short, slender, *c.* 2 × postorbital carapace length.

Mouthparts generally similar to other species of *Paranchistus*. Mandibles moderately robust, without palp; molar process stout, with several large blunt distal teeth, incisor process slender, three acute teeth distally, central tooth smallest.

Maxillula normal; palp with feebly developed lateral lobe, medial lobe normal with small hooked terminal seta; upper and lower lacinia broad, densely setose with strongly setulose seta; short, stout, feebly dentate spines distally on upper lacinia, spiniform setae on lower.

Maxilla with stout, proximally swollen palp, medial and lateral borders setose, distally slender, non-setose. Basal endite well developed, broad, deeply cleft, each lobe with numerous long, slender, setulose setae. Scaphognathite broad, *c.* 2·6 × longer than width; anterior lobe broad.

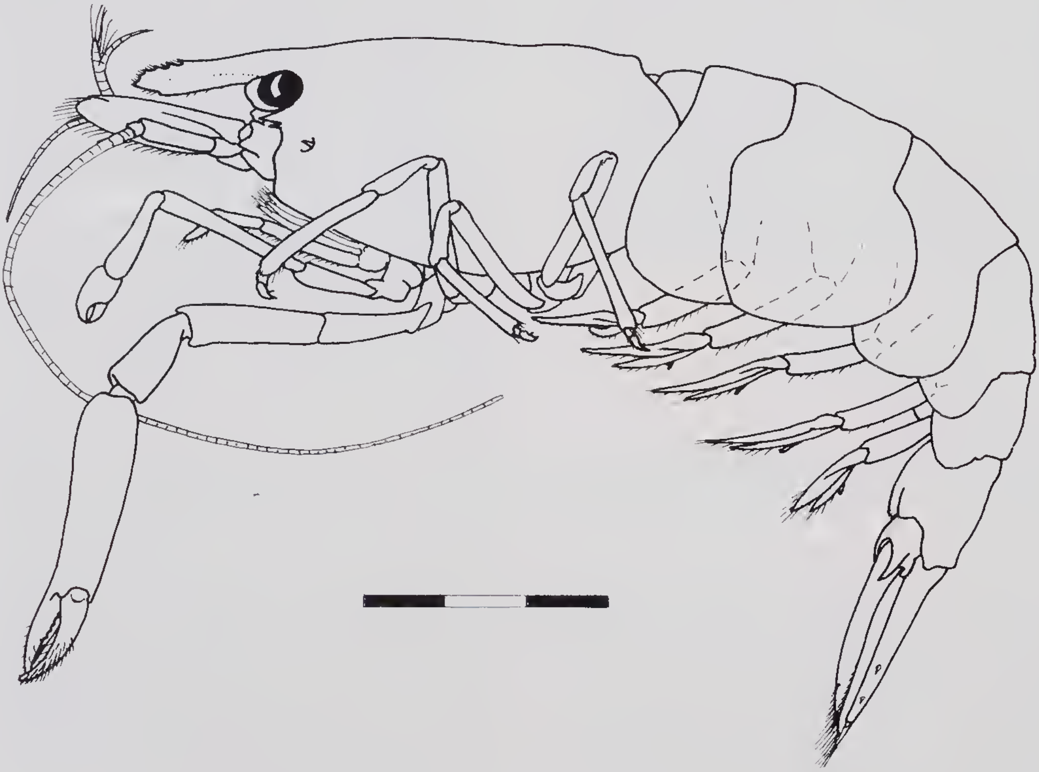

FIG. 1: *Paranchistus pycnodontae* sp. nov., holotype female, Heron Island, Queensland. Scale in mm.

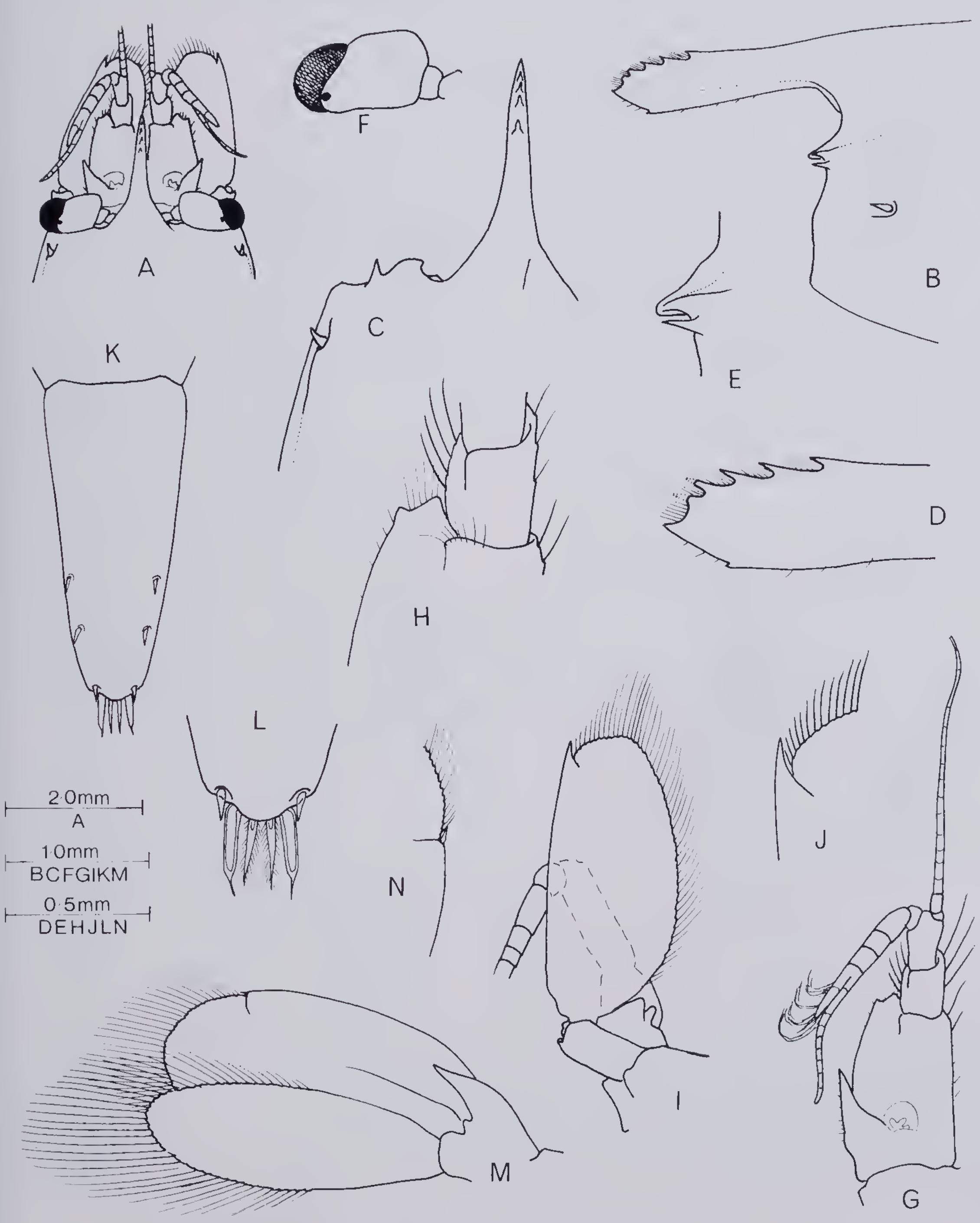

FIG. 2: *Paranchistus pycnodontae* sp. nov., holotype: A, anterior carapace, rostrum, and antennae, dorsal aspect; B, anterior carapace and rostrum, lateral; C, orbital region, dorsal; D, distal rostrum; E, inferior orbital angle and antennal spine; F, eye, dorsal; G, antennular peduncle; I, antenna; J, distolateral tooth of scaphocerite; K, telson; L, posterior telson spines; M, uropod; N, distolateral spine of exopod of uropod;

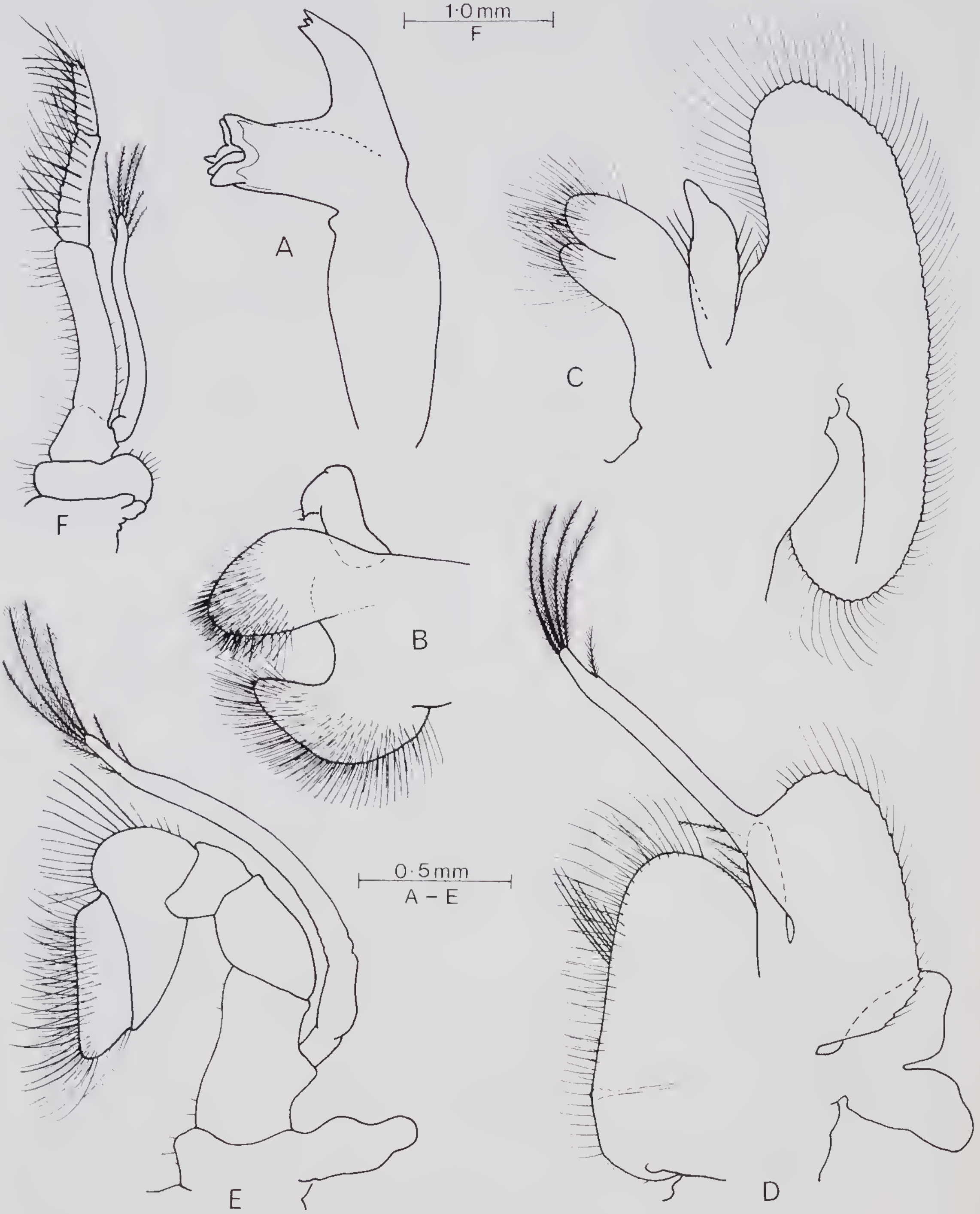

FIG. 3: *Paranchistus pycnodontae* sp. nov., holotype: A, mandible; B, maxillula; C, maxilla; D, first maxilliped; E, second maxilliped; F, third maxilliped;

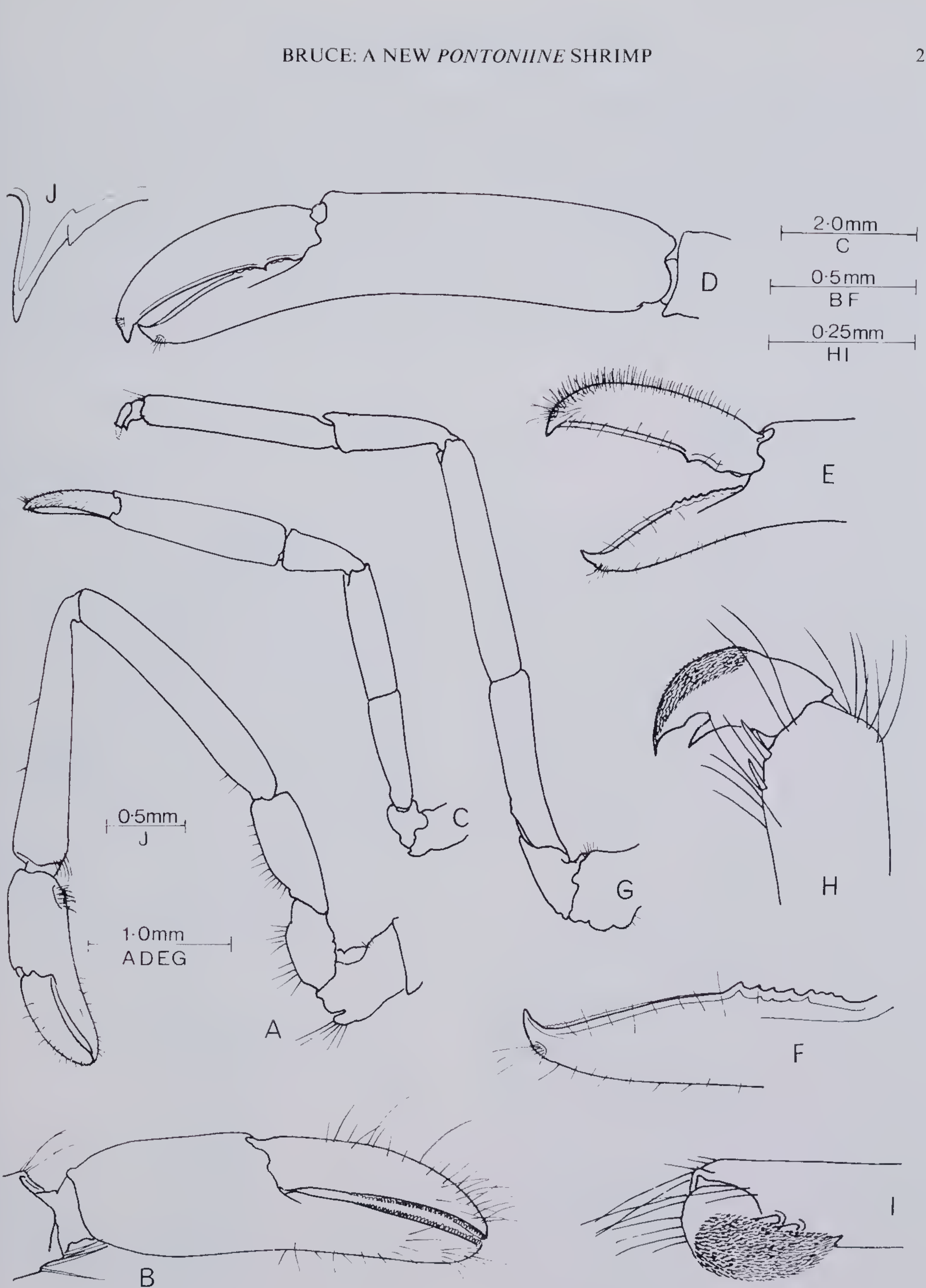

FIG. 4: *Paranchistus pycnodontae* sp. nov., holotype: A, first pereiopod; B, chela of first pereiopod; C, second pereiopod; D, chela of second pereiopod; E, fingers of chela; F, fixed finger of chela; G, third pereiopod; H, distal propod and dactyl of third pereiopod, lateral; I, *idem,* dorsal aspect of dactylus; J, accessory dactylar tooth of fourth pereiopod;

First maxilliped with subcylindrical palp, distomedially with setulose setae, exceeding anterior margin of endite but not caridean lobe; basal endite broad, rounded, medial border straight, confluent with coxal endite, junction indicated by minute protuberance, with numerous slender finely setulose setae; dorsal surface with oblique row of long, coarsely setulose setae; coxal endite sparsely setose. Exopod well developed, flagellum with four plumose distal setae only, caridean lobe small, broad. Epipod triangular, deeply bilobed.

Second maxilliped normal; dactylar segment *c.* 3 × longer than broad, numerous slender, finely setulose setae medially. Exopod with four plumose setae distally; epipod small, irregularly subrectangular; podobranch absent.

Third maxilliped moderately slender, reaching proximal end of carpocerite; ischiomerus feebly separated from basis, junction indicated medially by small notch; ischiomerus slightly tapering distally, moderately bowed, *c.* 4 × longer than proximal width, medial border feebly setose, short simple setae; penultimate segment *c.* 0·6 × ischiomerus, 3·2 × longer than width, with longer stouter setae medially and laterally; distal segment similarly setose, *c.* 0·5 × ischiomerus, tapering, *c.* 3·5 × width, Basis broad, sparsely setose medially, as long as wide: coxa stout, medially rounded, well developed epipod laterally. Exopod slightly exceeds ischiomerus, four plumose distal setae. Arthrobranch rudimentary.

Coxae of third maxillipeds widely separated; fourth thoracic sternite broad, unarmed.

First pereiopods slender proximally, stouter distally, exceeding carpocerite by carpus and chela; chela robust, palm subcylindrical, slightly compressed; fingers subequal to palm, broadly subspatulate, distally rounded with fine denticulations along distal third of cutting edge medially and two thirds laterally, slightly gaping proximally on medial side, densely setose. Palm *c.* 1·7 × longer than width, transverse rows of cleaning setae proximally. Carpus proximally slender, width increasing × 3 distally, *c.* 5 × longer than distal width, cleaning setae distomedially; merus subequal to carpus, slightly bowed, *c.* 6·4 × longer than width; ischium compressed, *c.* 2·6 × width, *c.* 6·5 × merus, medial border with row of short setae; basis 0·33 × merus, sparsely setose along medial margin, coxa robust, small setose ventromedian process present.

Second pereiopods well developed, slender, subequal, similar. Palm of chela subcylindrical, smooth, slightly compressed distally, *c.* 3·4 × width; fingers well developed, *c.* 0·6 of palm length, dactylus strongly curved, overreaching fixed finger, tip acutely hooked, cutting edge sharp, entire except for small tooth at 0·3 of length, outer surface with numerous short, erect setae; fixed finger similar, proximal half of cutting edge with eight small teeth, distal four subacute, proximal four rounded, distal part of cutting edge feebly denticulate. Carpus *c.* 0·47 × palm length, 2 × longer than distal width; distal margins feebly excavate, unarmed. Merus *c.* 0·75 × palm length, 4 × longer than width, uniform, with small distoventral tooth. Basis and coxa normal.

Ambulatory pereiopods slender, third extending beyond scaphocerite by 0·3 of carpus and chela; dactyl about 0·27 × propod length; unguis distinct from corpus, dorsoventrally compressed, hastate, surface covered with dense felt of short processes giving furry appearance; corpus with single well developed, slender acute accessory spine; short distal sensory setae present. Propod *c.* 6·6 × longer than width, uniform, with pair of distoventral spines and single preterminal ventral spine. Carpus 0·63 propod length, *c.* 3·2 × longer than distal width, unarmed; merus *c.* 1·27 × propod length; ischium *c.* 1·0 × propod length, *c.* 5 × longer than distal width; basis and coxa robust, all unarmed. Pereiopods 4–5 similar: 3, 5 subequal, 4 slightly shorter. Accessory spines on dactyls of pereiopods 4, 5, with small additional denticle on posterior margin.

Uropods slightly exceed telson tip, protopodite with large acute posterolateral tooth; exopod broad, *c.* 2·3 × longer than wide, broadly rounded distally, with small mobile spine only at posterior end of convex lateral border; endopod *c.* 3 × longer than width.

MEASUREMENTS: (In millemetres)

Total length (approx.)	18.7
Rostrum and carapace	6.2
Postorbital carapace	4.5
Second pereiopod chelae	3.8 (left and right)

COLOURATION: Semi-transparent with numerous small round evenly distributed red chromatophores, all over body, ambulatory pereiopods, antennae and caudal fan. Similar but slightly larger chromatophores over second pereiopods. Chromatophores absent from antennal flagella and propods of ambulatory pereiopods.

HOST: *Pycnodonta hyotis* L. (Ostreidea)

ASSOCIATES: One specimen of *Onuxoden parvibrachium* (Fowler) (Pisces: Carapidae), a species not previously known from Australia.

TABLE 1: Hosts of Species of Paranchistus and other Pontoniine Associates

Paranchistus spp.	*Hosts*	*Other associates*
P. armatus (H. Milne-Edwards)	*Tridacna gigas* (L.)	*Anchistus miersi* (De Man) *Conchodytes tridacnae* Peters
P. ornatus Holthuis	*Atrina vexillum* Born	*Anchistus custos* (Forskal) *Conchodytes biunguiculatus* (Paulson)
P. nobilii Holthuis	*Spondylus gaederopus* L.	—
P. spondylis Suzuki	*Spondylus barbatus* Reeve	—
P. pycnodontae sp.nov.	*Pycnodonta hyotis* L.	*Platypontonia hyotis* Hipeau-Jacquotte

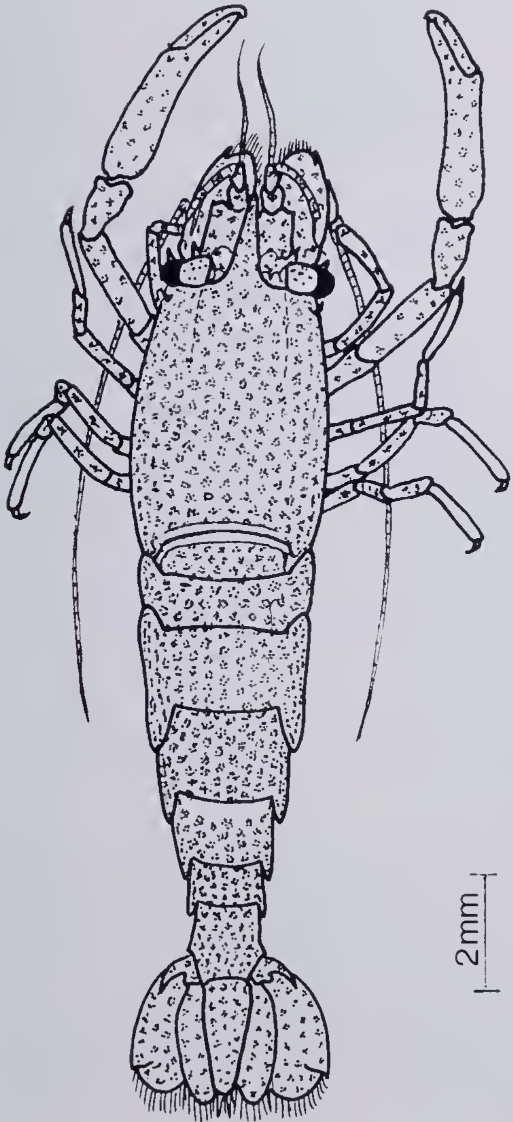

FIG. 5: *Paranchistus pycnodontae* sp. nov., holotype, colour pattern.

SYSTEMATIC POSITION OF *P. pycnodontae*

Paranchistus pycnodontae appears to be most closely related to *P. spondylis* Suzuki, and may be distinguished from that species by the sub-spatulate fingers of the first pereiopods. In all other features the morphology of the two species appears to be very similar. Other minor differences include: In *P. spondylis* (a) the palm of the chela of the second pereiopods appears to be stouter; (b) the accessory spines of the ambulatory pereiopods are shorter and stouter; (c) the accessory spines of the dactyls of the fourth and fifth pereiopods are without denticles; (d) the minute processes on the anterior aspect of the dactyls of the walking legs are perpendicular to the surface; (e) the lateral posterior telson spines appear to be marginal; (f) and the intermediate posterior telson spines are of uniform taper.

DISCUSSION

All species of the genus *Paranchistus* Holthuis are known to be associates of bivalve molluscs. The genus is not represented outside tropical Indo-West Pacific waters. The host molluscs belong to the families Tridacnidae, Pinnidae, Spondylidae and now also include the Ostreidae. *P. pycnodontae* is the only shrimp so far known to associate with *Pycnodonta hyotis* in Australian waters, but in the western Indian Ocean Hipeau-Jacquotte (1971) has recorded the occurrence of a different pontoniine shrimp, *Platypontonia hyotis* Hipeau-Jacquotte, which is also known to associate with *Pterostrea imbricata* (Lam.) in Japanese waters (Suzuki 1971). The only other ostreid bivalve known to have a pontoniine associate is *Lopha cristagalli* (L.), the host of *Platypontonia brevirostris* (Miers), (Bruce 1968).

The hosts of the species of *Paranchistus* are summarized in Table 1, which also indicates other pontoniine associates of the same host.

In addition to the morphological characters that distinguish *P. pycnodontae* from *P. spondylis*, it may be noted that the colour patterns also appear to be distinctive. In the figures of the latter given by Suzuki (1971), the specimen shows a comparatively coarse pattern of larger and more sparsely distributed red chromatophores than is found in *P. pycnodontae*. Most of the pontoniine associates of the bivalve molluscs present a colour pattern of uniformly distributed chromatophores over most of the body surface and appendages. These may be very small and numerous, as in *Anchistus custos, Paranchistus ornatus* or *Conchodytes tridacnae*. In *P. spondylis* and *P. pycnodontae* they are larger and more numerous, and in *Anchistus demani* and *A. miersi*, they are conspicuously larger and much less numerous. In complete contrast, the colour pattern of *Platypontonia hyotis* consists mainly of large spots and bands of red.

The dactyls of the ambulatory pereiopods are of particular interest as, in the genus *Paranchistus*, they exhibit a wide range of morphological variations of great value in distinguishing the species. *P. armatus* presents a simple condition, with a simple, well developed unguis distally and a broad accessory tooth. There is no trace of ornamentation on the unguis (Bruce 1975). In *P. ornatus* the unguis is still distinct from the corpus and the outer surface is covered with transverse rows of short spines which become obsolescent towards the tip. The ventral aspect of the unguis is also transversely ridged. The corpus has distal sensory setae present, but the accessory spine is absent, the region of the spine being provided with a low eminence covered with small tubercles. The pit described by Holthuis (1952) appears to be a vesicle below this eminence. In *P. pycnodontae*, the arrangement is essentially similar except that a well developed accessory spine is present and the unguis is very much larger. A comparable vesicular structure and sensory setae are also present. *P. nobilii* and *P. spondylis* have dactyls very similar to *P. pycnodontae*.

Fujino (1975) has provided scanning electron photomicrographs of the dactyl of the walking legs in *Anchistus miersi* (De Man). *Anchistus* Borradaile is a genus very closely related to *Paranchistus* Holthuis, from which it is separated principally by the complete absence of an hepatic spine. In *Anchistus* a comparable range of variation in dactylar morphology is also present and in species such as *A. demani* Kemp and *A. miersi*, with *A. gravieri* Kemp representing a less well developed stage, and the dactyls very closely resemble those found in some *Paranchistus* spp. SEM photomicrographs clearly show that the outer surface of the unguis of the dactyls is densely covered with large numbers of short erect spinules. In *Anchistus* the anterior aspect of the unguis has been reported as scoop-shaped (Kemp 1922; Fujino 1975) but in *Paranchistus* spp. this surface appears to be convex rather than concave. The precise function of the spinulations of the unguis is still obscure, but is presumably related to the grip of the shrimp upon its host. The function of the ventrally situated tooth on the corpus would appear to enable a good grip upon the host's tissues to be obtained during traction by the limb. The distally directed spinules of the unguis may function by preventing the penetration of the dactyl too far into the host's tissues and thereby avoiding excessive damage to the host in a commensal relationship.

ACKNOWLEDGMENT

I am grateful to Dr Paxton for the identification of the associated fish.

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PLATE 39

Paranchistus pycnodontae sp. nov., holotype, in *Pycnodonta hyotis* L.

Mem. Qd Mus. **18**(2): 243–63. [1978]

GASTROINTESTINAL NEMATODES FROM AQUATIC AUSTRALIAN SNAKES

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ABSTRACT

Three new nematodes are described, and another three species are recorded from six species of aquatic snake (Acrochordidae and Colubridae). Four nematodes are from genera which predominantly parasitise vertebrates of other Phyla or Orders, but which inhabit a similar aquatic environment to these snakes.

This paper is the first in a proposed series on the gastrointestinal parasites of Australian snakes. Little work has been done on the nematode parasites of the Australian tropical and subtropical aquatic snakes, most of it being confined to identifications and host records (Johnston and Mawson 1941, 1948), with no indication of intensity or prevalence of infection. This paper is concerned with the gastrointestinal nematodes from 26 Australian aquatic Colubrid and Acrochordid snakes preserved in the Queensland Museum, Brisbane. Representatives from all six Australian species in this group were examined, namely *Acrochordus javanicus, Acrochordus granulatus, Cerberus rhynchops, Myron richardsoni, Fordonia leucobalia* and *Enhydris polylepis*.

The nematodes recovered are as follows:

Subclass ADENOPHOREA
Order ENOPLIDA
Superfamily DIOCTOPHYMATOIDEA

Eustrongylides acrochordi sp. nov.
(Fig. 1, Table 1)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum G10275, ♀, collected by H. Jones from stomach of *Acrochordus javanicus*, QM J23191, collected by J. Covacevich and C. Tanner near Coen, North Queensland, June 1973.

PARATYPE: QM G10276, ♀, (incomplete), same data as holotype.

DIAGNOSIS

Double row of six apical papillae, marked terminal striations and row of lateral punctations, nerve ring anterior, oesophagus long and voluminous, anus terminal. Vagina opens into the rectum, forming a cloaca. No tail.

DESCRIPTION

Worm long, cylindrical and partly coiled. Very marked striations near both ends, diminishing until scarcely visible near centre of worm. Two lateral rows of very small punctate markings, situated in the striations, proceed posteriorly from anterior end, disappearing within a few mm. Two lateral rows of four evenly spaced small papillae at caudal end, replaced anteriorly by punctate markings as at anterior end, gradually disappearing. Body of fairly uniform thickness, tapering slightly at posterior end but more markedly at anterior end. Mouth elongated dorsoventrally, surrounded by six spined papillae, two laterally and four submedially. Another row of six rounded papillae below these. Another 12 much smaller papillae, two just below each lateral spined papilla, one just anterior to each lateral rounded papilla, and the remaining six at intervals between the two main rows of papillae.

A short straight pharynx leads into a wide undulating oesophagus; this increases slightly in width throughout its length, is without a bulb, and measures 0·2 × the total length of the worm. Nerve ring surrounds oesophagus just behind its origin. No excretory pore seen. A wide rectum, flattened

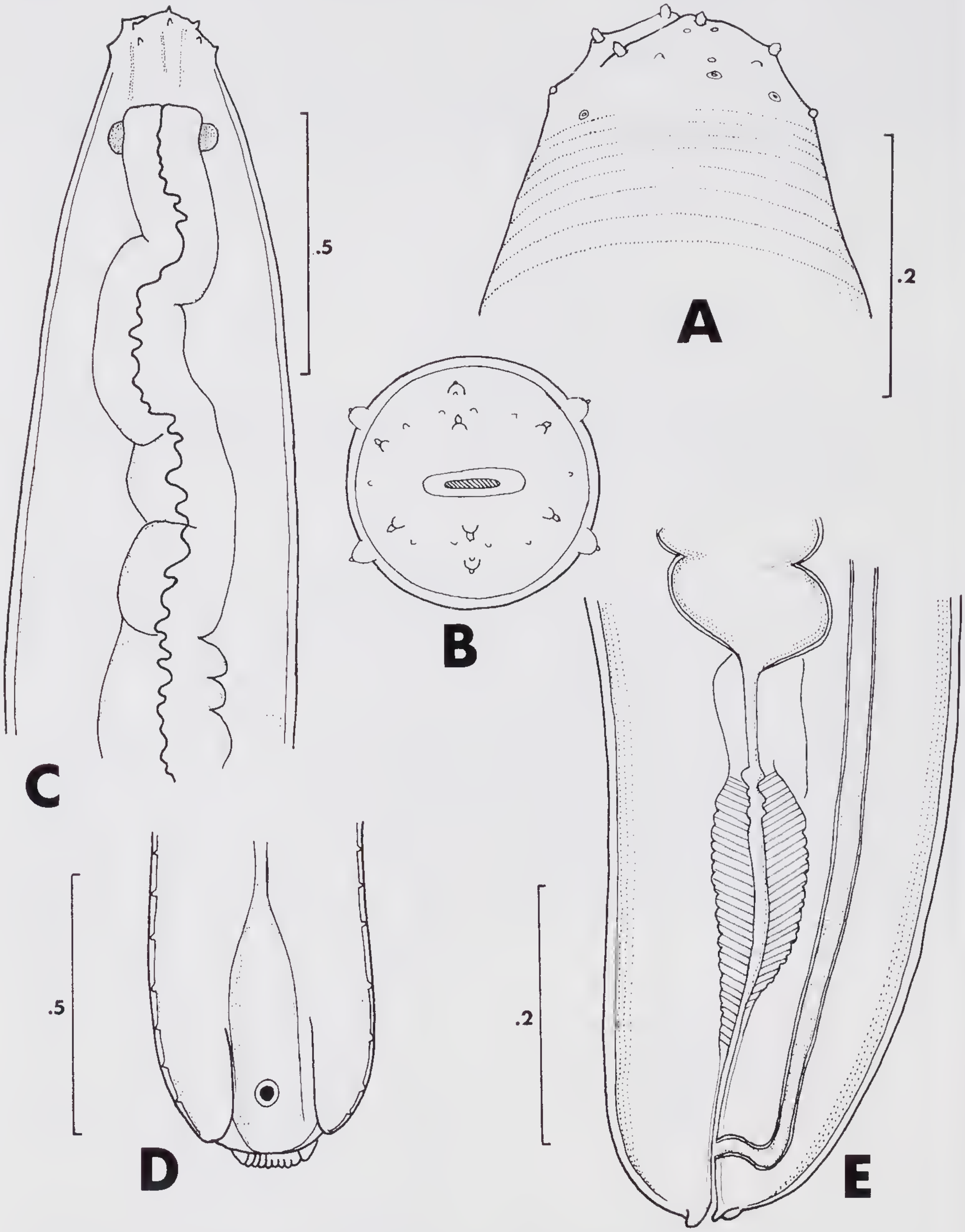

FIG. 1. *Eustrongylides acrochordi* sp. nov. Holotype ♀ G10275. A, anterior end; B, anterior extremity, *en face;* C, Anterior end and oesophagus; D, posterior end, dorsal; E, posterior end, lateral, showing insertion of vagina into rectum.

TABLE 1: BODY MEASUREMENTS (IN MM) OF HOLOTYPE IMMATURE FEMALE *Eustrongylides acrochordi* sp. nov.

Total length	84·50
Width at mid-point	1·03
Width at 2·0 mm from front	0·56
Head width at 1st row of papillae	0·15
Head width at 2nd row of papillae	0·22
Width at beginning of oesophagus	0·28
Oesophagus length	15·90
Oesophagus proportion of length	1/5
Oesophagus width near beginning	0·18
Oesophagus width c. 1/4 along	0·28
Oesophagus width c. 3/4 along	0·42
Pharynx length	0·19
Length of anterior papilla spines	0·01
Nerve ring fr. ant. extremity	0·24
Nerve ring fr. oesoph. beginning	0·03
Caudal papillae distance	0·08
Punctation spacing at anterior end	0·04
Punctation spacing proceeding posteriad	0·13
Anus width	0·10
Rectum length	0·38
Rectum width	0·13
Post. intestine-rectum	1·00
Width of uterus 4 mm fr. tail	0·15
Width of uterus near rectum	0·06
Lumen of uterus	0·04
Uterine wall thickness	0·01
Distance of post. edge of vagina fr. anus	0·08

dorsoventrally, leads into the terminal anus. This is widened laterally and is surrounded dorsally and ventrally by a rugose ridge. There is no tail. Ovary not seen. The vagina passes posteriorly and just before the rounded posterior end of the worm turns sharply medially and enters the rectum. The uterus was not fully developed and contained no eggs.

DISCUSSION

Both the holotype and the paratype (which lacked the anterior end) were lying freely in the stomach among a large number of *Tanqua ophidis*. The worms are characteristic of the genus, but differ from all described species in that the vagina opens into the rectum, forming a cloaca. This feature is sufficient to ascribe them to a new species, even though neither worm is mature. In all other *Eustrongylides* species the vulva opens terminally, very close to the anus. A cloaca has been described from only one other group of adenophorean nematodes, the free-living *Lauratonema* species (Gerlach 1953).

All previous records of *Eustrongylides* species have been from large aquatic birds, from the proventriculus or associated glands, and it is possible that this snake was acting as a paratenic host.

Subclass SECERNENTEA
Order OXYURIDA
Superfamily OXYUROIDEA

Spironoura fordoniae sp. nov.
(Fig. 2, Table 2)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum G10277, ♂, collected by H. Jones from rectum of *Fordonia leucobalia*, QM J23200, collected by J. Bredl from Edward River, North Queensland, 1973.

ALLOTYPES: QM G10278, 2 ♀♀, (poor condition), same data as holotype.

PARATYPES: QM G10279, 3 ♂♂, 7 ♀♀, same data as holotype; QM G10280, 8 ♂♂, 2 ♀♀, (poor condition), collected by H. Jones from stomach of *F. leucobalia*, QM J23924, collected by J. Bredl from Edward River, North Queensland, 1973.

DIAGNOSIS

Head with three lips surrounded by six papillae. Vestibule present. Pharynx short, oesophagus with hour-glass formation at posterior end, stout equal alate spicules, conspicuous oblique precaudal ventral muscle bands, ten pairs of caudal papillae, one unpaired precloacal papilla, lateral alae from cervical region to near posterior end, vulva just past mid-length.

DESCRIPTION

Worm tapering towards either end. No constriction behind head. Body finely striated. Lateral alae commence in cervical region and run most of the length of body, diminishing in size and finally disappearing in last quarter of body. Tail slender and finely pointed in both sexes. Mouth with three lips, with two papillae at base of each. Short vestibule leading into muscular pharynx, length about 2·5 × width. Oesophagus muscular, long, gradually increasing in diameter to a prebulbar swelling (preceded by a constriction) and a large spherical muscular bulb. Intestine straight and wide lumened. Nerve ring 0·25–0·20 from front of oesophagus. Small but distinct cervical papillae about 0·66 along oesophagus, excretory pore about 0·75 along oesophagus.

MALE: Length rather less than females. Caudal end coiled ventrally. Oblique precaudal ventral muscle bands conspicuous; no ventral sucking disc. No caudal alae. Ten pairs of sessile caudal papillae, arranged as three regularly spaced ventrolateral precloacal papillae, three closely set pairs of paracloacal papillae, and four pairs of caudal papillae of which the most anterior two are

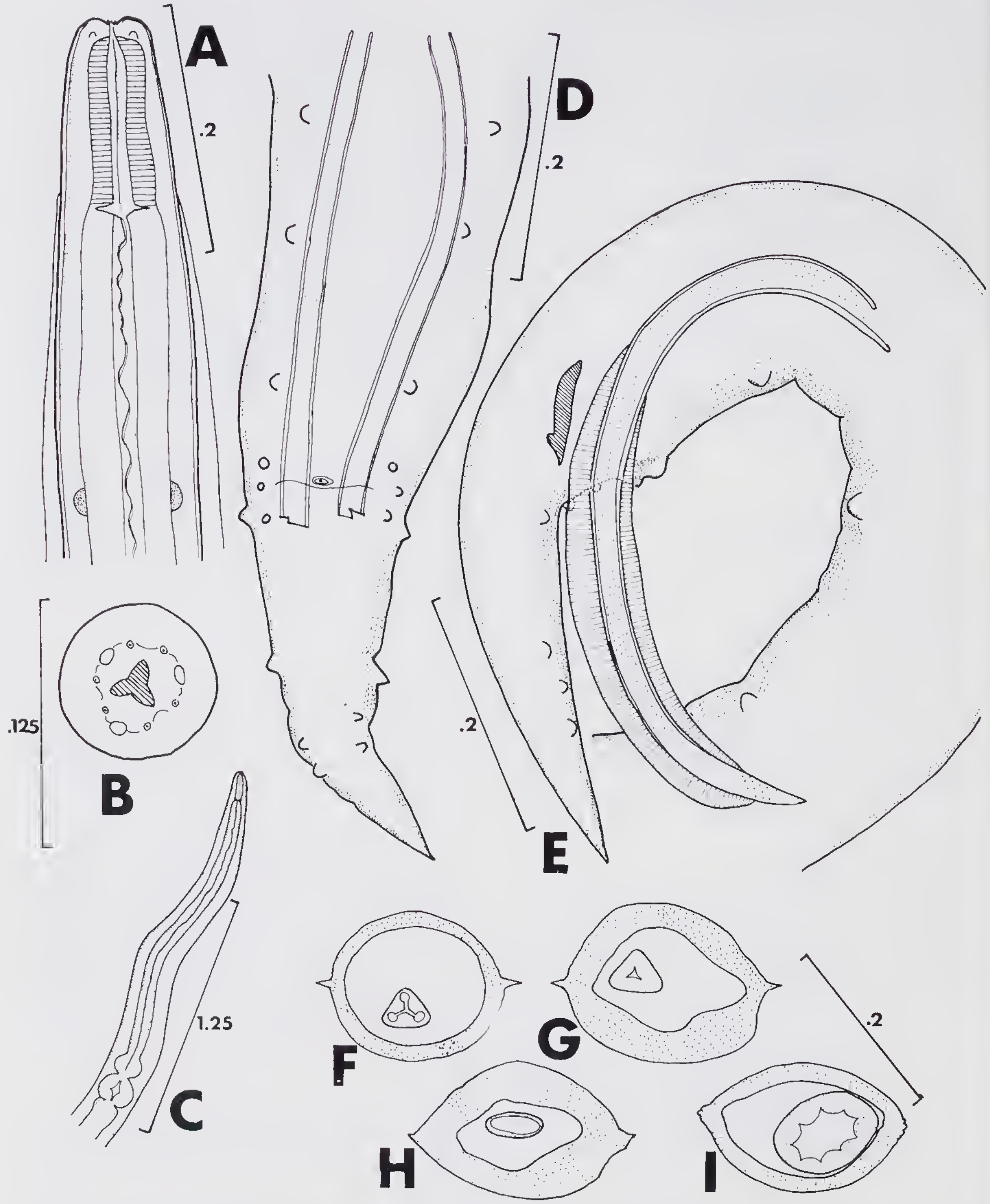

FIG. 2. *Spironoura fordoniae* sp. nov. Holotype ♂ G10277. A, anterior end; B, anterior extremity, *en face;* C, anterior end and oesophagus. D, posterior end, ventral; E, posterior end, lateral; F–I, sections at level of upper oesophagus, lower oesophagus, mid-body and near posterior end, respectively.

TABLE 2: Body Measurements (in mm) of *Spironoura fordoniae*, sp. nov. and *Camallanides cerberi* sp. nov.

	Spironoura fordoniae sp. nov.				*Camallanides cerberi* sp. nov.				
	Holotype	Paratypes (Male) (3)	Allotype	Paratypes (Female) (3)	Holotype	Paratypes (male) (3)	Allotype	Paratypes (Female) (10) range	$\bar{x} \pm s$
Length	10.72	9.07 –10.87	12.67	9.3 –13.27	10.5	9.0 –10.0	32.0	19.0 – 36.0	25.7 ±5.76
Maximum width	0.227	0.175– 0.245	2.45	1.92 – 2.80	—	—	—	—	—
Nerve ring*	0.38	0.36 – 0.38	0.39	9.38 – 0.40	0.210	0.190– 0.207	0.294	0.224– 0.308	0.269±0.030
Cervical papilla*	1.01	1.01 – 1.15	1.12	1.12 – 1.36	0.40	—	—	—	—
Excretory pore*	1.49	1.40 – 1.49	1.59	1.40 – 1.75	—	—	0.448	0.380– 0.452	0.410±0.024
Vestibule	0.011	—	0.011	—	—	—	—	—	—
Pharynx length	0.12	0.09 – 0.13	0.13	0.10 – 0.13	—	—	—	—	—
Pharynx width	0.055	0.042– 0.047	0.049	0.043– 0.049	—	—	—	—	—
Oesophagus length	1.78	1.70 – 1.86	1.72	1.70 – 2.1	—	—	—	—	—
Muscular eosophagus length	—	—	—	—	0.344	0.300– 0.329	0.385	0.378– 0.420	0.401±0.14
Glandular oesophagus length	—	—	—	—	0.413	0.392– 0.434	0.587	0.475– 0.636	0.543±0.053
Oesophagus width	0.073**	0.064– 0.067**	0.078	0.070– 0.101	—	—	—	—	—
Muscular oesophagus width	—	—	—	—	0.100	0.092– 0.112	0.160	0.115– 0.154	0.135±0.017
Glandular oesophagus width	—	—	—	—	0.106	0.087– 0.090	0.157	0.104– 0.174	0.131±0.023
First oesoph. bulb width	0.126	0.084– 0.115	0.109	0.098– 0.118	—	—	—	—	—
Second oesoph. bulb width	0.162	0.137– 0.160	0.168	0.137– 0.190	—	—	—	—	—
Ring (base of buccal capsule)	—	—	—	—	0.050	0.046– 0.050	0.087	0.073– 0.092	0.080±0.005
Buccal capsule depth	—	—	—	—	0.095	0.081– 0.092	0.162	0.120– 0.151	0.135±0.014
Buccal capsule width	—	—	—	—	0.095	0.076– 0.090	0.120	0.106– 0.148	0.126±0.013
Tail length	0.37	0.29 – 0.34	0.59	0.51 – 0.63	0.090	0.092– 0.140	0.420	0.392– 0.560	0.447±0.056
Spicule length, left	0.77	0.68 – 0.72	—	—	0.252	0.245– 0.315	—	—	—
Spicule length, right	0.77	0.68 – 0.72	—	—	0.406	0.400– 0.420	—	—	—
Spicule width (with alae)	0.050	0.046– 0.054	—	—	—	—	—	—	—
Gubernaculum	0.112	0.110– 0.112	—	—	—	—	—	—	—
Vulva position†	—	—	55	57 – 63					
Vagina length	—	—	—	—	—	—	2.92	2.72 – 2.96	2.87 ±0.05
Eggs	—	—	122–66μ	108–126×63–66μ	—	—	—	—	—

* from anterior end † % of body length from anterior end. ** excluding bulbs

lateral and the most posterior two ventral. One unpaired precloacal papilla. Spicules equal in length, curved and stout, with wide alae reaching almost to the bluntly pointed tips. Gubernaculum chitinized and elongated, with a pointed posterior end.

FEMALE: Vulva on a slight protrusion, just past mid-length. Vagina directed anteriorly. No caudal papillae. Eggs large, elongated, with thick shells, unembryonated.

DICUSSION

These worms differ from all previously described members of the genus in the possession of lateral alae. As absence of alae is given as part of the generic diagnosis (Yorke and Maplestone 1926; Yamaguti 1961), this must now be amended to read: alae present or absent.

The genus *Spironoura* is confined to the digestive tract of fish, amphibia and reptiles. However of the approximately 27 species which have been described from reptiles (Yamaguti 1961) all but three are from chelonians; only *S. mascula* (Rudolphi 1819) and *S. nitida* (Travassos 1920) have been described from snakes. The only previous Australian record of the genus is *S. elseyae* Johnston and Mawson 1941 from the turtle *Elseya dentata*.

Order ASCARIDIDA
Superfamily ASCARIDOIDEA
Family ANISAKIDAE

Goezia sp.

MATERIAL EXAMINED

Queensland Museum G10292, 2 ♀♀, collected by H. Jones from stomach of *Acrochordus granulatus*, QM J28740, collected by J. Covacevich and P. Filewood, Iron Range, North Queensland, June 1976.

It was not possible to assign these to a species, but they appeared to be the same as specimens recently recovered from Australian sea-snakes and crocodiles, to be described by Sprent (in press). Apart from these, the only previous record of this genus from a reptile has been *G. gavialidis*, (Maplestone 1930), from an Indian Gavial. All other species have been from fish.

Order SPIRURIDA
Suborder CAMALLANINA
Superfamily CAMMALLANOIDEA

Camallanides cerberi sp. nov.

(Fig. 3, Table 2)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum G10281, ♂, collected by H. Jones from upper oesophagus of *Cerberus rhynchops*, QM J23630, collected by J. Bredl, Edward River, North Queensland, June 1973.

ALLOTYPE: QM G10282, ♀, same data as holotype.

PARATYPES: QM G10283, 3 ♂♂, 11 ♀♀, and 9 incomplete specimens, same data as holotype; QM G10284, 1 ♂, oesophagus of *Enhydris polylepis*, QM J20282, collected by S. Sterling near Cairns, North Queensland, 1970.

DIAGNOSIS

Chitinised buccal valves with 12–14 internal longitudinal ridges. Dorsal and ventral chitinous rods projecting posteriorly from edge of buccal capsule. Four small perioral papillae. Seven or eight pairs of pedunculate precloacal papillae and eight or nine pairs of postcloacal pedunculate papillae in males. Unequal spicules. No gubernaculum. Vulva on a pedunculate prominence; female tail slender and ending in a slight knob. Viviparous.

DESCRIPTION

Fixed worms pale grey in colour, with a black streak running the entire length due to blood or blood products in intestine. Fairly uniform width, anterior end rounded, tail tapering. All specimens were collapsed so diameter could not be measured accurately. Head capsule chitinized, brown. Cuticle finely striated. Mouth elongated dorsoventrally, with four inconspicuous sessile papillae, one beside each corner. Buccal capsule consists of two buccal valves, each of which consists of two chitinous masses separated by a broad longitudinal groove. A smaller chitinous body anterior to each mass, from the median aspect of which is a small projection at the worm's anterior extremity. Twelve to fourteen longitudinal ridges inside each valve, only the central ones of which continue to base of capsule. Chitinous ring at base of buccal capsule. Thin curved chitinous bodies at dorsal and ventral edges of capsule run through ring at base of capsule to anterior end of oesophagus; from exterior aspect of each an irregularly-shaped chitinous bar extends posteriorly.

Oesophagus divided into two portions; anterior muscular portion stout, with pronounced swelling towards posterior end. Posterior glandular portion almost cylindrical in shape, widening slightly towards posterior end, lumen narrow and tortuous. Intestine broad lumened, filled with blood or blood products, running directly to anus. Nerve ring surrounds anterior portion of oesophagus,

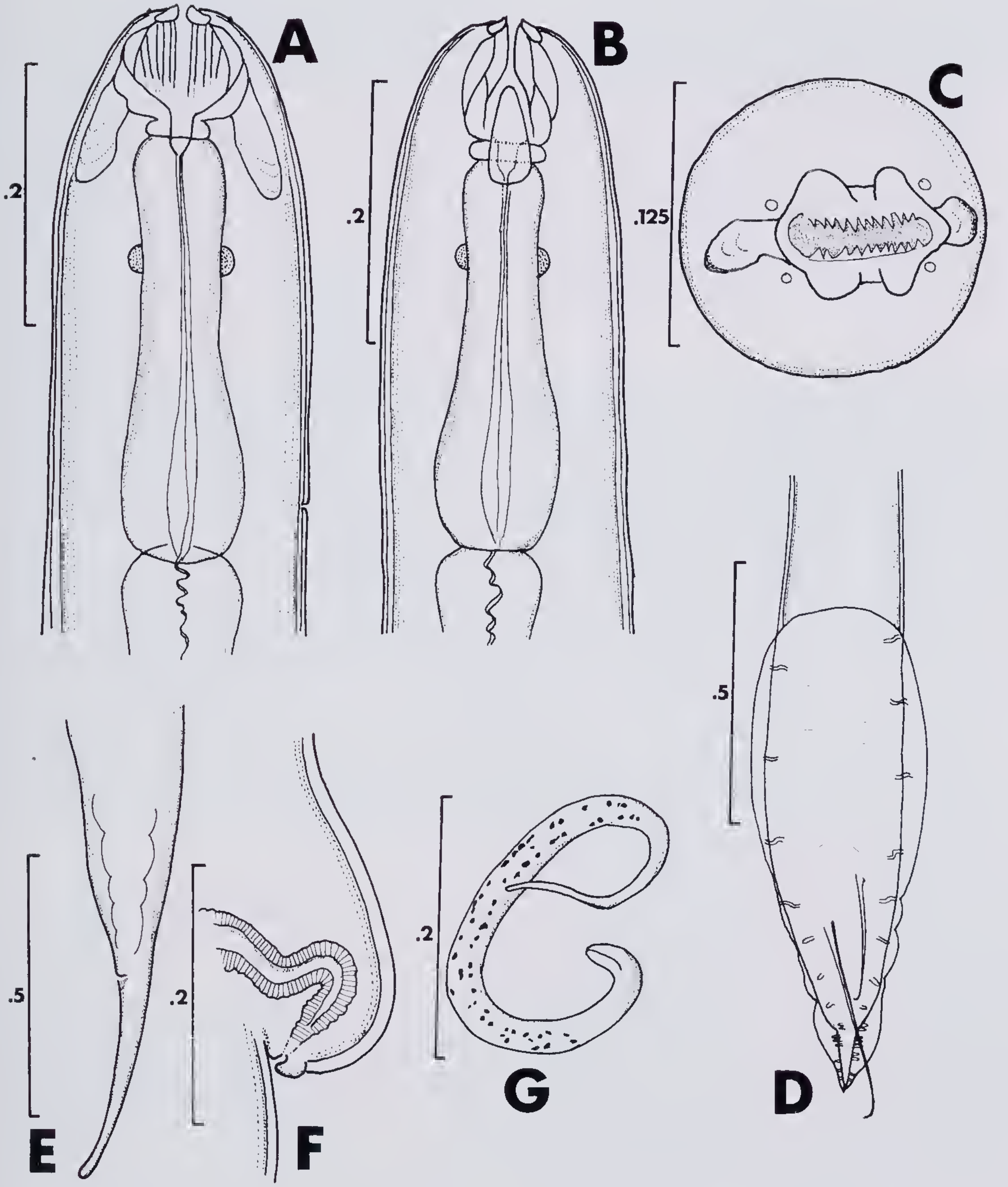

FIG. 3. *Callamanides cerberi* sp. nov. Holotype ♂ G10281, Allotype ♀ G10282. A, anterior end, lateral; B, anterior end, dorsal; C, *en face;* D, male tail, ventral; E, female tail, lateral; F, vulva, lateral; G, embryo in uterus.

excretory pore near posterior end of muscular oesophagus. Very small bristle-like cervical papilla seen in one female only.

MALE: Less than half length of female. Well developed caudal alae, terminating just before tip of pointed tail. Alae connected anteriorly (not in all specimens), supported by an inconstant number of papillae; six to nine regularly-spaced pedunculate papillae precloacally, and eight or nine smaller irregularly spaced papillae between cloaca and tip of tail. Spicules unequal in size and dissimilar in shape. Larger right spicule (projects from cloaca in all specimens) alate, tapering to fine slightly curved point. Smaller left spicule not alate, but also with a finely curved tip. No gubernaculum.

FEMALE: Mean length 27 mm. Tail long and tapering, terminating in an almost club-shaped knob, with or without a conical tip. Vulva situated just anterior to midpoint of body on rounded pedunculate appendage directly posteriorly. Vulval aperture on dorsal side of appendage, against body of worm, surrounded by two small lips. Muscular vagina runs anteriorly some distance before opening into opposed uterine tubes. All specimens contained many larvae, many of which contained numerous black granules, indicating that they were obtaining nutriment from the females' blood intake.

DISCUSSION

Five species of *Camallanides* are recognised at present, all from the Indian subcontinent: *C. prashadi* Baylis and Daubney 1922, *C. piscatori* Khera 1954, *C. ptyasi* Khera 1954, *C. dhamini* Deshmukh 1968, and *C. hemidenta* Majumdar 1965. *C. prashadi* was recovered from *Naja bungarus* and *Ptyas mucosus*, as well as from *Bungarus fasciatus* by Baylis (1929), and from a frog, *Rana tigrina* by Karve (1930), *C. piscatori* from *Natrix piscator*, *C. ptyasi* and *C. dhamini* from *Ptyas mucosus* and *C. hemidentata* from a freshwater fish, *Channa striatus*. In addition, Gupta (1959) recorded a single unidentified female *Camallanides* from a sea-snake, *Hydrophis cyanocinctus*. All were found in the intestine of their hosts. The five snake species from which these are recorded are not found in Australia, but their distribution overlaps with both that of *Fordonia leucobalia* and *Cerberus rhynchops* in the Indo-Malaysian archipelago. *C. prashadi* has been identified from *C. rhynchops* from Thailand (British Museum, unpublished).

Camallinides cerberi differs from those species described in being larger, in having four instead of six apical papillae, in the absence of a gubernaculum, and in the rounded anterior end. In addition, it differs from *C. prashadi* in the shape of the dorsal and ventral chitinous bodies which do not project forwards as in that species, in the thicker post-directed chitinous rods, and in the wider groove separating the chitinous masses of each valve. Whether or not *C. piscatori* and *C. ptyasi* have dorsal and ventral chitinous bodies seems uncertain (Deshmukh 1968). *C. cerberi* differs from *C. prashadi* and *C. dhamini* in having a relatively shorter and more bulbous vulval appendage; the vulval aperture is on the doral side of this appendage, and not on the ventral side as in *C. prashadi*, *C. ptyasi* and *C. piscatori*. In *C. dhamini* there are 14–16 longitudinal internal buccal ridges, and less inequality in spicule length. These specimens are assigned to a new species on the basis of these various features. Differences in the number and position of the caudal papillae, however, have not been taken into account; they have been used to some extent in differentiating species in this genus but, at least in *C. cerberi*, they are variable. *C. piscatori* and *C. dhamini* were described from one male, *C. ptyasi*, *C. hemidenta*, and the redescription of *C. prashadi* (by Agrawal 1967) were from two males. In view of this, and the fact that three of these *(C. prashadi*, *C. ptyasi* and *C. dhamini)* have been described from the same host, *Ptyas mucosus*, it seems desirable that a greater number of specimens be examined before differentiation based on these papillae can be relied upon. Further study may question the validity of these species.

Suborder SPIRURINA
Superfamily GNATHOSTOMATOIDEA

Tanqua ophidis Johnston and Mawson 1948

MATERIAL EXAMINED

Queensland Museum G10285, G10286, G10287, G10288 and G10293 from *Acrochordus javanicus* QM J23192, J23718, J23189, J23191 and J23718 respectively (see Table 4); 3 ♂♂ and 1 incomplete specimen in author's collection, stomach of *Enhydris polylepis*, J23215.

Apart from two in the oesophagus and two in the intestine, all specimens were in the stomach, in numbers ranging from seven to 179. Sexes were approximately equal, with a large number of young worms in the two most heavily infected

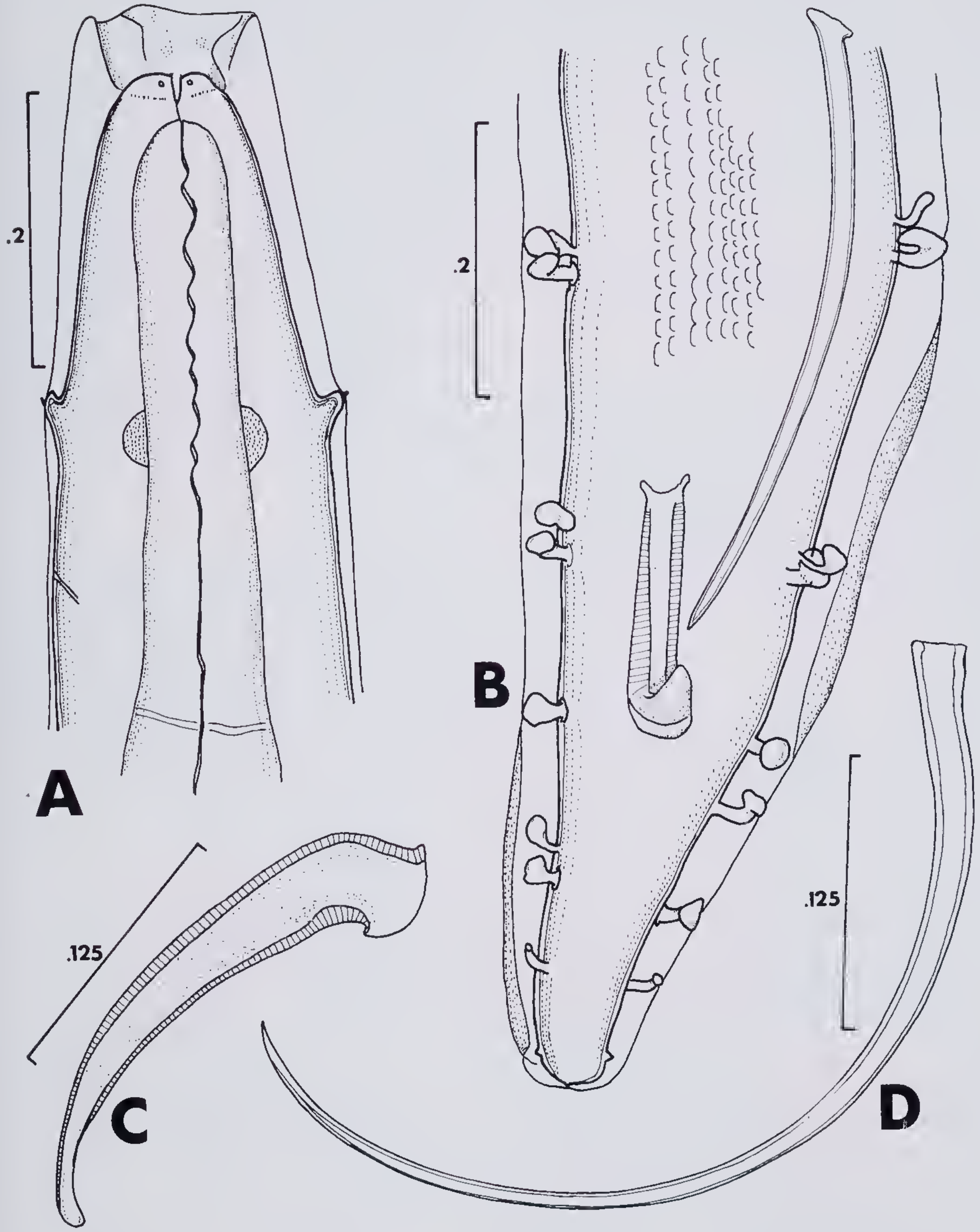

FIG. 4. *Heliconema longissima* (Ortlepp 1922), G10291. A, anterior end, lateral; B, male tail, ventral; C, right spicule; D, left spicule.

snakes; clearly it is a prevalent parasite in this species. It was originally described from a freshwater snake, *Amphiesma mairii*, and from *A. javanicus* (see Johnston and Mawson 1948), and has not been reported since then. *E. polylepis* is therefore a new host record.

Superfamily PHYSALOPTEROIDEA

Heliconema longissima (Ortlepp 1922)

(Fig. 4, Table 3)

MATERIAL EXAMINED

Queensland Museum G10291, 37 stomach, 3 oesophagus, 1 rectum *Fordonia leucobalia;* J10262; G10290, 12 stomach and 11 proximal small intestine, *F. leucobalia,* J877; G10289, one from stomach, *F. leucobalia,* J23200.

The characters and measurements of the worms agree in almost every particular with the original description by Ortlepp (1922) and the redescription by Ogden (1969), the only differences being that in these specimens there were never more than nine longitudinal tesselated ridges on the ventral surface of the male caudal region, instead of 12 in Ogden's description, and in the females the vulva was always just posterior to the midlength of the body.

DISCUSSION

In the measurements of this species by Ortlepp (1922), Li (1934) from *Anguilla pekinensis* from China and Ogden (1969), the vulva was always slightly anterior to the midlength of the body. These differences, however, together with the lesser number of tesselated ridges in the male, are not thought sufficient to warrant a new species, and may be host-induced variations.

There has been uncertainty about the hosts of the original material examined by Ortlepp (1922), which had been labelled 'snakes, Australia'. Chabaud and Campana-Rouget (1956) in suggesting that the genus *Ortleppina* erected for the type species by Schultz (1927) was synonymous with *Heliconema,* suggested that the original specimens had been wrongly labelled, and that they had probably come, as had all other known members of the genus, from eels, and this view was supported by Ogden (1969). The finding of these specimens in aquatic snakes now suggests that maybe the original labelling was correct. The present specimens are therefore the first certain records of the genus which were not recovered from eels.

DISCUSSION AND CONCLUSIONS

The nematode species recovered were: *Eustrongylides acrochordi* sp. nov., *Spironoura fordoniae* sp. nov., *Goezia* sp., *Camallanides cerberi* sp. nov., *Tanqua ophidis* Johnston and Mawson 1948 and *Heliconema longissima* (Ortlepp 1922). In 24 of the 26 snakes the stomachs were empty; two *Fordonia leucobalia*

TABLE 3: BODY MEASUREMENTS (IN MM) OF ***Heliconema longissima*** (ORTLEPP).

	Males (4)	Females (11)	
		range	$\bar{x} \pm s$
Length	17.85 –27.37	28.27 –38.55	32.19 ±3.19
Maximum width	0.192– 0.350	0.402– 0.542	0.499±0.069
Nerve ring*	0.231– 0.315	0.259– 0.350	0.298±0.026
Cervical papilla*	0.231– 0.315	0.245– 0.329	0.290±0.025
Excretory pore*	0.366– 0.413	0.406– 0.546	0.414±0.049
Muscular eosophagus length	0.371– 0.497	0.455– 0.532	0.425±0.028
Glandular oesophagus length	2.47 – 3.62	2.84 – 4.14	3.33 ±0.29
Muscular oesophagus width	0.063– 0.105	0.070– 0.112	0.091±0.006
Glandular oesophagus width	0.119– 0.189	0.140– 0.210	0.178±0.014
Tail length	0.231– 0.350	0.091– 0.203	0.145±0.028
Spicule length, left	0.482– 0.616	—	—
Spicule length, right	0.231– 0.259	—	—
Vulva position†		50–66	56±2

* from anterior end

† % of body length from anterior end

TABLE 4: NUMBERS OF WORMS RECOVERED FROM AUSTRALIAN AQUATIC SNAKES IN THE COLLECTIONS OF THE QUEENSLAND MUSEUM.

Host (Habitat and diet)	Qld. Museum Cat. No.	Locality and Date	*Tanqua*	*Eustrongylides*	*Camallanides*	*Heliconema*	*Spironoura*	*Goezia*
Enhydris polylepis (purely freshwater; various aquatic vertebrates)	J28060	Iron Range, N.Q., 1.vii.1976	—	—	—	—	—	—
	J489	No. data, 1912	—	—	—	—	—	—
	J20282	nr. Cairns, N.Q., 1970	—	—	1	—	—	—
	J22343	Mt. Molloy, May, 1972	—	—	—	—	—	—
	J23215	Mt. Carbine, 12.v.1973	4	—	—	—	—	—
	J23221	Mt. Molloy, 10.v.1973	—	—	—	—	—	—
Acrochordus javanicus (mainly freshwater; almost exclusively fish)	J23189	Edward River, N.Q., 1973	36	—	—	—	—	—
	J23190	Coen, N.Q., 1973	122	—	—	—	—	—
	J23191	Coen, N.Q., 1973	179	2	—	—	—	—
	J23192	Edward River, N.Q., June, 1973	7	—	—	—	—	—
	J23718	Coen, N.Q., June, 1973	30	—	—	—	—	—
	J24917	Coen, N.Q., June, 1973	15	—	—	—	—	—
	J28911	O'Shanassy Riv, N.W.Q., Oct., 1976	14	—	—	—	—	—
	J28912	O'Shanassy Riv, N.W.Q, Oct., 1976	9	—	—	—	—	—
Myron richardsoni	J16653	Normanton, N.Q., 1969	—	—	—	—	—	—
Cererus rhynchope (mainly esturine and mangrove; small crustaceans and fish)	J23630	Edward River, N.Q., June, 1973	—	—	23	—	—	—
	J23717	Edward River, N.Q., June, 1973	—	—	—	—	—	—
	J23948	Edward River, N.Q., June, 1976	—	—	—	—	—	—
		Edward River, N.Q., June, 1976	—	—	—	—	—	—
Fordonia leucobalia (saline waters, to open sea; mainly crustaceans, especially crabs)	J877	? Queensland, 1913	—	—	—	23	—	—
	J1510	New Guinea, 1914	—	—	—	—	—	—
	J10262	Northern Terrty, June, 1959	—	—	—	41	—	—
	J23200	Edward River, N.Q., 1973	—	—	—	1	15	—
	J23924	Edward River, N.Q., 1973	—	—	—	—	10	—
Acrochordus granulatus (saline waters, to open sea; mainly fish and crabs)	J142	Cairns, N.Q., 1912	—	—	—	—	—	—
	J5032	Cairns, N.Q., March, 1930	—	—	—	—	—	—
	J28740	Iron Range, N.Q., June, 1976	—	—	—	—	—	2

(J877 and J10262) contained remains of large crustacea.

The differing habitats of the snakes probably reflect the different composition of their food, and hence their largely different parasites. Data in Table 4 suggest that *T. ophidis* and *E. acrochordi* probably have fresh-water life cycles, *S. fordoniae*, *Goezia* sp. and *H. longissima* marine life cycles, and *C. cerberi* an estuarine life cycle.

These are the first records of snakes as hosts for parasites in the genera *Eustrongylides* and *Heliconema*. *Goezia* have recently been reported from sea-snakes and crocodiles (Sprent, in press), and the great majority of species in the genus *Spironoura* are found in fish or chelonians. The usual hosts for *Spironoura* spp. (fish and turtles), *Eustrongylides* spp. (aquatic birds) and *Heliconema* spp. (eels) are ones which live in similar environments to these snakes, and with which they may have common food and hence sources of infection. The presence of these parasites in snakes illustrates their physiological opportunism in adapting to phylogenetically different hosts which inhabit the same environment and may be involved in similar food-chains to their more usual hosts. Both *E. acrochordi* and *S. fordoniae* show morphological features not found in other members of these genera (cloaca in one; lateral alae in the other), suggesting that they may be evolving away from the main pattern of forms found in these genera.

ACKNOWLEDGMENTS

I would like to thank Miss. J. Covacevich for her great help in allowing me access to and facilities for the examination of the snakes in the Queensland Museum, and to Professor J. F. A. Sprent for helpful advice and discussion.

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Mem. Qd Mus. **18**(2): 255–63, pl.40. [1978]

SOME PARASITIC BARNACLES (RHIZOCEPHALA: SACCULINIDAE) FROM PORTUNID CRABS IN MORETON BAY, QUEENSLAND

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ABSTRACT

One new species of *Sacculina* and two new species of *Heterosaccus* are described and additional morphological features of *Sacculina granifera* Boschma 1973 revealed by scanning electron microscopy are recorded.

Only three sacculinids have been reported from Australian waters. Boschma (1933) described *Sacculina duracina* from *Parthenope longimanus* (Leach) at Port Molle, Queensland, and more recently *S. granifera* from *Portunus pelagicus* (Linnaeus) from Moreton Bay, Queensland (Boschma 1973). A further unnamed *Sacculina* sp. from *Thalamita sima* H. Milne-Edwards from Sydney was mentioned by Haswell (1888). *S. granifera* was described only recently although it is a serious parasite of the commercial sand crab (*P. pelagicus*) and has been known for many years (Thomson 1951). In the course of an investigation into the biology of this association, *S. granifera* and three other sacculinids found on different host species were examined primarily to determine whether the other crab species served as reservoir hosts of *S. granifera.* This paper contains descriptions of three previously unnamed sacculinids and further observations on the morphology of *S. granifera.*

MATERIALS AND METHODS

Externae of the parasites were fixed in 5% formalin, Bouin's fluid or 70% alcohol. For sectioning, a small part of the mantle and parts of the visceral mass containing colleteric glands, cypris cell receptacles and ducts were removed, dehydrated and embedded in wax. Sections were cut at 7 – 10μ and were stained in borax carmine or chlorazol black E. Retinacula were observed by mounting small pieces of mantle in balsam and examining the inner surface. Pieces of mantle taken from young, clean externae were prepared for scanning electron microscopy by dehydration in graded alcohols and xylol and coating with gold dust. All measurements are in millimetres unless otherwise stated, and follow the convention illustrated in Fig. 1a where A = anterior to posterior dimension, B = dorsal to ventral dimension (The parasite lies on one side), and C = the left to right dimension i.e. the thickness of the parasite between the crabs abdomen and cephalothorax. Abbreviations used in figures are as follows:

col. gl.	colleteric gland
ex.	excrescences
ext. cut.	external cuticle of mantle
g. coat.	granular coating of mantle
j.	junction of male duct and cypris cell receptacle
l. can.	lymph canals
l.c.r.	left cypris cell receptacle
l.m.d.	left male duct
mant.	mantle
me.	mesentery
m.o.	mantle opening
pap.	papillae
ped.	peduncle
r.c.r.	right cypris cell receptacle
r.m.d.	right male duct
rods	supporting rods of retinaculum
sept.	septae
visc. m.	visceral mass.

Sacculina amplituba nov. sp.
(Fig. 1a – j)

MATERIAL EXAMINED

HOLOTYPE Queensland Museum W7145, ex *Matuta granulosa*, Main channel, Moreton Bay, collector W. Phillips, 6. iv. 1973.

PARATYPES. W7146, a whole specimen, W7147, serial sections, same data as holotype.

DIAGNOSIS

Panduriform parasites occurring singly. Cypris cell receptacles and ducts outside visceral mass, completely separated, receptacles large, roughly globular without septae passing abruptly into ducts; left receptacle terminates on the right side of the mesentery; diameters of ducts widen until equal to that of receptacles, septate. Tubes of colleteric glands arranged in approximately seven rows, greatest division shows 150–160 tubes. External cuticle covered with spiny excrescences of 35μ length formed of hyaline chiton differing from that of the main layers. Retinacula not present. Parasitic on *Matuta granulosa* Miers.

DESCRIPTION

Body form: Mature externae are ovoid to rectangular in shape (Fig. 1a) and brownish in colour except for a pale patch surrounding the posterior stalk. Fine lines can be seen on the mantle, the opening of which is anterior on top of a short muscular tube. Although some specimens were examined other than those designated types, none were found on crabs bearing more than one externa. Dimensions of holotype: A = 15, B = 21, C = 8 and a whole paratype A = 10, B = 15, C = 6.

Cypris cell receptacles: The cypris cell receptables are in the anterior region of the stalk completely separated from the visceral mass (Fig. 1b,f-h). They are roughly globular and without septae and open into the ducts by a narrow aperture (Fig. 1e-g). The ducts widen till they become as wide as the receptacles (Fig. 1d) then narrow near the opening into the mantle cavity. The terminal portion is free in the mantle cavity (Fig. 1c). The internal surface of the duct bears septae (Fig. 1d). The left cypris cell receptacle terminates on the right side of the mesentery (Fig. 1h).

Colleteric glands: The colleteric glands are cushion shaped bodies in the middle portion of the left and right sides of the visceral mass (Fig. 1b). In transverse section in the area of greatest division of tubes, there are 150–160 tubes in up to seven rows. Fig. 1j shows 155 tubes.

Mantle: The external cuticle of the mantle is 75–100μ in thickness and bears clusters of spines 35–40μ in length. The spines are united at their bases in clumps of two to seven; they are of a hyaline chiton different from the cuticle of the mantle (Fig. 1i). As with all sacculinids, granular matter collecting round the excrescences may partially obscure them (Fig. 1i). No retinacula were observed.

REMARKS

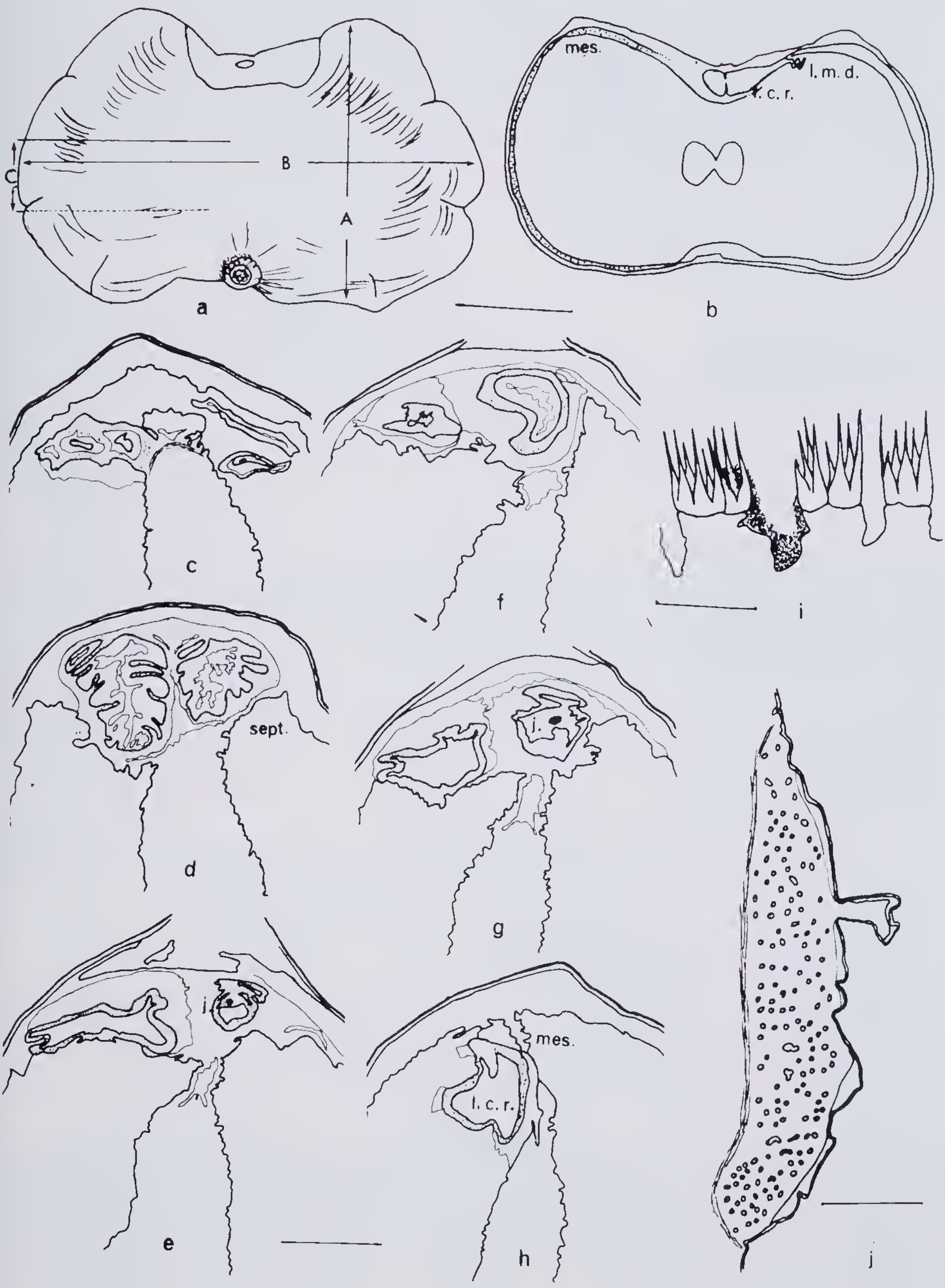
The name *Sacculina amplituba* nov. sp. is proposed because the male ducts widen to a diameter equal to that of the receptacles. In related species the ducts are narrower than the receptacles. *S. amplituba* is similar to *S. beauforti* Boschma 1949 from *Scylla serrata* (Forsk.), *S. leptodiae* Guirin-Ganivit from *Xantho exeratus* (H. Milne-Edwards) and *S. vankampeni* Boschma from *Ozius rugulosus* Stimpson, but differs from these in having (i) ducts as wide as the receptacles whose ends lie free in the mantle cavity as opposed to ducts not as wide as the receptacles and without free ends and (ii) the left receptacle terminating on the right rather than the left. Furthermore, the colleteric glands of *S. beauforti* divide into approximately 50 tubes and those of *S. leptodiae* into less than 20 (Boschma 1949) and so are quite different from the glands in *S. amplituba* which divide into more than 100 tubes. *S. beauforti* has the cuticle of the mantle of 120–130μ in thickness (Boschma 1955) considerably thicker than that of *S. amplituba* (75–100μ thick).

Apart from the morphological distinctions, *S. amplituba* should be considered a new species since each of the most similar species all occur in a different host genus and the work of Fratello (1968) on chromosomes indicates a high degree of host specificity among sacculinids.

Sacculina granifera Boschma, 1973

The most important characteristic of *S. granifera* is the structure of the excrescences of

FIG. 1: *Sacculina amplituba:* a, whole parasite — left side. A, B and C are the anterior to posterior, dorsal to ventral and left to right dimensions respectively; b, left side with left side of mantle removed, scale = 4 mm; c–h, transverse sections of posterior part of parasite showing male organs, scale = 1 mm; i, transverse section of external cuticle of mantle showing excrescences, scale = 40μ; j, transverse section of colleteric gland in region of greatest division of tubes, scale = 300μ.


C
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the external cuticle described as irregularly globular (Boschma 1973). Scanning electron micrographs (Plate 40, Fig. 1,b) reveal that each of the globular excrescences bears many small spines. Further more, Boschma described the colleteric glands of *S. granifera* as dividing into 40 tubes in one row. Specimens examined by me show the colleteric glands to be divided consistently into up to 100 tubes in the region of greatest division.

Heterosaccus lunatus nov. sp.
(Fig. 2 a–i)

MATERIAL EXAMINED

HOLOTYPE Queensland Museum W7148, ex *Charybdis callianassa,* Moreton Bay, collector R. Bishop, Feb. 1975.

PARATYPES Queensland Museum W7149 *ex Charybdis callianassa,* Moreton Bay, collector R. Bishop, Nov. 1974, three whole specimens on one host. Queensland Museum W7150, ex *C. callianassa,* Moreton Bay, collector W. Phillips, 24/v/1973, sections.

DIAGNOSIS

Kidney shaped parasite, more than one of which may occur on the one host. Cypris cell receptacles within visceral mass and deeply crescentic, terminating near colleteric glands and containing sponge-like meshwork. Receptacles open widely into straight ducts also with sponge-like meshwork; ducts open near stalk; receptacles and ducts surrounded by lymph spaces. Colleteric glands posterior, with 60–70 tubes in five to six rows in region of greatest division. External cuticle with papillae 15μ long and 10μ apart, of same material as mantle. Retinacula rounded flaps of tissue occurring singly each with four to six rods. Parasite of *Charybdis callianassa* (Herbst).

DESCRIPTION

Body form: The externa (Fig. 2a) is kidney-shaped having a wide mantle opening with poorly developed musculature. The numbers of externae per crab varies from one to three, the externae being smaller where there are more than one on one host. Dimensions of the holotype: A = 10, B = 19, C = 7; and of whole paratypes (i) A = 10, B = 20, C = 9, (ii) A = 8, B = 13, C = 6, (iii) A = 8, B = 11, C 6.

Cypris cell receptacles: The male organs are confined to the posterior dorsal portion of the visceral mass where they are surrounded by lymph canals. The rest of the visceral mass is without pronounced lymph canals. The ducts which open close to the stalk (Fig. 2,h) are of a consistent diameter of about 400μ and have a sponge-like structure for most of their length. The lumen of each duct is 40–50μ wide. The ducts are not significantly convoluted. They pass gradually into the receptacles which are only slightly wider than the ducts (Fig. 2 d–g). The receptacles have a deep curvature and terminate near the colleteric glands (Fig. 2g).

Colleteric glands: The colleteric glands are cushion-shaped bodies lying in the posterior half of the visceral mass near the middle. In the region of greatest division there are 60–70 tubes in five to six rows (Fig. 2i). There is no chitinous lining but villiform projections are present on the inside.

Mantle: The external cuticle of the mantle is 15–20μ thick and is covered with papillae approximately 15μ long and 10μ apart (Fig. 2c). The papillae are projections of the cuticle of the mantle and may be partially or wholly obscured by a granular coating (Fig. 2b). Scanning electron micrographs (Plate 40, Fig. b) clearly show the shape and distribution of the papillae and the granular coating.

Retinacula (Fig. 2c) are single rounded flaps of tissue about 20μ wide each containing four to six rod–like bodies. The retinacula are about 200μ apart.

REMARKS

The name *Heterosaccus lunatus* nov. sp. is proposed because of the deeply crescentic nature of the cypris cell receptacles.

Heterosaccus multilacinensis nov. sp.
(Fig. 3 a–i)

MATERIAL EXAMINED

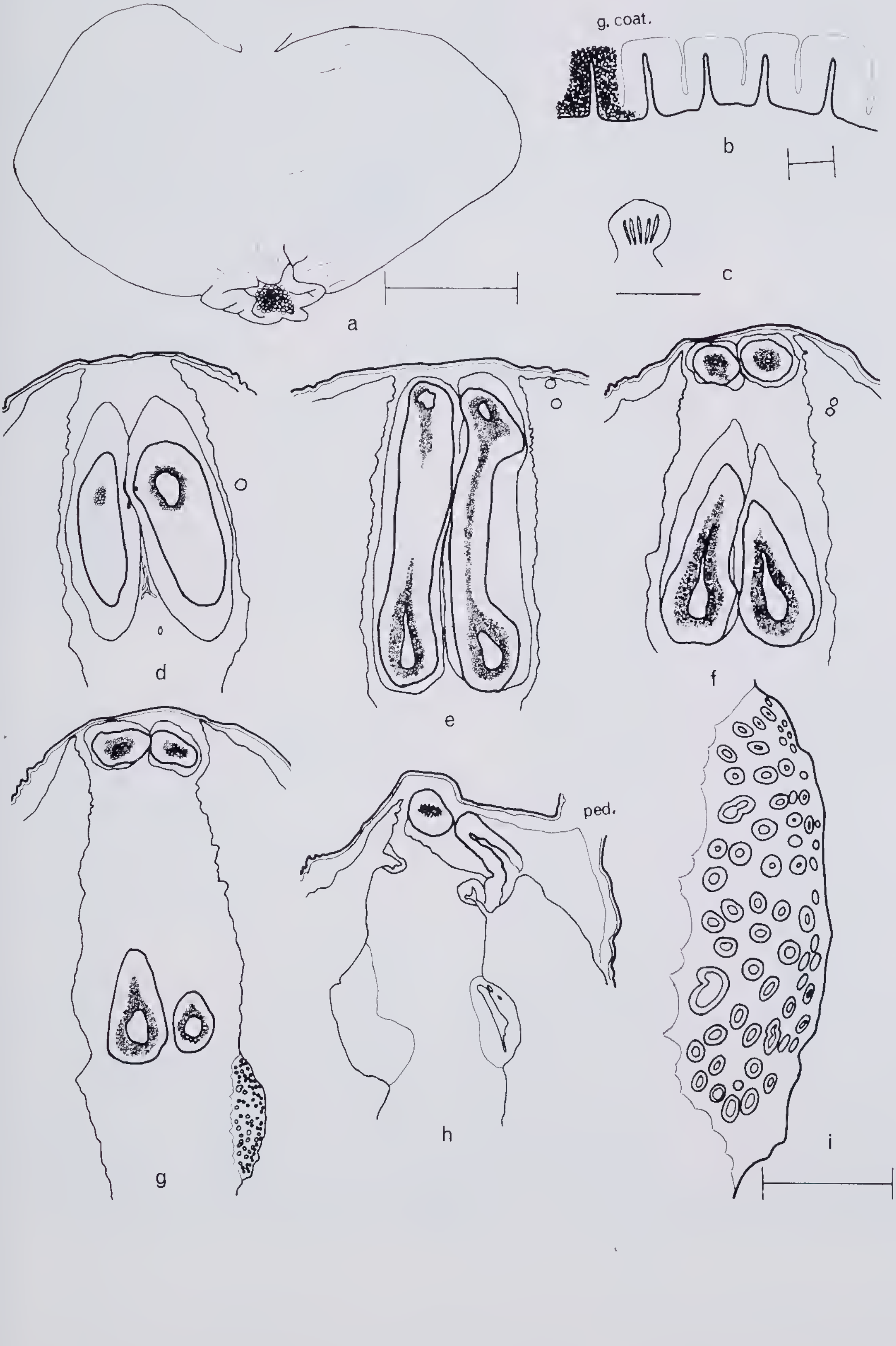
HOLOTYPE Queensland Museum W7151, sections, ex *Carybdis truncata,* East Moreton Bay, collector W. Phillips 6/iv/1973

PARATYPES W7152, ex *C. truncata,* four specimens on host, same data as holotype.

DIAGNOSIS

Kidney-shaped parasite more than one of which may occur on the one host. Cypris cell receptacles

FIG. 2: *Heterosaccus lunatus:* a, whole parasite — left side, scale = 3 mm; b, transverse section of external cuticle of mantle, scale = 10μ; c, internal retinacula, scale = 25μ; d–h, transverse sections of posterior part of parasite showing male organs, scale = 1 mm; i, transverse section of colleteric glands in region of greatest division of tubules, scale = 200μ.


g. coat.
b
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shallow crescentic, not surrounded by lymph spaces; ducts slightly convoluted opening away from stalk; meshwork present in receptacles but not in ducts. Colleteric glands in posterior part of visceral mass, region of greatest division of tubes shows 40–60 tubes in four to five rows. External cuticle with papillae 15μ long, close together at base and separated by 5μ at tip. Papillae of same material as cuticle. Retinacula of one to six rounded flaps on a common base with one rod per flap. Parasite of *Charybdis truncata* (Fabricius).

DESCRIPTION

Body form: The externae (Fig. 3a, b) are kidney-shaped with a wide mantle opening showing poorly developed musculature. The number of externae per crab may be more than one. Dimensions of paratypes (i) A = 10, B = 17, C = 4, (ii) A = 9, B = 10, C = 7, (iii) A = 10, B = 19, C = 6, (iv) A = 18, B = 14, C = 4.

Cypris cell receptacles: The male organs are confined to the posterior dorsal portion of the visceral mass and are not surrounded by lymph spaces although lymph spaces are seen commonly in the visceral mass (Fig. 3 a,d–g). The ducts which open close to the stalk are somewhat convoluted and do not possess a sponge-like structure (Fig. 3 e–g). They have a diameter of 220–240μ and the lumen is 50–70μ in diameter. The ducts pass gradually into the receptacles which have a shallow curvature and do possess a sponge-like structure. The receptacles are two to three times as wide as the ducts (Fig. 3 d,e).

Colleteric glands: The cushion shaped colleteric glands are situated in the posterior part of the visceral mass towards the middle. The region of greatest division of tubes shows 40–60 tubes in four or five rows (Fig. 3h). There is no chitinous lining, but the lumen is lined with villiform structures.

Mantle: The external cuticle of the mantle is approximately 50μ thick with papillae 15μ long which are extensions of the cuticle (Fig. 3b). The papillae touch at the bases and taper to a blunt point. They are about 5μ apart at the tips.

Retinacula (Fig. 3c) consist of one to six rounded flaps of chiton on a common base, each flap containing two or three rods which may project out of the flaps and appear to extend into the base. The flaps are from 18–20μ long and spaced about 200μ apart.

REMARKS

The name *Heterosaccus multilacinensis* nov. sp. is proposed because of the many flaps on each retinaculum.

Boschma (1963) described *Heterosaccus papillosus* from several species of the genus *Charybdis* including *C. callianassa*. It is similar to, yet distinct from, the two species described here. *H. lunatus* differs from *H. papillosus* in having (i) wider receptacle ducts opening close to the stalk, (ii) deeper curvature of the receptacles, (iii) greater division of the tubes in more posteriorly placed colleteric glands, (iv) longer more closely placed papillae on the mantle, and (v) retinacula consisting of flaps with rods rather than spindles. *H. multilacinensis* differs from *H. papillosus* in having (i) ducts opening close to the stalk rather than at a distance from the stalk, (ii) shallower curvature of the receptacles, (iii) greater division of tubules in more posteriorly placed colleteric glands, (iv) papillae closer together and of a different shape, and (v) retinacula consisting of many flaps with rods. *H. multilacinensis* differs from *H. lunatus* in having (i) narrower more convoluted male ducts without a sponge-like structure, (ii) less division of the tubes of the colleteric glands, (iii) longer, thicker, more closely packed papillae, and (iv) retinacula consisting of several flaps on one stalk.

DISCUSSION

Undoubtedly the rhizocephalan fauna of Australia will be found to be more numerous than is presently recorded. The influence of these parasites on the biology of their hosts is considerable and where the hosts are of commercial importance they produce considerable losses to the industry. As yet no sacculinid has been found to parasitize the commercial mud crab *Scylla serrata* in Australia although *S. beauforti* and *Loxothylacus ihlei* Boschma 1949 have been described from this species in Indonesia.

Discrimination of species of rhizocephala is difficult since insufficient is known of the details of their life cycles or the variability of characteristics with the age and maturation of the externa. Scanning electron micrographs of the exterior surfaces of the mantle of young externae should provide accurate and detailed information on one rather important taxonomic feature, viz. the form of the cuticular excrescences. Clear differences can be seen between *Sacculina amplituba* and *Heterosaccus lunatus* (Plate 40).

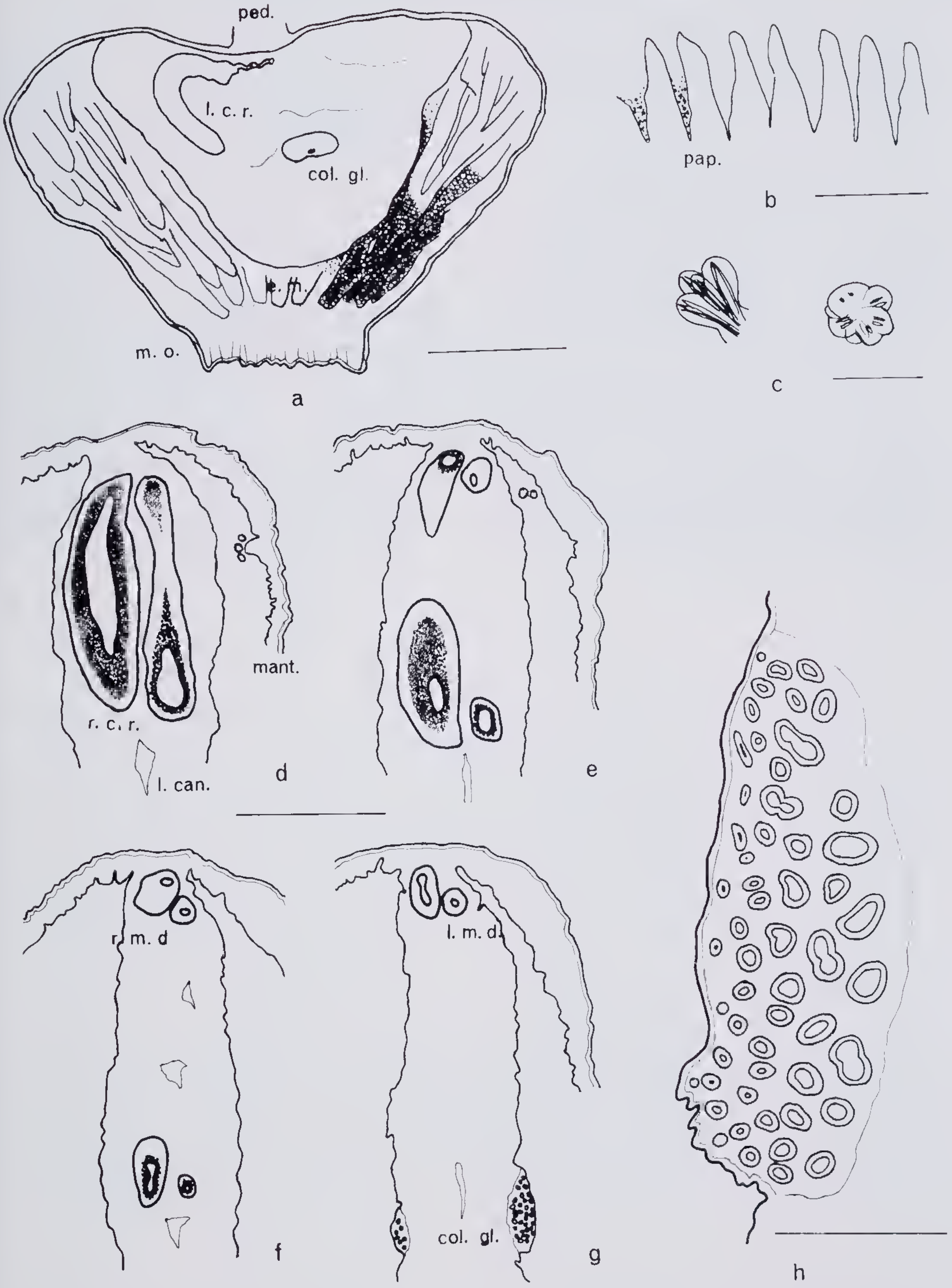

FIG. 3: *Heterosaccus multilacinensis:* a, whole parasite, left side, with left side of mantle removed, scale = 3 mm; b, papillae of external surface of mantle, scale = 10μ; c, retinacula, scale = 25μ; d–g, transverse section of posterior part of parasite showing male organs, scale = 1 mm; h, transverse section of colleteric glands in region of greatest division of tubes, scale = 300μ.

Probably the most promising means of discriminating species would be chromosome techniques as described by Fratello (1968) who was able to discriminate several species previously described as one.

ACKNOWLEDGMENTS

The sacculinids described in this paper were related to a post-graduate honours project in the Department of Parasitology, University of Queensland. I would like to express my thanks to Professor J.F.A. Sprent for permission to use departmental facilities.

I would also like to thank Dr L.R.G. Cannon for assistance in preparing the manuscript; the C.S.I.R.O., for use of its boat for collecting specimens, Mr J. Hardy of the Electron Microscope Unit and Mr J. Mines for advice on histological matters. The late Dr H. Boschma of Leiden Museum, Netherlands also provided valuable information concerning this work.

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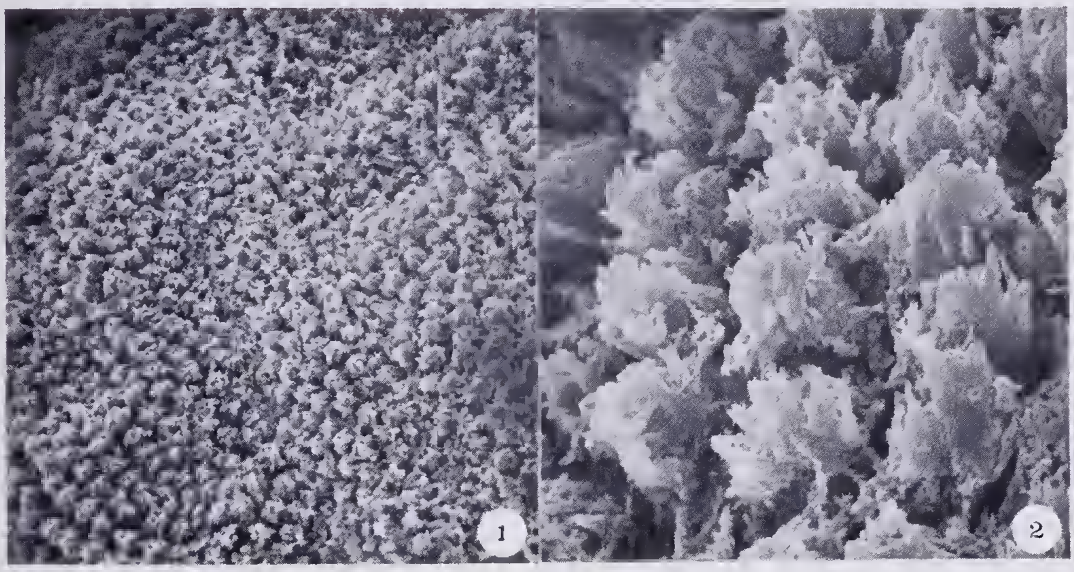
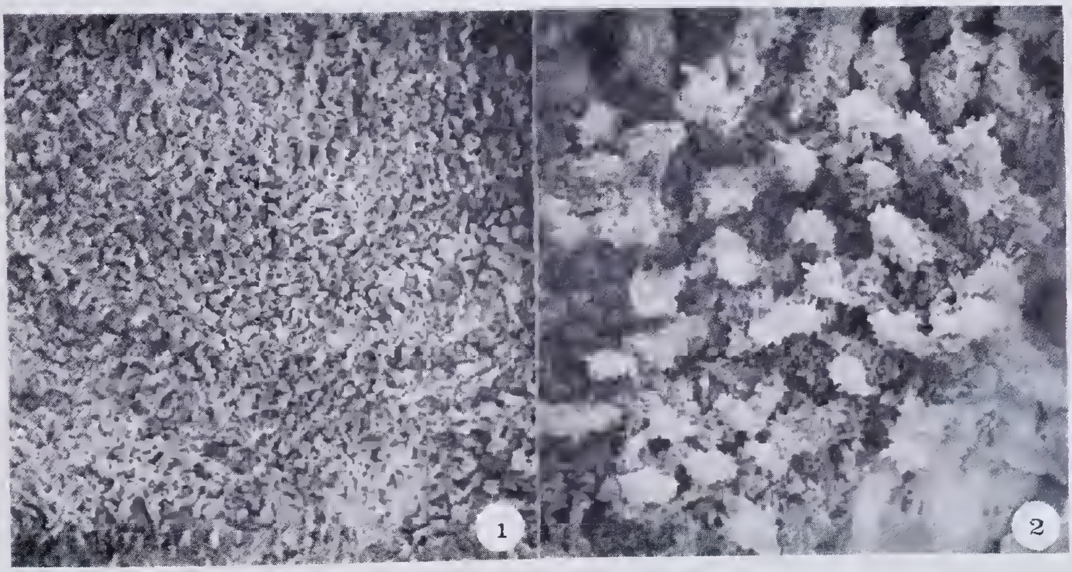
PLATE 40

A: External surface of mantle of *Sacculina granifera* 1. ×500; 2. ×2500

B: External surface of mantle of *Heterosaccus lunatus* 1. ×450; 2. ×1350.



A



B

Mem. Qd Mus. **18**(2): 265–71, pls. 41–42 [1978]

THE OLD BURIAL VAULT AT NORTH QUAY, BRISBANE

J. C. H. Gill
Queensland Museum

ABSTRACT

A brick structure accidentally uncovered in 1972 during construction of the Riverside Expressway, Brisbane, opposite the eastern side of the junction of Herschel Street and North Quay, has been determined to have been a burial vault dating from the penal settlement days of Moreton Bay and Brisbane Town. This probably represents the last convict structure to be located in this area. It has been assessed as fully as possible from the limited record able to be made at the time of discovery, as within an hour of this it had been destroyed totally.

In the Queensland Museum are eleven sand stock bricks, registered H9750 to H9760 inclusive, collected by the Museum on 23 August 1972; their *in situ* provenance is recorded as 'from suspected grave site on Brisbane River bank 100 yards [90 m] west of Tank Street'. They provide a slender base on which to assert they were part of a structure dating from the convict days of Brisbane Town, yet there is evidence which affords positive indications of the time when the bricks were used, of the structure of which they were part, and of the use to which that structure was put.

The narrative which follows will incorporate the historical evidence. Then the structure as such will be dealt with as far as it is possible to make a reconstruction from the relics available.

Historical Evidence

On 23 August 1972 a bulldozer working on the Brisbane Riverside Expressway construction opposite the junction of North Quay and Herschel Street dislodged some bricks buried in the soil, and disclosed an aperture in the sloping bank behind which lay a buried chamber. Examination revealed a barrel-vaulted, brick structure, over which a coating of lime mortar had been applied internally.

Main Roads Department officers supervising the construction halted work and informed the Royal Historical Society of Queensland of the find. The author was contacted and requested Queensland Museum assistance to assess the historical value of the discovery. Very limited time was allowed for investigation before construction work resumed. The urgent situation precluded detailed archaeological investigation. Fortunately a local television station, QTQ 9, filmed external and internal views, and later donated the film to the Queensland Museum. Rough sketches were made of the structure and some bricks were taken for later examination. As nothing further could be done, the Main Roads Department officers were informed and within minutes the bulldozer operator, who had kept his motor running all this time, had destroyed the structure. A press photographer arrived too late to do other than photograph a few bricks lying where the structure had been, resulting in coverage in the 'Courier-Mail', on 24 August 1972, p. 3.

With the wisdom of hindsight it seems to have been a rather inglorious episode. Yet the element of surprise and the pragmatic attitude of the people concerned with the site gave no opportunity for complete survey. Furthermore the nature and purpose of the structure was at first not clear. The situation could not compare, for example, with the discovery, again per medium of a bulldozer, on 30 March 1974, of an early brick vault in what had been the earliest official burial ground in

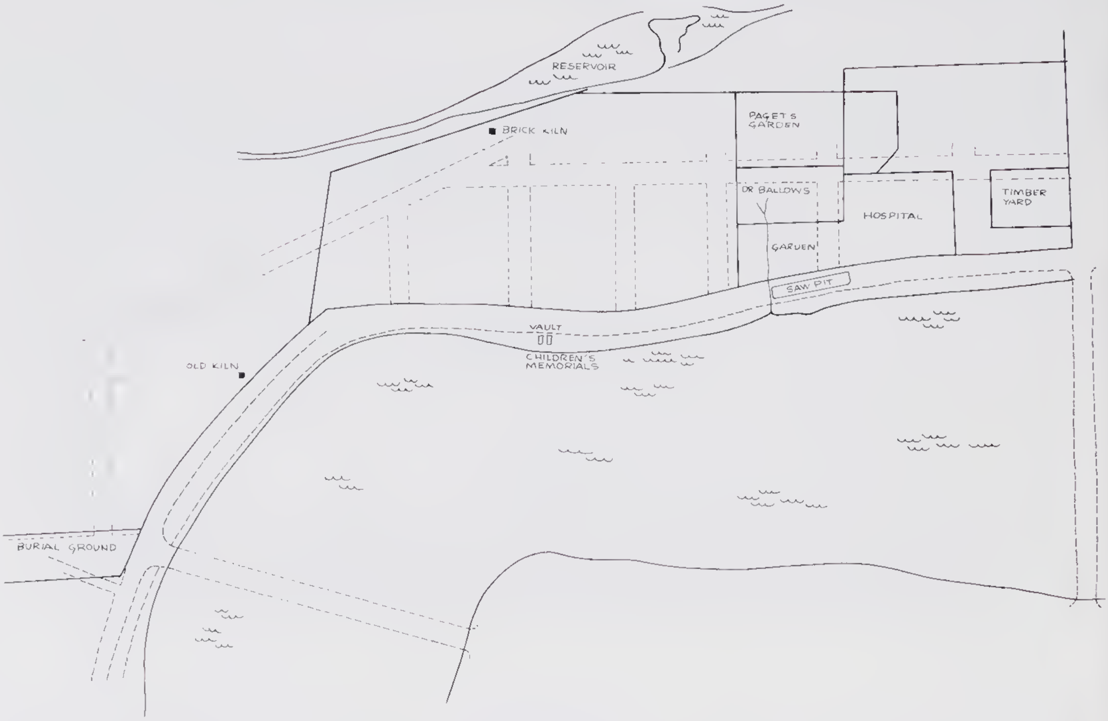


FIG. 1. Plan based on Assistant Surveyor R. Dixon's 1840 survey, with outlines of modern streets superimposed.

Sydney from 1793 to its closure on 27 January 1820. The purpose of the structure was clear — it contained a collapsed wooden coffin within which were bone fragments and Sydney University archaeologists had three days to assemble a team to survey it. Resulting public interest gave the vault a further reprieve and in the end it was dismantled for reconstruction at the Old Sydney Town Project. Finally a thoroughly researched monograph was published (Birmingham and Liston 1976).

The site of Brisbane's earliest burial ground was investigated previously by Gill (1959-60, 1974), who recalled that the structure was only yards away from isolated memorials on North Quay known as 'the children's graves'.

Relics from Brisbane's penal settlement era are few. The absence of a burial ground from this era is particularly notable when one considers the plethora of early memorials in the other states of Australia. Controversy has raged as to the site of Brisbane's earliest burial ground. Yet it has been proved beyond doubt that the penal settlement's earliest and only burial ground was that shown in the town maps of Assistant Surveyor Robert Dixon (1840)* and Surveyor Henry Wade (1842)† situated on the north bank of the Brisbane River at the northern end of the William Jolly Bridge in the area bounded by the present day Skew Street and Eagle Terrace.

One of the causes of controversy was the presence of three (at least) memorials on the river bank at North Quay directly opposite the eastern corner of North Quay and Herschel Street, immediately above a prominent rock face which rises abruptly out of the river. The Royal Historical Society of Queensland has a photograph (said to have been taken about 1876) which shows memorials *in situ* at this point (Plate 41, fig. 1). This photograph, acknowledged to Mr H.A. Jones was donated in 1921 and was reproduced in the 'Brisbane Courier' on 25 October 1913 at p. 12. It was captioned: 'The Soldiers Graves on North Quay. A controversy has for some time been waged in the "Courier" as to the exact location of the soldiers' graves in the old burial ground on North Quay. Our photo shows their position (indicated by a X).' The memorials have long been gone from North Quay but they are still to be seen in Toowong General Cemetery. On 5 October 1881 the memorials at North Quay and any remains (under licence

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* Queensland Survey Office Map M.T.3

† Queensland Survey Office Maps 6 and B.1182

issued by the Colonial Secretary on 23 August 1881) were removed to Toowong.*

Only three memorials and remains were removed. Whether there were any more burials on this site is a matter of doubt.

The three memorials all commemorate young children — William Henry Roberts, son of Charles Roberts of the Commissariat Department who died of illness on 15 November 1831 aged 3 years and 2 months†, Peter, son of Private Peter McCauley of H.M. 17th Regiment of Foot, accidentally drowned on 5 January 1832, aged 5 years and 8 months; and Jane, daughter of John Pittard, former Colour Sergeant of the 57th Regiment, who died on 29 January 1833, aged 12 months and 13 days (Plate 41, fig. 2).

The McCauley and Pittard memorials are the usual headstone and footstone types; the Roberts memorial is a catafalque or table monument type with the inscription on the flat top. The memorials show evidences of the ravages of time. In 1962 the Brisbane City Council took steps to refurbish them. The decay of the first two memorials has been arrested, but the inscription on the Roberts memorial is now lost and is, in fact, covered by a coat of stucco. Fortunately it was recorded in its entirety in 1913 with some errors which, except for the age (5 instead of 3 years) were corrected by Gill (1959-60).

Assistant Surveyor Dixon in his 1840 map, in addition to the official burial ground, showed two small squares, habitually used by surveyors to indicate isolated graves, at a point corresponding to the location of 'the children's graves' (Gill 1959-60).

Steele (1975) indicates that the Reverend John Vincent, in his initial report to Archdeacon Scott, complained that the settlement's 'burial ground is at a very remote distance, is too small and so very difficult to be dug . . . that two men with the utmost exertion are scarcely able to prepare a grave in six or seven hours'.

If the children were buried where the memorials were located, it would have required the cutting of kists in solid rock, and the purpose of the structure unearthed on 23 August 1972 now becomes clear. It was a burial vault sited on or slotted into the rock in which bodies were placed whilst sorrowing relatives were allowed to place memorials around it, a much easier process than cutting a full-size grave into the rock each time.

Evidence of the existence of the vault was available, but the disappearance of the structure beneath the earthen embankment of the widened North Quay in the latter part of the nineteenth century and the presence up to 1881 of the table monument to the Roberts' child led to the belief that references to the vault were references to the table monument.

The removal of the memorials from North Quay on 5 October 1881 excited no comment from the press of the day. In fact it was not until Friday, 21 October 1881 that the 'Brisbane Courier' on page 2 remarked:

> 'The old landmarks of Brisbane are rapidly disappearing and although by many the removal of these mementoes of early days may be regarded with some lingering feelings of regret the improvement which will result in the general appearance of the city must be a matter of satisfaction'.

The disappearance of the old convict barracks and old buildings on the corner of Queen and Albert Streets is favourably commented upon, whilst the fact that the dreary looking goal at Petrie Terrace will soon become a thing of the past also is editorially approved. Then:

> 'Another "landmark" that has disappeared from within the boundaries of the city are the old graves on the North Quay. In these graves were the remains of three bodies that have been under the ground for some fifty years. By the order of the Colonial Secretary, the remains with the tombstones that were over them, have been removed to the cemetery at Toowong, that being considered a more fitting place for them, where it will be less trouble to keep the graves in order, and where they will be subjected to less desecration'.

It was not on-the-spot reporting by any means and it is not surprising that the vault escaped notice by the press. There the matter rested for 32 years whilst improvement works along the North Quay greatly altered the old landscape.

Professor F. W. S. Cumbrae Stewart through the columns of the 'Brisbane Courier' of 30 September 1913 (p. 4) drew attention to the childrens memorials in Toowong Cemetery, expressed the belief that they had been removed thence from North Quay in 1876, and sought information as to where the gravestones originally stood on North Quay.

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* John Oxley Library MS.O.M. 65/18, Queensland State Archives [QSA.] COL/A319, 3694; QSA. COL/G15, p. 585, 81/1233.

† John Oxley Library. ibid. Mr Melville the sexton at Toowong Cemetery in 1940 says it appears to be 3 but could be 5 years, on account of weathering of the stone. In 1881 (59 years earlier) the age is given as 3 years and 2 months. The stone was then 50 years old and the inscription much more legibile.

Between 30 September and 5 November 1913 the 'Brisbane Courier' published fourteen letters on the subject of the 'Old Burial Ground' (Gill 1959-60).

On 7 October 1913 the 'Brisbane Courier' (p. 4) published a letter from a Mr Thos. Illidge who stated he was on the spot when the remains were dug up by Mr D. Hannah of Paddington. Published with the letter was an interview by a Courier reporter with Mr David Hannah of Rosalie who said he had assisted in the removal of headstones on the river bank from North Quay to Toowong. It is significant that Mr Hannah did not refer to the removal of remains.

On 16 October 1913 (at p. 7) 'Sixty Years a Queenslander' wrote about 'the monumental stone' which in earlier years marked the spot known to old residents as the 'soldiers' graves'. He referred to the difference of opinion which seemed to exist as to the exact site. This he regarded as quite natural for during the last few years (i.e. prior to 1913) 'surface appearances have changed or become obliterated'. He also says:

> 'In the 'fifties and 'sixties of last century much of the river frontage along the North Quay was covered with a tangled growth of lantana, which could only be penetrated by a bird-nesting boy or a billygoat. As the former, I have often "worked my passage" through this scrub and my memory fixes the site of the graves as about midway between Tank and Herschel Streets and just above a prominent rock which here rises abruptly over the river.' (Gill 1959-60).

He was almost on the correct site and indicates that with the profusion of under-growth making the site inaccessible the general public had come to refer to them as the 'Soldiers' Graves'.

On 20 October 1913 (p. 6) the 'Brisbane Courier' published a letter from a Mrs Lucy Sonnonschein (nee Wynn) of Warwick. She said:

> 'The old burial grounds were situated opposite the present Roma Streets goods shed gates. After the burial ground was removed, the land was built upon and occupied by Davies (Davis) the Jew, Joseph Jayes, Bill and Joe Jewell, carpenters, Joshua Peter Bell, and Bulger, a wine merchant. New shops have replaced these dwellings. This burial ground was known as the "Soldiers' Graves". On the bank of the river in North Quay there was a large vault, opposite Paddy Pacey's milking yard, which marked the spot where some officer was buried.' (Gill 1959-60).

The existence of the burial vault, rediscovered in 1972, being unknown, the author as already stated believed this to be a reference to the table monument to the Roberts' child.

Yet on 5 November 1913 the 'Brisbane Courier' published (in the Courier Home Circle Supplement at p. 6) the final two letters in the burial ground debate. Mr A. E. Campbell of Rockhampton refers to the sketch in the 'Courier' of 25 October of the "soldiers' grave".

> 'Yes, that is about the spot, only high up, about ten yards from the fence. [the X was placed too low on the photograph], and there is a high stone face projecting towards the river. It was the grave of an officer who went out riding and his horse carried him against a tree and broke his neck. I think his name on the top slab was "Lawson". The tomb must have been shifted in the early 'sixties. The bottom end near the river was broken, and it acted as a cave. Many a one slept there for the night, for it was a cosy camp for a cold night.' (Gill 1959–60).

Here again the author believed the reference was to the table monument; but it would have made cramped quarters and access would have been grossly difficult. The mean dimensions of the monument are only 1·905 m by 0·990 m by 0·852 m high. The brick vault was in a different category — in the 'fifties and 'sixties it was buried beneath lantana; any remains in it would have been moved in 1881; (in any event the remains of young children would not have the durability of those of adults); the access, if the end near the river had broken away, would have been easier, and air circulation and animal scavengers would have removed any associations with its grisly past by the time 'down and outs' began to camp in it.

It is considered that these reports provide sufficient evidence of the existence of a vault.

In addition to its existence we also have evidence of its use. A macabre story recounted by J. J. Knight (1895) furnishes this. Talking of the offences for which a convict could be sent to the triangle Knight says:

> 'A very common offence was the purloining of a few cobs of corn and potatoes, the chief ingredients of the convicts' much prized "fiddle-cake", the love for which caused many sore backs at the triangle, and weary legs on the treads. These two things having been obtained, the corn was ground on an improvised grater made usually of a piece of tin or zinc, in which holes had been punched.'

After describing the grating and recipe for the delicacy, Knight goes on

> 'But it was often more difficult to obtain the material for the grater than the corn and potatoes, and in one case at least a convict finding this so resorted to a very questionable means of gratifying his desires. The overseer at Eagle Farm was unfortunate enough to lose one of his children, and the body having been placed in a tin box, was laid in one of the vaults on the river bank near Herschel Street. This fact was, of course, known to the prisoners, and a day or so after the funeral one who had so urgently desired the possession of a "grater"

effected an entrance to the vault and taking out the dead body of the child found in the box the material for the manufacture of this necessary implement of the "fiddle-cake" maker. Fortunately for the sacrilegist, he was not found out, and was enabled to make many specimens of that delicacy, which was described by one who had often partaken of it as being "better than any pie going".'

Apart from anything else this indicates that a measure of improvisation was required still in the undertaking line. If there were no coffins readily available for children of officials one wonders what sort of hurriedly thrown together boxes were used for convict burials.

Knight talks of one of the vaults on the river bank near Herschel Street. The available evidence indicates there was only one such vault. It appears to have carried no marks of identification (the adjacent memorials made this unnecessary). Mr Campbell does mention the name Lawson, but he appears to be confusing the inscribed Roberts' monument with the vault. In Plate 41, fig. 1 the Roberts' monument is plainly discernible but the vault is not, although Mr Campbell has no doubt about the location of the latter. It was because the vault carried no identifying marks or inscription that all the stories about soldiers' graves and officers' burial places came into being. The correct function of the vault probably occurred to no one; the memorials were there and it would not be known generally that they were sited on solid rock. Once North Quay was widened in the late nineteenth century the footpath on the river side of the roadway was cut off from the steep river bank by a wooden picket fence of sturdy construction. Apart from wooden stairway accesses to the Commercial, Brisbane and Brisbane Grammar School Rowing Club Boatsheds there was no access and for upwards of half a century until World War II the North Quay river bank from the O'Connor Boathouse (Commercial Rowing Club) upstream to the Grey Street (William Jolly) Bridge became a terra incognita.

Even the erection of air raid shelters in 1942 resulting in the partial disappearance of the fence followed by its nearly complete demolition in the post-war period brought about no interference with the river bank itself.

It was not until the construction commenced of the Riverside Expressway section of the South East Freeway that the riverbank began to be altered substantially. In August, 1972 the work began on the expressway exit to Herschel Street. This meant carving away a section of the riverbank; before the bulldozer got down to the rock, it blundered into the old vault with the results already indicated. The vault could well have been coeval with the Windmill and the Commissariat store*, and may well be the last of the Brisbane Town convict structures which remained to be rediscovered.

DESCRIPTION OF THE VAULT

The vault itself was constructed of sand-stock bricks (as they are commonly known) with mean approximate dimensions of 205·9 mm × 63·5 mm × 107·9 mm. The dimensions of the vault as estimated by Mr A. Sweetser, Queensland Museum, in a drawing he made (Figure 2) are given as 1·53 m × 1·83 m with a barrel vaulted roof rising above 1·53 m high side and end walls. The entrance at the northern end had been bricked up after any remains had been cleared from the vault. Two wooden slabs lay on the floor covered by rubble and a partly burned piece of hardwood plank lay near the southern end of the vault. There was some evidence of dampness in the earth floor but no signs of the vault ever having been inundated with water; the run-off from North Quay to the Brisbane River was steep enough to prevent water from gathering and lying in the vault. The only wall of the structure to show up in full width in the movie film was the northern wall, and estimating from the known lengths of the bricks collected from the site the mean width of the wall could be 1·72 m, 0·19 m more than Mr Sweetser's estimate (Figure 2).

The side walls were grooved for their entire lengths at two levels, which indicated an intention to have the coffins resting on planks (fitted into the grooves) above ground level and provisions for an upper layer of coffins if needed.

An analysis of the lime mortar used to bind the bricks and plaster the interior of the vault has been made by the Queensland Government Chemical Laboratory. The analytical report (Appendix 1) established the source of the burnt lime used in the mortar as Ipswich; a clear link with the penal settlement days.

As regards the bricks, what were known as the old and new brick kilns respectively both were located within 230 m of the vault as shown on Figure i (Steele 1975). So the raw materials for the brickwork were close at hand.

Plate 42, fig. 1 shows the intrusion of some tree roots, but the lack of moisture had inhibited the growth of these.

Owing to the gross interference with ground levels, even before the discovery of the vault as

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*Both completed in 1829.

well as subsequently, no soil profile could be taken. However it was obvious to the eyewitness that the vault had been covered by fill from elsewhere than the river bank itself and that the river bank proper began at the base of the structure.

Apart from the planks within the vault no timber beams or lintels were noted in the walls of the structure; it appears to have been small enough not to require timber to span any openings or archwork which the bricks themselves could not support. No other features remain to be remarked upon.

Thus a few feet of film and eleven bricks at the Queensland Museum, with this account, will be the only record of a structure dating from the early penal settlement days of Brisbane Town.

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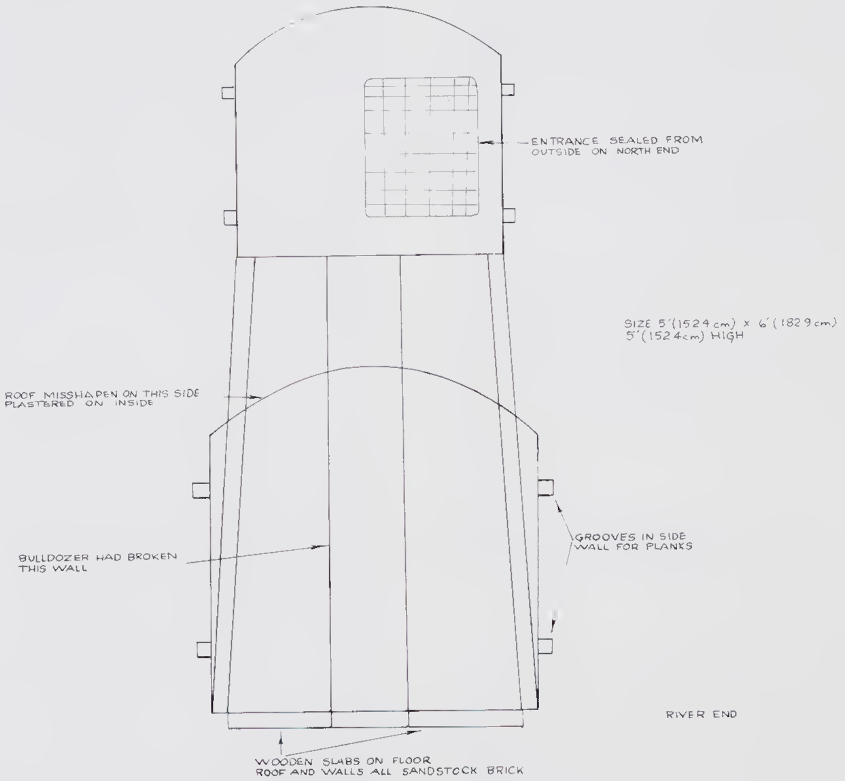

Fig. 2. Diagram of the vault, after a sketch by Mr A. Sweetser held in the Queensland Museum.

APPENDIX 1

Government Chemical Laboratory
William Street,
Brisbane, Q. 4000
16th November 1976

Dr. D. J. Robinson
Qld. Museum
Gregory Terrace &
Bowen Bridge Road,
BRISBANE.

Ref: DR:DF H10/5

Dear Sir,

On Tuesday 8th November, soft portions of the white material in mortar samples H9255 and 9578 provided by the Museum were scraped out and this material on analysis gave carbon dioxide, 9% acid soluble silica and 6% magnesium as magnesium oxide. Aslo present is calcium oxide, iron oxide and alumina.

The Geological Survey Office was contacted and confirmed that the results of an early analyses of the Limestone Hill Limestone was

Loss of Ignition	43.8%
Total Silica	5.7%
Iron oxide	0.9%
Alumina	1.1%
Calcium oxide	27.5%
Magnesium oxide	20.6%

This indicated that this mineral is an impure mixture of calcium and magnesium carbonates. Other areas of limestone in the Ipswich area have similar compositions. The presence of acid soluble silica and the magnesium oxide indicates that the burnt lime used in the mortar sample probably came from the Ipswich district which seems to be the only source of limestone in the local area other than sea shells. The Ipswich deposits have variable compositions but all seem to have more than 5% magnesium carbonate.

Microscopic and hand lens examination showed no shell particles and it is not expected that shells burnt to calcium oxide would contain acid soluble silica and magnesia.

Warwick and Gympie limestones are much lower in magnesia.

D. Mathers
Director

PLATE 41

FIG. 1: The memorials *in situ* ca. 1876 – photograph in Royal Historial Society of Queensland collections.
FIG. 2: Children's memorials at Toowong Cemetery.

1

2


Sacred
To
the Memory of
Peter (Son of Peter McCauley
Private in H.M. 17th Regt. of Foot) who
was accidentally drowned on 5th day of
Jany 1832 Aged 5 years and 5 months
A Lovely Boy Possessed of every charm
Could not the Tyrants fatal dart disarm
Engaging sweetness met the stroke
And bid farewell to every human
His Spotless Soul now to his God restored
Bless in reward
Then happy child my soul no more
Shall in poignant grief thy fate deplore
But humbly hope thro' an Almighty grace
One day to fold thee in a sweet embrace

PLATE 42

FIG. 1: Interior of vault-photograph from QTQ 9 16 mm film.
FIG. 2: Riverside Expressway showing remains of bold, rocky face above which the vault was located.

1

2

Mem. Qd Mus. **18**(2): 273–319, pls. 43–103 [1978]

THE CORAL GENUS *ACROPORA* (SCLERACTINIA: ASTROCOENIINA: ACROPORIDAE) IN THE CENTRAL AND SOUTHERN GREAT BARRIER REEF PROVINCE

CARDEN C. WALLACE
Queensland Museum

ABSTRACT

The genus *Acropora* (excluding subgenus *Isopora* Brook) is revised from zonation studies on two reefs, and incidental collecting from many other localities in the Great Barrier Reef Province. As a result of field studies, many species are placed in synonymy, and a resulting forty species are redescribed. The revision includes description of field characteristics of the species, many of which were previously known only from small skeletal series. Problems of identification and delimitation of the various species are discussed.

In the Great Barrier Reef Province, as in most Indo-Pacific reef areas, the regions of densest coral growth are regions dominated by the branching coral genus *Acropora*. Over 300 species have been described for this genus. Some 80 have been recorded from the Great Barrier Reef, and many more would have been added to this list had the reef slopes and deeper waters been more accessible to early collectors. The original 300 may be reduced to around 70 by synonymy, and the 40 species here treated are considered to represent at least 90% of the branching *Acropora* in the Great Barrier Reef Province.

The following is a working paper on the taxonomy of this neglected genus. It is based on regional studies in the Great Barrier Reef region, and in particular on line transect studies carried out at Big Broadhurst Reef (Wallace 1975, Wallace and Dale 1977) and Bushy-Redbill Reef (Wallace and Lovell 1977, Wallace unpublished). It is an attempt to open the study of the genus to workers in all aspects of coral study and to this end it concentrates on field description of the species.

It is clear to the author after some experience with the genus that few species can be fully understood by simple morphological studies of colonies, even with the addition of ecological information. Even the population cannot be considered a sufficient unit for study as there are often other key species in the surrounding assemblage which may look like, physically interact with, or affect the members of the population in some way. This paper seeks to indicate such problems.

TAXONOMIC HISTORY

The name *Acropora* Oken, 1815 was officially validated in 1963 (Boschma 1961, China 1963). It came into general use with Verrill (1902), although not without some argument and nostalgia for the previously widely used *Madrepora* Lamarck: 'it is with a feeling of regret that we are forced to abandon the use of a generic name which remained unquestioned by four generations of authors during the golden days of systematic zoology' (Mayor 1924, p.vii).

Many authors have described species in this genus. Few have attempted to synonymise or group species, fewer still to define and standardise terms. The most notable single contribution to the taxonomy of the genus was that of Dana (1846) who gave very careful attention to his specimens collected during the United States Exploring Expedition. His arrangement of species according to colony shape and radial corallite shape without defined subgeneric status remains the simplest and most acceptable treatment of the genus.

Brook (1893) produced the only true monograph of the genus, summarizing all previous work and re-describing all described species. He ordered the species into subgeneric groups, attempting to take into account all skeletal characters, but his subgenera have not found general acceptance: indeed, current synonyms often span the groupings. Brook unfortunately did not examine Dana's specimens, although he did see most of the European located types, and most Dana species can be shown to have a Brook synonym. Verrill (1902) also split many Dana species needlessly. Nemenzo (1967) revived the use of group names, although not affording subgeneric status to his groups.

Of the twentieth century authors, Vaughan (1918), Hoffmeister (1925), Crossland (1928, 1952) and Wells (1954) have treated the genus in detail, with ecological data, although not concentrating exclusively on *Acropora*.

Detailed underwater studies of *Acropora* were first made by J. Verwey in the Bay of Batavia in the 1930's, and the taxonomic results of his study are still unpublished (see Umbgrove 1939, p.56, 1940, p.303; Wells 1954, p.414). In discussions with Dr Verwey I have found that we are usually in agreement in our general assessment of species limits (though obviously not always on names). His opinions pre-date those of this paper by some forty years, and it is hoped that his work, which is to be a complete monographic treatment of the genus, will soon be available.

CHARACTERS AND TERMINOLOGY

(For coral terminology not specifically referrable to *Acropora* see Moore, Hill, and Wells 1956).

Acropora lacks most of the skeletal characteristics used in the species identification and study of variability of other corals, e.g. columella, dissepiments, septal structures. The main character defining the genus is the method of branching: an axial polyp builds a corallite of increasing length, and buds off radial polyps from its growing tip. Any radial polyp has the potential to take up an axial role. A variety of branching patterns occur, and these (with commonly applied terminology) are summarized in Figure 1.

The polyps have twelve tentacles, one of which (overlying a directive septum) is longer than the others. Two cycles of simple trabecular septa can be expressed in the corallites, although further cycles may be apparent in the walls. The walls, regarded as synapticulothecae (Wells 1956) have recently been shown to have septal contribution (Ricart y Menendez and Freidman 1977). See plate 43 and Figure 1 for a summary of these features).

The axial corallites are usually described by measurements, (in this paper expressed as inner and outer diameter) and by septal development (here expressed as maximum observed development, to an approximate fraction of the radius, e.g. to 1/3R). The radial corallites are described according to their shapes, summarized in Figure 2.

'Coenosteum' as described for *Acropora* commonly refers to both external corallite and intercorallite features. The walls of corallites are often clearly costate, in which case the intercorallite material is usually a spongy reticulum, with or without spines. Sometimes there is little or no difference between the appearance of the two areas. This is usually when the coenosteum is a dense arrangement of elaborated spines. With electron microscopy different categories of spines can be seen and the coenosteum can be more accurately described (Wallace and Grimmer, in preparation).

VARIABILITY

All Scleractina are capable of broad morphological variety, but in *Acropora* this can be

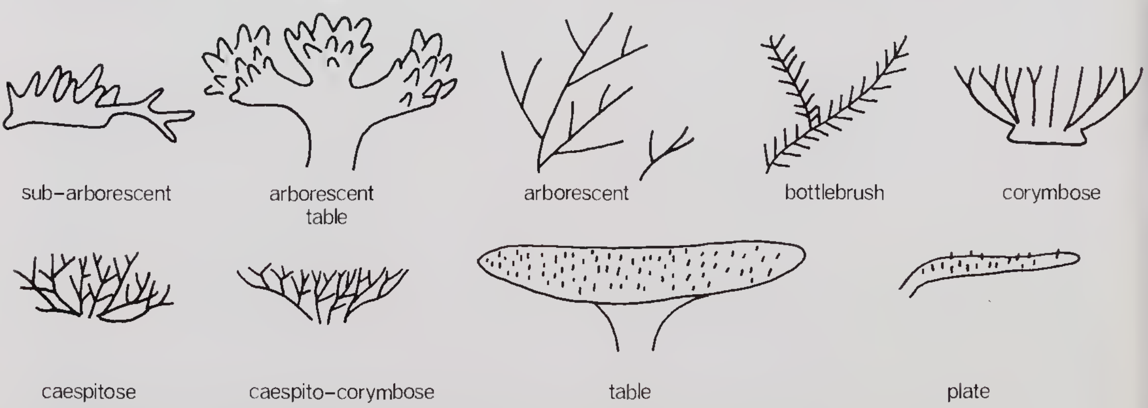

FIG. 1: Common colony shapes in Great Barrier Reef *Acropora* and their nomenclature.

particularly subtle. A number of features contribute: the axial method of growth allows a continuum of shape possibilities, which may be exploited differently by the species, the population, the colony, or even parts of the colony. The simplified skeletal structure allows the application of only a limited descriptive terminology, and description of small variations is always difficult. Detailed measurements for analysis of variation often show similar variability within the colony to that in the entire population (Wallace, unpublished, for *A. millepora* and *A. aspera;* similarly high variability in *Porites* is shown by Brakel 1977). In fact the absolute variation in size of most skeletal features within the entire genus is relatively small for a coral group.

In this much speciated genus there is a tendency for numbers of species to co-occur. Often differences between species can be seen in population strategies and slight differences in habitat preference.

Despite the above, some of the taxonomic confusion so repeatedly quoted in the literature disappears when the taxonomist enters the water. This is particularly so with reef slope species where growth form and other features can often be seen to alter gradually with depth. It can be stated unequivocally that the most complex species taxonomically are those occurring on the shallow reef flat, and none of these can be considered to be fully described in the present paper.

Some generalizations can be made, and should be born in mind when interpreting the taxonomic section:

(1) Some reef regions support predominantly characteristic colony shapes, which can be attributed to physical parameters (in particular low-profile corymbose shapes on the outer reef flat where exposure is great (low water depth); small flat plates on the deep reef slope where light availability is limited). In these areas the species composition can be expected to include (a) species capable of only that shape; (b) species having the shape within a range of phenotypic variability; (c) morphs of polymorphic species.

(2) All species which extend down the reef slope exhibit a gradual flattening out of shape with depth, and the ratio of radial to axial corallite numbers decreases. These flat colonies can be recognised for what they are if the observer investigates shallower sections of the populations. (In skeletal collections they are more difficult to sort). A few species are characteristically flat but with high radial to axial corallite ratio, and do not extend into deep water. At least one species *(A. granulosa)* is apparently adapted to low-light situations, and has a characteristic distribution which includes shallow but shaded situations.

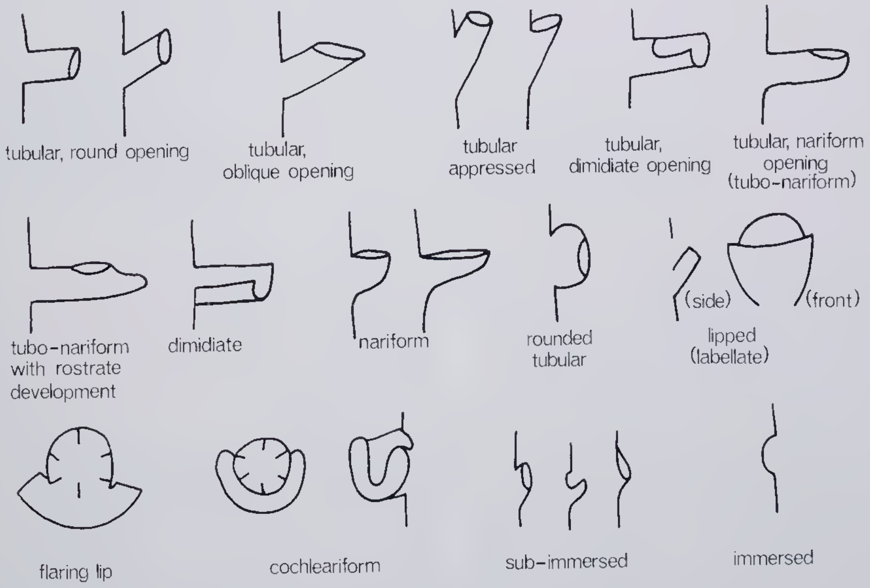

FIG. 2: Radial corallite shapes in Great Barrier Reef *Acropora* and their nomenclature.

(3) Some basically arborescent species which occur on the reef flat may exhibit diverse growth forms adapted to different habitats.

(4) The greatest variety of colony shape seems to occur in areas with good water cover and reasonable water çirculation, such as deep 'middle reef flat' areas and leeward patch reefs. Many species can be thought of as achieving their most 'characteristic' shape in these areas. Here also many colonies achieve colossal size.

Many species have characteristic colouration, at least locally, which can be used as a guide to identification but it should never be supposed that this is the only possible colour for the species.

METHODS

FIELD STUDIES: The observations in this paper are the result of a variety of studies on reefs in the Central and Southern Great Barrier Reef Province (see Maxwell 1968). They concentrate on reef slope and other below-L.W.M. areas, as the corals here have previously been least observed. On Big Broadhurst Reef (18°55'S; 147°44'E) observations and collections were made serially across the outer reef flat and down the reef slope (see Wallace 1975; Wallace and Dale 1977). Similar techniques were used on the reef flat at Redbill Island (20°57'S; 150°05'E) (Wallace, unpublished). Collections with habitat data were made at Bushy-Redbill Reef (see Wallace and Lovell 1977), Darley Reef (19°24'S; 148°05'E), Bowden Reef (19°02'S; 147°06'E), Prawn Reef (19°02'S; 148°05'E), Viper Reef (18°53'S; 148°10'E), Tryon Reef (23°15'S; 151°47'E), Lady Musgrave Reef (23°55'S; 152°24'E), and Heron Island reef (23°27'S; 151°55'E). Detailed samples of populations of *A. millepora* and *A. aspera* for a morphometric study were made at Heron Island. A reference collection was made in the Fiji Islands, type locality of many of the species. Occasional reference is also made to observations by the author at Enewetak, Marshall Islands and Tongatabu, Tongan Islands. A recent opportunity to study specimens at James Cook University (JCU) collected at Lizard Island (14°40'S; 145°28'E) and the Palm Island group (18°40'S; 146°33'E) allowed further notes to be added for some species.

Other workers contributed specimens from various parts of the Great Barrier Reef Province and the Murray Islands. Information on this material is given to the text, and locations of reefs can be seen in Maxwell (1968, figs. 17A-D). Other material examined in the Queensland Museum included the collections of the Great Barrier Reef Committee (G.B.R.C.) and specimens mentioned by Stephenson and Wells (1956).

TYPE MATERIAL: Types were studied in the Smithsonian Institution (USNM), Yale Peabody Museum (YPM), British Museum of Natural History (BM), Museum National d'Histoire Naturelle, Paris (PM), University of the Philippines (UP). Fragments of type material were received on loan from the first three institutions, and photographs of type specimens were received from the Museum für Naturkunde, Berlin (MNB), the USNM and the BM. Collections were examined at the Rijksmuseum van Naturlijke Historie, Leiden (Verwey collections), Zoological Museum Amsterdam, and the University of the South Pacific, Fiji.

LABORATORY STUDIES: Most specimens were stored as cleaned skeletons (preferably macerated and cleaned in water). Small fragments of some specimens have been preserved entire in buffered formalin. Observations on skeletons were made with a Wild M5 binocular microscope with linear measuring eyepiece. Where possible, particularly with type material, five observations per character were made for each specimen, but expediency prevented this procedure being used for all specimens. Additionally, representative specimens of each species were examined with scanning electron microscopy, and a standardized procedure for photographing axial and radial corallites and inter-corallite spines was followed. This information is sometimes used to clarify descriptions, but it is mainly to be used for a study further defining species groups and pursuing a phylogenetic grouping of them (Wallace and Grimmer, in preparation).

USE OF THE TEXT

Any taxonomic text has two main categories of readers: those interested in the taxonomic interpretation as such, and those requiring an identification tool. For this genus, I suspect the second category will be in the majority. I recommend that no attempt be made to identify single specimens without field observations, and conversely that field work (even when done without taxonomic emphasis) include casual assessment of affinities of colonies. Any field notes which allow specimens to be later grouped as series are useful.

For observing skeletal specimens with an incident light microscope a finger held between the light source and the specimen (to diffuse the light) enables corallite shape and septal features to be viewed clearly.

The photographic plates are considered to form a major part of the taxonomic description, because they (1) display field appearance of colony and habitat, (2) indicate size and shape of corallites, and where possible coenosteal texture, (3) indicate variety in all features. A fourth and most important role intended for the plates is that of a visual key. The identification process will be simplified if the user scans the plates before attempting to identify material. Reference to plate numbers is made once only for each description.

Where synonymy lists of other authors have been accepted without investigation these are quoted as (synonymy) after the author reference. Check-lists and catalogues (e.g. Rathbun 1887) are not used for synonymy lists. In this context Faustino (1927), being mainly a reiteration of previous descriptions, is regarded as a check list unless it makes an addition to information on a species.

The arrangement of species is partly in accordance with previous arrangements, and reflects my own views of affinities. Strongly supported affinities are grouped as species-groups. As both detailed morphological and phylogenetic affinities of species will be pursued in a later paper this arrangement must be considered a working guide only.

One species group, that including *A. palifera* (Lamarck) (i.e. the subgenus *Isopora* of Brook, 1893), has been omitted as this is under scrutiny in population studies by Potts (1976, 1977) and will be given separate taxonomic treatment (Potts and Wallace, in preparation).

Specimens quoted in the text are registered specimens, and in most cases further unregistered material and spirit specimens are located in the Queensland Museum (QM). Small reference collections will be lodged in the USNM, BM, and MNB.

Depth ranges recorded for species apply to the areas studied, and these may differ in other areas.

Finally, some of the taxonomic format used by other authors has been omitted. For example, many authors describe undersurface details of colonies. As these depend on general colony shape and are reductions of upper surface features their usefulness is questionable. Radial corallite measurements are not given, as a statistically acceptable assessment of these which is comparable across different shapes has not been arrived at (the illustrations and previous authors' descriptions give an indication of size range).

SYSTEMATICS

Family ACROPORIDAE Verrill, 1901

Acroporidae Verrill, 1901, p.163; Wells, 1936, p.99; Wells, 1956, p.F372.

Massive or ramose colonies by extratentacular budding; hermatypic. Corallites small, synapticulothecate or septothecate, pseudocostate or costate, slightly differentiated from coenosteum. Septa non-exsert, in 2 cycles, formed by simple spiniform trabeculae projecting inward and upward from vertical mural trabeculae, commonly fusing to form laminae. Columella absent or trabecular and weak. Dissepiments thin and tabular when developed. Coenosteum extensive, light reticulate, flaky, generally spinose or striate on surface. (Modified from Wells 1956, p.F372).

Genus **Acropora** Oken, 1815

Acropora Oken, 1815, p.66; Verrill, 1901, p.164; Verrill 1902, p.208 (synonymy); Vaughan, 1918, p.159; Wells, 1956, p.F373 (synonymy); Nemenzo, 1967, p.47.

TYPE SPECIES: *Millepora muricata* Linnaeus, 1758.

Acroporidae which are ramose, rarely massive or encrusting; branching with an axial or leading corallite larger than the more numerous radial corallites budded from it; united by light, reticulate, spinose or pseudocostate or costate coenosteum. Columella and dissepiments absent. (Modified from Wells 1956, p.F374).

THE '**Acropora robusta**' GROUP

The four species *Acropora palmerae, A. robusta, A. rotumana,* and *A. abrotanoides* are very similar in corallite morphology but not colony shape. *A. palmerae,* described as a completely encrusting species (Wells 1954) can bear short vertical branches (Wallace, in prep.). *A. rotumana* is stalked, with thick alciform branching units or even forming a sturdy arborescent table. *A. robusta* can vary phenotypically from encrusting to open branching. *A. abrotanoides,* still poorly categorized, occurs as clumps of mainly vertical branches.

Ignoring this last species, the other species have strong habitat preferences: *A. palmerae* for rocky (typically algal ridge) locations; *A. rotumana* for deeper-water reef flat areas, *A. robusta* for the shallow outer reef. On Enewetak atoll in the Marshall islands *A. palmerae* and *A. rotumana* are very abundant and *A. robusta* rare (Wallace, in prep.). On the Central Great Barrier Reef where there is no distinct algal ridge, *A. palmerae* is absent, any encrusting colonies being recognisable as members of an *A. robusta* population; *A. rotumana* appears as a rare species.

Within each species there is also a phenotypic component to radial corallite variation: the radials are best developed on the most freely branching parts of the colony.

These features, and the added fact that the clumsy colonies never lend themselves to the collection of a truly representative sample, have led to the naming of many species from single or few fragments. As well as the species placed in synonymy here, a number of more obscure species-names possibly belong with these species, e.g. *A. cyclopea* (Dana), *A. cuspidata* (Dana), *A. conigera* (Dana), *A. smithi* (Brook). With the current lack of geographic studies on *Acropora* it is difficult and unwise to lump these.

The separation of the three species treated here is maintained on the basis of their apparent distinctness in Great Barrier Reef populations, and pending further regional studies.

Acropora robusta (Dana, 1846)
(Plates 44, 45)

Madrepora robusta Dana, 1846, p.475, pl.39, fig.3, 3a, pl. 31, figs. 3a–c; Brook, 1893, p.42 (synonymy).

Madrepora pacifica Brook, 1891, p.465; 1893, p.39, pl.30, fig.B.

Acropora pacifica: Crossland, 1952, p.202, pl.31, fig. 2, pl.32, fig.2; Nemenzo, 1967, p.54, pl.18, fig.4.

Madrepora decipiens Brook, 1892, p.456; 1893, p.51, pl.14, figs. B to D.

Acropora decipiens: Vaughan, 1918, p.165, pl.67, figs. 2, 2a, 2b; Nemenzo, 1967, p.60.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. robusta* holotype 297.

BM: Samoa, Rev. Whitmore, *A. pacifica* holotype 1875.10.2.13.[1] Rocky Is., G.B.R. Saville Kent *A. decipiens* syntypes 1892.6.8.82; 1892.6.8.85.

QM: Big Broadhurst Reef: SW. side, reef slope: 4m, 27.iii.1973, C.W., G10190; 2·2m, 11.x.1973, C.W., G10250; 1·5m, 18.x.1973, C.W., G10191; 1m, 26.iii.1973, C.W., G10194; SW. side, Outer reef flat: 11.x.1973, C.W., G10246, 18.x.1973, C.W., G10248; 22.x.1973, C.W., G10247.

Bushy-Redbill Reef: SE. side, reef crest, 27.xii.1972, C.W., G10193; S side, reef crest; 27.xii.1972, E. Lovell, G10192; 25.xii.1972, E. Lovell, G10257; W. side, reef crest, 22.xii.1972, C.W., G10258; W. side, reef slope, 19.xii.1972, E. Lovell, G10259; NW. side, reef crest, 30.xii.1972, C.W., G10193; NNE side, reef slope, 30.xii.1972, C.W., G10193; NNE side, reef slope, 30.xii.1972, C.W., G10197.

Bowden Reef:[1] SW. side, reef crest, 15.vii.1972, C.W., G10198, G10199; slope of opening in SW. side, 26.vii.1972, C.W., G10256.

Bramble Cay: Dec. 1924, C. Hedley, G10201; Oct. 1924, C. Hedley, G10262.

Coates Reef, 13.viii.1924, 'Geranium', G10261.

Feather Reef, 11.viii.1924, 'Geranium', G10260.

Flinders Reef, Moreton Bay, W. side, 6.ix.1973, C.W., G10200.

Masthead Reef, NNE. side, reef crest, August 1974, J. Buhman, G10254, G10255.

FIELD DIAGNOSIS

Colonies have stout branches which can be vertical cones, distorted humps, or freely branching horizontal units on different parts of the same colony. Sections of the colony can be completely encrusting. Those parts of the colony on solid substrate have the solid vertical cones, but these extend horizontally and branch freely where small holes in the reef, or the reef edge itself, allow. The low, distorted rounded humps are formed in very shallow (e.g. reef crest) areas. Prominent tubular radial corallites mixed with shorter ones are obvious at the tips of the cones and branches. Common colours are bright green with deep pink branch-tips and pink-brown, yellow-brown or cream.

LABORATORY DIAGNOSIS

Laboratory difficulties occur because usually only a piece of the heavy colony is collected. Two very different fragments are illustrated in Plate 45 figs. a and e. Crossland's plate 32, fig.2, shows another shape the branches can take.

Branching pattern: This is described above. The free branches are usually 20 to 35 mm diameter, but branchlets as narrow as 10 mm can occur; maximum length measured is 250 mm. The cones may be as thick as 40 mm at the base. The humps are either solid or encrusting, taking the shape of the substrate.

Axial corallites: Outer diameter 2·5 to 3·0 mm; inner diameter 1·2 to 1·5 mm. Septation: primaries to 3/4R, secondaries to 1/4R, usually incomplete. The axial corallites are not strongly different from large radial corallites, and on the rounded humps they may be absent altogether.

Radial corallites: Tall and short radial corallites mixed. The differences between the two are emphasised at the growing tips where the tall radials may be 5 mm long. On the low humps the differences may disappear entirely. The tall radials are tubular, with rounded, oblique or dimidiate openings. Their angle of extension from the branch decreases from 90° at the base to about 45° at the tips. The short radials usually have only a small section of outer wall present. Septation is usually well-developed in the tall radials (primaries to 1/2R, secondaries to 1/3R), and less developed in the short radials (sometimes only the directives visible).

Coenosteum: Costate on corallites, reticulate with simple spines in between.

WITHIN REEF DISTRIBUTION

The species occurs only in the shallow outer flat–reef crest area, and flourishes at the windward (SE.) end of the reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

In the field this species is conspicuous and distinctive. In the laboratory the colony is poorly represented by fragments and there is the temptation to find a 'best fit' with one of the many described robust species, few of which have been described from the field. Only the most certain synonyms have been included: some of the robust species mentioned in the introduction may also be this species. The more slender free-growing branches resemble *A. intermedia*, and specimens of the two species can be confused in the laboratory (but never in the field). *A. palmerae* Wells may be synonymous. An encrusting colony of *A. robusta* with few vertical branchlets is illustrated in colour in Roughly 1936 (plate 6 upper).

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: China Sea, Philippines, Great Barrier Reef, Fiji Islands, Samoa, Marshall Islands (C.W.).

Acropora rotumana (Gardiner, 1898)
(Plate 46)

Madrepora rotumana Gardiner, 1898, p.258, pl.23, fig.2.

Acropora rotumana: Hoffmeister, 1925, p.69; Wells, 1954, p.419, p.112, fig.1–3, pl.113, figs.4, 5.

Acropora tutuilensis (part) Hoffmeister, 1925, p.71.

MATERIAL EXAMINED

USNM: Pago Pago Harbor, Tutuila, Samoa *A. tutuilensis* no. 4 (mentioned Hoffmeister, 1925); Rongerik Atoll 44477; Rongerlap Atoll 44478; Bikini Atoll, 44469, 44470, 44472, 44473, 44474, Enewetak Atoll 44475: *A. rotumana* (mentioned Wells, 1954).

QM: Big Broadhurst Reef: SW. side, outer reef flat: 14.x.1973, C.W., G10233; 22.x.1973, C.W., G10234, G10235; E. side, reef slope, 1m, 21.x.1973, C.W., G10236.

Bowden Reef: SW. side, reef crest, 15.vii.1972, C.W., G10263.

FIELD DIAGNOSIS

Mature colonies are about 1·5 m in height and width. They have a sturdy tree-like appearance due to the small number of very stout branches which have some proximal vertical growth component, then become horizontal for most of their extent, and proliferate into small branchlets at the tips. This is not the full range of shapes possible in the species. At Enewetak Atoll, for example, it can form a stalked table (Wallace, in preparation). Colours: deep pinkish-brown or apple green. (See Gardiner 1898 for detailed field diagnosis).

LABORATORY DIAGNOSIS

The fragments collected from this species are usually branch-tips with a greater or lesser amount of branch remaining. They often have a 'distorted' appearance, due to the irregular secondary branching pattern.

Branching pattern: described above.

Axial corallites: Outer diameter 2·0 to 2·5 mm (in the G.B.R. specimens); inner diameter 0·8 to 1·2 mm. Septation: primaries present to 1/2R, few secondaries, up to 1/4R.

Radial corallites: Tall and short radial corallites mixed. Tall radials extend from branch at 45° to 90° and are tubular with round, oblique, dimidiate or nariform openings. Short radials usually have less than half the wall developed, and range down to immersed. Primary septa not well developed, up to 1/3R; secondaries absent or a few just visible.

Coenosteum: Costate or pseudocostate on radials, reticulate with simple spines in between.

WITHIN REEF DISTRIBUTION

Occasional colonies found just below the reef top on the upper reef terrace or in surge channel openings on the outer reef. Elsewhere (e.g. on Enewetak Atoll) it occurs in deep-water reef flat situations.

IDENTIFICATION DIFFICULTIES AND HISTORY

This is one of the few *Acropora* species to be originally described from the field as well as from skeletal material. Both Hoffmeister and Wells regard it as a good species because of its distinctive colony shape. Gardiner states it to be 'by far the most abundant coral on the reefs of Rotuma'. It cannot be distinguished from *A. robusta* or *A. abrotanoides* on radial corallite shape.

GEOGRAPHIC DISTRIBUTION

Pacific Ocean: Great Barrier Reef, Rotuma, Samoa, Marshall Islands.

Acropora abrotanoides (Lamarck, 1816)
(Plate 47)

Madrepora abrotanoides Lamarck, 1816, p.280; Brook, 1893, p.56 (synonymy).
Acropora abrotanoides: Crossland, 1952, p.204; Wells, 1954, p.418, pl.123, figs. 1, 2.
non *Acropora abrotanoides:* Vaughan, 1918, p.166, pl.68, fig. 2.
Madrepora deformis [non Michelin]; Dana, 1846, p.484, pl.43, fig. 1.
Madrepora danai Milne Edwards and Haime, 1860, p.560.
Madrepora danae: Brook, 1893, p.57 (synonymy).
Acropora danai: Wells, 1954, p.418, pl.111, figs. 4–6.

MATERIAL EXAMINED

USNM: Tahiti, U.S. Expl. Exped., *A. danai* holotype 303 *(M. deformis* of Dana); Marshall Islands, J. W. Wells, *A. danai* 45175 (mentioned Wells 1954).

YPM: Tahiti, fragment of type (labelled *A. deformis)* 4162 (mentioned Verrill, 1864)

QM: Big Broadhurst Reef, patch reef in lagoon, 28.iii.1973, C.W., G10238.
Bushy-Redbill Reef, NW. side, reef crest, 22.xii.1972, C.W., G10239.
Bowden Reef, slope of opening in SW. side, 26.vii.1972, C. W., G10240–2.
Viper Reef, patch reefs in lagoon, 1·5m., 16.vii.1972, C. W., G10243.
Great Astrolabe Reefs, Fiji Islands, 1974, C. W., G10244.

FIELD DIAGNOSIS

Colonies occur as tufts of sturdy vertical to oblique branches with appearance roughened by the presence of numerous incipient branchlets. Colour: yellow-brown.

LABORATORY DIAGNOSIS

Branching pattern (taken from five specimens): From a basal area (usually dead) a small number of sturdy branching units is given off. Each branching unit has a small number of main branches which are vertical or almost so, and the branches may branch again. In addition, each branch is roughened by the presence of incipient branches. The longest branch is 150 mm, and the widest 40 mm.

Axial corallites (on main branches): Outer diameter 2·5 to 3·8 mm; inner diameter 0·8 to 1·2 mm. Septation: primaries present to 1/3R, secondaries sometimes complete to 1/4R.

Radial corallites: Tall and short radials mixed. Tall radials tubular with round, oblique or dimidiate openings. Those with round openings usually can be recognised as incipient axials, themselves budding radials from their circumference.

Coenosteum: Costate on radials, reticulate with simple spines in between.

WITHIN REEF DISTRIBUTION

This species seems to be restricted to upper reef areas, mainly the outer reef flat and crest, and the tops of patch reefs in deep lagoons.

IDENTIFICATION DIFFICULTIES AND HISTORY

Brook describes his specimens in detail, and apparently examined Lamarck's type, which I have been unable to locate. All other authors had meagre or immature specimens (e.g. Vaughan's 'three small immature specimens'). There are no morphological characters supporting the separation of *A. danai. A. listeri* (Brook) may also be a synonym, but its validity could be tested by a study on the Tongan reefs.

This species still remains categorized only as a group of specimens, with no field identity. The fact that it eludes categorization in the field suggests that it is not a 'good' species. The abundance of incipient branches is a poor species character, but this is at present the main feature defining this species.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Singapore, Great Barrier Reef, Marshall Islands, Tahiti.

Acropora intermedia (Brook, 1891)
(Plates 48, 49)

Madrepora intermedia Brook, 1891, p.463; 1893, p.31, pl.1, fig. C.
Acropora intermedia: Crossland, 1952, p.200, pl.32, fig. 1; Stephenson and Wells, 1956, p.16; Pillai and Scheer, 1976, p.24, pl.2, fig. 1.

MATERIAL EXAMINED

BM: Maldive Islands, *A. intermedia* syntype 1886.11.22.6.

QM: Big Broadhurst Reef, SW. side, reef slope: 2m, 11.x.1973, C. W., G11400; 2m, 26.iii.1973, C. W., G11295; 3m, 28.iii.1973, C.W., G11310; 5m, 25.ii.1973, C.W., G11302; 5.3m, 13.x.1973, C.W., G11576; 6m, 25.iii.1973, C. W., G11301; 6·1m, 13.x.1973, C. W., G11582; 6·3m, 13.x.1973, C. W., G11579; 7·6m, 13.x.1973, C. W., G11575; 7·7m, 14.x.1973, C. W., G11578, G11580; 8m, 26.iii.1973, C. W., G11300; 8·3m, 15.x.1973, C. W., G11581; 8·6m, 15.x.1973, C. W., G11577; SW. side, outer reef flat: 11.x.1973, C. W., G11308, G11583; 22.x.1973, C. W., G11327, G11584; SW. side, floor of surge channel opening: 20.x.1973, C. W., G11307, G11309, G11585.

Bowden Reef, SW. side, upper reef slope, 26.vii.1972, C. W., G11316.

Bushy-Redbill Reef, S. side, reef slope, 3m, 27.xii.1972, C. W., G11311; adjacent Redbill Is., reef crest, 18.xii.1972, C. W., G11305; NW. side, first reef crest, 22.xii.1972, C. W., G11312, G11313; NNE. side, reef slope, Jan. 1973, C.W., G11391.

Heron Is., W. side, reef flat, 6.vii.1973, Y. Loya, G11297.

FIELD DIAGNOSIS

Colonies vary from small clumps to small thickets of around 3m diameter and are sturdy-branched arborescent. The radial corallites are a mixture of tall and short tubular and are obvious under water. Colours are cream to pale brown, pale green or greenish brown or bright blue.

LABORATORY DIAGNOSIS

Branching pattern: Branches are given off at wide angles (45° to 90°) and branch width varies from 15 to 25 mm. Branches usually taper strongly.

Axial corallites: From barely exert to 2 mm exert. Outer diameter 3·0 to 4·0 mm (in QM specimens); inner diameter 1·1 to 1·5 mm. Septation: primaries well developed, often reaching 3/4R, secondaries usually present, up to 1/4R.

Radial corallites: Tall and short radial corallites are mixed. The tall radial corallites are tubular, up to 5 mm long, with round, oval or dimidiate openings and usually extend from the branches at 90° to 45°. Lower wall may be slightly thickened. Primary septa are developed up to 2/3R, and secondaries present, up to 1/4R. The smaller radials are tubular appressed or emergent, or sub-immersed, and oriented with their openings facing in random directions to the branch.

Coenosteum: Strongly costate on radial corallites, open reticulate with simple spines between radials.

WITHIN REEF DISTRIBUTION

Middle and outer reef flat, upper reef slope to about 12 m, surge channel floors and sandy bottoms around patch reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

This species appears to be morphologically similar in radial corallite and coenosteal features to the *A. robusta* group. Many specimens are difficult to place exactly in either this species, *A. formosa* or *A. grandis*, and clearly all three species require further field study.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Maldives, Great Barrier Reef.

Acropora grandis (Brook, 1892)

(Plate 50 A,B)

Madrepora grandis Brook, 1892, p.457; 1893, p.42, pl.1, figs. A, B.

Acropora grandis: Crossland, 1952, p.202, pl.31, figs. 1, 3, 4.

MATERIAL EXAMINED

BM: Palm Island, Saville-Kent, *A. grandis* syntype 1892.6.8.60; Herring Island, Bowen, Saville-Kent, *A. grandis* 1892.6.8.314; Rocky Island, Saville-Kent, *A. grandis* var. 1892.6.8.261.

QM: Big Broadhurst Reef, SW. side, reef slope: 6m, 25.iii.1973, C.W., G11320; 6·1m, 13.x.1973, C.W., G11366; 7m, 27.iii.1973, C.W., G11299; 7·1m, 13.x.1973, C.W., G11367; 7·7m, 14.x.1973, G11368.

Bushy-Redbill Reef, NW. side, first reef crest, 22.xii.1972, C.W., G11306, G11315, G11317.

Darley Reef, patch reef in lagoon, 4 m, 24.iii.1973, C.W., G11298.

FIELD DIAGNOSIS

Openly arborescent colonies have scattered radial corallites of mixed size with large obvious openings, and may be brown, bright blue, bright purple or even greenish-brown with blue tips.

LABORATORY DIAGNOSIS

Branching pattern: Branches commonly spread at from 60° to 40° . Branches are from 10 to 30 mm thick, and may be as long as 30 cm without branching. They usually taper gradually.

Axial corallites: Up to 3 mm exert; outer diameter 2·5 to 3·5 mm; inner diameter 1·0 to 1·7 mm. Septation: both cycles may be present, the primary septa up to 1/3R, the secondary up to 1/4R.

Radial corallites: Two sizes of radial corallite occur. Towards the branch tips the large radials reach 3 mm length, but elsewhere they are much shorter than this. The openings are round to oval, and are directed straight out from the branch, or nearly so. The septa are poorly developed: both cycles may be completely absent, or primary septa may be present up to 1/4R, plus a few secondaries.

Coenosteum: The surface has a light, crumbly appearance, the coenosteum being costate or reticulate on the radial corallites and open reticulate between.

Identification Difficulties and History

This species has only been recorded from the Great Barrier Reef, and in my experience it is not common on the outer reefs, but is more characteristic of the fringing reefs of the continental islands. Crossland treats the species in detail. Although this species is morphologically different from *A. formosa* and *A. intermedia* in many features, there remains a suspicion that it may be related to one or other of these, and all three species require further study in the field.

Geographic Distribution

Recorded from the Great Barrier Reef only.

Acropora formosa (Dana, 1846)

(Plates 51, 52)

Madrepora formosa Dana, 1846, p.473, pl.31, fig.2a, 2b, pl.38, fig.4.

Acropora formosa: Hoffmeister, 1925, p.55, pl.8, figs.1-3 (Synonymy); Wells, 1950, p.35; 1954, p.415, pl.102, figs.1-9, pl.103, figs.1-5, pl.104, fig.4 (synonymy); Stephenson and Wells, 1956, p.14 (synonymy); Nemenzo, 1967, p.61, pl.21, fig.3; Pillai and Scheer, 1974, p.453; Pillai and Scheer, 1976, p.23.

Madrepora brachiata Dana, 1846, p.474, pl.38, fig.3, 3a, 3b.

Madrepora gracilis Dana, 1846, p.482, pl.41, fig.3, 3a, 3b.

Madrepora nobilis Dana, 1846, p.481, pl.40, fig.3, 3a.

Acropora nobilis: Hoffmeister, 1925, p.59, pl.11, fig.1 (synonymy); Wells, 1954, p.416, pl.104, figs.1, 2; Nemenzo, 1967, p.62, pl.21, fig.5.

non *Acropora nobilis:* Pillai and Scheer, 1974, p.453, fig.3c.

Acropora laevis (part) Crossland, 1952, p.230, pl.45, figs.1, 2.

Material Examined

USNM: Fiji Islands, U.S. Expl. Exped., *A. formosa* syntypes 888, 282; Fiji Islands, U.S. Expl. Exped., *A. gracilis* holotype 333; Sooloo Sea, U.S. Expl. Exped., *A. brachiata* holotype 295; Singapore, U.S. Expl. Exped., *A. nobilis* holotype 427.

QM: Big Broadhurst Reef: SW. side, reef slope: 1·6 m, Oct. 1973, C.W., G11388; 2 m, 20.x.1973, C.W., G11339; 2 m, 11.x.1973, C.W., G11343; 2 m, 26.iii.1973, C.W., G11398, G11405; 2·3 m, 20.x.1973, C.W., G11349, G11353, G11360; 2·6 m, 22.x.1973, C.W., G11346; 2·8 m, 12.x.1973, C.W., G11356; 3·8 m, 12.x.1973, C.W., G11335, G11347; G11362; 5·3 m, 13.x.1973, C.W., G11365; 5·7 m, 23.x.1973, C.W., G11348, G11364; 6 m, 25.iii.1973, C.W., G11320; 6 m, 13.x.1973, C.W., G11336; 6·1 m, 13.x.1973, C.W., G11363, G11373, 6·3 m, 20.x.1973, C.W., G11334; 6·3 m, 23.x.1973, C.W., G11361; 6·3 m, 13.x.1973, C.W., G11369, G11371; 7·6 m, 13.x.1973, C.W., G11367; 7·7 m, 14.x.1973, C.W., G11333, G11341, G11368, G11372; 7·8 m, 14.x.1973, C.W., G11330, G11337, G11358, G11370; 8·1 m, 22.x.1973, C.W., G11340; 8·7 m, 15.x.1973, C.W., G11352; 12·4 m, 23.x.1973, C.W., G11363; 12·5 m, 17.x.1973, C.W., G11350, G11355; 28.iii.1973, C.W., G11396; SW. side, outer reef flat: 20.x.1973, C.W., G11331, G11354; 11.x.1973, C.W., G11359; 18.x.1973, C.W., G11344; SW. side, reef crest: 1·3 m, 22.x.1973, C.W., G11345; 1·3 m, 23.x.1973, C.W., G11351; SW. side, surge channel, 7·5 m, 20.x.1973, C.W., G11342.

Bowden Reef: SW. side, upper reef slope: 26.vii.1972, C.W., G11318, G11319, G11322, G11323, G11325; floor of opening in SW. side, 5 m, 26.vii.1972, C.W., G11380, G11381, G11375.

Bushy-Redbill Reef: NW. side, first reef crest: 23.xii.1972, E. Lovell, G11374, G11376, G11377; 22.xii.1972, C.W., G11306, G11378, G11379, G11384, G11385.

Darley Reef, patch reef in lagoon: 1 m, 24.iii.1973, C.W., G11401; 4 m, 22.iii.1973, C.W., G11404.

Viper Reef, July 1972, C.W., G11326, G11394.

Field Diagnosis

This is the common, thicket-forming arborescent species with numerous small tubular radial corallites, commonly coloured cream to brown, less often bright blue or blue-tipped.

Laboratory Diagnosis

Branching pattern: Branching is always openly arborescent. Branch diameters vary from slender (10 mm) to thick (35 mm).

Axial corallites: From barely exert to 1·5 mm exert. Outer diameter 2·0 to 2·8 mm; inner diameter 0·8 to 1·2 mm. Septation: Primary septa well developed, up to 1/2R; secondary septa usually present, but poorly developed, up to 1/4R.

Radial corallites: Tubular, varying from sub-immersed to 5 mm, prominent, with openings from round to sharply oblique, the corallites oriented at anything from 90° to the branch to fully appressed. Septal development varies greatly, but most commonly secondary septa are absent or only poorly represented.

Coenosteum: Costate or neatly arranged simple spines on radial corallites, reticulate with simple spines between.

Within Reef Distribution

Reef crest and slope to position of surge channel floor (10–12 m), lagoonal floors and lagoonal patch reefs (may even form entire basis of lagoonal patch reefs), middle reef flat, occasional small colonies on outer reef flat, fringing reefs.

Identification Difficulties And History

The interpretation that I have placed on this species follows that of Wells (1954) and Stephenson and Wells (1956) preceded by Hoffmeister (1925). The reader is referred to their discussions. The species, as interpreted, may well be a mixture and there is certainly no satisfactory interpretation of variability (for example slender and sturdy branched thickets may occur adjacent to each other). There is some suggestion (J. Collins, pers. comm.) that the sturdy branched colonies may be old colonies. The colonies offer no readily perceptable clues in the field. If there are several species involved, the mosaic of their variabilities may be adding to the confusion.

This species requires individual attention, and the only assistance that can be offered at present is in distinguishing from the field the other 'easily recognizable' arborescent species: *A. haimei, A. microphthalma, A. intermedia, A. aspera, A. pulchra* and *A. splendida. A. acuminata* Verrill does not seem to occur in the areas studied.

Geographic Distribution

Indo-Pacific: Ceylon, Cocos-Keeling, Amboina, New Ireland, Great Barrier Reef and Torres Straits, Fiji Islands, Samoa, Marshall Islands, Tahiti. (Further Indian Ocean localities in Pillai and Scheer, 1974).

Acropora splendida Nemenzo, 1967
(Plates 53, 54)

Acropora splendida Nemenzo, 1967, p.51, pl.17, fig.2.

Material Examined

UP: Hundred Islands, Pangasiman, 1959, A. de la Cruz, holotype C931.

USP: Fiji Reefs 3916.

QM: Big Broadhurst Reef, SW. slope: 23·5 m, 17.x.1973, C.W., G8715; 15 m, 16.x.1973, C.W., G8716; 9·7 m, 15.x.1973, C.W., G8714; 8 m, 28.iii.1973, C.W., G8704–6; 7·8 m, 15.x.1973, C.W., G8713; 7·5 m, 15.x.1973, C.W., G8712; 7 m, 26.iii.1973. C.W., G8701, G8702; 6·9 m, 14.x.1973, C.W., G8710, G8711; 6·6 m, 14.x.1973, C.W., G8708, G8709; 6 m, 25.iii.1973, C.W. G8699; 5 m, 26.iii.1973, C.W., G8700; 4·9 m, 13.x.1973, C.W., G8707; 3 m, 27.iii.1973, C.W., G8703.

Bowden Reef: Lagoon slope, Nov. 1972, R. Pearson, G8696; floor of opening in SW. end of reef, 26.vii.1972, C.W., G8697.

Darley Reef, patch reefs in lagoon, 4 m, C.W., G8698.

Field Diagnosis

Colonies are large (commonly around 1m diameter) bowl to bracket shaped, the shape given by long openly arborescent branches which curve and divide to varying extent, depending on their position within the colony. The bowl shape occurs in specimens on flat surfaces and attachment becomes lateral with steepness of the attaching surface. With increasing depth the colonies become flatter and smaller. A specimen collected at 23·5 m (G8715) is completely horizontal. Common colours are dark olive green with paler green tips to the branches, dark blue with paler blue tips, brown with pale blue tips, brown or cream.

Laboratory Diagnosis

Branching pattern: As the colonies are large, fragments are usually collected. These are often easily confused with other large arborescent species. Specimens from the centre of the bracket usually have long curving branches with little secondary branching; those from the edge zone are more proliferous, with shorter branches and some fusions, and may be flat underneath.

Axial corallites: Outer diameter 2·0 to 3·5 mm; inner diameter 0·8 to 1·5 mm. Septation: primaries to 2/3R, all or some secondaries present to 1/2R.

Radial corallites: Tubular, projecting from branches at 90° (less towards tips) with openings round, oval, nariform, or dimidiate. Radials are usually evenly sized and distributed but smaller radials may be present amongst these, and their openings may be variously directed. Septal development varies, but primaries are usually present to 1/3R, and some secondaries visible.

Coenosteum: Usually neatly costate on radial corallites, open reticulate with simple or laterally flattened spines in between.

Within Reef Distribution

Reef slope from a few metres below crest to limits of *Acropora* distribution (species no.3 in Wallace 1975); deep water lagoonal patch reefs; fringing reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

Nemenzo's species was based on a single fragment, and he was not aware of the shape of the colony. The species seems to have been neglected in all other literature, although it is possible that fragments may have been identified with other arborescent species. This is the only *Acropora* with an 'arborescent bracket' shape and it is very distinctive in the field. Laboratory specimens without field notes become unnecessarily confused with other arborescent 'problems'.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Philippines, Great Barrier Reef, Fiji Islands, (common in Fijian fringing reefs, from my personal observations), Palau (M. Pichon, pers. comm.).

Acropora horrida (Dana, 1846)
(Plates 55, 56)

Madrepora horrida Dana, 1846, p.472, pl.39, fig.2, 2a; Verrill, 1864, p.41; Brook, 1893, p.188 (synonymy).

Acropora horrida: Wells, 1954, p.417, pl.107, fig.1.

Madrepora angulata Quelch, 1886, p.160; Brook, 1893, p.195.

Madrepora inermis Brook, 1891, p.462; 1893, p.194, pl.29, figs. A, B.

Acropora inermis: Wells, 1954, p.431.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. horrida* holotype 291.

YPM: Fiji Islands, U.S. Expl. Exped., *A. horrida* fragment of type 2013.

BM: Zamboangana, 'Challenger' Exped., *A. angulata* holotype 1886.12.9.233; South Seas, purchased, *A. inermis* syntypes 1841.12.11.6, 1841.12.11.7.

QM: Big Broadhurst Reef: SW. side, reef slope: 7·3 m, 15.x.1973, C.W., G8755; 7·6 m, 23.x.1973, C.W., G8757, G8758; 5 m, 27.iii.1973, C.W., G8759; 8 m, 28.iii.1973, C.W., G8761; 4 m, 28.iii.1973, C.W., G8763; SW. side, surge channel, 8·5 m, 20.x.1973, C.W., G8756.

Bowden Reef: Slope of opening in SW. side: 26.vii.1972, C.W., G8764–7; 1–5 m, 26.vii.1972, C.W., G8768; 1–2 m, 26.vii.1972, C.W., G8769; 25.vii.1972, C.W., G8771; floor of opening in SW. side, 26.vii.1972, C.W., G8770.

Bushy-Redbill Reef: NW. side, floor outside slope: 12 m, 30.xii.1972, C.W., G9076; 8 m, 31.xii.1972, C.W., G9077; NW. side, middle reef flat, 22.xii.1972, C.W., G9078; 20.xii.1972, C.W., G9079; NW. side, reef patches, 12 m, 14.vi.1975, C.W., G9080; W. side, reef slope: 8 m, 3.vi.1975, C.W., G9081; Dec. 1972, C.W., G8774; adjacent Redbill Is., reef slope, 5 m, 2.vi.1975, C.W., G9084.

Darley Reef, patch reef in lagoon: 22.iii.1973, C.W., G8773; 6 m, 22.iii.1973, C.W., G8762, 23.iii.1973, C.W., G8760.

Heron Island, W. side, reef slope, July 1973, C.W., G8773.

Fiji Islands, Great Astrolabe Reefs (Kadavu), W.side of Yaukuvi Levu fringing reef, 1.ii.1974, C.W., G9085.

FIELD DIAGNOSIS

Occurs as sprawling arborescent to shrubby patches. Branches are slender and have a ragged appearance due to the scattered distribution of the radials and their poorly-formed walls. The polyps of this coral are usually extended, an unusual feature in *Acropora*. The colour is usually light powder-blue to light grey.

LABORATORY DIAGNOSIS

Branching pattern: Branching is primarily open-arborescent. Specimens from loose substratum areas tend towards horizontal primary growth; those from firmer substrates are more upright. Main branches are 7 to 15 mm in width, and taper gradually towards the tips. Secondary branchlets are irregularly sized and placed. They can be short, scattered twigs which alter the shape of the colony little, or bundles of branchlets which give a shrub-like appearance, or bottlebrush formations of subequal length arranged all over the branches.

Axial corallites: Outer diameter 1·6 to 2·3 mm; inner diameter 0·6 to 1·2 mm. Septation: Primary septa present, up to 2/3R, secondary cycle poorly developed, usually a few septa just visible.

Radial corallites: Scattered, sub-immersed to emergent tubular, sometimes appressed, with round openings. Walls are thin and very fragile around the opening. Primary septa developed, up to 1/3R, secondary septa usually absent, or one or two just visible.

Coenosteum: Open reticulate with simple to forked spines, both on corallites and between.

WITHIN REEF DISTRIBUTION

This species occurs where there is some constant water cover, down to at least 15 m, and apparently favours high sediment areas, i.e. deeper reef flat areas, reef slopes, rubble and sandy bottom areas around patch reefs and on surge channel floors. It occurs with *A. vaughani* in the deeper areas.

IDENTIFICATION DIFFICULTIES AND HISTORY

The species is distinctive in the field because of the extended polyps, ragged appearance and unusual colouring. The extended polyps also give it a silky sheen. Laboratory differences from *A. vaughani* are explained by Wells 1954 (p.417). Brook's *A. inermis* specimens are apparently slender branches of this species. Quelch's *A. angulata* is named from a single branch tip.

Geographic Distribution

Indo-Pacific: Philippines, Great Barrier Reef, Fiji Islands, Marshall Islands.

Acropora vaughani (Wells 1954)
(Plate 57)

Acropora vaughani Wells, 1954, p.416, pl.105, fig. 1, pl.106, figs. 1–8, pl.107, figs. 2–6.

Material Examined

USNM: Bikini lagoon, 18 fms, holotype 44452; Seaward slope, Bikini Atoll, 21–25 fms, paratype 44457.

QM: Big Broadhurst Reef, SW. side, reef slope: 9·8m, 16.x.1973, C.W., G10264; 8·1m, 14.x.1973, C.W., G10265; 7m, 13.x.1973, C.W., G10266; 6·1m, 13.x.1973, C.W., G10267, G10268; 3m, 27.iii.1973, C.W., G10269; 7m, 28.iii.1973, C.W., G10270; 8m, 28.iii.1973, C.W., G10271.

Bushy-Redbill Reef, NNE. side, off-reef floor, 12m, 30.xii.1972, C.W., G10272.

Field Diagnosis

Occurs as scattered 'shrubby arborescent' patches, particularly on areas of loose bottom material (sand or rubble). Scattered short final branchlets are given off from the main branches. Colour is usually cream or pale brown.

Laboratory Diagnosis

Branching pattern: Branching is basically arborescent, but the length and positioning of secondary branches varies greatly. Branch widths are from 10 to 20 mm. Secondary branches (or 'branchlets') can be regularly arranged along the main branches, or scattered. In general, the slender main branches tend to be more proliferous than the sturdy ones.

Axial corallites: Outer diameter: 1·6 to 2·5 mm; inner diameter: 0·6 to 0·9 mm Septation: both cycles usually complete, the primaries up to 2/3R, secondaries up to 1/4R.

Radial corallites: Tubular with round or occasionally oval to nariform openings. They are unequal in length and orientation (usually oriented within a range 45° to 90°, except towards basal areas, where they may be appressed).

Coenosteum: Spines are distributed evenly over corallites and inter-corallite areas. In heavily calcified specimens these have elaborated tips; in less calcified specimens the tips are simple to laterally flattened.

(For more detailed laboratory diagnosis see Wells, 1954).

Within Reef Distribution

From about 3m to 15m on reef slope, deep-water lagoons, and patch reef areas, on rubble or sandy floors, fringing reefs. Usually it occurs with *A. horrida* (Dana), from which it can easily be distinguished, on the Great Barrier Reef, because *A. vaughani* is more sturdy, does not usually extend the polyps in daylight, and is commonly cream or pale brown, while *A. horrida* is pale blue or grey. The upper range is more limited than for *A. horrida,* which can occur in some reef flat situations.

Identification Difficulties and History

The appearance of the branchlets can be very varied (see Wells), but with good field notes the species can be identified without confusion with other arborescent species.

Geographic Distribution

Pacific: Marshall Islands, Great Barrier Reef.

Acropora pulchra (Brook, 1891)
(Plates 58, 59, 60C)

Madrepora pulchra Brook, 1891, p.468; 1893, p.44, pl.28, fig. A.

Madrepora pulchra var. *stricta* Brook, 1893, p.44, pl.28, fig. B.

Madrepora pulchra var. *alveolata* Brook, 1893, p.45, pl.28, fig. C.

Acropora pulchra: Vaughan, 1918, p.162, pl.66, figs. 3, 3a; Crossland, 1952, p.203; Stephenson and Wells, 1956, p.17.

Acropora pulchra var. *stricta:* Crossland, 1952, p.204, pl.34, fig. 2.

Acropora pulchra var. *alveolata:* Vaughan, 1918, p.162, pl.66, figs. 1, 2; Crossland, 1952, p.203.

Material Examined

BM: Keeling Is., *A. pulchra* holotype 1884.2.16.1.

QM: Bushy-Redbill Reef, adjacent Redbill Is., reef flat: 7.vi.1975, C.W., G11102, G11105; 11.vi.1975, C.W., G11097, G11103, G11104; 12.vi.1975, C.W., G11093, G11095, G11096, G11100, G11101.

Heron Island, W. side, reef flat: 2.vii.1973, Y. Loya, G11117; 3.vii.1973, C.W., G11120; July 1973, C.W., G11115; G11119, 11.xii.1973, C.W., G11111, G11116, G11121, G11122; 15.xii.1973, C.W., G11118.

Fiji Islands, Great Astrolabe Reefs, Feb. 1974, C.W., G11123–5.

Low Isles, August 1954, W. Stephenson (Stephenson and Wells 1956): G2617–20; G2699–G2712, G2715, G2716, G2721–5.

North West Island, C. Hedley, 3–4 June 1924, G.B.R.C. 170.

FIELD DIAGNOSIS

Colonies of this species are arborescently branching, and can vary in overall shape from open thickets to compact corymbose form. Small radial corallites with oblique apertures give the branch surface a smoother appearance than that of other arborescent or corymbose species. Colour is pale to dark brown, often with pale blue tips.

LABORATORY DIAGNOSIS

Branching pattern: The angle of emergence, length, and width of branches varies widely, as the plates show. Branch widths are from 7 to 15 mm, and the overall general colony form can be anything from an arborescent thicket to a neatly caespito-corymbose clump.

Axial corallites: 1 to 2 mm exert; external diameter 2·0 to 3·5 mm, internal diameter 0·6 to 1·2 mm. Septation: primary septa well developed, up to 2/3R, secondary septa absent or poorly represented, occasionally all present, up to 1/4R.

Radial corallites: Mixed sizes, all very small, project at 90° from branch, upper wall poorly developed, lower wall extended and lip-like. The opening is oval to dimidiate. Primary septa may be present to 2/3R, or may be just visible; secondary septa not usually visible, or a few may be present to 1/4R.

Coenosteum: Costate on radial corallites, openly reticulate to costate between. General appearance is light and spongy.

WITHIN REEF DISTRIBUTION

This is a reef flat species, occurring particularly on the inner and middle reef flat. It occurs with *A. aspera*, often in close association, as plate 60C shows.

IDENTIFICATION DIFFICULTIES AND HISTORY

Brook (1893) described the radial corallities well and his descriptions should be consulted. The main problem with this species is seen when it occurs with *A. aspera*. The two species show similar colony shape variations, apparently in response to similar environmental conditions. Although the radial corallites are different in both shape and size, colonies sometimes appear to have a mixture of characteristics of both species. This problem was encountered on Redbill reef flat, at places where populations of the two species intermingled: some colonies suggest a hybrid appearance. It is possible that some of Vaughan's *A. pulchra* specimens were *A. aspera*.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Cocos-Keeling Islands, Great Barrier Reef.

Acropora aspera (Dana, 1846)
(Plates 60, 61, 62)

Madrepora aspera Dana, 1846, p.468, pl.38, fig. 1, 1a, 1b; Brook, 1893, p.62 (synonymy).

Acropora aspera: Crossland, 1952, p.205, pl.33, figs. 2, 3; Nemenzo, 1967, p.65.

Madrepora hebes Dana, 1846, p.468, pl.35, fig. 5; Brook, 1893, p.128 (synonymy).

Acropora hebes: Vaughan, 1918, p.174, pl.73, figs. 2, 2a, pl.74, figs. 1, 2, 2a, 2b, pl.13, fig. 6; Hoffmeister, 1925, p.57, pl.9, figs. 3a, 3b; Wells, 1950, p.36; Crossland, 1952, p.217; Wells, 1954, p.423, pl.104, fig. 3; Stephenson and Wells, 1956, p.14; Nemenzo, 1967, p.64, pl.22, fig. 1.

Madrepora cribripora Dana, 1846, p.470, pl.31, fig. 1, 1a–1c; Brook, 1893, p.123.

Madrepora manni Quelch, 1886, p.150, pl.9, fig. 1, 1a; Brook, 1893, p.63 (synonymy).

Acropora manni: Faustino, 1927, p.263, pl.85, figs. 6, 7; Nemenzo, 1967, p.63.

Acropora luzonica Verrill, 1902, p.231, pl.36c, fig. 4, pl.36F, fig. 9.

?Madrepora arabica Milne Edwards and Haime, 1860, p.145; Brook, 1893, p.66 (synonymy).

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. aspera* holotype 285; Fiji Islands, U.S. Expl. Exped., *A. hebes* syntypes 287, 286; Rewa River Mouth, Fiji Islands, U.S. Expl. Exped., *A. cribripora* holotype 289.

YPM: Manilla Bay, Luzon, Philippines *A. luzonica* holotype 1809.

PM: Mer Rouge, *A. arabica* holotype 331.

QM: Big Broadhurst Reef: S. side, surge channel on outer flat, 2 m, 21.x.1973, C.W., G10928; patch reef in lagoon, 28.iii.1973, C.W., G10929, G10930; SW. side, reef slope, 18.x.1973, C.W., G10962.

Bushy-Redbill reef: W. side, middle reef flat, 14.vi.1975, C.W., G10947; N. side, inner flat-algal bank area, 6.vi.1975, C.W., G10937–41, G10943, G10960, G10961; adjacent Redbill Is., reef flat, 7.vi.1975, C.W., G10944–6.

Bowden Reef, SW. side, reef slope, 1 m, 15.vii.1972, C.W., G10925.

Heron Island: July 1973, C.W., G10849–G10854; G10913–G10917; G10921; W. side, inner reef flat, 11.xii.1973, C.W., G10860–2; W. side, reef flat: 15.xii.1973, C.W., G10886–92; 17.xii.1973, C.W., G10893, G10896; N. side, reef flat, 11.xii.1973, C.W., G10855; N. side, reef flat (solid area), 14.xii.1973, C.W., G10883–5; N. side, inner reef flat, 11.xii.1973, C.W., G10856, G10857; N. side, middle reef flat, 11.xii.1973, C.W., G10858; S. side, outer reef flat, 12.xii.1973, C.W., G10865–72; SW.side, outer reef flat, 13.xii.1973, C.W., G10873–81; WSW. side, outer reef flat, 12.xii.1973, C.W., G10864; SE. side, outer reef flat, 17.xii.1973, C.W., G10897–902.

Low Isles, 1975, C. Limpus, G10931.

Masthead Reef, reef flat, August 1974, J. Buhmann, G10926.

Michaelmas Cay, 1975, C. Limpus, G10932, G10933.

Maer Island, Murray Island Group, N. side, outer reef flat, 17.vii.1974, G. Ingram, G10927.

Bramble Cay, Oct. 1924, C. Hedley, G.B.R.C. 7, 93–7, 149–52, 168, 169, 211.

Feather Reef, 11.viii.1924, 'Geranium', G.B.R.C. 181.

Ellison Reef, 25.vii.1924, Paradice, G.B.R.C. 2–6, 54–67, 176.

Surprise and Flora Reefs, Sept. 1924, 'Geranium', G.B.R.C. 8, 9, 12, 13, 16, 19–21, 24, 28.

Fiji Islands: Makaluvau Reef, 10.i.1974, C.W., G10955, G10957; Great Astrolabe Reefs, Feb. 1974, C.W., G10949–54.

Field Diagnosis

This is a basically arborescent species in which the colonies show considerable phenotypic flexibility. Different colonies or parts of a colony can have long, slender spreading branches with scattered radial corallites or shorter thicker branches, even to the extent of appearaing corymbose, with crowded corallites. Radial corallites are in two sizes and have poorly developed walls. Colours are commonly pale blue-grey, green-grey, or cream, less commonly bright blue. It is a characteristic of this species on the Great Barrier Reef that specimens, when collected, exude large quantities of mucous.

Laboratory Diagnosis

Branching pattern: Ranges from open branching (at 90°) to closed branching, the branches being given off vertically to obliquely to give a corymbose appearance. Branch widths vary from 10 to 15 mm.

Axial corallites: From non-exert to 3 mm exert. Outer diameter 3·5 to 4·5 mm; inner diameter 1·3 to 1·8 mm. Septation: Both septal cycles usually present, the primaries up to 2/3R, the secondaries up to 1/3R.

Radial corallites: Two sizes of radial corallite are mixed. These are best regarded as 'large diameter' and 'small diameter', although the 'large diameter' radials are also always more prominent. The 'large diameter' radials have round openings, upper wall undeveloped, and lower wall short and thickened, or extended horizontally as a lip, which may be rounded or pointed. The 'small diameter' radials are sub-immersed to immersed. In general colonies with short, thick branches tend to have the radial corallites crowded with short, thick lips, and colonies with long slender branches have radial corallites scattered, with thin pointed lips. On the larger radials primary septa are usually visible up to 1/3R; and secondary development varies, but often some septa are present, up to 1/4R.

Coenosteum: Open reticulate with simple to laterally flattened spines between radials, costate on radials.

Within Reef Distribution

This is a reef flat species, occurring from the inner reef flat to outer flat, but not on elevated outer flat platforms. It can occur in very silty and coral-depauperate areas and shallow lagoonal situations.

Identification Difficulties and History

The two species *'A. hebes'* and *A. aspera* are both 'well known' and typical specimens of the two species appear very different from each other. However, the relationship of the two can be easily established in the field. The placing of less known synonyms is more difficult, and possibly there are other species names still to be included. Two major problems of identification occur with this species. The first is in separating some corymbose specimens from sturdy specimens of *A. millepora,* the second in separating some arborescent colonies from arborescent *A. pulchra.* (see discussions for these species).

Geographic Distribution

Indo-Pacific: ?Red Sea, Cocos-Keeling, Philippines, Great Barrier Reef, Fiji Islands, Samoa, Marshall Islands, Tongan Islands (C.W.).

The '**Acropora corymbosa**' Group

A number of species have radial corallites with scale-like lips, and a disproportionately large number of species descriptions have been written to cover these species.

In the following list there is barely a species which has not been placed in synonymy or compared with, or mistaken for some other species in the list, and of the 'real' species that exist, each has been placed under a number of the commonest names. The main species concerned are: *A. corymbosa* (Lamarck), *A. efflorescens* (Dana), *A. cytherea* (Dana), *A. spicifera* (Dana), *A. hyacinthus* (Dana), *A. surculosa* (Dana), *A. millepora* (Ehrenberg), *A. prostrata* (Dana), *A. subulata* (Dana), *A. convexa* (Dana), *A. armata* (Brook), *A. reticulata* (Brook), *A. arcuata* (Brook), *A. cytherella* (Verrill), *A conferta* (Quelch), *A. pectinata* (Brook), *A. recumbens* (Brook), *A. squamosa* (Brook).

The most widely applied name on this list is the oldest, *A. corymbosa* (Lamarck). Three contenders for this name are the species I am identifying as *A. hyacinthus*, *A. cytherea* and *A. millepora*. Older interpretations of this species tended to favour an *A. cytherea*-like appearance. A specimen regarded as the type (of *A. corymbosa)* was seen and described by Brook (1893) who points out the similarity between *A. cytherea* and this. Professor J. Wells has kindly shown me photographs of (apparently) this type, sent to him some time ago by the Paris Museum. Neither my own search of the Lamarck collection, nor a later search by Dr J. P. Chevalier could locate a type.

My opinion is that the currently accepted view of this species (e.g. Wells 1954) is morphologically between *A. millepora* and *A. hyacinthus*. While it is possible that this is a true species, at least some of the specimens so identified are other species: for example Stephenson and Wells 1956 mention two specimens, of which one (G2626) is a small reef flat specimen of *A. hyacinthus*, and the other (G2623) a stunted *A. millepora*.

The species has been mentioned by many other authors since 1893, e.g. von Marenzeller (1907), Vaughan (1918), Hoffmeister (1925, 1929), Thiel (1932), Crossland (1952), Nemenzo (1967), Pillai and Scheer (1976), and is regarded as having a wide Indo-Pacific distribution. In the interests of taxonomic stability, I am not attempting to trace its synonyms on the basis of a regional study, but I feel a caution must be taken that the interpretation of this species by the various authors may not coincide. Hopefully, with extensive regional studies, this group will be given a more complete taxonomic treatment.

The species which I interpret as *A. hyacinthus* and *A. cytherea* are dominant members of the reef-front assemblage. They are the early colonizers and often influence the effective shape of some reef areas. Special problems are associated with the separation of these species at their overlapping limits. *A. spicifera* has not been present in my areas of study. *A. millepora* is a common reef-flat species which has usually (on the Great Barrier Reef) been identified as its synonym, *A. squamosa*.

Acropora hyacinthus (Dana, 1846)
(Plates 63, 64A-C, 65, 66A,B)

Madrepora hyacinthus Dana, 1846, p.444, pl.32, fig.2; Brook, 1893, p.107 (synonymy).

Acropora hyacinthus: Thiel, 1932, p.123, pl.16, fig.2; 1933, p.20; Stephenson and Wells, 1956, p.16; Nemenzo, 1967, p.115, pl.33, fig.1; Pillai and Scheer, 1976, p.29.

Acropora hyacinthus (?part): Hoffmeister, 1925, p.64, pl.13, fig.3; Wells, 1954, p.421.

?Madrepora conferta Quelch, 1886, p.164, pl.10, fig.3; Brook, 1893, p.108.

Madrepora pectinata Brook, 1892, p.460; 1893, p.95, pl.27, fig.D, E.

Madrepora recumbens Brook, 1892, p.461; 1893, p.106, pl.27, fig.F.

Acropora pectinata: Vaughan, 1918, p.172, pl.71, fig.1, 1a-1c, 2; Thiel, 1932, p.119, pl.14, fig.4 (synonymy).

Acropora corymbosa (part): Stephenson and Wells, 1956, p.12.

Madrepora surculosa var. *turbinata* Dana, 1846, p.446; Brook, 1893, p.200 (synonymy).

Madrepora turbinata: Verrill, 1864, p.42.

Acropora turbinata: Verrill, 1902, p.242.

Note: This synonymy does not include all references to synonyms, as their interpretations are difficult to trace.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. hyacinthus* holotype 246; Tahiti, U.S. Expl. Exped., *A. surculosa* (var. *turbinata)* syntype 251.

YPM: Tahiti, *A surculosa* var. *turbinata* type fragment 2017.

BM: Fiji Reefs, Challenger, *A. conferta* holotype 1885.2.1.12; Thursday Is., Saville Kent, *A. pectinata* syntype 1892.6.8.155; Low Woody Is., G.B.R., *A. recumbens* (var.) 1892.6.8.161.

QM: Big Broadhurst Reef: SW side, reef slope: 1m, 11.x.1973, C.W., G9860, G9861; 1m, 13.x.1973, C.W., G9862; 1·3m, 22.x.1973, C.W., G9863; 1·5m, 11.x.1973, C.W., G9859; 2·7m, 12.x.1973, C.W., G9864; 3m, 29.iii.1973, C.W., G9872; 5·3m, 13.x.1973, C.W., G9865; 6·3m, 13.x.1973, C.W., G9866; 8·3m, 15.x.1973, C.W., G9867; Oct. 1973, C.W., G9868; patch reef in lagoon, 21.x.1973, C.W., G9869; E. side, reef slope, 4m, 21.x.1973, C.W., G9870.

Bowden Reef, opening in outer reef, 26.vii.1972, C.W., G9877, G9878; SW side, reef crest, 0·6m, 15.vii.1972, C.W., G10716.

Bushy-Redbill Reef: S. side, outer flat, 31.v.1975, C.W., G9874; NW.side, top of patch reef off reef edge, 19.xii.1972, E. Lovell, G10727; W. of Redbill Is., edge of surge channel, 0·5m, 19.xii.1972, C.W., G10232.

Darley Reef, patch reef in lagoon, 24.iii.1973, C.W., G9876.

Great Keppel Island, E. side, fringing reef, Dec. 1975, R. Woolley, G10723, G10726.

Heron Island: reef flat, W. side: 2.vii.1973, Y. Loya, G9875; 6.vii.1973, Y. Loya, G10720. July 1973, C.W., G10718, G10722; N. side, 9.viii.1950, W. Stephenson, G9684; reef flat, April 1954, E. Grant, G2680; N. side, 14.v.1954, W. Stephenson, G2681–3.

Lady Musgrave Reef, W. side, outer slope, 16.vii.1971, I. Neuss, G6268.

Tryon Reef, E. side, reef flat, 12.vii.1971, C.W., G6267; NW. side, reef slope, 18.xii.1971, I. Neuss, G6478, G6480, G6494.

Viper Reef, patch reef in lagoon, 1m, 16.vii.1973, C.W., G10717.

Bramble Cay, Oct.1924, C. Hedley, G.B.R.C. 34–9, 86–92.

Coates Reef, 13.vii.1924, 'Geranium', G.B.R.C. 141, 195.

Flora Reef, 21.v.1924, Dr Paradice, G.B.R.C. 138.

Flinders Reef, Moreton Bay, NW. margin, 9.viii.1972, E. Lovell, G6984; NW. slope, 21.vi.1973, E. Lovell, G7297, G7298.

Field Diagnosis

Tabular to plate like colonies to over 3m diameter, formed by the developmental process described by Hoffmeister (1925). Colonies are sturdy in texture, and the vertical branchlets have a rosette like appearance due to the regular arrangement of labellate corallites around them. Colours are blue with pink growing edge (common reef flat colouration), pale to dark brown, pink-, yellow-, green- or blue-brown.

Laboratory Diagnosis

Branching pattern: From a central to lateral stalk, branching is horizontal, with branches anastomosing to a greater or lesser extent. Secondary branchlets are single or in groups of up to seven, from 1 mm to 22 mm long, and from 3 mm to 8 mm wide (commonly around 10 mm long and 4 mm wide). In very shallow reef flat situations, the branchlets may be reduced to mere buds, but very wide (up to 8 mm). The longest branchlets are in lagoonal specimens. In this species and in *A. cytherea,* layers may be added to the original plate.

Axial corallites: Up to 1·5 mm exert; outer diameter 1·4 to 2·0 mm; inner diameter 0·6 to 1·1 mm. Septation: primaries present to 2/3R, secondaries absent, or a few present to 1/4R.

Radial corallites: Tubular appressed, with only lower (or outer) wall developed (2/3 circumference or less) to form a rounded lip. Radials are arranged evenly and closely around the branchlet, giving a rosette-like appearance, typical of this species. Septation may be strongly developed, all primaries being present to 1/4R, plus a few secondaries, or so weakly developed that only the directive septa can be distinguished. On horizontal branches immersed corallites occur.

Coenosteum: Costate on radial corallites, reticulate with occasional laterally-flattened spines between.

Within Reef Distribution

This species occurs in lagoons, deep water reef flat situations, shallow outer reef flat, and on the reef slope to about 30 m (species no. 4 in Wallace 1975).

Identification Difficulties and History

Dana's type of *A. hyacinthus* (illustrated by Hoffmeister 1925) is a young specimen just in the 'vasiform' stage of development. This compares closely with juveniles of the species I have described, which is a sturdier species than *A. cytherea.* Much reef flat material of the species (well calcified) has probably been identified as *A. corymbosa,* while the interpretations of *A. hyacinthus* (e.g. by Hoffmeister) tend to be of a lighter-textured form. Whether his material was of *A. cytherea* or of a geographic variant of *A. hyacinthus* I am not able to judge. The deepest occurring colonies of *A. hyacinthus* are light textured with reduced radial corallite lips. These could be confused with *A. cytherea* from shallower depths but from a comparable depth *A. cytherea* has the distinctive *'A. reticulata'* form. *A. conferta* (Quelch) has slightly smaller axial corallite dimensions than those given here, but on radial corallite characteristics it appears to be a synonym. This is one of the most successful Indo-Pacific species of *Acropora:* it is an early colonizer, and occurs with great abundance in some areas. Hoffmeister's detailed treatment of a species under this name, without parallel detailed treatment of *A. cytherea* (or *'A. reticulata'*), leaves unsolved a taxonomic puzzle. A study of these two species on the Samoan reefs would be extremely useful.

Geographic Distribution

Widespread Indo-Pacific distribution from the Mascarene Archipeligo (G. Faure pers. comm.) to Tahiti. Exact localities cannot be quoted because of taxonomic confusion.

Acropora cytherea (Dana, 1846)

(Plates 63, 64A, D, 66C, D, 67)

Madrepora cytherea Dana, 1846, p.441, pl.32, fig.3a, 3b; Brook, 1893, p.99 (synonymy).

Acropora cytherea: Crossland, 1952, p.215.
Madrepora efflorescens Dana, 1846, p.441, pl.33, fig.6; Brook, 1893, p.35 (synonymy).
?*Acropora efflorescens:* Pillai and Scheer, 1976, p.26, pl.3, fig.3.
Madrepora armata Brook, 1892, p.452; 1893, p.100, pl.10, figs. A, B (synonymy).
Madrepora reticulata Brook, 1892, p.461; 1893, p.68, pl.4, figs. A, B.
Madrepora reticulata var. *cuspidata* Brook, 1893, p.69.
Acropora reticulata: Wells, 1954, p.422, pl.110, figs.4-6, pl.114, figs.1-6 (synonymy); Pillai and Scheer, 1976, p.28, pl.7, fig.1.
Madrepora arcuata Brook, 1893, p.102, pl.12; Studer, 1901, p.395.
Acropora cytherella Verrill 1902, p.253, pl.36, fig.7, pl.36a, fig.7, pl.36F, fig.1. (synonymy).
Acropora corymbosa 'cytherea Form': von Marenzeller, 1907, p.32, pl.1, figs.1, 2: pl.2, fig.3.
Acropora hyacinthus (part): Hoffmeister, 1925, p.64; Wells, 1954, p.421.

Material Examined

USNM: Tahiti, U.S. Expl. Exped., *A. cytherea* syntype 226; Samoa, *A. hyacinthus* (id. Hoffmeister), no.14 Mayor Collection.

YPM: Fiji Islands, U.S. Expl. Exped., *A. cytherella* holotype 2007; East Indies, *A. efflorescens* ?type 1799.

BM: Singapore, *A. armata* syntypes 1850.1.16.1, 1857.4.6.1; Amirante Islands, *A. reticulata* syntype 1882.10.17.131; Navigator Island, *A. arcuata* syntypes 1862.1.27.5, 1875.10.2.9.

QM: Big Broadhurst Reef: S W. side, reef slope: 1 m, 13.x.1973, C.W., G9841, G9842; 1·3 m, 11.x.1973, C.W., G9837, G9838; 2 m, 26.iii.1973, C.W., G9853; 2·3 m, 12.x.1973, C.W., G9839, G9840; 3 m, 28.iii.1973, C.W., G9856; 5 m, 27.iii.1973, C.W., G9855; 7 m, 13.x.1973, C.W., G9843; 8·1 m, 14.x.1973, C.W., G9845; 8·2 m, 14.x.1973, C.W., G9844; 8·3 m, 15.x.1973, C.W., G9847; 8·7 m, 15.x.1973, C.W., G9846; 9·7 m, 15.x.1973, C.W., G9849; 10·6 m, 6.x.1973, C.W., G9848; SW. side, surge channel floor, 5 m, 20.x.1973, C.W., G9850.

Bushy-Redbill Reef, NW. side, reef slope, 21.xii.1972, C.W., G9857.

Tryon Reef: NNE. side, outer slope, 21.xii.1971, I. Neuss, G6482; NW. side, outer slope, 6-10 m, 19.xii.1971, I. Neuss, G6479.

Viper Reef, patch reef in lagoon, 1 m from top, 16.vii.1972, C.W., G10717.

Flinders Reef, Moreton Bay: 1973, E. Lovell, G7290, G7291; NW. margin, 3-12 m, 9.viii.1972, E. Lovell, G6999, G7032; W. margin, 10 m, 10.iv.1972, E. Lovell, G7303, G7309.

Solitary Islands, 1972, J. Veron *et al.*, G7057, G7058.

Field Diagnosis

Tabular to plate-like colonies to over 3 m diameter, formed by the developmental process described by Hoffmeister (1925) for *A. hyacinthus*. Colonies have a light crumbly texture. Axial corallites are usually obviously exert, and contrast with slight scale-like radial corallites. Horizontal branches are reticulated to fully anastomosed. Colours are cream, pale brown, pink-, yellow-, green- or blue-brown or -grey.

Laboratory Diagnosis

Branching pattern: From a central to lateral stalk, branching is horizontal, with branches anastomosing to a greater or lesser extent. Secondary branchlets are vertical and single or in groups of up to six, from long and slender (up to 20 mm length, width around 3 mm at this length), to short bundles of tubular axials approximately 5 mm long with occasional proliferation of radial corallites at their base. In the series of specimens from lesser to greater depths on the Big Broadhurst Reef, a transition occurs from long branchlets with non-proliferous tips (identifiable with '*A. arcuata*' and '*A. armata*'), through shorter branchlets with proliferous tips, the proliferations often partially naked of radial corallites, to very short branchlets with few radial corallites (identifiable as '*A. reticulata*'). All specimens are openly reticulated and lightly calcified.

Lagoonal colonies are more anastomosed and heavily calcified and the branchlets are similar to those of deep reef slope colonies. Specimens from the geographically extreme southern locations (Flinders Reef, Moreton Bay and the Solitary Islands) have the main branches strongly anastomosed, and bundles of short thick proliferous branchlets: they identify with *A. cytherea sens. strict.*

Axial corallites: From 1·0 to 5·0 mm exert. Outer diameter 1·3 to 1·7 mm in Great Barrier Reef specimens, 1·6 to 2·5 mm in the Flinders Reef — Solitary Island specimens; inner diameter 0·7 to 1·0 mm. Septation: primary septa present, up to 2/3R; secondary septa often absent, never fully present, up to 1/4R.

Radial corallites: Tubular appressed with only lower (or outer) wall (1/2 circumference or less) developed, to form an elongate lip. In *A. cytherea s.s.* forms these lips are thickened: on the reef slope they are light structured and may be reduced to single or double points. Septal development of radials very poor: usually only directives can be seen, sometimes a few other primaries are present as fine points. On horizontal branches immersed corallites occur.

Coenosteum: Costate on radial corallites, reticulate with laterally flattened spines in between.

WITHIN REEF DISTRIBUTION

On the Great Barrier Reef this is a reef slope species (species no.5 in Wallace 1974), but occasional colonies occur in lagoonal and deeper water reef flat areas. On other reefs (e.g. Enewetak Atoll) it has a similar distribution (C.W.).

IDENTIFICATION DIFFICULTIES AND HISTORY

Two special taxonomic problems are associated with this species: (1) In combining *A. cytherea* with *A. reticulata,* and (2) In distinguishing between lightly structured colonies of *A. hyacinthus* and colonies of *A. cytherea* with good branchlet development.

A. cytherea s.s. occurs in geographically extreme locations (Tahiti, Solitary Islands, Moreton Bay). The temptation is to retain *A. reticulata,* which best describes the species in its main tropical range.

The second problem can also be stated as a problem of interpretation of *A. arcuata* and *A. armata.* These and *A. cytherea* have been combined with *A. hyacinthus* by recent authors. On *A. arcuata* and *A. armata* my own observations are of a co-occurrence of these 'species' with definite *A. hyacinthus* at the same depth on the Big Broadhurst reef front, and their graduation into typical '*A. reticulata*' with depth. Crossland's works are important to the ecological documentation of this species: in 1928 he identified *A. cytherea* as *A. hyacinthus,* in 1931 reversing the identification. In 1952 he notes that both species are common in Tahiti.

This species, as I have defined it, is easily separated from *A. hyacinthus* in the field by its light crumbly skeleton. The two species co-occur on the reef front, *A. cytherea* extending a little deeper, and *A. hyacinthus* extending more into reef flat areas.

GEOGRAPHIC DISTRIBUTION

The species has a wide Indo-Pacific distribution from the Mascarene Archipeligo (G. Faure, pers. comm.) to Tahiti.

Acropora millepora (Ehrenberg, 1834)
(Plates 68, 81 D)

Heteropora millepora Ehrenberg, 1834, p.109.
Madrepora millepora: Brook, 1893, p.116 (synonymy).
Acropora millepora: Verrill, 1902, p.257; Thiel, 1932, p.124, pl.18, fig.1, pl.19, fig.1; Nemenzo, 1967, p.94, pl.28, figs.1, 2.
Madrepora spathulata Brook, 1891, p.469; 1893, p.121, pl.32, fig.B.
Madrepora squamosa Brook, 1892, p.463; 1893, p.120, pl.20, fig. B;
Acropora squamosa: Vaughan, 1918, p.173, pl.72, figs.1, 2, 2a, 3; Crossland, 1952, p.216; Stephenson and Wells, 1956, p.18.
Acropora sarmentosa: Vaughan, 1918, p.17A, pl.72, fig.4.

MATERIAL EXAMINED

BM: Claremont Is., Great Barrier Reef, Saville Kent: *A. millepora* (mentioned Brook, 1893) 1892.6.8.165; *A. squamosa* syntype 1892.6.8.163; Treasury Is., Solomon Islands, D.A. Guppy, *A. spathulata* holotype 1884.12.11.25.

MNB: *A. millepora* holotype, 854 (photograph).

QM: Big Broadhurst Reef: patch reef in lagoon, 28.iii.1973, C.W., G11052–6; E. side (weather side), channel in outer flat, 21.x.1973, C.W., G11055.

Bushy-Redbill Reef: NW. side, outer reef flat, 23.xii.1972, C.W., G11047, G11049; NW. side, reef slope, 23.xii.1972, C.W., G11046.

Bowden Reef, SW. side, reef crest, 26.vi.1972, C.W., G11064.

Darley Reef, patch reef in lagoon, 1 m, 18.vi.1972, C.W., G11057; 3 m, 22.iii.1973, C.W., G11058; 4 m, 22.iii.1973, C.W., G11059.

Heron Island: N. side, reef flat, 14.xii.1973, C.W., G10996–G11001; S. side, outer reef flat, 12.xii.1973, C.W., G10973, G10976–83; SW. side, outer reef flat, 13.xii.1973, C.W., G10985–93; W. side, reef flat: 15.xii.1973, C.W., G11002–5; 17.xii.1973, C.W., G11006–8; SE side, reef flat, 17.xii.1973, C.W., G11009–16.

Great Keppel Is., Dec. 1975, R. Woolley, G11061.

Maer Island, Murray Island group, N. side, inner reef flat: 16.vii.1974, G. Ingram, G11060; 18.vii.1974, G. Ingram, G11062.

Masthead Reef, reef flat, Aug. 1974, J. Buhmann, G11063.

Michaelmas Cay, 1974, C. Limpus, G11067.

Low Isles, 1974, C. Limpus, G11066, G11068.

Fiji Islands, Great Astrolabe Reefs, Feb. 1974, C.W., G11033–43.

FIELD DIAGNOSIS

Low corymbose or stalked corymbose colonies, commonly with neat round outline; branches terete or slightly tapering, covered by evenly sized and closely arranged radial corallites with flaring, scale like lips. Commonest colouration (on both the Great Barrier Reef and Fijian reefs) is a dull to brilliant green with dull to bright orange branch tips. The colonies can also have multiple colouration, being predominately blue or pink, with touches of other pastel colours and a grey sheen, or bright orange to pale cream.

LABORATORY DIAGNOSIS

Branching pattern: Branches are given off vertically to obliquely from a central to lateral region which may be consolidated into a stalk. In some colonies from sandy situations a growing point is barely recognizable, and the growth is bush like and relatively indeterminate. A small amount of secondary branching occurs, and the top of the colony is in a single plane. Branch width varies from 7 to 13 mm.

Axial corallites: Barely exert. Outer diamter 2·4 to 3·9 mm; inner diameter 0·9 to 1·6 mm. Septation: primary cycle fully developed, up to 1/2R; secondary cycle usually represented, but not all septa developed, up to 1/4R.

Radial corallites: No upper wall is developed, the lower half of the wall is expanded as a rounded lip, and the outer edges of this lip may flare away from the opening of the corallite. The primary septa are often well developed, up to 2/3R, secondaries absent or a few present to 1/4R.

Coenosteum: Costate on radial corallite lips, reticulate with simple spines between radials.

WITHIN REEF DISTRIBUTION

Reef flat, from sandy middle reef flat to consolidated outer flat, occasionally to a few metres below the reef top; tops of lagoonal patch reefs and fringing reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

The usual name applied locally to this species is *A. squamosa*, but the material from the Great Barrier Reef identified as *A. millepora* by Brook (apparently the last person to observe and describe Ehrenberg's type) belongs to this species, and in fact forms a series from the same locality as his *A. squamosa* types. Verrill (1902) synonymised the two, but he has not been followed by later authors.

Two species regarded as being similar to *A. millepora* (or *'A. squamosa')* may now be dismissed: *A. sarmentosa* was misinterpreted by Vaughan (1918), and is a clearly definable species; *A. aspera* (= *A. hebes)* with many synonyms is a highly versatile reef flat species which in its low corymbose form appears very similar to this species. *A. millepora* has a more restricted reef flat distribution than *A. aspera*, and extends closer to the reef crest. In aggressive interactions observed at Heron Island and on Bushy-Redbill Reef *A. millepora* tissues appear to be inclined to overgrow those of *A. aspera*. Small colonies of the species have probably been identified as *'A. corymbosa'* by some authors. *A. imbricata* (Ehrenberg) is another possible synonym.

GEOGRAPHIC DISTRIBUTION

The most definite records of this species are only from the Great Barrier Reef, Solomon Islands, Fiji Islands (C.W.) and Marshall Islands (C.W.). Other less certain records extend the range to Ceylon, the Philippines, New Ireland, New Hebrides.

Acropora delicatula (Brook, 1891)
(Plate 69)

Madrepora delicatula Brook, 1891, p.461; 1893, p.109, pl.28, figs. D, E.

Acropora delicatula: Wells, 1954, p.420, pl.115, figs.1, 2.

non *Acropora delicatula:* Stephenson and Wells, 1956, p.12.

MATERIAL EXAMINED

BM: Solomon Islands, Guppy, *A. delicatula* holotype 1884.12.11.23.

QM: Big Broadhurst Reef, SW.side, reef slope: 2 m, 26.iii.1973, C.W., G11442; 6 m, 25.iii.1973, C.W., G11441; 6 m, 27.iii.1973, C.W., G11439; 8 m, 26.iii.1973, C.W., G11436; 8·1 m, 14.x.1973, C.W., G11434; 8·6 m, 15.x.1973, C.W., G11438; 13·4 m, 17.x.1973, C.W., G11437; 17 m, 23.x.1973, C.W., G11435.

Bushy-Redbill Reef, NW. side, reef slope, 3–7 m, 21.xii.1972, C.W., G11440.

FIELD DIAGNOSIS

Shallow caespitose or corymbose-plate colonies have slender vertical branchlets with small, scale-like radial corallites. Colours are cream, pale brown or greenish brown.

LABORATORY DIAGNOSIS

Branching pattern: From an attachment that is lateral or nearly so, branching is at first horizontal, then branchlets or bundles of branchlets are given off vertically upwards. The branchlet bundles can be as tall as 40 mm, and branchlet width is around 5 mm. A small amount of branching from the undersurface may occur.

Axial corallites: 0·5 to 1·5 mm exert. Outer diameter 1·5 to 2 mm; inner diamter 0·6 to 0·9 mm. Septation: primary septa well developed, up to 3/4R, secondary cycle usually absent, or a few septa may be present up to 1/4R.

Radial corallites: Appressed tubular, nariform or dimidiate, the outer wall only developed, and extended as a lip which is correspondingly rounded, elongate or spade-shaped. The septal development varies, but commonly all primary septa are visible, up to 1/4R, and two or three secondaries just visible.

Coenosteum: Costate or rows of simple spines on radial corallites, neat rows of simple spines, or reticulate with scattered spines, between.

WITHIN REEF DISTRIBUTION

I have observed only a very few colonies, all in reef slope situations. The species is much more commonly represented from fringing reefs, and a series in J.C.U. is from the Lizard Island and Palm Islands reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

This species is poorly documented, and working with a poor series I am unable to resolve some problems. *A. subulata* (Dana), may be a senior synonym. Stephenson and Wells' specimen from Low Isles (QM G2648) is *A. tenuis*.

GEOGRAPHIC DISTRIBUTION

Great Barrier Reef, Solomon Islands, Marshall Islands.

Acropora haimei (Milne Edwards and Haime, 1860)

(Plates 70, 71)

Madrepora haimei Milne Edwards and Haime, 1860, p.151; Brook, 1893, p.77 (synonymy); von Marenzeller, 1907, p.51 pl.16 figs. 45–48.

Acropora haimei: Vaughan, 1918, p.163, pl.70, figs.3, *3a, 3b, pl.66, figs. 4, 5; Crossland, 1952, p.207, pl.33, fig. 1, pl. 35, fig. 1; Rossi, 1954, p.48; Stephenson and Wells, 1956, p.14; Nemenzo, 1967, p.82, pl.25, fig. 1.*

MATERIAL EXAMINED

QM: Big Broadhurst Reef: SW. side, reef slope: 9·8 m, 16.x.1973, C.W., G10216, G10217; 9·6 m, 15.x.1973, C.W., G10215; 8·7 m, 15.x.1973, C.W., G10213, G10214; 8·6 m, 15.x.1973, C.W., G10212; 8·3 m, 15.x.1973, C.W., G10211; 8 m, 14.x.1973, C.W., G10210; 7·8 m, 23.x.1973, C.W., G10206–9; 7 m, 13.x.1973, C.W., G10205; 5–6 m, 23.x.1973, C.W., G10204; 6 m, 13.x.1973, C.W., G10224; 5·7 m, 23.x.1973, C.W., G10225; 5 m, 27.iii.1973, C.W., G10182, G10221; 5 m, 25.iii.1973, C.W., G10181; 4·2 m, 22.x.1973, C.W., G10222; 3·8 m, 12.x.1973, C.W., G10180; 1·6 m, 22.x.1973, C.W., G10223; 1·5 m, 12.x.1973, C.W., G10179; 1·3 m, 11.x.1973, C.W., G10202; 1·3 m, 14.x.1973, C.W., G10203; 1 m, 26.iii.1973, C.W., G10194; SW. side, surge channel opening, 10 m, C.W., G10183; patch reef in lagoon, 21.x.1973, C.W., G10184, G10185.

Bushy-Redbill Reef; NNE. side, reef slope, 3 m, 30.xii.1972, C.W., G10186, G10187, G11303; NW. side, reef crest, 30.xii.1972, C.W., G10195, G10227, G10228; W side, reef crest, 18.xii.1972, C.W., G10226.

Bowden Reef, opening in SW. side of reef, 26.vii.1972, C.W., G10188, G10189, G10229–31.

FIELD DIAGNOSIS

This is a medium sized compact arborescent species, which occurs as scattered turf like patches, bushes or thickets. It is distinguished from other arborescent species by very open radial corallites. Colour is usually cream or pale brown.

LABORATORY DIAGNOSIS

Branching pattern: Branching is open and irregular. Main branches are up to 15 mm wide and tapering.

Axial corallites: Outer diameter 2·2 to 3·5 mm; inner diameter 0·8 to 1·2 mm. Septation: primary septa present up to 2/3R; secondary septa all present, or mostly present, up to 1/3R.

Radial corallites: Tubular, extend at from 45° to 90° from branch; openings cochleariform; the upper part of the corallite wall (about 1/3 of the diameter) is thinner and shorter than the rest of the wall, and the thicker lower portion often flares slightly. Septal development is usually very marked: primaries can extend to R, and a full set of secondaries can be present. A good key to the identification of this species is the presence, on the proximal part of branches, of well formed cochleariform radials with strong septal development.

Coenosteum: Costate on radials, reticulate with simple or laterally flattened spines in between.

IDENTIFICATION DIFFICULTIES AND HISTORY

Although following Crossland's interpretation, I am still not fully satisfied that *A. haimei* is the correct identification of this species. Milne Edwards and Haime's type cannot be located. Other authors, particularly von Marenzeller, describe a greater variety of colony shapes than I have seen, including shallow water reef flat forms which approach corymbose. To a worker with some experience in the field, this species becomes easy to distinguish from other arborescent species because of its large open radial corallites.

WITHIN REEF DISTRIBUTION

The species occurs as small patches on middle and outer reef flats, but achieves its greatest abundance on the reef slope (to about 10 m), in surge channel openings and on sandy bottoms in deep lagoons and around broken reef-patch areas.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Red Sea, ?Diego Garcia, Maldive Islands, Ceylon, Mauritius, Singapore, Great Barrier Reef, Fiji Islands.

Acropora tenuis (Dana, 1846)
(Plates 72, 73)

Madrepora tenuis Dana, 1846, p.451; Ortmann, 1888, p.152; Brook, 1893, p.83 (synonymy).
?Madrepora eurystoma Klunzinger, 1879, p.16, pl. 1, fig. 8, pl. *A*, fig. 7, pl. 9, fig. 12.
Madrepora eurystoma: Brook, 1893, p. 137 (synonymy).
Madrepora macrostoma Brook, 1891, p.464; 1893, p. 105, pl. 19, fig. B.
Madrepora bifaria Brook, 1892, p.453; 1893, p.110, pl. 30, fig. A.
Madrepora kenti Brook, 1892, p.458; 1893, p. 110, pl. 11, fig. B.
Madrepora dilatata Brook, 1893, p.81.
Madrepora anthocercis Brook, 1893, p. 106, pl.13, fig. C (synonymy).
?Acropora anthocercis: Nemenzo, 1967, p. 109.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *Madrepora tenuis* holotype 259.

BM: Koseir, Red Sea, *A. eurystoma* 1886. 10.5.5; Diego Garcia, G. C. Bourne, *A. eurystoma* 1891.4.9.1. (mentioned Brook, 1893); Mauritius, *A. macrostoma* holotype 1878.2.4.7; Java, *A. bifaria* holotype 1859.12.12.2; Thursday Island, Saville-Kent, *A. kenti* holotype 1892.6.8.202; Palm Island, Saville-Kent, *A. anthocercis* syntype 1892.6.8.235; Rocky Island, Saville-Kent, *A. anthocercis* syntypes 1892.6.8.236, 1892.6.8.237.

QM: Big Broadhurst Reef, SW. side, reef slope: 1·9 m, 22.x.1973, C.W., G11413; 3·3 m, 22.x.1973, C.W., G11429; 4 m, 24.iii.1973, C.W., G11431; 6 m, 27.iii.1973, C.W., G11428; 7 m, 28.iii.1973, C.W., G11430; 7·8 m, 14.x.1973, C.W., G11456; 8 m, 26.iii.1973, C.W., G11433; 8 m, 14.x.1978, C.W., G11420; 8·1 m, 14.x.1973, C.W., G11424; 8·2 m, 14.x.1973, C.W., G11422, G11423; 8·6 m, 15.x.1973, C.W., G11425; 9·2 m, 15.x.1973, C.W., G11421; 9·8 m, 16.x.1973, C.W., G11426, G11432.

Bushy-Redbill Reef: W. side, outer reef flat, Dec. 1972, C.W., G11417; NW. side, reef slope: 19.xii.1972, E. Lovell, G11412, G11415, G11416; NW. side, floor outside slope, 22.xii.1972, C.W., G11427.

Darley Reef, patch reef in lagoon, 22.iii.1973, C.W., G11414, G11418.

Heron Island, W. side, reef flat, 6.vii.1973, Y. Loya, G11457.

Masthead Reef, SW. side, upper reef slope, Aug. 1974, J. Buhmann, G11419.

FIELD DIAGNOSIS

Colonies are 'thick plates' or caespito-corymbose. The radial corallites are evenly arranged and have distinctive, lip like, flaring outer wall and strong septal development, which can often be seen with the naked eye. Once learnt in the field, this species is always easily recognised. The commonest colour is cream, less commonly colonies are greenish-blue or bright blue. Polyps are often partly extended during the day, and in cream colonies these are often bright orange (axial polyps) and bright purple (radial polyps).

LABORATORY DIAGNOSIS

Branching pattern: From a growing area which may be central to lateral, branching is horizontal, then secondary branchlets or groups of branchlets are given off vertically to obliquely, their tips in one plane. Branching may also occur from the lower surface but these lower branches are never as long as the upper. Branchlet widths are from 6 to 8 mm. Shallow water specimens are 'thick plates' of up to 110 mm vertical depth; deeper water specimens may be thin plates as little as 35 mm thick.

Axial corallites: Up to 2 mm exert. Outer diameter: 1·9 to 3·0 mm; inner diameter 0·8 to 1·2 mm. Septation: both cycles usually developed, the primaries up to 2/3R, the secondaries up to 1/3R.

Radial corallites: Tubular, ascending, the inner wall less developed (both in thickness and length) than the outer; the outer wall flaring, so that the opening appears large and round or slightly oval. Towards the middle of the branches these radials have a classic 'cochleariform' appearance. Both septal cycles are usually developed, and in some reef flat and lagoonal specimens these may fill the corallite. The size of the radials is very even over the corallum. With increasing water depth the corallite wall becomes less flaring, the 'cochleariform' appearance is lost, and the corallites are more scattered.

Coenosteum: Either strongly costate or in rows of simple spines on the radial corallites, reticulate with simple spines between.

WITHIN REEF DISTRIBUTION

Reef flat (deeper water areas), lagoonal patch reefs, reef slope to about 10 m.

IDENTIFICATION DIFFICULTIES AND HISTORY

The synonymy list for *A. tenuis* is large, and possibly still incomplete. The synonyms differ in features such as length of branches and degree of calcification. In the field, the colonies look quite similar to those of *A. aculeus* (Dana). Some field experience is necessary to distinguish them. The main differences are:

(a) wide flaring lip and larger radial corallites in *A. tenuis;*
(b) colour pattern: *A. tenuis* is usually cream or pinkish brown while *A. aculeus* has a distinctive double colouration;
(c) *A. tenuis* very often has the polyps expanded, as noted.

The shape of the radial corallites shows some similarity to that in *A. haimei,* and strong similarity to that in *A. striata* Verrill, which does not occur in the Great Barrier Reef regions studied, but is a common species in the Marshall Islands. One specimen from Lizard Island in the J.C.U. with bottlebrush growth form is possibly *A. striata.*

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Mauritius, Red Sea, Diego Garcia, Indonesia, Philippines, China Sea, Great Barrier Reef, Fiji Islands.

Acropora tubicinaria (Dana, 1846)
(Plate 74)

Madrepora tubicinaria Dana, 1846, p.451, pl.32, fig.7; Brook, 1893, p.139 (synonymy).

Acropora tubicinaria: Verrill, 1902, p.219; Wells, 1954, p.423, pl.122, figs.3-5.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. tubicinaria* holotype 258.

QM: Bushy-Redbill Reef: W. side, inner reef flat: 28.v.1975, C.W., G11071–6, G11080; Jan. 1973, C.W., G11077; 18.xii.1972, C.W., G11081; NW. side, first reef crest, 22.xii.1972, C.W., G11082; S. side, microatoll zone, 2.i.1973, C.W., G11078, G11079, G11083.

Masthead Reef, August 1974, J. Buhmann, G11088. Great Keppel Island, Dec. 1975, R. Woolley, G11089.

FIELD DIAGNOSIS

Colonies are small rounded caespitose clumps (largest seen 25 cm diameter) in which the openings of the radial corallites are obvious. Colour is brown, occasionally with blue tips.

LABORATORY DIAGNOSIS

Branching pattern: From a central growing area branches are given off vertically to obliquely, and these branch again, sometimes infrequently, sometimes frequently. As colonies mature the base and basal parts of branches may die, and portions of the colony become separate from each other. Branches are from 8 to 10 mm thick, and may be truncate or strongly tapered.

Axial corallites: Non exert. Outer diameter 1·8 to 3·2 mm; inner diameter 1·0 to 1·2 mm. Septation: both septal cycles developed, primaries up to 3/4R, secondaries up to 1/4R.

Radial corallites: Short tubular, usually upper part of wall less developed than lower, opening circular. Usually both septal cycles are developed, but just visible, although on parts of the corallum primaries can reach 1/2R and secondaries 1/4R.

Coenosteum: On some colonies lines of simple spines are arranged both on and between radials. More commonly the coenosteum is costate or in lines of spines on the radials, and reticulate with simple spines between.

WITHIN REEF DISTRIBUTION

On Bushy-Redbill Reef, this species is common in the coral depauperate inner reef flat (recorded as *A. digitifera* by Wallace and Lovell 1977). With *A. palifera* and species of *Porites* it dominates this zone and it is rare on other parts of the reef.

IDENTIFICATION DIFFICULTIES AND HISTORY

This species is rarely mentioned in the literature. On my evidence and that of Wells, it tends to specialize in certain reef zones (which may be characterized by poor coral cover), but is common in these areas. It is rare in collections brought to the QM for identification, and I have not yet seen it from fringing reefs. *A. striata* Verrill mentioned by Wells (1954) as a 'related form' does not occur on the Great Barrier Reef.

GEOGRAPHIC DISTRIBUTION

Great Barrier Reef, Fiji Islands, Marshall Islands, Tahiti.

Acropora aculeus (Dana, 1846)
(Plates 75, 76)

Madrepora aculeus Dana, 1846, p.450, pl.32, fig.6; Brook, 1893, p.104 (synonymy).

Acropora aculeus: Faustino, 1927, p.269; Nemenzo, 1967, p.114.

Madrepora tubigera Horn, 1860, p.435; Verrill, 1864, p.41; Quelch, 1886, p.161; Brook, 1893, p.79 (+ further synonymies); Verrill, 1902, p.239, pl.36, figs.1, 2-2b, pl.36a, figs.1, 2-2b; pl.36f, fig.8.

Acropora tubigera: Crossland, 1952, p.208.
?*Madrepora nana* Studer, 1878, p.533, pl.2, figs. 6a, 6b; Brook, 1893, p.82.
Acropora nana: Wells, 1950, p.39, pl.10, figs.3, 4.
?*Acropora nana:* Nemenzo, 1967, p.85.
Madrepora patula Brook, 1892, p.460; 1893, p.111, pl.9, fig.E.
Acropora patula: Crossland, 1952, p.215; Stephenson and Wells, 1956, p.16; Nemenzo, 1967, p.102.
?*Madrepora elegantula* Ortmann, 1889, p.507, pl.12, fig.5.
Madrepora elegantula: Brook, 1893, p.115.

Material Examined

USNM: Fiji Islands, U.S. Expl. Expd., *A. aculeus* holotype 257; Cocos-Keeling, *A. nana* (mentioned Wells, 1950) 44322.

YPM: *A. tubigera* fragment of type 1483.

BM: Port Denison, Great Barrier Reef, *A patula* holotype? 1892.6.8.274.

QM: Big Broadhurst Reef: SW. side, reef slope: 13.x.1973, C.W., G9093; 3 m, 28.iii.1973, C.W., G9097; 5 m, 27.iii.1973, C.W., G9107; 5·1 m, 23.x.1973, C.W., G9086, G9087; 6 m, 13.x.1973, C.W., G9092; 6·1 m, 13.x.1973, C.W., G9090; 7 m, 28.iii.1973, C.W., G9106; 8 m, 26.iii 1973, C.W., G9108; 8·2 m, 14.x.1973, C.W., G9094; 8·5 m, 23.x.1973, C.W., G9100; 8·7 m, 15.x.1973, C.W., G9095; 9·2 m, 23.x.1973, C.W., G9088; 10 m, 20.x.1973, C.W., G9099; 10 m, 23.x.1973, C.W., G9101; 10·6 m, 16.x.1973, C.W., G9102; 13·3 m, 23.x.1973, C.W., G9089; 25 m, 17.x.1973, C.W., G9091; 25·1 m, 18.x.1973, C.W., G9104; SW. side, surge channel floor, 10 m, 20.x.1973, C.W., G9098, G9108.

Bushy-Redbill Reef: W. side, middle reef flat: 8.vi.1975, C.W., G9122–4; 14.vi.1975, C.W., G9125, G9126; W. side, outer reef flat, 31.vi.1975, C.W., G9116; W. side, reef slope, 1–8 m, 3.vi.1975, C.W., G9118, G9120; NW. side, middle reef flat, 30.xii.1972, C.W., G9114; NW. side, patch reefs: 19.xii.1972, E. Lovell, G9542; 15 m, 16.vi.1975, C.W., G9117; NW. side, reef slope, 3–7 m, 21.xii.1972, C.W., G9115; adjacent Redbill Is., reef crest: 19.xii.1972, C.W., G9113; 1.vi.1975, C.W., G9119; adjacent Redbill Is., reef slope, 20.xii.1972, C.W., G11463.

Darley reef, patch reefs in lagoon: 3 m, 18.vii.1972, C.W., G9110; 3 m, 22.iii.1973, C.W., G9109; 4 m, 22.iii.1973, C.W., G9111.

Prawn reef, patch reef in lagoon, 15.vii.1972, C.W., G9112.

Field Diagnosis

This species occurs as 'thick plates' or caespito-corymbose units. The colony can be one plate with a loose central or side attachment, or a number of tiers of plates can develop. The single plates occur on the outer reef flat and deeper water parts of the reef slope: the layering develops in deep water middle reef flat areas and on the reef crest. Small round colonies can occur on the outer reef flat. Colours are blue, grey, green, or brown on lower parts of branches, with tips of branches yellow, lime green, pale blue or brown.

Laboratory Diagnosis

Branching pattern: From a usually lateral attachment, main branches are horizontal and secondary branchlets or bundles of branchlets are given off horizontally to obliquely on both sides of them. Branchlets are slender (3 to 7 mm). The 'stout branches' of Dana was either a slip of the pen or a reference to the main stem. Small shallow reef flat specimens grow as vertical branchlets directly from an encrusting base.

Axial corallites: Outer diameter 1·8 to 2·4 mm; inner diameter 0·8 to 1·0 mm. Septation: primary septa well developed, up to 2/3R, secondaries usually partly but poorly developed, up to 1/4R.

Radial corallites: Tubular appressed to partly appressed, with round to slightly oval openings at 90° or more to the branch. Primary septa developed up to 1/2R, and some secondaries visible. Radials are usually evenly sized and distributed on branches and show little variation. Wall can be thickened.

Coenosteum: Lines of simple spines on and between radials, or sometimes a spongy appearance between radials.

Within Reef Distribution

Middle and outer reef flats, reef crest, reef slope to 20 m, lagoonal patch reefs.

Identification Difficulties and History

Much of the variability in this species is related to colony size. Some idea of the scale of this variability can be seen by comparing Well's *A. nana* specimen (1950, pl.10, figs.3, 4) and my Plate 76, Fig.D. Other features such as thickness of wall, angle of radial lip, and completeness of radial septation, vary little, but are responsible for the various species in synonymy. *A. elegantula* (Ortmann) as interpreted by Brook (1893) (BM 1892.12.5.18) is a heavily calcified specimen of this species.

Geographic Distribution

Indo-Pacific: Cocos-Keeling Islands, Philippines, Great Barrier Reef, Fiji Islands, Samoa, Marshall Islands.

Acropora cerealis (Dana, 1846)
(Plate 77)

Madrepora cerealis Dana, 1846, p.460, pl.35, fig.2; Brook, 1893, (part) p.91 (synonymy).
Acropora cerealis: Faustino, 1927, p.266, pl.86, figs.1, 3; Nemenzo, 1967, p.83, pl.25, fig.2.
Madrepora hystrix Dana, 1846, p.476, pl.40, fig. 1, pl.31, fig.5; Brook, 1893, p.176 (synonymy).
Acropora hystrix: Wells, 1954, p.425; pl.125, figs.1-4.
Madrepora tizardi Brook, 1893, p.89, pl.11, figs. C, D. (synonymy).
Acropora tizardi: Wells, 1954, p.425, pl.125, figs. 5, 6; Nemenzo, 1967, p.103

Material Examined

USNM: Sooloo Sea, U.S. Expl. Exped., *A. cerealis* syntype 269; East Indies, U.S. Expl. Exped., *A. cerealis* syntype 270, Fiji Islands, U.S. Expl. Exped., *A. hystrix* holotype 298.

YPM: Fiji Islands, U.S. Expl. Exped., *A. hystrix* fragment of type 2039.

BM: Tongatabu, J. J. Lister, 1891.3.6.9; Amboina, Challenger, 1885,2.1.1; *A. cerealis* (Brook 1893 mentioned specimens); Tizard Bank, *A. tizardi* syntype 1889.9.24.115.

QM: Big Broadhurst Reef, SW. side, reef slope: 4·5 m, 12.x.1973, C.W., G9532; 5·1 m, 14.x.1973, C.W., G9539; 6 m, 13.x.1973, C.W., G9535; 6·3 m, 23.x.1973, C.W., G9538, G9531; 8·6 m, 15.x.1973, C.W., G9533; 8·7 m, 23.x.1973, C.W., G9529; 10 m, 23.x.1973, C.W., G9541; 14·2 m, 23.x.1973, C.W., G9530; 13.x.1973, C.W., G9537; Oct., 1973, C.W., G9540.

Bowden Reef, slope of opening in SW. side, 3 m, 26.vii.1972, C.W., G9519, G9520.

Bushy-Redbill Reef, NW. side, reef crest, 22.xii.1972, C.W., G9543.

Darley Reef, patch reefs in lagoon: 5 m, 24.iii.1973, C.W., G9524; 1 m, 22.iii.1973, G9525, G9528; 3 m, 18.vii.1972, C.W., G9526.

Viper Reef, patch reefs in lagoon, 3 m, 6.vii.1972, C.W., G9521, G9523.

Field Diagnosis

Colonies can be untidy caespitose clumps in lagoonal situations, through caespito-corymbose on the upper reef slope, to corymbose plates on the deeper reef slope. Radial corallites are narrow tubo-nariform, with tendency for outer edge to be hooked upwards *('A. tizardi')*, with elongate oblique opening *('A. hystrix')* tubo-nariform tending to nariform *(A. cerealis s.s.)*. The resultant appearance is a colony similar to *A. nasuta*, but with 'spinier' appearance and slender, usually more complexly branching, branchlets. Colour is usually cream to pale brown.

Laboratory Diagnosis

Branching pattern: From a central to lateral attachment, main branches are given off vertically (mainly in lagoonal colonies) to horizontally. Secondary branching is on all sides of vertical branches or vertically to obliquely upwards from horizontal branches. There is a tendency for further secondary branching. Branchlet widths are around 10 mm, but much of this width is given by the spreading radial corallites.

Axial corallites: Outer diameter 1·8 to 2·1 mm, inner diameter 0·7 to 0·9 mm. Septation: primary septa well developed, up to 3/4R, secondaries absent or a few present to 1/4R.

Radial corallites: The shape of the radial corallites is nariform to tubo-nariform, but the opening varies from rounded to slightly oval (lagoonal specimens) to accentuated elongate. The lower wall may be slightly thickened or may be extended as a 'hook'. In lagoonal specimens, radials tend to be scattered. In reef-slope specimens with elongate radials these tend to be arranged in neat rows along the branches. Septal development varies, but primaries are always strongly visible, and secondaries usually at least partially visible.

Coenosteum: Costate or dense lines of spines on corallites, reticulate with simple spines in between.

Within Reef Distribution

Deep water reef flat areas, reef slope (to 15 m in present study), lagoonal patch reefs.

Identification Difficulties and History

Wells (1954) commented on the similarity between *A. tizardi* and *A. hystrix*. Unfortunately *A. cerealis sens. strict.* is the most difficult of the synonyms to place correctly. Without the accentuated oblique radial corallite opening it approaches *A. nasuta* in general appearance. Deeper reef slope specimens are very lightly structured, and are easily confused with specimens of *A. tenuis* from similar localities

Geographic Distribution

China Sea, Philippines, Great Barrier Reef, Fiji Islands, Marshall Islands, Tongan Islands.

Acropora nasuta (Dana, 1846)
(Plate 78)

Madrepora nasuta Dana, 1846, p.453, pl.34, fig.2; Brook, 1893, p.73 (synonymy).
Acropora nasuta: Verrill, 1902, p.257; Hoffmeister, 1929, p.364; Wells, 1954, p.424, pl.113, figs. 5, 6; pl.124, figs.1-3; Nemenzo, 1967, p.88, pl.26, fig.3.

Madrepora nasuta var. *crassilabia* Brook, 1893, p.74.
Acropora nasuta crassilabia: Wells, 1954, p.425, pl.124, fig.4.
Acropora nasuta var. *crassilabia:* Nemenzo, 1967, p.89, pl.26, fig.2.
Madrepora effusa Dana, 1846, p.455; Brook, 1893, p.76 (synonymy).
Acropora effusa: Verrill, 1902, p.229, pl.36, fig.16, 16a, pl.36B, fig.7, 7a.
Madrepora cymbicyathus Brook, 1893, p.86 (synonymy).
Acropora cymbicyathus: Hoffmeister, 1925, p.63, pl.13, figs.2a, 2b; Wells, 1954, p.425; pl.124, figs.5-7; Stephenson and Wells, 1956, p.12.

MATERIAL EXAMINED

USNM: Tahiti, U.S. Expl. Exped., *A. nasuta* holotype 260.

YPM: Point Pedro, Ceylon, *A. effusa* holotype 8147.

QM: Big Broadhurst Reef: patch reef in lagoon: 21.x.1973, C.W., G11212; 28.iii.1973, C.W., G11227; SW. side, outer reef flat, 22.iii.1973, C.W., G11209; SW. side, reef crest: 1·5 m, 11.x.1973, C.W., G11216; 1·5 m, 22.x.1973, C.W., G11213; 2 m, 11.x.1973, C.W., G11215, G11274; SW. side, reef slope: 7 m, 28.iii.1973, C.W., G11224; 7·6 m, 13.x.1973, C.W., G11217.

Bowden Reef, SW. side, reef crest, 1 m, 15.vii.1972, C.W., G11211.

Bushy-Redbill Reef: adjacent Redbill Is., reef flat: 18.xii.1972, C.W., G11204; 7.vi.1975, C.W., G11222; 12.vi.1975, C.W., G11223; W. side, middle reef flat; 5.vi.1975, C.W., G11226; 27.vi.1975, C.W., G11221, G11228; NW. side, first reef crest, 22.x.1973, C.W., G11214.

Darley Reef, patch reef in lagoon, 3 m, 22.iii.1973, C.W., G11218.

Heron Island: W. side, outer reef flat, 7.vii.1973, C.W., G11209; W. side, reef flat, July 1973, C.W., G11205; W. side, reef slope, 7 m, 7.vii.1973, Y. Loya, G11203.

Palm Islands, 1939, T. C. Marshall, G11206–8.

FIELD DIAGNOSIS

Corymbose to tabular colonies, the branchlets covered evenly and neatly with nariform corallites with elongate openings. Colour is most commonly cream to pale brown, usually with pale blue tips, but can also be yellowish or greenish.

LABORATORY DIAGNOSIS

Branching pattern: Branches arise from an encrusting plate, or a sturdy stalk. Secondary branches are vertical in the centre of the colony, and more curved towards the edges; they are not usually very proliferous.

Axial corallites: Outer diameter 2·0 to 3·0 mm; inner diameter 0·5 to 0·9 mm. Septation: primary septa present, up to 3/4R, secondary septa anything from all absent to all present up to 1/4R.

Radial corallites: Nariform, dimidate, or tubo-nariform, opening at 90° to branch or less. The walls of the corallites may be thickened. Primary septa present up to 1/3R, secondary septa poorly developed, usually less than a full cycle present, up to 1/4R.

Coenosteum: Laterally flattened or forked spines are arranged densely on radial corallites, sometimes joining as costae. Between radials coenosteum is reticulate.

WITHIN REEF DISTRIBUTION

Occurs on most parts of the reef flat, reef crest, upper reef slope (to about 8 m in studied areas). This is sometimes the only *Acropora* (other than *A. palifera*) occurring in shallow lagoonal patch reefs in inner lagoons adjacent to coral cays.

IDENTIFICATION DIFFICULTIES AND HISTORY

The close similarity of *A. nasuta* and *A. cymbicyathus* has been commented on by other authors. Although not well represented in the literature, this is a common *Acropora* on the Great Barrier Reef, occurring in a variety of habitats. Colonies are often very regularly formed, and easily recognised, although it can sometimes be confused with more regular colonies of *A. cerealis*. It is a good photographic subject, usually being identified in popular texts as *'A. surculosa'*.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Ceylon, Great Barrier Reef, Fiji Islands, Samoa, Marshall Islands, Tahiti.

Acropora diversa (Brook, 1891)
(Plates 79, 80A, B)

Madrepora diversa Brook, 1891, p.461; 1893, p.141, pl.16, fig.B.
Acropora diversa: Wells, 1954, p.424, pl.117, figs.3-6; Stephenson and Wells, 1956, p.13.
Madrepora concinna Brook, 1891, p.460; 1893, p.165, pl.17.
Acropora otteri Crossland, 1952, p.229, pl.43, figs.1, 2, pl.44, figs.1, 2.

MATERIAL EXAMINED

BM: Diego Garcia, G. C. Bourne, *A. diversa* holotype 1891.4.9.4; Mauritius, *A. concinna* syntypes 1878.2.4.3, 1878.2.4.8; Great Barrier Reef Expedition, *A. otteri* syntypes 1934.5.14.17; 1934.5.14.76; June Reef, outer moat *A. otteri* (? also a syntype) 1934.5.14.315.

QM: Big Broadhurst Reef: SW. side, outer reef flat: 22.x.1976, C.W., G11232, G11233; 18.x 1973, C.W., G11261, G11263, G11269, G11279, G11280; 22.x.1973, C.W., G11272, G11285; SW. side, reef slope: 1·3 m, 22.x.1973, C.W., G11245; 1·5 m, 18.x.1973, C.W., G11266; 3 m, 27.iii.1973, C.W., G11254; 3·3 m, 22.x.1973, C.W., G11237; 4·5 m, 23.x.1973, C.W., G11273; 5·1 m, 23.x.1973, C.W., G11236, G11270; 5·7 m, 23.x.1973, C.W., G11241; 6 m, 27.iii.1973, C.W., G11252; 7 m, 28.iii.1973, C.W., G11259; 7·1 m, 13.x.1973, C.W., G11276; 7·8 m, C.W., G11267; 8 m, 28.iii.1973, C.W., G11246, G11258; 8·1 m, 14.x.1973, C.W., G11231; 8·2 m, 14.x.1973, C.W., G11230, G11243, G11285; 8·6 m, 15.x.1973, C.W., G11240; 8·7 m, 15.x.1973, C.W., G11264; 9·6 m, C.W., G11265; 9·7 m, 15.x.1973, C.W., G11271; 9·8 m, 16.x.1973, C.W., G11239; 10·6 m, 23.x.1973, C.W., G11275; 12·5 m, 17.x.1973, C.W., G11242; 14·2 m, 23.x.1973, C.W., G11235; SW. side, reef crest; 1·5 m, 11.x.1973, C.W., G11278; 1·6 m, 22.x.1973, C.W., G11284; 22.x 1973, C.W., G11234.

Bowden Reef, SW. side, reef crest: 0·75 m, 15.vii.1972, R. Pearson, G11268; 1 m, 15.vii.1972, C.W., G11248, G11251, G11260; SW. side, reef slope: 26.vii.1973, C.W., G11238.

Bushy-Redbill Reef, NW. side, reef slope: Jan. 1973, C.W., G11249; 19.xii.1972, E. Lovell, G11257; G11262; G11282.

Darley Reef, patch reef in lagoon: 1 m, 24.iii.1973, C.W., G11250; 5 m, 19.vii.1972, C.W., G11244, G11256; 24.iii.1973, C.W., G11253, G11255.

Field Diagnosis

Corymbose, caespito-corymbose, tabulate to plate-like colonies have a mixture of tall and short tubular radial corallites which is usually distinctive. A variety of colours occur, vis. cream, yellow-brown, blue-grey, blue-brown.

Laboratory Diagnosis

Branching pattern: From an attachment region which is central to lateral, branches are given off upwards vertically to obliquely. These may be as short as 20 mm to as long as 70 mm, and may branch proliferously or rarely. Branch widths vary from 7 to 20 mm.

Axial corallites: 1 to 3 mm exert. Outer diameter 2·4 to 3·2 mm (slightly larger in *A. diversa* type); inner diameter 0·8 to 1·1 mm. Septation: both cycles usually present, the first cycle up to 3/4R, the second up to 1/3R.

Radial corallites: Tall and short corallites are mixed, in a pattern which may be regular (tall radials arranged in vertical rows) or very irregular. The form of the tall and short radials is similar — tubular, with round, or slightly oval openings, sometimes tubo-nariform. The outer wall may be thickened. The septal development is usually poor, primary septa being present, up to 1/3R, but usually less than this, the secondary cycle usually only partly present, up to 1/4R.

Coenosteum: Simple pointed to laterally flattened spines are densely arranged on the radial corallites, sometimes forming costae. Between the radials their arrangment is less dense.

Within Reef Distribution

Outer reef flat, reef crest and reef slope to about 15 m, lagoonal patch reefs.

Identification Difficulties and History

Amongst my material there is great variability in radial corallite features such as length, shape of opening, ratio of short to long, as well as the expected colony-shape variability. Both in the field and in the laboratory I find areas of overlap and difficulty in distinguishing some specimens from *A. nasuta* and others from *A. variabilis*. A study concentrating on these three species would be profitable.

Geographic Distribution

Indo-Pacific: Mauritius, Diego Garcia, Great Barrier Reef, Marshall Islands.

Acropora variabilis (Klunzinger, 1879)

(Plate 80C, D)

Madrepora variabilis Klunzinger, 1879, p.17, pl.1, fig.10, pl.2, figs.1, 5, pl.5, figs.1, 3, pl.9, fig.14; Brook, 1893, p.161.

Acropora variabilis: von Marenzeller, 1907, p.49, pl.15, figs. 40–44; Vaughan, 1918, p.181, pl.80, figs.2, 3, 3a, 3b: Faustino, 1927, p.276; Wells, 1950, p.38; 1954, p.428, pl.128, figs.1, 2, pl.130, figs. 1, 2; Rossi, 1954, p.52; Stephenson and Wells, 1956, p.19; Scheer and Pillai, 1974, p.23, pl.8, fig.2; Pillai and Scheer, 1976, p.31.

Acropora variabilis var. *pachyclados:* Crossland, 1952, p.222, pl.38, figs.1, 6.

Material Examined

MNB: Koseir, Klunzinger, *A. variabilis* var. *pachyclados* 2118; Koseir, Klunzinger, *A. variabilis* var. *cespitofoliata* 2120 (Klunzinger mentioned specimens, examined as photographs only).

QM: Big Broadhurst Reef, SW. side, outer reef flat: 11.x.1973, C.W., G11291; 18.x 1973, C.W., G11287–90.

Field Diagnosis

Colonies may be small round clumps of vertical to oblique branches or stalked corymbose colonies to about 30 cm across. Branches are covered by appressed tubular corallites with round openings. The sizes of the radial corallites may be similar or extremely variable. Colour may be brown, lavender-brown, greenish-brown, or yellow or cream with purple corallites.

Laboratory Diagnosis

As this species has been well described by other authors, and my series is poorly representative of the species, further description is not given. Refer to Vaughan 1918 for tables of measurements of skeletal features.

Within Reef Distribution

Shallow outer reef flat (particularly where an elevated platform is present), reef crest. A large series in the JCU comes from the fringing reefs of the Palm Islands and Lizard Island.

Identification Difficulties and History

Although this species is poorly represented in my areas of study, evidence suggests it may be common (a) on windward outer reef flat platforms (as small round clumps) and (b) on reef edges of the fringing reefs of continental islands (as caespito-corymbose colonies). The series in JCU from Lizard Island and the Palm Island group is in the second category. An allied species is *A. valida* (Dana) (see Hoffmeister, 1925, p.60). This latter species may also occur on the Great Barrier Reef, but is not represented in the QM collections, except by two specimens collected in the Fiji Islands, and closely comparable with Dana's type.

Geographic Distribution

Indo-Pacific: Red Sea, Nicobar Islands, Cocos-Keeling, Philippines, Great Barrier Reef, Marshall Islands.

Acropora humilis (Dana, 1846)
(Plates 81, 82, 83)

Madrepora humilis Dana, 1846, p.483, pl.31, fig.4, pl.41, fig.4.

Acropora humilis: Wells, 1954, p.425, pl.100, fig.1, pl.126, figs.1–6, pl.127, figs.3, 4, pl.128, figs. 3–5 (synonymy), Rossi, 1954, p.50; Stephenson and Wells, 1956, p.15; Pillai and Scheer, 1976, p.32.

This species has been given extensive taxonomic treatment by Wells 1954. He combined 17 species (some with additional synonyms designated by earlier authors), and concluded that three broad forms could be recognised. These he considered to be characteristic of different reef localities and related, in particular, to water level. Although a large suite of specimens is on hand at the QM, their description is withheld until a further study concentrating on this complex species can be carried out. For general purposes, this species is probably the best known and most easily recognised *Acropora*. Some additional information is added below on Well's first facies, forma alpha *(A. samoensis, A pelewensis)*.

Acropora humilis (Dana, 1846) forma α Wells, 1954

Material Examined

QM: Big Broadhurst Reef, SW. side, reef slope: 8·6 m, 14.x.1973, C.W., G1132, G1135; 8·6 m, 15.x.1973, C.W., G11131; 8·7 m, 15.x.1973, G11130; 9·8 m, 16.x.1973, G11134; 10·4 m, 16.x.1973, C.W., G11133; 12·5 m, 17.x.1973, C.W., G11137.

Bowden Reef, SW side, upper reef slope, 26.vii.1972, C.W., G11189.

Darley Reef, patch reef in lagoon: 24.iii.1973, C.W., G11128; 3 m, 22.iii.1973, C.W., G11129; 22.iii.1973, 5 m, C.W., G11611.

Field Diagnosis

Colonies may be low arborescent (with shrub-like growth) caespito-corymbose, or plate-like. Branches are terete (non tapering) or slightly tapering, with wide axial corallites, and large thick-walled radial corallites. Colours are cream-brown, sometimes with pale blue tips, or pale blue or lavender.

Laboratory Diagnosis

Branching pattern: Superimposed on the colony shape described above is usually a high degree of budding. The branches may be as broad as 20 mm, but in the plate like colonies (which occur on reef slopes) and particularly in deeper-water specimens, branches can be as narrow as 8 mm.

Axial corallites: About 2 mm exert. Outer diameter 3·0 to 5·0 mm; inner diameter 1·1 to 1·6 mm. Septation: both cycles present, primaries up to 3/4R, secondaries up to 1/2R.

Radial corallites: Tubular or appressed tubular, with round or oval openings, or nariform, the outer wall thickened. Primary septa are usually present, up to 1/3R; secondary septa not usually fully developed, but some present up to 1/4R.

Coenosteum: Costate to reticulate both on and between radial corallites, with spines that are laterally flattened and sometimes slightly elaborated at the tip.

Within Reef Distribution

This form extends down the reef slope and sloping surfaces of lagoonal patch reefs.

Identification Difficulties and History

Deep water specimens, because of the narrow and proliferous branches, are barely recognisable as *A. humilis*, and begin to have a similar general appearance to *A. sarmentosa*.

Geographic Distribution

A. humilis has a wide Indo-Pacific distribution.

Acropora digitifera (Dana, 1846)

(Plate 84)

Madrepora digitifera Dana, 1846, p.454; Brook, 1893, p.75.

Acropora digitifera: Verrill, 1902, p.228, pl.36, fig.12, pl.36B, fig.3; Vaughan, 1918, p.175, pl.13, fig.7; pl.76, figs.1, 1a, 2; Wells, 1954, p.427, pl.127, figs.1, 2; 1955, p.9; Stephenson and Wells, 1956, p.13 (synonymy).

Acropora fraterna Verrill, 1902, p.247, pl.36, fig.18, pl.36B, fig.9.

Material Examined

YPM: *A. digitifera* type (fragment, ex. Boston Soc. Nat. History) 4192; Tahiti, U.S. Expl. Exped., *A. fraterna* holotype 2032.

QM: Big Broadhurst Reef, SW. side, outer reef flat: 11.x.1973, C.W., G11170; 18.x.1973, C.W., G11169, G11171, G11172; 22.x.1973, C.W., G11168, G11187.

Bushy-Redbill Reef, adjacent Redbill Is., reef flat, 18.xii.1972, C.W., G11176; 2.vi.1975, C.W. G11173, G11174; 5.vi.1975, C.W., G11175; 10.vi.1975, C.W., G11188; 11.vi.1975, C.W., G11177.

Heron Island, W. side, reef flat, July 1973, C.W., G11180.

Oyster Cay, C. Limpus, 1975, G11179.

Fiji Islands: Great Astrolabe Reefs, Yaucuve Levu fringing reef, Jan. 1974, C.W., G11183, G11184, G11186; Vaga Bay, Beqa, patch reefs, 15.i.1974, C. J. Wallace, G11182.

Field Diagnosis

Colonies are corymbose, with central to lateral attachment, and tapering branches. Appearance is of a diminutive, 'neat' *A. humilis*. Colour is commonly cream to pale brown, with or without blue branch tips.

Laboratory Diagnosis

Branching pattern: From a growing area which may be central to lateral, and more or less stalk-like, main branches grow horizontally, and give off secondary branches or bundles of branches vertically to obliquely. These may taper to a point, or be terete, and are from 8 to 20 mm greatest width.

Axial corallites: Non exert. Outer diameter 2·8 to 3·8 mm; inner diameter 0·8 to 1·1 mm. Septation: both cycles developed, primaries up to 2/3R, secondaries up to 1/4R.

Radial corallites: A size gradation occurs from branch tip to proximal and small corallites are interspersed with large. Shape is dimidiate, or tubular with oval to dimidiate opening, radials spreading at 90° from branch. Outer wall is thickened.

Coenosteum: Costate or with regular lines of spines on corallites, spongy with spines in between.

Within Reef Distribution

Limited to the shallow middle reef and outer reef flat pavement *('A. digitifera'* from inner reef flat as interpreted by Wallace and Lovell 1977 is *A. tubicinaria.)*

Identification Difficulties and History

On some reefs (e.g. Enewetak, Marshall Islands) this species is well marked and easily recognised. On the Great Barrier Reef, where *A. digitifera* occurs with *A. humilis*, some colonies cannot be definitely assigned to one or other species on morphological grounds. As Stephenson and Wells (1956) point out, the main difference is in dimensions. A further analysis of one must include the other.

Geographic Distribution

Great Barrier Reef, Moreton Bay (Queensland), Fiji Islands, Marshall Islands, Tahiti.

Acropora multiacuta Nemenzo, 1967

(Plate 85)

Acropora multiacuta Nemenzo, 1967, p.133, pl.39, figs.1, 2, 3; Scheer and Pillai 1974, p.24, pl.6, fig.4.

Material Examined

USNM: (donated): Darley Reef, shallow patch reefs in lagoon, 1 m, 24.iii.1973, C.W.

BM: (donated): Darley Reef, shallow patch reefs in lagoon, 1 m, 24.iii.1973, C.W.

JCU: Philippine Islands, 1975: 3 m, M. Pichon, 2509/75; 5 m, M. Pichon, 2525/75.

QM: Darley Reef, shallow patch reefs in lagoon: 1 m, 19.vii.1972, C.W., G6721, G6722; upper surface, 23.iii.1973, C.W., G10465, G10470, G10471; upper surface, 24.iii.1973, C.W., G10466, G10467, G10469; 1 m, 24.iii.1973, C.W., G10464; 3 m, 22.iii.1973, C.W., G10468.

FIELD DIAGNOSIS

Irregular caespitose to caespito-corymbose colonies from an encrusting central to lateral base, with axial corallites sturdy and prominent, sometimes to the extent of the entire branch or one side of the branch being naked of radial corallites. Colour is whitish blue with pale blue polyps. The largest colony seen to date is 19·5 cm diameter.

LABORATORY DIAGNOSIS

Only twelve Great Barrier Reef specimens have been examined and these show much variation, particularly in the extent of radial corallite presence on the branches, the amount of secondary branching, and the length of the main branches. Some dimensions such as the width of the branches are not included in the diagnosis for this reason.

Branching pattern: From the encrusting base, the main branches arise vertically to obliquely, and may be variously curved. The longest branch in the present collection is 10 cm. At the base of main branches smaller branches may occur. These do not always alter the colony shape, but in the side attached specimens it appears they would contribute to the development of a bracket shape as the colony matured. Some specimens have prolific incipient branching along the main and secondary branches.

Axial corallites: (On the main branches) outer diameter 3·5 to 6·5 mm; inner diameter 1·0 to 2·0 mm. Septation: both cycles present, occasionally a third cycle partially developed, primaries up to 1/3R, secondaries up to 1/4R. On the basal and incipient branches axials are narrower and sometimes compressed so that the opening is oval. These are described as radial corallites by Nemenzo.

Radial corallites: Scattered, nariform, tubo-nariform, or partly appressed tubular; often oriented with opening down or across the branch. Septa not developed at all, or primaries just visible.

Coenosteum: Densely echinulate on both radial corallites and inter-corallite areas; the spines laterally flattened, occasionally some pseudocostate development on the axial corallite.

WITHIN REEF DISTRIBUTION

The only populations seen have been on the upper surface and edges of patch reefs, just below low water. The colonies occur on the surface or in depressions in the irregular reef surface, and the main branches may be curved to maintain an overall vertical orientation. The naked areas of branches are always upwards.

IDENTIFICATION DIFFICULTIES AND NOTES

Nemenzo used the species grouping Alticyathus for this species and for his *A. fastigata* (1967, p.134). The latter may be a synonym, or may be *A. digitifera.* I have not been able to locate Nemenzo's types in the UP collections. On the Great Barrier Reef, the species has only been seen from the Darley Reef lagoon, and it cannot yet be fully categorised.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Nicobar Islands, Philippines, Great Barrier Reef.

Acropora clathrata (Brook, 1891)
(Plates 86, 64C).

Madrepora clathrata Brook, 1891, p.459; 1893, p.49, pl.5, pl.6, fig.A, B.
Madrepora orbicularis Brook, 1892, p.460; 1893, p.37, pl.2 (synonymy);
Madrepora vasiformis Brook, 1893, p.37, pl.26, fig. A (Synonymy).
Acropora vasiformis: Pillai and Scheer, 1976, p.27, pl.3, fig.4.
Acropora tutuilensis (part) Hoffmeister, 1925, p.71, plate 19, figs. 1a–1e.

MATERIAL EXAMINED

BM: Mauritius, *A. clathrata* holotype 1893.4.7.78; Ceylon, *A. orbicularis* holotype 1883.3.24.7; Rodriguez, *A. vasiformis* holotype 1876.5.5.92.

USNM: Pago Pago Harbour, Tutuila, Samoa, *A. tutuilensis* no. 1; ?nos. 2, 3. (Mayor collection) (mentioned Hoffmeister, 1925).

QM: Big Broadhurst Reef, SW. side, reef slope: 5 m, 25.iii.1973, C.W., G9753; 8 m, 26.iii.1973, C.W., G9752; 1 m, 27.iii.1973, C.W., G9748; 3 m, 27.iii.1973, C.W., G9749; 4 m, 27.iii.1973, C.W., G9751; 5 m, 27.iii.1973, C.W., G9750; 1 m, 13.x.1973, C.W., G9742, G9746; 6·3 m, 13.x.1973, C.W., G9735; 7 m, 13.x.1976, C.W., G9743; 7·1 m, 13.x.1973, C.W., G9740, G9741; 7·3 m, 14.x.1973, C.W., G9739; 8 m, 14.x.1973, C.W., G9744, 8·1 m, 14.x.1973, C.W., G9738; 19·7 m, 15.x.1973, C.W., G9737, 4 m, 20.x.1973, C.W., G9745; 10 m, 20.x.1973, C.W., G9759; 1·9 m, 22.x.1973, C.W., G9747; 3·3 m, 22.x.1973, C.W., G9736.

Bowden Reef: slope of opening in SW. side: 0·5 m, 26.vii.1972, C.W., G9760; 1 m, 26.vii.1972, C.W., G9761; SW. side, reef slope, 1 m, 15.vii.1972, C.W., G9762.

Bushy-Redbill Reef: NW. side, reef slope, Dec. 1972, C.W., G9754; NNE. end, 30.xii.1972, C.J.W., G9755; S. end, reef slope, 3 m, 3.vi.1975, C.W., G9756; reef slope adjacent Redbill Is., 0·5 m, 1.vi.1975, C.W., G9758; 1 m, 2.v.1975, C.W., G9757.

Darley Reef: patch reef in lagoon, 3 m, 18.vii.1972, C.W., G9763.

FIELD DIAGNOSIS

Horizontal plate (reaching approx. 1·2 m diameter), developing by unilateral expansion from a vasiform shape with a single attachment, which becomes lateral as the colony develops. The plate has a flat appearance, due to the orientation of the secondary branchlets in the plane of the plate or obliquely to it. Common colours are pinkish brown, apple green and yellowish green.

LABORATORY DIAGNOSIS

Branching pattern: From the attaching stalk, branching is oblique to horizontal. Secondary branches arise in the same plane as primary branches, or obliquely to them, forming a single layer or a series of interlacing layers. All branches, except those towards the edge zone, are of similar diameter. Anastomosis of branches varies, so that anything from an open network to a solid plate (with branches either fused to the plate or projecting obliquely from it) is possible.

Axial corallites: Outer diameter 1·5 to 2·2 mm, inner diameter 0·6 to 0·9 mm. Septation: primary septa present, up to 1/3R, secondaries usually not visible, or a few present to less than 1/4R.

Radial corallites: A number of shapes are possible, and specimens may possess all, some, or only one of the possible types, viz. tubular, with round, oval, or dimidiate openings, tubo-nariform, nariform, rostrato-nariform, dimidiate, sub-immersed or immersed. Immersed corallites usually only occur along lines of fusion of branches. The other types project from the branch, at from 90° to 45°, occasionally less. There is a tendency for differential thickening or extending of the longer wall sometimes with bizarre extensions such as long points on nariform and horns on dimidiate corallites. Plate 86 shows:

(D) all uniform size, nariform or dimidiate with differential outer wall development.

(B) mixed size, tubular with round, oval, and dimidiate openings, immersed and sub-immersed.

(F) similar to B, but corallites more appressed and scattered.

Septation: septa are never well developed; usually only the directive septa are visible, or a few other primaries present as small spines. As the corallites are rarely appressed, they appear well spaced and there is always some coenosteum between.

Coenosteum: On unthickened corallites this may be visibly porous and is usually costate, on thickened radials it is composed of compactly arranged flattened spines, sometimes pseudocostate. Between corallites it is reticulate.

IDENTIFICATION DIFFICULTIES AND HISTORY

This coral occurs with the other large horizontal plate *Acropora (A. hyacinthus* and *A. cytherea)*, from which it is easily separated by its flattened appearance and by the lack of scale-like corallite lips. Identification difficulties occur at the laboratory stage, where so many different combinations of colony features and corallite size and shape are seen. This variety is demonstrated in the synonymy: *A. clathrata s.s.* has narrow branches, openly reticulated, and radial corallites are tubular, with a variety of sizes and opening-shapes; *'A. orbicularis'* and *'A. vasiformis'* are almost solid plates, *'A. vasiformis'* with rostrate thickening of many radial corallites, *'A. orbicularis'* with unthickened radials in a variety of shapes. Hoffmeister's no. 1. specimen of *A. tutuilensis* is a partly fused plate of this species. His no.4 is probably *A. rotumana*. All the type specimens can be compared with specimens in the QM series. *A. stigmataria* (Milne Edwards and Haime) (see Brook 1893, p.50), may be a senior synonym but its type cannot be located for examination.

WITHIN REEF DISTRIBUTION

The species appears to be restricted to sloping surfaces or good water cover. Very large specimens can occur around low water mark on the edge of surge channels, on the upper reef slope, and on the floor of surge channel openings (see Plate 64C).

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Mauritius, Rodriguez, la Reunion (G. Faure pers. comm.), Ceylon, Seychelles (?), Great Barrier Reef, Samoa.

Acropora divaricata (Dana, 1846)
(Plates 87, 88)

Madrepora divaricata Dana, 1846, p.477, pl.41, fig.2; Milne Edwards and Haime, 1860, p.140; Brook, 1893, p.64.

Madrepora tenuispicata Studer, 1880, p.20, figs.1a, 1b; Brook, 1893, p.96.

Acropora tenuispicata: Pillai and Scheer, 1974, p.455, fig.4b.

?*Madrepora complanata* Brook, 1891, p.459; 1893, p.70, pl.4, fig.C.

Acropora complanata: Pillai and Scheer, 1976, p.28, pl.7, fig.2.

?*Madrepora complanata* var. *informis* Brook, 1893, p.71.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. divaricata* holotype 299.

YPM: Fiji Islands, U.S. Expl. Exped., *A. divaricata* fragment of type 2008.

BM: Seychelles, H.M.S. Alert, *A. complanata* syntypes 1882.10.17.140, .147, .148; Macclesfield Bank, 13 fathoms, *A complanata* var. *informis* syntypes 1892.10.17.71, .72, .73.

Hessisches Landmuseum: *Acropora tenuispicata* (colour transparencies only) (mentioned Pillai and Scheer 1974).

QM: Big Broadhurst Reef: SW. side, reef slope: 12·4 m, 23.x.1973, C.W., G9162; 11 m, 16.x.1973, C.W., G9166; 9·8 m, 16.x.1973, C.W., G9167; 9·6 m, 15.x.1973, C.W., G9164; 8·7 m, 15.x.1973, C.W., G9170, G9173; 8·6 m, 15.x.1973, C.W., G9174, G9175; 8·3 m, 15.x.1973, C.W., G9163, G9172; 8·1 m, 14.x.1973, C.W., G9161, G9168; 8 m, 14.x.1973, C.W., G9160, G9165, G9178; 7·8 m, 14.x.1973, C.W., G9171, G9176, G9177; 7·6 m, 28.iii.1973, C.W., G9180; 7·1 m, 13 x.1973, C.W., G9169; 7 m, 28.iii.1973, C.W., G9181, G9188; 6 m, 26.iii.1963, C.W., G9179; 6 m, 25.iii.1973, C.W , G9184.

Bushy-Redbill Reef: W. side, reef slope: 8 m, 3.vi.1975, C.W., G9186; 2 m, 3.vi.1975, C.W., G9185; NW. side, reef patches, 12 m, 14.vi.1975, C.W., G9187.

Darley Reef: patch reefs in lagoon: 7 m, 22.iii.1973, C.W., G9182; 3 m, 18.vii.1972, C.W., G9184; 22.iii.1973, C.W., G10219.

Fiji Islands, Great Astrolabe Reefs (Kadavu), W. side of Yaukuve Levu, fringing reef, 1.ii.1974, C.W., G9781, G9782.

FIELD DIAGNOSIS

Occurs as bracket like colonies with central to lateral attachment, 'corymbose' in having all branches reaching up to a horizontal plane, and 'caespitose' in having divaricate branching within the boundaries of the colony shape. Reaches approximately 50 cm diameter. Branches appear rough because of projecting radial corallites. Colour is usually a drab dark brown or dark brown with blue tips.

LABORATORY DIAGNOSIS

Although the species is easily recognised in the field, skeletal fragments can be confusing. Branchlet dimensions and radial corallite shape are variable amongst colonies in a single population, and pieces taken from different parts of the same corallum may appear different because of their orientation.

Branching pattern: From a single area of attachment, branching is central to lateral. Periferal branches contribute to an oblique undersurface; inside these is a network of short branchlets at wide angles, the final branchlets being erect or nearly so, and ending in a horizontal plane. Branchlet widths vary from 7 mm to 15 mm.

Axial corallites: Outer diameter 2·3 to 3·0 mm; inner diameter 0·8 to 1·1 mm. Septation: primary septa present, up to 1/2R, secondary septa poorly developed, but usually some present, up to 1/4R.

Radial corallites: Shape and size of the radial corallites changes along the branches. On upper branchlets they are prominent (up to 3 mm long), usually extending at from 45° to 90°. They are usually tubular on branch tips, passing through tubo-nariform to nariform, then rounded to sub-immersed proximally. The prominent radials are sometimes extended by rostrate development (see Plate 88 C, D). Within the sequence from distal to proximal, radials are usually evenly graded and neatly arranged, but they can be unevenly graded, so that branches appear ragged (Plate 88 A), and downward directed radials can occur anywhere along the branch.

WITHIN REEF DISTRIBUTION

This coral occurs in the higher diversity (for *Acropora)* parts of the reef, where no particular colony shape predominates: middle reef slope, deeper outer reef flats, patch reefs in deep lagoons and leeward broken reef areas. The species, although common, has a drab appearance when alive, and is easily missed when subjective observation techniques are used.

IDENTIFICATION DIFFICULTIES AND HISTORY

The radial corallites of this species are similar to those of the flat plate species, *Acropora clathrata.* I have not found specimens of *Acropora divaricata* deep enough to form flat plates but am confident that *A. complanata* (Brook), a flat plate species dredged from deep water, represents deep water flattening of *A. divaricata.* For *A. tenuispicata* (Studer) I have drawn on Pillai and Scheer's (1974) interpretation of this species. The type is not in the MNB, where the remainder of the Studer types are located. The combination of a determinate bracket with divaricate branching is unique in the *Acropora*. The shape has not been emphasised in previous descriptions. A series in the JCU from Lizard Island fringing reefs shows more rounded colony shape, with slender branches, often naked of radial corallites on their upper surface.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Seychelles, Singapore, Fiji Islands, Great Barrier Reef.

Acropora sarmentosa (Brook, 1892)
(Plate 89)

Madrepora sarmentosa Brook, 1892, p.462; 1893, p.127, pl.22
Acropora sarmentosa: Nemenzo, 1967, p.90, pl.26, fig.4.
non *Acropora sarmentosa:* Vaughan, 1918, p.174, pl.72, fig.4, pl.73, fig.1.
Acropora rosaria form 1: Crossland, 1952, p.224, pl.40, fig.3.

MATERIAL EXAMINED

BM: Port Denison, Saville Kent, *A. sarmentosa* syntype 1892.6.8.228.

UP: Little Balatero Cove, Puerto Gaelera, Oriental Mindoro, Nemenzo 259; Muelle, Puerto Gaelera, Oriental Mindoro, Nemenzo 324 (mentioned Nemenzo, 1967).

QM: Big Broadhurst Reef, SW. side, reef slope: 17m, 24.x.1973, C.W., G9064, G9065; 15·7m, 23.x.1973, C.W., G9062; 15·4m, 17.x.1973, C.W., G9056; 9·7m, 15.x.1973, C.W., G9059; 8·1m, 14.x.1973, C.W., G9055; 8m, 28.iii.1973, C.W., G9054; 7·6m, 13.x.1973, C.W., G9057; 6·8m, 20.x.1973, C.W., G9058; 4·1m, 22.x.1973, C.W., G9061.

Bowden Reef, slope of opening in SW. side, 1–2m, 23.viii.1972, C.W., G9066.

Bushy-Redbill Reef, NW. side, reef slope: 30.xii.1972, E. Lovell, G9071; 3–7m, 21.xii.1972, E. Lovell, G9073; NW. side, reef crest, 30.xii.1972, C.W., G9070; NW. side, patch reefs: 12m, 15.vi.1975, C.W., G9075; 12m, 14.vi.1975, C.W., G9060; SW. side, reef crest, 24.v.1975, C.W., G9063; outer reef flat adjacent Redbill Island 1.vi.1975, C.W., G9072; 22.xii.1972, E. Lovell, G9074.

Darley Reef, patch reefs in lagoon. 6m, 22.iii.1973, C.W., G9067; 4m, 22.iii.1973, C.W., G9068; 2.5m, 24.iii.1973, C.W., G9069.

Heron Island, W. side, reef flat, 6.vii.1973, Y. Loya, G9704.

Ellison Reef: dredged 9 fathoms, 25.vii.1924, Dr Paradice, G9709; 24.vii.1924, C. Hedley, G9707.

Fiji Islands, Great Astrolabe Reefs: Qasilabe fringing reef, 4–6m, 4.ii.1974, C.W., G9710; Yaukuve Levu, W. side, fringing reefs, 8m, 1.ii.1974, C.W., G9705.

FIELD DIAGNOSIS

Colonies of this species usually have few (commonly 2 or 3) thick rounded branching units, consisting of a central horizontal to oblique branch or branches, with vertical branchlet bundles evenly distributed, but longer on the upper side. Colonies of more than 50 cm across are unusual, and attachment is usually from the side. The overall appearance is smooth — axial corallites are not exert, radial corallites are large, evenly distributed, uniformly sized and not projecting; secondary branching patterns are regular and branchlets terete. The usual colouration on the Barrier Reef is two-toned, and cryptic — most often a dull greenish-grey or -brown, with pale brown or pink tips to the branchlets. This colouration occurs also in the Fijian reefs. On patch reefs in deep lagoonal situations, the colony can assume a sturdy rounded shape with central attachment.

LABORATORY DIAGNOSIS

Branching pattern: From a side attachment, branching is horizontal or oblique, with two to several main branches. Vertical to acute branchlets occur at regular intervals along the main branches; these usually branch again, one to several times, and are shorter and narrower on the under surface. Upper surface branchlets are 5 to 9 mm wide.

Axial corallites: Outer diameter 3·0 to 4·0 mm, up to 7 mm in lagoonal specimens; inner diameter 1·0 to 2·0 mm. Septation: 12 septa or slightly less, usually well developed (primaries to 3/4R, secondaries to 1/2R).

Radial corallites: All of similar size, neatly and evenly arranged around the branchlet, appressed tubular. (Brook described them as 'swallow-nest shaped'). In shallow water specimens the wall is thick, and corallites are densely packed around the branchlet. With increasing depth, radial corallites become more scattered, thinner walled, and the wall may flare a little, and appear lip like.

Coenosteum: Spines which may be laterally flattened or slightly elaborated are arranged evenly both on radials and between: sometimes radial walls are costate.

WITHIN REEF DISTRIBUTION

Reef slope from crest to limits of depth of *Acropora* distribution (species no. 18 in Wallace 1975); deeper water diverse reef flats and lagoonal patch reefs; sporadically in shallow outer reef situations where there is space for outward growth; fringing reefs. The species is never very abundant, but is usually present in most reef habitats.

IDENTIFICATION DIFFICULTIES AND HISTORY

In the field, lower reef slope specimens of this species and of *A. florida* may appear similar. The two-toned colouration, thicker branchlets and smoother general appearance of *A. sarmentosa* can distinguish it. Vaughan (1918) suggested that *A. sarmentosa* may be a growth form of *A. squamosa* (= *A. millepora)*. His specimens were not *A. sarmentosa* but were indeed '*A. squamosa*'. His misidentification of this species may account for it being overlooked in much of the literature. Both Brook and Nemenzo describe their specimens well.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Philippines, Great Barrier Reef, Fiji Islands.

Acropora florida (Dana, 1846)
(Plates 90, 91, 92)

Madrepora florida Dana, 1846, p.466, pl.37, fig.1.
non *Madrepora florida:* Brook, 1893, p.53.
Madrepora gravida Dana, 1846, p.470; Brook, 1893, p.59 (synonymy).
Acropora gravida: Nemenzo, 1967, p.107, pl.31, fig.3; Scheer and Pillai, 1974, p.18, pl.5, fig.1; Pillai and Scheer, 1974, p.453.
Madrepora mirabilis Quelch, 1886, p.159, pl.10, fig.5; Brook, 1893, p.125.
Madrepora compressa Bassett-Smith, 1890, p.452; Brook, 1893, p.60, pl.33, fig.F.
Madrepora affinis Brook, 1893, p.60, pl.28, fig.F (synonymy).
Acropora affinis: Crossland, 1952, p.205, pl.34, fig.1; Nemenzo, 1967, p.77.
Acropora vermiculata Nemenzo, 1967, p.108, pl.31, fig.4.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. florida* holotype 282.

YPM: Fiji Islands, U.S. Expl. Exped., *A. florida* fragment of type 2002.

BM: Tizard Bank, China Sea, 5 fthms, *A. compressa* holotype 1889.9.24.117; Darnley Island, J.B. Jukes, *A. affinis* syntype 1846.7.30.29; Banda, Challenger, *A. mirabilis* holotype 1885.2.1.14; Claremont Is., G.B.R., Saville Kent, *A. ornata* var. (id. Brook) 1892.6.8.112.

QM: Big Broadhurst Reef: S W. side, reef slope: 15·3m, 17.x.1973, C.W., G8649; 11·3m, 17.x.1973, C.W., G8653; 9·3m, 16.x.1973, C.W., G8647; 9·3m, 17.x.1973, C.W., G8646; 8·6m, 17.x.1973, C.W., G8648, G8654; 8·6m, 16.x.1973, C.W., G8661; 8m, 28.iii.1973, C.W., G8664; 7·9m, 15.x.1973, C.W., G8650; 7·4m, 15.x.1973, C W., G8656, G8662; 6·6m, 14.x.1973, C.W., G8655, G8657, G8667; 6m, 27.iii 1973, C W., G8665; 6m, 25.iii.1973, C.W., G8666; 5·8m, 13.x.1973, C.W., G8651; 5·2m, 13.x.1973, C.W., G8645; 3m, 25.iii.1973, C.W., G8669; 2·3m, 11.x.1975, C.W., G8644; 2m, 25.iii.1973, C.W., G8661, G8663, G8668, G8670; S W. side, surge channel, 8·5m, 20.x 1973, G8658, G8659; S W. side, outer reef flat, 18.x.1973, G8652.

Low Isles, June 1974, C. Limpus, G8672.

Murray Islands (Maer Is.), 18.vii.1974, G. Ingram, G8671.

Bowden Reef, S. end, reef slope, 3·3m, 15.vii.1972, C.W., G6726.

Darley Reef, lagoonal patch reef, 3–5m, 19.vii.1972, C.W., G6725.

Viper Reef, lagoonal patch reef, 1·5m, 16.vii.1972, C.W. G6724.

Fiji Islands, Makaluvau Reef, outer reef flat, 10.i.1974, C.W., G10273.

FIELD DIAGNOSIS

This is a sturdy open arborescent species, in which the surface of the branches is covered by short secondary branchlets. It is highly variable in two aspects, the shape of the colony and the density and prominence of the secondary branchlets. The colony shape changes with depth and slope of the attaching surface. In shallow water and flat substrate it forms a rounded, open colony with central attachment; on sloping surfaces the attachment is more lateral, and the branches tend to extend horizontally. With increasing depth the branches become flatter. The secondary branchlets vary from evenly distributed with even lengths to scattered and variously sized and may even be undeveloped on some branches. The most irregular colonies occur in fringing reef situations.

LABORATORY DIAGNOSIS

Branching pattern: Sturdy main branches divide sparsely to form an upright bush. The shape of the colony and the cross-sectional shape of the branch become flatter with increasing water depth. The branches usually proliferate towards the branch tips into shorter branches. The surface of the branches is covered with short branchlets. Except on completely vertical branches the branchlets are shorter on the under-surface (to absent on horizontal branches).

Axial corallites: Outer diameter 2·0 to 3·0 mm; inner diameter 0·8 to 1·4 mm. Septation: primary septa present, up to 2/3R; secondary septa usually all developed, or at least 3 present, up to 1/2R.

Radial corallites: Evenly sized and distributed, appressed tubular with round opening, with wall which may flare slightly. Septation: primary septa present, up to 1/2R, some to all secondaries present, up to 1/4R.

Coenosteum: Costate or reticulate on radial corallites, reticulate in between, with scattered simple spines.

WITHIN REEF DISTRIBUTION

Entire reef slope from reef crest to limits of *Acropora* growths; deep water lagoonal patch reefs, fringing reefs. Occasionally on middle or outer reef flat. It is well known as an early recolonizer on the fringing reefs near Townsville, N.Q. (D. Tarca, pers. comm.).

IDENTIFICATION DIFFICULTIES AND HISTORY

The variability of the species is expressed in the synonymy. Brook misunderstood *A. florida:* his specimens in the BM are possibly *A. rotumana. A. florida s.s.* is atypical of the species as it appears on the Great Barrier Reef in that the corallites are larger and the branchlets poorly developed: G6725 is closest to this. The species is best described by *A. affinis*, which has evenly sized and distributed branchlets; its similarity to *A. gravida* was apparent to Brook. *A. compressa* is named from a flat plate specimen of this species. *A. mirabilis* is named for a single aberrant specimen which is probably this species under some environmental stress.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Singapore, Celebes, Philippines, Strait of Malacca, Nicobar Islands, Great Barrier Reef, Fiji Islands, Enewetak Atoll (C.W.).

THE **'Acropora echinata'** GROUP

The species *Acropora echinata, A. subglabra, A. carduus* and *A. longicyathus*, with their synonyms, have in common their shape, radial corallite structure and coenosteal structure.

The growth forms are comparable within the group, and nothing exactly similar is found outside the group. The branches are commonly labelled 'bottlebrush': secondary branchlets, or bundles of branchlets, are given off evenly around the main branches, giving a round brush like unit. The growth of a colony is indeterminate, the units being capable of openly branching or closely proliferating, giving a variety of form in collected specimens. The colonies tend to occur on rubble or sandy floors, and the bases of branch units are usually dead. If the colonies occur in deep sloping conditions, they are small and approach a flattened form.

The radial corallites are round tubular appressed or partly appressed, tending to develop into axial corallites. Their numbers relative to the number of axials are lower than in most other groups. In all species, the number of radial corallites per axial decreases distally on the branch unit, so that long naked axials may occur around the base.

The spines of the coenosteum have multiple tips, and the coenosteal appearance on and between radials is similar.

The main differences among the species are in the corallite dimensions and the amount of elaboration of the coenosteal spines.

These species occur only in the sheltered, deeper parts of reefs, where almost any *Acropora* species can survive. They appear to have poor differentiation of radial corallites from axials, and if this is accompanied by a similar lack of functional differentiation it may account for their lack of colonizing success.

Acropora echinata (Dana, 1846)

Madrepora echinata Dana, 1846, p.464, pl.36, fig.1, 1a; Brook, 1893, p.185 (synonymy).

Acropora echinata: Vaughan, 1907, p.158, pls.49, 50; Wells, 1954, p.423, pl.135, figs. 1–4, pl.136, figs 1–6 (synonymy); Nemenzo, 1967, p.126; Pillai and Scheer, 1976, p.33, pl.11, figs.1, 2.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exp., *A. echinata* syntype 275.

UP: Batangas Channel, Puerto Galera, Oriental Mindoro C1064 (mentioned Nemenzo, 1967).

I have not seen this species in the central and southern Great Barrier Reef. A single specimen in James Cook University was collected at Lizard Island on a sandy bottom. A large specimen in the Queensland Museum bearing no locality data has been presumed to be from the Great Barrier Reef. The species is well described and illustrated by other authors. Further notes are given with *A. subglabra*.

GEOGRAPHIC DISTRIBUTION

Philippines, Sulu Sea, Great Barrier Reef, Fiji Islands, Samoa, Marshall Islands.

Acropora subglabra (Brook, 1891)
(Plate 94A, B)

Madrepora subglabra Brook, 1891, p.470; 1893, p.186, pl.29, fig.c (synonymy).

Acropora subglabra: Thiel, 1933, p.24.
M. subglabra var. *rugosa* Brook, 1893, p.187.
Acropora subglabra var. *rugosa:* Nemenzo, 1967, p.125, pl.35, fig.2.
Madrepora procumbens Brook, 1893, p.188, pl.29, fig.d.
Acropora procumbens: Thiel, 1932, p.130, pl.10, fig.2; Nemenzo, 1967, p.127–128, pl.35, fig.1.

MATERIAL EXAMINED

BM: *A. procumbens* syntype 1843.3.6.131; South Seas, *A. subglabra* syntype 1841.12.11.1.

UP: *A. subglabra* var. *rugosa* C731 (mentioned Nemenzo, 1967).

QM: Lizard Island fringing reef, June 1973, R. Pearson, G10713, G10714.

FIELD DIAGNOSIS

Sprawling, shrubby bottlebrush colonies, of very slender proportions, colour pale brown or pinkish brown.

LABORATORY DIAGNOSIS

Branching pattern: Main branches may have any orientation from vertical to horizontal. Secondary branchlets distributed evenly around main branches, up to 30 mm long, undersurface branchlets being shorter than upper surface branchlets in horizontal branches.

Axial corallites: Outer diameter 0·9 to 1·5 mm; inner diameter 0·5 to 0·8 mm. Septation: primaries complete, to 3/4 R, secondaries absent or some present to less than 1/4R.

Radial corallites: Scattered appressed tubular, tubo-nariform or nariform, up to 3 mm long. Non-appressed tubular radials are incipient axials.

Coenosteum: Lines of elaborate spines both on and between radial corallites.

WITHIN REEF DISTRIBUTION

The species apparently does not occur in the Central and Southern Great Barrier Reef province, but is present further north, in situations below the reef flat.

IDENTIFICATION DIFFICULTIES AND HISTORY

This species requires field study. Brook's description of *A. procumbens* was on the basis of 'contracted (axial corallite) apertures', but in fact the internal axial diameter of the type is only an average 0·1 mm less than that of the *A. subglabra* type. *A. echinata* (Dana) is a similar species of slightly larger dimensions, and it is probable that this is a (senior) synonym.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Singapore, Philippines, Banda, Great Barrier Reef.

Acropora carduus (Dana 1846)
(Plates 93A, 94C, D)

Madrepora carduus Dana, 1846, p.464, pl.36, fig. 2; Brook, 1893, p.178 (synonymy).
Acropora carduus: Faustino, 1927, p.277, pl.93, figs.1, 2; Nemenzo 1967, p.123–4, pl.34, fig.3.

MATERIAL EXAMINED

USNM: Sooloo Sea, U.S. Expl. Exped., *Acropora carduus* paratype? 277 (N.B. Rathbun (1887) records 278 from Fiji as type).

QM: Big Broadhurst Reef, S W. slope: 6 m, 25.iii.1973, C.W., G10729, G10730; 6·3 m, 23.x.1973, C.W., G10738; 7·8 m, 14.x.1973, C.W., G10733; 8 m, 26.iii.1973, C.W., G10731; 8 m, 14.x.1973, C.W., G10734; 9·6 m, 15.x.1973, C.W., G10736; 9·8 m, 16.x.1973, C.W., G10737; 12·4 m, 23.x.1973, C.W., G10732; 16·2 m, 23.x.1973, C.W., G10735.

Bowden Reef, SW. side, reef slope, 2 m, 26.vii.1972, R. Pearson, G10741, G10742.

Bushy-Redbill Reef: NW. side, sandy floor around patch reefs, 15 m, 15.vi.1975, C.W., G10739; W. side, reef crest, 2 m, 3.vi.1975, C.W., G10740.

Fiji Islands, Great Astrolabe Reefs, Jan. 1974, C.W., G10744.

FIELD DIAGNOSIS

Arborescent to shrubby, bottlebrush branched colonies of dimensions intermediate between those of *A. subglabra* and *A. longicyathus.* Colour: cream, pale brown, or pink-brown.

LABORATORY DIAGNOSIS

Branching pattern: Growth indeterminate, main branches covered by short branchlets, which are evenly distributed, more or less equal in size and extending at 45° to 90° from the branch. Total diameter of this 'bottlebrush' is 15 to 30 mm, with branchlets up to 12 mm long and 5 mm wide. Main branches may be proliferous, giving a shrubby appearance, or sparsely branching, giving an arborescent appearance: usually both types of branching occur within a colony. In deep water (e.g. specimen G10735) the branchlets develop on the upper surface of the colony only, and the colony is effectively reduced to a small plate.

Axial corallites: From non exert (budding at tip) to 7 mm exert. Outer diameter 1·0 to 2·0 mm; inner diameter 0·5 to 0·8 mm. Septation: primary septa well developed, up to 3/4R, secondary septa absent, or some present, to 1/4R.

Radial corallites: On branchlets, scattered appressed tubular, sometimes approaching nariform, with round openings. On some colonies radials crowded, partly appressed tubular and extending out from branchlets. On the main branches radials are sub-immersed to immersed, or in some cases tubular appressed. Primary septa poorly to well developed to 1/2R, secondaries usually absent except in immersed corallites, where a few may be present. Radial corallites are best represented on distal parts of branches. At the bases of branches most have developed into long tubular axials.

Coenosteum: finely echinulate on radial corallites and between. Occasionally spines are arranged in rows or even joined as costae.

WITHIN REEF DISTRIBUTION

Reef slope, from below the area of rough water surge to about 20 m; deep water reef flat areas, sandy floors of lagoons and reef-edge patch reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

Being a deeper water species, *A. carduus* is poorly represented in older collections, and hence presents few historical problems. It occurs with *A. longicyathus*, and they can be easily separated by obvious differences in corallite dimensions.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Philippines, Sulu Sea, Great Barrier Reef, Fiji Islands.

Acropora longicyathus (Milne Edwards and Haime, 1860)
(Plates 93B, 95)

Madrepora longicyathus Milne Edwards and Haime, 1860, p.148; Brook, 1893, p.187 (Synonymy).
Acropora longicyathus: Nemenzo, 1967, p.128, pl.35, figs. 3, 4.
Madrepora prolixa Verrill, 1866, p.22.
Acropora prolixa: Verrill, 1902, p.237, pl.36, figs. 3, 3a, pl.36A, Figs. 3, 3a; pl.36F, fig.14; Hoffmeister, 1925, p.65, pl.16; Crossland, 1952, p.226.

MATERIAL EXAMINED:

PM: *A. longicyathus* type 303A.

USNM: Ousima, *A. prolixa* syntype 414.

QM: Big Broadhurst Reef, S W. side, reef slope: 6m, 25.iii.1973, C.W., G10763; 7m, 27.iii.1973, C.W., G10767; 8m, 26.iii.1973, C.W., G10762, G10764; 9m, 15.x.1973, C.W., G10751, G10752; 9·6m, 15.x.1973, C.W., G10753; 9·7m, 15.x.1973, C.W., G10754; 9·8m, 16.x.1973, C.W., G10755; 10·3m, 16.x.1973, C.W., G10756; 10·6m, 16.x.1973, C.W., G10757, G10758; 12m, 16.x.1973, C.W., G10759; 12·5m, 17.x.1973, C.W., G10760; surge channel, 10m, 20.x.1973, C.W., G10761.

Bushy-Redbil Reef: W. side, outer flat, 31.v.1975, C.W., G10745; reef slope near Redbill Is., 3m, 1.vi.1975, C.W., G10746; W. side, patch reefs (sandy floor), 8m, 3.vi.1975, C.W., G10747, G10748; N W. side, patch reefs (sandy floor) 12m, 14.vi.1975, C.W., G10749, G10750.

FIELD DIAGNOSIS

Arborescent to shrubby, bottlebrush branched colonies of sturdy dimensions. Colour: cream, pale to dark brown, or blue-brown.

LABORATORY DIAGNOSIS

Branching pattern: Growth indeterminate, main branches covered by evenly distributed proliferous branchlets or bundles of branchlets. These are directed at 45° to 90° to the branch, and may be as short as 5 mm all over branch, or all several centimetres long and much branched. Greatest total branch width is 80 mm, smallest (except for branch tips) 40 mm. Deep-water colonies can have little undersurface development, and approach a plate like shape.

Axial corallites: Sometimes exert (to 10 mm) near base of branch, more often one side naked of radial corallites, other side with 3 or 4 from their outer rim. Outer diameter 2·1 to 2·8 mm; inner diameter 0·8 to 1·3 mm. Septation: primary cycle present to 3/4R, secondary cycle present, or at least partly developed up to 1/4R.

Radial corallites: On branchlets, appressed or partly appressed tubular with round openings. When fully appressed, radials are scattered, only a few to each axial corallite: however, branchlets can have radials touching. In the first case, radials on main branches are immersed or (more usually) sub-immersed; in the second, main branch radials are usually similar to those of branchlets.

Coenosteum: Neatly echinulate on and between corallites, the spines laterally flattened with simple to forked or more elaborate tips.

WITHIN REEF DISTRIBUTION

Reef slope, from below the area of rough water surge to about 20m; deep water reef flat areas, sandy floors of lagoons and leeward patch reefs.

IDENTIFICATION DIFFICULTIES AND HISTORY

The two species *A. longicyathus* and *A. prolixa* have been combined by other authors: Verrill's specimens were small branch tips. This species is not well represented in collections.

GEOGRAPHIC DISTRIBUTION

Philippines, Ousima, Samoa, New Guinea, Great Barrier Reef.

THE '*Acropora squarrosa*' GROUP

The group of species *A. elseyi, A. rosaria, A. squarrosa* and *A. granulosa* has in common (1) dense echinulate coenosteum of elaborate spines, (2) large tubular to nariform radial corallites, and (3) a tendency for some branchlets to have an upper surface naked of radial corallites. The group is linked to the '*A. echinata*' group which has, however, less differentiated radial corallites.

The synonyms adopted here may be controversial. Most of the species involved seem to be well documented in the literature, but they still present extraordinary' identification problems. The synonymics are presented as hypotheses requiring further testing.

The oldest name for the group, *A. squarrosa* (Ehrenberg) has been treated by a number of authors (e.g. von Marenzeller 1907, Vaughan 1918, Wells 1954), but the interpretations are various and sometimes confusing. *A. granulosa*, with its synonyms here listed, links this group to the '*A. echinata*' group.

A. microphthalma, as here interpreted, is included in the group because of its coenosteal structure.

Acropora microphthalma (Verrill, 1869)
(Plate 96)

Madrepora microphthalma Verrill, 1869, pp.83, and 102.

Acropora microphthalma: Verrill, 1902, p.232, pl.36C, fig.1, 36F, fig.15.

?*Acropora microphthalma:* Wells, 1954, p.429, pl.126, figs. 7–9 (synonymy).

non *Acropora microphthalma:* Stephenson and Wells, 1956, p.10.

Acropora laevis (part) Crossland, 1952, p.230.

MATERIAL EXAMINED

YPM: Ryuku Islands, *A. microphthalma* holotype 774 (fragment).

QM: Big Broadhurst Reef, SW. side, reef slope: 3m, 28.iii.1973, C.W., G8684; 4m, 13.x.1973, C.W., G8688, G8689; 6m, 25.iii.1973, C.W., G8685; 6·4m, 14.x.1973, C.W.,, G8693; 7·8m, 15.x.1973, C.W., G8691; 8m, 26.iii.1973, C.W., G8683, G8686; 8m, 28.iii.1973, C.W., G8682; 9·1m, 16.x.1973, C.W., G8690; 9·4m, 16.x.1973, C.W., G8692.

Bowden Reef, SW. side, reef crest, 0·5m, 24.vii.1972, C.W., G8680.

FIELD DIAGNOSIS

An aborescent species forming small clumps (up to 100 cm across) the branches having slender dimensions, and radial corallites being small and crowded. Colour is most commonly a whitish-cream. Although because of its size it is not a conspicuous species, it is the most delicate arborescent coral in the Great Barrier Reef area, and is easily recognized.

LABORATORY DIAGNOSIS

Branching pattern: Branching is open arborescent, with many short branchlets being given off towards branch tips at 45° to 90° to the main branches. The greatest branch width measured in the collections is 14 mm, the smallest (excluding branchlets) 5 mm.

Axial corallites: Outer diameter 1·8 to 2·3 mm; inner diameter 0·8 to 1·00 mm. Septation: primary septa strongly developed, up to 3/4R, secondaries absent, to present up to 1/4R.

Radial corallites: Extend at about 45°, short tubular with round to oval opening to tubo-nariform, outer wall slightly thickened. First septal cycle well developed, up to 2/3R, second cycle usually partially represented. Radials are uniform in size and evenly distributed, giving a fine-grained appearance to the branches.

Coenosteum: When spines are well developed, they have elaborate tips and are distributed both on corallites and between. However, lightly calcified coralla may have simple pointed spines and a generally spongy appearance.

WITHIN REEF DISTRIBUTION

Middle reef flat, deeper reef flat areas, sandy floors around patch reefs, reef slope to surge channel floor.

IDENTIFICATION DIFFICULTIES AND HISTORY

Interpretation of *A. microphthalma* from Verrill's poor series is difficult and previous identifications have linked it with *A. exilis*. The *A. microphthalma* of Stephenson and Wells (1956) (no. G2697, QM) is in my opinion *A. nasuta*.

The species as here interpreted is distinctive, particularly in the field, and the fragment I have seen of Verrill's type compares well with the tips of the larger dimensioned specimens. At least one specimen of Crossland's *A. laevis* series (BM 1934.5.14.67) is this species.

GEOGRAPHIC DISTRIBUTION

Ryuku Islands, Great Barrier Reef, Fiji Islands (C.W.), Enewetak Atoll (C.W.).

Acropora elseyi (Brook, 1892)
(Plate 97 A, B.)

Madrepora elseyi Brook, 1892, p.456; 1893, p.172, pl.11, figs. E, F.
Acropora elseyi: Crossland, 1952, p.223; Pillai and Scheer, 1976, p.31, pl.9, fig.1.
Madrepora exilis Brook, 1892, p.457; 1893, p.172, pl.10, figs. C, D.
Acropora exilis: Crossland, 1952 (part), p.223, pl.39, fig.4; Stephenson and Wells, 1956, p.13, pl.1(b) (synonymy).

MATERIAL EXAMINED

BM: N. Australia, J. Elsey, *A. elseyi* syntypes 1857.11.18.214, 215, 216, 217, 218; Thursday Is., Saville-Kent, *A. elseyi* 1892.6.8.241–4, 6; Rocky Is. Saville-Kent, *A. elseyi* 1892.6.8.247 (mentioned Brook, 1893). Port Denison, Saville-Kent, *A. exilis* syntypes, 1892.6.8.103, 104, 106.

QM: Big Broadhurst Reef, E. side, side of reef flat channel, 21.x.1973, C.W., G10802.

Bushy-Redbill Reef: W. side, middle reef flat, 1m, 27.v.1975, C.W., G10793; G10794; W. side, outer reef flat, 8.vi.1975, C.W., G10797; N W. side, first reef crest, 23.xii.1972, C.W., G10798; adjacent Redbill Is., reef crest, 19.xii.1972, C.W., G10795; adjacent Redbill Is., reef slope, 19.xii.1972, C.W., G10796.

FIELD DIAGNOSIS

Low bushy to caespitose colonies with bottlebrush-type branches. Colour usually bright yellow, yellow-brown or lime green-brown.

LABORATORY DIAGNOSIS

Branching pattern: Main branches surrounded by regularly placed short branchlets which may be of equal or unequal length. Main branches up to 15 mm wide, branching units up to 100 mm wide, branchlets up to 8 mm wide.

Axial corallites: From non-exert to 2 mm exert. Outer diameter 1·6 to 3·2 mm; inner dimaeter 0·6 to 1·0 mm. Septation: primary septa well developed, up to 3/4R, secondary septa absent or few present to less than 1/4R.

Radial corallites: On both main branches and branchlets, radials are tubular with round openings, becoming round tubular distally. Radials are usually evenly distributed on branches, and almost touching, sometimes upper surface of small branchlets is naked of corallites. Septation: primaries well developed, up to 1/2R, secondaries absent or a few just visible.

Coenosteum: Neatly and densely costate both on and between corallites.

WITHIN REEF DISTRIBUTION

This is one of the few *Acropora* occurring in the shallow longitudinal patch reefs perpendicular to the reef edge, forming the windward edge of lagoons, and is characteristic of these areas. It also occurs in deeper reef flat areas, and reef crest and upper reef slope on some leeward reef areas. It is a common species of fringing reefs of continental islands.

IDENTIFICATION DIFFICULTIES AND HISTORY

Both species in synonymy were described from the Barrier Reef, *A. elseyi* being slightly sturdier than *'A. exilis'*. The species will be better understood when studied on fringing reefs.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Maldive Archipelago, Great Barrier Reef.

Acropora rosaria (Dana 1846)
(Plate 97 C, D)

Madrepora rosaria Dana, 1846, p.465, pl.36, fig.3.
Madrepora rosaria var. *diffusa* Brook, 1893, p.180.
Acropora rosaria: Vaughan, 1918, p.184, pl.82, figs.2, 2a, 2b; Wells, 1954, p.428, pl.130, figs.3, 4; Stephenson and Wells, 1956, p.18.
Acropora rosaria (part): Crossland, 1952, p.224, pl.40, figs.1, 4.
?*Madrepora syringodes* (part) Brook, 1892, p.463; 1893, p.177, pl.33, fig.E.

MATERIAL EXAMINED

USNM: Fiji Islands, U.S. Expl. Exped., *A. rosaria* holotype 281; paratype 933.

QM: Palm Islands, 1939, T. C. Marshall, G9192, G9193, G9194, G9195, G9196, G9197, G9200, G9202.

FIELD DIAGNOSIS

Not determined.

LABORATORY DIAGNOSIS

Branching pattern: Usually 'bottlebrush' branching units are formed, a central branch of up to 20 mm diameter bearing branchlets at even intervals all around.

Axial corallites: Exert 1·0 to 2·0 mm. Outer diameter 2·5 to 3·8 mm; inner diameter: 0·8 to 2·4 mm. Septation: first cycle well developed, up to 3/4R, second cycle usually present, or most septa present, up to 1/3R.

Radial corallites: Tubular, partly or fully appressed, or nariform. Walls thick, primary septa developed up to 1/3R and secondary septa partly developed, up to 1/2R.

Coenosteum: Densely arranged spines, sometimes laterally flattened, both on and between corallites.

Within Reef Distribution

The specimens described were collected on the fringing reefs of the Palm Island group.

Identification Difficulties and History

This species requires further study. The only material easily identifiable with *A. rosaria* available to me was collected in habitats not comparable with those I have studied. I am thus unable to pursue the possibility of a close relationship between this species and *A. squarrosa*. I consider it probable that the figured syntype of Brook's *A. syringodes* (BM 1892.6.8.209 from Palm Islands) is *A. rosaria*. Interpretations of *A. syringodes* are difficult to follow and seem to span a number of species, and it is likely that the latter species, as described, is a mixture.

Geographic Distribution

Great Barrier Reef, Fiji Islands, Samoa, Marshall Islands.

Acropora squarrosa (Ehrenberg, 1834)
(Plates 98, 99, 100)

Heteropora squarrosa Ehrenberg, 1834, p.112.
Madrepora squarrosa: Brook, 1893, p.65 (synonymy).
Acropora squarrosa: von Marenzeller, 1907, p.46, pl.14, figs.36-39; Vaughan, 1918, p.184, pl.83, figs. 2, 2a, 2b; Wells, 1954, p.427, pl.129, figs. 1, 2; Rossi, 1954, 1954, p.52; Nemenzo, 1967, p.69, pl.21, fig.4; Pillai and Scheer 1976, p.31.
Acropora murrayensis Vaughan, 1918, p.183, pl.82, figs.1, 1a, 1b; Nemenzo, 1967, p.71, pl.23, fig.2.
Madrepora syringodes (part) Brook, 1892, p.463; Brook, 1893, p.177 (not illus.).
Madrepora cancellata Brook, 1893, p.166, pl.32, fig.C.
Acropora cancellata: Crossland, 1952, p.225, pl.41, figs.3, 4.

Material Examined

USNM: Murray Islands, *A. murrayensis* holotype.

BM: *A. syringodes* 1893.4.7.163 (mentioned Brook, 1893); Louisade Archipelago, 15 fathoms, *A. cancellata* holotype 1851.9.29.39.

QM: Big Broadhurst Reef, SW. side, reef slope: 1·3 m, 23.x.1973, C.W., G10839; 1·9 m, 23.x.1973, C.W., G10840; 6·3 m, 13.x.1973, C.W., G10826, G10827; 6·3 m, 23.x.1973, C.W., G10841; 7 m, 13.x.1973, C.W., G10825; 7·8 m, 14.x.1973, C.W., G10828, G10830; 8 m, 14.x.1973, C.W., G10829; 8·1 m, 14.x.1973, C.W., G10824; 8·2 m, 14.x.1973, C.W., G10831; 8·7 m, 15.x.1973, C.W., G10832; 9 m, 15.x.1973, C.W., G10833, G10834; 9·2 m, 25.x.1973, C.W., G10842; 10·6 m, 16.x.1973, C.W., G10836; 11·4 m, 25.x.1973, C.W., G10843; 12·9 m, 23.x.1973, C.W., G10845; 13·4 m, 17.x.1976, C.W., G10837; 30 m, 18.x.1973, C.W., G10838; E. side, reef slope, 4 m, 21.x.1973, C.W., G10844.

Bushy-Redbill Reef: Reef crest adjacent Redbill Is.: 18.xii.1972, C.W., G10768, G10770; 19.xii.1972, C.W., G10769; 1.vi.1975, C.W., G10771; reef slope adjacent Redbill Is.: 20.xii.1972, E. Lovell, G10772, G10773; 20.xii.1972, C.W., G9189; W. side, middle reef flat; 1 m, 8.vi.1975, C.W., G10774, G10775; 14.vi.1975, C.W., G10776; NW. side, first reef crest: 22.xii.1972, E. Lovell, G10777; 22.xii.1972, C.W., G10778, G10779; NE. side, D. Hadley, 1.i.1973, G10780.

Bowden Reef, SW. side, reef slope: 24.vii.1972, C.W., G10789; 26.vii.1972, C.W., G10788.

Darley Reef, patch reef in lagoon: 1m, 18.vii.1972, R Pearson, G10782, G10785; 1 m, 22.iii.1973, C.W., G10783, G10784, G10786, G10787, G10790; 3 m, 18.vii.1972, C.W., G10846; 3 m, 24.iii.1973, C.W., G10791; 4 m, 22.iii.1973, C.W., G10792; 6 m, 22.iii.1973, C W., G10847; 7 m, 22.iii.1973, C.W., G10846.

Viper Reef, patch reef in lagoon, 2 m, 16.vii.1972, C.W., G10781.

Field Diagnosis

Colonies can be bottlebrush branching, caespitose to plate like, some of the variation being due to depth gradients. The surface of the branches has a general 'globular' appearance due to rounded, thickened corallites, and a whitish glow behind the general colouration due to dense coenosteum showing through semi-transparent tissue. Common colours are pale blue, lavendar, cream-brown and yellow-brown.

Laboratory Diagnosis

Branching pattern: Bottlebrush branching colonies have tapering branching units, and the branchlets extend widely from the main branch (90° or just less). In caespitose colonies there is a tendency towards development of a bottlebrush unit (incipient branchlets developed evenly around the branches) and even in plate-like colonies the short upright branches bear indications of incipient branchlets along their length. In most specimens of this species branchlets which are naked of radial corallites on their upper surface can be seen.

Axial corallites: From barely exert to 2·5 mm exert, Outer diameter 2·6 to 3·8 mm; inner diameter 0·7 to 1·4 mm. Septation: primaries usually well developed (up to 3/4R), secondaries completely absent to fully present, up to 1/3R.

Radial corallites: Tubular appressed to nariform, with round to oval openings at 90° or less to branch. Wall is thickened so that corallite may appear round tubular, or distorted rostrate hooks or horns may be developed. Septa are usually poorly developed: primaries can usually be just detected, and sometimes a few secondaries.

Coenosteum: Laterally flattened spines with elaborated tips are arranged densely and evenly over both the corallites and the inter-corallite region.

IDENTIFICATION DIFFICULTIES AND HISTORY

The material examined shows extraordinary variation in colony shape, branch size, and radial corallite distribution. However, I am unable to separate the collection into units on any of these characters. The evidence suggests a species where the role of the radial corallite is very flexible. The 'easiest' identification in this group is *A. murrayensis s.s.*, which was well described by Vaughan. This occurs particularly on sandy floor situations in lagoons and deep water reef flat areas. On the reef crest and upper reef slope it can also occur, but with shortened 'bottlebrush' branches. The caespitose to plate-like forms occur mainly on sloping surfaces, and on deep parts of the reef slope small flat plates approaching *A. granulosa* are formed, these being identifiable with *A. cancellata s.s.* At least one of Brook's syntypes of *A. syringodes* (BM 1893.4.7.163) from unknown locality, compares closely with caespitose specimens in the present collection. The biggest problem is in interpreting *A. squarrosa s.s*, which I have taken (following Vaughan 1918) to be caespitose, approaching corymbose, with very regularly arranged radial corallites and relatively thick branches. I suspect *A. austera* specimens are sometimes identified to this species.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Red Sea, Seychelles, Maldives, Minicoy, Philippines, Louisade Archipelago, Great Barrier Reef, Marshall Islands.

Acropora granulosa (Milne Edwards and Haime, 1860)
(Plates 101, 102)

Madrepora granulosa Milne Edwards and Haime, 1860, p.156; Brook, 1893, p.189 (synonymy).
Madrepora speciosa Quelch, 1886, p.163, pl.10, fig.1; Brook, 1893, p.191.
Madrepora clavigera Brook, 1892, p.455; 1893, p.183, pl.9, figs. A, A^1.
Acropora clavigera: Crossland, 1952, p.226, pl.40, fig. 2, pl.42, fig.3.
Madrepora rayneri Brook, 1892, p.461; 1893, p.191, pl.8, fig.A.
Acropora rayneri: Wells, 1954, p.431, pl.134, fig.6, pl.137, figs.1, 2, pl.139, figs.1, 2.

MATERIAL EXAMINED

PM: *Acropora granulosa* holotype 328a.

BM: *Acropora clavigera* holotype 1851.11.14.28. Fiji, *Acropora rayneri* syntypes, 1862.2.4.30, 1862.2.4.44.

QM: Big Broadhurst Reef, SW. slope: Oct., 1973, C.W., G11483; 5 m, 27.iii.1973, C.W., G11476; 7 m, 26.iii.1973, C.W., G11474; 7 m, 27.iii.1973, C.W., G11477, G11493; 8 m, 28.iii.1973, C.W., G11492; 8 m, 24.x.1973, C.W., G11481; 10 m, 23.x.1973, C.W., G11494; 10·4 m, 16.x.1973, C.W., G11487; 17·2 m, 17.x.1973, C.W., G11480; 25 m, 17.x.1973, C.W., G11485.

Bushy-Redbill Reef: adjacent Redbill Is., reef crest, 1 m, 1.vi.1975, C.W., G11490; 20.xii.1972, E. Lovell, G11491; NW. side, patch reefs, 15.vi.1975, 12 m, C.W., G11488.

Darley Reef, patch reef in lagoon, 2·5 m, 19.vii.1972, C.W., G6723.

Feather Reef, reef slope, 10 m, 24.x.1972, R. Pearson, G11479, G11482.

FIELD DIAGNOSIS

Colonies are side-attached thin plates, with anastomosing horizontal branches and short vertical branchlets or groups of branchlets. Axial corallites are long, tapering or rounded, and may be sinuous. Radials are relatively few and scattered.

LABORATORY DIAGNOSIS

Branching pattern: described above.

Axial corallites: From barely exert to as long as 10 mm bare of radials. Outer diameter 1·2 to 2·5 mm; inner diameter: 0·6 to 2·2 mm. Septation: primaries well developed, up to 3/4R, secondaries absent or poorly represented, to less than 1/4R.

Radial corallites: Appressed tubular to nariform with round to slightly oval opening, directed at 90° or less to branch. Radials, except at growing edge of colony, are few, and inconspicuous, the appearance of the colony being dominated by the axial corallites.

Coenosteum: Spines with pointed or laterally flattened tips are densely and evenly arranged on and between corallites.

WITHIN REEF DISTRIBUTION

Reef slope and sides of lagoonal patch reefs, usually at depths greater than 20 m, but can be much shallower on very steeply sloping surfaces, for example G11490 is a specimen from 1 m on the side of a steep and narrow surge channel opening.

IDENTIFICATION DIFFICULTIES AND HISTORY

The combination of the various species in synonymy seems barely possible from the type material, and also from much of my own material which identifies strongly with one or another species. A more acceptable combination would be two species, *A. speciosa* = *A. rayneri* and *A. granulosa* = *A. clavigera*. However some large specimens show a mixture of characteristics of all four species. The differences amongst the described species are in dimensions and the degree of tapering of the axial corallite: '*A. rayneri*' is very slight, and '*A. speciosa*' sturdier, both with tapering axials, *A. granulosa s.s.* and '*A. clavigera*' both have thick, rounded, non-tapering axials. In all the material there is little difference in inner axial diameter, axial septation, radial corallite shape and coenosteal spines. The locations of the specimens give no clue to the morphological differences. All categories except '*A. speciosa*' (one lagoonal specimen) co-occur on the reef slope. Their different appearances (whether genotypically or phenotypically determined) cannot be explained by reef slope gradients, and are probably related to microhabitat features.

Despite the variety in the species, extreme care must be taken in assigning a specimen to this species, as deeper water specimens of many other species appear (as cleaned specimens) similar to this species.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Mascarene Archipeligo (G. Faure, pers. comm.), Louisade Archipelago, Great Barrier Reef, Fiji Islands, Marshall Islands.

Acropora austera (Dana, 1846)
(Plates 103, 65C)

Madrepora austera Dana, 1846, p.478; Brook, 1893, p.56 (synonymy); Verrill, 1902, p.266, pl 36, fig. 10, pl. 36B, fig. 1.

MATERIAL EXMAINED

YPM: *Acropora austera* (fragment of type) 4190.

QM: Big Broadhurst Reef, S W. side, reef slope: 7·8 m, 14.x.1973, C.W., G10813, G10828; 8·0 m, 14.x.1973, C.W., G10814; 8·2 m, 14.x.1973, C.W., G10815; 9·0 m, 15.x.1973, C.W., G10816.

Bowden Reef, SW. end, reef slope, 26.vii.1972, C.W., G10817.

Bushy-Redbill Reef: adjacent Redbill Is., reef crest: 2.vi.1975, C.W., G10806, G10807; 4.vi.1975, C.W., G10808; S. side, reef slope, 3 m, 27.xii.1972, C.W., G10809, G10810; W. side, patch reef, 8 m, 15.vi.1975, C.W., G10811; N W. side, patch reef, 19.xii.1972, E. Lovell, G10812.

Darley Reef, patch reef in lagoon, 24.iii.1973, C.W., G10818, G10819.

Viper Reef, patch reef in lagoon, 16.vii.1972, C.W., G10820.

Fiji Islands, Great Astrolabe Reefs, Jan. 1974, C.W., G10821, G10822.

FIELD DIAGNOSIS

Patchy, irregularly branching colonies of bushy, bottlebrush or caespitose appearance; large, irregular-length rounded radial corallites with very large openings. Colour cream to pale brown or dirty yellow. Extended polyps may be bright orange (axials) and purple (radials).

LABORATORY DIAGNOSIS

Branching pattern: Main branches are up to 40 mm width. These give off secondary branches of such irregular spacing, angle, and length, that the colony may appear caespitose, bottlebrush, or low arborescent. Although growth is apparently indeterminate, colonies do not often reach more than about 1 m across, occurring usually in areas of high density cover.

Axial corallites: From barely exert to 3 mm exert. Outer diameter 2·4 to 3·8 mm; inner diameter 1·0 to 1·5 mm. Septation: all septa usually present, primaries up to 2/3R, secondaries up to 1/2R.

Radial corallites: On secondary branches radials are tubular, nariform or tubo-nariform, of mixed length. Similar corallites on main branches tend to become appressed, then rounded, distally. The shape of the opening approaches a square, and the lower (or outer) wall is sometimes thickened accentuating the angularity of the opening. Primary and most or all secondary septa are developed and, as Dana comments, these usually slope towards the centre deep in the corallite.

Coenosteum: Reticulate with elaborated spines on and between radial corallites.

WITHIN REEF DISTRIBUTION

Reef crest and upper slope, top and sides of lagoonal patch reefs. This species seems to occur particularly where there is a bend or edge on the reef surface (see plate 65C).

IDENTIFICATION DIFFICULTIES AND HISTORY

This species is neglected in the literature, although my experience has shown it to be widely distributed.

GEOGRAPHIC DISTRIBUTION

Indo-Pacific: Singapore, Philippines, Great Barrier Reef, Fiji (C.W.), Enewetak Atoll (C.W.).

Acropora brueggemanni (Brook, 1893)
(Plate 50C, D)

Madrepora brueggemanni Brook, 1893, p.145, pl. 24. (synonymy).
Acropora brueggemanni: Crossland, 1952, p.221.
Madrepora brueggemanni var. uncinata Brook, 1893, p.146, pl. 35, fig. E.
Acropora brueggemanni var. *uncinata:* Nemenzo, 1967, p.55.

MATERIAL EXAMINED

BM: Singapore, *A. brueggemanni* syntype 1878.4.1.1.

JCU: Palm Island Group, T. Done, 4 specimens; Lizard Island Group, M. Pichon and T. Done, 6 specimens.

QM: Big Broadhurst Reef, SW. side, reef slope, 5 m, 27.iii.1973, C.W., G11495; 6 m, 27.iii.1973, C.W., G11496–8.

Palfrey Islet, Lizard Island group, 30.vii.1977, P. Hutchings, G11499–506.

FIELD DIAGNOSIS

Sturdy arborescently branching colonies occur as either small clumps or extensive thickets. Axial corallites are obviously large and bulbous and there may be several axials at or near the branch tip. General appearance approaches that of *A. palifera* (see Wells 1954, p.430), but a definite branching pattern is achieved. Colour is pale brown to pale apple green.

LABORATORY DIAGNOSIS

Branching pattern: The branches may be round or irregular in cross section, from 15 to 30 mm diameter, and either tapering or truncate. The angle of branching is usually wide.

Axial corallites: Outer diameter 2·0 to 8·0 mm; inner diameter 0·8 to 1·4 mm. In general, when there is a single axial corallite, this is wider than the members of a bundle of axials. Septation: Both septal cycles usually developed, the primaries up to 3/4R, secondaries up to 1/3R.

Radial corallites: From short (barely emergent) to appressed tubular, with round openings. Primary septal cycle usually well developed, up to 1/2R; secondary cycle poorly developed, up to 1/4R.

Coenosteum: Dense arrangement of elaborated spines both on and between radials.

WITHIN REEF DISTRIBUTION

In my work, I have encountered this species only as a rare member of the upper reef slope assemblage. It is very common on the fringing reefs of the Lizard Island and Palm Island Groups, usually on sandy or poorly consolidated substrates.

IDENTIFICATION DIFFICULTIES AND HISTORY

Both Brook and Crossland note an approach to the characteristics of subgenus *Isopora* in this species. Strong affinities with *A. palifera* can be seen in the radial corallite structure, coenosteal texture, and tendency to multiple axial corallites. It is considered in the present paper in order to avoid field-identification problems.

GEOGRAPHIC DISTRIBUTION

Singapore, Philippines, Great Barrier Reef.

ACKNOWLEDGMENTS

I wish to express my gratitude to the following: Prof. Jan Verwey (whose taxonomic decisions on *Acropora* were made many years ago but whose search for perfection still keeps him from publication) for his generosity in discussing his work, and Mrs Verwey for her hospitality. Prof. John Wells for encouragement, constant assistance and hospitality. Other workers in coral taxonomy, in particular Maya Wijsman-Best, Richard Randall, Brian Rosen, Michel Pichon, Gerard Faure, John Veron, and members of the N.S.F. Enewetak Taxonomic Workshop (1976) for advice and discussion. Micky Watkins and Hugh Hope who took us to the reef. Robert Pearson whose unpublished observations contributed to the ground work of the study, and Colin Limpus who made large contributions of specimens and observations. Museum colleagues who helped in the field (Rolly McKay, Terry Tebble, Dianne Gleeson, David Joffe); in separate field collecting (Glen Ingram, Jan Buhmann) and back-up work (Alan Easton and staff, photography; Peter Berryman and staff, artwork); many members of technical and clerical staff, and Bruce Campbell and Lester Cannon for advice on the manuscript. Peter Beveridge and family and Bruce Carlson for hospitality in Fiji. The following Museum Curators and their staff for assistance with specimens and hospitality: Dr K. Reutzler and Dr F. Bayer (USNM), Dr P. F. S. Cornelius (BM), Dr J. P. Chevalier (PM), Dr W. Hartman (YPM), Dr D. Kuhlmann (MNB), Dr M. Wijsman-Best (RNHL), Dr Abad-Santos (UP), Dr Van Soest (Zoological Museum Amsterdam). Neville Coleman for considerable assistance with coloured underwater records. D. and M. Tarca of Townsville. Many other friends in the field, but in particular Ed Lovell, Robin Elks, Harvey Walsh and Carl Wallace. John Hardy and Bob Grimmer of the University of Queensland

Electron Microscope Unit. Michel Pichon and Terry Done for hospitality at James Cook University.

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INDEX TO SPECIES

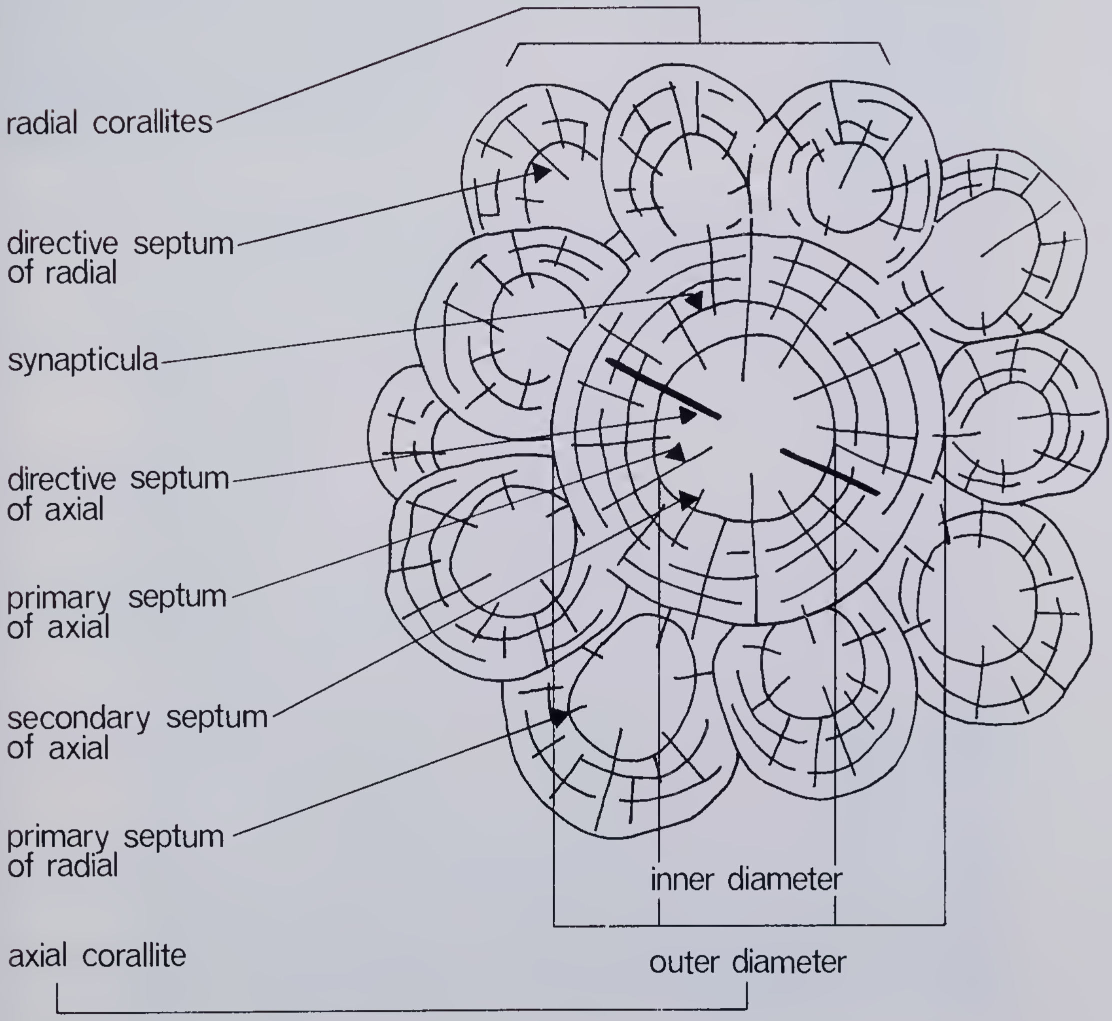


FIG. 3: Diagrammatic representation of Plate 43C indicating features used in the description of species.

PLATE 43

Features of *Acropora* displayed by scanning electron microscopy.

A. Side view of a branch tip (of *A. millepora)* from which tissues have been removed to display skeleton.
B. Side view of a branch tip (of *A. tenuis)* from which skeleton has been removed, to display soft tissues. The specimen is in a retracted state, so that tentacles are withdrawn.
C. Face view of skeletal branch tip of *A. millepora.*

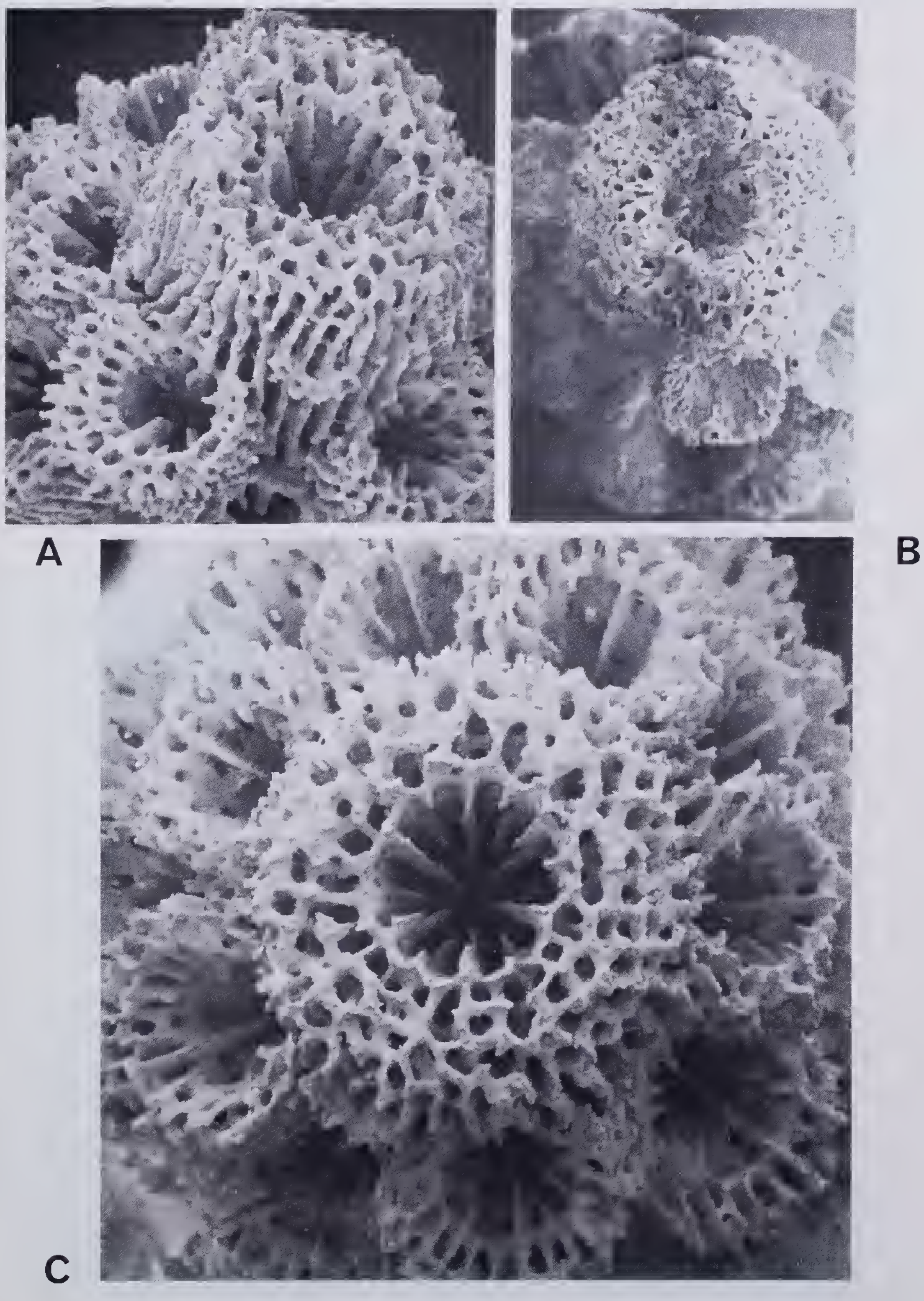

A
B
C

PLATE 44

Acropora robusta (Dana, 1846) on Bushy-Redbill Reef.

A. Large colony on SW. reef crest showing distorted humps, some vertical cones, and some free branching. Other corals in the picture are *Pocillopora*.
B. (Left hand side) colony on SW. reef crest with vertical cones and free branching. Other *Acropora* in the picture are *A. hyacinthus* (upper centre), *A. variabilis* (centre) and several *A. humilis*.
C. Small colony on SE. (weather) side of reef (arrow), with *A. cuneata* (centre), *A. humilis* (upper centre) and *Pocillopora*.

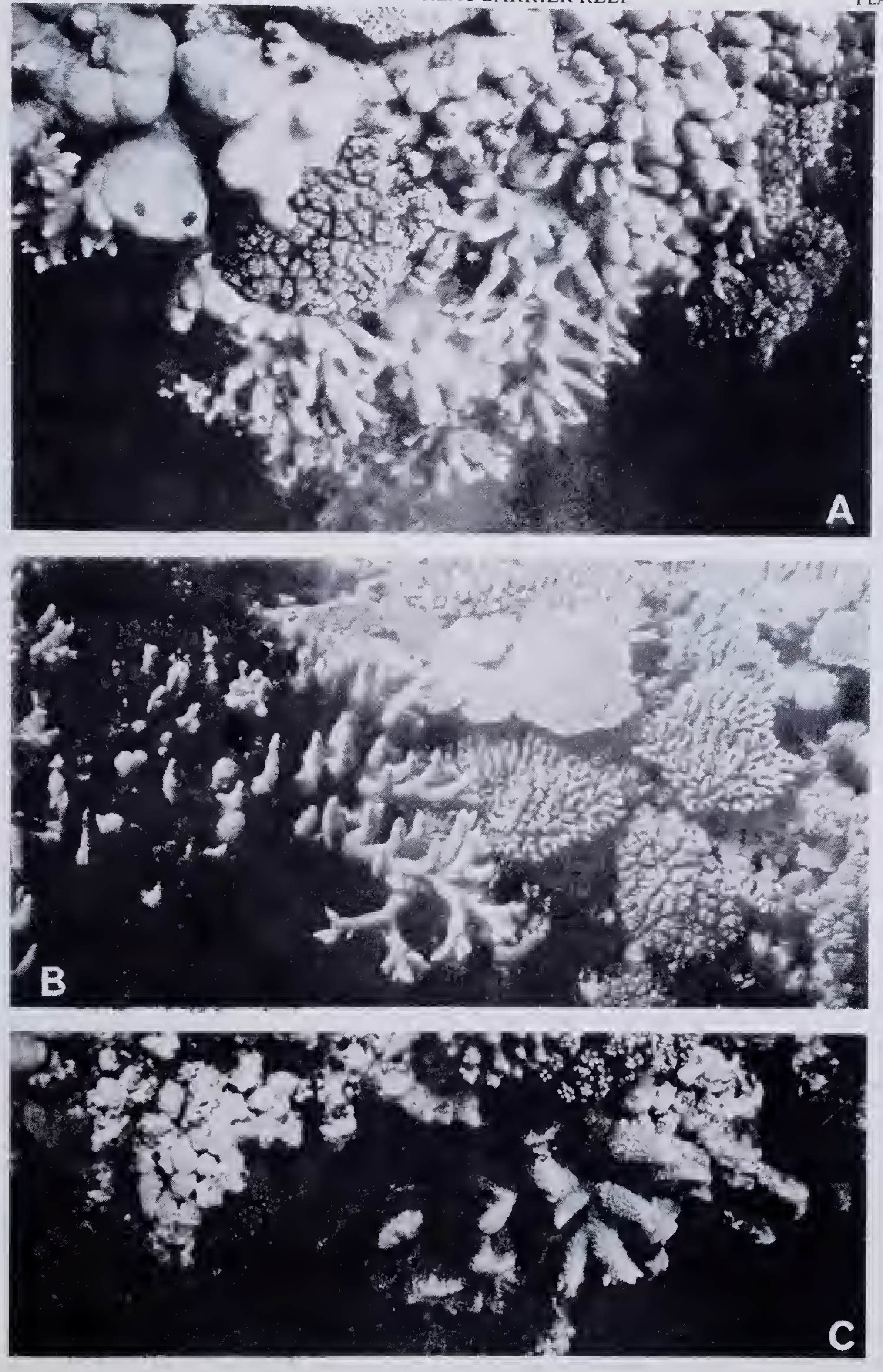
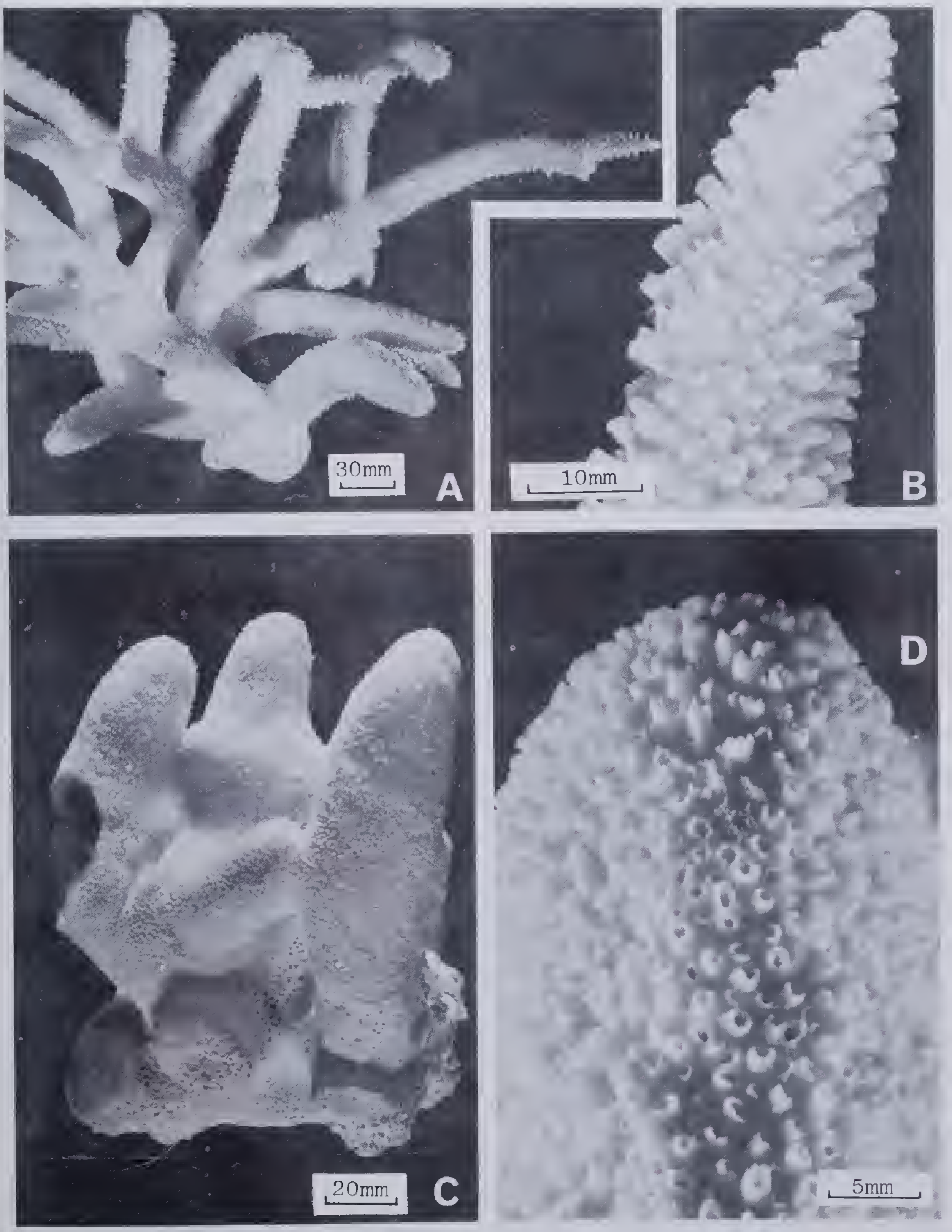

A
B
C

PLATE 45

Acropora robusta (Dana, 1846)

A, B. Free branching portion of colony, G10191, Big Broadhurst reef, SW. slope, 1·5 m, colour green, pink tips.

C, D. Sturdy vertical humps from colony, G10259, Bushy-Redbill Reef, W. slope, 10 m.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A
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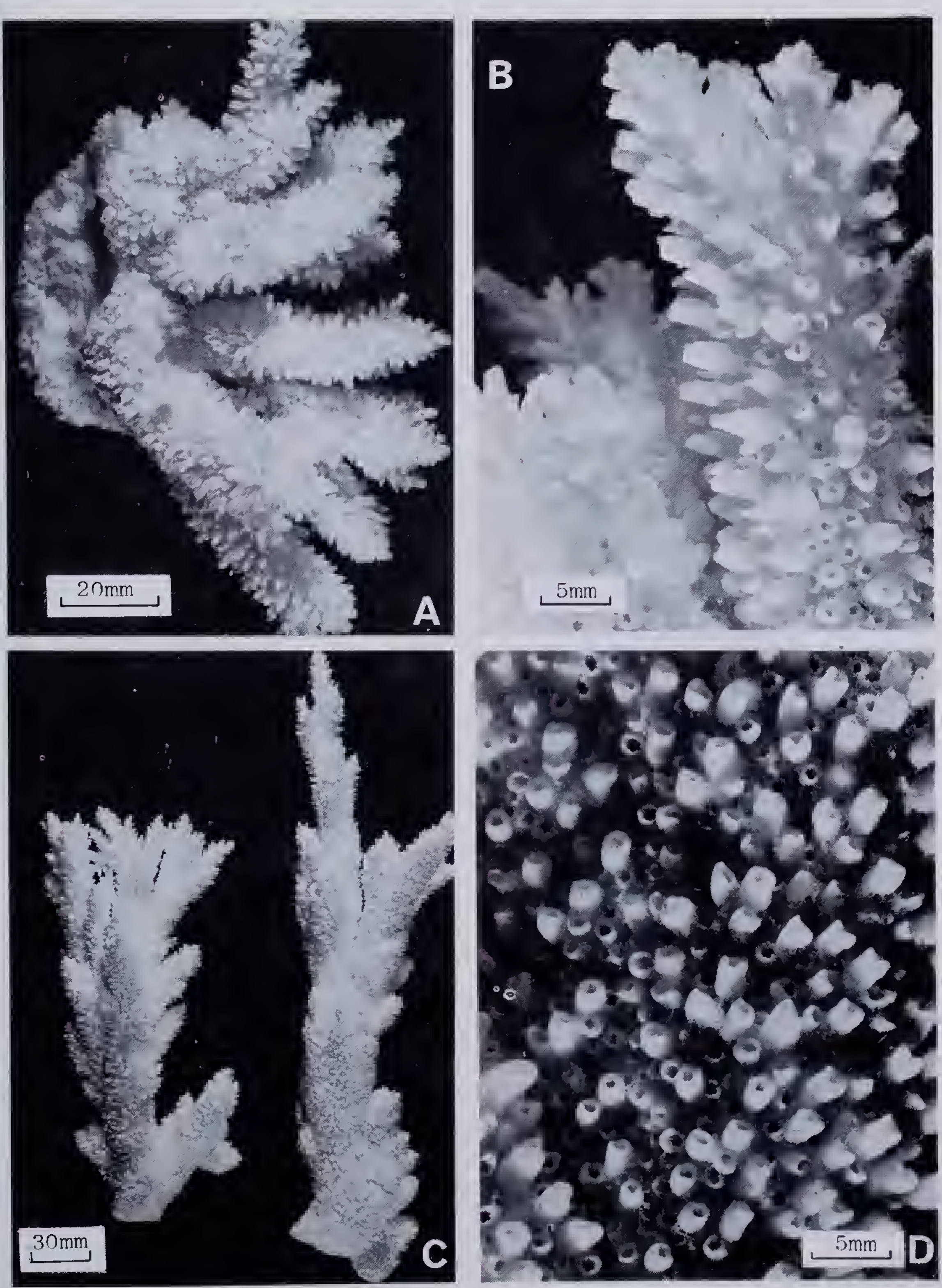
B
20mm
C
D
5mm

PLATE 46

Acropora rotumana (Gardiner, 1898)

A, B. Specimen from branch tip, G10235, Big Broadhurst Reef, SW. side, outer reef flat, colour pale green.
C, D. Two branches of colony, G10263, Bowden reef, SW. side, reef crest, colour pink-brown.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A
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C
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D

PLATE 47

Acropora abrotanoides (Lamarck, 1816)

A, B. G10239 Bushy-Redbill reef, NW. side, reef crest, colour yellow-brown.
C, D. G10238 Big Broadhurst reef, upper surface of a patch reef in the lagoon, colour yellow-brown.

PLATE 47

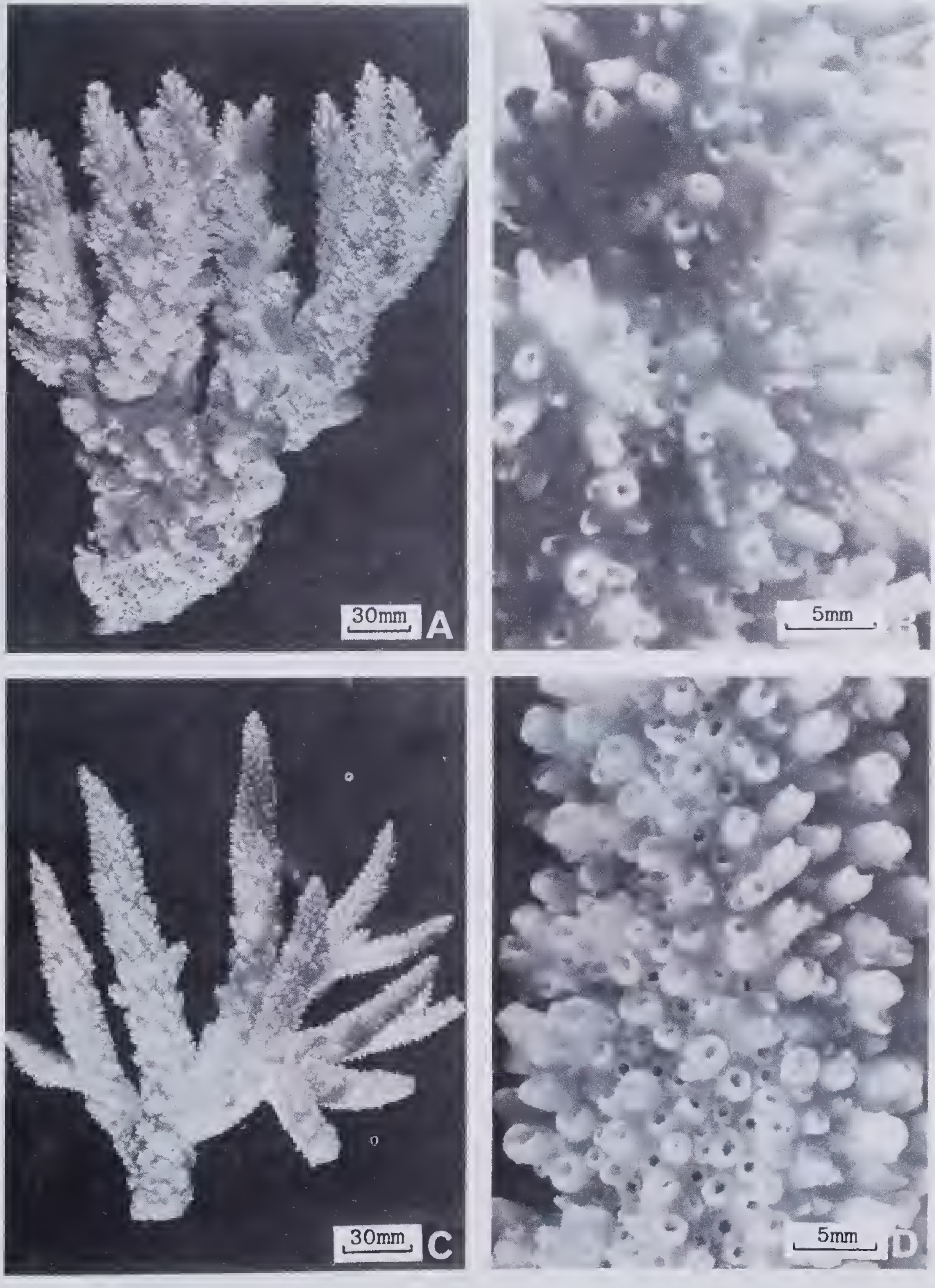

PLATE 48

Acropora intermedia (Brook, 1891) on Bushy-Redbill Reef.

A. Large thicket in deep water middle reef flat on leeward (W.) side.
B. Small patches with *A. digitifera* (centre) on reef crest, SW. side.
C. Small patch (left) with *A. aspera* on inner middle reef flat, SW. side.

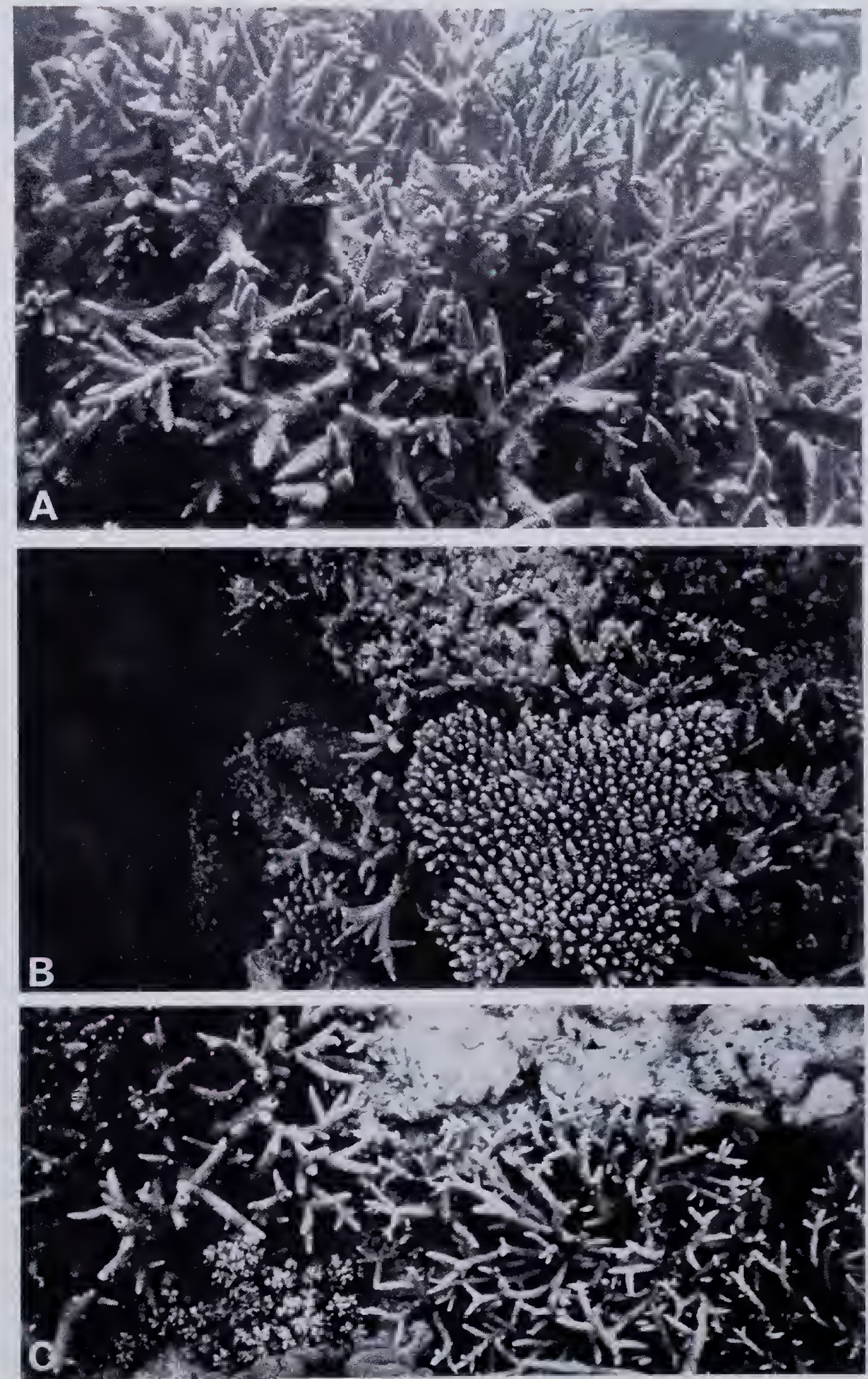
A
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PLATE 49

Acropora intermedia (Brook, 1891)

A, B. G11400 Big Broadhurst Reef, SW. slope, 2 m, colour bright blue.
C, D. G11295 Big Broadhurst Reef, SW. slope, 2 m, colour pale green.

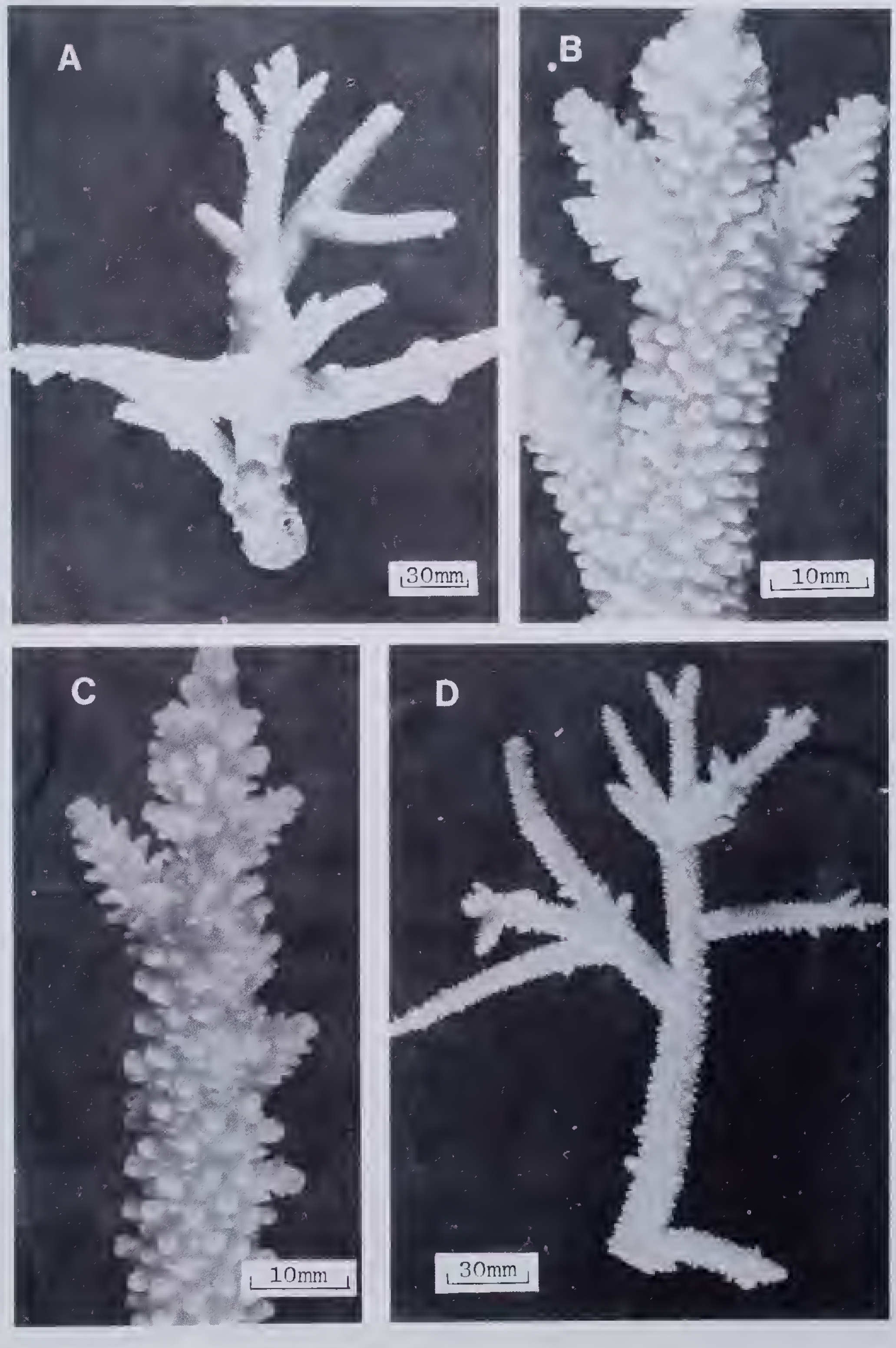
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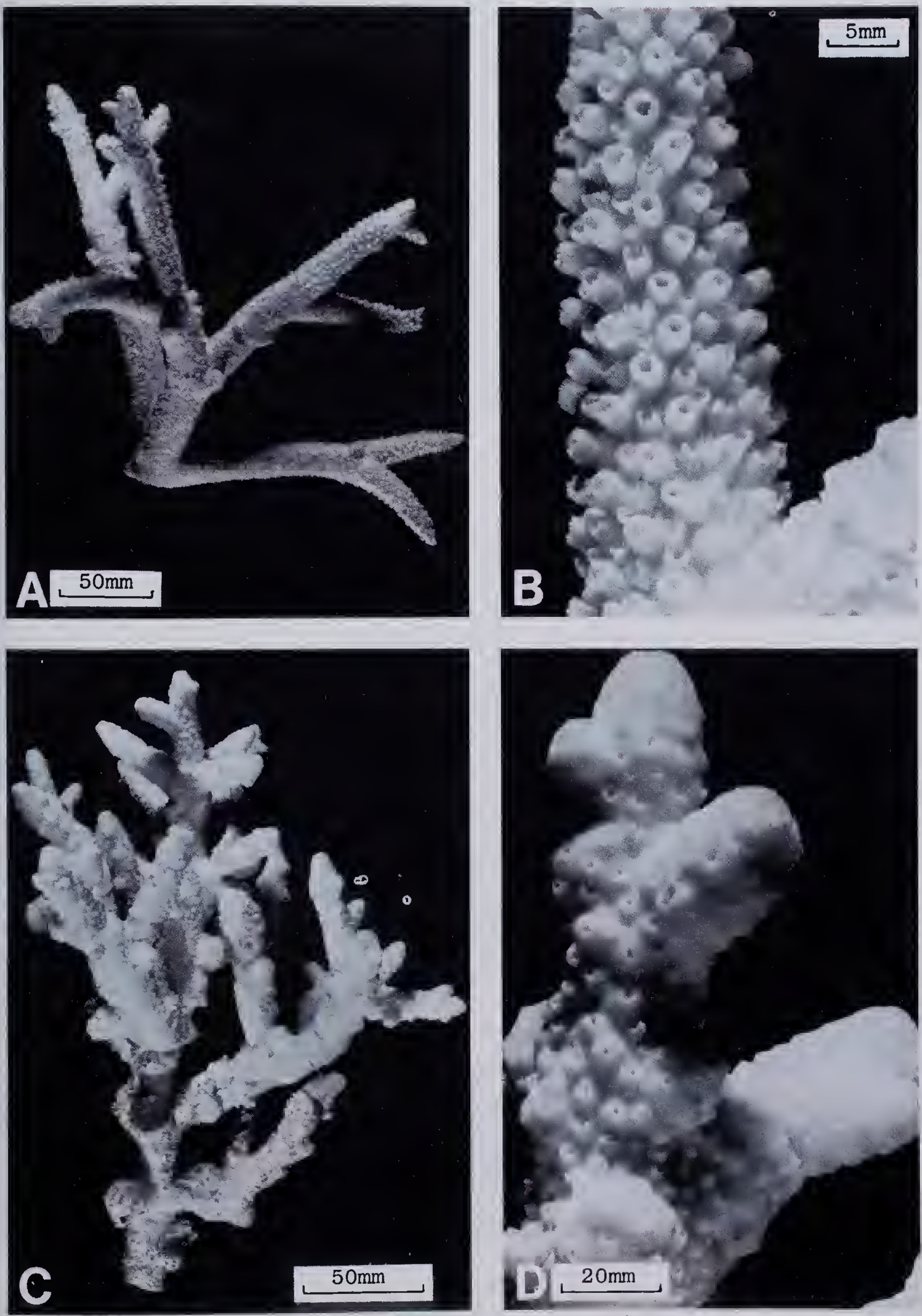
PLATE 50

A, B. *Acropora grandis* (Brook, 1892) G11298 Darley reef, patch reef in lagoon, 4 m, colour creamy brown.
C, D. *Acropora brueggemanni* (Brook, 1893) G11498 Big Broadhurst Reef, SW. slope, 6 m, colour brown.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B
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C
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D
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PLATE 51

Acropora formosa (Dana, 1846) on the reef.

A. Large thickets on sandy bottom in deep middle reef flat, Bushy-Redbill Reef, leeward (W.) side.
B. Thicket (foreground) with diverse *Acropora* assemblage in background, base of upper reef terrace, Big Broadhurst Reef, SW. side.


A
B

PLATE 52

Acropora formosa (Dana, 1846)

A, B. G11339, Big Broadhurst reef, 2 m, colour pink-grey.
C, D. G11381 Bowden Reef, floor of opening in SW. side, 5 m.

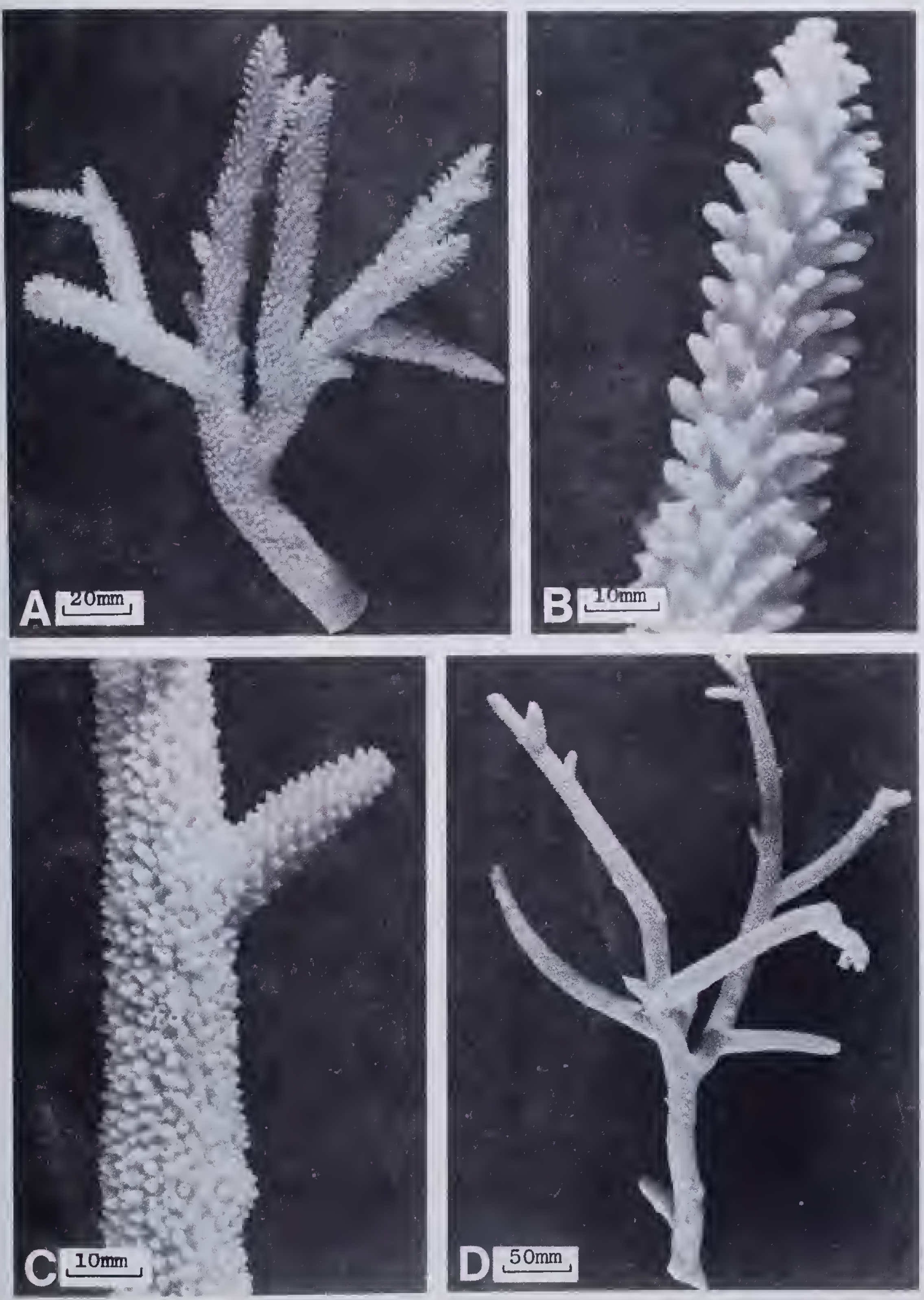
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PLATE 53

Acropora splendida Nemenzo, 1967 on Big Broadhurst Reef, SW. side.

A. Colony on gently-sloping upper reef terrace (about 7 m) surrounded by flat-plate species. The distinctive 'arborescent-bracket' shape can be seen.

B. Colony in a mixed assemblage at about 10 m (centre of plate). This colony is flatter than the previous, and its shape is somewhat disguised by another arborescent colony *(A. formosa*, lower left and right). The small flat colony upper left of *A. splendida* is *A. clathrata;* the large plate above this is *A. hyacinthus*, and above it to the right is *A. cytherea*. The small dense bushy colony (upper left) is *A. haimei*.


A


B

PLATE 54

Acropora splendida Nemenzo, 1967.

A, B. Specimen from inner part of large bracket, G8699, Big Broadhurst Reef, SW. slope, 6 m, colour brown, pale blue tips to branches.

C, D. Specimen from outer part of bracket, G8701, Big Broadhurst Reef, SW. slope, 7 m, colour olive green, pale green tips to branches.


30mm
A


5mm
B

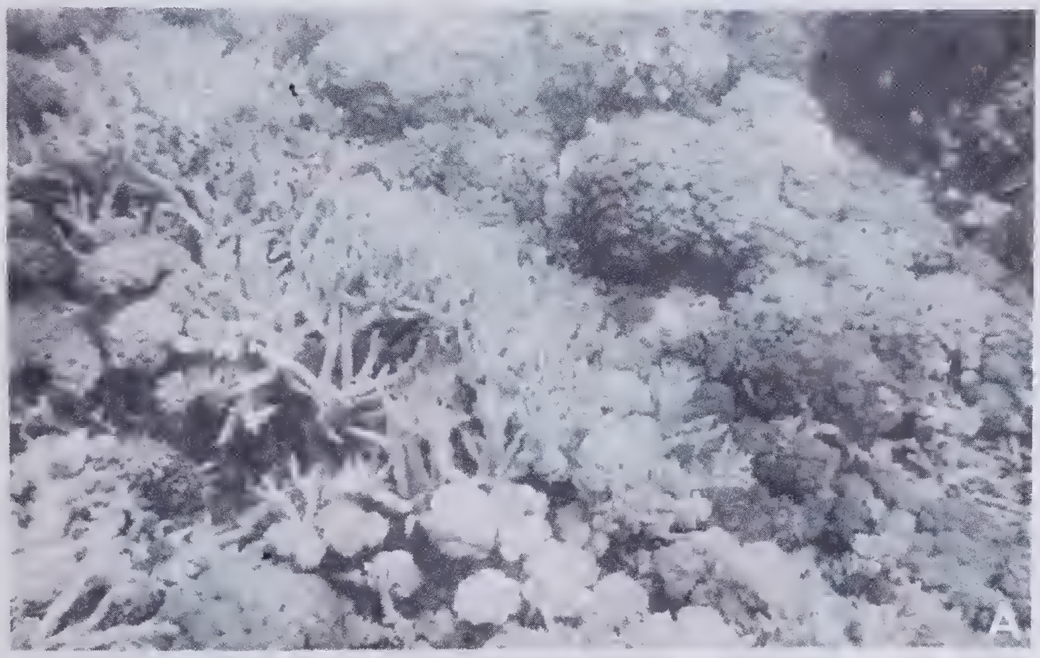

5mm
C


30mm
D

Plate 55

Acropora horrida (Dana, 1846)

A. Shrub like formations (centre) with soft corals in deep water leeward (W) middle reef flat on Bushy-Redbill Reef.
B. 'Bottlebrush' branch from C, below.
C. Sprawling arborescent formation on sandy bottom, 15 m depth, off-reef floor, Bushy-Redbill Reef, NW. side.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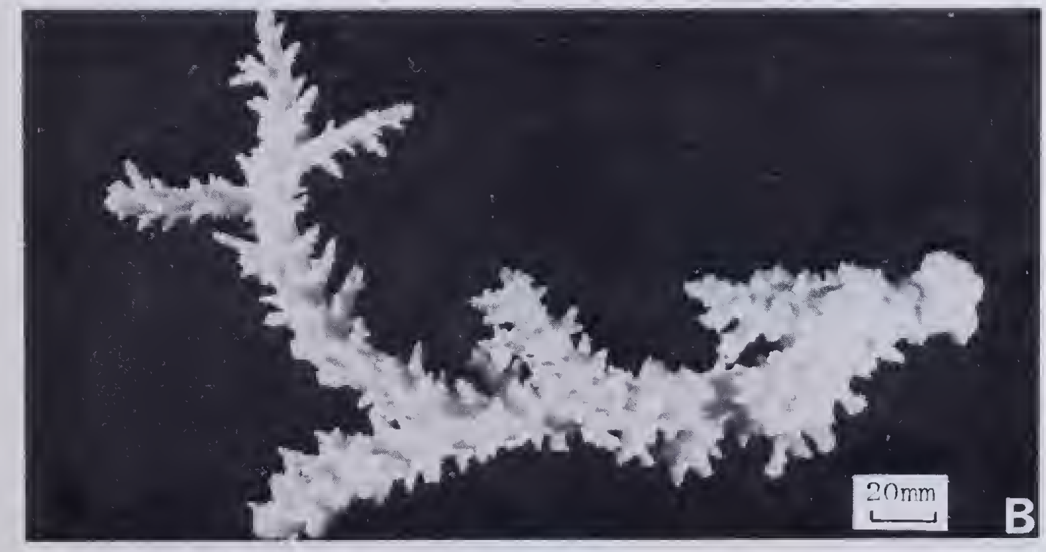
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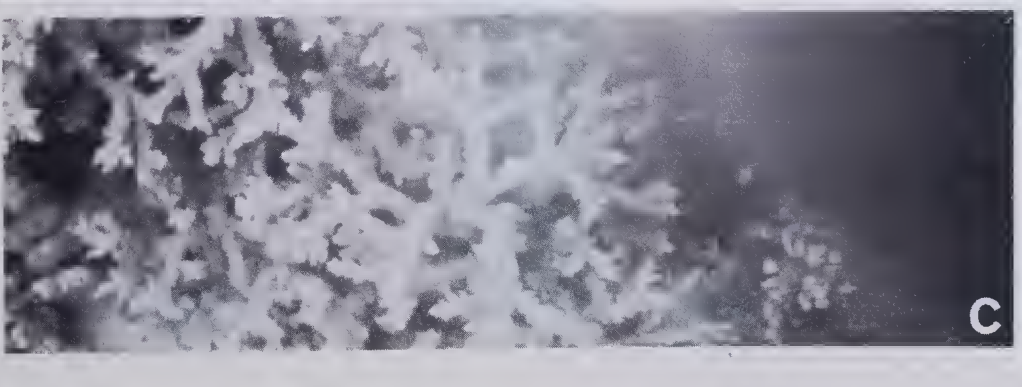
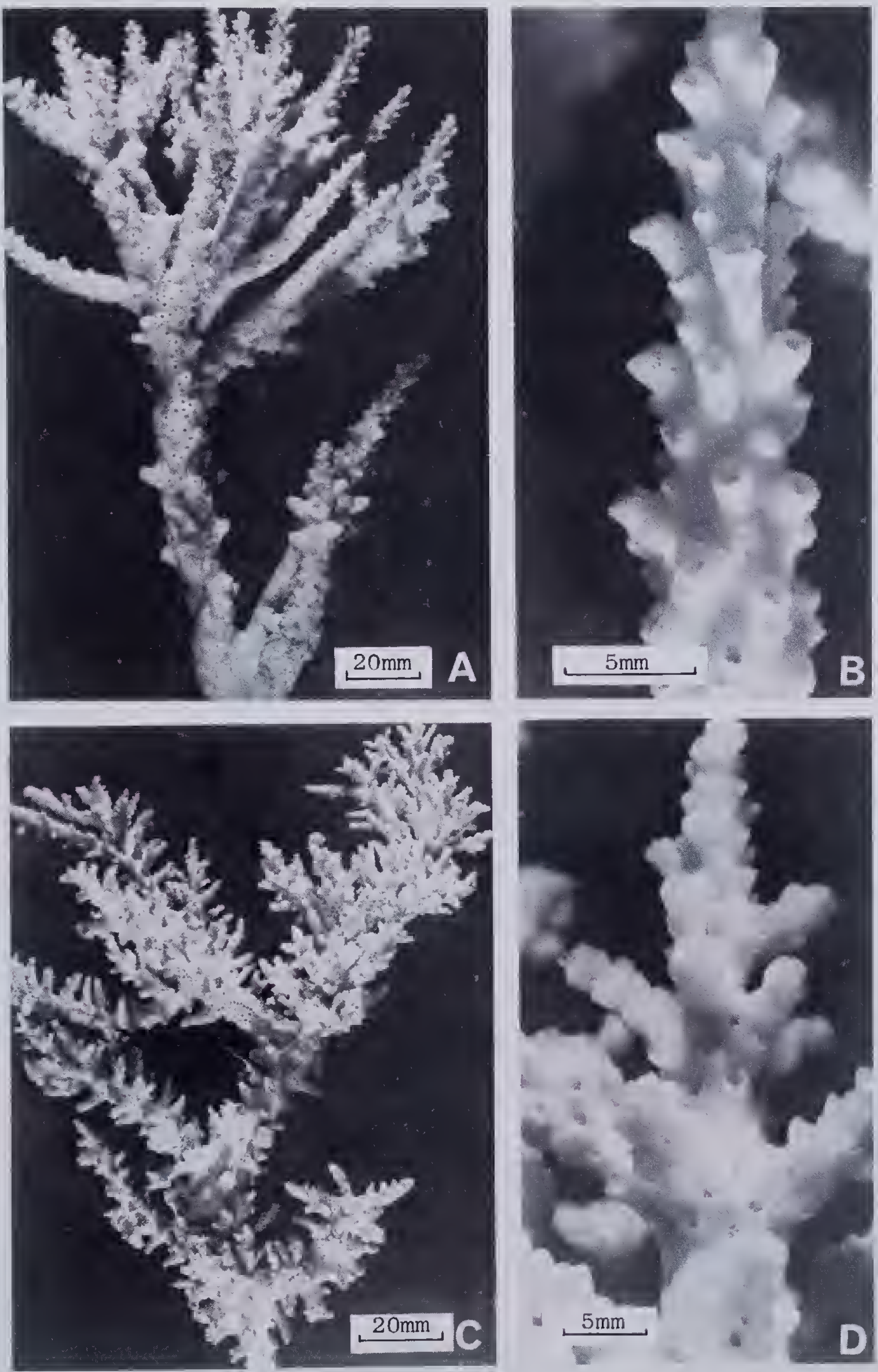

C

PLATE 56

Acropora horrida (Dana, 1846)

A, B. Piece of shrub-like colony, G9078, Bushy-Redbill Reef, NW. side, middle reef flat, colour lavender-grey.

C, D. Piece of colony, open arborescent, proliferous with short branchlets, G9077, Bushy-Redbill Reef, NW. side, floor outside slope, 8 m, colour pale blue.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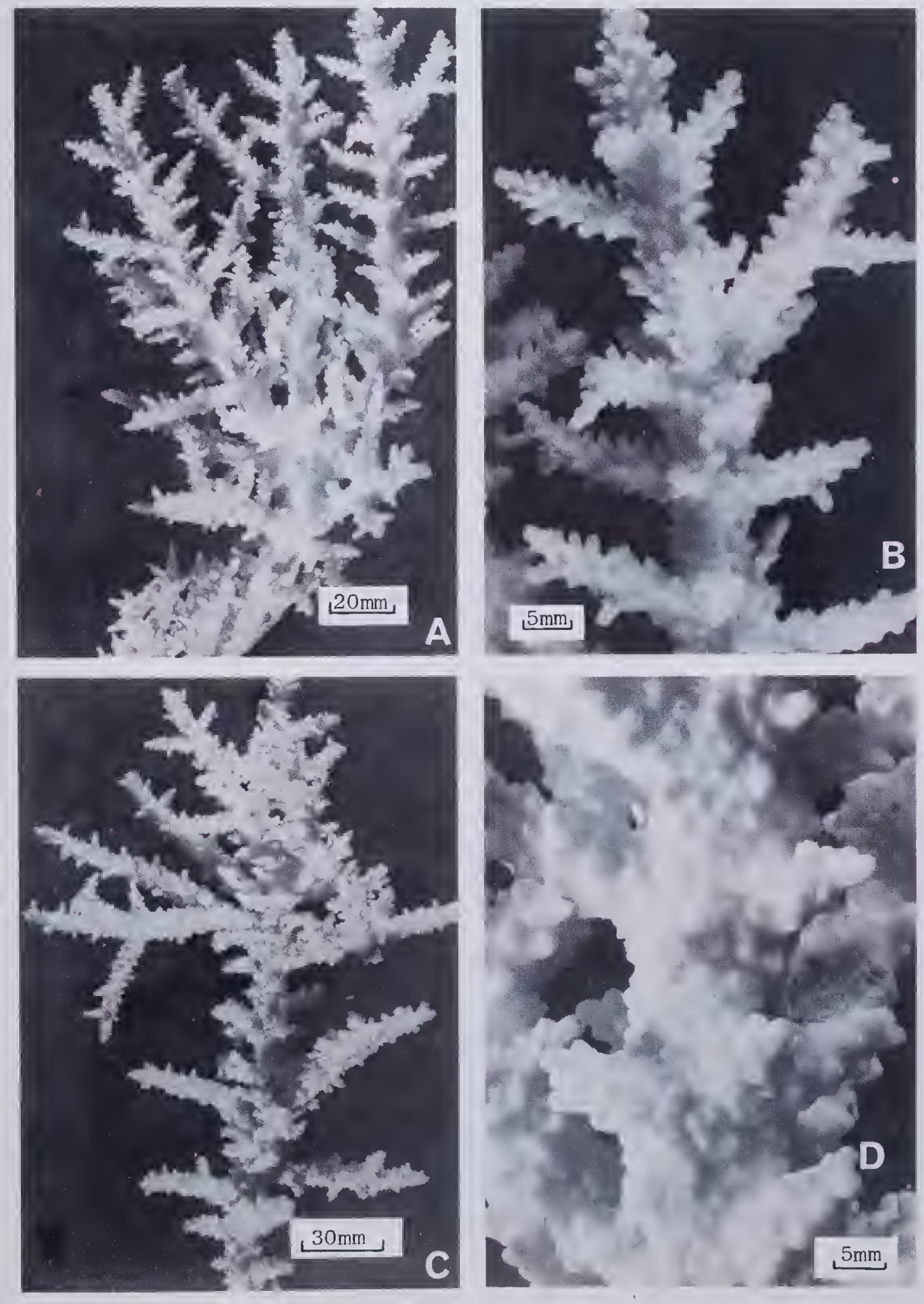
D

PLATE 57

Acropora vaughani Wells, 1954.

A, B. G10270, Big Broadhurst Reef, SW. slope, 7 m, colour pale brown.
C, D. G10271 Big Broadhurst Reef, SW. slope, 8 m, colour pale brown.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C
D
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PLATE 58

Acropora pulchra (Brook, 1891)

A, B. G11118, Heron Island reef flat. Low corymbose colony with slender branches.
C, D. G11116 Heron Island, W. side, reef flat, colour cream-brown, blue tips. Corymbose colony with thick branches.

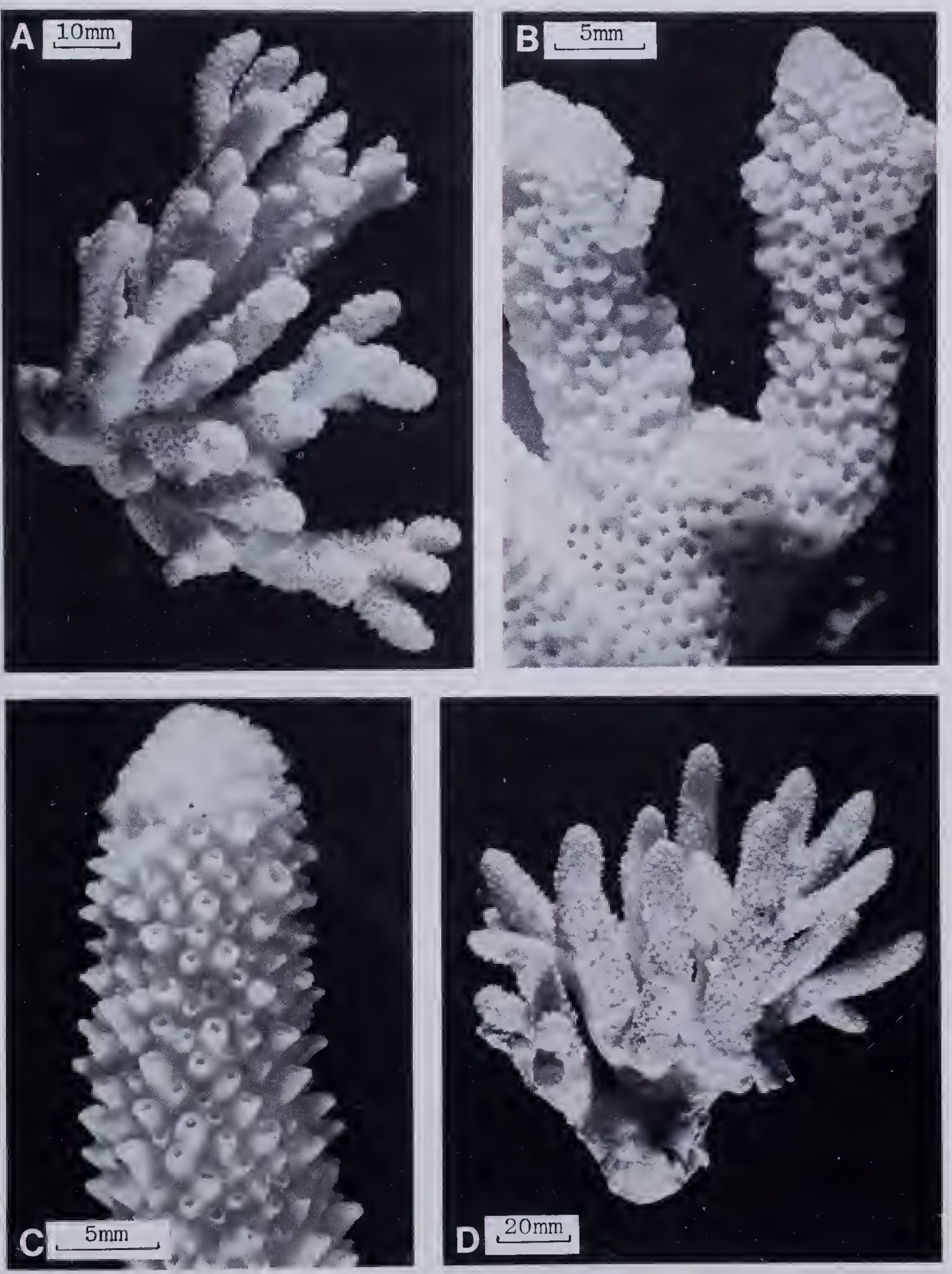
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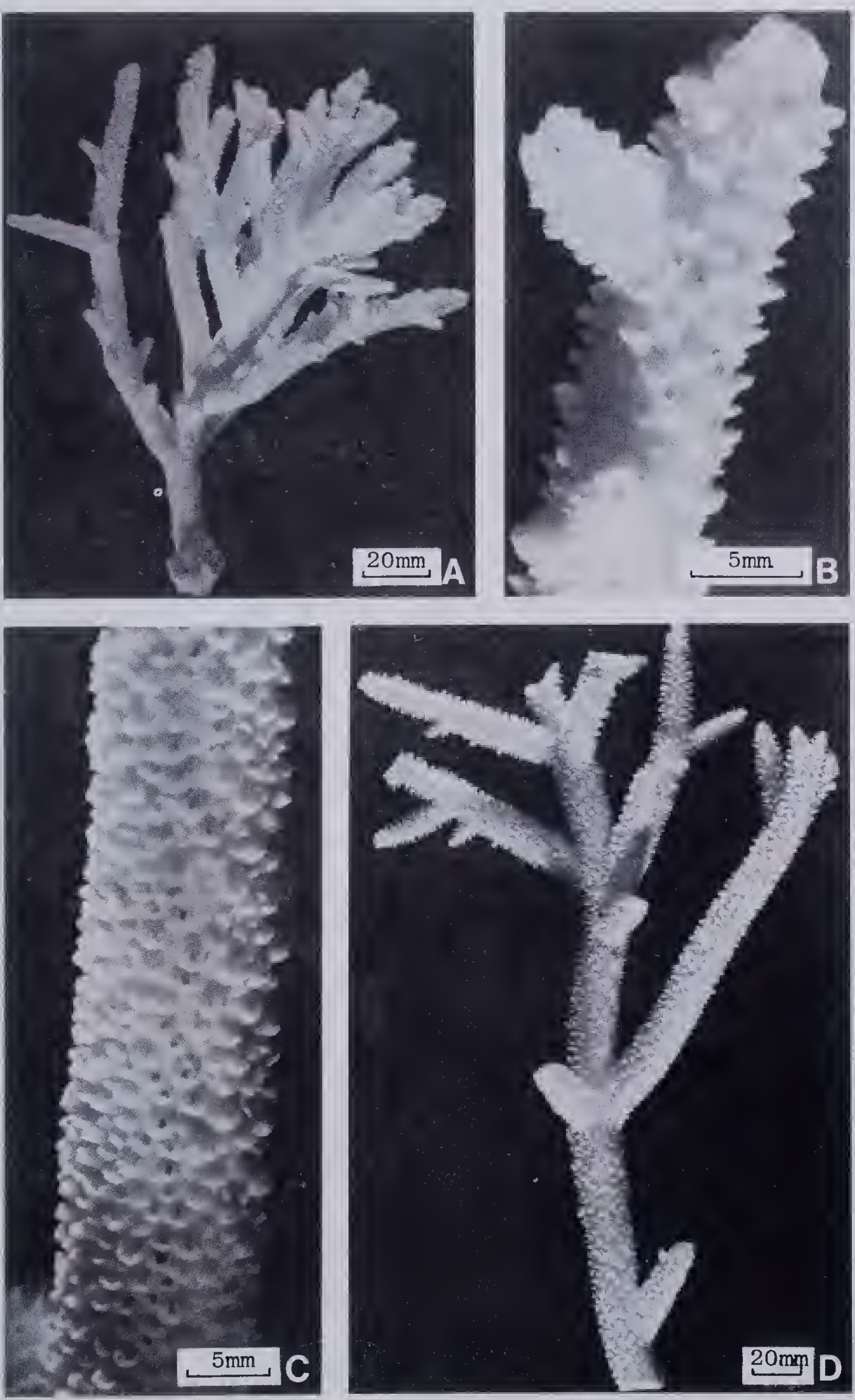
Plate 59

Acropora pulchra (Brook, 1891)

A, B. G11111 Heron Island Reef flat. Compact arborescent colony.

C, D. Specimen from reef flat adjacent to Redbill Island. Open arborescent colony.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D

Plate 60

Acropora aspera (Dana, 1846) on the reef.

A, B. Microatoll type development of corymbose colonies on middle reef flat, Heron Island reef, W. side. (Scale divisions are 2 cm).

C. Large thicket (left half of picture) in contact with thicket of *A. pulchra* (right hand side) on inner middle reef flat, Bushy-Redbill Reef, SW. side.

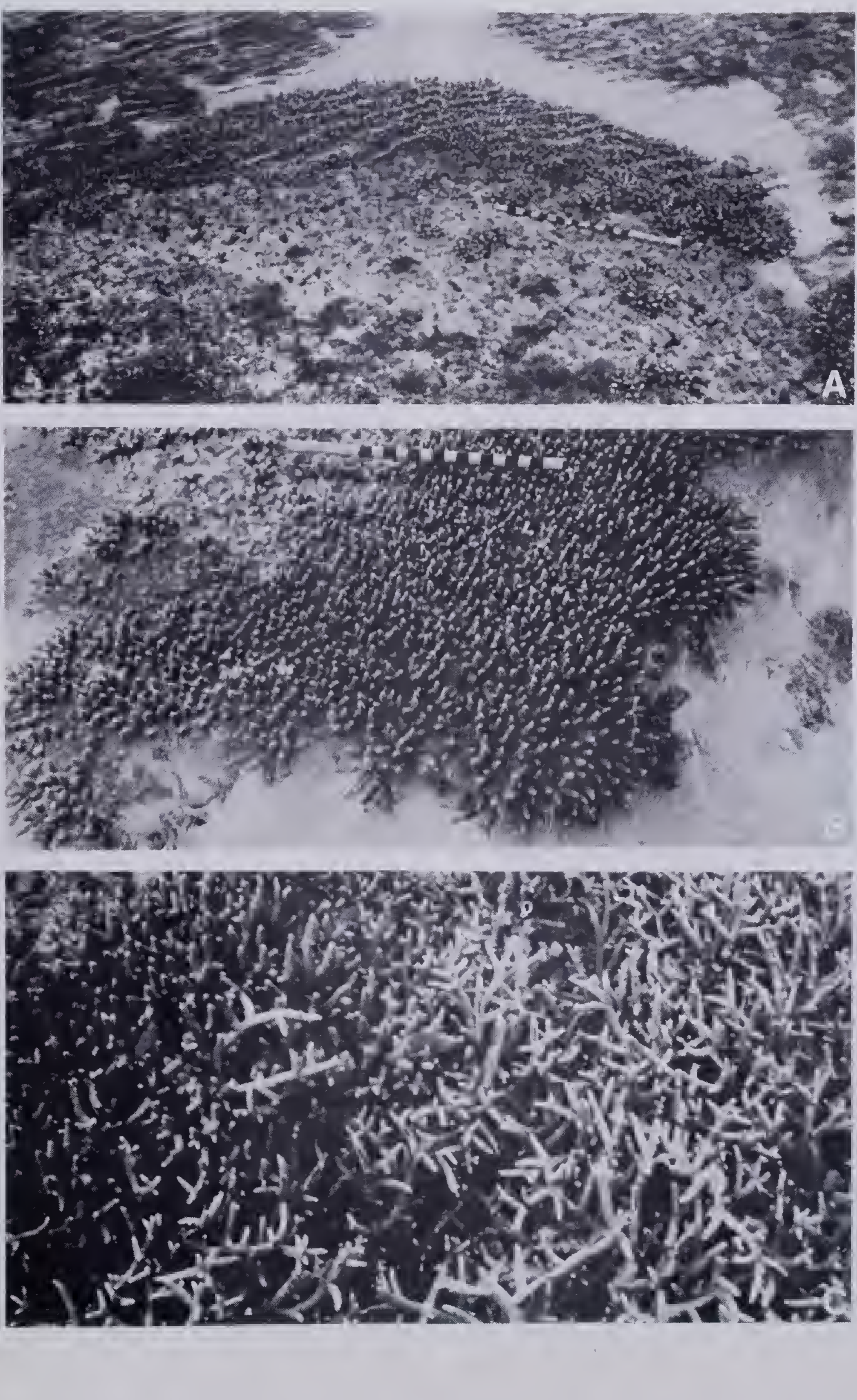
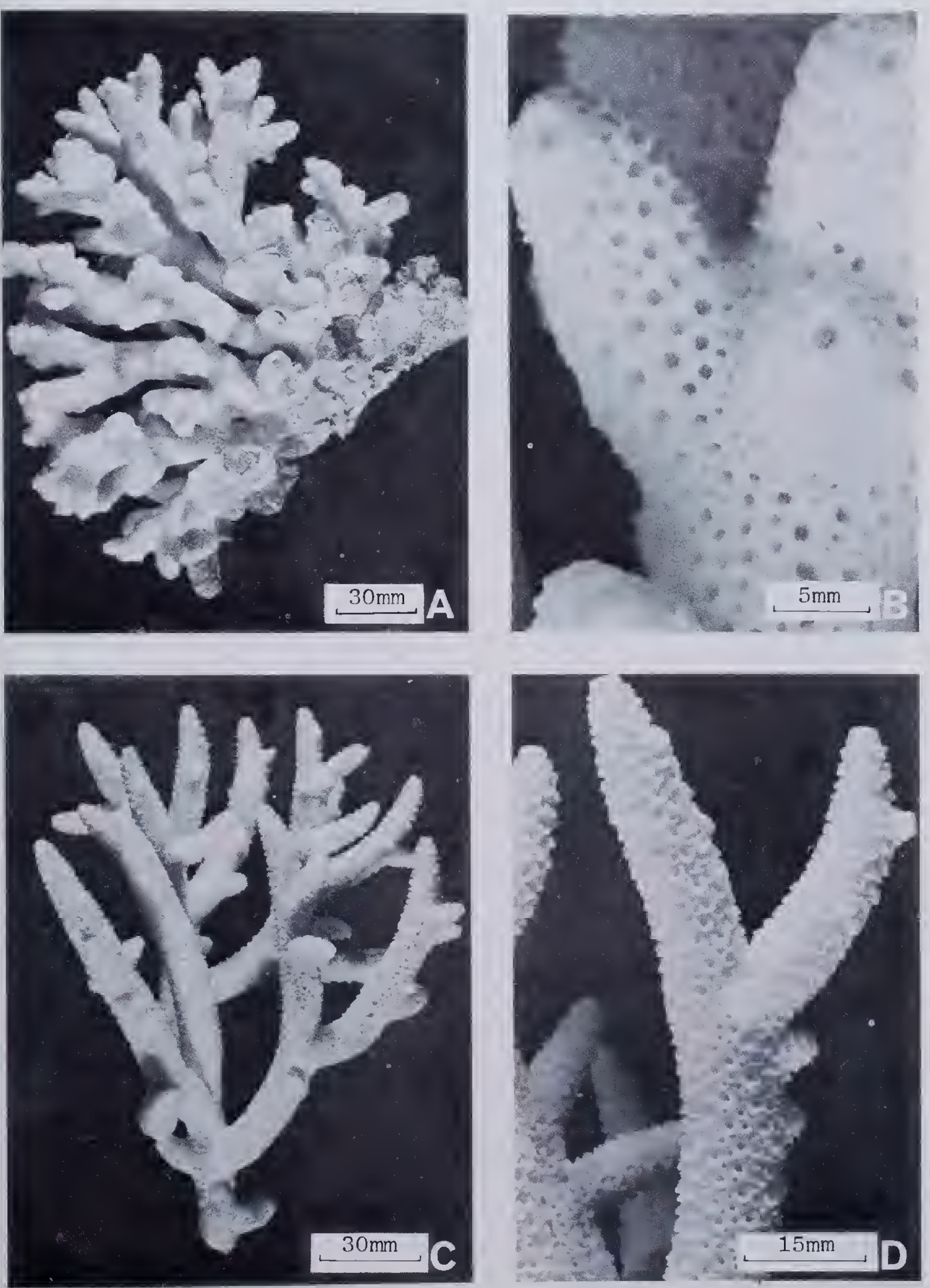

A
B
C

PLATE 61

Acropora aspera (Dana, 1846)

A, B. G10961, Bushy-Redbill Reef, N. side, inner flat-algal bank area, colour brown, blue tips.
C, D. G10930 Big Broadhurst Reef, patch reef in lagoon, colour pale green. (Specimen typical of *'A. hebes'*).


30mm
A
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D

PLATE 62

Acropora aspera (Dana, 1846)

A, B. G10929 Big Broadhurst Reef, patch reef in lagoon, colour pale green.

C, D. G10921 Heron Island reef flat, colour pale brown. (Specimen typical of *A. aspera s.s.*)

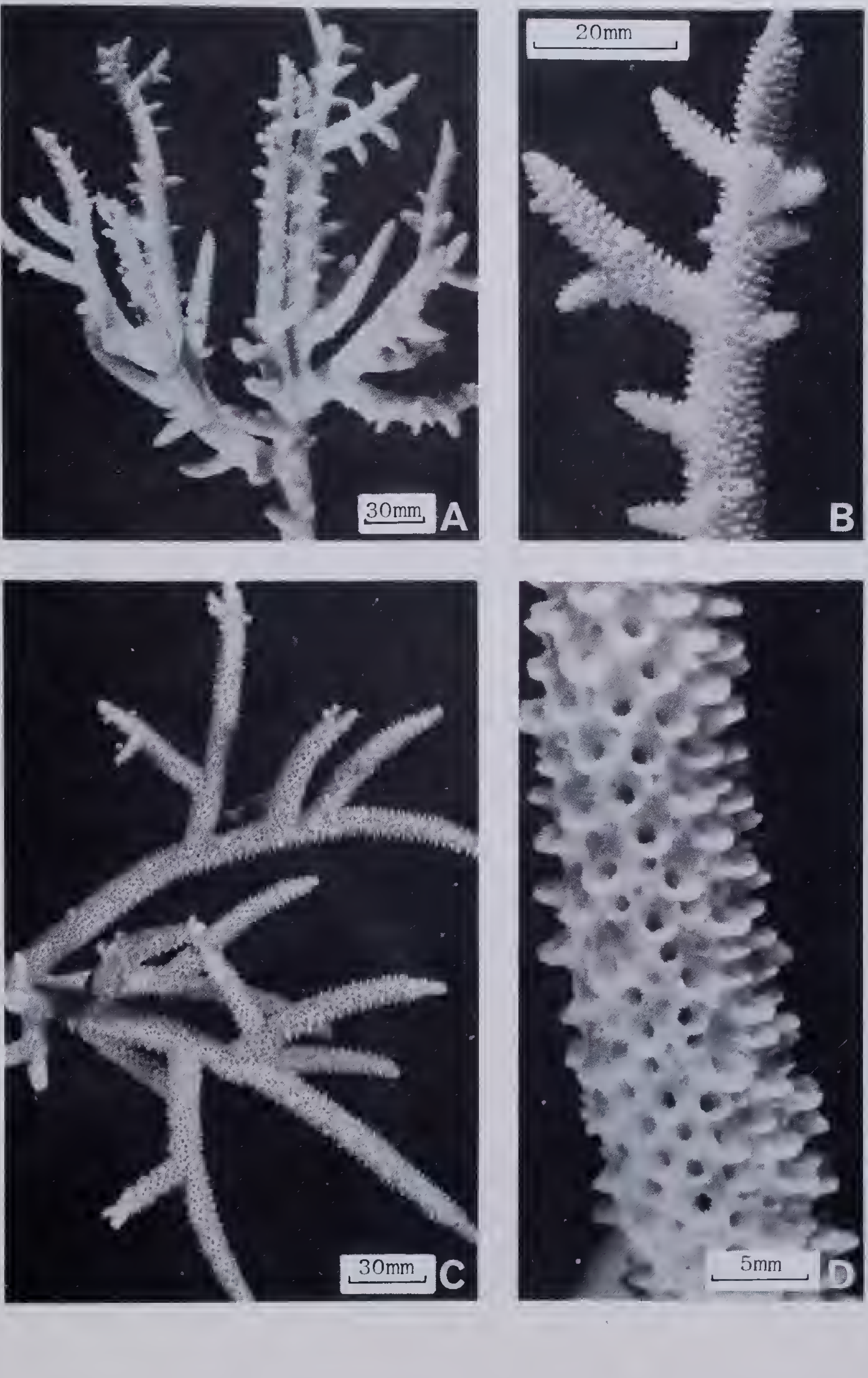
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PLATE 63

Large flat plates *(Acropora hyacinthus, A. cytherea* and *A. clathrata)* and arborescent species, on Big Broadhurst Reef. (N.B. species cannot be distinguished).

A. On upper reef terrace.
B. On surge channel floor. Note the change in arborescent to flat plate species ratio between this and the reef terrace in the background.


A


B

PLATE 64

Large flat plate species on the reef.

A. *Acropora hyacinthus* (upper left), *A. cytherea* (lower left), *A. clathrata* (centre). With *A. florida* (left of centre) and arborescent species on the surge channel floor (approx. 10 m) at Big Broadhurst Reef.
B. *A. hyacinthus* with other *Acropora* in the Darley Reef lagoon. Note oblique additions to the original flat plate.
C. *A. clathrata* (centre) with *A. hyacinthus* (right) and *A. formosa* (left) on the reef crest at Bushy-Redbill Reef.
D. Three juvenile *A. cytherea* colonies on the reef crest at Bushy-Redbill Reef.

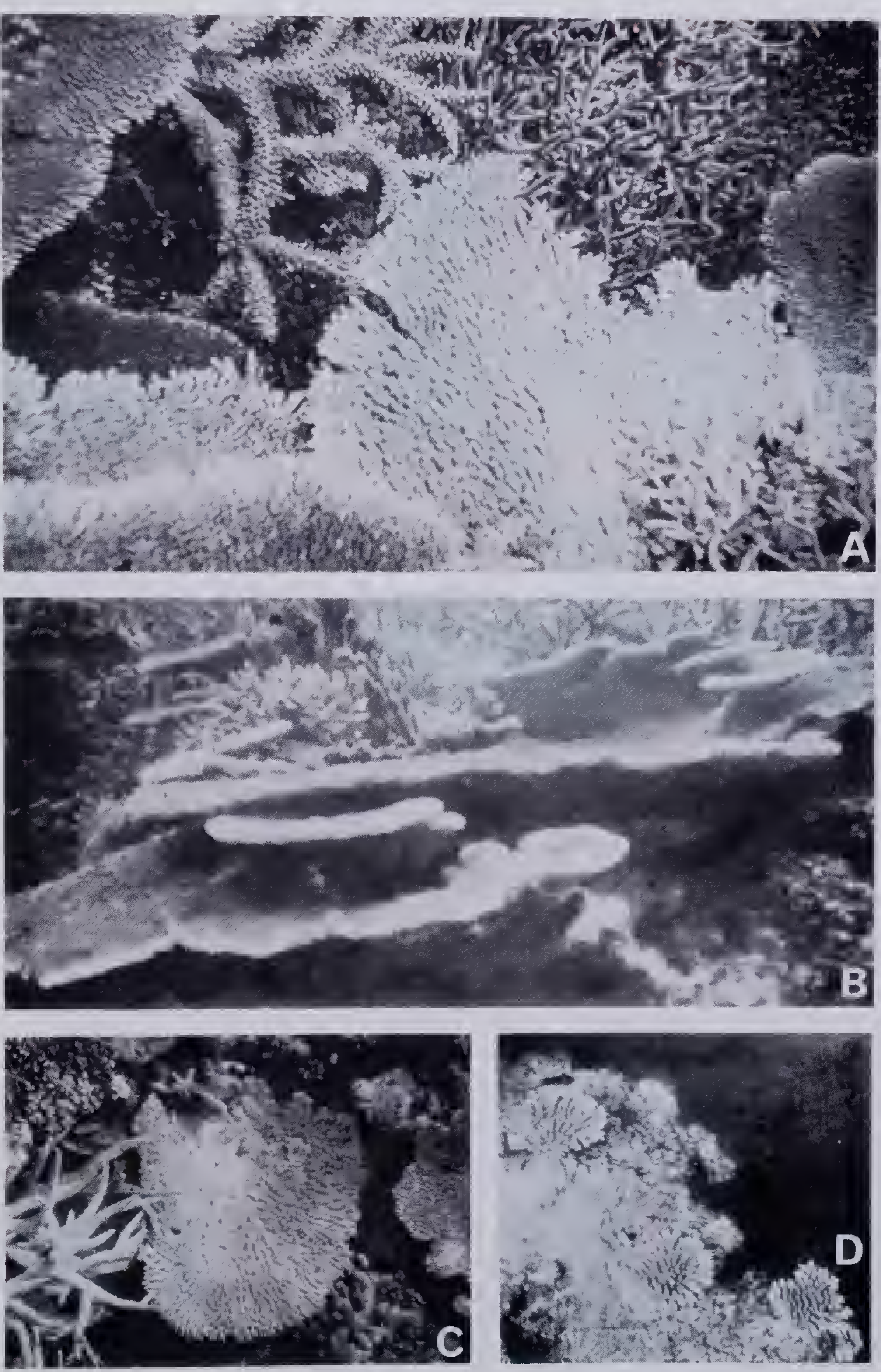
A
B
C
D

PLATE 65

Acropora hyacinthus (Dana, 1846) on Bushy-Redbill Reef.

A. Deep middle reef flat area on leeward (W.) reef (1·5 m at low tide), with *A. formosa.*
B. Outer reef flat, SW. side. Several colonies with *A. digitifera* (centre and lower centre) and *A. formosa.*
C. Reef crest, SW. side. Two colonies (arrows) with *A. austera* (centre left), *A. digitifera* (centre) and *A. humilis* (centre right).

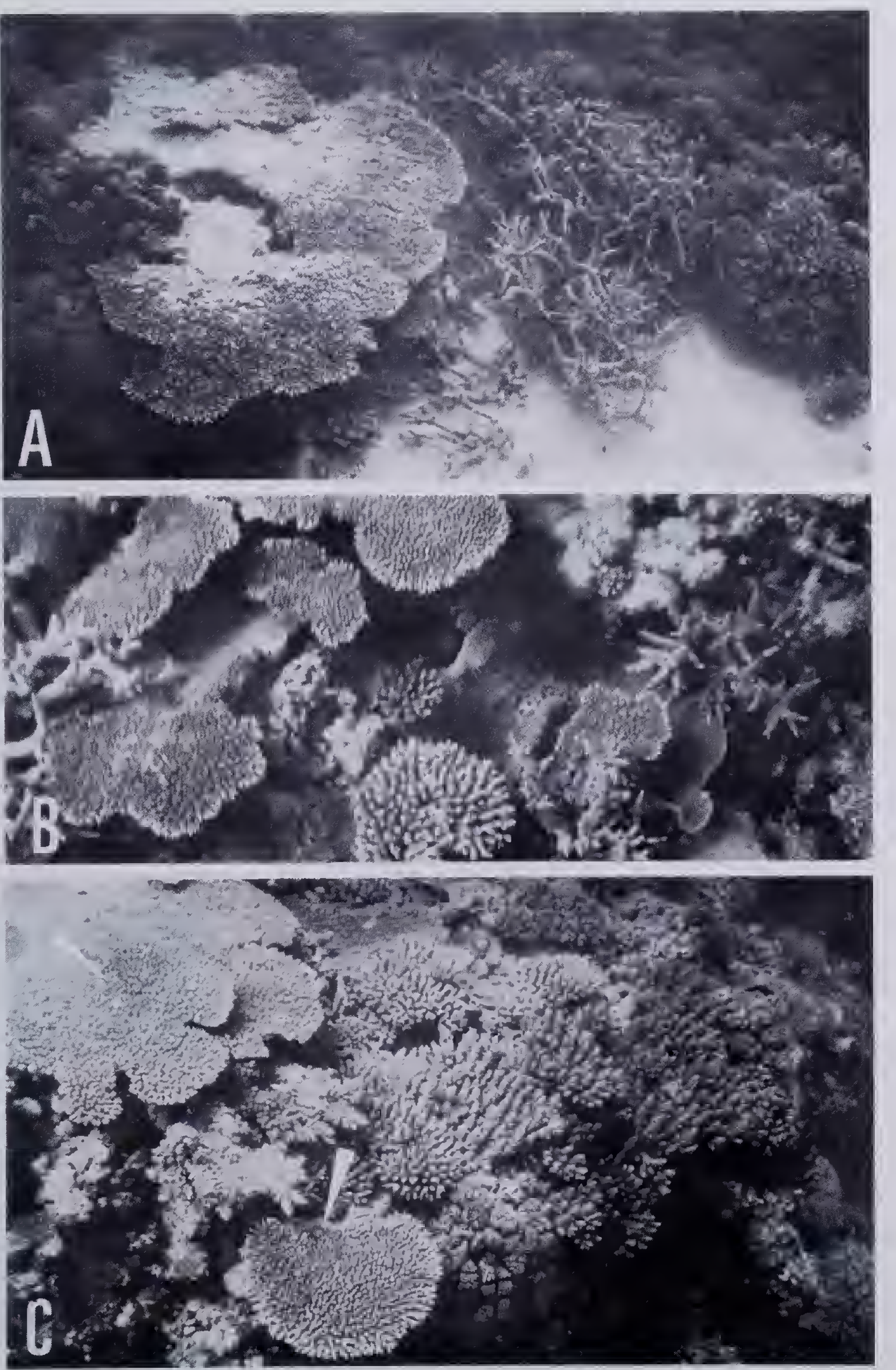
A
B
C

PLATE 66

Acropora hyacinthus (Dana, 1846) and *A. cytherea* (Dana, 1846)

A, B. *A. hyacinthus* portion of colony, G9865 Big Broadhurst Reef, SW. side, reef slope, 5·3 m, colour pink-brown.

C, D. *A. cytherea* portion of colony, G9856 Big Broadhurst Reef, SW. side, reef slope, 3 m, colour pink-brown.

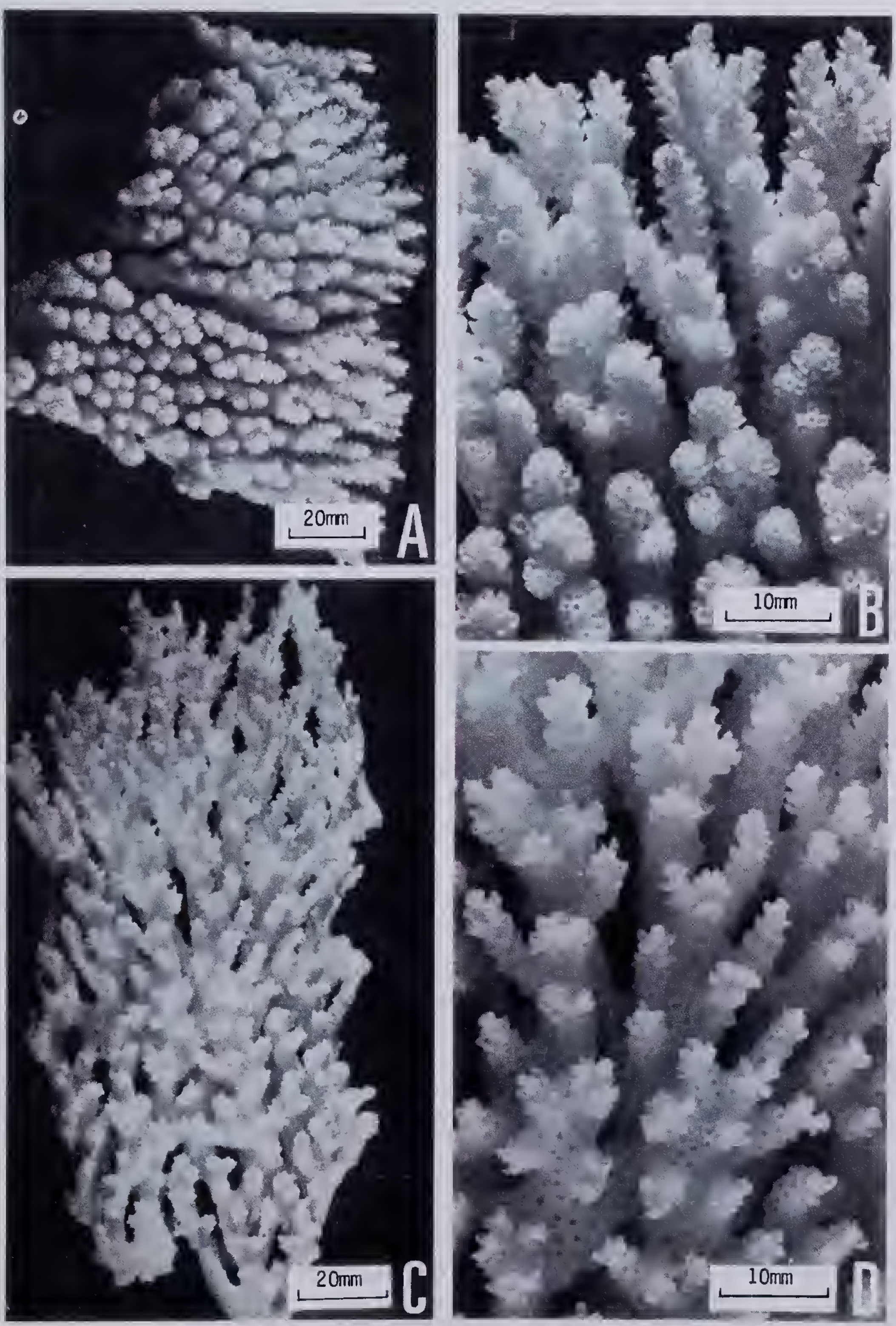
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PLATE 67

Acropora cytherea (Dana, 1846)

A. G7291 Flinders Reef, Moreton Bay, SE. Queensland.
B. G9855 Big Broadhurst Reef, SW. slope, 5 m, colour pale pinkish brown.
C. G9849 Big Broadhurst Reef, SW. slope, 9·7 m, colour yellow.

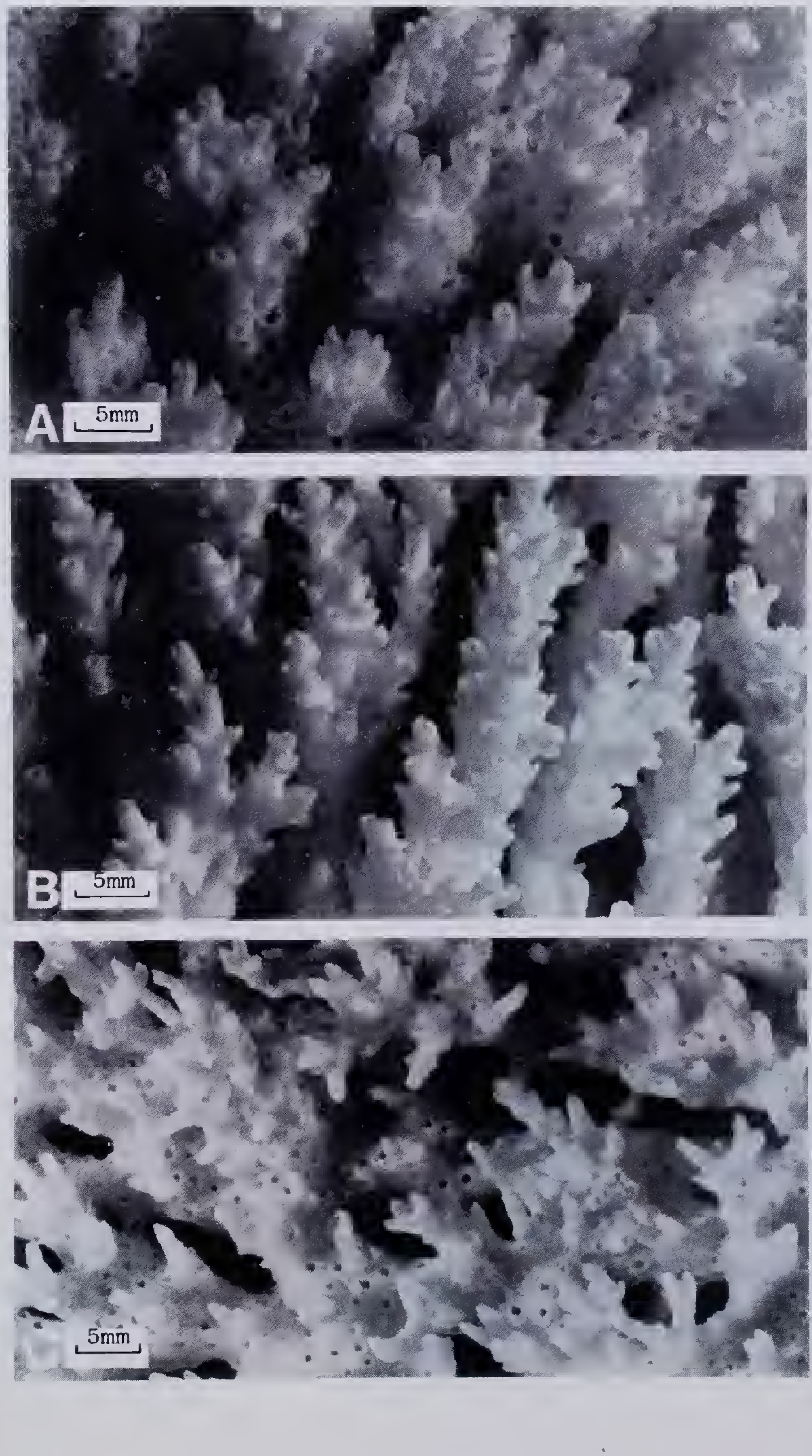
A
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PLATE 68

Acropora millepora (Ehrenberg, 1834)

A, B. G11064 Bowden Reef, slope of opening in SW. side, 2 m, colour orange.
C, D. G11049 Bushy-Redbill Reef, NW. side, outer reef flat, colour pale brown, yellow tips.

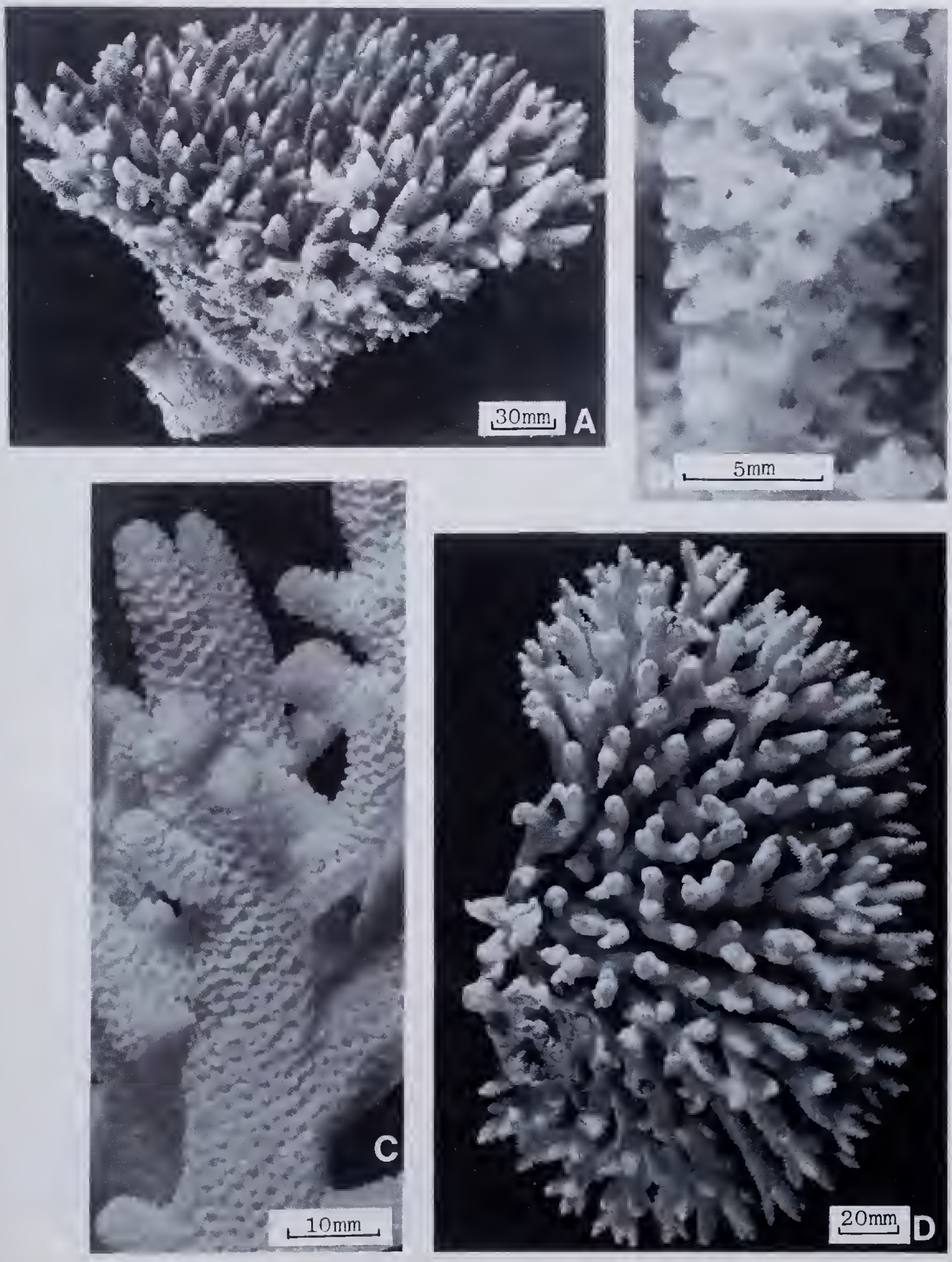
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Plate 69

Acropora delicatula (Brook, 1891)

A, B. G11441 Big Broadhurst Reef, SW. slope, 6 m, colour pale brown.
C. G11435, Big Broadhurst Reef, SW. slope, 17 m.

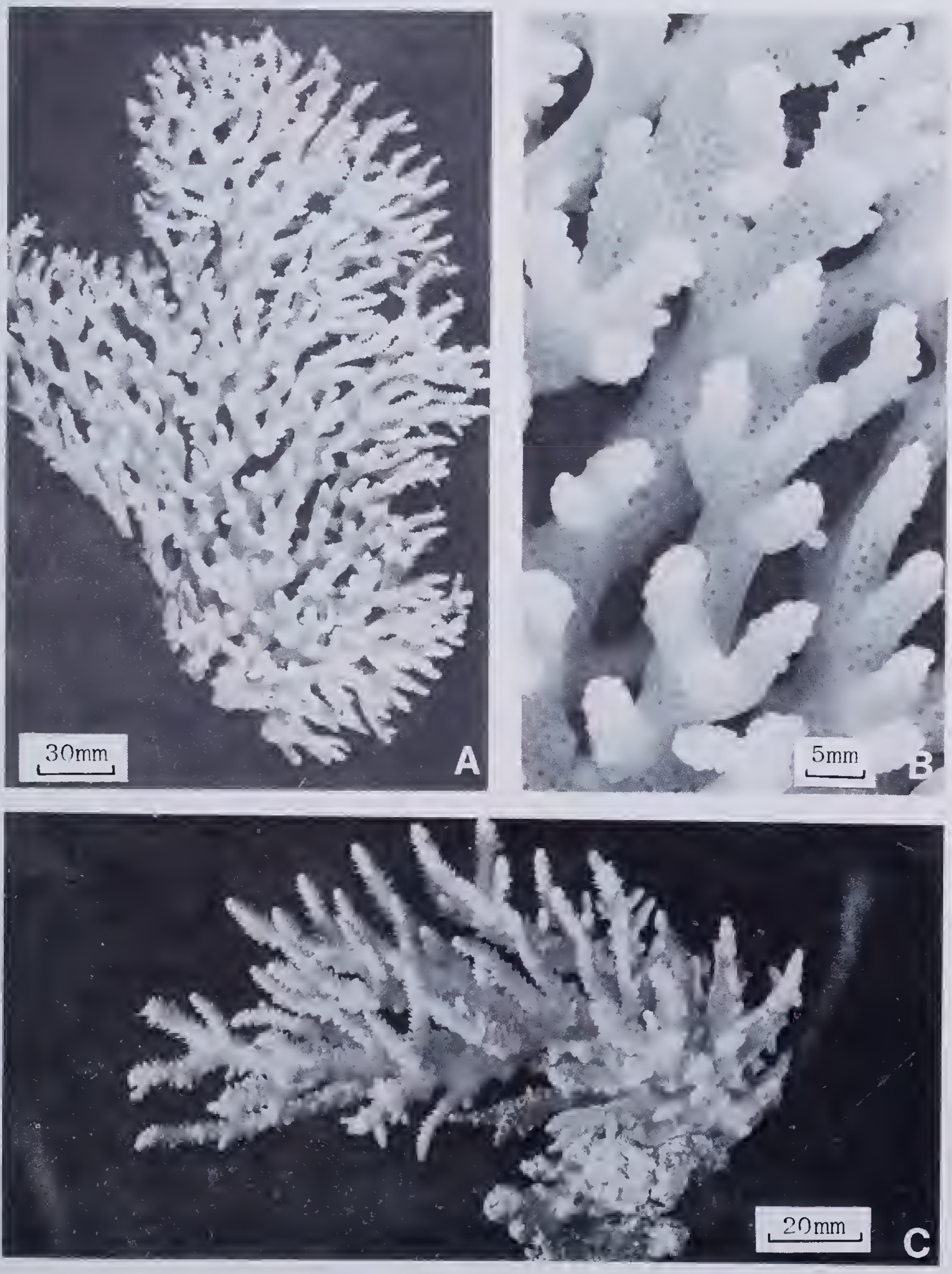
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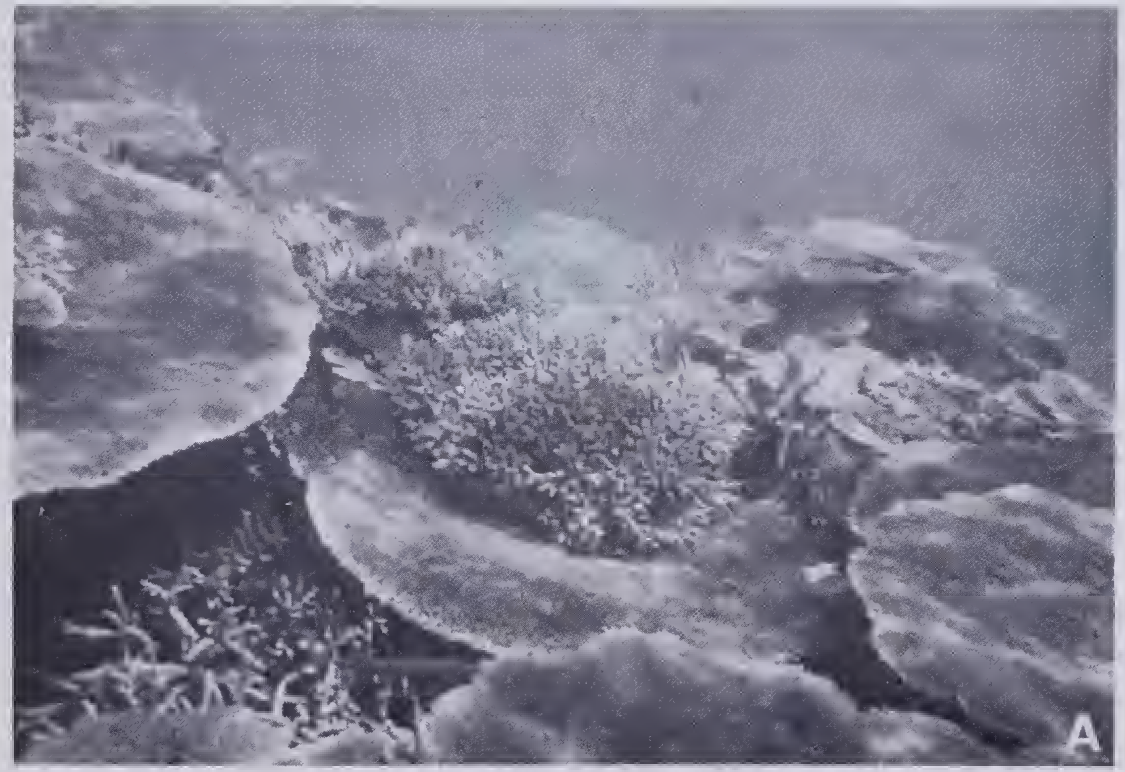
PLATE 70

Acropora haimei (Milne Edwards and Haime, 1860)

A. Compact arborescent clump on gentle reef slope on SW. side of Big Broadhurst Reef, about 5 m depth, (centre of picture) with flat plate species *A. hyacinthus* and *A. cytherea,* and other arborescent species.

B. Turf like patch on middle reef flat at Bushy-Redbill Reef, SW. side, with soft corals, *Seriatopora* (lower left) and *Acropora palifera* (lower right).


A


B

PLATE 71

Acropora haimei (Milne Edwards and Haime, 1860)

A, B. G10222 Big Broadhurst Reef, SW. slope, 4·2 m, colour cream.
C, D. G10217 Big Broadhurst Reef, SW. slope, 9·8 m, colour cream.

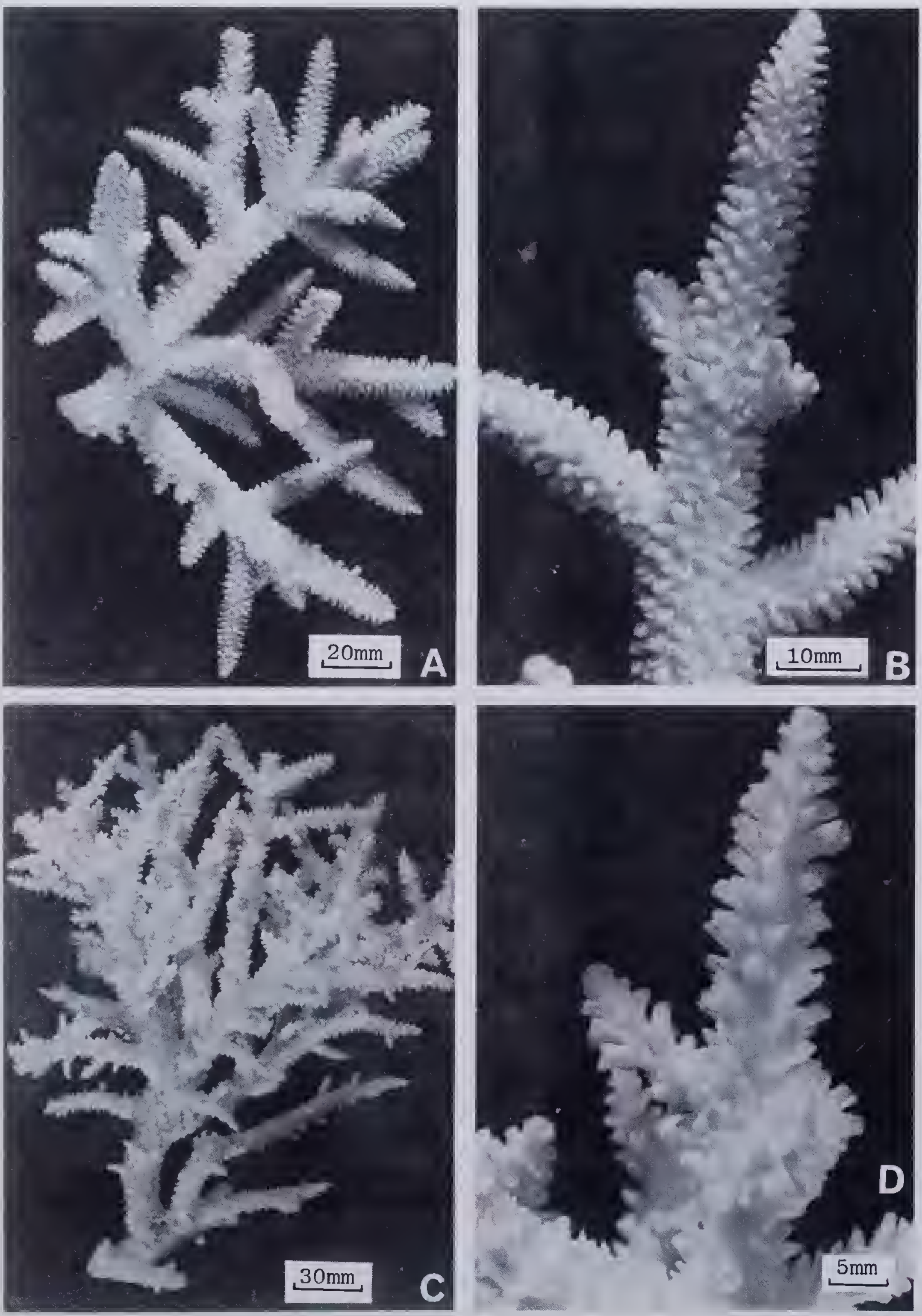

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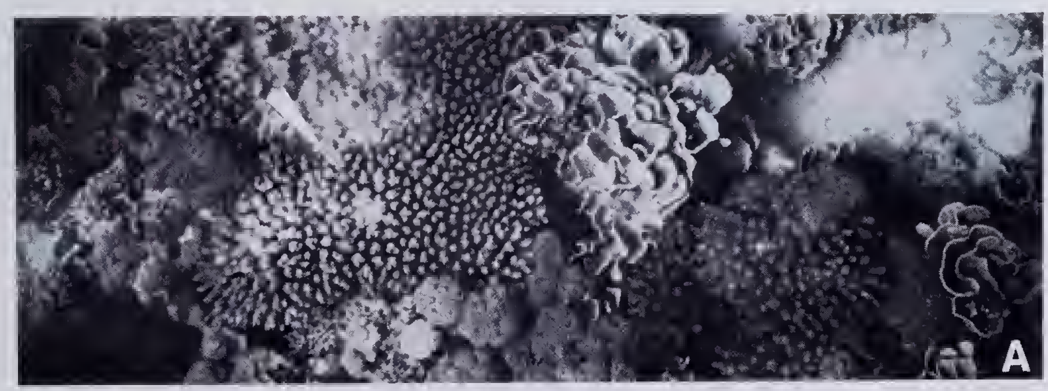
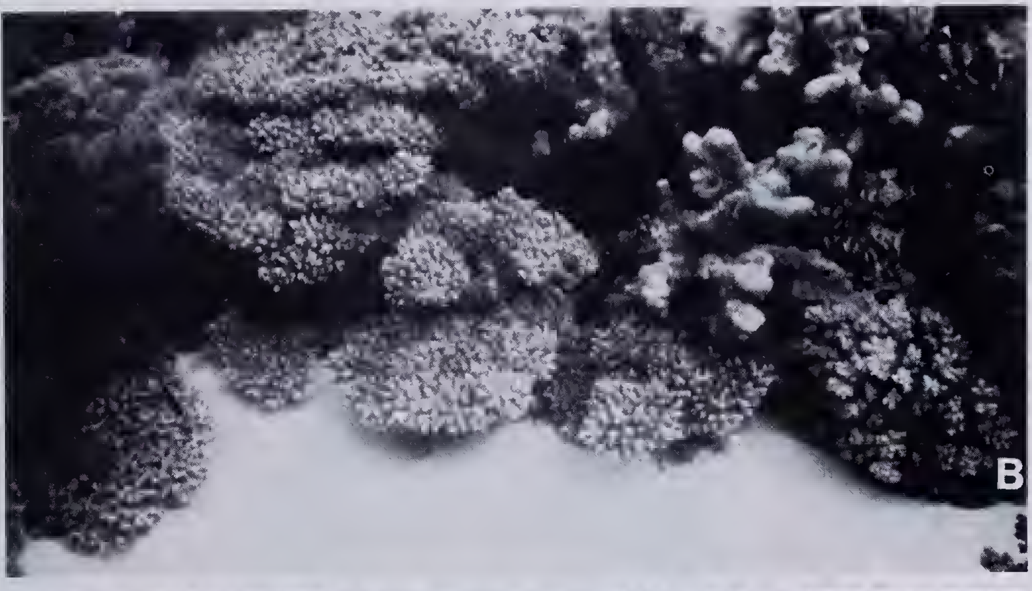
PLATE 72

Acropora tenuis (Dana, 1846) on the leeward (W.) side of Bushy-Redbill Reef.

A. Corymbose plate (arrow) on outer middle reef flat. With sponges and soft coral.
B. Layered colony in middle reef flat area, sandy bottom. With *A. palifera*, *Pocillopora* and *Seriatopora*.
C. Layered colonies on reef crest.


A


B

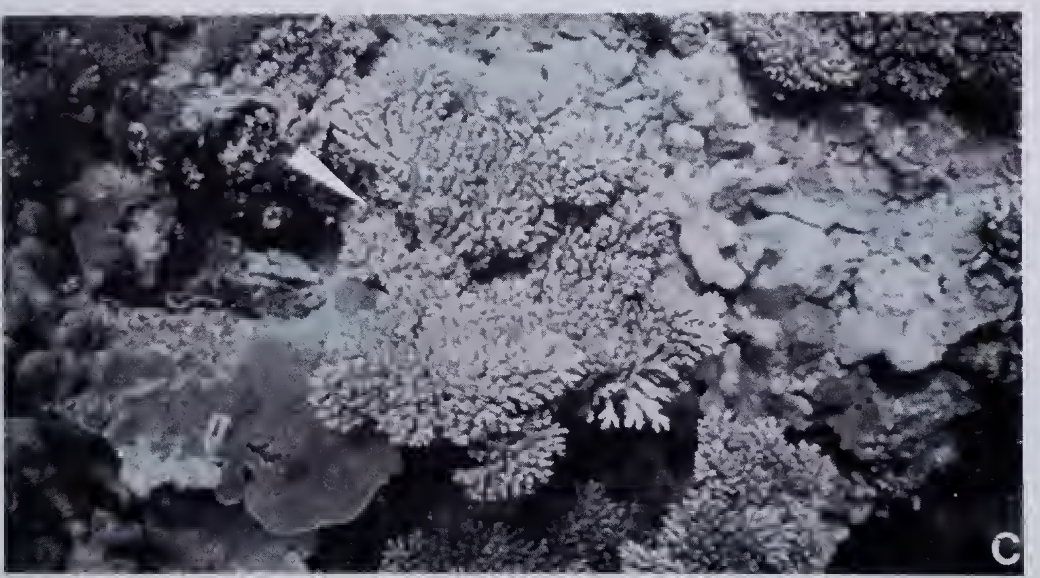

C

PLATE 73

Acropora tenuis (Dana, 1846)

A, B, E. G11418 Darley Reef, patch reef in lagoon, colour pale brown.
C, D. G11428 Big Broadhurst Reef, SW. slope, 6 m, colour pink-grey.

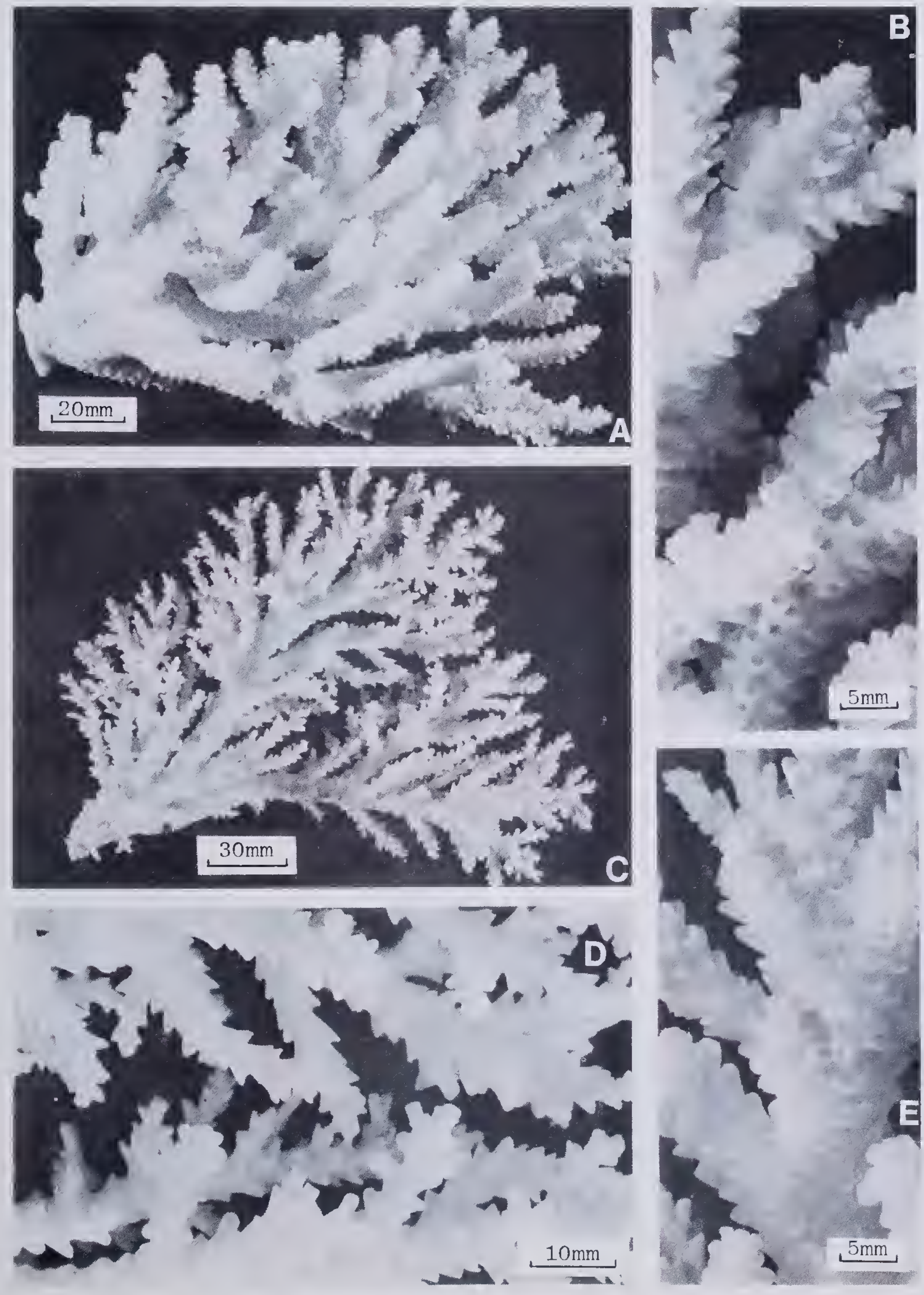

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PLATE 74

Acropora tubicinaria (Dana, 1846)

A, B. G11072, Bushy-Redbill Reef, W. side, inner reef flat, colour pale brown.
C, D. G11077, Bushy-Redbill Reef, W. side, inner reef flat, colour pale brown.

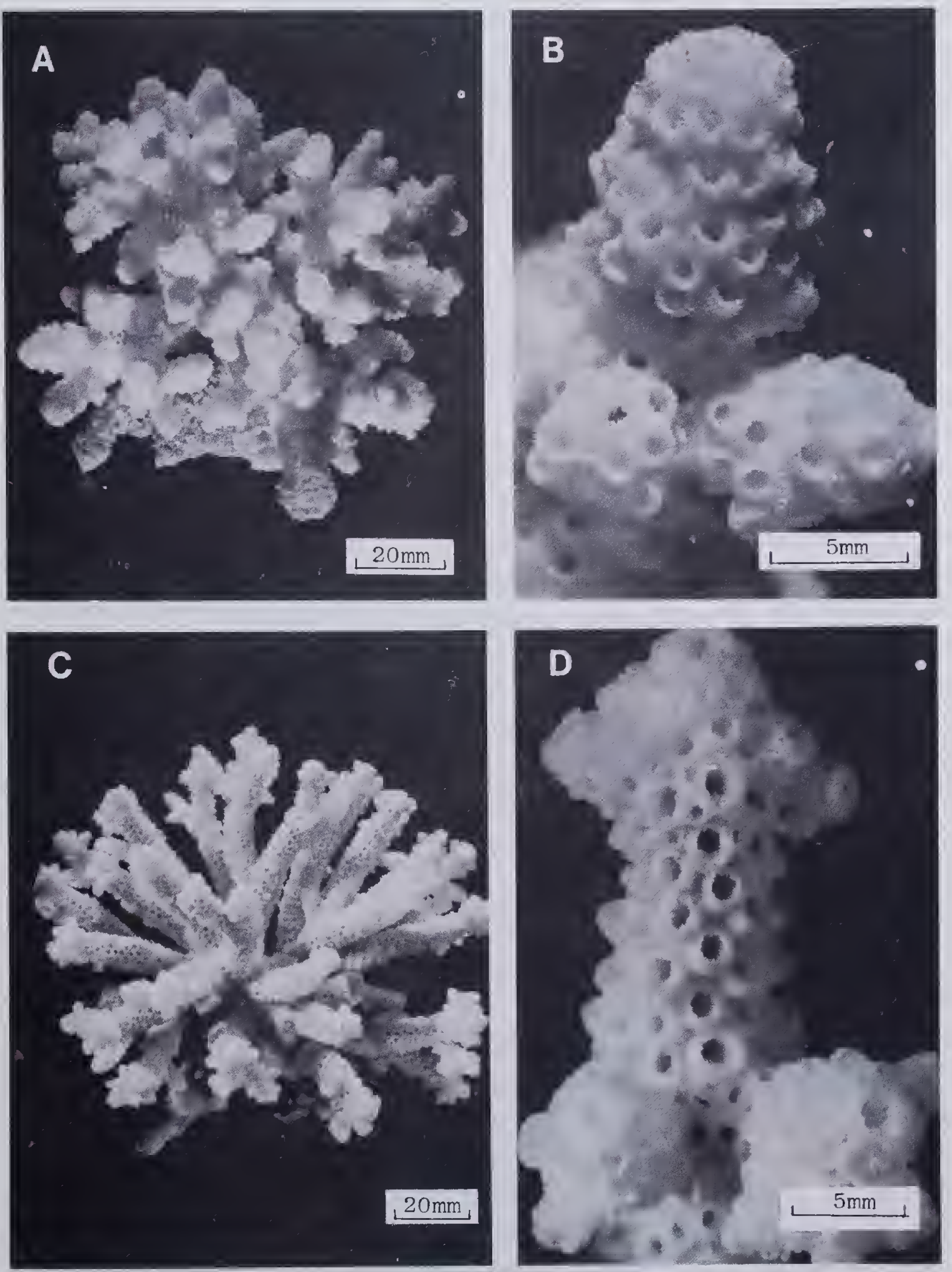
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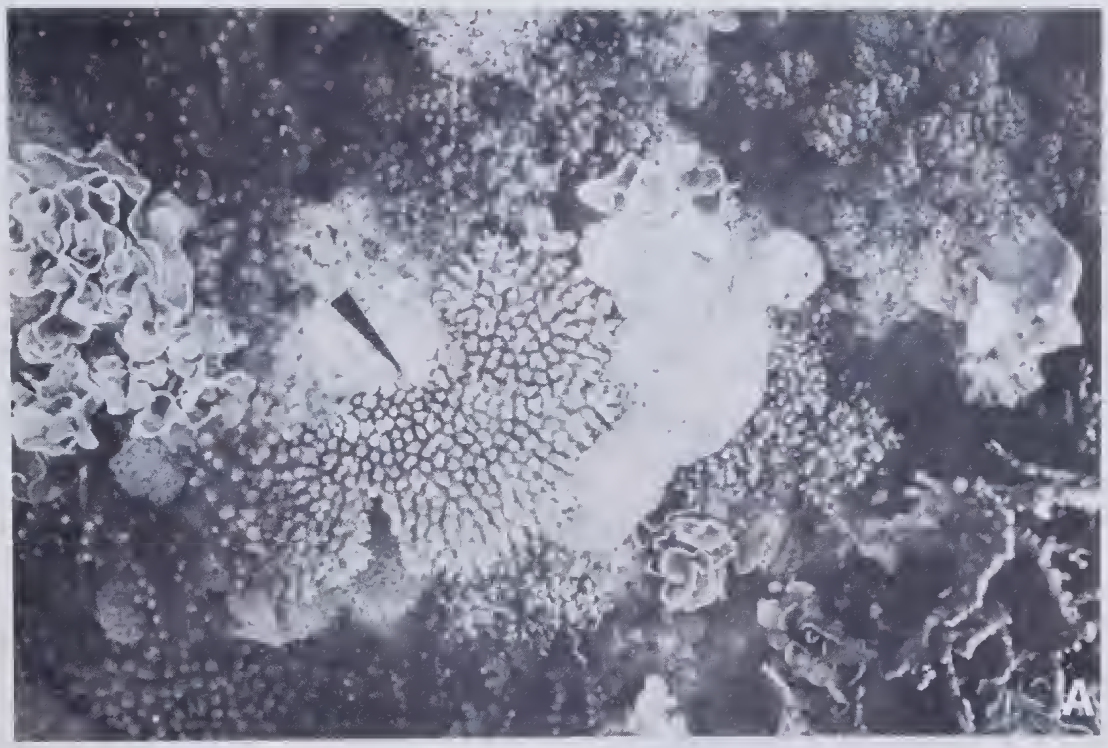
PLATE 75

Acropora aculeus (Dana, 1846) on the leeward side of Bushy-Redbill Reef

A. Plate like colony on middle reef flat (arrow) with soft corals and sponges.
B. Layered colony on reef crest (bottom of picture), with *A. formosa* (left), ?*A. haimei* (right), *A. palifera* (centre), *A. clathrata* (plate) and other corals.

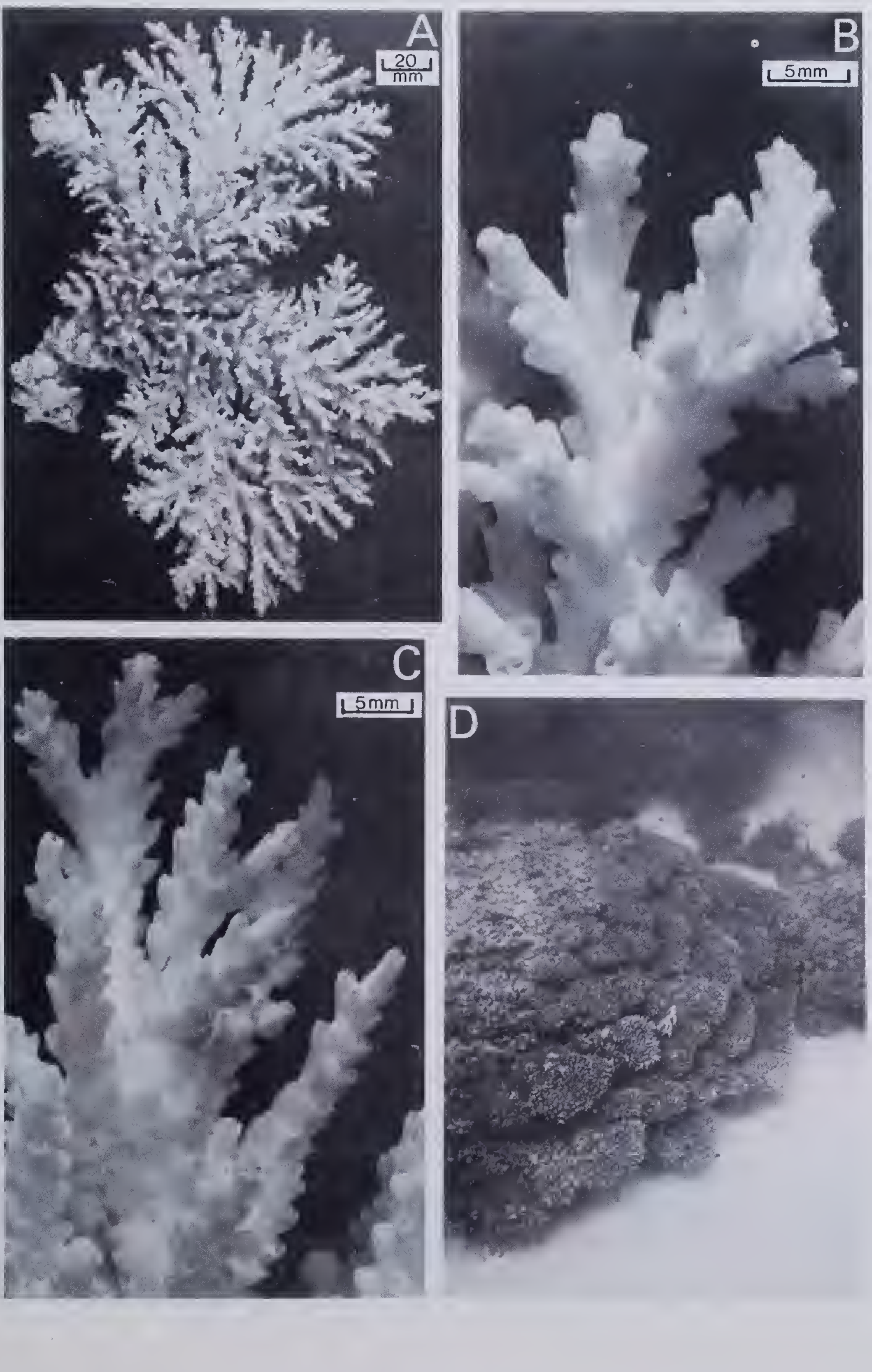

A


B

PLATE 76

Acropora aculeus (Dana, 1846)

A, B. From Big Broadhurst Reef, SW. slope, about 10 m. Small, thin plate specimen.
D. Large tiered plate colony in deep water middle reef flat area, Bushy-Redbill Reef, W. side.
C. Portion of a large tiered plate.


A
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B
5mm
C
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D

PLATE 77

Acropora cerealis (Dana, 1846)

A, B. G9519 Bowden Reef, slope of opening in SW. side, 3m, colour blue.

C, D. G9529 Big Broadhurst Reef, SW. slope, 8·7m, colour cream.

E, F. G9526 Darley Reef, patch reef in lagoon, 3m, colour pale brown-lavender.

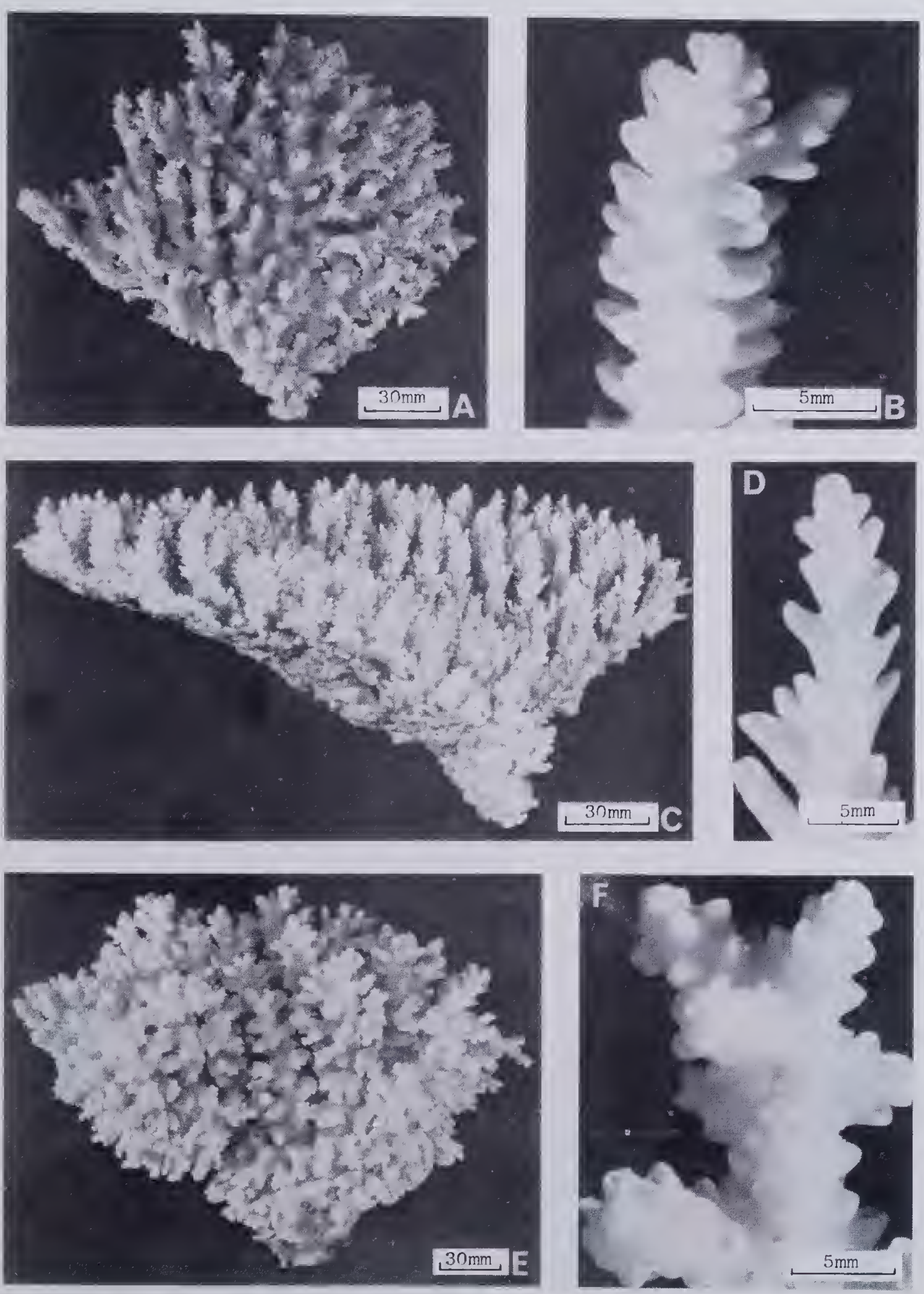
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PLATE 78

Acropora nasuta (Dana, 1846)

A, B. Colonies in the deep middle reef flat of Bushy-Redbill Reef, W. side with sandy bottom and soft corals.
C, D. G11224 Big Broadhurst Reef, SW. slope, 7m, colour grey.

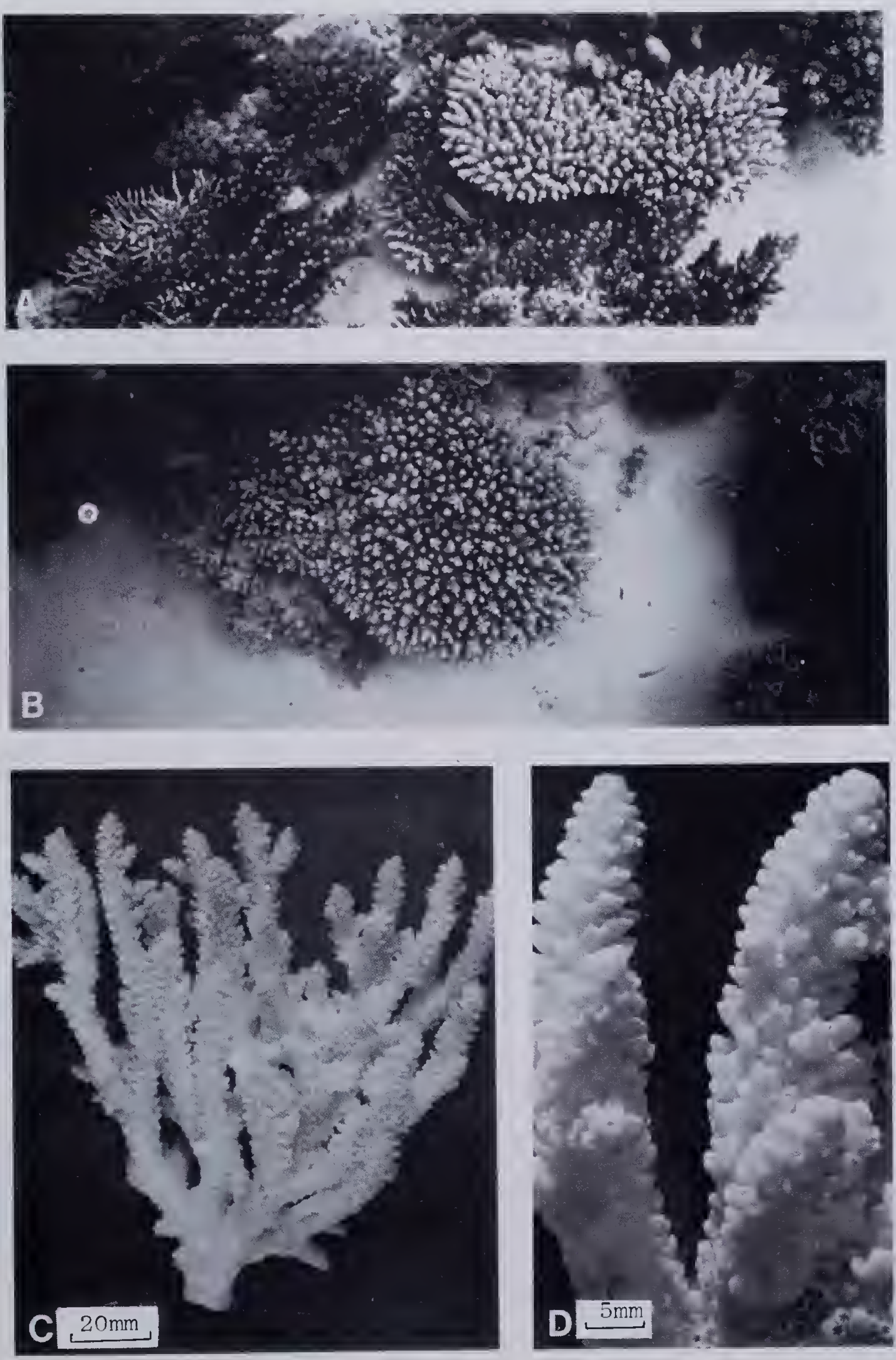
A
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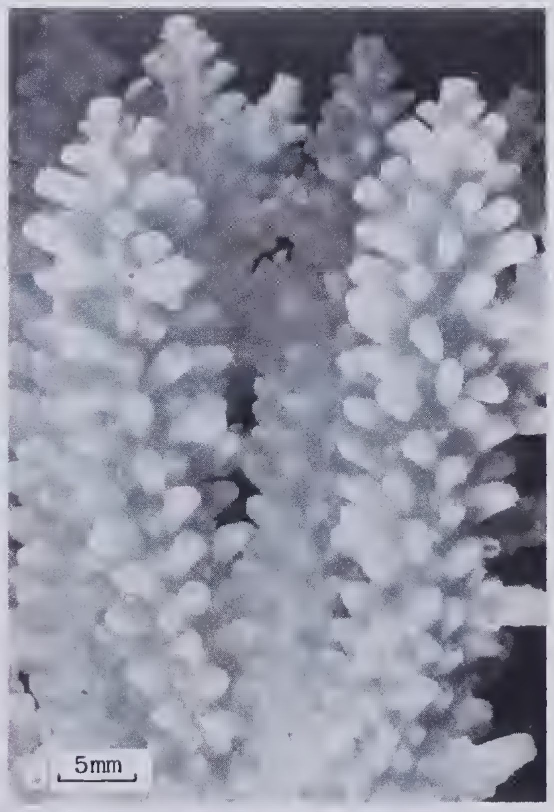
PLATE 79

Acropora diversa (Brook, 1891)

A, B. G11246 Big Broadhurst Reef, SW. slope, 8m, colour purple, cream tips.
C, D. G11245 Big Broadhurst Reef, SW. slope 1·3m, colour cream.


20mm
A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C

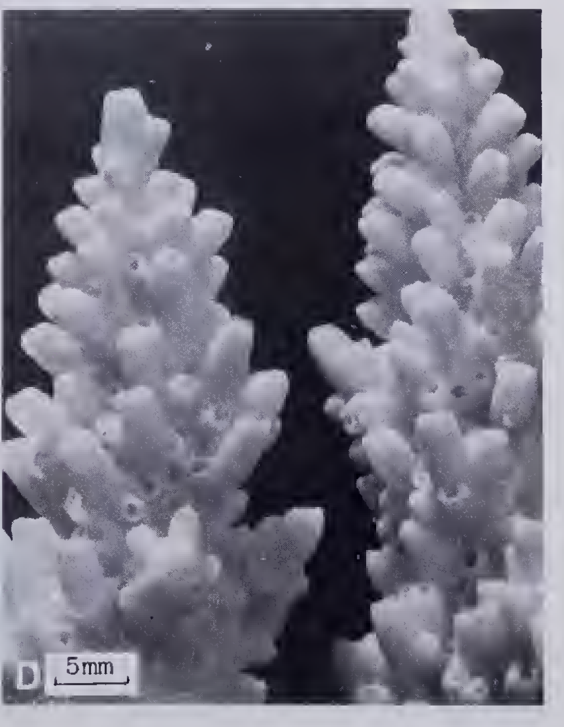
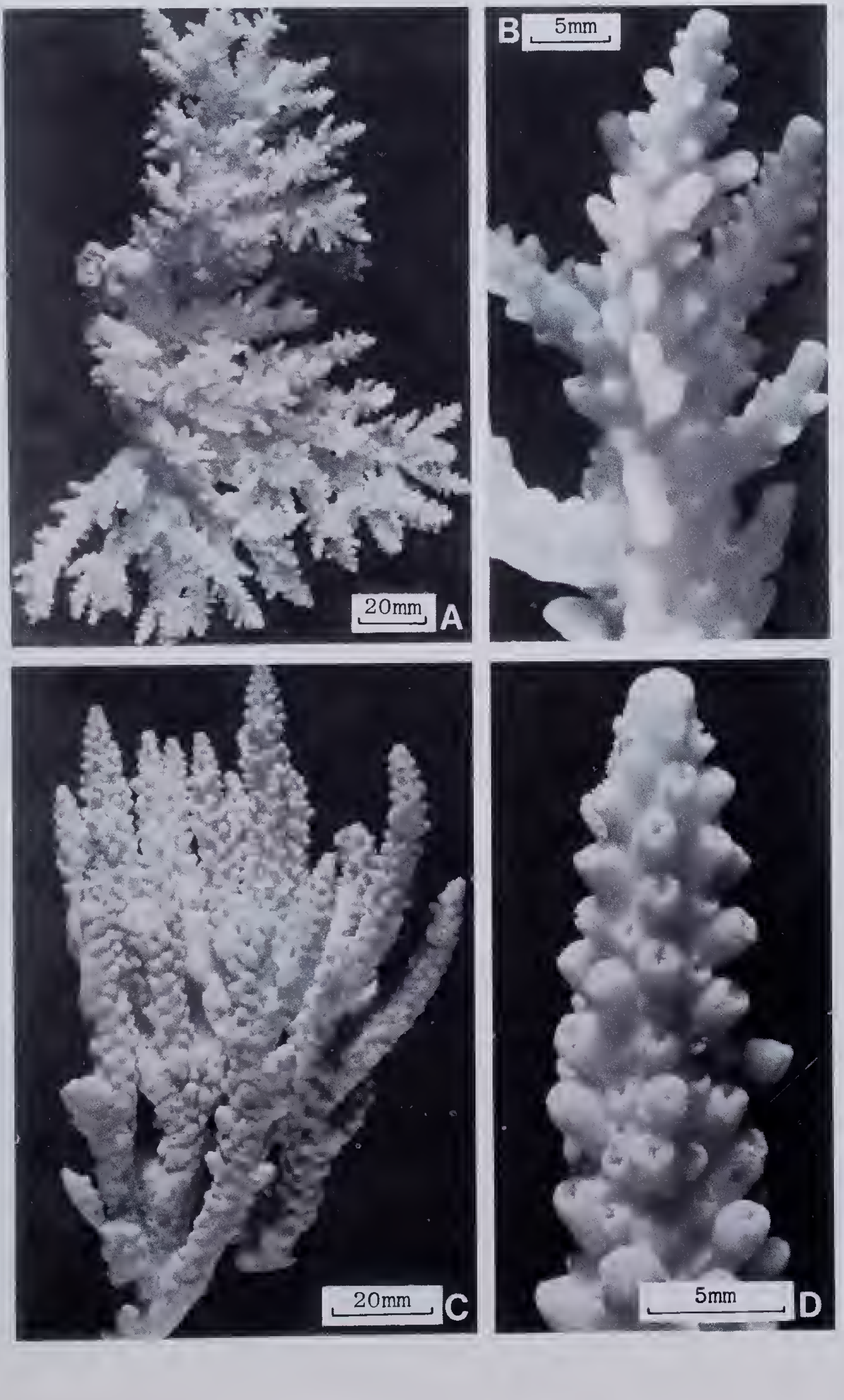

D
5mm

Plate 80

A, B. *A. diversa* (Brook, 1891) G11236 Big Broadhurst Reef, SW. slope 5·1 m, colour blue-brown.

C, D. *A. variabilis* (Klunzinger, 1879) G11290 Big Broadhurst Reef, SW. side, outer reef flat, colour cream.


B
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D

PLATE 81

Acropora humilis (Dana, 1846) and *A. millepora* (Ehrenberg, 1834) on the reef.

A. Reef edge at Big Broadhurst Reef, SW. side, looking back across the reef flat. *A. robusta* and *A. hyacinthus* in the foreground: most of the other colonies are *A. humilis.*

B. *A. humilis* colony on sandy bottom, deep middle reef flat, Bushy-Redbill reef, W. side. This colony could be regarded as forma α → forma β.

C. Outer reef flat on windward side (SE.) of Bushy-Redbill Reef. Colony in centre may be regarded as *A. humilis* forma γ, and that to its left as *A. humilis forma* β. To the right is another low *A. humilis,* and other corals are *A. palifera* and *Pocillopora.*

D. *A. millepora* (centre) on reef flat adjacent to Redbill Island; to its left is *A. humilis* forma γ, and another small *A. millepora* colony. To the right is *A. aspera.*

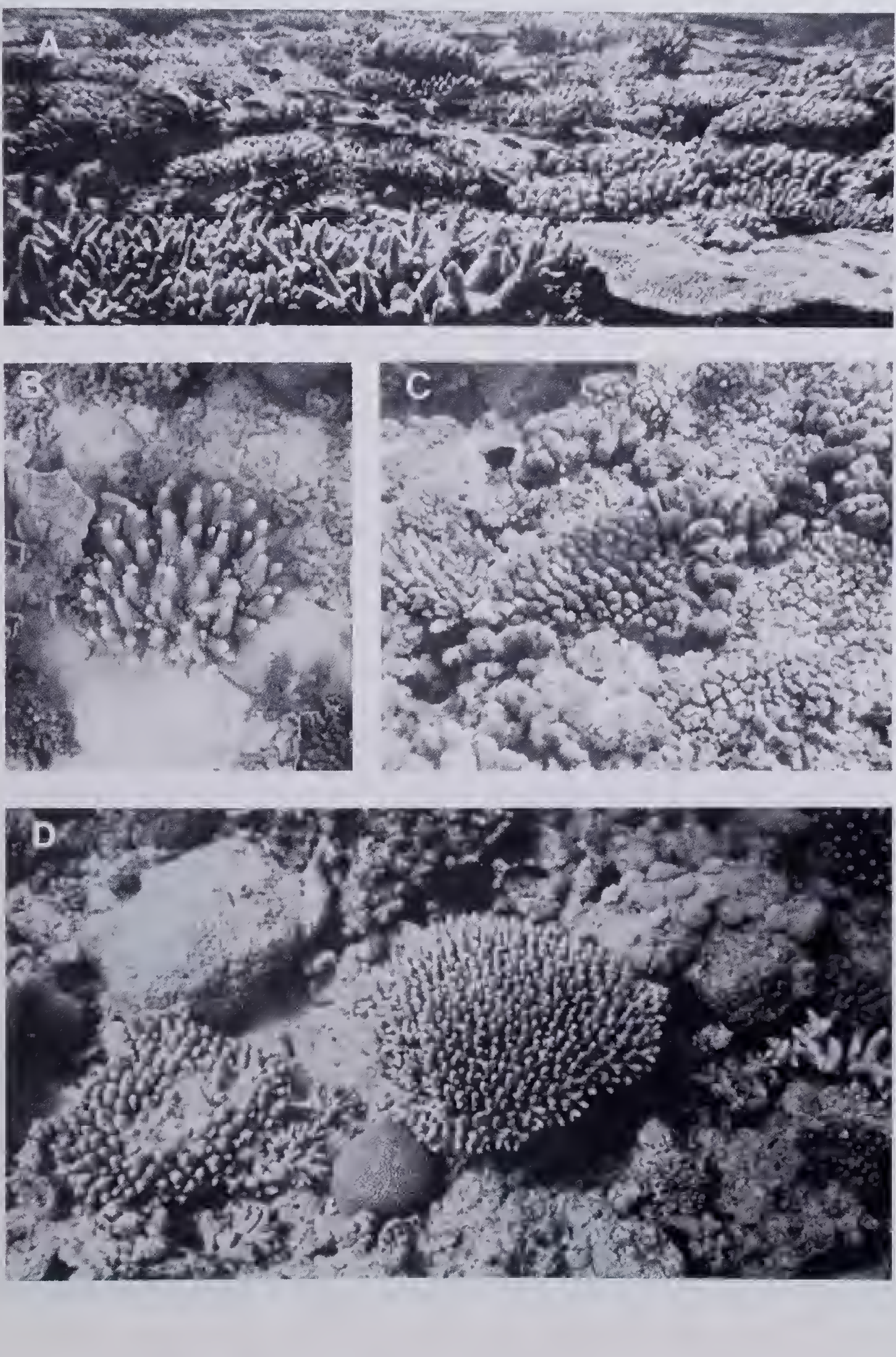
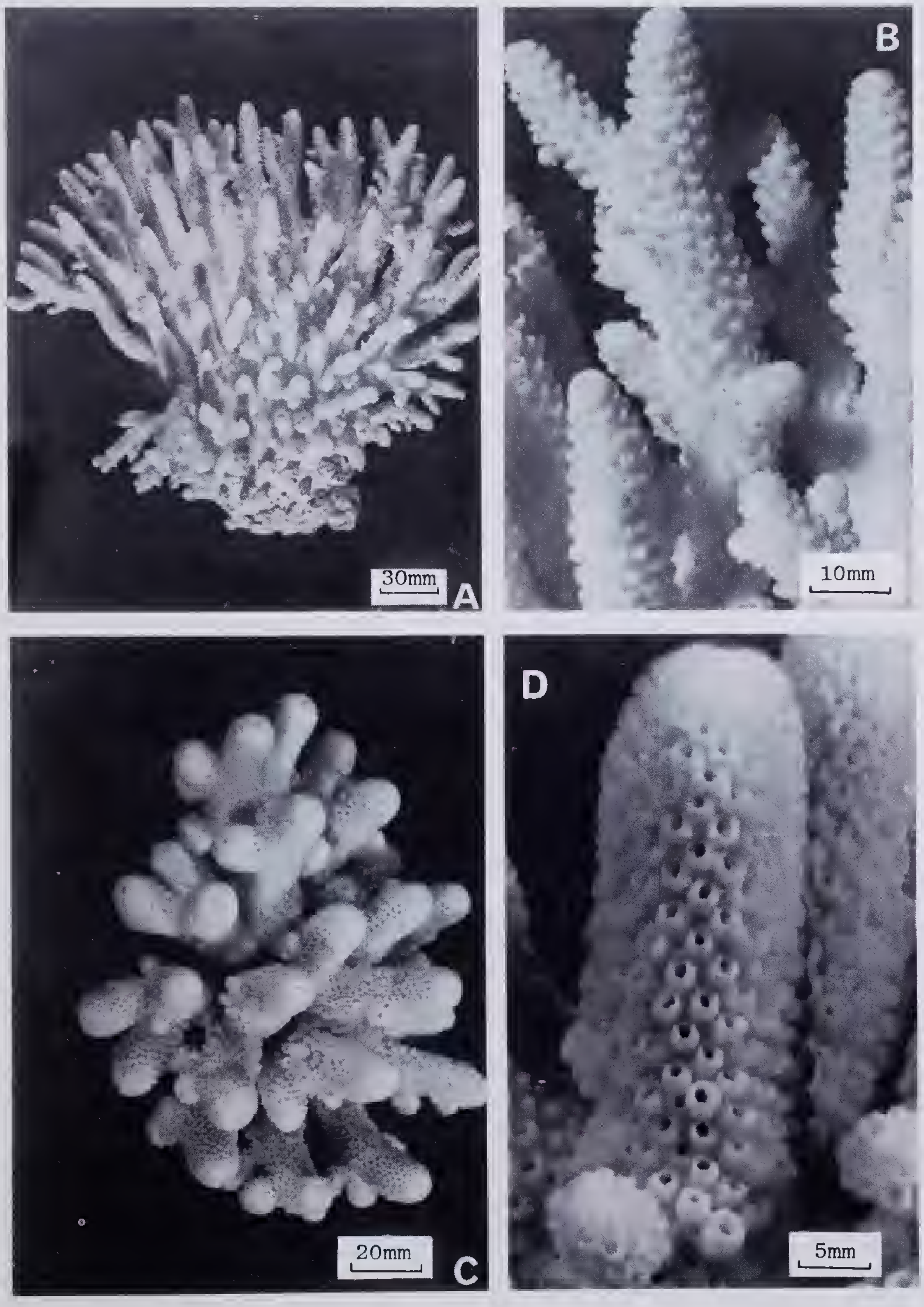

A
B
C
D

PLATE 82

Acropora humilis (Dana, 1846)

A, B. G11611 Darley Reef, patch reef in lagoon, 5m, colour pale brown, lavender tips. Forma α Wells.

C, D. G11189 Bowden Reef, slope of opening in SW. side. Forma α Wells.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A
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20mm
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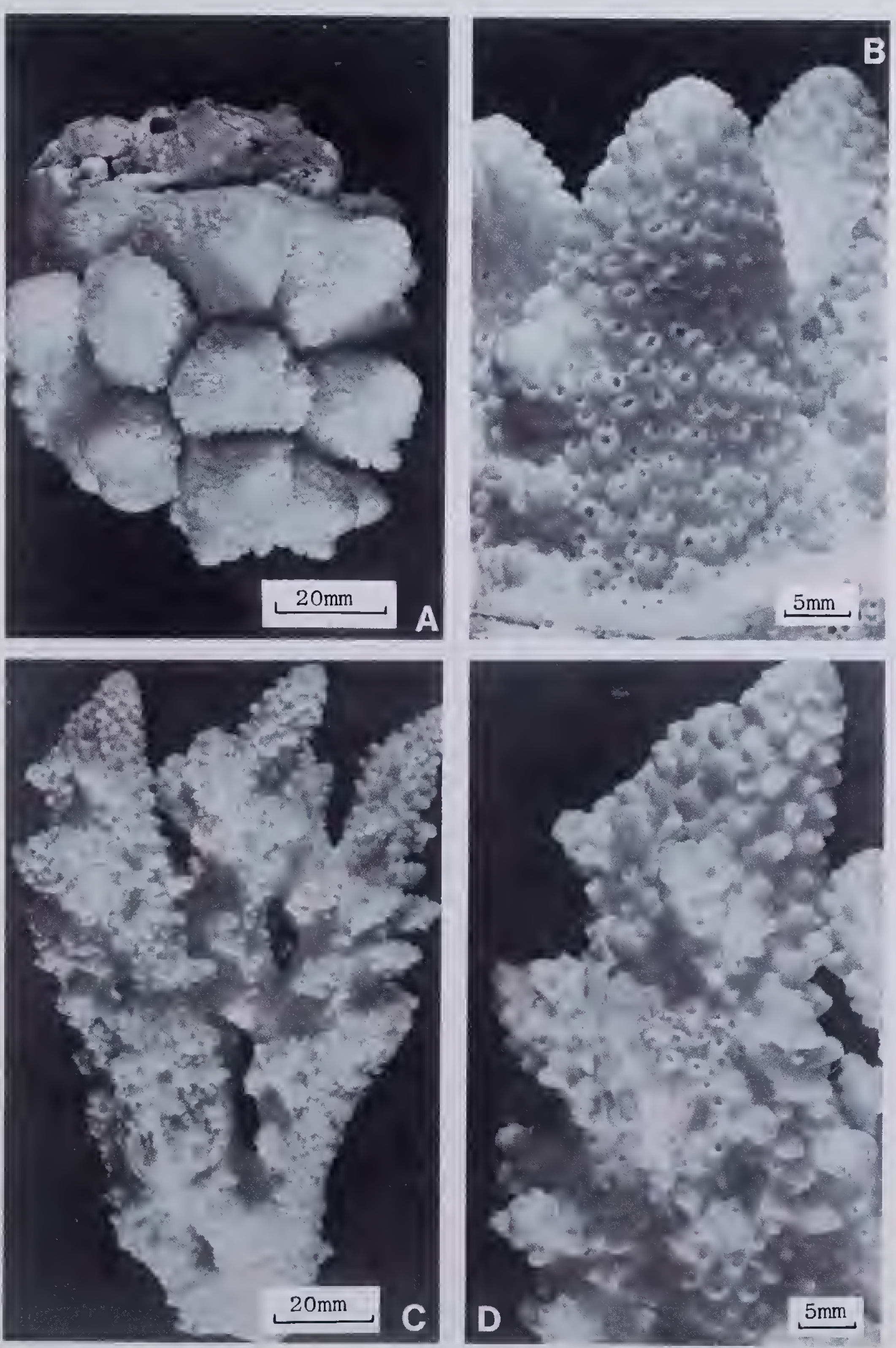
5mm

PLATE 83

Acropora humilis (Dana, 1846) (Specimens not mentioned in text).

A, B. G11150 Big Broadhurst Reef, weather (E.) side, 2m, colour blue. *A. humilis* forma γ Wells.
C, D. G11142 Big Broadhurst Reef, SW. slope, 2m. Forma α → forma β Wells.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A
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5mm

PLATE 84

Acropora digitifera (Dana, 1846)

A. Colonies on outer reef flat adjacent to Redbill Island (small colony centre left is *A. millepora)*

B, C. G11169 Big Broadhurst Reef, outer reef flat, colour cream, blue tips.

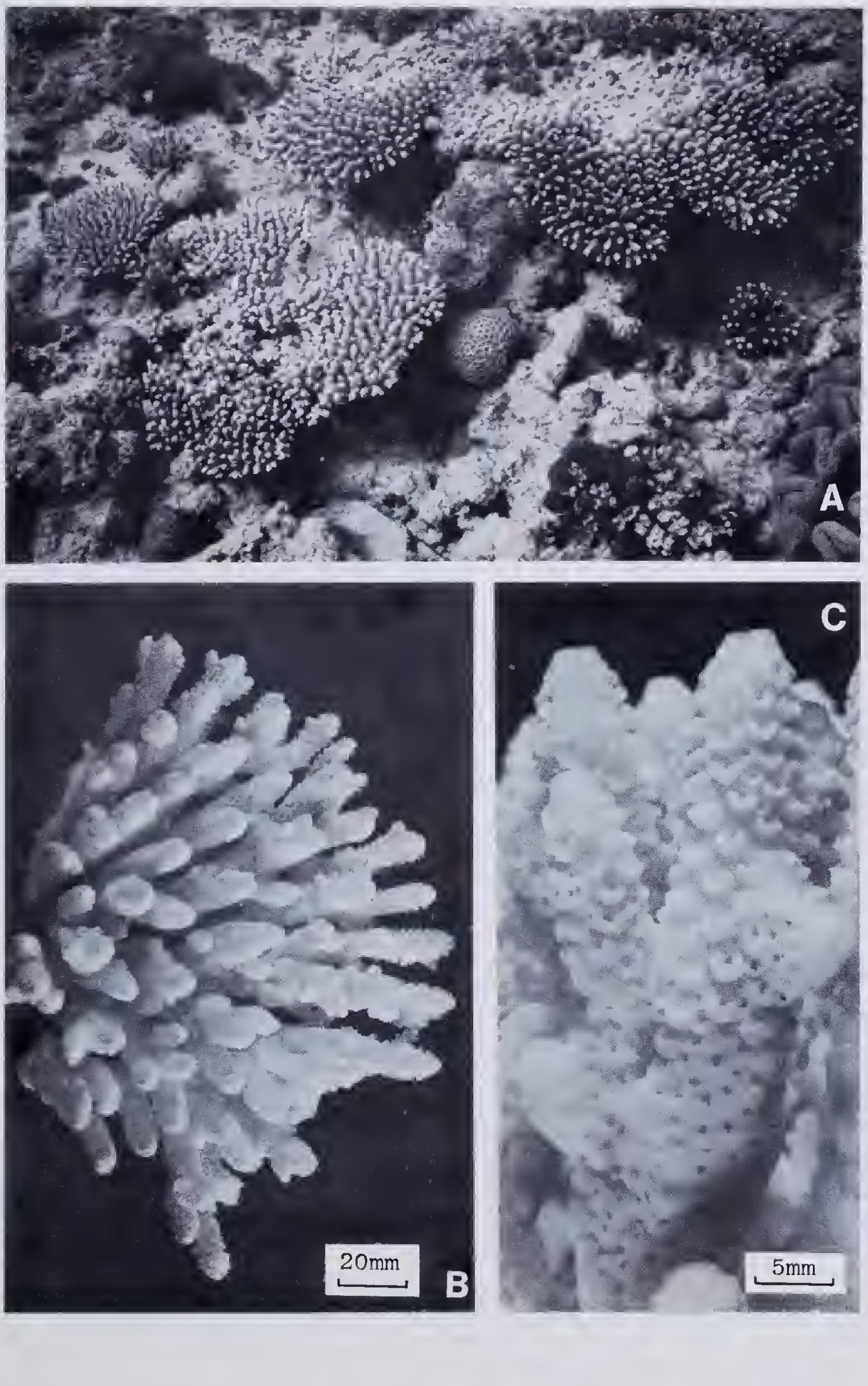
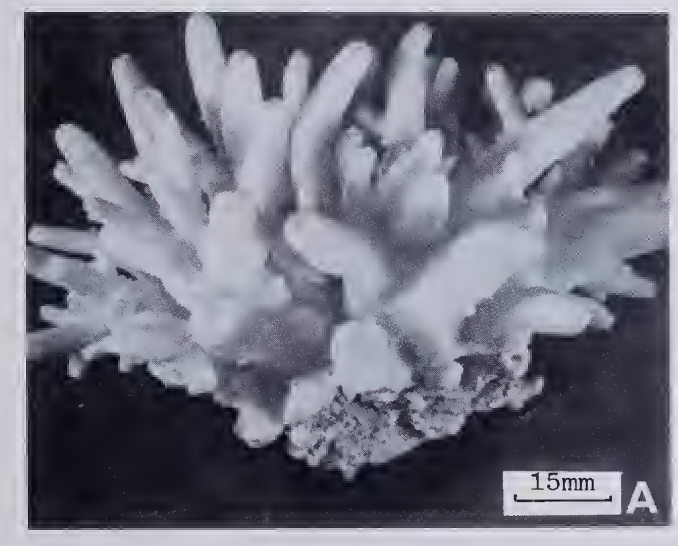

A
C
20mm
B
5mm

PLATE 85

Acropora multiacuta Nemenzo, 1967. All specimens from Darley Reef, patch reef in lagoon, all pale blue.

A. G10471.
B. G10468.
C, D. G6721.


15mm
A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C


10mm
D

PLATE 86

Acropora clathrata (Brook, 1891)

A, B. G9762, whole colony, Bowden Reef, SW. side, reef slope 1m, colour lavender-brown.
C, D. G9753, portion of colony, Big Broadhurst Reef, SW. side, reef slope, 5m, colour yellow-brown.
E, F. G9750, portion of colony, Big Broadhurst Reef, SW. side, reef slope, 5m, colour brown, with mauve tips to branchlets.

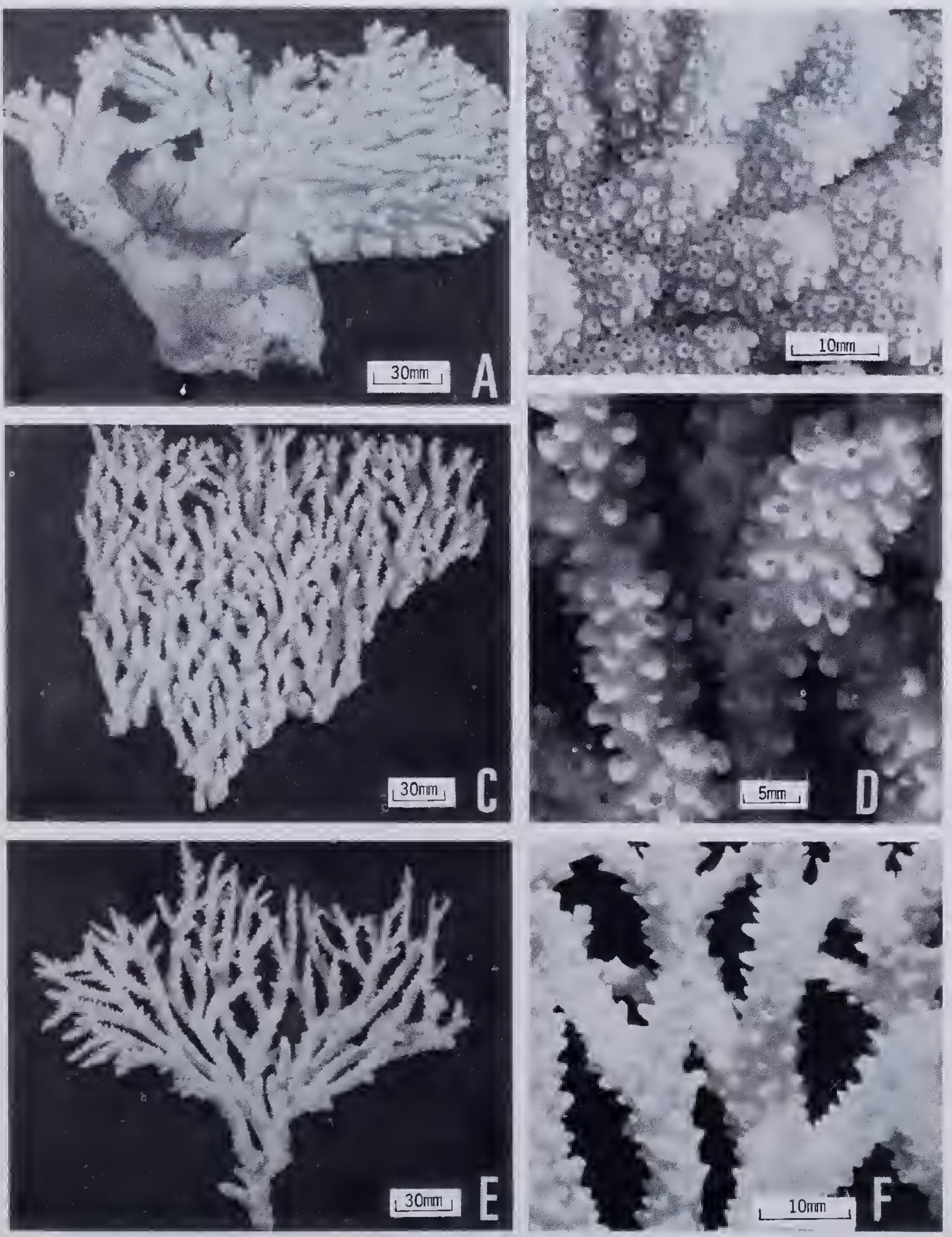
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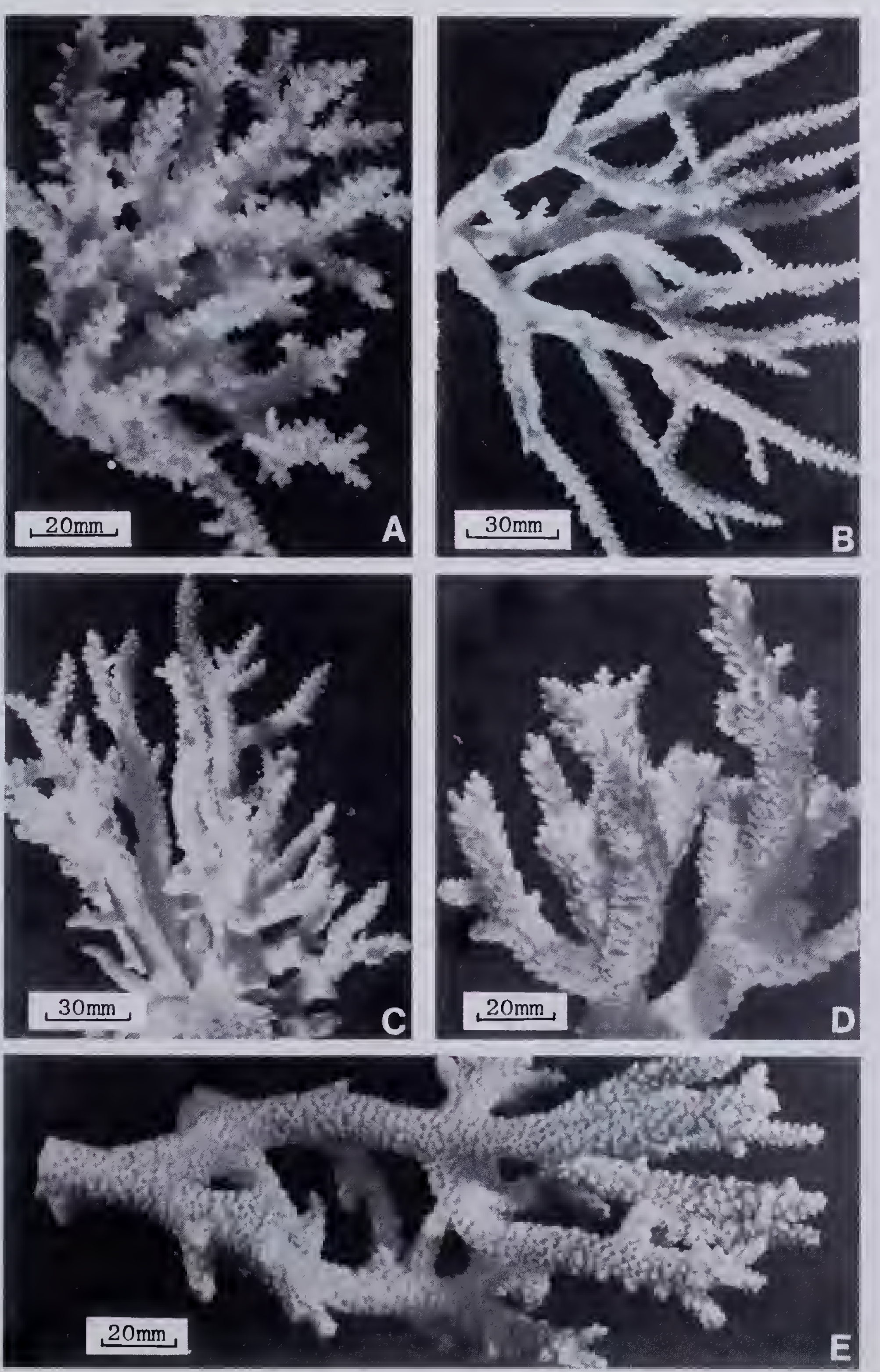
PLATE 87

Acropora divaricata (Dana, 1846) (C is a whole colony, others are portions of colonies).

A. G9162 Big Broadhurst Reef, SW. slope, 12·4m, colour brown, blue tips.
B. G9181 Big Broadhurst Reef, SW. slope, 7m, colour brown, blue tips.
C. G9182, Darley Reef, patch reef in lagoon, 7m, colour brown, lavender tips.
D. G9173 Big Broadhurst Reef, SW. slope, 8·7m, colour brown.
E. G9174 Big Broadhurst Reef, SW. slope, 8·6m, colour brown, blue tips.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E

PLATE 88

Acropora divaricata (magnified views of specimens in plate 87)

A. G9162, see Plate 87A.
B. G9181, see Plate 87B.
C. G9173, see Plate 87D.
D. G9174, see Plate 87E.

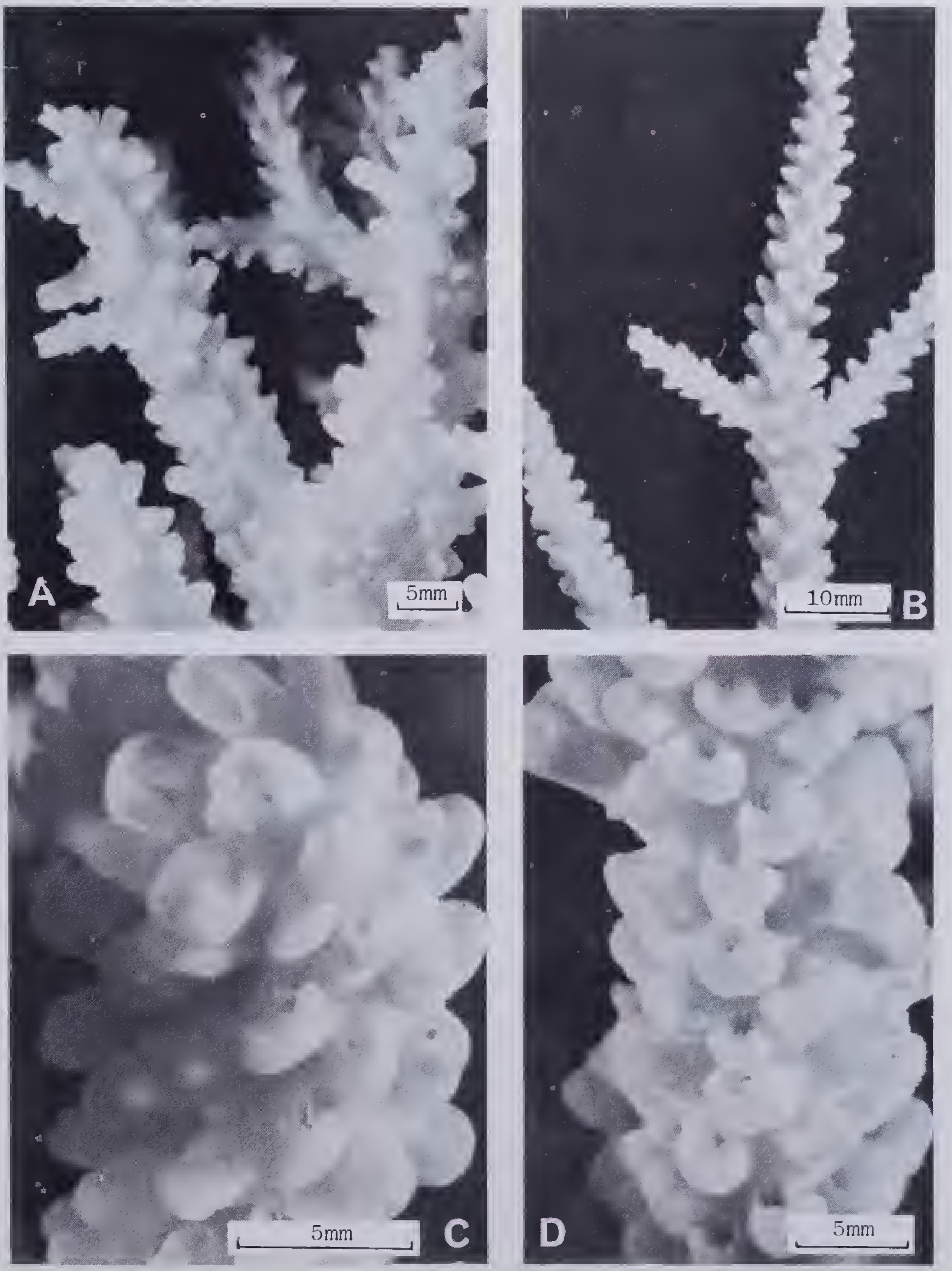
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PLATE 89

Acropora sarmentosa (Brook, 1892)

A, B. G9057, Big Broadhurst Reef, SW. slope, 7·6 m, colour cream-brown.

C, D. G9059, Big Broadhurst Reef, SW. slope, 9·7 m, colour green, pink-grey tips.

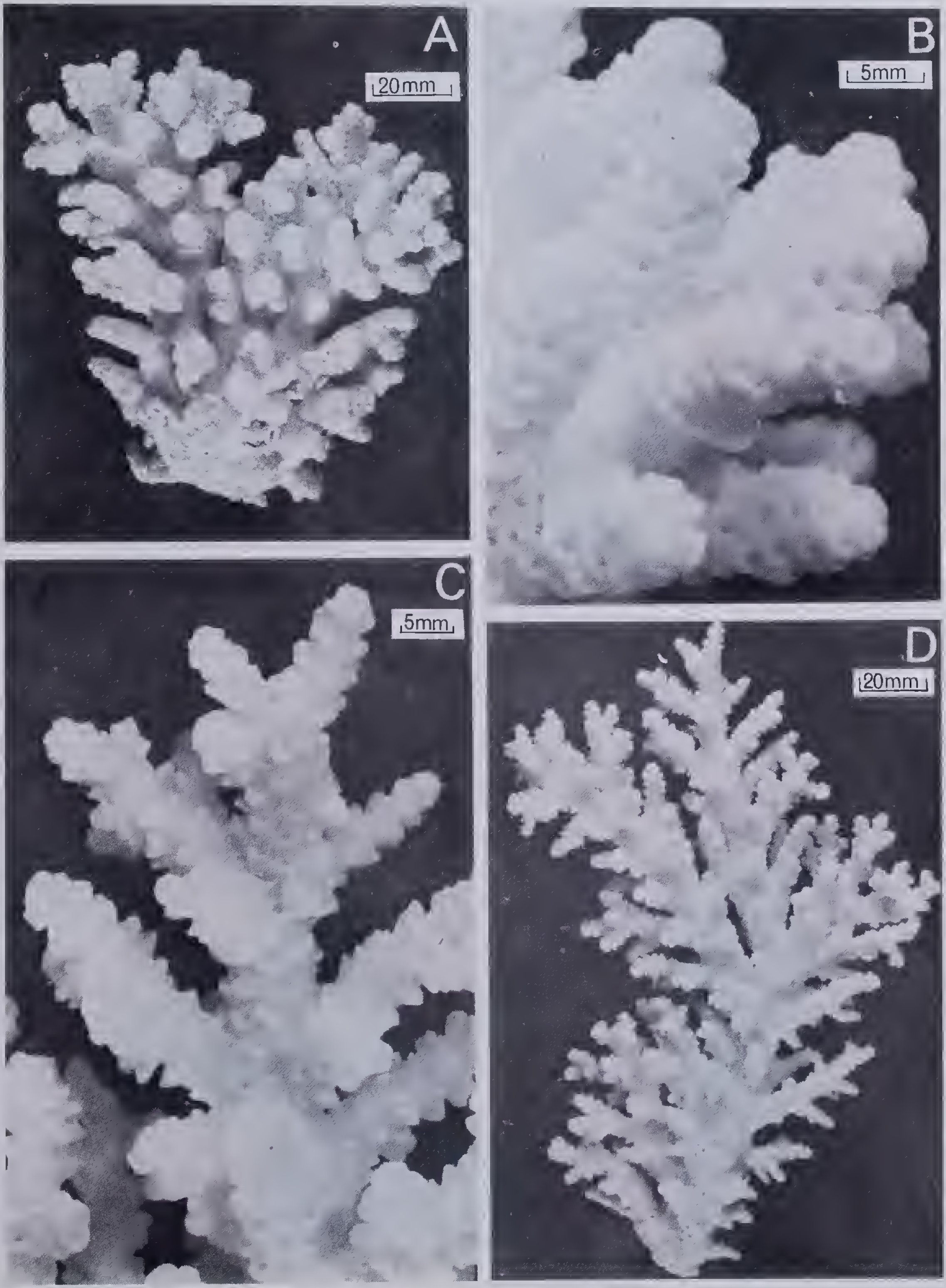
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PLATE 90

Acropora florida (Dana, 1846) on Big Broadhurst Reef.

A. In mixed assemblage on floor of surge channel at 10 m (centre). Rounded, open-arborescent colony. Branches are round in cross-section, secondary branchlets are evenly distributed and sized. Coral in bottom left corner is *A. splendida.*

B. Colony on reef slope, at about 10m (arrow). Branches here are more or less horizontal, and are flattened in cross-section. Secondary branchlets are differentially developed on the upper surface.

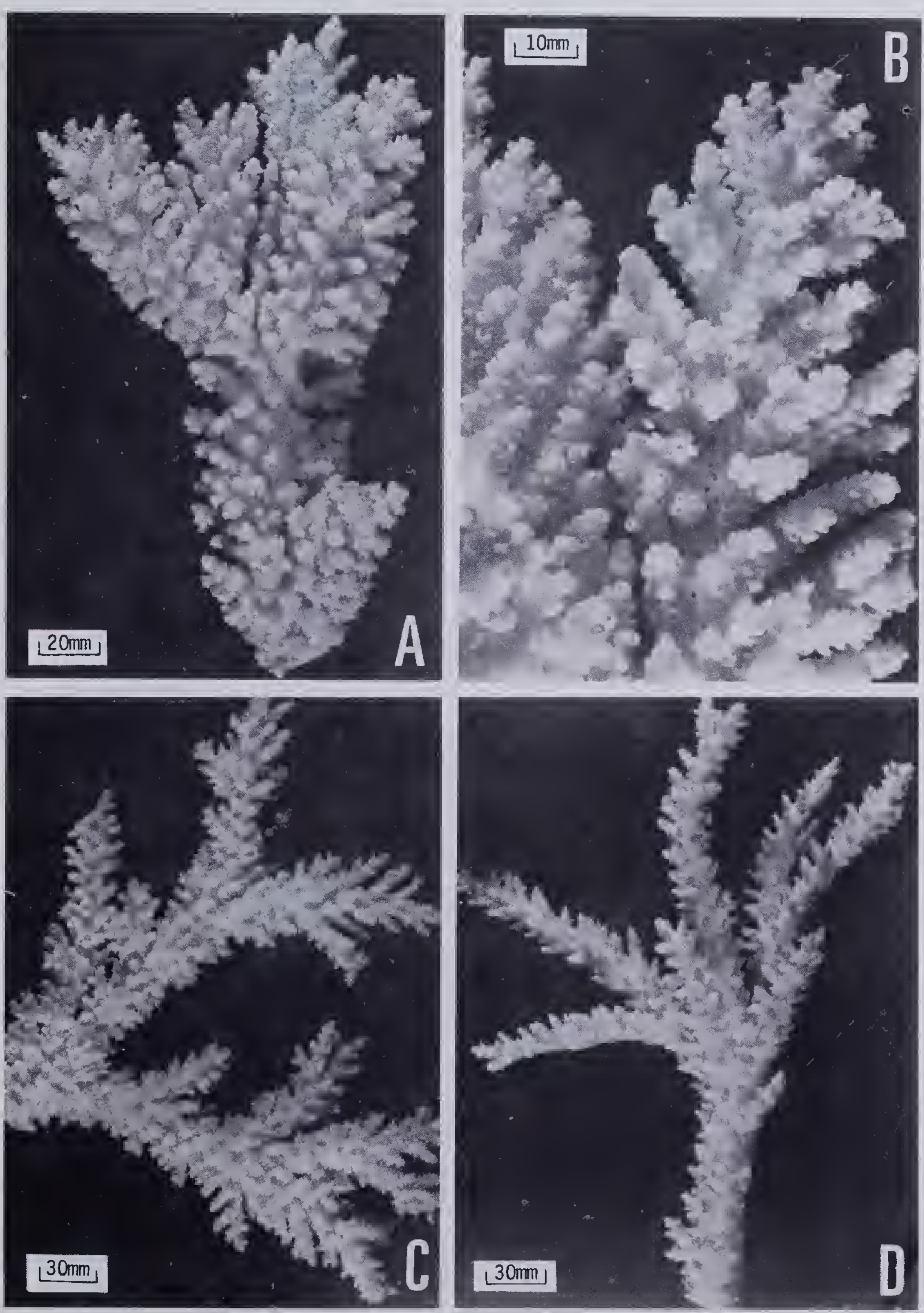

A


B

PLATE 91

Acropora florida (Dana, 1846)

A, B. G8651, portion of colony, Big Broadhurst Reef, SW. slope, 5·8m, colour brown.
C. G8665, whole colony, Big Broadhurst Reef, SW. slope, 6m, colour pink-brown.
D. G8657, portion of colony, Big Broadhurst Reef, SW. slope, 6·6m, colour green-brown.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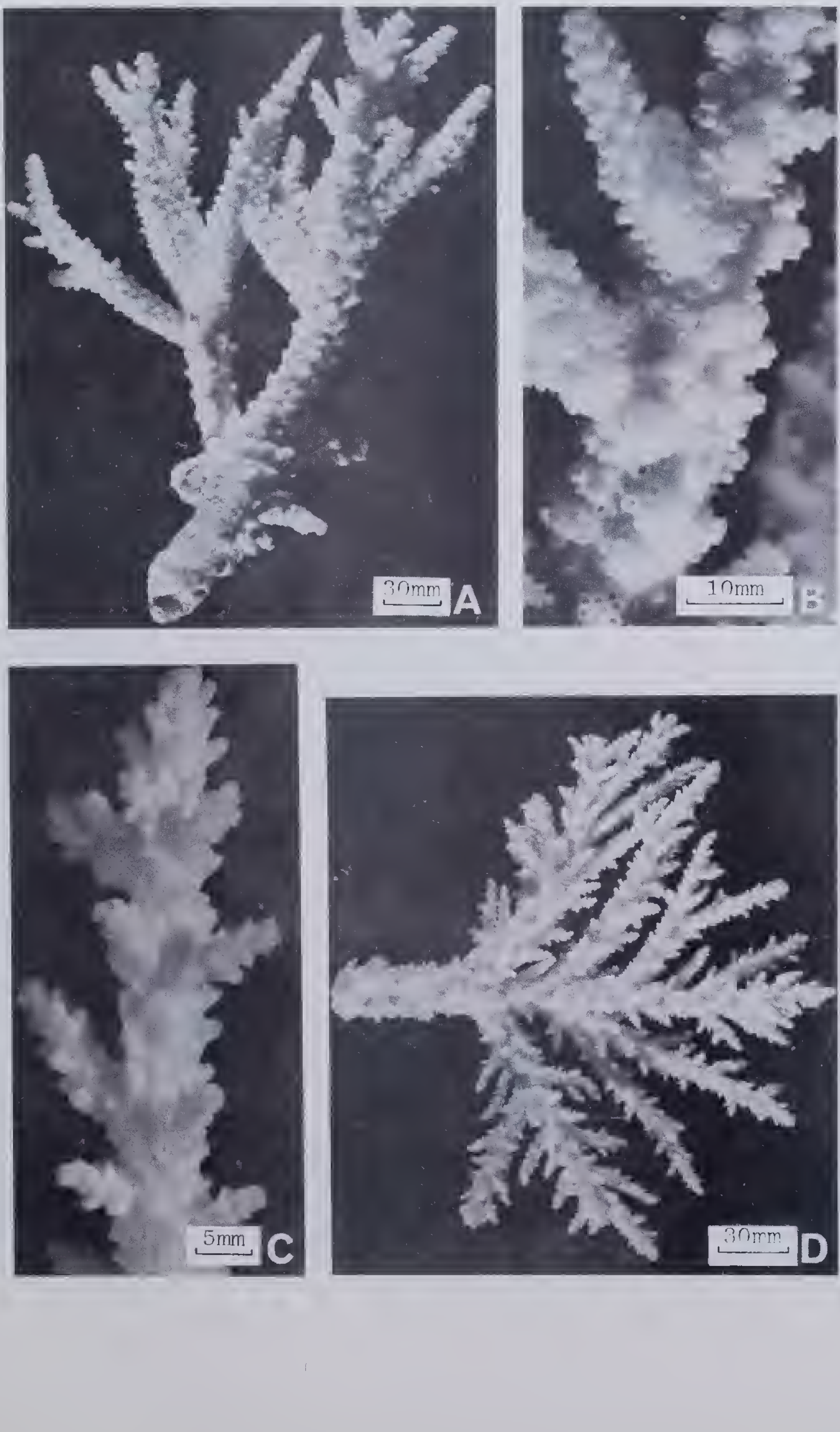
D

PLATE 92

Acropora florida (Dana, 1846)

A, B. G8655 Big Broadhurst Reef, SW. slope,. 6·6m, colour pale pinkish brown. (This specimen resembles *A. florida s.s.)*

C, D. G8647 Big Broadhurst Reef, SW. slope, 9·3m (flat plate specimen).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D

PLATE 93

Acropora echinata group on Big Broadhurst Reef, SW. side.

A. On surge channel floor at 10m. *A. carduus* (Dana, 1846). (arrow) with a small table (?*A. cytherea)* and *A. florida* (surrounding).
B. On gentle reef slope, about 12m. *A. longicyathus* (Milne Edwards and Haime, 1860) (arrow). Above this is *A. splendida*, and *A. divaricata*, upper right.


A

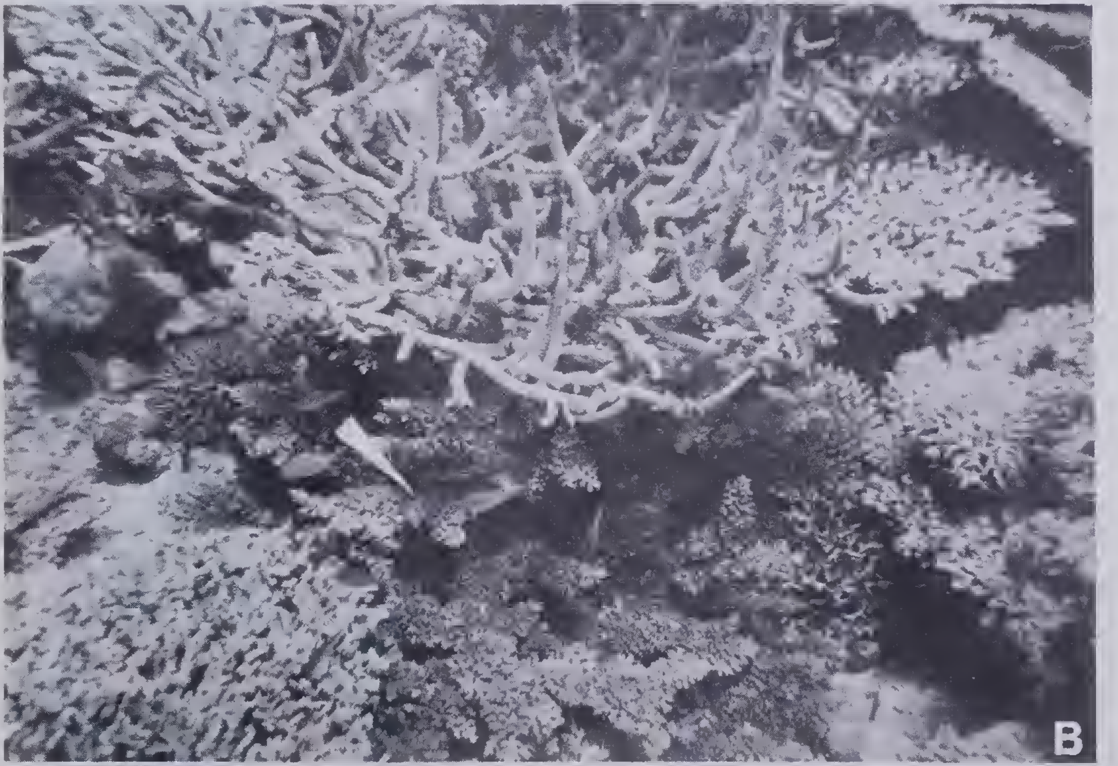
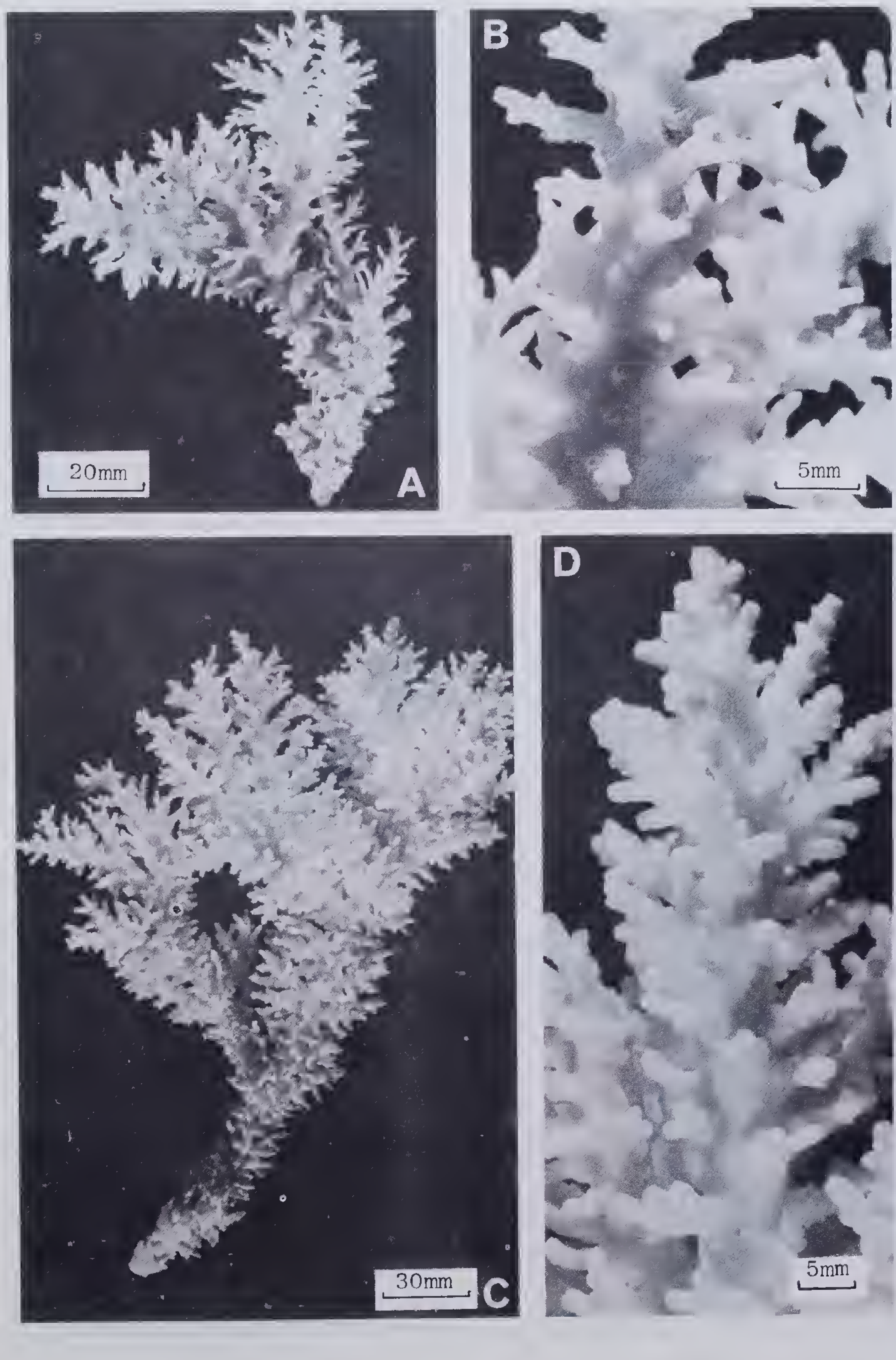

B

PLATE 94

A, B. *Acropora subglabra* (Brook, 1891) G10714 Lizard Island fringing reef, colour pinkish brown.
C, D. *Acropora carduus* (Dana, 1846) G10731 Big Broadhurst Reef, SW. slope, 8m, colour brown.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D
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PLATE 95

Acropora longicyathus (Milne Edwards and Haime, 1860)

A, C. G10767 Big Broadhurst Reef, SW. slope, 7 m, colour brown.
B. Portion of colony from similar location.

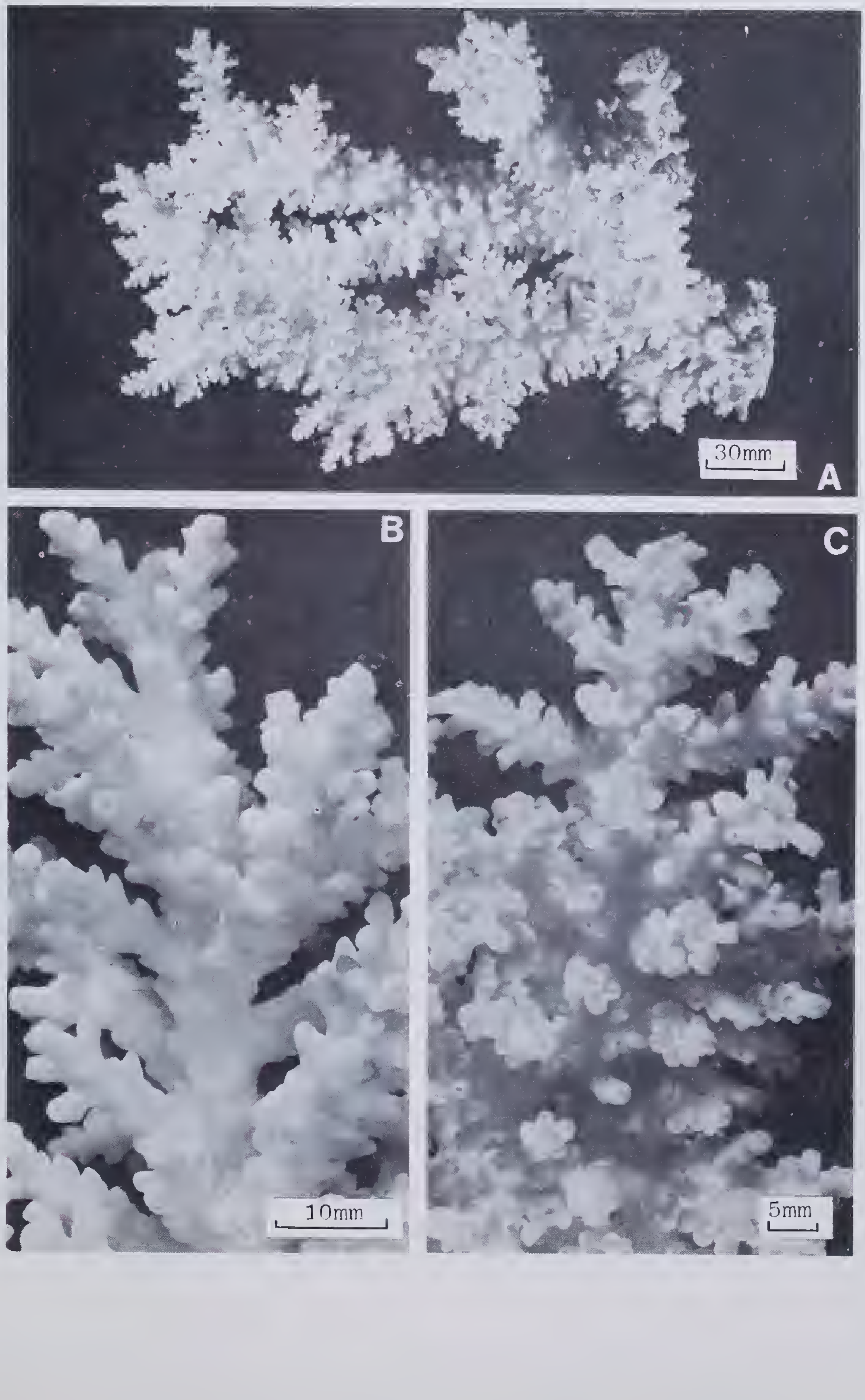
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PLATE 96

Acropora microphthalma (Verrill, 1869)

A, B. G8685, Big Broadhurst Reef, SW. slope, 6m, colour pale brown.

C, D. From Big Broadhurst Reef, SW. slope.

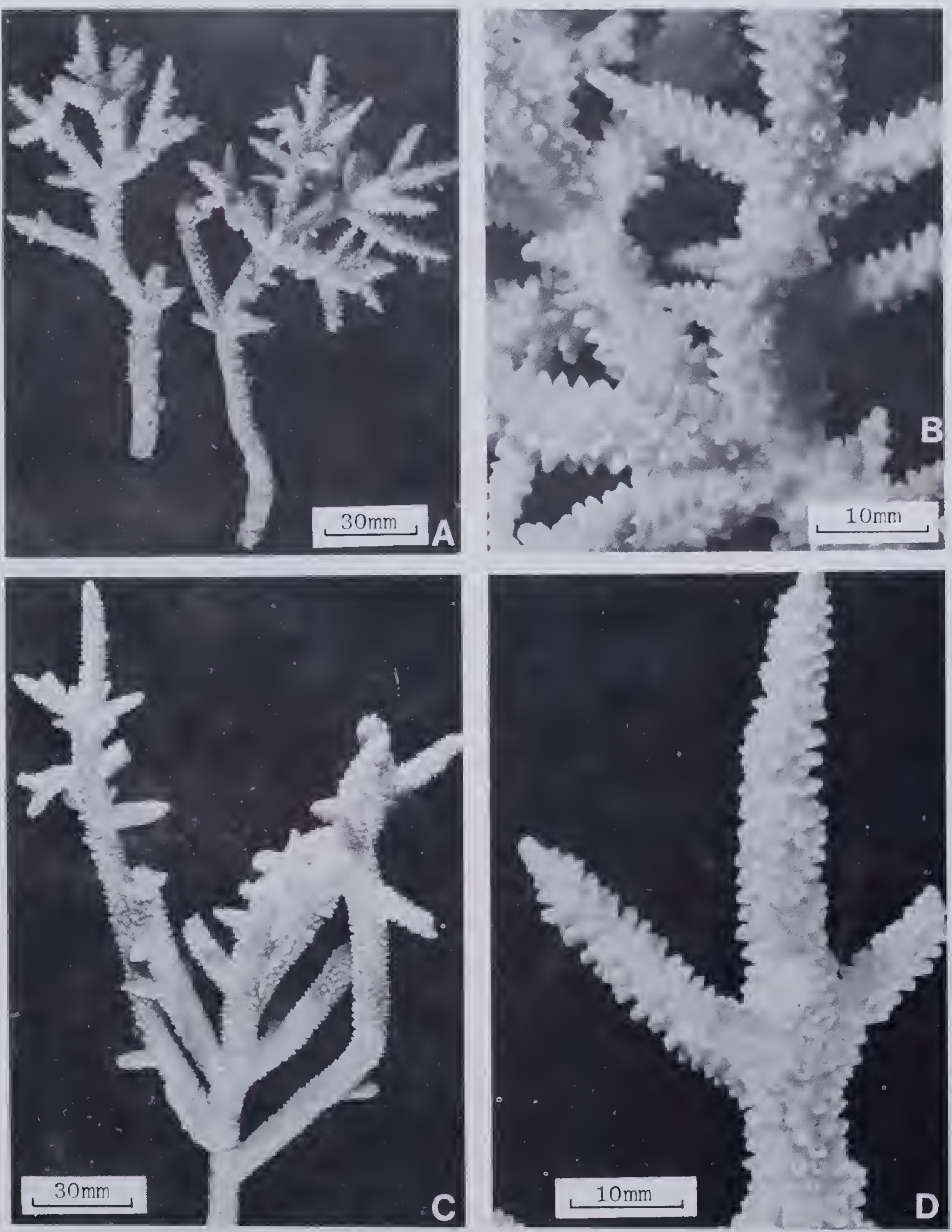
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PLATE 97

A, B. *Acropora elseyi* (Brook) G10793, Bushy-Redbill Reef, W. side, middle reef flat, 1 m, colour yellow.
C, D. *Acropora rosaria* (Dana) G9202, Palm Islands, 1929, T. C. Marshall.

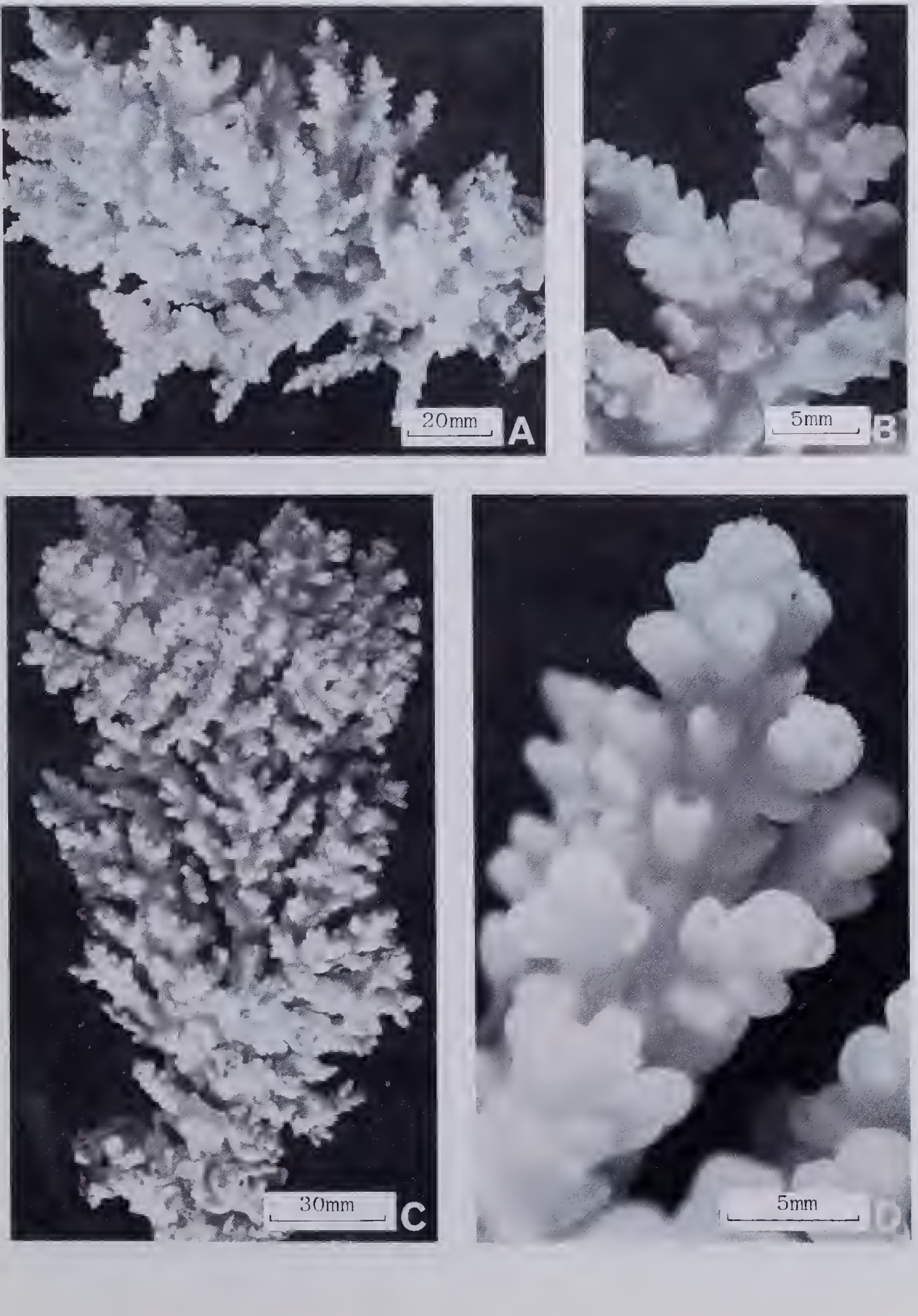
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PLATE 98

Acropora squarrosa (Ehrenberg, 1834) on the reef.

A. Bottlebrush branching colony on reef crest, Bushy-Redbill Reef, W. side, colour blue (arrow).
B. Bottlebrush branching colony, (with shortened brushes) on edge of hard/soft coral patch, middle reef flat, Bushy-Redbill Reef, W. side, colour yellow-brown (arrow).
C. Caespitose 'incipient bottlebrush' colony on lagoonal patch reef, Darley Reef (arrow).
D. Bottlebrush branching colony on sand, deep middle reef flat, Bushy-Redbill Reef, W. side, colour lavender-blue.
E. Bottlebrush thicket in deep water reef flat at Wistari reef, near Heron Island. (photo courtesy D. Ross Robertson).
F. Caespitose colony on lagoonal patch reef, Darley reef, colour pale blue.

PLATE 98

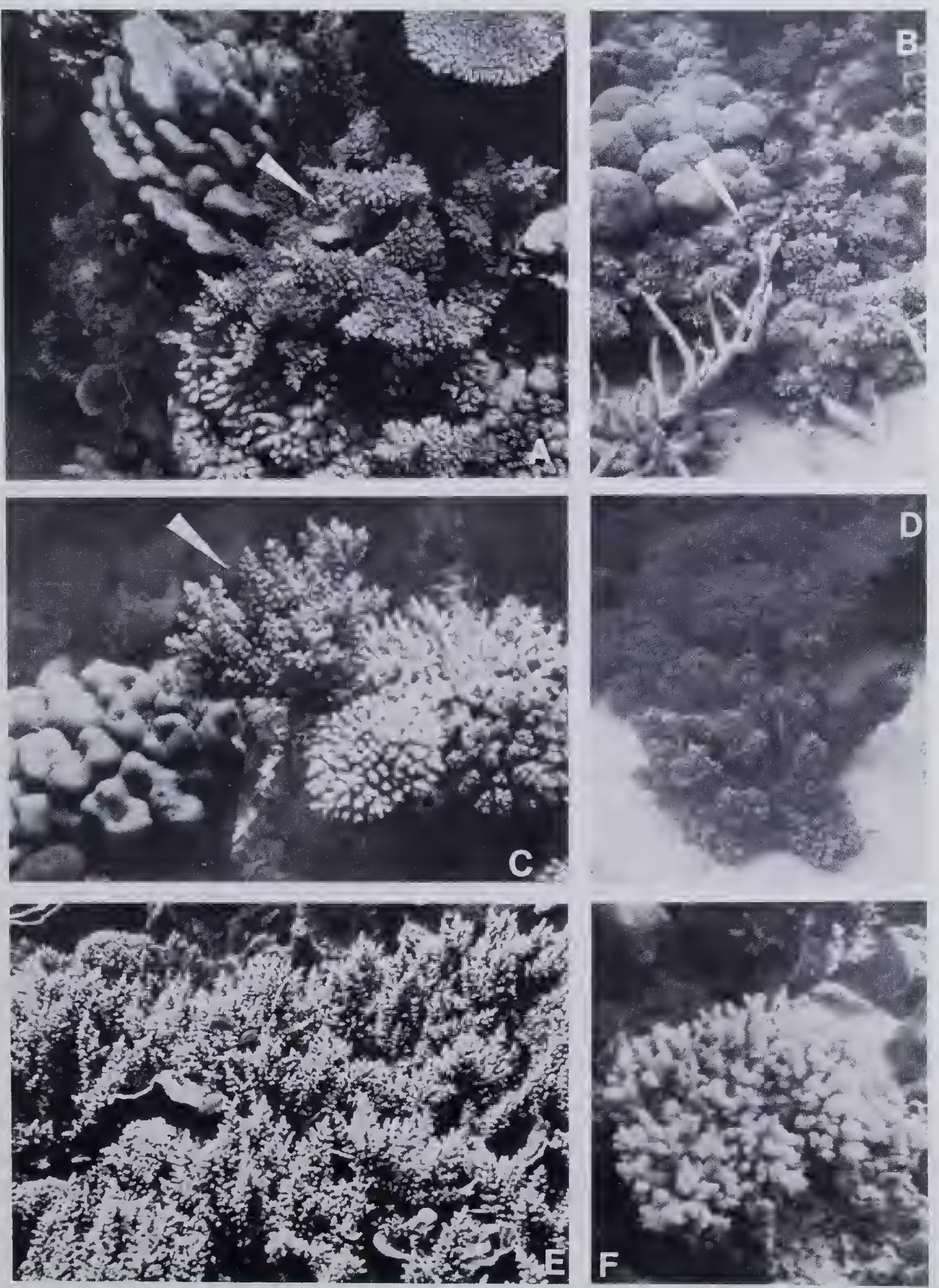

PLATE 99

Acropora squarrosa (Ehrenberg, 1834)

A, B. G10782 specimen comparable to *'A. murrayensis'* Darley Reef, patch reef in lagoon, 1 m, colour lavender.

C, D. G10842 specimen approaching *'A. syringodes'* (part). Big Broadhurst Reef, SW. side, reef slope, 9·2 m, colour cream.

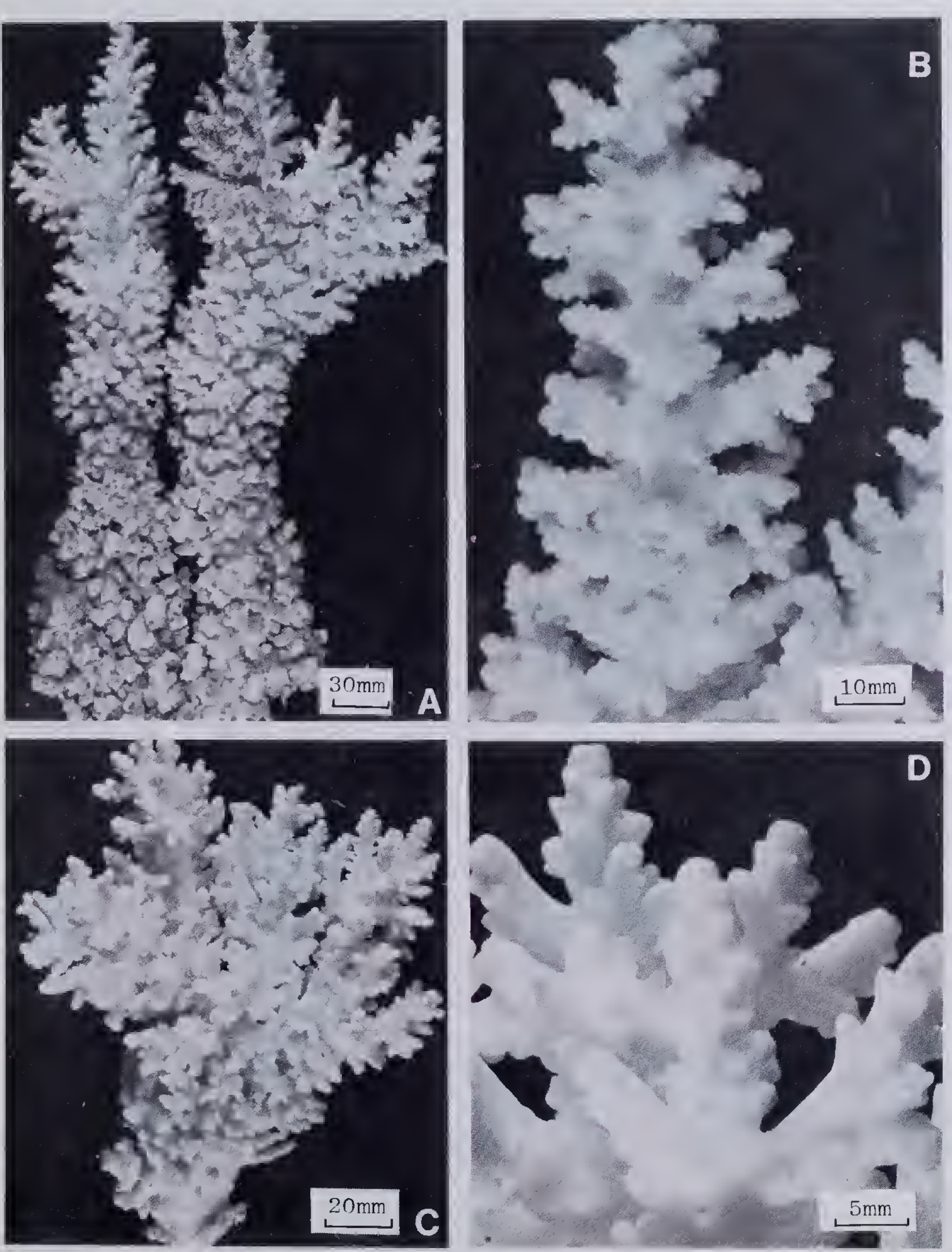
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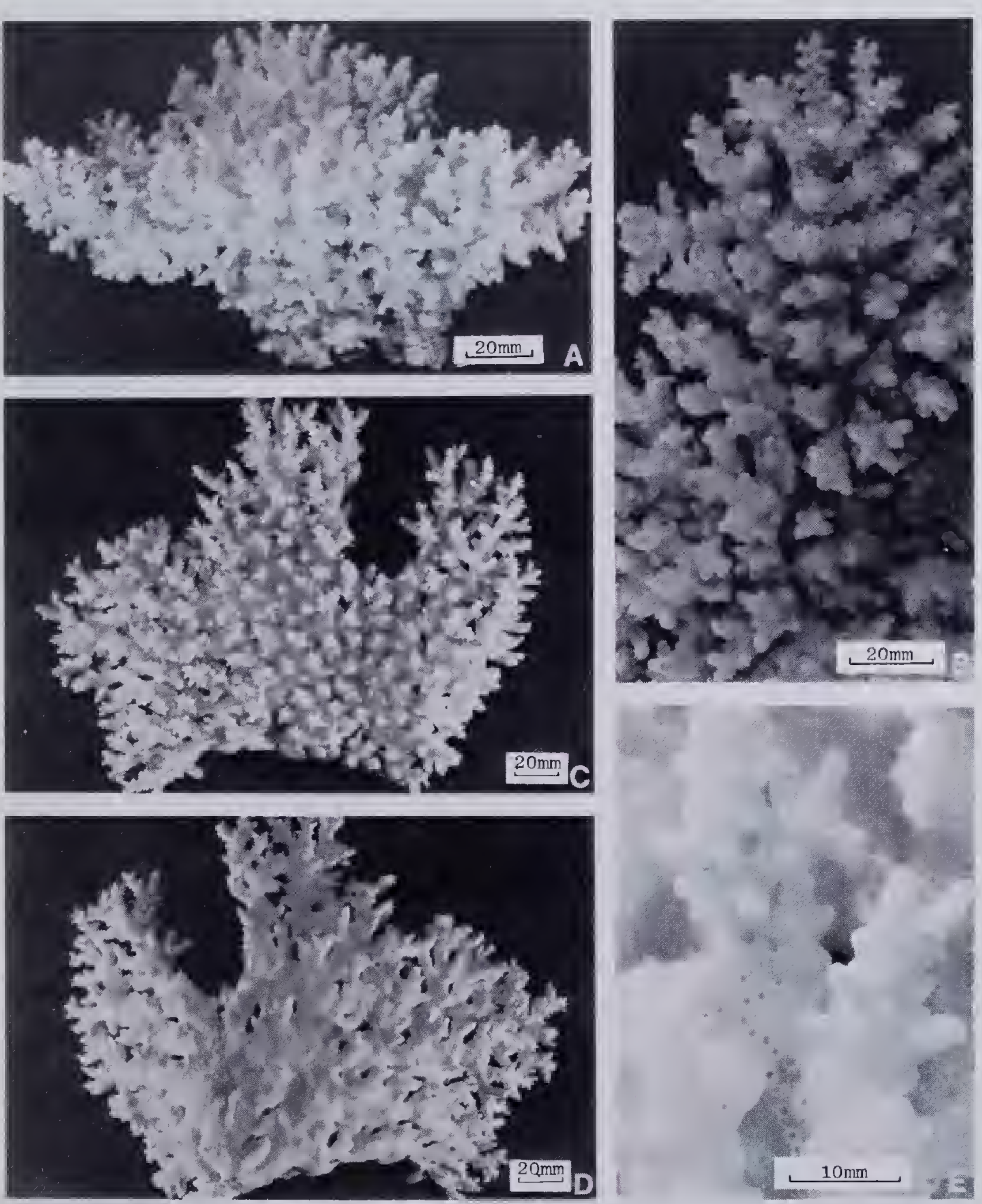
PLATE 100

Acropora squarrosa (Ehrenberg, 1834)

A, B. G10846 low caespitose specimen. Darley Reef, patch reef in lagoon, 3 m, colour patches of pale yellow, lavender and blue.

C, D, E. G10845 flat plate specimen (D is undersurface). Big Broadhurst Reef, SW. side, reef slope, 12·9 m, colour pale blue-brown.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D
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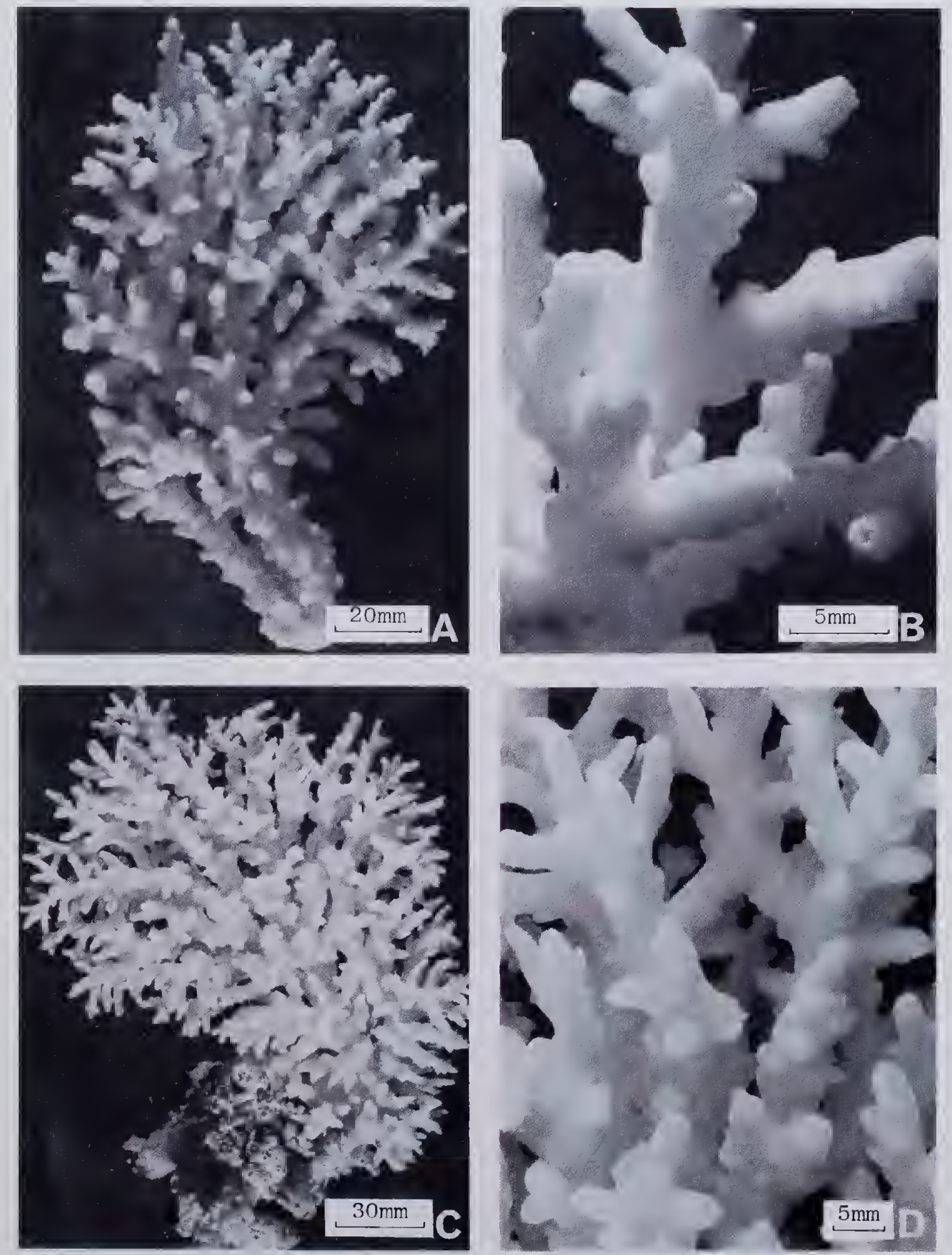
E

PLATE 101

Acropora granulosa (Milne Edwards and Haime, 1860). Specimens with blunt axial corallites.

A, B. G11487, Big Broadhurst Reef, SW. side, reef slope, 10·4 m, colour cream-grey.
C, D. G11492, Big Broadhurst Reef, SW. side, reef slope, 8 m, colour brown.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D

PLATE 102

Acropora granulosa (Milne Edwards and Haime, 1860). Specimens with tapering axial corallites.

A, B. G6723 (comparable with *'A. speciosa')*. Darley Reef, patch reef in lagoon, 2·5 m, colour pale brown.
C, D. G11476 (comparable with *'A. rayneri')*. Big Broadhurst Reef, SW. side, reef slope, 5 m, colour pale brown.

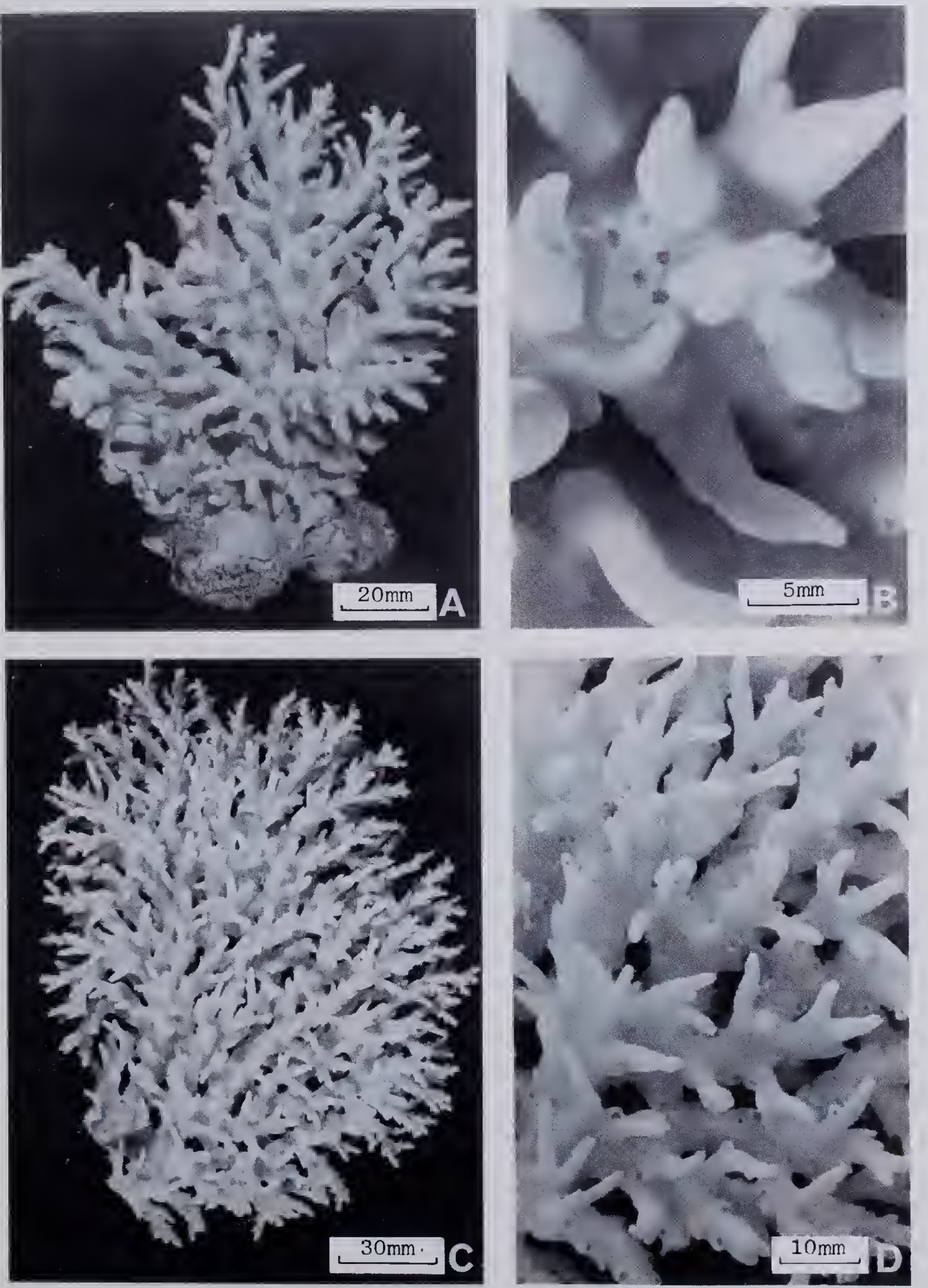
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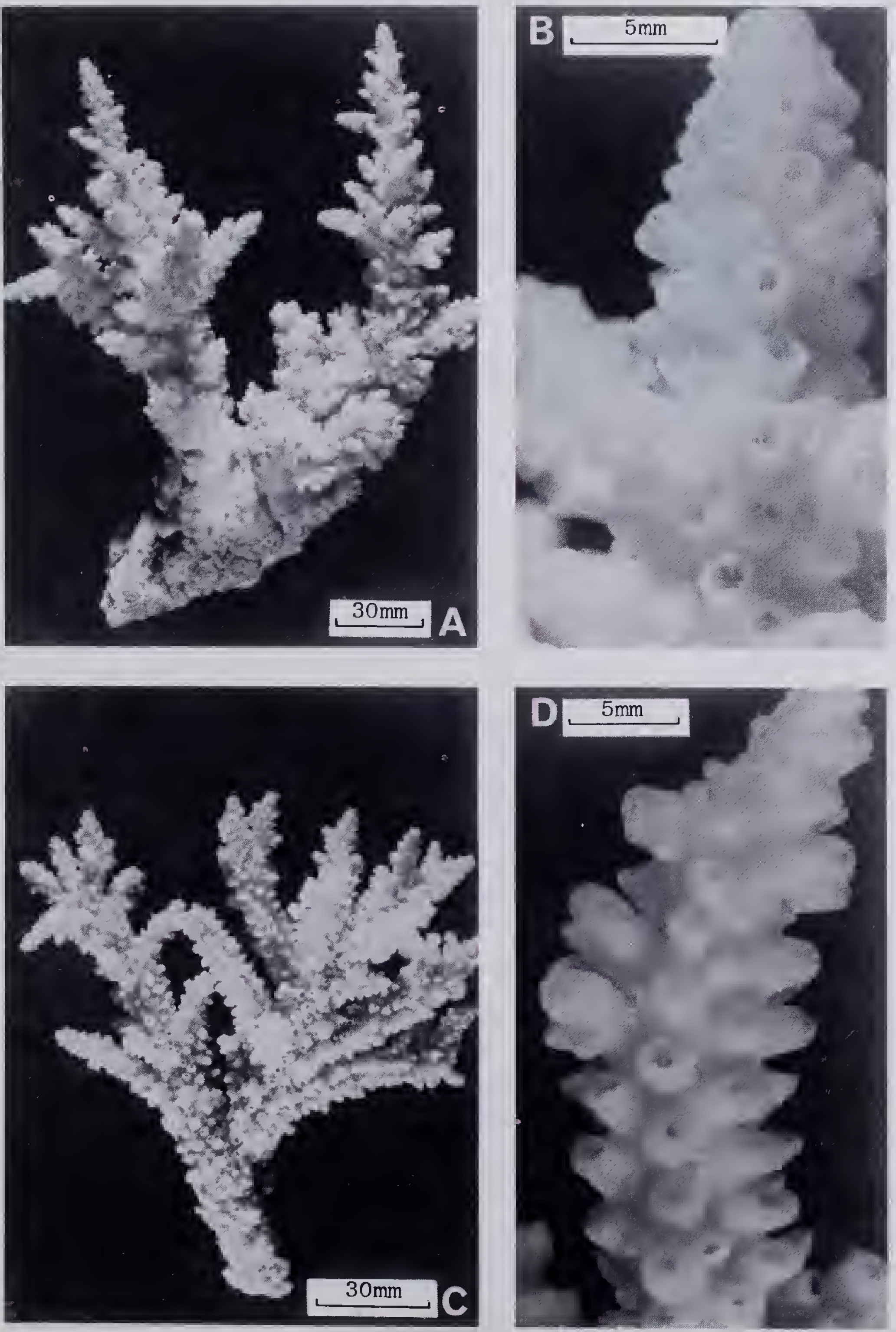
PLATE 103

Acropora austera (Dana, 1846)

A, B. G10828 Big Broadhurst Reef, SW. slope, 7·8 m, colour cream.
C, D. G10810 Bushy-Redbill Reef, S. side, reef slope, 3m, colour lavender.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