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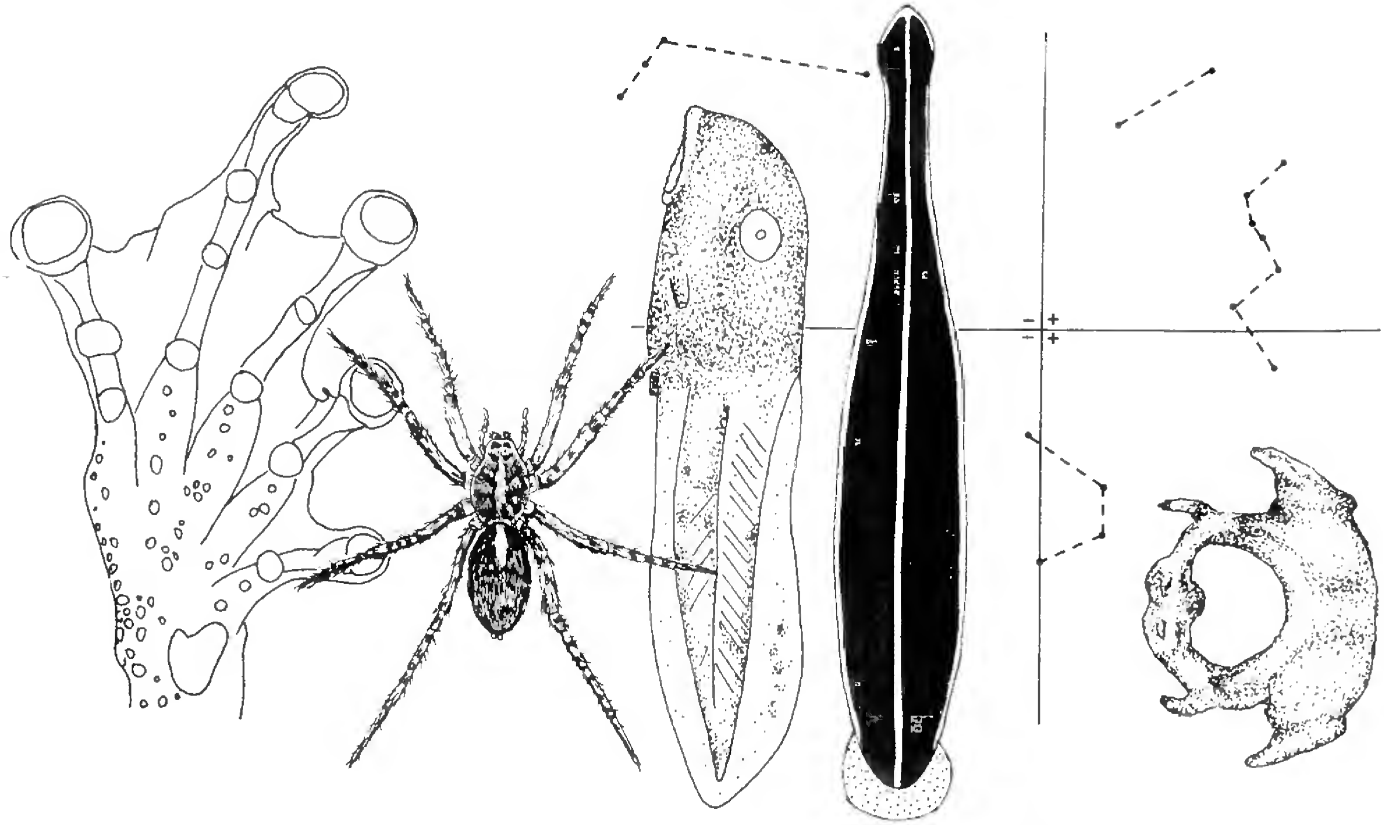

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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 2. THE ARENARIS GROUP

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ABSTRACT

Four species of Australian lycosid spiders are defined as the 'arenaris group' due to the presence of a distinct tubercle on the outer curve of the fang of mature males. *Lycosa celaenica* is a synonym of *L. arenaris*, *L. segregis* is a synonym of *L. pullastra*, *L. furcillata* is assigned to this group of species, and *L. lapidosa* is described as new.

In an attempt to arrange the Australian Lycosidae into a more natural classification, all species in which a distinct tubercle is present on the outer curve of the fang of mature males were placed together as forming a natural group of species. An analysis of this group indicates that the species are indeed related as some similarities can be observed in the shape of the epigynum, the structure of the male palp, and the internal genitalia of mature females. In addition to the morphological similarities, all species are found to occur in similar habitats such as river beds and in grassed areas near swamps or on watered lawns. A burrow consisting of an open shallow pit, or a webbed retreat among grasses or stones, is constructed by most species, rather than a well excavated burrow with a flap, door, or turret, as is frequently found in other members of the genus.

The function of the tubercle on the fang of mature males is unknown. As this tubercle is not present on the fangs of the female or immature males, it may be associated with courtship, and used to ward off the fangs of the female prior to copulation. *Lycosa pullastra* has been observed during courtship and copulation, but at no time were the fangs employed in any manner to suggest the function of the tubercle. The mature males frequently cluster around a sexually mature female during the breeding season, as the population density is normally very high. Little intra-specific mortality occurs between males despite frequent contact; the encounter is usually brief, although at times quite violent, and it is suggested that the tubercles on the fangs prevent a high mortality between courting males.

The family Lycosidae is currently under review by the writer. This contribution is part 2 of a series of papers on Australian Wolf Spiders. An introduction to the study is given by McKay (1973).

Lycosa arenaris Hogg, 1905
(Figure 1, a–m)

Lycosa pulvere-sparsa: Hogg, 1896, p. 351, MacDonnell Ranges, Palm Creek, Bagot's Creek, Paisley Bluff, Central Australia, [Not *Lycosa pulvere-sparsa*].

Lycosa arenaris Hogg, 1905, pp. 586–8, fig. 88, MacDonnell Ranges, (Northern Territory); Rainbow, 1911, p. 265; Bonnet, 1957, p. 2634.

Lycosa celaenica Rainbow, 1917, p. 488, pl. 32, figs. 10 and 11, Farina, South Australia; Bonnet, 1957, p. 2637; McKay, 1973, p. 379.

Varacosa arenaris: Roewer, 1954, p. 305; McKay, 1973, p. 381.

MATERIAL EXAMINED

SYNTYPES: 2, SAM, labelled '*Lycosa arenaris* Hogg, MacDonnell RNG. Horn Exp.' in ink, '*Lycosa arenaris* H. R. Hogg. 2 females Types. MacDonnell Range, Horn Exp.' in pencil, and 'F. 206' in pencil. A lectotype is here designated from this series.

LECTOTYPE: SAM ♀ M with a well developed epigynum, in a tube with the original labels.

PARALECTOTYPE: SAM ♀ P with the epigynum partly formed but in a penultimate condition, in the same tube as the lectotype.

HOLOTYPE OF LYCOSA CELAENICA: SAM, ♀ M, with abdomen detached labelled '*Lycosa caelonica* Rainb. Farina, Mus. Exp. Int. 1916 T' in ink (mis-spelt, = *Lycosa celaenica*), 'Farina to Spring, Mus. Exped. Interior 1916' in pencil, a small faded printed label 'TYPE' and '*Lycosa caelonica* Rainb. Farina to Spring TYPE' in pencil on a fourth label. This specimen fits the description of *L. celaenica* well except that the carapace is 5·9 mm long and 4·3 mm wide (Rainbow has '5·8 mm broad, 4·3 mm long', but this would not be possible for a *Lycosa*). The epigynum of the holotype is shown in Fig. 1, g.

OTHER MATERIAL: Western Australia: Avon River at Northam, 14.xii.1962, BYM, 4 ♀ M, 1 ♂ M, WAM 71-1000–4, 1 ♂ M, WAM 71.988; Behn River at Old Argyle Downs station, 9.x.1971, RJM, 1 ♀ M, 72-76, 24.x.1971, 2 ♀ M, 1 ♂ M, WAM 72-77–9; Broome Hill 15 miles east, 3.ii.1961, BYM, 5 ♀ M, 3 ♂ M, WAM 71-1546–53; Desperate Bay near Snag Island, 27.ii.1971, RJM, B. Ryle, 1 ♀ M, WAM 71-891; Fitzgerald River, 12.vii.1970, RJM, 4 ♀ M, 8 ♂ M, 4J, WAM 71-1904–19; Fortesque River, 22.ii.1962, BYM, 2 ♀ M, 1 ♂ M, 2J, WAM 71-1554–8; Hooley Station at Kylan Pool, Sept. 1969, RJM, 1J, WAM 71-946; Hotham River 71 mile peg Albany Highway, 27.x.1961, BYM, 1 ♀ M, 2J, WAM71-989–91; Kojonup 17 miles east, 3.xi.1961, BYM, 6 ♀ M, 3 ♂ M, WAM 71-1537–45; Maitland River, 23.ii.1962, A. R. Main, 4 ♀ M, 2 ♂ M, 1J, WAM 71-1513–20; Maitland River 30 miles south, 22.ii.1962, A. R. Main, 4J, WAM 71-1521–4; Millstream Station, Fortesque River, 23, 25.ix.1969, RJM, 3 ♀ M, WAM 71-942–4, 1 ♀ M, WAM 70-210; Mount Herbert at pool, 20.v.1961, BYM, 1 ♀ M, WAM 71-1562; Mugumba Creek, 26.ii.1963, A. R. Main, 1 ♀ M, WAM 71-1559; Murchison River at the Loop, 26.i.1969, RJM, JG, P. Snowball, 3 ♀ M, 1 ♂ M, WAM 69-335–40; Murchison River, 20.ii.1962, BYM, 8 ♀ M, 4J, WAM 71-1525–36, 27.i.1969, RJM, JG, 1 ♀ M, WAM 71-1564, 8.vi.1970, W. K. Youngson, 1 ♀ M, 70-166; Ongerup 85 miles east, 4.xi.1961, BYM, 1 ♀ M, WAM 71-1560; Ord River, 3.x.1971, RJM, 1 ♀ M, WAM 72-166, 21.x.1971, RJM, 2 ♀ M, WAM 71-153–4; Perth 80 miles east. 4.xi.1961, BYM 2 ♀ M, 6 ♂ M, WAM 71-992–9; Rudall River, 4.v.1971, RJM, R. W. George, 4 ♀ M, 2 ♂ M, 4J, WAM 71-1241–50; Susetta River, 12.vii.1970, RJM, 2 ♀ M, WAM 70-218–9; Twirtup Creek, Fitzgerald River, 15.vii.1970, AB, 6 ♀ M, 2 ♂ M, WAM 70-312–19· Wittenoom Gorge Pool, 30.ix.1969, RJM, R. Dear, 2 ♀ M, WAM 69-1043–4; Yannarie River, 13.v.1972, RJM, 1 ♀ M, QM W3854.

South Australia: Clayton Bore 33 miles north of Maree, 25.viii.1970, HB, W. D. L. Ride, 9 ♀ M, WAM 71-564–72; Kalamurina Homestead near Lake Eyre, 9.i.1902, Professor J. W. Gregory, 2 ♀ M, NM.

Victoria: Snowy and Broadbent Rivers, xii.1947, C. W. Brazenor, 1 ♀ M with young, NM.

Misidentified as *Lycosa pulveresparsa* by Hogg (1896): Central Australia, W. A. Horn, 2 ♀ M, BM 1897.1.18. 11-12; Palm Creek, Central Australia, Horn Expedition, 2 ♀ M, Hogg Coll., BM 1924, III.1.977-8. Hogg's (1896) record of *L. pulveresparsa* from Central Australia is in error, and was not rectified in his 1905 description of *L. arenaris*.

DESCRIPTION

Modified from Hogg: Female. Carapace yellow-brown with mixed black and white hairs on the cephalic part, and more posteriorly a wide white area constricted in the middle and extending on to the middle of the rear slope where it narrows abruptly as a thin white line; margin of carapace with a thin, frequently broken, sub-marginal white line; mandibles dark brown with pale brown hair; labium, maxillae, and sternum yellow-brown. Abdomen

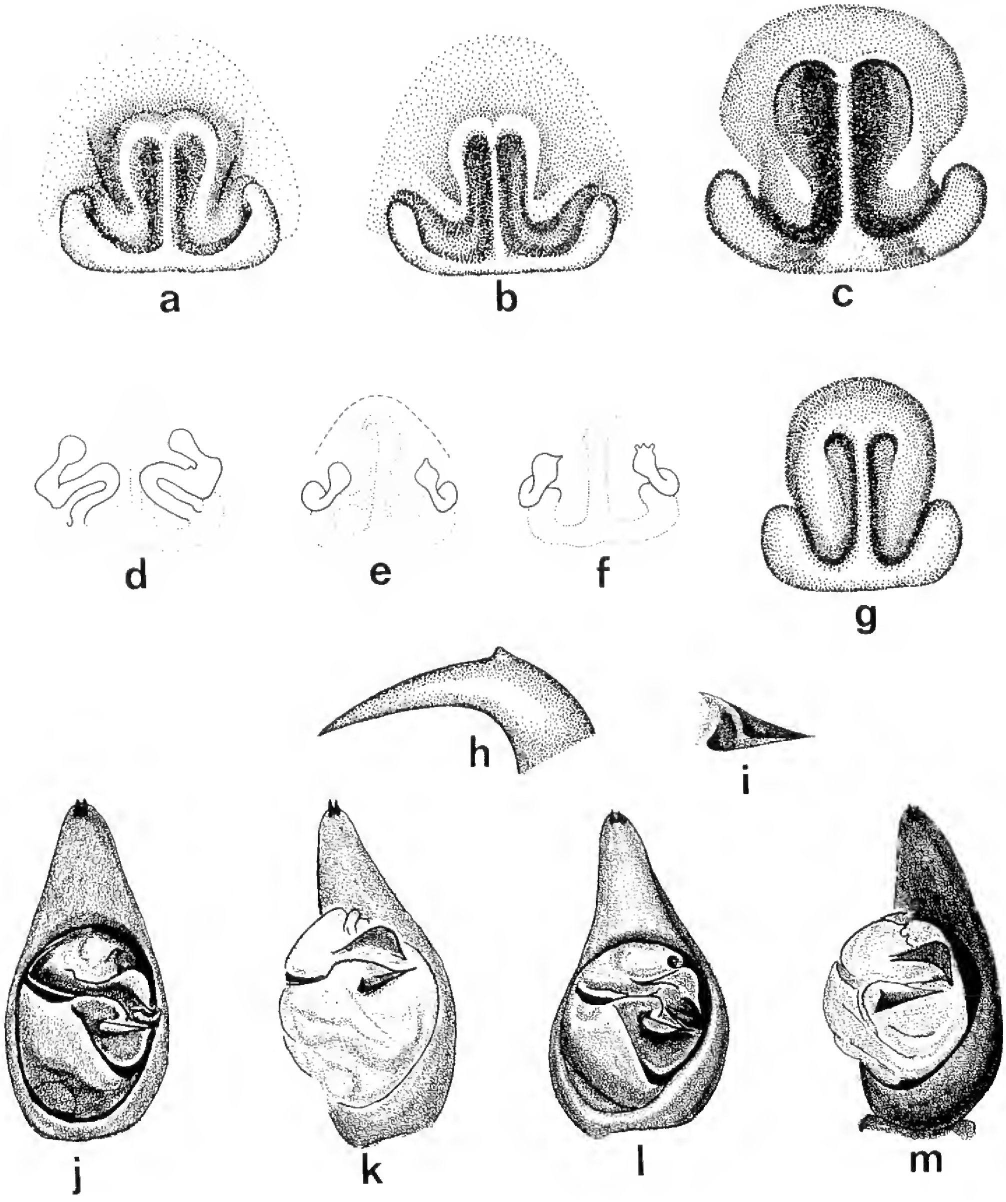

FIG. 1: *Lycosa arenaris* a–c, epigyna of WAM 69-340, WAM 69-335, and WAM 70-210; d–f, internal genitalia of WAM 70-312, WAM 70-313, and WAM 72-77; g, epigynum of holotype of *L. celaenica*; h, fang of mature male; i, median apophysis of male palp; j–k, unexpanded and expanded male palpal organ of WAM 71-988; l–m, unexpanded and expanded palpal organ of WAM 70-314.

dull brown, irregularly spotted with small patches of whitish hairs above; venter dull brown, the centre area rather paler than the sides. Legs and palpi yellowish with brown hairs and darker brown erect bristles; a ring of paler yellow around femur, middle of tibia, and metatarsal joints.

Anterior of carapace high and narrow with the clypeus about equal to or less than a diameter of the AM. Anterior row of eyes procurved, the AM larger than the AL and further apart than from the AL, PM less than a diameter apart.

Three equal sized retromarginal cheliceral teeth. Labium almost as wide as long. The epigynum is generally broader than long with a narrow median guide, and a wide transverse guide curled around the base of the lateral margin. Three epigyna are illustrated (Fig. 1, a–c). Legs slender, two spines above on tibiae III and IV, none on the first or second pairs; on the underside the spines are long and stout.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF *L. arenaris* IN MM FROM HOGG

Leg	Coxa	Trochanter and Femur	Patella and Tibia	Metatarsus and Tarsus
1	2½	5	5½	5
2	2	4½	5	5
3	2	4½	4½	5½
4	2½	6	6	8
Palp	1¼	3	2¼	1¾

VARIATION: The venter of the abdomen of mature males and females may be of a uniform yellowish-brown without markings, light brown with vague darker bars or spots, or honey-brown with transverse, longitudinal, or criss-cross smoky-grey markings. Legs uniform brown, mottled, or with brown rings. The mature male has a tubercle on the outer surface of the fang (Fig. 1, h), penultimate males lack the tubercle.

The eye measurements were found to vary in the ten specimens examined, each measurement is given below in Table 2 as a per cent of the total width of the first eye row. Hogg (1905, p. 587) describes the front row of eyes as straight, although his figure illustrates the anterior row as quite procurved; all specimens examined by me had the anterior row of eyes procurved, and the distance AM:AM always wider than the distance AM:AL (not equidistant as described by Hogg). The clypeus is not twice the diameter of the AM as described by Hogg, but about equal to or much less than the diameter of the AM.

The epigyna and the internal genitalia of three Western Australian females are illustrated (Fig. 1, a–f).

The male palpal organ is figured in the unexpanded (Fig. 1, j, l) and partly expanded condition (Fig. 1, k, m) to show variation in the shape of the median apophysis illustrated separately in Figure 1, i. Above the tip of the somewhat triangular blade of the median apophysis is the rather scoop-shaped membraneous secondary conductor in which the embolus lies in the unexpanded state. An unusual and very distinctive embolic guide (see

TABLE 2: EYE DIAMETERS AND INTERSPACES OF *Lycosa arenaris* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
WAM 72.77	♀ M	5·4	24	18	42	35	10	5	21	8
WAM 72.78	♀ M	4·9	24	18	44	36	12	4	24	11
WAM 72.79	♂ M	3·4	26	18	47	41	10	3	20	5
WAM 70.319	♂ M	5·0	24	17	46	41	6	3	22	9
WAM 70.210	♀ M	6·0	24	18	44	34	10	6	24	11
QM W3854	♀ M	5·9	23	17	46	36	8	4	21	9
WAM 70.312	♀ M	6·2	25	19	47	40	6	3	21	8
WAM 70.313	♀ M	5·6	23	18	44	36	8	4	21	10
WAM 70.314	♀ M	5·1	24	19	47	37	9	4	22	11
WAM 70.315	♀ M	5·0	25	17	47	38	10	6	19	8

Wallace, 1942, Fig. 1, a) is present as a well sclerotized, curved, medially expanded, plate-like structure. Figure 4 illustrates the terminology employed in the description of the epigynum and male palpal organ.

SIZE RANGE: Mature females C.L. 4·1 to 6·8 mm. Mature males C.L. 4·0 to 6·3 mm.

DIAGNOSIS: *Lycosa arenaris* differs from other members of the arenaris group in having the epigynum with a narrow median guide and a wide transverse guide, expanded terminally, and extending up the sides of the epigynal plate. The mature male has a curved plate-like embolic guide.

LIFE HISTORY

Mature males and females may be collected throughout the year, but are more numerous during the summer months. Females with egg cocoons and carrying young were collected during September at the Fortesque River, and were common in January at the Murchison River. One female carrying young was collected during December in Victoria (NM, C. W. Brazenor).

This species may be found in considerable numbers in suitable habitat, and although the spiders make frequent contact, little intra-specific mortality appears to occur. If disturbed, this species will run onto the surface of the water, and make rapid progress with the legs held in a horizontal manner. One specimen from the Fitzgerald River was quite unharmed after complete submersion in an inverted jar of water for 20 minutes. At the Murchison River this species was observed, on occasions, to occupy masses of floating aquatic plants, and would retreat below the surface of the water to escape capture.

During the day *Lycosa arenaris* will actively prey on diptera of many kinds, the free-living young of about 2 to 5 mm in total length are particularly adept at capturing sand flies (Ceratopogonidae), midges (Chironomidae) and mosquitoes (Culicidae), and are therefore to be considered important predators of these insects.

HABITAT

Wet sand, sand-silt, or coarse gravel on the wet or damp banks of rivers, streams, creeks, or pools in the arid or semi-arid areas of Australia. Most specimens are to be found at the edge of the water on wet substrates, and are rarely found on the dry sand of the river bed.

BURROW

An open, rather shallow burrow that extends down to, or almost to, the water-table in wet sand, within 2 feet of the waters edge. The mature females may seek the slightly drier sand or loam when carrying egg-cocoons or young. The spider is frequently to be found at the entrance of the burrow during the day. Burrows may be little more than shallow vertical or horizontal pits in wet sand; in the moist or damp soils the burrows may extend some 10 cm into the slope of the bank.

DISTRIBUTION

Western Australia, South Australia, Northern Territory and Victoria. Not yet recorded from Queensland, and New South Wales.

DISCUSSION

A direct comparison of the holotype of *Lycosa celaenica* with the lectotype of *Lycosa arenaris* shows these two nominal species to be synonymous. The epigynum of the holotype of *Lycosa celaenica* is illustrated in Figure 1g. *Lycosa arenaris* was placed in the genus *Varacosa* by Roewer (1954, p. 305), but using Roewer's key to the genera of the subfamily Lycosinae (Roewer, 1959, pp. 217–25) this species falls into *Allocosa* Banks, 1900, a subgenus of *Lycosa*. In the key to the subgenera of the subfamily given by Guy (1966, pp. 51–3) *Lycosa arenaris* also falls into the subgenus *Allocosa*.

Lycosa pullastra Simon, 1909
(Figure 2, a–p)

Lycosa pullastra Simon, 1909, pp. 184–5, fig. 2, Mundaring Weir (Perth), and Albany, Western Australia; Rainbow, 1911, p. 272; Bonnet, 1957, p. 2660; McKay, 1973, p. 379.

Lycosa segregis Simon, 1909, p. 186, fig. 4, Fremantle, Western Australia; Rainbow, 1911, p. 272; Bonnet, 1957, p. 2663; McKay, 1973, p. 379.

Hogna pullastra: Roewer, 1954, p. 253.

Hogna segregis: Roewer, 1954, p. 253.

MATERIAL EXAMINED

Western Australia: Australind at estuary foreshore, 22.x.1969, RJM, R. W. George, 1 ♀ M, 1 ♀ P, 3 ♂ M, WAM 71-363–7; Amelia Heights near Perth, 28.x.1970, M. Shepherd, 1 ♀ M, WAM 71-460; Applecross near Perth, 1963, G. M. Riley, 1 ♀ M, WAM 69-869; Attadale near Perth, 15.x.1960, BYM, 1 ♀ M, WAM 71-1496, 20.viii.1960, BYM, 1 ♀ M, WAM 71-1497, 4.ix.1960, BYM, 1 ♂ M, WAM 71-1499; Bibra Lake, BYM, 18.x.1960, 1 ♀ M, WAM 71-1455, 4.xi.1961, 4 ♀ M, 1 ♂ M, WAM 71-1456–60; 17.ix.1960, 6 ♀ M, 7 ♂ M, 2 ♂ P, 2J, WAM 71-1461–77, 11.xi.1960, 1 ♀ M, WAM 71-1478, 1.x.1960, 1 ♀ M, WAM 71-1479, 11.xi.1960, 1 ♀ M, WAM 71-1480, 4.xi.1961, 2 ♀ M, WAM 71-1481–2, 8.iii.1960, 2 ♀ M, WAM 71-1483–4; Boyup Brook 20 miles south east, 3.xi.1961, BYM, 1 ♂ M, WAM 71-1509; Brentwood Swamp, 23.iv.1969, RJM, 1 ♀ M, WAM 69-855, 6.xii.1970, RJM, 3 ♀ M, 3 ♂ M, WAM 71-158–63, 1 ♀ M, WAM 71-533; Bunbury, 22.x.1969, RJM, R. W. George, 1J, WAM

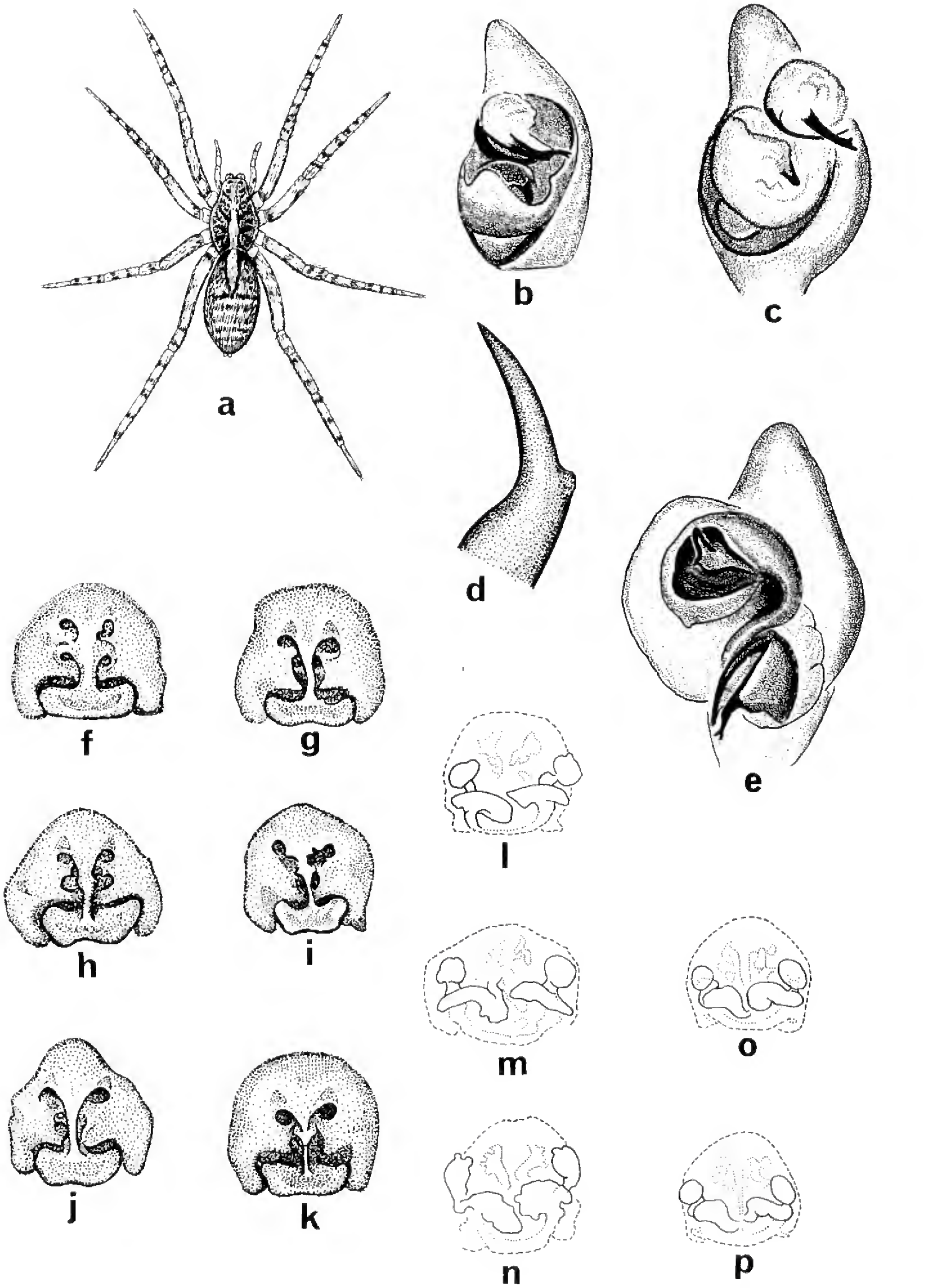

FIG. 2: *Lycosa pullastra* a, mature female WAM 70-3; b, male palpal organ of WAM 71-78; c, expanded male palpal organ of WAM 71-1492; d, cheliceral fang of mature male; e, expanded male palpal organ of WAM 71-77; f–k, epigyna of WAM 71-1461–6; l–p, internal genitalia of WAM 71-109, WAM 71-110, WAM 71-111, WAM 71-979, WAM 71-980.

71-355; City Beach near Perth, 16.ix.1968, I. Elliot, 1 ♀ M, WAM 69-856, 5 ♂ M, WAM 71-974–8; Collie, 16.x.1961, BYM, 1 ♀ M, WAM 71-1485, 3.viii.1961, BYM, 1 ♀ M, 1 ♂ P, WAM 71-1490–1, 18.x.1961, BYM, 1 ♂ M, WAM 71-1492; Collie 27 miles east, 26.x.1961, BYM, 2 ♀ M, 1 ♀ P, 1 ♂ M, WAM 71-1486–9; Cottesloe, 17.xi.1970, RJM, 1 ♀ M, 5J, WAM 71-152–7, 27.vii.1970, RJM, 3 ♂ M, WAM 71-545–7; Darkan, 13.ii.1969, RJM, 1 ♀ M, WAM 69-429; Eagle Bay near Cape Naturaliste turnoff, 22.x.1969, RJM, R. W. George, 1 ♂ M, WAM 71-550; Elliker, 16.ii.1969, RJM, R. W. George, 1 ♂ M, WAM 71-1508; Fitzgerald River, 11.vii.1970, JG, RH, 1 ♀ M, WAM 71-494; Harvey, 10,ix.1961, BYM, 2 ♂ M, WAM 71-1506–7; Jarrahwood, viii.1969, Miss V. Godridge, 1 ♀ M, WAM 71-500; Lake Grassmere, 16.ii.1969, RJM, 1 ♀ M, WAM 69-133; Lake Jandakot, 19.iv.1970, RJM, RH, 1 ♀ P, 1 ♂ M, WAM 71-458–9; Melville, 25.i.1960, BYM, 2 ♀ M, 2 ♂ M, 1 ♂ P, WAM 71-1501–5; Moodiarrup 4 miles south, 15.ii.1969, RJM, 1 ♀ M, WAM 69-522, 1 ♀ M, WAM 69-867; Nornalup, 16.ii.1969, RJM, 2 ♀ M, 3 ♂ M, 3J, WAM 71-444–51; Pinjarra, 10.ix.1961, BYM, 1 ♂ M, WAM 71-1500; Rossmoyne near Canning River, RJM, 149 specimens, WAM 69-47, 69-436–9, 69-845, 69-865, 69-868, 69-1040, 70-3, 70-244, 70-247–50, 71-77–86, 71-88–9, 71-90–6, 71-97–8, 71-106, 71-107–40, 71-143–6, 71-151, 71-245–58, 71-263–8, 71-270–1, 71-389–90, 71-391, 71-437–42, 71-513, 71-538, 71-540–3, 71-544, 71-563, 71-674–81, 71-682, 71-731–8, 71-739, 71-812–18, 71-894–97, 71-972–3, 71-983, 71-1493, 71-1494–5; Rottnest, 20.i.1954, BYM, 1 ♀ M, 3 ♂ M, WAM 71-979–82; Scarborough, 4.viii.1968, RJM, 1 ♀ M, WAM 71-269; Two People Bay, 7.ii.1970, J. Bannister, 3 ♀ M, WAM 71-489–91; Pemberton, at The Colonels, 19.ii.1969, RJM, 1 ♀ M, WAM 69-131, 1 ♀ M, WAM 69-132; Wanneroo, at Lake Badgerup, 12.iv.1969, RH, 1 ♀ M, WAM 69-872; Walpole at Coalmine Beach, 16.ii.1969, RJM, 2 ♀ M, WAM 69-520–1.

Description (After Simon, 1909)

Male. Cephalothorax black, with a narrow complete golden band in the middle; cheliceral and mouth parts black; sternum black. Abdomen black, slightly paler and reddish-tinged in the middle; marked nearer the front with a short yellow median band, fading posteriorly, and with a few small white points on both sides. Under surface golden, becoming yellowish, and faintly dark. Legs dark and ringed without order.

Anterior row of eyes moderately curved forward and almost equidistant. AM at least a third larger than the AL:PM separated by three-quarters of a diameter.

Female. Epigynum scarcely wider than long, the depression at the front moderately narrow but enlarged at the corner on both sides, and divided by a thick, black, strong wall becoming narrower and triangular; the depression is protected by a posterior reddish curtain that is transverse, finely striated, and with a moderately thin semicircular edge on both sides.

Variation: Many specimens are of an olive-green to brown colour. The abdomen may have a yellowish or orange-green area anteriorly on the dorsal surface in addition to the yellowish to orange-green longitudinal stripe; the venter of the abdomen may be may be uniform green-brown with or without darker markings or blotches. Legs olive-green to brownish with darker rings or blotches. The coloration of the species may vary according to habitat, and those taken on black mud or rotting vegetation may be quite dark. The size of the eyes and their interspaces may vary and frequently overlap the dimensions of *Lycosa segregis* as described by Simon. At first, *L. segregis* was thought to be a separate species but it soon became apparent that the two nominal species were synonymous after a large number of specimens of both forms and many intermediate examples were collected from a single locality at Rossmoyne. One mature female WAM 69-865, lacked both AL eyes. The first row of eyes is usually shorter than the second row but specimens with both rows of equal width, and a few in which the first row exceeded the second, were found. The ratios of the 14 specimens in Table 3 were as follows: 54:56, 57:56, 57:58, 50:52, 44:45, 40:43, 54:55, 48:48, 53:54, 45:58, 57:55, 56:55, 45:48, 43:46. Table 3 shows the dimensions and interspaces of the eyes expressed as a per cent of the total width of the first eye row. The eyes of lycosid spiders are difficult to measure accurately even when using an ocular micrometer under high power. I have taken the diameter of an eye to include the dark surround where the eye emerges from the carapace, and have measured the interspaces as the least width between the raised surface of the eye as above. In a number of cases the combined eye diameters and interspaces as per cent of the first row of eyes frequently exceeds 100 per cent by up to 10 per cent. This error appears unavoidable and is in part due to the slightly curved face of the spider. A number of repeat measurements on the same specimen indicates a human error of up to 5 per cent. The anterior row of eyes is measured under the ocular micrometer and is not calculated from the addition of the diameters and interspaces of the separate eyes (which would make the combined eye diameters and interspaces as per cent of the first eye row total 100 per cent).

TABLE 3: Eye Diameters and Interspaces of *L. pullastra* Converted to Percent of the Total Width of the First Row of Eyes

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
WAM 71.109	♀ M	5·0	24	17	43	35	9	1·9	26	13
WAM 71.110	♀ M	5·2	25	19	39	33	8	2·3	25	12
WAM 71.111	♀ M	5·6	23	19	40	33	9	3·5	26	14
WAM 71.112	♀ M	4·6	24	20	41	34	10	3·0	29	13
WAM 71.979	♀ M	4·2	22	18	44	36	9	4·5	24	13
WAM 71.980	♂ M	3·8	23	15	45	37	10	4·0	23	11
WAM 71.1455	♀ M	5·6	22	18	37	33	7	4·6	30	15
WAM 71.1493	♀ M	4·3	23	19	42	35	8	4·2	23	10
WAM 71.1497	♀ M	5·0	24	19	43	34	9	3·8	21	13
WAM 71.1498	♂ M	4·3	22	18	43	35	11	3·3	27	10
WAM 71.1501	♀ M	5·7	24	19	33	32	10	1·8	31	16
WAM 71.1502	♀ M	5·0	23	21	41	32	9	3·9	23	11
WAM 71.1503	♂ M	4·2	26	20	45	36	9	2·2	24	10
WAM 71.1504	♂ M	4·2	25	20	45	35	7	2·8	25	9

The number of cheliceral teeth in Lycosid spiders is frequently used as a generic character, but in *Lycosa pullastra* (and *Lycosa meracula*) the retromarginal cheliceral teeth are quite variable (see Table 4). The promarginal teeth number 3 + 3.

The male, like that of *Lycosa arenaris*, has a tubercle on the outer curve of the fang (Fig. 2d); this tubercle is lacking in immature or penultimate males.

Some individual variation can be seen in the shape of the epigyna illustrated in Figure 2, f–k, and in the morphology of the internal genitalia, Figure 2, l–p. The male palp has a short median apophysis bearing a conspicuous tubercle, and a long terminally bifurcate embolic guide (Fig. 2, b, c, e). Although the epigynum is quite distinct from that of *Lycosa arenaris*, some similarities can be noted.

TABLE 4: RETROMARGINAL CHELICERAE TEETH OF *Lycosa pullastra* FROM WESTERN AUSTRALIA

Regd No.	Locality	Retromarginal teeth
WAM 69.868	Rossmoyne	3 + 3
WAM 71.97	Rossmoyne	2½ + 2½
WAM 71.107	Rossmoyne	2 + 2¼
WAM 71.1494–5	Rossmoyne	2 + 2
WAM 71.1493	Rossmoyne	2½ + ¼
WAM 71.1455	Bibra Lake	3 + 3
WAM 71.1479–80	Bibra Lake	2 + 2
WAM 71.1481	Bibra Lake	2½ + 2½
WAM 71.1485	Collie	2½ + 2½
WAM 71.1491	Collie	2 + 2
WAM 71.1506	Harvey	2 + 2
WAM 71.1507	Harvey	3 + 3
WAM 71.1497	Attadale	2 + 2
WAM 71.1498	Attadale	3 + 3

SIZE RANGE: Mature females C.L. 2·7 to 5·6 mm. Mature males C.L. 3·2 to 4·5 mm.

DIAGNOSIS: *Lycosa pullastra* differs from *L. arenaris* in having the male palpal organ with a terminally bifurcate embolic guide, and the epigynum of complex shape (Fig. 2, f–k). *L. segregis* is regarded as a synonym.

LIFE HISTORY

Mature males may be collected throughout the year but are most abundant from July to February. Courtship commences early in July and reaches a peak in September and October when clusters of males may be found actively courting mature females; by November courtship declines and *Lycosa impedita* males become more common. The mature male *Lycosa pullastra* continues to court females through the summer months and this species has a prolonged breeding season on the watered suburban lawns. The courtship display of the male is elicited as soon as the male makes contact with the female pheromone; a slow drumming or scratching of the palpal cymbium on the ground commences, and the first pair of legs are held stiffly forwards and vibrated vigorously whilst the male moves forwards in a series of slow, deliberate stops and starts, rather unlike the male of *Lycosa impedita* which makes pronounced forward jerky movements. *Lycosa pullastra* males appear to use the anterior outer surface of the cymbium to locate the pheromone and the palps are frequently moved around as if in a sensing fashion. No courtship response from mature males exposed to the female pheromone occurred unless palpal drumming commenced. The male approaches the female whilst courting strongly, and mounts the female from above with both sexes facing opposite directions. The palpal organ is applied to the epigynum and mating takes place with the palpal organs being applied alternately, the left palp across the left side of the female. Mature male *Lycosa pullastra* that had previously responded to mature females of the same species did not respond to the pheromone of mature *Lycosa impedita* females.

Mature *Lycosa pullastra* females have been found throughout the year but are most common during the summer months. The first females carrying egg-cocoons are to be observed in July and become common during September and October. Females carrying young become common during the months of October and November, and may be found through to April. The female selects a clear space just outside the burrow, or may construct an open web retreat in which to lay the eggs. The ground is prepared, and a disc of silk laid down; the eggs are deposited as a heap in the centre of the disc, and then webbed over. The female pulls the periphery of the egg package up and folds it over the top of the egg mass to produce a rough ball; the egg cocoon is rotated, and reinforced by silk until a rounded cocoon is made and attached to the spinnerets. The operation of laying eggs to the final attachment of the egg cocoon may take over 12 hours. The female carries the cocoon at all times and may expose it to the morning sun by cradling the cocoon between the hind legs whilst remaining head down in the burrow. The eggs take from 17 to 65 days to hatch; the following data was collected from specimens held in the laboratory: 17 days in December, 1968, 28 days in November, 1968, 44 days in March, 1968, and 65 days during July, 1968. The young commence to leave the female 5 to 12 days after hatching, but some may remain up to 22 days on the abdomen. The egg cocoon varies in size from 5·0 to 9·0 mm in diameter; if a second egg-cocoon is laid during the breeding season it is noticeably smaller than the first. Table 5, gives the numbers of eggs laid by some females captured in the field. Between 150 and 169 juveniles have been counted from the dorsal surface of females captured in the field. The free living young do not construct burrows.

TABLE 5: NUMBER OF EGGS IN THE COCOONS OF *Lycosa pullastra*

Month	C.L.	Number of eggs
July	4·6	266
August	4·9	139+28 infertile
September	4·1	135
September	4·8	242
September	5·0	296
October	5·0	245
November	3·5	139

Adults prey on a wide variety of small insects especially Diptera and small beetles, but avoid those beetles with hard exoskeletons. A study of the prey of *Lycosa pullastra* was not undertaken.

As this species frequently hunts during the day a series of crude experiments were undertaken to establish the heat tolerance of the males during January, 1971. A shaded plastic container with a diameter of 10 cm was part filled with grass cuttings and fitted with a thermometer near the base; this container was exposed to the sun and the mature specimen introduced. Of the three males tested all appeared normal at a temperature of 40°C for a period of 10 minutes, but became agitated at a temperature of 43°C, crouched at 44°C, and became uncoordinated at 45°C. All recovered within 1 hour after transfer to a temperature of 32°C. Field temperatures taken adjacent to the spider varied from 11°C to 35°C.

HABITAT

The damp or moist areas near swamps, lakes, streams, rivers, and estuaries of southwestern Australia. *Lycosa pullastra* prefers grassed areas, or a plentiful supply of rotten vegetation, or leaf litter, on moist sand, loam, or clay soils. Specimens were collected by Mr J. Bannister of the WAM on the dry, rotting surface of washed up seaweed banks of Two People Bay. This species, with *Lycosa impedita*, inhabits lawns of Buffalo, Couch, and other grasses throughout the metropolitan area of Perth, and on some well watered suburban lawns may be extremely abundant during the summer months. Such populations may be significantly reduced if the lawn is mowed frequently or if insecticides are applied. If the grass becomes too high *Lycosa pullastra* will be found sheltering near the margins, particularly near paths and gardens, but if lawns are kept low by infrequent mowing the spider will be found over the entire area.

BURROW

Small open retreats among grass roots are constructed by males, penultimate females, and juveniles. The mature female may web the grass roots or stems into a simple tube-like burrow, and then close the entrance with pieces of grass or silk web after the egg cocoon is laid. On occasions, the burrow of the mature female is simply a webbed over hole in the lawn, a webbed retreat below leaves or rotten logs, or a small burrow up to 5 cm dug into a bank or below the edge of a lawn.

DISCUSSION

Roewer (1954, p. 253) placed both *L. pullastra* and *L. segregis* into the genus *Hogna* (AM–AL = AM–AM), but Simon (1909, pp. 184–5) states that the eyes of the first row are almost equidistant. In all specimens examined by me the distance AM–AL is always less than the distance AM–AM. Guy (1966) treats *Hogna* as a subgenus of *Lycosa*. In the key to the subgenera of the subfamily Lycosinae provided by Guy (1966) specimens of *L. pullastra* key down to the subgenera *Allocosa* (of *Lycosa*), *Arctosa* (of *Arctosa*) and *Allohogna* (of *Trochosa*). The use of eye diameters and interspaces as generic characters is once again of limited value when a series of specimens of such variable species is examined. I have placed *Lycosa pullastra* into the 'arenaris group' of species in the genus *Lycosa* as all mature males possess a conspicuous tubercle on the external surface of the cheliceral fang. The burrows and habitat of all species in the 'arenaris group' are similar, and some similarities can be observed in the shape of the epigyna. It remains to be seen if the 'arenaris group' is an assemblage of related species and thus worthy of generic distinction.

DISTRIBUTION

Southwest of Western Australia within the region receiving more than 400 mm annual rainfall.

Lycosa lapidosa sp. nov.

(Figure 3, a–b, e–j)

Material Examined

Holotype: Queensland Museum W3865, ♀ M, C.L. 7·8 mm, Black Duck Creek, near Junction View, SE. Queensland, collected by R. J. McKay and V. Davies, 24 January, 1973. In spirit.

Paratypes: Black Duck Creek, 24.i.1973, RJM, V. Davies, P. Walker, R. Hobson, 6♀M, 4♀P, 5♂M, QM W3864; East Branch, Blackfellows Creek, Junction View, Queensland, 14.iii.1973, RJM, V. Davies, QM W3866; Boolumba Creek, Kennilworth State Forest, Queensland, 29.i.1973, R. Raven, 1 ♀ M, QM W3867; Pike Creek Dam, Texas, Queensland, 8–9.ii.1973, RJM, M. & E. Archer, 6 ♀ M, 3 ♀ P, 2♂ M, QM W3868; Clarence River, 30 miles down river from Tabulam, New South Wales, 24.iv.1973, D. Gleeson, 1 ♀ M, QM W3869.

Description

Based on the holotype.

Carapace dull olive-green without a pattern, but becoming mid-brown with very vague radiating darker stripes after preservation in alcohol; face dark olive-green to ash-brown; paturon brown with ash-grey hair; labium and maxillae brown; sternum light brown to olive-brown without a dark mark. Abdomen olive-green to green-brown above; two longitudinal rows of very small faint white spots on the dorsal surface are present in life, but absent after preservation when the abdomen appears dark brown; ventral surface olive-brown, with three longitudinal dark brown bars converging posteriorly, the middle one divided anteriorly (Fig. 3b). Legs uniform pale olive-green to olive-brown above and below.

Anterior row of eyes procurved and about as wide as the second row, AM larger than AL. Ratio of eyes AM:AL:PM:PL = 21:15:37:32; distance AM:AM 9, AM:AL 6, AM:PM 11, AL:PM 13, PM:PM 22. Clypeus to AM 19. Width of first eye row 92; width of second eye row 94.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size.

TABLE 6: Measurement of Leg Segments of *L. lapidosa* in mm.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·6	2·9	4·8	4·5	3·0
2	5·4	2·7	4·4	4·4	2·7
3	5·0	2·4	4·0	4·8	2·5
4	6·6	2·9	5·7	6·1	3·6
Palp	2·9	1·3	1·8	—	2·0

Variation: Juveniles are dull olive-green or green-brown with an ash-grey sheen. Eye measurements are recorded for ten specimens; each measurement is expressed as a

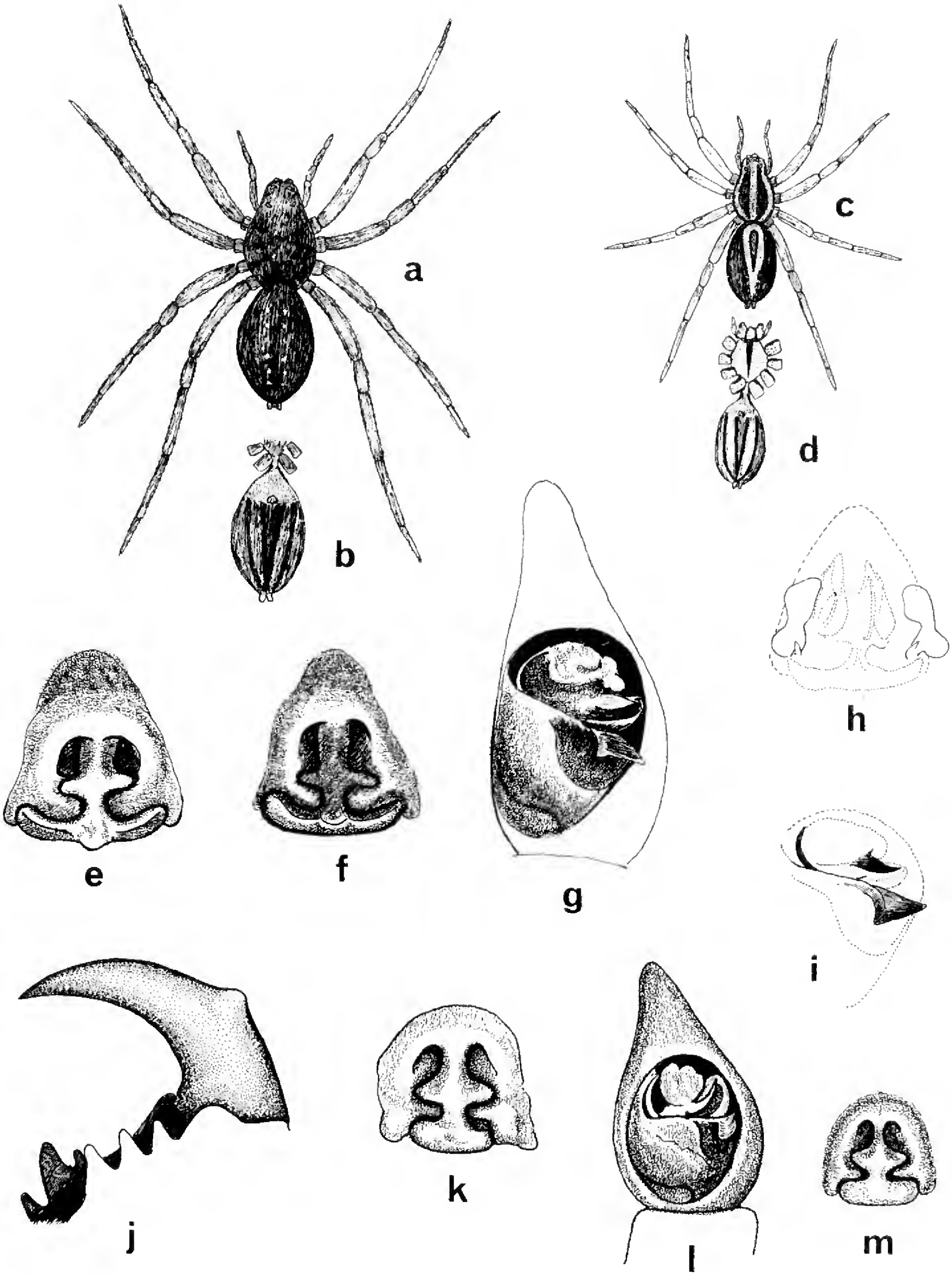

FIG. 3: a–b, e–j, *Lycosa lapidosa*. a, holotype; b, ventral surface of abdomen; e, epigynum of holotype; f, epigynum of QM W3864; g, male palpal organ of QM W3864; h, internal genitalia of mature female QM W3864; i, median apophysis and embolic guide of male palpal organ; j, fang of mature male.

c–d, k–m, *Lycosa furcillata*. c, lectotype; d, ventral surface of abdomen; k, epigynum of lectotype; l, palpal organ or paralectotype male; m, epigynum of QM W3862.

per cent of the total width of the first row of eyes, in Table 7; the first row of eyes may be narrower or wider than the second row, the ratios for the specimens in Table 7 are as follows: 95:96, 97:96, 90:92, 49:50, 92:83, 84:85, 49:52, 93:95, 100:100, 99:99. The epigynum of the holotype and one paratype is illustrated in Figure 3 e, f. The internal genitalia of a paratype female is illustrated (Fig. 3h). Mature males are coloured as above. A conspicuous tubercle on the outer curve of the fang is present in all mature males (Fig. 3j); the palpal organ has a well developed median apophysis and a short pointed embolic guide (Fig. 3i).

SIZE RANGE: Mature females C.L.7·9 to 8·7 mm. Mature males C.L. 6·5 to 7·9 mm.

DIAGNOSIS: *Lycosa lapidosa* is very similar to *Lycosa furcillata* but lacks a pattern on the carapace, does not have a pale loop-like stripe on the dorsal surface of the abdomen, and the sternum is uniformly coloured. *Lycosa lapidosa* is a much larger species at sexual maturity. *Pirata brisbanae* has a similar pattern on the venter, but differs in coloration, the shape of the epigynum, and the size at sexual maturity.

LIFE HISTORY

Mature females may be collected from January to April in southern Queensland; the mature males have been collected in January and February.

Females with egg cocoons were collected at Black Duck Creek and Pike Dam Creek in January and February. The cocoon measured 7·5–8·5 mm × 9·0–10·2 mm and four cocoons contained from 387 to 486 ova measuring 1·15 mm in diameter.

HABITAT

All specimens were collected on the margins or dry beds of creeks. This species shelters below large water-worn pebbles or rocks, and are most abundant where such rocks are piled into heaps or ridges near the waters edge. A webbed retreat is occasionally built by gravid females and those carrying egg cocoons, but other mature specimens and juveniles merely shelter within the crevices between rocks.

DERIVATION

From the latin 'lapidosus', abounding in stones.

Lycosa furcillata L. Koch, 1867
(Figure 3, c–d, k–m)

Lycosa furcillata L. Koch, 1867, pp. 201–2; L. Koch, 1877, pp. 903–6, pl. 78, Figs. 1, 1a, 1b, 2, 2a, 2b, Bowen, Brisbane, Mackay, Gayndah, Queensland; Sydney, New South Wales; Rainbow, 1911, p. 268; Rack, 1961, p. 37; McKay, 1973, p. 379.
Allocosa furcillata: Roewer, 1954, p. 206.

MATERIAL EXAMINED

SYNTYPES: 3, British Museum (N.H.), BM 1919.9.18. 363–5. The syntype recorded by Rack (1961) was not examined. A lectotype is here designated from this series.

LECTOTYPE: BM 1919.9.18.363, ♀ M, C.L. 6·7 mm, Sydney, epigynum as figured by Koch (1877) and redrawn in Figure 3k.

PARALECTOTYPES: BM 1919.9.18.364, ♀ M, C.L. 5·9 mm, Sydney. BM 1919.9.18.365, ♂ M, C.L. 5·4, Sydney, palpal organ as figured by Koch (1877) and redrawn in Figure 3l. One specimen in the Hamburg Museum (Rack, 1961).

OTHER MATERIAL: Queensland: Samford, near Brisbane. April 1973, D. Joffe, QM W3862, 1 ♀ M, May 1973 QM W3863, 1 ♂ M; Mackay, 28.vii.1973, C.L. Wilton, Otago Museum, New Zealand, 1 ♀ M; Everton Part, Brisbane, 4.iii.1973, RJM, QM W3870, 2 ♀ M.

DESCRIPTION (After Koch, 1877)

Female. Cephalothorax yellowish-brown; a very narrow pale yellow lateral margin with a broad parallel white band from the posterior margin to the anterior corners of the carapace; a broad brownish longitudinal band commences rather narrowly at the posterior margin and reaches the PM, at the anterior end this band is divided by a brown longitudinal stria; three black and white radiating stripes are present on each side of the thorax. Mandibles pitch-black, with yellow-brown hair. Maxillae and labium red brown. Sternum yellow-brown with a broad wedge-shaped black longitudinal spot pointing posteriorly.

Abdomen dark yellow-brown above with brown-yellow hair; a continuous longitudinal lighter stripe which is rounded anteriorly and tapers posteriorly is present on the dorsal surface, in the anterior part of the stripe is a similarly shaped brown spot with the dorsal sigilla within covered by white hair; the posterior half of the longitudinal band is bordered on either side by a row of brown serrations, between each two serrations is a white spot; sides of abdomen brownish-yellow with pale yellow and brown spots. Undersurface of abdomen pale yellowish with three black longitudinal stripes converging posteriorly; the middle stripe containing two yellow spots. Spinnerets yellow-brown. Palpi and legs brownish yellow.

Male. Almost identical in colour and pattern;maxillae are brown-yellow; labium black; the longitudinal wedge-shaped spot on the sternum is smaller; the spots on the longitudinal stripe on the upper side of the abdomen are brownish-yellow and lighter than in the female; the central longitudinal black stripe on the undersurface of the abdomen is split along almost the full length.

Female. Cephalothorax as long as patella plus tibia of the 4th leg. Anterior row of eyes slightly procurved, the eyes equidistant and separated by very narrow interspaces; AM considerable larger than AL and separated by more than a radius from the PM. PM more than a radius apart and about a diameter from the PL.

Male. Cephalothorax is narrower anteriorly than female; eyes similar to female. Mandibles thinner and longer with a denticle on the outside slightly before the middle.

VARIATION: The eye diameters and interspaces of seven specimens are given in Table 8 as a percentage of the total width of the first row of eyes. The anterior eye row is narrower than the second in the ratio 64:71, 58:64, 49:55, 60:66, 64:72, 63:72, 56:65. The clypeus

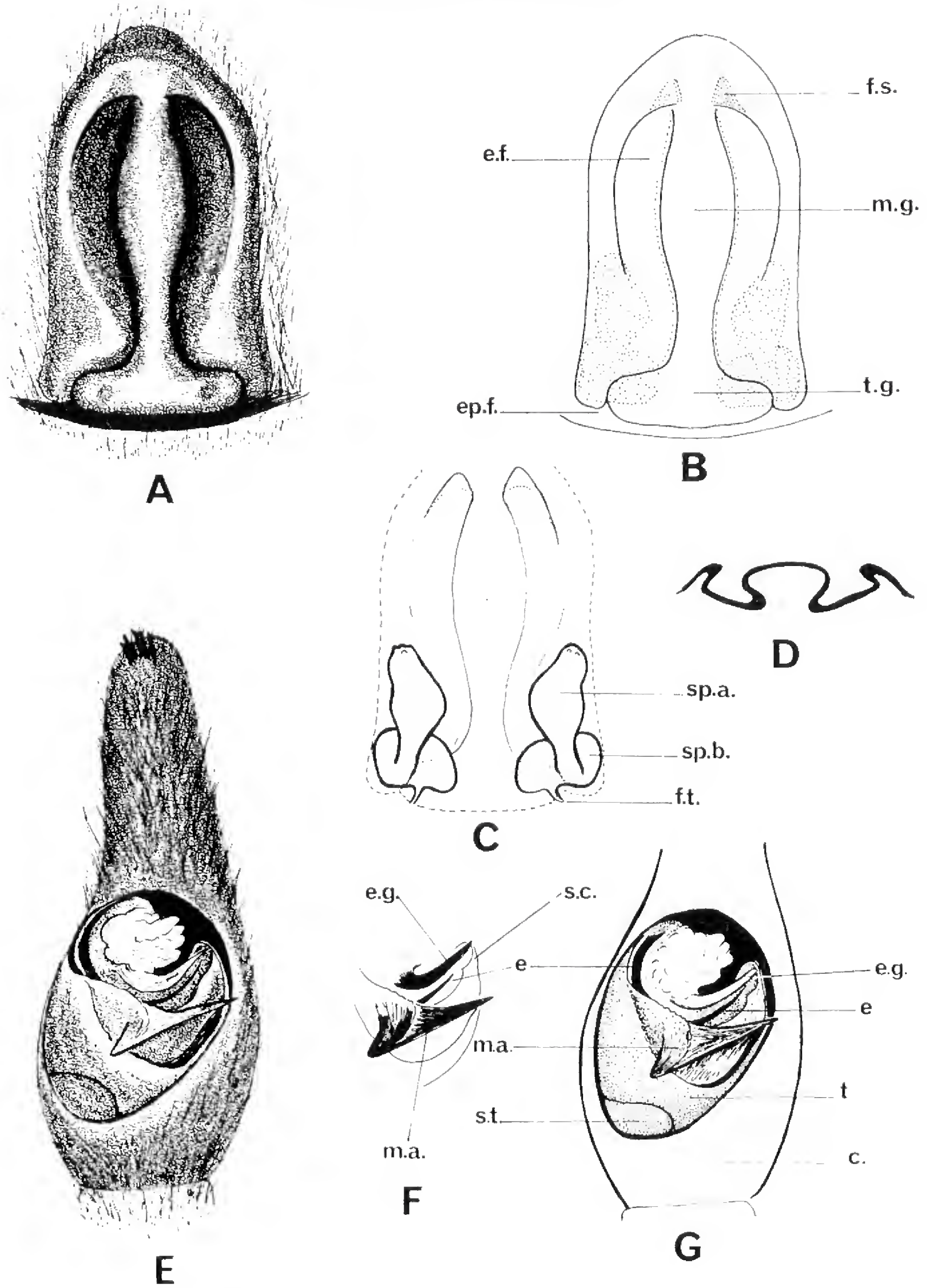

FIG. 4: The genitalia of lycosid spiders; A, external view of epigynum; B, terms used in description of epigynum; C, internal view of dissected epigynum showing spermathecae; D, cross section through B at level e.f; E, male palpal organ; F–G, terms used in description of palpal organ. Abbreviations: c = cymbium, e = embolus, e.f. = epigynal furrow, ep.f. = epigastric furrow, e.g. = embolic guide or terminal apophysis, f.s. = furrow sac, f.t. = fertilization tube, m.a. = median apophysis or conductor, m.g. = median guide, sp.a. = apical spermatheca, sp.b. = basal spermatheca, s.c. = membranous secondary conductor, s.t. = subtegulum, t = tegulum, t.g. = transverse guide.

TABLE 7: EYE DIAMETERS AND INTERPSACES OF *Lycosa lapidosa* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
QM W3864	♀ M	8·2	23	17	39	36	12	6	24	11	14
QM W3864	♀ M	7·6	24	17	37	35	9	7	25	11	15
QM W3864	♂ M	8·0	27	17	44	37	8	6	22	11	17
QM W3864	♀ M	8·7	23	16	39	33	8	6	26	10	14
QM W3864	♀ M	8·3	24	16	42	36	9	7	25	11	16
QM W3864	♂ M	7·3	27	20	42	35	8	4	25	10	12
QM W3867	♀ M	8·7	24	16	39	33	7	6	24	9	14
QM W3868	♀ M	7·3	26	18	42	34	9	5	23	8	11
QM W3868	♀ M	8·6	25	18	40	33	8	5	22	11	13
QM W3869	♀ M	8·3	24	18	41	33	9	6	23	10	13

TABLE 8: EYE DIAMETERS AND INTERSPACES OF *Lycosa furcillata* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
Lectotype	♀ M	6·7	21	17	45	41	10	6·0	28	12	15
BM 1919.9.18.364	♀ M	5·9	22	17	45	40	8	5·0	23	14	19
BM 1919.9.18.365	♂ M	5·4	23	19	47	40	7	3·5	26	12	18
QM W3862	♀ M	4·6	22	17	45	40	7	5·0	27	12	15
QM W3863	♂ M	4·9	24	18	48	39	6	4·7	23	10	16
QM W3870	♀ M	5·1	21	19	49	42	8	4·8	25	13	16
QM W3870	♀ M	4·4	23	18	48	39	9	5·3	27	15	18

varies in depth from about $\frac{3}{4}$ to a little more than the diameter of an AM. Retromarginal cheliceral teeth 3 + 3. The two mature males have a well developed tubercle on the outer curve of the fang. The epigynum of the lectotype and the female from Samford is illustrated (Fig. 3k, m). The male palpal organ has a well developed curved median apophysis and a curved tapering embolic guide (Fig. 3, l).

DIAGNOSIS: *Lycosa furcillata* is distinguished from all other members of the 'arenaris group' in having a distinctive pale longitudinal stripe on the dorsal surface of the abdomen.

LIFE HISTORY

A mature female collected from a grassed footpath at Mackay on 28 July, 1973, by Mr C. L. Wilton had an egg cocoon with the young emerging. The burrow is unknown; all specimens collected near Brisbane have been found on lawns or pasture grasses.

DISTRIBUTION

Queensland and New South Wales.

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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 3. A CORAL SHINGLE INHABITING SPECIES FROM WESTERN AUSTRALIA

R. J. McKay
Queensland Museum

ABSTRACT

A new species of Wolf Spider *Lycosa corallina* inhabiting the coral shingle on offshore islands of Western Australia is described.

McKay (1973) has provided an introduction to the present study of the Wolf Spiders of Australia. A number of undescribed species have been collected and these will be reported upon as the study progresses. Keys to the identification of the spiders of this family will be provided at a later date when the Australian species are more fully known.

Many species of Lycosid spiders are confined to a particular habitat and may be restricted to small local areas of suitable substrate despite their wide distribution. This contribution to the series of papers devoted to the systematic revision of the family describes one such species.

Lycosa corallina sp. nov.
(Figure 1a–h)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 71-1645, ♀ M, C.L. 13·0 mm, Wooded Island, Houtman Abrolhos, W.A., collected by R. J. McKay, July 10, 1971. In spirit.

PARATYPES: Abrolhos Islands, W.A.; Basile Island, 22.viii.1970, N. Sammy, 1 ♂ M, WAM 71-502, 24.viii.1970, B. Green, 1 ♀ P, WAM 71-503, 2 ♀ M, WAM 71-504–5, 8.vii.1971, RJM, 4 ♀ M, 1 ♂ M, 4 ♀ P, 2 ♂ P, 1J, WAM 71-1631–40; Beacon Island, 11.vii.1971, RJM, L. Baird, 4 ♀ M, 4 ♀ P, 8J, WAM 71-1649–65, 1 ♂ P, WAM 71-1989; Post Office Island, 9.i.1968, A. Slerkowski, 1 ♀ M, WAM 71-506, 8.vii.1971, RJM, L. Baird, 3 ♀ M, 3 ♀ P, 5 ♂ M, 2 ♂ P, 8J, WAM 71-1609–30, 4 ♀ M, 1 ♂ M, 1 ♂ P, 1J, WAM 71-1793–9, 1J, WAM 71-1990; Wooded Island, 10.vii.1971, RJM, 1 ♀ M, 2 ♀ P, 1 ♂ M, WAM 71-1641–4, 1 ♂ M, 2J, WAM 71-1646–8, 1 ♀ M, WAM 71-1800; Rosemary Island, Dampier Archipelago, W.A., 27–28.x.1971, RJM, 4 ♀ M, 2 ♀ P, 8J, WAM 71-1976–88.

DESCRIPTION

Based on the holotype.

Carapace dark brown, covered with fine grey-brown hair becoming green-brown around ocular quadrangle; some faint radiating darker markings visible in alcohol but barely visible in life; paturon dark brown to black below with ash-grey to grey-brown hairs above on the anterior and anterolateral surfaces; lateral condyle dark red-brown,

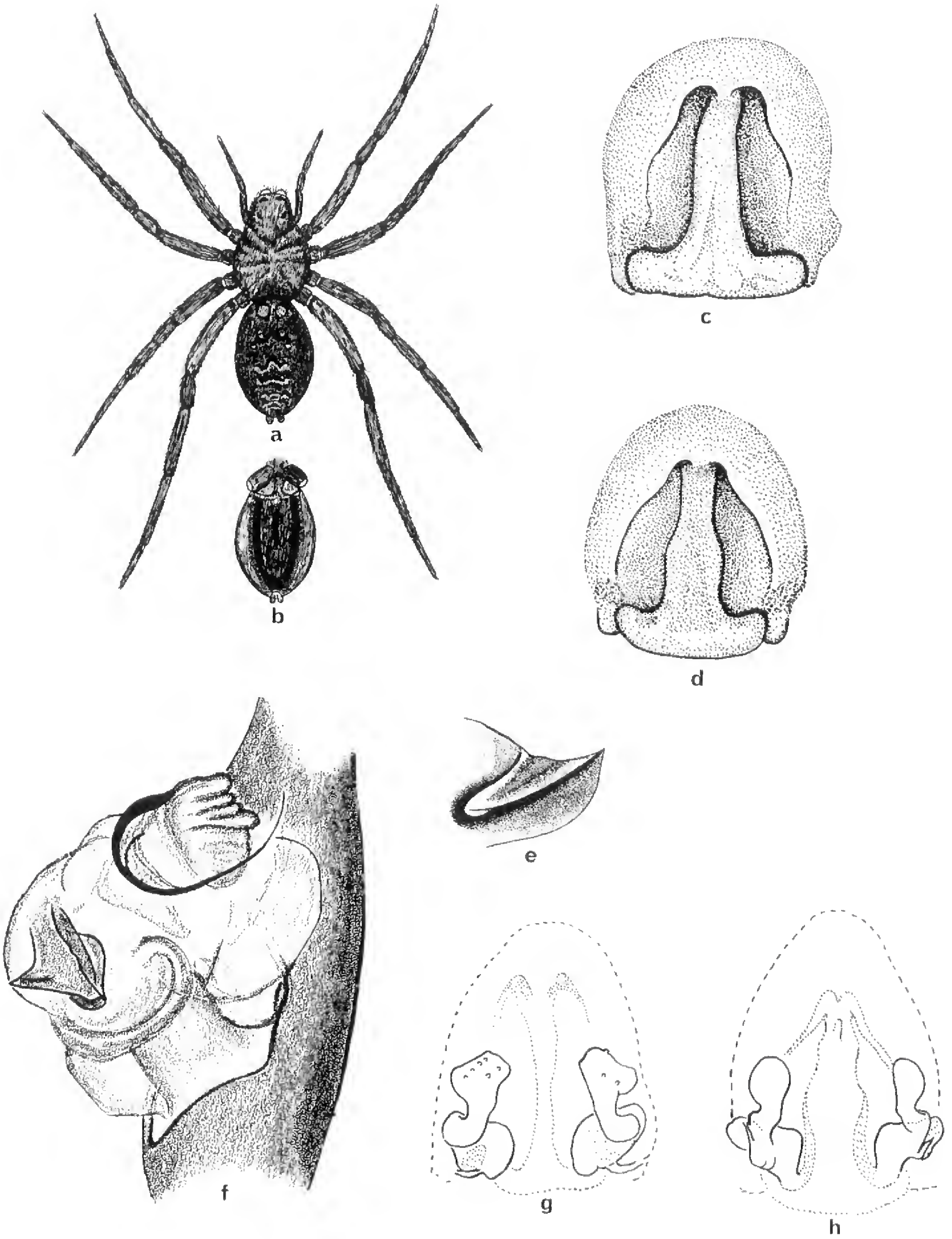

FIG. 1: *Lycosa corallina*. a, holotype, b, ventral surface of abdomen; c, epigynum of holotype; d, epigynum of WAM 71-1663; e, median apophysis of male palpal organ; f, male palpal organ of WAM 71-1643; g–h, internal genitalia of WAM 71-1797 and WAM 71-1663.

edged in black; fangs black; labium and maxillae dark brown; sternum and lower surface of coxae dark brown to blackish. Abdomen ash-grey to grey-brown above and on sides; anterior slope black with two black stripes extending on to the anterior dorsal surface to almost enclose a round light grey area on each side dorsally; more posteriorly are a pair of very small but distinct pale grey spots followed closely by a black inverted V-shaped chevron; two additional black-brown chevrons each followed by a thin pale grey line that expands somewhat at the lateral ends, are situated posteriorly, followed again by two tent shaped black spots narrowly joined by a thin dark brown line, and two thin, short, transverse black-brown chevrons just before the pale grey spinnerets; fine black spots are scattered all over the dorsal and lateral surfaces of the abdomen; venter with a dark brown to black-brown field with a super-imposed black triangular field out-lined by vague paler brown spots, both fields reaching the base of the spinnerets; lung book covers dark brown. Legs ash-grey to olive brown, becoming ash-grey after preservation in alcohol; the sides of the femora may become rubbed clear of hair and appear brownish; ventral surface of metatarsi and tarsi brownish; the ventral surface of the femora-patella joints are black; palpi grey brown.

Anterior row of eyes procurved, AM larger than AL, PM more than three times the diameter of the AM and almost 2/3 of their diameter apart. Ratio of eyes AM:AL:PM:PL = 10:8:36:27; distance AM:AM 8, AM:AL 7, AM:PM 7, AL:PM 5, PM:PM 22. Quadrangle of posterior eyes, length 81, width 115. Clypeus to AM 11. Length of first eye row 59, length of second eye row 90.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth, the inner one slightly larger than the remaining two. Labium longer than wide.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	9·0	5·1	7·6	7·2	3·9
2	8·3	4·9	6·9	7·1	3·7
3	7·8	4·4	6·3	7·4	3·6
4	10·0	4·8	8·4	11·1	4·6
Palp	4·4	2·4	2·8	—	3·2

Epigynum with a well developed median guide terminating in a somewhat flat transverse guide (Fig. 1c).

VARIATION: Juveniles may be slightly lighter in colour than the adults, and vary from a light ash-grey on bleached coral rubble to a dark green-brown on masses of decaying seaweed on the shore. The venter of adults may be a light grey colour with two distinct longitudinal black lines or heavy bars converging to meet just before the spinnerets; a median dark grey to black bar may be present. One adult male has the two wide black converging bars superimposed with a row of fine white spots, whereas in other specimens, the black bars have the row of fine white or pale grey spots on the lateral edge of the bar. Females from Dampier Archipelago have the venter as described above, or pale brown with indistinct markings. One female has a black venter with a large pale brown spot in the centre. Juveniles may have a dark grey venter with two converging rows of pale grey spots between which is an indistinct median darker grey longitudinal bar. The dorsal surface of the abdomen may be a dark grey to brown-grey with two rows of paler grey or pale brown spots converging towards the spinnerets where they may fuse to form a pale area. The carapace is with or without vague radiating dark stripes sometimes with adjacent paler stripes, or on occasions with a Union Jack-like pattern of radiating dark and ash-grey markings, no median longitudinal bar is present, and the carapace may become a polished dark brown if the hair is worn thin or removed. Specimens from Dampier Archipelago are more variable in coloration and may have a paler marginal stripe on the posterior part of the carapace; many mature females have the legs banded or blotched with fawn and dark brown rings. The eye diameters and interspaces vary slightly; 13 specimens are recorded in Table 2 below.

TABLE 2: Eye Diameters and Interspaces of *Lycosa corallina* Converted to Percent of the Total Width of the First Row of Eyes

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
HOLOTYPE	♀ M	13·0	20	14	61	46	14	12	37	12
WAM 71-504	♀ M	13·5	22	15	64	51	10	9	34	12
WAM 71-505	♀ M	11·8	22	15	63	50	9	9	34	11
WAM 71-506	♀ M	14·9	22	16	61	48	13	9	36	11
WAM 71-1621	♀ M	11·9	20	15	62	47	12	8	36	8
WAM 71-1634	♀ M	12·3	21	16	62	52	11	11	36	8
WAM 71-1642	♀ M	11·7	20	16	63	47	10	10	39	12
WAM 71-1643	♀ P	10·6	20	14	66	49	12	10	35	10
WAM 71-1644	♂ M	11·4	22	16	68	49	12	10	39	10
WAM 71-1655	♀ P	9·3	20	16	68	50	14	9	36	9
WAM 71-1976	♀ M	10·5	22	16	60	45	11	8	35	12
WAM 71-1977	♀ M	12·5	22	15	60	51	10	7	37	10
WAM 71-1978	♀ M	16·6	23	17	62	48	8	8	33	10

Variation in the internal genitalia is shown in Figure 1g, h, with the external surface of the epigynum of the holotype and WAM 71-1663 illustrated in Figure 1c, d.

Mature males are similar to females in coloration. The male palp is shown in a fully expanded condition in Figure 1f; the median apophysis is large and is illustrated in Figure 1e.

Size Range: Mature females C.L. 10·4 to 14·9 mm. Mature males C.L. 10·5 to 11·6 mm.

Diagnosis: *Lycosa corallina* is similar in coloration to *Lycosa lapidosa* but the epigynum is quite different in shape, and mature males lack a tubercle on the anterior edge of the fang.

LIFE HISTORY

Mature females have been collected in January and July and are therefore possibly present throughout the year. Mature males are present in July and August, and mating was observed at the Abrolhos Islands in July. Juveniles of all sizes, and penultimate males and females were collected in July, and it is possible that this species has an extended breeding season throughout the winter and spring months at the Abrolhos Islands. One female WAM 71-504, C.L. 11·8, had an egg cocoon 15·5 by 14·1 mm containing 515 ova, 1·5 mm in diameter. At night, this species was common on areas of coral shingle, and remained in a perched position on the tips of coral fragments. They were found to be most numerous near the shoreline where they ventured out on to masses of seaweed. In some areas near fishermen's huts they were rather more abundant, and although not observed feeding, they may prey on cockroaches and flies associated with the lobster bait stored nearby. Small specimens may prey on flies, maggots, or amphipods within the masses of stranded decomposing seaweed.

A few large specimens were liberated onto the surface of a slightly choppy sea near North Island, Abrolhos. The spiders had no difficulty in remaining afloat and were carried rapidly along the surface by the wind. One specimen was followed for over ten minutes before it was lost from sight. A large female that had been transported rapidly across the surface of the sea by a brisk wind was noticed on three occasions to remain motionless until it fell to leeward of a mass of semi-submerged floating seaweed, and then to swim vigorously up wind to the seaweed where it clambered onto the highest area, and was only dislodged with some difficulty. It is therefore possible that this species has a wide distribution.

HABITAT

At the Abrolhos Islands and Rosemary Island, Dampier Archipelago, *Lycosa corallina* was found to inhabit the extensive ridges and swales of coral shingle and to a lesser extent the deposits of seaweed washed ashore on coral shingle beaches. Some islands of the Abrolhos Group are composed entirely of coral shingle, and on such islands (Post Office, Basile, etc.) *Lycosa corallina* was abundant all over the island. On other islands with beach ridges of coral shingle on the periphery or in isolated areas, this lycosid was found to inhabit the shingle areas only. On islands without coral shingle *Lycosa corallina* was not collected despite a careful search of beaches, sand dune, limestone rubble and other habitats. On the mainland near Geraldton, coral shingle is not present, and this species was not collected.

Teichert (1947, p. 155) describes the coral shingle habitat as consisting of 'unsorted material. The coral fragments are arranged in all directions so that they form a densely packed and firmly interlocked mass which is not likely to undergo any further compaction when, in the later stage of its development, it is removed from the influence of the waves. Mixed with the coral fragments is a certain amount of more or less abraded gastropod and pelecypod shells, generally heavy shells of the rough water type such as *Turbo, Trochus, Chama, Tridacna,* etc. To these are added occasional echinoid tests, sponges, bryozoan skeletons, foraminiferal tests, etc., but such material is very subordinate'. Teichert describes the progressive darkening of the coral fragments from the freshly thrown up white coral fragments to the very dark grey colour of the oldest fragments. *Lycosa corallina* inhabits white coral shingle but is more abundant in the darker grey weathered coral shingle.

BURROW

This species was observed to lie motionless on the tops of exposed pieces of *Acropora* coral fragments, and move head-first into the interstices of the coral shingle when disturbed at night. They are difficult to capture and move down into the coral shingle when approached; once within the coral mass small specimens move with great agility between the coral fragments; large specimens may be found sheltering some 10 to 20 cm below the surface in slightly webbed irregular burrows, but most specimens appear to lack any kind of well webbed burrow and are found sheltering in crevaces or irregular spaces below the surface. Although abundant at night, their presence was unknown to many fishermen resident on the islands for many years.

DISCUSSION

This new species falls into the subgenera *Allocosa* (AM–AL shorter than AM–AM) and *Hogna* (AM–AL = AM–AM) of the genus *Lycosa* using the key to the subgenera provided by Guy (1966, p. 51). The limitation of the use of eye diameters and interspaces as characters of generic importance can be seen when a number of specimens are examined. A later paper in this series will attempt a more natural regrouping of the Australian species of the subfamily Lycosinae.

DISTRIBUTION

On coral shingle and beach ridges of the Abrolhos Islands, and Rosemary Island, Dampier Archipelago, Western Australia.

DERIVATION

Named in reference to the coral shingle habitat selected by this species.

ACKNOWLEDGEMENTS

I wish to thank Mr B. K. Bowen, the Director, Western Australian State Fisheries and Fauna Department, for transport to and from the Houtman Abrolhos Islands. My grateful acknowledgement of the assistance and cheerful company of the skipper Mr E. Little, and crewman Mr L. Baird of the Fisheries Patrol Vessel 'Dampier'. My thanks are also due to Mr E. (Ned) Kelly of Rosemary Island who actively assisted in the collection of specimens.

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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 4. THREE NEW SPECIES FROM MOUNT KOSCIUSKO, N.S.W.

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ABSTRACT

Three previously undescribed species of Wolf Spider, *Lycosa summa, Lycosa kosciuskoensis* and *Lycosa musgravei* are recorded from Mount Kosciusko, New South Wales.

Mount Kosciusko with an elevation of 2,230 m, situated on the Kosciusko Plateau near the border of New South Wales and Victoria, is the most elevated area in Australia. The highest portions of the plateau are covered with snow from eight to nine months of the year and some snow drifts may persist throughout the summer.

McLuckie and Petrie (1927) have drawn attention to the extreme shortness of the vegetative season at these high altitudes and their study of the plant communities of the Kosciusko Plateau led them to recognise three zones: the Montane zone from 3,000 to approximately 5,000 feet (900–1500 m), the subalpine zone from approximately 5,000 feet (1500 m) to the tree-line at 6,000 to 6,500 feet (1800–2000 m), and the alpine zone from the tree-line to the highest elevations. In the alpine zone the continuous cover of snow throughout nine months of the year has a very pronounced effect on the vegetation. All the herbaceous types die down when the snow comes, but perennate from season to season by subterranean organs of propagation. The snow grass *Poa caespitosa* occurs throughout the alpine zone into the subalpine zone, and provides some cover for small animals dwelling above the tree-line. The summits of certain peaks represent an extemely barren habitat with practically no soil. Dulhunty (1947) records the soil as consisting mainly of sand and gravel derived from granite. On the slopes and hill sides, the surface layer of soil, 6–8 inches deep, is of dark colour due to the accumulation of humus. Peat formation occurs in upland swamp areas, and Dulhunty recorded subsurface peat temperatures at 9 inches and 3 feet (ca. 200 mm and 1 m). The surface temperatures during the investigation in 1945–46 at an elevation of 6,200 feet (1900 m) ranged from 17·2°C during January to at least freezing point during winter; subsurface temperature within the peat deposit at 9 inches did not fall below 1·1°C during the 1945–46 winter. Gentilli (1971, p. 129) gives the lowest temperature so far recorded in Australia as −22°C, at 1830 m (about 6,000 feet) just below Charlotte Pass (Kosciusko Plateau) on July 14, 1945, and August 22, 1947. At Lakeside Inn (formerly Kosciusko Hotel: 1529 m) the mean annual temperature is 6·3°C. The mean daily minimum is below freezing from May to September inclusive. On Hotham Heights, Victoria (1860 m), the mean annual temperature is 4·7°C.

In such a harsh environment one would not expect to find lycosid spiders, but in January, 1929, a party from the Australian Museum consisting of Mr A. Musgrave, Curator of Insects and Arachnids, Mr H. O. Fletcher, Assistant in Palaeontology, and Mr W. Boardman, Assistant Zoologist, visited the Kosciusko plateau and camped inside a stone hut at the foot of Mount Kosciusko, where they spent a few days collecting. Two species of *Lycosa* were collected from burrows and from below stones among the clumps of snow grass at 7,000 feet (2140 m). Musgrave (1930) gives an account of the expedition and provides a photograph of 'an apparently new species of *Lycosa* or Wolf Spider which made its lair among the Snow grass on the sides of Mount Kosciusko' (here described as *Lycosa summa* sp. nov.). Three lycosid spiders are now known from Mount Kosciusko, and a related species *Venatrix fuscus*, from Mt. Hotham (6,000 feet).

The life history of these montane species is poorly known and would undoubtably make a very fascinating study considering the extremely short period available for feeding and reproduction. McKay (1973) has outlined the method of capture in a brief introduction to the revision of the Australian Wolf spiders.

Lycosa summa sp. nov.

(Figures 1a–c, g–i)

Lycosa sp.: Musgrave, 1930, pp. 103 (Fig.), 104.

MATERIAL EXAMINED

HOLOTYPE: Australian Museum AM K61669, ♀ M, C.L. 10·7 mm, Mount Kosciusko, 7000 feet (2140 m), N.S.W., collected by A. Musgrave and H. O. Fletcher, 7 January, 1929. In spirit.

PARATYPES: Mount Kosciusko, 7000 feet (2140 m); A. Musgrave, H. O. Fletcher, 7.i.1929, 1 ♀ M, 1 ♂ P, AM K61669, 2 ♀ M, 1 ♂ P, 4J, AM K61667, 1 ♀ M, AM K61668, 2 ♀ P, 1J, AM K61670; H. O. Fletcher, 7 ii.1929, 1 ♀ M, AM K61671.

DESCRIPTION

Based on the holotype.

Carapace light brown to fawn (white in life?) with a dark brown triangular shaped area extending over each side of the carapace from the PL eye; three dark brown stripes radiate from the fovea, but these do not reach the margin, the most posterior one is broad and wedge-shaped; paturon dark brown to black, the anterior surface with a buff coloured stripe reaching from the base to about 2/3 distance to the fang; fang black; labium, maxillae, sternum and ventral surface of coxae black-brown. Abdomen dark brown above becoming light brown on the sides; a wide pale brown to fawn (white in life?) longitudinal stripe, rounded anteriorly, pointed posteriorly, extends from the anterior dorsal surface to just before the spinnerets, and encloses a dark brown hastate stripe anteriorly, so that is appears to be a loop-like pale fawn marking; venter black, the anterior part extending up the sides of the abdomen where it is clearly outlined with pale brown. Legs dark brown, the ventral surface and lower sides of the femora pale brown to fawn; the ventral tips of the tibiae of the fourth legs fawn. The holotype is illustrated in Figure 1a–c (a photograph of a female is provided by Musgrave, 1930, p. 103).

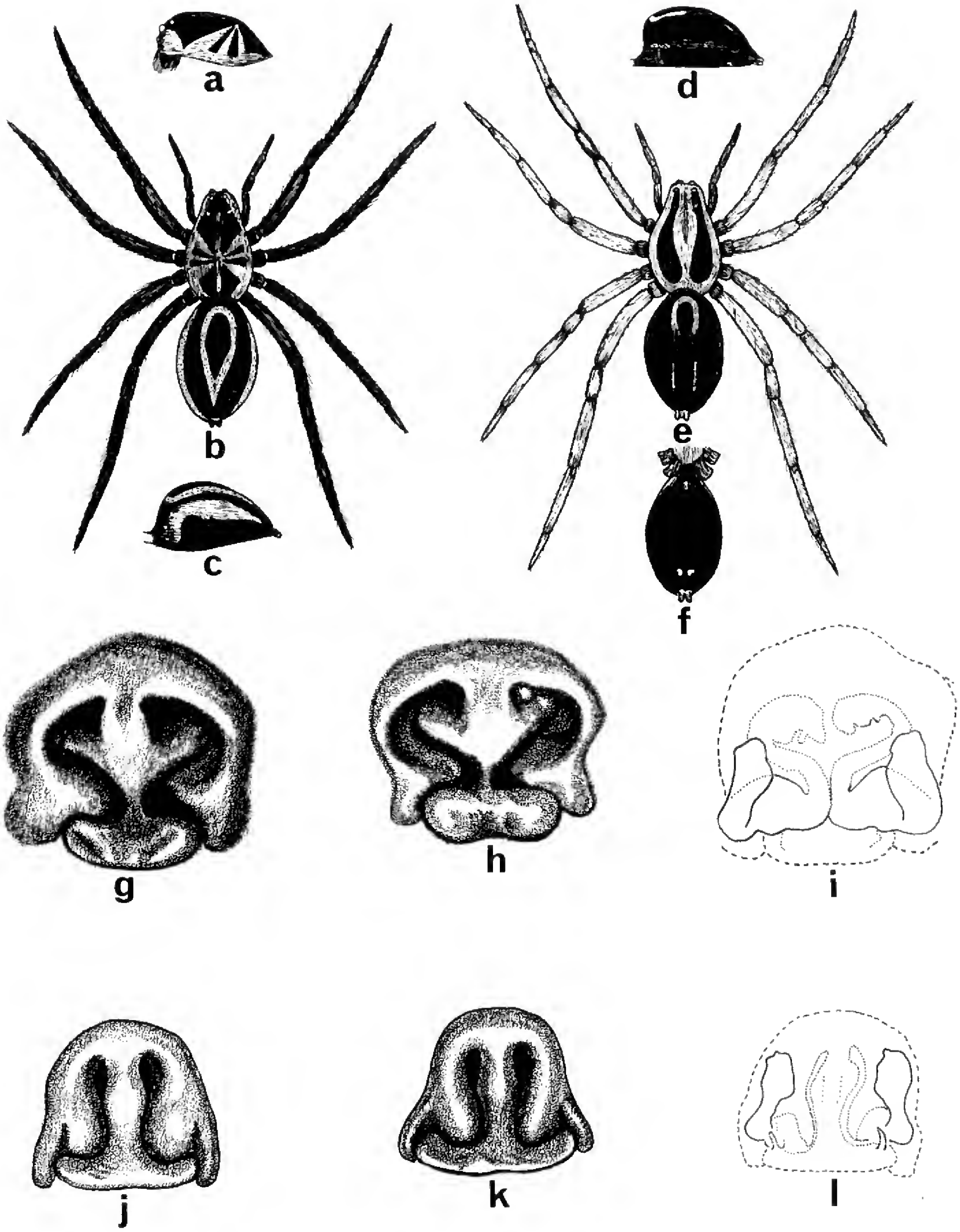

FIG. 1: a–c, g–i, *Lycosa summa*. a, lateral view of carapace; b, holotype; c, lateral view of abdomen; g, epigynum of holotype; h, epigynum of AM K61668; i, internal genitalia of AM K61668.

d–f, j–l, *Lycosa kosciuskoensis*. d, lateral view of abdomen; e, holotype; f, ventral surface of abdomen of AM K61673; j, epigynum of holotype; k, epigynum of paratype AM K61675; l, internal genitalia of AM K61675.

Anterior row of eyes very slightly procurved, AM about the same diameter as AL, PM little more than twice the diameter of the AM, and 2·3 of their diameter apart. Ratio of eyes AM:AL:PM:PL = 11:11:24:20; distance AM:AM 7, AM:AL 4, AM:PM 11, AL:PM 11, PM:PM 16. Clypeus to AM 20. Length of first eye row 61; length of second eye row 60.

Cheliceral with three promarginal teeth, the middle one largest and joined to the base of the outer tooth; three retromarginal teeth of equal size. Labium as broad as long.

TABLE 1: Measurements of Leg Segments of *L. summa* in mm.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	6·9	3·3	5·3	5·5	3·2
2	6·2	3·1	4·5	5·1	3·1
3	5·7	3·1	3·5	4·5	2·8
4	7·0	3·2	5·2	6·6	3·4
Palp	3·9	1·8	2·2	—	3·0

Variation: Penultimate males have the same colour pattern as the female. The epigynum of the holotype, and the epigynum and internal genitalia of a paratype is illusrated (Fig. 1g–i). The eye diameters and interspaces of the holotype and eight paratypes are given as a per cent of the total width of the first row of eyes in Table 2.

TABLE 2: Eye Diameters and Interspaces of *L. summa* Converted to Percent of the Total Width of the First Row of Eyes

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
Holotype	♀ M	10·7	18	18	39	33	11	7	26	18	18
K61669	♀ M	10·0	18	18	40	35	12	6	25	14	15
K61669	♂ P	7·6	18	18	38	32	12	7	30	18	18
K61667	♀ M	10·6	18	18	40	34	13	6	27	16	18
K61667	♀ P	8·9	18	19	40	33	13	8	26	18	18
K61670	♀ P	8·9	18	18	41	32	9	7	25	15	16
K61670	♀ J	6·3	19	19	39	33	13	7	29	16	15
K61671	♀ M	10·3	18	17	37	33	14	9	29	18	19
K61668	♀ M	9·8	19	17	38	35	12	7	26	18	19

The first row of eyes usually shorter than the second row, the ratio's for the holotype and paratypes are 61:60, 60:61, 50:50, 62:64, 54:56, 88:89, 69:70, 100:100, 95:96.

Size Range: Mature females C.L. 8·9 to 10·7 mm.

Diagnosis: *Lycosa summa* is similar to *Venatrix fuscus*, but differs in having a loop-like fawn or white marking on the dorsal surface of the abdomen, and no white longitudinal markings on the venter. The epigynum is of similar shape in possessing an expanded mid-section of the median guide, but the transverse guide is shorter than in *V. fuscus*. The penultimate male of *L. summa* has the loop-like fawn markings on the dorsum of the abdomen as in the female; *V. fuscus* males have a wide fawn bar that extends from the anterior dorsal surface of the abdomen and narrows to reach the spinnerets.

LIFE HISTORY

Mature females and penultimate males were collected in January, and one mature female in February. This species, as in *Lycosa kosciuskoensis*, presumably overwinters beneath the snow in the alpine regions of Mount Kosciusko.

BURROW

The specimens found among the snow grass on the sides of Mount Kosciusko, were dug from '. . . a simple hole in the ground sometimes surmounted by a turret' (Musgrave, 1930, p. 104, and on label with specimens).

DISCUSSION

Lycosa summa keys down to the genus *Venatrix* (type species *V. fuscus*) using Guy (1966), but differs in having the AM:AM larger than AM:AL, and in having the first row of eyes shorter than the second in some specimens. Those specimens with the first eye row shorter than the second would key down to *Orinocosa* as does *Lycosa kosciuskoensis*. I have placed my new species into the genus *Lycosa* pending a generic revision of the Australian Lycosinae.

DERIVATION

From the latin *summus* meaning highest or uppermost.

Lycosa kosciuskoensis sp. nov.
(Figure 1d, f, j–l)

MATERIAL EXAMINED

HOLOTYPE: Australian Museum AM K61675, ♀ M, C.L. 8·7 mm, near Lake Albina, Mount Kosiusko, N.S.W., collected by A. Musgrave, 6 January, 1929. In spirit.

PARATYPES: Mount Kosciusko; 7000 feet (2140 m), A. Musgrave, H. O. Fletcher, 7.i.1929, 1 ♀ M, AM K61691, 1 ♀ M, AM K61672, 3 ♀ M, AM K61674; near Lake Albina, A. Musgrave, 6.i.1929, 1 ♀ M, AM K61675: 7000 feet (2140 m), H. O. Fletcher, 7.ii.1929, 2 ♀ J, AM K61676; Summit 7328 feet (2235 m), A. Musgrave, H. O. Fletcher, 7.i.1929, 3 ♀ M, 2 ♀ P, AM K61673; near Lake Cootapatamba, H. O. Fletcher, A. Musgrave, 7.i.1929, 1J, AM K61680.

DESCRIPTION

Based on holotype.

Carapace dark brown with a well defined fawn to pale brown marginal band extending around the edge of the carapace and joining a wide fawn to pale brown longitudinal stripe that commences behind the PM eyes, extends between the PL eyes, and broadens noticeably to about the middle of the carapace where it tapers slightly to join the lateral band; some wedge shaped darker brown markings radiate across the sides at the middle of the carapace; paturon black with the anterior surface orange; lateral condyle dark brown; fangs black; labium and maxillae black; sternum and ventral surface of coxae dark brown to black. Abdomen brown above and on sides, but separated from the black venter by a pale fawn line; anterior slope of the abdomen darker brown with a very distinct narrow, hastate, dark brown longitudinal spot surrounded by a narrow fawn band that becomes somewhat diffuse posteriorly; more posteriorly on the dorsal surface are two distinct brown-edged cream parallel lines not quite reaching the spinnerets; venter jet black with two cream to pale yellowish dots located before the spinnerets (Fig. 1f). Legs brown, darker below, the femoral and metatarsal joints light brown, spines black.

Anterior row of eyes gently procurved, only slightly shorter than the second row, AM slightly larger than AL, PM about twice the diameter of the AM and two thirds their diameter apart. Ratio of eyes AM:AL:PM:PL = 10·7:9:21:18; distance AM:AM 4, AM:AL 3, AM:PM 8, AL:PM 9, PM:PM 14. Clypeus to AM 10. Length of first eye row 52; length of second eye row 55.

Chelicerae with three promarginal teeth, the middle one much larger than the minute laterals; three retromarginal teeth, the inner two larger than the reduced lateral. Labium about as wide as long.

TABLE 3: MEASUREMENTS OF LEG SEGMENTS OF *L. kosciuskoensis* IN MM.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5·8	3·3	4·2	4·1	2·5
2	5·5	3·0	3·8	3·8	2·7
3	4·9	2·9	3·2	4·4	2·9
4	6·5	3·3	5·0	6·5	3·1
Palp	3·2	1·9	1·8	—	2·2

The second right leg (not measured) is a replacement leg in the holotype.

VARIATION: The holotype has indistinct dark radiating wedge-shaped areas on the dark brown sides of the carapace, which disappear when the hair on the carapace dries; it is not known if these wedge-shaped marks are present in life. Two juvenile specimens have the adult coloration as described above, except that the venter has two tapering, parallel, yellowish bars from about the middle of the venter to near the spinnerets. The epigynum of the holotype and the epigynum and internal genitalia of a paratype is illustrated (Fig. 1j–l). The eye diameters and interspaces of eight paratypes are given as a per cent of the total width of the first row of eyes in Table 4. First row of eyes shorter than the second row in the ratio 56:57, 58:62, 56:61, 57:62, 47:51, 57:61, 55:58, 49:53.

SIZE RANGE: Mature females C.L. 8·1 to 9·9 mm.

DIAGNOSIS: *Lycosa kosciuskoensis* most clearly resembles *Lycosa summa* but lacks the expanded mid-section of the median guide of the epigynum, and has a different coloration. The longitudinal stripe on the carapace is conspicuously wider than in *L. summa*;

TABLE 4: Eye Diameters and Interspaces of *L. kosciuskoensis* Converted to Percent of the Total Width of the First Row of Eyes

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
K61676	♀ M	8·7	21	20	41	34..	7	4	25	14	11
K61673	♀ M	9·2	21	19	41	36	7	5	26	12	12
K61673	♀ M	9·3	21	19	43	36	8	6	25	14	12
K61673	♀ M	9·1	21	19	39	35	9	5	28	16	14
K61673	♀ P	7·7	21	19	45	38	7	6	25	14	15
K61674	♀ M	9·3	21	19	42	35	9	6	28	14	14
K61674	♀ M	9·0	20	20	42	35	7	6	25	16	16
K61674	♀ M	8·1	21	20	45	37	9	6	27	16	16

the loop-like pale marking on the dorsum of the abdomen is faint or indistinct posteriorly, and is followed by two narrow white parallel bars; the venter has two small white spots just before the spinnerets. *Venatrix fuscus* is a morphologically similar species but lacks the pale loop-like markings and parallel white bars on the dorsal surface of the abdomen, and has two parallel or converging white bars on the venter (as does *L. kosciuskoensis* juveniles) in adult females. The epigynum of *V. fuscus* differs from *L. kosciuskoensis* in possessing an expanded mid-section of the median guide.

Life History

Mature females were collected in January and February. One specimen AM K61672, C.L. 8·8 mm, ♀ M, had an egg cocoon measuring approximately 13 mm in diameter. Males were not collected.

Burrow

Musgrave (1930, p. 104) records this spider as 'making a tunnel and covering the opening with a web or else living under stones.' A further note included with the specimen states 'Makes nests with funnel of web at mouth opening of burrow or else simple depression in earth under a rock'.

Discussion

Lycosa kosciuskoensis falls within the genus *Orinocosa* as defined by Guy (1966). Chamberlin (1961, pp. 290–1) separates his genus *Orinocosa* from *Lycosa*, and related genera, due to the presence of the steeply sloping sides of the carapace, and the presence of stout median dorsal spines on the posterior tibiae. *Lycosa kosciuskoensis* has a carapace with gently sloping sides, lacks stout median apical spines on the dorsal surface of the posterior tibiae and the eyes differ in dimensions from that of the type species *Orinocosa aymara*. I therefore place my new species in the genus *Lycosa* pending a full generic revision of the Australian Lycosinae.

I believe that *Lycosa kosciuskoensis*, *Lycosa summa*, and *Venatrix fuscus* are closely related species despite some minor differences in the arrangement of the eyes. All can be montane species as the National Museum, Victoria, has specimens of *Venatrix fuscus* from 6,000 feet (1830 m) at Mt. Hotham, in addition to a number of records from localities of much lower altitude in Victoria and Tasmania. These three species may represent a natural grouping if the mature males of *L. kosciuskoensis* and *L. summa* have a distinct tubercle on the outer edge of the fang as do the mature males of *Venatrix fuscus*. Further collecting in the alpine areas of southeastern Australia may clarify the relationship between these three species.

Lycosa musgravei sp. nov.

(Figure 2a–c)

MATERIAL EXAMINED

HOLOTYPE: Australian Museum, AM KS23, ♀ M, C.L. 13·4 mm, Mount Kosciusko, N.S.W., collected by L. Voysey, 30 January, 1966, and donated by R. Mascord. Epigynum removed but retained with holotype. In spirit.

DESCRIPTION

Based on the holotype.

Carapace dark brown with a very narrow pale fawn longitudinal stripe extending from the light brown area within the ocular quadrangle to the posterior slope where it merges with the light brown marginal hand; four dark edged fawn stripes radiate from the middle of the carapace, the anterior-most stripe curved forward to below the PL eyes; paturon dark brown ventrally, mid-brown enteriorly; fang dark brown; labium, maxillae, sternum and ventral surface of coxae dark brown. Abdomen dark brown above, darker on the sides, and black-brown on the ventral surface; black rounded wedge-shaped spot with elongated posterior corners lies in a paler brown area on the anterior dorsal surface of the abdomen, this spot is followed by five light brown chevrons. Legs brown above, orange-brown below, becoming darker brown distally; the femora with the distal ventral tip devoid of hair and ash-grey to black in colour.

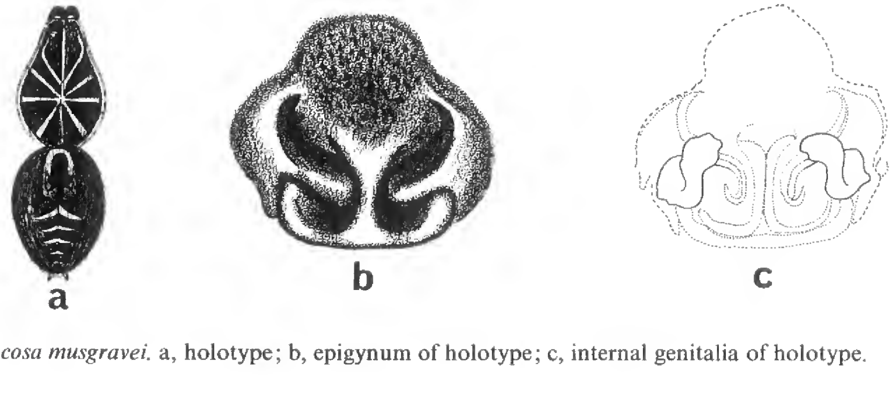

FIG. 2: *Lycosa musgravei*. a, holotype; b, epigynum of holotype; c, internal genitalia of holotype.

Anterior row of eyes slightly procurved, AM about the same diameter as AL, PM more than twice the diameter of the AM, and about 2/3 of their diameter apart. Ratio of eyes AM:AL:PM:PL = 15:13:34:29, distance AM:AM 7, AM:AL 6, AM:PM 15, AL:PM 12, PM:PM 23. Clypeus to AM about 25. Length of first rye row 74; length of second eye row 85. Chelicerae with three promarginal teeth, the middle one largest and joined to the base of the outer tooth; three retromarginal teeth of equal size. Labium a little longer than broad.

TABLE 5: MEASUREMENTS OF LEG SEGMENTS OF *L. musgravei* IN MM.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	9·5	4·9	7·0	6·7	3·9
2	8·8	4·7	6·0	6·5	3·9
3	7·8	4·1	5·3	6·3	3·7
4	9·9	4·5	7·7	9·1	4·3
Palp	4·9	2·2	2·6	—	3·3

Epigynum broader than the width of the anterior row of eyes but not as broad as the second row; the median guide broadens anteriorly into a low flat plate, and the transverse guide has the extremeties curved anteriorly (Fig. 2b). The internal genitalia is illustrated in Figure 2c.

DIAGNOSIS: *Lycosa musgravei* is similar in coloration to *Lycosa godeffroyi* but may be distinguished from the latter species by the shape of the epigynum; the transverse guide is wide with the ends curved anteriorly.

DISCUSSION

This new species is known from the holotype only. No information is available on the life history, burrow, habitat and altitude range. The epigynum appears to be distinctive and differs from all specimens of *Lycosa godeffroyi* examined by me. Further collecting is necessary to establish the degree of variation encountered within the species, and to describe the male palpal organ.

DERIVATION

Named in honour of Mr Anthony Musgrave, Curator of Insects and Arachnids at the Australian Museum, 1920–59, who collected the first lycosids from Mount Kosciusko, and published a number of papers on Australian spiders.

ACKNOWLEDGEMENTS

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APPARENT ASSOCIATION OF BONE AND CHARCOAL OF DIFFERENT ORIGIN AND AGE IN CAVE DEPOSITS

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ABSTRACT

It is pointed out that anomolies in the age of apparently associated organic materials in cave deposits are known. Experiments using a controlled laboratory situation are carried out which demonstrate that small skeletal elements differ in their ability to be transported by water, and charcoal is more mobile than all bone when transported by water. This could result in younger charcoal being associated with older bone. An analysis of materials from an actual cave situation confirms that some skeletal elements transport more readily than others. It also demonstrates that skeletal elements differ in durability. Other ways of producing anomolous associations of organic materials in cave deposits are discussed.

While carrying out paleontological excavations in caves in Western Australia, it became apparent that there were certain problems that might arise in interpreting doline and cave deposits. In particular, the selective nature of water transportation seemed a way in which anomolous associations of organic materials could occur. With this in mind a series of samples for radiocarbon dating was obtained from Horseshoe Cave on the Hampton Tableland of Western Australia. From one layer, a sample of small mammal bones and a sample of small charcoal pieces were submitted for radiometric dating. The date for the charcoal (Gak 3474) was 890 ± 300 years B.P. and the date for the bone (Gak 3814) was 5630 ± 120 years B.P. Many such anomolous radiometric dates are known from other cave excavations (e.g. Wright, 1971).

The effects of water transportation have been discussed in general terms (e.g. Krumbein and Sloss, 1963; Hjulstrom, 1939; Twenhofel, 1950) and in relation to the particular problem of selective transportation of organic materials (e.g. Leidy, 1869; Henshaw, 1942; Voorhies, 1969). Problems of sediment transportation, applicable to doline and cave situations, have been considered (Jewell, 1963, 1966; Simpson, 1946; Brain, 1958; Frank, 1971; Jennings, 1971). However, little research has been attempted into the possible effects of water transportation on dolines and in caves in producing anomolous assemblages of organic detritus. Voorhies (1969) carried out horizontal stream table experiments using sheep-sized animals and demonstrated that certain skeletal elements were more readily transported by water than others. In the present study an attempt was made to examine the relative transportability of small mammal bones in an experimental situation that more closely approximated the cave situation.

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*This work was largely carried out at the Western Australian Museum.

Problems connected with radiometric dates have also been discussed (e.g. Dyck, 1967; Shotton, 1967; Gill, 1971; Polach and Golson, 1966; Stuckenrath, 1965). These problems are either those involved with the radiometric methods themselves or those arising from a misunderstanding of how a radiocarbon sample relates to the event studied. In the present study, problems of the second sort are discussed in relation to the cave situation.

Caves mentioned in this paper are in Western Australia unless otherwise stated. Cave names used are given with the code designation of the Western Australian Speleological Group (pers. com. Mr P. J. Bridge). The mammal taxonomy is that used by Ride (1970). Representative specimens of taxa discussed are lodged with the Queensland Museum.

MOBILITY TESTS

THE SLUICE

A sluice 2·4 metres in length by 0·24 metres in width was covered with sheets of grade S2 glasspaper. The sluice was inclined at an angle of approximately 30 degrees to the horizontal. A perforated rubber hose was fixed across the top of the sluice. Murid (*Mus musculus* to *Rattus fuscipes* in size) and dasyurid (*Sminthopsis murina* to *Dasycercus cristicauda* in size) bones (Plate 1) of known average weights (Table 1) from a Quaternary owl pellet deposit collected from Brown Bone Cave SH17 and charcoal pieces of known weights from *Eucalyptus* and *Banksia* trees were used. All of the charcoal used had a visual-estimate sphericity rating of about 0·7 to 0·9 and a roundness rating of 0·1 to 0·3 (Krumbein and Sloss, 1963).

TABLE 1: AVERAGE WEIGHT AND VISUAL ESTIMATES OF SPHERICITY* AND ROUNDNESS* FOR SELECTED MURID (m) AND DASYURID (d) SKELETAL ELEMENTS.

Skeletal element	Weight (grams)	Sphericity	Roundness
scapula (m+d)	0·04	<0·3	<0·1
ulna (m+d)	0·04	<0·3	0·7
maxilla (d)	0·04	<0·3	<0·1
occipital (m)	0·05	<0·3	<0·1
bulla and periotic unit (m)	0·06	0·7	0·7
humerus (m+d)	0·06	0·3	0·7
dentary (d)	0·07	<0·3	0·4
pelvis (m+d)	0·08	<0·3	0·6
tibia (m+d)	0·10	<0·3	0·7
femur (m+d)	0·11	<0·3	0·9
dentary (m)	0·16	<0·3	0·4
rostrum (m)	0·40	<0·3	<0·1

*Figures for roundness are based on the cross-section of the long axis of the objects. Figures for sphericity are based on overall shape.

This experimental situation involved only variables directly involving water transportation. In the natural situation where organic detritus accumulates near a cave entrance and gets washed down onto the cave floor, many other variables are involved. These include among others slope stability, regularity, texture, vegetation, capacity and competence of the transporting water.

TEST 1. MOBILITY OF DIFFERENT BONES IN A WATER FILM

The first test attempted to determine if the different bones used were differentially mobile in water under constant conditions of slope, water velocity and substrate. Ten individual bones of 12 different types (such as femurs, pelves etc.) were mixed and placed 10 cm from the top of the sluice. Water was squirted from the perforated hose across the top of the sluice producing water velocities of about 0·8 m per second. The water moved down the slope in a sheet about 2 to 5 mm deep. As soon as the glass paper on the sluice became wet it wrinkled producing a rippled surface with crests and troughs transverse to the long axis of the sluice. The crests and troughs exhibited a slope relief of less than 10 mm. The flow of water was stopped when by visual estimate one quarter to one half of the objects had been washed clear of the sluice. The actual number of individual bones of each type that washed clear of the sluice was then recorded. The same test, using the same bones, was run ten times. The percentage that each bone type represented among all the bones washed clear of the slope is shown in Table 2.

TABLE 2: THE SUSCEPTIBILITY TO WATER TRANSPORTATION (ST)*.

Skeletal element	ST
bulla and periotic unit (m)	0·19
occipital (fused supra-, para- and basiocciptal) (m)	0·14
maxilla (d)	0·13
dentary (m)	0·11
dentary (d)	0·08
humerus (m + d)	0·07
ulna (m + d)	0·07
scapula (m + d)	0·07
tibia (m + d)	0·05
rostra (united L and R maxilla and premaxilla) (m)	0·05
femur (m + d)	0·04
pelvis (single fused ilium, ischium and pubis) (m + d)	0·01

* This was determined from the results of Test 1 by dividing the number of a particular type of bone that washed clear of the sluice by the total number of all bones that washed clear of the sluice.

During Test 1, the bulla and periotic units rolled down the sluice so readily that a slope angle of 30 degrees was found to be the steepest angle that would permit them to remain in place until the water was used. This determined the angle of the sluice for all future experiments. Certain bones such as murid dentaries, scapulas, occipitals and dasyurid maxillas possess a broad smooth surface on one or more faces. These enabled objects to float on the surface of the water probably by virtue of surface tension. However, some elements with flat surfaces also have irregularities on other surfaces such as spinous processes on scapulas and angular processes on dasyurid dentaries (Plate 1). As a result these objects were sometimes anchored by the projection sufficiently long enough for them to become oriented in a manner that stopped downslope progress. For the dasyurid dentary this position was with the anterior end pointing upstream, and the angle and tip of the coronoid process contacting the substrate and pointing downstream (Fig. 1). Other objects with fewer large flat surfaces achieved a stable orientation on the sluice relatively early in each trial. For example pelves quickly stabilized generally with the acetabulum up and the ilium pointing upstream. Similarly tibias stabilized with the distal epiphysis pointing upstream.

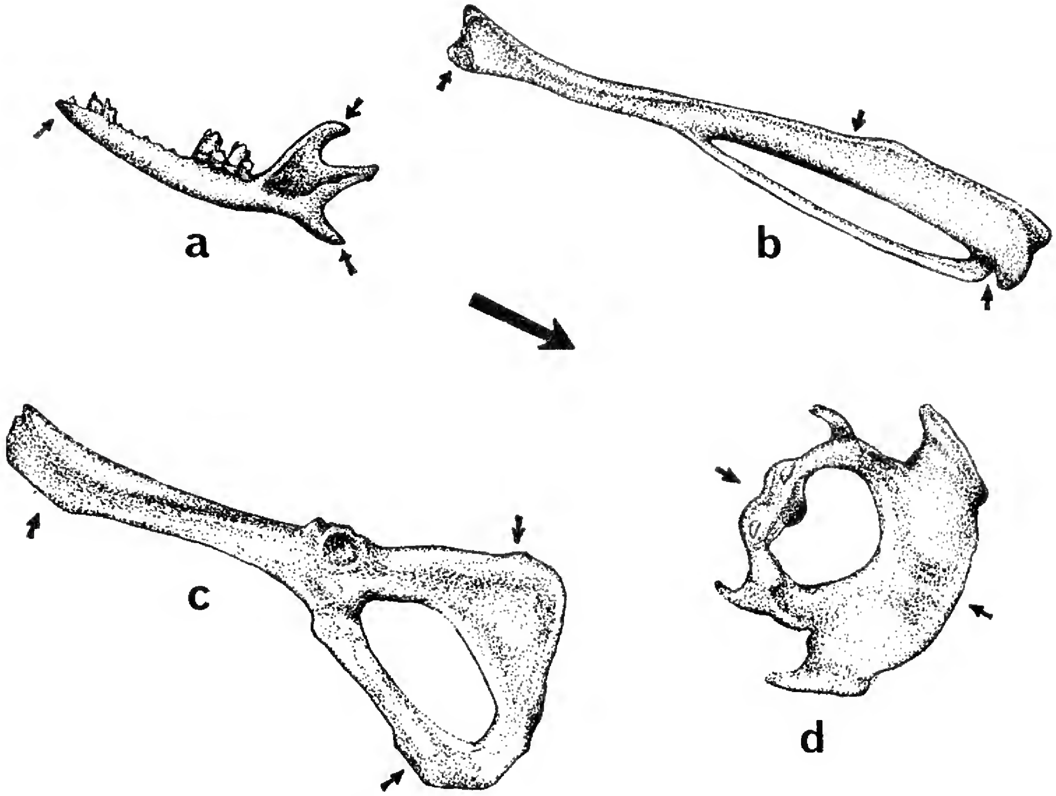

FIG. 1: Stable orientation for four skeletal elements observed during the sluice test trials: a, dasyurid dentary; b, murid tibia (and fibula); c, murid pelvis; d, murid occipital (basi-, para- and supraoccipital). The large arrow indicates the current direction and angle of the sluice. The small arrows indicate points of contact between the bone and the sluice surface.

TEST 2. RELATIVE MOBILITIES OF BONES AND CHARCOAL PIECES

The second test was carried out to determine if charcoal was transported by water more readily than bone (under constant conditions of slope, water velocity and substrate). Samples of particular bones and charcoal pieces, matched by weight, were placed 10 cm from the top of the sluice. For example one sample consisted of 50 tibias of average weight 0·1 gm and 50 charcoal pieces of average weight 0·1 gm. Another sample consisted of 50 dasyurid dentaries of average weight 0·07 gm and 50 charcoal pieces of average weight 0·07 gm. Twelve trials were run, each involving a different type of bone. The sluicing was carried out in the same manner as described above for the first test, except that only two trials were run for each type of bone, and the length of time for running each trial was not necessarily the same as that for each trial in the first test. The results of Test 2 are given in Table 3. In each case, a greater percentage of charcoal reached the bottom of the sluice than the skeletal element of the same weight.

TABLE 3: SUSCEPTIBILITY TO WATER TRANSPORTATION OF CHARCOAL AND BONE PIECES OF SIMILAR WEIGHTS

Skeletal element	Percentage of charcoal pieces reaching bottom of sluice	Percentage of bone pieces reaching bottom of sluice	Mean weight of charcoal and bone pieces (g)
bulla + periotic (m)	57	56	0·06
occipital (m)	80	36	0·05
dentary (m)	52	20	0·16
dentary (d)	36	12	0·07
scapula (m + d)	50	11	0·04
maxilla (d)	74	11	0·04
ulna (m + d)	54	5	0·04
femur (m + d)	33	1	0·11
humerus (m + d)	40	1	0·06
tibia (m + d)	63	1	0·10
pelvis (m + d)	65	0	0·08
rostra (m)	52	0	0·40

TEST 3. BONE FLOATATION

Although the water was too shallow for some of the bones to float in either test, the ability of small bones to float was tested in another way. Samples of bone types were tipped into a container full of fresh water. Each object that floated was tapped below the surface

TABLE 4: PERCENTAGE OF INDIVIDUAL BONES CAPABLE OF FLOATING, OR PARTLY FLOATING IN WATER.

Skeletal element	% float	% partly float (as described)	
sacrum (m)	28	0	
tibia (m + d)	15	9	proximal end floats
pelvis (m + d)	23	6	ilium floats
femur (m + d)	39	6	either end floats
humerus (m + d)	18	8	proximal end floats
periotic (m)	66	30	air bubble trapped in inner ear
premaxilla (m)	3	1	air bubble trapped in alveolus

to eliminate from the count any that were suspended by surface tension alone. Some bones were found to partly float, that is to have one end contacting the bottom and the other end waving free in the water. The results of these trials are shown in Table 4. Other types of bones tested did not float at all. In practice, the water on the sluice was not deep enough to take full advantage of floating bones. However, the ability to float may have helped some bones achieve a higher mobility rating (Table 2) in Test 1. Charcoal also floats and this undoubtedly helped the charcoal in Test 2 to consistantly surpass equal weighted bones in slope mobility (Table 3).

EXAMINATION OF BONE ACCUMULATIONS IN A CAVE SITUATION

The sluice test results demonstrate that differential transportation of organic materials by water can occur. It remains to be demonstrated however that differential transportation also takes place under natural conditions. In a doline and cave situation, there may be large slope irregularities, a loose soil substrate which washes downslope with the bone or ensnares and restricts the movement of bone, and water flow of varied speed and character. Field studies accordingly have been made.

Brown Bone Cave (SH 17)

Brown Bone Cave (SH 17), about 170 km north of Perth, has an owl roost on the wall about half way up the wall of its doline. Immediately beneath this roost are piles of small mammal bones, representing prey which the owls have eaten. Owls regurgitate pellets containing the indigestible parts of their meals, including mammal fur and bone. Virtually complete skeletons of thousands of small mammals have been accumulating beneath the roost in Brown Bone Cave. The bone deposit extends downslope from the roost, forming a carpet of progressively diminishing size as it approaches the base of the doline rubble pile. Most of the bone has disappeared into the rubble pile near its base. An intermittent stream (the Namban River) emerges from the base of the rubble pile and proceeds into Brown Bone Cave proper. Small mammal bones are abundant in the channel gravels and may be found in the stream bed and stream deposits as far into the cave as it is possible to crawl before a pool of water makes further progress difficult. Samples of this bone-bearing deposit were taken from beneath the roost on the doline rubble pile and from the stream bed about 75 m downstream from the owl roost. These samples were placed in linen bags and taken to Perth where part of the samples were sorted and counted. Some damage to fragile bones such as scapulas probably occurred during transport. This is discussed below.

The number and percentages of each skeletal type from the doline rubble pile and the stream channel samples are listed in Table 5. The most common skeletal element in both samples were murid dentaries.

For the purposes of the present study, the assumption has been made that the bone present in the stream channel sample was derived in large part from owl pellet piles on the doline rubble pile. There are only two other general areas where owls might have accumulated the bones now found in the stream channel sample. They might have roosted along the downstream section of Brown Bone Cave proper or farther upstream in areas now covered by the rock fall that produced the doline rubble pile. If the latter, the stream channel sample would still represent a sample transported some distance from the point of initial accumulation. On the other hand, if owls roosted along the downstream section in Brown Bone Cave, near the area from which the stream channel sample was collected, water transportation might not have played such an important part in the history of the deposit. However, it seems unlikely that bone was accumulated in the downstream area because there are no obvious owl roosts visible, no owl pellet piles are present (although the stream could have removed them) and the downstream area extends into the totally dark area of the cave, a situation not known to be suitable for owl habitation. In view of the fact that bone from the owl pellet piles on the doline rubble slope occurs near the base of the rubble pile and the point of emergence beneath the rubble pile of the Namban River, the simplest conclusion would seem to be that the bone on the rubble pile is the source of the bone in the channel deposit.

There are two species represented in the stream channel bone (the domestic dog, *Canis familiaris*, and the large Western Grey Kangaroo, *Macropus fuliginosus*) that are not represented in the doline owl pellet piles. Other species which have so far been identified are represented in both deposits. The species which are represented in the stream channel deposit and not the doline deposit may have walked, fallen or been carried into the cave. They do not effect the bone counts since only small mammal bones were involved in the analyses.

TABLE 5: DISTRIBUTION OF SKELETAL ELEMENT TYPES IN BROWN BONE CAVE.

Skeletal element	Rubble pile		Stream channel		Change in % of total
	No.	% of total	No.	% of total	
maxilla (m)	84	8	162	17	× 2·1
dentary (m)	145	13	219	23	× 1·8
half rostrum (m)*[1]	5	1	7	1	× 1·0
premaxilla (m)	75	7	104	11	× 1·6
occipital (m)*[2]	6	1	8	1	× 1·0
tibia (m + d)	127	12	133	14	× 1·2
periotic (m)*[3]	30	3	42	5	× 1·7
dentary (d)	27	3	26	3	× 1·0
sacrum (m + d)	18	2	18	2	× 1·0
pelvis (m + d)*[4]	88	8	38	4	× 0·5
ulna (m + d)	145	14	64	7	× 0·5
humerus (m + d)	142	13	56	6	× 0.5
scapula (m + d)	54	5	15	2	× 0·4
maxilla (d)	26	2	6	1	× 0·5
femur (m + d)	109	10	39	4	× 0·4
rostrum (m)*[5]	4	0·4	0	0	× 0·0

*[1] The half rostrum includes one premaxilla and one maxilla;

*[2] the occipital includes fused basi-, para- and supraocciptals;

*[3] the periotic has no bulla attached;

*[4] the pelvis includes only one fused ilium, ischium and pubis;

*[5] the rostrum is a unit that includes paired left and right maxilla and premaxilla.

It is obvious from the numbers of each skeletal type present in the doline sample (Table 5) that there had been some selectivity by the time the bone had reached the locus of the doline rubble pile sample. For example the murid occipital and scapula proportionate numbers are low. On the other hand the premaxilla, maxilla, dentary, humerus, ulna, pelvis, femur, and tibia proportionate numbers are all relatively high. It seems likely, and this is supported by the data presented in Table 4, that the doline rubble pile bone sample is much better representative of whole skeletons than is the stream channel bone sample. In the stream channel sample, although the maxilla is a proportionately more common element than the maxilla in the doline sample, most of the other skeletal elements are represented by lower proportionate figures. Because this apparent reduction in representation is by no means identical for all skeletal element types, it is probable that the processes of transportation involved have been selective. This will be discussed below.

TABLE 6: PERCENTAGE OF DAMAGED BONES OF VARIOUS SKELETAL TYPES FROM BROWN BONE CAVE

Skeletal element	Rubble pile	Stream channel	Criterion for damage
scapula (m + d)	93%	73%	outline incomplete
maxilla (d)	50%	50%	facial wing broken
dentary (d)	48%	74%	angular process broken
maxilla (m)	26%	43%	maxillary plate damaged
dentary (m)	18%	37%	less than half complete
occipital (m)	33%	75%	outline incomplete
humerus (r + d)	15%	30%	one or more ends broken
ulna (m + d)	36%	45%	one or more ends broken
tibia (m + d)	26%	46%	one or more ends broken
pelvis (m + d)	50%	76%	ischium broken

BONE DAMAGE: A damage analysis was also made of the two samples from Brown Bone Cave. Using certain criteria for each type of bone, every bone specimen was scored as damaged or not damaged. The percentages of damaged specimens and criteria for determining a damaged condition of each bone type from both samples are presented in Table 6. It is clear that almost all the bone from the stream channel sample exhibits more damage than the bone from the doline sample. This damage or attrition may be interpreted as a function of the distance of transportation.

ABRAKURRIE CAVE (N3)

This very large cave on the Western Australian Nullarbor has a side chamber whose floor is thick with damp organic detritus, largely plant, and whose walls bear the evidence of flooding to heights of two metres and more above the present floor level. It is possible that the surface organic material might have been representative of more than one episode of introduction by floods. After the organic material introduced during one flood dried it could be floated, mixed and re-deposited with the organic detritus of the next flood. Pieces of wood from the damp organic layer in this chamber were removed in polythene bags and two days later tipped into a dish of water. After seventy-two hours the wood was still floating. This suggests that the sticks in the chamber of Abrakurrie Cave would in fact float if the chamber filled with water. This process might effect bone as well since, as has been demonstrated above, some bone floats. There is therefore a possibility that a particular organic fragment could be continually maintained at the surface of the deposit throughout the cave's history of detritus accumulation. This is a distinct sort of selective transportation by water that may result in a difference between the association of organic materials found in a deposit and those found around the cave.

DISCUSSION

Both the sluice tests, as well as the Brown Bone Cave samples, demonstrate that selective transportation of organic materials by water may occur.

The first test demonstrates that different skeletal elements are differentially susceptible to water transportation. The skeletal elements could be grouped into three categories according to their relative susceptibility to water transportation (see Table 2):

GROUP 1 (easily transported)	GROUP 2 (intermediate)	GROUP 3 (difficult to transport)
bulla and periotic (m)	dentary (d)	pelvis (m+d)
occipital (m)	humerus (m+d)	femur (m+d)
maxilla (d)	ulna (m+d)	rostrum (m)
dentary (m)	scapula (m+d)	tibia (m+d)

The significance of this is that in a particular geological horizon in a cave deposit, a pelvis, for example might be on the average older than a murid dentary found in the same horizon. Voorhies (1969) reports on experiments with skeletal elements from sheep and coyotes using a stream table with water of varying depth. In the sluice tests reported in this paper, bones of rat-sized and smaller animals were used, and water depth on the sluice did not exceed 5 mm. As a result, Voorhies' (1969) results and the results reported in this paper are not directly comparable. Nevertheless, Voorhies' (1969) work demonstrates that the skeletal elements used in his tests are differentially mobile.

It was also noted during Test 1 reported above that some bones could assume orientations with respect to the current direction which frustrate further movement downslope (Fig. 1). It has been recognized (e.g. Twenhofel, 1950) that objects with one long axis, such as limb bones, may transport by traction as part of a stream's bed load until the long axis of the object is parallel to the direction of the stream current. The object may then cease to move. It may also be inclined upstream in such a way that turbulence beneath the object is reduced to a minimum. Voorhies (1969) shows that when water on a stream table is shallow and the bones are partly emergent, the stable orientation of the bone's long axis is transverse to the current direction. On the other hand, when the stream was deeper and the bones submerged, stable orientation of the long bones was parallel to the current direction. In the first test reported in this paper the water volume and velocity were not altered. As a result it is not clear what the stable orientations of small mammal long bones are under completely submerged conditions. It was noted above however, that under partly emergent conditions many of the small mammal bones exhibited a stable orientation which was parallel to the current (Fig. 1). It seems likely that under submerged conditions the stable orientation would remain parallel to the current.

The results of Test 2 (Table 3) reported above demonstrate that charcoal of particular weight is more easily transported than bone of the same weight. The significance of this in cave studies is that in a given sedimentary horizon in a cave deposit, the charcoal might be younger than the associated bone. How much younger would depend on actual transport rate differences and the geological aspects (e.g. angle of repose and length of the doline slope) pertinent to the particular situation being studied. In view of the general practice of using charcoal to date associated events or objects, this possible source of error should be examined in every doline and cave environment.

The results of Test 3 given above demonstrate that certain types of bone are capable of floating. The significance of this is that some bones may transport by water more readily than others. This ability may have given some bones, such as the periotics, an advantage in slope mobility during Test 1. Other bones which exhibit a tendency to float (Table 4) were not given a good chance to do so because of the shallowness of the water used on the sluice during the first test. In the field in Brown Bone Cave, water levels in the stream would become high enough to float bones. Voorhies (1969) states that in stream table experiments, both the sternum and the sacrum of sheep and coyotes float until they become water-logged. He suggests that this ability is the reason for these bones being relatively uncommon in concentrations of mammal bones.

The results of the damage analysis (Table 6) demonstrate another way in which selectivity can occur. For example, although the murid rostrum transported more readily than the murid pelvis in Test 1 (Table 2) there was a proportionately greater drop in the number of rostrums than pelves down the rubble pile and along the stream bed in Brown Bone Cave (Table 5). This apparent anomaly may be due to the effects of attrition. Complete rostrums were not present at all in the stream channel sample. Their fragility is obvious after having handled specimens from the doline pile sample. It is probable that the rostrums broke up during transportation (and this may in part account for the apparent increase down-stream, as shown in Table 5, of the murid maxillas, two of which partly compose each rostrum). In fact all bone types except the scapula and dasyurid maxilla showed evidence of increased attrition in the stream channel deposit (Table 6). The scapulas, which have paper thin edges, are so fragile that many of them may have been damaged while the bulk of the doline sample was transported back to the laboratory. This might account for the large number of damaged specimens from that sample. In the case of the dasyurid maxillas there are too few specimens (6) present in the stream channel sample to permit a reliable comparison. However, the proportionate reduction (85% shown in Table 5) in numbers of dasyurid maxillas is itself a suggestion that severe attrition effects this skeletal element. The same could be said of the scapulas which show a similar proportional reduction (82% shown in Table 5) in the stream channel sample.

In summary, there are various selective processes which may effect the relationships of organic materials during transportation and ultimately in doline and cave deposits. These processes include the ability of certain objects to be transported more easily by water, either by floating, skating on the water's surface, or simply by moving more easily as part of the traction load of flowing water. Of particular significance is the fact that charcoal transports more readily than bone. The results of the Brown Bone Cave analysis demonstrate that selective transportation does occur under natural conditions. As a result of the analysis of bone from Brown Bone Cave, it is clear that another significant factor in the selective nature of transportation is the extreme fragility of certain types of bone. These fragile elements may be under-represented in doline and cave deposits if transportation is involved.

It may be hard to decide in a particular situation which factor or factors are responsible for a disproportionate representation. For example, does a relative absence of small scapulas in a deposit indicate that they were floated past the site of the excavation or that they were thoroughly abraded and not available for deposition? When other aspects of selective accumulation are considered as well, does the relative absence of femurs in a deposit indicate that water competence was not great enough to transport them as far as the excavation site, or does it indicate that some predator removed the femurs before they could be available for transportation?

These are the sorts of problems of interpretation that are likely to arise as a result of excavations in caves. Each cave situation must be examined by the excavator with these potential problems in mind. It is important that every researcher should consider all aspects of any process that might effect the vertical and horizontal relationships of materials being studied and use these considerations to temper his conclusions.

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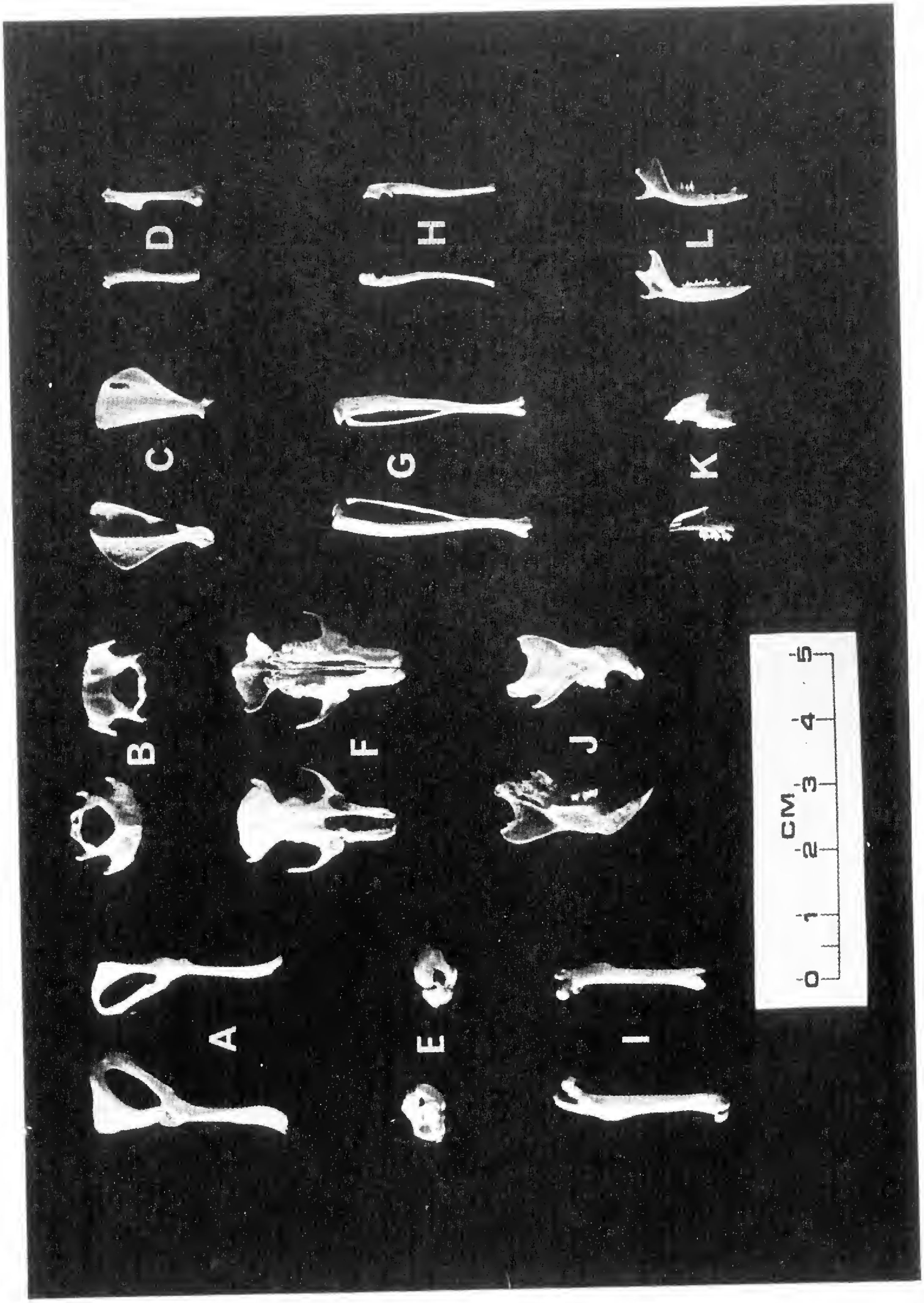
PLATE 1

Examples of the skeletal elements used in the sluice tests showing alternate profiles. A, murid pelvis; B, murid occipital; C, murid scapula; D, murid humerus; E, murid bulla and periotic unit; F, murid rostrum; G, murid tibia (and fibula); H, murid ulna; I, murid femur; J, murid dentary; K, dasyurid maxilla; L, dasyurid dentary.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Mem. Qd Mus. 17(1): 49–53. [1974]

THE STATUS OF *HYLA IRRORATA* DE VIS 1884 (ANURA: HYLIDAE)

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ABSTRACT

Opinions of the five authors who have commented on the status of *Hyla irrorata* are summarised and, following examination of the neotype and eleven specimens identified as *H. irrorata* by De Vis early in 1885, *H. irrorata* is synonymised with *Litoria caerulea* (White), 1790.

Hyla irrorata was described in a paper read on 8th August, 1884, from a series of specimens collected at Gympie in southeastern Queensland by Mr H. F. Wallman. In De Vis's original description the dorsum is described as 'lead blue to olive brown' (not or), and variation 'in young examples' is referred to (p. 129), so it seems reasonable to assume that De Vis had at least three specimens although only two sets of measurements are given in the description.

Eleven specimens (J12970–80) in the Queensland Museum collection were erroneously presumed to be De Vis's syntypes by Covacevich (1971, p. 53). These specimens were previously registered as collection 10, R 4826. Collection 10, in the 'Collection Register C1–C178 1884–1899' was made according to the register, by Mr H. F. Wallman in 1884 'during his geological investigations' at Gympie. The third entry in collection 10 is '*Hyla irrorata* De Vis 11'. The number R4826 accompanies this entry in different, apparently more recent, handwriting indicating registration of the eleven specimens in the 'General Catalogue 1887 (?)–1893 R1–R6219'. In this, R4826 refers to the same specimens—'*Hyla irrorata* De Vis 3, 8 Gympie'. This collection data agrees with that given by De Vis. Total lengths (= snout–vent length (S–V) after Tyler, 1968, p. 9) of these specimens are in mm:

J12870, 76·2; J12871, 54·8; J12872, 55·7; J12873, 69·2;
J12874, 52·5; J12875, 66·0; J12876, 72·3; J12877, 62·7;
J12878, 81·0; J12879, 72·7; J12880, 84·5.

The measurements are only approximate because of the brittle and shrunken condition of the specimens. They do not agree with the two sets given by De Vis (32 lines = 67·8 mm, 20 lines = 42·3 mm) although J12873 and J12875 are reasonably close to the first De Vis specimen measured. Other measurements given by De Vis have not been compared because it is impossible to determine where they were made.

This discrepancy in size and recently located correspondence between Wallman and the Director of the Queensland Museum on 6th January, 1885, cast doubt on the presumption, based on collection data, that these specimens are De Vis's syntypes although they were identified by him as *H. irrorata* apparently soon after he had described the species. The correspondence refers to a consignment of specimens and, read in conjunction with the 'Collection Register', shows that the eleven specimens were collected after De Vis described the species and could not be those on which the type description was based. As no trace of the original series can be found, the assumptions of Fry (1912, p. 100) and Copland (1962, p. 61) that the types were lost can now be confirmed.

THE STATUS OF HYLA IRRORATA

Five authors have commented on the status of *H. irrorata*. Their opinions, based solely on De Vis's description, are summarised below.

(i) Boulenger (1885, pp. 386–7) suggested 'comparison' with *H. infrataeniata* (= *H. infrafrenata* Günther, 1867, after Fry, 1912, p. 100.).

(ii) Fry (1912) examined 'what remain of Mr C. W. De Vis's typical specimens in the Queensland Museum' (p. 97). The *H. irrorata* type material was apparently not sent to him and he assumed it was lost (p. 100). He synonymised *H. irrorata* with *H. caerulea* rather than *H. infrafrenata* although he noted affinity with the latter, including De Vis's description of 'a short line, or series of spots, white' at the angle of the mouth in *H. irrorata*. This was regarded by Fry as characteristic of *H. infrafrenata* but not *H. caerulea*. He regarded colour pattern, position of the vomerine teeth, and distribution of the two species as important, and considered the apparent discrepancy in size of the finger discs as a probable *lapsus calami* by De Vis.

(iii) Loveridge (1935, pp. 39–40) agreed with Fry and treated both *H. irrorata* and *H. gilleni* Spencer, 1896 as synonyms of *H. caerulea*. *H. gilleni*, a central Australian form, has subsequently been reinstated as a subspecies, *H. caerulea gilleni*, by Copland (1957, pp. 30–31) and Mertens (1964, pp. 15–21, pls. 1–2). The 'short line, or series of spots, white' which confused Fry was present in several of Loveridge's specimens. The discrepancy in size of the finger discs was also noted by Loveridge.

(iv) Copland (1962, p. 261) followed Fry's assumption regarding the loss of the type series of *H. irrorata* and designated a Queensland Museum specimen, J9255 from Dalby, SEQ., the neotype of *H. irrorata*. After examining this specimen (J9255) Copland (1957, pp. 34–5) treated *H. irrorata* as a separate species, closer to *H. gracilenta* Peters, 1870, than to either *H. caerulea* or *H. infrafrenata*. This opinion was based largely on a comparison of size of the finger discs and percentages of webbing and was reinforced by Copland's consideration of colour patterns and size of tympana. The only discrepancy noted by Copland when comparing De Vis's description with J9255 was in the shape of the head.

(v) Mertens (1964, pp. 15–16) restated the opinions of Fry and Copland.

The generic name *Litoria* Tschudi (1838) is here used for all Australian and Papuan species formerly referred to *Hyla* following Tyler's proposal (1971, p. 351).

Litoria infrafrenata, with which both Boulenger and Fry considered *L. irrorata* possibly conspecific, may be excluded from further consideration. This species occurs in

TABLE 1: COMPARISON OF THE NEOTYPE OF *H. irrorata* WITH SPECIMENS IDENTIFIED BY DE VIS AS *H. irrorata* AND WITH PUBLISHED DESCRIPTIONS OF *H. irrorata*, *L. gracilenta* AND *L. caerulea*.

Character	J9255	J9255 (after Copland)	*L. caerulea* (after Copland)	*L. gracilenta* (after Copland)	*H. irrorata* (after De Vis)	J12870–80 (identified as *H. irrorata* by De Vis)
disc of finger 3/tympanum	0·7	0·66	0·75–1·7	>	0·4	0·9–1·0
eye/tympanum	1·5	1·3	1·25–1·5	1·5–1·8	1·33–1·5	1·3–1·5
head breadth/length	1·1	1·0	1·19	1·16	much <	1·14–1·3
% webbing						
right fingers 1–2	27·9	27·0	35·0	64·0	"webbed at base"	24·0–33·8
2–3	32·0	37·0	38·0	67·0		37·0–52·0
3–4	38·6	33·0	38·0–50·0	74·0		32·0–52·0
right toes 1–2	47·4	36·0	52·0	65·0	"toes two-thirds webbed"	48·0–53·4
2–3	46·8	44·0	48·0	83·0		42·0–52·7
3–4	50·0	61·0	61·0	71·0		55·1–68·8
4–5	61·5	61·0	63·0	82·0		58·4–63·4
line or series of spots from angle of mouth	+	+	+	—	+	+ (in four)
white spots on dorsum and groin	+ (dorsum only)	—	+	—	+	apparently lost with preservation
canthus rostralis line	—	—	—	+	—	—
forearm shield	—	—	—	+	—	—

only northeastern Queensland and New Guinea (Copland, 1957, pp. 32–3 and Tyler, 1968, pp. 109–110; Queensland Museum, 16 specimens). In all specimens seen by Copland there is a 'wide very prominent, white line which circles the lower jaw and then runs back from the angle to above the shoulder' and this is regarded as diagnostic. Tyler also described this 'conspicuous white stripe'. De Vis described *L. irrorata* from either live or freshly preserved specimens (the syntypes were collected and described in 1884). He does not mention this feature in his detailed description of colour and there is now no trace of any marking on the lower jaws of any of the eleven specimens identified as *L. irrorata* by him.

Examination of the neotype of *L. irrorata* and the eleven specimens identified by De Vis as *L. irrorata* in respect to the features used by Fry, Loveridge and Copland is now possible.

Table 1 compares variation in the disc of the third finger and diameter of the eye in relation to the tympanum; head length and breadth; percentages of webbing on the fingers and toes and colour pattern in *L. gracilenta*, *L. caerulea* (after Copland), De Vis's measurements and description of *L. irrorata*, the eleven specimens identified as *L. irrorata*, by De Vis and the neotype of *L. irrorata*.

Percentages of webbing of the digits have been calculated following Copland (1957, p. 10) and, where possible, his definitions of characters have been used. Where they are not given, those of Tyler (1968, p. 9) have been followed.

De Vis states 'disks two-fifths of the tympanum' in the original description of *L. irrorata*. The disc of the third finger in J12870–80 is almost equal to or equals the tympanum (0·9–1·0). It is impossible to known how and where De Vis made his measurements but such a great difference can not be attributed to changes with preservation. It is possible that De Vis took an average size but this seems unlikely as he does not mention it. The most acceptable explanation is that either the 'two-fifths' of De Vis is a *lapsus calami* as first suggested by Fry (1912, p. 100) or that is is a printer's error and should have been four-fifths, which would be within the range described by Copland for *L. caerulea*.

The vomerine teeth of *L. gracilenta* are 'well separated' and almost always lie between the choanae (Copland, 1957, p. 23). In *L. caerulea* they may be well separated, closely approximated or contiguous and are usually behind the choanae but may extend to the anterior edges of the choanae (p. 28). In the neotype the vomerine teeth are as described by Copland (p. 35)—'. . . well separated, . . . almost but not quite behind choanae'. In ten of the eleven specimens identified by De Vis as *L. irrorata* the vomerine teeth are adjacent and in one (J12870), slightly separated. They lie behind the posterior edges of the choanae in eight and level with them in J12873, J12878, and J12880.

The eleven *L. irrorata* identified by De Vis are within the range which could be expected for *L. caerulea*. Copland described variation in most of these features—size of the disc of the third finger and the eye compared with the tympanum, vomerine teeth, and colour. In the remaining two features for which no variation is described by Copland, (percentages of webbing and head breadth/length) they are much closer to *L. caerulea* than to *L. gracilenta*. They may be definitely excluded from *L. gracilenta* by tympanum size, position of the vomerine teeth, and colour pattern.

In all features considered the neotype of *L. irrorata* is within or very close to the range described for *L. caerulea*. Slight differences are undoubtedly due to its small size and shrunken and brittle condition which make obtaining measurements with any accuracy impossible. Dr H. G. Cogger of the Australian Museum, Sydney, has recently examined this specimen and considers it to be 'a typical specimen of *caerulea*' (pers. comm.) despite its shrunken condition and the distinct colour pattern which is also present in many Australian Museum and Queensland Museum specimens.

Examination of the eleven *L. irrorata* identified by De Vis and the neotype of *L. irrorata* therefore confirms Fry's opinion that *L. irrorata* (De Vis) is a junior subjective synonym of *Litoria caerulea* (White).

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A NUMERICAL STUDY OF A SMALL GROUP OF *ACROPORA* SPECIMENS (SCLERACTINIA: ACROPORIDAE)

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ABSTRACT

A small group of museum (skeletal) specimens belonging to four recognised species of *Acropora* with suggested affinities was subjected to a simple taxonometric analysis, using an information theory model. The results suggested distinct species groupings, with growth-form in one case influencing subgroupings. Implications were taken on the role and suitability of the various morphological attributes.

The coral genus *Acropora* is highly speciated, but species limits, species affinities, and growth form variability are poorly understood. Although skeletal morphology is only one aspect of species characterisation in the Scleractinia (see Lang, 1972) it requires further understanding in this particular genus before most experimental methods of species differentiation could be applied. A study of this nature has been commenced on the species *A. squamosa* (Brook) and *A. hebes* (Dana) from the Great Barrier Reef, and it is hoped that numerical methods could be employed to examine attribute variation within the species. In order to examine possible ways in which morphological features might be quantified, a simple numerical study was carried out, using a selection of skeletal attributes.

MATERIAL

SPECIMENS: Twenty-three dried skeletal specimens from the registered collections of the Queensland Museum, most of them identified by J. W. Wells and mentioned in Stephenson and Wells, 1956, were used as the individuals in the study. The specimens belong to the four species *Acropora squamosa* (Brook), *A. hebes* (Dana) (both placed by Brook, 1893, in subgenus *Lepidocyathus*) and *A. corymbosa* (Lamarck), *A. surculosa* (Dana) (both placed by Brook, 1893, in *Polystachys*). Information on this material is given in Table 1.

In some of its growth forms *A. hebes* is difficult to distinguish from *A. squamosa* in the field, as was noted by Crossland (1952, p. 217). The radial corallite structure of *A. corymbosa* and *A. surculosa* has some similarities with *A. squamosa*, and some growth forms approach those of *A. squamosa*. No synonymization has been suggested between members of the group, and it was hoped that the species would separate easily, and that the influence of growth form could be seen. Attention was focused on *A. hebes* and *A. squamosa*, the other species being employed for comparative purposes. The single specimen of *A. surculosa* (the only one available) contributed little to the study.

TABLE 1: INDIVIDUALS INCLUDED IN THE STUDY.

Number	Qd Museum Registration	Identification	Identified by*	Locality	Microhabitat‡
1	G2743	*A. squamosa*	S and W†	Low Isles	'tag missing'
2	G6612	*A. corymbosa*	C. Wallace	Tryon Reef	—
3	G2673	*A. hebes*	S and W†	Low Isles	'E. side, *Porites* pond'
4	G2663	*A. hebes*	S and W†	,, ,,	'traverse xi'
5	G2621	*A. corymbosa*	J. Wells	Heron Is.	'Reef flat'
6	G2623	*A. corymbosa*	S and W†	Low Isles	'Right up creek between mangroves, Traverse xxxvii'
7	G2754	*A. surculosa*	S and W†	,, ,,	'traverse xii'
8	G2664	*A. hebes*	S and W†	,, ,,	'W. of old Tripneustes spit, L.W.M.'
9	G2724	*A. squamosa*	S and W†	,, ,,	'traverse xii'
10	G2737	*A. squamosa*	S and W†	,, ,,	'Loc. xiv, below L.W.S.'
11	G2675	*A. hebes*	S and W†	,, ,,	—
12	G2674	*A. hebes*	S and W†	,, ,,	'traverse xxx sandy glade between mangroves, coral rich area'
13	G2626	*A. corymbosa*	S and W†	,, ,,	'traverse xii'
14	G2666	*A. hebes*	S and W†	,, ,,	'traverse xxxv, trickle zone from main mangrove outlet'
15	G2676	*A. hebes*	S and W†	,, ,,	'W. of old Tripneustes spit, L.W.M.'
16	G2739	*A. squamosa*	S and W†	,, ,,	'traverse xii'
17	G2671	*A. hebes*	S and W†	,, ,,	'L.W.M. Traverse xxv, trickle zone from main mangrove outlet on S. end of E. side'
18	G2740	*A. squamosa*	J. Wells	,, ,,	'traverse xii'
19	G2744	*A. squamosa*	J. Wells	Heron Is.	'Reef flat'
20	G2736	*A. squamosa*	J. Wells	,, ,,	'E. side anchorage very shallow water'
21	G2738	*A. squamosa*	S and W†	Fitzroy Is.	'Below M.L.W.'

*S and W refers to W. Stephenson and J. Wells.

†Mentioned in Stephenson and Wells, 1956.

‡Microhabitats as given on label by Stephenson and Wells, 1956 (see their map).

ATTRIBUTES: A list of 16 attributes measurable on the dried skeleton was devised. Attributes were chosen so as to give an even coverage of the various skeletal aspects: growth form, size, and corallite structure. The attributes, for this initial study, were expressed in unsophisticated terms, and all numerical measurements were an average of five scores. All attributes are listed in Table 2 (results of GROUPER).

TABLE 2: ATTRIBUTES EMPLOYED IN THE STUDY, AND THEIR RANKINGS IN THE GROUPER RESULTS.

Number	Attribute	Ranked contribution of the attribute to fusion number 38	39	40	41
	Qualitative:				
1	taper/non taper of final branch	1	5	8	13
2	occurrence/non occurrence of anastomosis	15	16	13	3
3	one/two cycles in radial corallites	14	13	9	16
4	one size/range of sizes in radial corallites	16	15	7	10
5	wide/narrow primary axial septa	7	7	15	14
6	one/two cycles in axial corallites	8	6	10	15
	Numerical:				
7	diameter of final branch	6	8	2	7
8	length of final branch	2	2	6	8
9	angle of final branching	12	12	5	1
10	axial corallite exertness	3	11	1	9
11	axial corallite width	4	3	4	5
12	maximum number of bifurcations before final branch	9	10	14	11
	Disordered multistate:				
13	growth form (3 states)	10	1	16	6
14	structure of undersurface (5 states)	5	14	3	4
15	shape of radial corallites (4 states)	13	9	11	2
16	degree of coenosteum development between radials (3 states)	11	4	12	12

PROGRAMMES: The sequence of programmes was chosen by M. Dale. It is now widely used for taxonomic studies in Australia, and available on the C.S.I.R.O. PDT 10 computer in Canberra. It runs as follows:

(1) MULTBET: an agglomerative method of sorting, associating individuals or groups by the successive gains in information associated with fusions. Results are expressed in a dendrogram (see Lance and Williams, 1967).

(2) GROUPER: analyses the major groupings in the MULTBET dendrogram, in terms of the ranked contributions of the various attributes.

(3) GOWER: a principal coordinates analysis (see Gower, 1966).

RESULTS

(1) MULTBET: A dendrogram expressing the results of the MULTBET programme is shown in Figure 1. The three largest groupings (fusions 37, 38, 39) are a basically

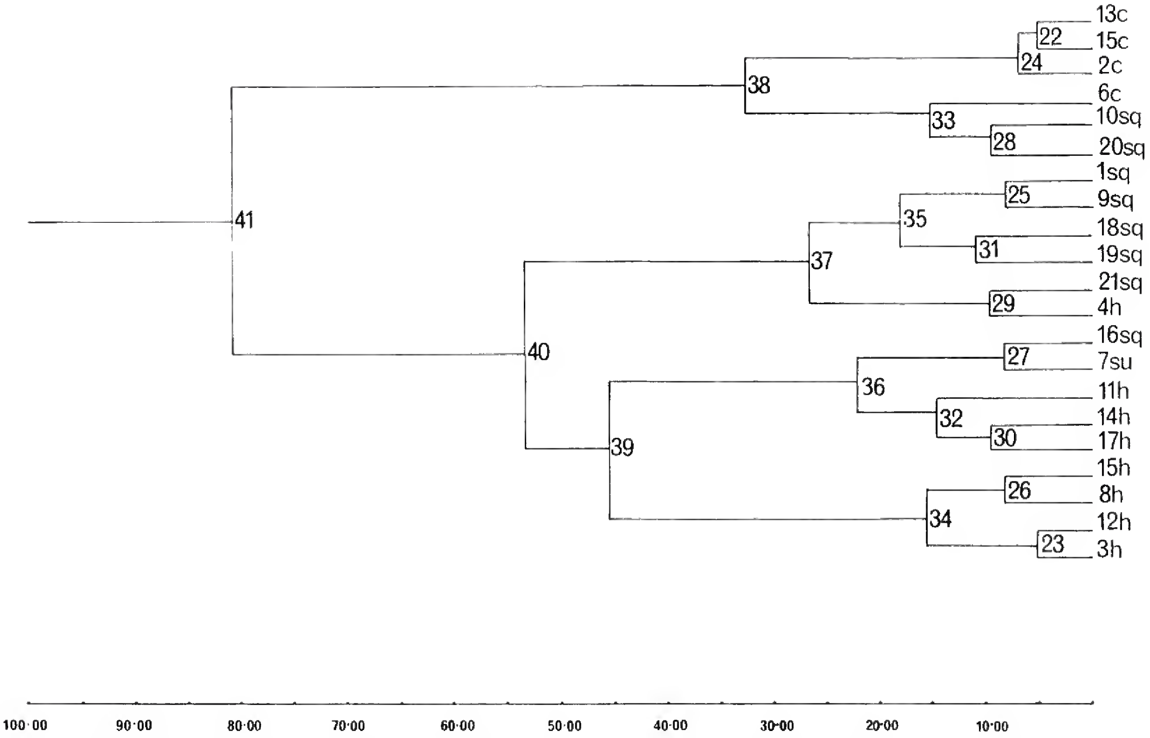


FIG. 1: Dendrogram of results of Multbet programme. Numbers at junctions indicate order of fusion. Scale represents coefficient (information gain).

c = *Acropora corymbosa* sq = *A. squamosa*
h = *A. hebes* su = *A. surculosa*

A. corymbosa, a basically *A. squamosa*, and a basically *A. hebes* group. The *A. hebes* group is composed of two sub-groups (36, 34). Group 34 has four members, all from inner reef flat areas, and all with similar appearance (low, open-arborescent, sprawling). The *A. hebes* specimens in group 36 are from outer flat regions; all have a 'simulated corymbose' appearance.

(2) GROUPER: Table 2 lists the attributes used and their ranked contributions to the four major groupings. An overall ranking shows that the attributes, as used, showed the following order of importance in forming the overall classification:

1. axial corallite width.
2. length of final branch.
3. diameter of final branch.
4. axial corallite exertness.
5. structure of undersurface.
6. taper of final branch.
7. angle of final branching.
8. general growth form.
9. shape of radial corallites.
10. one/two cycles in axial corallites.

11. degree of coenosteum development between radials.
12. wide/narrow primary axial septa.
13. maximum number of bifurcations before final branch.
14. occurrence/non-occurrence of anastomosis.
15. one size/range of sizes in radial corallites.
16. one/two cycles in radial corallites.

(3) GOWER: The results of the GOWER programme are expressed as two-dimensional ordinations (Fig. 2). The principle coordinates along the first and second, then the first and third vectors are plotted, and in each case a dotted line is drawn between each point and its nearest neighbour. When this is done in the 1/2 vector diagram, five interconnected 'groups' are formed: an *A. corymbosa* group, an *A. squamosa* (+ *A. surculosa*) group, a second *A. squamosa* group of individuals 10 and 20, an *A. hebes* 'corymbose' group, and an *A. hebes* 'arborescent' group. It will easily be seen that these groups are basically similar to those formed in sequence by the agglomerative process; when all three vectors are combined this similarity is emphasised.

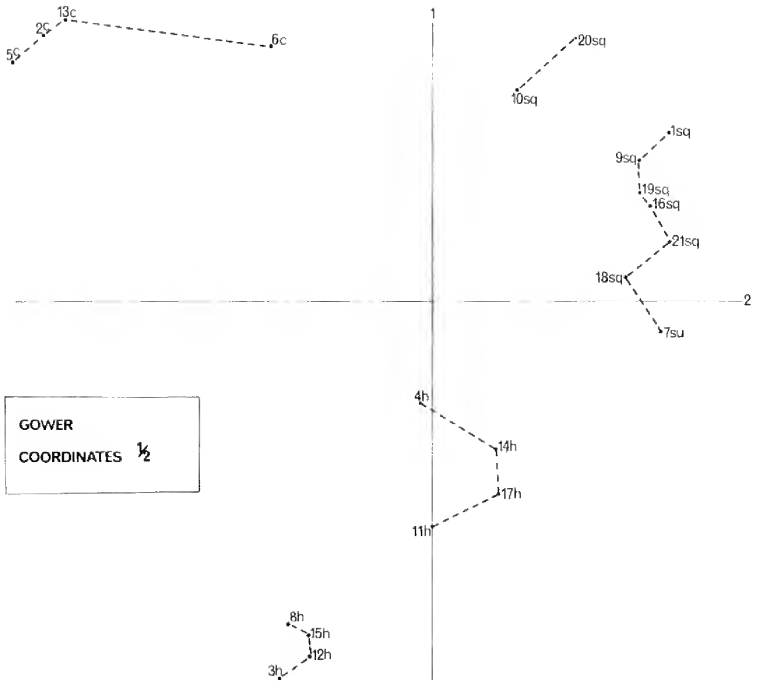
DISCUSSION

With the exception of the *A. surculosa* specimen, which did not have the opportunity to group with its own species, most of the specimens fell roughly into the species groupings they had previously been allotted by identification methods. This was expected, as most of the attributes used are taken into consideration for species definition. The programmes were run for the heuristic purpose of developing better definition of attributes for the study of morphological variation with location. With this in mind it is the GROUPER results which are given most consideration. GROUPER is employed only on the MULTBET process. The GOWER results are taken as a confirmation of the MULTBET groupings, as it is presumed that any anomalies in MULTBET would be contradicted in the GOWER results.

When the overall ranking of attribute 'importance' is considered, the highest ranked attributes are seen to describe dimensions: axial corallite width, length of final branch, diameter of final branch, and axial corallite exertness. The next four rankings describe corallum growth form: structure of undersurface, taper of final branch, angle of final branching, and general growth form. These were also the attributes which were the easiest to define and measure. They would probably be used in a similar form in a future study.

With two exceptions, the remaining attributes presented some difficulties of definition, and were probably expressed in an over-simplified form. The two exceptions were radial corallite structure and the possession of uniform as opposed to varying radial corallite size. These are attributes of 'key' importance in separating the three species, and for this reason they were simply expressed in disordered multistate and qualitive terms, respectively. It is evident that they are not, as used, sensitive to the sort of variation that might be expected between populations and between growth forms. In a future study they would be expressed as measurements, although this will provide difficulties, as it will be the dimensions of essentially different shapes which are measured.

The only GROUPER programme in which some attributes describing the corallites rather than the corallum are given high ranking is that from fusion 39, which unites two


13c
2c
5c
6c
1
20sq
10sq
1sq
9sq
19sq
16sq
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18sq
2
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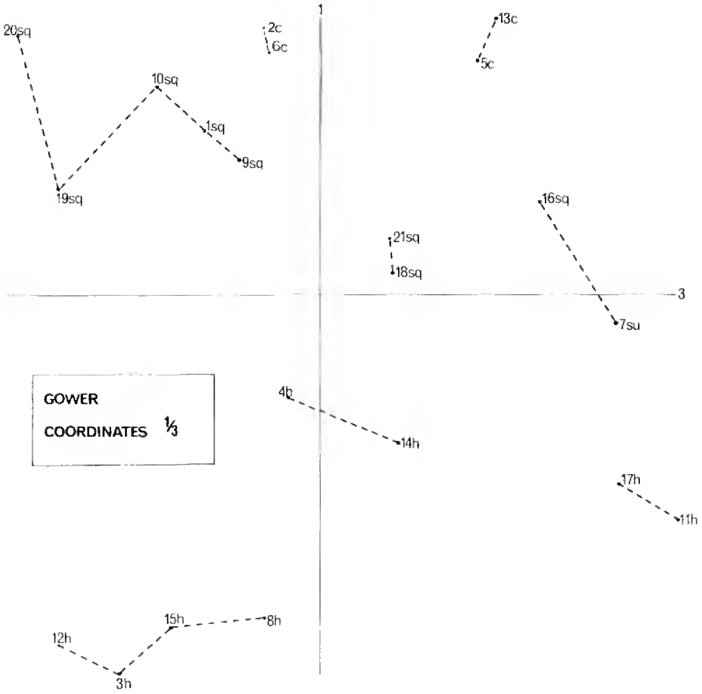
GOWER
COORDINATES ½
4h
14h
17h
11h
8h
15h
12h
3h


20sq
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4h
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11h
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essentially *A. hebes* sub-groups. In this case it is possible to give a definition of each sub-group in terms of the highest ranked attributes: Group 36 'of corymbose growth-form, short terete branchlets, crowded radial corallites, axial corallites with one cycle of well developed septa', and group 34 'of low arborescent growth form, tapering branchlets, radials more sparsely distributed, axial corallites with two cycles of poorly developed septa'.

The most obvious omission from the above definitions is a description of radial corallite differences. This should be rectified by a change in radial corallite definition as previously discussed. Septal cycle definitions for both axial and radial corallites would probably be better expressed as counts of the number of secondary septa, rather than as presence/absence of a secondary cycle.

CONCLUSIONS

It appears from the GROUPER results, that attributes expressed in binary terms will not prove very useful in a study at this low taxonomic level. It is also apparent that the structure and dimensions of the radial corallites need to be better quantified for them to play any part in the numerical classification, and in turn, for their effect on the classification to be examined. The results suggest that, if these changes are followed, the MULTBET–GOWER–GROUPER programme can be employed to sort specimens into groups, whose attribute-sets can be easily seen. When specimens are accompanied by detailed locality data, the possibility that groups so formed are population or zonation groups can be examined.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the advice and supervision of Dr Tom Hailstone, University of Queensland. The choice of programmes was made by Dr Mike Dale, C.S.I.R.O., who also provided helpful discussion. I wish to thank him and Mrs Kath Stephens for the running of the programmes.

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FIG. 2: First three vectors from the Gower ordination process. A dotted line has been drawn between each point and its nearest neighbour.

c = *Acropora corymbosa* h = *A. hebes* sq = *A. squamosa* su = *A. surculosa*

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Mem. Qd Mus. 17(1): 63–7, pl. 2. [1974]

SOME ASPECTS OF REPRODUCTIVE BEHAVIOUR AND THE MALE ERECTILE ORGANS OF *DASYURUS GEOFFROII* AND *D. HALLUCATUS* (DASYURIDAE: MARSUPIALIA)

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ABSTRACT

Male individuals of the marsupial species *Dasyurus geoffroii* and *D. hallucatus* have been kept live in captivity. Various types of sexual behaviour were observed. The erectile reproductive organs of both species, observed while the animals were asleep, are similar. In both there are two erectile structures, one evidently homologous with the penis of other mammals while the other is of uncertain homology. The male *D. geoffroii* was observed in courtship behaviour and an attempted copulation with a female. The peni of preserved specimens of *Sminthopsis leucopus*, a small dasyurid, have been dissected and found to differ from those of *Dasyurus geoffroii* and *D. hallucatus*.

Live dasyurids have been kept in captivity for five years as part of research into the diversity of this marsupial family. During this time various aspects of reproductive behavior and morphology were observed in Western Native Cats (*Dasyurus geoffroii*) Because these observations were made on captive individuals it is possible that some of the observed aspects of their reproductive behavior are unnatural. However, the morphology of the erectile structures of the males described below is clearly not affected by captivity.

DASYURUS GEOFROII

The male was obtained as a juvenile in July 1970. No sexual behaviour was observed until March 1971. At this time he was frequently observed to have an erection while asleep. By 17 March 1971 it was approximately 90 mm in length. On 23 April 1971 his brothers and sisters, held in cages in captivity by Miss V. Bristow, were mating. Miss Bristow noted (pers. com.) that copulation often lasted for three hours, with intermittent active thrusting by the males. A particular female copulated at least twice. No erections were observed in the male after April. On 10 March 1972 he was again observed to have an erection while asleep in a bureau drawer. The drawer was opened so that he could be observed. This opportunity lasted only a few moments after which he awoke and the erection subsided.

On 24 March 1972 he was presented with one of his sisters, with whom he had had no contact since July 1970. Her first reaction after being released into the living room of a house was to explore. After half an hour the male was released into the same room. She immediately hid beneath a bookcase. He located her by standing on his hind legs and sniffing intently. Each effort brought him closer to her hiding place. Having discovered her, he stiffened, with his tail held out straight. He made nose to nose contact with the female, also tense and alert, and then with very uncharacteristic, steady and smooth movements, he made a determined effort to get close. She fled and he followed, staying about 30 cm behind. His movements actually resembled the stalking behaviour of placental cats but differed from his own behaviour when pursuing live prey. At first, when she stopped, he stopped. When she started off again, he followed again. After a few minutes of this type of pursuit, when she stopped, he came up to her flank and carefully sniffed. At first she turned and ran at him. He instantly drew back. Finally he approached her again but this time put a hand on her rump. She remained motionless. He did the same with his other hand and then pressed his chest against her rump. Suddenly she flipped on her back, opened her mouth, made a sharp noise and spread out her arms in an attack posture. He reacted by rearing up on his hind legs, threatening attack with sharp sounds, open mouth and outspread arms. They leaped apart, but in a moment he was again in pursuit as if nothing had happened. Hand-rump contact was again made. This time there was a continuous huffing by both individuals. The female, however, while huffing, raised her rump towards the male and set her throat down on the floor. She occasionally half-closed her eyes. In spite of this seeming acceptance, she refused to let him actually mount. At the last moment she flipped over and threatened. When this happened his tail quivered violently. He ran rapidly around the female apparently very tense. At no time during this evening did he appear to have an erection. Relations between the two appeared to degenerate and after two hours of this behaviour he bit the female's tail, drawing blood. After this she refused to raise her rump or make any obvious attempts to induce mating. They were separated to different rooms for the rest of the night.

The following evening they were again put together in the same room, but she indicated her unwillingness to have anything to do with him by attacking or continually hiding. They were again separated.

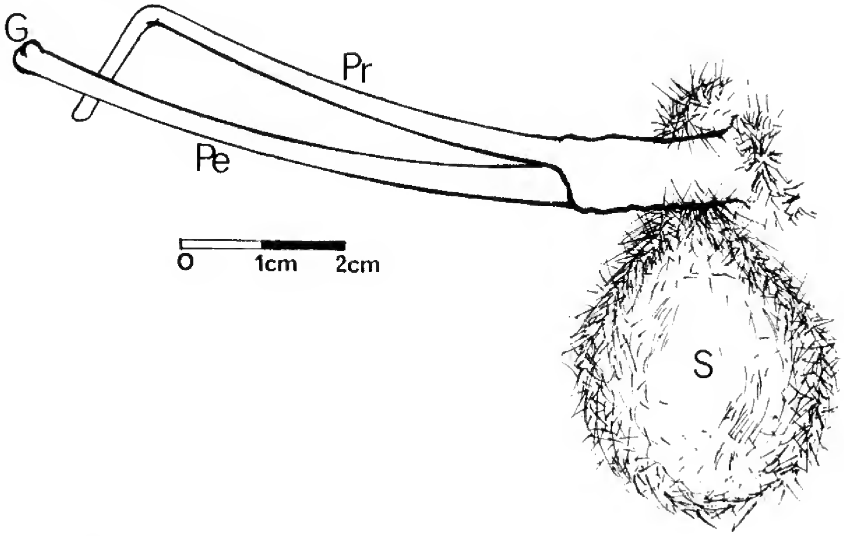

FIG. 1: Erectile reproductive organs of *Dasyurus geoffroii*. The dorsal structure (Pr) is only partially erect. The penis (Pe) is fully erect. The glans (G) and scrotum (S) are visible.

On 1 April 1972 another of the male's sisters, was put into the same room. She behaved in a manner very similar to the first female but appeared to be more interested in the male. When he followed her, she turned and chased him around the room. Several times she caught him and bit into his neck from above. He offered no resistance. After half an hour, he began to chase her. After catching her he grabbed the fur of her back with his hand and literally hauled her across the room to a secluded corner. He put her down and proceeded to mouth the thickened fur on the back of her neck. Both females had developed swollen necks at this time of year (a change noted by Miss V. Bristow, pers. comm., who held them in captivity for two years). Keeping his grip, the male mounted the second female. She remained quiet, with rump up and throat down. They stayed like this, not copulatlng for about three hours. His foot often vibrated against her leg. Several times he pulled her towards his abdomen with spasmodic jerks of his arms. These spasmodic jerks were highly regular in frequency, occurring every 1·5 seconds. These sessions lasted about one minute at a time with irregular pauses between. Ewer (1968) notes this type of behaviour in another dasyurid, *Sminthopsis crassicaudata.* After the first hour the male achieved a partially inflated erection (Fig. 1) but appeared unable to penetrate the vent. The female finally broke free. Mounting was not attempted again and he became aggressive, biting the female's tail. As a result they were separated.

Fig. 1 shows the erectile organs as noted while asleep. The intromittal penis has a slightly swollen glans, and a shaft. The other erectile structure emerges from near the base of the penis on its dorsal surface. Several times it was observed in full erection and it exceeded the ventral penis in length, the former reaching approximately 95 mm and the latter 90 mm. When both are inflated, they diverge. As a result it is difficult to envisage how they can both be intromittal organs. Although the male's attempt to mate was unsuccessful both organs were observed in partial erection while copulation was attempted (Plate 2B). The dorsal structure however was less rigid than the penis, and in fact when the animal was observed asleep, the dorsal structure was frequently only partially erect while the ventral penis was seemingly fully erect. Plate 2A shows the flaccid penal complex after it was physically pulled from the cloaca following death on 28 April 1973.

DASYURUS HALLUCATUS

A captive male was received on 1 July 1972. No sexual activity was observed until 9 July 1972, when he was observed, while sleeping, to have an erection. The erectile organs were identical to those of *D. geoffroii.*

SMINTHOPSIS LEUCOPUS

Preserved specimens of this species (e.g. Fisheries and Wildlife Department of Victoria D5343) have been examined and no evidence for an erectile structure dorsal to the penis was found. The glans was partly bifid at the tip. In the retracted state the penis exists in a pocket of the cloaca. When the glans is drawn out, the infolded pocket everts. The surface of the penal shaft was found to be covered by minute rough projections.

DISCUSSION

Descriptions of and remarks about the penis of dasyurids have been given by MacKenzie (1919), Sharman (1970), Fordham (1928), Gerhardt (1933), Jones (1949), and Marlow (1961). General observations on reproduction in dasyurids are given by Woolley (1966), Marlow (1961), Hill and O'Donoghue (1913), Fleay (1934, 1935a and b, 1940, 1961), Mack (1961), Ewer (1968), and Godfrey (1968).

Descriptions of and remarks about the penis of other marsupials have been given by Osgood (1921), Sharman (1970), Hartman (1921), MacKenzie (1919), Rotenburg and Glauert (1928), Young (1879) and Owen (1868). General studies on reproduction in marsupials are reviewed for example by Sharman, Calaby and Poole (1966), Sharman (1970), and Sharman and Calaby (1964).

Gerhardt (1933) illustrates the flaccid penis of *Dasyurus viverrinus* and indicates its complex structure. I can find no other description or suggestion of an erectile complex comparable with that reported here for *Dasyurus*. However, most of the studies noted above have been made on preserved specimens. Bifidy of the dasyurid glans is well-documented (e.g. Fordham, 1928) and it has been suggested that this corresponds to the two lateral vaginal horns (Hartman, 1922 and Sharman, 1970) of the female. However, the parts of the penal complex noted in the present study do not form a bilaterally symmetric pair and their total function is hence not so easily explained. The dorsal erectile organ in *Dasyurus* may be a modified prepuce, but this has not been satisfactorily determined. More work involving preserved specimens will be necessary to determine the homology of this dorsal structure.

ACKNOWLEDGEMENTS

I wish to thank my wife Elizabeth for patiently bringing up the male Western Native Cat for three years, Miss V. Bristow for allowing us the opportunity to raise the male, Mr R. Warneke for permission to examine specimens of *Sminthopsis* in his care, and Dr P. Woolley for kindly bringing Gerhardt's (1933) work to my attention and general comments on a draft of this work. While this research was carried out I was supported alternatively by a Fulbright Scholarship, a grant in aid from the American Explorer's Club and a Research Assistantship to Dr W. D. L. Ride, Director of the Western Australian Museum, who was in receipt of a Research Grant from the Australian Research Grants Committee.

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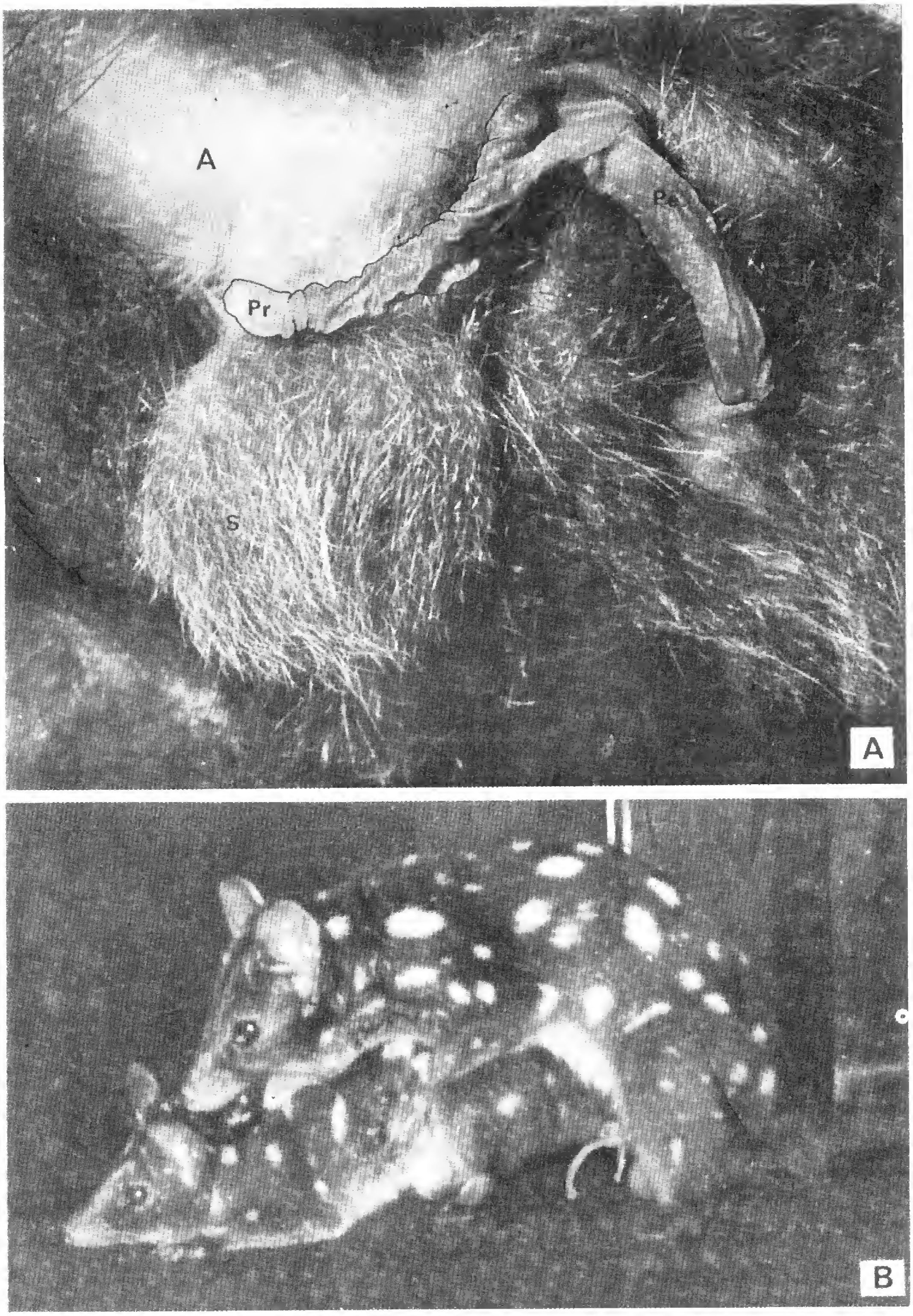
PLATE 2

A. The external genitalia of *Dasyurus geoffroii*, post-mortem, partially extruded from cloaca. S, scrotum; Pe, penis; Pr, possibly a modified and erectile prepu

B. Male and female *Dasyurus geoffroii* in attempted copulation. Male holds scruff of female's neck in his mouth. Generative organs of male partially erect. True penis appears the largest. Organ of unknown homology posterior to penis appears relatively flaccid. Female has her rump raised off the ground.


A
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A HOLOCENE MOLLUSCAN FAUNA FROM MAROOCHYDORE, QUEENSLAND

P. A. Wood
Geological Survey of Queensland
and
Helen King
Queensland Museum

Wood (1972) described the occurrence of a fossil tree stump (?*Eucallyptus rescrucera*) 145 m SW. of the present Maroochy River and 3 km W. of the coast line. This stump was in growth position and overlain by a black mud bed 4·9 m thick containing a fossil marine fauna. It was suggested that the shoreline was close to the site of burial of the tree stump and about 5·2 m below its present level about 7500 years B.P., the age given by radio Carbon for the wood.

The molluscan fauna in the 4·9 m marine bed has now been determined and is listed here. The list includes species which are known to occur at present on tidal flats and in estuaries.

FAUNAL LIST

The molluscan fauna of the middle black mud unit (Wood, 1972) contained 22 species, listed below.

The numbers refer to Queensland Museum catalogue numbers and the specimens have been deposited in that institution.

GASTROPODA
  TROCHIDAE
  Calliostoma ? similaris (Reeve, 1863) Mo5672
  POTAMIDIDAE
  Velacumantus australis (Quoy and Gaimard, 1834) Mo5673
  Pyrazus ebeninus (Bruguiere, 1792) Mo5674
  CERITHIIDAE
  Cerithium sp. Mo5675
  NATICIDAE
  Polinices conicus (Lamark, 1822) Mo5676
  Polinices sordidus (Swainson, 1821) Mo 5677
  MURICIDAE
  Bedeva hanleyi Mo5671
  NASSARIIDAE
  Nassarius ? pictus (Dunker, 1846) Mo5678
  Parcanassa ellana Iredale, 1936 Mo5679
  Plicarcularia thersites (Bruguiere, 1789) Mo5680

BIVALVIA
  ARCIDAE
  Anadara (Anadara) trapezia (Deshayes, 1839) Mo5681
  NOETIIDAE
  ? *Sheldonella* sp. Mo5682
  PLACUNIDAE
  Placuna quadrangularis (Retzius, 1788) Mo5683
  OSTREIDAE
  Saccostrea commercialis (Iredale & Roughley, 1933) Mo5684
  Unidentified Mo5685
  VENERIDAE
  Paphia (Paphia) undulata (Born, 1778) Mo5686
  Placamen calophylla (Philippi, 1836) Mo5687
  MACTRIDAE
  Spisula (Notospisula) trigonella (Lamark, 1818) Mo5688
  TELLINIDAE
  Tellina (Homalina) ? *deltoidalis* Lamark, 1818 Mo5689
  Tellina capsoides Lamark, 1818 Mo5690
  ? *Psammotreta (Tellinimactra)* sp. Mo5691
  Leporimetis spectabilis (Hanley, 1844) Mo5692

DISCUSSION

All the identified specimens belong to species that have living representatives. Also, all of the positively identified species are characteristic of modern tidal flats and estuaries (Dakin, 1953; Allan, 1959). One species, *Saccostrea commercialis*, also occurs on exposed coasts and its distribution is apparently dependent on the presence of firm substrates for attachment.

Only one of the species, *Velacumantus australis*, has been studied in any detail (Ewers, 1967). This species lives under a variety of tidal conditions and can tolerate a wide range of salinities. Many of the other species are said by MacIntyre (1959) to tolerate a wide diversity of tidal and salinity conditions. Included are *Pyrazus ebeninus*, *Bedeva hanleyi*, *Parcanassa ellana*, *Anadara trapezia*, *Spisula (Notospisula) trigonella*, and *Saccostrea commercialis*.

The junior author observed *Velacumantus australis*, *Pyrazus ebeninus* and *Polinices sordidus* on the tidal flats at the present mouth of the Maroochydore River.

CONCLUSIONS

It is reasonable to assume that a tree as large as this one grew at or above sea level. It then follows that the deposition of the fossiliferous black mud was the result of a marine inundation associated with a relative rise in sea level sufficient to deposit 4·9 m of sediment. It is not possible to estimate how much relative sea level has changed because the amount of compaction of the sediments is unknown.

The excellent preservation of the wood indicates quick burial by the middle black mud deposits containing the molluscan shells. The fauna indicates that the enclosing sediments were deposited in intertidal, estuarine or sheltered coastal environments characterised by low velocity currents. The black mud unit was deposited in a space of less than 7500 years and the good preservation of the shells is compatible with quick deposition.

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THE BENTHIC FAUNA OF SOFT BOTTOMS, SOUTHERN MORETON BAY

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ABSTRACT

Fifteen sites in a relatively small area south of Peel Island were sampled in quintuplicate using an $0 \cdot 1 m^2$ van Veen grab. Samples were repeated at three-month intervals for two years and in the middle of the investigations there was usually heavy rainfall.

Data were analysed by the three-dimensional method described by Williams and Stephenson (1973). This method was modified: (a) to allow tests of significance of species in site-groups and this permitted scanning of all species-in-sites data to locate 'conforming' species; (b) to allow search for an alternative site-grouping to be revealed by the 'non-conforming' species—no such grouping was evident; (c) to expand the species-times data to itself become three-dimensional and thus permit separate consideration of species-in-months and species-in-years. The method was not entirely satisfactory in delineating species-groupings; it considers variances of differences (from species-centred values). As a result species-groups were derived somewhat heuristically.

The site-groups, which revealed small scale patterns, showed an extraordinarily close similarity to the differences in sediments, and other abiotic differences between sites can be neglected. There were some significant changes in sediments during the course of the work.

Changes between years were more important than those between seasons, but the evidence that this was due to flood dilution is not convincing. The inadequacy of the sampling program with respect to temporal changes was revealed.

Species-relationships to sites, to months and to years are considered in terms of 'conformity' and 'importance' instead of dominance, constancy and fidelity. In a number of cases the same species conforms and is important and there is a Petersen-type association. The species which conform to sites often conform to one or the other time dimensions and these should not be excluded from site-analyses. Species-relationships are compared with those of other relevant investigations.

The contributions of different elements to biotic complexity is briefly discussed and it is suggested that limited environmental instability may increase diversity.

INTRODUCTION

Previous work on dredged samples in Moreton Bay (Stephenson, Williams and Lance, 1970) showed indistinct spatial associations of macrobenthic species and it was suspected

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that the 'real' patterns in certain areas were finer than those revealed. This is in part because stations were widely spaced and rarely less than ½ mile (0·8 km) apart, and partly because of the distance traversed in a single dredging—up to 20 m. Finer patterns were now sought and the dredge was replaced by an 0·1 m^2 van Veen grab. Because dredge and grab sample different fractions of the benthos, the present investigation is a new study in an area south of Peel Island whose complexity was indicated by the previous work,

It had been hoped to sample sites on a grid pattern at 100 m apart but this proved impossible. Eventually three main areas of sampling were selected, each containing five sites spaced so that relatively small-scale area patterns might be revealed.

The previous work stressed area patterns, but seasonal changes in certain species were noted. The present work was planned on a seasonal basis with samples at three-month intervals, thus permitting evaluation of area and seasonal effects. Seasonality has a particular importance because in the classical studies of benthic communities by the 'Petersen school' beginning with Petersen (1914), seasonally occurring species have been eliminated. Petersen himself stated (1914, p. 4) '. . . It is obvious beforehand, that every single species occurring on the valuation lists is not of the same importance . . .; many animals only occur in quantity at certain times of the year, hence called seasoned animals; from the different quantities in which they occur on the lists we are, therefore, in general not able to draw any conclusion as to the composition of the community.' Seasonal variations in benthic populations have been noted by several workers, for example Raymont (1949), Kitamori (1950) and Yamamoto (1952) but we know of no satisfactory attempts to obtain a relative measure of area and seasonal effects.

The initial intention was to sample a complete year plus one season of overlap. In the event, the proposed overlapping season (March 1971) followed an abnormally wet season which could be expected to cause a marked reduction in the biota. By extending the sampling it was possible to compare a 'normal year' with one involving recovery from a natural catastrophe. Here again a literature exists dealing with various catastrophes, for example Stauffer (1937), Parker (1955), Sandisson and Hill (1959), Dean and Haskin (1964) and Tulkki (1965).

The results indicated only a slight effect of the abnormal season, and are possibly more relevant to studies of annual changes in benthos generally. The literature which exists does not give relative evaluations of areas, seasons and years. It includes Moore (1933), Poulsen (1951), Ursin (1952), Birkett (1953), Segestråle (1960) and Kühlmorgen-Hille (1965).

As expected the survey revealed a large number of species or, in Hurlbert's (1971) terms, high 'species density'. Also there were many codominant species or, in the terms of Whittaker (1965) and Sanders (1968) high 'dominance diversity'. We could have approached the problem as a diversity study, along the lines reviewed by Whittaker (1972) but preferred for reasons given later to approach it in a classificatory context. The methodology has already been outlined (Williams and Stephenson, 1973).

AREA OF INVESTIGATION

POSITIONS AND DEPTHS OF SITES

Moreton Bay as a whole (Figure 1) has been described by Stephenson, Williams and Lance (1970) and by Maxwell (1970). In subtropical latitudes, it is partly an arm of the

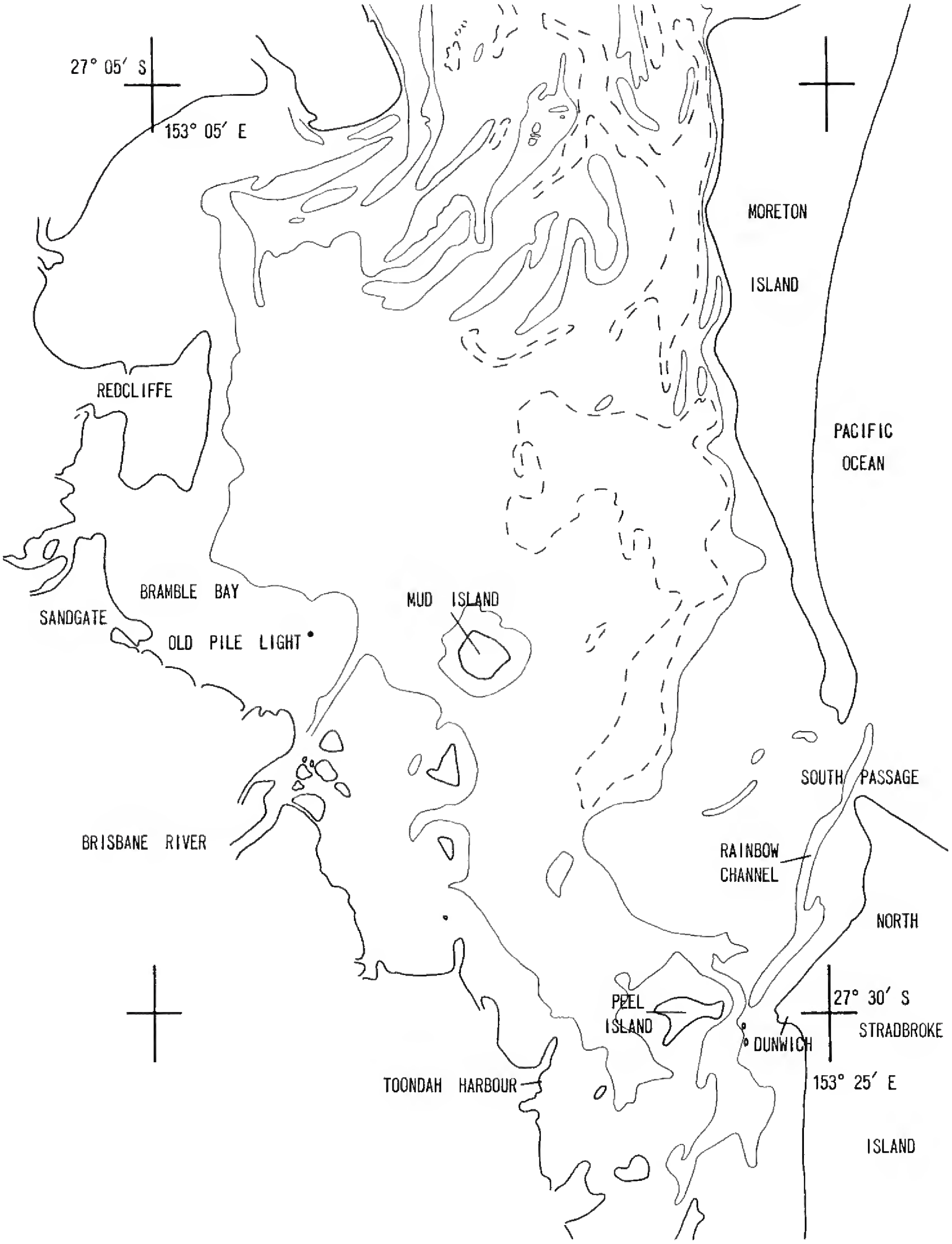

FIG. 1: Moreton Bay, showing localities mentioned in the text. Thin continuous lines = 3 fm (5·5 m); broken line = 10 fm (18·2 m).

Pacific and partly a complex estuarine system, with numerous islands in its southern portion. The present work was carried out in this southern portion and near Peel Island for the following reasons: (1) as established by our previous work, it is an area with a rich fauna and with a small scale patterning of 'communities', (2) relative shelter minimises interruption of sampling by bad weather; and (3) there is an abundance of navigation beacons for use as sighting marks.

Choice of sites was restricted by an underwater cable and the necessity to relocate sites with speed and accuracy; this required intersecting lines of sight using nearby beacons. Finally three areas each of five sites were selected in regions with contrasting bottom topographies as revealed in the published chart of the area (Department of Harbours and Marine—Queensland—Moreton Bay, Peel Island to Russell Island, surveys to 1969). After several surveys had been completed, a checking of depths at sampling sites revealed considerable differences from the above chart. More recent data have been provided through the kindness of the above State Department ('Survey by J. K. Slater and L. V. Lee, completed 29/11/69, Dunwich to Toondah Harbour, Hydrographic Plan'). In Figure 2 sites are plotted in this plan; their positions have been established by horizontal sextant angles of conspicuous fixed points (data filed in archives of Queensland Museum).

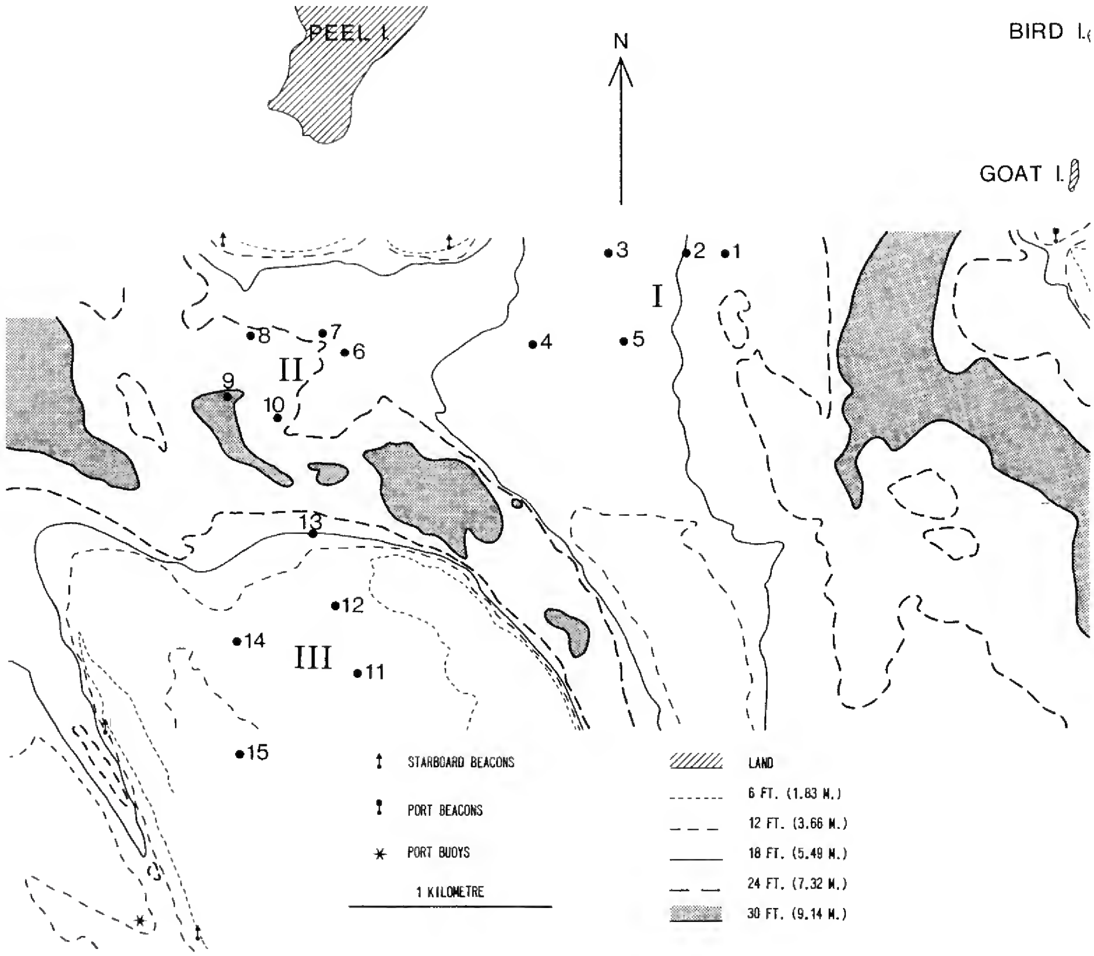

FIG. 2: Sampling sites (1–15) grouped in areas I, II and III.

Owing to the above, grouping of sites by proximity and by bathymetric features do not coincide. The proximity groupings are into a northeasterly area (I) comprising sites 1–5, a northwesterly area (II) of sites 6–10, and a southerly area (III) of sites 11–15. Areas encompass in km^2: I,0·24; II, 0·16; III, 0·36; all sites are enclosed within 3·08 km^2. Topographic grouping of sites gives: 'Goat Island slope' 1–5; 'Northwest gutter' 6–10, 13; 'Southern shallows' 11, 12, 14, 15. From the soundings on which Figure 2 is based sites can also be grouped by depths as follows: shallow (2·4–5 m) 3, 4, 5, 11, 12, 14, 15; medium (5·1–7·5 m) 1, 2, 6, 7, 13; deep (7·6–9·3 m) 8, 9, 10.

SEDIMENTS

Maxwell's (1970) results on the sediments of Moreton Bay were incorporated in the benthic studies of Stephenson, Williams and Lance (1970). In the present investigations it was found necessary to re-investigate sediments primarily because Maxwell's stations were too distantly spaced; for example they failed to reveal the muddy substrata in Area I.

About 5% of each grab sample was carefully hand sorted for specimens and used for sediment analysis. This was performed by elutriation methods with the pore sizes of sieves as follows in mm: 1·98, 1·02, 0·53,0·15, 0·211, 0·099. The grades retained are here described as gravel, very coarse sand, coarse sand, medium sand, fine sand and very fine sand respectively, and the non-retained grade as mud.

TABLE 1

MEAN PERCENTAGES OF SEDIMENT GRADES, FROM QUINTUPLICATE SAMPLES MARCH 1970 AND DECEMBER 1971.

Sites	Gravel	V. coarse sand	Coarse sand	Med. sand	Fine sand	V. fine sand	Mud
1	1·41	0·53	0·58	0·59	2·77	37·30	54·86
2	4·25	1·47	1·22	1·08	1·02	33·08	57·96
3	4·33	1·58	1·51	1·23	1·09	30·91	59·02
4	4·03*	1·01	0·96*	1·18*	2·31	47·61	42·55
5	3·24	1·22*	1·25*	1·86*	2·20*	35·25*	56.51
6	4·87*	5·19	17·14	34·78	35·10	6·47	14·08
7	10·94	10·22*	19·56	25·01	13·80	6·25	14·16
8	10·31*	10·08	19·68	24·50	12·63	7·50*	15·16
9	13·34	7·86	14·06	21·47	20·04	9·54	15·92
10	13·51*	8·25	14·52	19·40*	15·92	9·14	15·16
11	8·84	1·49	1·52	8·20	49·91	16·35	13·06
12	6·51*	1·08*	1·33*	8·67	35·48*	20·32	26.66
13	13·34*	10·96*	11·59*	14·75*	18·13*	17·95*	13·60*
14	7·50*	3·23*	5·03*	11·02*	40·33	28·15	25·02
15	5·28	1·45	2·03	15·57*	35·89*	19·43*	17·36*

*These values showed significant differences between the March 1970 and December 1971 samplings.

The main sets of samples were collected in quintuplicate at the beginning (March 1970) and end (December 1971) of the biotic sampling. An additional set was taken in March 1971 when, following the floods of 1970/71, a soft sediment layer in 5 mm thick was noted in area I. Single analyses performed on this surface layer at each of the sites 1–5, showed little change from March 1970 apart from a slightly increased percentage of fine sand and decreased percentage of mud.

Comparisons between March 1970 and December 1971 showed significant changes in many of the fractions (those affected are asterisked in Table 1). The important changes are: Stn 5, less mud; Stn 12, less fine sand and more mud; Stns 13 and 14, more very coarse and medium sand and less mud; Stn 15 less coarse, medium and fine sand and more very fine sand and mud. There is no consistent pattern in changes excepting their concentration in area III.

Mean values from the two main sets of analyses are given in Table 1. To facilitate understanding the grades in this Table are fused, giving: coarse sand comprising medium sand and grades coarser; fine sand (including very fine sand); and mud. The sediments may then be classified by the mode (using fused grades) and further subdivided by mud percentages as in Table 2.

TABLE 2

DISTRIBUTION OF SEDIMENTS CLASSIFIED BY MODE AND MUD PERCENTAGE

Mode	% Mud	Sites
Mud	>50	1, 2, 3, 5.
Fine sand	50–25	4, 12, 14.
	<20	11, 15.
Coarse sand	<20	6, 7, 8, 9, 10, 13.

Further perusal of data indicates that the most aberrant sites in the first, third and fourth groups are 1, 4 and 13 respectively. If required the fourth groups can be further subdivided by percentages of coarse sand into 6, 7, 8, with >60% and 9, 10, 13 with <60%.

WATER MOVEMENTS

North of Peel Island tides flood from and ebb to the north. Immediately south the tidal streams come from northeast and northwest round the island, leaving a 'slacker' area which includes area I. Conversely in area II the tidal currents are strong and during spring tides surface currents are 2–3 knots. No data are available on bottom currents.

The area as a whole is protected from oceanic swells and waves are due solely to local winds. The most relevant data are the annual wind-roses for Brisbane given in the Official Year Book of the Commonwealth of Australia for 1970. At 9 a.m. the most frequent winds are southerly and southwesterlies, while at 3 p.m. they are most frequent in an arc from northeast to southeast. Newell (1971) also includes wind data from Sandgate covering January 1967 to December 1968 and states (p. 5): 'A seasonal pattern emerges, with winds from north to east predominating between December and April, and from south to southwest between May and August. There is no obvious seasonal pattern in the occurence of strong or light winds.'

The longest wind-fetches in the sampling area are in an arc from south to southeast and the wave-action is severest when these winds blow against a flooding tide from the north. This and the shallow depths makes sites 11, 12, 14 and 15 the most wave affected. Area I is the most protected, particularly from the north-northwest and north; next is area II especially from the north-northeast. From all other northern directions waves curve round Peel Island to affect all areas.

SOURCES OF WATER IN THE AREA: Newell (1971, p. 31) notes that the southern end of Moreton Bay is relatively isolated from the aspect of water exchanges and notes that '. . . the Bay water is divided into an eastern fringe, a western and southern fringe, and a central zone.'

General observations supplemented by drogue data of Helbig (unpublished) shows that a stream of eastern or Pacific water enters the area from the South Passage via the Rainbow Channel with incoming spring tides. This will give the most oceanic influences in area I. The tidal flow into areas II and III is more from the western and central portions of the Bay which are under greater terrestrial influence. Newell (1971) has shown this includes greater dilution by flood waters and a greater temperature variation—it also includes higher turbidity and greater possibilities of pollution.

Newell's (1971) work did not encompass the occasional catastrophic effects of severe flooding from river run-off, which have been mentioned by Slack-Smith (1960) in a biological connection and Stephenson (1968) in a brief hydrographical survey. The main influence of floods in the area is from the Logan-Albert River which discharges from the south. These effects will be greatest in area III, and least in area I. This topic is further discussed under seasonal changes (see below).

SEASONAL CHANGES

DILUTION AND CONCENTRATION

No direct data are available on salinities within the area of investigation, but relative effects can be deduced from rainfall data and water discharge by the Logan-Albert Rivers. Unfortunately data upon flows in these rivers does not cover a sufficiently long and continuous period to be of present value. Rainfall data, kindly supplied by the Commonwealth Bureau of Meterology have been used. From the known rainfall pattern in the Logan-Albert catchment two weather stations were selected as typical of lower and higher rainfall areas; these are Beaudesert and Springbrook respectively. (In fact Springbrook is just outside the watershed but is still regarded as typical of the higher rainfall areas). Data upon monthly rainfalls at these sites from 1915 onwards are given in Table 3. From December to March is typically the wet season, and July to September is typically the driest part of the year.

Analysis of the total available rainfall data from the above stations showed that the year before the study (1969) was fairly typical except for an increase in August recordings. The late autumn and winter of 1970 (May–August) and of 1971 (April–June) were unusually dry and from this one would expect higher than usual salinities in the sampling data. The summer of 1970–71 (Dec. 1970–Feb. 1971) included two months of exceptionally heavy rainfall from which one would expect unusual summer dilution. Comparably ususual

TABLE 3

Rainfall in 1/100th inch for Selected Sites in Catchment of Logan-Albert Rivers.

Month	Beaudesert				Springbrook			
	Mean* (St. Dev.)	1969	1970	1971	Mean* (St.Dev.)	1969	1970	1971
Jan	514(361)	238	796	801	1680(1376)	181	1116	1646
Feb	529(445)	99	487	1173	1809(1468)	1037	1964	3823
March	397(288)	75	470	143	2310(2978)	1197	1022	1743
April	241(212)	65	82	23	1039(817)	237	501	611
May	204(226)	838	63	88	828(681)	1643	126	147
June	245(286)	83	70	22	799(1081)	111	67	91
July	177(199)	90	64	108	603(842)	184	160	295
Aug	137(114)	527	42	155	390(339)	539	202	339
Sept	163(121)	127	274	148	408(306)	167	504	237
Oct	274(200)	543	314	109	613(475)	2188	987	243
Nov	312(233)	334	499	306	830(697)	1480	1405	416
Dec	478(298)	332	1204	244	1037(789)	398	3125	728
Total	3680	3351	4365	3320	11975	10462	11179	10234

*Means and standard deviations are for 1915–1970 inclusive.

conditions, in both respects (low and high rainfalls), have not occurred since 1946–47, and for these reasons one might expect particularly accentuated seasonal patterns in the benthos.

TEMPERATURE

The most relevant available data are mean monthly temperatures at the Pile Light off the mouth of the Brisbane River, covering the period 1931–1950.

TABLE 4

Water Temperature in °C at (Old) Pile Light.

Month	Mean	Highest	Lowest
Jan.	25·6	27·8	23·9
Feb.	25·0	28·3	23·9
Mar.	25·0	26·1	23·3
Apr.	22·8	25·0	21·1
May	20·6	23·3	18·9
June	17·8	22·2	15·6
July	16·1	18·3	14·4
Aug.	16·7	18·9	14·4
Sept.	18·3	22·2	16·7
Oct.	21·1	22·8	19·4
Nov.	22·8	25·0	21·7
Dec.	25·0	26·7	22·8
Mean	21.1	22.8	20.6

These data were kindly made available by the Commonwealth Bureau of Meteorology and comprise 9 a.m. readings at depths of 6–8 ft (ca. 2–3 m) below water level. Converted to °C they are shown in Table 4.

No data are available during the years of the present study, but since there were no prolonged periods of unusual air temperatures, we may assume that the water temperature lay tolerably close to the mean values given above.

SAMPLING PROGRAM

Many authors have criticised the use of single 0·1 m^2 grab samples, for example Holme (1950, 1953, 1964) and M. L. Jones (1961). Clearly the number of samples required depends upon the small-scale heterogeneity of the area and Ford noted as long ago as 1923 that a slight alteration of the position of the ship sometimes gave a striking change in fauna and in substratum. Preliminary work in the present general area indicated that twenty-five 0·1 m^2 samples might be required at a given site. Sampling at this intensity for fifteen sites at each season was beyond the logistic possibilities, and would also have increased the risk of a second sample being collected from exactly the same area as a later one (see below). Eventually, following Steven (1930) and Longhurst (1958) five samples were taken at each site on each occasion.

Sampling was repeated at intervals of three calendar months from March 1970 to December 1971, and with one exception (March 1970) collections were made within a week. Difficulties in operating occurred initially. The boat was positioned accurately by drifting from an upwind or uptide position, but like Day, Field and Montgomery (1971 p. 7) we found the grab 'tended to strike the bottom on its side, and many attempts had to be made before the wire could be maintained sufficiently vertical for a reasonable sample to be obtained.' This was overcome firstly by working only during neap tides, secondly by not operating in wind speeds exceeding 20 knots, thirdly by using an anchored boat, and fourthly by lowering the grab gradually until within about 2–3 m from the bottom. With this method, the grab worked successfully in the present range of depths and substrates, excepting that repeat samples were sometimes required in area III (see later).

Problems of accurate relocation of sites arose as the work progressed. Although accuracy had been required it was discovered that only the boat anchor had been carefully positioned on each occasion. It was estimated that, owing to swinging in wind and tide, samples at each season were within an area of ca. 25 m^2, but that over the entire program they lay within a circle of just under 20 m radius, i.e. an area of ca. 1000 m^2. (On Figure 2 these circular areas are drawn to scale). Clearly some of the differences apparently due to seasons could be from sampling a different portion of the circular area.

The inaccuracy of site relocation has a counter-balancing fortunate effect. It greatly reduces the chance of the grab collecting a presampled spot. On only one occasion was there evidence (from the physical appearance and faunistic contents of the sample) that this had happened in one of the quintuplicate samples. This was discarded and recollected. No evidence was obtained of exact resampling of a spot after a seasonal interval, and because of the large area involved this would be unlikely.

The normal method of collecting the biota from grab samples was by on-board wet sieving, with the final apertures ca. 1·2 mm square. Particular care was taken over samples containing small specimens of bivalves and gastropods which fortunately were infrequent. The procedure was modified on grounds suspected to contain *Branchiostoma* because smaller specimens burrowed through the sieve holes, and in such cases the sample was hand sorted before the finer sieving. After collection all specimens were initially preserved in 10% formalin and within a month tranferred to the most appropriate final preservative.

In summary the sampling program allows investigation of three types of spatial patterns (a) at a given site (and a given time) within the groups of quintuplicate samples whose exact spacings are unknown; (b) between the five sites within each area, which range from 150 to 700 m apart—an alternative is between topographic groupings as listed earlier; (c) between the three areas, whose incentres are from 1400 to 2430 m apart. It also allows a variety of temporal patterns to be investigated. These include seasonal (March, cf. June, cf. September, cf. December), annual 1970 cf. 1971), and possible differences immediately after a flood (March 1971 cf. remainder).

BIOTIC DATA

IDENTIFICATIONS

Chace (1969) comments on '. . . a major and virtually insuperable problem which plagues any ecological survey in tropical waters today; that is, the imperfect knowledge of the existing fauna . . .'. This applies to Moreton Bay, despite systematic publications referred to in our dredging work (Stephenson, Williams and Lance, 1970). Because of anticipated difficulties in identification and in recognition of species, hydroids and amphipods were excluded from the investigation; the former were also excluded on other grounds. Amphipods were present in smaller numbers than in comparable surveys elsewhere, but nevertheless their omission is unfortunate.

The problems of identification were also responsible for the selection of a relatively coarse sieve (1·2 mm square) during collecting. This excludes the smaller species where the major taxonomic problems would lie. If these small species had been included a much more complex situation than that recorded would have been obtained.

Shortage of space precluded retention of all specimens collected, so reference collections were established with at least duplication of 'species' occurring twice or more. Initially species were segregated and given 'working names' with assistance from a reference collection of most species from the previous dredging work (Stephenson, Williams and Lance, 1970) housed in the Queensland Museum. This resulted in some over-splitting, and was resolved when group experts had identified collections. Over-splitting probably remains in the Nemertea. In one case (*Euclymene*) two or possibly three species are lumped because of uncertainty regarding early discarded specimens.

Reference specimens, and when possible entire collections, were referred to group experts for identification. Without this assistance (as acknowledged later) the present study would have been very incomplete or even impossible. There remained a sizeable collection with only 'working names' or incomplete identifications, some of which are likely to be in error. These have been deposited in the Queensland Museum and the attention of taxonomic experts is invited.

GROUPS EXCLUDED

In addition to those excluded because of taxonomic difficulty peneid prawns were eliminated; they are known to be common at certain seasons in Moreton Bay but a grab is an inefficient device for their collection. The few specimens which were obtained were discarded.

Acorn barnacles and limpets were recovered from superficial dead shells. These belong to the hard-bottom fauna and their distribution reflects the almost random recovery of large solid objects. All the hard-bottom fauna was excluded—serpulids, polyzoa, hydroids, most polyzoans and some algae. When species occurred on large dead shell fragments and also the substratum generally (e.g. some tunicates) they were recorded.

FORM OF THE DATA: Usually the number of individuals of each species from each grab sample was recorded, but problems arose over colonial forms. Where the numbers of discrete colonies was known this was noted, but where this was not known—for example with *Halophila* where separate shoots arise from one or several stolons—we have only obtained data in a presence/absence form. Presence was noted as for a single individual.

Material which was obviously dead was not retained. All colonies of the serpulid *Filograna implexa* (Berkeley) were excluded for this reason, as would have been most polyzoan and hydrozoan colonies but for their prior exclusion. In general, empty tubes of polychaetes were not recorded either because it was clear they had not been inhabited recently or because of uncertainty over the species. The exception was *Chaetopterus variopedatus* and when it appeared that tubes were currently inhabited, but the specimens had eluded capture, data were recorded. Complete tubes were never recovered (nor were intact specimens), and here two separate tube-ends were recorded as one worm and so was a single separate end.

SPECIES OBTAINED

The 420 species are listed in Appendix I. The richness of this biota is difficult to compare precisely with that of most other surveys because of methodological differences. However, a certain number of local comparisons are possible. In our dredging work in Moreton Bay, we covered a much greater variety of habitats and a much greater area (ca. 775 km^2 against ca. 3 km^2) but obtained fewer species, 335 in all, and 25 of these are in groups excluded from the present survey. The difference mostly reflects the loss of specimens during dredging operations. Current work by Raphael and Stephenson in Bramble Bay near the mouth of the Brisbane River, using the present grab and sieves, and over an area of ca. 30 km^2 seems likely to produce ca. 180 species, thus indicating a relatively impoverished fauna. Hailstone (1972) in the lower reaches of the Brisbane River has noted 136 species from carefully sifted dredgings obtained from an area of ca. 1 km^2 (but of varied habitats).

Comparisons from wider areas are more difficult but we can note 74 species from an area of ca. 4 km^2 in a single season at Sek Harbour, New Guinea, using the present technique (Stephenson and Williams, 1971) and 264 species from ca. 30,000 km^2 by Petersen (1914) in Danish waters (Stephenson, Williams and Cook, 1972). Summarising the above, we are clearly dealing with a species richness of a different order from the other authors quoted.

At the level of actual species present, the present is a pioneer study in eastern Australian waters. Hence there are numerous new Queensland records and a considerable number of undescribed species. This renders comparisons difficult and premature, and the only relevant ones are with surveys in Moreton Bay. Comparison with the dredge survey of Moreton Bay as a whole (Stephenson, Williams and Lance, 1970) is difficult because of the unidentified species in the two surveys (e.g. sponges) and because some species were confused in the earlier study. For example we suspect at least five species of ophiuroids were recorded previously as *Amphioplus* sp. (This was due to damage of specimens during collection and examination of insufficient samples.) Within comparable taxonomic groups 115 species were common to the two surveys, 150 were obtained by dredge only and 275 by grab only. This confirms the relative inefficiency of dredge sampling and that the two methods sample different fractions of the biota.

Comparison with incomplete data of Raphael and Stephenson indicates 70 species common to the two areas, 110 only at Bramble Bay and 350 only at Peel Island. Comparisons are not affected with Hailstone's data from the lower Brisbane River, much of which is incompletely identified.

ANALYTICAL METHODS

FUSION OF SAMPLES

Analyses of small scale topographic patterning within quintuplicate samples was attempted, but because precise positions are unknown and only five samples are available at each site, analyses were restricted, and results are not detailed. There were indications of small scale aggregations in at least half of the more ubiquitous species. To reduce data to moderate proportions, results from quintuplicate samples are fused and in general represent numbers obtained from $0{\cdot}5\ m^2$ samples. The presence/absence data upon such forms as *Halophila* now become meristic summations and hence all data are of substantially the same form.

CHOICE OF METHOD

The main problem is to produce conceptual order within the 420 species obtained in the survey. It could be approached by what have become almost traditional methods of studying diversity, using one of the multiplicity of diversity measures based upon the proportions of species present for example Simpson (1949), Margalef (1951), McIntosh (1967), Edden (1971), Hurlbert (1971); or the widely used measures depending upon information theory, the Shannon and Brillouin measures (see MacArthur, 1955; MacArthur and MacArthur, 1961; Lloyd and Ghelardi, 1964; MacArthur and Wilson, 1967; Lloyd, Zar and Kar, 1968; Pielou, 1969; Whittaker, 1972). There is a comparably extensive literature upon measures of equitabllity or evenness, as quoted in Hurlbert (1971) and Whittaker (1972), and upon explanations of why diversity and equitability are higher in some situations than in others (see Pianka, 1966; Recher, 1972; and Whittaker, 1972).

We believe that the best approach is by partitioning so that, for example, we can evaluate the contributions made by species in sites, seasons and years. There have been theoretical discussions of the partition of diversity information statistics for example by

Kullback, Kupperman and Ku (1962) and by Kullback (1968) and an ecological approach by Orloci (1968). Partitioning of information diversity has been explored in an ecological (rain-forest) problem by Williams et al (1973). There are two disadvantages as listed by Williams and Stephenson (1973); partitioning is incomplete and results seem ecologically unsatisfactory. An alternative method is to use a sum-of-squares partitioning as detailed in the last quoted paper and this we followed. Because it involves analysis of variance and euclidean distances (centred), results are likely to be unduly influenced by the more abundant species. In the earlier paper a cube-root transformation was used and incomplete investigations of effects of transformations suggested this was appropriate in the present case.

Our original data is in four-dimensional form viz 15 sites × 4 seasons × 2 years × 420 species, and desirably we should seek patterns between all possible pairs of these dimensions. When analysis commenced, no method of handling four-dimensional data had been developed, so our data was first regarded as three-dimensional and in the form of 15 sites × 8 times × 420 species. (The times 1–8 run sequentially from March 1970 at three month intervals to December 1971). The three-dimensional technique is as described by Williams and Stephenson (1973) and leads to three two-way coincidence tables, of sites and species, times and species, and sites and times. Flexible sorting with β at $-0{\cdot}25$ was used (see Lance and Williams, 1967; Stephenson, Williams and Cook, 1972).

CRITIQUE OF METHOD

We should first comment on the advantages of this method over the two approaches used previously. The first used a $qt \times s$ matrix (where q = quadrats, t = times and s = species). Analysis by any of the usual techniques of grouping samples usually reveals via the dendrograms whether the major influence is due to q or to t. Interpretation of subordinate groupings is difficult because they are variably homogeneous with respect to q and t attributes. Comparable difficulties arise if we make t separate analysis of q and s.

As quoted in an earlier paper (Stephenson, Williams and Cook, 1972) referring to work by Hailstone (1972) we stated: 'For each month of the year the data reveal site groups and species groups related through coincidence tables. But from month to month the site groups alter their composition and so do the species groups.'

Various sub-sets extracted from the present data had been separately analysed before the present main analysis began. These were the 55 species as related in Williams and Stephenson (1973), the ophiuroids (19 species) and tunicates (27 species). Details need not now concern us, the main conclusions were that the site-groupings obtained in each case were substantially similar, but the times-groupings were not. For example, with the tunicates the main picture was seasonal with grouping of times: 1 + 5, 2 + 6, and 3 + 7, but breaking down with 4 and 8. The 55 species and ophiuroids gave segregation of March data 1 + 5, with an annual pattern for the remainder, viz. 8 + 7 + 6, 4 + 3 + 2. With the 71 species selected as below yet another pattern emerged: 7, 8 + 6 + 5 + 1, 4 + 3 + 2.

It is evident that times-groupings give no overall conceptual picture. As in the case of $qt \times s$ matrices, groupings contained variable proportions of homogeneity with respect to two different variables. In the present case these are seasons (here m for months) and years (y). To resolve this difficulty one can again partition part of the data, converting times × species into the dimensional form of months × years × species (summed over all sites) i.e. $m \times y \times s$ where $m = 4$ and $y = 2$.

In the analyses which follow we commenced with a $q \times t \times s$ matrix, and following the methodology of the previous paper affect data reduction, consider the relative importance of the different comparisons and analyse them in a preliminary way. This leads to two extensions, firstly of the species/sites relationships ($s \times q$), and secondly to the species/times ones ($s \times t$) which are expanded to three dimensions ($s \times m \times y$).

ANALYSES OF SITES × TIMES × SPECIES

First Stages of Analysis

These involve species reduction and considerations related thereto.

We begin by summating and obtaining means (cube root data) of: (a) all species over all times at each site, and (b) all species over all sites at each time. Values are given in Table 5.

TABLE 5

Mean Values, Species Summated (Cube Root Data) in Sites 1–15, and in Times 1–8.

Site	Mean n	Times	Mean n
1	0·490	1	0·814
2	0·473	2	1·583
3	0·456	3	1·593
4	0·671	4	1·394
5	0·457	5	0·832
6	0·883	6	1·188
7	0·785	7	1·769
8	0·775	8	1·140
9	0·749		
10	0·739		
11	0·672		
12	0·664		
13	0·840		
14	0·806		
15	0·852		

The values in Table 5 are measures of total populations and are the transformed numerical equivalents of total biomass. These data already show some ‘ecological sense’, for example that (a) populations are least in the muddy sites 1, 2, 3, 5 and (b), a clear seasonal pattern exists with low populations in March, rising through June to a maximum in September and declining in December. Comparison of March 1971 (time 5) with March 1970 (time 1) fails to show the expected effects of the summer flood but there is possibly a delayed effect at June 1971 (time 6 cf. time 2).

The second step leading to species reduction is to determine the contribution each species makes in terms of squared euclidean distance to the differences between all pairs of sites—i.e. to site classification. Based upon these contributions we can have a method of species reduction which is quantified and can be subject to a single decision. In the earlier work, using 55 species, we showed an objective sum-of-squares chopping was much too drastic, replaced it by an arbitrary level and excluded species contributing less than 1% of the total variance. With the present full number of species (420) this would have left only 26 species. We reduced the level to 0·5% and retained 48 species.

In a similar way the contributions of each species to a time classification were evaluated, and taking the 0·5% level we retained 52 species. In the analysis detailed below we considered the 71 species which were present in one or another of the above lists. They are listed in Table 6 with only the generic name given when a single species of a genus is in the main list (see Appendix).

TABLE 6

71 SPECIES LIST, THE NEW ARBITRARY NUMBER IS GIVEN FOLLOWED BY THE ORIGINAL NUMBER IN PARENTHESIS.

1	(1)	*Discobotellina*
2	(29)	Nemertea—“pink”
3	(35)	? *Euleanira*
4	(36)	*Leanira*
5	(37)	*Sthenelais*
6	(58)	*Arabella*
7	(62)	*Eunice antennata*
8	(63)	*E. cf. indica*
9	(70)	*Onuphis* sp. (“long gill”)
10	(73)	*Chloeia*
11	(74)	*Eurythoe*
12	(75)	*Glycera americana*
13	(76)	*G. prashadi*
14	(77)	*Goniada*
15	(90)	*Nephtys*
16	(91)	*Amaeana*
17	(95)	*Loimia medusa*
18	(100)	*Pista* sp.3
19	(104)	*Terebellides*
20	(123)	*Chaetopterus*
21	(129)	*Euclymene*
22	(134)	*Magelona* sp.
23	(139)	*Petaloproctus*
24	(145)	*Spiophanes*
25	(159)	*Alpheus distinguentus*
26	(164)	*Axius*
27	(165)	*Callianassa*
28	(204)	*Carinapseudes*
29	(214)	*Columbella*
30	(221)	*Herpetopoma*
31	(236)	muricid 2
32	(244)	*Dentalium*
33	(258)	*Cycladicama*
34	(262)	*Modiolus ostentus*
35	(263)	*Ensiculus*
36	(265)	*Fulvia*
37	(267)	*Gari venta*
38	(269)	*Laternula*
39	(270)	*Leptomya pura*
40	(279)	*Malleus*
41	(283)	*Neosolen*
42	(285)	*Nucula astricta*
43	(288)	*Paphia gallus*
44	(289)	*P. subrugata*
45	(297)	*Placamen tiara*
46	(306)	*Tellina lilium*
47	(308)	*T. cf. solenella*
48	(316)	*Tucetilla*
49	(328)	*Golfingia*
50	(330)	*Thermiste*
51	(340)	*Amphioplus depressus*
52	(341)	*Amphipholis loripes*
53	(342)	*Amphioplus* sp.
54	(343)	*Amphiura bidentata*
55	(344)	*A. cataphes*
56	(350)	*Ophiocantha*
57	(356)	*Ophionereis*
58	(360)	*Hypselaster*
59	(364)	*Protankyra*
60	(367)	*Agnesia*
61	(373)	*Eugyra*
62	(381)	*Molgula exigua*
63	(382)	*M. rima*
64	(383)	*M. sabulosa*
65	(385)	*Polycarpa fungiformis*
66	(387)	*P. tinctor*
67	(390)	*Styela ramificata*
68	(394)	*Branchiostoma*
69	(413)	*Pseudocodium*
70	(419)	*Halophila ovalis*
71	(420)	*H. spinulosa*

The noteworthy groups are polychaetes (22 spp.), bivalves (16), tunicates (8) and ophiuroids (7); the noteworthy exclusions are all of the sponges, coelenterates and crabs, and all but one of the algae.

RELATIVE IMPORTANCE OF EACH COMPARISON

Using the 71 species, mean variances per comparison, as shown in Table 7, permit assessment of the relative importances of each comparison.

TABLE 7

MEAN VARIANCES PER COMPARISON

Nature of Comparison	Variance attributable to: sites	species	times	interaction
inter-sites	—	1·629	0·905	0·406
inter-species	1·629	—	1·123	0·406
inter-times	0·905	1·123	—	0·406

These data show that, with respect to species, site-groupings are about 50% more important than times-groupings. The site-times combination, which concerns the 'numbers' equivalent of the total biomass, is about 80% of the species-times combination. Its magnitude indicates that there are important chronological changes in total populations, as discussed earlier. The interaction is the variance left in the system when any two of the major variables have been eliminated. It is the smallest value in the table and is not readily amenable to commonsense ecological interpretation so is neglected.

SITE-SPECIES RELATIONSHIPS

Classifying the sites by the 71 species (fused over all times) and taking this to the four group level gives: I = 11 + 15, II = 6 + 7 + 8 + 9 + 10 + 13, III = 4 + 12 + 14, IV = 1 + 2 + 3 + 5. These are identical with those obtained in the preliminary analyses.

It is evident that there is small scale patterning within the area of study. With area I of 0·24 km^2 there is one site-group and part of a second; within area III of 0·36 km^2 there are elements of three site-groups; only area II of 0·16 km^2 appears biotically homogeneous. Further discussion of the site-groups is given later.

To determine how these site-groups are characterised by species, reference was made to the 2-way table, referred to in Williams and Stephenson (1973) as the *B* table which gives single values—these are the means of site-centred and species-centred deviations. Perusal suggested that many species-groups derived in the analyses were heterogeneous, and we reverted to the tables with double values i.e. site-centred values used in site classification and species-centred values for the species classification. Using the latter the species-groups now appeared more homogeneous internally, but still insufficiently so in some cases. While many species-groups contained species which conformed 'crisply' to the site-groups in others the sorting was more 'blurred'. A measure was sought of the extent to which species conformed to the site classification.

In general, the attributes used to define a numerical classification cannot be used as the basis for between-group tests of significance, since their differences have been optimized. It follows that the site-centred values could not be used for this purpose; it remains to consider whether the species-centred values can be used in their place. Unfortunately, the setting up of a two-way table implicitly assumes that the two sets of values are related, so that the between/within variance ratios will be conservative, not random, estimates. However, the variance ratio F can still be used as a measure of the extent to which a given species defines the different site-groups, and the values associated with the usual probability estimates can be taken as convenient points on an arbitrary scale. We shall henceforth refer to such tests as 'significance tests' for the sake of brevity; but it must be remembered that, though they are less biassed than would be the corresponding ratios obtained from the site-centred values, they are still biassed.

Using the above test for four site-groups and 15 sites, F values are as follows: 0·05–3·59, 0·01–6·22, 0·001–11·56. Although these values are conservative they can be used to grade species with respect to site-group conformation. Four grades were recognised with F values as follows: VH $>$ 11·56, H 11·56–6·22, M 6·21–3·59, and L $<$ 3·59.

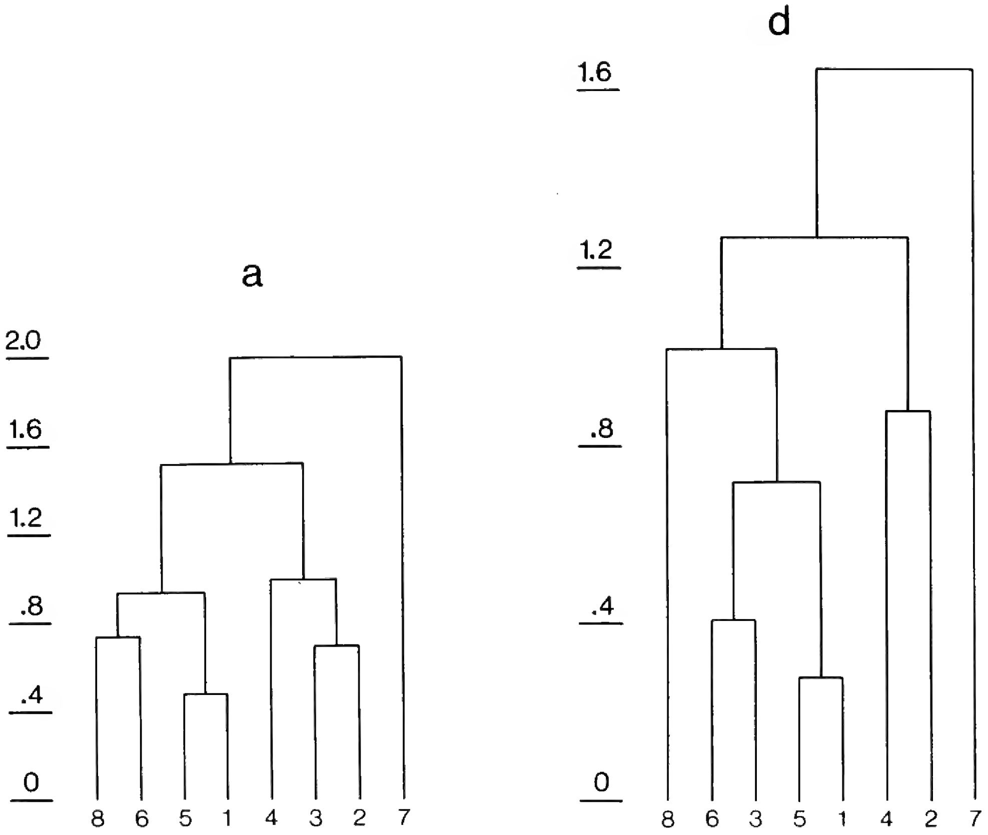

FIG. 3: Dendrograms showing classification of times by species (a) and sites (d); euclidean distance type of coefficient.

Of the 71 species classified, 22 were in the L grade, and this included species high on the list of contributions to site variance. Consideration of these and other species is given later.

TIMES-SPECIES AND TIMES-SITES RELATIONSHIPS

Using the 71 species list, four classifications were derived: (a) times by species, (b) species by times, (c) sites by times, and (d) times by sites. We consider first (a) and (d) above as shown in Figure 3.

In both cases the nearest pair of seasons (months) are 1 and 5 i.e. the 'normal' March of 1970 and the 'abnormal' March of 1971 immediately after the flood. It is evident that the immediate effects of the flood were minimal both on the total populations present (dendrogram d) and on the actual species present (dendrogram a).

In both cases the most isolated time is 7 (September 1971), suggesting a delayed flood effect. However in the times by sites analysis this time is characterised by a specially *abundant* total population. If there is a delayed flood effect it seems to have operated by allowing a transient increase in certain species which becomes evident after a delay of about nine months.

In neither case does the first or second dichotomy reflect a clear seasonal grouping or a clear annual grouping to indicate which factor is the more important. For this and other reasons stated earlier the analyses were expanded.

EXTENSIONS OF ANALYSES OF SPECIES-SITES

POSSIBILITY OF ALTERNATIVE SITE-GROUPING

Of the 71 species previously analysed it was considered that the 22 not fitting into the site-grouping earlier obtained, might conform to a different grouping. These species plus additional ones relatively high in the site variance hierarchy (= 34 in all) were used in a site reclassification. The site-groupings obtained were: 1 (very isolated), 12 + 14, 2 + 3 + 4 + 5, 13 + 15, 6 + 7 + 8 + 9 + 10 + 11. These do not reflect any obvious abiotic attributes nor an overall topographic pattern. Five of the six species highest in the variance hierarchy dominated the classification and gave almost individualistic distributions within the site-groups. While it is possible that another and more meaningful pattern would emerge if they were removed and the remainder re-analysed, it was considered more likely that yet more individualistic patterns would emerge. It was concluded that there is only a single important pattern of site-groupings.

No further mention is made of the species which failed to fit the general site-groupings, unless they appear in the later times-groupings. One species which seemed to characterise the area as a whole, and which was one of the characterizing species of the earlier dredge study, is eliminated from the present groups. It is *Leanira* (36).

CONSIDERATION OF ADDITIONAL SPECIES

The technique of testing species for significance of conformity to the major site-pattern was applied to all 420 species. Ninety-seven species conformed at the M grade or

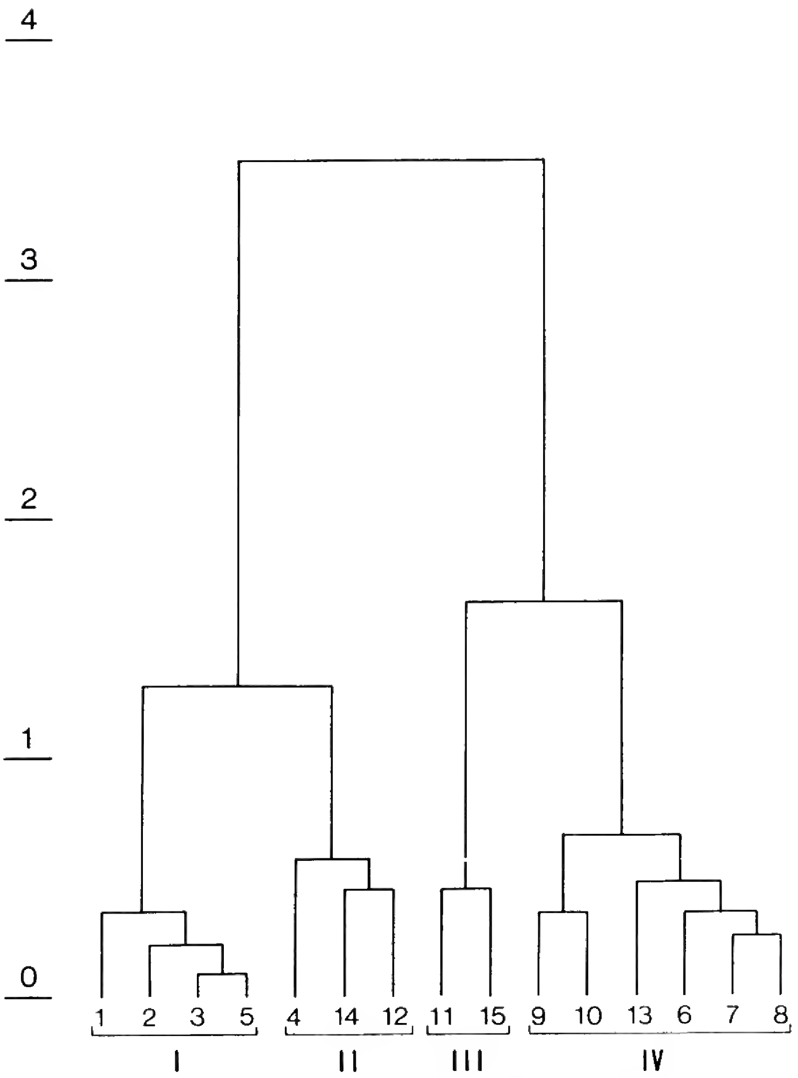

FIG. 4: Dendrogram of sites classified by 97 spp., euclidean distance type of coefficient. The site-groups (I–IV) do not refer to the area groups in Figure 2.

higher and these extended as low as 250th in the site-variance hierarchy. The matrix of 15 sites × 97 species was reclassified.

SITE-GROUPS

As expected, the four original site-groups were generated (see Figure 4) and as stated earlier these agree with those obtained using sedimentary attributes. The correspondence goes below the four group level; thus in site-groups I and II the 'aberrant' sites by both systems are 1 and 4 respectively. Site-group IV can readily be subdivided by both systems which agree in having sites 6, 7 and 8 in one subgroup and 9 and 10 in the other. The only discrepancy concerns site 13 which links with 6, 7 and 8 in the dendrogram and with 9, 10 by sediments.

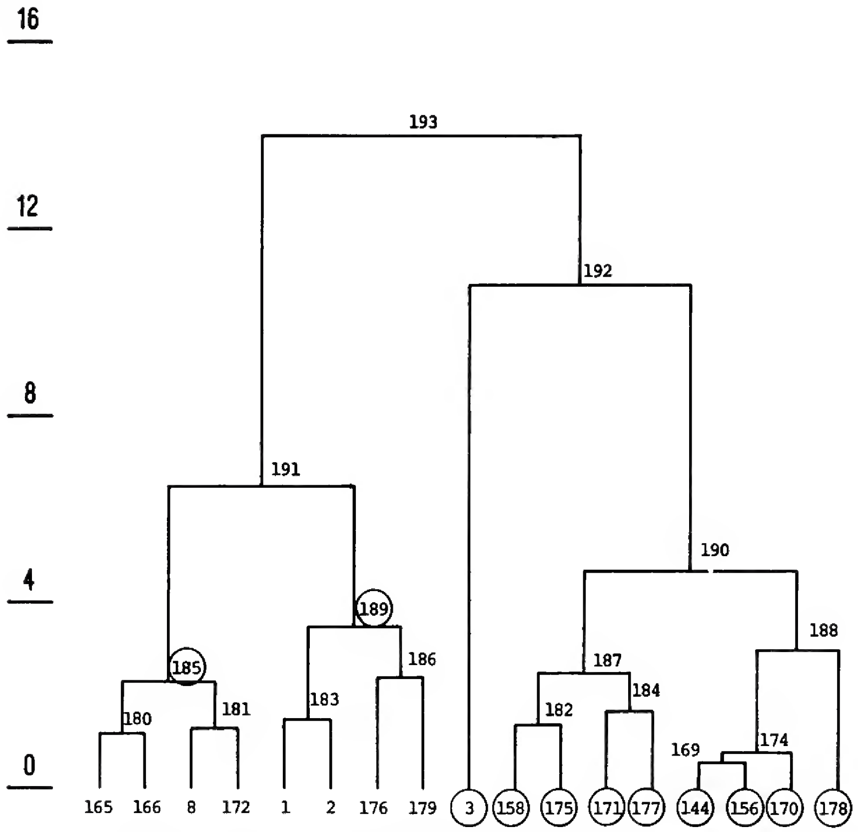

FIG. 5: Dendrogram of species-groups (involving 97 spp.) classified by sites, euclidean distance type of coefficient. The 17 groups originally considered were reduced to the eleven which are ringed.

SPECIES-GROUPS AND TWO-WAY TABLES

After generating an excess of species-groups, 17 were considered as shown in Figure 5. Further fusions within the exact framework of the dendrogram destroyed the conceptual sense of the species groupings as revealed in two-way tables. This sense was retained by accepting groups at different dendrogram levels, as shown in Figure 5, with a condensed two-way table in Table 8. In other cases we have investigated, acceptance at different levels has been due to group-size dependence, a phenomenon inherent in sharply clustering strategies such as the flexible strategy here employed. (See Williams et al, 1971 for discussion of group-size dependence). In the present case higher fusions were possible when the groups contained the more abundant species and this is discussed later.

Nine rows of Table 8 contain a single value distinctly higher than the remaining three, and here the species-groups characterize the site-groups in a positive way. Two rows contain two high values, and the relevant species-groups (189, 177) each positively characterize a pair of site-groups. There are only two possible species-groups with a single distinctly low value (189, 3) and in the discussion below we concentrate upon positive characterizations.

TABLE 8

MEAN DEVIATIONS OF SPECIES-GROUPS (SPECIES STANDARDIZED VALUES) IN SITE-GROUPS. SPECIES-GROUPS ARE AS IN FIGURE 5.

Species groups	Site-groups and sites therein I 1, 2, 3, 5	 II 4, 12, 14	 III 11, 15	 IV 6, 7, 8, 9, 10, 13
185	−1·8	−0·9	−1·6	2·0
189	−4·8	−2·3	3·5	3·2
3	−2·0	9·3	−4·4	−1·8
158	1·0	−0·1	−0·5	−0·4
175	−0·1	1·8	−0·4	−0·7
171	3·1	−0·4	−0·8	−1·6
177	2·3	1·3	−1·3	−1·7
144	−0·9	−0·4	2·0	0·1
156	−0·9	−0·6	−0·4	1·0
170	−1·9	−0·3	2·5	0·9
178	−0·1	0·2	4·4	1·5

Perusal of Table 8 shows that fusions of species-groups with similar positive characterisations are possible—for example species groups 144, 170 and 178 all characterize positively site-group III. Such heuristic higher groupings do not conform to those of the dendrogram (Figure 5), and the possibility of another classificatory strategy for species was considered. The heuristic species-groupings were retained and those given in Table 8 fused as follows:

A = 158 + 171, positive characterization of site-group I
B = 3 + 175, positive characterization of site-group II
C = 144 + 170 + 178, positive characterization of site-group III
D = 185 + 156, positive characterization of site-group IV
E = 177, positive characterization of site-groups I and II
F = 189, positive characterization of site-groups III and IV.

CHARACTERISTICS OF SPECIES IN SPECIES-GROUPS

Within each species-group, species were arranged in order of grades of conformity (VH, H and M) as defined earlier. Within these grades they were further graded in 'importance'. Importance values were estimated, within the 97 species, as the summated site-centred cube-root contributions of a given species to the site-classification. Values ranged from 79·2 to −24·1 and were graded: H $>$ 10, M 10 to 0, L $<$ 0. Within the conformity-importance groups species were arranged in systematic order, with numbering as in the Appendix, and are given in Table 9.

INTERIM SUMMARY OF SPECIES-SITES ANALYSES

Site-group III, comprising two sites (11, 15) and with a sediment of fine sand with a low percentage of mud, has the richest characterizing biota. This comprises the 24 spp. of

TABLE 9

CHARACTERISTICS OF SPECIES-GROUPS (SITE-ANALYSIS).

Species Group	Conformity grade	Importance grade	Species numbers (see Appendix)
A	VH	L	80, 358
	H	L	85, 204, 244, 311, 359.
	M	H	197, 420
		L	55, 66, 67, 126, 149, 214, 296, 303.
B	VH	H	364
		M	374
		L	306
	H	M	165
		L	277
	M	H	263
		M	342
		L	18, 97, 160, 286, 309, 346.
C	VH	H	129, 139
		L	109, 131, 255, 279, 395, 402, 419.
	H	H	62
		M	283
		L	120, 125, 210, 299.
	M	M	97, 100
		L	171, 193, 199, 233, 253, 372, 393.
D	VH	H	385
		M	316, 382
		L	132
	H	H	75, 288, 350
		M	221
		L	54, 72, 107, 156, 184, 267, 381, 390
	M	H	330
		M	1, 145.
		L	69, 70, 134, 140, 308, 356, 359, 366, 415.
E	VH	H	37, 285
	H	L	270, 274
	M	H	90, 104.
F	VH	H	63, 289, 297, 394
	H	H	35, 340, 386
	M	H	123

species-group A and the eight of species-group F. It also has the highest number of uniquely characterizing species with VH conformity—nine. Against the figures of 32 and 9 for site-group III there follow: site-group IV (coarse sand)—28 and 4; site-group I (mud)—23 and 2; and site-group II (fine sand with higher percentage of mud)—19 and 3. The composition of the species-groups is considered later.

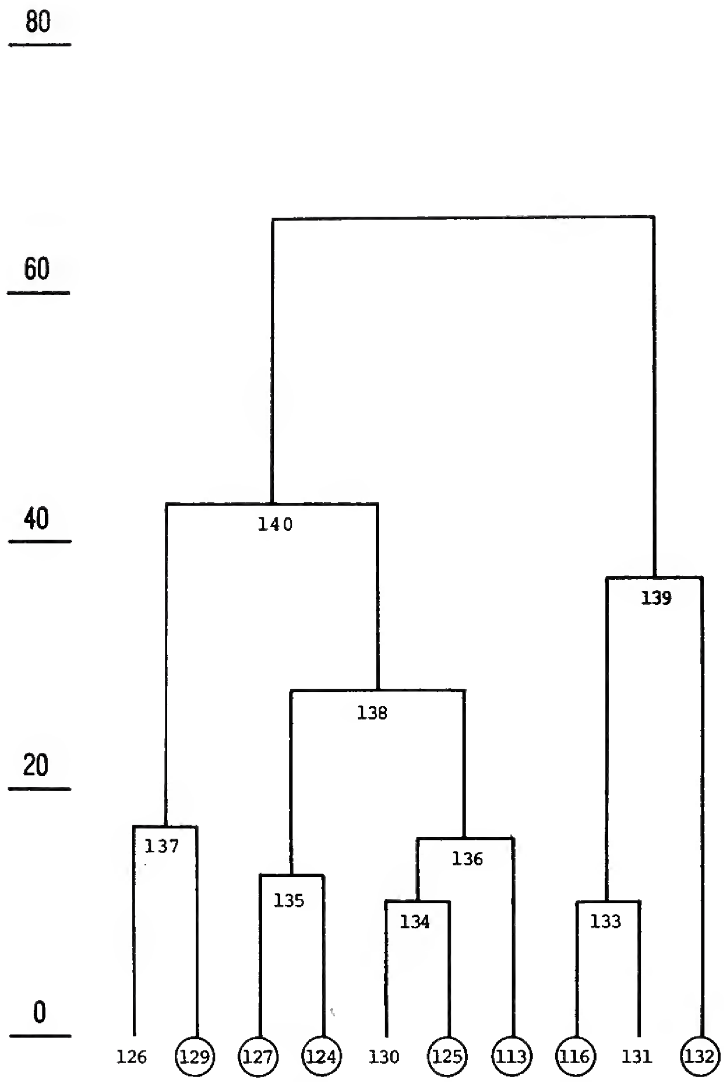

FIG. 6: Dendrogram of species classified by months. Species-groups with 'internal homogeneity' are ringed.

EXTENSIONS OF ANALYSES OF SPECIES-TIMES

Because the species-times relationships are of more interest than those of sites-times, expansion of times analyses were restricted to the former and now become a species × months × years situation in three dimensions.

RELATIVE IMPORTANCE OF EACH COMPARISON

Dealing with the original 71 species, mean variance per comparison is shown in Table 10. It will be noted that the total variance is half that of the species-times comparison listed in Table 7. The months × years comparison is approximately twice the importance of

TABLE 10

MEAN VARIANCES PER COMPARISON.

Nature of Comparison	months	Variance attributable to: years	species	interaction
Inter-months	—	0·270	0·077	0·055
Inter-years	0·270	—	0·129	0·055
Inter-species	0·077	0·129	—	0·055

the species × years, which in turn is almost double that of the species × months comparison. In other words, firstly changes in total populations with time are the most important elements and secondly that a monthly pattern of species common to the two years will be the 'weakest' of the three which emerge. This contrasts with the reasonable similarity of the month totals of species summated between the two years (see Table 5) and indicates that different species are replacing one another tolerably precisely from the months of 1970 to the equivalent months of 1971.

Seasonal and annual associations of species are investigated below, meanwhile the interaction values (0·055) should be noted. While low in absolute terms they are high relative to the species-months comparison. Again no ecological interpretation of this interaction is attempted.

SPECIES-MONTHS RELATIONSHIPS

Only four months (1, March; 2, June; 3, Sept.; and 4, Dec.) are involved. The months classification is of little interest, the dendrogram showing an initial dichotomy of 1+2 and 3+4. The similarity between 3 and 4 is slightly more than between 1 and 2.

The dendrogram of the species classification (Figure 6) was taken to the 10 group level, and the seven groups containing the species with the largest deviations of species-centred values were internally homogeneous in that all species characterized the same month in the same way. These groups are ringed in Figure 6. However the remaining three groups, which contained most of the species (46/71) each included species with either two or three types of month characterizations. This heterogeneity was not resolved by a finer classification. Even more so than in the study of species characterizing sites, was it necessary to alter the computer classification, and in the present case it was discarded.

Perusal of the values of species centred deviations showed, as with the species in site-groups, that some species had an outstanding positive deviation and hence positively characterized one of the four months. Others had negative characterizations and some appeared to have both positive and negative ones.

A method of quantifying an 'outstanding' deviation was required, bearing in mind that tests of significance are not possible with only four entities. That adopted was the proportion of the total variance of differences of the species-centred values contributed by the selected species-in-month values. Values for the 71 spp. ranged from ca. 0·3 to 0·76 and were graded arbitrarily as follows: 0·3–0·49, L (17 spp.); 0·50–0·59, M (21 spp.); 0·60–0·69, H (22 spp.); and 0·70–0·76, VH. Species with a L grade were eliminated.

When one of the remaining species appeared to characterize two seasons, one positively and the other negatively, it was accepted if (a) the variance due to these two seasons was 0·95 or more of the total, and (b) several such species showed similar characterizations. On these bases eight species with double characterizations were accepted.

It is appreciated that these criteria operate more stringently with respect to the month-groupings than those adopted for the site-groupings. This was done deliberately because in the present case there are not tests of significance and because there are fewer degrees of freedom.

TABLE 11

Species, with Numbers from Appendix, which Characterize Months.

Species group	Conformity grade	Importance grade	Species numbers
A	H	M	139
(+ve March)	M	H	123, 297
B	VH	L	165, 267
	H	H	73, 76
(+ve June)	M	M	385, 37
		L	360
C	VH	L	1, 373, 413
	H	M	29, 104
(+ve Sept.)		L	62, 100, 343, 367
	M	L	236, 241
D	H	L	145, 269, 306, 316
(+ve Dec.)	M	L	77, 283, 383
E	VH	H	289, 344
		M	387
	H	H	35, 364
(−ve March)		M	330, 420
		L	134, 263, 285, 342, 419
F	M	M	75
(−ve June)			
G	VH	L	221, 279
	H	L	288
(−ve Dec.)	M	H	90
		M	91
H*			
(−ve March)	H	H	63, 394
	M	H	36
		L	74, 204, 328
(+ve Sept.)	M	L	244, 341

*Double characterization −ve March, +ve Sept, grading restricted to outstanding cases.

Using these criteria and re-sorting the groups obtained by computer classification gave eight species groups. Conformity values of each species were obtained as previously—precise values differ because they were derived on different assemblages, one of 97 spp. and the other of 71. In Table 11 these data are given with the months they characterize positively, negatively and both.

Because only four months are considered and conformity grades are arbitrary the analysis was not extended beyond the 71 species of Table 6, and of the 54 species accepted 30 characterize months positively, 24 negatively, and 8 give double characterizations. The outstandingly 'weak' season is March with only three positive species and with 18 negative. It is followed by December with seven positive and five negative. The 'strongest' season is September with 19 positive and no negative species.

SPECIES-YEARS RELATIONSHIPS

The interest is in species-groupings, and the computer classification dissects an array of numbers in which each species bears balancing positive and negative deviations in the species-centred values. Groups are tabulated below by positive characterizations, also listed are the range of deviations in each group, the number of species it contains and the arbitrary grades of conformity which were given. Because there is only a single degree of freedom these grades were applied stringently.

TABLE 12

NUMBER OF SPECIES OF DIFFERENT CONFORMITY GRADES WHICH CHARACTERIZE POSITIVELY THE YEARS 1970 AND 1971.

1970		1971		Conformity grade
Range	No. spp.	Range	No. spp.	
0·44 – 1·1	10	0·0 – 0·7	11	discard
1·5 – 2·5	7	1·1 – 2·6	6	L
3·1 – 3·9	10	3·0 – 3·6	7	M
4·1 – 5·4	9	4·2 – 5·5	6	H
6·8 – 8·1	5	9·8	1	VH

Species are listed, with numbers from Appendix, in Table 13 for the upper three conformity grades, together with importance values obtained in the usual way.

MONTHS-YEARS RELATIONSHIPS

Data are given as a double 2-way table in Table 14 and show that the 1971 biota is less than that of 1970, suggesting adverse effects of the flood. This conclusion is negatived by the data in Table 5 (second column) which deals with all species and not merely the 71 used for Table 13. The lowest value in Table 5 is for March 1970, before the flood; this is confirmed in Table 14.

TABLE 13
Species, with Numbers from Appendix, which Characterize Positively the Years 1970 and 1971.

Species group	Conformity grade	Importance grade	Species numbers
A	VH	H	63, 344, 350, 364
		L	343
(+ve 1970)	H	H	73
		M	129, 159, 387
		L	37, 77, 360, 383, 390
	M	H	340, 394
		M	385
		L	1, 62, 204, 265, 279 285, 381
B	VH	L	342
(+ve 1971)	H	H	289
		M	104
		L	308, 341, 367
	M	H	35
		L	95, 145, 221, 236, 316, 382

TABLE 14
Two-Way Table of Months-Years; Upper Values Centred by Years, Lower Values by Months. Year Summations at Right, Monthly Ones Below.

		Months				Year Summations
		1, March	2, June	3, Sept.	4, Dec.	
Years	1, 1970	−0·5 −102·2	43·8 44·8	−1·3 43·0	25·7 14·3	y_1 67·7
	2, 1971	0·5 −67·3	−43·8 −9·0	1·3 79·5	−25·7 −3·2	y_2 −67·7
Monthly Summations		m_1 −169·5	m_2 35·8	m_3 122·5	m_4 11·1	

CONSIDERATION OF SPECIES-GROUPINGS

General Comparisons of Groupings

There are two difficulties. The first is that the species-groups derived by the computer analyses did not precisely coincide with those required on conceptual grounds—it was by using the latter that groups were accepted. The second is that a test of conformity of species to entity-groupings which had some statistical significance could only be applied to the species-in-sites data. This allowed acceptance of more species in sites data (97) than in months (54) or years (38) data.

A large fraction of the species which were above the M grade of conformity in the sites analyses were present in the other lists (39/97) and with lists of equal length the fraction would have increased. To exclude from site-classification all species with marked seasonal or annual patterns, as Petersen (1914) suggested, would greatly disturb the site-analyses and exclude much valuable data.

On general grounds one might have suspected that species of VH conformity to a particular entity group would include many cases of faithful species, which in turn would be uncommon and have low importance values. Survey of the data did not support this expectation; instead there are many cases of VH conformity coinciding with H importance. In these cases the diagnostic species are those of high dominance/constancy, and we have 'Petersen type communities' in the sense used in our previous paper (Stephenson, Williams and Cook, 1972). The difference is that these apply in an area sense (as did Petersen's) but also in a season and a year sense.

POST-ANALYTICAL DATA REDUCTION

Ninety-seven species can be accommodated in the site-groups. For each we have data in continuous form on the degree of conformity to the site-groups and on relative importance over all sites. Data involving this sort of detail are difficult to comprehend so both conformity and importance values have already been graded. As in earlier work (Stephenson, Williams and Cook, 1972) further data compression is necessary for comprehension and below we eliminate all except those with VH conformity or H importance. These reduced data are given in Table 15 and are discussed below, comparable data for month-groups and year-groups are given in Tables 16 and 17.

SPECIES IN SITE-GROUPS

Site-group I comprising the muddy sites is characterized uniquely by *Leocrates* (80) and *Ophiura kinbergi* (358) as VH conformity species and *Rhizopa* (197) and *Halophila spinulosa* (420) as H importance species. Ophiuroid 'communities' are known from muddy grounds from many parts of the world (see Thorson, 1957) and from our earlier work in Moreton Bay (Stephenson, Williams and Lance, 1970) and in New Guinea (Stephenson and Williams, 1971). This particular species has not been involved previously.

Site-group II comprising fine sand with a relatively high percentage of mud is characterized uniquely by three species at VH conformity levels. These are *Tellina lilium* (306), *Protankyra* sp. (364) and *Microcosmos* (374). The H importance species are *Ensiculus* (263) and *Protankyra* (364). Here the coincident occurrence of *Protankyra* indicates that a dominant species is characterizing a community in the classical manner (see Petersen, 1914: Stephenson, Williams and Cook, 1972). Community indicators, comparable to some of the present species, occur elsewhere, for example the many *Tellina* communities listed by Thorson (1957). The present species *T. lilium* has moderate constancy for a site-group which is predominantly muddy north of the mouth of the Brisbane River (Raphael and Stephenson 1972). In the present case it is, however also associated with *Protankyra*.

TABLE 15

SPECIES (IN GROUPS) CHARACTERIZING SITE-GROUPS* (CONDENSED FROM TABLE 9). POSITIVE CHARACTERIZATIONS.

Species group	Selected species VH conf.	H importance	Site-group characterized
A	80, 358	197, 420	I (sites 1, 2, 3, 5)—mud
B	306, 364, 374	263, 364	II (sites 4, 12, 14)—fine sand, high mud
C	109, 129, 131, 139, 255, 279, 395, 402, 419	62, 129, 139	III (sites 11, 15)—fine sand, low mud
D	132, 316, 382, 385	75, 288, 330, 350, 385	IV (sites 6, 7, 8, 9, 10, 13)—coarse sand
E	37, 285	37, 90, 104, 285	I and II
F	63, 289, 297, 394	35, 63, 123, 289, 297, 340, 386, 394	II and III

TABLE 16

SPECIES (IN GROUPS) CHARACTERIZING MONTHS-GROUPS* (CONDENSED FROM TABLE 11).

Species group	Selected species VH conf.	H importance	Month characterized
A	—	123, 297	March (+ve)
B	165, 267	73, 76	June (+ve)
C	1, 373, 413	—	Sept (+ve)
D	—	—	Dec (+ve)
E	289, 344	35, 364	March (−ve)
F	—	—	June (−ve)
G	221, 279	90	Dec (−ve)
H	—	63, 394	March (−ve), Sept (+ve)

*Only VH conformity and H importance species are listed. Species numbers are from the Appendix.

TABLE 17

SPECIES (IN GROUPS) CHARACTERIZING YEAR-GROUPS* (CONDENSED FROM TABLE 13). POSITIVE CHARACTERIZATION.

Species group	Selected species VH conf.	 H importance	Year
A	63, 343, 344, 350, 364	63, 73, 340, 344, 350, 364, 394	1970
B	342	35, 289	1971

*Only VH conformity and H importance species are listed. Species numbers are from the Appendix.

This latter species, under the name of *Leptosynapta* was one of the species which, in the earlier dredge survey (Stephenson, Williams and Lance, 1970) characterized the peripheries of the extensive sloping areas of mud to the north of the Brisbane River. In that earlier survey no '*Protankyra* grounds' were located in the Peel Island area. In the earlier survey *Ensiculus* was another characterizing species, but was not associated with the others now listed. It did characterize many of the areas near Peel Island, including the location of the present site-group.

Site-groups I and II are collectively characterized by two species of VH conformity—*Sthenelais* (37) and *Nucula astricta* (285), and four species of H importance—the two just cited together with *Nephtys* (90) and *Terebellides* (104). The three polychaetes have almost cosmopolitan distributions and have been involved in community descriptions elsewhere (see Thorson, 1957). Two (*Sthenelais* and *Terebellides*), like *Protankyra* in the dredge survey, characterized the muddy grounds to the north of the Brisbane River. Of these, one (*Terebellides*) is an important community indicator in the current work of Raphael and Stephenson. Again there is evidence of a 'Petersen-type community' in the co-occurrence of *Sthenelais* and *Nucula astricta* under both conformity and importance headings.

Site-group III comprising fine sand with a relatively low percentage of mud is uniquely characterized by nine species of VH conformity: sabellid 4 (109), the polyspecific *Euclymene* spp. (129), *Isolda* (131), *Petaloproctus* (139), *Circe* (255), *Malleus* (279), *Acetabularia* (395), *Gracilaria verrucosa* (402) and *Halophila ovalis* (419). Of these *Euclymene* and *Petaloproctus* are of H importance, as is another species *Eunice antennata* (62). Many of these species also characterized site-groups in our dredge survey but were spread between several species groups and there is little correspondence. None of the species characterize the areas being studied by Raphael and Stephenson.

Site-group IV comprising coarse sand is uniquely characterized by four species of VH conformity: *Lygdamis* (132), *Tucetilla* (316), *Molgula rima* (382), and *Polycarpa fungiformis* (385). The H importance species are *Glycera americana* (75), *Paphia gallus* (288), *Thermiste* sp. (330) and *Polycarpa fungiformis* (385). Again several species are common to one or another of the species-groups derived in the dredge survey, and none are amongst the important species just north of the Brisbane River (Raphael and Stephenson 1972).

There remain several species (species-group F) characterizing site-groups II and III. The VH conformity species are: *Eunice* cf. *indica* (63), *Paphia subrugata* (289), *Placamen tiara* (297) and *Branchiostoma* (394). All four have H importance values as have ?*Euleanira* (35), *Chaetopterus* (123), *Amphioplus depressus* (340) and *Polycarpa pedunculata* (386). Again most occurred in one or another of the groups from the dredge survey, but on preliminary results few appear important just north of the Brisbane river.

Summarizing the species in sites analysis: (a) there are several cases of 'Petersen-type communities' in which species of VH conformity also have H importance values, (b) many of the characterizing species of the present survey also characterized site-groups in the earlier dredge survey (Stephenson, Williams and Lance, 1970) but there are only slight correspondences in detail, (c) several of the species characterizing the more muddy sites of the present survey also in the current work, are characterizing muddy sites just north of the Brisbane river.

Several species which were intuitively thought to be characteristic of one area or another are not listed above. They include *Discobotellina* (1) which only has M conformity to site-group IV. Several species which occurred commonly and which might characterize the total area of investigation rather than sections of it are not listed. One such is *Leanira* (36), which did not conform to the major site pattern.

Species in Month-Groups

March has no species with VH positive conformity but two with H importance: *Chaetopterus* (123) and *Placamen tiara* (297). It is negatively characterized at the VH conformity level by *Paphia subrugata* (289) and *Amphiura catephes* (344), and at the H importance level by ?*Euleanira* (35) and *Protankyra* (364). Additional species are considered below.

June only has positive characterization at the levels now considered; the VH conformity species are *Callianassa* (165) and *Gari venta* (267) while the H conformity ones are *Chloeia* (73) and *Glycera prashadi* (76). September again only has positive characteristics with three species of VH conformity and none of H importance. The former are *Discobotellina* (1), *Eugyra* (373), and *Pseudocodium* (413). Additional species are considered later. December has no positive characterizations at the prescribed levels and is negatively characterized at VH conformity by *Herpetopoma* (221) and *Malleus* (279) and at H importance by *Nephtys* (90).

Finally, two species characterize March negatively and September positively at H importance; they are *Eunice* cf. *indica* (63) and *Branchiostoma* (394).

The results show only tenuous resemblance to the preliminary conclusions on seasonality from the earlier dredging work. In both studies *Protankyra* negatively characterized the warmer part of the year. In the previous work *Discobotellina* showed no seasonality, but now it does. This may relate to the different areas of sampling because the species is uniformly present in large numbers in the northern part of Moreton Bay but appears to occur in a patchy and spasmodic fashion near Peel Island. Studies by Stephenson and Rees (1965a, b) indicate that its normal life-span exceeds a year.

There are perplexing aspects to the results. One would have expected the seasonal species to be predominantly small, to include many algae and, following Kott's (1972) interpretation of our incomplete tunicate collections, to include many tunicates. In fact the species listed earlier include many of the larger forms, for example *Chaetopterus*, *Placamen tiara*, *Paphia subrugata*, *Chloeia* and *Malleus*. Moreover none of the above are highly mobile with the possibility of movement into and out of the area. This is the likely explanation of the seasonality of *Callianassa* which here occurs as juveniles and in which adults are likely to be more than one year old (Hailstone and Stephenson, 1961).

A possible explanation of this paradox is in the existence of topographical micropatterns with accidental concentration of sampling on certain patterns in certain seasons. As indicated elsewhere much more frequent sampling is required for adequate investigation of seasonality. Studies of populations of individual species which involve size measurements are also required; to date these have only done on *Discobotellina* (Stephenson and Rees, 1965a, b) and on intertidal populations of *Callianassa* (Hailstone and Stephenson, 1961).

SPECIES IN YEAR-GROUPS

The five species with VH conformity for 1970 are: *Eunice* cf. *antennata* (63), *Amphiura bidentata* (343), *A. catephes* (344), *Ophiacantha* (350) and *Protankyra* (364). Of these *Eunice*, *A. catephes*, *Ophiacantha* and *Protankyra* have H importance, as have *Chloeia* (73), *Amphioplus depressus* (340) and *Branchiostoma* (394). A single species characterizes 1971 with VH conformity—*Amphioplus* sp. (342) with two species of H importance—?*Euleanira* sp. (35) and *Paphia subrugata* (289). With the exceptions of *Chloeia* and *Paphia* all are small species and many are surface-dwelling ophiuroids whose populations might be expected to change from year to year. The surprising exclusions from the list are the smaller tunicates—these were below the arbitrary levels which were selected.

DISCUSSION

INTRODUCTORY

The objective of the present work was to investigate a suspectedly complex benthic biota and to attempt to resolve the complexity into a number of patterns in terms of area and of time. We use the term 'complexity' in deliberate avoidance of 'diversity' which means so many things to so many people.

Fifteen stations were sampled in quintuplicate at each of four seasons for two years. The method of analysis with which we began was developed by use of a selected array of the present data, has already been described (Williams and Stephenson, 1973), and has been discussed earlier in the present paper. It involves three arbitrary elements. The first is the stringency of transformation (we used cube roots), the second the level of data reduction (this we modified, excluding initially species contributing less than 0·5% of the variance to the two initial analyses), and the third the sorting strategy (we used flexible).

SITE-GROUPS

We first examined the site-groupings obtained using species as attributes (summed over all times). The past literature on soft-bottom benthos has sometimes stressed site-groupings and sometimes species-groupings, and there is uncertainty amongst ecologists generally as to which are the most important. Noy-Meir's (1970) canvassing of opinion of non-marine ecologists suggested a preference for site-groups. If, following Dahl (1908), communities are delimited biotopically, a view which appears (unforunately) to be gaining ascendency in ecological texts (see Stephenson, 1973), then clearly site-groups are at the core of the community concept. While we later concentrate on species-groupings, site-groupings are of great importance for two reasons. The first is that we can use their extrinsic abiotic attributes as criteria for choosing between classificatory methodologies (see Stephenson, Williams and Lance, 1970; Stephenson and Williams, 1971; Stephenson, 1973). The second is that we can use site-groups via two-way coincidence tables to link the species-groups to the abiotic environmental features.

We used the first in preliminaries to the present work and compared the site-groups which were generated by different transformations of three sub-sets of the present data. It was on this basis that a cube-root transformation was selected.

As regards the second, there is an extraordinary resemblance between the site-groups generated by using species as attributes and the sediment classification of the sites. The correspondence is so close that the effects of other abiotic variables are completely masked. This almost exact relationship was not apparent when date for our earlier paper (Williams and Stephenson, 1973) were at hand. Sediment data for this earlier work were obtained at the start of the survey (March 1970), the data used in the present work was the average of values for March 1970 and December 1971.

The differences between these two sets of values were greater than expected, and because sediment grades are so important it is evident that much more data should have been collected. This would have indicated whether sediments were changing on a short term basis (for example between spring and neap tides), on a long term basis (over several years) or whether the differences in the sets of data are due to different 'random' samplings of topographical micropatterns.

An original objective was to determine whether there were small scale area patterns in the area. They are clearly present. Within one area (I) of 0·24 km^2 there is one site-group and part of a second, and within another (area III) of 0·36 km^2 there are elements of three site-groups. Within our area it would have been desirable for the intersite distances to have been no greater than 0·25 km for adequate delineation of the kind of group we obtained. This indicates that close spacing is likely to be desirable in inshore sub-tropical areas with varying sediments and under some estuarine influences. Pearson (1970) has already suggested that the scale of inshore patterns is finer than offshore. We have already indicated (Stephenson, Williams and Cook, 1972) that Petersen's (1914) stations were too distantly spaced to show coherent area patterns, and the present work confirms this opinion.

A second kind of site-grouping was provided by the analyses—this is using times as attributes (with summation of species). It gives little conceptual advantage over consideration of the summed values of all species over all times in the sites—as in Table 5. The main conclusion is that the muddy sites (1, 2, 3 and 5) have the lowest total populations.

SPECIES IN SITES

As the present work progressed it became evident that interest was primarily focussed on species. It was equally evident that the 'inverse' classifications as revealed in the dendrograms were not producing optimal sense. This led to the first important modification of the Williams and Stephenson (1973) methodology. In the previous paper in order to produce a single two-way table showing site-groups and their constituents and species-groups with their constituents, we had to marry classifications using two different sets of derived data. These were site-centred deviations as used in the site classification and species-centred deviations as used in the species classification. We did this, in tables designated 'B', by taking the mean of the two differently centred values. In an attempt to resolve some of the problems of species classification we considered only species-centred values. This gave slightly greater conceptual sense, but difficulties remained. Their resolution, such as it was, was affected by concentrating on the species-centred values in site-groups obtained by using site-centred data.

The computer classification we used is based upon the euclidean distances of species one from another (using cube-root data) and these distances are greater with the more abundant species. The less abundant species tend to be 'lumped' into what are virtually discard groups.

The conceptual aim in a species/site situation is to determine which species characterize a site by predominantly occurring there (or by predominantly not occurring there). This predominance is not necessarily proportional to the abundances of the species, indeed on the assumption that species of high fidelity are relatively uncommon, the reverse might be expected.

In the species-in-sites classification, species-groups derived by variance of differences were acceptable at different levels on the dendrogram, and only at lower levels for the less common species. It was necessary to redesign the upper parts of the hierarchy by commonsense methods.

Neither the original strategy nor its commonsense substitute were satisfactory for deciding in doubtful cases whether a species was predominant in a particular site-group. Here a 'test of significance' was used—the ratio of between site-group variances to within site-group variances (the F test). The affinities between species on different branches of the dendrogram became obvious when this ratio was employed.

The availability of an approximate test of significance of a given species to a predetermined site-grouping is an important auxillary advantage of the present methodology. It allowed us to reject species of low conformity to the grouping, and also to scan the total species list (beyond those with high site variance values) to pick out further conformers. As a result almost one quarter of the biota are known to conform to the site-groups we had specified.

Having selected some species with high contributions to site-variance which did not conform to the original site-groupings we added species lower on the site-variance list and searched for an alternative site-grouping. None eventuated in the present case. There is no certainty that this would be so in other situations and it is quite possible that an area might contain sediment-sensitive and pollution-sensitive species which could generate alternative site-groupings. To be able to explore such possibilities is another advantage of the present technique.

The tests of significance were used to produce grades of conformity of species to site-groups, and we have used the term 'conformity' throughout. In our previous numerical analyses of benthic data we have characterized species by the terms long used by terrestrial botanists—dominance, constancy and fidelity. Previously the stress has been on dominance and constancy (see Williams, Stephenson and Lance, 1970; Stephenson and Williams, 1971; Stephenson, Williams and Cook, 1972). 'Conformity' combines the three concepts. Thus high positive conformity of a species to a site-group means that most individuals occur in that group. This is irrespective of the actual numbers there present. High positive conformity can occur with an uncommon species, in which case it equates to fidelity. It can also occur in an abundant species, in which case it is likely to equate to dominance/constancy. Another type of conformity occurs, although more obvious in later analyses. This is high negative conformity—it means that a species 'avoids' a site-group. To describe this in terms of negative dominance/constancy/fidelity introduces conceptual problems, so throughout we adhere to the terminology and concept of 'conformity'.

While dominance grades in a given site-group are thus discarded, relative abundances of species in a particular data matrix are readily obtained. They are the summations between site-groups of the site-centred deviations which are used in site-grouping. Because the term 'dominance' has a within site-group connotation we have used the term 'importance' for these summated values and graded them on an arbitrary basis. We might expect that the less common species with lower importance values would have the most discrete sorting into site-groups (i.e. show the highest fidelity) but the data did not show this—neither did it apply to the species in month-groups detailed later.

TIMES ANALYSES

The relative importance of times and sites with respect to species is indicated in Table 7 and is about 2:3. The times-sites comparison is a measure of the changes in total population (all species summated) and is less than that of species-times in the ratio of 4:5. The chronological changes in total population through time are also shown in Table 5.

Attempts to classify times by species were regarded as unsatisfactory because the dimension time involves two dimensions—months and years. The time-species data were expanded to three dimensions of species × months × years. This gives, overall, a partial partitioning in four dimensions. In general terms by successive paritioning of a matrix in which one dimension is species, there is no theoretical limit to the number of dimensions which may be explored.

Within the species-times data, Table 10 shows that the greatest amount of variance is between months and years—i.e. in total population of all species summated, rather than in either of the combinations involving species. This indicates considerable replacement of one set of species by another set (or sets) as time proceeds. The species-year variance is almost double that of species-seasons indicating that annual changes in species composition are more important than seasonal ones.

Data on the population changes from 1970 to 1971 are ambiguous (compare Tables 5 and 14) but it is clear that if there was any population reduction due to floods, there was a delay period of about six months, as evidenced the low values of June 1971. The smallest total population was in March 1970; then and previously there had been no obvious abiotic adversities. The highest total population was in September 1971 and because this followed an exceptionally dry winter, it may indicate that the salinities in the area are sub-optimal throughout. In summary explanations of differences in populations between 1970 and 1971 are tenuous.

Analyses of the species-months data were concentrated on delimiting species-groups characterizing particular months. Because there are only four months to consider, tests of significance of conformity could not be made. It is plain that, for a satisfactory study of season changes more frequent sampling, for example 12 times annually, is required. We estimated conformity by using ratios of variance and obtained arbitrary grades; because they were arbitrary we did not extend the selection to species beyond the 71 species list of Table 6. Seventeen of the 71 species were eliminated because of very low conformity, and the remaining 54 already present more data than is readily comprehensible. Values of importance for the 54 species were obtained and have been cited (Table 13).

The main difference in emphasis between the site-conforming species and the month-conforming species is that the latter contained a large fraction (24/54) giving negative characterization—almost exclusively of March.

Analyses of species/years were purely in terms of species, and grades of conformity are arbitrary. They were made by using the points of dissection in an essentially continuous array which were revealed by the classificatory programme. The flexible sorting strategy which was used here proved its value—it optimizes discontinuties. Again the inadequacy of the data are apparent. Because annual effects are clearly important (in the present case more important than seasonal ones), to document their reality in terms of significance and to elucidate their causes would require data extending over possibly a decade.

With the present data limitations each species which positively characterizes one year gives an equal negative characterization of the other. Comparisons of the numbers of positive and negative characterizations with those of other analyses are impossible.

The most important general comment on the species-times data is that it allows us to think of species-groups in seasons and species-groups in years as well as species-groups in sites. We are no longer like Petersen (1914) bound to eliminate 'seasonal animals' from our ideas of communities, or more strictly of associations (Mills, 1969; Stephenson, Williams and Cook, 1972). We return later to the contribution of these three kinds of species-groups to an understanding of the complexity of the area.

The most important pragmatic consideration is that if a sampling programme is limited to a single set of samples taken 'instantaneously', a great deal of relevant information is likely to be missing. We understand that such sampling programmes are normally all that are required by authorities considering whether or not an engineering project is likely adversely to effect an environment—these are the 'environmental impact' statements. It would clearly be impossible, even with the present fairly extensive data, for us to predict in any detail the natural changes which might occur in our sampled area. To predict with any degree of confidence, the possible effects of superimposed changes might require an initial survey of ten years duration.

COMPLEXITY AND DIVERSITY

In the extensive literature upon diversity which has developed since the later 1950's considerable attention has been paid to the comparison of diversities from different situations, and particularly from different latitudes. Recent reviews have been given by Recher (1972) and by Whittaker (1972) and critical earlier papers are by Fischer (1960), Klopfer and MacArthur (1969), Saunders (1968) and Thorson (1952). At the level of species richness there is an immense literature in faunistic and floristic treatments of various taxa.

There seems to be general agreement that diversity comparisons should either be within ecological units or between them. The units envisioned are sometimes habitats, and thus we have within-habitat α diversity and between-habitat β diversity. Sometimes diversity is considered within an 'ecological community' (Edden, 1971) and sometimes applying to a 'community biota' (Hendrickson and Ehrlich, 1971). The concepts and comparisons are valid when, and only when, there is agreement on what a habitat is or an ecosystem is. Delimitations of 'habitats' and 'ecosystems' involves human judgements which seem often to be made upon undefined bases. We suspect that a 'habitat' judgement is usually made by the human eyes or by instrumental measurements of the abiotic features in a situation. If so it is directly comparable to biotopic concepts of the community which originated with Dahl (1908). These notions seem open to severe criticism in that we determine the boundaries and hope that the organisms will respect them. The history of marine soft-bottom 'communities' which began with Petersen (1914) has not a tradition of accepting biotopic boundaries, probably because consideration of abiotic attributes produces continua. Boundaries have been set by the organisms, the 'communities' are biocoenoses. In fact as already stated by Mills (1969) and Stephenson, Williams and Cook (1972) the word 'associations' is more appropriate.

If the 'communities' are though of as site-groups derived by using species as attributes, if there is a complex situation and if one is not to discard data on most of the species, one is forced into one or another method of numerical classification using computer techniques. Different methodologies produce different groupings and techniques of handling data are still evolving. Some advances were made in the preliminary paper using some of the present data (Williams and Stephenson, 1973) and others are contained in the present paper. No satisfactory technique exists in which there are statistically acceptable tests of the level at which, in a classificatory hierarchy, a site-group can be accepted or rejected.

In comparisons between apparently similar 'habitats' at different latitudes it is possible that the sizes of site-groups which one would accept would differ. In more specific terms one explanation for increased tropical diversity could be the existence of topographical micropatterns of site-groups. Another term for this is 'patchiness', and references to this are given by Pielou (1966) and Lloyd (1967). Both deal with the topic somewhat theoretically. In studies of soft-bottom benthos there appear to have been no investigations of the scales of patterning in comparable tropical, subtropical and temperate soft bottom environments. We believe our own investigations have been of a finer scale than others and we have revealed small-scale topographical patterning. We suspect that the real scale may be finer than that which we have revealed.

Meanwhile, as Pearson (1970) has indicated, there may be obvious geographical change in patterning as one moves from inshore to offshore localities. This, as well as latitudinal changes, merits detailed investigation.

There are many problems centred around the time factor in ecological surveys, including the methodological problems with which we have been concerned earlier in this paper. There are also conceptual problems, for example whether or not the 'community concept' should or should not include chronological changes. Many of the earlier definitions of communities and associations exclude the time element deliberately or by implication. As stated in an earlier paper (Stephenson, 1973): 'For example Möbius (1877) spoke of a community in which the total of species is mutually linked under the *average external conditions of life*. Hesse (1924) said that the groupings correspond with *average prevailing conditions* [The italics are not in the originals] . . . It seems that the terrestrial botanists have adopted a similar view. Their associations are characterized by such things as constancy of species, and seasonal species are clearly inconstant on a continuous chronological scale'. Later definitions involve dynamic concepts, for example Resvoy's (1924) mention of dynamic balance, and Emerson's (1939) concept of a chronologically adjusting super-organism.

Once the notion is established that there are seasonal changes and 'seasonal communities' we are in danger of conflict with one of the shibboleths of current thinking about diversity. This is the belief that high diversity occurs in situations of high stability. This danger of confrontation cannot be avoided if there is a component of complexity which is due to different annual 'communities', in which there is no evidence of regularity of re-occurrence. We have demonstrated that there are differences between one year and another in our own situation and that they are more important than seasonal differences.

There is nothing intrinsically wrong with the argument that a situation showing annual instability should be more complex than one with annual stability. Indeed the argument appears as if it should run: biotic uncertainty equates to abiotic uncertainty; whence diversity equates to an environment showing differences from year to year. To this argument we should add two important riders.

The first is that, in our present situation, there is no clear evidence that the difference between the two years of the investigation was directly due to abiotic events. The second is that in discussing chronological instability in abiotic factors there are likely to be differences in scale. Gross instability is likely to lead to reduction in complexity, whereas instability within 'acceptable limits' may well increase it. The 'acceptable limits' will be in terms of the range and availability of organisms capable of immediate replacements in changed areas. What applies to an inshore situation with occasional reduction of salinities, or with changes in sedimentary patterns, can not be expected to apply to the terrestrial biota of an oceanic island devastated by a volcanic eruption.

Just after the above was written the senior author was given by W. Sakai (private communication) results of a startling simple demonstration of the effects of instability within 'acceptable limits' causing an increase in diversity. Sakai worked on clumps of mussels and showed that moderate mechanical disturbance increased diversity.

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APPENDIX I

SPECIES OBTAINED, WITH ORIGINAL ARBITRARY NUMBERS.

PROTOZOA
  FORAMINIFERA
  1 *Discobotellina biperforata* Collins

PORIFERA
  2 Cushion Sponge
  3 Sponge I
  4 Sponge 2
  5 Sponge 3
  6 Sponge 4
  7 Sponge 5
  8 Sponge 6
  9 Sponge 7
  10 Sponge 8
  11 Sponge 9
  12 Sponge 10
  13 Sponge 11

CNIDARIA, ANTHOZOA
  GORGONACEA
  14 'Whip coral'
  15 'Rusty wire' gorgonid
  PENNATULACEA
  16 *Scleroblemnon* sp.
  17 Sea pen
  CERIATHARIA
  18 cf. *Cerianthus* sp.
  ZOANTHARIA
  19 *Sphenopus marsupialis* (Gmelin)
  ACTINIARIA
  20 *Edwardsia* sp.
  21 Anemone 1
  22 Anemone 2
  23 Anemone 3

PLATYHELMINTHES
POLYCLADIDA
24 Sp. 1
25 Sp. 2

NEMERTEA
26 'Black'
27 'Brown'
28 'Pale'
29 'Pink'
30 'Speckled'
31 'Sunburnt'
32 'White striped'
33 'Red'
34 'Red and white'

ANNELIDA, POLYCHAETA
APHRODITIDAE
35 ? *Euleanira* sp.
36 *Leanira yhleni* Malmgren
37 *Sthenelais boa* (Johnston)
38 Sigalionid 1
39 Sigalionid 2
40 'Small aphroditid' 1
41 'Small aphroditid' 2
42 'Small aphroditid' 3
43 'Small aphroditid' 4
44 'Small aphroditid' 5
45 'Small aphroditid' 6
46 'Small aphroditid' 7
47 'Small aphroditid' 8
48 'Small aphroditid' 9
49 'Small aphroditid' 10
50 'Small aphroditid' 11
51 'Small aphroditid' 12
52 'Small aphroditid' 13

NEREIDAE
53 *Ceratocephala sibogae* (Horst)
54 *Nereis jacksoni* Kinberg
55 *Leonnates stephensoni* Rullier
56 *Platynereis insolita* Gravier
57 *Websterineris punctata* (Wesenberg-Lund)

EUNICIDAE
58 *Arabella iricolor* (Montagu)
59 *Drilonereis* sp. 1
60 *Driloenreis* sp. 2
61 *Drilonereis* sp. 3
62 *Eunice antennata* (Savigny)
63 *Eunice* cf. *indica* Kinberg
64 Eunicid ('4 antennae')
65 *Lumbrineris latreilli* Audouin and Milne Edwards
66 *L. maxillosa* (Ehlers)
67 *L. mirabilis* (Kinberg)

68 *L. mucronata* Ehlers
69 *Marphysa sanguinea* Montague
70 *Onuphis* sp. ('long gill')
71 *Onuphis* sp. ('short gill')
72 *Rhamphobranchium* sp.

REMAINING ERRANTIA
73 *Chloeia flava* (Pallas) (Amphinomidae)
74 *Eurythoe cf. parvecarunculata* Horst (Amphinomidae)
75 *Glycera americana* Leidy (Glyceridae)
76 *G. prashadi* Fauvel (Glyceridae)
77 *Goniada eremita* Audouin and Milne Edwards (Glyceridae)
78 Hesionid 1 (Hesionidae)
79 Hesionid 2 (Hesionidae)
80 *Leocrates cf. claparedii* (Costa) (Hesionidae)
81 Phyllodocid 1 (Phyllodocidae)
82 Phyllodocid 2 (Phyllodocidae)
83 Phyllodocid 3 (Phyllodocidae)
84 Pilargid 1 (Pilargidae)
85 Pilargid 2 (Pilargidae)
86 Pilargid 3 (Pilargidae)
87 Syllid 1 (Syllidae)
88 Syllid 2 (Syllidae)
89 Syllid 3 (Syllidae)
90 *Nephtys dibranchis* Grube (Nephtyidae)

TEREBELLIDAE
91 *Amaeana trilobata* (Sars)
92 *Amphitrite rubra* (Risso)
93 *Lanice conchilega* (Pallas)
94 *Loimia ingens* (Grube)
95 *L. medusa* (Savigny)
96 *Lysilla* sp.
97 *Pista typha* Grube
98 *Pista* sp. 1
99 *Pista* sp. 2
100 *Pista* sp. 3
101 *Streblosoma gracile* Caullery
102 *Streblosoma* sp.
103 *Telothelepus* sp.
104 *Terebellides stroemi* Sars
105 *Trichobranchus gracialis* Malmgren

SABELLIDAE
106 Sabellid 1
107 Sabellid 2
108 Sabellid 3
109 Sabellid 4
110 Sabellid 5
111 Sabellid 6
112 Sabellid 7
113 Sabellid 8
114 Sabellid 9
115 Sabellid 10
116 Sabellid 11

REMAINING SEDENTARIA

117 *Amphicteis gunneri* (Sars) (Ampharetidae)
118 *Anchenoplax* sp. (Ampharetidae)
119 *Armandia cf. intermedia* Fauvel (Opheliidae)
120 *Armandia* sp. (Opheliidae)
121 *Bucherta* sp. (Capitellidae)
122 Capitellid 1 (Capitellidae)
123 *Chaetopterus variopedatus* Renier (Chaetopteridae)
124 *Cirriformia ankylochaeta* (Schmarda) Cirratulidae)
125 *Coppingeria longisetosa* Haswell (Flabelligeridae)
126 *Dasybranchus caducus* (Grube) (Capitellidae)
127 *Diplocirrus* cf *capensis* Day (Flabelligeridae)
128 *Diplocirrus* sp. 2 (Flabelligeridae)
129 *Euclymene* spp. (Maldanidae)
130 *Haploscoloplos bifurcatus* Hartman (Orbiniidae)
131 *Isolda pulchella* Muller (Ampharetidae)
132 *Lygdamis cf. indicus* Kinberg (Sabellariidae)
133 *Magelona cincta* Ehlers (Magelonidae)
134 *Magelona* sp. (Magelonidae)
135 Maldanid ('parchment-grit tube') (Maldanidae)
136 *Mesochaetopterus minutus* Potts (Chaetopteridae)
137 *Notomastus giganteus* Moore (Capitellidae)
138 *Pectinaria antipoda* Schmarda (Pectinariidae)
139 *Petaloproctus terricola* Quatrefages (Maldanidae)
140 *Piromis cf. arenosus* Kinberg (Flabelligeridae)
141 *Piromis* sp. 2 (Flabelligeridae)
142 *Polydora* sp. (Spionidae)
143 *Polyophthalmus pictus* Dujardin (Opheliidae)
144 *Pseudocapitella* sp. (Capitellidae)
145 *Spiophanes* sp. (Spionidae)
146 Spionid 1 (Spionidae)
147 Spionid 2 (Spionidae)
148 Spionid 3 (Spionidae)
149 *Sternaspis scutata* (Renier) (Sternaspidae)

UNCERTAIN FAMILIES

150 Polychaete 1
151 Polychaete 2
152 Polychaete 3

ARTHROPODA, CRUSTACEA

STOMATOPODA

153 *Squilla anomala* Tweedie
154 *S. fasciata* de Haan

DECAPODA

155 *Achaeus brevirostris* (Haswell) (Majidae)
156 *A. lacertosus* Stimpson (Majidae)
157 *Actaea savignyi* (H. Milne Edwards) (Xanthidae)
158 *Actumnus* sp. (Xanthidae)
159 *Alpheus distinguentus* de Man (Alpheidae)
160 *A. stephensoni* Banner and Smalley (Alpheidae)
161 *Alpheus* sp. near*pacificus* (Alpheidae)
162 *Alpheus* sp. 1 (Alpheidae)
163 *Alpheus* sp. 2 (Alpheidae)

164 *Axius glyptocercus* von Marthens (Axiidae)
165 *Callianassa australiensis* Dana (Callianassidae)
166 *Calmania prima* Laurie (Xanthidae)
167 *Ceratoplax truncatifrons* Rathbun (Goneplacidae)
168 *Chlorinoides longispinus* (de Haan) (Majidae)
169 *Cryptodromia unilobata* Campbell and Stephenson (Dromiidae)
170 *Cryptopodia queenslandi* Rathbun (Parthenopidae)
171 *Dorippe australiensis* Miers (Dorippidae)
172 ? *Globopilumnus* sp. (Xanthidae)
173 'Hermit crab' (Paguridae)
174 *Hexapus granuliferus* Campbell and Stephenson (Goneplacidae)
175 *Hyastenus convexus* Miers (Majidae)
176 *H. diacanthus* (de Haan) (Majidae)
177 *Leucosia ocellata* Bell (Leucosidae)
178 *L. pubescens* Miers (Leucosidae)
179 *Leucosia* sp. (Leucosidae)
180 *Libystes paucidentatus* Stephenson and Campbell (Portunidae)
181 *Macrophthalmus* sp. (Ocypodidae)
182 *Myra affinis* Bell (Leucosidae)
183 *M. australis* Haswell (Leucosidae)
184 *Nursia plicata sinuata* Miers (Leucosidae)
185 *Parthenope harpax* (Adams and White) (Parthenopidae)
186 *Parthenope* sp. (Parthenopidae)
187 *Phalangipus australiensis* Rathbun (Majidae)
188 *Pilumnoplax* sp. (Goneplacidae)
189 *Pilumnus contrarius* Rathbun (Xanthidae)
190 *P. minutus* de Haan (Xanthidae)
191 *Pilumnus* sp. (Xanthidae)
192 *Pinnotheres spinidactylus* Gordon (Pinnotheridae)
193 *Pisidia dispar* (Stimpson) (Porcellanidae)
194 *P.* cf. *spinulifrons* (Miers) (Porcellanidae)
195 *Polyonyx transversus* (Haswell) (Porcellanidae)
196 *Raphidopus ciliatus* Stimpson (Porcellanidae)
197 *Rhizopa gracilipes* Stimpson (Goneplacidae)
198 *Scyllarus sordidus* (Stimpson) (Scyllaridae)
199 *Thalamita sima* H. Milne Edwards (Portunidae)
200 *Typhlocarcinops decrescens* Rathbun (Goneplacidae)
201 *T. tonsurata* Griffin and Campbell (Goneplacidae)
202 *Xenophthalmoides dolichophallus* Tesch (Goneplacidae)
203 *Xenophthalmus pinnotheroides* White (Pinnotheridae)

REMAINING CRUSTACEA

204 *Whiteleggia stephensoni* Boesch (Tanaidacea)
205 *Cyclaspis* sp. 1 (Cumacea)
206 *Cyclaspis* sp. 2 (Cumacea)
207 *Heterotanais* sp. (Tanaidacea)
208 *Pomacuma australiae* (Zimmer) (Cumacea)

MOLLUSCA

GASTROPODA

209 *Adamnestia thetidis* (Hedley) (Scaphandridae)
210 *Bedeva hanlyi* Angas (Muridae)
211 *Cancellophora amasea* Iredale (Cancellariidae)
212 *Cerithiopsis (Notoseila) crocea* Angas (Cerithiopsidae)

213 *Clavus* sp. (Turridae)
214 *Columbella (Atilia) conspersa* Gaskoin (Pyrenidae)
215 *Conuber conica* (Lamarck) (Naticidae)
216 *Daphnella cheverti* Hedley (Turridae)
217 *Diali* sp. 1 (Rissoidae)
218 *Diali* sp. 2 (Rissoidae)
219 *Etrema catapasta* Hedley (Turridae)
220 *E. spurca* Hinds (Turridae)
221 *Herpetopoma atratus* Gmelin (Trochidae)
222 *Inquisitor* cf. *lassulus* Hedley (Turridae)
223 *I. metcalfei* Angas (Turridae)
224 *Latirus recuvirostris* (Schub. Wagn.) (Fasciolariidae)
225 *Mesophora bowenensis* Laseron (Triphoridae)
226 *Nassarius pictus* (Dunker) (Nassariidae)
227 *Natica* cf. *colliei* Recluz (Naticidae)
228 *N. vitellus* L. (Naticidae)
229 *Natica* sp. (Naticidae)
230 *Philine angasi* Crosse and Fisher (Philinidae)
231 *Pseudorhaphitoma* cf. *axicula* (Hedley) (Turridae)
232 *Pupa* sp. (Acteonidae)
233 *Reticunassa paupera* Gould (Nassariidae)
234 *Talopia morti* Iredale (Trochidae)
235 Muricid 1 (Muricidae)
236 *"Bedeva" fischerianus (Tapparone canefri)* (Muricidae)
237 Nudibranch 1 (Nudibranchia)
238 Nudibranch 2 (Nudibranchia)
239 'Sea-hare' 1 (Opisthobranchia)
240 'Sea-hare' 2 (Opisthobranchia)
241 Triphorid (Triphoridae)
242 Trochid (Trochidae)
243 ? *Daphnella* sp. (Turridae)

SCAPHOPODA
244 *'Dentalium'*

PELECYPODA
245 *Aerosterigma oxygonum* Sowerby (Cardiidae)
246 *Antigona lamellaris* Schumacher (Veneridae)
247 *Arca (Arca) navicularis* Bruguiere (Pinnidae)
248 *Atrina (Servatrina) pectinata* L. (Pinnidae)
249 *Azorinus abbreviatus* (Gould) (Solecurtidae)
250 *Chama fibula* Reeve (Chamidae)
251 *C. pulchella* Reeve (Chamidae)
252 *Chlamys (Annachlamys) leopardus* Reeve (Pectinidae)
253 *C. (Chlamys) gloriosa* Reeve (Pectinidae)
254 *C. (C.) grossiana* Iredale (Pectinidae)
255 *Circe sugillata* Reeve (Veneridae)
256 *Clementia strangei* Reeve (Veneridae)
257 *Crytomya cf. elliptica* A. Adams (Myidae)
258 *Cycladicama (Toralimysia)* sp. (Ungulinidae)
259 *Decatopecten (Decatopecten) strangei* Reeve (Pectinidae)
260 *Diplodonta (Zemysina)* sp. (Ungulinidae)
261 *Dosinia (Dosinia) cf. sculpta* Hanley (Veneridae)
262 *'Modiolus' ostenatus* Iredale (Mytilidae)

263 *Ensiculus hilaris* Iredale (Cultellidae)
264 *Eufistulina* sp. (Teredinidae)
265 *Fulvia* sp. (Cardiidae)
266 *Gari (Gari) cf. simplex* Sowerby (Psammobiidae)
267 *Gari venta* Iredale (Psammobiidae)
268 *Gari* sp. (Psammobiidae)
269 *Laternula vagina* (Reeve) (Laternulidae)
270 *Leptomya pura* Angas (Semelidae)
271 *L. cf. pura* Angas (Semelidae)
272 *Limaria (Limaria) cf. delicatuta* Iredale (Limidae)
273 *Lunulicardia subretusum* (Sowerby) (Cardiidae)
274 *Macoma cf. donaciformis* Deshayes (Tellinidae)
275 *Macoma (Salmacoma) cf. vappa* Iredale (Tellinidae)
276 *Macoma* sp. 1 (Tellinidae)
277 *Macoma* sp. 2 (Tellinidae)
278 *Mactra (Electromactra) angulifera* Deshayes (Mactridae)
279 *Malleus albus* Lamarck (Malleidae)
280 *Modiolus micropterus* Deshayes (Mytilidae)
281 *'Modiolus' cf. pulvillus* Iredale (Mytilidae)
282 *Musculus cumingiana* Reeve (Mytilidae)
283 *Neosolen correctus* Iredale (Cultellidae)
284 *Notocorbula hydropica* Iredale (Corbulidae)
285 *Nucula (Leionucula) astricta* Iredale (Nuculidae)
286 *N. (L.) orekta* Iredale (Nuculidae)
287 *Ostrea cf. cristagalli* L. (Ostreidae)
288 *Paphia gallus* Gmelin (Veneridae)
289 *P. subrugata* Iredale (Veneridae)
290 *P. (Paphia) textile* Gmelin (Veneridae)
291 *P. (P.) undulata* Born (Veneridae)
292 *P. (P.) cf. undulata* Born (Veneridae)
293 *Phragmorisma* sp.? (Thraciidae)
294 *Pinctada albina sugillata* Reeve (Pteridae)
295 *Pinna* sp. (Pinnidae)
296 *Placamen sidneyense* (Menke) (Veneridae)
297 *P. tiara* (Dillwyn) (Veneridae)
298 *Regozara flava* L. (Cardiidae)
299 *Scapharea (Cunearca) hubbardi* (Iredale) (Arcidae)
300 *Solecurtis* sp. (Solecurtidae)
301 *Solen vagina* L. (Solenidae)
302 *Spondylus wrightianus* Crosse (Spondylidae)
303 *Syndosmya* sp. (Semelidae)
304 *Tapes (Tapes) watlingi* Iredale (Veneridae)
305 *Tellina (Semelangulus)* cf. *brazieri* Sowerby (Tellinidae)
306 *T. (S.) lilium* Hanley (Tellinidae)
307 *T. (S.) semitorta* Sowerby (Tellinidae)
308 *T. (S.)* cf. *solenella* Deshayes (Tellinidae)
309 *Tellina* sp. (Tellinidae)
310 *T. (Laciolena) texturata* Sowerby (Tellinidae)
311 *Tepidoleda* sp. (Nuculanidae)
312 *Tigamnona chemnitzi* Hanley (Veneridae)
313 *Timoclea (Glycodonta) cf. subnodulosa* Hanley (Veneridae)
314 *Trichomya hirsuta* (Lamarck) (Mytilidae)
315 *Trisidos trisidos* L. (Arcidae)

316 *Tucetilla tenuicostata* (Reeve) (Glycymeridae)
317 Aloidid
318 Venerid 1
319 Venerid 2
320 Bivalve E
321 Bivalve H
322 Bivalve I
323 Bivalve J
324 Bivalve Z

POLYZOA
325 Polyzoan

ECHIUROIDEA
326 *Listriolobus bulbocaudatus* Edmonds

SIPUNCULIDAE
327 *Aspidosiphon* sp.
328 *Golfingia longirostris* (Wesenburg-Lund)
329 *Sipunculus* sp.
330 *Thermiste* sp.

PHORONIDAE
331 Phronid 1
332 Phronid 2

BRANCHIOPODA
333 *Lingula tumidula* Reeve

PHYLUM UNCERTAIN
334 species 1
335 species 2
336 species 3
337 species 4

ECHINODERMATA
ASTROIDEA
338 *Luidia* sp.
339 Sea star
OPHIUROIDEA
340 *Amphioplus depressus* (Ljungman)
341 *Amphipholis loripes* Koehler
342 *Amphioplus* sp.
343 *Amphiura bidentata* H. L. Clark
344 *A. catephes* H. L. Clark
345 *A. magnesquama* H. L. Clark
346 *A. octacantha* H. L. Clark
347 *A. septemspinosa* H. L. Clark
348 *A. tenuis* H. L. Clark
349 *Amphiura* sp.
350 *Ophiacantha confusa* Koehler
351 *Ophiactis perplexa* Koehler
352 *O. savignyi* Müller and Troschel
353 *Ophiactis* sp.
354 *Ophiocentrus* sp.
355 *Ophionephthys* sp.

356 *Ophionereis stigma* H. L. Clark
357 *Ophiothrix stelligera* Lyman
358 *Ophiura kinbergi* Ljungman

ECHINOIDEA

359 *Brissopsis luzonica* (Gray)
360 *Hypselaster jukesii* (Gray)
361 *Salmacis belli* Döderlein

HOLOTHURIOIDEA

263 *Holothuria spinifera* Theel
363 *Mensamaria intercedens* (Lampert)
364 *Protankyra* sp.
365 *Thyone papuensis* Theel

TUNICATA

366 *Adagnesia opaca* Kott (Agnesiidae)
367 *Agnesia glaciata* Michaelson (Agnesiidae)
368 *Aplidium* sp. (Polyclinidae)
369 *Ascidia aclara* Kott (Ascidiidae)
370 *A. sydneyensis* Stimpson (Ascidiidae)
371 *Botrylloides nigrum* Herdman (Styelidae)
372 *Cnemedocarpa floccosa* Sluiter (Styelidae)
373 *Eugyra moretonensis* Kott (Molgulidae)
374 *Microcosmus australis* Herdman (Pyuridae)
375 *M. exasperatus* Heller (Pyuridae)
376 *M. nichollsi* Kott (Pyuridae)
377 *M. spinifera* Herdman (Pyuridae)
378 *M. stolonifera* Kott (Pyuridae)
379 *Microcosmus* sp. (Pyuridae)
380 *Molgula diversa* Kott (Molgulidae)
381 *M. exigua* Kott (Molgulidae)
382 *M. rima* Kott (Molgulidae)
383 *M. mollis* Herdman (Molgulidae)
384 *M. sphaera* Kott (Molgulidae)
385 *Polycarpa fungiformis* Herdman (Styelidae)
386 *P. pedunculata* (Heller) (Styelidae)
387 *P. tinctor* (Quoy and Gaimard) (Styelidae)
388 *Pyura vittata* Stimpson (Styelidae)
389 *Styela plicata* Lesuer (Styelidae)
390 *S. ramificata* Kott (Styelidae)
391 *S. stolonifera* (Herdman) (Styelidae)
392 *Sycozoa pedunculata* Quoy and Gaimard (Clavelinidae)

BALANOGLOSSIDAE

393 *Glossobalanus hedleyi* Hill

CEPHALOCHORDATA

394 *Branchiostoma moretonensis* Kelly

ALGAE

395 *Acetabularia caliculus* Quoy and Gaimard
396 *Asparagopsis taxiformis* (Delile) Collins and Hervey
397 *Ceramium* sp.
398 *Champia parvula* (C. Ag.) Harv.
399 *Chondria* sp.

400 *Dictyota dichotoma* (Huds.) Lamx. var *intricata* (G. Ag.) Grev.
401 *Gracilaria textorii* (Suringar) De Toni
402 *G. verrucosa* (Huds.) Pap.
403 *Gracilaria* sp.
404 *Griffithsia* sp.
405 *Hypnea cervicornis* J. Ag.
406 *Hypnea* sp.
407 *Laurencia rigida* J. Ag.
408 *Laurencia* sp.
409 *Martensia* sp.
410 *Microcoleus lyngbyaceus* (Kuetz.) Crow
411 *Polysiphonia macrocarpa* Harv.
412 *Polysiphonia* sp.
413 *Pseudocodium* sp.
414 *Solieria robusta* (Grev.) Kylin
415 *Solieria* sp.
416 *Sporochnus cosmosus* C. Ag.
417 *S. harveyanus* J. Ag.
418 *Spyridia filamentosa* (Wulf.) Harv.

ANGIOSPERMA
419 *Halophila ovalis* (R. Br.) Hook F.
420 *H. spinulosa* (R. Br.) Aschers

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AMICIBDELLA AND *MICOBDELLA* GEN. NOV. OF EASTERN AUSTRALIA (HIRUDINOIDEA:HAEMADIPSIDAE S.L.)

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ABSTRACT

Two new genera and three new species are described. *Amicibdella niger* sp.nov.: 5-annulate; contrast stripes lateral in the paramedian fields and along the lines of the supramarginal sense organs; nephropores in a dark band in the marginal fields; northeastern Queensland. Categories are defined for individual variations in pattern, and three forms of tertiary variation described for *A. niger. Micobdella gloriosi* sp.nov.: 4-annulate, contrast stripes in the dorsal median field, lateral in each intermediate field extending into the line of the supramarginal sense organs; nephropores in a dark band in the marginal fields; annuli of the midnephric somites equal in length; southeastern Queensland. *Micobdella auritus* sp.nov.: annuli of midnephric somites unequal in length; Sydney, N.S.W. *Micobdella* sp.?, (?) Tasmania.

Modification of the paramedian and intermediate palisades of dorsoventral muscles due to the ventral reduction of xxiii to xxvii, is briefly described.

Topographically defined pattern is proposed as a guide to generic separations among species exhibiting close morphological similarity.

This paper provides two new genera for eastern Australian land-leeches. One is 5-annulate, known only in the type species in northern Queensland; the second, 4-annulate, based on a species in southern Queensland, is represented by a second species in Sydney, N.S.W., and a specimen recorded as from Tasmania. The latter locality is possibly doubtful.

The two genera are defined in a combination of external and internal characteristics. Each has a distinctive pattern, as in other genera I have defined in this manner.

Preserved specimens of the 5-annulate show marked variation in individual pattern. In describing this, I differentiate the principle forms of individual variation in pattern as known to me in australian Haemadipsidae, some forms having such high frequency as to be characteristic of the species and systematic in value, as in this 5-annulate.

The Haemadipsidae occur in the Oriental, Australian, Oceanic, and Malagasian zoogeographic divisions. As known the family has been small, containing (Soos, 1967) 31 species in 9 genera, three of the genera based on australian species with a fourth genus in Papua based on an oriental species. Elsewhere, I will add two other new genera for Papua. Below, I give indications for other new genera in eastern Australia.

The diversity here is adequate for the testing of the principles on which the family had long been systematized.

One such principle has been that pattern is so highly variable as to be without systematic value (*v.* Blanchard, 1917). This was formulated in earlier practice in which 'genera' were characterized essentially on simple external meristic morphology. Such genera are heterogenous in content, present zoogeographic anomalies, and are zoologically inadequate (Soos, 1967; Richardson, 1969, 1971).

I review elsewhere (*Mem. Nat. Mus. Vict.* **35**) in more detail, the development of the concept of 'genus' in the Haemadipsidae. Briefly, early genera (*Haemadipsa* Tennent 1859, Oriental; *Chtonobdella* Grube, 1866, Australian) were defined on the nature of the ocular arch, the total number of annuli, and the number of annuli between the genital pores. Then, following Whitman, from 1893 to 1897, by Blanchard on the number of annuli in the fully annulate somite (*Mesobdella*, 3-annulate, Neotropical; *Planobdella*, 7-annulate and *Phytobdella*, 6-annulate, Oriental; *Philaemon*, 4-annulate, Australian) and species separated on the number of annuli between the genital pores or other detail in general somital annulation. Blanchard (1917) reduced *Chtonobdella* to synonymy under *Haemadipsa*, both being 5-annulate, although *Haemadipsa* was based on a trignathous leech. Blanchard's system (1917) continues to dominate the greater part of the Haemadipsidae (*v.* Soos, 1967).

A sound basis for departure from that system was provided by Miss A. M. Lambert (1898) in her closely detailed account of the morphology of *Philaemon pungens*, showing this to be duognathous, the postcaeca terminating in distinctive organs, now the lambertian organs, as also (1899) the same characteristics in two 5-annulate species in Australia.

Using this, Harding (1913) defined *Idiobdella* (Seychelle Is.): 5-annulate, duognathous, 11½annuli between the genital pores, lacking auricles and lambertian organs; Augener (1931) revalidated *Chtonobdella* as duognathous; Moore (1938) defined *Tritetrabdella* (Malay Peninsula): 4-annulate, trignathous, lacking lambertian organs; Nybelin (1943), *Nesophilaemon* (Juan Fernandez): 4-annulate, duognathous, lacking lambertian organs. *Idiobdella*, *Tritetrabdella*, *Nesophilaemon*, are monotypic.

Adding to these criteria the annulation of the somites anterior and posterior to the fully annulate series, and the morphology of the auricle, I established (1969) *Neoterrabdella* (Northern Territory): 4-annulate, duognathous, lacking lambertian organs, exceptional in having xxiv 3-annulate, xxv 2-annulate, and the auricles on xxiv to xxvii. *Neoterrabdella* is monotypic.

I demonstrated also the distinctive morphology of the reproductive systems in the Haemadipsidae, and on this basis removed *Nesophilaemon*, and later (1971) *Mesobdella* from this family.

Criteria of systematic significance additional to those above, are introduced in the present paper: jaws armed with an edentulous cutting ridge; salivary gland papillae on the jaws of the 5-annulate '*Geobdella*' *whitmani* Lambert 1899; a count of the annuli posterior to xxiii a_2, since xxiv commonly lacks detectable somital sense organs and the annulation of these two somites cannot always be determined with full confidence; the form, location, and the relative lengths of the lambertian organs and their ducts; the relative lengths of the two limbs of the primary loop of the female median region; and topographically defined pattern. In various combinations, these have generic value.

I show here for the first time in the Haemadipsidae, a separation of species on the relative lengths of the annuli in the mid-nephric somites.

With progress toward a more precise concept of genus and of species in the Haemadipsidae, variation in pattern in the individuals of a species can be closely analysed, categorized, and utilized systematically.

Additional to those genera which can be separated on morphological grounds, there are in the eastern australian Haemadipsidae assemblies of 4- and of 5-annulate species which are closely similar morphologically and cannot be separated in this manner.

Each assembly contains groups of species, the groups exhibiting differences in the topography of pattern of the same order as the differences in the distinctive patterns of those genera which have been defined on combinations of external and internal morphological characteristics.

This indicates that the knowledge of the systematic morphology of the Haemadipsidae is still incomplete; but I continue unable to locate and fill these gaps.

Unless there is acceptance of the principle that topographically defined pattern is in itself a reliable indication for the separation of genera among these assemblies in eastern Australia, the result will be a division of the Haemadipsidae here into genera, some defined on morphological terms and each with its distinctive pattern; and others in which pattern will be diversified and without systematic meaning as in the zoologically inadequate 'genera' of Blanchard.

This paper brings us to the point where the acceptance of the principle is warranted.

Amicibdella gen. nov.

DERIVATION: *amicus*, friendly; *bdella*, a leech. m.

Haemadipsidae; duognathous; lacking salivary gland papillae; somites ix to xxii, 5-annulate (total 14); viii and xxiii, 4-annulate; xxiv, 2-annulate; 7 annuli posterior to xxiii a_2; auricles posterior to xxiv, the margin lobed; wide contrast stripes lateral in the paramedian fields, narrow contrast stripes along the lines of the supramarginal somital sense organs; nephropores included in a wide dark band extending across the marginal and submarginal fields and including the submarginal and ventral intermediate somital sense organs; teeth minute, a nearly uniform row of about 95; pharynx terminates at viii/ix; lambertian organs, posterior, each about twice the length of its duct; genital pores, xi b_5/b_6, xiii b_1/b_2; reproductive systems, haemadipsoid: anterior region of male paired ducts reflected as a single primary loop in the median splanchnic chamber, a sperm duct on the procurrent or on both limbs; ejaculatory bulbs, present; median regions, hemimyomeric, the male a micromorphic atrium, the female formed on a posteriorly directed loop, the limbs equivalent in length, and the loop extended posteriorly as an oviducal glandular sac.

TYPE SPECIES: *Amicibdella niger* sp. nov. as below.

Amicibdella is characterized by: the absence of a contrast stripe in the dorsal median field; by the presence of a contrast stripe lateral in each paramedian field from in v to xxvii, the stripe including the intermediate sense organs along the posterior half of the body; by a narrow contrast stripe along and restricted to each line of supramarginal somital sense organs from in vi to in xxiv; by a dark band occupying the marginal and ventral intermediate fields from in v to in xxv, the band including the submarginal sense organs along its length, the ventral intermediate sense organs anteriorly, and the nephropores which are in the marginal field.

It differs in general somital annulation from a 5-annulate genus in Papua, (*Mem. Nat. Mus. Vict.* **35**) which has viii to xxiii 5-annulate (total 16); vii, incomplete 5-annulate; the lateral margin of the auricle, straight.

The general external meristic morphology and the internal morphology of *Amicibdella* is the same as in the other 5-annulates of eastern Australia. The majority of these have a contrast stripe in the dorsal median field from in iii (or shorter in some, from in ix) to in xxii or xxiii; a stripe lateral in the paramedian field from in v to in xxiv; some with one stripe in the medial half of the dorsal intermediate field, others with this stripe and a second stripe in the lateral half of this field, from in vi to in xxiii, xxiv, or xxv; the stripes of the paramedian and intermediate fields complete to much broken represented only by short to longer patches; a stripe in the ventral half of the marginal field, usually complete from the velum to the auricle, expanding into the dorsal half of this field as a lobe on the nephroporic annulus, the lobe including the nephropore which is in the marginal field.

Leeches in this assembly are known to me from southern Queensland, south to beyond Sydney, N.S.W. Moore (1944) and myself (Richardson, 1967, 1968a, b; Richardson and Hunt, 1968) were misled by Blanchard (1917) to identify leeches in this assembly as *Chtonobdella limbata* Grube, 1866.

'*Geobdella*' *whitmani* Lambert 1899 of southern Queensland is the only described leech in this assembly. I find it has salivary gland papillae on the jaws, not known previously in the Haemadipsidae. The median dorsal stripe terminates in xxi; a single stripe in each intermediate field, commonly broken into patches commencing and terminating on a_2; a stripe in the marginal field from the velum to the auricle, has straight edges, fills the field, and includes the nephropores. A new genus will be provided elsewhere for *whitmani*.

The 5-annulates lacking a dorsal median stripe are known to me only from north-eastern Queensland, and from eastern New South Wales south of Sydney.

Those in New South Wales are *Chtonobdella limbata* Grube 1866. I have studied the types and recently collected material. '*Geobdella*' *australiensis* Lambert 1899 is a synonym of *limbata*.

In *C. limbata* (*v.* Lambert, 1899) the dorsal pattern is restricted to the posterior end of the body, from xx/xxi to xxiii/xxiv: a single patch (gold in life) on each side of the midline on the contiguous annuli of xxi and xxii, also on these annuli for xxii and xxiii, and also on the posterior annuli of xxiii; a pair of patches in both intermediate fields at the same levels as the anterior and middle patches in the paramedian fields, together forming distinct transverse rows; a stripe (red in life) lateral in each paramedian field from xx/xxi into the anterior half of xxiii; erratic white patches in xxiv; a stripe in the ventral half of the marginal field from the velum to xxiii/xxiv, expanding dorsally on the nephroporic annuli as a lobe including the nephropore.

Amicibdella niger sp. nov.

(Figures 1, 2, 3)

HOLOTYPE: Preserved, 52·0 mm long. Herberton Range, north of the main road from Herberton to Atherton, North Queensland, map reference (1:100,000) CA 319850; Grassy clearing in rain-forest; Alt., 2,000 m; May 4, 1973; Collector, W. Whiteman; Per J. W. Winter. Dissected. Deposited: Queensland Museum, G5310.

PARATYPE: Preserved, 38·5 mm long. Herberton Range, north Queensland, map reference (1:100,000) CA 310980; grassy forest grading into wet sclerophyll; alt., 1,200 m; May 29, 1973; collector, J. Winter. Dissected, right ventrolateral jaw removed, mounted separately. Deposited: Australian Museum, Sydney, W4305.

DESCRIPTION OF HOLOTYPE (For details of the teeth, refer to the paratype description.)

GENERAL FORM: Moderately large; maximum extension in life, 55·0 mm.

Preserved, extended, 52·0 mm long; elongate tapering cylindrical, widest along the posterior half of the body, the width equal to the depth, reducing gradually anteriorly in width and depth to the narrow anterior sucker, more abruptly posteriorly to the sucker which is about two-thirds the maximum width of the body.

Total length, 52·0 mm; the width and depth, 2·0 mm at v/vi; 4·5 mm at x/xi, 10·0 mm from the tip of the velum; 6·0 mm at xiv/xv, 20·0 mm from the tip; 6·5 mm at xvii/xviii, 30·0 mm from the tip; 7·0 mm at xx/xxi, and posteriorly to 45·0 mm; reducing to the basis (4·0 mm) of the posterior sucker which is 5·0 mm in diameter.

COLOUR: In life: the dorsum black with a pair of wide-spaced longitudinal contrast stripes, golden along the greater length of the body, pale green at the anterior and posterior ends, extending onto the dorsum of the posterior sucker to enclose a black postanal patch; these stripes expanding briefly at regular intervals and wider on the posterior portion of the body. Lateral to these golden stripes, a wide reddish brown band maculated with dark brown on the posterior portion of the body extends onto the venter, the upper and lower borders of the band maculated. A very narrow gold stripe with straight margins divides the reddish brown band along the length of the body. The venter, light brownish, immaculate between the reddish brown bands.

Preserved in formalin: The black of the dorsum diminishes in intensity; a narrow pale brownish median dorsal band with irregular dark margins becomes vaguely indicated; green disappears from the paired dorsal stripes which, as also the outer stripes reduce to yellow; the paired reddish brown bands reduce to a pale brown with obvious dark brown maculation along both margins; the venter becomes a pale yellow.

PATTERN (Figs. 1, A–E): The wide median dorsal black band fills the ocular arch in ii to iv; in v posteriorly to in xxvii, the band includes the lines of the paramedian somital sense organs, extends across the medial half of the paramedian fields, and is represented by the postanal patch on the dorsum of the sucker.

The inner paired wide contrast stripes occupy the lateral half of the paramedian fields from in v to ix, progressively posterior to this expanding on a_2, then on b_2, a_2, b_5, to contact and then to include the sense organs of the intermediate lines from xv posteriorly, and to briefly enter the intermediate fields.

The outer paired narrow contrast stripes occupy and are restricted to the lines of the supramarginal sense organs from in vi to xxiv/xxv dividing the side paired bands into dorsal and marginal elements.

The dorsal element occupies the dorsal intermediate field from in vi to xxiii with the intermediate somital sense organs included marginally on the anterior portion of the body.

The marginal element is defined as such from in vi to xxiv/xxv; occupies the marginal field, includes the nephropores which are in this field, the lines of both submarginal and ventral intermediate sense organs and the ventral intermediate field on the anterior portion of the body, but only the lateral half of this field on the posterior portion of the body.

ANNULATION (Figs. 1, A–F): In life, moderately areolate; extended, preserved, areolae weakly defined. Somital and intersomital furrows equivalent; somital limits not directly recognizable; somital sense organs, each enclosed in a small white disc, generally

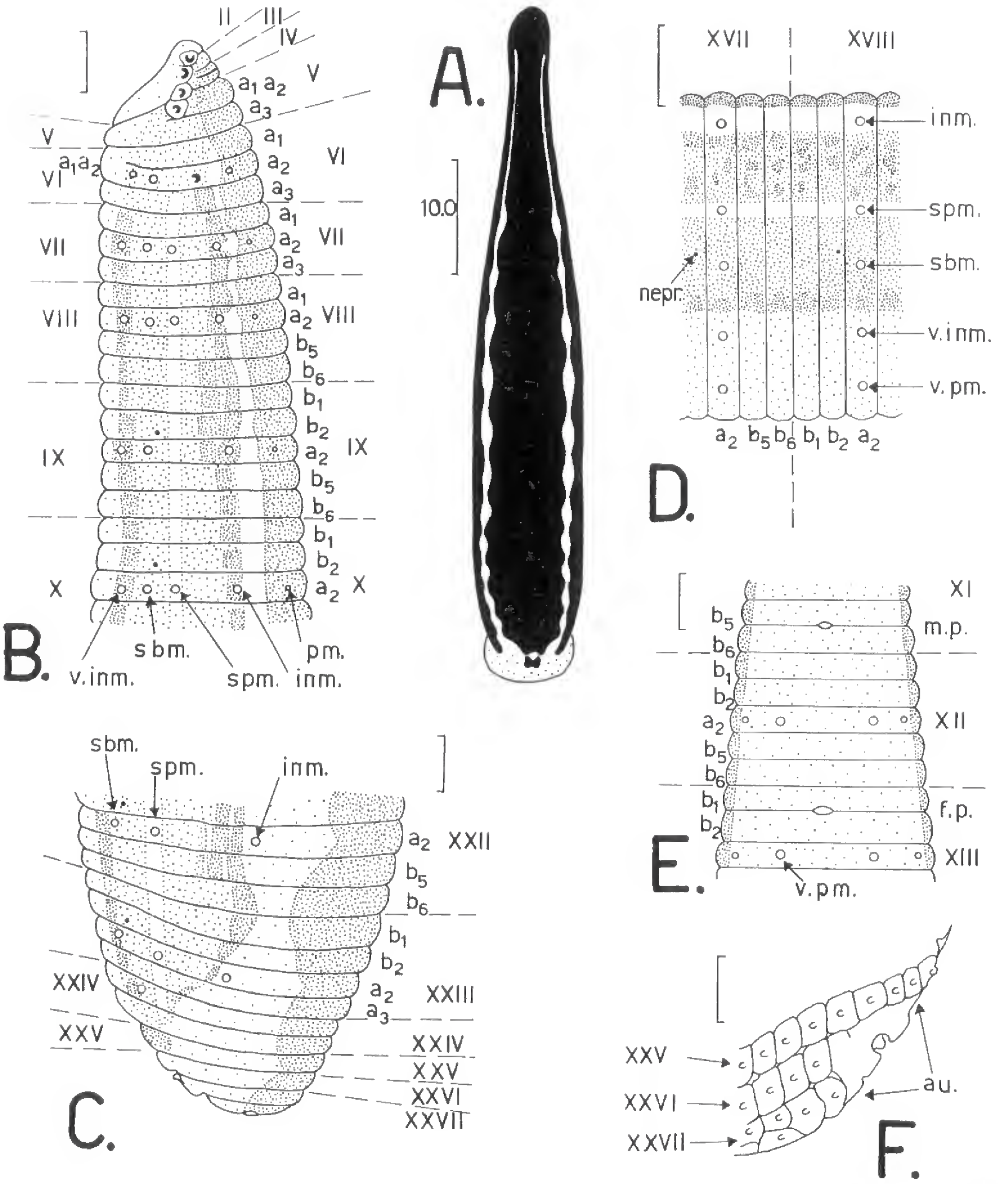

FIG. 1: *Amicibdella niger* gen. et sp. nov. Holotype. A, general form and dorsal pattern, showing contrast stripes in the paramedian fields. B, lateral aspect showing somital annulation of somites i to x, and detailed topography of pattern. C, the same, somites xxii to xxvii. D, the same, somites xvii and xviii. E, ventral aspect, somites xi into xiii. F, right auricle, dorsal view.

Somites and somital ganglia indicated by roman numerals; somital limits, by broken lines; annuli, 'a_2', etc.; somital ganglia represented at relative size. Scales in millimeters, 1·0 mm, or as indicated.

Abbreviations: an.gr., annular groove; at., atrium; au., auricle; cr., crop; dm.r., dorsomedian muscular ridge; ej.b., ejaculatory bulb; f.p., female pore; inm., intermediate somital sense organ; j., obvious as transverse and longitudinal series; sensillae, minute white points, central in the areolae, nephropores, located in the marginal field, generally obscure minute apertures in the posterior half of b_2 immediately dorsal to the level of the submarginal sense organ on a_2; width of the dorsal median field in xvi = half the width of the somite.

Somites ii and iii, uniannulate with the 1st and 2nd pairs of eyes, each eye in an ocular areola, the furrow ii/iii extending between these areolae, and iii with the 1st pair of paramedians; the 1st nephropores on the margin of the velum, lateral to the 2nd pair of eyes; iv, 2-annulate between the ocular areolae containing the 3rd pair of eyes; v, 2-annulate above, a_1a_2 with the 4th pair of eyes $= a_3$, a_1a_2/a_3 extending into the intermediate line, and uniannulate v forming the lateral and ventral margins of the sucker; vi, with the 1st complete series of somital sense organs, 3-annulate above, $a_1 = a_2$ with the 5th pair of eyes $< a_3$, a_1/a_2 extending into the ventral intermediate field, and vi 2-annulate below, $a_1a_2 > a_3$; vii, complete 3-annulate, $a_1 = a_2 = a_3$ (= viii a_1); viii, 4-annulate, $a_1 = a_2$ slightly $> b_5 = b_6$; ix to xxii 5-annulate (total 14); ix, $b_1 = b_2 < a_2 = b_5$ slightly $> b_6$, the second nephropores on b_2; x, $b_1 = b_2 < a_2 = b_5 = b_6$, as also xi and xii; xiii, $b_1 = b_2$ slightly $< a_2 = b_5 = b_6$; xiv to xvi, $b_1 = b_2 < a_2 > b_5 = b_6$; xvii to xix, $b_1 = b_2 < a_2$ slightly $> b_5$ slightly $> b_6$; xx to xxii, $b_1 = b_2 < a_2 = b_5 = b_6$; xxiii, $b_1 = b_2 < a_2 > a_3$, the 16th nephropores on b_2; xxiv, 2-annulate, $a_1a_2 = a_3$, an intermediate sense organ on the left, a_1a_2 the last annulus complete across the venter; xxv–vii, incomplete, transversely abbreviated, uniannulate; anus at the posterior margin of a supernumerary annulus.

Auricles, small, formed along the lateral edges of xxvi and xxvii; margined anteriorly by xxv; the lateral edge of the auricle with an anterior flange on xxvi separated from a posterior flange on xxvii by an open arch; the flange, roofing over a well formed chamber little deeper than the groove elsewhere between the posterior somites and the dorsum of the sucker.

Dorsum of the sucker with 5 concentric rings of areolae; ventral surface with a central papillate area about $\frac{1}{4}$ of the diameter of the sucker, and radiating muscular ridges dividing to terminate as about 80 at the margin.

Genital pores, xi b_5/b_6; xiii b_1/b_2.

CENTRAL NERVOUS SYSTEM (Fig. 2A): The ventral component of the anterior ganglionic mass is compact, situated at the level of the anterior annuli in vii, with ganglion vii narrowly spaced from the ventral component and situated in the posterior annulus of vii. Ganglion viii is widely spaced from vii, posterior in somite viii at the level of b_5/b_6; ganglion ix, widely spaced from viii and at the level of a_2/b_5 in ix.

BODY WALL AND MUSCULAR SYSTEM: All three muscular layers in the body wall are individually distinct in dissection.

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jaw; l.o., lambertian organ; m.p., male pore; nepr., nephropore; n.r., connectives of anterior ganglionic masses; ov., ovary; ovd.s., oviducal glandular sac; p.c., postcaecum; pm., paramedian somital sense organ; ph., pharynx; pr., prostate; pr.l., procurrent limb; re., rectum; re.l., recurrent limb; sbm., submarginal somital sense organ; sl.g.d., aggregated salivary gland ducts; sp.d., sperm duct; spm., supramarginal somital sense organ; te., testis; v.d., vas deferens; v.gl.m., ventral glandular mass of salivary glands; v.inm., ventral intermediate somital sense organ; vl.r., ventrolateral muscular ridge; v.pm., ventral paramedian somital sense organ.

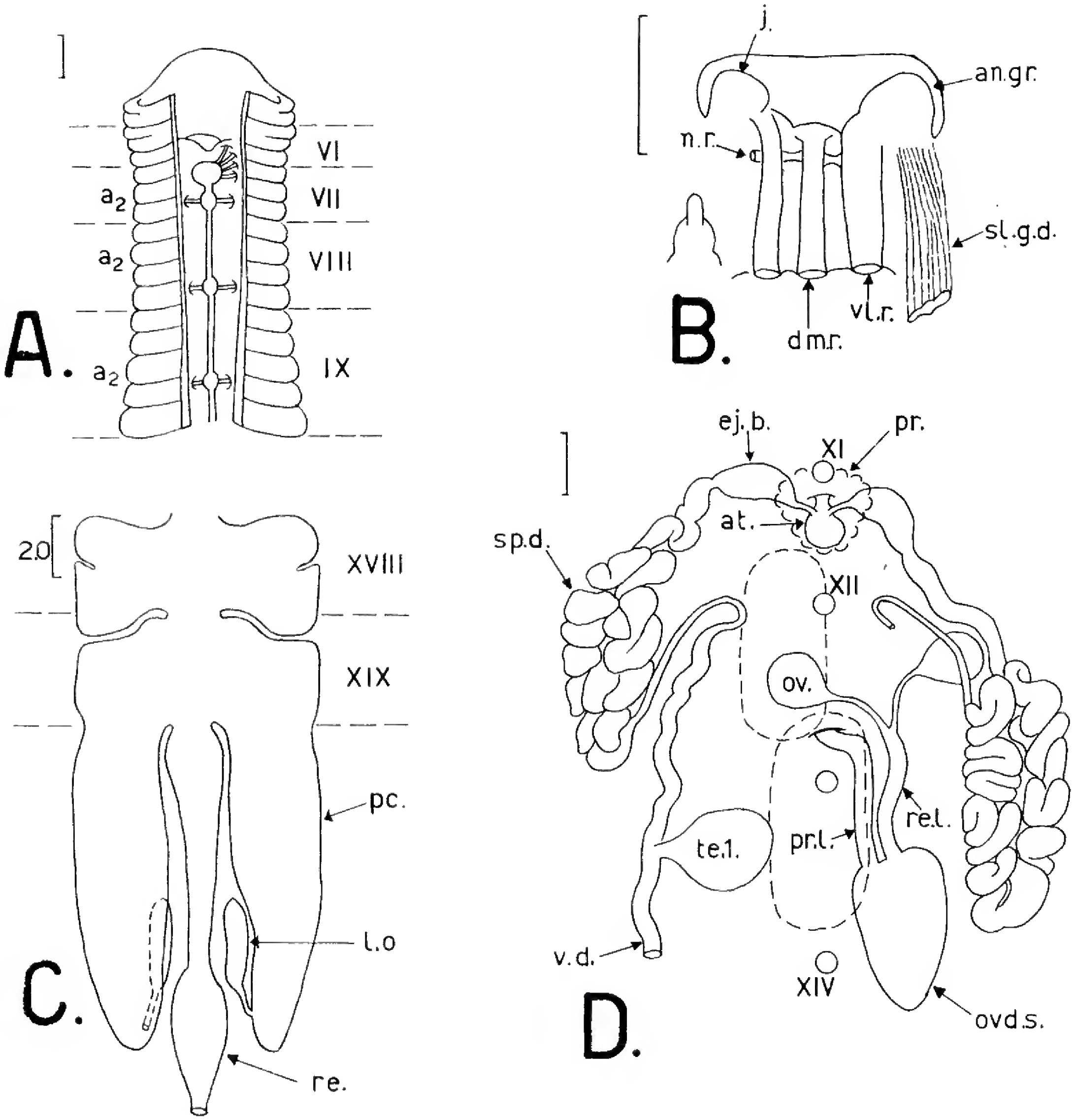

FIG. 2: *Amicibdella niger* gen. et sp. nov. Holotype. A, ventral aspect, somites v to ix opened by a median longitudinal incision to show the somital relationship of the ventral component of the anterior ganglionic mass and of ganglia vii to ix. B, pharynx opened along midventral line to show jaws, internal muscular ridges, column of aggregated salivary gland ducts. Inset, profile of median end of jaw. C, crop, engorged, caecation somites xviii, xix; lambertian organs; intestine; rectum. D, anterior region of male paired ducts, displaced laterally the broken lines indicating the original positions; male median region; female reproductive system.

For abbreviations, etc., see Fig. 1.

The paramedian palisades of dorsoventral muscles are obvious along the length of the crop only as clusters of strands at each intersomital level. In the intestinal region, the palisades are represented by three spaced flat pairs of strongly muscular bands, between the intestine and the postcaeca, and distinctly dorsoventrally oblique.

The bands appear to be at the intersomital levels: xx/xxi, xxi/xxii, xxii/xxiii.

Due to the greater development of these somites on the dorsal aspect, relative to the ventral aspect, with the dorsum longer than the venter, the dorsal end of each band is attached to the body wall at a level anterior to the ventral attachment, and since the ventral aspect narrows more rapidly than the dorsal, the dorsal ends are more widely spaced than the ventral.

In this way, the bands appear to be radiating from a limited ventral origin close to the base of the sucker, and more widely spaced at their dorsal insertions, as though possibly functional when the animal is erect.

The bands are adherent to the wall of the intestine in the preserved specimen.

The intermediate dorsoventral palisades are composed of a uniformly spaced series of individual strands.

Alimentary Tract (Figs. 2, B, C): The lower surface of the velum is smooth with a subcentral trifid opening, the apex ventral. The wall of the chamber of the sucker internal to this opening, is smooth, and terminates as a ridge forming the anterior wall of a distinct continuous annular groove, housing the jaws, and the posterior wall of the groove formed by the anterior end of the pharynx.

The jaws are transverse, subhorizontal, small, the base about 0·9 mm long, and the anterior end of the pharynx also carries a low obtusely triangular dorsomedian muscular pad and a similar pad in the ventromedian position, the pads much smaller than the jaws, the width not half of the length of the base of a jaw.

The entrance to the pharynx is very small, restricted, no wider than the dorsomedian pad; the wall weakly muscular, and the lumen tapering.

Each jaw and the muscular pads continue posteriorly as low undivided primary internal ridges on the wall of the pharynx. There are no salivary gland papillae on the jaws.

The pharynx terminates at viii/ix. The extrinsic radial musculature is an obvious system in vi, vii, viii, and in ix.

The engorged compartments of the crop obscure the distribution of the salivary glands. Very thick bands of aggregated ducts enter the jaws.

The caecation of the crop can only be assessed as each compartment with a pair of caeca at the anterior, and a second pair at the posterior levels; the pairs, equivalent; but this may not be correct since the postcaeca originate from the lateral aspects of the middle portion of the compartment in xix.

The postcaeca extend in the paramedian splanchnic chamber into xxiv.

The lambertian organs are ventral to the postcaeca; each elongate cylindrical, about 2·5 mm long and 0·5 mm wide; posterior in position, the anterior end at xxi/xxii; each longer than its duct which is about 1·0 mm in length and connects subterminally to the ventral face of the postcaecum. The lambertian organs are lined with a longitudinally rugose epithelium.

The intestine is compressed, tapering tubular, and connects terminally to the rectum at xxiii/xxiv.

Reproductive Systems (Fig. 2D): Assessed as adult, male gravid.

Typically haemadipsoid; ejaculatory bulbs present.

Testes, saccular, the anterior pair at xiii/xiv, the posterior pair at xxii/xxiii, total 10 pairs; vasa efferentia, very short, connecting laterally to the white, thin-walled, tortuous vas deferens extending anteriorly in the paramedian splanchnic chamber to the middle of xii; reducing then to a thin-walled narrow tube which passes through the paramedian palisade, enters the median chamber, and is developed as a posteriorly directed primary loop in this chamber; a much folded sperm duct on the procurrent limb of the left loop, and on both limbs on the right loop; the relationship, tandem.

Each sperm duct terminates in a small opalescent, muscular, fusiform ejaculatory bulb, reducing abruptly into a short narrow ejaculatory duct entering the anterior aspect of the atrium. The atrium, minute, entirely ventral to the nerve cord, thin-walled, and amyomeric, micromorphic.

The whole female system is ventral to the anterior region of the male paired ducts.

The single pair of thin-walled saccular ovaries are posterior in xii; each continuing as a long narrow, thin-walled transparent oviduct; the oviducts joining to form the median region. There is no obvious female atrium. The median region is formed on a posteriorly directed primary loop reflecting at xiii/xiv.

The two limbs of the loop are essentially equal in length; the initial recurrent limb, a wide thick-walled tube; the terminal procurrent limb, wider than the recurrent limb, more strongly muscular, terminates at the genital pore. The oviducal glandular sac originates from the posterior aspect of the elbow of the loop, extends into the posterior half of xiv, as an inflated thin-walled sac with a glandular lining.

The prostatic tissue forms a large glandular mass ventral to the nerve cord, completely investing the male atrium, the ejaculatory ducts, and extends onto the terminal portion of the bulbs. There is no indication of albumin glands investing the median region of the female system.

DESCRIPTION OF PARATYPE

GENERAL FORM: At rest, 25·0 mm long, maximum width, 6·0 mm; full extension, horizontal, 45·0 mm, erect 35·0 mm. Preserved, 38·5 mm.

COLOUR: As in the type.

PATTERN: As the type, excepting the posterior end of the contrast stripe in the paramedian field is narrower but still includes the somital sense organs of the intermediate lines.

ANNULATION: Distinct supramarginal sense organs immediately lateral to the 2nd, 3rd, and 4th eyes. Nephropores, as in the type excepting nearly exactly at the level of the submarginal sense organs.

General somital annulation, as in the type, with a_2 distincty the longest annulus in xii to xxii, $b_1 = b_2 < a_2 > b_5 = b_6$; xxiv, 2-annulate.

Auricle, the eave more extended than in the type; the notch deeper, wider; but the chamber beneath the eave no deeper than the groove lateral to xxiv.

ALIMENTARY TRACT: The anterior margin of the right ventrolateral jaw is 0·9 mm long; the medial portion, of the margin, convex, the lateral portion almost straight; teeth, 95 to 97, acutely conical and crowded along the medial half, progressively wider spaced reduced to be granular along the last quarter of the row; 0·016 mm tall at the medial end, the height diminishing uniformly and gradually along the row to be 0·014 mm in the middle of the row.

Differing from the type: the dorsomedian internal muscular ridge subdivided into two ridges, one wider; well-defined compartments on the crop in xiii to xviii, each with a single pair of long-based caeca originating along the middle level; xix, with long-based postcaeca extending posteriorly to xxiii/xxiv.

Lambertian organs as in type: the anterior end at xxii a_2, the posterior end at xxiii/xxiv, and the duct short, its length no more than the width of the organ.

REPRODUCTIVE SYSTEMS: As in type, excepting: the sperm ducts short; the primary loops on the anterior region of the male paired ducts, parallel in relationship; primary loop of the female median region reflecting in the middle of xiii, consequently the recurrent and procurrent limbs, short, but equal in length; the posterior end of the glandular sac at the level of ganglion xiv, and the sac relatively longer.

DISTRIBUTION

As known, northeastern Queensland, Cairns to Townsville, coastal into the Tablelands.

VARIATION IN PATTERN (Fig. 3)

For descriptive purposes, individual variation in pattern in the Haemadipsidae can be differentiated as:

A. Primary Variation: a deviation from a precisely defined topography, a band or contrast stripe extending into the lines of sense organs or into adjacent fields for one or a few somites; erratic; commonly asymmetric, occasionally symmetric; of such high frequency in some species as to be characteristic.

B. Secondary Variation: differing degrees in length or interruption and incompleteness of contrast stripes, or a combination of both; conforms to the defined topography; asymmetric, or some measure of symmetry when interruptions occur over the same annuli in somites; of such high frequency in some species as to be characteristic.

C. Tertiary Variation: forms of pattern appearing during growth; not constantly correlated with size; conforms to the defined topography; typically symmetrical; of such high frequency in some species as to be characteristic.

D. Pseudovariation: artefacts appearing in preserved specimens.

In *Amicibdella niger* primary variation has been seen in few specimens: the supramarginal sense organs lateral to the narrow contrast stripe on a few mid-body somites, the stripe then in the intermediate field—Caribou Falls, 45·0 mm, xvii b_5 to xix b_2; a small gold patch within the ocular arch. Secondary variation is rare, one specimen with a break in a supramarginal contrast stripe for three somites on one side.

Pseudovariation is common, many preserved specimens showing a very pale narrow median band along the length of the body, the edges vaguely defined, the band related to

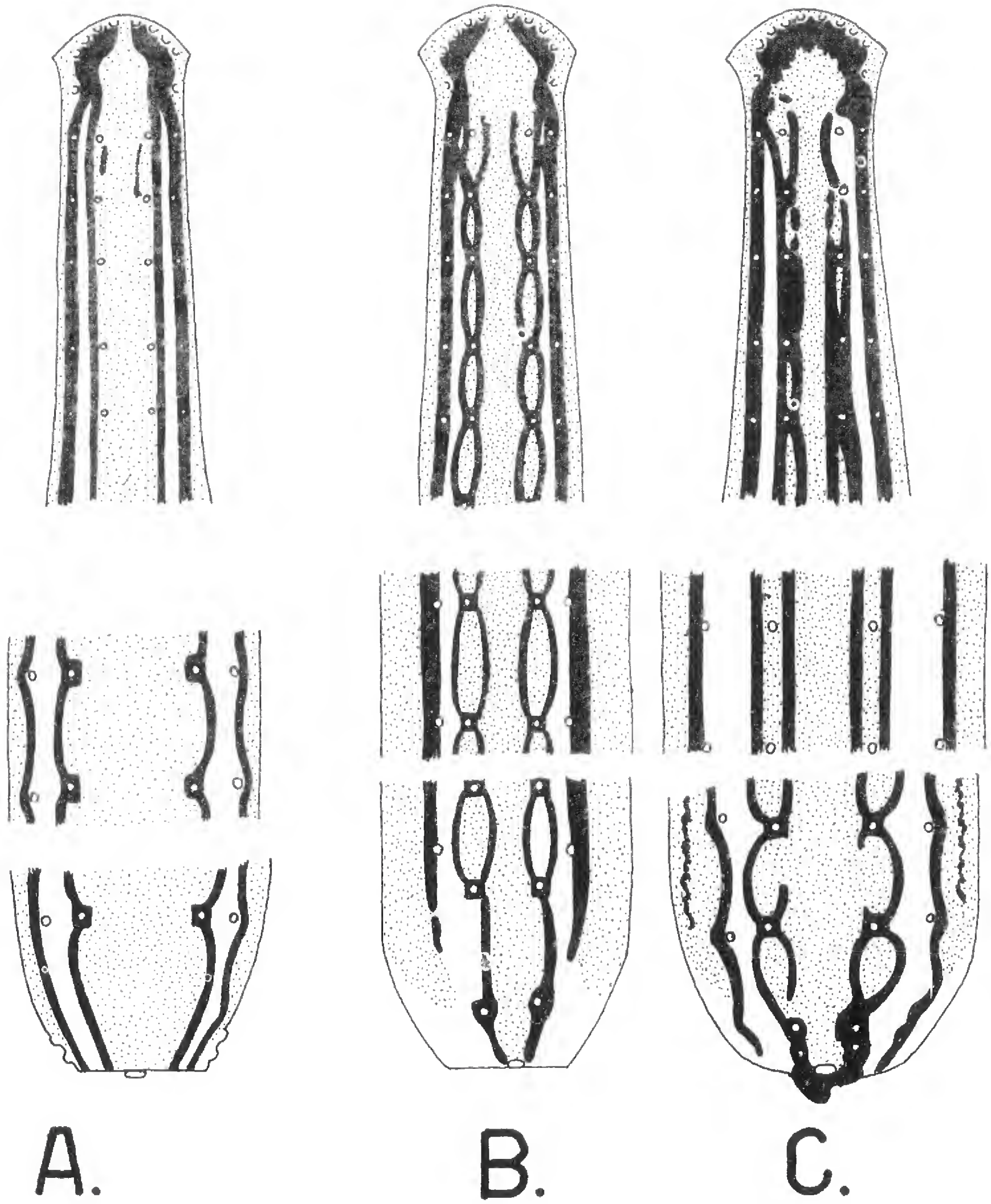

FIG. 3: *Amicibdella niger*. Tertiary variation in individual pattern in three specimens from Caribou Falls (v. Additional material, 3), shown at the same size for direct comparison. The lines of the paramedian and intermediate sense organs; stipple indicating the pale brown of the body of bands in the median, paramedian and intermediate fields; black, the dark brown margins on these bands, the dark brown line medial to the paramedian sense organs, and dark brown areolae including these sense organs; contrast stripes of the paramedian fields, white.

A, 28·0 mm, Unistriate along the length of the body; above, anterior region of the body back into xi; middle, xvii and xviii; below, posterior region of body, xxii to xxvii. B, 31·0 mm, the same, Catenulate along the length of the body. C, 45·0 mm, the same, Bistriate fused anteriorly, Catenulate on the posterior somites.

the absence along this line of the very dark internal botryoidal tissue and a thin body wall.

Tertiary variation has a very high frequency in *A. niger*, commonly very obvious in preserved specimens; only occasionally detectable in the living specimen.

It has three forms:

(a) Unistriate: a wide pale band extends across the dorsal median field to terminate in the paramedian field with a narrow dark margin. This form is general in specimens less than 30·0 mm and occurs also in larger specimens.

In others, less than 30·0 mm to full size, a second dark line is present. This is medial to the line of paramedian sense organs and is of the width of the line lateral to them. This provides two forms, one or the other, or in combination in the one specimen; the resultant, essentially symmetrical.

(b) Bistriate: the two dark lines parallel, the paramedians in a pale band between them; the dark lines may widen, the pale band narrow, or fuse to include the sense organs.

(c) Catenulate: the paramedian sense organs each in a dark areola; the two lines converging and connecting to the areolae, diverging between the areolae, and 'chain-like' in appearance.

AMICIBDELLA NIGER: ADDITIONAL MATERIAL

In all of the following, the annuli of the midnephric somites show differences in length with a_2 distinctly long.

(1) 3 specimens, 16·0, 20·0, 48·0 mm. Ridge above Christie's Pocket, due W. of Thornton's Peak, Q., Rainforest; June 16, 1973; Collector, J. W. Winter.

16·0 mm, unistriate; 20·0 mm, catenulate along the greater length of the body; 48·0 mm, bistriate anteriorly, the paramedian organs each in a dark areola, then catenulate back to xxi.

(2) 5 specimens, 18·0, 25·0, 32·0, 34·0, 52·0 mm. Townsville, Q.; August, 1968; collector, M. J. Grice.

18·0 mm, catenulate in xv to xviii; 25·0, catenulate ix to xvii; 32·0 mm, bistriate, the dark lines broad, female pore in xiii b_2; 34·0 mm, as 32·0 but catenulate from in xix to in xxvi; 52·0 mm, engorged, catenulate xviii to in xxiv.

Colour in life: As in type.

(3) 6 specimens, 28·0, 28·0, 30·0, 31·0, 45·0, 53·0 mm. Caribou Falls, near Lake Eachem, N. Queensland; August 31, 1969; collector, North Queensland Naturalists Club, Cairns.

Colour in life, as in type. Pattern (Fig. 3). Preserved in alcohol, the paired contrast stripe is defined below only by a maculate line separating the margin from the venter.

(4) Two specimens, 21·0, 32·0 mm. Tinaroo Creek, near Mareeba, N. Q.; Alt., 3,000 ft.; collector, North Queensland Naturalists Club, Cairns.

In life, 32·0 mm, generally dark brown, a paler brown band in the median field; bistriate, the lines partly fused from xii to xv, catenulate from xv to xxiv; the stripe of the supramarginal line extending briefly into the marginal field; venter, sparsely maculate.

(5) Four specimens, 19·0, 29·0, 50·0, 57·0 mm. No locality; August 11, 25, 1968; collector, North Queensland Naturalists Club, Cairns.

19·0 mm, viii to xii unistriate, xii to xvi bistriate, xvii to xxii catenulate; 29·0 mm, paramedian sense organs in brown areolae, bistriate, partly fused from xi to xv, catenulate to xxiv; female pore, xiii b_2; 50·0 and 57·0 mm, unistriate for the length of the body.

The 50·0 mm specimen has 4 small opaque white subspherical bodies, each about 0·20 mm in diameter, visible through the ventral body wall. They are erratic anatomically, and have the general appearance of parasitic cysts.

(6) One specimen, 29·0 mm. Broomfield Swamp, Atherton Tableland; in cleared rainforest, near a swamp; June 3, 1969; collector, B. Hyland; per. P. Ogilvie.

Preserved, very pale brown, the dorsal band, greyish, unistriate with some very weak indications of the dark line medial to the paramedian sense organs.

(7) One specimen, 29·0 mm. Forest Patch on Roaring Meg, North Daintree River, N. Queensland; June 17, 1973; collector, J. W. Winter; preserved, brown, pattern complete, catenulate viii to xxiii.

(8) Two specimens, curved, approx. 17·0, 23·0 mm. Grassy woodland, 800 to 1,200 ft. Gold Hill, end of ridge W. from Thornton Peak and Enterprise Mine; June 18, 1973; collector, J. W. Winter; preserved in formalin, pattern complete.

17·0 mm, bistriate vii to xv, then catenulate; a few supramarginals lateral to the stripe in the midbody; 23·0 mm, catenulate viii to xi and xix to xxiii, bistriate between xi and xix.

Micobdella gen. nov.

DERIVATION: *micere*, to move to and fro with a rapid motion; *bdella*, a leech. m.

Haemadipsidae; duognathous; lacking salivary gland papillae; somites viii to xxiii 4-annulate (total 16); xxiv, uniannulate; 6 annuli posterior to xxiii a_2; auricles, small, posterior to xxiv, the margin very weakly lobed; a contrast stripe in the dorsal median field from ii/iii into xxvii; a contrast stripe lateral in the intermediate field from in vi to in xxvii also includes the line of the supramarginal sense organs, and has straight edges; 1st nephropores lateral on iv, 2nd to 16th nephropores ventral in the marginal field, and included in the band in this field; jaws edentulous, each armed with a continuous low cutting edge; pharynx terminates at viii/ix; crop compartments each with a single pair of wide based caeca at the median level; lambertian organs in xxi to in xxii, elongate cylindrical, the organs shorter than the ducts; genital pores, xi b_5/b_6, xii b_5/b_6; reproductive systems, haemadipsoid: anterior regions of male paired ducts reflected in a single primary loop in the median splanchnic chamber, a sperm duct on the posterior halves of both limbs of the loop, ejaculatory bulbs present, weakly muscular; median regions, hemimyomeric, the male a micromorphic atrium, the female formed on a posteriorly directed loop, the limbs of the loop equal in length, and the loop extended posteriorly as an oviducal glandular sac.

TYPE SPECIES: *Micobdella gloriosi* sp. nov. as below.

OTHER SPECIES: *Micobdella auritus* sp. nov.

Micobdella is characterized in the combination of a general somital annulation as in *Philaemon* and other 4-annulates of eastern Australia; a contrast stripe along the length of the dorsal median field; a contrast stripe along the length of each intermediate field including the line of supramarginal somital sense organs; the jaws armed with a continuous cutting edge.

With the exclusion (Richardson, 1969) of the neotropical *Nesophilaemon* Nybelin 1943 from the Haemadipsidae, the previously established 4-annulate genera in the family are: *Philaemon* Lambert 1898; *Tritetrabdella* Moore 1938; *Neoterrabdella* Richardson 1969.

Tritetrabdella is based on a species from the Malay Peninsula: viii to xxii 4-annulate; trignathous, the jaws with 45 teeth; no salivary gland papillae; no lambertian organs. The pattern is not topographically defined.

Neoterrabdella is based on a species from the Northern Territory: viii to xxiii 4-annulate; xxiv 3-annulate; 8 or 9 annuli posterior to xxiii a_2; large lobed auricles formed on xxiv to xxvii; jaws, duognathous, with teeth; pattern: longitudinal contrast stripes—the middle half of the dorsal median field from ii/iii to xxvii, on each line of paramedian sense organs from in viii (or shorter, in ix, or in xii) to xxiv a_2, median in each paramedian field from in vi to xxiv a_2, median in each intermediate field from in ix to in xxiv a_2, and in each marginal field from the velum onto the auricle; nephropores in the marginal fields; no salivary gland papillae; no lambertian organs. This combination has not been seen in any 4-annulates from eastern Australia or Papua.

Philaemon is based on specimens probably from southern Victoria, possibly from Tasmania, the type species being *Philaemon pungens* as described by Lambert (1898). From Lambert, the characteristics are: viii to xxiii 4-annulate; xxiv,uniannulate; 6 annuli posterior to xxiii a_2; genital pores, xi b_5/b_6, xii b_5/b_6; auricles, posterior to xxiv; duognathous, with 'some seventy or more small teeth'; no salivary gland papillae (*v.* pl. xi. figs. 10 to 12); lambertian organs in xx and xxi, the organ about half the length of the duct; pattern: a pale brown band filling the median field from in vi a_2 to in xxvii; contrast stripe (green in life) along each line of paramedian sense organs from in vi a_3 to xxiii/xxiv, the stripe distinctly and regularly narrowed on a_2 in each somite; a stripe in each marginal field at least from in x to the auricle; location of the nephropore, ?.

The combination of characteristics as in *Philaemon* is found in 4-annulates from North Queensland to Tasmania. These constitute a complex assembly, as yet confusingly similar in pattern and external meristic morphology, such that I continue unable to sort them with any confidence.

One from Mount Glorious, southeast Queensland, differs in having also a contrast stripe in the lateral half of the intermediate field, the stripe extending to include the supramarginal sense organs; genital pores, xi b_6, xii a_2. It is brown in general colour, small, the largest specimen to date, 14·0 mm long.

Additional to the above, a new genus in Papua is based on a troglobitic 4-annulate lacking cutaneous pigment and pattern: the 1st nephropore on viii a_1; viii to xxiii 4-annulate; 6 annuli posterior to xxiii a_2; lambertian organs in xxi and xxii, the organ much longer than the duct (as in 5-annulates); recurrent limb of the female median region, short, about half the length of the procurrent limb, etc.

Micobdella gloriosi sp. nov.
(Figures 4, 5)

HOLOTYPE: Preserved, 55·0 mm long. Mt Glorious, SE. Queensland; rainforest; Feb. 28, 1972; collector, A. Hiller; per C. Wallace. Dissected, jaw removed, mounted separately. Deposited, Queensland Museum, G5309.

PARATYPE: Preserved, total length 55·0 mm. Same locality, date, collector, as type. Dissected. Deposited Australian Museum, Sydney, W4306.

DESCRIPTION OF HOLOTYPE

GENERAL FORM (Fig. 4 A): Preserved, elongate, slightly depressed; widest posteriorly, the width diminishing gradually anteriorly to the base of the narrow anterior sucker; more rapidly posteriorly to the base of the posterior sucker which is nearly as wide as the widest portion of the body.

Total length, 55·0 mm; the width at v/vi, 3·0 mm; the width and depth, 3·0 mm at ix/x, 8·0 mm from the anterior tip of the animal; 4·0 mm and 3·0 mm at xi/xii, 14·0 mm; 6·0 mm and 5·0 mm at 20·0 mm; 8·0 and 5·0 mm, at 30 mm; 7·5 mm and 5·0 mm, at xx/xxi, 40·0 mm; the base of the posterior sucker, 5·0 mm at 53·0 mm; and the sucker 7·0 mm wide and 9·0 mm long.

COLOUR: In life: the dorsum a deep dark brown sparsely maculate with black so as to be dusky; divided into a pair of dark bands by a continuous longitudinal brightly yellow median stripe along the full length of the body, and a single pair of continuous longitudinal brightly yellow stripes. The paired stripes divide the dorsum from the light brownish immaculate venter. Dorsum of the posterior sucker, immaculate pale grey.

Preserved in formalin: the dorsum diminishes to a pale brown excepting along the margins of the bands which are dark brown; contrast stripes diminish to off-white or pale cream; the venter to dusky faintly brownish pale grey. The narrow lower margin to the lateral stripe weakens to become broken, even difficult to detect.

PATTERN (Fig. 4, B to E): Preserved: the median contrast stripe is continuous from ii/iii, immediately behind the 1st pair of eyes into xxvii, reaching to and enclosing the anus. It almost fills the median field from ii/iii to v; elsewhere uniformly restricted to the middle half of the median field which is completed by the narrow medial dark margins of the dorsal bands. The medial margin of this band includes the line of the paramedian sense organs; the paler portion of the band occupies the paramedian field and the line of the intermediate sense organs; and the outer dark margin of the band is in the intermediate field, close to the line of intermediate sense organs in the pregenital region, progressively further from this line as the field widens along the genital and postgenital regions, with the greater part of the medial half of the field then occupied by the paler portion of the band.

The single pair of contrast stripes are narrow; commence immediately lateral to the 5th eye on vi, enclose the supramarginal sense organ close to the edge of the stripe. The stripe continues posteriorly in this relationship, occupying the lateral half of the intermediate field, the line of the supramarginal sense organs just within the outer edge of the stripe.

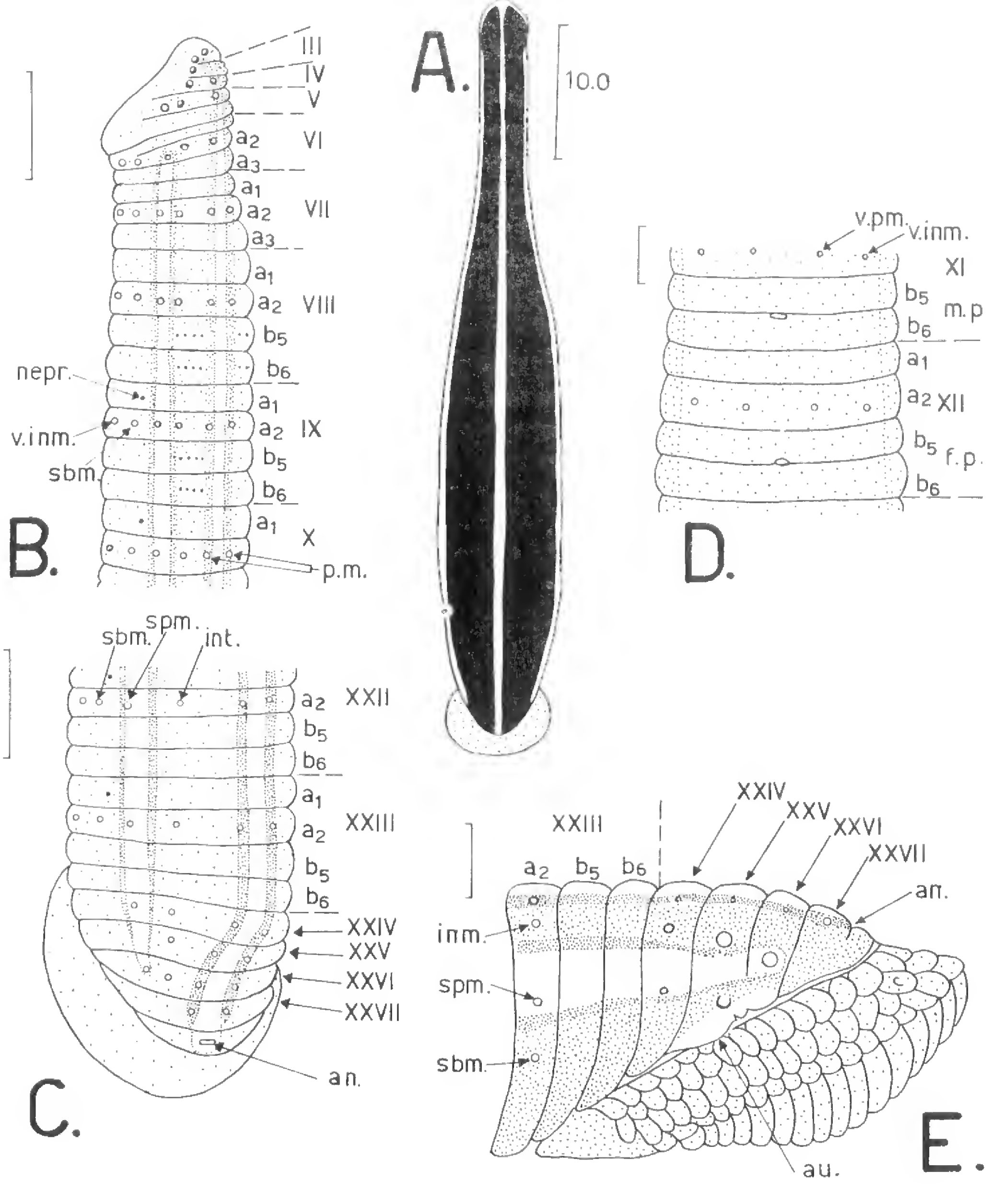

FIG. 4: *Micobdella gloriosi* gen. et sp. nov. Holotype. A, general form and dorsal pattern, contrast stripes in the median and intermediate fields. B, left dorsolateral aspect, somites i to ix, showing somital annulation and topography of pattern. C, the same, for somites xxii to xxvii. D, ventral aspect, somites xi and xii. E. Left lateral aspect, somites xxiii to xxvii, dorsum and ends of ventral muscular ridges on sucker, topography of pattern, and morphology of auricle.

For abbreviations, etc., see Fig. 1.

In this way, both edges of the paired contrast stripes are straight, and the stripe uniform along the greater length of the body.

The paired contrast stripes divide the dorsal pattern from the marginal and ventral pattern, which is uniform excepting the narrow dark margin dorsal in the marginal field.

The dark margins of the bands narrow behind xxiii.

The paired stripes continue posterior to this, reducing in width and terminate enclosing the supramarginal sense organ on xxvi.

There is no indication of pattern on the dorsum of the posterior sucker.

ANNULATION (Fig. 4, B–E): Interannular and intersomital furrows equivalent; somital limits not directly recognizable; no obvious couplets or triplets of annuli; somital sense organs, in life everywhere encircled in white and obvious, preserved, frequently obscure, detectable with difficulty; sensillae, obvious as small white points, relatively few in all fields; annuli, strongly areolate in life, areolae detectable only in the ocular somites in well extended specimens; nephropores obvious in life as small dark points central in the length of a_1, in the marginal field just dorsal to the level of the submarginal sense organ on a_2.

Fully extended, ii/iii is the first recognizable furrow, weak, restricted to the median field, with the 1st eyes anterior to it; iii, uniannulate with the 2nd pair of eyes; iii/iv, stronger, terminating in the intermediate lines; iv, uniannulate, with the 3rd pair of eyes and 1st detectable paramedian sense organs; v, 2-annulate, $a_1a_2 = a_3$, the 4th pair of eyes in a_1a_2 as also the 1st detectable supramarginal sense organs, a_1a_2/a_3 terminating at the level of the submarginal line, and v forming the posterior portion of the surface of the velum and extending ventrally as the lateral and ventral margin of the sucker; no defined dorsolateral lobe on the margin; the 1st nephropore on the lower surface of the velum close to the lateral margin at the level of v a_1a_2/a_3; vi, 3-annulate above, $a_1 < a_2 < a_3$, a_2 with the 5th pair of eyes and the 1st complete set of somital sense organs, a_1/a_2 extends into the ventral intermediate field, and below this, vi 2-annulate, $a_1a_2 > a_3$; vii, complete 3-annulate, $a_1 < a_2 < a_3$ (a_3 = viii a_1); viii to xxiii 4-annulate (total 16); viii, a_1 slightly $> a_2 = b_5 = b_6$; 2nd nephropore on ix a_1; ix to xx, $a_1 = a_2 = b_5 = b_6$, with b_6 slightly shorter than b_5 but the difference is so small that b_6 is not directly recognizable by length alone; xxi, $a_1 < a_2 = b_5 = b_6$, as also xxii; xxiii, $a_1 = a_2$ slightly $> b_5 = b_6$; 6 annuli posterior to xxiii a_2; xxiv to xxvii, uniannulate; xxiv, complete across the venter, but reduced, and carrying minute white dorsal paramedian, slightly larger intermediate and supramarginal somital sense organs; xxv and xxvi with minute paramedians and large obvious intermediate sense organs; xxvii, with minute paramedians, followed by a supernumerary annulus nearly divided by the anus.

Auricles distinctly small; the eave, narrow, differentiated as a thick flange on the edge of xxv, longer than a thin flange on xxvi, the two separated by a notch; no differentiated eave on xxvii; the groove between the eave on xxv and the dorsal surface of the sucker not appreciably deeper than the groove beneath xxiv. In life, the 17th nephropore elevated on a papilla below the notch in the eave; preserved, the papilla fully retracted and the nephropore a minute aperture on the inner wall of the groove.

Dorsum of the posterior sucker divided into about five concentric rows of areolae;

the venter with a prominent clamp, the surface divided into radiating muscular ridges which subdivide to end as about 80 at the margin of the sucker.

BODY WALL AND MUSCULATURE: The body wall thin, only the inner layer of longitudinal muscle strands detectable in dissection.

Paramedian palisades of dorsoventral muscles represented along the crop by small clusters at the intersomital levels. Posterior to xix/xx, four pairs of strong bands on each side of the intestine, serial, apparently intersomital, the pairs reducing in length posteriorly; the dorsal ends attached to the body wall anterior to and more widely spaced than the attachment to the ventral body wall where the ends are closely approximated. In this way the bands appear to rise from a common ventral attachment and radiate to individual spaced attachments on the dorsal body wall.

Intermediate palisade, uniformly spaced strands back to xx. Posterior to this, three pairs of distinct bands, much narrower than the paramedian bands, are closely approximated in their ventral attachment and more widely spaced dorsally.

CENTRAL NERVOUS SYSTEM (Fig. 5 A): The anterior ganglionic mass has right and left small dorsolateral components well spaced from the compact bilobed ventral component which innervates the velum, at least somites iii and iv, v and vi.

Ganglion vii in intimate contact with the ventral component and widely spaced from viii which is at the level of viiib_5.

ALIMENTARY TRACT (Fig. 5, A–C): The lower surface of the velum inflated, smooth, with a median subcentral trifid aperture; the rim of the aperture forming the anterior edge of a wide deep annular groove on the inner wall of the chamber of the sucker, the posterior wall of the groove formed by the anterior end of the pharynx; the groove, undivided excepting partially ventrally by a ventromedian thickening on the end of the pharynx.

Duognathous; dorsomedian and ventromedian muscular pads on the end of the pharynx; the ventrolateral jaws housed in the annular groove, horizontal, the obtuse convex anterior margin 0·75 mm long, the profile at the median end, obtusely convex, as tall as wide (0·5 mm) at the base.

The right ventrolateral jaw removed. Under high power, no indication of teeth; the edge armed with a thin low ridge, a cutting edge, 0·73 mm long, highest (0·03 mm) at the medial end, reducing gradually in height along its length to be 0·02 mm in the middle.

No salivary gland papillae on the jaws.

The entrance to the pharynx, narrow, restricted, not half the length of the anterior margin of the jaw, and closely embraced by the connectives between the dorsal and ventral components of the anterior ganglionic masses.

The wall of the pharynx, thin; internal muscular ridges present as undivided dorsomedian, ventromedian, and ventrolateral ridges; no dorsolateral ridges.

Salivary glands, sparse aggregations in vii, viii, and ix, and a compact ventral mass on each side posterior in viii; the ducts joining on each side to form heavy columns of aggregated ducts terminating in the jaws.

The pharynx supported by an obvious system of extrinsic radial muscles, terminates at viii/ix.

The crop thin-walled, narrowly tubular without obvious compartmentation in ix and x; then partly filled with blood, the compartments each extended laterally with a single pair of wide based simple caeca at the median level in xi to xviii; xix, with postcaeca originating from the anterior half of the compartment, the postcaeca entering the paramedian splanchnic chambers and extending posteriorly into xxiii; the outer aspect of the postcaeca, lobed.

Lambertian organs located in the paramedian chambers ventral to the postcaeca; the organs from in xxi to in xxii; elongate cylindrical, continuing as a very narrow duct connecting terminally to the postcaeca; the organs distinctly shorter than the ducts, about one third the length of the duct.

The crop terminates at xix/xx, connecting terminally to the tubular intestine which shows no indication of anterior caeca, and joins at xxii/xxiii to the end of the tubular tapering rectum.

REPRODUCTIVE SYSTEMS (Fig. 5D): Assessed as male mature.

Typically haemadipsoid; ejaculatory bulbs present.

Genital apertures, xi b_5/b_6, xii b_5/b_6.

Testes, saccular, the anterior pair at xiii/xiv, the posterior pair at xxii/xxiii, total 10 pairs; vasa efferentia, short, connecting laterally to the white tortuous vas deferens extending anteriorly in the paramedian splanchnic chamber, reducing in width in xiii, and entering the median chamber at xi/xii, developed here as a simple posteriorly directed loop, the two in parallel; a much folded sperm duct occupying the posterior half of the recurrent limb of the loop and of the procurrent limb; terminal portion of the procurrent limb narrowly tubular, terminating as a small elongate opalescent muscular ejaculatory bulb; the bulb continues as a very short ejaculatory duct, the two ducts entering independently into the anteroventral aspect of the male atrium; male atrium thin walled, small, standing just above the level of the ventral cord, amyomeric, micromorphic.

The single pair of small saccular ovaries, posterior in xii, each continuing as a short narrow delicate oviduct; oviducts joining just anterior to the female pore to form the median region; no distinct female atrium; median region formed on a posteriorly directed primary loop reflecting in xiv, the two limbs of the loop essentially equal in length; the initial recurrent limb, thick walled, narrower than the strongly muscular procurrent limb; the posterior wall of the elbow of the loop expanded as a thin-walled glandular sac extending into xv.

Prostatic tissue, a large glandular mass in xi a_2 to xi/xii, adherent to the ventral body wall, enclosing and concealing the atrium, the ejaculatory ducts and the terminal ends of the bulbs.

There is no glandular tissue recognizable as albumin glands.

DISTRIBUTION

Eastern Queensland: Cairns; Mount Glorious, Brisbane.

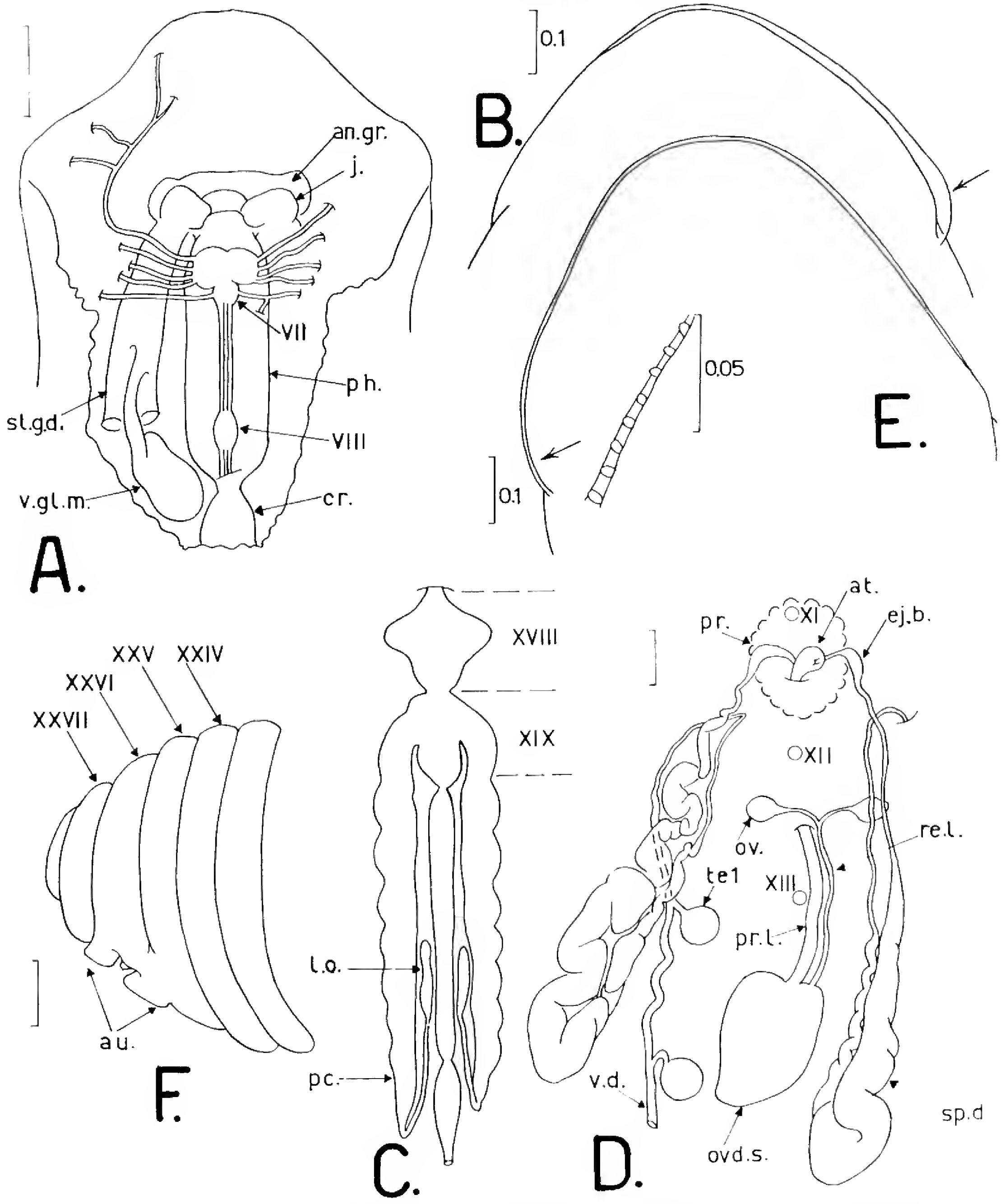

FIG. 5: A–G, *Micobdella gloriosi* gen. et sp. nov. Holotype. A, anterior ganglionic mass, somital ganglia vii and viii, jaws, pharynx, aggregated salivary gland ducts and ventral glandular mass as exposed by a median incision along the ventral aspect. B, jaw and cutting ridge, arrow marks medial end. C, caecation of crop, somites xviii and xix, lambertian organs and ducts, intestine, rectum. D,

E, F, *Micobdella auritus* sp. nov. Holotype. E, jaw with cutting ridge, arrow marks medial end. Inset, minute teeth of the medial end of the anterior margin of the jaw. F, right lateral aspect xxiv to xxvii, and the auricle.

ADDITIONAL MATERIAL

One specimen, 34·0 mm, Under a log, Road A, about two miles from Tinaroo Lake, near Atherton, N. Q.; Nov. 7, 1971; collector, North Queensland Naturalists Club, Cairns.

Sent alive, dead and dessicated on arrival. Placed on damp filter-paper, recovered form, colour and pattern.

Colour, as type. Preserved, dorsal bands, pale brown with narrow black margins; contrast stripes, cream; venter white, immaculate, with an incomplete narrow pale brown margin in the marginal field.

Pattern, general somital annulation, genital pores, nephropores, auricles, as type.

Somites xvii, xviii, the annuli essentially subequal in length, a_1 and b_6 slightly $<$ $a_2 = b_5$, but not regularly so along the midnephric series.

Micobdella auritus sp. nov.

(Figures 5 E, F)

HOLOTYPE. Total length, 67·0 mm. Killara, Sydney, N.S.W. (Moist valley); July 7, 1973; collector, Glen Hunt; per Dr P. Hutchings. Dissected, one jaw removed, mounted separately. Deposited, Australian Museum, Sydney, W5537.

DESCRIPTION OF HOLOTYPE

GENERAL FORM: A large 4-annulate land-leech, the size and general form as in *M. gloriosi.*

COLOUR: In life: margin of the velum pale grey; dorsum of the velum and of the body, intense black; contrast stripes, golden, tinged with green anteriorly; somital sense organs obscure; venter, dark red, immaculate, excepting large dark brown maculae just ventral to the outer paired stripes, each macula restricted to an annulus; dorsum of the posterior sucker, immaculate pale grey, the venter off-white.

Preserved in formalin: the dorsum remains black excepting posterior to xxiii which becomes pale reddish; the green tinge fades from the contrast stripes which become pale yellow; the venter and the maculae diminish in intensity.

PATTERN: As in *M. gloriosi*: a median dorsal contrast stripe with sharply defined parallel edges occupies the middle third of the median field from ii/iii to in xxvii, uniform in width along the greater length of the body, slightly wider anterior to viii; a single pair of contrast stripes with sharply defined parallel edges, each occupying the lateral half of the intermediate field and the line of supramarginal sense organs from in vi a_2, lateral to the 5th eye, to xxiv/xxv; nephropores below the stripe close to the line of submarginal sense organs.

ANNULATION: General somital annulation as in *M. gloriosi.* Somital annulation differs: iv, 2-annulate between the ocular areolae; vi, $a_1 < a_2 < a_3$ above; viii, $a_1 > a_2 < b_5 = b_6$; ix, $a_1 < a_2 < b_5 = b_6$; x, $a_1 = a_2 < b_5 = b_6$; xiii to xvi, $a_1 = a_2 = b_5 > b_6$; xvii, xviii, xix, $a_1 < a_2 > b_5 = b_6$; xx, xxi, $a_1 = a_2 < b_5 > b_6$; xxii, xxiii, $a_1 = a_2 > b_5 > b_6$; xxiii b_5, last annulus complete across the venter, b_6 reduced to a very thin ridge. A supernumerary annulus divided by the anus.

The relative lengths of the annuli in ix to xx are distinct, and fully recognizable.

Auricles, short, as an eave formed on the lateral ends of xxv and xxvi, terminating at xxiv/xxv and xxvi/xxvii, divided by a notch; the eave covering a groove no deeper than the groove beneath the end of xxiv; the eave more prominent than in *gloriosi.*

Genital pores, xi b_5/b_6, xii b_5/b_6.

ALIMENTARY TRACT: Velum, annular groove, housing of the jaws, entrance to the pharynx, the pharynx, crop, and intestine, as in *M. gloriosi.*

Jaws, compressed, taller, more convex along the anterior margin than in *gloriosi.* The anterior margin 1·4 mm long; minute, obtuse, low conical, blunt teeth 0·006 mm high, spaced at intervals of 0·01 mm, detectable along the medial portion for a distance of 0·4 mm, and a low cutting ridge of about the same height along the rest of this margin. The teeth are of such small size and stand at varying angles as though non-functional. No salivary gland papillae.

Lambertian organs in xxi and xxii, elongate cylindrical, each much shorter than its duct.

REPRODUCTIVE SYSTEMS: As in *M. gloriosi.* Assessed as male gravid. The sperm ducts occupy almost the entire length of both limbs on the primary loop. The two loops are parallel in relationship.

M. auritus differs from *gloriosi* in having a_2 and/or b_5 distinctly long in somites xiii to xxiii; in having minute (? non-functional, vestigial) teeth along a short portion of the anterior margin of the jaw additional to the cutting edge; and in being black on the dorsum, the black remaining through early preservation.

DISTRIBUTION

Known only from the holotype. This species has not been represented in the many other collections I have examined from south of Sydney, the Northern Rivers Region in N.S.W., or Queensland.

ADDITIONAL MATERIAL

Micobdella sp.? One specimen, 44·0 mm long. Tasmania. National Museum of Victoria, Melbourne, G852. (There is no other information).

Large, heavy-bodied; preserved in alcohol; faded; unsuitable for dissection.

General form, pattern and topography of pattern, general somital annulation, as in *Micobdella.*

Narrow brown lines define the edges of the contrast stripes, the median from in iii to in xxvii; the dorsal edge of the paired stripes from in viii (left), in ix (right), to in xxiv; venter immaculate.

The topography of the pattern is shown clearly in xxiii as: a contrast stripe occupying the middle half of the dorsal median field; the paired contrast stripes as in the lateral half of the intermediate field with the supramarginal sense organ immediately within the edge of the stripe; the nephropores in the marginal field immediately dorsal to the level of the submarginal sense organ.

The auricle, very small, a longer flange on xxv separated by a notch from a small flange on xxvi; the eave compressed and hardly recognizable.

Somites xv to xxi, $a_1 = a_2 = b_5 > b_6$; xxii, $a_1 = a_2 = b_5 < b_6$; xxiii, $a_1 > a_2 > b_5 = b_6$. In this G852 resembles *auritus* and differs from *gloriosi*. It differs from the 4-annulates previously recorded from Tasmania, *Philaemon pungens* Lambert 1898 and *P. grandis* Ingram 1957, both having a contrast stripe along the lines of the paramedian sense organs.

Although unsuitable for dissection, the jaws grossly contracted and unusable for detail, the combination of the somital annulation and the distinctive topographic pattern of *Micobdella* indicates that the specimen can be assigned with reasonable confidence to this genus.

I have had no other material from Victoria or Tasmania assignable to *Micobdella*; but with the experience of a single specimen from Sydney as the only evidence in many collections of this genus outside of Queensland, its occurrence in Tasmania cannot be seen as improbable.

G852 is not fully documented. Lambert's material of '*Geobdella australiensis*' and '*Geobdella*' *whitmani* carry the collection numbers G831 to 833 on printed labels with writing in the same hand as for G852, which may be only a coincidence of cataloguing such as happens with the use of a new label. At least there is this evidence that material had come to the National Museum from southern Queensland and from central eastern N.S.W.

For this reason, it seems best to accept the record of *Micobdella* as in Tasmania, as provisional.

ACKNOWLEDGEMENTS

This study initiated with collections sent to me by the North Queensland Naturalists Club, by Mr P. Ogilvie of the Forestry Department of Queensland, and Dr M. J. Grice, then of Townsville and now of Brisbane. These showed novelty which was not resolvable until I had extended my experience of the Haemadipsidae in eastern Australia. More recently, others have come to me from Mrs C. Wallace, the Queensland Museum, and associates; from Mr J. W. Winter, National Parks Zoologist for Queensland; and from Dr G. Hunt of Sydney through Dr P. Hutchings, Australian Museum. The majority were sent as live specimens, the later collections resolving the difficulties in the apparent changes in pattern following preservation.

I do most warmly acknowledge my debt to these persons and their associates; as also to the Directors of the Queensland Museum, the Australian Museum, and the National Museum of Victoria, to Mr B. Campbell and Mrs C. Wallace, Dr P. Hutchings, and Dr B. J. Smith of these institutions for the opportunity to study material coming to and in the collections of their institutions; to Miss E. Pope and Dr J. C. Yaldwyn, both formerly of the Australian Museum, for their help in previous years; and to the Librarians, New England University, Armidale, the Australian Museum, and C.S.I.R.O. Melbourne, for assistance with literature; as also Professor M. C. Meyer, University of Maine, Orono, for assistance with difficult literature.

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A REVIEW OF THE *LITORIA NANNOTIS* SPECIES GROUP, AND A DESCRIPTION OF A NEW SPECIES OF *LITORIA* FROM NORTHERN QUEENSLAND, AUSTRALIA (ANURA: HYLIDAE)

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ABSTRACT

The identity of *Hyla dayi* Günther was discussed and re-examined in the light of extensive study on taxonomy and biology of northern Queensland frogs. It is proposed that the original description of *Hyla dayi* was based on a northern Queensland *Nyctimystes*. *Litoria dayi* non Günther is described and is named *rheocolus*.

A new species of *Litoria* from northern Queensland similar to *rheocolus* and *nannotis* is described, and is named *nyakalensis*. Tadpoles of *rheocolus* and *nannotis* are described, and the male calls of *rheocolus* and *nyakalensis* are discussed.

Litoria nannotis species group consists of three species, *rheocolus*, *nyakalensis*, and *nannotis*, all restricted to northern Queensland. Phylogenetic relationships amongst these three species are discussed; it is proposed that *rheocolus* is the most primitive, *nannotis* the most specialized, and *nyakalensis* is intermediate and probably the immediate ancestral stock of *nannotis*. It is suggested that the *Litoria nannotis* species group evolved in northern Queensland from a New Guinean ancestral stock which crossed the Torres Strait land bridge in the Pleistocene.

During the course of taxonomic and biological studies on northern Queensland frogs I collected an undescribed *Litoria* which is closely related to *Litoria dayi* auctorum and *Litoria nannotis*. Because little is known on the biology of the above species group, the doubtful identity of *Hyla dayi* Günther, and erroneous description of *nannotis* tadpole, it is desirable to review the whole species group which occurs in northern Queensland.

MATERIALS AND METHODS

Observations and drawings were carried out under a Wild stereoscopic microscope. Techniques and abbreviations of measurements not given in an earlier paper (Liem and Hosmer, 1973), are as follows: interorbital width (IO) is the narrowest width of the fronto-parietal, upper eyelid width (EW) is the widest section of the upper eyelid, tympanum width (TW) is the width of the tympanum measured along its horizontal diameter, and eye diameter (ED) is measured along its horizontal diameter. DSL is abbreviation for David S. Liem collection, and QM for Queensland Museum collection.

SYSTEMATICS

Key to Species of the Litoria nannotis Species Group

1. Head rounded; IN/EN ratio more than 0·970; web on 1st toe on or just beyond proximal subarticular tubercle; ventral surfaces of posterior portion of body cream with reddish brown tinge .. .. *nyakalensis*
   Not as above 2

2. Snout shorter than eye diameter; snout bluntly rounded; loreal region strongly concave; prepollex enlarged; nuptial pad large with coarse spinules; single outer metacarpal tubercle; adult more than 40 mm in SV length .. .. *nannotis*
   Not as above .. .. *rheocolus*

Litoria rheocolus sp. nov.
(Figures 1,4C , D; Plate 3A)

Hyla dayi (non Günther, 1897): Loveridge, 1935, p. 38; Copland, 1957, p. 20; Tyler, 1968, p. 502.

Holotype: Adult male, QM J22631 from Kuranda, 50 km west of Cairns, N. Queensland, collected 21 May 1972 by David S. Liem.

Paratypes: 15 ♂—QM J22632–4, DSL 6187,6588, collected together with the holotype; QM J22635–9, from Bloomsfield Rd, 50 km SE. of Cooktown, collected 14 October 1972; QM J22640–42 from Cape Tribulation, 100 km N. of Cairns, collected 11 October 1972; DSL 6522 from Henrietta Creek, Palmerston N. P., collected 17 October 1972; DSL 6517 from the Boulders, 5 km W. of Babinda, collected 10 October 1972.

5 ♀—QM J22643–4 from Cape Tribulation, collected 11 October 1972; QM J22645, DSL 6547, 6554 from Shiptons Flat, 50 km S. of Cooktown, collected 14 October 1972; all localities are in N. Queensland; all specimens were collected by David S. Liem.

Other Material: 56 specimens—Amos Bay, 45 km S. Cooktown, QM J22383–86; Shiptons Flat, 50 km S. Cooktown, QM J17848; Bloomsfield Rd, 55 km S. Cooktown, QM J17847, DSL 6536–8, 6540, 6542–3, 6545, 6550–2; Cape Tribulation 100 km N. Cairns, DSL 6176, 6181, 6191, 6548, 6527, 6530–1,6533; Kuranda, 50 km W. Cairns, DSL 6606, 6173, 6175, 6178–80, 6183, 4925–30; Davies Creek Rd, 15 km SE. Mareeba, QM J18031; Tinaroo Creek Rd, 10 km SE. Mareeba, DSL 4932; Millaa Millaa Falls, DSL 6532–4; Henrietta Creek, Palmerston N. P., DSL 6518–21, 6523–4; The Boulders, 5 km W. Babinda, DSL 4839–45, 6514–16. Eleven tadpoles at stage 25 from Kuranda, 50 km W. of Cairns. All localities are in N. Queensland.

Diagnosis: A moderate sized treefrog, ranging from 27·0 to 37·8 mm in SV length. It could be distinguished from *nyakalensis* and *nannotis* by the following combination of characters: 1, snout bluntly pointed; 2, prepollex normal, not enlarged; 3, nuptial pad small, spinules fine; 4, forearm of males normal, not robust; 5, webbing on outer margin of 3rd finger reaches base of penultimate phalanx. Furthermore it differs from *nyakalensis* by its narrow IN/EN ratio (less than 0·970), cream ventral surfaces without reddish brown tinge, and from *nannotis* by its smaller size (adults less than 40 mm), two outer metacarpal tubercles, snout larger than eye diameter, absence of keratin spinules on chest of males, and the males call.

Description of Holotype: SV length 30·6 mm; TL 16·8 mm, 0·549 of SV length;

HW 11·0 mm, 0·359 of SV length; EN 3·3 mm; IN 3·0 mm; IN/EN ratio 0·909; IO 3·1 mm; EW 2·6 mm; IO/EW ratio 1·192; TW 1·5 mm; ED 3·1 mm; TW/ED ratio 0·405.

Tip of snout bluntly pointed; canthus rostralis sharp, angular in cross-section; loreal region slightly concave; dorsal view of head bluntly pointed (Fig. 1C), rounded blunt in profile (Fig. 1E); tympanum small; supratympanic fold present; tongue subovate, slightly nicked posteriorly; vomerine teeth in short, slightly oblique, oval rows just behind the level of the posterior edge of the choanae; upper jaw toothed; males without vocal sac.

Forearm not robust; a row of whitish tubercles present on lateral edge of forearm; distal segment of fingers expanded into disc; with ventro-marginal groove; 3rd finger disc larger than the diameter of the tympanum; length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; basal segment of 1st finger not enlarged and its disc moderate in size; subarticular tubercles roundish, one each on 1st and 2nd fingers, and two each on 3rd and 4th fingers; two small supernumerary tubercles on base of metacarpal of 3rd and 4th fingers; two oval (small medial and an elongated lateral) outer metacarpal tubercles on base of the palm, and an elongated inner metacarpal tubercle on the proximo-ventral inner surface of the metacarpal of 1st finger.

Fingers moderately webbed: between 1st and 2nd fingers free of web; web between 2nd and 3rd fingers reaching just beyond the proximal subarticular tubercle by a narrow fringe; webbing between the two outer fingers reaching by a narrow fringe the 2nd subarticular tubercle of 3rd finger, and just beyond the 2nd subarticular tubercle of 4th finger. Nuptial pad small, and consists of small fine darkbrown keratinous spinules.

Hindlimbs moderately long; distal segment of toes expanded into disc, with a ventro-marginal groove; length of toes from shortest to longest 1-2-5-4-3; phalangeal formula of foot 2-2-3-4-3 subarticular tubercles roundish, one each on 1st and 2nd toes, two each on 3rd and 5th toes, and three tubercles on 4th toe; a row of minute supernumerary tubercles is present on metatarsal of 5th toe; an oval inner and a small round outer metatarsal tubercles are present; foot webbing reaching base of disc of 1st toe, outer margins of 2nd and 3rd toes, and inner margin of 5th toe; web reaches by a narrow fringe the base of disc of 2nd and 3rd toes; web reaches halfway down the penultimate phalanx of 4th toe.

Cloacal opening at mid-level of the thighs; skin of dorsum shagreen, with small conical tubercles scattered on the head, upper eyelids, pectoral region, and throat; postero-ventral portion of femur granular; skin fold across chest absent. Pupil horizontal, roundish to oval; palpebral venation on lower eyelid absent.

Colour: In life, dorsal colour slate; proximal portion of thighs dirty brown; sides of body greyish brown; ventral surfaces of throat, body and anterior portion of thighs cream without pinkish tinge; palm of hands, ventral surfaces of tarsus, plantar surfaces of foot brownish slate; posterior and postero-ventral of femur, and postero-ventral of upperarm slate tinge with tan; margins of throat lightly spotted with brown. In preservative, dorsal colour slate, brownish tinge not distinct, and ventral surfaces cream white.

DESCRIPTION AND VARIATION: There is no marked difference amongst the males: fourteen male paratypes are 28·9–32·4 mm in SV length (mean 30·85 ± 3·981 mm); TL/SV 0·522–0·589; HW/SV 0·330–0·389; IN/EN 0·867–0·968; IO/EW 1·000–1·270.

Male paratypes and other male specimens have similar finger webbing as the holotype; web between the two outer fingers reaching on or just barely touching the 2nd subarticular tubercle; web on outer margin of 3rd finger reaches approximately two thirds down the length of the proximal phalanx in 5 specimens (DSL 6183, 6173, 6175, 6178, and 4930). Foot webbing is slightly variable: toe webbing in the majority of males examined reaches just the base of disc on outer margin of 2nd and 3rd toes.

Females are larger than males: nine females including the paratypes ranging from 32·7–37·8 mm in SV length (mean 34·01 ± 2·181 mm); TL/SV 0·534–0·569; HW/SV 0·320–0·365; IN/EN 0·882–0·970; IO/EW 1·067–1·147. In some females the toe webbing is less extensive, e.g. in two specimens it reaches outer margin of 3rd finger approximately two-thirds down the length of the proximal phalanx, and in two others the web reaches three-quarters the length of the proximal phalanx of the 1st toe. In females the supernumerary tubercles of palm and sole are distinct, arranged in rows along the metacarpals and metatarsals; inner and outer metatarsal tubercles are small and rounded. In two females (DSL 6525–26) the conical tubercles on back are large.

Colour: In life most males have similar colouration as the holotype; in some males however (QM J22635, J22637–8, J22642), the fore and hindlimbs are dark grey with brownish tinge. In QM J22632, J22642, the dorsal colour is brownish with a vague broken inverted triangular marking; in others (QM J22633, and DSL 6522) the fore and hindlimbs are greyish with distinct dark spots; ventral surfaces of hands and feet are grey with dark markings. In preservatives the following specimens are ashy grey dorsally: QM J22643–4, J22641, DSL 4927, and 4930. In life the ventral surfaces of body and throat are spotted with brown pigments or lightly dusted on margins of throat.

Female colouration differs from the male; dorsal background colour brownish tan with a distinct black inverted triangular marking on the back, stretching from between the eyes down to the coccygeal region; dorsal surfaces of fore and hindlimbs are brownish or grey, spotted with dark pigments, or with irregular vague cross-bands; background colour of ventral surfaces cream; throat, pectoral region, antero- and postero-ventral surfaces of thighs heavily dusted with darkbrown pigments; one individual (QM J22644) has a uniform cream whitish ventral surface dusted with greyish-brown on postero-ventral surfaces of the thighs.

MATING CALL: Regular repeated long drawn single note call, easily distinguished from the rasping call of *nyakalensis*. Details of the call structure will be reported elsewhere.

LIFE HISTORY: Amplexus pairs were observed from November to March; males call throughout the year except during cold winter nights; amplexus axillary. Males call from rocks or boulders in creeks or from vegetation overhanging water along streams and creeks. Eggs pigmentless, ovidiameter 1·4–1·8 mm; eggs are laid in compact gelatinous clumps under rocks in water.

Tadpoles at stage 25 ranging from 21·1–29·0 mm in snout-tail length (ST); tail height (TH)/tail length (TL) ratio 0·375–0·414; tail tip rounded; proximal half of dorsal and ventral tail fins are thick, and taper off posteriorly; muscular tail strong, and it is twice the height of the tail fins at base of tail (Fig. 4C); labia expanded and forms a large sucker-mouth (Fig. 4D); mouth width (MW)/body length (BL) ratio 0·512–0·702; the sucker-mouth consists of two continuous rows of labial papillae, one row along the edges of the labium, and another one on the inner surface of the mouth close to the labial tooth rows; additional labial papillar rows are present on the posterior portion of the labia, and at the anterior angles of the mouth (Fig. 4 D). Labial teeth consist of two entire upper and three entire lower labial tooth rows (II/III); the inner rows are stronger than the outer rows.

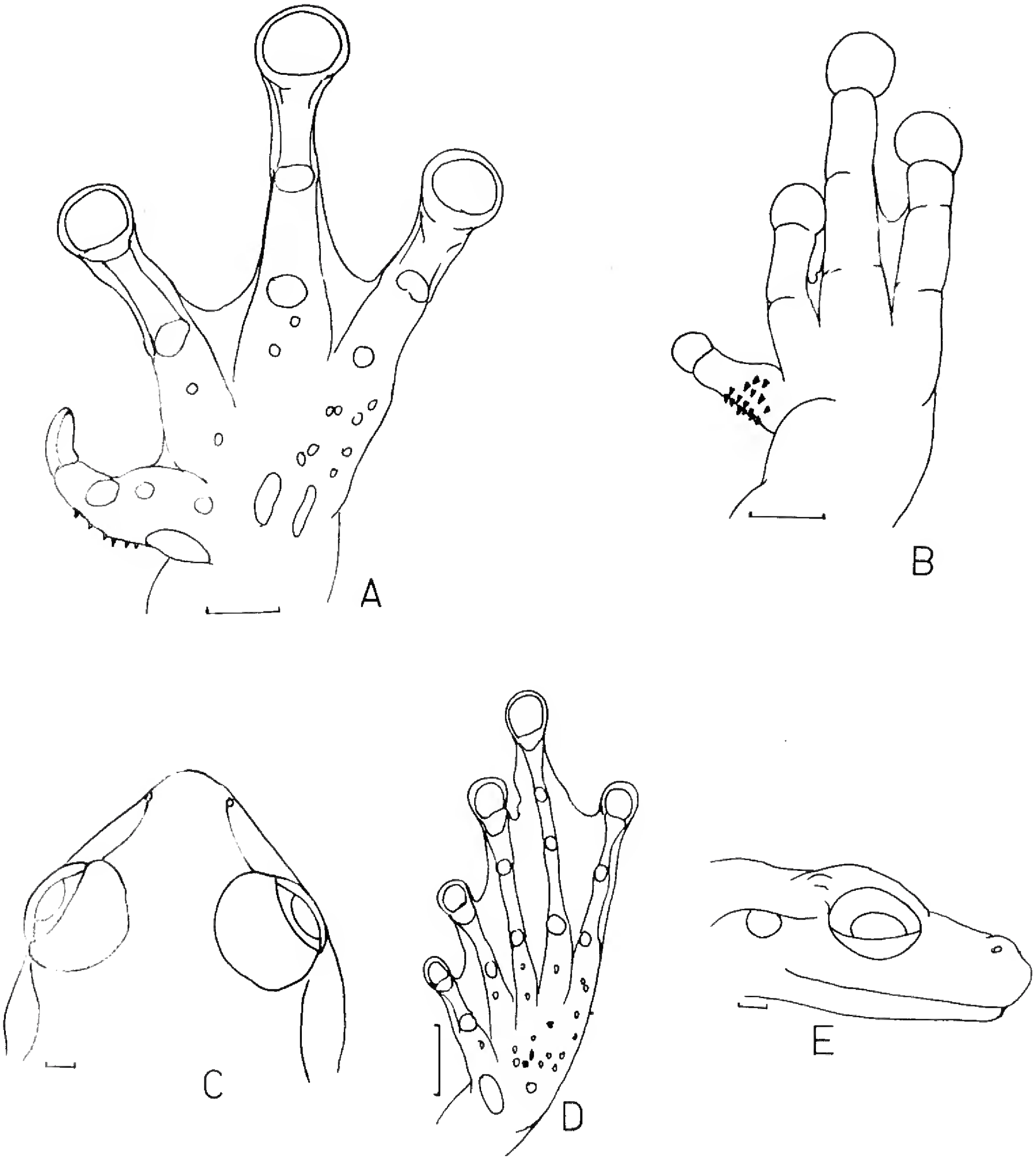

FIG. 1: *Litoria rheocolus*. A, ventral surface of hand (DSL 6187); B, dorsal surface of hand (DSL 6518); C, dorsal surface of head (DSL 6157); E, ventral surface of foot (QM J22645); F, lateral view of head (DSL 6517). Line equals 1 mm.

Upper jaw M-shaped; the lower jaw is V-shaped; both jaws are serrated (Fig. 4 D); spiracle opens at the end of a tube on ventro-lateral side of the body; anal opening median.

In life, body ground colour sandy; abdomen black and body darkbrown; the tail is transparent with reddish tinge; muscular tail lightly dusted with pale brown pigments. There is no marked differences between *rheocolus* and *nannotis* tadpoles.

Tadpoles live in fast flowing water current and are difficult to remove when clinging on rocks or other substrates. Efficient adaptation to fast water current is shown structurally by the large sucker-mouth, flattened head and body, and the strong muscular tail.

HABITAT: *Litoria rheocolus* is restricted along rocky fast flowing creeks and streams in rainforest as well as in wet sclerophyl forest. It ranges from sea level (Cape Tribulation and The Boulders) up to 1200 m above sea level (Mt. Lewis). This species is synchronopatric with *Litoria nyakalensis*, *nannotis*, *eucnemis*, *lesueuri*, *chloris*, and *infrafrenata*, *Nyctimystes hosmeri*, *tympanocryptis*, *Mixophyes schevili*, *Taudactylus acutirostris*, *rheophilus*, *Hylarana daemeli*, *Sphenophyrne pluvialus*, *Cophixalus ornatus* and *exiguus*.

DISTRIBUTION: It is distributed throughout the rainforest and wet sclerophyl forest from Palmerston N.P. (near Innisfail) in the south of Mt. Finigan (S. of Cooktown) in the north. *L. rheocolus* has yet to be discovered along the Cape York Peninsula rainforest chain.

ETYMOLOGY: The specific name is derived from the Greek *rheos* meaning creek or stream, and the latin suffix, *colus* meaning an inhabitant; it refers to the habitat of the frog.

DISCUSSION

In 1897 Günther described and named a treefrog *Hyla dayi* from a single specimen collected from Mt. Bartle Frere, northern Queensland by W. S. Day. The type probably lodged in the Tring Museum is now apparently lost (Tyler, 1968; H. G. Cogger and A. G. C. Grandison, *in litt.*).

Loveridge (1935) and Copland (1957) each refer one specimen collected to this species, and both add degrees of variation to the original description. Straughan (1966), studying 16 specimens, accepted Copland's modified description but noted variable webbing between fingers. Tyler (1968) using Loveridge and Copland specimens designated these *Hyla dayi* (Günther) whilst noting that they differed from the original description in extent of finger webbing, tympanum size, SV length and dorsal colouration—differences which he considered unimportant.

Included in a collection of practically all known northern Queensland frogs made personally during the past few years are approximately 50 specimens which correspond with *Hyla dayi* of Loveridge (1935), Copland (1957), Straughan (1966), and Tyler (1968), but careful examination convince me that these are not *Hyla dayi* Günther. The specimens studied come from various localities in northern Queensland, as far south as Mt. Spec, north of Townsville, and as far north as Mt. Finigan, south of Cooktown, and included specimens from part of Mt. Bartle Frere close to the type locality of *Hyla dayi* Günther. Specimens came from as low as sea level up to approximately 1000 m above sea level.

Distribution of characters which were used in the original description of *dayi*, amongst the small-eared northern Queensland treefrogs are presented in Table 1. As seen from

Table 1, SV length, dorsal colouration, and finger webbing are important and critical in establishing the status of the original description of *dayi*.

It is unfortunate that Günther (1897) did not define exactly the extent of webbing on the 3rd finger; he did not specify whether it reaches the base or the distal end of the penultimate phalanx of the 3rd finger. From his statement 'fingers strongly webbed', apparently the web on the 3rd finger extends beyond the base of the penultimate phalanx, probably close to the distal end. If this is true then the web of *dayi* holotype differs from *dayi* auctorum, but is similar to *Nyctimystes*. Live or preserved specimens of *dayi* auctorum, *nannotis*, and the undescribed *Litoria* are slate or olive with dark markings, but never uniformly brown. Females of *dayi* auctorum are brown dorsally, but they always have a distinct large inverted triangular black marking which extends from the level of the eye to the coccygeal region; Loveridge's (1935) specimen has a similar pattern and most likely it is a female. Amongst northern Queensland small-eared treefrogs, only females of *nannotis*, *Nyctimystes hosmeri* and probably also of *tympanocryptis* reach more than 50 mm in SV length. SV length of *dayi* holotype is substantially larger than *dayi* auctorum. Although *dayi* holotype is within the size range of *nannotis* females, they differ in other respects (see Table 1). Although texture of skin depends on the state of preservation, I believe that the large tubercles of *dayi* auctorum should have been detected were they present on the holotype.

Based on the above evidence I am convinced that *dayi* holotype was based on a *Nyctimystes* female; since uniform brown colour variant is present in *tympanocryptis*, *hosmeri* and *vestigea*. (The validity of *vestigea* is discussed by Liem, in MS). This makes specific identification impossible.

Litoria nyakalensis sp. nov.
(Figure 2 ; Plate 4)

HOLOTYPE: Adult male, QM J22624 from Henrietta Creek, Palmerston N. P., N. Queensland, Australia, 800 m above sea level, collected 17 October 1972 by David S. Liem.

PARATYPES: Nine males, QM J22625–8, DSL 6502, 6719 collected together with the holotype: QM J22629–30, DSL 6174, collected 29 November 1971 from Beatrice Creek, Palmerston N. P., N. Queensland. All specimens were collected by David S. Liem.

OTHER MATERIAL: Besides the type series, two other specimens from Beatrice Creek, Palmerston N. P. were studied (DSL 4320–1).

DIAGNOSIS: A moderate sized robust treefrog, males ranging from 29·7–32·3 mm (mean 31·6 ± 2·975 mm) in snout-vent length. It could be distinguished from *rheocolus* and *nannotis* by the following combination of characters: 1, snout rounded; 2, IN/EN ratio more than 0·980; 3, first finger enlarged, its disc small; 4, web on 1st toe on or just beyond the proximal subarticular tubercle; 5, inner tarsal fold absent or indistinct; 6, ventral surfaces of forearms, hindlimbs, and part of the pectoral region are washed with reddish pink; 7, males have a rasping call. It is distinguished from *rheocolus* by the robust forearms, and large nuptial pad with coarse spinules; from *nannotis* by the smaller size (less than 40 mm in SV length), longer snout (snout longer than eye diameter), two outer netacarpal tubercles present, moderate sized prepollex, absence of keratinous spinules on chest, throat, and sides of head, and the males call.

DESCRIPTION OF HOLOTYPE: SV length 32·3 mm; TL 17·5 mm, 0·542 of SV length; HW 12·0 mm, 0·372 of SV length; EN 3·4 mm; IN 3·1 mm; IN/EN ratio 0·912; IO 3·5 mm; EW 3·0 mm; IO/EW ratio 1·167; TW 1·4 mm; ED 3·9 mm; TW/ED ratio 0·359.

Tip of snout rounded; canthus rostralis rounded in cross-section and it is distinct (Fig. 2 A); loreal region slightly concave; dorsal view of head rounded; it is bluntly rounded in profile (Fig. 2 C); tympanum small, partly hidden under the skin; supartympanic fold present; tongue subovate, free posteriorly; vomerine teeth in a lightly oblique short oval rows just behind the level of the choanae; vocal sac absent; upper jaw toothed.

Forearm robust; a row of whitish tubercles is present on lateral edge of the forearm; distal segment of fingers expanded into large disc, with ventro-marginal groove; length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; first finger enlarged, but its digital disc is small (Fig. 2 D). Fingers slightly webbed: web between 2nd and 3rd fingers reaches the proximal subarticular tubercles; web between 3rd and 4th fingers reaches halfway down the proximal phalanx of 3rd finger, and the 2nd subarticular tubercle of 4th finger by a narrow fringe. Nuptial pad large with coarse black keratinous spinules (Fig. 2 B); subarticular tubercles roundish, one each on 1st and 2nd fingers, and one each on 1st and 2nd fingers, and two each on the two outer fingers; a row of supernumerary tubercles is present on metacarpal of 3rd and 4th fingers; a pair of outer metacarpal tubercles are present on the proximo-lateral portion of the palm, and an elongated tubercle on the proximo-ventral surface of the metacarpal of the 1st finger (Fig. 2 D).

Hindlimbs moderately long; distal segment of toes expanded into disc, with ventro-marginal groove; length of toes from shortest to longest 1-2-5-4-3; phalangeal formula of foot 2-2-3-3; one subarticular tubercle each of 1st and 2nd toes, two each of 3rd and 5th toes, and three on the 4th toe; supernumerary tubercles are present on ventral surfaces on metatarsal of toes; inner metatarsal tubercle oval; outer metatarsal tubercle indistinct or absent. Toes extensively webbed; web reaches halfway down the proximal phalanx of 1st toe by a narrow fringe; web reaches just below base of discs on outer margins of 2nd and 3rd toes, and it reaches by a narrow fringe the proximal subarticular tubercle of 2nd toe, and the 2nd subarticular tubercle of 3rd toe; web reaches the 3rd subarticular of 4th toe; it reaches the base of the disc of 5th toe.

Cloacal opening at mid-level of the thighs; skin of dorsum with conical tubercles, scattered on the head, upper eyelids and back; dorsal surfaces of fore- and hindlimbs smooth with some scattered tubercles on tibia and heels; ventral surfaces of abdomen, chest, throat, and posterior ventral portion of the thighs granular; skinfold across chest absent.

Pupil horizontal, oval; palpebral venation on lower eyelid absent.

Colour: Dorsal colour of head and body slate; fore- and hindlimbs greyish brown, with indistinct dark markings; ventral surfaces of body and thighs cream, reddish pink on ventral surfaces of fore- and hindlimbs. Palm and sole uniformly grey to slate colour without dark markings.

In life, dorsum brownish olive or greyish brown with dark olive irregular markings on extremities; eyes brown with black pupil; ventral surfaces cream and reddish pink on fore- and hindlimbs as well as the pectoral region.

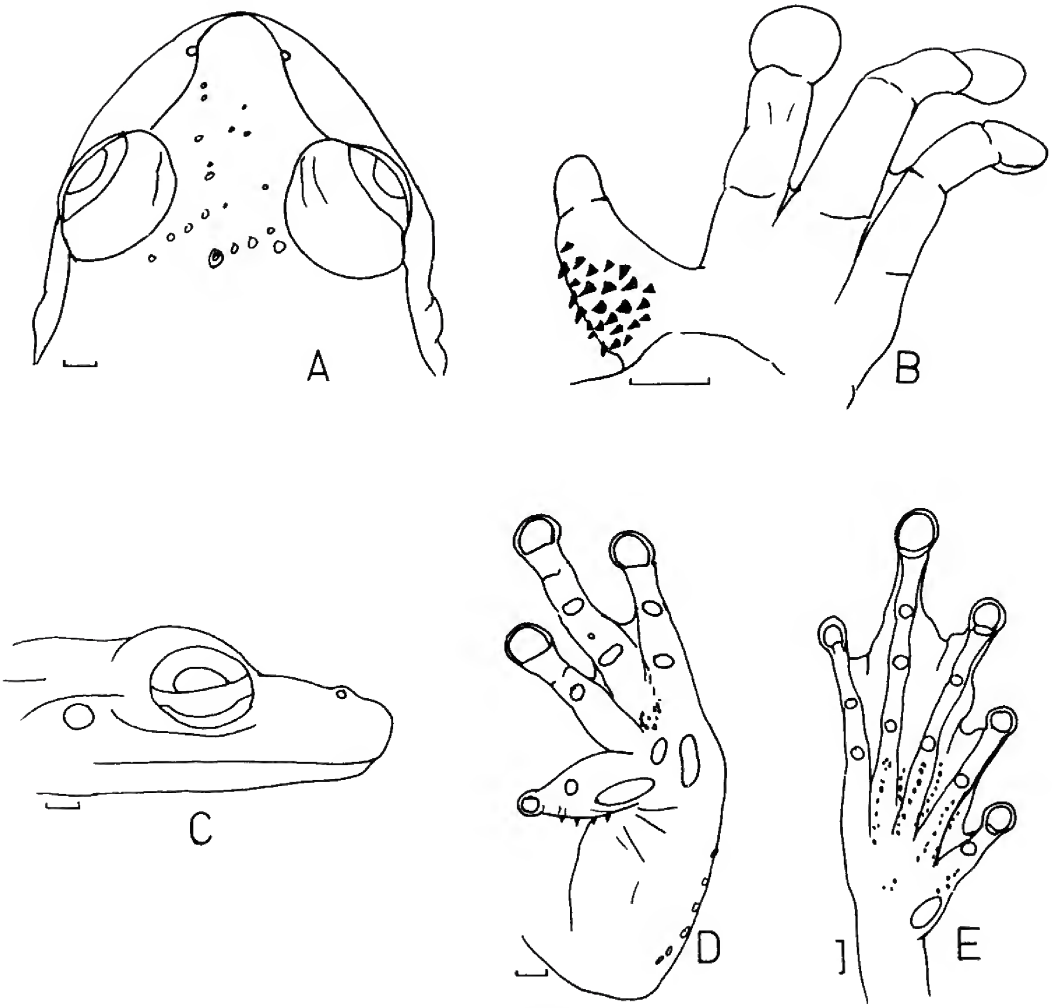

FIG. 2: *Litoria nyakalensis*. A, dorsal view of head (QM J22624, holotype); B, dorsal surface of hand (QM J22626); C, lateral view of head (QM J22624, holotype); D, ventral surface of hand (QM J22624, holotype); E, ventral surface of foot (QM J22625).

DESCRIPTION AND VARIATION: Six males from Henrietta Creek, Palmerston N.P. are 29·7–32·3 mm in SV length. Five males from Beatrice Creek Palmerston N.P., N. Queensland ranging from 30·8–33·1 mm in SV length. Because there is no marked differences between these two samples, their ratios are combined: TL/SV ratio 0·520–0·560; HW/SV ratio 0·330–0·377; IN/EN ratio 0·978–1·029; IO/EW ratio 0·999–1·133; TW/ED ratio 0·326–1·029.

There are slight variations in regard to the extend of finger webbing: in four specimens the web reaches only one-third down the length of the proximal phalanx on outer margin of 3rd finger, and not quite reaching the 2nd subarticular tubercle of 4th finger (QM J22629, J22625–6, DSL 6502). In QM J22625–7, J22629, DSL 4320–1, 6502, the web reaching the proximal subarticular tubercle of the 1st toe whereas in QM J22625–6, J22630, DSL 4320–1, 6502, the web barely reaches the base of disc on outer margins of 2nd and

3rd toes; in QM J22627 it reaches halfway down the penultimate phalanx of 3rd toe. in DSL 4320–1 the outer metatarsal tubercle is obscured, and in DSL 4320 the supernumerary tubercles of the foot area are absent or indistinct.

In life, the dorsal ground colour of *nyakalensis* varies from uniform slate colour to greyish brown, some specimens with dark irregular markings. In QM J22625–6 and J22628, the dorsal ground colour of fore- and hindlimbs are greyish brown, and is lighter than the dorsal colour of the body. In most individuals the ventral colouration is uniformly cream with reddish pink on forearm, pectoral region, thighs and tibia; in QM J22628–30, DSL 6174, 6502, 6719, the throat, pectoral region, lateral region of abdomen, antero- and postero-ventral surfaces of the thighs are heavily pigmented with brown markings washed with reddish brown pigmentation. The eye is brown, and with black pupil.

MATING CALL: Regular repeated rasping single note call, easily distinguishable from the long drawn single note call of *rheocolus*. Details of the call structure will be presented elsewhere.

LIFE HISTORY: Little is known about the life history of *nyakalensis*; mating call of males were heard from October to March. Females of this species are yet to be discovered, probably similar to *rheocolus* females. Tadpoles unknown; judging from the substantial similarities amongst the *Litoria nannotis* species group, *nyakalensis* probably has similar sucker-mouth tadpoles like the other two species.

HABITAT: *Litoria nyakalensis* occurs along creeks in rainforest and wet sclerophyl forest; it perches on rocks or on vegetation overhanging creeks. This species is synchronopatric with *Litoria rheocolus*, *eucnemis*, *lesueuri*, and *chloris*, *Nyctimystes tympanocryptis*, *Mixophyes schevili*, *Taudactylus acutirostris*, *Sphenophryne pluvialis*, *Cophixalus ornatus* and *exiguus*.

DISTRIBUTION: At present *L. nyakalensis* is known from three localities, Henrietta Creek and Beatrice Creek in Palmerston N.P., and Tinaroo Creek Rd, 15 km south of Mareeba, N. Queensland.

ETYMOLOGY: The specific name refers to Nyakali, an aboriginal tribal group who once lived in the vicinity of the type locality.

DISCUSSION

The new form of *Litoria* is intermediate between *rheocolus* and *nannotis*. In addition to characters listed in Table 1, the new form differs from *rheocolus* in the following respects: slightly larger IN/EN ratio, rounded snout, rounded canthus rostralis, first finger of males enlarged, moderate sized nuptial pad with large coarse spinules, males with robust forearm, less extensive webbing on 1st toe, and ventral surface cream with reddish brown tinge on posterior portion of the body.

It differs from *nannotis* by the smaller SV length, slightly larger IO/EN ratio, tympanum always distinct, slightly concave loreal, smaller prepollex in males, less extensive webbing on first toe, two outer metacarpal tubercles, and ventral surface cream with reddish brown tinge of posterior portion of the body. *Litoria nannotis* does not call; the rasping male call of the new form could readily be distinguished from the monotonous long drawn single note of *rheocolos*.

Litoria nannotis (Andersson)
(Figures 3, 4 A, B; Plate 3B)

Hyla nannotis Andersson, 1916, p. 16; Tyler, 1965, p. 94.
Hyla obsoleta: Loveridge, 1935, p. 50 (part).
Hyla obsoleta nannotis: Copland, 1957, p. 55.
Litoria nannotis: Tyler, 1971, pp. 351, 353.

MATERIAL EXAMINED: (31) Shiptons Flat, 50 km S. Cooktown, QM J17861–3; Mt. Spurgeon, QM J5570; Mt. Lewis, 100 km N. of Cairns, DSL 5015–16; Tinaroo Creek Rd, 10 km SE Mareeba, DSL 4931; Atherton Tableland, QM J17017; Palmerston N.P., DSL 4261–2; Mt. Spec, 120 km N. of Townsville, DSL 4996–5001, 5003, 5005–10, 5012–14, 6198, 6306, 6343, 6559–60. All localities are in northern Queensland.

DIAGNOSIS: A moderately large sized treefrog, adult males ranging from 40·1–47·9 mm, and adult females from 49·1–54·7 mm in SV length. It differs from *rheocolus* and *nyakalensis* by the following characters: 1, short snout (shorter than eye diameter); 2, strongly concave loreal; 3, extremely enlarged prepollex; 4, keratin spinules are present on chest, margins of throat, and sides of head; 5, males do not call; 6, adults more than 40·0 mm in SV length; 7, only one outer metacarpal tubercle is present. It differs from *nyakalensis* by its smaller IN/EN ratio (less than 0·970), and it is further distinguished from *rheocolus* by its evenly rounded canthus rostralis.

DESCRIPTION OF HOLOTYPE: See Andersson (1916), and additional information in Tyler (1965).

DESCRIPTION AND VARIATION: Although Tyler (1965) gave an adequate account of variation, it is noteworthy to add more in the light of fresh material collected from new localities outside the range of published reports.

Males range from 40·1–47·9 mm in SV length; TL/SV 0·514–0·584; HW/SV 0·342–0·397; IN/EN 0·896–0·960; IO/EW 1·043–1·275; TW/ED 0·303–0·315 or obscured.

Females are larger: 49·1–54·7 mm in SV length; TL/SV 0·510–0·570; HW/SV 0·351–0·379; IN/EN 0·793–0·963; IO/EW 1·070–1·195; TW/ED 0·303–0·378 or obscured.

Tip of snout bluntly rounded; snout shorter than eye diameters; loreal region strongly concave; canthus rostralis evenly rounded in section; tympanum barely visible or hidden under the skin; tympanum is distinct in 6 (DSL 6560, 5000, 5015–16, 5010, 4996) out of 26 individuals studied. Only one large outer metacarpal tubercle is present (Fig. 3D); inner metacarpal tubercle on base of thumb elongated; prepollex extremely enlarged (Figs. 3D and E); supernumerary tubercles are present on palm, on metacarpals, and on the phalanges; a row of tubercles along lateral side of lower forearm present.

Fingers moderately webbed; web between 2nd and 3rd fingers reaching their proximal subarticular tubercles; web between 3rd and 4th fingers reaching halfway down the proximal phalanx of 3rd finger, and between half to three-quarters down the length of the proximal phalanx of the 4th toe.

Webbing of the foot reaching the base or barely reaching the base of disc of 1st, 2nd, 3rd, and 5th toes; it only reaches the 3rd subarticular tubercle (or just beyond it) of 4th toe (Fig. 3A); web on inner margins of 3rd and 4th toes reaches the base of discs by a narrow fringe; metatarsals are separated by webbing. Supernumerary tubercles are arranged in rows on the metatarsals; ventral surfaces of tarsus heavily tubercular; outer metatarsal

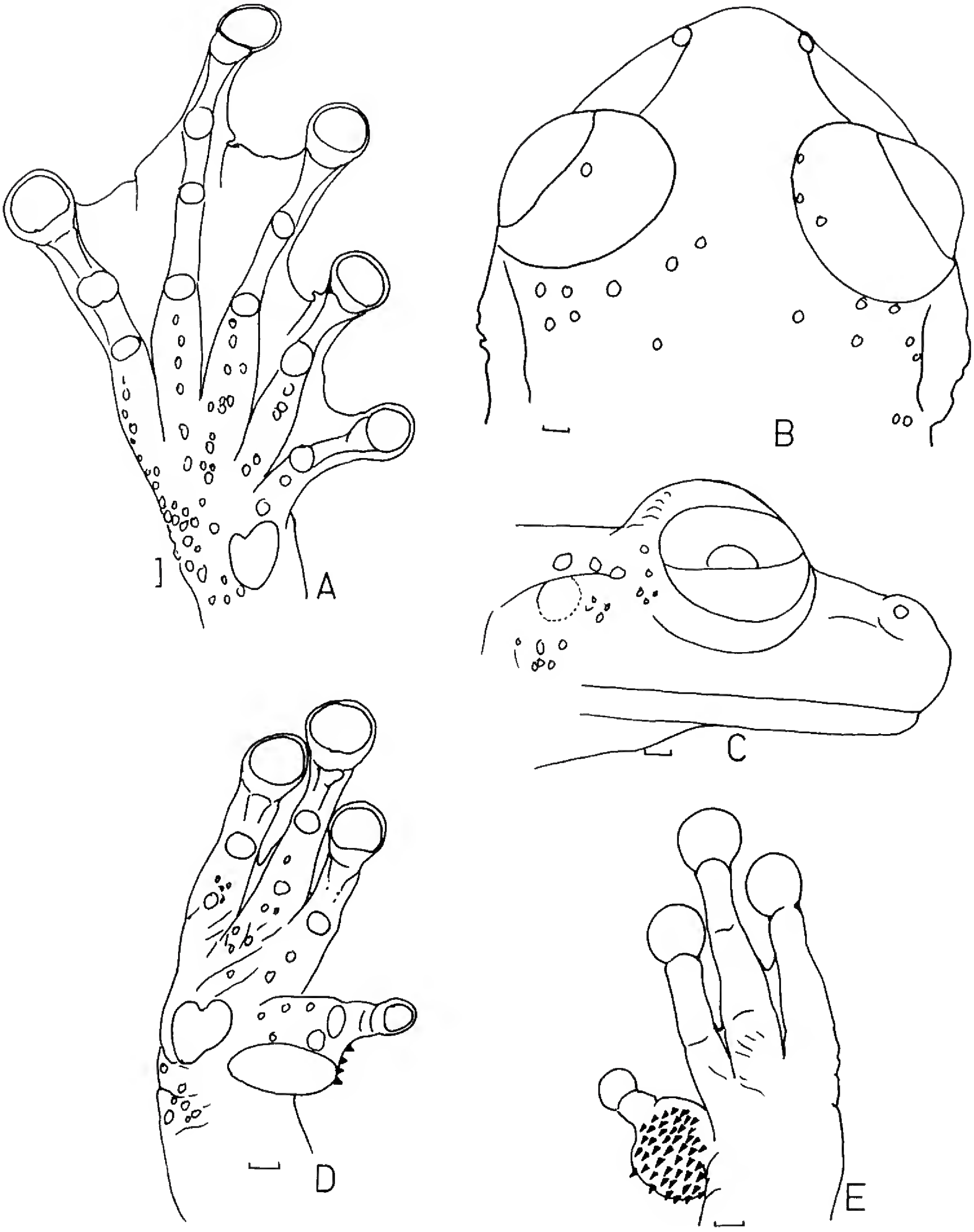

FIG. 3: *Litoria nannotis*. A, ventral surface of foot (DSL 5016); B, dorsal view of head (DSL 6960); C, lateral view of head (DSL 6960); D, ventral surface of hand (DSL 5016). E, dorsal surface of hand (DSL 5016).

tubercle small and rounded.

Tyler (1965) noted that in the holotype of *nannotis*, an internal vocal sac is present, but he failed to mention whether a vocal sac was present in other males. There is no trace of this vocal sac in any specimens examined. The report of the presence of a vocal sac in *nannotis* holotype is probably erroneous; short openings observed were probably artifacts.

Dorsal surface shagreen, with scattered tubercles on body, head and dorsal surfaces of the limbs; large tubercles are present on upper eyelids, posterior portion of eyes, tympanic region, on elbow and heel, on posterior and postero-ventral surfaces of the thighs. Ventral surfaces of the body (including the throat) are granular; only the anterior and antero-ventral surfaces of thighs, and inner surfaces of tibia and tarsus are smooth.

Adult males are easily distinguished from females by their smaller size, robust forearm, extremely large prepollex, heavily spinulated nuptial pad on the proximo-dorsal side of the thumb, and black tipped spinules on inner surfaces of forearm, base of forearm, along ventral and ventro-posterior region of the eyes, loreal region, and scattered on ventral surfaces of the thighs and inner surfaces of the tarsus.

Colour: In life, dorsal colour uniformly slate, or yellowish olive background with dark irregular markings (DSL 6343, 6559–60); in some individuals the extremities are washed with purplish colour (DSL 5010, 5005, 4997–8); dorsal colour of some individuals are pale slate (DSL 5000, 5007, 4999). Ventral surfaces of males cream; throat dusted with brown (DSL 6559, 6306, 5012). Ventral surfaces of females cream, and heavily pigmented with brown on the throat and ventral surfaces of the thighs; abdomen in four females (DSL 6343, 5000, 5014, 4999) is uniformly cream.

In preservatives the purplish brown colouration of the throat, ventral surfaces of fore- and hindlimbs disappeared; the majority of specimens are slate dorsally.

Mating Call: No call has been associated to *nannotis*; males do not call.

Life History: Pigmentless eggs (ovidiameter 2·7–3·4 mm) are laid in gelatinous eggmasses under rocks in water. Eggmasses laid by amplexus pairs were raised, and hatched tadpoles were substantially different than those described by Tyler (1965), and Martin and Watson (1971). Large tadpoles described by Tyler (1965) were undoubtedly those of *Mixophyes schevili* (will be reported elsewhere); W. Hosmer (pers. comm.) who collected tadpoles (AMNH 67115) upon which Tyler (1965) based his description agreed that they were not *nannotis* but the common *Mixophyes schevili* tadpoles.

Tadpoles of *nannotis* are similar to *rheocolus*; the former have sucker-mouth, very strong muscular tail, and narrow tail fins (Fig. 4 A): spiracle opens at the end of a tube on ventro-lateral left side of the body; anal opening median. The sucker-mouth consists of two complete papillar rows, one along the edge of the labium, and another close to the labial tooth rows; the posterior half of the latter consists of a single row whereas its anterior half consists of two papillar rows; in addition to the above rows two or more rows of papillae are present on the posterior of the labium between the inner and outer rows (Fig. 4 B). The labial tooth row consists of two entire upper and three entire lower rows (formula II/III); the inner labial tooth rows are stronger than the outer ones. Jaws are strong, lower jaw is V-shaped, and the upper jaw is slightly indented anteriorly (Fig. 4 B).

In life, body ground colour sandy, with dark abdomen; tail with yellowish tinge and numerous dark-brown blotches on muscular tail. Like *rheocolus* tadpoles they are highly adapted to fast flowing water current. Tadpoles of *nannotis* differ from *rheocolus* by their darker tail colouration and their yellowish tinge.

HABITAT: This species occurs along rocky fast flowing rainforest or wet sclerophyl forest creeks; *L. nannotis* is uually restricted near waterfalls. It is synchronopatric with *Litoria rheocolus*, *nyakalensis*, *eucnemis*, *lesueuri*, *infrafrenata*, and *chloris*, *Nyctimystes hosmeri*, *tympanocryptis*, *Mixophyes schevili*, *Taudactylus acutirostris*, *rheophilus*, *Hylarana daemeli*, *Sphenophryne pluvialis*, *Cophixalus ornatus* and *exiguus*.

REMARKS: *Litoria nannotis* is restricted in rocky stream habitats with fast flowing water current, behind waterfalls. Unlike other frogs, adults and juveniles form a colony amongst large boulders behind waterfalls. These aggregations were observed during the day as well as at night. On various occasions I observed that individuals perch close together (sometimes on top of each other) in a corner of a boulder. Loud background noise of

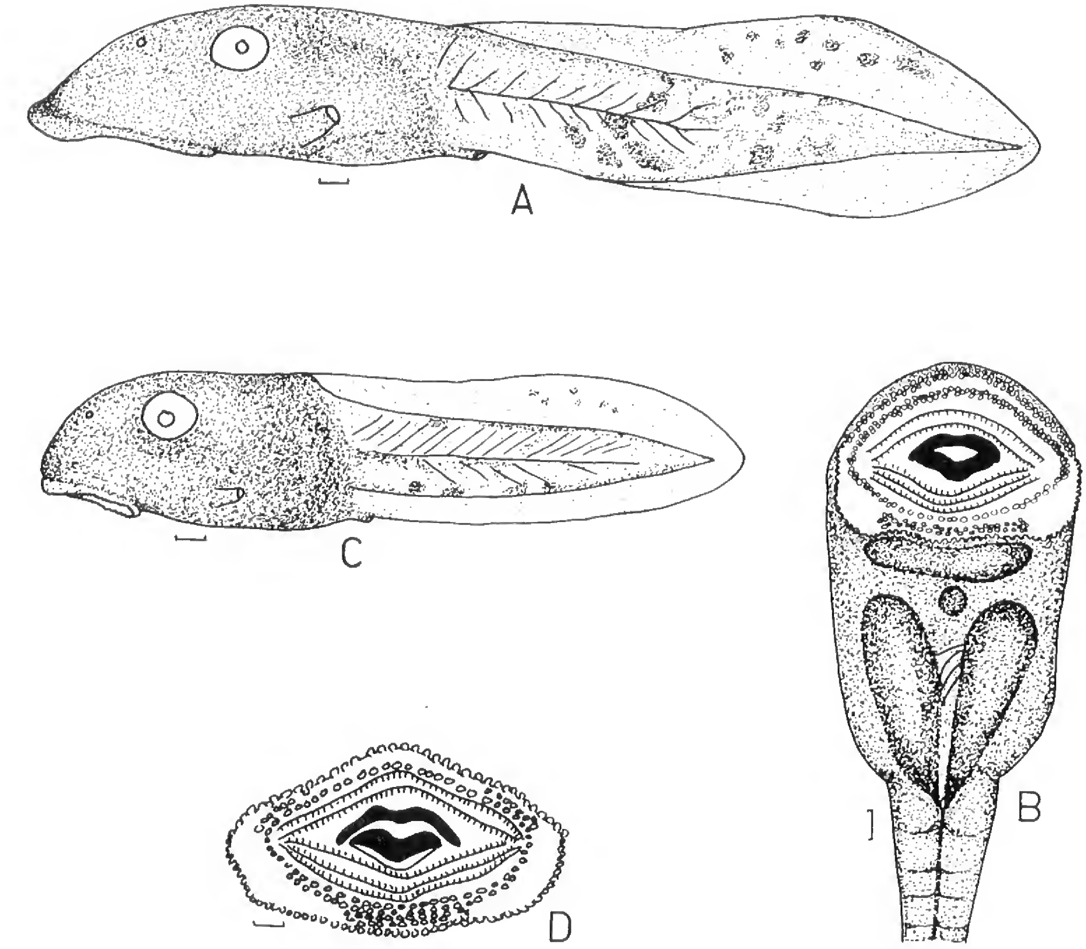

FIG. 4: A, B, *Litoria nannotis*. A, lateral view of tadpole, B, ventral view of body. C, D, *Litoria rheocolus*. C, lateral view of tadpole. D, mouth parts.

rushing waterfall probably resulted in the loss of the male call; consequently colony aggregations keep males and females close together for breeding or social contacts. The large number of females collected in one place on Mt. Spec, suggests that females do not wander far from males and from their microhabitats behind waterfalls; large numbers of females collected at one spot is unusual in frogs.

DISTRIBUTION: Before the present study, *nannotis* was known only from the Atherton Tableland (Andersson, 1916; Loveridge, 1935; Copland, 1957; Tyler, 1965). My recent survey in northern Queensland reveals that it has a much wider distribution: it extends in the south to Mt. Spec (120 km NW of Townsville) and in the north to Mt. Finigan (50 km SE of Cooktown), N. Queensland. It is also found on Mt. Lewis, Mt. Spurgeon, Shiptons Flat, Tinaroo Creek Rd (15 km SW of Mareeba), Palmerston N.P., and Tully's Falls, all in northern Queensland. Its presence along the northeastern rainforest chain of Cape York Peninsula has yet to be discovered.

PHYLOGENETIC RELATIONSHIPS WITHIN THE *Litoria nannotis* SPECIES GROUP

Three species, *rheocolus*, *nyakalensis* and *nannotis* are placed in the *Litoria nannotis* species group. It is characterized by the following combination of characters: 1, moderate to large sized rheocolous treefrog; 2, tympanum small, less than 0·4 the width of eye diameter; 3, prepollex small to large; 4, moderate to very coarse nuptial pad spinules; 5, fingers moderately webbed—web on 3rd finger reaches base of penultimate phalanx or less; 6, vomerine teeth in short or long rows, behind level of choanae; 7, eggs unpigmented, individually encapsulated; 8, eggs laid in a clump under rocks in water; 9, sucker-mouth tadpoles with median anal opening; 10, labial tooth row formula II/III.

Satisfactory interpretation of phylogenetic relationships requires knowledge (or reasonable assumption) of primitive and derived states. This method had been used by Ozeti and Wake (1969), and Liem (1970, and MS). I adopted Marx and Rabb's (1970) criteria for establishing primitive and derived states.

Nine characters utilized for deducing phylogenetic relationships amongst species of the *Litoria nannotis* species group are presented in Table 2. The best phylogenetic tree obtained from these characters is presented in Figure 5 (construction of tree see detail in Liem, 1970 and MS). Even scanning through Table 2, it is obvious that *nyakalensis* shares more states with *nannotis* than with *rheocolus*, and this is shown by the best tree (Fig. 5). Based on the above evidence I consider *rheocolus* the most primitive, and the ancestral stock of *Litoria nannotis* species group; *nannotis* is the most specialized, whereas *nyakalensis* is intermediate between *rheocolus* and *nannotis*. *Litoria rheocolus* which is the most common and widely distributed species and lives in generalized creek habitats in contrast to the restricted waterfall microhabitat of *nannotis* or the restricted distribution of *nyakalensis*, lends support to the above hypothesis.

Relationships between *Litoria nannotis* species group and New Guinean species is unclear. Its restricted distribution in northern Queensland rainforest and wet sclerophyl forest, and its 'rheocolous' habits, strongly suggests that *Litoria nannotis* species group is a recent arrival into northern Queensland from New Guinea. Probably its ancestral stock crossed the last Torres Strait land bridge in the Pleistocene together with *Rana daemeli*, *Nyctimystes*, and other microhylids (Liem and Hosmer, 1973).

TABLE 1

Distribution of Character States of *Hyla dayi* Günther, *Litoria dayi* (non Günther), *L. nyakalensis* sp.nov., *L. nannotis* (Anderson), *Nyctimystes tymapnocryptis*, (Anderson), and *N. hosmeri* Tyler.

Character	*H. dayi* Günther	*L. dayi* non Günther	*L. nyakelensis* sp.nov.	*L. nannotis*	*N. tympanocryptis*	*N. hosmeri*
Tongue subovate, nicked	yes	yes	yes	roundish	yes	yes
Vomerine tooth row	transverse	slightly oblique	slightly oblique	long, transverse	transverse	transverse
Head depressed	yes	moderate	yes	no	yes	yes
Snout longer than eye	yes	yes	yes	no	yes	yes
Canthus rostralis	angular	angular	rounded	rounded	angular	angular
Loreal	straight	slightly concave	slightly concave	concave	straight	straight
IO broader than EW	yes	yes	yes	yes	yes	yes
TW/ED	0·250	0·357–0·430	0·326–0·410	indistinct/0·303–0·403	0·300–0·422	0·226–0·362
Fingers strongly webbed	yes	no	no	no	yes	yes
Web of 3rd finger	?	base of penultimate phalanx	½ proximal phalanx	½ proximal phalanx	½ penultimate phalanx	base of penultimate phalanx
Toes fully webbed	yes	yes	yes	yes	yes	yes
Finger disc/tympanum	slightly smaller	smaller to larger	larger	larger	larger	larger
Inner tarsal fold	present	present	absent/indistinct	present	present	present
Dorsal skin	smooth	tubercular	tubercular	tubercular	smooth/shagreen	shagreen
Ventral skin	granular	granular	granular	granular	granular	granular
Supratympanic fold	present	present	present	present	present	present
Skin fold across chest	absent	absent	absent	absent	absent	absent
Ventral colouration	whitish	whitish cream	cream/reddish	cream with dark marking	cream white	cream white
Dorsal colouration	uniformly brown	males slate, females brown with black marking	slate	slate, olive with dark markings	brown, greyish-brown with/without spots	brown, grey with/without spots
SV length	52 mm	27·0–37·8 mm(N=60)	30·8–33·4 mm(N=12)	40·1–53·8 mm(N=29)	31·2–35·9 mm(N=39)	33·8–55·3 mm(N=39)

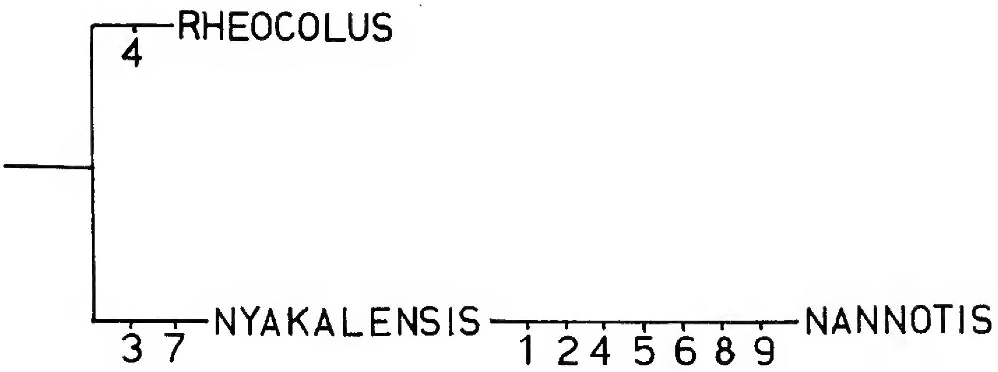

FIG. 5: Suggested phylogenetic tree of *Litoria nannotis* species group. Numbers along nodes are number of derived states (see Table 2).

TABLE 2

CHARACTER DISTRIBUTION OF *Litoria nannotis* SPECIES GROUP.

Character	Character State*	Species†
Snout	0, longer than eye 1, shorter than eye (1)	1, 2 3
Tympanum	0, distinct 1, indistinct or obscure (2)	1, 2 3
Canthus rostralis	0, angular 1, rounded (3)	1 2, 3
Inner tarsal fold	0, absent/indistinct 1, present (4)	2 1, 3
Outer metacarpal tubercle	0, two 1, one (5)	1, 2 3
Prepollex	0, moderate size 1, very large (6)	1, 2 3
Nuptial pad spinules	0, moderately fine 1, coarse (7)	1 2, 3
Chest keratin spinules	0, absent 1, present (8)	1, 2 3
Male call	0, present 1, absent (9)	1, 2 3

* Primitive state is coded 0 and the derived state 1. Numbers in brackets are derived states number and they are also used in the phylogenetic tree in Fig. 5.
† 1, *L. rheocolus*; 2, *L. nyakalensis*; 3, *L. nannotis*.

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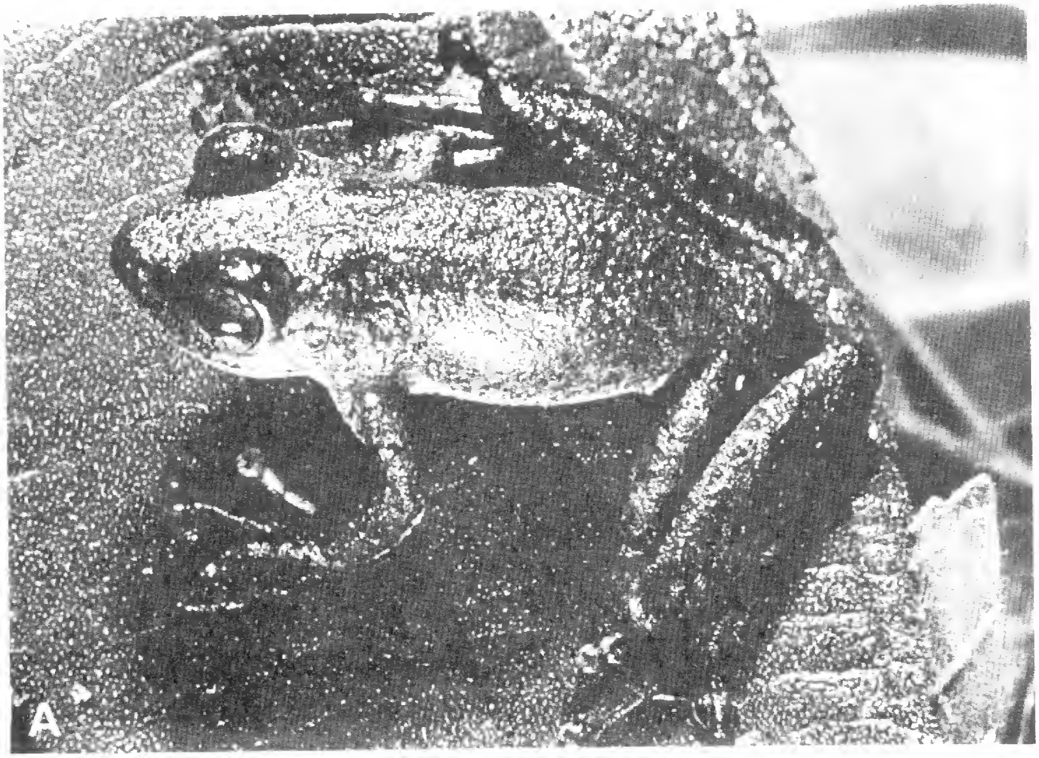
PLATE 3

A: Holotype of *Litoria rheocolus* (QM J22631).

B: *Litoria nannotis* (DSL 5001).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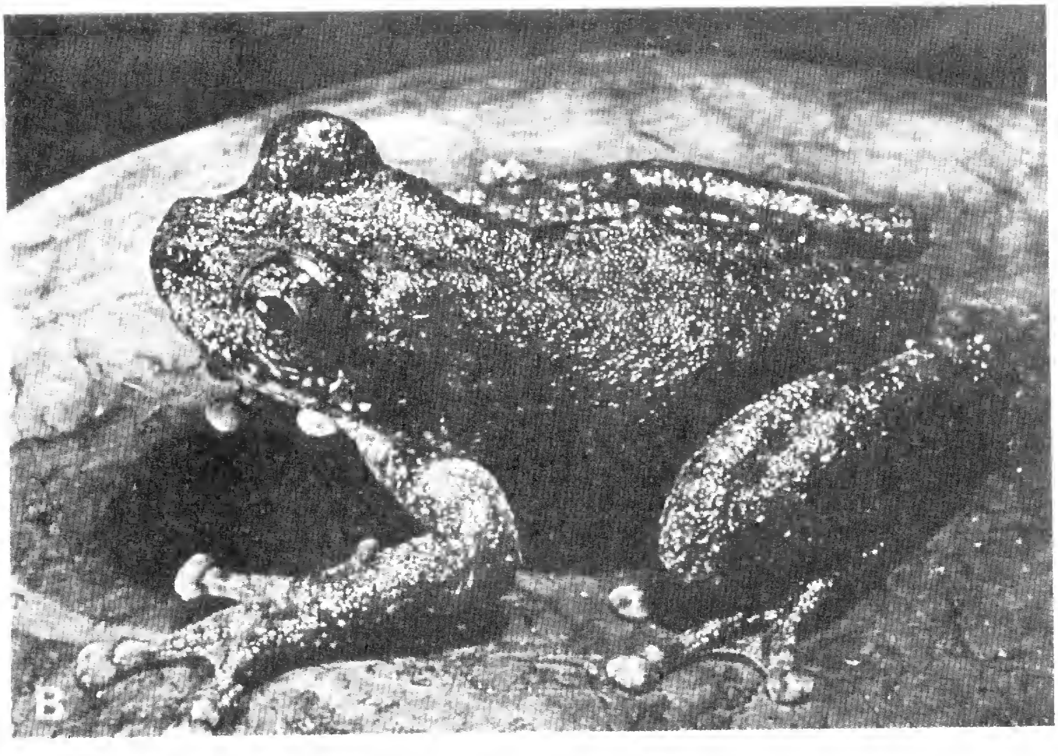
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PLATE 4

Holotype of *Litoria nyakalensis* (QM J22624).

Mem. Qd Mus. **17**(1): 169–74, pl. 5. [1974]

A NEW SPECIES OF THE *LITORIA BICOLOR* SPECIES GROUP FROM SOUTHEAST QUEENSLAND, AUSTRALIA (ANURA:HYLIDAE)

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ABSTRACT

A new species of treefrog of the *Litoria bicolor* species group is described from south-east Queensland. It is distinguished from other species of that group by the male mating call, broader head and snout, presence of dark brown spots and reticulations on dorsum, and a distinct brown purplish femoral streak bordering the dorsal green colour of the thighs.

It is closely related to *Litoria glauerti* (Copland), and it occurs along coastal sandy areas.

Early in 1971 I collected a series of small green treefrogs from a Freshwater Lake, Cooloola, and these appear to be an undescribed species closely related to *Litoria glauerti*. Subsequently similar frogs were collected from Fraser Island by Rick Shine, and from Lake Coolamera in Cooloola by Peter Ogilvie. Subsequent visits to Cooloola convinced me that these frogs represented an undescribed species.

During the course of this study I have examined *Litoria bicolor* and *L. glauerti* as defined by Straughan (1969).

Most of the specimens were collected by the author and are now deposited in the Queensland Museum (QM). Techniques and abbreviations of measurements are given elsewhere (Liem and Hosmer, 1973; Liem, MS). Head length (HL) is distance from tip of snout to angle of jaws. Mouth width of tadpoles is distance between most lateral portions of labial papillar row, and body length (BL) of tadpoles is distance between tip of snout and anal opening. The following ratios were computed, TL/SV, HW/SV, HW/HL, IN/EN, and TW/ED, but only HW/HL, IN/EN ratios and SV length were useful for distinguishing the three species of this species group.

SYSTEMATICS

Litoria cooloolensis sp. nov.

(Figure 1; Plate 5)

HOLOTYPE: Adult male, QM J22646 from Lake Coolamera, Cooloola, SE Queensland, collected on 27 September 1972 by David S. Liem.

PARATYPES: Eight adult males QM J22647–51 and DSL 6402, 6448, 6730, collected together with the holotype by David S. Liem.

OTHER MATERIAL: Besides the holotype and paratypes, eleven other specimens were examined: Freshwater

Lake, Cooloola (DSL 4531–39); and from Coomboo Lake, Fraser Island (DSL 5273–75). Fifteen tadpoles and eggmasses from Coolamera Lake were studied.

Fifteen individuals of *Litoria bicolor* from North Queensland were studied: Atherton Tableland, QM J12409–10; Ravenshoe, QM J10590–91; Mt. Molloy, QM J19501–02; Dimbullah, QM J16996–98, QM J17012; Yorkey Knob, QM J16992; Mareeba, QM J17016; Palm Island, QM J5306, J5309; and from Rockhampton, QM J15728.

Sixteen specimens of *Litoria glauerti* from southeast Queensland were studied: Tin Can Bay, DSL 4542, 4544, 4549; Montville near Nambour, DSL 6403–04; Samford, near Brisbane, DSL 4271, 4273, 4277, 4279, 5173, 5176, 5230, 5249, 5251; Mt. Glorious, DSL 5223–24.

DIAGNOSIS: A small sized green treefrog' less than 32 mm in SV length. It is distinguished from other Australian treefrogs by the following combination of characters: 1, small size; 2, absence of vomerine teeth; 3, dorsal background colour green with dark-brown spots and reticulations; and 4, posterior surface of thigh bright orange separated from the dorsal green colour by a distinct brown purplish femoral streak. It is distinguished from *glauerti* and *bicolor* by the longer SV length, broader head (HW/HL ratio more than 1·054), broader internarial width (IN/EN ratio more than 1·044), absence or indistinct maxillary cream streak, absence of brown loreal streak, and the peculiar diphasic male call.

DESCRIPTION OF HOLOTYPE: SV length 24·0 mm; TL 12·7 mm, 0·529 of SV length; HW 7·7 mm, 0·321 of SV length; HL 6·6 mm; HW/HL ratio 1·167; EN 2·3 mm; IN 2·4 mm; IN/EN ratio 1·044; ED 2·9 mm; TW 1·7 mm; TW/ED ratio 0·586.

Tip of snout bluntly pointed (Fig. 1A); snout slightly protruding beyond lower jaw; canthus rostralis evenly rounded; loreal region straight, slightly sloping outward; dorsal view of head bluntly pointed; tympanum more or less distinct; supratympanic fold weak or absent; tongue oval, free posteriorly; vomerine teeth absent; upper jaw toothed. Vocal sac with two slit-like openings.

Distal segment of fingers expanded into disc; disc of 3rd finger as large as tympanum; length of fingers from shortest to longest 1-2-4-3. Fingers with vestigeal webbing; web between 3rd and 4th fingers reaches their 2nd subarticular tubercles. Subarticular tubercle present, one each on 1st and 2nd fingers, two on 4th finger, and three on 3rd finger. There are three oval outer metacarpal tubercles, and an elongated inner one; supernumerary tubercles present on metacarpals and on the palm (Fig. 1B).

Hindlimbs moderately long; distal segment of toes expanded into disc with ventromarginal groove; length of toes from shortest to longest 1-2-3-5-4; subarticular tubercles simple, one each on 1st and 2nd toes, two each on 3rd and 5th toes, and three on 4th toe; supernumerary tubercles on plantar region weak or indistinct. Inner metatarsal tubercle oval, outer one absent. Foot extensively webbed; it reaches base of disc of inner margin of 5th toe, and outer margin of 2nd and 3rd toes; it reaches halfway down the proximal phalanx of 1st toe, and the 3rd subarticular tubercle of the 4th toe.

Dorsal surface shagreen; abdomen and postero-ventral surfaces of thighs coarsely granular; throat lightly tubercular.

Pupil horizontal, oval. Adult males have finely spinulated nuptial pad on base of thumb.

Colour: In life, dorsal colour green with dark-brown spots and reticulations; a narrow barely visible dark-brown loreal streak runs from anterior angle of eye to nostril, just along the ventral margin of canthus rostralis; a cream maxillary streak runs from below the eye to base of forearm; dorsal green colour of femur is bordered ventrally by a brown purplish femoral streak meeting along a sharp line; posterior surface of thigh orange, bordering the femoral brown purplish streak along a sharp line. Ventral surfaces of body and limbs cream.

In preservative the dorsal green colour change into bluish green; orange patch on posterior surface of thigh disappears and the femoral brown purplish streak is retained.

Description and Variation: Fifteen adult males: SV length 24·68 ± 1·480 mm (range 22·9–26·1 mm); TL length 10·9–13·6 mm, 0·452–0·535 of SV length; HW 7·0–8·5

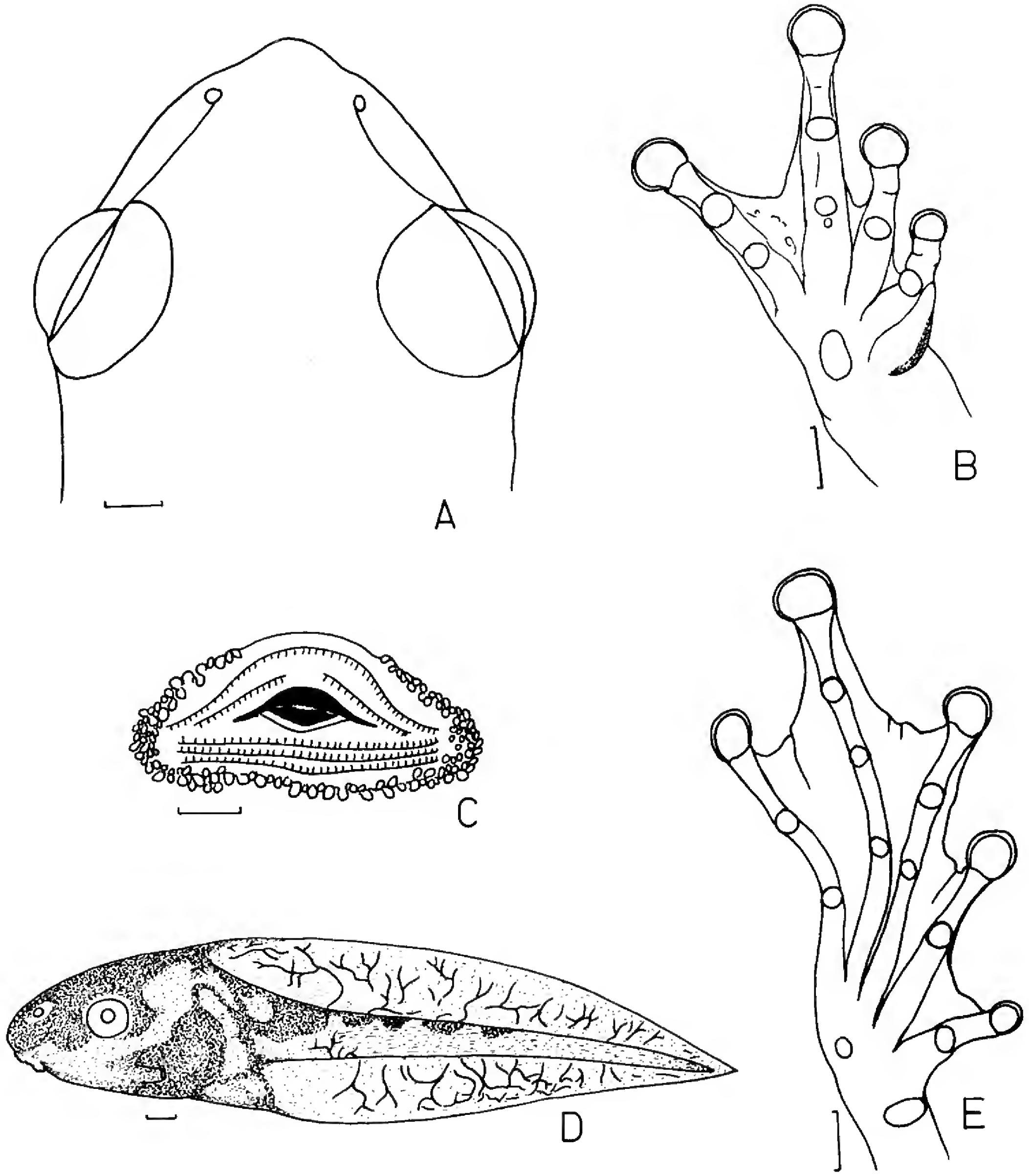

Fig. 1. *Litoria cooloolensis*. A. Dorsal aspect of head (holotype, QM J22646), B. ventral aspect of hand (QM J22651), C. mouth of a tadpole, D. lateral aspect of a tadpole at stage 25, E. ventral aspect of foot QM J22651). Line equals to 1 mm.

mm; HW/SV ratio 0·286–0·332; HL 6·6–7·8 mm; HW/HL ratio 1·039–1·167; EN 1·6–2·5 mm; IN 2·1–2·5 mm; IN/EN 1·044–1·313; ED 2·6–3·4 mm; TW 1·3–1·7 mm; TW/ED 0·457–0·586. Females are larger than males, 29·2–30·0 mm in SV length; TL 14·3–15·5 mm; TL/SV ratio 0·497–0·530; HW 9·0–9·2 mm; HW/SV ratio 0·300–0·315 ;HL 8·2–8·5 mm; HW/HL ratio 1·082–1·098; EN 2·5–3·0 mm; IN 2·9 mm; IN/EN 1·160–1·166; ED 3·4–3·6 mm; TW 2·0 mm; TW/ED 0·556–0·588. There are no marked differences in measurements amongst the males; females are significantly larger than males. Some individuals show less extensive foot webbing: web along outer margin barely reaching the base of disc of 2nd toe in two individuals (QM J22647, J22649); one individual (QM J22649) lacks the cream maxillary streak. Individuals from Freshwater Lake, Cooloola are darker; dark-brown spots and reticulations on dorsum and the brown loreal streak are barely visible; they also lack or with very small cream maxillary streak; foot webbing is less extensive in one individual (DSL 4534); in one individual (DSL 4538) the throat is extensively dusted with brown pigments. The brown purplish femoral streak is consistently present in all individuals studied and so is the orange patch on posterior surfaces of the thighs.

Mating Call: A diphasic call, a short creak followed by a rattling noise at the end (call structure will be reported elsewhere). With little practice one can easily distinguish by ear, *cooloolensis* from *glauerti* and *bicolor* calls.

Life History: Males call from August to May, but they may also call during warm winter nights. Amplexus pairs were observed during or after rain; amplexus axillary. Small jelly encapsulated eggs are deposited on submerged vegetation; eggs with light brown animal and cream vegetal hemispheres, similar to *glauerti* and most other Australian green treefrogs.

TABLE 1

Distribution of Characters useful for Distinguishing Species of *Litoria bicolor* Species Group.

Characters	*L. bicolor*	*L. glauerti*	*L. cooloolensis*
SV length (males)	22·10 ± 1·687 (N = 11)	23·54 ± 1·519 (N = 13)	24·68 ± 1·481 (N = 15)
HW/HL ratio	0·846–0·912	0·855–0·971	1·054–1·167
IN/EN ratio	0·864–0·957	0·863–0·926	1·044–1·313
Web on 1st toe	halfway penultimate phalanx	base of disc	$\frac{1}{2}$ to $\frac{2}{3}$ penultimate phalanx
Dorsal colour	bronze and green	uniform green	green with brown spots and reticulations
Brown loreal streak	present	present	indistinct/absent
Brown head streak	present	present	absent
Maxillary cream streak	prominent	prominent	small/absent
Tympanum colour	brown	brown	green
Upperarm colour	pale yellow	pale yellow/orange	orange
Colour of posterior of thighs	pale yellow	orange	orange
Brown purplish femoral streak	absent	indistinct/absent	present

Tadpoles have a typical Australian hylid habitus, blunt snout and a pointed tail. Fifteen tadpoles at stage 25 have the following dimensions: ST length 25·0–29·0 mm, TL/ST 0·643–0·680, TH/TL ratio 0·444–0·500, MW/BL ratio 0·300–0·750. Tail is relatively high; muscular tail narrow; spiracle opens at the end of a tube on ventro-lateral left side of the body; anal opening dextral. Mouth moderately large, directed antero-ventrally; labial papillar rows consist of 1–2 layers, more at angle of jaws and is interrupted at its anterior portion (Fig. 1C). Labial tooth row formula I,1/III, similar to some populations of *glauerti* tadpoles; jaw moderate in size and serrated. Unlike the spectacular coloured *glauerti* tadpoles (will be reported elsewhere), *cooloolensis* tadpoles are dull: tail fins transparent with dark brown reticulations; head, body, and base of tail with cream (light in preservatives) and brown markings (Fig. 1D). The dull colouration of the *cooloolensis* tadpole distinguishes it from the multicoloured tadpoles of *glauerti*.

Habitat: *Litoria cooloolensis* is restricted in sandy fresh water lakes along coastal SE. Queensland and on Fraser Island. It occurs in wallum habitats and lowland rainforest. It is synchonopatric with *Litoria peroni*, *olongburensis*, *Bufo marinus*, *Crinia signifera*, *Uperoleia laevigata*, *Pseudophryne bibroni*, *Platyplectron dumerili*, and an undescribed *Litoria*.

Distribution: At present it is known from only three localities: Freshwater Lake and Coolamera Lake in Cooloola, and in Coomboo Lake on Fraser Island, SE. Queensland.

Etymology: The specific name refers to the locality where the holotype was collected.

Status and Relationships

Only two species, *Litoria bicolor* (Gray) and *L. glauerti* (Copland), amongst the Australian treefrogs recognized, show any potential resemblance to the new form. Species of the *Litoria bicolor* species group are characterized by small size (less than 32 mm in SV length), dorsal green background colour, absence of vomerine teeth, vestigeal finger webbing, and a characteristic diphasic mating call. The only other Australian treefrog without vomerine teeth is *Litoria microbelos* from northern Queensland; it differs from *L. bicolor* species group by its smaller size, less extensive foot webbing, and the brownish dorsal colour.

Morphologically Straughan (1969) distinguished *bicolor* from *glauerti* by its narrower head width (HW/HL ratio less than 0·92), and more or less larger tympanum (TW/ED ratio 0·667–0·750). My sample however, did not show any significant differences in both ratios: HW/HL 0·846–0·912 and TW/ED 0·507–0·592 in *bicolor* as opposed to 0·855–0·971 and 0·500–0·636 for *glauerti*. In the present study *L. glauerti* sample came from SE. Queensland whilst Straughan (1969) used North Queensland sample and probably this attributed to the difference. Because *bicolor* and *glauerti* are sympatric in North Queensland the difference between these two species in North Queensland is probably due to character displacement.

Significant characters for distinguishing *bicolor*, *glauerti* and the new form are listed on Table 1. In SV length *bicolor* is not significantly different from *glauerti* at $p < 0{\cdot}05$ ($t = 2{\cdot}118$, $DF = 3$), however the new form differs significantly from either *glauerti* at $p < 0{\cdot}05$ ($t = 2{\cdot}163$, $DF = 25$) or from *bicolor* at $p < 0{\cdot}01$ ($t = 0{\cdot}054$, $DF = 21$); furthermore the new form is distinguished from the two other species by a broader head (HW/HL ratio more than 1·054), and broader internarial distance (IN/EN ratio more than 1·044).

Because the new form differs from *bicolor* and *glauerti* in SV length, HW/HL ratio, and IN/EN ratio, tadpole, colouration, and the male call structure, it merits specific recognition, and I propose to name it *cooloolensis.*

Its restricted occurrence in coastal SE. Queensland and on Fraser Island, and the presence of derived characters (presence of brown spots and reticulations on dorsum and purplish brown femoral streak, absence or indistinct loreal and head streaks in *cooloolensis*), suggests that *cooloolensis* is a derived species, probably it evolved from the widely distributed and generalized *glauerti* through isolation along SE Queensland coastal pocket during the Pleistocene similar to speciation of *Crinia tinnula* (Straughan and Main, 1966).

KEY TO THE SPECIES OF THE *Litoria bicolor* SPECIES GROUP

1. IN/EN and HW/HL ratios more than 1·000; dorsal colour green with darkbrown spots and reticulations; purplish brown femoral streak bordering the dorsal green colour of the thigh .. .. *cooloolensis*
   Not as above 2
2. Dorsal bicoloured, bronze and green; web on 1st toe halfway down the penultimate phalanx; posterior of thighs pale yellow .. .. *bicolor*
   Dorsal colour uniformly green or brownish; web of 1st toe reaches base of disc; posterior of thighs orange .. .. *glauerti*

ACKNOWLEDGEMENTS

I wish to thank Miss Jeanette Covacevich of Queensland Museum for the privilege to study specimens under her care, and Rick Shine and Peter Ogilvie for the valuable gifts.

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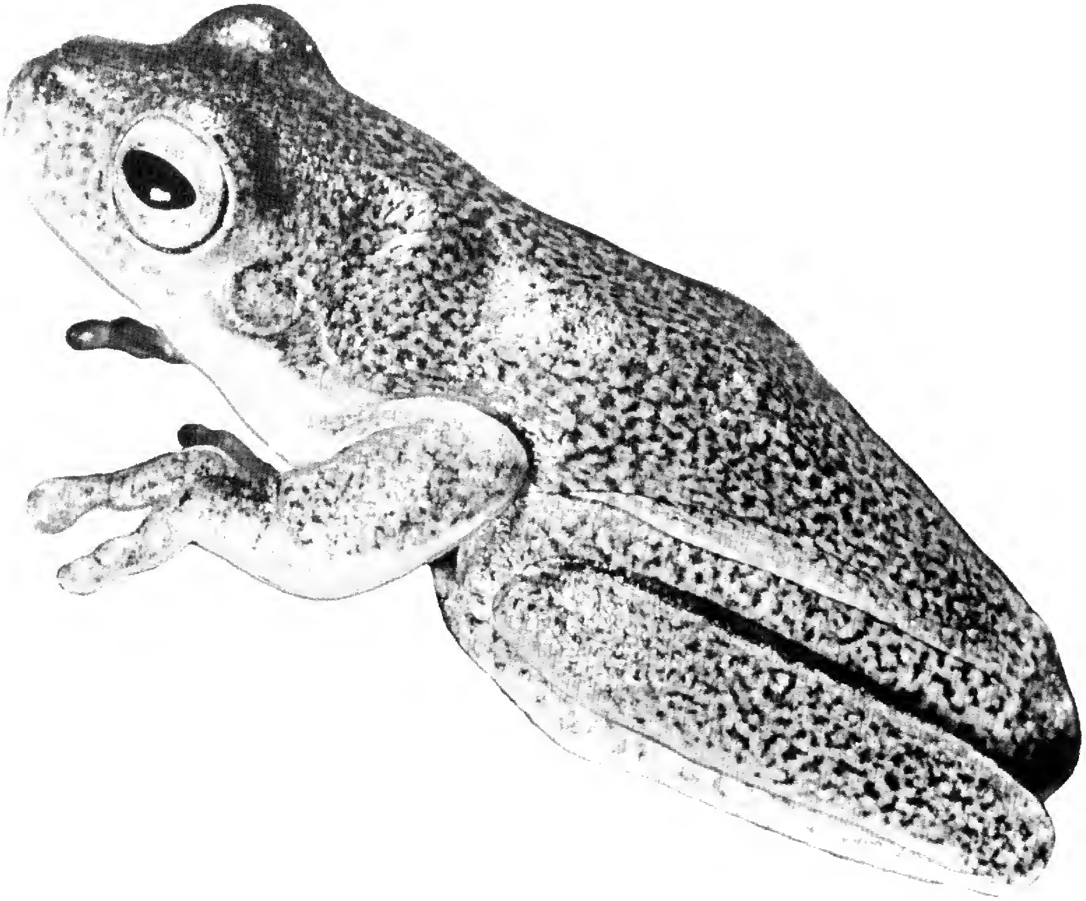
PLATE 5

Litoria cooloolensis (holotype, QM J22646).



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A REVIEW OF THE AUSTRALIAN CRABS OF FAMILY HIPPIDAE (CRUSTACEA, DECAPODA, ANOMURA)

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ABSTRACT

Five species of Hippidae are recorded from Australian waters. Keys, diagnoses, and illustrations are given for their identification, and the Australian literature of the family is reviewed. *Mastigochirus quadrilobatus*, *Hippa adactyla*, *H. pacifica*, and *H. celaeno* are tropical species and widely distributed in the Indo-West Pacific; *Hippa australis* is a warm-temperate Australian endemic.

The Hippidae are a small family of anomuran crustaceans of worldwide distribution, adapted for burrowing in sand. Because of this habit they are known in some areas as mole crabs or sand crabs, but in Australia no common name has been applied to the family as a whole. Hale (1927, p. 97) used the name 'southern mole-crab' for *Hippa australis*, and McNeill (1958, p. 491) referred to the tropical species collectively, under the name *H. adactyla,* as 'turtle crab'.

Hippa, the largest of the three genera comprising the Hippidae, is represented in the tropical Indo-West Pacific by at least ten species, most of which were the subject of an excellent revision by De Man (1896). The literature on the genus is in considerable confusion, however, because many identifications were based on an earlier revision by Miers (1878). Miers considered most of the nominal species of *Hippa* to be synonyms of a single, variable species, *Remipes testudinarius* (*adactyla* of some authors). Another source of confusion is the fact that the species-complex to which Miers applied the name *testudinarius* does not include the species to which that name properly belongs. For a discussion and partial solution of this problem, see Haig (1970).

Records in the literature give the impression that three species of Hippidae occur in Australia: *Mastigochirus quadrilobatus* Miers, from northern Queensland; *Hippa australis* Hale, confined to temperate waters; and *H. adactyla* Fabricius, widespread in the Australian tropics. Griffin and Yaldwyn (1968, p. 171) included *H. adactyla* among examples of decapod Crustacea that are widely distributed in Australia. This picture, however, proves to be somewhat inaccurate and misleading. The present study, in which I have used De Man's revision for the first time for the identification of Australian *Hippa*, has shown that there are at least three tropical species of that genus in Australia and that *H. pacifica* (Dana) is the common and widely distributed one, while *H. adactyla* appears to be relatively rare in the area.

Measurements mentioned in the text refer to carapace length (cl.), and were taken in the midline with a dial caliper.

In order to clarify the status of the Hippidae in Australia it was necessary to examine some material on which earlier records were based; I also examined unrecorded specimens from several sources. Museums in which material is deposited are abbreviated in the text as follows:

A.M.	Australian Museum, Sydney
B.M.N.H.	British Museum (Natural History), London
M.U.Q.	Museum of the Department of Zoology, University of Queensland, Brisbane
N.M.V.	National Museum of Victoria, Melbourne
Q.M.	Queensland Museum, Brisbane
S.A.M.	South Australian Museum, Adelaide
W.A.M.	Western Australian Museum, Perth
Z.M.H.	Zoologisches Museum, Hamburg

FAMILY HIPPIDAE

DIAGNOSIS: Carapace oval, strongly convex, with lateral extensions which cover all but the first pereiopods. Telson of abdomen elongate, lanceolate. Mandibles reduced, non-functional as feeding organs. Third maxillipeds without an exopodite; merus broadened. First pereiopods non-chelate. Dactyl of pereiopods 2–4 curved and flattened.

KEY TO THE GENERA OF HIPPIDAE

1. Antennal flagella very long; dactyl of first pereiopods oval and lamellate *Emerita*
(Nine species, including three from the Indo-West Pacific; not reported from Australia)
Antennal flagella short; dactyl of first pereiopods not oval and lamellate .. 2

2 (1). Dactyl of first pereiopods greatly elongated and multiarticulate *Mastigochirus*
Dactyl of first pereiopods styliform, not multiarticulate .. .. *Hippa*

Mastigochirus Miers, 1878

Mastigopus Stimpson, 1858, p. 230. Type-species: *Mastigopus gracilis* Stimpson, 1858, by original designation.
Mastigochirus Miers, 1878, p. 321. New name for *Mastigopus* Stimpson, 1858, preoccupied by *Mastigopus* Leuckart, 1853; *ipso facto* the same type-species: *Mastigopus gracilis* Stimpson, 1858.

Mastigochirus quadrilobatus Miers, 1878
(Figure 1)

Mastigochirus quadrilobatus Miers, 1878, p. 322, pl. 5 fig. 8 (type-locality: Guimaras, Philippine Is.); 1884, p. 280 (Prince of Wales Channel). Henderson, 1888, p. 39 (off Booby I., Flinders Passage).
Remipes adactylus: Grant and McCulloch, 1906, p. 33 (Port Curtis). Not *Hippa adactyla* Fabricius.
[?] *Emerita analoga:* Stephenson, Endean, and Bennett, 1958, p. 269 (Low Is.). Not *E. analoga* (Stimpson).

MATERIAL: Western Australia: Three specimens, Roebuck Bay, Mrs B. Grey, B.M.N.H. 1932.11.30.61–62.

Female, Broome, sand bar opposite jetty, R. W. George on 'Dorothea', 16.x.1962, W.A.M. 8–68.

Queensland: Male, two females, Albatross Bay near Weipa, Gulf of Carpentaria, H. Foley, vi.1962 to iii.1963, A.M. P14138. Three females, mouth of Embly R., Weipa, 200 yds offshore, 15 ft on sand, high tide, E. Gamberg, 29.i.1962, W.A.M. 311-62. Three females, Port Curtis, presented ii.1907 by Mrs F. E. Grant, A.M. G5759 (with label *'Remipes testudinaria'*). Female, 1 mile SE of Skirmish Pt, Moreton Bay, 2 fm on sand ripple, Dep. Zool. Univ. Qd, 14.viii.1967, Q.M. W2988.

DIAGNOSIS: Carapace covered with wavy, transverse lines. Frontal margin with four teeth; outer pair narrow, triangular, and projecting well beyond inner pair; latter close-set, rounded or triangular. No teeth on lateral margins. A row of about 20–24 shallow, setiferous pits near each lateral margin. First pair of legs longer than carapace plus dorsally visible portion of abdomen; dactyl heavily clothed with long hairs, and composed of about 20 articles.

MEASUREMENTS: Male 9·1 mm, non-ovigerous females 6·2 to 11·6 mm, ovigerous females 9·5 to 12·8 mm.

REVIEW OF AUSTRALIAN LITERATURE: *Mastigochirus quadrilobatus* was collected off Queensland by the 'Alert' (Miers, 1884) and the 'Challenger' (Henderson, 1888). Grant and McCulloch (1906) reported three specimens of *Remipes adactylus*, dredged at Port Curtis in 7 fm. The collections of the Australian Museum contain no *Hippa* that match these data; however, the three female *Mastigochirus* from Port Curtis, A.M. G5759, are almost certainly the basis of Grant and McCulloch's record.

The record by Stephenson *et al.* (1958) of *Emerita analoga* is undoubtedly erroneous; *E. analoga* (Stimpson) is a western American species, and none of three Indo-West Pacific members of the genus has been found in Australian waters. The collections from the 1954 Low Isles survey are housed in the Department of Zoology, University of Queensland, but the material on which this record was based cannot be located (Dr W. Stephenson, pers. comm.). It was probably *Mastigochirus quadrilobatus,* the only Australian hippid with a superficial resemblance to *Emerita.*

REMARKS: This species has one congener, which also inhabits the Indo-West Pacific. *Mastigochirus gracilis* (Stimpson) is distinguished from *M. quadrilobatus* by the presence of three teeth instead of four on the frontal margin of the carapace, and several teeth on the lateral margins.

DISTRIBUTION: Waltair coast, India; Guimaras, Philippine Is.; and Australia from Roebuck Bay, W.A., around the northern coast and southward to Moreton Bay, Qd. To depth of about 8 fm.

Hippa J. C. Fabricius, 1787

Hippa J. C. Fabricius, 1787, p. 329. Type-species: *Hippa adactyla* Fabricius, 1787, by subsequent designation of Rathbun, 1900, p. 301.

Remipes Latreille, 1804, p. 126. Type-species: *Remipes testudinarius* Latreille, 1806, by subsequent monotypy.

REMARKS: Most of the Indo-West Pacific members of this genus were treated by De Man (1896, 1898). Since it is highly probable that additional species of *Hippa* may yet be encountered in Australian waters, his revision should be consulted for the identification of any material that does not agree with the illustrations and diagnoses given in the present paper.

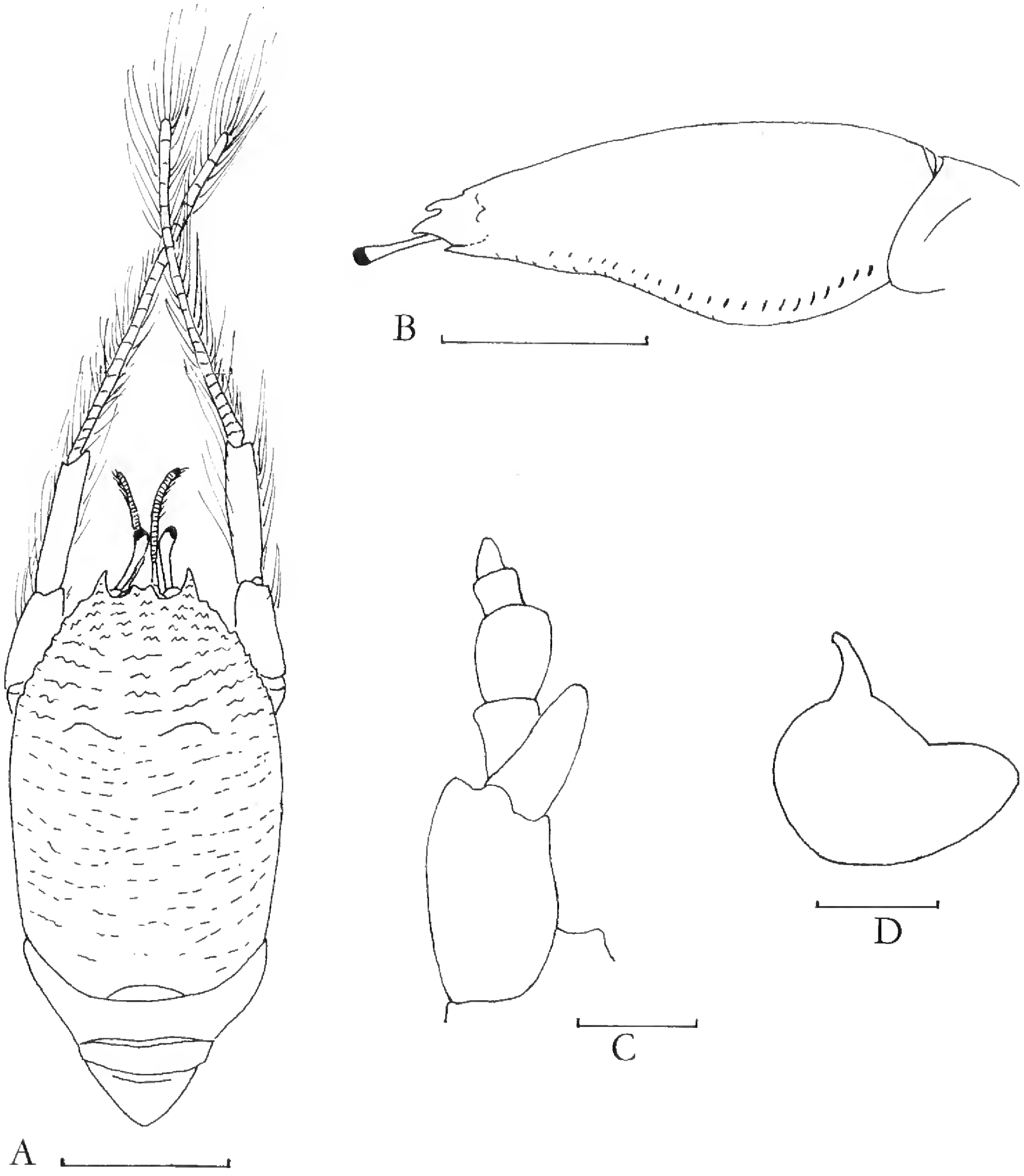

FIG. 1: *Mastigochirus quadrilobatus* (Stimpson). A, animal in dorsal view; B, carapace, lateral view; C, left antenna; D, dactyl of right second pereiopod. Scales A, B = 5 mm; C = 0.5 mm; D = 1 mm.

KEY TO HIPPA KNOWN FROM AUSTRALIA

1. Frontal margin of carapace with two (occasionally three) median and two lateral lobes or teeth; each lateral margin of carapace with a submarginal row of shallow, setiferous pits 2
Frontal margin of carapace with a broad median lobe, lateral lobes scarcely developed; no row of setiferous pits paralleling lateral margins *H. australis*
2 (1). All frontal lobes about equally projecting; concave margin of dactyl of legs 2 and 3 cut into an obtuse angle 3
Lateral lobes of frontal margin much more strongly projecting than median pair; concave margin of dactyl of legs 2 and 3 cut into a right angle *H. adactyla*
3 (2). Submarginal row with about 30–40 setiferous pits; antennal flagellum normally with two articles .. .. *H. pacifica*
Submarginal row with about 23–28 setiferous pits; antennal flagellum normally with a single article .. .. *H. celaeno*

Hippa adactyla J. C. Fabricius, 1787
(Figure 2; Plate 6)

Hippa adactyla J. C. Fabricius, 1787, p. 329 (type-locality: 'in Oceano australi'). Haig, 1970, p. 293 (Coff's Harbour; neotype designated).
Remipes testudinarius Latreille, 1806, p. 45 (type-locality: 'in Oceano Australasiae.); 1819, p. 141 ('Nouvelle-Hollande'). Desmarest, 1823, p. 285 ('Nouvelle-Hollande'); 1825, p. 175 ('Nouvelle-Hollande'). Guérin, 1825, p. 281 ('nouvelle Hollande'). H. Milne Edwards, 1837a, p. 114, footnote, pl. 42 figs. 1, 1a–j ('Nouvelle-Hollande'); 1837b, p. 206, pl. 21 figs. 14–20 ('Nouvelle-Hollande'). Haswell, 1882, p. 151 (no new records). De Man, 1896, pp. 461, 463; 1898, pl. 33 figs. 50, 50a–c.
Remipes [*testudinarius*]: Latreille, 1817, p. 28 (type-locality restricted to 'Nouvelle-Hollande').
Remipède tortue: Latreille, 1817, pl. 2 fig. 2.
Remipes denticulatifrons White, 1847, p. 57 (nomen nudum; type-locality: Phillippine Ils.).
Remipes testudinarius var. *denticulatifrons* Miers, 1878, p. 318 (in part), pl. 5 fig. 2.
Hippa testudinarius var. *denticulifrons*: Thomassin, 1969, pp. 150, 161, 164, 172, figs. 6, 7a, 8a, pl. 5.
[non] *Remipes testudinarius*: White, 1847, p. 57. Miers, 1878, p. 316, pl. 5 fig. 1. Ortmann, 1892, p. 537.
[non] *Remipes adactylus*: Grant and McCulloch, 1906, p. 33.
[non] *Hippa adactyla*: Stephenson, Endean, and Bennett, 1958, pp. 269, 274. McNeill, 1968, p. 39.

MATERIAL: Large dry specimen lacking most of carapace, Dunk I., Qd, presented by E. J. Banfield and registered ii.1920, A.M. P4660. Female, neotype, 25·1 mm cl., McCauley's Beach, Coff's Harbour jetty, N.S.W., low tide, C. Bowden, A.M. P17384. Female, 26·5 mm cl., and soft-shelled juvenile, 7·5 mm cl., same data as neotype, A.M. P15825 and P15826. Male and female, Australia, Z.M.H. K5053. Soft-shelled specimen, Australia, Lidth de Jeude, 1866, N.M.V. Male, old collection, Q.M. W381.

DIAGNOSIS: Carapace densely covered with sharply serrate, transverse lines. Frontal margin five-toothed; outer pair narrow, triangular, and sharp-pointed, and in adults projecting well beyond inner ones; inner pair rounded; between them a small median denticle, broadly triangular and scarcely produced. A row of 50–55 shallow, setiferous, slightly elongate pits near each lateral margin, forming a narrow band. Antennal flagellum with 3–6 articles, the number increasing with age. Dactyl of second and third legs deeply falcate, distal and proximal portions of the concave margin meeting at a right angle.

REVIEW OF AUSTRALIAN LITERATURE: *Remipes testudinarius* was described by Latreille (1806) from material collected by Péron and Lesueur at an unspecified Australian locality. This record was subsequently repeated several times (Latreille, 1817, 1819; Desmarest, 1823, 1825; Guérin, 1825). H. Milne Edwards' diagnoses and illustrations (1837a, 1837b) may have been based on other than type-material. Haswell (1882) recorded *Remipes testudinarius* in his catalogue of Australian Crustacea, but had no material and merely translated H. Milne Edwards' (1937b) diagnosis.

Haig (1970) selected as the neotype of *Hippa adactyla* a specimen of *Remipes testudinarius* from New South Wales, thereby reducing the latter name to synonymy.

REMARKS: This species is easily distinguished from all other members of the genus by the shape of the dactyl of the second and third pairs of legs. In the form of the frontal margin of the carapace it resembles *Hippa admirabilis* (Thallwitz), which is recorded from southern New Guinea and should be looked for in suitable habitats along the northern Australian coast.

DISTRIBUTION: From the west coast of Madagascar eastward through the East Indian Archipelago, north to Japan and east to the Marquesas Is. (for confirmed records see Haig, 1970, p. 294). In Australia the only precise localities on record are Dunk I. and Coff's Harbour on the east coast.

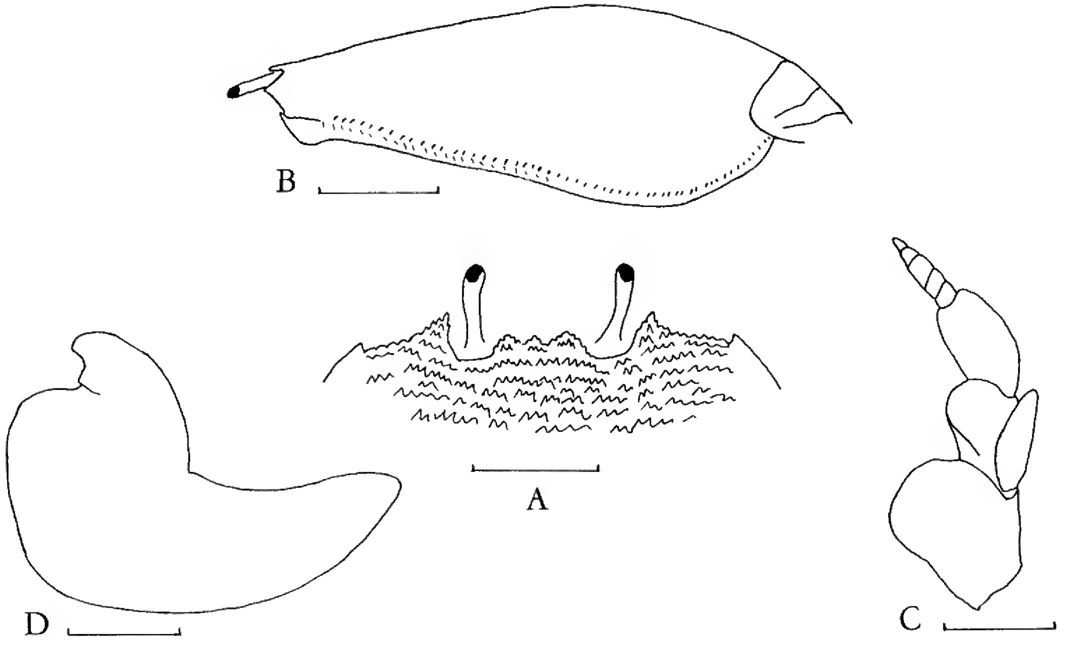

FIG. 2: *Hippa adactyla* Fabricius. A, frontal part of carapace; B, carapace, lateral view; C, left antenna; D, dactyl of right second pereiopod. Scale A = 4 mm; B = 6 mm; C, D = 2 mm.

Hippa pacifica (Dana, 1852)
(Figure 3)

[?] *Remipes testudinarius*: White, 1847, p. 57 (Australia). Ortmann, 1892, p. 537 (E. Australia). Not *R. testudinarius* Latreille = *Hippa adactyla* Fabricius.

[?] *Remipes marmoratus* Jacquinot *in* Jacquinot and Lucas, 18[?], pl. 8 figs. 22–26; 1853, p. 97 (type-locality: Raffles Bay, Australia).

Remipes pacificus Dana, 1852, p. 407 (type-localities: Fiji and Sandwich = Hawaiian Is.); 1855, pl. 25 figs. 7a–g. Miers, 1877, p. 74 (Australia, at least in part). De Man, 1896, pp. 462, 476; 1898, pl. 33 figs. 53, 53a–c.

Remipes testudinarius: Miers, 1878, p. 316 (in part: Australia), [?] pl. 5 fig. 1. Not *R. testudinarius* Latreille = *Hippa adactyla* Fabricius.

Hippa adactyla: McNeill, 1968, p. 39 (Murray I., Torres Str., in part). Not *H. adactyla* Fabricius.

Hippa pacificus: Thomassin, 1969, pp. 157, 161, 164, 172, figs. 7c, 8c, 10, pl. 7.

MATERIAL: Western Australia: Ten males, seven females, Pt Vlamingh, Rottnest I., in coarse sand at water's edge, W.A.M. 24/9-36 and 30/44-36. Three specimens, Cape Vlamingh, Rottnest I., in coarse sand at edge of water, low tide, B.M.N.H. 1938.2.24.1-3. One specimen, Rottnest I., Hymnus, ii.1920, W.A.M. 9612. Female, Pt Quobba near Carnarvon, P. Barrett Lennard, x.1959, W.A.M. 117-68. Female, Pt Cloates, W.A.M. 282-52. Six males, four females, near Yardie Creek Homestead, North West Cape, on beach, Alf Sneed, v.1959, W.A.M. 67-62. Male and female, between Cape Dupuy and Cape Malouet, Barrow I., intertidal rock flat, W. A. Mus-U. S. Nat. Mus. Barrow I. Exped., 13.ix.1966, W.A.M. 96-68. Female, Yampi Sound, in beach sand, G. H. Robinson, x.1959, W.A.M. 60-62.

Queensland: Sixteen males, forty-seven females, Murray I., Torres Str., C. Hedley and A. R. McCulloch, viii–x.1907, A.M. P2937. Male and female, Hope I. near Cooktown, A. R. McCulloch, viii.1906, A.M. P17395.

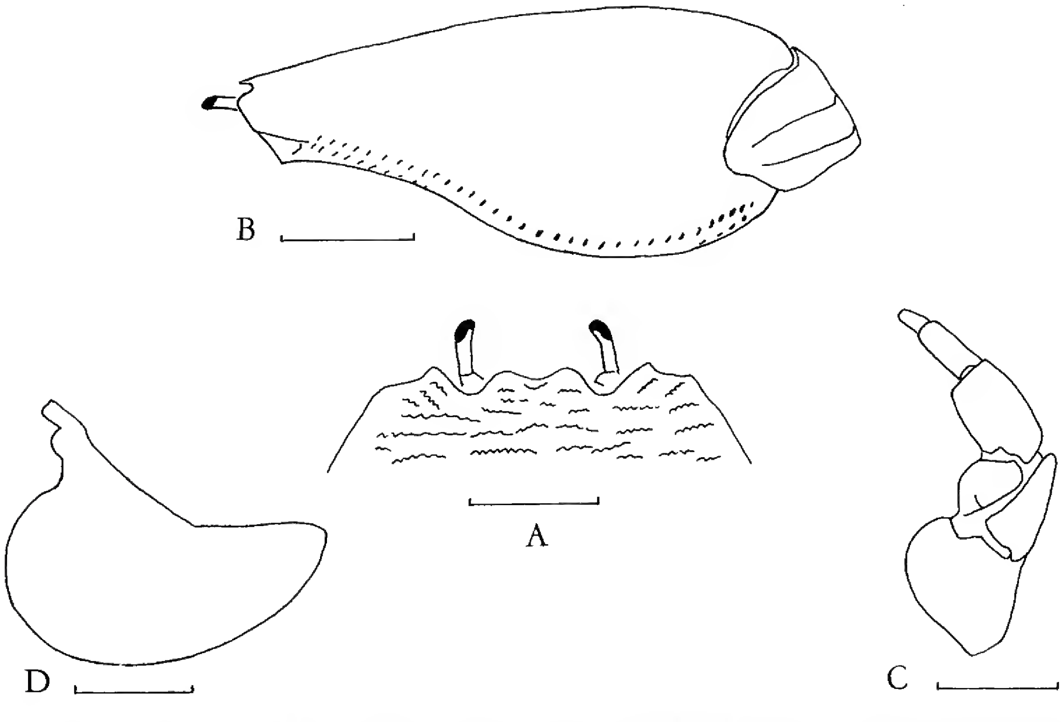

FIG. 3: *Hippa pacifica* (Dana). A, frontal part of carapace; B, carapace, lateral view; C, left antenna; D, dactyl of right second pereiopod. Scale A = 4 mm; B = 6 mm; C, D = 2 mm.

Female, Michaelmas Cay off Cairns, presented xi.1926 by C. Hedley, A.M. P8743. Male, Orpheus I., A. A. Cameron, 3.vii.1940, Q.M. W1109. Female, Townsville, found in surf, A. Collins, 8.ix.1923, Q.M. W109. Female, Wistari Reef near Heron I., Capricorn Grp, under the sand, A. A. Cameron, x.1939, A.M. P11164. Female, Caloundra, C. Y. Ross, 29.iv.1946, Q.M. W1677. Female, Redcliffe, F. Stott, 16.vi.1949, Q.M. W1706.

New South Wales: Female, Corindi Beach, 30 miles S. of Grafton, intertidal sandy beach, J. Knight, 20.ii.1964, A.M. P15801. Female, McCauley's Beach, Coff's Harbour, low tide, presented by C. Bowden and registered 26.ix.1957, A.M. P12973.

Lord Howe I.: Female, old collection, no data, A.M. P15806. Female, W. S. Thomson, collected before 1902, A.M. G4072. Female, presented xi.1923 by R. Baxter, A.M. P6764.

DIAGNOSIS: Carapace covered with wavy, transverse lines. Frontal margin with four rounded lobes, outer pair slightly more projecting than inner; lobes of inner pair separated by a shallow concavity; rarely a small median denticle. A row of about 30–40 shallow, setiferous, slightly elongate pits near each lateral margin. Antennal flagellum normally with two articles. Dactyl of second and third legs with a concave margin, distal and proximal portions of this margin meeting at an obtuse angle.

MEASUREMENTS: Males 9·0 to 17·7 mm, non-ovigerous females 11·3 to 24·9 mm, ovigerous females 14·5 to 27·5 mm.

REVIEW OF AUSTRALIAN LITERATURE: White (1847) listed six Australian specimens of *Remipes testudinarius* in the collections of the British Museum, and Miers (1877) noted that there were specimens of *Remipes pacificus* in the collections of that institution. Miers' Australian material, which would have included that listed by White, was probably based at least in part on *Hippa pacifica*; but until these specimens can be re-examined their status must remain uncertain. Miers (1878) published a revision of the Hippidea in which he combined most of the nominal Indo-West Pacific species of *Hippa*, including *H. pacifica*, under the name *Remipes testudinarius*. The record from E. Australia by Ortmann (1892), who followed Miers's broad interpretation of *R. testudinarius*, may have been based on *Hippa pacifica*.

McNeill (1968) referred to notes made in 1907 by A. R. McCulloch on *Hippa adactyla* from Murray I., Torres Str. Eighty-one specimens collected by C. Hedley and A. R. McCulloch on that occasion are in the collections of the Australian Museum; 63 of them proved to belong to *H. pacifica* and the rest to *H. celaeno*.

Jacquinot (in Jacquinot and Lucas, 1853) described a new species, *Remipes marmoratus*, with Raffles Bay as the type-locality. Miers (1876, p. 59) included it in his catalogue of the Crustacea of New Zealand, citing the Raffles Bay locality; but Thomson (1899, p. 169) pointed out that Raffles Bay is on the northern coast of Australia, and deleted *R. marmoratus* from the New Zealand faunal list.

De Man (1896) did not include Jacquinot's species in his revision of Indo-West Pacific *Remipes*, and its status has remained unknown. During a visit several years ago to the Paris Museum I examined the type-material, consisting of four soft-shelled specimens; although I did not compare them critically with material of *Hippa pacifica*, I noted that they agree with that species in the number of setiferous pits near the lateral margin of the carapace and in having a two-segmented antennal flagellum. The illustration of *R. marmoratus* was published before the desctription and probably earlier than 1852, since Dana

(1852, p. 408) mentioned the species in connection with his original description of *R. pacificus*. Should careful comparison of the two species prove them to be synonymous, the unused name *marmoratus* might have to be suppressed to insure the stability of *pacificus*.

REMARKS: From the study of *Remipes testudinarius* (probably = *Hippa pacifica*, at least in part) from the Philippine Is., Estampador (1939, p. 355) concluded that these animals are either predators or scavengers. *H. pacifica* was later reported feeding on *Physalia* on Hawaiian beaches (Bonnet, 1946, as *Emerita pacifica*). Matthews (1955, p. 382) also observed *H. pacifica* preying on *Physalia* in the Hawaiian Is., and discussed the mechanics of selective feeding in this species. No observations have been published on feeding of *Hippa* in Australian waters; but the label with ten specimens of *H. pacifica* from North West Cape, W.A., listed above, indicates that the animals were "attracted by fish.'

Hippa pacifica is most closely related to *H. ovalis* (A. Milne-Edwards), which differs chiefly in the form of the frontal lobes, and in having a three-segmented flagellum and about 45–55 setiferous pits near the lateral margins of the carapace (see De Man, 1896 and Thomassin, 1969).

DISTRIBUTION: *Hippa pacifica* is more widely distributed than are any of its congeners. It is apparently absent from the Red Sea, where all verified records refer to either *H. picta* (Heller) or *H. celaeno* (De Man) (Lewinsohn, 1969, pp. 172, 173). Most records from the E. and S. coasts of Africa under the names of *testudinarius* and *adactyla* probably refer to *H. ovalis* (A. Milne-Edwards), but I have seen material of *H. pacifica* from Tanzania. There are confirmed records throughout the tropical Indo-West Pacific as far east as the Hawaiian and Gambier Is. The species has also reached the west coast of the Americas where it occurs in the tropics from Mexico to at least as far south as Panama, and on various outlying islands (Clipperton, Revillagigedos, Cocos, Galapagos); Efford (1972) showed that all W. American records under the names *adactyla*, *denticulatifrons*, and *testudinarius* are based on material of *H. pacifica*.

In Australian waters the species is now shown to range from Rottnest I., W.A., around the northern coast and southward to Coff's Harbour, N.S.W.

Hippa celaeno (De Man, 1896)
(Figure 4)

Remipes celaeno De Man, 1896, pp. 462, 483 (type-localities: Makassar and Amboina); 1898, pl. 33 figs. 55, 55a–e.

Hippa adactyla: Stephenson, Endean, and Bennett, 1958, pp. 269, 274 (Low Is.). McNeill, 1968, p. 39 (off Low Is.). McNeill, 1968, p. 39 (off Low Is.; Murray I., Torres Str., in part). Not *H. adactyla* Fabricius.

MATERIAL: Queensland: Two males, sixteen females, Murray I., Torres Str., C. Hedley and A. R. McCulloch, viii–x.1907, A.M. P7552 and P14455. Male and female, Hope I. near Cooktown, A. R. McCulloch, viii.1906, A.M. P15863. Two females, off Low Is., Great Barrier Reef Exped. 1928–29, B.M.N.H. 1937.9.21.367–368. Dry specimen, Low Is., wet beach sand just above reef flat, 1954 Low Is. Survey, 14.viii.1954, M.U.Q. Male, three females, Horseshoe Bay near Bowen, Dep. Zool. Univ. Qd, 20.v.1966, W.A.M. 6-68. Female, Heron I., Capricorn Grp, Dep. Zool. Univ. Sydney, viii.1960, A.M. P15800.

DIAGNOSIS: Carapace covered with short, somewhat wavy, tranverse lines. Frontal margin with four rounded or rounded-triangular lobes, all about equally projecting, outer

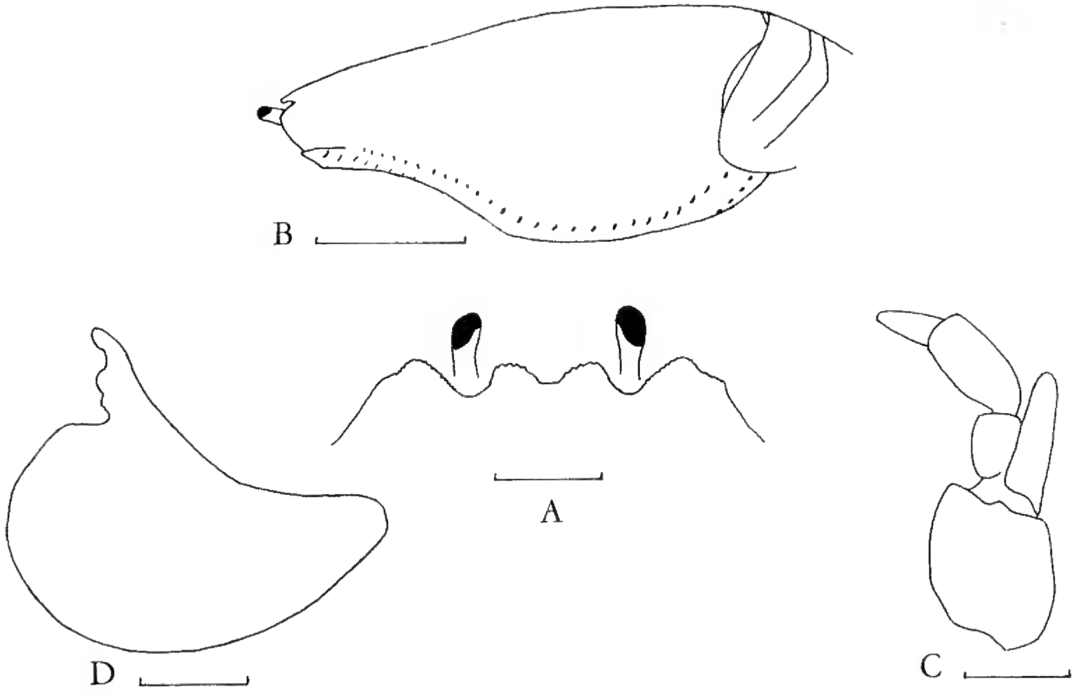

FIG. 4: *Hippa celaeno* (De Man). A, frontal part of carapace; B, carapace, lateral view; C, left antenna; D, dactyl of right second pereiopod. Scale A = 2 mm; B = 5 mm; C, D = 1 mm.

pair somewhat broader than inner ones. Anterior part of lateral margins rather markedly and evenly concave. A row of about 23–28 shallow, setiferous, slightly elongate pits near each lateral margin; this row sharply diverging from margin posteriorly. Antennal flagellum normally with a single article. Dactyl of second and third legs with a concave margin, distal and proximal portions of this margin meeting at an obtuse angle.

MEASUREMENTS: Males 6·0 to 9·1 mm, non-ovigerous females 7·8 to 16·0 mm, ovigerous females 11·0 to 16·9 mm.

REVIEW OF AUSTRALIAN LITERATURE: This species was not reported previously from Australian waters. The specimens collected at Low Is. during the Great Barrier Reef Expedition of 1928–29, and one from the 1954 Low Is. Survey, all of which had been reported as *Hippa adactyla,* were re-examined and found to be *H. celaeno.* As I have noted under the account of *H. pacifica,* McNeill's (1968) record of *H. adactyla* from Murray I. was based on both *H. pacifica* and *H. celaeno* which were collected together at that locality by C. Hedley and A. R. McCulloch.

REMARKS: *Hippa celaeno* may be easily recognized by the abrupt concavity of the anterior portion of the lateral carapace margin, and by the strong divergence from that margin of the last few setiferous pits. Only one other species, *H. picta* (Heller), has both a one-segmented antennal flagellum and fewer than 30 pits in the submarginal row.

DISTRIBUTION: Red Sea, East Indian Archipelago, Bismarck Archipelago, New Caledonia, and now reported from the east coast of Australia from Torres Str. to Capricorn Grp, Qd.

Hippa australis Hale, 1927
(Figure 5 A–F)

Hippa australe Hale, 1927, p. 97, fig. 94 (type-locality: Corney Pt at mouth of Spencer Gulf, Australia); 1928, p. 97 (Cottesloe).

MATERIAL: South Australia: Cast exoskeleton, holotype, Corney Pt, Yorke Peninsula, mouth of Spencer Gulf, Mrs Isobella Klem, 1.x.1923, S.A.M. C994.

Western Australia: Female, beach near Forest Grove, close to Black Rock, W.A.M. 540-31. Female, Bob's Hollow, Calgardup, W.A.M. 151-40. Female, beach near Margaret R., 1954, W.A.M. 4-68. Female, Gnoocardup, W.A.M. 37-44. Female, Bunker Bay, in fine beach sand at tide level, R.W. George, 5.iii.1959, W.A.M. 68-62. Eleven males, four females, beach W. of Harvey, W.A.M. 4/18-36. Two females, beach near Harvey, W.A.M. 213/4-35. Three males, twenty-four females, Harvey, received from Snell, W.A.M. 3-68. Female, Cockburn Sd, D. McCorkill, iii.1958, W.A.M. 64-62. Female, Naval Base, Cockburn Sd, W.A.M. 326-33. Female, Port Beach, Fremantle, G. Riley, 24.xi.1963, W.A.M. 2-68. Male, Leighton Beach, W.A.M. 33-45. Twenty-one males, twenty females, Cottesloe, W.A.M. 10174/93. Female, City Beach, W.A.M. 288-45. Female, Scarborough Beach, presented 27.xi.1963 by R. G. Mason, W.A.M. 5-68. Female, Triggs I., C. Tillbrook, iii.1959, W.A.M. 65-62.

DIAGNOSIS: Carapace covered with shallow, setiferous pits, nearly absent anteriorly, elsewhere arranged in more or less even, transverse rows; anterolaterally these close-set, forming a series of oblique lines near lateral margins. Front with a low, broad, obtusely triangular rostrum; orbits shallowly concave, outer orbital lobes rounded, obscure. Longer flagellum of antennule with about 32–40 articles, shorter with 5–7 (usually 6) in males, 7–12 (usually 8) in females. Antennal flagellum with two articles, the proximal one elongate. Concave margin of dactyl of second and third legs curved, distal and proximal portions not meeting at a sharp angle.

MEASUREMENTS: Males 5·7 to 10·2 mm, non-ovigerous females 6·4 to 18·2 mm, ovigerous females 8·5 to 17·1 mm.

REMARKS: Hale (1928, p. 98) suggested that *Hippa australis* might be identical with *H. truncatifrons* (Miers), a species known from China and Japan. Several years ago, at my request, Dr Isabella Gordon compared specimens of the Australian species with the female holotype of *H. truncatifrons* (B.M.N.H. 1936.8.25.1) and pointed out several diffrences. Later I was able to verify these by examination of four Japanese specimens of *H. truncatifrons* sent by Dr Sadayoshi Miyake. Although closely related, the two species may be distinguished by the following characters:

1. In *Hippa australis* the low, triangular lobe is flanked on either side, to the inside of the eye, by a weakly developed, rounded lobe (Fig. 5A). There is no trace of such lobes on the rostral area in *H. truncatifrons* (Fig. 5G).
2. In *Hippa australis* the longer flagellum of the antennule is elongate and more or less gradually tapering toward the tip (Fig. 5C), while in *H. truncatifrons* it is much shorter and less tapering (Fig. 5H). The shorter antennular flagellum may be consistently longer in *H. australis* than in *H. truncatifrons*, but the articles have been

counted in a very small sample of the latter species. In females (figured) the usual number of articles in *H. australis* is 8, in *H. truncatifrons* 6. In male *H. australis* there are usually 6 articles in the shorter flagellum; there are only 4 in the single male *H. truncatifrons* that I have examined.

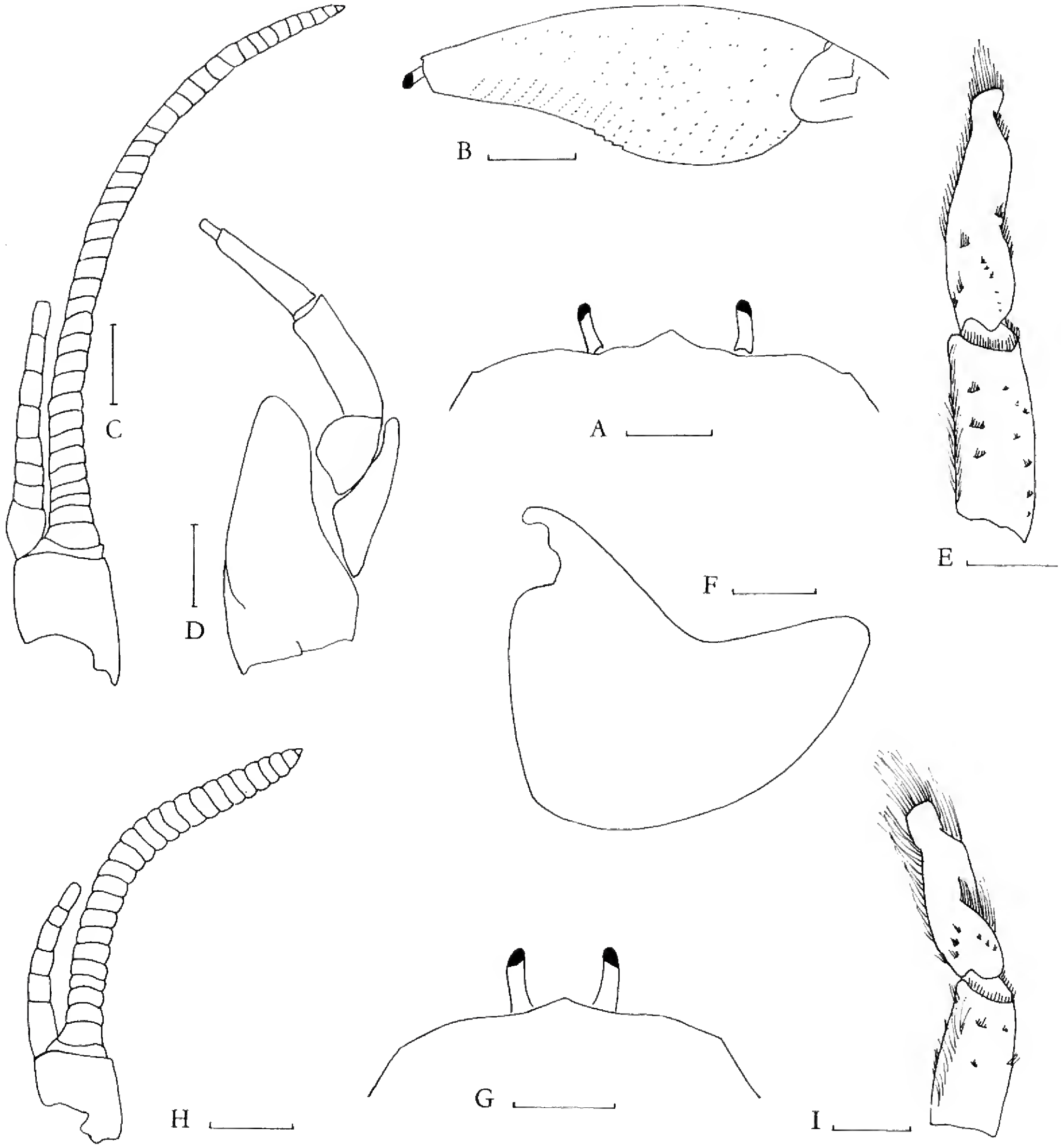

FIG. 5: A–F. *Hippa australis* Hale. A, frontal part of carapace; B, carapace, lateral view; C, left antennule; D, left antenna; E, F, dactyl of right first and second pereiopods, respectively.

G–I. *Hippa truncatifrons* (Miers) from Tosa Bay, Shikoku, Japan. G, frontal part of carapace; H, left antennule; I, dactyl of right first pereiopod.

Scales A, E, G, I = 2 mm; B = 4 mm; C, D, F, H = 1 mm.

3. The propodus and dactyl of the first pereiopods are more slender in *Hippa australis* (Fig. 5E) than in *H. truncatifrons* (Fig. 5I).

Hippa was placed on the Official List of Generic Names in Zoology and designated as feminine (International Commission on Zoological Nomenclature, 1963, p. 18). Therefore, the original spelling *australe* is changed to *australis* in this paper to agree in gender with *Hippa.*

DISTRIBUTION: The holotype of *Hippa australis* is a cast exoskeleton, which was picked up on the beach in South Australian waters. All subsequent records for the species are from temperate Western Australia.

DISCUSSION

Mastigochirus quadrilobatus, *Hippa adactyla*, *H. pacifica*, and *H. celaeno* are members of the tropical Indo-West Pacific fauna, and are widely distributed in the Indian and western Pacific oceans. The ranges of *H. adactyla* and *H. pacifica* extend to eastern Polynesia, and the latter species has crossed the Pacific faunal barrier to become established on the west coast of the Americas. With the exception of *H. pacifica*, the group of about eight species of *Hippa* to which the tropical Australian forms belong—all having two or three median frontal lobes or teeth, and a row of setiferous pits paralleling each lateral margin—has no representatives outside the Indo-West Pacific region. *Mastigochirus*, with two species in the Indian and western Pacific oceans, is an endemic Indo-West Pacific genus.

The fifth species treated in this paper, *Hippa australis*, is an Australian endemic and is confined to warm-temperate waters in the south and southwest part of the continent. It belongs to a second group of *Hippa* species, characterized by the presence of a single median frontal lobe and the lack of a submarginal row of setiferous pits. Its closest relative is *H. truncatifrons*, a subtropical Indo-West Pacific species that is apparently restricted to southern Japan and adjacent parts of the Chinese mainland. The other three members of this group are tropical with one representative each in the eastern Pacific, central and western Atlantic, and eastern Atlantic.

The division of the Australian hippid fauna into a southern temperate and a northern tropical component is consistent with the distribution of Australian marine decapods in general (Griffin and Yaldwyn, 1968, p. 168). Of the tropical species, *Mastigochirus quadrilobatus* and *Hippa pacifica* occur in suitable sandy habitats on both west and east sides of the continent and to the north, while *H. adactyla* and *H. celaeno* appear to be restricted to the east side. However, the distribution of these latter species may prove to be much wider when more collecting has been done.

Thomassin (1969, p. 172), in a study made on the west coast of Madagascar, found that the distributions of Hippidae in that area are influenced by wave action, salinity, and texture of the substrate. *Hippa adactyla* tolerates water of reduced salinity and lives in coarse sediments in the infralittoral zone; *H. pacifica* tends to be distributed according to age, with young postlarval stages (to 5 mm cl.) usually found in fine sands on the outer slope of the reefs, while adults live in coarser sediments, always in the region of breaking waves. The ecological requirements of the other Australian species have not been investigated.

ACKNOWLEDGMENTS

Without help from many sources, this study would never have been completed. My sincere thanks go to the following persons, who offered assistance when I examined material at their institutions, sent material for study at the Allan Hancock Foundation, or provided various kinds of information: D. J. G. Griffin and the late F. A. McNeill, Australian Museum; J. C. Yaldwyn, Australian Museum (now at National Museum, Wellington); A. Neboiss, National Museum of Victoria; Helene M. Laws, South Australian Museum; R. W. George, Western Australian Museum; B. M. Campbell, Queensland Museum; W. Stephenson, University of Queensland; Isabella Gordon and R. W. Ingle, British Museum (Natural History); J. Forest, Paris Museum; G. Hartmann, Hamburg Museum; and S. Miyake, Kyushu University. I also wish to thank F. Munger, who took the photographs from which I prepared some of the illustrations; J. S. Garth for reading the manuscript; and the administration of the Allan Hancock Foundation for providing working space.

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PLATE 6

Hippa adactyla Fabricius, neotype. McCauley's Beach, Coff's Harbour, N.S.W. (AM P17384).

Scale in millimetres.

[redacted]

OBITUARY

Henry Hacker

1876–1973

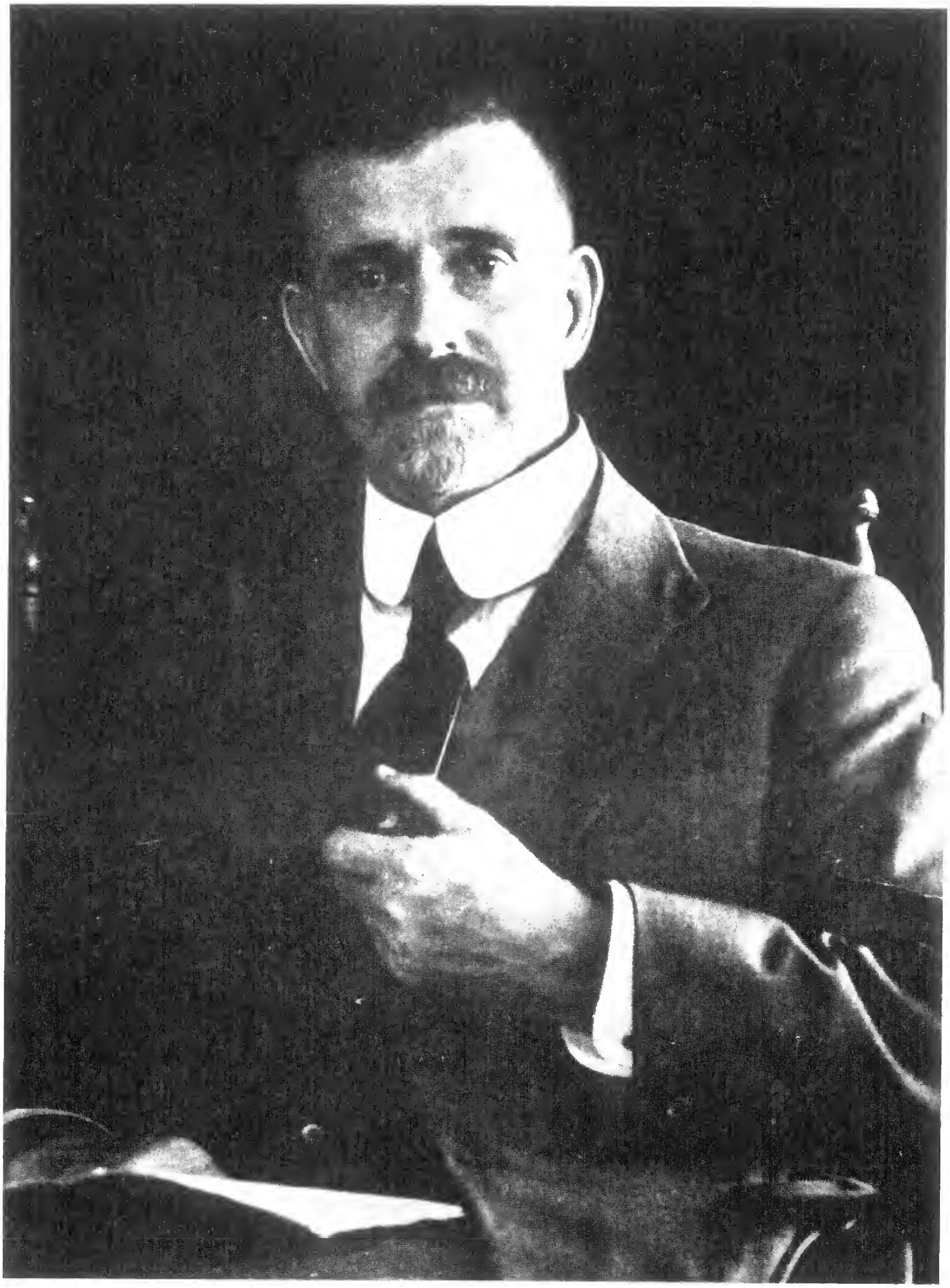
Henry Hacker, who had charge of the Queensland Museum's entomological collection from 1911 to 1943, was born at Slip, Walthamstow, Essex, England on 31st January, 1876 and died at Brisbane on 21st September, 1973.

He started his study of entomology at the British Museum and it is likely that he also acquired a grounding in bee-keeping in England. However, he soon embarked on a wandering, adventurous life. He came to Australia and gold fever seems to have caught him. He vistited Kalgoorlie and Coolgardie in Western Australia, and in November, 1898 took out a Miner's Right at Charters Towers. About 1897–8 he began collecting Australian insects.

He served as a Trooper in the Boer War and took his discharge at Durban on 27 November 1901, giving his trade as miner and his intended place of residence as Johannesburg. He was still in the Transvaal in June 1902 but later that year he made the first of three major collecting trips to parts of Australia which, previous to his visits, were entomologically unknown and of which he wrote interesting accounts. The first was a bicycle trip from Adelaide 300 miles by road to Port Augusta and then a further 258 miles northwest to Tarcoola (now on the Trans-Australia Railway) following camel pads, tracks about 2 feet wide. When riding he was so embedded in bundles that people used to wonder what it was coming along. For meat he depended on emus and rabbits which were present in thousands. His return journey was in winter and the beetles collected were left with Rev. T. Blackburn in Adelaide and the new species described by Blackburn, Sloane, Carter and Lea. (*Ent. Soc. Qd.* Minutes, 27 March, 1935).

In August 1904, Hacker took out a Miner's Right at Cairns. He travelled by boat to Port Stewart and cycled to Coen which he made his base. The bicycle was of little use for riding but was invaluable for transporting equipment and stores. After a mishap he joined the frame together with hardwood pegs and fencing wire and used it for hundreds of miles more. He got two sawyers to fell a small patch of scrub for him, and he visited this every night with a hurricane lamp. It was during the wet season, and although he had many wettings he made a good collection from this patch. There were dangerous episodes with sunstroke and with a group of aborigines at a spot where a man had been speared. From his collections, Lea, Sloane and Carter described 51 new species of beetles. (*Ent. Soc. Qd* Minutes, 8th August, 1932, 27 March 1935).

He was in Brisbane in 1907 but having business in Cloncurry took ship to Townsville and train to Charters Towers, whence he set out on 7 February to bicycle over 500 miles to Cloncurry, collecting beetles along the way. The weather was exceedingly hot and dry but four days beyond Richmond (where the railway ended) the rain fell in torrents. 'It was impossible to ride or even push my bicycle through the wet black soil, so I shouldered it at sunrise and started to walk to the next stopping place, Fisher's Creek, a distance of forty



miles.' With the help of a little riding he reached it at midnight and arrived at Cloncurry about midday on 20 February. Lea reported that Hacker sent him from this trip 128 species of beetles, probably more than half of them new to science, (*Tasm. Nat.* 1 (2): 12–13 1907).

In 1909 Hacker married Constance Callaghan (d. 1970), sister of a school-teacher friend. They had a happy family life and reared three sons and two daughters. They settled in the Upper Mulgrave valley south of Cairns, but their rubber farm was unsuccessful and they came to Brisbane. Perhaps it was of this period that Hacker wrote: 'Many years ago in N. Queensland I successfully worked large flowering blood-woods with the aid of a pair of climbing irons. Taking some lunch and a bottle of water I used to sit among the branches from early morning till about midday. The net was attached to a long bamboo so that all the branches could be reached. In catching large Buprestidae and Cetonidae, a tap on the underside of the branch with the rim of the net was sufficient to cause them to tumble in. Such fine species as *Calodema plebejus* and *regalis*, *Metaxyorpha hauseri* and *gloriosa*, besides many fine *Stigmodera*, large Cetonidae, and innumerable smaller insects were collected by this method.' (*Ent. Soc. Qd.* Minutes, 27 March 1935).

He sold (probably in 1910) his private collection of about 6000 species of Australian Coleoptera to the National Museum, Berlin. He applied for a position on the staff of the Queensland Museum citing A.M. Lea, C. French, A. J. Turner, H. Tryon, W. Froggatt and T. Sloane as all being acquainted with his work, and on 7 March 1911 he was appointed to the Museum staff.

As an entomologist he undoubtedly had skill and enthusiasm, and nowhere is this skill and enthusiasm more evident than in the collections and the *Memoirs* of the Queensland Museum. He was most outstanding in his collecting ability and in his powers of observation. Many of his contributions to the *Memoirs* consisted of notes and observations on the collection, life histories, and habits of Australian insects. In these he often passed collecting hints on to other entomologists, for example, in Vol. 6, page 107 he writes '. . . . . to take note of all the dams and waterholes in the district to be collected over, and visit them in November or December. About that time they will be nearly dry and the mud around the edges visited by many fine wasps and bees.' His other papers in the *Memoirs*, one of which was written in conjunction with T. D. A. Cockerell, concern the taxonomy of various Hymenoptera and Homoptera. Throughout the *Memoirs* there are papers by such authors as Lea and Cockerell in which Hacker's name constantly appears as the collector of many new species. Many other new species have been described by other authors and in other journals.

During Hacker's era not only were the collections increased but he encouraged specialists to identify his material. He would sort the material into conspecific groups and gave every group numbers. One or two specimens from each species group were forwarded to the specialist concerned who would return a list of identifications with the corresponding numbers. In such a system one would expect errors, but in fact, Hacker's eye for a species is proving very accurate when the material is re-examined by today's specialists.

His collecting ability and knowledge of insect life histories was also evident in the museum displays he prepared for the instruction and enjoyment of the public. Both the collection and displays still have examples of his skill at preserving caterpillars by inflation and drying. Another of his skills was also seen in these displays, notably photography, an interest stimulated by Tom Marshall, a young Museum Assistant who often accompanied Hacker on collecting trips to the Mt. Glorious area. The displays contained clear and sharp photo-micrographs of fleas, lice and mosquitoes which Hacker produced using equipment improvised from cardboard cylinders and rubber bands. Further evidence of his photographic skill can be seen in the plates accompanying his papers in the *Memoirs*.

In 1929 Robert Veitch arranged for Hacker to be seconded to the Department of Agriculture and Stock to identify and build up its reference collection, while continuing to work one or two days a week at the Museum. Though eventually he became an officer of the Department, this arrangement continued until his retirement on 30 June 1943. When the serious bee disease, American foulbrood, was identified at Clear Mountain in 1931, none of the senior entomologists in the Department was experienced in beekeeping. Hacker was appointed an Inspector of Apiaries in February 1931 and was actively engaged on this for about a year.

The beekeepers found him an unusual character to deal with, with his small goatee beard and rather dapper English-style suit, waistcoat and tie, which he wore even to the roughest spots. He was very knowledgeable about bees, particularly in relation to diseases and pests, and the youthful Charlie Roff found it very interesting and instructive to accompany him. On other occasions when he was issuing certificates for export of queen bees, John Weddell went with him. Both found it a very exciting experience, for at this time Hacker travelled with a motorcycle and sidecar in which was the apiary equipment as well as the passenger. He would 'go like hell' irrespective of the kind of road, never slackening at corners and, coming back into town among the slow traffic, would point at a gap between two vehicles and somehow pass through.

For the Department Hacker produced several extension articles on bees, the most important of these was the Department's first extension Bulletin for beekeepers, 'An introduction to beekeeping'. The basic information in it on the life history of the honey bee is as sound now as when it was written, though the equipment described is outdated.

It was fortunate indeed for Queensland and for entomology that in days when jobs for entomologists were few Henry Hacker was able to obtain a post at the Queensland Museum where he could give all his time to entomology.

His interest was extended to other orders besides Coleoptera by the need to build up the Museum's collection, and it was further stimulated by visits from and correspondence with leading specialists from other states and overseas. He was one of the founders of The Entomological Society of Queensland in 1923, and at its meetings, by his papers, exhibits and informed comments on the exhibits of others, he was able to pass on much of his great knowledge to younger entomologists. By consent of the Society's Council, parts of its tribute to him (Marks, E. N., 1973. *Ent. Soc. Qd News Bull.* **100**: 13–16) have been reproduced here.

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EDWARD DAHMS
Queensland Museum

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