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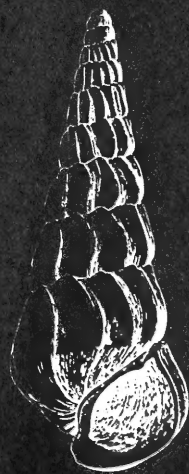
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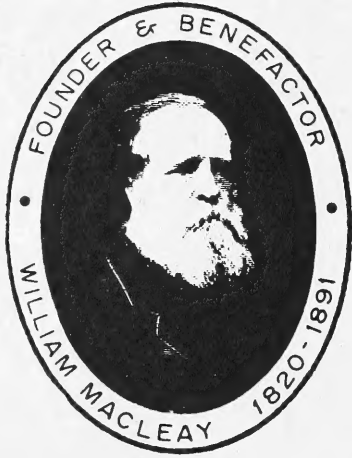
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THE LINNEAN SOCIETY OF NEW SOUTH WALES



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Cover motif: The gastropod collected '16 miles east of Wollongong' and described by Charles Hedley as *Stiva ferruginea* gen. et sp. nov. (*Proc. Linn. Soc. N.S.W.* 29, 1904: pl. IX, no. 23).

PROCEEDINGS

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VOLUME 111

NUMBER 1

Redistribution of Nutrients in Subtropical Rainforest Trees

MARCIA J. LAMBERT and JOHN TURNER

(Communicated by D. W. EDWARDS)

LAMBERT, M. J., & TURNER, J. Redistribution of nutrients in subtropical rainforest trees. *Proc. Linn. Soc. N.S.W.* 111 (1), 1989: 1-10.

Fresh foliage and leaf litterfall from trees and understorey plants in a N.S.W. subtropical rainforest were chemically analysed to estimate nutrient redistribution. In general, the proportion of nutrients redistributed in these species at time of leaf litterfall is low. Results available on nutrient redistribution from the same species in this area during heartwood formation showed that trees which redistributed phosphorus from foliage, redistributed little from heartwood and *vice-versa*. By way of contrast, species in sclerophyll forests were highly efficient at nutrient redistribution from both leaves and wood.

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INTRODUCTION

Nutrient cycling within forests is critical for long term maintenance of productivity and stability. It involves nutrient uptake, utilization and accumulation by vegetation, together with the return of nutrients to the soil through litterfall, leaching and root sloughing. Comparisons of nutrient cycles involve considerations of how species are able to obtain nutrients from soils with low nutrient status and then retain the nutrients within systems (Turner, 1975). In order to assess turnover of nutrients, various indices have been developed. For example, turnover of litter on forest floor has been compared by using a 'k' factor which relates the input of litter (L) to the mass of litter (F) on the forest floor. The 'k' factor = L/F and assumes a steady state forest floor weight (Jenny *et al.*, 1949; Olson, 1963; Richards and Charley, 1977) and gives an indication of the rate of loss (decomposition) by the litterfall in relation to accumulation on the forest floor.

Relative efficiency of nutrient acquisition from soil, nutrient utilization requirements and efficiency of redistribution of nutrients can be assessed within the tree component of an ecosystem. These comparisons are difficult, but some can be made. For example, an index of nutrient utilization within a tree is often obtained using foliage nutrient concentrations (Lambert and Turner, 1983; Lambert *et al.*, 1983). Nutrient redistribution may be estimated as withdrawal of nutrients, both during leaf abscission (Ashton, 1976; Attiwill, 1980; Turner and Lambert, 1983) and in heartwood formation (Lambert, 1981). Such estimates have been made in only a few forests in Australia and have been carried out predominantly in stands dominated by a single species (Hingston *et al.*, 1979; Attiwill, 1980; Turner and Lambert, 1983) where monthly leaf litterfall data were compared with those for live leaf material on the trees. In studies of forest stands including a variety of species, and particularly in conditions where organic matter decomposition and tissue leaching can be quite rapid, the use of monthly litterfall samples becomes inappropriate.

Subtropical rainforests are associated with relatively fertile soils (Baur, 1957; Webb, 1969; Lambert *et al.*, 1983) whereas eucalypt forests are on soils with much lower fertility (Baur, 1957; Webb, 1969; Turner and Kelly, 1981). Subtropical rainforests (Baur, 1965) have high species diversity with often in excess of 30 species ha^{-1} in the overstorey. They are notable in northern N.S.W. for the absence of *Eucalyptus* species, a genus which

dominates most other coastal and tableland forest types in N.S.W. During a programme of study in a subtropical rainforest located on the New South Wales Border Ranges, leaf material was sampled from a range of species in order to obtain indices of nutrient distribution and cycling patterns within this forest. Fresh litter was specifically sampled to provide estimates of nutrient redistribution in various species. These data were combined with differences in heartwood and sapwood nutrient concentrations and compared with similar data from coastal sclerophyll forests.

STUDY SITE

The study site was originally described by Lambert *et al.* (1983) and was located in forests of the Border Ranges (153°E, 28°38'S), west of Murwillumbah. The altitudinal range of the forest is 600-1200m above sea level. Annual rainfall is 3000mm. Plots were selected from within subtropical rainforest growth experiments (Burgess *et al.*, 1975; Horne and Gwalter, 1982). Soils from the region are derived from Tertiary volcanic rocks of the Mt Warning Shield and are predominantly of basaltic composition (Stevens, 1976). The basalts have given rise to kraznozems, that is, deep well-structured red clay loams with clay sub-soils having a relatively uniform appearance and depth (Beckman and Thompson, 1976). The soils are high in nutrients, particularly when compared with soils supporting sclerophyllous species (Lambert *et al.*, 1983).

METHODS

Trees were sampled for foliage and wood during logging operations near the study site. Within a species, nutrient variability in foliage concentration was found to be low (Lambert *et al.*, 1983; Lambert and Turner, 1986). Foliage samples were bulked from within the crown but only fully-formed leaves were used; that is, very young or damaged leaves were omitted. Samples were placed in paper bags, oven dried at 70°C, ground and analysed for various chemical elements (Lambert, 1983). The results for overstorey and understorey trees have been reported elsewhere. Wood discs were taken from the stem approximately 1m above the ground. These were air dried and then separated into bark, sapwood and, where present, heartwood. The individual components were ground and analysed for the same chemical elements as the foliage samples (Lambert, 1983).

Freshly-fallen leaf samples were sampled beneath the crown of selected species within the research plot and were those recently fallen so that there was minimal effect due to decomposition and leaching. Where leaves were caught on understorey vegetation, they were preferentially selected so that ground contact was minimized. Acquiring sufficient suitable material of many species was difficult and hence single, bulked samples were used rather than replicates. The leaf litterfall samples were dried, ground and analysed in the same way as foliage samples.

A list of the common names, scientific names and authorities of species sampled on the study site is given in the Appendix.

RESULTS

Results of the analyses are presented in detail in Table 1; trends are summarized in Table 2. Changes in concentration of nitrogen and phosphorus between overstorey leaf and litterfall were relatively minor in most cases. There were obvious exceptions, such as *Dendrocnide excelsa*, *Solanum aviculare* and *Solanum mauritianum*, these tending to be very high in nutrients initially. The other exception was *Orites excelsa* which has relatively low requirements for both phosphorus and nitrogen and appears to be also efficient at retranslocation, that is, there is high nutrient removal by retranslocation even in a situ-

TABLE 1
 Mean foliage nutrient concentrations (from Lambert et al., 1983), leaf litter concentrations and estimated concentration changes in tree species in a New South Wales subtropical rainforest

Species		Ash (%)	N (%)	P	Ca	Mg	K	Mn	Al (ppm)	Na	Zn	Fe	B	Cl
<i>Heritiera actinophylla</i>	— leaf	4.99	1.85	765	9930	4050	8450	745	165	150	22	75	43	2225
	— litter	6.09	2.02	950	10310	4625	12040	435	145	195	15	90	32	2280
	— change	+1.10	+0.17	+185	+380	+575	+3590	-310	-20	+45	-7	+15	-11	+55
<i>Neolitsea reticulata</i>	— leaf	3.69	1.80	760	5985	1130	8550	1580	230	2345	40	55	17	1230
	— litter	4.64	1.52	680	9795	1830	3440	1680	585	2825	50	250	23	1240
	— change	+0.95	-0.28	-80	+3810	+700	-5110	+100	+355	+480	+10	+195	+6	+10
<i>Calcduvia paniculosa</i>	— leaf	8.72	1.90	920	13080	12595	10200	1485	3635	1680	29	95	23	1870
	— litter	8.69	1.48	815	15900	11255	2330	2120	2155	645	30	95	32	365
	— change	-0.03	-0.42	-105	+2820	-1340	-7870	+635	-1480	-1035	+1	0	+9	-1505
<i>Euodia micrococca</i>	— leaf	8.50	2.15	1180	11110	3130	6580	800	135	1470	53	69	61	6545
	— litter	11.49	1.44	995	12035	3010	1280	800	275	1250	60	190	35	5315
	— change	+2.99	-0.71	-185	+925	-120	-5300	0	+140	-220	+7	+121	-26	-1230
<i>Dendrocnide excelsa</i>	— leaf	15.66	3.34	2120	30290	7790	25290	95	165	445	35	185	30	11925
	— litter	17.18	3.23	1630	41140	5340	8490	145	385	245	40	355	29	3385
	— change	+1.52	-0.11	-490	+10850	-2450	-16800	+50	+220	-200	+5	+170	+9	-8540
<i>Solanum aviculare</i>	— leaf	9.63	5.21	2660	7790	2800	34050	210	340	215	30	315	27	8040
	— litter	11.62	2.95	940	21790	2640	27900	150	140	235	25	140	50	5335
	— change	+1.99	-2.26	-1720	+1400	-160	-6150	-60	-200	+20	-5	-175	+23	-2705
<i>Cryptocarya erythroxylon</i>	— leaf	5.43	2.08	1150	9155	2410	12185	420	620	1080	75	63	23	2360
	— litter	5.31	2.10	1270	12190	1885	-6360	455	1400	590	65	165	35	860
	— change	-0.12	+0.02	+120	+3035	-525	-5825	+35	+780	-490	-10	+102	+12	-1500
<i>Orites excelsa</i>	— leaf	4.53	1.17	540	6225	1560	4300	1140	6790	220	25	70	22	30
	— litter	5.18	0.54	220	5073	1720	1630	2590	2105	550	10	100	20	380
	— change	+0.65	-0.63	-320	-1152	+160	-2670	+1450	-4685	+330	-15	+30	-2	+350
<i>Geissois benthamiana</i>	— leaf	7.14	1.30	595	15010	4715	7860	960	2285	1305	41	53	44	1640
	— litter	6.82	1.26	635	14940	4855	4380	1190	2130	1510	50	140	60	1145
	— change	-0.32	-0.04	+40	-70	+140	-3480	+230	-155	+205	+9	+87	+16	-495

TABLE 1 (concluded)

Species		Ash (%)	N (%)	P	Ca	Mg	K	Mn (ppm)	Al (ppm)	Na	Zn	Fe	B	Cl
<i>Dysoxylum fraserianum</i>	— leaf	6.67	2.17	1230	10550	4395	17200	35	115	805	25	80	31	6510
	— litter	9.16	1.82	905	18530	5110	11700	70	435	1470	25	325	44	6080
	— change	+2.49	-0.35	-325	+7980	+715	-5500	+35	+320	+665	0	+245	+13	-430
<i>Solanum mauritianum</i>	— leaf	6.95	4.54	885	15910	3545	18220	385	270	550	40	200	69	5070
	— litter	8.94	1.36	655	23220	3980	7950	190	510	600	60	560	54	4600
	— change	+1.99	-3.18	-230	+7310	+435	-10270	-195	+240	+50	+20	+360	-15	-470
<i>Heritiera trifoliolata</i>	— leaf	5.20	1.98	1110	8995	2795	12215	275	55	1170	25	55	27	3735
	— litter	4.32	1.95	970	6945	2395	9470	550	165	515	20	120	55	1410
	— change	-0.88	-0.03	-140	-2050	-400	-2745	+275	+110	-655	-5	+65	-15	-2325
<i>Sloanea woollsi</i>	— leaf	4.30	1.10	755	9255	2930	8025	1005	130	360	30	65	42	1590
	— litter	6.66	0.92	475	14900	4765	5140	815	885	810	15	150	47	1935
	— change	+2.36	-0.18	-280	+5645	+1815	-2885	-190	+745	-450	-15	+85	+5	+345

ation of high nutrient availability (Kelly *et al.*, 1983). Calcium typically increased in concentration in the litter of most species, an exception being *Orites excelsa*. The patterns of other elements were much more irregular (Table 2). Potassium and manganese tended to decline and accumulate respectively. *Caldcluvia paniculosa* and *Orites excelsa* accumulated aluminium in the foliage but the concentration of this element was lower in the litter, the *Orites excelsa* to a higher degree possibly showing different patterns of handling an antagonistic element. Of the 48 samples assessed, heartwood was detectable in only 12 and in these instances relatively few had significant retranslocation of nutrients (Lambert *et al.*, 1983).

Within the non-woody understorey species, nutrients were retranslocated between young and old tissues as in the woody species (Table 3). *Cyathea australis*, for example, redistributed 45% of phosphorus in the aging of fronds. *Archontophoenix cunninghamiana* was an efficient retranslocator of phosphorus (65%) and potassium (96%), although there may be a higher proportion leached as it is difficult to estimate when foliage of this species can be classified as litterfall as the older foliage hangs down next to the stem. *Asplenium nidus* retranslocated much smaller quantities during senescence.

DISCUSSION

Estimates of nutrient retranslocation are relative measures and to understand the ecological significance of nutritional patterns, comparisons with other forest types have been used. Within the subtropical rainforest, retranslocation of nutrients within foliage prior to abscission appears to be relatively low for most overstorey species, however, exceptions were: *Dendrocnide excelsa*, this species having fairly high nutrient requirements; *Orites excelsa*, which is an aluminium-accumulating species and appears to have an efficient system of retranslocation; and two solanaceous species (*Solanum aviculare* and *Solanum mauritianum* which invade and grow immediately after soil disturbance and live for only a relatively short time. It appears they have both high nutrient demands and efficient retranslocation. The level of retranslocation may be compared with that in sclerophyllous species and coachwood which generally grow on nutritionally poorer soils than the subtropical rainforest (Table 4). In these species, phosphorus, nitrogen, magnesium and potassium are all retranslocated, while calcium and aluminium are accumulated. The calcium pattern appears typical of mature foliage in many trees. Further, there were consistently high removals of nutrients in these species during heartwood development. The pattern of heartwood development and retranslocation was either absent or very low in the majority of species sampled in this rainforest.

Generally, nutrient redistribution is an important component, along with uptake, in fulfilling forest stand nutrient requirements (Turner and Lambert, 1983). However, if the general principle is that the subtropical rainforest tree species generally redistribute nutrients at a low level, whereas the sclerophyllous and cool temperate rainforest species are more efficient at redistribution, is this a function of generally higher soil nutrient availability? Further, if large fertilizer quantities were applied to eucalypt species or they were located on more fertile soils, would heartwood production be reduced or litter retranslocation lowered? Eucalypts growing naturally across a range of fertilities do not have significantly different foliage nutrient concentrations (Lambert and Turner, 1983) or nutrient redistribution patterns. This suggests that soil nutrients are not controlling the patterns but rather that they are evolutionarily determined. The reverse situation of growing subtropical rainforest trees on poor sites is harder to test, mainly because it appears that soil nutrients are delineators of species (Turner and Kelly, 1981) and hence rainforest species are out-competed on poor sites.

Within the subtropical rainforest there were some species such as *Orites excelsa*

TABLE 2
 Changes in nutrient concentrations between foliage and litter for all species in Table 1. It has been assumed that at least a 10% change in concentration is needed to be significant.
 If the change is less than 10%, a 0 is listed for that element

Species	Nutrient												
	N	P	Ca	Mg	K	Mn	Al	Na	Zn	Fc	B	Cl	
<i>Heritiera actinophylla</i>	0	+	0	+	+	-	-	+	-	+	-	+	
<i>Neolitsea reticulata</i>	-	-	+	+	-	0	+	+	+	+	+	0	
<i>Caldcluvia paniculosa</i>	-	-	+	-	-	+	(-)	-	0	0	+	-	
<i>Euodia micrococca</i>	-	-	0	0	-	0	+	-	+	+	-	-	
<i>Dendrocnide excelsa</i>	0	-	(+)	-	-	+	+	-	+	+	?	(-)	
<i>Solanum aviculare</i>	-	-	+	0	-	-	-	0	-	-	+	-	
<i>Cryptocarya erythroxylon</i>	0	+	+	-	-	0	+	-	-	+	+	-	
<i>Orites excelsa</i>	-	-	-	+	-	+	(-)	+	-	+	0	(+)	
<i>Geissois benthiana</i>	0	0	0	0	-	+	(0)	+	+	+	+	-	
<i>Dysoxylum fraserianum</i>	-	-	+	+	-	+	+	+	0	+	+	0	
<i>Heritiera trifoliolata</i>	0	-	-	-	-	+	+	-	-	+	-	0	
<i>Solanum mauritianum</i>	-	-	+	+	-	-	+	0	+	+	-	+	
<i>Sloanea woollarii</i>	-	-	+	+	-	-	+	-	-	+	+	+	

TABLE 3
Mean foliage and litter nutrient concentrations and the estimated changes in nutrient concentrations in understorey species

Species	Component	Ash (%)	N (%)	P	Ca	Mg	K	Mn	Al (ppm)	Na	Zn	Fe	B	Cl
<i>Cyathea australis</i>	— frond	6.44	1.73	970	2810	3780	13000	65	9755	1680	35	100	12	14320
	— litter	8.27		505	2670	4440	3420	65	8200	4665	55	140		11735
	— change	+1.83		-465	-140	+660	-9580	0	-1555	+2985	+20	+40		-2585
<i>Archontophoenix cunninghamiana</i>	— frond	6.59	1.20	865	3085	1730	18675	260	35	4945	15	60	6	28145
	— litter	3.33		302	5385	1490	825	365	175	255	15	155		90
	— change	-3.26		-563	+2300	-240	-17850	+105	+140	-4690	0	+95		-28055
<i>Nephrolepis</i> sp.	— frond	6.21		1300	7970	5410	14575	185	585	585	35	290	36	9940
	— litter	3.83	0.85	845	9000	4020	970	310	795	165	50	285	34	115
	— change	-2.38		-455	+1030	+1390	-13605	+125	+210	-420	+50	-5	-2	-9825
<i>Asplenium nidus</i>	— new	11.63	1.18	1580	5225	2170	50225	555	60	1240	23	75	31	
	— old	5.61	0.70	470	17910	7245	10605	995	160	1015	20	325	63	340
	— change	-6.02	-0.48	-1110	+12685	+5075	-39620	+440	+100	-220	-3	+250	+32	
— blade	— new	12.11	2.14	2820	13480	4930	37065	885	115	1185	43	100	45	
	— old	16.28	1.80	1465	40910	9415	7400	995	625	3080	55	425	95	850
	— change	+4.17	-0.34	-1355	+27430	+4485	-29665	+110	+510	+1895	+12	+325	+50	

TABLE 4

Published information for various Australian forest species on redistribution from foliage during abscission

Forest Type		N (%)	P	Ca	Mg (ppm)	K	Al	Reference
Wet Sclerophyll								
<i>E. grandis</i>	— foliage	1.47	895	4800	2690	6450	80	Turner and Lambert (1983)
	— litter	0.86	340	7065	2160	1955	230	
	— change	-0.61	-555	+2265	-530	-4495	+150	
<i>E. regnans</i> ^a	— foliage	0.79	780	5730		5730		Ashton (1976)
	— litter	0.87	300	5450		1240		
	— change	-0.12	-480	-280		-4490		
<i>E. pilularis</i>	— foliage	1.21	620	3420	3465	3810	120	Turner and Kelly (1981)
	— litter	0.70	300	12610	2390	1140	330	
	— change	-0.51	-320	+9190	-1075	-2670	+210	
<i>Lophostemon confertus</i>	— foliage	1.61	1205	9525	2735	11035	195	Turner and Kelly (1981)
	— litter	0.81	525	12220	2580	1750	820	
	— change	-0.80	-680	+2695	-155	-9285	+625	
Rainforest								
<i>Ceratopetalum apetalum</i>	— foliage	1.10	505	10365	2990	4540	7275	Turner and Kelly (1981)
	— litter	0.71	210	7890	1740	1030	8200	
	— change	-0.39	-295	-2745	-1250	-3510	+925	
<i>Nothofagus cunninghamii</i>	— foliage		1010					Ashton (1976)
	— litter		300					
	— change		-710					
<i>Athosporia moschatum</i>	— foliage		1500					Ashton (1976)
	— litter		890					
	— change		-630					
Dry Sclerophyll								
<i>E. sieberi</i>	— foliage		440					Ashton (1976)
	— litter		110					
	— change		-330					

^a 2nd year leaf and leaf litter analyses for a mature stand.

which gave a similar pattern to the sclerophyllous pattern of redistribution. Whether this is an indication that the species had evolved on poorer soils and now survive within the subtropical rainforest is difficult to ascertain, but it is suggested that the combination of high litter and heartwood redistribution efficiencies, particularly for phosphorus, is indicative of evolution on soils with low nutrient status.

A further question arises as to the relationship between redistribution during leaf abscission and that during heartwood formation for the rainforest species. For most nutrients there was no relationship, but for phosphorus and nitrogen, there was an inverse relationship (Fig. 1). That is, as the proportion of phosphorus redistributed in leaves increased, the proportion redistributed in heartwood formation or its formation at all, decreased. The exception to this was *Orites excelsa* which, as noted above, tends to have unusual patterns of nutrient utilization compared with other species.

The general pattern for phosphorus in rainforest trees, is that as phosphorus becomes more efficient at redistribution in one type of tissue, it becomes less efficient in another. The species which most noticeably form heartwood are not redistributing during leaf senescence. This is the opposite pattern to that found in *Eucalyptus* and other sclerophyllous species (Fig. 1) where there is simultaneous redistribution from leaf litter

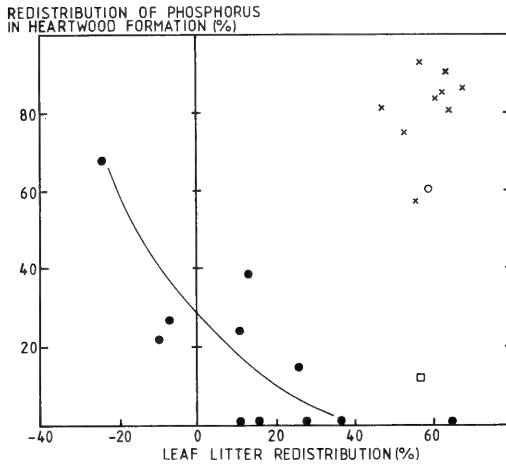


Fig. 1. Relationship between redistribution of phosphorus during heartwood formation and leaf abscission (● — rainforest species; x — eucalyptus and sclerophyllous species; □ — *Ceratopetalum apetalum*; ○ — *Orites excelsa*).

and heartwood. *Orites excelsa* relates closely to the 'sclerophyllous' pattern which includes *E. pilularis*, *E. dives*, *E. maculosa*, *E. rossii*, *E. rubida*, *E. obliqua*, *E. grandis*, *Lophostemon confertus* and *Casuarina torulosa*, these being the species where mature green leaf, leaf litterfall, sapwood and heartwood concentrations were available. The phosphorus redistribution pattern in coachwood, however, was similar to that found generally in the subtropical rainforest species even though this species grows in differently structured rainforest (Baur, 1965).

Comparisons with other species (Table 4) were based on results for mature leaves on the tree and fresh litter using comparable sampling techniques. Fully-developed younger leaves have nutrient concentrations different to those in older leaves, so that there are different patterns of redistribution taking place within the crown. Further, there are different patterns between different-aged forests of the same species (Ashton, 1975). The pattern for nitrogen was similar to that for phosphorus for the rainforest species. *Orites excelsa* was again found to form a different pattern. Nitrogen was generally not as efficiently redistributed as phosphorus during heartwood formation. *Ceratopetalum apetalum* and *Lophostemon confertus* in this case followed the rainforest pattern, while the eucalypts were differently distributed.

While for most nutrients there are relationships between foliage litter and heartwood redistribution which may be described as specific to species/site, phosphorus and nitrogen have given separate patterns of nutrient cycling. In rainforests, where phosphorus and nitrogen are usually readily available, a certain amount of 'energy' is apparently expended in retaining nutrients in biomass and hence not all tissues are affected. In the case of the lower phosphorus sclerophyllous forest, all available phosphorus is apparently redistributed, this being the primary limiting nutrient. The pattern of *Orites excelsa* possibly indicated that it evolved in a low phosphorus environment.

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APPENDIX

List of common names, scientific names and authorities of species from the study site

Common name	Botanical name
Bangalow palm	<i>Archontophoenix cunninghamiana</i> (H. Wendl.) H. Wendl. et Drude
Birds nest fern	<i>Asplenium nidus</i> L.
Black booyong	<i>Heritiera actinophylla</i> (F. M. Bail.) Kosterm.
Bollygum	<i>Neolitsea reticulata</i> (Meisn.) F. Muell.
Brushbox	<i>Lophostemon confertus</i> (R. Br.) Peter G. Wilson et J. T. Waterhouse
Coachwood	<i>Ceratopetalum apetalum</i> D. Don
Corkwood	<i>Caldcluvia paniculosa</i> (F. Muell.) Hoogl.
Doughwood	<i>Euodia micrococca</i> F. Muell.
Giant stinging tree	<i>Dendrocnide excelsa</i> (Wedd.) Chew
Kangaroo apple	<i>Solanum aviculare</i> Forst. f.
Lace fern	<i>Nephrolepis</i> sp.
Pigeonberry ash	<i>Cryptocarya erythroxylon</i> Maiden et Betche
Prickly ash	<i>Orites excelsa</i> R. Br.
Red carabeen	<i>Geissois benthamiana</i> F. Muell.
Rosewood	<i>Dysoxylum fraserianum</i> (A. Juss.) Benth.
Teak	<i>Flindersia australis</i> R. Br.
Tree fern	<i>Cyathea australis</i> (R. Br.) Domin
White booyong	<i>Heritiera trifoliolata</i> (F. Muell.) Kosterm.
Wild tobacco tree	<i>Solanum mauritianum</i> Scop.
Yellow carabeen	<i>Sloanea woollsi</i> F. Muell.

New Occurrences of Culmacanthid Acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia

G. C. YOUNG

YOUNG, G. C. New occurrences of culmacanthid acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia *Proc. Linn. Soc. N.S.W.* 111 (1), 1989: 11-24.

Two new species of the acanthodian fish *Culmacanthus* Long 1983 are described from the lower part of the Aztec Siltstone of southern Victoria Land, Antarctica, and Facies 3 of the Boyd Volcanic Complex of southeastern New South Wales. Both are represented only by cheek plates. That of *C. antarctica* sp. nov. has distinctive ornament, a longer lateral than dorsal lamina, and the infraorbital sensory groove passing off the ventral margin of the plate. *C. pambulensis* sp. nov. resembles the type species *C. stewarti* Long in the shape of the posterior margin of the cheek plate and the ventral course of the infraorbital sensory canal, but differs in its proportions, the shape of the anterior margin, and the much finer dermal ornament. *C. antarctica* sp. nov. is considered to be the oldest (?late Middle Devonian) because it is associated with turiniid thelodont scales. The two other species of *Culmacanthus* occur with bothriolepid and phyllolepid placoderms in assemblages considered to be early Late Devonian (Frasnian). The specific differences described herein suggest however that they are not precise correlatives. Culmacanthid acanthodians are only known from southeastern Australia and southern Victoria Land, a distribution pattern previously noted in chondrichthyans and placoderms from the same faunas, and suggesting that *Culmacanthus* was an east Gondwanan endemic.

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INTRODUCTION

The acanthodians are a major group of Palaeozoic gnathostome fishes, with a fossil record from Silurian to Permian. During the Devonian Period they were widely distributed in both non-marine and marine aquatic environments, and their tiny scales and characteristic fin-spines are commonly represented in microvertebrate assemblages. However articulated specimens are much less common, and knowledge of acanthodian morphology is based mainly on a few localities in Europe and North America which have yielded well-preserved complete specimens (for a comprehensive review of the group see Denison, 1979).

A. S. Woodward was the first to describe Australian acanthodians, from the Lower Carboniferous Mansfield group of Victoria (Woodward, 1906), and he also published the first descriptions of the group from Antarctica (Woodward, 1921). Isolated acanthodian scales and spines occur widely in Devonian rocks of eastern and central Australia (Fig. 1), and in recent years some well-preserved articulated acanthodians have been described from southeastern Australia (e.g. Long, 1983a, 1986a). The best-known locality is Mount Howitt in east central Victoria, which is the type locality for the genus *Culmacanthus* Long 1983, of which additional material is described in this paper. With these two new species the genus *Culmacanthus* is now known from three localities in southeastern Australia, and one locality in Antarctica (Fig. 1). Its distribution pattern matches that seen in several other taxa of Devonian fishes, the palaeogeographic significance of which is discussed below. All described specimens are housed in the Commonwealth Palaeontological Collection (prefix CPC), Bureau of Mineral Resources,

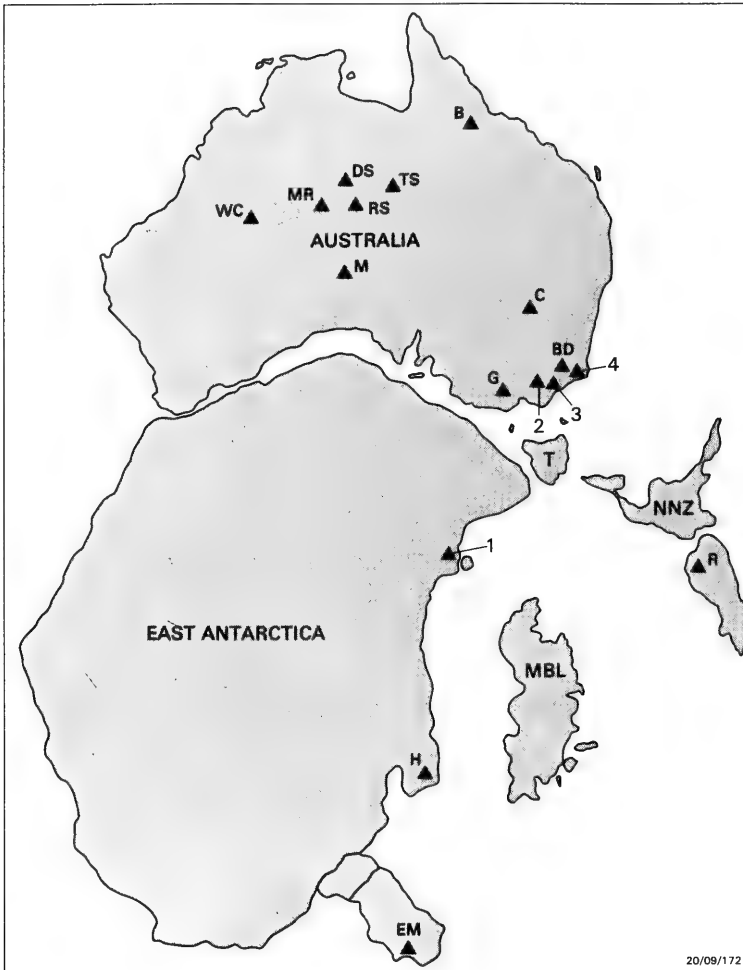


Fig. 1. Reconstruction of East Antarctica against Australia, modified from the Gondwana reconstruction of Lawver and Scotese (1987), showing the main localities of Devonian acanthodian fishes in the southwest Pacific region. Numbered localities are the only known occurrences of culmacanthid acanthodians, as dealt with in this paper; 1, Mount Crean, Lashly Range, southern Victoria Land (*Culmacanthus antarctica* sp. nov.); 2, Mount Howitt, east central Victoria (*Culmacanthus stewarti* Long); 3, Freestone Creek, east Gippsland, (culmacanthid indet.); 4, Pambula River, southeastern New South Wales (*Culmacanthus pambulensis* sp. nov.). Other abbreviations are: B, Broken River, Queensland; BD, Burrinjuck Dam, New South Wales; C, Cobar area, Darling Basin; DS, Dulcie Syncline, Georgina Basin; EM, Crashsite Quartzite, Ellsworth Mountains; G, Grampians, western Victoria; H, Horlick Formation, Ohio Range; M, Munyarai, Officer Basin; MBL, Marie Byrd Land, West Antarctica; MR, Macdonnell Range, Amadeus Basin; NNZ, New Zealand, North Island; R, Recfton, New Zealand, South Island; RS, Ross River Syncline, Amadeus Basin; T, Tasmania; TS, Toko Syncline, Georgina Basin; WC, Wilson Cliffs, Canning Basin.

Geology and Geophysics, Canberra, A.C.T. Material of the type species *Culmacanthus stewarti* Long is housed in the Museum of Victoria (prefix NMP).

PREVIOUS INVESTIGATIONS

The first samples of the Antarctic Aztec fish fauna were collected by F. Debenham on the British Antarctic 'Terra Nova' expedition of 1910-13, from moraine material at

Granite Harbour on the coast of southern Victoria Land. They were described by Woodward (1921), who identified eight taxa of Devonian fishes, including isolated acanthodian scales which were said to resemble those of *Cheiracanthus murchisoni* from the Middle Devonian of Scotland. *In situ* remains of the Aztec fauna were not discovered until the Trans-Antarctic Expedition of 1955-58 (see Gunn and Warren, 1962), when Devonian fish remains were collected from the Aztec Siltstone at three localities (Lashly Mountains, Mount Feather, Boomerang Range) in the region of the Skelton Névé of southern Victoria Land (locality 1, Fig. 1). Other fish remains from the same general area were recorded by Matz and Hayes (1966) and Matz, Pinet and Hayes (1972; their 'Fortress Formation') from west Beacon Heights, Mount Fleming, Mount Crean, and Aztec Mountain, and by Helby and McElroy (1969) from Aztec Mountain. Gunn and Warren's collection was described by White (1968). The most extensive collections of Devonian fishes from the Aztec Siltstone were made by Antarctic expeditions from Victoria University of Wellington in 1968-69 (see McKelvey *et al.*, 1972), and in 1970-71 (VUWAE 15), when the specimen described below was collected. Detailed measured sections through the Aztec Siltstone at most of the fossil localities are given in Askin *et al.* (1971) and Barrett and Webb (1973). Recent publications dealing with or discussing the Aztec fish fauna include Ritchie (1971a, b, 1974, 1975). Young (1982, 1988), and Grande and Eastman (1986). A detailed locality map and a summary of the 24 known localities for the Aztec Siltstone fish fauna are given in Young (1988).

In the material collected by Gunn and Warren, White (1968) identified several types of acanthodian spines. Ribbed spines from the upper fossiliferous horizon in the Boomerang Range were referred to a new species (*G. warreni*) of the genus *Gyracanthides*, originally described by Woodward (1906) from the Early Carboniferous of Mansfield in Victoria. A new genus and species (*Antarctonchus glacialis* White) was erected for long slender acanthodian spines with numerous strong longitudinal ribs. White also determined as an acanthodian some small spine fragments originally described by Woodward (1921) as an antiarch (*Byssacanthoides debenhamsi* Woodward). In addition to these named taxa from the Middle-Late Devonian, V. T. Young (1986) has referred to the genus *Machaeracanthus* two types of Early Devonian acanthodian spines from the Horlick Formation in the Ohio Range of the southern Transantarctic Mountains, and a similar specimen is recorded from the Ellsworth Mountains (H, EM, Fig. 1).

In southeastern Australia acanthodian remains have been known from Victoria for some time (Woodward, 1906; Hills, 1931). More recently Long (1983a) described *Culmacanthus stewarti* from the Mount-Howitt fish locality, and figured one incomplete specimen from Freestone Creek in eastern Victoria as a probable culmacanthid (localities 2, 3, Fig. 1). A second acanthodian from the Mount Howitt fauna (*Howittacanthus*) was described by Long (1986a). A summary of the Victorian Devonian fish localities and their biostratigraphy is given in Long (1983b; fig. 1). Placoderms associated with *Culmacanthus* are also described by Long (1984) and Long and Werdelin (1986).

Over the state border, in southeastern New South Wales, Devonian fish remains were discovered in the Eden-Pambula area in 1978 (locality 4, Fig. 1), and a preliminary report (Young, in Fergusson *et al.*, 1979) identified four assemblages ranging in age probably from latest Middle Devonian (Givetian) through to the end of the Late Devonian (Famennian). One specimen, first described as a possible osteichthyan plate (Fergusson *et al.*, 1979: 103), is referred below to *Culmacanthus* on the basis of Long's (1983a) description of this genus. Further collecting in 1979 produced the new specimens described below. Other described elements of the Devonian fish faunas from the south coast of New South Wales include sharks from the Bunga Beds near Bermagui (Young, 1982), and an asterolepid antiarch from the Pambula River area (Young, 1983). Elements still to be described include bothriolepid and remigolepid antiarchs, phyllo-

lepid placoderms, and rhipidistian and other acanthodian remains. A locality map of the region is given in Young (1983: fig. 1).

SYSTEMATIC DESCRIPTIONS
Subclass ACANTHODII Owen
Order CLIMATIIDA Berg
Suborder DIPLACANTHOIDEI Miles 1966
Family CULMACANTHIDAE Long 1983
Genus *Culmacanthus* Long

Remarks: The above taxa are defined in Denison (1979) and Long (1983a).

Culmacanthus antarctica sp. nov.
(Figs. 2A, 3A)

1986a. 'culmacanthid cheek plates' (*pars*) Long, p. 13.

Holotype: CPC 26579, a right cheek plate preserved in part and counterpart.

Locality: Mount Crean, east side of the Lashly Range (77° 53' S, 159° 33' E), southern Victoria Land, Antarctica (locality 8 of Young, 1988: fig. 3).

Horizon: From the lower part of the Aztec Siltstone, within 40 m of the base of the formation (unit 5 of section L2 measured by Askin *et al.*, 1971; for a detailed discussion of the stratigraphy of the Mount Crean section see Young, 1988).

Diagnosis: A *Culmacanthus* possessing a cheek plate in which the infraorbital sensory canal passes off the ventral margin, the anteroventral corner is pronounced, the ventral lamina is longer and deeper than the dorsal lamina, and the plate is fairly flat, ornamented with closely spaced ridges and elongate tubercles with a flat external surface, and has a breadth/length index of about 79.

Remarks: Long (1983a) did not present a diagnosis for the type species *C. stewarti*, but compared to the Antarctic specimen there are obvious differences in the form of the cheek plate. In the type species the coarser ornament of more widely spaced ridges have a rounded rather than flat dorsal surface, the anterior margin of the plate is distinctly notched (Fig. 3B), there is a more pronounced angle between the dorsal and lateral laminae, the dorsal lamina is longer than the lateral, and the latter has a concave external surface. The most obvious difference is in the course of the main sensory groove, with both dorsal and ventral sections passing off the anterior margin of the plate.

The articulated remains of *C. stewarti* show that *Culmacanthus* was a diplacanthoid acanthodian with two dorsal fin-spines, paired pectoral and pelvic spines, and an anal spine (Fig. 5). These spines are ornamented with approximately nine coarse longitudinal ribs, and they have a deeply inserted base which is finely striated (Long, 1983a). It is possible therefore that some of the similar acanthodian spines from the Aztec Siltstone named by White (1968) as *Antarctonchus* may also belong to *Culmacanthus*. Long (1983a) has already suggested this for the isolated spines from Freestone Creek in Victoria named *Striacanthus* by Hills (1931). However, in the absence of articulated material demonstrating this, and because the histology of *Culmacanthus* spines is at present unknown, I follow Long's (1983a) procedure here, and leave *Antarctonchus* as a form genus for isolated spines, until such time as new material or more detailed study can demonstrate that the spines and dermal cheek plates come from the same fish.

Description: The holotype and only referred specimen is an isolated dermal cheek plate preserved in part and counterpart. The external impression was cleaned in dilute hydrochloric acid to remove the bone, and the distinctive ornament is well displayed in a latex cast (Fig. 2A). The counterpart is preserved as bone except for the posterolateral corner, which is an impression of the visceral surface. All margins of the plate are

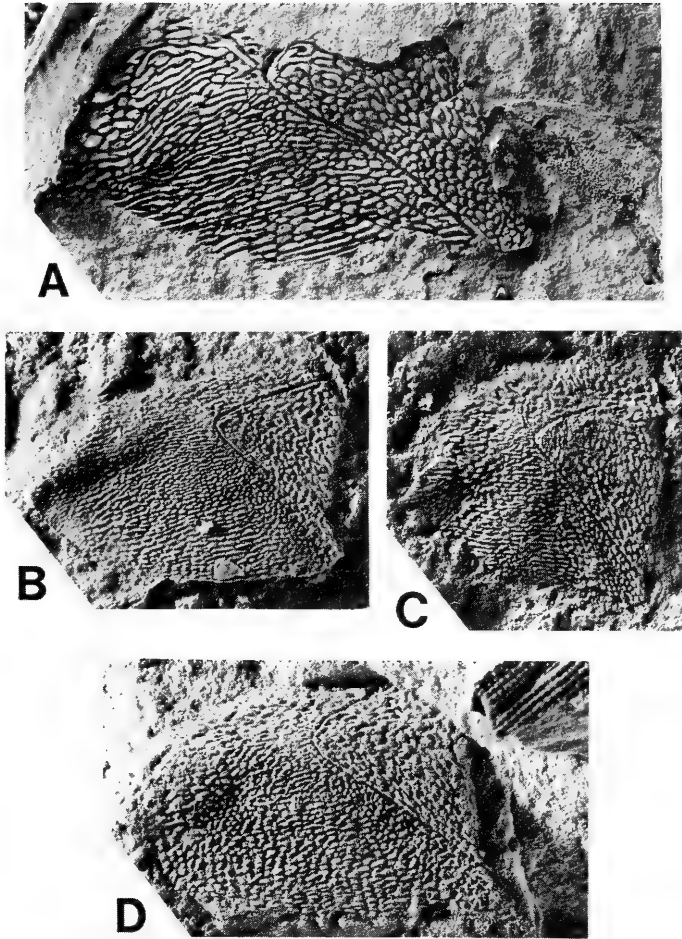


Fig. 2. Right cheek plates of *Culmacanthus* in external view (latex casts whitened with ammonium chloride). **A**, *C. antarctica* sp. nov., holotype, CPC 26579 (x4). **B-D**, *C. pambulensis* sp. nov.; **B**, holotype, CPC 26580 (x4); **C**, CPC 26581 (x3); **D**, CPC 26582 (x4).

complete. The orientation of such isolated cheek plates is not readily determined, but following the work of Long (1983a) on the articulated Mount Howitt material of *C. stewarti*, the position of the short sensory groove (ifc.b, Fig. 3A) shows this to be a right dermal cheek plate. It is about 21.5mm long, and relatively deep (breadth/length index of 79). The anterior margin lacks the distinct orbital notches seen in the type species (Fig. 3B), and slopes anteroventrally to a pronounced anteroventral corner, behind which the infraorbital sensory groove passes off the ventral margin of the plate.

The plate has a slight flexure at the level of the posterior angle of the infraorbital sensory groove (ifc, Fig. 3), as previously described by Long (1983a), but overall it is a much flatter plate than in the Victorian species (based on NMP 159838). The inflexion of the infraorbital groove is placed high on the plate, which gives it a much larger lateral than dorsal lamina. The short posterodorsal sensory groove (ifc.b), as described for *C. stewarti*, was interpreted by Long (1983a) as possibly part of the preopercular sensory groove, but this groove in fishes normally passes posterolaterally across the cheek towards the mandibular joint. It is considered more likely that the short groove on the

cheek plate of *Culmacanthus* is equivalent to the 'postero-median branch of the infra-orbital canal' of *Diplacanthus* identified by Watson (1937; 'central sensory line' of Miles, 1966).

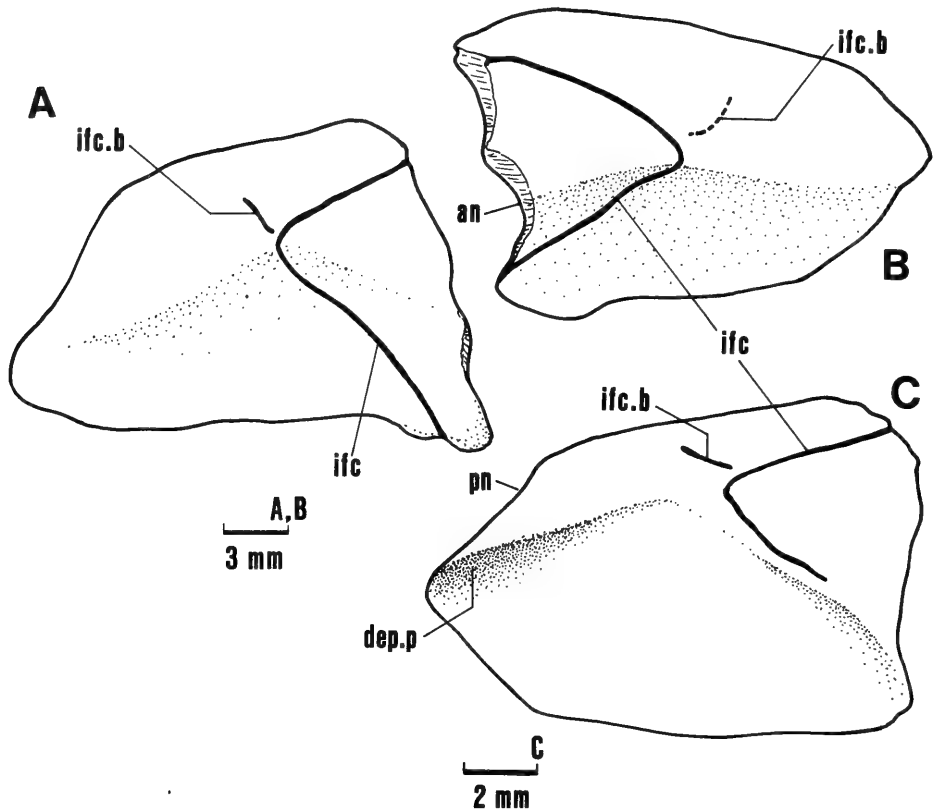


Fig. 3. Cheek plates of *Culmacanthus* restored in external view. A, a right plate of *C. antarctica* sp. nov., after the holotype, CPC 26579; B, *C. stewarti* Long, a left plate, restored after a latex cast of NMV P159838 (see Long 1983a: fig. 4B); C, a right plate of *C. pambulensis* sp. nov., after the holotype, CPC 26580. an, anterior notch; dep.p, posterior depression; ifc, infraorbital sensory groove; ifc.b, posterodorsal ('central') branch of infra-orbital sensory groove; pn, posterior notch.

The distinctive ornament of *C. antarctica* sp. nov. comprises cusp-like tubercles which change into elongate ridges towards the posterior margin. In front of the sensory groove the surface of each cusp slopes upwards from the bone surface in a posterodorsal direction, at which a point may be developed, to give some cusps a triangular shape. Behind the sensory groove the more elongate cusps and short ridges have their pointed ends directed posteriorly, and are separated by deep, narrow grooves. Most of the ridges and tubercles are ornamented with up to four very fine ridges which may branch towards the anterior. Typically the elongate primary ridges of the ornament which are most pronounced on the posterior half of the plate have a flat or slightly concave upper surface, with the edges clearly marked by two fine ridges. Compared to *C. stewarti* (NMP 159838, Fig. 3B) the ornament is more finely sculptured, with the ridges and tubercles more closely spaced. In the type species (Long, 1983a, fig. 4A, B) the ornament is

coarser, with wider intervening spaces, and scattered tubercles along the ventral margin. However some fine striations are also visible on the more elongate tubercles and ridges, and in larger specimens there are fewer tubercles and longer ridges (Long, 1983a, fig. 2B).

Culmacanthus pambulensis sp. nov.

(Figs. 2B-D, 3C, 4)

1979. 'osteichthyan, with an ornament of delicate subparallel ridges' Young, in Ferguson *et al.*, p. 103.

1983a. 'dermal cheek plate . . . from Pambula River' Long, p. 54.

1986a. 'culmacanthid cheek plates' (*pars*) Long, p. 13.

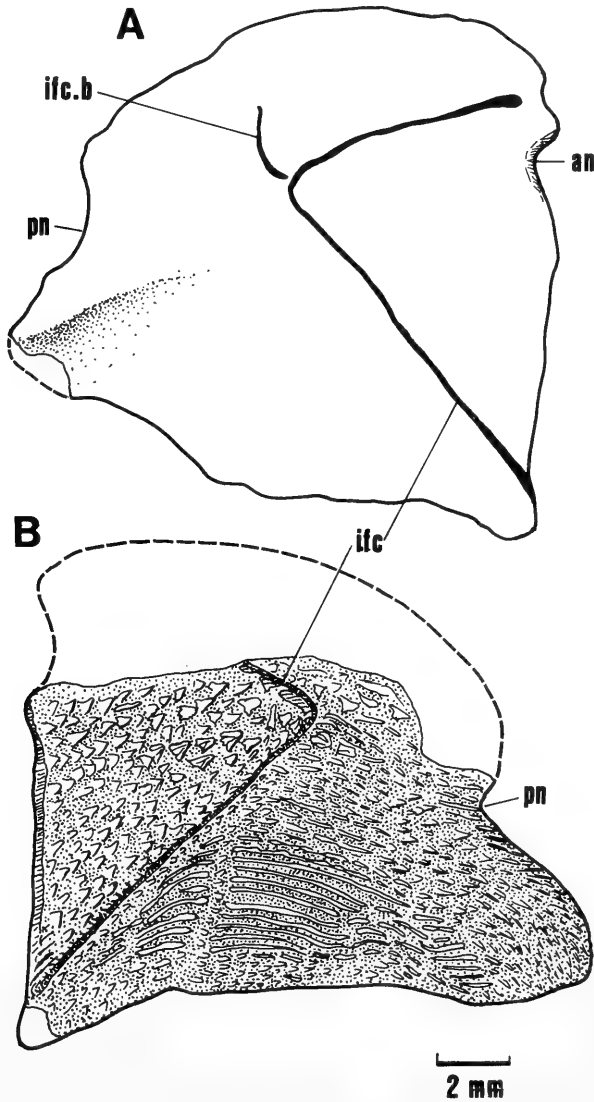


Fig. 4. *Culmacanthus pambulensis* sp. nov., check plates in external view. A, a right plate, after CPC 26581; B, a left plate, after CPC 26583. For abbreviations see caption to Fig. 3.

Name: Abbreviated from the nearby town of Pambula, N.S.W.

Holotype: CPC 26580, a right cheek plate.

Other Material: Right (CPC 26581, 26582) and left (CPC 26583) cheek plates, and another ornamented fragment (CPC 17004).

Locality: Grid Reference 7510E 59081N on the Pambula 1:25000 Sheet, about 5km west of the town of Pambula on the south coast of New South Wales (see Young, 1983: fig. 1).

Horizon: Facies 3 of the Boyd Volcanic Complex, as described by Fergusson *et al.* (1979).

Diagnosis: A *Culmacanthus* possessing a fairly flat cheek plate in which the infraorbital sensory canal passes off the anterior margin, the anterior margin has only shallow or indistinct notches, the ventral lamina is considerably deeper than the dorsal lamina, the closely spaced ornament comprises fine ridges and elongate tubercles, and the breadth/length index varies between at least 68 and 94.

Remarks: Apart from the obvious and consistent differences in ornament, the three measurable specimens of *C. pambulensis* are broader than in the type species, although for the smallest example described below (CPC 26580) this difference is only slight. Long (1983a: 56) regarded such differences in proportion to be generic rather than specific features, but the variability in proportions is clear in this new species, and the other obvious similarities indicate that these specimens are properly referred to the genus. *C. pambulensis* resembles *C. antarctica* rather than *C. stewarti* in the flatter cheek plate, the longer and steeper disposition of the ventral section of the infraorbital sensory groove, and the absence or slight development of notches on the anterior margin. It differs from *C. antarctica* but resembles *C. stewarti* in the fact that the infraorbital groove passes off the anterior margin of the plate. Long (1983a) noted other specimens from Freestone Creek in eastern Victoria with broader proportions than the type species, as in *C. pambulensis* sp. nov., but that material is at present too poorly known to permit useful comparisons.

Description: All specimens are preserved as external moulds, which have been studied by latex casting. The holotype (Figs 2B, 3C) is the smallest specimen (length 14mm), and the most complete. The infraorbital groove has an attenuated ventral section, not seen in other examples, and interpreted as an individual variation. The posterodorsal branch is a short separate groove (ifc.b, Fig. 3C) as in other examples with this part preserved. Compared to *C. stewarti* (represented by NMP 159838) the cheek plate is rather flat. The lateral lamina is slightly concave near the posterior corner (dep.p), and there may be another shallow depression running anteroventrally beneath the ventral section of the infraorbital canal, but otherwise both laminae of the plate are gently convex. The posterior depression is seen in all available specimens of this species (Fig. 2B-D). Two larger specimens are unusually broad (Fig. 4), although their posterior margins are somewhat irregular. This may be due to incomplete preservation, but an irregular margin abutting against small plates at the posterior margin of the gill cover is considered more likely. It is possible that breadth of the plate increased allometrically with size, but evidence against this is provided by *C. stewarti*, where the largest plate (Long, 1983a: fig. 2) is also the most elongate (erroneously stated as 'twice as broad as long' by Long, 1983a: 56). In both CPC 26581 and 26583 the lateral lamina projects posteriorly, as in *C. antarctica* described above, and all specimens with the region preserved show a shallow notch on the posterodorsal margin (pn, Figs 3C, 4). The general similarity of the delicate ornament in the two largest examples (Figs 2C, 4B) to other specimens from this locality suggests that they are conspecific, and that proportions of the cheek plate are more variable than previously thought. In the type species only three cheek plates have been described, with two from one individual, so further material is required to assess the variability of this feature.

The ornament in *C. pambulensis* is much finer than in *C. antarctica* or *C. stewarti*. Small triangular tubercles with posterodorsally directed points predominate in front of the sensory canal, as in the other species, and behind the canal these tubercles become more elongate and posteriorly directed (Fig. 2B, D), and may coalesce into subparallel ridges (Figs 2C, 4B). Specimen CPC 17004 previously mentioned by Young (in Ferguson *et al.*, 1979) is referred to *C. pambulensis* only on its similar ornament, since no sensory grooves are preserved.

DISCUSSION

Morphology and Systematics

Denison (1979) included two genera in his family Diplacanthidae — *Diplacanthus* Agassiz and *Gladiobranthus* Bernacsek and Dineley. Long (1983a) preferred to place *Gladiobranthus* as closely related to *Uraniacanthus*, as originally suggested by Bernacsek and Dineley (1977). However Bernacsek and Dineley supported this relationship by suggesting that *Uraniacanthus* may have possessed dermal plates and prepectoral spines, even though Miles (1973) expressed no doubt from detailed study of the specimens that these structures were absent in *Uraniacanthus*. Bernacsek and Dineley (1977) also inferred that *Gladiobranthus* had dentigerous jawbones, but the holotype shows anterior circum-orbital bones, indicating proximity of the snout, but no sign of ossified jaw elements. These may have been lost, but the available evidence favours the interpretation that *Gladiobranthus* did not possess them. Supporting this, and the climatiid affinities of *Gladiobranthus*, are the presence of dermal shoulder plates, prepectoral spines, and the large plates and tesseræ of the head (Denison, 1979). The scapulocoracoid of *Gladiobranthus* was restored by Bernacsek and Dineley (1977) as a low and broad element with a truncated dorsal end, but the specimen (Bernacsek and Dineley, 1977: pl. 7) suggests a higher narrow dorsal termination, with an anterior ridge and expanded posterior ventral part, just as in *Diplacanthus*. The two enlarged circumorbitals, one at the posterodorsal corner of the orbit, are special features shared with *Diplacanthus*, as Denison (1979) noted. Thus I follow Denison (1979) in considering *Gladiobranthus* better placed as a diplacanthoid acanthodian, rather than an ischnacanthid (see also Long, 1986b: 335).

Long (1983a) modified Miles's (1966) diagnosis of the Diplacanthoidei to include *Culmacanthus*. The most significant resemblances (Fig. 5) are in the large dermal cheek plate crossed by the infraorbital sensory groove, the relatively deep body, and the deeply inserted spines. *Culmacanthus* differs from *Diplacanthus* primarily in the larger size of the cheek plate, the absence of intermediate fin-spines, the probable absence of a mandibular bone, the high narrow scapulocoracoid, and the structure of the dermal shoulder girdle, with an unpaired loral plate, and no spines attached to the paired pinnals. Long (1983a) suggested that the cheek plate of *Culmacanthus* may have been homologous to the postorbital or preopercular bones of *Diplacanthus*, but since there is no sensory groove passing posterolaterally across the plate it seems more likely that it is only a much enlarged postorbital, which extended more dorsally than the corresponding bone of *Diplacanthus*, to include the junction of the posterodorsal branch of the infraorbital canal at its ossification centre. For functional reasons it is likely that the cheek plate only covered the region of the palatoquadrate, with a flexible hyoid gill cover situated between it and the scapulocoracoid. The well-ossified branchiostegal rays in this position in *Gladiobranthus* may be interpreted as a symplesiomorphy, by outgroup comparison with climatiids. It is unclear from Long's (1986b) analysis of the dermal shoulder girdle of climatiids whether the condition in *Culmacanthus* is primitive or specialized, but if intermediate fin-spines and pectoral spines firmly attached to the pinnal plates are

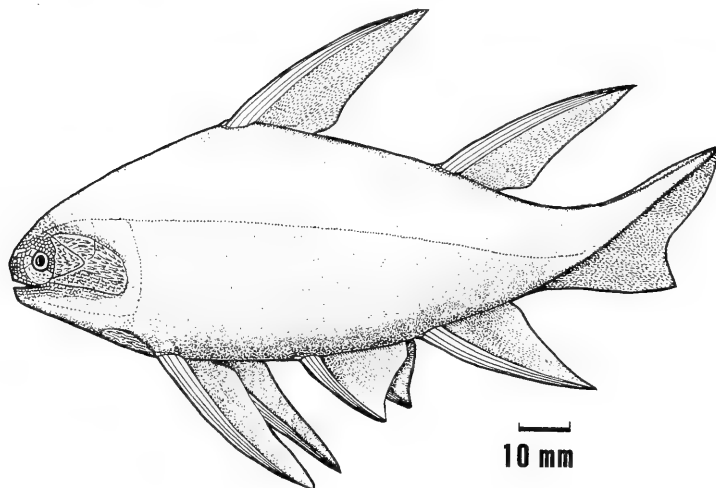


Fig. 5. *Culmacanthus stewarti* Long. Restoration of complete fish, slightly modified after Long (1983a: fig. 9).

synapomorphies of 'higher climatiids' as he suggests (1986b: 337), then *Diplacanthus* would be more closely related to some Early Devonian climatiids than to *Culmacanthus*. All students of acanthodian evolution have acknowledged the small number of reliable characters available to define the major groups, and in the case of *Culmacanthus* the main evidence still to be forthcoming concerns the histology of the scales and fin spines. This is not known in the Victorian material because the bone is badly weathered. Better-preserved material permitting histological study can be expected to clarify the relationships of this form to the Euramerican diplacanthids.

Biostratigraphy

A biostratigraphic analysis of the Aztec fish fauna based on the distribution of antiarchs was presented by Young (1988), in an attempt to resolve previous differences of opinion about its precise age. Woodward (1921) first proposed a Late Devonian age on the evidence of the antiarch *Bothriolepis*, and associated shark and large osteolepid scales, and Gross (1950) reached the same conclusion. However White (1968) noted the apparent mixing in the Aztec fauna of groups that elsewhere range in age from Middle or even Early Devonian, to Late Devonian or Early Carboniferous, and on this basis he favoured a late Middle Devonian rather than early Late Devonian age. Ritchie (1975) added the placoderms *Phyllolepis* and *Groenlandaspis* to the faunal list, and proposed a younger Late Devonian age. Young (1982) suggested correlations with southeastern Australia based on the sharks in the Aztec fauna, which were consistent with Helby and McElroy's (1969) assessment of a Frasnian age for a palynoflora dominated by the spore *Geminospora lemurata*. This species was assessed by Playford (1983) to have a known biostratigraphic range from early or middle Givetian to late Frasnian or early Famennian. However in Europe McGregor (1979) has estimated a much greater (Emsian-Famennian) range for the possibly synonymous *Geminospora svalbardiae*, so the spore evidence at present only dates the Aztec Siltstone within broad limits.

Other evidence supporting comparisons between the Aztec succession and the Devonian sequences of southeastern Australia include the acanthodian *Gyracanthides* described from Victoria by Woodward (1906), and from the upper Aztec succession by White (1968), the antiarch *Pambulaspis* from southeastern New South Wales (Young,

1983) and described by Young (1988) from the top of the Aztec, and the culmacanthid acanthodians just described. *Culmacanthus antarctica* is associated with turiniid thelodont scales and bothriolepid antiarchs, and may therefore be the oldest known species, since no thelodonts have been recorded from the successions in eastern Victoria and the south coast of New South Wales. Young (1988) noted that the association of bothriolepid antiarchs with thelodont scales is currently known from only one other locality, in the Hatchery Creek fauna from near Wee Jasper, New South Wales (Young and Gorter, 1981). A post-Emsian age for this fauna is indicated by conodonts in the underlying Murrumbidgee Group (*serotinus* Zone or slightly younger), but a younger age limit is uncertain. In contrast the two Australian species of *Culmacanthus* are associated with phyllolepid placoderms, which occur widely in southeastern Australia, in all other post-Emsian faunas currently known which contain placoderms. From eastern Victoria and the southern coast of New South Wales only the Bunga Beds fauna (Young, 1982) lacks phyllolepid, but this is an impoverished fauna in which placoderms have not been found. The abundant placoderms in the Aztec Siltstone includes phyllolepid only in the highest horizons, and Young (1988) suggested that the base of the phyllolepid zone preserved in the Aztec Siltstone, and the first appearance of the antiarch *Pambulaspis*, may be older than the occurrence of related forms in eastern Victoria and southeastern New South Wales.

In eastern Victoria, Long (1983b: fig. 3) used the appearance of *Bothriolepis* and phyllolepid to define the base of the Upper Devonian, with *Groenlandaspis* occurring in the latter half of the Frasnian. The fish fauna in the Boyd Volcanic Complex (Fergusson *et al.*, 1979; Young, 1982, 1983), which as well as *Culmacanthus* includes at least four taxa (*Bothriolepis*, *Pambulaspis*, *Antarctilamna*, phyllolepid) in common with the Aztec fauna, apparently lacks *Groenlandaspis*. The fact that both *Bothriolepis* and *Groenlandaspis* in the Aztec Siltstone occur in the lowest fossiliferous beds, and far below the phyllolepid zone, indicates again that these are earlier occurrences than the range of these forms in southeastern Australia. In western New South Wales and central Australia groenlandaspid arthrodires are associated with thelodont scales in the *Wuttagoonaspis* fauna (Ritchie, 1975; Turner *et al.*, 1981) but the only antiarchs from this fauna are asterolepids (Young, 1984a), so this appears to be older than the Aztec fauna. An Early-Middle Devonian age has been assigned to the *Wuttagoonaspis* fauna, but the occurrence of the Antarctic shark *McMurdochodus* (Turner and Young, 1987), otherwise only known from the Aztec Siltstone, may indicate less difference in age to the lower Aztec fauna than previously thought.

In southeastern New South Wales the Boyd Volcanic Complex provides evidence for a minimum age for the Aztec fauna, because the overlying Merrimbula Group contains a marine invertebrate fauna of probable late Frasnian age (e.g. Roberts *et al.*, 1972). A single early Late Devonian marine transgression in southeastern Australia may be assumed, for which the oldest reliable age is late Frasnian based on upper *gigas* Zone conodonts (Pickett, 1972). This implies a late Givetian — early Frasnian age for the underlying fishes and equivalent faunas in eastern Victoria, and an approximate younger limit to the age of the Aztec Siltstone based on the phyllolepid placoderms in its upper horizons. However, although the Victorian and southern New South Wales fish successions are broadly equivalent in age, detailed taxonomic work on placoderms common to the two areas (e.g. bothriolepids, phyllolepid) has not yet been done. The results of the present study show specific differences between the *Culmacanthus* remains from the two sequences, which may provisionally be regarded as indicating difference in age, but there is as yet no reliable evidence on which occurrence is the older. It should also be noted that according to Long (1983a) the culmacanthid from Freestone Creek is not conspecific with *C. stewarti*, although other species (e.g. *Bothriolepis cullodenensis* Long,

1983b) are shared between the two assemblages. Further detailed taxonomic work on the placoderms in the various faunas from southeastern New South Wales and Victoria should clarify the precise correlation between the two sequences.

Biogeography

The biogeography of the Aztec fish fauna has been discussed previously by Young (1981, 1982, 1984b, 1988) and Grande and Eastman (1986), whilst Long (1986a) has recently commented on acanthodian biogeography in the Devonian. The presence of species of *Culmacanthus* in southeastern Australia and southern Victoria Land, Antarctica, but nowhere else, corresponds with the pattern indicated previously by the elasmobranch *Antarctilamna* (Young, 1982), the antiarch *Pambulaspis* (Young, 1988), and possibly the placoderm *Antarctaspis* (if a relationship to phyllolepid is confirmed; see Young, 1987: fig. 5). These distributions are all consistent with grouping the two regions together in an 'East Gondwana Province' as proposed by Young (1981). It should also be noted that the only two fish assemblages recorded from any continent in which bothriolepid antiarchs and turiniid thelodonts are associated are in southeastern Australia and southern Victoria Land, and species group interrelationships for the cosmopolitan antiarch *Bothriolepis* again indicate an Antarctica-Australia connection (Young, 1988). All these fishes inhabited freshwater environments, but this does not mean that they were unable to cross marine barriers, and in this respect no specific data are provided on the Devonian palaeogeography of the Antarctic-Australian region. It is relevant to note however that the distinctive dermal cheek plates of *Culmacanthus* have not been found in the well-studied fish faunas from the classic Old Red Sandstone localities of the Northern Hemisphere, but that they do occur in the Southern Hemisphere in two areas separated today by the vast expanse of the Southern Ocean, and a distance in excess of 4500km, which exceeds by a considerable margin the 3000km-wide ocean postulated by some authors to have separated Gondwana from Euramerica during the Late Devonian. Thus the evidence of culmacanthid distribution is entirely consistent with reconstructions of a Palaeozoic Gondwana which minimize or remove oceanic barriers by juxtaposing southeastern Australia and Victoria Land (Fig. 1).

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A new Australian Species of *Argyrodes* Simon (Araneoidea: Theridiidae) which preys on its Host

M. R. GRAY and G. J. ANDERSON

GRAY, M. R., & ANDERSON, G. J. A new Australian species of *Argyrodes* Simon (Araneoidea: Theridiidae) which preys on its host. *Proc. Linn. Soc. N.S.W.* 111 (1), 1989: 25-30.

A new species of the web-parasite spider genus *Argyrodes* is described. This spider has a close association with its only known and larger host, the tent web spider *Achaearanea mundula*. It is a predator of both the host and its eggs and young and makes use of the host's leaf retreat as a shelter for its egg sac.

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INTRODUCTION

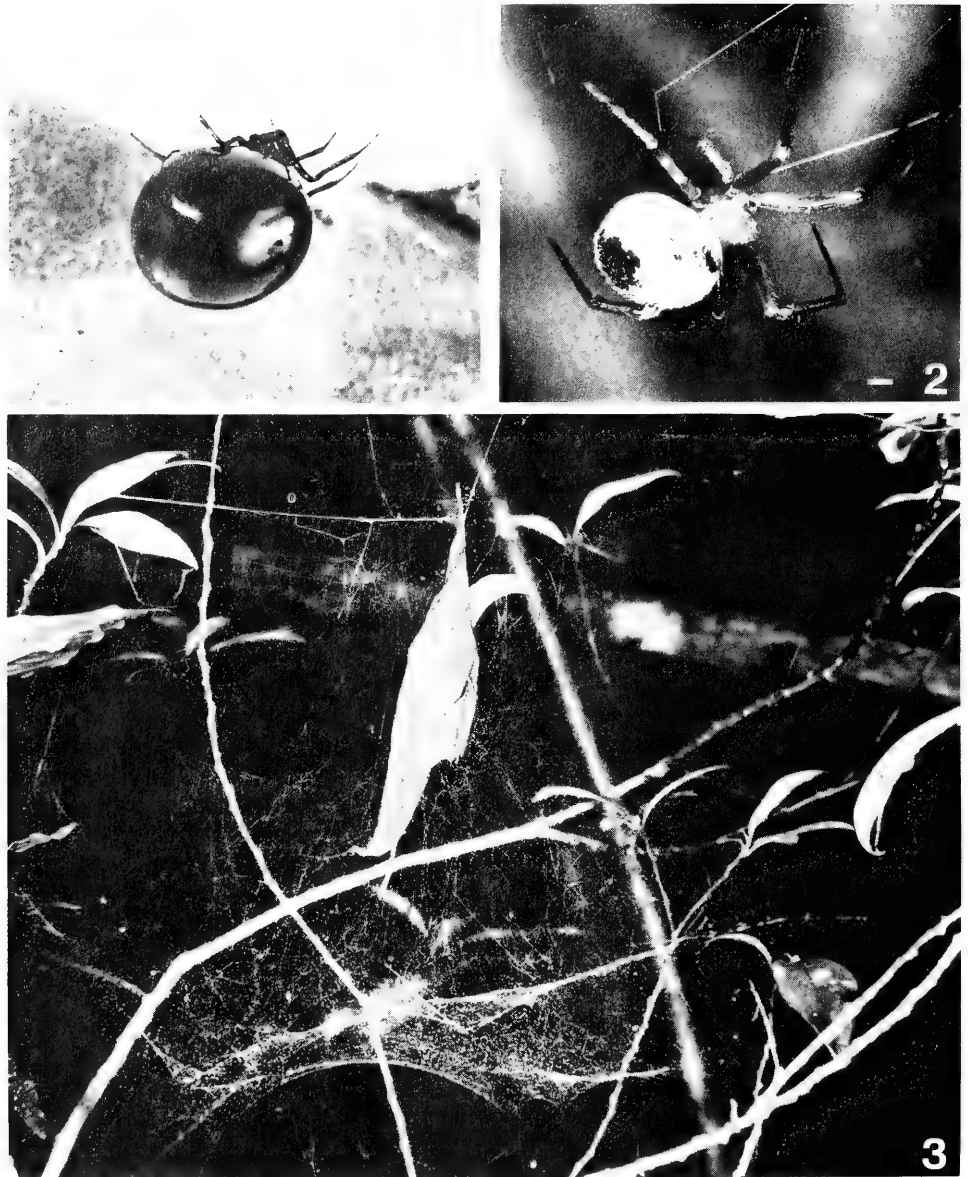
Large, complex or communal spider webs may harbour a variety of invertebrates as temporary or semi-permanent residents. The small spiders of the worldwide genus *Argyrodes* Simon (Exline and Levi, 1962) are common residents in the webs of araneoid spiders. Most live either as commensals which take small prey ignored by the host spider or kleptoparasites which steal prey captured by the host (Robinson and Robinson, 1973; Vollrath, 1979; Whitehouse, 1986). The host spider is often much larger (e.g. *Nephila* or *Argiope* spp.) than the resident *Argyrodes* so that competition for food resources would not seem likely. Several studies have shown, however, that prey stealing can have such an impact that some hosts abandon their webs and build elsewhere (Robinson and Robinson, 1976; Vollrath, 1981; Rypstra, 1981). A few temperate zone species of *Argyrodes* have become predators of both their hosts and spiderlings (Kaston, 1965). Trail (1980) has observed host predation by *A. fictitium* (Hentz) and *A. baboquivari* Exline and Levi upon linyphiid host spiders including *Frontinella* sp., and the uloborid *Philliponella oweni* Chamberlin. *A. trigonum* (Hentz) is a predator of the araneids *Metepeira labyrinthica* Hentz and *Mecynogea lemniscata* Walckenaer and the linyphiid *Neriene radiata* Walckenaer (Wise, 1982; Larcher and Wise, 1985). Whitehouse (1986) noted predation by *A. antipodiana* O.P. — Cambridge upon its araneid host *Araneus pustulosus* Walckenaer while the host was moulting and virtually defenceless. Gray (1983) briefly reported upon a distinctive *Argyrodes* species from eastern Australia which showed host predation behaviour. A description of this spider and some behavioural observations are given below.

Argyrodes incursus new species

Figs 4-12

Types: Holotype male (KS 18359), Blackbutt Reserve, Newcastle, New South Wales, March 1986, G. Anderson. Paratypes: Allotype female (KS 18360), 3 females (KS 18361), data as above; 2 females (KS 12254-55), Upper Causeway and Couranga Track, Royal National Park, near Sydney, New South Wales, 4.3.1983, M. Gray and C. Horseman. Australian Museum coll.

Material examined: 2 females, Station 32, southwest of North Hummock, Lord Howe Island, New South Wales, 6.2.1971, M. Gray.



Figs 1-3. 1, *Argyrodes incursus*, 'engorged' female. 2-3, *Achaearanea mundula*: 2, female; 3, web. Scale lines: Figs 1-2, 1.0mm.

Diagnosis. Male palp with marginal coiled embolus, abdomen with dorsal scute. Female with orange-red spot on posterodorsal abdomen, abdomen rounded.

Male. Total length 2.18. Carapace length 0.90, width 0.63. Abdomen length 1.27, width 0.89. Leg 1 segment lengths: femur 1.07, patella 0.33, tibia 0.63, metatarsus 0.65, tarsus 0.45. Carapace, sternum and mouthparts dark brown. Abdomen dark brown dorsally and basally; remainder black apart from 4 small orange spots placed around the base of the spinnerets (Figs 4, 5). Femora and tibiae of legs 1 and 2 dark brown, femora 2 lighter

ventrally; remaining segments reddish brown. Legs 3 and 4 reddish brown, femora lightest. Cheliceral groove with 3 promarginal, 1 retromarginal teeth. A.M.E. largest, other eyes subequal. A.M.E. separated from each other by almost 2 diameters and from A.L.E. by 0.5 diameters; P.M.E. separated by 1.75 diameters. Clypeus with wide, transverse groove with numerous anterodorsally directed setae in and below groove. Transverse stridulatory ridges run across the posterolateral carapace lobes. Abdomen ovoid, widest behind middle and covered with a dorsal scute which extends anteriorly around the pedicel. A separate scute surrounds the spinnerets (Fig. 5). Dorsal pedicel margin strongly sclerotised with evenly spaced enlarged hair bases as stridulatory picks. Male palp (Fig. 11) with tightly coiled embolus (3 turns) surrounding a raised central tegular area. Embolus supported marginally by a membranous conductor. Radix apical, triangular and lying adjacent to the elongate median apophysis.

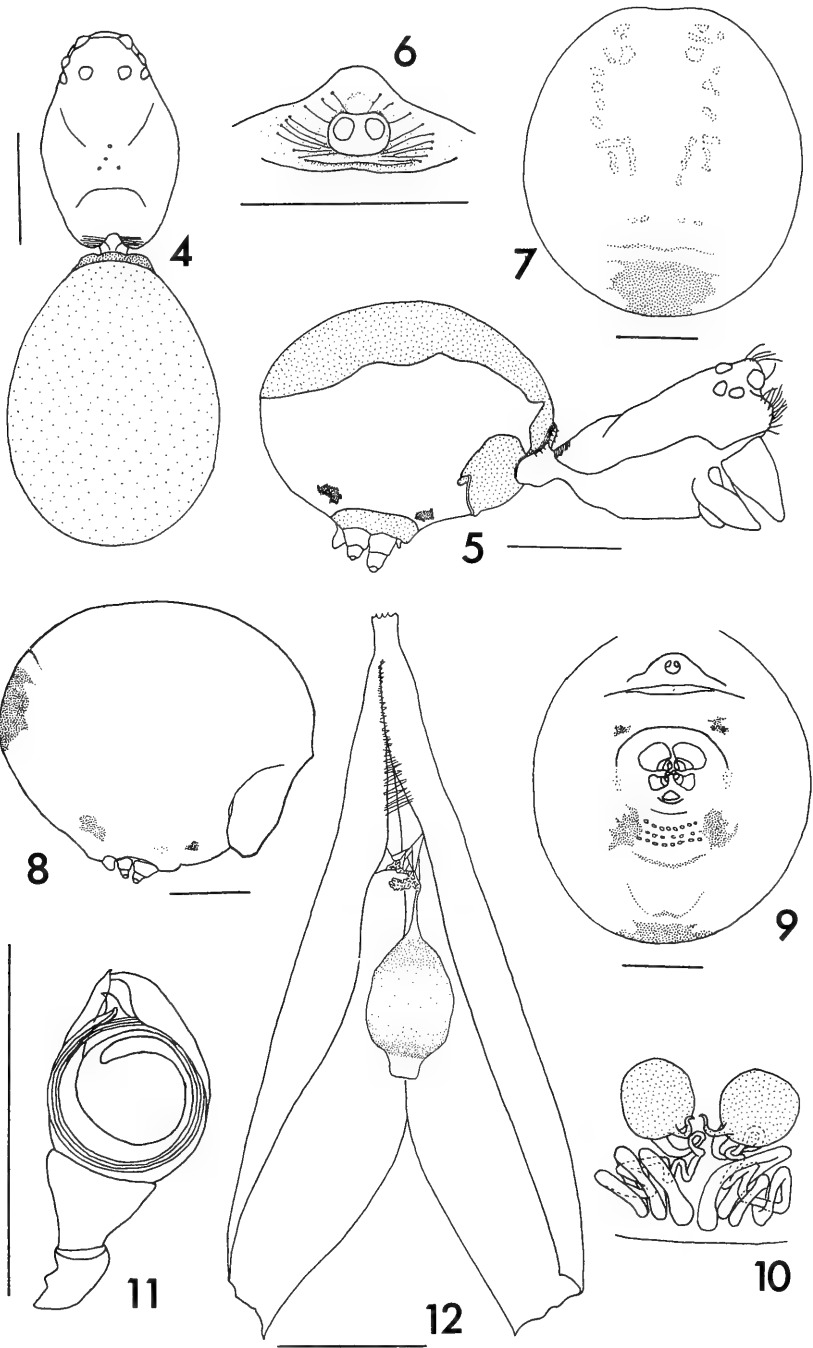
Female. Total length 3.36-4.33. Carapace length 1.29-1.35, width 0.88-0.92. Abdomen length 1.97-3.00, width 1.80-2.55. Leg 1 segment lengths: femur 1.20-1.25, patella 0.35-0.38, tibia 0.80-0.96, metatarsus 0.80-0.88, tarsus 0.50-0.62. Carapace, sternum and mouthparts dark brown. Legs 1-3 dark brown except metatarsi and tarsi which are reddish brown; leg 4 reddish brown. Abdomen ovoid to spherical, black with two indistinct rows of unpigmented spots anterodorsally. Posterodorsal abdomen with a large orange-red spot (occasionally divided into two unequal spots), bounded anteriorly and posteriorly by 1 or 2 narrow transverse orange bars (Figs 7, 8, 9). Four small irregular orange spots are grouped around the spinnerets. Epigynum (Fig. 6) a low mound surmounted by two ovoid fossae separated by about half a diameter. Internal genitalia (Fig. 10) with more or less spherical receptacula separated by about half their width. Spermathecae strongly convoluted.

MORPHOLOGY AND BEHAVIOUR

Both the shape and coloration of the abdomen of *Argyrodes incursus* are unusual. Elongation, shoulder or posterior tubercles and silvery ornamentation are common features of the *Argyrodes* abdomen (Exline and Levi, 1962). In unfed female specimens of *A. incursus* the abdomen is ovoid but expands considerably after feeding into a smooth sphere (Fig. 1). A prominent orange-red spot (absent in males) on the posterodorsal abdomen contrasts markedly with the shiny black coloration of the remainder. The function of this distinctive female colour pattern is not understood but may have some aposematic benefit, such as providing protection from other web-invading predators (e.g. mimetid spiders or wasps). A dark brown dorsal scute covers the male abdomen. The male palp is unusual in that the tegulum forms a central 'drum' around which the coiled embolus is wound.

A. incursus was always found in association with the 'tent web' spider, *Achaearanea mundula* (L. Koch). This spider (Fig. 2) is common in open forest habitats in eastern New South Wales and Queensland. Populations with which *A. incursus* was associated were located at Newcastle, Sydney, and Lord Howe Island, New South Wales. *Ach. mundula* builds a complex web consisting of a knockdown maze of threads above a finely woven horizontal sheet (Fig. 3). The curled leaf or litter retreat is placed at the centre of the knockdown maze; this provides a refuge for the spider and its egg sacs (up to 6). The webs are usually built among low understorey foliage. They also harbour commensal/kleptoparasitic species of *Argyrodes* plus uloborid and mimetid spiders; the latter are temporary residents, well known as predators of araneoid spiders.

Specimens of *A. incursus* were found singly inside the curled leaf retreats of *Ach. mundula* individuals during February and March. In the Newcastle population, however, the catching parts of 3 host webs harboured 8, 2 and 2 *A. incursus* individuals respec-



Figs 4-12. *Argyrodes incursus*. 4-5, male body: 4, dorsal; 5, lateral. 6, epigynum. 7-9, female abdomen: 7, dorsal; 8, lateral; 9, ventral. 10, female internal genitalia, dorsal. 11, male palp, ventral. 12, upper part of curled leaf retreat of *Ach. mundula* split open to show *A. incursus* egg sac near apex. Scale lines: Figs 4-11, 0.5mm; Fig. 12, 3.5mm.

tively, with the female hosts still occupying their retreats. Six observations were made of *A. incursus* females actually feeding upon the carcass of their host spider and/or its eggs or spiderlings, always within the leaf retreat. The dead host spiders were partially silk wrapped and their loosely woven egg sacs, if attacked, were torn open. In the Newcastle population *A. incursus* individuals also were found living inside the leaf retreats of empty *Ach. mundula* webs; in one case a male and female were found together. Some of these females had built single egg sacs at the leaf retreat apices (Fig. 12). Seven egg sacs were observed, all with the characteristic urn shape found in many species of *Argyrodes* (Exline and Levi, 1962). When present, the female sat above its sac on the stalk attachment.

At present *Ach. mundula* is the only known prey of *A. incursus*. The capacity for almost tick-like engorgement of the abdomen of *A. incursus* after feeding is particularly striking. Females may be able to survive and reproduce on the food reserves obtained from one successful predatory episode. The limited observations suggest that mating may occur within the *Ach. mundula* retreat. In addition, *A. incursus* females use the empty host leaf retreats for the protected placement of their egg sacs. All of this suggests a close, perhaps exclusive, association of *A. incursus* with its host/prey species, *Ach. mundula*.

In a study of *A. trigonum* (Hentz), Larcher and Wise (1985) observed a wide range of behaviour including commensalism, kleptoparasitism, web theft and host predation. They concluded that the nature of the interaction between *A. trigonum* and its hosts varied as a function of their relative individual sizes. This agrees with an earlier finding of Trail (1980) that *Argyrodes* species which attack their hosts are equal or larger in adult size compared with their host species. Presumably, this makes the attacker better able to overpower its prey. *A. incursus*, however is considerably smaller than its prey, *Ach. mundula*. Carapace length ranges for females of *A. incursus* and *Ach. mundula* are respectively 1.29-1.35mm (M = 1.32) and 2.17-2.58mm (M = 2.32). The mean difference of 1.00mm is highly significant ($P < 0.001$). The suggestion of Trail (1980) that an *Argyrodes* species smaller than its host would behave as a commensal or kleptoparasite rather than as a host predator is not supported in this case.

As yet, little information about the attack behaviour of *A. incursus* is available. It seems likely that the host is attacked in its retreat as all carcasses were found in retreats. Limited observations by Larcher and Wise (1985) suggest that *A. trigonum* simply approaches the host and bites it on a leg, resistance being negligible (though some hosts flee to avoid an attack). The venom is apparently quick to immobilise the prey which is wrapped after being bitten. An intriguing but anecdotal observation (Walker, 1983) notes that a spider purported to be an *Argyrodes* species entered the web of a red-back spider (*Latrodectus hasselti* Thorell) and squirted a milky substance (source unknown) onto the silk. The red-back readily ate the substance and became immobilized soon after. Such an indirect prey capture technique would provide an effective predation strategy in a small predator/larger prey system. Alternative hypotheses include stealth, the prey remaining unaware of the slowly approaching predator; or male behavioural mimicry, the predator imitating some aspect of the courtship repertoire of the prey's male.

The level and impact of *A. incursus* predation upon *Ach. mundula* populations are not clear. Data for a small sample of 17 *Ach. mundula* webs from Royal National Park near Sydney showed that only 2 webs harboured *A. incursus* individuals. By contrast 13 webs contained other presumptively kleptoparasitic/commensal *Argyrodes* residents. However, Newcastle *Ach. mundula* webs showed *A. incursus* occupancy rates of approximately 50%. This suggests that *A. incursus* predation may exert a considerable effect at least in small host populations.

ACKNOWLEDGEMENTS

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Two new Species of Amphientomidae (Insecta: Psocoptera), the first Record of the Family for Australia

C. N. SMITHERS

SMITHERS, C. N. Two new species of Amphientomidae (Insecta: Psocoptera), the first record of the family for Australia. *Proc. Linn. Soc. N.S.W.* 111 (1), 1989: 31-35.

Two new species of Amphientomidae, representing the first species of the family to be recorded from Australia, are described.

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INTRODUCTION

The psocopteran family Amphientomidae has not been recorded from Australia although Mockford (in lit.) has mentioned that the family occurs here. On this authority the family was noted as being Australian in the manuscript of the forthcoming revised edition of the 'Insects of Australia'. While sorting material in the collections of the Australian Museum two specimens have been found, each belonging to an undescribed species. They are described here.

The Amphientomidae now include nearly 80 species, grouped into 18 genera. In the main they are infrequently encountered insects of warm climates. Three genera are known only from amber and there are a few species in the genus *Amphientomum* Pictet which are also known from amber. Current generic definitions are based mainly on venational features but these are gradually being supplemented by other characters as additional material becomes available.

The Amphientomidae are unusual in that they are one of only two families in the order in which the body is clothed with scales, the other family being the unrelated Lepidopsocidae. The members of both bear a superficial resemblance to microlepidopterans and can easily be mistaken for them in the field.

Definitions and illustrations of the main distinguishing features of the family and genera have been given in Smithers (1972); they are not repeated here. The two new species fall clearly into the genera *Hemiseopsis* Enderlein and *Seopsis* Enderlein respectively.

SYSTEMATIC DESCRIPTIONS

Hemiseopsis alettae sp. nov.

FEMALE

Coloration (in alcohol). Head and body pale testaceous, the head a little darker than body and legs. Eyes reddish brown.

Morphology. Length of body: 3.1mm. Median epicranial suture fine but very distinct, anterior arms absent. Pilosity of head very fine. No hairs between ommatidia. Length of flagellar segments: f_1 : 0.14mm; f_2 : 0.19mm. First flagellar segment broader in basal half than in distal half, attachment to pedicel very narrow. Second flagellar segment longer than first. Antennal striations very fine and dense. Scape and pedicel broad. Eyes large, not protruding from head capsule except behind. Dorsal margin continuous with vertex. Seen from above eyes curve towards each other anteriorly continuing curvature of head. IO/D: 1.6; PO: 0.5. Lateral ocelli small, situated about a third of

distance from eye to median epicranial suture, opposite about middle of eye. Lacinia (Fig. 2) curved. Maxillary palp densely beset with microtrichia. Second segment with small sensory cone and broader than third and fourth segments. Measurements of hind leg: F: 0.6mm; T: 1.0mm; t_1 : 0.68mm; t_2 : 0.11mm; t_3 : 0.13mm; rt: 6.2:1:1.2; ct:27,0,0. Ctenidiobothria very strong with well developed basal combs. Femur of anterior legs without cones along internal margin. Tibia of second pair of legs with external spine about half way along length in addition to usual apical spines. Femur of third leg with strong, curved, dorsal apical spine. Tibia of third leg with seven ventral spines in distal half in addition to usual apical spines. Claws with one preapical tooth and row of setulae basad of tooth. Fore wing length: 2.5mm; width: 0.78mm. Fore wing (Fig. 1) almost parallel-sided, rounded apically. Basal section of Sc ends in somewhat thickened costa. Distal section of Sc absent. R_1 parallel with costal margin basad of the elongate stigmapophysis beyond which it bends to meet costal margin. Rs divides between origins of M_2 and M_3 . Cu_1 divides opposite stigmapophysis. Hind wing with R_1 present. M simple. Epiproct lightly sclerotized, simply rounded behind with preapical row of setae basad of which setae are sparsely and irregularly arranged. Paraprocts simple, without clearly defined trichobothrial field but with a few large setae without patterned area around base. Subgenital plate simple. Gonapophyses (Fig. 3) with ventral valve greatly attenuated ending in sharp point, with ventral membranous flange. Dorsal valve broad in basal half, narrowing abruptly to form long tapering extension which matches and lies adjacent to that of ventral valve. External valve tapering to bluntly rounded end, with strongly developed dorsal lobe.

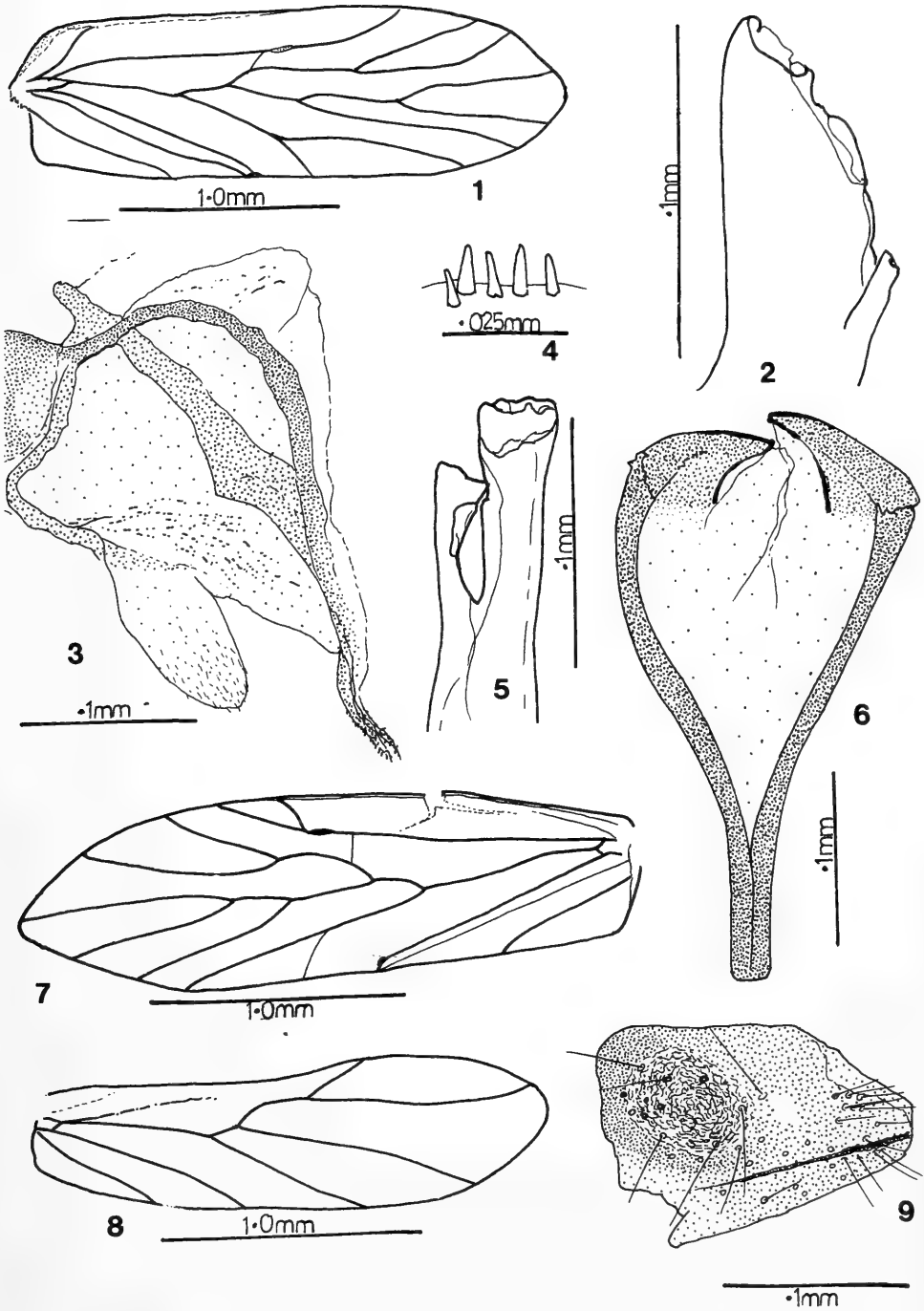
MATERIAL EXAMINED. Holotype female, Falbrook, N. Singleton, New South Wales, 26.i.1979. A. S. Smithers. Holotype in Australian Museum. This species is named for my wife who collected the type specimen.

DISCUSSION. Four species of *Hemiseopsis* have now been described, three from Africa and the present species from Australia. The genus may also occur in Jamaica (Turner, 1975). *H. alettae* is smaller than *H. fuellerborni* (Enderlein) from Tanzania, Zaïre, Angola and Zambia. In that species Rs divides opposite the origin of M_3 , Rs lies much further from R_1 and Cu_{1b} is much shorter than in *H. alettae*. The basal section of Rs is very much shorter than R_{2+3} . The genitalia of *H. fuellerborni* have not been described. *H. machadoi* Badonnel, from Angola, is only a little larger than *H. alettae* but can be distinguished by features of the wing venation and the female genitalia. In *H. machadoi* R_1 does not reach the wing margin and the crossvein from R_1 meets M basad of its separation from Rs. M_3 arises opposite the division of Rs and Cu_{1b} is much shorter than in *H. alettae*. The ventral and dorsal valves of the gonapophyses are not strongly attenuated, reaching only as far as the end of the external valve. In *H. alettae* they extend far beyond the end of the external valve. In *H. machadoi* the lacinia is straight with a different arrangement of apical teeth from that in *H. alettae*. In *H. obscurus* Broadhead and Richards, from Kenya, several of the veins of the fore wing in the basal half are weakly differentiated. The ventral and dorsal valves of the gonapophyses are not attenuated but are blunt; the dorsal lobe of the external valve is longer than the valve itself, a condition not found in any of the species of which the genitalia have been described. The head of *H. obscurus* has a distinctive colour pattern not found in any of the other species.

Seopsis incisa sp. nov.

MALE

Coloration (in alcohol). Head pale brown with brown markings. A narrow brown



Figs 1-9. *Hemiseopsis alettae* sp. nov. 1, female fore wing. 2, female lacinia. 3, female gonapophyses. *Seopsis incisa* sp. nov. 4, male femoral spines. 5, male lacinia. 6, male phallosome. 7, male fore wing. 8, male hind wing. 9, male paraproct.

mark on each epicranial plate along the ridge of the vertex; a diffuse, broad brown band across the front of the head from eye to eye; a narrow band in position usually occupied by anterior arms of epicranial suture, this broadened laterally to form a small patch just anterior to the lateral ocellus on each side; posterior half of postclypeus with a reticulate pattern in brown, part of which consists of narrow, longitudinal, parallel lines, the pattern extending further anteriorly in the midline than laterally: postclypeus pale in anterior half. Labrum pale. Lower half of genae brown. Antennae dark brown. Eyes black. Ocelli circled with dark brown. Thorax pale brown, darker along some sutures. Abdomen pale, darker dorsally on basal quarter and with suggestion of irregular segmental marks, laterally dark. Femora pale. Fore and middle tibiae pale in basal half, brown in distal half. Hind tibiae pale. First tarsal segment pale in basal half, darker in distal half but with pale tip. Second and third segments brown. Fore wing membrane hyaline, faintly tinged with brown, paler in distal third. Hind wing hyaline.

Morphology. Length of body: 2.3mm. Median epicranial suture fine but distinct. Anterior arms indistinct but position marked by brown band. Vertex slightly curved. Length of flagellar segments: $f_1:0.31\text{m}$; $f_2:0.34\text{mm}$. Antennal flagellum very fine, with very long setae from 7 to 15 times as long as flagellar width. Transverse striations of antennae very numerous. Eyes large, but hardly protruding. Upper margin almost level with vertex, extending a little behind head laterally. Fine, short setae between facets. Three ocelli. Lateral ocelli close to antero-medial angle of eyes, median ocellus in middle of frons so that the three ocelli are almost in a straight line. Lacinia (Fig. 5) almost straight, deeply divided at apex. Measurements of hind leg: F: 0.5mm; T: 0.98mm; $t_1: 0.54\text{mm}$; $t_2: 0.1\text{mm}$; $t_3: 0.1\text{mm}$; rt: 5.4:1:1; ct: 19,0,0. Front femur with long row of short spines (Fig. 4). Claws with one preapical tooth. Fore wing length: 2.5mm; width: 0.76mm. Fore wing (Fig. 7) narrows to somewhat pointed apex. Venation as usual in genus but distal section of Sc and Cu_{1b} evanescent and less obvious than other veins. Hind wing length: 2.0mm; width: 0.6mm. Hind wing (Fig. 8) with R_1 not reaching wing margin. IA curves distally towards hind margin. Epiproct simple, rounded behind, setose. Paraproct (Fig. 9) with finely and densely rugose, slightly raised area from which large setae arise. Bases of setae not surrounded by 'rosette' pattern often encountered in barklice. Hypandrium well sclerotized, simple, posteriorly and laterally slightly upturned. Eighth sternite more heavily sclerotized than more anterior sternites and forming an anterior extension to the hypandrium. Phallosome (Fig. 6).

MATERIAL EXAMINED. Holotype male, Malaise trap, $14^\circ 49'S$, $125^\circ 50'E$, mining camp, Mitchell Plateau, Western Australia, 9-19.v.1983. I. D. Naumann and J. C. Cardale. Holotype in Australian National Insect Collection, Canberra.

DISCUSSION. *Seopsis* is now a genus of ten species. There are three from Sri Lanka, two from the Philippines, two from Angola and one from each of Nepal, Singapore and Australia. *S. brunnea* New, from Singapore, differs from *S. incisa* in lacking the dark postclypeal pattern, in having a lacinia without a deeply divided apex and in lacking the row of spines on the fore femur. The male phallosome is similar to that of *S. incisa* in general form but differs in proportions. *S. luzonica* Banks, from the Philippines, differs in having a brown head with a pale transverse band at the level of the ocelli and in having two dark marks on each side on the vertex. In *S. metallops* Enderlein, from Sri Lanka, the head is black or dark brown with a pale spot in the middle of the front of the head and a similar spot on each half of the vertex. The lateral ocelli are much further from the eyes than in *S. incisa*. The membrane of the fore wing is dark. The basal segment of the hind tarsus is more than seven times the length of the second segment, whereas it is only 5.4 times as long in *S. incisa*. *S. nepalensis* New, from Nepal, has the posterior part of the postclypeus

pale, not dark as in *S. incisa*. The fore wing is acuminate and there are accessory sclerites internally at the posterior ends of the male parameres. The apex of the lacinia is not deeply divided. *S. pavonia* Badonnel, from Angola, has the fore wing strongly acuminate and the lacinia is not deeply divided. *S. termitophila* Badonnel, also from Angola, has much shorter wings than *S. incisa* (1.7mm as opposed to 2.5mm). The apex of the lacinia is not deeply divided and the male phallosome has a pair of pitted plates, internally, adjacent to the ends of the parameres. *S. superba* Hagen, from Sri Lanka, has a brown head with a darker longitudinal band on the vertex. The ocelli are close together. The basal tarsal segment of the hind legs is very much longer than in *S. incisa*, being about seven times as long as the second. *S. tricolor* Banks, from the Philippines, has a brown head and the lateral ocelli are set well away from the eyes. It is larger than *S. incisa* (fore wing length 3.5mm as opposed to 2.5mm). The illustration of the wing which accompanies the description shows no distal section to Sc, an unusual condition for this genus. *S. vasantasena* Enderlein, from Sri Lanka, has a brownish yellow head with four narrow, longitudinal streaks from the vertex down onto the front of the head; the postclypeus has a double, broad brown longitudinal band. The fore wing length is only 2.0mm.

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Redistribution of Amino Acids and Amides during Seedling Development in *Acacia iteaphylla* F. Muell. (Fabaceae: Mimosoideae)

ANITA B. BRADKE and DAVID R. MURRAY

BRADKE, ANITA B., & MURRAY, DAVID R. Redistribution of amino acids and amides during seedling development in *Acacia iteaphylla* F. Muell. (Fabaceae: Mimosoideae). *Proc. Linn. Soc. N.S.W.* 111 (1), 1989: 37-42.

The distribution of free amino compounds in the cotyledons and the organs derived from the embryonic axis has been studied in developing seedlings of *Acacia iteaphylla*. The results indicate that asparagine and pipercolic acid are the major forms of nitrogen translocated initially from the cotyledons to the hypocotyl and primary root. Selective transport of several 'non-protein' amino acids was indicated. *S*-carboxyethylcysteine became prominent in the hypocotyl after the pipercolic acid content of the hypocotyl had declined; it appeared also in the primary leaf, but was not strongly represented in the roots. *S*-carboxyisopropylcysteine appeared late in the hypocotyl, and was not detected in any other part of the axis. Albizziinc was not transported out of the cotyledons, but like arginine was metabolized *in situ*.

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INTRODUCTION

The cotyledons of *Acacia* seedlings undergo a transition from storage organs to photosynthetic organs (Ashcroft and Murray, 1979; Murray, 1981; Smith, 1981). During this transition, reserve materials appear to be mobilized in two stages. The first encompasses the initial growth of the radicle and hypocotyl, resulting in the elevation of the cotyledons. In *Acacia iteaphylla* F. Muell., the dry matter content of the cotyledons is depleted by about 70% during this stage, but only a slight net decline in the protein content of the cotyledons is observed (Ashcroft and Murray, 1979). In the second phase, more rapid net breakdown of protein in the cotyledons is associated with the synthesis of chloroplasts, as the cotyledons and then the primary leaf become effective photosynthetic organs.

It has long been known that *Acacia* seeds contain a high proportion of total seed nitrogen as free amino acids (Petrie, 1908, 1911). Many 'non-protein' amino acids have now been identified (Seneviratne and Fowden, 1968), and their distribution among species has indicated that there are four main sub-groups of *Acacia* throughout the world (Evans *et al.*, 1977; Murray, 1986b). In view of the early slow rate of net decline in the protein content of cotyledons, Ashcroft and Murray (1979) suggested that non-protein amino acids might represent the earliest mobilized form of nitrogenous reserve. Evidence has now been obtained that some, but not all, of the non-protein amino acids are transmitted to the axis, together with newly-synthesized asparagine.

MATERIALS AND METHODS

The seeds of *Acacia iteaphylla* were from the same batch studied previously (Ashcroft and Murray, 1979). To permit uniform imbibition, the seedcoats were cut with a razor blade at the end furthest from the embryonic axis. Except for seeds imbibed for 24h, which were placed in Petri dishes between moist Whatman No. 1 filter paper at 23°C (Krishna and Murray, 1988), seeds were placed in trays of sandy soil in a glass house,

with day temperatures around 30°C. At intervals up to 14 days, groups of 10 to 20 uniform seedlings were removed, dismembered and analysed.

Extracts from cotyledons, radicles and hypocotyls were prepared using a chilled mortar and pestle, acid-washed sand, and medium consisting of 25mM K⁺ phosphate (pH 7.5), 0.5mM 2-mercaptoethanol and 0.03% (w/v) Triton X-100 (Murray and Kennedy, 1980; Murray, 1983). The ratio of medium to tissue was 5:1 (mL per g fresh weight). The homogenates were centrifuged for 4min at 9,000g in a Microfuge and the supernatants removed. These were treated with ethanol (4:1, v/v) and insoluble material removed by centrifugation (Murray and McGee, 1986). Smaller samples (whole axes; balance of shoot) were extracted directly with ethanol (4:1, v/v). Aliquots of the ethanol-soluble fractions were assayed for amino nitrogen content by the procedure of Schnarrenberger *et al.* (1972), using L-serine as a reference standard (Murray, 1983).

Ethanol-soluble fractions were dried in a rotary evaporator, then redissolved in 0.5 to 1.0mL of 70% (v/v) ethanol, and applied to the origins of Whatman No. 1 papers prepared for 2-dimensional descending chromatography (Murray, 1983). Extracts available only in small quantities were applied without prior concentration. The solvents employed were 80% (w/v) phenol-water plus ammonia (200:1, v/v) in the first dimension, then either *n*-butanol: acetic acid: water 12:3:5 (v/v) or *n*-butanol: propionic acid: water 6:3:4 (v/v) in the second (Murray *et al.*, 1971; Murray, 1983). At least two chromatograms were run for each extract. Amino compounds were detected by their reaction with ninhydrin, and identified by comparison of their positions with those of authentic compounds. Information on the chromatographic behaviour of non-protein amino acids was kindly provided by Dr C. S. Evans and Prof. E. A. Bell. Authentic albizziine was purchased from Aldrich; other amino acids and amides were from Sigma Chemical Co.

RESULTS

The rate of seedling growth was faster than in the previous study because of higher temperatures and longer day-length. The 4-day, 8-day and 14-day stages chosen for analysis closely resembled the 8-day, 15-day and >21-day stages described previously (Ashcroft and Murray, 1979; Murray, 1981). At the 1-day stage, the amino nitrogen content of the cotyledons effectively represents that of the whole embryo (Fig. 1), as the axis was too small for accurate analysis (less than 1mg fresh weight). The amount of free amino nitrogen in the whole seedling progressively increased, doubling by 14 days (Fig. 1). Within the cotyledons, the amino nitrogen content did not alter substantially until between 8 and 14 days, when it declined. Within the axis, the hypocotyl gained a much higher proportion of the amino nitrogen exported by the cotyledons than did the radicle.

The amino acids and amides present in *Acacia* seedling tissues were identified as shown in Fig. 2. Changes in their relative abundance in the cotyledons are shown in Table 1. Many of the major nitrogenous solutes stored in the cotyledons initially are still among the most prominent forms present after 14 days, when the total free amino nitrogen content of the cotyledons had declined by 40% (Fig. 1). The content of asparagine increased, while the contents of albizziine, glycine, arginine, pipercolic acid, and finally glutamate and alanine, declined (Table 1).

The distribution of amino compounds in the roots and hypocotyls of seedlings aged 8 and 14 days is shown in Table 2. Pipercolic acid and asparagine were the most abundant forms of free amino nitrogen in both the roots and the hypocotyl of the 8-day-old seedlings. At this stage, *S*-carboxyethylcysteine was prominent in the hypocotyl, but was not detectable in the roots. At the 14-day stage, both *S*-carboxyethylcysteine and *S*-carboxyisopropylcysteine became prominent in the hypocotyl. The content of asparagine was

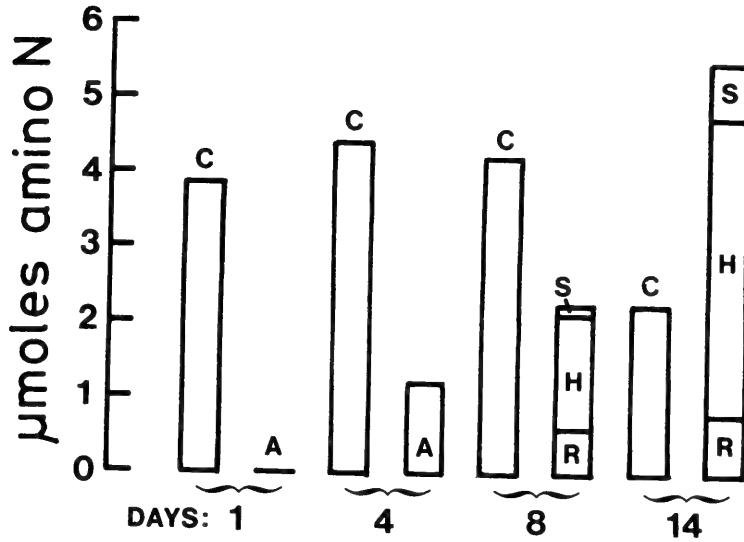


Fig. 1. Changes in the distribution of free amino nitrogen in the developing seedling of *Acacia iteaphylla*. C = cotyledon pair; A = whole embryonic axis; R = radicle or root system; H = hypocotyl; S = shoot system above the cotyledons.

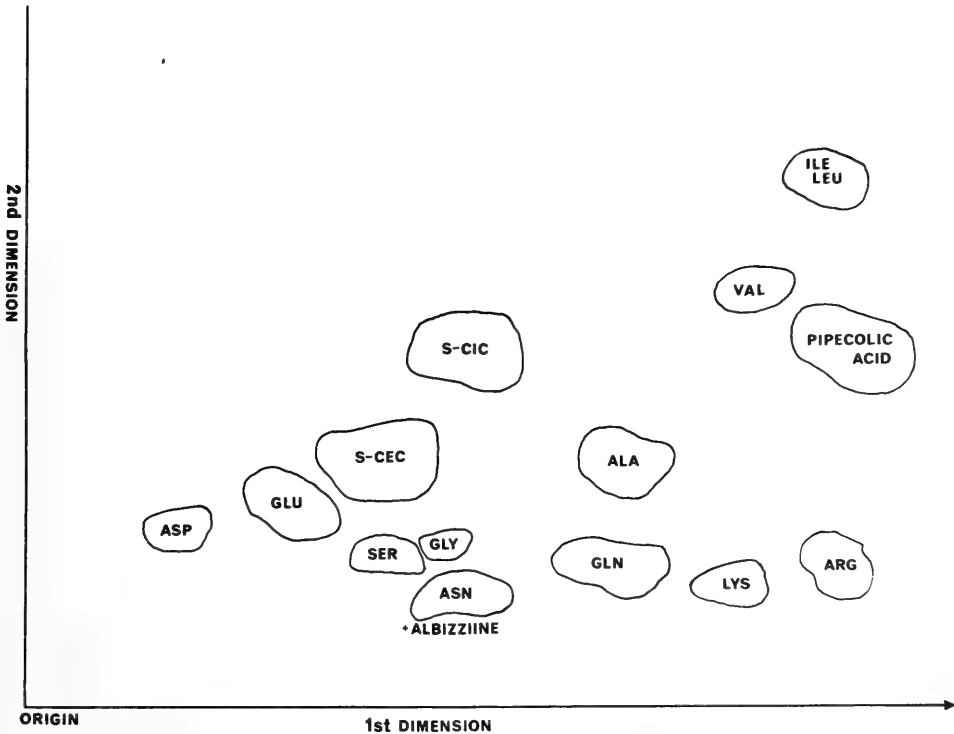


Fig. 2. The positions and identities of amino compounds separated from cotyledons of *Acacia iteaphylla* by 2-dimensional descending paper chromatography. Solvent 1, phenol-water-ammonia; solvent 2, *n*-butanol-acetic acid-water (see Materials and Methods). Abbreviations are standard, plus S-CEC = *S*-carboxyethyleysteine; S-CIC = *S*-carboxyisopropylcysteine.

TABLE 1

Changes in the Distribution of Free Amino Acids and Amides in the Cotyledons of Acacia iteaphylla Seedlings

Compound	Age of seedling (days)			
	3	4	8	14
S-carboxyethylcysteine	++++	++++	++++	+++
S-carboxyisopropylcysteine	+++	++++	++++	+++
Pipecolic acid	+++	++++	+++	++
Albizziiine + asparagine	++ ¹	++	++ ²	+++ ²
Glutamine	++	++	+++	++
Aspartate	tr	++	tr	+
Glutamate	+++	+++	+++	+
Serine	++	++	++	++
Glycine	++	+	+	+
Alanine	++	+++	++	tr
Valine	+	tr	tr	tr
Leucine + Isoleucine	+	tr	tr	tr
Lysine	tr	tr	tr	tr
Arginine	++	+	tr	n.d.

tr, trace; n.d., not detected.

¹ albizziiine predominant;² asparagine predominant — see text.

TABLE 2

Changes in the Distribution of Free Amino Acids and Amides in the Roots and Hypocotyl of Acacia iteaphylla Seedlings

Compound	Roots		Hypocotyl	
	8-day	14 day	8-day	14-day
S-carboxyethylcysteine	n.d.	+	++	+++
S-carboxyisopropylcysteine	n.d.	n.d.	n.d.	++
Pipecolic acid	+++	++	++++	+
Asparagine	+++	++	++++	+++
Glutamine	++	n.d.	++	n.d.
Aspartate	+	+	++	+
Glutamate	+	n.d.	++	tr
Serine	+	++	++	+
Glycine	tr	++	+	n.d.
Alanine	++	++	+++	tr
Valine	++	n.d.	+	n.d.
Leucine + Isoleucine	tr	n.d.	+	n.d.
Threonine	n.d.	n.d.	tr	n.d.

tr, trace; n.d., not detected.

maintained, but the contents of pipecolic acid and alanine declined sharply (Table 2). In the roots of the 14-day-old seedlings, some S-carboxyethylcysteine was present, but S-carboxyisopropylcysteine was not detected.

In the balance of the shoots from these seedlings (mainly the primary leaf at 14 days), serine and S-carboxyethylcysteine were most prominent. Pipecolic acid was also detected, along with aspartate, glycine, alanine, glutamate and glutamine, but asparagine, albizziiine and S-carboxyisopropylcysteine were not detected.

DISCUSSION

The net increase in free amino nitrogen in the seedling between 1 and 8 days was $2.55\mu\text{mol}$ (Fig. 1), which is within the maximum amount that could be met from limited breakdown of proteins in the cotyledons (Ashcroft and Murray, 1979). Our observations are consistent with the transport of selected forms of free amino nitrogen from the cotyledons to the hypocotyl, the root, and later the shoot, with the content of free amino nitrogen maintained close to $2\mu\text{mol}$ per cotyledon by proteolysis until after 8 days (Fig. 1). It must be noted that it is not possible for any uptake of exogenous nitrogen sources to have occurred through the roots; the axis-derived organs are gaining nitrogen entirely at the expense of the cotyledons.

Since the only way that the cotyledons can export nitrogenous solutes is through the phloem (Guardiola and Sutcliffe, 1972; Murray, 1984), an important question raised is whether the different organs of the axis are selective in the nitrogenous solutes they import, and if so, whether restrictions apply to phloem loading or unloading of individual compounds. In seedlings of jack bean (*Canavalia ensiformis* [L.] DC), Rosenthal and Rhodes (1984) have demonstrated that the non-protein amino acid L-canavanine is transported only to the above-ground parts of the shoot — none is translocated to the radicle.

Of all the non-protein amino acids potentially available from the cotyledons, only pipecolic acid appeared to be imported by very young roots of *Acacia iteaphylla* seedlings. Pipecolic acid and asparagine were abundant early in both the roots and the hypocotyl; quantitatively, they are the most important forms of nitrogen initially transferred from the cotyledons to the axis (Table 2). Outside the cotyledons, *S*-carboxyisopropylcysteine was detected only in the hypocotyl, relatively late in development (Table 2), whereas transport of the other derivative of cysteine was less restricted. *S*-carboxyethylcysteine became one of the more prominent nitrogenous solutes of the hypocotyl, and appeared also in the roots (late) and the primary leaf. The serine present in the primary leaf has probably accumulated from at least two biosynthetic pathways operating in the leaf itself (Murray, 1986a).

Arginine was not transported from the cotyledons (Table 2), but converted to other nitrogenous solutes *in situ* (Table 1). Urease was detected immunochemically in cotyledon extracts (for methods see Murray and Knox, 1977), which is consistent with this interpretation.

Finally, what is the role of albizziine (L- α -amino- β -ureidopropionic acid), a compound whose synthesis in *Acacia* cotyledons is known to be confined to seed development (Seneviratne and Fowden, 1968)? In our chromatographic systems, albizziine and asparagine could not be resolved (Fig. 2). This is in agreement with data on the mobility of albizziine reported by Cooper and Meister (1973). However, the colour of the reaction product with ninhydrin produced by authentic albizziine after paper chromatography was always mauve, whereas that produced by asparagine was always brown. On chromatograms where authentic albizziine and asparagine were loaded together, the final colour reflected the abundance of each compound; a brown colour consistently indicated the predominance of asparagine.

Initially albizziine is the prominent component of the combined albizziine-asparagine area from cotyledon extracts, but with increasing time following germination, asparagine predominates. When detected on chromatograms of *Acacia* root and hypocotyl extracts, the joint region was always brown, and if the unstained area was eluted from replicate chromatograms and hydrolysed with HCl, a ninhydrin positive product with the same mobility as aspartate was recovered. We have therefore concluded that asparagine is a major nitrogenous solute translocated to the roots and

hypocotyl (Table 2). This is in agreement with a transport function for newly synthesized asparagine determined for cotyledons of light-grown pea (Melcher, 1983) and peanut seedlings (Peoples *et al.*, 1986).

In *Acacia* cotyledons albizziine, like arginine, is converted to translocated forms of nitrogen, predominantly asparagine. It remains to be determined exactly how albizziine is metabolized, and whether, while present in cotyledons, it has any deterrent function against larvae of Australian insects.

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PROCEEDINGS

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John Vaughan Thompson, F.L.S.

HUGH CAMPBELL

(Communicated by T. G. VALLANCE)

CAMPBELL, HUGH. John Vaughan Thompson, F.L.S. *Proc. Linn. Soc. N.S.W.* 111 (2), 1989: 45-64.

John Vaughan Thompson (1779-1847) was a surgeon in the British Army Medical Service who made his name as a 'gentleman naturalist'. He became a Fellow of the Linnean Society in 1810 in recognition of his work in botany, but his great contribution to science was his discovery of metamorphosis in the Crustacea: a discovery which was received with disbelief and hostility in the 1830s, and not fully accepted until after Thompson died. He spent the last eleven years of his life in New South Wales, eight of them in charge of Convict and Military Medical Services. He failed as an administrator, and most Australian historians have not only blamed him unduly for his failure but have also neglected the scientific achievements which more than compensate for it. His life is an interesting study of the difficulties faced by an amateur scientist working alone without the support of personal wealth or powerful friends.

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INTRODUCTION — GIVING J. V. THOMPSON HIS DUE

John Vaughan Thompson (1779-1847) distinguished himself as a zoologist and botanist while quietly earning his living as an army surgeon in England, the West Indies, Mauritius, Madagascar, Ireland and Australia. He has been treated generously by his recent English biographers, who refer to his achievements before he went to Australia. Australians have been less kind to him: if they have noticed him at all, it is only in passing. For instance, although he spent his last eleven years in New South Wales, eight of them in charge of the convict and military medical services in the colony, the *ADB* contains no entry about him in his own right: he is mentioned only as a sort of *bête noire* in other men's lives.

It is true that he failed as a colonial administrator, and only natural that local historians should have reported accordingly. But most did not inquire further, and so overlooked both his zealous service during forty-five years as an army surgeon and his wide-ranging work in natural history, especially his discoveries about marine invertebrates. What is more, the writer believes they made their unflattering picture even worse by blaming him too much for his difficulties in New South Wales. As a result, biographers sympathetic to Thompson have usually thought it best to dismiss his years there in a single sentence and concentrate on the rest of his life. This paper is an attempt to repair the large gaps and unfair biases in what has hitherto been written about him.

There are other reasons, too, for the discrepancies. First, Thompson was inconsistent in himself: illness and bitterness changed him during the course of his service in New South Wales. Second, earlier biographers do not mention the Colonial Office files, reported for the first time in this paper, which contain a number of details of his personal life. Hence, they do not explain some of his actions. Third, several of his discoveries in natural history soon became such common knowledge that his later biographers forgot his part in discovering them.

Wheeler (1970) pointed out that most of Thompson's important achievements were recognized too late for him to enjoy the praise: he had that sort of luck all his life. By his own account, fortune first failed him in 1778, the year before he was born, when his father lost all his property in North America. In one part of a 'memorial' seeking a grant

of land in New South Wales, Thompson (1835) explained the setback: 'Memorialist's father . . . lost to his family by attachment to the Loyalist cause and the unfortunate result of the American War, a grant of land to the amount of 4,000 acres situated on the Mohawk River beyond Albany, . . . together with a good deal of other property, houses, &c at New York and Long Island, and a considerable stock of firing provided for the army under Sir John Vaughan, for which he was contractor — the above grants being given as the reward of services as an officer of the 96th Regiment at the taking of Pt Havana [sic] &c was totally lost by the precipitation with which he was obliged to fly when the King's troops took their final departure from Sandy Hook'.*

It was typical of Thompson to expect the government to compensate him for the loss his Loyalist father had suffered in the American War of Independence more than fifty years earlier — a loss he had probably heard of many times as a boy. But, as we shall see, to the end of his life, he remained surprisingly naive in political matters.

On 19 November 1779, a year after his father fled from Sandy Hook, John Vaughan Thompson was born at Berwick-on-Tweed. His mother was Jane Hall (*International Genealogical Index*, 1981).

Thompson grew up there, and gave that address as late as 1817. But he left home much earlier: the son of a dispossessed Loyalist army officer had to make his own way in the world. He studied medicine at the University of Edinburgh in the sessions of 1797-8 and 1798-9, enrolling in anatomy, surgery, obstetrics, chemistry and botany (Edinb. Univ., 1797-8); and on 3 March 1799, soon after his nineteenth birthday, he was appointed Assistant Surgeon to the Prince of Wales Fencibles. Without taking his degree, he accompanied the regiment to Gibraltar in December 1799.

THE WEST INDIES, 1800-1809

Appointment as Army Surgeon

On 3 July 1800 he became Assistant Surgeon of the 37th Foot, and embarked with them for the West Indies and Guiana to take part in the war against the French and Dutch: records show that he was engaged in the taking of Berbice and Demerara in Guiana. On 25 June 1803 he was promoted to Surgeon in the regiment. During his six years residence in Trinidad, with occasional visits to Grenada and St Vincent, he found time, while carrying out his military duties, to study the natural history of subjects as diverse as land crabs and ginger.

There is evidence that he paid at least one visit to England during his service in the West Indies. When he asked Lord Seaforth, F.L.S. and recently retired Governor of Barbados, to present his paper about *Kaempferia* to the Linnean Society, he headed his covering letter 'London, April 7th, 1807' (Linn. Soc., 1807). He took advantage of being in England that year to engage in other literary activity: he published his 'Catalogue of Plants in the vicinity of Berwick-on-Tweed' (a small octavo of 132 pages) (Thompson, 1807a), and had papers on *Kaempferia* (Thompson, 1807b) and *Piper* (Thompson, 1808) read to the Linnean Society.

Early Interest in Botany

Britten (1912), reviewing his first publication, wrote: 'Thompson must early have acquired considerable proficiency in botany. His *Catalogue of Plants . . . Berwick upon Tweed* was prepared before he left England — i.e. at or before the age of twenty — and

* The *Encyclopedia Americana* (1983) explains the reference to the capture of Havana in 1762; the *DNB* (1900a) entry on Sir John Vaughan gives an account of his service on the British side in the American War of Independence and his appointment as Governor of Berwick-on-Tweed, where Thompson's father appears to have joined him, a possible connection by a marriage in 1765 being suggested by the *International Genealogical Index* (1981); and the *EB* gives an account of the British flight from Sandy Hook in 1778.

shows a very complete knowledge of the plants of that region and of the literature of the period: the pretty coloured group which adorns the title page and a plate (also coloured) and dissections show him to have been a capable artist'.

In the same article, Britten points out that a paper on British birds has been wrongly attributed to Thompson (*DNB*, 1900b) because of a false entry in Royal Society (1871).

Thompson left the West Indies for good and returned to England in 1809. A year earlier he had been made an Associate of the Linnean Society, and in November 1809, four members signed the following certificate: 'John Vaughan Thompson, Esq., Surgeon of his Majesties [sic] 37th Regiment of Foot, & A.L.S., a Gentleman well versed in the study of Botany, being desirous of becoming a Fellow of the Linnean Society of London, we, the undersigned do from our personal knowledge beg leave to recommend him as likely to become worthy of that honour' (Linn. Soc., 1809).*

He was elected F.L.S. on 6 February 1810. Stebbing (1910), writing on the centenary of the occasion, described his election as 'prophetic insight', recognizing that Thompson's most important work was still to come.

On 3 March 1812, two of his papers were read to the Society — one about an unusual Pouched Rat he had observed in Trinidad (Thompson, 1813) and the other, reported by Wheeler (1970), on his observations of the genus *Myrtil* there.

SERVICE IN MAURITIUS AND MADAGASCAR, 1812-1816

Shortly afterwards, he was posted to Mauritius and Madagascar. On Christmas Day, 1812, he was appointed staff surgeon, though his official duties in the Mascarene Islands are not now known. It has been said that in two consecutive years he worked on 'introducing vaccine inoculation to Madagascar', and that for some time he was officially styled 'Government Agent for Madagascar'. In his 1835 letter seeking a land grant (Thompson, 1835), he himself refers to his appointment instructions and his journal 'sent to Governor Sir R. T. Farquhar and now, he presumes, in the Colonial Office'. Neither the instructions nor the journal have been found.

He claims (Thompson, 1835) that: 'amongst the important accessions to the culture of the Mauritius, [he] added 8 varieties of that estimable food, the plaintain, 10 valuable varieties of banana, 12 varieties of sugar cane, most of them vastly superior to those in common cultivation, 9 varieties of tobacco, 7 varieties of the indigo plant and 11 varieties of ordinary and upland rice'.

He also writes of: 'His efficient service as Civil Agent at Madagascar for the years 1814-15 a. During the period of his Agency he put a total stop to the traffic in slaves from those parts under his control. b. Repressed several efforts of rival chiefs to disturb the general tranquility [sic] by war. c. Introduced vaccine inoculation amongst the natives. d. Completed a survey of the extensive harbours of Loquez without loss of a single life. e. Paved the way for a friendly intercourse with the natives by a kind and generous treatment diametrically opposed to that of the French, our predecessors. f. Introduced and taught the cultivation of the potato and several other culinary vegetables'.

Vaughan (1953) refers to a 1902 work by Grandidier in which Thompson was credited with introducing *Albizzia lebbek* ('bois noir') to the treeless plains of Madagascar, having included a sack of seeds among his presents to the island's king, Radama I. The reference is further evidence that Thompson was engaged in some sort of diplomatic service in Madagascar.

* Apparently wishing, on second thoughts, to show their wholehearted endorsement of an Associate, the sponsors struck out 'likely to become'.

Thompson says that eventually he was 'attacked by the formidable remittent fever of the country which obliged him to relinquish a very lucrative post to return to Europe at great expense and finally to go on the half pay of his then rank of surgeon'.

In his informative 'land grant' letter, he also makes a particular point of mentioning that he had 'at the request of Governor Farquhar, drawn up and published at the Mauritius a systematic catalogue of all the plants cultivated in the three Government Gardens of Pamplemousses, Mon Plaisir and Redit, which cost [him] much labour, numerous journeys and a great deal of patient investigation'.

The title page of the *Catalogue of Exotic Plants Introduced to Mauritius* (Thompson?, 1816) does not show Thompson as the author. R. E. Vaughan (1953), however, based an article entitled *A Forgotten Work of John Vaughan Thompson* on yet another letter, which Thompson had written about the *Catalogue* in 1838. In that letter, he claimed to be the author of the work, which had in fact been published anonymously in 1816, shortly after he had left for England. He asserts that someone had suppressed the title page naming him as author, which had been ready for the press when he sailed, and replaced it with another. The 1838 letter was an appeal to the President of 'La Société d'Histoire Naturelle de Maurice' asking the Society to credit Thompson with the authorship. In the event, the President did nothing to advance Thompson's claim, partly because he thought that the *Catalogue*, based as it was on the Linnaean '*système sexuel*', was out of date by 1838.

Regardless of authorship, 'this was the first work on the plants of the island to be published locally, and is useful in listing the dates of introduction of many plants grown in the Botanic Gardens and elsewhere. It shows Thompson's interest in the importation of useful plants, an interest he shared with many other colonists of the time' (Wheeler, 1970). In fact, it contains references to a number of plants introduced by Thompson himself. Barnwell (1941) lists among these the honeysuckle, the jonquil, Guernsey and other lilies, Madagascar arrowroot and tobacco, weeping willow, walnut, chestnut, horse-chestnut and American lime; he also records that Thompson's name is inscribed on the Liènard Obelisk in the Pamplemousses Garden. But this first taste of having his scientific efforts and their worth doubted probably influenced Thompson's later decision to publish his own work.

Britten (1912) reports that during this period he also 'sent dried plants to Robert Brown, which are in the National Herbarium', later to become part of the British Museum (Natural History).

Reviewing his service between 1812 and 1816, Thompson later complained of the 'loss of property at the Madagascar and the Mauritius, being involved in the latter by the burning of Port Louis* and the extensive bankrupcies [sic] which occurred shortly after his departure for Europe on sick leave', and of the 'loss and expense entailed by the great length to which the regnal[?]' of the Madagascar was extended'.

When Thompson left Mauritius, he was thirty-seven. In the year of his departure, he suffered physically from the onset of malaria, financially from the fire at Port Louis, and psychologically from lack of recognition of his efforts. And his hardship was compounded because illness forced him to go on half pay for two years from 10 June 1817 (Johnston, 1917).

He had the consolation, however, of knowing that his paper on *Mus anomalis*, which had been read before he left England, had been published by the Linnean Society in 1813 (Thompson, 1813). The paper, accompanied by a plate which illustrates his

* 'A fire broke out in the commercial section of Port Louis [in 1815]. Efforts to extinguish it were unsuccessful and all the principal shops and warehouses were destroyed. Seven hundred houses were burned down, and millions of rupees of property lost. [Governor] Farquhar acted quickly and efficiently. People were clothed and fed and no one died of hunger, although many were ruined financially . . .' (Mannick, 1979).

meticulous drawing, contains a revealing statement of his views about scientific classification: 'But when we examine into nature with due attention, we find she delights to mock the vain efforts of mortals to shackle and confine her within the bounds of generic characters, which are found to run so into each other as to render all attempts at method more or less imperfect. This animal must remain an anomaly in the family'.

His curiosity about natural history was not dampened. He had taken advantage of his time in Mauritius to study 'the famous extinct Mascarene birds', although he waited until 1829 to publish his *Contributions towards the natural history of the Dodo . . .* (Thompson, 1829). More immediately, as Wheeler (1970) records, on the way home he observed south of Madagascar 'a puzzling luminosity in the sea. He trailed a muslin hoop over the stern of the ship and caught a profusion of small animals hitherto invisible in the water'. Wheeler goes on to note that 'Thompson has been credited with being the first to use a plankton net, and there is little doubt that his use of it in late July or August 1816 was his own idea entirely: but he was anticipated by John Cranch, who used a similar tow net on [Captain Tuckey's voyage to] the River Zaire (or Congo) in April 1816'.

Back in Berwick-on-Tweed on half pay, Thompson returned to medical school. He enrolled for the 1816-17 session at the University of Edinburgh in Clinical Medicine and Materia Medica. He paid 4/6d for lectures in Materia Medica from Professor James Home; among others on his page of the fees list were two Royal Navy surgeons and another army surgeon (Edinb. Univ., 1816).

ARMY MEDICAL SERVICE AND MARINE STUDIES AT CORK, 1819-1835

The next record of Thompson's movements appears when he was restored to full pay (on exchange) on 25 May 1819 (Johnston, 1917). By that time he was in Cork, and for the ensuing eleven years he remained on full pay in posts such as district medical officer at Cork and surgeon of the Cork Recruiting District. There is evidence that in 1819 he gave a course of lectures at the Cork Institute on the science of Botany (Wheeler, 1975).

Presumably he married soon after his return to England in 1816. The advice of his departure from Mauritius in June 1816 (*Gazette de l'Isle Maurice*, 1816) suggests that he had no wife then. Previous biographers have said nothing about his private life and family; Wheeler (1970), the latest, said, 'It is not known whether he married'. But it is a subject on which Thompson's (1835) revealing letter throws some light. In it, he describes himself as 'having a young family of six children, four girls and two boys, whose prospects have been materially affected' by the reverses in North America and Mauritius which he mentioned in the letter. Tantalizingly, the shipping record shows that, when he sailed for Hobart Town in 1835, he was accompanied by his wife and four children, the eldest sixteen (Colonial Office, 1836a): for some reason, two of the girls (probably older than 16) did not go.

Thompson remained at Cork until 1835. During his years there he made those discoveries of the life histories of the marine invertebrates in the Cove [Cobh] for which he is chiefly remembered. He announced the principal ones in the following order during the brief period between 1827 and 1830:

- the discovery of *Pentacrinus europaeus* (Thompson, 1827);
- the discovery of metamorphosis in the development of most Crustacea (Thompson, 1828);
- the classification and life history of barnacles (Thompson, 1830a); and
- the discovery of the animals he called *Polyzoa* (Thompson, 1830b).

As the *DNB* (1900b) has it, 'Our present conceptions of the structure of these forms, of

their zoological position, and of the metamorphoses which they undergo, date from Thompson's papers'.

His achievements resulted from his appreciation of the need for practical observation, his capacity for detecting and recording detail and, above all, his ability to realize the implications of what he saw. They were all the more remarkable because he worked alone, without the support of a university or other centre for scientific development, or the collaboration, it seems, of even a single colleague. Hence, for want of people to rally round him in his lifetime, his name is not well known today, even among specialists in marine zoology. Although his discoveries about marine invertebrates received a good deal of attention when he announced them, biologists soon began to take them for granted: and if scientists subsequently wondered who made those discoveries, they often attributed them to later workers.

Thompson announced his discoveries in a series of memoirs which he published at his own expense. Although nowhere does he say so, it is likely that his experience with his *Catalogue of Exotic Plants in Mauritius* made him wary of trusting his discoveries to others until he had published them.

Pentacrinus europaeus

The *DNB* (1900b), in its reference to his first discovery, the *Memoir on Pentacrinus europaeus* (Thompson, 1827), records that it: 'announced the presence of a stalked crinoid in the seas of the British Isles: until then crinoids (feather stars or sea-lilies) were known only from the West Indies. Thompson also revealed that the crinoidea were really 'radiata'; and (as shown more fully by a second paper in *New Philosophical Transactions*, Edinburgh 1836) that this *pentacrinus* was really the young stage of the *antedon*, or feather star'.

The discovery of this animal and Thompson's conclusions about the stages in its life history drew the attention of zoologists in France, Germany and elsewhere to his work, and many of his succeeding papers were translated or abstracted into journals abroad.

Thompson announced his other principal discoveries in a series of five scarce pamphlets, now reprinted in facsimile, which he published under the title of *Zoological Researches and Illustrations* (Thompson, 1828-34).

In the light of Thompson's later appointment to Sydney, it is interesting to note that a copy of the first *Researches* was sent to New South Wales, endorsed 'W. S. McLeay, Esq., with the author's compliments'. 'He was also the donor of seeds of cotton to A. McLeay in Sydney, as shown by the Seed Book' (Fletcher, 1920). In fact, Thompson corresponded regularly — and evidently was on familiar terms — with Alexander Macleay, the Treasurer of the Linnean Society of London from 1798 until 1825, and thereafter Colonial Secretary of New South Wales (Wheeler, 1970). Macleay, of course, was one of the four who had nominated him for F.L.S. in 1809.

Metamorphosis of Crustacea

Thompson published the first issue of his *Researches* at Cork in September 1828, price 3s.6d. 'It announced what is probably his most important contribution to zoology: the discovery that certain planktonic forms of crustacean, then known by the generic name *Zoea*, undergo changes of form (metamorphoses) until they become recognizable as the young of the European edible crab (*Cancer pagurus*)' (Wheeler, 1970).

The full title of the first memoir was: *On the Metamorphoses of the Crustacea, and on Zoea, exposing their singular structure and demonstrating that they are not, as has been supposed, a peculiar genus, but the Larva of Crustacea!!* (Thompson, 1828). Wheeler (1975) points out that 'the two exclamation marks as well as his text showed that he appreciated the revolutionary

nature of his discovery, but it is doubtful whether he could have anticipated the furore that his important discovery was to invoke among the zoological establishment'.

Wheeler (1975) goes on to explain how Thompson's discovery challenged one of the basic tenets of contemporary systematic zoology: 'The essence of the controversy lay in the distinction made by systematists between the classes *Insecta* and *Crustacea*. The insects, as was easy to observe, went through a series of metamorphoses to emerge as an imago, or perfect insect. The crustaceans, less easy to observe, were not known to develop through metamorphosis; consequently they were assumed not to do so. This difference was one of the principal characters distinguishing the classes'.

Wheeler's summary of Thompson's memoir is simple and elegant: 'Thompson's demolition of the character was based on practical observation. In 1816, while on the return journey from Mauritius, he had . . . captured small planktonic animals, which resembled species of the crustacean genus *Zoea*, described by earlier naturalists from mid-ocean. In the spring of 1822, Thompson "to his great surprise" found a considerable abundance of *Zoetas* in the harbour of Cove [Cobh], and in 1823 he succeeded in keeping a large specimen in fresh sea water between 14 May and 15 June, when it died in the process of casting its skin. He noted that the form of the *Zoea* was totally changed and that the limbs that had disengaged from the skin resembled those of the decapod crustaceans (crabs, lobsters, shrimps, etc.) in having four long walking legs and an anterior pair armed with pincers. The final confirmation was obtained four years later, in June 1827, when Thompson succeeded in hatching the eggs of the edible crab (*Cancer pagurus*) to find *zoea* larvae. From these observations he asserted that the decapod crustaceans generally undergo metamorphosis during their development. Not only did his announcement render invalid one of the major distinctions between the *Crustacea* and the *Insecta*, it accounted for the anomalous *Zoea* specimens of earlier naturalists, and it also explained previously unaccountable phenomena such as the migration to the sea of land crabs which he had observed in the West Indies'.

In fact, Thompson used his observations of land crabs to support his theory, pointing out that even such land dwellers must lay their eggs in the sea and give their young a perilous life there, so that they may undergo metamorphosis before going ashore in their adult form.

He points out, too, that fifty years earlier, in a work published at Haarlem, Slabber (1778) claimed that he had observed metamorphosis in *Zoea*. Thompson swiftly disposes of that claim: 'The metamorphosis, however, which this observer thought he witnessed is of so different a description that we must either suppose him to have fallen into some error or else there may be Crustacea which pass through some other forms'.

He concludes, 'from much experience', that Slabber 'lost his *Zoetas* in changing the sea water, and that the new form came from the added portion'.

Nevertheless, in his own first memoir, Thompson, too, had 'failed to prove the complete metamorphic cycle because his *zoea* died in the process of change; it was only by comparing them [sic] with ova from a berried female crab that he was able to deduce the relationship' (Wheeler, 1970). What is more, his announcement was accompanied by a second memoir 'On the genus *Mysis*' (Thompson, 1828), in which he showed that the mysidacean crustaceans hatch in a form very similar to that of the adult and undergo only slight metamorphosis, thus tending to contradict his assertions about metamorphosis as a characteristic of most crustaceans. And both memoirs appeared only months before the German scientist Rathke, unaware of Thompson's announcements, published his own observations on the development of the crayfish (*Potamobius*, formerly *Astacus*), now known to be one of the few exceptions to the general rule propounded by Thompson. Rathke's work demonstrated that the young crayfish hatch at a late stage of development and do not undergo metamorphosis.

One might ask why Thompson was in such a hurry to publish when his conclusion was not entirely proved and was supported by only a single observation. The answer lies in the comment made by Stebbing in relation to another of Thompson's discoveries, the *Polyzoa*, where an observation made in 1823 was not published for seven years, and so was not credited to him. 'As we all know, recognition of our discoveries has to date, not from the time when they were made, but from the time when they were published' (Stebbing, 1910). Thompson knew that others were studying marine invertebrates, and did not want to risk being beaten. As it happened, he was alone in detecting metamorphosis, and could have afforded to wait.

But given Thompson's reliance on deduction in his first memoir, it is not surprising that many established zoologists treated his claim of metamorphosis in the Crustacea with 'distinct and often derisory doubt'. They resented the overturning of the taxonomy in use at the time, as expounded by Leach and Cuvier. Nevertheless, Thompson continued to announce fresh examples to prove his hypothesis. By the end of the decade, Rathke and others had published admissions that their scepticism had been misplaced and that Thompson was correct (Wheeler, 1975).

In the middle of 1830, Thompson's military career blossomed briefly. On 22 July he was promoted to the rank of Deputy Inspector General of Hospitals (the next step on the promotion ladder for surgeons) as a reward for his long and zealous service. The promotion promised him an income sufficient both to support his family in the style he thought fitting and to continue publishing the results of his research. Then, as suddenly as his fortunes rose, they fell (Johnston, 1917). On 9th December 1830 he was retired to half pay, along with 13 other officers of his rank who experienced the same meteoric rise and fall. At age 51, with a wife and six children (under fifteen?), he saw his income drop from 30 shillings a day to 17. Not only did the reduction threaten the prospects of his family, but it also made it impossible for him to go on publishing his *Zoological Researches* without help. Some might think he should have been able to bring up a family on £300 a year. Thompson did not.

Consequently, the proceedings of a meeting of the Zoological Society of London a month later, on 11 January 1831, (Zool. Soc., 1831), show that it received 'an Address by Mr J. V. Thompson, Esq., "To the members of the Zoological Society, and the Zoologists of the United Kingdom in general", soliciting such support, by subscription, as may enable him to continue, without further loss, his *Zoological Researches and Illustrations*. This address is printed, together with a list of the subjects of some of the preceding memoirs, on the cover of the fourth number of the *Researches*, which was at the same time laid on the table'. Stebbing, writing eighty years later, referred to 'a pathetic appeal to the scientific world to furnish him with 150 subscribers, as his private income would no longer bear the sacrifice till then entailed by the publication of his researches' (Stebbing, 1910).

Thompson's financial setback did not prevent him from announcing further evidence of metamorphosis in the Crustacea, in response to a complaint from Vigers (1830) in the *Zoological Journal* that his conclusions had been too sweeping. His letter to the Secretary of the Zoological Society dated 'Cork, Dec. 16, 1830', is reported thus (Zool. Soc., 1830: internal quotations are from Thompson): 'In it, Mr Thompson urges, in support of the universality of a metamorphosis among the *Crustacea*, that he has ascertained the newly hatched animal to be a *Zoea* in eight genera of the *Brachyura*, viz. *Cancer*, *Carcinus*, *Portunus*, *Eriphia*, *Gecarcinua*, *Thelphusa*?, *Pinnotheres*, and *Inachus*; and in seven Macrourous genera, viz. *Pagurus*, . . . and *Astacus*. "These embrace all our most familiar native genera of the *Decapoda*". The Lobster, or *Astacus Marinus*, Mr Thompson states, "does actually undergo a metamorphosis, but less in degree than in any of the other enumerated genera, in its first stage being what I should call a modified *Zoea* . . . ; in short, such an animal as would never be considered what it really is, was it not obtained

by hatching the spawn of the Lobster". In the other indigenous species of *Astacus*, the River Crawfish, it would appear from the excellent treatise of M. Rathke on the developement [sic] of its eggs, that the young are hatched in a form according with that of the fully grown animal. Mr Thompson, however, suspects that some source of error may exist in these observations. "If it should be found otherwise, it can only be regarded as one solitary exception to the generality of metamorphoses, and will render it necessary to consider these two animals for the future as the types of two distinct genera" . . .'

This letter is an interesting demonstration of Thompson's confidence in the accuracy of his observations: he did not hesitate to question the opinions and observations of established and respected naturalists when they conflicted with his own.

The Cirripedes

Thompson's third important achievement in marine biology was his discovery that cirripeds are *Crustacea*: in the system proposed by Cuvier, they had been designated as a class of the *Mollusca*. He published his discovery in the third number of *Zoological Researches*, Memoir iv: *On the Cirripedes or Barnacles; demonstrating their deceptive character; the extraordinary Metamorphosis they undergo, and the Class of Animals to which they indisputably belong*' (Thompson, 1830a).

Wheeler (1975: internal quotation is from Thompson and Darwin) explains the significance of the discovery thus: 'Again this presented a revolutionary concept as far as the higher classification of barnacles was concerned. Among the barnacles two major groups are well known, the goose or ship's barnacles, which look somewhat like small, light coloured mussels on a stalk, and the acorn barnacles, which are so abundant on rock and timber on shore. Earlier naturalists had been much exercised about the true relationships of these animals.

'Thompson stumbled on the correct solution to their relationship by, as he put it, "the result of chance rather than of design and industry". In 1823, crossing on the ferry at Passage Cove, he trailed his small muslin net behind the boat to catch a quantity of marine zooplankton. Among them were translucent elliptical animals a tenth of an inch in length, evidently crustaceans but of a form undescribed by earlier naturalists. On 1 May 1826 he collected further specimens, and in the light of his knowledge that larval decapod crustaceans were entirely dissimilar to the adults kept them in order to observe any metamorphosis which might take place. He had the satisfaction on 8 May of seeing some of these elliptical animals metamorphose, and found them firmly attached to the bottom of the glass container, perfectly recognizable as young acorn barnacles. On 10 May another of these larvae was seen to cast its outer skin and settle to the bottom as a barnacle. In 1835 Thompson described the larvae of the goose barnacle, which he found on a ship's bottom in 1830.

'Again, though Thompson had firmly placed the barnacles within the Crustacea and showed that they too enjoyed a planktonic larval stage before settling, established zoologists were slow to accept his findings. However, Darwin (1851) in his monograph on the group recognized Thompson's contribution as a "capital discovery".'

Of course, Thompson would not have 'stumbled on the correct solution' had he not been looking with the eyes of one who *knew* that metamorphoses occurred in Crustacea.

The Royal Society's *Catalogue of Scientific Papers 1800-1863* (Royal Society, 1871) records some of the reprints of Thompson's papers which had appeared by 1831 in English and French journals.

An illustration of the way Thompson's name cropped up incidentally in scientific discussions in the early 1830s comes from the proceedings of the Zoological Society on 11 January 1831 (Zool. Soc., 1831). A question was raised at this meeting about the cause of phosphorescence in sea water. 'It was remarked that Commerson and others have

attributed the phenomenon described to putrefaction of animal matters, . . . Sir Joseph Banks, Dr Macartney, and others, on the contrary, have referred it to the presence of marine animals, principally Crustacea; and the existence of such, as the cause of this appearance, has been recently insisted on by Mr J. V. Thompson.'

Polyzoa

The last of Thompson's four important discoveries was that of *Polyzoa*, a new Animal discovered as an Inhabitant of some zoophytes (Thompson, 1830b). He showed that the term zoophytes had been used to cover a mixture of animals superficially alike but essentially different in structure. Relying on Wheeler again: '[*Polyzoa*] had been formerly included as part of a heterogeneous collection of enigmatic invertebrates, the so-called zoophytes; but he showed that they were distinct from the colonial hydroids and the ascidians, with which they had been sometimes confused. The term *Polyzoa* received considerable usage, especially in Great Britain, but it was eventually dropped in favour of *Bryozoa*, which had been proposed almost contemporaneously' (Wheeler, 1970; supported by Stebbing, 1910).

Because of Thompson's preoccupation with natural history, it is not surprising to find that he left only one paper on medical science. Although he was a prolific writer and despite more than forty years in the Army Medical Department, his only recorded publication in the field is an 1832 pamphlet entitled *The Pestilential Cholera Unmasked . . .*' Wheeler (1970) describes it as 'a work devoted to diagnosis and treatment of cholera, but exhibiting little understanding of the causative factors involved in the disease'. Perhaps the critic expected too much. At the time, no one else understood such matters, either. In fact, the pamphlet conveyed the prevailing wisdom about the disease and it was topical: cholera had been spreading westward from Asia during the 1820s, and the first major outbreak in the British Isles occurred in 1832.

Wheeler (1975) reports in passing that in 1833 Thompson's collection of invertebrates was purchased by the Royal College of Surgeons, Dublin. Unfortunately, the collection has not survived. In the light of his financial setback at the end of 1830, one wonders what domestic crisis forced Thompson to sell it.

SCIENTIFIC DISPUTES AND FINANCIAL DIFFICULTIES

Meanwhile, Thompson's conflict with the zoological establishment in London became more and more acrimonious as his new concepts threatened to overturn fundamental systematics. As Wheeler (1970) says, 'His correspondence and published writings of the time suggest a man impatient with the conservatism of his opponents, and eventually embittered by their opposition . . .' Elsewhere, Wheeler (1975) says: 'His tendency to write in a forthright style cannot have endeared him to his opponents'.

Meanwhile, too, Thompson's money problems became more and more embarrassing. On 8 May 1835 he informed the Treasurer of the Linnean Society that he was 'unable to send the large amount due' and 'craved the indulgence . . . in the hands of the Committee of remitting the payments in special cases of disability'. He pointed out that he had not been attending meetings or receiving copies of the Society's 'valuable Transactions' while his fees (at the time £3 per annum) were in arrears. He explained that he was claiming the indulgence ' . . . on account of the pecuniary loss sustained by the publication of my *Zoological Researches* and the great expense incurred by the prosecution of those discoveries by being obliged to keep up an establishment on the sea-side during a great part of the period, & the disbursements consequent on boat hire travelling back and forward, &c' (Linn. Soc., 1835).

According to its minutes for 22 May 1835, Council 'resolved that the request be

acceded to on account of his high merit as a naturalist and the papers he had supplied for the Transactions of the Society'.

In the middle of dealing with both his financial difficulties and a bitter scientific controversy, Thompson was removed from the scene. Colonial authorities in London had for some time been anxious to reduce the cost of the separated convict medical services and military medical services in New South Wales and Van Diemens Land. Early in 1835, the Government decided to combine both services in each colony under the supervision of senior Army surgeons (Colonial Office, 1834). Accordingly, in June 1835, John Vaughan Thompson was offered an appointment as Deputy Inspector-General of Hospitals in New South Wales (Colonial Office, 1835a). Distressed as he was, he could not refuse the offer, since it meant he would be restored to full pay from 7 August 1835 (Johnston, 1917).

Only money could have taken him so far abroad; and it could not have done so at a worse time, because scepticism about his *Zoological Researches* was at its height. In the very week that Thompson was offered his new appointment, his most implacable opponent, J. O. Westwood, F.L.S., secretary of the Entomological Society and through that office committed to retaining the old taxonomy, attacked Thompson's work by presenting a long paper to the Royal Society *On the supposed existence of Metamorphoses in the Crustacea*. Westwood (1835) used special cases and the opinions of a number of respected authorities to deny outright the evidence that Thompson presented. He was quite wrong, but the error did not make his criticism any less credible to many of his listeners and readers, who shared his misconceptions. Patronizingly, he pointed out that 'the accuracy of [Thompson's] beautiful figures deserves the highest praise' and summed up by saying, 'Although disagreeing with Mr Thompson in respect to his theory, I have already stated that his figures are very faithful delineations of nature'. In all else, he set out to discredit Thompson.

Perhaps that paper spurred others, some of them also severe critics, to take Thompson seriously and make their own observations. Nevertheless, it took some time to verify Thompson's work, and it was not until the end of the decade that impartial zoologists repeated his observations and admitted that he was right (Wheeler, 1975).

Not that Thompson himself had slackened in his efforts to substantiate his discoveries. He had been continuing his research and his writing, and a number of his papers appeared in various journals in 1835 and 1836 (Royal Society, 1871). Some of them appeared even in the heart of the enemy's territory, the *Entomological Magazine* (Royal Society, 1871).

DEPUTY INSPECTOR-GENERAL OF HOSPITALS, NEW SOUTH WALES, 1836-1844

Surgeon-Superintendent of the 'Boadicea'

In June 1835, however, Thompson had the more pressing problem of arranging passage to New South Wales for himself, his wife and four children. In his fifty-sixth year he was about to begin a new career in a new land, and turn his back on the researches which had occupied him for the past 20 years.

By the beginning of August 1835 he had settled most of his affairs in Ireland and returned to London. He left unpaid a seemingly trivial account for goods to the value of £6.10.7½ with Mrs Dwyer of 89 Grand Parade, Cork, which was to haunt him for years (Colonial Office, 1841a). On 7 August 1835, the day he returned to full pay, he wrote a memorial to the Secretary of State for the Colonies, seeking a grant of land in New South Wales as a recompense for losses he and his father had suffered in government

service (Thompson, 1835)*. The Secretary of State replied that the regulations did not allow him to make the grant (Colonial Office, 1835b).

To minimize his expenses, Thompson secured the post of Surgeon-Superintendent on the emigrant ship *Boadicea* taking 200 unmarried females and about 60 people in family groups to Van Diemens Land. For this service he received £50 and his own free passage, but he had to pay what seems an exorbitant price of £159 for cabin passages for his wife and children. On 8 August 1835 he signed his contract with the Secretary of the Emigration Committee, undertaking to be available from 26 September 'to inspect the emigrants and witness their promissory notes' (Colonial Office, 1835c). The *Boadicea* sailed on 1 October 1835, and arrived in Hobart Town on 4 February 1836. It is an extraordinary coincidence that Charles Darwin, who would later praise Thompson's work on barnacles, sailed into the Derwent River next day on the *Beagle*. There is no evidence that Thompson and Darwin met, although they were in Hobart Town at the same time for more than a fortnight.

There were no deaths on the 128-day voyage. The Surgeon-Superintendent reported that: 'I am quite confident that it was to [the] regulation of their diet, the withdrawal of their wine while in the Torrid Zone and the promptitude with which every case of sickness was met that under Divine Providence I am indebted for the preservation of very many lives — not that we escaped our share of sickness nor the occurrence of several very hopeless cases & almost miraculous escapes'† (Colonial Office, 1836b).

After almost a month waiting in Hobart Town, Thompson and his family secured a passage to Sydney on the *North Briton*, arriving on 15 March 1836 (*Herald*, 1836). He took up his new duties in the Office of Deputy Inspector General of the Convict [Civil] and Military Hospitals in the Colony of New South Wales on 1 April.

Sir James McGrigor, head of the Army Medical Department since 1815, was well aware of the qualities of his senior officers, and proved a good friend to Thompson in all that was to follow. He had sent Thompson his instructions on 20 August 1835 (Colonial Office, 1835d). The Deputy Inspector General's mission was to manage Convict and Military Hospitals as a single service, as far as possible under the Hospital Regulations of the Army. He was to give particular attention to keeping down costs, to controlling the requisition and issuing of medicines and making regular returns about their use, and to regulating the access by civil servants and other free residents to hospital services.

With uncanny prescience, McGrigor (Colonial Office, 1835d) advised Thompson against possible pitfalls: 'In the allotment of the duties civil and military you will take care as much as possible to preserve the harmony necessary to good order; and in assimilating the duties you will not unnecessarily disturb the Colonial Surgeons' appointments, and on all occasions obtain the approbation of the Governor and proper authorities in recommending any change of duty among inferior officers and servants.'

Early Administrative Problems

In 'preserving harmony' and 'not disturbing the Colonial Surgeons', Thompson failed utterly. Accordingly, his previous biographers have either discreetly ignored the New South Wales part of his career or written about that to the exclusion of all else.

Part of the reason for his failure was undoubtedly the forthright and abrasive personality that he had already revealed in his scientific disputes and in his rejection of an offensive complaint about rations from the sea-lawyers on the *Boadicea* (Colonial Office,

* This memorial has been mentioned already as the source of hitherto unknown information about Thompson's family and his service in Mauritius.

† In fact, it is the frankness and directness of Thompson's reports on the emigrants that first attracted the writer's attention to him. He seemed so determined to face opposition head on, and to do it in writing, (Campbell, 1988) that I was compelled to find out what happened to him afterwards — and before.

1836d). In 1838, Governor Gipps said of him: 'Dr Thompson, whatever may be his other merits, was not the man calculated to carry successfully into effect a measure in itself unpalatable to his subordinates, being on the one hand wanting in blandness of manner or conciliatory address, before which opposition might have gradually given way, and on the other in that firmness and decision of purpose which would have overruled it' (Colonial Office, 1838a).

But as McGrigor wrote: 'His situation was no easy one for any man of common patience and temper. It was perhaps to be expected that an officer experienced in the duties, sent out to control expenditure, diminish emoluments and supervise the manner in which the several officers discharged their duties would be unacceptable, let his address and manner be what they would' (Colonial Office, 1839).

First, he had to serve three masters: the Governor and Secretary of State for the Colonies in matters relating to the Convict [Civil] establishment, the Secretary at War in matters relating to the Army, and the Director General of the Army Medical Service in regard to professional reports and returns. What is more, running through his dealings with all three was an undercurrent of resentment from officials in the Colonial Office about the intrusion of the Army Medical Service and the War Office into their domain. Hence, the Governor and his London superiors seemed to take some pleasure in pointing out Thompson's failings to McGrigor, who was responsible for appointing him and for disciplining him thereafter.

Second, through an incredible bureaucratic bungle, he arrived in Sydney to find that Dr James Bowman, who had joined the colonial medical service in 1817 and had been its head since 1819, was still in that position, and no arrangements had been made to remove him from it. Consequently, one of the first recommendations Thompson had to make was that his predecessor should be stood down. In the event, it took two years for the despatches necessary to terminate Bowman's appointment to pass back and forth between Sydney and London. Meanwhile, Bowman remained on strength without duties, devoting himself to his extensive private practice and the pastoral schemes of his father-in-law, John Macarthur. Even without those supplements, his unearned salary was some £200 greater than the pay for Thompson's active Army rank.

Third, the other colonial surgeons, especially James Mitchell, who had been on good terms with Bowman, also resented Thompson's arrival. His lack of a medical degree did not go unnoticed, and the colonial surgeons were aware of his proposals to replace them by army surgeons at lower rates of pay when their posts became vacant. The security of their lucrative private practices was also threatened by their new liability to transfer. And Thompson was less than tactful towards them. He was critical, in reports to Sir James McGrigor, of their private practices, their drinking, and their failure to cooperate with him.

Fourth, to cap Thompson's difficulties, the Governor reported at the end of 1836 that 'Mr Thompson has not as yet presented any distinct and comprehensive arrangement for . . . hospitals in this Colony, chiefly I apprehend from the infirm state of health under which he has for some time been suffering' (Colonial Office, 1836c).

In fact, Thompson had devoted a good deal of time to pointing out that his travelling allowance did not cover the cost of the journeys he was required to make; comparing his own pay and allowances with those of other senior officials; confronting the colonial surgeons; and complaining to London about the obstacles the latter were putting in his path.

To put the matter bluntly, the duties Thompson was expected to carry out, and the circumstances in which he found himself, were beyond the powers of an elderly, ailing, quarrelsome and forthright army surgeon who had been five years retired, and who in

any case would rather have been working at his microscope. The consequences were inevitable.

Nevertheless, Sir James McGrigor in London argued in his support: 'Mr Thompson complains that he has met with vexatious obstruction from some of the Colonial Medical Officers at the outset; perhaps it is but natural that some of these gentlemen should, at first, feel a new control irksome, and complain of more duty being imposed on them than under the old system so as to interfere with lucrative private practice or their avocations as agriculturalists . . .

'I am not prepared in every instance to support the tone of Mr Thompson's querulous correspondence, and I have so expressed my disapprobation of it that I trust this zealous and experienced officer . . . will henceforth be most respectful in all his correspondence . . . and I am of the opinion that henceforth no infirmity of temper will be betrayed by the Deputy Inspector General of Hospitals.

'In justice, however, to Mr Thompson I ought to say that during a long period of service I have ever found him an able and honourable officer, one who has constantly evinced the most indefatigable zeal on every service on which he has been employed, acting with discretion, prudence and forbearance' (Colonial Office, 1837a).

Despite this testimonial and promise for the future, in September 1837 a dispute known as 'the Mitchell case' made public a conflict which had been festering since Thompson's arrival and which dragged on for almost four years. Briefly, Mitchell, who had been in rancorous disagreement with Thompson from the outset, claimed to have misunderstood an instruction, and so failed to attend as medical officer at a flogging. Consequently the Governor dismissed him for disobeying an order. In response to public support for Mitchell, Thompson inflamed the debate by writing a letter to a newspaper; in it he referred selectively to some comments made about Mitchell by the Governor. It is true that the Governor had more than once criticized the way the colonial surgeons, including Mitchell, responded to Thompson's instructions; but he had criticized the tone and nature of the instructions themselves almost as often. Mitchell sued Thompson for libel, and won. In the meantime, he had appealed against his dismissal.

The appeal led eventually to an inquiry by Governor Gipps: as a result, Mitchell was reinstated in 1841 for one day, for the sole purpose of allowing him to retire without a stain on his name. Although the finding supported Thompson's rank and office, he suffered more than Mitchell, who in fact had little to lose. But Thompson was left a broken man, after yet another acrimonious conflict which had simply deepened his bitterness and disillusionment.

An account of the quarrel between Thompson and Mitchell, distinctly unsympathetic to Thompson, is provided by McIntosh (1956). It contains a good deal of accurate detail but does not, in the writer's opinion, sufficiently recognize the problems Thompson faced in dealing with an entrenched Sydney establishment. A good summary of the evidence is given in Gipps' Report on his Review of the case (Colonial Office, 1841b).

Thompson made other administrative mistakes, too. Soon after his arrival, he was taken to task for writing personal letters to the Secretary of State for the Colonies about mismanagement by certain officers of the colony who were outside his jurisdiction. He was told to stop his 'political investigations and writings' (Colonial Office, 1837b), and concentrate on his public duties. And as time went on, he displayed an increasing reluctance to provide the reports and accountings required of him, leading to comments about his 'inflexible taciturnity' and 'habitual delay' (Colonial Office, 1842a). What is more, he did not bring about the hoped-for reduction in costs.

Sustained Interest in Natural History

Despite Thompson's difficulties with his official duties in New South Wales, he continued to show his interest in natural history. Except for the dedication of his *Zoological Researches* to Sir James McGrigor, he had scrupulously kept this interest separate from his life as an army surgeon.

He began optimistically. On 20 April 1836, he wrote to his old acquaintance, Alexander Macleay, the Colonial Secretary, expressing his disappointment at not finding 'the Society'* flourishing, and his hope that Macleay would re-establish it and name some original members. He also made a number of suggestions about the scope and purpose of a natural history society, recommending a wide membership (Thompson, 1836). It appears that this letter was Thompson's acceptance of an invitation to join 'A Committee of Superintendence of the Australian Museum and Botanical Garden' (*Gazette*, 1836). Macleay became chairman, and Thompson was a member. The minute books of the Committee show that he attended meetings regularly from 1836 to 1843 and was a member of the Sub-Committees for both the Botanical Gardens and the Australian Museum (Australian Museum, 1836.)

Meanwhile, he still found time to look to his scientific reputation and contacts. His letter to Julien Desjardins, President of the Natural History Society, Mauritius, claiming authorship of the *Catalogue of Exotic Plants in Mauritius* has been mentioned already. A letter from the Curator of the Australian Museum records that ten specimens of native birds were given to J. V. Thompson 'for the Mauritius' in 1837 (Australian Museum, 1837). He is also on record in 1839 as having sent cotton seeds to Mauritius in 1838; and the 1840 Annual Report of the Mauritius Natural History Society records that 'Thompson is the only one of our New South Wales correspondents who has not given us up' (Vaughan, 1953). Thompson would have been heartened, too, to find that in 1839 Du Cane, a friend of Macleay, was one of those who had confirmed his observations on the metamorphosis of the Crustacea (Fletcher, 1920).

Removal from Office

Ever since Thompson had left Cork in 1835 without settling his account with Mrs Dwyer, she had been trying to get her money. Failing in appeals directly to Thompson, she had then unsuccessfully sought to have Sir James McGrigor order Thompson to pay. Getting no satisfaction in that quarter either, on 28 October 1841 she complained to the Secretary of State for the Colonies. It was Thompson's bad luck that her letter arrived only a fortnight after the Secretary of State had been considering Governor Gipps's report on the Mitchell case, and so Thompson's name was fresh in his mind. There is no record to show that Thompson paid the bill, in spite of a fresh instruction to do so.

During 1842, Thompson's neglect in submitting reports and returns became intolerable to his superiors (Colonial Office, 1842b). Finally, in November, he was given six weeks to submit a particular return. When he did not meet the deadline, preliminary steps were taken to replace him (Colonial Office, 1843a). The Governor reported to the Secretary of State, who in his turn asked McGrigor to remove Thompson. By this time it was July 1843. In the letter to McGrigor, the Colonial Office reminded him of Mrs Dwyer's case, saying that 'this renewed proof of that officer's negligence' seemed to call for his suspension from duty (Colonial Office, 1843b).

McGrigor replied that he was already aware of the situation, and recognized the need to act: '. . . for some time back I have had occasion to notice to Mr Thompson many instances of neglect in conducting the public duties and of his rarely performing the duty of inspecting the hospital, but finding this proceeded from greatly impaired

* Presumably he was referring to the defunct Philosophical Society of Australasia.

health, with mental as well as bodily infirmity, I informed him of my intention . . . of his being placed on the half pay of his rank in the army' (Colonial Office, 1843c).

McGrigor followed up his official letter with a private one to Stephen, his counterpart in the Colonial Office, presumably to make sure that no one proceeded with the idea of suspending Thompson or dismissing him outright, and so cutting off his income: 'The neglect of his duties by Mr Thompson . . . is not unknown to me. I regret to say that for a considerable time back I have had cause to complain of the imperfect manner in which he has performed his duties. I have reason to believe that this has proceeded from the broken down health of Mr Thompson who is no longer equal to the multifarious duties of the responsible situation in which he is placed' (Colonial Office, 1843d).

It is curious that Governor Gipps made no mention of Thompson's deteriorating health, which had been mentioned by Bourke at the end of 1836 but ignored thereafter in despatches from New South Wales. Hence one wonders how McGrigor came to his conclusion that ill health was an important reason for Thompson's poor performance. But the question is academic: Gipps had secured Thompson's removal.

Thompson was allowed to remain in office until his successor arrived in New South Wales (Colonial Office, 1843e). He relinquished his position on 1 February 1844, and his retirement to half pay was gazetted on 11 February (Johnston, 1917).

It should be said in his defence that, despite the problems described above, he survived for almost eight years in a position which had been almost untenable from the outset — more than twice as long as his counterpart in Van Diemens Land, who had taken up duty at the same time and was superseded in 1839. And no one seems to have complained about the quality of the medical service under his regime. In fact, at the end of 1839 Gipps had made a special point of remarking that he had no complaint about the way the 'strictly professional duties of the Medical Department in this Colony are performed' (Colonial Office, 1838b).

Thompson's 'taciturnity' and failing health in the 1840s did not prevent him from returning to his old interest in botany, and four more papers from him on the cultivation of cotton and sugar cane were published in the *Indian Journal of Agriculture* between 1842 and 1845 (Royal Society, 1871).

When Thompson retired, one piece of business with the Colonial Office was still unfinished. On 6 April 1843, having heard of a plan for sending young prisoners from Parkhurst to the colonies for rehabilitation, Thompson wrote another characteristically naive proposal to the Secretary of State for the Colonies. He announced that he had 'just purchased a farm (part of Eagle Farm) about seven miles from Brisbane Town, and [had] at present about 200 acres of clear tillage land'. His scheme was hastily conceived and impracticable. He said he would be 'most happy to try the experiment with from 10 to 20 of the Parkhurst boys . . . [T]hey will be removed from all temptation to steal or pick pockets and will be employed in gardening, assisting the agricultural labourers and vine dressers and in looking after the farm work. My object is to give a fair trial to tropical agriculture and in particular to cotton, sugar cane and coffee in addition to the vine and other colonial productions' (Thompson, 1843).

Perhaps Thompson wanted only to tell someone that he had just bought a property to replace the land his father had lost sixty-five years earlier. Whatever he intended, his plan misfired. It was typical of his luck that his application for Parkhurst boys was considered and rejected just the day before the Secretary of State approved his transfer to half pay. His Lordship remembered the letter, and saw it as just one more proof of Thompson's inattention to his real duties (Colonial Office, 1843f).

Thompson's last official letter is a sad reminder that mail took several months to pass between London and Sydney. A week after Thompson had been retired to half pay, the Governor called for a copy of his letter about the Parkhurst boys. Jno V. Thompson,

Deputy Inspector General, replied on 21 February 1844: 'I have the honor to acknowledge receipt of your communication of the 17th instant (44/14), and regret that I am incapable of supplying the copy of the letter addressed to the Secretary of State of 6th April last, considering it to be a private affair and only a request, which, having been deprived of every means of accepting now by the loss of my appointment, I must of necessity relinquish' (Thompson, 1844).

As far as is known, Thompson remained in Sydney for the next three years, and so did not have a chance to occupy his land at Moreton Bay. He died at his residence in Liverpool Street on 21 January 1847, and was buried in the Parish of St Lawrence, County of Cumberland (Registrar General, 1847). Presumably his grave was in the old Devonshire Street cemetery, now the site of Central Railway Station.

He directed that the monies from his estate should be used in the first instance to pay his debts, and that what remained should be paid to his 'dear wife for her use entirely' (Supreme Court, 1847).

CONCLUSION

Since his death, John Vaughan Thompson's contribution to natural science has been recognized spasmodically. A crustacean, *Vaunthompsonia*, was named after him, as was a plant from Madagascar, *Deidamia thompsoniana*, though the latter was subsequently given another name. He merits a line in some histories of zoology (Singer, 1959); Lankester (1890) gives him a full paragraph in the Zoology article in *The Advancement of Science*, remarking that 'Thompson made . . . great discoveries, which seem to have fallen in his way in the most simple and natural manner, but must be regarded really as the outcome of extraordinary genius'; and he is the subject of entries in the *Dictionary of National Biography* and the *Dictionary of Scientific Biography* under his own name. His *Zoological Researches* were reissued in a facsimile edition in 1968. It is interesting that the burning issues of his day were not seen by later biographers to be controversial. For instance, metamorphosis in Crustacea, the subject of acrimonious debate in the 1830s, was overlooked by Lankester, and hardly mentioned by Stebbing (1910) in the paper he wrote to mark the centenary of Thompson's election to a Fellowship in the Linnean Society.

Today, however, 140 years after his death, the way he approached natural history is more important than the truths he revealed. He was one of the genuine discoverers in the age when gentleman naturalists played a significant part in scientific inquiry, and even in that he illustrates a point: he shows how hard it was for a man short of money, and working alone, to have his work noticed. Previous biographers have praised his perceptiveness, and shown how his discoveries resulted from acute practical observation. But they have not made enough of his persistence, his solitariness and the disappointments he suffered.

He was a 'difficult' man and yet he was able to make a notable contribution to both botany and zoology. And that is only one side of his life. It is too easy to forget that his eight-year stint in New South Wales, where the odds were against him from the first, was the only blemish on a career in the Army Medical Service spanning forty-five years. On balance, his unhappy inability to get on with people neither cancels out his work as a surgeon nor dulls the brilliance of his lonely scientific achievements.

It is a pity that he was not in England when his discoveries were finally recognized. There he might have been honoured instead of being ignored. The careful obituary in the *Sydney Herald* of 26 January 1847, with no mention of friends and colleagues who appreciated him, emphasizes his loneliness. And it was John Vaughan Thompson's usual luck that the age was wrong. He was in his 68th year, not his 63rd: ' . . . in his 63rd

year, after long-continued illness — distinguished for his achievements in zoology and botany — possessing talents of no common order — and estimable in every relative duty of life — he is deeply lamented by his afflicted family, to whom his loss is irreparable' (*Herald*, 1847).

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Key to abbreviations used in the text: *ADB* = *Australian Dictionary of Biography*, 1967; *DNB* = *Dictionary of National Biography*, 1900; *EB* = *Encyclopedia Britannica*, 1968; Linn. Soc. = Linnean Society of London; Zool. Soc. = Zoological Society of London.

Key to abbreviations used in the references: CO xx/xx = Colonial Office Item Numbers; AJCP xx = Numbers of Australian Joint Copying Project Microfilm Reels; *HRA* = Historical Records of Australia volumes. Otherwise standard abbreviations are used for societies and journals.

Since many of the references are to manuscript letters and other records, the references are presented in two parts: Part 1: Published Works and Part 2: Unpublished letters, etc.

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- , 1839. — *HRA* I, Vol. 20: 77. McGrigor to Stephen, 5 February 1839.
- , 1841a. — CO 201/313 (AJCP Reel 336). Mrs Dwyer to Sec. of State for Colonies, 28 October 1841.
- , 1841b. — CO 201/306 (AJCP Reel 331). Gipps to Sec. of State, 19 January 1841.
- , 1842a. — CO 201/321 (AJCP Reel 340). Gipps to Stanley, 20 June 1842, margin note.
- , 1842b. — CO 201/321 (AJCP Reel 340). Gipps to Stanley, 20 June 1842.
- , 1843a. — CO 201/331 (AJCP Reel 346). Colonial Sec. to Thompson, 7 January 1843.
- , 1843b. — CO 201/330 (AJCP Reel 346). Colonial Office to McGrigor, 22 July 1843.
- , 1843c. — CO 201/338 (AJCP Reel 351). McGrigor to Stephen, 26 July 1843.
- , 1843d. — CO 201/338 (AJCP Reel 351). McGrigor to Stephen, 1 August 1843.
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- , 1836. — Archives Office of New South Wales, 4.2539.3, file 41/10460. Thompson to Macleay, 20 April 1836.
- , 1843. — CO 201/343 (AJCP Reel 354). Thompson to Sec. of State for Cols., 6 April 1843.
- , 1844. — *HRA* I, Vol. 23: 439, J. V. Thompson to Colonial Secretary Thomson, 21 February 1844.

A List of the Cryptogams and Gymnospermous Plant Specimens in the British Museum (Natural History) gathered by Robert Brown in Australia 1801-5

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A list is here published for the first time of the cryptogams and gymnosperms gathered by Robert Brown in Australia and now preserved in the herbarium of the British Museum (Natural History), London. Brief remarks on Brown's Australian visit and collecting during 1801-5 are given. Correlation with the register of the collection prepared by J. J. Bennett is indicated.

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'... That full account of the Botanical discoveries made during Flinders's expedition, which the public had a right to expect, has never appeared...'

J. Lindley, 1844

INTRODUCTION

The work of Robert Brown during and after Flinders' expedition to Australia in 1801-5 is recognized as a significant contribution to Australian natural history in general and Australian botany in particular, but scientific records of the expedition are fragmentary. Flinders' (1814) account of the voyage of the *Investigator* concentrates on geographical, navigational and sailing aspects and is useful for the chronology of the expedition up to his departure in 1803 and subsequent imprisonment at Mauritius. But for botanical details we must rely on Brown. His *Prodromus* of 1810 was intended to be the main account of the botany, but only one volume of the two proposed was produced, and only a few copies were sold. In due course, this important work was withdrawn. Brown also contributed a modest botanical appendix to the Flinders volumes (1814: 2, 533-613).

After the death of the expedition's commander, Matthew Flinders [1774-1814], British interest in the voyage appears to have declined, and it was not until 1904 that Britten published an account of the plants collected by Brown in Madeira on the outward voyage. More recently Rourke (1974) has produced an account of Brown's activities at the Cape of Good Hope, but there appears to be no list of South African specimens collected by Brown in existence. Brown's Timor plants are also little known, being only briefly mentioned by Forbes (1885). In Australia Brown prepared lists of plants seen or collected, or both, at some of the anchorages. Where these lists are still extant they remain in manuscript, and as Lindley (1844) pointed out, no published list of Brown's Australian plant specimens was available forty years after Brown returned. It

was not until the 1870s that a manuscript list of Brown's specimens was prepared. This is the catalogue referred to below as the 'Bennett Register'.

Recent Australian interest in the voyage began with the account by Burbidge (1956) of Brown's nomenclatural system (based on Flinders' chart annotations) for the Australian collecting localities. A landmark in studies of Brown's Australian botanical work was reached a few years later when a facsimile edition of the *Prodromus* (Brown, 1810) was published with an introduction by Stearn (1960a). There has been renewed interest in the natural history aspects of the voyage in the United Kingdom recently with the publication of a paper on the expedition by Edwards (1976) and the publication of the diary of Peter Good [d. 1803] also by Edwards (1981). Some of the paintings by the botanical artist Ferdinand Lukas Bauer [1760-1826] are reproduced by Stearn (1960b), Stearn and Blunt (1976) and Norst (in press). Vallance and Moore (1982) have given an account of the geological aspects of the voyage and Mabberley's (1985) work on Brown has provided a much-needed biography. Clements (1983) has described the orchids collected by Brown which are in the Lindley Herbarium and is to give an account of those in the British Museum (Natural History) Herbarium. However, there are no published lists of all the 3400 plants collected by Brown in Australia.

Further work, which will be published in the near future, includes the edited transcription of Brown's Diary of the voyage (Vallance *et al.*, in preparation). An important outcome of the Diary publication project is the realization that considerably more specimens were collected by Brown than are mentioned in either the *Prodromus* (Brown, 1810) or the Diary accounts. In his Diary Brown uses a variety of plant names. These include names already published by, for example, Carl Linnaeus [1707-1778], William Aiton [1731-1793] and others. But he also used 'nicknames' for species he did not immediately recognize. These are sometimes manuscript names attributable to D. C. Solander [1736-1786]. Their use is hinted at in a letter (British Library Add. MS 32439, ff61-4 and *Historical Records of N.S.W.* 4: 776-9) written by Brown to Sir Joseph Banks [1743-1820] from Sydney on 30 May 1802 which contains the following passage: '... The list ... is partly compos'd of nicknames given at the moment the plants were collected, and not allow'd since. Some of them, I am afraid, may mislead, and the greater part I am aware are rather barbarous, especially where I have terminated specific names in oides, which I have done when uncertain whether the plant was distinct from a species already known, ...'

'Oides' names are mentioned in Brown's Diary text and as a result of work connected with editing the Diary for publication, the surviving plant specimens gathered by Brown have been located in the BM (NH) Herbarium in order to check if these 'nicknames' were mentioned on the original labels. Fortunately most of them are. The locating of Brown's plants led to the preparation of an index of over 3000 cards (Groves and Moore, 1986), and the cryptogams and gymnospermous representatives located in this way form the basis of this account.

ROBERT BROWN'S PLANT COLLECTION

A letter from Sir Joseph Banks to Sir John Barrow [1764-1848], written on 9th October 1805 (B.L. Add. MS 32439, f185), reveals that twelve boxes of dried plants and eleven boxes of Bauer's natural history drawings were landed at Liverpool from the *Investigator*. There were, in all, 38 cases of natural history specimens (cf. Edwards, 1976). Banks indicates in a letter of 3rd January 1807 (B.L. Add. MS 32439, ff237-245) that about 3600 specimens were in the boxes of plants. Edwards (1976), citing Banks, stated that there were about 700 plant specimens from the south coast of Australia, 500 from the east coast, 500 from the north and 700 from Tasmania; there were some 1000

specimens from the neighbourhood of Port Jackson, and 200 from the island of Timor (not discussed here).

Brown wrote relatively little on the lower plants, but the existence of his paper on mosses (Brown, 1811) indicates he was to some extent interested in Bryophytes. But his greatest contribution to the plants that are our concern in this paper was the realization that the cycads had coniferous similarities (Brown, 1826).

Having survived the voyage to England in a leaking ship, impounding at the Custom House of Liverpool, and a journey to London by the roads of 1805 (Vallance *et al.*, in prep.), it is appropriate to examine what befell the specimens after their arrival in London. They appear to have gone initially to Banks's house in Soho Square. There and later at the British Museum, they were a major part of Brown's herbarium (Murray, 1904). During his lifetime Brown kept his own herbarium separate from the British Museum material and did not allow free access (Edwards, 1976), but George Bentham [1800-1884] consulted it in the preparation of his *Flora* (Bentham and Mueller, 1863-1878) (cf. Stearn, 1981). The next to feature as custodian of Brown's plants was J. J. Bennett [1801-1876]. Bennett became assistant to Brown at the British Museum in November 1827 and Brown's herbarium was left to him at Brown's death (Woodward, 1904; Mabberley, 1985). In his turn Bennett kept the Brown herbarium separate from the main herbarium but on his death (February 1876) his wife gave it to the British Museum and it was then incorporated into the General Herbarium. Duplicates, and material which today would not necessarily be considered as duplicate, were later distributed to other institutions in Europe and Australia. Those sent to Ireland have been listed by Powell and Morley (1976).

Unlike the practice in other British Museum departments, the Botany Department never prepared formal registers, so there are no present-day BM (NH) herbarium numbers as such.

There are indications that some Brown Herbarium vascular plant specimens were given to Banks's librarian Jonas Dryander [1748-1810] during his lifetime. The Brown specimens listed in the Bennett register do not include these duplicates. In our list we have included them only where we believe the original is lost and where we can relate them to the Bennett register entries. These Dryander duplicates are recognizable by Dryander's later label, but bear neither a Brown original label nor the blue sticker of Bennett's plants (see below), nor a number. Some are unique while others are plants from the same gathering as that to which a Bennett number was given. The actual numbering was done by James Britten [1846-1924], assistant and later librarian, in the Botany Department and was probably undertaken soon after Brown's herbarium was acquired on the death of Bennett.

Not all species given by Brown (1810) are in our list, as Brown sometimes selected Banks and Solander specimens for his descriptions. As an example, *Mitrasacme prolifera* R.Br., Spigeliaceae (Bennett 2894) bears a Brown label indicating that it came from the Endeavour River, Queensland, in 1770. The description of this taxon in the *Prodromus* (Brown, 1810: 453, entry 8) then, is of a Banks and Solander gathering, not Brown's.

Fortunately, Brown annotated his algal and pteridophyte original labels after the publication of Turner's (1807-19) *Fuci* and his own *Prodromus* (Brown, 1810). So we have reason for thinking that certain specimens are illustrated, or at least noticed, in these works. A fern example is Bennett 104 (*Gleichenia rupestris* R.Br., see below). Bryophyte and gymnosperm labels are not annotated in this way.

THE BENNETT REGISTER

After coming into possession of Brown's Herbarium Bennett instituted a register of

the material. This gave the plants both a number and a name. But it was left to Britten, assisted by Henry Trimen [1843-1896], to complete the task (Edwards 1976). No locality or ecological data are recorded in this 'Bennett Register'. Such detail as Brown committed to paper is obtainable only from the original labels on the herbarium sheets, and, in some instances, from Brown's descriptions in the Botany Library (the 'Brown Slips'). In the herbarium the Brown specimens catalogued by Bennett and his followers are recognized by a blue label bearing Britten's hand-written number and the printed words 'Iter Australiense 1801-5'.

One hundred and twenty-three numbers were allocated to Brown's algae and charophytes in the Bennett register. Of these, we have been able to find eighty-four. Because Bennett's workers missed specimens which we include, it is difficult to make numbers of 'found' taxa agree with the Bennett register. Some of Brown's algae were described by Dawson Turner [1775-1858], and in the list below, dates of publication of parts of Turner's *Fuci* (1807-1819) are given according to Price (1984). Fortunately, the specimens described by Turner (1807-19) are recognizable because Brown annotated his labels to the effect 'this is the specimen sent to Mr Turner'.

The absence of Brown's original labels in some cases means there is no locality information for some specimens. Also, the Brown locality 'South Coast' is disappointingly vague. But better locality data are often available where a specimen is mentioned in Turner (1807-19). In our list nomenclature, where appropriate, is in accordance with Womersley (1967, 1984, 1987). The charophyte nomenclature used in our list is that of Wood (1965) and we have located four out of five of Brown's charophytes.

The lichens were never given space in the Bennett register. It would appear that they were handed in the 1870s to the Rev. J. M. Crombie [1830-1906] to investigate, probably with a batch of blank 'Iter Australiense' labels. It is Crombie's writing on the blue labels accompanying Brown's original lichen labels and it would appear that Crombie also applied the series of numbers. The numbers used are between 500 and 579 (thus not duplicating any numbers assigned by Bennett and Britten). It is these numbers which were quoted by Crombie (1879). It can be seen from the lichen list that there are several species given the same number. This is because since the 1870s many have received revision and so now consist of more than one species under one number. Many of Brown's lichens were collected in Tasmania, and Kantvilas (1983) warns of the unreliable nature of many of Brown's labels. But, as others have found (Vallance and Moore, 1982), the original labels may give reliable provenance data and should not be regarded lightly.

Assuming that originally there were seventy-nine lichens, and each was allocated a number by Crombie, we have been unable to trace twenty-four of them.

The fungi too are somewhat neglected by the Bennett register. They were allocated numbers 142-156 (inclusive), but no identifications or other data were entered against the numbers. The specimens, probably all mounted, were transferred to Kew Herbarium when the BM(NH) fungal collection was passed to Kew as a result of the Moreton agreement of 1961 (cf. Stearn, 1981: 309-310). They have since been incorporated into the Kew collections. A search made there by one of us (EWG) to trace Brown's fungi, with the aid of the list of the ten names in Brown's appendix to Flinders (1814: 2, 592-4), has revealed only one possible fungus. This is 'Clavaria coralloides L.' (= *Clavaria cristata* var. *coralloides* Corner). While not attributed to Brown on the sheet, the writing beneath the specimen and the watermark of the paper appear to be contemporary with other Brown sheets at the BM(NH).

The majority of Brown's bryophytes in the BM(NH) remain unmounted and have still to be critically examined. As they lack Bennett numbers they have not been included here. But a minority were allocated Bennett numbers and subsequently

incorporated in the herbarium. These appear to be mostly from Tasmania. There is Brown material on some sheets from the Hooker herbarium (*ex Kew*) but this does not have original labels. From Brown's Diary (cf. Vallance *et al.*, in prep.) we know that Brown visited only Port Dalrymple, and the Esk Rivers and the River Derwent/Mt. Wellington areas of Tasmania in 1804. Despite this, we have accounted for all the spaces in the Bennett register assigned to bryophytes.

In the 1870s Bennett assigned one hundred and forty-four numbers to Brown's pteridophytes. We have found all but two.

Brown (1810) indicated by letters the provenance of the species described, for example 'D' for Tasmania, and 'J' for Port Jackson. The original labels were annotated by Brown so there is reason for thinking that certain specimens are the ones that formed the basis of the descriptions in Brown (1810).

Three cycadophytes are noted in the Bennett register. While we have traced two, there remains uncertainty over the identity of 'Zamia spiralis' of Flinders (1814: 1, 81). It appears to be a late entry to the Bennett register and thus existed in the 1870s. We have not traced it. Brown (1810: 348, entry 1 'J' & 'M') indicated his specimen was not tropical and from study of Brown's Diary (Vallance *et al.*, in prep.; cf. Flinders, 1814: 1, 348) we believe the specimen came from Lucky Bay, Western Australia. Consequently, we think it was, in fact, *Macrozamia riedlei* (Fisch. ex Gaudich.) C. A. Gardn., Zamiaceae (cf. Johnson, 1959: 103). This is 'Macrozamia spiralis Miq.' of Mabberley (1985: 86).

In our list of Brown's conifers we follow the nomenclatural recommendation of Mr K. Hill of the Royal Botanic Gardens, Sydney. Bennett assigned nineteen spaces in his register to this group. We have found fourteen specimens.

The manuscript Bennett register (now housed in the Botany Library, BM (NH)), is the only document to list the plant specimens gathered by Brown in Australia. But it was written seventy years after the voyage ended and is a somewhat inadequate document for curatorial purposes. There were, for example, 3900 numbers allocated but considerably fewer than this number of actual specimens; there are blank numbers in the register and the numbers do not run consecutively. For example, the bryophytes finish at 295 and the next entry, the Asteraceae (Compositae), start at 2000. So, as the sequential arrangement in the Bennett register bears no chronological relation to the order of collection, and exhibits only a rudimentary grouping into families, there is no advantage in giving our list in this manner. Consequently in our list the genera are arranged in alphabetical order under their respective groups. The number we have given to each entry has been applied merely to aid reference.

NOTES ON THE SPECIMEN LIST

1. In the following list we give Brown's original label entry, with his geographical and ecological data as they are set out on the labels. Keys to the geographical localities and anchorages around Australia will be found in Burbidge (1956) and Stearn (1960a).
2. For some listed specimens there is more than one original label per herbarium sheet, but in numerous instances there is more than one sheet per label and more than one plant per sheet. In some cases it is not always clear which label goes with which plant.
3. We have kept editorial comment on the texts of Brown's original labels (given here in single quotation marks) to a minimum, but we have indicated any references on the original labels to Turner's *Fuci* (1807-1819), Crombie (1879) and Brown (1810). The note 'Icones Bauer' found on some higher-plant labels appears not to be present on the pteridophyte labels. Our claim that the Bauer painting of, for example, *Azolla*, is based on a particular herbarium specimen is circumstantial and visual.

ALGAE

CHLOROPHYTA

1. *Anadyomene brownii* (Gray) J.Ag. Bennett 205
Lacks a Brown original label, and is thus unlocalized. An annotation on the sheet indicates that this is 'Calomena brownii' of Gray (1866: t.44, fig. 3) and has type status.
2. *Caulerpa brownii* (C.Ag.) Endl. Bennett 173
'Actaia selago? [sic] Kents Islands'
There are two sheets of this material with identical labels.
3. *Caulerpa cactoides* (Turn.) C.Ag. Bennett 166
'Actaia opuntia South Coast the specimen sent to Mr Turner'.
'Fucus cactoides' of Turner (1809-11: 3, 89-90, t.171). Type status.
4. *Caulerpa flexilis* Lam. Bennett 172
(Syn. 'Caulerpa hypnoides' (R.Br.) C.Ag.)
'Actaia hypnoides Kents Islands'. Turner (1809-11: 3, 93-4, t.173).
Two specimens, one with type status.
5. *Caulerpa geminata* Harv. Bennett 167
(Syn. 'Caulerpa sedoides' (R.Br.) C.Ag.)
Two identical labels on the sheet. 'Actaia sedoides L Kents Islands. The specimens sent to Mr Turner'. In fact, 'Fucus sedoides' of Turner (1809-11: 3, 92, t.172). There is an annotation on another sheet *ex* Turner herb. (formerly at Kew) by I. R. Price, 16 xii 1974 to the effect that the specimen was the basis of Turner's figure. Type status.
6. *Caulerpa racemosa* var. *laetevirens* (Mont.) Weber van Bosse Bennett 168
No original labels, and specimen is consequently unlocalized, but a note by I. R. Price of 10 xii 1974 indicates he considered the material to be possibly of the tropical var. *lamourouxii* (Turn.) Weber van Bosse.
7. *Caulerpa racemosa* (Forsk.) J.Ag. var. *laetevirens* (Mont.) Weber van Bosse Bennett 169
'Actaia clavata South Coast'. I. R. Price in a note of 10 xii 1974 considers this locality incorrect.
8. *Caulerpa racemosa* (Forsk.) J.Ag. var. *laetevirens* (Mont.) forma *cylindrica* (Sonder) Unnumbered
Weber van Bosse
(Syn. 'Caulerpa cylindracea' Sonder)
Two specimens on one sheet, the lower one is labelled 'Actaia clavata South Coast'.
9. *Caulerpa scalpelliformis* (R.Br. ex Turn.) J.Ag. Bennett 171
Two labels: 1st reads 'Actaia scalpelliformis South Coast'; 2nd reads 'Actaia scalpelliformis South Coast the spec sent to Mr Turner'. Turner (1809-11: 3, 95-6, t.174).
Type status.
10. *Caulerpa sertularioides* (S.Gmel.) Howe Bennett 170
(Syn. 'Caulerpa taxifolia' (Turn.) C.Ag.)
Two sheets, label reads 'Caulerpa taxifolia Fucus taxifolius Turn South Coast'.
'Fucus taxifolius' is featured in Turner (1807-8: 1, 120-122, t.54). In a note on the sheet of 10 xii 1974 I. R. Price considered this taxon to be tropical.

11. *Caulerpa simpliciuscula* (Turn.) C.Ag. Bennett 174
There are two sheets 'Actaia conglobata Kents Islands'. Turner 1809-11: 3, 98, t.175).
12. *Codium australicum* Silva Bennett 181 (pro parte)
No Brown label, consequently unlocalized.
13. *Codium duthieae* Silva Bennett 181 (pro parte)
No Brown label.
14. *Codium fragile* (Suringar) Hariot ssp. *tasmanicum* (J.Ag.) Silva Bennett 181
'SC' [?South Coast]. (pro parte)
15. *Codium muelleri* Kütz. Bennett 181a
No Brown label and unlocalized.
16. *Polyphysa peniculus* (R.Br. ex Turn.) C.Ag. Bennett 203
(Syn. 'Acetabularia peniculus' (R.Br. ex Turn.) Solms-Laubach)
Has type status but sheet on loan in November 1988.

PHAEOPHYTA

17. *Acrocarpia paniculata* (Turn.) Aresch. Bennett 213
Two labels: 1st reads 'The sp sent to Mr Turner Fucus scoparino Kents Islands Bass Strait'; 2nd reads 'Fucus paniculatus Turn. hist 3 p.99 t.176 Cystoseira paniculata Agardh [1823-8] Sp. alg. 1 p.76'. Turner (1809-11: 3, 99-100, t.176). Type status.
18. *Asperococcus bulbosus* Lam. Bennett 179
'F[ucus] ampullaceus is an incorrect name for a plant wch when perfect is filld with a dense gelatinous material' [reverse reads] 'Kents Islands & South Coast'.
19. *Carpoglossum confluens* (R.Br. ex Turner) Kütz. Bennett 226
'Fucus confluens Port Dalrymple'. 'Fucus confluens' of Turner (1809-1811: 3, 17, t.141), Agardh (1823-8: 1, 95). Type status.
20. *Cystophora brownii* (Turn.) J.Ag. Bennett 208
'Fucus Browni Turn Hist 4 p1 t 197 Cystoseira Brownii Agardh sp algar; 1 p.73' [reverse] 'sent to Mr Turner, you proposd to give it my name South coast frequent'. According to Turner (1811-19: 4, 2-3), the specimen is from King George Sound. See also, Agardh (1823-8: 1, 73). H. B. Womersley appended a note, dated 31 v 1952, to the effect that the lower of the two specimens on the sheet is the type of 'C. brownii', but the upper may be 'C. monilifera'.
21. *Cystophora moniliformis* (Esper.) Womersley & Nizamuddin ex Womersley Bennett 214
Two labels, 1st reads 'non logica F barbata sed distincta & prope F thuyoid: Herb Banks' [reverse] 'Fucus paniculatus litt. Kents Group'; 2nd reads 'Fucus spartioides Turn hist. 4 p.85 t.232. Mr Turner did not return the specimen which is in fructification RB'. Turner (1811-19: 4, 86, t.232). Type status.
22. *Cystophora retroflexa* (Labill.) J.Ag. Bennett 209
Two labels: 1st reads 'Fucus ramosissimus South Coast sent to Mr Turner'; 2nd reads

- '*Fucus retroflexus* Labill. Turn. hist. 3 p.47 t.155 *Cistoseira retroflexa* Agardh [1823-8] sp Alg. 1 p. 74'. Turner (1809-11: 3, 48, t.155).
23. *Cystophora torulosa* (R.Br. ex Turn.) J.Ag. Bennett 211
 'Fucus torulosus Kents Islands Bass Strait 1803-4 The sp sent to Mr Turner'. Turner (1809-11: 3, 51, t.157). Another sheet (ex Kew herbarium), lacks a Bennett number, but is almost certainly another portion of the same gathering. It has a label which reads 'dup Fucus torulosus N Sp Turn fuc 3 [. . .] t157 Kents Group *Cystophora torulosa* Agardh'. Turner (1809-11: 3, 52, t.157). Type status.
24. *Cystophora* sp.indet. Bennett 219
 'Fucus vagus the sp sent to Mr Turner Fucus vagus South Coast'. The Turner illustration implied by the original label is untraced.
25. *Cystophora* sp.indet. Bennett 221
 'Cystoseira (?) affin retroflexa Dr Agardh has a perfect specimen from Dr Greville'. Unlocalized.
26. *Cystophora* sp.indet. Bennett 224
 'Cystoseira [. . .] retroflexa'. Unlocalized.
27. *Cystoseira trinodis* (Forsk.) C.Ag. Bennett 218
 (Syn. '*Cystophyllum muricatum*' (Turn.) J.Ag.)
 Two labels: 1st reads 'Fucus angustifolius North Coast of New Holland F muricatus Mr Turner's writing'; 2nd reads 'Cystoseira muricata North Coast Cystoseira trinodis Ag [1823-8], Sp Alg p.67 [. . .] 24 June 1833'. Turner (1808-09: 2, 107-8, t.112).
28. *Cystoseira trinodis* (Forsk.) C.Ag. Bennett 223
 No original labels, and unlocalized.
29. *Dictyopteris woodwardia* (R.Br. ex Turn.) J.Ag. Bennett 177
 Two identical labels which read 'Fucus woodwardia North Coast [reverse reads] a F membranaceo divers frondibus spinulo-denticula'. A third sheet ex Herb. Kew, although lacking the Bennett number, is of the same gathering. Type status.
30. *Dictyota* sp.indet. Bennett 251
 'Kents Islands'.
31. *Ecklonia biruncinata* (Bory) Papenfuss Bennett 229
 (Syn. '*Ecklonia radiata*' (Turn.) J.Ag.)
 'Fucus radiatus Turn. hist 2 p.161 t.134 Port Dalrymple too young for Baptism [sic]'. Turner (1808-09: 2, 161-2, t.134).
 An annotation on the sheet indicates this specimen was identified by H. B. S. Womersley 25. v. 1952 as the type of Turner's var. *exasperata* of *F. radiatus*.
32. *Homoeostrichus sinclairii* (Hook. & Harv.) J.Ag. Bennett 175
 (Syn. '*Zonaria stiposa*' R.Br. ex J.Ag.)
 Two labelled sheets: 1st reads 'Zonaria Nov sp'; 2nd reads 'Kents Islands'. Type status.
33. *Hormosira banksii* (Turn.) Decaisne No Bennett number
 No sheet bearing Brown's original label exists. There is, however, a label in Brown's

hand ex Herb. Kew which reads 'Nov. Holl. or occident. Herb. Mus. Paris Sep 1816 [added later] *Cystoseira expansa* Ag' [a third sheet is labelled] '*Cistoseira Banksii*'. Type status.

34. *Macrocystus pyriforme* (L.) C.Ag. Bennett 231
'*Fucus pyriformis* King's Island'.

35. *Perithalia caudata* (Labill.) Womersley Bennett 227
Two labels: 1st reads '*Fucus inermis* Port Dalrymple & South Coast of New Holland'; 2nd reads '*Fucus inermis* distinct from *F aculeatus* with minute globules terminating the ramuli'. Type status.

36. *Phyllospora comosa* (Labill.) C.Ag. Bennett 230
Two identical labels reading '*Fucus polyphyllus* South Coast of New Holland *F comosus*'. We note Turner (1809-11: 3, 18, t.142) gives the locality as 'Van Diemens Land'.

37. *Platythalia quercifolia* (R.Br. ex Turn.) Sond. Bennett 217
Three labels: 1st reads '*Fucus quercifolius* South Coast New Holland 1802 [. . .]'; 2nd reads '*Fucus quercifolius* South Coast of New Holland Turn hist 3 p37 t.151 *Cystoseira quercifolia* Ag'; 3rd label reads '*Fucus quercifolius* Turn hist 3. p.37 t.151'. Turner (1809-11: 3, 37, t.151). Type status.

38. *Sargassum decipiens* (Turn.) J.Ag. Unnumbered
Two labels: 1st reads '*Fucus polymorphus* [struck through] *decipiens* Port Dalrymple the sp sent to Mr Turner'; 2nd reads '*Fucus decipiens* Ag Turn fuc 3 p79 t166'. Turner (1809-11: 3, 79, t.166). Type status.

39. *Sargassum decurrens* (Turn.) J.Ag. Bennett 157
'*Fucus decurrens* Turn hist 3 p143 t194 North Coast (I believ) [sic] only specimen sp figured'. See Turner (1809-11: 3, 143, t.194). Type status.

40. *Sargassum heterophyllum* C.Ag. Unnumbered
Turner (1808-9: 2, 62, t.92) cites a Brown specimen of '*Fucus heterophyllum*' from 'Coast of New Holland' but this material is untraced.

41. *Sargassum lacerifolium* (R.Br. Turn.) J.Ag. Bennett 158
'*Fucus lacerifolius* Turn hist 3 p81 t.167 *Sargassum lacerifolium* Agardh [1823- 8] sp alg. 1- p15 [. . .]. From Port Dalrymple, Tasmania, according to Turner (1809-11: 3, 81-2, t.167). Type status.

42. *Sargassum paradoxum* (R.Br.) Harv. Bennett 210
Two labels: 1st reads '*Fucus paradoxus* South Coast'; 2nd reads '*Fucus paradoxus* Mss Turn Fuc 3 p.49 t156 *Cystoseira paradoxa* Agardh [1823-8] in sp. alg. 1 p.15'. Turner (1809-11: 3, 49, t.156). Type status.

43. *Sargassum vestitum* (R.Br. ex Turn.) C.Ag. Bennett 159
Two labels: 1st reads '*Fucus vestitus* Kents Islands Bass strait & South Coast The specimen sent to Mr Turner'; 2nd reads '*Fucus vestitus* Turn. hist. 3 p101 t177 *Sargassum vestitum* Agardh [1823-8] Sp. Alg. 1 p24'. Turner (1809-11: 3, 101-2, t.177). Type status.

44. *Sargassum* sp.indet. Bennett 161
 'Sargassum North Coast of New Holland'.
45. *Sargassum* sp.indet. Bennett 162
 'Sargassum cum *S. ilicifolia* receptaculis convenit North Coast'.
46. *Sargassum* sp.indet. Bennett 163
 'Sargassum North Coast of New Hollnad'
47. *Scytothalia dorycarpa* (Turn.) Grev. Bennett 216
 Two sheets and two labels: 1st reads 'Fucus platycarpus South Coast of New Holland The specimen sent to Mr Turner'; 2nd reads 'Fucus dorycarpus Turn hist 3. p.21 t.143 Cystoseira dorycapa Agardh [1823-8] Sp alg 1 p.80'.
 'It is not clear in Turner (1809-11: 3, 24, t.144) if the illustrated specimen was collected by Menzies or Brown.
48. *Seirococcus axillaris* (R.Br. ex Turn.) Grev. Bennett 215
 Two sheets, three labels in all: 1st reads 'Fucus axillaris Port Dalrymple The sp sent to Mr Turner sp fig'; 2nd reads 'Fucus axillaris Turn hist 3 p.27 t146 Cystoseira axillaris Agardh [1823-8] sp. alg p.80'; 3rd reads 'Cystoseira axillaris Port Dalrymple'. Turner (1809-11: 3, 28, t.146). Type status.
49. *Splachnidium rugosum* (L.) Grev. Bennett 225
 Two labels: 1st reads 'Fucus rugosus Kents Islands shallow water on rocks. You say [sic] *Ulva rugosus* Herb[?] Lad'; 2nd reads 'Fucus rugosus Turn. hist 3 p.119 t.185 Agardh [1823-8] Sp alg. 1 p100 Kents Islands'. Turner (1809-11: 3, 118, t.185).
50. *Sporochnus radiceformis* (R.Br. ex Turn.) C.Ag. Bennett 228
 'Fucus ?radiceformis is it a Fucus Kents Islands Bass Strait. Type status.
51. *Xiphophora chondrophylla* (R.Br. ex Turn.) Montague ex Harv. Bennett 271
 Two labels: 1st reads 'Fucus chondrophyllus Port Dalrymple'; 2nd reads 'Fucus chondrophyllus Mss Turn. hist 4 p. 60 t.222'. Turner (1811-19: 4, 60, t.222).
52. *Zonaria* sp.indet. Bennett 182
 No Brown label and consequently unlocalized.

RHODOPHYTA

53. *Brongniartella australis* (J.Ag.) Schmitz Bennett 195
 'Griffithsia australis Ag [. . .]'. Unlocalized. Agardh (1823-8: 2, 135).
54. *Champia parvula* (C.Ag.) Harv. Bennett 240
 No orig. label, consequently unlocalized.
55. *Coelarthrum muelleri* (Sonder) Borges. Bennett 245
 'Fucus compar Kents Islands Bass Strait & South Coast of New Holland'. Another sheet ex Herb. Kew, of the same gathering, bears the locality in Brown's handwriting as 'South & East coasts of New Holland'.

56. *Gelidiella acerosa* (Forsk.) J. Feldmann & Hamel Bennett 264
(Syn. 'Gelidiopsis rigida' Grev.)
'Spharococcus rigidus Ag [1823-8] Sp. Alg. p.285 [. . .]'. No locality or other data on original label.
57. *Gelidium australe* J.Ag. Bennett 250
'F corneus? [sic]'. No locality given.
58. *Gelidium glandulaefolium* Hook. & Harv. Bennett 272
No Brown label. Secondary label reads 'Fucus Kents Group'.
59. *Gracilaria edulis* (S.Gmel.) Silva Bennett 269
(Syn. 'Gracilaria corniculata' (R.Br. ex Turn.) J.Ag.)
Two labels: 1st reads 'Fucus ceratophyllus [struck through] corniculatus The sp sent to Mr Turner Kents Islands 1803-4 proxe cornea a distinc: spec? [sic]'; 2nd reads 'Fucus corniculatus Turn 3 p.113 t.182'. Turner (1809-11: 3, 112, t.182). A note appended by H. B. S. Womersley on 27.v.1952 indicates 'this specimen may well be a Gigartina'. Type status.
60. *Griffithsia* sp. indet. Bennett 193
'Griffithsia'. No locality given.
61. *Hymenocladia divaricata* (R.Br.) Harv. Bennett 254
'Fucus divaricatus Mss in fructific only specimen Fucus divaricatus Turn hist 3 p.110 t181'. Turner (1809-11: 3, 110, t.181) localizes Brown's material as from 'on the coast of New Holland'. Type status.
62. *Hymenocladia usnea* (R.Br.) J.Ag. Bennett 259
'Fucus usnea Mss Kents Group Basses Strait 1803-4'. A second label, not Brown's, reads 'Fucus usnea Ag Turner Hist 4 p70 t225. Chondria usnea Agardh [1823-8] Syn Alg. XVIII. Turner (1811-19: 4, 70, t.225). Type status.
63. *Hypnea musciformis* (Wulf.) Lamour. Bennett 236
'F musciformis'. Unlocalized.
64. *Laurencia botryoides* (Turn.) Gaill. Bennett 253
On loan at time of compilation.
65. *Laurencia pinnatifida* (Huds.) Lam. Bennett 257
Two sheets with identical labels; 'Fucus pinnatifidus Kents Islands'.
66. *Leptophyllis conferta* (R.Br. ex Turn.) J.Ag. Bennett 263
Two labels: 1st reads 'Fucus confertus Kents Islands 1803 Scopula nov sp? [sic]'; 2nd reads 'Fucus confertus Mss Turn. 3 p177 t184 Delesseria ?conferta Ag. [1823-8] Sp. alg. p. 177? [sic]'. Turner (1809-11: 3, 116, t.184). Type status.
67. *Melanthalia obtusata* (Labill.) J.Ag. Bennett 260
Two labels: 1st reads 'Fucus strictus Port Dalrymple F obtusatus Labill?'; 2nd reads 'Fucus obtusatus Labill Turn. hist 3 p.25 t.145'. Turner (1809-11: 3, 25-6, t.145).

68. *Osmundaria prolifera* Lamour. Bennett 206
 (Syn. 'Polyphacum proliferum' C.Ag.)
 'Polyphacum proliferum Agardh [1823-8] Sp. alg. 1. p.106. *Osmundaria prolifera*
 Lamour Port Dalrymple the only specimen'
69. *Peyssonnelia australis* Sond. Bennett 176
 No Brown label, consequently unlocalized.
70. *Phacelocarpus labillardieri* (Mert. ex Turn.) J.Ag. Unnumbered
 No Brown gathering of this taxon has been traced in the BM (NH) herbarium, but there
 is a specimen marked 'Australia R Brown' (not in Brown's writing) and a fragment on
 another sheet labelled 'F scolopendrum Mss Mr Brown 1807 [sic]'. Both sheets were
 formerly in the Kew herbarium. Turner states regarding '*Fucus labillardieri*' that 'This
 plant has also been gathered upon the coast of New Holland by our own countryman,
 Mr Brown'. Turner (1809-11: 3, 8, t.137).
71. *Plocanium* sp.indet. Bennett 251
 'Fuci pulchilli var? [γ] Junior planta? Kents Islands Bass Strait according to you may be
 F aspenoides in herb.' Secondary label reads 'Delessaria plocanium [a]'
72. *Plocanium* sp.indet. Bennett 252
 'Fucus pulchellus Kents Island in Bass Strait & Port Dalrymple 1803-4.
73. *Polyopes constrictus* (Turn.) J.Ag. Bennett 268
 Two labels: 1st reads 'Fucus densus Kents Islands 1803-4'; 2nd reads 'Fucus constrictus
 Turn. hist 3 p39 t152'. See Turner (1809-11: 3, 39-40, t.152). Type status.
74. *Polysiphonia decipiens* Mont. Bennett 235
 (Syn. 'Polysiphonia cancellata' Harv.)
 Lacks original label, and consequently unlocalized.
75. *Pterocladia lucida* (R.Br. ex Turn.) J.Ag. Bennett 266
 'Fucus lucidus Mss Turn. hist. 4 p99 t238'. Turner (1811-19: 4, 99, t.238) gives the locality
 as 'on the southern coasts of New Holland'.
76. *Rhabdonia verticillata* Herv. Bennett 244
 'Fucus is it diffit from Compar [sic] Kents Islands'.
77. *Rhodymenia cuneifolia* (Hook.f. & Harv.) Taylor Bennett 249
 (Syn. 'R. corallina' Grev.)
 No Brown label, consequently unlocalized.
78. *Trematocarpus concinnus* (R.Br.) De Toni Bennett 233
 'Fucus caespitosus according to you a var. of F plicatus Kents Islands One spec in fructif'.
 Type status.
79. *Trematocarpus concinnus* (R.Br.) De Toni Bennett 267
 Two labels: 1st reads 'Fucus scoparius [struck through] concinnus Kents Islands 1803-4';
 2nd reads 'Fucus concinnus Mss Turn. hist 3 p41 t153'. See Turner (1809-11: 3, 41-2,
 t.153). Type status.

80. *Vidalia fimbriata* (R.Br.) J.Ag. Bennett 261
Two labels: 1st reads 'Fucus fimbriatus North Coast of New Holl spec unic (?) [sic]'; 2nd reads 'Fucus fimbriatus Mss Turn. Hist. 3. p87 t170'. Turner (1809-11: 3, 87-8, t.170).
Type status.

CHAROPHYTA

81. *Chara corallina* Klein ex Willd. Bennett 277
(Syn. 'Chara australis' R.Br.)
'Chara crassifolia Port Jackson'
82. *Chara corallina* Klein ex Willd. Bennett 279
(Syn. 'Chara plebeja' R.Br.)
'Chara A Carpentaria Point [sic, locality not given]'
83. *Nitella congesta* (R.Br.) A.Br. Bennett 276
'Chara cfr B a Bay I South Coast'. Lucky Bay, Western Austalia (cf. Burbidge, 1956).
84. *Nitella hyalina* (DC.) J.Ag. Unnumbered
Two sheets with identical data 'Chara B Point T Carpentaria'. Cape Shield, Northern Territory (cf. Burbidge, 1956).

LICHENES

85. *Cladia aggregata* (Sw.) Nyl. Bennett 532
'Lichen multiflorius Cladonia multiflora ericet elevat aust:' (cf. Crombie, 1879: 393), a type according to Filson (1981: 15).
86. *Cladia ferdinandii* (Müll. Arg) R. Filson Bennett 533
'Lucky Bay Cladia retipora'. Another sheet without a Bennett number, but of the same gathering, bears the label 'On the ground Lucky Bay Tasmania [sic]'. A note by R. Filson of 8 vi 1983 states that 'this specimen was probably collected at Lucky Bay, W Australia [. . .]'. The identification of this material has been confirmed by D. J. Galloway as *Cladia ferdinandii*.
According to Crombie (1879: 393) Brown's 'Lichen cribrosus' was from 'Mountain heaths, Australia'.
87. *Cladia retipora* (Labill.) Nyl. Bennett 534
'Lichen cribrosus Cladonia cribrosa enceta Montes que ora australis & Ins Diemen'. Tasmania, cf. Crombie (1879: 393) and Filson (1981: 23).
88. *Cladia retipora* (Labill.) Nyl. Bennett 534
No original label, probably another part of the gathering above.
89. *Cladonia squamosa* Müll. Arg. Bennett 531
(Syn. 'Cladonia subsquamosa' (Nyl.) Wain var. 'pulverulenta' (R.Br.) Vain. and 'C. pulverulenta' R.Br.)
No original label; Crombie's handwriting reads 'on the ground Table Mt. Tasmania R. Brown Cladonia acuminata (Ach)'.
Brown's 'Cladonia pulverulenta' was from Mt Wellington (cf. Crombie 1879: 392).

90. *Cladonia pleurota* (Flörke) Schaerer Bennett 530
(Syn. 'Cladonia deformis' Hoffm.)
'lat. sax. Mont. Tabul prom Dieman'. Brown's 'Lichen deformis' was from Mt Wellington, Tasmania, cf. Crombie (1879: 393).
91. *Cladina confusa* (R. Sant.) Follm. & Ahti Bennett 527
'Lichen rangiferinus mons Tabul & encet'. Crombie (1879: 393) gives 'Mt Wellington on the ground'.
92. *Coenogonium implexum* Nyl. Bennett 504
'Lichen spongiosus arb cort: laevi in sylvis umbrosus humidis ad radis Mont Tabul prom Diemen'. Mt Wellington, Tasmania (cf. Crombie, 1879: 399).
93. *Collema durietzii* Degel. Bennett 511
'Lichen fascicularis? rip & arb Musc insula Diemen'. This specimen had been earlier identified by Crombie as 'Collema implicatum' Nyl. From trees near the River Derwent, Tasmania according to Crombie (1879: 391).
94. *Collema leucocarpum* Hook.f. & Tayl. Bennett 549 (bis)
'Lichen obductus rup & arb orce australis N Holl & Ind Dieman'. Crombie (1879: 391-2). See also entry below.
95. *Collema subconveniens* Nyl. Bennett 549 (bis)
We have not been able to trace this specimen, but Degelius (1974: 139) appears to have seen and cited it 'as *C. nigr[esens]* Lichen obductus (BM) N.W. Tasm'. According to Crombie (1879: 392) Brown's 'Lichen obductus' was from trees near the River Derwent, Tasmania.
96. *Diploschistes ocellatus* (Vill.) Norman Bennett 563
'Lichen lateritus [. . .] prope Risdon Cove'. Tasmania (cf. Crombie, 1879: 399).
97. *Dirinaria picta* (Sw.) Clem. & Shear Bennett 546
No original label; secondary label reads 'Lichen pictus Sw near Kingstown, Newcastle' (cf. Crombie, 1879: 397).
98. *Ephebe fruticosa* Henssen Bennett 522
Two species on sheet: label reads 'Lichen pubescens Lin Ach L. exilis Lightf rup & sax inundat'. Specimen from the Grose River, NSW, according to Crombie (1879: 391).
99. *Ephebe tasmanica* Cromb. Unnumbered
According to notes on the sheet there are three species present. The first is *Ephebe tasmanica* Cromb. The second *Ephebe fruticosa* A. Henssen. The third is *Pseudephebe pubescens* (L.) M. Choisy. (Syn. 'Electoria pubescens'(L.) Howe). According to Crombie (1879: 391) 'Lichen pubescens' was from River Grose, NSW.
100. *Flavoparmelia rutidota* (Hook.f. & Tayl.) Hale Bennett 539
'Lichen cfr L caperatum fl Derwent'. Tasmania (cf. Crombie, 1879: 394).
101. *Graphis intricata* Fée Bennett 561
'Lichen Opegrapha dendritica arb: trunche rip: fl Grose [. . .]'. According to Crombie

(1879: 401), the specimen was from the bark of trees, near the River Grose, New South Wales.

102. *Graphis platycarpa* (Eschw.) A. Zahlbr. Bennett 560
 'Lichen Opegrapha plebja cor: arb: prope P Jackson'. (*Graphis sophistica* Nyl. and *Opegrapha plebja* of Crombie, 1879: 401).

103. *Haematomma puniceum* (Ach.) Mass. var. *collatum* (Stirt.) Zahlbr. Bennett 569
 (Syn. 'Haematomma collatum' (Stirt.) Dodge)
 'Ad cortices Port Jackson'. Probably 'Lichen guttatus' gathered from bark of trees near Middle Harbour, Port Jackson; cf. Crombie (1879: 399).

104. *Haematomma puniceum* (Ach.) Mass. var. *infusum* (Stirt. ex Bailey) Zahlbr. Bennett 507
 (Syn. 'Haematomma infusum' (Stirton ex Bailey) R. W. Rogers)
 'Lichen guttatus Middle Harbour Port Jackson' (cf. Crombie, 1879: 399).

105. *Hypogymnia lugubris* (Pers.) Krog Bennett 526
 'Lichen nem aff L physodi lat Mont Tabularis'. Mt Wellington, Tasmania (cf. Crombie, 1879: 395).

106. *Hypogymnia mundata* (Nyl.) Rassad. Bennett 550 (bis)
 According to an annotation by J. A. Elix (of x 1977) this specimen, noted by Crombie as 'Parmelia mundatum var. pulverata Nyl. [. . .] Lichen dendrosme on trees base of Table Mt, Tasmania', is a mixture of the above species and *H. pulverata* (Nyl. ex Crombie) Elix.

107. *Hypogymnia pulverata* (Nyl. ex Cromb.) Elix Bennett 515 (on some sheets as 550)
 No original label, but has been written up by Crombie (1879) as a mixture of *Parmelia mundata* Nyl. (ex Derwent River) and 'Parmelia angustata' Pers. (ex Port Jackson). Remounting seems to have removed *P. mundata*, and the latter has been identified by J. A. Elix (x 1977) as the above.

108. *Hypogymnia tabularis* (Taylor) Elix Bennett 550
 'Lichen dendrosma [. . .] in sylvis umbrosis ad radic Montis Tabularis prope fl Derwent'. Determined by Crombie (1879: 395) as 'Parmelia mundata' Nyl., more recently by J. A. Elix (ix 1977) as the above.

109. *Lecidea flindersii* Cromb. Bennett 565
 'Superce [?] terra Risdon Cove'. Tasmania (cf. Crombie, 1879: 400).

110. *Melaspilea circumserpens* Nyl. Bennett 566
 'Lichen ambiguens I terra nude rarius in saxis In collibus prope Risdon Cove' Tasmania (cf. Crombie, 1879: 401).

111. *Nephroma cellulosum* (Ach.) Ach. Bennett 543
 'Lichen antarcticus rup umbrosos humid adrip fl Anna Maria infra calaratum'
 'Anna Maria River' appears to be Margate Rivulet, southeastern Tasmania, (cf. Vallance *et al.*, in prep.).

112. *Pannaria rubiginosa* (Thunb. ex Ach.) Del. Bennett 556
 'South coast Bay 3'. Fowlers Bay, South Australia (perhaps Crombie, 1879: 397).

113. *Parmelia tenuirima* Hook.f. & Tayl. Bennett 537
Two sheets: 1st reads 'Lichen amplissimus in saxis & rupibus collium prope fl: Derwent'
2nd sheet has no orig. label. 'Lichen amplissimus' of Crombie (1879: 394).
114. *Pseudephebe pubescens* (L.) M. Choisy Bennett 521
'Lichen lanatus sum Mont Tabul prom Diemen' (cf. Crombie, 1879: 395).
115. *Pseudocyphellaria billardierei* (Delise) Räsänen Bennett 536
'Lichen linearis in trunc arbor prope fluv Derwent' Tasmania (cf. Crombie, 1879: 396).
116. *Pseudocyphellaria crocata* (L.) Vainio Bennett 540 (bis)
'Lichen crocatus Dicks: Hoffm: rup & Sax in montosis' (cf. Crombie, 1879: 396). See *P. neglecta*, below, for second label.
117. *Pseudocyphellaria glabra* (Hook.f. & Tayl.) Dodge Bennett 538
'Lichen latissimus rup & sax Montis Tabularis'. Mount Wellington, Tasmania (cf. Crombie, 1879: 396). Determined as '*Sticta freycinetii*' Del. by Crombie.
118. *Pseudocyphellaria multifida* (Nyl.) D. Galloway & P. James Bennett 516
'Lichen dichotomus rup: umbros: [. . .] ad rep fl Anna Maria prope Calaractam' (cf. Crombie, 1879: 396). Perhaps Margate Rivulet, Tasmania.
119. *Pseudocyphellaria neglecta* (Müll. Arg.) H. Magn. Bennett 540 (bis)
'Lichen crocatus'. Locality as 116 above?
120. *Psoroma decipiens* (Hedw.) Hoffm. Bennett 567
(?Syn. '*Lecidea decipiens*')
'Lichen decipiens [. . .] supra terra Risdon Cove' Tasmania (cf. Crombie, 1879: 400).
121. *Psoroma asperellum* Nyl. Bennett 547
'Lichen adscendens [. . .] ad latus Mont: Montis Tabularis'. Mt Wellington, Tasmania (cf. Crombie, 1879: 398).
122. *Psoroma hypnorum* (Vahl) S. F. Gray Bennett 554
'Lichen cfr: L hypnorum lat sax: Montis Tabularis prope Derwent'. Mount Wellington, Tasmania.
123. *Psoroma leprololum* (Nyl.) Räsänen Bennett 553
No original label, secondary label suggests specimen is 'Lichen denrosmae' from base of Mt Wellington, Tasmania, cf. Crombie (1879: 398).
124. *Psoroma soccatum* R.Br. ex Crombie Bennett 502
'Lichen soccatus trunce emiort ad radi Mont Tabularis' (cf. Crombie, 1879: 398-9).
Lectotype (Galloway, 1985: 481).
125. *Psoroma sphinctrinum* (Mont.) Nyl. Bennett 553
'Lichen Dendrosma reniles Derwent River' Tasmania (?Crombie, 1879: 398).
126. *Ramalina inflata* (Hook.f. & Tayl.) Hook.f. & Tayl. Bennett 519
'Lichen fastigiatus arb [. . .] prope P Jackson' (cf. Crombie, 1879: 393).

127. *Ramalodium succulentum* Nyl. ex Cromb. Bennett 551
 'Lichen succulentus arb: trunc & rup umbros ad rip fl Grose [. . .] 2 rami and musci' (cf. Crombie, 1879: 392).
128. *Relicina limbata* (Laurer) Hale Bennett 544
 Two specimens, but one original label missing; secondary label suggests 'Lichen pinnatus on rocks from Port Jackson. 2nd (original) labels reads 'Lichen pinnatus in saxis prope P Jackson' (cf. Crombie, 1879: 394).
129. *Siphula coriacea* Nyl. Bennett 501
 'Lucky Bay S Ct'. Another sheet, without a Bennett label, bears a label in Crombie's hand 'on the ground Lucky Bay Tasmania [sic]'.
 See also number 86, above. Crombie (1879: 393), however, has number 501 from Mt Wellington, Tasmania.
130. *Sphaerophorus melanocarpus* (Sw.) DC. Bennett 517
 Two sheets: 1st label reads 'Lichen fragilis arb trunc semi putrid ad rip flu alpinor Mon Tabul prom Diemen'; 2nd has no original label (cf. Crombie, 1879: 392).
131. *Sphaerophorus tener* Laurer Bennett 524
 'Lichen globiferus lat sax Mont Tabul prom Diemen' (cf. Crombie, 1879: 392).
132. *Stereocaulon ramulosum* (Sw.) Räsichel Bennett 526
 'Lichen ramulosus men alt L paschali lat Mont Tabul & rip fl Grose &' (cf. Crombie, 1879: 392).
133. *Stricta subcaperata* (Nyl.) Nyl. Bennett 555
 'Lichen filix Lin: fil. In lat umbros supra summitato Montis Tabularis insul. Dieman'. Mount Wellington, Tasmania (cf. Crombie, 1879: 396).
134. *Teloschistes chrysophthalmus* (L.) Th. Fr. Bennett 545
 'Lichen chrysophthalmus [. . .] Kents Group'. Bass Strait (cf. Crombie (1879: 396-7).
135. *Thamnolia vermicularis* (Sw.) Ach. ex Schaerer Bennett 528
 'Lichen vermicularis Cladonia vermicularis lat & sum: Mon Tabul prom Diemen'. Mount Wellington, Tasmania (cf. Crombie, 1879: 393).
136. *Thelotrema lepadinum* (Ach.) Ach. Bennett 520
 'Lichen ? [sic] occulatatus Cort laevi: arbor ad ripas fluv: Grose [. . .]' (cf. Crombie, 1879: 399).
137. *Umbilicaria cylindrica* (L.) Delise in Duby Bennett 558
 Two specimens: 1st has no original label, secondary label suggests 'Lichen proboscideus summit of Table Mtn.' 2nd (original) reads 'Lichen proboscideus [. . .] sum: Mont Tabularis prope fl Derwent'. Mount Wellington, Tasmania (cf. Crombie, 1879: 397).
138. *Usnea acromelana* Stirt. var. *decipiens* (Lamb) Lamb Bennett 523
 (?Syn. 'Neuropogon acromelanus')
 'Lichen ustulatus rup sum: Mont Tabularis prom Diemen'. (cf. Crombie, 1879: 395). Holotype of variety (Walker, 1985).

139. *Usnea ceratina* Ach. Bennett 518 (bis)
(cf. Crombie, 1879: 394). Specimen untraced.
140. *Usnea florida* (L.) Wigg. Bennett 518 (bis)
'Lichen floridus' from the River Grose, N.S.W., specimen untraced. (cf. Crombie, 1879: 393).
141. *Xanthoparmelia australiensis* (Cromb.) Hale Bennett 525
'Scyphophorus lat Mont Tabul In Diem [sic]'. Mt Wellington, Tasmania according to Crombie (1879: 395), but this locality could be an error (Kantvilas 1983). According to Bibby (1951), and Elix *et al.* (1986) the locality is the Nullarbor region and Flinders Ranges. Holotype of species (Elix *et al.*, 1986).
142. *Xanthoparmelia multipartita* (Cromb.) Hale Bennett 542
'Lichen multipartitus in saxis prope P Jackson'. (cf. Crombie, 1879: 394-5). There is other material in the gathering with no original label; secondary label reads 'Lichen multipartitus rocks near Port Jackson'.
Taxon distributed in south-eastern Australia and this number is described as type by Elix *et al.* (1986).

BRYOPHYTA

LEAFY LIVERWORTS

143. *Jamesoniella colorata* (Lehm.) Spruce ex Schiffn. Bennett 293
Secondary label reads 'Tasmania'. The taxon is known to occur in Tasmania according to Scott (1985).
144. *Frullania falciloba* Taylor ex Lehm. Bennett 290
Secondary label reads 'Tasmania'. Known in Tasmania (Scott, 1985).
145. *Gackstroema weindorfii* (Herzog) Grolle Bennett 294
Secondary label reads 'Tasmania'. Known to occur, frequently in *Nothofagus* forests, in Tasmania (Scott, 1985).
146. *Lepicolea scolopendra* (Hook.) Dum. ex Trev. Bennett 292
Secondary label reads 'Tasmania'.
147. *Plagiochila* sp. indet. Bennett 291
Secondary label reads 'Tasmania'.

THALLOID LIVERWORTS

148. *Hymenophyton flabellatum* (Labill.) Dum. ex Trev. Bennett 295
(Syn. 'Symphyogyna flabellata' (Labill.) Mont.)
Secondary label reads 'Tasmania'. Known in Tasmania, Scott (1985). The specimen is unmounted, and in a folded and re-used sheet of Brown's herbarium drying paper on which is written 'Carpentaria Island s [. . .] 21 Jan'y 1803 [. . .]' but this is struck through in pencil.

149. *Symphyogyna podophylla* (Thunb.) Mont. & Nees Bennett 296
 (Syn. 'Symphyogyna obovata' Hook.f. & Tayl.)
 Secondary label reads 'Tasmania'. The label is annotated 'Syn Hep p.480' (cf. Gottsche *et al.*, 1844-7).
 Scott (1985) confirms the Tasmanian occurrence of this taxon.

MUSCI

150. *Blindia magellanica* Schimp. Bennett 284
 Secondary label reads 'Tasmania'. Tasmanian occurrence is confirmed by Scott and Stone (1976).
151. *Breutelia affinis* (Hook.) Mitt. Bennett 288
 Secondary label reads 'Tasmania' (cf. Scott and Stone, 1976).
152. *Breutelia pendula* (Sm.) Mitt. Bennett 289
 Secondary label reads 'Tasmania' (cf. Scott and Stone, 1976).
153. *Bryum billardieri* Schwaegr. Bennett 287
 Secondary label reads 'Tasmania' (cf. Scott and Stone, 1976).
154. *Campylopus clavatus* (R.Br.) Wils. Bennett 282
 Secondary label reads 'Tasmania' (cf. Scott and Stone, 1976).
155. *Campylopus introflexus* (Hedw.) Brid. Bennett 281
 Secondary label reads 'Tasmania' (cf. Scott and Stone, 1976).
156. *Dawsonia polytrichoides* R.Br. Unnumbered
 1st original labels reads: 'Nova Cambria Australis: ad radices montium prope Port Jackson Jan 1 1804 RB [sic]'; 2nd original label reads 'Dawsonia polytrichoides to show that part of the peristomium originates from the columnale or Placenta'. But an annotation on the wrapping paper of an unmounted specimen in a 'Herb. Brown' cover reads 'Genus Muscor frondos Proxim: Polytricho lesser division of the first branch of the River Grose Jan 1 1805 desc'.
 The 1st original label is incorrectly dated. Brown was in Tasmania 1 January 1804 (cf. Vallance *et al.*, in prep.). The date 1 Jan 1805 is consistent with the New South Wales locality. Probably material from this gathering was described by Brown (1811) where the locality was given as 'Port Jackson'. Scott and Stone (1976) note the occurrence of this taxon in Tasmania, Victoria, New South Wales, A.C.T. and Queensland.
157. *Dicranoloma dicarpum* (Nees) Par. Bennett 285
 Secondary label reads 'Tasmania' (cf. Stone and Scott, 1976).
158. 'Dicranoloma robustum' of BM (NH) Herbarium Bennett 283
 Secondary label reads 'Tasmania'.
159. *Leptostomum erectum* R.Br. Unnumbered
 Secondary label reads 'New Holland Mr Brown'. The mounted Hooker specimen (*ex* Kew Herbarium) bears a secondary label which reads 'New Holland Mr Brown'. Taxon known in Victoria, New South Wales and Queensland (Scott and Stone, 1976).
 Possibly gathered with Brown's (1811) material from the 'Hawkesbury and Grose'.

160. *Leptostomum inclinans* R.Br. Bennett 286
Possibly this material was gathered with that described by Brown (1811) and from 'Van Diemens Land'. A Hooker specimen of this gathering (*ex* Kew Herbarium) has a secondary label which reads 'Table Mountain Van Diemens Land Mr Brown at an elevation of 3000-3500ft'. A label on the sheet indicates this specimen is the basis of the illustration by Brown (1811: 320, t.23, fig 2). A secondary label with the unmounted material reads 'Tasmania' (cf. Scott and Stone, 1976).
161. *Leptostomum macrocarpum* (Hedw.) Pyl. Unnumbered
Secondary label reads 'Leptostomum macrocarpum, Br Australia R Brown'. Known from Tasmania, New South Wales and Queensland according to Scott and Stone (1976).
162. *Tayloria octoblepharum* (Hook.) Mitt. Bennett 280
Secondary label reads 'Tasmania'. Scott and Stone (1976) confirm the occurrence in Tasmania.

PTERIDOPHYTA

LYCOPSIDA

163. *Lycopodium deuterodensum* Herter Bennett 126 (on same sheet as Bennett 127)
'Lycopodium candelabrum Derwent Huon &c' (Lycopodium densum of Brown, 1810: 165, entry 3-D).
164. *Lycopodium deuterodensum* Herter Bennett 127 (on same sheet as Bennett 126)
'Lycopodium venustum Port Dalrymple Jan 1804 [reverse] Lycopodium candelabrum'.
165. *Lycopodium deuterodensum* Herter Bennett 128
'Lycopodium candelabrum B & S Port Jackson [reverse] 3 Lycopodium densum' (Brown, 1810: 165, entry 3-J).
166. *Lycopodium fastigiatum* R.Br. Bennett 129
Two labels, 1st reads '4 Lycopodium fastigiatum Summit of Table Mountain VDL (Brown, 1810: 165, entry 4-D); 2nd reads 'Lycopodium quadrifarium Port Jackson'.
167. *Lycopodium laterale* R.Br. Bennett 130
'Lycopodium diffusum Port del Esperance V D Land' (Brown, 1810: 165, entry 5-D).
168. *Lycopodium laterale* R.Br. Bennett 131
'Lyopodium laterale [. . .] Port Jackson' (Brown, 1810: 165, entry 6-J).
169. *Lycopodium myrtifolium* Forst.f. Bennett 123
'Lycopodium varium [alpha][. . .] Table Mountain' (Brown, 1810: 165, entry 1-D).
170. *Lycopodium myrtifolium* Forst.f. Bennett 124
'Lycopodium varium [beta] alpinae Mont Tabule' (Brown, 1810: 165, entry 1-D). Holotype of 'Lycopodium varium [beta] alpinum', according to an annotation on the sheet by J. M. Beitel 1981.
171. *Lycopodium scariosum* Forst.f. Bennett 125
'Lycopodium decurrens affr L reptans B & S: Mont Tabularis and fluv Derwent' ('Lycopodium decurrens' of Brown, 1810: 165, entry 2-D).

172. *Selaginella uliginosa* (Labill.) Spring Bennett 133
 'Lycopodium quadrilineum var Port Phillip'.

173. *Selaginella uliginosa* (Labill.) Spring Bennett 132
 'Lycopodium uliginosum Labill' (Port Jackson, cf. Brown, 1810: 165, entry 7-J).

PSILOPSIDA

174. *Psilotum nudum* (L.) Beauv. Bennett 120
 Two labels: 1st reads 'Lycopodium nudum Broad Sound [reverse] 1 Psilotum triquetrum'; 2nd reads 'Lycopodioides nuda P.Jackson' ('Psilotum triquetrum' of Brown, 1810: 164, entry 1-J).

175. *Tmesipteris billardieri* Endl. Bennett 122 (on same sheet as Bennett 121)
 'Lycopodioides truncata [. . .] Derwent [reverse] 2 Psilotum truncatum' (Brown, 1810: 164, entry 2-D).

176. *Tmesipteris truncata* R.Br. Bennett 121 (on same sheet as Bennett 122)
 'Lycopodioides truncata [. . .] Port Jackson [reverse] 2 Psilotum truncatum' (Brown, 1810: 164, entry 2-J).

FILICOPSIDA (TRUE FERNS)

177. *Acrostichum aureum* L. Bennett 2
 Two labels: 1st reads 'Acrostichum fraxinifolium prod 145 Arnhem South Bay Feb 6 1803', Caledon Bay, Northern Territory (Burbidge, 1956); 2nd reads 'Acrostichum fraxinifolium [. . .] Port II prod 145', Port Clinton, Queensland (Burbidge, 1956). Brown was there in August 1802 (Vallance *et al.*, in prep.; Brown, 1810: 145, entry 2-T).

178. *Adiantum aethiopicum* L. Bennett 69
 'Adiantum assimile Shoal Water Bay Keppel Bay prodr 155.' *A. aethiopicum* of Beadle *et al.* (1972), perhaps Brown (1810: 155, entry 4). Brown, however, does not note a tropical specimen ('T').

179. *Adiantum aethiopicum* L. Bennett 70
 'Kangar[oo] Island' (Brown, 1810: 155, entry 4-M).

180. *Adiantum aethiopicum* L. Bennett 71
 'Adiantum ebenum Port Jackson' (Brown, 1810: 155, entry 4-J).

181. *Adiantum formosum* R.Br. Bennett 67
 'Adiantum formosum prodr 155 Port Jackson' (Brown, 1810: 155, entry 3-J).

182. *Adiantum formosum* R.Br. Bennett 68
 'Adiantum cfr formosum Port Jackson [. . .]' (Brown, 1810: 155, entry 3-J).

183. *Adiantum hispidulum* Sw. Bennett 64
 'Adiantum hispidulum Shoal Water Bay prodr 155' (Brown, 1810: 155, entry 2-T).

184. *Adiantum hispidulum* Sw. Bennett 65
 'Adiantum [. . .] hispidulosa Port Jackson' (Brown, 1810: 155, entry 2-J).

- 185.** *Adiantum hispidulum* Sw. Bennett 66
 Three labels: 1st reads 'Adiantum cfr A. hispidulum Port Jackson; 2nd reads 'North rocks 8 August 1802'; (Brown, 1810: 155, entry 2-J). 3rd reads 'Dove Dale Feb 1804 - '.
- 186.** *Arthropteris tenella* (Forst.f.) J.Sm. Bennett 12
 'Polypodium tenellium Forst prodr 147 Polypodium fimiculus rupibus & rare in loc umbrosis in rip[as] Grose' (Brown, 1810: 147, entry 8-J).
- 187.** *Asplenium aethiopicum* (Burm.f.) Bech. Bennett 33
 (Syn. 'Asplenium furcatum' Thunb.)
 'Asplenium praemorsum prodr 150 rup umbrose: Grose' (Brown, 1810: 150, entry 7-J).
- 188.** *Asplenium attenuatum* R.Br. Unnumbered, but corresponds to Bennett register entry 25
 No original label; secondary label reads 'Nova Cambria Australis: Port Jackson R Brown' (Brown, 1810: 150, entry 2-J).
 A duplicate of this in Kew Herbarium, as No 26, is from the 'Grose' River, Blue Mountains.
- 189.** *Asplenium bulbiferum* Forst.f. Bennett 35
 Two labels: 1st reads 'Asplenium [. . .] laxum prodr 151'; 2nd reads 'Asplenium laxum prodr 151 (Brown, 1810: 151, entry 10-D).
- 190.** *Asplenium flabellifolium* Cav. Unnumbered, but corresponds to Bennett register 30
 'Asplenium flabellifolium Van Diemens Land' (Brown, 1810: 150, entry 6-D).
- 191.** *Asplenium flabellifolium* Cav. Unnumbered but corresponds to Bennett register 31
 'Asplenium flabellifolium Port Jackson' (Brown, 1810: 150, entry 6-J).
- 192.** *Asplenium nidus* L. Unnumbered but corresponds to Bennett register 25 (bis)
 'Asplenium nidus Port Jackson' (Brown, 1810: 150, entry 1-J).
- 193.** *Asplenium nidus* L. Unnumbered but corresponds to Bennett number 25 (bis)
 Three labels: 1st reads 'Asplen. nidus North Coast'; 2nd reads 'Asplenium nidus Linn prodr 150 Broad Sound West Peaked Hill In sylvis umbrosis ad radices arborum spec parasiticum' [cf. Brown, 1810: 150, entry 1-T]; 3rd reads 'Grose 1804' (cf. Brown 1810: 150, entry 1-J).
- 194.** *Asplenium obtusatum* Forst.f. Bennett 27
 No original label; secondary label reads 'Insula Van Diemen 1804' (probably Brown, 1810: 150, entry 3-D).
- 195.** *Asplenium paleaceum* R.Br. Unnumbered but corresponds to Bennett register 29
 No original label, secondary label reads 'Nova Cambria australis in monte prope Broad Sound 1802 Robert Brown' (cf. Brown, 1810: 150, entry 5-T).
- 196.** *Asplenium polyodon* Forst.f. Unnumbered but probably corresponds to Bennett register 28
 (Syn 'A. falcatum' Lam.)
 No original label; secondary label reads 'Nova Cambria australis Port Jackson' (perhaps corresponds with Brown, 1810: 150, entry 4-J).

197. *Azolla pinnata* R.Br. Bennett 134
Two labels: 1st reads 'Azolla pinnata Nob in stagnis prope Richmond in Nov Camb: durt'; 2nd reads 'Azolla pinnata Nob in stagnes & fluv len: fluat Richmond Hawkesbury' (Brown, 1810: 167, entry 1-J).
Bauer painting 229 (BM (NH) Botany Library) is probably based on this plant or the specimen below.
198. *Azolla pinnata* R.Br. Bennett 135
'Azolla filiciloides [sic] pinnata Patersons River Oct 1804' (Brown, 1810: 167, entry 1-J).
BM (NH) Bauer painting 229 perhaps based on this plant, but see above.
199. *Azolla filiculoides* Lam. var. *rubra* (R.Br.) Strasburger Bennett 136
'Azolla rubra Patersons River Oct 1804' ('Azolla rubra' of Brown, 1810: 167, entry 2-J).
200. *Blechnum camfieldii* Tindale Bennett 49
'Blechnum mutatum var. Port Jackson 8 Stegania procera prodr 153' ('Stegania procera' of Brown, 1810: 153, entry 8-J).
201. *Blechnum ambiguum* (Presl.) Kaulf. ex C.Chr. Bennett 41
Two sheets, with identical labels '3 Blechnum laevigatum Prodr 152 Port Jackson' (Brown, 1810: 152, entry 3-J).
202. *Blechnum cartilagineum* Sw. Bennett 39
'Blechnum paludosum Port Jackson [. . .] 1 Blechnum cartilagineum (Sw) prodr 152' (cf. Brown, 1810: 152, entry 1-J).
203. *Blechnum chambersii* Tindale Bennett 42
'2 Stegania lanceolata prodr 152 Van Diemens Land' (Brown, 1810: 152, entry 2-D).
204. *Blechnum fluviatile* (R.Br.) E. J. Lowe Bennett 43
'Pteris fluviatilis rivul alp Mont tabul. Derwent [. . .] 3 Stegania fluviatilis prodr 152' (cf. Brown, 1810: 152, entry 3-D).
205. *Blechnum indicum* Burm.f. Bennett 40
'2 Blechnum striatum prodr 152 Port Jackson' (Brown, 1810: 152, entry 2-J).
206. *Blechnum minus* (R.Br.) Ettingsh. Unnumbered but probably corresponds
'Insula Van Diemen 1804 RB' (Brown, 1810: 153, entry 7-D). to Bennett register 47
207. *Blechnum nudum* (Labill.) Mett. ex Luerss. Bennett 45
'Blechnum pteroides Port Dalrymple Jan 1804 5 Stegania nuda prodr 153' ('Stegania nuda' of Brown, 1810: 153, 5-D).
208. *Blechnum nudum* (Labill.) Mett. ex Luerss. Bennett 46
'Blechnum ?discolour Osmunda discolor B&S Kings Id 6 Stegania falcata prodr 153 [. . .]' ('Stegania falcata' of Brown, 1810: 153, entry 6-D).
209. *Blechnum penna-marina* (Poir.) Kuhn Bennett 44
'Pteris alpina desc cat Mont Tabul Derwent 4 Stegania alpina prodr 152 ('Stegania alpina' of Brown, 1810: 152, entry 4-D).

210. *Blechnum penna-marina* ssp. *alpina* (R.Br.) Kuhn Unnumbered but probably corresponds to Bennett register 44
 'Insula Van Diemen in summitate Montis Tabularis 1804 RB *Stegania alpina* prodr [. . .]' (probably another sheet of the above, cf. Brown, 1810: 152, entry 4-D).
211. *Blechnum watsii* Tindale Bennett 48
 '*Blechnum mutatum* desc Kings Island 8 *Stegania procera* prodr 153' (Brown, 1810: 153, entry 8-D).
212. *Blechnum watsii* Tindale Bennett 49 (bis)
 'Port Jackson 8 *Stegania procera* prodr 153' (cf. '*Stegania procera*' of Brown, 1810: 153, entry 8-J). The label bears an annotation by T. C. Chambers dated 6. xii. 1977 which reads 'Maybe a hybrid but closest to *Blechnum watsii* Tindale.'
213. *Botrychium australe* R.Br. Bennett 119
 '1 *Botrychium australe* prodr 164 Paramatta Port Jackson' (Brown, 1810: 164, entry 1-J).
214. *Cheilanthes austrotenuifolia* Quirk & Chambers Bennett 74
 '*Adiantoides crispa* Kangar[oo] Id'
 See Quirk *et al.* (1983: 510-3) regarding the relationship of *Cheilanthes austrotenuifolia* and *C. tenuifolia*.
215. *Cheilanthes austrotenuifolia* Quirk & Chambers Bennett 76
 '*Adiantoides crispa* Port Jackson' (see above, and Quirk *et al.*, 1983: 510-3).
216. *Cheilanthes austrotenuifolia* Quirk & Chambers Bennett 77
 'Goose Id Bay South Coast *Adiantoides crispa* var' (see above, and Quirk *et al.*, 1983: 510-3).
217. *Cheilanthes brownii* (Desv.) Domin Bennett 5(a)
 'Arnhem South Bay Point U₁ Feb^y 6 1803 2 *Notholaena vellea* prodr 146'.
 Mt. Caledon, Caledon Bay, Northern Territory (Burbidge, 1956; Vallance *et al.*, in prep.). '*Notholaena vellea*' of Brown (1810: 146, entry 2-T). Holotype (Quirk *et al.*, 1983: 529-31).
218. *Cheilanthes brownii* (Desv.) Domin Bennett 5(b)
 'Shoalwater Bay Conical Pine Hill' (Perhaps '*Notholaena vellea*' of Brown, 1810: 146, entry 2-T).
219. *Cheilanthes caudata* R.Br. Bennett 78
 '*Pteris* [struck through] *Cheilanthes caudata* prodr 156 Port II' Port Clinton, Queensland (Burbidge, 1956). Visited by Brown in August 1802 (Vallance *et al.*, in prep.). Brown (1810: 156, entry 2-T). Holotype (Quirk *et al.* 1983: 540-1).
220. *Cheilanthes distans* (R.Br.) Mett. Bennett 4(a)
 '*Adiantoides palacea* Port Jackson [. . .] *Notholaena distans* prodr 146' ('*Notholaena distans*' of Brown, 1810: 146, entry 1-J). Holotype (Quirk *et al.*, 1983: 526-9).
221. *Cheilanthes lasiophylla* Pichi-Serm. Bennett 4b
 '*Adiantoides paleacea* Inlet XII [. . .] *Notholaena* cfr *N. distans*'
 At the Head of Spencer Gulf (Burbidge 1956), but Brown (1810: 146, entry 1) indicates

Port Jackson as the source of the material. The *Prodromus* entry should have the 'M' annotation if Spencer Gulf is meant. See Quirk *et al.* (1983: 531-2) and Pichi-Sermolli (1951) regarding relationship with 'Notholaena canescens'.

- 222.** *Cheilanthes nudiuscula* (R.Br.) T. Moore Bennett 60
 'Pteris denudata v[ar] N Coast Id. y2'
 Pibassoo's Island, Northern Territory (Burbidge, 1956). 'Pteris nudiuscula' of Brown (1810: 155, entry 8-T). Holotype (Quirk *et al.*, 1983: 537-40).
- 223.** *Cheilanthes tenuissima* Bailey Bennett 61
 'Adiantoides pubescens North Coast Island y2 & C'. Pibassoo's Island, as above.
- 224.** *Cheilanthes tenuissima* Bailey Bennett 3
 'Acrostichum gracile [struck through] pteroides prodr 145 North Coast Islands 1803 RB' (Brown 1810: 145, entry 3-T). Type of 'Acrostichum pteroides' R.Br. (Quirk *et al.*, 1983: 541-3).
- 225.** *Cheilanthes tenuifolia* (Burm.f.) Sw. Bennett 72
 (Syn. ssp. *queenslandica* Domin., see remarks on relationship of *C. austrotenuifolia* and *C. tenuifolia* by Quirk *et al.* (1983: 506-13). 'Adiantoides crispa var. North Coast Islands' (Brown, 1810: 155, entry 1-T).
- 226.** *Cheilanthes* sp.indet. Bennett 73
 'Adiantoides crispa Port II', Port Clinton area, Queensland (Burbidge, 1956).
- 227.** *Cheilanthes* sp.indet. Bennett 75
 'Adiantoides cicutaria Pteris [sic] Port II'
- 228.** *Christella dentata* (Forsk.) Browns. & Jermy Bennett 21(a)
 '5 Nephrodium molle Prodr 149 [reverse reads] Plenosouris Polypod: molle Jacq. Grose' (Brown, 1810: 149, entry 5-J).
- 229.** *Christella dentata* (Forsk.) Browns. & Jermy Bennett 21(b)
 'Polypodium molle Jacq adrip: Patersons Hunter William Rivers det 1804 [reverse reads] 5 Nephrodium molle Prodr 149' (Brown, 1810: 149, entry 5-J).
- 230.** *Ctenopteris heterophylla* (Labill.) Tindale Bennett 13
 'Polypodium arbor prope in caulis Dicksonia Derwent 9 Polypodium grammitidis prodr 147' ('Polypodium grammitidis' of Brown, 1810: 147, entry 9-D).
- 231.** *Culcita dubia* (R.Br.) Maxon Bennett 86
 Two labels: 1st reads 'Cfr D. cicutarian [struck through] Banks of Hunter's River Nov 1804 4 Davallia dubia prodr 157'; 2nd reads 'Davallia dubia Port Phillip' (Brown, 1810: 157, entry 4-J and D).
- 232.** *Culcita dubia* (R.Br.) Maxon Bennett 87
 '4 Davallia dubia adripes fl. Patersons & Hunters Rivers Oct: Nov: 1804' (Brown, 1810: 157, entry 4-J).
- 233.** *Culcita dubia* (R.Br.) Maxon Bennett 88
 Two identical sheets '4 Davallia dubia Pt Jackson' (Brown, 1810: 157, entry 4-J).

234. *Culcita dubia* (R.Br.) Maxon Bennett 89
'4 *Davallia multiflora* [struck through] *dubia* Port Jackson' (Brown, 1810: 157, entry 4-J).
235. *Culcita dubia* (R.Br.) Maxon Bennett 90
'4 *Davallia dubia* prodr 157 Port Dalrymple Jan 1804' (Brown, 1810: 157, entry 4-D).
236. *Cyathea australis* (R.Br.) Domin Bennett 94
'*Cyalloides* Kings Island Basses Strait' ('*Alsophila australis*' of Brown, 1810: entry 1-D).
A tree fern, occurring in gullies near the sea. Lectotype (Tindale, 1956: 350).
237. *Cyathea australis* (R.Br.) Domin Bennett 95
'1 *Alsophila australis* prodr 158' (probably '*Alsophila australis*' of Brown, 1810: 158, entry 1-J).
238. *Davallia pyxidata* Cav. Bennett 84
'*Davallia glycopoda* P Jackson in rep' (Brown, 1810: 156-7, entry 1-J).
239. *Davallia pyxidata* Cav. Bennett 85
Two sheets: 1st reads '*Davallia pyxidata* b Hunters River, Ash Island'; 2nd reads '*Davallia glycopoda* P Jackson in rup Grose [sic]' (Brown, 1810: 156-7, entry 1-J).
240. *Dennstaedtia davallioides* (R.Br.) T. Moore Bennett 93
'*Davallia tenera* Banks of Patersons River Oct: 1804 *Dicksonia davallioides* prodr 158' (Brown, 1810: 158, entry 2-J).
241. *Dicksonia antarctica* Labill. Bennett 92
Two sheets: 1st reads '*Dicksonia australis* Kings Island'; 2nd reads '*Dicksonia antarctica* Van Diemen [sic] Kings Island' (second label relates to Brown, 1810: 157, entry 1-D. See also next).
242. *Dicksonia antarctica* Labill. Bennett 91
Two labels: 1st reads '*Dicksonia australis* Derwent'; 2nd reads '*Dicksonia antarctica* prodr 157 Derwent' (Brown, 1810: 157, entry 1-D).
243. *Dicranopteris linearis* (Burm.f.) L. Underw. Bennett 111
'*Polypodium dichotomum* Shoalwater bay passage [. . .] 8 *Gleichenia Hermanni* prodr 161' (Brown, 1810: 161, entry 8-T).
244. *Diplazium australe* (R.Br.) Wakef. Unnumbered, but probably corresponds to Bennett register entry 24
No original labels, but on back of sheet, not in Brown's hand, '*Nova cambria australe* Port Jackson' (perhaps '*Allantodia tenera*' R.Br., cf. Brown, 1810: 149, entry 2-J).
245. *Doodia aspera* R.Br. Bennett 36
'*Woodwardia aspera* Banks of Hunters River frequent Oct-Novr 1804 *Doodia aspera* prodr 151' (Brown, 1810: 151, entry 1-J).
246. *Doodia caudata* (Cav.) R.Br. Bennett 37
'*Woodwardia blechnoides* sp5 [sic] Port Jackson [. . .] *Doodia caudata* prodr 151' (Brown, 1810: 151, entry 3-J).

247. *Doodia caudata* (Cav.) R.Br. Bennett 38
'Woodwardia Port Dalrymple Jan: 1804' (Brown, 1810: 151, entry 3-D).
248. *Doryopteris concolor* (Langsd. & Fisch.) Kuhn Bennett 62
'Pteris pedata prodr 155 Broad Sound in Montibus prope Upper Head' (Brown, 1810: 155, entry 9-T).
249. *Drynaria rigidula* (Sw.) Bedd. Bennett 14a (but should be 15)
'Polypodium anomalum Carpentaria Groote Eyland Frondes sterilis sumatae breviores latiores [reverse reads] Polypodium quercifolium B non Lin.' (Brown, 1810: 147, entry 10-T).
250. *Drynaria sparsisora* (Desv.) T. Moore Bennett 14b (bis)
'10 Polypodium quercifolium Prodr 147 Carpentaria Coen River' (Brown, 1810: 147, entry 10-T).
251. *Drynaria sparsisora* (Desv.) T. Moore Bennett 14b (bis)
'Polypodium Keppel Bay' (Brown, 1810: 147, entry 10-T).
252. *Gleichenia alpina* R.Br. Bennett 105
'3 Gleichenia alpina desc prodr 160 Summitat Table Mountain Derwent' (Brown, 1810: 161, entry 3-D).
253. *Gleichenia dicarpa* R.Br. Bennett 108
(Syns. 'Gleichenia circinnata' Sw., 'Calymella circinnata' (Sw.) Ching.?)
'Gleichenia pubescens sp [. . .] P Dalrymple desc' (possibly Brown, 1810: 161, entry 5-D).
254. *Gleichenia microphylla* R.Br. Bennett 106
(Syn. 'Calymella circinnata' (Sw.) Ching.?)
'Gleichenia cfr speluncae Port Jackson' (Brown, 1810: 161, entry 4-J).
255. *Gleichenia microphylla* R.Br. Bennett 107
Two labels: 1st reads '4 Gleichenia microphylla Prodr 161 Kings Island'; 2nd reads 'Port Jackson' (Brown, 1810: 161, entry 4-D (label 1) and J (label 2)).
256. *Gleichenia microphylla* R.Br. Unnumbered
No original label: secondary label reads 'New Holland Kents Group Dec 1803' (Brown, 1810: 161, entry 4-D).
257. *Gleichenia rupestris* R.Br. Bennett 104
(Syn. 'Calymella rupestris' (R.Br.) Ching.)
'Gleichenia austriaca desc Port Jackson [. . .] 2 Gleichenia rupestris Port Jackson prodr 160' (Brown, 1810: 160, entry 2-J).
258. *Gleichenia speluncae* R.Br. Bennett 103
(Syn. 'G. circinnata' var.?, or 'G. microphylla R.Br. ?).
'Gleichenia subsimplex desc rup [. . .] Port Jackson' (Brown, 1810: 160, entry 1-J).

259. *Grammitis billardieri* Willd. Bennett 6 b & c
Label 6b reads 'Ceterach polypodiodes rupestris in later Mont Tabul Derwent Grammitis australis prodr 146' (Brown, 1810: 146, entry 1-D); 6c reads 'Grammitis australis prodr 146 Port Jackson 1804 RB' (Brown, 1810: 146, entry 1-J).
260. *Histiopteris incisa* (Thunb.) J.Sm. Bennett 52
'3 Pteris vespertilionis P Jack[son and] Derwent' (Brown, 1810: 154, entry 3-J).
261. *Histiopteris incisa* (Thunb.) J.Sm. Bennett 54
'3 Pteris vespertilionis prodr 154 Kings Island' (Brown, 1810: 154, entry 3-D).
262. *Histiopteris incisa* (Thunb.) J.Sm. Bennett 55
'Pteris vespertilionis B Port Jackson' (Brown, 1810: 154, entry 3-J).
263. *Hymenophyllum cupressiforme* Labill. Bennett 100
'Hymenophyllum tunbridgense prodr 159 Derwent' (Brown, 1810: 159, entry 4-D).
264. *Hymenophyllum flabellatum* Labill. Bennett 98
'Hymenophyllum nitens prodr 159 Derwent' (Brown, 1810: 159, entry 2-D).
265. *Hypolepis rugosula* (Labill.) J.Sm. Bennett 16a
'12 Polypodium rugosulum Prodr 147 [reverse reads] Polypodium affine Kings Island' (Brown, 1810: 147, entry 12-D).
266. *Lastreopsis decomposita* (R.Br.) Tindale Bennett 22
'Pteridioides acuminata Polypodium Involuc renif. adip. Hunters River Oct 1804 7 Nephrodium decompositum prodr 149'.
(*Nephrodium decompositum*' of Brown, 1810: 149, entry 6-J). Holotype of *L. decomposita* (cf. Tindale, 1965: 320-3).
267. *Lastreopsis decomposita* (R.Br.) Tindale Bennett 23
'Polypodium tenerum Broad Sound Peaked West Hill in sylvis umbrosis [. . .] 7 Nephrodium decompositum [struck through] tenerum prodr 149' (*Nephrodium tenerum*' of Brown, 1810: 149, entry 7-T).
268. *Lindsaea ensifolia* Sw. Bennett 80
'Lindsaea lanceolata Prodr 156 [reverse reads] Lindsaea pleroides [*Vittaria*' struck through] Port II Shoal Water Bay passage' (Brown, 1810: 156, entry 2-T). This specimen has been determined by K. U. Kramer in 1965 as the ssp. *agati* (Brack.) Kramer.
269. *Lindsaea ensifolia* Sw. Bennett 81
'2 Lindsaea lanceolata [β] [reverse reads] Lindsaea polymorpha North Coast Island Y₂' Arnhem Bay area, N.T. (Burbidge, 1956; Brown, 1810: 156, entry 2-T). Determined by K. U. Kramer in 1965 as the ssp. *agati* (Brack.) Kramer.
270. *Lindsaea linearis* Sw. Bennett 79
Two labels: 1st reads 'Lindsaea recurifera Port Jackson [reverse reads] Lindsaea linearis Prodr 156'; 2nd reads '1 Lindsaea linearis' (Brown, 1810: 156, entry 1-J, and Kramer and Tindale, 1976: 112-3).

271. *Lindsaea microphylla* Sw. Bennett 83
Original label damaged, remaining part reads '[. . .] Port Jackson' (Brown, 1810: 156, entry 4-J, and Kramer and Tindale, 1976: 95-8).
272. *Lindsaea media* R.Br. Bennett 82
'*Lindsaea irregularis* North Coast Island y2 Feb 18-24 1803 Z' Pibassoo's Island (Burbidge, 1956). (Brown, 1810: 156, entry 3-T, and Kramer and Tindale, 1976: 98-101).
273. *Lygodium flexuosum* (L.) Sw. Unnumbered but probably corresponds
to Bennett register entry 116
'Nova Hollandia or septen trionalis 1803 RB' ('*Lygodium semibipinnatum*' of Brown, 1810: 162, entry 2-T).
274. *Lygodium microphyllum* (Cav.) R.Br. Unnumbered but probably corresponds
(Syn. '*Lygodium scandens*' (L.) Sw.) to Bennett register entry 115
No original label; secondary labels reads 'Nova Cambria australis inter tropicum RB'
('*Lygodium microphyllum*' of Brown, 1810: 162, entry 1-T).
275. *Marsilea angustifolia* R.Br. Bennett 141
'3 *Marsilea angustifolium* Carpentaria Island g Dec 25 1802', Vanderlins Island (Burbidge, 1956; cf. Vallance *et al.*, in prep.). (Brown, 1810: 167, entry 3-T).
276. *Marsilea hirsuta* R.Br. Bennett 138
'*Marsilea hirsuta* Carpentaria Island f, Bountiful Island (Burbidge, 1956). Brown was there on 3 December 1802 (Vallance *et al.* in prep.). (Brown, 1810: 167, entry 2-T).
277. *Marsilea hirsuta* R.Br. Bennett 139
'2 *Marsilea* [quadrifolia struck through] *hirsuta* Broad Sound in frales de popes scites temporebus inundatis' (perhaps Brown, 1810: 167, entry 2-T). '*Marsilia quadrifolia*' of Brown's Diary, collected on 15 September 1802 (Vallance *et al.*, in prep.).
278. *Marsilea hirsuta* R.Br. Bennett 140
'2 *Marsilea villosa* [struck through] *hirsuta* in [. . .] Port Jackson' (Brown, 1810: 167, entry 2-J).
279. *Marsilea mutica* Mett. Bennett 137
(Syn. '*M. brownii*' R.Br., cf. Beadle *et al.* (1972), in index.)
'1 *Marsilea quadrifolia* Port Jackson' (Brown, 1810: 167, entry 1-J).
280. *Marsilea mutica* Mett. Unnumbered
Two labels: 1st reads 'Nova Cambria australis Port Jackson R Br'; 2nd reads '*Marsilia australis* RB *Marsilia quadrifolia* prodr [blank]' (probably Brown, 1810: 167, entry 1-J).
281. *Mecodium australe* (Willd.) Copel Bennett 99
'3 *Hymenophyllum flabellatum* ['undulatum' struck through] Labill prodr 159 Derwent' ('*Hymenophyllum flabellatum*' of Brown, 1810: 159, entry 3-D).
282. *Mecodium rarum* (R.Br.) Copel. Bennett 97
Two labels: 1st reads '1 *Hymenophyllum rarum* prodr 159 Derwent'; 2nd reads '*Hymenophyllum rarum* prodr [. . .] Van Diemens Island 1804 RB' (Brown, 1810: 159, entry 1-D).

283. *Microsorium punctatum* (L.) Copel. Bennett 10
 '5 Polypodium irioides ['punctatum' struck through] Prodr 147 Keppel Bay Shoal Water Bay Broad Sound'. Another sheet of the same gathering has a secondary label which reads 'Nova Cambria Australis intra tropicum 1802 RB' (Brown, 1810: 147, entry 5-T).
284. *Nephrolepis hirsutula* (Forst.f.) C. Presl Bennett 20
 'Nephrodium exaltatum prodr 148 Plendioides davilliastrum desc ['Davallioides' struck through] Port II East Coast'. Port Clinton, Queensland (Burbidge, 1956), (Brown, 1810: 148, entry 2-T).
285. *Ophioglossum costatum* R.Br. Bennett 118
 '2 Ophioglossum costatum Arnhem N Bay Feb 14 1803 desc 55' (Brown, 1810: 163, entry 2-T).
286. *Pellaea falcata* (R.Br.) Fee Bennett 59
 'Kents Islands & Hawkesbury 6 Pteris ['adiantoides' struck through] falcata prodr 154' ('Pteris falcata' of Brown, 1810: 154, entry 6-J and D).
287. *Pellaea paradoxa* (R.Br.) Hook. Bennett 63
 'Port Jackson 1 Adiantum paradoxum prodr 155' ('Adiantum paradoxum' of Brown, 1810: 155, entry 1-J).
288. *Phymatosorus diversifolia* (Willd.) Pichi Serm. Bennett 11a-c
 Three sheets: 1st (Bennett 11a) reads '6 Polypodium billardieri prodr 147 Port Dalrymple in umbrosis & truncus arbor Jan 1804'; 2nd reads (Bennett 11b) 'Polypodium polymorphum var Port Jackson'; 3rd (Bennett 11c) reads 'Kents Group Bass Strait 7 Polypodium ['lycopodioides' struck through] Billardieri prodr 147' ('Polypodium billardieri' of Brown, 1810: 147, entry 7-D). The indication would appear to be that the Port Jackson specimen did not feature in the description.
289. *Platyserium bifurcatum* (Cav.) C.Chr. Bennett 1
 Two labels: 1st reads 'Acrostichum alcicorne prodr p145 Port Jackson 1802-5 Rocks & Trees'; 2nd reads '1 Acrostichum alcicorne prodr 145' (Brown, 1810: 145, entry 1-J).
290. *Platyzoma microphyllum* R.Br. Bennett 101
 (?Syn. 'Gleichenia platyzoma' F. Muell.)
 'Platyzoma microphylla Carpentaria Island h' (North Island cf. Burbidge 1956) (Brown, 1810: 160, entry 1-T).
291. *Platyzoma microphyllum* R.Br. Bennett 102
 (? Syn. 'G. platyzoma' F. Muell.)
 'Acrostichum? Gleichenia? Facing Island Port I' (Queensland, cf. Brown, 1810: 160, entry 1-T).
292. *Pleurosorus rutiflorus* (R.Br.) Fee Bennett 7
 'Derwent Risdon 2 Grammitis rutaefolia prodr 146'. Another specimen on this sheet bears the secondary locality 'Nova Hollandia ora australis Kangaroo Island 1802 RB' (probably 'Grammitis rutaefolia' of Brown, 1810: 146, entry 2-D).

293. *Polyphlebium venosum* (R.Br.) Copel. Bennett 96
 'Derwent 1 Trichomanes [‘repandum’ struck through] venosum prodr 159’ (Brown, 1810: 159, entry 1-D).
294. *Polystichum australiense* Tindale Bennett 18
 No original label; secondary annotation reads ‘Derwent’. Separated out from material of Bennett 17 (see below) and assigned by Bennett’s workers to No 18.
295. *Polystichum proliferum* (R.Br.) C. Presl Bennett 17
 ‘Aspidium proliferum prodr 147 desc Port Jackson [and] Derwent’ (Brown 1810: 147-8, entry 1-D). Lectotype (Tindale, 1961: 50).
296. *Pteridium esculentum* (Forst.f.) Cockayne Bennett 57
 ‘Pteris esculenta var P Jackson’ (Brown, 1810: 154, entry 5-J).
297. *Pteridium esculentum* (Forst.f.) Cockayne Bennett 58
 ‘5 Pteris esculenta prodr 154 Derwent’ (Brown, 1810: 154, entry 5-D).
298. *Pteris tremula* R.Br. Bennett 53
 ‘Grose’ (Brown, 1810: 154, entry 4-J).
299. *Pteris tremula* R.Br. Unnumbered but corresponds to Bennett register entry 56
 ‘Pteris tremula prodr 154 Port Jackson’ (Brown, 1810: 154, entry 4-J).
300. *Pteris umbrosa* R.Br. Bennett 51
 ‘Pteris umbrosa First branch of the Grose Pteris’ (Brown, 1810: 154, entry 1-J).
301. *Pyrrosia confluens* (R.Br.) Ching Bennett 9
 ‘Pteroides varia [struck through] Polypodium confluens prodr 146 cfr Plenopiloselloides ad rip Hunters & Patersons Rivers Oct: Nov 1804’ (‘Polypodium confluens’ of Brown, 1810: 146, entry 3-J).
302. *Pyrrosia rupestris* (R.Br.) Ching Bennett 8
 ‘Polypodium rupestre prodr 146 [reverse] Polypodium serpens B & S Forst Prod: Vahl Symb Port Jackson’ (‘Polypodium rupestris’ of Brown, 1810: 146, entry 2-J).
303. *Rumohra adiantiformis* (Forst.f.) Ching Bennett 19
 ‘2 Aspidium coriaceum prodr 148 Polypodium adiantiforme Forst prod Derwent adras montis’ (‘Aspidium coriaceum’ of Brown, 1810: 148, entry 2-D).
304. *Schizaea bifida* Willd. Bennett 113
 Two labels: 1st reads; ‘3 Schizaea furcata [struck through] bifida prodr 162 Port II’; 2nd reads ‘Schizaea furcata Richmond’ (Brown, 1810: 162, entry 3-J. The provenance annotation is J and D; perhaps T and J are meant).
305. *Schizaea bifida* Willd. Unnumbered — Dryander duplicate, see introduction.
 ‘Acrostichum pectinastordes Nova Cambria australis Port Jackson’.
306. *Schizaea dichotoma* (L.) J.Sm. Bennett 114
 ‘Schizaea dichotoma 4 Schizaea aspera scabr cfr S dichotom: prodr 162’ (Brown, 1810: 162, entry 4-T).

307. *Schizaea fistulosa* Labill. Unnumbered
'Terra Dieman' ('Schizaea fistulosa' of Brown, 1810: 162, entry 2-D).
308. *Schizaea fistulosa* Labill. Unnumbered
(Syn. 'Microschizaea fistulosa' (Labill.) Reed).
'Schizaea fistula [. . .]'. Locality probably Tasmania as above (cf. Brown, 1810: 162, entry 2-D).
309. *Schizaea rupestris* R.Br. Bennett 112
'Schizaea rupestris prodr 162 desc 25 nep [. . .] Port Jackson' (Brown, 1810: 162, entry 1-J).
310. *Sticherus flabellatus* (R.Br.) St. John Bennett 109
'Port Jackson 6 Gleichenia ['prolifer' struck through] flabellata prodr 161' ('Gleichenia flabellata' of Brown, 1810: 161, entry 6-J).
311. *Sticherus tener* (R.Br.) Ching Bennett 110
'7 Gleichenia tenera prodr 161 in rup. hum ad rip rivul alpin Mon[tis] Tabul[aris]' ('Gleichenia tenera' of Brown, 1810: 161, entry 7-D).
312. *Todea barbara* (L.) T. Moore Bennett 117
'Osmunda barbara prodr 163 Port Jackson' (Brown, 1810: 163, entry 1-J).
313. *Vittaria elongata* Sw. Bennett 50
'Vittaria acostata Broad Sound Peaked West Hill parasit: super Asplen[ium] nidus' (Brown, 1810: 153, entry 1-T).

CYCADOPHYTES

Cycadaceae

314. *Cycas angulata* R.Br. Bennett 3106 (pro parte)
No original label. According to an annotation by J. R. Maconochie of 18 November 1976, the specimen is probably from Bountiful Island, Gulf of Carpentaria, and the 'T' entry confirms the tropical provenance (Brown, 1810: 348, entry 2-T). In his Diary (Vallance *et al.*, in prep.) Brown does not mention a cycad being collected from Bountiful Island but Good mentions a 'Cycas circinalis' which his editor (Edwards, 1981: 104) identified as *C. media* R.Br. But we believe that *C. angulata* is correct. Bauer painting 159/60, Botany Library, BM (NH), is probably based on this plant.
315. *Cycas media* R.Br. Bennett 3106 (pro parte)
No original label. According to an annotation by J. R. Maconochie of 18 November 1976, the specimen is probably from Cumberland Islands, Queensland. The 'T' entry (Brown, 1810: 348, entry 1-T) confirms this (cf. Mabberley, 1985: plate 4). Certainly Brown collected a specimen of 'Cycas circinalis' at Calder Island (Cumberland Islands) on 16 October 1802 which could be this specimen. BM (NH) Bauer painting 157/8 is probably based on this plant (Vallance *et al.*, in prep.).

CONIFEROPHYTES

Araucariaceae

316. *Araucaria cunninghamii* Ait. Bennett 3115

'Araucaria cunninghamii Port Bowen 1802 RB' (probably the specimen collected 21 August 1802 according to Brown's Diary (Vallance *et al.*, in prep).

Cupressaceae

317. *Callitris gracilis* R. Baker Bennett 3108
(Syn. 'Frenela robusta' A. Cunn.)

Two labels: 1st reads 'Callitris glauca Nob Mount Brown Spencers Gulf 1802 RB'; 2nd reads 'Genus Conifer Inlet XII South C'. Gathered from Mount Brown, 10-11 March 1802 (cf. Vallance *et al.*, in prep.).

318. *Callitris gracilis* R. Baker Bennett 3109
(Syns 'Frenela robusta' A. Cunn., 'Callitris propinqua' R.Br.)

'Callitris propinqua Nob Kangaroo Island 1802 RB'. Gathered March 1802 (cf. Vallance *et al.*, in prep.).

319. *Callitris muelleri* (Parl.) F. Muell. Bennett 3112
(Syn. 'Frenela muelleri' Parl., cf. Garden, 1956: 383).
'Callitris Nova Holland loc incerta'.

320. *Callitris rhomboidea* R.Br. ex A. & L. C. Rich Bennett 3107
(Syn. Holotype of 'Callitris ventenatii' Mirb., Garden, 1956: 386)
'Callitris ventenatii Nob Port Jackson 1804-5'.

321. *Callitris rhomboidea* R.Br. ex A. & L. C. Rich Bennett 3114
(Syn. 'Callitris australis', cf. Garden, 1956: 386).
'Genus Coniferar: adripas saxosus fluvii Cataract River Port Dalrymple Jan 10 1804
[. . .] Callitris australis'.

322. *Callitris tuberculata* R.Br. ex R. T. Baker & H. G. Smith Bennett 3110
(Syn. 'Frenela robusta var. verrucosa', also 'Callitris preissi' Miq.).
Two labels: 1st reads 'Middle Island of Goose Island Bay 1802 RB'; 2nd reads 'Genus Conif Bay II South Coast 1802 Jan^y 12'. Gathered January 1802 from the Archipelago of the Recherche (cf. Willis, 1959: 99; and Vallance *et al.*, in prep.).

323. *Callitris* sp.indet. Bennett 3111
'Port Jackson'.

324. *Callitris columellaris* F. Muell. Bennett 3113
'Nov gen Conifer Sandy Cape Arbor Mediocris cortice ramoso crasso'. Collected 30 July 1802, Vallance *et al.* (in prep.).

Podocarpaceae

325. *Lagarostrobos franklinii* (Hook.f.) C. J. Quinn Bennett 3120
'Huon Pine'. No locality given on original label. This taxon *sensu* Quinn (1982).

326. *Phyllocladus aspleniifolius* (Labill.) Hook.f. Bennett 3119
(Syn. 'Podocarpus asplenifolia' Labill.).
'Derwent [. . .] Podocarpus asplenifolia'.

327. *Podocarpus elatus* R.Br. ex Endl. Bennett 3117
Two labels: 1st reads 'Taxus cfr T elongatum Hunters River'; 2nd reads 'Taxus cfr T elongatum In sylvis prope ripas fluvio Paterson A A Ash Island Insulas que adjacent Cabbage tree swamp & C Desc In mscr N C No95'. Probably gathered 14 October 1804 (cf. Vallance *et al.* in prep.).
328. *Podocarpus lawrencei* Hook.f. Bennett 3116
(*'Podocarpus alpinus'* of de Laubenfels, 1985).
'Taxus emersa No120 desc Misc fl Derwent In Summitate saxosa Montis Tabularis prope fluio: Derwent Apr: Mai 1804'.
329. *Podocarpus spinulosus* (Sm.) R.Br. ex Mirb. Bennett 3118
No original label.

INDEX

Poorly-localized material is unindexed, but material from the **south coast** is given below. This is broadly equivalent to Brown's (1810) annotation 'M':
3, 7-10, 14, 18, 20, 22, 24, 35, 36-7, 42-3, 47, 55, 75, 83, 86, 122, 129, 172, 179, 214, 317-8 and 322.

Material from **Tasmania**, and **Bass Strait**, approximately equivalent to Brown's (1810) 'D' annotation:

2, 4, 5, 11, 17-19, 21, 23, 31-32, 34, 38, 41, 43, 48-51, 55, 59, 62, 65-8, 71-3, 78-9, 87, 89, 90-6, 100, 105-11, 113-15, 117-8, 120-25, 130-35, 137-8, 141, 143-55, 157-8, 160-64, 166-7, 169-71, 175, 189-90, 194, 203-04, 206-11, 230-1, 235-6, 241-42, 247, 252-3, 256, 261, 263-5, 281-2, 286, 288, 292-3, 295, 297, 303, 307-8, 311, 321, 326 and 328.

Material from **New South Wales**, equivalent to Brown's (1810) 'J' annotation:
97-9, 101-04, 126-28, 136, 140, 142, 156, 165, 168, 173-74, 176, 180-82, 184-88, 191-93, 196-202, 205, 212-13, 220, 228-29, 232-34, 237-39, 240, 244-46, 257-60, 262, 266, 270-71, 278-80, 287, 289, 296, 298-302, 304, 309-10, 312, 320, 323 and 327.

Tropical material, equivalent to Brown's (1810) 'T' annotation:
27, 29, 44-6, 80, 82, 84, 177-78, 183, 195, 217-19, 222, 224-25, 243, 248-51, 267, 268-69, 272-77, 283-85, 290-91, 304, 306, 313-16, 324 and 327.

INDEX OF BENNETT NUMBERS vs GROVES & MOORE NUMBERS

There are no Bennett numbers: 8, 33, 38, 40, 70, 84, 99, 156, 159, 161, 188 [=25], 190 [=30], 191 [=31], 192 [=25], 196 [=28], 206 [?=47], 210 [?=44], 244 [?=24], 256, 273 [?=116], 274 [?=155], 280, 299 [=56], 305, 307 and 308. Possibly equivalent Bennett numbers are given in brackets — see text for each such entry. For Groves & Moore numbers marked with an asterisk (*) there is no Bennett number.

Bennett	Groves & Moore	Bennett	Groves & Moore	Bennett	Groves & Moore
1	289	9	301	19	303
2	177	10	283	20	284
3	224	11a-c	288	21a	228
4a	220	12	186	21b	229
4b	221	13	230	22	266
5a	217	14a[=15]	249	23	267
5b	218	14b	250 & 251	24	244*
6b & c	259	16a	265	25	188, 192 & 193*
7	292	17	295	27	194
8	302	18	294	28	196*

Bennett	Groves & Moore	Bennett	Groves & Moore	Bennett	Groves & Moore
29	195*	81	269	131	168
30	190*	82	272	132	173
31	191*	83	271	133	172
33	187	84	238	134	197
35	189	85	239	135	198
36	245	86	231	136	199
37	246	87	232	137	279
38	247	88	233	138	276
39	202	89	234	139	277
40	205	90	235	140	278
41	201	91	242	141	275
42	203	92	241	157	39
43	204	93	240	158	41
44	209 & 210*	94	236	159	43
45	207	95	237	161	44
46	208	96	293	162	45
47?	206*	97	282	163	46
48	211 & 212	98	264	166	3
49	200	99	281	167	5
50	313	100	263	168	6
51	300	101	290	169	7
52	260	102	291	170	10
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61	223	111	243	181	12, 13 & 14
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65	184	115?	274*	195	53
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70	179	120	174	209	22
71	180	121	176	210	42
72	225	122	175	211	2
73	226	123	169	213	17
74	214	124	170	214	21
75	227	125	171	215	48
76	215	126	163	216	47
77	216	127	164	217	37
78	219	128	165	218	27
79	270	129	166	219	24
80	268	130	167	221	25

Bennett	Groves & Moore	Bennett	Groves & Moore	Bennett	Groves & Moore
223	28	284	150	539	100
224	26	285	157	540	116 & 119
225	49	286	160	542	142
226	19	287	153	543	111
227	35	288	151	544	128
228	50	289	152	545	134
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230	36	291	147	547	121
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253	64	516	118	565	109
254	61	517	130	566	110
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The Lichens of Norfolk Island

1: Introduction and the Family Parmeliaceae

JOHN A. ELIX and HEINAR STREIMANN

ELIX, J. A., & STREIMANN, H. The lichens of Norfolk Island. 1: Introduction and the family Parmeliaceae. *Proc. Linn. Soc. N.S.W.* 111 (2), 1989: 103-121.

The historical records of lichens of the Norfolk Island complex are discussed and synonymy given. The 16 species (from 7 genera) of the Parmeliaceae which currently grow there are examined critically. Each species is described fully (including chemistry) and its distribution is recorded. The endemic *Flavoparmelia norfolkensis* Elix & Streim. is described as new to science. All 16 species on these geologically recent, oceanic islands possessed vegetative dispores, attesting to the efficiency of this method of reproduction.

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KEY WORDS *Flavoparmelia norfolkensis* Elix & Streim., *Neofuscelia verrucella* (Essl.) Essl., *Paraparmelia scotophylla* (Kurok.) Elix & Johnston, *Parmelia erumpens* Kurok., *Parmelinopsis spumosa* (Asahina) Elix & Hale, *Parmotrema austrocetratum* Elix & Johnston, *Parmotrema chinense* (Osbeck) Hale & Ahti, *Parmotrema crinitum* (Ach.) Choisy, *Parmotrema cristiferum* (Taylor) Hale, *Parmotrema gardneri* (Dodge) Sérusiaux, *Parmotrema rampoddense* (Nyl.) Hale, *Parmotrema reticulatum* (Taylor) Choisy, *Parmotrema sancti-angelii* (Lyngé) Hale, *Parmotrema tinctorum* (Despr. ex Nyl.) Hale, *Xanthoparmelia amplexula* (Stirton) Elix & Johnston, *Xanthoparmelia australasica* D. Gall., Parmeliaceae, chemotaxonomy, Norfolk Island, lichens.

INTRODUCTION

The Norfolk Island complex (including Norfolk, Phillip and Nepean Islands with the satellite islands) is an isolated volcanic outcrop in the South Pacific Ocean between longitudes 167°55' and 168°00' E and latitudes 28°59' and 29°08' S. The islands lie on a narrow, steep-sided submarine ridge (the Norfolk Ridge) which extends from New Caledonia to New Zealand (Jones and McDougall, 1973). The closest land is New Caledonia, 670 kilometres to the north. Norfolk Island lies approximately 1610 kilometres north-east of Sydney and 1100 kilometres north-north-west of Auckland (Fig. 1).

The islands are an Australian territory: Norfolk Island (the largest) is 8 kilometres long and 6 kilometres wide; Phillip Island is 2 kilometres long and 1 kilometre wide, while Nepean Island is approximately 500 metres long and 300 metres wide (Figure 2).

Norfolk and Phillip Islands have similar geology: both are almost completely volcanic in origin. Olivine basalt lavas predominate on Norfolk Island, with basaltic tuffs relatively more common on Phillip Island. This volcanic activity occurred 2.3-3.2 million years ago, during the Pliocene epoch (Jones and McDougall, 1973). Nepean Island and part of Norfolk Island (near Kingston) consist of coarse marine calcareous rock of late Pleistocene origin (Ovington, 1984).

The highest point on Norfolk Island is Mt Bates, which is 319 metres above sea level. Mt Pitt is slightly lower (318m), but these peaks are only 600 metres apart and together form the summit complex. The southern half and north-west corner of the island are gullied plateaux 90-120 metres a.s.l. and are distinct from the Mt Pitt — Mt Bates summit area. Most of the coastline, except for a length on the southern coast (Kingston area) and several bays, consists of cliffs up to 140m high (Jones and McDougall, 1973; Ovington, 1984).

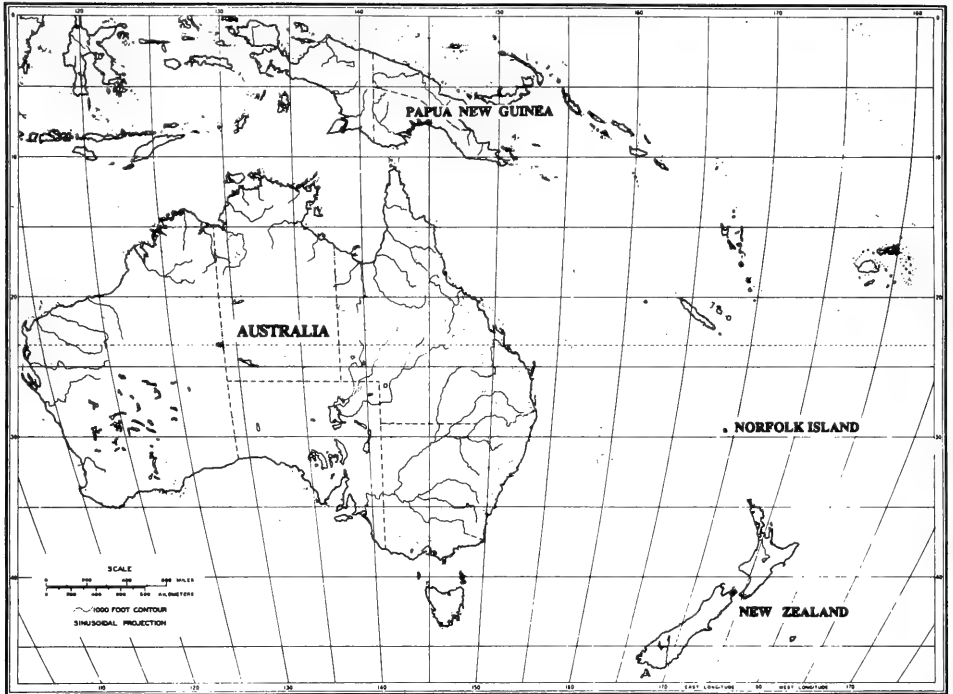


Fig. 1. Location of Norfolk Island.

Phillip Island is even more rugged and precipitous, rising to its highest point at Jacky Jacky (280 metres a.s.l.) and surrounded by coastal cliffs. Largely defoliated by feral rabbits, pigs and goats, the island is eroded extensively, with many exposed boulders and rock outcrops. The plateau above the coastal cliffs consists of a series of eroded valleys which rise towards the summit, where the slope ends abruptly at a near-vertical cliff, 280 metres a.s.l. (Coyne, 1982). Nepean Island, an uninhabited limestone island a few acres in extent, rises to 32 metres (Hoare, 1965).

The climate of Norfolk Island is sub-tropical with no extremes of temperature and moderate relative humidity (72-81%) with no seasonal pattern. Mean monthly temperature fluctuates from minima near 12°C (in winter) to maxima near 25°C (in summer) and the daily range is rarely more than 8°C. Rainfall (mean annual precipitation 1313mm) occurs throughout the year with a winter maximum (June average of 163mm). Droughts of some weeks duration may occur (Ovington, 1984).

HISTORY OF LICHENOLOGICAL INVESTIGATIONS

Captain James Cook discovered Norfolk Island on October 10, 1774, during his second voyage around the world. The following day he landed at Duncombe Bay and named the island after the then Duchess of Norfolk. Although uninhabited at the time, Polynesian stone adzes have been discovered since, suggesting earlier settlement. Fourteen years after discovery, the first of two penal settlements was established and maintained until 1814. A second penal settlement was established in 1826 and abandoned 30 years later. In 1856, descendants of the 'Bounty' mutineers left their home on Pitcairn Island and established the first free settlement on Norfolk, and today the 'Islanders' still comprise some 30% of the total population of approximately 2,000 (Hoare, 1965).

Norfolk Island has been visited by a number of scientific expeditions in the course of its short history. Few of the early expeditions contributed greatly to the lichen flora.

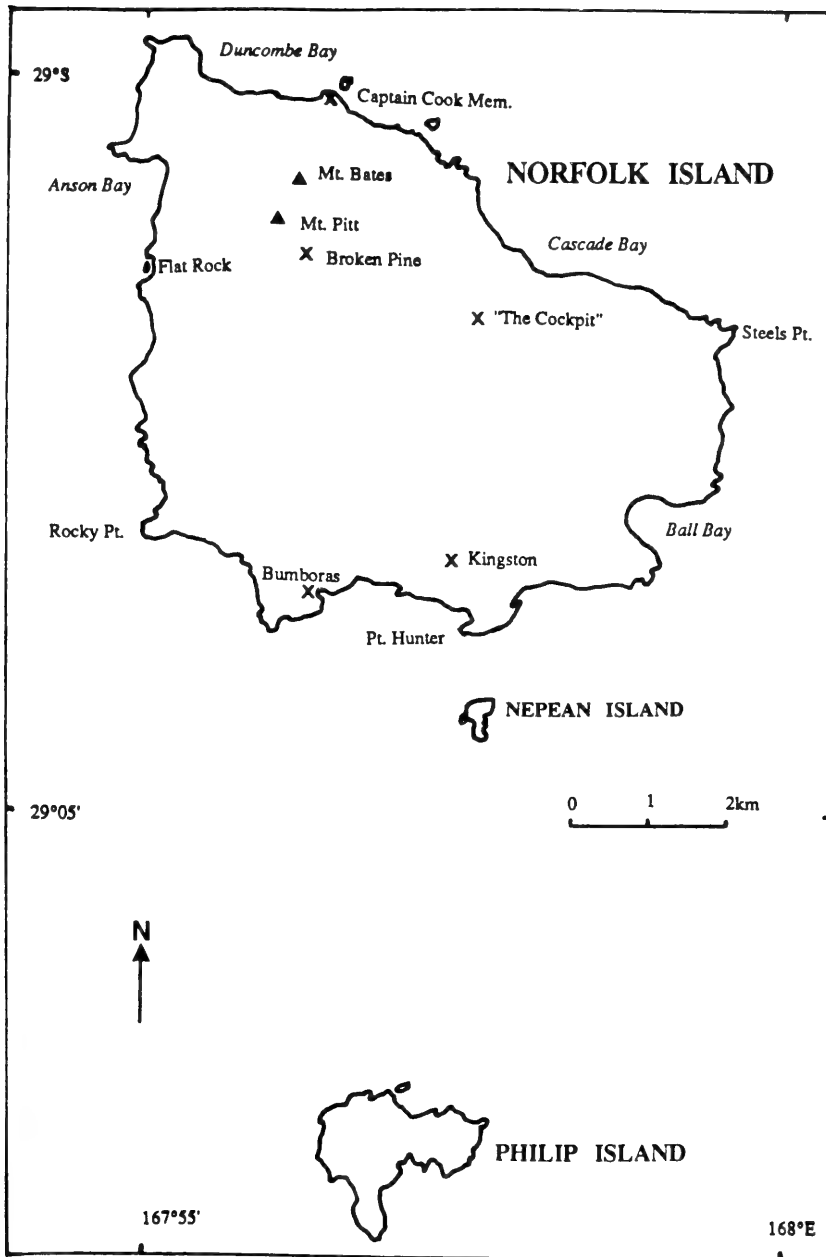


Fig. 2. Map of the Norfolk Island complex. Here, and on Fig. 3, 'Philip Island' should be Phillip Island.

In 1804-5 Ferdinand Bauer visited the island and his collections and drawings were submitted to Stephan Endlicher of Vienna, who published a *Prodromus* (Endlicher, 1833) to the plants which listed four lichens: *Evernia* (*Usnea*) *melaxantha* Ach., *Parmelia* (*Parmotrema*) *perlata* Ach., *Parmelia* (*Physcia*) *caesia* Ach., and *Sticta* (*Pseudocyphellaria*) *aurata* Ach.

In 1830 Allan Cunningham visited the island and augmented the knowledge of its

botany; his notes were published posthumously in Heward (1842). A lichen not enumerated by Endlicher was listed, namely *Ramalina scopulorum* Ach.

Baron Ferdinand von Mueller subsequently investigated the botany of the island on the basis of specimens collected by Isaac Robinson, a resident and agent for the Sydney Botanic Gardens. The identity of the lichen collections was communicated subsequently to J. H. Maiden (see below).

In 1904 J. H. Maiden (Director of the Botanic Gardens in Sydney) reported a total of 29 lichen species for Norfolk Island. This list was prepared by Edwin Cheel (Botanic Gardens, Sydney) after examining the collections of Maiden and Boorman (made during a visit to the island in 1902), and was supplemented by F. von Mueller (Melbourne), who supplied the names of six species identified by J. Müller of Aargau, Switzerland.

This list is presented here using currently-accepted names for taxa (bold) followed, where appropriate, by the synonyms used by Maiden in brackets. [?] infers a dubious identification — according to Maiden. The species list included: *Anaptychia ciliaris* (L.) Körb. [?]; *Catinaria grossa* (Pers. ex Nyl.) Vainio {*Patellaria grossa* Müll. Arg.}; *Catinaria versicolor* (Fée) Sipman {*Patellaria versicolor* Fée}; *Chiodecton perplexum* Nyl.; *Clathroporina eminentior* Nyl.; *Coenogonium implexum* Nyl.; *Dirinaria confluens* (Fr.) Awasthi {*Physcia confluens* Mitt.}; *Glyphis verruculosa* Zahlbr. {*Glyphis verrucosa* Knight}; *Leptogium cyanescens* (Rabenh.) Körb {*L. tremelloides* L.}; *Letrouitia bifera* (Nyl.) Hafelln. {*Heterothecium biflorum* Nyl.}; *Ochrolechia pallescens* (L.) Massal. {*Lecanora pallescens* Fr.} [?]; *Parmentaria ravenellii* (Tuck.) Müll. Arg. {*Parmentaria havenlii* Tuck.} [?]; *Parmotrema chinense* (Osbeck) Hale & Ahti [*Parmelia perlatus* L.]; *Pertusaria* sp.; *Phyllopsora parvifolia* (Pers.) Müll. Arg. {*Psora parvifolia* Müll. Arg.}; *Physcia caesia* (Hoffm.) Fűrnr.; *Physma byrsinum* (Ach.) Müll. Arg.; *Pseudocyphellaria aurata* (Ach.) Vainio {*Sticta aurata* Ach.}; *Pyrenula nitida* (Weigel) Ach. [?]; *Pyxine cocoes* (Sw.) Nyl.; *Ramalina farinacea* (L.) Ach.; *Ramalina glaucescens* Krempelh. {*R. leiodea* Nyl. var. *fastigiata* Müll. Arg.}; *Ramalina siliquosa* (Huds.) A.L. Sm. {*R. scopulorum* Ach.} [?]; *Ramalina thrausta* (Ach.) Nyl. {*R. thrausta* (Ach.) Fr.} [?]; *Teloschistes flavicans* (Sw.) Norm.; *Usnea aurantiaco-atra* (Jacq.) Bory {*Evernia melaxantha* Ach.} [?]; *Usnea barbata* (L.) Weber ex Wigg. {*U. barbata* Ach.}; *Usnea florida* (L.) Weber ex Wigg. {*U. barbata* Ach. var. *florida* (L.) Fr.}; *Usnea intercalaris* Krempelh.

Since then only scattered individual reports of lichens occurring in Norfolk Island have appeared in the literature, such as that of *Usnea nexilis* Motyka and *U. propinqua* Stirton (Motyka, 1938), *Ramalina arabum* (Dill. ex Ach.) Meyen & Flot. (Riedl, 1976) and from preliminary reports of the present work (Elix and Streimann, 1985).

PRINCIPAL VEGETATION FORMATIONS

The vegetation of the Norfolk Island complex was divided into five major formations: sub-tropical rainforest, open *Araucaria* woodland, pastures and foreshores, weedy forests dominated by *Psidium* and *Olea*, and Phillip Island (Elix and Streimann, 1985; Ovington, 1984). Brief notes are given below for these, together with the dominant lichen genera occurring in each formation.

Sub-tropical Rainforest

No doubt the Mt Pitt Reserve, with its remaining areas of sub-tropical rainforest, is the major habitat for lichens on the island and has the richest lichen flora. Dominant spermatophytes including *Araucaria heterophylla* together with varying amounts of native hardwoods — *Elaeodendron cirtipendulum*, *Nestegis apetala*, *Rapanea crassifolia* and *Baloghia lucida*. The understorey comprises smaller trees and sometimes scattered palms (*Rhopalostylis baueri*), tree ferns (*Cyathea* spp.) and the exotics red guava, *Psidium littorale*

and *Citrus limon*. Within this reserve, the eastern and south-eastern slopes of Mt Bates appear to be the richest site for lichens. Corticolous species abound: the richest substrates are the trunks of *Elaeodendron* and the base of the trunks and branches of *Araucaria heterophylla* and *Citrus limon*. The macrolichen genera *Heterodermia*, *Parmotrema*, *Ramalina*, *Teloschistes* and *Usnea* are prominent in the canopy while *Coccocarpia*, *Pannaria*, *Physma* and *Pseudocyphellaria* species occur in the wetter areas at the base of trees. *Elaeodendron curtispiculum* is by far the richest substrate for crustose lichens, including many species of Graphidaceae, *Pyrenula* and extensive cover by *Clathroporina* and *Megalospora*. One of the most conspicuous lichens of the forest is the beautiful *Pseudocyphellaria aurata*, with its brilliant yellow and emerald green (when wet) thallus, which commonly inhabits the trunks of *Cyathea*, *Citrus* and *Araucaria*.

Open *Araucaria* Woodland

Open *Araucaria* woodlands, which occur at sites such as Anson Bay Reserve, Selwyn Recreation Reserve and Ball Bay Reserve, constitute the second most important lichen habitat on the island. The *Araucaria* trees throughout the island are characterized by a prodigious growth of *Ramalina arabum* and *Usnea* sp. on the canopy branches in particular, as well as on lower branches. *Dirinaria*, *Pyxine* and *Physcia* species as well as various *Ramalinae*, are very abundant and well developed on the branches of most *Araucaria* trees, while *Xanthoria* and *Caloplaca* species are limited to *Araucaria* in coastal situations.

Pastures and Foreshores

Here old fence posts are colonized by a few corticolous lichens (*Usnea*, *Ramalina*, *Lecanora* sp.). Remnant *Araucaria* trees which occur in scattered stands or as individuals are much better substrates, with more species present and larger populations of lichens. However their communities are impoverished compared with those on woodland or forest trees of similar age. Exposed rock surfaces in pasture and along the foreshores are more interesting substrates. Their communities include representatives of *Neofuscelia*, *Paraparmelia*, *Parmotrema* and *Xanthoparmelia* plus a variety of microlichen genera including *Diploschistes*, *Lecanora* s.l. and *Lecidea* s.l. Interestingly the limestone outcrops near Emily Bay provide a suitable habitat for several calciphilic species, including a very unusual *Buellia*.

Weedy Forest dominated by *Psidium littorale* and *Olea africans*

Areas of Mt Pitt Reserve dominated by thickets of *Psidium littorale* (guava) are extremely poor in lichens. *Psidium* supports no lichens and its dense canopy prevents growth on soil or other small trees and shrubs. Lichens in these areas are found virtually only on scattered remnant *Araucaria* or other native trees. *Olea africans* dominates other drier areas on the Reserve and, like *Psidium*, it is a very poor lichen host. Only scattered depauperate *Usnea*, *Ramalina* and *Parmotrema* species are found on *Olea* in such areas.

Phillip Island

The Phillip Island lichen flora is rather depauperate because of the rarity of host trees. The branches of remnant *Lagunaria patersonia* are moderately well covered with lichens, but are relatively poor in taxa, mainly species of *Dirinaria*, *Physcia* and *Pyxine*. However saxicolous lichens are quite well developed in some areas of Phillip Island (e.g. upper Long Valley), although again the number of species is not large, with *Parmotrema reticulatum* being particularly common. Oddities include *Teloschistes flavicans* growing on soil and rocks, usually a corticolous species, and *Xanthoria*, *Caloplaca* and *Lecidea* growing on consolidated soil, imitating the soil crust lichens of arid inland Australia.

THE LICHEN FAMILY PARMELIACEAE

Representatives of the genera *Flavoparmelia*, *Neofuscelia*, *Paraparmelia*, *Parmelia*, *Parmelinopsis*, *Parmotrema* and *Xanthoparmelia* are detailed and a key to the species is given. A full description of each species (including chemical constituents) and its distribution are provided. Interestingly all (16) species have vegetative diaspores, illustrating the ease of dispersal of such units in reaching such isolated oceanic islands, and hence the effectiveness of such a mode of reproduction.

Artificial Key to the Parmeliaceae in Norfolk Island

1. Thallus brown *Neofuscelia verrucella*
1. Thallus grey or yellow-green 2
2. Thallus yellow-green 3
2. Thallus grey 5
3. Thallus with a pale lower surface *Xanthoparmelia amplexula*
3. Thallus with a black lower surface 4
4. Thallus with cylindrical isidia, medulla white throughout *Xanthoparmelia australasica*
4. Thallus with pustulate isidia, lower medulla yellow-orange *Flavoparmelia norfolkensis*
5. Lobes narrow, less than 1.5mm broad 6
5. Lobes broad, greater than 2mm broad 7
6. Thallus isidiate, saxicolous *Paraparmelia scotophylla*
6. Thallus pustulate, usually corticolous *Parmelinopsis spumosa*
7. Upper surface pseudocyphellate *Parmelia erumpens*
7. Upper surface lacking pseudocyphellae 8
8. Thallus isidiate or sorediate 9
8. Thallus lacking soredia or isidia, but with flaking upper cortex *Parmotrema austrocetratum*
9. Thallus isidiate 10
9. Thallus sorediate 11
10. Thallus ciliate, medulla K+ yellow, C- *Parmotrema crinitum*
10. Thallus eciliate, medulla K-, C+ red *Parmotrema tinctorum*
11. Upper surface reticulately cracked *Parmotrema reticulatum*
11. Upper surface lacking reticulate cracks 12
12. Medulla K+ yellow or K+ yellow-red 13
12. Medulla K- 14
13. Medulla K+ yellow-red, containing salazinic acid *Parmotrema cristiferum*
13. Medulla K+ yellow, containing stictic acid *Parmotrema chinense*
14. Medulla C+ rose, containing gyrophoric acid *Parmotrema sancti-angelii*
14. Medulla C- 15
15. Thallus ciliate, medulla P-, UV+, containing alectoronic acid *Parmotrema ramppoddense*
15. Thallus eciliate, medulla P+ brick-red, UV-, containing protocetraric acid *Parmotrema gardneri*

Specimens Examined

Collectors and location of specimens examined are as follows: *JAE* were collected by *J. A. Elix and H. Streimann* and are held in ANUC; *HS* were collected by *H. Streimann* and are held in CBG with duplicates distributed as indicated.

Collection site details (for map see Fig. 3):

S1: open *Araucaria* woodland, Picnic Area, end of Martins Road, 29°03'30"S, 167°59'E, 80m, 1.xii.1984.

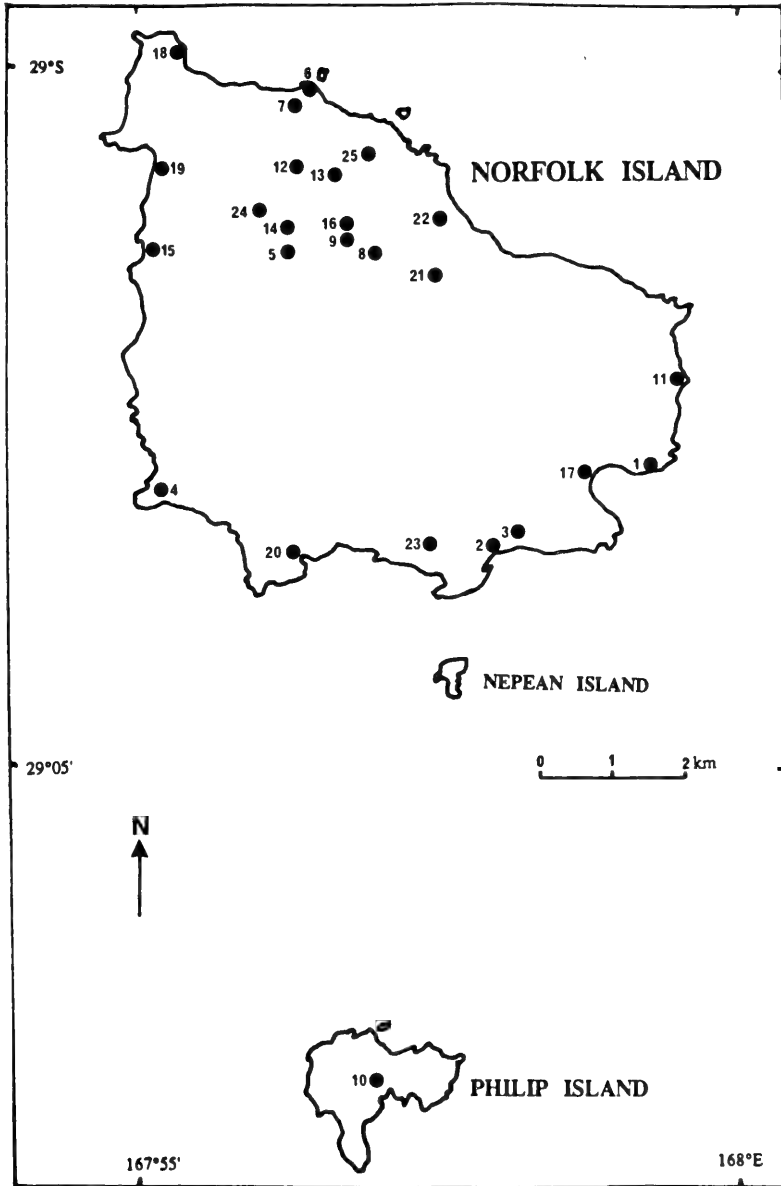


Fig. 3. Collection sites on Norfolk Island.

- S2: pasture, Cemetery road, Kingston, 29°03'30"S, 167°58'E, 15m, 2.xii.1984.
- S3: *Araucaria heterophylla*-dominated grassland, Bloody Bridge, Cemetery Road, 29°03'30"S, 167°58'E, 20m, 2.xii.1984.
- S4: mixed exotic and *Araucaria* woodland, Rocky Point Reserve, 29°03'S, 167°55'20"E, 60m, 2.xii.1984.
- S5: mixed sub-tropical rainforest, near Broken Pine, Mt Pitt Reserve, 220-240m, 29°01'30"S, 167°56'20"E, 2.xii.1984.
- S6: stand of *Araucaria heterophylla* along the margin of grassland and forest, Captain Cook Memorial, Duncombe Bay, 29°00'S, 167°56'30"E, 100m, 3.xii.1984.
- S7: regrowth forest, just south of the Captain Cook Memorial, Duncombe Bay, 29°00'20"S, 167°56'30"E, 100m, 3.xii.1984.
- S8: mixed sub-tropical rainforest, Filmy Fern Trail, Mt Pitt Reserve, 29°01'20"S, 167°56'40"E, 130m, 3.xii.1984.
- S9: open woodland with kikuyu grass, Mt Pitt Reserve, track at end of Selwyn Pine Road, 29°01'S, 167°56'30"E, 215m, 3.xii.1984.
- S10: *Olea africans*-dominated valley, Upper Long Valley, Phillip Island, 29°07'30"S, 167°57'E, 80m, 4.xii.1984.
- S11: open *Araucaria* woodland, Point Blackbourne Reserve, end of Two Chimneys Road, 29°03'S, 167°59'E, 3m, 4.xii.1984.
- S12: mixed sub-tropical rainforest, Mt Bates summit trail, Mt Pitt Reserve, 29°00'30"S, 167°56'30"E, 300m, 6.xii.1984.
- S13: mixed sub-tropical rainforest, track from Red Road to Mt Bates, Mt Pitt Reserve, 29°00'40"S, 167°56'40"E, 220m, 6.xii.1984.
- S14: mixed sub-tropical rainforest, King Fern Valley, Mt Pitt Reserve, 29°01'S, 167°56'20"E, 260m, 7.xii.1984.
- S15: grassland with scattered *Araucaria heterophylla*, Flat Rock Bay Picnic Area, Anson Bay Road, 29°01'30"S, 167°55'E, 40m, 7.xii.1984.
- S16: *Psidium*- and *Olea*-infested lowland forest, track at end of Selwyn Pine Road, 29°01'S, 167°56'30"E, 200m, 8.xii.1984.
- S17: rocky foreshore, Ball Bay Reserve, 29°03'S, 167°59'E, 2m, 8.xii.1984.
- S18: rocky cliffs at north-west point, Duncombe Bay, 29°00'S, 167°55'30"E, 50m, 9.xii.1984.
- S19: grassland with scattered *Araucaria heterophylla*, near Jacobs Rock, Anson Bay Road, 29°01'S, 167°55'E, 50m, 9.xii.1984.
- S20: *Araucaria*-dominated grassland, Bumboras Reserve, 29°03'30"S, 167°56'20"E, 10m, 9.xii.1984.
- S21: open pasture, 'The Cockpit', Cascade Creek Valley, 29°01'S, 167°58'E, 35m, 9.xii.1984.
- S22: open woodland, Prince Philip Drive, 29°01'S, 167°58'E, 35m, 9.xii.1984.
- S23: open pasture, Kingston, 29°03'30"S, 167°57'30"E, 8m, 9.xii.1984.
- S24: regrowth rainforest, Mt Pitt Reserve, just south of summit of Mt Pitt, 29°01'S, 167°56'E, 230m, 10.xii.1984.
- S25: mixed sub-tropical rainforest, Bird Rock Track, Mt Pitt Reserve, 29°00'30"S, 167°57'E, 210m, 10.xii.1984.

FLAVOPARMELIA Hale

Flavoparmelia norfolkensis Elix & Streim. sp. nov. (Fig. 4)

Species cum thallo ut in *Flavoparmelia euplecta* sed ad hac specie isidiis cylindricis, coral-loideis demum inflatis, apicibus saepe erumpentibus sed esorediosis differt.

Type: Norfolk Island. On *Elaeodendron* in open woodland in forest clearing, Mt Pitt

Reserve, track at end of Selwyn Pine Road, 29°01'S, 167°56'30"E, 215m, *J. A. Elix 18738* and *H. Streimann*, 8.xii.1984 (CBG-holotype; MEL, US-isotypes).

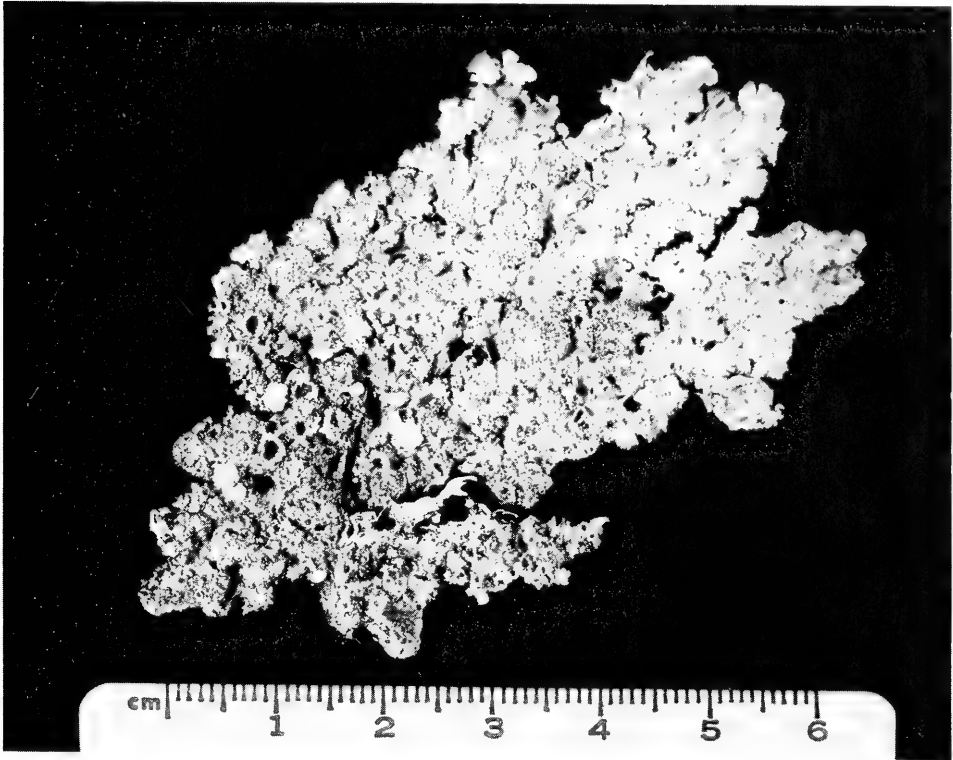


Fig. 4. Holotype of *Flavoparmelia norfolkensis*.

Thallus foliose, corticolous or saxicolous, adnate, pale yellow-green, to 5cm in diameter.

Lobes irregular, 1.0-3.0(-5.0)mm wide, becoming laterally imbricate, \pm contiguous, plane, rotund at the apices. **Upper surface** plane to \pm undulating, dull to slightly shiny, with reticulate, white maculae towards the apices, isidiate; **isidia** laminal, cylindrical at first and becoming coralloid, ultimately becoming inflated at the apices and erumpent-pustulate, hollow within (dactylate), very rarely with traces of granular soredia; medulla white for the most part, but with a yellow-orange zone adjacent to the lower cortex. **Lower surface** black with a very narrow, naked, brown rim, sparsely rhizinate, rhizines short, simple or tufted at the apices, concolorous with the lower surface. **Apothecia** up to 5mm in diam., disc strongly concave, dark cinnamon brown, dull; margin persistent, strongly inrolled, pustulate-isidiate; spores ellipsoid, 19-21 \times 8-9 μ m. **Pycnidia** rare, black, punctiform, immersed; conidia weakly bifusiform, 4-6 \times 1 μ m.

Chemistry: Cortex K-; medulla K+ pale brown, C-, P+ brick red; pigmented lower medulla K+ claret; containing usnic acid, protocetraric acid (major), atranorin (\pm trace), euplectin (minor), virensic acid (trace), gyrophoric acid (trace), skyrin (trace).

This species is characterized by the adnate, yellow to yellow-green thallus, the pustulate isidiate upper surface and a medulla pigmented orange (adjacent to the lower cortex) with the anthraquinone, euplectin. In many respects this new species resembles the common Australian species, *F. euplecta* (Stirton) Hale, as both have a similar, pigmented lower cortex and analogous chemistry. However the upper surface of *F. euplecta* is sorediate, with laminal, erumpent-pustulate soralia, which are subcapitate at first but coalesce and spread over the upper surface as granular soredia, whereas *F. norfolkensis* is isidiate with the cylindrical isidia ultimately becoming coralloid, inflating at the apices and bursting open, but remaining esorediate for the most part. This species is quite common throughout the island.

Specimens Examined:

NORFOLK ISLAND. On tree trunk and dead log, S5, *JAE 18333, 18352*; on *Elaeodendron*, S7, *JAE 18379*; on canopy of fallen tree, S8, *JAE 18421*; on *Elaeodendron*, S9, *JAE 18440*; on *Citrus limon*, S12, *JAE 18580*; on fallen *Araucaria heterophylla*, S12, *HS 34354*; on dead treelet branch, S13, *HS 34396*; on *Citrus limon*, S14, *JAE 18669*; on volcanic rocks, S20, *JAE 19269*; on volcanic rocks, S21, *JAE 18787*; on *Citrus limon*, S24, *JAE 18815*; on rock shaded by old building, S23, *HS 34806* (US).

PHILLIP ISLAND. On volcanic rocks with a southerly aspect in the open, S10, *JAE 18501*.

NEOFUSCELIA Esslinger

Neofuscelia verrucella (Essl.) Essl., *Mycotaxon* 7: 53 (1978).

Parmelia verrucella Essl., in C. F. Culberson, W. L. Culberson and T. L. Esslinger, *Bryologist* 80: 132 (1977).

Type: Australia. Victoria: Rock Bore, about 33km NNW of Murrayville, *Dahl* (O-holotype).

Thallus saxicolous, moderately to loosely adnate, yellow-brown to dark brown, 4-6cm in diam. **Lobes** irregular, 1.0-2.5mm wide, often markedly imbricate to entangled. **Upper surface** smooth, shining at margins, wrinkled and cracked in the centre, emaculate, \pm lightly pruinose, moderately to densely isidiate; **isidia** laminal, cylindrical, simple or branched, to 1.5mm tall; medulla white. **Lower surface** black, smooth and shining at margins, matt and wrinkled at centre, sparsely to moderately rhizinate, rhizines simple, black. **Apothecia** rare, to 2mm in diam., sessile, deeply concave when young, becoming \pm flat with age, disc smooth, light to dark-brown, margins entire or sparsely isidiate; spores broadly ellipsoid, 8-9 \times 4-6 μ m. **Pycnidia** not seen.

Chemistry: Cortex K-, HNO₃ + dark blue-green; medulla K-, C-, KC- or KC+ faint rose, P-; containing divaricatic acid (major), nordivaricatic acid (minor).

A common and widespread species in Australia, also occurring in both islands of New Zealand and South Africa. Rare in Norfolk Island.

Specimen Examined:

NORFOLK ISLAND. On volcanic rocks, S21, *JAE 18791*.

PARAPARMELIA Elix & Johnston

Paraparmelia scotophylla (Kurok.) Elix & Johnston, *Mycotaxon* 27: 281 (1986).

Parmelia scotophylla Kurok., in Kurokawa and Filson, *Bull. natn. Sci. Mus. Tokyo* B, 1: 46 (1975).

Type: On rocks, Ardglen Gap, Liverpool Range, 8.5km north of Murrurundi, Great Dividing Range, New South Wales, *S. Kurokawa 5174*, 28.x.1965 (TNS-holotype; MEL-isotype).

Thallus saxicolous, adnate, mineral grey but blackening with age, 5-10 (-20)cm diam. **Lobes** irregular to sublinear, 1.0-3.0mm wide, slightly imbricate, apices subrotund. **Upper surface** smooth, shining at margins, flat to slightly convex, becoming cracked in the centre, emaculate; moderately to sparsely isidiate; **isidia** laminal, cylindrical, simple or sparingly branched, to 0.2mm tall; medulla white. **Lower surface** pale to light brown, sparsely to moderately rhizinate, rhizines simple, concolorous. **Apothecia** rare, to 6mm in diam., substipitate, deeply concave, disc smooth, pale brown, margins thin, involute, isidiate; spores 7-11 x 5-8 μm . **Pycnidia** not seen.

Chemistry: Cortex K+ yellow; medulla K+ yellow then dark red, C-, P+ orange; containing atranorin, salazinic acid (major) and consalazinic acid.

A common and widespread species in Australia, also occurring in both islands of New Zealand. Rare on Norfolk Island.

Specimen Examined:

NORFOLK ISLAND. On volcanic rocks, S21, JAE 18793.

PARMELIA Acharius

Parmelia erumpens Kurok., *Lich. rar. Critic. Exsicc.* no. 74 (1969)

[Based on *Parmelia tenuirima* J. D. Hook. & Taylor f. *corallina* Müll. Arg.]

Parmelia tenuirima J. D. Hook. & Taylor f. *corallina* Müll. Arg., *Flora*, Jena, 66: 46 (1883).

Type: Gippsland, Australia, *Stirling* (G-lectotype; UPS, US-isolectotypes).

Thallus corticolous or saxicolous, adnate to loosely attached, pale greenish to light mineral-grey, 8-20cm in diam. **Lobes** short, subirregular to apically rotund, imbricate, 2-8mm wide. **Upper surface** shiny, plane, white-reticulate at first but becoming conspicuously cracked to the margin, **pseudocyphellae** effigurate, 0.2-1.0mm long, somewhat raised, dense, fusing into a reticulate network over the whole surface, sorediate; the **soredia** coarse and isidioid, often bursting apically, forming dense marginal and laminal soralia and/or extended, granular, coralloid-isidioid outgrowths; medulla white. **Lower surface** black, moderately rhizinate, rhizines simple or squarrosely branched at maturity, 1-2mm long, black. **Apothecia** rare, stipitate, to 15mm in diameter, disc dark brown, concave at first then flattening, margin inrolled at first but splitting radially at maturity, the amphithecium reticulately cracked, pseudocyphellate, sorediate; spores ellipsoid, 10-12 x 6-8 μm . **Pycnidia** scattered, punctiform, black, conidia cylindrical to weakly bifusiform, straight, 5-7 x 1 μm .

Chemistry: Cortex K+ yellow; medulla K+ yellow becoming deep red, C-, P+ red-orange; containing atranorin, chloroatranorin, salazinic acid (major), consalazinic acid (minor), lobaric acid (minor), protocetraric acid (\pm trace).

P. erumpens is a widespread species on rocks and trees in coastal and hinterland areas of Australia, both islands of New Zealand and Lord Howe Island. It also occurs in South Africa, India, Indonesia, Taiwan and Japan. This species is scattered on both rocks and trees in Norfolk Island and is easily recognized by the deeply reticulate-fissured cortex, the abundant coarse, pustular soredia and the lack of cilia. Uncommon in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On exposed volcanic rocks, S2, JAE 18316, HS 31746; on *Elaeodendron*, S5, JAE 18310; on tree, S7, JAE 18360, 18385; on *Elaeodendron*, S16, JAE 18737.

PARMELINOPSIS Elix & Hale

Parmelinopsis spumosa (Asahina) Elix & Hale, *Mycotaxon* 29: 243 (1987).

Parmelina spumosa (Asahina) Hale, *Phytologia* 28: 483 (1974).

Parmelia spumosa Asahina, *J. Jap. Bot.* 26: 259 (1951).

Type: Higashi-Murayama, Kita-Tama-gun, Prov. Masashi, Japan, *Asahina* (TNS-lectotype).

Thallus corticolous, adnate, fragile, pale mineral grey to pale olive grey, 2-6cm in diam. **Lobes** sublinear, narrow, 0.5-2.0mm wide, ciliate, the marginal cilia distinct and evenly dispersed, *ca.* 0.5mm long. **Upper surface** plane, emaculate, continuous, densely pustulate-isidiate; **pustules** laminal, bursting open but sparingly or not sorediate; medulla white or faintly yellow. **Lower surface** smooth, shiny, black, moderately rhizinate, rhizines simple or furcate, short, *ca.* 0.1-0.2mm long. **Apothecia** very rare, laminal, adnate, concave, 1-3mm in diam., disc brown, imperforate, margin and amphithecium pustulate; spores ellipsoid, 12-14 x 7-8 μ m. **Pycnidia** not seen.

Chemistry: Cortex K+ yellow; medulla K-, C+ rose, KC+ red, P-; containing atranorin, chloroatranorin, gyrophoric acid (major), 5-O-methylhiascic acid (minor), umbilicic acid (minor).

P. spumosa is a cosmopolitan species which is widespread throughout the tropical and sub-tropical areas of the world, but is much less common at temperate latitudes. In Australasia it is common in Australia, Papua New Guinea and New Zealand. Exposed trees at the forest margins or isolated individuals are the preferred habitat. Rare in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On *Citrus limon*, S12, *JAE 18584*; on *Elaeodendron*, S22, *JAE 18798*; on *Elaeodendron*, S25, *JAE 18839*, 10.xii.1984.

PARMOTREMA Hale

Parmotrema austrocetratum Elix & Johnston, *Mycotaxon* 31: 495 (1988)

Type: New Zealand. North Island. On tree trunk in remnant forest, Burgess Park, New Plymouth, 60m, *J. A. Elix 4645*, 7.v.1980 (CHR-holotype, CBG-isotype).

Thallus corticolous or saxicolous, loosely attached, light mineral-grey, 6-12cm in diam. **Lobes** rotund, imbricate or not, 10-20(-30)mm wide, apices often lacinate, the lacinae flat or convex, 0.5-1.5mm wide, 1-5(-8)mm long, lobes moderately ciliate, the cilia 0.2-1.0(-1.5)mm long, simple or sparingly branched. **Upper surface** white-reticulate at first but becoming conspicuously cracked to the margin, developing raised closed dactyls, dactyls \pm curved, laminal, ultimately becoming fused and forming laminal ridges, the older parts of the thallus eventually becoming cracked-areolate, with the areolae flaking off and exposing the white medulla in eroded areas; lacking soredia and isidia. **Lower surface** black with a bare, brown marginal zone 1-2mm wide, moderately to densely rhizinate, rhizines simple or sparsely branched, slender, black. **Apothecia** rare, stipitate, to 10mm in diameter, disc perforate, pale tan, concave at first then concave-distorted, margin eciliate, thin, \pm stellate-cracked; spores ellipsoid, 12-16 x 8-9 μ m. **Pycnidia** scattered, punctiform, black, conidia filiform, 9-16 x 1 μ m.

Chemistry: Cortex K+ yellow; medulla K+ yellow becoming deep red, C-, P+ red-orange; containing atranorin, chloroatranorin, salazinic acid (major), consalazinic acid (minor), protocetraric acid (\pm trace).

P. austrocetratum is a widespread species on rocks and trees in coastal and hinterland areas along the sub-tropical and tropical east coast of Australia and the north island of New Zealand. Uncommon in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On *Cyathea* stem, S5, *HS 31905*; on *Elaeodendron*, S8, *JAE 18439*, *HS 32190* (B, H, US); on *Elaeodendron*, S16, *JAE 18742*.

Parmotrema chinense (Osbeck) Hale & Ahti, *Taxon* 35: 133 (1986).

Lichen chinensis Osbeck, *Dagb. Ostindisk resa.*: 221 (1757).

Type: Specimen and pl. 20, fig. 39B, Dillenius, *Hist. Musc.*: 147 (1742) (OXF-lectotypotype).

Lichen perlatus Huds., *Fl. angl.*: 448 (1762), (incl. type of *L. chinensis* Osbeck).

Parmelia perlata (Huds.) Ach., *Meth. Lich.*: 216 (1803).

Parmotrema perlatum (Huds.) Choisy, *Bull. mens. Soc. linn. Lyon* 21: 174 (1952).

Thallus corticolous, moderately to loosely adnate, membranaceous to coriaceous, pale mineral grey to whitish-grey, 4-15cm in diam. **Lobes** irregular, 3-8mm wide, in part rounded and deeply crenate, in part irregularly incised and lacinate, imbricate, sparingly to moderately ciliate, cilia 0.2-3.0mm long, \pm branched. **Upper surface** dull, smooth, sorediate; **soralia** submarginal, causing lobe margin to become revolute and suberect, ultimately appearing labriform, soredia granular; medulla white. **Lower surface** black, shining, with a broad, brown, naked marginal zone, moderately rhizinate, rhizines simple, to 2mm long. **Apothecia** very rare, laminal, substipitate, concave, to 7mm in diameter, disc pale brown to cinnamon brown, imperforate, margin thick, inrolled, sorediate; spores ellipsoid, 25-27 x 16-18 μ m. **Pycnidia** not seen.

Chemistry: Cortex K+ yellow; medulla K+ yellow, C-, P+ orange-red; containing atranorin, chloroatranorin, stictic acid (major), constictic acid (major), cryptostictic acid (trace), menegazziaic acid (trace), norstictic acid (trace).

P. chinense is a cosmopolitan species which is widespread throughout the tropics and temperate areas. In Australasia it is common in Australia and New Zealand, but also occurs in Fiji and Papua New Guinea. It is very rare on Norfolk Island, and although it was the first '*Parmelia*' reported for the island (Endlicher, 1833), this may well have referred to *P. reticulatum*, a morphologically similar and common species.

Specimen Examined:

NORFOLK ISLAND. On treelet stem, S24, *HS 34830* (US).

Parmotrema crinitum (Ach.) Choisy, *Bull. mens. Soc. linn. Lyon* 21: 175 (1952).

Parmelia crinita Ach., *Syn. Lich.*: 196 (1814).

Type: North America, *Muhlenberg* (H-holotype).

Thallus corticolous or saxicolous, coriaceous, adnate, pale mineral grey to grey-green, 5-6cm in diameter. **Lobes** subirregular, crenate or irregularly incised, imbricate, 2-5mm wide, the margin ciliate, cilia simple or branched, 0.5-3.0mm long. **Upper surface** plane, emaculate, smooth to rugose with age, cortex fragile, isidiate; **isidia** laminal and marginal, short-cylindrical at first, \pm becoming coralloid, granulose or occasionally dissolving into soredia, often ciliate at the apices; medulla white. **Lower surface** black, with a narrow brown, naked marginal zone, densely rhizinate, rhizines slender, simple, to 1.0mm long. **Apothecia** and **pycnidia** not seen.

Chemistry: Cortex K+ yellow; medulla K+ yellow, C-, P+ orange; containing atranorin, chloroatranorin, stictic acid (major), constictic acid (minor), cryptostictic acid (trace), norstictic acid (trace), menegazziaic acid (\pm trace), connorstictic acid (\pm trace).

P. crinitum is a cosmopolitan species, widespread in humid habitats in temperate and tropical regions. In Australasia this species is common in Australia, New Zealand and Papua New Guinea. Common in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On base of *Araucaria heterophylla*, S1, JAE 18133; on base of *Araucaria heterophylla*, S4, JAE 18216, 18246, 18323, HS 31821 (US); on tree and dead branches, S5, JAE 18276, 18293; on *Araucaria* stem, S6, HS 32018 (US); on *Elaeodendron* S7, JAE 18384; on *Lagunaria*, S8, HS 32181 *pr. p.*; on *Campsis grandiflora*, S9, JAE 18469; on base of *Araucaria heterophylla*, S11, JAE 18513; on *Citrus limon*, S12, JAE 18579, 18581, 18588, 18590; on treelet stem, S12, HS 34376; on palm and *Citrus limon*, S14, JAE 18670, 18679, 18692, HS 34515; on volcanic rocks, S17, JAE 18749; on volcanic rocks, S20, JAE 19268; on *Citrus limon*, S24, JAE 18812, 18817.

Parmotrema cristiferum (Taylor) Hale, *Phytologia* 28: 335 (1974).

Parmelia cristifera Taylor, *Hooker's Lond. J. Bot.* 6: 165 (1847).

Type: Calcutta, Wallich (FH-lectotype; BM-isolectotypes).

Thallus corticolous, adnate to loosely adnate, coriaceous, pale mineral grey, 3-10cm in diam. **Lobes** irregular, 5-20mm wide, rotund at the apices, entire or weakly crenate, imbricate or subsascending at the margins, main lobes eciliate, lateral lobes and lobe axils not or sparingly ciliate, cilia 0.5-1.5mm long. **Upper surface** dull, emaculate, continuous, sorediate; **soralia** mainly marginal on lateral lobes, sorediate lobes more or less ascending, soredia granular; medulla white. **Lower surface** smooth, shiny, black, with a broad, brown, naked marginal zone, sparsely rhizinate, rhizines simple, short, ca 0.1-0.2mm long, coarse. **Apothecia** very rare, laminal, adnate, concave, to 3mm in diameter, disc brown, imperforate, margin thick; spores ellipsoid, 25-30 x 13-15µm. **Pycnidia** not seen.

Chemistry: Cortex K+ yellow; medulla K+ yellow then dark red, C-, P+ orange-red; containing atranorin, chloroatranorin, salazinic acid (major), consalazinic acid (± minor).

P. cristiferum is a cosmopolitan species that is widespread throughout tropical and sub-tropical areas. In Australasia and Oceania it is common in Australia, Fiji, Papua New Guinea, Pitcairn Island, Raratonga and New Zealand. Common in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On base of *Araucaria heterophylla*, S1, JAE 18138; on dead branches and shrubs, S5, JAE 18279, 18282, 18301, HS 31908; on *Elaeodendron* stem, S7, HS 32061; on *Elaeodendron*, S8, JAE 18420, 18427; on *Elaeodendron*, S9, JAE 18444; on *Citrus limon*, S12, JAE 18581, 18588, 18590, HS 34264 (B, H, US); on dead treelet stem, S13, HS 34397, 34414 (US); on palm, S14, JAE 18692; on treelet stem and stump, S14, HS 34513, 34516; on crown of *Araucaria*, S15, HS 34596; on *Elaeodendron*, S16, JAE 18735 (*Lich. Australasic Exsicc.* Fasc. 4: 88); on palm stem and dead tree, S16, HS 34633, 34674, 34675 (US); on *Citrus limon*, S24, JAE 18812.

Parmotrema gardneri (Dodge) Sérusiaux, *Bryologist* 87: 5 (1984).

Parmelia gardneri Dodge, *Ann. Mo. bot. Gdn.* 46: 179 (1959).

Type: Brazil, Gardner (FH-holotype).

Thallus corticolous, adnate to loosely adnate, coriaceous, pale mineral grey, 4-6cm in diam. **Lobes** irregular, 8-15mm wide, rotund at the apices, imbricate or subsascending at the margins, crenate, irregularly incised or sublaciniate, eciliate or rarely sparingly ciliate, cilia 0.2-0.5mm long. **Upper surface** dull, emaculate, becoming rugose with age, continuous or ± cracked, sorediate; **soralia** marginal, linear along the margins to subcapitate on somewhat revolute lobes or short marginal laciniae, sometimes spreading submarginally, soredia granular; medulla white. **Lower surface** wrinkled, black, with a

broad, brown, naked marginal zone, sparsely rhizinate, rhizines simple, short, *ca.* 0.1-0.2mm long, slender. **Apothecia** rare, laminal, adnate, concave, to 3mm in diameter, disc dark brown, imperforate, margin thick, eciliate, margin and amphithecium sorediate; sores ellipsoid, 18-22 x 8-10 μ m. **Pycnidia** rare, punctiform, conidia sublageniform, 6-7 x 1 μ m.

Chemistry: Cortex K+ yellow; medulla K+ pale brown, C-, P+ brick-red; containing atranorin, chloroatranorin, protocetraric acid (major), unknown fatty acids (\pm minor).

The presence of the marginal soralia and medullary protocetraric acid plus the absence of cilia distinguish this from other species of *Parmotrema* on the island. It is a pantropical species known from Africa, Australia, Papua New Guinea and South America. Rare in Norfolk Island.

Specimen Examined:

NORFOLK ISLAND. On *Araucaria* trunk, S1, JAE 18156.

Parmotrema rampoddense (Nyl.) Hale, *Phytologia* 28: 338 (1974).

Parmelia rampoddensis Nyl., *Acta Soc. Sci. Fenn.* 26: 7 (1900).

Type: Ramboda, Ceylon, *Almquist* (H-NYL 35555-holotype; S-isotype).

Thallus corticolous, loosely adnate, coriaceous, pale grey to mineral grey, 10-20cm in diam. **Lobes** irregular, 5-20mm wide, rotund at the apices, crenate, ciliate, cilia conspicuous, 3-6mm long, simple or bifurcate. **Upper surface** dull, emaculate, rugulose towards the centre, sorediate; **soralia** mainly marginal, linear, sometimes spreading submarginally, soredia farinose; medulla white, often pigmented orange-red adjacent to the lower cortex. **Lower surface** smooth, shiny, black, with a broad, brown, naked marginal zone, sparsely rhizinate, rhizines simple, to 6.0mm long, slender. **Apothecia** not seen in Norfolk Island material. Hale (1965) reports apothecia 3-10mm in diam., disc imperforate, amphithecium sorediate and spores 10-12 x 6-7 μ m. **Pycnidia** not seen.

Chemistry: Cortex K+ yellow; medulla K-, C-, KC+ red, P-; pigmented lower medulla K+ purple; containing atranorin, chloroatranorin, alectoronic acid (major), α -collatolic acid (major or minor), skyrin (\pm).

P. rampoddense is a common and widespread pantropical species. In Australasia it is known from Australia and Papua New Guinea. Rare in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On fallen branch, S5, JAE 18125; on treelet stem, S14, HS 34532.

Parmotrema reticulatum (Taylor) Choisy, *Bull. mens. Soc. linn. Lyon* 21: 175 (1952).

Parmelia reticulata Taylor, in Mackay, *Fl. Hibern.* 2: 148 (1836).

Type: Ireland, County Kerry, near Dunkerron (FH-holotype).

Thallus corticolous or saxicolous, loosely adnate, membranaceous to coriaceous, pale mineral grey to grey-green, 4-20cm in diam. **Lobes** irregular, 5-15mm wide, in part rounded and deeply crenate, in part irregularly incised and lacinate, imbricate or subsending at the margins, sparingly to moderately ciliate, cilia 0.2-3.0mm long. **Upper surface** dull, reticulately maculate and cracked, sorediate; **soralia** marginal, linear along the margins to subcapitate, commonly on short marginal laciniae, sometimes submarginal and punctiform, soredia granular; medulla white. **Lower surface** black, rhizinate or papillate to the margins or with a brown, naked marginal zone, densely rhizinate, rhizines simple or squarrose, to 2mm long, slender. **Apothecia** rare, submarginal to laminal, substipitate, concave, to 8mm in diameter, disc pale to mid-brown, imperforate or narrowly perforate, margin thick, eciliate, margin and amphithecium sorediate; spores ellipsoid, 13-18 x 8-11 μ m. **Pycnidia** rare, punctiform, conidia filiform, 12-16 x 1.0-1.5 μ m.

Chemistry: Cortex K+ yellow; medulla K+ yellow then dark red, C-, P+ orange-red; containing atranorin, chloroatranorin, salazinic acid (major), consalazinic acid (\pm minor).

P. reticulatum is a very common and highly variable species. Specimens growing in drier, exposed sites tend to become coriaceous, have weakly developed maculae and often submarginal soralia, while those from moist, shady habitats are usually membranaceous, have marginal soralia and well-developed maculae. *P. reticulatum* is a cosmopolitan species, widespread throughout the tropics and temperate areas. In Australasia it is common in Australia, New Zealand and Papua New Guinea. Very common in Norfolk Island and occasional in Phillip Island.

Specimens Examined:

NORFOLK ISLAND. On *Araucaria* trunk, S1, *HS* 31718, 31723, 31728, 31734 (US); on exposed boulder, S2, *HS* 31748 (H, US); on small rock outcrop, S3, *HS* 31768, 31769 (B, H, US); on *Grevillea robusta*, and *Melia*, S4, *JAE* 18222, 18231, 18250, *HS* 31791, 31839 (US); on dead branch, S5, *JAE* 18308; on rocks, S6, *JAE* 18371, 18374, *HS* 31997, 32022 (US); on old wooden steps, S8, *HS* 32189 (H, US); on *Cyathea* stem, S14, *JAE* 18665, *HS* 34537 (US); on *Araucaria* trunk, S15, *HS* 34578A, 34588 (US); on volcanic rocks, S17, *JAE* 18745, 18746, 18837, *HS* 34695, 34699, 34707 (US); on volcanic rocks, S18, *JAE* 18764, *HS* 34736; on *Lagunaria patersonia* trunk, S19, *JAE* 18778; on volcanic rocks, S20, *JAE* 18833 (*Lich. Australasici Exsicc.* Fasc. 4: 89), 18834, 19267, *HS* 34769 (H, US); on shaded rocks, S21, *HS* 34782.

PHILLIP ISLAND. On south-facing volcanic rocks in the open, S10, *JAE* 18502, 18503, *HS* 32204.

Parmotrema sancti-angelii (Lynge) Hale, *Phytologia* 28: 339 (1974).

Parmelia sancti-angelii Lynge, *Ark. Bot.* 13: 35 (1914).

Type: Santo Angelo, Rio Grande do Sul, Brazil, 25 January 1893, *G. A. Malme* (S-lectotype).

Thallus corticolous, adnate to loosely adnate, membranaceous to coriaceous, pale grey to pale grey-green, 3-10cm in diam. **Lobes** irregular, 5-15 mm wide, rotund at the apices, crenate, often deeply divided and with ascending margins, ciliate, cilia slender, 1.0-3.5mm long, simple or bifurcate. **Upper surface** dull, emaculate, wrinkled or rugose towards the centre, sorediate; **soralia** mainly marginal, linear, sometimes spreading submarginally, soredia farinose; medulla white. **Lower surface** smooth, shiny, black, with a broad, brown or mottled, naked marginal zone, densely rhizinate, rhizines simple, elongate, to 2mm long, slender. **Apothecia** not seen in Norfolk Island material. Hale (1965) reports apothecia imperforate, spores 13-18 x 7-10 μ m. **Pycnidia** rare, conidia weakly sublageniform, 6-8 x 1 μ m.

Chemistry: Cortex K+ yellow; medulla K-, C+ pale red, P-; containing atranorin, chloroatranorin, gyrophoric acid (major), lecanoric acid (\pm trace).

P. sancti-angelii is a common and widespread pantropical species. In Australasia it is known from Australia and Papua New Guinea. Rare in Norfolk Island.

Specimen Examined:

NORFOLK ISLAND. On *Elaeodendron*, S5, *JAE* 18349.

Parmotrema tinctorum (Despr. ex Nyl.) Hale, *Phytologia* 28: 339 (1974).

Parmelia tinctoria Despr. ex Nyl., *Flora*, Jena 55: 547 (1872).

Type: Canary Islands, *Despréaux* (H-NYL 35365-holotype).

Thallus corticolous or saxicolous, loosely adnate, membranaceous to coriaceous, pale grey to grey-green, 10-30cm in diam. **Lobes** irregular, 10-20mm wide, rotund at the

apices, entire or crenate, eciliate. **Upper surface** shiny, becoming dull towards the centre, emaculate, cortex sometimes cracking and flaking, isidiate; **isidia** sparse to abundant, laminal and eventually marginal, confluent or in scattered groups, brown tipped or concolorous with the thallus, simple or branched, thin and cylindrical or coarse and irregularly inflated, rarely \pm interspersed with lobules; medulla white. **Lower surface** smooth, shiny, black, with a broad, brown, naked marginal zone, sparsely rhizinate, rhizines simple, short, *ca* 0.5-2.0mm long, coarse. **Apothecia** very rare, laminal, substipitate, concave or \pm radially split, to 20mm in diameter, disc dark brown, imperforate or with a small perforation, margin thick, margin and amphithecium isidiate; spores ellipsoid, 13-15 \times 7-8 μ m. **Pycnidia** rare, conidia filiform, 12-16 \times 1.0-1.5 μ m.

Chemistry: Cortex K+ yellow; medulla K-, C+ red, P-; containing atranorin, chloroatranorin, lecanoric acid (major), orsellinic acid (trace).

Parmotrema tinctorum is a cosmopolitan species that is widespread throughout tropical and temperate regions. In Australasia and Oceania it is common in Australia, Fiji, Papua New Guinea, Vanuatu, Samoa and the North Island of New Zealand. Very common in Norfolk Island and Phillip Island.

Specimens Examined:

NORFOLK ISLAND. On base of *Araucaria heterophylla*, S1, *JAE 18137*, *HS 31739* (H, US); on *Grevillea robusta*, S4, *JAE 18221*; on *Elaeodendron* and dead branches, S5, *JAE 18285*, *18307*, *18350*; on *Araucaria* trunk, S6, *HS 32017*, *32035* (US); on canopy of fallen tree, S8, *JAE 18411*; on *Elaeodendron*, S8, *HS 32164*, *32196* (H, US); on *Elaeodendron* and *Citrus limon*, S12, *JAE 18558*, *18570*; on *Araucaria* trunk, S15, *HS 34589* (B, MICH, US); on *Elaeodendron*, S16, *JAE 18736* (*Lich. Australasici Exsicc.* Fasc. 4: 90); on rock outcrop, S20, *HS 34860* (US); on tree trunk, S22, *HS 36482* (B, US); on *Citrus limon*, S24, *JAE 18816*; on tree in open area, Mt Pitt Reserve, R. *Goldsack 4*, 25.xii.1981 (ANUC).

PHILLIP ISLAND. On south-facing volcanic rocks in the open, S10, *JAE 18499*, *HS 32225* (B, H, US); on *Lagunaria* stem, S10, *HS 32213*, *32225*.

XANTHOPARMELIA Hale

Xanthoparmelia amplexula (Stirton) Elix & Johnston, *Bull. Br. Mus. nat. Hist. (Bot.)* 15: 192 (1986).

Parmelia amplexula Stirton, *Trans Proc. Roy. Soc. Victoria* 17: 69 (1881).

Type: Australia. Near Brisbane, Queensland, *Bailey 262* (BM-holotype).

Parmelia violascens Stirton, *Trans Proc. New Zeal. Inst.* 32: 77 (1899).

Type: Australia. Grampian Mountains, Victoria, *Sullivan* (BM-holotype).

Thallus foliose, adnate to moderately adnate on rocks, yellow-green or commonly blackening towards the centre as a result of the dark-tipped, dense isidia; subirregularly lobate, 5-10cm in diam. **Lobes** sublinear-elongate, sparingly imbricate or not so, 0.8-2.0 (3.0)mm wide. **Upper surface** opaque, emaculate, with sparse to numerous isidia, isidia cylindrical, simple or branched and coralloid up to 2mm high; medulla white. **Lower surface** pale brown to dark brown, sparsely to moderately rhizinate, the rhizines concolorous with the lower surface, simple, slender. **Apothecia** rare, 1.5-6.0mm in diam.; disc strongly concave to \pm flat at maturity, dark brown, shining; margin thin, persistent, involute at first, isidiate; spores 7-12 \times 5-6 μ m. **Pycnidia** not seen.

Chemistry: Cortex K-; medulla K-, C-, KC+ rose, P-; containing usnic acid, loxodin (minor), norloboridone (major), unknown (trace).

A common and widespread species in Australia (occurring in all States and Territories) and both islands of New Zealand. It also occurs in Lord Howe Island and South Africa. Rare in Norfolk Island.

Specimen Examined:

NORFOLK ISLAND. On treelet stem, S25, *HS 34916A*.

Xanthoparmelia australasica D. Gall., *N.Z. J. Bot.* 18: 531 (1980).

Parmelia australasica (D. Gall.) Filson, *Aust. J. Bot.* 30: 519 (1982).

Type: New Zealand, North Auckland, Karekare Beach, on andesitic conglomerate, 8 October 1977, J. Bartlett (CHR 314047 – holotype; CHR – isotypes).

Thallus foliose, moderately to loosely adnate, yellow-green, 5-12 (-20)cm in diam. **Lobes** irregular, 2.0-3.5 (-5.0)mm wide, often markedly imbricate, secondary lobes similar to the marginal lobes, sometimes building the thallus up into a thick mat, apices subrotund. **Upper surface** smooth, shining at margins, wrinkled and cracked in the centre, emaculate, moderately to densely isidiate; **isidia** laminal, often forming a dense areolate crust, robust, broad, cylindrical, extensively coralloid-branched, to 2.5mm tall; medulla white. **Lower surface** black with a narrow brown, naked, marginal zone, smooth and shining at margins, matt and wrinkled at centre, sparsely rhizinate, rhizines simple, black. **Apothecia** rare, 2-6 (-8)mm in diam., sessile, deeply concave when young, becoming shallowly convex with age, disc smooth, red-brown, margins conspicuously isidiate, exciple wrinkled, shining, becoming isidiate with age; spores 8-11 x 4-6 μ m. **Pycnidia** not seen.

Chemistry: Cortex K-; medulla K+ yellow then dark red, C-, KC+ red, P+ orange; containing usnic acid, salazinic acid (major) and consalazinic acid, protocetraric acid (\pm trace), norstictic acid (\pm trace).

A common and widespread species in Australia, which occurs in all States and Territories. It also is found in both islands of New Zealand, the continental United States and South Africa. Relatively uncommon in Norfolk Island.

Specimens Examined:

NORFOLK ISLAND. On rock in shaded track cutting, S13, *HS 34371A*; on volcanic rocks, S18, *JAE 18765*; on volcanic rocks, S21, *JAE 18788, 18789, 18790, 18794, 18797, HS 34792* (US).

ACKNOWLEDGEMENTS

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Conicochernes doyleae, a new Australian Species of the Chernetidae (Pseudoscorpionida: Arachnida)

CLARICE M. A. KENNEDY

KENNEDY, C. M. A. *Conicochernes doyleae*, a new Australian species of the Chernetidae (Pseudoscorpionida: Arachnida). *Proc. Linn. Soc. N.S.W.* 111 (2), 1989: 123-129.

A new species of the genus *Conicochernes* Beier, *C. doyleae*, is described from the Sydney region. It is corticolous, being associated in the sampled area specifically with the 'Brush Box', *Lophostemon confertus* (R.Br.) Peter G. Wilson et J. T. Waterhouse.

Clarice M. A. Kennedy, School of Biological Sciences, Macquarie University, North Ryde, Australia 2109; manuscript received 16 August 1988, accepted for publication 15 February 1989.

INTRODUCTION

The Chernetidae are the largest family of pseudoscorpions currently including nearly 100 genera and over 550 species distributed over much of the world (Harvey, 1985). Of these only 12 genera, represented by 26 species, occur in the Australian region.

The species described herein is a representative of the genus *Conicochernes* Beier which is endemic to Australia. Four species are currently known namely: *C. brevispinosus* (L. Koch), *C. crassus* Beier, *C. globosus* Beier and *C. incrassatus* (Beier).

Measurements are based on the examination of 10 specimens of each stage made in accordance with those advocated by Chamberlin (1931). Those in parentheses are the female and follow those of the male.

Abbreviations for chelal trichobothria and setal formulae follow those devised by Chamberlin (1931).

Genitalic terminology follows Legg (1974a, 1974b). All specimens are preserved in spirit.

SYSTEMATIC DESCRIPTION CHERNETIDAE Chamberlin 1931 *Conicochernes* Beier 1948

Type species: *Chelifer brevispinosus* L. Koch 1885.

For synonymy list refer to Harvey 1981: 246.

KEY TO SPECIES OF CONICOCHERNES

1. 3rd distal blade of flagellum serrate 2
3rd distal blade of flagellum not serrate 3
2. At least 2 galea setae, eye spots present *C. doyleae* sp. nov.
1 galea seta, eye spots absent *C. incrassatus* (Beier)
3. 3rd distal blade of flagellum pinnate 4
All blades of flagellum pinnate *C. globosus* Beier
4. Serrula exterior with 16-17 lamellae *C. brevispinosus* (L. Koch)
Serrula exterior with 21 lamellae *C. crassus* Beier

Conicochernes doyleae sp. nov.
(Figs 1-4)

Etymology: This species is named after Suzanne Doyle, a colleague who has been of great assistance to me in the field.

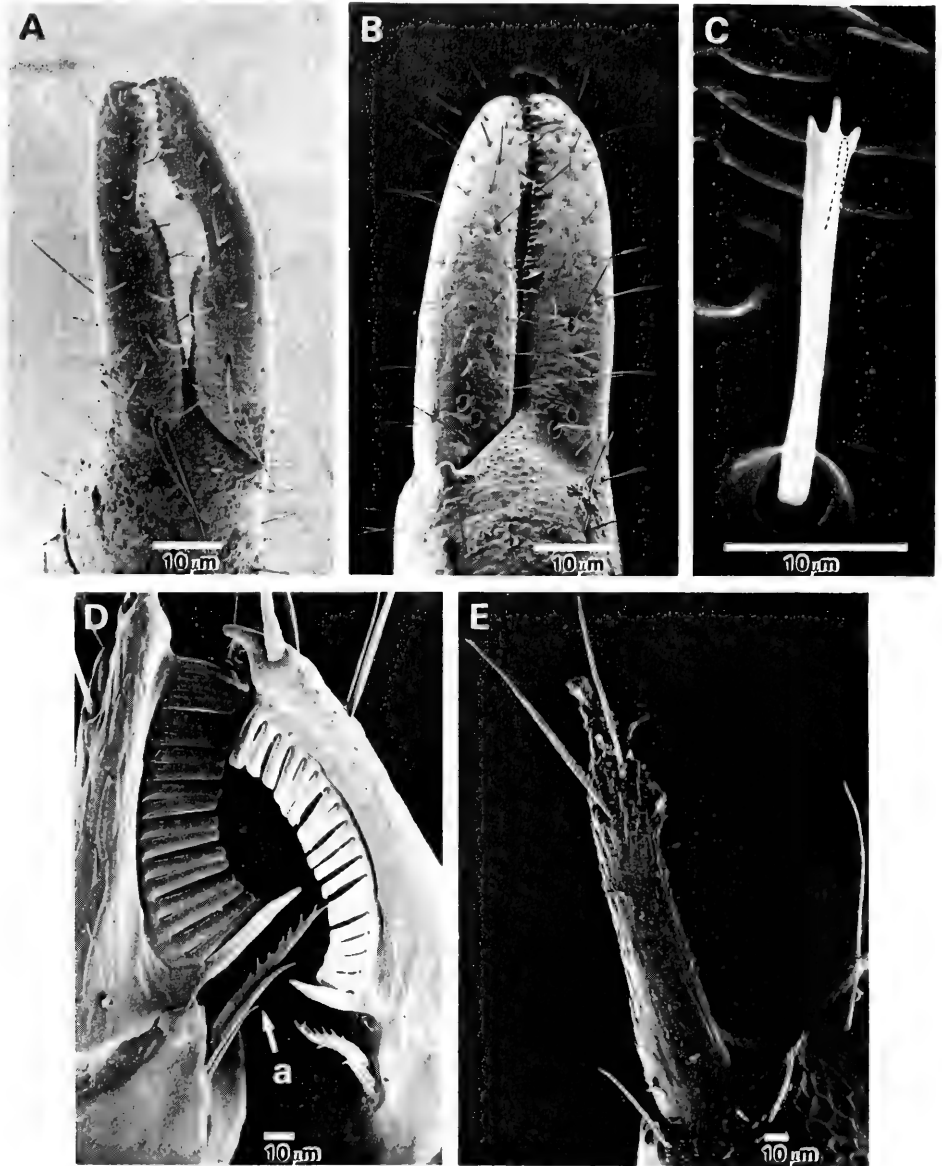


Fig. 1. *Conicochernes doyleae* sp. nov., scanning electron micrographs of paratypes: **A**, right chela, lateral aspect, male; **B**, left chela, lateral aspect, female; **C**, dorsal seta of tergite 4; **D**, serrula exterior of chelicerae, female; **E**, flagellum of left chelicera; **F**, movable finger of left chelicera.

Holotype: ♀, Australian Museum, Sydney (KS 17445).

Type locality: Stanley Street, Chatswood, 10km NW of Sydney G.P.O., N.S.W., lat. 33°48'10"S, long. 151°11'30"E, under bark of *Lophostemon confertus* (R.Br.) Peter G. Wilson et J. T. Waterhouse, 17. iv. 1985, C. Kennedy.

Paratypes: same data as holotype, Australian Museum, 4♂ (KS 17446), 4♀ (KS 19207), 4 nymphs (KS 19208).

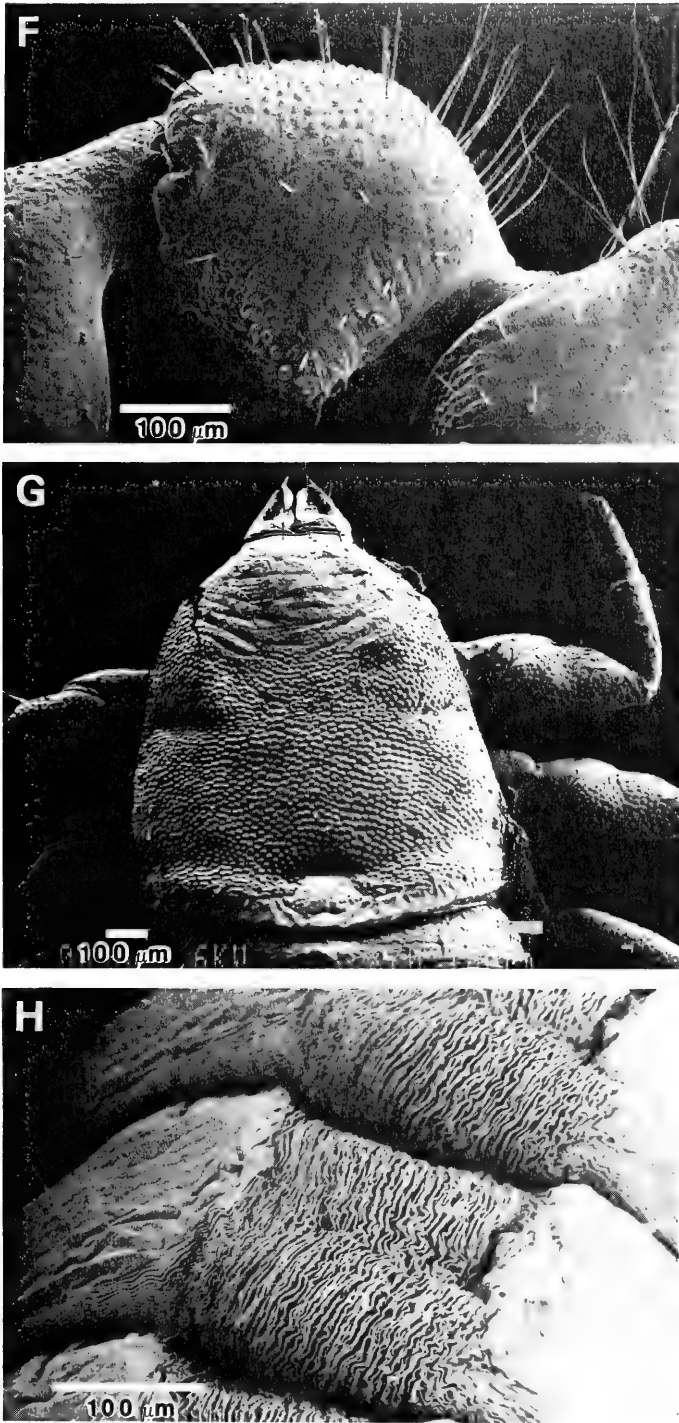


Fig. 2. *Conicochernes doyleae* sp. nov., scanning electron micrographs of female paratypes: **F**, trochanter of right pedipalp; **G**, carapace, dorsal aspect (pedipalps dissected); **H**, pleural membrane.

Diagnosis: A species of the genus *Conicochernes* with the following characters: trichobothrium *it* widely separated distally from *ist*; serrula exterior with 16-17 equidimensionally broad, blunt lamellae and a long, narrow acuminate proximal lamella; 2 galea setae present, eye spots distinct.

Description: Adults. Colour dark red-brown, body dorso-ventrally compressed, surface of carapace predominantly papillate; pleural membrane with closely set undulating longitudinal folds (Fig. 2H). Pedipalp stout, trochanter with gently rounded anterior margin, setae very long and acuminate proximally (Fig. 2F), elsewhere short, straight, longitudinally ribbed in upper distal third and terminating in 3-4 small denticles of different lengths (Fig. 1C); sculpture coarsely papillate; L/W ratio 1.15-1.40 (♂), 1.20-1.40 (♀); femur stout, anterior margin relatively straight, posterior margin well rounded proximally, abruptly pedicellate, setae short, terminally denticulate as described above, 2.75-3.00 (♂), 2.56-3.00 (♀); tibia stout, anterior margin gently rounded, distinctly pedicellate 1.69-2.40 (♂), 1.63-2.33 (♀); chela very stout, chelal hand broad proximally, narrowing distally and longer than chelal fingers, lateral margins relatively straight, chela (with pedicel) 2.93-3.44 (♂), 3.02-3.44 (♀), chela (without pedicel) 2.43-3.17 (♂), 2.75-3.25 (♀) × longer than broad. Fixed chelal finger with 8 trichobothria (Fig. 4M, N), *it* well separated distally from *ist*; movable finger with 4 trichobothria, venom tooth large; marginal teeth on each finger 40-50 contiguous, accessory teeth present; sense spots present; male chelal fingers with extensive medial gape (Fig. 1A); female chelal fingers without gape (Fig. 1B). Chelicera small with 5 setae, lamina exterior present, serrula exterior attached throughout with 18-19 (♂), 17-18 (♀) equal broad, blunt lamellae and a long acuminate proximal lamella (Fig. 1D); galea well developed, ♂ with 3-5 small rami, ♀ 5-6 rami, in most cases 2 galea setae present (Fig. 1E); flagellum with 3 blades of unequal length, distal blade long with 8-9 small spines, approximately 3.40 μm in length, spaced 4.0-4.70 μm along the anterior face (Fig. 1Da). Carapace: anterior margin truncate; pars cephalica covered with transverse discontinuous ridges and corresponding furrows that may be modified by very small, transversely aligned papillae, the remaining part of carapace coarsely and densely papillate; posterior margin slightly angulate with centrally elevated disc, lateral margins slightly converging distally (Fig. 2G); setae short, terminally denticulate, 6: 10: 60-70 (♂), 6: 13-14: 50-60 (♀); L/W ratio 1.05-1.16 (♂), 1.00-1.16 (♀) × longer than broad, eye spots present. Tergites: interscutal membrane in shallow folds, setae short, terminally denticulate; chaetotaxy: ♂ 12-14: 14:: 14-16: 14: 16-17: 16-18: 18-20; 18-20: 17-18: 18-20: 14-16: ?; ♀ 10-14: 12-15: 16-17: 16-18: 18-20: 18-20: 18-20: 18-20: 18-20: 13-15: 10: ? Uniseriate. Coxal chaetotaxy: ♂ 2: 3: 24-25, 0: 3: 10-12, 0: 4: 11-12, 0: 3: 10-12, 0: 3: 15-16; ♀ 2: 3: 10-16, 1: 2: 7-8, 1: 2: 9, 1: 2: 7-8, 1: 2: 14-15. Male genitalia: dorsal apodemes elongate, tapering; paired lateral apodemes extend ventrally and laterally to curve upwards terminally (Fig. 3K). Chaetotaxy: anterior operculum large, posterior margin with row of 7 acuminate setae curling into genital aperture, anterior to these, a row of 9 short setae above which are 3-4 long setae forming a pyramidal effect and surrounded by 11-12 very short setae; posterior operculum small with only 10-12 scattered setae (Fig. 3I). Female genitalia: with lateral apodemes which provide for muscle attachment and support of the genital atrium; two median cribriform plates associated with the medium accessory glands and two lateral cribriform plates on the anterior wall of the lateral diverticula, each plate cuticular and perforated by pores; spermathecae two blind, digitate projections resulting from antero-dorsal evagination of median diverticulum. Scattered cells occur in epithelium of median diverticulum (Fig. 3L). Chaetotaxy: posterior margin of anterior operculum with row of 27-30 acuminate setae, long over small genital aperture, becoming short laterally, anterior to these and

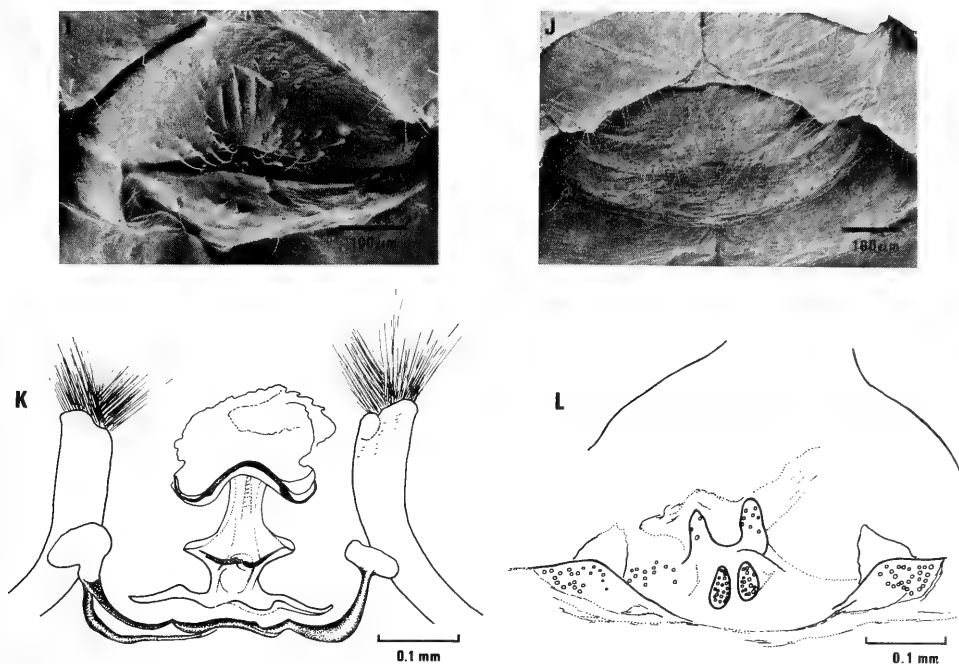


Fig. 3. *Conicochernes doyleae* sp. nov., I and J, scanning electron micrographs of genital region, external aspect, male and female paratypes respectively. K, male genitalia; L, female genitalia.

centrally situated 6-7 very long setae above which are 7-8 short setae; posterior operculum with 7-10 setae distributed centrally at random, posterior margin with 17-18 uniseriate acuminate setae (Fig. 3J). Sternites: setae short, acuminate; chaetotaxy: ♂ 0: 27-30: 12-14: 16-18: 20-23: 18-20: 18-20: 18: 18: 10-12: 10: ?; ♀ 0: 30-40: 20-24: 16-18: 16-18: 20: 18: 18: 16-18: 24-26: 28: ?, sternites 4-11 uniseriate.

Dimensions (mm): body length 2.70-3.28 (2.92-3.46); pedipalps: trochanter 0.36-0.43/0.27-0.34 (0.36-0.39/0.27-0.30), femur 0.77-0.90/0.27-0.30 (0.75-0.84/0.27-0.30), tibia 0.59-0.72/0.30-0.39 (0.56-0.66/0.27-0.36), chela (with pedicel) 1.08-1.30/0.34-0.43 (1.18-1.26/0.36-0.41), chela (without pedicel) 1.02-1.24/0.34-0.43 (1.08-1.17/0.36-0.41), movable finger length 0.46-0.54 (0.43-0.56); chelicera 0.18-0.23/0.10-0.14 (0.21-0.25/0.11-0.14) movable finger length 0.12-0.16 (0.12-0.18); carapace 0.84-0.98/0.75-0.89 (0.86-1.03/0.84-0.98); cucullus length 0.14-0.19 (0.16-0.22) ocular breadth 0.56-0.64 (0.56-0.64); leg I: coxa width 0.30-0.36 (0.32-0.36), trochanter 0.13-0.16/0.11-0.16 (0.14-0.16/0.11-0.16), basifemur 0.16-0.22/0.14-0.18 (0.16-0.25/0.14-0.17), telofemur 0.22-0.33/0.13-0.16 (0.22-0.33/0.12-0.16), tibia 0.16-0.28/0.10-0.14 (0.22-0.28/0.10-0.14), tarsus 0.16-0.22/0.08-0.10 (0.16-0.22/0.07-0.08); leg 4: coxa width 0.28-0.33 (0.30-0.36), trochanter 0.18-0.25/0.14-0.16 (0.19-0.28/0.14-0.19), basifemur 0.25-0.30/0.16-0.25 (0.19-0.28/0.16-0.22), telofemur 0.39-0.50/0.19-0.24 (0.41-0.50/0.21-0.28), tibia 0.28-0.42/0.12-0.14 (0.28-0.40/0.11-0.15), tarsus 0.22-0.28/0.08-0.10 (0.16-0.20/0.07-0.11).

Tritonymph. L/W ratio: pedipalpal trochanter 1.36-1.73, femur 2.12-3.21, tibia 1.56-2.05, chela (with pedicel) 3.00-3.65, chela (without pedicel) 2.78-3.30 x longer than broad. Fixed finger with 7 trichobothria, movable finger with 3 trichobothria, *sb* and *ist* absent; serrula exterior of chelicera with 13 broad lamellae, distal and proximal lamellae long and narrow. Carapace: posterior margin angulate, 6: 10: (50-60) setae, 1.04-1.20 x

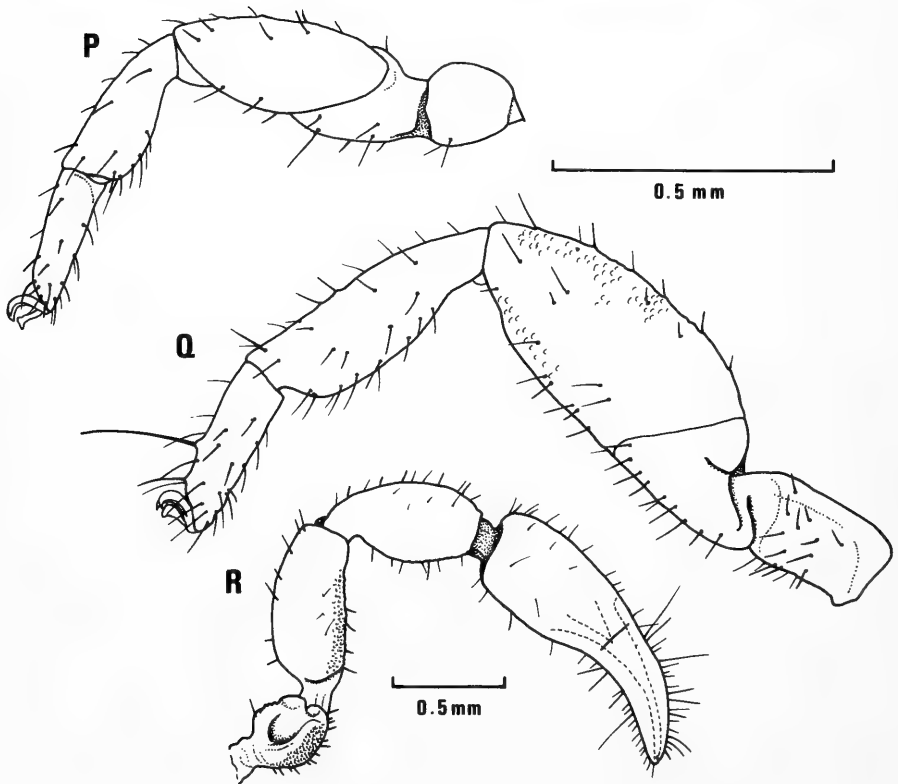
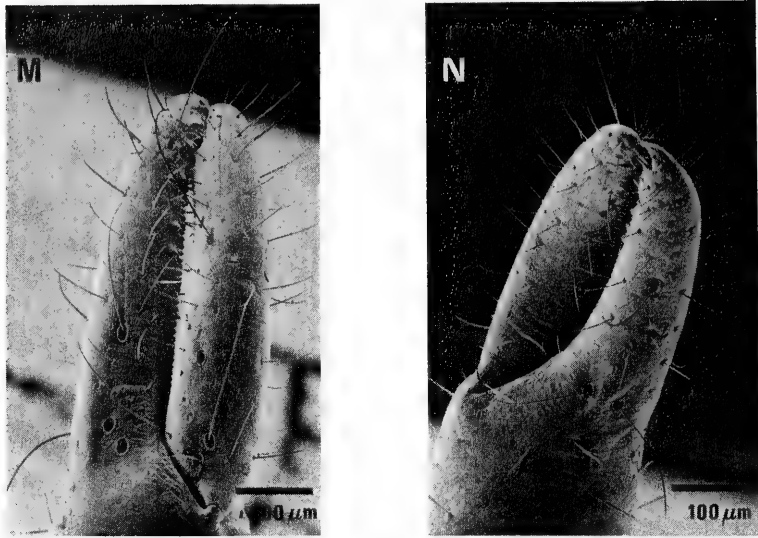


Fig. 4. *Conicochernes doyleae* sp. nov., female paratypes: **M** and **N**, scanning electron micrographs of right chela, lateral, external and internal aspects respectively showing position of trichobothria; **P**, 1st left leg; **Q**, 4th left leg; **R**, left pedipalp, dorsal.

longer than broad. Tergal chaetotaxy: 10-12: 12: 12: 12: 13-14: 11-12: 14-15: 14-15: 12: 10-12: 12-14: 2. Sternal chaetotaxy: 0: 6-8: 8-10: 12: 14-16: 16: 16-18: 10-14: 12-18: 10-12: 12-14: 2. Coxal chaetotaxy: 0: 3: 4, 0: 2: 7, 0: 2: 6-7, 0: 2: 10-13. Monotarsate.

Dimensions (mm): body length 2.38-2.88; pedipalps: trochanter 0.26-0.33/0.19-0.22, femur 0.47-0.61/0.19-0.25, tibia 0.39-0.47/0.19-0.25, chela (with pedicel) 0.84-0.95/0.25-0.30, chela (without pedicel) 0.78-0.86/0.25-0.30, movable finger length 0.35-0.45; carapace 0.61-0.70/0.56-0.64.

Deutonymph. L/W ratio: pedipalpal trochanter 1.35-1.72, femur 2.14-2.57, tibia 1.56-2.00, chela (with pedicel) 3.19-4.06, chela (without pedicel) 2.76-3.68 x longer than broad. Fixed finger with 6 trichobothria, movable finger with 2 trichobothria, *st*, *sb*, *ist*, *esb* absent, serrula exterior of chelicera with 11 blunt lamellae, distal and proximal lamellae long and narrow. Carapace 6: 8: (30-40) setae, 1.00-1.07 x longer than broad. Tergal chaetotaxy: 8: 8: 8: 10-12: 12: 10: 10-12: 12: 12: 10-12: 8: 2. Sternal chaetotaxy: 0: 0: 0: 4-6: 6-10: 7: 8-10: 9-11: 10-12: 9-10: 10: 1. Coxal chaetotaxy: 0: 2-3: 6-7, 0: 3: 5-6, 0: 2: 5, 0: 3: 5.

Dimensions (mm): body length 1.48-2.24; pedipalps: trochanter 0.19-0.25/0.11-0.16, femur 0.30-0.42/0.14-0.19, tibia 0.25-0.33/0.12-0.19, chela (with pedicel) 0.61-0.73/0.16-0.22, chela (without pedicel) 0.56-0.65/0.16-0.22, movable finger length 0.25-0.31; carapace 0.39-0.47/0.37-0.45.

Protonymph. L/W ratio: pedipalpal trochanter 1.20-1.33, femur 1.75-2.50, tibia 1.58-1.91, chela (with pedicel) 3.14-4.30, chela (without pedicel) 3.00-3.90 x longer than broad. Fixed finger with 3 trichobothria, *t*, *et*, *eb*, *isb* present. Serrula exterior of chelicera with 10 broad lamellae, distal and proximal lamellae long and narrow. Carapace with 6: 7-8: (25-30) setae, 1.04-1.10 x longer than broad. Tergal chaetotaxy: 6: 8: 6: 6: 6: 8: 6-8: 8: 8: 6: 4: 2. Sternal chaetotaxy: 0: 2-3: 4: 4-5: 5-6: 6-8: 6-8: 6-8: 6-8: 8: 6: 1-2. Coxal chaetotaxy: 0: 2: 4; 0: 2: 3, 0: 2: 2-3, 0: 2: 3.

Dimensions (mm): body length 1.10-1.45; pedipalps: trochanter 0.12-0.16/0.10-0.13, femur 0.19-0.28/0.10-0.12, tibia 0.18-0.23/0.10-0.12, chela (with pedicel) 0.43-0.54/0.12-0.14, chela (without pedicel) 0.39-0.48/0.12-0.14, movable finger length 0.18-0.21; carapace 0.28-0.48/0.26-0.43.

ACKNOWLEDGEMENTS

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Mckenziartia and *Pectocythere* (Pectocytheridae, Ostracoda, Crustacea) in Lake Macquarie, New South Wales

IRADJ YASSINI and MARY MIKULANDRA

YASSINI, I., & MIKULANDRA, M. *Mckenziartia* and *Pectocythere* (Pectocytheridae, Ostracoda, Crustacea) in Lake Macquarie, New South Wales. *Proc. Linn. Soc. N.S.W.* 111 (2), 1989: 131-139.

The distribution pattern of four species of *Mckenziartia* and one species of *Pectocythere* in Lake Macquarie, New South Wales, is investigated and three new species: *Mckenziartia thomi* sp. nov., *Mckenziartia mowbrayi* sp. nov. and *Pectocythere royi* sp. nov., are described.

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INTRODUCTION

The genus *Mckenziartia* was described by Bentley (1988) on the basis of carapace morphology. The genus was erected to designate a group of pectocytherid ostracodes characterized by the presence of a crescentic fossa over the central muscle field, a large anterior vestibulum with short, simple or occasionally-branched marginal pore canals, and an antimerodont hinge structure. The crescentic fossa over the central muscle field was described as a diagnostic feature of the genus. Examination of a large population of the species from different estuaries of New South Wales shows, however, that the size and shape of fossa may vary and is often integrated with the ornamentation pattern of the valves. The size and the shape of the vestibulum and the distribution of the anterior marginal pore canals remain unchanged, and they present a more stable diagnostic feature for the genus.

Mckenziartia Bentley is a typical inhabitant of the estuarine environment and has been reported from several estuaries around Australia (Bentley, 1988).

Present work investigated the distribution pattern of four species of *Mckenziartia*: *Mckenziartia portjacksonensis* (McKenzie, 1967), *Mckenziartia foveata* (Hartmann, 1978), *Mckenziartia thomi* sp. nov. and *Mckenziartia mowbrayi* sp. nov., as well as distribution of *Pectocythere royi* sp. nov., another member of the Pectocytheridae in Lake Macquarie. The type specimens are deposited at the Australian Museum. Some paratype specimens were also deposited at the Commonwealth Palaeontological collection in the Bureau of Mineral Resources, Canberra.

AREA STUDIED

Lake Macquarie is located some 85km north of Sydney, on the central coast of New South Wales. With an extremely irregular outline, the lake extends in a north-south direction for over 22km, has a width of 10km and a surface area of 110km².

The average depth of the lake is 6.7m and its maximum depth never exceeds 12m. A narrow inlet channel 3.5km in length and 240m to 400m wide connects the lake to the Pacific Ocean.

The lake has a total catchment area of 770km². Three major creeks; Mannering Creek in the south, Dora Creek in the west and Cockle Creek in the north, contribute up to 4% of the total lake volume (Bass Becking *et al.*, 1959). Some seven other minor creeks

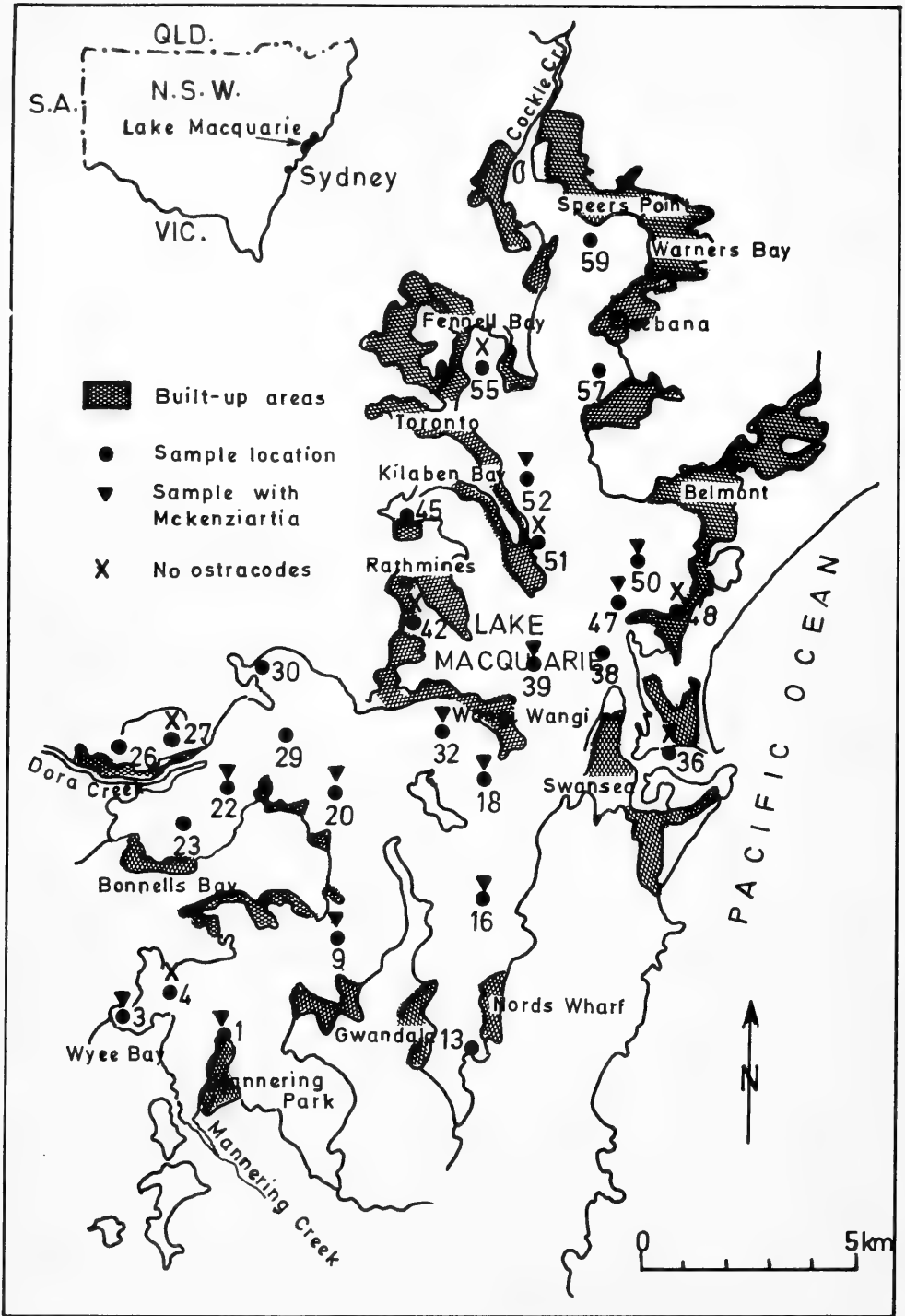


Fig. 1. Location map of the samples studied.

TABLE 1
Species and number of valves in 30ml of samples

Species	Samples											
	52	50	47	39	32	22	20	18	16	9	3	1
<i>Mckenziartia portjacksonensis</i>	26	10	245	74	24	8	18	40	23	14	3	2
<i>Mckenziartia thomi</i>	—	—	48	—	—	—	—	—	—	—	—	—
<i>Mckenziartia foveata</i>	—	—	12	—	—	—	—	—	—	—	—	—
<i>Mckenziartia mowbrayi</i>	—	—	—	2	—	—	—	—	—	—	—	8
<i>Pectocythere royi</i>	—	—	22	—	—	—	—	—	—	—	—	—

also flow into the lake during the rainy periods. A total of 26 grab samples were taken from the bottom sediment of the lake; Fig. 1 indicates the location of the samples studied. Table 1 shows the number of valves of each species in 30ml of unwashed sample.

SYSTEMATICS

Class OSTRACODA Latreille, 1802

Order PODOCOPIIDA Müller, 1894

Family PECTOCYOTHERIDAE Hanai, 1957

Genus *Mckenziartia* Bentley, 1988

MCKENZIARTIA PORTJACKSONENSIS (McKenzie, 1967)

Fig. 2A-D and Fig. 4A

'Hemicytheridea' portjacksonensis McKenzie, 1967: p. 85, pl. 12, figs 3i-j,6.

'Munseyella' tumida Swanson, 1979: p. 158, fig. 4q.

Pectocythere portjacksonensis (McKenzie), Hartmann, 1980: p. 122, pl. 5 fig. 17.

Pectocythere portjacksonensis (McKenzie), Yassini and Jones, 1987: p. 826, pl. 2, fig. 21.

Mckenziartia portjacksonensis (McKenzie), Bentley, 1988: p. 445, pl. 1, figs. e-f, text fig. 4a-b.

Distribution: The species has been recorded from many estuaries and shallow open marine environments around Australia (McKenzie, 1967; Hartmann, 1978, 1980; Yassini and Jones, 1987; Bentley, 1988) and from New Zealand (Swanson, 1979). In Lake Macquarie, it was recorded from 12 stations but it was particularly abundant at station 47 at the mouth of the inlet channel (Table 1).

Mckenziartia foveata (Hartmann, 1978)

Fig. 2G-I, Fig. 3G and Fig. 4B

Pectocythere foveata Hartmann, 1978: p. 144, pl. 14, figs. 12-13.

Pectocythere foveata Hartmann, Yassini and Jones, 1987: p. 826, pl. 2, figs. 18-20.

Remarks: The hinge structure and vestibulum pattern justify attribution to the genus *Mckenziartia*.

Distribution: The species has been recorded from several estuaries and shallow open marine environments around the continent (Hartmann, 1978; Yassini and Jones, 1987). In Lake Macquarie it was only found in sample 47, dredged from a seagrass bed close to the inlet channel (Table 1).

Mckenziartia thomi sp. nov.

Fig. 3A-F and Fig. 4C

Diagnosis: Carapace elongate, length about 2.6 times height. Anterior broadly rounded, posterior rounded ventrally, subvertical medio-dorsally. Dorsum straight,

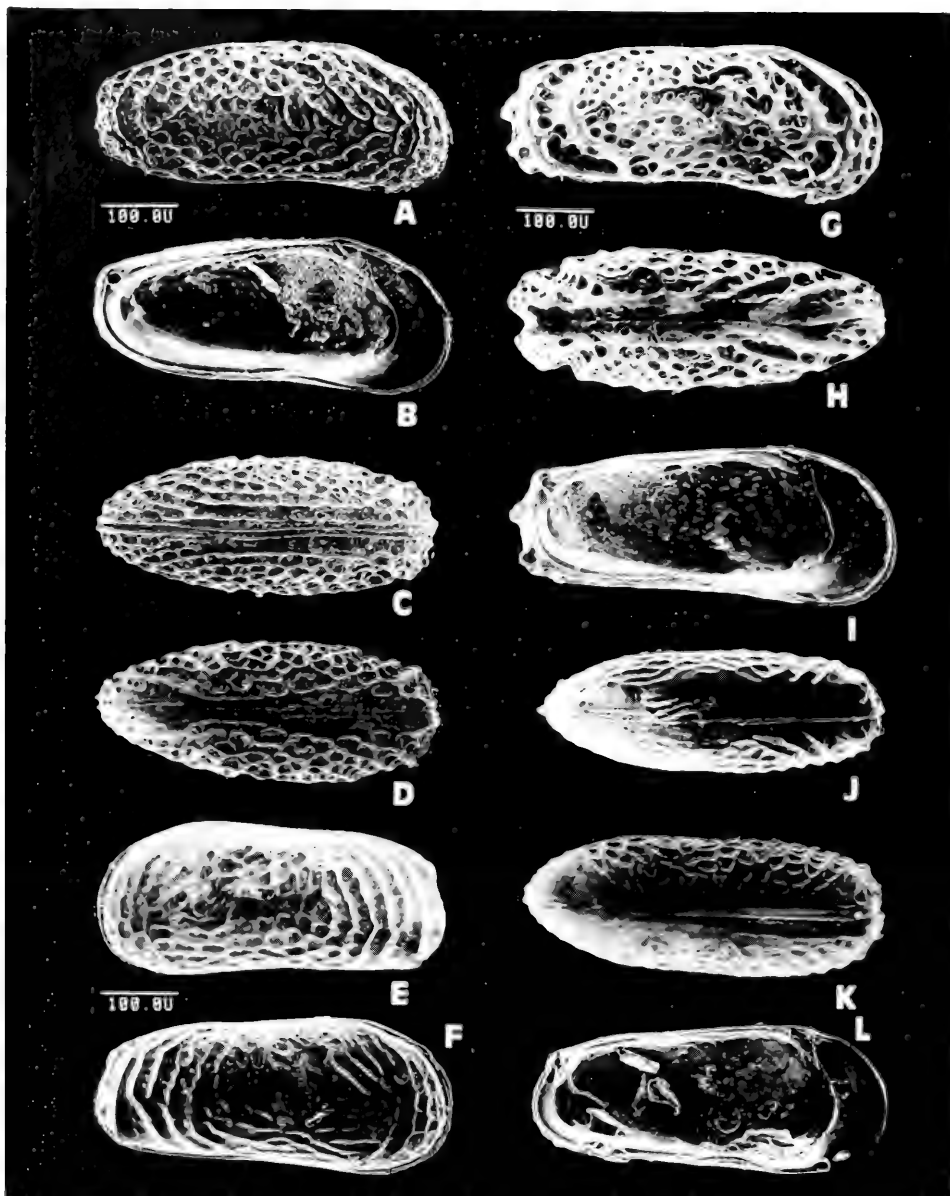


Fig. 2. **A-D.** *Mckenziartia portjacksonensis* (McKenzie): **A.** RV, ♂, external view; **B.** ♂, LV, internal view; **C.** ♀, ventral view of the carapace; **D.** ♂, dorsal view of the carapace, sample 47. **E, F, J-L.** *Mckenziartia mowbrayi* sp. nov.: **E.** LV, ♀, external view, holotype AM P37639; **F.** RV, ♂, external view, paratype AM P37641; **J.** ♀, ventral view of the carapace, paratype AM P37641; **K.** ♀, dorsal view of the carapace, paratype AM P37642; **L.** LV, ♂, internal view, paratype AM P37642, sample 1. **G-I.** *Mckenziartia foveata* (Hartmann): **G.** RV, ♂, external view; **H.** ♂, dorsal view of the carapace; **I.** LV, ♂, internal view, sample 47.

ventrum gently concave. Valves equal in size. In dorsal and ventral views, carapace elongate with parallel borders. Internally: inner lamella broad, anterior vestibulum deep, narrow, posterior vestibulum broad and elongate. Marginal pore canals simple, few and

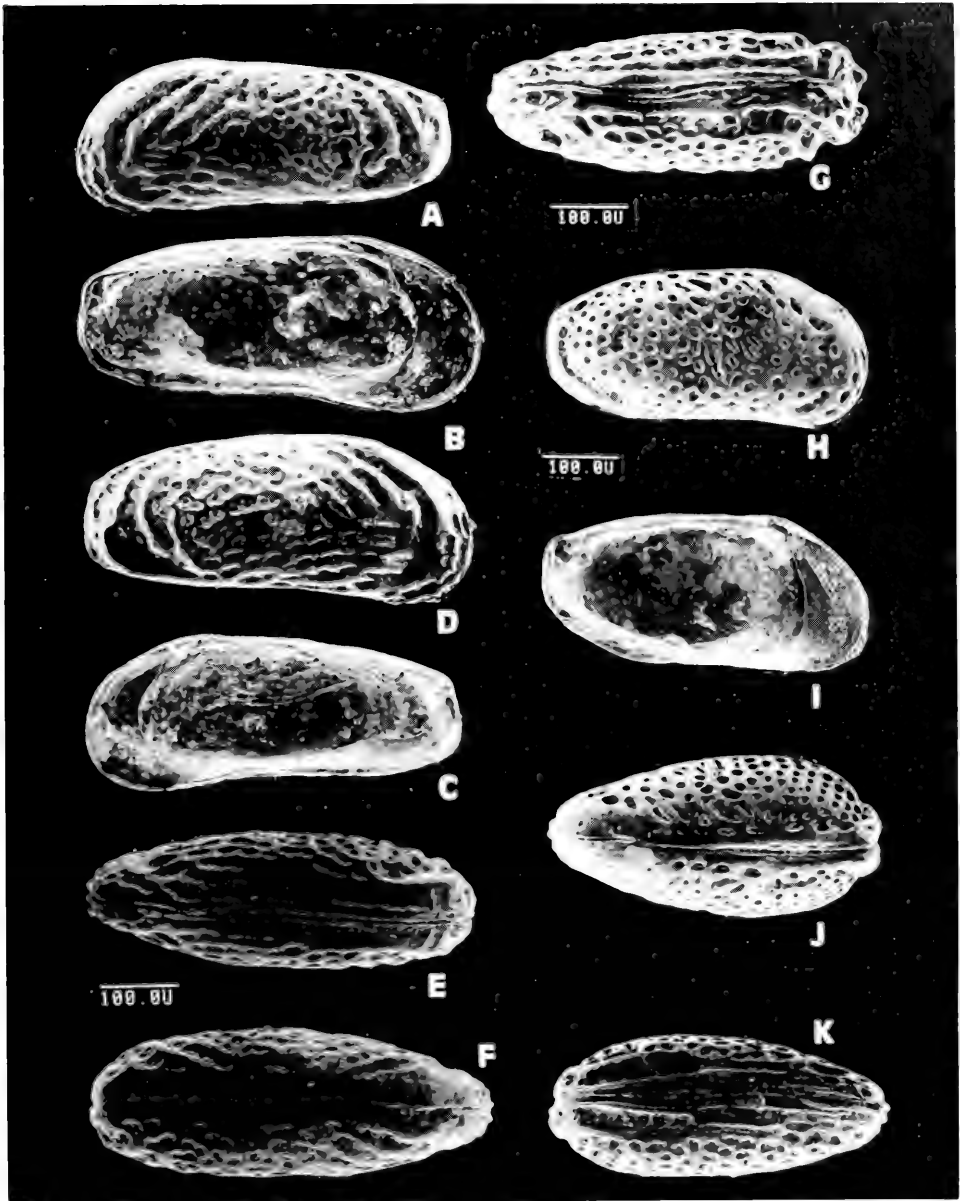


Fig. 3. **A-F**, *Mckenziartia thomi* sp. nov.: **A**, LV, ♂, external view paratype AM P37647; **B**, IX, ♀, internal view, paratype AM P37648; **D**, RV, ♀, external view, holotype AM P37646; **C**, RV, ♂, internal view, paratype AM P37649; **E**, ♂, ventral view of the carapace, paratype AM P37650; **F**, ♂, dorsal view of the carapace, paratype CPG 26554, sample 47. **G**, *Mckenziartia foveata* (Hartmann) ♂, ventral view of the carapace, sample 47. **H-K**, *Pectocythere royi* sp. nov.: **H**, RV, internal view, holotype AM P37661; **I**, IX, internal view, paratype AM P37662; **J**, dorsal view of the carapace, paratype AM P37663; **K**, ventral view of the carapace, paratype AM P37664, sample 47.

scattered. Hinge antimerodont. Muscle scars: four adductor scars in a subvertical row; two frontal scars and a large furcal scar. Valve surface reticulated, with three distinct

concentric ridges parallel to posterior margin and a set of oblique ridges joining the ventral ridge.

Remarks: With a crenulate posterior socket, and a straight and crenulate median bar the species clearly belongs to the Pectocytheridae and it can be differentiated from the allied species (*Mckenziartia portjacksonensis* (McKenzie) and *Mckenziartia mowbrayi* sp. nov.) in the details of surface ornamentation.

Material: Holotype AM P37646, right valve, adult male; length 0.51mm. Paratypes AM P37647, AM P37648, AM P37649, AM P37650 and CPC 26554. All from type locality.

Type locality: Lake Macquarie entrance tidal channel, New South Wales, Australia (lat. 33°03'00"S; long. 151°38'00"E); Recent, estuarine, muddy sand, with *Zostera capricorni* (Aschers.); depth 5.2m; on the sampling day salinity was 35.8‰, water temperature 22.8°C, and dissolved oxygen 6.6mg/l.

Etymology: The species is named after Professor Bruce Thom, Geography Department, University of Sydney.

Distribution: The species has also been recorded from Heron Island, off Queensland (Labutis, 1977) and Broken Bay, New South Wales (Yassini, unpublished).

Mckenziartia mowbrayi sp. nov.

Fig. 2E-F, J-L and Fig. 4D

Diagnosis: carapace elongate, length about 2.3 times height. Anterior broadly rounded, posterior rounded to gently subacute. Dorsum straight, ventrum gently concave in the middle. Valves equal in size. In dorsal and ventral views, sides of the carapace are parallel. Internally: inner lamella broad, anterior vestibulum shallow and broad. Posterior vestibulum narrow. Marginal pore canals straight, well-spaced and few. Hinge antimerodont. Valve surface reticulate, with a few distinct, concentric low ridges at the posterior end, and three at the anterior end. In ventral view, the ridges form a series of chevron-type grooves converged toward anterior and posterior ends. Muscle scars are typical of the genus *Mckenziartia* (Bentley, 1988).

Remarks: When compared with *Mckenziartia thomi* sp. nov. and *Mckenziartia portjacksonensis* (McKenzie), it differs in its typical surface reticulation.

Material: Holotype AM P37639, carapace, male; length 0.46mm. Paratypes AM P37640, AM P37641, AM P37642, AM P37643 and CPC 26553. All from type locality.

Type locality: Lake Macquarie (Sample 1), north of Mannering Park, New South Wales, (lat. 33°09'00"S; long. 151°33'00"E); Recent estuarine, sandy mud; depth 3.7m; on the sampling day salinity was 36.22‰, water temperature 22.8°C, and dissolved oxygen 4.4mg/l.

Etymology: After Mr William Mowbray, Chairman of Lake Illawarra Management Committee.

Distribution: Outside Lake Macquarie, the species has also been found in Broken Bay (Yassini, unpublished) and off Queensland (Labutis, 1977).

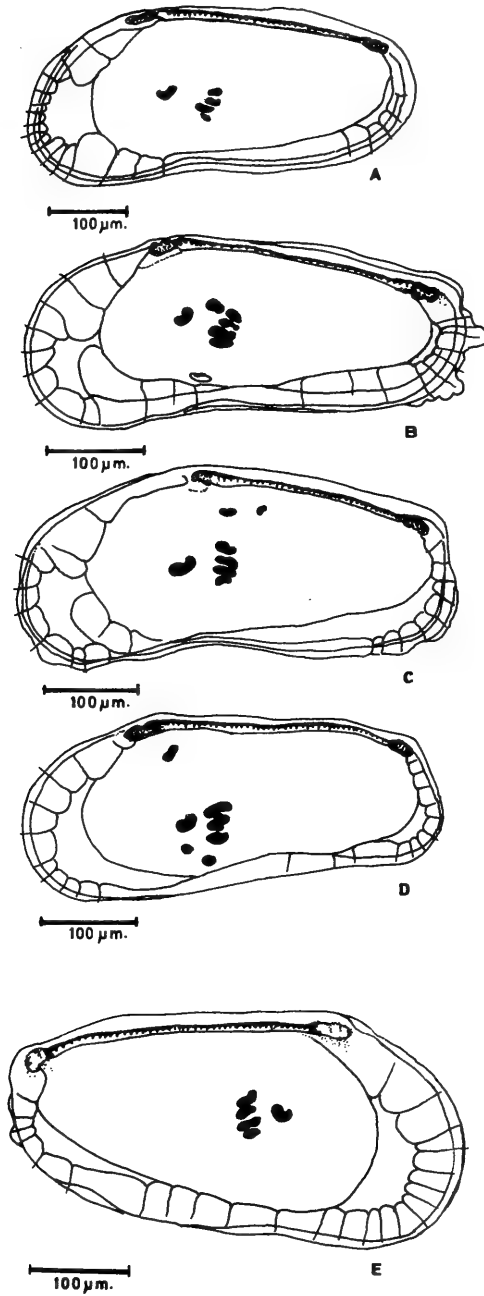


Fig. 4. **A**, *Mckenziartia portjacksonensis* (McKenzie), RV, internal structure; **B**, *Mckenziartia foveata* (Hartmann), RV, internal structure; **C**, *Mckenziartia thomi* sp. nov., RV, internal structure, holotype AM P37546; **D**, *Mckenziartia mowbrayi* sp. nov., RV, internal structure, paratype AM P37644; **E**, *Pectocyther ruyi* sp. nov., LV, internal structure, paratype AM P37638.

Genus *Pectocythere* Hanai, 1957

Pectocythere royi sp. nov.

Fig. 3H-K and Fig. 4E

Pectocythere sp. (Ceduna 120), Hartmann; (*Nec* Hartmann, 1980) Yassini and Jones, 1987; p. 826, pl. 2, fig. 14-17.

Diagnosis: Carapace elongate, small, length about 2.1 times height. Anterior broadly rounded, posterior with an elevated rim and postero-ventrally oblique. Dorsum straight, slightly inclined posteriorly. Ventrum straight, valves ornamented with irregularly distributed rounded or elongated alveoli. In dorsal view, broader posteriorly. Internally: inner lamella broad, anterior vestibulum broad and shallow, marginal pore canals few and straight. Hinge merodont, consisting in the right valve of an elongate anterior tooth, distinctly crenulated median groove and coarsely lobated posterior terminal tooth. Central muscle scars comprising a row of four adductors and a V-shaped antennal scar. Sex dimorphism is not known.

Remarks: The only described species with closely similar shape is *Pectocythere* sp. (Ceduna 120) Hartmann (1980) which is easily distinguished from the present species by the depression of the postero-ventral region and lack of the raised posterior rim.

Material: Holotype AM P37661, right valve: 0.43mm length. Paratype AM P37662, AM P37663, AM P37664 and CPC 26555. All from type locality.

Type locality: Lake Macquarie (Sample 47), entrance tidal channel, New South Wales (lat. 33°03'00"S, long. 151°38'00"E); Recent, estuarine, muddy sand with *Zostera capricorni* (Aschers.); depth 5.2m; on the sampling day, salinity was 35.8‰, temperature 22.8°C and dissolved oxygen 6.6mg/l.

Etymology: After Dr Peter Roy, Geological Survey, New South Wales.

Distribution: Widely distributed in estuarine environments along the coast of New South Wales.

DISCUSSION

Among the five described species, *Mckenziartia portjacksonensis* is the only one which is widespread and abundant in all the estuarine environments along the eastern coast of Australia; from Heron Island in the north (Labutis, 1977) to Bass Strait in the south (Yassini and Blom, in preparation). *Pectocythere royi*, has also been found in limited numbers in Broken Bay, Twofold Bay and Bass Strait. *Mckenziartia foveata*, initially described by Hartmann (1978) from Port Hedland, Western Australia, was also found in several estuaries of New South Wales (Lake Illawarra, Botany Bay, Broken Bay, Brisbane Waters). The species was also reported by Labutis (1977) from the Great Barrier Reef, off Queensland. The other two species; *Mckenziartia thomi* sp. nov. and *Mckenziartia mowbrayi* sp. nov. appear to be limited to the northern (Labutis, 1977) and central coast of New South Wales.

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NUMBER 3

Wetlands of the Lower Clarence Floodplain, Northern Coastal New South Wales

R. L. PRESSEY
(Communicated by P. ADAM)

PRESSEY, R. L. Wetlands of the lower Clarence floodplain, northern coastal New South Wales. *Proc. Linn. Soc. N.S.W.* 111 (3), 1989: 143-155.

The wetlands on the lower Clarence floodplain, on the far north coast of New South Wales, were mapped and described during a detailed survey in 1982. The survey identified 755 wetlands with a total area of about 14,700 ha. Most wetlands were smaller than 10 ha but the relatively few large wetlands made up most of the total area. Open water occupied only 5% of the total wetland area at the time of the survey although some open water occurred in 45% of wetlands. The most important plant families, in terms of extent and frequency of occurrence, were Poaceae (covering 23% of the wetland area, occupying 82% of the total number of wetlands), Cyperaceae (20% area, 36% number), Myrtaceae (17% area, 36% number), Polygonaceae (12% area, 76% number) and Juncaceae (10% area, 75% number). Most wetlands were fringed by dense stands of herbaceous plants but, due to clearing, had few trees on their margins. Ninety-eight percent of wetlands were grazed to some extent and 92% of the total wetland area was affected by drainage. Most wetlands are seasonal with relatively small catchments. Only 28% had catchments on the bedrock slopes surrounding the floodplain. Most catchments have been completely cleared for agriculture. Most wetlands are freehold tenure.

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KEY WORDS: Wetlands, survey, plant taxa, catchments, Clarence floodplain.

INTRODUCTION

The coastal wetlands of New South Wales have been mapped and classified in a number of broad-scale surveys. Hannah's (1968) landscape approach dealt mainly with the wetlands of the dune systems and was restricted to the north coast. West *et al.*, (1985) mapped and classified the vegetation of the State's estuarine wetlands. The surveys of Goodrick (1970) and the Coastal Council of New South Wales (1985) were of dunal, estuarine and floodplain wetlands along the whole coast. The Coastal Council study simply delineated wetlands for the purposes of development controls under State Environmental Planning Policy No. 14. Goodrick's survey provided a useful classification based on dominant vegetation and water regime and is the best overview of wetlands on the coastal floodplains. It does not, however, provide sufficiently detailed information on individual floodplain wetlands for conservation or management.

On the Clarence floodplain, none of the previous local, more detailed studies of flora and fauna has covered the wetlands comprehensively. They have concerned only one or a few wetlands and have had a variety of purposes and approaches. For example, Broome (1978) surveyed waterbirds in several areas and two environmental impact statements (Clarence River County Council, 1978, 1980) include vegetation maps and descriptions of some large wetlands. Most other publications on the Clarence floodplain wetlands deal with soils and specific occurrences of birds (Pressey, 1981).

Wetland surveys for the National Parks and Wildlife Service, designed to be both detailed and comprehensive, covered the lower floodplains of the Hunter, Clarence and Macleay Rivers in 1981, 1982 and 1984, respectively, and the coastal lowlands of Tweed Shire in 1986.

The main aims of these surveys were to: plot wetlands with accuracy and, in the

Tweed survey, associated coastal communities on 1:25 000 topo-cadastral maps; describe the wetlands and their catchments from features that could be recorded during a single field visit or remotely from maps and aerial photographs; rank the wetlands for nature conservation, based on a combination of selected criteria.

This paper summarizes the results of the inventory and description of wetlands on the lower Clarence floodplain. Full data, the results of conservation evaluation, and reduced wetland maps have all been incorporated in a consultancy report (Pressey, 1987).

STUDY AREA

The Clarence is one of the major coastal rivers in New South Wales and has an extensive floodplain, some 500 km north-east of Sydney (Fig. 1). The lower Clarence floodplain was defined as alluvium below the 10 m contour, a broad expanse of flood-prone land downstream of the very narrow, upper floodplain. Virtually all of the alluvial wetland area in the Clarence system occurs on the lower floodplain. The survey was also restricted to non-estuarine wetlands (those without saltmarsh and mangroves), although it included brackish areas intermediate between fresh and full tidal waters.

The study area occupies approximately 700 sq. km (Fig. 1). To the north of the river, it extends upstream as far as Whiteman Creek and includes extensive alluvial flats to the north of Grafton, south of Lawrence and around the Broadwater. The major wetland on this side of the river is the Everlasting Swamp. South of the river the survey covered areas downstream of Seelands including large expanses of floodplain between Swan Creek and Tyndale and around Wooloweyah Lagoon. The main wetlands in these areas are the Harrington Lagoon complex, the heavily wooded Shark Swamp and a group of large wetlands on the Coldstream River, one of the Clarence's lower tributaries. The survey also covered Woodford, Harwood and Chatsworth Islands which lie either in the course of the river or in its broad estuary.

Virtually all of the floodplain is cleared for farming. The major agricultural use is grazing of beef and dairy cattle. Sugar cane is an important crop in the eastern parts and relatively small areas are planted with poplars, vegetables and other crops. Drainage of wetlands began soon after European settlement. Around the turn of the century, drainage unions or trusts were formed to enable adjacent landholders to arrange for drainage in co-ordinated systems, with design and construction provided by the Department of Public Works. This work was to promote the growth of vegetation considered valuable as pasture and to encourage closer settlement in the region. From the late 1950s to the 1970s, under flood mitigation schemes, many drains, levees and floodgates were constructed and integrated to exclude floods from certain areas and to accelerate the recession of floodwaters. The alteration of wetlands continued during this period.

Goodrick (1970) found that about 47% of all wetlands in the far north coast region had been destroyed or significantly altered by 1969, mainly by drainage and flood mitigation. About 85% of the total affected area consisted of shallow floodplain wetlands, with more wetland now affected since flood mitigation on the Clarence has continued since Goodrick's survey (Pressey and Middleton, 1982). In addition, many private developments have recently drained and cleared wetlands.

METHODS

The units of the survey were discrete wetland basins which were initially identified on black and white aerial photographs as areas of darker tone or as stands of trees. The available aerial photographs were taken between August 1978 and March 1979 and varied in scale from 1:25 000 to 1:40 000. The minimum size for recognition of wetlands

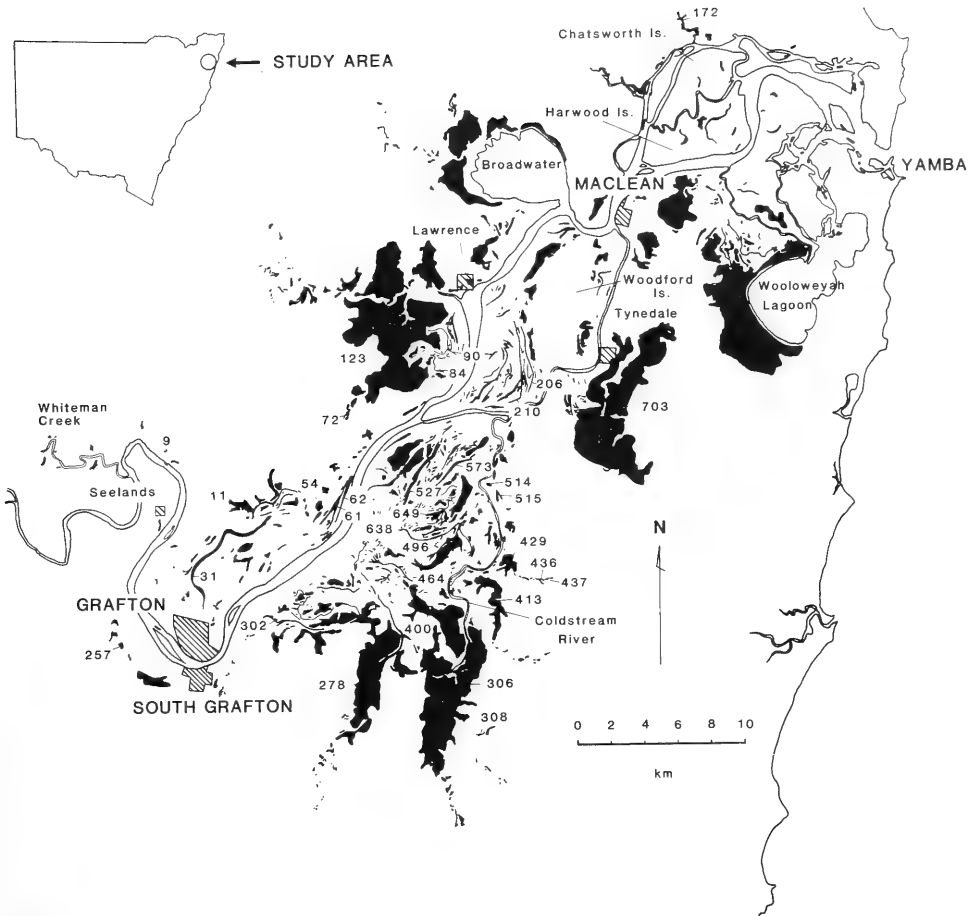


Fig. 1. The study area. Numbers are those given to named wetlands during the survey. The names corresponding to these numbers are: 9 Double Swamp; 11 Bunyip Creek; 31 Alummy Creek; 54 Southgate Lagoon; 61 Southgate Creek; 62 Franks Creek; 72 Long Waterhole; 84 Hannons Lagoon; 90 Harrisons Creek/Coxs Creek; 123 Everlasting Swamp; 172 Mororo Creek; 181 Duckpond Creek; 206 Elbow Creek; 210 Roberts Creek; 257 Cowans Ponds; 278 Cassons Creek/Harrington Lagoon/McLachlan Waterhole; 302 Swan Creek; 306 Ellis Swamp/Crowsnest Swamp; 308 Horseshoe Waterhole; 400 Morans Swamp/Colletts Swamp; 413 Chaffin Swamp; 429 Champions Swamp; 436 Stokes Waterhole; 437 Stokes Waterhole; 464 Sweeneys Creek; 496 Sweeneys Swamp/Oregon Creek; 514 McPhees Swamp; 515 McPhees Swamp; 527 Calliope Creek; 573 Calligans Creek; 638 Alummy Creek; 649 Swampy Creek; 703 Shark Swamp/Tyndale Swamp.

was about 0.1 ha. A few small wetlands of 1 ha or less were omitted because of difficult access.

Final boundaries of wetlands were marked on aerial photographs during a single field visit to each one, either in summer (3.2.82-28.2.82) or winter (19.7.82-17.8.82). These boundaries were later transferred onto 1:25 000 topo-cadastral maps. Scale differences and lens distortion were corrected in the transfer by enlarging or reducing the images on the photographs and by matching features such as fencelines, roads and drains between photographs and maps over small areas.

The number and types of attributes recorded for each wetland were constrained by the time available. In particular, fauna could not be described reliably, and faunal

habitat and importance in each wetland were generally inferred from open water and the type and structure of vegetation.

Of the twelve attributes listed for each wetland, five were used solely for ranking the wetlands for conservation (see Pressey, 1987). The remaining seven were used descriptively and are as follows.

i) *Size*

Size of wetlands was estimated from corrected boundaries on topo-cadastral maps using a dot grid.

ii) *Vegetation/habitats*

Vegetation and faunal habitat of the wetlands were described by plant species or genera and two categories of open water: deep (>60 cm) and shallow (<60 cm). Authorities for plant names are those in Jacobs and Pickard (1981) as amended by Jacobs and Lapinpuuro (1986), unless indicated otherwise. Water depth was judged from fence-lines and from the slope of the bed. Submerged plants were not recorded, nor were species from the families Azollaceae or Lemnaceae. The percentage of each wetland occupied by each taxon or open water category was estimated by eye in the field. Percentages were later converted to absolute areas when the sizes of wetlands were measured. Taxa or open water categories occupying less than 0.1 ha in a wetland were listed only as present.

Small wetlands were described by walking through or around them, large swamps by walking through them, by scanning with binoculars from vantage points, and by visiting areas with distinctive tone or texture on aerial photographs. Some inconsistencies in description would have resulted from differences in sampling intensity between wetlands. The accuracy of estimates of the percentages of wetland areas occupied by plant taxa and open water categories would probably be inversely related to wetland size.

iii) *Marginal vegetation*

Vegetation on wetland margins was rated in the field according to the percentage of perimeter lined with trees or emergents (rushes, tall herbs or grasses) and the average density and width of the fringing emergent band. Fringing plants not typical of wetlands, such as tall pasture grasses, were not taken into account as emergents.

iv) *Alteration*

Signs of obvious alteration such as grazing, drainage and impoundment were recorded in the field and from aerial photographs.

v) *Catchment areas*

Wetland catchments were categorized according to whether they were completely on alluvial flats or at least partly on bedrock slopes. Catchments on bedrock above the 10 m (lowest) contour were delineated and their areas measured on topographic maps.

vi) *Catchment land use*

Broad types of land use in wetland catchments were recorded in the field and from maps and aerial photographs. They were listed for each catchment in order of the proportion occupied. Categories recognized were agriculture (including grazing and cropping), forestry, industrial areas, mining (only surface extraction of sand, gravel etc. in the case of the Clarence survey area), natural vegetation, urban areas and waste disposal (including sewage treatment works).

vii) *Tenure*

Land tenure, easements and any other relevant land designations were listed for each wetland in order of the proportion of the wetland affected.

RESULTS AND DISCUSSION

The survey covered 755 wetlands with a total area of 14,728 ha. The majority of wetlands are small (Table 1), 88% of them 10 ha or less in size. These small wetlands account for only 9% of the total wetland area. The bulk of the wetland area (77%) is made up by the relatively small number of wetlands (3% of total number) greater than 100 ha in size.

TABLE 1
Size distribution of wetlands

Area (ha)	No. of wetlands	% Total no.	Wetland area (ha)	% Total area
0-1.0	343	45.4	174.5	1.2
1.1-5.0	255	33.8	626.6	4.3
5.1-10.0	69	9.1	480.4	3.3
10.1-50	57	7.6	1155.4	7.8
51-100	12	1.6	878	6.0
101-500	13	1.7	2713	18.4
501-1000	1	0.1	520	3.5
>1000	5	0.7	8180	55.5
	755	100.0	14,727.9	100.0

Seventy-three plant taxa were systematically recorded. Their occurrence in the study area, with that of the two recorded categories of open water, is summarized in the Appendix. Some plants were identified only to genus. The most common of these were:

- *Juncus* spp. refers to species in the Section Genuini, the relative areas of which were not determined. The only two species identified were *J. usitatus* and *J. polyanthemus*. From subsequent work on the Macleay floodplain, it is likely that hybrids of these species are common and widespread.
- *Persicaria* spp. were not recorded individually. Species collected during the survey were *P. hydropiper* (most extensive), *P. lapathifolia*, *P. strigosa* and *P. sp. B*. Another species occurring in the area but not found in the wetlands surveyed is *P. sp. A*.
- *Typha* spp. were also combined. Both *T. domingensis* and *T. orientalis* occur in the area, with the latter species by far the more common.

Open water was relatively unimportant in terms of the overall area occupied (Appendix). Shallow open water was more extensive and more commonly recorded than deep open water. Goodrick (1970) recorded a relatively small area of wetlands dominated by open water on the far north coast generally. The floodplain wetlands in this region, including those of the Clarence, are largely in the five categories of Goodrick's classification that are dominated by herbaceous emergents or by trees: fresh meadows, seasonal fresh swamps, semi-permanent fresh swamps, teatree swamps and reed swamps (Table 2). Wetlands in these categories contain relatively little open water.

Of the plant taxa recorded, the monocotyledons accounted for nearly 59% of the total wetland area and dicotyledons about 35% (Appendix). Monocots occurred in 97% of wetlands and dicots in 89%. The most extensive and commonly recorded monocot families were Poaceae (23% of wetland area, 82% of wetland number), Cyperaceae (20% area, 36% number) and Juncaceae (10% area, 75% number). *Paspalum distichum* (water couch) dominated the area occupied by the Poaceae and was the most commonly recorded grass. *Eleocharis equisetina* was the commonest and by far the most extensive member of the Cyperaceae. The most extensive and commonly recorded dicot families were Myrtaceae (17% of wetland area and 36% of wetland number) and Polygonaceae

(12% area, 76% number). *Melaleuca quinquenervia* was the most extensive dicot species, occupying 17% of the total wetland area. *Casuarina glauca* was the most commonly recorded dicot species, occurring in 33% of wetlands, although it is likely that most or all of the 76% of wetlands containing *Persicaria* spp. contained *P. hydro Piper*.

TABLE 2

Extent and decline of wetland types on the far north coast of New South Wales (modified from Goodrick, 1970)#

Wetland type	Original area (ha)	1969 area (ha)	% Decline
<u>fresh meadows</u>	22680	(2150)	59.4
<u>seasonal fresh swamps</u>		(7050)	
<u>semi-permanent fresh swamps</u>	360	320	11.1
<u>open fresh waters*</u>	450	450	—
<u>teatree swamps</u>	4010	2390	40.4
<u>salt meadows</u>	1380	1380	—
<u>reed swamps</u>	1460	730	50.0
<u>salt flats</u>	530	530	—
<u>mangrove swamps</u>	1860	1780	4.3
<u>coastal bogs</u>	570	570	—
<u>coastal <i>Lepironia</i> swamps</u>	320	320	—
	33620	17670	47.4

estimates excluded two wetland types: shallow estuarine waters and sheoak swamps.

* open fresh waters is the only floodplain wetland category identified by Goodrick as being dominantly open water, although relatively small areas of open water occur in other categories on the Clarence floodplain.

Underlined categories are those occurring on the Clarence floodplain.

Cyperaceae and Poaceae were the most diverse families, with 24 and 12 species respectively, together representing nearly half the total plant taxa. Most plant taxa occurred in relatively few wetlands and occupied only small percentages of the total wetland area (Table 3). The maximum number of native plant taxa recorded in a wetland was 31, although most wetlands contained relatively few (Table 4).

Four recorded plant species are introduced: *Salvinia molesta*, *Echinochloa crus-galli*, *Nymphaea capensis* and *Eichhornia crassipes* (water hyacinth). At the time of the survey, these covered about 1.9% of the total wetland area. Water hyacinth was by far the most extensive of these, occupying some 250 ha, and had completely blanketed and infilled some wetlands.

Several native species, such as *Eucalyptus robusta*, *Juncus kraussii*, *Sporobolus virginicus* and *Triglochin striata*, occur only marginally in floodplain wetlands and are more typical of other wetland types.

The survey provided records of some rare or uncommon plant species. These include:

- *Brasenia schreberi* (Cabombaceae): present in 1 wetland; very few records for coastal New South Wales; listed as 3V by Briggs and Leigh (1988);
- *Cyperus odoratus* (Cyperaceae): present in 2 wetlands; very few records for the state;
- *Cyperus platystylis* (Cyperaceae): present in 1 wetland; a plant of floating organic mats in northern Australia and a very rare plant in New South Wales (K. Wilson, Natnl. Herb. N.S.W., pers. comm.); found on a mat of water hyacinth;
- *Eleocharis philippinensis* (Cyperaceae): present in 1 wetland; only one previous record for the state;

TABLE 3

Frequency of occurrence of plant taxa in wetlands according to % number of wetlands and % total wetland area (bracketed figures indicate number of introduced species in percentage classes)

Percentage class	No. taxa (% no. wetlands)	No. taxa (% wetland area)
0-1.0	28(2)	57(3)
1.1-2.0	9	5(1)
2.1-3.0	5	2
3.1-4.0	1	2
4.1-5.0	8	1
5.1-6.0	2	—
6.1-7.0	2	—
7.1-8.0	2(1)	—
8.1-9.0	—	—
9.1-10.0	1	1
10.1-20	8	4
21-30	1	—
31-40	2(1)	—
41-50	—	—
51-60	—	—
61-70	—	—
71-80	3	—
81-90	—	—
91-100	—	—

TABLE 4

Numbers of native plant taxa in wetlands

Taxa	No. wetlands	% Total no.
>20	5	0.7
16-20	10	1.3
11-15	49	6.5
6-10	171	22.6
0-5	520	68.9
	755	100.0

- *Maundia triglochinosoides* (Juncaginaceae): present in 34 wetlands over a total area of 13.5 ha; known range only on the east coast between Wyong and the Brisbane area (Aston, 1973; Sainty and Jacobs, 1981); considered rare on the New South Wales central coast by Beadle *et al.* (1982); generally rarely reported and of uncertain status (S. Jacobs, Natnl. Herb. N.S.W., pers. comm.).

Despite dry conditions over most of New South Wales in 1982, the results of the botanical survey should be generally representative of the Clarence floodplain wetlands. Good rains preceded the February survey when wetland vegetation was well developed and most basins were full or nearly so. However, some plants would have been missed or underestimated during the winter part of the survey because of seasonal growth patterns, absence of inflorescences, or the drier conditions typical of winter in the area.

The majority of wetlands had few trees on their margins (Table 5), a result of the widespread clearing of the floodplain. Fringing herbaceous emergents were, however, generally well developed in terms of density, width and the average percentage of perimeters occupied. The major taxa classed as fringing emergents were *Juncus* spp. and *Pericaria* spp. Others were *Carex appressa*, *Leersia hexandra* and *Lepironia articulata*. *Casuarina glauca* and *Melaleuca quinquenervia* were the most common fringing trees.

TABLE 5
Summary of records for condition of marginal vegetation

A			B		
Percentage of perimeter with trees			Percentage of perimeter with emergent vegetation		
Percentage	No. wetlands	% Total no.	Percentage	No. wetlands	% Total no.
91-100	44	5.8	91-100	410	54.2
66-90	36	4.8	66-90	79	10.5
36-65	58	7.7	36-65	74	9.8
10-35	65	8.6	10-35	42	5.6
0-9	552	73.1	0-9	150	19.9
	755	100.0		755	100.0

C. Average density and width of emergent vegetation		
Rating	No. wetlands	% Total No.
5 (very dense and wide)	331	43.8
4	69	9.1
3	122	16.2
2	76	10.1
1 (very sparse and narrow)	157	20.8
	755	100.0

About 98% of the total number of wetlands were grazed to some extent. Drainage had directly affected 295 wetlands (39% of total number) and a wetland area of 13,500 ha (92% of total area). Drainage has reduced the persistence and depth of standing water in these wetlands with consequent changes in the distribution and abundance of plants and animals. The severity of drainage effects has varied depending on the depth of drains, the original nature of the wetlands, and the extent of their catchments. The overall effects of drainage on the Clarence floodplain wetlands are probably underestimated by these statistics for two reasons. Firstly, drainage may have lowered local water tables and so affected wetlands not directly drained. Secondly, drainage has fragmented some previously large wetlands into remnant sub-basins that are not directly drained but have had their water regimes altered.

Few, if any, wetlands on the Clarence floodplain have been completely eliminated by drainage. The main reason for the inconsistency between this statement and Goodrick's (1970) estimates of the decline of fresh meadows and seasonal fresh swamps in the region (Table 2) is that Goodrick's survey was primarily concerned with waterfowl habitat. His estimates of the decline of wetlands therefore included any areas whose value to waterfowl had been largely eliminated. Many such areas, though, can still be defined by wetland vegetation.

Wetlands were placed in two broad hydrological categories on the basis of the nature of their catchments. The first (Category 1) comprises 544 wetlands with an area of 2456 ha (72% total number, 17% total area) which have small catchments confined to alluvial flats below the 10 m contour. Their water levels would generally be less stable and would fall more quickly during dry periods than those in other wetlands.

The second type of wetlands (Category 2) have catchments extending above the 10 m contour beyond the alluvial flats on which they occur. This category includes 211 wetlands with a total area of some 12,272 ha (28% of total number, 83% of total area). Most of these wetlands have catchments smaller than 1000 ha although most of the wetland area in Category 2 is filled from larger catchments (Table 6). The largest catchment area, that of Ellis Swamp and Crowsnest Swamp (No. 306 in Fig. 1), is 17,200 ha. Most

also have ratios of catchment area/wetland area of less than 100 and nearly 80% of the wetland area in Category 2 has a ratio of 10 or less (Table 7). Wetlands with large catchments and with large ratios of catchment area/wetland area will generally have more persistent and stable water levels and will contract more slowly in dry periods. At least some of these would be important local foci for fauna during droughts and may be significant in a broader context, particularly for the more mobile species of waterbirds.

TABLE 6
Catchment sizes for wetlands with catchments above the 10 m contour (Category 2)

Catchment size (ha)	No. wetlands	% Total no. Cat. 2	Wetland area (ha)	% Total area Cat. 2
0-10	62	29.4	112.4	0.9
11-100	66	31.3	421.3	3.4
101-1000	44	20.8	2566.8	20.9
> 1000	39	18.5	9171.4	74.7
	211	100.0	12272.9	100.0

TABLE 7
Ratios of catchment area/wetland area for wetlands with catchments above the 10 m contour (Category 2)

Catchment/wetland ratio	No. wetlands	% Total no. Cat. 2	Wetland area	% Total area Cat. 2
0-10	106	50.2	9433.0	76.8
11-100	66	31.3	2722.8	22.2
101-1000	26	12.3	95.0	0.8
> 1000	13	6.2	21.1	0.2
	211	100.0	12271.9	100.0

Twenty-one combinations of land uses were recognized in wetland catchments. The occurrence of each broad land use is summarized in Table 8. Agriculture is by far the major catchment land use, although areas of natural vegetation are also relatively common. Seventy-seven percent of catchments are completely under agriculture, and nearly all of these are restricted entirely to the alluvial flats. Only two catchments are completely covered by natural vegetation.

TABLE 8
Land use occurrence in wetland catchments

Land use	Present (% no. catchments)	Dominant or sole use (% no. catchments)
Agriculture	99.7	87.3
Forestry	5.7	1.1
Industrial area	0.5	—
Mining	3.2	—
Natural vegetation	21.3	11.5
Urban area	3.0	0.1
Waste disposal	0.5	—

In 95% of wetlands, land tenure is solely or dominantly freehold. One wetland (Cowans Ponds, No. 257 in Fig. 1) is within a Wildlife Refuge under the National Parks and Wildlife Act, 1974.

The survey reported here is the first comprehensive and detailed description of wetlands on the Clarence floodplain. However, the results are accurate for the wetlands and their catchments only for the period of the field survey and for the dates of the aerial photography. Subsequent developments and changes in land use will have affected and will continue to affect the condition of many wetland catchments, the condition of marginal vegetation, and the occurrence of plant taxa and open water. In particular, the future applicability of the data on plants and open water categories will depend on the extent of short-term irregular and long-term successional changes in the wetlands. The nature of these changes is difficult to predict with the presently poor understanding of the dynamics of Australian wetlands. Nevertheless, general observations by the author over several years on the Clarence floodplain suggest that:

- the distribution and abundance of plant taxa in some wetlands alter over periods of months or years, although the suites of plant species in these areas generally remain similar;
- the distribution and abundance of plant taxa in other wetlands, particularly those which are seasonal and have small catchments, appear to change very little over months or years.

Without research on the vegetation dynamics of these areas, the characteristics of the wetlands that determine variability or stability of plant distributions, and the nature and extent of short-term variability, must remain conjectural.

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APPENDIX

Occurrence of open water categories and plant taxa (* indicates introduced species; + indicates no occurrence greater than 0.1 ha; ns indicates less than 0.1%)

Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area	Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area
Shallow open water	317	42.0	554.5	3.8	<i>E. tetralophila</i>	9	1.2	0.2	ns
Deep open water	91	12.1	315.5	2.1	<i>Leersia hexandra</i>	56	7.4	24.2	0.2
Total open water	337	44.6	870	5.0	<i>Panicum paludosum</i>	2	0.3	+	ns
PTERIDOPHYTES					(1) <i>Panicum/Pseudoraphis</i>	152	20.1	309.4	2.1
BLECHNACEAE					<i>Paspalum distichum</i>	569	75.4	2211.5	15.0
<i>Blechnum indicum</i> Burm.f.	10	1.3	+	ns	<i>P. vaginatum</i>	8	1.1	344.7	2.3
MARSILEACEAE					<i>Phragmites australis</i>	31	4.1	455	3.1
<i>Marsilea maitica</i> Mett.	31	4.1	11.4	0.1	<i>Sacciolepis indica</i>	2	0.3	+	ns
SALVINIACEAE					<i>Sporobolus virginicus</i>	4	0.5	14	0.1
* <i>Salvinia molesta</i>					Total Poaceae	622	82.4	3364.5	22.9
D. S. Mitchell	3	0.4	2	ns	PONTEDERIACEAE				
Total Pteridophytes	43	5.7	13.4	0.1	* <i>Etichornia crassipes</i>	266	35.2	246.7	1.7
MONOCOTYLEDONNS					POTAMOGETONACEAE				
ALISMATACEAE					<i>Potamogeton tricarlinatus</i>	31	4.1	6	ns
<i>Damasonium minus</i>	2	0.3	+	ns	TYPHACEAE				
CYPERACEAE					<i>Typha</i> spp.	29	3.8	24	0.2
<i>Baumea articulata</i>	7	0.9	+	ns	Total Monocotyledons	733	97.1	8627.1	58.6
<i>Bolboschoenus? caldwelli</i>	2	0.3	25.2	0.2	DICOTYLEDONNS				
<i>B. fluviatilis</i>	21	2.8	3.8	ns	APIACEAE				
<i>Carex appressa</i>	52	6.9	24.6	0.2	<i>Lilaeopsis polyantha</i>	5	0.7	+	ns
<i>Cladium procerum</i>	4	0.5	2.1	ns	ASTERACEAE				
<i>Cyperus exaltatus</i>	33	4.4	2.4	ns	<i>Cotula coronopifolia</i>	9	1.2	10.5	0.1
<i>C. haspan</i>	5	0.7	+	ns	CABOMBACEAE				
<i>C. odoratus</i>	2	0.3	+	ns	<i>Brasenia schreberi</i>	1	0.1	+	ns
<i>C. pilosus</i>	1	0.1	0.5	ns	CASUARINACEAE				
<i>C. platyphyllis</i>	1	0.1	+	ns	<i>Casuarina glauca</i>	250	33.1	601.8	4.1
<i>C. polystachyos</i>	37	4.9	17.7	0.1	HALORAGACEAE				
<i>C. sanguinolentus</i>	3	0.4	+	ns	<i>Myriophyllum latifolium</i>	23	3.0	3.4	ns
<i>Eleocharis dietrichuana</i>	48	6.4	4.1	ns					
<i>E. equisetina</i>	110	14.6	2118	14.5					

APPENDIX (continued)

Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area	Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area
<i>E. minuta</i>	83	11.0	146.5	1.0	LOBELIACEAE				
<i>E. philippinensis</i>	1	0.1	0.1	ns	<i>Isotoma ? armstrongii</i>	1	0.1	0.3	ns
<i>E. sphacelata</i>	98	13.0	168.7	1.1	<i>I. fluviatilis</i>	1	0.1	+	ns
<i>Fimbristylis ferruginea</i>	2	0.3	+	ns	<i>Isotoma</i> sp.	6	0.8	+	ns
<i>F. nultans</i>	3	0.4	+	ns	Total Lobeliaceae	8	1.1	0.3	ns
<i>Isolepis inundata</i>	10	1.3	26.4	0.2	MENYANTHACEAE				
<i>Lepironia articulata</i>	45	6.0	189.8	1.3	<i>Nymphoides geminala</i>	9	1.2	1.3	ns
<i>Schoenoplectus litoralis</i>	17	2.3	203.7	1.4	<i>N. indica</i>	38	5.0	39.5	0.3
<i>S. mucronatus</i>	9	1.2	0.2	ns	Total Menyanthaceae	45	6.0	40.8	0.3
<i>S. validus</i>	5	0.7	+	ns	MYRTACEAE				
Total Cyperaceae	274	36.3	2933.8	19.9	<i>Callistemon satignus</i>	21	2.8	1.2	ns
ERIOCAULACEAE					<i>Eucalyptus robusta</i>	3	0.4	6.1	ns
<i>Eriocaulon scariosum</i>	3	0.4	+	ns	<i>Leptospermum juniperinum</i>	3	0.4	5	ns
HYDROCHARITACEAE					<i>Melaleuca linariifolia</i>	117	15.5	62.8	0.4
<i>Ottelia ovalifolia</i>	40	5.3	1.7	ns	<i>M. quinquenervia</i>	140	18.5	2479.3	16.9
JUNCACEAE					<i>M. styphelioides</i>	79	10.5	3.9	ns
<i>Juncus kraussii</i>	7	0.9	15.1	0.1	Total Myrtaceae	273	36.2	2558.3	17.3
<i>J. prismatocarpus</i>	32	4.2	2.2	ns	NYMPHAEEACEAE				
<i>Juncus</i> spp.	557	73.8	1395.9	9.5	<i>*Nymphaea capensis</i>	58	7.7	25.2	0.2
Total Juncaceae	565	74.8	1413.2	9.6	<i>N. gigantea</i>	10	1.3	13	0.1
JUNCAGINACEAE					Total Nymphaeaceae	63	8.3	38.2	0.3
<i>Maundia triglochinoides</i>	34	4.5	13.5	0.1	ONAGRACEAE				
<i>Triglochin procerum</i>	95	12.6	22	0.1	<i>Ludwigia peploides</i>	119	15.8	31.9	0.2
<i>T. striata</i>	11	1.5	24	0.2	POLYGONACEAE				
Total Juncaginaceae	129	17.1	59.5	0.4	<i>Persicaria</i> spp.	574	76.0	1705.0	11.6
PHILYDRACEAE					SCROPHULARIACEAE				
<i>Philydrum lanuginosum</i>	74	9.8	577.7	3.9	<i>Bacopa monnieri</i>	19	2.5	227.2	1.5
POACEAE					Total Dicotyledons	669	88.6	5217.4	35.4
<i>Diplachne fusca</i>	1	0.1	0.5	ns	SURVEY TOTAL	14727.9	100.0		
<i>*Echinochloa crus-galli</i>	2	0.3	5	ns					

(1) *Panicum obseptum* and *Pseudoraphis spinescens* were not always reliably distinguished. *Panicum obseptum* was by far the more extensive and commonly recorded.

Wetlands of the Lower Macleay Floodplain, Northern Coastal New South Wales

R. L. PRESSEY
(Communicated by P. ADAM)

PRESSEY, R. L. Wetlands of the lower Macleay floodplain, northern coastal New South Wales. *Proc. Linn. Soc. N.S.W.* 111 (3), 1989: 157-168.

A survey of wetlands on the lower Macleay floodplain in 1984 involved mapping and description of 432 wetlands with a total area of nearly 12,800 ha. Most wetlands were less than 10 ha and the three largest accounted for 73% of the total area. One hundred and eighteen plant taxa and two categories of open water were recorded. Open water occupied only 2.5% of the total wetland area but some open water occurred in 54% of wetlands. The most extensive and frequently occurring plant families were Polygonaceae (covering 26% of the wetland area, occurring in 97% of the total number of wetlands), Poaceae (28% area, 91% number), Juncaceae (10% area, 91% number), Cyperaceae (20% area, 63% number) and Myrtaceae (6% area, 21% number). Broad fringing bands of herbaceous plants were typical of the wetlands. Most wetlands had few trees on their margins due to clearing. About 99% of wetlands were grazed. Drainage affected 51% of the total number and 96% of the total wetland area. Most wetlands are seasonal and have relatively small catchments restricted to the alluvial flats. Twenty-one percent of wetlands have catchments on adjacent hillslopes and ranges. Agriculture was by far the dominant land use in wetland catchments. Most wetlands were freehold and only one is covered (partly) by a reserve for nature conservation.

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KEY WORDS: Wetlands, survey, plant taxa, catchments, Macleay floodplain.

INTRODUCTION

The wetlands of the Macleay floodplain have not previously been mapped or surveyed in a detailed and comprehensive way. In a broad-scale survey of the State's coastal wetlands, Goodrick (1970) mapped and classified many on the Macleay floodplain, including all the major ones. His study outlined the types and distribution of coastal wetlands and estimated their decline up to 1969. However, it lacked the detailed information needed to decide priorities for conservation and management. The only other inventory of wetlands on the Macleay floodplain was by the Coastal Council of New South Wales (1985) which mapped many of them for zoning purposes without describing or classifying them. Another broad survey by West *et al.*, (1985) dealt exclusively with the estuarine wetlands of the Macleay and other parts of the coast.

There are few detailed studies on the flora and fauna of the Macleay floodplain wetlands and none of these has covered more than a few of the total number of wetlands. Broome (1978) identified the habitat associations of waterbirds and studied the dynamics of their populations at a few selected sites. The remaining studies on the wetlands of the floodplain are mainly concerned with geomorphology and soils (Pressey, 1981).

This paper summarizes the results of a detailed inventory and description of all the wetlands on the lower Macleay floodplain (see Pressey, 1987). The survey was part of a series of studies on coastal wetlands undertaken for the New South Wales National Parks and Wildlife Service. The area and aims of the surveys and the types of data collected are outlined in the accompanying paper on the Clarence floodplain wetlands (Pressey, 1989).

STUDY AREA

The Macleay River floodplain is situated on the mid-north coast of New South Wales, approximately 350 km north-east of Sydney (Fig. 1). As for the Clarence survey, the lower Macleay floodplain was defined as alluvium below the 10 m contour. This boundary contains virtually all of the alluvial wetland in the Macleay system and encloses the extensive deltaic alluvial plain that has formed during and since the last rise in sea level. The floodplain above the 10 m contour is restricted to a narrow strip along the river and the wetlands are generally small and scattered. The survey was also restricted to predominantly fresh wetlands and excluded estuarine and most brackish areas.

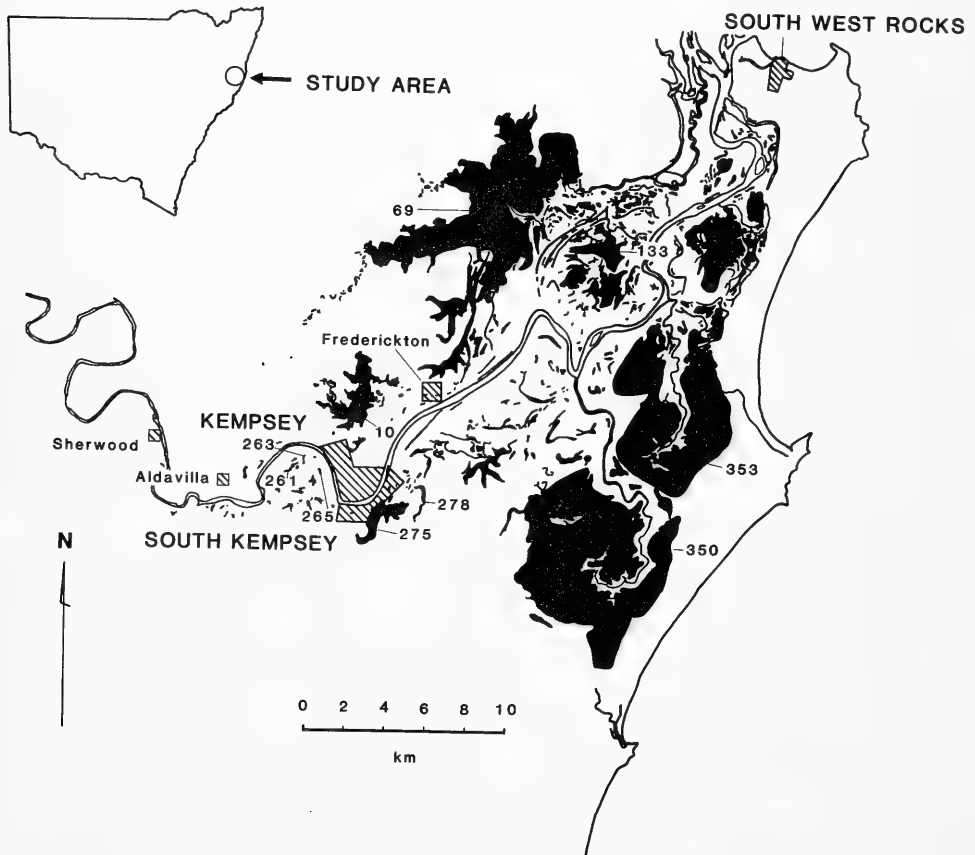


Fig. 1. The study area. Numbers are those given to named wetlands during the survey. The names corresponding to these numbers are: 10 Christmas Creek; 69 Doughboy Swamp/Sevenoaks Swamp/Clybucca Swamp; 133 Cooroobongatti Swamp; 261 Chapmans Creek; 263 Chapmans Creek; 265 Chapmans Creek; 275 East Kempsey Swamps/Bridge Creek; 278 Pola Creek; 350 Belmore Swamp; 353 Swan Pool/Kinchela Swamp.

The study area occupies about 400 sq. km (Fig. 1). To the north of the river it extends upstream as far as Aldavilla. On this side, a large area of alluvium lies adjacent to Christmas Creek, immediately north of Kempsey, but the bulk of the northern floodplain is to the north and east of Frederickton where continuous alluvium extends for some 140 sq. km. The dominant wetland area here is the large Doughboy, Sevenoaks or

Clybucca Swamp in the north-west of the study area. To the south of the river the study area extends upstream almost to Sherwood. Most of the southern alluvium lies in a continuous tract of about 180 sq. km downstream of South Kempsey. The largest wetland areas here are the Swan Pool, formerly known as Kinchela Swamp, and Belmore Swamp.

The main land use on the Macleay floodplain is grazing for dairying and beef. Relatively small areas have been planted to poplars and to crops such as sorghum and corn. As on the Clarence floodplain, drainage of wetlands began late in the nineteenth century to improve pasture production. Drainage trusts or unions were formed around the turn of the century to co-ordinate drainage schemes. From the late 1950s, under flood mitigation schemes, drains, floodgates and levees were constructed and integrated to minimize damage to urban and agricultural land from flooding. They extended and intensified the alteration of wetlands caused by earlier drainage.

Goodrick (1970) found that about 49% of all wetlands on the mid-north coast, which includes the Macleay floodplain, had been lost or significantly altered before 1970, mainly to drainage and flood mitigation. This decline or alteration includes about 14,800 ha of shallow floodplain wetlands, representing about 68% of the wetlands lost or altered. The impacts on floodplain wetlands are likely to be more extensive today since flood mitigation on the lower Macleay has continued since Goodrick's survey (Pressey and Middleton, 1982).

METHODS

Initial identification of wetlands was from black and white or colour aerial photographs taken between 1979 and 1981 at scales of 1:25 000 and 1:50 000. The wetlands were each visited at least once during two field surveys (6.12.83 – 21.12.83 and 6.1.84 – 27.1.84).

Of thirteen attributes of each wetland recorded in the field and/or remotely from maps and aerial photographs, six were used only for ranking the wetlands for conservation (see Pressey, 1987). The remaining seven – size, vegetation/habitats, marginal vegetation, alteration, catchment areas, catchment land use, and tenure – were used descriptively and are discussed in this paper.

Methods of recording the seven descriptive attributes are given in the preceding paper on the Clarence wetlands (Pressey, 1989). Differences in recording plant taxa in the Macleay wetlands were that more time was spent searching for plants, species in the families Azollaceae and Lemnaceae were included, and all plants were identified at least to species level. Authorities for plant names are those in Jacobs and Pickard (1981) as amended by Jacobs and Lapinuro (1986), unless indicated otherwise.

RESULTS AND DISCUSSION

The survey covered 432 wetlands with a total area of 12,772 ha. Most of the wetlands are small, 90% being 10 ha or smaller (Table 1). These small wetlands account for less than 6% of the total wetland area. The bulk of the wetland area (89%) is made up by the relatively small number (3% of the total) greater than 100 ha in size. The three largest wetlands account for 73% of the total wetland area.

The recorded plant taxa, including a hybrid *Juncus*, an undescribed species of *Myriophyllum*, and two forms of *Pericaria strigosa*, totalled 118. Their occurrence in the study area, with that of the two recorded categories of open water, is summarized in the Appendix.

The two forms of *Pericaria strigosa* differed in features and habitat. *P. strigosa* FORM 1 was the less common. It is characterized by large green leaves with cordate bases,

bristles beneath the dense glandular hairs on the peduncles, and white flowers in a large, compact, ovate spike. It was found generally along the edges of relatively permanent, steep-sided channels and in other sheltered, damp areas that are rarely inundated. *P. strigosa* FORM 2 has reddish leaves that are more lanceolate than FORM 1, frequently with hastate bases. In addition, there are no bristles beneath the glandular hairs on the peduncles and the spike of white flowers is linear to ovate and occasionally interrupted. It was found growing in dense meadows in relatively persistent standing water, particularly in wetlands with large catchments or in those adjacent to perennial streams. FORM 2 is the more similar to *P. sp. B* in terms of leaf shape and inflorescence structure.

TABLE 1
Size distribution of wetlands

Area (ha)	No. of wetlands	% Total no.	Wetland area (ha)	% Total area
0-1.0	190	44.0	107.5	0.8
1.1-5.0	162	37.5	368.8	2.9
5.1-10.0	37	8.6	254.5	2.0
10.1-50	28	6.5	526	4.1
51-100	3	0.7	200	1.6
101-500	8	1.8	1415	11.1
501-1000	1	0.2	530	4.1
>1000	3	0.7	9370	73.4
	<u>432</u>	<u>100.0</u>	<u>12771.8</u>	<u>100.0</u>

Open water was relatively unimportant in terms of the overall wetland area occupied (Appendix). Some shallow open water occurred in about half the number of wetlands but totalled, at the time of the survey, only about 290 ha or 2.3% of total wetland area. Deep open water was much more restricted in distribution and extent. The scarcity of open water in the wetlands of the mid-north coast generally is indicated by estimates from Goodrick's (1970) report (Table 2). The five categories of Goodrick's classification that make up the bulk of the wetland area in the region, and on the Macleay floodplain, contain relatively little open water and are dominated by herbaceous emergents and by trees.

Completion of all the field work in mid-summer following heavy rains provided ideal conditions for the identification of a large number of wetland plant taxa. Some shallow seasonal wetlands contained so much water that the results of the survey may be atypical to some extent. Of the plant taxa recorded, one is a liverwort, seven are ferns, 67 are monocotyledons and 43 are dicotyledons. The most diverse families were Cyperaceae (30 taxa), Polygonaceae (12), Juncaceae (11) and Poaceae (10). The largest number of native taxa recorded in a wetland was 46, although most wetlands contained relatively few (Table 3). There is a significant relationship between wetland size and number of plant taxa in the wetlands on the Macleay floodplain (Margules *et al.*, 1988) although there is considerable variability in the number of taxa in wetlands of any size. Most taxa occurred in relatively few wetlands and occupied a relatively small overall area (Table 4).

Monocotyledonous plants occupied some 62% of the total wetland area and occurred in all but one wetland (Appendix). The most important monocot families, in terms of extent and frequency of occurrence, were Poaceae (28% of total wetland area, 91% of total number of wetlands), Juncaceae (10% area, 91% number) and Cyperaceae (22% area, 63% number). *Paspalum distichum* (water couch) and *Juncus polyanthemus* x *usitatus* were the most extensive and frequently occurring taxa in the Poaceae and

Juncaceae, respectively. *Eleocharis equisetina* made up most of the area occupied by the Cyperaceae and was one of the most frequently occurring sedges. Dicotyledons occupied 35% of the wetland area and occurred in all but three wetlands. Polygonaceae (26% area, 97% number) and Myrtaceae (6% area, 21% number) were the major dicot families. *Persicaria hydrophiper* and *Melaleuca quinquenervia* were, respectively, the most extensive and commonly recorded species in these families.

TABLE 2

Extent and decline of wetland types on the mid-north coast of New South Wales (modified from Goodrick, 1970)#

Wetland type	Original area (ha)	1969 area (ha)	% Decline
fresh meadows	18590	(2430)	79.7
seasonal fresh swamps		(1340)	
semi-permanent fresh swamps	120	120	—
open fresh waters*	40	40	—
shallow saline lagoons	650	650	—
teatree swamps	7490	6560	12.4
salt meadows	3520	3520	—
reed swamps	2880	810	71.9
salt flats	160	160	—
mangrove swamps	1170	1170	—
coastal bogs	1940	1940	—
coastal <i>Lepironia</i> swamps	40	40	—
	36600	18780	48.7

estimates excluded two wetland types: shallow estuarine waters and sheoak swamps.

* open fresh waters is the only floodplain wetland category identified by Goodrick as being dominantly open water, although relatively small areas of open water occur in other categories on the Macleay floodplain. Underlined categories are those occurring on the Macleay floodplain.

TABLE 3

Numbers of native plant taxa in wetlands

Taxa	No. wetlands	% Total no.
>30	4	0.9
26-30	3	0.7
21-25	9	2.1
16-20	31	7.2
11-15	101	23.4
6-10	174	40.2
0-5	110	25.5
	432	100.0

Twenty of the species recorded are introduced. They occupied about 180 ha or 1.5% of total wetland area at the time of the survey. The most extensive were *Eichhornia crassipes* (94 ha), *Salvinia molesta* (33 ha) and *Echinochloa crus-galli* (31 ha). The first two mentioned are particularly troublesome floating weeds and had completely blanketed and infilled some wetlands. *Cyperus brevifolius* may be native to parts of northern Australia although it is considered to be introduced to the study area (K. Wilson, Natnl. Herb. N.S.W., pers. comm.).

Four recorded species, *Commelina cyanea*, *Cyperus polystachyos*, *Pseudognaphalium luteoalbum* and *Ranunculus plebeius*, are widely distributed in non-wetland habitats, particu-

larly in higher rainfall areas. A further six species, *Bacopa monnieri*, *Bolboschoenus caldwellii*, *Juncus kraussii*, *Schoenoplectus litoralis*, *Sporobolus virginicus* and *Triglochin striata*, are typical of brackish and estuarine habitats and occur only marginally in freshwater floodplain wetlands.

TABLE 4

Frequency of occurrence of plant taxa in wetlands according to % number of wetlands and % total wetland area (bracketed figures indicate number of introduced species in percentage classes)

Percentage class	No. taxa (% no. wetlands)	No. taxa (% wetland area)
0-1.0	39(9)	107(20)
1.1-2.0	14(1)	1
2.1-3.0	12(1)	3
3.1-4.0	4(2)	—
4.1-5.0	4	1
5.1-6.0	5(3)	1
6.1-7.0	5	—
7.1-8.0	3	—
8.1-9.0	4	2
9.1-10.0	2	2
10.1-20	12(2)	1
21-30	5(1)	—
31-40	1	—
41-50	2(1)	—
51-60	1	—
61-70	2	—
71-80	1	—
81-90	2	—
91-100	—	—

Four rare or uncommon plant species were recorded during the field survey:

- *Cyperus platystylis* (Cyperaceae): present in six wetlands over a total area of 0.1 ha; very rare in New South Wales although more common in northern Australia where it occurs on floating organic mats (K. Wilson, Natnl. Herb. N.S.W., pers. comm.); recorded only on mats of the introduced *Salvinia molesta* and *Eichhornia crassipes*;
- *Eleocharis philippinensis* (Cyperaceae): present in one wetland; third and southernmost record for the State;
- *Maundia triglochinosoides* (Juncaginaceae): present in 30 wetlands and over a total area of 12.1 ha; known range only between Wyong and the Brisbane area (Aston, 1973; Sainty and Jacobs, 1981); considered rare on the New South Wales central coast by Beadle *et al.* (1982); generally rarely collected and of uncertain status (S. Jacobs, Natnl. Herb. N.S.W., pers. comm.);
- *Potamogeton javanicus* (Potamogetonaceae): present in one wetland; only known from the central and north coast regions of the State (Sainty and Jacobs, 1981) and recorded very rarely over this range although it is widespread in northern Australia and overseas (Aston, 1973); given as rare on the central coast by Beadle *et al.*, (1982) and rarely collected from the Sydney region in recent years (R. Coveny, Natnl. Herb. N.S.W., pers. comm.).

The majority of wetlands had dense, broad bands of herbaceous emergents around most of their perimeters (Table 5). The major fringing emergents, by far, were *Persicaria hydropiper* and *Juncus polyanthemus* x *usitatus*. Few wetlands had more than 10% of their margins lined with trees, the result of clearing for grazing. The commonest fringing trees were *Casuarina glauca* and *Melaleuca quinquenervia*.

TABLE 5
Summary of records for condition of marginal vegetation

A			B		
Percentage of perimeter with trees			Percentage of perimeter with emergent vegetation		
Percentage	No. wetlands	% Total no.	Percentage	No. wetlands	% Total no.
91-100	10	2.3	91-100	324	75.0
66-90	12	2.8	66-90	19	4.4
36-65	15	3.5	36-65	32	7.4
11-35	27	6.2	11-35	12	2.8
0-10	368	85.2	0-10	45	10.4
	432	100.0		432	100.0

C. Average density and width of emergent vegetation		
Rating	No. wetlands	% Total No.
5 (very dense and wide)	316	73.2
4	26	6.0
3	26	6.0
2	19	4.4
1 (very sparse and narrow)	45	10.4
	432	100.0

About 99% of the wetlands were grazed to some extent by cattle. At least five wetlands had been separated from tidal influence by floodgates or earthen block banks. Drainage had directly affected 220 wetlands (51% of total number) and a wetland area of 12,236 ha (96% of total area). Additional, indirect effects of drainage on other wetlands include separation into undrained sub-basins and could include local lowering of water tables.

The actual hydrological effects of drainage would vary with factors such as the depth of drainage and of water tables and the size of catchments. In general, however, drained wetlands will have reduced storage capacity and will dry more readily compared to undrained ones. It is unlikely that any wetlands on the lower Macleay floodplain have been completely eliminated by drainage, despite Goodrick's (1970) estimates of wetland decline in the region (Table 2). His estimates are based on the elimination of value to waterfowl whereas wetlands were defined in this study by the occurrence of plants adapted to at least seasonal inundation. Many wetlands defined in this way are no longer of value as waterfowl habitat. Some 33% of the wetland area covered by the survey reported here was occupied by two taxa (*Juncus polyanthemus* x *usitatus* and *Persicaria hydropiper*) typical of marginal wetland conditions. Wetland drainage has probably been a major cause of the extensive distribution of these taxa.

Two broad hydrological categories of wetlands were distinguished from the nature of their catchments. The first (Category 1) contains 342 wetlands (79% of total number) with a combined area of nearly 4800 ha (37% of total area) which have catchments extending no higher than the 10 m contour. They are filled only by groundwater and localized runoff from the surrounding alluvial flats and will generally have less stable water levels and will dry more readily than those in Category 2. The second type of wetlands (Category 2), with additional drainages on the bedrock slopes surrounding the floodplain, number 90 (21% of total number) and have an overall area of about 8,000 ha (63% of total area).

Most wetlands in Category 2 have catchments on bedrock smaller than 100 ha but the few large wetlands which make up most of the area of this type are fed by catchments

larger than 1000 ha (Table 6). The catchment sizes for these wetlands are 1100 ha (East Kempsey Swamps, No. 275 in Fig. 1), 1790 ha (Belmore Swamp, No. 350), 5060 ha (Christmas Creek, No. 10) and 13,400 ha (Doughboy Swamp, No. 69). The other very large catchment covers 1880 ha and supplies wetland No. 249 which has an area of only about 1 ha. About 90% of wetlands in Category 2 have catchment area/wetland area ratios of 100 or less (Table 7). About 95% of the area in this type of wetland is fed by catchments that are at most 10 times larger than the individual wetlands. Larger catchments and larger ratios of catchment area/wetland area will generally confer greater permanence on wetlands or on particular parts of large, complex basins. Water levels in these wetlands would generally be more persistent because of the greater effectiveness of any rainfall in refilling the basins and perhaps because of greater base flow from groundwater in large catchments.

TABLE 6
Catchment sizes for wetlands with catchments above the 10 m contour (Category 2)

Catchment size (ha)	No. wetlands	% Total no. Cat. 2	Wetland area (ha)	% Total area Cat. 2
0-10	43	47.8	67.9	0.9
11-100	29	32.2	75.1	0.9
101-1000	13	14.4	503.0	6.3
>1000	5	5.6	7340.8	91.9
	90	100.0	7986.8	100.0

TABLE 7
Ratios of catchment area/wetland area for wetlands with catchments above the 10 m contour (Category 2)

Catchment/wetland ratio	No. wetlands	% Total no. Cat. 2	Wetland area	% Total area Cat. 2
0-10	54	60.0	7553.8	94.6
11-100	28	31.1	417.7	5.2
101-1000	7	7.8	14.5	0.2
>1000	1	1.1	0.8	—
	90	100.0	7986.8	100.0

Table 8 summarizes the occurrence of seven broad land uses in the catchments of the Macleay floodplain wetlands. Every wetland catchment contains some agricultural use and agriculture is the dominant or sole use in 93% of catchments. Areas of natural vegetation occur in 21% of catchments but occupy the largest parts of only 4% of catchments. None of the wetlands surveyed had completely natural catchments. Forestry, industrial areas, mining (only surface extraction of sand, gravel etc. in the case of the Macleay survey area), urban areas and waste disposal occurred in relatively few catchments and rarely or never occupied the largest proportions.

The tenure of about 98% of the wetlands was solely or dominantly freehold. A small part of the Swan Pool (wetland No. 353) is within Hat Head National Park.

The results reported here are estimates that are strictly valid only for the period of the field survey and for the dates of the aerial photography. The condition of wetlands and their catchments and the tenure of the wetlands will have since changed to some extent with new developments and changes in land use. In particular, short-term dynamics of wetland vegetation will have altered the occurrence of plant species and open water. Further surveys of the wetlands and research on the temporal variability of coastal freshwater wetlands are necessary to quantify and explain such changes.

TABLE 8

Land use occurrence in wetland catchments

Land use	Present (% no. catchments)	Dominant or sole use (% no. catchments)
Agriculture	100.0	93.3
Forestry	1.4	0.9
Industrial area	0.7	—
Mining	2.1	—
Natural vegetation	21.3	4.2
Urban area	5.8	1.6
Waste disposal	1.4	—

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APPENDIX

Occurrence of open water categories and plant taxa (* indicates introduced species; + indicates no occurrence greater than 0.1 ha; ns indicates less than 0.1%)

Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area	Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area
Shallow open water	227	52.5	287.6	2.3	IRIDACEAE				
Deep open water	39	9.0	28.4	0.2	* <i>Sisyrinchium micranthum</i>	1	0.2	+	ns
Total open water	232	53.7	316.0	2.5	JUNCACEAE				
HEPATIC					* <i>Juncus acuminatus</i>	3	0.7	+	ns
RICCIACEAE					* <i>J. acutus</i>	1	0.2	+	ns
<i>Ricciocarpus natans</i>					* <i>J. articulatus</i>	2	0.5	+	ns
(L.) Corda	1	0.2	+	ns	<i>J. bufonius</i>	1	0.2	+	ns
PTERIDOPHYTES					* <i>J. cognatus</i>	2	0.5	+	ns
AZOLLACEAE					<i>J. kraussii</i>	9	2.1	4.1	ns
<i>Azolla filiculoides</i> Lam.	96	22.2	10.8	0.1	<i>J. planifolius</i>	2	0.5	+	ns
<i>A. pinnata</i> R. Br.	72	16.7	12.2	0.1	<i>J. polyanthemus</i>	97	22.5	68.4	0.5
Total Azollaceae	160	37.0	23.0	0.2	<i>J. polyanthemus</i> x <i>ustulatus</i>				
BLECHNACEAE					<i>J. prismatocarpus</i>	313	72.5	1117.6	8.8
<i>Blechnum indicum</i> Burm. f.	13	3.0	22	0.2	<i>J. ustulatus</i>	36	8.3	1.5	ns
MARSILEACEAE					Total Juncaceae	395	91.4	1253.4	9.8
<i>Marsilea hirsuta</i> R. Br.	7	1.6	0.6	ns	JUNCAGINACEAE				
<i>M. mutica</i> Mett.	34	7.9	14.7	0.1	<i>Mauandia triglochinoides</i>	30	6.9	12.1	0.1
Total Marsileaceae	41	9.5	15.3	0.1	<i>Triglochin procera</i>	243	56.3	151.2	1.2
SALVINIACEAE					<i>T. striata</i>	10	2.3	0.3	ns
* <i>Salvinia molesta</i>					Total Juncaginaceae	254	58.8	163.6	1.3
D. S. Mitchell	14	3.2	32.9	0.3	LEMNACEAE				
THELYPTERIDACEAE					<i>Lemna minor</i>	31	7.2	0.1	ns
<i>Cyclosorus interruptus</i>					<i>Spirodela oligorhiza</i>	107	24.8	8.2	0.1
(Willd.) H. Ito	1	0.2	+	ns	Total Lemnaceae	110	25.5	8.3	0.1
Total Pteridophytes	193	44.7	93.2	0.7	PHILYDRACEAE				
MONOCOTYLEDONS					<i>Phylidrum lanuginosum</i>	31	7.2	6.5	0.1
ALISMATACEAE					POACEAE				
<i>Alisma plantago-aquatica</i>	10	2.3	0.1	ns	* <i>Echinochloa crus-galli</i>	214	49.5	31.4	0.3
					<i>Isachne globosa</i>	4	0.9	+	ns
					<i>Leersia hexandra</i>	38	8.8	4.1	ns

COMMELINACEAE	10	2.3	+	ns				127	29.4	266.5	2.1
<i>Commelina cyanea</i>								350	81.0	2094.8	16.4
CYPERACEAE								11	2.5	1134.6	8.9
<i>Baukea articulata</i>	10	2.3	0.5	ns				7	1.6	+	ns
<i>Bolboschoenus caldwellii</i>	7	1.6	0.8	ns				2	0.5	25.2	0.2
<i>B. fluviatilis</i>	25	5.8	576.4	4.5				5	1.2	20.7	0.2
<i>B. medianus</i>	2	0.5	0.7	ns				1	0.2	+	ns
<i>Carex appressa</i>	175	40.5	293.7	2.3				393	91.0	3577.3	28.0
<i>C. fascicularis</i>	3	0.7	0.5	ns							
<i>C. neurochlamys</i>	1	0.2	+	ns				71	16.4	94.3	0.7
<i>Cladium procerum</i>	1	0.2	+	ns							
* <i>Cyperus brevifolius</i>	53	12.3	4.3	ns				1	0.2	+	ns
<i>C. difformis</i>	6	1.4	+	ns				37	8.6	1.3	ns
* <i>C. eragrostis</i>	23	5.3	+	ns				37	8.6	1.3	ns
<i>C. exaltatus</i>	55	12.7	0.7	ns							
<i>C. haspan</i>	5	1.2	+	ns				1	0.2	+	ns
<i>C. platystylis</i>	6	1.4	0.1	ns				1	0.2	+	ns
<i>C. polystiachyos</i>	38	8.8	2.8	ns				18	4.2	17	0.1
<i>C. sanguinolentus</i>	5	1.2	+	ns				19	4.4	17	0.1
<i>C. trinervis</i>	2	0.5	+	ns							
<i>Eleocharis dietrichiana</i>	1	0.2	+	ns				431	99.8	7930.2	62.1
<i>E. equisetina</i>	42	9.7	1844.4	14.5							
<i>E. minuta</i>	27	6.3	10	0.1							
<i>E. philippinensis</i>	1	0.2	+	ns							
<i>E. sphacelata</i>	49	11.3	38.2	0.3							
<i>Fimbristylis dichotoma</i>	1	0.2	+	ns				22	5.1	+	ns
<i>F. velata</i>	1	0.2	+	ns							
<i>Isolepis inundata</i>	14	3.2	4	ns							
<i>Lepironia articulata</i>	4	0.9	27	0.2				22	5.1	5	ns
<i>Rhynchospora browneii</i>	1	0.2	+	ns				2	0.5	+	ns
<i>Schoenoplectus litoralis</i>	8	1.9	0.7	ns				24	5.6	5	ns
<i>S. mucronatus</i>	10	2.3	+	ns							
<i>S. validus</i>	8	1.9	2.2	ns				2	0.5	+	ns
Total Cyperaceae	270	62.5	2807.0	22.0				7	1.6	2	ns
HYDROCHARITACEAE								8	1.9	2	ns
<i>Ottelia ovalifolia</i>	52	12.0	1.4	ns				3	0.7	0.4	ns
								13	3.0	+	ns
<i>Panicum obsequeum</i>											
<i>Paspalum distichum</i>											
<i>Phragmites australis</i>											
* <i>Polygogon monspeliensis</i>											
<i>Pseudoraphis paradoxa</i>											
<i>P. spinescens</i>											
<i>Sporobolus virginicus</i>											
Total Poaceae											
PONTERIACEAE											
* <i>Eichhornia crassipes</i>											
POTAMOGETONACEAE											
<i>Potamogeton javanicus</i>											
<i>P. tricarinalus</i>											
Total Potamogetonaceae											
SPARGANIACEAE											
<i>Sparganium antipodum</i>											
TYPHACEAE											
<i>Typha domingensis</i>											
<i>T. orientalis</i>											
Total Typhaceae											
Total Monocotyledons											
DICOTYLEDONS											
AMARANTHACEAE											
<i>Alternanthera denticulata</i>											
APIACEAE											
* <i>Hydrocotyle bonariensis</i>											
<i>Lilaeopsis polyantha</i>											
Total Apiaceae											
ASTERACEAE											
* <i>Aster subulatus</i>											
<i>Genitipeda minima</i>											
<i>Gotula coronopifolia</i>											
<i>C. longipes</i>											
<i>Eclipta prostrata</i>											

APPENDIX (continued)

Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area	Taxon/open water category	No. wetlands	% Total no.	Total area (ha) occupied	% Total wetland area
<i>Enhydra fluctuans</i>	4	0.9	+	ns	NYMYPHAEACEAE <i>*Nymphalaea capensis</i>	25	5.8	8.3	0.1
<i>Pseudognaphalium lateoalbum</i>	1	0.2	+	ns					
Total Asteraceae	29	6.7	4.4	ns	ONAGRACEAE <i>Ludwigia peploides</i>	270	62.5	26.1	0.2
CALLITRICHACEAE <i>*Callitriche stagnalis</i>	2	0.5	+	ns					
CASUARINACEAE <i>Casuarina glauca</i>	85	19.7	371.7	2.9	PLANTAGINACEAE <i>*Plantago major</i>	10	2.3	+	ns
GOODENIACEAE <i>Goodenia paniculata</i>	5	1.2	+	ns	POLYGONACEAE <i>Persicaria attenuata</i>	1	0.2	+	ns
HALORAGACEAE <i>*Myriophyllum aquaticum</i>	3	0.7	7.5	0.1					
<i>M. latifolium</i>	28	6.5	4	ns	<i>P. hydropiper</i>	383	88.7	3088	24.2
<i>M. sp. (undescribed)</i>	11	2.5	1.2	ns	<i>P. lapathifolia</i>	82	19.0	1.1	ns
Total Haloragaceae	42	9.7	12.7	0.1	<i>P. orientalis</i>	60	13.9	+	ns
LOBELIACEAE <i>Isotoma armstrongii</i>	7	1.6	+	ns	<i>P. strigosa FORM 1</i>	21	4.9	2.2	ns
LYTHRACEAE <i>Lythrum hyssopifolia</i>	4	0.9	+	ns	<i>P. strigosa FORM 2</i>	60	13.9	118.2	0.9
MALVACEAE <i>Hibiscus diversifolius</i>	1	0.2	+	ns	<i>P. sp. A</i>	41	9.5	0.5	ns
MENYANTHACEAE <i>Nymphoides geminata</i>	2	0.5	+	ns	<i>P. sp. B</i>	60	13.9	59.9	0.5
<i>N. indica</i>	10	2.3	1.2	ns	<i>P. sp. C</i>	1	0.2	+	ns
Total Menyanthaceae	12	2.8	1.2	ns	<i>*Polygonum arenastrum</i>	4	0.9	+	ns
MYRTACEAE <i>Callistemon salignus</i>	27	6.3	2.3	ns	<i>*Rumex conglomeratus</i>	99	22.9	0.2	ns
<i>Melaleuca linariifolia</i>	20	4.6	5.1	ns	<i>*R. crispus</i>	16	3.7	+	ns
<i>M. quinquerivra</i>	63	14.6	689.9	5.4	Total Polygonaceae	419	97.0	3270.1	25.6
<i>M. styphelioides</i>	28	6.5	0.1	ns	RANUNCULACEAE <i>Ranunculus inundata</i>	162	37.5	31	0.3
Total Myrtaceae	92	21.3	697.4	5.5	<i>R. plebeus</i>	17	3.9	+	ns
					Total Ranunculaceae	168	38.9	31	0.3
					SCROPHULARIACEAE <i>Bacopa monnieri</i>	18	4.2	3.9	ns
					Total Dicotyledons	429	99.3	4431.8	34.7
					SURVEY TOTAL	12771.8			100.0

The Ordovician-Silurian Stratigraphy of the Cudgegong-Mudgee District, New South Wales

JOHN W. PEMBERTON

PEMBERTON, J. W. The Ordovician-Silurian stratigraphy of the Cudgegong-Mudgee district, New South Wales. *Proc. Linn. Soc. N.S.W.* 111 (3), 1989: 169-200.

Ordovician and Silurian rocks of the Cudgegong-Mudgee district crop out in a narrow belt separating Devonian sequences on the northern Capertee High.

The basal unit consists of Late Ordovician basaltic and andesitic lava and their fragmental equivalents (*Cudgegong Volcanics*) which are unconformably overlain by a thick Wenlockian to Ludlovian sequence of shallow marine to emergent units. The lowermost *Willow Glen Formation* (fossiliferous clastic sediments and limestone) was deposited in a coastal environment affected by a series of transgressive/regressive cycles. It is overlain by a thick and persistent sequence of dacite lava and breccia (*Windamere Volcanics*) with associated mass flow detritus (*Toolamanang Formation*), followed by volcanic quiescence with continuing shallow marine sedimentation (*Millsville Formation*).

The Ordovician-Silurian rocks occupy the core of a shallowly plunging northwest-trending anticline, the northeast limb of which is overturned. The rocks of this belt are disconformably overlain by Early Devonian units, a continuation of shallow marine conditions on the northern Capertee High, whereas the fluvial Late Devonian Lambie Group overlies the strata with slight angular unconformity.

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LOCATION

Mudgee is 260km northwest of Sydney in the central tablelands of New South Wales (Fig. 1). The village of Cudgegong, 35km to the southeast, and surrounding properties have been resumed by the Water Resources Commission as part of the Windamere Dam and Recreation Park, along the Cudgegong River valley. Consequently, parts of the study area including Cudgegong township have, since 1984, been flooded by the infilling Windamere Dam.

GEOLOGICAL SETTING

The Cudgegong-Mudgee district lies near the northeast margin of the Lachlan Fold Belt and comprises sequences mainly deposited on the Capertee High (Fig. 1). In this paper, a detailed stratigraphy is presented for the southeast-trending belt of Late Ordovician to Late Silurian rocks which crops out along the Cudgegong River valley from Mudgee to Cudgegong. The belt is flanked to the northeast and southwest by Devonian sequences whereas in the south, the belt is intruded by the Carboniferous Aarons Pass Granite and unconformably overlain by Permian strata.

There are no known Cambrian rocks in the northeast Lachlan Fold Belt. However, by the Early Ordovician deep water flysch sequences were common with scattered mafic volcanic centres and associated shoalwater limestones developing in the Parkes, Wellington, and Molong areas (Cas, 1983). These conditions continued into the Late Ordovician where the dominant feature in the eastern Lachlan Fold Belt was the north-northwest-trending Molong High — a volcanic arc producing andesitic centres with flanking shoalwater limestones and volcanoclastics in an otherwise flysch-dominated environment (Powell, 1983b; Cas, 1983).

Deformation at the end of the Ordovician apparently continued into the early Middle Silurian (Crook *et al.*, 1973) and heralded the onset of a tensional regime in the

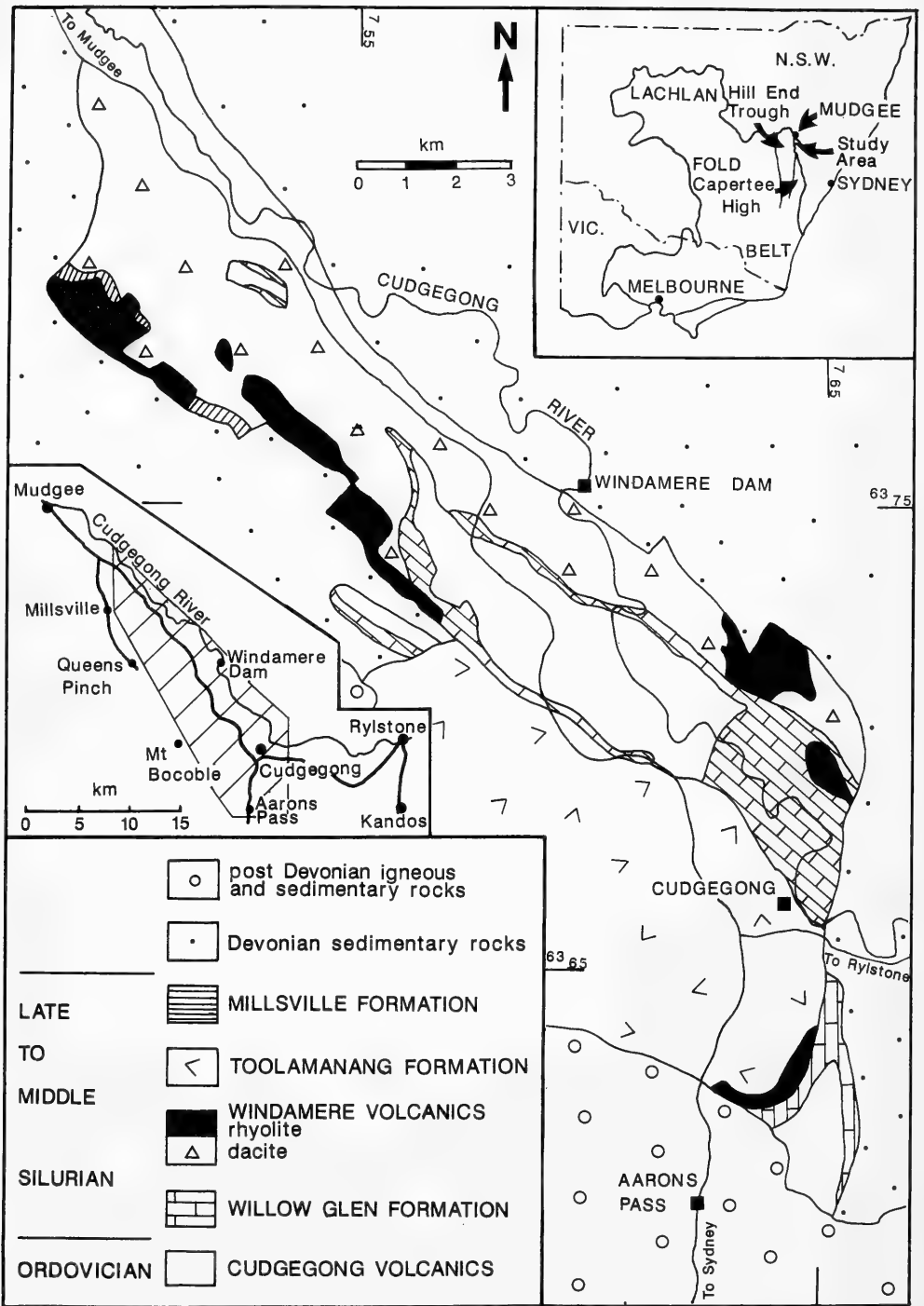


Fig. 1. Ordovician-Silurian geology of the Cudgong-Mudgee district.

Late Silurian which produced regionally extensive silicic magmatism and extensional marine basins (Pickett, 1982b; Powell, 1983b). In the northeast, the deformation initiated rifting of the Molong High producing the opening of the Hill End Trough as a deep-water basin flanked to the east by a rifted fragment which produced the Late Ordovician basement for the developing Capertee High (Gilligan and Scheibner, 1978). Limestones, epiclastics, and extensive silicic volcanics represent Late Silurian shallow marine deposition on both the Molong and Capertee Highs whereas detritus for the infilling Hill End Trough was derived from the volcanism (Pickett, 1982b). On the east margin of the Lachlan Fold Belt, this configuration continued through the Early Devonian.

By the Middle Devonian, much of the Lachlan Fold Belt had been uplifted and intensely deformed, and proven Middle Devonian strata are limited to the Capertee High (Pickett, 1982b). However, there is a marked facies difference between the Early and Late Devonian sequences, accompanied by low angle discordant contacts along the northeast margin. The Late Devonian fluvial and marine conditions (Powell, 1983a) continued into the Early Carboniferous and the orogenic history of the Lachlan Fold Belt concludes with terminal deformation in the late Early Carboniferous (Powell and Edgecombe, 1978; Cas, 1983).

PREVIOUS GEOLOGICAL INVESTIGATIONS

The first major treatment of the geology of the district was that of Game (1935) in which he mapped a wide tract of Silurian and Devonian strata from Mudgee to Aarons Pass and Kandos. He considered that a central belt of Upper Devonian rocks was faulted against Upper Silurian sequences. Mapping by the present author in the southwest Silurian belt has shown that: the sequence includes both Ordovician and Late Silurian rocks; conformable and unconformable contacts exist; the Ordovician-Silurian rocks are folded into a large scale anticline; and the strata may be locally overturned. Clearly this revised stratigraphy greatly affects part of Game's interpretation.

Wright (1966) produced a major contribution to the understanding of the Devonian stratigraphy and faunas and, in particular, to the subdivision of Game's Upper Devonian sequences on the basis of Early and Late Devonian faunas. In addition, he recognized that many of Game's limestones in the Queens Pinch area were, in fact, Early Devonian.

On the Dubbo 1:250 000 geological sheet, Offenberg *et al.* (1971) portrayed, in the Cudgong-Mudgee district, the Devonian sequences of Wright (1966) flanking a central area in which they recognized the Ordovician Sofala Volcanics and the Siluro-Devonian Gulgamree Beds. However, mapping by Powis (1975), Michie (1975) and Pemberton (1977) raised doubts as to the validity of this nomenclature. Recent mapping by the author indicates that the proposed extent of the Sofala Volcanics of Offenberg *et al.* includes both Ordovician basaltic sequences and Silurian dacitic sequences. In addition, Wright (pers. comm.) considers their use of the Gulgamree Beds to far exceed his original description of the unit which, in any case, is probably a lateral equivalent of the Mullamuddy Formation in the Queens Pinch Belt. Most of the sedimentary rocks placed in the Gulgamree Beds by Offenberg *et al.* (1971) are now mapped as the Willow Glen Formation (Pemberton, 1980b).

CUDGONG VOLCANICS (Lavers 1960)

The Cudgong Volcanics, the oldest rocks in the district (Fig. 2), were first mentioned by Lavers (1960) and subsequently by McManus *et al.* (1965). These rocks, to the southeast of Cudgong, have subsequently been described by Pemberton (1980a).

Further mapping has revealed four separate outcrop areas of the Cudgegong Volcanics (Fig. 1; I, II, III and IV from Fig. 3).

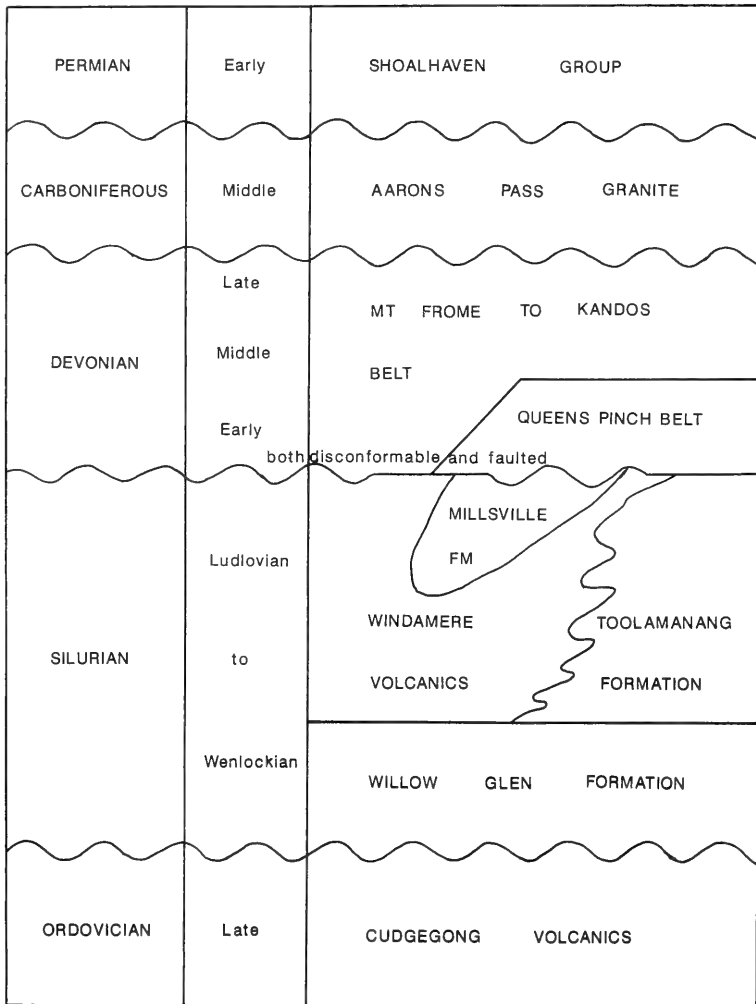


Fig. 2. Stratigraphy of the Cudgegong-Mudgees district.

Stratigraphic Relationships

In each of the four outcrop areas, the Cudgegong Volcanics are unconformably overlain (the contact is not exposed) by the Willow Glen Formation, or are faulted against younger rocks. The base of the Volcanics is not exposed.

The areas consist mainly of fine- to medium-grained andesitic arenite, basaltic rocks being generally rare. Exceptions include: the southeast area (IV) where abundant basaltic textures and compositions are modified by the contact metamorphism of the Aarons Pass Granite; common basaltic arenite throughout the southwest area (II); and the larger central area (III, Fig. 3) which provides the best exposures of the basaltic rocks and andesitic lava. In the northwest of the latter area, lava, with probable pillows, fine- to coarse-grained arenite and breccia together with andesite lava and possible

syenite sills suggest proximity to a basaltic source (Cas and Wright, 1987). To the southeast, near Limestone Creek, there is a fining in fragment sizes within near continuous basaltic exposures and here the fine- to medium-grained basaltic arenite may indicate a more distal aspect from the possible northwest source. The basaltic exposure, near the southwest margin (GR 615695), consists of lava, with probable pillows, arenite and minor breccia.

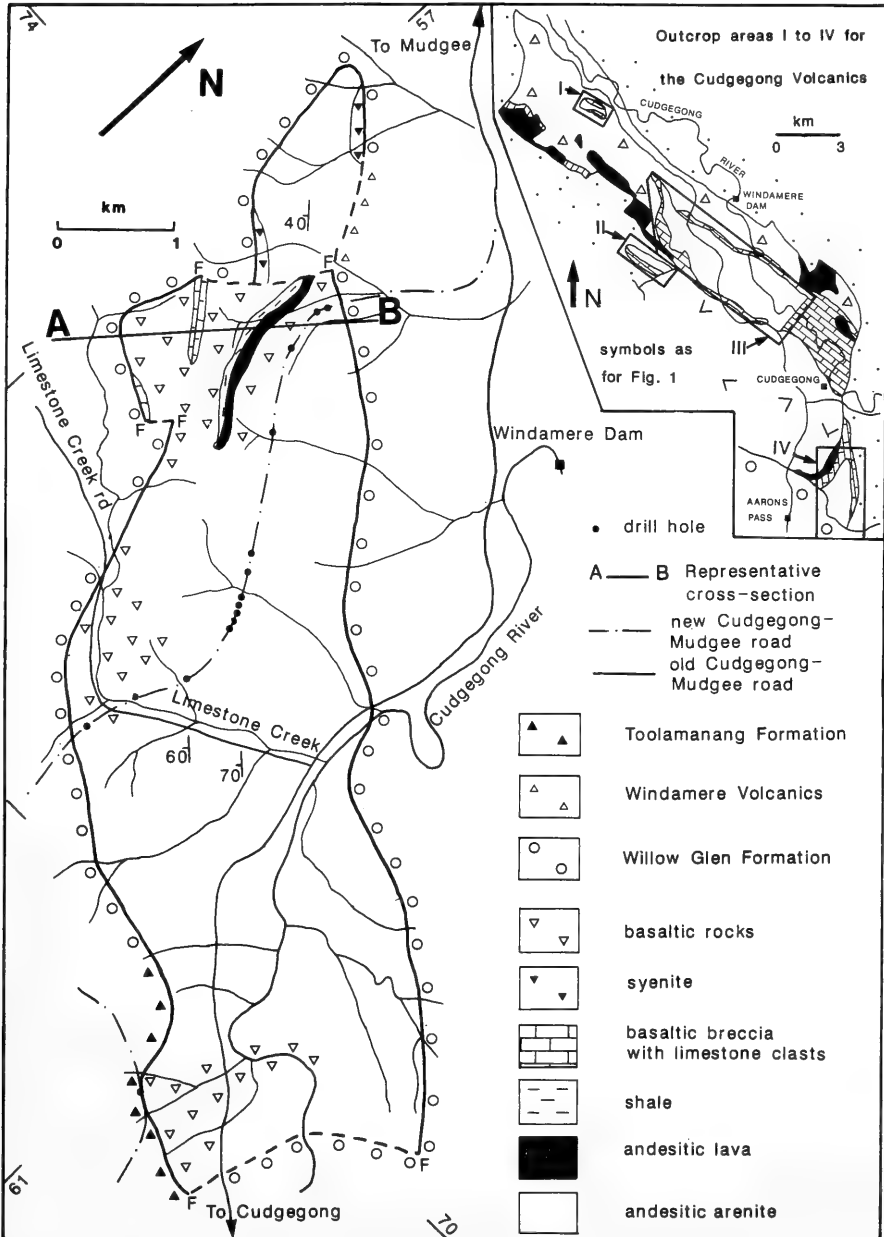


Fig. 3. Geology of the central area (III) of the Cudgegong Volcanics.

All areas display rapid lateral lithological variation and recognition of marker horizons is difficult. The exception is in the northwest of the central area (Fig. 3) where a number of distinctive horizons of the less common rock types are exposed. These include andesite lava, shale, breccia with abundant limestone clasts and syenite horizons.

TABLE 1

Petrography of the main rock types in the Cudgong Volcanics

basalt lava SiO ₂ =48-54% (in basalt to basaltic andesite range)	Porphyritic with phenocrysts of subhedral to euhedral clinopyroxene (glomeroporphyritic, twinned, zoned, diopside to augite, 11 to 34%) to 7mm across; subhedral to euhedral plagioclase (albite, 0 to 18%) to 5mm long; and rare subhedral amphibole (pargasite, X=colourless, Y=light green, Z=green/brown) to 2mm across. Groundmass (50 to 59%) pilotaxitic to cryptocrystalline (usually recrystallised) of albite laths, clinopyroxene and rare amphibole subhedra, tremolite, sphene, chlorite, calcite, epidote and pyrite. Rare ovoid amygdales contain chlorite and calcite. Clinopyroxene chemistry and significance detailed in Pemberton and Offler (1985); relatively unaltered with chlorite and calcite along fractures in cores, and tremolite rims on more altered grains. Albite strongly altered to sericite, chlorite and calcite. Initial glassy groundmass devitrified and now dominated by chlorite and sphene. Calcite, chlorite, epidote, albite, prehnite, pumpellyite and quartz common in porphyroblastic aggregates.
basaltic arenite	Very fine- to very coarse-grained (0.01 to 2mm), moderately sorted in ash fractions to poorly sorted in coarser rocks, immature. Angular (larger grains are more rounded) phenoclasts of clinopyroxene (5 to 35%), plagioclase (albite, 15 to 34%) and rare pargasitic amphibole (0 to 8%); basaltic groundmass clasts (with or without phenocrysts, 19 to 43%). Matrix formed by recrystallisation and devitrification of finest fractions. Minor bedding and clast alignment; erosional contacts between size fractions suggest numerous pulses of activity rather than gravity settling; grain size gradational to basaltic breccia.
basaltic breccia	Very fine sand to cobble size (0.05mm to 10cm, rare boulders to 1m), very poorly sorted, immature. Angular (larger clasts are more rounded) basaltic lava cobbles and boulders; basaltic groundmass clasts (with or without phenocrysts, 26 to 61%); phenoclasts of clinopyroxene (15 to 28%), plagioclase (albite, 3 to 11%) and rare amphibole; limestone cobbles to 15cm and calcite grains to 3mm. Matrix recrystallised and devitrified material. Rare calcite cement. Larger limestone component (cobbles and grains) than basaltic arenite; clast alignment indicates minor current activity; slump deposit emphasised by sorting and clast size decrease away from larger clasts.
andesite lava SiO ₂ =53-57%	Porphyritic with phenocrysts of subhedral to euhedral plagioclase (albite, glomeroporphyritic, 25 to 35%) to 5mm long, and rare subhedral clinopyroxene (0 to 9%). Groundmass (50 to 58%) pilotaxitic, of albite laths with interstitial chlorite and sphene. Albite partially altered to sericite, chlorite and rare calcite. Clinopyroxene grossly altered to calcite and sphene. Original groundmass partly glassy; devitrified and now mainly chlorite and sphene. Porphyroblastic aggregates of calcite, epidote, chlorite and prehnite.
andesitic arenite	Very fine to coarse sand size (0.01 to 3mm), moderately sorted. ash fraction to very poorly sorted in coarser rocks, immature. Angular (larger clasts are more rounded) phenoclasts of plagioclase (albite, 34 to 43%) and rare clinopyroxene; andesitic groundmass (with or without phenocrysts, 36 to 55%). Matrix formed by recrystallisation and devitrification of finest fractions; rich in chlorite and sphene. Minor bedding, clast alignment and size grading indicate some current activity.

Petrography

The Cudgegong Volcanics consist of lavas of basaltic, basaltic andesite and andesitic composition together with associated very fine- to coarse-grained arenite and breccia (Table 1). The rocks show the imprint of prehnite-pumpellyite to greenschist facies metamorphism (Offler and Pemberton, 1983).

Fauna, Age and Correlation

The only recognized fossils in the Cudgegong Volcanics are found in a thin marl, up to 20cm thick, underlying the basaltic breccia with limestone clasts marker horizon in the central area (Figs 3 and 4; GR 568733). Pickett (1982a) identified the coral *Plasmoporella* sp. and the alga *Vermiporella* sp. from autochthonous limestone beds in the marl. Pickett (1978) reported the same coral and alga, together with a Gisbornian conodont fauna, from limestone clasts in a breccia towards the top of the Sofala Volcanics.

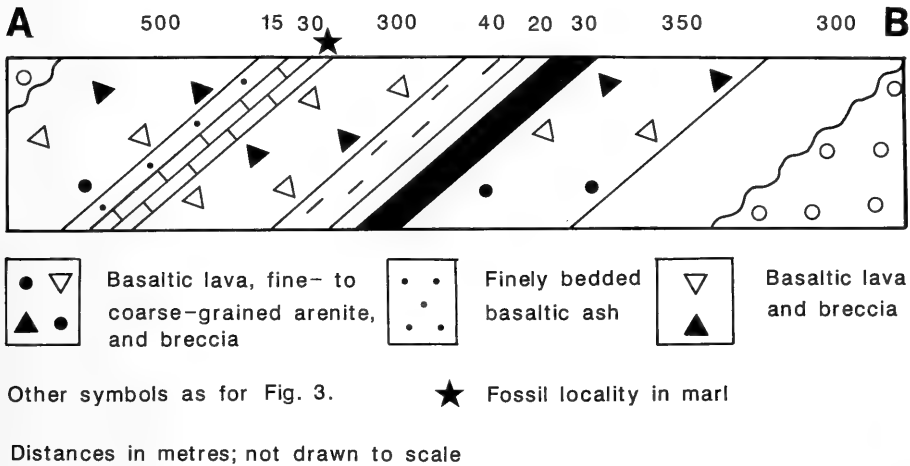


Fig. 4. Representative cross-section through the Cudgegong Volcanics.

The Cudgegong Volcanics are here correlated with the upper parts of the Sofala Volcanics on the basis of similarities in lithologies (Packham, 1968; Barron, 1976; Gilfillan, 1976), clinopyroxene chemistry (Pemberton and Offler, 1985) and fauna. The fauna occurs towards the south margin of the Cudgegong Volcanics where the strata are southwest dipping and apparently upright, and as this suggests the fauna occurs towards the top of the unit, a Gisbornian age is indicated for this part of the Cudgegong Volcanics.

Structure

The Cudgegong Volcanics in the central, northwest and southeast areas (III, I and IV respectively in Fig. 3) form the core of a northwest-trending anticline, with an overturned northeast limb. The southwest area (II) is considered part of a southwest-dipping Ordovician-Silurian block faulted into position against Devonian rocks.

Folding within the Volcanics cannot be recognized. Marker horizons, where present, are traceable only over short distances yet they strike parallel to the contact with the Willow Glen Formation and do not indicate any sequence repetition. In the central area (III), the sequence is apparently simply southwest dipping (data from finely laminated ash, flat bedded arenite and crudely aligned clasts in breccia) and younging, from

the reworked top of an andesitic lava, indicates strata, near the south margin at least, are upright. Possible internal folding hinders attempts to produce a representative section for the Volcanics and as a compromise, a representative cross-section has been compiled for the northwest of the central area (Fig. 4).

Environment of Deposition

The majority of rocks in the Cudgegong Volcanics are immature, grain-supported arenite containing poorly sorted, randomly-oriented angular clasts of their respective lavas forming thick apparently structureless outcrops. The arenites satisfy many of Cas and Wright's (1987) criteria for formation by volcanoclastic debris flow.

The majority of arenites were derived from an andesitic parent; however, the outcrops display no features indicating possible source areas. Exposures of basaltic rocks are limited, yet in the northwest of the central area (III), a possible near-vent location is suggested by outcrops of basaltic breccia with limestone clasts, andesitic and basaltic lava and possible syenite sills which fulfil some of the required near-vent criteria (Williams and McBirney, 1979; Cas and Wright, 1987).

Preservation of limestone clasts in breccia together with the underlying marl in the northwest of the central area (III), calc-silicate and chert horizons in the southeast area (IV), and the identification of probable pillow lava (GR 619696 and GR 580747) indicate a marine environment for both the volcanic and quiescent periods. The autochthonous fauna in the marl indicate that in some areas, at least, shallow marine conditions prevailed.

The data suggest the Cudgegong Volcanics formed by slumping of unstable andesitic and basaltic debris from volcanic island slopes in a subaqueous environment.

WILLOW GLEN FORMATION (Pemberton 1980a)

The Willow Glen Formation, named after the former Willow Glen property 3km southeast of Cudgegong, was initially described and named by Pemberton (1980a). The extensive exposure of the unit was noted by Pemberton (1980b) and in this paper the previous description of the unit is reviewed and expanded.

Stratigraphic Relationships

The formation crops out in a number of separate areas (Fig. 1; areas (a) to (f) in Fig. 5). In each area, the unit is conformably overlain by the Windamere Volcanics (contact clearly exposed in the new Cudgegong-Mudgee road at GR 575748); the exception is the southeast area (f) where it is overlain conformably by the Toolamanang Formation.

The formation consists of conglomerate (dominated by silicic volcanic clasts) grading to pebbly litharenite and litharenite, shale, fossiliferous limestone, and rare rhyolite horizons (Table 2).

In the southeast area (f), Pemberton (1980a) established a sequence of basal litharenite, lower limestone bed (biomicrite with silty interbeds), massive dacitic ash grading to well-bedded shale, and upper limestone bed (biomicrite with abundant silicic volcanic clasts and common pentamerid brachiopods).

To the northwest, the formation differs markedly with the introduction of abundant lensoidal conglomerate horizons and thinly bedded shale and arenite with common limestone lenses. The most complete and representative exposure of these rocks occurs in the eastern portion of the central area (e from Fig. 5). Unfortunately these exposures lie close to the Cudgegong River and now the majority of these, together with several important fossil localities, are covered by the waters of Windamere Dam. Rocks typically exhibit rapid lateral facies change which produces considerable variation in

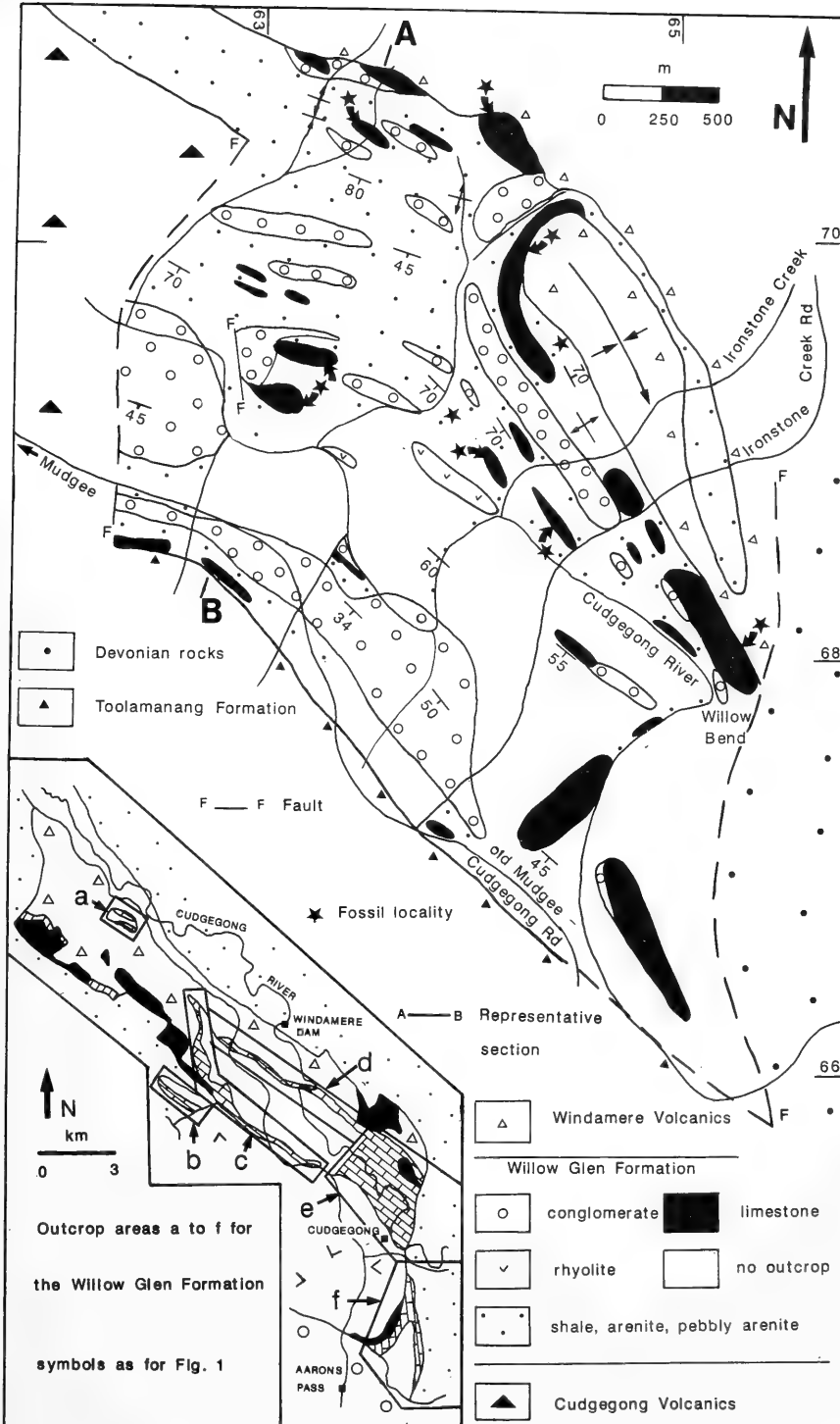


Fig. 5. Geology of the eastern portion of the central area (c) of the Willow Glen Formation.

both thickness and extent of the outcrops. Consequently the prominent conglomerate horizons, within the recessive shale, arenite and limestone, cannot usually be traced as marker horizons for distances greater than several hundred metres.

TABLE 2

Petrography of the main rock types in the Willow Glen Formation

conglomerate	Grey/white to red, very fine sand to cobble size (4cm), very poorly sorted, immature. Subrounded to rounded white and black silicic volcanic clasts (80%), fragmental plagioclase and quartz grains to 3mm, and rare shale, arenite and limestone clasts. Matrix of fragmental quartz and plagioclase; strongly recrystallised. Very fine siliceous cement, commonly with iron oxide or chlorite. Gradational to pebbly arenite. Plagioclase grains altered to sericite and calcite; matrix texture obscured by recrystallisation and abundant secondary calcite veining.
litharenite	Grey/brown to red, very fine- to coarse-grained (2mm), moderately to poorly sorted, immature. Angular to subrounded (larger grains are more rounded) silicic volcanic, plagioclase, quartz and calcite grains with rare shale clasts. Matrix strongly recrystallised; cement siliceous with common secondary iron oxide and chlorite. Common secondary calcite veins and irregular-shaped aggregates mask much of texture.
shale	Grey/brown, very fine-grained siliceous material with rare angular quartz and plagioclase grains to 0.1mm. Abundant aligned secondary white mica.
limestone	Unsorted biomicrite and biosparite, and intrasparite; all with common detrital silicic volcanic clasts, and quartz and plagioclase grains. Silicic volcanic pebbles (3cm) abundant in upper limestone bed of southeast outcrop area. Jones et al. (1987) report oolitic limestone (intrasparite) from GR 652679.

Stratigraphic sections from all outcrop areas are included in Fig. 6. The thickness of section 2 may be exaggerated as the sequence through area (e) is probably repeated by folding. Comparison of these sections has emphasized a number of similarities and differences.

First, the majority of the Willow Glen Formation consists of lensoidal conglomerate, arenite and pebbly arenite horizons within a fossiliferous sequence of thinly bedded shale and arenite with limestone lenses. The two obviously different areas are: the southeast area (f; section 1 of Fig. 6) where conglomerate is absent and shale with limestone lenses are sparse; and at the northwest of area (d) (section 6 of Fig. 6) which is dominated by thick lensoidal conglomerate.

Second, the distinctive pebbly limestone (abundant silicic volcanic clasts and common pentamerid brachiopods) of the upper limestone bed, southeast area (f) also occurs in the limestone horizon in the southwest area (b); the southeast limestone bed of area (c) (GR 612698); and numerous limestone lenses in the eastern portion of the central area (e). Similar limestones are not recorded in the northwest of the district.

Third, the thickness of the sections and the outcrop width of the areas varies dramatically and this suggests that the top of the formation was not a flat topographic surface, rather that the essentially conformable Windamere Volcanics filled erosional or nondepositional depressions on this surface.

Fauna, Age and Correlation

Numerous fossil localities have been recorded from shales (brachiopods and trilobites) and limestones (brachiopods and corals) in the Willow Glen Formation (faunal

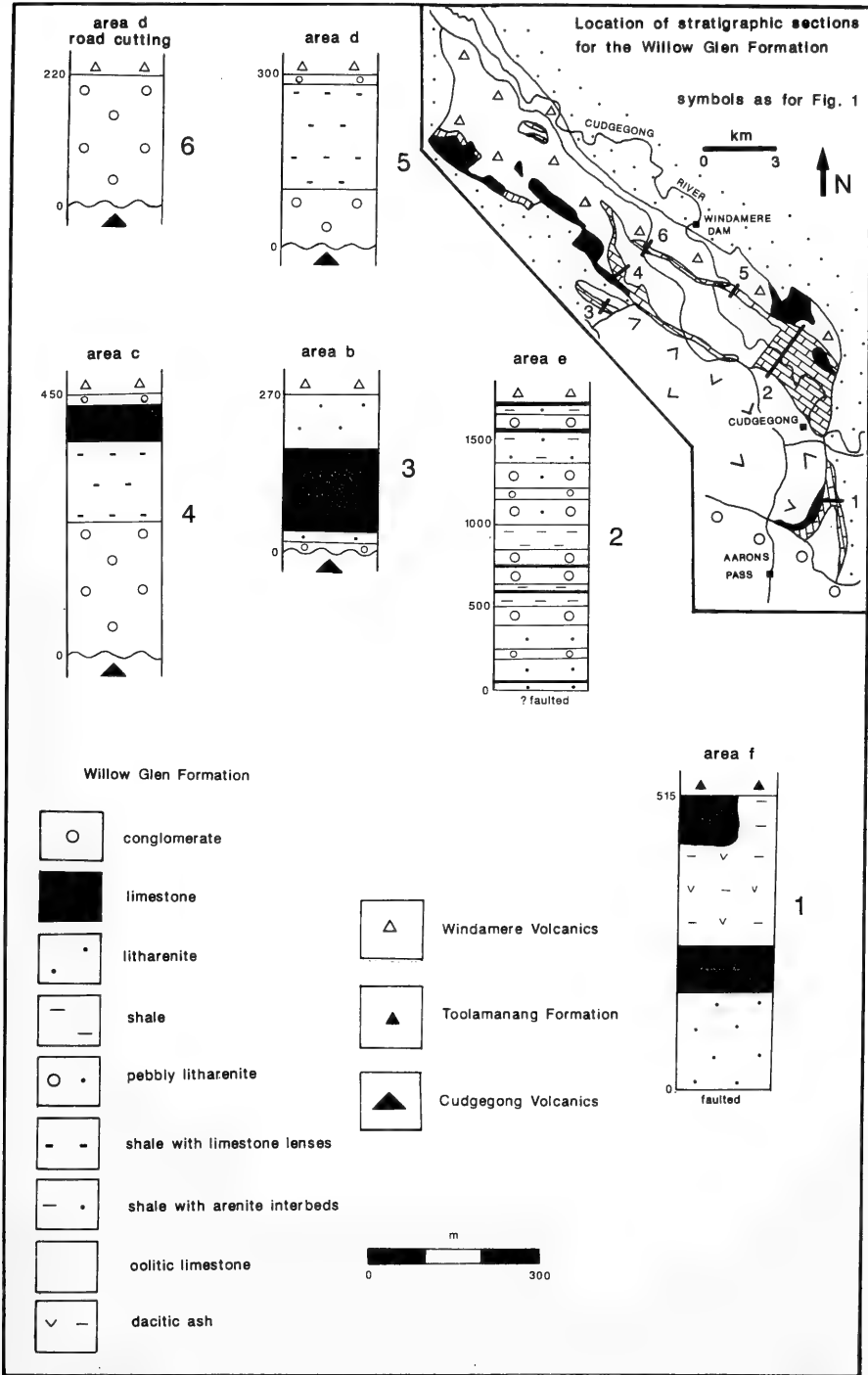


Fig. 6. Representative stratigraphic sections for the outcrop areas of the Willow Glen Formation. No section from the northwest area.

lists in Appendix). Pickett (1982a) proposed a Wenlockian to Ludlovian age based on the identification of the brachiopod *Kirkidium* and the corals *Phaulactis*, *Halysites orthopteroides*, *Desmidopora multitabulata*, and *Pycnostylus scalariformis* from the limestone localities. Recovery of conodonts from limestone samples was low with the best-preserved specimens being referable to *Ozarkodina ranuliformis*, a species considered to occur over a broad Silurian age in Australia (Pickett, 1982a).

Strusz (pers. comm., 1984) recognized that the Willow Glen Formation shale fauna was similar to part of the fauna from Coppin's Crossing, near Canberra (Strusz, 1982). He identified the brachiopods *Salopina ?mediocostata*, *Aegiria* cf. *norvegica*, *Morinorhynchus oepiki* and *Coelospira cavata*, together with *Maoristrophia* (Strusz, 1983) and the trilobite *Encrinurus mitchelli* (Strusz, 1980). He suggested a Late Wenlockian to Early Ludlovian age for the fauna.

Silurian sedimentary sequences unconformably overlie Sofala Volcanics equivalents at at least four known localities: Sofala and east of Wattle Flat (Packham, 1968); Palmers Oakey (Powell, 1984, based on Bischoff and Fergusson, 1982) and now at Cudgegong. In the Sofala-Wattle Flat area, Packham (1968) identified a coral-trilobite-brachiopod fauna, with sparse graptolites, from the Tanwarra Shale. Based on tentative identification of the graptolites, he suggested the Tanwarra Shale may be as old as Late Llandovery. However, in the Tanwarra Shale equivalents at Palmers Oakey, Bischoff and Fergusson (1982) recognized a very Late Wenlockian age for an extensive conodont fauna. The Late Wenlockian to Early Ludlovian age proposed for the Willow Glen Formation, after Pickett's and Strusz's faunal identifications, is consistent with the age of the strata at Palmers Oakey and perhaps the age of the Tanwarra Shale at Sofala.

Structure

The southeast, northwest and central areas (f; a; and c, d and e respectively from Fig. 5) lie on the limbs of an anticline whereas the southwest area (b) is part of an Ordovician-Silurian block faulted against Early Devonian strata.

In both the southeast and northwest, bedding data are limited and mapping of formation boundaries and age relationships indicate the anticlinal structure. Bedding data from the upright southwest-dipping area (c) have a mean limb dip of 35° with a modal strike of 315° whereas data from the southwest-dipping overturned (facing from cross-bedded pebbly arenite) areas (d) and (e) have a mean dip of 75° with a modal strike varying from 310° to 320°. Combined limb data indicate a near-horizontal fold plunge with both southeast and northwest plunge components. Within-limb parasitic folding is common, with similar fold styles and plunge to the large scale structure.

Environment of Deposition

Conglomerate, arenite and pebbly arenite horizons

These horizons have many features indicative of a fluvial channel-fill origin. These include the very poorly-sorted yet well-rounded nature of the clasts; common interbedding of lithologies producing flat lamination, with clast alignment in the coarser beds; cross-bedding with pebbles aligned parallel to, and with fining upwards sequences in, the cross beds as well as low angle beds asymptotic to the cross-bed base; and their lensoidal shape. The lenses vary greatly in thickness (a few metres up to 200m) and lateral extent (10m up to several km) providing evidence for an extensive channel system preserving single channel-fill events (thickness in the order of 5m) as well as multiple channel-fill build-up.

Shale and arenite with limestone lenses

Strusz (pers. comm., 1984) noted the faunal and lithological similarity of these

rocks to the strata near Coppin's Crossing, Canberra (Strusz, 1982). He considered the latter to represent Boucot's (1975) benthic assemblage 3 — the subtidal zone with both quiet and rough water reef communities below 6m water depth. The thinly bedded fossiliferous shale, arenite and *in situ* limestone of the Willow Glen Formation represent a dominantly quiet water, low energy environment. The thicker lensoidal limestones may indicate local mounds with rough water conditions, as indicated by the pentamerid-coral fauna (Boucot, 1975), and provide the higher velocity currents necessary to transport and deposit the silicic volcanic pebbles typical of some of these limestones.

The detailed study of the strata at Willow Bend (GR 652681 from Fig. 5; Jones *et al.*, 1987) demonstrates a thin clastic regressive unit within open-marine limestone. The basal shale (low energy subtidal environment below storm wave base) is sharply overlain by a very shallow marine oolitic limestone which was later subjected to evaporation on supratidal flats. The sequence was then partly eroded by fluvial scours prior to transgression with initially another localized oolitic limestone and then by more open-marine limestone.

In summary, the majority of the formation represents deposition on subtidal to supratidal flats affected by transgressive/regressive cycles. The overall pattern is one of fluctuating sea level and energy regimes with localized rough water limestone mounds surrounded by quiet water deposition. The inferred flats were incised by fluvial channels accompanying periods of sea-level regression.

Variations

The northwest of area (d) and the southeast area (f) are lithologically different from the majority of the formation. In the former area, thick conglomeratic horizons represent substantial fluvial channel-fill accumulations possibly providing the source direction for the channel system incising the tidal flats to the southeast and southwest. By comparison, in the southeast area, the absence of conglomeratic horizons, and the thick ash/shale and arenite beds with poorly fossiliferous limestone suggest open-marine conditions to the southeast of the tidal flats.

Depositional setting

Comparison of the Willow Glen Formation from the northwest to the southeast of the district indicates a typical 20-25km wide coastal zone, similar to present-day examples along the north and northeast Australian coast, with progression from the fluvial channel zone through a tidal flat to more open-marine conditions.

WINDAMERE VOLCANICS (Pemberton 1980b)

These rocks were included by Offenberg *et al.* (1971) in the Sofala Volcanics. However, recognition of their Late Silurian age and dacitic nature led Pemberton (1980b) to propose the Windamere Volcanics, named after the former property upstream from the Windamere Dam wall.

Stratigraphic Relationships

The formation crops out to the northwest of Cudgegong initially as a 1km-wide belt which widens northwest of Windamere Dam reaching a maximum width of 4km in the Millsville area (Fig. 1). These exposures lie on the limbs of the major northwest-trending anticline and have been described (data summarized in Table 3) as the northern limb (Fig. 7) and southern limb (Fig. 8).

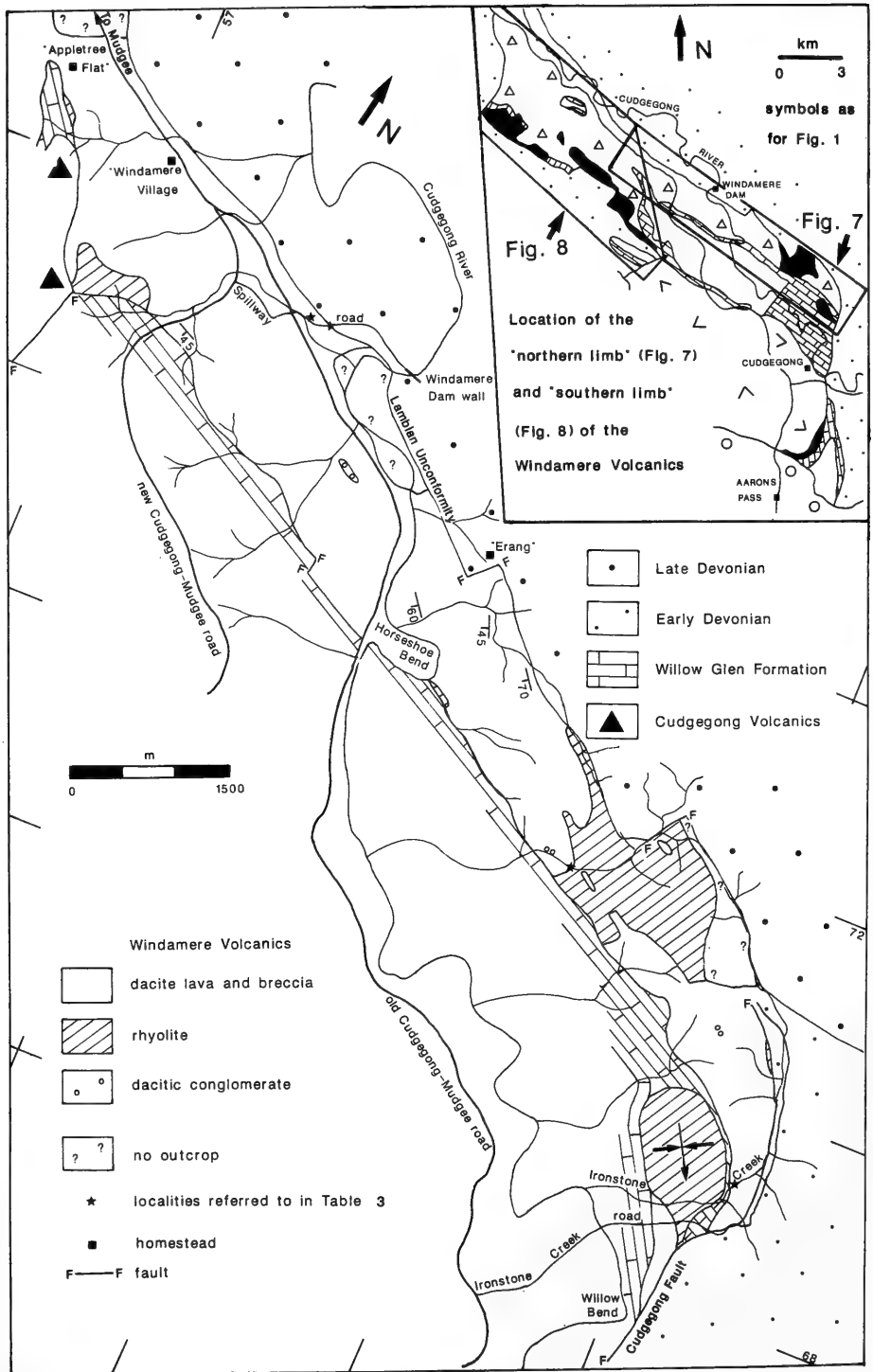


Fig. 7. Lithological variation for the northern limb of the Windamere Volcanics.

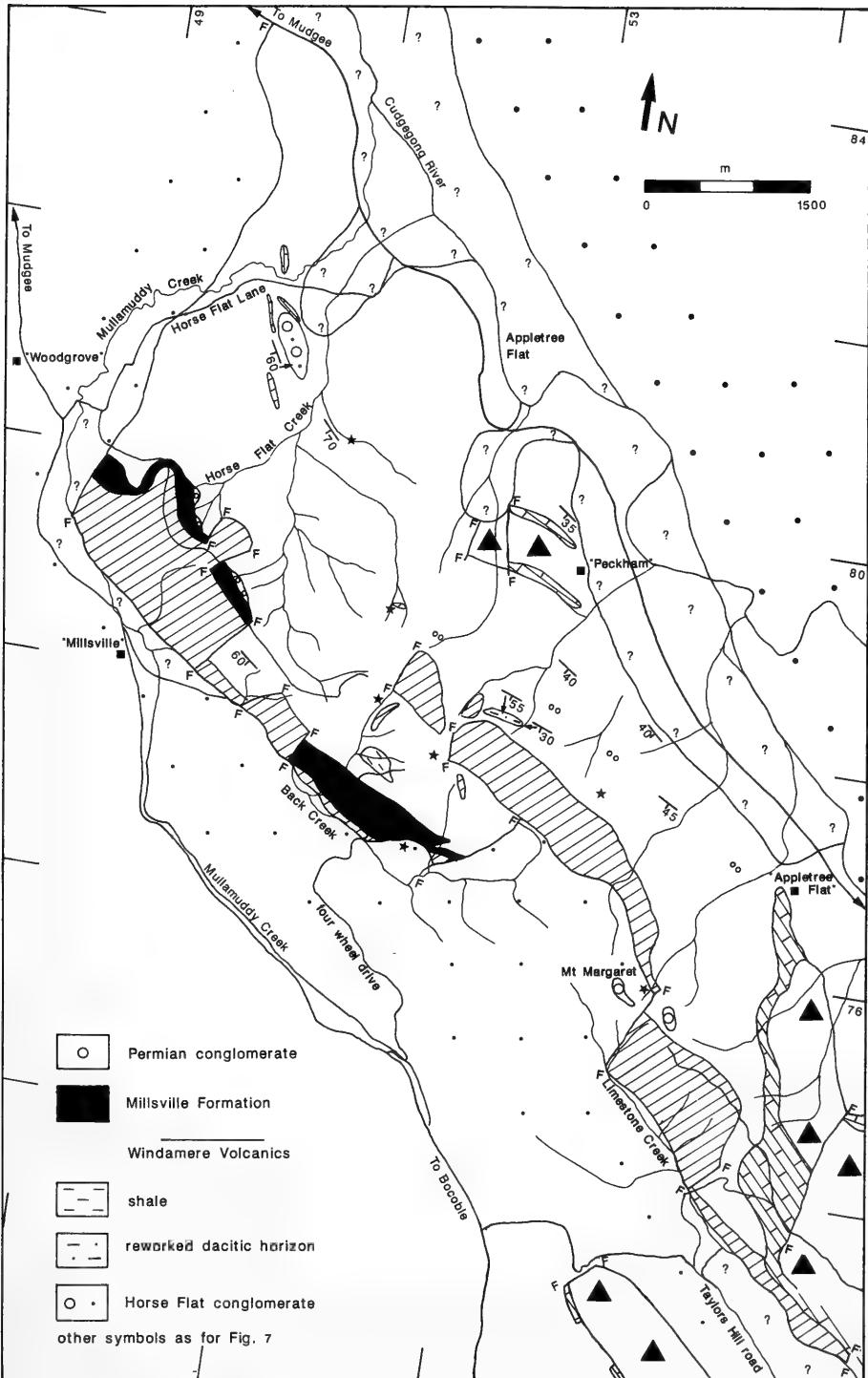


Fig. 8. Lithological variation for the southern limb of the Windamere Volcanics.

Petrography

The Windamere Volcanics are characterized by thick and extensive exposures of undifferentiated dacite lava and breccia, with common rhyolite horizons at all stratigraphic levels (Table 4). Less common rock types include dacitic arenite (with sparse pebbles) to rare ash-size rocks; dacitic conglomerate; dacitic breccia with limestone clasts; flow layered dacite lava; and shale, with rare limestone clasts. Positions in the sequence and best exposures are included in Table 3.

TABLE 3

Extent of and sequence within, the Windamere Volcanics Extent

Northern limb	Overtured limb bounded by unconformity with Late Devonian rocks along Cudgegong River valley and to southeast by Cudgegong Fault. Unit top not exposed yet conformably underlain by Willow Glen Formation over outcrop length.
Southern limb	Provides more complete sequence with both conformable underlying (Willow Glen Formation) and overlying (Millsville Formation) contacts, the latter only in certain northwest localities. The Millsville Formation and rhyolite of Windamere Volcanics are both disconformable and faulted with Early Devonian strata of Queens Pinch Belt.

Sequence and best exposures

Basal sequence	Dominated by dacite lava and breccia. Variations include: numerous conformable rhyolite horizons, to several m thick, both at base and slightly higher in sequence; in Ironstone Creek (GR 657692), 5m of dacitic arenite with limestone and rhyolite clasts, and black shale, with limestone lenses, occur above an initial 20m of dacite lava (contact not exposed); and on Horse Flat (GR 503810) Willow Glen equivalents are sharply overlain by 100m of coarse conglomerate (dacite and rhyolite clasts), pebbly arenite and arenite.
Middle sequence	Dacite lava and breccia dominant (extensively exposed in new road cuttings and dam spillway), with greater diversity of less common rock types. Include: dacite lava with polygonal cooling joints; dacite lava with rounded mafic xenoliths to several cm across; flow layered dacite lava; discontinuous dacitic conglomerate beds; rare dacitic breccia with limestone clasts; coarse dacitic breccia with flow layered clasts to 1m across (GR 522774); common thin conformable rhyolite horizons; and 25m thick reworked dacite horizon (GR 528781) of thinly bedded arenite, shale with sandy interbeds (ripple marks), coarse breccia, conglomerate with arenite beds (cross-beds and scour and fill structures). Facing from sedimentary structures indicate horizon upright.
Upper sequence	Proportion of detrital dacitic rocks increases within dominant dacite lava and breccia. Detrital lithologies include: breccia with limestone clasts; arenite and pebbly arenite; 100m thick shale bed (GR 518774) with rare thin limestone and conglomerate lenses; and 10m thick dacite boulder horizon (GR 518771) only a few m below conformably overlying Millsville Formation.
Rhyolite	Flow layered lava, with rare breccia and conglomerate, occurs at all stratigraphic levels. Thickness varies from few m to 100m, with thicker horizons as prominent ridges. On the southern limb, one such 100m thick apparently conformable body of flow layered lava forms prominent steeply southwest-dipping scarp for 5.5km length. Best conformable contacts with dacite at GR 507777 and GR 630716.

Primary dacite lava is distinguished from the fragmental rocks by the lack of fragmental phenocrysts (rounded, embayed quartz, subhedral to euhedral plagioclase and amphibole); the glomeroporphyritic nature of phenocryst aggregates; the presence of rare amygdaloids; and the clear distinction between phenocrysts and groundmass (15 to 35% phenocrysts with the maximum density 49%). However, recognition of primary

textures is hindered by the effects of prehnite-pumpellyite to greenschist facies metamorphism. Moreover, recrystallization of the groundmass produces granoblastic quartz masses. Further, breakdown of the groundmass varies from the minor development of fine-grained interstitial chlorite to the major development of distinct chlorite-rich and quartz-rich portions, the latter producing a brecciated appearance. Another feature hindering the recognition of primary textures, especially in rocks towards the top of the formation, is the secondary silicification of highly fractured dacitic rocks and the development of siliceous spherulitic concretions in numerous rhyolite horizons.

TABLE 4

Petrography of the main rock types in the Windamere Volcanics

dacite lava SiO ₂ =65-69%	Porphyritic with phenocrysts of subhedral plagioclase (albite, glomeroporphyritic, 11 to 32%) to 5mm long; embayed quartz (fractured, 0 to 6%, fine-grained recrystallised margins) to 3mm across; and rare subhedral to euhedral amphibole (hornblende, 0 to 9%, X=pale brown, Y=light brown, Z=brown/green) to 1mm long. Fine-grained and recrystallised groundmass (51 to 87%) dominated by anhedral quartz and plagioclase. Rare ovoid amygdaloids contain chlorite. Albitised plagioclase phenocrysts and groundmass grains partially altered to chlorite, sericite, epidote, pumpellyite, prehnite and calcite. Chlorite very common in groundmass (to 16%) as interstitial material in less altered rocks, and as irregular-shaped masses, to several mm across, and as pseudomorphs after plagioclase and amphibole in more altered rocks. In the most altered rocks, groundmass segregates into quartz-rich and chlorite-rich portions.
dacite breccia	Very fine-grained to cobble size (0.01mm to 10cm; rare boulders to 1m), very poorly sorted, immature. Angular (rounded larger clasts) dacite lava cobbles and boulders, dacite groundmass clasts, plagioclase and quartz phenocrysts. Matrix of finest sized dacite fragments (dominated by recrystallised quartz and plagioclase). Rare primary calcite cement. Alteration of phenocrysts and groundmass similar to that described for dacite lava. Development of metamorphic textures, in particular breakdown of groundmass, may hinder recognition of primary fragmental nature.
dacite arenite	Very fine-grained to very coarse-grained sand (0.01 to 3mm), poorly sorted, immature. Angular dacite groundmass clasts, quartz and plagioclase phenocrysts, and rare dacite lava clasts. Matrix formed by recrystallisation and devitrification of finest dacitic fraction. Alteration as described for dacite lava and breccia. Sharp erosional contacts between varying grain sizes.
rhyolite lava	Sparsely porphyritic with phenocrysts of embayed quartz (finely recrystallised margins) to 3mm across, and rare subhedral feldspar (strongly altered, untwinned) to 5mm long. Coarsely recrystallised groundmass of polygonal quartz and irregularly-shaped altered feldspar. Common flow layering as compositional banding of quartz-rich and -poor horizons to 5mm thick. Feldspar phenocrysts very strongly to completely altered to sericite and chlorite; groundmass grains less severely sericitised. Spherical siliceous concretions, to 4cm across, are very abundant towards the top of the unit.

Age and Correlation

No fauna has, as yet, been found in the Windamere Volcanics. However, the unit is considered Late Silurian as it is conformably underlain and overlain by Wenlockian to Ludlovian strata — the Willow Glen Formation and the Millville Formation. Rhyolite overlying the latter is disconformably overlain by Early Devonian strata.

In the Sofala district, rhyolite lava, arenite and breccia (the Wenlockian Bells Creek Volcanics of Packham, 1968) conformably overlies the Tanwarra Shale and is overlain conformably by the deep water Chesleigh Formation deposited on the eastern margin of the Hill End Trough.

Structure

The outcrop areas of the Windamere Volcanics lie on the limbs of the major anticline. On the southern limb, facing (from the reworked dacitic horizon and the conformably overlying Millsville Formation) indicates the southwest-dipping sequence is upright. A composite representative section (Fig. 9) has been compiled from the basal contact with the Willow Glen Formation on the Peckham property (Fig. 8), incorporating a number of northeast-southwest traverses, to the uppermost rocks, including the Millsville Formation, below the Early Devonian disconformity along Back Creek (GR 521766). The southwest-dipping strata of the northern limb are considered overturned, based on the relationship with older units as well as cleavage vs bedding orientation.

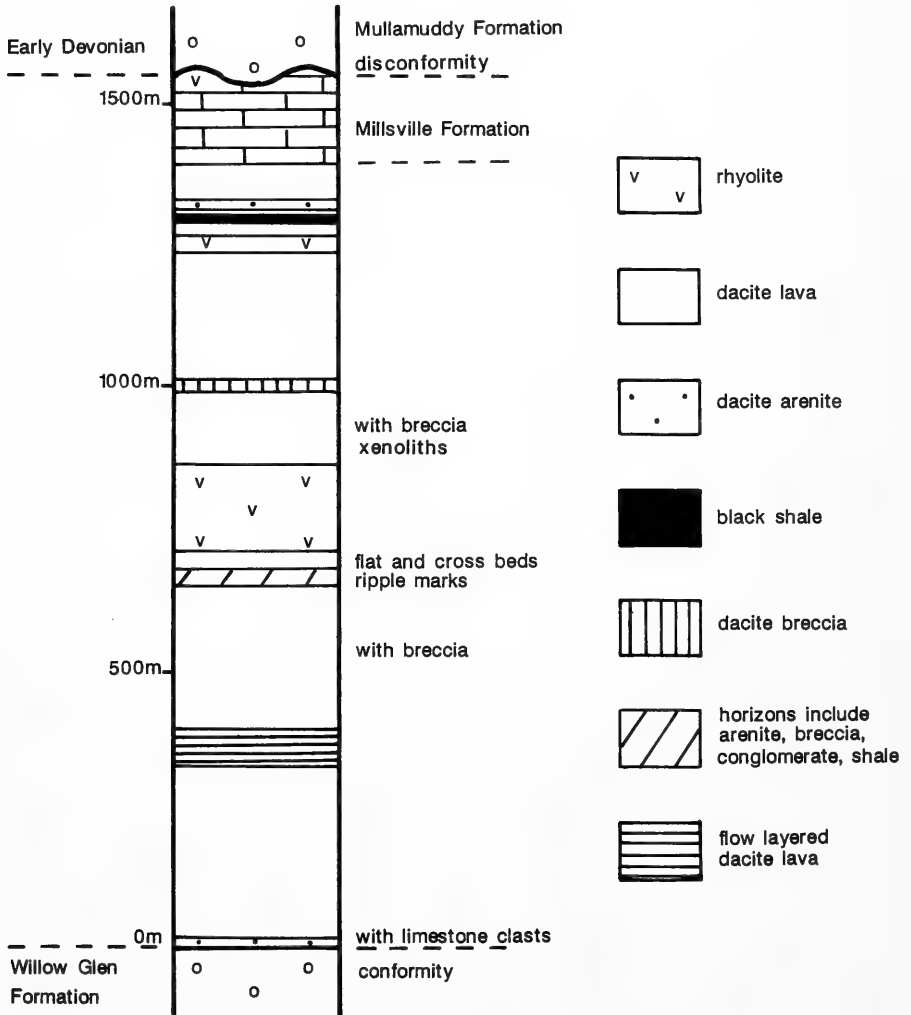


Fig. 9. Composite representative section through the Windamere Volcanics.

Common northeast-trending faults clearly offset rhyolite horizons on the southern limb (Fig. 8), as well as the Millsville Formation; the Cudgegong Volcanics-Willow Glen

Formation sequence; contacts with the Devonian strata and Devonian sequences in the Queens Pinch Belt. A similar pattern of faults affects strata on the northern limb (Fig. 7). The displacement along the faults varies from small scale (several metres) up to hundreds of metres. The faulting is approximately normal to the regional fold axis and probably represents tear or compartmental faults (Davis, 1984) which formed during the regional folding and acted as transverse strike-slip faults accommodating the deformation of a thick rock mass.

Environment of Deposition

The eruptive environment, at least during periods of volcanic quiescence, is considered to have been shallow marine to probably emergent. Evidence includes: shale, with apparently *in situ* limestone lenses, at the base and top of the unit; shale, arenite and breccia, all with limestone clasts; and traction current structures (in the reworked horizon [GR 528781]) indicating fluctuating energy conditions in a shallow marine environment. In addition, the lensoidal conglomeratic body on Horse Flat (GR 510815, Fig. 8) together with other common conglomeratic lenses (Table 3) suggest a fluvial channel origin. Further, the underlying Willow Glen Formation was deposited in a shallow marine to supratidal environment with regression to subaerial conditions and the overlying Millsville Formation includes shallow marine and beach deposits.

The eruption of silicic lava into a shallow marine to subaerial environment should produce dominantly pyroclastic detritus with short thick lava bodies of limited aerial extent (Cas and Wright, 1987). However, the Windamere Volcanics are dominated by dacite lava, with less common breccia and rhyolite horizons.

An explanation for the high volume of dacite lava could be emplacement as a lava dome. The growth of silicic domed masses around vents, and shallow intrusions (cryptodomes), is preceded by highly explosive activity followed by long periods of non-explosive dome growth capable of producing thick lava masses. Recent subaerial examples include activity at Mt St Helens (Swanson *et al.*, 1987), the islands of Lipari and Vulcano (Sheridan *et al.*, 1987) and the South Sister volcano (Scott, 1987). The initial explosions decrease the volatiles available for later magmatic pulses thus providing the degassing mechanism for emplacement of thick non-explosive lava bodies (Fink and Manley, 1987). However, Newhall and Melson (1983) record numerous examples of post-dome explosions which activated partial dome collapse and led to autobrecciation of parts of the lava body.

If the Windamere Volcanics were emplaced as a thick domal body, the initial degassing mechanism may have produced the fragmental material of the Toolamanang Volcanics, a lateral mass-flow equivalent of the Windamere Volcanics. The common breccia may have formed from later explosive events causing autobrecciation by small scale dome collapse. In this model the abundant conformable rhyolite horizons could be either extrusive (with the thicker bodies towards the top of the volcanics representing terminal activity) or emplaced as contemporaneous sills.

TOOLAMANANG FORMATION (Pemberton 1980a)

The unit was named after the historic Toolamanang property, south and southwest of Cudgegong. To the southeast of Cudgegong, Pemberton (1980a) recorded rhyodacite lava, breccia and arenite (the Toolamanang Volcanics); these rocks had been assigned by Offenberg *et al.* (1971) to the Sofala Volcanics. Subsequent mapping to the southwest of Cudgegong (Pemberton, 1980b) revealed much greater exposure of the unit with a lack of primary volcanic features; thus the original description of the Toolamanang Volcanics has been considerably modified.

Stratigraphic Relationships

To the southeast of Cudgong, the Toolamanang Formation overlies the Willow Glen Formation with apparent conformity (Pemberton, 1980a). However, to the north-west along Limestone Creek valley, the unit is faulted against Ordovician and Silurian rocks where the contact is marked by a prominent ferruginous zone tens of metres thick.

The unit crops out over 14km in length with a width up to 5km (Fig. 1). Near Mt Bocoble, an apparently conformable overlying contact is exposed with limestone (with pentamerid brachiopods and halysitid corals), breccia (limestone clasts in a sandy matrix), conglomerate and shale which resemble, from the fauna and lithology, parts of both the Willow Glen Formation and Millsville Formation. To the southeast of Mt Bocoble, this contact is poorly exposed and the overlying rocks are discontinuous unfossiliferous limestone beds.

Lithologies

The Toolamanang Formation is a massive, structureless succession of fine- to coarse-grained arenite with common black mud horizons and sporadic basaltic outcrops. The main rock types consist of dacitic detritus as lithic arkose and feldspathic litharenite; with common very fine ash size rocks and fine-grained breccia. The rocks are texturally similar, being very poorly sorted with angular plagioclase (albite), less common quartz and rare hornblende fragments, up to 3mm across, and a highly variable content of dacite groundmass clasts ranging from several mm to 3cm across. Clasts are tightly packed, with a recrystallized matrix of fine dacitic detritus. Lithological variation in the succession, in which no sequence or marker horizons could be established, is minor and involves rapidly varying grain sizes. Basaltic blocks, petrographically and chemically similar to basaltic rocks in the Cudgong Volcanics (Pemberton and Offler, 1985) occur throughout the unit, varying in size from tens of centimetres up to 3m across.

The best exposures occur in several cuttings on the new Cudgong-Mudgee road (GR 631661 to GR 618681) and their associated drill cores. They are dominated by fine- to coarse-grained arenite with massive black mud (fine-grained dacitic ash) beds, from several cm to 1m thick. The bases of the sandy horizons show loading and slumping of the sand squeezed and injected into the mud whereas the tops are generally flat and sharp. Several of the basal zones, which vary from a few cm to 1m thick, have a disoriented fabric of irregularly-shaped sandy masses representing intensely churned and squeezed sand within the mud layers. Fine-grained breccia patches (with randomly aligned arenite and black mud clasts) and angular and rounded basaltic blocks are common.

Both the cuttings and the cores show: firstly, that the basaltic material is fragmental, varying greatly in size and that this material has been deposited in the muddy and sandy detritus; and secondly, that the grain size of, and thickness of the units within, the dacitic detritus varies rapidly, indicating multiple depositional episodes, and that contacts between units are sharp and show evidence of loading and slumping.

Age and Correlation

No fauna has, as yet, been found in the Toolamanang Formation. The unit is considered Late Silurian on the basis of the Wenlockian to Ludlovian age of the conformably underlying Willow Glen Formation and the preliminary dating of the fauna from overlying limestone near Mt Bocoble as Late Silurian.

Lithologies in the formation consist principally of volcanic detritus of similar composition to dacite lava, the dominant rock type in the Windamere Volcanics. Together with similarities in age and underlying and overlying formations, the

Toolamangang Formation is considered a lateral equivalent, and fragmental version, of the Windamere Volcanics.

Correlatives of the Windamere Volcanics, the Bells Creek Volcanics (Packham, 1968) and the Mullions Range Volcanics on the Molong High (Hilyard, 1981); both contain a high proportion of fragmental rhyolitic and dacitic material as does the Toolamanang Formation.

Structure

Rare bedding data display the regional southeast strike with steep southwest dips. R. Oflfer (pers. comm.), in a study to the northeast of the new Cudgegong-Mudgee road (Fig. 1), confirmed the southwest-dipping trend yet he noted dip reversals within and between outcrops indicating small scale southeast-plunging folds.

There has been no attempt to compile a representative section due to the lack of established sequence, the unknown internal structure and the poorly known southern portion of the formation. If the apparently overlying strata are Millsville Formation equivalents, the formation may be simply dipping to the southwest and the 5km outcrop width produces a thickness of approximately 3.5km. Alternatively, the outcrop pattern near Cudgegong suggests a synclinal structure (Pemberton, 1980a) with an upright sequence on the eastern limb and, if the overlying rocks are Willow Glen Formation equivalents, the larger scale structure may be a northwest-plunging syncline with the southwest limb overturned. As a consequence the unit thickness may be nearer 1.5 to 2km.

Environment of Deposition

The pervasive arenite of the Toolamanang Formation consists of angular, poorly sorted, ash- to fine lapilli-sized dacitic detritus in massive structureless outcrops and suggests deposition as an unsorted crystal and lithic ash formed from dense, gravity-driven, volcanoclastic flows (Cas and Wright, 1987).

The black muddy rocks are composed of very fine-grained dacitic detritus and vary from massive bodies to intensely-churned zones formed by slumping and loading of the overlying sands. The rocks suggest deposition as mud flows associated with the coarser ash-flow events. The black mud clasts in the breccia indicate transport of partially lithified mud.

The basaltic rocks are considered part of the Cudgegong Volcanics basement which has been included in the debris flows by erosion, or possibly explosive ejection, from the flanks of the Late Silurian volcano and subsequently transported, with minor reworking, prior to the dumping of the load into the sandy and muddy strata.

There are no direct indicators of a subaqueous or subaerial environment for the debris flows, although the underlying, tentatively overlying and laterally equivalent units exhibit shallow marine to emergent characteristics. The slumping so typical of the arenaceous rocks can occur on fairly gentle slopes and this suggests the detritus was deposited into slightly deeper water conditions than that of the northwest source.

It has been previously implied that the processes which initiated the debris flows of the Toolamanang Formation may have provided the mechanism to erupt the thick Windamere Volcanics lava body. The emplacement of similar silicic bodies produces a variable yet significant volume of pyroclastic material, which acts as the explosive degassing mechanism preceding thick lava growth (Heiken and Wohletz, 1987; Scott, 1987). There is no evidence of explosive activity preserved in the Toolamanang Formation; however, the variable grain size within the thick flow succession clearly represents a large number of flow episodes. It remains to be proven that the episodes

were explosively initiated thus providing the volatile release necessary to allow the Windamere Volcanics emplacement.

MILLSVILLE FORMATION (Powis 1975)

Offenberg *et al.* (1971) included these rocks in the Siluro-Devonian Gulgamree Beds. However, Powis (1975) recognized their Late Silurian age and demonstrated mappable differences from the nearby Early Devonian sequences. He proposed the name Millsville Beds, after the nearby property. Further mapping by Pemberton (1980b, and more recently) has confirmed Powis' ideas and herein the sequence is formally named the Millsville Formation.

Stratigraphic Relationships

There are two main outcrop areas of the Millsville Formation here described as the southeast and northwest exposures (Fig. 10; location from Figs 1 and 8).

The major rock type is breccia with dominantly limestone and minor dacite and rhyolite clasts in a dacitic matrix. Subordinate rocks include: limestone (biosparite and biomicrite); a gradational sequence of shale, arenite and fine-grained conglomerate of calcareous and dacitic detritus; and well-defined dacitic conglomerate and breccia horizons (Table 5). In addition, thick rhyolite lava, with rare breccia, occurs at the top of the formation.

In both areas, the formation conformably overlies dacite of the Windamere Volcanics, with gradational contacts recognized by an increase in fragmental dacitic material and the appearance of limestone lenses and detritus. However, the basal rocks in certain localities in the northwest area are discontinuous (up to 100m long) dacitic conglomerate lenses up to 10m thick (Fig. 10).

The pervasive breccia is present throughout the formation with little lithological variation. Limestone horizons vary from rare thin lenses, from several cm to 1m thick, to several prominent *in situ* bodies up to 300m long with thickness to 100m (Fig. 10). Thinly-bedded fossiliferous shale, and flat-bedded arenite to fine-grained conglomerate occur as discrete horizons or as gradational lenses within the breccia succession.

The northwest area and certain localities in the southeast area are conformably overlain by a persistent rhyolitic succession. The rhyolite and remaining Millsville Formation are disconformably overlain by the Early Devonian Mullamuddy Formation (Fig. 10).

In general, the formation is typified by rapid facies change. Marker horizons are few and include the basal dacitic conglomerate in the northwest area and a prominent 10 to 15m thick dacite breccia horizon, outcropping for over 1.5km length, towards the middle of the southeast area sequence (Fig. 10).

Fauna, Age and Correlation

Powis (1975) reported four fossil localities (Fig. 10), in limestone and shale, to which he assigned a Silurian age. His faunal lists included: limestone — *Phaulactis*, heliolitids, favositids, stromatoporoids, and pentamerid brachiopods; shale — *Halysites cf. bellensis*, *Encrinurus*, *Rhizophyllum*, *Eospirifer*, *Leptaena* together with orthid, atrypid and rhyonellid brachiopods. Pickett (1982a) noted *Kirkidium*, *Thamnopora*, *Amphipora*, and *?Propora*, together with rare conodonts (not age-diagnostic), within the prominent limestone of the northwest area. The fauna is clearly Silurian and the recognition of faunal similarities with the Willow Glen Formation, together with the relationship of the formation to the underlying Windamere Volcanics and the overlying Lochkovian to

Pragian Mullamuddy Formation, indicates a Late Silurian (Wenlockian to Ludlovian) age for the Millsville Formation.

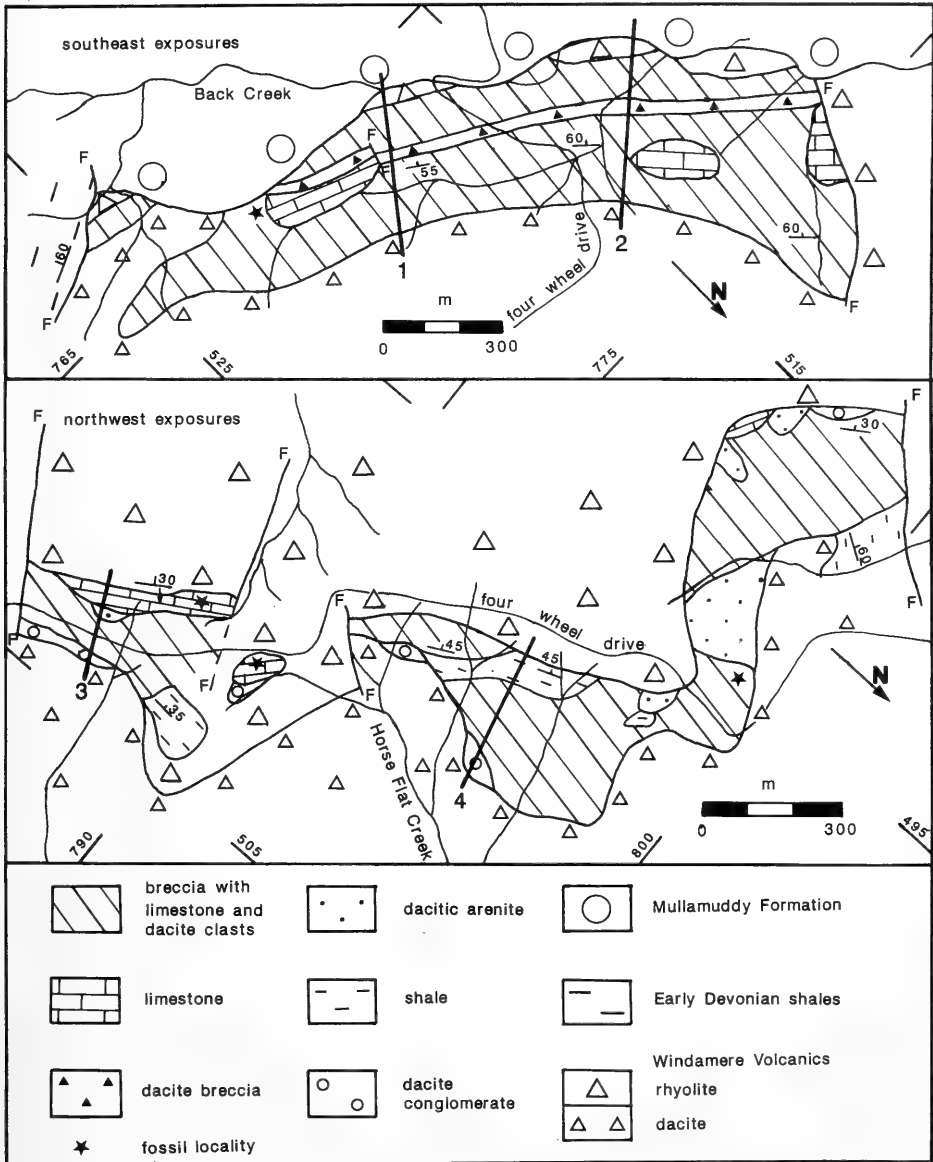


Fig. 10. Geology of the two outcrop areas of the Millsville Formation.

The Ordovician-Silurian sequences at Cudgong and Sofala are similar; however, Windamere Volcanics-Toolamanang Formation equivalents in the Sofala area are conformably overlain by deep water rocks of the Hill End Trough sequence (Packham, 1968). However, in the Cudgong-Mudgee district, Late Silurian rocks overlying silicic volcanic sequences (the Millsville Formation) are deposited in a shallow marine environment.

TABLE 5

Petrography of the rock types in the Millsville Formation

breccia	Grey to pink, very fine sand to boulder size (1m), very poorly sorted, immature. Angular to subangular (larger clasts more rounded) dominantly limestone (poorly washed biosparite with limy mud fraction) clasts, from 5cm to 1m across, with subordinate dacite (lava and arenite), rhyolite lava, shale, and siliceous clasts to 10cm across. Matrix supported; matrix consists of fine- to coarse-grained arenaceous dacitic and calcareous detritus.
limestone	Grey, cream to red; poorly washed biosparite (rich in corals, brachiopods and stromatoporoids) with limy mud horizons; sparse to packed biomicrite; and calcirudite patches (Powis, 1975).
dacitic conglomerate	Grey, fine sand to boulder size (0.5m), very poorly sorted. Rounded to angular dacite lava clasts, from 10cm to 30cm across, with rare boulders to 0.5m. Clast-supported with minor dacitic matrix. No clast alignment. Boulder horizon in southeast exposures similar texture yet clasts angular and coarser.
dacitic breccia	Grey to brown, fine sand to boulder size (0.5m), very poorly sorted, immature. Angular dacite (lava and arenite) clasts from several cm to 20cm across, rarely to 0.5m; with common limestone clasts to several cm across. Matrix supported; matrix of dacitic detritus.

Structure

There is no evidence of folding within the formation. Limited bedding data indicate a consistently southwest-dipping unit up to 220m thick. Further, geopetals (brachiopod and stromatoporoid orientations) in the limestone indicate upright horizons. Consequently four representative sections (Fig. 11, locations from Fig. 10) have been produced for areas of best exposure. Horizons within each outcrop area may be crudely correlated; however, it is not possible to correlate between outcrop areas.

Environment of Deposition

The appearance of limestone and shale horizons at the top of the Windamere Volcanics signals the start of volcanic quiescence in a shallow marine environment. The basal dacitic conglomerate does not show features indicative of a fluvial channel origin and the very poorly sorted, clast-supported lenses are likely to represent beach deposits.

The autochthonous limestone bodies contain a distinctive pentamerid brachiopod-coral fauna typical of rough water limestone bank or mound communities (Boucot, 1975) on a shallow marine shelf. The shale horizons (*in situ* coral growth and a low degree of brachiopod and trilobite fragmentation) formed during quiet water periods and together with the limestone represent bank to lagoonal deposition.

The pervasive breccia suggests collapse of the limestone banks, possibly due to storm activity, and the subsequent dumping of this material into dacitic detritus in slightly deeper water.

The Millsville Formation represents deposition on a shallow marine shelf where initially extensive bank to lagoonal areas, with minor beach deposits, were subsequently affected by limestone bank collapse into slightly deeper water.

Persistent volcanism was then resumed as thick rhyolite masses conformably overlie the shelf deposits, especially in the northwest area.

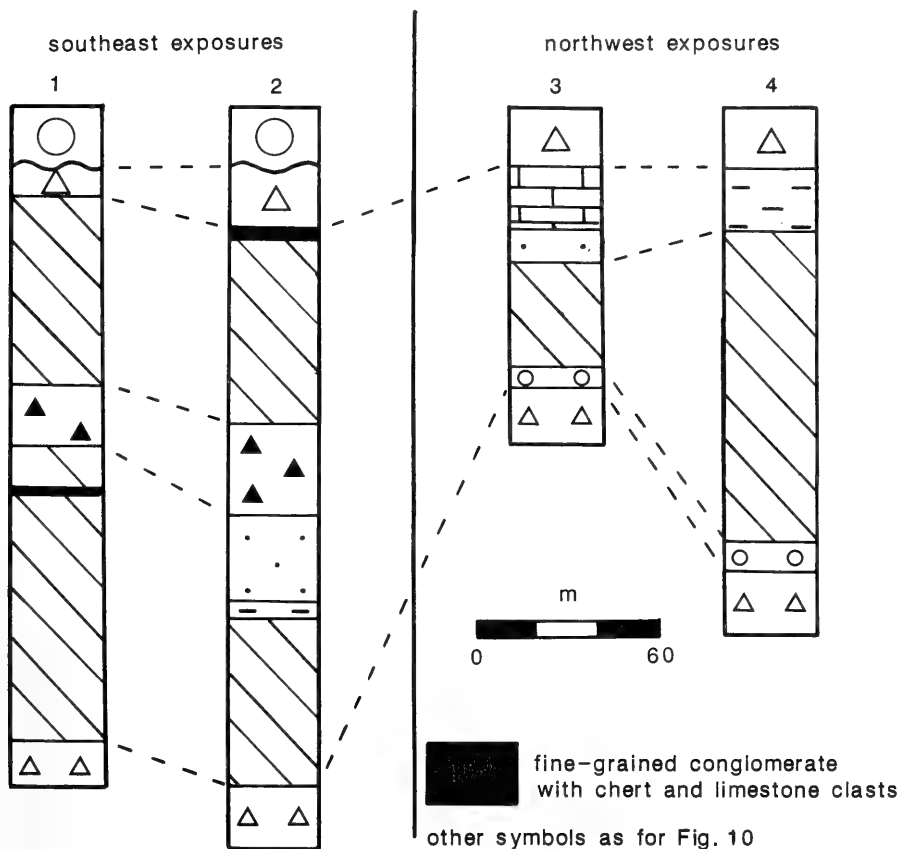


Fig. 11. Representative sections through the Millsville Formation.

DISCUSSION

Nature of the Contacts with the Overlying Strata

Wright (1966) recognized that the Ordovician-Silurian sequences, described in this paper, separated two belts of Devonian rocks — the Queens Pinch Belt and the Mt Frome to Kandos Belt (Fig. 12).

Queens Pinch Belt (Carne and Jones 1919)

The belt consists of a number of fault-bounded slices of Early Devonian shelf and turbidite facies rocks deposited on the western margin of the Capertee High (Wright, pers. comm. and in Strusz, 1972). Contacts with the Ordovician-Silurian rocks are mainly faulted, particularly in the Limestone Creek area; however, disconformable contacts have been identified between the oldest unit in the Queens Pinch Belt, the Lochkovian to Pragian Mullamuddy Formation, and the Wenlockian to Ludlovian units — the Windamere Volcanics near Mt Margaret (GR 545757) and the Millsville Formation along Back Creek (GR 520765).

Immediately north of Mt Margaret, the top of the Late Silurian rhyolite has been reworked and at the base of the Mullamuddy Formation, a black shale, up to 1.5m thick,

containing abundant rhyolite clasts grades up to an *in situ* limestone horizon. Near Back Creek, the base of the Mullamuddy Formation has eroded deeply into the Millville Formation as the contact cuts through rhyolite and breccia successions as well as the prominent dacite breccia horizon (Fig. 10). Here, the Mullamuddy Formation is a breccia of unsorted rhyolite and limestone cobbles and boulders.

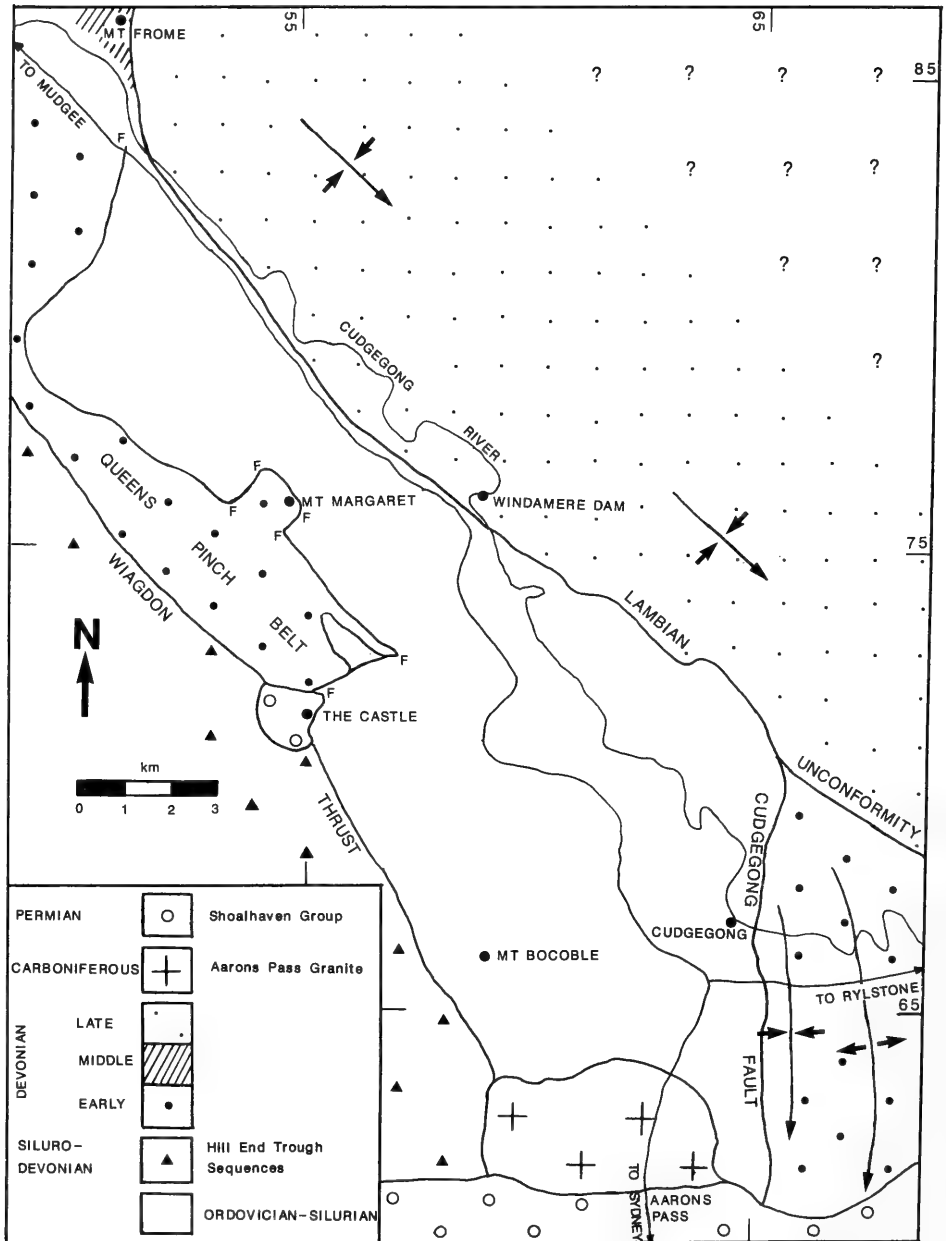


Fig. 12. Post-Silurian geology of the Cudgong-Mudgee district.

Mt Frome to Kandos Belt

The belt comprises a thick sequence of Late Devonian fluvial and shallow marine successions (Wright, 1966) together with Early Devonian shallow marine sediments and volcanics in the Cudgegong-Rylstone district (Pemberton, 1977; Campbell, 1980; Millsted, 1985; Cook, 1988; Colquhoun, 1989).

Cudgegong Fault (Game 1935)

Game (1935) proposed a large scale strike-slip fault (the Cudgegong Fault) separated Ordovician-Silurian and Devonian sequences along the Cudgegong River valley and to the southeast of Cudgegong. Pemberton (1980a) and Millsted (1985) have confirmed a faulted contact between Late Silurian and Early Devonian strata from the Permian plateau to the headwaters of Ironstone Creek (Figs 5 and 12). Evidence for the Cudgegong Fault in this area includes the truncation of folded Early Devonian units and several members of the Late Silurian sequence. The fault plane is marked by a thick linear ferruginous zone and a restricted fault breccia. In addition, C. L. Fergusson (pers. comm., 1987) noted the development of a prominent zone of tectonic melange in a road cutting (GR 652653) on the Cudgegong-Rylstone road along the line of the fault.

Lambian Unconformity (Powell and Edgecombe 1978)

A low angle discordance between the Late Devonian Lambie Group and a variety of older rocks, the Lambian Unconformity, has been recorded from numerous localities in the northeast Lachlan Fold Belt. In the Mudjee district (Fig. 12), the basal Late Devonian unit, the Buckaroo Conglomerate of Wright (1966), crops out continuously from Mt Frome to the Carwell Creek district.

Near Mt Frome, Powell and Edgecombe (1978) record an angular discordance of 5° to 24° where the Buckaroo Conglomerate overlies the latest Early to early Middle Devonian sequence (Garratt and Wright, 1988). To the southeast, the contact is covered by the Cudgegong River floodplain. An exception exists near the Windamere Dam spillway where the Lambian Unconformity can be recognized along the road from the spillway to the observation deck. Here the top of the Windamere Volcanics is represented by 5m of intensely weathered dacite in sharp contact with the northeast-dipping Buckaroo Conglomerate. Gross (1982) noted a discordance of up to 28° with the Buckaroo Conglomerate.

To the south of Cudgegong, the Ordovician-Silurian strata are intruded by the Middle Carboniferous (320 Ma, Vickary, 1983) Aarons Pass Granite, a massive biotite granite/adamellite stock of 10km diameter. The strata are unconformably overlain by thin flat-lying veneers of Sydney Basin outliers at Aarons Pass, Mt Margaret, the Castle and Mt Bocoble (Fig. 12). At these localities, polymictic conglomerate and pebbly litharenite represent the basal unit in the Snapper Point Formation of the Shoalhaven Group (Bembrick, 1983).

Geological History of the Cudgegong-Mudjee District

Ordovician

The oldest rocks in the Cudgegong-Mudjee district, the Late Ordovician (Gisbornian) Cudgegong Volcanics consist of basaltic and andesitic arenite, breccia and rare lava associated with volcanoclastic debris flows on the flanks of submarine volcanoes with fringing shallow marine areas. These rocks are correlated with the upper parts of the Sofala Volcanics in the Sofala district. Other strata tentatively assigned an Ordovician age on the northern Capertee High are flysch-like sequences to the northwest (Lue Beds, Offenber *et al.*, 1971) and west of Rylstone (Colquhoun, 1989). The

Cudgegong Volcanics-Sofala Volcanics association constitutes a Late Ordovician volcanic arc providing a number of basaltic and andesitic eruptive centres with fringing shallow water environments, with possibly deeper water flysch conditions to the east.

Silurian

The Cudgegong Volcanics are unconformably overlain by Wenlockian to Ludlovian sequences. Similar contacts occur at Sofala and possibly west of Rylstone, and the absence of Llandoveryan units confirms that deformation of the volcanic arc continued through the Benambran/Quidongan event (Crook *et al.*, 1973; Cas, 1983).

There is a thick and persistent succession of Wenlockian to Ludlovian shallow marine to possibly emergent units exposed in the Cudgegong-Mudgee district. The lowermost unit, the Willow Glen Formation (conglomerate, pebbly arenite and arenite; fossiliferous shale and limestone) was deposited in a southeast-facing coastal environment which included a fluvial channel zone; subtidal to supratidal flats, affected by a series of transgressive-regressive cycles including common incision by fluvial channels; and more open marine shelf conditions.

The conformably overlying Windamere Volcanics-Toolamanang Formation eruptive episode produced up to 1500m of undifferentiated dacite lava and breccia (the Windamere Volcanics) possibly emplaced as a thick lava dome; and between 2 and 3km of fine- to coarse-grained dacitic detritus with common fragmental basaltic blocks (the Toolamanang Formation). The latter unit was produced by dense, gravity-driven volcanoclastic ash- and mud-flows which incorporated eroded basement material. This was followed by a period of volcanic quiescence represented by the Millsville Formation (up to 220m of dominantly limestone with dacitic and rhyolitic detritus) deposited on a shallow marine shelf.

Late Silurian shallow marine sediments with minor dacite/rhyolite lava and fragmental rocks also occur to the north of Mudgee (Armstrong, 1983), west of Rylstone (Colquhoun, 1989) and tentatively northwest of Rylstone (Offenberg *et al.*, 1971). In the Sofala district, equivalents of the Willow Glen Formation (the Tanwarra Shale) and the Windamere Volcanics-Toolamanang Formation (the Bells Creek Volcanics) are known (Packham, 1968); however, they are far more restricted in extent and thickness than on the northern Capertee High. There is no Millsville Formation equivalent in the Sofala district as the shallow marine rocks are conformably overlain by the deep water Hill End Trough sequence.

Post-Silurian

Contacts with the Early Devonian strata are either faulted or disconformable, the latter representing the effects of the Bowning deformational event (Cas, 1983) on the northern Capertee High.

During the Early and part of the Middle Devonian, the deposition of shallow water to emergent, richly fossiliferous sediments with silicic volcanic outpourings continued on the northern Capertee High (Wright, 1966, 1967, 1981); however, the Queens Pinch Belt consists of both shallow and deep water strata at the western margin of the Capertee High, adjacent to the deep water Hill End Trough. The marked facies change to Late Devonian fluvial conditions is preceded by deformation resulting in the Lambian Unconformity. Fluvial conditions, with an increasing shallow marine component, continued possibly into the Early Carboniferous when the effects of the cratonizing Kanimblan deformational event (Cas, 1983) produced folding of the Late Devonian and older rocks, and emplacement of the Middle Carboniferous Aarons Pass Granite.

Neplanation of much of the Cudgegong-Mudgee district took place before the

Early Permian where the thin, flat-lying remnants of the basal Snapper Point Formation of the Shoalhaven Group represent a sandy transgressive shoreline, at the western margin of the Sydney Basin.

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APPENDIX

Faunal Lists for the Willow Glen Formation

Locality Details	Author (Source)	Fauna Recorded and Age
Locality 1 GR 618725; known locally as Woolleys Flat	Pickett (1982a)	corals: <i>Syringopora</i> , <i>Halysites orthopterooides</i> , <i>Desmidopora multitalulata</i> , <i>Pycnostylus scalariformis</i> brachiopods: pentamerids conodonts: <i>Panderodus</i> , <i>Ozarkodina ranuliformis</i> , <i>Distomodus</i> , 'Ozarkodina' <i>media</i> , 'Neoprioniodus' cf. <i>bicurvatus</i> age: Wenlockian to Ludlovian
	Strusz (pers. comm., 1984)	brachiopods: <i>Spirinella</i> , <i>Aegiria</i> cf. <i>norvegica</i> , ? <i>Howellella</i> , <i>Coelospira</i> , <i>Salopina</i> , <i>Stropheodontacea</i> trilobites: <i>Encrinurus mitchelli</i> , proctacean, ? <i>Staurocephalus struzsi</i> (check only) crinoids: <i>Pisocrinus</i> age: Late Wenlockian to Early Ludlovian
Locality 2 GR 642692 to GR 648687; area just west of Ironstone Creek	Pickett (1982a)	corals: <i>Favosites</i> , <i>Heliolites</i> , <i>Tryplasma</i> , <i>Alveolites</i> , <i>Thamnopora</i> stromatoporoids: <i>Amphipora</i> brachiopods: <i>Kirkidium</i> conodonts: 'Ligonodina', ? <i>Lonchodina</i> , <i>Panderodus</i> , <i>Ozarkodina ranuliformis</i> age: Wenlockian to Ludlovian
	Strusz (pers. comm., 1984)	brachiopods: <i>Spirinella</i> , ? <i>Howellella</i> , <i>Coelospira cavata</i> , <i>Salopina</i> ? <i>mediocostata</i> , <i>Morinorhyncus oepiki</i> , <i>Maoristrophia</i> , <i>Leptostrophia</i> trilobites: <i>Encrinurus mitchelli</i> , proctacean corals: <i>Entelophyllum</i> age: Late Wenlockian to Early Ludlovian
Locality 3 GR 563740; just south and west of four wheel drive track north of Limestone Creek	Pickett (1982a)	corals: <i>Phaulactis</i> , <i>Tryplasma</i> , <i>Alveolites</i> stromatoporoids: <i>Amphipora</i> brachiopods: <i>Kirkidium</i> conodonts: <i>Ozarkodina ranuliformis</i> age: Wenlockian to Ludlovian
	Strusz (pers. comm., 1984)	brachiopods: <i>Aegiria</i> , <i>Coelospira</i> , ? <i>Howellella</i> trilobites: <i>Encrinurus mitchelli</i> corals: <i>Halysites</i> , <i>Tryplasma</i> age: Late Wenlockian to Early Ludlovian

Locality Details	Author (Source)	Fauna Recorded and Age
Locality 4 GR 600732; just west of Horseshoe Bend on Cudgegong River	Strusz (pers.comm., 1984)	corals: <i>Cystiphyllum</i> , <i>Tryplasma ?lonsdalei</i> , <i>Phaulactis shearsbyi</i> , <i>Syringopora</i> , <i>Palaeophyllum</i>
	Pemberton (additional specimens identified by A. J. Wright)	corals: <i>Halysites</i> , <i>Favosites</i> , <i>Heliolites</i> age: probably Wenlockian to Ludlovian
Locality 5 GR 653637; in the upper limestone bed just west of track along Oakey Creek, southeast of Cudgegong	Pickett (1982a)	corals: <i>Propora</i> , <i>Tryplasma</i> , <i>Favosites</i> , <i>Phaulactis</i> brachiopods: <i>Kirkidium</i> age: Wenlockian to Ludlovian
Locality 6 GR 560761; approx. 2km west of 'Windamere Village'	Pemberton (identified by A. J. Wright)	corals: <i>Tryplasma</i> , <i>Thamnopora</i> , <i>Phaulactis</i> , <i>Favosites</i> , <i>Halysites</i> brachiopods: pentamerids age: Late Silurian
Locality 7 GR 612698; just north of new Cudgegong-Mudgee road, approx. 3km east of Limestone Creek	Pemberton (identified by A. J. Wright)	corals: <i>Halysites</i> , <i>Favosites</i> brachiopods: pentamerids age: Late Silurian
Locality 8 GR 562717; approx. 1km south of Limestone Creek road, at east margin of southwest area	Pickett (1982a)	conodonts: ' <i>Ligonodina</i> ', ' <i>Spathognathodus</i> ', ' <i>Hindeodella</i> ', ' <i>Ozarkodina denckmanni</i> ', <i>Distomodus</i> , <i>Panderodus</i> , <i>Ozarkodina</i> cf. <i>remscheidensis</i> , <i>Delotaxis</i> cf. <i>elegans</i> , ' <i>Belodella</i> ' <i>triangularis</i> age: very Early Devonian
	Pemberton (identified by A. J. Wright)	corals: <i>Halysites</i> , <i>Favosites</i> , <i>Heliolites</i> brachiopods: pentamerids age: Late Silurian
Locality 9 GR 528796; approx. 0.5km southeast of Appletree Flat, northwest area	Pemberton (identified by A. J. Wright)	corals: <i>Heliolites</i> brachiopods: pentamerids age: Late Silurian

Aspects of the History and Fishery of the Murray Cod, *Maccullochella peelii* (Mitchell) (Percichthyidae)

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Aspects of the history and fishery of Australia's most famous and largest inland freshwater fish, the Murray cod, *Maccullochella peelii*, are briefly reviewed. Information and data on fossil records, the prominence of Murray cod in aboriginal mythology and culture, observations of cod by explorers and early settlers, and the development and subsequent decline of a commercial fishery are presented. Possible factors contributing to the reduced abundance of Murray cod are discussed. It is suggested that overfishing caused a decline between the late 1800's and the 1930's, but that extensive environmental modification of the Murray-Darling river system has adversely affected larval recruitment resulting in the dramatic decline in abundance of *M. peelii* since the 1950's.

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INTRODUCTION

The Murray cod, *Maccullochella peelii* (Mitchell, 1838) is an Australian, native, warmwater, percichthyid fish found naturally throughout most of the Murray-Darling river system (Fig. 1) with the exception of the headwaters of some tributaries in Victoria and southern New South Wales (Lake, 1971).

M. peelii is Australia's, and one of the world's largest freshwater fish. Whitley (1955) stated that Murray cod grow to 1.8 m (6 ft) and 83 kg (182 lb); however, a cod of 113.6 kg (250 lb) is reported to have been captured from the Barwon River near Walgett in 1902 (Noble, 1955). Although cod in excess of 50 kg are rarely captured, small numbers of cod between 20 and 40 kg are regularly taken by experienced commercial and recreational fishermen, particularly in the Darling, Barwon and Edward rivers, the lower reaches of the Murray and Murrumbidgee rivers, Lake Mulwala on the Murray River, and Lake Burrinjuck on the headwaters of the Murrumbidgee River. Because of its size and excellent edible qualities, Murray cod is highly valued by both commercial and recreational fishermen.

Despite its importance, there has been little research into the natural history of *M. peelii*. This paper briefly reviews the part played by Murray cod in aboriginal mythology and culture, the observations made of the species by explorers and early settlers, and the development, decline and current status of the Murray cod fisheries. Possible causes of the dramatic decline in abundance of Murray cod are discussed.

HISTORICAL ASPECTS OF MURRAY COD

Origin and Fossil Records

Most Australian freshwater fishes, including *M. peelii*, are considered to have a relatively recent marine ancestry (Whitley, 1959; Darlington, 1965). MacDonald (1978) suggested that the *Maccullochella* and *Macquaria* groups (both percichthyids) diverged from a common ancestor during a marine stage of their evolutionary development and made separate colonizations of Australian freshwaters.

Hills (1946) recorded fossil Murray cod from diatomaceous earth in the Warrum-

bungle Mountain areas and considered the remains to be not older than Pliocene (started 7 m.y.a.). However, Browne (1972) stated that the basalt overlaying these diatomaceous earths had been dated as Upper Miocene, and Taylor *et al.* (1980) reported Murray cod fossils from diatomite in the Cooma region to be of Miocene age (26-7 m.y.a.). The diatom flora associated with these fossils is of the type found with Lower Tertiary basalts (Gill, 1970) and so the ancestral *Maccullochella* may be up to 60-65 million years old. Hills (1946) stated that the former distribution of *M. peeli* (*M. macquariensis* as used by Hills, 1946, synonymous with *M. peeli*) in the western drainage, as determined by fossil records, was similar to the current distribution.

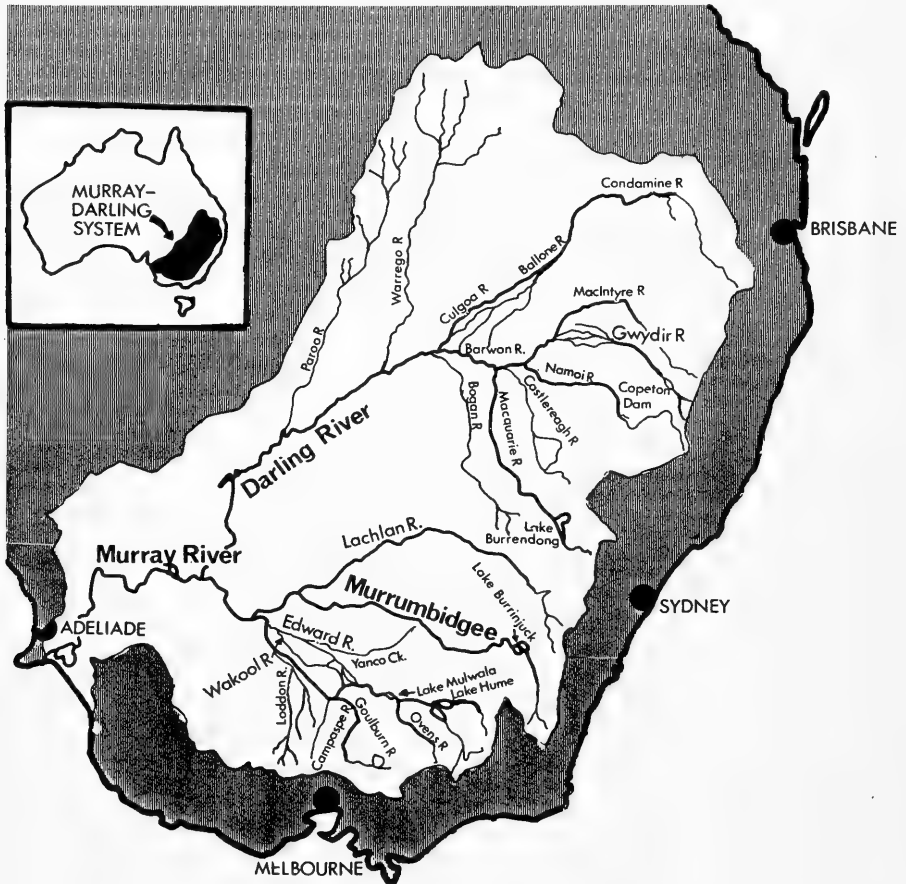


Fig. 1. The Murray-Darling river system.

Aboriginal Mythology and Culture

The Murray cod plays a prominent part in aboriginal mythology (Ramsay Smith, 1930; Berndt, 1940). According to legend, a huge fish, the Murray cod (called 'ponde' by the aborigines*) burst forth from the depths of the earth at the source of the Murray

* According to Ramsay Smith (1930) and Berndt (1940) the aborigines of the lower Murrumbidgee and Murray River regions called the Murray cod 'ponde', but Bennett (1834) states that aborigines in the Yass region on the upper Murrumbidgee River called the river cod 'mewuruk' and the aborigines in the Tumut [sic] country called the varieties of river cod 'bewuk' or 'mungee'.

River, which was then only a small stream of water trickling to the southern ocean. The Murray cod struggled along the narrow stream digging with its head and swinging its powerful tail making the river deep and forming all the bends. Then Nepelle, the Great Prophet, speared it at a site now known as Lake Alexandrina and with the help of the creative hero Ngurunderi, cut it into pieces and threw the fragments into the water, naming them 'tarki' (golden perch, *Macquaria ambigua*), 'tukkeri' (bony bream, *Nematolosa erebi*), 'tinuwarre' (silver perch, *Bidyanus bidyanus*) and all the other fishes of the system. When they had finished they threw the remainder back and said 'You keep on being ponde'.

Murray cod were a major food item of those tribes living adjacent to inland waters (Lawrence, 1971; Tindale, 1981) and as with all animal life, the aborigines made a detailed study of inland fishes, in particular the Murray cod which was considered *the* fish (Ramsay Smith, 1930). The aborigines were excellent fishermen and amazed early explorers and settlers with their prowess. They commonly used spears, nets and poisons to capture their prey, but also constructed different types of traps using brush fences, stones or hollow logs (Bennett, 1834; Lawrence, 1971; Tindale, 1951, 1981).

Explorers and Early Settlers

The inland explorers and early settlers were astounded by the abundance, size and delicacy of the Murray cod or as it was generally known by the pioneers 'River cod' or 'codfish'. The explorer John Oxley (1820) wrote of cod in the Lachlan River 'If however the country itself is poor, the river is rich in the most excellent fish, procurable in the utmost abundance. One man in less than an hour caught eighteen large fish, one of which was a curiosity from its immense size and the beauty of its colours . . . It weighed an entire 70 pounds, . . . Most of the other fish taken this evening weighed from fifteen to thirty pounds each'.

The holotype of *M. peeli*, which has since been lost (Berra and Weatherley, 1972), was collected from the Peel River, N.S.W., by the explorer Major Thomas Mitchell (Mitchell, 1838). There is an excellent drawing, dated 14th December, 1831, of a Murray cod in Major Mitchell's sketch book. Members of the expedition led by Charles Sturt down the Murrumbidgee and Murray rivers, caught and ate Murray cod (Sturt, 1899).

Bennett (1834) wrote that large quantities of the delicious 'River Cod' weighing up to 120 lbs were caught in the Yas [sic] and Murrumbidgee rivers, and in 1863 he recommended to the Acclimatization Society of N.S.W. that every endeavour should be made to propagate them (Bennett, 1864). Murray cod were held in such high esteem that Dr Gunther considered the species worthy of acclimatization in England (O'Connor, 1897) and Ramel (1868; cited in Berra and Weatherley, 1972) suggested that Murray cod be introduced into Europe. Although this did not eventuate, Murray cod were stocked, during the 19th century into many waters where they were not found naturally. These included the Yarra River, Victoria (Wilson, 1857), the easterly-flowing Cox's, Nepean and Wollondilly rivers on the N.S.W. central coast (Phillips, 1863; Hill, 1864), Mulwarree Ponds near Goulburn and Lake George near Canberra (Macleay *et al.*, 1880), the easterly-flowing Mary river system in southern Queensland (S. H. Midgley, pers. comm.), and the Avon River and Lake Grassmere, Western Australia (Morrissy, 1970). Apart from an occasional specimen captured from the upper reaches of the Yarra River, Murray cod are no longer found at any of these sites. The population of cod in the Mary river system is genetically and morphometrically distinct from *M. peeli*, but its taxonomic status has not been determined (Rowland, 1985).

During the 20th century, Murray cod have been successfully stocked into Lake Bathurst and Lake George in N.S.W. (Whitley, 1937), Lake Charlegrark, Green Lake, Taylor's Lake and the Wimmera River, in the western Wimmera region of Victoria

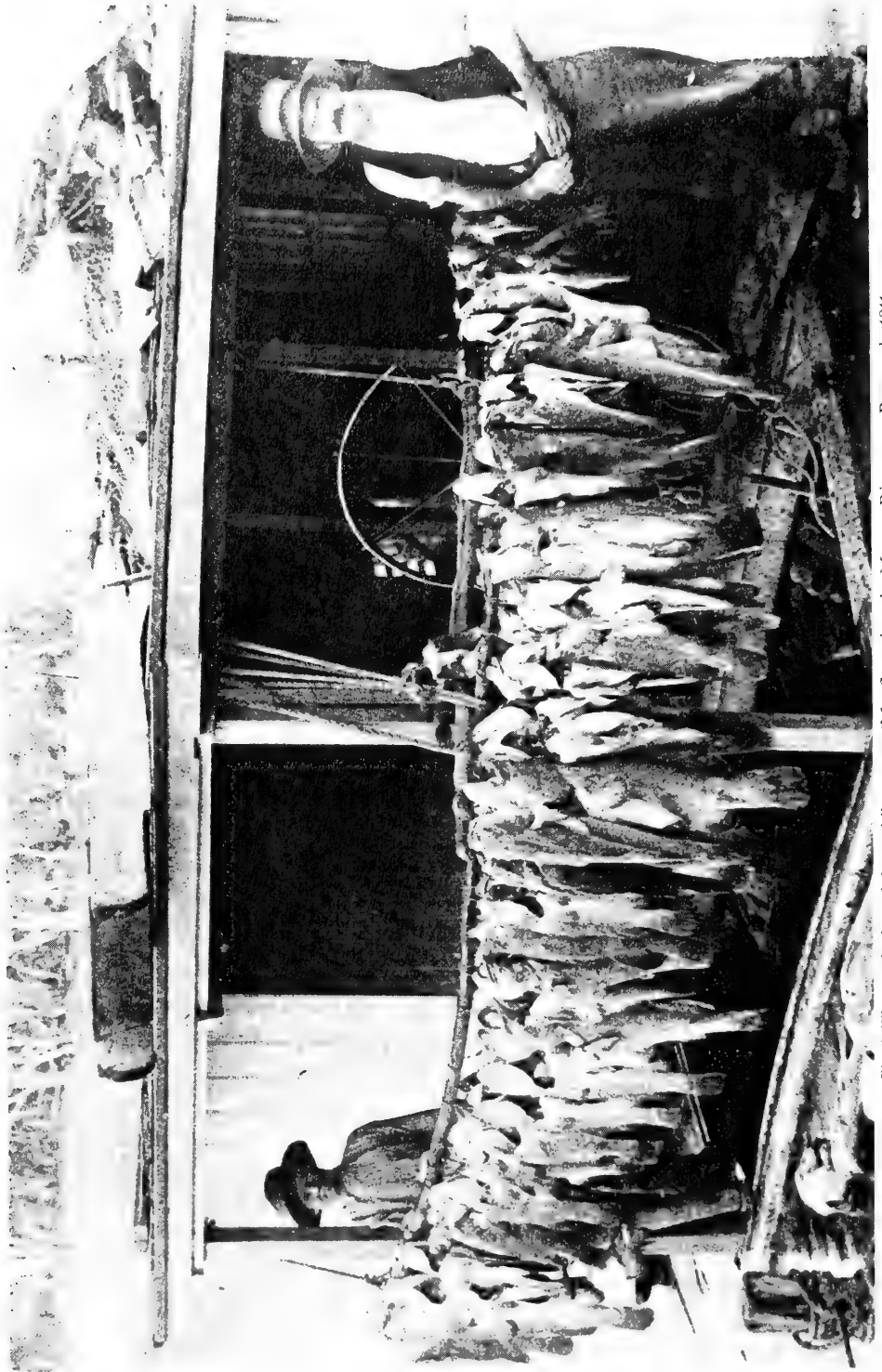


Fig. 2. The catch aboard the paddlesteamer 'Mayflower' on the Murray River near Renmark, 1911.

(Cadwallader and Backhouse, 1983), Cataract Dam (Anderson, 1916) and several other Sydney water supply dams (Lake, 1959, 1971) and numerous farm dams in the eastern states of Australia.

MURRAY COD FISHERIES

Development

During the mid to late 1800's a large inland, commercial fishery developed and was based mainly on the Murray and Murrumbidgee rivers (Macleay *et al.*, 1880; Dannevig, 1903; Stead, 1903). Large-scale operators used paddlesteamers as fishing boats (Fig. 2) and set up to 200 drum nets per vessel (Pollard and Scott, 1966). The drum net was introduced into the inland fishery in 1880 (Dannevig, 1903) and has remained the most common method of netting Murray cod and golden perch in the inland rivers and creeks. By 1883 the Murray River fisheries formed a considerable factor in the fish supply to Victoria and during this year more than 147 tons were sent to Melbourne from Moama (Cox, 1884). In 1900 the value of the inland fisheries within the South Australian portion of the Murray River was worth £25,000-£30,000 per annum (Whitley, 1937).

Although few quantitative data are available, it appears that the fishery was based primarily on Murray cod. In 1862 a company of six men and a number of aborigines captured two to three tons of fish per week from the Murray River, south of Deniliquin, which 'abounded with fish, particularly the Murray River cod' and sent them to Bendigo and Melbourne (Jervis, 1952). A professional fisherman from Tailem Bend, South Australia, reported catching '... three bags (170 lb each) of Murray cod in one morning' (Stead, 1903). The Fisheries Enquiry Commission of 1879-80 (Macleay *et al.*, 1880) was told by Mr. F. A. Tompson of Wagga, in relation to the fish in the Murrumbidgee River, that 'The cod is the most prominent and remarkable... It is brought to market more plentifully than the others... a ton of fish is brought in here every week... I saw 150 large cod alive in a cart... They were sold in two hours or less'.

In 1900, cod accounted for 75% of the river fish available at the Melbourne market, the remainder being golden perch (Poole, 1984). The dominance of Murray cod in professional catches is shown in Fig. 2, the catch aboard the paddlesteamer 'Mayflower' near Renmark in 1911. Dakin and Kesteven (1938) referred to 'the overwhelming importance of cod, the quantity of golden perch and silver perch taken is small compared with quantity of cod'.

Besides the commercial fishery, large numbers of Murray cod were easily caught and used as food by early settlers (Bennett, 1834; Macleay *et al.*, 1880). By 1955 the popularity of inland fishing had increased tremendously and with the aid of motor vehicles, a large recreational fishery had developed (Anon., 1956). During the 1950's large catches of Murray cod could be made by experienced recreational fishermen.

Decline

Dakin and Kesteven (1938) presented the available data on the catch of native fish from the inland waters between 1883 and 1938, and allowing for the limitations as discussed by those authors, the data indicate that although large fluctuations of fish populations occurred in the Murray-Darling river system, there had been a gradual decline in the overall catch from a peak in 1918. By the mid 1930's it was apparent that the commercial fishery had declined to an unprofitable level for the large-scale operators (Whitley, 1937; Pollard and Scott, 1966).

Catch statistics from the commercial fishery in inland N.S.W. between 1940/41 and 1983/84 are presented in Fig. 3. The annual catch of Murray cod increased between

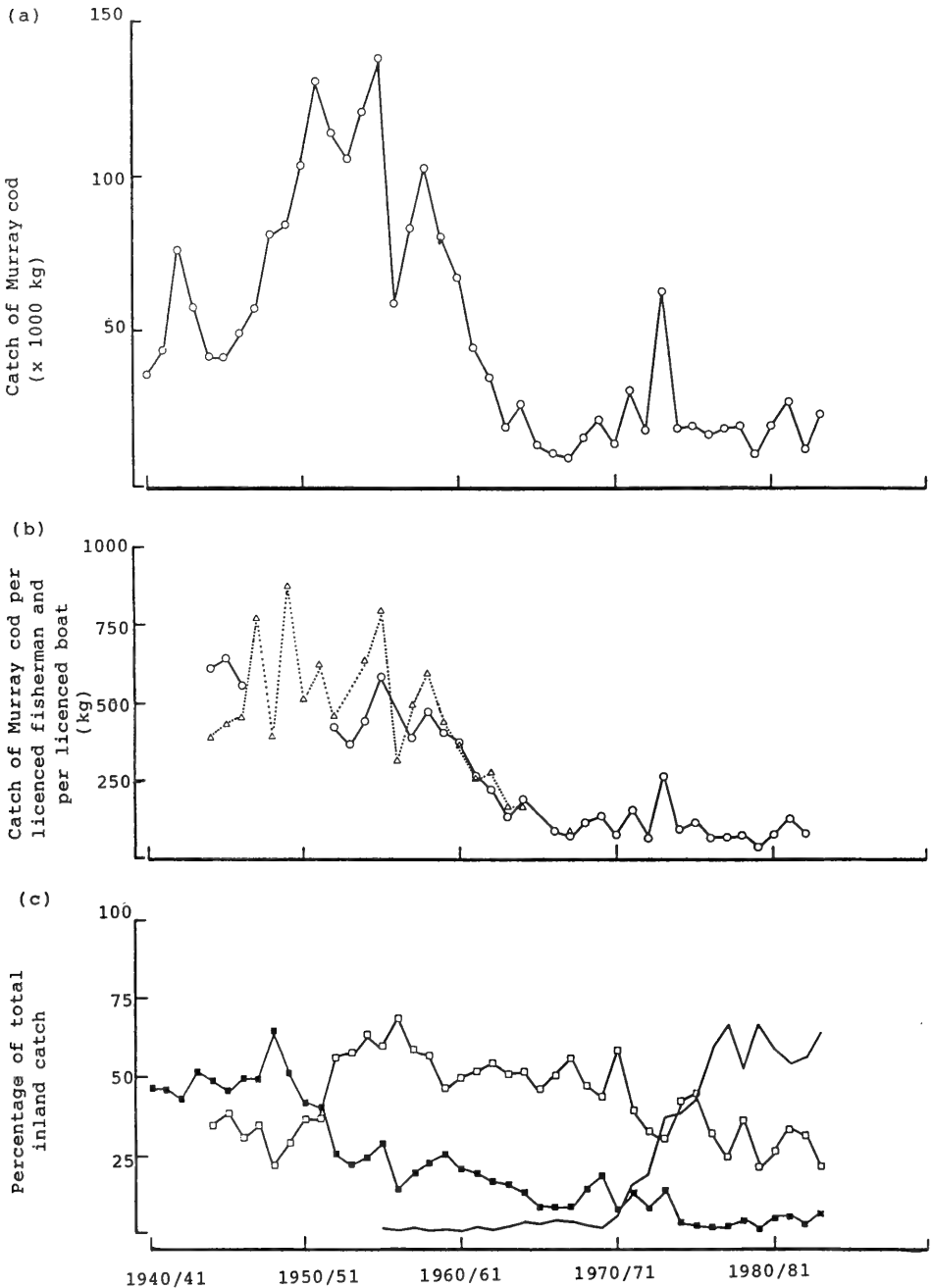


Fig. 3. The total annual catch (a) and catch per licensed fisherman and per licensed boat (b) of Murray cod, and the percentage composition of Murray cod, golden perch and common carp (c) in the commercial catch from inland waters in N.S.W. between 1940/41 and 1983/84 (data from annual reports, N.S.W. State Fisheries).

(b) ○—○ catch per licensed fisherman
 △-----△ catch per licensed boat

(c) ■—■ Murray cod
 □—□ golden perch
 — common carp

1940/41 and 1955/56, but then the total catch and the catch per licenced fisherman declined dramatically (Fig. 3a, b). Murray cod was the major species in the inland fishery until 1951/52, and between 1940 and 1951 cod comprised 42-65% of the total annual catch from inland N.S.W. However, after 1951/52, golden perch (*Macquaria ambigua*) replaced Murray cod as the major native species in the N.S.W. inland fishery (Fig. 3c). The total catch, catch per licenced fisherman and the percentage composition data all strongly suggest that there was a dramatic decline in the abundance of *M. peeli* between 1955 and 1964. There was a concurrent decline in the commercial catch of Murray cod from the Murray River in South Australia (Reynolds, 1976). Between 1940/41 and 1962/63 the annual total catch of Murray cod in N.S.W. exceeded 35,000 kg; however since 1963/64, with the exception of 1974/75, the annual catch has remained below 30,000 kg and the catch per licenced fisherman below 200 kg.

The continued small catch and low catch per licenced fisherman of Murray cod in the N.S.W. commercial fishery since 1960/61 (Fig. 3) indicate that the fishery remains in a depressed state. These catch statistics also indicate that there has been no major reduction or increase in the abundance of Murray cod since the mid 1960's. Consequently, it appears that stocks of Murray cod have remained stable, but at relatively low levels over the last 25 years.

Reduced Distribution

There has also been a reduction in the distribution of *M. peeli*. Many historical reports indicate that the species was common in rivers where cod are now rare or no longer found. The explorer George Evans, the first European man to see the species (Stanbury and Phipps, 1980), observed cod in the Fish River before he reached the present site of Bathurst. The type locality of *M. peeli* is the Peel River, N.S.W. probably near the present site of Tamworth (Mitchell, 1838) and in 1836 an enormous 120 lb 'River codfish of the Colonists' was found entangled and struggling near the bank in a pond of the Cudegong River (Bennett, 1864). Murray cod are now extremely rare in the Fish, Peel and Cudegong rivers.

In Victoria, Murray cod abounded in the Loddon, Campaspe and Goulburn rivers and their tributaries, even where the waters 'dwindled into the most insignificant streams' (Wilson, 1857). By the late 1940's the populations of Murray cod and other native fishes had declined in these rivers (Langtry, in Cadwallader, 1977) and there are now very few localities in Victoria where Murray cod can be considered common (Cadwallader and Backhouse, 1983).

Fisheries Management and Research

Concern about the stocks of Murray cod was expressed as early as the 1880 Royal Commission enquiring into the Fisheries of N.S.W. (Macleay *et al.*, 1880) and from 1883 until about 1895 there was some supervision of inland waters (Dakin and Kesteven, 1938). Dannevig (1903) detailed measures for restricting gear, protecting fry and young fish and the imposition of a closed season. From 1905 to 1910 serious attempts were made to improve the cod fishery, including experiments conducted in 1905 by H. C. Dannevig on the artificial propagation of cod (Farnell, 1906; Dakin and Kesteven, 1938). Whitley (1937) briefly discussed the available information on the distribution, fishery, breeding and taxonomy of Murray cod and included a complete bibliography containing mostly taxonomic references. In 1936, a conference on the Murray River fisheries, attended by representatives from N.S.W., Victoria and South Australia, adopted a closed season of September, October and November for the taking of Murray cod; set minimum legal lengths; suggested that hatcheries be established; asked the Murray River Commission to construct a fishway at Lock 15 at Euston; and suggested

that the breeding habits and migration of freshwater indigenous fishes be studied by each State (Isherwood, 1939).

However, since that time only five studies have contributed significantly to the knowledge of the biology of *M. peeli*. Dakin and Kesteven (1938) presented brief notes on the natural history, behaviour in captivity and the spawning season of Murray cod; they also discussed the cod fishery including the evidence for, and possible causes of the decline of cod stocks. Dakin and Kesteven artificially bred cod by capturing and stripping ripe fish; the eggs, embryonic development, larvae and fry were described. However, this part of the study was restricted by the difficulty of procuring ripe brood-fish from the wild. The need for future research into the biology and breeding of this species was emphasized.

J. O. Langtry conducted an ecological survey of the Murray River and some of its tributaries in 1949-50. Unfortunately, his report was not published, and it wasn't until 1977 that the manuscript was rewritten and presented by Cadwallader (1977). The report contains data on the relative abundance of fishes in the study area and describes the differences between Murray cod and trout cod (*Maccullochella macquariensis*). Langtry also made observations and collected some quantitative data on the distribution, diet, breeding biology and growth rate of Murray cod.

During the 1960's, John Lake studied the reproductive biology of native fishes at the Inland Fisheries Research Station, Narrandera, N.S.W. and his research demonstrated that critical temperatures and rising water levels in ponds (and presumably a flood or fresh in the wild) triggered the spawning of some species (Lake, 1967 a,b). Cadwallader and Gooley (1985) collected data on the spawning of Murray cod in earthen ponds, and developed techniques for the artificial propagation and rearing of *M. peeli*. Rowland (1985) conducted research into the biology and artificial breeding of *M. peeli*, and some of his findings form the basis of the following discussion.

POSSIBLE CAUSES OF THE DECLINE

Reduced Larval Recruitment

The high survival of fish larvae is dependent on the availability of relatively high concentrations of suitable-sized food organisms at the commencement of exogenous feeding; suboptimal feeding conditions generally result in death due to starvation or predation (May, 1974; Pitcher and Hart, 1982). Hjort (1926) hypothesized that the degree of mortality of larvae during a 'critical period' after the completion of yolk sac absorption determined the strength of year-classes in natural populations. Although the relationship between larval mortality during the 'critical period' and year-class strength is difficult to determine in nature (May, 1974) it is generally thought that the survival rate of fish larvae is the most important factor determining the strength of year-classes (Beverton, 1962; Gulland, 1965; May, 1974; Pitcher and Hart, 1982).

Many overseas studies have shown that strong year-classes of freshwater fishes are established when the breeding season coincides with rising or high water levels (e.g. Aggus and Elliott, 1975; Stevens, 1977; Marshall, 1982; Beam, 1983). Although *M. peeli* spawned annually in the southern tributaries of the Murray-Darling river system between 1977 and 1980, relatively strong year-classes were only established when the breeding seasons coincided with high river levels or floods (Rowland, 1985), demonstrating that floods in October and November provide optimum conditions for the survival and recruitment of *M. peeli* larvae.

The floodplain areas of the Murray-Darling river system are highly productive. When they are inundated in spring or summer, a rich source of terrestrial nutrients, plus the plankton, aquatic insects (in particular chironomid larvae) and other organisms

of the billabongs become available to the aquatic community of the rivers (Frith, 1959; Shiel, 1980; Maher and Carpenter, 1984). Zooplankton, chironomid larvae and other aquatic insects are the major food items of the larvae and fry of Murray cod and golden perch in earthen ponds, and a delay of several days in the availability of food to larvae after the completion of yolk sac absorption results in reduced survival in both species (Rowland, 1985, 1986).

The construction of dams, high-level weirs and levee banks on the major tributaries of the Murray-Darling system has altered the natural flow and temperature regimes and dramatically reduced the frequency, extent and duration of floods (Lake, 1971; Reynolds, 1976; Cadwallader, 1978; Walker *et al.*, 1978; Walker, 1979). The Murray River no longer floods annually in spring and much of the vast anabranch, billabong and floodplain areas of the Murray and Murrumbidgee rivers have been eliminated and do not flood except under extraordinary circumstances (Langtry, in Cadwallader, 1977; Shiel, 1980). Consequently optimum conditions for the survival of the larvae of Murray cod, which usually spawn in October or November, now rarely occur. It is suggested that the reduced frequency, extent and duration of spring flooding in the Murray-Darling river system has led to an overall reduction in larval recruitment and that this is a major cause of the decline in the abundance of *M. peeli*.

This hypothesis is supported by the change in the relative proportion (by weight) of Murray cod and golden perch in the commercial catch from inland N.S.W. (Fig. 3c). Prior to 1951/52, *M. peeli* was the major species; however, since then golden perch have formed a much greater percentage of the annual catch than have Murray cod. Golden perch require a substantial rise in water level, when temperatures are about 23°C, to induce spawning (Lake, 1967a); if suitable conditions do not occur in the wild, adults remain at an advanced stage of gonadal development until March or April (Mackay, 1973). Therefore *M. ambigua* can delay spawning over a six month period whereas *M. peeli* spawns only during spring and early summer when the water temperature is about 20°C (Rowland, 1983, 1985; Cadwallader and Gooley, 1985). The reduced frequency and extent of flooding, in particular the reduction of flooding which usually occurred each spring in the Murray and Murrumbidgee rivers (Langtry, in Cadwallader, 1977; Walker *et al.*, 1978; Walker, 1983) would be expected to affect larval recruitment to a greater extent in *M. peeli* than in *M. ambigua*.

The major impoundments on the Murray-Darling river system in N.S.W. were constructed between 1907 and 1976; Burrinjuck Dam 1907 (enlarged 1957), Hume Dam 1936 (enlarged 1961), Wyangla Dam 1936 (enlarged 1971), Yarrawonga Weir 1939, Keepit Dam 1960, Menindee Lake Storage Scheme 1960, Burrendong Dam 1967, Blowering Dam 1968, Pindari Dam 1969, Copeton Dam 1976 (Anon., undated; Walker, 1980). By 1950, the effects of Hume Dam and Yarrawonga Weir on the flow in the Murray River were clearly evident (Langtry, in Cadwallader, 1977). The cumulative effects of the major impoundments and water storage schemes would have been substantial by 1960 when there was an apparent rapid decline in the abundance of Murray cod.

Overfishing

The relatively large inland commercial fishery which existed between the mid 1800's and the late 1930's and which was based primarily on Murray cod (Macleay *et al.*, 1880; Dannevig, 1903; Stead, 1903; Dakin and Kesteven, 1938) would have placed intense fishing pressure on cod populations. Previously unfished populations of long-lived fishes consisting of 12 or more year-classes are extremely susceptible to exploitation; and with unchanging recruitment the absolute size of the total stock will decline markedly, or even catastrophically under moderate exploitation (Ricker, 1963). It is

therefore probable that the decline in abundance of Murray cod, at least until the 1930's, by which time the inland commercial fishery had become unprofitable for large-scale operators (Pollard and Scott, 1966), was caused primarily by overfishing.

A possible reduction in the exploitation of cod populations after the 1930's due to the depressed state of the fishery, the Depression and World War II, may have resulted in numbers and the catch per licenced fisherman/boat remaining reasonably stable or even increasing (Fig. 3) until the late 1950's when, as suggested, the effects of reduced larval recruitment became apparent by the rapidly declining stocks. It is also possible that the recreational fishery which developed in the 1950's (Anon., 1956; Poole, 1984) contributed to the decline of cod stocks during this period.

English Perch (Redfin)

English perch, *Perca fluviatilis*, were abundant and sympatric with *M. peeli* in the southern tributaries of the Murray-Darling system between the late 1940's and the 1960's. Langtry (in Cadwallader, 1977) found that the diet of *P. fluviatilis* was identical to that of *M. peeli* and *M. ambigua*, and small fishes become a major part of the diet of larger English perch (Lake, 1967c). English perch larvae and juveniles feed on zooplankton, crustaceans and insect larvae, and because *P. fluviatilis* spawns in early spring when temperatures are about 12°C; usually the last week or so in August in southern N.S.W. (Lake, 1967c), juvenile English perch may prey on, and possibly compete for food with Murray cod larvae and fry, particularly during drought periods when food resources are limited. The catch data on fishes from the Kerang Lakes, Victoria, between 1919 and 1949 (Figure 1 in Cadwallader, 1977) demonstrated that when English perch were abundant, native fish were scarce and *vice versa*. It is therefore possible that English perch have contributed to the decline of Murray cod in the southern parts of the Murray-Darling river system.

Other Factors

Factors such as siltation, desnagging, channelization, depressed water temperatures below impoundments, and barriers preventing spawning migrations have been implicated in the decline of native fishes (see Merrick and Schmida, 1984). While some of these factors may be responsible for the decline of some species in certain areas, because of the great size of the Murray-Darling river system it is unlikely that they have been major contributing factors to the decline of *M. peeli* which is widely distributed throughout the system (Lake, 1971) and does not undergo extensive migrations (Reynolds, 1983).

SUMMARY

Historical aspects of Australia's most famous and largest inland freshwater fish, the Murray cod, *Maccullochella peeli*, are briefly reviewed. Fossil records suggest that ancestral Murray cod are of, at least Miocene age. The Murray cod played a prominent part in the mythology and culture of some aboriginal tribes. Explorers, including George Evans, John Oxley, Thomas Mitchell, and Charles Sturt, and the early, inland settlers were astounded by the abundance, size and delicacy of Murray cod. The species was held in such high esteem that it was considered worthy of acclimatization in England and Europe, and although this did not eventuate *M. peeli* was extensively translocated within and outside its natural range of the Murray-Darling river system during both the 19th and 20th centuries.

During the late 1800's a large, inland, commercial fishery developed. It was based on Murray cod and was located mainly on the mid and lower reaches of the Murray and

Murrumbidgee rivers. Historical records and catch statistics indicate that there has been a dramatic decline in the abundance and a reduction in the distribution of *M. peeli*. Possible causes of the decline are briefly discussed. It is suggested that overfishing contributed to a decline between the late 1800's and the 1930's, but that the reduced frequency, extent and duration of spring flooding in the Murray-Darling river system, caused by the construction of dams, high-level weirs and levee banks, has adversely affected larval recruitment in *M. peeli*. This has caused the dramatic decline in abundance of cod during the 1950's and the maintenance of stocks at relatively low levels over the last 25 years.

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Microhydromys musseri n. sp., a New Murid (Mammalia) from the Torricelli Mountains, Papua New Guinea

T. F. FLANNERY

FLANNERY, T. F. *Microhydromys musseri* n. sp., a new murid (Mammalia) from the Torricelli Mountains, Papua New Guinea. *Proc. Linn. Soc. N.S.W.* 111 (3), 1989: 215-222.

Microhydromys musseri n. sp. differs greatly from the only previously described species of *Microhydromys* (*M. richardsoni*) in its larger size, brown dorsum with a markedly contrasting venter, broader skull, palate morphology, and dentition details. Both species however share synapomorphies not seen in other hydromyine murids. *Microhydromys musseri* n. sp. is thus far known from a single specimen collected near the summit of Mt Somoro, Torricelli Mountains (part of the North Coast Ranges). It is the third mammal species endemic to these ranges to be described. Three additional specimens of *Microhydromys richardsoni*, which was previously known only from the holotype, are described. These add significantly to knowledge of the species distribution and morphology.

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KEY WORDS: *Microhydromys musseri*, New Guinea, Hydromyinae, zoogeography.

INTRODUCTION

The murid subfamily Hydromyinae consists of 10 genera in the Australo-Papuan region. Thomas (1898) and Misonne (1969) have referred Asian taxa to the Hydromyinae, but Musser (1982) notes that it is not yet clear if any of these taxa do indeed represent part of the hydromyine radiation. All of the Asian taxa are readily distinguishable from members of the Australo-Papuan group and none resemble the species of *Microhydromys*. For this reason, and because of their uncertain status, I have restricted comparisons of the new species to Australo-Papuan taxa.

Within the New Guinean Hydromyinae are a group of six species, placed in four genera, that are known as microhydromyines. They are small, shrew-like murids with short, sleek coats, tiny eyes and pointed snouts. Included are some of the rarest and least known Melanesian mammals. The genera *Mayermys* and *Neohydromys* are monotypic, while *Pseudohydromys* includes two similar, probably parapatric species. *Microhydromys* includes two species that differ greatly in morphology, one of which is described here as new.

Previous taxonomic work upon microhydromyines has been limited, and it is not yet clear whether these species represent a monophyletic group, or are simply phenetically similar and paraphyletic. Likewise, the generic limits are in some cases poorly understood, and it is possible that in future some genera will be synonymized.

Microhydromys richardsoni Tate and Archbold, 1941 was described on the basis of a single adult male taken at an altitude of 850m near Bernhard Camp, Idenburg River, Irian Jaya. It is one of the more distinctive microhydromyines, possessing grooved upper incisors and a broad skull with a short rostrum. A brief mention of the existence of an additional specimen (Menzies and Dennis, 1979) constitutes the only other reported occurrence of this species.

In this work a new species of *Microhydromys*, from the North Coast Ranges, is described; descriptions of 3 additional specimens of *M. richardsoni* are provided. Although the new species is known only from a single specimen its description as a new

taxon is considered justified on the basis of its highly distinctive morphology. The likelihood of additional material being found in the near future is also low.

MATERIALS AND METHODS

Dental terminology follows Musser (1981), and colours where capitalized follow Smithe (1974). Measurements are in millimetres and weights in grams. Abbreviations are as follows: AM M, Australian Museum mammal specimen; AMNH, American Museum of Natural History mammal specimen; BBM, Bishop Museum mammal specimen.

SYSTEMATICS

Microhydromys Tate and Archbold, 1941

Microhydromys musseri n. sp

(Figs 1-2, Table 1)

Holotype and Type Locality: BBM101737, puppet skin and skull with dentaries of an adult male, collected on 12 November 1972 by A. B. Mirza at 1,350m on Mt Somoro (3° 22' S, 142° 09' E), Torricelli Mountains, West Sepik Province, Papua New Guinea.

Etymology: For Dr Guy Musser, who has contributed so abundantly to systematic research on the murids of Asia and Melanesia, and who has so greatly increased our understanding of the shrew-like murids of the region.

Diagnosis: *Microhydromys musseri* n. sp. can be distinguished from *M. richardsoni* in the following ways: it is larger (Table 1); the dorsum is Ochre Brown and the sharply demarcated venter Cinnamon (as opposed to the nearly uniform grey colouration of *M. richardsoni*); there is no longitudinal groove on the upper incisors; the palate is more deeply concave; the skull is absolutely and relatively broader; I/1 is less procumbent; a posterior cingulum is present on M/1.

Description: Fur short and dense, tail and ears appearing naked to the unaided eye. Dorsum near Ochre Brown, grading to Cinnamon Brown on flanks. Venter sharply demarcated and Cinnamon with two small, irregular white patches on thorax. Throat Cinnamon, crown of head Fuscous. Eyes surrounded by a circle of blackish hairs. Most vibrissae pale, but a few black; similar in length, distribution and density to those of other microhydromyines such as *M. richardsoni* and *N. fuscus*. Hands and feet thinly furred with pale hairs on dorsal side. Tail slightly paler below than above and mottled with light patches becoming prominent distally. Flesh of ears dark. Tail scales ill-defined but form regular rings with a single hair per tail scale. Flesh of the hands and feet shrivelled, but enough can be seen to determine that the pads of the forefeet were striated. Tiny rhinarium naked, toes unwebbed.

Upper incisors ungrooved and enamel orange. Lower incisors with paler orange enamel and less procumbent than in most other hydromyines. Molars heavily worn, with much crown detail lost. M1/ elongate, narrow, subrectangular. T2 large, obvious, much worn. A slight groove on the anterolingual face separates T1 and T2. Distinct enamel basin separates anterior and median lophs. Wear has obliterated almost all detail distal to this point. However, a slight groove discernable between median and posterior lophs on buccal face. T4 present as well-developed ridge. All M2/ crown details obliterated by wear. M2/ triangular in outline, with apex facing posteriorly. M/1 heavily worn. Protolophid horseshoe-shaped dentine basin surrounded by remnant of enamel crown. Hypolophid similar, but subrectangular shaped basin. Posterior cingu-

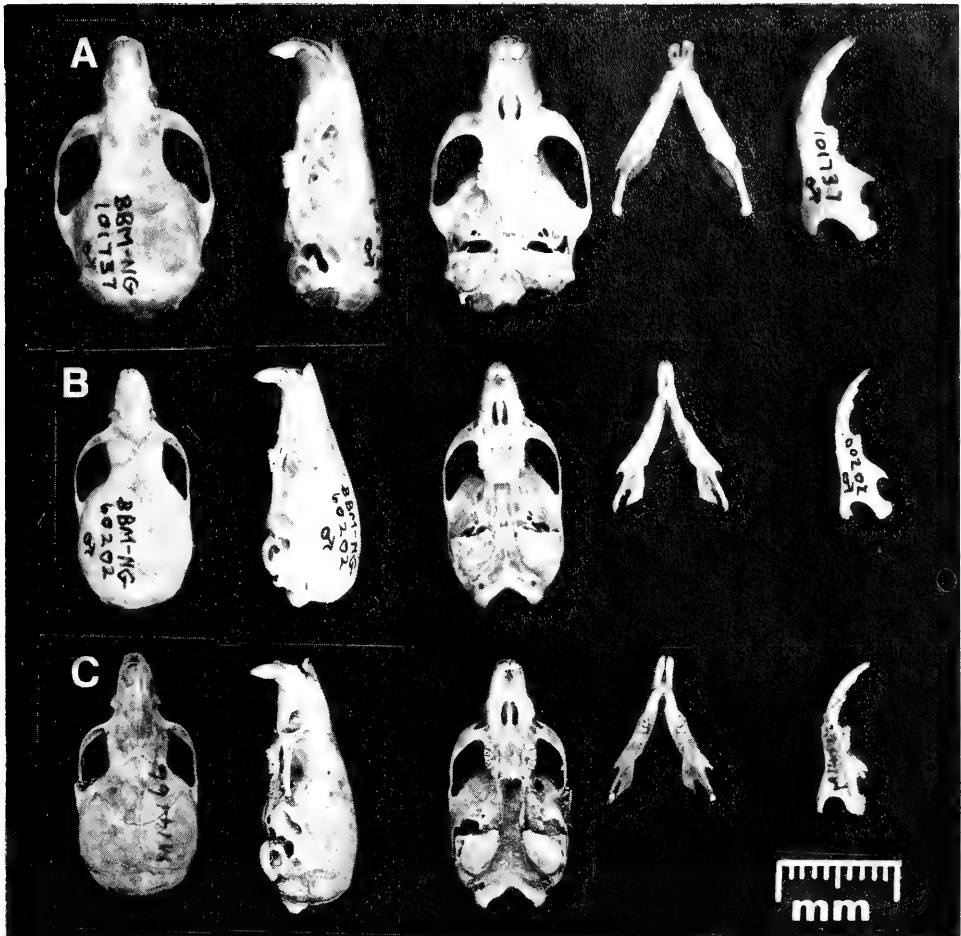


Fig. 1. The crania of **A**, *Microhydromys musseri* (holotype) BBM 101737. **B**, BBM 60202, *M. richardsoni*. **C**, AM M14166, *M. richardsoni*.

lum large and ovoid, positioned at anterolingual margin of tooth. M/2 smaller than M/1. Protolophid subrectangular and heavily worn basin. Hypolophid crescent shaped basin. Lophids separated by simple interlophid valley.

Cranium slightly damaged; left occipital condyle sheared off and basoccipital shattered then reglued. Rostrum shorter than in other microhydromyines, and broadened posteriorly. Premaxillae do not extend beyond incisors. Masseteric foramen lunette shaped and sloping anterodorsally, but with vertical orientation at posterior end. Infraorbital foramen moderate in size, not expanded as in *Hydromys*, *Parahydromys* and *Crossomys* species. Incisive foramina short and bowed, posterior ends located just posteromedial to zygomatic plates. Zygomatic plates broad and flared laterally. Zygomatic arch thin. Braincase moderately inflated. Bregmatic anteroposteriorly very short but broad. Palate deeply excavated, with molar alveolar margin raised into a ridge which extends well ventral to palate floor. Palatal foramina partially obscured by overhang of this ridge. Well-defined grooves run from palatal to incisive foramina. Left pterygoid broken away. Otic notch large, bulla unexpanded.

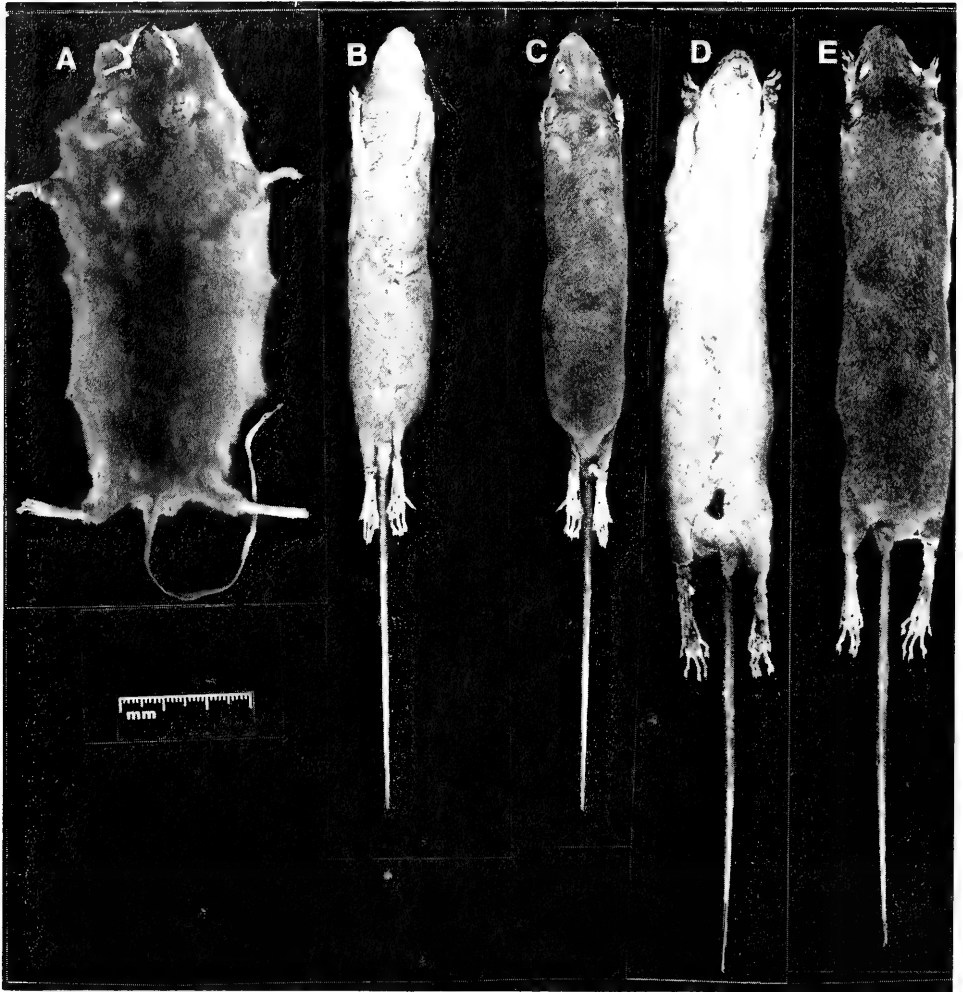


Fig. 2. Skins of **A**, *M. richardsoni* (AM M14166) **B**, ventral view and **C**, dorsal view of *M. richardsoni* (BBM60202), **D**, ventral view and **E**, dorsal view of *Microhydromys musseri* n. sp. (holotype) BBM101737.

DISCUSSION

Systematics

The assignation of the newly described species to the genus *Microhydromys* is based upon a cladistic interpretation of aspects of hydromyine morphology. Phenetically, *M. musseri* n. sp. and *M. richardsoni* appear to be rather different. However they share a number of key, apparently derived, features that are either rare or are not seen elsewhere among the Hydromyinae. These include the following.

- 1) The M1/ is extremely narrow and elongate, and more nearly rectangular in occlusal outline than in other hydromyines. This feature is unique in the subfamily and is not seen among other Australo-Papuan murids. Thus on the basis of outgroup comparison this feature is likely to be derived.
- 2) The lingual end of the interloph valley between the anterior and medial lophs of M1/ is very narrow, and partially closed off by a low ridge from T1. The entire lingual

margin of the tooth thus forms a continuous linear face which is parallel with the skull midline. Again, this feature is not seen in other hydromyines and is doubtless derived.

3) The rostrum is short relative to skull length and yet the interorbital canals are not greatly enlarged. The only other hydromyines with such a short rostrum are the species of *Hydromys*, *Crossomys* and *Parahydromys* (here called the '*Hydromys* group'). These very large hydromyines however all possess greatly enlarged infraorbital canals. Most murids (including the plesiomorphic hydromyine *Leptomys elegans*) have longer rostra. Thus it seems likely that the presence of a short skull is a derived feature. Because in other aspects the morphology of members of the '*Hydromys* group' and the species of *Microhydromys* is so different it seems likely that this similarity is due to convergence.

4) The palatal foramina are partially closed posteriorly and are narrow. Again, these features are unique in the subfamily and on the basis of outgroup comparison are likely to be derived.

Other aspects of morphology of the two *Microhydromys* species are however not shared between these taxa, but are either unique, or are shared by one or the other species with other hydromyines. These features are interpreted as being either retained symplesiomorphies or as being due to convergence; the features are as follows. The pelage of *M. musseri* n. sp. is bright. Its warm brown and cinnamon tones and sharply contrasting venter are not approached in any other microhydromyines. Among other hydromyines, only the species of *Leptomys* and one species of *Paraleptomys* possess such colouration. The species of *Leptomys* are particularly plesiomorphic hydromyines in many aspects of their morphology, and no other features would suggest a relationship with *Microhydromys*. Thus this feature may well be due to either convergence or else be a retained symplesiomorphy.

Another striking feature of *M. musseri* n. sp. that is most closely approached only in apparently distantly related taxa is the extremely concave palate. Only in *Xeromys myoides*, among other hydromyines, is the condition seen in *M. musseri* n. sp. approached. However, here details of actual palatal structure differ, suggesting that palatal concavity in these taxa is the result of convergence. The palatal foramina in *X. myoides* are not overhung by the ridges supporting the cheekteeth as in *M. musseri* n. sp., but are subovate and open. Furthermore, in cross section the palate of *M. musseri* is more angular than in *X. myoides* (where the cross section is arch shaped).

Overall skull shape at first suggested that a close relationship might exist between *M. musseri* n. sp. and the '*Hydromys* group' species, for these taxa have a short rostrum and are superficially similar in skull shape. However, in species of the '*Hydromys* group' T1 and T4 on M1/ are not extended posteriorly as they are in other New Guinean hydromyines. Posterior extension of these cusps must be regarded as derived, as it is not seen in plesiomorphic murid groups. This suggests that all hydromyines except members of the '*Hydromys* group' may be monophyletic, and that similarities between *M. musseri* n. sp. and the species of *Hydromys* are either plesiomorphic or due to convergence.

A final striking feature of *M. musseri* n. sp. is the presence of a distinct and large posterior cingulum on M/1. Only in the species of *Leptomys*, *Paraleptomys* and *Neohydromys* among hydromyines is this structure otherwise retained. The widespread presence of a posterior cingulum on the lower molars of other murid groups (including all non-hydromyine Australo-Papuan taxa) suggests that the loss of this structure is derived. That the posterior cingulum appears to have been retained in several unrelated hydromyine taxa indicates that its loss within the subfamily has occurred independently in several lineages.

Microhydromys richardsoni possesses one feature that is unique in the Hydromyinae. This is the presence of longitudinally grooved incisors. Such grooved incisors are, however, seen in a number of other murid taxa, such as the species of *Mylomys*, *Pelomys*

and *Golunda*. In *Vandeleuria oleracea* the incisors are only occasionally grooved, while in *Mus xenodontus* only one incisor is grooved. Misonne (1969) suggests that this indicates that the presence of grooves on the upper incisors of murids is under relatively simple genetic control and that it has only limited systematic importance. These data, together with the fact that the grooved incisors of *M. richardsoni* are unique (autapomorphic) among near relatives, suggests that not too much importance should be placed upon this feature in phylogenetic analysis.

In summary, it would appear that *M. musseri* n. sp. and *M. richardsoni* are each other's nearest relatives, but that both possess a number of independent specializations not seen in the other. This may in turn indicate that these taxa have been evolving separately for a considerable period of time. On this basis, a case could be made for either placing each in a monotypic genus, or retaining both in *Microhydromys*. The latter course has been chosen because I feel that the recognition of yet another monotypic genus of microhydromyine murid is not desirable until relationships within the group are clarified; furthermore such a decision would not indicate the nature of the relationship between *M. richardsoni* and *M. musseri* n. sp.

Biology and Zoogeography

A note on the label of the type specimen of *M. musseri* n. sp. indicates that it was taken at an altitude of 1,350m in a snap trap in 'forest'. At altitudes above about 1,200m Mt Somoro and the other high peaks of the North Coast Ranges are covered by mossy forest which differs sharply from the forest at lower altitudes. It is now becoming clear that these forests harbour a distinctive mammal fauna unlike that found anywhere else in New Guinea. The first endemic mammal to be described from these ranges (in this case the Cyclops Mountains) was also a hydromyine, *Paraleptomys rufilatus* Osgood, 1945. It has subsequently been found in the Mt Somoro area. Zeigler (1981) described a second endemic, the large petaurid *Petaurus abidi* from Mt Somoro. This paper describes a third endemic, which is yet another hydromyine. Furthermore, recent fieldwork undertaken in the Somoro area has revealed the presence of additional, as yet undescribed, endemic mammal species. In addition to these taxa, a number of slightly more widespread species are found in this habitat. These include *Pseudocheirops albertisii*, also known from the Vogelkop and Japen Island, and *Dendrolagus inustus*, which has a similar distribution. The area of mossy forest available to these species in the Torricelli Mountains is tiny (ca. 39 km²), but in the recent past was probably larger, when Ice Age cooling depressed altitudinal zones. However, it appears that at no time in the last few million years was this region in contact with the mossy forests of the Central Cordillera. This is reflected in the 'unbalanced' assemblage of species in this habitat. For example, no endemic dasyurids are known from these ranges, while the Central Cordillera has 6 species found exclusively at mid-high altitudes. Perhaps the fact that two out of the three described endemic mammals from the North Coast Ranges are insectivorous hydromyines reflects this lack. In the absence of the insectivores and carnivores which inhabit this forest type elsewhere, it may well have been that the hydromyines that could invade the habitat underwent a modest radiation. Whatever the case, it is apparent that no similar event happened elsewhere, as no endemic hydromyine species have been found on other isolated mountain ranges in New Guinea.

Additional Specimens

The only detailed information previously published regarding *Microhydromys richardsoni* is that contained in the type description and paraphrases of it. The holotype is an adult male, taken, presumably in a snap trap (the posterior part of the skull is broken in a way that suggests snap trap damage), at an altitude of 850m 4km SW of Bernhard

camp on the Idenburg River, Irian Jaya on 16 March 1939. Only three further specimens have been collected since that time, and two of these have been examined for this study. The first collected is an adult male (AMNH 198790). This was snap trapped under a small log in secondary growth at an altitude of 670m at Wanuma in the Adelbert Mountains, Madang Province by A. C. Zeigler on 21 October 1967. I have been unable to examine this specimen but Dr G. Musser kindly made the following notes for me; the terminal 35mm of the tail is mottled white, and the skull is so shattered that measurements could not be made. The Adelbert Range is a small, relatively low mountain range (most of it barely exceeding 1,000m) which is isolated from the New Guinean Central Cordillera.

The second additional specimen to be collected is another adult male (BBM60202). This was snap trapped in an area of secondary forest-Eucalypt savannah near Sirinum Dam, Sogeri area, Central Province Papua New Guinea on 28 October 1968. Sirinum Dam lies at an altitude of *c.* 550m. This is a most unexpected locality, as the Idenburg River and Adelbert Range specimens must have come from much wetter forest. The measurements of this specimen closely approach those of the holotype for the most part (Table 1). The pelage and cranial morphology are also similar to that of the holotype. They differ primarily in that: approximately 37mm of the distal part of the tail is white tipped as opposed to 10mm in the holotype; the grey of the dorsum is interrupted by irregular and inconspicuous ginger blotching (the individual blotches being 1-2mm in diameter).

TABLE 1

Measurements for the 5 known specimens of *Microhydromys*. Measurements for AMNH 152079 are from Tate (1951). Measurements in mm and weight in grams. *l* = length, *w* = width, *inc.* = incisive

Measurement /Weight	<i>M. musseri</i>		<i>M. richardsoni</i>		BBM-NG 60202
	BBM-NG 101737	AMNH 198790	AMNH 152079	AM M 14166	
head body l.	108	83	80	86	86
tail vent l.	101	84	92	79	83
hindfoot (su) l.	22	19	20	—	19
ear (n) l.	13	11	8	—	12
weight	—	9	—	12	—
condylobasal l.	23.6	—	—	20.2	19.6
bizygomatic w.	13.4	—	9.2	10.1	9.6
palate l.	13.6	—	10.0	9.5	9.7
rostral w.	5.7	—	—	4.1	4.0
inc. foramen l.	2.2	—	2.5	2.1	1.9
interorbital w.	5.2	—	4.4	4.6	4.2
nasal l.	8.0	—	6.4	7.0	5.9
maximum nasal w.	3.0	—	2.6	2.6	2.3
mastoid w.	10.7	—	9.4	8.8	9.3
bullae l.	4.4	—	3.8	4.2	4.2
M1-2/ l.	2.9	—	2.4	2.0	1.9
M1-1/ w. internal	3.5	—	2.4	2.7	2.7
M1/ l.	2.1	—	1.6	1.4	1.2
M1/ w.	0.9	—	0.8	0.8	0.6
M2/ l.	0.8	—	0.8	0.7	0.7
M2/ w.	0.8	—	0.7	0.6	0.6

The most recently collected specimen is AM M14166. It is an adult female snap trapped on 18 September 1979 at 1,450m on the southern slopes of Mt Sisa, Southern Highlands Province by P. Dwyer. Although most measurements are similar to those for the other *M. richardsoni* individuals known, it differs in a number of ways. The nasals are

longer and the mastoid width narrower than in the male specimens (Table 1). The palate does not extend as far posteriorly behind M2/ as in the Sogeri specimen. The skin of the Mt Sisa specimen is flat. It closely resembles that of the Sogeri individual except that it lacks the ginger blotching and has a small patch of pure white hairs on the throat. The most distal 25mm of the tail is pure white, while a light and dark mottled area extends a further 30mm proximally.

It is unclear as yet whether the differences between AM M14166 and the other *M. richardsoni* specimens represent sexual dimorphism, intra, or possibly even interspecific variation. However from the specimens described here it is clear that this species, or taxa closely related to it, are relatively widely distributed across New Guinea, both geographically and in differing environments.

CONCLUSION

Microhydromys musseri n. sp. is described. Known from a single specimen collected in mossy forest high in the Torricelli Mountains, it differs in many aspects of its morphology from *M. richardsoni*. Three additional specimens of *M. richardsoni* are described. They indicate that this species has a wide geographic distribution and that it exhibits considerable morphological variation. *Microhydromys richardsoni* can inhabit drier habitats than had previously been suspected.

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Tidal and Diel Variations in the Abundance of Larval Fishes in Botany Bay, New South Wales, with Emphasis on Larval Silverbiddy *Gerres ovatus* (Fam. Gerreidae) and Gobies (Fam. Gobiidae)

ALDO S. STEFFE

STEFFE, A. S. Tidal and diel variations in the abundance of larval fishes in Botany Bay, New South Wales, with emphasis on larval silverbiddy *Gerres ovatus* (Fam. Gerreidae) and gobies (Fam. Gobiidae). *Proc. Linn. Soc. N.S.W.* 111 (4), 1989: 225-232.

Surface plankton samples were collected from an area of strong tidal flow in Botany Bay, during early autumn 1981, to examine tidal and diel variations in the abundance of larval fishes. The sampling program was restricted to one 24 hour period, and yielded 2,898 larvae consisting of 30 distinct larval types from 21 families. Larval gobies (Fam. Gobiidae) and silverbiddy *Gerres ovatus* (Fam. Gerreidae) dominated the assemblage, and together accounted for 82.5% of the standardized total catch. On the selected sampling day the composition of the larval assemblage differed at either end of the tidal range. Gobiid larvae were more abundant at low tide both day and night, whereas abundances of *G. ovatus* were greater at high tide both day and night. Night catches of gobiid and *G. ovatus* larvae were greater than day catches. The great majority of *G. ovatus* larvae had deflated gas bladders during the day and inflated gas bladders at night. The limitations of these findings are acknowledged; due to the short sampling period it is possible that effects of other variables were confounded with effects of the main factors being tested.

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INTRODUCTION

Although the nursery function of Australian estuaries has been studied (Lenanton, 1977; Robertson, 1980; SPCC, 1981; Young, 1981; Bell *et al.*, 1984; Middleton *et al.*, 1984) little is known about larval fish distributions or the factors which affect larval recruitment in these estuarine areas (Steffe and Pease, 1988).

The common problem facing both recruiting larvae and those already in the estuary is how to maintain their position in the estuary and avoid being flushed out on the ebb tide. Weinstein *et al.* (1980) proposed that successful recruitment and/or retention in a stratified estuarine system involved selective vertical migrations by larval fishes in conjunction with changes in tide and photoperiod. There is also evidence that the larvae of other estuarine dependent species respond to tidal or diel stimuli, or both (Fore and Baxter, 1972; Graham, 1972; Eldridge, 1977; Melville-Smith *et al.*, 1981; Fortier and Leggett, 1982; Norcross and Shaw, 1984; Roper, 1986), but the mechanism(s) by which larval fishes achieve this are poorly understood.

Here, the findings of a sampling program designed to analyse variation in larval fish abundances with respect to changes in tidal and diel conditions are reported. The main question asked was: on the selected sampling day did larval fish abundances at the surface vary with respect to changes in tide and/or diel conditions?

MATERIALS AND METHODS

Study Area

Botany Bay (34°01'S, 151°11'E) is a large, semi-landlocked estuary on the east coast of Australia (Fig. 1). It is dominated by ocean swell and wind waves (Roy *et al.*,

1980), is vertically well mixed (Rochford, 1951), and at most times is best described as a marine embayment.

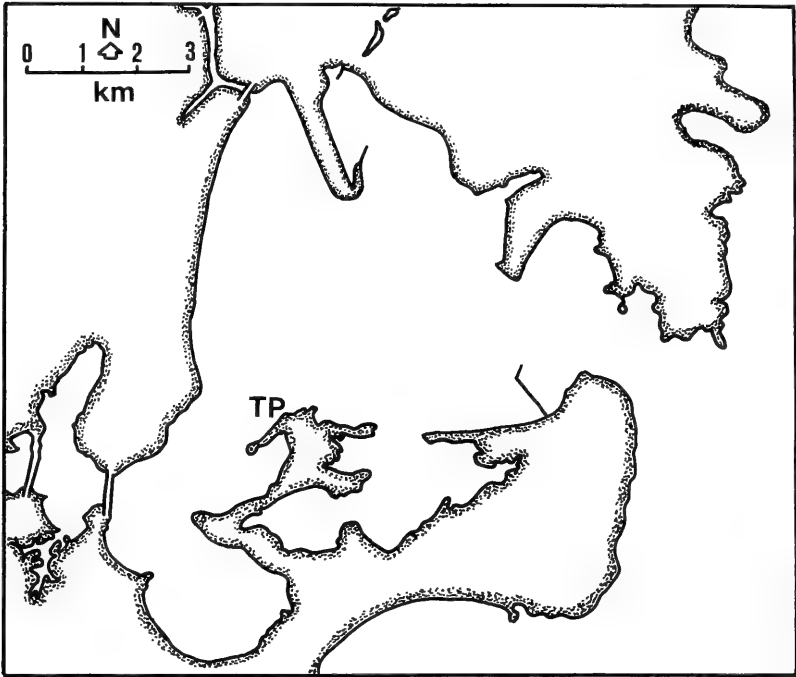


Fig. 1. Map of Botany Bay showing location of sampling station. Abbrev.: TP = Towra Point.

A sampling station (Fig. 1) was selected off Towra Point because of its position in the main tidal stream and its close proximity to large *Posidonia australis* and *Zostera capricorni* seagrass meadows, and an extensive mangrove stand. These habitats are important fish nursery areas (Bell *et al.*, 1984; Middleton *et al.*, 1984). Samples were collected during March (early Autumn) as juveniles of many economically valuable fishes are most abundant in the Bay shortly after this period (Bell, 1980; SPCC, 1981; Bell *et al.*, 1984; Middleton *et al.*, 1984). The maximum depth at the sampling station was about 4m.

Field Procedures

The sampling program was designed to analyse variances in larval fish numbers between stage of tide (high vs low) and diel condition (day vs night) at one station. The design was orthogonal and required that both high and low tides be sampled during daylight, and at night. High and low tide were defined as a two hour period with the tidal prediction at its centre. Four replicate samples were collected at each consecutive high and low tide over the 24 hour sampling period. Tidal height ranged from 0.2-1.6 m above I.S.L.W. during the sampling period.

Day sampling commenced 40 minutes after sunrise (05.57h) on 19 March 1981 and

night sampling commenced one hour after sunset (18.09h). Plankton samples were collected from a small (4m) boat using a net with a square mouth (area 0.25m^2), a mesh of $500\ \mu\text{m}$, and a length of about 2.5m. The net was towed in a circular path at the surface at a constant speed of about 2m sec^{-1} for 5 minutes ($\pm 5\ \text{sec.}$). This procedure kept the net out of the engine wash and thus avoided unnecessarily increasing net escapement. A General Oceanics (model 2030) flowmeter was used to measure the volume of water filtered. Volume filtered per tow averaged 133.7m^3 (s.d. 13.2). A salinity ($\pm 0.1\text{‰}$) and water temperature ($\pm 0.2^\circ\text{C}$) reading was taken during each of the consecutive tides sampled.

Samples were preserved immediately after collection in 5% Steedman's preservative and were sorted entirely under a dissecting microscope. All larval fishes were identified to the lowest possible taxonomic level and then stored in 4% buffered formalin. Standardized larval abundances are expressed as the number of larvae per 100m^3 water filtered. Terminology follows the definitions of Leis and Rennis (1983).

Size Distribution and Gas Bladder Inflation Incidence

Some 200 day-caught and 200 night-caught larvae of *Gerres ovatus* and of gobiids were randomly selected. These larvae were measured to the nearest 0.1 mm using a dissecting microscope with mounted ocular micrometer. Notochord length was recorded for preflexion and flexion stages whilst standard length was measured for post-flexion stages. The numbers of larvae with deflated, or inflated gas bladders were then recorded separately for day-caught and night-caught *G. ovatus* only. This was easily done as the gas bladder in this species is clearly visible when inflated. This procedure was not repeated for gobiid larvae as they have a permanently inflated gas bladder.

RESULTS

The sampling program yielded 2,898 larval fishes consisting of 30 distinct larval types from 21 families (Table 1). Silverbiddy *Gerres ovatus* and gobiid larvae dominated the larval fish assemblage. *G. ovatus* larvae accounted for 31.3% of the standardized total catch whilst gobiids (four spp.) made up 51.2% of this total. The remaining 19 families contributed 17.5% of the standardized total catch but were not sufficiently abundant, or were present in too few samples, to warrant statistical analysis (Table 1).

More *Gerres ovatus* were caught at night and during high tide (Fig. 2a, Table 2). The interaction term was not significant. Similarly, significantly more gobiid larvae were caught at night, however unlike *Gerres ovatus*, significantly more gobiids were caught during low tide (Fig. 2b, Table 2). There was no significant interaction (Table 2).

Total fish larvae reflected the contrasting patterns of *Gerres ovatus* and gobiids. Night catches were significantly greater than day catches, but there was no significant tidal effect or interaction (Fig. 2c, Table 2).

The length frequency of night-caught *Gerres ovatus* larvae was similar to that for day caught larvae (Kolmogorov-Smirnov test, $D_{\text{max.}} = 0.075$, $p > > > 0.05$) (Fig. 3a). Ninety-eight percent of day-caught larvae ($n = 200$) were found to have deflated gas bladders and ninety-five percent of night-caught larvae ($n = 200$) had strongly inflated gas bladders.

The length frequency distribution of gobiid larvae caught during daylight was significantly different to that of gobiids caught at night (Kolmogorov-Smirnov test, $D_{\text{max.}} = 0.23$, $p < 0.001$) (Fig. 3b). In contrast to *G. ovatus*, more larger gobiid larvae were taken at night.

Salinity and water temperature did not fluctuate greatly during sampling (temp.

22.8-24.0°C; sal. 32.7-34.0‰) and rainfall had not been reported for the previous ten days in the area (Bureau of Meteorology, 1981).

TABLE 1

Number of distinct larval types, occurrence, and the percentage of the standardized total catch for each taxon in the larval assemblage. Note that each larval type may not be monospecific

Taxon	No. Larval Types	Occurrence (Max. = 16)	% Standardized total catch
Gobiidae	4	16	51.2
Gerreidae	1	16	31.3
Ambassidae	2	15	4.7
Syngnathidae	4	16	3.7
Blenniidae	2	12	1.5
Sillaginidae	1	8	0.7
Sparidae	2	7	0.7
Monacanthidae	1	7	0.5
Carangidae	1	5	0.4
Atherinidae	1	4	0.3
Anguilliformes	1	3	0.2
Clupeidae	1	5	0.2
Hemirhamphidae	1	1	0.1
Platycephalidae	1	1	0.1
Pempherididae	1	3	0.1
Soleidae	1	3	0.1
Tetraodontidae	1	3	0.1
Scorpaenidae	1	1	} 0.1
Mugilidae	1	1	
Sphyraenidae	1	1	
Callionymidae	1	1	
Damaged larvae	—	16	

TABLE 2

F ratios and significance levels derived from two way fixed effects ANOVA of effects of tide (high vs low) and diel period (day vs night) for *Gerres ovatus*, Gobiidae and sample totals. Data tested for heteroscedasticity using Cochran's test ($p < 0.1$). A = log transformed data, B = raw data

Source of Variance	df	<i>Gerres ovatus</i> ^A	F ratio Gobiidae ^B	Sample Totals ^B
Tide	1	16.10**	5.17*	0.08 NS
Diel	1	12.55**	19.11***	11.71**
TxD	1	1.85 NS	0.06 NS	0.08 NS
Residual	12			

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS $p > 0.05$

DISCUSSION

Gerres ovatus larvae were significantly more abundant on high tides whilst gobiid larvae were caught in significantly greater numbers during low tides. As *G. ovatus* and numerous gobiid species are known to spawn within Botany Bay (State Pollution Control Commission, 1981) their centres of larval abundance may have been expected to coincide. Yet, they have become spatially separated, occurring at either end of the tidal range. This larval distribution was found both during daylight and at night. Two hypotheses, not mutually exclusive, to explain this are: (1) spawning aggregations of *G.*

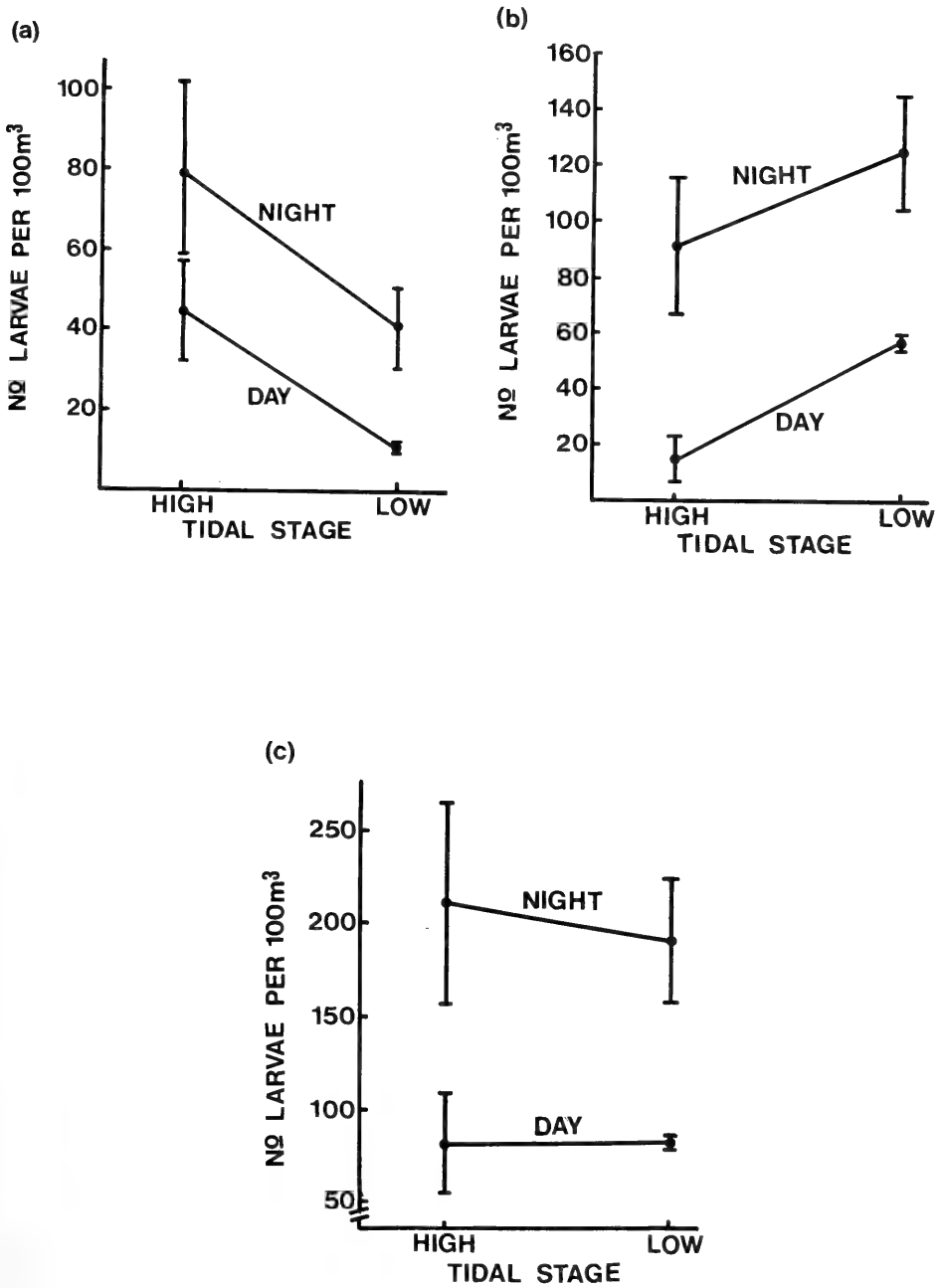


Fig. 2. Mean and \pm one SE for the standardized larval abundances at each of the consecutive tides, both day and night, over the 24 hour sampling period for (a) *Gerres ovalis*, (b) *Gobiidae*, and (c) sample totals.

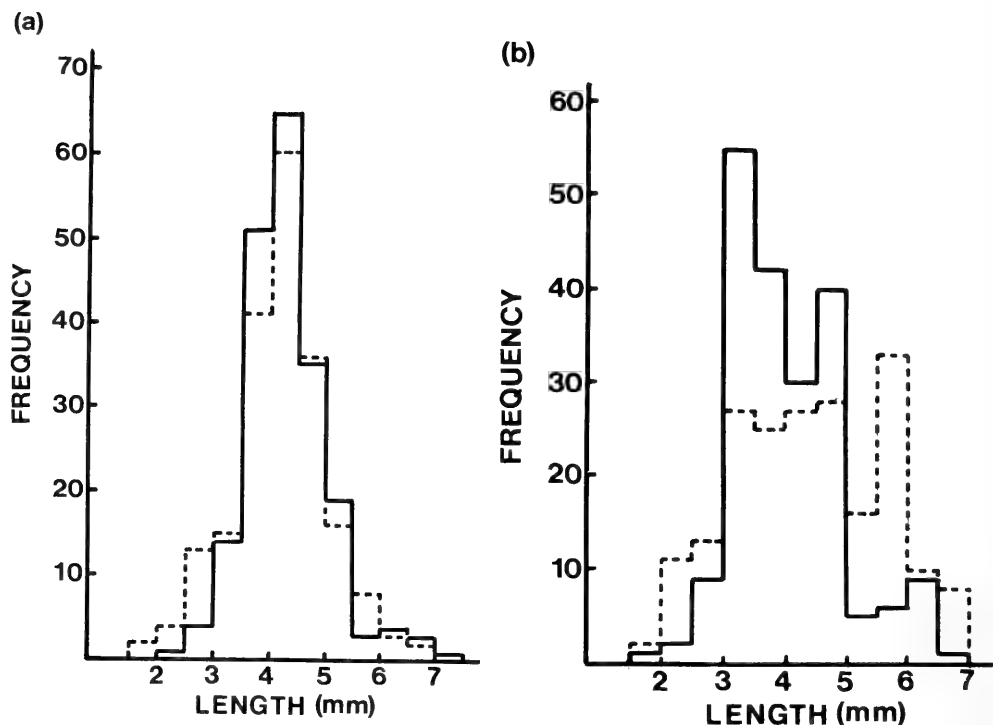


Fig. 3. Length frequencies of randomly selected day-caught ($n = 200$) and night-caught ($n = 200$) larvae for (a) *Gerres ovatus*, and (b) Gobiidae. Solid lines denote day-caught, and broken lines denote night-caught.

ovatus occur near the Bay entrance and seaward of gobiid spawning sites; and (2) both groups spawn at a similar distance into the Bay, but the demersal eggs of gobiids are more effective than the pelagic eggs of *G. ovatus* at reducing the net transport of offspring seaward from spawning sites by currents. This could occur because demersal eggs, unlike pelagic eggs, are not subject to passive transportation by currents, and because at hatching, larvae from demersal eggs tend to be relatively larger, more developed, with better swimming capabilities than those from pelagic eggs (Steffe and Pease, 1988).

Larval catches of *Gerres ovatus* and gobiids were found to be significantly greater at night (Table 2). There was no difference in the size structure of *G. ovatus* between day and night (Fig. 3a) suggesting that differential net avoidance was minimal and that the higher night catches could be mainly attributed to the effects of diel vertical migration.

The effects of differential net avoidance and diel vertical migration could not be separated for gobiids as more large larvae were caught at night (Fig. 3b).

Most *Gerres ovatus* larvae had deflated gas bladders during the day whilst the reverse was true at night. This phenomenon appears to be common and occurs in many taxonomically diverse teleost groups (Hunter and Sanchez, 1976; Leis and Rennis, 1983; Liew, 1983; Hoss and Phonlor, 1984; Kitajima *et al.*, 1985; A. Steffe, unpub. data). Hunter and Sanchez (1976) found that nocturnal gas bladder inflation can provide considerable energy savings to northern anchovy *Engraulis mordax* larvae by retarding sinking. It is likely that larval *G. ovatus* gain a similar benefit.

The silverbiddy, *G. ovatus*, has been found to recruit almost exclusively to mangrove areas in Botany Bay (State Pollution Control Commission, 1981). The observed larval distribution of *G. ovatus* at a site near its preferred nursery habitat supports the hypothesis that larval silverbiddy may be using flood tides to assist their transportation into mangrove areas. This hypothesis appears tenable because mangrove areas are wholly dependent on tide for water exchange.

The data presented and interpreted here are based on collections made during a single 24 hour period. Consequently, it is possible that the effects of other variables which were not specifically tested may have, by chance, been confounded with the effects of the tidal and diel factors examined during the selected sampling day; in view of the relatively constant temperature and salinity conditions it is unlikely that larval catches were influenced by these parameters. Further sampling, that is, the same experiment repeated on other 'replicate' days, is required to eliminate this possible source of error and to possibly allow the conclusions drawn here to be accepted with greater confidence.

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Redescription of *Austrochthonius australis* Hoff (Chthoniidae: Pseudoscorpionida)

CLARICE M. A. KENNEDY

KENNEDY, C. M. A. Redescription of *Austrochthonius australis* Hoff (Chthoniidae: Pseudoscorpionida). *Proc. Linn. Soc. N.S.W.* 111 (4), 1989: 233-240.

An examination of approximately 150 specimens of *Austrochthonius australis* Hoff from various locations in southeastern Australia suggests a considerable size variation within the species when compared with the two published descriptions of adults (Hoff, 1951; Beier, 1966). For the first time the nymphal stages are described.

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INTRODUCTION

A. australis is widely distributed in a variety of habitats throughout Australia. The description of the holotype is based on a single female specimen from Mt Slide, Victoria. Beier (1966) has briefly described male and female specimens based on an examination of material from Western Australia, Victoria, New South Wales, Australian Capital Territory and Tasmania.

Investigation of specimens from Western Australia, identified as *A. australis*, has revealed a number of differences from the holotype suggesting that an undescribed species is represented. In addition, individuals of a population in the Sydney region are much smaller, when compared with the two published descriptions of the adult by Hoff (1951) and Beier (1966); this prompted examination of some 150 specimens from various locations in Victoria, New South Wales and Tasmania to determine if specimens identified as *A. australis* are in fact a single species. Apart from size, specimens examined are morphologically similar to the holotype.

The results of this research are presented below and represent a more comprehensive description of the species which for the first time, incorporates the nymphal stages.

MATERIALS AND METHODS

Specimens were borrowed from the following institutions: American Museum of Natural History, New York; Australian Museum, Sydney; Museum of Victoria, Melbourne and 34 samples from the private collection of Dr. M. S. Harvey, Western Australian Museum, Perth.

Measurements are based on the examination of at least 5-15 adults of each sex from various locations in south eastern Australia made in accordance with those described by Chamberlin (1931). Figures in parentheses are female values and follow those of the male. The morphological nymphal information is based on measurements of 10 specimens of each stage collected from the Sydney region. Nymphs from the other regions within the distribution of the species are, at present, unavailable for comparison.

Abbreviations for chelal trichobothria and setal formulae follow those devised by Chamberlin (1931). Genitalia terminology follows that of Legg (1975). Specimens of *A. australis* from the Sydney region are deposited in the Australian Museum, 6 ♂ (KS 20186), 6 ♀ (KS 20187), 6 nymphs (KS 20188).

SYSTEMATIC DESCRIPTION

CHTHONIIDAE Hansen 1893

Austrochthonius Chamberlin 1929**Type species:** *Chthonius chilensis* Chamberlin 1923*Austrochthonius australis* Hoff

(Figs 1-4)

Diagnosis: Chelicera with 5 setae on hand; palpal teeth quadrate and separated; 6 pinnate coxal spines present on coxa 2; intercoxal tubercle absent. L/W ratio of chela (with pedicel) range 1:1.05-1.33 (1: 1.03-1.45) x longer than broad.

Description: Adults. Colour light golden brown; carapace surface smooth; pleural membrane with series of irregularly spaced longitudinal ridges, each with minute, elevated, white nodules (Fig. 1A). Pedipalp: trochanter stout, femur with lateral margins virtually parallel, abruptly converging distally, L/W ratio range 1: 1.00-1.65 (1:

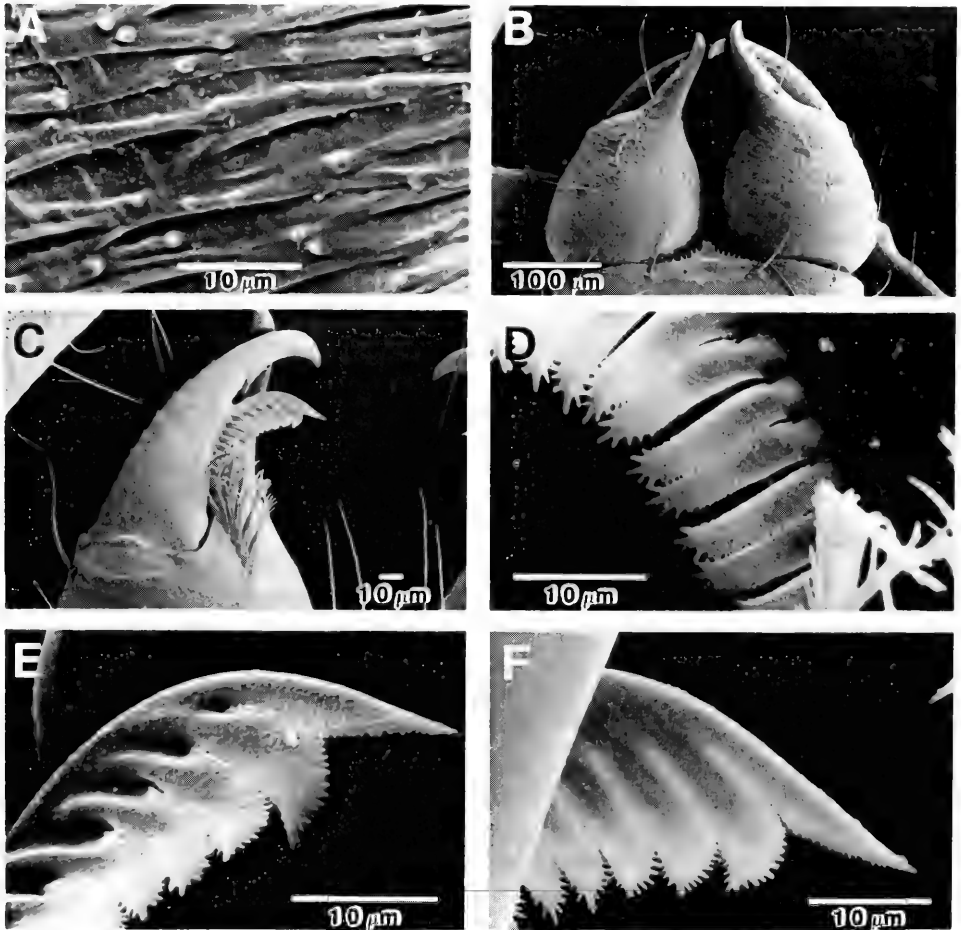


Fig. 1. *Austrochthonius australis* Hoff, scanning electron micrographs, male: A, pleural membrane; B, chelicerae, dorsal aspect; C, right chelicera movable finger, ventral aspect; D, left chelicera, serrula exterior proximal blades; E, right chelicera, serrula exterior distal blades, ventral aspect; F, right chelicera, serrula exterior distal blades, dorsal aspect.

1.00-1.65), tibia calyciform; chelal hand broad and shorter than chelal fingers, lateral margins very slightly rounded, poorly developed pedicel, L/W ratio of chela (with pedicel) range 1: 1.05-1.33 (1: 1.03-1.45), chela (without pedicel) 1: 1.03-1.31 (1: 1.01-1.42) x longer than broad. Chelal fingers long and tapering, fixed finger with 8 trichobothria, *ib* and *isb* medial on dorsum of chelal hand; movable chelal finger with 4 trichobothria; marginal teeth quadrate, separated and retrorse on fixed finger, teeth smaller on movable finger becoming broader with rounded apices and laterally fused proximally, 46-50 (♂) 45-46 (♀) (Fig. 4T); venom apparatus absent. Chelicera large, stout with 5 setae on hand, fingers cross distally (Figs 1B, 4S), fixed finger with reticulate sculpture, teeth 15-16 (♂) 15-17 (♀), distal one large, remainder diminishing in size proximally; movable finger with 18 well-spaced smaller teeth which become almost indistinguishable proximally; lamina exterior absent. Serrula exterior detached in upper half with 14-

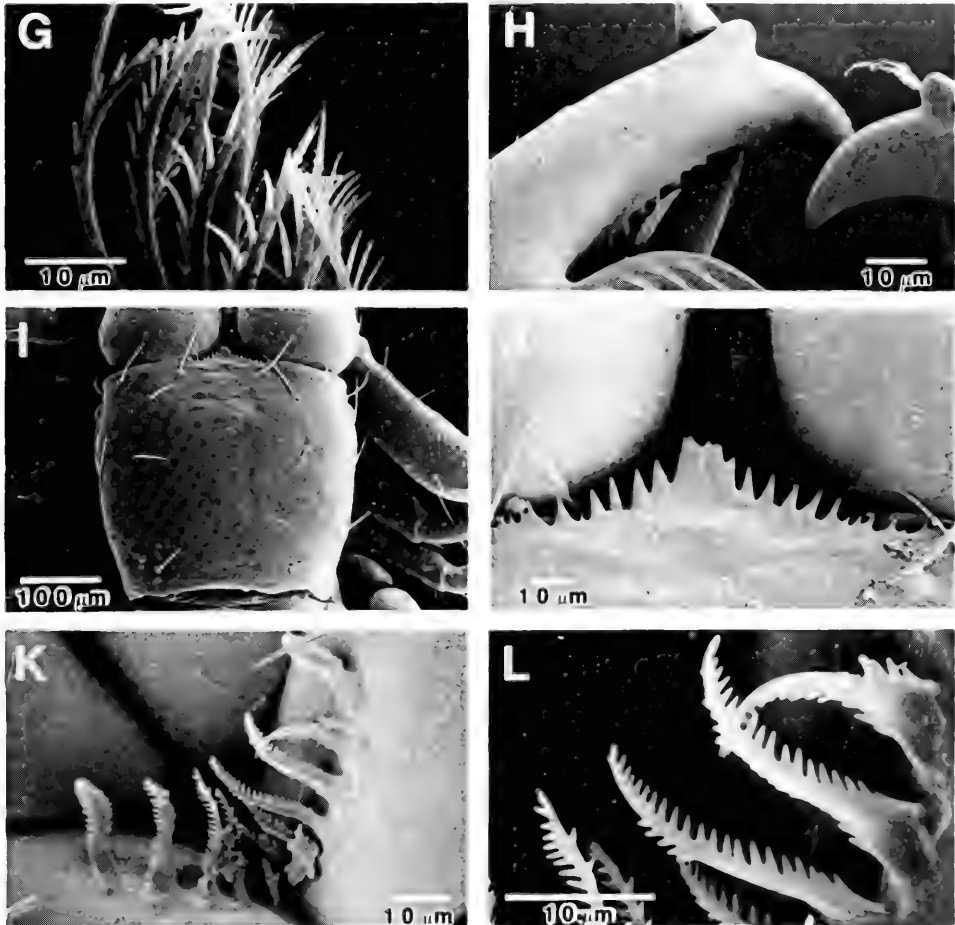


Fig. 2. *Austrochthonius australis* Hoff, scanning electron micrographs, male: G, right chelicera, flagellum blades, ventral aspect; H, female, right chelicera showing galea a sclerotic tubercle; I, carapace; J, male, epistome; K, coxal spines; L, enlargement of pinnate coxal spine blades.

15 (♂) 14 (♀) lamellae (Fig. 1C), lamellae relatively broad, elongate, with parallel sides proximally, terminally each blade digitate (Fig. 1D) becoming broad distally (Figs 1E.

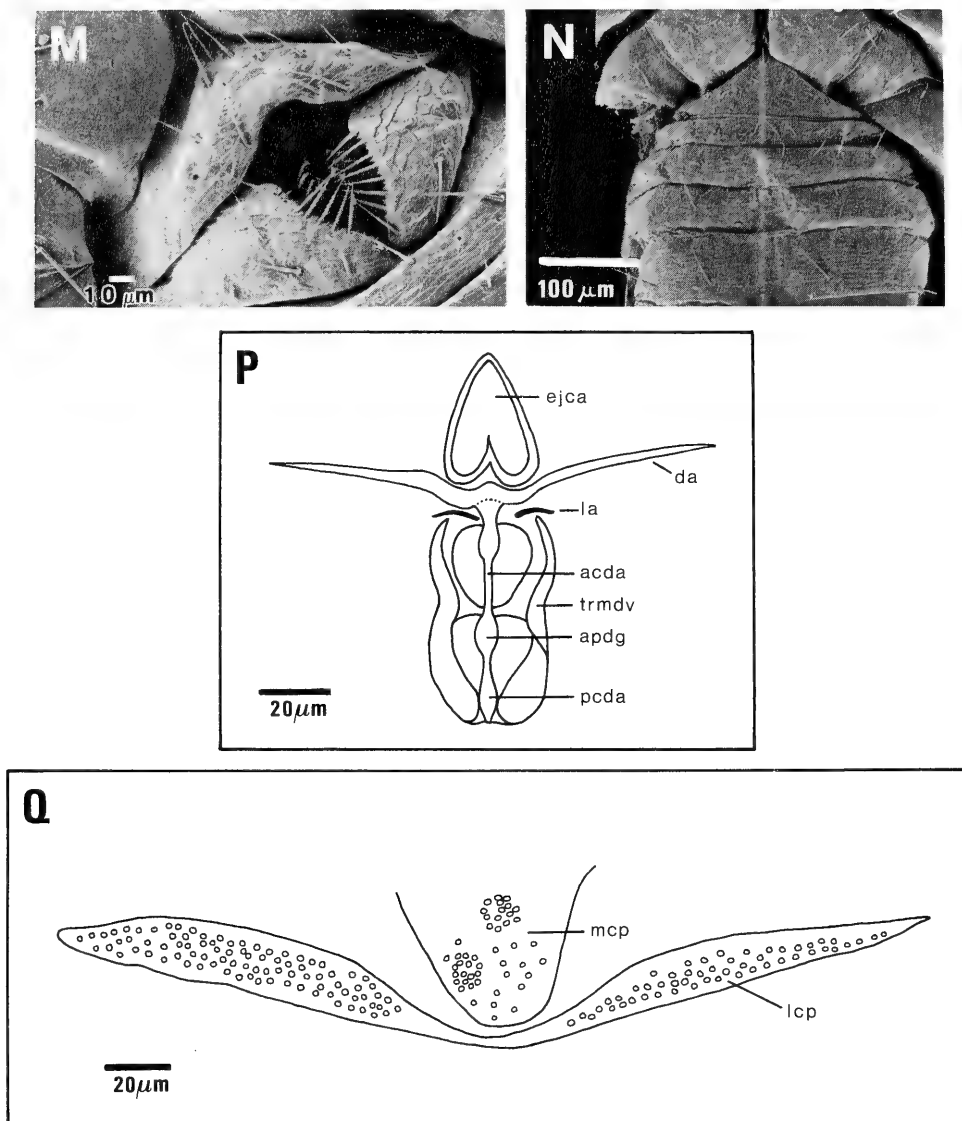


Fig. 3. *Austrochthonius australis* Hoff, scanning electron micrographs: **M**, male genital region, external aspect; **N**, female genital region, external aspect; **P**, male genitalia, internal aspect; **Q**, female genitalia, internal aspect.

F); galea a sclerotic tubercle in ♀ (Fig. 2H), absent in ♂; galea seta basad of mid-point of movable finger. Flagellum with 8 stalk-like blades each arising separately along a diagonal slit basad of fixed cheliceral finger (Fig. 1C) becoming unipinnate distally (Fig. 2G). Carapace: subquadrate, surface smooth; anterior margin slightly serrate laterally with prominent, blunt, dentate epistome (♂) (Fig. 2J), more or less acute (♀), weakly reticulate sculpture; lateral margins distinctly narrowed posteriorly (Fig. 2I); posterior margin relatively straight; setae long, acuminate 4: 2: 12 (♂), 4: 2: 12-14 (♀); L/W ratio

(based on ocular width) range 1: 1.00-1.13 (1: 1.03-1.36), (based on posterior width) 1: 1.07-1.52 (1: 1.12-1.33) x longer than broad. Anterior eye well developed, posterior eye flattened disc. Tergal chaetotaxy: setae relatively long, acuminate, ♂ 4: 4: 3-4: 2-4: 6: 6-7: 6: 4: 4-5: 4: 4: 2; ♀ 4: 4: 4: 4: 4: 4: 6: 6: 6: 4-5: 2. Uniseriate. Coxal chaetotaxy: 6 pinnate coxal spines placed anterior-ventrally along proximal half of coxa 2 (Figs 2**K**, **L**) ♂ 2: 2: 1, 0: 3: 1, 0: 3: 2, 0: 2: 3-4, 0: 2: 4; ♀ 2: 2: 1-2, 0: 3: 2, 0: 3: 1, 0: 2-3: 4-5, 0: 2: 3. Intercostal tubercle absent. Male genitalia (Fig. 3**P**): ejaculatory canal atrium (ejca) pear-shaped; roof of each medial diverticulum thickened (trmd) to form two elongated structures, anterior horns of each free but fused posteriorly, in mid-line is atrium of posterior dorsal gland (apdg). Cuticle of genital atrium thickened and extended to form apodemes; dorsal apodeme (da) well developed with Y-shaped structure below ejaculatory canal atrium (ejca), posterior extension of Y forms anterior crest of dorsal apodeme (acda), posterior to atrium of posterior dorsal gland (apdg) the posterior crest of the dorsal apodeme (pcda) arises in mid-line above duct of median genital sac; lateral apodemes (la) reduced and thickened to provide attachment for muscles of ejaculatory canal and support for anterior region of genital region of genital atrium. Chaetotaxy: anterior operculum with 8-9 relatively long setae along anterior margin, 4-5 along posterior margin which is deeply concave medially; posterior operculum with 8 relatively long acuminate setae on each side of a deep median notch. These setae project into the centre forming a grill-like pattern across the genital atrium (Fig. 3**M**). Female genitalia (Fig. 3**Q**): lateral cribriform plates (lcp) clearly differentiated with numerous pores; median cribriform plate (mcp) — pores scattered over the surface with some aggregations. Chaetotaxy: anterior operculum a triangular plate; posterior operculum a simple elongate plate (Fig. 3**N**). Sternites with reticulate sculpture, chaetotaxy: ♂ 0: 13-14: 26-27: 4: 4: 3-4: 4: 6: 6: 4-6: 4-6: 2; ♀ 0: 10: 10-12: 8: 6: 4-6: 6: 6: 6: 2, setae long, acuminate. Sternites 4-11 uniseriate.

Dimensions (mm): body length 0.75-1.17 (0.77-1.62); pedipalp: femur 0.21-0.36/0.07-0.10 (0.21-0.46/0.07-0.10), chela (with pedicel) 0.43-0.61/0.09-0.13 (0.45-0.70/0.10-0.16), chela (without pedicel) 0.41-0.59/0.09-0.13 (0.41-0.68/0.10-0.16), movable finger length 0.25-0.37 (0.28-0.45). Carapace 0.27-0.37/ocular width 0.27-0.41/posterior width 0.21-0.34 (0.28-0.46/ocular width 0.30-0.48/posterior width 0.26-0.43).

Tritonymph. L/W ratio: pedipalpal trochanter 1.00-2.00, femur 2.28-3.00, tibia 1.28-1.42, chela (with pedicel) 3.55-4.33, chela (without pedicel) 3.33-4.11 x longer than broad. Fixed finger with 7 trichobothria, movable finger with 3 trichobothria, *isb* and *sb* absent; serrula exterior of chelicera with 11-12 broad, elongate lamellae, each blade digitate terminally. Carapace: anterior margin slightly serrate laterally, epistomal process prominent; posterior margin relatively straight; lateral margin narrowing at point of union with abdominal segments, 4: 2: 8, setae long, acuminate. L/W ratio (based on ocular width) 1.08-1.25, (based on posterior width) 0.96-1.00 x longer than broad. Tergal chaetotaxy: 4: 4: 4: 4: 4-6: 4-6: 6: 6: 6: 4: 4-6: 2. Sternal chaetotaxy: 0: 3-4: 6-7: 6: 6: 4: 4: 6: 6: 6-7: 5-6: 2. Coxal chaetotaxy: 4-5 coxal spines in medial position along anterior margin of 2nd. coxa, 2: 2: 1, 0: 3: 0, 0: 3: 2-3, 0: 1: 2-4, 0: 1: 3-4.

Dimensions (mm): body length 0.66-0.79; pedipalp: trochanter 0.07-0.09/0.05-0.07, femur 0.16-0.21/0.07, tibia 0.09-0.10/0.07, chela (with pedicel) 0.32-0.39/0.07-0.09, chela (without pedicel) 0.30-0.37/0.07-0.09, movable finger length 0.19-0.27; carapace 0.27-0.30/ocular width 0.27-0.31/posterior width 0.22-0.25.

Deutonymph. L/W ratio: pedipalpal trochanter 1.20-1.40, femur 2.00-3.20, tibia 1.00-1.75, chela (with pedicel) 3.75-4.50, chela (without pedicel) 3.28-4.16 x longer than broad. Fixed finger with 6 trichobothria, movable finger with 2 trichobothria, *isb*, *esb*, *sb*, *b* absent; serrula exterior of chelicera with 9-10 broad, elongate lamellae, each blade

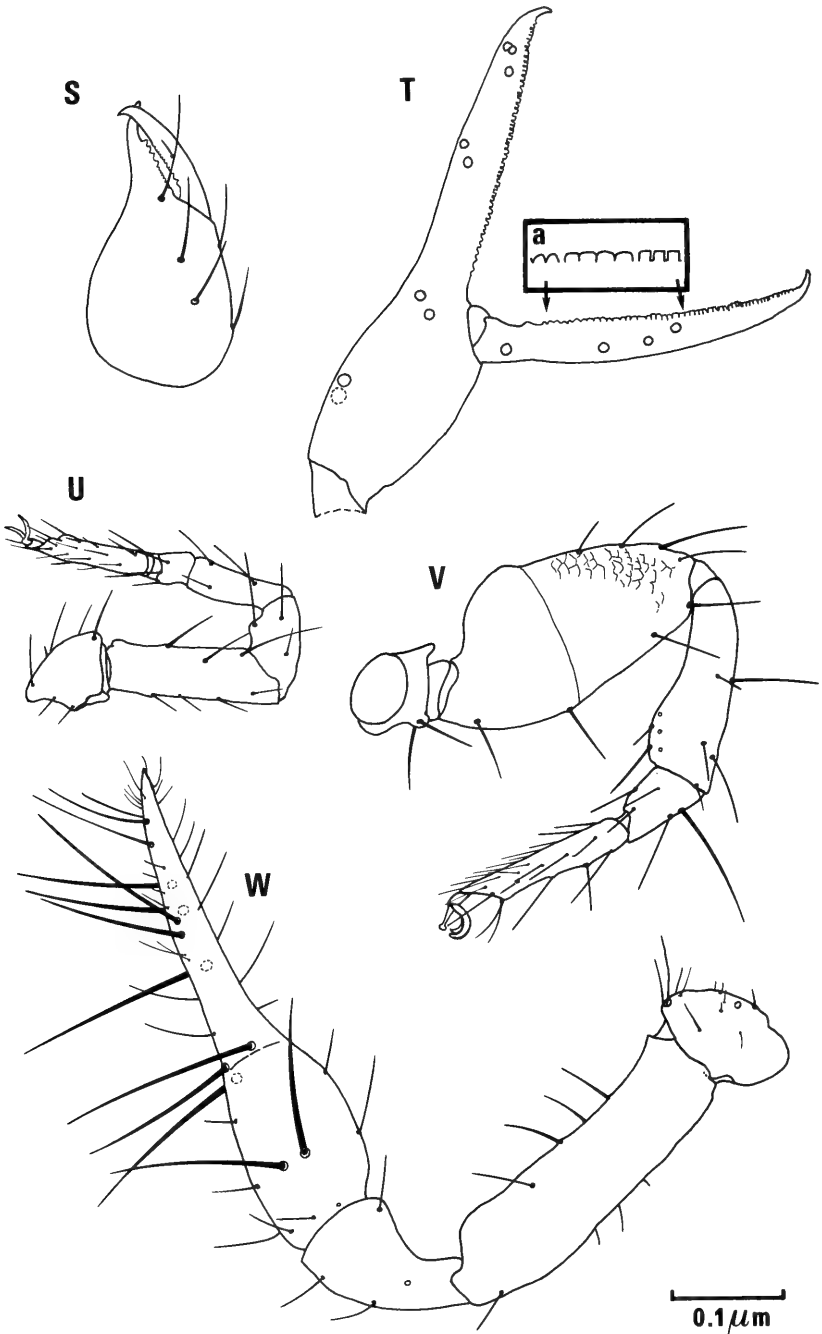


Fig. 4. Austrochthonius australis Hoff, male: **S**, right chelicera, dorsal aspect; **T**, right chela, lateral aspect; **Ta**, inset, enlargement showing dentition type (not to scale); **U**, first right leg; **V**, fourth right leg; **W**, left pedipalp, dorsal aspect.

digitate terminally. Carapace: anterior margin serrate, epistome prominent; 4: 2: 8: 3-6 relatively long setae, 1.05-1.18 x longer than broad (ocular and posterior width equal). Tergal chaetotaxy: 4: 4: 4: 2-4: 4-6: 4-6: 4-5: 5-6: 4-5: 4-6: 5-6: 2, setae, long, acuminate posteriorly. Sternal chaetotaxy: 0: 4: 4: 4-6: 4-6: 6: 4: 4: 4-6: 4-6: 6: 2. Sternites 3-5 divided. Coxal chaetotaxy: 3-4 coxal spines in medial position along anterior margin of 2nd. coxa, 2: 2: 1, 0: 2-3: 0, 0: 2: 1, 0: 1-2: 1, 0: 1: 2.

Dimensions (mm): body length 0.48-0.63; pedipalp: trochanter 0.06-0.07/0.05, femur 0.12-0.16/0.04-0.07, tibia 0.07/0.05-0.07, chela (with pedicel) 0.25-0.28/0.06-0.07, chela (without pedicel) 0.23-0.27/0.06-0.07, movable finger length 0.14-0.19; carapace 0.19-0.23/0.16-0.20.

Protonymph. L/W ratio: pedipalpal trochanter 1.25-1.33, femur 2.20-3.00, tibia 1.25-1.50, chela (with pedicel) 3.33-4.00, chela (without pedicel) 3.16-3.80 x longer than broad. Fixed finger with 3 trichobothria, *ist*, *et*, *eb* present; movable finger with 1 trichobothrium, *t* present; serrula exterior of chelicera with 7-8 broad, elongate lamellae.

Carapace: anterior margin smooth, slightly dentate medially, 4: 2: 5: 3 setae, 1.06-1.16 x longer than broad (ocular and posterior width equal). Tergal chaetotaxy: 2: 2-3: 2-3: 2-3: 4: 3: 3-4: 3: 4: 3-4: 4-5: 2. Sternal chaetotaxy: 0; 2-3: 3: 4: 2-3: 2-4: 4: 4: 3-4: 3-4: 4: 2. Coxal chaetotaxy: 3-4 small coxal spines along anterior margin of coxa 2, 2: 2: 1, 0: 2: 0, 0: 2: 0, 0: 1-2: 1, 0: 1: 1.

Dimensions (mm): body length 0.36-0.45; pedipalp: trochanter 0.04-0.05/0.03-0.04, femur 0.09-0.11/0.03-0.05, tibia 0.05-0.06/0.04, chela (with pedicel) 0.17-0.22/0.05-0.06, chela (without pedicel) 0.16-0.21/0.05-0.06, movable finger length 0.11-0.14; carapace 0.14-0.17/0.12-0.16.

DISCUSSION

Only two species of the genus *Austrochthonius* Chamberlin are recorded from Australia namely: *A. australis* Hoff and *A. cavicola* Beier (1968). Results of this investigation are based on the examination of specimens from locations ranging from lat. 33°45' S, long. 150°57' E to lat., 41°49' S, long. 145°37' E and suggest a considerable size variation exists within *A. australis* which is not consistent with clinal variation.

While size is important, body length was not considered a reliable guide in itself because measurements can vary considerably due to a number of factors; for example, the freshness of material, the inclusion of gravid specimens, the nature of preservative and length of time in fixative. Consequently, the results of this research are based on measurements of important specific morphological features which remain relatively constant within populations.

A comprehensive description of the nymphal population is presented for the first time and is therefore applicable only to the small specimens recovered from the Cumberland State Forest, Sydney, N.S.W. Lack of material representative of southeastern Australia precluded a reliable assessment in this respect.

ACKNOWLEDGEMENTS

I wish to thank Dr. N. I. Platnick (American Museum of Natural History), Dr. M. Gray (Australian Museum), Dr. M. S. Harvey (Western Australian Museum) for loan of material and Dr. N. N. Tait for reviewing the manuscript.

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Pied Currawongs (*Strepera graculina*): their Diet and Role in Weed Dispersal in suburban Sydney, New South Wales

ROBIN A. BUCHANAN

BUCHANAN, R. A. Pied Currawongs (*Strepera graculina*): their diet and role in weed dispersal in suburban Sydney, New South Wales. *Proc. Linn. Soc. N.S.W.* 111 (4), 1989: 241-255.

In this dietary study of an abundant population of pied currawongs (*Strepera graculina*) 1009 regurgitated pellets, collected over 25 months, were analysed. The percentage of pellets containing plant parts, mostly seeds of fleshy fruit, was high throughout the year (79-98%). The fruit of introduced plants was present in 45-91% of pellets containing plant material. The seeds of 46 species, of which 36 were introduced, were identified in their pellets.

Fruits of the family Oleaceae, including the three introduced species, *Ligustrum sinense* (small-leaved privet), *Ligustrum lucidum* (large-leaved privet) and *Olea africana* (wild olive) were the most significant part of the currawong diet for three months of the year, when at least one of these species was present in 54-74% of the pellets analysed. Other major plant species in the diet included the introduced *Pyracantha angustifolia*, *Morus nigra*, *Ochna atropurpurea*, *Solanum pseudocapsicum*, and the native *Elaeocarpus reticulatus*.

The proportion of pellets containing animal parts decreased from a value of 50-75% in the warmer months to 11-12% in the coldest months of the year. Few vertebrate remains were found in the pellets; the major animal components identified were bullants (*Myrmecia* spp.), beetles, and other insects.

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INTRODUCTION

A varied diet, intelligence and bold behaviour have contributed to making the pied currawong (*Strepera graculina*) one of the most successful and abundant birds in suburban environments throughout eastern Australia (Readshaw, 1968; Wimbush, 1969; Blakers *et al.*, 1984). Within twenty years of European colonization, pied currawongs had exploited new habitats and foods provided by settlement (Currey, 1966); and by the 1920's they were listed as one of the main dispersal agents of *Opuntia* spp. (Anon, 1920; 1927). More recently it has become clear that they are also agents for the dispersal of two abundant privet species (*Ligustrum sinense*, *L. lucidum*) in suburban Sydney (Walsh, 1965; Vellenga, 1966; Rose, 1973; Clyne, 1980). Despite their large size (41-51cm), abundance and role in weed dispersal, the diet of pied currawongs has not been studied in detail.

Rose (1973) systematically sampled regurgitated pellets, but many other accounts are largely anecdotal. Reports of their animal prey occur in Lea and Grey (1936), Marshall (1935), Roberts (1942), Readshaw (1965), Recher (1976), and Cooper and Cooper (1981) and include many insect orders as well as worms, snails, crabs, birds, mammals and carrion. Items of fruit eaten are frequently listed in catalogues of regional birdlife (Table 1).

From October 1976 to October 1978 the pellets regurgitated by pied currawongs in a garden in suburban Sydney were collected and their contents analysed. Objectives of this survey were: to record details of the larger contents of pellets, relating them to seasonal abundance of dietary components; to discuss the dietary findings in relation to the role of pied currawongs in weed dispersal in the Sydney region.

TABLE 1

Fruits and seeds reported in previous studies and additional to those recorded from Thornleigh

Identification ^x	Author	Type of Record +
MONOCOTYLEDONES		
Poaceae		
*Maize	Edwards 1922	N
DICOTYLEDONES		
Anacardiaceae		
* <i>Schinus molle</i>	Rose 1973	P
*Pepper Tree	Cheney 1915	O
*Pepper Tree	Bourke 1949	O
Aquifoliaceae		
*Holly Tree	Vallenga 1966	O
Cactaceae		
*Prickly Pear	Morse 1922	N
*Prickly Pear	Anon 1920	N
*Prickly Pear	Anon 1927	N
Loranthaceae		
Mistletoe	Cleland, Maiden, Ferguson & Musson 1918	S
Loranthus	Lea and Gray 1936	S
Mistletoe	Keast 1958	N
Mistletoe	Rose 1973	P
Malvaceae		
# <i>Lagunaria patersonia</i>	Smith, Larkins & Pegler 1984	N
Mimosaceae		
# <i>Paraserianthes lophantha</i>	Smith, Larkins & Pegler 1984	N
Moraceae		
Moreton Bay Fig	Agnew 1922	O
<i>Ficus macrophylla</i>	Robertson 1969	O
Myrtaceae		
# <i>Eucalyptus caesia</i>	Smith, Larkins & Pegler 1984	N
Philesiaceae	Rose 1973	P
Rosaceae		
*Loquat	Roberts 1942	N
*Wild Raspberry	Marshall 1935	O
*Rowan	Vallenga 1966	O
*English Laurel	Vallenga 1966	O
Rutaceae		
*Orange and Lemon	Roberts 1942	O
Santalaceae		
<i>Exocarpos stricta</i>	Lea & Gray 1936	S
Solanaceae		
*Chillies	Bravery 1970	O
Vitaceae		
Native Grape	Cleland, Maiden, Ferguson & Musson 1918	S

x = The common or scientific name is listed in the same form as that given in the relevant paper.

* = introduced to Australia.

= indigenous to Australia but not to the Thornleigh area.

+ N = not stated.

O = observation while feeding.

P = pellet

S = stomach content.

SITE DESCRIPTION

The study was carried out at Thornleigh, 19km north-west of Sydney, New South Wales; area features are illustrated in Fig. 1. Thornleigh is situated on a ridge 1-3km wide with the steep-sided valleys of the Lane Cove River to the south-east and Berowra Creek to the north-west. Both valleys are forested and the land to the west of Berowra

Creek is rural. Most of the suburban development consists of detached dwellings in gardens well vegetated with native and introduced trees and shrubs. The percentage of suburban development within a one to three kilometre radius of the study site ranges from 50 to 67% respectively, with the remainder being natural vegetation.

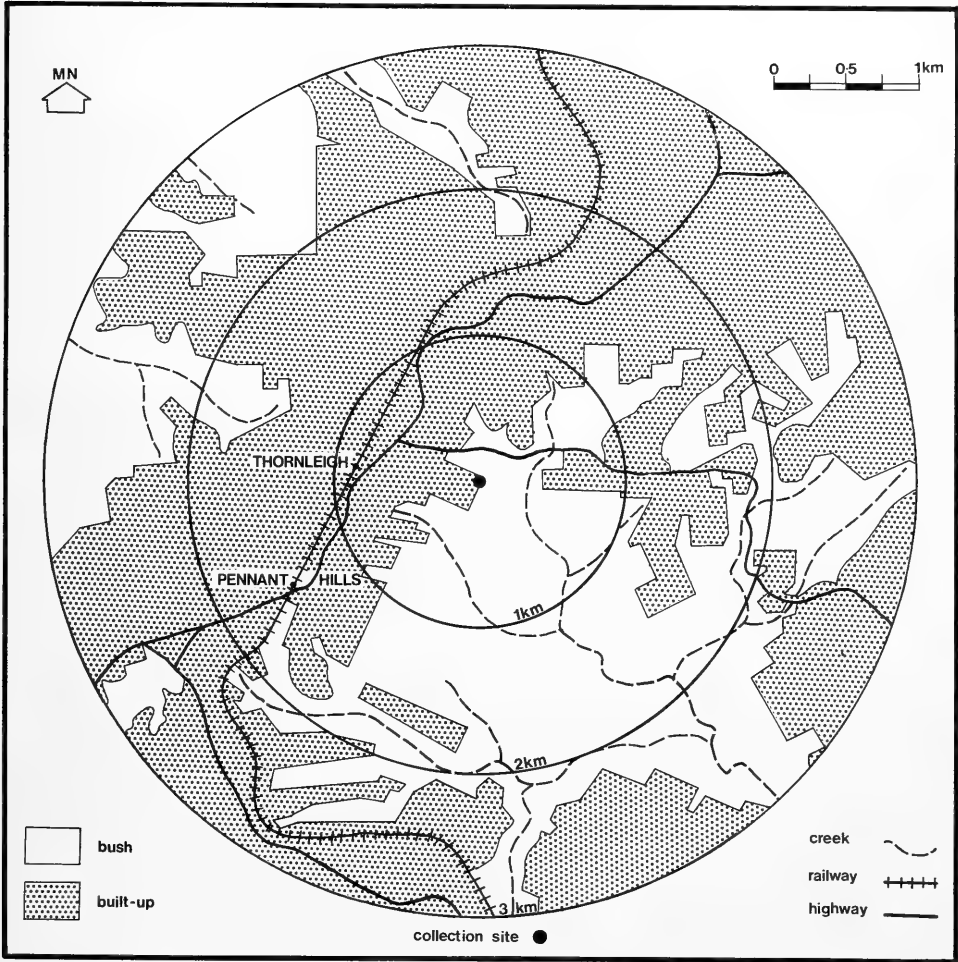


Fig. 1. Map of the environs of the collection site showing the distribution of the built-up areas and native vegetation.

The majority of the natural vegetation is woodland/open-forest (Specht, 1970) and is included in the Sandstone Complex, both wet and dry sclerophyll, of Specht *et al.*, (1974). Most of the slopes are free of weeds but *L. sinense* and other weeds are abundant along the creek and river banks.

Regurgitated pellets were collected at the junction of built-up and forested areas on the eastern side of Thornleigh. The collection site was a lawn surrounded by a dense growth of shrubs and trees; pied currawongs were attracted by bread, honey, seed, meat and water.

METHODS

Pellets

Pellets were collected twice a week over an area of approximately 150 m² from October 1976 to October 1978. In total 1 009 pellets were examined; the highest number sampled in any one month was 53 and the lowest 8 (Table 2). In October 1978 some 41 pellets were analysed.

TABLE 2

Number of pellets analysed in the 24 month period (October 1976–September 1978) and collected in the second year

Year	O	N	D	J	F	M	A	M	J	J	A	S
1 (Analysed)	51	41	39	51	43	22	39	49	43	53	49	40
2 (Analysed)	48	41	46	45	24	20	8	41	46	44	40	45
2 (Collected)	119	64	90	96	24	20	8	53	114	57	120	132

The sampled pellets were divided into three classes of coherence; coherent (collected intact or almost intact), partly coherent (collected in more than one piece), not coherent (collected completely fragmented). The lengths and widths of coherent pellets were measured and the contents of coherent and partly coherent pellets were then separated by stirring them in water and filtering. All pellets separated into individual fragments with this treatment. Only the larger fragments, identifiable at 40x magnification, were noted.

Component Identification

Most seeds were identified by comparison with seeds from known plants and by identification of young plants grown from seeds in the pellets. Some of the rarer seeds in the pellets were identified by the National Herbarium (Sydney). Scientific and vernacular names are listed in Table 3; botanical and common names follow the National Herbarium of New South Wales. Classification of invertebrates — based on Commonwealth Scientific and Industrial Research Organization, 1970 — was only attempted to class or order and rarely to genus. Many tiny invertebrate fragments remained unidentified. Some bone fragments were identified by the Australian Museum, Sydney. The number of different components, identified to class or genus for insects, and species for plants was tallied for each pellet.

The plant species most frequently present in pellets was assessed by counting the number of pellets in which a species was present in each month.

Bull-ants (*Myrmecia* species)

As the number of pellets containing bull-ants showed a strong seasonal pattern, an estimate of the activity of bull-ants was obtained by observing six nests for 5-10 minutes on one afternoon a week during the second year of the study. The largest number of ants present on the surface of the nest during this time was recorded. The average number of observed bull-ants was then calculated for each month.

TABLE 3
Species of fruit recorded in pellets

Classification (Common Name)	Highest frequency in any one month (%)				
	0-10	10-30	30-50	50-70	70-90
GYMNOSPERMAE					
Cupressaceae					
* <i>Juniperus</i> sp. (Juniper)	X				
MONOCOTYLEDONES					
Arecaceae					
* <i>Phoenix</i> sp. (Palm)		X			
Asparagaceae					
#0* <i>Protasparagus aethiopicus</i> (Asparagus Fern)	X				
Asteliaceae					
+ <i>Cordyline rubra</i>	X				
Phormiaceae					
<i>Dianella caerulea</i> (Flax Lily)	X				
Smilacaceae					
<i>Smilax glycyphylla</i> (Thornless Smilax)	X				
Zingiberaceae					
#0* <i>Hedychium gardnerianum</i> (Ginger Lily)	X				
DICOTYLEDONES					
Anacardiaceae					
#0* <i>Toxicodendron succedaneum</i> (Rhus)		X			
Araliaceae					
0* <i>Hedera helix</i> (Ivy)	X				
<i>Polyscias sambucifolia</i>		X			
Cornaceae					
* <i>Dendrobenthamia capitata</i>	X				
Ebenaceae					
* <i>Diospyros kaki</i> (Persimmon)			X		
Elaeocarpaceae					
<i>Elaeocarpus reticulatus</i> (Blueberry Ash)		X			
Euphorbiaceae					
<i>Omalanthus populifolius</i> (Poplar-leaved Omalanthus)	X				
Lauraceae					
#0* <i>Cinnamomum camphora</i> (Camphor Laurel)					X
Magnoliaceae					
0* <i>Magnolia grandiflora</i> (Evergreen Magnolia)	X				
Malvaceae					
+ <i>Lagunaria patersonia</i> (Norfolk Island Hibiscus)	X				
Meliaceae					
0 + <i>Melia azedarach</i> (White Cedar)				X	
Moraceae					
* <i>Ficus carica</i> (Commercial Fig)			X		
<i>Ficus rubiginosa</i> (Port Jackson Fig)		X			
0* <i>Morus alba</i> (Mulberry)					X
Myrtaceae					
<i>Eucalyptus resinifera</i> (Red Mahogany)	X				
+ <i>Syzygium paniculatum</i> (Lilly Pilly)		X			
Ochnaceae					
#0* <i>Ochna atropurpurea</i> (Ochna)		X			
Oleaceae					
#0* <i>Ligustrum lucidum</i> (Large-leaved Privet)			X		
#0* <i>Ligustrum sinense</i> (Small-leaved Privet)				X	
#0* <i>Olea africana</i> (Wild Olive)		X			
Phytolaccaceae					
#0* <i>Phytolacca octandra</i> (Ink Weed)	X				
Pittosporaceae					
<i>Pittosporum undulatum</i> (Pittosporum)		X			

TABLE 3 (Cont'd.)

Classification (Common Name)	Highest frequency in any one month (%)				
	0-10	10-30	30-50	50-70	70-90
Proteaceae					
<i>Persoonia pinifolia</i> (Pine-leaf Geebung)		X			
Rosaceae					
#0* <i>Cotoneaster glaucophyllus</i> (Cotoneaster)	X				
#0* <i>Duchesnea indica</i> (Wild Strawberry)	X				
* <i>Fragaria ananassa</i> (Strawberry)		X			
* <i>Malus</i> sp. (Apple)		X			
* <i>Prunus</i> sp. (Plum and Cherry)		X			
#0* <i>Pyracantha angustifolia</i> (Orange Firethorn)			X		
* <i>Pyrus</i> sp. (Pear)	X				
#0* <i>Raphiolepis indica</i> (Indian Hawthorn)	X				
* <i>Rubus x loganobaccus</i> (Loganberry)	X				
Rubiaceae					
<i>Morinda jasminoides</i>	X				
Rutaceae					
* <i>Citrus sinensis</i> (Orange)	X				
Solanaceae					
#0* <i>Solanum pseudocapsicum</i> (Madeira Winter Cherry)		X			
Sterculiaceae					
0+ <i>Brachychiton acerifolius</i> (Illawarra Flame Tree)	X				
Verbenaceae					
#0* <i>Lantana camara</i> (Lantana)		X			
Vitaceae					
0* <i>Parthenocissus</i> sp. (Virginia Creeper)	X				
* <i>Vitis labrusca</i> (Grape)		X			

* = introduced to Australia
 + = indigenous to Australia but not to the Thornleigh area
 0 = present in the forest
 # = reproductive in the bushland
 No notation = native to the area

RESULTS

Pellets

Occurrence

The smallest number of pellets collected occurred in the autumn months (Table 2), a period which coincided with a seasonal decrease in the number of birds visiting the site (Buchanan 1983). Only eight pellets were collected in April, a deposition rate of 0.05 per square metre per month. The highest number occurred in September when 132 were collected, a deposition rate of 0.9 per square metre per month. The decrease in the number of pellets collected in July cannot be explained.

The average width of coherent pellets was 15mm with a standard deviation of 0.32. The average length of coherent pellets was 27mm with a standard deviation of 0.64. The maximum number of non-coherent pellets (Fig. 3) was recovered over the late autumn and winter months of April, May, June, July and August, when the pellets lacked animal remains to bind the seeds together (Fig. 4). The maximum number of coherent pellets was recorded in October (58%) and November (71%) when pellets contained large amounts of mulberry (*Morus alba*). The majority of these multiple fruits were relatively intact.

The data collected over 25 months showed that feeding is concentrated on one or a few items during the time needed to produce a pellet (Fig. 2). Almost 40% of pellets contained one component and more than 70% contained one or two.

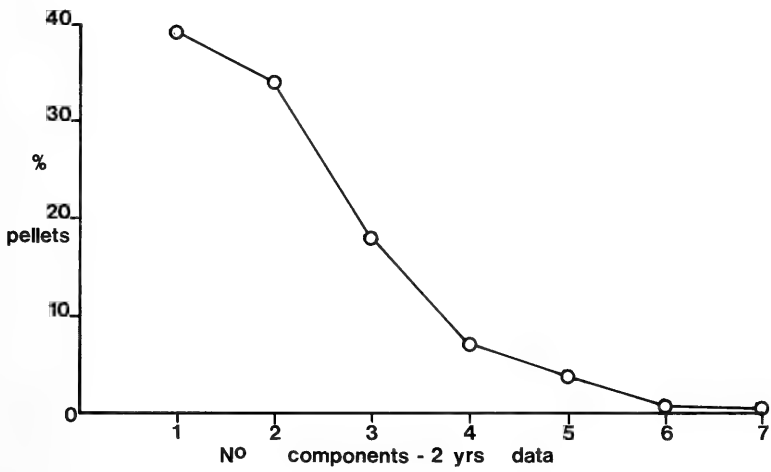


Fig. 2. Percentages of pellets containing different numbers of different components for the 25 month period.

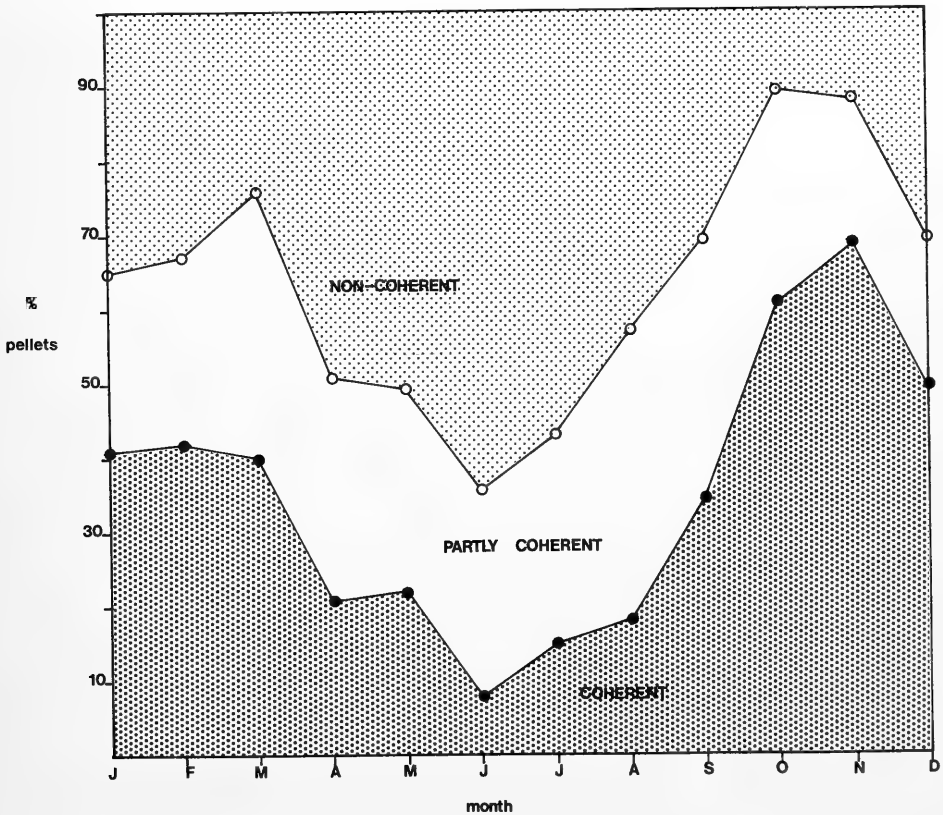


Fig. 3. Average monthly percentages of coherent, partly coherent and non-coherent pellets.

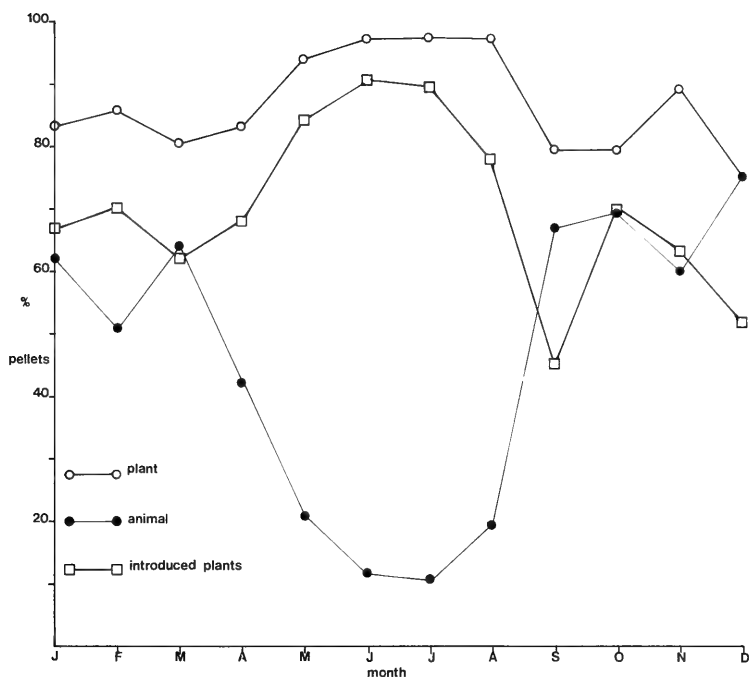


Fig. 4. Average monthly percentages of pellets containing plant parts, introduced plants and animal parts for the 25 month period.

Components and Seasons

Plant Content

The percentage of pellets containing plant parts remained high (79-98%) throughout the two years (Fig. 4). Fruit and seed was the major component (Table 3) but leaves and flowers were recorded in 3% and 0.6% of pellets examined. Almost half (22) of the 46 recorded fruits and seeds were present in less than 10% of the pellets in any one month (Table 3). Twenty-one species were abundantly represented, (Fig. 5).

Oleaceae, including *Ligustrum sinense*, *L. lucidum* and *Olea africana* were present in over 20% of pellets from May to September and peaked at 74% in July. *L. sinense* was the most abundant and was present in over 20% of pellets for three months of the year (Fig. 6). The consumption of *Olea africana* was highest in the early winter months but never peaked above 20% and *L. lucidum* was the most important in the later part of winter (26% in August).

Two other common weeds of urban native vegetation, *Ochna atropurpurea* and *Cinnamomum camphora*, were a prominent part of the diet in summer and autumn respectively. Insufficient sampling may have exaggerated the importance of *Cinnamomum*

camphora in April of the second year — only eight pellets were collected. *Morus alba* dominated the diet in October and November and *Pyracantha angustifolia* was consumed for several months of the year (Fig. 5).

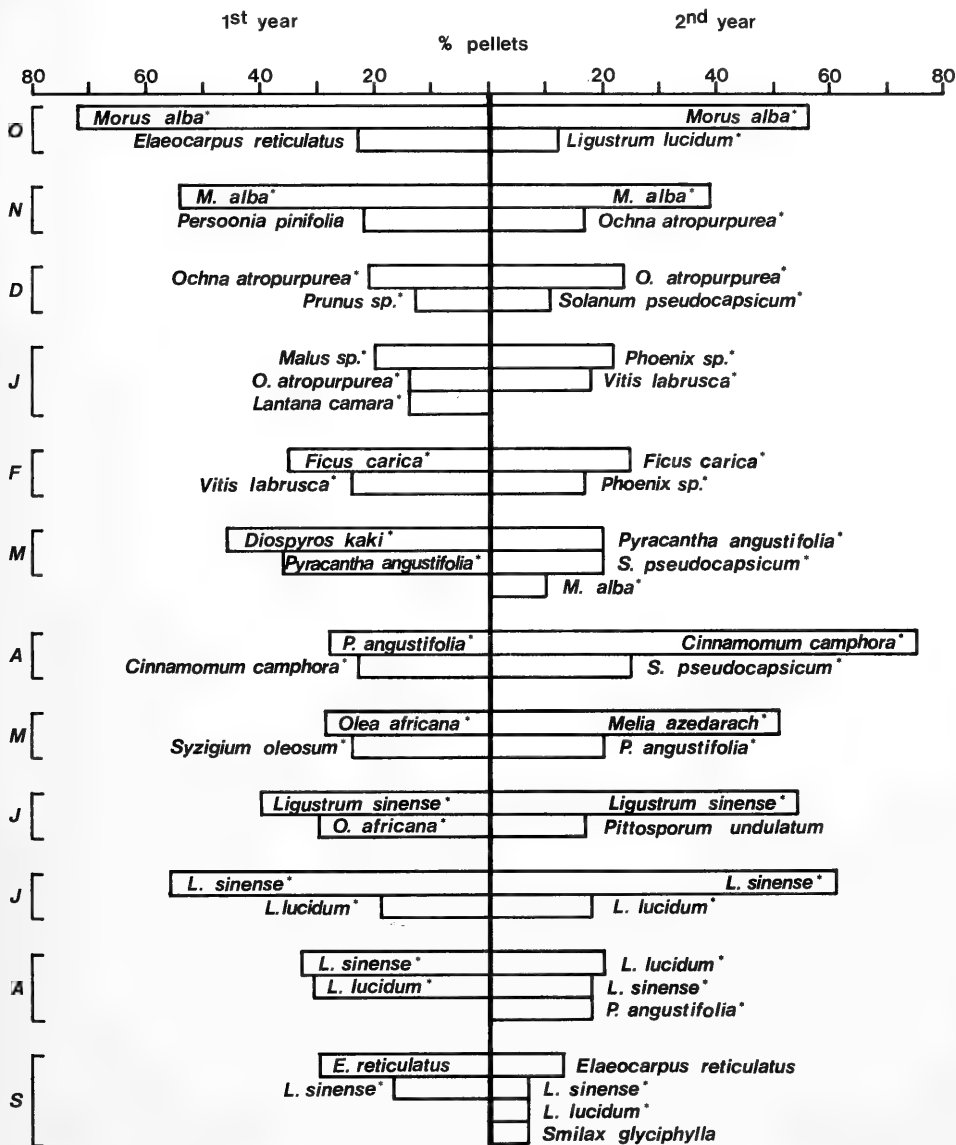


Fig. 5. The two plant species most frequently present in pellets for each month, showing changes between the first and second years of the 25 month period.

Introduced plants were present in 50-90% of pellets in all but one month (Fig. 4). Twenty-one of the 36 introduced plants recorded are present in the bushland and at least 15 of these produce seed in this situation. Only 10 of the 46 species were native to the Thornleigh area. The most important of these were *Elaeocarpus reticulatus*, *Persoonia pinifolia*, *Pittosporum undulatum* and *Smilax glycyphylla* (Fig. 5). Only *Elaeocarpus reticulatus* was

the dominant native species in any month (September). *Pittosporum undulatum*, which has a similar habit and similar habitat requirements to *Ligustrum sinense* and which is dispersed over the same months as the Oleaceae, was sparingly eaten.

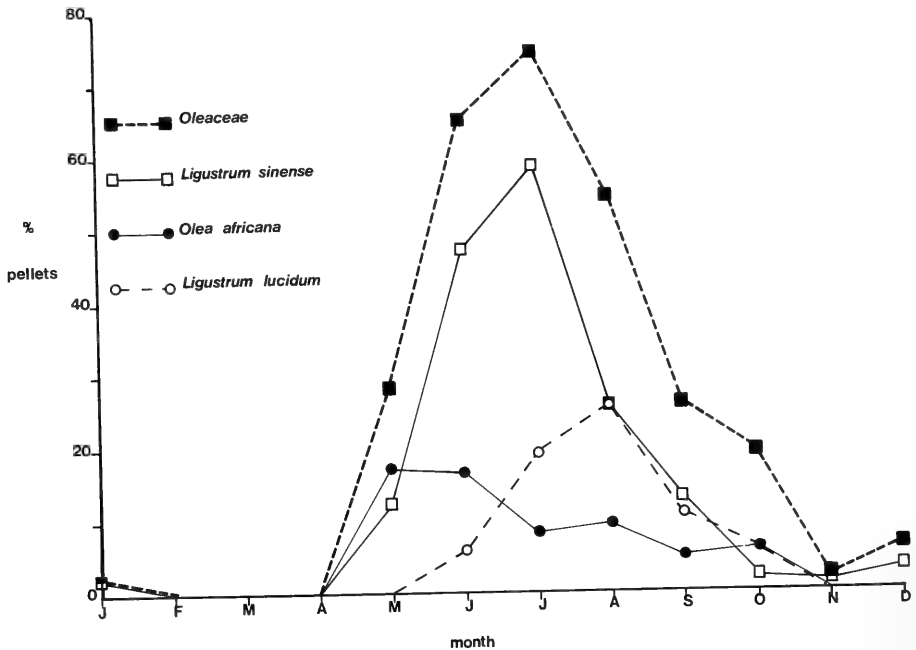


Fig. 6. Average monthly percentages of pellets containing Oleaceae, *Ligustrum sinense*, *Ligustrum lucidum* and *Olea africana*.

The data in Table 4 indicate that the fruit of the most favoured species have an average diameter greater than 5mm. Fruits of several species (*Morus alba*, *Ficus* sp., *Solanum pseudocapsicum* and *Pittosporum undulatum*) contained many seeds; but, the majority of fruit eaten contained only one or two seeds. For this latter group, the smaller the fruit is, the higher the number of seeds contained in a pellet. Fruits 5-6mm in diameter were represented by an average of 8-42 seeds per pellet while large fruit such as *Persea pinifolia* (14mm), *Syzygium paniculatum* (14mm) and *Melia azedarach* (13mm) were only represented by 2-5 seeds per pellet. Flesh and skin, but no seeds, of the very large fruited apple and persimmon were recorded in the pellets. The maximum number of seeds per pellet for *Ligustrum sinense* was 162, *Lantana camara* 131, *Ligustrum lucidum* 67, and *Ochna atropurpurea* 42.

The major fruits in the currawong diet ranged in colour from bright orange (*Diospyros kaki*, *Pyracantha angustifolia* and *Solanum pseudocapsicum*) to green (*Vitis labrusca* and *Persea pinifolia*) to black-blue for 7 of the 21 most frequent species.

Fruit Selection

Only ripe fruit was eaten or ingested by the pied currawongs. For green and pale-coloured fruit pied currawongs appeared to use means other than colour to determine ripeness. Just before *Melia azedarach* fruit first appeared in pellets, individual currawongs were observed to visit the tree; in each case the bird selected several fruits, held each one in the beak for a few seconds, and then dropped it. It is suggested that the birds were

assessing the yellowish coloured fruit for ripeness by testing the softness of the pericarp with their beaks or tasting the flavour of exuded juices.

TABLE 4

Fruit size and colour, number of seeds per fruit, average and maximum number of seeds in pellets

Species	Colour of fruit	Av. diam of fruit (mm)	No. seed per fruit	Av. No. seed per pellet	Max No. seed per pellet
<i>Malus domestica</i>	green or red	fruit very large — only skin and flesh ingested, no seed			
<i>Diospyros kaki</i>	orange	fruit very large — only skin and flesh ingested, no seed			
<i>Morus</i> sp.	dark red	may have many hundreds of seeds per pellet			
<i>Phoenix</i> sp.	red	26x15	1	3	10
<i>Ficus</i> sp.	brown	may have many hundreds of seeds per pellet			
<i>Prunus nigra</i>	dark red	approx 20	1	1	10
<i>Pittosporum undulatum</i>	orange	only consume seed	many	approx 50	approx 200
<i>Vitis labrusca</i>	green & purple	10-15	0-3	3	10
<i>Persoonia pinifolia</i>	green	14	1	2	9
<i>Syzygium paniculatum</i>	light purple	14	1	3	7
<i>Melia azedarach</i>	pale yellow	13	1	5	23
<i>Solanum pseudocapsicum</i>	orange	10	many	approx 60	approx 300
<i>Cinnamomum camphora</i>	black	10	1	4	23
<i>Elaeocarpus reticulatus</i>	blue	9	1	7	22
<i>Pyracantha angustifolia</i>	orange	8	5	approx 60	204
<i>Olea africana</i>	black	7	1	8	23
<i>Ligustrum sinense</i>	black	6	1	36	162
<i>Ligustrum lucidum</i>	black	6	1 or 2	18	67
<i>Ochna atropurpurea</i>	black	6	1	8	42
<i>Lantana camara</i>	black	5	1	42	131
<i>Smilax glyciphylla</i>	black	5	1 or 2	10	54

Animal Content

The percentage of pellets containing animal parts was highest (50-75%) in the warmer months but decreased to a low of 11-12% in the two coldest months of the year, June and July (Fig. 4). Remains of 7 major animal groups were recorded; these were Gastropoda, Arachnida, Diplopoda, Insecta, Amphibia, Aves and Mammalia.

Vertebrate remains were rare in the collected pellets and only 14 contained bone fragments (Table 5). The fragments in seven of the pellets were too small for identification, but of the remaining seven, two were from birds, two from frogs, two from house mice (*Mus musculus*) and one was a chicken bone.

The majority of the animals eaten were invertebrates — especially insects. Adult beetles, lepidopteran larvae and hymenopterans, — particularly bull-ants — were the most abundant remains (Table 5). The percentage of pellets containing bull-ants was high in the summer months, peaking at 47% in December, but fell to 0.4% during the winter months. This decrease was correlated with reduced bull-ant activity outside the nest (Fig. 7).

TABLE 5
Animal remains identified in pellets

Categories of Animal Remains	Month and Number of Pellets Containing Item											
	J	F	M	A	M	J	J	A	S	O*	N	D
Gastropoda (snails)							2		2			
Arachnida (spiders)											1	
Diplopoda (millipedes)					1							
Insecta												
Ephemeroptera (mayflies)											1	
Blattodea (cockroaches)					1							1
Mantodea (praying mantids)	1											
Dermaptera (carwigs)	3									1		
Orthoptera (grasshoppers & crickets)			1	1			1		1	2		1
Hemiptera (bugs)												2
Coleoptera (adult beetles)	30	16	9	8	10	3	4	7	40	61	28	38
Lepidoptera (moth & butterfly larvae)	5	2	1	1	1	2	3	3	12	19	9	10
other	1		2	1	1	1		1	1	2		
Hymenoptera (sawflies, wasps, bees & ants)												
<i>Myrmecia</i> sp. (bull-ant)	23	19	14	6	4	3		3	20	52	26	40
other	3	3	4	2	5		1	1	3	3	1	10
Unidentified	20	12	10	6	5		2	2	11	20	25	13
Bone	2	1	2	1		1	1	1	2	2		1
Egg shell								1	2	4		
Number of pellets examined	96	67	42	47	90	89	97	89	85	140	82	85

* = 3 months' data

DISCUSSION

Pellets and Diet

The examination of regurgitated pellets does not reflect the complete diet since only indigestible items are recorded (Dorst, 1971). The comparative volume of items in the pellets is also only a general guide to their importance in the bird's diet. For example, remains of lepidopteran larvae were usually only represented by the head capsule even though the larvae may have contributed a significant portion of the day's intake of food. On the other hand, favoured fruit items such as *Elaeocarpus reticulatus*, *Olea africana*, *Ligustrum sinense* and *L. lucidum* have thin fleshy layers around a hard endocarp and lost very little of their volume after digestion.

Despite the drawbacks outlined above the pellet studies reported here have augmented information on currawong diets in several ways. The importance of plant material in the omnivorous diet has been confirmed, but the wide diversity of fruits and seeds ingested — including many introduced species — has been documented in detail; the variety of animals eaten has also been demonstrated. Seasonal frequency in a number of animal and plant remains, and the small number of dietary components in individual pellets constitutes further evidence that currawongs are opportunistic feeders.

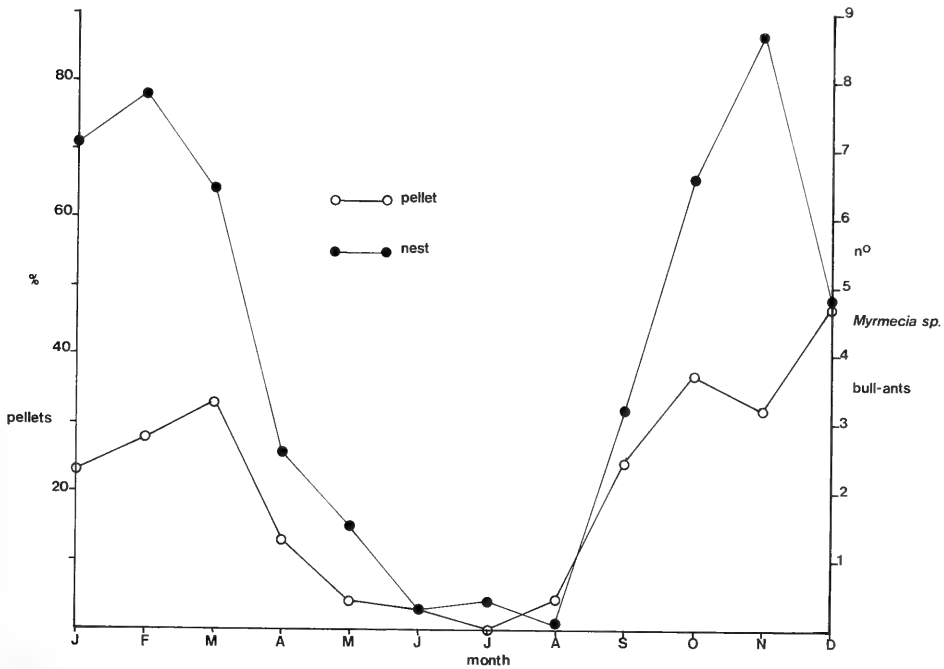


Fig. 7. Percentages of pellets containing bull-ants (*Myrmecia* spp.) in the 25 month period and the average number of bull-ants recorded at nest surfaces for one year.

Fruit Selection and Dispersal

The utilization of a large number of introduced plants as food resources by the currawong has wider implications, because of the potential for dispersal of weed species. Dispersal is only possible if the seed is undamaged by ingestion. Many seeds included in the pied currawong pellets were identified by germinating them and viability was high. *Ligustrum sinense* viability ranged from 83-91% (three samples of 50, 46 and 12 seeds), *Pittosporum undulatum* 100% (8 seeds) and *Toxicodendron succadaneum* 100% (6 seeds).

The Oleaceae (*Ligustrum sinense*, *L. lucidum* and *Olea africana*) seem to be ideally suited to dispersal by pied currawongs. The prolific crop is produced in winter at a time when pied currawongs form large feeding flocks in the warmer parts of their range, including Sydney (Buchanan, 1983). The black-blue colour of the fruit is one of the colours preferred by birds (Turcek, 1963). The size of the fruit is at the lower limit of the size taken by pied currawongs so that large numbers of fruit, and hence seeds are consumed. The ratio of fruit to animals eaten also increases in the winter months so that a higher proportion of fruit may be eaten than in summer. Deposition of at least some of the seed in suitable conditions for germination and establishment (i.e. along creeks and

rivers) is ensured by the fact that pied currawongs usually regurgitate pellets after drinking (Robertson, 1969; Clyne, 1980).

The average number of seeds deposited per square metre can be large; in June 1977 approximately 12 *Ligustrum sinense* seeds were dropped on every square metre of the collection site. The density of deposition away from the collection site would be much less, but the common occurrence of clustered *Ligustrum sinense*, *L. lucidum* and *Cinnamomum camphora* seedlings in natural vegetation confirms that seed dispersal by birds is important.

Some fruit appeared to be rejected by the birds. For example, *Cotoneaster glaucophyllus* is abundant in the study area and carried a prolific crop of fruit each autumn and winter, but was never present in more than 10% of pellets in any one month (Table 3). Rejection of *Cotoneaster glaucophyllus* cannot be explained. It was not on the basis of the thickness of the flesh (1.4mm) as this was greater than for *Elaeocarpus reticulatus* and the Oleaceae (0.8-1.2mm). Fruit size was within the range of the most frequently eaten species (Table 4) and by the colour it should have been selected (Turcek 1963).

As well as the dispersal of obviously palatable items, pied currawongs may also distribute the seed of woody fruit. The fruit of *Eucalyptus resinifera* was found in one pellet. Even if the inclusion of such fruit and viable seeds is a rare event, the possibility for dispersal of minor dietary items is important.

ACKNOWLEDGEMENTS

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Nine New Deep-water Species of Echinodermata from Norfolk Island and Wanganella Bank, northeastern Tasman Sea, with a Checklist of the Echinoderm Fauna

FRANCIS W. E. ROWE

ROWE, F. W. E. Nine new, deep-water species of Echinodermata from Norfolk Island and Wanganella Bank, northeastern Tasman Sea, with a checklist of the echinoderm fauna. *Proc. Linn. Soc. N.S.W.* 111 (4), 1989: 257-291.

Nine new species comprising 3 holothurians, 2 echinoids, 3 asteroids and 1 crinoid are described from the deep waters surrounding Norfolk Island and Wanganella Bank, northeastern Tasman Sea. A checklist of the echinoderm fauna shows at least 123 species are now known for that region, which includes the nine new taxa and seven taxa identified only to the level of genus. Taxonomic notes are included in the checklist for the taxa *Bathyplotes punctatus* (Sluiter); *Holopneustes inflatus* Lütken in Agassiz; *Ophiothrix (Acanthophiothrix) lepidus* de Loriol; *Fromia polypora* H. L. Clark; *Coscinasterias muricata* Verrill; *Astrostole rodolphi* (Perrier); *Oxycomanthus plectrophorum* (H. L. Clark) and *Cenolia spanoschistum* (H. L. Clark).

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INTRODUCTION

Norfolk Island (29°S, 168°E) and Wanganella Bank (c. 32°32'S, 167°32'E) lie to the northwest of the northwest tip of New Zealand. A number of recent, published accounts describe, or include records of echinoderms from those regions (Pawson, 1965b; McKnight, 1967, 1968a,b, 1975, 1977; H. E. S. Clark, 1970, 1982; Baker, 1979, 1980; Rowe, 1977, 1985; Edgecombe and Bennett, 1983; Rowe and Albertson, 1987). During the course of an investigation of the systematic composition and zoogeographic relationships of the echinoderm fauna of New South Wales (Australia), Lord Howe Island and Norfolk Island (Tasman Sea), the author has examined echinoderm material held in the collections of the Australian Museum (AM), Museum of Victoria (MV), National Museum of New Zealand (NMNZ) and the collections of the New Zealand Oceanographic Institute (NZOI). This latter collection includes, particularly, a great deal of material from Norfolk Island and Wanganella Bank along the Norfolk Ridge. Previous publications have recorded nearly 70 species from those regions. The present study has revealed not only nearly double that number (123 species) can be recorded, but that 9 of those are species which are new to science and seven taxa are identified as far as genus. The purpose of this paper is to provide descriptions of the new species and present a preliminary, updated checklist of all the taxa now recognized. The checklist includes a citation of the reference recording the taxon from the vicinity of Norfolk Island or Wanganella Bank; a general distribution similarly with an appropriate reference and/or indication to 'this work' indicating the present author's view; depth range; brief taxonomic note for each of 8 species where a comment is required. New records from Norfolk Island or Wanganella Bank are denoted by an asterisk (*). For the purposes of this report an area delimited by the latitudes 28°-33°S and longitudes 167°-169°E is used to include records from waters surrounding both Norfolk Island (28°-30°S, 167°-169°E) and Wanganella Bank (>30°-33°S, 167°-169°E).

SYSTEMATIC ACCOUNT
 Class HOLOTHURIOIDEA
 Family Holothuriidae

Holothuria (Vaneyothuria) uncia n. sp.
 Fig. 1A-D

Diagnosis: A species in the subgenus *Vaneyothuria* which is distinctively coloured uniformly cream with a chocolate brown ring around each tube-foot and with the rim of the disc of the 3-dimensional table spicules smooth.

Material examined: Holotype, AM J21696, 29°24.8'S, 168°10'E, off Norfolk Island, 342-360 m (NZOI stn I91).

Description: The contracted holotype is about 135mm long and about 57mm wide at the middle of the body. There are 17 tentacles. The tube feet are in three bands along the ventral ambulacra. The ventral-lateral bands are formed by a zigzag alignment of the pairs of tube feet. The mid-ventral band comprises two discrete rows of paired tube feet, the rows spaced about 6-8mm apart. Dorsally the tube feet are more or less scattered, without linear arrangement. The body wall is relatively thin. The calcareous ring is stout and not unusual (Fig. 1A). Tentacle ampullae are present. The gonad comprises a large bunch of branched and unbranched tubules on the left hand side of the dorsal mesentery. It lies about 20mm from the anterior end of the body, and the tubules are up to 60mm long. The respiratory trees are not unusual. The gut is full of sand.

Spicules of the tentacles comprise curved spinous rods. The largest rods, from the tentacle stalk, measure up to about 480 μm long x about 50 μm wide. The smallest rods, from the tentacle branches, measure 50-150 μm x 5-7.5 μm (Fig. 1B).

Spicules from the dorsal and ventral body walls comprise tables and buttons. The disc of the tables are squarish to irregularly rounded, smooth-rimmed, 90-105 μm in diameter and with a single ring of 8-10 holes (Fig. 1C). The spire comprises four pillars, joined by one or two cross-beams. The crown of the spire is small (c. 20-25 μm diameter), with a variable number of small spines. The spire is between 70-90 μm in height. The buttons are usually smooth, irregular in outline and usually have three pairs of holes (Fig. 1D). Rarely one or two low knobs may occur along the midline. They measure between 52 μm long x 37 μm wide to 127 μm long x 97 μm wide, with the majority measuring 90 μm x 52 μm . Tables in the dorsal tube feet range up to 112 μm disc diameter, with up to 16 small, peripheral holes, either in a single ring or with some holes offset into a partial, second ring. Buttons are present, but in addition curved and straight supporting rods occur. An irregular end-plate is also present, c. 180 μm diameter. Spicules in the ventral tube feet are often of similar type but the tables range in size from disc diameter 50-90 μm and spires from 40-55 μm in height. The buttons are often elongate (165 μm long x 52 μm wide), with up to 6 pairs of holes. Supporting rods are similar to those in the dorsal appendages and the end-plates range up to 400 μm diameter.

Colour: Uniformly cream, with a narrow basal ring around the ventral tube feet and a much broader (3-4mm diameter) ring of chocolate brown around the dorsal tube feet.

Etymology: Named for *Uncia*, the snow-leopard.

Remarks: This species (*uncia*) is clearly related to *H. (V.) integra* Koehler and Vaney, of which *H. neozaelanica* Mortensen is a synonym (Rowe, 1969; Cherbonnier and Feral, 1981) and which is distributed from the Bay of Bengal, off Port Hedland, northwest Australia, the Philippines and New Zealand. The spiny-discs of *integra* easily separate the two species. Also, the colour of *uncia* is distinctive among known deeper-water species of *Holothuria*.

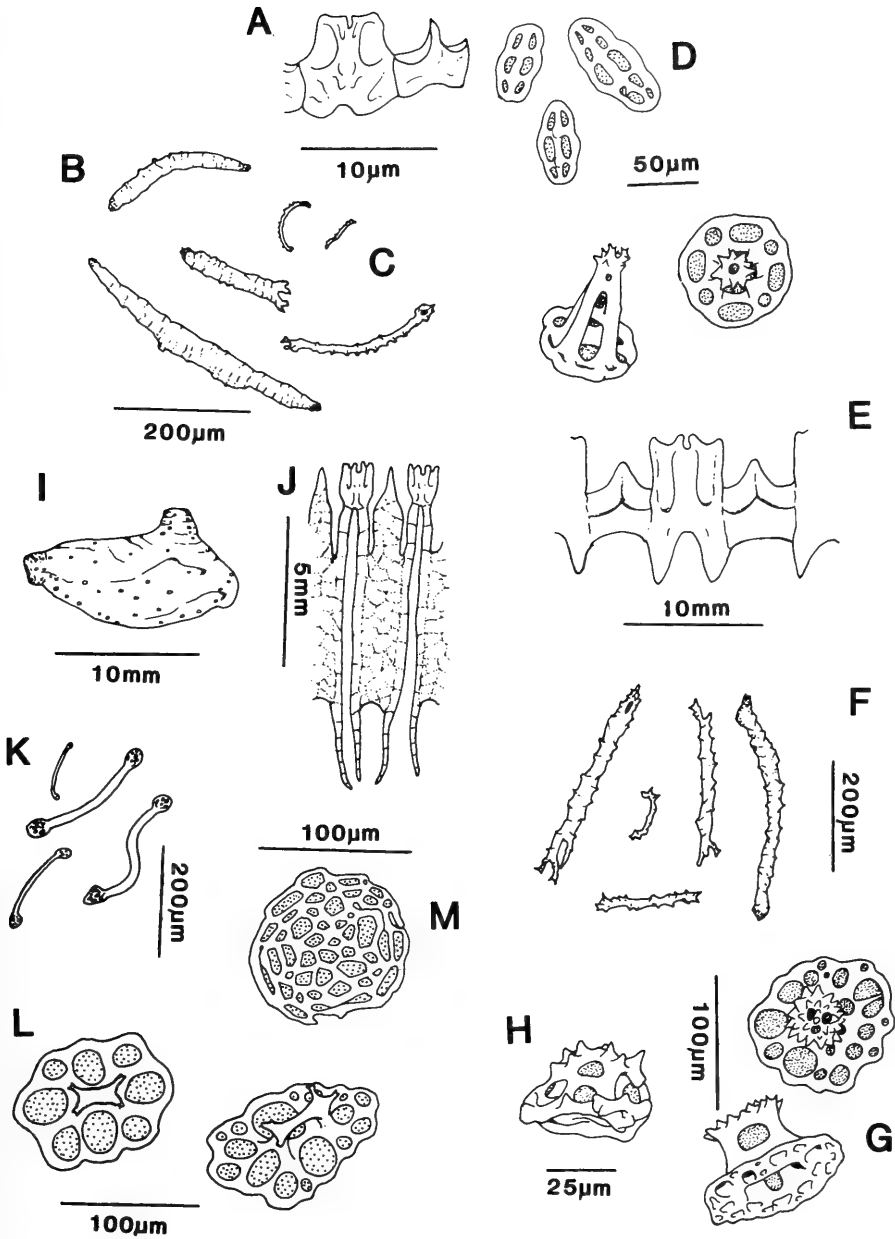


Fig. 1. **A-D** *Holothuria* (*Vaneyothuria*) *uncia* n. sp. (holotype AMJ21696), **A** = calcareous ring, interradial and radial plate, **B** = rods from tentacle, **C** = tables from body wall, **D** = buttons from body wall; **E-H** *Mesothuria* (*Penichrothuria*) *norfolkensis* n. sp. (holotype AMJ21697), **E** = calcareous ring, **F** = rods from tentacle, **G** = tables from body wall, **H** = 'reduced' table from tube-foot; **I-M** *Neothyonidium parvipedum* n. sp. (holotype, AMJ21698), **I** = lateral view of left side of holotype, **J** = calcareous ring, **K** = rods from tentacle, **L** = tables from body wall, **M** = end plate from tube foot.

Family Synallactidae

Mesothuria (Penichrothuria) norfolkensis n. sp.

Fig. 1E-H

Diagnosis: A species in the subgenus *Penichrothuria* which is uniformly creamy-grey in colour; tube feet are scattered over the body but most prominent along the ventral-lateral ambulacra; reduced tables few; normal tables with 4 pillars which are crowned with ring of numerous small spines.

Material examined: Holotype, AM J21697, 28°57.9'S, 167°45.5'E, off Norfolk Island, 392-423m (NZOI stn P35).

Description: The holotype measures about 165mm in length and about 67.5mm in width. It has 17 tentacles. The tube feet are scattered over the body, but are most prominent along the ventral-lateral ambulacra.

There are no tentacle ampullae. The polian vesicle is single. The madreporite lies to the right hand side of the dorsal mesentery. The gonad is a single tuft on the left hand side of the dorsal mesentery. It comprises some 25 tubules, each ending in a number of bifid lobes giving the gonad the appearance of a bunch of grapes. The water vascular ring is separated from the posterior end of the calcareous ring by about 15mm. The gut is packed with fine sand. The calcareous ring is stout, with radial plates deeply notched posteriorly (Fig. 1E).

Spicules from the tentacles comprise more or less straight, or slightly curved, spiny rods. The largest, from the stem, range in length and width up to about 400 μm x 75 μm , respectively. The smallest rods occur in the branches of the tentacles and range between about 60-120 μm in length (Fig. 1F).

Spicules from the body wall comprise tables only. Supporting rods and perforated disc plates are additionally present in the tube feet. Rarely in the tube feet are there small, reduced tables. The tables of the dorsal body wall have a disc diameter of 65-130 μm (Fig. 1G). There is either a single peripheral ring of 8-10 holes or an inner ring of 8 larger holes alternating with a partial or complete outer ring of 4-10 holes. The spire comprises four pillars with one cross beam. The spires are 52-75 μm high and crowned with a ring of numerous small spines. The tables of the ventral body wall are slightly smaller, with disc diameter up to about 112 μm . The tables of the dorsal tube feet are smaller with disc diameters ranging from 50-90 μm and spires up to 52 μm high. Otherwise, the tables have similar appearance to those of the body wall. The supporting rods are curved, perforated terminally and either side centrally. They are up to 187 μm long. The end plates are up to 300 μm in diameter. Small, irregular, reduced tables are present, but very few in number (Fig. 1H). Spicules of the ventral and ventral-lateral tube feet are similar, in all respects, to those of the dorsal tube feet, except that the end plate of the ventral-lateral tube feet have a diameter up to 550 μm .

Colour: Uniformly creamy-grey.

Etymology: Named for the locality of discovery, Norfolk Island.

Remarks: The form of the tables, with a complete ring of numerous small spines at the apex of the spire easily separates this species from all others, including *M. (P.) verrilli* (Theel) and *M. (P.) carnosa* Fisher, in the subgenus *Penichrothuria*. Were it not for the occurrence of 'reduced' tables, albeit few, in the tube feet, I would consider *M. (P.) norfolkensis* closely related to *M. (Allantis) intestinalis* (Ascanius), though separable from it on the shape of the normal tables (the spire is more slender in *intestinalis*). Heding (1942) is quite emphatic that the absence of 'reduced' tables gives a clear limit to the subgenus *Allantis* in which he placed *intestinalis*. Because of the apparent rarity of the 'reduced' tables in *M. (P.) norfolkensis*, a fresh assessment of this character would be usefully undertaken. This is particularly relevant because, in their rarity, these tables can easily be

overlooked. It is on this somewhat shaky character alone that *norfolkensis* is subgenerically separated from its apparent nearest relative, *intestinalis*.

Family Phyllophoridae

Neothyonidium parvipedum n. sp.

Fig. 1I-M

Diagnosis: A species of *Neothyonidium* with a caudal process, small tube feet in double or irregular quadruple rows on the ventral ambulacra, more or less scattered dorsally; calcareous ring tubular, polyplacous, radials with very long posterior processes, interradials almost as long as the processes of the radials; two-pillared tables in body wall.

Material examined: Holotype, AM J21698, 32°36.32'S, 167°30.7'E, Wanganella Bank, 126m (NZOI stn P4).

Description: The contracted holotype is about 15.25mm long and about 6mm wide at mid body. The body is bluntly tapered anteriorly, but narrowing to a distinct caudal process (tail) posteriorly. The tail is dorsally directed, about 2.5mm from the ventral, backward projection of the body (Fig. 1I). The tube feet are small, in double rows in the ambulacra anteriorly and posteriorly. Mid-ventrally the tube feet are widely spaced in somewhat irregular rows with 4 rows of tube feet in each ambulacrum. Dorsally the podia are fewer in number and without apparent regular arrangement.

There are 20 tentacles, 5 pairs of larger alternating with 5 pairs of small tentacles. The calcareous ring is polyplacous, massive, tubular, about 13.25mm long. The radial plates are notched anteriorly, and have very long posterior processes. The interradial plates are pointed anteriorly and long posteriorly, extending to within about 3mm of the end of the ring. The interradials do not have posterior processes (Fig. 1J). The polian vesicle and madreporite are each single. The form of the gonad is difficult to determine but appears branched. It is preserved in a fused condition.

Spicules of the tentacles comprise smooth, straight, curved, S-shaped or, rarely, X-shaped rods (Fig. 1K). The rods are terminally expanded and perforated. They range in size from 75 μm long x 3.5 μm wide to 240 μm long x 17 μm wide.

Spicules in the introvert comprise two-pillared tables. The disc is irregularly oval to squarish. It has 4 large central holes surrounded by up to about 26-30 smaller holes in one or two alternate rings. The disc reaches a maximum diameter of 112 μm . The spire measures up to 75 μm in height, has a single cross-beam and each of the two terminally divergent pillars bears 2-3 spines at the tip.

Spicules in the body wall comprise scattered, two-pillared tables (Fig. 1L). The disc of the tables range from 90 μm x 75 μm to 112 μm x 105 μm . The disc comprises 4 large, alternating with 4 small peripheral holes. Rarely, an outer, incomplete third row of 3-4 smaller holes is present. The spire comprises two pillars joined by a cross-beam. The tips of the pillars diverge and each is usually minutely bifid. The spires range from 40-60 μm in height.

There are only end plates in the tube feet and these range in diameter from 75 μm (anteriorly and posteriorly) to 100 μm (mid-ventrally) (Fig. 1M).

Colour: Uniformly greyish-white.

Etymology: Named for its small tube feet.

Remarks: This species is most closely related to *N. hawaiiense* (Fisher). It differs from *hawaiiense* in possessing a caudal process, in the slightly smaller disc plates from the tube feet, in possessing rods in the tentacles, and in the smaller number of perforations in the discs of the tables in the introvert. It is possible that *parvipedum* will be found to be conspecific with *hawaiiense*, but insufficient material does not permit such a conclusion at this time. I am not convinced by Heding and Panning's (1954) synonymy of Fisher's

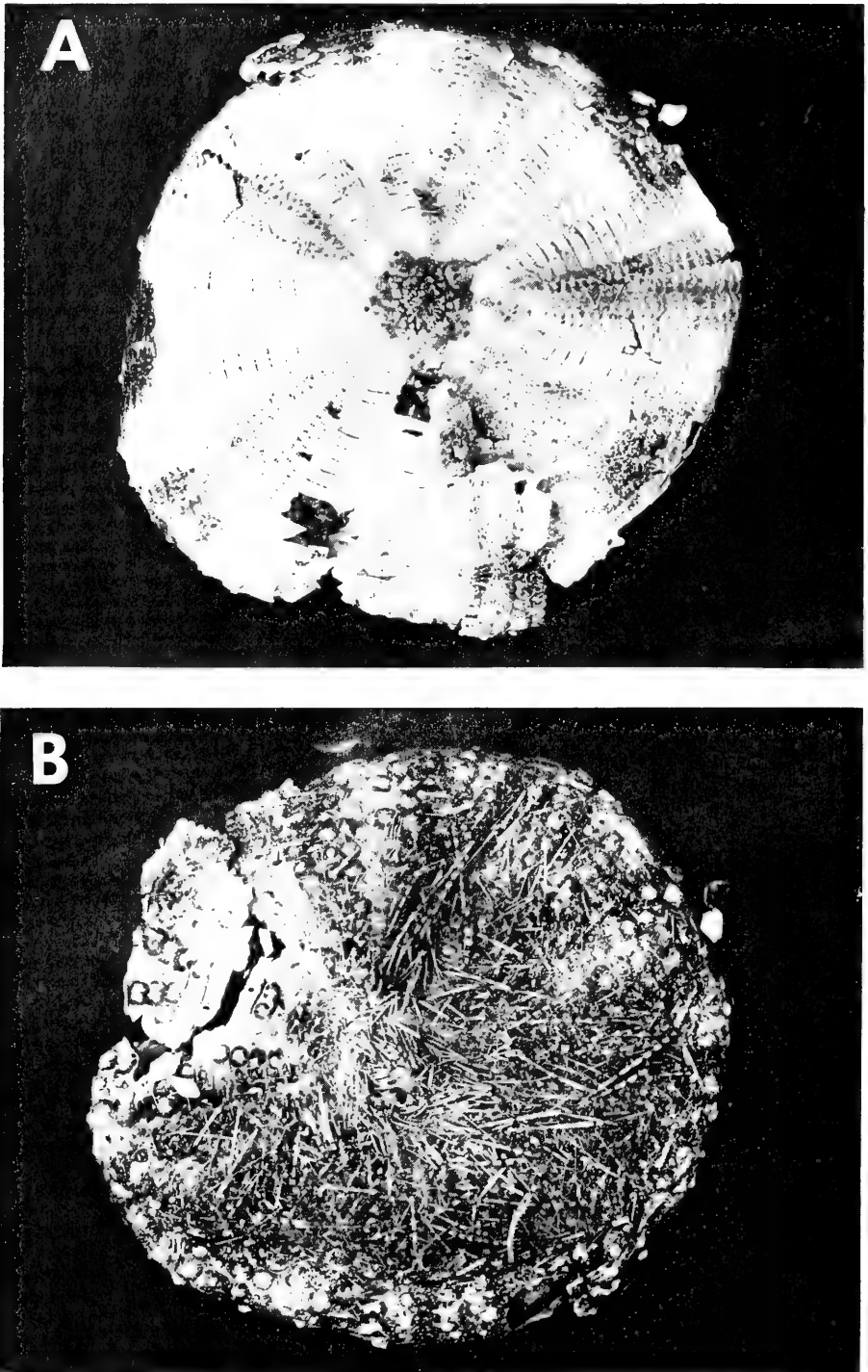


Fig. 2. *Hapalosoma pulchrum* n. sp. (holotype, AMJ21699). **A** = aboral view, **B** = oral view (h.d. = 67.4mm).

(1907) second Hawaiian species *N. alexandri* with *hawaiiense*. There appears to be as close a relationship between *alexandri* and *N. armatum* Pawson, 1965c, from New Zealand as between *hawaiiense* and *parvipedum*.

Class ECHINOIDEA
Family Echinothuriidae

Hapalosoma pulchrum n. sp.
Figs. 2A-B, 3A-B

Diagnosis: A species of *Hapalosoma* lacking aboral primary tubercles.

Material examined: Holotype, AM J21699, 29°54.90'S, 44°0.80'E, off Norfolk Island, 130-301m (NZOI stn P26).

Description: The test is flattened, more or less circular in outline, with h.d. = 67.4mm (Fig. 2A-B).

Apical system: Measures 13mm in diameter. Ocular plates are insert, anvil-shaped, contiguous with the more or less kite-shaped genital plates. The genital pores are large, indicating the probability of a female. A number (8-12) of small tubercles occur on a discrete convexity of the plates adapically to the genital or ocular pores respectively. The madreporite is large and prominent, extending over most of the plate. Apical plates each bear 1 or 2 tubercles (Fig. 3B).

Ambulacra: There are 55 plates in each ambulacral column. Two demi-plates, each pierced by a pore pair, are associated with each ambulacral plate. The pore pair piercing the ambulacral plate lies adjacent to the interambulacral plate. The pore pairs form three columns. A large primary tubercle occurs on each second and/or third plate, internal to the pore pairs on the oral surface as far as the ambitus of the test. A smaller tubercle occurs on each plate between the outer demi-plate and pore-pair piercing the ambulacral plate. A second even smaller tubercle occurs regularly under the pore-pair piercing the ambulacral plate. The latter two tubercles form a regular double series to the ambitus in the oral side. Three or four additional smaller tubercles occur in a median transverse line across the plate. Above the ambitus there are no primary tubercles but a row of 6, diminishing to 0-1 adapically, small tubercles forming a median transverse row on the plates. Skin areas are very narrow, almost obliterated between the plates. The ambulacral width at the ambitus is 14.2-15.6mm (Fig. 3A).

Interambulacra: There are 37 plates in each interambulacral column. The width of the interambulacrum is about 27mm at the ambitus. A large primary tubercle occurs on each of the first 14 plates from the edge of the peristome to the ambitus on the oral side. These tubercles form a regular series adjacent to the ambulacra. One or two additional tubercles, one usually close to the mid interambulacral margin of the plate, also occur, but irregularly on these plates. Up to about twelve minute tubercles occur scattered between the large tubercles. Above the ambitus, from about the 15th plate from the peristome, there are no large primary tubercles. Instead, a median transverse row of small, but equisized tubercles occur on each plate, the number diminishing from 13-14 at the ambitus to 0-1 adjacent to the apical system. Areas of skin between the plates are minimal (Fig. 3A).

All tubercles are perforate and non-crenulate.

Peristome: The peristome measures approximately 14mm in diameter. The plates carry flattened but club-shaped spines and pedicellariae.

Pedicellariae: These are typical of the genus though there is a tendency for the shaft of the bifid-tipped, reduced dactylus pedicellariae to be perforated by up to three small holes.

Colour: Test is pale green, the green being more intense on the ambulacral plates. The

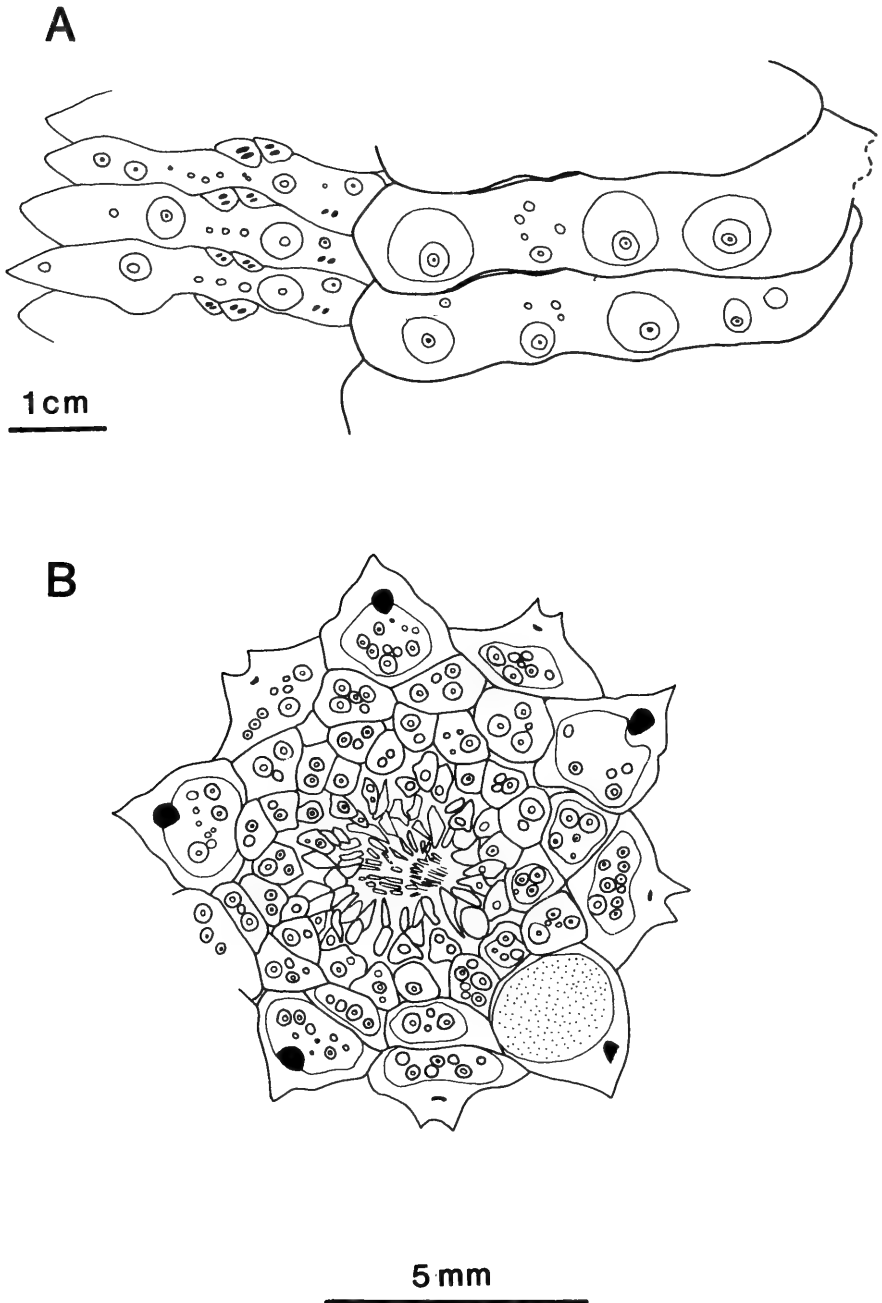


Fig. 3. *Hapalosoma pulchrum* n. sp. (holotype, AMJ21699), A = plates of ambulacrum and interambulacrum, B = apical system.

apical system is purplish. A wide purplish longitudinal band occurs in each ambulacral and interambulacral area orally, extending just above the ambitus as a purple patch.

The larger oral spines are very pale greenish with 5-6 narrow purplish bands. Remains of the white 'hoofs' indicate they are not prominent. The smallest secondary spines are uniformly whitish to pale green as are the abactinal spines.

Etymology: *pulcher* (Lat.) = beautiful, referring to its striking colour pattern.

Remarks: This species differs from its only congeners *H. pellucidum* (A. Agassiz) and *H. gemmiferum* Mortensen primarily by the absence of aboral primary tubercles and spines. The pierced blade of the dactylus pedicellariae and the colour pattern may also be useful differences separating the species. The genus *Hapalosoma* was last reviewed by Mortensen (1935).

Family Pedinidae

Caenopedina alanbakeri n. sp.

Figs. 4A-B, 5A-D

Diagnosis: A species of *Caenopedina* with relatively short primary spines (1.37 x h.d.); apical system 33% h.d.; peristome 25% h.d.; interambulacral plates with large primary tubercle and prominent secondary tubercle the remaining plate surface covered with small tubercles of 2-3 sizes; milled ring of spines 10% wider than the spine; test pale pink, primary and secondary spines uniformly deep pink basally, lighter towards the tip.

Material examined: Holotype AM J21700, 29°24.80'S, 168°13.20'E to 20°23.70'S, 168°13.80'E, off Norfolk Island, 570-578m (NZOI stn I92).

Description: The test is circular at the ambitus, flattened aborally and orally, the sides strongly arched (Fig. 4A-B). The h.d. = 41 mm, v.d. = 26 mm. There are 19 coronal plates.

Apical system: This measures 13.5mm in diameter (33% h.d.) (Fig. 5A). It is dicyclic with oculars all widely exsert. The male genital pores are small, horizontal, slit-like, with a channel extending from the pore to the lower border of the 8th interambulacral plate. The genital plate bearing the madreporite is not enlarged, the madreporite occupying a triangular, central portion of the septagonal plate. There are, more or less, two distinct groups of tubercles on each genital plate. A triangle of 10-11 tubercles occupies the periproctal edge of the plate while a further 9-10 tubercles form a more or less double transverse band across the plate, the remainder of the plate is bare (Fig. 5A). The oculars bear 5-6 small tubercles of which 4-5 form a transverse line straddling the ocular pore, the remaining tubercle occurring towards the inner edge of the plate. The periproct is covered by small plates, the anal aperture more or less centrally placed.

Ambulacra: The ambulacra measure 6.2mm in width at the ambitus (= 35.8% of interambulacra). Ambulacral plates are trigeminate, the pore pairs being in arcs of three on the oral surface from the peristome to the ambitus. Aborally, from about the ambitus to the apical system the pore arcs become more vertically aligned so that the pore pairs form a somewhat sinuous line. The middle component of each plate bears a conspicuous, perforate, non-crenulate, primary tubercle whose areole extends onto the plate components above and below it. These tubercles form a regular vertical series in each column, decreasing in size towards the apical system. Small secondary tubercles, of two sizes, occupy the remaining surface of the ambulacral plates (Fig. 5B).

Interambulacra: The interambulacra measure 17.3mm in width at the ambitus. The plates each bear a large primary tubercle more or less in the middle of each plate. The tubercles form a vertical series. The areoles are large and confluent between plates on the oral surface. On the aboral surface, above the ambitus the areoles are separated adapically by a simple row of small, secondary tubercles. A prominent, secondary tubercle occurs near the mid-interradial edge of each plate, forming a second vertical series below the ambitus but a more or less zigzag series above the ambitus. The remain-

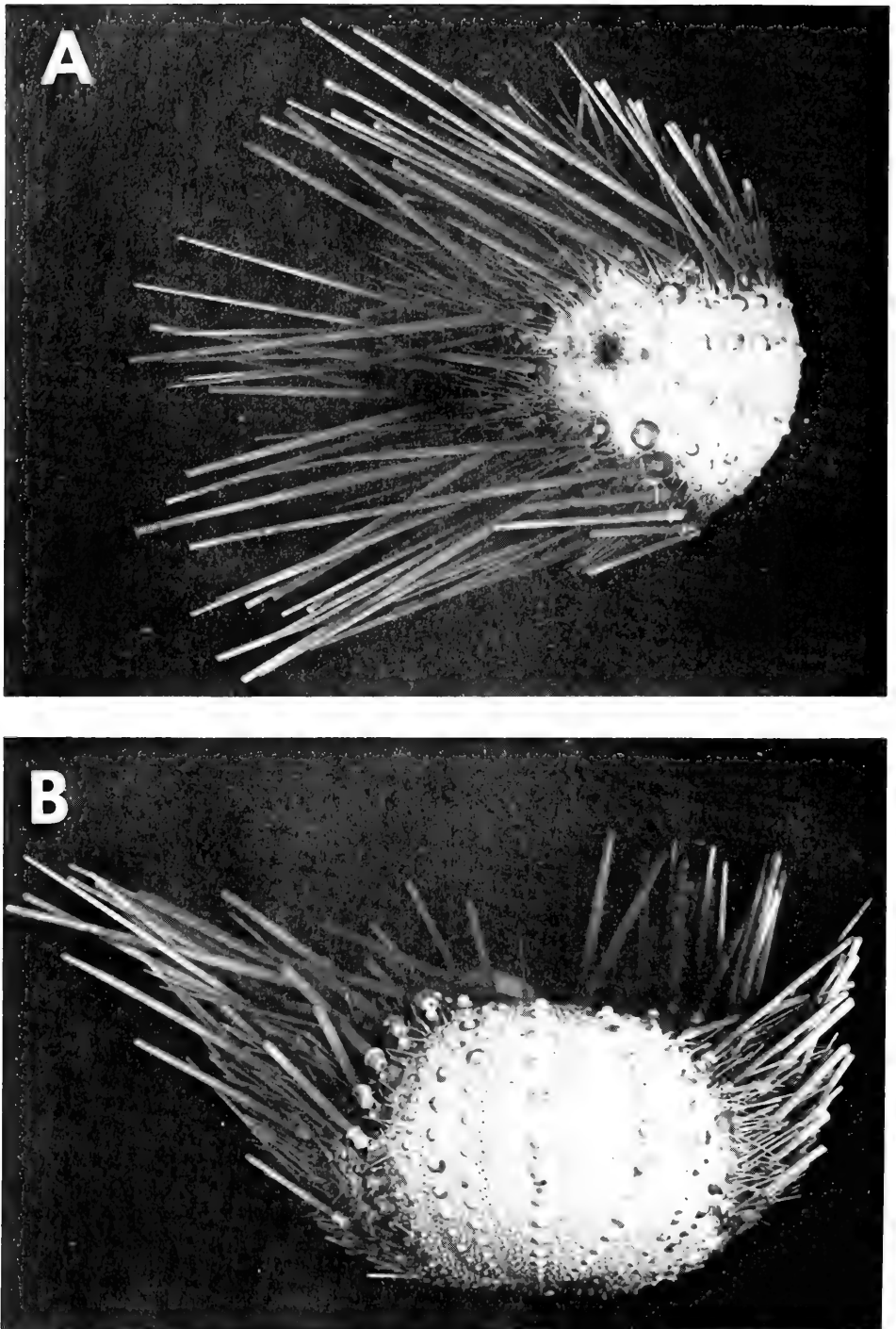


Fig. 4. *Caenopedina alambakeri* n. sp. (holotype, AMJ21700). **A** = oblique aboral view, **B** = lateral view (h.d. = 41mm).

ing surface of each plate is crowded with smaller, secondary tubercles of 2-3 different sizes. All tubercles are perforate and non-crenulate (Fig. 5B).

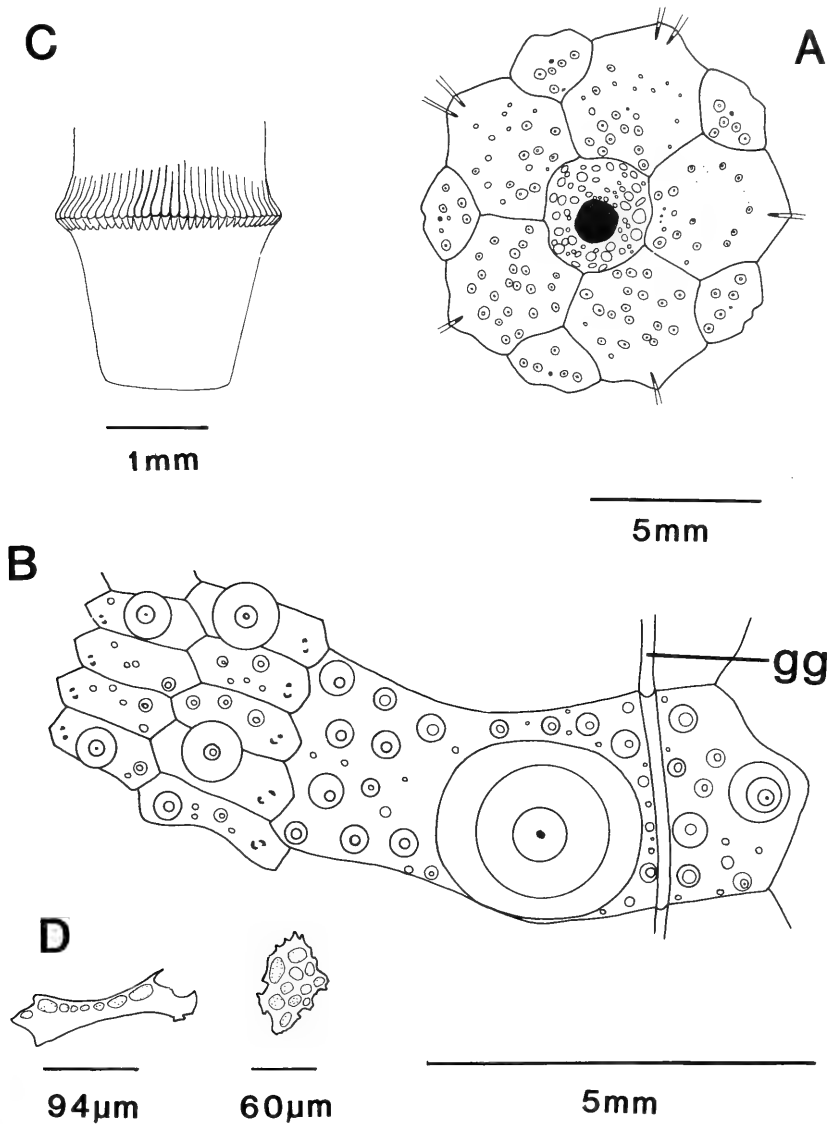


Fig. 5. *Caenopedina alambakeri* n. sp. (holotype, AMJ21700), **A** = apical system, **B** = plates of ambulacrum and interambulacrum, **C** = milled ring of primary spine, **D** = spicules from tube-foot. (gg = genital groove).

Peristome: The peristome measures 10.3mm (+ 25% h.d.). It is finely plated as well as containing the conspicuous buccal plates which bear pedicellariae.

Spines: The longest spines are 56.4mm, slender, tapering, longitudinally striated with minute thorns. The milled ring is conspicuous but not widely produced so that it is only 10% wider than the spine (Fig. 5C). Secondary spines are similar to the primaries but much smaller, about 1/5-1/4 the length of the primaries.

Spicules: The tube feet contain spicules which are slightly curved, irregularly elongate, perforated plates or smooth rods with marginal perforations (Fig. 5D).

Pedicellariae: These do not appear unusual for the genus, or to be distinctive, though the ophicephalous pedicellariae are rare on the test of the holotype.

Colour: The dried test is uniformly a very pale pink (when cleaned with domestic bleach the test is white except for a persistent pink on the plates of the apical system and immediately adjacent coronal plates). The spines are not banded but are deeper pink basally, becoming paler along their length, the distal $\frac{1}{3}$ to $\frac{1}{2}$ of the spine being a pale yellowish/lime colour. The secondary spines are similarly coloured only even paler. The poison sacks of the globiferous pedicellariae are violet/purple. The tube feet are pale brown with the tip sienna brown.

Etymology: This distinctive species is named for Dr Alan N. Baker, National Museum of New Zealand, who has contributed significantly to ophiuroid and echinoid taxonomy in this geographical region.

Remarks: The genus *Caenopedina* A. Agassiz has been reviewed by Mortensen (1940). More recently two species have been described from New Zealand waters; *C. novaezealandiae* Pawson (1964) and *C. otagoensis* McKnight (1968c). *C. alanbakeri* is immediately distinguished from its geographically nearest congener *C. novaezealandiae* Pawson by the colour; the size of the milled ring of the primary spines; the relative sizes of the apical system and peristome to h.d.; the relative number of coronal plates and tuberculation of the plates. Although the primary spines are not banded, *C. otagoensis* McKnight is otherwise distinguished from *C. alanbakeri* on similar comparative features to those of *C. novaezealandiae*. Despite the fact that the primary spines are only 1.37 x h.d., their slender form and the test plate ornamentation immediately distinguish *C. alanbakeri* from either of the short-spined *C. pulchella* (A. Agassiz and H. L. Clark) or *C. superba* H. L. Clark. These features clearly also distinguish *C. alanbakeri* from all other congeners.

Class ASTEROIDEA
Family Astropectinidae

Tethyaster tangaroae n. sp.
Figs. 6A-B, 7A-B

Diagnosis: A species of *Tethyaster* which has stout tabulae (about twice as high as wide); actinal plates with 1-3 prominently elongate central spinelets; adambulacral plates and some actinal and oral plates usually bear a large, elongate bivalved pedicellaria.

Material examined: Holotype, AM J21701, 28°57.90'S, 167°45.50'E, off Norfolk Island, 392-423m (NZOI stn P35), 2 paratypes, NZOI, 28°54.60'S, 167°44.20'E, off Norfolk Island, 390-402m, (NZOI stn P27).

Description: The holotype measures R = 46.5mm, r = 11.3mm, br (at 2nd inferomarginals) = 10.8mm; R/r = 4.1, R/br = 4.3 (Fig. 6A-B). The arms are slender, tapering to a narrow tip which is occupied by a prominent, convex, longitudinally elongate terminal plate. The terminal plate has a bumpy surface when cleaned of the minute spinelets which cover it. The spinelets give the plate a shaggy, felt-like appearance. The abactinal plates have a six-lobed base and are tabulate. They reduce in height towards the tip of the arm. The tabulae are about twice as high as they are wide, somewhat waisted and of two sizes, mixed, which are arranged, more or less, in longiseries on the arms. There are thirteen series at the base of the arm, reducing to four series at the arm tip. It is possible to detect a carinal row of spaced, larger tabulae when the tabulae are cleaned of their spinelets. The centre of the tabulae is occupied by up to 25 short, blunt-tipped spinelets of mixed sizes, and the periphery by up to 25 slender spinelets.

The madreporite is at about $\frac{2}{3}$ r from the disc centre. It bears small spinelets on its

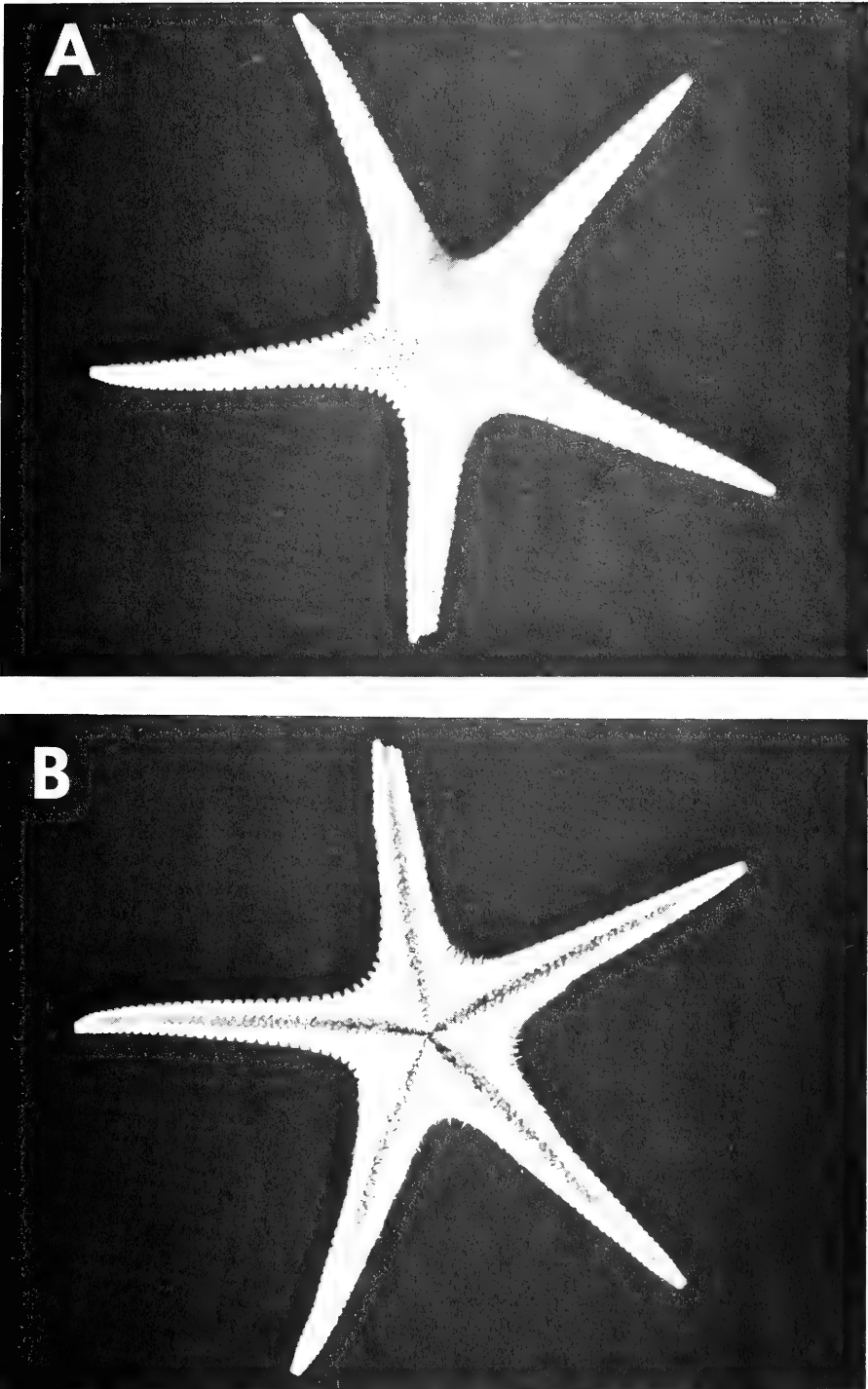


Fig. 6. *Tethyaster tangaroae* n. sp. (holotype, AMJ21701). A = aboral view, B = oral view (R = 46.5mm).

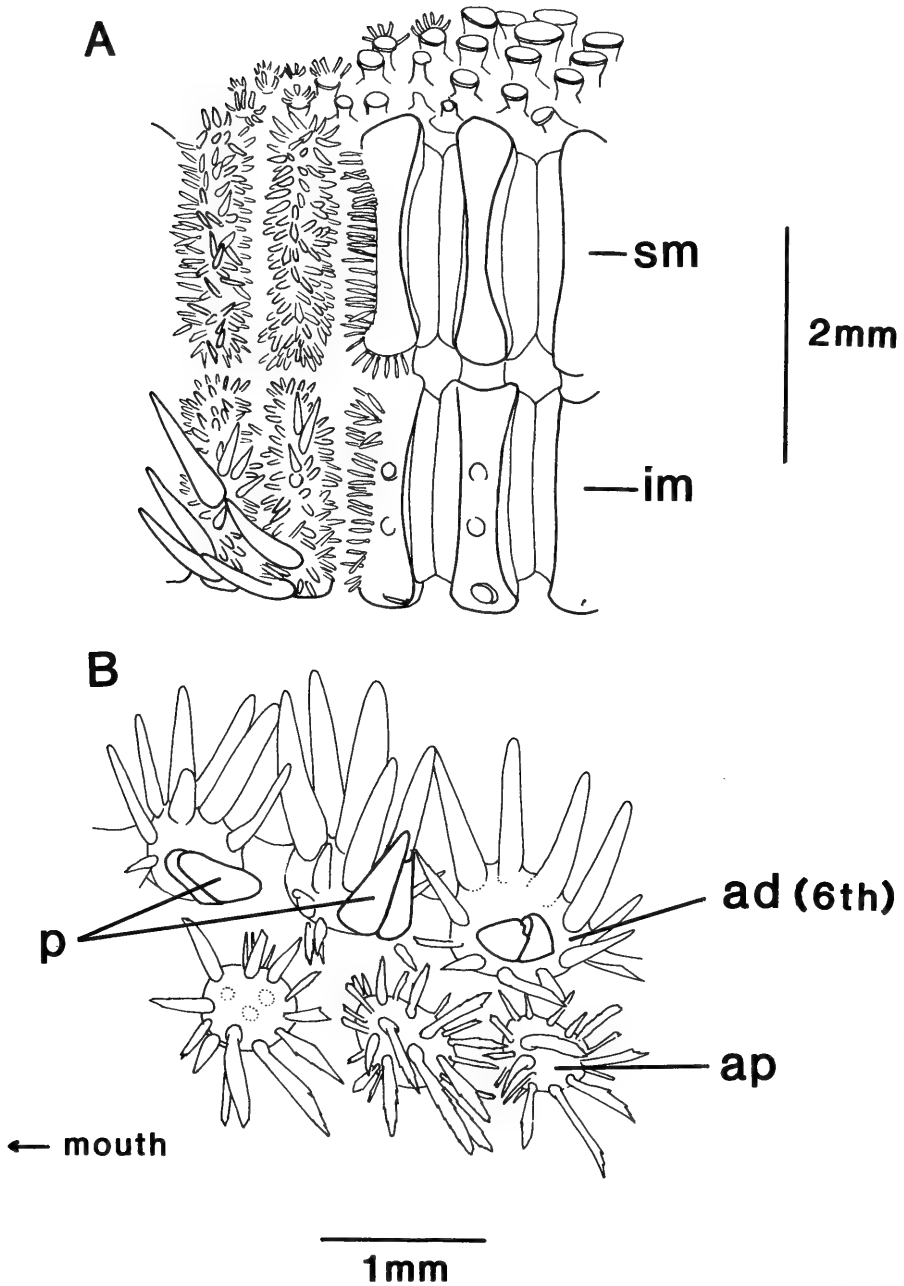


Fig. 7. *Tethyaster tangaroae* n. sp. (holotype, AMJ21701), **A** = superomarginal (sm) and inferomarginal (im) plates in interradial arc, **B** = 4th-6th adambulacral plates (ad) and adjacent actinal plates (ap), showing spines and pedicellariae (p).

corrugated surface and is almost hidden by the spinelets of adjacent tabulae. The disc is more or less flat, though the radial regions, at the base of the arms, are slightly convex.

The papulae are single and occur between the tabulae over the whole abactinal surface, extending to the arm tips.

The supero- and inferomarginal plates are similar in size and shape. There are 34 superomarginals and 35 inferomarginals, the distalmost 2-3 inferomarginals being very small and extending under the terminal plate each side. The marginal plates are vertically elongate, with a raised, flat-topped, rectangular median ridge which leave deep, straight-sided fasciolar channels between successive ridges. The flat-topped surface of the ridges are covered with low bumps, each bump bearing a short, stout spinelet. On the superomarginal plates these spinelets become elongate towards the edge of the ridge where together with those on the adjacent plates the spinelets span and cover the fasciolar channels between. The inferomarginal plates bear a vertical series of 3, proximally, reducing to 1 distally, large flattened, acicular spines across the ridged surface. Additionally, smaller slender, but otherwise similar spinelets cover the remaining surface with fasciolar spinelets, similar to those on the superomarginal plates, at the periphery of the ridge (Fig. 7A).

The actinal surface is relatively small, with 4 rows of plates on each side and a supplementary row of three plates extending along the mid-interradial line between the oral plates and first inferomarginal plates (Fig. 6B). The first actinal row extends to about the 10th inferomarginal plate; the second row extends to about the 6th inferomarginal plate; the third row comprises 3 plates and the 4th is a single plate. The actinal plates have a central convexity which bears elongate spinelets, 1-3 central ones being more prominent, elongate, tapering spines. Several plates bear a large, elongate, bivalved pedicellaria, replacing one or more of the central spines.

The adambulacral plates are somewhat wedge-shaped from actinal aspect, thereby projecting, slightly, into the furrow. There are 3-5 furrow spines, the middle spine being the longer and it is compressed. The actinal surface of the plates bear 3-4 central, elongate spines, one or two of which are replaced by a single, large, bivalved pedicellaria on many plates. The first two adambulacral plates each bear 2-3 such pedicellariae. The periphery of the plates bear a number of smaller, slender spinelets (Fig. 7B).

The oral plates bear 6-7 furrow spines. The two adjacent apical spines are so closely appressed as to appear to be fused together. Along the median crest between the adjacent oral plates is a row of 10-11 elongate spines, the 3rd and 4th of which are replaced by a large bivalved pedicellaria on several of the plates.

Neither of the paratypes possess pedicellariae, otherwise they are similar in almost all other respects to the holotype. One paratype measures $R = 34.6\text{mm}$, $r = 9.2\text{mm}$, $br = 7.6\text{mm}$; $R/r = 3.76$, $R/br = 4.6$. It has 27 superomarginal and 30 inferomarginal plates. There are 3 actinal rows and 2-3 plates form the median interradian row. The second paratype measures $R = 10.3\text{mm}$, $r = 4.2\text{mm}$, $br = 4.7\text{mm}$; $R/r = 2.45$, $R/br = 2.2$. It has 14 superomarginal and 16 inferomarginal plates. The inferomarginal spines are hardly prominent. There are two actinal rows and 2 plates form the median interradian row.

Remarks: *T. tangaroae* differs from its geographically nearest neighbour *T. aulophora* (Fisher) principally by the stouter tabulae, form of the large bivalved pedicellariae, and spinulation of the actinal plates. *T. tangaroae* differs from the South African *T. paei* (Mortensen) by the actinal spinulation and pedicellariae.

The discovery of a species of *Tethyaster* in the Tasman Sea is not an unexpected extension in range of this widespread genus which has been revised by A. M. and A. H. Clark (1954).

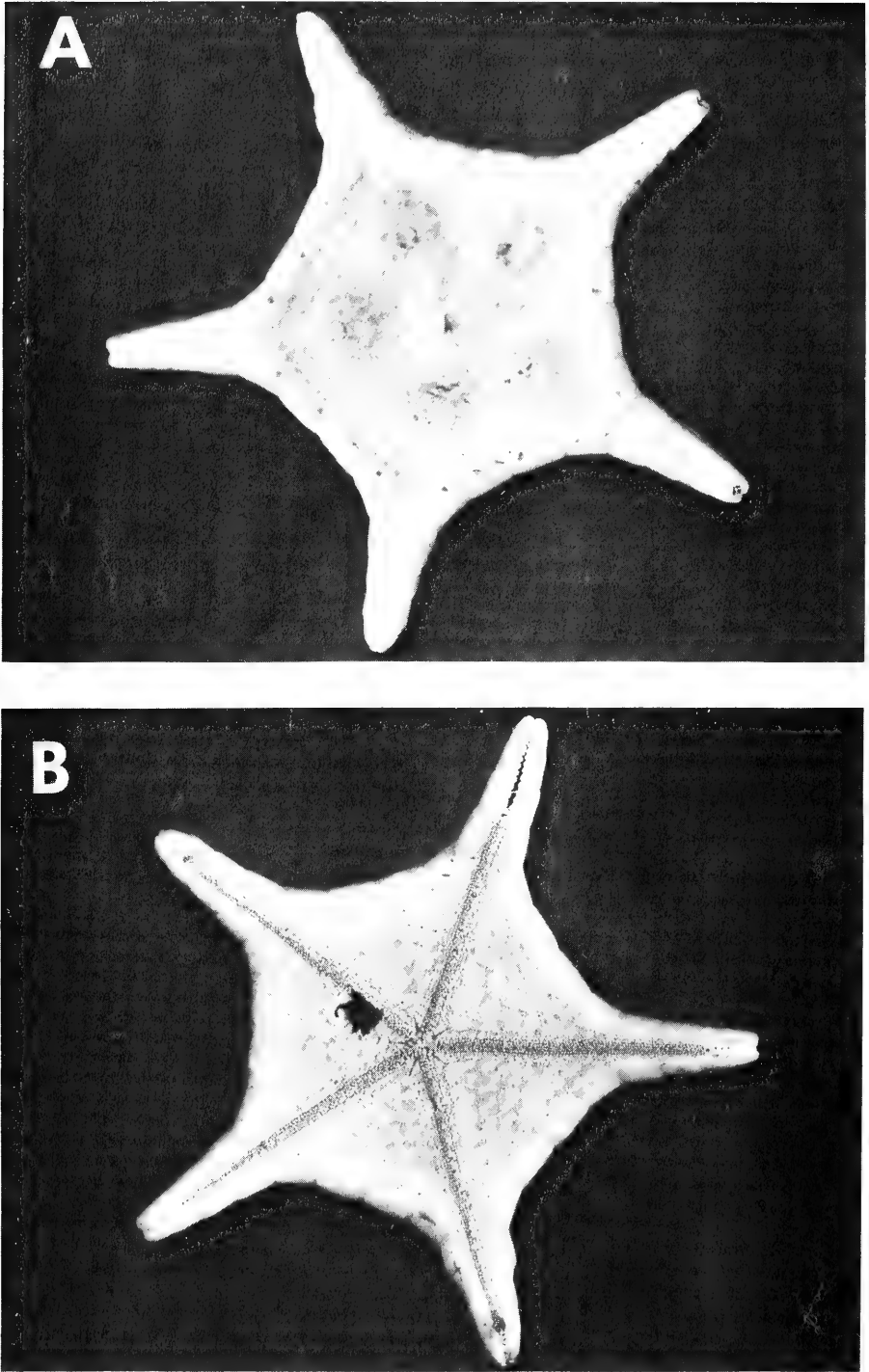


Fig. 8. *Glyphodiscus mcknighti* n. sp. (holotype, AMJ21702), A = aboral view, B = oral view (R = 23mm).

Family Goniasteridae

Glyphodiscus mcknighti

Figs. 8A-B, 9A-B

Diagnosis: A species of *Glyphodiscus* with smooth, flat abactinal plates, smooth marginal plates and few papulae which are restricted to the radii on the disc.

Material examined: Holotype, AM J21702, 28°42.30' S, 167°56.70' E, Norfolk Island, 475-450m (NZOI stn P46).

Description: The holotype measures R = 23mm, r = 11.5 mm, br = 4.2mm (at 2nd inferomarginals); R/r = 2.0, R/br = 5.5.

The abactinal area is pentagonal, slightly produced at the angles and sunken below the level of the superomarginal plates. The abactinal plates are smooth, flat, without crystal bodies. The plates are rounded-polygonal, the interradial plates being slightly larger than the radial plates. A row of narrow, transversely rectangular plates occurs adjacent to the superomarginals. A small, triangular madreporite occurs $\frac{1}{3}$ r from the centre of the disc (Fig. 8A).

The supero- and inferomarginal plates are similar in shape, size and number. They are block-like, smooth, longer than wide with a rounded dorsal-lateral or actinal-lateral edge respectively. There are 6 of each on each side of the disc and arm, the first 2 supero- and inferomarginals of adjacent radii respectively delimiting the pentagonal abactinal and actinal disc surfaces. The remaining 4 supero- and inferomarginals on each side of the arms unite across the arm along the median line. The terminal plate is small, with a convexity at its tip on either side of the actinal channel which houses the terminal tube foot. This channel is guarded by 3-4 minute granules.

The actinal plates are flat, smooth, rather transversely diamond-shaped. They form a regular pavement arrangement (Fig. 8B).

The abactinal, marginal and actinal plates are each surrounded by a single row of minute granules so that a double row of granules occurs between adjacent plates.

Papulae are restricted in each radius abactinally and are delimited as 5 rounded, convex areas each comprising about 10 plates.

Usually 1, occasionally 2, small spatulate pedicellariae occur at the edge of a number of actinal plates, also at the actinal edge of several of the inferomarginal plates (Fig. 9A). Pedicellariae are not present on the superomarginal or abactinal plates of this specimen.

The adambulacral plates bear five laterally compressed furrow spines (Fig. 9B), behind which stands a row of 3 enlarged (subambulacral) granules. The remaining actinal surface of the plate bears 2-3 rows each of 3-4 smaller wedge-shaped granules which merge in size with those surrounding the actinal plates (Fig. 9A).

The oral plates bear 7-8 furrow spines, 4-5 enlarged (suboral) granules and a triangular group of 8-10 wedge-shaped granules on the remaining actinal surface of the plate.

Etymology: Named for Mr D. McKnight of NZOI who has described much of the Tasman echinoderm fauna.

Remarks: I have placed this new species in the herein elevated subgenus *Glyphodiscus* Fisher on the grounds that the species characters are consistent with those outlined for the genus by Fisher (1917, 1919). I believe the smooth plates which lack glassy bumps (crystalline bodies), the complete ring of peripheral granules around all plates and the form of the adambulacral armature are quite reasonably sufficient to distinguish members of this genus from those in either *Iconaster* Sladen, *Lithosoma* Fisher or *Astroceramus* Fisher.

G. mcknighti is clearly distinguished from its only congener *G. perierctus* Fisher which

has roughened superomarginal plates, tumid peripheral abactinal disc plates and papulae distributed over the disc. In respect of size and shape, the two species are very closely similar.

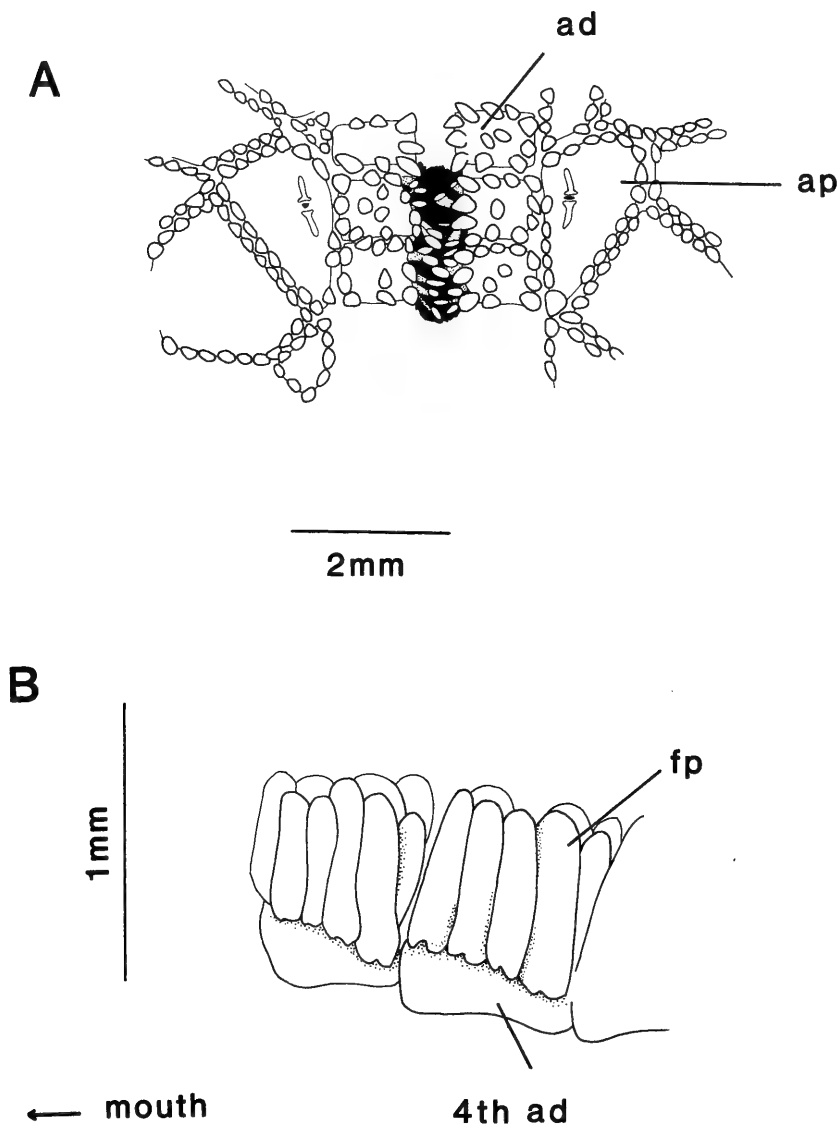


Fig. 9. *Glyphodiscus mcknighti* n. sp. (holotype, AMJ21702), **A** = spine and granule arrangement on adambulacral (ad) and adjacent actinal (ap) plates with pedicellariae, **B** = furrow spines (fp).

Family Brisingidae

Novodinia helenae

Figs. 10A-B, 11A-C

Diagnosis: A species of *Novodinia* with 12 arms, disc with papulae in groups of up to 10,

single madreporite, membranous, unskeletonised genital region of arm, and single adambulacral spine.

Material examined: AM J21703, 29°20.20'S, 168°10.79'E, off Norfolk Island, 308m (NZOI, stn I94).

Description: The holotype has 12 rays; $dd = 14\text{mm}$, $R = 75\text{mm}$, $br = 3.8\text{mm}$ (at base), 5.5-5.9mm (at widest part of genital expansions 12mm from base of ray), 3.0mm (at $\frac{1}{2}R$); $R/r = 10.7$ (Fig. 10A-B).

The disc is circular, 3.7mm high, flattened abactinally. It is covered by overlapping scale-like, and convex abactinal plates which form an open reticulum in which groups of up to 10 (occasionally single) papulae occur. Sharply pointed spines (up to 1.2mm), wreathed almost to their tips with crossed pedicellariae (Fig. 11C) occur on a number of the convex plates. These spines may stand singly, in pairs or triplets. In the latter two cases the spines are united by a web across which the pedicellariae span.

The genital region, at the base of the arm, is covered by a thin, unskeletonised membrane. This region is crossed by 4-5 complete costae. The costae comprise the marginal plate each side of the arm, linked more or less regularly by 7-10 rod-shaped abactinal plates. Costae 1 and 2 may be irregularly linked by a few abactinal plates extending mid-dorsally between them. Most of the plates of the costae, except for the marginal plates of the first two costae, bear a single, sharply pointed, slender spine. Most of these spines are encased in a gland-like sheath of pedicellariae. Beyond the 4th-5th costae the spine bearing marginal plates and abactinal plates form incomplete costae, that is to say a marginal and 4-5 small abactinal plates project dorsalwards along the side of the arm on each side but do not link over the abactinal surface. The link is made instead by a wide band of crossed pedicellariae. The abactinal surface of the arm is then covered by a very thin membrane for the rest of the length of the arm. Abactinally, between each of the incomplete costae a rounded patch of pedicellariae also occurs along the arms. The incomplete costae occur opposite every 4th-5th adambulacral plate along the arm (Fig. 11A).

The adambulacral plates are block-like, wider than long and each bears a large, cylindrical spine (2.5mm) which at least for the length of the genital area are flared into a bi-quadrifid tip. Beyond the genital area these spines are slender and pointed. These spines bear numerous pedicellariae, but these are confined to the outer surface and do not ensheath the spines. The first adambulacral plate of each arm is fused across the interradial line to its adjacent neighbour. However the first two adambulacral plates on each side of each arm are united by a syzygy. Thereafter the plates are united by muscle blocks, the interstices between each successive pair of adambulacral plates being half the length of the plates themselves.

The actinosome is 8mm in diameter and the mouth is 3.6mm wide. The peristome is thin but translucent. The oral plates are as usual for the genus, with lateral processes meeting mid-radially. In well-developed oral angles each plate bears 5 spines in a fan-shaped, marginal arrangement. The innermost spine is usually very small, rarely is it long and bearing pedicellariae. The second spine is always long and pointed and bears pedicellariae. The remaining 3 spines are small, non-pedicellariae bearing and decrease in size towards the furrow. Where arms are being regenerated, the mouth angle plates bear fewer spines (3-4) of which the elongate pedicellariae bearing spine is in the apical position. A small additional spine can be seen to develop in the interradial side of this spine in angles with more advanced regeneration. There are no spines on the actinal surface of the oral plates. The furrow margin of each oral plate is excavate to accommodate the first pair of tube feet (Fig. 11B).

The madreporite (1.2mm diameter) is small, subtuberculate, coarsely furrowed.

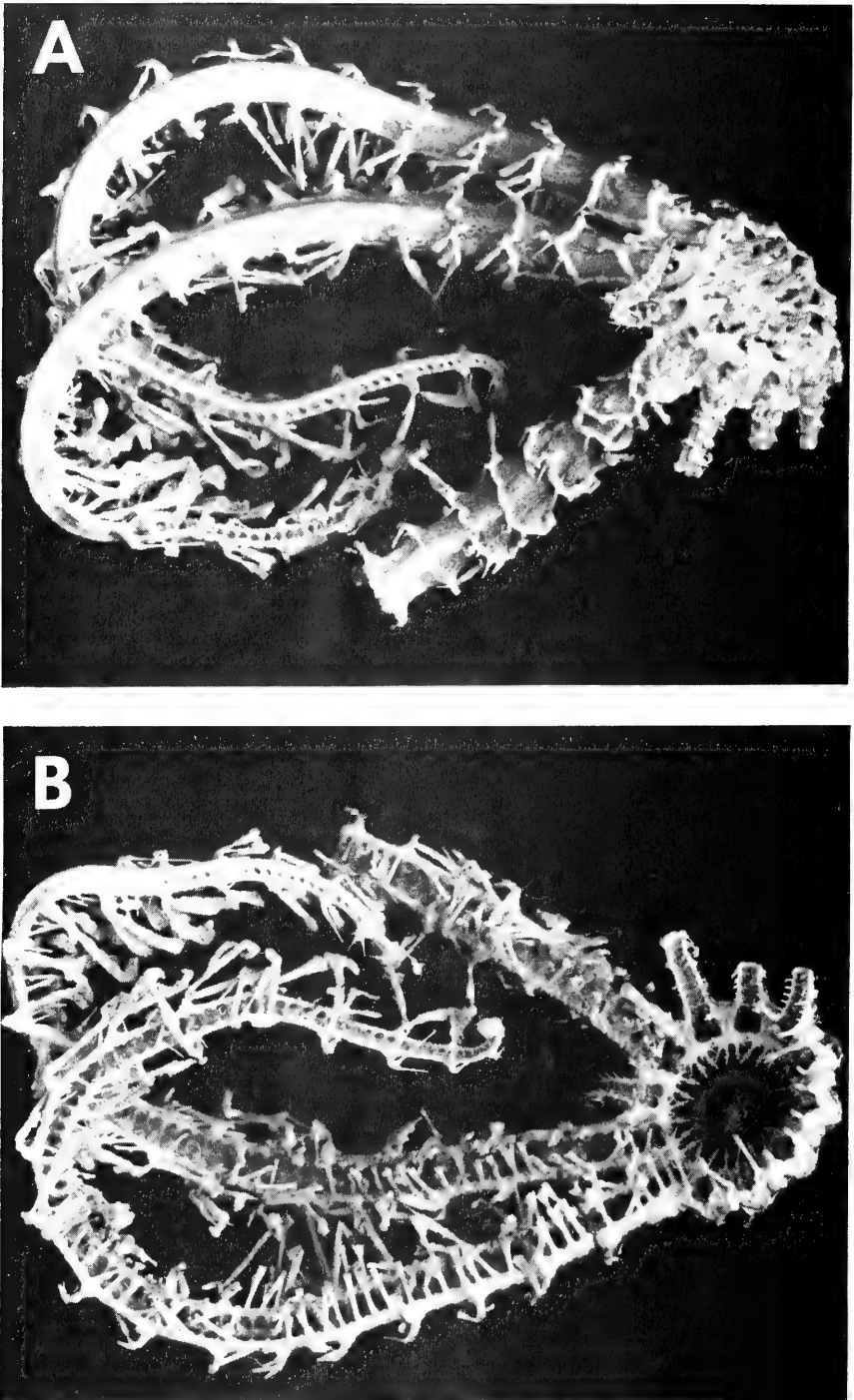


Fig. 10. *Novodinia helenae* n. sp. (holotype, AMJ21703), **A** = aboral view, **B** = oral view (dd = 14mm, R = 75 mm).

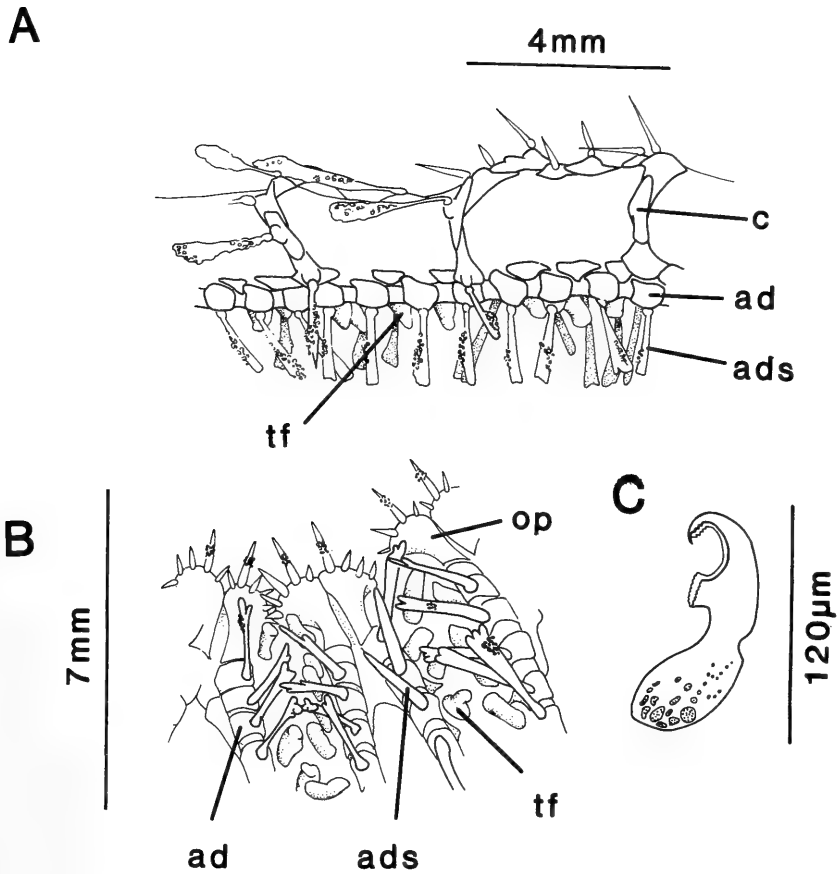


Fig. 11. *Novodinia helenae* n. sp. (holotype, AMJ21703), **A** = costae (c) in genital region of arm, **B** = oral plates (op) and arm bases with spine arrangements, **C** = value of crossed pedicellaria (ad = adambulacral plate; ads = adambulacral spine; tf = tube-feet).

Etymology: Named for Dr Helen E. S. Rotman (nee Clark) who has contributed to our knowledge of Tasman and Antarctic asteroids.

Remarks: The new species clearly belongs in the genus *Novodinia* Dartnall et al., as most recently redefined by Downey (1986). Only two species of *Novodinia* are recorded from the Tasman/New Zealand region. *N. australis* (H. L. Clark), from southeastern Australian waters and *N. novaezealandiae* (H. E. S. Clark), from off the Chatham Islands, east of New Zealand. *N. helenae* is immediately distinguished from each of these species by a number of characters: firstly, low arm number (12) as opposed to 14-16 (*australis*) or 18 (*novaezealandiae*); secondly, abactinal skeletal arrangement of the disc with groups of papulae (in each of *australis* and *novaezealandiae* the skeletal network is close and papulae occur singly); thirdly, the genital area of the arm is membranous in *N. helenae* but plated in the other two species. The number of madreporites (1 in *helenae* but 4 in *australis*) and the number of adambulacral spines (1 in *helenae* but 3-4 spines in *novaezealandiae*) are also features of distinction. Arm number and ornamentation of disc and genital regions readily distinguish *N. helenae* from its other congeners.

Class CRINOIDEA
Family Antedonidae

Nanometra duala n. sp.

Fig. 12A-E

Nanometra johnstoni. McKnight, 1977: 136 (non *N. johnstoni* John)

Diagnosis: A species of *Nanometra* with a pair of wing-like extensions to the segments of P_3 and subsequent pinnules.

Material examined: Holotype, AM J21704 and 2 paratypes, NZOI, 29°20.20'S, 168°10.79'E, off Norfolk Island, 308m (NZOI, stn I94).

Description: The holotype has 10 arms broken at about 20br and measuring about 10mm in length. The estimated length of the arms is not more than 20mm (Fig. 12A). The cirri are XXIV-XXVI, 19-22. The first 2 segments are twice as broad as they are long, the third segment is 1.5 x as long as it is broad, 4th-5th segments twice as long as broad, 6th segment 1.75 x as long as broad, 7th segment 1.25 x as long as broad. Distally, the segments are as long as they are broad. The segments do not bear a dorsal spine but the distal end is expanded (Fig. 12A-B).

The centrodorsal is conical, with a rugose apex. The cirri are arranged in vertical rows of 2 or 3 (Fig. 12B).

The radials are narrow, almost hidden, with a tubercle at each of the exposed corners of the plate.

The 1Br₁ is twice as broad as it is long, with the proximal and distal edges more or less straight but with the distal edge everted. There is a rounded or chisel-shaped tubercle arising on each side of the ossicle and one or two spinulose tubercles below each of these on the dorsal-lateral surface of the ossicle. The axillary (1Br₂) is triangular, slightly broader than long (1.25:1). The proximal border is slightly convex, the distal border everted and spinulose. There are one or two spinulose tubercles occurring on the lateral surfaces of the ossicle (Fig. 12B-C).

Br₁ is quadrate, about 2-2.5 times as wide as long. Up to 4 spinulose tubercles may occur on the lateral surface of the ossicles. Remaining brachials are more or less elongate, wedge-shaped, with the distal edge everted and spinulose (Fig. 12C-D). Syzygies occur at 3+4 and usually 9+10, but occasionally the second syzygy occurs at 8+9 or 11+12 or 13+14. The third syzygy occurs at 14+15 or 15+16. P₁ is the longest pinnule and the stoutest. It is 3mm long, comprising 11 segments. The first segment is broader than long, the second is quadrate, the remaining segments are up to 2 times as long as broad. P_a is about 1.5mm long and comprises 6 segments. P₂ is smaller and more slender than P₁, is about 2mm long and comprises 9 segments. The segments of these pinnules are strongly everted and spinulose on their distal edge. P₃ is the first gonadal pinnule. On P₃ and subsequent pinnules (for the length of the broken arms) the lateral edges of the 2nd to 4-5th segments are expanded into thin, wing-like processes, giving the pinnules a very characteristic form (Fig. 12D).

One paratype is very similar indeed to the holotype in being a relatively intact, if broken armed, specimen. The second paratype comprises the calyx of a specimen with many broken arm pieces. The form of the segments of the pinnules is, however, unmistakable in uniting the specimens within a single species.

Etymology: duo = two; ala = wing (Lat.) referring to the 2-winged appearance of the pinnular segments.

Remarks: The very distinctive form of the pinnule segments immediately distinguishes this species from its congeners *N. johnstoni* John (from S.E. Australia); *N. clymene* A. H. Clark (from the East Indian region) and *N. bowersi* (A. H. Clark) (from southwestern Japan), which have been reviewed by A. H. Clark and A. M. Clark (1967). McKnight's

(1977) record of *N. johnstoni* from the same locality (NZOI stn I94) refers instead, I believe, to the new species *N. duala*.

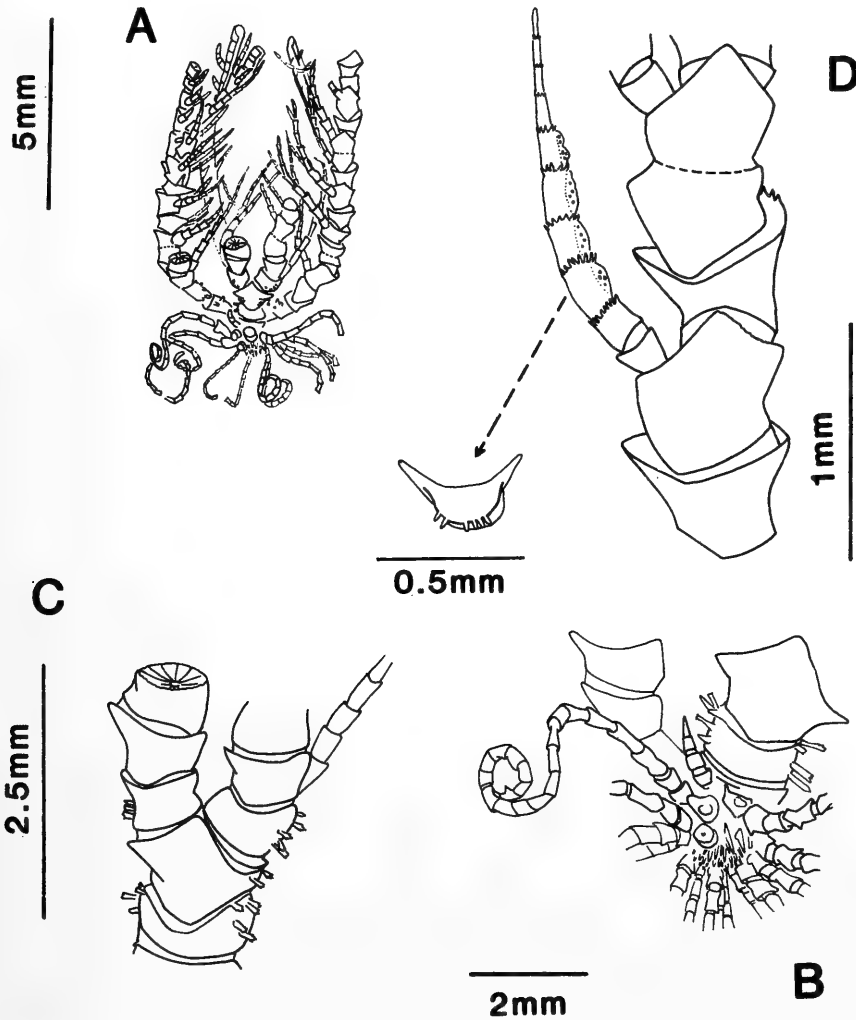


Fig. 12. *Nanometra duala* n. sp. (holotype, AMJ21704), **A** = lateral representation of holotype, **B** = cirri, centrodorsal and 1Br, **C** = 1Br and arm bases, **D** = P_3 with cross-section of pinnule segment showing wing-like extensions.

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TABLE 1
 Checklist of echinoderms from Norfolk Island and Wanganella Bank, northern Tasman Sea, with general distributions and depth ranges. (* = new record.)

Taxon	Norfolk Island 28°30'S, 167° ^a 169°E	Wanganella Bank > 30° ^a 33'S, 167° ^a 169°E	Other Distribution/Authority/Comments	Depth (m)
Holothuroidea				
Family Holothuriidae				
1. <i>Holothuria (Vaneyothuria) uncta</i> Rowe	*	—	This work.	342-360
2. <i>H. (Halodeima) atra</i> Jaeger	Edgecombe & Bennett (1983)	—	Indo-west Pacific; ?eastern tropical Pacific; Clark & Rowe (1971); Rowe (1985).	0-30
3. <i>H. (Lesonothuria) lineata</i> Ludwig	Edgecombe & Bennett (1983)	—	Indo-west Pacific; ?eastern tropical Pacific; Clark & Rowe (1971); Rowe (1985), as <i>H. (L.) parvatis</i> Selenka, non Selenka, 1867.	0-10
4. <i>H. (Mertensiothuria) leucospilota</i> (Brandt)	Edgecombe & Bennett (1983)	—	Indo-west Pacific; ?eastern tropical Pacific; Clark & Rowe (1971); Rowe (1985).	0-10
5. <i>H. (Platyperona) difficilis</i> Semper	Edgecombe & Bennett (1983)	—	Indo-west Pacific; ?eastern tropical Pacific; Clark & Rowe (1971); Rowe (1985).	0-13
6. <i>H. (Stauropora) doyleini</i> Augustin	*	—	Indo-west Pacific; this work.	0-20
7. <i>H. (Thymiosycia) hilla</i> Lesson	Edgecombe & Bennett (1983)	—	Indo-west Pacific; ?eastern tropical Pacific; Clark & Rowe (1971); Rowe (1985).	0-30
Family Synallactidae				
8. <i>Mesothuria (Pentichrothuria) norfolkensis</i> Rowe	*	—	This work.	492-423
9. <i>Bathyplotes natans</i> (Sars)	—	*	Widespread in Atlantic and Pacific Oceans; New Zealand; Southeastern and southern Australia, Pawson (1965a); this work.	200-1600
10. <i>Bathyplotes punctatus</i> (Sluiter)	—	*	Philippines; Malay Archipelago, Cherbon- nier & Féral (1981). I include <i>Karenella gracilis</i> Heding (1940) in the synonymy of <i>B. puncta- tus</i> . Similarly I am of the opinion that <i>Bathy- herpystikes punctatus</i> Sluiter (type-species of <i>Bathyherpystikes</i> Sluiter, 1901) is congeneric with <i>Stichopus natans</i> Theel (type-species of <i>Bathyplotes</i> Ostergren, 1896), so that both <i>Karenella</i> and <i>Bathyherpystikes</i> are regarded by me, herein, as synonyms of <i>Bathyplotes</i> .	310-614
Family Lactmogonidae				
11. <i>Laetmogone violacea</i> (Theel)	*	—	Cosmopolitan; Hanscn (1975).	—

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganella Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
12. <i>Laetmogone maculata</i> (Theel)	*	—	Japan; Malay Archipelago; N.E. Tasmania; Victorian coast, Australia; Hansen (1975); this work.	
Family Phylloporidae				
13. <i>Neothyonidium parvipadum</i> Rowe	—	*	This work.	126
Family Synaptidae				
14. <i>Leptosynapta dolabrifera</i> (Stimpson)	*	—	Southern Australia; Lord Howe Island (Tasman Sea); H. L. Clark (1946).	0-46
Echinoidea				
Family Cidaridae				
15. <i>Prionocidaris callista</i> Rowe & Hoggatt	Rowe & Hoggatt (1986)	—	Southeastern Australia; Lord Howe Island; Kermadec Islands; Rowe & Hoggatt (1986).	10-85(?198)
16. <i>Phyllacanthus imperialis</i> (Lamarck)	—	McKnight (1975)	Indo-west Pacific; Kermadec Islands Clark & Rowe (1971); Rowe & Hoggatt (1986).	0-73(?130)
17. <i>Syllectidaris brevicollis</i> (de Meijere)	*	—	Malay Archipelago; Lord Howe Island (Tasman Sea); Rowe & Hoggatt (1986).	69-301
18. <i>Stereocidaris</i> sp.	—	McKnight (1975)	? = <i>S. microtuberculata</i> (Yoshiwara); Rowe & Hoggatt (1986).	500
19. <i>Salenocidaris hastigera</i> (A. Agassiz)	McKnight (1968a)	—	Indian Ocean; Malay Archipelago; North Cape, New Zealand; McKnight (1968a).	370-2565 83-720
20. <i>Rhopalocidaris gracilis</i> (Döderlein)	*	—	Japan; Shigci (1986).	
Family Echinothuriidae				
21. <i>Hoplotosoma pulchrum</i> Rowe	*	—	This work.	130-301
22. <i>Calvertosoma gracile</i> (A. Agassiz)	*	—	Japan; Philippines; Malay Archipelago; Shigci (1986).	160-950
Family Aspidodiematidae				
23. <i>Aspidodiadema tonsum</i> A. Agassiz	*	—	Japan; Philippines; Malay Archipelago; Kermadec Islands; NE coast Australia; Mortensen (1940); this work.	180-1135
Family Arbaciidae				
24. <i>Coelopleurus maculatus</i> A. Agassiz & H. L. Clark	*	—	Japan; Philippines; Malay Archipelago; Shigci (1986).	60-360

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganello Bank >30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
Family Diadematidae				
25. <i>Centrostephanus rogersi</i> (A. Agassiz)	*	—	Southeastern Australia; Lord Howe Island (Tasman Sea); Kermadec Islands; northern coast of North Island, New Zealand; Pawson (1965b).	0-30
26. <i>Diadema savignyi</i> Michelin	—	—	Indo-west Pacific; Clark & Rowe (1971).	0-70
27. <i>Diadema palmeri</i> Baker	*	—	New Zealand; coast of New South Wales; Lord Howe Island (Tasman Sea); Baker (1967); this work.	10-50
Family Pedinidae				
28. <i>Caenopodina alabakeri</i> Rowe	*	—	This work.	570-578
29. <i>Caenopodina novaezealandiae</i> Pawson	—	McKnight (1975)	North Island, New Zealand; McKnight (1975).	324-500
Family Temnopleuridae				
30. <i>Holopneustes inflatus</i> Lütken in Agassiz	?	—	Southeastern Australia; this work. Mortensen (1943) based this record on examination of two old specimens. He considered the provenance Norfolk Island as doubtful).	0-30
31. <i>Trigonocidaris micropora</i> Mortensen	*	—	Philippines; Malay Archipelago; Mortensen (1943).	186-350
32. <i>Orechinus monolini</i> (A. Agassiz)	—	McKnight (1975)	Indo-Pacific, including Kermadec Islands; Mortensen (1943); McKnight (1975).	318-2300
Family Toxopneustidae				
33. <i>Toxopneustes pileolus</i> (Lamarck)	*	—	Indo-west Pacific; Clark & Rowe (1971).	0-90
34. <i>Triopneustes gratilla</i> (Linnaeus)	—	—	Indo-west Pacific, including Kermadec Islands; northern coast, North Island, New Zealand; Clark & Rowe (1971); Pawson (1965b).	0-75
35. <i>Pseudoboletia indiana</i> (Michelin)	—	—	Indo-west Pacific; Kermadec Islands and northern coast, North Island, New Zealand; Clark & Rowe (1971); this work.	0-100

TABLE 1 (Contd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganello Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
Family Echinidae				
36. <i>Gracilechinus multidentatus</i> (H. L. Clark)	—	McKnight (1975)	Kermadec Islands; New Zealand; southeastern Australia; McKnight, 1968b&c; this work.	510-1324
Family Echinometridae				
37. <i>Echinometra mathaei</i> (Blainville)	Edgecombe & Bennett (1983)	—	Indo-west Pacific; Lord Howe Island, Tasman Sea; Kermadec Islands; Clark & Rowe (1971); Pawson (1965b).	0-139
38. <i>Helicidaris tuberculata</i> (Lamarck)	Edgecombe & Bennett (1983)	—	Southeastern Australia; Lord Howe Island (Tasman Sea); Kermadec Islands; northern coast, North Island, New Zealand; Pawson (1965b).	0-54
39. <i>Heterocentrotus mammillatus</i> (Linnaeus)	Edgecombe & Bennett (1983)	—	Indo-west Pacific; Clark & Rowe (1971).	0-30
Family Clypeasteridae				
40. <i>Clypeaster australasiae</i> (Gray)	Pawson, 1965b	?McKnight (1975)	Southwest Pacific; Japan; Eastern Australia; Lord Howe Island (Tasman Sea); northern coast, North Island, New Zealand; ?Kermadec Islands; Pawson (1965b).	3-50
41. <i>Clypeaster virescens</i> (Döderlein)	*	—	Japan; Philippines; Indo-China; Australia and New Zealand; Shigei (1986).	40-301
Family Fibulariidae				
42. <i>Echinocyamus polyporus</i> Mortensen	Pawson, 1965b	—	North Island, New Zealand; Pawson (1965b).	9-536
Family Laganidae				
43. <i>Laganum decagonale</i> (Blainville)	*	—	Eastern Indian Ocean; Philippines; Malay Archipelago; Clark & Rowe (1971).	5-301
44. <i>Peronella hinemoae</i> Mortensen	Pawson (1965b)	McKnight (1968a)	New Zealand; Kermadec Islands; McKnight (1968a).	17-260
Family Apatopygidae				
45. <i>Oligopodia epigonus</i> (von Martens)	Pawson (1965b)	—	Indo-west Pacific; Lord Howe Island (Tasman Sea); Pawson (1965b).	35-141
Family Brissidae				
46. <i>Brissus agassizi</i> Döderlein	Baker (1967)	—	Japan; eastern coast Australia; Lord Howe Island (Tasman Sea); northern coast, North Island, New Zealand; Baker (1967).	0-120

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganelia Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
47. <i>Brisopsis oldhami</i> Alcock	Pawson (1965b)	—	Western Indian Ocean; Malay Archipelago; Philippines; New Zealand and Chatham Rise; Kermadec Islands; Mortensen (1951); Pawson (1965b).	18-2736
Family Astero stomatidac				
48. <i>Heterobrysis nitidus</i> (Döderlein)	Baker & Rowe (in press)	—	New Caledonia; Eastern Indian Ocean; Baker & Rowe (in press).	420-475
Ophiuroidea				
Family Astero schematidac				
49. <i>Asteroschema tubertjerum</i> Matusumoto	Baker (1980)	—	Japan; Hawaii; Baker (1980).	325-965
50. <i>Asteroschema igloo</i> Baker	Baker (1980)	—	Kermadec Islands; Baker (1980).	450-501
Family Gorgonocephalidac				
51. <i>Astrothroax waiteti</i> (Benham)	Baker (1980)	—	South Africa; southeastern Australia; New Zealand; Baker (1980).	73-998
52. <i>Astrothrombus vercors</i> (Kochler)	Baker (1980)	—	Malay Archipelago; northeastern New Zealand; Baker (1980).	204-751
53. <i>Asteroporpa australiensis</i> H. L. Clark	—	McKnight (1975)	Southeastern Australia; Kermadec Islands; New Zealand; Baker (1980); McKnight (1975) as <i>A. wilsoni</i> Bell.	55-508 71-301
54. <i>Asteroporpa (Astromoana) reticulata</i> Baker	Baker (1980)	—	New Zealand; Baker (1980).	92-508
Family Euryyalidac				
55. <i>Astroceras elegans</i> (Bell)	Baker (1980)	Baker (1980)	Bonin Islands; Philippines; Malay Archipelago; Guille (1981).	35-308
Family Hemiteuryyalidac				
56. <i>Ophioglyptis nodosa</i> Kochler	*	—	Japan; Philippines; Malay Archipelago; eastern Australian coast; Kermadec Islands; Baker (1979).	210-308
Family Ophiuridac				
57. <i>Ophiura micranantha</i> H. L. Clark	*	—	Hawaii; Philippines; Ceram Sea; Baker (1979).	204-1236 138
58. <i>Amphiophiura insolita</i> (Kochler)	Baker (1979)	—		
59. <i>Amphiophiura taranui</i>	—	McKnight, 1968a		

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganella Bank >30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
60. <i>Ophiomusium scalare</i> Lyman	*	—	Japan; Philippines; Malay Archipelago; Kermadec Islands; Guille (1981); McKnight (1975). Indo-west Pacific; Clark & Rowe (1971).	124-1100 0-30
61. <i>Ophioplocus imbricatus</i> (Müller & Troschel)	—	McKnight (1975)	—	130
62. <i>Ophiomionida parva</i> McKnight	—	McKnight (1975)	—	438-500
Family Ophioteuclidae				
63. <i>Ophiopyrum bispinosum</i> Koehler	Baker (1979)	—	Andaman Islands (Indian Ocean); Baker (1979). East Africa; Philippine Islands; Baker (1979); Guille (1981).	170-500
64. <i>Ophiopallas paradoxo</i> Koehler	Baker (1979)	—	—	0-30
Family Ophiocomidae				
65. <i>Ophiocoma dentata</i> Müller & Troschel	Edgcombe & Bennett (1983)	—	Indo-west Pacific; Clark & Rowe (1971).	0-30
66. <i>Ophiocomella sexradia</i> (Duncan)	*	—	Indo-west Pacific and tropical east Pacific; Clark & Rowe (1971).	0-15
Family Ophiodermatidae				
67. <i>Bathypectinura heros</i> (Lyman)	Baker (1979)	—	Widespread in tropical seas; New Zealand; Australia; Baker (1979).	240-2960
Family Ophiacanthidae				
68. <i>Ophiacantha cornuta</i> Lyman	*	—	Kermadec Islands; Fiji; H. L. Clark (1915).	308-1080
69. <i>Ophiacantha pentagona</i> Koehler	—	McKnight (1975)	Indo-Pacific; Macquarie Island; McKnight (1975).	82-1724
70. <i>Ophiacantha serrata</i> Lyman	Baker (1979)	—	Admiralty Islands (west Pacific); Baker (1979).	278-500 318-383
71. <i>Ophiacantha</i> sp.	—	McKnight (1975)	—	190-520
72. <i>Ophiocamax rugosa</i> Koehler	*	—	Malay Archipelago; Philippines; Japan; Guille (1981).	350-4239
73. <i>Ophiomyces delata</i> Koehler	Baker (1979)	—	Malay Archipelago; Baker (1979).	500
74. <i>Ophioprium larissae</i> Baker	Baker (1979)	—	—	500-1624
75. <i>Ophiophthalmus relictus</i> (Koehler)	Baker (1979)	—	Indian Ocean; Japan; Malay Archipelago; Baker (1979).	204-1171
76. <i>Ophioplinthaca pulchra</i> Koehler	—	McKnight (1975)	Philippines; Malay Archipelago; McKnight (1975).	

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganelia Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
77. <i>Ophiurothamnus stultus</i> (Kochler)	—	McKnight (1975)	Philippines; Malay Archipelago; McKnight (1975).	742-1705
Family Ophiactidae				
78. <i>Ophiactis profunda</i> Lutken & Mortensen	—	McKnight (1975)	Widespread in Pacific; McKnight (1975).	46-1644
Family Amphiruridae				
79. <i>Amphiura lymani</i> Studer	Baker (1979)	—	South Georgia; Southern Australia; Baker (1979).	5-500
80. <i>Amphiura psilopora</i> H. L. Clark	Baker (1979)	—	North Pacific; Japan; New Zealand; Baker (1979).	40-700
81. <i>Amphiura</i> sp.	—	McKnight (1975)	Cosmopolitan; Baker (1982).	954-951
82. <i>Amphipholis squamata</i> (Delle Chiaje)	McKnight (1967)	—	—	0-500
Family Ophiothricidae				
83. <i>Ophiothrix (Ophiothrix) ciliaris</i> (Lamarck)	*	—	Eastern Indian Ocean; Indo-China; Philippines; Malay Archipelago; western Pacific; tropical Australian coast; Clark & Rowe (1971).	0-308
84. <i>Ophiothrix (Acanthophiothrix) leptidus</i> de Lortoi	*	McKnight (1975)	Indo-west Pacific; southeastern Australia; Kermadec Ridge; I recognize this species as distinct from <i>O. purpurea</i> Von Martens with which it has been synonymized (see Clark & Rowe, 1971) principally on form of radial shields and colour. I consider <i>Ophiogymna saltatrix</i> McKnight (1968b) conspecific with <i>Ophiothrix (Acanthophiothrix) leptidus</i> de Lortoi; this work.	10-508
Asteroida				
Family Luidiidae				
86. <i>Luidia avicularia</i> Fisher	*	—	Indian Ocean; Japan; Philippines; Malay Archipelago; ? South Pacific Islands; N.W. Australia; Elizabeth Reef (Tasman Sea); A. M. Clark (1989 in press).	9-308
Family Astropocetinae				
86. <i>Astropoceten celebensis</i> Döderlein	*	—	Malay Archipelago; A. M. Clark (1989 in press).	394-472

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganella Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
87. <i>Astropecten polyacanthus</i> Müller & Troschel	*	—	Indo-west Pacific; Kermadec Islands; New Zealand; Clark & Rowe (1971); H. E. S. Clark (1970). This work.	0-185 390-423
88. <i>Tethyaster tangaroae</i> Rowe Family Benthocetinidae	*	—	Malay Archipelago; A. M. Clark (1981) This work.	260-402 308-310
89. <i>Cheiraster (Luidiaaster) teras</i> (Sladen)	*	—	This work.	450-475
90. <i>Cheiraster (Luidiaaster)</i> sp. Family Goniasteridae	*	—	Philippines; east coast Australia; this work.	194-472 422-437
91. <i>Glyphodiscus mcknighti</i> Rowe	*	—	Philippine Islands; Chatham Rise; Alderman Islands; H. E. S. Clark (1982).	200-920
92. <i>Athenoides rugulosus</i> Fisher	*	—	Japan; Eastern coast Australia; Kermadec Islands; Rowe (1985).	71-108
93. <i>Millettiphaster wanganellensis</i> H. E. S. Clark	—	H. E. S. Clark (1982)		
94. <i>Rosaster mimicus</i> Fisher Family Asterodiscididae	—	H. E. S. Clark (1982)		
95. <i>Asterodiscides grayi</i> Rowe Family Ophidiasteridae	Rowe (1977)	—	Southeastern Australia; Lord Howe Island; McKnight (1967).	0-50 500
96. <i>Ophidiaster confertus</i> H. L. Clark	McKnight (1967)	—	Indo-west Pacific; Clark & Rowe (1971). Southern and Southeastern Australia; Zeidler & Shepherd (1982). I am convinced that because of similarities in body form, granulation, spination and papular distribution, <i>Austrofromia polypora</i> (type species of <i>Austrofromia</i> H. L. Clark (1921)) is congeneric with <i>F. milleporella</i> (Lamarck) (type species of <i>Fromia</i> H. L. Clark (1840)) so that I commit <i>Austrofromia</i> H. L. Clark (1921) to the synonymy of <i>Fromia</i> Gray (1840); this work.	0-30
97. <i>Ophidiaster</i> sp.	—	McKnight (1975)		
98. <i>Fromia milleporella</i> (Lamarck)	*	—		
99. <i>Fromia polypora</i> H. L. Clark	*	—		

TABLE 1 (Contd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganello Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
100. <i>Heteronardoa carinata</i> (Koehler)	*	—	Indian Ocean; Japan; Philippines; Malay Archipelago; Tasman Sea; Kermadec Islands; Rowe (1976).	34-301
101. <i>Leiaster leachi</i> (Gray)	*	—	Indo-west Pacific; Clark & Rowe (1971).	10-30
102. <i>Linckia guildingi</i> Gray	*	—	Tropicopolitan; Rowe (1985).	0-20
Family Pterasteridac				
103. <i>Pteraster (Apterodon) obesus</i> H. L. Clark	*	—	Japan; Hayashi (1973).	65-308
Family Asterinidac				
104. <i>Asterina alba</i> H. L. Clark	*	—	Lord Howe Island, Elizabeth & Middleton Reefs (Tasman Sea); this work.	0-20
105. <i>Patiriella exigua</i> (Lamarck)	*	—	Southern Indian Ocean and South Africa; St. Paul's Island; Southern and southeastern Australia; Lord Howe Island (Tasman Sea); Dartnall (1971).	littoral
Family Asteropectridac				
106. <i>Patricia vernicina</i> (Lamarck)	*	—	Southern Australia; Kermadec Islands; this work.	0-60
Family Echinasteridac				
107. <i>Echinaster colemani</i> Rowe & Albertson	Rowe & Albertson, 1987	—	New South Wales, Australia; Rowe & Albertson (1987).	5-22
Family Asteriidac				
108. <i>Coccinasterias muricata</i>	*	—	Southern Australia; Lord Howe Island (Tasman Sea); New Zealand. This species is recognized herein as a valid species and taken out of the synonymy of <i>Coccinasterias calamaria</i> (Gray); this work.	0-91
109. <i>Astrostele rodolphi</i> (Perrier)	A. M. Clark (1950)	—	New South Wales, Australia; Lord Howe Island (Tasman Sea); Kermadec Islands; northern coast, North Island, New Zealand (Rowe). This species includes synonyms <i>A. inauularis</i> H. L. Clark (1938) and <i>A. multisipina</i> A. M. Clark (1950); this work.	0-250
110. <i>Coronaster haliceps</i> Fisher	—	McKnight (1975)	Philippine Islands; McKnight (1975).	192-545

TABLE 1 (Cont'd.)

Taxon	Norfolk Island 28°30'S, 167°-169°E	Wanganello Bank > 30°33'S, 167°-169°E	Other Distribution/Authority/Comments	Depth (m)
Family Brislingidae				
111. <i>Novodinia helenae</i> Rowe	*	—	This work.	308
Crinoidea				
Family Isocrinididae				
112. <i>Metacrinus nodosus</i> P. H. Carpenter	McKnight (1977)	—	Kermadec Islands; McKnight (1977).	570-1152
113. <i>Metacrinus</i> sp.	McKnight (1977)	—	—	669-732
114. <i>Saracrinus varians</i> (P. H. Carpenter)	—	McKnight (1977)	Philippines; Malay Archipelago; Kermadec Islands; McKnight (1977, as <i>Metacrinus</i>).	304-1152
Family Comasteridae				
115. <i>Oxycomanthus plectrophorum</i> (H. L. Clark)	McKnight (1975)	McKnight (1975)	Southeastern Australia; New Zealand. Records by McKnight (1977; 1975) are based on his misidentification of specimens as <i>Comanthus</i> (= <i>Cenolia</i>) <i>benhami</i> A. H. Clark; Rowe et al. (1986).	37-924
116. <i>Cenolia spanoschistum</i> (H. L. Clark)	McKnight (1977)	—	Southern Australia; New Zealand. The record by McKnight (1977) is based on his misidentification of specimens as <i>Comanthus</i> (= <i>Cenolia</i>) <i>trichoptera</i> (J. Müller); Rowe et al. (1986).	18-310
117. <i>Comissia norfolkensis</i> McKnight	McKnight (1977)	—	Hoggett & Rowe (1986).	450-578
Family Charitometrididae				
118. <i>Charitometra basicarua</i> (P. H. Carpenter)	—	McKnight (1975)	Kermadec Islands; A. H. Clark (1950).	716-1159
119. <i>Glyptometra crassa</i> (A. H. Clark)	McKnight (1977)	—	Bay of Bengal (Indian Ocean); Malay Archipelago; McKnight (1977).	73-1023
Family Antedonidae				
120. <i>Antedon incommoda</i> Bell	McKnight (1977)	—	Southern coast of Australia; A. H. & A. M. Clark (1967).	0-68
121. <i>Antedon deltonna</i> McKnight	McKnight (1977)	—	—	15-24
122. <i>Nanometra duala</i> Rowe	McKnight (1977)	—	McKnight (1977), as <i>Nanometra johnstoni</i> John; this work.	308
123. <i>Tionometra</i> sp.	—	McKnight (1977)	—	500

A Review of the Family Caymanostellidae (Echinodermata: Asteroidea) with the Description of a New Species of *Caymanostella* Belyaev and a New Genus

FRANCIS W. E. ROWE

ROWE, F. W. E. A review of the family Caymanostellidae (Echinodermata: Asteroidea) with the description of a new species of *Caymanostella* Belyaev and a new genus. *Proc. Linn. Soc. N.S.W.* 111 (4), 1989: 293-307.

The history of the deep-sea asteroid family Caymanostellidae is reviewed. A recently proposed close relationship between *Caymanostella* and the concentricycloid genus *Xyloplax* is discussed and refuted. A new species in the genus *Caymanostella* is described from the Tasman Sea and a new genus, *Belyaevostella*, is described to accommodate the Indonesian species *C. hispida* Aziz and Jangoux. New observations for caymanostellid asteroids are the occurrence of papulae in the new genus, varied position of the gonopore associated with the proximal-most supermarginals and internal structure of some abactinal plates.

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INTRODUCTION

The family Caymanostellidae was described by Belyaev (1974) to accommodate the then unique species *Caymanostella spinimarginata* Belyaev, collected from depths of 6740-6780m in the Cayman Trench and living on sunken wood. Belyaev included the family in the asterozoan order Phanerozonia because of the prominence of the marginal plates. He was uncertain whether the distinctive features including the shape of the oral plates, lack of ventro-lateral (actinal) plates, and the actinal spinulation represent primitive (plesiomorphic) features or derived (apomorphic) characters related to the specific habitat of the sea-stars. Consequently, he was also uncertain of relationships of the Caymanostellidae with other phanerozoan families.

Later (1977) Belyaev and Litvinova described a second species, *C. admiranda*, which had been collected in 5220m from the northern part of the Coral Sea, West Pacific. They made no further comment on the relationships of the family.

Aziz and Jangoux (1984) have described a third species *C. hispida*, from 2350m in the Strait of Macassar (Indonesia), West Pacific. They suggest that because of the form of the abactinal and marginal skeleton, the family has closer affinities with members of the order Spinulosida, and in particular the family Asterinidae.

Smith (in Smith and Tranter, 1985) described a fossil sea-star, *Protremaster uniserialis*, from Sinemurian (Lower Jurassic) deposits on Alexander Island, Antarctica. He considered the species a tremasterin asterinid, but compared it, also, with *Caymanostella*. Rowe *et al.* (1988) and Rowe (1988), however, consider *Protremaster* to be an early caymanostellid asteroid, thus concluding that the family Caymanostellidae is of relatively ancient lineage and that early members possessed at least one row of actinal-lateral plates.

Blake (1987), in a major reclassification of post-paleozoic asteroids, refers the Caymanostellidae to the order Velatida, which he re-established to include also the Korethrasteridae, Solasteridae, Myxasteridae and Pterasteridae. The Velatida are

included with the monofamilial Spinulosida within the superorder Spinulosacea. Blake (1987) contends that the Caymanostellidae are aberrant velatidans and that characters shared between *Caymanostella* and members of the Valvatida are '... best explained by convergence.' Unlike Aziz and Jangoux (1984), Blake (1987) does not draw a direct comparison with the Asterinidae, which latter family he had earlier (1981) transferred from the Spinulosida, (e.g. Spencer and Wright, 1966) to the Valvatida. Rowe *et al.* (1988) maintain the Caymanostellidae, Korethrasteridae and Asterinidae should be retained within the same order, the Valvatida. Rowe *et al.* (1988), in discussion of the origin of the Class Concentricycloidea, suggest that the caymanostellids and korethrasterids may warrant a supra-familial taxon of their own.

Smith (1988) classifies the Caymanostellidae as a sister group to *Xyloplax medusiformis* Baker, Rowe and Clark (1986) within the order Velatida (sensu Blake, 1987). He argues against the recognition of the Class Concentricycloidea erected by Baker *et al.* (1986) for *Xyloplax*.

In this paper, and following examination of over 250 specimens of caymanostellids, the family Caymanostellidae is comprehensively re-diagnosed and its relationships, including that with *Xyloplax* are discussed. A new species of *Caymanostella* is described and a new genus described for *C. hispida* Aziz and Jangoux. Two paratypes of *C. spinimarginata* Belyaev, one paratype of *C. admiranda* Belyaev and Litvinova and the holotype and paratype of *C. hispida* Aziz and Jangoux have been re-examined. In the text, Institution abbreviations are AM = Australian Museum; BM(NH) = British Museum of Natural History, London; NMNZ = National Museum of New Zealand, MNNH = National Museum of Natural History, Paris.

SYSTEMATIC ACCOUNT

Family CAYMANOSTELLIDAE Belyaev

Caymanostellidae Belyaev, 1974: 1502

Diagnosis (emended): Body pentagonal to circular in outline; aborally slightly convex, orally flat; body covered with thin or very thick epidermis; madreporite relatively simple; disc plate arrangement distinct or not, from arms, aborally; disc plates variously imbricated include centrodorsal, primary radial and interradiial plates, a pair of distinctive distal-lateral disc plates (dldp) in each interradius and several intercalary plates; each dldp has an internal, horn-like process which abuts with its opposite number in the mid-interradiial line, forming, with the oral plates, internal buttressing points between which a T-shaped odontophore is braced (Figs. 1, 5F); aboral arm plates imbricate proximally, comprising a carinal and one or more dorsal-lateral rows each side; aboral plates hexagonal, to fan-shaped, thin delicate and scale-like or thicker lenticulate and robust; superomarginals not conspicuous in fossil taxon but more or less rectangular conspicuous in Recent taxa, entirely abactinal, first pair usually markedly larger than succeeding ones, supermarginal plates either similar in size or smaller than inferomarginal plates; inferomarginals rectangular, delimiting margin of body at oral/aboral angle; terminal plates each with central perforation; actinal-lateral plates absent in Recent forms, present in known fossil taxon; adambulacral plates bar-like, extending between ambulacral and inferomarginal plates in Recent taxa; first adambulacral plate very short, second and third longest; furrow margin straight, furrow spines few (1-3); ambulacral grooves narrow or broad/petaloid; two rows of suckered tube-feet; 10 gonads, 1 pair to each interradius, visible from oral surface through thin, membranous, triangular 'window', actinal membrane with or without perforated plate spicules (Fig. 7); 10 gonopores one pair to each interradius, associated with proximalmost superomarginal plate of each plate series, as a marginal notch or piercing the plate, or

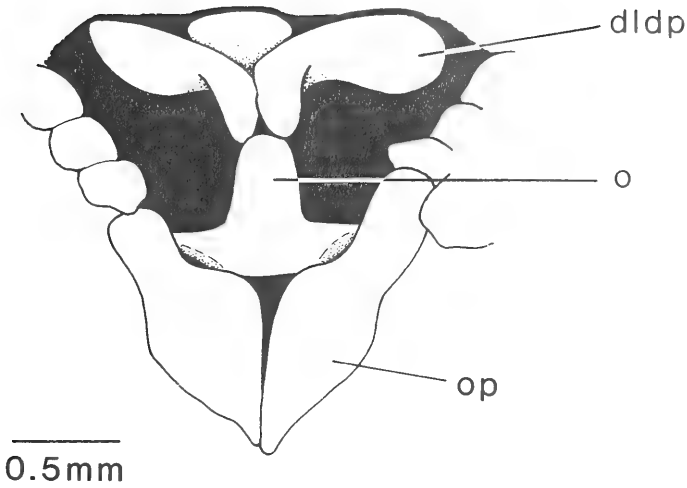


Fig. 1. Internal juxtapposition of horns of distal lateral disc plates (lldp), odontophore (o) and oral plate (op), viewed from oral surface.

positioned adjacent to first supermarginal plate (Fig. 2) (position of gonopores not determined in Fossil taxon); sexually dimorphic, male gonopores minute compared with size of female gonopores; abactinal plates bear granuliform or long, slender spinelets; adambulacral plates bear spike-like spinelets, inferomarginal plates bear 1-3 short, clavate or slender spines on their outer edge, forming an ambital fringe to the asteroid; no pedicellariae; papulae present or absent; habitat of Recent taxa sunken, waterlogged wood; Lower Jurassic — Recent.

Type genus: *Caymanostella* Belyaev, 1974 (own designation).

Other general included: *Protremaster* Smith, 1985; *Belyaevostella* gen. nov.

Remarks: The Caymanostellidae share with the Korethrasteridae Danielssen and Koren, 1884, the form of the adambulacral plates, the occurrence of an actinal membrane, though this latter is better developed in caymanostellids, and the absence of actinal-lateral plates in Recent taxa. Lack of fossil material of korethrasterids prevents comparison of early actinal morphology between the two families. Both families have taxa which possess abactinal papulae and taxa which do not. They differ, however, in shape, korethrasterids are stellate whereas caymanostellids pentagonal; abactinal plating, (3 of 4 genera of korethrasterids — *Peribolaster* Sladen, 1889, *Remaster* Perrier, 1894 and *Anareaster*, Fell and Clark, 1959) have cruciform plates; abactinal spination, korethrasterids have paxilliform plates whereas caymanostellids have an even covering of granuliform spinelets or spaced, elongate spinelets; and the more prominent development of marginal plates in caymanostellids.

Unless the form of the adambulacral plates and occurrence of an actinal membrane in both families can be shown to be the result of convergence, then they may be considered to be related, commonly derived and included within the same asteroid order. As far as the caymanostellids are concerned, the form of the Fossil *Protremaster* indicates Recent forms have lost actinal plates, though the adambulacral structure was already evolved in the Jurassic genus. There is no evidence to suggest that the bar-like adambulacral plates resulted from fusion with actinal-lateral plates. It can only be speculated that the extension of the adambulacral plates and loss of actinal-lateral plates is a response to specialized habitat/environmental pressures.

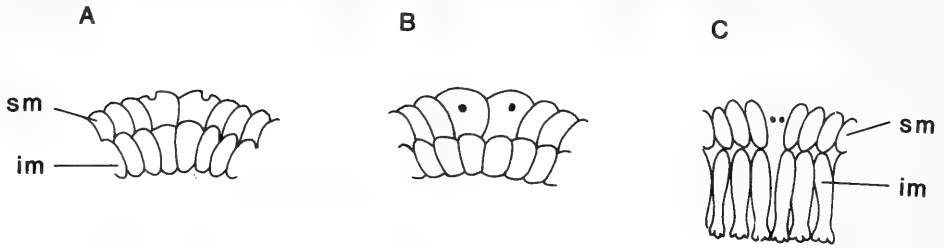


Fig 2. Position of gonopores in *Caymanostella* (A = marginal, B = piercing) and *Belyaevostella* (C = interproximal-most superomarginals).

Smith (1985) clearly saw in *Protremaster* close affinities with asterinid taxa rather than with *Caymanostella*. Paradoxically, therefore, there is a measure of agreement between Smith (1985) and Rowe *et al.* (1988) regarding the relationship of caymanostellids and asterinids when Smith concludes *Caymanostella* may be a specialized offshoot from tremasterins. I would support this proposition in referring to the possible derivation of caymanostellids from asterinids since I am unconvinced of the subfamilial relationship of tremasterins within the family Asterinidae (Rowe and Berents in prep.) and Smith's genus is not a tremasterin in any case. This view places the families Caymanostellidae and Korethrasteridae with the Asterinidae in the order Valvatida under Blake's recent reclassification. Whether a separate supra-familial taxon is warranted (Rowe, 1988) for this group of families, remains to be determined.

However, I would contend that Smith's (1988) comparison of *Caymanostella* and *Xyloplax* contains errors of interpretation due to his reliance on inadequately detailed published data and lack of examination of relevant specimens. Full descriptions of *Xyloplax* spp., including sperm development and morphology, are now available (Rowe *et al.*, 1988; Rowe, 1988; Healy *et al.*, 1988). The Caymanostellidae are detailed herein. It can now be shown that a number of characters chosen by Smith (1988), to show a close relationship between *Caymanostella* and *Xyloplax*, are incorrect (see Table 1). I would also point out that caymanostellids reach a diameter of at least 27mm (R = 13.6mm in *Belyaevostella hispida*), three times the 9mm recorded by Smith (1988: 20).

There can be, in my view, no support for a progenetic origin for *Xyloplax* (Smith 1988: 20) based on the early form of the asteroid water vascular system. Smith contends that in metamorphosing asteroids, before arm and ambulacral skeletal development '... the first few tube feet in effect form a peripheral circle.' In my view, this would be due to the juxtaposition of a small, primary (terminal) tube-foot adjacent to which, and on either side, are one or two larger ambulacral tube feet developing along a primordial radial canal. There is no evidence of an incipient double-ring arrangement as evolved in *Xyloplax*. Such an arrangement, if it occurred, would have profound implications in the development of the radial structure of the ambulacral water vascular system in adult echinoderms. There is no embryological evidence that such is the case in asteroids or any other echinoderms.

Contrary to Smith's (1988) reliance on the superiority of his cladistic approach to the relationship between *Caymanostella* and *Xyloplax*, I do not believe that his use of cladistics has increased the objectivity of approach to this particular problem. In my view the relationship between *Caymanostella* and *Xyloplax* remains as remote as that described by Baker *et al.*, 1986; Rowe *et al.*, 1988; Rowe, 1988 and Healy *et al.*, 1988.

TABLE 1

Comments on characters chosen by Smith (1988) in cladistic analysis

Character chosen by Smith (1988)	Comments
1. Calcinal ring	Inappropriate for use above generic if not species level.
2. Superomarginals	Palaeontological evidence does not support Smith's use of this character in such a narrow sense.
3. Hyaline spines	Highly derived; presence or absence of these specialized spines is too widespread in the Asteroidea for use to compare the Concentricycloidea. In any case they are absent in both caymanostellids and xyloplacids.
4. Ambulacrals	Interpretation is critical. Rowe <i>et al.</i> , (1988) and Rowe (1988) interpret ambulacrals of <i>Xyloplax</i> as having fused with the adambulacral/oral plate to form the expanded oral frame.
5. Oral plates	Interpretation is critical. The oral plates are not unusual in the asteroid <i>Caymanostella</i> , but substantially altered in <i>Xyloplax</i> , forming, with fusion to ambulacral plates a uniquely widened oral frame (Rowe <i>et al.</i> , (1988); Rowe (1988)).
6./14. Adambulacral arrangement	In caymanostellids the adambulacrals, except the first one, have extended in width across the actinal surface. The first adambulacral is NOT reduced to rudimentary state as claimed by Smith (1988: 20). The adambulacrals are NOT lost from <i>Xyloplax</i> but have changed roles to act as 'ambulacral' plates. Articulation between the adambulacrals and the ambulacral/oral frame ossicles is substantially altered (see Rowe <i>et al.</i> , 1988).
7. Actinals	These are present in caymanostellids, even if only in the fossil taxon, <i>Protremaster</i> , described by Smith (1985).
8. Terminal plates	Perforated terminal plates occur across a diverse range of taxa (Rowe, 1985) including Caymanostellids, but not <i>Xyloplax</i> .
9. Inferomarginals	These are differentiated in each of the groups included in Smith's (1988) cladogram.
10. Peristome/oral plates	The oral frame of <i>Xyloplax</i> comprises a ring of ossicles formed by fusion of adambulacral oral/ambulacral plates.
11. Madreporite	Caymanostellids have a small but typical madreporite.
12. Abactinal plates/papulae	One caymanostellid (described herein) DOES possess papulae; the type genus of the korethrastrids, <i>Korethrastra</i> , does NOT possess papulae; plates are imbricate, not tessellate; caymanostellids bear granuliform and spiniform abactinal armament on plates.
13. Tube-feet	Caymanostellids possess suckered tube-feet NOT pointed tube-feet. This was a mistake made by Belyaev (1974) and perpetuated by Smith (1988) clearly without reference to any specimens. The pointed tube-feet of <i>Xyloplax</i> are explained by Rowe (1988) to be probably functionally associated with living in a soft substrate.
14.	See 6.
15. Ambulacral plating	A critical difference in interpretation by Rowe <i>et al.</i> (1988) and Rowe (1988) who consider the perradial plates between which the tube-feet protrude to be modified adambulacrals.

Genus *Caymanostella* Belyaev

Caymanostella Belyaev, 1974: 1502

Diagnosis (emended): Caymanostellid sea-stars with hexagonal to fan-shaped, lenticulate abactinal plates; thin epidermis not obscuring skeletal plates (in adults); granuliform abactinal armament; ambital spinelets club-shaped; gonopores form a notch in aboral edge of plate (Fig. 2A) or pierce the first superomarginal plates (Fig. 2B); spicules absent from actinal membrane; papulae absent, distributed in the Caribbean and West Pacific.

Type species: *C. spinimarginata* Belyaev, 1974, by own designation.

Other species included: *C. admiranda* Belyaev and Litvinova, 1977; *C. phorcynis* sp. nov.

Remarks: *Caymanostella* is distinguished from *Belyaevostella* gen. nov., the latter genus possesses delicate, scale-like abactinal plates embedded in a thick epidermis (in adults), spiniform abactinal and marginal armament, abactinal papulae and spicules in the actinal membrane. The gonopores of *Belyaevostella* occur adjacent to but do not pierce or notch the superomarginal plates.

Caymanostella spinimarginata Belyaev

Figs 2A, 3A-B

Caymanostella spinimarginata Belyaev, 1974: 1504, figs 1-2.

Material examined: 2 specimens (paratypes, BM(NH) 1987.3.26.1 (R = 4.8mm) and 1987.3.26.2 (R = 4.3mm)), 19°38.5'N, 76°37.5'W, 6740-6780m (Oriente depression, eastern part of Cayman Trench, Stn 1267), R/V 'Akademik Kurchatov', 25.3.73.

Diagnosis: A species of *Caymanostella* in which the abactinal plates imbricate in a similar direction, only the primary interradial plates (including the madreporite) are distinguishable on the disc; there are at least two alternating, dorsal-lateral rows of plates either side of the carinal row along each of the arms; the supero- and inferomarginal plates are of similar size to each other; the gonopore is positioned in a notch on the upper margin of the proximal-most superomarginal plate in each series; the oral plates each with 3 oral, and a single suboral, coarsely thorned spines; adambulacral plates with a single furrow and up 10 coarsely thorned spines, these latter mostly in two alternating rows along the actinal surface of the plate; outer edge of inferomarginals each with 2 elongate, club-shaped spines, actinal membrane triangular to heart-shaped; abactinal granulation homogenous, blunt, club-shaped; maximum known size for species R = 4.8mm; distribution, Cayman Trench.

Remarks: The marginal position of the gonopore on the proximal-most superomarginal plates immediately separates this species from *C. admiranda* Belyaev and Litvinova and *C. phorcynis* sp. nov. Differences in abactinal plate arrangement also separate the species.

Caymanostella admiranda Belyaev and Litvinova

Fig. 4A-B

Caymanostella admiranda Belyaev and Litvinova, 1977: 1983, figs 1 and 2.

Material examined: 1 specimen (paratype, BM(NH) No. 1987.3.26.3 R = 3.4mm) 7°31.1'S, 149°51.1'E, (Coral Sea), 5220m, R.V. 'Dm Mendeleev' (Stn. 1234), 15.12.75; 2 specimens (Amsterdam Museum, R = 4mm; R = 2.1mm) 10°39'S, 123°40'E (off Timor) 520m, (soft grey mud with brown upper layer), 'Siboga' Expedition, (Stn. 297).

Diagnosis: A species of *Caymanostella* in which the abactinal plates imbricate and are arranged in two distinct fields; on the disc the centrodorsal plate is surrounded by an inner ring of 7 plates, 5 large trapezoidal radial plates and, in each of 2 of the interradial, a small squarish plate, there is an outer ring of 10 plates, 5 large, hex-heptagonal interradial plates and 5 smaller hexagonal, rather shield-shaped radial plates; between the primary interradial plate and radial plate on the outer ring of the disc plates, and the proximal carinal plate and dorsal-lateral plate is an obliquely directed, oblong distal-lateral disc plate; along the arms are 3 heptagonal-fan-shaped carinal plates, with 2-3 dorsal-lateral plates alternating either side; the terminal plate is radially longer than wide, with a relatively small perforation towards its distal edge; there are 6-7, more or less equal-sized superomarginal and inferomarginal plates, with the exception that the proximal-most superomarginal in each series is about twice as broad as its immediate neighbour, a small, wedge-shaped plate separates the upper half of the proximal-most two superomarginals across the mid-interradial line: a small gonopore (male) pierces the centre of each of the first superomarginal plates; the oral plates each bear 2 oral and

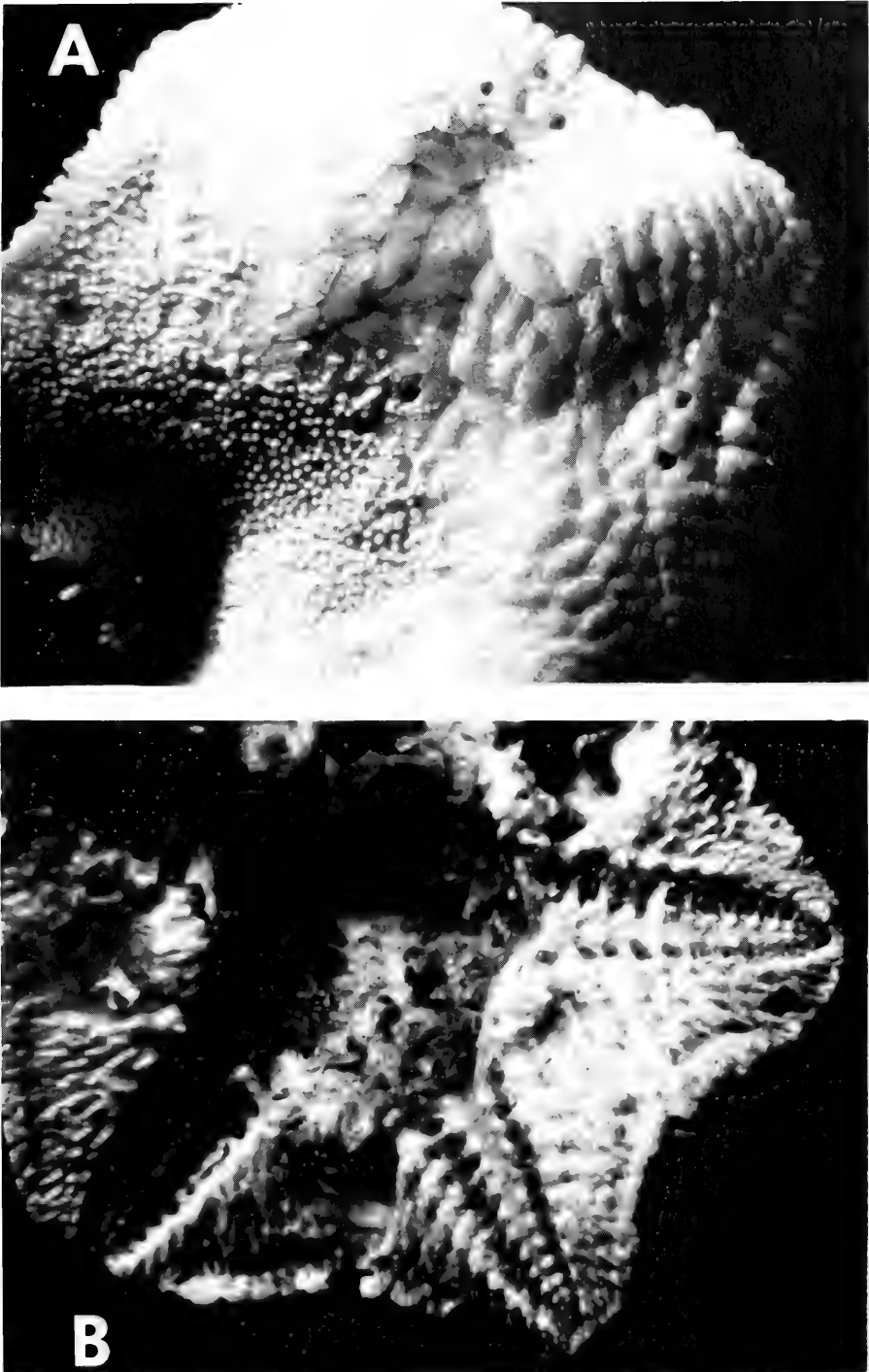


Fig. 3. *Caymanostella spinimarginata* Belyacv (paratype, BM(NH) 1987.3.26.1). **A** = aboral view, **B** = oral view (R = 4.8mm).

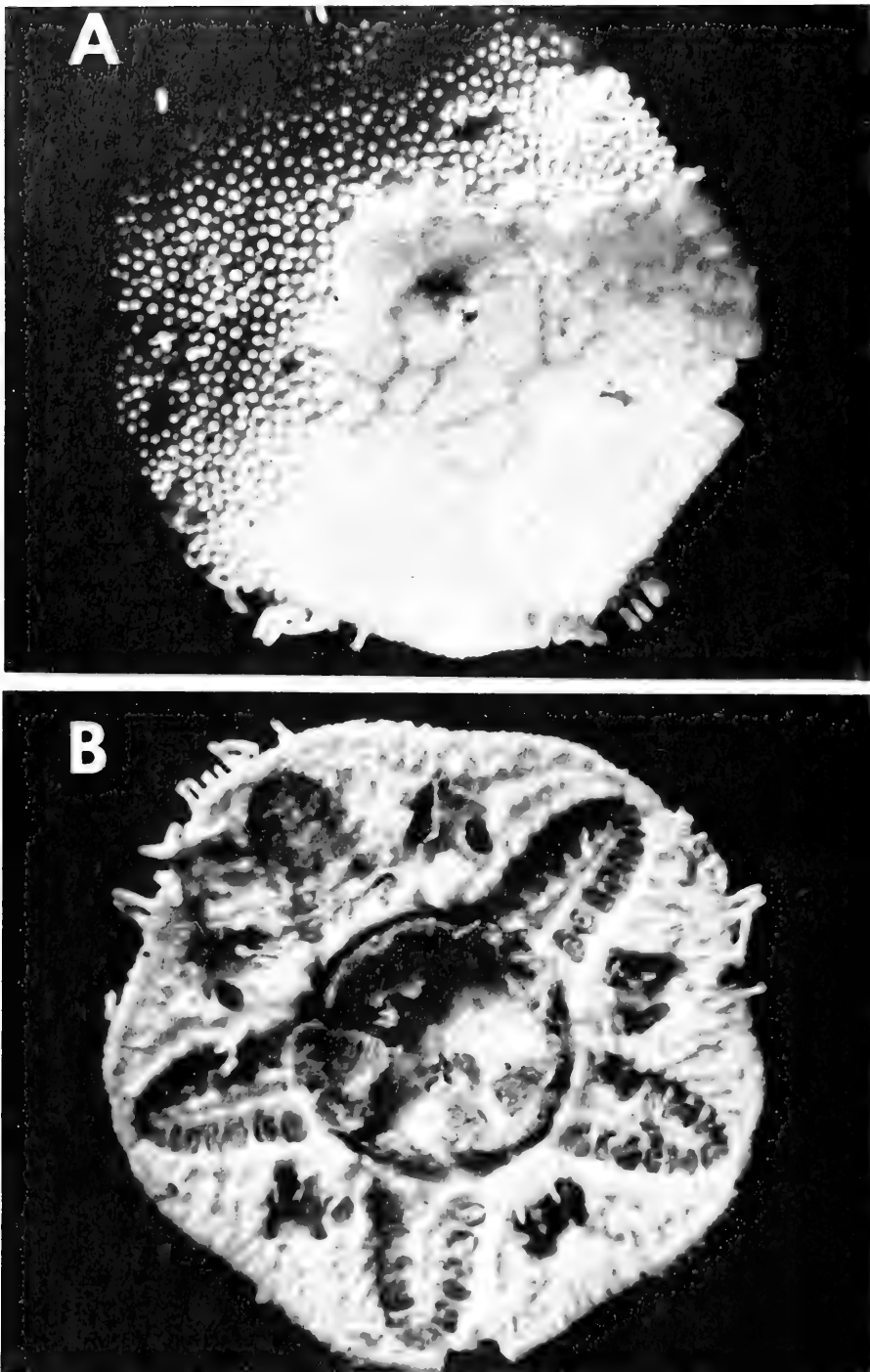


Fig. 4. *Caymanostella admiranda* Belyaev and Litvinova (paratype, BM(NH) 1987.3.26.3). **A** = aboral view, **B** = oral view (R = 3.4mm).

one suboral, rather coarsely thorned spines; adambulacral plates bear a single furrow spine and only one or two coarsely thorned spines on the actinal surface of the plate; the outer edge of the inferomarginal plates bear 2 marginal spines; the actinal membrane is heart-shaped; furrows are petaloid with up to 8 pairs of tube-feet; abactinal granulation even, over abactinal surface, granules low, rounded, 2 sizes more or less apparent; maximum known size, $R = 4.90\text{mm}$; distribution Coral and Timor Seas.

Remarks: Belyaev and Litvinova (1977) neither described nor adequately figured the abactinal plate arrangement for their species. The diagnosis, therefore, includes information based on one of the two paratype specimens which has been donated to the British Museum (Natural History) in London by Dr. G. Belyaev. Both of the 'Siboga' specimens ($R = 4\text{mm}$, $r = 3.3\text{mm}$, $R/r = 1.2\text{mm}$; $R = 2.1\text{mm}$, $r = 1.8\text{mm}$, $R/r = 1.16$) are in very poor condition, broken, and have apparently dried out at some time prior to this examination. The specimens are currently stored in alcohol, but dissociation of some plates indicate probable original storage in formaldehyde solution. Because of the fragility of the specimens, the abactinal granules have not been removed to examine the plate arrangement. However, where granules have already been lost, it is evident that the hex-heptagonal shape of the plates and abactinal plate arrangement is similar to that described for *C. admiranda*. This second record for *C. admiranda* therefore requires confirmation when better preserved material becomes available from the Timor Sea, particularly considering the shallow depth from which the specimens were collected.

The shape and arrangement of the abactinal plates clearly identifies *C. admiranda* from its congener *C. phorcynis* sp. nov., with which it shares the feature of the gonopores piercing the superomarginal plates. Currently, the geographical range of *C. admiranda* is considered to extend between the Coral and Timor Seas in depths of 5220m and 520m respectively.

Caymanostella phorcynis sp. nov.

Figs. 2B, 5A-D

Material examined: 3 specimens (holotype, AM J18911, 2 paratypes, (1 dissected for SEM) AM J17880) $34^{\circ}54'S$, $151^{\circ}14'E$ to $34^{\circ}50'S$, $151^{\circ}15'E$, 993-1030m (off Shoalhaven Bight, New South Wales, Australia). N.S.W. State Fisheries R/V 'Kapala', 26.10.83; 3 specimens (paratypes, AM J18910 (1), AM J17830 (2)) $35^{\circ}31'S$, $150^{\circ}50'E$ to $35^{\circ}28'S$, $150^{\circ}53'E$, 938-994m (off Shoalhaven Bight, New South Wales, Australia), N.S.W. State Fisheries R/V 'Kapala', 8.9.83; 2 specimens (paratypes, AM J16365) $33^{\circ}40'S$, $151^{\circ}56'E$ to $33^{\circ}37'S$, $151^{\circ}56'E$, 736m (off Broken Bay, New South Wales, Australia), N.S.W. State Fisheries R/V 'Kapala', 6.12.77; 9 specimens (paratypes NMNZ 4248(5), AM J18912(2), AM J18913(2), $37^{\circ}23.7'S$, $177^{\circ}39.5'E$ to $37^{\circ}23.7'S$, $177^{\circ}36.6'E$, 1075-1100m (off White Is. north island of New Zealand), USSR f/v 'Kalinovo', on/in large waterlogged log of *Coriaria arborea*. 3 specimens (paratypes, NMNZ 4252) $42^{\circ}47.1'-42^{\circ}48.2'S$, $175^{\circ}45.6-175^{\circ}47.2'W$, 1174-1180m, (NE of Chatham Islands), F.V. 'Otago Buccaneer', 22.7.84, on wood; 230+ specimens (NMNZ 4247), $37^{\circ}23.7'S$, $177^{\circ}39.5'E$ to $37^{\circ}23.7'S$, $177^{\circ}36.6'E$, 1075-1100m (off White Is, north island of New Zealand), USSR f/v 'Kalinovo', on/in large waterlogged log of *Coriaria arborea*; 7 specimens (Amsterdam Museum) $3^{\circ}27.1'N$, $125^{\circ}18.7'E$, 2053m, fond dur, traces de sable fin, foncé et dur, 'Siboga' Expedition (Stn. 126).

Diagnosis: A species of *Caymanostella* with fan-shaped plates; gonopores piercing the proximal-most superomarginal plates; 8-15 supero- and inferomarginal plates similar in size (except larger proximal-most superomarginals); ambulacral furrows narrow;

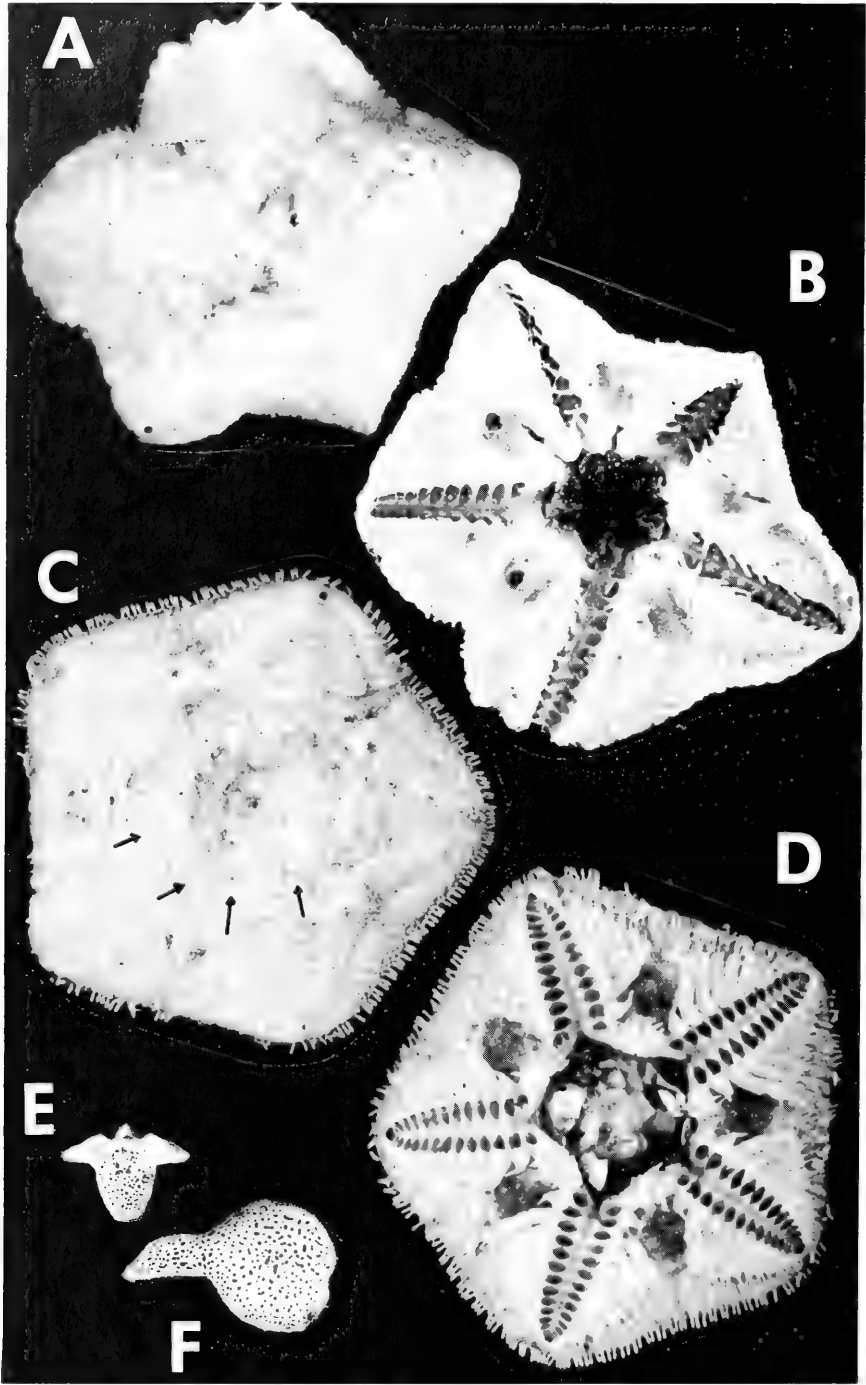


Fig. 5. *Caymanostella phorcynis* sp. nov. (holotype, AMJ 18911) **A** = aboral view, **B** = oral view ($R = 5.0\text{mm}$). (Paratype, NMNZ 4248), **C** = aboral view (arrows indicate positions of distal-lateral disc plates), **D** = oral view ($R = 5.0\text{mm}$). **E** = distal-lateral disc plate ($\times 22$), **F** = odontophore ($\times 22$).

adambulacral plates with 1-2 furrow spines, 10-12 spines on the actinal surface; abactinal granulation even, granules dome-shaped.

Description: The specimens range in size from $R = 2.8-10.5\text{mm}$, $r = 2.2-8.5\text{mm}$, $R/r = 1.05-1.30$ (holotype: $R = 5.0\text{mm}$, $r = 3.9$, $R/r = 1.28$). The abactinal surface is covered with imbricating plates almost all of which imbricate in a similar direction, with the proximal edge of each plate overlying the distal edge of the preceding plate (Fig. 5A, C). On the disc imbrication is less regular. However, the only plates which can be most easily distinguished are the 5 primary interradians by virtue of their larger size than the surrounding plates and by the location of the madreporite in interradius CD. Also recognizable is a fan-shaped plate distal to the primary interradiial plate and between it and the proximal-most two superomarginals. A small distal-lateral disc plate is separated either side of the overlap between the primary interradiial plate and the more distal fan-shaped plate described above (Fig. 5C, E). An additional series of 3 small plates separates the dldp and interradiial fan-shaped plate from the primary interradiial in the large specimens. The anus is surrounded by 4-5 plates.

Along the arms is a carinal row of 5-8 fan-shaped plates, either side of which is a row of 3-6 dorsal-lateral plates (Fig. 5A, C). These latter plates alternate with the carinal plates. Occasionally, on some arms, 2 or 3 small intercalary plates are present, which disturbs the regularity of the dorsal arm plate arrangement. In the largest specimen (NMNZ 4252; $R = 10.5\text{mm}$) 3 plates form a second dorso-lateral series, alternating with the plates of each of the first series. The terminal plate bears a large, more or less central perforation.

There are 8-15 superomarginal and inferomarginal plates which are elongate at right angles to the periphery. These plates decrease in size regularly towards the arm tips. The first superomarginal on adjacent arms is about twice as large as the next adjacent plate. It bears, towards its centre, a gonopore. The other marginal plates are of similar size to each other along the length of the arms. The edge of each of the inferomarginals bears two spines.

The furrows are narrow, or at the most in smaller specimens, sub-petaloid (Fig. 5B, D). There are 9-14 pairs of well-developed tube-feet in each ambulacrum, the number increasing with growth. The ambulacral plates are dumb-bell-shaped.

With the exception of the first plate, the adambulacrals are typically elongate, obliquely perpendicular to the groove, extending to the proximal edge of the inferomarginal plates. These plates decrease in size towards the arm tip. The adambulacral plates bear rugose, tapering spines. The first plate bears 3-5 spines, of which the innermost 2, occurring slightly obliquely on the adradial edge are interpreted as furrow spines. Up to 10-12 spines occur on each of the remaining adambulacral plates of which 2 furrow spines occur regularly on the adradial edge of the first 4 plates and irregularly alternating with 1 furrow spine to the seventh plate, thereafter 1 furrow spine occurs on the adradial edge of each of the adambulacral plates. The remaining spines are in two alternating rows across each plate. The lower surface of each inferomarginal plate bears spinelets similar in form to, but smaller than, those on the adambulacral plates (Fig. 5B, D).

The oral plates bear 3-4 furrow spines, 5 on the largest specimen (NMNZ 4252; $R = 10.5\text{mm}$) and 2-3 suboral spines.

The gonads on either side of the interradiial membrane, can be seen through a more or less triangular actinal membrane. This membrane is delimited by the oral plates, the first 2 adambulacral plates and the innermost 2 inferomarginal plates.

The actinosome is large, about $\frac{1}{3}$ diameter of the preserved animals.

Abactinal granulation is fine, even, with granules slightly longer than broad, dome-shaped, slightly spaced, 9-12 per mm.

Both the anus and gonopores are surrounded by 7-9 granules.

Etymology: *Phorcynis*, daughter of the sea god *Phorcus* and *Medusa*.

Remarks: The shape and arrangement of abactinal plating easily separates *C. phorcynis* from *C. admiranda* Belyaev and Litvinova, which otherwise share the feature of the gonopore piercing the proximal-most superomarginal plates.

Although they do not appear to differ significantly from Tasman Sea specimens, the seven 'Siboga' specimens are identified as *C. phorcynis* with some hesitation due to their very poor state of preservation. Further material in better preserved state is required to confirm the occurrence of *C. phorcynis* in the Indonesian region. Otherwise *C. phorcynis* is known from both sides of the Tasman Sea in depths between 736-1208m. The 'Siboga' specimens were taken in deeper water at a depth of 2053m.

Belyaevostella gen. nov.

Description: A caymanostellid sea-star with body becoming invested in thick skin with growth which includes, aborally, very thin, finely perforated, scale-like abactinal plates, irregularly imbricating and in no apparent order; superomarginal plates squarish in juvenile specimens, becoming elongate in adults but smaller than the elongated inferomarginals; proximal-most and interradially adjacent superomarginals abut in juveniles, becoming divergent in large adults (Fig. 1C); gonopores open between the diverging, proximal-most superomarginals (Fig. 1C); aboral papulae present; actinal membrane with perforated plate-like spicules (Fig. 7A, B); adambulacral and oral plates as for family; distributed in East Indian region and off NE coast of Australia in depths of 1301-1350m; habitat sunken, waterlogged wood.

Type species: *Caymanostella hispida* Aziz and Jangoux, 1984, by designation.

Other species included: None.

Etymology: Named for Dr. G. Belyaev who described the family. Gender feminine.

Remarks: The form and arrangement of the skeleton on the oral surface clearly shows this genus to be a member of the family Caymanostellidae. However, the form and arrangement of the abactinal plates, position of the gonopores, presence of spicules in the actinal membrane and more particularly the presence of abactinal papulae, all distinguish *Belyaevostella* from *Caymanostella* at generic level.

Belyaevostella hispida (Aziz and Jangoux)

Figs. 2C, 6A-B, 7A-B

Caymanostella hispida Aziz and Jangoux, 1984; 190, pl. 3.

Material examined: 2 specimens (holotype MNHN, ECAS 10056; paratype MNHN, ECAS 10057), Station 220 (0°13.79'S, 188°12.73'E), 2350m, Macassar Strait, Expedition franco-indonésienne 'Corindon.' 1 specimen (Amsterdam Museum), Station 88 (0°34.6'N, 119°8.5'E), 1301m, Macassar Strait, 'Siboga' Expedition. 1 specimen (Australian Museum J21783), Station 16 (11°41.55'S, 145°36.65'E), 2006-2053m, off NE coast (Queensland) of Australia, collected from log, 'Franklin' Cruise.

Diagnosis (emended): as for genus; additionally inferomarginal plates with 3-4 elongate, acutely tipped spinelets along their margin in smaller specimens (R = <8mm) (not observed in largest specimen, R = 13.6mm); adambulacral plates with 3-5 spines forming a simple transverse row across the plates; oral plates with 3 (not 2; Aziz and Jangoux, 1984) furrow spines and a single suboral spine.

Remarks: The investment of the body in a thick skin, the presence of aboral papulae and the occurrence of spicules in the actinal membrane are all new observations for this species. The holotype (R = 8mm) and paratype (unmeasurable) are dried specimens which are in generally poor condition. It is not surprising, therefore that the papulae

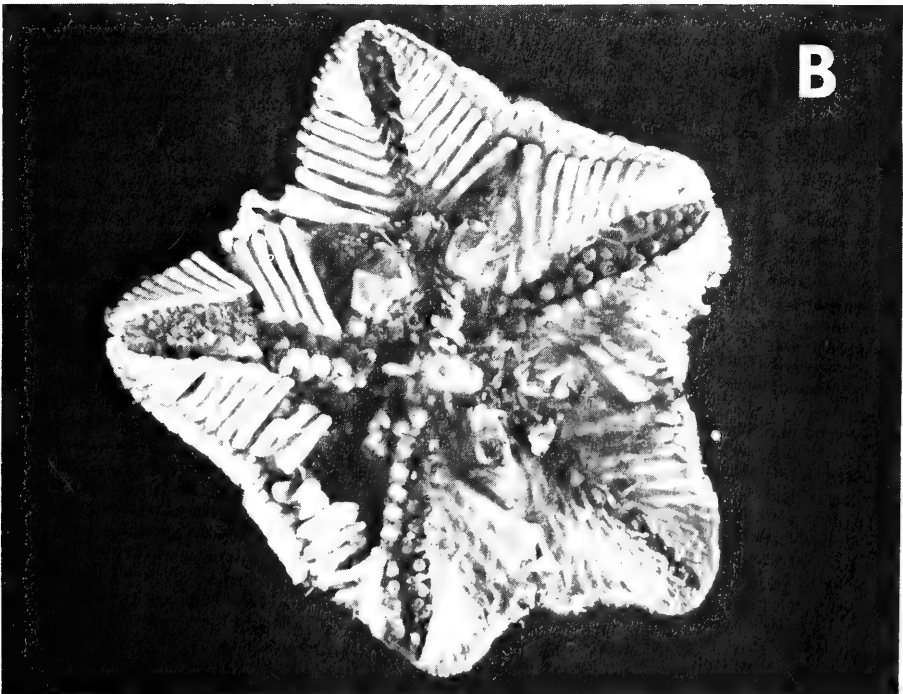
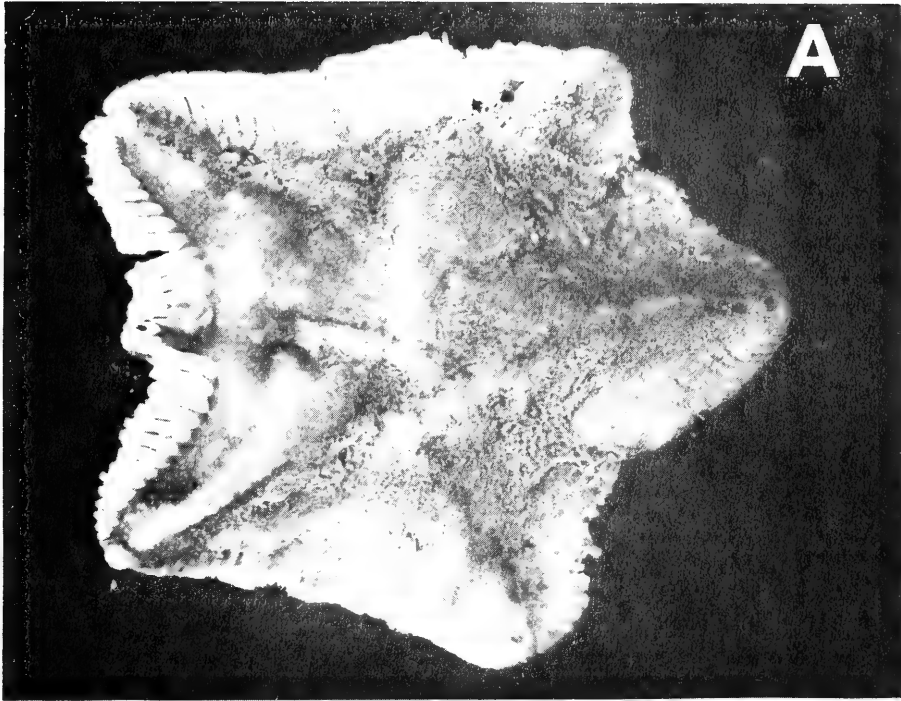


Fig. 6. *Belyaevostella hispida* (Aziz and Jangoux) (AMJ 21783) **A** = aboral view, **B** = oral view (R = 13.6mm).

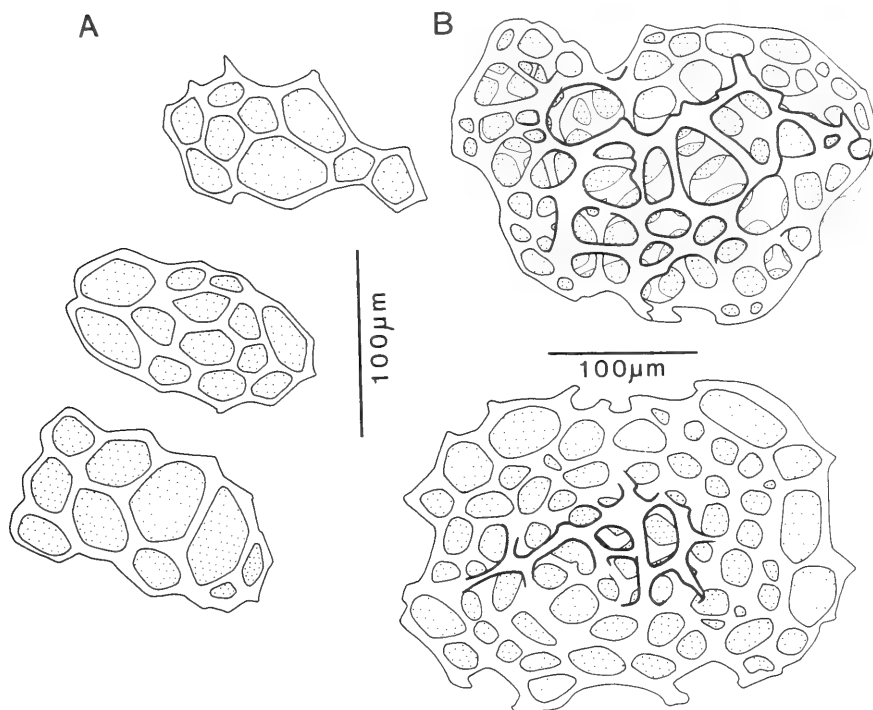


Fig 7. Spicules from actinal membrane of *Belyaevostella hispida*. **A** = specimen $R = ? < 8\text{mm}$ (paratype, MNHN ECAS 10057), **B** = specimen $R = 13.6\text{mm}$ (AMJ21783).

were not observed by Aziz and Jangoux (1984). Also the skin investing the body is thin and not readily apparent. However, I was able to find relatively simple spicules (Fig. 7A) in the actinal membrane of these specimens. A third specimen, from the Macassar Strait (Siboga Expedition) is smaller than the type specimens ($R = 5.3$, $r = 4.5$, $R/r = 1.17$). Although now stored in alcohol it is apparent the specimen has been dried at some point during its storage. It therefore does not have thick investing skin cover. It does appear to me that the investing skin develops with growth of the animal. A further growth feature appears to be the change in shape of the interradially adjacent pair of superomarginal plates. In the smallest (Macassar) specimen these plates are squarish and distinctly smaller than the first pair of inferomarginal plates. However, in the type specimens the shape of these superomarginals is already changing to becoming elongate. In the largest specimen, which I do not hesitate to identify with the type specimens, despite a much larger size, these superomarginals are as slender as the first pair of inferomarginal plates, though still only about half as long. Curiously, also the two superomarginals diverge from each other and away from the mid-interradial line. Dissection from the ventral surface shows the gonoducts to lie in the space between the divergent superomarginals so that the gonopores do not either notch or pierce the adjacent marginal plates.

This distinctive caymanostellid genus interestingly shows a convergent possession of papulae with the genera *Peribolaster* Sladen, 1889, *Remaster* Perrier, 1894 and *Anareaster* Fell and Clark, 1959 in the closely related family Korethrastridae, but without the development of cruciform and paxilliform abactinal plates.

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