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NOTICE TO AUTHORS

Papers will be considered for publication in *The Australian Zoologist* if they make an original contribution to whole animal biology of the Australian fauna. Papers submitted will be subjected to review and thence to the normal editorial process, in the course of which authors will receive edited galley proofs for correction. A manuscript is accepted on the understanding that it is to be published exclusively in *The Australian Zoologist*.

MANUSCRIPTS (original and one copy) should be sent to the Editor, "The Australian Zoologist", School of Biological Sciences, Macquarie University, North Ryde, N.S.W. 2113. They should be typewritten (double spaced) on good quality paper. All pages of the manuscript must be numbered consecutively, including those containing references, tables and figure legends, which should all be placed after the text.

On the first page of the manuscript should appear the title of the paper, name of the author, the name of the Institution where the work was done and the present postal address if different from that of the Institution. Titles should be as brief, but as informative, as possible. A short title, to serve as a running head and consisting of not more than 50 letters (including spaces) must also be given on the title page.

The abstract (up to 200 words) should state concisely the scope of the work and the principal findings and should be suitable for direct use by abstracting journals. The section headings should be Introduction, Materials and Methods, Results, Discussion, Acknowledgements and References. Presentation must be clear and concise and all unnecessary repetition especially in consecutive sections should be avoided. Footnotes should be avoided.

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TABLES should be numbered with arabic numerals, be accompanied by a title and be typed on separate sheets. Their approximate position in the text should be indicated by a note in the margin.

ILLUSTRATIONS AND DIAGRAMS should be larger than the size of the finished block. Drawings must not exceed 30 x 20 cm. If the originals exceed this they should be photographically reduced and good quality prints provided. Half tone prints should be arranged as plates and mounted on stiff white board up to a maximum size of 30 x 20 cm. Authors will be allowed up to two plates free of charge, but will be expected to pay the cost of any additional plates.

Observations on the Behaviour of the Macropodid Marsupial *Thylogale billardieri* (Desmarest) in Captivity

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ABSTRACT

Observations were made on the diurnal behaviour of a captive group (3♂♂, 11♀♀) of *Thylogale billardieri* (the rufous-bellied pademelon). The daily activity pattern, postures, locomotion, feeding, grooming, vocalisations, agonistic and sexual behaviour are described, and comparisons made with the behaviour of other macropodids.

INTRODUCTION

The rufous-bellied pademelon, *Thylogale billardieri* (Desmarest) is one of the smaller members of the Macropodinae, adult males standing approximately 70 cm and adult females approximately 60 cm tall. A mature female weighs about 5.5 kg. There is wide variation in coat colour, ranging from rufous to dark brown. Some animals possess a pale hip-stripe or faint facial markings, but these vary between individuals. The pademelon is restricted to Tasmania and the Bass Strait islands, although it formerly also occurred in Victoria and south-eastern South Australia (Calaby, 1971). Information on the biology of *T. billardieri* is sparse. It has been described as an "extremely gregarious" species (Troughton, 1965) which lives in "colonies" (Sharland, 1962). Mollison (1960) summarised its favoured habitats in Tasmania as mixed forests of lower slopes, bracken or grassland on forest fringes, and burnt and cutover buttongrass and *Poa* savanna. Troughton (1965) noted that runways are constructed through dense scrub.

The maintenance of a group of rufous-bellied pademelons by the Melbourne Zoological Gardens provided the opportunity to make behavioural observations on the species. While captivity undoubtedly results in artificialities and modifications of normal behaviour, studies of captive animals have nevertheless contributed useful data. For example, the observations of Packer (1969) on captive quokkas (*Setonix brachyurus*) and Russell (1970a) on captive red kangaroos (*Megaleia rufa*) gave results consistent with field-derived behavioural data. The present study is a preliminary assessment of aspects of pademelon behaviour, which may provide a basis for more definitive studies.

MATERIALS AND METHODS

The composition of the pademelon group during the study is shown in Table 1; most data in the table are drawn from Zoo records. Females preponderate over males, due to the Zoo's policy of removing most male neonates from the pouch in order to maximise breeding stock.

TABLE 1
COMPOSITION OF PADEMELON GROUP

Zoo Code No.	Sex	Date of Leaving Pouch	Offspring	Origin	Removal From Group
502	Male	?		Healesville 1967	d. March 30
501	Female	?	505, 504, 35	Healesville 1967	d. August 9
505	Female	Sept. 1968	42	Zoo	
504	Male	Oct. 1969		Zoo	Escaped April 29
598	Female	1969	43	King Is. 1970	
2	Female	?	33	Tasmania 1970	
5	Female	?		Tasmania 1970	d. August 20
32	Female	1970	37	Zoo	d. August 11
33	Female	1970		Zoo	d. May 11
35	Female	1971		Zoo	
37	Female	1971		Zoo	
42	Male	May 1971		Zoo	
43	Female	April 1971		Zoo	
*44	Male	?		*May 1971	

*44, a mature male, was introduced into the group from a bachelor stock kept elsewhere in the Zoo.

Three rectangular enclosures housed the pademelons at different times during the study. The first enclosure (March 18 to April 19, 1971) was about 180 m² in area and contained a shed, water trough, trees along the northern boundary, and scattered shrubs elsewhere. The second enclosure (April 20 to May 20) was the same as the first, but contained several more trees and some scattered boulders as well as a shed and trough. The third enclosure (May 21 to October 6) was about 360 m² in area, and contained a shed and trough but fewer trees than the previous enclosures. In this last enclosure there were seven red-necked wallabies (*Macropus rufogrisus*) as well as the pademelons. Hay, bran and carrots were placed in the sheds as supplementary food.

Observations of behaviour totalling 81 hours were made between March 18 and October 6, 1971. All observations were made during daylight hours from

outside the enclosure, sometimes with the aid of 6 x 30 binoculars. Individual animals were readily recognised by combinations of characteristic facial markings, coat colour and size. In addition, each animal had a Zoo registration number on an eartag; in this report these numbers are used to identify individuals. The duration of observation periods varied between 30 minutes and 180 minutes, with the majority being about 90 minutes. Initially, observations were made at various times of the day, but as it was found that activity was greatest in the late afternoon, observations were later concentrated in this period.

RESULTS

(1) Daily Activity Pattern:

Pademelons are said to be crepuscular in habits, emerging from cover during dusk and early mornings to feed (Troughton, 1965). Limitations of the Zoo study did not allow this aspect of activity to be analysed. However, there was often activity — grooming and grazing — in the mid-morning and always in the late afternoon. During periods of inactivity the animals assumed a resting posture and often slept for periods of more than an hour. Diurnal activity appeared to vary with daily weather pattern and season, with greatest activity occurring on cool and cloudy days.

A preference for shade was normally shown, the animals moving into direct sunlight only when grazing. However this preference altered with season, being most marked in summer. On two occasions (July 25 and September 24) some pademelons were observed lying stretched out in the sun.

(2) Body Postures:

When asleep or resting, the pademelons adopted a characteristic pose (Fig. 1). The tail was thrust forward between the hind legs and the head rested on the tail. In general this attitude was adopted with the back to a tree or fence, although depressions in the ground were sometimes used.

The lying-down pose characteristic of the red kangaroo (Russell, 1970a) was rarely adopted, and then only when lying in the sun in winter.

During rain the pademelons adopted a semi-upright stance, with tail extended posteriorly and head thrust forward.

(3) Locomotion:

The hopping gait of the pademelon is basically similar to that of other small macropodids, but shows some differences. Pademelons hold their forelegs against the chest, and their gait is not markedly saltatorial. When alarmed they showed great speed and agility.

The walking gait was employed when grazing or when a male was "inspecting" females (see Sexual Behaviour). Unlike the red kangaroo (Russell, 1970a), the tail is not used as a support during walking.

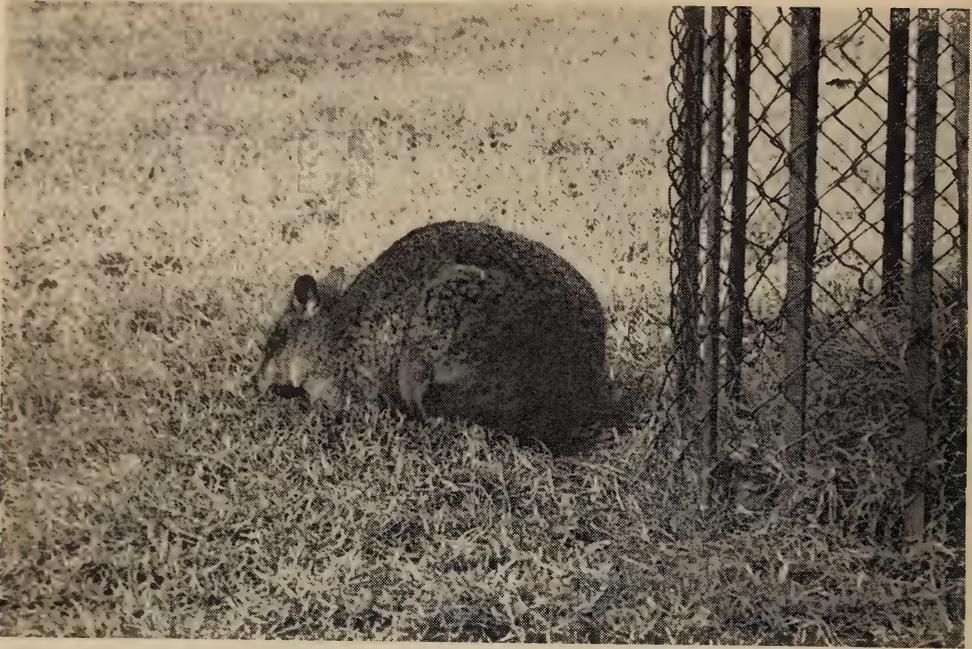


Figure 1—Resting posture: This position with the back towards a large object is typical.



Figure 2—Grooming: Parting fur with the forepaws and licking.

(4) Feeding and Drinking:

In the wild, pademelons eat a wide variety of grasses, shoots and leaves (Mollison, 1960). In captivity all grasses in the pens were grazed, as well as leaves, bark and supplementary foods. Forepaws were sometimes used for picking up food and parting thick grass.

Regurgitation in the rufous-bellied pademelon appeared to be comparatively infrequent, being observed only six times during the period of study. The process seemed identical to, but less frequent than, that described for the quokka (Moir, Somers and Waring, 1956). Pademelons re-ate all spilled material after regurgitation, and chewed the bolus in every case.

Drinking was most commonly seen when the animals began grazing in the late afternoon.

(5) Grooming:

Grooming was a prominent activity throughout the day. Three general modes of grooming were observed:—

(a) Licking — Mainly used for pouch and abdominal cleaning. The tongue was used to clean while the snout nuzzled into the fur. Forepaws were often used to part fur to facilitate licking (Fig. 2).

(b) Scratching with Forepaws — Used in grooming flanks, tail, back, abdomen, chest and face. The forepaws scratched vigorously through the fur and were often licked clean.

(c) Scratching with Hindfeet — Used in grooming head and shoulders. The hindfoot has a syndactylous inner claw which Wood Jones (1924) considered to be an adaptation for combing fur.

Pouch cleaning may be considered as a specialised type of grooming (Fig. 3). It was observed in females both with and without pouch-young, and was essentially as described for the red kangaroo (Russell, 1970a).

Pademelons groomed at various times during the day while at rest. They awoke, stood erect, and groomed for varying periods (1 to 10 minutes), then lapsed back into the resting posture and returned to sleep. This pattern of waking, grooming and sleeping often continued for some hours. Finally in the late afternoon the animals became more active and groomed again for a considerable period (usually more than 15 minutes) before beginning to graze. Grooming appeared to increase after rain, and in some observation periods after heavy rain it was the predominant activity.

Mutual grooming is discussed under mother-young interactions.

(6) Vocalisations:

The following vocalisations were heard:—

(a) Growling — Low intensity sounds made by the dominant individual in an aggressive interaction. Both males and females used this sound, which was

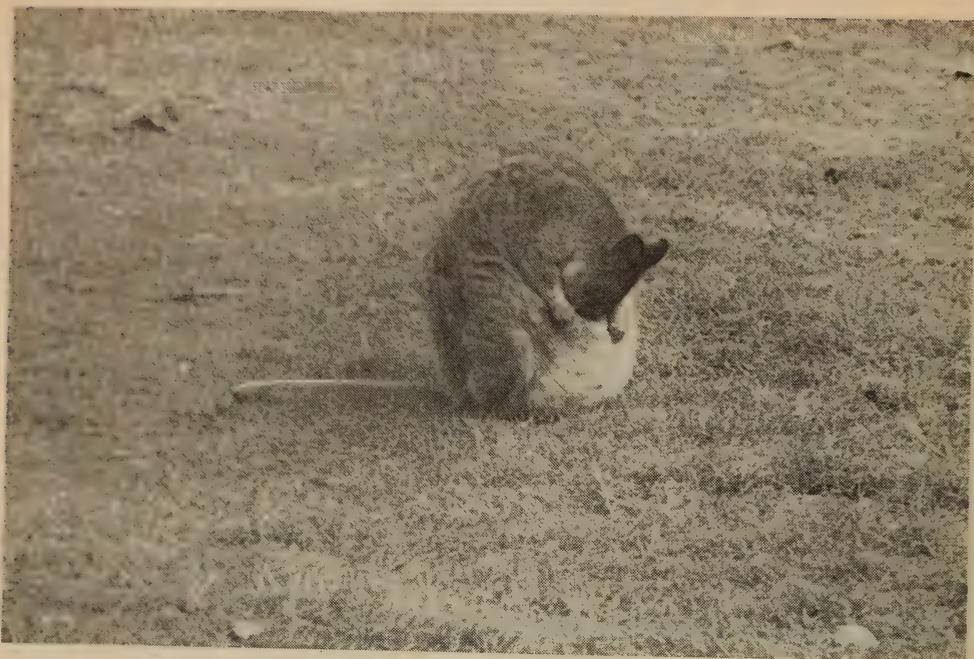


Figure 3—Grooming: Pouch cleaning.



Figure 4—Sexual behaviour: "Inspection" by male (right) of a female. The third individual is another female. (Photos: A. A. Martin).

BEHAVIOUR OF *THYLOGALE BILLARDIERI*

difficult to pinpoint accurately. This vocalisation is probably equivalent to the "snort" of the red kangaroo (Frith and Calaby, 1969; Russell, 1970a).

(b) Clucking — This was heard in three different situations:

(i) Emitted by a male in sexual following, and presumably analogous to the "soft clucking" of the red kangaroo (Russell, 1970a).

(ii) Emitted by a male in aggressive interactions, and probably equivalent to that described for the red kangaroo (Sharman and Calaby, 1964) and Bennett's wallaby (LaFollette, 1971).

(iii) Emitted by a female to her young. This seems equivalent to the "loud clucking" of the red kangaroo (Russell, 1970a). No distinction could be made between the clucking in each of these situations, but because of the low intensity of the sound it is possible that differences went unnoticed. Sounds equivalent to the distress squeak of young red kangaroos (Sharman and Calaby, 1964; Russell, 1970a) were not heard. However, this may also be due to the difficulty of hearing vocalisations adequately.

(7) Aggressive Interactions:

(a) Male-Male — Two males (502 and 504) were present in the enclosure together for a period of only two weeks, but 10 hours of observation during this period showed 12 aggressive interactions between them. All these resulted in the younger, smaller 504 retreating. Most interactions occurred when 504 came within about 2 m of 502, and the result was immediate chasing by 502 for a distance of approximately 5 m. The two never came close enough together to actually fight. On one occasion 504 approached the resting 502 and adopted a pose face to face with him, his front paws on the ground and his body stretched horizontally so that his quivering snout was almost touching that of 502. When

TABLE 2
AGGRESSIVE INTERACTIONS BETWEEN FEMALES

		DOMINANT								
		505	2	598	35	32	33	37	5	43
SUBORDINATE	505	—								
	2	9	—	1						
	598	17	7	—						
	35	6	12	7	—	2			5	
	32	5	8	2	1	—				
	33	2	1	1	3	0	—			
	37	5	13	3	12	5	0	—	4	
	5	9	3	3	1	1	0	0	—	
	43	1	5	19*	1	0	0	8	1	—

*All these interactions occurred after August 20 when weaning occurred.

502 began to rise after about 15 sec 504 fled. The pose adopted by 504 is tentatively termed a threat pose. It is not certain that 504 was sexually mature at this time, but he engaged in sexual following (see Sexual Behaviour) often with penis erect.

(b) Female-Female — Table 2 is a summary of the results of aggressive interactions between females: the data suggest that a near linear hierarchy exists. The types of interaction observed and included in the table were:

- (i) One animal retreating from another with no apparent provoking action from the dominant.
- (ii) One animal chasing another for varying distances.
- (iii) One animal cuffing another with the forepaws.
- (iv) Fighting, i.e., mutual cuffing or wrestling with forepaws. Hindfeet were not used in fighting.

The latter three types of interaction often included growling. Between females the threat pose as described for males was observed 15 times, but quivering of the muzzle was not always seen. Usually the animal adopting the pose subsequently cuffed or chased the other.

The level of aggression of females varied throughout the study, and there is evidence that this was related to the presence or absence of pouch-young. For example, 60 per cent of the observed aggressive interactions of female 5 occurred between July 11 and her death on August 20. Pouch inspection on August 12 revealed the presence of a 4 cm pouch-young (estimated age about 25 days). Similarly, 68 per cent of the observed interactions of female 37 occurred between July 6 and October 6, compared with 32 per cent between March 18 and July 6. She carried a 5 cm pouch-young (estimated age about 35 days) on August 12. Again, 67 per cent of the observed interactions of female 505 occurred before May 20, when her young first left the pouch. Of her later observed interactions, 50 per cent were with females 5 and 37 who were then acting more aggressively. The increased aggression of females did not affect their hierarchical position. The ability to dominate in an interaction appeared to be positively correlated with body size (Table 3).

TABLE 3

RELATION BETWEEN BODY SIZE AND POSITION IN DOMINANCE HIERARCHY IN FEMALES

Order of size (largest to smallest by visual assessment)	505	<u>2</u>	<u>598</u>	5	35	32	37	43
		equal						
Position in hierarchy	1	2	3	<u>4</u>	<u>4</u>	<u>4</u>	7	8
				equal				

(c) Male-Female — Aggression between a male and a female was noted several times. During attempts at courtship (described below), cuffing was used by

a female to break the male's hold, and the male often retaliated by cuffing or chasing the female. Males were also cuffed about the face whenever they attempted to sniff a female's pouch area, and the males retaliated by cuffing but rarely by chasing. On one occasion female 5 was chased extensively by male 504 for no apparent reason. The threat pose described above was observed twice in females during male-female interactions.

(8) Sexual Behaviour:

A daily occurrence was the "inspection" of females carried out by a male, during which he walked around the enclosure, stopping to sniff the genital area and/or pouch region of each female encountered (Fig. 4). Often there was no further interaction, but on each occasion the male attempted to court at least one female. This involved the male's standing at full height, sometimes with head raised, in front of the female. The female either raised her head until it was just under the male's, or the male wrestled her or cuffed her under the chin until she adopted this position. At this stage the male either bent to sniff the female's genital area again, or, more often, placed his forearms around the female's neck, and, retaining his grip with one arm, moved behind the female. The male then held the female's flank with the free arm and slipped the other back until the female was held by both flanks; then he attempted to mount. The female reacted to this by either turning to cuff the male, or, more frequently, hopping forward out of the male's grasp. The male usually followed, sometimes making a clucking sound, and repeated the courtship attempt. This pattern of courtship, escape, pursuit, courtship often continued for some time, and on one occasion male 44 made 28 attempts to court female 42 over a period of 15 minutes. At any stage of the courtship sequence the male erected his penis, sometimes by licking it. On two occasions the male was seen to perform a brief copulation-like display in front of a female (505 and 42), in which, with penis erected, he jerked his pelvis 5 or 6 times.

Only once was copulation observed: between male 44 and female 505 (1630 hours, September 3). After the initial sniffing, the male licked the female's genital area. The female pushed him away and adopted the resting posture. Shortly afterwards, while the female was cleaning her pouch, the male groomed himself and licked his penis, which was erect. He then groomed the female's ears by licking, and pushed his snout in under her chest and licked her genital area. Then he stood upright with his head raised vertically, and wrestled the female until she was also upright (but without head raised). He then moved behind the female as described above, gripping her flanks so tightly that his forearms were hidden in the folds of skin formed by her hind legs and side. He then mounted and mating occurred.

Three phases were observed in mating:—

(a) Intromission, during which the female was almost lifted off her hind legs, and strained forward with forepaws on the ground. Sometimes her head lay on the ground, sometimes it stretched forward horizontally. On one occasion she

ate briefly. At times she "walked" sideways on her forepaws so that the pair moved in a circle as copulation proceeded. No lateral tail movements took place.

(b) A rest phase in which both animals relaxed. The male retained his firm grip, but his penis relaxed and both animals stood still. Occasionally the male's head rested on the female's back.

(c) A phase in which the male vigorously massaged the female's flanks. His penis was relaxed in this phase.

These phases were repeated in seemingly random order during each of the three mountings. The durations of these mountings were respectively 8, 2 and 8 minutes, and approximately half the time in each was spent in copulation, the rest of the time being equally shared between rest and massage. Between mountings the animals groomed themselves and fed briefly. The times between mounts were 4 and 15 minutes respectively. After the third mounting the two animals fed and groomed side by side. There may have been subsequent mountings but the closure of the Zoo terminated observations.

Following this copulation an attempt was made to learn the gestation period, assuming successful fertilisation on September 3. Because the lowest recorded macropodid gestation period is 22 days (in the boodie, *Bettongia lesueuri*; Frith and Calaby, 1969), pouch checking of 505 did not commence until 24 days later. On this day a young was present in the pouch and from its development Zoo staff estimated its age as 2 weeks. Either the pademelon has an extremely short gestation period or the female was pregnant at the time of mating.

Zoo records indicate that pademelons breed throughout the year in captivity, and that females have only one young per year.

(9) Mother-Young Interactions:

The exact period of pouch life has not been determined, but is estimated to be about 25 weeks, as in the quokka (Waring, Sharman, Lovat and Kahan, 1955).

When young first left the pouch for short periods they were easily alarmed and dashed back to the mother on any disturbance. The time spent out of the pouch increased gradually until about 5 weeks later, when it increased sharply over about 2 days, so that the young no longer entered the pouch. The young-at-foot continued to suckle, but with decreasing frequency. About 4 months later weaning occurred. This appeared to involve a significant amount of aggression, as can be seen from the interactions of 598 and 43 in Table 2. These interactions mostly consisted of cuffing, and sometimes chasing, by the mother. Aggression towards the young tapers off rapidly and in one instance the mother was seen to briefly suckle the young one month after weaning.

Further interactions involved what is best termed mutual grooming. The mother and her offspring cleaned and groomed each other's head and neck, licking and using forepaws. While not doing so, the two often rested side by side for periods of over an hour, but the actual grooming rarely persisted for longer than 15 minutes. Such grooming occurred between all mother-offspring pairs in the

group, but the male offspring appeared less inclined to take part in it than the females. Male 504 was seen to groom 501 on only two brief occasions, and male 42 (left the pouch in June) began grooming less with his mother after September.

On the other hand, mutual grooming between mother and female offspring appeared to persist for a longer time, although with gradually decreasing duration. For example, 505 left 501's pouch in September 1968 and was seen grooming with her in April 1971. The strength of this bond is also evidenced by observation of mutual grooming between a mother and an offspring which was carrying a large pouch-young, and between a mother and two different offspring simultaneously. Thus mutual grooming is a persistent phenomenon, although its frequency and duration slowly decrease.

Sparring between mother and offspring, as described for red kangaroos by Russell (1970a) was observed only once in the pademelon group.

DISCUSSION

General Behaviour:

The general activity and body postures resemble those of other small macropodids. Thus the diurnal rhythm of activity is very similar to those described for the red kangaroo, *Megaleia rufa* (Caughley, 1964; Russell, 1970a), and grey kangaroo, *Macropus giganteus* (Caughley, 1964) and clearly, at least in captivity, pademelons are not strictly crepuscular. The resting posture seems suited to conservation of body heat, and may be additionally adaptive in making the animal less conspicuous to predators. The lying-down posture characteristic of the red kangaroo was seen on only two days in winter, when animals lay in the sun; this may also relate to regulation of body warmth. The resting and threat postures are virtually identical to those recorded for the quokka by Packer (1969).

Social Organisation:

The aggression displayed by female pademelons is more pronounced than that described for captive groups of boodies (Stodart, 1966), quokkas (Packer, 1969), Bennett's wallabies (LaFollette, 1971) or red kangaroos (Russell, 1970a, b). In captive groups of all these animals, however, some form of dominance between females was observed. The relevance of this aggression in captive animals to their behaviour in the wild is questionable. Caughley (1964) and Frith and Calaby (1969) concluded that red kangaroo mobs showed little social cohesion. Dunnet (1962) stated that quokkas were non-gregarious and lacked any social organisation, although Holsworth (1967) demonstrated the existence of group territories within which individual quokkas inhabited home ranges. Boodies appear to live in social groups (Finlayson, 1958), but the field behaviour of Bennett's wallabies is undescribed. Hence the presence of dominance interactions between female macropodids in captivity is not proof that natural groups have definite social organisations.

The degree of aggression shown may, however, illuminate differences in organisation. Stodart (1966) gave some evidence of a hierarchy amongst female

boodies, while Packer (1969) concluded that no linear hierarchy could be distinguished in female quokkas. Similarly, interactions between female red kangaroos (Russell, 1970a, b) appear to be of a much lower intensity than those seen between boodies, even though Russell (1970b) demonstrated the existence of a hierarchy in groups of female red kangaroos. These differences may well be due to the differences in social organisation, and because female pademelons appear to be more aggressive it may be that pademelons have a definite social structure. Both Troughton (1965) and Sharland (1962) state that pademelons live in colonies or communities, and the latter writes of their aggressive temper. It is, therefore, possible that the aggression and dominance hierarchy observed in captive pademelons form part of their natural behaviour. Artificiality does, however, arise from the heterogeneity of the group of pademelons studied (see Table 1), the lack of males, and the limited area of the enclosures.

Sexual Behaviour:

The mating behaviour of the pademelon affords interesting comparisons with that described for other macropodids: red kangaroo (Sharman and Calaby, 1964), grey kangaroo (Poole and Pilton, 1964), the boodie (Stodart, 1966), and the quokka (Packer, 1969).

(a) Licking — The licking by the male of the urinogenital area of the female is known in the boodie, but is not described for the other three macropodids. In the boodie, licking was observed on the day preceding presumed copulation whereas it was observed immediately before copulation in the pademelon.

(b) Circling during Intromission — The female grey and red kangaroo are both described as adopting a "submissive posture" during intromission. The boodie was observed circling in one of the three matings described by Stodart.

(c) Repeated mating — Not observed in the boodie, observed only once in the red kangaroo, but "typical" of the grey kangaroo.

(d) Rest periods — These occur in the other macropodids, but there is no description for any of them of the vigorous and unmistakable flank massage which was seen in each mating in the pademelon.

Breeding in pademelons occurs throughout the year in captivity, but field behaviour may be different (Guiler, 1960). Quokkas breed continuously in captivity but seasonally in the field (Shield, 1968).

The anomalous result obtained for gestation period may be explained either by an anoestrous mating or by the existence of an extremely short gestation period. While the former is more likely, Poole and Pilton (1964) and Frith and Calaby (1969) have shown how rare anoestrous mating is in grey and red kangaroos.

Mother-Young Association:

The sequence of mother-young interactions in the pademelon closely parallels that described for the red kangaroo by Russell (1970a), but mother-offspring relations appear to persist longer in the pademelon. Russell (1970a) showed that although there was a long period of association between mother and offspring in red kangaroos, there was no evidence that such associations persisted beyond

sexual maturity. Similarly, association of euro (*Macropus robustus*) mother and offspring may continue for only two years (Ealey, 1967). There is evidence of association of young quokkas in their natal territories (Holsworth, 1967), but there is no evidence of any persistent mother-offspring bond. Association in the above examples is related to suckling, whereas in the rufous-bellied pademelon there is stronger association through mutual grooming. No evidence regarding the adaptive significance of this persistent bond is available.

Weaning may also be marked by differences from other macropodids, as aggression towards the young-at-foot during weaning is quite evident in pademelons. In other species weaning appears to involve mere rejection of the young (e.g., Russell, 1970a).

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Breeding Biology of some Species of *Pseudophryne* (Anura: Leptodactylidae) of the Southern Highlands, New South Wales

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ABSTRACT

Populations of *Pseudophryne corroboree*, *P. dendyi* and *P. bibroni* in the highlands and tablelands of south-eastern N.S.W. breed when temperatures are decreasing. In *P. corroboree* the onset of breeding is negatively correlated with altitude. Modal clutch sizes of the three species are as follows: *corroboree* (20-29), *dendyi* (80-89), *bibroni* (80-99). In general fecundity is not related to female body length.

INTRODUCTION

Most species of the genus *Pseudophryne* are terrestrial breeders, laying their eggs in burrows in soil, under leaf litter, or in moss in areas which are subject to seasonal inundation. The number of relatively large, heavily yolked eggs laid varies from 20 in *P. australis*, to well over 100 in *P. bibroni*. From the information available (Table 1), it appears that most species breed during the late summer to late autumn or early winter. Both *P. australis* and *P. occidentalis* are atypical in this respect as the former species is reported to breed throughout the year after rain (Harrison, 1922) and the latter "breeds after summer rains and when these fail . . . breeds after the first warm rains of winter" (Main, 1965).

In *P. corroboree*, *P. dendyi* and *P. bibroni*, the male constructs the burrow which also serves as a calling site (Pengilley, 1971a). Colefax (1956) reported that in *P. corroboree* the female performs this task as he observed in the laboratory, females making burrows in moss after injection with *Bufo marinus* pituitaries. In nature, no female has been observed to make a burrow.

From the literature, species appear to differ in their behaviour after egg laying. Males of *P. douglasi* (Main, 1964), *P. coriacea* (Straughan, 1963, pers. comm.), *P. dendyi* (Moore, 1961), *P. corroboree* (Jacobson, 1963) and females of *P. australis* (Harrison, 1922) have been found in burrows containing eggs. Jacobson (1963) reported that both sexes of *P. bibroni* remain with the eggs. This is contrary to my observations on this species, where only males have been found in nests containing eggs.

TABLE 1.

Summary of breeding biology of <i>Pseudophryne</i> species						
Species	Calling season	Breeding season	Clutch Size	Egg Diam. (mm)	Length of Larval life (days)	References
<i>Pseudophryne bilbroni</i>		Apr.-June	130	2.0	150-180	Fletcher, 1889
		Apr.-June		2.1		Harrison, 1922
		Apr.-May	260	2.0		Moore, 1961
		Mar.-May Feb.				Jacobson, 1962 Littlejohn, 1963 Pengilley, unpubl.
	Mar.-June	Apr.-May	80-99 ^b		120-150	New England, N.S.W. Southern Highlands, N.S.W.
<i>P. dendyi</i>		Feb.	85	2.2	180-210	Pengilley, unpubl. Martin, 1965
	Jan.	Jan.-Feb. Feb.	80-99 ^a		180-210	Jindabyne, N.S.W. Snowy Mts., N.S.W.
		March			180-210	Clyde Mtn., N.S.W. Coree Flats, N.S.W.
<i>P. corroboree</i>		Dec.-Jan.	12	3.5	180-210	Colefax, 1956
		Jan.-Feb.	20-30 ^b		180-210	
		Jan.-Feb.	20-30 ^b		180-210	
		Jan.-Apr.	20-30 ^b		180-210	Pengilley, unpubl.
<i>P. semimarmorata</i>		Mar.-May				
		Mar.-May			180-210	Melbourne, Vic. Tasmania Melbourne, Vic.
<i>P. australis</i>		Nov., Jan., May Sept.				Fletcher, 1889
		All year?	20	2.8	28	Harrison, 1922
		Aug.-Mar.	15		30-40	Moore, 1961
		Aug.	10-20	3.0-3.5		Jacobson, 1962 Pengilley, unpubl.
<i>P. coriacea</i>		Jan.				near Mittagong, N.S.W.
		March	110-180			Sydney, N.S.W. Pengilley, unpubl.
		Feb.				North Coast, N.S.W. Straughan, 1963 (pers. comm.)
<i>P. guentheri</i>		Mar.-June			40-50	
		Apr.-May			90-120	Main <i>et al.</i> , 1959 Main, 1965
<i>P. occidentalis</i>		Jan.-June			40-50	Main <i>et al.</i> , 1959
		Dec.-Mar.			40-50	Main, 1965
		Summer-early winter				
<i>P. douglasi</i>		Summer-early winter				
		May	89		90-120	Main, 1964

^a based on 1964 data^b modal class size

Because of the paucity of information available on the breeding biology of species of this genus, a number of populations of *P. corroboree*, *P. dendyi* and *P. bibroni* in the Southern Highlands and Southern Tablelands were examined as frequently as possible during the breeding seasons. During the examination of these areas, particular attention was placed on obtaining fairly accurate information on the onset and duration of the calling and breeding seasons of the three species. In the case of the calling season, it was thought that the time when the males were first heard calling probably indicated that males were beginning to move into the breeding areas. Known burrows in the breeding areas were periodically checked to see whether there were any males present. The examination of burrows during these visits also provided information on fecundity and on the date of commencement of breeding and fecundity.

MATERIALS AND METHODS

Locations of the study areas have been given elsewhere (Pengilley, 1971a). Most of the areas that were visited more than once during the calling and breeding seasons are situated in the montane or subalpine zones of Costin (1954) within south-eastern N.S.W.

The main study area, which is located at Coree Flats (alt. 1036m) on the Brindabella Range near the north-western corner of the N.S.W.-A.C.T. border, is a wet heath surrounded by dry-wet sclerophyll forest (*Eucalyptus dalrympleana*-*E. robertsoni* alliance). Within the wet heath, the majority of breeding animals were concentrated at the northern and southern parts where the vegetation had been partly modified by man. In these small areas, the herbaceous layer consisting of a diverse assemblage of snow grass (*Poa caespitosa*), species of *Agrostis*, and various herbs and mosses, (Fig. 1) provided suitable breeding sites for *P. corroboree* and *P. dendyi*. Snowy Flats (alt. 1646 m) is situated on the Brindabella Range approximately 27 km south of Coree Flats. It is essentially a valley bog surrounded on the slopes by subalpine woodland (*E. pauciflora*) underlain by a well-developed and virtually continuous sward of snow grass (*Poa caespitosa*). The bog is an example of the *Carex gaudichaudiana*-*Sphagnum cristatum* bog alliance (Costin et al., 1959) of which a large part consists of active sphagnum moss showing hollow-hummock development (Fig. 2). Most burrows of *P. corroboree* were found in sphagnum bordering pools or in between pools.

The area here called Smiggin Holes is about 3.2 km north of the village of Smiggin Holes on the Smiggin Holes-Guthega road at an elevation of about 1650 m. It is a small sphagnum bog surrounded by disclimax heath (Costin, et al., 1959), which was originally subalpine woodland.

Boggy Plain (alt. 1585 m) is located about 5 km south-east of Smiggin Holes on the same mountain range. As the name suggests, this was once a very wet sphagnum bog but due to repeated burning off and grazing of sheep, it is now very dry and there is little actively growing sphagnum.

Round Mountain is 39 km NNW of Smiggin Holes at an elevation of 1585 m. It is a small bog surrounded by subalpine woodland. Little Thredbo River Flats

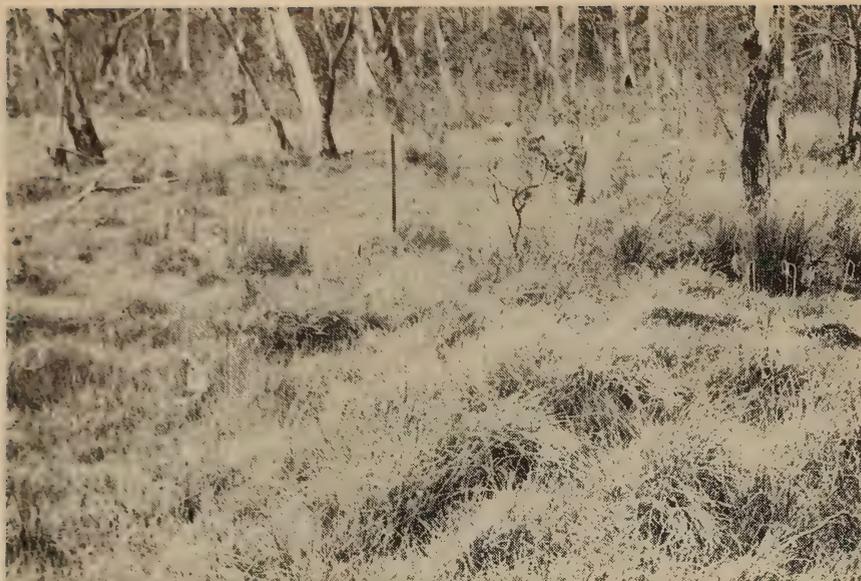


Fig. 1. Breeding sites of *P. corroboree* and *P. dendyi* at the southern end of Coree Flats. Burrows of both species tended to be concentrated around ill-defined depressions in the heath similar to the one shown in the extreme right of the photograph.



Fig. 2. Breeding site of *P. corroboree* at Snowy Flats, A.C.T. The majority of breeding adults were found in the sphagnum bordering the pool (arrowed).

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(alt. 1280 m) is located near the junction of the Little Thredbo and Thredbo Rivers in the Thredbo Valley, approximately 7 km south of Smiggin Holes. The area consists of a disturbed sphagnum bog surrounded by wet sclerophyll forest.

The area here called Yarrangobilly is actually 2 km south-east of the village of Yarrangobilly on Highway 18 at an elevation of approx. 1260 m. It is part of the western montane zone of Costin (1954) and consists mainly of wet sclerophyll forest.

Weather data for two highland localities (Smiggin Holes and Yarrangobilly) and one tableland locality (Canberra) are shown in Fig. 3.

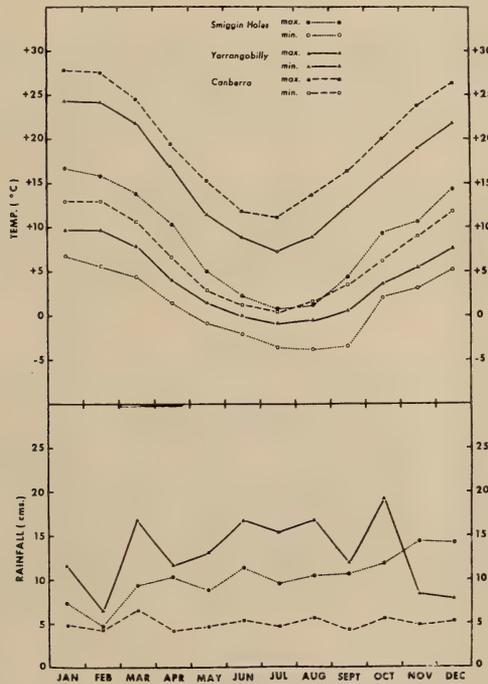


Fig. 3. Upper Graph. Mean maximum and minimum monthly screen temperatures of three selected stations in the Southern Highlands and Tablelands of N.S.W. Lower Graph. Mean monthly rainfall in centimetres for the same three stations.

Rainfall and temperature data for Coree Flats for the years 1963 to 1965 have also been reported in another publication (Pengilly, 1971b). During the early part of 1965, drought conditions prevailed over most of south-eastern N.S.W. Very little rain was recorded at Coree Flats during the months of January and February, and no rain was recorded in March. Less than 5 cms of rain fell in each of the four subsequent months.

A preliminary statement on the taxonomic status of the three species studied has been given in an earlier publication (Pengilley, 1971a).

The number of eggs laid by each of the three species was determined (1) by counting the number of eggs in the body cavity and oviducts of females that had ovulated, and (2) by counting eggs, which were of one embryological stage of development, that were deposited in burrows. The snout-urostyle measurements refer to those obtained from preserved adults which were collected during the breeding season.

OBSERVATIONS

Size at Sexual maturity

Snout-urostyle lengths of males *P. corroboree* found in burrows during the breeding season and of gravid females are given in Table 2. At any given locality, males are generally a few millimetres smaller than females. There is a gradual but parallel increase in the mean size of both males and females with increase in altitude.

At Coree Flats, *P. corroboree* probably attains sexual maturity at 3 years. This rather crude estimate of the length of the pre-reproductive period is based on size attained by juveniles at the end of first year of their terrestrial phase, but in their second year of growth following fertilization. At this stage in the

TABLE 2.

Snout-urostyle lengths of adult male and adult female *P. corroboree*.
Southern Highlands, N.S.W.

Locality	MALES		FEMALES	
	No. in Sample	Mean Snout-urostyle length (mm) \pm SE \ddagger	No. in Sample	Mean Snout-urostyle length (mm) \pm 2SE
Coree Flats* (alt. 1040 m)	51	22.0 \pm 0.30	57	24.6 \pm 0.26
Bull's Head* (alt. 1220 m)	—	— — —	8	25.2 \pm 1.02
Snowy Flats* (alt. 1650 m)	53	22.7 \pm 0.26	5	26.0 \pm 0.62
Yarrangobilly (alt. 1280 m)	20	22.0 \pm 0.56	5	25.0 \pm 1.16
Smiggin Holes \dagger (alt. 1650 m)	70	23.7 \pm 0.22	12	27.0 \pm 0.70
Round Mountain \dagger (alt. 1590 m)	42	24.0 \pm 0.34	9	27.6 \pm 0.92

* Localities in the Brindabella Range

\dagger Localities in the Snowy Mountains

\ddagger SE = Standard error

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life cycle, juveniles ranged from 7.5 to 10.0 mm in snout-urostyle length and at the end of their first year of terrestrial growth they range from 9.0 to 14.0 mm.

P. dendyi males are also slightly smaller than females, but they tend to be slightly larger than males of *P. corroboree* from the same altitude (Fig. 4), but unlike the situation in *P. corroboree*, there is no clearly defined trend in size with altitude. There are, however, some differences between localities differing greatly in altitude over a short distance. For example, males from Boggy Plain (alt. 1585 m) are larger than those from Little Thredbo River Flats (alt. 1158 m) and similarly males from Clyde Mountain (alt. 610 m) on the Coastal Range are significantly larger than those from near sea level at Moruya.

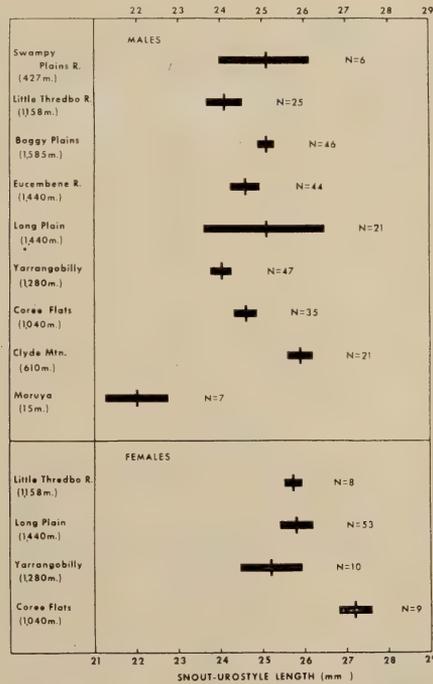


Fig. 4. Snout-urostyle lengths of adult males and females of *P. dendyi*. Thin vertical lines represent the means and the thicker horizontal bars represent the means \pm 2SE.

Both adult male and adult female *P. bibroni* (Table 3) are approximately the same size as most of the Southern Highland populations of *P. dendyi*.

Number of eggs laid

P. corroboree

The clutch size of *P. corroboree* based on counts of eggs in gravid females ranged from 16 to 38, the mean clutch sizes for the two samples (Snowy Mts.

and Brindabella Range) being 26.4 and 24.0 respectively. The larger mean clutch size of the Snowy Mountains females is attributable to the larger mean size of these females (Table 2). However, from the small sample of 24 females obtained from the Snowy Mountains there is no relationship between snout-urostyle length of the female and fecundity, although fecundity is correlated with size in the sample from the Brindabella Range (Fig. 5).

TABLE 3.

Snout-urostyle lengths (sub) of adult male and female *P. bibroni*, Southern Tablelands, N.S.W.

Locality	MALES		FEMALES	
	Number in Sample	Mean SUL (mm) \pm 2SE	Number in Sample	Mean SUL (mm) \pm 2SE
11.2 km. south of Yass, N.S.W.	25	24.8 \pm 0.5	5	25.6 \pm 1.2
Mountain Creek Road, N.S.W.	11	23.8 \pm 0.8	2	24.2
Uriarra, A.C.T.	19	24.4 \pm 0.5	2	25.4

TABLE 4.

Percentage of nests of *P. corroboree* containing a given number of clutches*.

Locality	Year	Number of nests examined	Percentage of nests containing a given number of clutches				
			1	2	3	4	5
Coree Flats	1963	104	48.3	31.7	13.3	5.0	1.6
	1964	136	60.0	34.3	5.0	0.6	0.0
	1965	7	77.8	22.2	0.0	0.0	0.0
	1967	21	33.3	25.0	23.0	9.0	0.0
Snowy Flats	1964	83	45.7	43.8	7.7	1.9	1.0
	1965	14	75.1	18.8	6.3	0.0	0.0
Smiggin Holes	1964	14	49.9	42.8	7.1	0.0	0.0
	1965	58	67.2	29.5	3.2	0.0	0.0
Round Mtn.	1965	28	61.8	38.2	0.0	0.0	0.0

* For this purpose, a clutch consisted of less than 30 eggs at the same stage of development. If two batches of eggs were at different stages of development, they were considered to be two clutches even though each batch may have consisted of less than 15 eggs.

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Colefax (1956) reported that *P. corroboree* (Snowy Mountains) lays 12 eggs. It is evident from the counts of eggs in gravid females and the number of eggs per nest (Figs. 6 and 7) that this number represents only part of the egg complement of a female. A small percentage of burrows, generally less than 20% do contain less than the minimum clutch size recorded. Most, however, contain one or more clutches of eggs (Figs. 6 and 7 and Table 4) indicating that a burrow is used by more than one female as an oviposition site.

P. dendyi

The only report in the literature on the number of eggs laid by *P. dendyi* is that of Moore (1961) who found 85 eggs in a nest near Jindabyne, N.S.W. The number of mature eggs contained in the ovaries of 30 gravid females ranged from 35 to 102. There was no relationship between size of female and fecundity.

In 9 nests of *P. dendyi* at Coree Flats examined in 1963, the number of eggs ranged from 45 to 154, the mean being 101.1. Examination of 36 nests during the 1964 breeding season showed that modal clutch size was within the range 80-89 (Fig. 8) and the mean was 81.8. In 1965, there was a reduction in the modal (40-49) and mean (65.0) 'clutch' size.

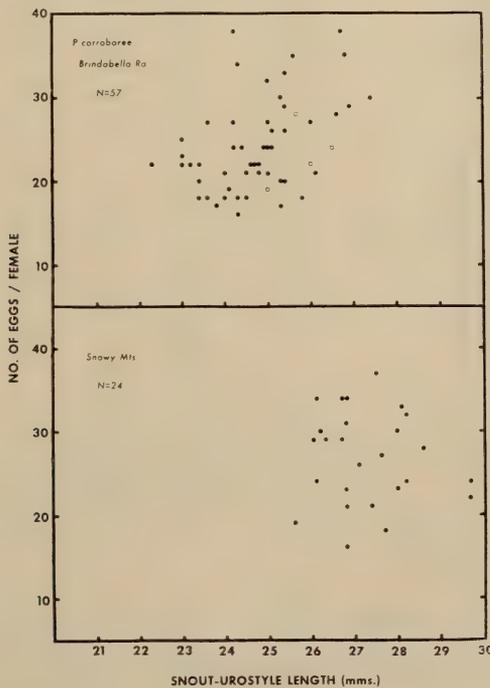


Fig. 5. Plot of the number of eggs found per female against snout-urostyle length. The open squares represent specimens obtained from Snowy Flats, Brindabella Range.

TABLE 5.
 Calling and Breeding Seasons of *P. corroboree*, Southern Highlands, N.S.W.

Locality	Season	Males in breeding area, not calling or only a few calling	Large numbers of males calling	Breeding season	Last male seen in breeding area
Smiggin Holes	1963-64	—	4th week Dec.	3rd week Jan.-?	2nd week Feb.
	1964-65	—	—	4th week Jan.-	1st week April
	1965-66	—	—	2nd or 3rd week Jan. 1st week Jan.-?	—
Round Mountain	1964-65	—	—	4th week Jan.-	—
	1965-66	—	—	4th week Feb. 1st week Jan.-?	—
	1963-64	2nd week Dec.	1st week Jan.	3rd week Jan.-	1st week Mar.
Snowy Flats	1964-65	—	—	2nd week Feb.	—
	1965-66	—	1st week Jan.	1st week Feb.-? 4th week Jan.-?	1st week April
	1962-63	—	—	1st week Mar.-	4th week April
Coree Flats	1963-64	2nd week Jan.	2nd week Feb.	3rd week Mar. 1st week Mar.-	2nd week April
	1964-65	1st week Jan.	3rd week Jan.	4th week Mar.	4th week April
	1965-66	4th week Dec.	—	4th week Mar.-?	—
	1966-67	3rd week Dec.	—	1st week Mar.-?	? 2nd week April

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P. bibroni

This species is recorded as laying 130 (Harrison, 1922) and 260 eggs (Jacobson, 1962). From 12 nests at Uriarra, A.C.T., the modal 'clutch' size was between 80-99 (Fig. 8) the mean being 85.3. Since only three gravid females were dissected, it is not known whether there is any relationship between body length and egg complement. The clutch size of these females ranged from 82 to 109 (Fig. 9).

Calling and Breeding Seasons

Male *P. corroboree* have been heard calling from early December until early April at Snowy Flats and from late December until mid-April at Coree Flats (Table 5). Thus males are present in the breeding areas 4 to 8 weeks before breeding commences and some males remain until 2 to 4 weeks following egg

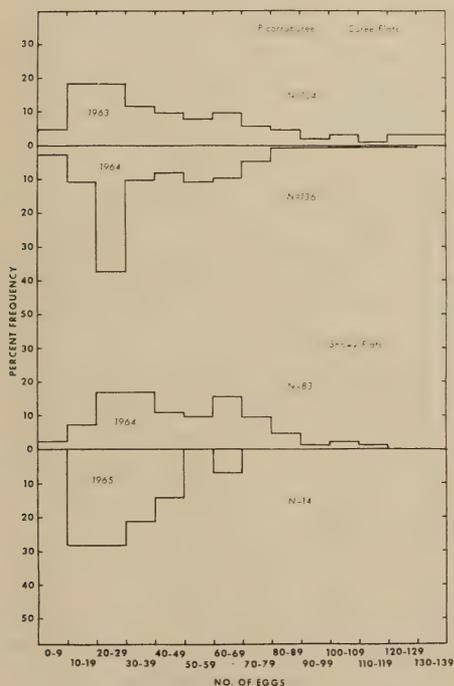


Fig. 6

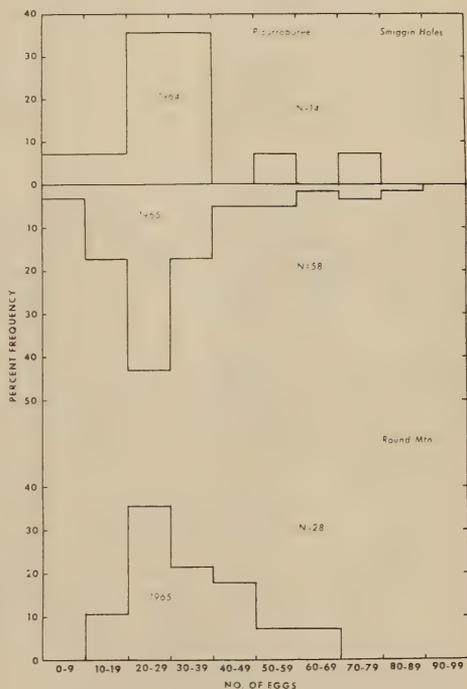


Fig. 7

Fig. 6. Frequency distribution of the number of eggs found in nests of *P. corroboree* at two localities on the Brindabella Range. The number of nests (N) and the year during which they were examined are shown on the diagram.

Fig. 7. Frequency distributions of the number of eggs found in nests of *P. corroboree* at two localities in the Snowy Mountains region. The number of nests (N) and the year during which they were examined are shown on the diagram.

laying. On the limited and qualitative information available, both migration of males into and out of the breeding areas appears to be related to altitude.

The onset of breeding as evidenced by the presence in burrows of recently-laid eggs or of eggs in the early stages of development is more clearly related to altitude than is the initiation of the influx of males into the breeding area. Populations of *P. corroboree* in the sub-alpine zone (>1524 m) generally begin breeding in the latter half of January, but those at lower altitudes (about 1000 m) do not commence until early March. This negative relation between altitude and the commencement of egg laying appears to be consistent from year to year (Fig. 10 and Table 5).

However, in 1965, breeding was much later at all localities except for Round Mountain and Smiggin Holes in the Snowy Mountains when recently-laid eggs were found on January 24 and 25. If allowances are made for errors

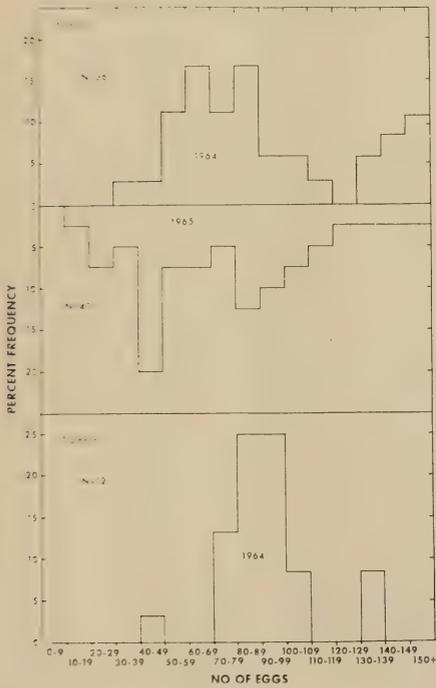


Fig. 8

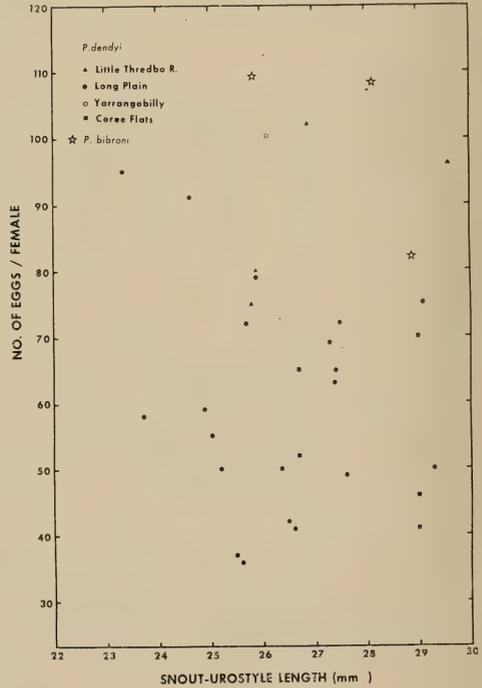


Fig. 9

Fig. 8. Upper Graph. Frequency distribution of the number of eggs found in nests of *P. dendyi*.

Lower Graph. Frequency distribution of eggs found in 12 nests of *P. bibroni* at Uriarra, A.C.T. during the 1964 breeding season.

Fig. 9. Plot of the number of eggs found in gravid females of *P. dendyi* and *P. bibroni* against snout-urostyle length.

PSEUDOPHRYNE BREEDING BIOLOGY

in estimating the date of commencement of breeding, the dates given do not differ greatly from those of the previous year. At both Snowy and Coree Flats, however, breeding was two to three weeks later than the previous year.

Colefax (1956) recorded *P. corroboree* breeding in the latter half of December at Alpine Hut (alt. approx. 1768 m). If 1964 is considered to be a normal season for *P. corroboree*, then from the relationship between altitude and the onset of breeding, the Alpine Hut population would have started breeding towards the end of December.

P. dendyi and *P. bibroni*

The breeding of *P. dendyi* and *P. bibroni* tends to follow the same pattern as of *P. corroboree* in that the males migrate into the breeding areas some weeks before breeding commences.

During 1965, males of *P. dendyi* were observed in the breeding areas towards the end of January at both Boggy Plain and Little Thredbo River Flats, but were not heard calling until early March at Coree Flats. By the second week of April, the majority of males had moved out of the breeding area at Boggy Plain, but this did not take place until at least early May at Coree Flats as males were still present on April 26.

The close correspondence seen in breeding schedule and altitude of *P. corroboree* was not so apparent in *P. dendyi* during 1964 and 1965. In 1964 at 1585 m breeding began towards the end of January and at 1219 m eggs were first noticed towards the end of the second week in February. Delayed breeding was also observed in 1965 when most populations bred approximately two weeks later than in the previous year.

Male *P. bibroni* were first heard calling at 610 m on April 13, 1964, but as these populations were not visited before this date, calling possibly could have begun much earlier. Males were last heard calling towards the end of May of the same year.

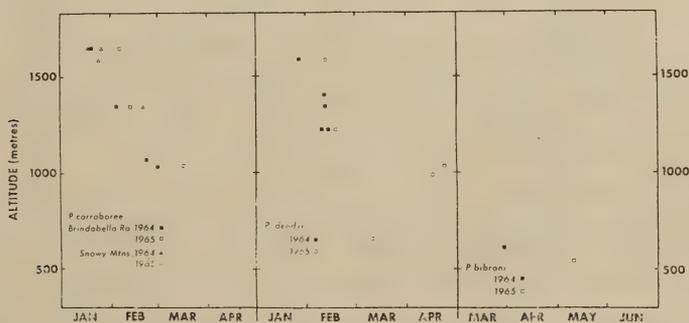


Fig. 10. Time of onset of breeding in *P. corroboree*, *P. dendyi* and *P. bibroni* at various altitudes in the Southern Highlands and Southern Tablelands, N.S.W.

The data available for *P. bibroni* are too limited to indicate whether breeding schedule is related to altitude. However, some observations made in 1963 suggest that breeding in this species is partially dependent on latitude. *P. bibroni* was found breeding near Pt. Lookout (alt. approx. 1 200 m) New England Tablelands, N.S.W. on January 16, 1963. Three days later (January 19) in the Blue Mountains, males were found calling in burrows but no eggs were present. At Canberra, however, males were not heard calling until towards the end of March.

DISCUSSION

Where *P. corroboree* and *P. dendyi* are sympatric, there is some overlap in breeding seasons, with *P. corroboree* tending to breed much earlier than *P. dendyi*. At Coree Flats, *P. dendyi* males begin to move into the breeding area at the time when *P. corroboree* is just beginning to breed. There is always the possibility then that *P. dendyi* males could mate with *P. corroboree* females. However, the courtship calls of the two species are quite different (Pengilley, 1971a) and this undoubtedly plays some part in enhancing reproductive isolation between the two species.

Where *P. corroboree* and *P. dendyi* are allopatric there is some evidence which suggests that there is greater overlap in breeding seasons. During 1964, in the Snowy Mountains, *P. dendyi* began breeding about one week later than *P. corroboree*, and if a correction is made for the difference in altitude between the two localities, there is very little difference between the times at which they bred. In 1965, however, the overlap was not as great as the time of breeding of both species (at the same altitude, but at different localities) differed by three weeks.

The drought of 1965 affected the breeding of all populations below 1560 m. in one of two ways: breeding was either restricted to very wet places in the breeding areas, or it was totally inhibited. No breeding of *P. corroboree* occurred in the main study area at the southern end of Coree Flats. A total of seven nests containing eggs were found, however, in two small areas bordering a small stream in the northern and western edges of the wet heath. In this area, male frogs were largely confined to the relatively moist, peripheral, ecotone of *Leptospermum myrtifolium* and *Epacris breviflora*. Only a few males were located in the central part which, in 1963 and 1964 had provided the most favourable breeding sites. It was estimated that the area suitable for breeding in this small part of the flat had been reduced to about 1% or less of the 1964 value.

At Coree Flats, *P. dendyi* was not as greatly affected by the drought as *P. corroboree* because it bred much later in the year when climatic conditions were less severe.

Populations of *P. bibroni* on the tablelands were also greatly affected by the drought. Males migrated to the breeding areas at 5 localities but eggs were found at only one of these.

At localities about 1500 m. on the Brindabella Range, and the Snowy Mountains, all populations of *P. corroboree* and *P. dendyi* bred. However, the breeding was not entirely successful as large numbers of eggs became desiccated and died as a result of the sphagnum drying up.

The demonstration of well-defined seasonal breeding in these species of *Pseudophryne* suggests that their reproductive activities are controlled by climatic conditions. Temperature and rainfall are considered as being the two most important climatic factors affecting reproduction in amphibia (Gallien, 1959; Noble and Noble, 1923; Smith, 1955). Although experimental evidence is available only for the effects of temperature (Van Oordt, 1960), there is much evidence (e.g. Savage, 1961) which suggests that one or both factors are influential in determining the onset of breeding. In *P. corroboree* and to a lesser extent in *P. dendyi*, it appears that the breeding schedule is determined by temperature but the precise thermal conditions necessary to induce breeding are not known, primarily because of the lack of records from different localities extending over a number of years. However, the rate of decline of temperatures during the period January to May may be of some importance. At Coree Flats, breeding was much later in 1965 than in 1964. In 1965, temperatures declined at the mean daily rate of 0.06°C, whereas in 1964 the rate was 0.12°C. Robinson (1965, pers. comm.) suggested that the slower rate observed in 1965, may have been responsible for delayed breeding in the winter-breeding lyre bird, *Menura novae-hollandiae* at a locality about 17 km. south of Coree Flats.

The rate of decline of temperatures is probably not the prime factor responsible for breeding of *Pseudophryne* in the subalpine zone, because these species begin breeding when temperatures are just beginning to decrease.

Although rainfall has been implicated as a stimulus for breeding in some species of *Pseudophryne* (Fletcher, 1889; Jacobson, 1963; Main, 1965) it seems from the data obtained on *P. corroboree* and *P. dendyi* that there is very little relationship between the two. Both species breed from late summer to mid-autumn, a period during which rainfall is generally minimal. The absence of rain, however, can affect reproduction by making the breeding sites too dry for egg deposition. In moist areas, at the same localities, breeding will occur.

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Three New Species of Deep-dwelling Damsel-fishes (*Pomacentridae*) from the South-West Pacific Ocean

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ABSTRACT

Three new species of damselfishes are described which were collected during 1971-1972 while conducting ichthyological investigations aboard the research vessel *El Torito* at Madang, New Guinea; Fergusson Island, D'Entrecasteaux Group; Osprey Reef, Coral Sea; and the Great Barrier Reef. These species were taken in depths ranging from 31 to 50 metres. *Abudefduf starcki* and *A. caeruleolineatus* appear to have no close relatives. The remaining species, *Pomacentrus nigromarginatus*, belongs to the complex which include *P. melanochir*, *P. melanopterus*, *P. nigromanus* and *P. philippinus*. It is most closely related to the latter species, but differs on the basis of habitat preference and counts for the gill rakers and tubed lateral line scales.

INTRODUCTION

The use of SCUBA (self-contained underwater breathing apparatus) by marine scientists has become increasingly popular. However, in spite of its widespread application, there are few ichthyologists who regularly employ this equipment below 100 feet, primarily because of the physiological hazards involved. During the period extending from November 1971 to June 1972, I had the opportunity to work with Dr. Walter A. Starck II aboard his 65-foot research vessel *El Torito*. This ship was designed by Dr. Starck for support of deep-diving and is equipped with both conventional SCUBA and closed circuit, electronically controlled, mixed gas apparatus. Other equipment includes air compressors, two decompression chambers, and a host of accessories designed for probing the deeper reefs. Our itinerary included the following localities: Palau Archipelago, Western Caroline Islands; Madang, Cape Nelson and Samarai Island, along the north-east coast of Papua New Guinea; Goodenough, Fergusson and Normanby Islands, D'Entrecasteaux Group; Egum Atoll, Solomon Sea; Osprey Reef, Coral Sea; portions of the Great Barrier Reef off Cairns, Queensland. A significant amount of our collecting effort was expended between depths of 100 and 250 feet. The collections were made with rotenone, quinaldine, dipnets and small multi-prong spears. They contain at least 20 new species including three species of deep-dwelling pomacentrids which are described below.

METHODS OF COUNTING AND MEASURING

The methods of counting and measuring are the same as those described in Allen (1972) except the length of the dorsal and anal spines are measured proximally at the base of the spine rather than the point at which the spine emerges from the scaly sheath. Measurements were made with needlepoint dial calipers to the nearest one-tenth millimetre (mm). Standard length is abbreviated as SL. The fraction $\frac{1}{2}$ which appears in the dorsal and anal fin ray formulae refers to a bifurcate condition of the last ray.

The counts and proportions which appear in parentheses under the description section for each species apply to the paratypes when differing from the holotype. A summary of counts for the dorsal, anal and pectoral fin rays, gill rakers on the first gill arch, and tubed lateral line scales are presented in Tables 1 and 2.

Type material has been deposited at the following institutions: Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London (BMNH); Museum National d'Histoire Naturelle, Paris (MNHN); United States National Museum, Washington, D.C. (USNM).

DESCRIPTIONS

Abudefduf starcki, new species
Figure 1

Holotype — AMS I.16477-001, 44.7 mm SL, collected with multi-prong spear on outer slope of Osprey Reef, Coral Sea (13°58'S, 146°41'E; U.S.H.O. Chart No. 2002) in 37 metres by G. R. Allen on June 22, 1972.

TABLE 1

Dorsal and Anal Fin Ray Counts for New Pomacentrids from Papua New Guinea and the Coral Sea

SPECIES	DORSAL RAYS										ANAL RAYS						
	XIII	XIV	11	11½	12	12½	13	13½	14	14½	15	II	13	13½	14	14½	I5
<i>Abudefduf starcki</i>			2							2		2			1		1
<i>A. caeruleolineatus</i>	10			1		8	1					10	2	6	2		
<i>Pomacentrus nigromarginatus</i>	5									1	2	2	5		1	2	2

TABLE 2

Pectoral Ray, Gill Raker, and Tubed Lateral Line Scale Counts for New Pomacentrids from Papua New Guinea and the Coral Sea.

SPECIES	Pecoral Rays			Gill Rakers				Tubed Lateral Line Scales					
	15	16	17	20	21	22	23	12	13	14	15	16	
<i>Abudefduf starcki</i>		1	1		1	1							2
<i>A. caeruleolineatus</i>	1	9			1	4	4	1	2	1	4	2	
<i>Pomacentrus nigromarginatus</i>		2	3		1	4					1	4	

NEW SPECIES OF DAMSELFISHES

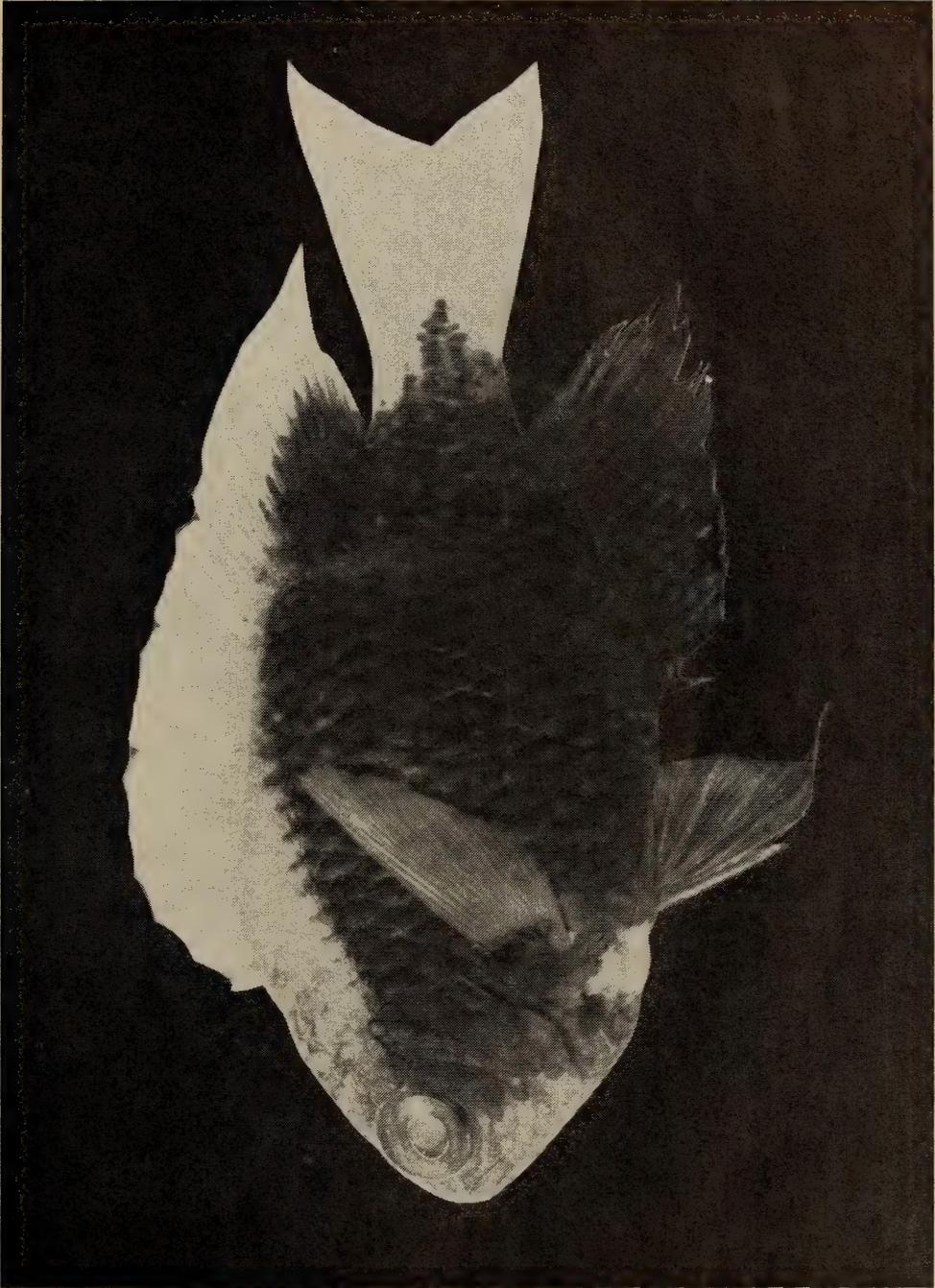


Fig. 1. *Abudefduf starcki*, holotype, 44.7 mm SL, from Osprey Reef, Coral Sea.

Paratype — AMS I.16478-001, 36.0 mm SL, same collecting data as holotype.

Diagnosis — A species of *Abudefduf* with the following combination of characters: Dorsal spines 13; horizontal scale rows between middle of lateral line and dorsal fin base $1\frac{1}{2}$; scales on upper part of head reaching to nostrils; teeth uniserial; preorbital and suborbital naked; body mostly blue with mid-dorsal stripe, dorsal fin and caudal fin yellow.

Description — The proportional measurements for the type specimens are expressed as percentage of the standard length in Table 3.

Dorsal rays XIII,14; anal rays II,14 (II,15); pectoral rays 17 (16 on right side of paratype); pelvic rays I,5; branched caudal rays 13; gill rakers on the first gill arch 22 (21) with bifurcate raker at angle of gill arch; tubed lateral line scales 15 or 16 (damaged on both specimens); vertical scale rows from upper edge of gill opening to base of caudal fin 28; horizontal scale rows from base of dorsal fin to middle of lateral line (exclusive of dorsal base sheath scales) $1\frac{1}{2}$; from lateral line to anal fin origin 9; predorsal scales about 20 extending well forward of anterior edge of orbits, about to level of nostrils; teeth uniserial, close-set, somewhat incisiform with rounded tips, about 36 to 38 in the lower jaw and about 48 to 50 in the upper.

Body ovate and laterally compressed, the greatest depth 2.2 in the standard length. Head profile conical, the head length contained 3.4 (3.3) times in the standard length; snout 4.9 (5.2), eye diameter 2.3 (2.2), interorbital width 3.8 (4.6), least depth of caudal peduncle 2.1 (2.3), length of caudal peduncle 2.5 (2.7), of pectoral fin 1.0 (0.9), of pelvic fin 1.0, of middle caudal rays 1.3 (1.4), all in the head length

TABLE 3

MORPHOMETRIC PROPORTIONS (IN % OF SL) OF TWO SPECIMENS
OF *ABUDEFDUF STARCKI* FROM OSPREY REEF, CORAL SEA

Morphometric measurement	N	Range (% SL)	Mean (% SL)
Standard length (SL)	2	36.0-44.7	—
Body depth	2	45.0-46.1	45.5
Head length	2	29.4-30.4	29.9
Snout length	2	5.8-6.1	5.9
Eye diameter	2	12.8-13.9	13.3
Interorbital width	2	6.7-7.9	7.3
Least depth of caudal peduncle	2	13.1-13.9	13.5
Length of caudal peduncle	2	11.1-11.6	11.3
Snout to origin of dorsal fin	2	32.5-33.4	32.9
Snout to origin of anal fin	2	62.4-62.8	62.6
Snout to origin of pelvic fin	2	40.0-40.0	40.0
Length of dorsal fin base	2	60.8-63.0	61.9
Length of anal fin base	2	31.1-33.0	32.0
Length of pectoral fin	2	29.5-32.3	30.9
Length of pelvic fin	2	29.1-30.6	29.8
Length of pelvic spine	2	17.5-20.0	18.7
Length of 1st dorsal spine	1	—	6.6
Length of 6th dorsal spine	2	15.0-16.7	15.8
Length of last dorsal spine	2	15.0-16.4	15.7
Length of longest soft dorsal ray	2	19.7-20.3	20.0
Length of 1st anal spine	2	7.6-8.1	7.8
Length of 2nd anal spine	2	12.3-13.4	12.8
Length of longest anal ray	2	20.0-22.0	21.0
Length of middle caudal rays	2	22.3-23.3	22.8

NEW SPECIES OF DAMSELFISHES

Single nasal opening on each side of snout, difficult to distinguish from surrounding sensory pores; mouth oblique, terminally located; lateral line gently arched beneath dorsal fin, terminating below base of first few soft dorsal rays; preorbital, most of suborbital (2-3 scales on posterior portion), tip of snout, lips, chin, and isthmus naked, remainder of head and body scaled; most of head scales cycloid, remainder of scales finely ctenoid; preopercle with two horizontal scale rows with additional row of smaller scales on inferior limb; small sheath scales covering about basal $\frac{1}{2}$ of membranous portions of dorsal, anal and caudal fins; lower margin of preorbital and suborbital entire; margin of preopercle and opercle entire.

Origin of dorsal fin at level of second tubed lateral line scale; spines of dorsal fin gradually increasing in length to sixth spine, remaining spines about equal; length of first dorsal spine 6.6, of sixth and thirteenth dorsal spines 2.0 (1.9), of longest soft dorsal ray 1.5, of first anal spine 3.9 (3.8), of second anal spine 2.4 (2.3), of longest soft anal ray 1.3 (1.5), all in the head length; caudal fin emarginate; pectoral fins pointed.

Colour of holotype in alcohol: Ground colour of body dark blue grading to blackish posteriorly; broad pale yellow mid-dorsal stripe extending anteriorly from origin of soft dorsal fin to forehead, covering most of region above lateral line; head dusky, paler ventrally; spinous dorsal fin pale with fine black margin; soft dorsal fin blackish basally, pale distally with fine black margin; caudal fin and upper and lower portions of caudal peduncle pale; pelvic and anal fins blackish; pectoral fins pale with blackish basal bar.

The paratype is coloured similarly except the interorbital, snout, and ventral portion of the head are less dusky.

Colour of holotype and paratype in life: Most of body royal blue, broad mid-dorsal stripe of canary yellow extending anteriorly from origin of soft dorsal fin to tip of snout, also engulfing spinous dorsal fin and distal half of soft dorsal fin; ventral portion of head yellow; most of opercle, posterior portion of preopercle and suborbital royal blue; basal half of soft dorsal fin, anal fin, and pelvic fins bluish-black; caudal fin and upper and lower portions of caudal peduncle canary yellow; pectoral fin pale yellow with blackish basal bar.

Remarks—*A. starcki* does not appear to have any close relatives. The combination of characters listed under the diagnosis in addition to the colour pattern are distinctive. About 15 specimens were encountered in the vicinity of the type locality in depths ranging from 35 to 52 metres. The type locality consisted of a steep slope intersected by sand channels. Individuals of *A. starcki* were seen around rocky outcrops and near crevices on the reef slope and also around outcrops in the sand channels. They typically feed on plankton a short distance above the bottom. The stomach contents of the types consisted of 99 per cent copepods with a small quantity of gastropod fragments and polychaetes.

Named *starcki* in honour of Dr. Walter A. Starck II, who first pointed out the species to me while diving at Osprey Reef.

Abudefduf caeruleolineatus, new species

Figure 2

Holotype — USNM 207941, 34.9 mm SL, collected with quinaldine and dipnets on outer reef slope off middle of Kranket Island (5°12'00"S, 145°50'52"E; Aus. Chart No. 648), about 1.5 nautical miles north of Madang, New Guinea in 40 metres by G. R. Allen on April 9, 1972.

Paratypes — AMS I.16480-001, 2 specimens, 36.4 and 37.4 mm SL, collected with multi-prong spear on outer slope of Osprey Reef, Coral Sea in 50 metres by W. A. Starck II on June 23, 1972; BMNH 1972.8.14.4-5, 2 specimens, 30.1 and 37.4 mm SL, same collecting

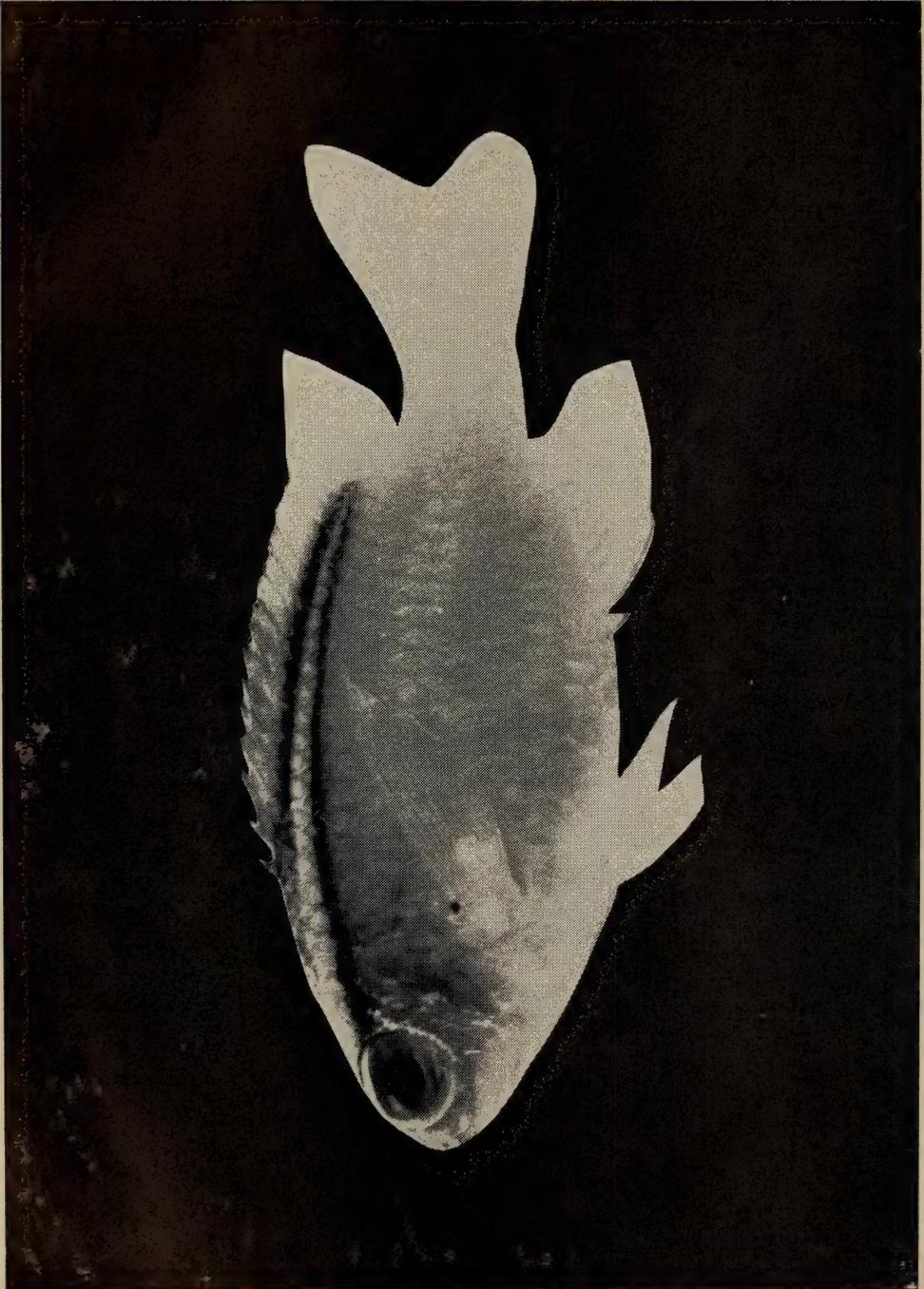


Fig. 2. *Abudefduf caeruleolineatus*, holotype, 34.9 mm SL, from Madang, New Guinea.

NEW SPECIES OF DAMSELFISHES

data as the holotype; BPBM 13227, 2 specimens, 31.8 and 34.9 mm SL, same collecting data as the holotype except collected on April 4, 1972; MNHN 1972-87, 2 specimens, 32.5 and 36.3 mm SL, same collecting data as the holotype except collected on April 4, 1972; USNM 207942, 36.3 mm SL, same collecting data as the holotype.

Diagnosis — A species of *Abudefduf* with the following combination of characters. Dorsal spines 14; pectoral rays usually 16; tubed lateral line scales 12 to 15; horizontal scale rows between middle of lateral line and dorsal fin base $1\frac{1}{2}$; predorsal scales extending to mid-interorbital; head scales cycloid; teeth uniserial; greatest body depth 2.3 to 2.7; colour bright yellow with iridescent blue stripe above lateral line, extending from anterior portion of soft dorsal fin to snout.

Description — The proportional measurements for the type specimens are expressed as percentage of the standard length in Table 4.

Dorsal rays XIV, $12\frac{1}{2}$ (XIV, $11\frac{1}{2}$ to 13); anal rays II, $13\frac{1}{2}$ (II, 13 to 14); pectoral rays 16 (one paratype with 15); pelvic rays I, 5; branched caudal rays 13; gill rakers on the first gill arch 21 (20 to 23, usually 22); tubed lateral line scale 15 (12 to 15, usually 13 or 14); vertical scale rows from upper edge of gill opening to base of caudal fin 28 (27 to 28); horizontal scale rows from base of dorsal fin to middle of lateral line (exclusive of dorsal base sheath scales) $1\frac{1}{2}$, from lateral line to anal fin origin 8 (7 to 8); predorsal scale about 12 (about 10 to 14), extending to about mid-interorbital; teeth uniserial, conical with rounded tips, about 40 to 44 in each jaw.

TABLE 4

MORPHOMETRIC PROPORTIONS (IN % OF SL) OF TEN SPECIMENS OF *ABUDEFDUF CAERULEOLINEATUS* FROM MADANG, NEW GUINEA AND OSPREY REEF, CORAL SEA

Morphometric measurement	N	Range (% SL)	Mean (% SL)
Standard length (SL)	10	30.1-37.4	—
Body depth	10	37.7-44.0	40.9
Head length	10	29.1-32.9	31.6
Snout length	10	4.7-7.5	6.3
Eye diameter	10	12.0-14.0	13.1
Interorbital width	10	6.9-8.4	7.6
Least depth of caudal peduncle	10	14.1-16.1	14.9
Length of caudal peduncle	10	9.2-12.9	10.2
Snout to origin of dorsal fin	10	36.0-40.0	38.4
Snout to origin of anal fin	10	64.9-71.5	67.2
Snout to origin of pelvic fin	10	37.0-44.8	40.4
Length of dorsal fin base	10	54.8-63.8	59.6
Length of anal fin base	10	24.5-26.3	25.5
Length of pectoral fin	10	28.9-35.8	32.0
Length of pelvic fin	10	21.9-25.1	23.4
Length of pelvic spine	10	14.0-15.2	14.8
Length of 1st dorsal spine	10	4.4-6.2	4.7
Length of 7th dorsal spine	10	8.7-13.2	11.6
Length of last dorsal spine	10	10.3-13.2	12.1
Length of longest soft dorsal ray	10	17.3-20.4	19.0
Length of 1st anal spine	10	4.7-6.3	5.7
Length of 2nd anal spine	10	11.4-15.2	13.3
Length of longest anal ray	10	15.0-19.6	17.9
Length of middle caudal rays	10	20.9-26.7	22.6

Body relatively elongate and laterally compressed, the greatest depth 2.4 (2.3 to 2.7) in the standard length. Head profile rounded, the head length contained 3.2 (3.0 to 3.4) times in the standard length; snout 4.3 (4.6 to 6.9), eye diameter 2.3 (2.2 to 2.7), interorbital width 3.9 (3.8 to 4.5), least depth of caudal peduncle 2.2 (2.1 to 2.3), length of caudal peduncle 3.4 (2.3 to 3.1), of pectoral fin 1.0 (0.9 to 1.1), of pelvic fin 1.3 (1.3 to 1.5), of middle caudal rays 1.5 (1.2 to 1.5), all in the head length.

Single nasal opening on each side of snout; mouth oblique, terminally located; lateral line gently arched beneath dorsal fin, terminating one scale row below base of 13th (11th to 13th) dorsal spine; preorbital, suborbital, snout, lips, chin, isthmus and anterior portion of interorbital naked; remainder of head and body scaled; scales of the head region cycloid, those of the body finely ctenoid except most of scales above lateral line which are cycloid; preopercle with two horizontal scale rows with additional row of smaller scales on inferior limb; small sheath scales covering about basal $\frac{1}{2}$ to $\frac{2}{3}$ of membranous portions of dorsal, anal and caudal fins; margin of preorbital, suborbital, preopercle and opercle entire.

Origin of dorsal fin at level of fourth tubed lateral line scale; spines of dorsal fin gradually increasing in length to about seventh spine, remaining spines about equal in length; length of first dorsal spine 5.0 to 7.4 (paratypes only, holotype damaged), of seventh dorsal spine 2.6 (2.4 to 3.8), of last dorsal spine 2.7 (2.4 to 3.2), of longest soft dorsal ray 1.8 (1.5 to 1.9), of first anal spine 5.5 (4.2 to 7.1), of second anal spine 2.1 (2.2 to 2.8), of longest soft anal ray 1.7 (1.6 to 2.0), all in the head length; caudal fin emarginate; pectoral fins pointed.

Colour of holotype in alcohol: Head and body entirely pale yellowish except black-edged bluish stripe, about $\frac{1}{2}$ eye diameter in width extending forward from base of anteriormost soft dorsal rays to tip of snout (passing through dorsal half of eye), and covering most of dorsal portion of body above lateral line; mid-dorsal region between stripe of each side including spinous dorsal fin brownish; remainder of fins pale; small black spot superiorly at pectoral base.

Colour of holotype in life: Head and body entirely yellow except black-edged iridescent blue stripe above lateral line; mid-dorsal region between stripe of each side dusky; spinous dorsal fin bluish, remainder of fins yellow; small black spot superiorly at pectoral base.

Remarks — *A. caeruleolineatus* does not appear to have any close relatives. The dorsal spine count of 14 is a rare feature among the *Abudefduf*. The colour pattern of *A. caeruleolineatus* is very similar to that of *A. leucopomus* Lesson as figured by Jordan and Seale (1906, colour plate XLIII, fig. 1) except it lacks the small black spot at the base of the posteriormost soft dorsal rays and the larger triangular blotch at the base of the caudal fin. *A. leucopomus* is a very common species throughout the western tropical Pacific and is restricted to shallow surge areas.

A. caeruleolineatus was the deepest dwelling member of the genus which we observed. It lives on outer exposed reef slopes among rubble or small rocky outcrops which are usually situated in sandy areas at depths ranging from 38 to at least 62 metres. At Madang, New Guinea, it was moderately common in such areas. It was sighted, but not collected, at 60 metres depth on the outer reef off Seymour Bay, Fergusson Island, D'Entrecasteaux Group.

The name *caeruleolineatus* refers to the distinctive blue stripe on the upper back.

Pomacentrus nigromarginatus, new species

Figure 3

Holotype — USNM 207937, 57.3 mm SL, collected with quinaldine and dipnets on outer reef slope off north end of Kranket Island (5°11'24"S, 145°50'54"E, Aus. Chart No.

NEW SPECIES OF DAMSELFISHES

648), about two nautical miles north of Madang, New Guinea, in 35 metres by G. R. Allen on April 17, 1972.

Paratypes — AMS I.16655-001, 57.1 mm SL, collected with multi-prong spear at Thedford Reef, Great Barrier Reef, off Cairns, Queensland, Australia, in 30 metres by G. R. Allen on August 15, 1972; BMNH.1972.8.14.3, 60.2 mm SL, same collecting data as the holotype except collected with multi-prong spear; BPBN 13226, 2 specimens, 49.6 and 50.5 mm SL, collected with multi-prong spear on isolated pinnacle reef about two nautical miles off south-west side of Seymour Bay, Fergusson Island, D'Entrecasteaux Group in 35 metres by G. R. Allen on May 29, 1972; USNM 207938, 59.9 mm SL, same collecting data as the holotype except collected by W. A. Starck II with multi-prong spear in 31 metres on April 4, 1972.

Diagnosis — A species of *Pomacentrus* with the following combination of characters: dorsal spines 13; preorbital and suborbital naked; slight notch between preorbital and suborbital; inferior edge of suborbital entire; teeth biserial; tubed lateral line scales usually 15; colour basically medium-grey with black margin about $\frac{1}{3}$ to $\frac{1}{2}$ pupil diameter on posterior edge of dorsal and caudal fins; base and axil of pectoral fin black.

Description — The proportional measurements for the type specimens are expressed as percentage of the standard length in Table 5.

Dorsal rays XIII,15 (XIII,14½ to 15); anal rays II,14½ (II,14½ to 15); pectoral rays 16 on right side, 15 on left side (16 to 17); pelvic rays, 1,5; branched caudal rays 13; gill rakers on the first gill arch 21 (20 to 21); tubed lateral line scales 14 on right

TABLE 5

MORPHOMETRIC PROPORTIONS (IN % OF SL) OF FIVE SPECIMENS OF *POMACENTRUS NIGROMARGINATUS* FROM MADANG, NEW GUINEA AND FERGUSSON ISLAND, D'ENTRECASTEAUX GROUP

Morphometric measurement	N	Range (% SL)	Mean (% SL)
Standard length (SL)	5	49.6-60.2	—
Body depth	5	46.8-48.1	47.4
Head length	5	28.5-30.0	29.4
Snout length	5	6.1-6.9	6.5
Eye diameter	5	10.7-11.5	11.0
Interorbital width	5	7.0-8.4	7.6
Least depth of caudal peduncle	5	13.7-15.0	14.4
Length of caudal peduncle	5	8.5-10.7	9.0
Snout to origin of dorsal fin	5	36.2-40.9	37.8
Snout to origin of anal fin	5	65.6-68.0	66.3
Snout to origin of pelvic fin	5	37.8-39.8	39.0
Length of dorsal fin base	5	62.0-66.6	63.7
Length of anal fin base	5	28.1-29.7	28.6
Length of pectoral fin	5	31.4-34.5	33.3
Length of pelvic fin	5	29.1-33.1	31.2
Length of pelvic spine	5	16.1-18.0	16.7
Length of 1st dorsal spine	5	6.3-9.4	7.4
Length of last dorsal spine	5	15.2-16.7	16.1
Length of longest soft dorsal ray	5	20.9-26.0	23.6
Length of 1st anal spine	5	6.3-8.6	7.4
Length of 2nd anal spine	5	15.1-17.4	16.5
Length of longest anal ray	5	19.0-22.4	20.6
Length of middle caudal rays	5	22.2-25.3	23.4

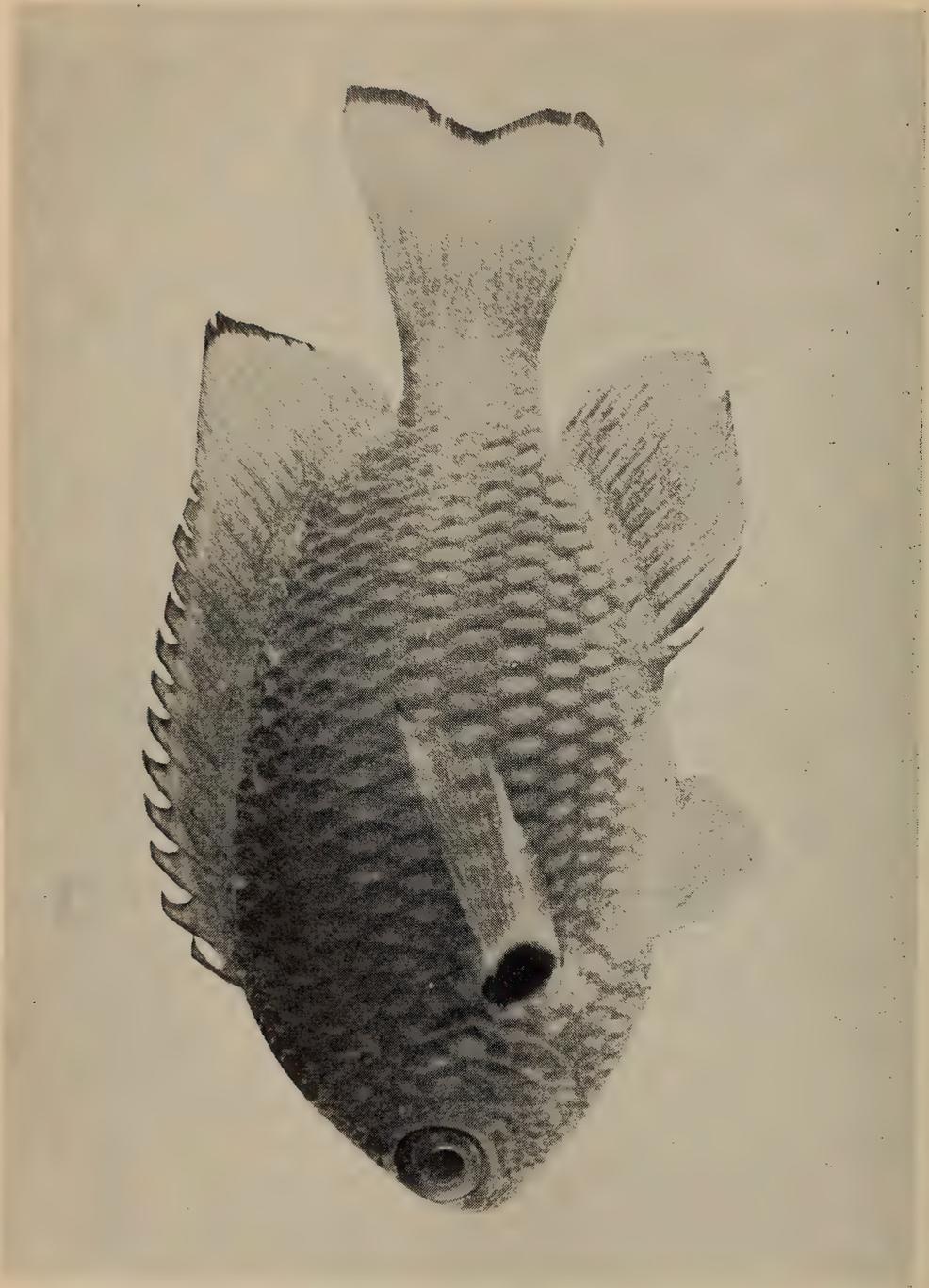


Fig. 3. *Pomacentrus nigromarginatus*, holotype, 57.3 mm SL, from Madang, New Guinea.

NEW SPECIES OF DAMSELFISHES

side, 13 on left side (15, except 17 on left side of one paratype); vertical scale rows from upper edge of gill opening to base of caudal fin 28; horizontal scale rows from base of dorsal fin to middle of lateral line (exclusive of dorsal base sheath scales) $1\frac{1}{2}$; from lateral line to anal fin origin 9; predorsal scales about 20 (about 18 to 22), extending well forward of anterior edge of orbits, about to level of nostrils; teeth biserial at front of jaws, remainder uniserial, conical in shape with gently rounded tips, about 32 in the lower jaw and 42 in the upper.

Body ovate and laterally compressed, the greatest depth 2.1 in the standard length. Head profile conical, the head length contained 3.4 (3.3 to 3.5) times in the standard length; snout 4.8 (4.4 to 4.6), eye diameter 2.7 (2.5 to 2.8), interorbital width 3.5 (3.7 to 4.3), least depth of caudal peduncle 2.0 (1.9 to 2.2), length of caudal peduncle 2.8 (3.4 to 3.5), of pectoral fin 0.9, of pelvic fin 0.9 (0.9 to 1.0), of middle caudal rays 1.2 (1.2 to 1.3), all in the head length.

Single nasal opening on each side of snout; mouth oblique, terminally located; lateral line gently arched beneath dorsal fin, terminating $1\frac{1}{2}$ scale rows below base of posteriormost dorsal spines; preorbital, suborbital, tip of snout, lips, chin and isthmus naked; remainder of head and body scaled; scales finely ctenoid; preopercle with 2 or 3 transverse scale rows with additional row of scales on inferior limb; small sheath scales covering about basal $\frac{1}{2}$ to $\frac{2}{3}$ of membranous portions of dorsal, anal and caudal fins; margin of preorbital and suborbital entire except for very slight denticulations on two of the paratypes; posterior margin of preopercle denticulate; posterior margin of opercle entire.

Origin of dorsal fin at level of third tubed lateral line scale; spines of dorsal fin gradually increasing in length to last spine; length of first dorsal spine 3.9 (3.2 to 4.7), of last dorsal spine 1.8 (1.7 to 1.9), of longest soft dorsal ray 1.2 (1.1 to 1.4), of first anal spine 4.2 (3.5 to 4.5), of second anal spine 1.8 (1.7 to 1.9), of longest soft anal ray 1.4 (1.3 to 1.5), all in the head length; caudal fin emarginate; pectoral fins pointed.

Colour of holotype in alcohol: Head and body greyish-brown with reddish suffusion, scale margins and dorsal portion of body slightly darker; spinous dorsal greyish with translucent submarginal band on outer half of fin; basal half of soft dorsal and caudal fins greyish-brown, outer half pale grey to translucent; dorsal and caudal fins with black margin, about $\frac{1}{3}$ to $\frac{1}{2}$ pupil diameter, especially prominent on posterior edges of soft dorsal and caudal fins; pelvic fins pale; pectoral fins pale with prominent black spot covering entire base and axil of fin.

The paratypes are lighter, nearly whitish on the ventral portion of the head and body, and their overall colouration lacks the reddish suffusion of the holotype.

Colour of holotype in life: Head and body pale grey, whitish ventrally; scale margins brownish, but not detracting from the overall pale colouration of the body; prominent black spot covering pectoral fin base and axil; fins greyish with prominent black margin on edge of dorsal and caudal fins.

Remarks—*P. nigromarginatus* belongs to an Indo-Australian Archipelago species complex which includes *P. melanochir* Bleeker, *P. melanopterus* Bleeker, *P. nigromanus* Weber, and *P. philippinus* Evermann and Seale. These species share similar counts and possess a prominent spot which covers the base and axil of the pectoral fin. *P. nigromarginatus* is clearly separable from *melanochir*, *melanopterus* and *nigromanus* on the basis of colour pattern and number of tubed lateral line scales. The latter group of species usually have 17 to 19 tubed scales compared with a modal count of 15 (holotype with 13 to 14) for *P. nigromarginatus*. *P. melanochir* is further separable by the presence of a strongly denticulate suborbital and one or more spinules on the rear margin of the opercle. *P. melanopterus* usually has a few weak denticulations on the suborbital and a flattened spinule

on the upper edge of the opercular margin. The suborbital and opercle are virtually entire in *P. nigromarginatus*.

P. nigromarginatus appears to be most closely related to *P. philippinus* with regards to morphology and colour pattern. They differ appreciably, however, in number of tubed lateral line scales and total gill rakers on the first arch. Furthermore, the suborbital width of *philippinus* fits about 4.5 to 5.0 in the width of the bony orbit compared to about 6.0 to 7.0 for *nigromarginatus*. The suborbital of *philippinus* also differs by possessing scales on its posterior half. There appears to be a great deal of latitude in the colour pattern of *philippinus*, but the species is invariably much darker than *nigromarginatus*. According to Montalban (1927), specimens from the Philippines are predominantly blackish with pale streaks on the scales. The caudal fin and posterior portions of the dorsal and anal fins are yellow. Specimens of *philippinus* collected by the author at the D'Entrecasteaux Group, Egum Atoll (Solomon Sea, near Woodlark Island), and Osprey Reef (Coral Sea) were basically dark brownish with a red-orange suffusion, particularly noticeable on the ventral surface. The caudal and posterior portion of the dorsal and anal fins were also red-orange and had blackish margins similar to those of *P. nigromarginatus*. Specimens of *P. philippinus* collected at Pixie Reef, on the Great Barrier Reef, off Cairns, Queensland, Australia were entirely blackish, including all the fins except the pectorals, and had pale streaks on the scales. *P. nigromarginatus* and *P. philippinus* are further separable on the basis of ecology. Both species occur on exposed outer reef slopes. However, *P. philippinus* lives in depths ranging from 1.5 to 12 metres, usually around coral outcrops or in the shadows of overhanging cliffs and ledges. *P. nigromarginatus* is usually restricted to depths ranging from 30 to at least 46 metres and frequents rocky outcrops which are usually situated on sandy slopes. It was common in this habitat at Madang, Fergusson and Normanby Islands, Egum Atoll, and Osprey Reef. The stomach contents of one of the paratypes consisted mainly of copepods and algal fragments.

The name *nigromarginatus* refers to the characteristic black margin on the dorsal and caudal fins.

ACKNOWLEDGMENTS

I would like to thank Dr. Walter A. Starck II for making possible my participation on the "El Torito" cruises of 1971-1972. Dr. John E. Randall provided the initial stimulus for my studies of Indo-Pacific damselfishes under National Science Foundation Grant GB-8732. Thanks are also due my wife, Connie, who typed the manuscript.

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Aspects of Reproduction in the Whiptail Wallaby, *Macropus parryi*

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The whiptail wallaby, *Macropus parryi* Bennett, 1835, is a large slender macropodid which is common in Queensland and locally common in northern New South Wales. Relatively little is known about its biology. Calaby (1966) briefly reported on the habitat, habits and numbers of this species in the Upper Richmond and Clarence Rivers area of northern New South Wales. Clark and Poole (1967) mentioned in passing that the whiptail wallaby resembled the grey kangaroo, *Macropus giganteus*, in not having a post-partum oestrus. Calaby and Poole (1971) quoted unpublished data of Merchant for the length of oestrous cycles, gestation periods and pouch life. However, no data are available to indicate whether embryonic diapause occurs in the species.

This paper reports data on reproduction obtained from a small sample of whiptail wallabies collected in September, 1971 at Coombadjha (29° 21' S, 152° 31' 42" E) on the Clarence River about a mile from its junction with the Mann River. The habitat was partly cleared, dry sclerophyll forest essentially the same as described and figured by Calaby (1966). The sample of *M. parryi* was collected to investigate the mode of inheritance of the enzyme phosphoglycerate kinase (P.G.K.) and to further studies on X chromosome inactivation in macropodids. These results are reported elsewhere (VandeBerg, Cooper and Sharman, 1973). In addition some data were collected on reproduction and are reported here.

Half of each ovary and a piece of uterus were collected from all females carrying pouch young. These were fixed in Bodian's solution, embedded in paraffin, sectioned at 7 or 8 μ m and stained in haematoxylin and eosin. A blastocyst was recovered from female 27 (Table 1) using Sharman's (1955) method. Standard body measurements were recorded for all animals and weights and pouch depth or scrotal size were recorded for all adults and juveniles. A total of 41 adults and juveniles was collected.

18 breeding females ranged in weight from 8.5 kg (molar eruption stage MII.O, (Maynes, 1972) primiparous) to 12.8 kg (multiparous); while 12 mature males ranged from 13.4 kg (almost MII.2) to 25 kg.

Table 1 gives the body measurements of the pouch young of 16 females taken during the period 23-27 September, 1971. Limited data on growth of pouch young in captivity and comparison with the growth of pouch young of other

species (*M. parma* (Maynes, 1972); *M. eugenii* (Murphy and Smith, 1970) and *Megaleia rufa* (Sharman, Frith and Calaby, 1964)), suggests a range in age from about 1 week to about 35 weeks. Thus the whiptail wallaby would appear to breed at least from January to September. The data do not exclude the possibility that they breed year round.

TABLE 1

Body measurements of pouch young of whiptail wallaby (all measurements in mm)

Parent No.	Sex of P.Y.	Head	Ear	Arm	Leg	Foot	Body	Tail
30	♂	9.4	2.2	5.1	3.0	4.1	25.8	7.2
34	♀	19.5	5.3	11.1	14.0	10.1	56.1	25.2
54	♂	20.0	6.6	12.3	15.1	11.8	65.6	23.2
32	♀	21.2	6.8	12.9	18.0	12.8	67.6	32.6
16	♂	28.9	9.9	18.2	28.1	20.9	93.9	45.4
9	♂	34.8	11.4	22.3	37.0	28.2	109	68.2
46	♀	36.1	11.9	22.2	39.0	28.5	106.1	62.5
5	♀	36.1	13.4	23.5	43.2	32.4	117	76.0
42	♂	38.5	13.3	23.8	40.2	31.2	112.4	69.2
57	♂	48.1	17.8	31.0	55.7	42.9	137	90
48	♀	48.0	18.9	31.7	64.5	50.5	145	100.8
7	♂	49.5	17.8	30.7	59.2	45.2	145	93
14	♀	52.1	21.5	34.4	71.1	56.5	162	104
23	♀	70.6	38.7	57.0	132	107	236	216
19	♂	73.3	37.5	58.5	130	111	245	211
27	♀	91.6	73.6	83.9	196	168	348	395

Examination of the ovaries and uteri of those females carrying a pouch young showed that all except female 27 were anoestrous. The uterine glands of anoestrous females were small and scattered with little or no lumen present. They consisted of low columnar epithelial cells with oval nuclei occupying about half to two-thirds of the cell. The uterine lumen was lined with cuboidal epithelial cells having mainly oval nuclei which occupied most of the cell. A few females had large atretic follicles up to 1 mm diameter. Female 19 had a large non-atretic follicle of 1.5 mm diameter.

Female 27 had a blastocyst, with an external diameter of 257 μ m (measured after fixation), present in the right uterus. Tall pseudostratified columnar epithelial cells with mainly oval, basally-situated nuclei lined the uterine lumen. The uterine glands had tall columnar cells with rounded nuclei. The lumina of most glands were open and had some material present in them (Fig. 1). There was no evidence of either coagulated semen or sperm in the uterine glands or the uterine lumen. Neither was there any sign of mitoses in the uterine glands or lining. The right ovary had a large corpus luteum with large luteal cells possessing rounded nuclei (Fig. 2). No mitoses were observed in the luteal cells. It is concluded that this female was either in a quiescent state (Clark and Poole, 1967) or just coming out of it.

REPRODUCTION IN *MACROPUS PARRYI*

These data support the statement by Clark and Poole (1967) that *M. parryi* does not have a post-partum oestrus. The presence of a large functional follicle in female 19 and the blastocyst in female 27, suggest that mating may occur while females are carrying a large pouch young. Following mating, the embryo derived from it would become quiescent and would not begin to develop until towards the end of pouch life of the primary young. During the early period of pouch life there is direct inhibition of ovarian activity by the suckling young as shown by females 30-23 (Table 1). Such a reproductive pattern has been observed in the eastern grey kangaroo, *M. giganteus*, by both Kirkpatrick (1965) and Clark and Poole (1967).

Direct inhibition of ovarian activity by a suckling young appears to be the ancestral form of ovarian inhibition (Sharman and Berger, 1969). It has been retained to varying degrees by the parma wallaby (*M. parma*), the whiptail wallaby (*M. parryi*) and the grey kangaroos (*M. giganteus* and *M. fuliginosus*). In all other macropodids that have been studied in detail, this primitive form of ovarian inhibition has been lost completely. In these species, ovarian inhibition while carrying a pouch young is maintained by the suckling stimulus acting via the corpus luteum of lactation derived from a pre- or post-partum oestrus (Sharman, 1970). The reproductive patterns shown by *M. parma*, *M. parryi*, *M. giganteus* and *M. fuliginosus* are thus regarded as being representative of different stages

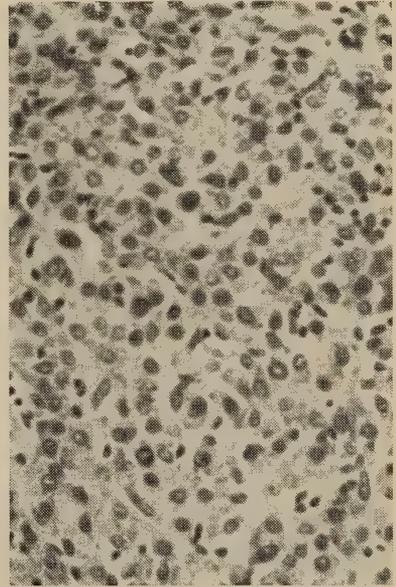
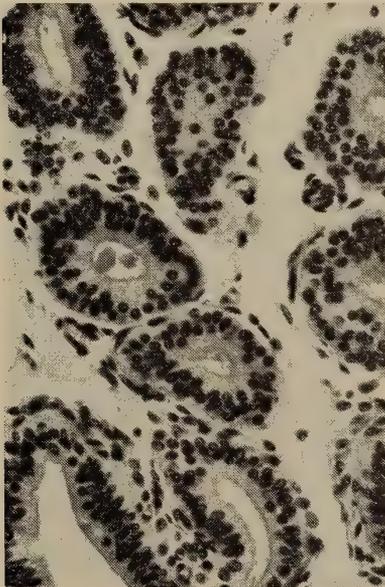


Fig. 1. (left): Uterine glands associated with 257 μm blastocyst of the whiptail wallaby. Uterine lumen lower left.

Fig. 2. (right): Corpus luteum associated with 257 μm blastocyst in the whiptail wallaby.

in the evolution of embryonic diapause and ovarian inhibition as observed in other macropodids.

The retention of transitional reproductive patterns in some species of the genus *Macropus* cannot be regarded alone as evidence for, or an indication of, a close affinity between these species.

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Feeding Mortality in a Deep Sea Angler Fish (*Diceratias bispinosus*) due to a Macrourid Fish (*Ventrifossa* sp.)

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A number of deep sea fishes are known to prey on other fishes which exceed them in size. Large mouths and highly distensible stomachs characterize such fishes as the swallows (*Chiasmodontidae*), gulpers (*Saccopharyngidae*), and anglers (*Ceratioidea*); all have been recorded with stomach contents containing fishes either considerably longer than the abdominal cavity of the predator or larger than the whole fish. The morphological specializations enabling some fishes to consume large prey have been described by Tchernavin (1953). The maximum size of food organisms can only be inferred from the relatively few known instances where the predator has succumbed due to the size of the prey attempted. Unequivocal evidence of such circumstances is usually available only when both animals are found floating at the surface or washed upon a beach.

Recently a 112 mm diceratiid angler fish, *Diceratias bispinosus*, was found floating on the surface in the Bismarck Sea off New Ireland with a 369 + mm macrourid of the genus *Ventrifossa* protruding from its mouth (Fig. 1). The finding has prompted us to make a survey of the known occurrences of this phenomenon.

Our specimens were taken floating at the surface south-east of the island of New Ireland, Papua New Guinea (3° 48' S, 153° 32' E) at 1600 hours on 30 April 1968. Both specimens were dead, although little sign of decay is present and both are in relatively good condition. The macrourid has been engulfed to a point just behind the tips of the pectoral fins. The head of the macrourid has distended the stomach and body wall of the angler posteriorly and ventrolaterally to such a degree that the caudal fin was no longer the most posterior portion of the angler's body. With such a mass filling the entire mouth and body cavity of the angler, both fishes probably died because they could not pass enough water over the gills to obtain sufficient oxygen.

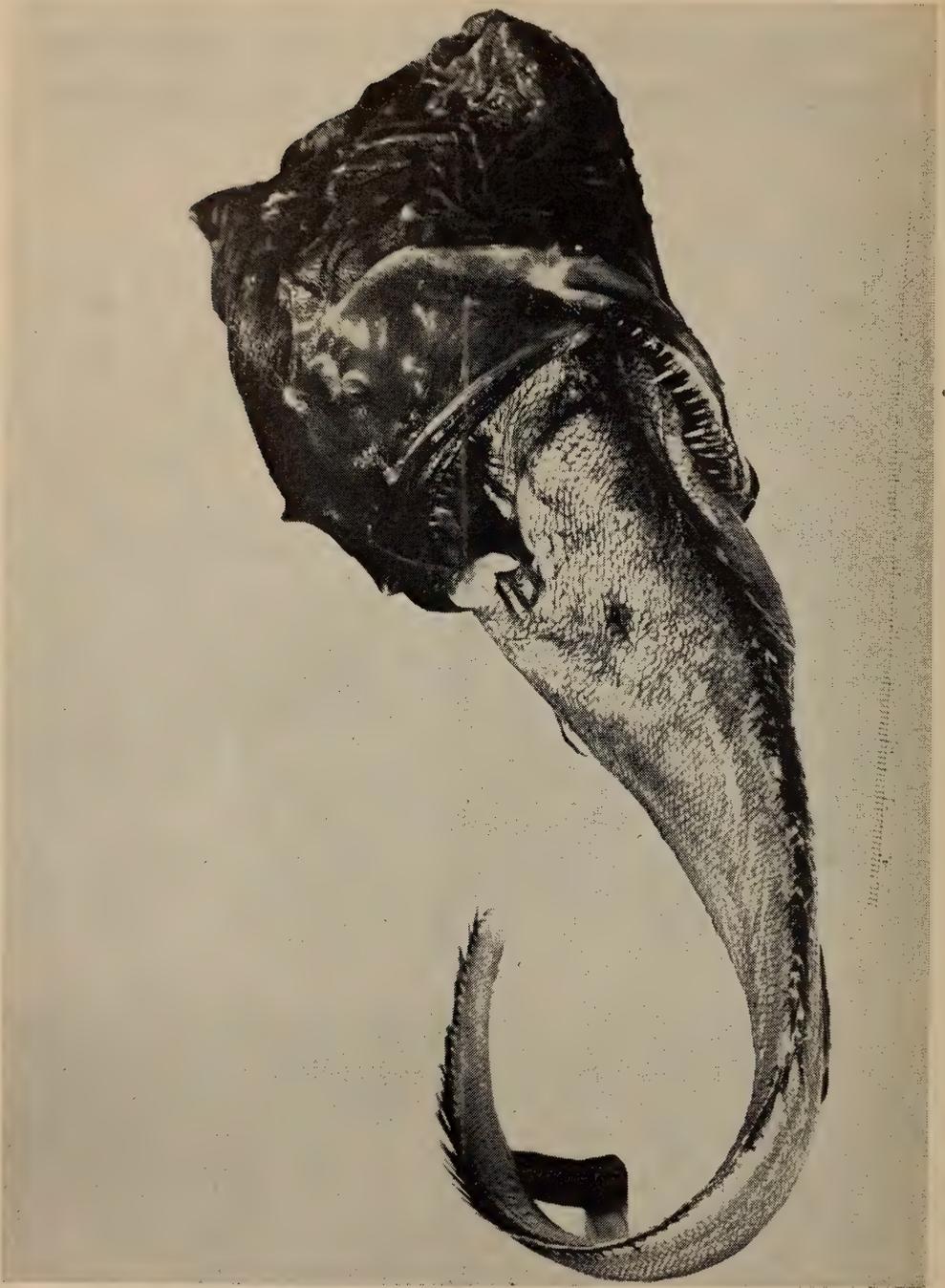


Fig. 1. *Diceratias bispinosus* with partially engulfed *Ventrifossa* sp.

FEEDING MORTALITY IN A DEEP SEA ANGLER FISH

The long, depressible teeth of the angler effectively prevented the macrourid from escaping; some dissection was necessary to remove the latter. With the exception of the area around the tooth marks on the body and in the midventral area between the anal and ventral fins, no visible digestion of the macrourid has occurred, as even the eyes are in good condition. One of us (R.J.L.) has previously noted that fishes from the stomach of gigantactid angler fishes had the greatest amount of digestion around the tooth marks. Although the cause could be the ease with which digestive enzymes of the stomach entered the wounds, possibly a digestive enzyme is associated with the teeth themselves. The presence of digested areas associated with the tooth wounds on our macrourid specimen supports this hypothesis for ceratioid angler fishes.

The difference in size between predator and prey is exaggerated when standard lengths are considered, due to the elongate and narrow tail of the macrourid. A more meaningful relationship for these two species is biomass; wet weight of the angler is 175 grams, that of the macrourid 258 grams.

The following list is a literature compilation of deep sea fishes found floating at the surface with a large food organism in the stomach and/or mouth; *Saccopharynx ampullaceus* body 215 mm long with 230 mm *Halargyreus johnsoni* in stomach (Günther, 1887: 256, Fig. 66); *S. ampullaceus* body 510 mm long with unidentified fish 180 mm in circumference presumably in mouth (Günther, 1887: 256); *S. flagellum* body 355 mm long with 255 mm unidentified fish in stomach (Günther, 1887: 256); 50 mm *Omosudis lowei* with *Argyropelecus* sp. 25 mm long and 25 mm high in stomach (Günther 1887: Fig. 52C'; Marshall, 1954: 142); 95 mm *Chiasmodon niger* with 145 mm *Gonostoma denudata* in stomach (Johnson, 1863: 410); 165 mm *C. niger* with 265 mm *Neoscopelus macrolepidotus?* in stomach (Carte, 1866: 35, Fig. 2); *C. niger* with unidentified fish in stomach (Goode and Bean, 1896: 292, Fig. 264); 49 mm *Linophryne*



Fig. 2. Esca of *Diceratias bispinosus*; scale equals 2 mm.

Lucifer with 70 mm scopeloid fish in stomach (Collett, 1886: 138, Fig. 15); 3 *Melanocetus johnsoni* 75 to 95 mm, each with a 180 to 205 mm *Lampanyctus crocodilus* in stomach (Günther, 1864: 301, Fig. 25; Regan, 1913: 1097).

A number of deep sea fishes taken in trawls have had extremely large prey organisms in the stomach (for example see Marshall, 1954: 142), yet presumably have not been adversely affected. The 12 known surface captures indicating feeding mortality give little information as to the relative frequency of the phenomenon. However, it is surprising that all of the previous reports were made prior to 1900, considering the larger number of oceanographic vessels at sea today. In the present case the macrourid is very close to the maximum circumference possible for the angler to ingest with extreme jaw expansion. Since the dental morphology of the angler does not allow a large food organism to be rejected once swallowed, the trial and error method of learning maximum food size must be severely limited.

The present angler (Austr. Mus. Sydney, I.15602-001) is the fourth recorded metamorphosed female of *Diceratius bispinosus*. Others have been taken from the Banda Sea (Günther, 1887), the Indian Ocean off Malabar (Alcock, 1899) and the western Atlantic off South America (Grey, 1959); all three were taken with bottom fishing gear (Grey, 1959). Most macrourids, including species of *Ventrifossa*, are benthic, and apparently *D. bispinosus*, while having no obvious morphologic adaptations for benthic life, lives and feeds close to the bottom. Bertelsen (1951) recorded two larval females from the upper waters of the Indian Ocean and Celebes Sea.

The present specimen agrees in almost all respects with that described by Grey (1959), although there are no illicial papillae on our specimen. The outer primary appendages of the esca (Fig. 2) are more highly developed than in the specimen figured by Regan and Trewavas (1932: Fig. 85A). A moderately large pore is on the right or dorsal side of the middle appendage of the esca. We cannot ascertain whether the esca is normally held in a lateral or dorsoventral position over the mouth, but the pore is definitely not on the left side, as in Günther's (1887) specimen. Grey (1959: 226) described a subcutaneous structure over the dentary which she considered a gland or possibly a tentacle. Pietsch (1972: 31) called the structure a labial cartilage. In the present specimen the structure is not cartilagenous, but filled with an opaque substance of jelly-like consistency after formalin preservation. The skin over the organ is thickened and darkly pigmented, somewhat as the 'cavernous luminous tissue' found in some whale fishes of the family Cetomimidae (Harry, 1952). However, the functional significance of the structure is unclear.

The specimen of *Ventrifossa* (AMS I.15602-002) does not match the description of any species described by Gilbert and Hubbs (1920) or Parr (1946). The fish is partially digested between the anal and ventral fins and the obscurity of the often diagnostic luminous organs and associated lenses and scaleless areas precludes formal naming and description.

FEEDING MORTALITY IN A DEEP SEA ANGLER FISH

We are indebted to the Papua New Guinea Department of Agriculture, Stock and Fisheries and particularly to W. A. Filewood of the Fisheries Research and Survey Station, Port Moresby, for making the specimens available. Father W. Hager of the Catholic Mission, Tonga collected the specimens, forwarded them to fisheries authorities, and made available additional collecting details. C. V. Turner took the photograph. B. B. Collette, T. W. Pietsch and F. H. Talbot kindly reviewed the manuscript. To all go our appreciation.

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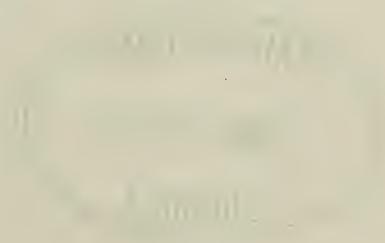
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Physiological Adaptations of Anuran Amphibians to Aridity: Australian Prospects

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ABSTRACT

We attempt to assess research on Australian anurans in the light of recent discoveries involving species outside Australia and consequently question the relevance of several studies of frogs in laboratory conditions.

Amphibians generally avoid water loss by burrowing or otherwise selecting favourable microclimates. Although it has been thought that the evaporative water loss from anurans is high and uncontrolled, several species from arid environments greatly reduce water loss under certain conditions. Some arboreal frogs apparently secrete a lipid-like substance onto the skin. Other fossorial species produce "cocoon" of dead epidermis.

Uricotelism, once thought excluded from the amphibia as a major form of nitrogen excretion, has been demonstrated in several arboreal species, one of which may excrete over 80% of the waste nitrogen as urates. Several Australian *Litoria* should be examined because they exploit niches similar to those of the uricotelic frogs from Argentina and Rhodesia.

Virtually nothing is known about the thermal relations or energy economy of Australian anurans. Desert species, studied elsewhere, feed intensely throughout a limited season of activity and show rapid gains in fat reserves correlated with a high calorogenic effect. Basking in some species may be significant in taking maximum advantage of a transient food supply typical of arid environments.

Long periods of dormancy characterized by temperature independent reduction of metabolic rate occur in some desert toads.

INTRODUCTION

Bentley (1966a), Mayhew (1968), Schmid (1969), and Shoemaker (1974) have thoroughly reviewed the physiology of desert amphibians, and Thorson (1955), Chew (1961), Heatwole *et al.* (1969), and Bentley (1971) have considered specific aspects of their water economy. The intent of this report is not to offer another review of the literature because that cannot be justified at this time. Our purpose is to assess research on Australian desert anurans in the light of a number of interesting discoveries, published primarily since 1969, which have not yet appeared in review. Most of this new information

comes from outside Australia but some of it may ultimately apply to Australian species. It is tempting to suggest Australian candidates which may be profitably examined. Our task has been eased by an excellent review of the ecology of Australian frogs by Main (1968). This report is restricted to the physiological adaptations of adult anurans. Very little has been added to our knowledge of the ecology and life histories of the larvae of desert anurans.

WATER ECONOMY

Evaporative Water Loss—Because amphibians generally show little physiological capacity to restrict evaporation from the skin and none is known to produce hypertonic urine, many investigators have been drawn to study amphibians in deserts where free water is seldom available and the potential evaporation is high. The results show that few species are physiologically adapted to arid conditions to the standards set by higher vertebrates. Most adaptations are behavioural.

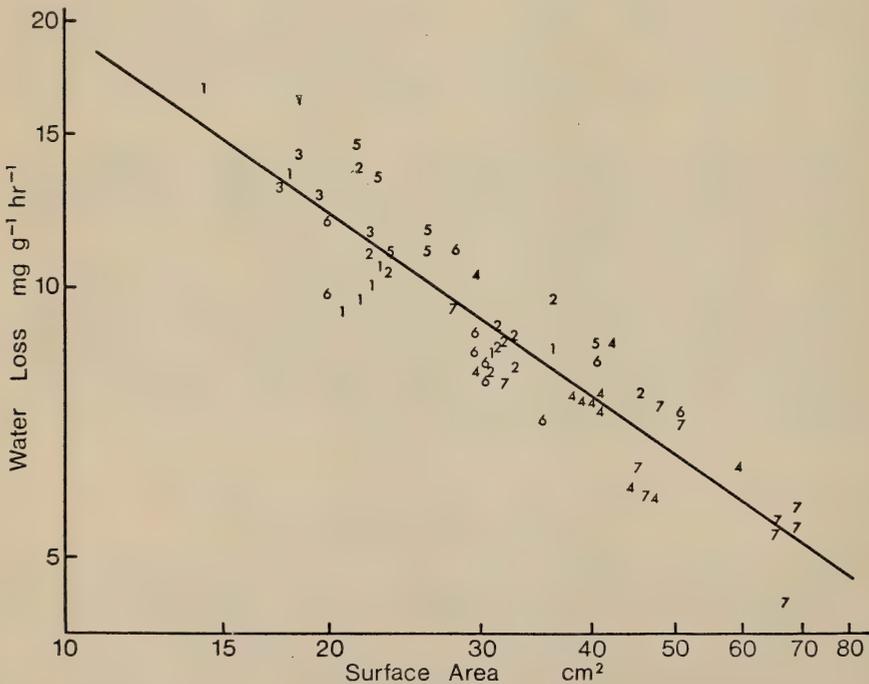


Fig. 1. Evaporative water loss from seven species of Australian frogs ranked according to decreasing aridity of habitat: *Cyclorana platycephalus* (1), *Cyclorana alboguttatus* (2), *Neobatrachus pictus* (3), *Litoria caerulea* (4), *Limnodynastes dumerili* (5), *Litoria aurea* (6), *Mixophyes fasciolatus* (7). Data from Clyne (1969).

PHYSIOLOGICAL ADAPTATIONS OF ANURANS

Among the majority of amphibians, there have been no large or consistent differences in evaporative water loss (EWL) between terrestrial species from mesic and xeric habitats (see Bentley, 1971) (Fig. 1). The lowest rate of EWL from a North American species is about 50 times the rate in lizards (Claussen, 1969). It is important to note that most measurements have been obtained by placing the animals in conditions favouring a rapid water loss (e.g. over drying agents, in streams of dry air, in wire cages indoors, etc.). As experiments designed to compare *maximal* rates of water loss, they have been successful, but there have been only a few studies which assess evaporation rates under natural conditions (Packer, 1963; Lee, 1968). If by behavioural means most frogs naturally avoid these extreme drying conditions, there should be little selective pressure for physiological mechanisms limiting water loss. On the other hand, there is apparently great selective advantage in maintaining the skin as an organ of gas exchange and water uptake. Both of these functions require a skin permeable to water.

The majority of desert species burrow into the soil where humidities are high and where water is available to be absorbed through the skin. Examples include the species of *Notaden*, *Cyclorana*, and *Neobatrachus* from Australian deserts. A few desert species remain close to permanent water such as *Litoria rubella* and *L. caerulea*, although *L. rubella* may exist away from permanent water and seek refuge in moist crevices.

Until recently it has been assumed amphibian skin had no influence on the rate of evaporation. However, various dormant anurans produce cocoons of shed skin which restrict water loss. The cocoons may be as many as 50 cell layers thick, as in the Argentinian toads, *Ceratophrys ornatus* and *Lepidobatrachus llanensis* (McClanahan *et al.*, 1974), or only one cell layer as in the Australian burrowing frogs, *Cyclorana platycephalus*, *C. alboguttatus* and possibly *Limnodynastes spenceri* (Lee and Mercer, 1967). The isolated cocoon of *Cyclorana alboguttatus* limits water transfer from a saturated atmosphere into a dry atmosphere to $0.65 \text{ mg H}_2\text{O cm}^{-2}\text{h}^{-1}$ at 25°C . The rate of water loss from the intact animal is some $7\frac{1}{2}$ times higher. Shoemaker, Ruibal, and McClanahan have observed cocoon formation in two species of burrowing ceratophrid frogs from Argentina. Cocoons form during exposure to room air and are also produced by buried frogs as the soil dries. The EWL from frogs with cocoons is about one-tenth of that from frogs without cocoons. *Lepidobatrachus llanensis* exhibits a progressive decrease in EWL when exposed to room air (Fig. 2). After 5 months underground, EWL in dry air was extremely low.

Most other measurements of EWL in burrowing frogs have been made on animals taken immediately from moist conditions and dehydrated at an extremely rapid rate. It is not surprising that the EWL was high and death occurred quickly even in frogs known to produce cocoons. However, under conditions of long-term, low-level dehydration, such as beneath gradually drying soil, amphibians may be given enough time to physiologically adjust the rate of

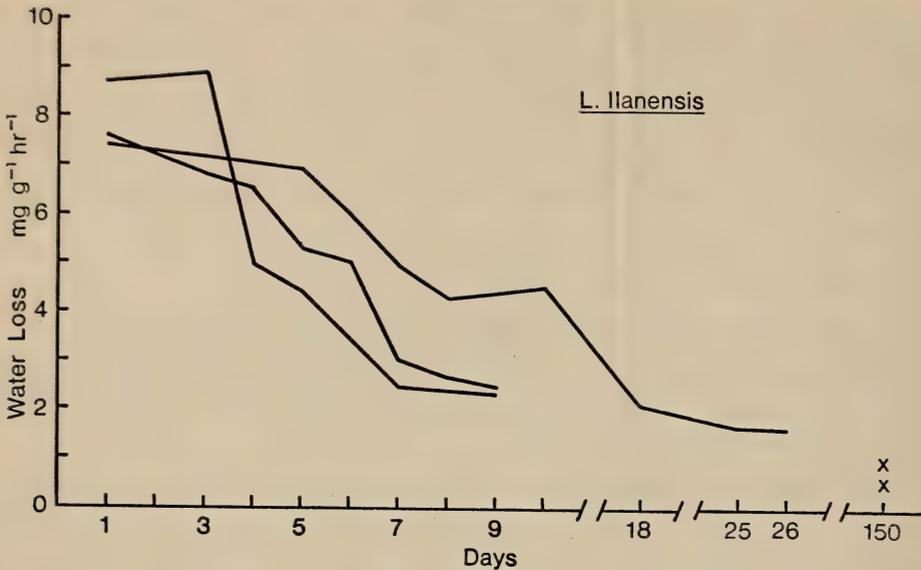


Fig. 2. Evaporative water loss of *Lepidobatrachus llanensis* related to number of days exposed to room air. Cocoons were visible after three days. X symbolize values from two frogs after about five months under dried soil. Data from McClanahan *et al.* (1974).

water loss by producing a cocoon. Short-term experiments by Warburg (1965, 1967) suggest that EWL decreases with time in *Neobatrachus pictus*, *N. centralis*, *Limnodynastes dumerili*, *L. ornatus* and *Cyclorana* spp. All of these frogs probably produce cocoons. However, Packer (1963), found no change in the rate of EWL from *Heleioporus eyrei* over a period of six days in dry sand. It is not known if *Heleioporus* spp. produce cocoons during dormancy. None of the experiments on EWL of Australian anurans was directed toward an assessment of the effect of changes in the skin so none is conclusive. We feel that more work is needed to determine the role of the cocoon on water loss as well as gas exchange and water uptake. The cocoons of the Australian frogs which have been examined are continuous over the eyes and the cloaca, but the nostrils remain open. Seymour (1973c) has shown that all gas exchange occurs cutaneously in dormant spadefoot toads (*Scaphiopus*) without cocoons, but it is possible that the buildup of shed skin limits respiratory gas exchange to a point necessitating pulmonary ventilation. The cocoons may also function to limit contact of the frogs with the soil thus reducing water exchange. In very moist soil, a cocoon could limit an influx of water which may be harmful to arid-land anurans (Schmid, 1965). On the other hand, if the soil dries sufficiently to pull moisture out of a frog by virtue of a high soil moisture tension, a cocoon may effectively break capillary contact between the soil and the frog's skin.

PHYSIOLOGICAL ADAPTATIONS OF ANURANS

Recently, some arboreal frogs from semi-arid habitats in Argentina (*Phyllomedusa* spp.) and Rhodesia (*Chiromantis xerampelina*) have attracted attention because their rates of EWL are characteristic of reptiles (Loveridge, 1970; Shoemaker *et al.*, 1972). These moderately sized tree frogs may spend many months in exposed situations which would quickly kill other anurans. The nature of the cutaneous barrier to water loss is currently being analyzed by V. H. Shoemaker, R. Ruibal, and L. McClanahan and their associates. They found that water beaded when placed on the skin of the Argentinian frog, *Phyllomedusa sauvagii*, and detergent washes destroyed the barrier. This implied that a lipid layer covers the skin, possibly spread by stereotyped wiping movements whereby each leg wipes the dorsal and ventral surfaces of the body after the frog emerges from water. Histological sections revealed that the skin contains glands which react intensely with lipid stains, and thin-layer chromatography of skin extract showed lipid constituents not present in a closely related frog having high rates of water loss.

It is even more surprising that both frogs (*Chiromantis xerampelina* from Rhodesia and *P. sauvagii* from Argentina) excrete primarily urates, the salts of uric acid. Urates were formerly thought to be excreted by amphibians only in trace amounts (Deyrup, 1964). However, in *P. sauvagii*, urates account for over 80% of the nitrogen excreted, even when free water is available (Shoemaker, pers. comm.). Under conditions of restricted water, urates are stored in the bladder, and are subsequently voided within a mucous envelope when water is available. Thus *P. sauvagii* maintains plasma electrolyte and urea concentrations at relatively low levels even when the only source of water is in insect food. Under the same conditions, *Hyla pulchella* shows a pronounced rise in plasma urea and electrolytes.

It is interesting to note that uricotelism and low evaporative water loss occur in a rhacophorid from Africa and in several phyllomedusids from South America. This may represent convergent evolution in an arboreal and semi-arid niche. Several Australian *Litoria* spp. occupy this niche, and should be examined for these adaptations. *L. rubella* may be found close to dry gilghis in the semi-arid areas of western New South Wales where they may spend months without free water. *L. peronii* commonly calls from trees some distance from free water, and *L. caerulea* resides in crevices though near to water.

Measurements of EWL have been made on some Australian *Litoria* spp. by Warburg (1972) and Clyne (1969). The values Warburg obtained for xeric anurans from Australia and Israel are extremely low and these frogs would seem superficially better adapted than frogs elsewhere. However, values obtained by Clyne on some of the same species under identical conditions are roughly 20 times higher and compare favourably with values from other literature. Clyne showed no consistent relationship between water loss and habitat (Fig. 1). Furthermore, EWL in *L. caerulea* was not significantly different (on a surface specific basis) than that in *L. aurea*, and the large rain forest frog, *Mixophyes*

fasciolatus had significantly the lowest surface specific EWL. There are, however, no careful measurements of EWL of Australian semi-arid and arid land frogs under conditions favouring gradual water loss for periods longer than six days.

Cutaneous Uptake of Free Water.—Many studies have attempted to define a correlation between the rate of cutaneous water uptake and independence of water in amphibians. (Thorson, 1955, McClanahan, 1967, Claussen, 1969, Fair, 1970). In general, no reasonably consistent relationship has appeared. Bentley *et al.* (1958) found a significant correlation in four species of *Neobatrachus*, but not in five species of *Heleioporus* from habitats of varying aridity. Warburg (1965, 1972) claimed to have demonstrated a relationship in several Australian anurans, but his results are equivocal, and the degree and rate of dehydration were not adequately controlled.

All of the published studies compare water uptake based on body weight or total skin area and thus ignore possible regional differences in skin permeability. McClanahan and Baldwin (1969) have shown that the water uptake through the ventral pelvic "seat patch" accounts for about 70% of the total uptake in dehydrated *Bufo punctatus*. This regional difference in skin permeability may not be universal in desert anurans, but it may be considered adaptive in allowing the animal to take advantage of transient wet surfaces resulting from dew or rain. *Bufo punctatus* cannot be distinguished from other North American anurans when the rate of water uptake is expressed in terms of total surface area (Claussen, 1969). However, with access to wet surfaces, this toad may rehydrate more rapidly than other species not possessing a "seat patch". Stille (1958) and Johnson (1969) have described various postural adjustments in dehydrated American and Australian frogs which appear to enhance contact between the frog and wet surfaces.

It has been generally assumed that a high rate of cutaneous water uptake, *per se*, has adaptive value for an anuran in arid conditions. Main (1968) summarized the rates in 19 species of Western Australian frogs and attributed the significant differences to selection favouring individuals which dehydrate quickly. Thus these frogs could begin calling immediately after rain following a severe drought. Bentley (1971, p. 172) rationalized the failure to find universally higher rates in desert species by suggesting that the differences between species "arose and persisted in response to ecological stresses on the Amphibia during their evolutionary history, even though they may not today be precisely related to the life of all contemporary species". For several reasons, these conclusions must be viewed with caution. First, experiments where frogs are immersed in water may not be relevant because rapid rates of dehydration in the laboratory and regional differences in water uptake may obscure the natural rate of uptake in the field. Second, if dehydration occurs gradually over a long period during dormancy as in American spadefoot toads (Shoemaker *et al.*, 1969), it seems energetically disadvantageous for frogs to produce short-lived neurohypophysial hormones continuously in preparation for rehydration. Moreover, the hormones could con-

ceivably enhance the rate of water loss from the frogs by increasing the permeability of the skin in the face of a drying soil. It may be significant in this connection that Jasinski and Gorbman (1967) found only minimal differences in stainable hypothalamic neurosecretion between hydrated and naturally dehydrated spadefoot toads in the field. It should be interesting to determine the titres of hormones and rates of water uptake in dehydrated frogs emerging in response to summer rain. Finally, the difference in average time for replacement of a 25% water deficit between the desert toad, *Neobatrachus wilsmorei*, and its most mesic relative, *Neobatrachus pelobatoides*, is only one hour (Bentley *et al.*, 1958). Even if complete hydration is a prerequisite to chorusing in these frogs, it seems unlikely that this small difference has much effect on the frogs' reproductive success.

Uptake of Water from Soil.—In even the driest deserts, moist soil may occur close to the surface. Amphibians may be the only tetrapods which can directly absorb moisture held by soil. The rate at which water moves between an amphibian and the soil depends basically on (1) the osmotic pressure of the animal's body fluids, (2) the permeability of the skin, (3) the osmotic pressure of the soil water and (4) the affinity of the soil particles for water (soil matric potential). The effect of the soil matric potential on the water economy of American spadefoots has been examined by Ruibal *et al.* (1969), Shoemaker *et al.* (1969) and McClanahan (1972). Soils of fine particle size have a higher affinity for water than do sandy soils with identical water content. Therefore it is more difficult for toads to obtain water from silty soil than sandy soil when the water content is low. When soil dries to a point where the soil matric potential is greater than the equivalent osmotic pressure of the body fluids, the frogs deaminate protein, producing urea which is retained along with electrolytes. The effect is to balance, to a certain extent, the soil matric potential with elevated total osmotic pressure. This response is similar to that observed in *Rana cancrivora* and *Bufo viridis* which swim in saline water (Gordon *et al.*, 1961; Gordon, 1962).

Aside from one experiment by Packer (1963), there have been no investigations of water uptake from soil in Australian species. It should be interesting to compare the responses of *Neobatrachus* spp. which burrow in silty soil with those *Heleioporus* spp. which prefer sand (Main, 1968).

Water Storage and Tolerance to Dehydration.—Amphibians generally have a greater tolerance to water loss than most vertebrates and a number of studies have shown still greater tolerance in desert species (Thorson and Svihla, 1943; Thorson, 1955; Main and Bentley, 1964; Schmid, 1965). Desert anurans also have large urinary bladders (Bentley, 1966b) which may serve to store water to replace evaporative losses (Ruibal, 1962; Shoemaker, 1964; Clyne, 1969). Thus the production of hyposmotic urine and the active transport of ions through the bladder wall result in a significant store of very dilute urine. Spencer (1896, p. 163-164) popularized *Cyclorana platycephalus* as the "water holding frog", familiar to early settlers (and the aborigines before them) along the Diamantina

River for their capacity to hold "a wine glass full of clear sweet water". This species together with *Notaden nicholsi* and *Neobatrachus wilsmorei* have capacities which approximate 50% of the rest of the body weight (Main and Bentley, 1964). However, Clyne (1969) obtained similar values for *Mixophyes fasciolatus*, a frog from wet sclerophyll and rain forest in eastern Australia. Thus large bladders are not always correlated with arid conditions, and their function in Na⁺ retention may complicate this relationship.

Because water losses are replaced by bladder reserves, we expect that large bladders should be favoured in arboreal frogs which bask away from water. However, not enough reliable data are available to judge this issue. *Litoria moorei* has a bladder capacity between 20 to 30% (Main and Bentley, 1964), or similar to North American desert toads (Ruibal, 1962; McClanahan, 1967), and this frog may bask like the related species, *L. aurea*.

The value of bladder water in an Australian frog under natural conditions has been demonstrated only once (Lee, 1968). *Heleioporus eyrei* may evaporate over 20% of the body weight during one night of foraging. If food is available, the water loss is regained to an extent by eating. However, it is assumed that losses from the body are also met by reabsorption from the bladder at night, and ultimately by reabsorption from the soil during the day.

The "water balance response" whereby dehydration stimulates release of neurohypophysial hormones, which, among other things, increase the rate of water uptake from the environment and from the bladder, has been well described elsewhere (see Bentley, 1971). We therefore wish only to point out a long overlooked feature of some amphibian kidneys which may be functionally related to reabsorption of bladder water. Many investigators during the 19th and early 20th centuries described the nephrostomes opening from the kidney into the coelomic cavity of adult anurans (see Smith, 1961). Sweet (1907) determined that they also open into the renal veins and associated blood vessels, since carmine injected into the body cavity appeared later in the peritubular blood sinuses, renal veins, and post cava, but not in the tubules. Sweet suggested that water reabsorbed from the bladder into the coelom entered the vascular system through the nephrostomes and was distributed from there to peripheral regions. There appears to be a correlation between the number of nephrostomes and arid habitats in Australian anurans (Table 1). Those species with large bladders have the largest number of nephrostomal openings, and among the *Litoria*, it may be significant that *L. aurea* basks whereas *L. lesueurii* apparently does not. We surmise that the rate of reabsorption of water from the bladder in a basking frog would be higher than in a non-basking frog under natural conditions but this remains to be demonstrated.

THERMAL RELATIONS

When amphibians seek shelter, they avoid not only drying conditions but also stressful temperatures. Accordingly, their absolute temperature tolerance is low

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TABLE 1
NUMBER OF NEPHROSTOMAL OPENINGS PER KIDNEY IN AUSTRALIAN ANURANS FROM VARIOUS HABITATS (SWEET, 1907).

Species	Number	Habitat
<i>Crinia signifera</i>	"small number"	Mesic—ponds and marshes
<i>Litoria lesuerii</i>	300	Mesic—rivers and streams
<i>Neobatrachus pictus</i>	105	Mesic, Xeric—ephemeral ponds
<i>Litoria aurea</i>	150-200	Mesic—ponds, billabongs, rivers (basks)
<i>Cyclorana alboguttatus</i>	210	Xeric—ephemeral ponds
<i>Notaden bennetti</i>	1067	Xeric—ephemeral ponds

compared to other vertebrates (see Bentley, 1966a; Brattstrom, 1970). Most differences in tolerance among anurans from different habitats can be ascribed to acclimation and acclimatization within a genetically fixed range (Brattstrom, 1970).

Body temperatures of desert anurans in the field are generally below 30°C (see Mayhew, 1968, for references), but a few species have higher temperatures. The highest body temperatures, 39.2°C, come from Australian *Cyclorana* spp. captured in shallow pools (Main, 1968); this temperature is close to maximum burrow temperatures experienced by spadefoot toads in North America (Ruibal *et al.*, 1969).

High body temperatures also occur in species which bask. Juvenile *Bufo californicus* and *Bufo debilis* are active diurnally and reach maximum temperatures of 37°C and 34°C respectively (Cunningham, 1962; Seymour, 1972). We have no field body temperatures of basking Australian frogs.

ENERGY METABOLISM

In addition to the problems of heat and water, deserts are characterized by an inconsistent, if not low, supply of food. Further, desert frogs feed only when surface conditions permit and consequently do not feed for most of the year. Hence desert frogs must build up substantial energy reserves within a relatively brief period to survive long periods of dormancy.

North American spadefoot toads (*Scaphiopus* spp.) show several behavioural and physiological adaptations which optimize the utilization of transient food sources during the summer rainy season. Like most anurans, they are opportunistic predators which accept a large range of prey size (R. S. Seymour, unpubl. data; see also Heatwole and Heatwole, 1968). They feed during the night, especially following rains which also promote the emergence of insects, and enter shallow burrows during the day where humidity and temperature are high (Ruibal *et al.*, 1969). The high burrow temperatures (27-39°C) doubtless facilitate digestion. A high calorogenic effect following feeding in *S. hammondi* suggests that proteins

are rapidly converted into non-protein products, probably chiefly fat (Seymour, 1973b). The rate of fat deposition appears to be higher in *S. couchii* and *S. hammondii* than in mesic anurans, and the relative weight of fat stored is higher (Seymour, 1973b). These differences are consonant with longer periods of dormancy at higher ambient temperatures in desert toads.

Rates of oxygen consumption and heart beat decrease during dormancy in spadefoot toads (Seymour, 1973b, c). Oxygen consumption during dormancy is about 20% of values from toads resting on the surface in the same season (Fig. 3). At this low metabolic rate, fat reserves are sufficient for the toads to remain in dormancy for at least 10 months. When additional resources of energy in body protein and eggs are considered, it is evident that some individuals in a population could survive for two or more years without feeding, even with an average body temperature of 15°C.

The aerobic metabolic scope for activity and the tolerance of exercise are high in *S. hammondii* and *Bufo cognatus* compared to *Rana pipiens* and *R. catesbeiana* (Seymour, 1973a). This may be related to the regular occurrence of

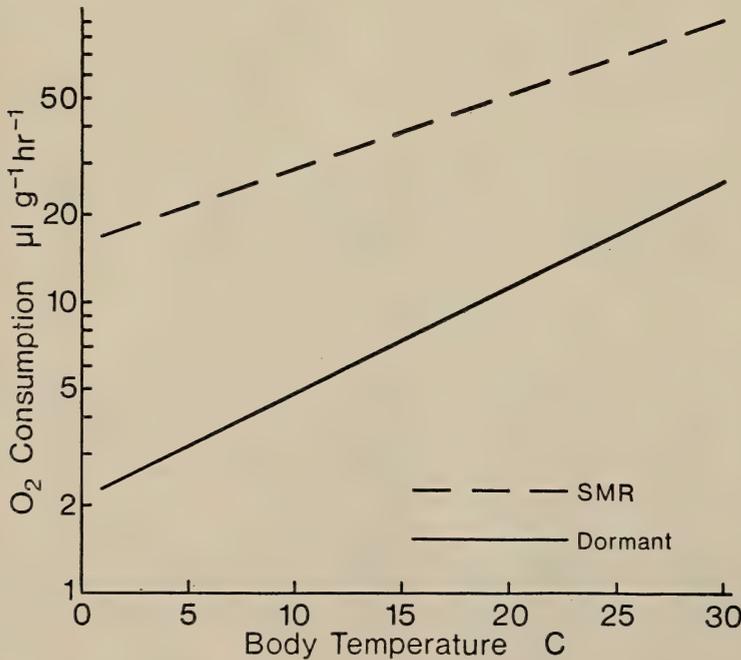


Fig. 3. Regression lines of oxygen consumption of *Scaphiopus couchii* during dormancy beneath soil and after arousal from dormancy during the same season. Measurements from aroused toads were taken under conditions required to produce the accepted concept of standard metabolic rate (SMR). Data from Seymour (1973b).

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burrowing in the two desert toads. Burrowing demands a sustained high rate of energy supply whereas the short bursts of activity exhibited by the two ranids may occur largely anaerobically. These observations have been confirmed in certain Australian frogs by D. Bromell (pers. comm.). The leptodactylids, *Limnodynastes dumerili* and *L. tasmaniensis*, have higher aerobic scopes than the hylids, *Litoria aurea* and *L. verreauxi*. Low aerobic scope appears to be complemented by high anaerobic scope in anurans (Bennett and Licht, 1973).

NEW DIRECTIONS

The mainstream of research into the adaptations of amphibians to arid conditions has been directed largely at aspects of water economy and particularly at assessment of tolerances and capacities under laboratory conditions. Recently emphasis has shifted to studies of water economy in natural environments, and to energetics. Several attributes new to our knowledge of amphibia have emerged—uricotelism, cocoons, lipid barriers to water loss, etc. This report suggests Australian species which may show adaptations similar to these. However, we feel that it would be most rewarding to search for new mechanisms which are not variations on a theme. It must be remembered that studies on the performance of desert amphibia in natural environments have been based largely upon species from North American deserts characterized by a relatively predictable climate. Therefore the prospect of discovering new strategies in Australia seems good since Australian deserts are characterized by frequent yet unpredictable drought.

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The Status of *Pseudomys novaehollandiae* (the New Holland Mouse)

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ABSTRACT

The New Holland Mouse, *Pseudomys novaehollandiae* (Waterhouse), has been found to have a wide if somewhat patchy distribution from the north coast of New South Wales to the Kangaroo Valley south of Sydney. It occurs again on the Mornington Peninsula in Victoria. In many of the places where it has been found, it is very abundant and can not be considered endangered. Rather, its ecology and habitat requirements are suggestive of an opportunistic species which flourishes during certain successional stages after fire.

INTRODUCTION

After a long period when it was considered that it might be extinct, *Pseudomys novaehollandiae* (the New Holland Mouse) was rediscovered in 1967. Reporting on the rediscovery, Mahoney and Marlow (1968) considered that the apparent rarity of *P. novaehollandiae* resulted from its being confused with the abundant and widespread introduced House Mouse (*Mus musculus*) and from the limited amount of trapping which has been done on the east coast of Australia in past years. However, the exact status of *P. novaehollandiae* has remained in doubt and both Calaby (1969) and Ride (1970) considered it an 'endangered species'. The animal is listed in the IUCN handbook on rare and endangered species as endangered.

In the course of studies on the small mammal fauna of coastal heaths in New South Wales, we trapped *P. novaehollandiae* at a number of places in northern New South Wales and found it to be abundant and widely distributed. Other workers have also taken *P. novaehollandiae* since 1967 and it seems appropriate at this time to review its status. Additionally though our work has been confined largely to heaths it provides information on the features of the habitat which influence the distribution and abundance of *P. novaehollandiae*. Detailed analyses of the relation between habitat and small mammals in coastal heaths will be presented elsewhere, but are discussed briefly in this paper with specific reference to the status of *P. novaehollandiae*.

DISTRIBUTION

Previous to 1967, *P. novaehollandiae* was known from only four specimens taken in northern New South Wales near Scone, upper Hunter River, and from

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the vicinity of the Richmond River. In 1967 a single specimen was collected in Ku-ring-gai Chase National Park near Sydney (Mahoney and Marlow, 1968) and in 1968 a number of specimens were taken from a locality near Port Stephens (Keith and Calaby, 1968). Subsequently, specimens have been collected at Smiths Lake near Forster (Batt *et al.*, 1972) and from south of Sydney in the Royal National Park (P. Foster, pers. comm.) and the Kangaroo Valley (Mahoney, pers. comm.). A second specimen was taken in Ku-ring-gai Chase in October 1973 from a place near the original record. We have collected it ourselves at a number of localities on the north coast of New South Wales from Port Stephens to the Richmond River (Evans Head).

Though *P. novaehollandiae* is likely to occur on the south coast of New South Wales, the specimen from the Kangaroo Valley is the only record from that part of the state. We have not trapped it in an extensive trapping programme in the Nadgee Nature Reserve south of Eden nor has it been taken at Jervis Bay despite intensive trapping by Douglas (pers. comm). However, in an interesting extension of its known modern range, Seebeck and Beste (1970) have taken *P. novaehollandiae* on the Mornington Peninsula in south-eastern Victoria and further trapping could well extend the animal's known range. Mahoney and

TABLE 1
NUMBERS OF SMALL MAMMAL SPECIES

Locality	Trapnights	No. of individuals										
		<i>Rattus lutreolus</i>	<i>R. fuscipes</i>	<i>R. rattus</i>	<i>Melomys</i> sp.	<i>Pseudomys gracilicaudatus</i>	<i>P. novaehollandiae</i>	<i>Mus musculus</i>	<i>Antechinus stuartii</i>	<i>A. swainsonii</i>	<i>Sminthopsis murina</i>	<i>Cercartetus nanus</i>
Kingscliff	988	—	—	3	—	—	—	9	—	—	—	—
Evans Head	3648	25	—	—	4	—	18	16	1	—	—	—
Yamba	252	—	—	8	—	—	—	5	—	—	—	—
Diggers Camp	3648	—	7	—	—	—	8	22	—	—	—	—
Bonny Hills	524	49	2	2	—	3	—	94	1	—	1	—
Port Stephens	5472	1	1	2	—	—	31	14	—	—	5	—
Pearl Beach	1920	5	9	1	—	—	—	2	4	—	—	—
Nadgee Nature Reserve	15240	94	21	—	—	—	—	—	1	9	—	2
Total	35692	174	40	16	4	3	57	162	7	9	6	2

Marlow (1968) point out that there are subfossil bone deposits from caves in Tasmania and western Victoria which are remains of *P. novaehollandiae*.

HABITAT REQUIREMENTS

Previous to our studies, *P. novaehollandiae* was reported mainly from dry sclerophyll forest with a sclerophyllic understorey (Keith and Calaby, 1968; Seebeck and Beste, 1970; Batt et. al., 1972). Keith and Calaby (1968) also found it between dunes at swamp edges and we have trapped it extensively in coastal heaths. In these places, *P. novaehollandiae* is as abundant as other native and introduced small mammals (Table 1). However, on the north coast of New South Wales, the distribution of *P. novaehollandiae* is not uniform and there appears to be extensive areas where it is absent or rare. The reason for this patchy distribution is not clear, but is probably in part historical and in the part the animal's response to differences between and within habitats.

In our studies of small mammal communities, we attempt to relate the presence or absence of a species to the structure of the habitat. Plant species composition, soil firmness, total vegetation density, foliage height density, extent of bare ground, number of plant species and amount of leaf litter are measured and the presence or absence of small mammals is determined by trapping. A brief analysis of the major habitat requirements of *P. novaehollandiae* is essential to an understanding of its distribution and abundance.

TABLE 2
OCCURRENCE OF *P. NOVAEHOLLANDIAE* AND *M. MUSCULUS* IN DIFFERENT HEATHS

Substrate	Heath Type	No. of Plots	<i>P. novaehollandiae</i>		<i>M. musculus</i>		
			A	B	A	B	C
Rock	headland—dry	26	0	0.0	0	0.0	0
	headland—moist	9	0	0.0	1	0.1	0
Sand	foredune	5	0	0.0	3	1.6	0
	moist	22	6	0.5	11	3.1	2
	dry	18	13	1.6	10	1.6	8
	heavily disturbed	8	2	0.6	4	0.9	1
	Total	88	21		29		11

A—Number of plots with animals

B—Average number of animals per plot

C—Number of plots with both species

Various workers have commented on the possible importance of the seeds of legumes (e.g. *Acacia*, *Dillwynia*) as food of *P. novaehollandiae* in forest habitats (e.g. Keith and Calaby, 1968). Our observations support this suggestion: the forest habitats in which we have taken this mouse comprise a dense sclerophyllic understorey with a high proportion of legumes. However, in coastal heaths,

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the presence of *P. novaehollandiae* is associated with a small number of habitat variables, but not obviously with the proportion of legumes.

The heaths sampled in this study have been grouped according to substrate, substrate moisture and degree of disturbance (Table 2). Moisture relations and the level of disturbance were ranked and each plot placed in the appropriate class. All of the heaths sampled have a modern history of fire and grazing. The heaths at Nadgee on the south coast of New South Wales differ from those on the north coast in having been protected from fire and grazing for the last 20 years. The north coast heaths showed the effects of more recent disturbances. *P. novaehollandiae* was not found on any of the plots at Nadgee and on the north coast it was most abundant in dry and only moderately disturbed heaths (Table 2). Numbers were lower in recently and heavily disturbed heaths and where *P. novaehollandiae* occurred in wet heaths, it was where such heaths were associated with and surrounded by dry heaths. The wet heaths sampled have probably been less affected by fire and grazing than the dry heaths.

The grouping of heaths into rather broad habitat types does not tell us why *P. novaehollandiae* occurs in one place and not another. To answer this question we need to know the features of the habitat which are important to the animal and how these features differ between plots where the animal is present and where it is absent. One method of analysis is to use 'stepwise discriminant analysis' (Sokal and Rohlf, 1969) to obtain a measure of how well the respective environmental parameters which we measured separate the plots in which the mouse is present from those in which it is absent. The results of this analysis are summarized in Table 3. Only the foliage density at the 20 cm height level was used as this variable was highly correlated with foliage densities at other heights (i.e. 10, 50, 100 and 150 cm) and of all the foliage densities measured it gave the best association with the presence of *P. novaehollandiae*.

The analysis presented in Table 2 is based on fifty plots which were sampled twice in different years. We found that there was no association with the number of plant species, with soil firmness or with the composition of the plant community. There was a positive but insignificant association with the

TABLE 3

ASSOCIATION BETWEEN *P. NOVAEHOLLANDIAE* AND HABITAT VARIABLES

Variable	Association	F-value	d.f.	p
Vegetation density at 20 cm	positive	3.25	1.48	0.1
Bare ground	positive	16.25	1.48	0.001
Total vegetation	negative	4.62	1.48	0.05
Bare ground and vegetation at 20 cm	positive	15.15	2.47	0.001

The results have been derived from 50 plots trapped twice.

amount of leaf litter. It is interesting that while there was a positive association with vegetation density at 20 cm, there was a negative association with total vegetation. The most important single variable was the amount of bare ground. Using two variables, the amount of bare ground and vegetation density at 20 cm increases the separation between plots with and without *P. novaehollandiae*. Studies now in progress suggest that these features are characteristic of heaths regenerating after fire.

DISCUSSION

Our observations suggest that an optimum habitat for *P. novaehollandiae* is a dry heath which has been disturbed by fire and is actively regenerating. The positive association with bare ground, foliage density at 20 cm and leaf litter and the negative association with total vegetation support this conclusion. Similarly its abundance in sclerophyll forests with a well developed sclerophyllic understory and a high proportion of legumes suggest an animal which does well in the early and middle successional stages following fire.

Habitats protected from fire are as unsuited for *P. novaehollandiae* as are the first stages of succession after fire or habitats in which succession is disrupted by too frequent burning, heavy grazing or mining. A similar set of habitat requirements has been reported by Ahlgren (1966) for granivorous rodents in North America. Baker (1971) also noted that granivores invaded disturbed areas because seeds and insects became more abundant and readily available during the early stages of succession. It is particularly interesting that Christensen (pers. comm.) working in Western Australia, Leonard (1973) in Victoria and Recher in southeastern New South Wales (unpub. data) have found that *Mus musculus* invades recently burned forests and heaths, increases rapidly in abundance and then becomes rare as succession proceeds and food presumably becomes less abundant. Based on the evidence available, it is not unreasonable to assume that *P. novaehollandiae* has a similar ecology.

One other variable merits discussion. The introduced *M. musculus* is widely distributed on the coast of New South Wales and occurs abundantly in habitats used by *P. novaehollandiae* (Table 2). As these rodents are very similar in size, appearance and probably in feeding habits, it is possible that they use similar resources. If so, the distribution and abundance of the native mouse might be affected by the presence of the introduced animal. Of the 88 plots sampled one or more times in this survey, *P. novaehollandiae* occurred on 21 and *M. musculus* on 29 (Table 2). They occurred together on 11 of the plots, but there is no indication that the abundance or distribution of *P. novaehollandiae* has been affected by the introduced *M. musculus*. Of the 18 plots on which *M. musculus* was present without *P. novaehollandiae*, only two had habitat characteristics (i.e. extent of bare ground and foliage density at 20 cm) suitable for *P. novaehollandiae*. There is a negative association between *M. musculus* and *P. novaehollandiae* which is almost significant (0.1 p 0.5). It is possible,

STATUS OF *PSEUDOMYS NOVAEHOLLANDIAE*

therefore, that the two species have apportioned the available range of heath habitats among themselves and that the modern habitat range of *P. novaehollandiae* is less than that used prior to the advent of *M. musculus*. Historically, *M. musculus* has been present in Australia since the later part of the 18th century and there has been adequate time for any competitive interactions between *P. novaehollandiae* and *M. musculus* to have come to an equilibrium with a separation by habitat.

Regardless of any past interactions that may have occurred between *M. musculus* and *P. novaehollandiae*, the latter has a wide range from northern New South Wales to southern Victoria and occurs in forest as well as heath habitats. Though its distribution within this range is patchy, it can not be considered an endangered species. We prefer to consider this mouse an opportunistic or fugitive species; one which responds quickly to favourable conditions with a great increase in numbers and then becomes uncommon or rare as the habitat changes or as other species of small mammals colonize the area.

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Occurrence and Field Recognition of *Macropus parma*

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ABSTRACT

The parma wallaby, *Macropus parma*, is recorded from the Dorrigo Plateau for the first time in 40 years. The parmas were found feeding in areas of disturbed wet sclerophyll forest and appeared to be coming from areas of rainforest and wet sclerophyll forest with a rainforest understorey. Characteristics of the species which will aid in field recognition are detailed.

INTRODUCTION

The parma wallaby, *Macropus parma*, was originally discovered in the Illawarra district of New South Wales by John Gould who listed the name *Halmaturus parma* for the species (Gray, 1843). Gould, however, failed to describe the species and this was done by Waterhouse in 1846.

In the early 1840's, Gould wrote to John Gilbert, "Three kinds of wallaby run in the brushes of Illawarra, viz. *Halmaturus ualabatus* [= *Wallabia bicolor*], *H. tithys* (the common pademellan, a red-necked kind [= *Thylogale thetis*]) and a nearby allied species called 'Pama' by the natives. Of this latter which is very like *Derbyanus*, [= *Macropus eugenii*], I wish as many specimens and crania as convenient" (Longman, 1922). Unfortunately, Gilbert was speared to death by aborigines during the ill-fated Leichhardt expedition to Port Essington in 1845 before he could collect further specimens for Gould.

Twenty years later, Gould wrote, "In these brushes, it doubtless still exists, as since my return, other specimens have been sent to me by the late Mr. Strange. How far its range may extend westwardly [south] to Port Phillip or eastwardly [north] in the direction of Moreton Bay, I am unable to state" (Gould, 1863).

Ride, in 1957, could find only 12 specimens in the world museums and records of 4 others which could no longer be located. He reported the species as apparently extinct (Ride, 1957).

Prior to the turn of the century, all specimens came from the south coast region of New South Wales. The last specimen recorded south of Sydney was taken at Mawarra, Sassafras (approx. 35° 05' S, 150° 15' E) in 1889.

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In 1921, a single specimen was taken at Point Lookout Gorge ($30^{\circ} 30' S$, $152^{\circ} 24' E$) near Ebor by H. Raven who was collecting for the American Museum of Natural History. This locality may now lie inside the boundary of the New England National Park.

Two other specimens were taken by P. J. Darlington at Cascade ($30^{\circ} 16' S$, $152^{\circ} 47' 18'' E$) 22 km. north of Dorrigo in February, 1932. Darlington recorded taking the male in a pen gum forest (sic) on a ridge and the female in an open space in a pen gum forest (sic) on the side of a ridge (Darlington, field notes).

Johnson and Mawson (1939, 1940) described several parasites from the parma wallaby using material collected by Luke Gallard in the Ourimbah region ($33^{\circ} 03' S$, $151^{\circ} 21' E$) in 1909-11. The Gallard collection is of parasites only and no voucher specimens were entered with the collection. However, in 1965, Mr. E. Worrell of the Australian Reptile Park at Gosford received a female *M. parma* with a male pouch young, reportedly from the same general district. The skin and skull of the female are now lodged in the National Museum of Victoria register number C 10725. The exact locality of the population from which this animal came is yet to be determined.

In 1967, a population of the parma wallaby was reported on Kawau Island, New Zealand ($36^{\circ} 25' S$, $174^{\circ} 51' E$) where they had been taken about 1870 by Sir George Grey (Wodzicki and Flux, 1967).

A field survey to determine the current distribution and status of the parma wallaby in New South Waes was commenced in 1972. This paper reports the discovery of a population of *M. parma* in Moonpar State Forest ($30^{\circ} 12' S$, $152^{\circ} 41' 25'' E$) on the Dorrigo Plateau and details field recognition characters for this species.

METHODS

A single specimen of *M. parma* was collected in Moonpar S.F. on the last night of a nine day field trip to Cascade in March, 1972. A further four weeks was spent in Moonpar S.F. between June 26 and July 21, 1972 during which time I attempted to determine recognition characters for separating *M. parma* from the two pademelons *Thylogale thetis* and *Thylogale stigmatica*.

The survey was conducted from a Land-Rover as outlined by Calaby (1966). During the day much of the area was inspected on foot.

Ages were estimated using data in Maynes (1972).

RESULTS

(a) *Habitat*

(i) *Topography and Soil*

Moonpar State Forest ($30^{\circ} 12' S$, $152^{\circ} 41' 25'' E$) lies on the northern edge of the Dorrigo Plateau at the junction of the Blicks and Nymboida Rivers and

TABLE 1
 MEAN MONTHLY RAINFALL AT THREE STATIONS
Mean Rainfall in m.m.

Station	Yrs.	Altitude	Location	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
DORRIGO	59	730 m	30° 21' S 152° 43' E	255	280	293	194	138	163	118	89	81	107	123	186	2027
BOBO	20	570 m	30° 15' S 152° 51' E	197	235	279	109	86	153	88	91	60	105	125	155	1683
CLOUD'S CREEK	25	610 m	30° 04'18" S 152° 37'30" E	207	198	180	91	66	87	67	62	54	95	119	152	1378

TABLE 2
 MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURES (°C)

Station	Yrs.	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
BOBO	16	25.8 15.4	25.3 16.4	24.1 14.9	21.6 10.4	19.1 5.8	16.8 3.3	16.3 1.8	18.1 3.6	20.3 6.4	23.3 7.1	25.2 12.2	26.4 14.6
CLOUD'S CREEK	16	25.6 13.9	25.0 13.9	23.3 11.7	21.1 7.2	18.9 3.3	16.1 1.7	15.6 0.5	17.2 0.5	19.4 2.7	22.2 6.7	24.4 9.4	26.1 12.2

covers approximately 3 360 ha. It is an area of undulating hills ranging from 425 m, in the river valleys to a maximum height of 855 m, with the majority of the forest between 550 m, and 730 m. (Forestry Commission N.S.W. Map. Misc. F 842).

McArthur (1964) has surveyed the soils of the Dorrigo Plateau and described a Moonpar Association comprised of red podzolic soils on granite. The surface layer of soil is a dark brown gritty loam below which is a red gritty clay at about 0.5 m. (McArthur, 1964). Although McArthur did not survey Moonpar S.F. itself, one of his sample profiles was 400 m. from the southern entrance to the forest. It would appear that this association applies throughout most of the State Forest.

(ii) *Climate*

The area has a high annual rainfall with the period December-March being the most reliable. Table 1 gives the mean annual rainfall for the three nearest stations to Moonpar S.F. These are Bobo (13 km. east), Cloud's Creek (13 km. north north west) and Dorrigo (13 km. south west).

Table 2 records the mean temperature data for Bobo and Cloud's Creek stations. The average frost-free period at these stations is 241 days and 200 days respectively. The winters are mild with heavy frosts at times, especially within small openings in the forest.

(iii) *Vegetation*

The dominant forest types have been mapped by the Forestry Commission of New South Wales. Moonpar S.F. consists mainly of rainforest and wet sclerophyll forest with some scattered areas of dry sclerophyll forest (Forestry Commission Map Misc. F 842). The rainforest generally occupies the gullies while the eucalypt forest is usually on the ridges.

The rainforest is a coachwood (*Ceratopetalum apetalum*)—Crabapple (*Schizomeria ovata*) type in which coachwood is clearly dominant. Associated species include Hoop Pine (*Araucaria cunninghamii*), Red Carabeen (*Geissois benthamii*), Silver Sycamore (*Cryptocarya glaucescens*), Sassafras (*Doryphora sassafras*), Corkwood (*Endiandra sieberi*), Lilly Pilly (*Acmena smithii*) and Black Myrtle (*Backhousia myrtifolia*).

The areas of wet sclerophyll forest are dominated by Sydney Blue Gum (*Eucalyptus saligna*), Tallowwood (*E. microcorys*) and Blackbutt (*E. pilularis*). There is generally a dense mesophyllic shrub layer of rainforest species.

In the northern section of the forest, control burning and grazing is maintaining an open woodland habitat dominated by Sydney Blue Gum, Blackbutt, Tallowwood and New England Blackbutt (*E. campanulata*) (G. Grey, pers. comm.). The forest oak (*Casuarina torolosa*), black she-oak (*Casuarina littoralis*),

TABLE 3
FLESH MEASUREMENTS OF PARMA WALLABIES FROM MOONPAR S.F.

Field No.	Sex	M.I.	M.E.S.	Age	Head	Ear	Arm	Leg	Foot	H & B	Tail	Scrotum		Wt.
												Pouch		
72/1P	♀	—	I.2(.3)	54 wks	—	66.3	71.3	167	125	386	395	39.2	—	2.4
72/2P	♀	1.35	I.4	74 wks	93.3	62.8	71.7	175	122	404	390	41.0	—	2.5
72/3P	♀	2.70	III.3	245 wks	110.0	72.0	93.2	206	136	483	479	103	—	4.4
72/4P	♂	—	—	145 d	56.7	31.0	37.3	80.3	68.0	180	136	7.3	—	0.4
72/5P	♀	1.35	I.4	76 wks	97.0	67.3	75.2	172	128	424	406	87	—	2.8
72/6P	♀	—	—	37 d	21.5	6.7	11.0	17.5	12.5	64.6	26.1	—	—	—
72/7P	♀	0.60	I.0	38 wks	83.0	55.5	61.8	149	116	349	318	—	—	1.6

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black wattle (*Acacia irrorata*), Sally wattle (*Acacia floribunda*), bracken fern (*Pteridium* sp.), blady grass (*Imperata* sp.), kangaroo grass (*Themeda australis*), Poa (*Poa caespitosa*), Dogwood (*Jacksonia coperia*) and other species were observed in this area.

(b) Field recognition of *M. parma*

(i) *Flesh measurements*

Body measurements of the parma wallabies collected in Moonpar S.F. are given in Table 3.

There is considerable overlap in the size of the hind foot between *M. parma* (103-147 mm), the red-necked pademelon (*Thylogale thetis*) (102-151 mm) and the red-legged pademelon (*Thylogale stigmatica*) (122-134 mm, adults only). Consequently, attempts to determine specific differences between the foot prints were abandoned.

TABLE 4
TAIL LENGTH AS A PERCENTAGE OF BODY LENGTH

Species	n	$\bar{x} \pm \text{S.E. } \%$	Range %
<i>M. parma</i>	28	99.91 \pm .65%	106.2-94.0
<i>T. thetis</i>	23	88.05 \pm .81%	95.4-81.1
<i>T. stigmatica</i>	6	78.52 \pm 1.72%	85.6-73.8

Table 4 gives the value of the tail length expressed as a percentage of the body length for *M. parma* and both *T. thetis* and *T. stigmatica*. The parma value is based on animals from Kawau Island, New Zealand, while the pademelon values are from animals collected in northern New South Wales. (All measurements were taken by the author). Values for the five parmas taken in Moonpar S.F. were 91.1, 95.8, 96.5, 99.2 and 102.3%.

As can be seen from Table 4, parmas have the longest tail relative to the body size of all three species. This can be observed, under suitable conditions, in the live animal at some distance.

(ii) *Gait*

The appearance of *M. parma* and *T. thetis* in profile are shown in Figs 1 and 2. When hopping at medium pace, parmas carry their tail curved upwards in a shallow U-shape. Pademelons in contrast tend to carry the tail either straight out behind them or only slightly curved. Pademelons' tails appear to bob up and down more obviously and vigorously than do parmas. When travelling at



Fig. 1. Profiles of parma wallabies.



Fig. 2. Profiles of red-necked pademelons.

speed, the tail is held straight out behind in all species. Parmas appear to remain close to the ground when hopping and maintain an almost horizontal position. Pademelons seem to "bounce" more when hopping.

Pademelons generally appear to be somewhat stockier than parmas and tend to be heavier in the lower abdominal and pelvic regions. From rear view, parmas generally appear thinner in the hips than pademelons which are more circular in outline.

(iii) *Pelage*

In the hand, *T. thetis* is readily recognized by its prominent rufous-brown shoulders and the lack of any cheek stripe or nuchal stripe. *T. stigmatica* has the back and shoulders a uniform dark grey. The cheeks, a patch above the eyes and the base of the ears are reddish-brown. There is an indistinct white cheek-stripe and an indistinct dark nuchal stripe.

M. parma has a uniform brownish grey back with a black stripe down the spine that ends in the mid-back. There is a well developed white cheek stripe along the upper lip and the rest of the head is a grizzled grey. The shoulders appear only slightly lighter than the rest of the back.

In some *M. parma*, there is a white tip to the tail which is usually 20-40 mm long when present. White tail tips have also been observed in some *T. stigmatica* but never in *T. thetis*.

Although parmas invariably have a white chest and throat, some specimens of both species of pademelon have been observed with this same condition. The presence of reddish-brown heels cannot be considered alone as a sufficiently good character for identifying *T. stigmatica* in the field. Some *T. thetis* have heels almost as red as those observed in *T. stigmatica* while the *M. parma* collected in Moonpar also had very red-brown heels. Faint hip stripes have been observed in all three species.

(iv) *Skull characteristics*

M. parma can be readily separated from the two species of pademelons by the position of the groove on the labial surface of i^3 . The outer lamina is about 60% of the length of the whole tooth in *M. parma*, about 80% in *T. stigmatica* and about 95% in *T. thetis* (Fig. 3). The permanent premolar is about equal in length to m^1 in *M. parma* while it is 20% and 70% larger than m^1 in *T. thetis* and *T. stigmatica* respectively (Fig. 3).

The differences in the shape of the nasal bones between the three species is shown in Fig. 3.

In *M. parma* the suture between the maxilla and palatal bones on the bridge between the palatal foramina lies about a third from the front. This suture is in the middle of the bridge in both species of pademelon (Fig. 3).

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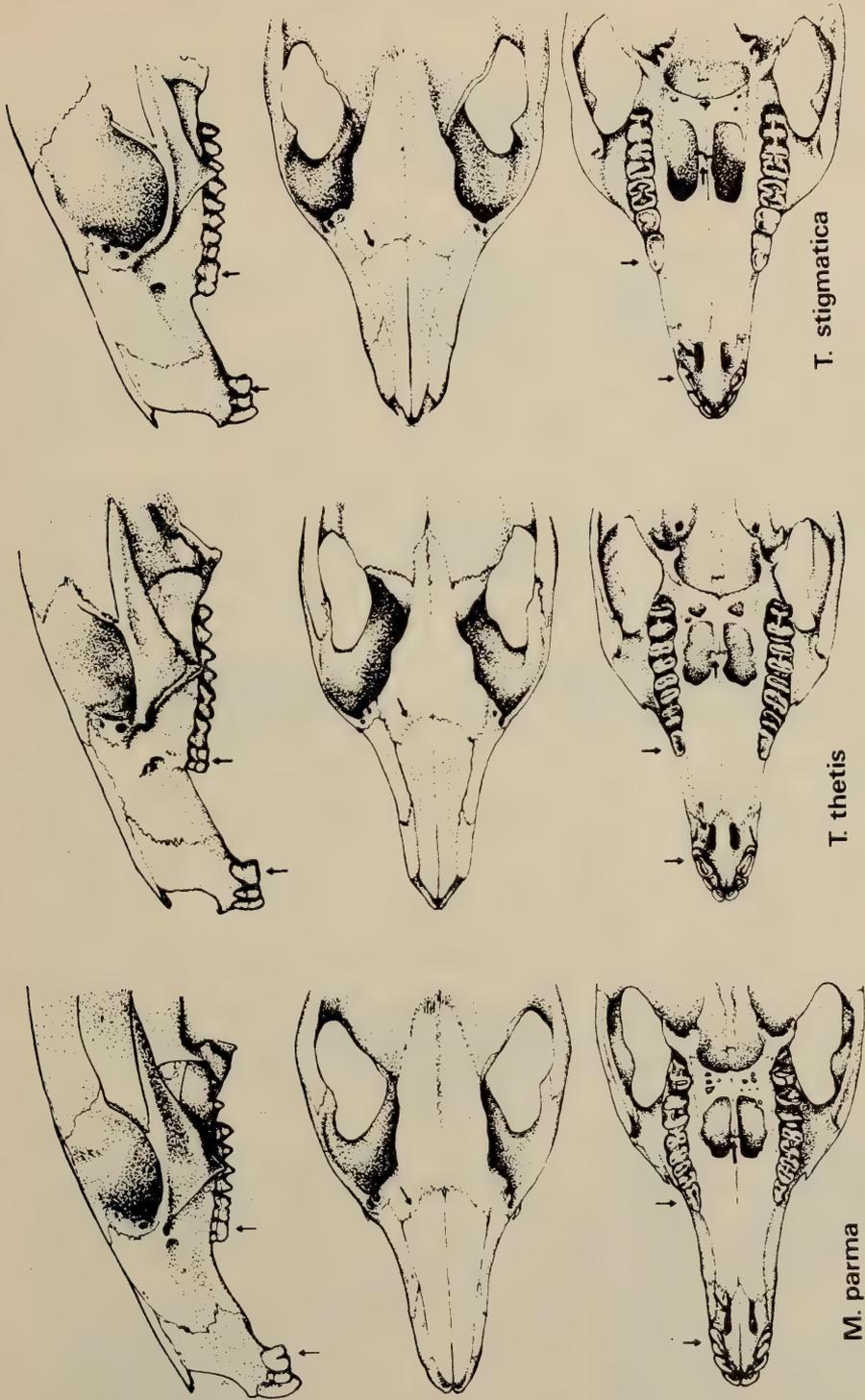


Fig. 3. Skull characteristics for separating parma wallabies from red-necked and red-legged pademelons.

The incisive foramina (Fig. 3) are long and thin in *M. parma* (about 6.5 mm long) whereas they are more uniform in outline and smaller in the pademelons. They are about 4.5 mm long in *T. thetis* and about 5.4 mm in *T. stigmatica*.

(v) *Faecal Pellets*

Two distinctive types of small macropodid droppings were found in the study area. Identification of the species producing the droppings was done by examining the rectal contents of shot animals.

Parma droppings are flattened, square to slightly rectangular pellets (Figs. 4, 5). Faecal pellets produced by the red-necked pademelon are elongate cylinders and tend to be less regular in outline (Figs. 5, 6). The few droppings collected from *T. stigmatica* resembled those from *T. thetis* rather than *M. parma*.

A collection of faecal pellet groups from four separate sites was taken on the last day of the July field-trip to assess whether the pellet-group count technique could be applied to a study of the biology of *M. parma*. No *T. stigmatica* were seen or collected at any of these sites during the entire period spent in Moonpar S.F. so all pademelon droppings were attributed to *T. thetis*.

TABLE 5

SPECIES COMPOSITION OF FAECAL PELLET GROUPS AT FOUR SITES IN MOONPAR STATE FOREST

Site	n	<i>M. parma</i>	<i>T. thetis</i>	Uncertain	Other Species
1	293	50%	32.7%	9.2%	8.1%
2	260	3.5%	86.1%	4.6%	5.8%
3	112	24.1%	33.0%	10.7%	32.2%
4	91	23.0%	32.0%	3.3%	41.7%

Table 5 gives the percentage species composition of the pellet groups at the four sites. Specimens of *M. parma* were collected at all sites except site 2 where a single parma was observed but not collected. Not all pellet groups could be

CAPTIONS FOR PLATE OPPOSITE

Fig. 4. Upper surface view of two parma wallaby faecal pellet groups. Juvenile on left, adult on right.

Fig. 5. Lateral view of parma wallaby pellet (upper) and pademelon pellets (lower). Note the much greater flattening of the parma pellet.

Fig. 6. Upper surface view of three faecal pellet groups from red-necked pademelons. All figures natural size.



Fig. 4

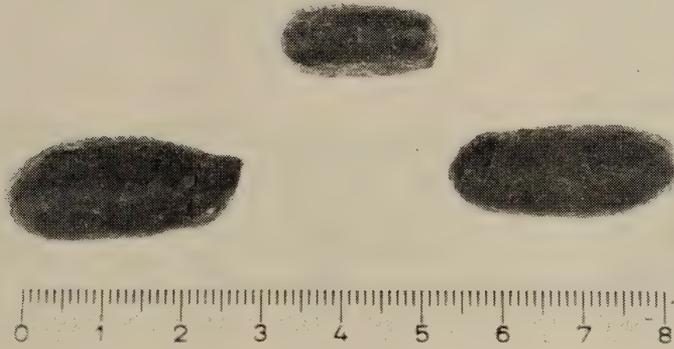


Fig. 5



Fig. 6

identified with certainty as either parma or pademelon and these have been recorded as uncertain. The other species category is mainly *Wallabia bicolor* but includes some *Macropus giganteus* and *Macropus rufogriseus* droppings.

There is no apparent difference in the pattern of production of pellet groups between *M. parma* and *T. thetis* (Table 6).

TABLE 6
NUMBER OF PELLETS PER GROUP

Number	1 %	2 %	3 %	4 %	5 %	6-8 %	Total Groups
<i>M. parma</i>	23.6	40.0	24.1	7.4	3.0	2.0	203
<i>T. thetis</i>	24.4	40.4	20.2	11.4	2.6	0.8	386

(c) Mammal Distribution

The platypus, *Ornithorhynchus anatinus*, occurred in both the Blicks and Nymboida Rivers which flank Moonpar S.F. Within Moonpar, were six species of macropodids besides *M. parma*. Both species of pademelon, *T. thetis* and *T. stigmatica*, occurred in the rainforest and wet sclerophyll forest areas. *T. stigmatica* was observed on only a few occasions and would be considered one of the less common species of the area. *Wallabia bicolor*, the swamp wallaby, was widely distributed throughout the forest in both rainforest and wet sclerophyll forest areas.

A single wallaroo, *Macropus robustus*, five eastern grey kangaroos, *Macropus giganteus*, and six red-necked wallabies, *Macropus rufogriseus*, were observed feeding on Mills Farm and the adjacent areas which had been opened up for grazing. Both the grey kangaroos and the red-necked wallabies were more common in the open forest to the west. *M. parma*, *T. thetis* and *W. bicolor* have all been observed feeding in the same areas at one time or another. These three species have also been seen feeding in areas grazed by the grey kangaroos and red-necked wallabies.

Five species of phalangerids were observed in Moonpar. *Trichosurus caninus* and *Pseudocheirus peregrinus* were observed in rainforest areas, while *Trichosurus vulpecula*, *Petaurus breviceps* and *Petaurus australis* were seen in the dry sclerophyll forest and open woodland area in the north.

Several tiger cats, *Dasyurus maculatus*, were heard and one was observed crossing the road in a rainforest area. A small mammal which appeared to be an *Antechinus* was also observed on the road.

Feral cats, *Felis catus*, were present in the forest as was the dingo, *Canis familiaris dingo*.

(d) Biology of *M. parma*

Examination of the area in which parmas were most common based on the analysis of faecal pellet groups indicated that kangaroo grass (*Themeda australis*) was the preferred food in that area. Patches of kangaroo grass were grazed to lawn level whereas only small amounts of *Poa* had been eaten and the blady grass (*Imperata* sp.) was virtually untouched.

Evidence was found of predation by both the carpet snake (*Morelia spilotes*) and the dingo upon the red-necked pademelon. It must be assumed that these species would also take parmas if the opportunity arose. The tiger cat and feral cat are other potential predators but no evidence was found for predation by either of these species upon macropodids.

Four of the five specimens of *M. parma* collected were feeding with other animals, but there was no other evidence that they were part of a social group. All animals appeared to make for the rainforest and thicker wet sclerophyll forest areas when disturbed.

The estimated months of birth of the four animals less than two years old and the two pouch young are February (2), March (2), June and October. Estimated age at first birth for 73/5P was 70 weeks old which agrees with the data obtained from yard animals (Maynes, 1973). Both 72/1P and 72/2P would appear to have begun to mature sexually as judged by their pouch condition. Thus the weight at sexual maturation is probably between 2.5 and 2.8 Kg in the female.

DISCUSSION

The habitat of the parma wallaby would appear to be rainforest and wet sclerophyll forest. This agrees with Gould's statement that he had seen it in the brushes (i.e. rainforest) of the Illawarra area (Gould, 1863). Both Darlington's specimens and my own were taken in eucalypt forest where they were feeding. It may be that the parmas feed in the more open eucalypt forest areas and shelter in or on the edges of the rainforest areas.

One reason for the apparent rarity of the parma wallaby may be the difficulty in recognising it in the field from the two species of pademelon. Most sightings are at night, of short duration, and of moving animals as they run into the brush on the side of the road or as they cross the road. Under such conditions, some experience is needed in recognising the three species. Parmas are generally lighter in build than the pademelons. The length of the tail in relation to the body is considered the most useful character for recognising parmas in the field. If one observes a pademelon-sized animal with a long white-tipped tail, it is a

parma wallaby. The presence of the distinct white cheek stripe can also be used for identifying them provided one can observe them long enough.

The presence of distinctive parma wallaby pellets in Moonpar S.F. suggests that this may be a useful means of checking for the presence of the species. It also holds promise as a means of assessing the relative use of different areas by parmas, pademelons and other species.

The parma wallaby appears to be in no immediate danger in Moonpar S.F. provided there is no radical change in current management practices. It is to be hoped that it will be found to be more widely distributed in the state forests of the district. Further field survey work is required to assess the distribution, habitat preference and status of this species in New South Wales.

The discovery of this population of parma wallabies in New South Wales suggests that there may be no need to repopulate Australia with animals from Kawau Island as has been contemplated in some quarters (Anon., 1973). It is strongly recommended that no releases into the wild be attempted until detailed studies have revealed the ecological consequences of such an action.

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***Craterocephalus dalhousiensis* n.sp., a Sexually Dimorphic Freshwater Teleost (Atherinidae) from South Australia**

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ABSTRACT

Craterocephalus dalhousiensis n.sp. is described from specimens collected in shallow water of artesian springs at Dalhousie Springs, South Australia and represents the first Australian record of a sexually dimorphic atherinid. *C. dalhousiensis* appears to be closely related to *C. lacustris* and *C. stercusmuscarum* although meristic and morphometric differences make the new species readily distinguishable. A number of specimens of *C. dalhousiensis* has been examined internally for gonad condition, gut content and presence of parasites. Water temperature, salinity and pH were measured at the time of collection and upper and lower thermal tolerances were also determined.

INTRODUCTION

As a result of aquatic surveys conducted by the South Australian Museum in the Far North of South Australia since 1968, the known distributions of several species of fishes have been extended and some new forms have been collected, including the species described here.

Preliminary field observations and experiments on this new species' environment, activity and thermal physiology can be compared with the findings of Brown and Feldmeth (1971) on desert pupfish (*Cyprinodon* spp.) in southern California.

(A) TAXONOMY

MATERIALS AND METHODS

The technique used for counts and measurements was the same as used by Munro (1967) except for the inter-dorsal count where the scales were counted from the origin of the last spine of the first dorsal to the origin of the second dorsal. Transverse scale rows count was made diagonally across the body from the

origin of the first dorsal to the origin of the ventral fin. Relative positions of the fins were recorded in numbers of scales in front or behind the origins or tips of fins.

All measurements were made with dial calipers to the nearest one-tenth of a millimetre (mm). Body measurements were expressed as proportions of standard length or as otherwise indicated in Table 1. A mean and range (in brackets) was also given for the ten male and ten female specimens examined.

Type material has been deposited at the following institutions: Australian Museum, Sydney; American Museum of Natural History, New York; British Museum of Natural History, London; Museum National d'Histoire Naturelle, Paris; Zoologisch Museum, Amsterdam.

List of abbreviations used in Table 1:

SL	standard length
B	behind
F	in front of
OD1	origin of first dorsal fin
OD2	origin of second dorsal fin
OV	origin of ventral fin
T. Pec.	tip of pectoral fin
TV	tip of ventral fin

DESCRIPTION

Craterocephalus dalhousiensis, new species

Figure 1

Holotype—SAM F3453 (male), allotype—SAM F3453 (female), type locality, Dalhousie Springs, Main Spring, South Australia, 26° 25' S., 135° 30' E. (Map ref. 1:250,000 Topographic Maps, Series R502, Commonwealth Government Printer, Canberra. Map Sheet: Dalhousie SG 53-II. Grid ref.: 345718). Holotype and allotype in South Australian Museum (SAM). Paratypes in South Australian Museum and The Australian Museum, Sydney (AMS).

Material examined:

Main Spring, Dalhousie Springs, South Australia, designated holotype SAM F3453 (male), 51 mm SL, designated allotype SAM F3453 (female), 63 mm SL, designated paratypes SAM F3453, AMS I.17756-001; Spring, 2.4 km south-west of Dalhousie Main Spring, South Australia, SAM F3466.

General description—The material examined ranged from 27 to 63 mm SL. In both sexes, the lips are thick and fleshy with the skin of the upper jaw fusing with the skin over lower jaw about half way along the premaxilla. Premaxilla never reaches the anterior margin of the orbit.

The lower jaw is massive when compared with other species of this genus, the anterior end expanding to form a wide horseshoe-shaped band with many rows of small but easily visible curved teeth. Upper jaw is similarly toothed. The rest of the mouth is edentulous. Both the preopercle and opercle are covered with scales. Body scales are cycloid, round in smaller specimens but becoming elongated vertically in older fish. The ridges on scales do not extend to the posterior part of the scale in specimens examined. As in all other Australian hardyheads, the midlateral scales are pierced with pores, but in many specimens scales on the dorsal surface and on the lateral sides are likewise pierced.

Specimens preserved in alcohol are dark brown above the midlateral band due to presence of many small chromatophores uniformly dispersed along the back. Occasionally, spots immediately above the midlateral band form a faint discontinuous line. A dark band extends from the snout through the eye and opercle, then continues as a midlateral band formed by large pigment spots in the centre of each midlateral scale. Scales beneath the midlateral band have smaller pigment spots usually forming two or three discontinuous lines along the abdomen. Very young fish are dusky brown with few or no spots below midlateral band.

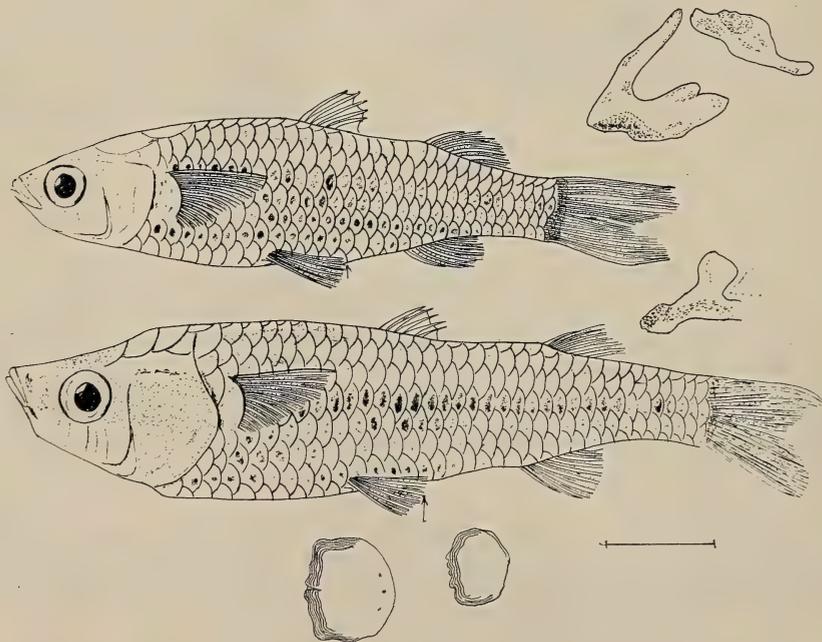


Fig. 1. Line drawings of holotype male (above) and allotype female (below) showing external features. Scales (6th along the midlateral band) from both specimens. Line diagrams of premaxilla, maxilla and dentary are also included. Position of anus is indicated by arrow. Projected scale, 10 mm.

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TABLE 1

BODY MEASUREMENTS AND COUNTS OF TWENTY-TWO SPECIMENS OF *C. DALHOUSIENSIS* FROM DALHOUSIE SPRINGS

	Holotype	Allotype	Mean, range of 10 males	Mean, range of 10 females
Head in SL	3.4	3.1	3.5(3.3-3.7)	3.3(3.0-3.5)
Greatest body depth in SL	3.9	3.8	4.0(3.7-4.7)	4.1(3.7-4.5)
Premaxillary process in eye	1.1	1.1	1.3(1.1-1.7)	1.2(1.0-1.6)
Eye in the head	3.8	4.4	3.6(3.0-3.9)	3.8(3.3-4.4)
Interorbital in head	2.6	2.4	2.6(2.3-2.9)	2.6(2.4-3.1)
Snout in eye	1.1	1.0	1.1(1.0-1.3)	1.1(0.9-1.2)
Premaxilla in eye	1.0	1.0	1.0(1.0-1.4)	1.0(0.8-1.1)
Least depth of caudal peduncle in SL	8.7	10.2	9.5(8.7-10.0)	10.0(9.4-10.1)
Midlateral scales	30	31	29.6(29-30)	29.9(29-31)
Transverse scales	7.5	7.5	7.1(6-8)	7.3(6.5-7.5)
Predorsal scales	17	26	15.9(15-17)	16(15-18)
Interdorsal scales	6	8	7(6-8)	7.6(7-8)
Dorsal fin count	V,li6	VI,li6	V-VI, li4-6	IV-VI, li5-6
Anal fin count	li7	li7	li6-7	li6-8
Pectoral fin count	li12	li12	li11-13	li11-12
Gill rakers in lower gill arch	8	7	7.1(7-8)	7.1(7-8)
Vertebral count	32	32	31.6(31-32)	31.2(30-32)
OD1, in relation to TV (scales)	F 3.5	F 3.5	F 3.3(2.0-4.5)	F 3.9(3-5)
OD2, in relation to OA (scales)	B 1	B 1	B 1(0.5-1.5)	B 1.5(0.5-1.5)
OD1, in relation to T. Pec. (scales)	B 1.5	B 2	B 2.4(1.5-3.0)	B 2(1.5-3.0)
OV, in relation to T. Pec. (scales)	F 1	directly below	F 0.6(0-1.5)	F 1.1(0-3)
Position of anus to TV (scales)	B 0.5	B 1	B 1(0-2 B)	B 0.5(F0.5-B0.5)

Remarks—*C. dalhousiensis* is sexually dimorphic, a condition which is exceptional amongst the Australian hardyheads, except for some sexual differences during the breeding season (Llewellyn, 1971). It is, however, quite normal for blue eyes (*Pseudomugilinae*) and rainbow fish (*Melanotaeniidae*) their close relatives. Fish longer than 40 mm SL are easily sexed (see Fig. 1), externally. On the average (in a sample of 64) the adult male is shorter than the adult female. The dorsal surface in males tends to be almost horizontal from the snout to the origin of the first dorsal; the abdomen on the other hand is gently arched from the isthmus to the tips of ventrals. In the female, the belly is flat, but the head slopes sharply towards the snout with the interorbital space being flat to concave, depending on maturity. No other differences can be observed between males and females externally. Specimens less than 40 mm SL are difficult to sex although ripe gonads were

found in a 34 mm male and a 27 mm female. Immature individuals tend to resemble adult males, but the abdomen is flat. Gonads in both sexes lie below and to one side of the intestine. The ovary, a long cylindrical sac is completely enclosed by black mesovarium. It lies below and to the right side of the intestine with its duct extending past the rectum to open just posteriorly to the anus. The testis is a yellow-white mass lying below and to the left side of the intestine with its duct extending past the anus to open posteriorly as in the female. Gonads were checked histologically to confirm the relationship between sex and external morphology. In a 34 mm male collected in November, sperm was found in great abundance. In a thin section of an ovary from a 37 mm female collected in August, no ripe oocytes were visible, although the more immature stages were clearly evident.

Superficial examination of adult females suggests a close affinity with *C. lacustris* Trewavas. Apart from significant colour differences, the size range, vertebral, midlateral scale and gill raker counts are very different. Coloration and spot pattern suggests a closer similarity to *C. stercusmuscarum* (Gunther), but none of the 64 specimens of *C. dalhousiensis* examined for colour and spot pattern had more than one row of spots above the midlateral band as seen in *C. stercusmuscarum*. However, immature specimens of the two species are easily confused because of their similar pigmentation. *C. dalhousiensis* is deep bodied, *C. stercusmuscarum* is slender, the midlateral scales, vertebral and gill raker counts are also different. A comparison with other allied species also shows meristic and morphometric differences (Table 2).

TABLE 2

MERISTIC AND MORPHOMETRIC DIFFERENCES (EXPRESSED AS MEANS AND RANGES) OF FOUR CLOSELY ALLIED SPECIES OF *CRATEROCEPHALUS*

	<i>C. lacustris</i>	<i>C. stercusmuscarum</i>	<i>C. marjoriae</i>	<i>C. dalhousiensis</i>
Greatest body depth in SL	4.6(3.5-6.0)	4.9(3.5-5.6)	4.1(3.7-4.5)	4.1(3.7-4.7)
Midlateral scales	34.3(32-38)	32.6(30-34)	28.5(24-30)	29.8(29-31)
Transverse scales	7.3(6.0-8.5)	7	6(5.5-7.0)	7.1(6.5-7.5)
Vertebral count	36.5(35-39)	36.8(35-39)	31.4(30-32)	31.4(30-32)
Gill rakers in lower gill arch	10.7(9-12)	9.1(8-10)	10.1(9-11)	7.1(7-8)

On the basis of body colour, pattern and body shape, *C. dalhousiensis* appears to be closely related to *C. lacustris* and *C. stercusmuscarum*. Counts and measurements also suggest a close affinity with *C. marjoriae* Whitley. A comparative study of the premaxillary bone of five species of *Craterocephalus* confirms the relationship with *C. lacustris* and suggests affinity with *C. eyresii* (Steindachner) (Fig. 2). Counts and measurements do not confirm close relationship with *C. eyresii*.

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Diagnostic features—*C. dalhousiensis* can be distinguished from its congeners by the following characters: it is a deep bodied fish which is dark brown above and with two to three rows of brown spots below the midlateral line, 7 to 8 gill rakers in the first lower arch, 29 to 30 midlateral scales, $6\frac{1}{2}$ to $7\frac{1}{2}$ transverse scales; females have a head which slopes sharply towards the snout whilst the abdomen tends to be flat. Mature males have a sloping abdomen and a relatively horizontal dorsal surface.

Range—At present, this species is only known from Dalhousie Springs, South Australia which is about 120 km north of Oodnadatta. It may have a wider range as has proved to be the case with *C. eyresii* which has been recorded (unpublished

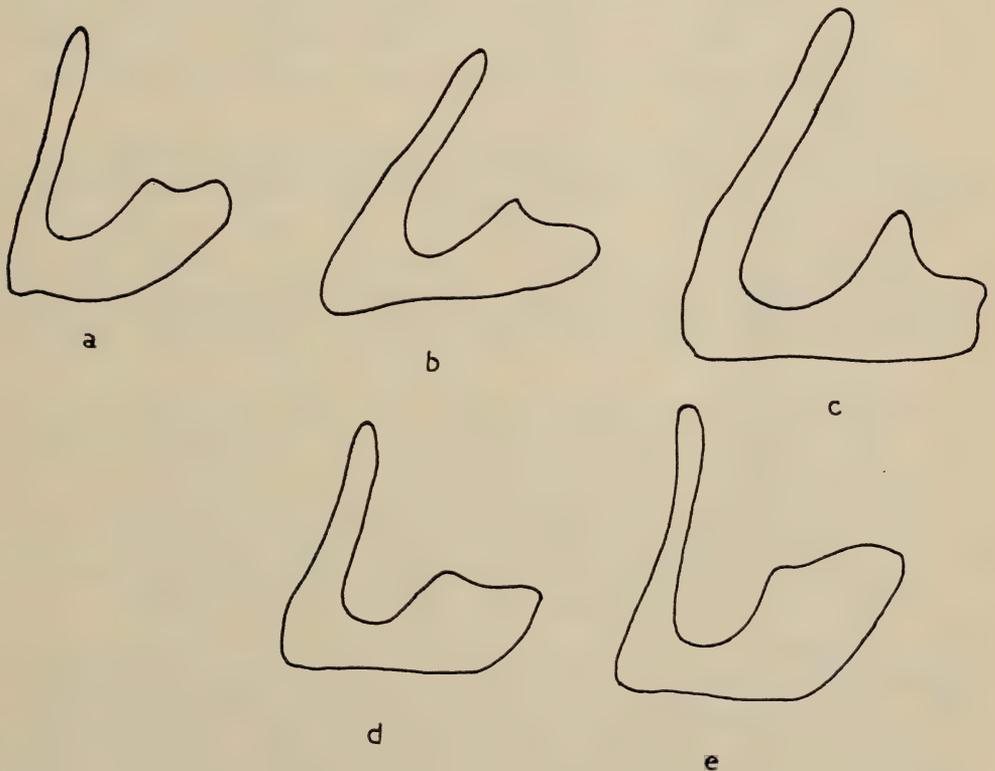


Fig. 2. Comparison of the premaxillary bones of 5 species of *Craterocephalus*.

- (a) *C. lacustris*
- (b) *C. dalhousiensis*
- (c) *C. marjoriae*
- (d) *C. eyresii*
- (e) *C. stercusmuscarum*

data) from the Namoi, Peel and Murray Rivers and the inland lakes of Victoria and South Australia.

The name given to the species is derived from the name of the type locality, a major area of mound spring development, embracing about thirty-three artesian springs of varying size and activity, scattered over an area of nearly 75 km².

(B) BIOLOGICAL NOTES

MATERIALS AND METHODS

The fish were collected with wire mesh traps (26 gauge wire, 2 mm mesh) 31 x 15 x 15 cms. Each end of the cage had an aperture with an internal collar 3.5 cms in diameter. Traps were set both during the day and night. The size and the composition of catches was noted and recorded. Each species was identified and examined for gut content.

Water temperatures were recorded at five stations over a distance of approximately 1 km along the course of Dalhousie Main Spring stream. pH and salinity were also taken at the time of trapping.

Observations of movements of *C. dalhousiensis* were made at Dalhousie Springs (by C.J.M.G.) on two occasions. The observations were followed up by a series of simple field experiments to determine upper and lower thermal tolerances of the hardyheads.

- (a) In one experiment the fish trapped in a cage were transferred to a point 5 metres upstream where the temperature recorded was higher. The experiment was repeated later in the day with a metal baffle inserted over the upstream end of the cage to reduce the force of the water current.
- (b) Captive hardyheads and catfish (*Neosilurus* sp.) from Dalhousie Main Spring were held in non-heated, non-aerated tanks in which the temperature was allowed to drop to well below 20°C.

To determine whether thermal acclimation takes place, freshly retrieved hardyheads were subjected in batches of four to rising water temperature by placing the holding tank (one litre polythene beaker) in a large water bath (an enamel bucket) containing water at 100°C. The fish were taken from waters of various temperatures to determine whether fish inhabiting the warmer sections of Dalhousie Main Spring were tolerant to higher temperatures than those from cooler regions. Constant agitation of water in the holding tank by stirring with a hand-held glass bulb thermometer, produced rapid and uniform transfer of heat, enabling the upper thermal limit of fish to be reached in about 10 minutes. A total of sixteen specimens from each of the two regions of the Spring stream were tested for thermal acclimation.

RESULTS AND DISCUSSION

Trapping—Far greater numbers of hardyheads (*C. dalhousiensis*) are trapped in daylight than during equivalent periods at night. In the case of the catfish (*Neosilurus* sp.) the reverse applies. A comparison of day and night catches (Table 3), made with a wire trap set along the Dalhousie Main Spring stream for five hour periods, confirms these catch patterns which presumably reflect activity patterns.

Associated fish—In the Dalhousie Main Spring (Table 3), an extremely large population of hardyheads (*C. dalhousiensis*) is found in association with an equally abundant population of catfish (*Neosilurus* sp.) together with very much smaller populations of two other small species, the desert goby (*Chlamydogobius eremius*) and the spotted gudgeon (*Mogurnda mogurnda*).

The catfish (*Neosilurus* sp.) appears to be an undescribed form.

Similar associations were found in all but one of the other inhabited springs inspected at Dalhousie; in one large spring approximately 0.8 km west of the main spring the species collected were *C. dalhousiensis*, *C. fluviatilis* McCulloch and *Madigania unicolor*.

Diet—Examination of gut contents in all specimens from a series of *C. dalhousiensis* yielded a large number of small unidentified gastropods and remnants of plant tissue.

Parasites—No external or internal parasites were noted on or in any of the *C. dalhousiensis* specimens examined.

TABLE 3

NUMBERS OF FISH TRAPPED DURING FIVE HOUR SETTINGS

Temperature and pH data recorded on morning of 19/11/69.

(a) day trapping—1100-1600 hours, 18/11/69.

(b) night trapping—2100-0200 hours, 18-19/11/69.

Station	<i>C. dalhousiensis</i>		<i>Neosilurus</i> sp.		<i>M. mogurnda</i>		<i>C. eremius</i>		Surface water temp.	Water pH
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)		
a	309	0	0	0	0	0	0	0	43.0°C	7.2
b	283	0	0	136	3	3	2	0	35.6°C	7.2
c	15	0	17	126	1	0	0	0	35.0°C	7.2
d	62	0	1	24	1	0	0	0	33.5°C	7.2
e	37	0	0	0	8	5	0	0	21.6°C	7.2
Total	706	0	18	286	13	8	2	0		

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Water temperature, pH and salinity—Surface temperatures recorded at five stations over a distance of approximately 1 km along the course of Dalhousie Main Spring stream during summer in 1967 varied from 43°C in a narrow channel feeding into the main body of the spring at the west end, down to 21.6°C in the shallows of the swamp at the east end into which the spring waters spread (Fig. 3).

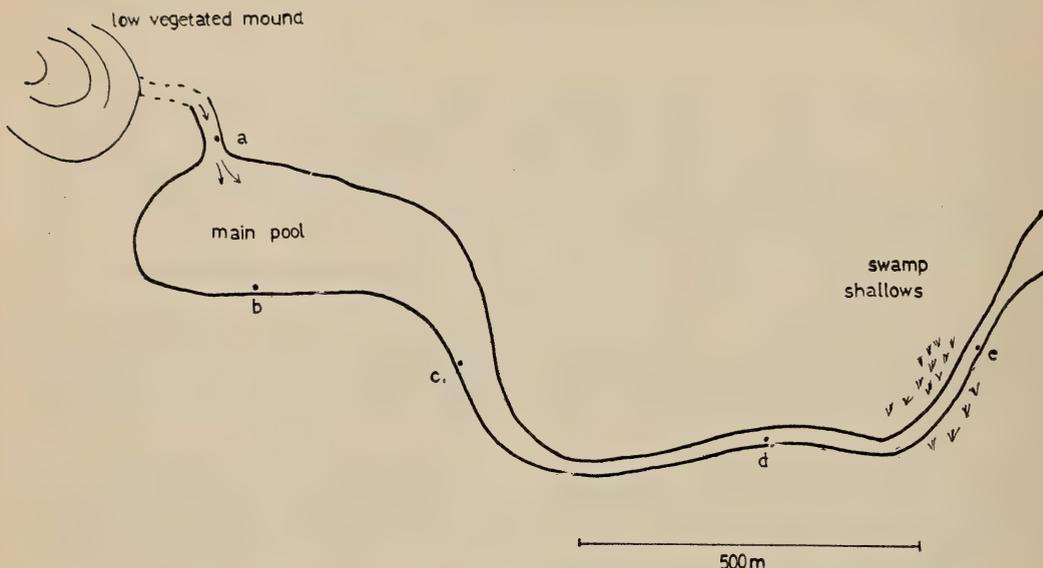


Fig. 3. Diagrammatic representation of Dalhousie Spring and stream with collecting stations indicated.

Water pH (Table 3), measured at each of the above stations was consistent at 7.2, a fairly typical value for swiftly flowing artesian waters of the Lake Eyre drainage region. The pH of outflowing waters is usually about 7.0; this often rises along the stream path, minimally in swiftly flowing waters, more steeply in slowly flowing shallow streams and terminal waters, especially in the presence of large quantities of algae or other aquatic vegetation when pH may rise to very high levels.

Water sampled about mid-way along the Dalhousie Main Spring stream and subsequently analysed (Table 4), indicated relatively low salinity (as total dissolved solids) compared with other artesian waters of the central Australian region.

Thermal tolerance—(a) Upper thermal tolerance

Large numbers of *C. dalhousiensis* have been observed making brief solitary excursions of up to one minute's duration from the edge of the main body

TABLE 4

ANALYSIS* OF WATER SAMPLED FROM THE MAIN SPRING AT DALHOUSIE SPRINGS, SOUTH AUSTRALIA, 6/6/68.

(*Analysis performed by the Australian Mineral Development Laboratories, South Australia).

Constituent	ppm	Assumed composition of salts	ppm	Hardness (as Ca CO ₃)	ppm
Anions					
Cl	370				
SO ₄	150	Ca HCO ₃	186	Total	245
HCO ₃	140				
NO ₃	trace	Ca SO ₄	41	Temporary	115
F					
Cations					
Na	252	Mg SO ₄	119	Permanent	130
K					
Ca	58	Na SO ₄	38	Due to Ca	145
Mg	24				
F		Na Cl	610	Due to Mg	100
Total dissolved solids				Total alkalinity as Ca CO₃	
	994				115

of the Main Spring into the narrow channel of rapidly inflowing shallow water, originating from the spring's outlet higher up on an adjacent vegetated mound.

Specimens of *C. dalhousiensis* and *Neosilurus* sp. trapped near the entrance to the channel at 30 cm depth, where the water temperature was 38.8°C, were put back into the water about 5 metres upstream in depth of 10 cm and temperature of 41.8°C. It was observed that all the hardyheads collapsed rapidly and died within 16 minutes of the transfer. The catfish died 2 to 3 minutes later.

When the force of the current was reduced by the insertion of a metal baffle over the upstream end of the trap, the hardyheads and the catfish survived approximately 60 and 120 minutes respectively.

Clearly those fish inhabiting the surface waters in the vicinity of the channel's outlet into the spring's large pool are living close to their upper thermal limit and in fact the hardyheads intrude briefly into water which, if their stay is prolonged, proves lethally warm.

Although the motivation for these incursions is not clear it is probable that they are foraging upon blue-green algae that grows abundantly over the bed of the channel, parallelling the findings of Brown (1971) who reported that the desert pupfish (*Cyprinodon* spp.) in southern California feed on blue-green algae in water of about 42°C which is close to their upper thermal limit.

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(b) Lower thermal tolerance:

Fish held in tanks where temperature was allowed to fall below 20°C rapidly became comatose. None survived overnight in this situation by which time the water temperature had dropped to 8.7°C.

In one experiment where water temperature had fallen to 16°C, a comatose catfish was revived by raising the water temperature above 20°C. This experiment was not repeated with the hardyheads.

Thermal acclimation:

The results obtained for thermal acclimation are summarized in Table 5. The data collected suggest the occurrence of direct acclimation by *C. dalhousiensis* to the thermal gradient along the Main Spring stream. Similar results were obtained with the catfish from the same spring and with desert gobies (*Chlamydogobius eremius*) elsewhere (C.J.M.G., unpublished data).

TABLE 5

SUMMARY OF RESULTS FOR THERMAL ACCLIMATION BY *C. DALHOUSIENSIS*

Station	Surface water temperature at collecting station	Standard lengths range (16 specimens)	SL mean	Critical thermal maxima range	Critical thermal maxima mean
a	38.8°C	30-52 mm	36 mm	41.8-44.6°C	43.6°C
d	32.8°C	37-50 mm	43 mm	37.8-42.5°C	40.2°C

These results are similar to those of Brown and Feldmeth (1971) who found that the upper thermal limit of desert pupfish (*Cyprinodon* spp.) freshly collected from thermal springs correlated with the temperatures of their habitats.

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The Fauna of Careel Bay with Comments on the Ecology of Mangrove and Sea-Grass Communities

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ABSTRACT

Careel Bay, Pittwater, New South Wales can be divided into five zones, salt marsh, mangroves, *Zostera* and *Posidonia* weed beds and sandy beach. The flora and fauna of each of these zones are described with comments on the seasonal abundance of animals in the weed beds and on the sandy beach. Finally the inter-relationship of these zones to each other especially in relation to the detritus food chain is discussed.

INTRODUCTION

It is widely accepted that salt marsh, mangrove and sea-grass communities are important components of estuarine ecosystems (Lyford and Plinney, 1968; Odum, 1961; Odum and de La Cruz, 1967. These communities act as nurseries for many organisms and produce large quantities of organic matter which forms the base of estuarine food chains. These communities have been little studied in Australia (Clarke and Hannon, 1967, 1969, 1970, 1971; Collins, 1921; Goodrick, 1970; Hamilton, 1919; Kratochvil, Hannon and Clarke, 1972; Macnae, 1966, 1967) and even basic descriptions of fauna are lacking.

During 1972, the New South Wales Division of the Australian Littoral Society surveyed the biology of Careel Bay in Pittwater on the Central Coast of New South Wales (Hattersley, Hutchings and Recher, 1973). The survey considerably expanded our knowledge of the fauna of estuarine habitats on the Central Coast, but in view of the limited data available for the fauna of mangrove and sea-grass communities in Australia, it was decided to extend the survey for an additional year. The results of the work during 1972 and 1973 are presented in this paper and although emphasis is on a description of the fauna, its distribution within Careel Bay and seasonal changes, the role of salt marsh, mangrove and sea-grass communities in the ecology of the estuary is also considered.

Careel Bay

Careel Bay (33° 37' S; 151° 20' E) is situated on the southeastern shore of Pittwater. Pittwater is part of the Hawkesbury River-Broken Bay estuary (Fig. 1): an extensive drowned river valley 32 km north of Sydney. No major

river flows into Pittwater and it is unlikely that any significant amount of freshwater reaches Pittwater from the Hawkesbury River. The volume of fresh water coming down the Hawkesbury River is irregular and carries a heavy silt load. At times of flood on the Hawkesbury we have not observed any intrusion of river water into Pittwater or Careel Bay.

Development on the watershed of Pittwater is primarily residential with substantial areas along the northern shores reserved as National Park. Careel Bay is shallow, but well protected from prevailing winds. Surrounding lands have been developed for residential purposes and water flowing into the Bay

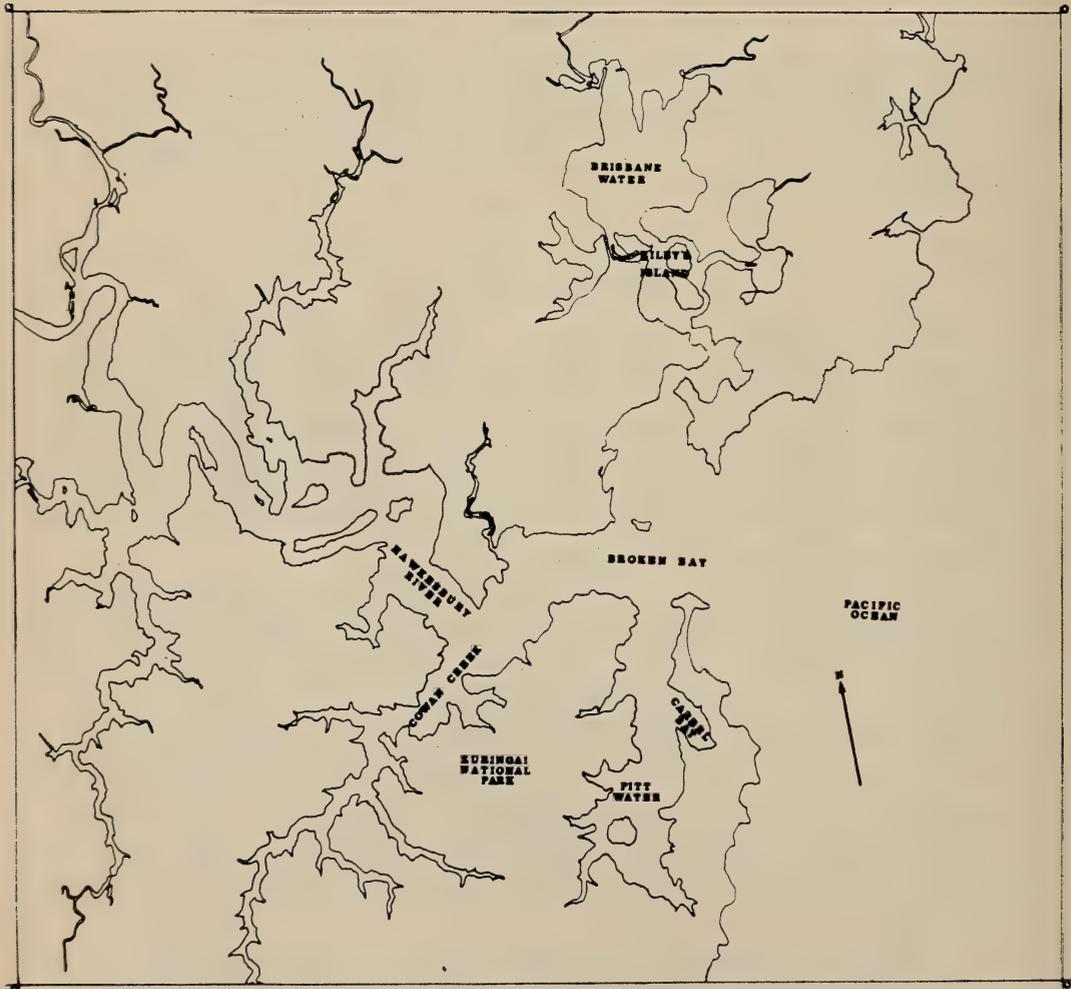


Fig. 1. Map of Pittwater, Hawkesbury River and Brisbane Waters, showing the relationship of Careel Bay to these areas.

FAUNA OF CAREEL BAY

comes primarily as runoff from the storm water drainage system. There is some seepage from septic systems and runoff from the garbage tip. Other than minor local effects, water pollution, however, is not a problem. The Bay opens widely to Pittwater and the tidal range is 2 m. The entrance to Careel Bay is marked by a sand bar which consists of sediments transported from the ocean side of Pittwater. The bar prevents sand from entering the Bay, but does not seem to impair the exchange of water with Pittwater. Sediment deposition is occurring at the head of Careel Bay and over the last century, 1.3m of sediment has been deposited (Hattersley, Hutchings and Recher, 1973). The mangroves and sea grass flats at the head of the Bay appear to trap and retain most of these sediments. It is likely that these sediments have been derived from disturbances associated with the residential development of the foreshores and surrounding areas and the rate of sedimentation may decline when the area is fully developed.

TABLE 1
AREA OF MAJOR LITTORAL HABITATS

Zone	Area (m ²)	%
Sandy beach	149.0	15
Salt marsh	32.9	3
Mangroves	82.9	7
<i>Zostera</i>		
Sea grass flats	427.5	38
<i>Posidonia</i>		
Sea grass flats	410.0	37

The estuarine environment of Careel Bay (Fig 2) can be conveniently divided into five zones, sandy beach, salt marsh, mangrove (Fig. 3), *Zostera* grass flats and *Posidonia* grass flats. The extent of each zone is given in Table 1. The zones and their approximate distributions are shown in Fig. 4.

METHODS

Between January 1972 and December 1973 a number of general collecting trips were made to Careel Bay. These included night collecting. A representative sample of all the animals collected during this survey has been deposited in the Australian Museum, Sydney. In addition quantitative sampling was carried out in February, June and November, 1973. In February only the upper zone of *Zostera* was sampled, but in June and November the upper and lower zones were sampled separately.

During each period of quantitative sampling ten samples were collected from the *Posidonia* and *Zostera* weed beds and sandy beach. Using a spade 9000 cm³ of



Fig. 2. Aerial photograph of Careel Bay.

Photo: Peter Whalan.



Fig. 3. The salt marsh mangrove junction. Numerous small bushes of *Avicennia marina* in the foreground, amongst the salt marsh vegetation. Photo: Peter Whalan.

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mud or sand and associated plants (if any) was collected and passed through a 2.0 mm sieve. In taking the samples, only the surface layer of the substrate to a depth of 10 to 20 cm was collected. Fast swimming and deep burrowing animals were probably missed or underestimated by this method. In the *Posidonia* zone, a different method was adopted for the June and November samples. Divers with SCUBA pulled out plants with their root systems and adhering mud until 9000 cm³ of material had been collected. Again 10 samples were collected, but these are not comparable with the samples taken in January or from the other zones. We found collecting in the *Posidonia* difficult and this zone was not well sampled.

In addition to the volumetric samples, the population density and size distribution of the Sydney cockle *Anadara trapezia* was measured using a 0.25m² quadrat in the lower *Zostera*. A 0.25m² quadrat was used also to estimate the biomass of *Zostera* and *Posidonia*. The quadrat was placed randomly ten times in each zone and all plant material was removed from within the quadrat. The plants were washed, excess moisture and epiphytes removed and the plants weighed. The samples were then dried at a constant humidity and temperature (21°C) and re-weighed until constant weight.

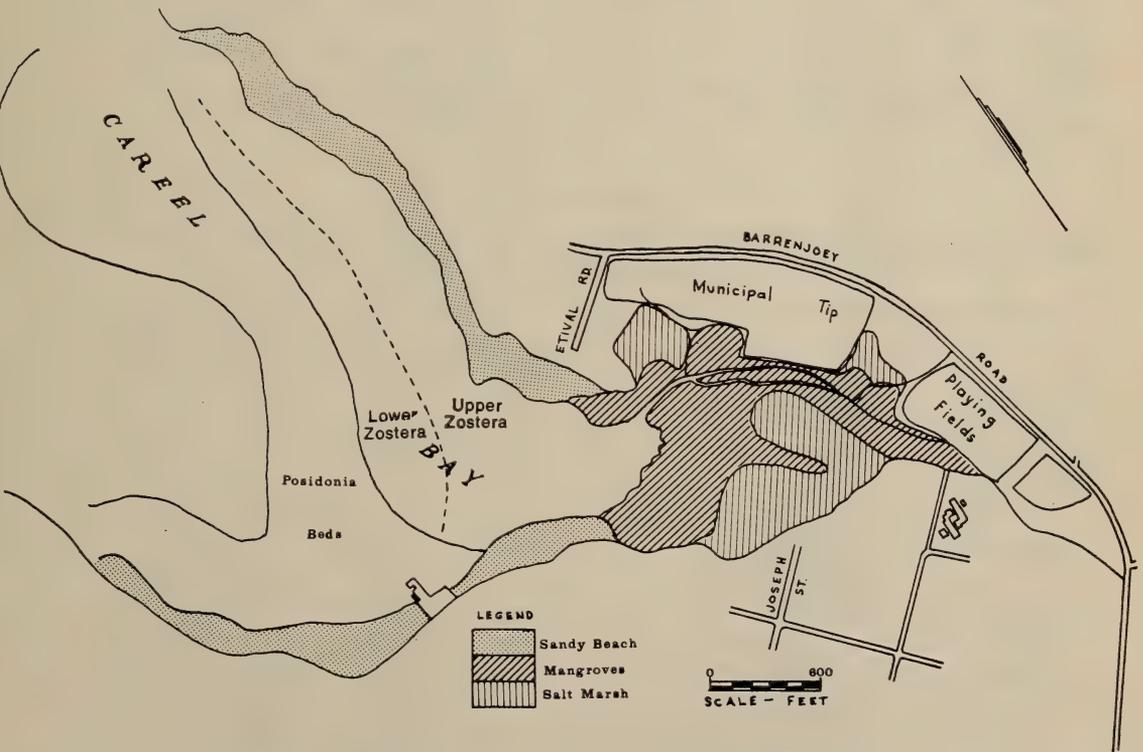


Fig. 4. Careel Bay showing the extent of the 5 zones. The reclaimed areas of the Municipal Tip and Playing Fields are also shown.

FAUNA

The fauna of Careel Bay will be presented in two ways. First we describe the major groups of animals which occur in Careel Bay. Second we relate the distribution and abundance of the fauna to each of the five major habitats (zones) in Careel Bay.

Marine Invertebrates

A list of the marine invertebrates collected during 1972 and 1973 at Careel Bay is presented in Table 2. This table also shows the distribution of species by zones and an indication of species abundance on a scale of \log_e throughout the year. Absolute values of abundance are not given as we have insufficient quantitative data for most animals to justify giving precise figures. Also some of the species are very patchy in their distribution. The *Zostera* has been considered as a single zone in this Table. The faunal lists for the five zones present in Careel Bay are not complete, as even after 2 years of regular collecting, new records for the Bay continue to be obtained. These probably represent seasonal visitors to the Bay or species which are sparsely represented in the Bay. The species list for the mangrove zone is incomplete in that the infauna of the mud was inadequately sampled. For practical reasons it was only possible to sample areas adjacent to the creek. Other invertebrates occur in Careel Bay such as encrusting organisms on pilings, moorings or rocky habitats, and these were not sampled during this survey.

TABLE 2

DISTRIBUTION AND ABUNDANCE (WHERE AVAILABLE) ON A SCALE \log_e OF MARINE INVERTEBRATES IN CAREEL BAY

		Salt marsh	mangroves	Zostera	Posidonia	Sandy beach
Coelenterates	<i>Edwardsia</i> sp.			1	1	
Platyhelminthes	Turbellarian			1		
Nemertean	Heteronemertean			2	2	1
Polychaetes						
F. Polynoidae	<i>Paralepidonotus</i> cf. <i>ampuliferus</i>			1	1	
F. Phyllodoceidae	<i>Phyllodoce</i> <i>novaehollandiae</i>			1		
	<i>Phyllodoce</i> sp.			1		
F. Syllidae	<i>Syllis</i> sp. 1			1	1	
	<i>Syllis</i> sp. 2			1		
F. Nereidae	<i>Australonereis ehlersi</i>			1		4
	<i>Ceratonereis</i> <i>erythraeensis</i>	1		1		
	<i>Ceratonereis mirabilis</i>			1		
	<i>Neanthes vaalii</i>		1	1		
	<i>Nereis (Hediste) diversicolor</i>		1	3		1

FAUNA OF CAREEL BAY

TABLE 2 (continued)

		Salt marsh	mangroves	Zostera	Posidonia	Sandy beach
F. Nephtyidae	<i>Nephtys australiensis</i>		1	4	1	1
F. Glyceridae	<i>Glyceria americana</i>			1	2	
F. Eunicidae	<i>Marphysa sanguinea</i>			1	1	
F. Lumbrineridae	<i>Lumbrineris latreilli</i>			1	1	
F. Orbiniidae	<i>Haploscoloplos</i> n. sp.		1	1	1	3
	<i>Naineris</i> sp.				1	
	<i>Orbinia</i> sp.			1	1	
	<i>Phyllo</i> sp.			1	1	
	<i>Scoloplos</i> sp.			1		
F. Spionidae	<i>Boccardia</i> sp.	1				
	<i>Dispio</i> sp.				1	
	<i>Malacoceros</i> sp.				1	
	<i>Polydora</i> sp.		2	2	1	1
	<i>Prionospio</i> sp.			1	2	
F. Magelonidae	<i>Magelona</i> sp.			1		1
F. Chaetopteridae	<i>Chaetopterus</i> sp.			1	1	1
F. Cirratulidae	<i>Cirratulus</i> sp.					1
F. Flabelligeridae	<i>Pherusa</i> sp.				1	
F. Opheliidae	<i>Armandia lanceolata</i>			1	1	
F. Capitellidae	<i>Barantolla leptae</i>			3	1	1
	<i>Capitella capitata</i>	1		1		1
	<i>Heteromastus</i> sp.				1	
	<i>Mediomastus</i> sp.			1	1	
	<i>Notomastus hemipodus</i>			5	2	
F. Maldanidae	—incomplete specimen			1		
F. Arenicolidae	<i>Arenicola bombayensis</i>			1		
F. Oweniidae	<i>Owenia fusiformis</i>			3	1	1
F. Ampharetidae	<i>Amphicteis</i> sp.			1		
	<i>Lysippides</i> sp.				1	
	<i>Samytha</i> sp.			1		
F. Terebellidae	<i>Lysilla pacifica</i>			2	1	
	<i>Thelepus setosus</i>				1	
	<i>Rhinothelepus lobatus</i>			2	1	
	<i>Pista</i> sp.			1		
F. Serpulidae	<i>Spirorbis</i> sp.			3	3	
	<i>Hydroides</i> sp.				1	
<i>Phoronids</i>	<i>Phoronis</i> sp.			1		
<i>Crustaceans</i>						
Sub-Class. Cirripedia						
F. Balanidae	<i>Balanus amphitrite</i>		1			
Order Isopoda						
F. Anthuridae					1	
F. Sphraeromidae	<i>Cymodoce coronata</i>				1	
F. Ligidae	<i>Ligia australiensis</i>		x		1	
Order Amphipoda						
F. Ampithoidae	<i>Ampithoe</i> sp.		x	2	2	
F. Gammaridae	<i>Melita</i> sp.			2		
F. Liljeborgidae	<i>Liljeborgia</i> sp.				1	
F. Haustoriidae	<i>Urohaustorius</i> sp.				1	1

TABLE 2 (continued)

		Salt marsh	mangroves	Zostera	Posidonia	Sandy beach
Order Decapoda						
F. Penaeidae	<i>Penaeus plebejus</i>		x	2	2	1
	<i>Penaeus esculentus</i>			1	1	
	<i>Penaeus</i> sp.			1		
F. Palaemonidae	<i>Macrobrachium intermedium</i>				1	
F. Alpheidae	<i>Alpheus euphrosyne</i>			2	2	
	<i>Alpheus</i> sp. B			1	1	
	<i>Alpheus</i> sp. C			x		
F. Hippolytidae	<i>Hippolyte tenuirostris</i>				1	
F. Laomeiidae	<i>Laomeia healyi</i>		x			
F. Callianassinae	<i>Callianassa</i> sp.			1	1	2
F. Paguridae				x		
F. Hymenosomatidae	<i>Halicarcinus ovatus</i>				1	
F. Portunidae	<i>Portunus pelagicus</i>			1	1	
	<i>Thalamita sima</i>			1	1	
	<i>Thalamita crenata</i>			x		
	<i>Scylla serrata</i>		x			
F. Xanthidae	<i>Heteropanope serratifrons</i>			1	1	
F. Grapsidae	<i>Sesarma erythroductyla</i>	x	x			
	<i>Paragrapsus laevis</i>	x	x			
F. Ocypodidae	<i>Heloeccius cordiformis</i>	x	x			
	<i>Macrophthalmus setosus</i>		x	2		
	<i>Macrophthalmus crassipes</i>			2		
	<i>Macrophthalmus</i> cf <i>punctulatus</i>			x		1
	<i>Macrophthalmus</i> sp. 1			x		1
	<i>Macrophthalmus</i> sp. 2			x		x
	Species A			2		
	Species B			1		1
	<i>Australoplax tridentata</i>		x	x	1	
F. Mictyridae	<i>Mictyris longicarpus</i>			x		3
Molluscs						
F. Arcidae	<i>Anadara trapezia</i>		x	3	x	
F. Mytilidae	<i>Modiolus pulex</i>		x	x		
	<i>Mytilus edulis</i>			x		
	<i>Xenostrobus securis</i>			1		
F. Laternulidae	<i>Laternula tasmanica</i>			1		
F. Lodabiidae	<i>Cavatidens omissa</i>			2	1	1
F. Leptonidae	<i>Mysella</i> sp.			1	1	
F. Ostreidae	<i>Saccostrea cucullata</i>		x			
F. Veneridae	<i>Eumarcia fumigata</i>			1		1
	<i>Tapes watlingi</i>			1		1
F. Macturidae	<i>Notospisula parva producta</i>			2	1	2
F. Garidae	<i>Florisarka onuphria</i>					1
F. Tellinidae	<i>Macoma deltoidalis</i>			2	2	1
F. Teredinidae	<i>Teredo</i> sp.		x			
F. Trochidae	<i>Austrocochlea obtusa</i>	x	x	1		
	<i>Calliostoma australe</i>		x		1	
	<i>Salsipotens meyeri</i>		x			
F. Liotidae	<i>Liotia</i> sp.			1		

FAUNA OF CAREEL BAY

TABLE 2 (continued)

		Salt marsh	mangroves	Zostera	Posidonia	Sandy beach
F. Acmaeidae	<i>Chiazacmea flammea</i>		x			
F. Neritidae	<i>Nerita atrementosa</i>			x		
F. Littorinidae	<i>Littorina scabra</i>		x	x		
	<i>Bembicium auratium</i>	x	x	1		
F. Dialiidae	<i>Diala</i> sp.				1	
F. Tateidae	<i>Tatea rufilabris</i>	x				
F. Cerithidae	<i>Cacozeliana lacertina</i>			1	2	1
F. Potamiidae	<i>Pyrazus ebenensis</i>			1		
	<i>Velacumantus australis</i>		x	1		
F. Epitoniidae	<i>Epitonium</i> sp.			1		
F. Naticidae	<i>Conuber sordidum</i>			1		1
	<i>Conuber</i> sp.					1
F. Nassariidae	<i>Nassarius burchardi</i>		x	1	1	1
	<i>Nassarius jonasi</i>			x		
F. Muricidae	<i>Bedevea hanleyi</i>				1	1
F. Pythidae	<i>Melosidula zonata</i>	x				
	<i>Ophicardelus sulcatus</i>	x	x			
	<i>Ophicardelus ornatus</i>	x				
	<i>Ophicardelus quoyi</i>	x	x			
F. Amphibolidae	<i>Salinator solida</i>	x				
	<i>Salinator</i> sp.					1
F. Onchidiidae	<i>Onchidium damelli</i>		x	x		
F. Akeridae	<i>Haminoea wallissi</i>			2		
F. Aplysidae	<i>Aplysia dactylomela</i>			x	x	
	<i>Aplysia juliana</i>			x	x	
F. Elysiidae	<i>Elysia australis</i>			x	x	
F. Dorididae				1		
F. Sepiolidae	<i>Euprymna stenodactyla</i>			x	x	
Echinoderms	<i>Astropecten polycanthus</i>			x		
Ascidian	<i>Botrylloides nigrum</i>				x	

The sea anemone *Edwardsia* sp. and an unidentified turbellarian were collected in the upper *Zostera* zone. A single species of heteronemertean was collected from the sandy beach, *Zostera* and *Posidonia* zones. This species is being described by Gibson (Liverpool Poly., U.K.).

Forty-six species of polychaetes representing 22 families were collected including 21 identified to species level. Many of the polychaetes are new records for New South Wales and some undescribed species are present. These will be described in a paper by Hutchings (in prep.). No species of polychaete was found throughout the Bay although *Haploscoloplos* n. sp. was found in all zones except the salt marsh (Table 2). Twenty-three species occurred in two or three zones while 19 species were confined to a single zone. The *Zostera* weed beds had the richest fauna of polychaetes many of which are tubicolous including the abundant nereid *Australonereis eblersi*. The salt marsh, mangroves and sandy

beach had few species present although some in the sandy beach (e.g. *Australonereis ehlersi* and *Haploscoloplos* n. sp.) were abundant. A phoronid was found living in the empty tubes of the polychaete *Owenia fusiformis*, in November, 1973.

The majority of the polychaetes found in Careel Bay are detritus feeders. Some like *Arenicola* and all the capitellids actively ingest the substrate and digest the algae and bacteria adhering to the surface of the mud particles. Newell (1965) and Longbottom (1968) have shown how the resulting faecal material is enriched with nitrogen compounds which are then utilized by the bacteria and algae in the sediment. Subsequently this sediment is re-ingested and the cycle is repeated. The terebellids are surface deposit feeders, (Dales, 1955). Other species of polychaetes present are filter feeders, feeding on suspended detritus material and phytoplankton, these include *Chaetopterus*, and the serpulids. It is likely that *Nephtys australiensis* and many of the nereids are omnivorous scavengers although some experimental work has indicated that the polynoid *Paralepidonotus* cf. *ampuliferons*, the glycerid *Glycera americana* and the syllids are probably active carnivores feeding on small worms and crustaceans (pers. obser.).

Thirty-eight species of crustaceans were recorded from Careel Bay, most of these (31) occurred in the *Zostera* and *Posidonia* zones with only eight species present on the sandy beach. Three species occurred in the salt marsh and eleven species among the mangroves. Amphipods, isopods and other smaller crustacea were poorly sampled.

Many of the larger crustaceans were extremely abundant and show precise patterns of zonation with reference to high and low water marks. On the sandy beach a new species of *Callianassa* has been found and this is being described by Poore (Fisheries & Wildlife, Victoria, Australia). Three species of the snapping prawns *Alpheus* sp. were present in the weed beds and these are being described by Banner (Hawaii). Two crabs species, A & B, as yet unidentified, were especially abundant in the lower *Zostera*, but also occurred in the upper *Zostera* zone. Species A (Table 2) may be *Camptandrium paludicola* a species recorded by Snelling (1959) from the Brisbane River, Queensland. Three species of penaeid and carid prawns, *Penaeus plebejus* and *P. esculentus* and *Macrobrachium intermedium* were very abundant in the weed beds.

Many of the crabs in the mangroves feed on the algae growing on the bases of the mangrove trees and pneumatophores. Large numbers of crabs were observed feeding at night during low tide. For example *Paragrapsus laevis* was present in numbers ranging from 24-30 individuals /m², *Sesarma erythrodractyla* varied from 13-88/m², *Heloecius cordiformis* 3/m² and *Australoplax tridentata* 9/m². Similar measurements made during the day at low tide were in the order of 10-15 crabs/m². The amphipods, *Callianassa* and the alpheids are predominantly detritus feeders; and the soldier crab *Mictyris longicarpus* ingests the sand removing organic material.

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Forty-six species of molluscs were collected during the survey. Gastropods were the most numerous (31 species) followed by pelecypods with 14 species. We did not collect any chitons (Placophora), but they occur at Careel Bay along the rocky foreshores. Two species of cephalopods occur, *Octopus cyaneus* and *Sepia* sp., (Dakin, Bennett and Pope, 1952), but were not collected in this survey. The opisthobranchs, *Aplysia dactylomela* and *Aplysia juliana*, were particularly abundant during the spring and early summer on the sea grass flats. In contrast to the polychaetes, many of the molluscs were confined to a single zone. No species occurs in more than three of the five zones.

The molluscs can be divided into two main feeding categories, filter feeders and grazers. The bivalves which would represent the greatest biomass amongst the molluscs are all filter feeders; these are present in all zones except the salt marsh. In the weed beds, common species are *Anadara trapezia*, *Macoma deltoidalis* and in the mangroves *Saccostrea cucullata*. The grazers are represented by the gastropods, which feed either on the film of epibiota on the surface of the sea grasses or on the surface of the mud in the salt marsh or mangroves.

The only other marine invertebrates collected during the survey were the burrowing starfish *Astropecten polycanthus* in the lower *Zostera* and *Posidonia*, and the compound ascidian *Botrylloides nigrum*. This ascidian was found encrusting the leaves of the *Posidonia* in the November samples.

TABLE 3
SPIDER FAUNA OF CAREEL BAY

Order. Araneae		Salt Marsh	Mangroves
F. Clubionidae	<i>Clubiona robusta</i>		x
	<i>Miturga</i> sp.	x	
F. Pisauridae	<i>Dolomedes facetus</i>		x
F. Lycosidae	<i>Anoteropsis longipes</i>	x	x
	<i>Lycosa furcillata</i>		x
	<i>Lycosa</i> sp.	x	x
F. Hersiliidae	<i>Tama novaehollandiae</i>		x
F. Thomisidae	<i>Diaea</i> sp.	x	
F. Therididae	<i>Argyrodes antipodanus</i>		x
F. Tetragnathidae	<i>Tetragnatha bituberculata</i>		x
	<i>Tetragnatha</i> sp.	x	
F. Argiopidae	<i>Aranea insuta</i>	x	x
	<i>Aranea</i> sp.		x
	<i>Argiope aethera</i>	x	
	<i>Nephila ornata</i>		x
F. Linyphiidae	<i>Erigoninae</i> sp.	x	x
	<i>Laetesia</i> sp.	x	
	<i>Linyphiinae</i> sp.		x

Many of the spiders identified only to genus are juveniles.

Non Marine Invertebrates

A list of the spiders collected during the survey is presented in Table 3. Many species were collected only once and information on the seasonal occurrence of species is not available. Many of the spiders were identified to genus only as they were juveniles. In Appendix I, a list of insects which have been recorded from Careel Bay is given, this was compiled by D. McAlpine and G. Holloway of the Australian Museum from their Departmental records. Two interesting flies of the tropical genera *Merodonta* and *Pemphigonotus* have been found in the Bay and constitute new southern records for the genera. *Chelonus unimaculatus* and *C. australiensis* have been recorded for the first time since their original description in 1905. The larvae of the mangrove plume moth *Cenoloba obliterated* which are restricted to the fruit and young shoots of *Avicennia marina* were present. Also present is the mangrove fruit fly *Euphranta* sp. which is restricted to mangrove habitats as its larvae live in the fruits of *A. marina*.

TABLE 4
WADING AND SEA BIRDS OF CAREEL BAY
(species which occur regularly)

White-faced Heron	<i>Ardea novaehollandiae</i>
Mangrove Heron	<i>Butorides striatus</i>
White Egret	<i>Egretta alba</i>
White Ibis	<i>Threskiornis molucca</i>
Straw-necked Ibis	<i>Threskiornis spinocollis</i>
Black Billed Spoonbill	<i>Platalea regia</i>
Yellow Billed Spoonbill	<i>Platalea flavipes</i>
Little Pied Cormorant	<i>Phalacrocorax melanoleucos</i>
Australian Pelican	<i>Pelecanus conspicillatus</i>
Black Cormorant	<i>Phalacrocorax carbo</i>
Black Duck	<i>Anas superciliosa</i>
Dusky Moorhen	<i>Gallinula tenebrosa</i>
Grey Teal	<i>Anas gibberifrons</i>
Spur Winged Plover	<i>Vanellus miles novaehollandiae</i>
Bar-tailed Godwit	<i>Limosa lapponica</i>
Eastern Curlew	<i>Numenius madagascariensis</i>
Whimbrell	<i>Numenius phaeopus</i>
Red-necked Stint	<i>Calidris ruficollis</i>
Grey tailed Tatler	<i>Tringa brevipes</i>
Southern Stone Curlew	<i>Burhinus magnirostris</i>
Sacred Kingfisher	<i>Halcyon sancta</i>
Azure Kingfisher	<i>Alcyon azurea</i>
White Breasted Sea Eagle	<i>Haliaetus leucogaster</i>
Whistling Kite	<i>Haliastur sphenurus</i>
Silver Gull	<i>Larus novaehollandiae</i>
Crested Tern	<i>Sterna bergii</i>
White Fronted Tern	<i>Sterna striata</i>

FAUNA OF CAREEL BAY

Marine Vertebrates

Two groups of marine vertebrates need to be considered; fish and birds. Both groups are conspicuous and important parts of the Bay and the Hawkesbury River-Broken Bay estuary. Indeed, in the context of immediate social concern and economic value, both groups are of special interest. It is difficult to sample either group quantitatively and our observations are necessarily qualitative. Birds and fish are highly mobile animals and changes in numbers and species composition occur with each tide and season.

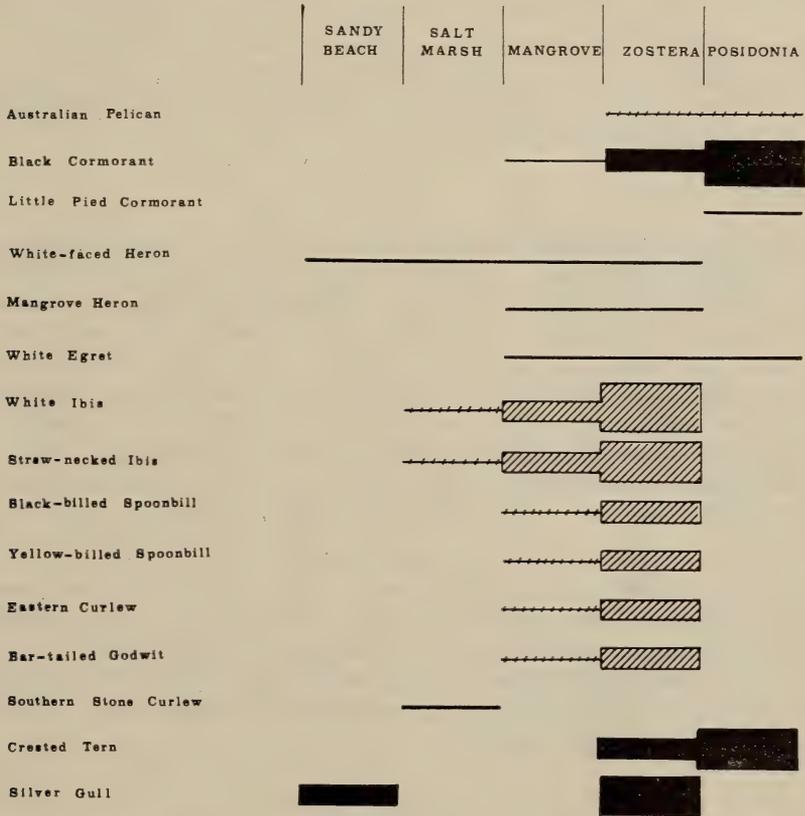
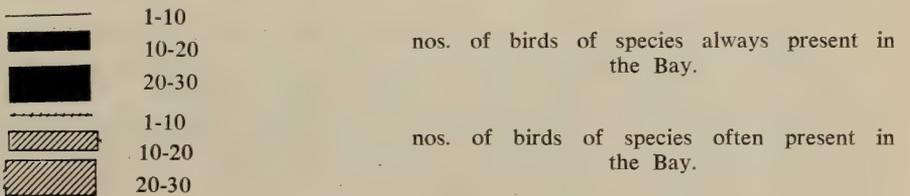


Fig. 5. Schematic diagram showing the abundance and feeding zones of the common Careel Bay Birds.



a. *Fish*

Fish were sampled using a 8 m seine with a fine 6 mm mesh. Thus, small fish and juveniles rather than large fish were taken. The grass flats of Careel Bay supported large numbers of young fish of commercially important species. For example, numerous juveniles of trevally, blackfish, bream, tarwhine, whiting and leather jackets were taken. These fish depend on the shallow waters of the estuary for their early growth and survival. Other species are resident on the grass flats and among the mangroves. Some, such as mullet, form important parts of the estuarine food chain and channel the organic production of the sea grasses and mangroves into larger and economically important species (Odum and Heald, 1972). A list of fishes collected in Careel Bay and elsewhere in the Hawkesbury system are presented in Appendix II; all the species listed are expected to occur in Careel Bay.

b. *Birds*

The estuarine food chains which begin with the sea grasses and mangroves often terminate with birds. At Careel Bay, wading and diving birds are a conspicuous part of the fauna (Table 4). Wading birds forage on the sea grass flats and among the mangroves at low tide while others such as terns, cormorants and pelicans feed when the flats are covered by water. The *Zostera* zone is the most important feeding area for the birds at Careel Bay and relatively few forage in the mangroves or on the salt marsh. However, the mangroves and salt marsh are important refuges at high tide and the mangroves provide nesting sites for herons. The salt marsh at Careel Bay is one of two places on the Central Coast where the Southern Stone Curlew *Burhinus magnirostris* nests.

In Fig. 5 we have shown the most common birds recorded at Careel Bay during 1972 and 1973 and the habitats in which they fed. Birds are highly mobile animals and their numbers tend to fluctuate with tide, weather and seasonal conditions. Probably most of the birds which forage on the tidal areas of Careel Bay range widely throughout the Hawkesbury River-Broken Bay estuary. In Fig. 5, we have, therefore, given relative numbers based on consistency of occurrence and absolute numbers.

HABITATS

Sandy Beach

The beach is made up of coarse clean sand. Some sediment and freshwater is carried onto the beach by a storm water drainage channel which empties directly on the beach. The beach gradually merges into the *Zostera*. On the land side of the beach there is limited development of *Juncus maritimus* and *Salicornia quinqueflora*. Residential development adjoining the beach has limited the area occupied by these plants.

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Polychaetes were the most abundant and diverse group of invertebrates found in this zone. The most abundant species were *Australonereis eblersi* and *Haploscoloplos* n. sp., both of which bred successfully during the year. This was indicated by their increase in numbers per sample due to the settlement of juveniles (Table 6). *Haploscoloplos* n. sp. bred between June and November and juveniles were abundant in the November sample. There was no evidence of mass mortality of the adults occurring after breeding. *Australonereis eblersi* bred earlier in the year; in the June sample, numerous newly settled individuals were present, suggesting breeding had begun in April or May. Breeding was still occurring in June as many of the females were gravid. Juveniles were present in November samples. It is not known whether breeding occurred continually throughout this period or if there were distinct outbursts of spawning, as found in many nereids (Clark, 1965; Schroeder, 1968). Hartman (1954) suggests *A. eblersi* may be viviparous no evidence of this was found. The numbers present in November are greater than those found in the preceding February suggesting that either 1972 was a less successful breeding season than 1973 or that many of the spawned worms will die during the subsequent summer months. Most species of nereids which have been studied breed once and then die (Clark, 1961; Dales, 1950).

The soldier crab *Mictyris longicarpus* was the most abundant crustacean in the sand, and newly settled individuals were numerous in June and November samples. The juvenile stages were more easily sampled by our methods than the adults and appear more abundant in our samples. Nevertheless, Careel Bay has a large population of adult soldier crabs. All other crustaceans were sparsely represented in the samples (Table 6).

Notospisula parva producta was the most abundant mollusc present in this zone and numbers increased in June due to the settlement of juveniles between February and June. Many of the other molluscs were represented only by one or two individuals e.g. *Eumarcia fumigata*, *Cacozeliana lacertina* and *Macoma deltoidalis*. A single juvenile of *Salinator* sp. was found in June.

Salt Marsh

The salt marsh occupies the area between the mangroves and fully terrestrial habitats. This zone has been affected by land fill operations and was probably bordered originally by paperbarks *Melaleuca* sp. and she-oak *Casuarina glauca*. The terrestrial margin of the salt marsh is dominated by the sedges, *Cyperus polystachyos* and *Juncus maritimus* var. *australiensis*, among which are scattered *Casuarina glauca*. Between the sedge zone and the mangroves is a region with bare mud and a patchy vegetation of *Salicornia quinqueflora* and *Triglochia striata*. Towards the mangroves there is a scattering of stunted mangroves *Avicennia marina* (Fig. 3). The patchy distribution of *Salicornia*, *Triglochia* and *Avicennia* in this zone reflects different levels of soil moisture and soil salinity (Clarke and Hannon,



Fig. 6. Inside the mangroves, looking towards the weed beds.
Photo: Dan Lunney.



Fig. 7. The upper *Zostera* weed beds. In the foreground are numerous seedlings of *Avicennia marina*.
Photo: Dan Lunney.

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1967, 1969, 1970, 1971). The mangroves for instance, invariably occupy depressions in the substrate surface.

The marine invertebrate fauna of the salt marsh was limited but the species present were usually represented by large numbers of individuals. The gastropods *Salinator solida* (1080/m²), *Tatea rufilabris* (74/m²), *Ophicardelus sulcatus* (264/m²) and *O. quoyi* (217/m²) were the most abundant molluscs present. These animals were found on the surface of the mud, and were closely associated with the vegetation. The crabs *Sesarma erythroductyla*, *Paragrapsus laevis* and *Heloecius cordiformis* were also common, especially in wetter areas.

Polychaetes appear to be entirely restricted to the mangrove margin of the salt marsh where residual pools of water remain. Three species were found, *Ceratonereis erythraeensis*, *Boccardia* sp. and *Capitella capitata*. All these species were represented by one or two individuals.

Mangroves

The mangrove zone is dominated by the grey mangrove *Avicennia marina* var. *australasica* which is the common mangrove on the Central Coast (Fig. 6). Adjoining the salt marsh there is a small number of the river mangrove *Aegiceras corniculatum*, a species which is more abundant in brackish waters. Despite intrusions by the Council garbage tip, mangroves occupy a significant area of Careel Bay (Table 1) and the stand appears to be colonizing the upper part of the *Zostera* zone (Fig. 7). The bases of the mangrove trees and pneumatophores are covered with a tufted red algae. The species has not been determined.

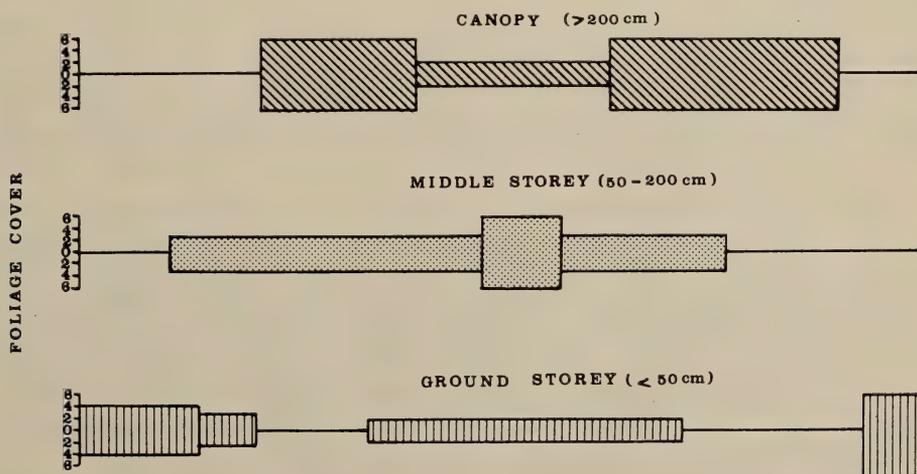


Fig 8. Schematic diagram of the Mangrove community in Careel Bay.

The mangrove zone is inundated on each high tide and the size of an individual tree is closely related to its position in the inter-tidal zone. The best growth of mangroves at Careel Bay occurs immediately adjacent to the *Zostera* flats; that is, just about mid tide level. A transect through the mangroves (represented schematically in Fig. 8) shows that tree height declines behind the first line of trees, with trees being noticeably smaller and more widely spaced in the central portion of the stand and adjacent to the salt marsh. The small size of the trees and the wide spacing of trees in the central portion of the stand may indicate that this part of the stand is higher above low water than areas along the fringe of the stand. Associated with changes in the height of trees and their spacing are changes in the density of foliage cover of the seedling and sapling layers. Throughout the mangrove stand is a layer of seedlings persisting at the two or four leaved stage. The leaves of these seedlings are arranged horizontally to the ground to intercept a maximum amount of the light diffusing through the rather dense canopy layer (Fig. 8) (see Horn, 1972 for a discussion of the adaptive morphology of trees). Whenever there is an opening in the canopy, the seedlings shoot towards the light and a dense middle storey rapidly develops.

TABLE 5
DENSITY DETERMINATIONS OF MOLLUSCS IN THE MANGROVES

Species	Site Nos.					
	1	2	3	4	5	6
<i>Saccostrea cucullata</i>	671	171	307	157	1342	167
<i>Bembicium auratum</i>	125	48	51	73	250	52
<i>Modiolus pulex</i>	5	2	2	3	10	1
<i>Chiazacmea flammea</i>	37	12	23	16	74	15
Unknown bivalve	4	1	2	—	8	1
<i>Calliostoma</i> sp.	3	—	—	—	6	—
Total no. of individuals per m ²	845	234	385	249	1690	236

The marine invertebrate fauna of the mangroves was richer than that found in the salt marsh both in terms of number of species and individuals. This was particularly noticeable among the molluscs where 16 species were recorded. The oyster *Saccostrea cucullata* was abundant on the lower trunks of mangrove trees especially those close to the weed beds and creek. *Littorina scabra* was commonly found grazing on the epibiota on the surfaces of the mangrove leaves. The densities of some of the common molluscs found in this zone are given in Table 5. Though not numerically abundant the pulmonate *Onchidium damelli* was common in this zone.

Crabs were common in the mangroves and several species occur, *Sesarma erythrodractyla*, *Paragrapsus laevis*, *Heloeius cordiformis* and *Scylla serrata*. Some

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indication of the densities of these crabs observed feeding at night were given in the preceding section on marine invertebrates. The amphipod *Ampithoe* sp. was also common. Odum and Heald (1972) have shown that amphipods are important in the shredding of mangrove leaves. The shredding makes the leaves available to other detritus feeders. A single specimen of *Laomedea bealyi* was found on the surface of the mud at low tide during night collecting.

The polychaete fauna of the mangroves was virtually restricted to the channels and creek which flow through the mangroves, *Nereis (Hediste) diversicolor* and *Nephtys australiensis* were the most common species. The nereid *Neanthes vaalii* was found in the oyster communities at the bases of the mangrove trees.

Between 0.8m above low water to 1.2m depth contour, the shallows of Careel Bay are dominated by the marine angiosperm, *Zostera capricornis* (Fig. 7). *Halophila ovalis* was also present, though during the period of our survey it was not abundant. Among the *Zostera* were the red algae, *Gracilaria verrucosa*, and *Hypnea valentiae* and the brown alga *Dictyota dichotoma*. The algae are seasonal in occurrence and reach a maximum density in late spring and early summer. The blades of *Zostera* commonly supported a well developed epibiota community.

The *Zostera* zone can be conveniently divided into an upper and lower zone (see Fig. 4). The junction of the upper and lower *Zostera* occurs at Indian Spring low water. The lower zone was distinguished by a greater biomass of *Zostera* and the presence of the Sydney cockle, *Anadara trapezia*. The upper zone was characterized by a sparser plant growth and the occurrence of the Hercules club-shell or Sydney whelk *Pyrazus ebeninus*. Biomass measurements were not made in the upper *Zostera*. Though the *Zostera* of the lower zone gave the impression of a fairly uniform density, biomass measurements indicated a rather patchy distribution (mean 80.60 gm/m² SD ± 90.32). Such figures are within the range that McRoy (1970) found. The *Zostera* in the upper zone was noticeably patchy with much bare space. In the lower *Zostera* and in the *Posidonia* zone there were scattered circular spots devoid of plant growth and animal life. The origin of these spots is not known, but may be resting places for rays.

a. Upper *Zostera*

Far greater numbers of species and individuals were present in this zone in comparison to the sandy beach. Polychaetes and molluscs dominated the samples both in terms of numbers of species and individuals.

The dominant polychaete in all samples was *Nephtys australiensis* but in the November samples, large numbers of juvenile *Haploscoloplos* n. sp. were also present (Table 6). Also in November, large numbers of *Nereis (Hediste) diversicolor* were found although this species was previously only found in small numbers (e.g. February).

The most abundant species of molluscs were *Macoma deltoidalis* and *Nassarius burchardi* which was commonly found grazing on the epibiota of the *Zostera*. In November, many juveniles of *M. deltoidalis* were collected. Similarly numerous juveniles of *Notospisula parva producta* were present in June and November samples. Two juveniles of *Anadara trapezia* were found in February and June but no adults were found in this zone. Many of the other molluscs were present in very few numbers e.g. *Laternula tasmanica*, *Eumarcia fumigata*, and *Austrocochlea obtusa*.

The crustaceans were represented by more species than in any of the preceding zones, but many species were collected in small numbers (Table 6). The amphipod *Melita* sp. was numerous in two samples collected in November, but absent from most others. Relatively similar numbers of *Macrophthalmus setosus* and *M. crassipes* were found in both the upper and lower *Zostera* zones. The numbers of *M. setosus* increased greatly in June in both zones. In the June and November samples, species A and B were collected (see note in marine invertebrates section). Both these species were more abundant in the lower *Zostera*.

b. *Lower Zostera*

Quantitative samples were collected only in June and November. In February no division of the *Zostera* into upper and lower zone was made and all the samples collected in February were from the upper *Zostera*.

The lower *Zostera* was the richest of all the zones sampled (Table 6) with an average of 14-15 species per sample. Polychaetes dominated this zone. The capitellids *Notomastus hemipodus* and *Barantolla lepte* were particularly abundant. Less common but invariably present were the terebellids, *Lysilla pacifica* and *Rhinothelepus lobatus*. In November large numbers of juvenile *Owenia fusiformis* were present indicating successful breeding had occurred between June and November. The *Zostera* blades were covered in *Spirorbis* sp. but no attempt to quantify them was made. Virtually all the species of polychaetes which were found in the upper *Zostera* also occurred in the lower *Zostera*, but additional species noticeably the terebellids and spionids were restricted to the lower *Zostera*.

The rich mollusc fauna of this zone was characterized by *Macoma deltoidalis*, *Nassarius burchardi* and *Anadara trapezia*. In June and more notably in November very small specimens (5-8 mm in length) of *A. trapezia* were found. The volume of sediment collected in these quantitative samples 9000cm³ was insufficient to collect adequate numbers of adults for determination of their relative abundance. Using a quadrat 0.25 m² in size, the average density of *A. trapezia* was 8.59/m², although there was some evidence of clustering. Within a quadrat anything from 0.6 specimens could be found. The adults range in size from 42-64 mm in height and no obvious year groups could be distinguished (Fig. 9). While collecting *A. trapezia* from 40 quadrats, two specimens of the echinoderm *Astropecten polycanthus* were found.

TABLE 6

SEASONAL DATA FROM SANDY BEACH AND WEED BEDS

(For each species, the mean value and standard deviation of number of animals found in 10 consecutive quantitative samples is given).

	Sandy Beach			Upper Zostera			Lower Zostera			Posidonia		
	Feb.,	June,	Nov.,	Feb.,	June,	Nov.,	June,	Nov.,	Feb.,	June,	Nov.,	
Polychaetes												
<i>Paralepidonotus cf. amputiferons</i>												
F. Phyllodoctidae												
Syllid sp. 1						0.1, 0.31	0.2, 0.4					
Syllid sp. 2							0.1, 0.31				0.1, 0.31	
<i>Australonereis ehlersi</i>	0.9, 1.41	12.9, 10.0	14.3, 10.0		0.2, 0.63		0.2, 0.63	0.1, 0.32				
<i>Ceratonereis mirabilis</i>		0.1, 0.32	0.1, 0.32	0.1, 0.32			0.3, 0.48	0.2, 0.47				
<i>Nereis (Hediste) diversicolor</i>				0.7, 0.95			0.2, 0.47	0.2, 2.26				
<i>Nephtys australiensis</i>	0.9, 1.0	0.3, 0.48					0.8, 1.03	0.2, 2.26	0.4, 0.96		0.1, 0.32	
<i>Glycera americana</i>							0.2, 0.42		0.1, 0.32		0.7, 0.67	
<i>Marphysa sanguinea</i>							0.3, 0.67	0.1, 0.32	0.1, 0.32		0.3, 0.48	
<i>Lumbrineris latreilli</i>								0.1, 0.32	0.2, 0.47		0.1, 0.32	
<i>Haploscoloplos n. sp.</i>	4.0, 1.9	2.5, 1.78	10.9, 4.24			11.8, 10.2		0.1, 0.32	0.1, 0.32		0.1, 0.32	
<i>Naineris</i> sp.							0.1, 0.32		0.9, 0.99		0.2, 0.63	
<i>Phylo</i> sp.							0.4, 1.27				0.4, 0.69	
<i>Scoloplos</i> sp.											0.1, 0.32	
<i>Dispio</i> sp.											0.1, 0.32	
<i>Malacoceros</i> sp.											0.6, 0.96	
<i>Polydora</i> sp.			0.2, 0.42				2.1, 2.33		0.2, 0.42		1.9, 2.3	
<i>Priotospio</i> sp.							0.7, 1.25	0.3, 0.67			0.8, 1.03	
<i>Magelona</i> sp.	0.3, 0.67										0.1, 0.32	
<i>Chaetopterus</i> sp.											0.1, 0.32	
<i>Cirratulus</i> sp.											0.2, 14.94	
<i>Pherusa</i> sp.											0.2, 0.42	
<i>Armanidia intermedia</i>							0.1, 0.32				1.0, 1.34	
<i>Barantolla lepte</i>	0.1, 0.31	0.3, 0.67		0.4, 1.0	1.3, 1.56		1.9, 1.19	1.6, 1.34	0.2, 0.42		0.6, 0.96	
<i>Capitella capitata</i>	0.1, 0.32			0.1, 0.32	0.1, 0.32						1.2, 1.68	
<i>Heteromastus</i> sp.							0.1, 0.32		0.2, 0.42		0.3, 0.48	
<i>Mediomastus</i> sp.							7.5, 4.14	5.4, 1.95	2.1, 1.66		0.1, 0.32	
<i>Notomastus hemipodus</i>				0.1, 0.32	2.0, 1.89	0.8, 0.92					1.8, 1.32	

	Sandy Beach		Upper Zostera		Lower Zostera		Postidonia		
	Feb.,	June,	Nov.,	Feb.,	June,	Nov.,	Feb.,	June,	Nov.,
<i>Arenicola bombayensis</i>					0.1, 0.32				
<i>Owenia fusiformis</i>		0.1, 0.32			1.3, 1.59	1.0, 1.6	0.1, 0.32	0.4, 0.96	
<i>Amphictetis</i> sp.					0.1, 0.32	0.5, 0.97	0.2, 0.42	0.2, 0.42	
<i>Lysippides</i> sp.									
<i>Samytha</i> sp.						0.2, 0.42			
<i>Lysilla pacifica</i>						1.5, 0.85		0.1, 0.32	0.2, 0.42
<i>Rhinothelopus lobatus</i>						1.9, 1.66		0.2, 0.42	0.2, 0.42
<i>Thelepus setosus</i>							0.1, 0.32		
<i>Pista</i> sp.									0.3, 0.67
Coelenterates									
<i>Edwardia</i> sp.					0.4, 0.69				0.1, 0.32
Turbellarian					0.2, 0.42				
Nemertean									
Heteronemertean									
Phoronid									
Crustaceans									
F. Anthuridae									
<i>Cymodoce coronata</i>								0.1, 0.32	
<i>Sphaeromidae</i> sp. A								0.1, 0.32	
<i>Ampithoe</i> sp.								0.1, 0.32	1.4, 1.51
<i>Melita</i> sp.					1.9, 3.78				0.9, 1.1
<i>Liljeborgia</i> sp.									0.1, 0.32
<i>Urohaustorius</i> sp.									
<i>Penaeus plebejus</i>									
<i>Penaeus</i> sp.									
<i>Macrobrachium intermedium</i>									
<i>Alpheus euphosyne</i>									
<i>Alpheus</i> sp. B									
<i>Hippolyte tenuirostris</i>									
<i>Callinassa</i> sp.									
<i>Halicarcinus ovatus</i>									
<i>Portunus pelagicus</i>									
<i>Thalamita sima</i>									
<i>Heteropanope serratifrons</i>									
<i>Macrophthalmus setosus</i>									
<i>Macrophthalmus crassipes</i>									
<i>Macrophthalmus</i> cf. <i>punctulatus</i>									
<i>Macrophthalmus</i> sp. 1									
Species A									

Species	Sandy Beach			Upper Zostera			Lower Zostera			Posidonia		
	Feb.,	June,	Nov.,	Feb.,	June,	Nov.,	June,	Nov.,	Feb.,	June,	Nov.,	
Species B												
<i>Australoplax tridentata</i>			0.1, 0.32		0.5, 0.97	0.1, 0.32	0.3, 0.48	1.8, 1.03				
<i>Mictyris longicarpus</i>	0.8, 1.03	2.0, 1.63	9.8, 4.47						0.6, 1.26			
Molluscs												
<i>Anadara trapezia</i>				0.1, 0.32	0.1, 0.32		0.5, 0.52	0.5, 0.71			0.1, 0.32	
<i>Xenostrobus securis</i>				0.3, 0.67	1.6, 1.42		0.1, 0.32					
<i>Laternula tasmanica</i>				0.2, 0.42		0.4, 0.69	2.0, 1.94	0.8, 0.78				
<i>Cavatidens omissa</i>	0.1, 0.32					0.1, 0.32	1.1, 1.52	1.1, 1.52	0.3, 0.67		0.2, 0.42	
<i>Mysella</i> sp.						0.1, 0.32	0.1, 0.32				0.2, 0.63	
<i>Eumarcia fumigata</i>	0.1, 0.32	0.1, 0.32					0.3, 0.67	0.1, 0.32				
<i>Tapes watlingi</i>							0.3, 0.67	0.1, 0.32				
<i>Notospisula parva producta</i>	0.1, 0.32	10.1, 16.10		1.3, 2.12	2.6, 3.02		0.3, 0.67	0.1, 0.32			0.2, 0.42	
<i>Florisarka onuphria</i>		0.1, 0.32									0.1, 0.32	
<i>Macoma deltoidalis</i>	0.1, 0.32			3.5, 1.9	3.1, 1.52	4.5, 3.41	3.5, 2.36	10.1, 6.67	0.6, 1.26		0.2, 0.42	
<i>Austrocochlea obtusa</i>				0.6, 1.26		0.5, 0.84						
<i>Calliostome australe</i>											1.0, 1.41	
<i>Liota</i> sp.					0.1, 0.32	0.1, 0.32	0.1, 0.32				1.8, 2.14	
<i>Diala</i> sp.												
<i>Cacozeliana laceritina</i>	0.2, 0.42					0.1, 0.32	0.5, 1.08	0.9, 0.87	0.1, 0.32		0.1, 0.32	
<i>Pyrazus ebenensis</i>					0.1, 0.32	0.1, 0.32					2.6, 1.78	
<i>Epitonium</i> sp.						0.1, 0.32	0.1, 0.32				4.8, 2.34	
<i>Conuber sordidum</i>						0.1, 0.32	0.1, 0.32					
<i>Conuber</i> sp.												
<i>Nassaritis burchardi</i>												
<i>Bedeva hanleyi</i>	0.63, 0.2			6.9, 4.93	3.7, 2.2	1.4, 1.71	6.3, 4.99	9.0, 11.6	0.1, 0.32		0.3, 0.48	
<i>Salinator</i> sp.	0.3, 0.67											
F. Dorididae												
<i>Haminoea wallissi</i>				0.1, 0.32			0.1, 0.32					
Fish												
<i>Centropogon australis</i>					0.1, 0.32	0.1, 0.32					0.1, 0.32	
<i>Rhabdosargus sarba</i>											0.1, 0.32	
<i>Gerres ovatus</i>				0.2, 0.42								
<i>Bathygobius krefftii</i>												
<i>Favonigobius lateralis</i>				0.5, 0.84			0.1, 0.32				0.1, 0.32	
<i>Lizagobius olorum</i>				0.2, 0.42								
Total Nos. of individuals	96	290	347	314	293	469	395	512	75	184	156	
Total Nos. of species	16	15	8	19	24	31	46	27	23	42	31	

In comparison with the molluscs and polychaetes, crustaceans were poorly represented in this zone. The amphipod *Ampithoe* sp. and the crabs *Macrophthalmus setosus* and species A and B were the most abundant species.

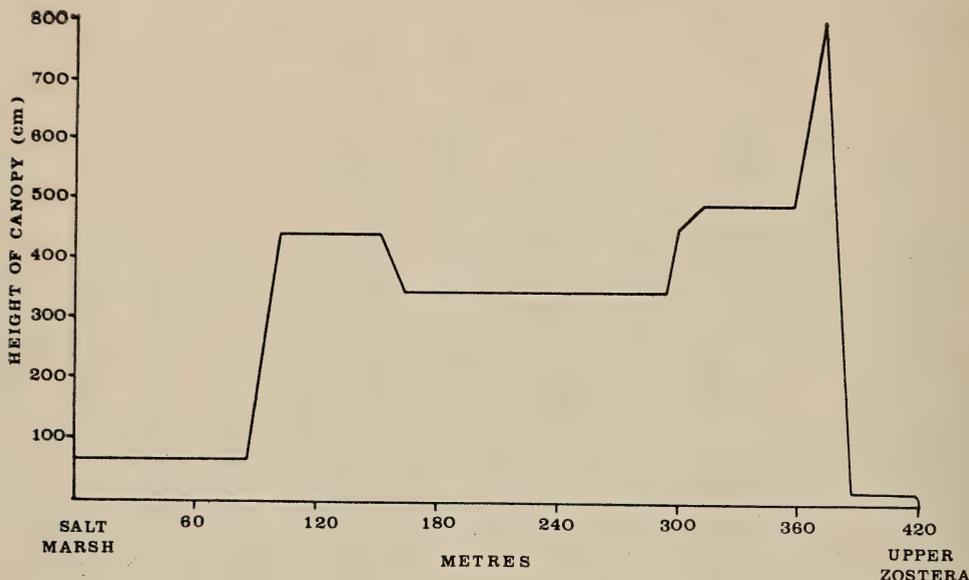


Fig. 9. Size distribution of the Sydney Cockle *Anadara trapezia* at Careel Bay.

Posidonia

The *Posidonia* flats extend from 1.2m depth contour to a depth of approximately 11m. The marine angiosperm, *Posidonia australis*, dominates this zone and other plant life is absent or epiphytic. Collections of epiphytes on the leaves of *Posidonia* were made and sorted, but these have not yet been identified. Polychaetes and small crustaceans were well represented in these collections. From 11m, plant growth becomes increasingly sparse and gives way to a sandy sea floor. The depth to which *Posidonia* can grow is determined by water clarity and its occurrence in 10-12 m of water in Careel Bay attest to the lack of turbidity or of the intrusion of Hawkesbury River water. Biomass measures in the *Posidonia* zone showed less variation than those made in the lower *Zostera* (287g/m^2 - $\text{SD} \pm 57.88$).

The *Posidonia* zone had a large number of species but relatively few individuals in any one sample in comparison to the lower *Zostera* zone (Table 6). This was particularly true of polychaetes where many species were represented only by one or two individuals e.g. *Armandia intermedia*, *Mediomastus* sp.,

FAUNA OF CAREEL BAY

Chaetopterus sp. and *Cirratulus* sp. This zone had some very large species of polychaetes present, *Glycera americana*, *Marphysa sanguinea* and *Chaetopterus* sp. and it is possible that the biomass of polychaetes would be greater in the *Posidonia* than in the lower *Zostera*, even though far fewer species are present.

Molluscs were poorly represented in this zone and the only numerically abundant species was *Cacozeliana lacertina*. Similarly crustaceans were poorly represented in the quantitative samples but this was probably a reflection on sampling techniques. As in the lower *Zostera* the amphipod *Ampithoe* sp. was common.

DISCUSSION

Without measuring energy flow, comments on the ecology of Careel Bay and its importance to the total estuary must necessarily be speculative. However, to judge by the number of species, the presence of many juvenile fish and the total standing biomass of plants and animals in Careel Bay, there is a significant production of organic matter in the salt marsh, mangrove and sea grass habitats. The invertebrate fauna of the salt marsh, mangrove and sea grass habitats is dominated by detritus feeding animals. It appears similar to the mangrove-invertebrate system described in detail for Florida by Odum and Heald (1972). Organic matter in the form of leaves and fruits enter the estuary where they are attacked by bacteria, fungi and small invertebrates. These break down the material to a size which can be ingested by other detritus feeders. Through a long series of steps in which the original matter of a mangrove leaf may be reingested many times, the complex molecular structure of the leaf is broken down and its energy released. The detritus feeders are in turn fed upon by predators. A later paper will discuss the possible reasons for the zonation of animals in the Bay and the potential food web operating both within and between the zones.

Our results have shown that Careel Bay is a very rich area in terms of numbers of species present. A similar ecological and geographical area to Careel Bay is Towra Point in Botany Bay which has been sampled by Weate (pers. comm.) using the same quantitative methods used in Careel Bay. She found in June, 30 species of animals in the *Zostera* and 13 species in the *Posidonia* weed beds. By comparison in Careel Bay, 51 and 54 species were found respectively in the *Zostera* and *Posidonia* weed beds. The reasons for the greater number of species being present in Careel Bay are not fully understood but parts of Botany Bay are heavily industrialized and extensive dredging occurs. Dredging must have deleterious effects on pelagic larvae which pass through the dredge. The majority of animals found in estuarine situations have pelagic larvae.

We have looked at other areas in the Hawkesbury-Broken Bay system, notably Patonga Creek (Broken Bay), Spectacle Island (Hawkesbury River) and Riley's Island (Brisbane Waters), which have many fewer species compared to Careel

Bay. However, individual species (e.g. *Macrophthalmus setosus*, *Mictyris longicarpus* and *Callianassa* sp. achieve considerably greater population densities on the tidal flats of Patonga than at Careel Bay.

One of us (Hutchings, 1974) has sampled in Wallis Lake, N.S.W. This is a coastal lagoon continually open to the sea but at times it receives large volumes of freshwater. A total of 32 species of polychaetes were found along the eastern shores of the lake in the weed beds of *Zostera* and *Halophila*. All the species present in Wallis Lake are also present in Careel Bay. Weate (pers. comm.) has sampled in the adjacent Smiths Lake, which is often closed to the sea. Sampling in December, using a hand operated corer, a total of 28 animal species were found. Similarly, surveys conducted by the N.S.W. Division of the Australian Littoral Society have shown that the numbers of species of animals decreases progressively up the estuary as the salinity falls. All the areas mentioned above have some species in common, e.g. Polychaetes, *Australonereis ehlersi*, *Nereis (Hediste) diversicolor*, *Marphysa sanguinea*, *Haploscoloplos* sp. and *Notomastus hemipodus*; Molluscs, *Nassarius jonasi*, *Pyrazus ebeninus*, *Macoma deltoidalis*; Crustaceans, *Paragrapsus laevis*, *Macrophthalmus* sp. and *Halicarcinus ovatus*.

It appears that Careel Bay represents the richest estuarine area yet sampled in N.S.W. This can partially be attributed to its almost totally marine situation, but other factors may be involved. We hope to elucidate these other factors by continuing to survey wetland areas on the N.S.W. coast.

It is very difficult to compare our work with studies done overseas as sampling techniques vary widely, but some comments can be made on geographically similar temperate areas. Day (1967) working on South African estuaries has found that estuaries vary in the richness of their fauna and he attributes this to the amount of freshwater entering the estuary and to the clarity of the water. The richest area comparable to Careel Bay that he has studied is the Knysna estuary which has clear water, allowing dense beds of sea grasses to flourish. Only small quantities of fresh water enter the river throughout the year. Other estuaries in the same temperate region are subjected to flooding and have eroding river banks, reducing clarity of water, hence weed growth is diminished and far fewer species of animals are present. Day (1967) also suggests that a wide opening to the sea (such as Careel Bay has) is important in maintaining water exchange and tidal movement. Day has recorded 350 species from Knysna estuary including, 69 polychaetes, 12 crabs, and 40 fishes. Considering that Careel Bay in comparison is a very small area and only the larger components of the fauna have been collected, the number of species of polychaetes is of the same order of magnitude. The number of species of polychaetes (at present 46) seems certain to increase, once the epibiota of the *Posidonia* and *Zostera* is analysed. Careel Bay is thus similar in species diversity to temperate South African estuaries and is the richest wetland area yet sampled in New South Wales.

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APPENDIX I

Insects Recorded from Careel Bay, N.S.W.

Diptera

Family:

Tephritidae

Euphranta n. sp.

Dacus (Strumeta) tryoni

Family:

Platystomatidae

Rivellia n. sp.

Family:

Lauxaniidae

Panurgopsis n. sp.

Prochaetops n. sp.

Chilocryptus sp.

Trigonometopsis n. sp.

Trigonometopus sp.

Family:

Carnidae

Australimyza sp.

Family:

Milichiidae

Desmometopa sp.

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Family:

Cryptochetidae
Cryptochetum sp.

Family:

Tethinidae
Dasyrhicnoessa sp.

Family:

Canaceidae
Canace sp.
Xanthocanace sp.

Family:

Chloropidae
Merodonta sp.—Southern Record for genera
Pemphigonotus sp.—Southern Record for genera

Lepidoptera

Family:

Oxychirotidae
Cenoloba oblitteratis

Hymenoptera

Family:

Ichneumonidae
Echthromorpha intricatoria Fabricius
Lissopimpla excelsa Costa
Netelia producta Brullé
Eriborus sp. (parasite of *Coenoloba* sp.)
Sphinctus sp.

Family:

Braconidae
Priaspis sp.
Chelonus unimaculatus Szepligeti—first record since original description
Chelonus australiensis Szepligeti—first record since original description
Phanerotoma australiensis Ashmead
Apanteles ruficrus Haliday
Microgaster sp.
Opius sp. (parasitic on *Euphranta* sp.)

Family:

Evaniidae
Evania appendigaster Linné

Family:

Sphexidae
Sphex fumipennis
Sphex globosus
Sceliphron laetum
Isodontia nigella
Isodontia sp.
Larra sp.
Pison sp.

Family:

Tiphiidae
Diamma bicolor

Family:

Vespidae
Polistes tasmaniensis

Family:

Apidae

Apis mellifera

Many of these insects which have been identified only to genus, are new species.

APPENDIX II

The following fishes were collected in Careel Bay at various times of the year, and in the Hawkesbury River estuary on November 23, 1972, at low tide by 20' seine. The following are the individual collecting localities: (1) beach at eastern side of Dangar Island; (2) Fisherman's Beach, Cowan Creek, Broken Bay; (3) Head of Jerusalem Bay, Cowan Creek; (4) Careel Bay. The numbers after the species refer to the various localities.

- | | |
|--|--|
| Family Urolophidae—stingrays | Family Sparidae—bream, tarwhine, snapper |
| <i>Urolophus testaceus</i> 2 | <i>Acanthopagrus australis</i> 2, 3 |
| Family Clupeidae—sardines, herrings, sprats | <i>Rhabdosargus sarba</i> 2, 3, 4 |
| <i>Hyperolophus vittatus</i> 2 | Family Mullidae |
| Family Syngnathidae—pipefishes and seahorses | <i>Upeneichthys tragula</i> 4 |
| <i>Hippocampus</i> sp. 4 | Family Mugilidae—mullet |
| <i>Stigmatophora nigra</i> 2, 4 | <i>Myxus elongatus</i> 1, 2, 3 |
| <i>Urocampus carinirostris</i> 1, 3 | Family Pomatomidae—tailor |
| Family Hemiramphidae—garfishes | <i>Pomatomus saltatrix</i> 2 |
| <i>Hyporhamphus ardellio</i> 2 | Family Clinidae |
| Family Atherinidae—hardyheads and blue eyes | <i>Cristiceps australis</i> 4 |
| <i>Pranesus ogilbyi</i> 2 | Family Gobiidae—gobies |
| <i>Taeniomembras microstomus</i> 3 | <i>Arenigobius frenatus</i> 1, 3, 4 |
| <i>Pseudomugil signifer</i> 3 | <i>Bathygobius krefftii</i> 1, 2, 3, 4 |
| Family Scorpaenidae—fortesques and red perches | <i>Favonigobius exquisitus</i> 3, 4 |
| <i>Centropogon australis</i> 1, 2, 3, 4 | <i>Lizagobius olorum</i> 3, 4 |
| Family Centropomidae—glass perches | <i>Nesogobius pulchellus</i> 4 |
| <i>Velambassis jacksoniensis</i> 1, 2, 3, 4 | <i>Redigobius macrostomus</i> 1, 3 |
| Family Platycephalidae—flatheads | Family Bothidae—left eyed flounders |
| <i>Platycephalus</i> sp. juv. 2 | <i>Pseudorhombus jenynsii</i> 1 |
| Family Enoplosidae—old wives | Family Balistidae |
| <i>Enoplosus armatus</i> 2 | <i>Meuschenia skotlower</i> 4 |
| Family Theraponidae—grunters | Family Aluteridae—leatherjackets |
| <i>Pelates sexlineatus</i> 1, 3, 4 | <i>Navodon skottowei</i> 2, 3 |
| Family Carangidae | <i>Monocanthus macrolepis</i> 4 |
| <i>Caranx</i> sp. 4. | Family Tetraodontidae—toados |
| Family Gerridae—silver biddies | <i>Torquigener hamiltoni</i> 2, 3, 4 |
| <i>Gerres ovatus</i> 3, 4 | Family Diodontidae—porcupine fishes |
| Family Scorpidae—luderick, sweep | <i>Dicotylichthys myersi</i> 2, 3 |
| <i>Girella tricuspidata</i> 3, 4 | <i>Diodon punctulatus</i> 4 |

Population Movements of the Agamid Lizard *Amphibolurus nobbi*

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Amphibolurus nobbi nobbi Witten is associated with arenaceous soils. It occurs commonly in the granite belt of southern Queensland, is present in many of the sandy granite areas of northern N.S.W. and also inhabits sand dunes of the northern N.S.W. coast (Witten, 1972). During a study of its taxonomic status and thermoregulation, population movements became evident and are presented here.

Snout-vent lengths were measured on preserved specimens, and these were related to the date and area of collection. Specimens of less than 35 mm s-v length were considered hatchlings, specimens from 35 to 50 mm as juveniles and specimens over 50 mm as adults. These categories were established on the basis of (1) minimum size of breeding adults, (2) the condition of the yolk sac scar, and (3) the size at which yellow and red secondary colouration first appeared. Only specimens from the northern tablelands of N.S.W. were studied, as breeding areas outside this region were not so clearly defined topographically.

Two types of area were inhabited, breeding areas, and areas into which animals dispersed. Three breeding areas are considered in this study. All were estimated to have an area of between one and two hectares. Each consisted of a steep north-facing slope. Similar, though less extensive data were obtained from areas outside the region.

In Autumn and Spring large numbers of adult *A. n. nobbi* are found in the breeding areas (Fig. 1) but desert them during the summer months. Adults emerge from hibernation in the first half of October. Dispersal of adults from the breeding areas takes place before the second week of December. Adults return to the breeding areas in autumn, from mid-February to the first week of March. Adults retreat for hibernation in late March or early April.

Emergence of hatchlings occurs from mid-October until mid-April. There are peaks in numbers of hatchlings in October and March-April. The emergence of hatchlings in spring (October) indicates that eggs or young overwinter in the soil. As it is normal for smaller individuals to emerge earlier in the spring (Cowles, 1941; Fitch, 1956), emergence of hatchlings later than adults may indicate that eggs complete their development in the spring and then hatch.

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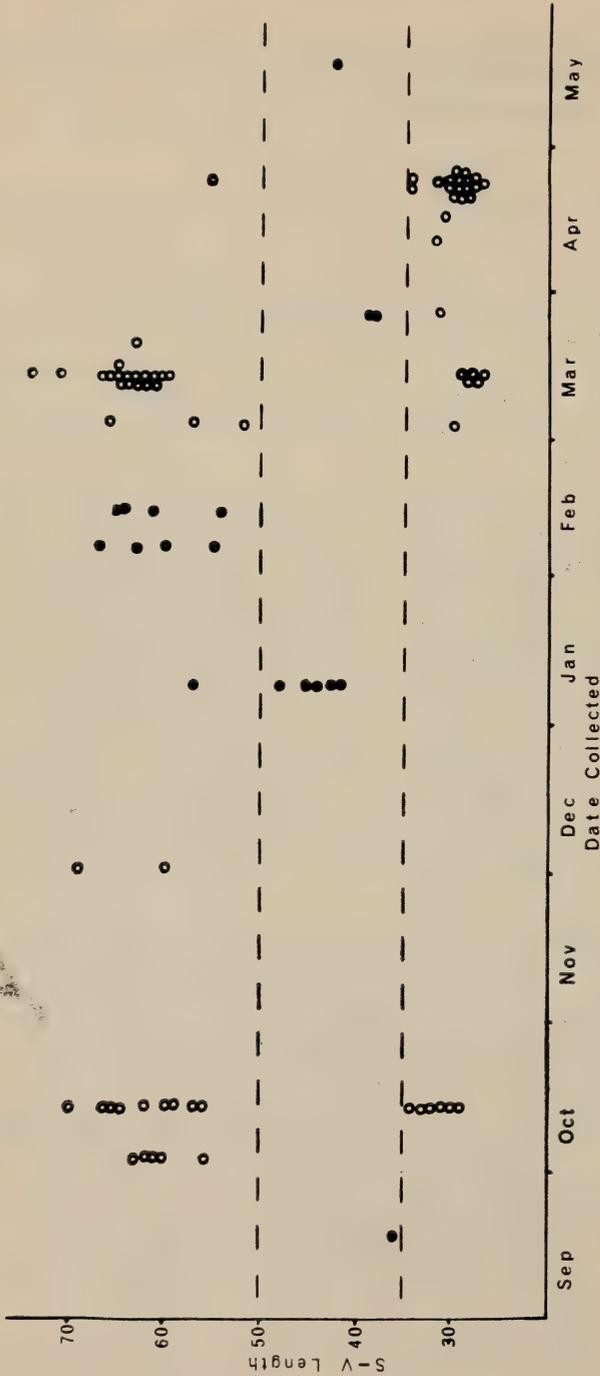


Fig. 1. Snout-vent lengths of specimens plotted against the date of their collection. Open circles designate specimens from breeding areas, closed circles indicate non-breeding areas. Horizontal lines divide categories of hatchlings, juveniles and adults. Note that all juveniles are from non-breeding areas, and that adults collected in January and February are from outside breeding areas.

POPULATION MOVEMENTS OF *AMPHIBOLURUS*

Similar observations have been made on several species of turtles (Sexton, 1957; Gibbons, 1969), but to the author's knowledge no such observations are available for lacertilians.

Hatchlings with fresh yolk sac scars were from 25 to about 32 mm in s-v length. They move out of the breeding area almost immediately; no juvenile of more than 35 mm s-v was collected within a breeding area. Juveniles apparently grow to adult size outside the breeding areas, and migrate to such sites upon attaining sexual maturity. Bradshaw (1971) observed juvenile emigration from an area dominated by adults in another agamid species, *A. ornatus*. However, this species demonstrates territorial behaviour and this movement was explained by Bradshaw on the basis of adult aggression against juveniles. *A. n. nobbi* is apparently not territorial in behaviour, and at least some juveniles vacate the breeding area while it is unoccupied by adults.

Territorial behaviour has been observed in several species of *Amphibolurus* (Carpenter *et al.*, 1970; *A. inermis*, *A. barbatus*, *A. muricatus*). Neither in the field, nor under confined laboratory conditions was territorial behaviour ever observed in *A. n. nobbi*. The presence of bright colouration (which is largely lacking in its territorial relatives) is puzzling, but may be involved in courtship displays; however, none were observed. This hypothesis is supported by the fact that sexual dichromatism is much more pronounced during the spring months than at other times of the year.

Migration to oviposition areas has been observed in *Iguana iguana* (Hirth, 1963; Rand, 1968); in that species only gravid females undertake the migration. This movement is of short duration, and activity in the oviposition area is concerned with finding a suitable nest site, nest digging and oviposition. Spent females return to their usual habitat within a few days after oviposition (Montgomery *et al.*, 1973). In *A. n. nobbi* the entire adult population is resident in the breeding area for 4 of the 6½ month adult activity season. *A. n. nobbi* also differs from *I. iguana* in that the breeding and non-breeding areas are basically similar, differing in gradient of slope and in the aspect presented to the sun.

There was no direct observation of individuals moving between two areas. A number of specimens were collected at a distance of six km. from known breeding areas in two localities, and one was taken some fifteen km. from the nearest known breeding area (coastal sand dunes). These observations suggest that the lizards are capable of moving relatively long distances, but further study is required to obtain reliable estimates.

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Capture and Marking of the Platypus, *Ornithorhynchus anatinus*, in the Wild

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We began trapping platypus in early 11971 as part of our investigation of temperature regulation (T.R.G.) and reproductive physiology (F.N.C.) in this species. Standard gill nets have been used in the past (Temple-Smith personal communication) to capture platypus but accidental drowning of some animals has always been a problem with the use of these nets. Over the last two years we have been able to modify this technique to minimise the risk of drowning animals.

As part of our studies we wish to observe animals in the wild to determine how long platypus remain in water and to investigate the relationship of this to ambient temperatures. This requires the capture and identification of

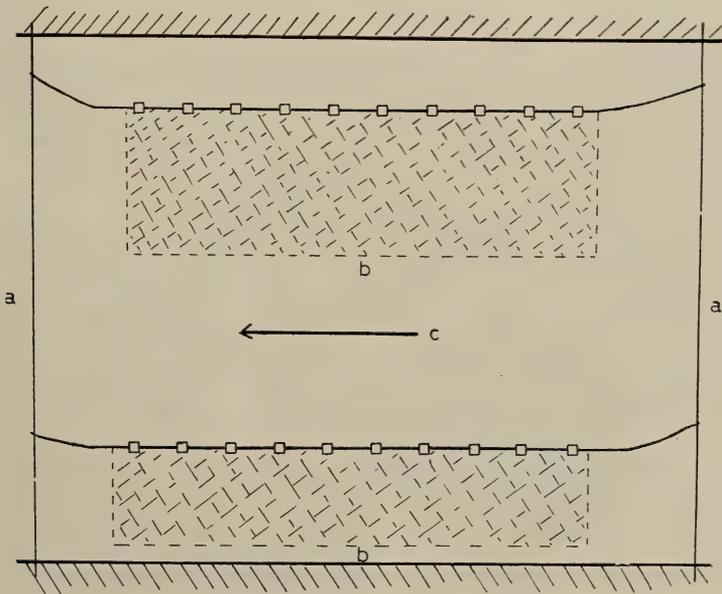


Fig. 1. Placement of nets in a stream
a. ropes b. nets c. direction of water flow

platypus with visible, individual marks. With a view to possible longer term studies these animals are also being marked with leg bands.

The increasing interest in the biology of the platypus in recent years has induced us to write this short paper to make our experiences available to others.

For *capture* we normally use two $3\frac{1}{8}$ -3" mesh nets laid in the stream or lake parallel to the bank (Fig. 1). These nets vary between 50 and 150 feet in length and in deep water nets having a drop of 8 feet are used, while in shallow water or over weed beds nets of 4 feet drop are necessary.

The standard fishing net has floats on the top and weights on the bottom. We have modified our nets by painting the floats white and removing the weights. The white floats allow the nets to be seen easily in the beam of a spotlight to facilitate checking at regular intervals during the night. The lack of weights makes it easier for an entangled animal to carry the net to the surface. It is necessary to use some weights in areas of stronger currents. However, the selection of the waterway is very important, and areas of rapid water flow, large numbers of snags, or rapidly changing water levels should be avoided. In such areas the risk of drowning animals is high and in our experience capture rates are usually low. In areas where the water temperature is very low, the need to remove animals from nets as soon as possible after capture is an important consideration. However, platypus are also very susceptible to heat stress and should be kept cool after capture and during transport in hot weather.

Snags, fish and other heavy objects caught in the nets account for quite a number of drownings. To lessen this hazard the nets are lifted every hour, to release fish and remove inanimate objects. Brief scanning of the nets every 10-15 minutes with a spotlight allows the detection of movement and seems to have no marked effect on capture rates.

Since we began using unweighted nets in December 1972, we have caught 40 platypus (which have been marked and released except for the small number of animals taken back to be maintained in the laboratory) without a single incident of drowning. It must be noted however that the capture of platypus in the wild is far from simple. It is time consuming, arduous and rates of capture can be quite low in some areas. The procedures outlined above only serve to show that these animals *can* be caught safely if certain precautions are taken.

Visible marks consist of adhesive bandage tape, painted with oil-based fluorescent paint attached to the tail. Plain colours are visible with field glasses at distances of up to 100 yards, and patterns can be distinguished at shorter distances. When applied firmly to the animal they will stay attached for around 10 days to a month. These tail marks are satisfactory for individual recognition of animals for short term observation work. We also intend to use them to allow visual location of animals to which transmitters have been attached. This

CAPTURE AND MARKING OF THE PLATYPUS

should remove the necessity to locate an animal by the radio signal and allow the use of transmitters with only a moderate range.

Leg bands of stainless steel rings 2.0 cm in diameter and 0.5 cm in width are applied to the shank of the rear foot using pliers to overlap the ends (Fig. 2). These are inscribed with a number and address. These bands were tried on captive animals before being used to mark wild ones. No damage to the legs of two captive platypus occurred and three wild animals caught after being banded for 7 months also showed no ill effect from the bands. These bands can be seen when an animal grooms itself in the water, but they are of limited use for observational purposes. They can, however, be used in mark and recapture studies.

We wish to thank Stockbrands Pty. Ltd., Mt. Hawthorn, W.A. for manufacturing the bands to our specifications. Bryan Shadbolt made the initial suggestion to remove all the weights from one of our nets. Thanks also go to various technicians and friends who have spent many hours helping to tend nets. The N.S.W. National Parks and Wildlife Service and N.S.W. State Fisheries Branch are acknowledged for allowing us to trap platypus in N.S.W. Part of the support for this work was provided by a grant from the Australian Research Grants Committee.



Fig. 2. Marked animal showing leg band
(photo: Bob McBlain).

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***Eptatretus longipinnis*, n. sp., A New Hagfish (Family Eptatretidae) from South Australia, with a Key to the 5-7 Gilled Eptatretidae.**

R. STRAHAN

Australian Museum, College St., Sydney, N.S.W. 2000

ABSTRACT

A new species of hagfish, *Eptatretus longipinnis* (Family Eptatretidae) based on a specimen from coastal waters near Robe, South Australia, is described. The species differs from other members of the genus in having a well developed ventral fin-fold extending into the branchial region. The genus *Paramyxine* is regarded as a junior synonym of *Eptatretus*. A key is given to the species of *Eptatretus* having 5-7 pairs of gills.

INTRODUCTION

Until 1971 no hagfishes had been recorded from Australian waters. Since then a number of specimens of *Eptatretus cirrbatus* have been taken from the Pacific Ocean off the coast of New South Wales in deep trawls (300-700m). Also in 1971, a quite different hagfish was taken from the south-eastern Indian Ocean near Robe, South Australia from a depth of approximately 40m. The hagfish had burrowed into the flesh of the abdomen of a spiny lobster and was still embedded when the lobster was brought to the surface. The specimen, preserved in alcohol, was forwarded to the author by Dr. C. J. M. Glover of the South Australian Museum.

DESCRIPTION OF *EPTATREUS LONGIPINNIS*, N. SP.

Holotype: A specimen 422mm long from south-eastern Indian Ocean off Robe, South Australia (149°43'E, 37°10'S) at depth of approximately 40m. In the South Australian Museum, Adelaide, South Australia (registration number F4042).

Major dimensions	mm	% length
Rostrum to first branchial aperture	120	29
Rostrum to last branchial aperture	139	33
Rostrum to origin ventral fin-fold	112	26
Rostrum to posterior border cloaca	387	92
Maximum depth of body	18	4

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Mucous glands	range	mean
Prebranchial series	27-29	28
Branchial series	5-6	6
Abdominal series	64	64
Caudal series	8-9	9
Total	104-108	106

Lingual teeth: inner 2+5; outer 3+5.

The body is elongate and subcylindrical, slightly deeper than broad, tapering towards either extremity from the middle. The skin is dusky-brown dorsally, clearer brown ventrally. A very slight paling of the skin marks the position of the eyes on the dorsolateral surface of the head, about 18mm behind the rostrum. The distal thirds of the nasal and anterior oral barbels are yellow, as are the margins of the caudal fin and ventral fin-fold. There is no change of pigmentation to mark the borders of the external branchial apertures.

The nasal rostrum is bluntly curved, overlying the nostril which is approximately three times wider than high. The nasal barbels are 7mm long, slender, and taper evenly to a point. (The left ventral nasal barbel is bifid at the tip, possibly the result of injury and regeneration). The anterior oral barbels are 8mm long and similar in shape to the nasal barbels. The posterior oral barbels, which partially overlie the mouth in the anterior midline, are approximately 4mm long and 2.5mm wide.

Six pairs of gills communicate with the exterior by short, nearly vertical, efferent branchial ducts which are approximately equal in length except for the most anterior, which is approximately twice the length of the others due to dorsad displacement of the first gill. The branchial apertures are ventral, arranged on each side of the body in a longitudinal series curving towards the midline as it passes posteriorly. The aperture of the pharyngocutaneous duct, shared with the efferent duct of the sixth gill on the left side, is irregular in outline, somewhat longer than wide.

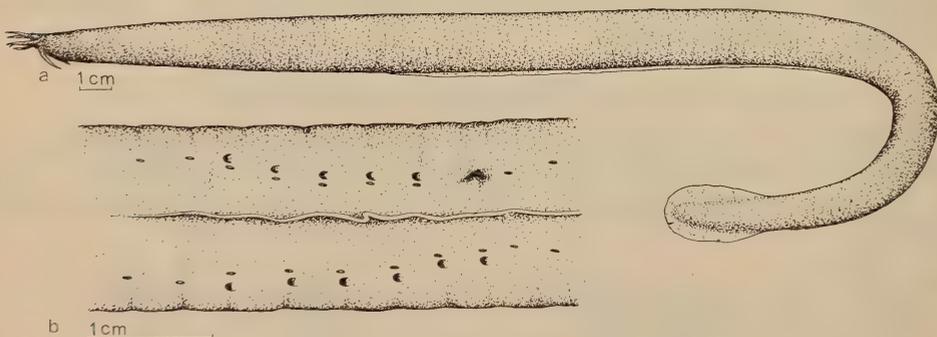


Fig. 1. *Eptatretus longipinnis*, n. sp., holotype. (a) lateral view; (b) ventral view of branchial region showing external branchial apertures, mucous glands and ventral fin-fold.

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The cloacal aperture is a longitudinal slit surrounded by lateral lips. The caudal fin, which originates dorsally and ventrally at the level of the posterior end of the cloacal aperture, is bluntly rounded and has a height equal to the maximum height of the body.

A prominent mid-ventral fin-fold originates anterior to the branchial region and extends between the branchial apertures to the anterior border of the cloacal aperture. It reaches a maximum depth of 4 mm in the branchial region.

The prebranchial series of mucous glands begins about 30 mm behind the rostrum on the ventral surface and extends to just in front of the first branchial aperture. The branchial mucous glands are immediately mesial to each branchial aperture except that of the sixth gill on the left side which lacks an associated gland. The abdominal series extends from the posterior end of the branchial region to about 10mm in front of the border of the cloacal aperture. The caudal series extends from the level of the middle of the cloacal aperture to about half the length of the tail.

The lingual tooth plates bear eight teeth in the outer row and seven in the inner. The bases of the anteriormost three teeth of the outer row are fused together, as are those of the anteriormost two of the inner row.

TAXONOMY OF POLYBRANCHIATE MYXINOIDS

The status of *Bdellostoma* and *Paramyxine*

The most recent comprehensive review of the Order Myxinoidea (Holly, 1933) recognises two genera of polybranchiate myxinoids: *Bdellostoma* and *Paramyxine*. There is long-standing disagreement on the proper name of the former genus, European workers tending to favour *Bdellostoma* Muller, 1835, while others favour *Eptatretus* Cloquet 1819. Supporters of *Bdellostoma* (e.g. Rauther, 1924; Holly, 1933) argue that *Bdellostoma* has had greater usage but, while this maybe true, it cannot be maintained that *Eptatretus* (or *Heptatretus*) is a forgotten name, resurrected on formal grounds of priority, for it has been in continued use since its introduction. Apstein (1915) included *Bdellostoma* in a list of recommended *nomina conservanda* but the International Commission on Zoological Nomenclature has ruled (Opinion No. 74) that it has no power to adopt this list *en bloc*. In the absence of a ruling to the contrary by the International Commission, the genus is properly called *Eptatretus*.

The retention of *Eptatretus* as a subgenus to include the 5-8 gilled polybranchiate myxinoids has little value and has been criticised by Bigelow and Schroeder (1948), Adam and Strahan (1963), and Hubbs (1963). However, full consideration of this must await a revision of the entire genus, including those species at present included in the subgenus *Polistotrema*.

The diagnosis of the genus *Paramyxine* Dean, 1904 is based on the branchial anatomy of the type of *P. atami* Dean: "Hyperotretes with branchial apertures ventrad of sacs. Ectal branchial ducts of distinctly unequal length, the most anterior several times the length of the most posterior. The duct of the most anterior gill opening at the surface opposite the fourth (or fifth) gill sac. Openings of the branchial ducts drawn close together and compressed transversely, that of the ductus oesophageus, however, longitudinally, the latter aperture of large size, its length equalling the sum of the interspaces of several gills. Transverse constrictor muscles of the branchial region developed as a distinct element in the region of the branchial sacs". (Dean 1904, p. 22).

Studies subsequent to Dean's erection of the genus have called these criteria into question. (1) Although the branchial apertures of the species assigned to *Paramyxine* tend to be closer to the mid-ventral line than in those traditionally assigned to *Eptatretus*, the distinction is difficult to assess, and, in the case of *E. longipinnis*, not valid. (2) Differences in length of the anterior and posterior efferent branchial ducts does not separate *Paramyxine* from *Eptatretus*: in *E. burgeri* the anteriormost efferent branchial duct is 2-3 times longer than the most posterior (Strahan, 1962). In *E. cirrhatus* it is approximately twice the length, three randomly chosen specimens having the respective ratios 23:12, 24:11, 2:1. In *E. longipinnis* the anteriormost efferent branchial duct is twice the length of the others but this is due to a dorsad displacement of the first gill rather than a caudad displacement of its efferent branchial aperture. (3) The first branchial aperture of *P. atami* Dean commonly opens at the level of the fourth or fifth gill but may open at the level of the third gill, as in *E. cirrhatus*. (4) The shape of the branchial apertures of *P. atami* Dean is extremely variable (Matsubara, 1937; Strahan and Honma, 1961): in *P. springeri* Bigelow and Schroeder, the apertures are almost circular and in *P. yangi* Teng they are semicircular. (5) The common aperture of the pharyngocutaneous duct and the last gill of the left side is not normally elongated longitudinally in *P. atami* Dean but is subject to considerable variation (Strahan and Honma, 1961): it is almost circular in *P. springeri* Bigelow and Schroeder and *P. yangi* Teng: its size does not bear the relationship to the intervals between the branchial apertures suggested by Dean. (6) The transverse branchial constrictor muscles of *E. burgeri* and *E. cirrhatus* are as well developed as those of *P. atami* Dean.

On the above considerations, I am of the opinion that *Paramyxine* must be regarded as a junior synonym of *Eptatretus*.

Taxonomic characters

Regan (1912) diagnosed the polybranchiate myxinoids in terms of the number of gills, the position of the anteriormost branchial aperture, and a rigidly defined dental formula. Holly (1933) followed Regan's general plan but indicated a range of variation in the dental formula and followed Dean in taking note of the position of the posterior end of the lingual musculature with respect to the gill series.

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None of those characters is constant. Large samples of a population of myxinoids usually include individuals with more or less than the model number of gills or gill apertures, and the range of variation in the dental formula is so great that there is considerable overlap between species. Moreover, these characters are not readily accessible: the number of gills may be inferred from the number of branchial apertures but these do not always correspond. In most preserved specimens the lingual teeth are retracted within the buccal cavity and a deep incision must be made to reveal them. The smaller teeth lie under a fold of buccal epithelium and are easily overlooked. Clearly it would be advantageous if species of myxinoids could be diagnosed by their external characters.

Studies of variation in the external characters of *E. atami* and *E. burgeri* (Strahan and Honma, 1961; Strahan, 1962) have demonstrated that the position of the first and last branchial apertures, cloaca, and ventral fin-fold; the depth of the body; and the number and distribution of mucous glands provide a constellation of individually variable characters which, taken together, are usually sufficient to define an eptatretid species.

COMPARISON OF *EPTATRETUS LONGIPINNIS* WITH OTHER 5-7 GILLED EPTATRETIDS

The six-gilled hagfish, *E. longipinnis* does not fit the description of any of the six-gilled species of *Eptatretus* (= *Bdellostoma*) listed by Holly (1933). However, in view of known variation in the characters considered by Holly, it is reasonable to establish that *E. longipinnis* is not a variant of a species with one more or one less pair of gills. These are: *E. yangi* (Teng) 1958; *E. springeri* (Bigelow and Schroeder) (1952); *E. atami* (Dean) 1904; *E. profundus* Barnard 1923; *E. burgeri* (Gunther) 1870; *E. hexatrema* (Muller) 1835; and *E. cirrhatus* (Bloch and Schneider) 1801.

Not all of these species have been described in sufficient detail to compare them character by character. Where possible, therefore, specimens have been re-examined and described in a standard manner. This has not been possible with *E. yangi* or *E. springeri* but the relatively recent descriptions of these species contain all the information necessary for the present purpose.

Eptatretus yangi

A description of the type and seven paratypes has been given by Teng (1958). The following is a summary.

Length: 198-250 mm.

Major dimensions as percentage of length	range	mean \pm S.D.
Rostrum to first branchial aperture	29 — 33	32 \pm 1.3
Rostrum to last branchial aperture	31 — 35	33 \pm 1.0
First to last branchial aperture	1 — 2	1.7 \pm 1.2
Rostrum to origin ventral fin-fold	39 — 55	47 \pm 4.5
Rostrum to posterior border cloaca	86 — 88	86 \pm 1.8
Maximum depth of body	5 — 8	6 \pm 0.7

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Number of mucous glands	range	mean \pm S.D.
Prebranchial series	17 — 20	18 \pm 1.0
Branchial series		nil
Abdominal series	35 — 40	37 \pm 1.5
Caudal series	7 — 10	9 \pm 1.1
Total	60 — 69	64 \pm 2.8

Lingual teeth: inner 2+6-8; outer 3+6-7.

Five pairs of branchial apertures in two irregular rows on the ventral surface. Violet-brown to violet-grey, paler ventrally; white border to ventral fin and to branchial apertures. South-western coast of Taiwan.

Eptatretus profundus

Only the holotype (SAM 13035) in the South African Museum is known. The following data are based on a re-examination of this specimen.

Length: 620 mm.

Major dimensions	mm	% length
Rostrum to first branchial aperture	125	20
Rostrum to last branchial aperture	160	26
Rostrum to origin ventral fin-fold	290	45
Rostrum to posterior border cloaca	505	81
Maximum depth of body	55	9

Number of mucous glands	range	mean
Prebranchial series	13	13
Branchial series	4	4
Abdominal series	50-51	51
Caudal series	15	15
Total	82-83	83

Lingual teeth: inner 2+8; outer 2+8.

Five pairs of ventrolateral branchial apertures arranged in regular rows. Branchial mucous glands dorsal to branchial apertures. Dark brown dorsally and ventrally. Atlantic Ocean, off Cape Pt., South Africa, 720 m depth.

Eptatretus springeri

The summary below is based on the detailed description of the holotype and two paratypes (Bigelow and Schroeder, 1952).

Length: 338-590 mm.

Major dimensions as percentage of length	range	mean \pm S.D.
Rostrum to first branchial aperture	23 — 24	23 \pm 0.4
Rostrum to last branchial aperture	26 — 28	27 \pm 1.0
First to last branchial aperture	2 — 6	4 \pm 1.4
Rostrum to origin ventral fin-fold	37 — 50	42 \pm 5.5
Rostrum to posterior border cloaca	82 — 87	85 \pm 1.7
Maximum depth of body	8 — 9	8 \pm 0.5

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Number of mucous glands	range	mean \pm S.D.
Prebranchial series	15 — 19	17 \pm 1.7
Branchial series	3 — 6	4 \pm 1.4
Abdominal series	44 — 57	52 \pm 5.5
Caudal series	11 — 14	12 \pm 1.0
Total	77 — 92	86 \pm 5.6

Lingual teeth: inner 2+9-10; outer 3+10-11.

Six pairs of branchial apertures in two regular rows on the ventral surface. Greyish-brown dorsally and ventrally; branchial apertures fringed with white. Gulf of Mexico, 400-500 m; Atlantic Ocean off Florida, 800-900 m; Caribbean, 500 m.

Eptatretus atami

Variation in the dimensions of 146 specimens has been described by Strahan and Honma (1961) who diagnosed an eastern and a western form of the species.

The following is a summary.

Eptatretus atami (western form)

Length: 130-583 mm.

Major dimensions as percentage of length	range	mean \pm S.D.
Rostrum to first branchial aperture	21 — 36	28 \pm 1.6
Rostrum to last branchial aperture	24 — 39	32 \pm 1.5
First to last branchial aperture		4 \pm 0.3
Rostrum to origin ventral fin-fold	39 — 54	47 \pm 2.7
Rostrum to posterior border cloaca	81 — 92	88 \pm 1.1
Maximum depth of body	5 — 8	6 \pm 0.5

Number of mucous glands

Prebranchial series	16 — 22	19 \pm 1.2
Branchial series		nil
Abdominal series	81 — 92	88 \pm 1.1
Caudal series	9 — 14	11 \pm 1.0
Total	68 — 79	75 \pm 2.6

Lingual teeth: inner 3+6-8; outer 3+5-9.

Six (sometimes 5) pairs of branchial apertures arranged in irregular (rarely regular) rows on the ventral surface. Purplish-brown dorsally, grey ventrally. Sea of Japan, coastal waters of north-western Honshu, Japan, 60-160 m depth.

Eptatretus atami (eastern form)

Length: 318-444 mm.

Major dimensions as percentage of length	range	mean \pm S.D.
Rostrum to first branchial aperture	25 — 28	27 \pm 1.0
Rostrum to last branchial aperture	28 — 32	30 \pm 1.3
First to last branchial aperture	2 — 4	3 \pm 0.2
Rostrum to origin ventral fin-fold	29 — 34	31 \pm 1.2
Rostrum to posterior border cloaca	86 — 87	87 \pm 0.3
Maximum depth of body	8 — 10	9 \pm 0.5

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Number of mucous glands	range	mean \pm S.D.
Prebranchial series	15 — 18	17 \pm 1.1
Branchial series		nil
Abdominal series	44 — 47	46 \pm 1.1
Caudal series	8 — 9	9 \pm 1.1
Total	68 — 72	71 \pm 2.1

Lingual teeth: inner 3+8-9, outer 3+8-9.

Six pairs of branchial apertures arranged in regular or irregular rows on the ventral surface. Purplish-brown dorsally, grey ventrally. Pacific Ocean, coastal waters of north-eastern Honshu, Japan, 50-490 m depth.

Eptatretus burgeri

The summary description below is based upon six specimens in the collection of the Imperial University of Tokyo and six in the collection of the Enoshima Aquarium, Japan.

Length: 235-435 mm.

Major dimensions as percentage of length	range	mean \pm S.D.
Rostrum to first branchial aperture	26 — 30	29 \pm 1.3
Rostrum to last branchial aperture	32 — 35	34 \pm 1.0
First to last branchial aperture	4 — 6	5 \pm 0.6
Rostrum to origin ventral fin	46 — 54	50 \pm 2.0
Rostrum to posterior border cloaca	84 — 90	87 \pm 1.5
Maximum depth of body	7 — 8	7.5 \pm 0.3

Number of mucous glands	range	mean \pm S.D.
Prebranchial series	19 — 22	21 \pm 0.9
Branchial series	5	5
Abdominal series	45 — 50	48 \pm 1.3
Caudal series	11 — 14	12 \pm 0.8
Total	81 — 89	85 \pm 2.1

Lingual teeth: inner 2+6-7; outer 3+6-7.

Six (rarely 5 or 7) pairs of branchial apertures in regular ventrolateral rows. Light brown to purplish-brown dorsally, paler ventrally; thin unpigmented mid-dorsal stripe; conspicuous pale patch of skin (translucent in life) over eye; tips of barbels pale. Southern Japan, southern Korea, 5-10 m depth.

Eptatretus hexatrema

The summary description below is based on six specimens in the British Museum and eight in the South African Museum.

Length: 112-720 mm.

Major dimensions as percentage of length	range	mean \pm S.D.
Rostrum to first branchial aperture	27 — 32	30 \pm 1.7
Rostrum to last branchial aperture	32 — 39	36 \pm 1.9
First to last branchial aperture	5 — 6	6 \pm 0.4
Rostrum to origin ventral fin	47 — 54	51 \pm 2.6
Rostrum to posterior border of cloaca	85 — 88	86 \pm 1.1
Maximum depth of body	6 — 7	6.5 \pm 0.3

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Number of mucous glands		
Prebranchial series	24 — 27	26 ± 1.0
Branchial series	5	5
Abdominal series	50 — 60	54 ± 3.4
Caudal series	11 — 14	13 ± 1.1
Total	91 — 105	98 ± 4.9

Lingual teeth: inner 2+8-10; outer 3+8-10.

Six (rarely 5) pairs of branchial apertures opening ventrolaterally in regular rows. Light brown to blackish-brown dorsally, paler ventrally. South Atlantic Ocean off Cape of Good Hope, 10-45 m depth.

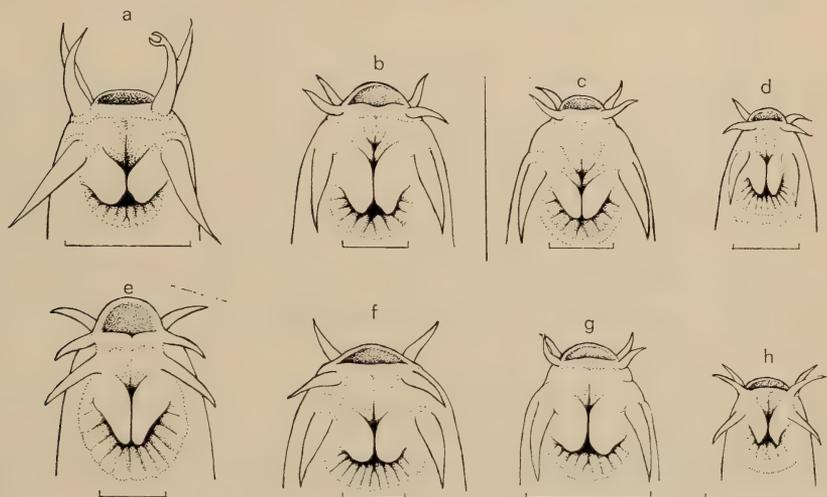


Fig. 2. Ventral view of heads of 5-7 gilled species of *Eptatretus*. (a) *E. longipinnis*, n. sp., 422 mm long, holotype; (b) *E. cirrhatus*, 660 mm long; (c) *E. burgeri*, 400 mm long; (d) *E. atami*, 350 mm long. (e) *E. springeri*, 590 mm long (after Bigelow & Schroeder); (f) *E. profundus*, 620 mm long; (g) *E. hexatrema*, 285 mm long; (h) *E. yangi*, 212 mm long (after Teng). Note that figures differ in scale: line below each figure is equivalent to 10 mm in length.

Eptatretus cirrhatus

The following summary description is based upon three specimens in the British Museum and ten from the National Museum, Wellington, New Zealand.

Dimensions as percentage of total length	range	mean ± S.D.
Rostrum to first branchial aperture	21 — 26	23 ± 1.8
Rostrum to last branchial aperture	28 — 33	31 ± 1.3
First to last branchial aperture	6 — 9	7 ± 1.1
Rostrum to origin ventral fin	47 — 55	52 ± 3.5
Rostrum to posterior border cloaca	80 — 86	84 ± 1.4
Maximum depth body	7 — 9	8.5 ± 0.3

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Number of mucous glands	range	mean \pm S.D.
Prebranchial series	15 — 18	16 \pm 1.0
Branchial series	6 — 7	6.5 \pm 0.2
Abdominal series	49 — 54	51 \pm 1.7
Caudal series	12 — 14	13 \pm 1.0
Total	83 — 92	87 \pm 2.7

Lingual teeth: inner 3+6-9; outer 3+6-9.

Seven (rarely 6) pairs of branchial apertures opening ventrally. Blackish-brown to brown dorsally, paler ventrally; prominent clear area over eye; white borders to branchial apertures. South Pacific Ocean off both islands of New Zealand, 8-10 m depth; off south-eastern coast of Australia, 300-700 m depth.

DISCUSSION

It is not difficult to separate *E. longipinnis* from the other species described above. In four characters—the anterior position of the ventral fin, the posterior position of the cloaca, the large number of abdominal mucous glands, and the small number of lingual teeth—values for *E. longipinnis* fall outside the combined range of the other species. In two characters, position of the ventral fin and position of the cloaca, values for *E. longipinnis* fall outside three standard deviations from the mean values for any of the other species. Indeed, in respect of the characters under consideration, *E. longipinnis* differs more from each of the other species or varieties than any two of them differ from each other.

KEY TO THE SPECIES OF *EPTATRETUS* HAVING 5-7 PAIRS OF BRANCHIAL APERTURES

- 1a Origin of ventral fin-fold anterior to third gill aperture *longipinnis*
- 1b Origin of ventral fin-fold posterior to third gill aperture 2
- 2a First gill aperture to last gill aperture more than 6% of total length *cirrhatius*
- 2b First gill aperture to last gill aperture less than 6% of total length 3
- 3a Pale mid-dorsal stripe *burgeri*
- 3b No mid-dorsal stripe 4
- 4a Less than 22 prebranchial mucous glands *hexatrema*
- 4b More than 22 prebranchial mucous glands 5
- 5a Rostrum to origin ventral fin less than 40% of total length *atami* (western)
- 5b Rostrum to origin ventral fin more than 40% of total length 6
- 6a Branchial mucous glands absent 7
- 6b Branchial mucous glands present 8
- 7a First gill aperture to last gill aperture more than 3% of total length *atami* (eastern)
- 7b First gill aperture to last gill aperture less than 3% of total length *yangi*
- 8a Branchial mucous glands dorsal to gill apertures *profundus*
- 8b Branchial mucous glands ventral to gill apertures *springeri*

ACKNOWLEDGEMENTS

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A NEW HAGFISH FROM SOUTH AUSTRALIA

ADDENDUM

While this paper was in press, a second specimen, 443 mm long, from South Australia "off Cape Douglas" (South Australian Museum No. F3611) came to hand. In this specimen the branchial region is slightly longer (1% total length) than in the type, and is slightly asymmetrical, the anteriormost branchial aperture on the right side being anterior (0.2% total length) to that on the left. The origin of the ventral fin-fold is at the level of the latter. Otherwise, this specimen corresponds well with the type.

Major dimensions	mm	% length
Rostrum to first branchial aperture	133-134	30
Rostrum to last branchial aperture	154	35
Rostrum to origin ventral fin-fold	134	30
Rostrum to posterior border cloaca	410	93
Maximum depth of body	21	5
Mucous glands	range	mean
Prebranchial series	27-28	28
Branchial series	5-6	6
Abdominal series	60-63	62
Caudal series	9	9
Total	102-105	104

Lingual teeth: inner 2+5; outer 3+5-6.

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A Taxonomic Revision of the *Litoria aurea* Complex (Anura: Hylidae) in South-Eastern Australia

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ABSTRACT

Four subspecies of *Litoria aurea* have been previously recognised in south-eastern Australia. In the present paper it is proposed that two of these subspecies (*Litoria aurea aurea* and *Litoria aurea raniformis*) be raised to specific status as *Litoria aurea* and *Litoria raniformis* respectively; that an isolated population from the New England region of N.S.W. be recognised as a new species *Litoria flavipunctata*; and that the remaining two subspecies, *Litoria aurea ulongae* and *Litoria aurea major* be synonymised with *Litoria aurea* and *Litoria raniformis* respectively.

This revision in taxonomy is proposed on the basis of morphological evidence and the apparent lack of hybridisation in areas of sympatry.

INTRODUCTION

Frogs of the *Litoria aurea* complex, representing a number of taxa, are extensively distributed in the south-east of Australia, including Tasmania, and in the south-west of Western Australia.

The group was first described as a single species, *Rana aurea* (Lesson 1831), the type locality being the Macquarie River at Bathurst, N.S.W. Günther (1858) placed the species in the genus *Hyla*. Keferstein (1867) described *Chirodrysia raniformis* from a specimen of unknown locality, but later (1868) sank this species into the synonymy of *Hyla aurea*. Parker (1938) recognised two subspecies of *Hyla aurea* in eastern Australia, the N.S.W. coastal form, *Hyla aurea aurea* and the inland and southern form, *Hyla raniformis*. In Western Australia, Parker recognized *Hyla aurea raniformis* and raised a further subspecies, *Hyla aurea cyclorhynchus* (Boulenger 1882) to specific status. Copland (1957) described the *raniformis* type from Western Australia as a new species, *Hyla moorei*. This was based on cross-fertilisation experiments reported by Moore (1954). *Hyla aurea ulongae* (Loveridge 1950) was described from Ulong, N.S.W. Yet another subspecies was erected when Copland (1957) re-named the Tasmanian group, previously ascribed to *Hyla aurea raniformis*, *Hyla aurea major*. Subsequently, Tyler (1971) has proposed that all Australo-Papuan species of *Hyla* be attributed to the genus *Litoria* Tschudi (1839) because of differences in vocal sac musculature compared with hylids from elsewhere.

Thus, two Western Australian species of the *Litoria aurea* complex are recognised, *Litoria cyclorhynchus* (Parker) and *Litoria moorei* (Copland). Until now, four subspecies of *Litoria aurea* have been recognized in south-eastern Australia, as follows:

- Litoria aurea aurea* (Lesson), a coastal form in N.S.W. and eastern Victoria,
- Litoria aurea raniformis* (Keferstein), distributed in southern inland N.S.W., Victoria and through the Murray R. Valley into South Australia,
- Litoria aurea ulongae* (Loveridge), from near Dorrigo, N.S.W.,
- Litoria aurea major* (Copland), from Tasmania.

There has been uncertainty of the taxonomic status of these south-eastern forms. Moore (1961) and Littlejohn, Martin & Rawlinson (1963) have suggested that the first two taxa may deserve full specific status. *Litoria aurea ulongae* was described from a single preserved specimen (Aust. Mus. No. R13817) (Loveridge 1950). *Litoria aurea major* was differentiated from *Litoria aurea raniformis* only on the basis of size (Copland 1957).

The present taxonomic revision is based on morphological evidence and apparent lack of hybridisation in zones of sympatry. We propose:

- (i) that *Litoria aurea aurea* and *Litoria aurea raniformis* be raised to full specific status as *Litoria aurea* and *Litoria raniformis*,
- (ii) that *Litoria aurea ulongae* and *Litoria aurea major* be synonymised with *Litoria aurea* and *Litoria raniformis* respectively; and
- (iii) that the geographically isolated population of *Litoria aurea raniformis* on the New England tableland be recognised as a new species, *Litoria flavipunctata*.

MATERIAL AND METHODS

Data on morphology and geographic distribution were obtained from our collections made throughout Victoria and New South Wales, and from preserved material in the Australian Museum. In addition, literature records were taken into consideration. Traverses were made near Canberra, Australian Capital Territory, and in East Gippsland, Victoria, to investigate the relationship between *Litoria aurea aurea* and *Litoria aurea raniformis* in sympatry.

In morphological studies, the following measurements were taken using vernier calipers (Peacock); snout-vent length (SV), tibia length (TL), head length (HL), and head width (HW) as defined by Goin and Netting (1940); foot length (FL) measured from outside heel to tip of toe; distance between eye and naris (EN), measured along the canthus rostralis; internarial span, (IN), diameter of the tympanum (T) and diameter of the eye (E). Using an ocular grid in a binocular microscope, the width of the third digit of the hand (DW) at the narrowest part between the digital pad and the next joint, and the width of the third digital pad (PW) were measured.

TAXONOMY OF *LITORIA AUREA* COMPLEX



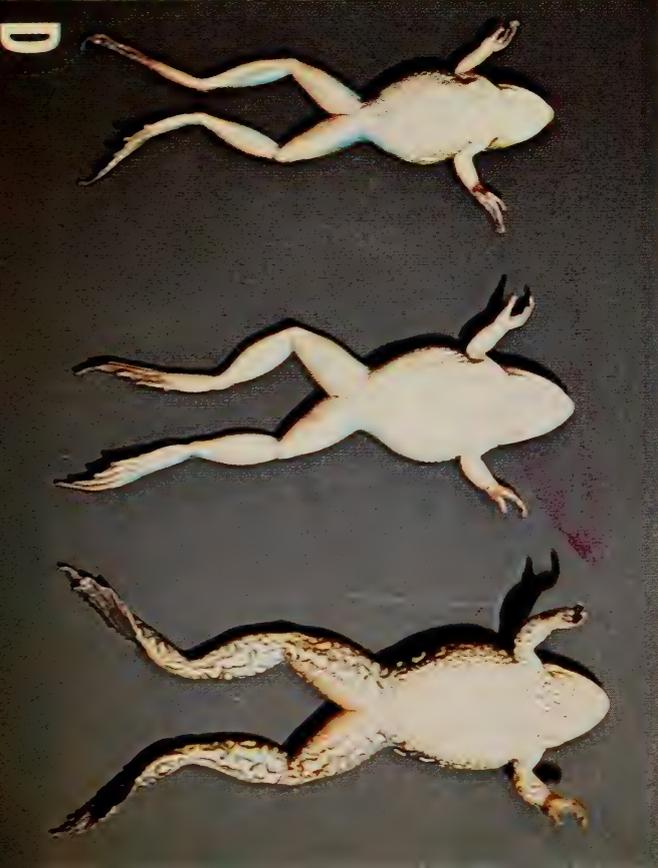
Fig. 1. View of foot and hand of *Litoria aurea* (top), *Litoria raniformis* (centre) and *Litoria flavipunctata* (bottom).



Fig. 2. Map of south-eastern Australia showing distribution of the *Litoria aurea* complex. The distribution of *L. raniformis* in Tasmania is based on Littlejohn (1967).



A



D

TAXONOMY OF *LITORIA AUREA* COMPLEX

COMPARISONS BETWEEN TAXA

To avoid confusion in the ensuing discussion, we will use the proposed names *Litoria aurea*, *Litoria raniformis* and *Litoria flavipunctata*.

(a) *Morphology*

(i) Dorsal stripe. *Litoria raniformis* and *Litoria flavipunctata* have an obvious mid-dorsal stripe. This is absent in *Litoria aurea* (Plate I).

(ii) Digital pads (Fig. 1). *Litoria raniformis* and *Litoria flavipunctata* have digital pads the same widths as the digits, whereas the pads of *Litoria aurea* are wider than the digits.

(iii) Colouration. *Litoria flavipunctata* is characterised by having large yellow spots in the groin and on the ventral surfaces of the legs. Smaller yellow spots are usually evident on the posterior surface of the thigh. Individuals of *Litoria raniformis* occasionally have a few small yellow spots on the posterior surface of the thigh. *Litoria aurea* never has yellow spots in these regions. In preservative, these spots are white.

(iv) Webbing (Fig. 1). The extent of foot webbing is consistently different in each of the three species. The fullest web is seen in *Litoria flavipunctata* where webbing extends to the tip of each toe. This webbing is usually covered with large yellow spots as found on the ventral surfaces of the hind limb. In *Litoria raniformis* the webbing is somewhat reduced, whereas in *Litoria aurea* the foot is only one half to three quarters webbed.

(b) *Zones of Sympatry*

The population on the New England tableland (*Litoria flavipunctata*) is geographically isolated from related taxa, so no interactions can occur.

Between *Litoria aurea* and *Litoria raniformis* however, two limited areas of sympatry are known. These areas are near Canberra, A.C.T. and on the Gippsland coast of Victoria near Orbost (Fig. 2). In both these areas, specimens of each species were collected, often in the same pond and even within less than a metre of each other. Using the morphological criteria given earlier, each species was clearly recognisable and no evidence of hybridisation was apparent. Littlejohn, Martin and Rawlinson (1963), from collections in East Gippsland between Metung and Orbost, noted that both types occurred in sympatry without hybridisation

CAPTION TO COLOUR PLATE

Plate I: A. *Litoria aurea*.

B. *Litoria raniformis*.

C. *Litoria flavipunctata*.

D. Ventral views of *Litoria aurea* (left), *Litoria raniformis* (centre) and *Litoria flavipunctata* (right).

Of another collection made in East Gippsland, Littlejohn (1969) writes: "specimens may be assigned to the subspecies *H. aurea aurea* with the exception of a series from Orbost in which there are indications of *raniformis* characteristics". The *raniformis* type is common to the east of 148°E, well within East Gippsland as defined by Littlejohn (1969) and yet no further mention of it appears in his checklist. Therefore we consider his statement indicative of his uncertainty of the taxonomic relationship between these taxa rather a clear implication that hybridisation occurs near Orbost. Moore (1961) refers to specimens that he considered to be intermediates between the two taxa. We have examined some of these specimens in the Australian Museum (R.9482-9484 from Koonadon near Leeton, R.7344 from Emu Plains near Urana, R. 5233 from Berridale, Monaro and the series R.5959-5962, R.6683 from Narracoorte, S.A., two of which Moore suggested may be intergrades). By our criteria these are all specimens of *Litoria raniformis*. Furthermore, these four localities are far distant from any known area of sympatry so that occurrence of intergrades at these localities is unlikely. Another specimen mentioned by Moore (1961) as a possible intergrade is in the British Museum (No. 96.6.17.17). It was collected from the Yarra River, Victoria. Unfortunately we have been unable to examine it.

In our view, the evidence suggests that *Litoria aurea* and *Litoria raniformis* maintain their distinctiveness in sympatry. The isolating mechanisms which operate to maintain this situation are, at present, unknown.

(c) *Litoria aurea ulongae*

This subspecies was described by Loveridge (1950) from a single preserved specimen from Ulong, N.S.W. No other specimen is known. Loveridge based its validity as a separate taxon on the lack of a dorso-lateral fold and the presence of an undivided ridge of vomerine teeth. Collections made in the area by one of us (G.P.C.) revealed no further specimens. The type specimen in the Australian Museum (R.13817) was examined carefully and it appears to be a somewhat unusual specimen of *Litoria aurea*. Hence we consider that *Litoria aurea ulongae* should be placed in the synonymy of *Litoria aurea*.

(d) *Litoria aurea major*

Copland (1957) ascribed the Tasmanian frogs of the "*raniformis*" type to a new subspecies, *Litoria aurea major*, solely on the basis of their supposed larger size. He wrote that "In large series of *raniformis* 60 mm was only exceeded in about 6% of specimens, and 70 mm only once (about 1%), and then only by 1 mm (71 mm). It must be noticed, however, that Keferstein gave the body length of his type of *raniformis* at 82 mm, which can only be regarded as very exceptional." (Copland 1957, p. 80.) Moore (1961) questioned the validity of this sub-species. He reported that several *raniformis* individuals which he had collected exceeded 72 mm, the length of the largest *major* referred to by Copland (1957).

In the present study, 66% of those *Litoria raniformis* measured exceeded 60 mm (compare 6% recorded by Copland, 1957) and one female caught at Nar-

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randera, N.S.W. was 90 mm in length. It would seem that no basis exists for retaining the Tasmanian frogs in a separate taxon and we propose that *Litoria aurea major* should be placed in the synonymy of *Litoria raniformis*.

SYSTEMATICS

The observations in the previous section support the validity of recognising three separate species within the *Litoria aurea* complex in south eastern Australia. Full descriptions of the three species will now be given.

Litoria aurea (Lesson 1831)

Synonymy:

- Rana aurea* Lesson 1831 (1830);
- Ranoidea jacksoniensis* Tschudi, 1839;
- Ranoidea resplendens* Girard, 1853;
- Hyla jacksonii* Bibron & Dumeril, 1854;
- Hyla castanea* Steindachner, 1867 (1869);
- Fanchonia elegans* Werner, 1893;
- Hyla blandsuttoni* Proctor, 1924.
- Hyla aurea ulongae* Loveridge, 1950;
- Hyla aurea ulongensis* Loveridge, 1950;
- Hyla aurea major* Copland, 1957.

Type Locality: Macquarie River, Bathurst, N.S.W.

Diagnosis: This species can be recognised in life by the following characteristics: smooth green band with irregular gold spots, yellow dorsolateral fold and a brilliant turquoise colour in the groin and on the back of the thigh.

In preservative the green and gold colours of the dorsum become smoky grey and light brown respectively. The dorsolateral fold becomes white. The groin colouring is grey.

Description of a female collected from Ourimbah, N.S.W. in October 1972. Australian Museum No. R42156.

The dorsal surface is smooth and green with irregular gold spots. A yellow dorsolateral fold extends from the eye to the groin. Another short yellow line extends from under the eye to above the shoulder.

The belly and ventral surfaces of the thighs are white and coarsely granulate. The skin is more finely granulate under the forelimbs and the throat. The groin, the posterior surface of the thigh and the ventral surfaces of the tibia are coloured brilliant turquoise.

The head is obtusely pointed and slightly longer than broad (HL/HW ratio 1.15). The head length is approximately 1/3 of the snout to vent length (HL/SV

ratio 0.34). The snout is not prominent and does not project conspicuously beyond the anterior limit of the mandible. The distance between the eye and the naris is greater than the internarial span. The canthus rostralis is distinct and straight; the loreal region is concave.

The tympanum is distinct and gold in colour. Its diameter is 0.72 x that of the eye. The vomerine elevations are large, paired and obliquely convergent posteriorly; they lie between the choanae. The tongue is broad, free and nicked posteriorly.

Fingers are long and free from webbing. They are, in order of length, $3 > 4 > 2 = 1$. Terminal discs are wider than the digits.

The hind limbs are long and slender (TL/SV ratio 0.50). Toes are, in order of length, $4 > 3 = 5 > 2 > 1$. They are approximately $3/4$ webbed (see Fig. 1).

In preservative, the dorsal surface is a greyish green and the ventral surfaces and the yellow lines become immaculate white.

Dimensions

SV 76.9 mm; TL 38.7 mm; FL 55.1 mm; HL 26.3 mm; HW 23.0 mm; IN 4.2 mm; E 8.7 mm; T 6.3 mm.

Variability

The snout to vent distances of 24 frogs of this species had a mean of 58.3 mm and a range of 46.9-76.8 mm. The amount of gold colouring on the dorsal surface varied greatly; this variation seemed to be unrelated to any geographic pattern.

Specimens examined

Australian Museum, N.S.W.; R18484, Wollongong, N.S.W.; R19424-7, (1890) Richmond, N.S.W.; R19643-5, (1890) Manly, N.S.W.; R4194-6, 4198-203, 4205, (1908) Maroubra, N.S.W.; R4452, (1909) Sans Souci, N.S.W.; R4665-8, (1910) Woonona, N.S.W.; R3388-9, (1911) North Sydney, N.S.W.; R5849, (1912) Cooks River, N.S.W.; R7325, (1921) Capertree, N.S.W.; R7376 (1921) Burrawang, N.S.W.; R7446-1, (1922) Pambula, N.S.W.; R7974, (1922) Upper Colo, N.S.W.; R8454, 8456, 8483, (1924) Sydney, N.S.W.; R9424, R9426-7, (1928) Wentworthville, N.S.W.; R9532, (1928) Botany, N.S.W.; R9558, (1928) Five Dock, N.S.W.; R9644, Tumut, N.S.W.; R18768, (1957) Shoalhaven Heads, N.S.W.; R19669-81, (1958) Singleton, N.S.W.; R2455, (1965) Londonderry, N.S.W.; R27635, (1968) Cobargo, N.S.W.; R29446, (1972) Lake Lidell, N.S.W.; R29441-3, (1972) French's Forest, N.S.W.

Author's collections

Goulburn, N.S.W. (4 specimens); Pearl Beach, N.S.W. (50 spec.); Tomerong, N.S.W. (3 spec.); nr. Jacqua, N.S.W. (2 spec.); Liddell Lake, N.S.W. (4 spec.); Cann River, Vic. (4 spec.); 12 m E. of Orbost, Vic. (10 spec.); 1 m E. of Orbost,

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Vic. (4 spec.); 5 m SE of Orbost, Vic. (2 spec.); Marlo, Vic. (6 spec.); Foxlow, N.S.W. (1 spec.); near Maclean, N.S.W. (2 spec.); Bungonia, N.S.W. (20 spec.); 12 m NE Canberra, N.S.W. (4 spec.); 12 m NE Tarago, N.S.W. (2 spec.).

Literature records

These records do not include material in the Australian Museum which has been examined by the authors.

Lower Clarence River, N.S.W.; Gurravembi, Nambucca River, N.S.W.; Warrell Creek, Nambucca River, N.S.W.; Nambucca River, N.S.W.; Botany Bay, N.S.W.; Bulahdelah, N.S.W.; Sydney, N.S.W.; East Lakes, Sydney, N.S.W.; Burradoo, N.S.W.; Bodalla, N.S.W.; Eden, N.S.W.; Nowra, N.S.W.; (Moore 1961). Jervis Bay, N.S.W.; (Fletcher 1894, cited in Moore 1961). Razorback Mt., near Picton, N.S.W.; Bundanoon, N.S.W.; Tallong, N.S.W.; Fitzroy Falls, N.S.W.; Barrengarry Mt., N.S.W.; Waverley, N.S.W.; (Copland 1957). Thirroul, N.S.W.; (Harrison 1922). Gypsy Point, Vic.; Orbost, Vic.; Corringale Beach, Vic.; 6 miles N of Lake Entrance, Vic.; Metung, Vic.; Genoa, Vic.; Nowa Nowa, Vic.; (Littlejohn *et al.* 1963). Goongerah, Vic.; Fairhaven, Mallacoota Inlet, Vic.; 1 ml N of Marlo, Vic.; 11 miles E of Orbost, Vic.; 8 miles E of Bendoc, Vic.; (Littlejohn 1969).

Biology

This species inhabits permanent ponds, farm dams and the still backwaters of rivers. Their habitat usually can be identified by the presence of beds of tall reeds. The frogs can be found on these reeds at night, feeding. They call in open water, and eggs are laid on top of the water but later sink (Littlejohn 1971).

Larvae

The tadpoles are large and dark. The anus is dextral; the spiracle sinistral; eyes lateral. The dorsal fin extends nearly halfway up the back. The mouth disc has two rows of upper labial teeth, and three rows in the lower labium. The inner row in each labium is divided. A narrow row of papillae extend around the lateral and posterior margins of the mouth.

Litoria raniformis (Kerferstein 1867).

Synonymy:

Chirodryas raniformis Kerferstein 1867.

Hyla aurea major Copland 1957.

Diagnosis: This species can be recognised by its green and gold warty back with a green middorsal stripe. The groin and back of thigh are coloured blue, slightly less brilliant than that of *Litoria aurea*. There are sometimes small yellow spots on the back of the thigh.

In preservative the mid-dorsal stripe and the dorsolateral folds stand out as pale grey markings against a darker grey back, on which longitudinal rows of darker warts are seen.

Description of a male collected from Narrandera, N.S.W., August, 1972. Australian Museum No. R42155.

The dorsal surface is green and brown with rows of black spots and a distinct green mid-dorsal stripe extending from between the eyes to the cloaca. There is a dorsolateral gold line which starts on the eye and fades out just before the groin. There is another line from below the tympanum to the shoulder.

The belly and most of the ventral surfaces of the thighs are coarsely granulated. The region of the vocal sac has a yellow tinge. The groin, the posterior surface of the thigh and the inner surface of the tibia and foot are blue in colour.

The head is obtusely pointed and approximately as long as it is broad (HL/HW ratio 1.02). The head approximately 1/3 of the snout to vent length (HL/SV ratio 0.37). The snout is not prominent and does not project conspicuously beyond the anterior limit of the mandible. The distance between the eye and naris is greater than the internarial span. The canthus rostralis is distinct and straight, the loreal region is concave.

The tympanum is distinct and gold in colour. Its diameter is 0.59 x that of the eye.

The vomerine elevations are paired, and are slightly convergent posteriorly. The anterior ends are directly between the choanae. The tongue is broad, free and indented posteriorly.

Fingers are long and free from web. Fingers are, in order of length $3 > 4 > 2 = 1$. Terminal discs are approximately the same width as the digit.

The hind limbs are long and robust (TL/SV ratio 0.50). Toes are, in order of length, $4 > 3 = 5 > 2 > 1$. They are extensively webbed (see Fig. 1).

In preservative the dorsal surfaces become a dirty green or brown and the ventral surfaces and the dorsolateral lines become dirty white.

Dimensions

SV 60.3 mm; TL 30.3 mm; FL 42.8 mm; HL 22.5 mm; HW 22.0 mm; EN 4.5 mm; IN 3.2 mm; E 7.8 mm; T 4.6 mm.

Variability

Members of this species usually have a green dorsum with brown and black warts arranged in longitudinal rows. Some individuals have a few small yellow spots on the posterior surfaces of the thighs. Males have a yellow tinge in the region of the vocal sac.

TAXONOMY OF *LITORIA AUREA* COMPLEX

Specimens examined

Australian Museum: R3121-3, (1900) Fish River, Tarana, N.S.W.; R5233, (1911) Berridale, N.S.W.; R7344, (1921) Emu Plains, Urana, N.S.W.; R8421, (1924) Tumut, N.S.W.; R10661-8, (1932) Yanco, N.S.W.; R10669-88, (1932) Tubbo Stn., Riverina, N.S.W.; R25852-55, (1966) Bombala, N.S.W.; R26181, (1966) Tumberumba, N.S.W.; R27605, (1967) Mt. Beauty, Vic.; R5959-62, R6683 (1912) Narracoorte, S.A.

Author's collection

Bywong, N.S.W. (1 specimen); Boorowa, N.S.W. (2 spec.); Narrandera, N.S.W. (15 spec.); Morundah, N.S.W. (1 spec.); Wagga, N.S.W. (5 spec.); Delegate, N.S.W. (2 spec.); 12 m NE Canberra, N.S.W. (15 spec.); near Bungendore, N.S.W. (2 spec.); Booligal, N.S.W. (10 spec.); Saucy Ck., Bombala, N.S.W. (2 spec.); Maclaughlin R. nr. Nimmitabel, N.S.W. (4 spec.); Swan Hill, Vic. (2 spec.); Whittlesea, Vic. (3 spec.); 10 m SE Orbost, Vic. (8 spec.).

Literature records

These do not include specimens in the Australian Museum already examined by the authors.

Albury, N.S.W.; Delegate, N.S.W.; Canberra, A.C.T.; Gunbower, Vic.; Melbourne, Vic.; Healesville, Vic.; Yarra River, Vic.; Millgrove, Vic. (Moore 1961). Tocumwal, N.S.W.; Gol Gol, N.S.W.; Darlington Point, N.S.W.; Balranald, N.S.W.; 10 m W of Narrandera, N.S.W.; 8 m S of Bombala, N.S.W.; Adaminaby, N.S.W.; Bacchus Marsh, Vic.; 13 m SE of Horsham, Vic.; Cobungra, Vic.; Macedon, Vic.; 18 m W of Bairnsdale, Vic.; Brighton, Vic.; Mordialloc, Vic.; Tailem Bend, S.A. (Copland 1957). Lock No. 9, Murray R.; 3 m E of Mildura, Vic.; Lake Cullulleraine, Vic.; 6 m SE of Red Cliffs, Vic.; Carwarp, Vic.; Nangiloc, Vic.; Boundary Bend area, Vic.; Nyah, Vic.; Sea Lake, Vic.; Wycheproof, Vic.; 16 m W of Nhill, Vic.; Kaniva, Vic.; Mildura, Vic.; Lake Boga, Vic.; 5 m NW of Dimboola, Vic.; Wail, Vic.; 15 miles W of Kaniva, Vic. (Littlejohn 1966). Flinders Is., Bass Strait; King Island, Bass Strait (Littlejohn and Martin 1965).

Biology

These frogs occupy a similar habitat to *Litoria aurea*. However, they are often found during the day on a grassy bank near water, basking in the sun. This habit is not usually observed in *L. aurea*.

Larvae

Martin (1965) has described the tadpole of this species.

Litoria flavipunctata sp. nov.

Synonymy:

Hyla aurea raniformis Moore 1961 *partim*.

Holotype

A male, No. R40676 in the Australian Museum, from a swamp on the Booralong Creek Road, 12.8 km west of Guyra, N.S.W. (30° 16'S. 151° 33'E). (Paratypes Aust. Mus. R40677-82).

Derivation of name

The name *flavipunctata* is from the Latin meaning "yellow spots". This refers to the large yellow spots found in the groin and on the ventral surfaces of the hind limb of these animals. The presence of these spots is a distinguishing feature of this species.

Diagnosis: This species can be recognised by its dorsal colouration: green with small brown and black spots and a green mid-dorsal stripe, together with large and conspicuous yellow spots in the groin and on the ventral surfaces of the hind limb. These large yellow spots are not found in *Litoria aurea* or *Litoria raniformis*.

In preservative the dorsum appears very similar to that of preserved *Litoria raniformis* with a slightly less obvious mid-dorsal stripe. Spots in the groin and on the legs are white.

Description of the type specimen

The dorsal surface is green with brown and black spots, giving it a warty appearance. There is a distinct green mid-dorsal stripe extending from between the eyes to the cloaca.

The belly and part of the ventral surface of the thigh are white and coarsely granulate. The skin is more finely granulate under the forelimbs and the throat, and there is a hint of pale yellow in the region of the vocal sac. In the groin, on the ventral surface of the thigh and the ventral surface of the tibia and the foot, there are very large, distinct, yellow spots. Smaller yellow spots are found on the posterior surfaces of the thighs.

A gold line extends dorsolaterally from behind the eye to behind the shoulder, where it continues as a series of gold warts almost to the groin. Another short yellow line extends from under the tympanum to above the shoulder.

The head is obtusely pointed and slightly longer than broad (HL/HW ratio 1.15). The head length is approximately 1/3 of the snout to vent length (HL/SV ratio 0.27). The snout is not prominent and does not project conspicuously beyond the anterior limit of the mandible. The distance between the eye and the naris is greater than the internarial span (IN/EN ratio 0.70). The canthus rostralis is distinct and straight; the loreal region is concave.

The tympanum is distinct, gold in colour with a green centre. Its diameter is 0.6 x that of the eye. The vomerine elevations are paired, obliquely convergent

TAXONOMY OF *LITORIA AUREA* COMPLEX

posteriorly. The anterior ends are directly between the choanae. The tongue is broad, free and nicked posteriorly.

The fingers are long and free from web. Fingers are, in order of length, $3 > 4 > 2 = 1$. Terminal discs are approximately the same width as the digit.

The hind limbs are long and robust (TL/SV ratio 0.53). Toes are, in order of length, $4 > 3 = 5 > 2 > 1$. They are fully webbed (see Fig. 1).

In preservative the dorsum becomes a dark grey colour with a lighter grey stripe. The large yellow spots become white.

Dimensions

SV 64.3 mm; TL 34.1 mm; FL 46.8 mm; HL 23.9 mm; HW 20.7mm; EN 5.3 mm; IN 3.7 mm; E 6.9 mm; T 4.1 mm.

Variation

There is a variable amount of gold on the dorsal surfaces of these frogs, but the dorsal stripe remains distinct at all times. The ventral yellow spots are sometimes outlined in black. The size of the digital pad in relation to the digit on the hand and the amount of foot webbing were the same in every frog examined. A series of 21 adult specimens had a range of SV lengths from 52.6-84.8 mm.

Biology

This species occupies a similar habitat to *Litoria aurea* and *Litoria raniformis*. It is found also in ponds or slow moving streams with overhanging grassy banks in the absence of reed beds.

It has been found to overwinter in the hollow centres of rotting logs and in the earth surrounding the roots of uprooted trees.

Specimens examined

Australian Museum, N.S.W. R32183-9, (1971) Guyra, N.S.W.; R32560, (1971) Llangothlin Lagoon, N.S.W.; R32547, (1971) Llangothlin Lagoon; R34814-7; (1972) Black Mt. Lagoon, nr Guyra, N.S.W.; R33816, (1972) Sattern Gully, nr Armidale, N.S.W.; R34937, (1972) Abby Green Stn., nr Guyra, N.S.W.

Author's collection

Black Mt., near Guyra, N.S.W.; Llangothlin Lagoon, N.S.W.; 4 m S of Guyra, N.S.W.; Booralong Ck., New England, N.S.W.

Literature records

Booralong Ck., N.S.W. (Moore, 1961), recorded as *Hyla aurea raniformis*.

To our knowledge, this is the only reference in the literature which specifically refers to the individuals on the New England tableland.

KEY TO SOUTH-EASTERN SPECIES

- 1 (a) Mid dorsal stripe present
 Digital pads same width as digits 2
 (b) Mid dorsal stripe absent
 Digital pads 1½ times width of digits *Litoria aurea*
- 2 (a) Large yellow spots (white in preservative) in groin and ventral surfaces of
 legs
 Toes completely webbed *Litoria flavipunctata*
 (b) No large yellow spots covering groin and ventral surfaces of legs
 Toes less than completely webbed *Litoria raniformis*

ACKNOWLEDGEMENTS

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Courtship of the Platypus, *Ornithorhynchus anatinus*

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ABSTRACT

An account is given of the courtship of a pair of captive platypuses over a period of 16 weeks and of subsequent incubation by the female over a period of six weeks.

The female takes the initiative in the courtship. Nine components are described in the behaviour of the female and five in that of the male. The male marks objects under water with cloacal secretion.

The findings are compared with the observations of other authors on the sexual behaviour of wild and captive platypuses.

INTRODUCTION

Spending most of its life in burrows or under water, and being inactive by day, the platypus is a difficult animal to study in the wild and little is known of its normal behaviour. Courtship and mating, which in many mammal species attract attention because of striking differences from normal, year-round, behaviour, are virtually undescribed for the platypus, and the few existing accounts are at some variance with each other.

Verraux (1848), who collected platypuses in tributaries of the Derwent River near New Norfolk, Tasmania, observed an apparent instance of mating one evening in September. According to him, the male pursued the female on or near the surface of the water for about an hour, driving her into the rushes at the edge of the river. There, he seized her with his bill by the nape of the neck, with his spurs clutching her rump. The female swam about, struggling violently and emitting cries like those of a piglet. Copulation lasted 5-6 minutes, after which the animals 'played' together for more than an hour.

Burrell (1927) was sceptical of Verraux's account, asserting that the male's bill is so constructed that it could not be used to grasp the female's neck: ". . . he manifestly did not understand that the extent to which the upper mandible overlaps the lower would render that impossible, quite apart from the pliable nature of the lips and the fact that both jawbones are divided at their extremities and

are pliable as far back as the secateuring ridges" (p. 168). Burrell also states that platypuses do not make the sound attributed to the female by Verraux.

Burrell (1927) claims to have seen two matings in the Namoi River, New South Wales. On 27 August 1909 at 0730, two platypuses came to the surface and one began to swim in a circle around the other. The second soon followed so that they swam in a circle. "After about one minute of this circling, one of the animals (which proved to be the female) submerged its body and tail and floated perfectly still with its head above the water. The male then came slowly up and mounted in a leisurely fashion. The whole process offered a very close resemblance to the early stages of copulation of a drake and duck with the exception that the male platypus did *not* take a grip with its bill. The male then threw himself back into a sitting posture, partly out of the water, but at this moment there was a great splash and both animals disappeared" (p. 168).

On 23 September 1921 at 0700, on the Namoi River three miles from the site of his 1909 observations, Burrell observed "a pair of platypuses coupled in an extraordinary position. The tail of each was laid flat along the belly of the other. . . . The precise position of the hindlimbs could not be made out, as no movement thereabouts was discernible; but it must have been the grip of these (spurs) that kept the animals together. So closely were they apposed that they appeared at times like a giant platypus" (p. 169). The conjoined pair, female in a normal position, male upside-down and tail-forward, dived and surfaced repeatedly for a period of three minutes, then separated and swam on the surface. Since the animals were already coupled before Burrell saw them, the actual period spent in this posture was not less than three minutes.

Home (1802) proposed a sexual role for the venomous spurs of the foot of the male platypus. "It is probably by means of these spurs, or hooks, that the female is kept from withdrawing herself in the act of copulation, since they are very conveniently placed for laying hold of the body on that particular occasion" (p. 72). Burrell agrees with Home and suggests that the spurs of the male fit into corresponding sockets in the foot of the female and proposes a rather complex manoeuvre by which a male could proceed from the sitting posture that he observed in 1909 to that observed in 1927.

Fleay (1944) observed the apparent onset of courtship in two platypuses in captivity at the Sir Colin Mackenzie Sanctuary, Healesville, Victoria. In mid-September 1943, "Jack seized Jill's tail in a firm grip with his bill and the two animals swam slowly in a processional circle" (p. 11). This behaviour was observed several times over the next 27 days. Mating took place on 11 October but the details are somewhat obscure. "It is worth noting that during the act when the animals were fast for nearly ten minutes, no spur grip was noted. A good deal of splashing and floundering about occurred, and in the first place the male doubled his body under him while maintaining his grip on the female's tail with his bill" (p. 29). The male was removed from the enclosure on 18 October and the mating

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was followed by the hatching and successful incubation of one young (the only such breeding in captivity).

Burrell (1927) and other authors reviewed by him have described the nest of leaves and grass used by the female as a brooding chamber. Fleay (1944) described the way in which the female collects wet leaves and carries them to her burrow, clamped between the ventrally curled tail and the abdomen. On 23 October, twelve days after copulation, the female collected leaves vigorously and apparently completed her nest. She fed 'ravenously' on 25 October, then retired to her burrow, returning to the water briefly on 31 October and 1 and 3 November, but not eating again until 6 November, 12 days later, when she resumed feeding at a level much greater than normal. It is reasonable to assume, with Fleay, that the period of fasting approximates to the period of incubation of the eggs, and that subsequent heavy feeding is related to lactation.

Collins (1973) states that two platypuses in the Bronx Zoo, New York, displayed tail-holding and circular swimming from 21 June to 23 June, 1953. Sixteen days later the female displayed nest-building behaviour.

MATERIALS AND METHODS

The Platypus House, Taronga Zoo, Sydney, was designed to the brief of the senior author with the following major provisions: (i) the animals are exhibited in subdued light in a long glass-sided tank containing flowing water, and surrounded by a darkened viewing gallery; (ii) the animals feed in two large tanks of still water, open to air and daylight; (iii) separate nesting boxes are provided for the male and female and these are connected with the exhibition tank and feeding tanks in such a way that the male and female have free and independent access to each (it being possible to restrict animals to separate feeding tanks if required). The system is designed so that there is no need to handle the animals and so as to provide them with sufficient information on day-length to maintain annual rhythms.

The exhibition tank has glass sides 6.1 m long and 1.3 m high. It contains approximately 8,000 l of slowly running fresh water and is lit from above by diffuse indirect sunlight, supplemented by fluorescent lamps when the animals are exhibited: the viewing gallery is illuminated only by the light from the tank. A tunnel from the exhibition tank leads to the male and female nesting boxes, and paired tunnels lead from these to two feeding tanks, each 5.2 m long and each containing approximately 4,000 l of water. Approximately one month prior to the observations recorded below, an annex 120 cm long x 46 cm x 46 cm was connected to the female's nesting box. This was filled with damp earth and leaves in the hope that it would be used for an incubation burrow.

Animals are enticed from their nesting boxes, via the tunnels, to the exhibition tank for about two hours each day (1100-1200, 1400-1500). A small amount of food (mealworms, woodlice, scarabaeid larvae, small crayfishes) is

placed in the exhibition tank and the shutter leading to it opened. The animals have learned that operation of the shutters is a signal for food and enter the feeding tank without being handled or driven. Once in the tank, the shutter is closed and the animals compelled to remain there except on the rare occasions when the female has persisted in attempts to return to her nest. After an hour, the shutter is opened and the animals usually retire 5-10 minutes later.

Food is placed in the outside feeding tanks at about 1500 each day and the considerable debris is removed when the tanks are cleaned and refilled at about 0800 each day. Although they have free access to the feeding tanks, the animals seldom enter during daylight.

The behaviour described below was recorded during the two hours of daily exhibition by one of the authors (D.E.T.), assisted by keepers of the Mammal Department, Taronga Zoo.

The male and female platypus were taken from the Kangaroo River, New South Wales, and introduced directly to the newly-completed Platypus House in May, 1969. Both animals were sub-adult. At the time of writing (January, 1975), they were still in good health.

FEMALE BEHAVIOUR

The courtship behaviour of the female comprises a number of components that may be performed as isolated acts or in sequences. These are briefly described below.

Interest in the male

For most of the year, the male and female show no interest in each other, swimming past without reaction or apparent recognition. In view of the solitary habits of platypuses in the wild, their relatively distant spacing along river banks, and reports of combat (Burrell, 1927) one might expect aggressive behaviour between individuals: lack of such behaviour in these captive animals may be due to habituation.

In late August 1971, the female began to evince interest in the male. If the male came near her while she was grooming (out of the water) she ceased this activity and entered the water, lying passively until the male moved away—when she would leave the water and resume grooming. This unoriented approach is the simplest component of the female repertoire.

From September to December, the interest of the female in the male increased and, as described below, involved specific, oriented, approaches to the male. It should be noted that sequences of interaction were usually of short duration, separated by much longer periods in which the animals ignored each other.

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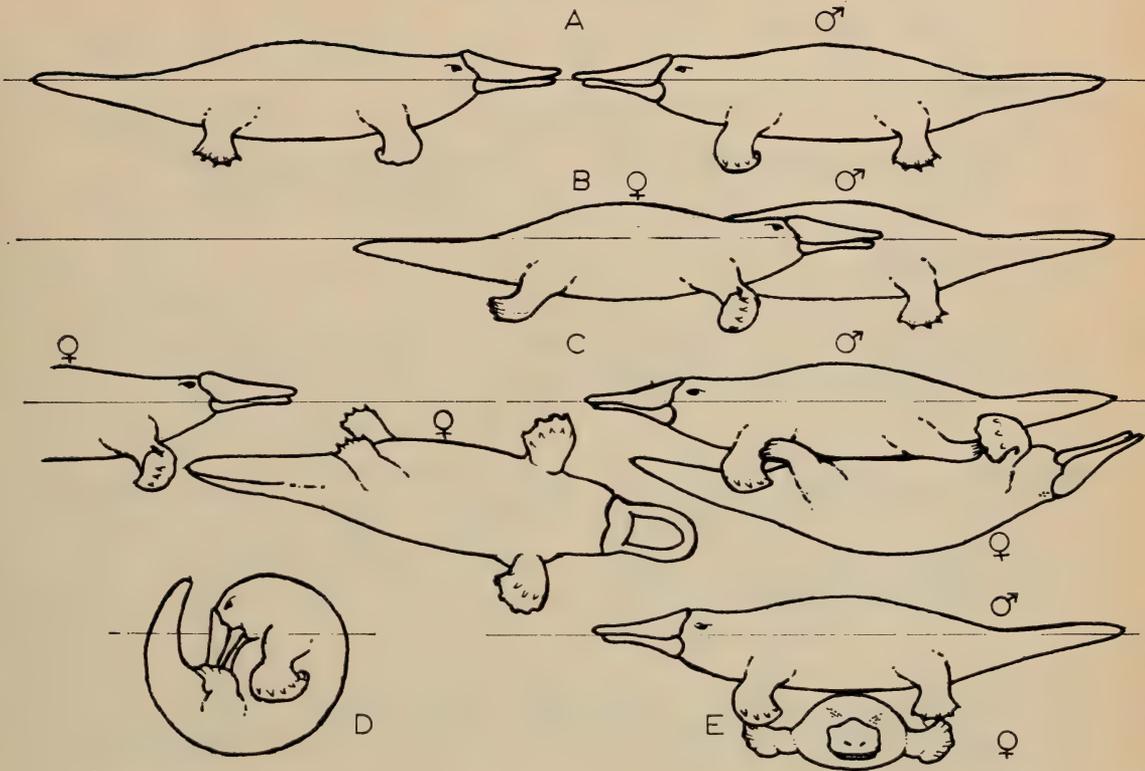


Fig. 1. Female courtship behaviour. A, frontal approach; B, side-passing; C, ventral-passing; D, cloacal grooming; E, under-passing.

Frontal Approach

The female approaches the male head-on. As the male rests on the surface of the water, the female swims to him and rests with her bill touching, or nearly touching his, the two bodies in a straight line (Fig. 1A). This relationship may be retained for as long as ten minutes.

Side-passing

The female swims to the male as in a frontal approach, then passes alongside him, rubbing against his side (Fig. 1B).

Ventral-passing

The female swims to the male as in a frontal approach but rolls over just before meeting him, so that her ventral surface rubs against his as she glides beneath him, upside down (Fig. 1C). Often the male responds by grasping her tail and following her (see 'tail-holding', p. 171).

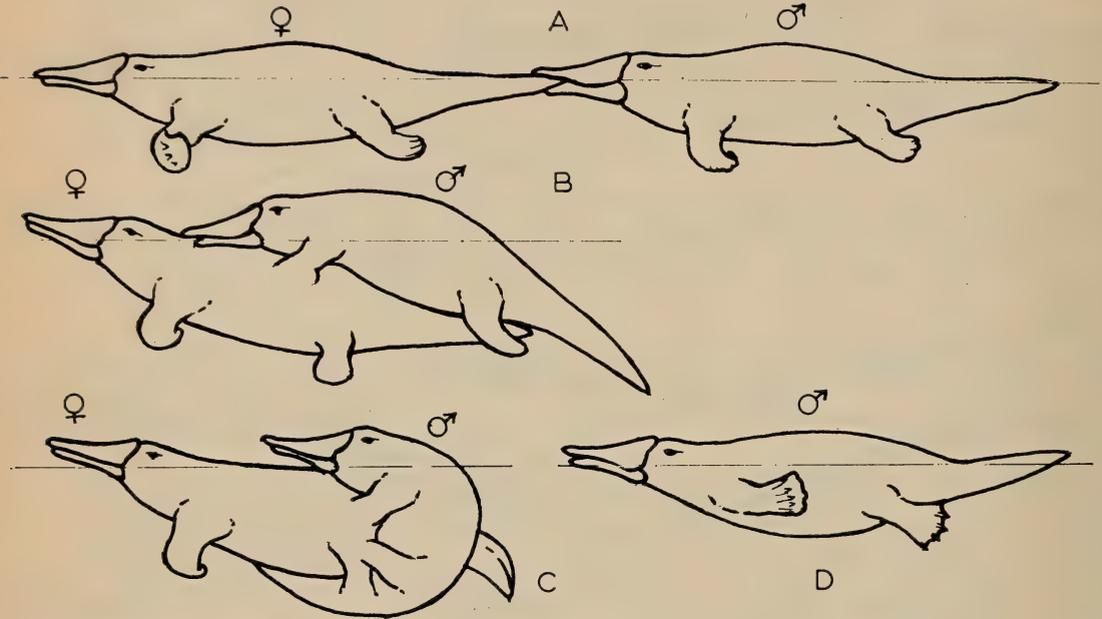


Fig. 2. Male courtship behaviour. A, tail-holding. B, neck-holding; C, sitting posture (possibly copulation); D, stretching. Where the position of the limbs is uncertain, the outline is incomplete.

Under-passing

The female approaches the male from one side as he rests on the surface, dives under his body, and surfaces again (Fig. 1E), the male may respond by tail-holding.

Circling

The female swims in a tight circle (always clockwise in our female) on the surface of the water. The male may follow and engage in tail-holding.

Grooming of cloacal region

While at the surface of the water, the female curls forward, almost into a ball, and grooms the cloacal region with her bill for 10-20 seconds (Fig. 1D). The animal may take up this posture lying on its side.

Regurgitation

The female, lying motionless on the surface, regurgitates a muddy vomit. As this sinks to the bottom in a cloud, the male swims through it repeatedly

COURTSHIP OF THE PLATYPUS

and the female follows him. The male grasps her tail and swims with her to the surface.

Clasping

When the male grasps the nape of the female's neck, she rolls onto her back, presents her ventral surface to his and the pair roll over in the water for 10-20 seconds. It is not clear which animal is clasping, or whether both are involved.

Leaf-carrying

Strictly speaking, this is an aspect of maternal behaviour rather than courtship. The behaviour is as described by Fleay (1944). The female picks up leaves, either from the bottom or the surface, by tucking them between the ventrally curled tail and the abdomen.

MALE BEHAVIOUR

The greater part of the behaviour of the male is in response to stimulation by the female. Distinguishable components of male courtship are described below.

Following

The male follows the female as she swims in a circle.

Tail-holding

The male seizes the tip of the female's tail in his bill and is towed behind her at, or below, the surface of the water (Fig. 2A). The male may assist locomotion with his forelegs or be pulled along passively. As mentioned above, the male may be stimulated to this behaviour by the female's circling, ventral-passing, under-passing, or regurgitation.

Continued grasping of the female's tail leads to loss of hair in two patches on either side of the midline (possibly from pressure by the tips of the male's premaxillae). We have no evidence that these paired bald patches arise, as suggested by Burrell (1927) from the use of the tail to plug the burrow with balls of mud, although generalised wear of the hair at the tip of tail in either sex may well be due to this.

Neck-holding

The male, previously engaged in tail-holding, releases his grip and climbs upon the female's back, grasping the fur on the nape of the female's neck with his bill (Fig. 2B). She responds by rolling onto her back (see 'clasping', above).

Marking

The male swims to the bottom, settles over a stone or other object, and everts the cloaca, from which is produced a yellow, mucilaginous liquid which

forms a cloud, settling over the object. After secretion of the substance, the male swims forwards, away from it. Although we have no direct proof of its function, we regard this as marking behaviour. Interestingly, the female has not been observed to show any interest in these marks.



Fig. 3. Platypus eggs in nest. This photograph was taken on Day 113 (13 November 1971) while the female was in the exhibition tank. The only disturbance involved was removal of the lid of the nesting box and the placing of two pieces of card (handled with surgical gloves and forceps) alongside the eggs. The three compartments of the nesting box are connected by small apertures to form an S-shaped chamber with a single entrance (out of sight) at the lower left of the photograph.

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Stretching

When normally at rest at the surface, the male has its four legs extended downwards and outwards from the body; the bill and tail are horizontal and half-submerged. During the period of courtship, the male was seen on a number of occasions to stretch itself at the surface, raising its bill and tail above the surface and extending its forelegs backwards and upwards along its sides (Fig. 2d). The significance, if any, of this behaviour is not known. It has not been observed outside the mating season.

COURTSHIP

Daily observations of the behaviour of the two animals was initiated on August 22, 1971 (Day 1) when it was noticed that the female had been making pellets of earth ("pugs" of Burrell, 1927, p. 129) from the material in the annex to her nesting box (described above). We thought that she might be about to seal herself off for oviposition, but this proved not to be the case, and pellets were not seen again, although the nesting box and annex were opened every 14 days thereafter for four months.

To summarise the records of 22 weeks, these are grouped below into five successive 28-day periods and a final period of 20 days.

Period 1 (Days 1-28, 22 August-19 September)

The female showed interest in the male from Day 3 and would enter the water when he came near. Tail-holding in response to circling was observed from Day 5 onwards. Frontal approaches and side-passing were first observed on Day 10, as was the single instance of regurgitation. Ventral passing was first observed on Day 11 and on this day very small bare patches were seen on the female's tail. Under-passing was first observed on Day 13. Marking was first observed on Day 16, as was stretching.

From Day 1 to Day 23 there was a gradual increase in intensity of female-male interactions, all of the above-mentioned components of behaviour (except regurgitation) increasing in frequency. From Day 24 onwards, the male was notably less responsive.

There was no obvious succession of the components of female behaviour, but it seemed that the frontal approach developed into side-passing, and ventral passing. Under-passing was always less frequent than side-passing.

By Day 28, two distinct bare patches had been worn on the female's tail.

Period 2 (Days 29-56, 20th September-17th October)

Although all components of behaviour observed during Period 2 were displayed during Period 1, the frequency and intensity were less, particularly on

the part of the male, who was often unresponsive to repeated approaches by the female.

Period 3 (Days 57-84, 18th October-14th November)

Early in this period, i.e. from about Day 60, the intensity of courtship increased. The male occasionally chased the female for the length of the exhibition tank.

Period 4 (Days 85-112, 15th November-12th December)

The general intensity of male-female interactions increased and new components were added. On Day 85 the male was first observed in neck-holding: the female responded almost immediately by rolling over on her back and apposing her ventral surface to his, but the two did not clasp. Claspings in response to neck-holding was observed on Days 86 and 105: on the latter occasion the pair remained clasped together for about 20 seconds, rolling over and over in the water. On Day 104 the male displayed an element of female behaviour, ventrally passing the female.

Cloacal grooming, by the female, was first observed on Day 86 and subsequently almost daily until Day 112. On Day 104 the female was observed to carry leaves from the bottom of the tank to the exit platform of the exhibition tank.

Period 5 (Days 113-140, 13th December-9th January)

On Day 113, the female entered the exhibition tank as usual at 1100. Examination of her quarters revealed two eggs (Fig. 3) in the nesting box (not in the adjoining earth-filled annex). While the female was in the exhibition tank, the male engaged in tail-holding, which the female accepted normally.

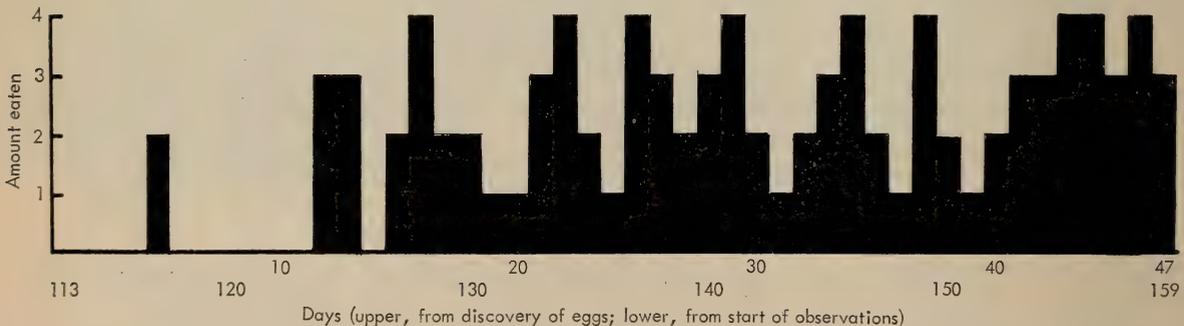


Fig. 4. Feeding behaviour during incubation and subsequently. 0, no feeding; 1, small amount eaten; 2, normal amount eaten; 3, more than normal amount eaten; 4, much more than normal amount eaten.

COURTSHIP OF THE PLATYPUS

The male was separated from the female at 1200 and the Platypus House closed indefinitely to the public. The female was given free access to the exhibition tank and one feeding tank, and close attention was paid to the amount of food eaten by her each night. The female did not leave the nest between Day 113 and Day 117 (when she emerged at night and fed normally). She did not feed again until Day 124. The pattern of feeding during Periods 5 and 6 is illustrated in Fig. 4.

The female made very few daylight excursions during Period 5, being seen only on Days 126, 127, 135 and 136. When in the water she was notably shyer than usual.

Period 6 (Days 141-161, 10th January-30th January)

Over this period the female fed every night, usually eating more than the normal (non-courting) amount. She made more frequent excursions in daylight and was less shy.

The nesting box was opened on Day 159 and the eggs were found to be shrivelled and without any sign of embryonic development. The male and female were reintroduced on Day 161 and showed no courtship behaviour or any obvious interest in each other apart from occasional slight aggression (bill-snapping) on the part of the female when the male passed near her.

DISCUSSION

We are aware of many shortcomings in the observations recorded above. The observational methods were not planned in advance and the system of recording involved several persons with no previous experience. The records are qualitative and we recognise from the daily notes that behaviour that was regularly repeated tended not to be logged by some observers: we have made some allowance for this in the analysis given above and in Table I in which the behaviour is further summarised.

It could be objected that it is inappropriate to study the behaviour of a crepuscular-nocturnal species in the middle of the day — and we accept this. It should be recognised, however, that daytime activity had been “grafted onto” the normal activity cycle two years previously and had been reinforced daily since then. It is likely that the intensity of male-female interactions was much greater outside the periods of observation and that the behaviour observed in the late morning and early afternoon did not cover the full span: certainly it seems not to have included copulation. Nevertheless, the behaviour described has a self-consistency that indicated ‘naturalness’, and our findings are reasonably in accord with those of other workers. Comparing our observations with theirs, a number of points of interest arise.

TABLE 1

RELATIVE FREQUENCY OF COMPONENTS OF COURTSHIP BEHAVIOUR

Period	1	2	3	4	5	6
Day no.	1-28	29-56	57-84	85-112	113-140	141-161
<i>Female behaviour</i>						
frontal approach	++	++				
side-passing	++	++	+++	+++		
ventral-passing	+	++	++	+++		
under-passing	+	+	+	+		
circling	*					
cloacal grooming				++		
regurgitation				*		
claspings	+++	+++	+			
leaf-carrying				++		
<i>Male behaviour</i>						
tail-holding	+++	+	+++	++	*	
neck-holding				++		
marking	+	+	++	++		
stretching	+	+	+	++		
claspings				++		

Note: + indicates infrequent (less than daily)
 ++ indicates relatively frequent (at least daily)
 +++ indicates frequent (several times daily)
 * indicates observed occurrence on only one day

Duration of courtship

It is possible that a low level of courtship may have passed unnoticed prior to our institution of regular observations in late August. Thus the period of 110 days between the beginning of observations and the discovery of eggs would appear to be the minimum duration of courtship in this case. Burrell (1927) has no direct information to offer on the duration of courtship. Fleay (1944) observed courtship over a period of 27 days. Courtship in the Bronx Zoo (Collins, 1973) was observed for no longer than 16 days.

At least two possible reasons come to mind for the great discrepancy between our observations and those mentioned above. The first is that the situation in Taronga Zoo was abnormal (although hardly more so than that obtaining in New York). The second is that observers who were limited to a view of the animals from above the water surface were able to see much less than we were able to through the glass walls of the display tank and therefore failed to observe much of the behaviour. We are inclined to the latter explanation, while not excluding the possibility of some abnormality in the behaviour of our animals such as the possible habituation mentioned earlier, and the possibility, mentioned below, that our records extend over an ovulatory cycle subsequent to the normal one.

COURTSHIP OF THE PLATYPUS

Time of mating

Burrell's two observations of mating were made in late August and late September. Less direct, but convincing evidence for the time of mating comes from the collection of eggs from nests. He found none in New South Wales earlier than 24th August or later than 6th November (Burrell, 1932). Based on records of egg-collecting elsewhere, Burrell suggests that mating is from July to August in central Queensland; from August to September in New South Wales; and from September to October in Victoria. If this is so, oviposition in our female was three months late.

A possible explanation for this is suggested by the events that led to the institution of regular observations; unusual behaviour of the female in September. As mentioned earlier, she had been making balls of earth and it is possible that this was either an expression of an earlier, failed, mating that took place at the usual time, or overflow activity arising from a strong but unfulfilled mating drive. It seems probable that the courtship observed by us was the outcome of a second oestrus, such as suggested by Burrell (1932), but we cannot tell whether or not this led to an unusually long courtship.

Role of the female

Our observations clearly demonstrate that the initiative of courtship rests largely with the female. The components of her stimulatory behaviour proceed in increasing complexity from initial interest, through the frontal approach, to side-passing, and ventral passing. Under-passing does not fit neatly into this sequence and is less frequently observed.

Role of the male and copulation

We agree with the other authors that following the female in a circle and tail-holding are early components of the male's responses to the female. Tail-holding is also released by ventral passing and under-passing on the part of the female, and by her regurgitation. We have observed transition from tail-holding to climbing on the back of the female and assert (contrary to Burrell) that the male can, and does, grip the neck of the female with his bill.

In 1971 we were convinced that copulation took place head to head and abdomen to abdomen, for such behaviour was observed at its peak 8 days prior to the discovery of eggs. However, this behaviour lasted only 20 seconds and we now interpret it as pre-copulatory. In a chance observation during the breeding season of 1974, the male was seen to move from a grip on the neck of the female to a sitting posture with his tail wrapped under the side of the female's tail (Fig. 2c), as described by Burrell in his 1909 observation and by Fleay (1944). For the position described by Verraux to have been functional, the tails of the two animals would also have needed to be oriented in this way. This sequence and final posture seems natural, whereas that observed by Burrell in 1921 does not. A possible explanation of his observation is that the male became dislodged from

the sitting posture while his barbed penis was still lodged within the female and that he was towed helplessly behind her, upside-down.

Burrell's assertion that the spurs of the male are used to lock into sockets in the feet of the female is based on his supposition that the tail-to-tail, upside down position of the male is normal for copulation. In the absence of any evidence that the spurs are so employed, his hypothesis is extremely weak: the copulatory position of the platypus seems to conform to the general mammalian pattern.

Marking

The platypus has a prominent sternal gland which increases in size in the male during the breeding season and is used to mark burrows with 'a foxy odour' (Burrell, 1927, p. 163). As we have shown, the male platypus also marks underwater. The nature of the secretion is unknown, but it is not faecal. The two mucous glands opening on either side of the wall of the cloaca by multiple apertures (Home, 1802) seem to be suitably situated for this function.

Cessation of feeding during incubation

Our observations are in accord with those of Fleay (1944) that the female does not feed for some days following oviposition. In the case recorded by Fleay, the female fasted for 12 days; in our case for 11 days (with one feeding on the fifth day).

ACKNOWLEDGEMENTS

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Mammals of Sturt National Park, Tibooburra, New South Wales

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ABSTRACT

A survey of mammals inhabiting a national park in the north-western corner of N.S.W. was undertaken during 1973 and 1974. Fourteen species were identified, many of which were new records for this region. Detailed observations were made of the habitat preferences, distribution and population numbers of several of the small mammals. It would appear that up to five mammal species can inhabit one area at the same time, particularly an area subjected to periodic flooding. However several of these mammals have discrete distributions and there is little overlap between different species. Numbers of animals changed noticeably during the study period, particularly those associated with periodic flooding. It is suggested that many of the small mammals living in the region surveyed are not arid-adapted but are dependant upon those areas scattered throughout the arid zone which have a habitat similar to that of a more temperate climate.

INTRODUCTION

In 1972 a large area of land in the north-western corner of New South Wales was set aside for the formation of a national park. This park, called Sturt National Park, now encompasses an area of approximately 200,000 hectares and further land acquisition will increase its size. Sturt National Park is situated approximately 340 km north of Broken Hill and comprises a variety of landforms typical of an arid and semi-arid environment. At the northern end of the park is the southern extremity of the Grey Range, with its associated mesa formations and eroded gullies. The remainder of the Park consists of the occasional stoney hill and numerous drainage basins which are influenced by Frome and Twelve-mile creeks (Figure 1).

Three major plant communities are recognized for this area (Beadle, 1948). These are the Mulga (*Acacia aneura*) association, the saltbush (*Atriplex*) association and the bluebush (*Kochia*) association. Because of the unusually good seasons during 1973-74 many grasses were also present, Mitchell (*Astrebla* spp.) and Flinders grass (*Iseilema membranaceum*) the most common. Climatically, Sturt National Park can be classified as within the arid area of Australia having a mean rainfall of under 200mm whilst the mean annual temperature is 27.4°C. Maximum temperatures are as high as 49°C. However during the survey period, record quantities of rain fell (over 760 mm of rain was recorded for the first five months of 1974).

During 1973 and 1974 I was able to live within the National Park and, in conjunction with other research, I conducted a survey of the mammals in this relatively little known area.

MATERIALS AND METHODS

Sampling of the mammal population was mainly achieved by use of Elliott live animal traps baited with a mixture of rolled oats, peanut butter and fried bacon. Over 4000 trap-nights were accomplished with an average trapping success of 14.5% (range 2-50%). Estimation of population numbers of the House Mouse (*Mus musculus*) and the Long-Haired Rat (*Rattus villosissimus*) was achieved by use of the Capture-Mark-Release Recapture method (C.M.M.R.). The calculations used are those outlined by Davis (1963). All animals were marked by using coded earholes and sprayed with a coloured dye (Vasco Stock Mark, V.S. Supplies Ltd.) to ensure rapid identification.

RESULTS AND DISCUSSION

1 EUTHERIANS

Order: Rodentia

Family: Muridae

(a) Forrest's Mouse (*Leggadina forresti*). Until recently this animal had not been recorded in N.S.W. Morton (1974) obtained two specimens from Fowler's

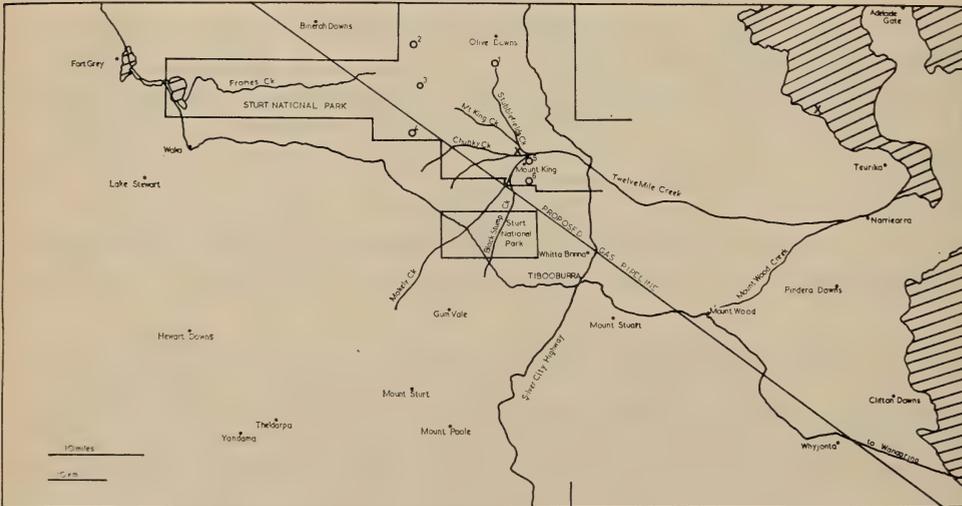


Fig. 1. Map of the north-western corner of N.S.W., showing principal study sites and the then western boundary of Sturt National Park. The eastern boundary had not been precisely delineated at time of writing.

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Gap Station, 110 km north of Broken Hill. To date only one specimen has been found in Sturt National Park. This animal was caught by hand after being disturbed from its nest. The nest consisted of a shallow burrow about 20 cm long made in the cracking soil underneath a flat rock. The area where the mouse was found was unusual for this species, being a flat-topped outcrop at the edge of the Grey Range. This type of outcrop is characterized by a silcrete type duricrust surface, cracking soil and shallow depressions similar to gilgais. Morton (1974) caught both specimens on flat, treeless plains whilst Watts (1972) and Parker (1973) describe the habitat of *L. forresti* as black soil alluvial flats and grassy plains. However, the areas at Fowler's Gap and Sturt National Park are similar in one respect, both contain cracks in the soil which are probably used for shelter.

The distribution of *L. forresti* is not limited to the Grey Range in Sturt National Park as several fragments of Forrest's Mouse have been found in owl pellets in an area surrounded by flat grassy plains.

(b) Sandy Inland Mouse (*Pseudomys hermannsburgensis*). According to Finlayson (1961) this murid is not commonly found east of Sturt's Line, however Watts (1974) recently found *P. hermannsburgensis* in three localities within Western Queensland. Only one specimen was captured within Sturt National Park, this animal was trapped in a sandy creek bed within the low hills found at the edge of the Grey Range. The area comprised of sandy soil with the dominant vegetation being shrubs (hakea etc.) and trees (gidgee, mulga, corkwood etc.). There was also extensive grass cover as well as many fallen trees.

(c) House Mouse (*Mus musculus*). Unlike Morton (1974) and Watts and Aslin (1974) I have found that the Tibooburra region was experiencing a virtual plague of these ubiquitous rodents. For instance, an area which yielded a 20% trapping rate (all animals trapped were *M. musculus*) was not uncommon during 1973-74. Systematic trapping along 48 km of the Gidgealpa-Sydney Gas Pipeline route (see Figure 1) covering eight different habitat types ranging from sandy creek beds to stoney hills, yielded a predominance of house mice in all habitats.

There appear to be two types of *M. musculus* in the area. One type was uniformly brown both dorsally and ventrally whilst the other type was fawn coloured dorsally with white belly fur. These two types have been previously described by Cleland (1918) and Jones (1923) whilst Johnson (1964) also mentions the phenomenon and likens the white form of mouse to the Mediterranean sub-species *M. musculus brevivostris*. Of 105 house mice examined at Sturt National Park, 56 were of the white form. No relationship between the colour forms of *M. musculus* and their distribution could be found.

To obtain some estimate of the numbers of house mice C.M.R.R. studies were carried out in an area where these animals were known to reside. This area was beside a small creek (Chunky Creek, see Figure 1) about 3 km from Mt. King homestead. Because of the closeness of semi-permanent water the vegetation was

relatively constant throughout the study period. The dominant plants being a mixture of sedge, *Leptochloa digitata* and a small bush (*Chenopodium* species) with a scattering of Coolabah trees (*Eucalyptus microtheca*) and an undergrowth of native clover (*Medicago* sp.). Twenty-five traps were laid at 10m intervals during a week in September 1973, then again, immediately after a large flood in March 1974. During the second period ninety-one traps were used.

Three mathematical methods were used to estimate population numbers:

- (i) the Schnabel (Krumholz) formula (Schnabel, 1938).
- (ii) the Schumacher-Eschmeyer Procedure (Davis, 1963).
- (iii) a graphical method outlined by Hayne (1949).

During September 1973, the three estimates of the mouse population using the three above methods were 14.7, 11.0 and 13.3. Considering the differences in the three methods the estimates were comparable and the mean of three estimates will be used, i.e. 13. The results of the 1974 trapping study were as follows. The three estimates of population size were; 36.3, 30.5 and 35.7. This gives a mean estimate of 34.

The difference between the two mean estimates was not entirely due to the difference in the number of traps used and the resultant larger area covered in 1974. By relating population numbers to the length of trap line (250mm in 1973, 400mm in 1974) the density of mice in 1973 was 0.05 mice per metre and in 1974 0.09 mice per metre. Consequently a higher density of mice in 1974 would seem to indicate a larger population in the trapping area during March 1974. A similar picture of population fluctuation has been observed by Newsome in his study of house mice inhabiting a reed bed in South Australia (Newsome, 1969a and b). Newsome found that population numbers fell during the dry months when soil suitable for nest-making (by burrowing) was limited. During the wetter months, particularly if in summer, numbers increased because of a greater availability of food and particularly nesting sites. It is interesting to note that a soil of similar characteristics to that found by Newsome (1969a) occurred at that site studied in the National Park. The ground consisted of a red soil (classified as Ug 5.3 by Stace *et al.*, 1968) and due to its high proportion of clay, tends to form large cracks when dry. During the drier months of 1973 the house mice had a limited amount of soft cracking soil in which to burrow and make nests. During the early months of 1974, particularly after the flooding experienced in January, the soil was ideal for breeding and there was a consequent increase in numbers of mice. The importance of the cracks in the soil is emphasized by Newsome (1969a), who points out that the microclimate within the crack provides a cool, moist shelter during the drier months.

(d) Plague or Long-haired Rat (*Rattus villosissimus*, Figure 2). This animal has only been seen occasionally in the area over the last century (Plomley, 1972). According to Finlayson (1961), its distribution appears to depend on local seasonal conditions, the animals spreading from western Queensland and the Northern



Fig. 2. Long-haired Rat (*Rattus villosissimus*)

Territory during wet periods. However, Watts and Aslin (1974) believe that *R. villosissimus* are always present in small numbers in pockets of favourable habitat from which they spread out during wet seasons. If this is so, then a pocket of favourable habitat for the long-haired rats was the area studied at Sturt National Park (the same area as described for *Mus musculus*. Here the rodents had established two types of burrow system.

The most common type was a shallow hollowing out of the soft, moist ground which lies beneath the dry, hardened crust of surface soil. This type of burrow appears to be used as temporary cover for the rats, possibly as protection against predators. The other type of burrow is more extensive and many of those dug up contained a nesting chamber of dried grass. This burrow resembled a small rabbit warren in that several side passages were always present and several separate burrow systems were usually found together in an area of soil suitable for burrowing. Finlayson (1939) describes a similar burrow system for *R. villosissimus* from the Lake Eyre Basin and I have found these burrows in the Cooper's Creek region (Windorah, Queensland). Nesting chambers would indicate that these rodents

were breeding and although no pregnant females were caught several immature animals were found.

However extensive trapping prior to the 1974 floods yielded no evidence of *R. villosissimus* either at the study site or in the surrounding area. If pockets of long-haired rats did occur in the Tibooburra area during the drier periods of the year they must have been spread out over a vast area and consequently migrating rats would have had to move a relatively long distance and from other reports they appear capable of such movements. There is evidence that *R. villosissimus* reached Spencer's Gulf via the Lake Eyre district in 1887 (Plomley, 1972).

Order: Chiroptera

Suborder: Microchiroptera

So far four species of bat have been found in Sturt National Park. These are the Little Brown Bat (*Eptesicus pumilus*), Lesser Long-eared Bat (*Nyctophilus geoffroyi*), Gould's Wattle Bat (*Chalinolobus gouldii*) and the White-Striped Mastiff Bat (*Tadarida australis*). All have been accidental captures either due to hitting a moving car or a windmill or else captured alive by mist net. Considering the number of deep caves found within the Grey Range it was expected that bats



Fig. 3. *Sminthopsis froggatti*

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would be found inhabiting these sites, but after thoroughly inspecting twenty of these caves no evidence of bat occupancy has been found.

2 MARSUPIALS

Order: Polyprotodonta

Family: Dasyuridae

Three species of this family have been found within Sturt National Park. The three are:

- (i) *Sminthopsis crassicaudata*
- (ii) *Sminthopsis froggatti* (Figure 3)
- (iii) *Planigale gilesi* (Figure 4)

Studies on *P. gilesi* and the two *Sminthopsis* species show an interesting ecological picture of several little-known species of marsupial. These three species have been found in similar areas within the National Park, however there is little overlap in habitat.



Fig. 4. *Planigale gilesi*

The habitat of *Planigale gilesi* is perhaps the simplest to describe. This habitat is as described for that of house mice at the Chunky Creek study site, i.e. red cracking soil, thickly covered by vegetation which is predominantly sedge and canegrass. This area is subject to periodic inundation with water. Other areas where *P. gilesi* have been found are the Bulloo Overflow (near Teuriko, see Figure 1) and the Channel country associated with Cooper's Creek (Windorah, Queensland). It is interesting to note that Aitken (1972) described the habitat of *P. gilesi* similarly and Troughton (1928) states that the habitat for two species of planigale (*P. ingrami brunneus* and *P. tenuirostris*) was beside large rivers in Queensland and N.S.W. and Parker (1973) gives a similar habitat for *P. ingrami*.

Both species of *Sminthopsis* also occur at the Chunky Creek site but are also much more widely spread. *S. crassicaudata* was found throughout the Park mainly associated with claypans and flood plains. *S. froggatti* was found primarily near creeks, recently flooded areas and gilgais as well as in the sandy hills of the Grey Range. This animal does not appear to be as widespread as *S. crassicaudata* and is perhaps restricted to a more specialized habitat which requires either soft ground for burrows or vegetation for cover. Where the three species were found together (Chunky Creek) there is a definite separation of the *Planigale* from the *Sminthopsis* species. Figure 5 shows the area at Chunky Creek where a trap line was laid and it can be seen that this line cuts through three different types of vegetation. Firstly the canegrass-chenopod association close to the creek, then a vegetation complex of *Bassia quinquecupis* as the dominant species and finally a stand of grass containing such species as Mitchell, Flinders, Umbrella (*Chloris acicularis*) and Ray (*Sporobolus actinocladius*). The results from five days trapping in June 1974 are shown in Figure 6, where the species of mammal found in each trap is given. It can be seen that the range of *S. froggatti* and *S. crassicaudata* does not extend into the chenopod complex whilst the planigale is only found within that particular habitat. Previous trapping has shown that when larger numbers of *P. gilesi* are present the same distribution occurs.

A similar situation appears to occur for the marsupial mice caught within the Park as that found for *Mus musculus*. *Planigale* appeared to utilize the cracks in the soil as cover and/or nesting sites and are possibly dependant on the periodic wetting of the ground to ensure the correct condition for burrowing. The influence of favourable conditions upon population numbers was illustrated by the numbers of *Planigale* caught at Chunky Creek during 1973-74. In January 1973, when the creek still contained pools of water, four *Planigale* were caught, then again in May another three were captured (all were released). After this, despite several months trapping, no more *Planigale* were found until February and March 1974 when eleven were caught. Similarly, no *Sminthopsis froggatti* were trapped during 1973, but sixteen were trapped in June 1974 at Chunky Creek.

The fall in numbers of *Planigale* during 1973 was perhaps due to the changed conditions during the drier months of the year but was possibly aggravated by the increasing numbers of house mice that occurred during that year. There is evidence

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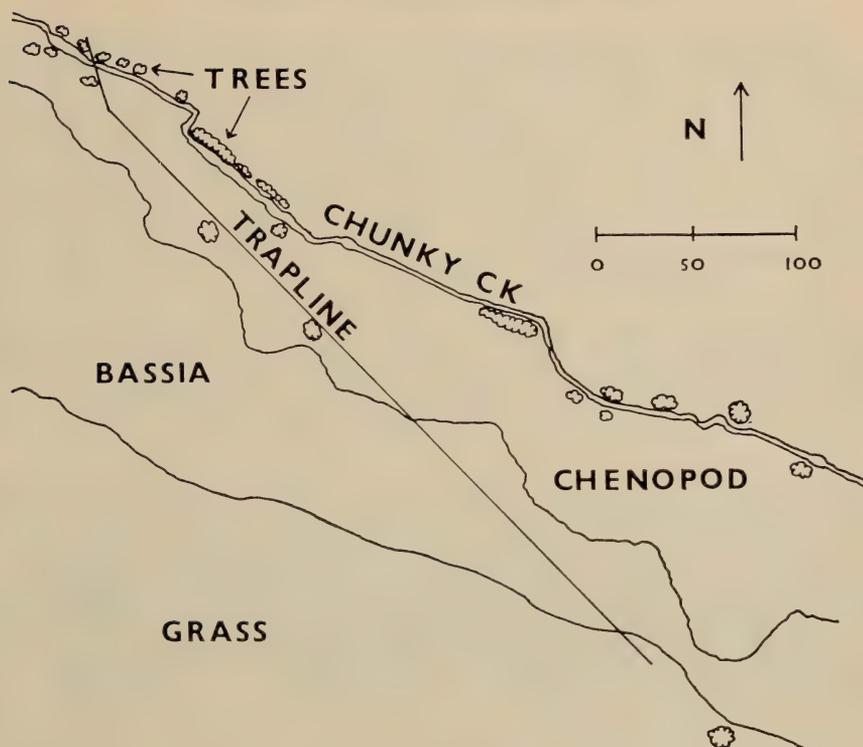


Fig. 5. The area of Chunky Creek used as a study site. Distances in metres.

of competition between *Mus musculus* and other mammal species not only for food (Caldwell and Gentry, 1965) but also for a place to live (Briese and Smith, 1973). In the present study competition for food eaten by both species would not have been intense as there were large numbers of insects (particularly the Spur-throated locust, *Austracis guttulosa*) in the area during 1973. Consequently an inability to occupy the cracks in the soil by *Planigale* when facing competition by house mice could have caused the fall in the number of marsupials. It is feasible that the marsupials were forced to move further away from the study site during the drier months, this bringing with it the greater possibility of predation. Aitken (1972) points out that the dense covering of vegetation associated with the habitat of *P. gilesi* would provide a barrier against aerial and terrestrial predation. Predators of small mammals in the Sturt National Park include feral cats, foxes, owls (remains of *Sminthopsis* sp., *L. forresti*, *Planigale* sp. and *Mus musculus* have been found in owl pellets) and fork-tailed kites. In appendix I is given a table of flesh measurements of these three marsupials.

Family: Macropodidae
 Subfamily: Macropodinae

Three species of the kangaroo family are found within Sturt National Park. The two most common are the Red Kangaroo (*Megaleia rufa*) and the Euro (*Macropus robustus erubescens*) whilst the Eastern Grey Kangaroo (*Macropus giganteus*) is not often encountered. The distribution of these marsupials within the Park is as would be expected from their known habitat preferences (Frith and Calaby, 1969). The occurrence of *M. giganteus* at Sturt National Park is the most westerly record of this kangaroo in this area of N.S.W. and it would appear that these animals are gradually moving westwards, their numbers increasing in areas west of the Darling River.

Some preliminary data is given in appendix II on various measurements taken from over 100 red kangaroos trapped in Sturt National Park during 1973-74 (the locations of the traps are shown in Figure 1, numbered 1 to 6). This data is being incorporated into a larger study on the migratory habits of red kangaroos.

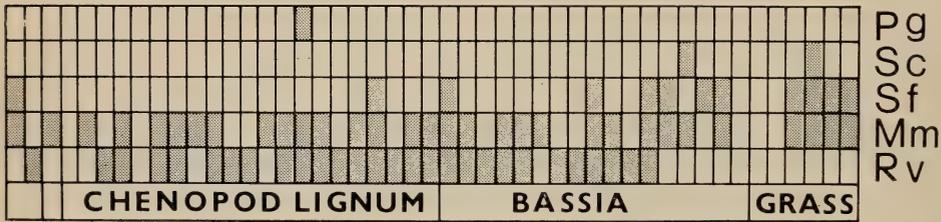


Fig. 6. Results of a trapping study in June 1974. Explanations of lettering is given in Table 1.

3 MONOTREMES

Although there is indirect evidence to show the existence of the Echidna (*Tachyglossus aculeatus*) in Sturt National Park, none have been sighted by the author. Use by the echidnas of the caves mentioned above appears to have occurred in the past. In the majority of caves echidna droppings were found. These droppings vary in length from two to eight cm and have a diameter of about two cm. They are composed almost entirely of clay mixed with crushed insect cuticle. This cuticle was found to be from ants, i.e. no termites (the predominant food for echidnas) were eaten by echidnas in this area. This is possibly due, not to any dietary preference for ants but to a low incidence of termites in the Tibooburra area (M. Griffiths, pers. comm.).

In the Cheviot Range in south-western Queensland a similar type of dropping as well as echidna quills and a nest made of grass (similar to that used by echidnas) were found in caves of the same structure as those occurring in the Grey Range.

4. FLOODING AND WILDLIFE

It is perhaps relevant here to give some general observations upon the influence of flooding on wildlife. There appear to be two patterns of flooding occurring

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during heavy rains. The first to be experienced is the "local" flooding formed by the large quantity of rain falling in a relatively short time, for instance approximately a year's rain (150mm) fell in Tibooburra within 24 hours during January, 1974. Local flooding has three major characteristics:

(a) It is quick to begin, does not last long, and the ground rapidly dries out after inundation.

(b) There is a strong water current not only draining off the slopes and across the claypans, but also down the various creeks in the area.

(c) Large depositions of silt occur. This can be as deep as 1.5m and is commonly found near the creeks and on the extensive claypans surrounding the waterways. Deposition of silt implies removal of soil from other areas. This removal is seen in the higher areas where channels are cut into the top 2m of ground.

Effects of local flooding are superficially disastrous. Any terrestrial animal unable to reach high ground will risk being swept away in the ensuing water movement. This, in fact, occurred during the floods in 1974 when large numbers of *Rattus villosissimus* were washed away and drowned in the Cooper's Creek. A few dead (presumably drowned) kangaroos were also seen in creeks draining into the Bulloo River Overflow (Narriearra Station, see Figure 1). Not all animals washed away would die however, many were capable of surviving on trees or small rises until the water drained away then they were able to repopulate an area. This appeared to be the case with *Sminthopsis crassicaudata*, one being caught just leaving the water after having been washed down Twelve Mile Creek.

Slow flooding occurs after the rains have fallen, sometimes over a fortnight later, when the larger rivers and lakes in the area gradually fill to capacity then spread out from their banks. This type of flooding was slow to occur and lasted a long time. The time factor involved in the slow inundation of the area allowed most animals to seek safety from the waters, but if local flooding occurred when the rivers were rising, many animals were trapped and died either from drowning or starvation. Consequently, slow flooding can be more disastrous than local flooding.

The effects of flooding upon populations of animals appeared to be influenced by three factors:

- (i) Habitat Selection
- (ii) Mobility; and
- (iii) Population Numbers.

(i) *Habitat Selection*. Because the habitat for *Planigale gilesi* was the "cracking" soils found near creeks or low flooding areas, these animals were sensitive to the spread out of water that occurred during slow flooding. For example, when the Bulloo Overflow flooded areas of cane-grass over 16 km from the main channel, the *Planigale* in that area were not able to escape the waters and endeavoured to exist on the cane-grass left exposed above the water.

(ii) *Mobility*. This applied mainly to the larger mammals, particularly the red kangaroo. These animals, even during small rainstorms, seek the highest point in the immediate area. Previous observations have shown that red kangaroos were to be found on the stony undulating hills around Mt. King and Olive Downs during the wet months and on the flats (using the shade trees in the creeks) during the drier months. Aerial traverses of flooded areas during early 1974 showed that few kangaroos were seen on the still wet flood plain or near the creeks. Most kangaroos sighted were found in the hills except those trapped by the rising flood waters.

During local flooding kangaroos sought high spots, e.g. sandhills, and stayed there until the surface water had run off, then spread out to drier areas being able to travel through mud up to 1m deep. Kangaroos staying on the sandhills and small rises were in danger of being trapped if the slow flooding due to river risings isolated their refuge. This was seen in areas flooded by the Bulloo River where one "island" in the flooded Overflow held 137 kangaroos.

(iii) *Population Numbers*. Large populations of mammals were more susceptible to flooding and its after effects than smaller populations. For instance the portion of long-haired rats killed by drowning in the Windorah (Qld.) area was far in excess of any other animal observed (over 60 carcasses were seen). Those left would also find it difficult to survive because of the relatively small area of dry land left. The trapping frequencies found during this survey were high compared with other surveys carried out in Australia. Calaby (1971) pointed out that in the United States catches are in the order of 20%, sometimes higher, whereas in Australia catches average 2 to 5%. Trapping frequencies up to 50% were found in the present study. Calaby then states that in times of high population density of particular species, large numbers of animals may be caught. It was this situation that was found during the survey described here, considering the high densities of *Mus musculus*. However small islands may also represent a situation where high densities of mammals may be found (Calaby, 1971). An island does not necessarily have to be a piece of land surrounded by water but is better defined as an area hospitable to certain species surrounded by an area through which movement is limited because of the vastly different environment found there, i.e. an area of acceptance surrounded by a sea of inhospitality.

Arid and semi-arid land cannot be strictly defined by an overall description because closer inspection yields a mosaic of differing habitats. Sometimes these may only be the size of a fallen log or a small pool of water. In a forest environment this mosaic is more complicated with numerous microhabitats existing in a small area (Calaby, 1966; Brereton, 1973). In the drier areas, although not as numerous, many such microclimates exist and some clearly defined examples are the surrounds of creeks (whether permanently watered or periodically flooded), stony outcrops areas of cane-grass found in drainage basins and even rubbish tips (now an established feature of a pastoral area).

It is this situation that exists in Sturt National Park. Small mammals, other than *Mus musculus*, were not caught in all places but only in those areas that can

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be defined as "islands". For instance, the trapping site at Chunky Creek yielded five different mammal species during a single night's trapping (*Mus musculus*, *Rattus villosissimus*, *Sminthopsis froggatti*, *S. crassicaudata* and *Planigale gilesi*) and gave a mean capture rate of 50%. An area away from the creek on the open ground, yielded only house mice and gave a capture rate of 5%. To further illustrate this point several different areas were chosen within the park and trapped for mammals. The results of this survey are shown in Table 1. It is apparent that those areas containing adequate ground cover for small mammals were the areas where the highest trapping frequency and species diversity were found, i.e. at Chunky Creek, Mulga Hills and gilgai.

Other examples of high densities of mammals in "island" situations were found outside the park. Fifteen *Planigals gilesi* were rescued from the cane-grass stalks protruding above the water in the flooded Bulloo Overflow. This was in an area of about 120 hectares and no other small mammals were found during several journies over the Overflow. Another example was seen on the Cooper's Creek where fourteen *Sminthopsis* (a mixture of *froggatti* and *crassicaudata*) were spotlighted along fourteen miles of road running near the creek.

A single similarity exists between all habitats where mammals were caught, i.e. the need for shelter from climatic extremes. Whether at Cooper's Creek, Bulloo Overflow, Chunky Creek etc., all habitat sites contained ground shelter which appeared to be used by the animals during the day. Consequently, these mammals are not necessarily adapted to desert living but are animals living within a more temperate environment within an arid area. Even during extensive dry times the characteristic shelters still exist and, as long as food supplies hold out, these animals should be able to survive. The recent geological past was climatically easier on the animals in the area. During the late Pleistocene the climate was cooler and more humid with perhaps a higher rainfall. Since the end of the Pleistocene the climate has become drier with several climatic fluctuations occurring (Keast, 1968; Jones, 1968). Such a sequence would allow establishment of arid adapted species in the drier areas. Those species adapted to a more temperate environment would either move further toward the still moist coastal areas or establish colonies in the islands of less arid habitat still retained in the arid areas. Such animals would possibly have been the native mice caught within Sturt National Park.

There is need for further work to be carried out on the situation of small native mammals within the arid zone, particularly in regards the situation described here, where periodic flooding occurs. Sheppe (1972) describes a similar situation in a Zambian floodplain and points out the remarkable adaptability of the small mammals to such an unstable environment. It would appear that those mammals associated with periodic flooding in Sturt National Park are equally adaptable.

TABLE 1

Species diversity and trapping frequency at various sites in Sturt National Park

Site	Habitat	Trapping frequency (mean %) and date	Species diversity
Mokely Ck.	Dense low vegetation beside creek, cracking soil.	19 (5/74) 28 (7/74)	1 (M.m.) 1 (M.m.)
Mokely Ck. (upstream)	Sandy creek bed.	20 (7/74)	1 (M.m.)
Mokely Ck. (branch)	Dense vegetation, cracking soil.	21 (7/74)	3 (M.m., R.v., S.f.)
Whittabreena Creek	Sparse vegetation, dry creek.	9 (6/74)	1 (M.m.)
Gilgai	Dense, low vegetation, damp cracking soil.	35 (6/74)	3 (M.m., R.v., S.f.)
Olive Downs Hills I	Sparse grass, sandy soil.	12 (6/74)	1 (M.m.)
Olive Downs Hills II	Tree cover, sandy and stony soil, logs.	36 (6/74)	3 (M.m., P.h., S.f.)
Flood Plain	Sparse, low vegetation, soft, silty soil.	12 (6/74)	3 (M.m., S.f., S.c.)
Chunky Creek	Dense low vegetation beside creek, cracking soil.	27 (3/74) 50 (6/74)	4 (M.m., R.v., S.f., P.g.) 5 (M.m., R.v., S.f., S.c., P.g.)
Sand Hill	Sparse vegetation, sandy soil.	14 (7/74)	1 (M.m.)

Dates trapped in parenthesis.

M.m. denotes *Mus musculus*

R.v. denotes *Rattus villosissimus*

P.h. denotes *Pseudomys hermannsburgensis*

S.f. denotes *Sminthopsis froggatti*

S.c. denotes *S. crassicaudata*

P.g. denotes *Planigale gilesi*

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APPENDIX I

Flesh measurements of three species of marsupials taken from live animals

Species	Head Length	Head and Body Length	Tail Length	Foot length
<i>Planigale gilesi</i>	2.14 ± 0.077 (10)	6.69 ± 0.94 (10)	6.74 ± 0.114 (10)	1.11 ± 0.017 (10)
<i>Sminthopsis crassicaudata</i>	2.77 ± 0.068 (8)	6.79 ± 0.091 (8)	6.37 ± 0.085 (8)	1.51 ± 0.032 (8)
<i>Sminthopsis froggatti</i>	2.78 ± 0.056 (18)	7.70 ± 0.155 (18)	9.59 ± 0.199 (18)	1.74 ± 0.045 (18)

All measurements in centimetres and given as mean ± standard error, number of animals in parenthesis.

APPENDIX II

Data on red kangaroos (*Megaleia rufa*) caught in Sturt National Park during 1973 (in collaboration with G. Wilson, National Parks and Wildlife Service).

- Body weights : Male: 57.7 ± 2.82*kg (n=53)
(range 9 to 95 kg)
Female: 25.1 ± 0.61 kg (n=74)
(range 9 to 37 kg)
- Pouch young : Mean age: 106 days (n=31)
(range 2 to 220 days)
Sex ratio: 20 ♂; 7 ♀

* Mean ± standard error.

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Observations on the Ecology of the Crayfish *Parastacoides tasmanicus* (Decapoda; Parastacidae) from South-Western Tasmania

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ABSTRACT

A typical habitat of the crayfish, *Parastacoides tasmanicus*, in south-west Tasmania is described. Data were collected in 1970 on the rainfall, temperatures, burrow water properties, soil and vegetation in a study area containing a thriving population of *P. tasmanicus*. Information is given on the structure of the crayfish burrows and the distribution of occupied burrows in relation to vegetation. The breeding cycle of the crayfish was determined and observations were made on the food of the crayfish. A provisional list of animals dwelling in occupied crayfish burrows is given.

INTRODUCTION

Parastacoides tasmanicus was first described as *Astacus tasmanicus* by Erichson (1846). Subsequently Haswell (1882) named it *Astacopsis tasmanicus*. Clark (1936a) in her taxonomic revision of Australian crayfish formed the genus *Parastacoides* and renamed *Astacopsis tasmanicus*, *Parastacoides tasmanicus*. The endemic Tasmanian genus *Parastacoides* has been the subject of considerable taxonomic attention, notably by Clark (1936a, 1939), Riek (1951, 1967, 1969, 1972) and Sumner (1971). At present six species of *Parastacoides* are formally recognized, though the Honours study of Sumner (1971) with its statistical analysis of morphological characters suggests that there may be only two distinct species, *P. tasmanicus* (Clark) and *P. inermis* (Clark).

Parastacoides tasmanicus is confined in its distribution to the south-western corner of the State, where it reaches its greatest abundance in areas of wet button grass (*Gymnoschoenus sphaerocephalus*) moors. If one accepts the species definitions of Sumner (1971), the distribution of *P. tasmanicus* becomes more extensive with the focus of distribution being still in the south-west of the State, but with populations extending to the central west coast and to the central north-western region of Tasmania (Sumner 1971, J. L. Hickman, B. Knott and P. Suter pers. comm.).

In contrast to the taxonomic attention, ecological studies of the freshwater crayfish of south-eastern Australia have been very limited. Prior to the study of

Newcombe (1970), no ecological study had been made of crayfish in the genus *Parastacoides*. General observations on the biology of Tasmanian parastacid crayfish have been made by Clark (1936a), Smith (1912), Smith and Schuster (1913), Lynch (1969), Williams (1968, 1974) and Riek (1969, 1972).

The present paper describes some aspects of the habitat and life history of *Parastacoides tasmanicus*. The species remarkable tolerance to pH has been described in another paper by Newcombe (In press).

OBSERVATIONS

The major portion of the data on the habitat of *Parastacoides tasmanicus*, the structure of the burrows, population structure and food was gained from the investigation of a population in an area near McPartlan Pass in south-west Tasmania (about 146° 13' west, 42° 52' south), (320m., a.s.l.). The study area contained a thriving population of *P. tasmanicus* and can be regarded as being

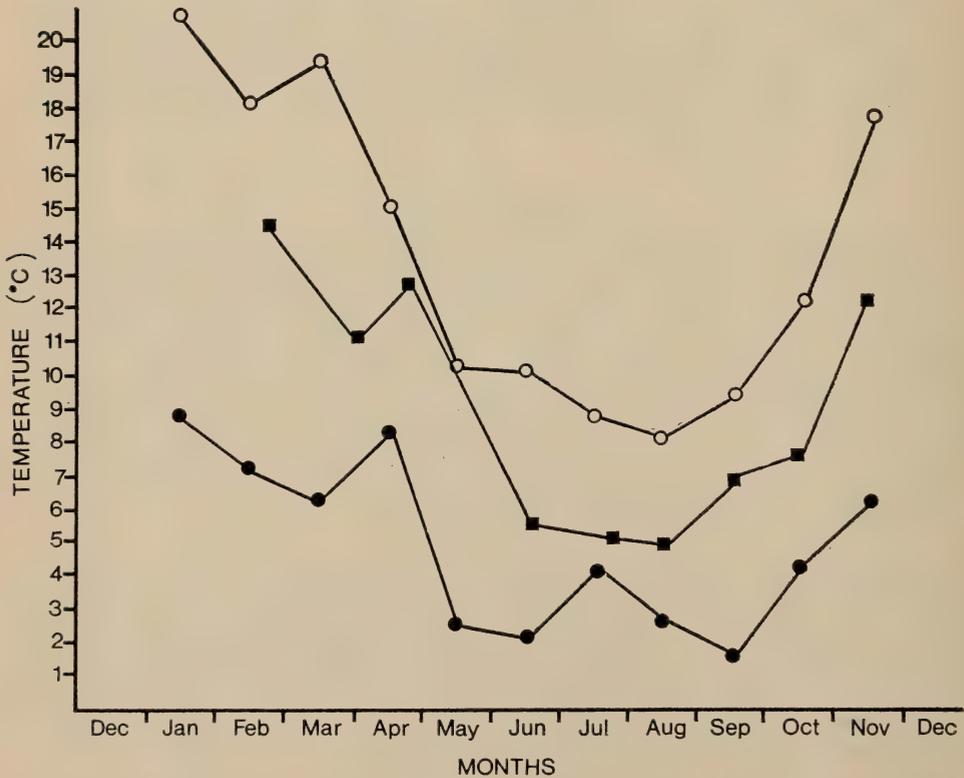


Fig. 1. Graph of mean monthly maximum air temperatures (O—O) and mean monthly minimum air temperatures (●—●) at Strathgordon and burrow water temperatures (■—■) in the study area in 1970.

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typical of the areas in south-western Tasmania populated by *P. tasmanicus*. An area, 91.44m (100 yds) by 91.44 m (100 yds), was marked out and field observations were made within this area, apart from the weather data which were obtained from nearby weather stations at the Knob and Strathgordon.

The soil of the study area conformed to the definition of moor podzol peat of Nicolls and Dimmock (1965) except for the frequent presence of a quartzite gravel bed, 16 to 90 cms from the surface.

Figure 1 is a plot of the mean minimum and maximum monthly air temperatures for 1970 near the area, along with the mean of burrow water temperature for each field trip. The burrow temperature was measured at a point 10 cms down from the burrow entrance. The burrow water temperatures as measured in three separate field trips (February, April, June, 1970) indicated that there was very little diurnal change in burrow water temperatures.

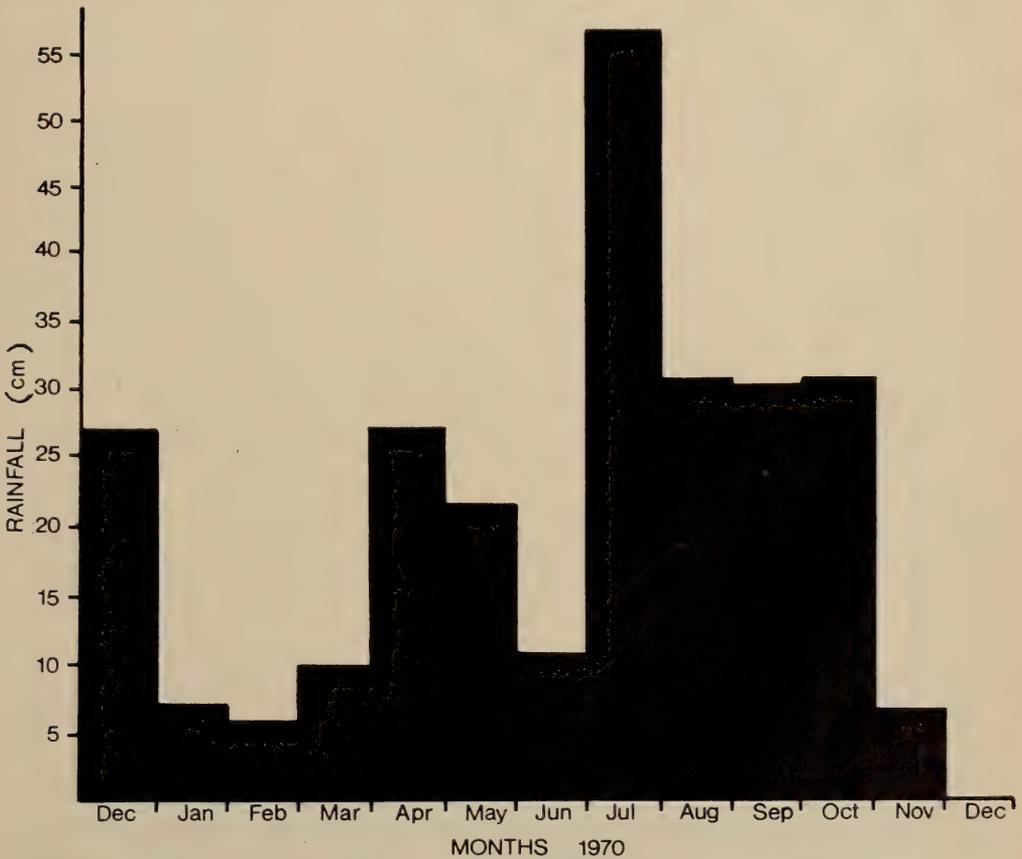


Fig. 2. Histogram of the rainfall recorded at Strathgordon in 1970.

As indicated in Figure 2, the area is subject to a high rainfall (circa 267 cms for 1970) with the maximum fall in late winter and spring.

Oxygen concentrations of water collected 10-15 cms down from the burrow entrances were determined by the standard Winkler procedure. As indicated in Fig. 3 the lowest oxygen concentration (circa 1 p.p.m. or 11% saturation) occurred in the hottest month of the year (February) and also at the driest time of the year. The months of February and March appear to be the period of greatest stress for the crayfish, with high burrow water temperatures and low concentrations of oxygen.

The pH of the burrow water was acidic and did not fluctuate through the year. The mean pH of the burrow system water was 4.4 ± 0.3 . Calcium concentrations in the burrow water are indicated in Figure 4. As can be seen they range from 0.125 p.p.m. (12.5 $\mu\text{eq/L}$) in June to 0.98 p.p.m. (49 $\mu\text{eq/L}$) in March. An analysis of burrow water from one field trip in November, 1970, gave mean values for the water of 5 burrows of:

Na : 173 $\mu\text{eq/L}$
 K : 17.9 $\mu\text{eq/L}$
 Mg : 75 $\mu\text{eq/L}$
 Ca : 35 $\mu\text{eq/L}$
 pH : 4.4

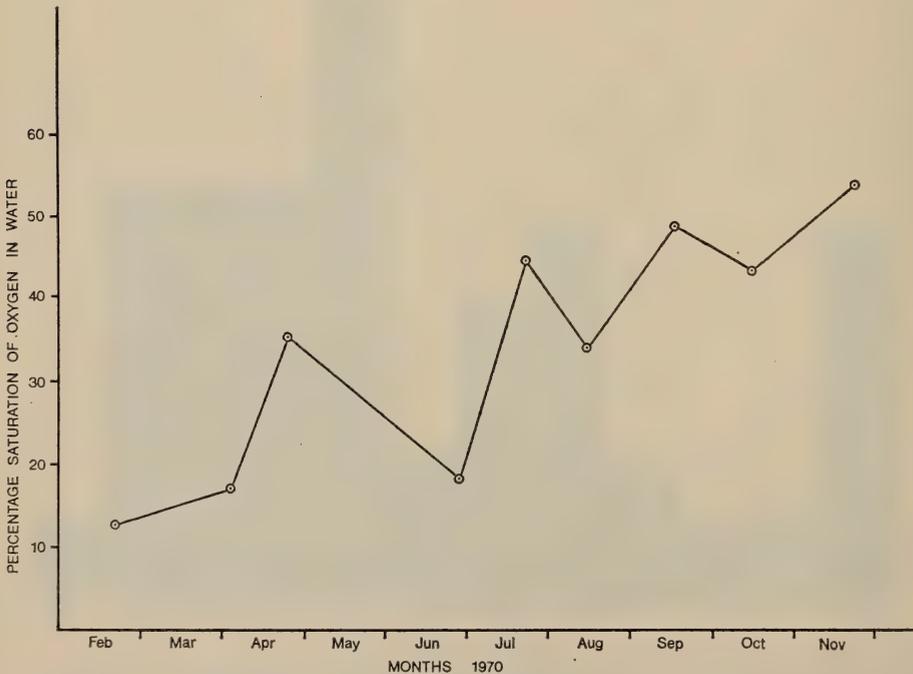


Fig. 3. Graph of oxygen levels in burrow water determined on each field trip.

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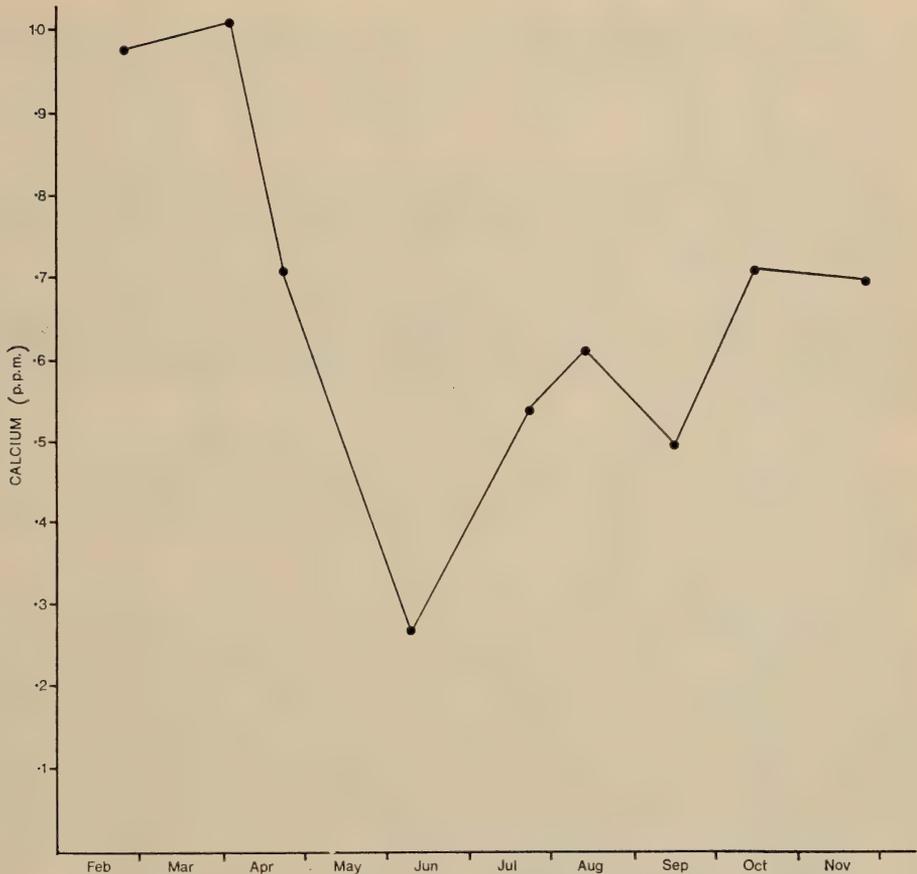


Fig. 4. Calcium levels in burrow water determined on each field trip in 1970.

These results indicate that the water chemistry is similar to that described by Buckney and Tyler (1973 a, b) for waters of south-western Tasmania. The burrow water is of a deep brown colour.

BOTANICAL DATA ON STUDY AREA

Five distinctive types of plant communities were found in the study area. The names given to the types of plant communities are not accepted definitions. Briefly the plant communities are:

1. *Button Grass Moor*. Large clumps of button grass (*Gymnoschoenus sphaerocephalus*) represent the dominant species and claim about 60% of the available ground. *Sprenglia incarnata*, *Bauera rubioides*, *Leptospermum nitidum*, *Boronia pilosum*, *Restio oligocephalus*, *Xyris* sp., were common sub-dominants in this community.

2. *Button Grass Swamp*. The button grass in small clumps claims about 20 to 30% of the available ground. With the clumps also occurs *Xyris operculata*, *Sprengelia incarnata*, *Bauera rubioides*, *Leptospermum nitidum*, while in the spaces between the clumps *Leptocarpus tenax*, *Baeckea leptocaulus*, *Lepyrodia tasmanica* and *Lycopodium* sp. occur.

3. *Marsh*. This community is dominated by *Leptocarpus tenax* and *Gleichenia microcarpa*. Dense entwining patches of *Hypolaena longissima* are present. In the understorey, *Lycopodium* occurs.

4. *Heath Sedgeland with Emergent Shrubs*. The common species in this community are *Bauera rubioides*, *Leptospermum nitidum* and *Gymnoschoenus sphaerocephalus*. Other species present include *Sprengelia incarnata*, *Restio oigocephalus* and *Boronia pilosa*.

5. *Swamp*. This community harbours a similar species range to that of the marsh community, with the addition of *Meloleuca squarria*, *Restio complanatus* and *Sprengelia incarnata*. The area consists of small islands of soil scattered over a complex of anastomosing channels. The channels have a characteristic white sandy substrate.

The communities described for the McPartlan Pass study site resemble some of those described in the Lake Edgar area by Macphail and Shepherd (1973). The Button Grass moor community resembles their button grass moor community, while the button grass swamp resembles their sedge swamp (*Gymnoschoenus-Xyris* association). The marsh community is somewhat similar to their swamp sedgeland community (*Lepidosperma-Leptocarpus-Xyris* association,) with the difference being an abundance of *Gleichenia* and an absence of *Lepidosperma* at McPartlan Pass. The heath sedgeland with emergent shrub community of this study is similar to that of the same name in MacPhail and Shepherd (1973), while the creek community of this study shows a similarity to their sedge swamp community.

DISTRIBUTION OF CRAYFISH IN RELATION TO PLANT COMMUNITIES

The various plant communities undoubtedly reflect varying levels of soil moisture, free water availability, water table levels and extent of soil development. Such factors can be expected to be of major importance in determining the distribution of crayfish. Within the study area, over a period of 25 days in August-September, 1970, a planned excavation of ten 9.144 m (10 yds) by 9.144 m (10 yds) plots, chosen at random, was carried out. All the burrows in each plot were dug up, the position of the burrow recorded and all the animals in the burrows collected.

As can be seen from Figure 5, the crayfish were largely confined to the three wetter plant communities; button grass swamp, marsh and swamp. Visual inspection revealed no burrows in the small area of heath sedgeland with emergent shrub community. While these data may apply for the area investigated, in many

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other areas *P. tasmanicus* occurs in a considerable diversity of wet plant communities ranging from closed scrub to rain forest gullies.

STRUCTURE OF BURROWS

A knowledge of burrow structure came from the excavation exercise and from the extensive sampling of *P. tasmanicus* populations that has been carried out by members of the Zoology Department in recent years in south-western Tasmania. A diagrammatic depiction of a typical burrow is presented in Figure 6.

The structure and depth of the burrow appears to be dependent on the amount of water available and the depth of the water table. In more swampier areas, with free surface water available, the burrow entrance is often found at the bottom of a pool, usually tucked underneath overhanging vegetation. Often

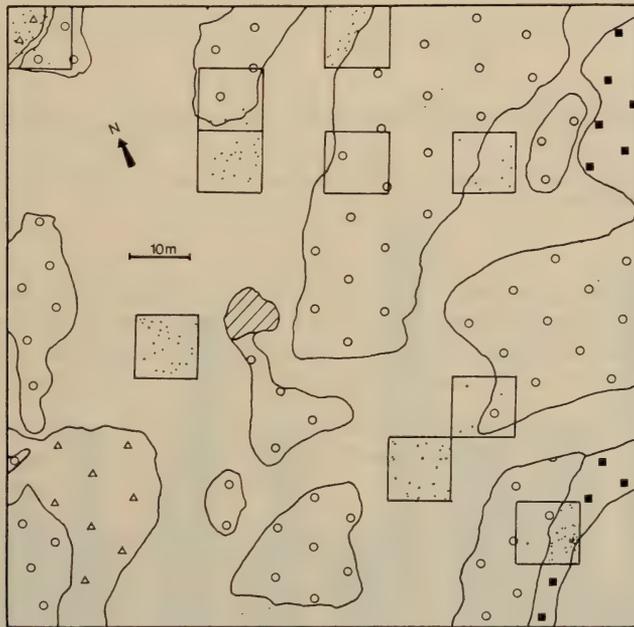


Fig. 5. Distribution of plant communities in the study area. The squares represent randomly selected areas which were excavated. Dots represent the occurrences of crayfish in the excavated areas.

- | | | | |
|---|---------------------|---|---------------------------------------|
|  | Button grass moor. |  | Heath sedgeland with emergent shrubs. |
|  | Button grass swamp. |  | Swamp. |
|  | Marsh. | | |



Fig. 6. Diagrammatic transverse section of a typical burrow system occupied by one adult *Parastacoides tasmanicus*.

two or three holes may open to the surface, but these usually meet below the surface. From the major burrow entrance, a branch may sometimes be found, leading to a small chamber beneath a large clump of vegetation. On drier soils, the burrow entrance is frequently found in clumps of vegetation.

The main burrow from the entrance invariably in going deeper takes a number of twists and turns and finally terminates in all systems, in a bottom chamber.

Where there is a quartzite gravel layer, the level of the bottom chamber is fixed, for the crayfish do not penetrate deeper than 1 to 2 cms into the quartzite layer. In drier areas, the burrows are deeper, because the water table is deeper. The burrows were from .4 to 1 metre deep in the study area. In the tunnel system of the study area, the burrows usually open at the base of vegetation clumps and are not very deep (7.7 to 15 cms). Recent digging activity in burrows may be indicated by shall chimneys, but these are never as well developed or as large as those created by species of *Engaeus*.

In the study area in the August-September excavation 185 burrows were dug up. The percentage of burrow occupancy was 83.5%. Of the burrows dug up, only four burrows were found which were interconnected. In each of these cases the interconnecting passages were full of mud and detritus and may be regarded as being disused. The relatively large diameter of the burrows suggest that adults

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carry out the active digging. Signs of small surface holes indicating possible digging by young crayfish were very uncommon. Young animals may build their burrows *de novo*, but it seems more likely that they occupy vacated adult burrows.

As a rule, there is one crayfish per burrow system, except for the case of females which have recently shed their young, in which case up to ten young hatchlings may be found in the burrow system. Adult individuals if kept together in captivity are very aggressive to one another. Leggett (1971) has described the agonistic encounters between individuals. If kept in a pair, the larger animal invariably wins.

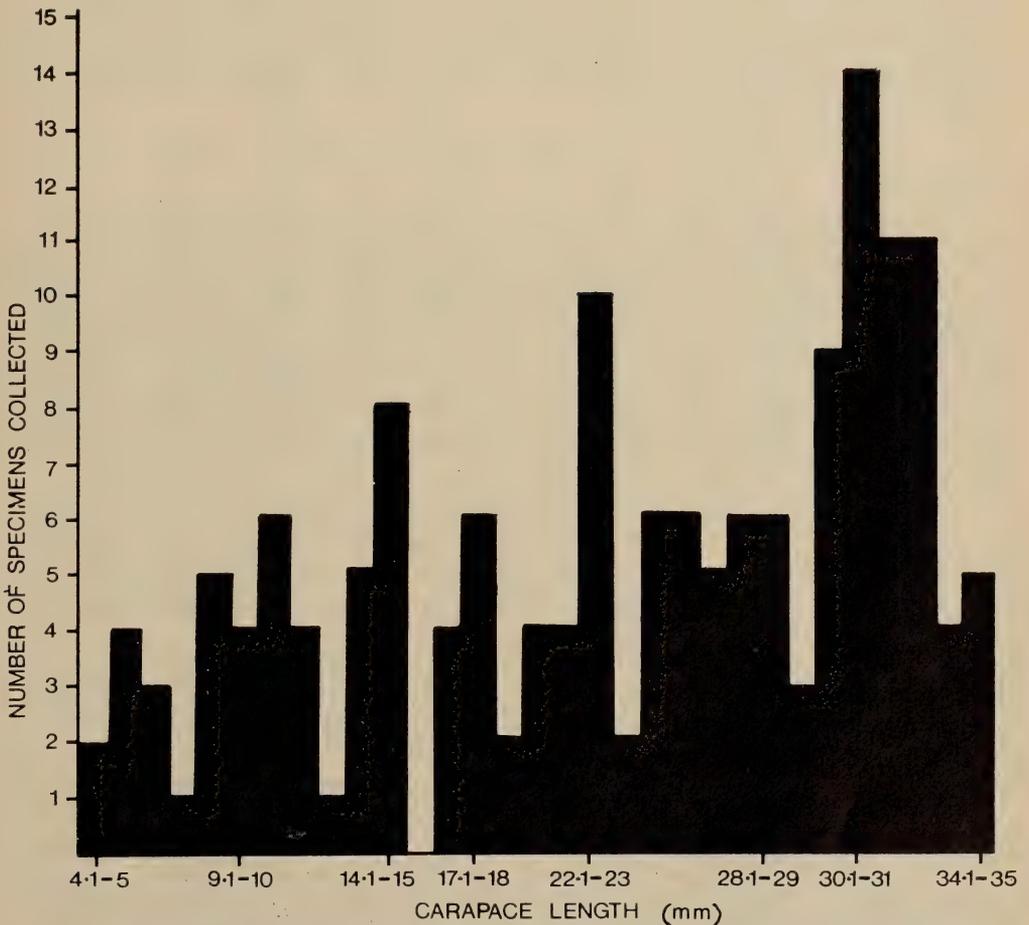


Fig. 7. Histogram of number of crayfish collected in the excavation of ten areas of the study area against carapace length.

POPULATION STRUCTURE AND DENSITY

In the excavation of ten plots in August-September, 1970, 154 crayfish were dug up. For the study area as a whole, at that time, this gives an upper population limit of 2,316 and a minimum population limit of 764 at the 95% confidence level. In terms of density, there is a maximum density of 1 animal per .985 m². A notable feature of the population at that time was the dominance of the population by large adults (22 to 35 mms carapace length). As the burrow sampling was very thorough, it is highly unlikely that many small individuals were missed. At the time of excavation, one could have reasonably expected to find a considerable number of small juveniles in the population, as a result of the young that presumably left their mothers in February-March of that year. This suggests that the population consists of slow growing mature adults (Figure 7) and that there is a high mortality of the juveniles each year with only a small fraction of them surviving the first year. The sex ratio in the study area was 40% males and 60% females.

BREEDING

From dissections of females collected in the field and on the basis of those carrying eggs, it appears that females in the study area become sexually mature at a carapace length of at least 24 mms. It appears that larger individuals with a carapace length from 32 to 36 mms are the most fertile. However, the percentage of females judged on the basis of carapace length to be sexually mature but which did not carry eggs was quite high. Only 40% of the eligible females carried eggs. Females of the eligible carapace length, dissected in September, contained mature but unfertilized oocytes. The relatively low level of fertilization in the population may partly explain the female-biased sex ratio.

The number of eggs carried per female ranged from 38 to 80, and the number of eggs carried per female increases linearly with increase in carapace length. Where y = number of eggs and x = carapace length in mms, the relationship between them is of the form, $y = 3.86x - 61.11$ with b having 95% confidence limits of -7.30 and $+14.02$.

As can be seen from Table 1, of the total number of eggs carried per female, the fraction carried per pleopod pair increases toward the tail, with the 2nd, 3rd and 4th pairs each carrying almost the same fraction of eggs.

Females carry eggs over winter from April through to November. The hatchlings then remain attached to the pleopods of the females through to February-March. The hatchlings are attached to the female's pleopods by their last two pairs of pereopods. The young leave the parent individually and not as a single group. Their carapace length at departure ranges from 3.5 to 3.8 mm. In captivity in a small container the young are at great risk from being eaten by the mother and they seek any shelter available. In the burrows, the young leave the mother and presumably flee from her and seek cover. When one digs up a

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burrow containing a female with young leaving her it is rare to find the young in close proximity of the mother.

TABLE 1

Distribution of eggs in relation to pleopod pair.

Animal No.	First pair Observed number (Decimal fraction of total)	Second pair Observed number (Decimal fraction of total)	Third pair Observed number (Decimal fraction of total)	Fourth pair Observed number (Decimal fraction of total)	Total number of eggs
1.	11 (.15)	18 (.25)	15 (.21)	27 (.38)	71
2.	13 (.21)	15 (.24)	18 (.29)	16 (.26)	62
3.	10 (.16)	17 (.27)	20 (.32)	15 (.24)	62
4.	14 (.19)	21 (.29)	21 (.29)	17 (.23)	73
5.	10 (.17)	17 (.28)	13 (.22)	20 (.33)	60
6.	11 (.18)	15 (.25)	17 (.28)	17 (.28)	60
7.	1 (.02)	14 (.33)	14 (.33)	14 (.33)	43
8.	9 (.21)	13 (.31)	10 (.24)	10 (.24)	42
9.	10 (.15)	14 (.21)	21 (.32)	21 (.32)	66
10.	8 (.17)	11 (.23)	13 (.28)	15 (.32)	47
Mean	fraction (.16)	(.27)	(.28)	(.29)	

The young appear to remain in the burrow system of the mother until the level of the water table rises with the rains and decreased evapo-transpiration in autumn and early winter. At this time of the year young crayfish may be picked up in hand-nets in small pools, tunnels and depressions. The young may be found in surface water under debris, stones, etc., or in unoccupied burrows. The reproductive cycle of the females largely agrees with the annual moulting cycle of *P. tasmanicus* meticulously determined by Mills (1973). Moulting was observed in March-April, which would, in females, be prior to oviposition and after the young had left.

Food

Ten specimens fixed in the field on field trips in March, June, August and October had the contents of the gastric mills examined. From this examination a list of food items may be compiled.

1. *Phylum Arthropoda:*

Class Insecta:

O. Hymenoptera,

F. Formicidae.

Pheidole sp. (only in one crayfish).

2. Order Coleoptera. Adults and larvae. (In 3 crayfish).

3. Class Crustacea:

O. Amphipoda,

Family Gammaridae.

Neoniphargus sp. (Only in one crayfish).

4. *Phylum Annelida.*

Class Oligochaeta. Setae regularly found.

5. *Plant Material:* By far the greatest amount of material in the gastric mills was plant material and by far the greatest amount of the plant material consisted of root material.

6. *Miscellaneous:* All gastric mills contained fine quartzite granules.

Thus, animal material is consumed by the crayfish, when this is available. Plant material is digested by the animals and forms the major part of their diet. Root material is the dominant type of plant material. There is good evidence for a cellulase enzyme being present in the crayfish gut (Newcombe 1970).

ANIMALS LIVING IN OCCUPIED *PARASTACOIDES TASMANICUS* BURROWS

For this part, the assistance of Mr. B. Knott and Dr. J. L. Hickman of the Zoology Department, University of Tasmania, was invaluable. From many field trips involving the digging up of *P. tasmanicus* burrows, a list of animal species in the burrows was compiled. Earthworms (Megascolidae) may be found in the soil surrounding the burrows, but in the water of the burrows all the macroscopic animals so far collected are crustaceans.

Class Crustacea

Order Copepoda

Sub-Order Cyclopoida

1. One species (South-West Tasmania).

Order Syncarida

2. *Micraspides calmani* (Crotty).
3. *Allanaspides helonomus* (South-West Tasmania).
4. *Allanaspides hickmani* (South-West Tasmania).

Order Isopoda

Sub-Order Phreatoicoidea

Family Phreatoicoideae

5. Undescribed genus. One sp. (South-West Tasmania).
 6. *Colubotelson* sp. (Same as large species on Pedder Beach (Bayly 1973).
- Family Amphisopidae
7. *Phreatoicoides* sp. 1 (Olga River Valley).

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- | | |
|--|--|
| <p>8. <i>Phreatoicoides</i> sp. 2 (Crotty).
<i>Asellota</i>
Family Janiridae</p> <p>9. Undefined Genus — possibly
<i>Heterias</i> (South-West Tasmania)</p> <p>10. <i>Pseudasellus</i> sp. Unpigmented
(West Tasmania e.g. Crotty)</p> <p>Order <i>Amphipoda</i>
Family Gammaridae</p> <p>11. <i>Neoniphargus</i> sp. 1 (eyed) large
(South-West Tasmania)</p> <p>12. <i>Neoniphargus</i> sp. 2 (eyed) small
(South-West Tasmania and West
Tasmania)</p> | <p>13. <i>Neoniphargus</i> sp. 3 (blind)
(South-West Tasmania and West
Tasmania)</p> <p>14. <i>Neoniphargus</i> sp. 4 (blind)
South-West Tasmania)</p> <p>15. Undescribed genus. Blind animals
very similar to <i>Niphargus pul-</i>
<i>chellus</i> (Crotty)</p> <p>16. Undescribed genus. Very similar
to <i>Gammarus australis</i> (South
West and West Tasmania)
Family Eusiridae</p> <p>17. <i>Paracalliope</i> sp. (Crotty)</p> <p>18. <i>Paraleptamphopus</i> sp. (South
West and West Tasmania)</p> |
|--|--|

It is very surprising that no insect adults or larvae occur in the burrows.

DISCUSSION

A brief description of some major features of a typical habitat of *P. tasmanicus* has been given. From the distribution of the species in Tasmania it is clear that it is restricted to areas of high rainfall and high water table level. Its distribution closely coincides with the distribution of tussock sedgeland and sedge swamp plant communities, where these communities have button grass, *Gymnoschoenus sphaerocephalus* as one of the dominants. As opposed to the judgment of Riek (1972), we do not regard *P. tasmanicus* as having streams and lakes as part of their normal habitat. All members of the genus *Parastacoides* are found in swampy ground; occasionally young individuals may be found in streams. One population of mature *P. tasmanicus* has been found in a small creek near Penguin in northern Tasmania in early December, 1973 (B. Knott and P. Suter, pers., comm.). Such a situation is highly unusual.

Previous accounts of parastacid crayfish burrow structure have been few. The depth of the burrows of *P. tasmanicus* appears to be primarily determined by the depth of the water table in the driest period of the occupied burrow's life. Consequently it varies considerably from locality to locality. *Parastacoides tasmanicus* has a burrowing ability, as has been often reflected upon by the authors in wet swamps under inclement conditions. We would not regard, as Riek (1972) does, *Parastacoides* as a 'moderate burrower', or *Geocharax* for that matter, especially in comparison to Riek's (1972) definition of 'strong burrowers' in the genus *Engaeus*. In our opinion, burrowing ability as opposed to burrow structure and choice of burrow site does not distinguish *Parastacoides* from *Engaeus* in Tasmania. The structure of engaeid burrows has been noted by Smith and Schuster (1913), Clark (1936 a&b), Riek (1969, 1972), Clark (1936b) noted that some

species of *Engaeus*, e.g. *E. fossor*, have solitary burrows while other species, e.g. *E. victoriensis*, form 'community' burrows. Riek (1969) describes some engaeids as living in family groups; with a family consisting of 'a mature pair of individuals and juveniles of one or two age groups'. *Parastacoides* lives in solitary burrows, and as observed by Leggett (1971) in the laboratory, individual *Parastacoides* when kept together are very aggressive to one another. Such aggression between individuals appears to greatly diminish any likelihood of social community or even grouping.

For *Engaeus fossor* in Tasmania it is our impression that this species also normally lives in solitary burrows and thus does not conform to the pattern of burrow occupancy ascribed to engaeids by Riek (1972). The same applies for *E. leptorhynchus*. Prior to this study very little had been published on the life history of parastacid crayfish. Clark (1936 a, b) concluded that the breeding season is in spring, after moulting. Hatching of the young, she concluded, occurred in December and January. Breeding and development in *Euastacus kershawi* has been described by Clark (1937) and aspects of the life history of the Marron, *Cherax tenuimanus*, have been described by Shipway (1951 a, b), Morrissy (1970 a&b, 1974). In New Zealand, Hopkins (1966, 1967 a&b) has described growth and breeding in the stream dwelling *Paranephrops planifrons*. The domination of the *P. tasmanicus* population by mature adults suggests that the population size is very stable and that both recruitment to the population and adult mortality are low in relation to the population size. A high mortality of juveniles can be expected. A situation of density limitation of recruitment is suggested for the marron (Morrissy 1970 b, 1974), and also for unexploited populations of *Astacus astacus*, Abrahamsson (1966).

P. tasmanicus females carry eggs over winter; the eggs hatch in spring (November) and the young leave the parent in February or March. Clark (1936 a&b) thought that for Tasmanian and Victorian parastacids the breeding season was a short one from spring to early summer (16 weeks or so). She overlooked the long over-wintering period of egg incubation. Hopkins (1967 a) found in *Paranephrops* the incubation of eggs extended from April to November and that the young left the mother in early December. Thus the breeding period for *Paranephrops* is long (25-26 weeks). However, as opposed to the situation in *Paranephrops* and *Parastacoides*, the marron *Cherax tenuimanus* appears to have a short breeding season covering spring and early summer (Morrissy 1970 b). Possibly the short breeding season may be due to high rate of larval development induced by relatively high water temperatures (bottom temperatures from 14-17°C in October and 16-25°C in December, Morrissy 1974), as opposed to the slow rate of egg and larval development in the low water temperatures experienced by *Parastacoides* and *Paranephrops*.

The majority of northern hemisphere astacid crayfish have a short breeding season usually occurring over spring and early summer, e.g. *Orconectes rusticus* (Langlois 1937), *Cambarus longulus* (Smart 1962), *O. obscurus*, *O. sanborni*,

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O. propinquus (Fielder 1972), *O. virilis* (Weagle and Ozburn 1972), or for a short period in late summer and autumn, *Procambarus clarkii* (Penn 1943), *Procambarus hayi* (Payne 1972). A relatively long breeding season involving egg-carrying over winter and the release of young in late spring has been found for European species of *Astacus* and for the North American crayfish, *Pacifastacus leniusculus* (Riegel 1959) and *P. trowbridgei* (Mason 1970). The method of attachment of the eggs to the female pleopods in parastacids has been described by Clark (1937) and Hopkins (1967 a). The number of eggs carried per pleopod pair in *P. tasmanicus* increases posteriorly.

This differs from the pattern in *Paraneohrops* (Hopkins 1967 a), where the greatest number of eggs are carried on the second and third pair of pleopods. The number of eggs carried by *P. tasmanicus* females varied from 36 to 79, which is higher than the 20 to 30 noted by Riek (1967). As for other crayfishes (e.g. Hopkins 1967 a, Abrahamsson 1966, 1971, Weagle and Ozburn 1972), the number of eggs carried per female increases linearly with increase in length of the female.

A number of observations have been made on the food of parastacids. Smith and Schuster (1913) noted that *Engaeus* species probably had a carnivorous diet. They found earthworms, insect larvae and 'probably land crustacea' in their gastric mills. Clark (1936 a&b) noted that in captivity species of *Euastacus*, *Cherax* and *Engaeus* ate earthworms, raw meat, fish and tadpoles. In their gastric mills Clark (1936 a) found 'mud and debris'. Clark (1936 b) also noted the propensity for cannibalism in captive parastacids. In the marron, *Cherax tenuimanus*, Shipway (1951 a&b) reported that they are omnivorous, while Morrissy (1970 b, 1974) found that the gastric mills of marron in farm ponds contained allochthonous plant material. Shireman (1973) found that marron in captivity preferred crayfish tails, fresh fish and catfish pellets in that order. They also ate plant material. In astacids, there is considerable evidence to support the idea that crayfish eat considerable amounts of plant material (e.g. Tack 1941, Bovbjerg 1952, 1970, Abrahamsson 1966). In *Parastacoides tasmanicus* plant material, especially root material, dominates the diet, though oligochaetes, some insects and amphipods may be eaten. Newcombe (1970) found good evidence for cellulase being present in the gut of *P. tasmanicus*. Whether this enzyme is produced by the cells of the crayfish or by symbionts is not clear. In both amphipods (Wildish and Poole 1970) and *Procambarus clarkii* (Yokoe 1960) cellulase has been found, and in both cases it appears that the cellulase is both of symbiotic and animal cell origin.

From the list of macroscopic animals found in *P. tasmanicus* burrows it appears that only crustaceans are found, in spite of the fact that oligochaetes, insects and molluscs are to be found in the surface pools of areas with high crayfish populations. The crustaceans found with *P. tasmanicus* have presumably evolved means to live a subterranean existence and also to evade or offset crayfish predation. There must be a strong selection pressure to push the crustaceans in such an adaptive direction. Possibly such a pressure is the need to survive in

dry periods, when in the button grass swamp areas of South-West Tasmania, the amount of standing surface water is very greatly reduced. At such times insects, oligochaetes and bivalve molluscs may survive by burrowing into the mud. In the case of some insects, this period may be spent in the adult phase. However, the requirement for continual free water by the crustaceans has forced them to adapt to living in the only standing free water readily available; that in the burrow systems of *Parastacoides tasmanicus*.

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The Identity of the Common Keyhole Limpet of South-Eastern Australia (Fissurellidae)

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The common, large species of *Diodora* from south-eastern Australia has been known since 1924 as *Elegidion audax* Iredale (1924). This binomen was introduced by Iredale to replace *Fissurella lineata* Sowerby, 1835, described from unknown locality, and its synonym *F. incii* Reeve, 1850 which was said to have been collected from "Raine Island, Torres Straits". Examination of material in the British Museum (Natural History) has shown that specimens of *F. incii* were wrongly localised and agree exactly with shells from New South Wales (compare figs. 1-6 with 7-15). There is also no known species in the Torres Straits north-eastern Queensland area that closely resembles *F. incii* (i.e. *lineata*).

Iredale (1924) argued that a new name was warranted on the basis of locality (in the case of *incii*) and on a point in Sowerby's (1835) description (in the case of *lineata*). Sowerby described the internal margin of the foramen (i.e. of the surrounding callus) as being truncated posteriorly in *F. lineata* and Iredale states that the southern Australian shell does not show this feature. However, Iredale's figured syntype (figs. 9-11) (a small specimen), and most small specimens of this species, do show a posterior truncation of the callus. Because Sowerby's original figure (which is presumably actual size) is only 23.3 mm long it would also be expected to show this feature.

A brief synonymy of *F. lineata* appears below.

Diodora (Elegidion) lineata (Sowerby, 1835). Plate 1, figs 1-15.

Fissurella lineata Sowerby, 1835: 7, pl. 78, fig. 68; Sowerby, 1866: 195, pl. 241, figs. 134, 135.

Fissurella incii Reeve, 1850, pl. 10, figs 69a, 8.

?*Fissurella australis*; T. Woods, 1877: 44 (non Krauss, 1848).

Glyphis lineata; Hedley, 1900: 95, pl. 3, fig. 11 (animal).

Fissurella mccoysi (T. Woods MS) Pritchard & Gatliff, 1903: 185 (nomen nudum).

Elegidion audax Iredale, 1924: 220, pl. 35, figs 5, 6.

Elegidion (err.) *audax*; Macpherson, 1966: 207.

It appears that the types of Sowerby's (1866) figured specimen of *F. lineata* probably came from the same lot as *F. incii* and both names appear on the labels with the material. None of the

specimens in the British Museum (Natural History) agree exactly with the figures given by Sowerby or Reeve, but in the case of Sowerby's figures these were often composite. One specimen closely fits the dimensions of one of the original figures of *F. incii* and all agree well in all but individual, minor details. There is little doubt that the specimens examined are part of the original series of *F. incii* and can be regarded as syntypes of *F. incii*. The types of *D. lineata* (Sowerby) appear to be lost. They were 2 specimens from the G. Humphreys collection and Sowerby (1835) states that they were "now in Mr. Cuming's (collection)". No trace of these can be found in the British Museum, but the original figure is a good one and there can be little doubt as to its specific identity.

<i>Dimensions:</i>	Length	Width	Height	Length of foramen
Figured syntypes of <i>lineata</i>	44.82 mm	29.60 mm	16.93 mm	3.84 mm
	38.22 mm	23.86 mm	12.80 mm	3.46 mm
Syntypes of <i>E. audax</i>				
Iredale				
largest	54.60 mm	35.20 mm	23.84 mm	4.62 mm
Iredale's figured specimen	18.17 mm	11.06 mm	5.76 mm	1.94 mm

Range: Burleigh Heads, S. Qld. (C. 98620) to Port Phillip Bay (Macpherson, 1966) and Flinders, Vic. (Burn, 1959). T. Woods (1877) recorded the South African species *Fissurella australis* Krauss from Tasmania and this was regarded by Tate & May (1901) as being a misidentification of *lineata*. May (1921), however, rejected the Tasmanian record of *lineata*.

Elegidion Iredale, 1924 is used as a subgenus of *Diodora* Gray, 1821 following Knight *et al.* (1960). The external appearance of the living animal is described by Hedley (1900) and Burn (1959).

ACKNOWLEDGEMENTS

I am grateful to the staff of the Mollusc Section, British Museum (Natural History) for their help during my visit. This work was supported by travel funds provided by the Ian Potter Foundation, the British Council, the Australian Research Grants Committee, the Science and Industry Endowment Fund, and the Trustees of the Australian Museum. I am particularly grateful to my wife for her assistance and for taking the photographs of the types in the British Museum. The other photographs were taken by Mr. G. Millen of the Australian Museum.

THE IDENTITY OF THE COMMON KEYHOLE LIMPET

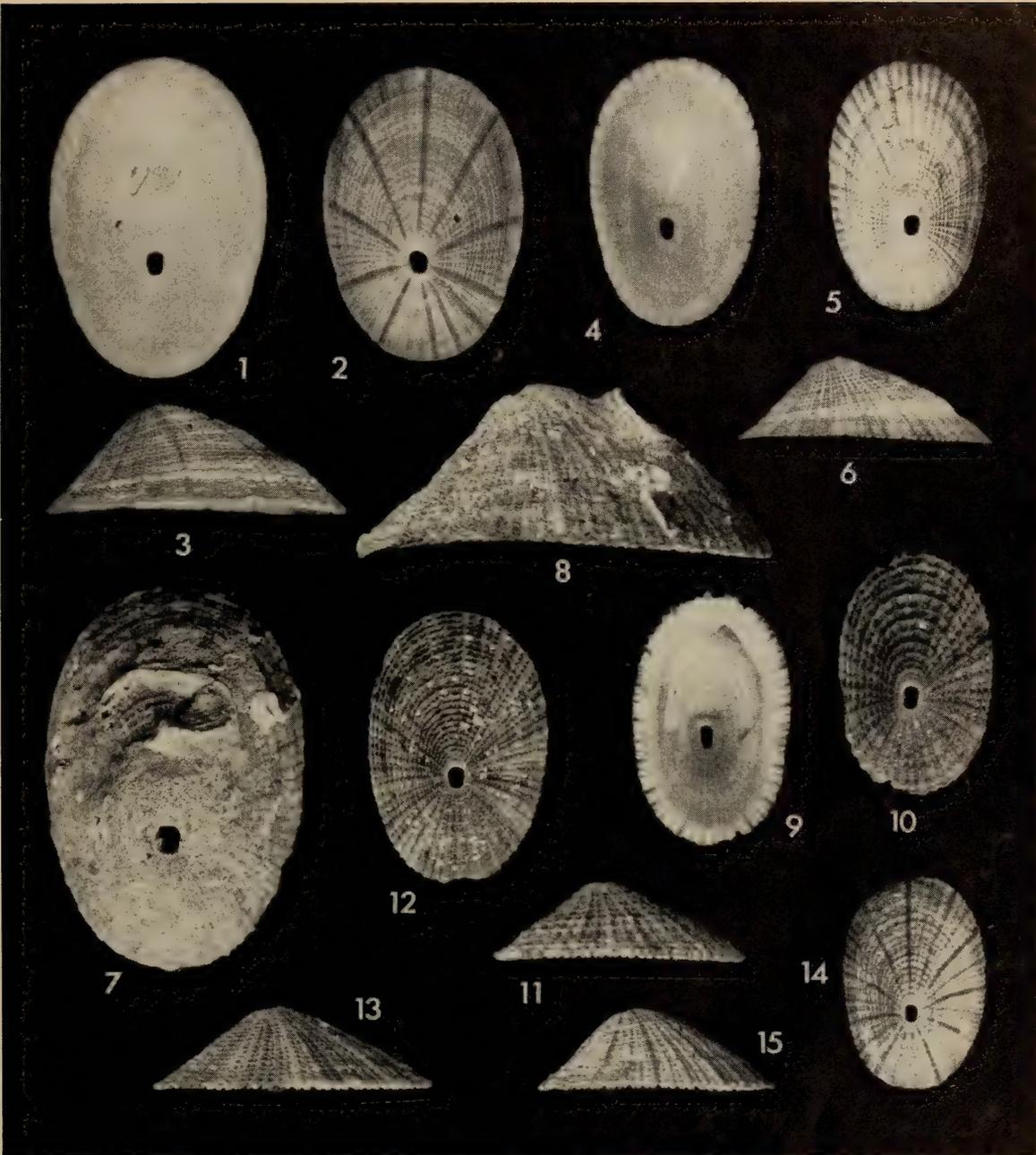


Plate 1. *Diodora (Elegidion) lineata* (Sowerby).

Figures 1-6 Probable syntypes of *Fissurella incii* (British Museum (Natural History registered number 197546).

7-11 Syntypes of *Elegidion audax* Iredale Twofold Bay, N.S.W. (C. 99178).*

12-13 Balmoral, Sydney Harbour, N.S.W. (C. 76384).

14-15 Kurnell, Botany Bay, N.S.W. (C. 88654).

* Australian Museum registered number.

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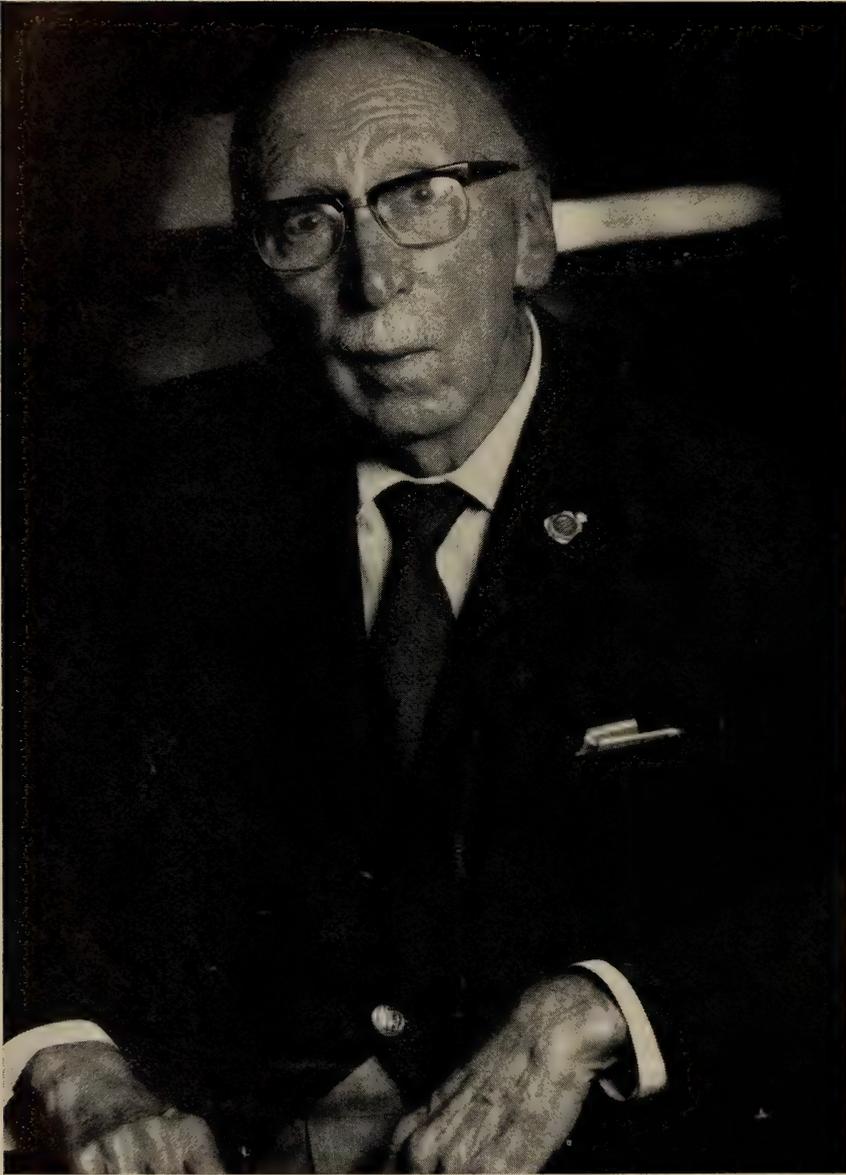
by the late GILBERT P. WHITLEY

ELLIS LE GEYT TROUGHTON, C.M.Z.S., F.R.Z.S. (1893-1974)

The death, at Concord, Sydney, on 30 November 1974 of Mr. E. Le G. Troughton ended the career of one who had served longer on the scientific staff of the Australian Museum than any other person in that institution's long history. He was the first full-time Curator of Mammals in any museum in Australia, a staunch conservationist, and a sociable friend of considerable charm. For over fifty years we were colleagues, working in adjoining rooms, so here I try to record some recollections of his life and work, albeit inadequately, so that he may be placed in his deserved niche in the history of zoology in Australia.

Ellis Le Geyt Troughton was born at Oxford, Kellett Street, Darlinghurst, Sydney on 29 April 1893. His birthplace is unrecognizable now, having been demolished for the King's Cross extensions to the Eastern Suburbs Railway. The *Sydney Morning Herald* (4 May 1893: 1) announced his birth to the wife of Donald E. Troughton, police magistrate, of Moree. His mother's maiden name was Elizabeth M. Ryrie. His boyhood haunts have also been largely destroyed by the inundation of the countryside for the Jindabyne Dam, New South Wales. Troughton was educated at West Bush Public School.

Troughton was one of several young Cadets appointed to the Australian Museum early in 1908. He was a general assistant at first, helping Hedley to label mollusca, many of which were mounted on nearly 25,000 tablets at that time. Next Troughton worked in the Department of Ethnology (the term Anthropology was not used in those days) and then Allan McCulloch trained him in taking care of the collections of all the vertebrates, in cataloguing literature, and in field work. Troughton helped McCulloch with the editing of the first part of the *Australian Zoologist* sixty years ago. Robert Etheridge was Director of the Australian Museum when Troughton joined the staff. There was no superannuation in those days and working conditions were poor, like the pay! Troughton was told that it was a privilege for him to hold a "gentleman's job" and that he was lucky to receive a salary of ten shillings (nominally one dollar) a week. Over the years, Troughton was to fight for the betterment of the underdogs. In 1909 and 1910 he studied zoology at Sydney Technical College and at the University of Sydney under Professor Thomas Harvey Johnston and passed the required examinations. "By way of a stimulus" the fees of successful students were refunded; otherwise cadets had to pay their own way. On 1 January 1913 Troughton was promoted to the permanent scientific staff as a Second Class Assistant, until he enlisted in the Army (First A.I.F.) in July 1916. He served as a stretcher-bearer



Ellis Le Geyt Troughton, C.M.Z.S., F.R.Z.S. in 1973.

Photograph by courtesy of the Linnean Society of New South Wales

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in the Fourth Australian Field Ambulance on the battlefields of France in 1917-1918. He visited London when on leave and was hospitably received at the British Museum (Natural History), where he studied Australian specimens, as he also did in the museums of Paris, Cologne and Monaco. On his way back to Sydney, he visited the museums of Cape Town and Durban and those of the mainland Australian States. He then became the first full-time Curator of mammals in any museum in Australia, when in October 1919, he was placed in charge of a new Department [of Mammals and Skeletons] in the Australian Museum. A year or so later he was promoted to First Class Scientific Assistant. He had already been largely responsible for the fine display of bleached skeletons against a plain black background in the public gallery.

The *Records of the Australian Museum*, part 3 of volume 13, published in December 1920, was facetiously referred to as the "Children's Supplement", because the early efforts of several young men on the staff therein saw the light of day: these included Troughton's "Notes on Australian Mammals, No. 1". His writings are fully listed in the Bibliography below. On the proposal of Professors T. Thomson Flynn and J. P. Hill, Troughton in 1936 was given the honorary status of Corresponding Member of the Zoological Society of London (C.M.Z.S.). Though writing did not come easily to him, Troughton was the author of many papers and popular articles on mammals. The book *Troughton's Furred Animals of Australia* recently passed its ninth edition and Iredale & Troughton's *Check-list of the Mammals recorded from Australia* (1934) still has not been supplanted. Troughton discovered numerous unnamed rats (studied in connection with Weil's Disease in Queensland and scrub typhus in Papua New Guinea), many bats, some whales and several marsupials from Australia and the Pacific. He has gone into historical details regarding the identity of Captain Cook's Kangaroo, the Grampus, Koala, New Guinea Dog, and other noteworthy mammals. Troughton revised Professor W. A. Haswell's mammal articles for the first edition of the *Australian Encyclopaedia*, to which he added one of his own, and he wrote a number of entries for the second edition. Though he worked principally on rats and marsupials, the bats seem to have been his favourite subject.

In 1922, he reported on Australian seals and sealing for the Commonwealth Institute of Science and Industry, appreciation of which was expressed by the then Prime Minister (Hon. W. M. Hughes). Another report was on "matters arising out of the invasion of Lord Howe Island by rats", at the request of the Lord Howe Island Board of Control (Chief Secretary's Department, Sydney) in 1923. Troughton proposed that owls be introduced to reduce the rats (a course of action induced by his observations on these birds and the rats on the Nullarbor Plain) and his recommendations were adopted. His curatorial work at the Museum involved care of human crania, whales, horses, cattle, sheep and all placental, marsupial and monotreme specimens, and the skeletons of all vertebrates. He supervised the setting up of habitat groups and gallery displays and attended to public enquiries. The latter included identification of human remains for Police; rats, etc., for the Health Department, and advising the Chief Secretary's

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Department concerning animal protection, open seasons and the issuing of collecting permits. He was on Government committees concerning Koala Park and on fur-farming and one formed to advise State and Commonwealth Governments on the export of animals through H.M. Customs. He was a member of the Green Committee concerning confiscated birds' eggs which came to the Australian Museum, and of the Grant Bird Collection Committee of 1926. He delivered many lectures and broadcasts.

Troughton joined the Royal Zoological Society of New South Wales in 1920 and was elected a Councillor in 1925. He was President in 1931-1932 and a Fellow in 1940. He was elected a member of the Linnean Society of New South Wales in 1921, became a Life Member, was on the Council from 1939 to 1972, President 1943-1944 and Vice-President 1944-1947. In 1928 he was a member of the Australian National Research Council. In 1932, as Secretary of Section D (Zoology) of ANZAAS, he sponsored a resolution that the Federal and State Governments conduct a biological survey of Australian fauna and flora. At the Auckland Congress (1937) he was Secretary of the Biological Survey Committee of ANZAAS whose recommendations about a decade later led to the establishment of the Wildlife Research Division of CSIRO. Troughton was a foundation member of the Fauna Protection panel of New South Wales, since replaced by the National Parks and Wildlife Service, serving on the panel from 1949 to 1963.

During the final phases of the Second World War, Troughton served in New Guinea with the Tropical Scientific Section, A.I.F., investigating the mammal reservoirs of scrub typhus, on the recommendation of, and reporting to, the U.S.A. Typhus Commission. I have not traced a copy of his official report, which was probably a "restricted" publication, but Mr. Troughton told me that no new species were named therein. Troughton had received medals for his army services in two World Wars: General Service and Victory Medals and Pacific Star and War Medal 1939-45.

"Troughtie", as he was known to his many friends, was of a mercurial disposition, very fond of company, and a member of numerous clubs, societies and sporting bodies. He was suntanned and wiry and had played much tennis, enjoyed climbing at Lord Howe Island, and kept fit at gymnasium in his younger days. He took part in swimming races at the Bondi Diggers' Club gatherings, and rode horseback on his field work in Mount Kosciusko National Park. He was a prominent member of a Lodge of Freemasons.

When so many younger people were away on war work, Troughton returned from New Guinea to find himself in charge of all the vertebrates again and referred to himself, with characteristic good humour as the Mammalornithoichthyherpetologist! In those days, curators were officially classed as "scientific assistants", a disparaging designation and always a handicap. Then we were known as ichthyologists, mammalogists, etc., which always had to be spelt over the telephone. In 1948, mercifully, the term was changed to "Curators".

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To give him his due, well before the Piltown skull was denounced as a fake in 1953, Troughton had always maintained that the mandible could not possibly have belonged to that skull.

Troughton was a life-long follower of the theatre and ballet and was fond of classical music. His memories of ballet went back to Adeline Genée, Anna Pavlova, and many later eminent artists and companies. When he was a boy, he may have seen Sir Henry Irving. Later, Troughton took small parts or was an extra on stage in various productions, not so much for the pay, but to study great acting. He could not sing but mimed and danced as a "galloping major" in one play, and he had a very strong vein of comedy. I remember him in jet doublet and hose in "Elizabeth and Essex". He acted in Gregan McMahon's Sydney Repertory Theatre Society productions in the 1920s and later in Miss Doris Fitton's Independent Theatre, North Sydney. He was a personal friend of Errol Flynn, Sir Laurence Olivier, Vivien Leigh, Elsa Lanchester, Bette Davis and other actors, of Sir Robert Helpmann and many ballet performers, as well as the entrepreneur, Hugh Ward, and his actor-zoologist son, Melbourne Ward. Because of his stage experience, Troughton was always in much demand at museum "smokos", when he alternated serious recitations (such as "The Hell-Gate of Soissons") with excruciatingly funny ones ("Mary", for example, or the young subaltern addressing his troops on the uses of the "Wife"), when anything was likely to happen—and did!

Troughton used to work back at the museum on his mammal books and papers until night-time, when the only sounds to disturb him were the newsboy's call and the clop-clop of horses' hooves on the roads now choked with motor traffic. On two occasions he was to encounter burglars: on one of these, in 1935, an intruder was hiding on the roofing of the "Birds of the Admiralty Islets" case—it was a wonder that he did not crash through the glass. "We know you're there, we've got you covered," called the police as Troughton crouched behind a pillar. The man came down (he had stolen some gold) and was arrested. Troughton, always the loyal public servant, pointed out to him the disgraceful nature of his offence, emphasizing that a museum is an educational institution. "Oh," said the culprit, "who cares? It's only the Government." Monty Hey, the genial policeman on point duty outside the Museum, moaned afterwards, "Only once in a hundred years the museum has a burglary and they didn't send for me!"

Ellis Troughton never married and his only brother predeceased him. Up to the time of his death, after a heart attack, he was a Research Associate of the Australian Museum, a Councillor of the Royal Zoological Society of New South Wales, and an Honorary Fellow of the Museums Association of Australia.

ACKNOWLEDGEMENTS

I am grateful to the Australian Museum for access to relevant material. Most of my account is based on memories of my long friendship with Ellis Troughton and on his *curricula vitae* and manuscript lists of papers. Portraits of him appeared in the *Australian*

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Museum Magazine (2, 1926:413 and 12, 1958:338) and in the newspapers, *Sydney Morning Herald*, 10 August 1931 and *Aftenposten* (Oslo, Norway), 15 October 1964. Others are held by scientific societies or are in private hands. I am grateful to the Linnean Society of New South Wales for the photograph of him, taken in 1973, reproduced herewith.

FIELD WORK AND TRAVELS

Mr. Troughton had travelled widely, always with the interests of the Australian Museum at heart. For example, during a brief stop at Canton Island, when being flown across the Pacific, he collected a shark for me. He had no preservatives, so informed a Customs official in Sydney that if he held the shark much longer, it would "declare" itself!

He had visited China, flown over the Burma Hump, and had had several trips to England, Europe and the United States, also visiting Japan and Antarctica. An argumentative old bushman, debating with him about the mode of reproduction of kangaroos, once scornfully referred to Troughton as a "Pitt and George Street naturalist". Nothing could have been further from the truth, for Troughton spent considerable periods in the bush, in many parts of Australia remote from those Sydney thoroughfares, and he also collected in the Santa Cruz Islands, New Guinea, the Moluccas and elsewhere. He preserved not only mammals but birds, fishes, insects, etc., for the Australian Museum.

His more important collecting localities, roughly in chronological order, were as follows.

His first field trip in 1912 at the age of 19 was to the Capricorn Group, Queensland, with A. R. McCulloch and Professor Thomas Harvey Johnston. The period from December 1919 to April 1920 was spent in South Australia (Farina, Eyre's Peninsula and Kangaroo Island) with C. M. Hoy, a representative of the United States National Museum, Washington. Troughton then secured 1,416 specimens for the Australian Museum at a total cost of £74. In 1920 and 1921, he collected at the Myall Lakes, Blue Mountains and the Nepean River, New South Wales, and made one of what was to be many trips to Lord Howe Island. From October to December 1921, with J. H. Wright as assistant, Troughton collected at several stations along the Trans-Australian Railway, across the Nullarbor Plain to south-western Australia, securing over 1,000 specimens for a total cost of £105. A long series of bats was collected at Hunter's Hill, near Sydney, in 1926. Later that year (July-August 1926), he visited Vanikoro and other islands of the Santa Cruz Group with A. A. Livingstone; these places were important as being the type-locality of some of Quoy and Gaimard's species. Good collections of marine life and ethnographical material were made at the same time, so that the Museum received rich stores of mammals (notably bats), birds, reptiles, fishes, shells, corals and insects.

In 1931, Troughton visited the National Park and Minnamurra, New South Wales, with A. J. Marshall. In 1934, at his own expense, he visited remote parts

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of Queensland and the Northern Territory with H. O. Fletcher (Atherton, Mount Isa, Alexandria Downs, Alroy Downs, the Barkly Tablelands and Avon Downs, etc., to the Gulf of Carpentaria). After travelling overseas in the 1930s, he had collected in every State of Australia and had visited New Zealand for ANZAAS.

His movements in New Guinea and environs in 1945 were shrouded in wartime secrecy, but he investigated mammal carriers of scrub typhus thereabouts with the Tropical Science Section of the Australian Imperial Forces and the American Typhus Commission. At about this period Troughton visited: Morotai (Moluccas, Indonesia), Biak, Schouten Island, and Japen Island (West Irian), Hollandia [now Sukarnapura] (West Irian), and in Papua New Guinea, the foot of the Cyclops Ranges and the Mount Lamington district (six years before the famous eruption), Lae, Port Moresby, Buna, and Dobodura, as well as Kiriwina in the Trobriands and Torokina, Bougainville, Solomon Islands.

In 1946, Troughton was one of a party to make a zoological reconnaissance of the Mount Kosciusko region, New South Wales. He spent long service leave abroad in 1949 and was Australian delegate to the International Technical Conference for the Protection of Nature, under the auspices of UNESCO and the International Union for the Protection of Nature, held at Lake Success, U.S.A.

He revisited Papua New Guinea with Norman Camps on the Australian Museum 1954 Expedition, paying his own expenses (£75). I have given elsewhere (*Rec. Austr. Mus.*, 24, 1956: 23) a map of their route. This was the first expedition on behalf of any museum in Australia to undertake field work in general zoology in New Guinea. In 1950-1951 Troughton revisited Mount Irvine, New South Wales and, after retirement, went abroad and to Japan and Papua New Guinea for science congresses and to Antarctica on a cruise.

He collected or discovered various new species of mammals, birds, reptiles, fishes, shells, insects and the external and internal parasites of animals. Some of these were very appropriately named after him. His own new names for taxa are listed at the end of his bibliography, below.

The Cave Owl was named *Tyto novaehollandiae troughtoni* by Cayley (*What bird is that?* 1931:32, pl. 5, fig. 4). I named one of his Vanikoro fishes *Teuthis troughtoni*, and Iredale a clam (*Tridacna*). Musgrave named a nycteribiid bat parasite, Livingstone a star-fish (*Parasterina*) and Johnston & Mawson, in 1941, a nematode (*Physaloptera troughtoni*), and doubtless there are, or will be, other taxa named in his honour.

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BIBLIOGRAPHY OF THE PUBLISHED WRITINGS OF
ELLIS LE GEYT TROUGHTON, C.M.Z.S., F.R.Z.S.

Books and papers are listed in chronological order, exact dates of publication being given when possible. Names of joint authors are given in brackets after titles of papers. Most items were published in Sydney unless otherwise stated.

1920

1. Notes on Australian mammals: No. 1.
Rec. Austr. Mus., 13 (3), Dec. 4, 1920, pp. 118-122, figs. 1-6.

1921

2. Exhibition of skull of *Bettongia cuniculus*.
Abstr. Proc. Linn. Soc. N.S.Wales, 356, Sept. 2, 1921, p. 2; *Proc. Linn. Soc. N.S.Wales*, 46, Nov. 2, 1921, p. 350.
3. Exhibition of yellow-footed pouched mouse, *Phascogale flavipes*.
Abstr. Proc. Linn. Soc. N.S.Wales, 356, Sept. 2, 1921, p. 2; *Proc.*, 46, Nov. 2, 1921, p. 350.

1922

4. A horse's hardship.
Austr. Mus. Mag., 1 (5), July 1922, pp. 150-151, fig. [Osteological note.]
5. Notes on Australian bats and the occurrence of *Chalinolobus gouldii*, Gray at Norfolk Island.
Australian Zoologist, 3 (1), Sept. 15, 1922, pp. 39-41.

1923

6. Exhibition of skins of a rare native rat, *Rattus mondraineus*.
Proc. Linn. Soc. N.S.Wales, 47, 1922 (Feb. 15, 1923), p. xxiv. [Not in Abstract.]
7. Exhibition of skulls of white-necked hair seal, *Eumetopias albigollis*.
Proc. Linn. Soc. N.S.Wales, 47, 1922 (Feb. 15, 1923), p. xxiv. [Not in Abstract.]
8. A revision of the rats of the genus *Leporillus* and the status of *Hapalotis personata* Krefft.
Rec. Austr. Mus., 14 (1), Feb. 28, 1923, pp. 23-41, pls. 5-6.
9. The 'honey mouse', *Tarsipes spenseerae*.
Austr. Zool., 3 (4), Aug. 15, 1923, pp. 148-156, pl. 23 and text-figure.

1924

10. Singular nesting sites of birds of the Nullarbor Plain.
The Emu, 23 (3), Jan. 7, 1924, pp. 215-217, pl. 33.
11. The stick-nest building rats of Australia.
Austr. Mus. Mag., 2 (1), late Jan. 1924, pp. 18-23, 5 figs.
12. Exhibition of insectivorous bat, *Nyctinomus australis* Gray, 1838, from Mittagong, N.S.W.
Abstr. Proc. Linn. Soc. N.S.Wales, 381, June 27, 1924, p. 1; *Proc.*, 49, 1924 (Feb. 18, 1925), p. xxv.
13. Exhibition of white-backed wren (*Malurus leuconotus*).
Abstr. Proc. Linn. Soc. N.S.Wales, 381, June 27, 1924, p. 2; *Proc.*, 49, 1924 (Feb. 18, 1925), p. xxv.
14. The honey eating marsupial mice of Australia.
Austr. Mus. Mag., 2 (4), Oct. 9, 1924, pp. 127-132, 3 figs.
15. The fruit bat group.
Austr. Mus. Mag., 2 (4), Oct. 9, 1924, p. 140, fig.

1925

16. The fruit bats or 'flying foxes' of Australia.
Austr. Mus. Mag., 2 (5), early Jan. 1925, pp. 169-174, 5 figs.

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17. Captain Cook's kangaroo. (By Tom Iredale & Troughton.)
Austr. Zool., 3 (8), Jan. 14, 1925, pp. 311-316, pl. 41.
18. Some strange African fruit-bats.
Austr. Mus. Mag., 2 (6), early April 1925, pp. 201-204, 3 figs.
19. A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms.
Rec. Austr. Mus., 14 (4), April 9, 1925, pp. 313-341, pls. 47-48 and text-figs. 1-2.
20. Exhibition of skull of adult female aboriginal showing remarkable recovery from injury.
Abstr. Proc. Linn. Soc. N.S.Wales, 394, Oct. 30, 1925, p. 2; *Proc.*, 50, 1925 (Feb. 15, 1926), p. xlv.
21. Exhibition of mounted specimen of *Caenolestes fuliginosa* from Ecuador.
Abstr. Proc. Linn. Soc. N.S.Wales, 395, Nov. 27, 1925, p. 2; *Proc.*, 50, 1925 (Feb. 15, 1926), p. xlvii.

1926

22. 'Vampire' bat.
Sunday News (newspaper, Sydney), March 1926, and fig.
23. Allan Riverstone McCulloch.
Austr. Mus. Mag., 2 (10), March 31, 1926, p. 346.
24. The mystery of marsupial birth and transference to the pouch.
Austr. Mus. Mag., 2 (11), July 13, 1926, pp. 387-391, frontispiece and 2 figs.
25. Recent expedition to the Santa Cruz Group.
Austr. Mus. Mag., 2 (12), Oct. 8, 1926, pp. 413-414, fig.
26. Striped opossums (*Dactylopsila*).
Austr. Encyclopaedia, 2, Oct. 11, 1926, p. 508. [Troughton also revised Haswell's articles on mammals for this encyclopaedia.]
27. A chapter on the bats of Australia and New Guinea.
In A. S. Le Souef and H. Burrell, *Wild Animals of Australasia* (London: Harrap), Oct. 1926, pp. 21-88, illustrated, plates, figs. 2-8 and 8 text-figs.
28. [Exhibition of the] skull of large bandicoot, *Isoodon macrourus*, from Clarence River, New South Wales.
Abstr. Proc. Linn. Soc. N.S.Wales, 403, Oct. 29, 1926, pp. 1-2; *Proc.*, 51, 1926 (Feb. 23, 1927), p. xlii.

1927

29. Fixation of the habitat, and extended description, of *Pteropus tuberculatus*, Peters.
Rec. Austr. Mus., 15 (5), April 6, 1927, pp. 355-359, fig. 1.
30. Cruising in the Santa Cruz. (By Troughton & A. A. Livingstone.)
Austr. Mus. Mag., 3 (2), April 11, 1927, pp. 41-48, 9 figs.
31. Further notes on marsupial birth.
Austr. Mus. Mag., 3 (2), April 11, 1927, pp. 53-56.
32. The Isles of Santa Cruz. (By Troughton & A. A. Livingstone.)
Austr. Mus. Mag., 3 (3), July 8, 1927, pp. 77-85, 11 figs.
33. Last days at Santa Cruz. (By Troughton & A. A. Livingstone.)
Austr. Mus. Mag., 3 (4), Oct. 13, 1927, pp. 113-125, 13 figs.
34. Hints for collectors: mammals.
Austr. Mus. [Circular, 4], Dec. 1927, pp. 1-6.

1928

35. A new genus, species and sub-species of marsupial mice (Family Dasyuridae).
Rec. Austr. Mus., 16 (6), June 11, 1928, pp. 281-288, pl. 39.
36. Sea cows. The story of the dugong.
Austr. Mus. Mag., 3 (7), July 13, 1928, pp. 220-228, 7 figs.

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1929

37. A new genus and species of bat (Kerivoulinae) from the Solomons, with a review of the genera of the sub-family.
Rec. Austr. Mus., 17 (2), June 26, 1929, pp. 85-99, fig. 1.
38. New forms of mosaic-tailed rats (*Melomys* and *Uromys*) from Hinchinbrook Island, Queensland. (By Troughton & A. S. Le Souef.)
Austr. Zool., 6 (1), Aug. 13, 1929, pp. 96-99.
39. Note on the occurrence of a second species of fruit-bat (*Pteropus scapulatus*) in New South Wales.
Austr. Zool., 6 (1), Aug. 13, 1929, pp. 104-106.
40. A new fruit-bat (*Pteropus rayneri* Group) from the Solomons.
Rec. Austr. Mus., 17 (4), Sept. 4, 1929, pp. 193-198.
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1930

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1935

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 [Ed. 7], 1962, " "
 [Ed. 8], 1965, " "
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1948

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1950

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1952

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1955

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1956

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1957

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1958

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Cats, Marsupial, 2, pp. 287-288. z
Dolphins, 3, pp. 266-267.
Dugong, 3, p. 307.
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Koala, 5, pp. 203-205, pl. 202 A and text-fig.
Mammals, 5, p. 471, coloured pl. 470 A.
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Rodents, 7, p. 476.
Seals, 8, pp. 54-56.
Spiny ant-eaters, 8, pp. 241-243, fig.
Tasmanian Devil, 8, pp. 437-438, fig.
Thylacine, 8, pp. 495-496, fig.
Water-rats, 9, p. 195.
Whales, 9, pp. 268-273.
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1959

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149. The marsupial fauna: its origin and radiation.
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1960

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1962

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1963

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1964

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Abstr. Proc. Linn. Soc. N.S.Wales, 727, June 3, 1964, p. 3; *Proc.*, 89 (3), 1964 (May 7, 1965), p. 382; correction to *Abstract* 727, 1964.
154. Koala — orphan of the gum-trees.
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1965

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158. Note from an Australian mammalogist on usage of the common name 'possum'.
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1966

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1967

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In D. F. McMichael (ed.) *A Treasury of Australian Wildlife* (London: Ure Smith), Nov. 15, 1967, pp. 22-31, 7 figs.
162. Bandicoots — rare and otherwise.
Ibid., pp. 32-41, 5 figs.
163. Kangaroos and wallaroos.
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164. The koala.
Ibid., pp. 54-60, 2 figs.
165. Marsupial native and tiger cats.
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1968

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1971

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A.N.Z.A.A.S. 42nd. Congress (Port Moresby, Papua) Programme, 1970, p. 98 (title only); *Proc. Linn. Soc. N.S.Wales*, 96 (2), Sept. 15, 1971, pp. 93-98, figs. 1-2.

1973

168. Troughton's furred animals of Australia.
(Sydney: Angus & Robertson), 8vo., pp. i-xviii + 1-314, col'd. pls. 1-25 and map. Ninth edition revised and abridged of no. 83, above, 1973. [Virtually 10th ed., 1974.] Mr. Troughton also wrote to the Daily Telegraph newspaper, Sydney, protesting against the building of an airstrip on Lord Howe Island.

LIST OF JOINT AUTHORS

Finlayson, H. H.	See item no. 155.
Iredale, T.	17, 54, 55, 69 & 151.
Kirkpatrick, T. H.	155.
Le Souef, A. S.	38, 41, 63 & 65.
Livingstone, A. A.	30, 32 & 33.
McMichael, D. F.	155.
Morrison-Scott, T. C.	155.

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**Studies of an Island Population
of *Antechinus minimus* (Marsupialia, Dasyuridae)**

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ABSTRACT

Field studies including a grid trapping and mark, release, recapture programme, of an island population of *Antechinus minimus* indicated that population density was exceptionally high (80 individuals per hectare). Males were significantly more mobile than females. Although the sequence of life history events closely corresponds to that of most other members of the genus, the timing of breeding is 2-3 months earlier than in the other south-east Australian species. An hypothesis for this reproductive phase difference is put forward.

INTRODUCTION

Of the four south-east Australian species of the dasyurid marsupial genus *Antechinus*, *A. minimus* (the swamp phascogale) is the least common and most restricted in distribution. The mainland subspecies *A. minimus maritimus* seems to be limited to a few scattered coastal localities from Robe in South Australia to Wilson's Promontory in Victoria (Wakefield and Warneke, 1963, 1967) and the Casterton district in western Victoria.

The only member of the genus on which there is much recent literature is *A. stuartii*, a common eastern Australian species (Barnett, 1973, 1974; Braithwaite, 1973, 1974; Marlow, 1961; Wood, 1970; Woollard, 1971; Woolley, 1966). Most work on *A. minimus* has been taxonomic (Finlayson, 1958; Tate, 1947; Wakefield and Warneke, 1963) although Green (1972) supplied notes on some broader aspects, including field observations, of the Tasmanian and Bass Strait islands nominate form.

The present paper reports on some findings, principally concerning population density and reproductive biology, of a field study of an insular population of *A. minimus*.

MATERIALS AND METHODS

1. STUDY AREA

Field work was carried out on Great Glennie Island, an island in Bass Strait about 6 km west of Wilson's Promontory. The island is elongate (N-S), about 2.5 km long, with an area of approximately 66 hectares (160 acres). The study area was on a northern slope in the Glennie Cove region at an altitude below 50 m.

The parent material is a grey, coarse-grained granite which is locally weathered with the development of coarse, sandy and often humus-rich soil.

Being a relatively small unprotected land mass, Glennie Island has a uniform maritime macroclimate. It is assumed that weather conditions are comparable with those of the nearest Bureau of Meteorology weather station, the Lighthouse at South-East Point, Wilson's Promontory, at an altitude of 100 m (see Bureau of Meteorology, 1969).

The vegetation of the study area is relatively uniform in character and typical of vegetation of much of the island. In the more rocky and sheltered situations there is a closed heath structural formation to a height of about 2 m. The upper stratum of dominant plants consists of a diversity of shrubs including silver banksia (*Banksia marginata*), coast tea tree (*Leptospermum laevigatum*), white correa (*Correa alba*), dusty daisy bush (*Olearia phloggopappa*) and common boobialla (*Myoporum insulare*). There is usually an understorey of *Poa* tussocks, the density of which appears to depend upon the intensity of light penetrating the shrub layer. In exposed areas where soil is often humus-rich and moderately deep, tussock grassland of the blue tussock grass (*Poa poiformis*) predominates, often interspersed with small shrubs, especially hoary sunray (*Helipterum albicans*), and many low succulent herbs including bower spinach (*Tetragonia implexicoma*), saloop (*Rhagodia hastata*) and rounded noon-flower (*Disphyma australe*).

2. FIELD TECHNIQUE

Three visits to Glennie Island in 1975 took place in April, May and September. For the collection of data on movement, home range and population density a programme of grid live-trapping was undertaken, using aluminium Elliott Type B traps (32 cm x 9 cm x 9 cm). A rectangular grid of five columns and six rows (30 stations) was laid out with adjacent trap stations placed 10 m apart. Since many *Rattus fuscipes* also entered the traps, three traps were placed at each station.

3. MOVEMENTS AND POPULATION DENSITY

As some individuals from outside the periphery of the grid entered traps it was necessary to estimate the effective area trapped to calculate abundance of *A.*

ISLAND POPULATION OF *ANTECHINUS MINIMUS*

minimus. The measure used was the average distance moved between successive captures (Av.D.), which was shown by Brant (1962) to be a good measure of the width of the boundary strip around the grid from which individuals were trapped. Av.D. was calculated for each recaptured animal and mean values for males, females and the population were obtained.

To estimate the number of animals in the effective area trapped a mark, release, recapture programme was conducted. The grid was trapped on three nights in May when animals were marked by toe-clipping and released at the site of capture.

RESULTS

1. TRAPPING SUCCESS

(a) GENERAL

A total of 65 individual *A. minimus* (33 ♂, 32 ♀) was trapped at Glennie Island in the 1500 trap-nights of the study. Of these, 15 (10 ♂, 5 ♀) were recaptured in a later trapping session. There were 74 recaptures in all with from one to seven recaptures per individual. With a total of 152 captures the overall trapping efficiency was 10%/trap-night. Trapping efficiency in May was 23%/trap-night.

(b) GRID TRAPPING

Over the three nights of grid trapping 34 animals (22 ♂, 12 ♀) were captured, with a total of 99 captures (74 ♂, 25 ♀). The average number of captures per male was 3.36 and per female was 2.08. Therefore the ratio of males to females captured was 1.62.

2. MOVEMENT

The mean Av.D. values for the 16 males and 7 females trapped more than once on the grid were 19.3 m and 13.4 m respectively. These values are significantly different at the 95% probability level. The Av.D. for the population was 16.4 m.

3. DENSITY ESTIMATE

Table 1 shows grid recapture trapping results. The three Lincoln Index (Lincoln, 1930) estimates of population size between trapping nights 1 and 2, 1 and 3, and 2 and 3 are 42, 26 and 34 respectively. The population size calculated using Hayne's method (Hayne, 1949) is 36, the value used for the density estimate. Using 15 m as an approximately minimum value of Av.D. and diameter of the boundary strip, the area of effective trapping was 0.45 hectares (1.1 acres). The population density was therefore 80 individuals per hectare (32 per acre).

TABLE 1

Recapture trapping results of *A. minimus* on the grid at Glennie Cove, May, 1975.

Night	Number of animals trapped			Number of animals recaptured		
	♂	♀	Total	♂	♀	Total
May 24th	18	5	23	—	—	—
May 25th	15	9	24	11	2	13
May 27th	16	7	23	16	7	23

4. REPRODUCTION

(a) SEX RATIO

The sex ratio of males to females in April was 1.73:1 (19 ♂, 11 ♀) and in May was 1.50:1 (24 ♂, 16 ♀). The preponderance of males is probably partly due to their greater mobility. The total number of each sex trapped (33 ♂, 32 ♀) gives a false idea of the overall sex ratio since the September trapping session took place after the postmating male die-off.

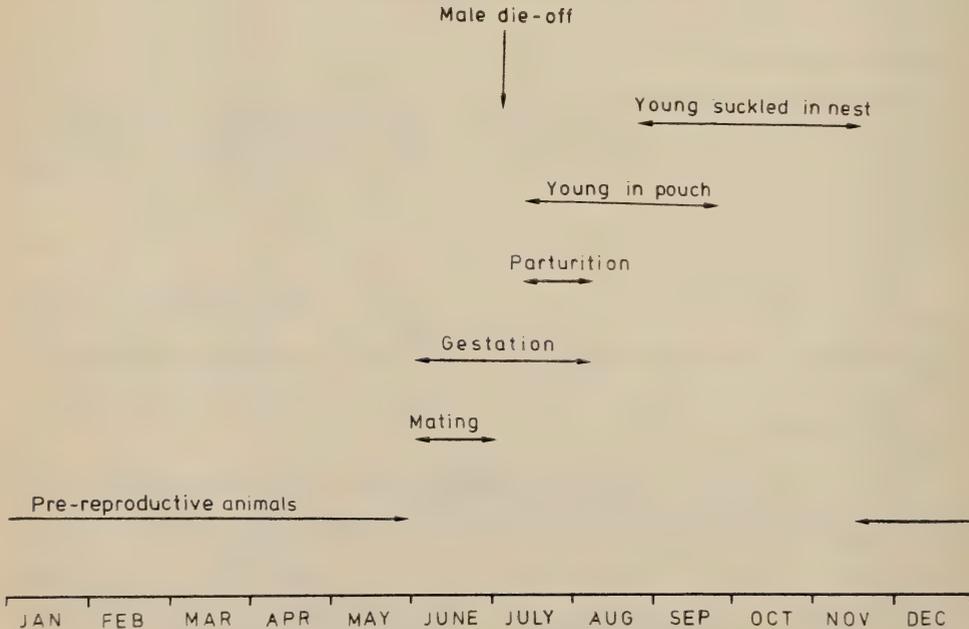


Fig. 1. Timing of life history events of *A. minimus* at Glennie Island.

ISLAND POPULATION OF ANTECHINUS MINIMUS

(b) LIFE CYCLE

An estimate of the timing of the important features of reproduction at Glennie Island is shown in Fig. 1. In late May, mating was occurring. Most parturitions occurred in July and the neonates remained in the pouch until late August to mid September. In early September some females had nest-young and others still had pouch-young. Young were then suckled in the nest until mid or late November; in early November 1975 no juveniles were found, whereas in early December 1974 they were abundant (Barnett, pers. comm.). Although conclusive evidence is wanting, the male die-off, which is universal, probably occurs early in July, because in late July 1973 only females with pouch young were present (Robinson, pers. comm.). No second-year females were encountered.

(c) LITTER SIZE

Of the 10 females captured in September three had pouch-young, the litter sizes being 6, 8 and 8. All females examined possessed 8 teats. The number of well developed nipples of females with nest-young is a reliable indication of the number of nest-young (Woolley, pers. comm.), and the five females with nest-young had 6, 7, 8, 8 and 8 well developed nipples; therefore the average number of young per mother for the 8 females with young was 7.4. The remaining two of the 10 animals captured had not bred.

DISCUSSION

TRAPPING SUCCESS

The trapping efficiency values at Glennie Island of 10%/trap-night overall, and 23%/trap-night during winter, when trapping is most productive, are much higher than values obtained elsewhere. At the Parker River Inlet, Otway Ranges, Vic., in November when juveniles were mobile, a trapping efficiency of 3.6% was obtained (Norris, pers. comm.), and Green (1972) found an efficiency of approximately 2.5% for Tasmanian populations in the most suitable habitat in winter.

MOVEMENTS AND POPULATION DENSITY

Close trap spacing gives capture points too close to disclose the true home range (Chitty, 1937; Stickel, 1954). All or nearly all of the animals on the grid were trapped on the first two nights of the grid trapping programme, suggesting that the area was saturated by traps. Thus Av.D. was kept at a minimum, giving underestimates of the effective area of trapping. Nevertheless, the Av.D. values for males and females, 19 m and 13 m respectively, are 50%-70% those found by Wood (1970) and closer to those found by Braithwaite (1973), both for *A. stuartii*.

Mobility of males was found to be significantly greater than that of females, possibly because males were actively defending territories at this time.

REPRODUCTION

Breeding is restricted to winter, conforming with the limited information available on Tasmanian individuals (Green, 1972). As in the three other south-east Australian species of *Antechinus* (Wakefield and Warneke, 1963, 1967; Woolley, 1973), *A. minimus* appears to be monoestrous. Males and females are sexually quiescent except during the very limited breeding season. There is a total postmating mortality of males, a phenomenon which Lee *et al.* (in press) have investigated in *A. stuartii*.

Breeding is 2-3 months earlier than in *A. stuartii*, in which mating occurs in late August in southern Victoria (Lee *et al.*, in press). This difference in timing may be related to their habitats and availability of food. *A. stuartii* shows extensive arboreal activity (Wood, 1970) and probably hunts for much of its food, consisting of invertebrates including adult insects, on the trunks of trees. Thus it synchronises its breeding with the spring flush of insects. On the other hand *A. minimus* is terrestrial and a large part of its diet consists of larval insects from the soil as well as other terrestrial arthropods (Wainer, 1975). In spring and early summer when *A. stuartii* females are rearing young, and as a result probably require relatively more food, adult insects are at a peak of abundance; however *A. minimus* appears to synchronise its breeding with the peak of larval insects in winter.

In the Glennie Island population no parous second year females, which can be distinguished from virgin females on the basis of development of nipples (Woolley, 1966), were found. The situation in *A. minimus*, therefore, may differ from that in *A. stuartii* where some females survive to a second breeding season (Wood, 1970).

ACKNOWLEDGEMENTS

The National Parks Service of Victoria kindly granted permission to conduct a live-trapping programme at Glennie Island and their co-operation is gratefully acknowledged. Also I wish to express my gratitude to Dr. Angus Martin and Mr. Stephen Morton for reading and commenting on the manuscript, and to Dr. Martin for supervising the project.

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Maturational and Seasonal Moulting in the New Holland Mouse, *Pseudomys novaehollandiae*

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ABSTRACT

The post-juvenile moult is described in a captive colony of *Pseudomys novaehollandiae*. This moult, which may be found in animals aged 35 to 105 days, progresses from the ventral to the dorsal surface of the body, ending on the head and near the base of tail. There appears to be no post-subadult moult in this species. The occurrence of moulting in a wild population was also studied. The post-juvenile moult occurs mainly from October to January and a seasonal moult between January and June.

INTRODUCTION

Moult is the process of losing hair or replacing one pelage with another. Two major types of moult may be recognised in small rodents, those which are of a seasonal nature and occur irrespective of age and those which are associated with the development of the animal and are therefore called maturational moults. Two maturational moults, post-juvenile and post-subadult, separate three pelage phases (juvenile, subadult and adult) in almost all species of Cricetidae (Buhlow, 1970; Ecke and Kinney, 1956; Layne, 1968; McManus and Zurich, 1972), Muridae (Borum, 1954; Saint-Girons, 1967) and Heteromyidae (Eisenberg, 1963), studied to date. However, Linzey and Linzey (1967) found only one maturational moult in the cricetid, *Ochrotomys nuttalli*. Brief mention has been made of moult in the Australian genus *Pseudomys* (Green, 1968; Finlayson, 1944) but not enough information was presented to say whether one or two maturational moults were present in the two species studied.

Seasonal moults, in spring and autumn, are known to occur in several species of small rodents (Buhlow, 1970; Layne, 1968; Linzey and Linzey, 1967; Saint-Girons, 1967) but Brechner and Kirkpatrick (1970) reported that moulting occurred throughout the year in *Mus musculus*.

The New Holland mouse, *Pseudomys novaehollandiae* is an Australian rodent inhabiting several localities in New South Wales and Victoria. In the wild it is a seasonal breeder, giving birth between September and December each year. It is

weaned during the fourth week of age but does not usually appear in trapped samples until at least five weeks. In the course of studying the growth and development of *P. novaehollandiae* information was obtained on the post-juvenile moult. It was felt that this might prove useful in the age determination of wild populations so information was gathered on all trapped animals. As a result, it was found that seasonal moult existed as well.

MATERIALS AND METHODS

The sequence and timing of the post-juvenile moult was observed in 35 live *P. novaehollandiae* from 10 litters. These laboratory-raised animals were progeny of mice obtained from the Nelson Bay and Smith Lake areas of New South Wales. They were maintained under the laboratory conditions described in Kemper (1976).

A pelage dye (Durafur Black) was applied to the first litter studied but this proved detrimental to the health of the animals so all other animals used were not treated in any way. The new pelage was simply noted to be present beneath the juvenile pelage by its shorter length and browner colouration. The chin, manus, pes and tail were not investigated for moulting because of the difficulty in observing the new fur in these areas. Not all animals were followed through from before the beginning to the end of moult and observations were made at different ages for each animal. To facilitate computations these were grouped into five-day intervals. Table 1 was obtained by totalling the number of animals of a certain age interval for each moult stage and taking that figure as a percentage of the total number of observations for that age. This was necessary because of the different sample sizes and because some of the animals were observed more than once during an age interval.

The skins of 150 field-trapped animals (from the same localities as the original laboratory stock) were examined for evidence of moulting. These were obtained over a two-year period from June 1972 to May 1974. Most were prepared as museum round skins but some were made into flat pelts. Moult was noted either by the emergence of new fur or by recording the position of darkly pigmented areas on the inside of the skin (pigment is deposited at sites of new hair formation), or both.

RESULTS

POST-JUVENILE MOULT

The sequence of the post-juvenile moult was much the same for all animals observed so it was possible to categorise this progression into a set pattern of phases which are listed below. An illustration of each phase appears in Fig. 1. The values in parentheses are ages when most animals were in the phase in question.

MOULT IN THE NEW HOLLAND MOUSE

Phase I

Moulting begins in the mid and anterior ventral regions. This may include the ventral surfaces of the forelimbs (35-50 days).

Phase II

Moulting is occurring over most of the ventral surface, except that of the hindlimbs, and may have reached the dorsal surfaces of the forelimbs (45-55 days).

Phase III

Moulting has progressed to the sides of the body including the dorsal and ventral surfaces of both fore- and hindlimbs. The new pelage in the mid-ventral region has grown enough so that it is indistinguishable from the juvenile pelage (50-75 days).

Phase IV

The ventral surface has completed moulting, except for the hindlimbs. On the dorsal surface the moult has spread to the mid-back to form a saddle joining the sides and is complete on the forelimbs (60-80 days).

Phase V

Moulting is visible all over the dorsal surface except the limbs, head and base of the tail (55-100 days).

Phase VI

Moulting is only visible on the head and near the base of the tail (65-105 days).

Observations on each animal were later placed into one of the above phases even though slight variations did exist when different body parts were moulting. Table 1 presents these data as a percentage of total observations for each five-day age interval. Two additional categories were included (not started and finished moulting) to give some idea of when most animals begin and end the moult. It can be seen from Table 1 that most animals begin the post-juvenile moult at 35-45 days of age and that all have started by 55 days, and end it by 100 days but this may occur as early as 70 days and as late as 110 days.

Only 13 of the 35 animals were followed from before the beginning of moulting to its completion. The average age at commencement was 43-46 days and at completion was 85-91 days (Table 2). The average duration of the moult for these animals was 41-50 days. Although the sample size is small, there appears

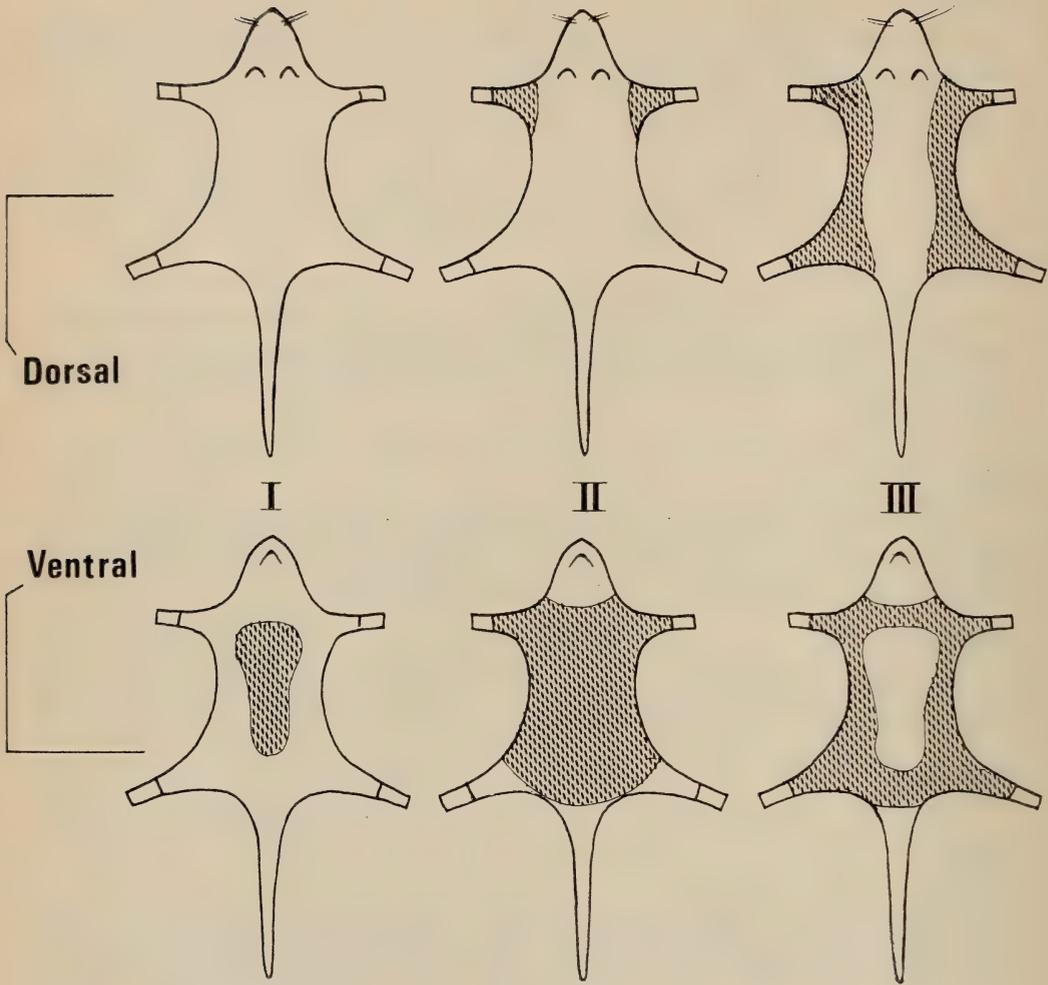
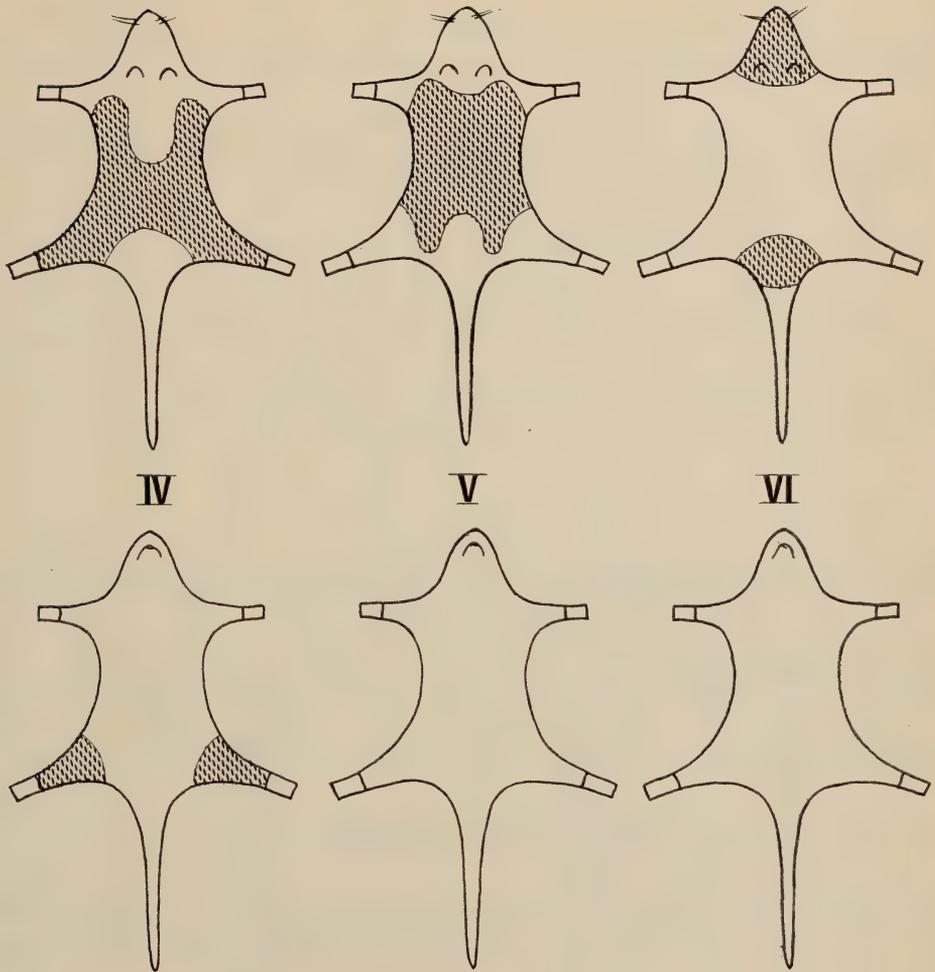


Fig. 1. Phases of the post-juvenile moult in *P. novaehollandiae*. Stippled areas indicate

to be no obvious difference in timing of the post-juvenile moult between sexes. Some variation in timing was observed between litters. In all three litters examined, from beginning to end of moulting, littermates began the moult within a few days of each other. The time of completion was more variable than the time of onset, although this may have been due at least in part to the difficulty in telling exactly when the moult ended. Individuals of other litters also showed similar phases of the moult at most times of observation.

MOULT IN THE NEW HOLLAND MOUSE



parts of the body in the process of fur replacement.

OTHER MATURATIONAL MOULTS

The skins of 41 laboratory animals, between 100 and 200 days of age, were examined for evidence of a post-subadult moult. Forty-two percent of these had areas of pigmentation on the inside of the skin. In most this was confined to the anterior and mid-ventral regions and to the head and none had extensive areas of pigmentation on either surface as is the case with the post-juvenile moult. It is suspected, therefore, that this is not a post-subadult moult but one of the periodic moults which adults experience.

CATHERINE M. KEMPER

TABLE 1

Percentage of *P. novaehollandiae* at moult stages for age intervals from 35-110 days.

Moult stage	Age															
	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110
Not started	80	44	20	6	0	0	0	0	0	0	0	0	0	0	0	0
I	20	50	20	13	6	0	0	0	0	0	0	0	0	0	0	0
II	0	6	48	19	28	3	0	0	0	0	0	0	0	0	0	0
III	0	0	8	52	38	70	42	25	18	5	0	0	0	0	0	0
IV	0	0	0	6	6	9	13	38	29	32	0	0	0	0	0	0
V	0	0	4	4	16	15	32	6	41	26	77	36	0	22	0	0
VI	0	0	0	0	6	3	13	19	12	26	15	55	0	11	100	0
Finished	0	0	0	0	0	0	0	12	0	11	8	9	0	67	0	100
Total animals	5	16	21	30	18	25	22	16	14	17	13	11	0	9	1	1

TABLE 2

Age at commencement and completion of the post-juvenile moult in three litters of *P. novaehollandiae*. The sixth member of the first litter was not included because it was developmentally retarded.

Litter size	Sex	Age at commencement (days)	Age at completion (days)	Duration
6	♂	37	67-70	40
	♂	38-40	78-82	39-44
	♂	38-40	73-78	33-40
	♀	38-40	67-70	27-32
	♂	38-40	83-87	43-49
4	♀	52-57	91-99	34-37
	♂	47-51	91-99	40-52
	♂	52-57	91-99	37-47
	♀	47-51	105-110	54-63
4	♂	41-43	92-100	49-59
	♂	41-43	85-91	42-50
	♂	41-43	92-100	49-59
	♀	41-43	92-100	49-59
Mean		43-46	85-91	41-50

SEASONAL MOULT

Fig. 2 illustrates the percentage of wild animals moulting during each month of the year for two age classes (C1 — those less than one year of age; and C2 — those older than one year). Two different types of moult were found in C1, the post-juvenile moult and another, which was assumed to be a seasonal one. Although

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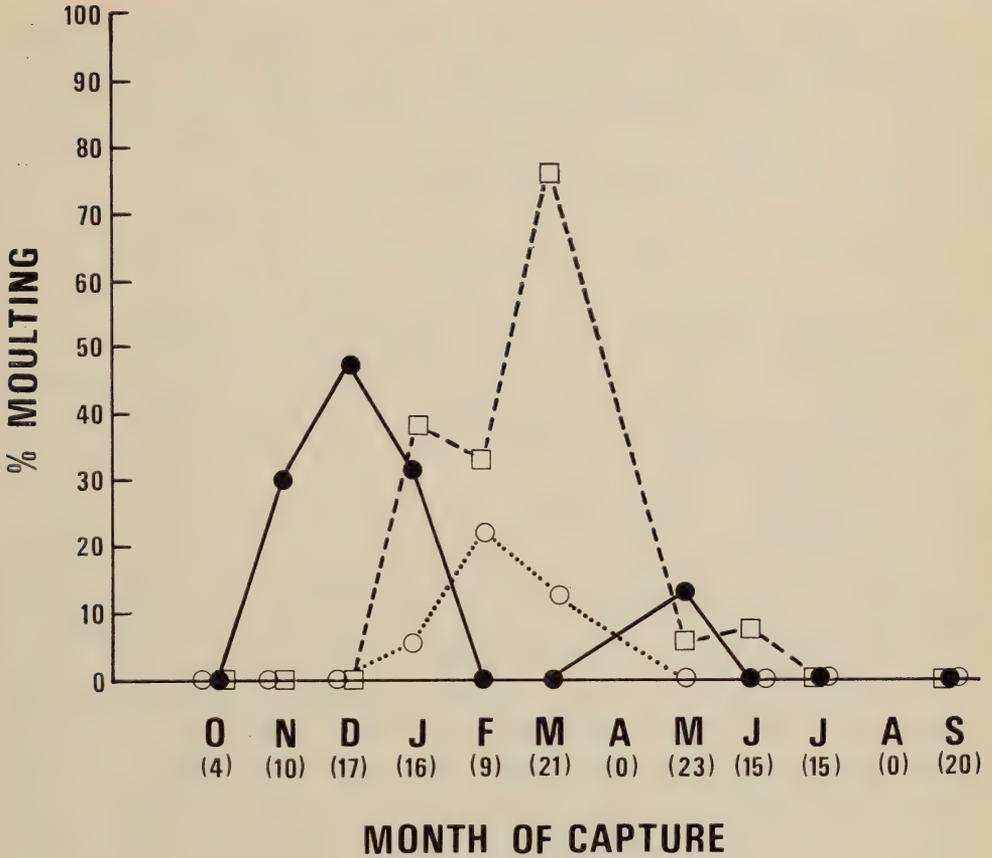


Fig. 2. Percentage of monthly captures of *P. novaehollandiae* in the process of moulting. Age class C1, — post-juvenile moult, - - - seasonal moult; age class C2 seasonal moult. Numbers in parentheses are sample sizes.

there is a possibility that the second type is a post-subadult moult this was discounted in view of the laboratory findings and because a seasonal moult was being experienced by C2 at the same time. Some of the observations of seasonal moult in C1 in January and February may have been, in fact, post-juvenile moults because it is difficult to differentiate these two moults in the later stages.

The post-juvenile moult was found from October to January and also in May, the latter resulting from a trapping period at Smith Lake in 1973 when a small population was found to be breeding out of season. Seasonal moult was found in C1 from January to June and in C2 from January to March (Fig. 2).

The seasonal moult in both age groups did not appear to follow the same pattern as the post-juvenile moult, although this was difficult to tell without following several animals through. The summer pelage is easily distinguished from the winter one because of its less dense nature and more grizzled appearance. As would be expected there seems to be a greater proportion of guard hairs in the summer pelage thus adding to its uneven texture.

DISCUSSION

The juvenile pelage covers the whole body surface by 13 days of age in *P. novaehollandiae* although it is not of maximum length (Kemper, 1976). It is soft, fine and grey in colour and is thus distinguishable from the coarser, brown pelage which replaces it. If, as suspected from the results in this study, there is only one maturational moult in this species, then, the later pelage is the adult one. This is in contrast to most species of rodents studied to date which have three basic pelage phases — juvenile, subadult and adult.

Buhlow (1970) has reviewed the literature pertaining to the timing of both maturational moults in the Muridae and Microtinae. In all species which experience a second moult this follows within two weeks of the end of the first. The duration of the post-juvenile moult is generally much shorter (12-31 days) than in *P. novaehollandiae* in which it lasts about 45 days. *Rattus norvegicus* also has a longer post-juvenile moult of 33-42 days duration (Buhlow, 1970). In *Ochrotomys nuttalli*, which has only one maturational moult, it lasts 25 (females) and 29 (males) days (Linzey and Linzey, 1967). In the small sample investigated no sex differences were found in *P. novaehollandiae*. Both other species of *Pseudomys*, in which moult has been reported, have long post-juvenile moults. *Pseudomys albocinereus* (= *apodemoides*) has a first moult (probably the post-juvenile one) at 7-15 weeks old (Finlayson, 1944) and *Pseudomys higginsi*, at 50-100 days (Green, 1968).

The progression of the post-juvenile moult follows roughly the same pattern in all species studied (Borum, 1954; Buhlow, 1970; Ecke and Kinney, 1956; Layne, 1968; Linzey and Linzey, 1967; McManus and Zurich, 1972; Saint-Girons, 1967). Moult begins on the ventral surface, spreads to the dorsal surface and ends on the head and at the base of the tail. However, it may be that *P. higginsi* and *P. albocinereus* differ somewhat in that the former begins to moult on the flanks (Green, 1968) and the latter on the nape of the neck (Finlayson, 1944).

Most mammals in temperate climates have two pelage phases related to season, the winter one being denser for protection against cold. In *P. novaehollandiae* the moult which results in the winter pelage takes place between January and June but there is no obvious new growth of fur in the spring. It

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may be that the spring moult is simply a result of thinning of the underfur by loss of hairs rather than a complete new pelage. This change could be so gradual that it would not be detected by the methods used in this study.

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Relative Efficiency of Two Types of Small Mammal Trap in Eastern Australia

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ABSTRACT

A comparison of the response of small mammals to snap traps and live traps was carried out using two methods. Overall captures indicate that at the 5% level of significance snap traps are more effective than live traps. Subtotals for each method and for each genus, however, show no significant difference. Advantages to be gained from the use of both types of trap are discussed. It is concluded that snap traps should be used for large-scale survey work unless the quality of the specimens is of prime importance.

INTRODUCTION

There are no published records in Australia on the response by small mammals to different types of traps. Cowan and Barnett (1975) do discuss new-object reactions but under laboratory conditions. Work done overseas indicates that the trap response may be species specific (Edwards, 1952). Some authors found live traps to be more efficient (Cockrum, 1947; Sealander and James, 1958), others that snap traps were more efficient in trapping small mammals overall (Smith, 1972; Buckner, 1957; Van Vleck, 1968). Response to traps is also discussed by Calhoun (1959), Crowcroft and Jeffers (1961), Golley (1961) and Eberhardt (1969).

The authors of this paper have experience in trapping small mammals on the East Coast of New South Wales using live and snap traps, and have found no apparent difficulty in trapping any particular species effectively using either type of trap. In view of the differential findings by the authors quoted above, and the often species specific response, we found it necessary to look at trap response in Australia. With many more groups now studying small mammal field biology in Australia we hope that other more specific studies will follow this one.

In this paper two types of traps, live and snap traps, were tested for their relative efficiency in the field. The work was carried out during a survey of the

rainforests on the East Coast of Australia, jointly undertaken by the Australian Museum, Sydney, and the Queensland Museum, Brisbane. Besides trap response, the advantages of both trap types are discussed.

METHODS

The trapping program was carried out at six sites in different eastern Queensland rainforest types between Bundaberg and Mackay. Trap types compared were: snap trap — household break-back rat trap; live trap — Elliott 33 x 10 x 10 cm collapsible aluminium live trap. All traps were baited with a mixture of peanut butter, rolled oats and bacon fat. Traps were checked each morning and rebaited or reset where necessary.

Trap response was compared using two methods:

A. Comparison on adjacent areas

At each site one area was set with six snap trap plots 100 m apart at the corners of a hexagon, each plot comprised 20 traps equally spaced on a cross with four 15 m arms. A central plot was set with 32 live traps equally spaced on a cross with four 16 m arms. The adjacent area was identical except that the central plot was set with snap traps and the six radial plots with live traps.

B. Comparison by use of paired traplines

At each site one or two index lines of 20 or 25 points was set up with trapping points 10 m apart. At each point one snap trap and one live trap were set within 1 m of each other but not immediately adjacent, being placed to catch small mammals (next to logs, tree trunks, etc.).

Method A was used on the first three sites while method B was used at all sites. At the first three sites the number of traps set off without a mammal capture was noted for each site.

TABLE 1
RATTUS AND *MELOMYS* CAPTURES

Site No.	Number of Nights	<i>Rattus</i>		<i>Melomys</i>	
		Snap Trap	Live Trap	Snap Trap	Live Trap
1	5	4	4	1	0
2	5	3	1	2	0
3	5	0	0	19	13
4	4	5	2	1	1
5	4	18	18	0	0
6	4	25	16	0	0
	37	55	41	23	14

SMALL MAMMAL TRAP EFFICIENCY

RESULTS AND DISCUSSION

Five species were trapped: *Rattus fuscipes*, *R. tunneyi*, *R. leucopus*, *Melomys* sp. and *Antechinus stuarti*. The low capture rate, 136 animals in 5574 trapnights (2.4%), meant that data could only be analysed at a genus rather than a species level (Table 1). No significant difference is apparent between trap types when considered at a genus level. There is no significant difference between types when each method is considered separately (Table 2). The paired trapline method was considered to be the better method to use for comparing trap types. The Chi-square test used was a one sample test with one d.f. testing equal probabilities of capture (Siegal, 1956).

All species taken in this study entered both types of trap and previous experience provided similar findings for other east Australian species of small mammals. The greater overall efficiency of snap traps may be related to the greater accessibility of bait on snap traps or to a lesser new object response toward snap traps compared to live traps. The latter view is also held by Buckner (1957) and supported by two direct observations by the authors, where animals shied away from a live trap and readily approached the snap trap nearby. A single animal was also observed attempting to get at the bait near the back of a live trap from the rear of the trap and left without finding the open entrance to the trap. Reduced new object response towards snap traps would mean that they could effectively sample a given population of small mammals sooner than live traps. Due to low capture rates this could not be evaluated directly in this study.

The results of this study certainly indicate that differences in trap response to the two types of traps used are not sufficient to exclude the consideration of other factors in the choice of traps. These factors depend on the type of study and data required. If good specimens are required then live traps should be employed to ensure fresh specimens and avoid skull damage. However, if a large survey or short-term studies are envisaged the use of snap traps is suggested as handling is simpler due to their smaller size, lighter weight and reduced cleaning time. These

TABLE 2
ANALYSIS OF TRAP DATA FOR ALL SPECIES

Trapnights		Snap Trap	Live Trap	Chi-Square
1622	Paired Trapline Captures	55	39	2.72
3952	Adjacent Area Captures	25	17	1.52
5574	Total Captures Both Methods	80	56	4.24*
5102	Traps Sprung Without Mammal Capture	473	74	326.00**

*Significant at 5% level

**Significant at 0.1% level

factors together with the much lower cost of snap traps mean that many more snap traps can be used in any study thus increasing trap density and so overcoming problems such as having traps sprung without mammal capture and bait loss both of which occur more frequently with snap traps (Table 2). Extensive trapping experience in eastern N.S.W. has not shown such loss of effective traps to be a significant problem (Posamentier and Recher, 1974; Posamentier, 1975).

From the results of this study and the reasons outlined above the authors suggest the use of snap traps for large-scale general surveys of small mammals. However, the variability in species trap response (Smith, 1972) indicates the need for further studies looking at individual species, a variety of habitats and other trapping techniques to provide more specific information. In addition, a study comparing the rates of capture by different types of traps is needed to indicate whether snap traps sample a given population of small mammals in a shorter period than live traps.

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Mammals of Clouds Creek, North-Eastern New South Wales, and their Distribution in Pine and Native Forests

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ABSTRACT

A survey was made of mammals in an area of 118 km² in Clouds Creek State Forest in north-eastern N.S.W. This area is being converted to *Pinus* spp. Twenty-seven species of indigenous mammals and seven introduced species were recorded. The distribution of these species in native and pine forest indicated that only *Rattus rattus*, *R. lutreolus* and *Mus musculus* inhabited pine forest (4-7 years old) exclusively, although this association was less obvious in older pines (25 years old) where they were trapped only on the periphery.

Changes in the habitats resulting from forestry practices influenced the distribution and abundance of mammals in the area. Individuals of *Rattus fuscipes* and *Macropus rufogriseus* were able to survive in pine plantings and their associated grasslands. No individuals of *Trichosurus caninus* or *T. vulpecula* used pine areas exclusively and they are dependent on adjacent native forest. Other phalangers were sighted only in native forest, including altered habitat such as grazed woodland. No populations of either *Antechinus stuartii* or *Melomys cervinipes* were found away from native forest and the latter species was trapped only in moist forest.

Macropods were similarly sensitive to habitat changes. *Macropus giganteus* was widespread in both native and pine areas, *Thylogale thetis* occurred on the pine periphery and *M. parma*, *T. stigmatica* and *Aepyprymnus rufescens* were restricted to closed and tall open forests.

INTRODUCTION

Tyndale-Biscoe and Calaby (1975) used the eucalypt forests of southern Australia to illustrate the dependence of certain mammals on specific forest types. They stressed the scarcity of information on distribution of Australian fauna with respect to vegetation type.

Calaby (1966) surveyed a large area of the upper Richmond and Clarence Rivers and demonstrated that north-eastern N.S.W. had a diverse mammalian fauna. Much of this area has been included as a target area in various proposals for a woodchip industry currently being considered for northern N.S.W. In addition, native forests are being cleared for the planting of exotic pines.

This paper reports on a long, intensive survey of a small area of highly productive native forest and of pine plantations in northern N.S.W. Emphasis is made of the distribution of the more abundant species between vegetation types.

STUDY AREA AND METHODS

In 1968 an ecological study of two possum species, *Trichosurus caninus* and *T. vulpecula*, was commenced in an area of forest that was partially being converted to *Pinus* spp. (How, 1972). This study was extended in 1975 to include the small mammals in the area. The study area was visited regularly from

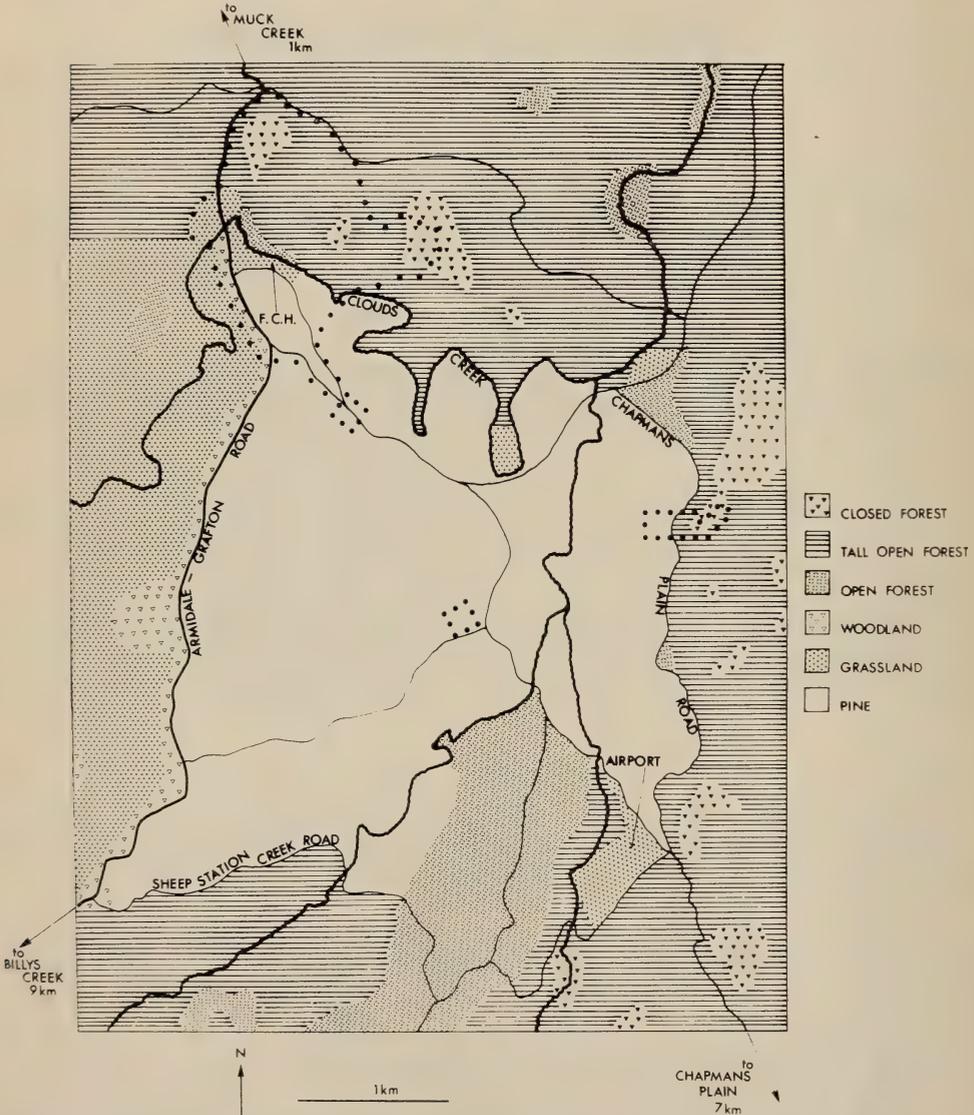


Fig. 1. Map of the Clouds Creek area showing the localities mentioned in the text. Solid circles enclose areas of fixed trap localities.

MAMMALS OF CLOUDS CREEK

1968, except for a period from January 1972 to August 1974. During the five and a half years spent in the area, various methods were used to assess the mammal populations, including live trapping, break-back trapping, spotlighting, the collection of roadkills and chance sightings.

STUDY AREA

The study area of 118 km² is at Clouds Creek (30° 05' S, 152° 37' E) in north-eastern N.S.W. (Fig. 1). Clouds Creek is situated on the eastern escarpment of the New England Tableland, about 120 km north-east of Armidale, and is on the northern edge of the Dorrigo Plateau, 24 km north-east of Dorrigo. Based on the classification of Specht (1970), four types of tree-dominated communities occur in the area. These are closed forest, tall open forest, open forest and woodland; pine plantation and grassland communities also occur in the study area.

Small areas of closed forest occur to the north and the east of the pine plantation. Species commonly found in this association are Coachwood (*Ceratopetalum apetalum* D. Don) and Sassafras (*Doryphora sassafras* Endl.) along with several others of commercial value. A southern area of closed forest was cleared in early 1970 and planted with pines.

In the transitional zone between closed forest and tall open forest, Brush Box (*Tristania conferta* R. Br.) is prominent, while tall open forest in the area is dominated by Tallowood (*Eucalyptus microcorys* F. Muell.), Sydney Blue Gum (*E. saligna* Sm.), White Mahogany (*E. acmenoides* Schau), Dunns White Gum (*E. dunni* Maiden) and Turpentine (*Syncarpia glomulifera* Sm.).

There is a large area of open forest to the north-west of the plantation dominated by Blackbutt (*E. pilularis* Sm.), while the area immediately to the south of the Forest Commission Headquarters (F.C.H.; Fig. 1) was New England Blackbutt (*E. campanulata* Baker and Smith) and Camerons Stringybark (*E. cameronii* Blakely and McKie), as codominants prior to its clearing in 1970.

Grazed woodland to the west of the F.C.H. is mainly Broadleafed Stringybark (*E. caliginosa* Blakely and McKie) and Ribbon Gum (*E. viminalis* Labill.). Along the creek Water Gum (*Tristania laurina* R. Br.) forms a dense association.

Grasslands in the region range from the "anomalous grassland communities associated with rainforest on basalt" (Baur, 1962) to improved pasture with white clover.

The central feature of the study area was the pine plantation. *Pinus elliotii* Engel. and *P. taeda* L. were first planted in 1950-51. Planting was recommenced in 1965 mainly with *P. taeda* but other species, *P. radiata* D. Don. and *P. patula* Schl et Cham. were also planted.

The principle climatic features are the cold dry winter and the wet summer months. The lowest minimum temperature over the 25 years previous to 1972 was -11.1°C and the highest maximum temperature was 39.5°C. Rainfall is

concentrated over the summer months; 55 per cent of the average annual rainfall of 1443 mm falls between November and March.

LIVE TRAPPING

Live trapping for small mammals was with Elliott folding aluminium traps (Elliotts Scientific Co., Upwey, Victoria) baited with a mixture of peanut butter and rolled oats. Medium sized mammals were trapped with three sizes of open-mesh wire traps. Two sizes of non-collapsible traps (Mascot Wire Works, Enfield, N.S.W.) 61 x 30 x 30 cm and 76 x 30 x 30 cm, and one size of collapsible trap (Tomahawk Live Trap Co., Tomahawk, Wisconsin, U.S.A.) 66 x 22 x 22 cm were used. These were usually baited with apple but on occasions peanut butter and rolled oats, tinned dog food, bread, and bread and honey were used.

There were 30,500 trap nights with the open-mesh traps of which 500 trap nights were on survey work, the remainder being in fixed locations. There were 10,621 trap nights with small mammal traps in fixed locations and 2,624 trap nights on survey work. The majority of the survey work where traps were either moved daily or every two days to a new location was generally on road edges separating pine and native vegetation.

Small mammals were individually marked by toe clipping and possums by ear nicks.

BREAK-BACK TRAPPING

Certain pine areas used as fixed locations for small mammal traps gave <1% trap success. In February 1976 a trap success of 7.5% was obtained in these areas from 120 trap nights with break-back rat traps baited with peanut butter and rolled oats. The only species caught in this way were *Rattus rattus* and one juvenile *R. fuscipes*.

SPOTLIGHTING

There was a total of 38 spotlight hours both on foot and from a moving vehicle. Spotighting from a vehicle was in general along the periphery of the pine plantation and when on foot was generally along the roads associated with Clouds Creek.

ROADKILLS

During 1975/76 regular journeys were made along the road between Clouds Creek and Billys Creek, a distance of 13 km. All roadkills were collected, decapitated and skulls subsequently prepared. Fifteen animals were collected in this way. Roadkill specimens and animals that died in traps are located at La Trobe University.

DAYLIGHT SIGHTINGS

During the time spent in the study area any mammals observed during the day were identified and recorded.

MAMMALS OF CLOUDS CREEK

TABLE 1

SYSTEMATIC LIST OF MAMMALS OF THE CLOUDS CREEK AREA INDICATING THEIR OBSERVED ABUNDANCE IN EIGHT HABITATS

1 — closed forest; 2 — tall open forest; 3 — open forest; 4 — woodland; 5 — central pines; 6 — peripheral pine; 7 — grassland; 8 — creek association
 abundant (A) >50; common (C) 10-50; uncommon (U) 5-10; scarce (S) < 5 animals observed

Common name	Scientific name	Habitat							
		1	2	3	4	5	6	7	8
Order Monotremata									
Family Tachyglossidae									
1. Echidna	<i>Tachyglossus aculeatus</i> (Shaw)								S
Order Marsupialia									
Family Dasyuridae									
3. Brown phascogale	<i>Antechinus stuartii</i> Macleay	A	A	U		S	S		S
4. Tiger-cat	<i>Dasyurus maculatus</i> (Kerr)	S	S				S		
Family Peramelidae									
5. Short-nosed bandicoot	<i>Isoodon macrourus</i> (Gould)			S	S	C		U	C S
6. Long-nosed bandicoot	<i>Perameles nasuta</i> Geoffroy			S		S			S
Family Phalangeridae									
7. Brush-tailed possum	<i>Trichosurus vulpecula</i> (Kerr)				C	A		C	C U
8. Mountain possum	<i>Trichosurus caninus</i> (Ogilby)	A	A	C	U			C	S C
Family Petauridae									
9. Ringtail possum	<i>Pseudocheirus peregrinus</i> (Boddaert)			S					S
10. Sugar glider	<i>Petaurus breviceps</i> Waterhouse			S	S				
11. Yellow-bellied glider	<i>Petaurus australis</i> Shaw			S					S
12. Greater glider	<i>Schoinobates volans</i> (Kerr)			C	C	U			S U
Family Burramyidae									
13. Feathertail glider	<i>Acrobates pygmaeus</i> (Shaw)			S					
Family Phascolarctidae									
14. Koala	<i>Phascolarctos cinereus</i> (Goldfuss)					S			
Family Macropodidae									
15. Grey kangaroo	<i>Macropus giganteus</i> Shaw				S	U		C	A
16. Wallaroo	<i>Macropus robustus</i> Gould			S	S				
17. Red-necked wallaby	<i>Macropus rufogriseus</i> (Desmarest)					C	S	A	A
18. Parma wallaby	<i>Macropus parma</i> Waterhouse			S	U				
19. Swamp wallaby	<i>Wallabia bicolor</i> (Desmarest)			U	U	U		S	U U
20. Red-necked pademelon	<i>Thylogale thetis</i> (Lesson)			U	C	C			C
21. Red-legged pademelon	<i>Thylogale stigmatica</i> Gould			U	S				
22. Rufous rat-kangaroo	<i>Aepyprymnus rufescens</i> (Gray)				S				
23. Potoroo	<i>Potorous tridactylus</i> (Kerr)	?	?			S		?	?
Order Chiroptera									
Family Vespertilionidae									
24. Bent-winged bat	<i>Miniopterus schreibersii</i> (Kuhl)							aerial	
Order Rodentia									
Family Muridae									
25. Bush rat	<i>Rattus fuscipes</i> (Waterhouse)			C	C	C		S	C U
26. Swamp rat	<i>Rattus lutreolus</i> (Gray)								U
27. Black rat	<i>Rattus rattus</i> (L.)							U	C U
28. Mosaic-tailed rat	<i>Melomys cervinipes</i> (Gould)			C	C				
29. House mouse	<i>Mus musculus</i> L.								C C S

Common name	Scientific name	Habitat							
		1	2	3	4	5	6	7	8
	Order Lagomorpha								
Family Leporidae									
30. Rabbit	<i>Oryctolagus cuniculus</i> (L.)					s	s	s	
	Order Carnivora								
Family Canidae									
31. Dog/dingo	<i>Canis familiaris</i> L.	s	s	s	s	s	s	s	s
32. Fox	<i>Vulpes vulpes</i> (L.)				s				
Family Felidae									
33. Feral cat	<i>Felis catus</i> L.		c	s	s	s	s	s	s
	Order Artiodactyla								
Family Bovidae									
34. Cattle	<i>Bos taurus</i>	c	a	a	a	a	a	a	a

RESULTS

A systematic list of the species of mammals observed in the study area is given in Table 1; Rides' (1970) classification is used. Twenty-seven indigenous and seven introduced species were recorded.

1. Echidna, *Tachyglossus aculeatus*

During the entire study period only one echidna was seen; this was in the grassland area near the Forest Commission Headquarters (F.C.H.).

2. Platypus, *Ornithorhynchus anatinus*

Platypus were sighted on three occasions in the same area although a considerable amount of time was spent along creeks at all times of the day and during all seasons. The sightings were in Clouds Creek near the F.C.H. in a region where the water was moving slowly and there were large pools. Both the monotremes must be considered uncommon.

3. Brown phascogale, *Antechinus stuartii*

A total of 131 individual *A. stuartii* were trapped, mainly in 1975/76. They were found in closed forest and tall open forest near the F.C.H. and to the east of Chapmans Plain Road in open forest, and in the pine plantation itself. Of the nine animals trapped in pine compartments, only two, both males, were trapped in the central plantation (in August at the time of mating); the others were caught in areas adjacent to native forest.

4. Tiger-cat, *Dasyurus maculatus*

Three tiger-cats were trapped during winter months, all in different vegetation types. One was in pines and another in closed forest near the F.C.H., and the other in tall open forest to the east of Chapmans Plain Road.

MAMMALS OF CLOUDS CREEK

5. Short-nosed bandicoot, *Isodon macrourus*

Seventy-seven short-nosed bandicoots were trapped in the grazed woodland adjacent to the Armidale-Grafton Road, in the grassland, tall open forest, open forest and pines near the F.C.H. One roadkill was collected at Billys Creek and others were spotlighted in pines, in grassland around the F.C.H. and at the airport. No short-nosed bandicoots were trapped during November, December and January; 42 of the specimens were trapped between May and August.

6. Long-nosed bandicoot, *Perameles nasuta*

The long-nosed bandicoot was considerably less common than *I. macrourus*. Four specimens were trapped in grassland, tall open forest and grazed woodland, all in the vicinity of the F.C.H.

7. Brush-tailed possum, *Trichosurus vulpecula*

This was one of the target species of the ecological study. There was a total of 593 captures representing 98 individuals. None were trapped in tall open forest or closed forest and they occurred less frequently in pines than in grazed woodland, open forest and grassland.

8. Mountain possum, *Trichosurus caninus*

This species was the other major possum species. There was a total of 2,597 captures representing 193 individuals. They occurred mainly in tall open forest and closed forest. They were also found in the other vegetation types although few occurred in grazed woodland. They were widely distributed over the whole of the study area, and all individuals were of the grey colour phase.

9. Ringtail possum, *Pseudocheirus peregrinus*

This species was considered rare in the area. One specimen was trapped in tall open forest near the F.C.H. and two were spotlighted along the creek in the same area.

10. Sugar glider, *Petaurus breviceps*

Three sugar gliders were observed during the day emerging from nest holes in open and tall open forest near the F.C.H. They appeared to have been forced out by *T. caninus* and *T. vulpecula* which climbed the trees after being released from traps.

11. Yellow-bellied glider, *Petaurus australis*

This species was not sighted but its characteristic calls were heard several times in trees along the banks of the creek and in tall open forest near the F.C.H.

12. Greater glider, *Schoinobates volans*

This species was widely distributed throughout the study area; it was not observed in pines or grassland.

13. Feathertail glider, *Acrobates pygmaeus*

Only one dried skin of this species was found in tall open forest near the F.C.H.

14. Koala, *Phascolarctos cinereus*

One koala was found dead after a "control burn" in grazed woodland approximately 2 km to the west of the Armidale-Grafton Road.

15. Grey kangaroo, *Macropus giganteus*

This species was common and widely distributed in the study area and was sighted in grassland, grazed woodland, open forest and pines.

16. Wallaroo, *Macropus robustus*

This species is considerably less common than the grey kangaroo. One skull was collected opposite a transition of tall open and open forest approximately 5 km south of Clouds Creek. One live specimen was observed in a similar forest type near the F.C.H.

17. Red-necked wallaby, *Macropus rufogriseus*

This species was found extensively throughout the pines and in areas of grazed woodland and grassland.

18. Parma wallaby, *Macropus parma*

Four roadkills of this species were collected, one near closed forest and two near tall open forest ca. 3 km to the south towards Billys Creek, and one at Muck Creek. This species is probably quite common throughout the area.

19. Swamp wallaby, *Wallabia bicolor*

Two specimens were trapped in pine and along the creek in tall open forest near the F.C.H. This species was observed mainly during the day in closed forest, tall open and open forest.

20. Red-necked pademelon, *Thylogale thetis*

This small macropod was common throughout the whole study area and was sighted mainly on roads between the pines and native forest. Two roadkills were collected near grazed woodland.

21. Red-legged pademelon, *Thylogale stigmatica*

This pademelon was less common than *T. thetis* and was observed only along roads near closed forest.

22. Rufous rat-kangaroo, *Aepyprymnus rufescens*

Only one specimen was collected as a roadkill near tall open forest 10 km towards Billys Creek.

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23. Potoroo, *Potorous tridactylus*

Only one specimen was trapped in grazed woodland near the F.C.H. However, spotlight sightings gave only a glimpse of many small macropods throughout the study area which were probably potoroos; this species is probably more common than indicated by the one capture and lack of positive sightings.

24. Bent-winged bat, *Miniopterus schreibersii*

The only bat collected was one specimen of this species which was brought in by a cat. Numerous bats were observed in the area but these remain unidentified.

25. Bush rat, *Rattus fuscipes*

Eighty-five individual *R. fuscipes* were trapped in closed forest, tall open forest, open forest and on the periphery of the pines. They were scattered throughout the study area, but were nowhere in high numbers; only one individual was caught in the central pine area. The nipple formula $1 + 3 = 8$ and $2 + 3 = 10$ occurred in the ratio of 3:1.

26. Swamp rat, *Rattus lutreolus*

Nine individuals were trapped in February and May 1975. They were all trapped within 35 m of the edge of the eastern pine compartments.

27. Black rat, *Rattus rattus*

A total of 16 individuals were trapped in both central and peripheral pines with live and break-back traps. None were trapped in native forest. Two colour phases, the black-backed and the brown-backed, occurred in the ratio of 7:1.

28. Mosaic-tailed rat, *Melomys cervinipes*

Twenty-six individuals were trapped in closed forest and tall open forest to the east of Chapmans Plain Road. Of these only two were trapped along the edge of a road.

29. House mouse, *Mus musculus*

Only eight individual mice were trapped, all in peripheral pines near the F.C.H. and in the eastern pines. None were trapped in native forest. Others have been brought in by cats and observed in grassland near the F.C.H.

30. Rabbit, *Oryctolagus cuniculus*

No rabbits were seen during 1975/76 and they must now be considered rare or absent from the area. However, in 1971 they were present in the one to two-year-old pine compartments.

31. Dog/dingo, *Canis familiaris*

One dog skeleton was found in grassland at Chapman Plain 11 km south-east of F.C.H., and numerous pads and faeces were observed along the pine periphery.

Three known individuals have been seen together in open forest near the airport, along Sheep Station Creek Road, and along a road through the pines near the F.C.H. Dogs probably roam throughout the area.

32. Fox, *Vulpes vulpes*

Only one roadkill fox was collected 6 km along the Armidale-Grafton Road towards Billys Creek; this species must be considered rare.

33. Feral cat, *Felis catus*

Feral cats are common and widely distributed throughout the study area except for no sightings in closed forest. Specimens have been trapped in both tall open forest and in pines.

34. Cattle, *Bos taurus*

This species is included as cattle are allowed to graze in the State Forest. They are wide-ranging and occur throughout the whole study area in all vegetation types.

DISCUSSION

The mammal fauna of Clouds Creek State Forest is very diverse. There are 27 species of native mammal and seven introduced species; this list will undoubtedly be considerably extended when more bats and some of the small macropods are collected and identified. The faunal diversity compares favourably with that of the area drained by the upper Richmond and Clarence Rivers (100 km to the north) where 45 native species (12 of which were bats) and seven introduced species were recorded (Calaby, 1966) in an area of 2,400 km² (cf. 118 km² in the Clouds Creek study area) and a smaller survey in Moonpar State Forest 15 km to the south where 17 species were recorded (Maynes, 1974).

The small mammals, however, were not particularly abundant; trap success with live small mammal traps averaged 4.4% ranging from 0.4% in the central pines to 8% in native forest to the east of Chapmans Plain Road. This latter area held three species, *A. stuartii*, *R. fuscipes* and *M. cervinipes*, the two rodents being present in relatively low numbers.

The distribution of mammals throughout the area showed that only *R. rattus*, *R. lutreolus* and *M. musculus* were trapped only in pines. This appears dependent on the age of the pines; in the older pines *R. rattus* and *M. musculus* were very strongly associated with the periphery. Although *R. lutreolus* were trapped in pines, this species was a transient in the study area and all captures were again very strongly associated with the periphery. Little is known of the biology of this species, but Braithwaite (pers. comm.) believes their distribution is closely correlated with the penetrability of the soil in which they burrow. High summer and early autumn rainfall could explain the patchy temporal distribution of this species.

MAMMALS OF CLOUDS CREEK

Individual *R. fuscipes* and *M. rufogriseus* and possibly some *M. giganteus* and *I. macrourus* also occurred in pines and associated grasslands, but other individuals of these species occurred solely in other vegetation types. Although a few (nine out of 131) *A. stuartii* were trapped in pines, none were recaptured. Two transient male *A. stuartii* were trapped in the central pine area during the mating period, but females appeared absent from this area. Other species were observed in pines but they appeared dependent on nearby native forest areas; these included *D. maculatus*, *Trichosurus caninus*, *T. vulpecula* and *Thylogale thetis*.

The species found solely in association with native forest were *S. volans*, *Melomys cervinipes*, *Thylogale stigmatica* and probably *Perameles nasuta*, *Pseudochairus peregrinus*, *Petaurus breviceps*, *P. australis*, *Acrobates pygmaeus*, *Phascogale cinereus*, *Macropus robustus*, *M. parma*, *M. dorsalis* and *Aepyprymnus rufescens*; none of these species were observed in anything other than native forest although several occurred in grazed woodland.

None of the forest in the Clouds Creek area has been left untouched by man. Disturbance varies from selective logging in closed forest areas to complete clearfelling of native forest and subsequent planting with *Pinus* spp. The remaining closed and tall open forests are probably the least disturbed. Grazing obviously alters the vegetation association and clearing and replacing with pines is a serious perturbation.

The replacement of native forest by pines has a range of effects on the fauna depending upon the age of pines and the distance from native vegetation. *Melomys cervinipes*, *Schoinobates volans* and *Thylogale stigmatica* are always lost, while *Trichosurus caninus* and *T. vulpecula* utilize the pine margins but do not live solely in pines (How, 1972). In the central pines no native small mammals occur and are replaced by *R. rattus* and *Mus musculus*.

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ADDENDUM

Continued survey of the area since submission of the manuscript has resulted in the following additions. An individual male of each of *Mus musculus* and *Pseudocheirus peregrinus* was trapped in closed forest and one male *Rattus lutreolus* was trapped in creek-associated grassland.

Aggressiveness, Body Weight and Injuries in Long-haired Rats (*Rattus villosissimus*)

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ABSTRACT

This paper details methods used to objectively estimate the aggressiveness of male *Rattus villosissimus*. The principal technique involves ranking rats in a series according to their incidence of dominance and subordination in encounters. A second measure, attack latency, is used to test the established rankings. A very high correlation of body weight and the incidence of wounding is examined to show the usefulness of the technique.

INTRODUCTION

During a study of the visual, tactile and auditory signals involved in the agonistic behaviour of *Rattus villosissimus* (Begg and Nelson, in press), it was evident that individual rats differed greatly in aggressiveness, defined here as the tendency to attack conspecifics.

A prelude to any investigation of the causal factors for individual differences in aggressiveness, or a correlation of this variable with other factors (e.g. reproductive success), is a reliable technique for the measurement of aggressiveness.

This task has been attempted in several ways, involving the estimation of one or more of the variables listed below:

- (i) the frequency of occurrence of selected behaviour patterns;
- (ii) attack latency;
- (iii) total duration of attack;
- (iv) the general outcome of encounters (i.e. "win" or "loss");
- (v) rating scales of aggressiveness (e.g. Bevan *et al.*, 1958).

Application of the last method has not produced many useful results, "due to the arbitrary ranking of behaviours that are not highly correlated or not correlated at all, on a linear scale" (Scott, 1966).

To be reliable, any method chosen to estimate individual aggressiveness, should give the same result for each animal tested. Working with *Mus musculus*, Catlett (1961), found measures (i), (ii), or (iii), above, to give consistent

results for the same animal on successive days. However, he was only able to obtain a correlation of 0.66 between measures.

There is usually a clear-cut dichotomy in the behaviour of two adult *R. villosissimus* engaged in an encounter. After an initial period of intense activity (usually very brief), one rat adopts a "subordinate" role and usually crouches alone, when undisturbed. Subsequently the opponent initiates all attacks and is termed "dominant". The subordinate rat usually attempts to defend itself or flee, when approached by a dominant opponent. This behaviour is described fully by Begg and Nelson (in press).

The terms "dominant" and "subordinate", as used in this context, do not imply any social values found under natural conditions. They are simply used to describe the different kinds of behaviour that may be observed in two rats involved in a conflict.

These terms follow Scott's (1956) definition of a "dominance-subordination relationship", as "antagonistic behaviour, where the behaviour of one individual consists of threat, or actual fighting, while the other individual remains passive or attempts to escape".

MATERIALS AND METHODS

All rats used were trapped in the wild as adult males and kept as described previously (Begg, 1975). Encounters were run between pairs of rats in a pine-board cage measuring 90 x 55 x 45 cm, with a clear Perspex front. A thin metal slide inserted through a longitudinal slot in the Perspex divided the cage floor into two equal areas. The cage floor was covered with wood shavings which were changed after each encounter to minimise the effects of strange odours.

For each encounter one rat was placed in each section of the cage and allowed five minutes to settle down. Most rats spent this time exploring the area in which they were placed. The slide was then removed and the rats were observed for 15 minutes.

The time between the removal of the partition and the initiation of the first aggressive act by one rat was measured and termed the attack latency for that encounter. If no aggression occurred during the 15-minute period the encounter was termed neutral.

Each rat was scored as dominant or subordinate for each encounter in which it participated. At the end of each encounter each rat was weighed to the nearest gram and all visible injuries were recorded. This included: the number of cuts per rat; the areas in which cuts were located; and a subjective estimate of the severity of each wound.

One hundred and five encounters were run between pairs of rats, randomly chosen from a stock of 19 animals. No rat was used more than once per day.

AGGRESSIVENESS IN RATS

TABLE 1
 AGGRESSIVE RANK, MEAN ATTACK LATENCY, AND MEAN BODY WEIGHT FOR MALE-MALE ENCOUNTERS

Rat	Number of encounters dominant	Number of encounters subordinate	Number of neutral encounters	Ratio of dominant to subordinate	Aggressive rank	Mean attack latency (secs)	Log ₁₀ latency	Mean body weight (gms)
738	11	0	0	—	1	8	0.90	311
743	9	1	1	9.00	2	9	0.95	289
761	9	1	1	9.00	3	20	1.30	282
717	5	1	5	5.00	4	8	0.90	275
747	6	2	3	3.00	5	40	1.60	244
763	5	3	3	1.70	6	50	1.70	247
736	6	4	1	1.50	7	34	1.53	224
713	3	3	5	1.00	8	9	0.95	251
711	5	5	1	1.00	9	71	1.85	192
725	4	5	2	0.80	10	62	1.79	226
767	3	5	3	0.60	11	81	1.91	221
745	2	5	4	0.40	12	104	2.02	224
756	2	6	3	0.33	13	120	2.08	199
765	2	6	3	0.33	14	182	2.26	261
757	1	4	6	0.25	15	183	2.26	195
753	1	5	5	0.20	16	480	2.68	322
740	0	5	6	0.00	17a*	—	—	285
749	0	6	5	0.00	17b*	—	—	241
764	0	6	5	0.00	17c*	—	—	282

* Rats 740, 749, 764 were never dominant. Thus, all three were grouped on the lowest rank (i.e. 17).

RESULTS

CALCULATION OF AGGRESSIVE RANKING

A ratio of the number of encounters in which the rat was dominant to the number in which it was subordinate, was calculated for each rat.

The more aggressive a rat is the higher the ratio may be expected to be. Thus, by comparing the ratios for each rat in a group it was possible to establish a ranking from the most aggressive rat (listed as number one) to the least aggressive rat in the group (Table 1). If any pair of rats had the same ratio the dominant rat in an encounter between the two was given the higher ranking.

All that this ranking is meant to imply is the tendency for a rat to be dominant under the conditions of the study. It does not imply that a linear dominance hierarchy (with associated ordering of access to food, water, mates, etc.) would exist if the animals were grouped. In fact Barnett (1958) showed that, at least for *R. norvegicus*, such a system does not exist.

STABILITY OF AGGRESSIVE RANKING

To test the stability of rankings, 10 encounters between pairs of rats, chosen from a table of random numbers, were repeated four months after the initial series of trials.

Of the 10 encounters repeated, eight resulted in the same rat being dominant on both occasions. The other two encounters resulted, on the second occasion, in

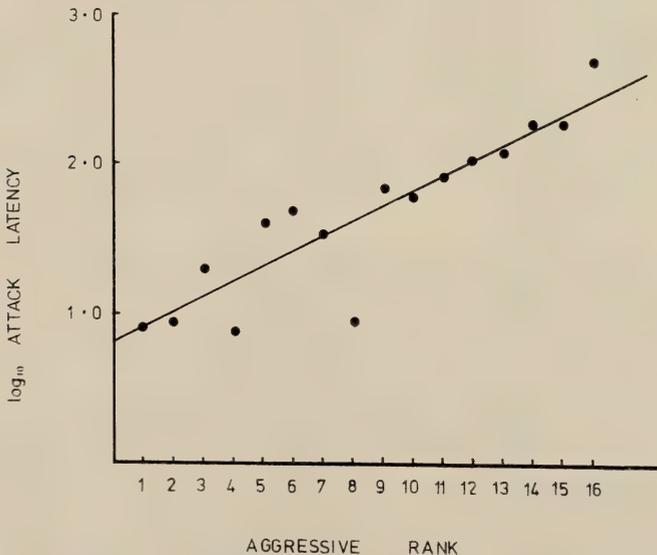


Fig. 1. \log_{10} attack latency vs aggressive rank.

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some aggression between pairs of rats that had previously had neutral encounters. In both cases, however, the dominant rat on the second occasion was of a higher aggressive rank than its opponent. Thus, although certainly not conclusive, these results tend to indicate that the relationships between rats are fairly stable over long periods.

ATTACK LATENCY

A mean attack latency was calculated for each rat over all encounters in which the rat initiated the first attack (Table 1).

To test the correlation between aggressive ranking and attack latency as estimates of the aggressiveness of individuals, the logarithm to base 10 of the mean attack latency of each rat was plotted against the established aggressive rank of that rat (Fig. 1). Logarithmic values were used for the ordinate as the relationship was found to be non-linear. A linear regression analysis was used to test the fit between these two variables. The regression line ($y = a_0 + a_1x$) is plotted in Figure 1 ($a_0 = 0.104$, $a_1 = 0.785$, with $r = 0.90$, $d.f. = 14$, and $P \leq 0.01$).

AGGRESSIVE RANK AND BODY WEIGHT

To test if body weight is a factor in aggressiveness, the mean body weight of each rat over the total period of observations was computed (Table 1). The mean

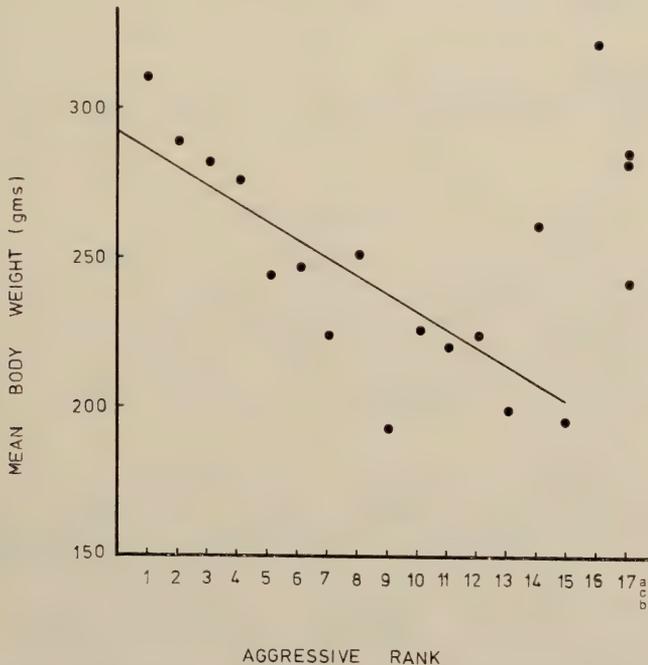


Fig. 2. Mean body weight vs aggressive rank.

body weight of each rat involved was then plotted against the aggressive rank of that animal (Fig. 2) and a linear regression analysis carried out. Taking rankings one to 19 in male-male encounters resulted in a correlation coefficient of -0.226 , $d.f. = 17$, $P > 0.05$. However, a linear regression analysis on rankings one to 15 produced a correlation coefficient of -0.764 . This value is significant at a 0.1% level ($d.f. = 13$). This regression line ($a_0 = 292.3$, $a_1 = -6.079$) is plotted in Figure 2.

Thus, for rats with aggressive rankings from one to 15, there is a highly significant correlation between aggressive rank and body weight. For animals with a lower ranking, the relationship is lost.

AGGRESSIVE RANK AND THE INCIDENCE OF WOUNDING

In 105 male-male encounters, 79 cuts resulted. All but one of these were to subordinate rats. The numbers of cuts delivered or received by rats were plotted against the aggressive rank of each rat (Figs. 3, 4). For cuts delivered to opponents $a_0 = 11.64$, $a_1 = -0.78$, with $r = -0.583$, $d.f. = 15$, $P \leq 0.02$. Thus the number of wounds caused by an attacker was significantly correlated with the aggressive rank of the attacking rat. For cuts received, however, $a_0 = 3.57$,

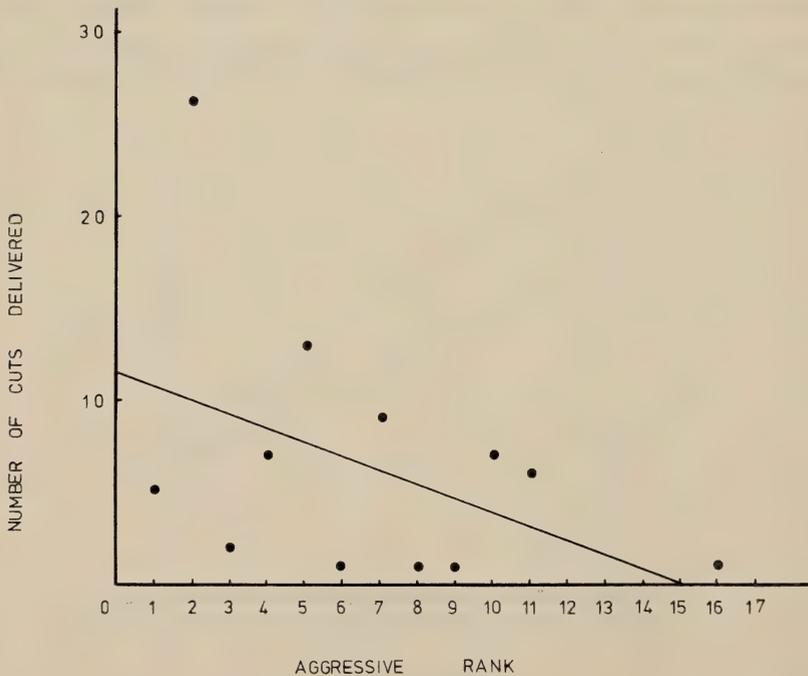


Fig. 3. Number of cuts delivered by rats vs aggressive rank.

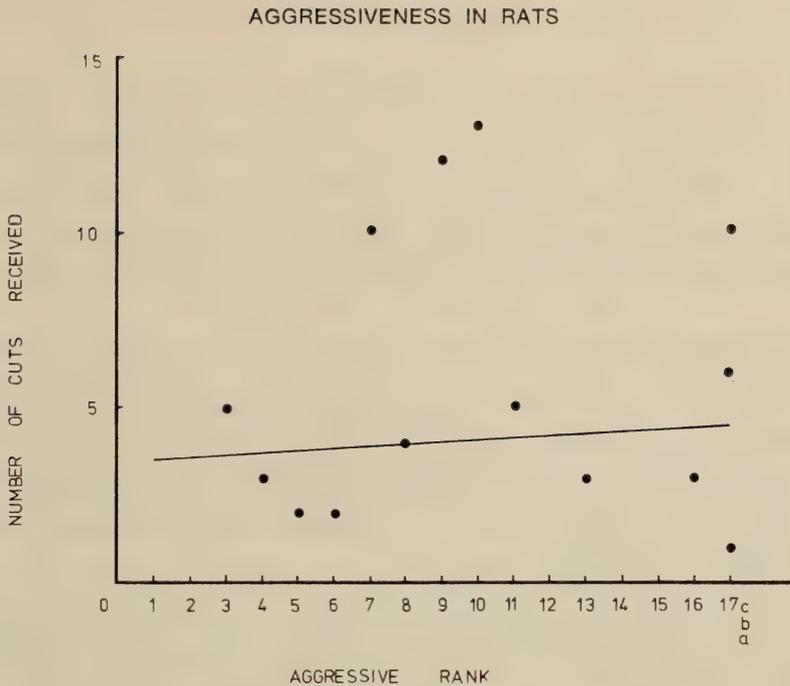


Fig. 4. Number of cuts received by rats vs aggressive rank.

$a_1 = 0.05$, with $r = 0.055$, $d.f. = 15$, $P > 0.05$. Thus the number of wounds received by a rat in encounters was not significantly correlated with the aggressive rank of the injured rat.

DISCUSSION

Ranking rats according to their incidence of dominance and subordination in encounters proved to be an effective method of representing the aggressiveness of male *R. villosissimus*. When compared with attack latency, a more commonly used measure, both methods gave the same estimate of the aggressiveness of individual rats. Previously Catlett (1961) was only able to obtain a correlation of 0.66 between different techniques for estimating the aggressiveness of *Mus musculus*.

It must again be stressed that the estimates of aggressiveness discussed in this study were obtained under specific conditions of cage size and construction, and experimentation, and thereby do not necessarily hold for a field situation. Aggression is probably heightened under these conditions of study, as caged animals have no avenue of escape, as discussed by Begg and Nelson (in press).

A series of encounters repeated four months after the original series of trials indicated that the rankings assigned to rats apply over a long period of time, as

almost all encounters gave the same results on both occasions. Lerwill and Makings (1971) found that for golden hamsters (*Mesocricetus auratus*) "relationship tends to be the same for any particular pair of hamsters, whenever they meet in similar circumstances". These facts tend to indicate that the establishment of a dominance-subordination relationship between rats probably does not depend on learning between two animals, as in the first series of encounters each pair only met once. More likely, some physical characteristics such as body weight, which was shown to be correlated with aggressiveness, are involved.

There was found to be a highly significant correlation between mean body weight and positions one to 15 on the aggressive ranking of male rats. Thus heavier rats tend to be dominant in more encounters. Barnett (1958) found that for colonies of *R. norvegicus* "most of the rats which grew well were dominant over the other males", and "alpha males were always large by comparison with other members of the colony". Similarly, Calhoun (1962) found that for *R. norvegicus* "for their respective ages, winners have greater than mean weights, and losers less than mean weights".

Thus, positions 16 to 19 on the aggressive ranking represent heavy rats that for some reason are subordinate in more encounters than may be expected. It is suggested that these rats are older (and thus heavier) than the other rats in the series and are not able to assert dominance over younger, stronger rats, and are thus subordinate in more encounters. Ewer (1971) found that both male and female wild *R. rattus* become less belligerent and show a general decline in activity as they become old. As Ewer says, males "become heavy, less agile, and a top ranking male is distinctly lazy". Newsome (1969) also suggested that with wild *Mus musculus* living in reed beds, old mice may be unable to maintain social superiority.

It was not possible to age the rats used in this study accurately as, firstly, they were needed for further experiments; secondly, one of the major methods used for aging *R. villosissimus* by Carstairs (1971) was to weigh the eye lenses of the animals. The curve for the relationship age/eye lens weight flattens out between the ages of 300-400 days and is thus inaccurate at the upper limits.

The number of injuries caused by a rat was found to be significantly correlated with its aggressive rank. That is, more aggressive rats deliver more wounds to opponents. While this may appear to be a truism, the converse did not hold. That is, the number of cuts received by a rat was not significantly correlated with its aggressive rank. Calhoun (1962) in his enclosure study of wild *R. norvegicus*, found more cuts and scars on animals of lower social rank. This measure is thus often used as an index of social status in the field. In *R. villosissimus*, however, this correlation probably does not hold. In this case animals toward the centre of the established aggressive ranking tended to receive the most injuries in encounters. These individuals may be attacked more by rats higher in the aggressive ranking, as they are closer to the latter in terms of body weight and behaviour.

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More Fish Genera Scrutinized

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New South Wales, 2000.

ABSTRACT

More than 16,000 generic or subgeneric names have been given to fishes. With a view to eradicating preoccupied or otherwise invalid names, all of them have been checked with nomenclators. Each doubtful genus is discussed below in alphabetical order, the style following the author's "Some fish genera scrutinized" which appeared in *Proc. Roy. Zool. Soc. N.S. Wales*, 1964-65, pp. 25-26.

INTRODUCTION

An overall modern classification of fishes in the broadest sense (to include lancelets, lampreys, elasmobranchs, teleosts, etc., and all recent and extinct families) down to generic level is still a desideratum.

More than 16,000 generic or subgeneric names (including nomina vana such as synonyms, homonyms, emended or variant spellings, etc.) have been bestowed on fishes since 1753 when Artedi listed the 50 genera known in his time. Thus there are many more names than natural genera. One way of reducing the excess is to eradicate preoccupied names; another is to dispose of synonyms. All of the known names published between 1758 (Linnaeus) and the early 1970s have been personally checked with nomenclators (for references see Whitley, *Austr. Zool.*, 13, 1966, p. 234). In this paper, certain generic names are purged.

The old name of each genus discussed is set out in alphabetical order below, following the same style as my earlier paper, "Some fish genera scrutinized" (*Proc. Roy. Zool. Soc. N.S. Wales*, 1964-65, pp. 25-26).

Sometimes (e.g. *Acropholis*, *Mesocyprinus*, *Palaeogadus*) new generic names were ascribed to more than one author by nomenclators, yet they were evidently duplicated publications of the new names, the later not preoccupied by the earlier ones. The nomina nuda of Agassiz, and Woodward's old names, restored in Casier's papers (especially his *Faune ichth. London Clay*, 1966) are other cases in point (examples: *Orvikuina*, *Percostoma*, *Podocephalus* and *Rhinocephalus*). These need not be considered further.

REMARKS

Ankistrorhynchus (Family Pristidae):

Ankistrorhynchus Casier (Bull. Inst. r. Sci. nat. Belg., 40(11), 1964, pp. 13-17) should be invalidated by *Ancistrorhyncha* Ulrich & Cooper (J. Paleont., 16, 1942, p. 624) in Brachiopoda and preoccupied by *Ancistrorhynchus* L'Hardy (Cah. Biol. Mar., 4, 1963, p. 220), a genus of turbellarian worms.

Ateleopus (Fam. Ateleopidae):

Ateleopus Temminck & Schlegel (Fauna Japonica, Pisces, 1846, p. 255, pl. 112, fig. 1) was a genus caelebs, that is a new genus without a specifically named type-species. It was published in May 1846 according to Mees (Zool. Verhand., 54, 1962, p. 79) and validly so. In the same year an amphibian generic name was emended to *Ateleopus* by Agassiz (Nomencl. Zool., 1846, Index Univer., p. 39). Whose name was earlier? The Index Universalis was prefaced December 1845, with title-page dated 1846. Bowley & H. M. Smith (J. Soc. Bibliogr. Nat. Hist., 5 (1), 1968, p. 35) do not specify a month in 1846, so we must give the fish name the benefit of the doubt and regard Agassiz's amphibian name as preoccupied. Furthermore, current usage will not be upset.

Temminck & Schlegel's unnamed species was called *Ateleopus schlegelii* by J. van der Hoeven (Handboek Dierkunde, 2, 1855, p. 326; Handbook of Zoology, 1858, p. 125). I have not seen the early editions of van der Hoeven's Handbook, but Sherborn (Index Animalium (2) 1, 1922, p. lxxviii of the bibliography) lists them and they are mentioned in Opinion 487 of the International Commission on Zoological Nomenclature. Some of van der Hoeven's generic names were discussed by Gill (Proc. U.S. Nat. Mus., 28, 1904, p. 119), Jordan (Genera of Fishes, 1919, p. 243) and Whitley (Rec. Austr. Mus., 16, 1928, pp. 294-295). *Ateleopus schlegelii* van der Hoeven, 1855 (if it were of earlier date, it would have been in Sherborn's Index) is however a synonym of *Ateleopus japonicus* Bleeker (Verh. Bat. Gen., 25, 1853, p. 21) likewise based on Temminck & Schlegel's type-species.

A genus related to *Ateleopus* is *Güntherus* Osório (Arq. Univ. Lisboa, 4, 1917, p. 117). *Guentherus* Walters (Copeia, 1963 (3), p. 456) is simply an emended spelling, not a new genus.

Barombia (Fam. Cichlidae):

Barombia Trewavas (Bonn Zool. Beitr., 13, 1962, p. 184), according to Neave (Nomencl. Zool.) is preoccupied by *Barombia* Karsch, 1891, in Orthoptera and by Jacoby, 1903, in Coleoptera.

Bertella (Fam. Oneirodidae):

Bertella Pietsch (Copeia, 1973 (2), p. 193) is not preoccupied by *Bertella* Paetel, 1875, because, according to Neave (Nomencl. Zool., 1, 1939, p. 422) the latter was an error for *Berthella* de Blainville, 1842, in Mollusca.

Brachypterus (Fam. Scorpaenidae, subfam. Pteroinae):

Brachypterus Catala (Carnaval sous la mer, 1964, p. 95), with type-species *Brachyrus zebra* [Quoy & Gaimard, 1825], was a substitute for *Brachirus* Swainson, 1839, of which it is a synonym. Neave's Nomencl. Zool. shows that *Brachypterus* is preoccupied by Kugelann, 1794, and by other authors in entomology and ornithology.

Buritia (Fam. Serrasalmidae):

Buritia Brant, 1972 — Brant & Marzulo (Bol. Mus. Hist. Nat., U.F.M.G. (Brasil), Zool., 17, p. 1, figs. 1-10) is preoccupied by a genus of Hemiptera, *Buritia* Young (Univ. Kansas Sci. Bull., 35, 1952, p. 67).

Byssacanthus (indet. Ichthyodorulite):

Byssacanthus Salter (Mem. Geol. Soc., 1861, p. 244, without type-species) is preoccupied by Agassiz (Poiss. F.V.G.R., 1845, p. 116) and is an unnamed ichthyodorulite allied to Chimaeridae according to Fowler (Quart. J. Taiwan Mus., 23, 1970, p. 152; Cat. World Fishes, 1 (13), p. 656), so Salter's name may be allowed to lapse as his genus appears to be unidentifiable.

Coridodax (Fam. Odacidae):

Coridodax Gunther (Cat. Fish. Brit. Mus., 4, 1862, pp. 69 & 243) is a new synonym of *Coregonoides* Richardson (Ann. Mag. Nat. Hist., 11, 1843, p. 426). L. D. Ritchie, quoted by Doak (Fishes of the New Zealand Region, 1972, p. 97) shows that the type-species of these two generic names are conspecific; as a corollary the genera are synonymic and the type-species should be known as *Coregonoides pullus* (Bloch & Schneider, 1801), comb. nov.

Cretaspis (Fam. Odontaspidae):

Cretaspis M. Sokolov (Byull. mosk. Obshch. Ispyt. Prir. Geol., 40 (4), 1965, p. 132) is preoccupied by *Cretaspis* Joleaud (Ann. Mus. Marseille, 15, 1916, p. 43), a genus of Crustacea.

Doryaspis (Fam. Lyktaspididae):

Doryaspis White (Phil. Trans. Roy. Soc. Lond., (B), 225, 1935, p. 444) was considered by Denison (J. Linn. Soc. Lond., 47, 1967, pp. 31 & 34) to be preoccupied, evidently by *Doryaspis* Dejean (Cat. Coleopt., ed. 2, 1835, p. 301), but that is a nomen nudum according to Neave's Nomenclator Zoologicus. Halstead (Biol. Reviews Cambridge, 48 (3) 1973, p. 326) places the fish genus in the synonymy of *Lyktaspis* Heintz, 1968.

Endemichthys (Fam. Dictyopygidae):

Endemichthys Forey & Gardiner (Palaeont. Africana, 15, 1973, p. 29, fig. 1) is preoccupied by *Endemichthys* Hopkirk (Diss. Abstr., 29B, 1968, p. 414), a genus of Cyprinid fishes.

Galeaspis (Ordo Liuaspidinida, nov., Fam. Liuaspidinidae, nov.):

Galeaspis Liu Yü-hai (Vert. Palasiat., 9 (2), 1965, p. 130), a genus of the Class Cephalaspides and of a new family named Galeaspidae by Liu, was placed in the then new Order Galeaspidiformes. The generic name is preoccupied by *Galeaspis* Ivshin (in Borukaev, Prepaleozoic & Lower Paleozoic N.E. centr. Kazakhstan. Acad. Sci. Kazakhstan S.S.R. (Inst. Geol. Sci.), Moscow, 1955, p. 276) a genus of trilobites, recorded in the Zoological Records for 1962 as well as for 1957.

"Goniophorus"

"*Goniophorus*" Toombs, Miles & Patterson (Zool. Rec., 104 (15) for 1967, Pisces, 1970, p. 118; and Ricketts, Zool. Rec., 104 (20) for 1967, index, p. 8) is a mis-spelling of *Goniporus* Gross, 1967. It is preoccupied by *Goniophorus* Agassiz (Mon. Ech., 1, 1838, p. 30) in Echinodermata.

Humbertia (Ordo Salmoniformes):

Humbertia Patterson (Bull. Brit. Mus. (Nat. Hist.) Geol., 19 (5), 1970, p. 207, plates & figs.) is preoccupied by *Humbertia* de Beaumont (Bull. Soc. vaud. Sci. nat., 69, 1965, p. 142), a genus of fossil mammals.

Katoporus (Fam. Phlebolepididae):

Katoporus Gross (Palaeontographica, (A) 127, 1967, pp. 5, 24, etc., pls. 2 & 3) is preoccupied by *Katoporus* John (Ann. Mus. Congo Belg. (Ser. 8) Sci. Zool., 51, 1956, p. 384) in Insecta.

Logania (Fam. Phlebolepididae):

Logania Gross (Palaeontographica, (A) 127, 1967, pp. 5, 31, etc., pl. 5) is preoccupied by *Logania* Distant (Rhopal. Malay., 1884, pp. 197 & 208), a genus of Lepidoptera.

Nybelinea (Fam. Roachiidae, nov.):

Nybelinia Nielsen (Galathea Rept., 10, 1969, p. 12 etc.) was preoccupied by *Nybelinia* Poche (Arch. Naturgesch., 91, 1925, A. 2-3, 1926, Syst. Platodaria, p. 364) a genus of Cestode worms, and has been renamed *Nybelinella* in the family Aphyonidae by Nielsen elsewhere.

Palaeotroctes (Fam. Alepocephalidae):

Palaeotroctes Daniltshenko (Akad. CCCP, 78, 1960, p. 15, pl. 4, fig. 3) is preoccupied by *Palaeotroctes* Enderlein (Palaeontographica, 58, 1911, p. 350), a genus of Insecta (Psocoptera).

Priacanthopsis (Fam. Serranidae):

Priacanthopsis Arambourg (Notes Mém. Moyen-Orient, 8, 1967, p. 103) is preoccupied by another genus of fishes, *Priacanthopsis* Fowler (Proc. Acad. Nat. Sci., Philad., 58, 1906, p. 122).

Pseudorhegma (Fam. Grammistidae):

Pseudorhegma Schultz (Ichthyologica, April 1966, p. 185).

Not *Pseudoregma* Doncaster (Entomologist 99, 1966, p. 158), a genus of Insecta (Aphids).

Quebecaspis (Arthrodira: Dolichothoraci):

Quebecaspis Pageau (Naturaliste canad., 96, 1969, p. 832) is preoccupied by *Quebecaspis* Rasetti (J. Paleont., 18, 1944, p. 254), a genus of Trilobita.

Siberiaspis (Subclass Heterostraci):

Siberiaspis Obruchev (Osn. pal., 11, 1964, p. 68) is preoccupied by *Sibiriaspis* Repina (Trudy SN 11 GGIMS, 19, 1960, p. 252) a genus of Trilobita.

Tangia (Fam. Lutjanidae):

Tangia Chan (Hong Kong Fisher. Res. Bull. 1 (F.R.S. Contrib. 17, 1970, p. 19) is preoccupied by *Tangia* Stål (Berlin ent. Z., 3, 1859, p. 317), a genus of Insecta (Hemiptera).

Thysia (Fam. Cichlidae):

Thysia Loisel & Welcomme (Rev. Zool. Bot. Afr. 85, 1972, pp. 37-58) is preoccupied by *Thysia* Thomson (Essai Class. Cerambyc., 1860, p. 96), a genus of Coleoptera.

Trewavasia (Fam. Cichlidae):

Trewavasia Thys van den Audenaerde, 1967-71 (*vide* Trewavas, Bull. Brit. Mus. Nat. Hist. (Zool.), 25 (1), 1973, p. 15 & footnote) is preoccupied by another genus of fishes in fossil Siluridae (White & Moy-Thomas, Ann. Mag. Nat. Hist. (11) 7, 1941, p. 400). A new name for the type-species, *Tilapia guinasana* Trewavas, is evidently being supplied elsewhere.

Trigonocephalus (Fam. Gobiidae, subfam. Tridentigerinae):

Trigonocephalus Okada (Studies on the freshwater fishes of Japan, 1961, p. 265) is preoccupied by *Trigonocephalus* Oppel (Ann. Mus. Hist. Nat. (Paris), 16 (95), 1811, pp. 377 & 388), a genus of reptiles. Okada's name was a lapsus calami for, and therefore a synonym of, *Tridentiger* Gill (Ann. Lyc. Nat. Hist. New York, 7, 1858, p. 16) according to Hubbs (Copeia, 1962 (1), p. 238).

Ulapiscis (Fam. Lutjanidae):

Ulapiscis Whitley (Rec. Austr. Mus., 19, 1933, p. 78) is a hitherto unreported synonym of *Aphareus* Cuvier & Valenciennes (Hist. Nat. Poiss., 6, 1830, p. 485). The type-species, *Ulapiscis kennedyi* Whitley from the Ellice Islands, agrees with *Aphareus furcatus* (Lacepede, 1802) as described and figured by Schultz (U.S. Nat. Mus. Bull., 202, 1953, p. 539, pl. 48, fig. B).

MORE FISH GENERA SCRUTINIZED

Yukonaspis (Heterostraci: Fam. Traquairaspididae):

Yukonaspis Obruchev (Osnovy Paleont., 2, 1964, p. 63) is preoccupied by *Yukonaspis* Kobayashi (J. Paleont., 10 (3), 1936, p. 164), a genus of Trilobita.

Zisius (Fam. Xiphiidae):

Zisius Oken (Lehrb. Naturg., 3, Zool. 2, 1816, pp. ii & 151) is a synonym of *Xiphias* Linnaeus 1758, the swordfish.

ACKNOWLEDGEMENTS

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EDITOR'S FOOTNOTE

While the original manuscript contained new generic names for most of the synonyms, the editor has followed reviewer's suggestions that the new generic names be deleted and left for future workers.

A Redescription of *Heteroclinus adelaidae* Castelnau (Pisces: Clinidae), With Description of a Related New Species

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ABSTRACT

Heteroclinus adelaidae, a southern Australian clinid, is redescribed from the holotype and numerous specimens from Tasmania, Victoria, South Australia and Western Australia. A new and closely related species is described from Tasmania and South Australia. The generic classification of the Australian clinids is briefly discussed.

INTRODUCTION

Clinids are one of the more poorly known groups of Australian marine fishes. The previous taxonomic studies have been based on limited material, primarily from one geographical area at a time. Castelnau described several species from southern Australia in the late 1800s, while Günther described various species from eastern and western Australia. McCulloch (1908) was the first Australian worker to extensively examine the group, although he treated only eight species, primarily from eastern Australia. Little subsequent work was done on the group until Whitley (1941, 1945) examined types in Europe. Scott (1955, 1966 and 1967) has treated the known Tasmanian species extensively. Milward (1967) revised the species known from Western Australia, and McKay (1970) described an additional Western Australian species.

At present 34 species have been described from Australia. Whitley (1964) recognized 18 species, two of which had been regarded as uncertain species. Types of these two species, *Heteroclinus adelaidae* and *Neoblennius fasciatus*, were examined in this study. Previously no thorough attempt has been made to examine the group on a widespread geographical basis, due to lack of adequate material. Recent field work in New South Wales, Victoria, Tasmania and South Australia has alleviated this problem to some extent, with 25 species now being known, but many of the species are still represented by few specimens. Most of the collecting has been restricted to depths shallower than five metres. Springer (pers. comm.) suggested that the ophiclinids are clinids, bringing the total number of Australian species to over 30, comparable in number to the South African fauna.

DESCRIPTIONS OF *HETEROCLINUS* SPECIES

Many of the Australian species are superficially similar, although many differ in live colour pattern, particularly of the head. In alcohol the colour fades, and important species characters are often lost. The body colouration, however, tends to be highly variable. Inadequate comparative material has led earlier workers to incorrectly synonymize species and not separate closely related ones. It is apparent that the range of variation in meristics within a species is narrower than previously suspected.

With the exception of a species of *Springeratus*, the Australian species are confined to temperate regions of eastern, southern, and south-western Australia. Two of the Australian species occur at Lord Howe Island and one occurs in New Zealand. The species occur in rocky tidepools, in association with algae around rocky reefs, or in grass flats over mud or sand bottoms. All the species are undoubtedly live-bearers.

METHODS

The following abbreviations are used in reference to material examined: AMS, Australian Museum, Sydney; MNHN, Museum National d'Histoire Naturelle; NMV, National Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; QVM, Queen Victoria Museum, Launceston; SAM, South Australian Museum, Adelaide; TM, Tasmanian Museum and Art Gallery, Hobart; WAM, Western Australian Museum, Perth.

In material examined lists, the number of specimens are given followed by the size range of standard length in mm. All fish lengths given are standard lengths (SL).

Counts and measurements follow those given by Hubbs and Lagler (1958). The last anal ray and last dorsal ray are counted as separate. Vertebral counts were determined from radiographs and cleared and stained specimens.

GENERIC CLASSIFICATION OF AUSTRALIAN CLINIDS

The generic classification of Australian clinids has not been thoroughly studied. Five nominal genera (*Heteroclinus*, *Neoblennius*, *Petraites*, *Clinus*, and *Cristiceps*) have been recorded from Australia, and a sixth, *Springeratus*, has been collected from the Great Barrier Reef. *Cristiceps* has long been regarded as distinct. Some Australian species have been placed in the African genus *Clinus* while other species have been placed in *Petraites*, with the two genera separated on the basis of the dorsal spine count. Recently, Penrith (1969) suggested that *Petraites* was a synonym of *Clinus*, and McKay (1970) has followed Penrith. Shen (1971), however, has noted that African clinids lack the genital flaps characteristic of Australian species. While it is apparent that the Australian species, all of which are undoubtedly live bearers, are related to African genera, no thorough comparison

has been made. Two of the Australian genera, *Heteroclinus* and *Neoblennius*, have been treated as uncertain genera. Examination of the holotype of *Heteroclinus adelaidae* Castelnau (1873) reveals it to be a distinct species subsequently described as *Cristiceps phillipi* Lucas (1891). Similarly, the syntypes of *Neoblennius fasciatus* Castelnau are representatives of the previously described *Cristiceps perspicillatus* Cuvier and Valenciennes (1836). At present no attempt is made to resolve *Heteroclinus*, *Petraites*, and *Neoblennius* problem. However, since *Heteroclinus* is the oldest of the three genera, the type species is redescribed and compared with a new closely related species.

The type species of *Petraites*, *P. heptaeolus*, and four closely related species (*P. wilsoni* and three undescribed species) differ from *H. adelaidae* complex in having three stout pelvic rays, a strongly compressed head, and the last two dorsal rays widely separated from the preceding. It is unlikely that *P. roseus* and *P. fosteri* also are referable to *Heteroclinus*. Other Australian species generally have a more robust head, and many species have biserial head pores. Whether or not these species belong in other genera is the subject of further study.

The species of the *H. adelaidae* and *H. heptaeolus* complexes differ substantially from the African genus *Clinus*. Of the characters used to define *Clinus* (Penrith, 1969), the shape of the orbital tentacle and presence of clusters of cirri on the dorsal spines are often different between closely related Australian species and do not seem of generic importance in these species. The species of these two complexes differ from *Clinus* in the arrangement of lateral line pores, in having three or more rows of teeth in the upper jaw, in having a more compressed head and body, and in always having the anterior scales overlapping. In general body form *Heteroclinus* is more similar to the African genus *Pavoclinus* than *Clinus*.

Heteroclinus Castelnau

Heteroclinus Castelnau 1873: 68 (type species, *Heteroclinus adelaidae* Castelnau, by monotypy)

Since the Australian clinids are heterogeneous and require further study, only the two species of the *Heteroclinus adelaidae* complex are characterized below:

Last two dorsal rays evenly spaced, not widely separated from the preceding ray or spine. Head moderately compressed; body strongly compressed. Snout pointed to rounded in lateral view. Body elevated along first dorsal margin. Infra-orbital and preopercular mandibular pores small and uniserial. Nasal tentacle short to moderately elongate, simple or weakly bilobed. Orbital tentacle short and rounded, elongate and pointed, or elongate with numerous lateral lobes. Dorsal origin above a point before preopercular margin to near end of eye. First three dorsal spines usually separate from rest; membrane of first dorsal connected at very base of first spine of second dorsal fin or to back before spine, rarely connected to tip of first spine of second dorsal fin. Segmented caudal rays 11. Pectoral rays typically 11 or 12. Second dorsal spines typically 29-31. Segmented

DESCRIPTIONS OF *HETEROCLINUS* SPECIES

dorsal rays 2-5. Branchiostegals 6. Mouth small, ending below eye. Pelvics 1, 2, two segmented rays slender and elongate reaching to near anal fin; an inner rudimentary ray, visible only by dissection. Vomer with 1-2 rows of teeth forming an inverted V. Precaudal vertebrae 13 to 15. Anteriorly, lateral line scales overlapping, with a posteromedian pore; posteriorly, near end of pectoral fin scales separated with tubes at each end; behind pectoral fin lateral line scales few and separate or absent.

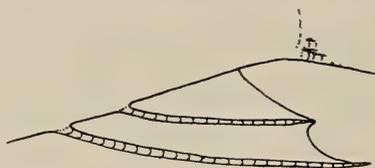


Fig. 1. Attachment of last anal ray to caudal peduncle in *Heteroclinus adelaidae* and *H. macrophthalmus*.

Considerable confusion has occurred over the identity of *Heteroclinus adelaidae* and *H. antinectes*. Whitley (1945) designated a lectotype of *Cristiceps antinectes* Günther (1861) and indicated that it was a senior synonym of *Petraites phillipi* (= *H. adelaidae*). Although one paralectotype is *H. adelaidae*, the lectotype and two paralectotypes are of a different and distinct species. Milward (1967) followed Whitley in treating *Cristiceps phillipi* Lucas as a synonym of *Petraites antinectes*. However, the species treated by Milward (1967) as *P. antinectes* is an undescribed species with biserial circumorbital pores not closely related to *H. antinectes*. Recent sampling has revealed a new species closely related to *H. adelaidae* from South Australia and Tasmania.

The two species treated here are easily distinguished from other Australian clinids by the combination of the two slender pelvic rays, the broad connection of the last anal ray to the caudal peduncle (Fig. 1) and the reduction of the lateral line.

Heteroclinus adelaidae Castelnau

Figures 2, 3a, and 4

Heteroclinus adelaidae Castelnau 1873: 68 (type locality, Adelaide, South Australia).

Cristiceps phillipi Lucas 1891: 11, pl. 3, fig. 2 (type locality, Port Phillip Bay, Victoria).

Petraites phillipi — McCulloch 1908: 43, pl. 10, fig. 3 (Western Port, Victoria).
Scott 1966: 109, fig. 1d (Green's Beach, northern Tasmania). Scott 1967: 194 (in part, Green's Beach, Tasmania).

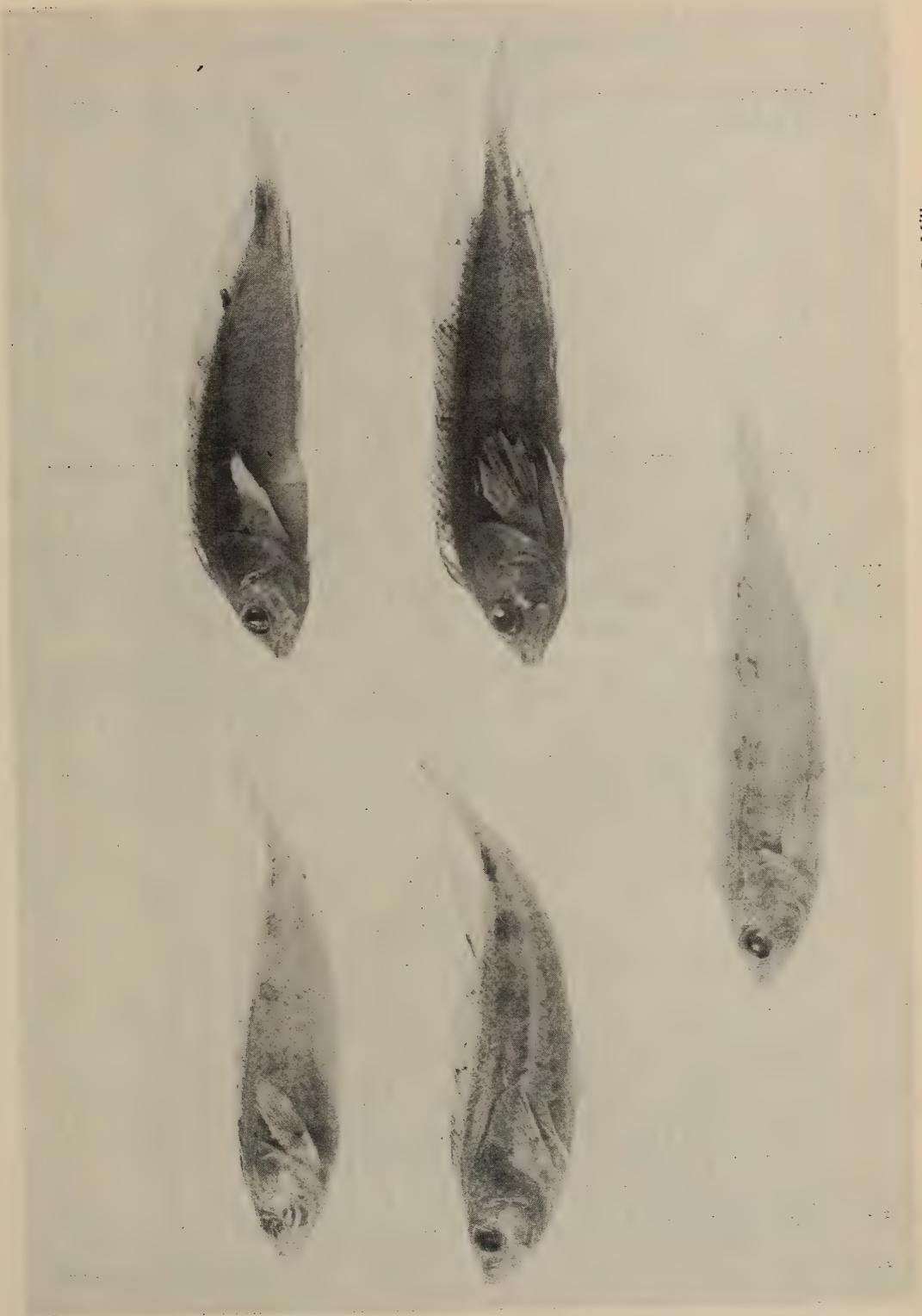


Fig. 2. Colour variation in *Heteroclinus adelaidae* from northern Tasmania. Photo by G. Millen.

DESCRIPTIONS OF *HETEROCLINUS* SPECIES

Description based on specimens 30 mm to 76 mm SL. An asterisk indicates count of holotype.

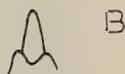
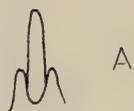


Fig. 3. Intromittant organ of males of *Heteroclinus adelaidae* (A) and *H. macrophthalmus* (B).

Pectoral rays 10 (in 1), 11 (in 71)*, 12 (in 10), 13 (in 1). Segmented caudal rays 11 (in 84)*. Gill rakers usually 2 + 6, total rakers 6 (in 1), 7 (in 6), 8 (in 39), 9 (in 3). Branchiostegal rays 6 (in 17). Dorsal, anal, and lateral line counts given in Table 1 and 2. Longitudinal scale rows 86 to 118.

Head moderately compressed, width 14.5 to 17.2% of SL. Body strongly compressed. Snout obtusely pointed, snout length less than eye diameter. Eye moderate, length 7.5 to 9.0% of SL. Interorbital narrow, about one half of eye diameter. Mouth short, reaching to a point below pupil; upper jaw length 11.0 to 14.3% of SL in males, shorter in females, 9.7 to 11.7% of SL. Anterior nostril tubular with a short, slender, posterior, simple or bilobed flap, positioned midway

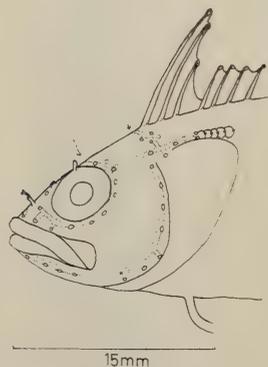


Fig. 4. Head of *Heteroclinus adelaidae* showing head flaps and sensory pores.

TABLE 1

DORSAL SPINE AND ANAL RAY COUNTS OF VARIOUS POPULATIONS OF *HETEROCLINUS ADELAIDAE*.
 An asterisk indicates count of holotype. Localities are arranged north to south within each State

Population	Second dorsal spines				Second dorsal rays				Total dorsal spines and rays						Anal rays					
	28	29	30	31	32	33	2	3	4	34	35	36	37	38	39	21	22	23	24	25
VICTORIA																				
Petersborough	—	1	2	4	1	—	—	7	1	—	1	2	4	1	—	—	2	5	1	—
Westernport Bay	—	2	4	2	3	—	—	11	—	—	—	2	4	4	1	—	—	2	6	2
Port Phillip Bay	—	1	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	1	—
TASMANIA																				
Green's Beach	—	2	10	17	3	—	9	22	1	—	4	14	11	3	—	—	4	14	13	1
Kelso	—	—	15	5	1	—	—	20	1	—	—	14	7	—	—	—	3	12	6	—
Port Latta	—	—	1	1	—	—	—	2	—	—	—	1	1	—	—	—	1	—	1	—
Coles Bay	—	2	2	2	1	—	3	3	1	—	2	3	2	—	—	—	4	2	1	—
Port Arthur	—	—	—	1	—	1	—	1	1	—	—	1	—	1	—	—	—	—	1	1
Wedge Bay	—	—	—	—	—	—	—	2	—	—	—	—	2	—	—	—	—	1	1	—
Bruny Island	—	—	—	—	1	—	1	—	—	—	—	—	1	—	—	—	—	—	1	—
SOUTH AUSTRALIA																				
Adelaide	—	1*	—	—	—	—	—	1*	—	—	—	1*	—	—	—	—	—	1*	—	—
Port Vincent	1	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	1	—	—
Venus Bay	—	2	—	1	—	—	1	2	—	—	1	1	1	—	—	2	1	—	—	—
Port Lincoln	—	—	—	—	1	—	—	1	—	—	—	—	—	1	—	—	—	—	1	—
Marion Bay	—	—	—	1	—	—	2	—	—	—	—	1	1	—	—	—	—	—	2	—
Kangaroo Island	—	—	—	—	—	1	—	1	—	—	—	—	—	—	1	—	—	—	—	1
WESTERN AUSTRALIA																				
1	4	4	3	—	—	—	2	9	1	—	—	5	6	1	—	2	3	5	2	—
TOTALS																				
2	15	39	39	11	2	—	18	84	6	—	2	18	46	34	6	2	4	21	49	30

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DESCRIPTIONS OF *HETEROCLINUS* SPECIES

TABLE 2
 LATERAL LINE SCALE COUNTS OF VARIOUS POPULATIONS OF *HETEROCLINUS ADELAIDAE*
 An asterisk indicates count of holotype

Population	Scales in arched part of lateral line										Scales in straight part of lateral line								
	18	19	20	21	22	23	24	25	26	27	0	1	2	3	4	5	6	7	8
VICTORIA																			
Petersborough	—	—	—	—	—	3	3	3	—	—	—	1	—	3	1	2	—	—	1
Westernport Bay	—	—	—	1	1	3	1	—	—	—	5	—	1	—	—	—	—	—	—
TASMANIA																			
Green's Beach	—	2	5	6	4	3	7	2	—	1	30	2	—	—	—	—	—	—	—
Kelso	—	—	2	1	6	3	4	2	3	—	18	3	—	—	—	—	—	—	—
Port Latta	—	—	—	—	—	—	1	1	—	—	1	1	—	—	—	—	—	—	—
Coles Bay	—	—	—	—	1	1	2	2	—	1	5	—	—	—	2	—	—	—	—
Port Arthur	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
Wedge Bay	—	—	1	1	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
Bruny Island	—	—	—	—	1	—	—	—	—	—	2	—	—	—	—	—	—	—	—
SOUTH AUSTRALIA																			
Adelaide	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1*	—	—	—
Port Vincent	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Venus Bay	—	—	1	—	—	—	1	—	—	1	2	1	—	—	—	—	—	—	—
Port Lincoln	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Marion Bay	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Kangaroo Island	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—
WESTERN AUSTRALIA																			
—	—	1	2	2	3	1	3	—	—	—	5	1	1	1	1	3	—	—	—
TOTALS																			
2	3	12	14	17	15	23	8	4	2	57	6	3	4	4	4	4	0	0	1

between upper jaw and posterior nostril. Posterior nostril a pore above anterior margin of eye. Orbital tentacle (Fig. 4) low and rounded, sometimes elongate, width varying from equal to length to twice as long as length; margin smooth; length 1.0 to 3.4% of SL.

First dorsal fin higher than second; first and second spines longest and about equal in length, third spine slightly shorter; fin lower in females. Second dorsal spine varying from about 10.5% of SL in young males, less than 50 mm SL to 14-17% of SL in larger males; varying from 8.6 to 15.3% of SL in females. First dorsal origin over end of preopercular margin, last spine above a point behind middle of operculum. Membrane of first dorsal usually connected basally to second dorsal, varying from attaching to body before second dorsal fin to tip of first spine of second dorsal. Flaps from dorsal spines bound in interspinal membranes, never free. Second dorsal origin above a point behind pelvic insertion. Anteriorly spines in second dorsal short, becoming progressively longer posteriorly, last spine 10.0 to 12.5% of SL; first ray longer than last spine. Dorsal rays evenly spaced. Last dorsal ray connected by membrane to caudal base. Anal origin below 10th or 11th spine in second dorsal fin. Anal II, 21-25, posterior rays becoming progressively longer; last ray shorter than preceding and broadly connected to two thirds of caudal peduncle. Caudal short and rounded, with 11 segmented rays and smaller procurrent rays above and below. Caudal length 19 to 22% of SL. Pectoral rays elongate, middle rays largest reaching to a point above or behind anal origin. Pelvics with a hidden spine, 2 elongate rays and a third rudimentary ray visible only upon dissection; two developed rays slender and about equal in length or inner ray slightly longer, reaching approximately to anal origin.

Gill rakers short and simple. Tongue tip broadly rounded, or tapering to a point. Intromittant organ elongate and curved forward, with bilobed papillae attached anteriorly at base. (Fig. 3a).

Head pores shown in Figure 4. Circumorbital and preopercular pores uniserial. Circumorbital pores (exclusive of median pores and pore below anterior nostril) 12 (in 47), 13 (in 9), 14 (in 17), 15 (in 1), number constant over size range studied.

Head naked, body scales small and cycloid, extending forward to above operculum below first dorsal. Scales overlapping and forming rows anteriorly, becoming nonimbricate and irregular posteriorly. Anterior lateral line scales overlapping with a small terminal and median or dorsomedian pore; first scale also with a ventral pore; posteriorly scales separate with pores at each end, extending in an elevated arch curving downward near end of pectoral fin; usually no scales along midside beyond pectoral tip, but occasionally up to 8 widely spaced scales in a line extending to below middle of second dorsal.

Upper jaw with outer row of conical teeth slightly enlarged extending over most of premaxilla. Anteriorly five inner rows of small conical teeth tapering posteriorly to a single row. Lower jaw with outer row of conical teeth slightly

TABLE 3
 VERTEBRAL COUNTS OF VARIOUS POPULATIONS OF *HETEROCLINUS ADELALDAE*

Population	Precaudal vertebrae					Caudal vertebrae					Total vertebrae				
	13	14	15	28	29	30	31	32	41	42	43	44	45	46	
N. E. Tasmania	2	11	—	—	8	5	—	—	—	1	8	4	—	—	
S. Tasmania	—	1	1	—	—	—	1	1	—	—	—	—	—	2	
South Australian Gulfs	4	1	1	3	2	1	—	—	1	3	2	—	—	—	
Kangaroo Island	—	—	1	—	—	1	—	—	—	—	—	—	—	—	

enlarged covering all of dentary. Anteriorly three inner rows of smaller conical teeth tapering posteriorly to a single row. In males smaller than 50 mm a single row of vomerine teeth in an inverted V. In larger males an incomplete inner row present. In females, usually only a single row of vomerine teeth. Palatine edentulous.

Colouration in alcohol variable (Fig. 2). Head and body varying from tan to dark brown. In some (including holotype) an oblique white bar extending from eye across preoperculum and operculum to pectoral base, continuing onto pectoral base divided by a dark brown bar. Stripe continues on body from base of pectoral to end of caudal peduncle. Head often with several dark brown spots, less than pupil diameter; spots occasionally extending onto body. Spots usually larger and forming a row along margins of head bar when present. In holotype a second white stripe present directly below anterior base of dorsal fins. Body often with 5 to 8 dark brown irregular vertical bands, sometimes broken into one upper and one lower row of larger irregular shaped blotches, with upper blotches darkest. Some specimens uniform tan or brown. Lateral line scales usually black anteriorly. Fins varying from uniform tan to mottled to banded. First dorsal fin sometimes black and darker than second dorsal fin. Banded individuals often with narrow extensions of bands onto second dorsal and anal fins either continuous with body bands or as separate blotches. Caudal and pectoral clear, dusky, or narrowly banded (pectoral banded in holotype). Pelvic fins light tan.

A moderate sized species reaching a size of 80 mm.

Variation.—*H. adelaidae* is peculiar among Australian clinids in being sexually dimorphic in jaw length and first dorsal spine height (Table 4). Males have a larger mouth and a higher dorsal fin than in females.

Lateral scale counts show considerable variation. Counts of 8 specimens from each of 3 States gives counts of 86 to 99 for South Australia, 95 to 103 for Victoria and northern Tasmania and 97 to 118 for southern Tasmania.

TABLE 4

SEXUAL DIMORPHISM OF *HETEROCLINUS ADELAIIDAE* IN JAW LENGTH AND SECOND DORSAL SPINE LENGTH

Measurements expressed as a percentage of standard length, rounded to the nearest per cent. The size distributions for the two sexes are similar, ranging from 47 to 65 mm SL. Based on sample from Green's Beach, Tasmania, January 1968.

Sex	Jaw length as a per cent of standard length					Second dorsal spine length as a per cent of standard length									
	10	11	12	13	14	8	9	10	11	12	13	14	15	16	
Males	1	5	9	8	1	—	—	1	2	6	6	4	4	1	
Females	7	14	2	—	—	2	3	11	3	4	—	—	—	—	

DESCRIPTIONS OF *HETEROCLINUS* SPECIES

As noted above colouration is highly variable. Although variation within a sample is high, from the limited material available it appears that the variation is greater between samples from different geographical areas.

Too few specimens are available to determine the extent of geographical variation. However, the data suggest that there is probably population variation in the height of the first dorsal fin and in the number of the lateral line scales along the straight portion of the lateral line. The meristic data suggest that there may be clinal variation in the number of second dorsal spines and anal rays and vertebrae in South Australia and Tasmania, with counts tending to be higher in the southern areas of these States (Tables 1 and 3).

The species ranges throughout Tasmania, Victoria, South Australia and is known from southern Western Australia.

In general head shape, body form, reduction of the lateral line, the broad connection of the last anal ray to the caudal peduncle, the presence of two slender pelvic rays and in the shape of the intermittent organ *H. adelaidae* is closest to *H. macrophthalmus*. *H. adelaidae* differs from that species in lacking free lobes from the dorsal spines, supraorbital and tentacle shapes and in segmented dorsal ray counts.

While most Australian clinids occur in association with algae around rocky reefs, *H. adelaidae* was taken in this study only from seagrass beds in shallow water. One specimen was dredged from 10 to 18 metres.

MATERIAL EXAMINED

Holotype. MNHN A.1077, a female 76.0 mm SL.

Victoria: Petersborough, AMS I.16987-011 8 (35-40). Port Phillip Bay, AMS I.2511, 1 (33). Westernport Bay, NMV (uncatalogued, dredged between Crawfish Point and Eagle Rock), 7 (28-79); AMS IA.1318, 1 (64); AMS I.7610, 2 (48-69); AMS I.9006-9008, 3 (60-75).

Tasmania: Green's Beach, QVM (out of 1972/5/231 (B)), 2 (47-90). QVM (out of 1972/5/225 (B)), 63 (46-66). Kelso, QVM (out of 1972/5/212 (C)), 10 (46-65); QVM 1972/51377, 11 (51-67). Port Latta, AMS I.17588-001, 2 (60-80). Port Arthur, AMS I.17550-003, 2 (41-63). Coles Bay, AMS I.17553-006, 7 (50-74). Wedge Bay, AMS I.17193-001, 2 (27-33). Bruny Island, TM D.593, 1 (53).

South Australia: Port Vincent, AMS IB.7133, 1 (71). Venus Bay, SAM F.3410, 2 (68-69). Port Lincoln, NMV (uncatalogued), dredged 10-18 m Spencer Gulf off Port Lincoln, taken with holotype of *H. macrophthalmus*, 1 (64). Marion Bay, Yorke Peninsula, SAM F.3629, 2 (30-55). Kangaroo Island, SAM F.348, 1 (75).

Western Australia: Emu Point, near Albany, WAM P.21687, 1 (66). Freycinet Harbour, BM (NH) 1974.11.29.3 (formerly part of 1858.12.27.67), male 66.5 mm SL, a paralectotype of *Cristiceps antinectes*. Cockburn Sound off Rockingham, WAM P.25258-002, 10 (38-64).

Heteroclinus macrophthalmus n. sp.

Figures 3b, 5, 6 and 7

Petraites phillipi.—Scott 1967: 194 (in part, "abnormal specimen" from Green's Beach only).

Based on 39 mm male and 64 to 83 mm females.

Measurements of types given in Table 5. Counts of holotype marked with an asterisk. Pectoral rays 12* (in 4), 13 (in 1). Segmented caudal rays 11* (in 5). Gill rakers 2 + 6 (in 1), 3 + 6 (in 1). Branchiostegal rays 6 (in 2). Dorsal III, XXXI, 4 (in 1); III, XXXI, 5* (in 4). Anal rays II, 25* (in 3); II, 26 (in 1); II, 27 (in 1). Lateral line scales — arched and straight part of lateral line 28 + 14 (in 1), 25 + 12 (in 1), 26 + 24 (in 1), 25 + 13* (in 1), 23 + 19 (in 1). Longitudinal scale rows 127 (in 1), 119 (in 1), 110 (in 1).

TABLE 5

MEASUREMENTS OF HOLOTYPES OF TWO SPECIES OF *HETEROCLINUS*
(in millimetres)

Measurement	<i>H. adalaidae</i> MNHN A 1077	<i>H. macrophthalmus</i> NMV A.495
Standard length	76.0	64.0
Head length	21.6	18.0
Predorsal length	15.0	11.2
Body depth at anal origin	15.5	13.8
Caudal peduncle depth	3.5	3.0
Caudal peduncle length	6.9	6.2
Upper jaw length	8.3	8.2
Eye length	6.3	6.9
Snout length	4.1	3.4
Pectoral length	14.5	12.8
Pelvic length	15.1	15.0
First dorsal spine length	8.8	8.2
Last dorsal spine length	9.5	7.6
First dorsal ray length	11.4	9.1
Caudal length	15.1	14.3
Orbital tentacle length	1.5	3.1

DESCRIPTIONS OF *HETEROCLINUS* SPECIES

Head moderately compressed, width 17.0 to 17.3% of SL. Body strongly compressed. Snout blunt, rounded in dorsal view, much shorter than eye diameter. Eye large 9.7 to 10.8% of SL. Interorbital narrow, about half eye diameter. Mouth short reaching to a point below middle to end of pupil. Upper jaw length 11.6 to 12.7% SL in females and 11.7% SL in male. Anterior nostril tubular with a large posterior branched tentacle, composed of 3 to 6 elongate lobes; anterior nostril positioned about half way between snout tip and posterior nostril. Posterior nostril with a raised rim, positioned above anterior margin of eye. Orbital tentacle (Fig. 7) flattened with 5 to 10 slender lobes extending from base; length 4.9 to 6.1% of SL.

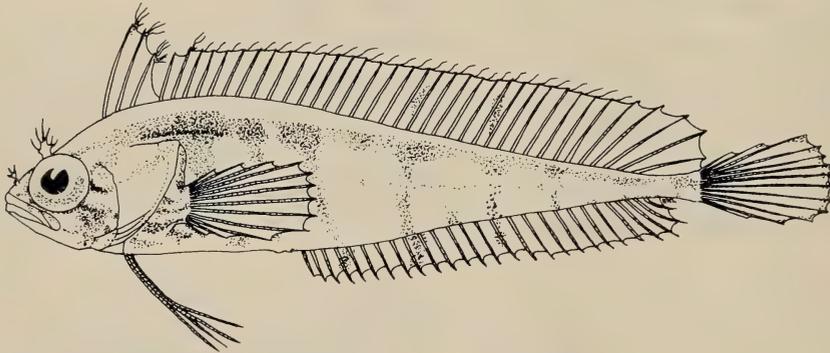


Fig. 5. Female holotype of *Heteroclinus macrophthalmus*, 64 mm SL, based on preserved colouration.

First dorsal fin higher than second; first and second dorsal spines about equal in length, third spine slightly shorter. Second spine 9.2% SL in 39 mm male and 12.6 and 14.6% SL in large females. First dorsal origin over end of posterior margin of preoperculum, last spine above a point behind middle of operculum. Membrane of first dorsal fin separate from second dorsal or connected to second dorsal at very base. Tips of first 3 dorsal spines with 3-6 elongate free flaps. First spine in second dorsal fin without flaps. Tip of second spine in second dorsal fin with 1 or 2 free flaps. Tips of remaining dorsal spines with an elongate free flap. Second dorsal origin above a point behind pelvic insertion. Anteriorly spines in second dorsal fin short, becoming progressively longer posteriorly, last spine 10.2 to 11.8% of SL; first ray longer than last dorsal spine. Dorsal rays evenly spaced. Last dorsal ray connected by membrane to caudal base. Anal origin below 11th and 12th spine in second dorsal fin. Posterior rays of anal becoming progressively longer; last ray shorter than preceding and broadly connected to about two thirds of caudal peduncle. Caudal short 17.9 to 22.4% of SL and rounded, with 11 segmented rays and smaller procurrent rays above and below. Pectoral rays elongate, middle rays longest. Pelvic rays I, 3, third ray a short rudiment visible

only upon dissection; 2 slender outer rays about equal in length, reaching approximately to anal origin.

Gill-raker short and simple. Tongue tip free, tapering to a point.

Intromittent organ elongate and curved forward, with bilobed papillae attached anteriorly at base (Fig. 3b).

Head pores shown in figure 7. Circumorbital and preopercular pores uniserial. Circumorbital pores (exclusive of median pore below anterior nostril) 13 (in 3).

Squamation as in *H. adelaidae*, except that straight part of lateral line more extensive, with 12-24 scales, reaching well beyond tip of pectoral fin.

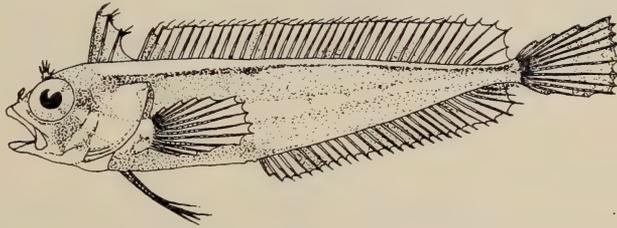


Fig. 6. Male paratype of *Heteroclinus macrophthalmus*, 39 mm SL, based on Kodachrome of fresh specimen.

Live colouration of male paratype from Kodachrome. Head and anterior half of body dark with brown or maroon; belly black; posterior half of body lighter brown. A prominent oblique silver bar, less than an eye diameter in width, extending from posteroventral margin of eye over preoperculum and operculum. Midside of body with silver stripe anteriorly, broken into irregular shaped silver blotches, posteriorly. Two faint narrow vertical bars below eye. Two white spots at angle of preoperculum. a broken black stripe on body below dorsal fin. Second dorsal fin with 2 narrow reddish brown longitudinal stripes, more prominent posteriorly. Six broad, faint yellow vertical bands on second dorsal fin. Anal fin reddish brown, with some yellow along base. Caudal clear with 7 reddish brown irregular bands. Pectoral clear with several narrow irregular reddish brown bands. Ventrals maroon. No black along anterior part of lateral line.

Colouration in alcohol of male paratype. Head and body tan. Silver and white blotches and stripes of fresh specimens tan in alcohol. Dark brown stripe behind eye continuing on body to near caudal base, upper margin of stripe below dorsal base sharply defined; ventral margin diffuse. Cheek dark brown. Sides of belly dark brown; rest of belly tan. First dorsal black anteriorly. Second dorsal dusky with 2 faint narrow horizontal dark stripes. Caudal clear with 7 irregular dusky bands. Anal dusky. Pectoral clear with several faint wavy dusky bands. Pelvic fin

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clear. Female colouration. Colour pattern of holotype shown in figure 5. Head and body tan. A diffuse dark brown, broken stripe on back, from behind eye to caudal peduncle. Six narrow transverse bands extend dorsally and ventrally from stripe, some extending on to dorsal and anal fins. Sides of head with dark brown mottling. Fins clear.

The Tasmanian and the largest South Australian paratype differ from the South Australian specimens in having a more extensive lateral line and in having 2 (rather than 1) rows of vomerine teeth. Since the extent of the lateral line raises geographically in *H. adelaidae* and the number of vomerine teeth increase in size in *H. adelaidae* these differences are not regarded as indicating any specific differences. Since only one small male has been studied, it is not known if *H. macrophthalmus* exhibits the sexual dimorphism characteristic of *H. adelaidae*. Although the male paratype has a different colouration from the female, it may not reflect sexual dimorphism since *H. adelaidae*, which has a similar colour variation, may not be sexually dichromatic.

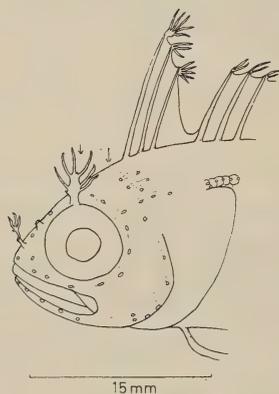


Fig. 7. Head of *Heteroclinus macrophthalmus* showing head flaps and sensory pores.

The species is known only from South Australia and northern Tasmania. It is closest to *H. adelaidae* (see discussion of that species). *H. macrophthalmus* differs from that species in having a larger eye, the free lobes on the dorsal spines, the branched orbital and nasal tentacles with numerous elongate lobes, a typically higher number of dorsal, anal and pectoral rays, a different snout shape, and more numerous lateral line scales.

This species has been taken only from grass flats subtidally and from 10-18 metres, twice in association with *H. adelaidae*.

MATERIAL EXAMINED

Holotype — NMV A.495, a 64 mm female, off Port Lincoln South Australia. Coll. J. Vestch 13 Mar. 1969. Dredged 10-18 m.

Paratypes — AMS I.17609-001, a 39 mm male, Victor Harbour, South Australia, West Island Aquatic Reserve; coll. D. F. Hoese and W. Ivantsoff, 20 Dec. 1973. 0-2 m, grass flat and algae, boulders. QVM 1974/5/131, a 75 mm female, Green's Beach, Tasmania; coll. R. H. Green, 9 Dec. 1965, grass flat and rocks. SAM F.1540, an 83 mm female, Spencer or St. Vincents Gulf, 19 Feb. 1931. SAM F.2589, a 73 mm female, Spencer or St. Vincents Gulf.

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Mosquitoes Feeding on Ectothermic Vertebrates: A Review and New Data

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ABSTRACT

The literature on feeding by mosquitoes on ectothermic vertebrates is reviewed. Original observations of the feeding of *Uranotaenia argyrotarsis* on *Rana daemeli* on Cape York Peninsula are presented.

LITERATURE REVIEW

Gilett (1971) in a review of mosquito biology lists lizards, snakes and frogs as hosts of filarial parasites transmitted by *Anopheles quadrimaculatus* and *Aedes taeniorhynchus*, mentions a trematode lung fluke of frogs which is transmitted from snails via larvae of *Anopheles maculipennis* to frogs (mosquito perhaps eaten by frog), and indicates that lizards and frogs are known to have non-human *Plasmodium* malarias which are presumably transmitted by mosquitoes. He also mentions that *Culex tarsalis* feeds on snakes and cites his personal observations of *Coquillettidia fuscopennata* feeding on a variety of vertebrates including frogs and toads. Some species of *Culex* feed exclusively on ectotherms (Woke, 1937a).

Aedes aegypti has frequently been observed to feed on ectotherms. Yuill (1964) developed the ingenious technique of using individuals of this species as micro-syringes for withdrawing small blood samples from Thailand geckos (*Hemidactylus frenatus* and *Platyurus platyurus*) for viraemia determinations of Japanese encephalitis; in the laboratory this same species fed on two species of Puerto Rican lizards, *Anolis cristatellus* and *Anolis pulchellus*. (Fox and Bayona, 1964), and on the Oriental lizards *Gecko verticillata* and *Calotes* sp. (Toumanoff, 1949); the latter reported that *Aedes albopictus* also feed on *G. verticillata* and *Calotes*. Woke (1937a, b) records *A. aegypti* feeding on a turtle (*Terrapene carolina*) and on a frog (*Rana clamitans*). Gordon and Lumsden (1939) induced this species to feed on frogs (*Rana sphenoccephala*) but could not get *Anopheles maculipennis*

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Fig. 1. *Uranotaenia argyrotarsis* feeding on *Rana daemeli* in the field. Note blood-engorged mosquito piercing upper eyelid and the swollen appearance of the eyelid.

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or *Culex molestus* to do so. Although *A. aegypti* obviously has wide food preferences, it does not feed on all species of ectothermic vertebrates, as in their literature review of this species, Fox and Bayona (1964) mention reports of failure to induce it to bite the lizard *Urocentron azureum* and some Brazilian geckos. Woke (1937a) also reports this species rejecting a lizard.

There is disagreement as to the relative nutritive value of the blood of ectotherms and homeotherms for this species. Woke (1937a,b) found that ectotherm blood was equal or superior to that of some homeotherms whereas Toumanoff (1949) found that *A. aegypti* feeding on lizards matured fewer eggs than those feeding on humans.

Thomas and Ekland (1960) found that garter snakes (*Thamnophis sirtalis parietalis* and *T. ordinoides vagrans*) experimentally infected with western equine encephalitis virus could transmit it to a mosquito vector of the disease (*Culex tarsalis*) even after having overwintered under artificial conditions subsequent to infection with the virus. Gebhardt *et al.* (1964) further showed that at least four species of snakes (*Thamnophis elegans vagrans*, *T. sirtalis*, *Pituophis catenifer* and *Coluber constrictor*) served as natural overwintering hosts for the virus. Under certain climatic conditions (especially high per cent of available sunshine in late spring or early summer), favourable both for large mosquito hatches and viraemia in infected snakes, epidemics resulting from transmission to warm-blooded hosts might result.

Craighead *et al.* (1962) suggest that lizards (*Ameiva*, *Cnemidophorus*, *Basiliscus*, *Iguana*) may play a role in the natural history of eastern equine encephalitis in Panama. A number of papers have recently indicated that a number of snakes, lizards and turtles can be experimentally infected by Japanese encephalitis virus or by western equine encephalitis virus and that natural reptilian populations often have high levels of antibodies to such viruses (see review by Shortridge *et al.* 1975). Hoff and Trainer (1973) in a review list 7 species of *Aedes*, 6 species of *Culex*, 2 of *Culiseta*, and *Mansonia perturbans* and *Anopheles quadrimaculatus* having been reported to feed on lizards, turtles and snakes. To the above records Tempelis and Galindo (1975) recently added 4 species of *Culex* that feed predominantly on reptiles and mention that some *Deinocerites* feed preferentially on ectotherms. Pinger and Rowley (1975) additionally record *Aedes trivittatus* as sometimes feeding on amphibians and reptiles.

The genus *Uranotaenia* seems to have a predilection for amphibian hosts. Remington (1945) records *Uranotaenia lowii* feeding on the frog *Rana sphenoccephala*, the tree frog *Hyla cinerea*, and the toad *Bufo valliceps* in the field, and upon *H. cinerea*, *B. valliceps*, *B. woodhousii fowleri* and the salamander *Desmognathus fuscus auriculatus* in the laboratory; only the salamander reacted to the bites. In laboratory tests, this mosquito rejected box turtles, two species of lizards, and humans; it seems to be largely restricted to amphibians.



Fig. 2. *Uranotaenia argyrotarsis* piercing the eyelid of *Rana daemeli* in the field. Note the whitish swelling on the frog's right eyelid.

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Marks (1960) records *Uranotaenia albescens* and *Culex* (*Lophoceraomyia*) sp. biting the hylid frog *Litoria caerulea*; this frog harbors a hemogregarine parasite in its blood and Marks suggested these mosquitoes may act as the invertebrate host. Her observations represent the only previous record of mosquitos feeding on ectothermic vertebrates in the Australian region.

OBSERVATIONS AND DISCUSSION

The present paper reports still another species of *Uranotaenia* feeding on amphibians, again from Australia. While collecting frogs at night along a small stream 16 km north-west of Iron Range, Queensland, on 6 September 1972, we noticed that a number of *Rana daemeli* were being bitten by mosquitoes. Many of the mosquitoes were observed to be blood-filled. Nine mosquitoes were collected and subsequently proved to be female *Uranotaenia argyrotarsis* Leceister. No other species was observed on the frogs. We subsequently approached the frogs cautiously using flashlights. The frogs remained motionless as long as the light was kept upon them and they could be closely observed. Of the 12 specimens captured and about three times that number observed but unmolested, nearly all were being bitten by at least one mosquito (Fig. 1) and some had as many as six biting simultaneously. The site of biting was always on the head, especially the upper eyelids, while no mosquitoes were observed biting the body or legs although these areas were exposed. The bites resulted in raised whitish swellings (Fig. 2). On no occasion did any frog give evidence of being irritated by the insects or in fact to be even aware of their presence.

We do not know how host-specific these mosquitoes are. However, we did not observe them biting any other species of frog in the area and they did not attempt to bite us although we were in close proximity to them for the several hours we observed the frogs. It is certain that they are not restricted to *R. daemeli* however, as the mosquito's geographic range is much wider than that of the frog. *U. argyrotarsis* occurs in Malaya, the Moluccas, the Philippines, New Guinea, the Solomon Islands and in Australia in the Northern Territory and north Queensland (Marks, pers. comm.). *R. daemeli* is found only on Cape York Peninsula, Australia. Some herpetologists consider *R. daemeli* as a subspecies of *Rana papua*. Even the range of *R. papua* in this broad sense is much smaller than the range of the mosquito, encompassing only New Guinea and Cape York.

We had the opportunity to collect *R. daemeli* at a different locality. On 7 September 1972, 24 km east of Iron Range, we obtained frogs from around small ponds and found that frogs are attacked in this area also. The swelling caused by mosquito bites are ephemeral except on the eyelids where they persist for some time, even in preservative. The preserved collections from the two sites were

examined in November 1975. On the 12 frogs collected on the 6th, 5 (45%) had one or both eyelids swollen; the corresponding value for the 40 collected by a pond on the 7th was 18 (45%). Thus, the incidence of biting seems to be similar in both localities. However, at the time of collection, no mosquitoes were seen on the frogs in the second area despite the fact that the collection was made at approximately the same time of evening as before. Weather conditions were probably responsible. The 6th was a calm night and no wind was noticeable. The 7th was windy and this may have inhibited mosquito activity.

Our observations in conjunction with similar ones from the literature suggest that feeding of mosquitoes on ectothermic vertebrates may be more common than generally realised. There may be economic and/or medical implications. A possible benefit which might accrue from examination of mosquito-transmitted diseases to amphibians could be the selective control of introduced amphibian pests in Australia such as the cane toad (*Bufo marinus*).

Studies are badly needed which survey (1) the range of hosts attacked by different species of mosquitoes, (2) the range of mosquito species biting particular species of amphibians and reptiles, (3) the diseases and/or parasites transmissible between mosquitoes and ectotherms, and (4) the environmental factors related to such transmission. Also studies evaluating ectotherms as potential reservoirs of viral or other mosquito-borne diseases attacking man, domestic animals or wildlife would be extremely valuable.

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Biology of *Neophyllaphis brimblecombei* Carver (Homoptera: Aphididae) in the Sydney Region

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The annual cycle of *Neophyllaphis brimblecombei* Carver in Sydney is described. The aphids generally occur only on young shoots of their host plants, *Podocarpus elatus* and *P. spinulosus*. Fundatrices hatch and colonise new shoots on *P. elatus* in late July or August. Winged oviparous females are present by the end of September. Alatae viviparae and males are uncommon. The shoots mature in November, and the aphid population then disappears. The eggs laid by the oviparae diapause until the following July or August. The cycle is similar on *P. spinulosus*, but is correlated with the variable commencement of shoot development in the host plant. Shoots produced on *P. elatus* in response to pruning are colonised by *N. brimblecombei*, as are naturally occurring autumn shoots on *P. spinulosus*. Annual cycles of other *Neophyllaphis* spp. on *Podocarpus* are compared with that of *N. brimblecombei* and possible factors controlling production of sexuales are discussed. The relatively low success of aphids in Australia is discussed in relationship to factors controlling production of sexual forms.

INTRODUCTION

Only 130 species of Aphidoidea are known from Australia, including 17 species probably restricted to native plants and known only from Australia (Carver, pers. comm.). A large proportion of the species now found here are thought to have been introduced accidentally on their host plants. As the total number of described aphid species exceeds 3600 (Eastop, 1970), the Australian aphid fauna is disproportionately small.

The biology of aphids occurring primarily on native plants in Australia is virtually unknown, the only exception being *Sensoriaphis furcifera* (Carver and Hales, 1974). Yet the subject is of considerable interest, particularly in view of the small representation of aphids in the Australian fauna. It appears that the Australian environment has been unfavourable for radiation of this group.

The genus *Neophyllaphis* has many primitive characteristics and is associated with the ancient plant genus *Podocarpus*, which originated in the Gondwanaland flora and has since spread into Asia and Africa. (Some species of *Neophyllaphis* occur on host plants belonging to other genera, e.g. *N. rappardi* Hille Ris Lambers

on *Agathis* in West Irian, *N. michelbacheri* (Essig) on *Pilgerodendron* in South America, *N. araucariae* Takahashi on *Araucaria* in Australia, New Guinea, Hawaii, Mauritius.) *Neophyllaphis brimblecombei* Carver occurs on *Podocarpus elatus* R. Br. ex Endl. in coastal regions of New South Wales and Queensland. It is very similar morphologically to *N. podocarpi* Takahashi on *Podocarpus* spp. in Japan and Taiwan. The present paper describes its annual cycle in the Sydney region. We have already described its unusual adhesive vesicles (White and Carver, 1972) and its flattened eggs and oviposition behaviour (Carver and Hales, 1974).

STUDY SITES

Neophyllaphis brimblecombei Carver was studied on four trees of *Podocarpus elatus* R. Br. ex Endl. growing in a street in the Sydney suburb of Mosman. The trees were approximately 10 m tall; collections were taken from the lowest branches at weekly or fortnightly intervals for one full season, and less frequently at other times, between 1971 and 1975. Aphids occurring on *Podocarpus spinulosus* (Sm.) R. Br. ex Mirb. are considered by Dr. Carver to belong to *Neophyllaphis brimblecombei*. *P. spinulosus* is a small scrambling shrub and occurs naturally in the bush around Sydney Harbour; some observations were made on populations on this host, also in Mosman. When found on *P. spinulosus*, *N. brimblecombei* is covered in a coating of long closely packed strands of wax wool, whereas on *P. elatus* it is only slightly pulverulent.

RESULTS

OBSERVATIONS ON THE HOST PLANTS

In the mature trees of *Podocarpus elatus* which were studied, shoots were produced almost synchronously in August, with only slight differences between the trees studied. The new leaves, at first pinkish and soft, became pale green and eventually reached a size of about 9 x 1 cm. Thereafter they began to darken in colour and became hard and stiff. Hardening and darkening of the leaves was evident, but incomplete, in mid-October; the leaves were not fully mature and hardened until late November.

In untouched trees, no further shoots were normally produced until the following August. Two of the trees studied were periodically pruned to prevent them touching powerlines and fresh shoots were present on these for long periods. Accidental damage also induced formation of new shoots out of season.

Although *P. elatus* is native to the Sydney region (as defined by Beadle *et al.*, 1972) most specimens in Sydney itself are cultivated as street or garden plants, and therefore are subject to pruning.

Podocarpus spinulosus commences shooting between late July and late September, the onset varying between plants in different situations. The leaves

BIOLOGY OF *NEOPHYLLAPHIS BRIMBLECOMBEI*

reach a maximum length of 6 cm before hardening. Hardening is completed in about 10 weeks from the beginning of shooting. Occasional new shoots are produced in natural conditions in April (mid-autumn). *P. spinulosus* is not cultivated and its normal growth cycle is not affected by human activities.

ANNUAL CYCLE

The annual cycle of *N. brimblecombei* in the study area can be summarised as follows: On *Podocarpus elatus*, the fundatrices hatch in late July or early August; they may survive briefly on old leaves if the new shoots have not developed, but transfer to new shoots before maturity. Fundatrices are characterised by a deep purple pigmentation and relatively short antennae. They give birth to apterae viviparae on the new shoots in the second half of August. Fundatrigeniae and later apterous generations are cream in colour with patches of purple pigment around the siphunculi. The population increases rapidly, reaching a peak in late September or early October. At this stage, before mid-spring, oviparae (which are always alate) become the dominant morph. Alate viviparae and alate males were never observed to be numerous but were usually collected in small numbers in October and November. Eggs were present on maturing leaves from October onwards and could be collected at any time until hatching. No signs of embryonic development were noted until shortly before hatching. The aphid population waned during late October and November, when only isolated specimens were found. Table 1 shows the occurrence of different morphs on a month-by-month basis.

TABLE 1
RECORDS OF MORPHS OF *N. BRIMBLECOMBEI* ON *P. ELATUS*

al = alate viviparae ap = apterous viviparae
f = fundatrix — = no survey

		1971-2	1972-3	1973-4	1974-5	1975-6
SPRING	Sept.	ap	f, ap, ♀	ap, ♀	—	f, ap, al, ♂, ♀
	Oct.	—	ap, ♀, ♂	ap, al, ♀, ♂	ap, al, ♀, ♂	
	Nov.	ap, al, ♀, ♂	ap	—	ap, al, ♀ (few)	
SUMMER	Dec.	nil	few larvae only	nil	ap	
	Jan.	—	nil	nil	—	
	Feb.	—	nil	—	nil	
AUTUMN	Mar.	—	nil	—	nil	
	Apr.	—	nil	—	nil	
	May	nil	nil	—	—	
WINTER	June	—	few ap	—	nil	
	July	—	—	—	—	
	Aug.	—	f	—	f	

When new shoots were produced on *P. elatus* out of season in response to pruning or damage, they were usually colonised by *N. brimblecombei*. The succession of morphs in these colonies has not been studied, but in the early stages of their development they contain apterae and apteriform nymphs. Neither fundatrices nor alatae have been collected in these situations. However, the colonies are presumably founded by migrants from locally more favourable host plants.

The collections from *P. spinulosus* indicate a similar annual cycle, with some differences. While fundatrix nymphs were collected in August 1975, the initiation of colonies sometimes appears to be delayed until October (no specimens were found in August and September 1973) and this may be correlated with the variable commencement of shooting of the host plant (see Table 2). The peak population size and production of sexuales also occurs later than on *P. elatus*, so that the aphids are still numerous in November and even December. Small colonies recur in April or May but do not persist. The aphids are absent in mid-summer. Specimens on this host retain their deep purple colouration in all generations, but it is only apparent when the dense wax wool coating is removed.

TABLE 2

RECORDS OF MORPHS OF *N. BRIMBLECOMBEI* ON *P. SPINULOSUS*

(Abbreviations as in Table 1)

		1971-2	1972-3	1973-4	1974-5	1975-6
SPRING	Sept.	—	—	nil	—	f, ap, al
	Oct.	—	—	—	—	ap, al, ♀
	Nov.	ap, al	—	—	ap, al, ♀, ♂	
SUMMER	Dec.	ap, al, ♀	—	—	♀	
	Jan.	—	—	—	—	
	Feb.	—	—	—	ap	
AUTUMN	Mar.	—	—	—	nil	
	Apr.	—	larvae only	—	larvae	
	May	ap	nil	—	nil	
WINTER	June	—	—	—	—	
	July	—	—	—	—	
	Aug.	—	nil	—	f	

Neophyllaphis brimblecombei is preyed on by *Micromus tasmaniae* Walker and *Drepanacra humilis* McLachlan (Neuroptera: Hemerobiidae), by *Leis conformis* (Boisduval) and *Coelophora inaequalis* (F.) (Coleoptera: Coccinellidae) and by *Melangyna viridiceps* (Macquart), *Simosyrphus grandicornis* (Macquart), *Beta-syrphus serarius* Wiedemann (Diptera: Syrphidae) and another syrphid which has not been successfully reared. The syrphid identifications are tentative as the group is in need of revision. No parasitised *Neophyllaphis brimblecombei* have been observed.

DISCUSSION

ANNUAL CYCLE OF *Neophyllaphis brimblecombei* COMPARED WITH CYCLES OF OTHER *Neophyllaphis* spp.

The annual cycle of *Neophyllaphis brimblecombei* in the Sydney region is basically a very short one, with only one or at the most two generations intervening between fundatrix and the first ovipara. Facultative parthenogenetic reproduction can continue, however, if suitable young growth is available on the host plants, as happens occasionally in natural conditions and frequently on cultivated plants. The fundatrix hatches late in winter (July-August) and from October to July the major part of the population is in the form of eggs.

Takahashi (1920, 1923) has given brief notes on the biology of *Neophyllaphis podocarpi* Takahashi in Japan and Taiwan. As mentioned above, *N. podocarpi* is very similar morphologically to *N. brimblecombei*. In Japan, *N. podocarpi* produces sexuales in late spring and they occur together with apterous and alate viviparae until the end of autumn. In Taiwan, on the other hand, *N. podocarpi* is continuously viviparous throughout the year and sexuales are rare. It is evident that the host plants (*P. macrophylla* and *P. nageia*) remain suitable for extended periods in Japan and continuously in Taiwan. The aphids are said to attack the young leaves, but it is not stated whether they can survive on mature leaves. Each apterous sexupara can produce both sexuales and apterous viviparae (Takahashi, 1923).

Neophyllaphis gingerensis Carver occurs on *P. alpina* R. Br. in alpine conditions in the Australian Capital Territory (Carver, 1959). It is mostly confined to young shoots of its host plant, and its season is again a short one. The first aphids are observed in December, with sexuales and viviparae both present from January onwards. By May no aphids remain.

The New Zealand species *Neophyllaphis totarae* Cottier produces sexuales in spring on *P. totara*, but can apparently continue reproducing parthenogenetically all the year round (Cottier, 1953, p. 24). The present author has collected both viviparae and sexuales in February in several South Island localities on *P. totara*, *P. nivalis* and *P. ballii*.

No published information is available on the annual cycles of the other *Podocarpus*-feeding species of *Neophyllaphis*.

Certain common features emerge from the annual cycles outlined above. Most species produce sexuales soon after the fundatrix generation. Sexuales and parthenogenetic forms can be produced concurrently, thus allowing facultative viviparous reproduction to occur in suitable conditions, while still ensuring early deposition of diapausing eggs. In some cases the aphids are present only for a short time; in *N. brimblecombei* the limiting factor appears to be the availability of young shoots, while in some species climatic factors may be more important.

The absence or rarity of sexuales in *N. podocarpi* in Taiwan is an exception to the pattern found elsewhere. The loss of ability to produce sexuales after a long period of parthenogenetic reproduction is well known in the most advanced aphid sub-family, the Aphidinae (see Lees, 1966), and it is interesting to note a similar phenomenon in a primitive aphid such as *N. podocarpi*.

MECHANISM OF INDUCTION OF SEXUALES

Sexual forms in most aphids that have been studied experimentally are induced by short photoperiods and low temperatures (see Lees, 1966 for references). There is usually an obligatory delay or "interval timer" which prevents production of sexuales until a certain time has elapsed from the fundatrix generation. This has been shown, for example, in *Aphis chloris* (Wilson, 1938), *Brevicoryne brassicae*, *Myzus persicae* and *Sappaphis plantaginea* (Bonnemaison, 1951) and *Megoura viciae* (Lees, 1961), all members of the sub-family Aphidinae.

Dixon (1971, 1972) has demonstrated a similar phenomenon in *Drepanosiphum platanoides* and *Eucallipteris tiliae*, both of which belong to the sub-family Drepanosiphinae, as does *Neophyllaphis*. In *D. platanoides* the obligate delay was much shorter than in the Aphidinae listed above, and could be overcome completely by very short experimental photoperiods. With the passage of time from the fundatrix generation, the critical photoperiod became longer, i.e. the threshold of response became lower. In *E. tiliae* even the fundatrix produces some oviparae in natural conditions.

The observations reported here on *N. brimblecombei* are consistent with a short obligatory delay and a low threshold of photoperiodic response. On the other hand, nutritional factors have been shown to induce the production of sexuales in some aphids, e.g. *Dysaphis devectora* (Forrest, 1970) and also in the closely related Pemphigidae, e.g. *Tetraneura ulmi* (Schwartz, 1932), *Pemphigus bursarius* (Dunn 1959, 1974) and *Eriosoma pyricola* (Sethi and Swenson, 1967). The hypothesis that host plant factors are involved in production of sexuales in *N. brimblecombei* is attractive, as it would account for the close correlation between aphid and host plant cycles.

ADAPTIVE VALUE OF THE *Neophyllaphis* ANNUAL CYCLE

Aphids have radiated and diversified most strongly in the north temperate regions, and the number of species endemic to Australia is small. It is rather surprising that so few north-temperate species have become established in Australia since the time of European settlement. One might seek the explanation in the annual cycles of northern aphids, which are specialised to avoid the harsh winter. A long obligate delay between fundatrix and sexuales, such as occurs in most holocyclic Aphidinae, forces species to rely on continuous parthenogenetic reproduction in summer. Long hot, dry periods, common in most parts of the Australian mainland in summer, reduce the suitability of host plants and put aphid populations at risk. The more primitive *Neophyllaphis* is better adapted to avoid the

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rigours of both summer and winter by producing diapausing eggs in the spring. Other factors related to the control of diapause may also limit the success of holocyclic strains of northern aphids in Australasia (Eastop, 1966, Lowe, 1973).

Early production of sexuales is characteristic of *Sensoriaphis* (Drepanosiphinae) (Carver and Hales, 1974) and *Schoutedenia* (Greenideinae) (Hales and Carver, 1976), two other genera associated with Australian native plants. The apparently native species belonging to the Aphidinae are anholocyclic as far as is known, and tend to be uncommon compared with *Neophyllaphis*, *Schoutedenia* and *Sensoriaphis*. The *Neophyllaphis* type of annual cycle thus appears to have a high adaptive value in Australian conditions.

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A Study of *Schoutedenia lutea* (van der Goot, 1917) (Homoptera: Aphididae)

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ABSTRACT

Observations on a population of the aphid *Schoutedenia lutea* have been made over a period of several years. The annual cycle is described. Sexuales occur concurrently with parthenogenetic females throughout summer and autumn. Some morphological and taxonomic notes are provided on the fundatrix, a green viviparous form, the sexuales and the eggs. *Schoutedenia viridis* is confirmed as a synonym of *S. lutea*. A number of insect parasites, hyperparasites and predators of *S. lutea* have been reared and are listed.

INTRODUCTION

Schoutedenia lutea (van der Goot) is a member of a small group (Schoutedeniini) of eight known genera in the subfamily Greenideinae, which is distributed in South America, Africa, India, Australia and in eastern Asia, northward to Japan, and includes two indigenous Australian genera, *Anomalaphis* Baker and *Meringosiphon* Carver.

S. lutea itself occurs naturally in Australia, S.E. Asia and India and probably Africa and China also, but its true range will not be determinable until the species composition of *Schoutedenia* is elucidated. The following species and subspecies of *Schoutedenia* have been described: *S. ralumensis* Rübsaamen, 1905; *S. lutea* (van der Goot, 1917); *S. viridis* (van der Goot, 1917); *S. bougainvilleae* (Theobald, 1920); *S. formosanus* (Takahashi, 1929); *S. emblica* (Patel and Kulkarni, 1952); *S. emblica andbraka* David and Hille Ris Lambers, 1956. However, some synonymy is suspected (Ghosh *et al.*, 1972; Eastop, 1966; Tao, 1962) and it is likely that the genus actually contains only one or two species.

Schoutedenia has been recorded from woody plants of the family Euphorbiaceae. The only known host plant of *S. lutea* in Australia is *Breynia oblongifolia* J. Muell., a small bush growing to 2 m high in or near rainforest and in sandstone bushland in New South Wales and Queensland, northward to Cape York.

MATERIALS AND METHODS

All collections were made in sandstone bushland in the Sydney suburb of Mosman. Observations were made from 1972 to 1975 inclusive, during spring, summer and autumn. At each inspection, notes were made of the morphs present. Predators and parasites were collected and reared for identification.

For taxonomic studies, microscopic mounts were made according to the method recommended by Stroyan (van Emden, 1972). Dissections were carried out in saline solution and serial sections were prepared from material fixed in alcoholic Bouin's solution containing 0.5% trichloroacetic acid and stained with Mayer's haemalum and celestin blue, or with Regaud's iron haematoxylin and phloxin or fast green.

ANNUAL CYCLE

The following account is a composite summary based on three seasons' observations. Table 1 gives a full month-by-month summary of morphs present. Fundatrices hatched in mid-September, although fresh shoots were present on the host plant from the beginning of August. Production of viviparae commenced at the end of September and, by late October, the first males were observed. Thereafter, apterae viviparae, alatae viviparae, oviparae and males were present in the population until May, except in 1974, when no aphids were observed after February. Occasional monthly samples after October lacked males and/or alatae viviparae.

TABLE 1
COLLECTIONS OF *SCHOUTEDENIA LUTEA* (VAN DER GOOT)

		1972/1973	1973/1974	1974/1975
SPRING	Sept.	—	Fundatrices	—
	Oct.	—	apt; ♂♂	nil
	Nov.	apt; al; ♀♀; ♂♂	apt; al; ♀♀	—
SUMMER	Dec.	apt; al; ♀♀; ♂♂	apt; al; ♀♀	—
	Jan.	apt; al; ♀♀; ♂♂	apt; ♀♀; ♂♂	apt; al; ♀♀; ♂♂
	Feb.	apt; ♀♀	apt; ♀♀; ♂♂	apt; al; ♀♀; ♂♂
AUTUMN	Mar.	apt; al; ♀♀	nil	apt; al; ♀♀; ♂♂
	Apr.	apt; al; ♀♀; ♂♂	nil	apt; al; ♀♀; ♂♂
	May	apt; al; ♀♀	nil	apt; al; ♀♀
WINTER	June	—	—	apt; al
	July	—	—	nil
	Aug.	nil	—	nil

apt. = apterae viviparae
al. = alatae viviparae
nil = no live aphids found

♀♀ = oviparae
♂♂ = males
— = no survey

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Eggs were laid continuously from November to May but presumably did not hatch until the following spring, as fundatrices were found only in spring.

The aphid was not confined to fresh shoots and could be found on young leaves, older leaves and on stems of *B. oblongifolia*. Although the host plant was common in the area, few individual plants were colonised by *S. lutea*. On colonised plants, however, aphid numbers rose to very high levels; over 80 individuals per leaf were counted, corresponding to a density of about 40 cm⁻². In late December or early January, alatae viviparae initiated secondary colonies on neighbouring bushes. These however did not usually reach the size of the primary colonies. Large populations of aphids appeared to damage the plants; the leaves turned yellow and were shed.

MORPHOLOGICAL AND TAXONOMIC NOTES

EGG

When freshly laid, the egg is light orange in colour and has a white papilla at the apex of the posterior (wider) end. Elongated but not flattened and somewhat irregular in cross section, it might best be described as banana-shaped (Fig. 1). Length of 20 eggs of *S. lutea* laid in the laboratory: 0.62-0.73 mm (mean = 0.68); width: 0.18-0.24 mm (mean = 0.21). Field-laid eggs may be a little larger. Within a day or so of being laid the eggs turned black. They were generally laid in leaf axils or in cracks in the bark, and were curved to fit the contours of the substratum. Eggs within macerated oviparae lack the papilla and instead appear truncate or faintly concave in this area. The papilla is presumably lost during maceration. Macerated eggs of *S. bougainvilleae* are similarly truncated at the posterior end (Eastop, 1961).

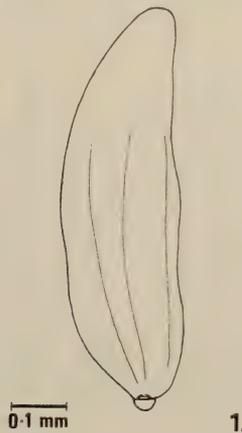


Fig. 1. Egg of *Schoutedenia lutea* (van der Goot).

TABLE 2
COMPARISON OF MORPHS OF *SCHOUTEDENIA LUTEA* (VAN DER GOOT)

	fundatrix	aptera vivipara green	aptera vivipara yellow	ovipara	alata vivipara	male	intermediate males
Mean body length (mm)	1.53	1.49	1.66	1.71	1.60	1.43	1.22
antennal length (mm)	0.76	0.81	1.04	1.17	1.19	1.22	0.92
ant. sgt. III (mm)	0.40	0.28	0.40	0.46	0.45	0.45	0.29
ant. sgt. IV (mm)	—	0.17	0.22	0.25	0.26	0.28	0.22
ant. sgt. IV base or Vb (mm)	0.17	0.15	0.19	0.22	0.23	0.23	0.20
ant. sgt. IV p.t. or V p.t. (mm)	0.08	0.08	0.10	0.12	0.12	0.12	0.10
antennal length/body length	0.47-0.53	0.49-0.56	0.56-0.69	0.62-0.74	0.72-0.82	0.82-0.88	0.72-0.78
p.t./base	0.45-0.48	0.42-0.59	0.44-0.63*	0.52-0.61	0.45-0.61	0.50-0.60	0.49-0.59
ant. sgt. III/p.t.	5.00-5.10	3.02-4.12	3.15-4.75*	3.47-4.00	3.50-4.20	3.33-4.00	2.70-2.90
ant. sgt. III/IV + V	—	0.66-0.77	0.65-0.86*	0.76-0.82	0.69-0.76	0.68-0.80	0.55-0.58
u.r.s./h.t.2	—	0.60-0.77	0.60-0.77	—	—	—	—
length spinal process/body length	0.16-0.18	0.15-0.17†	0.14-0.18	0.14-0.17	0.09-0.12	0.08-0.10	0.12
hind tibia/body length	0.23-0.24	0.24-0.25†	0.27-0.31	0.28-0.31	0.36-0.40	0.36-0.41	0.34-0.37
No. of specimens studied	3	9	7	6	8	8	2
Month of collection	ix	ii	ii, iii, iv	ii, iii, iv	ii, iii, iv	ii, iii, iv	iv

p.t. = processus terminalis u.r.s. = ultimate rostral segment h.t.2 = second hind tarsal segment

*Includes values obtained from measurements of 15 yellow apterae viviparae collected concurrently with green apterae viviparae tabled in previous column

†Values from three specimens only

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Oviposition was observed but had no unusual features. The ovipara stretched the abdomen posteriorly at the commencement of laying and gradually drew the tip forwards as the egg was extruded. The ovipara then moved away without giving further attention to the egg.

FUNDATRIX

Readily identifiable in field; deeper yellow than other apterae viviparae and with patches of brown on head and dorsum of thorax and abdomen. Antennae shorter than those of other morphs and only 4-segmented, segment III being proportionately longer than in other morphs; without secondary rhinaria; flagellar hairs about 9 μm in length, short, blunt, pale, sparse, i.e. usually no more than one hair near each rhinarium (in addition to apical hairs). Body pale; dorsal body hairs 5-8 μm long; a little shorter and sparser than in other apterae viviparae; siphuncular hairs 5-13 μm long; hairs on spinal processi 13 μm long; tergite VII with two pleural hairs, lateral to spinal processi; tergite VIII with two hairs, 7-19 μm long. Legs proportionately shorter than those of other morphs. Subanal plate apical, small, pale, spinosely imbricated, with 8-12 short and fine to long and stout hairs, symmetrically arranged. Subgenital plate pale, spinosely imbricated, with 4 anteriorly placed hairs and 5-8 posterior hairs. Gonapophyses consist of 4 groups each of 2-4 minute hairs. For further comparison with other morphs, see Table 2.

APTERA VIVIPARA

Apterae viviparae of *S. lutea* are usually a clear, uniform lemon-yellow in colour. Green viviparous specimens were found from time to time intermingled with yellow ones; on closer inspection, the green specimens proved to be alatoid individuals with varying degrees of development of wings, thorax, ocelli and compound eyes. Yellow alatoid apterae also occurred and once (2.ii.75), a collection was made which contained only green apterae viviparae (and darker, olive-green oviparae). These specimens possessed no alatoid characteristics and gave birth in the laboratory to the usual yellow apterae. The field colony contained only yellow specimens when next checked (20.iii.75). A comparison of these green *Schoutedenia* with yellow apterae viviparae collected on the same day from a locality a few kilometres distant showed no significant differences except perhaps one of size (see Table 2).

OVIPAROUS FEMALE

Apterous. Living specimens olive-green in colour, in contrast to the lemon-yellow or lighter green colour of the apterae viviparae; orange coloured eggs often visible through the body wall. Antennae 5-segmented, without secondary rhinaria; flagellar hairs as in aptera vivipara, 8-12 μm long; segment III with only 5 hairs, segment IV with only 2, near rhinarium; segment V with only 1, near rhinarium (in addition to apical hairs). Legs with 9-20 pseudosensoria on the hind *femur*;

these are difficult to distinguish from the pronounced gland-like ornamentation of the femora. Body hairs as in aptera vivipara, sparse; on anterior abdominal tergites, with a maximum of 2 spinal hairs, 8-9 μm long, and 2 submarginal hairs on each side; tergite VII with 2 pleural hairs lateral to spinal process; hairs on spinal processi approximately 13 μm long; tergite VIII with 2 hairs, 16-43 μm long. Posterior abdominal segments somewhat attenuated. Subanal plate apical, large, pale, spinosely imbricated, with 80-90 hairs varying in size from small and fine to long and stout (cf. that of vivipara with only 10-12 hairs): subgenital plate large but not obviously demarcated; presence indicated by 2 transverse groups of variously sized, fine, pale hairs; each group with 30-40 hairs (cf. that of aptera vivipara, with 2 rows each of usually 6 hairs). Gonapophyses borne on 3 pronounced tubercles, the outer tubercles, 42-64 μm long, both inclined posterolaterally and each with 4-6 hairs; inner tubercle shorter, 35-50 μm long, sometimes appearing faintly bifid at apex; with 6-8 hairs (cf. viviparae whose gonapophyses consist of 4 groups each of 2-5 hairs, which are very rarely borne on 3 very small, flat, pale tubercles). For further comparison with other morphs, see Table 2.

An internal structure, which persists after maceration, is very conspicuous in the abdomen of some oviparae. This structure consists of two large, broad, irregularly shaped, greenish arms which are united posteriorly by a narrow isthmus. It is also present in oviparoid nymphs, but the arms are not united. Dissection and serial sections showed that the structure corresponded to the accessory glands of the reproductive system. The sections also showed that the accessory glands contain a refractile green substance which is not removed by ordinary histological solvents. The precise nature and function of this substance are not known but presumably it forms a protective or adhesive layer on the surface of the eggs as they are deposited. Dissection of several oviparae showed four ovarioles on each side of the body cavity. Each ovariole contained one or

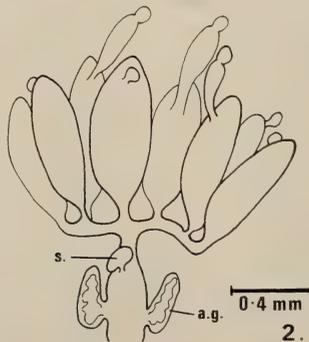


Fig. 2. Reproductive system of *S. lutea* (ovipara). Abbreviations: s.—spermatheca; a.g.—accessory gland.

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two large eggs. A diagrammatic representation of the reproductive system is given in Figure 2.

The presence of pseudosensoria on the hind femora is very unusual, the only other published instances being *S. bougainvilleae* and the related *Eonaphis euphorbiae* (Eastop, 1961; Quednau, 1964). These observations conflict with the references to the occurrence of pseudosensoria on the tibiae of oviparae of *S. lutea* and *S. emblica andbraka* (Ghosh *et al.*, 1972; David and Hille Ris Lambers, 1956).

MALE

Alate. Antennae proportionately longer than those of other morphs; 5-segmented, with 47-59 circular secondary rhinaria on antennal segment III, 13-24 on segment IV and 0-2, usually 0, on segment V (compared with 27-37 secondary rhinaria on segment III and 0-7 on segment IV in alata vivipara); concentrated on ventral surface. Tibiae and spinal processi spinosely imbricated, as in alata vivipara. Genitalia comparatively simple, not heavily sclerotized; claspers roughly trapezoidal in shape and medially acutely triangular; armature not extensive; penis short, sparsely haired; about 19 hairs at base of genitalia, which are anterior to or are a continuation of subanal plate. For further comparison with other morphs, see Table 2.

On at least two occasions (30.iv.73, 8.i.75), a few small, apparently functional males were collected, possessing varying combinations of apteroid and alatoid characteristics. The genitalia appeared to be normal, and compound eyes and ocelli were present but the specimens possessed abortive wings, a variously developed thorax and a varying and intermediate number of secondary rhinaria on the oddly proportioned antennal segments. In addition, they were noticeably smaller than specimens of any other morph studied.

Ghosh *et al.* (1972) have briefly described the male of *S. lutea* and David and Hille Ris Lambers (1956) the apteroid male of *S. emblica andbraka*.

The males, alatae viviparae and alatiform nymphs were green in colour.

PREDATORS AND PARASITES

The populations of *S. lutea* were subject to attack by a range of other insects. Where possible, the predators, parasites and hyperparasites were reared and identified.

A. Predators

1. Diptera: Syrphidae. Larvae of *Simosyrphus grandicornis* (Macquart) and a second species, probably *Melangyna viridiceps* (Macquart). Predation by larvae of these species was heavy, particularly in spring. *Diplazon laetatorius* (F.) (Hymenoptera: Ichneumonidae) was reared from *S. grandicornis*.

2. Diptera: Chamaemyiidae. *Leucopis* sp. (probably undescribed). This species was very common, the larvae consuming large numbers of *S. lutea* throughout the summer. Their passage through a colony was marked by the presence of dead, brown aphids hanging by their stylets.
Two specimens of *Euryischia* sp. (Encyrtidae: Eriaporinae) were reared from two puparia of this predator. Species of this genus are hyperparasites through parasitic Diptera (Riek, pers. comm.).
3. Coleoptera: Coccinellidae. *Coelophora inaequalis* (F.), *Amidellus ementitor* (Blackburn), *Leis conformis* (Boisduval). Adults and larvae of these were observed from time to time. They did not appear to affect well-established colonies greatly. On one occasion, *L. conformis* was found to be parasitised by dipterous larvae, *Phalacrotophora* sp. (Phoridae: Metopinae) probably undescribed. Four parasite larvae emerged from the remains of the host pupa, and pupated separately, alongside their host.
4. Neuroptera: Hemeroibiidae. *Micromus tasmaniae* Walker. Not common. Surprisingly, no Chrysopidae were observed.

B. Parasites

1. Hymenoptera: Chalcidoidea: Aphelininae. *Aphelinus gossypii* Timberlake. *Aphelinus gossypii* is at times a common parasite, in N.S.W. and South Australia at least, of many species of Aphidinae. While parasitism of *S. lutea* by this species sometimes reached moderate levels (the brownish gut contents of the parasite larva could be seen through the body wall of the living host), few mummified aphids and adult *Aphelinus* were obtained.

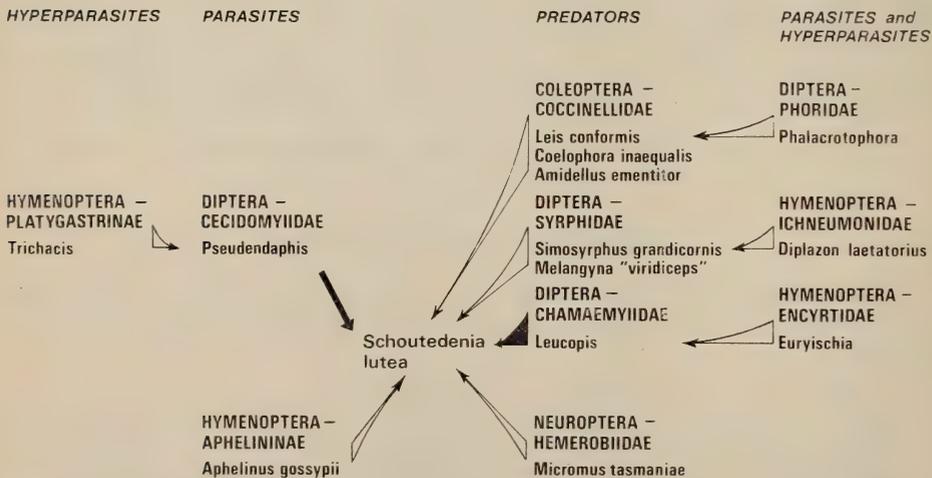


Fig. 3. Parasites and predators of *Schoutedenia lutea*.

2. Diptera: Cecidomyiidae. *Pseudendaphis* sp. This may be an undescribed species but its status will be uncertain until there has been a thorough revision of cecidomyiid endoparasites of aphids (Harris, pers. comm.). The species was extremely common from January to May as an endoparasite of *S. lutea*. The cecidomyiid larvae were in turn parasitised by a minute wasp, *Trichacis* sp. (Proctotrupeoidea: Platygastriinae). Members of the Platygastriinae are usually parasites of gall-forming Cecidomyiidae. Cecidomyiids have not previously been recorded as aphid parasites in Australia.

C. Relationships with ants

At least four species of ants were observed from time to time collecting honeydew from colonies of *S. lutea*.

The relationships of *S. lutea* with other insects are shown diagrammatically in Fig. 3. With the exception of *Pseudendaphis* sp. specimens of those insects not identified to species have been deposited in the Australian National Insect Collection, C.S.I.R.O., Canberra, A.C.T.

DISCUSSION

The annual cycle of *Schoutedenia lutea* in the Sydney region can be summarised as follows: fundatrices hatch in early spring (mid-September) and produce a generation of apterous fundatrigeniae. Adult males were first noted in late October, and oviparae in mid-November. It is therefore probable that the third generation can include males, and the following generation oviparae. After this time, alate and apterous viviparae as well as sexuales occur concurrently until the onset of the following winter. There is no evidence in the literature to indicate whether or not the life cycle of *S. lutea* has similar unusual features in other parts of its geographical range.

Other species producing sexuales early in the season either as the final morphs of an abbreviated life cycle or concurrently with viviparae include some Japanese species of *Greenidea*, *Paratrichosiphum* and *Eutrichosiphum* (Takahashi and Sorin, 1959; Takahashi, 1962), some species of the unrelated *Neophyllaphis* in Australia, New Zealand and Japan (see Hales, 1976), and *Sensoriaphis furcifera* in Australia (Carver and Hales, 1974).

Eastop (1961) describes the apterae of *S. bougainvilleae* as "yellow or green" and according to Hille Ris Lambers (pers. comm.), *Schoutedenia* collected in Java were "repeatedly yellow apterae, sometimes yellow apterae with green alatae".

The present study has established that *S. lutea* occurs in two distinct colour forms, yellow and green. Ghosh *et al.* (1972) are of the opinion that *S. lutea*, *S. viridis* and also *S. bougainvilleae* are synonymous. Tao (1962) lists *S. bougainvilleae* and *S. formosanus* as synonyms of *S. viridis* and Eastop (1966) says that *S. bougainvilleae* may be a synonym of *S. viridis*. Van der Goot (1917) described

(as *Setaphis*) the apterous and alate morphs of two species of *Schoutedenia* viz. *S. lutea*, a yellow aphid, and *S. viridis*, a green aphid, which were additionally distinguishable from one another, in both morphs, by a longer third antennal segment in *S. lutea* relative to the processus terminalis (4:1 in *S. lutea*, 3:1 in *S. viridis*).

It can be seen from Table 2 that this distinction does not hold for our specimens and further comparison of our colour forms and apterous and alate morphs with van der Goot's two descriptions leads to the conclusion that *S. lutea* and *S. viridis* are synonymous.

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Observations on *Bdellasimilis barwicki*, A Marine Triclad from Australian Freshwaters (Platyhelminthes: Turbellaria)

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ABSTRACT

Bdellasimilis barwicki, an aquatic planarian ectoconsortic on turtles from Australian freshwaters, is re-described from type material. Corrective remarks are made and new taxonomic data provided. The species is here regarded as a member of the Maricola that has invaded freshwaters and it is assigned to the family Procerodidae.

INTRODUCTION

Bdellasimilis barwicki is a probursal planarian originally described as an ectoconsort from the limb-pits of turtles from Lake Wyangan, near Griffith, New South Wales (Richardson, 1968). Subsequently further specimens were obtained from a turtle on the flood-plain of the Lower Clarence Valley, Northern Rivers Region, New South Wales, and there is a possibility that a second species occurs in Queensland (Richardson, 1970). There are many unusual morphological features of this species that made its taxonomic assignment difficult and pointed to the possibility that the genus may require a new suborder within the Tricladida (Richardson, 1970). Through the kindness of Professor L. R. Richardson I have been able to examine two paratypes of the species and from my detailed study of these I am able to correct some aspects of the original description and to provide new data that enhance our understanding of the systematic position of this animal.

Originally the species was assigned by Richardson (1968) to the Paludicola, the freshwater planarians, "provisionally and with much reservation". In my opinion the species is a true maricole that has invaded freshwaters (Ball, 1974a: 343) a phenomenon that has occurred in some other marine planarians (Ball, 1974b: 29). Kenk (1974) has also expressed doubt as to the paludicolan affinities of this form.

MATERIALS AND METHODS

The two paratypes from Professor Richardson were received preserved in glycerine. They were transferred to alcohol and then embedded in paraffin in the usual way. Sagittal and transverse serial sections were cut, at a thickness of 8 microns, and the sections were mounted on 2 in x 3 in glass microslides. The ribbons were arranged in vertical rows with the first section in the upper left corner when the slide label is to the right. The sections were stained in Mallory-Heidenhain stain (Gurr, 1963) but the fixation technique used by the original collector proved not to be entirely compatible with this stain and so the sections were only weakly coloured.

The two paratypes are now in the collections of the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum, as follows: sagittal sections on four slides (ROM C418a) and transverse sections on three slides (ROM C418b). The original type material is a whole-mount in the Australian Museum (W417c).

SYSTEMATIC SECTION

Infraorder MARICOLA

Family PROCERODIDAE Dising

Genus *Bdellasimilis* Richardson, 1968

The assignment of the genus to the Procerodidae may prove to be a temporary measure. The classification of the Maricola is in a state of flux (Holmquist and Karling, 1972; Mitchell and Kawakatsu, 1972) and it is more than likely that our concept of the Procerodidae, a family defined only by primitive characters, will undergo considerable revision in the near future (e.g. Ball, 1973, 1975).

Bdellasimilis barwicki Richardson, 1968

CORRECTIVE REMARKS

The original description (Richardson, 1968) and subsequent biological notes (Richardson, 1970) are here supplemented and corrected by my own observations on the two paratypes.

The eyes, which may be of taxonomic importance in both the Paludicola and the Maricola (Ball, 1974b, 1975), consist of a single-celled pigment cup containing about three large retinal cells. Across the opening of the pigment cup there is a thick corneal structure like that described in some other Procerodidae and in some

REVISION OF *BDELLASIMILIS BARWICKI*

Bdellouridae (Böhmg, 1906). I am unable to determine if this is a true lens in the sense of Lehmsick (1937).

Richardson (1968: 93) found the testes to be a paired tubular system. I find them to be represented by numerous small round follicles extending from near the anterior end of the animal, and well anterior to the eyes and ovaries, to the level of the pharyngeal pore. They are principally ventral in position though anteriorly they extend over the ovaries.

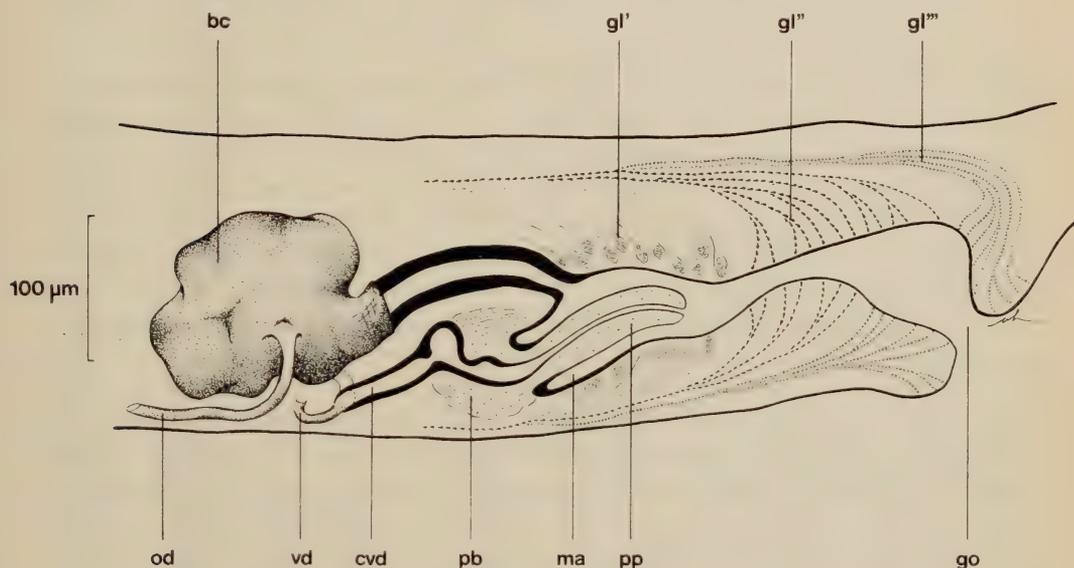


Fig. 1. *Bdellasimilis barwicki*, paratype, ROM C418a. Sagittal section of the copulatory apparatus, viewed from the left side. bc, bursa copulatrix; cvd, common vas deferens; gl, atrial glands; go, gonopore; ma, male atrium; od, left oviduct; pb, penis bulb; pp, penis papilla; vd, left vas deferens.

A sagittal view of the copulatory apparatus was not provided by Richardson; this is done here as Fig. 1. My interpretation of the sections differs in some respects from that of the original author (cf. Fig. 1 with Richardson, 1968: Fig. 2).

The penis consists of an elongate weakly muscular bulb, and a long slender papilla projecting into the atrium. The vasa deferentia unite to a stout common duct, with thick walls, anteriorly to the penis bulb and it is this duct that enters the frontal face of the bulb. Within the bulb it forms a small vesicle that narrows posteriorly to form an ejaculatory duct opening terminally.

The bursa copulatrix is a large sacciform organ lying anteriorly to the penis as above the common vas deferens. The wide and thick-walled bursal canal passes over the penis bulb and opens into the atrium in an unusually anterior position. The thin musculature of the bursal canal, which overlies a nucleate lining epithelium, continues the sequence of layers found in the atrium and the bodywall; there is no reversal of the circular and longitudinal layers. The two oviducts, which were not seen by Richardson, are most unusual in that they enter the lateral walls of the bursa copulatrix.

The single, ventral, gonopore lies between the two posterior adhesive discs. It opens into a large chamber into the walls of which numerous and extensive fine glands open. These glands appear as fine yellow-brown granules that extend into much of the mesenchyme (Fig. 1 gl'''). Entally to these the atrium narrows to form a tubular duct and into this zone there open numerous coarser glands which stain purple (Fig. 1 gl''). The ental part of the atrium, surrounding the penis, is larger once more and its walls are pierced by very coarse and very extensive eosinophil glands (Fig. 1 gl'). It is my belief that Richardson (1968) mistook this glandular complex for muscle tissue, which also may be eosinophil in nature, and thus erred in his interpretation of the penis bulb and atrium.

These corrections to the original description make necessary a new diagnosis of the genus.

DIAGNOSIS OF THE GENUS *Bdellasimilis*

Translucent marine planarians, ectoconsortic on turtles, with long pre-ocular region and broad posterior end with two adhesive discs. Eyes two, with single-celled pigment cup with lens, and three retinal cells. Bursa copulatrix anterior; oviducts enter the lateral walls of the bursa. Ovaries behind the eyes. Testes numerous, and ventral, and extending posteriorly to the level of the single gonopore. Penis with a weak bulb and slender papilla extending into a spacious and highly glandular atrium. Common vas deferens enters the penis bulb. Cocoons slender, ovoid or cylindroid, and with a slender stalk. Type and only known species: *Bdellasimilis barwicki* Richardson, 1968.

COMPARATIVE DISCUSSION

The eye-structure of *Bdellasimilis* is quite unlike that of the Dugesidae (Ball, 1974b, 1974c), the sole family to which the paludicolan planarians of Australasia belong, for in this family the multi-cellular pigment cup embraces numerous small retinal cells. In contrast the single-celled pigment cup, containing three large retinal cells, of *Bdellasimilis* is similar to that of many of the Maricola. This, together with the facts that there is a long, diverticulated pre-ocular duct of the anterior ramus of the intestine, a primitive feature found only in the Maricola

(Meixner, 1928), and many testes anterior to the ovaries, strongly suggests that *B. barwicki* cannot be a paludicolan triclad, notwithstanding the fact that it is probursal. In fact, the small size and large number of the testes are reminiscent of the condition found in species of the maricolan families Bdellouridae and Micropharyngidae (Böhmgig, 1906; Wilhelmi, 1909) and they are unlike those of the Australasian Dugesiidae that I have examined. The probursal condition is unusual because in most Maricola the bursa is behind the penis, but there is one marine family, the Probursidae of Hyman (1944), in which the probursal condition is present and presumably this is an independent acquisition in the two groups.

Most of the unusual structures of *Bdellasimilis* are paralleled by similar features in other marine planarians; whether the similarities are homologous or analogous cannot yet be stated. The extremely long atrium is also found in *Micropharynx parasitica* and *Nexilis epichitonius*, and *Nexilis* also possess an unusually ental opening of the bursal canal into the atrium (Ball, 1975). Interestingly enough, both these species, like *B. barwicki*, live in close association with higher aquatic organisms for *N. epichitonius* is usually ectocommensal on chitons and *M. parasitica* is ectoparasitic on skates in the North Atlantic Ocean (Jägerskiöld, 1896; Jennings, 1971; Ball and Khan, 1976). *M. parasitica* shows additional similarities with *B. barwicki* because it, too, has a long common vas deferens and the oviducts may open into a small vesicle that may be homologous with the bursa copulatrix of other Maricola (Ball and Khan, 1976). Apart from *Bdellasimilis*, and to the best of my knowledge, *Micaplana misae*, a marine planarian from Japan, is the only other aquatic planarian in which there is a well developed bursa into which the oviducts open (Kato, 1937).

The extreme glandular nature of the atrium of *B. barwicki* is without parallel in the Maricola. In the Paludicola, however, there seems to be a similar glandular complex within species of the genus *Cura*, particularly in the North American species *C. foremanii*, as described by Kenk (1935), and in the Australasian species *C. pinguis* (Weiss, 1910). In both these species the bursal canal opens into the atrium far more anteriorly than is usual in freshwater planarians and its terminal part, beneath the oviducal openings, is expanded to form a wide female atrium (Weiss, 1910: Fig. 32; Kenk, 1935: Fig. 15). The extensive shell glands open into this chamber. The posterior part of the atrium, leading to the gonopore, is quite extensive and its walls receive the openings of large numbers of glands. In *C. foremanii* Kenk recognised two sorts of glands, whereas Weiss (1910) refers simply to eosinophil glands in *C. pinguis*. But from my own slides of these two species I can confirm that in both there are two types of atrial glands. Those surrounding the gonopore stain brownish-yellow in Mallory-Heidenhain, and the more ental ones are coarser and eosinophil in reaction. The similarity of this

arrangement to that of *B. barwicki* is quite striking for if the ental atrial glands (gl') of *B. barwicki* are homologous with the shell glands of the *Cura* species, then the remaining two sets of glands (gl'', gl''') are identical with respect to position and structure with the two types of atrial glands in the *Cura* species. The origins of the freshwater planarians from their marine ancestors are obscure (Ball, 1974a) but it is interesting to note that *Cura* is generally considered to be one of the most primitive genera (Ball, 1974b) and is therefore most likely to show retention of maricole characters.

For the above-discussed reasons there can be little doubt that *Bdellasimilis* is a true marine planarian that has invaded freshwaters. A final analysis of its phylogenetic relationships within the Maricola must await a much-needed revision of the entire suborder something that has not been undertaken since the work of Wilhelmi (1909).

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Small Mammals Trapped in Dorrigo National Park, New South Wales

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New South Wales, 2076

Small mammal trapping was carried out in Dorrigo National Park for the first time in April 1975. Elliott live traps and a few wire cage traps were baited with a mixture of oats, peanut butter, and bacon grease. Three distinct habitats were sampled:

- A. Cool temperate rainforest regrowth, altitude 731 m.
- B. Dense canopied subtropical rainforest, altitude 609 m.
- C. Alluvial subtropical palm forest, altitude 76 m.

Some specimens were taken for the preparation of study skins and skulls and are deposited in the reference collection of the N.S.W. National Parks and Wildlife Service, Mount Colah Depot.

TABLE 1

Mammal captures. Animals indicated with an asterisk (*) were captured in wire cage traps. All others were captured in Elliott live traps.

Site	Trap nights	<i>Melomys cervinipes</i>	<i>Rattus fuscipes</i>	<i>Rattus rattus</i>	<i>Mus musculus</i>	<i>Antechinus stuartii</i>	<i>Trichosurus caninus</i>	<i>Felis catus</i>
A	294	8	10	—	1	7	—	—
B	253	5	39	1	—	8	2*	1*
C	144	4	15	1	1	1	—	—
Total	691	17	64	2	2	16	2	1

The results are shown in Table 1. Captures of *Rattus fuscipes* in habitat A (0.034 captures per trap night) were significantly, at the 1% level, lower than in habitat C (0.104 captures per trap night) and habitat B (0.154).

Identification of *Melomys cervinipes* on external characteristics was difficult due to general similarities with *R. fuscipes*. However, female *M. cervinipes* could be distinguished on the basis of nipple count (Table 2), and the body weight of

TABLE 2

Comparative data from *Melomys cervinipes* and *Rattus fuscipes*.

Species	Area	Body wt (gm) (mean \pm s.d.)	Mammary formula (thoracic & inguinal)
<i>M. cervinipes</i>	Dorrigo	63.75 \pm 15.3 (n = 16)	0 + 2 = 4
<i>R. fuscipes</i>	Dorrigo	134.3 \pm 28.9 (n = 59)	1 + 3 = 8
<i>R. fuscipes</i>	Ku-ring-gai	93.35 \pm 28.6 (n = 51)	2 + 3 = 10

this species was much lower than that of *R. fuscipes* trapped in the same area. However, as shown in Table 2, this relationship might not hold throughout the range of these species, as the mean body weight of bush rats from Ku-ring-gai (Sydney region) is closer to that obtained for *M. cervinipes* in this study. Members of the genus *Melomys* are frequently called 'mosaic tailed rats', but this character was not readily apparent in the Dorrigo population. The scales on the tail appeared to be arranged in rings (similar to the bush rat), and only upon close examination of the base of the tail of prepared study skins could a clear mosaic pattern be seen. There was some difference in the arrangement of hairs on the tail. *M. cervinipes* appeared to have a naked tail on first sight, but close examination disclosed short appressed hairs no longer than the scales. *R. fuscipes* had longer hairs emerging from under the scale rings. Further details for individuals of these two species collected at Dorrigo are given in Table 3. Colour is omitted, as there was considerable overlap in general coat colour. Most Dorrigo *R. fuscipes* did however have white patches of fur on the ventral surface. *M. cervinipes* did not.

TABLE 3

Measurements taken prior to preparation of study skins from Dorrigo rodents.

Sex	<i>M. cervinipes</i>			<i>R. fuscipes</i>		
	F	M	Juv.	F	M	Juv.
Weight (gm)	60	71	40	150	138	50
Head and body (mm)	122	128	106	162	169	123
Tail	152	166	126	151	152	113
Hindfoot without claw	27	27.5	26	31.5	33	30.9
Ear	20.4	20	17	23.3	23	19.6

A further characteristic that might be useful in distinguishing between these two rodent species in the field is the ready inclination of *M. cervinipes* to climb. A typical animal, when released from the trap, climbed 12 m up a sapling and

MAMMALS TRAPPED IN DORRIGO NATIONAL PARK

disappeared. *R. fuscipes* on the other hand could not be induced to climb, preferring in all cases observed to jump to the ground and run off.

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An Occurrence of Albino Frog Tadpoles in New South Wales

NORMAN GRADWELL

7 Centennial Avenue, Lane Cove, N.S.W. 2066.

In a review of albinism in amphibians, Noble (1931) states: "The albino axoltl is known to differ from the normal colored phase merely by a single Mendelian factor (Haecker, 1908), although there appear to be various degrees of albinism in this species which may be due to other genetic factors." More recently, Browder (1972) has discussed the literature relevant to the genetics of albinism in the Anura. However, there appear to have been no publications on the occurrence in nature of albinism among Australian anurans. The present report is on the finding and laboratory development of tadpoles of *Limnodynastes*, of which about half were albinos. Although no genetic data are presented, some references on this aspect of albinism are discussed.

On 7 October, 1974, a small population of both albino and normally pigmented frog tadpoles (Fig. 1A, B, C) were found near the golf links at La Perouse, ca. 8 km south of Sydney, N.S.W. A few normally pigmented adult *Limnodynastes* frogs were seen, but there were no albino adults. Normally pigmented tadpoles of *Ranidella signifera* were plentiful. The habitat consisted of muddy pools (ca. 0.5 m maximum depth) surrounded by patches of grass and wattle. Scattered refuse such as motor car chassis, tyres, and corrugated iron roofing, was also present. A random collection with dip nets yielded 27 albinos and 18 normally pigmented tadpoles of *Limnodynastes*. Both normal and albino tadpoles were of about the same size at corresponding stages of development (Table 1).

TABLE 1

Length in mm

Tadpole	Entire	Snout-to-vent	Stages of Gosner, 1960
Melanated	47.7 ± 11.1	20.7 ± 3.2	27—35
Albino	44.5 ± 12.3	19.2 ± 4.0	26—35

In dissection, the albinos were found to contain no melanin in their blood vessels, in their retinas, or anywhere else. Other slight anatomical differences between the two kinds of tadpole were also found. For example, the albinos had a wider median gap in the posterior tooth row of the upper jaw, than the normal pigmented tadpoles (Fig. 1D, E). These differences were enhanced during metamorphosis (Fig. 1C) by the appearance of patterns of distinctive non-melanated pigment. However, the beaks and teeth of the albinos were black like those of normally pigmented tadpoles (Fig. 1D, E). Both kinds of tadpole were identified by their mouth parts as belonging to the genus *Limnodynastes*.

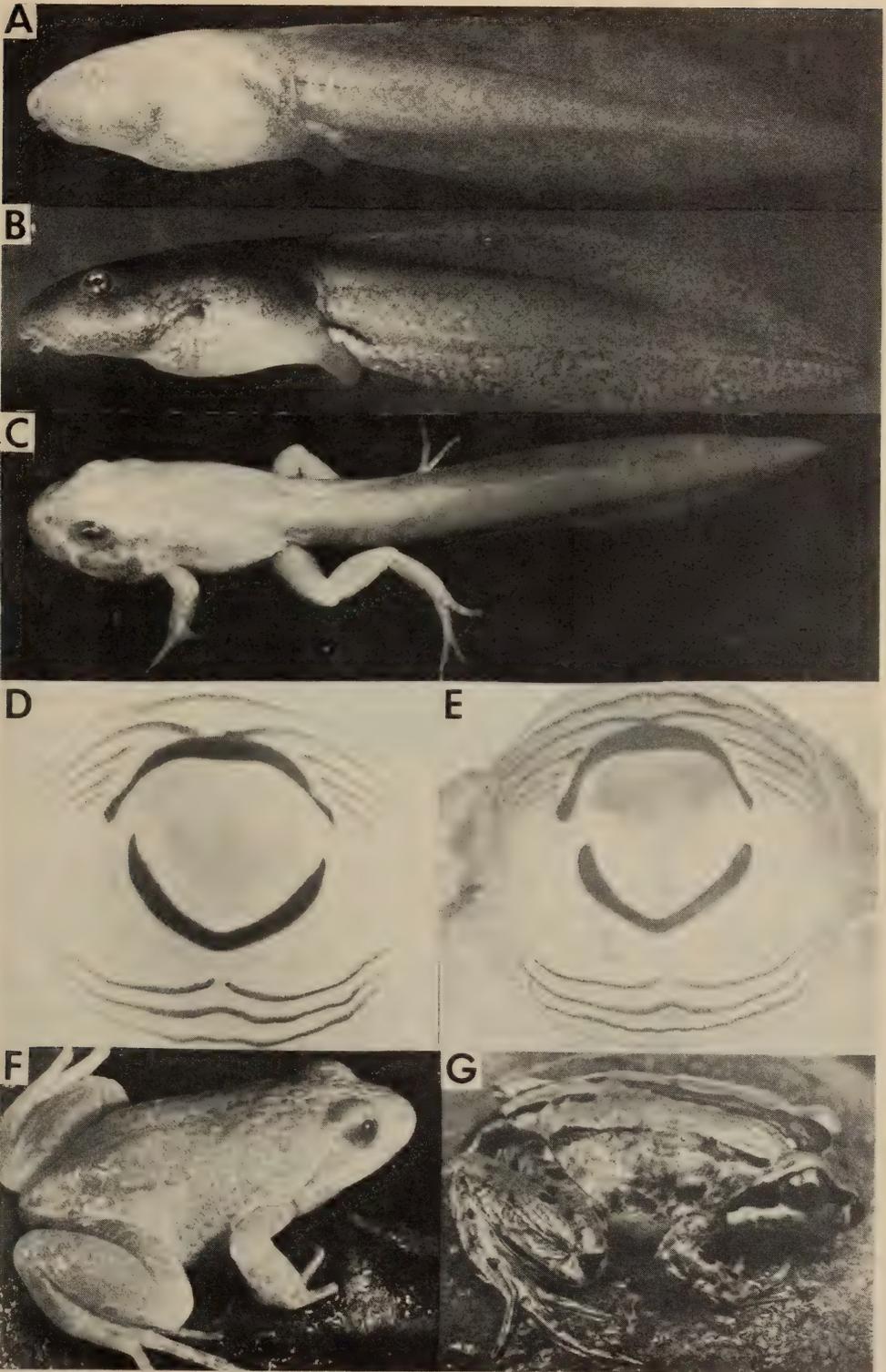
The bioreaction whereby melanin is produced has been summarised by Bell, Davidson, and Scarborough (1950). In the skin of several pigmented Amphibia, as in many other animal tissues, this reaction is catalysed by tyrosinase, but as Smith-Gill, Richards and Nace (1972) point out, albinism is not dependent on tyrosinase function alone. As this enzyme, like those associated with certain other genes, may become active only at specific stages of ontogeny, it was decided to determine whether albinism is restricted to the tadpole stage of the life history. In addition, Smith-Gill, Richards and Nace report on the failure of certain albino tadpoles of *Rana pipiens* to metamorphose.

The above findings encouraged the laboratory rearing and metamorphosis of the La Perouse tadpoles. Ten melanated and 10 albino tadpoles were kept in aerated aquaria containing Sydney municipal tap water at 20°C, and fed on boiled spinach for three to four weeks. They were illuminated with subdued incandescent light. To investigate the possibility of water-borne chemical interactions between the two kinds of tadpole, five albino and five melanated tadpoles were placed in one aquarium, and five tadpoles of each kind were placed separately in two other aquaria.

The albino tadpoles all became frogs of *Limnodynastes tasmaniensis* and the melanated tadpoles all became frogs of *Limnodynastes peroni* (Fig. 1F, G). However, from stage 42 onward (Fig. 1C, G), yellow-orange and white pigment appeared on the dorsum of only the albino animals. These pigments occurred in areas corresponding to the brown-orange and pale areas respectively of normally pigmented frogs of *L. tasmaniensis*.

Fig. 1. A. Albino tadpole of *Limnodynastes tasmaniensis*. B. Normal pigmented tadpole of *L. peroni*. C. Metamorphosing tadpole of *L. tasmaniensis*. D. Mouth parts of an albino tadpole of *L. tasmaniensis*. E. Mouth parts of a melanated tadpole of *L. peroni*. F. Young albino adult of *L. tasmaniensis*; slightly over-exposed photograph to emphasise the area of yellow-orange pigment bordered by white. G. Young normal pigmented adult of *L. peroni*.

OCCURRENCE OF ALBINO FROG TADPOLES



NORMAN GRADWELL

The present research has shown that under laboratory conditions the natural occurrence of albinism in certain tadpoles of La Perouse persists into the frog stage of the life history. However, the immaturity of the newly metamorphosed frogs precluded sexing them by dissection and it could not be established if albinism is a sex-linked character in these forms. Another finding concerns the fact that keratin itself is not black, even in darkly pigmented mammals, and therefore it is of interest to note that the keratinised beaks and teeth of all the albino tadpoles were black. In addition, there appears to be no melanin-influencing chemical interaction between the normally pigmented and the albino tadpoles during late larval growth and metamorphosis. Neither did melanin appear in the young albino frogs fed for three to five days on insects. However, as Browder (1972) points out, amelanotic melanophores may still be present in albinos. Finally, the failure to find albino frogs at La Perouse need not indicate a lethal genetic association between albinism and the assumption of life as a frog. It is more likely that poor eyesight in the albinos and their conspicuousness to predators, reduces viability. In this respect, Browder reports that even in laboratory conditions free from predators, the albinos of *Rana pipiens* are less viable than their melanated siblings.

Apart from melanation, no significant taxonomic differences were found between albino and normally pigmented tadpoles of *L. tasmaniensis* (from Sydney and Oberon districts).

A representative collection of the two kinds of tadpole and the frogs obtained by laboratory metamorphosis has been lodged at the Australian Museum, Sydney (registration numbers R47257 to R47278). The collection consists of 12 albino tadpoles, 10 melanated tadpoles, 11 albino frogs, and 8 melanated frogs.

ACKNOWLEDGEMENTS

I am grateful to Mrs. G. Goldsack for drawing my attention to her chance discovery of the tadpoles. I also thank Dr. H. Cogger for his assistance and Mr. M. J. Tyler for reading the manuscript and identifying and attempting to sex the frogs. This research has been supported by a grant from the Australian Biological Resources Study Interim Council.

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Memorial Notice



GILBERT PERCY WHITLEY, F.R.Z.S. (1903-1975)

Photograph by courtesy of Dr. J. R. Paxton

Mr. Gilbert Whitley died in Sydney after a short illness in July, 1975. Details of various facets of his life and work have been published elsewhere and need not be repeated here. The opportunity remains, however, for this journal to record the extent of the contributions made by Mr. Whitley to the Royal Zoological Society of New South Wales.

A brief review of Mr. Whitley's association with the Society presents a picture of extraordinary service extending over half a century. He was a Member of the Society from 1926 until his death, a Life Member from 1938 and a long-time Fellow. He served as a member of Council for many years and was President or Vice-President on several occasions. A gentle, knowledgeable, industrious man with a charming sense of humour, he was highly esteemed as a Council Member whose views always deserved consideration.

MEMORIAL NOTICE

The contributions made by Gilbert Whitley to the publications of the Society are unlikely to be equalled. His first paper in *The Australian Zoologist* (on parasitism in lower animals) appeared in 1925 in Volume 3, Part 8, and almost every issue since then (including the present one) contains one or more of his articles. The name of G. P. Whitley first appears in *The Proceedings of the Royal Zoological Society of N.S.W.* in 1936 and again he was a regular contributor to subsequent volumes. Many of his original scientific papers deal with fishes, but the remainder cover a wide variety of animal groups, as one would expect from a naturalist with such broad zoological interests. Other articles, such as book reviews, biographies and historical notes also appeared frequently.

In 1947 Gilbert Whitley became editor of both *The Zoologist* and *The Proceedings*. He edited all issues of *The Zoologist* from Volume 11, Part 2, to Volume 16, Part 1 (except for 13(2)) and all volumes of *The Proceedings* until 1970. In all these issues, a painstaking attention to detail and an editorial precision of professional standard is clearly evident. His editorial as well as his literary talents are also seen in the Handbooks he produced on scientific and historical subjects.

The Society has lost one of its most distinguished supporters whose level of scholarship and productivity were quite exceptional. Many members have felt the loss of a colleague and a friend.

E.S.R.

Erratum

Vol. 18(2), 1974. In the article by P. A. Hutchings and M. F. Recher entitled "The fauna of Careel Bay with comments on the ecology of mangrove and sea-grass communities", Figure 8 was split into Figures 8 and 9 and the correct Figure 9 was not included.

Figure 8 should be a composite of the published Figure 8 (top) and the published Figure 9 (bottom).

Figure 9 should be the following:

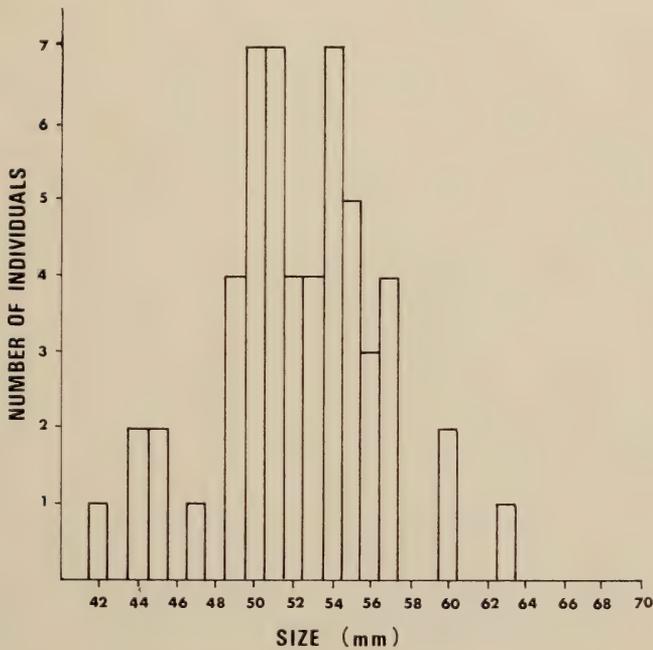


Fig. 9. Size distribution of the Sydney Cockle *Anadara trapezia* at Careel Bay.

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Papers will be considered for publication in *The Australian Zoologist* if they make an original contribution to whole animal biology of the Australian fauna. Papers submitted will be subjected to review and thence to the normal editorial process, in the course of which authors will receive edited galley proofs for correction. A manuscript is accepted on the understanding that it is to be published exclusively in *The Australian Zoologist*.

MANUSCRIPTS (original and one copy) should be sent to the Editor, "The Australian Zoologist", New South Wales State Fisheries, Fisheries House, 211 Kent St., Sydney, N.S.W. 2000. They should be typewritten (double spaced) on good quality paper. All pages of the manuscript must be numbered consecutively, including those containing references, tables and figure legends, which should all be placed after the text.

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Maintenance of the Platypus (*Ornithorhynchus anatinus*) in Captivity Under Laboratory Conditions

T. R. GRANT, R. WILLIAMS and F. N. CARRICK

School of Zoology, University of New South Wales, P.O. Box 1 Kensington,
New South Wales, 2033

ABSTRACT

Platypus were kept in captivity during studies of their temperature regulation and reproductive biology. They were housed in a complex consisting of a tank, a tunnel and three nest boxes, and were fed on various live and dead invertebrate and vertebrate species. Details of the dimensions of the housing facilities and descriptions of the diet provided are outlined, and general considerations on the maintenance of this species for research purposes are discussed.

INTRODUCTION

Burrell (1927) described the attempts of the early naturalists at keeping the platypus in captivity. All of these attempts were notable failures due to a lack of understanding of the animals' requirements. Bread, milk, and rice were common in the diets offered to the animals which were kept as house pets, in the absence of water! Burrell himself had little success with the species in captivity, although he made quite an effort to provide his captives with suitable food (worms, fresh water shrimps, insect larvae and pond snails) and living conditions. He maintained that "the platypus can be kept alive in captivity; and it is very probable that with sufficient pain and interest, it can be satisfactorily exhibited".

Sufficient "pain and interest" have been taken and the platypus has been successfully kept and exhibited in captivity since early this century (Table 1, modified from Collins, 1973). At present the Sir Colin MacKenzie Sanctuary in Victoria, David Fleay's Fauna Sanctuary in Queensland, Taronga Zoological Park in Sydney and the Australian Reptile Park at Gosford, N.S.W. all display *Ornithorhynchus anatinus*.

These animals, however, have been kept mainly for exhibition purposes and until the initiation of studies of the thermal biology and reproduction of the platypus at the University of New South Wales, the difficulties of handling the species in a laboratory situation were thought to be insurmountable. In 1972 the Director of Targona Park Zoo, Mr. Ron Strahan, conveyed his opinion of the impossibility of laboratory studies on the platypus. Smyth (1970) tried to maintain

TABLE 1

LONGEVITY DATA FOR EIGHT *ORNITHORHYNCHUS ANATINUS* IN CAPTIVITY (MODIFIED FROM COLLINS, 1973)

	Sex	Dates	Captivity	Institution
1	M	1939-1956	17y 0m	Sir Colin Mackenzie Sanctuary
2	F	1943-1955 (escaped)	12y 0m	"
3	F	1938-1947	9y 0m	"
4	M	1933-1937	4y 1m	"
5	M	1946-1957	11y 4m	"
6	F	1946-1957 (escaped)	11y 3m	and Bronx Zoo Bronx Zoo
7	F	—	4y 11m	Melbourne Zoo
8	—	1913-1917	4y 3m	Budapest Zoo

platypus in the animal house at the Department of Zoology at the Australian National University, but eventually in his experiments he had to use animals taken immediately from the wild, after losing four within 7-10 days after bringing them into captivity.

During the present studies, commenced in 1972, three platypus died in captivity. Seven animals were kept and used in experiments for periods of time ranging from three months to slightly under a year. Six of these seven animals were subsequently released. Hopefully the experience gained during the maintenance of these animals will be of benefit to other workers, and more particularly be of benefit to *Ornithorhynchus anatinus* in captivity.

MATERIALS AND METHODS

HOUSING

The first successful enclosures used for platypus by Eadie (1934) and Fleay (1944) were quite large; attempts being made to imitate a "natural" situation. Fleay's platypusary was 90 feet long and included an artificial bank, into which the animals could burrow. More recently constructed platypus displays, such as that at the Targona Zoological Park have also proved to be successful, despite their less elaborate design. Concrete maintenance tanks, wooden sleeping boxes and glass sided display tanks have increased the practicability of keeping the species in an artificial environment. However, even this type of facility was beyond the scope of the resources available and the size of the installation is not feasible in most research institutions (the feeding tank alone at the Taronga Zoo measured 5.2 metres in length, Strahan and Thomas, 1975).

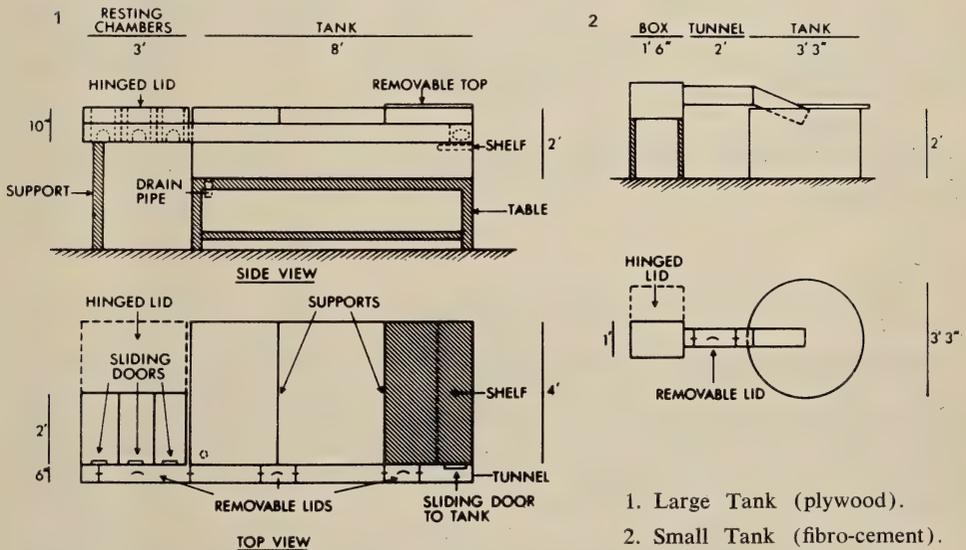
The facilities finally set up at the University of New South Wales were largely governed by space available, although valuable suggestions on minimum dimensions

THE PLATYPUS IN CAPTIVITY

were received from Mr. D. Thomas of Taronga Zoo. The first tank built (Fig. 1) was constructed from 1.1 cm waterproof plywood with the dimensions of 2.4 m by 1.2 m by 0.6 m. The tank was filled to approximately 0.3 m in depth, which put the water level just below a shelf placed at one end. From this shelf a tunnel was built along the outside of the entire length of the tank, ending in a unit of three sleeping boxes. These could be closed individually.

After the failure of the original coating (polyurethane) the joints of the tank were filleted with fibreglass cloth, and the whole complex was recoated with a tar epoxy resin (Epirez 304)*. The resin was reapplied after nearly a year because of abrasion of the surface by ice used in experiments in the tank, and this second coating remained waterproof after 2 years of further continual use. A second tank was built and because of the slight odour left with the tar epoxy, a ketimine cured epoxy was used as a coating (Epirez 235)*. Waterproof plywood was replaced by marine plywood in the construction of this second tank.

Figs. 1 & 2. Specifications of platypus enclosures.



The whole complex was mounted on a table and sloped slightly from one end. This allowed drainage through a 5.1 cm plug and waste. Water from the fur of animals was able to escape through drain holes in the floor of the tunnel. Collins (1973) mentions the use of rubber "squeegees" to remove excess water from animals moving along the tunnels of enclosures. All of the platypus which lived

* Indelab Pty. Ltd., Granville, N.S.W.

in captivity groomed and dried themselves before entering the sleeping chambers without the aid of these devices.

Sleeping chambers were lined with soft dry grass and condensation was dried off the roof and walls daily, when the animals were weighed and grass was checked for dryness and/or replaced. Initially soil was used under the grass but this proved a hinderance to the closing of doors in the tunnel and nest unit and became very soggy when new animals did bring water into the sleeping chambers. Platypus were at first carried and housed in hessian bags but this practice was quickly abandoned as it produced severe abrasions to the animals' feet.

During an experiment by one of the authors a female platypus was maintained in a small circular tank (0.6 m x 1 m in diameter, Fig. 2) with a simply constructed tunnel and sleeping box complex, for 3 months. However, a male animal had to be returned to the large tank when it did not settle in the small one, and another female kept in it for a short time died soon after its return to the large tank. In this latter instance the large tank had been vacated to enable replacement of the original coating. The smaller complex was more convenient and proved satisfactory in the instance mentioned, but in view of experience, the larger model has proved to be the most satisfactory enclosure for housing platypus in an animal house situation for any length of time.

In all instances tanks were drained, cleaned and refilled daily and were scrubbed with running fresh water every 4 or 5 days to stop the accumulation of algal growth.

FOOD

Platypus are known to eat a variety of food items in captivity but the provision of an ample supply of acceptable food has always hindered their maintenance in zoos and sanctuaries. Reports in the literature suggest that the weight of food taken by a platypus in one day can amount to over half its own body weight. Burrell (1927) recorded one of his captives devouring 70 earthworms, 10 ground grubs, and 600 salt water prawns in 72 hours and Fleay (1944) lists the food eaten by a lactating female as 400 earthworms, 338 grubs and 38 live yabbies during one 24 hour period.

Table 2 compares the daily diets given in two other institutions with the food supplied to the animals during the present studies. These lists can be noted as little more than guidelines because food intake by an individual is never static, being modified by factors such as activity, ambient temperature, animal size and individual diet preferences. In dealing with the platypus experience always played a great part in determining diet offered, and amounts and types of food given varied from week to week and from animal to animal. Most animals took some time to begin eating prawns. Some never ate them in any quantity, and in these instances many more earthworms and cockroaches had to be supplied. Mosquito fish (*Gambusia sp.*) were eaten by some of the captive platypus,

THE PLATYPUS IN CAPTIVITY

TABLE 2
DAILY DIETS GIVEN TO PLATYPUS IN CAPTIVITY

A. *Bronx Zoo, New York**

<i>Items</i>	<i>Details</i>	<i>Quantities</i>
1. Earthworms	—	454g
2. Crayfish	—	24
3. Frogs	—	2
4. Eggs	steamed	2
5. Cockroaches and Mealworms	—	1 handful

B. *Taronga Zoo, Sydney *+*

1. Earthworms	—	454g
2. Prawns	—	227g
3. Egg yolks	hard boiled	2
4. Mealworms	—	} small quantities in display tank.
5. Woodlice	—	
6. Scarabaeid larvae	—	
7. Small crayfish	—	

C. *School of Zoology, University of N.S.W.*

1. Earthworms	given with some soil (live)	160g
2. Prawns	heads removed	340-510g
3. Cockroaches	killed	12-24
4. Mealworms	live	12-36
5. Mosquito fish	} only to some animals on occasions	up to 100 in place of 3 & 4.
6. Small crayfish		6-12

* Collins (1973);

+ Strahan and Thomas (1975).

TABLE 3

ACCEPTANCE OF VARIOUS FOOD ITEMS BY THE EIGHT PLATYPUS KEPT IN CAPTIVITY

<i>Food Items</i>	♀1	♀2	♀5	♀31	♀48	♂8	♂20	♂22
Earthworms	A	A	A	A	A	A	A	A
Mealworms	—	A	—	A	A	A	A	S
Cockroaches	—	—	—	A	A	—	A	S
Mosquito fish	—	—	—	A	A	U	S	N
Insect larvae	—	—	—	A	A	A	A	A
School prawns	N	A	N	U	S	A	U	U
Yabbies	—	A	—	A	N	—	—	—
Eggs	—	N	—	N	—	N	—	N
Squid	—	N	—	—	—	N	—	—
Mussels (marine)	—	N	—	—	—	N	—	—

A = always

U = usually

S = seldom

N = never

— = not offered

while others showed little or no interest when these fish were released live into the tank. Data showing diet preferences of the individual animals are summarised in Table 3.

Earthworms were the most preferred food item and large worm cultures were established to cope with the demand. These were in pits, 0.5 m to 0.6 m in depth and of various sizes, the bottoms and sides being lined with galvanised iron. Soil was placed in the pits and over a period of several weeks, organic matter in the form of grass clippings and leaves was worked into the soil. Earthworms of various species were introduced into these beds, which were kept moist (but not sodden) and supplied with more organic matter, including horse manure, at regular intervals for several months.

Lumbricus terrestris in Britain takes up to a year to reach maturity after 10 weeks of incubation in the cocoon. Environmental factors such as food supply, temperature and soil moisture are known to influence rates of production in this and other species (Edwards and Lofty, 1972) but even if optimal conditions could be supplied in the worm beds, turnover rates are still likely to be quite slow. For this reason beds were kept unused for as long as possible and when harvested, only the smaller worms were removed. In times of very high demand breeding worms were taken, but where possible these were replaced by new stock at a later date. One set of beds were established in a lawned area and migration of worms from the lawn into the beds helped to supplement numbers.

Slowing of growth and a reduction in reproductive capacity in the winters proved to be a problem but the establishment of beds in a temperature-controlled glass house permitted ample supply of worms during the final winter of the study. An attempt was made to heat the outside cultures using trenches with a mixture of grass clippings and slaked lime, kept moist to produce heat. No noticeable effect on worm populations was observed.

Cultures were always covered with a layer of organic material and hessian bags which were kept moist. The organic material was mixed into the soil and replaced every time worms were removed. One large bed was kept entirely for "red" and "tiger" worms (probably *Eisenia sp.*), being supplied with rotting fruit, as well as leaves and grass. These worms seemed to have a higher turnover rate. Platypus usually only ate these in the first few weeks of captivity but their utilisation of them at this time of maximum demand eased the burden on the other cultures.

Various methods of extraction of the worms from the soil were tried (electrical current, chemicals and heat) but forking through the soil was the most successful and also served to mix in fresh organic material.

Because of their slow rate of reproduction, earthworms are not the most ideal food for captive platypus being maintained in a laboratory situation. It was fortunate that the animals could be kept on the mixed diet given in Table 2. Mealworms were the only other food item cultured during this study. Other

THE PLATYPUS IN CAPTIVITY

food was either purchased or supplied from cultures existing in other parts of the School of Zoology.

ANIMALS

Platypus were captured using the methods detailed in Grant and Carrick (1974). They were weighed daily, or once every two days after their capture. This was done in an attempt to keep a check on their condition and to slowly adapt them to being handled.

RESULTS AND CONCLUSIONS

Weight changes in eight of the animals kept are summarised in Table 4. All animals showed an initial weight loss before beginning to regain weight and stabilise. During experimentation, which was not commenced until animals had regained at least 80% of their original weight, some fluctuations of body weight normally occurred. If a steady decline commenced, experiments were terminated until this trend ceased.

Platypus released after being maintained in captivity were, with one exception above their original weight at capture. Male number 8 reached 91% of its original weight while telemetry experiments were in progress but lost weight during attempts at metabolic determinations. These experiments were terminated and after a recovery period the animal was released. Throughout its captivity this male retained substantial tail fat deposits.

Initial attempts to maintain platypus in the laboratory for a prolonged period were not successful. Both the platypus which died within a month of their capture did not regain lost weight (Table 4). Female number 2 was kept successfully for several months but died after a rapid decline in its condition, whilst housed in a small tank during emergency repairs to the main tank. In

TABLE 4
WEIGHT CHANGES IN THE EIGHT PLATYPUS KEPT IN CAPTIVITY

ANIMALS	♀ 1	♀ 2	♀ 5	♂ 8	♀ 31	♂ 20	♂ 22	♀ 48
Capture Wt. (g)	764	790	950	2350	1000	1348	1430	992
Date	26.6.72	26.6.72	9.12.72	3.2.73	6.2.74	19.6.74	7.1.75	24.5.75
Min. Wt.	618	604	665	1843	822	1122	1344	950
Date	4.7.72	17.7.72	10.1.73	21.2.73	18.2.74	4.7.74	15.1.75	3.6.75
Max. Wt.	764	956	950	2350	1002	1680	1708	1078
Date	26.6.72	17.9.72	9.12.72	3.2.73	13.5.74	20.12.74	5.4.75	17.8.75
Death Wt.	618	628	665	—	—	—	—	—
Date	4.7.72	28.11.72	10.1.73	—	—	—	—	—
Release Wt.	—	—	—	1982	1002	1680	1634	1046
Date	—	—	—	18.12.73	13.5.74	20.12.74	18.4.75	27.8.75
Duration (months)	.33	5	1	11	3.25	6	3.33	3

these three instances 20-30% of their original body weight was lost by these animals. Post mortem examination suggested that death was caused by septicaemic pneumoenteritis, possibly caused by bacterial proliferation associated with stress-induced lowering of immunological mechanisms. Similar symptoms were noted in a platypus which died at the Australian Reptile Park, Gosford, N.S.W. (Mr. George Wilson, personal communication).

Platypus were kept in a laboratory situation during this project with some success. It must be noted that any researchers considering the maintenance of this species in captivity should make provision for the considerable commitment of time required for the routine animal husbandry and culturing of the live-food component of the diet. As Burrell (1927) indicated, the platypus "demands a varied diet, and will starve to death in the presence of food which no longer pleases it. It must have clean, clear water, and sweet, dry sleeping-quarters. It is impatient of observation, and resents being handled. It is easily killed by too much excitement". Perhaps the most disturbing aspect of keeping this species in captivity is the realisation that, in spite of all the care and precaution taken, some of the animals may die.

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The Need for Joining Illawarra Wilderness Areas

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ABSTRACT

An examination of proposed and existing reserves between Royal National Park and the Shoalhaven River shows that each is ecologically valuable and contributes towards the preservation of existing flora and fauna. Due to the altering pattern of land usage and wide road construction, it has become apparent that a number of mammal species at present inhabiting the reserves may cease to do so when these reserves become small isolated wilderness areas.

A system of corridors is suggested to aid in making possible mammal movements between all reserves and other areas of significant biological value.

INTRODUCTION

A mammal survey of the whole area was conducted between 1966 and 1970 inclusive with work carried out since in selected areas. Every nature reserve and national park has been surveyed or check listed as well as all sections of bushland of significant size. The methods and results of this survey are contained in "Mammals of the Illawarra and Surrounding District" (Robinson, in press).

The major wilderness areas in the region are —

(1) Catchments of the Metropolitan Water Sewerage and Drainage Board; (2) Morton National Park; (3) Royal National Park — Heathcote National Park; (4) Illawarra Escarpment which includes land donated by A.I.S. Pty. Ltd. to the National Parks and Wildlife Service.

The smaller national parks and nature reserves are —

(1) Macquarie Pass National Park; (2) Seven Mile Beach National Park; (3) Barren Grounds Nature Reserve; (4) Red Rocks Nature Reserve; (5) Black Ash Nature Reserve; (6) Rodway Nature Reserve; (7) Devils Glen Nature Reserve.

RESULTS AND DISCUSSION

EFFECTIVE POPULATION NUMBER AND RESERVE SIZE:

Tyndale-Biscoe and Calaby (1975) stated: "Effective population number is the population size that will retain the original genetic diversity of the species, or a large fraction of it, in perpetuity and provide the genetic means for continued evolution. It must take account of natural fluctuations and be large enough to

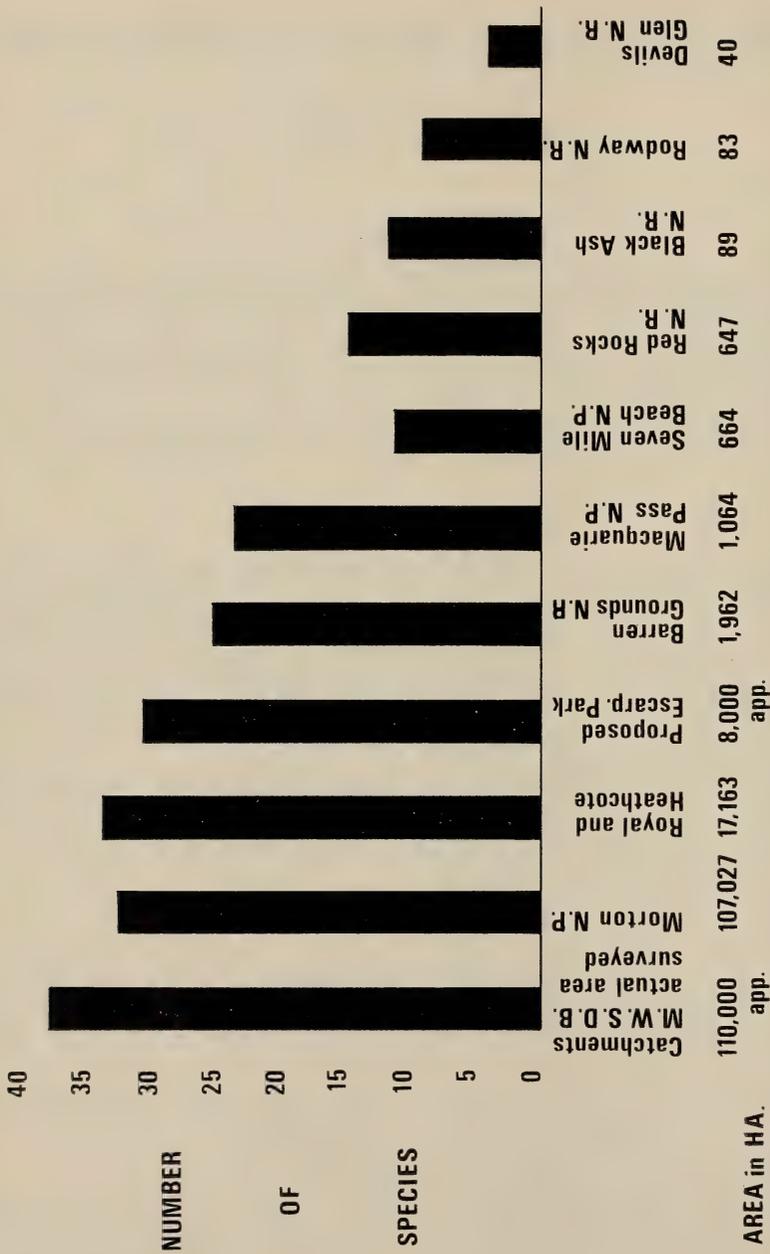


Fig. 1. Illawarra wilderness areas and mammal species within them.

ILLAWARRA WILDERNESS AREAS

withstand the vicissitudes of fire, disease and drought, it is the lowest number that the population can fall to under these circumstances."

After examining the work of Crow and Kimura (1970) and Main and Yadav (1971) they point out that the relatively abundant species such as the greater glider, *Schoinobates volans*, needs a reserve of no less than 6,000 ha. Species dependent on forest and less abundant, would need a proportionately increased area to accommodate a minimum effective population. Main and Yadav (1971) suggest selected areas of more than 20,000 ha which are likely to retain their characteristic biotic diversity.

Tyndale-Biscoe and Calaby (1975) also state: "The evidence at present available indicates that species with high attachment to their home sites do not move to other areas because these are already occupied and secondly, the number of animals that the small reserve can support in isolation is quite inadequate for the species long term survival."

The author has shown this to be so during studies on this district's reserves. The commonest large native mammal in Illawarra is the swamp wallaby, *Wallabia bicolor*, which inhabits forest or natural areas containing thick undergrowth. Edwards and Ealey (1975) studied the home range and territory of this species in Victoria. They stated: "The averages of the areas enclosed by the most widely separated records was 4.5 ha (males) and 7.2 ha (females). In any case these values are minimum estimates of the real dimensions." The second most commonly observed mammal is the wombat, *Vombatus ursinus*. McIllroy (1973) found a density of approximately one wombat per 4½ ha. in tall open forest near Tumut. With an effective population of 1,000 individuals of a species appearing to be near to the minimum for the continuance of genetic variability, Tyndale-Biscoe and Calaby consider 5,000 as a safe number, as this figure is the total population, including non-breeding juveniles, etc.

From this it can be seen that swamp wallabies and wombats need a large area to ensure their ultimate survival. In the Illawarra where some species are, overall, thinly distributed, as in the case of the wallaroo, *Macropus robustus*, very large areas are necessary. Only the larger mammals are given as examples because the smaller species such as *Antechinus* and *Rattus*, utilize smaller home ranges and these should survive if areas of sufficient size for large species remain.

ILLAWARRA RESERVES AND SPECIES:

Figure 1 shows the reserve size and number of recorded mammal species excepting bats and marine mammals. The numbers might well be increased with additional work. The following points should be noted in relation to Fig. 1.

- (a) The Catchments surveyed were Cataract, Cordeaux, Avon, Nepean, Woronora and O'Hares.
- (b) Extensive additions have been made to Morton National Park since the completion of the field work which led to the compiling of the check list.

- (c) Seven Mile Beach National Park has long been isolated by rural development. The largest terrestrial native mammal recorded was the long-nosed bandicoot, *Perameles nasuta*.
- (d) Field work is still progressing on Red Rocks and Devils Glen Nature Reserves, the boundaries of which are largely undefined. Devils Glen is predominantly a deep, steep sided gully, difficult of access.

NOTES ON RESERVES:

The Metropolitan Water Sewerage and Drainage Board Water Catchments and the Illawarra Escarpment are as one whole at present with Royal National Park joined by existing forest to the Illawarra Escarpment. Royal National Park and Heathcote National Park have effectively been separated by an expressway and the urban spread.

Morton National Park and Red Rocks Nature Reserve are joined at present by narrow natural or near natural belts of vegetation. Rodway Nature Reserve is isolated to a considerable degree but only a short distance separates it from the Barren Grounds Nature Reserve which is joined to Morton National Park via the proposed Buderoo National Park and belts of natural forest. Black Ash and Devils Glen Nature Reserves are almost joined together but are isolated at present from any large wilderness area.

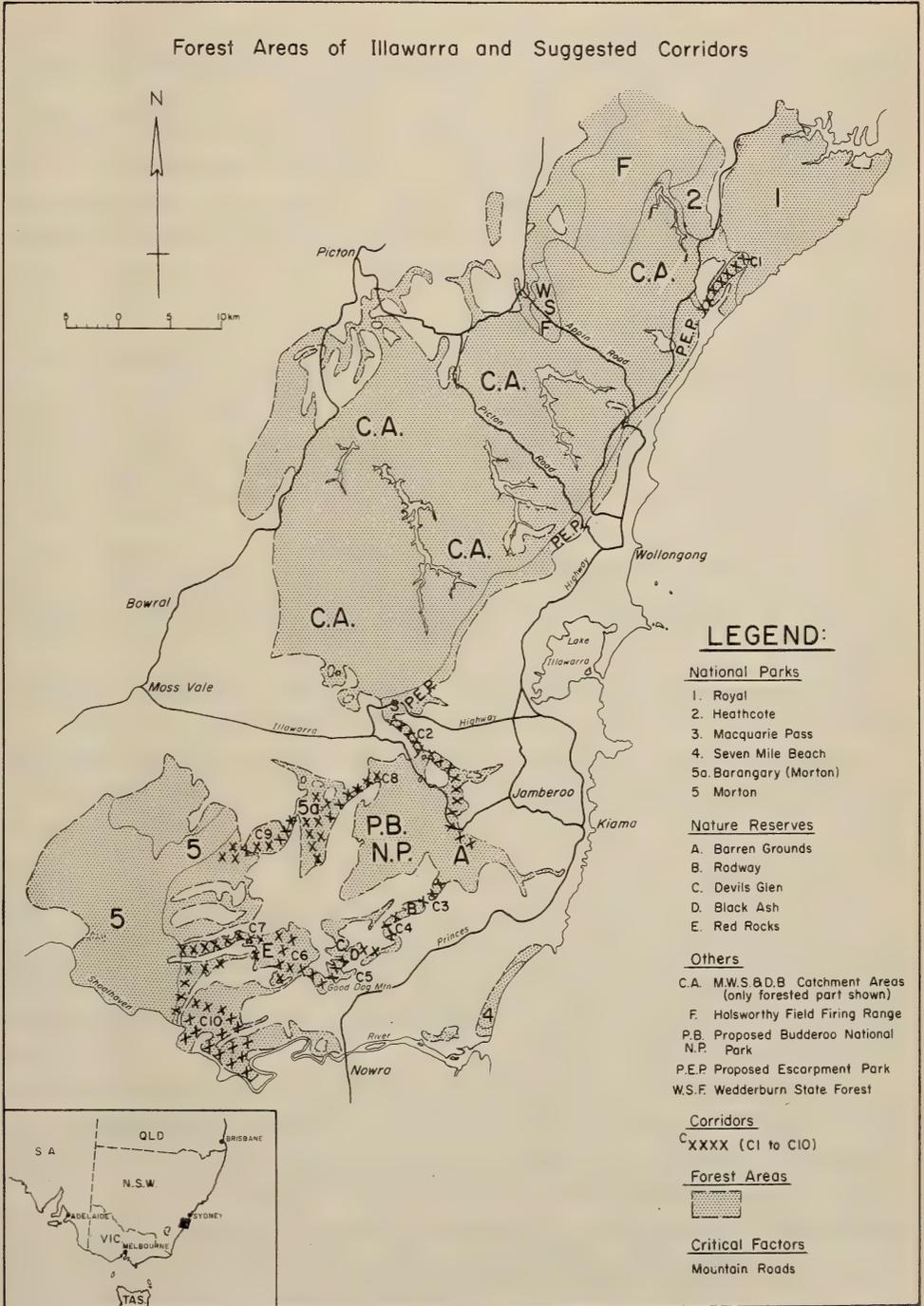
It can be seen from Fig. 1. that only the three largest wilderness areas contain sufficient biotic diversity to support a normal range of species typical of this part of Australia. A number of the species currently inhabiting most of our reserves will cease to do so if these reserves are isolated by the changing pattern of land usage

One example is the Barren Grounds Nature Reserve of 1,962 ha. It was surveyed during the years of 1966-1970. Twenty-five (25) species excluding bats were recorded. Of these, five were seen on no more than one occasion each, because of low numbers e.g. red-necked wallaby, *Macropus rufogriseus*, or cryptic behaviour, e.g. pigmy glider, *Acrobates pygmaeus*.

At present the reserve is part of a large wilderness area. If it was to become an "island" due to surrounding development, it is doubtful whether any large native mammal species would ultimately survive because much of the area is unsuitable for them. They utilize the surrounding wilderness as well at this time. Even Royal National Park, covering 14,912 ha., will probably lose a number of its large mammal species unless it is rejoined by corridors to Heathcote National Park and the proposed Illawarra Escarpment Park. Examples are the wombat, *Vombatus hirsutus*, and the wallaroo, *Macropus robustus*.

Only the catchments of the M.W.S.D.B. and Morton National Park appear large enough in isolation to retain their present species. Even on the catchments, there is a definite threat to some larger species through the effects of proposed very wide roads or expressways unless provisions are made in the design and construction of such roads to allow mammals to cross.

ILLAWARRA WILDERNESS AREAS



To try to keep maximum ecological values in all the National Parks, Nature Reserves and large wilderness areas, a system of corridors is suggested to make possible faunal movements between them. Corridors linking these would contribute towards one whole rather than having three major wilderness areas and a number of smaller ones, each of which is very valuable in many ways and which contribute towards the preservation of existing flora and fauna.

Once a framework is established, it might be possible to enlarge upon it if these minimum sized corridors are found to be of insufficient width and habitat variety.

CRITERIA USED IN CORRIDOR SELECTION:

The distance between areas to be linked is important. Where possible short corridors have been chosen. Vegetation types are crucial and eucalypt forest and rainforest together in this district form a near ideal link, with the eucalypts on the exposed sections and escarpment top, while the rainforest usually grows in the sheltered parts such as along gullies or escarpment sides. Unfortunately there are vegetation gaps in several corridors. Regrowth however, would eventually grow to form a corridor.

The composition of species and their habits, where known, can have a big bearing. Wombats and red-necked wallabies in this district generally keep to the escarpment top, although around the Shoalhaven River area, red neck wallabies do descend.

At the top of Macquarie Pass, the belt of existing vegetation is crucial because wombats do not move below the escarpment at this particular place.

Existing land usage has to be considered. Steep hillsides on water catchments such as on the rim of the Kangaroo Valley, or elsewhere, are best vegetated by natural forest to assist soil conservation.

PROPOSED CORRIDORS:

The corridors suggested are shown on the accompanying map (Fig. 2). The actual boundaries, description of geology and vegetation, mammals currently inhabiting each, immediate threat and other relevant comments have been submitted to the National Parks and Wildlife Service. For the purpose of this paper, only the mammals inhabiting each corridor are shown. The map shows the existing forested areas.

It is hoped that in future satisfactory crossings can be provided between both sides of the expressway and Princes Highway between Bulli and Engadine.

CORRIDOR 1 would link the Royal National Park to the proposed Illawarra Escarpment Park and M.W.S.D.B. Catchments.

CORRIDOR 2 would link the proposed Illawarra Escarpment Park and M.W.S.D.B. Catchments to Macquarie Pass National Park and the Barren Grounds Nature Reserve.

ILLAWARRA WILDERNESS AREAS

TABLE 1
 REFERENCE CHECK LIST OF MAMMALS INHABITING THE PROPOSED
 CORRIDORS

SPECIES	CORRIDORS									
	1	2	3	4	5	6	7	8	9	10
<i>Tachyglossus aculeatus</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Ornithorhynchus anatinus</i>	✓	✓							✓	✓
<i>Antechinus stuartii</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Dasyurus viverrinus</i>	*✗	✓				*✗	*✗	*✗	*✗	*✗
<i>Dasyurus maculatus</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Perameles nasuta</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Vombatus hirsutus</i>		✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Acrobates pygmaeus</i>	✓	✓		✓			✓	✓	✓	✓
<i>Cercartetus nanus</i>								✓		
<i>Petaurus australis</i>	✓	✓		✓				✓	✓	✓
<i>Petaurus norfolcensis</i>		✓								✓
<i>Petaurus breviceps</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Trichosurus vulpecula</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Trichosurus caninus</i>	✓	✓		✓		✓	✓	✓	✓	
<i>Pseudocheirus peregrinus</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Schoinobates volans</i>	✓	✓		✓			✓	✓	✓	✓
<i>Phascolarctos cinereus</i>		✓								
<i>Potorous tridactylus</i>	✓	✓		✓				✓	✓	*✗
<i>Petrogale penicillata</i>							✓			✓
<i>Thylogale thetis</i>		✓						✓	✓	
<i>Macropus rufogriseus</i>						✓	✓	✓	✓	
<i>Macropus robustus</i>	*✗						✓	✓	✓	✓
<i>Macropus giganteus</i>							✓			✓
<i>Wallabia bicolor</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Rattus fuscipes</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Hydromys chrysogaster</i>	✓	✓								
<i>Oryctolagus cuniculus</i>	✓	✓	✓	✓	✓	✓	✓	✓		✓
<i>Felis catus</i>	✓	✓	✓	✓		✓	✓	✓	✓	✓
<i>Canis familiaris</i>								✓		✓
<i>Vulpes vulpes</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Cervus timoriensis</i>	✓	✓								✓
<i>Capra hircus</i>	✓	✓				✓	✓	✓		

*No recent record

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- CORRIDOR 3 would link the Barren Grounds and Rodway Nature Reserve.
CORRIDOR 4 would link Rodway to Black Ash and Devil's Glen Nature Reserves.
CORRIDOR 5 would link Black Ash and Devils Glen reserves to Good Dog
CORRIDOR 6 would link Good Dog Mountain to Red Rocks Nature Reserve.
CORRIDOR 7 would link Morton National Park to Red Rocks Nature Reserve.
CORRIDOR 8 would link the Barren Grounds through the proposed Buderoo
National Park to Barangary Park, an isolated part of Morton.
CORRIDOR 9 would link Barangary Park to Morton National Park.
CORRIDOR 10 would link Bengalee Creek to Bugong Creek's edges westwards
to Morton National Park.

The long term planning of Region II, embracing the whole of the Illawarra and more, is being carried out. Unless provision is made to include mammal corridors, only the largest wilderness areas will retain maximum wildlife value. Some species at present widespread will eventually contract in range to only the largest parks or reserves.

It is suggested that similar corridor schemes be instituted where possible in other parts of Australia. Unless this is done, the future of a number of species is indeed bleak in many areas.

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A New Species of *Python* from Arnhem Land

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ABSTRACT

A new species of *Python* (Family Boidae) is described from two male specimens from the Arnhem Land escarpment of northern Australia. The new species is considered to belong to the *reticulatus* group of the genus *Python* and may be distinguished from all other species by its high ventral and subcaudal scale counts. An account is given of meristic variation of the dorsal scale rows of the new species and comparison made with other species.

INTRODUCTION

About ten species of pythons belonging to four genera are known from Australia (Cogger, 1975). The most recent critical work concerning the Pythoninae is that of McDowell (1975) whose generic definitions are followed here. McDowell has divided the genus *Python* into the *molurus* and *reticulatus* groups; the latter possessing infralabial pits set in a deep groove, slit-like supralabial pits set diagonally, hemipenis with proximally directed chevron-like flounces, and the upper lip below the eye light-coloured and similar in colour to the rest of the upper lip. The *reticulatus* group includes *Python amethistinus*, *P. boeleni*, *P. spilotus*, *P. reticulatus* and, possibly, *P. timorensis*. Two specimens of a boid snake from Arnhem Land in northern Australia appear to belong to this group also and are described herein as a new species. The specific name is derived from Oenpelli, the settlement nearest to the type locality.

Python oenpelliensis n. sp.

Holotype: ♂; 6.5 km S.W. of Oenpelli, Northern Territory, Australia (12° 21' S., 133° 01' E.), hereby designated type locality. Coll. Mr. B. Jukes, 17.VI.1975. Specimen in Museums and Art Galleries of the Northern Territory, Darwin (Reg. No. R0840). *Measurements* (in mm): Total length 3560; snout to vent 3037; tail 523; head length 69; snout to eye 25.4; interorbital distance 21.7; snout to nostril 4.7; orbit to nostril 17.3; internasal distance 11.3.

Paratype: ♂; Little Nourlangie Rock, N.T., Australia, (12° 51' S., 132° 48' E.). Coll. Dr. R. Begg, 9.VI.1976. Specimen in Australian Museum, Sydney (Reg. No. R55009). *Measurements* (mm): Total length 3593; snout to vent 3043; tail 550; head length 71.5; snout to eye 25; interorbital distance 22.2; snout to nostril 4.6; orbit to nostril 18.6; internasal distance 10.7.

DESCRIPTION OF HOLOTYPE

A large boid snake with a strongly prehensile tail. Scales without apical pits and without granular gular scales bordering the mental groove.

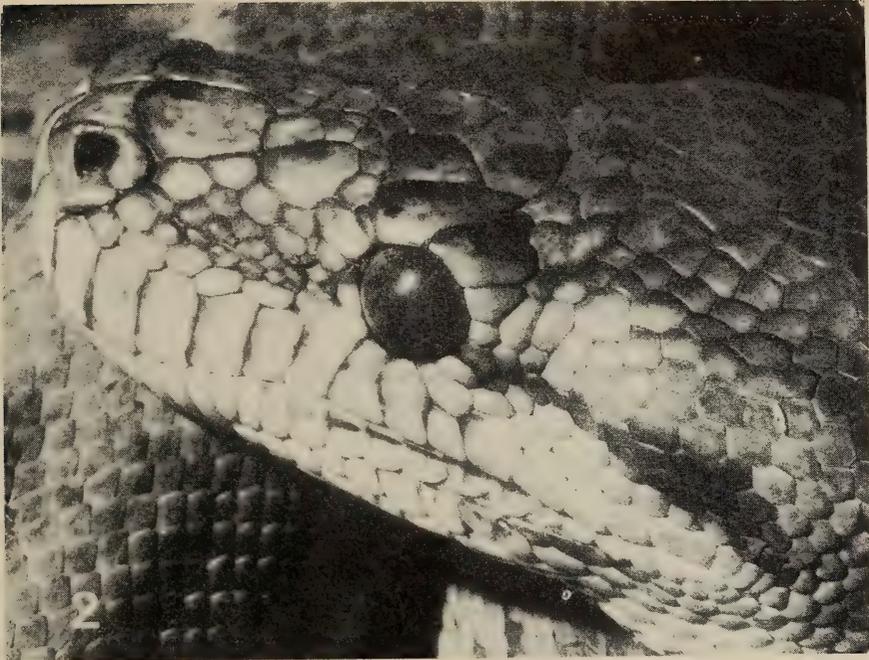
Rostrum visible from above, slightly broader than long, with a pair of deep slit-like sensory pits. Supralabials 15, the seventh and eighth on the left side and the seventh, eighth and ninth on the right entering the eye. First three supralabials with deep sensory pits; pit of first supralabial a long diagonal slit broadening dorsally and contacting ventral edge of the nasal. The slit of the second supralabial almost contacts ventral edge of nasal; third supralabial slit is distinct but shorter and broader than first two. Fourth supralabial without a distinct slit but an obscure elongate mark is present. Infralabials 24, six of the more posterior infralabials with deep rectangular pits. The row of infralabial pits begins beneath the eye and is sunk in a longitudinal groove. The row is preceded by an infralabial with a shallower pit.

One pair of prefrontals is present, each almost twice as long as broad. Internasals preceded by a pair of small scutes. The posterior prefrontal area, extending to the anterior frontals and supraoculars, consists of 22 subequal scales.



Fig. 1. *Python oenpelliensis* n. sp., holotype, in life.

A NEW SPECIES OF PYTHON



Figs. 2 & 3. *Python oenpelliensis* n. sp., holotype,

2, dorso-lateral view of head.

3, dorsal aspect of head.

Frontal plate divided into three; an equal anterior pair followed by a single plate. Parietal scutes absent, the top of the head covered with numerous subequal scales. Nasal partially divided; nostril directed upwards and outward; fissure extending from nostril to anterior loreal scutes. Loreal scutes, including small granules, 30 on right and 26 on left side. Preoculars 4 right, 3 left; postoculars 6 right, 5 left. Supraocular entire on right side (with partial division), divided on left with anterior portion the largest.

Mental groove relatively long, bordered anteriorly by first infralabials; two scales lie in rear of groove. Lateral border of groove of 9 and 10 scales similar in size to other gulars.

Dorsal scales smooth without apical pits; the first row large but less than half as broad as ventrals. At one head length behind head scales in 53 rows; at midbody, 70 rows; one head length anterior to the cloaca, 35 rows. About 50% of dorsal scale rows doubled (see discussion).

Ventrals 429. Subcaudals 155, mostly divided (7, 18, 19, 34, 35, 36, 37, 118, 119 are entire). Anal single. Cloacal spurs present.

One pair of premaxillary teeth. Maxillary teeth; 11 on right maxilla (estimated 6 missing), 14 on left (est. —3); estimated maxillary total 17. Palatine teeth; 10 on right (est. —5), 15 on left (intact series). Dentary teeth; 15 on right (est. —3), 14 on left (est. —4); estimated dentary total 18.

Hemipenis forked extending for about 10 subcaudals forked about 3 subcaudals proximal to this. Chevron like flounces of organ, 7.

DESCRIPTION OF PARATYPE

As for holotype with the following exceptions (figures in brackets refer to holotype).

Supralabials 17 (15); 8, 9 meet eye (7, 8) on left; 8, 9, 10 meet eye (7, 8, 9) on right. Infralabials 24 right, 22 left (24); seven on left pitted. Posterior prefrontal area 25 (22). Loreals 45 (30) right, 43 (26) left. Postoculars 5 (6) right, 7 (5) left. Supraoculars right divided, left entire (opposite arrangement in holotype). Ventrals 445 (429). Subcaudals 163 (155), mostly divided; 15 single subcaudals (9).

COLOUR NOTES

Pale fawn above merging into a lighter putty grey on the lower sides. A series of dark grey-brown blotches on the dorsal surface is irregularly arranged in four to five longitudinal rows. These dark blotches and streaks are largest in the vertebral series and much smaller laterally. Many of the dorsal scales carry an indistinct dark brown or black spot at the apex. The dorsal pattern becomes more obscure posteriorly. The dorsal scales of the tail are dark-edged producing a reticulated effect. The top of the head is pale fawn intermixed to a lesser degree with dark brown. Several of the head shields have the centre or the edge coloured dark

A NEW SPECIES OF PYTHON

brown. A dark brown supraocular streak about two scales wide extends from the supraoculars down each side of the head to the nape. A similar streak, indistinct anteriorly, runs from the nostril through the eye and is bordered above and below by equal areas of pale fawn. The ocular and supraocular streaks are joined by a diffuse band of dark spots in the post-temporal region. The supralabials and infralabials are fawn, the latter partially edged with dark brown below. The sublingual and gular area is white and the ventral surface of the body off white to pale yellow.

Holotype and paratype do not differ markedly in colour.

LOCALITY AND COLLECTING NOTES

Both specimens of *P. oenpelliensis* were collected near sandstone rock outcrops; the holotype specimen was collected crossing a road bordered by sandstone. More data is available for the locality from which the paratype was collected. The area is Myrtle-Pandanus savannah and mixed scrub. The specimen was collected a short distance from a sandstone outcrop (Dr. R. Fox, pers. comm.).

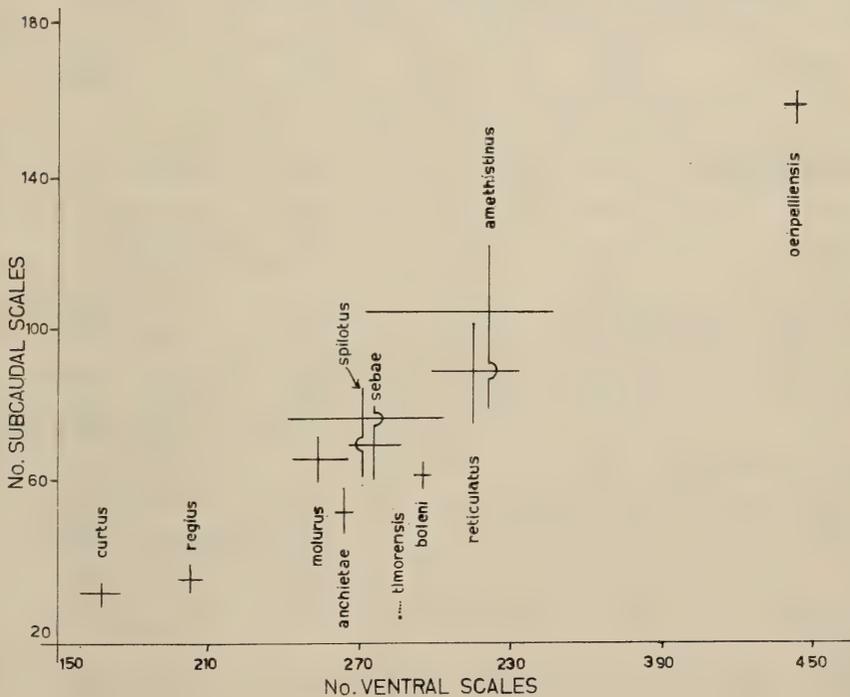


Fig. 4. Ranges of ventral and subcaudal scale counts for eleven species of the genus *Python*. Data from Boulenger (1893 & 1912), Cogger (1975), Fitzsimons (1962), Gow (1976), McDowell (1975) and Taylor (1965).

It was noted by both collectors and subsequent handlers that both specimens were docile during and after capture. Anecdotal evidence suggests that individuals of this new species may be longer than the specimens recorded herein.

DISCUSSION

Python oenpelliensis n. sp. adds a further species to the diversity of Pythoninae known from the Australasian region (see McDowell, 1975 p.3). The new species may be distinguished from other species of the genus *Python* by the high ventral and subcaudal scale counts, no other species possessing more than 346 ventrals or 122 subcaudals (maximum counts recorded for *Python amethistinus*; MacDowell *loc. cit.*). The distribution of numbers of ventrals and subcaudals for eleven species of *Python* are shown in Fig. 4. These characteristics are also adequate to separate the new species from all other Australian boid snakes.

TABLE 1
DOUBLE DORSAL SCALE ROWS OF 9 SPECIES OF PYTHONS

Species	Number of ventrals	Number of double dorsal scale rows	% ventrals/double dorsal rows	Locality and comments
<i>Python oenpelliensis</i>	429	221	51.5	Holotype
" "	445	223	50.1	Paratype
<i>P. amethistinus</i>	343	16	4.7	Queensland
<i>P. boeleni</i>	314	57	18.2	Sepik R., P.N.G.
<i>P. spilotes</i>	296	76	25.7	Oenpelli, N.T.
"	282	98	34.8	Central Australia
"	291	109	37.5	Central Australia
"	283	90	31.8	Melville Is., N.T.
<i>Liasis olivaceus</i>	353	107	30.3	Adelaide R., N.T.
<i>L. childreni</i>	261	65	24.9	Central Australia
<i>L. boa</i>	267	56	20.9	New Ireland
<i>L. mackloti</i> *	275	83	30.2	Katherine, N.T.
<i>Aspidites melanocephalus</i>	329	124	37.7	Katherine, N.T.

* *Liasis fuscus* Peters, 1847 is a synonym of *Liasis mackloti* Dumeril and Bibron according to McDowell (1975, 6.34 *et. seq.*).

A NEW SPECIES OF PYTHON

The dorsal scalation also distinguishes *P. oenpelliensis* from other species of Pythoninae. The number of dorsal scale rows of the new species is not the same as the number of ventral scales. About 50% of the ventral scales correspond to double, not single, rows of dorsal scales. It is believed that this is the first time that this meristic variation has been reported in the Pythoninae. The degree of doubling of dorsal scale rows in relation to the number of ventral scales is shown in Table 1.

It is apparent, from the limited data available, that the doubling of dorsal scale rows is very much greater in *P. oenpelliensis* than in the other species investigated. It is not apparent, by inspection at least, whether any pattern is present in the distribution of double dorsal scale rows either in a specific or an individual sense. Such analysis must await more data but it is suggested that the meristic variation of dorsal doubling in pythons is worth further investigation.

ACKNOWLEDGEMENTS

Thanks are due to Mr. B. Jukes and Dr. R. Begg who collected the specimens. Many people have helped in many ways and grateful acknowledgement is made to Mr. A. J. Dartnall, Dr. R. Fox, Mr. M. Gillam, Dr. R. Pengilly and Mr. R. Wells. I am also grateful to Dr. H. Cogger, of the Australian Museum, Sydney, who made the paratype specimen available to me after preservation.

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Tail Regeneration and Other Observations in a Species of Agamid Lizard

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ABSTRACT

Evidence of tail regeneration is reported for the first time in an agamid lizard contrary to the long held belief that lizards in this family are unable to regenerate damaged tails. This evidence was obtained in a study of the common Australian agamid lizard, *Physignathus lesueurii lesueurii*. Observations are also reported on mass-length relationships, food, and a lower temperature limit for activity for this lizard.

INTRODUCTION

The family Agamidae (dragon lizards) contains about three hundred species which are found in many of the warmer areas of the world including Australasia, and forty of these species occur in Australia. Agamid lizards have up to the present been considered to be unable to regenerate the tail once it is broken, compared with many other families of lizards, e.g. Geckonidae (geckos), Pygopodidae (legless lizards), and Scincidae (skinks).

During a study of the eastern water dragon (*Physignathus lesueurii lesueurii*) in suburban and country habitats several specimens showed evidence of new growth on damaged tails, and a few specimens were selected for detailed study in captivity. The resulting observations on tail regeneration, mass-length relationships, food, and a possible lower temperature limit for activity, are reported as being of interest to the study of this and other species of the Agamidae family in Australia and in other parts of the world.

DESCRIPTION AND HABITATS OF THE EASTERN WATER DRAGON

The type locality of the eastern water dragon is given by Worrell (1963) as Queensland, but it is also found close to water courses east of the Great Dividing Range from southern New South Wales to Cape York and it has also been reported in New Guinea. The lizard is brownish-grey to olive-green on the upper surface with black bands on each side of the ventral line and a broad black stripe from the eye to the temporal region on both sides. The belly in both sexes in mature specimens may be bright red. The lizard is reported to grow to a length of 1 metre. It has a large angular head, long strong hindlimbs, and a

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Figs. 1 & 2. Eastern water dragon with regenerated tail. 1: Specimen III (Table 2) in Sept. 1974 photographed on 100 mm square grid. 2: Close up of regenerated tail.

TAIL REGENERATION IN AN AGAMID LIZARD

bicarinated (doubly-keeled) tail which may be up to 2.5 times the body length, and which is compressed laterally for swimming. It is a shy animal and if disturbed takes refuge under rock ledges or in water, in which it can remain submerged for long periods. Worrell (1958) described the behaviour of specimens of this lizard along river banks and observed young lizards sunning themselves outside the nesting burrows in which they hatched from eggs after an incubation period of about three months.

A small colony of eastern water dragons was observed regularly for three years in a small reserve in the densely populated suburb of Vacluse in Sydney. In this habitat a small stream passes over a waterfall in a cliff face in which there are many rock ledges on which the lizards bask. The colony has suffered considerable disturbance during this period due to workmen clearing the rough native undergrowth and large areas of alien lantana (*Lantana spp.*) to landscape the slopes with large native plants. The removal of many of the small plants has reduced the plant food available to the colony and has exposed the lizards to predators, particularly large birds such as kookaburras (*Dacelo gigas*). However, the colony was still breeding in 1975 and four very young lizards were seen, although two large mature specimens seen in 1974 had apparently disappeared. The maximum number of specimens seen at any one time over the three years was ten.

Specimens were also observed and photographed at a large colony at Jenolan Caves, about 150 km west of Sydney in New South Wales. This colony is distributed over a wide area along a river through the caves and State Park and some of the lizards have grown accustomed to the public approaching them to within a few metres.

RESULTS AND DISCUSSION

MASS-LENGTH RELATIONSHIPS

During the three years eleven specimens were captured, weighed, measured, and photographed in close-up for reference in case of recapture. Five of these had perfect tails, and two had apparently had the tip broken off. Three specimens had distinct changes in tail thickness and appearance part way along the tail when captured, with evidence of regenerated growth of 38, 52, and 75 mm. One specimen in the colony at Jenolan Caves had two tails, a perfect main tail 399 mm long and an accessory tail 67 mm long growing from a point at the side of the main tail, 108 mm from the anus. The mass-length data are given in Table 1 together with data for five newly hatched dragon lizards reported by Longley (1947), but for which no masses were given.

The total length per g for perfect specimens decreases markedly with total mass, and therefore with age, e.g., from 18-26 mm.g⁻¹ at 9-11 g to 1.2-1.4 mm.g⁻¹ at 446-665 g. The ratio of tail length to body length for five specimens with perfect tails was in the range 1.6-2.6, whereas the ratio for five specimens with single regenerated tails was in the range 1.1-1.6.

TABLE 1
MASS-LENGTH DATA FOR SPECIMENS IN NATURAL HABITAT

Mass g	Total length mm	Body length mm	Length of regenerated tail mm	Total length† per g mm.g ⁻¹	Notes
9	234	65	—	26	Perfect tail
11	200	77	—	18	Perfect tail
41	300	100	—	7.3	Perfect tail
102	285	135	52	—	Specimen I (Table 2)
136	380	156	—	—	Specimen II (Table 2)
156	556	157	67	—	Double tail
270	480	185	75	—	Specimen III (Table 2)
446	613	213	—	1.4	Perfect tail
596	558	236	—	—	Tip of tail broken
660	570	250	38	—	
665	790	235	—	1.2	Perfect tail
—	127	38	—	—	5 specimens at birth: Longley (1947)

† For perfect specimens

The body length (BL, mm), defined as the length from the tip of the nose to the anus, correlates very well with the total body mass (M,g). The data points for the 11 specimens are fitted by a curve:

$$BL = M^{0.3} + 34$$

with a standard deviation of 5 mm. Seven of the calculated values of BL from this equation are within \pm one standard deviation of the measured values, and the maximum deviation of a calculated from a measured value is two standard deviations.

There is a considerable degree of scatter in the correlation of total length (TL, mm) with mass, but the data can be fitted by a curve:

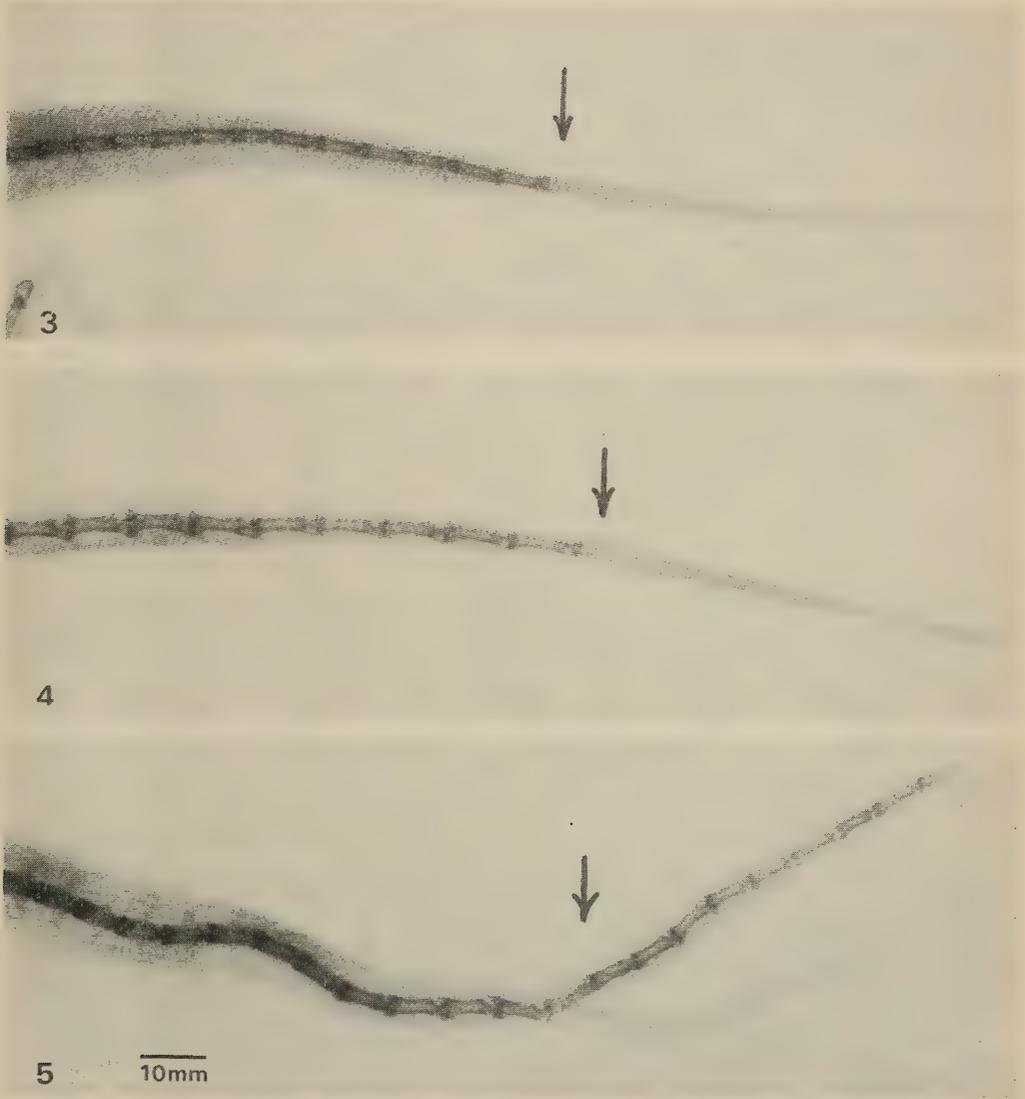
$$TL = M^{0.267} + 116$$

with a standard deviation of 74 mm. The much larger degree of scatter compared with the correlation of BL and M is due to the variability of tail length which in turn arises from the different extent of tail loss and extent of regeneration for different specimens.

TAIL REGENERATION

A specimen captured for study in May, 1973 broke off a piece of its tail a month later. This specimen has now been kept in captivity for over three years in a large outdoor cage containing large slabs of rock, a pool, and areas of native plants, and its tail growth and behaviour with respect to temperature

TAIL REGENERATION IN AN AGAMID LIZARD



Figs. 3-5. X-radiographs of regenerated tails. Arrows mark start of regenerated growth. Conditions: 0.06 sec. exposure at 75 mA and 60 KV with stationary grid to collimate beam. 3: Specimen I (Table 2). 4: Specimen III (Table 2). 5: Double-tailed specimen (Table 1).

variations studied periodically. After the tail broke the specimen had a mass of 136 g and a length of 380 mm (Table 1) and several months later it showed new growth at the end of the tail. After one year the new tail section was 65 mm (Table 2). The new tail had smaller scales than those on the old tail and was a uniform dark brown colour, not striped with lighter coloured bands as on the old tail, or on the whole length of perfect tails of other specimens. Clear differences between the appearance of regenerated and original tails of lizards in the families of geckos, skinks, and legless lizards are well established (Bustard, 1970).

TABLE 2

RATE OF TAIL REGENERATION FOR THREE SPECIMENS IN CAPTIVITY

Specimen (Table 1)	Mass g	Date	Length of regenerated tail mm	Rate of increase of length of regenerated tail mm.y ⁻¹
I	102	22.11.75	52	—
	106	8.2.76	112	280
II	136	15.5.73	0	—
	156	23.3.74	65	78
	256	19.1.75	79	17
	227	7.2.76	93	13
III	270	22.8.74	75*	—
	267	22.11.75	102	22
	327	7.2.76	109	34

* See Figure 1 for photograph of tail.

The rates of tail regeneration for three specimens studied in captivity are given in Table 2. Specimen I gained only 4 g in mass (4%) in ten weeks in captivity, but it increased in total length by 69 mm (24%) and in tail length by 64 mm (43%). Most of this tail growth was in the regenerated section of the tail, which increased by 60 mm (115%) compared with 4 mm on the original tail (4%). This very large rate of growth may be due to this specimen having broken its tail much closer to the body than where the breaks occurred with the two other specimens and therefore it having a greater area of blood supply to the new tail.

Specimens II and III (Table 2) did not increase smoothly in mass with time. Specimen II increased in mass rapidly in the first eighteen months in captivity and its tail grew rapidly in the first year. It decreased in mass by 11% in the last year but increased in length in this time and added 14 mm of new growth to its tail. Specimen III showed tail growth during the first year in captivity even though its mass remained constant. These observations indicate that these lizards were able to redistribute mass from the body to new tail

TAIL REGENERATION IN AN AGAMID LIZARD

growth during periods when they may have had insufficient food, or a poor variety of food, available to maintain a steady increase in mass.

The specimen with a double tail (Table 1, 156 g) probably developed the accessory tail following damage sufficiently deep to expose the spinal cord. This possible mechanism has been discussed briefly for other species of lizards by Goss (1969) who stated that lizards regenerate an unsegmented cartiliginous tube within the tail instead of vertebrae.

Accordingly, X-radiographs were taken of three of the lizards with regenerated tails, and prints of these are shown in Figs. 3-5. The regenerated parts of the tails can be clearly seen to contain a cartiliginous tube, as compared with the original tails in which normal vertebrae can be seen. The X-radiograph of the double-tailed specimen shows that the vertebra from which the accessory tail emerged has a central diameter of 2.5 mm compared with 2.0 mm for the vertebrae on either side and has the same density on the negative print as the cartiliginous tube. It appears that a sheath of cartilage formed around the vertebra and extended into the accessory tail which is therefore strongly attached to the main tail. This thickening of the cartiliginous tube around the vertebra at the point of breakage can also be seen in the X-radiographs of the two other specimens.

LOWER TEMPERATURE LIMIT FOR ACTIVITY

One drazon lizard (Specimen II) was observed in relation to its appearance from, and return to, hiding on sunny and dull days. The temperature was recorded at hourly intervals over a period of two weeks in May, 1973 and the time noted when it emerged from and returned to its overnight hiding place. The lizard basked on the rocks during the day whether the sun was shining or the sky was overcast provided that the temperature was above about 17°C. Observations on the specimens in captivity and in the small colony in Vacluse indicate that the lizards hibernate in this area in the winter months because the temperature is usually below 17°C.

In summer months the temperature at night is usually over 17°C on the east coast of Australia. The lizard then shows the normal daytime behaviour of many species of lizard of basking in the sun, and when the ambient temperature is high, in order to raise its body temperature before foraging for food, and then returning to shade or to its hole to prevent overheating or to escape from predators. Bustard (1967) reported that the variegated gecko (*Gehyra variegata*) often stopped foraging for food when the temperature dropped below 18°C, and studies on other species may show that they also have a similar temperature limit for activity.

OBSERVATIONS ON FOOD

The authors of many general books on Australian lizards have stated that the eastern water dragon takes a wide variety of food. Davey (1970) quoted mice, young rats, snails, grubs, worms, crustaceans, native flowers and berries. Observations of food taken in the wild are very difficult with this lizard because

of its shy nature, and because it forages for food in crevices in rocks and within vegetation.

Samples of faeces freshly deposited by large lizards in the wild were therefore collected and analysed. These were usually firm cylindrical pieces about 5 mm diameter and 10-15 mm long. After they were dried the components could be separated with tweezers and grouped into animal and plant remains. A large part consisted of the hard indigestible parts of beetles and other insects, e.g. legs and wing cases. There were also many small hard seeds, a large number of which were from lantana plants. Pieces of fern and other small plants were found, as well as powdery white lumps of dried salts. An unusual discovery in one sample was a 200 mm length of nylon thread. Young dragons observed near their nesting burrows spend most of the day picking up small flies and other small insects within easy reach, but have not been seen to take plant food.

In captivity these lizards will eat a variety of food, small pieces of meat, live insects (beetles, flies, cicadas), snails, worms, and whole or chopped fruit such as tomatoes and strawberries, of which the latter appear to be very attractive.

BODY COLOURATION

The eastern water dragon develops a bright red belly colouration in early summer after it has shed the old skin which is usually a dull-red-brown in that region. Both sexes are said to develop the colour. However, it is not possible to differentiate between the sexes in the field, and this can only be done reliably by a careful examination of the anal slit. Generally the whole of the underside from between the forelegs to between the hindlegs is uniformly coloured red. One of the specimens captured, a large mature dragon (660 g), had a ring of deep red-brown skin around the belly with the centre the normal grey-green colour.

It is not clear, from the few specimens studied, at what age or mass the red colour develops. The 106 g Specimen I (Table 2) in early February, 1976 was a deep red colour over the whole belly region, with the colour suffused into the legs and under the throat. The larger specimen (156 g, Table 1) with the double tail had only a slight tinge of red at the same date, and the much larger Specimens II and III (227 and 327 g, Table 2) both had distinctly red coloured bellies, but no colour on legs or throats.

ACKNOWLEDGEMENT

We are grateful to Dr. A. D. Tucker for taking the X-radiographs of the specimens.

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Electrophoretic Evidence for the Specific Status of the Lizards *Lampropholis guichenoti* (Dumeril & Bibron, 1839) and *L. delicata* (de Vis, 1887)

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ABSTRACT

Electrophoretic differences in two of the five enzymes studied indicate that sympatric populations of *Lampropholis guichenoti* and *L. delicata* are maintaining separate gene pools and should be recognised as separate species. Coloration was found to be the most useful feature for distinguishing the two species in the field.

INTRODUCTION

Lampropholis guichenoti (Dumeril & Bibron, 1839) and *L. delicata* (de Vis, 1887) are small ground lizards of the family Scincidae. In his original description of *L. delicata*, de Vis (1887) stated that the differences between it and *L. guichenoti* were "enlarged preanals . . . slender form, feebler limbs and completely different physiognomy".

Loveridge (1934) grouped the two together as subspecies *L.g. guichenoti* and *L.g. delicata*. Worrell (1963) supported this conclusion but applied the subspecies name *delicata* only to the type specimen from Warra, Queensland and to some specimens from Groote Eylandt.

Cogger (1975) listed them as separate species distinguishable by their coloration. He noted that they had similar scalation, size and habits and that their distributions overlapped considerably.

Clark (1965) attempted to differentiate between the two species using scale counts, body proportions and coloration. She found that the ranges of scale counts and body proportions were similar and decided that only coloration and the number of supraciliaries could be used to separate the two species.

On morphological grounds it is clearly difficult to distinguish between these putative species. Coloration appears to be the most reliable character but even this shows considerable variation.

Electrophoretic methods have been used successfully to investigate taxonomic problems in a wide range of species (see Avise, 1974). It was therefore decided

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to employ electrophoresis as well as morphology to investigate sympatric populations of these lizards with the aim of clarifying their taxonomy.

MATERIALS AND METHODS

Sixty adult lizards were collected in a suburban garden in Epping, N.S.W. They were divided into two groups according to their coloration. One group classified as *L. delicata* had a definite pale stripe above the dark lateral stripe with a pale stripe below the lateral stripe less obvious or missing. The other group classified as *L. guichenoti* had a pale stripe below the dark lateral stripe which was at least as obvious as the pale stripe above the lateral stripe. Using these criteria 33 specimens were classified as *L. guichenoti* and 23 as *L. delicata*. It was not possible to classify four individuals using these criteria.

MORPHOLOGY

The supraciliaries and 4th toe lamellae were counted and snout-vent length measured. The amount of overlap of adpressed limbs and the size of the preanals were also examined on some specimens. The presence or absence of a dark vertebral stripe, pale stripes above or below the dark lateral stripe and small pale and dark spots on the back was noted.

ELECTROPHORESIS

Livers were removed and homogenised in an equal volume of distilled water, using a micro mortar and pestle. The homogenates were then applied to starch gels or cellulose acetate "cellogel" (Chemetron, Milan). Electrophoresis conditions, buffers and stains for lactate dehydrogenase (LDH), malate dehydrogenase (MDH) and phosphoglucumutase (PGM) are described in Johnston (1973). The methods of Shaw and Prasad (1970) were used for detecting esterases and α glycerophosphate dehydrogenase (α GPDH).

TABLE 1

Length and scale counts of *L. guichenoti* and *L. delicata*

		n	\bar{x}	s	range
Supraciliaries	<i>L. guichenoti</i>	35	6.58	0.91	5-9
	<i>L. delicata</i>	22	6.41	0.84	5-8
4th toe lamellae	<i>L. guichenoti</i>	32	21.77	1.34	18-24
	<i>L. delicata</i>	21	24.83	1.13	22-26
Snout vent length (mm)	<i>L. guichenoti</i>	27	40.30	3.30	34-46
	<i>L. delicata</i>	20	37.28	2.69	31-41

ELECTROPHORETIC DIFFERENCES IN LIZARDS

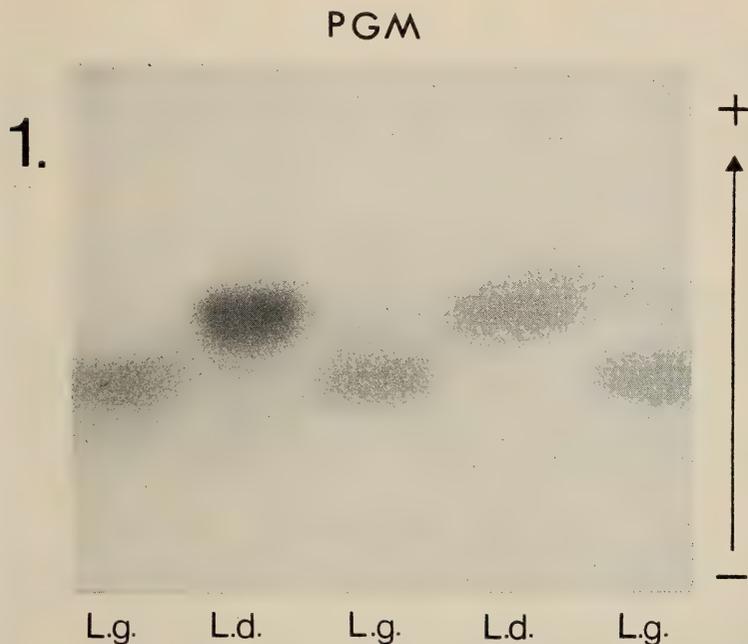


Fig. 1. Phosphoglucosmutase patterns of *L. guichenoti* (L.g.) and *L. delicata* (L.d.) after cellophore electrophoresis.

RESULTS

MORPHOLOGY

Table 1 gives the mean, standard deviation and range of values for the characteristics measured. Student's "t" test showed that the number of 4th toe lamellae and snout-vent length differed significantly between the two groups at the 5% level of significance. The difference in the number of supraciliaries was not significant.

No difference was observed in the size of the preanals or amount of limb overlap between the two groups.

COLOUR

Table 2 gives the percentage of lizards in each group with each of the coloration features studied. All *L. delicata* had a pale stripe above the dark lateral stripe, but no dark vertebral stripe or pale spots on the back. *L. guichenoti* was more variable. The majority of them had a dark vertebral stripe, pale stripes above and below the dark lateral stripe and pale spots on the back. However, none of these features was possessed by all the lizards in the group.

TABLE 2

Percentage of lizards showing coloration features

	<i>L. guichenoti</i> (n=37)	<i>L. delicata</i> (n=23)
Dark vertebral stripe	86%	0%
Pale stripe above lateral	83%	100%
Pale stripe below lateral	95%	17%
Pale and dark spots on back	92%	0%

ELECTROPHORESIS

Phosphoglucomutase: *L. delicata* and *L. guichenoti* showed different electrophoretic patterns for PGM. In all cases the band of *L. delicata* was faster migrating and was easily distinguished from the slower migrating band of *L. guichenoti* (Fig. 1).

Esterases: The electrophoretic patterns observed were complex. However each species had a distinct pattern and could be easily classified (Fig. 2).

ESTERASES

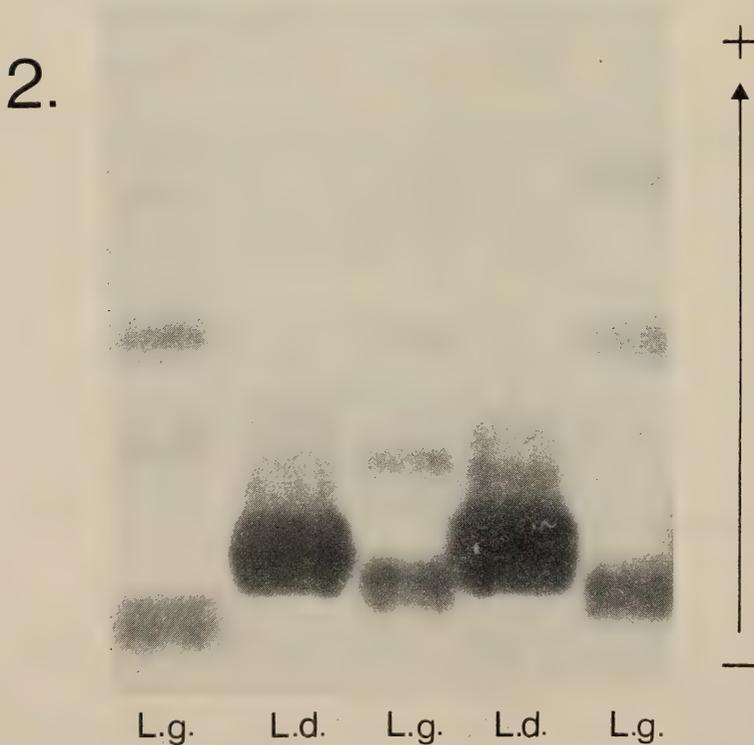


Fig. 2. Esterase patterns of *L. guichenoti* and *L. delicata* after starch gel electrophoresis.

ELECTROPHORETIC DIFFERENCES IN LIZARDS

Malate dehydrogenase, lactate dehydrogenase and a glycerophosphate dehydrogenase: These enzymes were monomorphic and had identical electrophoretic mobilities in both species. The four lizards which could not be classified on the basis of their colour patterns all had PGM and esterase patterns typical of *L. guichenoti*. These lizards were treated as *L. guichenoti* for the morphological studies.

DISCUSSION

The morphological data showed no significant difference between groups in the number of supraciliaries. The two characters that showed significant differences between groups were snout length and the number of 4th toe lamellae. These results contrast with those of Clark (1965) who found a significant difference between species in the number of supraciliaries but not in the number of 4th toe lamellae. It is thus apparent that these characters show considerable intra and interpopulation variation in both groups and are therefore not satisfactory for differentiating the two groups.

As has been found by other workers coloration is the most useful method for identification in the field. However, like the other morphological characters that have been used, there is some overlap and it was not possible to classify all the specimens on their colour patterns. Electrophoresis, on the other hand, clearly separates the lizards into two groups with no overlap. The PGM and esterase patterns were distinctive for each group. It has been established that PGM is a monomer in a wide variety of species (see Manwell and Baker 1970). Double banded phenotypes representing heterozygotes would therefore be expected if gene exchange was taking place between these groups. No double banded phenotypes were observed in any of the lizards examined.

The interpretation of the esterase variation is not so straightforward because of the unknown number of loci involved, but as with the PGM results, there is no evidence of heterozygotes being formed between the two groups. The electrophoretic results indicate that two groups are maintaining separate gene pools and that reproductive isolation exists between them. These results support the conclusion of Clark (1965) and Cogger (1975) that *L. guichenoti* and *L. delicata* are separate species.

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Voluntary Submergence Time and Breathing Rhythm in the Homalopsine Snake, *Cerberus rhynchops*

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Characteristics of breathing and submergence were analyzed for captive *Cerberus rhynchops*, a homalopsine aquatic snake. Some aspects of diving behavior differed markedly from that of sea snakes. Inactive snakes either hid in tubes on the bottom of the aquarium or rested with the head at the surface and the nostrils in air. Activity resulted in a reduction of submergence time. Within a given activity category, no diel difference in submergence time was observed, differences among individuals were large, and oxygen and CO₂ content of the water had only a weak effect on submergence time. Within the range 20°-30° C submergence time was only weakly temperature-dependent. Number of breaths per breathing episode showed great differences among individuals but little dependence upon time of day or gaseous content of the water. Individuals submerged for long periods tended to take a greater number of breaths per breathing episode.

Snakes at the surface for prolonged periods breathed regularly with the interval between breaths being longer than when they were alternatively surfacing and diving. Interbreath interval was independent of O₂ and CO₂ content of the water or of temperature between 20° and 33° C.

INTRODUCTION

Except for a few species scattered throughout various other taxa, the truly aquatic snakes belong to 5 major groups in 4 families. These are the sea kraits¹ (family Laticaudidae), the sea snakes¹ (family Hydrophiidae), the file snakes (family Acrochordidae) and two subfamilies of the Colubridae, the Homalopsinae and the Natricinae. Each of these five groups has probably developed their aquatic habits independently of the others and consequently it is of evolutionary significance to compare their diving adaptations.

Various aspects of the diving physiology and behavior of representatives of four of these groups have been investigated (Johansen 1959, Murdaugh and

1. The two families Laticaudidae and Hydrophiidae are sometimes lumped with their terrestrial relatives into the single family Elapidae (McDowell 1969) but were historically treated as subfamilies of the family Hydrophiidae (Smith 1926). It is now clear that they represent two independent marine radiations from the elapids and treatment as two separate families, as recently done by Burger and Natsuno (1974) seems the most appropriate procedure.

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Jackson 1962, Pough 1973, Standaert and Johansen 1974, Graham 1974, Graham *et al.* 1975, Heatwole and Seymour 1975a, 1975b, 1976, Heatwole 1975, 1977, Heatwole *et al.* in press, Seymour 1974, 1976, Seymour and Webster 1975, Jacob and McDonald 1976, Irvine and Prange 1976). The only previously uninvestigated group is the Homalopsinae. The present paper broadens the base of comparison by providing information on several aspects of diving and breathing in a homalopsine species, *Cerberus rhynchops*.

All of the 10 genera and 36 species of homalopsines are aquatic and have anterodorsally located nostrils which are lunate in shape and are valvular. Most are restricted to freshwater whereas others occur in brackish or marine situations. *Cerberus rhynchops* frequents tidal rivers and estuaries, both in the upper reaches where the water is fresh and in salt waters along coasts. It is widely distributed in suitable habitat from India throughout southeast Asia, Sunda Islands, Philippines, and into the Pacific to Palau (Gyi 1970). The animals used in the present study were collected in August-September 1975 in mangrove swamps at the United States Naval Base at Subic Bay, Republic of the Philippines, and at Jagoliao Island, Bohol, Republic of the Philippines. At the former locality, snakes were active at night in water 5 to 20 cm deep. The same area had been previously searched by day and no snakes observed.

MATERIALS AND METHODS

Except for an experiment on the effect of temperature on diving time, which was carried out in October, 1975, in Armidale, Australia, and using a snake that was transported there from the Philippines, all experiments and observations were carried out aboard the RV Alpha Helix in Philippine waters in September 1975.

Several limitations were imposed on the study by the animals and by the time available: (1) Individual snakes varied significantly from each other in respect to a number of characteristics and hence data from different animals could not be grouped for comparing experimental procedures. (2) Not all snakes engaged in all the types of behavior studied, and consequently some types of comparisons had to be omitted for some animals. (3) The submergence times were long and accumulation of a sufficient number for valid comparisons was time-consuming; available time was limited. Thus, some sample sizes are smaller than desirable.

The snakes were housed in 60-litre aquaria containing 20-35 cm of sea water maintained at a temperature of 25-28° C. Opaque polyvinyl tubes 3 cm in inside diameter and 40 cm long were provided as shelter for the snakes in the bottom of the aquaria. Lights in the laboratory were turned on at 0700 hrs and off at 1900 hrs each day. However, at night light from an adjacent laboratory entered through a large window and was of sufficient intensity that observations could be made. The snakes ranged in body weight from 93 to 222 g.

A total of 187 submergences on 6 individuals under a variety of different conditions were timed; when the snakes were not submerged data was recorded

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on the number and frequency of breaths. Two experiments were conducted to ascertain the possible effect of dissolved gases on the submergence time and breathing rhythm. In one of these, pure nitrogen was bubbled through the water of the aquarium until the oxygen level was lowered. O₂ level prior to bubbling was 5.2 ppm (measured by a YSI Model 57 oxygen meter) but dropped to 2.8 ppm after 1 hr 15 min of bubbling. Bubbling was discontinued during timed submergences but was maintained between observation periods, in some cases an entire day. O₂ levels in the aquarium were between 1.3 and 2.8 ppm during timed submergences; at the completion of the experiment O₂ was 1.4 ppm. By the following morning it had risen only to 1.6 ppm in the absence of bubbling.

A second experiment involved the same procedure except instead of nitrogen a gas mixture of 600 ppm CO₂ in nitrogen was bubbled through the water in order to raise the CO₂ level as well as to deplete oxygen. O₂ levels during timed submergences ranged from 1.4 to 1.6 ppm and after bubbling was discontinued had risen only to 3.9 ppm overnight.

The room in which these experiments were carried out was temperature-controlled and ventilated. There were no decreases in O₂ levels of the air above the water greater than 0.1 ppm and usually values were the same there as elsewhere in the room. Thus, any effect on submergence time or breathing rhythm would be a result of the change in dissolved gases rather than of alteration of composition of inspired air.

The temperature experiment carried out in Australia involved keeping a snake in an aquarium as described above but periodically altering the water temperature and then recording submergence times and breathing characteristics.

Time is expressed in minutes and tenths of minutes (rather than minutes and seconds) to facilitate calculation of means and standard errors.

RESULTS

GENERAL BEHAVIOR

When snakes were placed in the aquaria, they swam actively for several hours in what appeared to be escape behavior. However, by the end of the first day, all had found the tubes and entered them, alternating periods of swimming with periods of retreat into the tubes. Usually the head was just at the entrance of the tube and facing out, or the head and neck protruded from the pipe by a distance of up to 15 cm. Initially, disturbance such as sudden movements or substrate vibrations would result in the snake jerking backwards into the tube with a rapidity unexpected from the slow, deliberate movements generally characterizing this species. The first night one animal escaped from the aquarium and moved rapidly and as agilely as a terrestrial snake over a rather smooth sink top when the investigator entered the room. By the third day, overt fright responses were seldom observed (and then only in response to some unusual stimulus) and the snakes seemed accustomed to movement of people in the laboratory.

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BREATHING

When *C. rhynchops* breathes, it first exhales, then inhales and finally partially exhales. There is then a brief, or a prolonged period of apnea (depending on circumstances) before the next breath. Breathing movements are usually easily detectable by observing expansion and contraction of girth of the anterior part of the body. On some occasions when breathing was shallow it was difficult to detect individual breaths and they could not be counted.

The initial exhalent phase seems to be the active one; it is more rapid than the subsequent inhalent and second exhalent phase and sometimes the snake's body sways with the effort.

When a snake emerges it remains a short time with the nostrils out of the water before it takes a breath (mean 0.32 min; range 0.10-0.67 min). Subsequently, it breathes at short intervals, maintaining its nostrils continuously above water for the entire series of breaths. This series of breaths is called a breathing episode and the time elapsing between two consecutive breaths in that episode, the inter-breath interval. After the last breath of the episode, the animal almost immediately submerges (the time elapsing between the last breath and submergence averaging 0.06 min; range 0.03-0.27 min). The time between breaths of an inactive snake remaining continuously at the surface is also referred to as the inter-breath interval.

ACTIVITY AND INACTIVITY

During active periods, the snakes slowly swam along the bottom of the aquarium, poking the nose along the crevices at the sides of the plastic tubes or along the edges of the aquarium, or swam at the surface with occasional forays to the bottom and back. Movements were slow and deliberate. Activity took place chiefly at night. Snakes interspersed prolonged periods of inactivity with activity. There was considerable individual variation in level of activity, one animal seldom engaging in more than momentary periods of activity during the study; others were active much of the night with only occasional periods of rest.

There were two distinct behavioral patterns adopted by inactive snakes. One was to lie motionless in the tube except for periodic trips to the surface to breathe. Even during breathing the snake would not completely leave the tube but would extend the head and neck just far enough to protrude the nostrils and eyes above the surface. Upon termination of breathing, the snake backed slowly into the tube and again became motionless. While the head was on the surface, the body and neck stretched toward the surface either nearly vertically or at an angle of about 45°. The body was held straight without conspicuous bends or curves.

The second posture adopted during inactivity was to remain motionless at the surface with the nostrils and eyes emergent. The body extended to the bottom of the aquarium and the posterior part and the tail trailed on the bottom in a sinuous curve; in some cases the tail and part of the body were in a tube. Occasionally a snake would lower the head into the water and look around or even sub-

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merge briefly so that the head and anterior part of the body pointed upward from the bottom of the aquarium at about an angle of 45°, with the head at about mid-water. Bouts of activity were interspersed with this type of inactivity more frequently than with inactivity in shelter, and emergent inactivity is probably an indication of an alert state bordering on activity. Individual snakes differed greatly in their preference for inactivity at the surface as opposed to inactivity in shelter. Some snakes never were observed at the surface except for brief periods of breathing; others spent most of their inactive time with their heads at the surface.

VOLUNTARY SUBMERGENCE TIME

During the first two days in the aquarium, mean submergence times for a given activity category were low (31-37% those of the same individuals after 3 or more days) and no values even of inactive snakes, exceeded 28 mins.

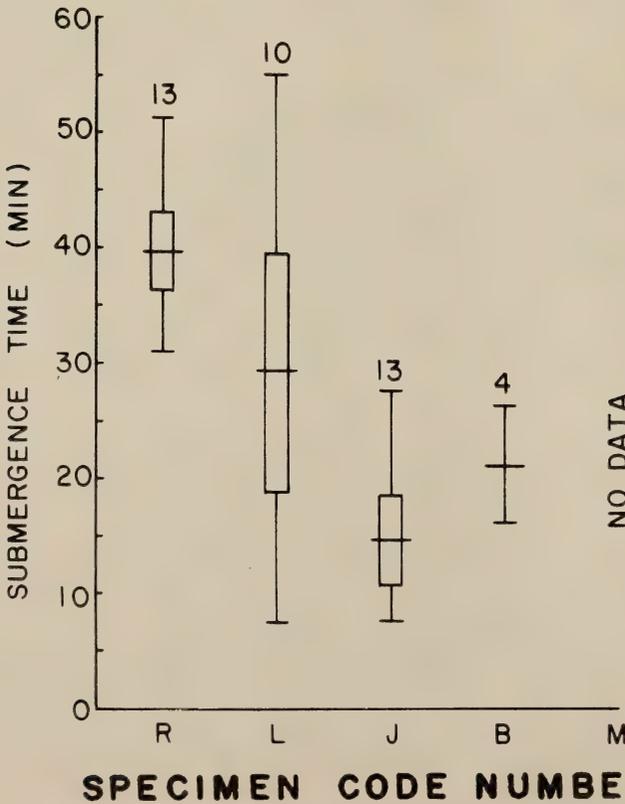
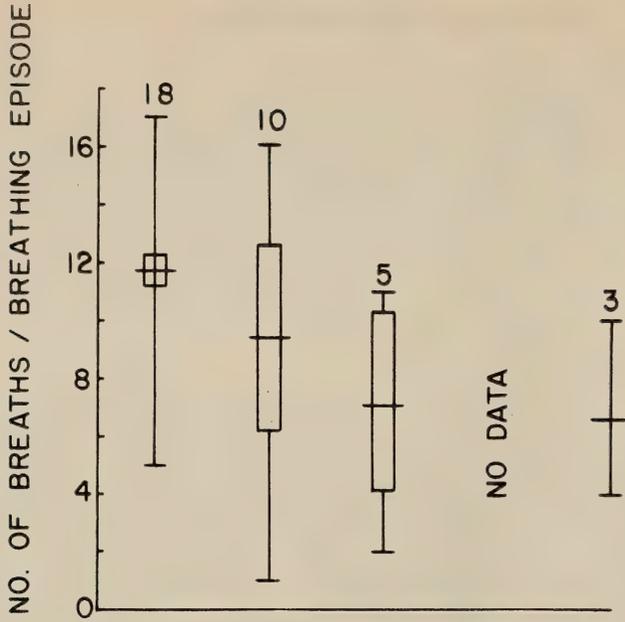
Underwater time of individual active snakes averaged 0.7-3.5 min, or 3.3 — 26% of the inactive values for the same snakes under comparable conditions. There was one exception in which active values were 84.4% of inactive ones; this exception occurred, however, during the second day in the experimental container when inactive values were abnormally low, probably because of the unfamiliar conditions. Pairing active and inactive means by animal, date and experimental conditions for all periods in which both inactivity and activity occurred, a Wilcoxon Matched Pairs Signed Ranks test revealed that the above differences were highly significant ($P < 0.005$, one-tailed; 8 pairs of means). Thus, activity greatly affects submergence time.

There was very little difference in submergence time between day and night for a given activity category and set of conditions. It was predicted that since the species is nocturnal, submergence times would be shorter at night. However, pairing day and night mean values by animal, activity category, date and type of experiment, a Wilcoxon Matched Pairs Signed Ranks test indicated no statistical diel differences ($P > > 0.05$, one-tailed, 9 pairs of means). Consequently values for night and day were lumped for further analyses but including only data from inactive snakes after the initial 3-day period of becoming accustomed to the new environment.

TABLE 1. RELATION OF SUBMERGENCE TIME OF *CERBERUS RHYNCHOPS* TO GASEOUS CONTENT OF THE WATER

Individual Snake Designation	Mean Submergence Time in Minutes (\pm s.e.)				% Re-duction	Water Bubbled with CO ₂ in nitrogen		
	N	Untreated Water	N	Water Bubbled with N ₂		N	% Re-duction	
R	13	39.58 \pm 1.72	7	36.01	9	4	33.06	16
L	10	29.12 \pm 5.16	6	22.01	24	—	—	—

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Under equivalent conditions, different individuals had markedly and significantly different mean submergence times (Fig. 1). These differences bore no consistent relation to body weight, e.g., the animal with the longest submergence times was the smallest individual and the one with the shortest submergence times was the second smallest snake. There did seem to be a general relationship with tendency toward activity. Qualitatively it was observed that the snakes with short submergences during inactive periods tended to be those which were most frequently active.

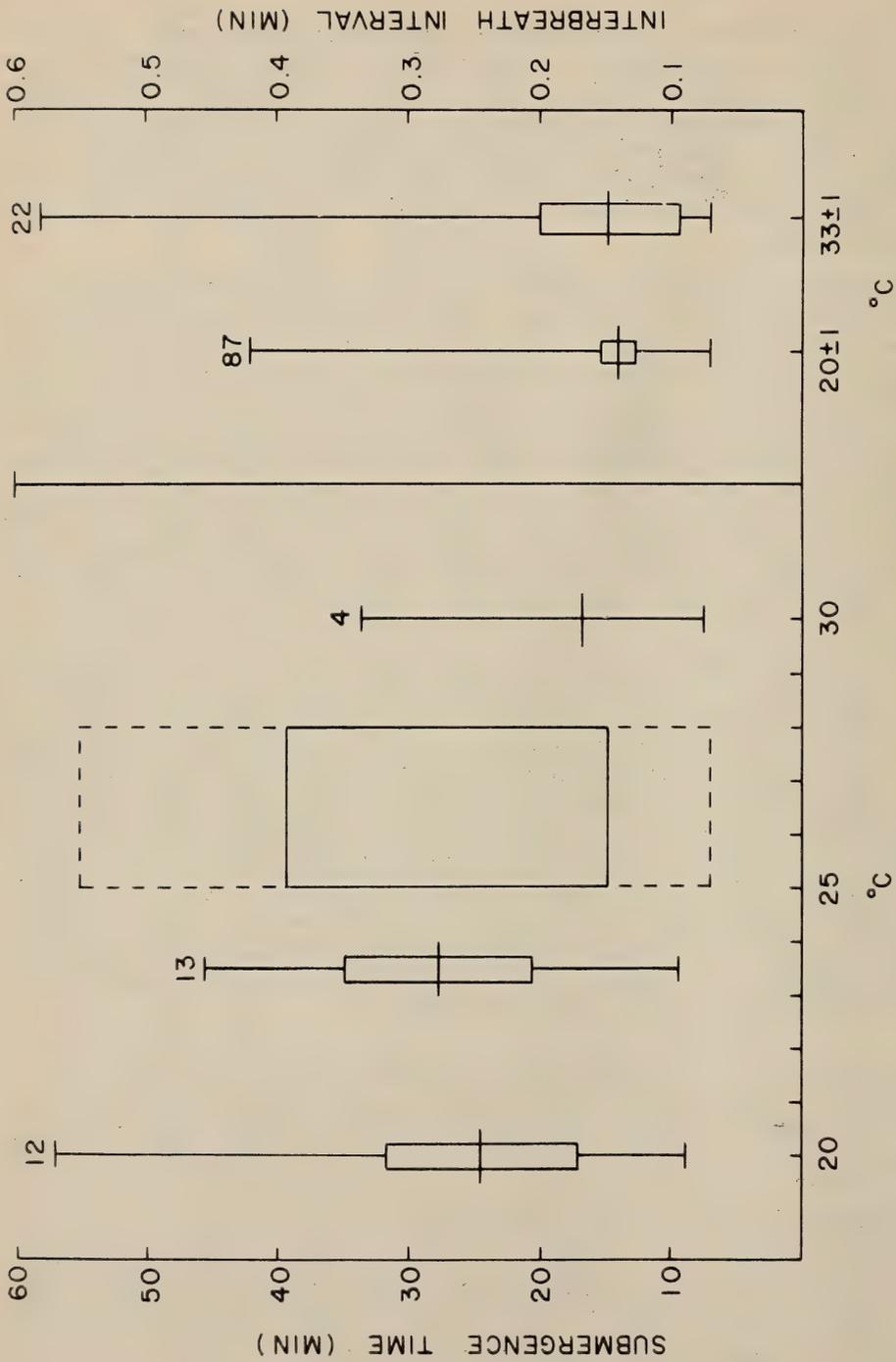
Mean submergence time decreased in oxygen depleted water in both individuals tested (Table 1). The differences were not statistically significant, however (Mann-Whitney U-test), as P values were just slightly greater than 0.05 in both cases. In water that was oxygen poor and CO₂ rich, there was a further (but not significant; P > 0.05) decrease in submergence times. Some of the differences were near the level of significance and all were in the direction predicted. It is possible that failure to achieve significance was largely a reflection of the small sample sizes. At present, however, it can only be concluded that the differences may have been due to chance. In any event, the reductions in submergence time possibly arising from bubbling N₂ and/or CO₂ were of less magnitude than individual differences and it can be concluded that if gaseous content of the water does influence submergence time, the effect is not great.

Voluntary submergence time is surprisingly independent of temperature within the range 20°-30° C. For the single individual tested at several temperatures, mean submergence time did not differ significantly between 20° and 23.5° C (Fig. 2) and even the value of the animal at 30° C was not greatly reduced from that at the other two temperatures (differences between 23.5° and 30° C not significant; Mann-Whitney U-test, P slightly greater than 0.05, one-tailed). The shortest submergences timed were practically identical at all temperatures (Fig. 2). However, the maximum values progressively decreased with increasing temperature. It seems that the snakes do not greatly alter their submergence times within the range of temperatures tested but that there may be a tendency to dispense with the exceptionally long ones at higher temperatures. Differences in submergence times at different temperatures for a given individual were less than differences among individuals at the same temperature (Fig. 2).

THE NUMBER OF BREATHS PER BREATHING EPISODE

Number of breaths taken when a snake surfaced to breathe varied from 1 to 17. There was considerable and significant variation among individuals, inter-individual means varying almost 2-fold for a given set of environmental conditions

Fig. 1. Submergence times and number of breaths per breathing episode in individuals R, L, J, B, and M of *Cerberus rhynchops*. Numbers above figures indicate number of submergences or breathing episodes involved. Vertical line indicates range, horizontal line the mean, and rectangles, 2 standard errors on either side of the mean.



TEMPERATURE

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(Fig. 1). In contrast to submergence times, the number of breaths per breathing episode did not show consistent differences between the periods before and after the snakes became familiar with their new environment, nor did it vary significantly between night and day (half of the day values were higher than night ones and half were lower) or dissolved gaseous content of the water (Mann-Whitney U-test, $P > 0.10$ in all comparisons). Insufficient data on this characteristic were available for active snakes for evaluation to be made.

It appears that for a given individual, various environmental factors have little effect on number of breaths per episode but that each individual has its own characteristic in this regard and individuals differ. Inspection of the two sets of figures in figure 1 indicates that the individuals that submerge the longest tend to take a larger number of breaths than those which have shorter submergence times, suggesting that there may be a relation between these two breathing characteristics. However, when the number of breaths taken were related to the corresponding previous submergence time for each individual snake, no significant correlations were obtained (Spearman Rank Correlation Test; $P \gg 0.10$ for each snake). Thus it seems that the number of breaths taken does not depend upon the length of submergence immediately preceding a given episode even though snakes that submerge long times tend also to take a large number of breaths per breathing episode.

INTER-BREATH INTERVAL

The intervals between the breaths of a given breathing episode (inter-breath intervals) were very short; means were less than half a minute in all snakes and averaged from 0.4% to 3.0% of the submergence times for given individuals. As was true of other breathing characteristics, there were significant differences among individuals in inter-breath interval (Fig. 3); difference among individuals varied as much as 3-fold.

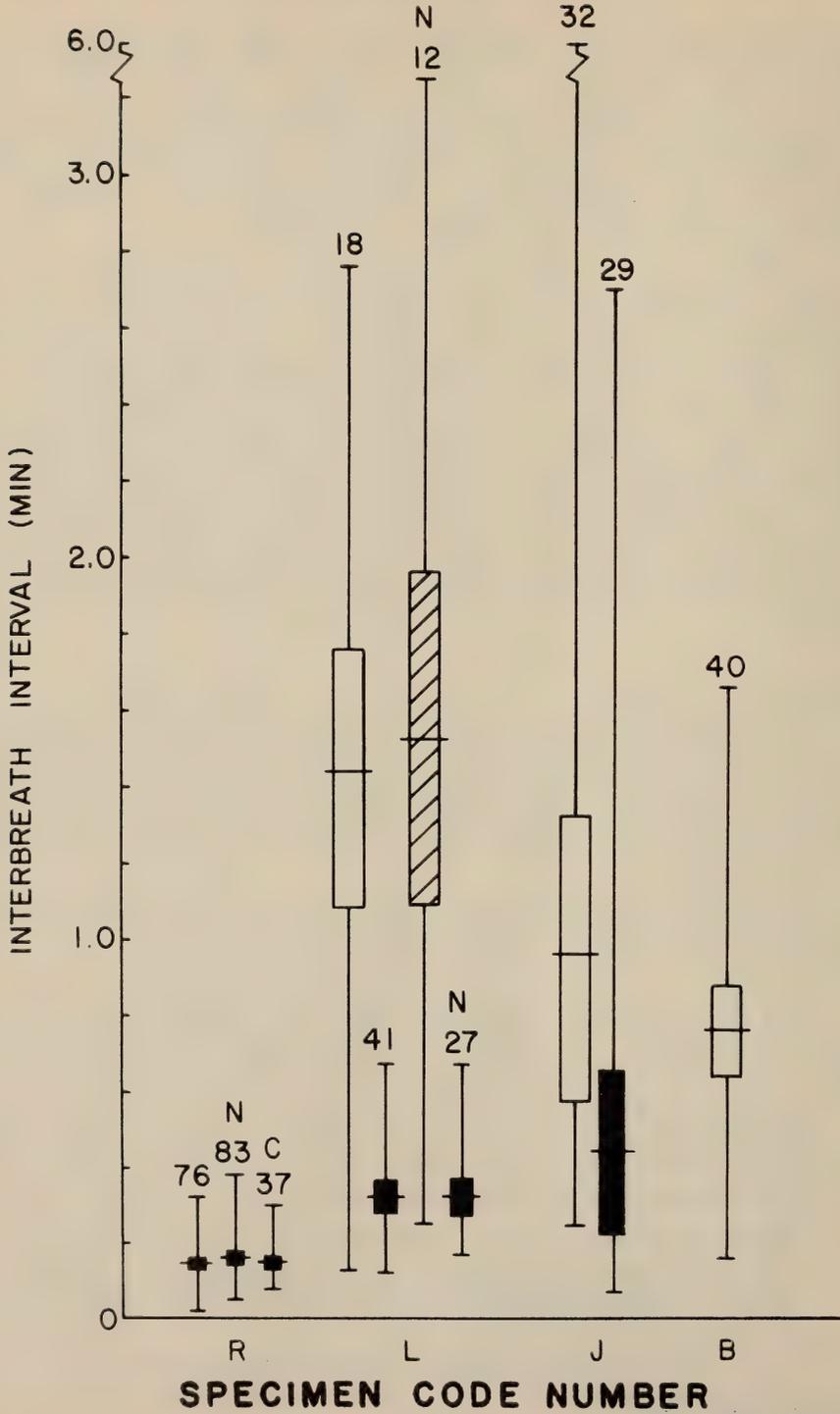
Those individuals that had long submergence times and high numbers of breaths per episode tended to be those with shorter inter-breath intervals (compare Figs. 1 and 3).

For a given individual, inter-breath interval was remarkably similar under a variety of conditions. For example, bubbling nitrogen or nitrogen and carbon dioxide through the water did not affect it (Fig. 3), nor did temperature (Fig. 2).

Inter-breath intervals were greatly different when inactive snakes remained continuously on the surface as compared to the brief breathing episodes between

Fig. 2. Relation of submergence times and inter-breath interval of *Cerberus rhynchops* to water temperature. Narrow figures as in Figure 1; all are of individual A. The wide rectangle indicates the range in means of snakes R, L, J, B and M over the temperature range indicated by the width of the box. The dotted lines extending the rectangle indicate the range of values.

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submergences (Fig. 3). For given individuals the inter-breath intervals between the two situations varied by 2-3 fold, more rapid and deeper breathing occurring in the latter case. As in other characteristics, inter-breath intervals of snakes remaining at the surface showed significant variation among individuals and was not affected by bubbling nitrogen through the water (Fig. 3).

The change between these two patterns of inter-breath interval when a snake emerges and then remains on the surface for a long time, is rather abrupt. For example, snake "L" emerged and had deep breaths at intervals of 0.20 to 0.32 minutes (mean 0.26). It then abruptly began to engage in shallow breathing with inter-breath intervals of 0.42-0.65 min (mean 0.51). The difference in inter-breath interval between these two periods was significant (Mann-Whitney U-test, $P < 0.002$). This observation also suggests that breathing frequency is related to tidal volume.

Prolonged apnea in *Cerberus* is related to submergence. When snakes are at the surface inter-breath intervals are short, yet there are some occasions when snakes at the surface did suspend breathing for rather long periods (usually 1-4 mins although some longer ones were observed). These apneic periods were usually coincident with some unusual disturbance in the laboratory and were probably fright responses. They were not included in the calculations of mean inter-breath intervals. Eleven such apneic periods occurred in snakes with the nostrils emergent during the study.

DISCUSSION

Breathing rhythm of sea snakes has been studied by Heatwole and Seymour (1975a, b, 1976) and Heatwole (1975). Breathing rhythm in *Cerberus* differs from that of sea snakes in several important ways. (1) Sea snakes undergo prolonged periods of apnea not only when submerged but also when they are at the surface, whereas *Cerberus* does so only when submerged (or when frightened) and (2) sea snakes usually take only 1-3 breaths per breathing episode whereas *Cerberus* takes a much larger number. The breathing rhythm of *Cerberus* when emergent resembles that of land snakes in air and it would appear to be somewhat intermediate in breathing rhythm between land snakes and sea snakes, or more likely, has retained the land rhythm and can switch between it and one more appropriate to aquatic animals depending upon circumstances. Sea snakes on the other hand seem to have lost the characteristics of the land rhythm and have exaggerated the apneic interval under all circumstances.

Fig. 3. Inter-breath interval of individuals of *Cerberus rhynchops* during breathing episodes between submergences (solid figures), and when remaining on the surface for extended periods in normal water (open figures) and when nitrogen was bubbled through water (cross-hatched figure). N indicates that nitrogen was bubbled through the water, and C indicates that CO₂ in nitrogen was bubbled through the water. Numbers above figures indicate number of submergences. R, L, J, B, and M refer to code numbers of individual snakes; other symbols as in Figure 1.

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The relatively slight (if any) effect dissolved gases have on submergence times of *Cerberus* may be related to other respiratory features of this species. Sea snakes are capable of cutaneous respiration to a greater extent than are land snakes. (Graham 1974, Standaert and Johansen 1974, Heatwole and Seymour 1975a, b, 1976). Such a capability would seem to be advantageous to any aquatic snake which remained submerged for extended periods. However, the relatively slight (if any) effect dissolved gases have on submergence times in *Cerberus* suggests that its aerial breathing rhythm is not greatly influenced by a capacity for underwater respiration. Heatwole and Seymour (in prep.) have found that this species has much lower cutaneous oxygen uptake than did four sea snakes tested under the same conditions. The waters of mangrove swamps (an habitat of *Cerberus rhy-nchops*) are often relatively depleted of oxygen and are rich in carbon dioxide. There would be little selection for cutaneous respiration in such an environment and the insensitivity of *Cerberus* to dissolved gases may be a reflection of its particular ecology.

ACKNOWLEDGMENTS

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The Labrid Fish Genus *Pseudojuloides*, with Description of a New Species

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ABSTRACT

Pseudojuloides elongatus n.sp. is described from specimens collected in New Zealand, Norfolk Island, New South Wales and Western Australia, and Japan. The genus *Pseudojuloides* Fowler and the type and only other species in the genus, *P. cerasinus* (Snyder), are redescribed.

INTRODUCTION

The genus *Pseudojuloides* was created by Fowler (1949) to separate *Pseudojulis cerasina* Snyder (1904) from other species of the genus *Pseudojulis* Bleeker (1862). Fowler differentiated *Pseudojuloides* by its much larger thoracic scales, shorter pectoral fins, greater number of scale rows on the caudal fin base, and differences in colouration. These characters alone seem insufficient to warrant separate generic status and probably for this reason there has been some confusion as to the validity of the genus, Randall (1973) for example, has referred *Pseudojuloides cerasinus* to the genus *Leptojulius*.

The discovery of a new species of *Pseudojuloides* in northern New Zealand waters led us to closely re-examine the status of the genus. Comparing our specimens and those of *P. cerasinus* with Fowler's description revealed several major discrepancies in the original description of *Pseudojuloides*. These necessitate a review of the genus.

In this paper we redescribe *Pseudojuloides* and the type species *P. cerasinus*. The new species of *Pseudojuloides* collected from northern New Zealand and subsequently found also in eastern and western Australia, at Norfolk Island, and in southern Japan, is described.

METHODS

Measurements were made with vernier calipers to the nearest half millimeter. Standard length is abbreviated as SL. In the description, counts and proportions follow Randall (1972). For the new species, those for the holotype are given

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first while those for the paratypes, when different from the holotype, appear in parentheses.

Type material has been deposited in the following institutions: Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); National Museum of New Zealand, Wellington (NMNZ); Tanaka Memorial Biological Station, Tokyo (TMBS); Western Australian Museum, Perth (WAM).

DESCRIPTIONS

Pseudojuloides Fowler

Pseudojuloides Fowler, 1949: p. 119 (type species: *Pseudojulis cerasina* Snyder, by original designation).

DESCRIPTION:

Dorsal rays IX, 11-12; anal rays III, 12; pectoral rays i, 10-11; pelvic rays I, 5; principal caudal rays 14. Lateral line continuous, abruptly bent downward beneath soft portion of dorsal fin, 27 scales in lateral line, an additional enlarged scale beyond caudal base. Lateral line pores simple, unbranched. Scale rows above lateral line beneath origin of dorsal fin $2\frac{1}{2}$, below lateral line to origin of anal fin $7\frac{1}{2}$. Gill rakers small, 13-16 on first arch. Branchiostegal rays 6. Vertebrae 10+15.

Body elongate, moderately compressed, snout pointed. Interorbital convex, low; eye small. Mouth terminal, lips moderately broad and well developed; lower lip with prominent downward projecting flap on each side, inner surface of upper lip plicate. Single pair of well-developed, forwardly projecting canines in front of jaws, upper pair splayed apart, those of lower jaw fitting between them; teeth on sides of jaws small and laterally compressed, restricted to anterior part of jaw. Larger individuals with a posterior canine in the angle of jaw on each side. Lower pharyngeal plate broadly Y-shaped, posterior row of teeth laterally compressed and elongate, those in centre somewhat enlarged and asymmetrically conical, remainder molariform with 4-5 small conical teeth extending in single row onto anterior shank of bone. Upper pharyngeals with teeth in triangular patch, anterior row of which are asymmetrically conical, remainder molariform (Figs. 1-6).

Preoperculum entire with free lower edge, about 1.5 times longer than posterior free edge; gill membranes broadly attached to isthmus with very narrow free fold posteriorly. Nostrils small, anterior nostril in short tube, posterior nostril with small dermal flap on anterior margin.

Head naked except for patch of small scales on nape or on side of head above operculum. Thoracic scales smaller than those on rest of body. No scales on fins except for caudal which has about 4 rows of small scales on base.

Caudal fin rounded. Dorsal fin long, its origin slightly forward of vertical through upper pectoral base. Anal fin elongate, its origin below last dorsal spine.

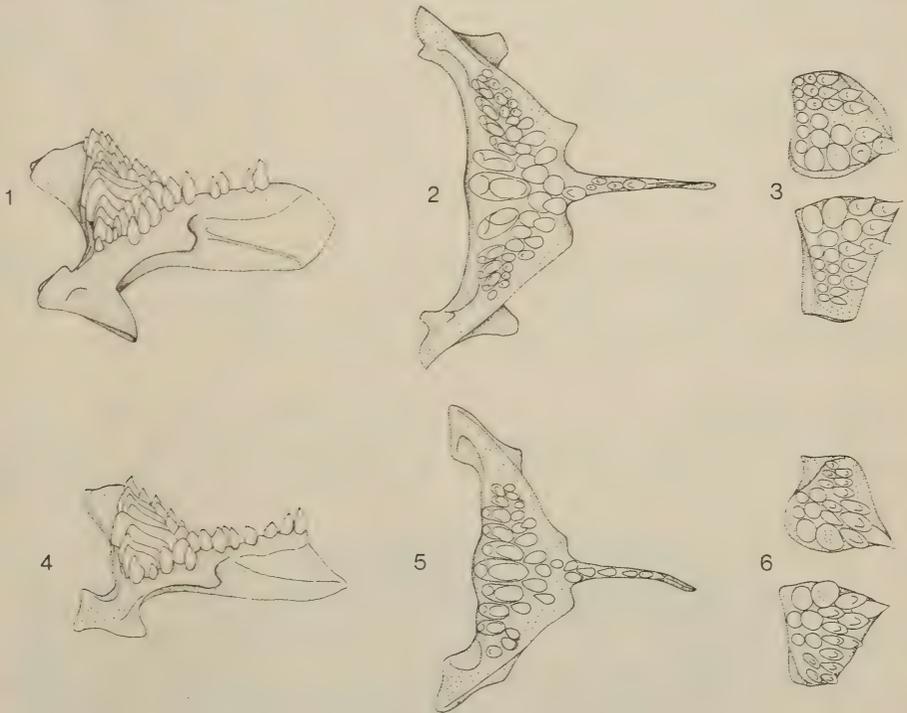
A NEW SPECIES OF PSEUDOJULOIDES

Pectoral fins rounded, first soft ray longest. Pelvic fins pointed, first two rays longest.

Sexually dimorphic; males brightly coloured, females drab.

REMARKS:

Fowler (1949) appears to have erred in his original description of *Pseudojuloides*. His description of colouration as "little contrasted, largely uniform" applies only to female specimens. A more important discrepancy is in his description of the teeth as "uniserial, largest in front of jaws, gradually smaller to last or posterior, all simple, pointed, conical." In all the specimens we have examined, the teeth in the sides of the jaw are laterally compressed. John R. Paxton, who has examined the type of *P. cerasinus* for us in the U.S. National Museum, reports that the teeth in that specimen also are small and laterally compressed.



Figs. 1-6. Pharyngeal bones of two species of *Pseudojuloides*.

1-3 *P. cerasinus* 63 mm SL. Fig. 1. Oblique lateral view of lower pharyngeal bone. Fig. 2. Dorsal view of lower pharyngeal bone. Fig. 3. Ventral view of upper pharyngeal bones.

4-6 *P. elongatus* 54 mm SL, same sequence as above.

The relationships of *Pseudojuloides* to the related genera *Pseudojulis*, *Leptojulis* and *Halichoeres* are not clear. All are characterised by small thoracic scales, naked head, absence of scales on dorsal and anal bases and 9 pungent dorsal spines. The type of *Pseudojulis* (*P. girardi* Bleeker) appears to be a juvenile *Halichoeres* and the status of this genus is doubtful. Separation of the other genera has been mainly on the basis of differences in jaw dentition. *Leptojulis* (type *L. cyanopleura* Bleeker) differs from both *Pseudojuloides* and *Halichoeres* in possessing two pairs of large canine teeth at the front of the jaws, although in small specimens of *L. cyanopleura* (less than 45 mm SL) the second pair are not well developed. In *Halichoeres* (type *H. bimaculatus* Rüppell) the jaw teeth are small and conical and clearly distinct from those of *Pseudojuloides*. The presence of more laterally compressed jaw teeth in *H. biocellatus* Schultz, although less widely separated than in *Pseudojuloides*, however, suggests that the structure of the jaw teeth in *Halichoeres* may be somewhat variable. Similarly, the presence of a posterior canine in the angle of the jaw, used as a diagnostic character by some authors, appears to be variable among species of *Halichoeres* which we have examined. The posterior canine in *Pseudojuloides elongatus* is developed only in specimens greater than about 100 mm SL. For the present we regard *Pseudojuloides* as a valid genus distinct from *Halichoeres* by its more elongate body and compressed, widely separate jaw teeth.

Pseudojuloides cerasinus (Snyder)

Figs. 1-3, 7

Pseudojulis cerasina Snyder, 1904: p.528 (type locality, Honolulu, Hawaii).

Pseudojuloides cerasinus — Fowler, 1949: p.119 (Hawaiian Is.).

Leptojulis cerasinus — Randall, 1973: p.197 (Society Is.).

MATERIAL EXAMINED:

AMS I.17470-004, (1) 73 mm SL., Uvea Atoll (20°23'S, 166°40'E), Loyalty Islands, 10-25 m, speared by G. R. Allen and W. A. Starck 18 June, 1973. AMS I.18094-002, (1) 78.5 mm SL., One Tree Island (23°30'S, 152°05'E), Great Barrier Reef, 20 m, speared by A. M. Ayling and B. C. Russell 16 September, 1974. AMS I.18366-001, (2) 60-71 mm SL., off Lahelahe Point (21°27.5'N, 158°13'E), Oahu, Hawaii, 28 m, speared by J. E. Randall 13 July, 1968.

DIAGNOSIS:

A species of *Pseudojuloides* with the following combination of characters: Dorsal rays IX,11; pectoral rays i, 11; lateral jaw teeth 6-7; triangular patch of small predorsal scales on nape; male dark green with deep blue midlateral line, below which is light green line, belly blue; lower part of head and cheeks blue with distinctive blue band passing from back of eye across operculum down to pectoral base, distinctive blue band on caudal fin separating dark outer half; female uniform reddish-brown.

A NEW SPECIES OF PSEUDOJULOIDES

DESCRIPTION:

Dorsal rays IX, 11; anal rays III, 12; pectoral rays i, 11; pelvic rays I, 5; principal caudal rays 14; gill rakers on first arch small, 7+6.

Body elongate, depth in front of anal fin 4.1-4.2 in SL, width 1.9-2.1 in depth; head pointed, length 2.9-3.2 in SL; snout including lips 3.1-3.2 in head; eye diameter 1.4-1.9 in snout; interorbital space convex, bony width 4.9-5.4 in head; least depth of caudal peduncle 2.7-3.1 in head; length of caudal peduncle 1.0-1.1 in least depth of peduncle.

Upper jaw nearly reaching a point vertically below anterior nostril; single pair of pointed, well-developed, forward projecting canines at front of jaws; 6-7 small and laterally flattened teeth, well-spaced, in anterior part of jaws along each side. Pharyngeal teeth (Fig. 1): upper bones with 20-22 teeth forming triangular patch, anterior row in each patch asymmetrically conical, remainder molariform; lower bone broadly Y-shaped, row of 10-11 laterally compressed elongated teeth, centre three teeth somewhat enlarged and asymmetrically conical, remainder molariform; 4-5 conical teeth extend uniserially on to anterior shank of the bone.

Caudal fin length 1.5-1.8 in head length; first dorsal spine 1.7-2.1 in snout length; second dorsal spine about one and a quarter times as long as first; ninth dorsal spine about one and a half times as long as first; length of longest dorsal ray 3.2-3.3 in head length; first anal spine 2.3-2.7 in first dorsal spine; third anal spine about three times as long as first; longest anal ray about equal to longest dorsal ray. Pectoral fins 1.8-2.1 in head length; origin of pelvic fins below lower base of pectoral fins; pelvic fins 2.1-2.7 in head length, first pelvic ray longest, reaching almost to vent.

Head naked except for a triangular patch of small predorsal scales on nape.

COLOUR: (from colour transparencies)

Male — body colour dark green, a deep blue row of scales midlaterally, below which is a row of light green or yellowish scales. Scattered indistinct

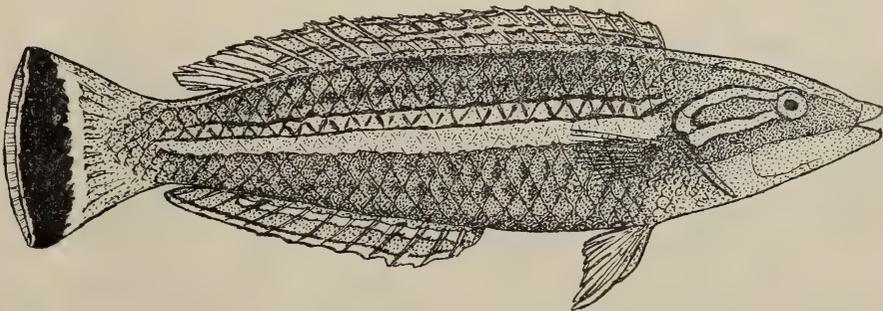


Fig. 7. *Pseudojuloides cerasinus* ♂ 75 mm SL.

blue spots on belly giving an overall blue diffusion. Head dark green above, a diffuse broad blue band passing from upper lip to just behind eye. A narrower dark blue band beginning behind eye, crossing preopercule, bending downwards across operculum and ending just above pectoral base. Lower part of head and cheeks blue. Iris green with a blue rim. Dorsal and anal fins dark green with blue margin, a second narrower blue line medially along fin. Caudal dark green at base, a narrow deep blue band separating the outer half which is black. Pectorals hyaline; pelvics dark green with blue markings. Colours in preservative are largely faded but in the male the dark blue midlateral line remains as a dusky line, the light green band below it somewhat lighter than the rest of the body. The dark outer margin and band on the caudal fin remain distinct.

Female — uniform reddish brown, fins translucent reddish brown.

DISTRIBUTION:

Hawaii, Loyalty Islands, Great Barrier Reef. John W. Shepard reports that this species also occurs in southern Japan and the Ryuku Islands.

***Pseudojuloides elongatus* n. sp.**

Figs. 4-6, 8-10; Table 1

Leptojulid sp. Masuda *et al*, 1975: p. 304 (Izu Oceanic Park, southern Japan)

HOLOTYPE:

NMNZ 6153, 123 mm SL, Nursery Cove (35°28.5'S, 174°44'E), Poor Knights Islands, New Zealand, 12 m, speared by A. M. Ayling 4 December, 1974.

PARATYPES:

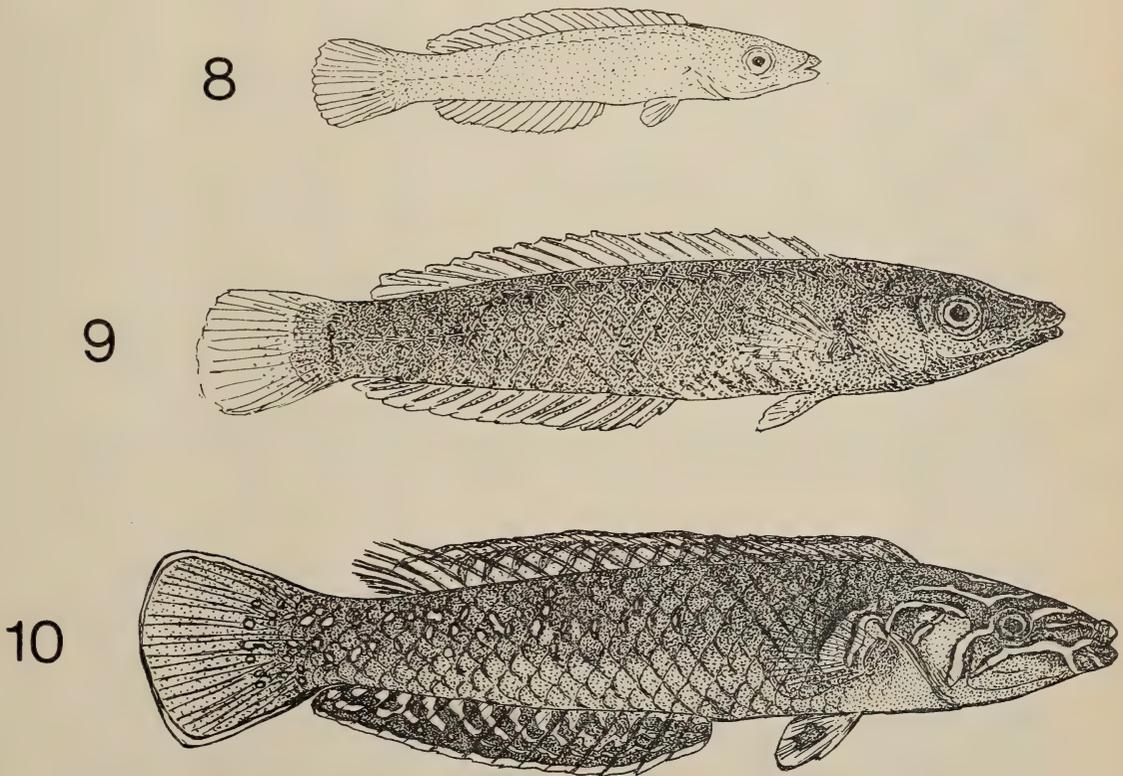
AMS I.17033-036, (1) 49.5 mm SL., North Head (33°49'S, 151°16'E), Sydney Harbour, 7 m, collected with rotenone by G. R. Allen, D. F. Hoese, G. McPherson, J. Paxton, D. Pollard, B. C. Russell, 6 April, 1974. AMS I.17735-008, (1) 58 mm SL., Camp Cove (33°50'S, 151°16'E), Sydney Harbour, 5 m, hand-netted by R. Kuitert 28 April, 1974. AMS I.17743-004, (3) 56.5-60 mm SL., Watsons Bay (33°50'S, 151°16'E), Sydney Harbour, 5 m, hand-netted by R. Kuitert 13-14 April, 1974. AMS I.17767-001, (6) 47.5-67 mm SL., between Watsons Bay and Parsley Bay (33°49.5'S, 151°16'E), Sydney Harbour, 5 m, hand-netted by R. Kuitert 5 May, 1974. AMS I.17800-001, (3) 66.5-75 mm SL., Sugarloaf Point (31°26'S, 152°32'E), Seal Rocks, 8 m, hand-netted by R. Kuitert 13 May, 1974. AMS I.18772-001, (1) 66 mm SL., Phillip Island (29°07'S, 167°56.5'E) Norfolk Island, 15 m, speared by B. C. Russell and A. Piper 20 September, 1975. BPBM 18022, (1) 67 mm SL., Balmoral Beach (33°49'S, 151°15'E), Sydney Harbour, 5 m, hand-netted by R. Kuitert 3 May, 1974. NMNZ 6155, (1) 106 mm SL., Nursery Cove, Poor Knights Islands, New Zealand, 15 m, speared by A. M. Ayling 18 April, 1974. NMNZ 6157, (1) 95 mm SL., Sandager's Reef (35°28.5'S, 174°44'E), Poor Knights Islands, New Zealand, 10 m, speared

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by A. M. Ayling 20 February, 1974. NMNZ 6156, (1) 126.5 mm SL., same data as holotype. NMNZ 6154, (1) 121 mm SL., Sandager's Reef, Poor Knights Islands, New Zealand, 10 m, speared by A. M. Ayling 2 February, 1975. TMBS 750819-1, (1) 115 mm SL., Igaya Bay (34°05'N, 124°10'E), Miyake-jima, Izu Islands, Japan, 14 m, screen netted by K. Meyer and J. T. Moyer. WAM P25110-001, (3) 88-97 mm SL., Kendrew Island (20°28.5'S, 116°32'E), Dampier Archipelago, Western Australia, 10 m, speared by G. R. Allen 2 November, 1974. WAM P25318-007, (1) 106.5 mm SL., Batavia wreck site (28°30'S, 113°44'E), Abrolhos Island, Western Australia, 8-10 m, speared by G. R. Allen 22 May, 1975. WAM P25318-008, (1) 112 mm SL., same data as previous specimen.

DIAGNOSIS:

A species of *Pseudojuloides* with the following combination of characters: dorsal rays IX, 12; pectoral rays i, 10; lateral jaw teeth 3-4 (upper jaw), 4-5 (lower jaw); predorsal scales absent; male olive green, back dusky, head



Figs. 8-10. *Pseudojuloides elongatus*. Fig. 8. Juvenile 28 mm SL. Fig. 9. ♀ 72 mm SL. Fig. 10. ♂ 78 mm SL.

TABLE 1

MORPHOMETRIC PROPORTIONS OF HOLOTYPE AND 5 PARATYPES OF
PSEUDOJULOIDES ELONGATUS

Proportions are as a percentage of the standard length

Registration number	NMNZ 6153	NMNZ 6156	NMNZ 6154	AMS I.17800-001	WAM P25318-007	TMBS 750819-1
Sex	♂	♂	♀	♂	♀	♂
Standard length (mm)	123.0	126.5	121.0	75.0	106.5	115.0
Depth of body	22.8	21.7	23.1	19.3	19.7	21.7
Width of body	12.6	12.3	14.9	10.7	8.5	13.0
Head length	29.3	30.4	29.3	30.0	30.0	29.1
Snout length	11.4	12.3	11.6	11.3	10.3	11.3
Eye diameter	4.3	4.2	5.4	5.0	5.6	5.2
Bony interorbital width	6.1	5.9	6.0	6.0	5.2	6.5
Length of upper jaw	7.1	7.7	6.6	7.7	6.1	5.7
Least depth of caudal peduncle	11.4	10.7	10.7	10.7	10.3	11.3
Length of caudal peduncle	9.4	8.7	9.5	8.7	12.2	11.7
Snout to origin of dorsal fin	28.1	29.3	29.8	28.7	28.6	27.8
Snout to origin of anal fin	52.0	50.6	52.5	48.7	49.8	49.6
Snout to origin of ventral fin	32.5	34.4	31.4	32.0	30.0	30.9
Length of caudal fin	19.9	20.6	19.0	20.0	19.7	20.9
Length of pectoral fin	14.2	14.6	14.9	14.7	15.5	13.0
Length of ventral fin	11.4	11.5	11.2	12.7	12.2	12.1
Length of first dorsal spine	3.7	4.0	3.9	3.3	3.8	4.3
Length of second dorsal spine	4.7	5.9	5.6	5.7	5.2	5.7
Length of last dorsal spine	8.1	6.9	9.1	8.7	8.0	8.7
Length of longest dorsal ray	10.6	10.7	10.7	11.3	10.3	11.7
Length of first anal spine	3.1	2.8	2.5	3.3	2.3	2.6
Length of second anal spine	4.3	4.6	5.2	5.0	4.7	4.3
Length of third anal spine	5.9	6.5	7.4	6.7	5.6	6.5
Length of longest anal ray	10.2	9.9	9.9	10.7	9.9	10.8
Length of dorsal fin base	58.1	58.1	58.7	56.0	59.2	60.4
Length of anal fin base	41.3	41.9	39.7	39.3	39.4	43.9

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brownish with four distinctive blue lines on each side, a dusky patch behind the pectoral fin base; female a uniform olive green.

DESCRIPTION:

Dorsal rays IX, 12; anal rays III, 12; pectoral rays i, 10; pelvic rays I, 5; principal caudal rays 14; gill rakers on first gill arch small, 9 + 7.

Body very elongate, depth in front of anal fin 4.4 (3.2-5.6) in SL, width 1.8 (1.5-2.5) in depth; head pointed, length 3.4 (3-3.4) in SL; snout including lips 2.5 (2.5-3.1) in head; eye diameter 2.7 (1.5-2.9) in snout; interorbital space convex, bony width 4.8 (4.5-5.8) in head; least depth of caudal peduncle 2.6 (2.7-3.3) in head; length of caudal peduncle 0.8 (0.7-1) in least depth of peduncle.

Upper jaw nearly reaching a point vertically below anterior nostril; single pair of pointed, well-developed, forward projecting canines at front of jaws; upper jaw with 3-4 small laterally flattened teeth, well-spaced in anterior part of jaw; lower jaw with 4-5 teeth similarly shaped and arranged. Pharyngeal teeth (Fig. 1): upper bones with 19-20 teeth forming triangular patch, anterior row in each patch asymmetrically conical, remainder molariform; lower bone broadly Y-shaped, posterior row of 9 laterally compressed elongate teeth, centre three somewhat enlarged and asymmetrically conical, remainder molariform; 4-5 small conical teeth extend uniserially onto anterior shank of bone.

Caudal fin length 1.5 (1.4-1.7) in head length; first dorsal spine 3.1 (2.2-4.4) in snout length; second dorsal spine about one and a half times as long as first; ninth dorsal spine about twice as long as first; length of longest dorsal ray 2.8 (2.6-3.4) in head length; first anal spine 1.2 (0.7-2.2) in first dorsal spine; third anal spine about twice as long as first; longest anal ray about equal to the longest dorsal ray. Pectoral fins 2.1 (1.3-2.6) in head length; pelvic fins 2.6 (2.3-3.2) in head length, first pelvic ray longest, reaching about two thirds of way from fin base to vent. See Table 1.

Head naked except for 4-5 diagonal rows of small scales on each side of head in forward projecting V-shaped patch above operculum; no midline predorsal scales.

COLOUR:

Male (from holotype) — Body colour olive green with lines of irregularly shaped turquoise blue spots and scattered irregular orange-brown patches on the dorsal scales; head brown above, orange-brown on the sides and green beneath chin with four blue lines on each side; the upper line originating above the eye and passing back to the upper origin of the opercular flap; the second beginning dorsally on the snout and passing back through the eye before slanting upwards to run around the upper edge of the opercular flap; the third line originating on the upper lip and immediately breaking into two, one part passing down around the lips, the other back through the eye and slanting abruptly downwards towards the isthmus; the fourth arching from the lower lip up past the lower rim of the

eye and down to the preopercular margin; on the operculum between the second and third lines is another short diagonal blue line that combined with the posterior portion of the second line separates a dusky patch on the opercular flap. Iris orange with a blue rim. A dusky patch behind pectoral fin base and an orange, blue bordered patch on the body behind this. Dorsal fin pale olive with red-brown diagonal lines and a narrow blue margin; anal fin red-brown with a prominent blue margin and a series of irregular diagonal blue lines. Caudal pale olive with a faint red rim, a blue line on upper and lower margins and blue spots at the base of the fin rays. Pectoral fins hyaline; pelvics blue with red-brown streaks. Colours in preservative are faded, body colour pale green, the blue lines on the male becoming dusky, but the dark back and dusky patch behind pectoral fin remain prominent.

Female — Uniform olive green with pale brown fins.

REMARKS:

This species may be distinguished from *Pseudojuloides cerasinus* by its extra dorsal soft ray; one fewer pectoral ray; slightly more elongate body; fewer jaw teeth; absence of predorsal scales, head scales being limited to a small patch on either side of the head above operculum; and differences in colour.

Male specimens from Western Australia and from Japan that we have examined are much more darkly pigmented on the back, some almost black compared with those from eastern Australia and New Zealand.

Named *elongatus* in reference to the elongate body form.

DISTRIBUTION:

North-eastern New Zealand, Norfolk Island, New South Wales, Western Australia and southern Japan.

ACKNOWLEDGEMENTS

We wish to thank Rudi H. Kuitert for his drawings of *Pseudojuloides* and Dr. John R. Paxton for his constructive criticism of the manuscript. Dr. Gerald R. Allen, Rudi H. Kuitert and Dr. John W. Shepard provided additional information and specimens of *P. elongatus*. Collecting trips in New Zealand were supported by the New Zealand University Grants Committee.

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A Juvenile Gempylid Fish, *Nealotus tripes*, from Eastern Australia

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ABSTRACT

The gempylid fish *Nealotus tripes* Johnson is newly recorded from eastern Australia, based on one juvenile specimen 49.8 mm standard length taken off Sydney. The juvenile has relatively larger, serrated fin spines than 24 larger specimens from Lord Howe Island. The species is also known from Papua-New Guinea, on the basis of a single specimen previously identified as *Promethichthys prometheus*.

INTRODUCTION

The fishes of the family Gempylidae are widely distributed in tropical and temperate waters of both the Atlantic and Indo-Pacific Oceans. The family consists of 14 genera and 15 species (Parin and Bekker, 1972) considered to be predaceous and mostly inhabiting deep waters. However, the systematics of the family is not understood comprehensively. There is also a paucity of life history information on these fishes.

Around Australia very few species of gempylid fishes have been recorded. Munro (1958a) reported only four species in his "Handbook of Australian fishes", *Leionura atun* (= *Thyrsites atun*), *Rexea solandri*, *Lepidocybium flavobrunneum* and *Ruvettus tydemani* (= *Ruvettus pretiosus*). Of these, both *Thyrsites atun* and *Rexea solandri* are important commercially. The other two are rather rare. Five more species, which are all uncommon, are recognised around Australia (Nakamura, unpublished data; Parin and Bekker, 1972). They are *Epinnula orientalis*, *Gempylus serpens*, *Rexea prometheoides*, *Nealotus tripes* and *Promethichthys prometheus*.

Nealotus tripes Johnson, a cosmopolitan species, has been recorded from Lord Howe Island (Ogilby, 1899; Allen *et al.*, 1976) and off north western Australia (Parin and Bekker, 1972). Recently, a juvenile specimen of the species was obtained off Sydney by F. R. V. Kapala, and is a new record of occurrence from the waters of the east Australian continental shelf. This paper compares the juvenile specimen with the specimens collected from Lord Howe Island and deposited in The Australian Museum (AMS, 23 specimens) and the Queensland Museum (QM, 1 specimen, Ogilby's type of *Machaerope latispinus*).

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MATERIALS AND METHODS

A juvenile specimen of *Nealotus tripes* (AMS I. 17887-006, 49.8 mm standard length) on which this description is based, was obtained from off Sydney, N.S.W. (34°13'S, 150°22'E) in a midwater trawl fishing from 0-145 m over a bottom of 165 m on May 6, 1974 by F. R. V. Kapala of New South Wales Fisheries. Twenty-four specimens collected from the beach at Lord Howe Island were used for the comparison (AMS IA. 1398-1404, I. 4121-4123, I.4312, I.5189, I.5590-5595, I.5597, I.5598, I.7858, I.7859, I.10700; 130.5-236.1 mm in standard length and QM 11/74 137.5 mm in standard length). The methods of measurement follow Hubbs and Lagler (1949). The drawings were made with the aid of a binocular microscope and vertebral counts from X-rays.

DESCRIPTION OF THE JUVENILE

Counts, measurements and description of the juvenile specimen (1) are followed by those of the Lord Howe Island specimens (24) in parentheses. Dorsal fin rays XX, I, 18+2 (XIX-XXI, I, 16-19+2); anal rays II, 16+2 (II, 15-19+2); pectoral rays 14 (12-14); pelvic rays I,1(I,1); gill-rakers on first arch 5+1+11 (5-8+1+10-17); branchiostegals 7 (7); intramuscular bones — (31-34); vertebrae including urostyle 37 (20+17=37 or 21+16=37); pyloric caeca — (8).

The following measurements are expressed as percent standard length: head length 28.1 (25.6-28.3); snout to insertion of first dorsal 24.7 (24.0-26.4); snout to insertion of second dorsal 75.7 (73.1-75.9); snout to insertion of pectoral 26.7 (26.3-28.5); snout to insertion of pelvic 26.3 (27.3-31.4); snout to anus 72.5 (67.2-71.7); snout to insertion of anal 73.4 (66.9-76.2). The following measurements are expressed as percent of head length: body depth 41.4 (43.0-56.2); body width 17.9 (12.0-31.2); snout length 35.0 (36.2-42.9); upper jaw length 42.0 (43.6-48.2); orbit length 25.0 (19.4-23.4); interorbital width 15.0 (17.1-20.6); pectoral fin length 43.6 (37.9-60.5); pelvic spine length 37.1 (7.8-15.9); length of longest first dorsal ray (spine) 30.7 (27.7-33.3); length of longest second dorsal ray (soft ray) 31.5 (25.8-34.0); length of first

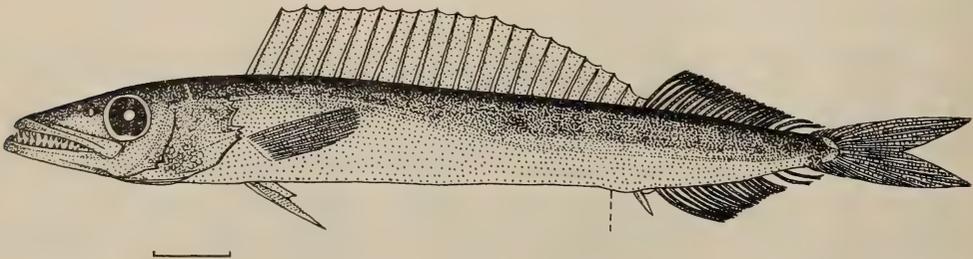


Fig. 1. Juvenile of *Nealotus tripes* (AMS I. 17887-006) obtained from off Sydney. Ventral broken. Line shows the position of anus. Scale equals 5 mm.

GEMPYLID FISH FROM AUSTRALIA

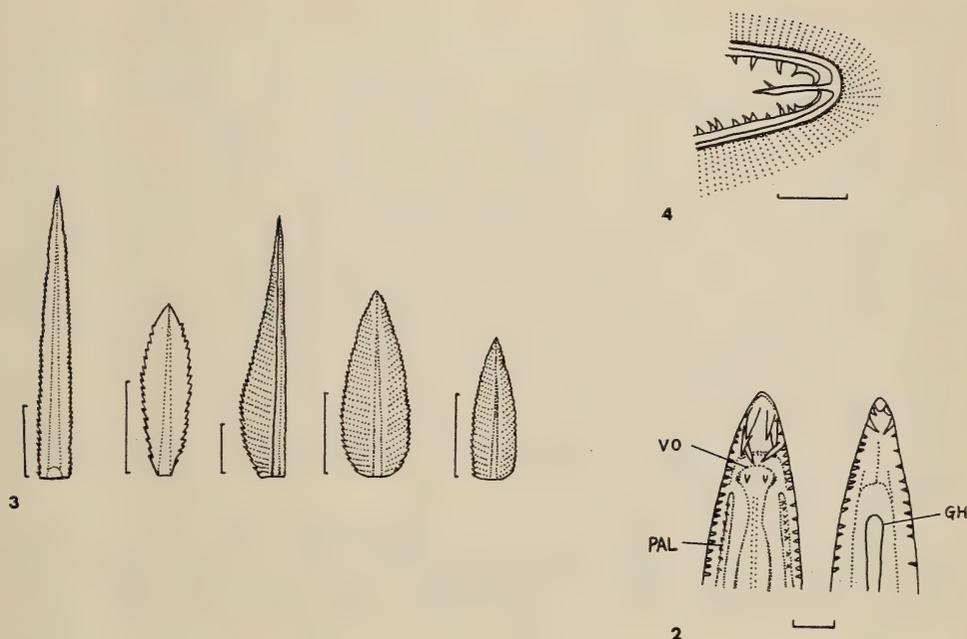


Fig. 2. Inside of upper (left) and lower (right) jaws of the juvenile. VO: vomer, PAL: palatine, GH: glossohyal. Scale equals 1 mm.

Fig. 3. Outer surface of first gill arch (left side) of the juvenile. Scale equals 1 mm.

Fig. 4. Spines in anterior view of the juvenile. From left to right: first dorsal spine, 20th dorsal spine, pelvic spine of left side, first anal spine and second anal spine. Each scale indicates 1 mm respectively.

anal spine 15.0 (5.4-14.2); length of longest anal ray (soft ray) 29.2 (24.5-35.4); caudal peduncle depth 14.3 (14.3-20.6).

Body elongate and compressed (Fig. 1). Greatest body width less than greatest body depth. Upper profile of head slightly convex from tip of snout to insertion of first dorsal fin (nearly straight in Lord How Island specimens). Snout less than twice as long as eye (slightly more than twice in larger specimens). Jaws bluntly conical; lower jaw projecting forward beyond tip of snout. Mouth large, maxillary scaleless, extending backward slightly beyond front edge of pupil. Three fangs on each side of upper jaw near tip of snout. A pair of canines near symphysis of lower jaw. A pair of minute teeth on vomer (vomer edentulous in larger specimens). A single series of small teeth on palatines (Fig. 2). Eye large, almost round. Infraorbital space very narrow, its least width less than diameter of pupil. Interorbital space narrower than eye. Lower part of preopercle armed with 2 spines. Several spines on hind part of opercle and subopercle (spines inconspicuous on hind part of opercle and subopercle in larger specimens). Lateral line single from near upper margin of opercle almost straight backward and

gradually downward from middle of first dorsal fin to base of caudal fin. Scales small, cycloid, imbricate in regular rows, but rather deciduous. Dorsal fin inserted above upper margin of opercle, base of first dorsal fin about three times as long as base of second dorsal fin. Soft rays of second dorsal fin preceded by a small spine, almost the same as soft rays of anal fin in shape and size. A flattened, dagger-shaped, serrated spine followed by a small, embedded, serrated spine between anus and insertion of soft anal (a dagger-shaped, smooth spine followed by a small, embedded, smooth spine in larger specimens). Soft rays of second anal fin inserted under third soft ray of second dorsal fin. Finlets 2 in dorsal and anal fins. Pectoral fin rather long, extending to vertical from base of seventh dorsal spine. Pelvic fin consists of a long flattened spine with serration followed by a soft ray (pelvic fin reduced to a small, single, smooth spine followed by a minute soft ray in larger specimens), inserted below origin of pectoral fin. All fin spines (20 first dorsal, 1 second dorsal, 1 pelvic and 2 anal) flattened and serrated more or less as shown in Fig. 3 (all fin spines smooth, elongated, dagger-shaped in larger specimens). Gill-raker at angle of first arch long, Y-shaped, other rakers short and acute (Fig. 4).

Colour of juvenile specimen fixed by formalin and preserved in ethanol, head and dorsal side of body dark brown; ventral side of body pale brown; pectoral fin dark brown; other fins pale brown. All fin membranes pale.

DISCUSSION

There have been few records of *Nealotus tripes* from waters around Australia. Some twenty specimens were recorded from Lord Howe Island (Ogilby, 1899; Allen *et al.*, 1976). Several specimens were recorded from off north western Australia (Parin and Bekker, 1972). There is no record from around New Zealand (Whitley, 1968), although four specimens were known from Kermadec Island (Waite, 1910). There is hitherto no record from around Papua-New Guinea (Munro, 1958b, 1967; Kailola, 1971, 1973, 1974). However, *Promethichthys prometheus* (Cuvier), recorded from Papua-New Guinea on the basis of two specimens by Munro (1958b) as species number 1128, represents two species. The Laughlan Island specimen (C.S.I.R.O. B.620) is *Nealotus tripes*, while the Collingwood Bay specimen (C.S.I.R.O. C.1616) is *Promethichthys prometheus*. The juvenile described here is a new record of *Nealotus tripes* to the waters of the east Australian continental shelf. This species is rather rare and distributed in chiefly circum-tropical and sub-tropical zones throughout the world.

The pelvic fin consists of a spine and a soft ray in both the juvenile fish and specimens from Lord Howe Island, although Matsubara and Iwai (1952) described the ventral reduced to a single smooth spine. The senior author re-examined the materials of Matsubara and Iwai deposited in Kyoto University and found that they missed a minute soft ray because of the bad condition of the materials. Strasburg (1964) gave a spine and 0.2 (mostly 2) soft rays as the pelvic fin elements in postlarval stages. The relative length of the pelvic spine (expressed as percent of standard length) decreases with growth (Fig. 5).

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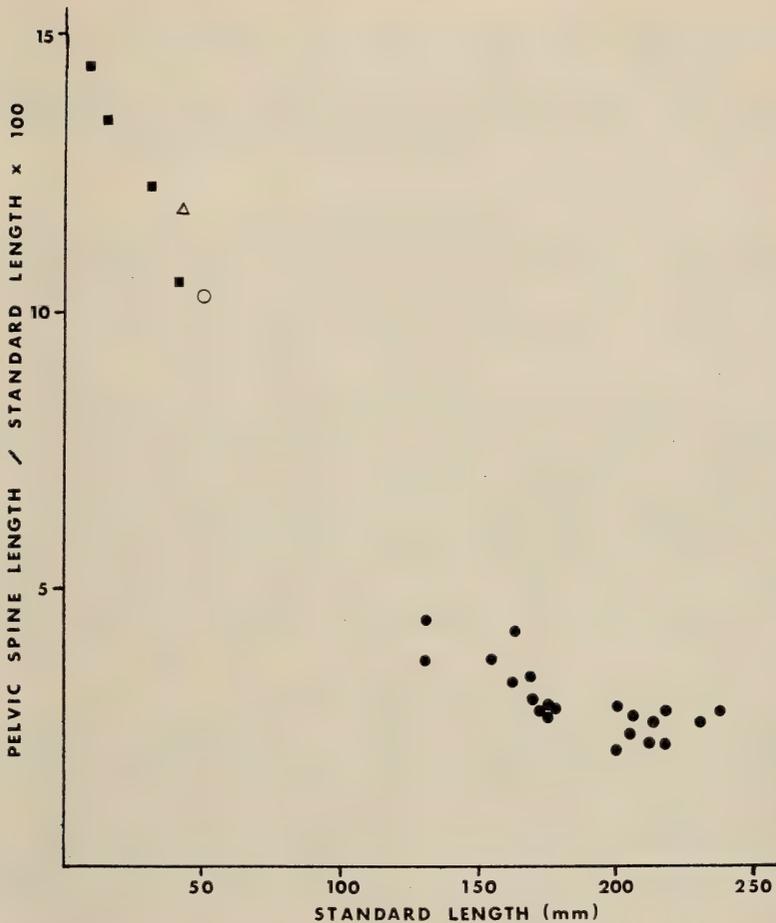


Fig. 5. Relative length of pelvic spine in *Nealotus tripes*. Pelvic spine lengths are plotted against the standard length. Squares: after Strasburg (1964); triangle: AMS IA.1424, from Lord Howe Island (smallest specimen of the Australian Museum collection); open circle: juvenile from off Sydney; closed circles: Lord Howe Island specimens.

The second anal spine is embedded along the ventral margin of the body, following the erected longer first anal spine in both juvenile and fishes from Lord Howe Island, although both the first and second anal spines are erected in Fig. 11 of Matsubara and Iwai (1952). The second embedded anal spine is thought to be one of the specific characteristics (adult phase) of *Nealotus tripes*. According to the figures shown by Strasburg (1964), both the first and second anal spines are erect in the postlarval stage.

Comparing our juvenile with a juvenile of *Nealotus tripes* (41.5 mm in standard length) described by Strasburg (1964) from southwest of Hawaii, both

are similar in external appearance. But they show some differences, such as head contour ("almost straight" of the former to "round" of the latter), spines on opercular and subopercular region (several spines on opercle and subopercle of the former to two opercular spines only of the latter) and the condition of the second anal spine (embedded of the former to erect of the latter).

ACKNOWLEDGEMENTS

We acknowledge with thanks the help of the captain and crew of F.R.V. Kapala of New South Wales State Fisheries for obtaining the juvenile specimen. We are very grateful to Roland J. McKay of the Queensland Museum and Ian S. R. Munro of C.S.I.R.O., Division of Fisheries and Oceanography, Cronulla for their permission to examine specimens deposited there. We wish also to thank Reiko K. Nakamura for her help.

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Sex Change in the Wrasse *Pseudolabrus gymnogenis* (Labridae)

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ABSTRACT

In *Pseudolabrus gymnogenis* there is a sexually undifferentiated primary germ cell, here referred to as a protogonium that divides mitotically to produce a slightly smaller yet similar deuteronogonium cell. At this stage the germ cells differentiate, prospective oocytes enter meiotic prophase and prospective spermatogenic cells begin a phase of chromatin condensation prior to meiosis. Meiotic stages and maturation stages of oocytes and sperm cells are described. The only evidence of intersexuality in females was seen from two specimens where small cysts of primary spermatogonia were located in the lamellar epithelium although this was not regarded as evidence for an impending sex inversion. A few meiotic stage oocytes were found in males and many males displayed remnants of degenerate mature oocytes.

INTRODUCTION

The origin of primordial germ cells from the extra embryonic endoderm or mesoderm and the early development of the teleost gonad has been investigated by many authors (D'Ancona, 1945; Okkleberg, 1921). It has been well established that primordial germ cells undergo a period of rapid mitotic increase when they reach the gonadal primordium. However, the terminology of the early derivatives of primordial germ cells is confusing.

In the teleost *Oryzias latipes*, Satoh and Egami (1972) reported mitotic divisions of the primordial germ cells in sixteen day old fry. D'Ancona (1945) believed the primordial germ cells (which he called protogonia) multiplied for a number of generations, giving rise to smaller daughter cells or deuteronogonia. As the deuteronogonia (as defined by D'Ancona, 1945) were believed to divide mitotically to produce oogonia or spermatogonia, then this term is equivalent to primary germ cell used by other workers, such as Barr (1963), Henderson (1962) and Ahsan (1966).

In the lamprey, *Lampetra planeri*, Hardisty (1965) recognised three forms of undifferentiated gonial cells, a primordial germ cell, a protogonium and a deuteronogonium with total diameters of 22.5, 12.9 and 10.2 μm respectively. Although the dimensions of the three gonia differed, Hardisty (1965) indicated

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TABLE I
SUMMARY OF THE NUMBER AND SIZE RANGE OF SPECIMENS COLLECTED THROUGHOUT THE YEAR

Locations Sampled	Juveniles		Mature Females		Males	
	No.	SL Range	No.	SL Range	No.	SL Range
JANUARY Ulladulla; Jervis Bay			2	200-212	21	204-255
FEBRUARY Batemans Bay	1	119	2	156-169		
MARCH Cronulla; Long Reef	33	54-124	2	155-158	1	208
APRIL Sydney Harbour; Long Reef	42	38-103	4	158-196	1	208
MAY Cronulla					12	215-275
JUNE Sydney Harbour; Long Reef	11	82-114	3	130-194	14	213-234
JULY Cronulla; Long Reef; Sydney Harbour	6	84-105	3	130-152	8	225-283
AUGUST Long Reef; Palm Beach; Sydney Harbour	11	91-120	10	140-220	17	193-246
SEPTEMBER Long Reef	3	64-70	1	155		
	107	38-124	27	130-220	74	193-283

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similar histological characteristics such as a prominent nucleolus, a nuclear membrane and a relatively chromatin-free reticulum. He showed that the primordial germ cells divide to form the small protogonia which in turn keep dividing to produce either more protogonia or the smaller deuteroogonia. The deuteroogonia then enter meiotic prophase in definitive females, although they still retain the capacity to divide mitotically.

Pseudolabrus gymnogenis is the most common species of labrid found along the rocky foreshores of the N.S.W. Central Coast. However little is known of its reproductive biology. This paper describes only the development of germ cells in *P. gymnogenis*.

MATERIALS AND METHODS

Thirty-two collecting stations were made between 29th December, 1972, and 3rd October, 1973 from Long Reef, Sydney Harbour, Cronulla, Palm Beach, Jervis Bay, Ulladulla and Batemans Bay, N.S.W. (Table 1).

Most specimens were collected by spearfishing. A fine mesh drop trap and a wire trap 4 feet long, 2 feet in diameter and enclosed in one inch wire mesh were also used. Badly damaged specimens were rejected.

Since fixation was not always possible immediately after death, post mortem changes were inevitable in some instances.

All fish were preserved in 10% formal saline. The right lobe of two mature ovaries, and the entire gonad of 10 juveniles were fixed in sea water Bouin's solution. The middle portion of one lobe from each gonad was embedded in paraffin wax. Testes and immature females were sectioned at 5 μ m, mature oocytes filled with large yolky masses crumbled if sectioned at less than 10 μ m.

Seven slides were prepared from each gonad, five were stained in Delafield's haematoxylin and alcoholic eosin and were used for the standard identification of oocyte and sperm maturation stages. The remaining two slides were later selected for more specific staining techniques. Feulgen proved to be successful for the identification of mitotic and meiotic division stages. Azan was useful for the differentiation of oocyte stages and spermatogenic stages. Periodic Acid Schiff (PAS) was used to test for mucopolysaccharides in oocytes. Nile Blue A localised lipofuscin pigments in testis tissue.

Sections of formalin fixed tissue from 10 males and 5 females were embedded in gelatin, and sectioned at 8 μ m (usually 10 μ m for mature ovaries) on a freezing microtome. Two slides were prepared, one was stained with Sudan Black B, the other was subjected to the Schultz test for cholesterol (Lillie, 1965).

RESULTS

UNDIFFERENTIATED GERM CELLS IN *P. gymnogenis*

In *Pseudolabrus gymnogenis* protogonia and deuteroogonia (as defined by Hardisty) have been found in females and males. The interphase protogonium of

TABLE 2
SIZES OF GERM CELLS AND THEIR NUCLEI FROM OVARIAN TISSUE
(approximate ranges only are given for mature oocytes)

	TOTAL CELL MEASUREMENTS % Increase			NUCLEUS			CYTOPLASM NUCLEUS RATIO
	Diameter	Range	Increase	Diameter	Range	Increase	
PROTOGONIA	7.4	6.2- 6.9		5.5	5.1- 6.0		1.3
INTERPHASE DEUTEROGONIA	6.5	6.2- 6.9	—12%	3.9	3.3- 4.6	—28%	1.6
MEIOTIC OOCYTES							
(a) LEPTOTENE	6.92	6.1- 7.3	5%	4.2	3.4- 4.6	2%	1.6
(b) ZYGOTENE		not resolved		5.0	4.6- 5.9	19%	—
(c) PACHYTENE	8.0	6.9- 9.7	17%	5.9	5.4- 6.5	20%	1.3
(d) LATE PACHYTENE/ EARLY DIPTOTENE	10.9	8.0-14.5	36%	6.4	6.2- 6.6	9%	1.6
(e) LATE DIPTOTENE		variable		20.0	15.0-30.0		
MATURING OOCYTES							
(a) PERINUCLEOLAR		55- 90			30-40		
(b) YOLK VESICLE		120-160			50-70		
(c) PRIMARY YOLK		210-260			70-80		
(d) SECONDARY YOLK		330-360			80-90		
(e) TERTIARY YOLK		330-360			80-90		
(f) MATURE		about 600					

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TABLE 3
SIZES OF GERM CELLS AND THEIR NUCLEI FROM TESTICULAR TISSUE

	TOTAL CELL MEASUREMENTS			NUCLEUS			CYTOPLASM NUCLEUS RATIO
	Diameter	Range	% Decrease	Diameter	Range	% Decrease	
PROTOGONIA	7.5	7.1-7.6		5.6	5.2-5.9		1.3
INTERPHASE DEUTEROGONIA	7.1	5.9-8.0	5%	4.1	3.4-4.7	25%	1.7
LATE STAGE DEUTEROGONIA or PRIMARY SPERMATOGONIA	5.1	4.7-5.3	30%	3.4	3.1-4.2	17%	1.4
SECONDARY SPERMATOGONIA	3.9	3.6-4.6	23%	2.8	2.5-3.2	16%	1.3
PRIMARY SPERMATOCYTES	3.6	3.1-3.8	7%	2.3	2.1-2.6	16%	1.5
SECONDARY SPERMATOCYTES		not resolved		1.9	1.6-2.4	17%	
SPERMATIDS		not resolved		1.4	1.1-1.5	28%	
SPERMATOZOA		not resolved		1.0	0.8-1.3	25%	

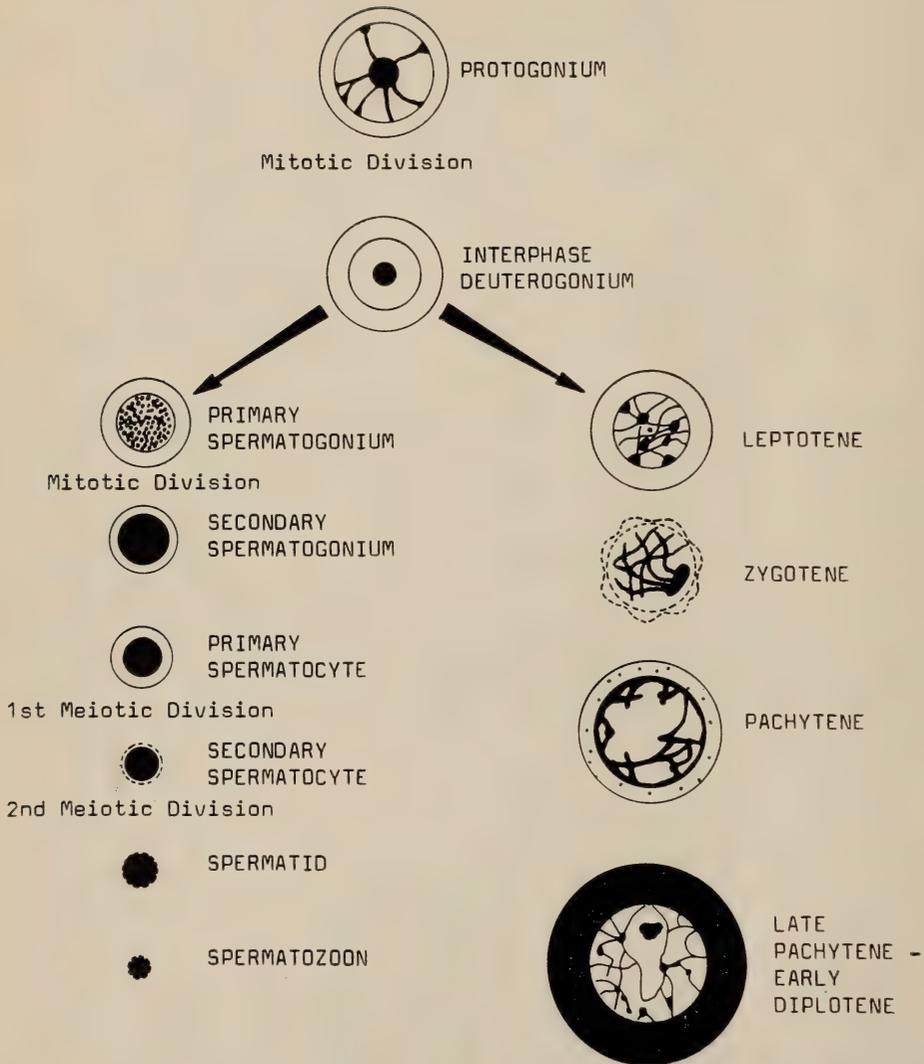


Fig. 1. Diagrammatic representation of the germ cell stages of *P. gymnogenis*. Mature oocyte stages are not represented.

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P. gymnogenis is a large cell with an average nuclear diameter of 5.5-5.6 μm , total diameter of 7.4-7.5 μm , and large nucleolus of 1.4 μm and a well defined nuclear membrane (Table 2 and 3). The reticulum is free of chromatin except for a number of chromatin bridges extending from the nucleolus to the nuclear membrane. Small clumps of chromatin may be seen around the nuclear periphery. Prior to their mitotic division the protogonia lose the nucleolus and the chromatin bridges disappear as the reticulum develops a high number of chromatin granules. During mitotic prophase the nucleus elongates slightly and condensed chromosomes are occasionally seen within the cell membrane, (Figure 2).

Deuterogonia result from the mitotic division of protogonia and may be distinguished from the latter by the higher cytoplasm/nucleus ratio (of 1.6). The average nuclear diameter ranges from 3.9-4.1 μm and the total diameter is 6.59-7.19 μm . Interphase deuterogonia with a distinct nucleolus and clear nuclear reticulum are not often seen.

At this stage the germ cells differentiate, prospective oocytes enter meiotic prophase, and prospective spermatogenic cells begin a phase of chromatin condensation prior to meiosis (Figure 1).

OOCYTE DEVELOPMENT

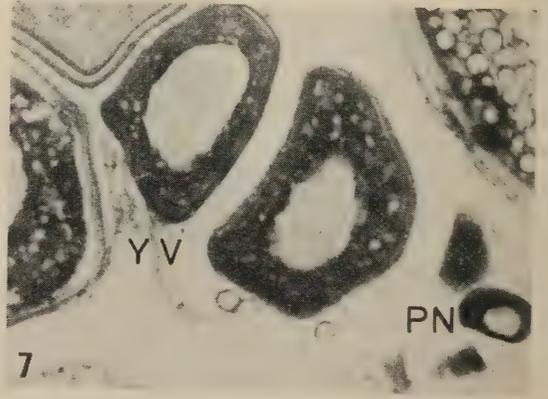
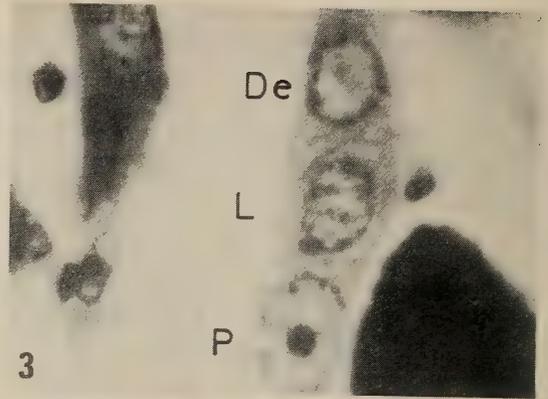
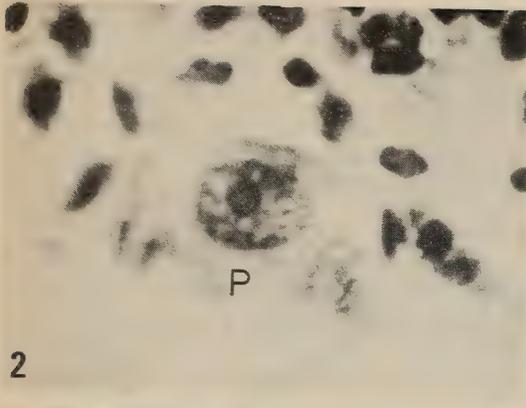
Meiotic Stages

Although meiotic prophase oocytes were not recorded for counts of ovarian maturity, details of their morphology are necessary for the identification of oocyte remnants in testes. The following description of *P. gymnogenis* was made from sea water Bouin fixed material.

Although protogonia are common in juvenile females (Figure 3) interphase deuterogonia are not often seen as they rapidly enter meiotic prophase. In what may be described as the leptotene stage the nucleolus rapidly decreases in size, there is an increase of coarse peripheral chromatin and fine chromatin threads appear across the reticulum. The outline of the nuclear membrane tends to become less distinct.

In zygotene, the chromosome threads progressively lengthen, thicken and stain intensely. The progression from leptotene to early zygotene is seen as a sudden concentration of chromatin to form a large mass of nuclear material in the centre of the nucleus (Figure 4). The nuclear membrane is extremely faint. As the nuclear diameter increases, the chromosomes spread out across the reticulum and may be resolved as long thin strands. In the European Lamprey, in many zygotene oocytes, a number of chromosomes at one pole of the nucleus condense into a small crescentic mass, called a synapsis figure by Hardisty (1965). In the other stages of zygotene, the chromosomes condense and orientate towards the faintly defined nuclear periphery. Later stages develop a variable ovoid configuration which gains a more extreme expression in pachytene.

While the leptotene nucleus shows little increase in size over that of the interphase deuterogonia (3.9 μm to 4.2 μm), this is a 19% increase at the



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zygotene stage (5.0 μm). The cytoplasm of the zygotene oocyte does not stain well with haematoxylin and the presence of many nuclei in very close proximity would suggest that the nucleus has expanded at a faster rate than the total cell diameter.

The most sharply defined nuclear configuration is described as pachytene (nuclear diameter 5.9 μm , total diameter 8.0 μm) which is marked by the condensation of chromatin around the nuclear periphery.

The chromosomal threads contract and are predominantly restricted to the periphery of the nucleus. At the points where the chromosomal threads intersect or are in contact with the inner surface of the nuclear membrane, there are often distinct chromatin granules (Figure 5). The nucleus at pachytene shows 20% increase over the zygotene stage, while the cell diameter has only increased by 17% over the leptotene stage.

Hardisty (1965) regarded the reappearance of the nucleolus as marking the transition to the pachytene stage. In *P. gymno-genis* the nucleolus is not evident until late pachytene when it appears as a small round structure near the nuclear periphery. The transition from late pachytene to early diplotene is difficult to distinguish, although the most obvious change is the acceleration of cytoplasmic growth (36% over pachytene, 18.0-10.9 μm) and its rapid increase in basophilia. The nucleus is 6.4 μm in diameter.

The final stage in oocyte proliferation is the development of diplotene oocytes. This stage is marked by a further rapid increase in nuclear diameter to 15-30 μm . The cytoplasm also increases at a comparable rate, although the cell shape is variable. The nuclear reticulum is more finely granular than in late pachytene — early diplotene stage oocytes, and a very large basophilic nucleolus is present (Figure 6).

Nuclei up to the pachytene stage are always present in cysts scattered along the lamellar epithelium. Late pachytene — early diplotene oocytes are invariably located around the interior periphery of these epithelial cysts while the late diplotene oocytes are always free of the lamellar epithelium. They are scattered by a surrounding layer of connective tissue, which contributes to the formation of the granulosa layer in mature oocytes.

Fig. 2. A mitotic prophase protogonium (P) in a testis.

Fig. 3. Protogonium (P) in an ovary. A late stage deutergonium (De) and a Leptotene nucleus (L) are also shown.

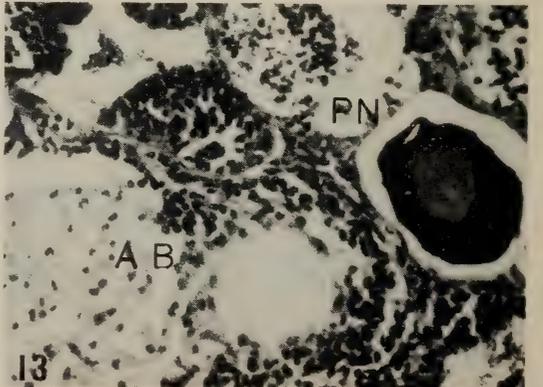
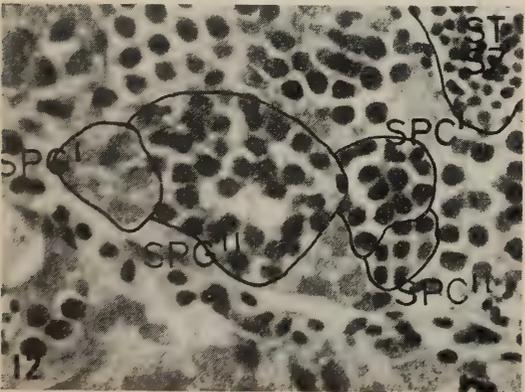
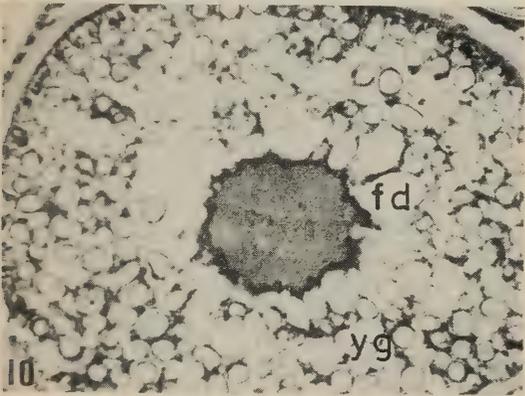
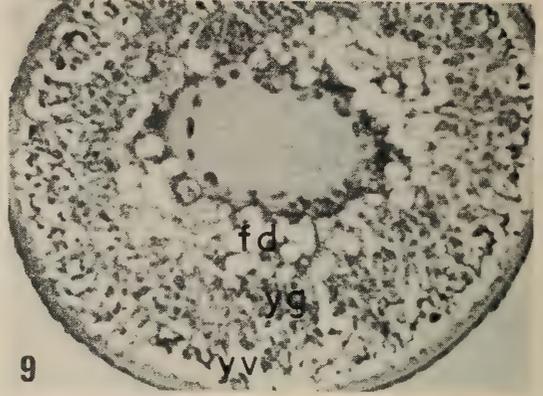
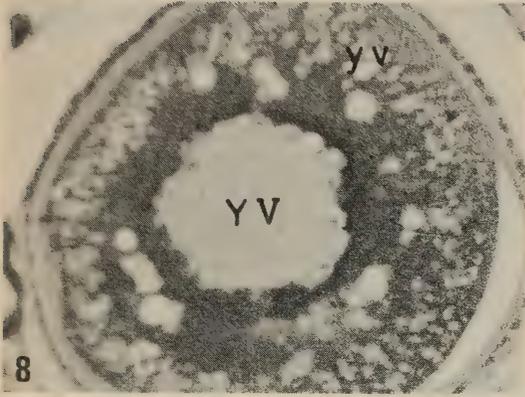
Fig. 4. Early zygotene (EZ) and typical zygotene (Z) nuclei. In zygotene, synapsis figures are often shown.

Fig. 5. Pachytene nuclei (PT) showing a marked peripheral condensation of chromatin.

Fig. 6. Late pachytene/early diplotene (PT/ED) oocyte. The nucleolus (n) is reappearing.

Fig. 7. Early yolk vesicle oocyte (YU). Perinucleolar oocyte (PN).

(Figs. 2-6 x 3,300; Fig. 7 x 370)



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Maturation Stages

(a) *Perinucleolar Stage* (Figure 7)

This stage is rarely seen in juveniles and represents the first stage of oocyte maturation, the nuclear diameter ranges from 30-40 μm . The cell shape is far more regular than that of diplotene oocytes and the nucleoli become closely associated with the nuclear periphery and change from a spherical to a hemispherical or elliptical configuration.

(b) *Yolk Vesicle Stage* (Figures 7 and 8)

Oocytes at this stage usually have a nuclear diameter range of 40-50 μm , a total diameter range of 120-160 μm and are characterised by the appearance of PAS positive yolk vesicles in the outer half of the cytoplasm. The vesicles first appear as small, scattered vacuoles (often containing basophilic granules) which become organised into a relatively distinct ring around the oocyte periphery, the largest vesicle reaching about 7 μm in diameter. Almost immediately after the appearance of the yolk vesicles in the outer cytoplasm, small fatty droplets develop in the inner half of the cytoplasm. The fatty droplets increase in size and coalesce with others to form a ring of droplets around the nucleus, with individual droplets up to 10 μm .

(c) *Primary Yolk Stage* (Figure 9)

Oocytes with a nuclear and total diameter of 70-80 μm and 210-260 μm respectively, develop small eosinophilic yolk globules between the yolk vesicles. These globules are first noticed with a diameter of 3-5 μm and they rapidly increase to 8-10 μm while still restricted to the outer half of the cytoplasm.

(d) *Secondary Yolk Stage* (Figure 10)

During this stage the yolk globules rapidly increase in size to a maximum of 15 μm . The nucleus diameter and total diameter increases to 80-90 μm and 330-360 μm respectively. As the globules increase in size they occupy all the remaining free cytoplasm. The largest fatty droplet increases to a maximum of 25 μm . The expansion of the yolk and fat within the cytoplasm restricts the yolk vesicles to a narrow band around the periphery of the cytoplasm, the largest vesicle being reduced to about 6 μm .

Fig. 8. Yolk vesicle stage oocyte (YU) with peripheral yolk vesicles (YU).

Fig. 9. Primary yolk stage oocytes with yolk vesicles (yv) and yolk globules (yg). Fatty droplets (fd) appear around the nucleus.

Fig. 10. Secondary yolk stage oocyte with fatty droplets (fd) and yolk globules (yg). In tertiary yolk stage, yolk globules begin to rupture.

Fig. 11. Interphase deuterogonium (De).

Fig. 12. Spermatogenic maturation stages. Primary spermatogonia (SPG I), Secondary spermatogonia (SPG II), primary spermatocytes (SPC I), secondary spermatocytes (SPC II), spermatids (ST) and spermatozoa (SZ).

Fig. 13. Perinucleolar oocyte (PN) and atretic bodies (AB) in a testis.

(Figs. 8, 9, 10, 13 x 370; Fig. 11 x 3,300; Fig. 12 x 700)

(e) *Tertiary Yolk Stage* (Figure 10)

Oocytes at this stage are of similar dimensions to secondary yolk oocytes. The yolk globules rupture, releasing their finely granular basophilic contents into the cytoplasm.

(f) *Mature Oocytes*

The final stage in oocyte maturation occurs when the external membrane of the tertiary yolk oocyte rapidly expands to a diameter of about 600 μm . The increase in cytoplasmic volume decreases the density of the free yolk material. The result of this is a large translucent oocyte with a single large fat droplet up to 150 μm . These mature oocytes are released into the ovarian lumen.

SPERMATOGENESIS

(a) *Protogonia, Deuterogonia and Primary Spermatogonia*

Protogonia are seen in the interstitial areas and are similar to those seen in ovaries. These cells divide to form an interphase deuterogonia which in testicular tissue rapidly become basophilic, although the nucleolus and the distinctive cytoplasm/nucleus relationship (ratio of 1:6) are evident (Figure 11). It is an increase in basophilia that marks the male orientation of deuterogonia. In this study, this basophilic stage is referred to as the primary spermatogonium stage. In the later stages of primary spermatogonium chromatin condensation, there is a further increase in basophilia as well as a reduction in the nucleus diameter from 4.1 μm to 3.4 μm , and the total cell diameter from 7.1 to 5.1 μm . The presence of a primary spermatogonial stage prior to the regular, the intensely basophilic spermatogonial phase, reported by most workers, has been described in only two teleosts, *Couesius plumbeus* (Ahsan, 1966) and *Salvelinus fontinalis* (Henderson, 1962). In both these teleosts, in the primary germ cell, there is a prominent nucleolus and a relatively clear nuclear reticulum.

Occasional mitotic divisions are seen among cysts of late primary spermatogonia to produce secondary spermatogonia.

(b) *Secondary Spermatogonia*

Secondary spermatogonia represent a marked increase in haematoxylin affinity over the latter stages of the primary spermatogonial chromatin condensation (Figure 12). The nucleus is slightly ovoid with a mean diameter of 2.8 μm and a total cell diameter of 3.9 μm . The condensed chromatin occupied the entire nucleus and the presence of a nucleolus is only evident with Feulgen staining which is not specific for RNA.

As reported by Ahsan (1966) the divisions of the primary spermatogonia are slow or infrequent and the large cysts of secondary spermatogonia are produced by numerous mitotic divisions within the cyst.

(c) *Primary Spermatocytes*

Within many cysts of secondary spermatogonia a few nuclei show a further decrease in nuclear diameter to the primary spermatocyte stage. They have a

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nuclear and total diameter of 2.3 μm and 3.6 μm respectively. No nuclear detail is evident (Figure 12). Apart from the spermatozoa, these cells are the most commonly seen in the testis.

Meiotic figures are often seen within primary spermatocyte cysts. Leptotene is characterised by a slight increase in nuclear diameter from the primary spermatocyte average of 2.3 μm to 2.6 μm . If a nucleolus is seen it is very small. Zygotene figures are not common. They lack a nucleolus, return to the diameter of interphase spermatocytes, and demonstrate fine and clearly demarkated chromatin threads that extend across the nucleus. The chromosomes at the pachytene stage are difficult to resolve. They appear in 5-6 large clumps which are radially arranged in a star-like pattern. Metaphase spreads are common.

(d) *Secondary Spermatocytes*

Secondary Spermatocytes have a nuclear diameter of 1.9 μm (Figure 12). The chromatin is highly condensed and is often located near meiotic prophase figures. These cells divide (Meiosis II) to form spermatids.

(e) *Spermatids*

Spermatids have a nuclear diameter of 1.4 μm (Figure 12). They are distinguished from secondary spermatocytes by their smaller nuclear diameter and crimson staining with Azan (in contrast to yellow-orange) and from spermatozoa by their larger nucleus, and absence of a flagellum.

(f) *Spermatozoa*

Spermatozoa have a nuclear diameter of 1.0 μm and a fine long flagellum. Often they appear within the spermatogenic lobules (or tubules) in "parachute shaped" clumps (Pollard, 1972), although they are usually distributed with varying densities within the lobules (Figure 12).

INTERSEXUALITY

Spermatogenic Cells in Ovaries

The only evidence of intersexuality in females was seen in two specimens (169 and 196 mm) from the April sample in which a few small cysts of primary spermatogonia were found. They were always located in the lamellar epithelium and were sometimes adjacent to groups of early meiotic prophase oocytes. The cysts were rare and there was no evidence to suggest an impending sex inversion as perinucleolar oocytes were developing and the colour pattern was quite normal. It is more likely that these cells were formed during the period of oocyte proliferation that appears to occur around April when deuterozoa normally differentiated to leptotene oocytes. However, a few entered the male germ cell line.

Oocyte Remnants in Testes

Early meiotic stage oocytes were only found in one male of 206 mm SL with a prominent anal bar, no red on the sides and 15% area of primary spermatogonia.

Figure 13 shows an intact diplotene or perinucleolar oocyte surrounded by testicular tissue. The empty vacuoles located around this oocyte were probably formed around oocytes which have since been resorbed. In this male, the vacuoles are surrounded by connective tissue; in established males similar structures are usually filled with spermatogenic stages.

The only other oocyte remnants were of collapsed mature oocytes and most commonly, atretic bodies (or atretic oocytes) that remain throughout the testicular phase of the gonad (Figure 13). Atretic bodies are formed only from oocytes in the yolk globule stage of development. Upon atresia, the granulosa cells that surround the mature oocyte enter through the ruptured membrane and envelop and resorb the yolk and fat material. In haematoxylin and eosin stained sections, the bodies are irregularly shaped masses of faintly eosinophilic cytoplasm with small densely basophilic nuclei. No comparable structure appears in ovaries, yet frozen sections of testes stained with Sudan Black B showed that atretic bodies had numerous black and dark green staining masses, identical to the black staining fatty droplets and the dark green yolk globules of similarly stained yolky oocytes. Intact yolk globules may sometimes be identified in haematoxylin and eosin stained sections viewed under bright blue fluorescent microscope (with a Schott BG 12 blue filter and a Wratten G 15 yellow filter). In some bodies large round globules fluoresce with a bright green colour (as do the many small nuclei), like the yolk globules of mature oocytes.

The remains of mature oocytes are more easily identified. They never contain connective tissue, but have a basophilic granular cytoplasm, give a positive lipid reaction with Sudan Black B and retain an intact, though grossly misshapen outer membrane.

DISCUSSION

Reinboth (1962) presented the only description of gametogenesis in sex reversing species within the sub-order Labroidei. He failed to provide a description of the stem germ cells in *Coris julis*, although he recognised their similarity in females and males and called them deuterogonia following the terminology of D'Ancona (1945). Reinboth believed that deuterogonia merely transformed into oogonia or spermatogonia and found great difficulty in differentiating between early forms of the two, especially in females where both were sometimes present. In *P. gymnogenis*, the stem germ cells (protogonia) divide mitotically to form interphase deuterogonia, a transient cell type that rapidly differentiates as a leptotene oocyte or a primary spermatogonium.

In two descriptions of natural sex reversal in labrids, in *Coris julis* (Reinboth, 1962) and *Halichoeres poecilopterus* (Okada, 1964) rapid spermatogenic proliferation was concomitant with ovarian degeneration. In *Coris julis* the testicular tissue was restricted to the periphery of the gonad, the ovarian lamellae collapsing completely. In contrast, Okada reported that the germ cell proliferation originated from stem germ cells located within the lamellae. Okada's photo-

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micrographs demonstrate that there was not a marked reduction in the size of the gonad with sex inversion; this was probably because *H. peocilopterus* usually transforms at the end of the breeding season when the gonads are free of large yolk stages and mature oocytes. A marked reduction in the gonad size was a feature of sex inversion in *P. gymnogenis* as the gonads of the transforming females were often distended with large maturing oocytes.

On a morphological basis there appears to be no difference between the stem germ cells in females and males of *P. gymnogenis*, yet they divide and differentiate into either female or male germ cells. In the crustaceans Charniau Cotton (1965) has shown that the titre of hormone produced by the androgenic gland decides whether the gonidia enter oogenesis or spermatogenesis. The reviews of Pickford and Atz (1957), Hoar (1965) and Barr (1968) have shown that teleosts present a more complicated picture; however, it is generally accepted (Reinboth, 1970) that undifferentiated gonidia are sexually bipotent and may be directly influenced by heterologous sex hormones.

In one male *P. gymnogenis* the remnants of a few small meiotic stage oocytes were seen in the central zone of a lamella, and not around the lamellar wall where meiotic oocytes are normally found in functional females. Although the nuclei were smaller than those of normal meiotic oocytes, they have been shown to be oocytes, and not degenerate lobule boundary cells. Okada (1964) believed that in transforming *H. poecilopterus*, oocytes were formed for some time, but gradually decreased in total diameter from 25 μ m to 5 μ m. As Okada (1964) makes no reference to normal meiotic stage oocytes it is likely that the 25 μ m cells were diplotene oocytes which had been present prior to the sex inversion. These small early meiotic prophase stages may have differentiated during the sex inversion period if low concentrations of oestrogen were still present, as was the case in the natural sex inversion of the protogynous synbranchid eel, *Monopterus albus* (Chan and Phillips, 1969).

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A new Genus and Two New Species in the Family Mithrodiidae (Echinodermata : Asteroidea) with Comments on the Status of the Species of *Mithrodia* Gray 1840

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ABSTRACT

A new genus and two new species of mithrodiid asteroids from the Pacific and Indian Oceans are described. *Mithrodia gigas* Mortensen, from South Africa, is referred to the new genus. The status of the species of *Mithrodia* is discussed. *Mithrodia fisheri* Holly and *Mithrodia clavigera* (Lamarck) are retained as valid species but *Mithrodia victoriae* Bell and *Mithrodia bradleyi* Verrill are provisionally referred to the synonymy of *M. clavigera*.

INTRODUCTION

During a visit to the Aquarium of Nouméa, New Caledonia, in 1969, the senior author was brought a giant asteroid, taken locally by the Aquarium's scuba divers. It clearly represented an undescribed form of the family Mithrodiidae. For several years this specimen was thought to be unique. Subsequently a specimen was sent from Guam by Dr. L. G. Eldredge in 1971 and a juvenile from the Ogasawara Islands, taken in 1974, was forwarded to us by Dr. M. Yamaguchi. Finally two further specimens were taken in 1975 by M. Labout and Mr. A. Birtles, near the original locality, in the lagoon off Nouméa. Photographic evidence also exists of an undoubted specimen of this species from the Philippine Islands, recorded on the cover of a Japanese periodical, "Marine Diving" 1972, No. 15 (cover picture).

Two specimens from the Seychelles Islands, Indian Ocean, forwarded to us by Miss A. M. Clark of the British Museum (Natural History), proved to be closely allied to but specifically distinct from the Pacific specimens.

Research of the literature indicated that both of these forms are not only closely related to *Mithrodia gigas* Mortensen from South Africa, but also to the "peculiar specimens of *Mithrodia*" described and illustrated by Fisher (1906). It seemed to both of us, however, that their features were sufficiently distinctive

to separate them generically from other species included in the genus *Mithrodia* Gray by Engel, Dilwyn John and Cherbonnier in their 1948 revision of that genus. We also concluded that some of these authors' findings were incorrect and we therefore felt it appropriate that, while describing and justifying the new taxa, we should include our comments on the status of species within the genus *Mithrodia*.

DESCRIPTIONS

Order: Spinulosida.

Family: Mithrodiidae.

Genus *Mithrodia* Gray, 1840 p. 288.

DIAGNOSIS:

Slender-armed forms, usually 5-rayed (4- to 6-rayed), with R (centre of disc to arm tip) up to about 300 mm, r (centre to edge of disc) up to about 20 mm, so that R:r lies between 7.5 : 1 and 15 : 1 (usually about 10-12 : 1). Arms tapering to a fairly acute tip. Skeleton open or compact, reticulate, with plates and trabeculae bearing tubercles. The whole (body and spines) covered by a thick skin beset with scales or thorn-like granules.

Large, stout spines occur actinally and abactinally, forming up to 9 longitudinal rows (including the rows of subambulacral spines). Tubercles or spines absent from the papular areas. Marginal plates inconspicuous but their position indicated by two of the rows of stout spines. Infero- and supero-marginal rows separated, connected by trabeculae. Actinal intermediate areas narrow, with only one row of plates. Abactinal spines and spines of the first actinal intermediate row usually longer than the inner, subambulacral spines and first actinal spines occurring irregularly, one adjacent to every 1 to 7 of the subambulacral spines. Furrow spines finger like, 10 to 12 in webbed fans. Pedicellariae multi-valved, typical of the family, present actinally and abactinally.

TYPE SPECIES:

- Asterias clavigera* Lamarck, 1816
= *Mithrodia spinulosa* Gray, 1840. Type species by monotypy: a synonym of *M. clavigera* fide Perrier, 1875; de Loriol, 1885 and subsequent authors.

OTHER SPECIES INCLUDED:

Mithrodia fisheri Holly, 1932; (*M. bradleyi* Verrill, 1867; *M. victoriae*, Bell, 1882 are provisionally referred to synonymy of *M. clavigera*)

Genus *Thromidia* gen. nov.

DIAGNOSIS:

Large, obese, 5-rayed forms with R up to 350 mm, r up to 85 mm. R:r as 4 : 1 up to 7 : 1. Arms with more or less parallel sides, tapering only distally

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to a blunt, rounded tip. Skeleton is open or compact, reticulate. Skeletal plates bear small tubercles, the whole being covered by a thick skin with scale- or thorn-like granules. The larger, stout spines are restricted to a subambulacral plus one (rarely two) actinal rows. Tubercles occur in the papular areas. Marginal plates inconspicuous and without spines. Actinal intermediate areas wide, with several rows of plates. Spines of the first actinal intermediate row usually shorter than the inner, subambulacral spines and forming a regularly arranged line, one to each 2 (proximally) — 4 (distally) subambulacral spines. Furrow spines number up to 12, in webbed fans. Multi-valved pedicellariae, typical of the family, present only actinally and usually restricted to areas adjacent to and between the spines of the first actinal and subambulacral rows.

The only exception to the above diagnosed arrangement of spines is seen in a juvenile specimen (R = 58 mm) bearing an even distribution of small spines over the whole body (see p. 204, figs. 5-6 and p. 205).

ETYMOLOGY: Anagram of *Mithrodia*; gender, feminine.

TYPE SPECIES: *T. catalai* sp. nov.

OTHER SPECIES INCLUDED: *T. seychellesensis* sp. nov., *Mithrodia gigas*, Mortensen, 1935.

REMARKS:

This genus is separated from *Mithrodia* because of its much greater bulk, the shape of its arms, the restriction of the stout spines to the subambulacral and first (rarely the second) actinal rows, the regularity of the actinal row of spines, the wide actinal intermediate area and the presence of tubercles in the papular areas.

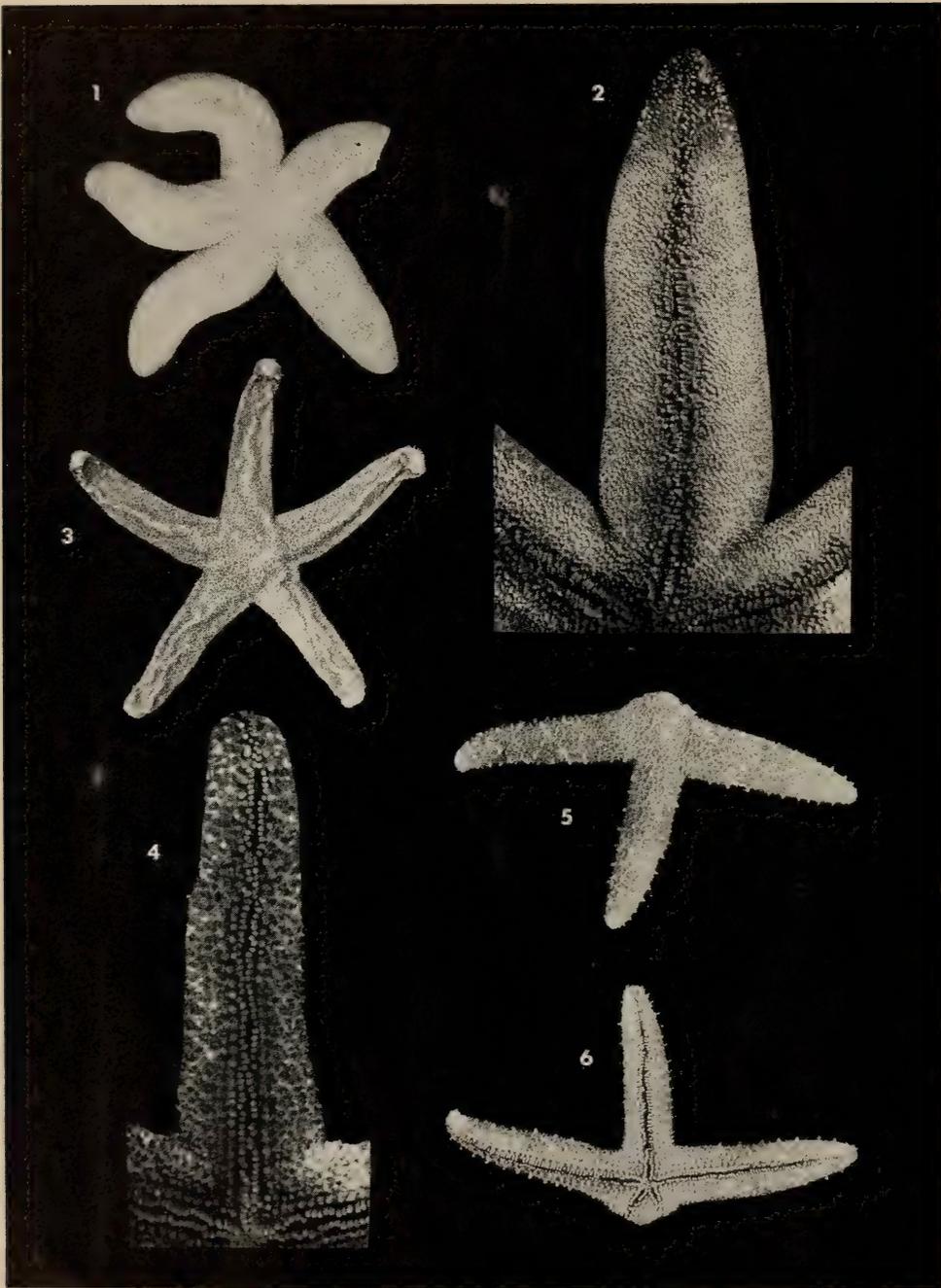
***Thromidia catalai* sp. nov.**

Figs. 1-6 and 9

Mithrodia sp., "peculiar specimen" Fisher 1906, p. 1069, Pl. XXXVII, figs. 2-3.
Mithrodia fisheri, Engel, Dilwyn John and Cherbonnier, 1948, p. 27 part.
(non *Mithrodia fisheri* Holly, 1932).

MATERIAL EXAMINED:

Holotype, R = 352 mm (in life), 283 mm after preservation in alcohol (Australian Museum No. J. 7792), near base of Tabu Reef, off Îlot Amedée, New Caledonia, circa 10 m depth, on sandy bottom with boulders, 14.IX.1969, collected by M. B. Conseil and M. G. Bargibant for the Aquarium of Nouméa. Two paratypes: (Australian Museum No. J. 9926 R = 238 mm) and British Museum (Natural History) No. 1976.10.14.1, R = 225-250 mm after preservation and drying), both taken in the same locality as the holotype, on 11.VII.1975, collected by M. M.P. Labout and Mr. A. Birtles in a depth of c. 10 m; one paratype, (R = 245 mm preserved dry) from the vicinity of Guam Island, taken by scuba divers



Figs. 1-6. *Thromidia catalai* n. sp. 1, holotype, A.M. No. J7792, abactinal view, R = 283 mm. 2, paratype, B.P.B.M. No. W2507, actinal view of one arm, R = 245 mm. 3-4, juvenile, A.M. No. J10134, whole abactinal view (3); actinal view of one arm (4), R = 125 mm. 5-6, juvenile, U.S.N.M. No. 32271, abactinal (5) and actinal (6) views, R = 58 mm.

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(no other data supplied), deposited at the Bernice P. Bishop Museum, Hawaii (W2507); one specimen (juvenile), $R = 125$ mm, preserved dry (Australian Museum No. J.10134) from Miyano-hama, Chichi-jima, Ogasawara Islands, 10 m depth, collected by Mr. T. Matuura, 24.III.1974; one specimen (juvenile) $R = 58$ mm (United States National Museum No. 32271) "Albatross" Station 4158, off the Bird Islands, Hawaii, 38-45 m, on coral and coralline bottom; one specimen (size not recorded; colour print only), Hansa Bay, 200 km north of Madang, Papua New Guinea, print sent by Dr. M. Jangoux, December, 1976.

DESCRIPTION:

A large obese species. In life adults range from $R = 355 - 384$ mm, $r = 82 - 90$ mm, $R/r = 4 - 4.6$; after preservation $R = 220 - 296$ mm, $r = 50 - 66$ mm and $R/r = 4 - 5.2$. The arms are slightly constricted at their origin from the disc, which is relatively small. The five arms are cylindroid with a taper which becomes marked only from approximately $2/3 R$. The madreporite is single, small and situated halfway between the centre of the disc and the interradial margin (Fig. 1).

The skeleton of plates and radiating trabeculae form an open meshwork enclosing large papular areas (up to 10-11 mm in adults) in which finer, minute ossicles are present. Tubercles (about 1 mm wide by 1.5 mm high) are extremely numerous and crowded over the whole surface, occurring on the skeletal elements. Smaller tubercles occur in the papular areas. On the distal $1/7$ of the arm only the larger tubercles are present, becoming more widely spaced. There are no stout spines abactinally (Fig. 9).

The whole surface, including all the tubercles and actinal spines (even including a few of the furrow spines) is covered by a thick skin in which are scale- or thorn-like granules. These granules become enlarged and pointed towards the apical regions of the spines and tubercles. Marginal plates are inconspicuous and do not bear spines.

Actinal intermediate areas are broad, with 5-6 rows of plates between the adambulacral and ventral lateral (inferomarginal) margin (Fig. 2). Adambulacral plates each bear a webbed fan of 6-7 (sometimes 5-8) finger-like furrow spines, backed by a single, stout, scale-covered subambulacral spine, up to 8 mm high and 2 mm in breadth. The inner side of the subambulacral spine is often rubbed bare. A regular row of spines which are slightly shorter than the subambulacrals (6 mm high and 3 mm in breadth) are found on the first actinal row of plates. Each actinal spine occurs adjacent to every second subambulacral spine. A second row of spines, intermediate in size between those of the first actinal row and the tubercles covering the rest of the actinal surface, is evident particularly on the distal part of the arms (Fig. 2).

Pedicellariae are multi-valved, occurring only actinally between the first actinal and subambulacral rows of spines. Tube feet are large, with a double ampulla and large terminal disc.

A dried juvenile $R = 125$ mm and $r = 30$ mm, $R/r = 4.5$ from Ogasawara Islands, which judging from its photograph in life has become very shrunken, has tubercles which are restricted to the plates and do not occur on the trabeculae (Fig. 3). Usually only one or two tubercles occur in its papular areas. The spines of the second row of the actinal intermediate plates are more prominent, particularly distally, than in the adult specimens. There are only three rows of actinal intermediate plates (Fig. 4).

The larger of the two "peculiar specimens" recorded from Hawaii by Fisher (1906) is only about half the size of the holotype but his description and figures of it (plate XXXVII, figs. 2 and 3) do not indicate any major differences from the one we examined from the Ogasawara Islands. We have, unfortunately, been unable to locate the whereabouts of Fisher's larger specimen. The smallest specimen we examined (USNM No. 32271), labelled "*M. bradleyi* Verrill", coming also from the vicinity of Bird Islands, Hawaii, but from "Albatross" Station 4158, has proved something of an enigma (Figs 5-6). We believe it to be the smaller of the two "peculiar specimens" of *Mithrodia* recorded by Fisher (1906, p. 1096). Its Station number and locality data agree with Fisher's record but there is a discrepancy in the measurement he gives for R ($= 38$ mm according to Fisher). In all other respects it agrees with his short description. We found $R = 58$ mm, $r = 12$ mm, $R/r = 4.8$. Unfortunately Fisher did not figure this specimen so we cannot be absolutely certain that it is the specimen to which he refers. However, a simple typographical error (mistaking a 5 for a 3) would account for the difference in the measurements. There is no doubt, however, that this is a juvenile *Thromidia*. It exhibits characters which are not visible in the larger juvenile from Ogasawara Islands. This at first led us to believe it might represent a fourth species of *Thromidia* since it has small spines scattered abactinally. These are only slightly smaller than the subambulacral spines but are similar to those of the first actinal row. It is not unknown, however, for juvenile forms in this family to have abactinal spines which later disappear with growth (Engel et al. 1948, pp. 7-10). The position of the marginal plates is determinable by the spines carried on them. This is a feature not shown by the adults. The papular areas vary in diameter between 2-2.5 mm. In our present state of knowledge we agree with Fisher, that this is a still earlier stage of his larger "peculiar specimen". However, we conclude further that it should also be regarded as a juvenile of the giant Pacific species *T. catalai*. The colour note given by Fisher adds convincingly to the argument for considering this specimen a juvenile of *T. catalai*.

COLOUR:

In life (adults), uniformly pink abactinally, deeper pink actinally, with arm tips cinnamon-brown; actinal and subambulacral spines rose-red with their flattened tips cream; furrow spines cream; tube feet whitish with the terminal disc muddy-brown. A colour print of the live juvenile from Ogasawara Islands shows it to be rose red, with arm tips a darker red. Fisher recorded the life colour of the larger of the "peculiar specimens" as "dull, light cinnamon-pink and

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maroon at end of the arms, the cinnamon mottled in places with buff. Actinal surface is light pinkish buff or vinaceous, darkest on tubercles. Ambulacral feet raw sienna”.

HABITS:

In the field the starfish have been observed lying in the open, on the bottom, in depths of 10 m or more. In one instance one was observed with its stomach everted over a grey, encrusting sponge, growing on a coral boulder (A. Birtles, personal communication). The holotype and the larger of the two specimens captured by Labout and Birtles were kept alive over periods of up to 10 months in the Aquarium of Nouméa and Mme. Catala reported that no solid food (flesh of fish, crustacea and molluscs) such as was fed to the fish and other inhabitants of their tank was taken by *Thromidia*, but it survived by feeding on encrusting growths on the boulders and side walls of the tank. The animals are more active by night and are capable of moving on their tube feet at speeds of up to 25 mm per second. The specimen now selected as the holotype A.M. J7792 lived unmolested for several months in the largest tank at the Aquarium which it shared with a number of species of fish, molluscs and stingrays. However, a newly introduced fish (a balliste) immediately attacked the starfish, tearing a hole in one arm. The attack was not repeated but the starfish responded to the injury by emitting a stream of whitish eggs upon which the fish fed. At this stage the *Thromidia* was removed from the tank for preservation.

When *Thromidia* lay on the bottom it was frequently observed to become covered abactinally by pebbles and shellgrit which rained down on it as a result of the feeding activities of certain species of fish. It seemed incapable of cleaning itself while flat on the bottom but the rubbish fell off when the starfish climbed vertical surfaces. The starfish could move on its tube feet with equal facility over a loose or solid substratum.

ETYMOLOGY:

The species is named in honour of Mme. Stucki and Dr. René Catala of the Aquarium of Nouméa who sponsored the collection of the Nouméa specimens and also kept *Thromidia* alive in their Aquarium making notes and observations on its behaviour.

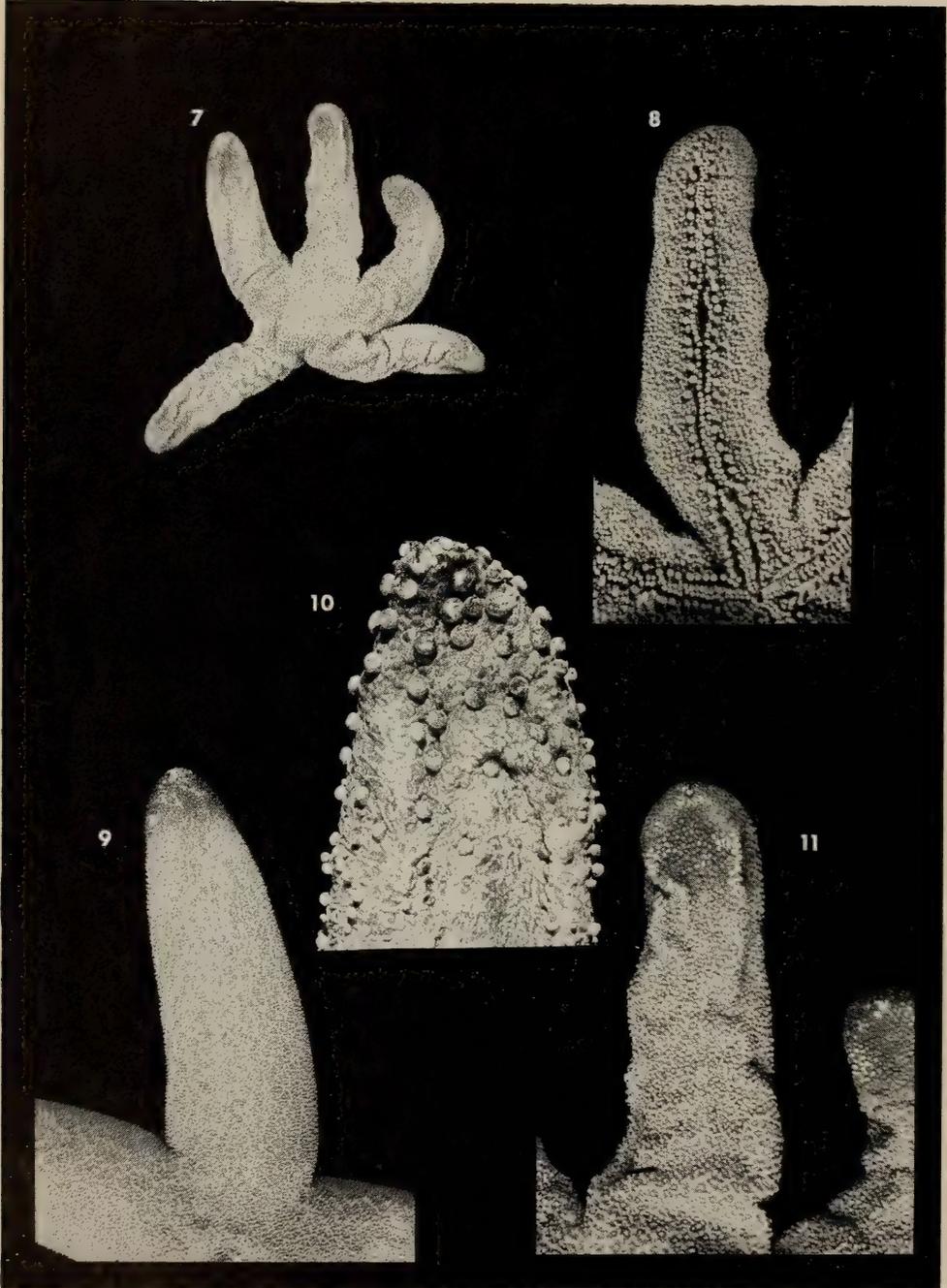
Thromidia seychellesensis sp. nov.

Figs. 7-8 and 11

Mithrodia fisheri, Jangoux, 1974, p. 791 (non *M. fisheri* Holly, 1932).

MATERIAL EXAMINED:

Holotype R = 123 — 124 mm (British Museum [Natural History] No. 1974.9.25.18); Recife d'Anse a la Mouche, Mahé Isle, Seychelles, Indian Ocean, collected by Dr. M. Jangoux, 1972; Paratype R = 135 mm (B.M. [N.H.] No.



NEW SPECIES OF MITHRODIIDAE

1976.10.14.2) Seychelles, Cousin Id, 12 m, October, 1972, collected by R. A. Birtles.

DESCRIPTION:

A species with five cylindroid arms which have parallel sides along the greater part of the length, tapering only slightly to a rounded, blunt tip. $R = 123 - 124$ mm, $r = 22 - 23$ mm, $R/r = 5.5$ (Holotype); $R = 135$ mm, $r = 27 - 28$ mm, $R/r = 4.9$ (Paratype). The madreporite is rather insignificant and positioned half way between the centre of the disc and the interradial margin (Fig. 7).

The skeletal plates and radiating trabeculae form a compact meshwork enclosing small papular areas (up to 3.5 mm diameter). Tubercles (about 0.6 mm wide by 0.75 mm high) are numerous and crowded over the actinal and abactinal surfaces, occurring on the skeletal elements. A smaller tubercle occurs in each of the papular areas (Fig. 11). On the distal $1/5 - 1/4$ of the arms the plates are rounded convex and are closely packed together, giving the tip of the arms the appearance similar to that of a cobbled pavement (Fig. 11). The distal papular areas are so small that they contain only one or two papulae. Occasionally the smaller tubercles persist on these papular areas. Trabeculae connecting the larger plates are very reduced. There are no stout spines abactinally.

The whole surface, as in *T. catalai*, is covered with a thick skin beset with scale- or thorn-like granules. These granules become slightly enlarged towards the apical region of the spines and tubercles but the distal arm plates are characterised by the even size of the granules covering them (Fig. 11). The marginal plates are inconspicuous.

Actinal-intermediate areas are broad, with 3-4 rows of plates between the adambulacral plates and the ventro-lateral (inferomarginal) margin (Fig. 8). Adambulacral plates each bear a webbed fan of 6-8 furrow spines backed by a single, stout subambulacral spine up to 4.5 mm high and 1.5 mm in breadth. The inner side of the subambulacral spine is often rubbed bare. A regular row of spines, shorter than the subambulacrals (3.5 — 4.5 mm by 1.5 — 2.0 mm) is found on the first actinal row of plates. The actinal spines are spaced, proximally, adjacent to every second subambulacral spine, but more distally (beyond $1/2R$), particularly on the holotype, adjacent to every 3rd or 4th subambulacral spine. A second row of spines, intermediate in size between those on the first actinal

Figs. 7-8. *Thromidia seychellesensis* n. sp., holotype, B.M. (N.H.) No. 1974.9.25.18, whole abactinal view (7); actinal view of one arm (8), $R = 123-124$ mm

Fig. 9. *T. catalai* n. sp., paratype, B.P.B.M. No. W2507, abactinal view of arm, $R = 245$ mm.

Fig. 10. *T. gigas* (Mortensen), holotype, S.A.M. No. A 22561, abactinal view of arm, $R = 330-347$ mm.

Fig. 11. *T. seychellesensis* n. sp., holotype, B.M. (N.H.) No. 1974.9.25.18, abactinal view of arm-tip, $R = 123-124$ mm

row and the tubercles covering the rest of the actinal surface, is evident particularly on the distal parts of the arms (Fig. 8).

Pedicellariae are typical of the family and distributed as in *T. catalai*. It is possible that the specimens of *seychellesensis* described above represent a young stage of the species.

COLOUR:

The dried holotype is museum colour with darker tips to the arms. The dried paratype is generally museum colour, with some trace of pink abactinally and actinally while the arm tips are a darker museum brown. A colour transparency sent to the authors by Dr. Jangoux (1976, pers. comm.) shows the species to be uniformly light orange abactinally, with arm tips darker.

HABITS:

This species is relatively common in the Seychelles Archipelago (Jangoux, 1976, pers. comm.) where Jangoux (1974) records it frequently as host to the fish parasite, *Carapus homei*. The fish occurs within the body cavity of the starfish.

ETYMOLOGY: Named after the area where it was taken.

***Thromidia gigas* (Mortensen)**

Fig. 10

Mithrodia gigas Mortensen, 1935, p. 1, fig. 1, plate 1; Cherbonnier, 1975, p.639, pls. I-II.

MATERIAL EXAMINED:

Holotype (South African Museum No. A 22561) off Point Morgan, East London, South Africa, in a depth 45-54 m, on 28 January, 1934, collected by Mr. Bell Marley. The starfish was taken on a fish-hook, after taking the bait.

DESCRIPTION:

There is little to add to the detailed description given by Mortensen (1935). There are, however, some slight discrepancies in his measurements and in the number of furrow spines Mortensen recorded. We found $R = 330 - 347$ mm, $r = 45$ mm, $R/r = 7.3 - 7.7$, and the furrow spines number from 5 — 6 generally and sometimes up to 8 per plate. We have included a new photograph of an arm tip of the holotype (Fig 10) for direct comparison with those of *T. catalai* and *T. seychellesensis*.

Cherbonnier (1975) has recorded a specimen off the west coast of Madagascar thus extending the range of the species. His specimen is about two thirds of the size of the holotype and rather contorted. Whether the measurements given by Cherbonnier correspond to the conventional way of measuring R and r is unclear.

NEW SPECIES OF MITHRODIIIDAE

We think that by "le diametre due disque . . ." Cherbonnier may refer, in fact, to r giving his specimen a R/r ratio of 6.6 — 7.6, and this conforms with his illustration and our diagnosis of the genus.

COLOUR:

In life the holotype was purplish-pink abactinally with the tips of the arms more cinnamon red, actinally it was pale yellowish, with the tube-feet white.

COMPARISON OF *T. CATALAI*, *T. SEYCHELLESENSIS* AND *T. GIGAS*

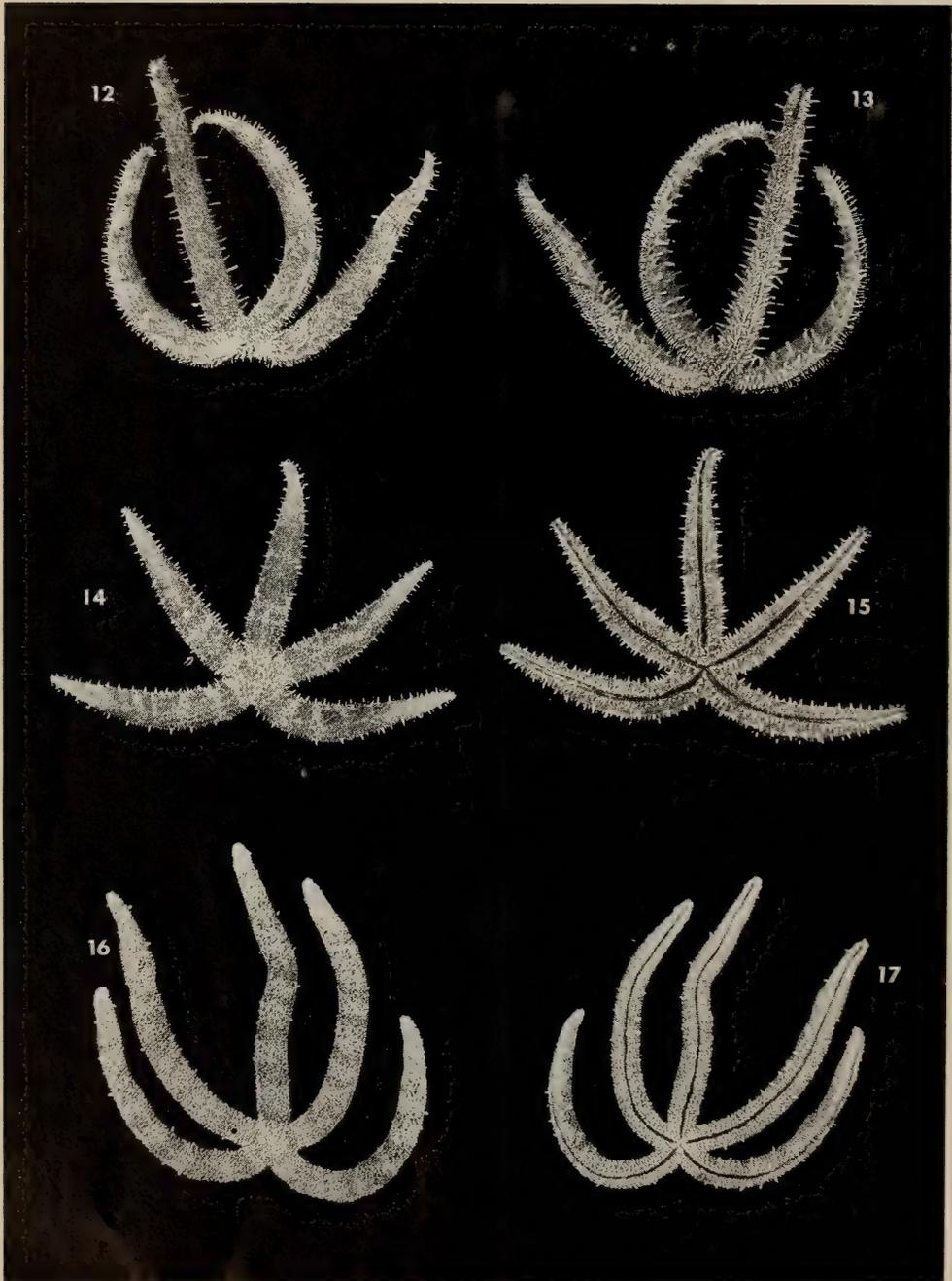
T. catalai differs markedly from *T. seychellesensis* (comparing two specimens of similar size, one from each species), in the arrangement of the skeletal reticulum, size of the papular areas and arrangement of plates and tubercles near the arm tips. Both of these new species are distinguished from *T. gigas* in their arm proportions, which are shorter and stouter than in the South African species, and in the lack of the very prominent, globular bosses on the arm tips.

KEY TO SPECIES OF *THROMIDIA*

- 1 $R/r = 6.5-7.6/1$; arm tips with large globular bosses (5 mm diameter) (Fig. 10); S.E. Africa (East London) — west coast Madagascar *T. gigas* (Mortensen)
- 1¹ $R/r < 6/1$, arm tips without large globular bosses 2
- 2 $R/r = 4.9 - 5.5/1$, arm tips with closely packed rounded, slightly convex plates, covered with even granules, giving cobbled appearance (Fig. 11); Seychelles (Western Indian Ocean) *T. seychellesensis* sp. nov.
- 2² $R/r = 4.5.2/1$, arm tip with spaced plates bearing small tubercles (Fig. 9); Pacific Ocean (Hawaii, Japan, Philippines, New Caledonia, New Guinea) *T. catalai* sp. nov.

DISCUSSION

The first two representatives of *Thromidia* were collected by the U.S. Fisheries ship "Albatross" off the Bird Islands, Hawaii in 1902. These were the juvenile specimens referred to by Fisher (1906, p. 1069) as "A peculiar specimen of the genus *Mithrodia*". They differed somewhat from other specimens of the species collected by the "Albatross" which Fisher identified as *Mithrodia bradleyi* Verrill. He did not, however, propose a new name for the peculiar specimens. We have not been able to locate the whereabouts of the larger of the two "peculiar specimens" but what we believe to be the smaller one is discussed above (p. 205).



NEW SPECIES OF MITHRODIAE

Holly (1932) described a new *Mithrodia* from Hawaii, *M. fisheri*, from a damaged, obviously juvenile specimen. He wrongly synonymised Fisher's "peculiar specimens" with his new species and failed to appreciate that it was the specimens identified and figured by Fisher (1906) in Plate XXXVI and Plate XXXVII Fig. 1, as *M. bradleyi* that in reality represented an adult of his *M. fisheri* (see below).

Mortensen (1935), in describing *M. gigas*, compared it with *M. bradleyi* sensu Fisher (1906), non Verrill (1868) and he failed to recognise in *M. gigas* differences considered by us to be of generic significance. He listed *M. bradleyi* as a valid species, not realising that Fisher's Hawaiian record in reality referred to Holly's species which had been undescribed at the time of Fisher's report. The validity of *M. bradleyi* Verrill, from the west coast of America is dealt with below (p. 214).

Engel et al. (1948) also did not realise the significance of Fisher's "peculiar specimens" but did realise Fisher's blunder in the identification of *M. bradleyi*. They referred both *M. bradleyi* sensu Fisher and his "peculiar specimens" to the synonymy of *M. fisheri* Holly.

There are no further records of the capture of specimens of *Thromidia* until the senior author encountered the first of the very large specimens, now the holotype, of *T. catalai*, from the lagoon off Noumea, New Caledonia in 1969. All subsequent known records are set out above.

COMMENTS ON THE STATUS OF THE SPECIES OF *MITHRODIA*

In a major review of the genus *Mithrodia*, sensu lata, Engel, John and Cherbonnier (1948) listed five species as follows: *M. clavigera* (Lamarck, 1816); *M. victoriae* Bell, 1882; *M. bradleyi* Verrill, 1867; *M. fisheri* Holly, 1932 and *M. gigas* Mortensen, 1935. Of these *M. gigas* has been referred in this paper to the new genus, *Thromidia*, for the reasons stated. Of the remaining four, we believe that *M. fisheri* is clearly defined and that the relationship between *M. clavigera*, *M. bradleyi* and *M. victoriae* still needs clarification.

Holly correctly recognised a new species, *M. fisheri* for a Hawaiian form (Figs. 16-17) even though his description was based on a damaged specimen. We do not agree with him, however, in identifying Fisher's "peculiar specimens" with

Figs. 12-13. *Mithrodia clavigera* (Lamarck), A.M. No. J5845, abactinal (12) and actinal (13) views, R = 200 mm. (Great Barrier Reef [Capricorn Group]). One arm broken off.

Figs. 14-15. *M. clavigera* (Lamarck) (identified as *M. bradleyi* Verrill), Allan Hancock No. 245 — 12, abactinal (14) and actinal (15) views, R = 165 mm. (California [Mexico]).

Figs. 16-17. *M. fisheri* Holly, Allan Hancock No. 726 — 1, abactinal (16) and actinal (17) views, R = 152.5 mm (Hawaii).

his new species as we have stated above (p. 213). In fact, part of the confusion in the recognition of *M. bradleyi* has arisen from Fisher's (1906) identification of that species from Hawaii. It appears he had examined at least one of Verrill's specimens from La Paz and confused the identity of his Hawaiian specimens with what he thought to be Verrill's species. Fisher's material was clearly in a good state of preservation when examined and photographed. He probably did not directly compare his specimens against Verrill's description (1867) and (1914) of the holotype of *bradleyi* but rather with one of the poorly preserved La Paz specimens, this being inferred in a letter which he subsequently wrote to, and was quoted by, Engel et al (1948, p. 18) admitting his mistake. We therefore concur with Engel et al in recognising the validity of *fisheri* for the reasons set out by them.

The status of *M. victoriae* is doubtful. Miss A. M. Clark examined the two syntypes in the British Museum (Natural History) (No. 1879.8.19.97) and concluded that she could find no difference between them and similar sized specimens of *M. clavigera* from Macclesfield Bank, South China Sea (personal communication to senior author, 1972) and that there seemed little doubt as to the origin of the specimens from Victoria Bank, Brazil (personal communication to the junior author, 1976). The junior author examined Bell's specimens of *M. victoriae* in 1975 and was unable to draw any different conclusions from those of Miss Clark. Engel et al were certainly very doubtful of both the validity of this species and its actual origin from Brazil, together with a second similar specimen also labelled "Brazil", held in the Leiden Museum, Netherlands. The authors therefore believe that *M. victoriae* should be considered a synonym of *M. clavigera*.

That *M. clavigera* is a valid species is without doubt. However, on referring to Verrill's description of the holotype of *M. bradleyi* (1867) and his subsequent photographic illustration (1914, pl. CXII) of the type-specimen, we can see little justification for the separation of this form from *clavigera*. We have compared a specimen from Lower California (Allan Hancock Foundation Cat. No. 275.12), labelled *M. bradleyi* (Figs. 14-15) with a comparably sized specimen of *M. clavigera* from North Reef, Capricorn Group of Islands, Queensland (Australian Museum No. J5845) (Figs. 12-13) and with a whole range of specimens in the Australian Museum from localities across the Pacific and from Mauritius, Indian Ocean. Taking point for point the characters discussed by Engel et al in distinguishing *M. bradleyi*, considering the wide variation in the characters of *M. clavigera* admitted by those authors, we find it difficult to detect any character which would justify the recognition of a specific distinction between eastern and western Pacific forms. The only two features of distinction appear to be the stouter arms and shorter spines of *bradleyi*, both features being present also in a large specimen (R = 225 mm, r = 32 mm; A.M. No. J9927) collected from New Caledonia. If these features are considered of specific importance then *M. bradleyi* and *M. clavigera* are sympatric (at least in the central Pacific area). It is unfortunate that the type specimens of *M. clavigera* and *bradleyi* cannot be directly compared

NEW SPECIES OF MITHRODIIIDAE

and that the two specimens from La Paz identified by Verrill as *bradleyi* are in such a poor state of preservation. Interestingly, Perrier (1875, p. 117) in a footnote commented that *M. bradleyi* was "peut-être identique elle aussi à l'espèce de l'Île de France (*M. clavigera*)", though Engel et al did not agree. We conclude that until a greater amount of comparative material has been examined (Engel et al compared only 4 specimens including at least 2 poorly preserved specimens of *bradleyi* against 47 specimens of *clavigera*), firm conclusions on the relationship between these two species are difficult to draw, but we feel that *bradleyi* is little more than an eastern Pacific form of the widely distributed and variable *M. clavigera*.

DISTRIBUTION

The distribution of the genus *Mithrodia*, like that of *Thromidia*, is Indo-Pacific. The Atlantic records for *Mithrodia victoriae* (synonym of *M. clavigera*) may be doubtful (Engel et al. 1948). *Mithrodia clavigera*, omitting the above doubtful record, is therefore distributed from Mauritius and the Red Sea through the Pacific to Lower California and Panama. *Mithrodia fisheri* occurs around Hawaii. It is also reported from Arica, Peru by H. L. Clark (1910) under the name of *M. bradleyi* (sensu Fisher) and while it is obvious from his figured specimen that he was dealing with *M. fisheri* his suspicions concerning its locality of origin might be well founded and should be taken into account. Engel and his co-authors (1948) report a specimen of *fisheri* from New Ireland, Bismarck Archipelago (originally identified as *M. clavigera* by Sluiter 1895) and one from the Philippine Islands. We have not examined these specimens.

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The authors wish to thank Dr. René and Madame Stucki Catala of the Aquarium of Nouméa for their generous help in donating specimens of *Thromidia* to the Australian Museum and for allowing the senior author to use the facilities of their Aquarium during the course of this investigation. We also thank them for their continued interest in keeping two of the specimens alive and under observation for long periods, recording habits and food preferences.

We also thank George Bargibant and Bernard Conseil (Collectors of the holotype) and M. Labout of Nouméa and Alistair Birtles of Townsville, Queensland (collectors of the paratypes) who supplied data as well as specimens. We are also grateful to Professor L. G. Eldredge of Guam University for allowing us to examine a beautifully preserved specimen from that island; to Dr. M. Yamaguchi, at present stationed at James Cook University of North Queensland, Townsville for presenting an important juvenile specimen from the Ogasawara Islands, accompanied by a colour print of the live animal, to the Australian Museum thus making it available to us for study; to Dr. M. Jangoux of Université Libre de Bruxelles for supplying data and colour photographs of *T. catalai* and *T. seychellesensis*; and to Dr. Maria E. Caso for allowing us to examine photographs of a *Mithrodia* from the New Hebrides.

The authors are indebted to a number of institutions and fellow echinodermologists for the loan of specimens and for supplying data as follows:— to Dr. D. L. Pawson and Miss Maureen Downey of the U.S. National Museum (Smithsonian Institution) Washington.

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A Redescription of *Periclimenes aesopius* (Bate, 1863) (Crustacea : Decapoda) with Remarks on Related Species

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ABSTRACT

The pontoniine shrimp *Periclimenes aesopius* (Bate, 1863) is redescribed in detail. It is considered to be endemic to southern Australia. Other records of this species are referred to *P. indicus* (Kemp) or *P. holthuisi* Bruce, species which may be found in association with actinarians or other coelenterates, and which also occur in Australian waters. It is considered probable that *P. aesopius* is involved in a similar association.

Periclimenes aesopius is remarkable for the great enlargement of postero-dorsal lobe of the third abdominal segment. Several closely related species have conspicuous colour markings on this segment and are also involved in fish-cleaning symbioses. It is also considered likely that the development of this process has the result of increasing the effectiveness of this signal and that *P. aesopius* may also be a fish-cleaning species.

Periclimenes aesopius is considered to be a member of a widely distributed group of closely related species, generally associates of actinarians, including the Indo-West Pacific species: *P. indicus* (Kemp), *P. tosaensis* Kubo, *P. holthuisi* Bruce; the east Atlantic-Mediterranean *P. scriptus* (Risso), *P. amethysteus* (Risso); and the tropical western Atlantic *P. yucatanicus* (Ives), *P. pedersoni* Chace, *P. magnus* Holthuis and *P. anthophilus* Holthuis & Eibl-Eibesfeldt. The group is not represented in the eastern Pacific region.

INTRODUCTION

The pontoniine shrimp *Periclimenes aesopius* was first described by C. Spence Bate as *Anchistia aesopia* in 1863. It is of particular interest in that it was the first pontoniine shrimp to be recorded from Australian waters and also that it has not subsequently been reported from any other localities and is still known only from St. Vincent Gulf, South Australia. Other records from the Indo-West Pacific region have proved to be erroneous, and Bate's species appears to be endemic to South Australia.

DESCRIPTIONS

Periclimenes aesopius (Bate) (Figs. 1-6).

Anchistia aesopia Bate, 1863, Proc. zool. Soc. Lond., 1863: 502-503, pl. 41, fig. 5.

Anchistia aopia—Haswell, 1882, Catal. Aust. Crust.: 194.

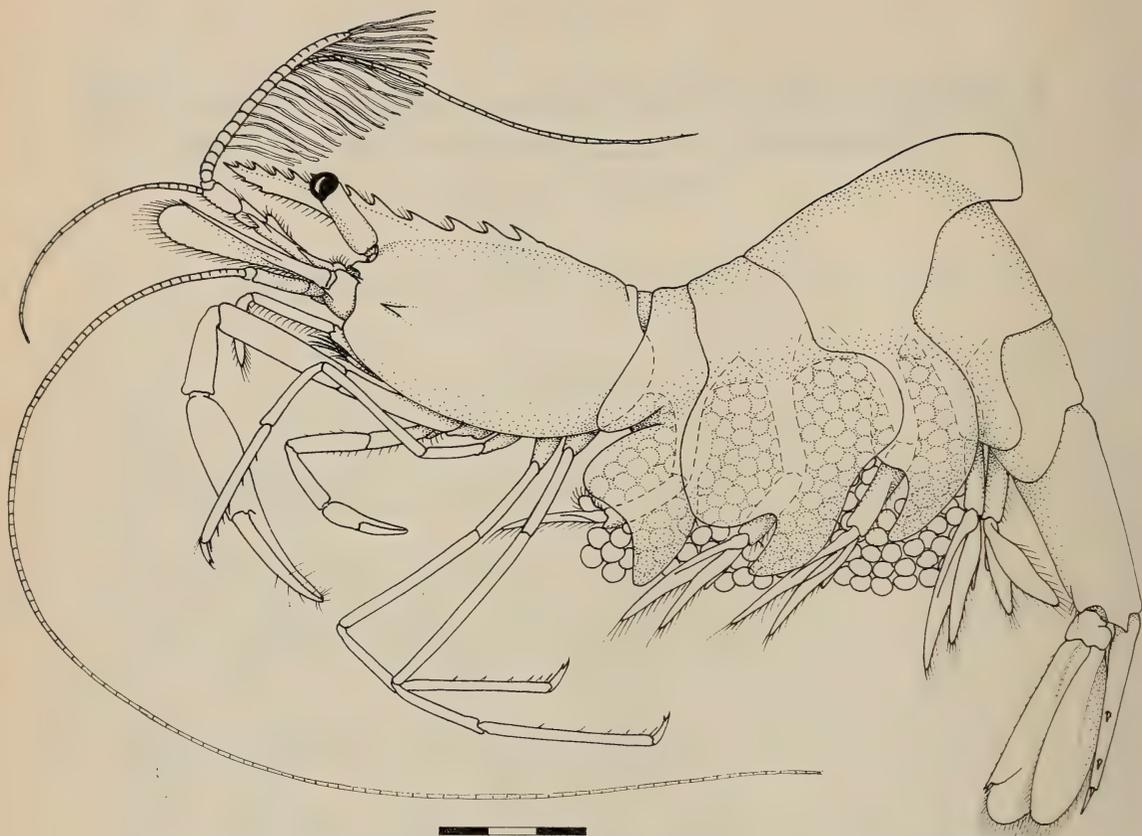


Fig. 1. *Periclimenes aesopius*, ovigerous female. Graduated scale = 3 mm.

Periclimenes aesopius— Borradaile, 1898, Ann. Mag. nat. Hist., (7)2:382.

Urocaris aesopius —Borradaile, 1917, Trans. Linn. Soc. Lond. Zool., (2) 17:354 (key), 354.

Periclimenes (Periclimenes) aesopius— Kemp, 1922, Rec. Indian Mus., 24:140.

Periclemenes aesopius— Kemp, 1922, Rec. Indian Mus., 24:142-143, fig. 12 — Hale, 1927, Crust. S. Aust., 1, 56, fig. 50; 1928, Rec. S. Aust. Mus., 4:95. — Bruce, 1969, Zool. Meded., Leiden, 43(20):258.

nec *Periclimenes (Periclimenes) aesopius* Holthuis, 1952; Siboga Exped. Mon., 39 a¹⁰:34-37, figs. 5-6. — Bruce, 1966, Crustaceana, 10(1): 19, 21, fig. 3b; 19, 21, fig. 3b, 4ef.

nec *Periclimenes (Periclimenes) aesopius* Johnson, 1961, Bull. Mus. Nat. Singapore, 30:58, 61, 75, tab. 1.

nec *Periclimenes aesopius* Bruce, 1967, Zool. Verhand., Leiden, 87:51-53.

A REDESCRIPTION OF *PERICLIMENES AESOPIUS*

MATERIAL EXAMINED:

(i) 1 ♂, 1 ♀, Gulf of St. Vincent, South Australia, British Museum (Natural History), registration No. 68-81, Types. (ii) 2 ovig. ♀, St. Vincent Gulf, South Australia, South Australian Museum, Cat. Nos. C626, C628. (iii) 1 ovig. ♀, 5 miles off Semaphore Beach, South Australia, South Australian Museum, Cat. No. C1063.

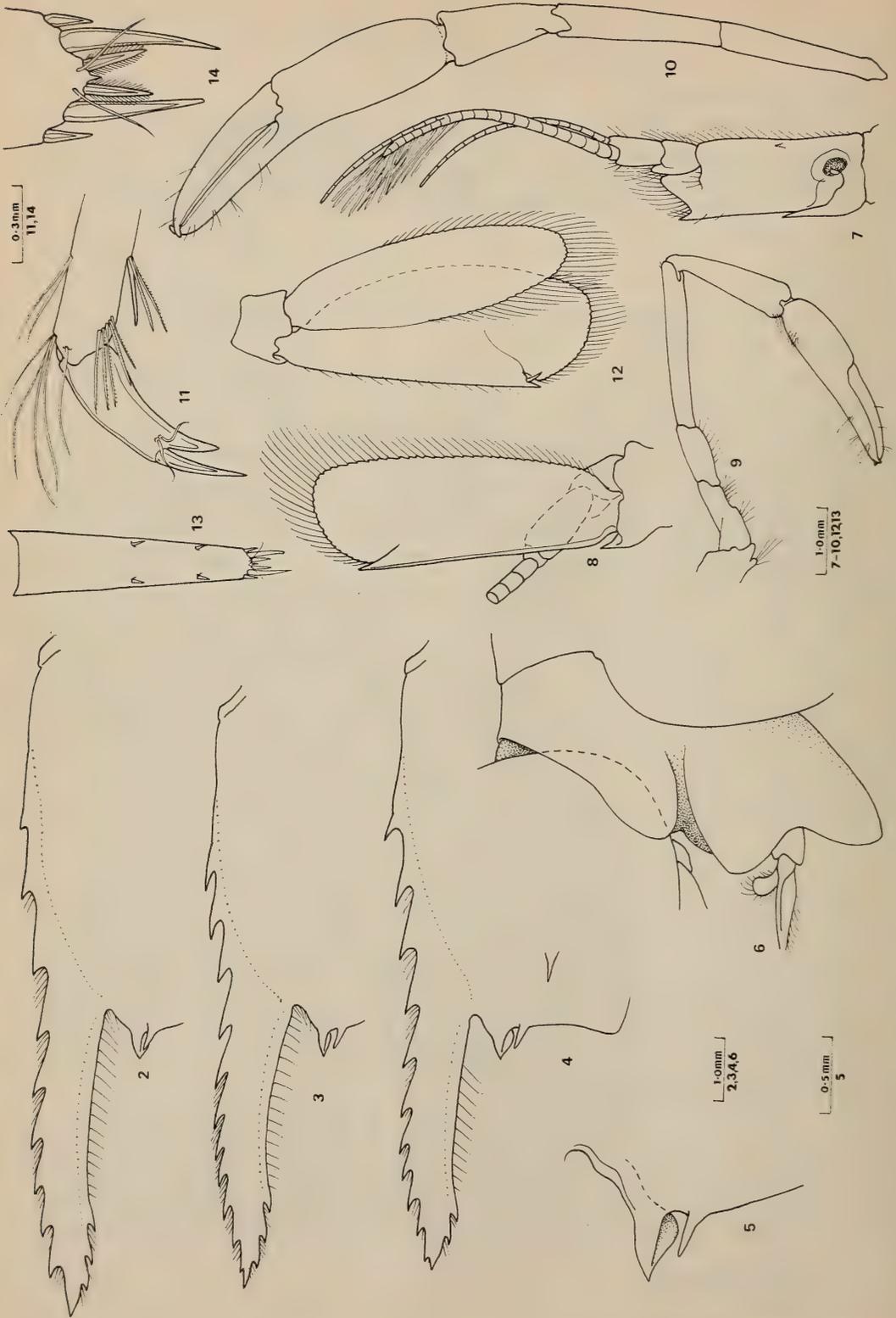
DESCRIPTION:

A relatively large and slenderly built species of *Periclimenes*, with a smooth carapace and abdomen.

The rostrum reaches almost to the end of the antennular peduncle and is feebly to moderately curved, directed slightly upwards in relation to the longitudinal axis of the carapace (from the posterior orbital notch to the median postero-dorsal point of the carapace, in lateral view). The lamina tapers feebly, with poorly developed lateral carinae, situated nearer to the ventral margin, which is straight or feebly concave, than to the dorsal margin. The dorsal margin is armed with from 9 to 11 acute teeth, of which 3 or 4 are situated on the carapace posterior to the level of the orbital margin. The first tooth is situated at a level of half the post-orbital carapace length or more from the orbital margin. The teeth on the carapace are larger and more widely spaced than those on the dorsal lamina, which gradually decrease in size towards the tip. The ventral border of the lamina bears 2 or 3 teeth on the distal fourth. The orbit is obsolescent and there is no supra-orbital spine. The inferior orbital angle is acutely produced, with a short medial ventral flange, and extends far beyond the tip of the antennal spine. The antennal spine is slender, acute, marginal and situated closely below the inferior orbital angle. The hepatic spine is well developed, larger than the antennal spine and situated more posteriorly at a distinctly lower level. The antero-lateral angle of the carapace is bluntly rounded.

The third abdominal segment is strongly produced postero-dorsally as a compressed rounded lobe projecting backwards, from the posterior half of the segment. The fifth segment is about 0.4 of the length of the sixth, which is 2.3 times longer than wide. The postero-lateral angle is acutely produced and the postero-ventral angle blunt and setose. In the male, the pleura are normal, all broadly rounded posteriorly. In the non-ovigerous female they are similar but larger. In the ovigerous female, the first three are greatly expanded, with the first and third broadly notched and the second deeply notched antero-ventrally. The pleuron of the first abdominal segment is strongly produced antero-ventrally and the lower part separated by a deep notch from the upper part of the pleuron, which is also produced anteriorly.

The telson is about 0.8 of the length of the sixth abdominal segment. It is about 3.5 times longer than the anterior width, tapering with straight sides to half that width posteriorly. The two pairs of dorsal spines are situated at 0.5 and 0.75 of the telson length and are equal to about 0.6 of the telson length. The posterior margin is moderately produced, with a slender acute median point.



A REDESCRIPTION OF *PERICLIMENES AESOPIUS*

The lateral pair of posterior spines is similar to the dorsal spines. The intermediate spines are long and robust, equal to 0.2 of the telson length. The submedian spines are also robust, equal to 0.4 of the intermediate spines and finely setulose. A pair of simple setae are also present dorsally.

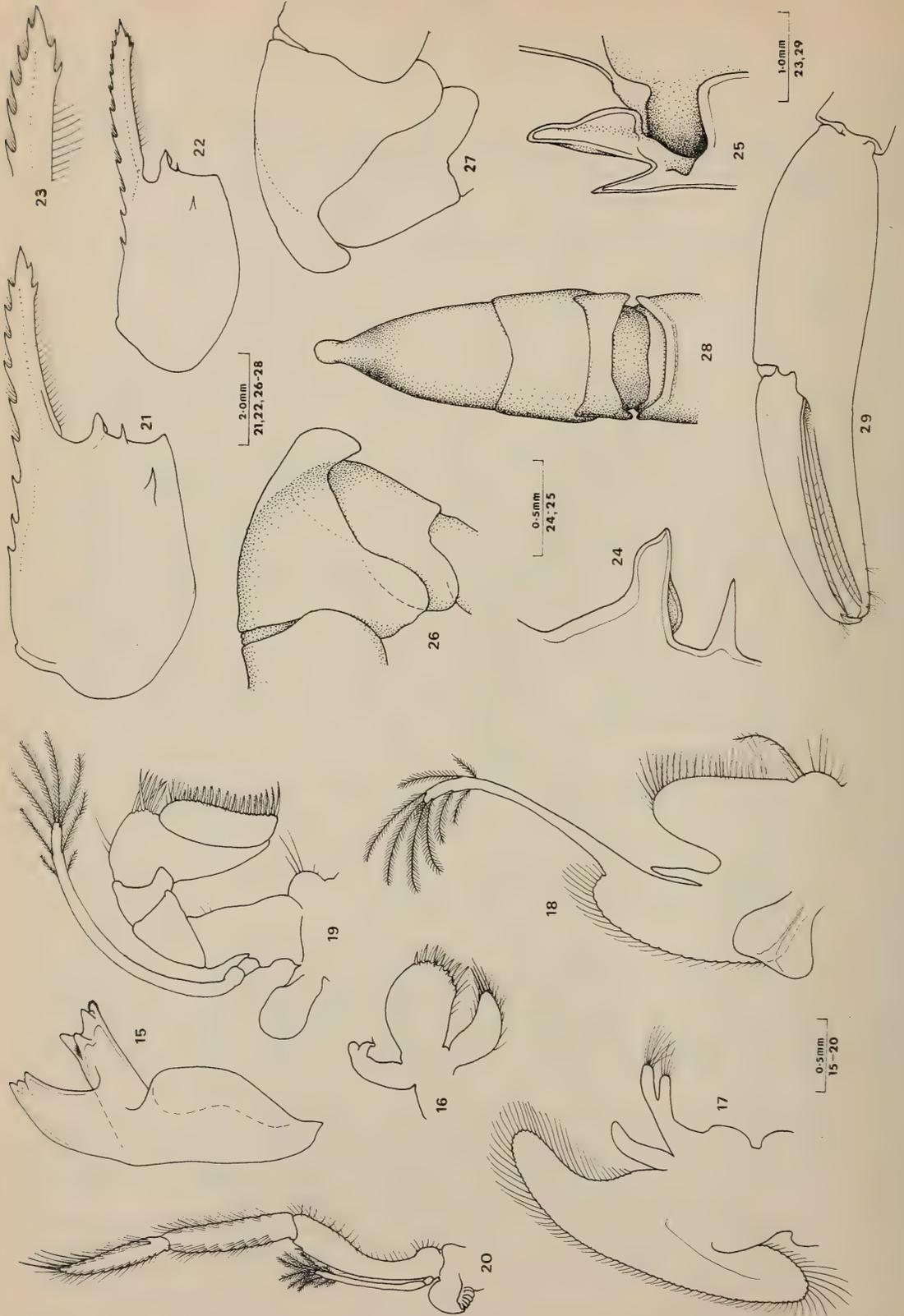
The cornea is globular, of slightly greater diameter than the distal end of the eyestalk, which is subcylindrical, about 2.3 times longer than wide at the base. An accessory pigment spot is distinct. The ophthalmic somite bears an acute median, anteriorly directed hook-like process.

The antennular peduncle slightly exceeds the tip of the rostrum but not the spine of the scaphocerite. The proximal segment is about 2.7 times longer than wide at half its length, with the antero-lateral lobe strongly produced with numerous marginal setae, and medially inclined to reach the level of the proximal end of the distal peduncular segment. The lateral margin is straight, with a strong distal tooth at a level just distal to the proximal end of the intermediate segment and far exceeded by the antero-lateral lobe. The ventro-medial margin bears a short acute tooth. The stylocerite is well developed, slender and acute, reaching to the level of the middle of the medial border. The statocyst is normal with a regular oval statolith. The intermediate and distal segments are together equal to half the length of the medial margin of the proximal segment, with the former segment equal to two thirds of the length of the latter and with a small setose antero-lateral lobe. The lower flagellum is biramous, with the rami fused for the twelve proximal segments. The shorter free ramus, in the dissected female specimen, consists of seven segments. The larger ramus is filiform and has about 20 segments. About 15 groups of aesthetascs are present.

The basicerite of the antenna is robust, with a strong lateral tooth. The carpcerite exceeds the tip of the stylocerite, and is about twice as long as broad and compressed. The scaphocerite is almost three times longer than broad, with the greatest width distally at the level of the disto-lateral spine. The anterior margin of the lamella is broadly rounded, slightly medially orientated and extending far beyond the disto-lateral spine, which is at the end of the straight lateral margin. The flagellum is long and slender.

The mouthparts are typical of the genus *Periclimenes*. The mandible is without a palp. The corpus is stout and the incisor process is robust, tapering distally to three stout terminal teeth. The molar process bears several large blunt teeth distally. The maxillula has a slender bilobed palp, the lower lobe having a simple hook-like seta disto-ventrally. The upper lacinia is broad, with 7-8 finely denticulate spines and numerous setae distally. The lower lacinia is

Figs. 2-14. *Periclimenes aesopius*. 2-4, rostral variation in ovigerous females. 5, inferior orbital angle. 6, pleuron of first abdominal segment, left lateral. 7, antennule. 8, antenna. 9, first pereopod. 10, second pereopod. 11, dactyl or fifth pereopod. 12, uropod. 13, telson. 14, posterior telson spines.



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slender and setose distally. The maxillula has a slender, non-setiferous palp. The basal endite is slender and tapering, with slender blunt distal lobes. The upper lobe is distinctly longer than the lower and both bear a small group of slender simple terminal setae. The coxal endite is absent and the margin is broadly rounded. The scaphognathite is well developed, long and slender, about 3.3 times longer than broad at the level of the base of the palp. The anterior lobe is slender, with the medial margin strongly concave. The first maxilliped has a small slender palp, non-setiferous, falling far short of the anterior margins of the basal endite or caridean lobe. The basal endite is large, broad, rounded with numerous setae along the antero-medial margins. The coxal endite is distinct, but small and rounded, with a few short, simple setae and a single long plumose seta. The caridean lobe is well developed, elongated and narrow. The epipod is small and feebly bilobed. The endopod of the second maxilliped is typical. The dactylar segment bears numerous stout denticulate spines along its medial margin. Longer spines are present on the disto-medial angle of the propod. The coxa is produced as a rounded medial lobe, with a few simple setae, and a small sub-rectangular epipod, without a podobranch, is present laterally. The third maxilliped is slender and exceeds the carapocerite by the length of the terminal segment. The antepenultimate segment consists of the ischio-merus and basis, which are completely ankylosed, with the medial border of the latter slightly produced, broadly rounded and setose. The segment is strongly bowed, about 5 times longer than broad, with a small spine at the distal end of the lateral margin and the medial border is sparsely setose. The penultimate segment is slightly shorter than the antepenultimate, about 5 times longer than wide, with numerous groups of finely denticulate setae. The terminal segment is about 0.9 of the length of the penultimate, about five times longer than wide, tapering distally, with more numerous groups of denticulate setae. The coxa is not produced medially, but a well developed rounded epipod is present laterally with also a small multilamellar arthrobranch. All three maxillipeds have the flagella of the exopods well developed, with about six large plumose setae distally and several shorter ones.

The fourth thoracic sternite is without a median process.

The first pereopod is moderately stout, exceeding the carapocerite by the length of the fingers. The palm of the chela is about twice as long as wide, slightly compressed and scarcely tapering. The fingers are subequal to the palm length, compressed, with feebly hooked tips and entire cutting edges. The carpus is 0.75 times the length of the chela, 3.5 times longer than the distal width,

Figs. 15-29. *Periclimenes aesopius*. 15, mandible. 16, maxillula. 17, maxilla. 18, first maxilliped. 19, second maxilliped. 20, third maxilliped. Types 21,22, carapace and rostrum. 23, tip of rostrum. 24, inferior orbital angle, lateral aspect. 25, inferior orbital angle, ventral aspect. 26, 27, third abdominal segment, lateral aspect. 28, first three abdominal segments, dorsal aspect. 29, chela of second pereopod. 21, 24, 25, 26, 28, 29, allotype. 22, 23, 27, holotype.

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twice as wide distally as proximally. The merus is slender, 7.5 times longer than wide and slightly shorter than the chela. The ischium is short, 0.4 of the length of the merus and feebly setose along the medial border. The basis is 1.1 times the length of the ischium and is also sparsely setose medially. The coxa is more robust, with a small setose ventro-medial process.

The second pereopods are subequal and similar. The carpoperite is exceeded by the carpus and chela. The palm of the chela is about 2.5 times longer than wide, feebly compressed and slightly tapering distally. The fingers are slightly bowed and a little shorter than the palm length. The tips are hooked and the cutting edges straight and entire. The carpus is short and stout, 0.6 of the palm length, moderately expanded distally and unarmed. The merus and ischium are also unarmed, the merus subequal to the palm length and 5.5 times longer than wide, the ischium more slender, subequal in length to the merus and 6.0 times longer than wide.

The ambulatory pereopods are slender, the third exceeding the basipereopod by dactyl, propod and carpus. The dactylus is slender and curved, about 4.0 times longer than the width at the base. The unguis is slender, equal to 0.6 of the length of the corpus, which bears a stout distal accessory spine. Sensory setae are present disto-laterally. The propod is about 10 times longer than wide, with 5-6 ventral spines. The carpus is 0.6 of the propod length and the merus is subequal; both are without spines. The fourth and fifth pereopods are similar but longer, the ratios of the segments being, in the dissected female specimen:

	P3	P4	P5
Propod	35	39	45
Carpus	23	23	25
Merus	35	43	52

The pleopods are normal. The appendices internae of the ovigerous female are very well developed. The appendix masculina bears numerous long spiniform setae.

The uropods are normal. The protopodite is without a postero-lateral spine. The exopod is broad, 2.6 times longer than wide, with the lateral margin straight, setose, terminating in an acute tooth distally, with a strong mobile spine medially. The endopod is about 3.4 times longer than broad and falls short of the end of the exopod.

TYPES:

Bate's specimens are preserved in the collections of the British Museum (Natural History). His description and figure 5 are based on the female specimen, with a rostral dentition of 9/2. This specimen is now in a fragmented state. The carapace is detached from the cephalothorax, which is also separated from the abdomen. The mouthparts, except the third right maxilliped, the eyes and the antennae are detached, but all pereopods are still attached to the cephalothorax.

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The male specimen, with a rostral dentition of 11/2, is almost intact, and lacks only the right third pereopod. The female specimen is now designated as the holotype and the male as allotype.

COLORATION:

Bate has reported that preserved specimens were spotted with red on rostrum, antennae and pereopods. Hale (1927, 1928) has also reported a similar coloration in his specimens and illustrated the colour pattern.

MEASUREMENTS:

Post-orbital carapace length, ♂ (allotype) 3.4 mm; ♀, (holotype), non-ovigerous, 5.0 mm; ovigerous, 4.6-5.6 mm. Length of ovum, 0.5 mm.

Periclimenes holthuisi Bruce (Fig. 7).

Urocaris longicaudata Pearson, 1905, Rep. Ceylon Pearl Oyster Fish., 4:78, pl. 1 fig. 5.

Periclimenes (Periclimenes) aesopius— Holthius, 1952, Siboga Exped. Mon., 39a¹⁰:34-37, figs. 5-6.

Periclimenes aesopius— Bruce, 1966, Crustaceana, 10(1):21, fig. 1b, 2ef.

Periclimenes holthuisi Bruce, 1969, Zool. Meded., Leiden, 43(26):258-259. —Monod, 1969, Cahiers Pacifique, 13:216-220, figs. 69-73. —Bruce, 1972, Crustaceana, 23(2):300-302; 1973, Crustaceana, 24(1):99; in press.

MATERIAL EXAMINED:

4 spms., Bowen, Queensland, Coll. E. M. Rainford. British Museum (Natural History) registration no. 1923.8.22.8-10.

DESCRIPTION:

The specimens agree well with the previously available information (Holthius, 1953; Bruce, 1969). The rostral dentition is 8.9/1.2. The dorsal lobe on the third abdominal segment is distinctly smaller than in *P. aesopius*. The inferior orbital angle is particularly long and acutely produced. All specimens are in a good state of preservation.

HOST:

The collector noted that the specimens were obtained from an anemone.

REMARKS:

The type material, from Hong Kong, was also found in association with an anemone. The species has also been found in association with the jellyfish *Cassiopea andromeda* Forsskål in Zanzibar (Bruce, 1972) and with the coral *Fungia actiniiformis* (Quoy & Gaimard). It has also been recorded from Peloris Island, Queensland (Bruce, in press).

DISTRIBUTION:

Type locality, Hong Kong. Also recorded from Zanzibar; Maldivé Islands; Ceylon; Indonesia, New Guinea; South China Sea; Japan; New Caledonia and Queensland, Australia.

Periclimenes indicus (Kemp) (Fig. 8)

Urocaris indica Kemp, 1915, Mem. Indian Mus., 5:275, fig. 26, pl. 13 fig. 9. —Borradaile, 1917, Trans. Linn. Soc. Lond. Zool., (2)71:323.

Periclimenes (*Periclimenes*) *indicus*— Kemp, 1922, Rec. Indian Mus., 24:104 (key), 144, 145, 146, fig. 13; 1925, Rec. Indian Mus., 27:323. —Holthius, 1952, Siboga Exped. Mon., 39a¹⁰:9, 32, 33, 39-40, fig. 8.

Periclimenes indicus— Kemp, 1922, Rec. Indian Mus., 42:115. —Fujino & Miyake, 1970, J. Fac. Agric., Kyushu Univ., 16(3):255.

Periclimenes indica— Panikkar & Aiyar, 1939, Proc. Indian Acad. Sci., 98:253.

Periclimenes (*Periclimenes*) *aesopius*— Johnson, 1961, Bull. Mus. Nat., Singapore, 30:58, 61, 75 tab. 1.

MATERIAL EXAMINED:

(i) 31 spms., (8 ovig. ♀, 4 juv.) Siglap, Singapore, 6 ins. below L.T., 25 February 1952, coll. D. S. Johnson, British Museum (Natural History) registration no. 1954.11.5.11-15.

(ii) 3 ♀ (2 ovig.), 4 juv., Myora, North Stradbroke Is., Queensland, Australia, 31 January 1968, coll. A.J.B., (no. 836).

(iii) 4 ♂, 14 ♀ (13 ovig.), Myora, North Stradbroke Is., as above) (no. 837).

(iv) 2 ovig. ♀, Peel Island, Moreton Bay, Queensland, Australia, 24 September 1968, coll. A.J.B., (no. 963).

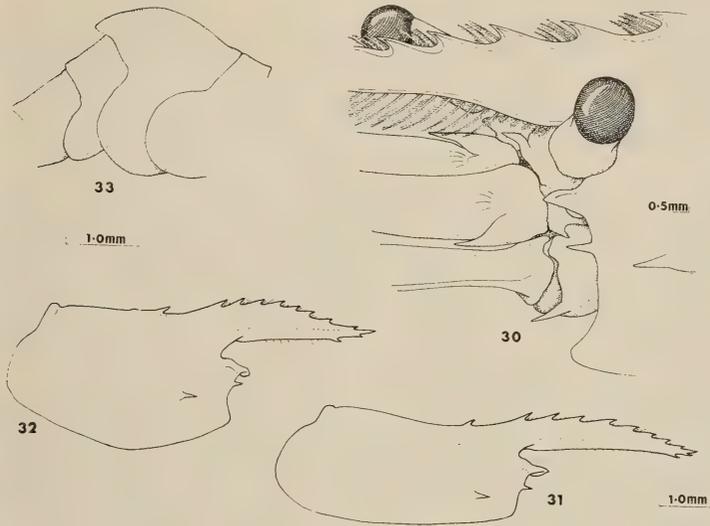
(v) 2 ♂, 2 ovig. ♀, Chilka Lake, no date, Zool. Survey India. (no. 952).

DESCRIPTION:

This species has been well described by Kemp (1922) and the Australian specimens agree closely with his description and with the specimens from the type locality, Chilka Lake, Orissa, India.

The specimens reported by Johnson (1961) as common in the *Enbalus* beds at Singapore, and referred then to *P. aesopius*, have been deposited in the collections of the British Museum (Natural History). These have been re-examined and found to belong to *P. indicus* (Kemp). Of six ovigerous females with undamaged rostra the dentition was 9/2 (4); 9/3 (1) and 10/2 (1), and the proximal part of the dorsal crest is distinctly elevated. The epigastric spine is situated well behind the posterior orbital margin. The inferior orbital angle is produced, but short and distally blunt, with a small ventral flange. The third abdominal segment is only slightly produced in the postero-dorsal midline and is not elevated to form a hump.

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Figs. 30-33. *Periclimenes* spp. 30, *P. aesopioides* ophthalmic somite, dorso-lateral view. 31, *P. holthuisi* Bruce, ovigerous female, Bowen, carapace and rostrum. 32, *P. indicus* (Kemp), ovigerous female, Siglap, Singapore, carapace and rostrum. 33, same, third abdominal segment.

COLORATION:

Generally transparent but mottled with red-brown; especially along ventral aspect of body, and dorsally over posterior margins of third and fourth abdominal segments, tip of scaphocariate, ventral eyestalk, coxae of pereopods and tip of caudal fan. Scattered small white dots over branchiostegite and pleura. Ovary and ova bright green.

HOST:

Macroactylus aspera Haddon & Shackleton (Actiniaria). All 18 specimens (no. 837) were obtained from the single host anemone.

REMARKS:

This species has not been previously recorded from Australia and these records represent a considerable extension of the known range of this species. The association of this species with an actinarian host has also not been previously reported and is of interest. It is thought probable that the other Australian specimens, as well as those from Singapore, may have been also associated with anemones but that on disturbance these hosts had withdrawn into the soft substrate leaving the shrimps among the surrounding phanerogams to be caught by the collector's net.

DISTRIBUTION:

Type locality, Chilka Lake, Orissa, India. Also reported from the Gulf of Manaar; and Madras, India; the Nicobar Islands, and Sumbawa and Celebes, Indonesia. Now also from Singapore and Queensland, Australia.

DISCUSSION

Periclimenes aesopius (Bate) is not known outside the restricted region of South Australia and appears to be an endemic relict species confined to that area. It belongs to a group of widely distributed species that are characterised particularly by the posterior production of the dorsal margin of the third abdominal segment and a produced inferior orbital angle with a ventral flange. Most of the species have a biunguiculate dactylus on the ambulatory pereopods but this is lacking in some species. In the Indo-West Pacific region this group is represented by *P. aesopius*, *P. holthuisi*, *P. indicus* and also *P. tosaensis* Kubo, which differs from the first three species in the lack of an accessory spine on the dactyls of the ambulatory pereopods (Kubo, 1951). In the Eastern Atlantic and Mediterranean Seas the group is represented by *P. amethysteus* (Risso) and *P. scriptus* (Risso), while in the Western Atlantic and Caribbean region there are *P. anthophilus* Holthuis & Eibl-Eibesfeldt, *P. pedersoni* Chace, *P. yucatanicus*

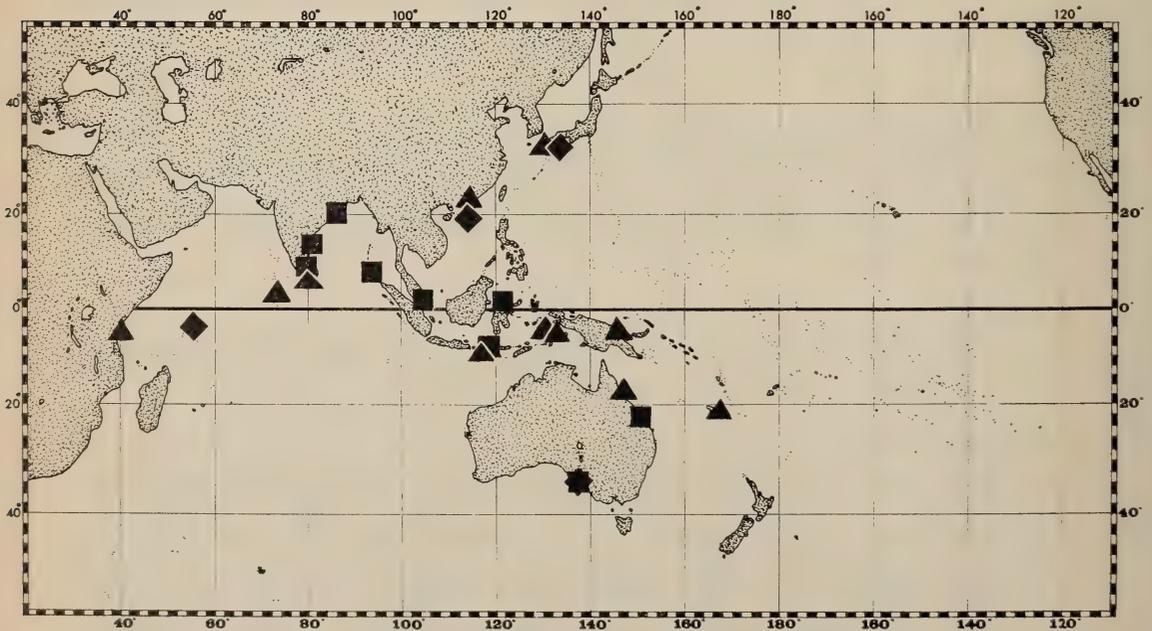


Fig. 34. Distribution of *Periclimenes aesopius* (Bate) ★, and related Indo-West Pacific species: *P. holthuisi* Bruce ▲, *P. indicus* Kemp ■, *P. tosaensis* Kubo ●.

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Ives and *P. magnus* Holthuis, the latter species also differing from the others in the lack of an accessory spine on the dactyls of the ambulatory pereopods (Holthuis, 1952).

In the Pontoniinae there are no established examples of free-living species that have biunguiculate dactyls on the walking legs. Of the species mentioned above *P. holthuisi*, *P. indicus*, *P. anthophilus*, *P. pedersoni* and *P. yucatanicus* are all known associates of sea anemones, (Holthuis & Eibl-Eibesfeldt, 1964; Limbaugh et al, 1961). In the Mediterranean Sea *P. amethysteus* and *P. scriptus* are also associates of actinarians (Svoboda, per. comm.) and other coelenterates. The hosts of *P. aesopius*, *P. tosaensis* and *P. magnus* have not yet been identified but it seems probable that they will also be associates of sea anemones, or other coelenterates.

The four American species all have the maxilla with a simple distal endite. This contrasts with all the other species, East Atlantic and Indo-West Pacific, in which this endite is normally distinctly bifid, although in *P. amethysteus* it may be simple or bifid (Holthuis, 1952), suggesting that the two groups have originated by radiation from different ancestral species. Of the species known at present *P. indicus* is the least morphologically specialized but *P. scriptus* and *P. amethysteus* also show little indication of specialization. In *P. tosaensis* and *P. magnus* the simple dactylus of the ambulatory pereopod is due to the secondary loss of the accessory tooth.

Periclimenes aesopius may be distinguished from all the related species by the remarkable hump-like process developed dorsally on the third abdominal segment, and by the presence of three or four post-rostral teeth on the dorsum of the carapace, as well as the biunguiculate dactylus of the ambulatory pereopods. In the other species usually only a single post-rostral tooth is present but in *P. holthuisi* and *P. anthophilus* there may be 1 or 2, and *P. yucatanicus* generally has two. The abdominal hump is less well developed in the other species but is distinct in *P. pedersoni*, *P. yucatanicus* and *P. magnus*, as well as *P. holthuisi*. In *P. scriptus*, *P. amethysteus* and *P. indicus*, it is very feebly developed, but the postero-dorsal margin of the third abdominal segment is produced backwards but not elevated, as it is also in *P. anthophilus*. In *P. tosaensis* a feebly elevated hump is present. The antero-ventral emargination of the pleura of the ovigerous female is also apparently unique in the Pontoniinae. With respect to these features, *P. aesopius* appears to be the most highly specialized species.

The function of the dorsal abdominal hump is obscure but this region is often conspicuously marked with bright colours in related species, (Chace, 1958; Limbaugh, et al 1961), often fish cleaners, and so it is probably to increase the visibility of the displayed signals.

Hale (1927) has described and illustrated the appearance of *P. aesopius* in life. The body of the shrimp is largely transparent but the dorsum of the first three abdominal segments, including the hump of the third segment, is white outlined in red. This must present a conspicuous signal. This region is similarly

conspicuously coloured in the cleaner shrimp *P. pedersoni*. A large tan coloured saddle shaped spot, ringed with white is present on the third abdominal segment in *P. yucatinicus*, another cleaner shrimp. Conspicuous red and white patches are also present on the third abdominal segment dorsally in *Leandrites cyrtorhynchus* Fujino & Miyake. In this palaemonine shrimp the third abdominal segment is posteriorly produced and it is also reported to be a fish cleaning species (Holzberg 1971). The markings in this shrimp are also red and white (Bruce, 1975).

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A System of Intersomital Dorsoventral Muscles in the Posterior Body Somites of Land-leeches (Hirudinea : Haemadipsoidea)

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ABSTRACT

Six pairs of dorsoventral muscles have their origins in somites xxii to xxvii, and insertions in xix to xxiii. The system is known only in Haemadipsoidea.

INTRODUCTION

Somatic dorsoventral muscles are known in Hirudinea as extending from the ventral to the dorsal body wall with the origin and insertion of a strand essentially in the same transverse plane.

There is described here a system of six pairs of strap-like dorsoventral muscles having their origin in the vicinity of ganglia xxii to xxvii and the posterior ganglionic mass, ascending to insertions on the dorsal body wall in somites xix to xxiii, and accordingly intersomital. Dissections of some land-leeches also show paired strap-like vertical muscles originating on the ventral body wall in the middle of somites xxii and xxiii, and inserted onto the intestine. These and the intersomital system are known to me only in land-leeches.

I have observed the intersomital system in land-leeches in the Haemadipsidae s.s., and in all four subfamilies of the Domanibdellidae. The system is detailed here as seen in *Chtonobdella limbata* Grube 1866, with brief comparative notes on the system in three other species of the Chtonobdellinae.

The anatomy of the intersomital system indicates function in such actions as: the maintenance of the extended body elevated at angles up to the vertical; torsion on the longitudinal axis of the elevated extended body; the lateral swing through an arc up to 160° of the body extended in the near horizontal plane; and the positioning of the relatively large and heavy posterior sucker adjacent to the anterior sucker during rapid dicotylal locomotion.

Excepting longitudinal undulation which I have not seen in land-leeches, these and other actions are performed with precision, slowly to rapidly, and this without the advantage of relief from gravitational and other mechanical stresses such as the surrounding medium provides for aquatic leeches.

It is proposed that the system be named the mm. Habenaе (habena, -ae: the thing holding a thing in place; the reins of a bridle; etc.).

The mm. habenae are assessable as dorsoventral muscles modified along with the reduction on the venter of the posterior body somites, a combination representing an early specialization in land-leeches for terrestrial locomotion.

RESULTS AND DISCUSSION

GENERAL ANATOMY OF THE POSTERIOR BODY SOMITES AND DORSOVENTRAL MUSCLES IN EUTHYLAEMATOUS LEECHES:

In aquatic euthylaematous sanguivorous and macrophagous leeches, somites xxiii and xxiv are fully formed on all aspects of the body wall, as also xxv which may be shortened on the venter by a reduction in the length or number of annuli. Somite xxv is commonly the most posterior somite formed on the venter, in some xxvi may be represented by a very short thin ridge. Somite xxvii is formed only on the dorsum. In these leeches, somital ganglia xxiii to xxvii are spaced apart, and xxvii narrowly spaced from the posterior ganglionic mass. The posterior end of the body cavity tapers gradually to the narrow base for the posterior sucker.

In land-leeches, somite xxiii (xxiv in nearly all Domanibdellinae) is the most posterior somite formed on the venter, and reduced in length on this aspect. Somites xxiv (xxv) to xxvii are transversely abbreviated, progressively reduced in length on the dorsum and margins, and not represented on the venter. The reduction of the venter is reflected in the central nervous system in which somital ganglia xxii and xxiii are well spaced apart; xxiii spaced narrowly from xxiv; and xxiv to xxvii are in intimate contact, with xxvii in contact with the posterior ganglionic mass (Richardson, 1975).

The posterior end of the body cavity in land-leeches has the form of a broad shallow basin, the dorsal and dorsolateral walls formed by xxiv to xxvii, and the wide floor by the base for the posterior sucker.

The dorsoventral muscles in euthylaematous leeches are arranged in four longitudinal rows extending from the pharyngeal region into the intestinal region. A pair of paramedian rows define a median splanchnic chamber between them. The body cavity on each side of this is divided by a lateral row into a paramedian and a lateral splanchnic chamber (Richardson, 1969).

The four rows are complete palisades in macrophagous leeches. In the sanguivorous leeches, the paramedian rows are represented along their length by intersomital clusters of strands, embracing and dividing the crop into compartments which extend into the paramedian chambers.

In aquatic sanguivores, the paramedian rows are represented by intersomital clusters in the intestinal region at xix/xx to xxv/xxvi.

In land-leeches, the paramedian rows have the typical sanguivorous form, with clusters in the intestinal region at xix/xx to xxii/xxiii, some lacking clusters at xxi/xxii.

INTERSOMITAL MUSCLES OF LEECHES

Dissection: An incision through the margin of the body wall at xviii/xix is continued across the dorsum into the opposite margin. From this, an incision is made along the midline of the dorsal median field to the anus. This displays the paramedian dorsoventral muscles, and the intestine and the rectum in the median splanchnic chamber. The intestine is transected at the junction to the rectum, and these organs reflected.

Dissection on each side of the ventral nerve cord exposes the origins of the mm. habenae, and the course and insertions of the individual muscles can be followed. The somital levels of the origins can be assessed from the somital ganglia; the insertions, from the annulation of the dorsal body wall.

ANATOMY OF THE MM. HABENAE IN *Cbtonobdella Limbata* GRUBE 1866.
(Figs. 1 to 3)

Bilaterally symmetrical, elongate, thin, strap-like muscles originating close to the midline on the floor of the median splanchnic chamber in xxii and the following preanal somites; ascending anteriorly, laterally to transversely wide spaced insertions on the body wall roofing the paramedian and lateral splanchnic chambers in somites xix to xxiii.

In terms of their origins, the mm. habenae are divisible into:

- a) anterior habenae, two pairs originating in the adjacent halves of xxii and xxiii;
- b) middle habenae, two pairs originating adjacent to ganglia xxiv to xxvii and the posterior ganglionic mass; and
- c) posterior habenae, two pairs originating posterior to the middle pair.

The anterior and middle habenae have their origins in the ventral body wall, and the posterior pairs essentially on the base for the posterior sucker.

The two pairs at each level differ in their origins, courses and insertions. The most suitable anatomical description is provided in the following groupings:—

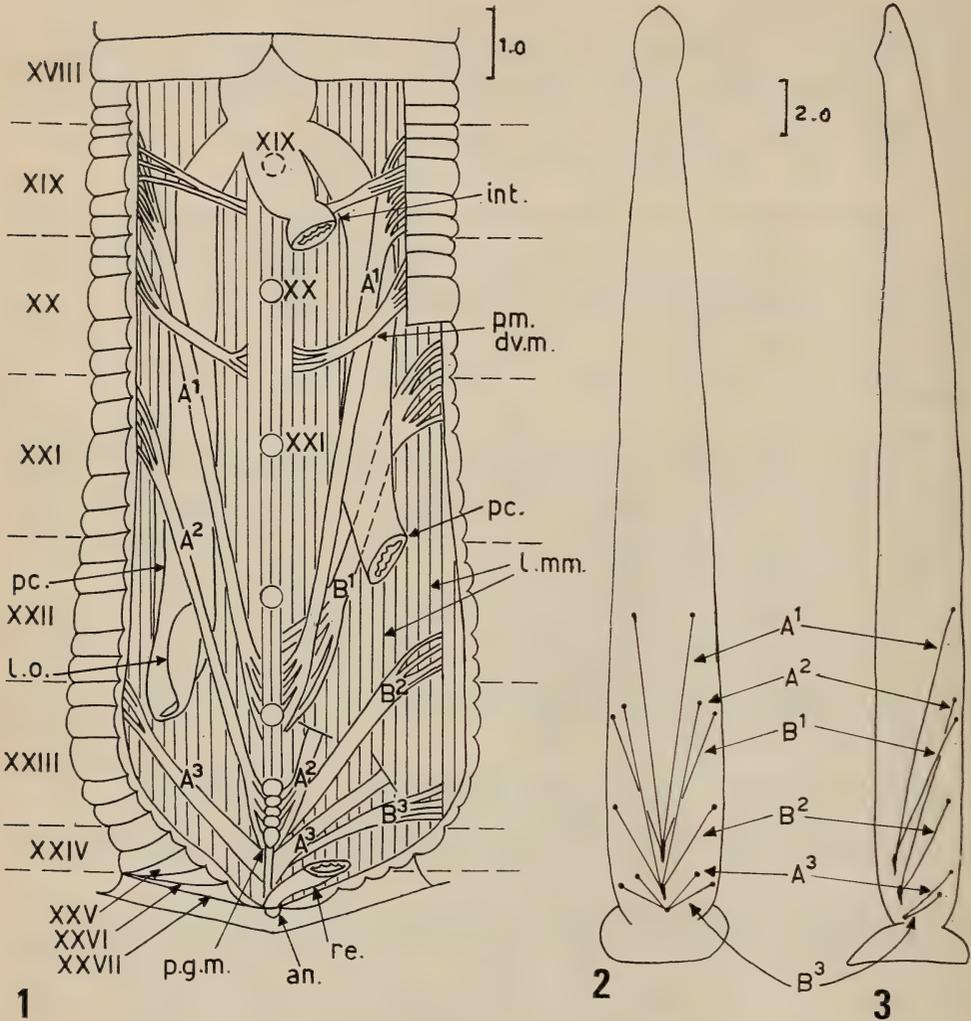
GROUP A.

Three pairs of habenae, anterior (A^1), middle (A^2), and posterior (A^3), the origins close to the midventral line, entering and ascending in the paramedian splanchnic chambers to insertions on the body wall roofing these chambers.

A^1 : origins in the contiguous halves of xxii and xxiii; ascending in the paramedian chamber medial to the postcaeca, to insertions in xix.

A^2 : origins lateral to ganglia xxiv to xxvii and the posterior ganglionic mass; course as A^1 ; insertions on the anterior half of xxi.

A^3 : origins posterior to the posterior ganglionic mass; ascending in the paramedian chambers posterior to the postcaeca; insertions on the anterior half of xxiii.



Figs. 1-3. The mm. habenae in *Chtonobdella limbata* Grube 1866. 1, Dissection of somites xix to xxvii from the dorsal aspect to show the origins, courses and insertions of the mm. habenae: Group A, on the left; on the right, A¹, the origins of A² and A³, and Group B. Only two pairs of dorsoventral clusters of the paramedian row are shown, others and the lateral palisades omitted for clarity. 2 and 3, semidiagrammatic representations of the dorsal and lateral views showing the general relationships of the habenae in the entire extended specimen.

Somital limits indicated by broken lines; somites and somital ganglia, by roman figures; annuli, a₂, etc.; somital ganglia represented at relative size. Scales, mm.

Abbreviations: an., anus; int., intestine; l.mm., longitudinal muscular layer in the body wall; l.o., lambertian organ; pc., postcaecum; p.g.m., posterior ganglionic mass; pm. dv.m., paramedian dorsoventral muscle; re., rectum.

INTERSOMITAL MUSCLES OF LEECHES

GROUP B.

Three pairs of habenae, anterior (B^1), middle (B^2), and posterior (B^3), the origins immediately lateral to the origins of the corresponding habenae of Group A, entering and crossing the floor of the paramedian chamber, to enter and ascend in the lateral splanchnic chambers to insertions on the body wall roofing these chambers.

B^1 : origins in the contiguous halves of xxii and xxiii; crossing the paramedian chamber ventral to the postcaeca, ascending lateral to the postcaeca, to insertions on the contiguous halves of xx and xxi.

B^2 : origins lateral to ganglia xxiv to xxvii and the posterior ganglionic mass; course, as B^1 ; insertions on the posterior half of xxii.

B^3 : origins posterior to the posterior ganglionic mass; course posterior to the postcaeca; insertions on the posterior half of xxiii.

The above provides a longitudinal alternation of the insertions of the habenae of Groups A and B, with the individual habenae of the B group having their insertions posterior to the corresponding habenae of the A group.

COMPARATIVE ANATOMY OF THE MM. HABENAE IN SOME CHTONOBDELLINAE:

The Chtonobdellinae contains the 5-annulate 2-jawed land-leeches of continental Australia east of the Great Divide (Richardson, 1975). The species considered here are *C. limbata*, central New South Wales, zoogeographically central eastern Bassian; *Quaesitobdella bilineata* Richardson 1975, central to northern New South Wales, central and northern eastern Bassian; *Jaabdella whitmani* (Lambert, 1899), southern and central Queensland, southern eastern Torresian; and *Amicibdella nigra* Richardson 1975, northern Queensland, northern eastern Torresian.

The annulation of the posterior body somites, the form of the posterior end of the body cavity, and the general anatomy of the mm. habenae are similar in the four species. One specimen of *J. whitmani* had a fourth pair of dorsoventral muscles originating posterior to the posterior ganglionic mass and inserted in the posterior half of xxiii. These were not seen in other specimens.

The summary given below shows the origins of A^2 and B^2 as the same in all four species. Groupings based on the differences in the origins and/or insertions of other pairs, show some peculiar to one species: e.g. the origin of A^1 more posterior in *J. whitmani*; the insertion of A^1 and the origin of B^1 more posterior in *A. nigra*; the insertion of B^3 more posterior in *C. limbata*; etc.

A major difference separates the bassian and torresian species: the origins of A^3 and B^3 are posterior to the posterior ganglionic mass in *C. limbata*, *Q. bilineata*; lateral to ganglia xxiv to xxvii and the posterior ganglionic mass in *J. whitmani*, *A. nigra*.

A^1 : origins in the contiguous halves of xxii and xxiii in *C. limbata*, *Q. bilineata*, *A. nigra*, the posterior half of xxiii in *J. whitmani*; insertions in the middle half

of xix in *C. limbata*, the posterior half of xix in *Q. bilineata*, *J. whitmani*, the anterior half of xx in *A. nigra*.

A²: origins lateral to ganglia xxiv to xxvii and the posterior ganglionic mass in all four species; insertions in the anterior half of xxi in *C. limbata*, *J. whitmani*, the posterior half of xxi in *Q. bilineata*, *A. nigra*.

A³: origins posterior to the posterior ganglionic mass in *C. limbata*, *Q. bilineata*, lateral to ganglia xxiv to xxvii and the posterior ganglionic mass, common with A² in *J. whitmani*, *A. nigra*; insertions, the anterior half of xxiii in *C. limbata*, contiguous halves of xxii and xxiii in *J. whitmani*, posterior half of xxii in *Q. bilineata*, *A. nigra*.

B¹: origins in the contiguous halves of xxii and xxiii in *C. limbata*, *Q. bilineata*, *J. whitmani*, in the posterior half of xxiii in *A. nigra*; insertions in the contiguous halves of xx and xxi in *C. limbata*, *J. whitmani*, *A. nigra*, posterior in xx in *Q. bilineata*.

B²: origins lateral to ganglia xxiv to xxvii and the posterior ganglionic mass in all four species; insertions in the posterior half of xxii in *C. limbata*, the contiguous halves of xxi and xxii in *Q. bilineata*, *J. whitmani*, the anterior half of xxii in *A. nigra*.

B³: distinct separate origins posterior to the posterior ganglionic mass in *C. limbata*, *Q. bilineata*, a common origin with B² in *J. whitmani*, *A. nigra*; insertions in the posterior half of xxiii in *C. limbata*, the contiguous halves of xxii and xxiii in *Q. bilineata*, *J. whitmani*, *A. nigra*.

ACKNOWLEDGEMENTS

This study has been conducted under an award from the Australian Research Grants Committee for studies on the zoology of Australian freshwater and terrestrial leeches.

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Short Paper:

Artificial Hybridization Techniques For Anuran Amphibians

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The general characteristics of most anurans (for example, their availability, external fertilization, lack of opaque covering on the egg, and ease of laboratory maintenance of embryos and larvae) make them particularly suitable for experimentation involving *in vitro* hybridization tests. This approach has been used both in studies of postmating isolation in closely-related species groups, and in establishing phylogenetic relationships in larger taxonomic groupings. For example, both applications have been used extensively in studies of the genus *Bufo* (see review by Blair, 1972).

Females for crosses should be freshly-collected, naturally ovulated individuals which are used within six hours of collection. Males can be stored for up to three months in cool cabinets (5-8°C) without any detectable effect on production of sperm. All animals should be killed by pithing immediately prior to use.

The following instruments have been found useful in performing artificial crosses. The Lawton Instrument Company catalogue number is given in parentheses to aid in instrument selection.

- 1 pair straight iris scissors (05-1450)
- 2 pairs small thumb dressing forceps, serrated (23-0560)
- 1 pair large angular forceps, serrated (09-0196)

All instruments should be clean and kept free of chemical contamination.

In addition, the following materials should be prepared before beginning the experiment:

- 500-1000 ml of distilled water (cold)
- 500-1000 ml of distilled water (boiling)

For each male in the experiment, a new sterilized, disposable plastic petri dish (e.g. 9.0 cm petri dish from Sterimed, Melbourne) should be marked on the lid and base with a permanent code to identify each cross, filled with about 10 ml of pond water [half strength Holtfreter's solution (Rugh, 1962) can be used instead of pond water] and placed so that the base is tilted and supported on one side by the lid.

The following techniques are modifications of the basic methods outlined in Rugh (1962) and have proved highly successful in crosses within all Australian genera of anurans which have been studied to date, viz. *Crinia*, *Geocrinia*, *Limnodynastes*, *Litoria*, *Neobatrachus*, *Pseudophryne*, and *Ranidella* (Watson, 1974, unpub. obs.).

A sperm suspension is prepared by dissecting testes from a male and macerating them (angular forceps facilitate this step) in water in a petri dish. Not more than 50 eggs should be used in each cross, so depending on the number of eggs available several males can be crossed to one female (for example, four to five males can be crossed to females of *Ranidella*, while 12 or more may be used with females of *Limnodynastes*).

After allowing 5 to 10 minutes for the sperm to become active, the female is killed and oviducal eggs dissected out and distributed among the sperm suspensions in such a way that each suspension receives eggs from different regions of both oviducts. After adding eggs to the sperm suspension the petri dish should be shaken gently to spread the eggs into a monolayer.

During all the above procedures it is important to prevent cross contamination of sperm suspensions. This is achieved by placing the dissecting instruments into boiling water and then into cold water between each operation.

For all artificial hybridization experiments it is essential to perform a partial control for each experimental series by fertilizing some of the eggs from the female with conspecific sperm.

Techniques for maintenance of embryos will vary according to the life history characteristics of the species involved.

In species where embryonic development is wholly aquatic, the petri dishes are filled with pond water after the eggs have rotated (rotation, resulting in the animal pole of each egg being uppermost, indicates successful fertilization). Organic debris, and damaged and infertile eggs should be removed. The egg clumps, which normally adhere to the bottom and sides of the petri dishes should be freed so as to float in the water, thus maximizing the exposed surface area of the clumps to ensure adequate gaseous exchange for the developing embryos. The dishes should then be covered.

In groups where embryonic development normally occurs on land in a saturated atmosphere (e.g. *Geocrinia*, *Pseudophryne*) the following procedure is followed. After rotation of the eggs and hydration of the egg capsules, excess water, organic debris, and damaged and infertile eggs are removed. The developing eggs should be arranged in a monolayer such that the eggs are in contact in order to provide an adequate exposed surface for gaseous exchange, while reducing to a minimum the surface area through which water loss from the egg capsules can take place. A wad of water-soaked paper tissue is placed in each dish out of contact with the egg capsules, and the dishes are covered. The egg capsules should be maintained in a fully hydrated state prior to hatching of the embryos

HYBRIDIZATION TECHNIQUES FOR AMPHIBIANS

by daily addition of drops of distilled water directly on to the eggs and by keeping the tissue wad saturated.

All developing embryos should be examined regularly for the presence of developmental abnormalities (see examples in Rugh, 1962). All abnormal embryos should be removed from the cultures.

After hatching, the young larvae should be transferred immediately to larger aquaria. Clean, plastic, glass or enamelled metal dishes containing 2 to 3 litres of pond water or Holtfreter's solution (Rugh, 1962) are suitable for this purpose.

Conditions for larval culture vary with species. Most species seem to grow well when fed par-boiled lettuce (clean lettuce leaves boiled for 5 to 6 minutes; a large quantity can be prepared and deep frozen for future use). However, some taxa, in particular members of the Myobatrachinae, require an additional high protein supplement for successful larval development. This can be provided by using high protein breakfast cereal, or by short duration addition of liver, or by making a suspension of fine-ground, dried pet food (e.g. Dog-Chow) in agar gel which when set can be cut up into small cubes and added to the aquarium. Particular care must be taken, especially when using high protein food sources, to keep the aquarium water clean and free of large-scale bacterial contamination.

When larvae reach stage 42 (Limbaugh and Volpe, 1957; i.e. when the fore-limbs are free) they should be removed from the culture dishes and placed in containers with tight-fitting lids. A small amount of pond water is added to each container and the containers should be kept in a tilted position so that the froglets can climb out of the water when metamorphosis is complete.

For most experimental purposes, raising hybrids to metamorphosis is sufficient. If adult hybrid progeny are required, the froglets should be transferred to terraria and feed live food appropriate to the size of each individual.

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NOTICE

The Royal Zoological Society of N.S.W. is sponsoring a symposium on Monotreme Biology, to be held at the University of N.S.W. on 15th-16th May, 1978.

Prof. G. B. Sharman (Macquarie University) is the symposium chairman.

Papers are invited dealing with unpublished material concerning any aspect of Monotreme Biology. The deadline for abstracts is 1st December, 1977.

All persons wishing to attend the symposium, whether speaking or not, are requested to write to the symposium secretary for a registration form not later than 1st March, 1978. There will be a registration fee of \$5.00.

Symposium Secretary,
M. L. Augee,
Zoology U.N.S.W.,
P.O. Box 1,
Kensington, N.S.W. 2033,
Australia.

Authors presenting papers to the symposium may have them published in a special issue of the society's scientific journal 'The Australian Zoologist'. All members of the society will receive this issue free of charge, and non-members are requested to order a copy (price \$5.00) in advance.

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NOTICE TO AUTHORS

Papers will be considered for publication in *The Australian Zoologist* if they make an original contribution to whole animal biology of the Australian fauna. Papers submitted will be subjected to review and thence to the normal editorial process, in the course of which authors will receive edited galley proofs for correction. A manuscript is accepted on the understanding that it is to be published exclusively in *The Australian Zoologist*.

MANUSCRIPTS (original and one copy) should be sent to the Editor, "The Australian Zoologist", New South Wales State Fisheries, Fisheries House, 211 Kent St., Sydney, N.S.W. 2000. They should be typewritten (double spaced) on good quality paper. All pages of the manuscript must be numbered consecutively, including those containing references, tables and figure legends, which should all be placed after the text.

On the first page of the manuscript should appear the title of the paper, name of the author, the name of the Institution where the work was done and the present postal address if different from that of the Institution. Titles should be as brief, but as informative, as possible. A short title, to serve as a running head and consisting of not more than 50 letters (including spaces) must also be given on the title page.

The abstract (up to 200 words) should state concisely the scope of the work and the principal findings and should be suitable for direct use by abstracting journals. The section headings should be Introduction, Materials and Methods, Results, Discussion, Acknowledgements and References. Presentation must be clear and concise and all unnecessary repetition especially in consecutive sections should be avoided. Footnotes should be avoided.

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SHORT PAPERS these should be no more than six typewriter pages long and should deal with a technique experiment or important observation not reaching lengthy treatment. Isolated factual notes would not be considered suitable.

A Survey of Central Australian Ichthyology

C. J. M. GLOVER & T. C. SIM

South Australian Museum, Adelaide, South Australia, 5000

ABSTRACT

The history of Central Australian ichthyology is reviewed from its inception in the 1840's to the present. Hampered by geographical isolation, an initial period of slow development preceeded the start of concerted scientific exploration towards the close of the nineteenth century. Occurrences and distributions of the Centre's fishes are now well documented and a provisional check-list is herein given. Taxonomic studies are well underway and increasing interest is now evident in the ecological field.

INTRODUCTION

For the present purpose "Central Australia" is regarded as virtually all of arid Australia, thereby embracing the drainage divisions of the Western Plateau and Lake Eyre as defined by Map 5 of the Review of Australia's Water Resources 1975 (1976), but excluding the Bulloo-Internal and Murray-Darling divisions (see Figure 1).

Except for one isolated occurrence (see later, Basedow 1918), no fishes were, until very recently, recorded from the mainly ephemeral waters of the Western Plateau. Most of the following commentary will therefore be almost entirely restricted to the Lake Eyre division.

Good general accounts of the country within the Central Australian region are given in Scenic Wonders of Australia (1976), whilst the Review of Australia's Water Resources 1975 (1976), provides concise descriptions and summarised data of the drainage divisions themselves.

The Lake Eyre drainage division embraces an arid area of 1.17 million km². Major rivers periodically flow in the relatively high-rainfall country of the north-east sector, in times of heavy seasonal precipitation, towards the interior and Lake Eyre itself. Flows reach the latter, and other major salt pans, irregularly, following

TABLE ONE

A PROVISIONAL CHECK-LIST OF CENTRAL AUSTRALIAN FISHES

All species listed, except *Carassius auratus*, have been recorded from the Lake Eyre Drainage. Those marked with a dagger (†) have also been recorded from the Western Plateau Drainage. Those with an asterisk (*) appear to be endemic to the Central Australian region.

Class TELEOSTOMI

Sub-Class ACTINOPTERYGII

Family Clupeidae

†*Nematalosa erebi* (Günther, 1868)

Family Retropinnidae

Retropinna semoni (Weber, 1895)

Family Plotosidae

Neosilurus hyrtilii (Steindachner, 1867)

†**Neosilurus argenteus* (Zietz, 1896)

**Neosilurus* sp. nov. (Ms., Feinberg & Nelson)

Neosilurus spp. nov. (3?)

Family Poeciliidae

†*Gambusia affinis* (Baird & Girard, 1853)

Gambusia dominicensis Regan, 1913

Family Melanotaeniidae

†*Melanotaenia tatei* (Zietz, 1896)

Family Atherinidae

Craterocephalus stercusmuscarum (Günther, 1867) (= *C. fluviatilis* McCulloch, 1913)

Craterocephalus eyresii (Steindachner, 1884)

**Craterocephalus dalhousiensis* Ivantsoff & Glover, 1974

Craterocephalus sp. (nov.?)

Family Centropomidae

†*Ambassis castelnaui* (Macleay, 1881)

Denariusa bandata (Whitley, 1948)

Family Serranidae

Plectroplites ambiguus (Richardson, 1845)

Family Teraponidae

†*Leiopotherapon unicolor* (Günther, 1859)

Amniataba percoides (Günther, 1864)

**Hephaestus* sp. (nov.?)

**Bidyanus welchi* (McCulloch & Waite, 1917)

Scortum hilli (Castelnau, 1877)

**Scortum barcoo* (McCulloch & Waite, 1917)

Family Gobiidae

Glossogobius giurus (Hamilton-Buchanan, 1822)

Mogurnda mogurnda (Richardson, 1844)

**Chlamydogobius eremius* (Zietz, 1896)

Hypseleotris spp. nov. (2?)

Family Cyprinidae

†*Carassius auratus* (Linnaeus, 1758)

CENTRAL AUSTRALIAN ICHTHYOLOGY

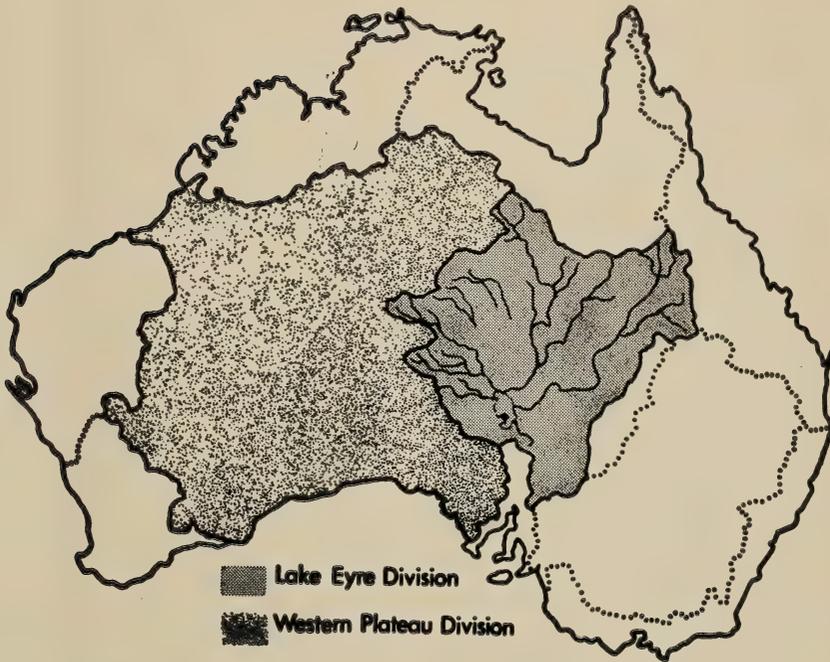


Fig. 1. The drainage divisions of Central Australia. Partly after Map 5 in Review of Australia's Water Resources 1975 (1976).

periods of exceptional rainfall and flooding in the north-east. Excluding the latter region, most of the *freshwater* of the Lake Eyre system is ephemeral, consisting mainly of scattered waterholes and rivers and creeks, which only fill with seasonal rains. Apart from the present phenomenal and prolonged flooding of Lake Eyre, permanent aquatic habitats in the arid interior are only represented by some large permanent waterholes, man-made dams and reservoirs, and surface waters associated with scattered artesian springs and bores.

The Western Plateau division, an immense area of 2.5 million km² of uncoordinated drainage, is, on the other hand, a region of *very* few permanent aquatic habitats. Creeks and rivers only flow for brief periods, following sporadic heavy rains, before the surface water is rapidly lost by high evaporation and absorption into the porous ground. The absence of fish throughout most of this division is therefore understandable.

Despite paucity of permanent water, a variety of fish, about twenty-nine species to date (some undescribed), are known to inhabit the Lake Eyre division, six of which (together with *Carassius auratus*) are also known from the Western Plateau division. These thirty species therefore constitute the total known fish

fauna of Central Australia (see Table 1). Often found in small populations, especially in ephemeral waterways, many of these fishes in the Centre also maintain themselves in great abundance in some of the more permanent waters, including those of artesian origin.

In view of the many taxonomic problems remaining, either under current investigation or awaiting attention, it must be emphasised that the list given in Table 1 is provisional and subject to revision. For example, although Nelson and Rothman (1973) tentatively referred the cluipiid of the Lake Eyre drainage to *Nematalosa erebi*, recent examination of larger collections than were available to Nelson and Rothman leave this designation open to doubt (C.J.M.G., unpublished data). Furthermore, although Vari's (1978) recent world revision of the Teraponidae advocated a number of changes to the Centre's teraponids, the region's plotosids remain very poorly known.

The following resumé traces the more noteworthy discoveries and observations pertaining to Central Australian fishes. Many of the early observations were clearly incidental to the then main task of geographical exploration. It was not until the last decade of the nineteenth century that the impetus of scientifically oriented exploration was evident. Whitley (1964) strangely omitted any mention (other than a scant and indirect reference) of this aspect of Australian ichthyology in his otherwise full and comprehensive survey.

Early references to specific, but otherwise formally undescribed fishes, are accompanied, where possible, by suggested probable current species names. Limited though these early reports may be, they do enable some comparisons to be made with existing occurrences of fish in Central Australia: changes accompanying European settlement have been thus deduced (see Glover & Sim, 1978).

Detailed route maps of major expeditions are, in some instances, appended to relevant reports and journals, and the routes of some expeditions are conveniently mapped together in certain publications such as those of Landsborough (1862), Calvert (1895) and Robinson (1927).

RESULTS

EARLY DISCOVERIES, 1840-1900

Documentation of the fish fauna of Central Australia commenced with the earliest European exploration of the region. Eyre (1845) certainly recognised that fish were a major food item of the Central aboriginal peoples, whilst Sturt (1849) observed "immense numbers of fish in reservoirs" adjacent to the desert later to bear his name and queried how they gained access to such an isolated place. Sturt (1849) appears to have provided the first description of a Central Australian fish, which seemed "to be identical with the silver perch of the Murray . . . but deeper and thinner" (*Scortum barcoo* or *Bidyanus welchi?*).

Babbage *et al* (1858) noted small fish at Gregory Creek and Finnis Springs west of Marree, whilst Stuart (1861, 1865) frequently sighted fish during his travels, including his epic 1861-62 journey across the continent. Stuart's (1865)

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account of stranded dead fish "resembling bream" (*Nematolosa erebi?*), at Lake Eyre and elsewhere, appears to be the first record of a phenomenon later noted in The Report of the Lake Eyre Committee (1955) following the Lake's flooding of 1949-50, and in more recent years by Ruello (1976) and Dulhunty and Merrick (1976a, 1976b). Waterhouse (1863), who accompanied Stuart's 1861-62 expedition, reported small fish "resembling gudgeon" (*Chlamydogobius eremius?*) at Strangways Springs. Although Waterhouse made collections of these and other natural history material (evidently the first to do so in the Central Australian region), many of the more delicate specimens, including the fish, did not survive the return journey. Moreover, as pointed out by Hale (1956), unpublished portions of Stuart's diary suggest that Stuart himself was little interested in Waterhouse's work, being as he was, preoccupied with crossing the Continent, and thus adverse to allowing adequate time for collecting.

Burke and Wills *et al* (1861) frequently referred to fish obtained from aborigines or that they themselves caught during their ill fated expedition. These included a variety "nine to ten inches (229-254 mm) long and two to three inches (51-76 mm) deep" (a Teraponid?); another termed by the aborigines "cupi"—"five to six inches (127-152 mm) long and not broader than an eel" (*Neosilurus* sp.?); one termed a "peru" (see later, Gason 1879 re "paroo", and Horne and Aiston 1924)—a "common one with large coarse scales" (*Nematolosa erebi?*); "calwichi"—"a delicious fish up to two pound" (0.9 kg); and "silver perch" (*Bidyanus welchi?*).

McKinlay (1862) observed fish in Lake Blanche and elsewhere, Landsborough (1862) speculated on the origins of fish in waterholes on the southern side of the Barkly Tablelands, and Giles (1894-95) reported "a number of small fish of a bright brown color" at Dalhousie Springs (*Craterocephalus dalhousiensis?*). Giles (1875a, 1875b, 1889) sighted great concentrations of fish in waterholes south-west of Alice Springs, including "a species up to three pounds" (1.3 kg) weight that "had a great resemblance to Murray Cod", and many small fish in the Finke river. Gosse (1874), on the other hand, although he inspected numerous permanent and ephemeral waters in the Centre, made only one direct reference to "a hole of water with fish in it" south-west of Alice Springs. Gason (1879), writing of the Dieri tribe of the lower Cooper, states, in relation to food, that "fish and other freshwater habitants . . . are few and unimportant, being caught in the waterholes and lakelets, which can only be called creeks or rivers when the floods come down; the last of which occurred in 1864". Gason (1879) listed three fish species—"paroo", "a small bony flat fish" (*Nematolosa erebi?*) (see Burke & Wills *et al* 1861 above re "peru" and Horne & Aiston 1924); "multhoomulthoo"—"a fish weighing from 3 to 3½ lbs" (1.4-1.6 kg); and "moodlakoopa"—"a fish averaging 2 lbs" (0.9 kg).

The Lake Eyre Expedition, under the leadership of Lewis (1875), collected what was to constitute the type material of *Craterocephalus eyresii*, the first fish from the Centre to be formally described (Steindachner, 1884).

It is interesting to note here, in the South Australian Museum Annual Report of 1886, that "we have only three species (of fish) from Lake Eyre any small fish from creeks or waterholes in the interior, would, even if not new, at least add to the knowledge of the distribution of species". As indicated by South Australian Museum Annual Reports, and that Museum's fish register, acquisitions of small collections of fish from the Centre were received intermittently from individual donors in subsequent years. Lucas (1894) reported two fish from near the MacDonnell Ranges, namely *Chatoessus erebi* (= *Nematolosa erebi*) and *Therapon fasciata* (= *Amniataba percoides*).

To this point in time very little effective collecting had in fact been accomplished, the number of recognisable fishes reported from the Centre amounting to no more than six species, only three of which could be considered as adequately described forms. These six species represented the families Clupeidae (1), Teraponidae (2), Atherinidae (1), Plectroplitidae (1) and Gobiidae (1). The absence of Central Australian localities from Macleay's (1881) Catalogue of Australian Fishes, and other checklists of the period, e.g. Tension-Woods (1883) and Ogilby (1886), is indicative of the then sparse knowledge of the Centre's fish fauna. Indeed, Lucas (1894) prophetically wrote . . . "It is to be hoped that the (then underway) Horn Expedition will bring back abundant material by means of which further light may be thrown on the distribution of Australian fresh-water fish . . ."

The Horn Scientific Expedition to Central Australia (1896) in fact heralded a major break-through in the region's ichthyology. From a substantial collection of fish, eight species representing five genera were recognised, six of which comprised new records for the Centre and all (at that stage) evidently new forms (Zietz 1896a, 1896b). The number of known fishes in the Centre now amounted to nine, but three of the above "new" species later proved to be synonymous with species described beforehand from elsewhere. In lieu of an apparent absence of affinity with Murray River forms, likely northern origins were now suggested for these fish in the above Horn Expedition's report. Furthermore, a lack of evidence to support aestivation, the probable role of floodwaters in dispersal and a suggestion of aerial transport of fish eggs by attachment to the feet of birds were also noted and commented upon in the expedition's report. In addition to the general narrative in Part I of this report, and Zietz's formal descriptions in Part II, Spencer & Gillen (1912) added further data and comment to the discoveries of fish by this expedition. Thus, at one stroke, the Centre's known *described* fish fauna had been increased from three to nine species, and basic but significant observations made relating to their ecology.

DISCOVERIES SINCE 1900

A scurry of scientific exploration, including biological collecting, now followed.

First, Basedow's (1914) journal of the 1903 Government North-West (of South Australia) Expedition reported what, in the context of the time, were

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particularly interesting observations, i.e. that there were "countless small fish in pools, along the overflow . . . of the highly mineralised Oodnadatta bore water" and that "the temperature of the water in which they were swimming, without the least sign of discomfort, was as high as 45°C". Basedow reported that this phenomenon, "induced the local folks to suppose the fish came up with the water from below". Having "disproved" that theory "by tying a net over the outlet of the bore for the greater part of the day without catching a fish", Basedow commented that "it is more probable that the fish came there as eggs, through the agency of the water fowl that occasionally frequent the water". Basedow further reported that he had also seen fish in hot springs at the Douglas River in the Northern Territory.

Next White's expedition (White *et al.*, 1914) noted fish at a number of bore sites, and collected *Leiopotherapon unicolor* elsewhere, in the Centre.

A South Australian Museum expedition to Strzelecki and Cooper Creeks in 1916 resulted in a further two species being described: *Bidyanus welchi* and *Scortum barcoo* (McCulloch & Waite, 1917).

Basedow (1918) next reported *Leiopotherapon unicolor* as having been collected in the Patterson Ranges of North-Western Australia. Interestingly, this last record was, until recently, the one and only fish record from the Western Plateau drainage division, despite earlier and subsequent explorations of the region by Warburton (1875), the Elder Expedition party (Lindsay, 1893; Stirling & Zietz, 1893; Helms, 1896), Slater and Lindgren (1955), the Western Australian Museum (Western Australian Museum Annual Reports 1963-64, 1964-65, 1969-70), the Australian Museum (Australian Museum Annual Reports 1951-52, 1952-53) and the Western Australian Wildlife Research Centre (Burbidge *et al.*, 1976). Allen (1977, in press) certainly did not record any species from the Western Plateau in his checklist of Western Australian freshwater fish. However, in October 1977, a South Australian Museum Expedition collected a number of species in the north east sector of the Western Plateau drainage (Wiso and Barkly basins) i.e. *Nematolosa erebi*, *Neosilurus argenteus*, *Melanotaenia tatei*, *Ambassis castelnaui* and *Leiopotherapon unicolor*. In 1978 *Carassius auratus* and *Gambusia affinis* were reported and confirmed present (personal communication from P. Burdon) in a dam at Woomera in the south-east sector of the Western Plateau drainage (Gairdner basin): this solitary occurrence of *Carassius auratus* is almost certainly the result of human introduction (both wild and domestic colour varieties being present), whilst the poeciliids (both here and in the Lake Eyre drainage) have probably also been similarly introduced (see Glover & Sim, 1978). Furthermore there are reports (personal communication from R. J. McKay) of fish having been found by railway fitters on the Nullabor Plain during the period 1917-22, and of "blind fish" in cave pools on the Nullabor Plain close to the railway line. In 1968 the South Australian Museum received a report of "blind fish" having been sighted in a cave pool north of the main road between Nullabor Homestead and Yalata Mission Station.

By now McCulloch (1929-30) listed but nine species as being specifically from "Central Australia".

Fletcher (1937) reported *Leiopotherapon unicolor* in Waroona Creek near Camooweal (Queensland), whilst the Simpson Desert Expedition of 1939 obtained *Ambassis castelnaui*, a new record, together with *Leiopotherapon unicolor* and *Bidyanus welchi*, all from temporary waters (Whitley, 1945).

The early 1950's saw a series of South Australian Museum trips to the then flooded Lakes Eyre and Callabonna, resulting in a variety of fish being collected from both (South Australian Museum Annual Reports 1952-53, 1954-55). In the late 1960's the Arid Zone Research Institute (Alice Springs) collected extensively in the Northern Territory, thereby establishing new locality records for a number of fishes in the north-western sector of the Lake Eyre drainage division (personal communication from S.A. Parker).

Following on from an embryological study of *Retropinna semoni* by Milward (1966), there then appeared a spate of breeding and physiologically oriented works. Although not based directly on Central Australian stock, many of these studies were upon species or closely allied forms known from that area, and thus are of direct relevance. Lake (1967a, 1967b) investigated the breeding and development of *Plectroplites ambiguus*, *Bidyanus bidyanus* and *Carassiops klunzingeri*, whilst Llewellyn (1968, 1971, 1973) examined aspects of the ecology, including thermal tolerance and breeding, of *Leioptherapon unicolor* and other species. McKay (1973) later examined aspects of the reproductive cycle of *Plectroplites ambiguus*, whilst more recently Beumer (1976) has further examined thermal (and salinity) tolerance, and aestivation, in *Leioptherapon unicolor*.

In 1967 a South Australian Museum investigation of the taxonomy and ecology of *Chlamydogobius eremius*, a fish known to inhabit artesian springs and bores, was initiated by one of the present authors (C.J.M.G.), and reported by Glover and Inglis (1971). This study revealed interesting ecological adaptations to an unusual habitat, in addition to many new locality records in the far north of South Australia, and provided further insight into fish dispersal mechanisms in the Centre (Glover 1971, 1973).

By this time Lake (1971) had listed seventeen species from nine families from the Lake Eyre division, but none from the Western Plateau.

A party from the Australian Museum collected a series of fishes from Cooper Creek, near Innamincka, including an evidently undescribed neosilurid, in 1971 (personal communication from J. R. Paxton). A joint party from the Australian Museum and New South Wales State Fisheries, in 1975, collected in the same place and from Lake Callabonna and other localities in the vicinity (personal communication from D. F. Hoese).

Following a visit to Dalhousie Springs, as reported by Souter (1974a, 1974b), Ivantsoff and Glover (1974) described a new atherinid from that locality and reported ecological observations made there on previous occasions.

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Stemming from earlier South Australian Museum studies, the present authors, in 1975, embarked upon a field survey of waters throughout the entire Lake Eyre division. Initial results of this project, augmented with complementary taxonomic/ecological studies, were reported by Glover (1975-78, 1977, in press) and Glover & Sim (1978).

CONCLUSION

It is evident that Central Australian ichthyology has experienced a checkered career, but that the last twenty-five years have seen an increasing impetus in fundamental field surveys and collecting, and more recently in taxonomic and ecological studies.

Suffice to say at this stage that adequate field observations and collections probably now exist to provide a nearly complete picture of the overall occurrence and incidence of the Centre's fishes, though not all forms are yet described or their relationships yet clear. These collections should engage systematists for some time yet in unravelling the taxonomic complexities of the respective groups, particularly of such lesser known ones like the notoriously obscure neosilurids. Other workers known to be at present examining Central Australian fishes include D. F. Hoese (Australian Museum : Gobiidae), W. Ivantsoff (Macquarie University : Atherinidae), J. R. Merrick (Sydney University : Teraponidae) and M. N. Feinberg & G. J. Nelson (American Museum of Natural History : Plotosidae).

Although little is known of the general biology of most of the Centre's fishes, it is this avenue of research, upon specific species, that probably offers especially promising and interesting results, particularly relating to their environmental adaptations.

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Observations on some Buprestidae (Coleoptera) from the Blue Mountains, N.S.W.

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ABSTRACT

Forty-two species of Buprestidae in nine genera were collected and observed in the Glenbrook area of the Blue Mountains N.S.W. during 1975-77. Specimens of three of these species were also collected from Wentworth Falls and Medlow Bath, in the higher Blue Mountains, during early 1977. A list of the jewel beetles, their occurrence, food plants and dates of collection, is included. Field observations on flight behaviour, feeding, defence and escape mechanisms, grooming and pollination are recorded and discussed. All of these aspects were not observed in every species mentioned. *Stigmodera macularia* (Don.), *S. variabilis* (Don.) and *Cisseis leucosticta* (Kirby) are figured.

INTRODUCTION

The Buprestidae commonly referred to as "jewel beetles" are well represented in Australia, with over 800 described species (Britton, 1970). When conditions are suitable e.g. high temperatures and profuse flowering and nectar-bearing by food plants, some species may be found in abundance, especially those of the dominant nectar-feeding genus *Stigmodera*. Individuals of foliage feeding genera e.g. *Cisseis*, *Ethon*, *Germanica* and *Paracephala* may be found during the summer months on their food plants, e.g. *Acacia* spp. (Mimosaceae) or *Casuarina* spp. (Casuarinaceae) (Froggatt, 1907; Tillyard, 1926; McKeown, 1945).

Some species have a widespread distribution, e.g. *Stigmodera erythroptera* Boisd. found in all states (Carter, 1931a), but others have somewhat limited distribution, e.g. *Stigmodera magnetica* Cart., from Western Australia (Glauert, 1948; Barker *et al.*, 1956; Barker *et al.*, 1960; Barker and Edward, 1963).

Despite the wide occurrence of some species, the great number of species and their abundance, very little is known about their biology (Hughes, 1975). This may be due, in part, to the difficulty of locating many species, as it appears from data at hand that numbers of individuals fluctuate from season to season; one species may be rare or absent one year in a particular area but be common the next season (Whitlock, 1947; Williams, 1977; and the present work).

Since very little has been written about any aspect of the biology of Australian Buprestidae, this study was undertaken in order to discover, within a relatively small area in the Blue Mountains, N.S.W., the species present and aspects of their behaviour in their natural habitat.

MATERIALS AND METHODS

(a) STUDY AREAS

The majority of observations were made on living insects in an area of radius approximately 6 km from the centre of Glenbrook, N.S.W. This area includes the townships of Lapstone, Blaxland and Warrimoo, 2 km S.E., 3 km N.W. and 6 km N.W. respectively, from the Glenbrook Post Office. Specimens of three species of buprestid were also collected from Wentworth Falls and Medlow Bath, in the higher Blue Mountains.

The township of Glenbrook is situated about 70 km (43 miles) by road, west of Sydney, at an altitude of 163 m (535 ft) above sea-level. Much of the natural bushland in the immediate vicinity of Glenbrook and other areas in the Blue Mountains has made way for residential development and no doubt the flora and fauna have been affected in various ways by this disturbance.

(b) COLLECTION TIMES AND MAIN FLOWERING SPECIES

Most field data and specimens were collected between December 1975 and February 1976 when *Angophora floribunda* (Sm.) Sweet, *A. bakeri* C. Hall, and *Leptospermum phyllicoides* (A. Cunn. ex Schau.) Cheel, major food plants for *Stigmodera*, flowered profusely and between December 1976 and February 1977, when *Leptospermum flavescens* Sm. was a dominant flowering plant in the areas studied. Specimens of foliage-feeding species of *Cisseis* were collected during both seasons but *Germarica*, *Paracephala* and *Astraeus* were only collected during the 1976/77 season. Specimens of *Cyria imperialis* Fabr. were only collected during 1975/76 when its main food plant in the area, *Banksia spinulosa* Sm. was in flower.

Specimens were collected by hand and/or net, released after examination, or kept for later examination and identification.

The majority of observations were made during periods of one to three hours, between 1200 and 1700 hrs (Eastern Standard Time).

(c) WEATHER CONDITIONS

The Glenbrook area receives an average annual rainfall of about 80 cm (32 inches) and temperatures range broadly from 1°C to 40°C. Weather conditions during the two seasons were variable with daily temperatures ranging from 15°C to 39°C. Good summer rains in excess of 203 mm (8 inches) fell during both seasons. During days when observations took place, conditions were mainly fine and clear with temperatures usually varying from 21°C to 39°C. The hottest day

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recorded during the two-year period of observation occurred during the summer of 1976/77, when 41.5°C was recorded at Glenbrook on the 5th January, 1977.

(d) NOMENCLATURE

The nomenclature used for plant species follows that of Beadle *et al.*, (1972). The nomenclature used for Buprestidae are as follows: for *Stigmodera* (Carter, 1916; 1929; 1931a; 1931b), for *Germanica*, *Paracephala*, *Curis*, *Cyria* and *Torresita* (Carter, 1929), for *Melobasis* (Carter, 1923b; 1929), for *Cisseis* (Carter, 1923a, 1929) and for *Astraeus* (Barker, 1975).

VEGETATION

The present vegetation of the Glenbrook area is one of dry sclerophyll forest dominated by scribbly gum, *Eucalyptus haemastoma* var. *sclerophylla* Blakely, the yellow bloodwood, *E. eximia* Schau., the red bloodwood, *E. gummifera* (Gaertn.) Hochr., and the Sydney peppermint, *E. piperita* Sm., as well as the angophoras, i.e. *Angophora costata* (Gaertn.) Druce, *A. floribunda* (Sm.) Sweet and *A. bakeri* C. Hall. The understorey vegetation is largely composed of species of *Acacia* (Mimosaceae); *Persoonia*, *Hakea*, *Banksia* and *Grevillea* (Proteaceae);

Pultenaea, *Bossiaea*, *Dillwynia*, *Oxylobium*, *Gompholobium*, *Daviesia* and *Phyllota* (Fabaceae); *Leptospermum* (Myrtaceae); and *Casuarina* (Casuarinaceae). Other small plants belonging to various plant families, including the grasses (Poaceae) occupy the ground zone strata. In deep gullies and gorges numerous ferns and rainforest tree species may be found, e.g. *Syncarpia glomulifera* (Sm.) Niedenzu (Myrtaceae). Many of the plants mentioned above, e.g. *Angophora*, *Leptospermum* and *Acacia* are food-plants for members of the Buprestidae (see Tables 1 and 2).

OBSERVATIONS AND DISCUSSION

(a) *List of species, occurrence, food plants and dates of collection*

This information is summarised in Table 1. The occurrence of buprestid species was rated on a per season basis similar to that of Williams (1977). The term "rare" indicates less than three specimens, "few" three to 10 specimens, and "common" more than 10 specimens captured and/or observed during each season of collection. Since this system was used by Williams (1977), comparisons can be made with his findings.

One fact that has emerged as a result of the two seasons of observations is the marked synchronization between the flowering of the food plants and the appearance of the nectar feeding species of *Stigmodera* and *Cisseis* upon the blossoms of these plants. Williams (1977) noted that he collected the most species and the highest number of individuals during the final flowering phase of the food plant (*Leptospermum flavescens* Sm.) at East Minto, New South Wales, during 1972-1975. This observation generally agreed with those at Glenbrook.

TABLE 1

List of species of Buprestidae collected in the Blue Mountains, 1975-1977.

SPECIES	SEASON							
	1975/76			SEASON		1976/77		
	Occurrence	Locality	Food Plant(s)	Dates of Collection	Occurrence	Locality	Food Plant(s)	Dates of Collection
Subfamily Buprestinae								
Tribe Buprestini								
1. <i>Astraeus pygmaeus</i> van de Poll	*	—	—	—	few	G	1, 2	7-20 Jan.
2. <i>Melobasis costata</i> Macleay	*	—	—	—	rare	G	4(?)	10 Jan.
3. <i>Melobasis cupriceps</i> (Kirby) (?)	*	—	—	—	rare	G	5, 6	28 Aug., 5 Dec.
4. <i>Torresita cuprifera</i> (Kirby)	rare	G	10	8 Dec.	few	G	9, 10	5, 22 Dec.
Tribe Stigmoderini								
5. <i>Stigmodera macularia</i> (Don.) (Fig. 1A and B)	common	G	10	2 Dec.-15 Jan.	rare	G	9	1-2 Dec.
6. <i>Stigmodera variabilis</i> (Don.) (Fig. 2A)	few	G	10, 11	3-15 Jan.	*	—	—	—
7. <i>Stigmodera andersoni</i> C. & G.	few	G	11	3-8 Jan.	*	—	—	—
8. <i>Stigmodera bella</i> Saund.	rare	G	12	18 Dec.-16 Jan.	few	G, B	9	2-8 Dec.
9. <i>Stigmodera bicincta</i> Boisd.	rare	G	12	5 Jan.	rare	B	9	6, 8 Dec.
10. <i>Stigmodera brutella</i> Thoms.	rare	G	11	4 Jan.	*	—	—	—
11. <i>Stigmodera crenata</i> (Don.)	rare	G	10	15, 18 Dec.	common	G, B	9, 10	1-11 Dec.
12. <i>Stigmodera cruenta</i> L. & G.	few	G	10, 12, 14	10-15 Dec., 22 Jan., 18 Feb.	rare	G	9	18 Dec.
13. <i>Stigmodera octospilota</i> L. & G.	few	G	10	12-15 Dec. 6 Jan.	few	G, B, MB	9, 10	1-18 Dec., 20 Dec.
14. <i>Stigmodera erythroptera</i> Boisd.	few	G	10	8-15 Dec.	common	G, B, W	9, 10	1-18 Dec.
15. <i>Stigmodera (?) flavopicta</i> Boisd.	*	—	—	—	rare	G	15	18, 29 Dec.
16. <i>Stigmodera kerremansi</i> Blackburn	rare	G	12	5-6 Dec.	rare	G, B	9	1, 7 Dec.
17. <i>Stigmodera kirbyi</i> Guer.	rare	G	12	8 Dec.	rare	WW	9	19 Jan.
18. <i>Stigmodera luteipennis</i> L. & G.	rare	G	10	15, 28 Dec.	*	—	—	—
19. <i>Stigmodera nasuta</i> Saund.	rare	G	10	12 Dec.	*	—	—	—
20. <i>Stigmodera decemmaculata</i> (Kirby)	few	G	10	6-22 Dec., 5 Jan.	*	—	—	—
21. <i>Stigmodera puella</i> Saund.	*	—	—	—	rare	B	9	9 Dec.
22. <i>Stigmodera rufipennis</i> (Kirby)	few	G	10	5-23 Dec.	common	G, B	9, 10	1-10 Dec.
23. <i>Stigmodera scalaris</i> Boisd.	rare	G	12	12 Dec.	common	G, B	9, 16	2-9 Dec.
24. <i>Stigmodera spilota</i> L. & G.	rare	G	5(?)	8 Feb.	*	—	—	—
25. <i>Stigmodera spinolae</i> L. & G.	rare	G	10	12 Dec.	*	—	—	—
26. <i>Stigmodera subpura</i> Blkb.	*	—	—	—	few	B	9	2-10 Dec.
27. <i>Stigmodera undulata</i> (Don.)	few	G	10, 11	3-12 Dec., 28 Jan.	few	G, B	9	2, 8, 10 Dec.
28. <i>Stigmodera vigilans</i> Kerr. (?)	rare	G	11	18 Dec.	(?) rare	G, B	9, 12	6-11 Dec., 3 Jan.
29. <i>Curis caloptera</i> (Boisd.)	rare	G	11	15 Dec.	*	—	—	—
Tribe Agrilini								
30. <i>Paracephala cyaneipennis</i> Blkb.	*	—	—	—	rare	G	2	5 Jan.
31. <i>Germarica lilliputana</i> (Thoms.)	*	—	—	—	common	G, MB	2, 3	9, 17-19 Jan.
32. <i>Cisseis acuducta</i> (Kirby)	rare	G	6	14 Dec.	rare	G, L	6, 17	18, 28 Dec.
33. <i>Cisseis atroviolacea</i> Thoms.	*	—	—	—	few	B, W	9	1-12 Dec.
34. <i>Cisseis cupripennis</i> Guer.	*	—	—	—	few	G	6	22, 26 Dec., 10, 20 Jan., 25 Feb.
35. <i>Cisseis leucosticta</i> (Kirby) (Fig. 2B)	common	G	6	25, 28 Jan., 3-5 Feb.	rare	G	7	4 Jan.
36. <i>Cisseis maculata</i> L. & G.	*	—	—	—	rare	B	9	5, 12 Dec.
37. <i>Cisseis marmorata</i> L. & G.	rare	G	8	16 Dec.	few	L	7, 8	14, 15, 20 Feb.
38. <i>Cisseis notulata</i> Germ.	rare	G	5	5 Jan.	common	G, B	5, 18	20-28 Dec., 2-15 Jan.
39. <i>Cisseis pygmaea</i> Blkb.	few	G	21	16-24 Jan., 14-16 Feb.	few	G	21	3-18 Jan.
40. <i>Cisseis roseo-cuprea</i> Hope	*	—	—	—	few	G	19	29 Aug. 77.
41. <i>Cisseis vicina</i> Kerr.	*	—	—	—	few	G, B, W	9, 10	1-8 Dec., 12 Feb.
Subfamily Chalcophorinae								
Tribe Chalcophorini								
42. <i>Cyria imperialis</i> (Fabr.)	few	G	20	22-31 Dec., 1-3 Jan.	*	—	—	—
No. of species present	29				32			

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Key to Table 1.

Occurrence

- * = no specimens observed or collected
- rare = ≤ 3 specimens collected
- few = 3-10 specimens collected
- common = > 10 specimens collected.

Locality

- G = Glenbrook;
- B = Blaxland;
- L = Lapstone;
- W = Warrimoo;
- WW = Wentworth Falls;
- MB = Medlow Bath.

Food Plants

Casuarinaceae

1. *Casuarina torulosa* Ait.; 2. *C. littoralis* Salisb.;
3. *C. nana* Sieb. ex Spreng.

Poaceae (Gramineae)

4. *Themeda australis* (R.Br.) Stapf.

Mimosaceae

5. *Acacia linifolia* (Vent.) Willd.; 6. *A. longiflora* (Andrews) Willd.;
7. *A. decurrens* (Wendl.) Willd.; 8. *A. parramattensis* Tindale

Myrtaceae

9. *Leptospermum flavescens* Sm.; 10. *L. phyllicoides* (A. Cunn. ex Schau.) Cheel;
11. *Angophora floribunda* (Sm.) Sweet; 12. *A. bakeri* C. Hall;
13. *Eucalyptus piperita* Sm.

Pittosporaceae

14. *Bursaria spinosa* (Cav.) Druce.

Asteraceae (Compositae)

15. *Cassinia compacta* F. Muell.; 16. *C. uncata* A. Cunn. ex DC.

Fabaceae (Papilionaceae)

17. *Jacksonia scoparia* R. Br.; 18. *Dillwynia retorta* (Wendl.) Druce var. *retorta*;
19. *D. floribunda* var. *teretifolia* Blakely.

Proteaceae

20. *Banksia spinulosa* Sm.

Sapindaceae

21. *Dodonaea triquetra* Wendl.

TABLE 2

Numbers of buprestid species collected from dominant flowering plants during each season in the study area

Food Plant	Number of Species	
	1975/76	1976/77
<i>Leptospermum flavescens</i> Sm.	0	19
<i>L. phyllicoides</i> (A. Cunn. ex Schau.) Cheel	13	6
<i>Angophora floribunda</i> (Sm.) Sweet	6	0
<i>A. bakeri</i> C. Hall	6	1

During the 1975/76 season the dominant flowering species upon which beetles were observed were *Angophora bakeri*, *A. floribunda* and *Leptospermum phyllicoides*. Flowering of *A. bakeri* in the lower Blue Mountains occurred throughout most of December and into the first half of January, while *A. floribunda* flowered later in December and extended into late January. Six species of *Stigmodera* were collected from *A. bakeri* (see Table 2), mainly during early to middle January, while five species of *Stigmodera* and *Curis caloptera* were collected from the latter plant species, mostly during early January (Tables 1, 2). Generally, buprestid species were not very common and often long waiting for beetles to arrive at blossoms and intensive searching failed to locate any specimens.

Leptospermum phyllicoides yielded 12 species of *Stigmodera* and *Torresita cuprifera*. Flowering of this plant began in the last week of November and reached a peak flowering period during middle to late December. Many plants were still flowering by mid-January, 1976. *Stigmodera macularia* was the only buprestid collected from this plant during the second week of January.

No buprestids were observed before December, but specimens may have been present on early flowering plants of *L. phyllicoides* in other localities where collection did not occur.

Most species of *Stigmodera* showed preference for one or two food plants, and only *S. variabilis* and *S. cruenta* were found on three different plant species during the 1975/76 season (see Table 1).

During 1976/77 the angophoras, eucalypts and *L. phyllicoides* flowered poorly in the Glenbrook area, while the yellow tea-tree *L. flavescens* flowered profusely, yielding 15 species of *Stigmodera*, three species of *Cisseis* and *Torresita cuprifera* (see Tables 1, 2). Flowering of this species at Glenbrook began in the last week of November, reached a peak during 8-10 December and had ceased by the 14 December, by which time petals had fallen off or blown off and fruit development was well advanced. No buprestids were collected after the 18 December from *L. flavescens* at Glenbrook. This represents a marked synchronization between the flowering of the food plant and the appearance of adult beetles.

One specimen of *Stigmodera kirbyi* was collected on the 19 Jan. 1977 from a late-flowering plant of *L. flavescens*, 5.5 km S.E. of Wentworth Falls, and a

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single example of *S. octospilota* was collected from a poorly flowering *L. phyllicoides* near Medlow Bath, in the higher Blue Mountains on the 20 Dec. 1976. These were the only *Stigmodera* collected from *Leptospermum* after the 18 Dec. 1976.

Williams (1977) collected 16 species of *Stigmodera* from *L. flavescens* at East Minto, N.S.W., during 1972-75, which is 50 km S.E. of Glenbrook; of these only six species were collected during 1976/77 at Glenbrook, while *Stigmodera bicincta*, *S. crenata*, *S. octospilota*, *S. erythroptera*, *S. kerremansi*, *S. scalaris*, *S. subpura* and *S. vigilans* (?) were not collected in any season by Williams, but most of the above were present both seasons at Glenbrook. Williams (1977) records the interesting observation of *Neocuris guerini*, *Curis caloptera* and *Cyria imperialis* on *L. flavescens*; none of these species were observed on *L. flavescens* at Glenbrook (*N. guerini* was not collected at all from any plants); on the other hand *Torresita cuprifera*, *Cisseis atrovioleacea*, *C. maculata* and *C. vicina* also found on *L. flavescens* at Glenbrook were not recorded by Williams. Williams (1977) noted considerable seasonal variation both in number of species and numbers of individuals present during his three years of observation. This observation was also noted during this study (Tables 1, 2).

It appears that the presence of many feeding beetle species is strongly associated with the species of plant flowering, and rainfall and temperature appeared to have little effect on their occurrence. One example is *Cyria imperialis*, which usually shows specificity to *Banksia* spp. (Froggatt, 1907; Tillyard, 1926; McKeown 1945), but was recorded on *Leptospermum flavescens* by Williams (1977). At Glenbrook it was only found during late December and early January 1975/76 on *Banksia spinulosa* Sm., which flowered well during this season. This plant did not flower during 1976/77 and extensive searching amongst *Banksia* bushes during the summer failed to find any of these buprestids.

Other examples of nectar-feeding buprestids showing apparent specificity for one species of plant and appearing only during one season include *Stigmodera andersoni*, *S. brutella*, *S. flavopicta*, *S. luteipennis*, *S. nasuta*, *S. decemmaculata*, *S. spinolae*, *S. subpura*, *Curis caloptera*, *Cisseis atrovioleacea* and *C. maculata*. It is felt, however, that with further observations many of these species may be found to frequent more than one species of plant.

(b) Flight behaviour

Observations on flight were obtained during the 1976/77 season. Periods spent in flight varied from one to greater than 70 seconds, depending on the genus and size of species (Table 3). Generally, the larger species, such as *Stigmodera rufipennis* and *S. undulata*, were more sedentary than the smaller more active species, e.g., *S. scalaris* and *S. crenata*. The very active *Cisseis atrovioleacea*, *C. vicina* and *C. maculata*, observed during the 1976/77 season, spent most of their time amongst the flowers of *Leptospermum flavescens*, and usually flew when disturbed or closely approached. Observations showed that standing or movement

of the author at distances of 15 to 50 cm from the feeding beetles aroused them, causing them to take immediate flight or to display the "free-fall and flight-escape mechanism" (see later). Beetles, when disturbed while feeding, usually ceased movement for about one second, quickly opened their elytra outwards and flew rapidly upwards or slightly horizontally.

One small specimen of *S. macularia*, the largest species examined, observed on the 2 Dec. 1976 at Blaxland, was very inactive, remaining motionless for more than five minutes before being collected, examined and later released (Table 3).

TABLE 3

Data on flight, feeding, defence and escape mechanisms for some species of Buprestidae observed in the study area during 1975-1977

Species	Periods spent feeding (secs)	Periods in flight (secs)	Feeding heights (m)	Defence and escape mechanisms +				
A. Small species 5-13 mm (total length)								
1. <i>Stigmodera crenata</i> (Don.)	3-15	10->25	1.2-2.0	1	2	3	4	
2. <i>Stigmodera erythroptera</i> Boisd.	2-25	5-30(?)	1.2-3.2		2	3		5
3. <i>Stigmodera kerremansi</i> Blkb.	5-15	>5(?)	0.7-2.0, 6.0	1		3	4	
4. <i>Stigmodera scalaris</i> Boisd.	3-20	5-25(?)	1.2-2.2	1		3	4	
5. <i>Cisseis atroviolacea</i> Thoms.	>120	>3(?)	1.1-2.5	1		3		
6. <i>Cisseis maculata</i> L. & G.	>90	*	1.5-2.0	1		3		
7. <i>Cisseis pygmaea</i> Blkb.	*	1-10	0.5-1.3	1				
8. <i>Cisseis vicina</i> Kerr.	>120	*	1.5-2.0	1		3		
B. Large species >13 mm (total length)								
9. <i>Stigmodera macularia</i> (Don.)	20->300	15-30	0.8-2.5		2	3		
10. <i>Stigmodera rufipennis</i> (Kirby)	25-195	15-70(?)	1.4-2.8			3		5
11. <i>Stigmodera undulata</i> (Don.)	25-125	3-20(?)	1.0-2.0		2	3	4	
12. <i>Stigmodera variabilis</i> (Don.)	>180	>5(?)	3.2, 6.0-9.0					4

KEY

(?) Specimens of these species were observed to fly away from food plants into surrounding bushland or out of sight. Hence the larger time(s) given is the time from departure of the food-plant to the time when the beetle(s) disappeared from sight.

* = No data available or not observed.

+ Defence and escape mechanisms

1 = Free-fall and flight

2 = Free-fall and death feign

3 = Upward flight

4 = Bright colour(s) on dark background

5 = Batesian mimic.

When in flight, all species of *Stigmodera* flew with abdomen pointed downwards, elytra positioned horizontally, and head and pronotum pointed slightly forward. They made circular flights around the largest bushes of *L. flavescens*, which had the most flowers open. They often reversed direction and circled back

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and forth over and around the tops of the bushes before landing. Slight disturbances, causing branches to move suddenly, caused individuals to take flight.

Barker (1975) first recorded the presence of a spring mechanism, involving the release of the elytra from the closed position, in the genus *Astraeus*. When the beetle releases the spring, the elytra flick open with considerable force, enabling the insect to be flung upwards. Barker (1975) recorded the height achieved by some species as "several metres"; observations on *A. pygmaeus* at Glenbrook, on the 7 Jan. 1977, showed the height obtained before flying in other directions to be approximately 0.3-0.6 m. Beetles observed were quite active and when approached would quickly flick to another branchlet, often turning in one direction, reversing and flying (?) or flicking off again. Occasionally individuals were observed to fall quickly to another *Casuarina* branchlet, [species of *Astraeus* are mainly found on *Casuarina* plants, Barker, (1975)], either resting there or flicking off to a higher altitude (up to 2.5 m). From the observations of these uncommon insects at Glenbrook it appears that individuals fly rarely and mainly remain on branchlets of their food plant *Casuarina torulosa* Ait; it appears that the spring mechanism is used to propel the insect upwards or downwards, and the wings used only to reach a convenient resting post, which was unable to be reached by the spring mechanism alone.

Germarica lilliputana, observed during January, 1977, at Glenbrook and Medlow Bath, tended to remain on *Casuarina torulosa* Ait., or *C. nana* Sieb. ex Spreng. branchlets, and flight was not observed.

Cyria imperialis, a strong flier producing a loud whirring noise while in the air, was observed during January, 1976, at Glenbrook. The species appears to be a wary insect, and flies far and fast when disturbed or approached; three specimens, observed 2.2 km N.E. of Glenbrook, displayed the "free-fall and death feign" escape mechanism (see later).

Flight was not observed in *Melobasis*, *Curis*, *Paracephala* or *Torresita*.

(c) Feeding biology

The *Leptospermum*, *Angophora* and *Eucalyptus* flowers (Family Myrtaceae), upon which many species of *Stigmodera* were observed and/or collected during 1975/77, are constructed so as to give easy access to the nectar supply for sugar-requiring species of Buprestidae and other species of insects. (Fig. 1 A and B, and Fig. 2 A and B).

The small species of buprestid, upon landing on a blossom, proceed to move through or over the series of stamens surrounding the ovary of the flower and to the areas where the numerous secretory cells are situated. The nectar collects in a hollow or groove formed by the edge of the ovary summit and the inner surface of the floral tube, but may spread over the top of the ovary in flowers with a considerable nectar supply. The nectar of these plant genera is sweet-

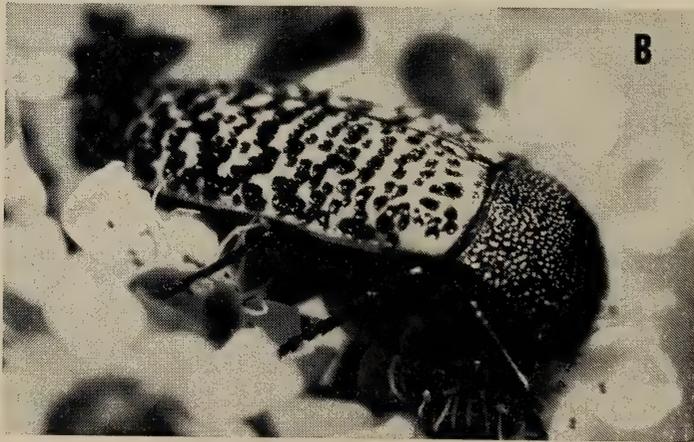


FIG. 1.—A. *Stigmodera macularia* on flowers of *Angophora bakeri*.

B. *S. macularia* on *Leptospermum flavescens*.

(Note deep pits on elytra and puncturing on pronotum).

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smelling and the sugar content appears to be composed, in *Leptospermum* at least, of glucose and fructose (Dr. H. A. Ford, pers. comm.), which is the necessary energy source for these active beetles. The buprestid, with head extended or placed downwards into the flower, is able to draw up through the rostrum (present in *Stigmodera*) the sugary liquid.

Small species of *Stigmodera* examined, e.g. *S. scalaris*, *S. bella*, *S. bicincta*, *S. erythroptera*, *S. kerremansi*, *S. nasuta* and *S. subpura*, alight on a flower (*Leptospermum*) and, aided by quick movements of their legs and quivering movements of the antennae, proceed to the nectar-bearing areas and position themselves head down into the flower. The elytra remain closed and extend above the stamens, while the legs are used for balance during feeding.

Time spent feeding on *Leptospermum flavescens* varied from two seconds to approximately five minutes, most probably depending on the amount of nectar present in the flowers and the activity of the species (Table 3). The larger and slower moving species, e.g. *S. rufipennis*, spent more time feeding on the flowers of the tea-tree and less in flight than did the smaller species. The latter moved quickly and readily from flower to flower (although they often remained several minutes feeding within one flower).

Of the beetles observed feeding, either on *Leptospermum phyllicoides* during 1975/76, or on *L. flavescens* during 1976/77 (both at Glenbrook), most species of *Stigmodera*, *Cisseis atrovioleacea*, *C. vicina* and *C. maculata* fed singly and but for a few occasions remained isolated and relatively distant (15 cm or more away) from members of the same species, and also individuals of other species of buprestid. On the 5 Dec. 1976 a pair of *S. rufipennis* was observed feeding from 1 to 8 cm away from each other. However, since most species feed singly, this suggests that a spacing mechanism is involved, possibly enabling individuals to feed undisturbed and to gain a more equal share of the available nectar. However, the latter suggestion would be difficult to prove under field or laboratory conditions.

Most specimens of *Stigmodera* and *Cisseis* which were observed on *Leptospermum* visited flowers which were more than 1 m above ground level. The smaller bushes of *L. flavescens*, less than 1 m in height, were seldom visited by any buprestid. One specimen of *S. macularia*, collected on the 1 Dec. 1976 frequented a group of flowers of *L. flavescens* situated 0.8 m above ground level. Specimens of *Cisseis pygmaea*, observed during Jan.-Feb., 1976 and 1977, frequented young plants of *Dodonaea triquetra* Wendl., less than 1.3 m in height (Table 3). For *Leptospermum flavescens*, the height range for flower visitation was > 1 and < 3.5 m. *Stigmodera* flew at heights also within this range and seldom flew higher than 4 m. One individual of *S. rufipennis* flew approximately 7 m into the air after being disturbed on the 3 Dec. 1976. *Stigmodera variabilis* preferred greater heights when feeding. Specimens of this species were observed or collected only during Jan., 1976, feeding on the flowers of *Angophora bakeri* and *Eucalyptus piperita* at heights ranging between 6-9 m, and on the 6 Jan.

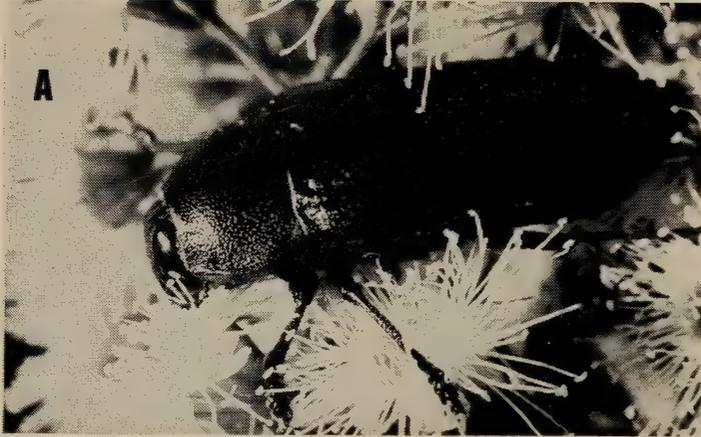


FIG. 2.—A. *Stigmodera variabilis* on flowers of *Angophora bakeri*.
B. *Cisseis leucosticta* feeding on a stem of *Acacia decurrens*.

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1976 one individual was collected on a large *Leptospermum phyllicoides* plant at a height of about 3.2 m. *Curis caloptera*, *Stigmodera kerremansi* and other species of *Stigmodera* collected during January, 1976, at Glenbrook, fed upon flowers of *Angophora floribunda* at heights of over 6 m. Most species of *Stigmodera* found feeding on *Leptospermum phyllicoides* during 1975/76 frequented flowers at heights of > 1 m and < 2 m. It appears, then, that nectar-frequenting species of Buprestidae have a height preference for flowers (depending on the species of food plant); those flowers less than 1 m above ground level are seldom visited. Those flowers visited appear to be mainly the top flowers, or flowers at tips of branches. It may be that the top flowers contain more nectar than the bottom flowers, and so these attract more insects. However, only superficial examination of the nectar supply of bottom and top flowers by the naked eye could be undertaken. From this examination it appeared that the bottom flowers were similar in condition to those higher up on the plant.

There appears to be no height preference at Glenbrook for species which are foliage eating, i.e. *Cisseis*, *Melobasis*, *Paracephala* and *Germarica*.

(d) Flower pollination by buprestids

Because of the habit of nectar-feeding *Stigmodera*, their movements over flowers and the structures of the *Leptospermum*, *Angophora* or *Eucalyptus* flowers themselves, it would appear that buprestid beetles as a whole are important pollinators of these plants. Many *Stigmodera* examined during Dec.-Jan., 1975/76 and 1976/77, had pollen attached to the sides of the pronotum and head region, as well as on the tarsi, other leg segments and the elytra.

Some species of *Stigmodera* have deep pitting on the elytra (Fig. 1B). These pits may act as reservoirs for fallen pollen, which may be carried by the beetle to other flowers. *S. macularia* is one such species; observations so far on this species, however, have not shown that the deep pits of the elytra are used for the transfer of pollen.

Several specimens of *Cisseis atrovioleacea* and *C. vicina*, collected on the 4 Dec. 1976, near Blaxland, were copiously covered in pollen from *Leptospermum flavescens*.

(e) Defence and escape mechanisms

(i) *Bright colours*—many species of jewel-beetle observed were brightly coloured with dominant colours of red, yellow, orange, green and/or blue, i.e. bright colours on a dark background (see Tables 3, 4).

(ii) *Dull colours*—most species of *Cisseis*, *Germarica lilliputana*, *Paracephala cyaneipennis* and *Melobasis* collected were dull in colour—browns, dull greens, blues and dark shades. The green tint of a vivid species of *Melobasis* (Table 4) appeared to match the colour of *Acacia longiflora* (Andrews) Willd. leaves upon

which the insect was resting; this cryptic colouration may aid the species to escape from would-be predators. Small size and colouration of *Germarica lilliputana* are two factors which may aid in the protection of this species.

TABLE 4

Heights at which beetles were collected on host plants and defence and escape mechanisms observed for some species of Buprestidae from the Blue Mountains, N.S.W. (1975-1977)

	Heights (m)	Defence and escape mechanisms +		
A. <i>Small species</i> < 16 mm (total length)				
1. <i>Cisseis leucosticta</i> (Kirby)	0.7-1.2	2	4	
2. <i>Cisseis marmorata</i> L. & G.	0.6-1.2		4	
3. <i>Cisseis notulata</i> Germ.	0.9-1.5	1		
4. <i>Cisseis roseo-cuprea</i> Hope	0.4-0.6	2		
5. <i>Germarica lilliputana</i> (Thoms.)	0.5-3.5			5
6. <i>Melobasis cupriceps</i> (Kirby) (?)	1.0-2.0			5
7. <i>Paracephala cyaneipennis</i> Blkb.	0.3	*		
8. <i>Stigmodera</i> (?) <i>flavopicta</i> Boisd.	1.2-1.5	1	3	6
B. <i>Large species</i> > 16 mm (total length)				
9. <i>Cyria imperialis</i> (Fabr.)	1.1-1.5	2		6

KEY

+ Defence and escape mechanisms

1 = Free-fall and flight

2 = Free-fall and death feign

3 = Upward flight

4 = Defence secretions

5 = Cryptic colouration

6 = Bright colour(s) on a dark background

* = Not observed or no data available

? = The identification of this species is uncertain.

(iii) *Batesian mimicry*—this phenomenon has been noted in *Stigmodera* (Nicholson, 1927; Britton, 1970). Batesian mimics in the author's collection were *S. rufipennis*, *S. nasuta*, *S. erythroptera*, *S. subpura* and *S. spinolae*. Nicholson (1927) and Britton (1970) illustrate in colour other mimics from the beetle families Cerambycidae, Curculionidae (Belidae), Buprestidae, Cantharidae and Oedemeridae. These beetles mimic the distasteful beetles of the genus *Metriorrhynchus* Lycidae (or Lampyridae of older works). The most common of these beetles is *M. rhipidius* Macleay. It is interesting to note that this and other species of *Metriorrhynchus* were also present on *Leptospermum flavescens*, together with most species of buprestid mentioned above. (See also list of insects recorded visiting *L. flavescens*, apart from members of the Buprestidae, Table 5).

(iv) *Free-fall and flight*—several species of *Cisseis* (including *C. pygmaea* and *C. notulata*) and *Stigmodera crenata*, *S. scalaris*, *S. karremansi* and *S. (?)*

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flavopicta, were observed to fall from a branch or flower when disturbed or approached, and then to fly away to a safer location immediately before hitting the ground (Tables 3, 4). This is no doubt a successful escape mechanism when attacked from above by a predator such a bird.

(v) *Free-fall and death feign*—*Stigmodera crenata*, *S. macularia*, *S. erythroptera*, *S. bella*, *S. undulata*, *Cisseis leucosticta*, *C. roseo-cuprea* and *Cyria imperialis*, all exhibited this escape mechanism when disturbed (Tables 3, 4). Hawkeswood (1977) has made a brief comment about this escape mechanism exhibited by

TABLE 5

The occurrence of identified insect species, other than the Buprestidae, visiting the leaves or flowers of LEPTOSPERMUM FLAVESCENS Sm., observed and/or collected at Glenbrook and Blaxland, N.S.W., during December 1-12, 1976

Order	Family	Genera and Species	Occurrence
Hymenoptera	Apidae	<i>Apis mellifera</i> L.	common
	Sphécidae	<i>Exeirus lateritius</i> Shuck.	rare
	Psammocharidae (Pompilidae)	<i>Cryptochielus fulvidorsalis</i> Turn.	rare
	Formicidae	<i>Iridomyrmex</i> sp. <i>Polyrhachis ammon</i> Fabr.	few rare
Lepidoptera	Amatidae (Syntomidae)	<i>Eressa paurospila</i> Turn. (?)	common
Hemiptera	Reduviidae	<i>Poecilosphrodus</i> sp. (?)	few
Diptera	Asilidae	<i>Chrysopogon crabroniformis</i> Roder.	rare
Coleoptera	Mordellidae	<i>Mordella leucosticta</i> Germ.	rare
		<i>Mordellisterna</i> spp. (2)	common
	Scarabaeidae	<i>Phyllotocus macleayi</i> Fisher	common
		<i>Phyllotocus</i> sp.	common
		<i>Polystigma punctata</i> (Don.)	rare
		<i>Liparetrus discipennis</i> Güer.	few
		<i>Repsimus manicatus manicatus</i> (Swartz) <i>Glycyphana brunnipes</i> (Kirby)	rare few
	Lycidae	<i>Metriorrhynchus rhipidius</i> Macleay	common
		<i>M. irregularis</i> Waterhouse	few
		<i>M. heterodoxus</i> Lea	few
		<i>M. eremitus</i> Fabricius	few
	Cantharidae	<i>Chaulignathus pulchellus</i> (Macleay)	rare
		<i>Heteromastix anticus</i> Blackburn	common
		<i>H. simplex</i> Lea	common
<i>Selenurus sydneyensis</i> Blackburn		few	
Chrysomelidae	<i>Paropsis</i> spp. (2)	rare	
Cleridae	<i>Trogodendron fasciculatum</i> Schreib.	rare	
	<i>Scrobiger</i> sp.	few	
	<i>Aulicus</i> sp.	few	
Elateridae	<i>Opilo congruus</i> Newman	common	
	<i>Anilicus</i> sp.	common	

KEY

rare = < 3 specimens observed; few = 3-10 specimens observed; common = > 10 specimens observed; ? = identification of these species is uncertain.

some Australian members of the Chrysomelidae (Coleoptera), but, from the literature available, little has been noted on this escape mechanism in the Buprestidae. Whitlock (1947), noting observations in the field on some Western Australian buprestids, records "jewel-beetles I am acquainted with have the habit of dropping down in an inert condition" when he approached or disturbed feeding beetles. The buprestid beetles observed at Glenbrook exhibited an immediate fall to the ground from heights ranging from 0.6 m to 2.0 m. On the ground they would lie positioned upside-down with a uniform coloured undersurface facing upwards. Between small pebbles, small rocks, sand, or amongst grass and other plants, the beetles appeared well camouflaged.

(vi) *Upward flight*—most species of *Stigmodera* immediately flew off in a vertical or angular direction if violently disturbed by a gust of strong wind causing a branch to move suddenly where an individual was feeding.

(vii) *Defence secretions*—Defence secretions have been noted to be exuded by *Torresita cuprifera*, *Cisseis leucosticta* and *C. marmorata*.

One specimen of *T. cuprifera*, captured on the 13 Dec. 1976 on *Leptospermum flavescens* exuded, from the mouth, a non-odorous crimson-coloured liquid when handled. A pale yellow non-odorous liquid was also exuded from the mouth in *Cisseis leucosticta* and *C. marmorata*, which stained the skin of the author's fingers.

(f) *Tarsal and antennal cleaning*

These aspects of grooming in Buprestidae were only observed in *Stigmodera undulata*, *S. rufipennis* and *S. macularia* in this study.

Individuals observed stroked the tarsal segments of the forelegs through the mouth region, starting at tarsal segment I and continuing to tarsal segment IV. Having completed one to three strokes in this manner for one tarsus, individual beetles would then repeat this action for the tarsus of the other foreleg. The exchange from one foreleg to the other was occasionally repeated twice or more, but usually one series of cleaning for each foreleg was administered. After the completion of tarsal cleaning, the antennae would be wiped several times by the previously cleaned tarsi of the forelegs. This is most probably an effective method in removing dust and pollen grains, which may impede the sensory function of the antennae. Tarsi of legs II and III were not observed to be cleaned; this is most probably because the beetles are unable to reach them with their mouthparts. However, these tarsi may be cleaned by other tarsi, although this was not observed.

(g) *Predators and relationships with other insects*

Table 5 lists the main insect species collected and observed feeding or visiting flowers of *Leptospermum flavescens*, excluding the Buprestidae. The list excludes unidentified members of the Diptera (Tabanidae, Muscidae and Syrphidae) and Hymenoptera (Sphecidae, Ichneumonidae). Several spiders of the family Argiopidae were also observed living amongst the branches of the tea-tree.

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Predation of insect species by other insects was observed in *Apis mellifera* L., which was predated upon by the red and black assassin-bug *Poecilosphrodus* sp. (?), a resident insect amongst the leaves of the tea-tree. *Araneus* spiders, resident amongst the foliage of the tea-tree, had caught numerous specimens of *Selenurus sydneyensis* Blkb., *Metriorrhynchus* spp., and *Chaulignathus pulchellus* (Macleay), but careful examination of webs failed to find any captured buprestids.

Observations also showed no physical contact between buprestids and other species of insects.

On the 4 Dec. 1976 a ♂ eastern spinebill (*Acanthorhynchus tenuiostris*) spent about 10 minutes feeding on insects frequenting a stand of *L. flavescens* 1.7 km E. of Blaxland; however, due to quick movements of the spinebill through and over the tea-tree shrubs, the author was unable to determine if buprestids were included in the bird's diet.

SUMMARY

(a) There appears to be a marked synchronization between flowering of food plants and the appearance of adults of nectar-feeding species of *Stigmodera*, *Cisseis* and *Torresita*. Generally, most individuals and species were found just before and during the final flowering phases of the food plants when most flowers were open and contained large quantities of nectar. No nectar-feeding buprestids were found on plants either before or after flowering had occurred.

(b) Most species of *Stigmodera* showed preference for one or two food plants and only *S. variabilis* and *S. cruenta* were collected on three different plant species during 1975/76. Many species of *Stigmodera* were collected only during one of the two seasons, while some, e.g. *S. macularia*, were collected during both seasons. Since a strong degree of specificity for a particular food plant appears to exist with certain nectar-feeding buprestids, the absence of beetles may have been due to the plants' failure to flower, or flower poorly.

A dead specimen of *Melobasis costata* was collected on a grass stalk during January, 1976, while a slow-moving specimen of *Stigmodera spilota* was collected from a non-flowering plant of *Acacia linifolia* (Vent.) Willd. during February, 1976, so it is unlikely that these are the food plants for these buprestids. For the remaining 40 species of buprestid collected, data on food plants have been given.

(c) Generally, larger species of *Stigmodera* were more sedentary than the smaller, more active species of *Stigmodera* and *Cisseis*.

Specimens of three species of *Cisseis* observed on *Leptospermum flavescens* during 1976/77 flew upwards or exhibited the "free-fall and flight" escape mechanism when approached within 15-50 cm from where beetles were feeding. This appears to indicate an acute awareness of predators and efficient methods of escape.

Many *Stigmodera* made circular flights and often flew back and forth over and around the tops of *Leptospermum* bushes before landing to feed. It appears that there is some type of spacing mechanism which exists between nectar-feeding buprestids, enabling beetles to feed undisturbed and to procure an adequate supply of nectar. More observations, however, are needed on this behaviour.

Barker (1975) was the first to record the presence of a spring mechanism in the genus *Astraeus*. Observations on *A. pygmaeus* at Glenbrook showed that beetles were quite active and used the spring mechanism to propel themselves upwards or downwards to reach other resting posts. Heights obtained were found to be about 0.3-0.6 m.

(d) Larger and slower moving species of *Stigmodera* spent more time upon and feeding within flowers between flights than did the smaller species, which usually spent only several seconds feeding within one flower before flying to another flower.

There appears to be a height preference for nectar-feeding species of *Stigmodera* and *Cisseis*. For *Leptospermum flavescens* height visitation was mostly between 1 and 3.5 m, for *L. phyllicoides* 1 to 2 m, *Angophora floribunda* > 6 m, and for *A. bakeri* 6 to 9 m. The blossoms visited appeared to be the topmost flowers, or flowers at tips of branches. Superficial examination showed that the lower flowers were in similar condition to those above; therefore quantity of nectar did not appear to determine the height preferred for feeding.

There appears to be no height preference for buprestids which are foliage feeders, e.g. *Paracephala*, *Germarica* and *Cisseis* which were found at various heights on different food plants.

(e) Many specimens of *Stigmodera* and nectar-feeding *Cisseis* were observed to carry pollen of their food plants. It appears that these beetles may be important pollinators of these plants.

(f) Several escape mechanisms have been observed, two of which have been descriptively termed in this paper, the "free-fall and flight" and the "free-fall and death feign" escape mechanisms. They appear to be efficient methods of escape (as verified by human disturbance), but there have been no observations on escape from natural predators.

The defence secretions occurring in three species of buprestid appear to represent the first record of such secretions in the Australian Buprestidae. The usefulness of these secretions in defence against natural predators has not been observed.

(g) Observations on tarsal and antennal cleaning by three species of *Stigmodera* have been recorded.

(h) A large number of insect species belonging to numerous families were found visiting blossoms of *Leptospermum flavescens* at Glenbrook and near

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Blaxland, N.S.W., during December, 1976. Spiders (*Araneus* sp.) had captured numerous beetles, but careful examination of the webs showed that no buprestids had been captured.

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Gait of the Brush-tailed Possum (*Trichosurus vulpecula*)

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ABSTRACT

Locomotion of *Trichosurus vulpecula* was studied on the treadmill and under quasi-natural conditions in a wire enclosure. On the treadmill *Trichosurus* used a walk and a half-bound. In the enclosure a third gait, the bound, was also observed. The walk was used at low speed and during climbing, and the bound on steeply inclined surfaces. Modified gaits were also observed.

INTRODUCTION

Analysis of locomotion has usually been conducted on the larger forms of both marsupials and placentals. To date there has been no detailed work on the locomotion of *Trichosurus vulpecula* (the brush-tailed possum), or, indeed, on most non-macropod marsupials. *T. vulpecula* has often been used in physiological experiments (e.g. Anderson, 1937; Burke, 1954; Dawson, 1969; Gilmore, 1969, etc.), and for these reasons description of the normal locomotion is of interest. Such study would help to characterize the normal behaviour of *T. vulpecula*, as well as to add to our knowledge of the locomotion of small mammals.

Trichosurus is an arboreal, nocturnal, mainly herbivorous creature. Their numbers are not being reduced by the expansion of civilisation in Australia, and they have successfully colonized New Zealand. Further information about the biology of *T. vulpecula* may be found in Troughton (1941) and Tyndale-Biscoe (1973).

To help elucidate the locomotion of *T. vulpecula* we undertook to study the locomotion both under laboratory and quasi-natural circumstances.

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METHODS

The gaits of *Trichosurus vulpecula* were studied under two conditions, on a treadmill and in a wire enclosure (10 feet square). In the enclosure were placed a number of cut tree branches, from about 5 to about 30 cm in diameter. These branches were placed in orientations ranging from nearly horizontal to vertical. Locomotion under both conditions was recorded using high-speed cinematography.

Cinematography of the two animals on the treadmill was conducted by Dr. R. Baudinette of the Department of Zoology, Flinders University, who kindly made his films available to us. The treadmill formed the floor of a small cage with transparent sides. The animals were trained to move at speeds of 2.8, 4.2, 5.5 and 6.8 km hr⁻¹. A mirror inclined at 45 degrees to the back wall, and placed in front of the animal, permitted filming of the anterior and lateral aspects simultaneously. The film was exposed at 128 frames per second. These films were analysed using the methods of Hildebrand (1966; 1977) and Dagg and de Vos (1968a; 1968b). Consecutive frames of the film were individually inspected during projection upon a screen. The gait diagram was then constructed by noting which limbs were in contact with the substrate in each frame, and representing this contact as a horizontal line in the gait diagram (e.g. Fig. 1).

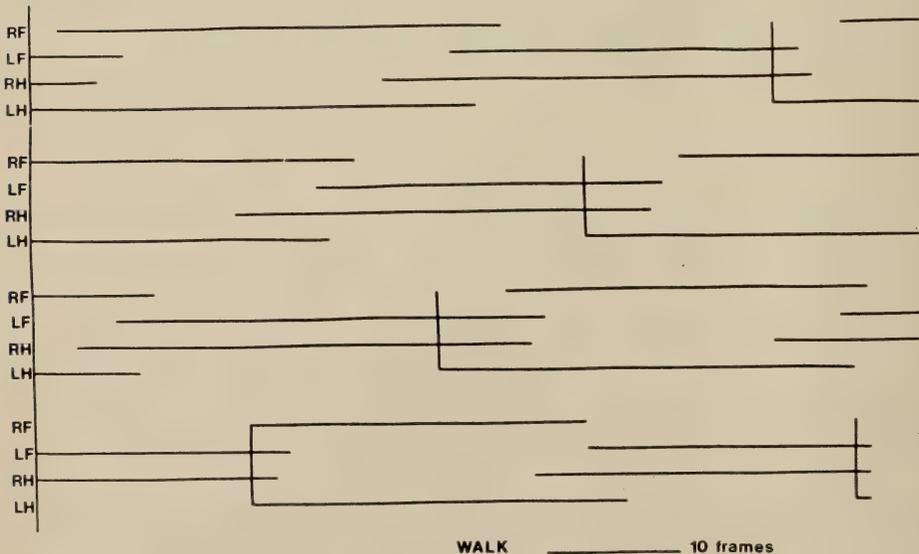


FIG. 1.—Gait diagram of five walking strides of *Trichosurus vulpecula* (on a treadmill). The diagram is “read” from upper left to lower right. Each vertical bar marks the beginning of a stride. Further explanation is given in the text. Ten frames of the film represent 0.08 seconds. The individual feet are indicated on the vertical line at the left, RF indicating the right fore-foot, LF the left fore-foot, RH the right hind-foot, and LH the left hind-foot.

Hildebrand has used two sets of variables (one set for each type) to characterise symmetrical and asymmetrical gaits. These variables are determined from the inspection of gait diagrams. Suitable combinations of these variables are then plotted as graphs, each point representing a stride. The fields of these graphs may be divided into areas each representative of a specific type of gait.

In the enclosure films were made after allowing several days for the animals to adjust to the enclosure. The films were exposed at 72 frames per second and analysed, as were the treadmill films. Due to the problems of filming free-ranging animals, relatively few film sequences were adequate for analysis, but it was possible to construct gait diagrams of at least one full stride of each gait reported.

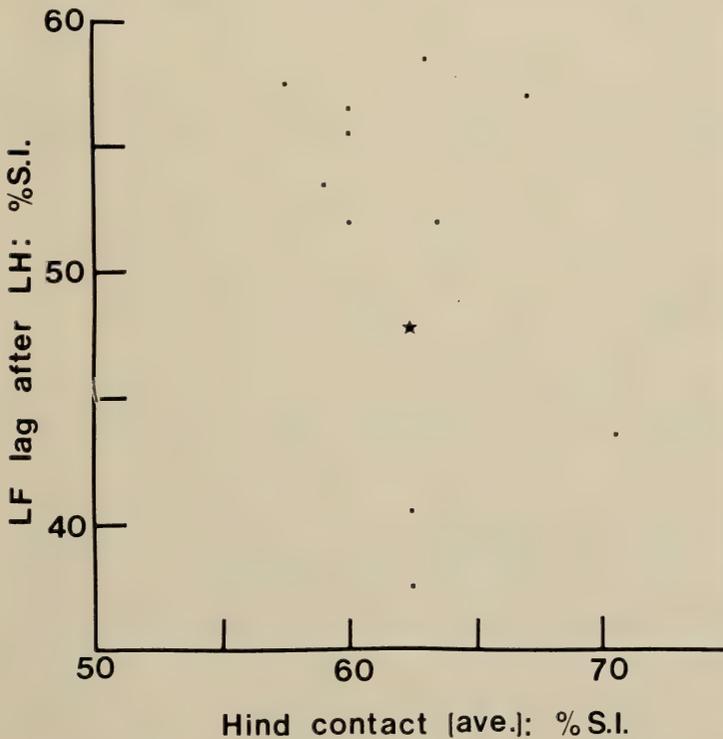


FIG. 2.—Results of analysis, after the method of Hildebrand (1966), of walk by *T. vulpecula* (on a treadmill). Each point represents one stride, and the average is indicated by the star. The ordinate presents the period by which the left fore footfall lags after the left hind footfall taken as a percentage of the stride interval, and the abscissa, the average duration of substrate contact of one or both hind feet taken as a percentage of the stride interval. Further explanation is given in the text. LF: left fore footfall; LH: left hind footfall; SI: stride interval (duration of the stride).

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RESULTS

Two gaits were observed to be used by *Trichosurus vulpecula* on the treadmill. For speeds less than 5.5 km hr^{-1} a walk was observed, whilst at greater speed a half-bound was used.

The gait diagram of *T. vulpecula* walking on the treadmill is presented in Fig. 1. The vertical axis indicates each of the four feet, and the contact of each foot with the substrate is represented by a horizontal bar. The whole sequence is "read", like a printed page, from left to right, and the sequences follow one another from top to bottom. The horizontal dimension represents time, and the vertical bars indicate the beginning of each stride, the first stride (but not necessarily any subsequent strides) beginning with the vertical line at the left of the diagram. Each stride commences with the initiation of substrate contact by the left hind foot.

The results of the analysis are presented in Fig. 2. Hildebrand (1966) has shown that the strides of symmetrical gaits may be represented as points in a two-dimensional space. This space is characterised by two variables, in turn

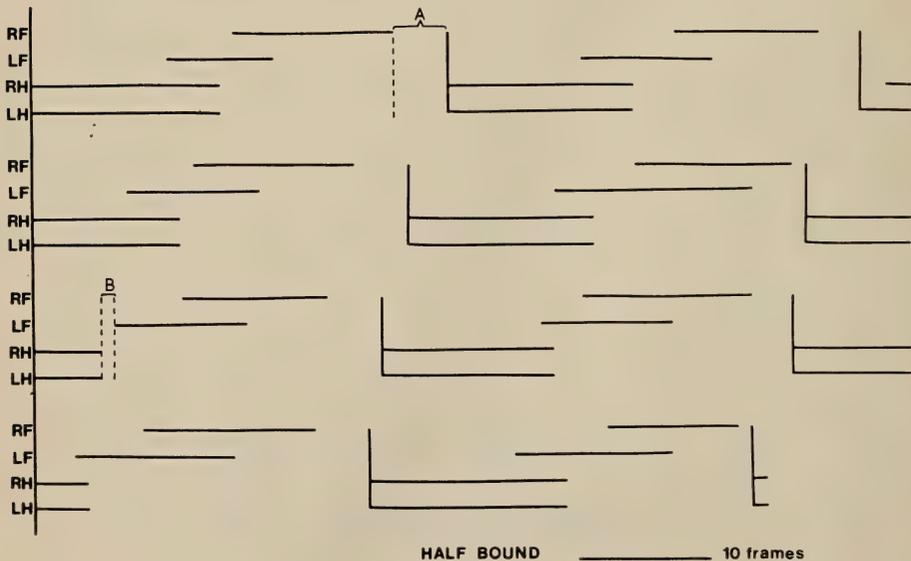


FIG. 3.—Gait diagram of *T. vulpecula* half-bounding (on a treadmill). Explanation of gait diagrams is given in caption of Fig. 1 and in text. Gaps, not occupied by any horizontal lines, indicate periods of suspension referred to in text. A indicates the first period of flexed suspension (present at the end of each stride), whilst B indicates one (the only one present in the diagram) of the periods of extended suspension. Ten frames of the film represent 0.08 seconds. Other abbreviations as in Fig. 1.

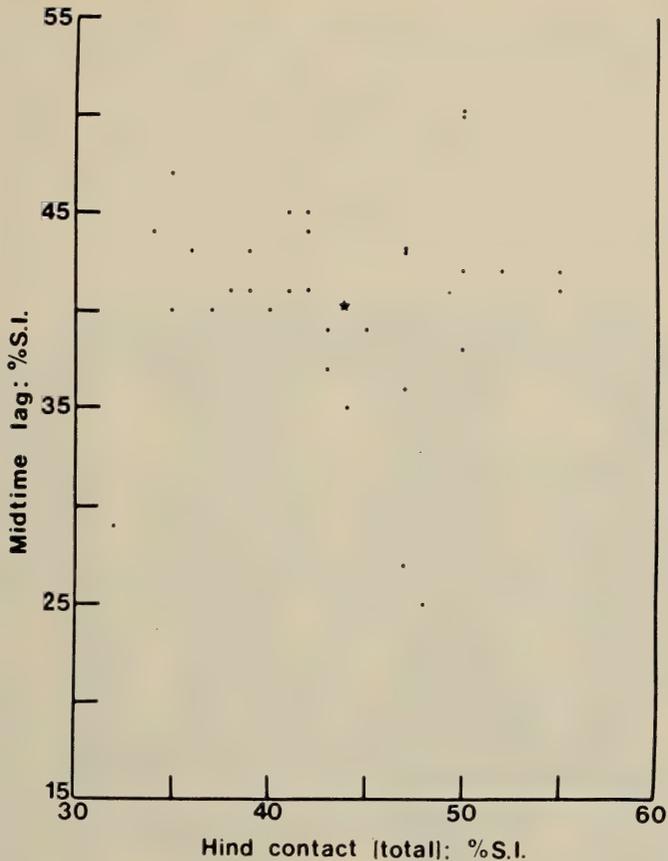


FIG. 4.—Results of analysis, after the method of Hildebrand (1977), of half-bound by *T. vulpecula* (on a treadmill). As in Fig. 2, each point represents one stride and the average is represented by the star. The ordinate represents the midtime lag, which is the period by which the middle of the period of substrate contact of the forelimbs follows the middle of the same period of the hind limbs. The abscissa represents the period during which one or both hind feet are on the substrate during the stride. Further explanation is given in the text, SI: stride interval.

represented as the two axes of a graph (Fig. 2). Indicated on the ordinate is the period of time by which each fore footfall follows the corresponding hind footfall expressed as a percentage of the stride interval, i.e. the duration of the stride. We found that this period (lag) was not usually equal for both left and right sets of limbs, and arbitrarily chose to use that of the left set of limbs. The second variable, indicated on the abscissa, is the period of time for which each foot is in contact with the substrate, again expressed as a percentage of the stride interval. In *T. vulpecula* these periods were not equal for each of the four feet, and we have

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arbitrarily chosen to use the average of the two hind contact durations, keeping in mind that Hildebrand (1977) found this variable of use in analysing asymmetrical gaits. The inequality between the duration of the left and right substrate contacts was due both to variations between individuals and between successive strides of one individual. The right members of a pair of limbs contact the ground about 50 per cent of the stride after the left footfall and vice versa. Hind contact is 55 to 70 per cent of the stride interval, and forelimb lag ranges from 40 to 60 per cent.

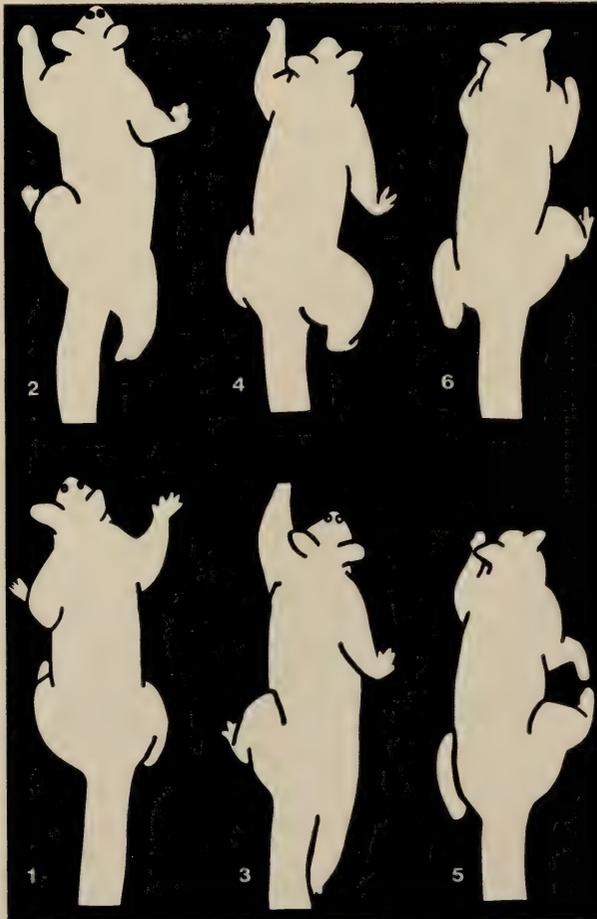


FIG. 5.—*T. vulpecula* climbing a flat vertical surface, using the walk.

Fig. 3 shows the gait diagram for the half-bound on the treadmill. Unlike the walk, there is a period, termed a suspension, at the end of each stride, during which there is no substrate contact. *T. vulpecula* shows a relatively long period of flexed suspension (during which the vertebral column is flexed, the forelimbs retracted and the hind limbs protracted) between loss of forelimb contact with the ground and hind footfall. On occasion a short period of extended suspension (during which the vertebral column is extended, the forelimbs protracted and the hind limbs retracted) was observed prior to fore footfall.

Fig. 4 presents the results of Hildebrand's (1977) method of analysis of asymmetrical gaits applied to *T. vulpecula*. Hildebrand (1977) shows that at least

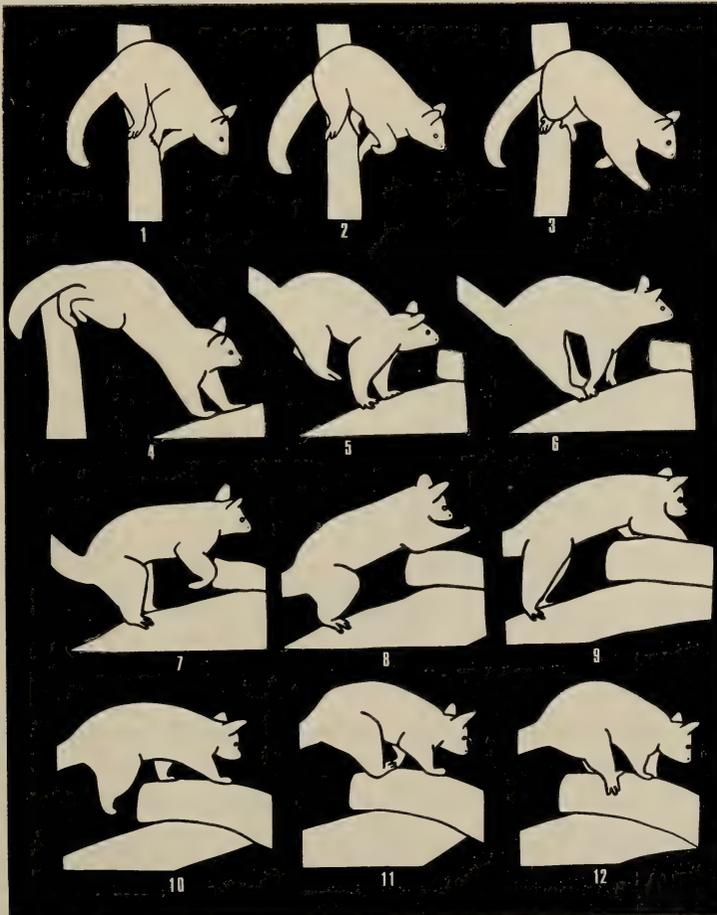


FIG. 6.—*T. vulpecula* half-bounding between branches and on to a log. Two successive strides are shown.

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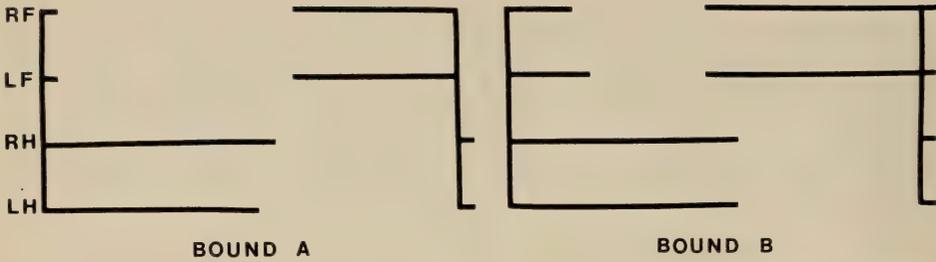


FIG. 7.—Gait diagram of one stride each of the two types of bounds used by *T. vulpecula*. Explanation of gait diagrams is given in caption of Fig. 1 and in text. A period of suspension may be seen in bound A that is not found in bound B. Abbreviations as in Fig. 1. Each stride represented is 0.35 seconds in duration.

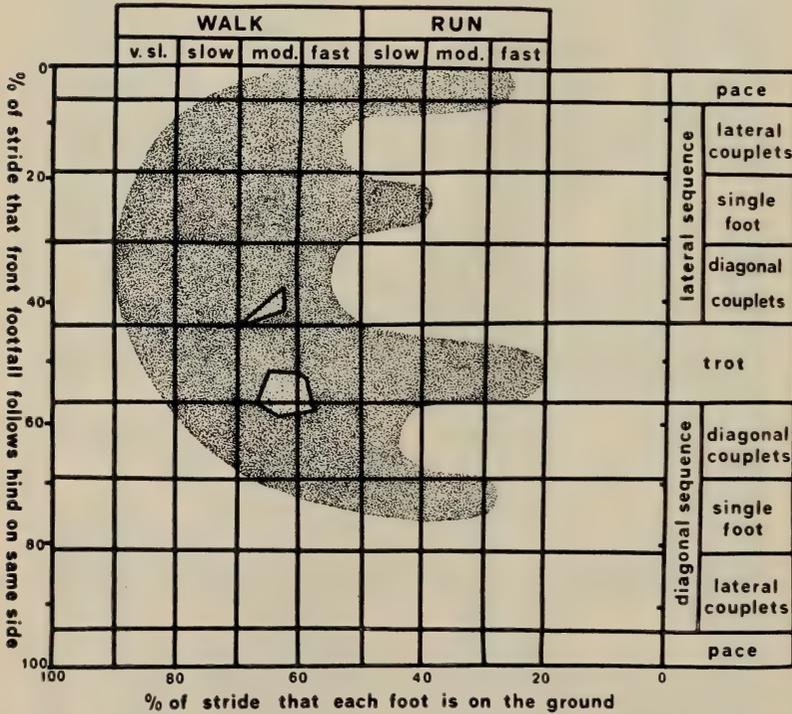


FIG. 8.—The symmetrical gait of *T. vulpecula* (in the two lightly stippled envelopes) compared with those of the mammals studied by Hildebrand (1966) (densely stippled). The descriptive terms labelling the upper and right borders are those of Hildebrand. It may be seen that *T. vulpecula* largely uses a moderate walk with diagonal couplets. Although points for *T. vulpecula* fall within the area designated 'trot' by Hildebrand, this gait was not observed. Further discussion is given in the text. (Diagram modified from Hildebrand, 1966).

five variables are necessary to characterise asymmetrical gaits. Five variables require 9 graphs for their graphic expression. Rather than work with all 9, Hildebrand chose to represent points on a graph analogous to that used for the analysis of symmetrical gaits. On this diagram the ordinate indicates the duration (midtime lag) by which the middle of the period of substrate contact of the forelimbs follows the middle of the period of contact of the hindlimbs represented as a percentage of the stride interval. The abscissa represents the period during which one or both hind feet are in contact with the substrate, again expressed as a percentage of the stride interval.

Three gaits were observed to be used by *T. vulpecula* in the enclosure. The walk was frequently used both on the ground and along inclined branches, as well as in climbing vertical surfaces (Fig. 5). In the latter case, as with movement on inclined branches, a slow diagonal sequence with two- and three-limb support was used.

The second gait observed was the half-bound, used often in movement along horizontal and inclined branches and in jumping from one branch to another (Fig. 6).

The third gait observed, which was never seen on the treadmill, was the bound. Simultaneous movement of both fore- and hindlimbs characterises this gait (Dagg, 1973). Two types of bounds were observed in the enclosure (Fig. 7). The first type, "A", agrees with Dagg's description. The second type, "B", also showing simultaneous movement by both pairs of limbs, is slower: two-limb support alternates with four-limb support. Speed appears to be the only criterion determining the choice between these two gaits. Bounding was observed mainly on vertical or near-vertical surfaces.

DISCUSSION

Hildebrand found that the points on his graph (Hildebrand, 1966, Fig. 10) for all mammalian symmetrical gaits observed fell within a restricted area of the total graph. Points in proximity indicate similar gaits. Fig. 8 compares walking by *Trichosurus vulpecula* with those gaits studied by Hildebrand. *T. vulpecula* shows a moderate to fast walk using diagonal couplets, to use the terminology of Hildebrand.

The portion occupied by gaits of *T. vulpecula* in Fig. 8 extends into the region designated by Hildebrand as the trot. It is thus important to point out that *T. vulpecula* was never observed to trot. This discrepancy may have arisen from the modification necessary to accommodate our data to Hildebrand's method of analysis. The most important of these modifications (arising from the inequality of the contact duration for different limbs) is probably the replacement of Hildebrand's variable, "per cent of stride that each foot is on the ground", by our variable, "per cent of stride of average hind contact". Gambaryan (1974) avers that gaits are not discrete, but fade one into another, forming a continuum over

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different speeds. These points on our graph fall at the gradation (under his interpretation) between the trot and the two walks with diagonal couplets, and provide support for his contention.

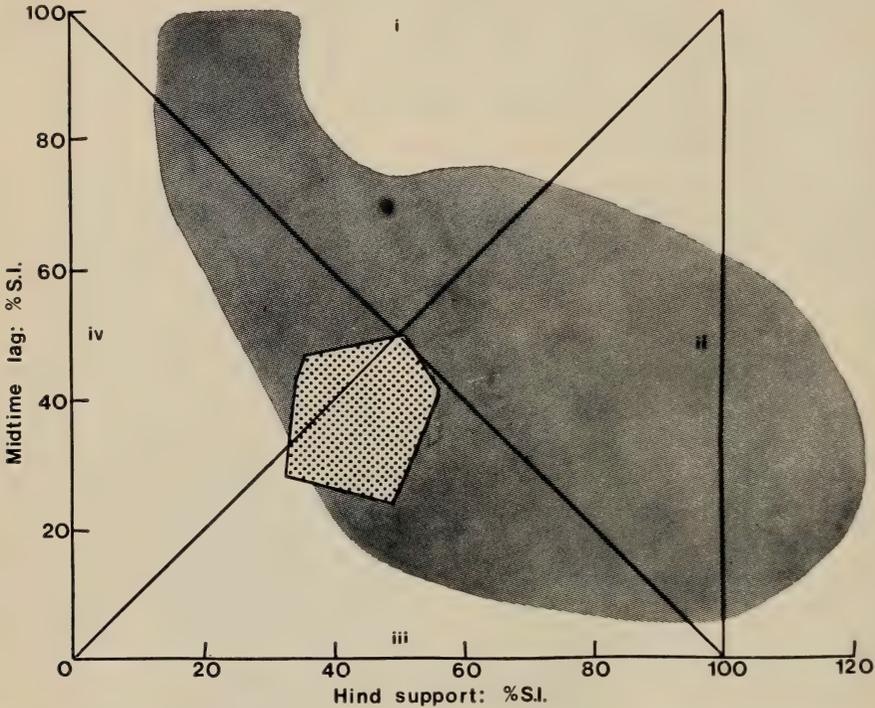


FIG. 9.—The asymmetrical gaits of *T. vulpecula* (coarsely stippled envelope) compared with those of the mammals studied by Hildebrand (1977) (finely stippled). Hildebrand presents this graph with the origin at upper right, and we have rotated it to put the origin at lower left as is the convention. The field of the graph is divided into four quadrants: i, extended suspension; ii, no suspension; iii, flexed suspension; and iv, flexed and extended suspension. *T. vulpecula* uses gaits with one (flexed) or two periods of suspension per stride. SI: stride interval. (Diagram modified from Hildebrand, 1977).

Hildebrand found that, as for symmetrical gaits, all observed asymmetrical gaits fall within a restricted area of the graph (Hildebrand, 1977, Fig. 9). Hildebrand included asymmetrical gaits of 79 genera of mammals, including five genera of Marsupialia, one of Chiroptera, two of Insectivora, 13 of Primates, one of Lagomorpha, 11 of Rodentia, 15 of Carnivora, two of Pinnipedia (which he considers separate from Carnivora), one of Hyracoidea, three of Perissodactyla and 25 of Artiodactyla. Fig. 9 compares half-bounding by *T. vulpecula* on the treadmill with the gaits studied by Hildebrand. *Trichosurus*' half-bound may be described as a medium speed gait with one (flexed) or two periods of suspension.

In the half-bound the hindlimbs strike the ground together, but the forelimbs do not. The forelimb striking second is the leading forelimb, as it is placed in front of the other fore-limb. While half-bounding *T. vulpecula* was able to change the leading forelimb without breaking the rhythm of movement. This may reduce fatigue. However, because of this change, use of Hildebrand's method of analysis proved difficult. Midtime lag was impossible to calculate, as the delays in contact by either forelimb were unrelated to loss of contact by the same limb. Variability was frequently observed between strides of a single individual.

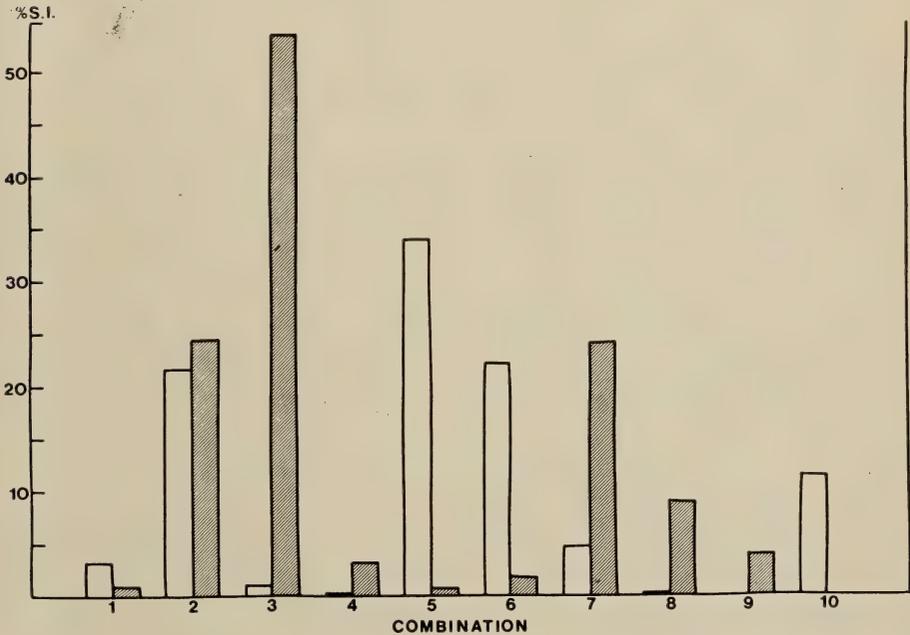


FIG. 10.—Possible combinations of support as percent of stride interval (S.I.), for the walk (shaded) and the half-bound (unshaded) of *T. vulpecula* on the treadmill.

- | | |
|-----------------------|---------------------------------|
| 1: single hindlimb; | 6: both forelimbs; |
| 2: single forelimb; | 7: both hind- and one forelimb; |
| 3: diagonal limbs; | 8: both fore- and one hindlimb; |
| 4: ipsilateral limbs; | 9: all limbs; |
| 5: both hindlimbs; | 10: no limbs. |
| | (i.e. suspension). |

Dagg and de Vos (1968a; 1968b) have considered combinations of support limbs. Histograms (Fig. 10), indicating each possible combination of support as a percentage of the stride interval, allow direct comparison of the two gaits used on the treadmill. Diagonal limbs support the body for more than half the stride interval whilst walking. Support by one (fore) or three (two hind and one fore)

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limbs allows transference between both pairs of diagonal limbs. These three support patterns account for nearly the entire stride during walking.

The walk is a slow gait without suspension and with support usually by diagonal pairs of limbs. Gray (1944) demonstrated that this pattern is the most stable for slow-moving tetrapods. The half-bound is a medium to high speed gait often used to clear obstacles by mammals with short limbs and a flexible vertebral column. Howell (1944) suggested that it is a more efficient gait than the bound, in which more energy may be expended in overcoming the deceleration of landing. In the half-bound (as compared with the walk) stability is compromised for speed. During approximately 13 per cent of each stride of the half-bound *T. vulpecula* is not in contact with the substrate. Such suspension allows the animal to increase its stride length, although each stride is of shorter duration than walking (cf. Figs. 1 and 6). Suspension usually precedes landing on both hindlimbs.

Rarely, the half-bound is modified by the introduction of a short hind lead, never comprising more than three per cent of the stride interval. The fore lead is long, to 22 per cent of the stride interval, which equals the duration of support by both forelimbs. A second modified gait was seen during walking, when the footfalls became almost simultaneous and the gait approached the trot (as defined by Dagg, 1973). As stated previously, the trot itself was not observed. Such examples demonstrate that consideration of any gait as a single entity may be misleading, and support the contention of Gambaryan (1974) that all gaits should be considered to form a continuum over different speeds. Gaits appeared more discrete upon the treadmill than in the enclosure, and we suggest that this arises from the discrete speeds at which the treadmill was run.

Under quasi-natural conditions in the enclosure the presence of four-limb (and absence of single-limb) contact during the walk indicates that walking is normally undertaken at a slower speed than on the treadmill (cf. Dagg, 1973). The diagonal support pattern seen in walking is quite stable (Howell, 1944; Gray, 1944) and may reflect adaptation to locomotion over an irregular substrate.

The half-bound was used in the enclosure for jumping from branch to branch and for clearing obstacles. Both forelead and the period of flexed suspension are reduced from those exhibited on the treadmill. Extended suspension was not observed, although all limbs were extended immediately prior to forelimb contact. The tail was apparently used as an anchor, being wound around the branch during jumping, as in *Pseudocheirus herbertensis* and *P. archeri* (Breden and Breden, 1970).

CONCLUSIONS

In the enclosure, and hence presumably under natural conditions, *Trichosurus vulpecula* exhibited three gaits: the walk, half-bound and bound. Only the first two of these were exhibited upon the treadmill.

The walk was used to move along horizontal and up inclined surfaces. Half-bounds were used to jump from branch to branch, to move along ground with grass and other low cover and to move up strongly inclined surfaces. The bound was used on steeply inclined and vertical surfaces. *T. vulpecula* avoided moving down steeply inclined branches, preferring to use more nearly horizontal branches or to jump down. Modified gaits were also seen.

Study of animals on a treadmill is useful if considered as an introduction to some (not all) of the gaits used in the wild. This supports Hildebrand's (1977) contention that gaits exhibited on a treadmill may not be characteristic of those exhibited in the wild.

ACKNOWLEDGEMENTS

Dr R. Baudinette very kindly made available for study films of two possums, Fred and TV 33, on the treadmill. Likewise Dr Milton Hildebrand generously made available for our use a manuscript, at the time unpublished, and we wish to express our gratitude to both. We would also like to thank Mr M. Oakey for his assistance in filming, the School of Zoology, University of New South Wales, for the use of their enclosure, and the Department of Medical Illustration, University of New South Wales, for their aid in preparation of the illustrations.

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Preliminary Assessment of Defecation Patterns for the Eastern Grey Kangaroo (*Macropus giganteus*)

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As faecal pellets of the eastern grey kangaroo (*Macropus giganteus*), wallaroo (*M. robustus*) and red-necked wallaby (*M. rufogriseus*) differ in shape and size, each animal can be identified from its faeces.

Number of pellets per defecation for grey kangaroos was found to vary markedly between different habitats. It is therefore suggested that individual pellets are more suitable than pellet groups as the foundation for survey work based on pellet counts.

A four-day trial monitored daily defecation rate for five kangaroos. Average for the group was 412 pellets per animal per day (co-efficient of variation 16 percent).

The defecation rate for night was approximately twice that for day periods, there being a strong association between defecation and feeding activity.

INTRODUCTION

An appraisal has been made of the faecal pellet count technique as a base for research into the ecology and distribution of the grey kangaroo (*Macropus giganteus*) within Queensland. Successful application of pellet counts, particularly if census work is envisaged, must be based on tedious preliminary investigations. The primary concern in any feasibility study is the defecation patterns of the target species. Depending upon the stability of pellet form, defecation rate and defecation in relation to activity cycles, the animal will vary in its suitability for study by this method. In accordance with these problems, a programme has been initiated to monitor defecation patterns of the grey kangaroo. Details are given of trials conducted with a captive population at Lone Pine Koala Sanctuary, Brisbane. Free ranging kangaroos were studied in the Durikai State Forest and an adjoining property "Eddington", 40 km west of Warwick, southern Queensland.

METHODS

SPECIES IDENTIFICATION

The usefulness of pellet surveys revolves around the assumption that an animal can be accurately identified from its faeces. In most cases pellet shape is

the most reliable guide for identification purposes (Riney, 1957). At Durikai, grey kangaroos live in association with sizable populations of wallaroos (*Macropus robustus*) and red-necked wallabies (*M. rufogriseus*). Comparisons were made between the faeces of these three species. At Lone Pine pellets were collected from the enclosures of caged animals while at Durikai; observation of feeding animals allowed collection of fresh pellets under natural conditions.

DEFECATION RATE

A preliminary trial at Lone Pine into defecation rate for grey kangaroos was conducted over four consecutive days during June, 1977. Five animals (two adult males, two adult females and one juvenile male) were placed in a 0.7 ha section of the grey kangaroo enclosure. The area was well grassed and the animals had access to supplementary feed. The enclosure was cleared of pellets twice daily.

Results were tabulated as pellet totals and pellet group totals. A group was classed as any assemblage of one or more pellets judged to be separate from surrounding pellets on the basis of distance, pellet size, shape and age. No minimum distance rule was adopted for separating adjacent groups, and the results probably reflect "splitting" rather than "lumping" of pellet groups (Neff, 1968: 607).

For any pellet survey or assessment of defecation rate the problem of what is to be counted must be resolved. The choice lies between individual pellets, pellet groups, presence or absence of pellets and mass of pellets. Research into kangaroos has made use of presence or absence of pellets (Caughley, 1964a) and mass of pellets (Warren, 1971). However, from the viewpoint of conducting a census or extracting maximum quantifiable data from the survey, the use of individual pellets or pellet groups is more appropriate. The pellet count technique was developed around deer surveys and has traditionally been based on pellet group totals (Bennett et al, 1940). For deer, the number of defecations per day (pellet groups) varies much less than total number of faecal pellets (Riney, 1957; Smith, 1964). As deer defecate less frequently than kangaroos, but pass a higher number of faecal pellets per day, it does not necessarily follow that pellet groups are the most suitable base for kangaroo surveys.

If it can be assumed that grey kangaroos from different areas have similar defecation rates, the problem is to determine whether pellet group totals or individual pellet totals best reflect this constancy.

Work with pellet groups from Durikai and Lone Pine suggested that the average number of pellets per defecation was quite different for the two populations. Data were therefore recorded to quantify this observation.

For Lone Pine, early morning counts were made of fresh, undisturbed groups of pellets deposited by 25 grey kangaroos housed in a 1.4 ha enclosure.

DEFACATION PATTERNS OF THE GREY KANGAROO

A systematic sampling pattern was completed for each count, although no attempt was made to cover the entire area.

At Durikai, pellet groups judged to be less than one month old were recorded from 0.001 ha circular plots. These were positioned at regular intervals along randomly located transects straddling varying habitat types. Twenty-eight days prior to this survey 120 fresh pellets from Lone Pine and Durikai were placed on 60 permanent plots (three rows of 20 pegs). This provided a control group of pellets of known age for use in the survey. As less than one per cent of the control group (one pellet from 120) disappeared during the 28 days, results of the survey were not biased significantly through pellet losses.

DEFECATION AND DAILY ACTIVITY

For the trial study of defecation rates the enclosure was cleared twice daily to correspond roughly with the late afternoon to early morning feeding session (4 p.m. to 8 a.m.) and the day resting session (8 a.m. to 4 p.m.). A separate defecation rate for these two periods could therefore be calculated. Classification of these activity periods was based on published material dealing with behavioural

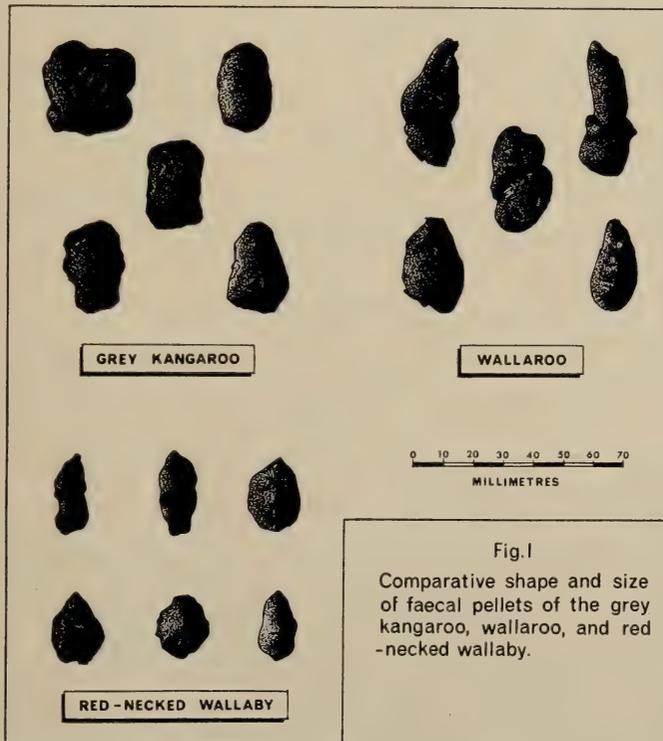


Fig.1
Comparative shape and size
of faecal pellets of the grey
kangaroo, wallaroo, and red-
necked wallaby.

patterns of grey kangaroos (Caughley, 1964b & Kaufman, 1975) and on personal observation.

RESULTS

SPECIES IDENTIFICATION

As reported by Caughley (1964a) and Grant (1974), grey kangaroo pellets have a distinctive shape. Opposite sides of the pellet are approximately equal in size and are usually rectangular in shape. Pellets often resemble rectangular prisms with rounded edges (Fig. 1). During the defecation process pellets are normally passed separately and pellet groups are therefore a collection of individual pellets.

The faeces of the wallaroo are of comparable size to those of the grey kangaroo. However, the pellets are more elongated and flattened and show a tendency to taper towards one end (Fig. 1). Unlike the grey kangaroo, wallaroos may pass a string of pellets compressed together.

Pellets of the red-necked wallaby are generally smaller than those of the two larger macropods. The shape is usually rounded, although tapered pellets are not uncommon (Fig. 1).

In Fig. 1 pellets were selected to illustrate the range that commonly occurs in pellet shape for each species. While variations in shape, that could result in wrong identification, have been noted, errors of this nature are not likely to be significant. Most variations of this type occurred with the Lone Pine animals, and these were attributed to reliance on a concentrate diet. This has been observed to cause similar problems in other herbivores (Smith, 1964).

Several weeks of sampling work at Durikai have confirmed that recognition of pellets from each species can be achieved quickly and confidently in the field.

DEFECATION RATE

TABLE 1

Daily defecation rate for five kangaroos over a four day period.

	Range	Mean	Co-efficient of variation
Pellets per animal	319-465	412.2	16%
Groups per animal	53-79	68.4	16.5%

Although the trial was too short to be given great significance, it does provide a rough guide line for comparing census estimates from pellet surveys with other survey methods. The conversion figure allows unwieldy population estimates of pellet totals to be reduced to a more easily interpreted form.

Monitoring of defecation rate for the Lone Pine kangaroos suggested that for this population individual pellet totals and pellet group totals were equally suited as a survey base. Co-efficients of variation for the two are similar (Table 1).

DEFACATION PATTERNS OF THE GREY KANGAROO

However, comparison of the frequency distributions of pellets per group for captive and wild kangaroos (Fig. 2a & b) indicates that other factors must be taken into consideration. Average number of pellets per group (6.2 and 3.7 respectively) and the skewness of the two distributions differ markedly (significant difference, 0.1 per cent level, Kolmogorov-Smirnov two-tailed test).

Unless the Lone Pine kangaroos pass approximately twice as many faecal pellets per day as the wild kangaroos, pellet group totals cannot be a reliable indicator of defecation rate for grey kangaroos.

Observation of feeding kangaroos implies that the number of pellets deposited in any one group depends on animal movement patterns.

For the captive kangaroos in a confined space, and with ample food, movement was minimised and the number of pellets passed at one situation large. At

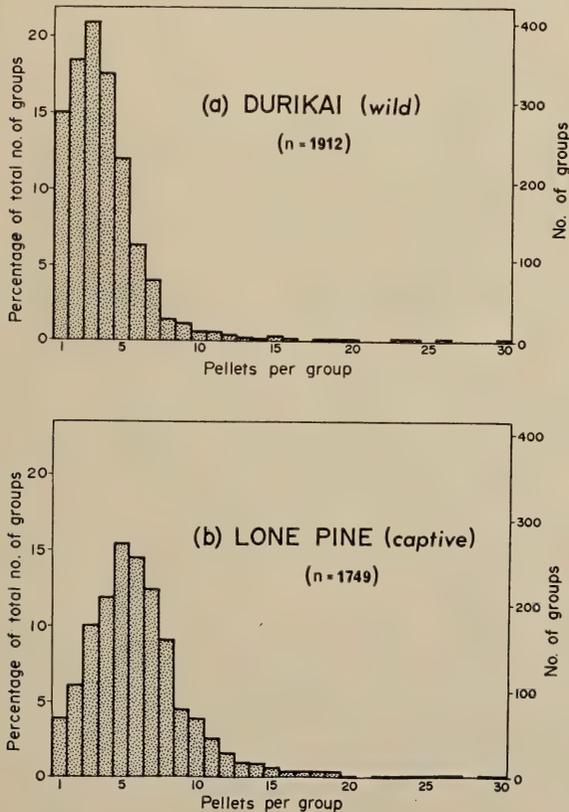


Fig. 2. Distribution of pellets per group.

Durikai, on the other hand, where pasture conditions were variable, feeding animals moved more often than their Lone Pine counterparts. Here defecation was characterised by fewer pellets per group.

During feeding kangaroos defecate frequently, both while stationary and when moving. For any short time-span a certain number of pellets will be deposited. Whether these form one large group or several small groups depends largely on the density of the pasture being utilised. This hypothesis is supported by comparison of the frequency distributions of pellet groups collected from well-grassed and sparsely-grassed plots located within the one paddock on Eddington Station at Durikai (Fig. 3a & b).

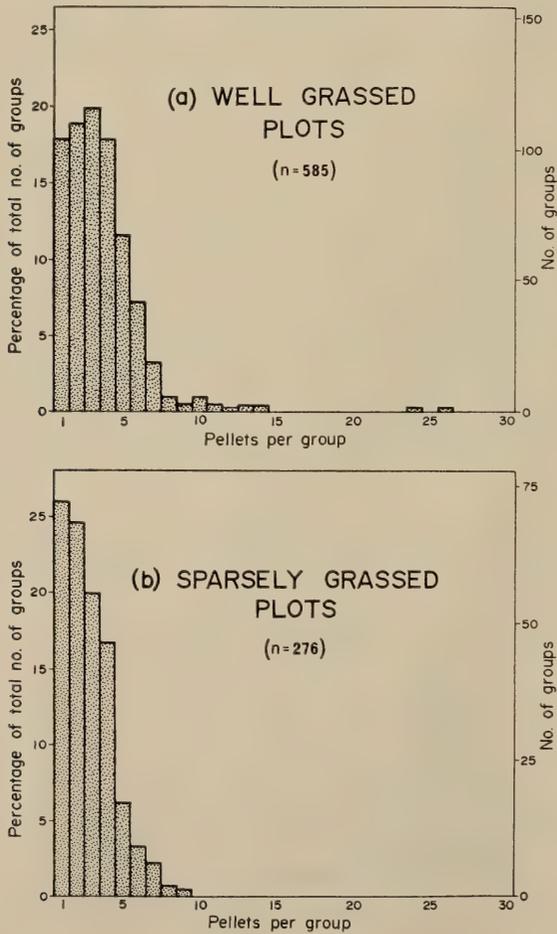


Fig. 3. Distribution of pellets per group at Eddington.

DEFACATION PATTERNS OF THE GREY KANGAROO

The two distributions are significantly different (0.1 per cent level, Kolmogorov-Smirnov two-tailed test). Where food is plentiful, the number of pellets per group is higher, as kangaroos stay in the one position for longer.

Comparisons between separate surveys in the spatial or temporal context could lead to serious interpretation errors if pellet groups are used. For example, should relative abundance of two kangaroo populations be compared by a pellet group survey, estimates will be positively biased toward the population utilising the more widely dispersed forage resource.

The pellet survey for Durikai described earlier in this paper provides data to illustrate the point. During this survey a 90 km² block of forested country had been sampled by 515 circular plots of area 0.001 ha. Each plot was searched for pellets judged to be less than four weeks of age. Averages were 1.22 pellets per plot with 0.3 pellet groups per plot. These estimates were converted to kangaroos/km² using the formula:

$$D = \frac{\bar{y} \times 100,000}{28 \times r}$$

where D = kangaroos/km²
 \bar{y} = mean per plot
(pellets or pellet groups)
100,000 = number of 0.001 ha plots/km²
28 = survey period in days
 r = daily defecation rate
(412 pellets or 68 pellet groups)

Result using pellet totals was 10.6 kangaroos/km², while pellet groups returned an estimate of 15.8 kangaroos/km². Although the accuracy of these estimates cannot be checked on the wild population, a density of 15.8 kangaroos/km² does appear very high for the country involved. On the other hand, 10.6 kangaroos/km² corresponds reasonably well with the density estimates of Fox for similar habitats (AREA, 19) close by across the New South Wales border (Fox, 1974: 95).

As a common yardstick for comparing different populations, pellet totals appear to be the most suitable base for surveys.

DEFECATION AND DAILY ACTIVITY

Any use of pellet surveys as a guide to habitat usage must be finely attuned to known behaviour of the animal involved. Correlations between pellet density and habitat type cannot take for granted that density of pellets is related to time spent in a particular area or is indicative of animal preferences.

Caughley (1964a: 242) states: "As most faeces are dropped at night when the animals are feeding, the dispersion of faeces gives an indication of how kangaroos utilise their habitat over a period of time".

Observations at Lone Pine and Durikai both substantiate Caughley's findings, although several points need to be clarified. For the Lone Pine study on defecation rates, pellet production per hour for the night period (4 p.m. to 8 a.m.) was higher than that of the day period.

TABLE 2
DEFECATION RATES FOR DAY AND NIGHT

Time Period	Weather	Pellets per Roo per Hr.
Tuesday	fine	11.2
Tuesday night	fine	21.6
Wednesday	fine	15.1
Wednesday night	fine	22.7
Thursday	overcast	11.2
Thursday night	rain	13.0
Friday	clearing	13.9

For the last day rain appears to have reduced overall defecation rate and evened out the differences. A similar phenomenon for rabbits is described by Taylor *et al* (1956).

When examining the data presented in table 2 it should be noted that these virtually domesticated animals actively foraged in their preferred feeding areas sporadically during the day. Wild kangaroos rarely follow this behaviour pattern. The major portion of daylight hours is spent in habitat types that offer concealment but little in the way of forage. In this case then, the data presented probably overestimate the pellet contribution for day periods.

One point gleaned from field work at Durikai is that heavy defecation is not usually associated with the daily bedding sites in the scrub. Resting kangaroos at Lone Pine have only been observed to defecate when they get up to shift position.

These observations and the data from table 2 indicate that defecation is strongly associated with feeding. This activity is most common during the period from late afternoon to early morning. In this context it must also be stated that pellet counts will not necessarily offer an indication of overall habitat usage by grey kangaroos. Day time shelter zones for example may exhibit very low pellet densities unless good ground cover is present that will keep kangaroos in the area during the feeding cycle.

DISCUSSION

Prolonged monitoring of average defecation rates is necessary before accurate population estimates can be made through pellet counts. However, this does not detract from the value of the technique in providing indices of kangaroo abundance. Greatest potential exists for areas where other survey methods prove unsatisfactory.

DEFACATION PATTERNS OF THE GREY KANGAROO

Heavily timbered country can be placed in this category. As only a small proportion of the kangaroo population is visible to observers, census estimates are not accurate. For habitats of this type, the reliability of aerial or ground counts of kangaroos is also doubtful because of seasonal movement patterns of the animals. To test this assumption an aerial survey programme has begun at Durikai to compare successive kangaroo counts with seasonal changes in pellet density distributions.

Pellet counts also offer considerable scope in providing distributional data of ecological and management significance. Habitat preference and seasonal movement pattern studies appear well suited in this regard. These factors are relevant in appraising issues such as competition with domestic stock, seasonal vulnerability to hunting and likely impact of land management programmes.

A factor favouring the use of pellet counts for research into grey kangaroos is the high defecation rate in terms of groups passed per day. Faecal material is therefore distributed widely across usage zones. In areas with a moderate density of animals, counts based on short deposition periods should return pellet densities high enough for surveys to be completed with success. Success can be defined in terms of workload required for acceptable statistical manipulation of data.

Defecation patterns of the target animal are only one of several aspects that must be examined when assessing the usefulness or feasibility of pellet counts. Determining pellet age, pellet decay rates and pellet visibility poses its own set of problems, as does the design of the survey itself. Success or failure however relies in the main on defecation patterns. The study outlined in this paper suggests that the defecation patterns of the grey kangaroo make it a suitable subject for research by the pellet count method.

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Permission to Traverse state forestry reserves was granted by the Queensland Forestry Department and Mr Tom Thornton has permitted research to be carried out on his property Eddington.

Without the co-operation of the above the project would not have been possible.

Mr E. E. Savage produced the graphs and Mr H. Stewart-Kellick sketched the faecal pellets.

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Eye Closure During Agonistic Behaviour of *Rattus villosissimus*

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Several groups of workers have noted the eye closure that may occur in a rat involved in certain acts or postures of flight or defence (Chance, 1962; Grant and Mackintosh, 1963; Barnett and Evans, 1965). Various hypotheses have been advanced to explain the significance of this response.

Chance (1962) proposed that closing of the eyes, turning away of the head, and similar responses when they occur in an agonistic context act as "cut-off" postures. They result in a reduced stimulus input from an attacking opponent and reduce the drive for flight in the actor. Thus, the rat under attack may remain in the proximity of its opponent. According to Chance, the advantage to the rat under attack is inherent in the idea that the formation of dominance-subordination relationships involves a fluctuating balance of attack and defence. Then, "cut-off" postures would allow the lability necessary for a fleeing rat to return to social contact.

Grant and Mackintosh (1963) working on a series of rodents including laboratory rats and mice, stated that "one of the general features of defensive and submissive postures is the withdrawal of attention from the aggressive animal". This they claim, reduces the tendency for the defender to retreat, thus concurring with the findings of Chance (1962). Barnett and Evans (1965) add the possibility that eye closure in agonistic situations, may be a product of autonomic activation. Secondly, this response may change "the visual stimulus provided by the defender, and so reduces the likelihood of further assault". Thus, closing of the eyes may affect the subsequent behaviour of both the actor and reactor.

During a study of the agonistic behaviour of *Rattus villosissimus* (Begg and Nelson, 1977), rats were found to close one or both eyes partly or wholly, during many different acts or postures observed in agonistic situations. It occurred spontaneously (with no obvious preceding change in the behaviour of an opponent), or as a result of some direct action by another rat. All situations in which *R. villosissimus* were seen to display this response, are listed in Table 1. A full

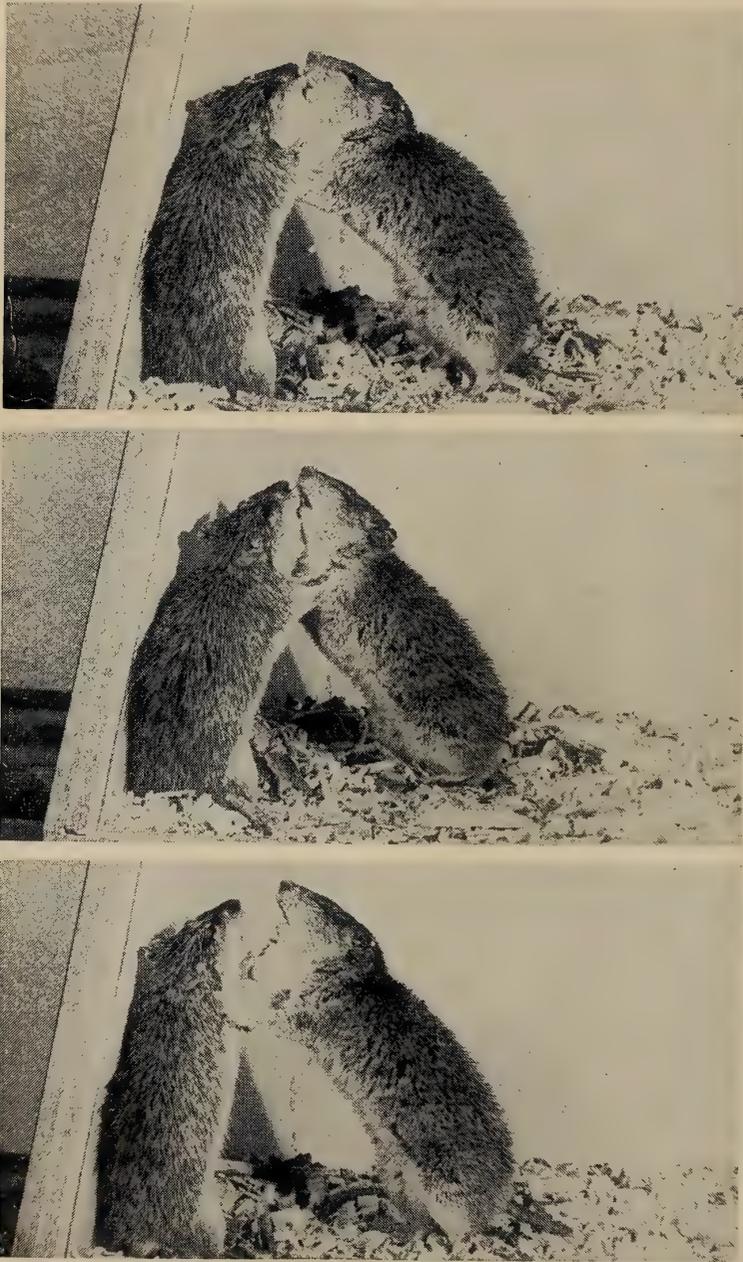


FIG. 1.—Variability of eye closure in one bout of OFFENSIVE (right) and DEFENSIVE (left) UPRIGHT posture in *Rattus villosissimus*.

EYE CLOSURE IN *RATTUS VILLOSISSIMUS*

description of the behaviour involved is given in Begg and Nelson (1977). No measures of frequency are given as it is hard to quantify this response due to rapid movements, variable orientation of rats involved, and differences in degree of eye closure.

TABLE 1

Postures and Acts Involving Eye Closure in Rattus villosissimus

Behaviour of Dominant Rat	Behaviour of Subordinate Rat	Rat with Eye, or Eyes, Closed
LUNGING	CROUCHING	D
APPROACH	LUNGING	D and/or S
CROUCHING during a lull in a ROLLING WRESTLING FIGHT	LUNGING	S
CROUCHING during a lull in a ROLLING WRESTLING FIGHT	ESCAPE LEAP	D
ATTACK LEAP		
(a) as D makes contact with mouth and forelimbs	DEFENSIVE SIDEWAYS POSTURE	D
(b) D releases grip with teeth and BITES again	DEFENSIVE SIDEWAYS POSTURE	D
OFFENSIVE UPRIGHT POSTURE	DEFENSIVE UPRIGHT POSTURE	D and/or S
OFFENSIVE SIDEWAYS POSTURE	DEFENSIVE SIDEWAYS POSTURE	D and/or S
STANDING OVER	"SUBMISSIVE" POSTURE	D or S
STANDING OVER	SUBMISSIVE CROUCH	D or S
CROUCHING	SUBMISSIVE CROUCH	S
GROOMING SELF	SUBMISSIVE CROUCH	S
SUBMISSIVE CROUCH	SUBMISSIVE CROUCH	D
INVESTIGATE	CROUCHING	S
GROOMING SELF	CROUCHING	S
CROUCHING	GROOMING D	D

D = dominant rat

S = subordinate rat

Eye closure occurred during acts and postures associated with offence or defence. It also occurred simultaneously in both attacking and defending rats (Fig. 1 shows a single instance of OFFENSIVE and DEFENSIVE UPRIGHT postures where eye closure occurred first in neither rat, then in the attacker, then in both rats). During postures which were maintained for several seconds or more, often only the eye nearer the opponent was closed. However rats closed both eyes while carrying out rapid acts (such as ATTACK LEAP, LUNGING, BITING), or following the performance of such rapid acts by an opponent. This was observed frequently when an animal made an ATTACK LEAP. Just before making contact with its forelimbs and mouth on an opponent, the attacking rat often briefly closed both eyes. Some rats have also been observed, during an ATTACK LEAP, to release

a grip with their teeth, and take a second bite further over the back of the defender, closing their eyes as they do so. In situations such as this, eye closure does not result in an obvious reduction of an attack drive as a theory such as that of Chance (1962) would propose. The animals still press home the attack.

Situations involving eye closure do however have some features in common. Most importantly they almost always involve some tactile contact between rats. Thus the eyes of each rat, which are particularly vulnerable due to their large size and degree of protrusion from the orbit, are placed in a situation of potential danger from the nearness of the opponent's teeth. Thus, in the situations outlined above, eye closure (which does, as detailed, often only involve the eye nearer to the opponent) may serve to protect the eyes from possible damage by an opponent. Vine (1970) suggests that a similar mechanism operates in many gulls and terns where the head-turning that occurs in many agonistic encounters may be a defensive reaction, removing vulnerable aspects of the face from the proximity of an opponent's bill.

Eye closure during sudden movement by either the actor or reactor then probably serves as a protective mechanism. Landis and Hunt (1936) demonstrated that a sudden loud noise may produce eye closure in man. Andrew (1963) lists a series of "protective responses" found in mammals, one of which is closing of the eyes. These responses may be evoked by an intense stimulus contrast, such as a sudden loud noise or a blow towards the face. They serve to protect the major sense organs against possible noxious effects from the source of contrast.

Thus, rather than forming some sort of "cut-off" mechanism, in *R. villosissimus* at least, eye closure in agonistic situations is probably a defensive reaction, evoked by the proximity of an opponent, or sudden movement by an opponent, or during sudden movement towards an opponent.

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A Triploid Male Individual *Amphibolurus nobbi nobbi* (Witten (Lacertilia: Agamidae))

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INTRODUCTION

Triploidy has been observed in representatives of three lizard families (Agamidae, Geckonidae, Teiidae; see Gorman, 1973, for review). Most of these are parthenogenetic species (Hall, 1970; Lowe *et al*, 1970b). The only previous report of triploidy within the Agamidae is an apparently parthenogenetic population of *Leiolepis belliana* (Hall, 1970).

MATERIALS AND METHODS

Live males of *Amphibolurus nobbi* in breeding condition were injected intraperitoneally with 0.2% solution of colchicine at the rate of 0.05 mls/g body weight within 2-3 days of collection. After 5 hours at room temperature (24-28°C) the animal was sacrificed. A testis was chopped finely, macerated in 1% sodium citrate solution for 10 minutes, then centrifuged. The cell button was fixed in three changes of freshly prepared acetic acid: methanol (1:3), and resuspended after the third change of fixative. Three drops of the suspension were spread on a slide, ignited, allowed to burn out, and the residue flung off. The preparation was then stained for 15-20 minutes in Giemza and air-dried before mounting.

RESULTS

Of three *Amphibolurus nobbi* karyotyped, one was triploid. The most common karyotype for Australian agamids consisting of 12 macrochromosomes and 20 microchromosomes ($2n = 32$) (Witten, unpubl.) was recorded in the other two individuals. A comparison with a normal diploid figure demonstrates that triploidy has resulted from an extra haploid complement, with no observable difference in any of the macrochromosomes (Figs. 1, 2). The triploid specimen (Austr. Mus. Field tag 11392) appeared to be normal.

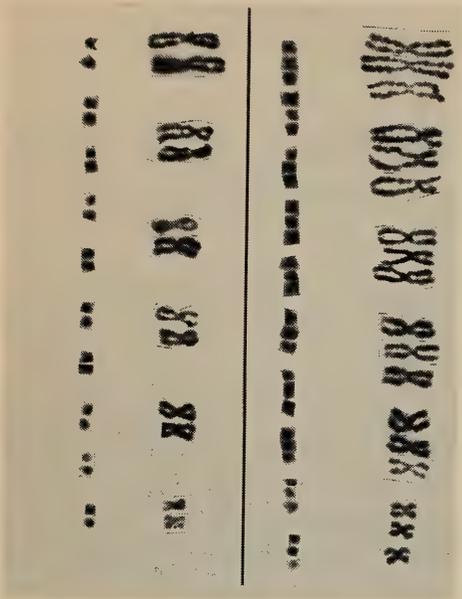


Fig. 1



Fig. 2

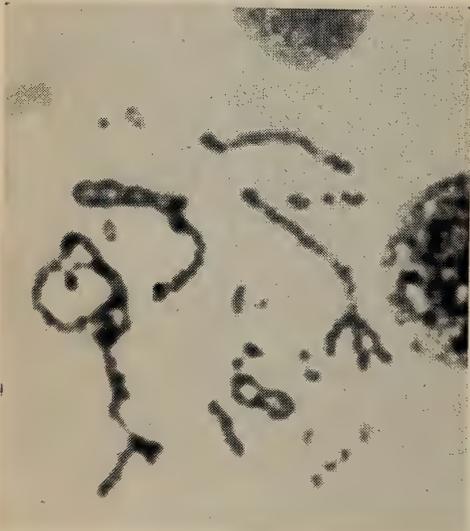


Fig. 3

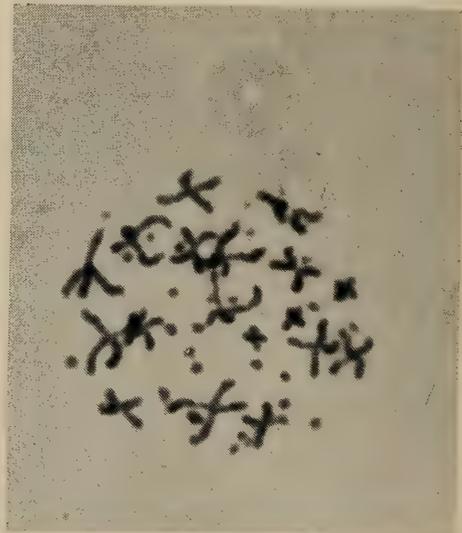


Fig. 4

FIG. 1 — Cut-out representation of karyotype of diploid (left) and triploid *A. nobbi*.

FIG. 2 — Photomicrograph of triploid mitotic figure. Bar represents 10 μ .

FIG. 3 — Diakinesis of triploid individual. Most figures of this stage showed even less organisation.

FIG. 4 — Metaphase II of meiosis in triploid *A. nobbi*, c.f. Fig 2 for appearance of chromosomes.

A TRIPLOID INDIVIDUAL AGAMID

It was apparent that diakinesis did not always result in the organisation of chromosomes into triplets (Fig. 3). Many cells representing this stage were observed, but no consistent pattern emerged.

Cells representing the second meiotic metaphase are distinguishable in normal testis preparations by the thinner appearance of the arms, the non-alignment of these arms away from the centromere, and by their haploid number. Using the first two of these criteria, second meiotic metaphase cells were identified in the triploid individual, but all such cells had a triploid complement (Fig 4). From this observation it was assumed that no reduction of chromosome number occurred in meiosis I.

DISCUSSION

Triploidy has been associated with parthenogenesis in all three families where it has been reported (Teiidae; Pennock, 1965; Geckonidae; Kluge and Eckardt, 1969; Agamidae; Hall, 1970). In the teiid genus *Cnemidophorus*, Lowe *et al* (1970b) have suggested that the triploid condition in at least some parthenogenetic species has arisen through hybridisation between diploid males and females of diploid parthenogenetic species. It is improbable that the present example of triploidy is due to hybridisation: the animal in question is sympatric with only two other agamid species. One is *Lophognathus gilberti*, which has a distinctively different karyotype (Witten, unpubl.). The other is *Amphibolurus barbatus* which is about 50 times the weight of *A. nobbi* and therefore is unlikely to produce a hybrid under natural conditions.

The presumed failure of meiosis I in this study is in contrast with the conclusions but not the results of Lowe *et al* (1970a). In an allotetraploid hybrid they noted an "infrequency of cells exhibiting meiosis II", and concluded that this was due to a "delayed testicular cycle". It is interesting to speculate that the failure to divide in meiosis I observed in this study could be due to polyploidy. If this is the case, then 'accidental' triploid females would produce triploid gametes. It has long been established in the amphibia that haploid individuals are less viable than diploids or polyploids (Fankhauser, 1945). If this holds true for reptiles, then gynogenetically or parthenogenetically developing triploid ova are more likely to be viable than haploid ova, and the strong correlation between triploidy and parthenogenesis could in part be explained.

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Sexual Dimorphism in an Australian Galaxiid (Pisces: Galaxiidae)

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(Fisheries Research Publication No. 328)

ABSTRACT

Sexual dimorphism in the diminutive Australian galaxiid *Galaxiella pusilla* (Mack) is described; this is the only galaxiid in which sexual dimorphism has been reported; its significance is discussed.

INTRODUCTION

The family Galaxiidae contains about 34 species, and is widely distributed in the southern cold temperate zone — Australia, New Zealand, South America, South Africa, and smaller islands near these areas. The species have been described in considerable detail (McDowall, 1968, 1970, 1971, 1973a; McDowall and Frankenberg, In Prep.), but in no instance was sexual dimorphism described. Massola (1938), however, in a popular article for aquarists, described the colouration of the tiny Australian species *Galaxiella pusilla* (Mack) (Fig. 1). He noted that there is a bright orange longitudinal stripe in males but not in females, a colour difference that has eluded recognition by later workers. Scott (1971) and Andrews (1976) described colouration in *G. pusilla* in considerable detail but made no mention of sexual dimorphism; it was not recognised by McDowall (1973b), nor by McDowall (1978) when describing the genus *Galaxiella* to contain *G. pusilla* (Mack), and two similar and related species from Western Australia — *G. nigros-triata* (Shipway) and *G. munda* McDowall.

The observation of live material, by the author, at the Arthur Rylah Institute for Environmental Research, Melbourne, and the collection of a substantial further sample of live material, showed that sexual dimorphism does occur in *G. pusilla*.

MATERIAL EXAMINED

Description of dimorphism in *G. pusilla* is based primarily on a sample of 43 specimens (22 males, 21 females) collected from a small, overgrown farm drain,



FIG. 1 — *Galaxiella pusilla* (Mack), 28.5 mm T.L., Narracan Creek, Victoria; female.

flowing intermittently, and entering Narracan Creek, a tributary of the La Trobe River, near Yallourn, southern Victoria (30 August, 1977); the sample is in the author's collection of galaxiid fishes.

A series of 26 body measurements was taken, and counts of the number of fin rays, gill rakers and vertebrae, following techniques described elsewhere (McDowall, 1970; McDowall and Frankenberg, In Prep.). Scanning of data from five specimens of each sex suggested that there are differences in three body proportions — body depth, pectoral-pelvic length, and pelvic-anal length; these dimensions were measured for the entire sample.



FIG. 2 — *Galaxiella pusilla* (Mack), Narracan Creek, Victoria; above — female 36 mm T.L.; below — male 25 mm T.L.

SEXUAL DIMORPHISM IN A GALAXIID

RESULTS

DIMORPHIC CHARACTERS

1. Size: Males are much smaller than females (Table 1; Fig. 2).
2. Body proportions: Ripe males are more slender-bodied than ripe females (Table 1). This is primarily a reflection of the swollen abdomens of the ripe females and the difference has little significance. The pectoral-pelvic and pelvic-anal intervals are less in males than in females (Table 1). Examination of plots of pectoral-pelvic length/standard length and pelvic-anal length/standard length suggested that there is allometric growth in this fish; the higher ratios in females are produced by allometry common to the two sexes, but which continues further in females than in males because the females grow to a greater size (Fig. 3).

TABLE 1

Sexual dimorphism in size and body proportions in Galaxiella pusilla (22 males, 21 females, Narracan Creek, Victoria).

		Range	Mean	S.D.
Size (total length — mm)	male	24.5 - 29.5	27.19	1.24
	female	31.0 - 39.0	34.20	1.86
Body depth/standard length (%)	male	16.8 - 21.5	18.70	1.27
	female	19.0 - 23.3	21.09	0.99
Pectoral-pelvic length/standard length (%)	male	23.7 - 29.1	26.06	1.44
	female	26.7 - 34.7	30.79	1.87
Pelvic-anal length/standard length (%)	male	15.9 - 19.3	17.40	0.83
	female	17.0 - 22.6	19.00	1.74

3. Ventral keel and genital papilla: In both sexes there is a fleshy keel along the ventral abdomen, beginning at about the pelvic fin bases, and extending back as far as the vent. The relative depth of the keel is slightly greater in males than in females. In the male the vent is followed by a low, fleshy genital papilla that projects slightly more than the vent; in the female the genital papilla is a distinct fleshy mound.

4. Colour: When alive the male *G. pusilla* is a dull olive-amber on the back and upper sides, with three black, longitudinal stripes along the trunk (Fig. 1); the upper stripe is weakest and merges medio-dorsally with darker pigment on the back. The middle stripe is much thinner and very distinct, and is positioned at about the lateral line; it is above and well-separated from a characteristic and very bright orange stripe along the abdomen, but converges with it on the caudal peduncle. The lower dark stripe is strongly developed and forms the lower margin of the orange stripe. Ventrally there is a pair of black lines, originating together in the isthmus, diverging, and then running parallel along the belly to the pelvic fin bases; the pelvic-anal interval is more or less unpigmented but there are black lines along the

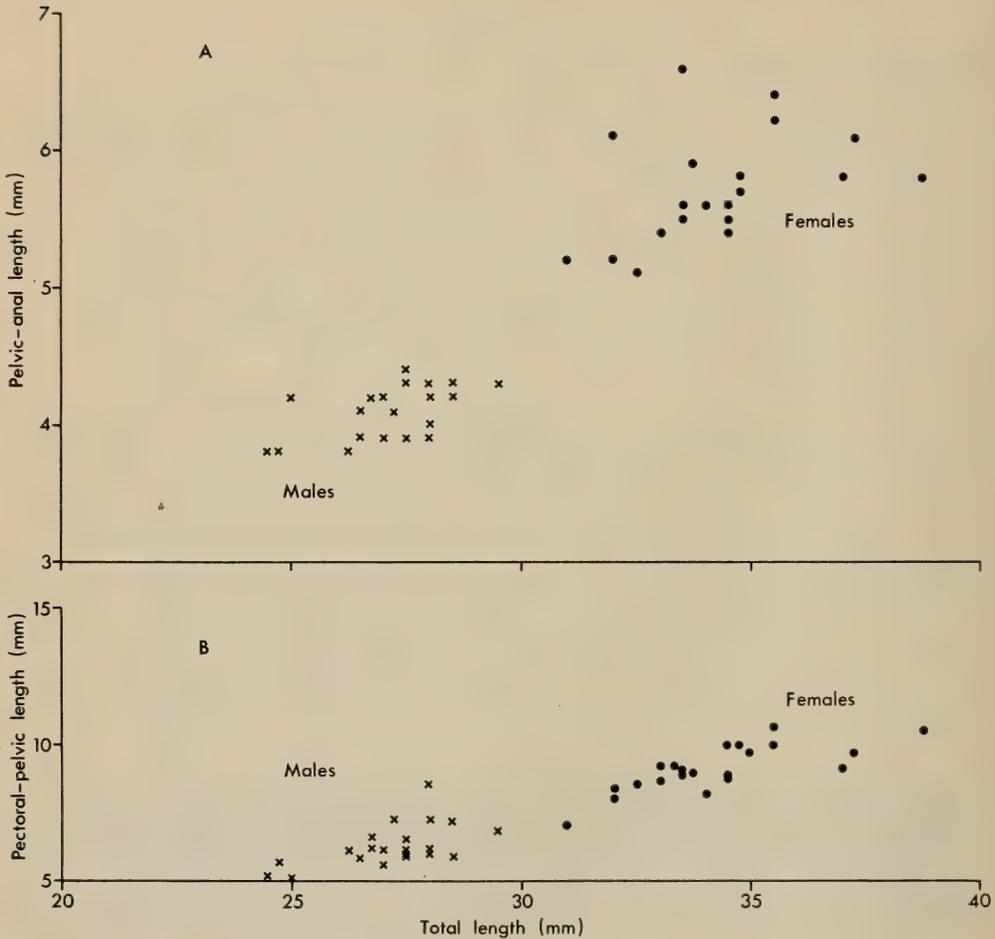


FIG. 3— Relationship between pelvic-anal length and pectoral-pelvic length, and total length in *Galaxiella pusilla*.

anal fin base and the ventral margin of the caudal peduncle, becoming more or less confluent with the lowermost dark lateral stripe. The belly is silvery-white, and the eyes are silvery-gold, with small areas of bright orange as a continuation of the lateral orange stripe.

The female differs from the male primarily in lacking the bright orange stripe. The longitudinal dark lines occur, but these are a little less bold, and there is a lateral band of silvery iridescence comparable in position to the orange stripe in the male.

DISCUSSION

Little is known about reproductive patterns in galaxiid fishes, particularly about their spawning behaviour. Breeding has been reported in a few galaxiids — *Galaxias olidus* Günther (Walford, 1940 — as *G. coxii* Macleay); *G. divergens* Stokell (Hopkins, 1971); *G. vulgaris* Stokell (Benzie, 1968; Cadwallader, 1976); *Neochanna apoda* Günther (Eldon, 1971, 1978); *N. burrowsius* (Phillipps) (Cadwallader, 1975). However apart from the report by Massola (1938) of spawning in *Galaxiella pusilla*, only in *Galaxias maculatus* (Jenyns) has spawning actually been observed (Hayes, in Hefford 1931a, b, 1932; Pollard, 1971) — small to large shoals of fish were observed to spawn together, releasing the eggs haphazardly over the substrate. In none of these species has sexual dimorphism, like that described for *G. pusilla*, been observed.

Galaxias maculatus is one of very few species of galaxiid that is known to live in shoals as an adult, and it is likely that its spawning habits are distinctive in the family. *Galaxiella pusilla* was reported by Massola (1938) to spawn in pairs, the female depositing its eggs singly on aquatic vegetation and the male subsequently fertilising them. Massola's report agrees with more recent observations of spawning in *G. pusilla* by R. W. Vanner and G. D. Backhouse, of Victoria, Australia, both of whom have seen the fish spawning in indoor aquaria (pers. comm.). Unlike most galaxiid fish, *G. pusilla* is a mid-water, free-swimming species. This behavioural distinction and the formation of pairs for spawning seem likely to be related to the occurrence of sexual dimorphism.

G. pusilla has recently (McDowall, 1978) been placed, with *G. nigrostriata* (Shipway) and *G. munda* McDowall, in the genus *Galaxiella* on account of similarities between these obviously closely related species, and differences from the remainder of the family Galaxiidae, in particular differences from the genera *Galaxias* Cuvier and *Brachygalaxias* Eigenmann.

There are not yet sufficient data available to indicate whether dimorphism occurs in the two Western Australian species of *Galaxiella*. *G. nigrostriata* very closely resembles *G. pusilla* (it has been regarded as a subspecies by some workers — Shipway, 1953; Munro, 1957), and sexual dimorphism seems likely in this species. *G. munda* less resembles the other *Galaxiella* species; it lacks the brilliant orange stripe and has instead a dull brick-orange stripe. Colour photographs of some specimens of *G. munda* show silvery iridescence along the lower sides, perhaps indicating that these are females comparable with the females of *G. pusilla*.

If the two Western Australian species are sexually dimorphic, the occurrence of such dimorphism in this small, distinctive radiation of galaxiid fishes would add to the array of characters setting *Galaxiella* apart from other galaxiid fishes, and thus add weight to the recognition of the genus as distinct.

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Comments on the Technique of Acid Dissolution of Coral Rock to Extract Endo-Cryptolithic Fauna

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ABSTRACT

Comparisons of fauna recovered by hammer and chisel technique and acid dissolution technique are made. A modified technique for acid dissolution of coral rock is described in which complete identifiable animals are recovered.

INTRODUCTION

Brock and Brock (1977) described a technique for dissolving coral rock in dilute acid to extract the infauna. The term infauna according to Hutchings (1974) includes the true borers and the opportunistic species which cannot themselves bore but utilise the burrows made by the true borers. As the term infauna is normally used for describing infaunal communities in soft sediments, we propose that the term infauna be replaced with the term endo-cryptolithic fauna indicating its two components, the endolithic fauna the true borers and the cryptolithic fauna the opportunistic species.

Previously two main methods of extracting this endo-cryptolithic fauna have been used. Clausade (1970) put coral samples into freshwater for several hours to force the mobile cryptolithic fauna out. Similarly Leviten (1976) allowed coral samples to stand in seawater for several hours and as the water became anoxic the mobile cryptolithic fauna evacuated the sample. Subsequently both these workers broke up the coral to extract the sessile endolithic fauna. However, as the samples are not preserved immediately many of the smaller animals may decompose either in or out of the coral rock and the results are thus only semi-quantitative (Brock and Brock, 1977). The other main method used by McCloskey (1970), Grassle (1973), Kohn and Lloyd (1973) and Hutchings (1974, 1978) is to crush the coral with a hammer and chisel after rapid fixation and then to sort the resulting residue under a microscope. These latter methods, although tedious, give quantitative results and are extensively quoted when discussing the biomass or numbers of individuals of endo-cryptolithic fauna in coral rocks. It is presumed however, that the acid bath technique of Brock and Brock (1977) will be used in

TABLE 1
The composition of the endo-cryptolithitic fauna recovered by the hammer and chisel method (A) and the subsequent fauna recovered by the acid dissolution technique (B)

	Sample 1		Sample 2		Sample 3	
	687.9	0.077	652.1	0.14	618.3	0.02
Original dry weight of block (g)						
Biomass extracted (g)	0.72		4.14		0.50	
Faunal composition	nos mean range* (mm)					
Polychaetes	61 6.8 1.0-18.0	28 2.8 2.0-22.0	168 8.2 2.0-40.0	66 5.5 1.5-15.0	15 6.3 1.0-12.0	14 4.0 1.5-8.0
Sipunculans	2 9.2 8.5-10.0		12 5.1 2.5-10.0	3 5.0 3.5-6.0		1 5.5 5.5
Platyhelminthes	4 4.1 3.0-6.0		2 5.2 4.5-6.0	1 3.0 3.0		
Molluscs	3 2.0 1.0-3.5	1 5.0 5.0	10 5.3 1.5-15.0	2 3.7 2.5-5.0	3 3.5 1.5-7.5	
Mysids	1 2.5 2.5					
Galatheids	3 2.3 1.5-3.0		1 3.0 3.0		3 2.3 1.0-3.0	
Crabs	1 3.0 3.0		2 1.5 1.5		1 8.5 8.5	
Carids	1 3.0 3.0				2 9.5 5-14.0	
Alpheids	3 2.1 1.0-3.5		6 3.1 2.5-4.0			
Amphipods	70 2.7 1.5-4.0	4 3.1 2.0-4.5	23 3.0 1.0-6.0	5 2.7 2.0-3.5	12 3.4 2.0-5.5	
Tanaids	18 2.8 1.5-4.0	3 2.3 2.0-2.5	11 2.5 1.5-4.0	2 3.8 3.5-4.0	5 3.2 2.0-3.5	1 3.0 3.0
Isopods	6 5.2 1.5-7.0		3 3.0 2.0-4.0	2 3.2 2.0-4.5	4 4.1 2.0-7.0	1 2.0 2.0
Stomatopods					1 2.5 2.5	
% of total biomass missed in extraction by hammer and chisel		8.8%		3.3%		3.8%

* Polychaetes, platyhelminthes, molluscs, mysids, amphipods, tanaids, isopods — total length
 Galatheids, carids, alpheids — carapace length
 Crabs — carapace width
 Sipunculans — trunk length

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future studies as it is rapid and efficient. Brock and Brock suggest that the biomass and numbers of individuals of the endo-cryptolithic fauna extracted by other methods are dependent on the patience and ability of the worker, which makes absolute quantification and comparative studies between these methods and the acid bath technique difficult. Brock and Brock did not attempt to quantify the percentage of endo-cryptolithic fauna overlooked by the hammer and chisel extraction method. Such quantification is essential to see whether all the earlier work using this extraction technique is valid and can therefore be compared with any future work using the acid bath technique. Therefore the coral residue or chips remaining after the extraction of the endo-cryptolithic fauna by the hammer and chisel method were dissolved using the acid bath technique to determine the percentage of fauna which had been missed. As it was our intention to process all our future samples using acid dissolution, the technique of Brock and Brock (1977) was modified to obtain faster dissolution and to ensure that the extracted fauna was intact and readily identifiable.

Finally glacial acetic acid was tested as a dissolving agent for the dead coral since it had been suggested as a potentially suitable acid.

METHOD

The residue of 3 samples which had been processed by breaking them up with a hammer and chisel to extract the fauna were selected at random from over 100 samples. The fauna of these samples is currently being analysed. The 3 samples had an original dry weight of 687.9, 652.1 and 618.3 g respectively before being used as part of an experimental series to determine the rate of colonisation by endo-cryptolithic fauna of coral rock (Hutchings and Weate, in press). The residue of each sample which consisted of small coral chips (10%-10-20 mm, 30%-5-10 mm, 40%-2-5 mm and 20%-1-2 mm, in diameter), was dissolved in an acid solution (5% formalin acidified with nitric acid to 4% by volume) using the technique described by Brock and Brock (1977). The rate of acid dissolution was increased by using six plastic ice-cream buckets (21., 15 cm x 15 cm x 10 cm) the sides and bottom of which were replaced with 0.3 mm polyester mesh. They sat on a removable tray in a bath in which the volume of acid was increased to 45l, thus necessitating less frequent replacement. The solution was agitated by 2 magnetic stirrers. The acid solution however, was still replaced as it became neutralised every 2-3 days. The residual pulp remaining after the coral chips were dissolved, was sorted under a microscope and the fauna such as molluscs, crustaceans, sipunculans and polychaetes were extracted, weighed and counted.

In order to ensure that the majority of the endo-cryptolithic fauna is removed intact and well preserved from dead coral samples using the acid dissolution technique, the following procedure is recommended. After a sample has been collected and put into a polythene bag and sealed, it should then be left for approximately an hour sitting in cool water to allow many of the mobile cryptolithic organisms

to evacuate the sample of their own accord. Care should be taken to prevent the sample becoming too anoxic. This fauna is then removed and fixed separately and the rock sample is then broken into small pieces and all additional visible fauna is removed. The remaining coral chips and separated faunal samples are fixed in 7% formalin. Several days later, the coral chips are dissolved in the acid solution as outlined above to extract the smaller elements of the fauna.

Experiments were also carried out using glacial acetic acid to dissolve the coral block after having been previously fixed in gluteraldehyde.

RESULTS

The percentage of faunal biomass recovered in the pulp in comparison to the total, previously extracted by the hammer and chisel method is 8.8, 3.3 and 3.8% respectively for the 3 samples. Therefore the majority of the endo-cryptolithic fauna (91.2, 96.7, 96.2% respectively) is extracted by the hammer and chisel method. In Table I, a breakdown of the biomass in terms of number and size of individuals extracted by the hammer and chisel technique and from the resultant coral chips by acid dissolution is given. The animals recovered from the coral chips, i.e. the fauna missed by the hammer and chisel technique, were predominantly polychaetes and were mainly small thin worms. The relatively high figure of 8.8% for one sample is mainly due to the presence of one gastropod whose weight minus the shell was 0.04 g, representing 4.8% of the fauna missed. Most of the fauna including the sipunculans were well preserved and easily identifiable. The vast majority of molluscs whose shells would dissolve in the acid had been removed during the hammer and chisel extraction. Trial runs with ophiuroids which are relatively rare (none were in the 3 samples dissolved) showed that their skeleton is partially dissolved in acid but they are generally still identifiable.

The rest of the pulp remaining after 4 to 6 days of acid dissolution, consisted mainly of fragments of sponges, bryozoans and algae. These fragments are difficult to identify and separate into species, and this technique is therefore not suitable for determining the biomass of these colonial animals or algae. MacGeachy (1977) has described a more suitable technique using ultra thin sections to determine the biomass of boring sponges and this could probably be adapted for the bryozoans, ascidians and algae.

Dissolving coral rock in glacial acetic acid to extract the endo-cryptolithic fauna is not recommended as many of the animals are partially or completely dissolved.

DISCUSSION

Our results show that the majority of the endo-cryptolithic fauna is extracted by the hammer and chisel method and therefore the figures quoted by workers such as McCloskey (1970), Kohn and Lloyd (1973), Hutchings (1974) and Hut-

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chings and Weate (1977) are comparable to those obtained by Brock and Brock (1977). Kohn and Lloyd's (1973) figures are probably more accurate than those of Hutchings (1974) as they pulverised their coral chips to powder. However, they may have rendered a few species unidentifiable by such harsh treatment (pers. comm). Although we recommend the acid dissolution technique for rapid extraction of the endo-cryptolithic fauna, we have modified it to ensure that the majority of animals are removed intact and well preserved. This is important since much of the fauna is new or represents new records.

Direct comparisons between biomass, numbers of individuals and species composition of different blocks of dead coral rock are still difficult. For the physical and biological nature of the coral rock such as surface area, percentage cover of epifauna and flora, density of the coral skeleton and the percentage of boring in the coral rock profoundly influence the biomass, numbers and species composition of the endo-cryptolithic community (Hutchings and Weate, 1977). Many workers have shown that live coral has a poor endo-cryptolithic fauna and that the fauna does not develop until the coral dies. However, when sampling in the field, one has no idea of how long that block of coral has been dead and therefore how old the community is. Also the community has a finite existence as eventually the endolithic fauna will destroy the block of coral completely. This probably explains much of the between sample variation reported by various workers, and perhaps more emphasis in the future should be put on determining the rates of colonisation of newly dead coral and the rates of boring by the endolithic fauna to determine the age of the community.

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The Introduction into Western Australia of the Frog *Limnodynastes tasmaniensis* Gunther

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INTRODUCTION

There is a number of records of the establishment of anurans in geographically extralimital areas as a result of intentional or accidental releases. The intentional introductions are usually well documented, such as the initial release of *Bufo marinus* in Australia (Mungomery, 1935), and the repeated releases of three Australian species of *Litoria* in New Zealand (McCann, 1961). However, we are unaware of any documented accounts of the establishment of an Australian species following an unintentional release.

In 1977, in the course of field studies of frogs in the East Kimberley region of north-western Australia, we found a small population of the frog *Limnodynastes tasmaniensis* Gunther at Kununurra. Formerly the species was known from eastern and south-eastern Australia 1,800 km distant; thus it was clearly evident that the Kimberley isolate had been introduced.

Further observations at Kununurra in 1978 revealed a significant expansion of the population there, leading us to deduce that the original introduction had occurred only a few years previously.

Here we document details of the Kununurra population and discuss the likely manner of its introduction.

ECOLOGICAL NOTES

Limnodynastes tasmaniensis is a moderate-sized frog (40-50 mm snout to vent length) inhabiting an extremely wide variety of environmental niches. It

occurs commonly amongst vegetation in damp situations near static or flowing water, but is adept at avoiding periods of temporary drought. For example, in the arid north-east of South Australia the frogs spend the day within fissures in the soil, emerging at night to feed. Throughout its range the species tends to be an opportunistic breeder, spawning most commonly in static water. In south-eastern Australia three call races of *L. tasmaniensis* are recognised (Loftus-Hills, 1973; Littlejohn and Roberts, 1975; Roberts, 1976).

GEOGRAPHIC DISTRIBUTION

Limnodynastes tasmaniensis occurs in an arc from the Eyre Peninsula of South Australia to northern Queensland (Fig. 1). Moore (1961) listed a specimen from Somerset at the northern extremity of Cape York Peninsula, but Cogger (1975) indicates the northern limit to be near Townsville, and we have adopted that modification here.



FIG. 1.—The distribution of *Limnodynastes tasmaniensis* in Australia. The distribution is based on Cogger (1975), Roberts (1976) and unpublished data; the position of the Kununurra isolate is shown by an arrow.

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THE KUNUNURRA ISOLATE

On 18 and 23 February 1977 we heard *L. tasmaniensis* calling from an area of flooded land in Coolibah Drive, Kununurra. Subsequently we recorded the calls of four individuals, and obtained a reference sample of four specimens now deposited in the Western Australian Museum (WAM R58830-33).

Observations in the surrounding district established that the species was confined to the north-western periphery of the Kununurra township, extending from the junction of Coolibah Drive with the Parry Creek Road to a point 1.8 km distant on the Parry Creek Road.

In 1978 we returned to the site, and on January 25 we plotted the population in more detail by making road traverses and noting the presence or absence of calling male frogs at intervals of 300 m. The extension of range beyond the 1977 limit was considerable, involving a continuous northern extension of 6.7 km, and a total range (in road km) of 8.5 km. However, no expansion of range east or west of the road had occurred; the population was confined to a roadside zone no more than 20 m wide. A single reference specimen has been deposited in the South Australian Museum (SAM R16919).

The population is currently restricted to roadside vegetation, where cover is provided by a rich growth of mixed grasses to a height of 1 m. The road runs through flat pastures dissected by irrigation channels. The frogs breed in a continuous, shallow, flooded depression on the western side of the road, between the road and a parallel irrigation channel. In the same area we collected *Limnodynastes convexiusculus*, *L. ornatus*, *Cyclorana australis*, *C. cultripes*, *Cyclorana* sp., *Litoria nasuta* and *L. rothi*.

CALL CHARACTERISTICS

The call is a short, staccato rattle consisting of 5-7 notes. One individual gave calls with five or six notes; calls of the second all had six notes; and calls of the other two individuals all had seven notes. Note duration ranged from 12-16 msec and call duration from 150-228 msec. The dominant frequency of the calls of all individuals lay at 1,900-2,000 Hz.

Water temperatures at the calling sites of the four recorded individuals ranged from 29.1 to 31.2°C.

POSSIBLE MANNER AND DATE OF INTRODUCTION

We examined the vicinity of Coolibah Drive, Kununurra, seeking information about possible modes of introduction of the frogs. Several of the nearby houses were pre-constructed transportable units, and enquiries revealed that these had been imported from South Australia. The manufacturer is Atlas Industrial Housing Pty Ltd, whose construction plant is at Pooraka, 12 km north of Adelaide. Enquiries directed to the manufacturer showed that the company had provided the transportable modular accommodation at the Lake Argyle construction camp

(now the Lake Argyle Tourist Village), and several hundred transportable homes throughout Kununurra. Most of the latter homes had been despatched from Adelaide between 1969 and 1971.

Resting directly on the soil at Pooraka prior to transportation, the home foundations would have provided ideal refuges for *L. tasmaniensis*. The frogs often form aggregations of a dozen or more during dry conditions (our unpublished observations); this could result in a number adequate for colonisation being transported together. We suggest that *L. tasmaniensis* was introduced into W.A. via one or more of the units.

The substantial expansion of the range of the population observed between February, 1977, and January, 1978, is best accounted for in terms of an extremely recent introduction. For this reason we suggest 1971, this being the last possible date for entry via the transportable homes.

DISCUSSION

Roberts (1976) showed that only one call race of *L. tasmaniensis*, the Western, occurs west of the Murray River in South Australia. Hence our supposition that the Kununurra population of *L. tasmaniensis* originated in the Adelaide area can be tested by comparing the call structure of the Kununurra isolate with that of the Western Call Race.

Unfortunately the temperatures at which our recordings were made considerably exceed those in Roberts' study (6.0-25.0°C); thus direct comparisons are not valid. However, the most striking call difference between the three races is in the number of notes per call; values are generally 1 in the Southern Race, 2-4 in the Northern Race and 3-8 in the Western Race (Roberts, 1976). In this characteristic the Kununurra population coincides with the Western Call Race, and the other aspects of call structure analysed, except dominant frequency, also fall within the range of this race. Dominant frequency of the Kununurra population lies above the range recorded by Roberts; possibly this is a temperature effect.

Thus the call data are consistent with the hypothesis of an Adelaide origin of the Kununurra population of *L. tasmaniensis*.

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Insulin Receptor Proteins in the Erythrocytes of Monotremes and other Vertebrates

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ABSTRACT

The membranes of mature red blood cells (RBC's) from a variety of vertebrate species were examined for insulin binding activity. A strong correlation was found between the presence or absence of a nucleus in the mature cell and the presence or absence of insulin binding activity in the erythrocyte membrane. An hypothesis is presented that the nucleus is involved in the production of an insulin receptor protein on the surface of the RBC. The RBC's of monotremes and marsupials are of particular interest, as these taxa represent a phylogenetic dividing line in the evolution of the mammalian non-nucleated erythrocyte. Reasons for the course of evolution of the enucleate form of the RBC are discussed.

INTRODUCTION

Mature erythrocytes of mammals are enucleate, although they are derived from nucleated precursors (e.g. reticulocytes). The erythrocytes of other vertebrate groups remain nucleated throughout their life span. The distinction between animals whose erythrocytes do not have nuclei and those whose erythrocytes have nuclei is complicated by the fact that some mammals have relatively high reticulocyte numbers. The camel, for example, has a high reticulocyte count which has been related to the ability of the red blood cells to withstand osmotic stresses of dehydration and rehydration (Banjaree *et al* 1962; Perk 1963, 1966).

Enucleation may be related to changes in the life span of erythrocytes. As shown in Table 1, mean life span for erythrocytes in the circulation is much greater in reptiles and amphibians (both groups possess nucleated erythrocytes) than it is in the mammals. However, birds have nucleated erythrocytes, and a mean erythrocyte life span similar to, and in some cases shorter, than mammals. Short erythrocyte life span might therefore be related to the high body temperature and high metabolic rate of mammals and birds. Basal heat production (Rodnan *et al* 1957) and metabolic rate (sp. Altland and Brace, 1962) have been correlated with erythrocyte turnover. That being the case, the enucleate condition of mammalian erythrocytes, as opposed to the nucleate erythrocyte of birds, must have an

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TABLE 1

COMPARISON OF THE TURNOVER RATES AND LIFE SPANS
OF A VARIETY OF VERTEBRATE RBC.

TAXA	Species	Mean RBC Life Span (Days)	Mean RBC Turnover (% RBC vol. replaced/ day)	References
Eutheria	Mouse	22	4.5	Burwell et al. 1953
	Marmot	36	.8	Brace 1953
	Rabbit	65	1.8	Sutherland et al 1959
	Cat	73	1.4	Kaneko et al 1966
	Dog	108	1.0	Weissman et al 1960
	Auodad*	65 & 170	—	Cornelius et al. 1959
	Horse	145	—	Cornelius et al. 1960
Pro- and Metatheria		NO	DATA	
Aves	Pigeon	40	2.5	Marvin and Lucy 1957
	Chicken	28	3.3	Hevesy and Ottesen 1945
	Duck	39	2.4	Brace and Altland 1956
Reptilia	Turtle	c 700	<0.2	Altland and Brace 1962
	Alligator	c 294		Cline and Waldmann 1962a
Amphibia	Cane Toad	c1000	—	Altland and Brace 1962
	Frog	c 200	—	Cline and Waldmann 1962b

*In the Auodad sheep two populations of enucleate red-blood cells were found.

evolutionary basis. Information about monotremes and marsupials might, on phylogenetic grounds, be expected to shed some light on the question, but as seen in Table 1 there are no comparative data on erythrocyte life span or turnover from those mammals. Data are needed from as many monotreme and marsupial species as possible, since evolutionary trends may be difficult to sort out from differences of longevity and body weight in various species.

In this study the metabolic significance of enucleate vs. nucleate erythrocytes was approached from a different angle. Instead of measuring erythrocyte life-span, red-blood cell membranes were prepared and analysed for insulin binding activity, which should be a more direct measure of the metabolic activity of the cell. The relatively long lived, nucleated cells should have a greater variety of enzymes and a greater metabolic capacity than enucleate cells. Along with this there should also be differences in insulin binding activity and an examination of a wide range of vertebrate species might shed light on the phylogenetic adaptations of erythrocyte function.

RBC INSULIN RECEPTORS

MATERIALS AND METHODS

Blood was obtained from 19 vertebrate species. The red cells were separated from the white cells and plasma by centrifugation. To each ml of compacted red cells an equal volume of distilled water was added and then mixed to ensure complete hemolysis. Erythrocyte membranes were collected and washed repeatedly (until colourless) following the method of Dodge *et al* (1963). Compacted membranes were stored at -20°C .

To test for insulin binding activity, 0.25 ml of compacted membranes was suspended in 0.75 ml cold (4°C) phospho-saline buffer (40 mM) containing 1.5% bovine serum albumin and adjusted to pH 7.4. All further steps were carried out at 4°C .

Each 1 ml volume of suspended membranes was subdivided into 10 $100\ \mu\text{l}$ parts, to each of which was added $100\ \mu\text{l}$ of I^{125} labelled human insulin (98% T.C.A. precipitable; prepared by the Endocrine Unit, University of Sydney Medical

TABLE 2
PERCENTAGE OF SPECIFIC COUNTS OF BOUND INSULIN
OVER FOUR INCUBATIONAL PERIODS AT 4°C .

TAXA	Species	Time of Incubation at 4°C			
		$\frac{1}{2}$ hr.	1 hr.	2 hrs.	4 hrs.
Reptilia	<i>Egernia cunninghami</i>	2.681	1.913	<M.E.	<M.E.
	<i>Tiliqua scincoides</i>	1.884	1.675	<M.E.	<M.E.
	<i>Crocodylus porosus</i>	3.044	2.806	1.717	<M.E.
Aves*	Chicken	2.531	2.211	1.856	<M.E.
	Galah	2.922	2.016	2.002	<M.E.
Monotremata	Platypus	<M.E.	<M.E.	<M.E.	<M.E.
	Echidna	<M.E.	<M.E.	<M.E.	<M.E.
Marsupialia	<i>Macropus giganteus</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Macropus robustus erub.</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Macropus fuliginosus f.</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Macropus eugenii</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Macropus rufus</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Potorous tridactylus</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Dasyuroides byrnei</i>	=M.E.	<M.E.	<M.E.	<M.E.
	<i>Dasyurus maculatus</i>	<M.E.	<M.E.	<M.E.	<M.E.
	<i>Trichosurus vulpecula</i>	1.643	<M.E.	<M.E.	<M.E.
Placentalia	Rat	<M.E.	<M.E.	<M.E.	<M.E.
	Rabbit	<M.E.	<M.E.	<M.E.	<M.E.
	Mouse	<M.E.	<M.E.	<M.E.	<M.E.

The calculated maximum error (M.E.) for the experimental design was 1.590%.

*In 1977 Ginsberg *et al.* demonstrated the presence of insulin receptors on turkey erythrocytes.

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School). One of the 10 aliquots was set aside for the determination of total protein (Lowry *et al* 1951) to ensure that the total membrane content of each sample was approximately equal.

In order to determine the non-specific binding component, 100 μ l samples of porcine insulin (20 μ g/ml) were added to three of the tubes for each sample. These three tubes, with remaining six, were treated together as follows:

Binding trials were carried out over 0.5, 1, 2 and 4 hours at 4°C. At the completion of that incubation period the vials were spun for 20 minutes at 6,000 g. The supernatant was discarded, and 1 ml chilled buffer was added to each vial before being centrifuged for 20 minutes at 6,000 g. The supernatant was discarded and the activity of the bound labelled insulin was determined with a gamma counter.

The maximum error of the system was determined by processing 12 vials of labelled insulin through the incubational procedure and scoring any differences in the counts obtained.

TABLE 3

COMPARISON OF INSULIN RECEPTOR ACTIVITY AGAINST THE PRESENCE OR ABSENCE OF A NUCLEUS IN ERYTHROCYTES.

TAXA	Species	Condition of Erythrocytes	Presence or Absence of Insulin Receptor Activity
Reptilia	<i>Egernia cunninghami</i>	Nucleated	Present
	<i>Tiliqua scincoides</i>	Nucleated	Present
	<i>Crocodylus porosus</i>	Nucleated	Present
Aves	Chicken	Nucleated	Present
	Galah	Nucleated	Present
Monotremata	Platypus	Non-nucleated	Absent
	Echidna	Non-nucleated	Absent
Marsupialia	<i>Macropus giganteus</i>	Non-nucleated	Absent
	<i>Macropus robustus erub.</i>	Non-nucleated	Absent
	<i>Macropus fuliginosus ful.</i>	Non-nucleated	Absent
	<i>Macropus eugenii</i>	Non-nucleated	Absent
	<i>Macropus rufus</i>	Non-nucleated	Absent
	<i>Potorous tridactylus</i>	Non-nucleated	Absent
	<i>Dasyuroides byrnei</i>	Non-nucleated	Weak
	<i>Dasyurus maculatus</i> <i>Trichosurus vulpecula</i>	Non-nucleated	Absent Weak
Placentalia	Rat	Non-nucleated	Absent
	Rabbit	Non-nucleated	Absent
	Mouse	Non-nucleated	Absent

RBC INSULIN RECEPTORS

RESULTS

Table 2 sets out the results of insulin binding trials on a number of vertebrate species expressed as "percentages of specific counts bound", calculated as:

$$\% \text{ specific counts bound} = \frac{\text{Bound counts} - \text{nonspecific counts}}{\text{total counts}}$$

The presence or absence of insulin receptor activity for each species indicated by the detectable specific binding of radioactive insulin, or lack of such binding, is compared with the erythrocyte condition in Table 3. It is clear from this Table that nucleated erythrocytes possess insulin receptors while enucleated erythrocytes do not.

DISCUSSION

In terms of erythrocyte longevity there is no significant difference between birds and mammals (Table 1). However, in terms of RBC insulin receptor activity, there is a marked difference (Table 2), and monotremes and marsupials are the same as other mammals in lacking detectable receptor activity and are clearly different from birds. Monotremes and marsupials are also like the eutherians in erythrocyte morphology. The echidna (Bolliger and Backhouse 1960a, Parer and Metcalfe 1967a, Lewis *et al* 1968), and the platypus (Parer and Metcalfe 1967b), possess non-nucleated erythrocytes and have low reticulocyte numbers. Parsons *et al* (1970) have likewise shown 18 species of marsupials to have mainly enucleate RBCs. Therefore the presence of enucleate erythrocytes coincides with lack of detectable insulin receptor activity, suggesting that the nucleus is essential for the production of the insulin receptor on the erythrocyte membrane.

Two marsupials, *Trichosurus vulpecula* and *Dasyuriodes byrnei*, seem to be an exception to the above, since they both have some (although weak) receptor binding activity. However both species have unusually high reticulocyte numbers (1.4% and 1.2% of the total RBCs respectively), and the low binding activity shown by *T. vulpecula* and *D. byrnei* could be explained by circulating reticulocytes at that level. Some other species of marsupials which were not available for the present study have also been shown to have high reticulocyte counts; koala (Bolliger and Backhouse 1960b), hairy-nosed wombat (Parsons *et al* 1970), and opossum (Giacometti *et al* 1972).

Another experimental result which appears to be an exception to the lack of mammalian erythrocyte insulin binding reported above is the demonstration of insulin binding sites on human erythrocytes by Gambhir *et al* (1977). However, they used a much more sensitive technique, and the interpretation of their results is difficult. It seems likely that the binding found by Gambhir *et al* (1977) is due to remnant receptor protein in the cell membrane. Certainly such receptors could have no physiological significance in mature enucleate erythrocytes. The

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fact that receptor proteins still exist beyond the reticulocyte stage indicates that the apparatus which normally degrades these molecules has itself become non-functional after enucleation.

Further evidence of the essential role of the RBC nucleus in production of protein within the RBC is provided by the work of Silber *et al* (1961). They related the nucleus to the production of RBC surface antigens. Enucleation was correlated with loss of transplantation antigens (and thus could explain the survival of transfused erythrocytes).

Therefore the RBC nucleus has important functions throughout its life span in most vertebrates and in reticulocytes in mammals. The loss of the nucleus in both ontogeny and phylogeny of mammals has led to a loss of synthetic ability of the erythrocyte, loss of receptor proteins and decreased erythrocyte life span. Clearly two strategies exist in the vertebrates: 1. The production of nucleated erythrocytes with a complete metabolic repertoire and capable of supporting themselves in a functional state in the circulation for relatively long periods; 2. The production of non-nucleated erythrocytes with reduced metabolic capacity and with reduced functional circulating life span; i.e. RBC turnover rates are relatively high. The adaptive advantage of one strategy over the other must depend on the energetic cost of producing a small number of cells capable of supporting themselves for a long time as opposed to producing a large number of cells which have a relatively short lifespan, but which utilise very little of the blood energy substrate.

This study has shed some light on the phylogeny of RBC enucleation to the extent that it has shown that all mammals, including monotremes, lack detectable insulin binding on the erythrocytes in marked contrast to other vertebrates.

A promising area for further studies of the functional significance of the RBC nucleus in mammals would be studies on the blood of pouch young of monotremes and marsupials. Marsupial pouch young have high circulating stem erythrocyte counts. Richardson and Russell (1969), and Yadav (1972), have found large numbers of eosinophilic megaloblasts in newly born pouch young of kangaroos. The embryonic young of monotremes and marsupials are, of course, much more readily available for study than eutherian young of similar development.

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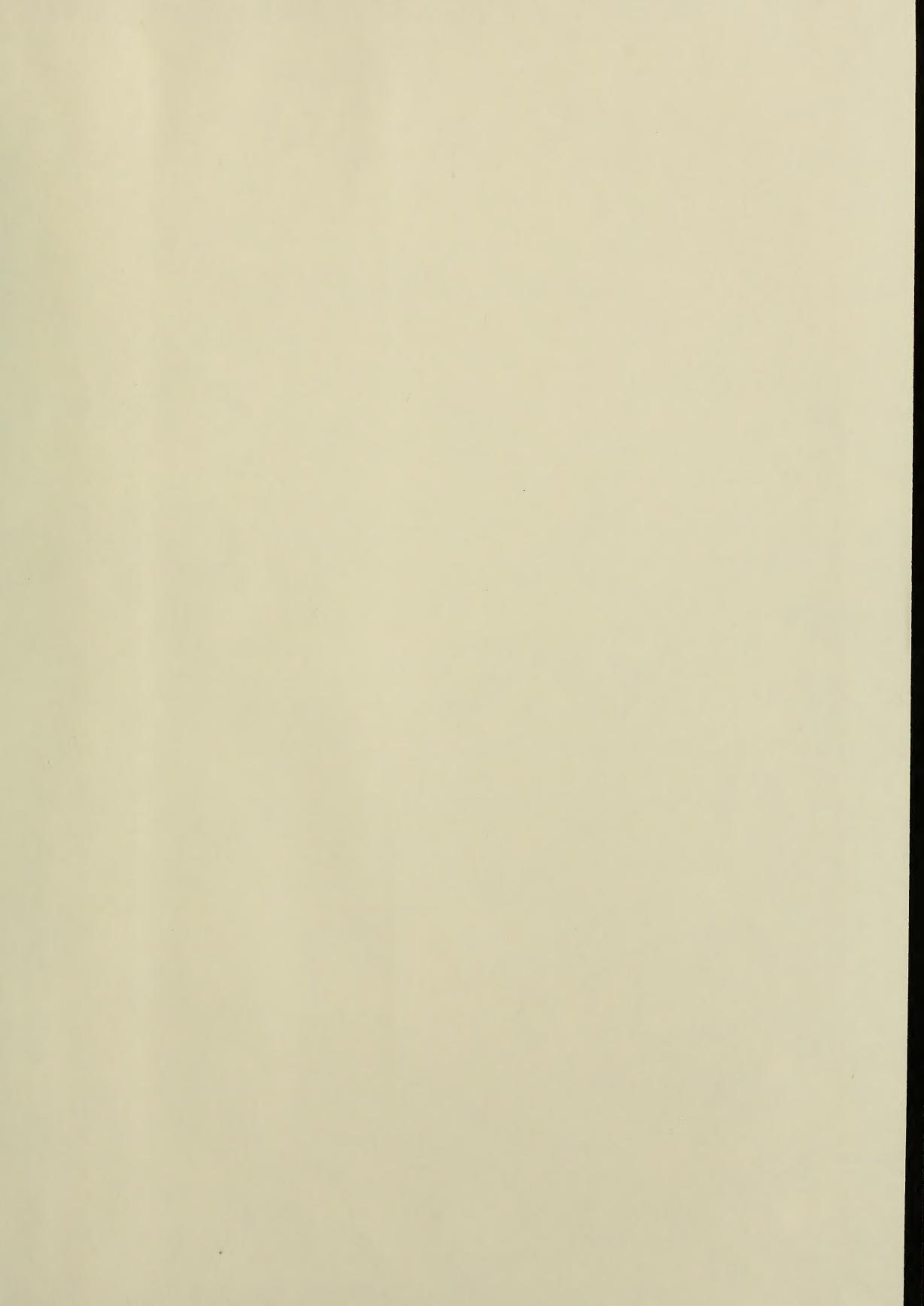
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