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THE SECOND CENTURY

Summary

The Royal Society of London was conceived more than 300 years ago when, following a lecture by Christopher Wren, it is recorded that "something was offered about a designe of founding a Colledge for the promoting of Physico-Mathematicall, Experimental1 Learning". Charles I1 became interested and granted the Society its first Charter in 1662, naming it "The Royal Society". A second Charter, in 1663, granted the body Arms, bearing the motto "Nullius in verba", as an expression of the determination of the Society to resist all dogma and to verify all information and statements by appeal to observation. At the same time, the full title of the Society became "The Royal Society of London for Improving Natural Knowledge".

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Sir Mark Oliphant, K.B.E., Patron of the Royal Society of South Australia

A little more than 200 years later, the Royal Society of South Australia was born, and 1976 is the centenary of its Transactions. Throughout this time the South Australian Society has played an invaluable role in recording, in proper scientific manner, manifold observations and descriptions of the geology, the fauna and the flora of this State. For long, the Society has emulated in its activities the search for natural knowledge which was the objective of the founders of the original Royal Society. However, for very practical reasons, such bodies are reappraising their activities and ever questioning whether they can continue to exist. Strangely enough, the problems arise from the very success of their past work. The technology, the application of knowledge for practical purposes, which arises from increasing understanding of nature, has made of science an ever growing national and international activity. Through their control of money, governments now determine the level of scientific enquiry and its content, while the rapidly increasing cost of publication means that they become the arbiters of what science shall be printed.

There are other factors which have a pronounced influence on comparatively small societies attempting to cater for those interested generally in science. Foremost is the growth of specialist societies interested only in a very narrow area of natural knowledge. It is almost impossible today to attract a biochemist to a discussion of relativity or cosmology, or to persuade a nuclear physicist that the nature of the chemical bond can be an interesting subject of study. The particle physicist cannot understand the entomologist, or the computer electronics expert the ornithologist. A broad interest in nature generally is now rare. There are few today whose interests are as broad as those of Lord Rayleigh, who wrote learnedly of the bending of marble mantlepieces and developed the mathematical theory of the waveguide. Publication of the results of scientific enquiry becomes more and more confined to specialist journals, or specialist sections of older journals.

Secondly, it is the national bodies, like the Academies of Science of the United States and Russia, which are government agencies, or the Royal Society of London and the Australian Academy of Science, which are not controlled directly by government, which represent science internationally for their countries, and which receive the greatest financial backing. It is they who can afford to organise conferences, national or international, they who can provide the expenses for travel by members and by visitors. They are prestigious societies whose activities are of world-wide significance.

The Royal Society of South Australia cannot emulate these giants. However, I am convinced that it will have a vital part to play in the second century of its existence. The growing interest, among scientists and the general public, in the preservation of the environment, in pollution, ecology, our national heritage of fauna and flora, natural resources, and the beauty of landscape, encourages belief in a return to deep interest in nature generally, rather than in one aspect only. If, as I believe, our Royal Society is to be revitalized to become a significant social influence through science, it must espouse causes, after full and frank discussion to determine an agreed approach, and then speak loudly and in public of its conclusions.

As instances of broad issues to which the Society could contribute much, there are preservation of the Mt Lofty Ranges and the Flinders Ranges, the salinity of the River Murray, the deterioration of our desert areas. We should not be deterred by the existence of C.S.I.R.O., of State instrumentalities, or of the Australian Academy of Science, from choosing areas of comprehensive, interdisciplinary study, which can be exciting scientifically and could be rewarding socially. A paper describing a new species of coleoptera from the Lake Frome area should be published, but will not rouse much interest in a general scientific audience. On the other hand, if this discovery is significant in indicating climatic change, or ecological upset on the eastern borders of the Flinders Ranges, it could become an important contribution to wide discussion.

South Australia faces a multitude of problems, most of which are relegated to investigation by governmental bodies. Our future depends critically upon assured supplies of water and of energy. Water, gas, and electricity authorities are too busy with immediate questions to exercise the imaginative responses necessary for creation of new approaches to longer term problems. On the other hand, a Royal Society which stimulates constructive discussion of such problems, in their widest context, might generate completely new ideas.

Where are we going? That is the first question we must answer in the early part of our second hundred years.

GOVERNOR OF SOUTH AUSTRALIA

COMPARATIVE OSTEOLOGY OF THE PELVIC GIRDLE OF AUSTRALIAN FROGS AND DESCRIPTION OF A NEW FOSSIL GENUS

BY *M. J. TYLER**

Summary

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Introduction

Of all bones of the anuran skeleton, the ilium has been shown to vary considerably and consistently between families, genera and even species. Ilia are commonly well preserved amongst disarticulated skeletal material, and their features are sufficiently diagnostic to permit identification; for this reason ilia have provided the basis for the recognition of genera and erection of new fossil species (Lynch 1963; Chantell 1964; Holman 1965).

Data on extant species so essential for identification and general comparative purposes are frequently limited, and in the case of Australian frogs, data are particularly deficient. Lynch (1971) provides the only comparative contribution. Confining his interest to leptodactylids, Lynch described the ilia of representatives of nine genera. Since then a fossil ilium of a previously undescribed genus has been reported from the Australian Tertiary by Tyler (1974), and it has proved necessary to examine and describe representative ilia of all of the known living genera in order to describe the new genus and species.

Material and methods

The dry specimens of the modern species studied were dissected from representatives of 4 families, 25 genera and 60 species, including all genera known in Australia. This material is in the author's collection. The fossil described herein is in the Palaeontology collection of the South Australian Museum.

With only minor variation, the descriptive terminology used follows Lynch (1971), and the features recognised are shown in Figure 1. Morphometric data were obtained with dial callipers or an eyepiece micrometer. The length of the animals from snout to vent was measured before dissection. Subsequently, the distances between the tip of the dorsal acetabular expansion and the end of the ilial shaft and the span between the anterior margin of the dorsal prominence and the ventral acetabular expansion were measured. The bone measurements were examined to establish relationships between ilial size or proportions and the size of the donor frog.

Features of the Anuran pelvis

(A) *Pubis*

The pubis is customarily a small, roughly triangular, cartilaginous wedge of tissue separating and underlying the ventral borders of the ischium and ilium (Fig. 1). In particularly large species (rarely in small ones), where there is a more intimate degree of fusion of the pelvic components, the pubis is often calcified or ossified.

(B) *Ischium*

The ischium is a bony or cartilaginous disc anteriorly fusing with the ilium to provide the posterior half of the acetabulum, and pos-

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000. (Present address: Department of Zoology, University of Adelaide, Adelaide, S. Aust. 5000).

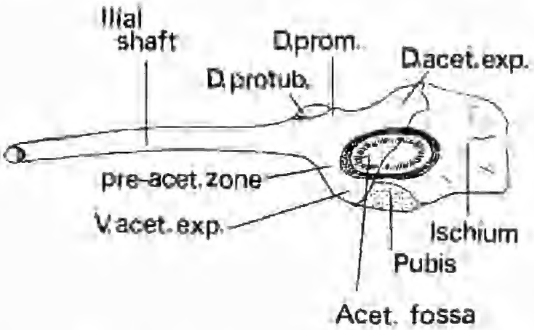

Fig. 1. Left lateral aspect of anuran pelvic girdle. *Abbreviations:* Acet. fossa—acetabular fossa; D. acet. exp.—dorsal acetabular expansion; D. prom.—dorsal prominence; D. protub.—dorsal protuberance; pre-acet. zone—pre-acetabular zone; V. acet. exp.—ventral acetabular expansion.

teriorly forming a plate occupied by numerous muscles communicating with the femur.

The shape of the ischium varies considerably at a specific level and is associated with differences in habits. For example, the development of a particularly large plate posterior to the acetabular fossa is found only in rotund species with exceptionally short and muscular hind limbs. Similarly, the development of a high, dorsally projecting extension is characteristic of large but agile frogs with powerful hindlimbs. Viewed with the femur as the reference point it is clear that a major shift in the muscle mass can only be brought about by concurrent changes in the development of the ischium.

(C) *Ilium*

The ilium is the largest pelvic bone, and consists of an elongate shaft terminating in an axe-head shaped body. It is a paired structure articulating anteriorly with the ventral surface of the sacral diapophysis and posteriorly abutting the ischium and pubis. Various areas of the ilium are recognisable as distinct components:

(a) *Ilial shaft:* The ilial shaft is an elongate and usually slightly curved structure varying from a cylindrical section through vertically oval to more elaborate forms in which there are grooves on the lateral or medial surfaces.

(b) *Dorsal crest:* A smooth bordered crest, rising high as a thin blade, occurs in numerous species of frogs, but is rare amongst Australian forms. It usually arises from the dorsolateral surface of the shaft, and reaches its maximum height within the anterior one-third of the shaft (Fig. 4*L*).

(c) *Dorsal prominence:* The dorsal prominence is a differentiated area rising on the superior margin of the shaft in a position above or slightly anterior to the acetabulum. It is not present in all species and is scarcely detectable in many others (e.g. in those exhibiting a dorsal crest).

(d) *Dorsal protuberance:* From the body of the dorsal prominence the dorsal protuberance arises as an elongate, rounded or pointed knob. To it attaches the Musculus gluteus maximus.

(e) *Dorsal acetabular expansion:* The body of the ilium extends dorsally into a triangular portion of bone superior and posterior to the acetabulum. This projection is termed the dorsal acetabular expansion. It may rise steeply and so meet the ischium in a vertical plane, whilst the anterior face can be at an acute or obtuse angle to the ilial shaft.

(f) *Acetabulum:* Variation in the acetabulum consists of differences in size (relative to adjacent structures), in position in relation to the ilial shaft, and in the width and extent of development of the acetabular rim.

(g) *Ventral acetabular expansion:* The superior segment of the ventral acetabular expansion has been termed the preacetabular zone by Lynch (1971). The considerable variation in this portion of the pelvis is difficult to express, because of the instability of potential reference points such as the acetabulum. Nevertheless, the basic shapes range from the form of a straight line extending ventrally and posteriorly (Fig. 2*A*, *D*), a gradual concavity (Fig. 2*B*), or a concavity of the preacetabular zone and a convexity beneath (Figure 2*C*).

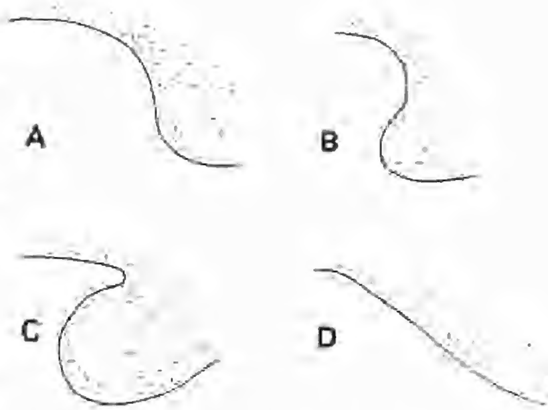

Fig. 2. Variation in the shape of the ventral acetabular expansion viewed from left aspect. See text for explanation.

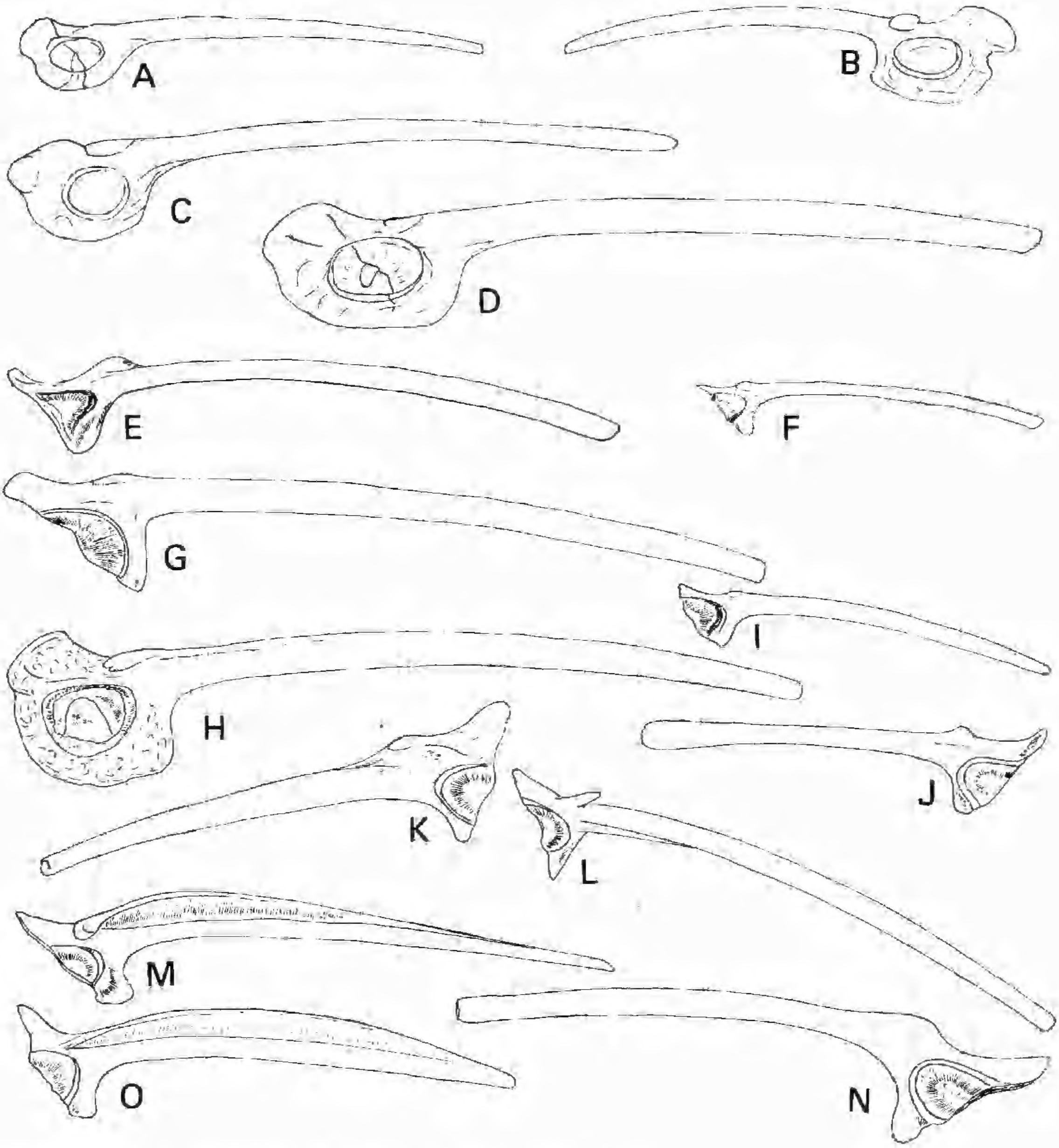

Fig. 3. Pelvis or isolated ilium of hylid and leptodactylid frogs:
A. Litoria caerulea, x 2; *B. L. lesueuri*, x 2; *C. L. eucnemis*, x 5; *D. Nyctimystes zwiefeli*, x 2; *E. Adelotus brevis*, x 5; *F. Assa darlingtoni*, x 5; *G. Crinia georgiana*, x 5; *H. Cyclorana novae-hollandiae*, x 2; *I. Geocrinia laevis*, x 5; *J. Glauertia orientalis*, x 5; *K. Heleioporus albopunctatus*, x 2; *L. Kyarranus* sp., x 5; *M. Lechriodus fletcheri*, x 5; *N. Limnodynastes peroni*, x 5; *O. Mixophyes fasciolatus*, x 2.

POST-MORTEM CHANGES

Disintegration of the pelvic girdle into its component bones has been observed in species in which cartilage is most extensive. Species that are heavily ossified remain intact.

During the process of dehydration, the acetabular fossa may become distorted and, in the material available, such distortion takes the form of compression in a dorsoventral direction. The dorsal crest of the ilium is par-

TABLE 1

Characteristics of the Ilium in species of Litoria

Species	Profile of ventral acetabular expansion	Dorsal prominence/ anterior rim of Acetabulum	Acetabular rim/ventral ilial shaft margin	Pubis	Position of medial rim on Ilium
adelaidensis	concave	level	above	cart.	ant. ¼
*angiana**	concavo-convex	posterior	level	cart.	absent
aurea	concave	½ anterior	above	cart.	ant. ¼
bicolor	concave	⅓ anterior	above	cart.	?absent
booroolongensis	concavo-convex	⅓ anterior	level	bony	central 1/5
brevipalmata	concave	level	above	cart.	ant. 1/3
caerulea	concave	level	level	cart.	absent
citropa	concave	level	above	cart.	ant. ⅔
*dorsalis**	concavo-convex	½ anterior	level	cart.	ant. ¾
eucnemis	concavo-convex	level	above	bony	ant. ¼
ewingi	concave	level	above	cart.	post. ½
gracilenta	concavo-convex	½ anterior	above	cart.	absent
infrafrenata	concave	⅓ anterior	above	cart.	ant. ¾
lesueuri	concavo-convex	⅓ anterior	level	bony	central 1/3
microbelos	concavo-convex	level	above	cart.	ant. ⅔
nannotis	concavo-convex	level	above	bony	absent
nasuta	concavo-convex	½ anterior	above	cart.	ant. 1/5
nigrofrenata	concavo-convex	¼ anterior	above	bony	ant. ⅔
rubella	concave	½ anterior	above	cart.	?absent
rothi	concave	⅓ anterior	above	cart.	absent
*thesaurensis**	concavo-convex	level	above	bony	ant. ¾

* Species restricted to New Guinea. ant.—anterior; cart.—cartilaginous.

ticularly subject to post-mortem distortion, commonly bending medially from a perfectly vertical orientation to form a quadrant. Even more conspicuous is the distortion amongst material recovered from owl pellets where there has been an induced medial curvature of the ilial shaft in several specimens.

Account of modern genera and species

Family **HYLIDAE**

LITORIA Tschudi

FIG. 3*A-C*

Species examined: L. adelaidensis (Gray), *L. angiana* (Boulenger), *L. aurea* (Lesson), *L. bicolor* (Gray), *L. booroolongensis* (Moore), *L. brevipalmata* Tyler, Martin & Watson, *L. caerulea* (White), *L. citropa* (Tschudi), *L. dorsalis* Macleay, *L. eucnemis* (Lönnberg), *L. ewingi* Dumeril & Bibron, *L. gracilenta* (Peters), *L. infrafrenata* (Gunther), *L. lesueuri* Dumeril & Bibron, *L. microbelos* (Cogger), *L. nannotis* (Andersson), *L. nasuta* (Gray), *L. nigrofrenata* (Gunther), *L. rubella* (Gray), *L. rothi* (de Vis), *L. thesaurensis* (Peters).

Variation in this morphologically and ecologically diverse genus renders a generic definition a difficult proposition. For this reason comparative data are included in Table 1, and only the following generalisations are possible:

The pubis is cartilaginous or ossified and the ischium is ossified.

The ilial shaft lacks a dorsal crest but invariably bears a narrow rim on at least a portion of the medial surface. In *L. aurea* there is also a lateral groove exhibiting a distinct ontogenetic trend in becoming progressively less conspicuous. The acetabular fossa tends to be rather large. The ventral acetabular expansion is of a variety of forms, from a narrow, concave profile to concavo-convex.

The dorsal protuberance and dorsal prominence are usually well differentiated but are not raised high above the level of the ilial shaft.

NYCTIMYSTES Stejneger

FIG. 3*D*

Species examined: N. tympanocryptis (Andersson and *N. zweifeli* Tyler of New Guinea.

TABLE 2

Generic features of Ilia

	Ilial shaft crest	Ilial shaft rim	Dorsal protuberance	Dorsal prominence/ anterior rim of acetabulum
Adelotus	absent	present	prominent	anterior
Assa	absent	absent	inconspicuous	level
Cophixalus	absent	absent	inconspicuous	anterior
Crinia	absent	present	inconspicuous	anterior
Cyclorana	absent	present or absent	inconspicuous	anterior
Geocrinia	absent	absent	absent	level
Glauertia	absent	absent	inconspicuous	anterior
Heleioporus	absent	absent	prominent	anterior
Kyarranus	absent	present	prominent	anterior
Lechriodus	present	absent	moderate	posterior
Limnodynastes	present or absent	present or absent	prominent	ant. or level
Litoria	absent	present or absent	moderate	usually anterior
Mixophyes	present	absent	inconspicuous	anterior
Myobatrachus	absent	absent	absent	posterior
Neobatrachus	absent	absent	prominent	anterior
Notaden	absent	absent	prominent	posterior
Nyctimystes	absent	absent	moderate	level
Philoria	absent	present	inconspicuous	anterior
Pseudophryne	absent	absent	moderate	level
Rana	present	absent	inconspicuous	posterior
Ranidella	absent	absent	moderate	anterior
Rheobatrachus	absent	absent	prominent	posterior
Sphenophryne	absent	absent	inconspicuous	posterior
Taudactylus	absent	absent	prominent	anterior
Uperoleia	absent	absent	prominent	anterior

The ilium and ischium are ossified in both species. The pubis is ossified in *zweifeli* and cartilaginous in *tympanocryptis*.

The ilial shaft is long, curved distally and very slightly compressed mediolaterally. The ventral acetabular expansion is gently rounded in a single, uninterrupted concave arc. The acetabular fossa is prominent, with its upper margin level with the centre of the ilial shaft. The dorsal prominence and dorsal protuberance are small and project laterally rather than superiorly. The anterior margin of the dorsal protuberance is on a level with the anterior margin of the acetabular rim. The dorsal acetabular expansion is only slightly raised.

Family LEPTODACTYLIDAE

ADELOTUS Ogilby

FIG. 3*E*

Species examined: A. brevis (Gunther).

The ischium is bony and the pubis is entirely cartilaginous.

The ilial shaft is distinctly curved and bears a narrow indentation on the medial surface. This indentation is deepest in the midsection of the shaft. The acetabulum has a narrow peripheral rim which superiorly is on a level with or is slightly superior to the ventral surface of the ilial shaft. The ventral acetabular expansion is only slightly developed, and the preacetabular zone is extremely narrow. The dorsal acetabular expansion is elongate and raised moderately. The dorsal prominence is poorly defined. The dorsal protuberance is extremely large, inclined posteroventrally and is almost entirely anterior to the anterior rim of the acetabular fossa.

ASSA Tyler

FIG. 3*F*

Species examined: A. darlingtoni (Loveridge).

The pubis and ischium are bony except for the portion associated with the posterior half of the acetabular fossa.

The ilial shaft is slightly curved, lacks ridges and indentations and is circular in cross section. The acetabulum has an exceptionally well developed peripheral rim which superiorly is very slightly above the ventral margin of the ilial shaft. The ventral acetabular expansion is slightly developed into a narrow preacetabular zone. The dorsal acetabular expansion is very poorly developed. The dorsal prominence is only slightly defined. The dorsal protuberance is small but prominent, its anterior margin on a level with the anterior margin of the acetabular rim.

CRINIA Tschudi

FIG. 3G

Species examined: C. georgiana Tschudi.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is curved, flattened mediolaterally over the posterior half and dorsoventrally over the anterior half. There is no dorsal ilial crest but there is a very slight longitudinal medial indentation. The acetabulum is large, has a fairly broad peripheral rim which superiorly is very slightly above the level of the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly developed; the subacetabular zone does not protrude anteriorly. The dorsal acetabular expansion is poorly developed. The dorsal prominence is low, but quite distinguishable from the ilial shaft. The dorsal protuberance is just detectable. Slightly less than one-half of the dorsal protuberance is anterior to the anterior rim of the acetabulum.

CYCLORANA Steindachner

FIG. 3H

Species examined: C. australis (Gray), *C. dahli* (Boulenger), *C. novaehollandiae* Steindachner and *C. platycephalus* (Gunther).

The ischium is bony and fused to the ilium, whereas the pubis can be extensively ossified and similarly fused (*C. dahli* and *C. novaehollandiae*), or completely cartilaginous (*C. australis* and *C. platycephalus*).

The ilial shaft is slightly curved and either bears a narrow dorsal rim, rendered conspicuous by a longitudinal indentation on the medial surface of the shaft (*C. australis, C. dahli* and *C. novaehollandiae*), or else lacks a dorsal rim (*C. platycephalus*). The acetabulum has a narrow peripheral rim which superiorly is above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly developed and the preacetabular zone is narrow. The dorsal acetabular expansion is prominent and conspicuous. The dorsal prominence is distinguishable from the ilial shaft but only slightly raised. The dorsal protuberance is inclined ventrolaterally, extends far from the prominence, and is approximately one-half anterior to the anterior rim of the acetabular fossa.

GEOCRINIA Blake

FIG. 3I

Species examined: G. laevis (Gunther).

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is short, slightly curved and flattened laterally in cross-section. The acetabulum is moderate with a narow peripheral rim. The superior margin of the acetabulum lies slightly above the level of the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly dilated. The dorsal acetabular expansion is not pronounced. The dorsal prominence is small and the dorsal protuberance is not detectable as a distinguishable area. The dorsal prominence is on a level with the anterior rim of the acetabulum.

GLAUERTIA Loveridge

FIG. 3J

Species examined: G. orientalis Parker.

The pubis and ischium are entirely cartilaginous.

The ilial shaft has an almost horizontal dorsal surface, and a slightly curved ventral one, so creating a slight broadening at the extremities of the shaft. There is neither a rim nor a crest to the shaft. The acetabulum has a scarcely detectable peripheral rim which superiorly is above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly developed and the preacetabular zone is slender. The dorsal acetabular expansion is poorly developed. The dorsal prominence is difficult to distinguish from the prominent and evenly rounded dorsal protuberance which appears to be inclined laterally. Approximately one half of the length of the dorsal protuberance lies anterior to the anterior rim of the acetabulum.

HELEIOPORUS Gray

FIG. 3K

Species examined: H. albopunctatus Gray.

The pubis and ischium are ossified.

The ilial shaft is not curved but has a slightly undulating superior face, raised into a thickened ridge on the posterior half. The acetabulum is small and is surrounded by an obliquely tapering rim. The acetabulum is high and is bisected by the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly dilated but the dorsal acetabular expansion rises sharply. The dorsal prominence is vast and the dorsal protuberance simply an elongate, semi-cylindrical ridge. At least two-thirds of the dorsal protuberance lies anterior to the anterior rim of the acetabulum.

KYARRANUS Moore

FIG. 3*L*

Species examined: K. sphagnicolus Moore, *Kyarranus* sp.

The pubis and ischium are almost entirely bony, only the central portion of the acetabular fossa remaining cartilaginous.

The ilial shaft is strongly curved and almost circular in cross section, but for an indistinct and narrow rim on the posterior half. This rim is created by an indentation of the medial surface of the shaft. The ventral acetabular expansion is poorly developed and the preacetabular zone is very narrow. The dorsal acetabular expansion is quite prominent. The dorsal expansion is scarcely distinguishable from the large and oval, posteroventrally inclined dorsal prominence. The anterior margin of the dorsal prominence is considerably anterior to the anterior rim of the acetabulum.

LECHRIODUS Boulenger

FIG. 3*M*

Species examined: L. melanopyga (Doria).

The pubis is cartilaginous and the ischium ossified.

The ilial shaft is slightly curved and bears an enlarged, fanlike dorsal crest arising from the posterior three-quarters of the shaft. The acetabulum is small and has a broad peripheral rim; the dorsal margin lies above the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly developed. The dorsal acetabular expansion is long and projects posteriorly. The dorsal prominence is small but detectable and the dorsal protuberance can be distinguished. The anterior margin of the dorsal protuberance is slightly posterior to the anterior rim of the acetabulum.

LIMNODYNASTES Fitzinger

FIG. 3*N*

Species examined: L. convexiusculus (Macleay), *L. dumerili* Peters, *L. ornatus* (Gray), *L. peroni* (Duméril & Bibron), *L. salmini* Steindachner, *L. spenceri* Parker, *L. tasmaniensis* Gunther, *L. terraereginae* Fry.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is slightly curved and highly variable in structure. There is an elongate groove on the medial surface in *L. dumerili*, a short groove in *L. terraereginae*, a short lateral groove in *L. tasmaniensis*, and there is a distinct dorsal crest in *L. ornatus* and *L. spenceri*. The acetabulum is small and high, bisected in most species by the ventral margin of the ilial shaft. The ventral acetabular expansion is small and not particularly expanded. The dorsal acetabular expansion rises into a moderate or else high and acutely pointed spike. The dorsal prominence is conspicuous in all species except those with crests on the shafts. It tends to form a conical shape in profile, but is somewhat broader and rounded in the largest species. The dorsal protuberance is an elongate ridge or expanded knob upon the tip of the dorsal prominence. The dorsal protuberance is on a level with or slightly anterior to the anterior rim of the acetabulum.

MIXOPHYES Gunther

FIG. 3*O*

Species examined: M. fasciolatus Gunther.

The pubis and ischium are completely ossified.

The ilial shaft is slightly curved and bears an enlarged fan-like dorsal crest arising dorsolaterally from the length of the shaft. The acetabulum has a broad peripheral rim, the dorsal margin of which lies above the ventral margin of the ilial shaft. The ventral acetabular expansion is moderately developed but with a rather narow preacetabular zone. The dorsal acetabular expansion rises high to abut the enlarged superior portion of the ischium. There is no dorsal prominence, and the dorsal protuberance is entirely laterally directed and so poorly developed that it is detectable only when the area is viewed from the dorsal or ventral aspects. The anterior margin of this weak protuberance is located anterior to the anterior rim of the acetabulum.

MYOBATRACHUS Schlegel

FIG. 4*A*

Species examined: M. gouldii (Gray).

The ischium is a large and almost circular bony plate, and the pubis is reduced to a small, triangular wedge of cartilage.

The ilial shaft is distinctly curved, lacks crests and indentations and is slightly flattened

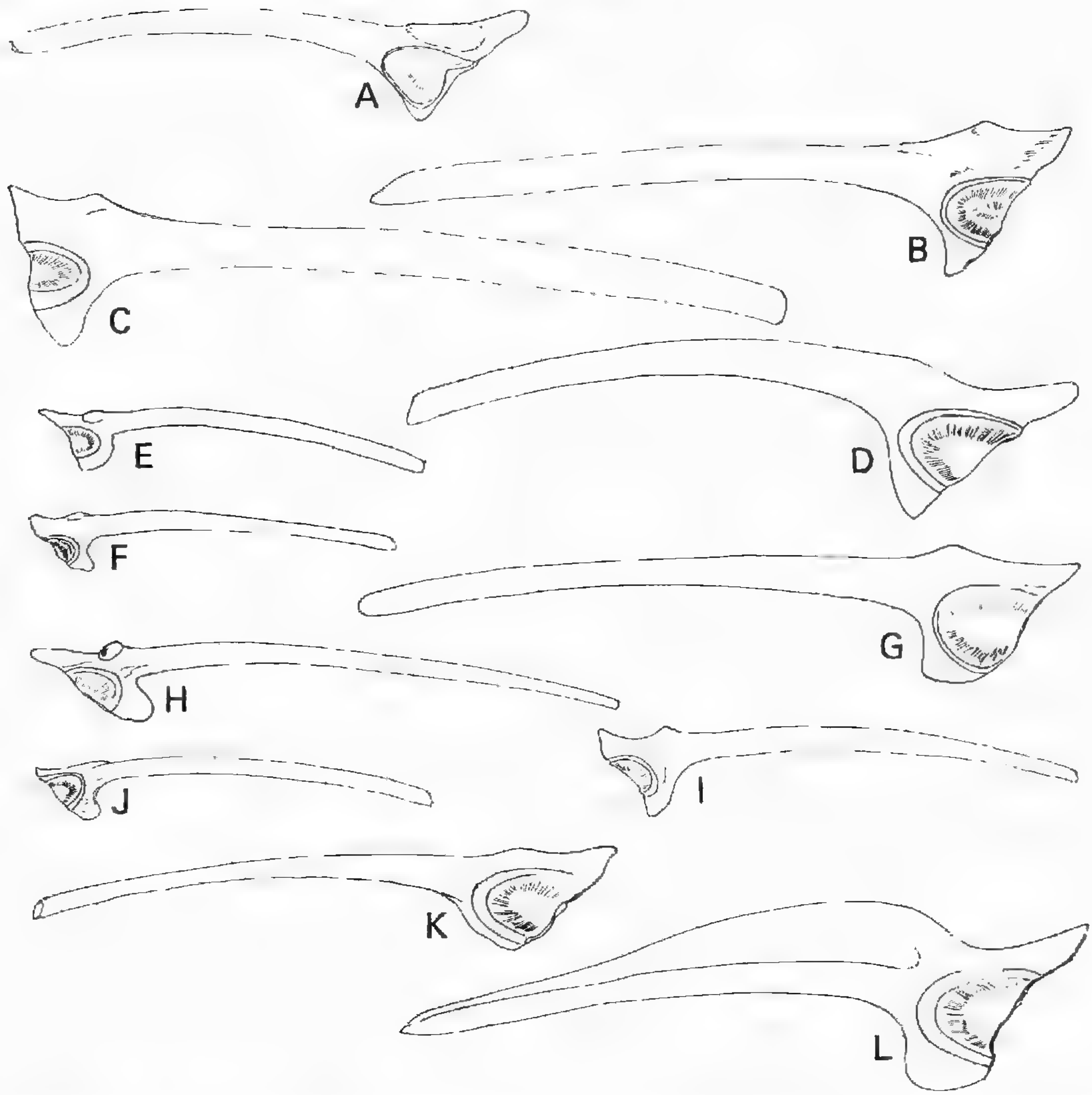

Fig. 4. Pelvis or isolated ilia of leptodactylid, microhylid and ranid frogs:
A. Myobatrachus gouldii, x 5; *B. Notaden melanoscaphus*, x 5; *C. Neobatrachus centralis*, x 5; *D. Philoria frosti*, x 5; *E. Pseudophryne bibroni*, x 5; *F. Ranidella parinsignifera*, x 5; *G. Rheobatrachus silus*, x 5; *H. Taudactylus diurnus*, x 5; *I. Uperoleia* sp., x 5; *J. Cophixalus ornatus*, x 5; *K. Sphenophryne robusta*, x 12.5; *L. Rana papua*, x 5.

laterally, producing an oval cross section. The acetabulum is large and has a narrow peripheral rim whose superior margin is considerably above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is greatly reduced, consisting of just a slender slip of bone bordering the acetabular rim. The dorsal acetabular expansion is a more prominent feature, rising above the ilial shaft. There is no dorsal prominence, and the dorsal protuberance is replaced by an oval, dorsolaterally inclined plate, consisting of a weak peripheral rim surrounding a very shallow depression. The anterior margin of this structure is far posterior to the anterior margin of the rim of the acetabular fossa.

NEOBATRACHUS Peters

FIG. 4*C*

Species examined: N. centralis Parker.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is almost perfectly straight. The acetabulum is small and high, the ventral margin of the ilium being on a level with the anterior one-third of the acetabulum. The ventral acetabular expansion is only slightly dilated, the preacetabular zone being particularly reduced. The dorsal acetabular expansion is high. The dorsal prominence is very large and the dorsal protuberance is a pointed nodule upon it. Approximately one-half of the dorsal protuberance lies anterior to the anterior rim of the acetabulum.

NOTADEN Gunther
FIG. 4*B*

Species examined: N. melanoscaphus Hosmer.

The pubis and ischium are cartilaginous, the latter with a median calcified zone.

The ilial shaft is only very slightly curved, lacks ridges and indentations and is circular in cross section. The acetabulum has a distinct, flattened peripheral rim which superiorly is on a level with the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly developed with a narrow preacetabular zone. The dorsal acetabular expansion is small and moderately developed. The dorsal prominence is broad and clearly demarcated from the ilial shaft. The dorsal protuberance is small and located on a level above the centre of the acetabular fossa.

PHILORIA Spencer
FIG. 4*D*

Species examined: P. frosti Spencer.

The pubis is cartilaginous and the ischium ossified.

The ilial shaft is strongly curved and has a medially directed dorsal rim. The acetabulum is large, its superior margin on a level with the ventral margin of the ilial shaft. The ventral acetabular expansion is not obviously dilated. The dorsal acetabular expansion is moderately well developed. The dorsal prominence is not conspicuous and the dorsal protuberance scarcely detectable as a separate entity. The dorsal protuberance is almost entirely anterior to the anterior rim of the acetabulum.

PSEUDOPHRYNE Fitzinger
FIG. 4*E*

Species examined: P. bibroni Gunther, *P. coriacea* Keferstein.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is almost straight and is circular in cross section. The acetabulum is large and has a narrow peripheral rim. The superior margin of the acetabulum lies on or slightly above the level of the ventral margin of the ilial shaft. The ventral acetabular expansion is dilated. The dorsal acetabular expansion is only very slightly raised. The dorsal prominence is small (scarcely detectable in *P. coriacea*, but quite distinct in *P. bibroni*) and the dorsal prominence a very small knob on its tip. The dorsal protuberance is on a level with the anterior rim of the acetabulum.

RANIDELLA Girard
FIG. 4*F*

Species examined: R. parinsignifera (Main), *R. signifera* Girard.

The pubis is cartilaginous and the ischium is bony.

The ilial shaft is curved, compressed laterally and possesses neither a rim nor a crest. The acetabulum has a broad peripheral rim which superiorly is on a level with the ventral margin of the ilial shaft. The ventral acetabular expansion is greatly enlarged, the subacetabular zone protruding anteriorly. The dorsal acetabular expansion is poorly developed. The dorsal prominence is broad and the dorsal protuberance is rounded, inclined posteroventrally and moderately prominent. Approximately one-half of the dorsal protuberance is anterior to the anterior rim of the acetabulum.

RHEOBATRACHUS Liem
FIG. 4*G*

Species examined: R. silus Liem.

The pubis is cartilaginous and the ischium ossified.

The ilial shaft is exceptionally slender, very slightly curved and cylindrical in cross section. The acetabulum is very large with a conspicuous rim, its superior margin slightly above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly dilated. The dorsal acetabular expansion is slightly developed, projecting posteriorly. The dorsal prominence is well developed and the dorsal protuberance is conical and situated posterior to the anterior rim of the acetabulum.

TAUDACTYLUS Straughan & Lee
FIG. 4*H*

Species examined: T. diurnus Straughan & Lee.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is gently curved, slightly compressed laterally and possesses neither a rim nor a dorsal crest. The acetabulum is large with a well developed rim creating a deep acetabular fossa. The ventral acetabular expansion is slightly dilated. The dorsal acetabular expansion is directed posteriorly and overlies the superior margin of the ischium. The dorsal prominence is only slightly distinguishable from the large, raised, oval, dorsolaterally directed dorsal protuberance. Approximately one-half of the dorsal protuberance lies anterior to the acetabular rim.

UPEROLEIA Gray

FIG. 4I

Species examined: U. marmorata Gray, *Uperoleia* sp.

The pubis and ischium are cartilaginous.

The ilial shaft is almost straight and is circular in cross section, lacking a rim and a crest. The acetabulum is large and has a broad peripheral rim. The superior margin of the acetabulum lies above the ventral margin of the ilial shaft. The ventral acetabular expansion is of moderate width with the subacetabular zone very slightly expanded. The dorsal acetabular expansion is not pronounced. The dorsal prominence is large and the dorsal protuberance conical and rising far above the level of the shaft. The anterior margin of the dorsal protuberance is situated anterior to the anterior rim of the acetabulum.

Family MICROHYLIDAE

COPHIXALUS Boettger

FIG. 4J

Species examined: C. ornatus (Fry).

The ischium is small but ossified, and the pubis is cartilaginous.

The ilial shaft is compressed mediolaterally, has neither a rim nor a crest, and is very slightly curved. The ventral acetabular expansion is concave and very narrow. The acetabular fossa is extremely large and very high, its superior margin nearer to the dorsal than the ventral margin of the ilial shaft. The dorsal protuberance is not distinguishable from the dorsal prominence, and lies slightly anterior to the anterior margin of the acetabular rim. The dorsal acetabular expansion is very poorly developed.

SPHENOPHRYNE Peters & Doria

FIG. 4K

Species examined: S. robusta (Fry).

The ischium is extremely small and only partly ossified. The pubis is cartilaginous.

The ilial shaft is compressed mediolaterally, has neither a rim nor a crest, and is very slightly curved. The ventral acetabular expansion is slightly concave and very narrow. The acetabular fossa is large and high, and is partly bisected by the ventral border of the ilial shaft. The dorsal protuberance is not distinguishable from the dorsal prominence, and lies entirely posterior to the anterior margin of the acetabular rim. The dorsal acetabular expansion is only slightly developed.

Family RANIDAE

RANA Linné

FIG. 4L

Species examined: R. papua Lesson.

The pubis is cartilaginous and the ischium is bony.

The ilial shaft curves gently downwards and bears a massive fin-like and tapering dorsal crest. The acetabulum is large and bears a broad peripheral rim. The superior margin of the acetabular rim extends considerably above the ventral margin of the ilial shaft. The ventral acetabular expansion has a reduced preacetabular zone and greatly dilated subacetabular zone. The dorsal acetabular expansion is well developed, tapering to a point posteriorly. There is no dorsal prominence and the dorsal protuberance is an oval and almost vertical expansion of the base of the ilial shaft. This protuberance lies entirely posterior to the anterior rim of the acetabulum.

Fossil genus

AUSTRALOBATRACHUS new genus

Type species: Australobatrachus ilius new species.

This taxon was first reported on by Tyler (1974, p. 711, fig. 1).

Extending from the acetabular region the ilial shaft bears a deep, curved groove on its lateral surface. The acetabular fossa is exceptionally high in relation to the ilial shaft, its superior border reaching a position equivalent to midway up the shaft. The acetabular rim is poorly developed. The dorsal protuberance is gently rounded, and not distinguishable from the dorsal prominence. The anterior limit of the dorsal protuberance is on a level with the anterior margin of the acetabular rim. The ventral acetabular expansion is neither protuberant nor concave, the ilial/preacetabular zone forming almost a straight line extending gradually posteriorly. The dorsal acetabular expansion probably does not project superiorly.

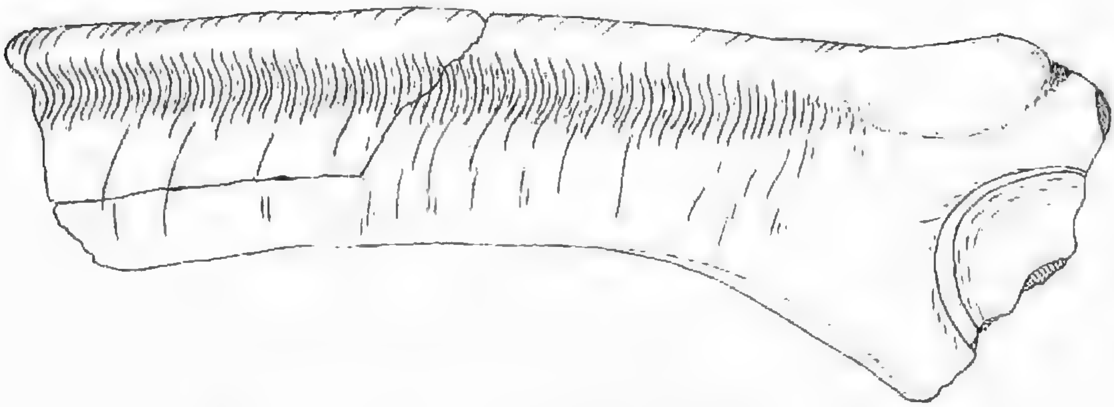

Fig. 5. Left ilium of *Australobatrachus ilius* holotype, SAM. P18021.

Australobatrachus ilius new species

Holotype: Two fragments comprising the distal 6.7 mm of a single left ilium. SAM. P18021 (Fig. 5).

Type locality: Tedford Quarry, on the west side of Lake Palankarrina, S.A. (University of California Museum of Palaeontology locality V-5375.)

Horizon: Etadunna Formation.

Age: Ngapakaldi Fauna, Tertiary; probably mid-Miocene.

Description of holotype: As for genus.

Comparison with other species: Of the existing families of frogs that do not have modern representatives in Australia, the Leiopelmatidae, Pipidae and Pelobatidae have members in the southern hemisphere and could all be regarded as potential contributors to the ancestral Australian frog fauna; hence they merit comparison with *Australobatrachus*.

The Leiopelmatidae of New Zealand have simple ilia with a slender, cylindrical ilial shaft and a poorly developed ventral acetabular expansion (Stephenson 1960). There is not the slightest resemblance to *Australobatrachus*.

According to Trueb (1973), the pipids are quite unique in possessing a lateral crest (not groove) to the ilial shaft. Any resemblance to *Australobatrachus* has to be weighed against the condition of the dorsal prominence (vast and projecting high above the shaft in pipids; reduced and not raised above the shaft in *Australobatrachus*) and of the ventral acetabular expansion (vestigial in pipids as opposed to being highly developed).

To judge from the descriptions and illustrations of Zweifel (1956) and Kluge (1966) the pelobatid ilium has typically a bow-like dorsad curvature, creating a totally different form from that of *Australobatrachus*. In addition the species illustrated by them have poorly-developed ventral acetabular expansions and more prominent acetabular fossae than has the new genus.

In comparison with the ranids of Australia and New Guinea, *Australobatrachus* is readily distinguished by its total lack of the dorsal crest which rises high above the ranid ilial shaft. Similarly many microhylids (and also some leptodactylids) exhibit such a crest, but the microhylids lacking a dorsal crest may be distinguished by the poor development of the ventral acetabular expansion.

Establishing means of distinguishing Australian hylids from leptodactylids has proved difficult. In general it would apear that a well-developed, dorsally-projecting dorsal prominence is almost characteristic of the leptodactylids, whereas it tends to be poorly developed or else laterally disposed in hylids. Most of the leptodactylids which are exceptional in having poorly-developed dorsal prominences, are those in which the upper section of the ilial shaft is modified in some way. Hence the prominence is scarcely differentiated in *Lechriodus* and *Mixophyes* which have a dorsal crest because the prominence is upon this thin flange of bone. It could be argued that the poor development of the dorsal prominence in *Australobatrachus* conflicts with my interpretation of the groove as an intrinsic modification of the ilial shaft. Hence an alternative hypothesis is that the upper rim is the supra-ilial structure, comparable to a dorsal crest. This latter explanation is not favoured, simply because the end section of the ilial shaft is 8-shaped, and the nature of the acetabulum (a poorly developed rim) is not usually developed on a pelvic girdle in which the acetabulum reaches the upper segment of the shaft.

Amongst the Australian hylids and leptodactylids there is considerable variation in the shape of the ventral acetabular expansion. *Cyclorana australis* and several species of *Litoria* approach the condition displayed by *Australobatrachus*, but in each the dorsal prominence is more highly developed and the lateral groove is lacking.

If *Australobatrachus* lacked a lateral groove the nature of the dorsal prominence and the ventral acetabular expansion would cause me to favour referring the genus to the Hylidae. Hence to avoid over-interpreting the presence and form of the lateral groove, *Australobatrachus* is assigned tentatively to this family.

Extrapolation of musculature: The lateral surface of the ilial shaft is the site of origin of the musculus iliacus externus. Any extreme broadening of the lateral surface of the ilial shaft increases the surface area available to this muscle. Unquestionably these are modifications most common in aquatic frogs or species inhabiting streamside situations, members of such genera as *Xenopus, Rana, Lechriodus* and *Mixophyes*. Certainly it is tempting to attribute a similar functional association for *Australobatrachus*, and hence assume that this animal lived close to permanent water.

Acknowledgments

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NEW AUSTRALIAN ALLODAPINE BEES (SUBGENUS EXONEURELLA MICHENER) AND THEIR IMMATURES (HYMENOPTERA: ANTHOPHORIDAE)

*BY T. F. HOUSTON**

Summary

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Three new species of *Exoneura* Smith (*E. eremophila*, *E. setosa* and *E. tridentata*) are described and figured. They are assigned to the formerly monotypic subgenus Exoneurella Michener and both adults and immatures of the new species are compared with those already described for the type-species, *E. lawsoni* Rayment. A key for identification of adults is provided.

Females of *E. tridentata* vary greatly in size and exhibit allometric variation of the head and metasoma.

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Females of *E. tridentata* vary greatly in size and exhibit allometric variation of the head and metasoma.

Introduction

The chief purpose of this paper is to provide names for three species of bees whose ethology is to be dealt with in a subsequent work. An exhaustive examination of material from collections has not been attempted and the descriptions to follow are based on specimens in the collections of the author and the South Australian Museum.

The three new species are assigned to the subgenus *Exoneurella* Michener (of *Exoneura* Smith) which formerly contained only the type-species, *E. lawsoni* Rayment. Since *Exoneurella* was founded partly on the basis of the larval characteristics of *E. lawsoni*, it seemed of interest to describe and compare immatures of the new species. Generally, the characteristics of the new species support retention of *Exoneurella* as a discreet taxon.

The size-correlated variation of females of *E. tridentata* sp. nov. is detailed below as it is significant in terms of the bionomics of the species. Such variation is unusual amongst allodapine bees and in the family Anthophoridae as a whole.

The following abbreviations are used for the names of institutions and collections referred to in the text below: ANIC (Australian National Insect Collection, C.S.I.R.O., Canberra), HC (author's private collection, to be deposited in SAM), KU (Snow Entomological Museum, University of Kansas, Lawrence, Kansas, U.S.A.), SAM (South Australian Museum, Adelaide) and WADA (Western Australian Department of Agriculture, Perth).

Except where stated otherwise, all specimens listed in this paper were collected by the author.

Genus EXONEURA Smith

Exoneura Smith, 1854, p. 232. See Michener, 1965, pp. 223-226 for detailed description, subgenera and species.

Subgenus EXONEURELLA Michener

Exoneurella Michener, 1963, p. 257 (erected as a genus); 1965, pp. 223-224 (relegated to subgeneric status; diagnosis provided).

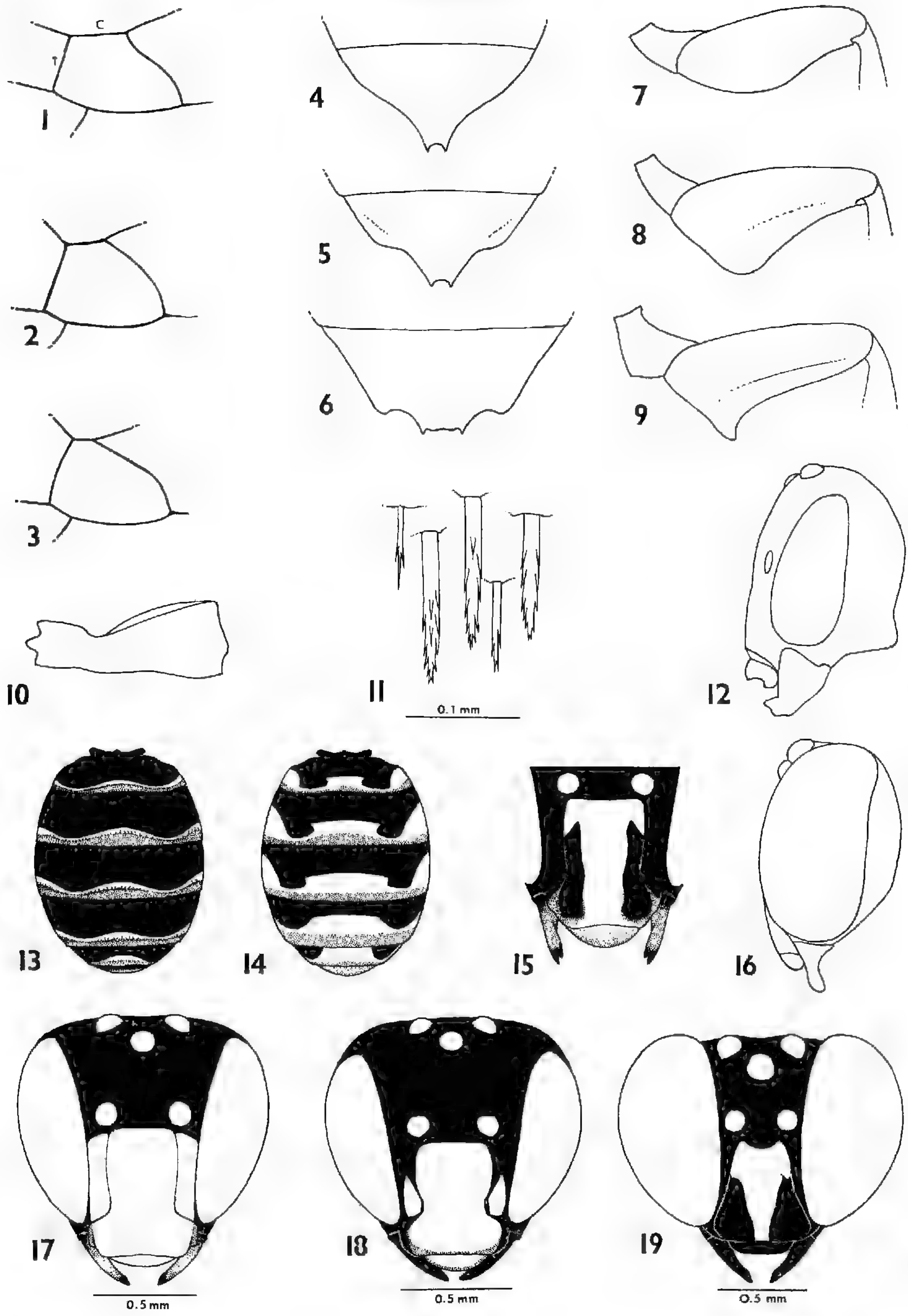
THE ADULTS

Key to the species of Exoneurella

1. Second cubital cell of fore wing with subequal costal and medial borders (Fig. 1); 6th metasomal tergum of female with simple non-bifid apex and a pair of lateral projections (Fig. 24, 25); compound eyes of male strongly swollen (Fig. 19) .. *E. tridentata*

1. Second cubital cell of fore wing with costal margin conspicuously shorter than medial margin (Figs 2, 3); 6th metasomal tergum of female with bidentate apex and with or without lateral

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000.



FIGS 1–19

projections (Figs 4–6); compound eyes of male not swollen (Figs 17, 18) . . . 2

2. Sixth metasomal tergum of female without lateral prominences, margins smoothly sinuate (Fig. 4); hind femora of male obtusely produced and carinate ventrally (Fig. 8); metasomal terga of both sexes black without cream or creamy-brown pigmentation and without numerous conspicuously thickened setae . . . . . . *E. lawsoni*

2. Sixth metasomal tergum of female with distinct lateral projections or prominences (Figs 5, 6); hind femora of male unmodified (Fig 7) or not modified as in Fig. 8; metasomal terga of both sexes with faint to distinct cream bands; terga 3 and 4 (females) or 4 and 5 (males) with numerous conspicuously thickened setae (Fig. 11) 3

3. Metasomal terga yellow-brown to black with wide cream bands (Fig. 14); 6th metasomal tergum of female with subacute lateral projections (Fig. 6); hind femora of male each with an acute ventral projection (Fig. 9) . . . . . . *E. eremophila*

3. Metasomal terga largely black with narrow (sometimes faint or incomplete) cream subapical bands (Fig. 13); 6th metasomal tergum of female with very obtuse lateral prominences (Fig. 5); hind femora of male unmodified (Fig. 7) . . . . . . *E. setosa*

Exoneura (Exoneurella) eremophila n.sp.

Figs 2, 6, 9, 14, 15, 17

Types

Holotype: ♂ (SAM, I 20961), New Kalamurina Homestead, S. Aust. (27°44'S, 138°15'E), 9–11.iii.1972, on *Wahlenbergia*.

Allotype: ♀ in SAM. Paratypes: 42 ♂, 44 ♀ in SAM; 2 ♂, 2 ♀ in ANIC; 1 ♂, 1 ♀ in KU.

Diagnosis: This species differs from all other *Exoneurella* as follows. Lateral face marks of male filling spaces between clypeus and compound eyes (Fig. 17); metasomal terga of both sexes yellow-brown to black with extensive cream maculations (Fig. 14); pronotum with a pair of cream marks sublaterally; hind femora of male each with an acute ventral projection (Fig. 9); 6th metasomal tergum of female with bidentate apex and a pair of subacute lateral projections (Fig. 6).

Description

Male. Body length 3.8–4.1 mm; head width 1.1–1.2 mm.

Head capsule as broad as long; compound eyes of usual relative size (Fig. 17); face narrowed to about 43% of head width; ocelli approximately equal in size to antennal sockets; scapes failing to reach level of median ocellus; flagella 85% as long as head width, the middle segments about as long as broad; genae viewed laterally almost half as wide as compound eyes and evenly convex; fore legs not especially slender, the fore tibiae about 3.5x as long as wide; hind femora laterally compressed, each with an acute ventral projection (Fig. 9); costal margin of 2nd cubital cell of fore wing about half as long as 1st transverse cubital vein (Fig.2).

Integument glossy generally with sparse fine pitting or none; metasomal terga very finely lineate.

Pubescence white, virtually absent dorsally but fairly long and dense ventrally and on legs and mesepisterna; 4th and 5th metasomal terga (except laterally) with a sparse covering of thickened bristle-like setae.

The following areas white or cream: lower face, labrum and middle portions of mandibles (Fig. 17), scapes and pedicels ventrally, tubercles and dorsal margin of pronotum (except medially), spots on tegulae, basal parts of wing veins, subapical bands on metasomal terga (Fig. 14), apices of femora, bases of tibiae, anterior edges of fore tibiae, and basitarsi. The following areas yellow-brown: scapes dorsally, flagella ventrally, most parts of legs (except for cream areas), metasoma

Figs 1– 3. Second cubital cells of right fore wings (in dorsal views) of *Exoneura* (*Exoneurella*) *tridentata*, *E.* (*E.*) *eremophila*, and *E.* (*E.*) *setosa* respectively. C = costal margin, T = first transverse cubital vein.

Figs 4– 6. Sixth metasomal terga (dorsal views) of females of *E.* (*E.*) *lawsoni*, *E.* (*E.*) *setosa* and *E.* (*E.*) *eremophila* respectively.

Figs 7– 9. Trochanters, femora and apices of tibiae of left hind legs (anterior views) of males of *E.* (*E.*) *setosa*, *E.* (*E.*) *lawsoni* and *E.* (*E.*) *eremophila* respectively.

Fig. 10. Left mandible of female of *E.* (*E.*) *tridentata* (ventral view).

Fig. 11. Thickened bristle-like setae from fourth metasomal tergum of female of *E.* (*E.*) *setosa*

Fig. 12. Head capsule of a relatively large female of *E.* (*E.*) *tridentata* (left lateral view).

Figs 13 and 14. Metasomae (dorsal views) of males of *E.* (*E.*) *setosa* and *E.* (*E.*) *eremophila* respectively showing cream bands (white) and translucent tergal margins (stippled).

Fig. 15. Lower portion of head of female of *E.* (*E.*) *eremophila* (anterior view) showing T-shaped clypeal mark.

Fig. 16. Head capsule of male of *E.* (*E.*) *tridentata* (left lateral view).

Figs 17–19. Head capsules (anterior views) of males of *E.* (*E.*) *eremophila*, *E.* (*E.*) *setosa* and *E.* (*E.*) *tridentata* respectively.

ventrally and partially or extensively dorsally. Remaining areas black or dark brown.

Female. Body length 4.0–5.5 mm; head width 1.1–1.2 mm.

Head form similar to that of male (Fig. 17); flagella about 67% as long as head width; mandibles tridentate but not constricted subapically; metasoma fairly elongate; 6th metasomal tergum with a bidentate apex and a pair of small but almost acute upturned lateral projections (Fig. 6); hind femora unmodified.

Integument and pubescence much as in male but thick bristle-like setae occur only on terga 3 and 4.

Coloration as in male except that white on face is limited to a full-length T-shaped mark on clypeus (Fig. 15).

Variation

The extent of yellow-brown coloration on the metasoma varies considerably amongst individuals collected together and some specimens have creamy-brown maculations on the lateral margins of the scutum and scutellum.

The specific name, derived from Greek, means loving solitude and alludes to the arid habitat of the species.

Distribution

Central regions of Australia including portions of the Northern Territory, Queensland, New South Wales and South Australia.

Specimens examined: The holotype and the following. *QLD:* 9 ♂, 8 ♀, 3 miles (4.8 km) W. of Windora, 17.iv.1969, ex nests (HC). *N.S.W.:* 1 ♀, 82 miles (132 km) W. of Cobar, 31.i.1971, on *Ptilotus* (SAM); 1 ♂, 14 ♀, 70 miles (113 km) E. of Wilcannia, 31.i.1971, on *Helichrysum, Goodenia* and *Wahlenbergia* (SAM). *S. AUST.:* 1 ♀, Amata (Musgrave Park) settlement, 14.x.1972, on *Calandrinia, H. E. Evans & T. F. Houston* (SAM); 1 ♀, 33 miles (53 km) W. of Amata, 17.x.1972, ex nest in pithy twig, *H. E. Evans & T. F. Houston* (SAM); 7 ♀, Bettys Well (132°26'E, 27°2'S), Everard Park Stn, 1–5.xi.1970, on *Hibiscus farragei* (SAM); 45 ♂ (paratypes), 48 ♀ (allotype and paratypes), New Kalamurina HS. (27°44'S, 138°15'E), 9–11.iii.1972, on *Wahlenbergia* (7 ♂, 5 ♀ pinned), ex dead stems of *Myriocephalus* (38 ♂, 43 ♀ in alcohol) (ANIC, KU, SAM); 2 ♀, Morgan, 19.xii.1963, on *Wahlenbergia* (HC); 4 ♂, 4 ♀, 10 miles (16 km) S. of Mt Davies airstrip, 21.x.1972, on *Ptilotus, H. E. Evans & T. F. Houston* (SAM); 2 ♀, Mt Miccollo (32°31'S, 136°36'E), Siam Stn, 20.iv.1971, ex nest (SAM); 1 ♀, S. of Tomkinson Ranges (129°8'E, 26°10'S), 18.x.1972, on *Scaevola, H. E. Evans & T. F. Houston* (SAM); 2 ♀, 31 miles (50 km) W. of Welbourn Hill HS, 13.x.1972, on blue *Eremophila, H. E. Evans & T. F. Houston* (SAM); 2 ♀, 10 miles (16 km) SE. of William Creek, 28.x.1972, on *Hakea, H. E. Evans & T. F. Houston* (SAM).

Exoneura (Exoneurella) lawsoni Rayment, 1946, pp. 230-232, fig. 2 (male, not female or larva).

FIGS 4, 8

Exoneurella lawsoni (Rayment) Michener, 1963, p. 257.

Exoneura (Exoneurella) lawsoni Rayment, Michener, 1965, p. 224.

Holotype: ♂ (in ANIC), Canberra, A.C.T., Newton R. Lawson, July 1945.

I have not examined the holotype but Ms Josephine Cardale (ANIC) made a critical examination of it on my behalf and confirmed that it agrees with the male characteristics given in the diagnosis below.

Michener (1963, p. 258) pointed out that the females and larvae described by Rayment in the original description of *E. lawsoni* are of another species and are referable to the subgenus *Brevineura*.

Diagnosis: E. lawsoni differs from all other *Exoneurella* as follows. Hind femora of male carinate and broadly produced ventrally (Fig. 8); 6th metasomal tergum of female lacking lateral prominences, the margins gently sinuate (Fig. 4). Differs from *E. setosa* and *E. eremophila* in complete absence of cream pigmentation from metasoma and in absence (or only feeble development) of thickened bristle-like setae on dorsum of metasoma.

For a detailed description of both sexes see Michener (1963, p. 259). Note, however, that the pale maculations of the face of the male are white, not pale yellow.

Distribution: On and near Great Dividing Range of south-eastern Queensland, New South Wales and eastern Victoria.

Specimens examined: QLD: 4 ♂, 5 ♀, Bunya Mountains, 8.x.1968, ex nests (HC). *VIC.:* 1 ♂, 2 ♀, Tambo Valley, 22.i.1966, on *Wahlenbergia* (HC).

Exoneura (Exoneurella) setosa n.sp.

FIGS 3, 5, 7, 11, 13, 18

Types

Holotype: ♂ (SAM, I 20962), West Beach, Adelaide, S. Aust., 25.iv.1975, ex dead *Euphorbia* stem, C. A. & T. F. Houston.

Allotype: ♀ in SAM. Paratypes: 7 ♂, 10 ♀ in SAM; 4 ♂, 4 ♀ in ANIC; 2 ♂, 2 ♀ in KU.

Diagnosis: Very like *E. lawsoni*, differing as follows. Hind femora of male unmodified, lacking ventral flanges and projections (Fig. 7); 6th metasomal tergum of female with a pair of lateral convexities (Fig. 5); metasomal terga of both sexes with narrow subapical bands of creamish pigment (sometimes faint or incomplete, especially medially) and translucent brown apical margins (Fig. 13); metasomal terga 4 and 5 (male) or 3 and 4 (female) with numerous conspicuously thickened, bristle-like setae (Fig. 11).

Description

Male. Body length 3.8–4.7 mm; head width 1.1–1.2 mm.

Head capsule 1.1x as broad as long; compound eyes of usual size (Fig. 18); face narrowed to about 42% of head width in lower part; ocelli approximating size of antennal sockets; scapes just failing to reach level of median ocellus; flagella about 72% as long as head width; middle flagellar segments slightly broader than long; genae viewed laterally 2/3 as wide as compound eyes and evenly convex; fore legs not unusually elongate, the fore tibiae about 3.5x as long as wide; hind femora unmodified (Fig. 7); costal margin of 2nd cubital cell of fore wing about 1/4 to 1/2 as long as 1st transverse cubital vein (Fig. 3).

Integument almost entirely glossy; clypeus and scutellum finely pitted; dorsal area of propodeum dulled by extremely fine sculpturing; metasomal terga finely lineate.

Pubescence white, sparse on head and body, densest laterally and ventrally on thorax and basal parts of legs; 4th and 5th metasomal terga with numerous short but thick bristle-like setae (Fig. 11) on dorso-apical areas.

The following areas white: almost all of clypeus and a spot of variable size on each side (Fig. 18), labrum, anterior stripe on fore tibia, spots at bases of mid and hind tibiae, pronotal tubercles and alar sclerites. The following areas off-white to cream: ventral edges of scapes, mid and hind basitarsi, narrow subapical bands on metasomal terga (Fig. 13; sometimes faint or incomplete especially medially). Fore legs (largely) and mid femora and tibiae anteriorly yellow-brown. Hind margins of metasomal terga translucent pale brown; remaining areas black or blackish brown.

Female. Body length 4.3–5.5 mm; head width 1.1–1.2 mm.

Head form similar to that of male: flagella 64% as long as head width; mandibles tridentate but not constricted subapically; metasoma elongate, the 6th tergum with bidentate apex and a pair of obtuse lateral prominences (Fig. 5).

Integument sculptured as in male.

Pubescence much as in male but bristle-like setae occur on hind margin of 3rd metasomal tergum and dorsal area of 4th.

Coloration differs from that of male as follows: clypeus with a full-length white T-shaped stripe; paraocular areas without white spots; labrum entirely brownish; legs lacking yellow-brown coloration.

The specific name, derived from Latin and meaning 'bristly', alludes to the setation of the metasoma.

Distribution

Lowlands of southern South Australia (West to Spencer Gulf) and of south-eastern Queensland.

Specimens examined: The holotype and the following. *QLD:* 1 ♀, 2 miles (3.2 km) S. of Nanango, 7.x.1968, on *Wahlenbergia* (HC), 1 ♂, 3 ♀, 3 miles (4.8 km) N. of Peregian Beach (near Noosaville), 9.xii.1966, ex. nests (HC). *S. AUST.:* 2 ♂, 5 ♀, Glenelg North (dunes), Adelaide, 24.x.1963, 6.xii.1964 and 14-16.i.1965, on pigface and *Wahlenbergia* flowers (HC); 1 ♀, Mambray Creek Rail Siding, 13.xi.1970, ex pithy stem (SAM); 3 ♀, Morgan, 18–19.xii.1963, on *Wahlenbergia* (HC): 13 ♂ (paratypes), 17 ♀ (allotype and paratypes), West Beach, Adelaide, same data as for holotype (ANIC, KU, SAM): 4 ♂, 3 ♀, West Beach, Adelaide, 5 and 24.ii.1965, 27.ix.1965, on *Wahlenbergia* and ex hollow stems (HC).

Exoneura (Exoneurella) tridentata n. sp.

FIGS 1, 10, 12, 16, 19-30

Types

Holotype: ♂ (SAM, I 20963), Lake Gilles National Park (136°46'E, 33°2'S), S. Aust., 31.xii.1973, ex short tunnel in twig of *Heterodendron.*

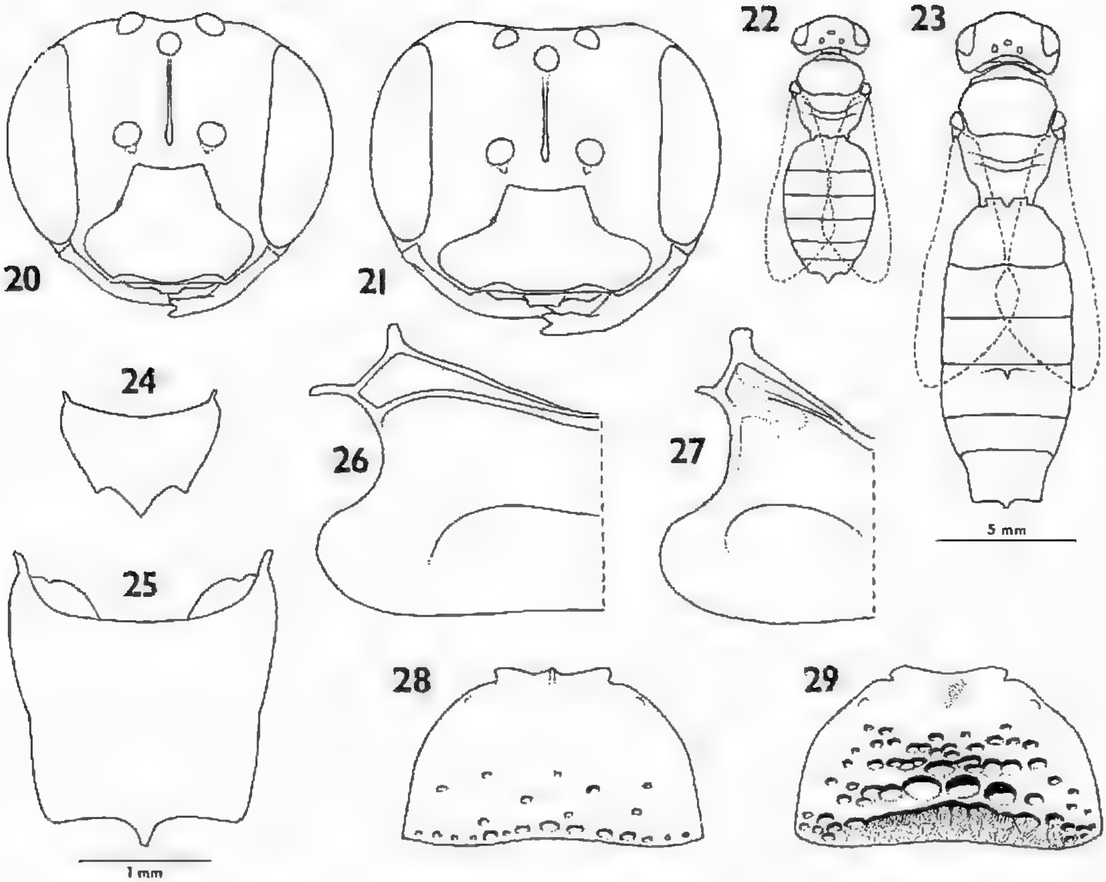
Allotype: ♀ in SAM. Paratypes: 39 ♂, 29 ♀ in SAM; 2 ♂, 5 ♀ in ANIC; 1 ♂, 2 ♀ in KU.

Diagnosis: E. tridentata differs from all other *Exoneurella* as follows. Costal margin of 2nd cubital cell of fore wing equal to or slightly longer than 1st transverse cubital vein (Fig. 1); scapes reaching to above level of median ocellus; male with swollen compound eyes and relatively narrow face (Fig. 19) and fore legs conspicuously elongated; female with angular genae (Fig. 12), mandibles constricted subapically (Fig. 10) and 6th metasomal tergum with non bifid apex (Figs 24, 25).

Description

Male. Body length 4.5–4.9 mm; head width 1.6–1.9 mm.

Head capsule 1.3x as broad as long; compound eyes strongly swollen so that face appears sunken between them; face narrowed to about 1/4 of head width (Fig. 19); ocelli relatively large (about 1.4x as wide as antennal sockets); genae viewed laterally (Fig. 16) much narrower than compound eyes and not angular; scapes slender, reaching to just above



Figs 20–29. *Exoneura* (*Exoneurella*) *tridentata* female. Figs 20, 21.—Head capsules (anterior views) of smallest and largest known specimens respectively, drawn to same length. Figs 22, 23.—Smallest and largest known specimens respectively (dorsal views) (antennae and legs omitted, fore wings represented by broken lines). Figs 24, 25.—Sixth metasomal terga (dorsal views) of smallest and largest known specimens, respectively. Figs 26, 27.—Left halves of fourth metasomal sterna (dorsal views) of smallest and largest known specimens, respectively, drawn to same length. Figs 28, 29. –First metasomal terga (dorsal views) of smallest and largest known females, respectively, drawn to same size to illustrate differences in surface pitting.

level of median ocellus; flagella relatively short, 1/2 as long as head width, all segments but apical one broader than long; fore legs very slender, the tibiae 5x longer than wide; hind femora unmodified; costal margin of 2nd cubital cell of fore wing equal to or longer than 1st transverse cubital vein (Fig. 1); metasoma relatively short, broad and depressed.

Integument of face smooth but dull with close small pitting on clypeus; scutum and scutellum glossy with very sparse fine pitting; mesepisterna dulled by shallow coarse pitting; anterior half of 1st metasomal tergum glossy and impunctate, the posterior half and most of tergum 2 pitted and finely roughened, dull except laterally; tergum 3 shiny but coarsely pitted; terga 4 to 7 duller with fine reticulate sculpture.

Pubescence white, fairly long and sparse generally, densest on clypeus, posterior of head, sides and venter of thorax, sides of propodeum, basal areas of legs and 1st metasomal tergum.

Colour black generally except for the following: clypeal mark (Fig. 19), ventral edges of scapes, patches on tegulae and wing bases and spot at base of each tibia white to cream; apical portions of femora, all tibiae and tarsi orange-brown; wing veins and ventral surfaces of flagella brown.

Female. Size extremely variable; body length 4.8–10.0 mm; head width 1.3–2.1 mm.

Head (viewed anteriorly) grading from fairly round in small females (Fig. 20) to rather quadrate in large females (Fig. 21); accordingly the inner orbits vary from slightly converging to slightly diverging below; genae (viewed laterally) almost as wide as compound eyes and very angular, especially in large specimens (Fig. 12); scapes slender and reaching median ocellus; flagella 65% as long as head width; labrum with a stout carinate median tubercle; mandibles tridentate, strongly constricted subapically (Fig. 10); legs not as slender as those of male; metasoma elongate and rather parallel-sided, more so in large females (Figs 22, 23); 6th tergum upturned, slightly to strongly concave dorsally, rather triangular with small lateral projections in small females (Fig. 24) grading to quadrate in large females (Fig. 25).

Integument largely glossy with few scattered small pits; dorsal and lateral areas of propodeum dull with fine roughening; 1st metasomal tergum of small specimens with relatively few pits concentrated along posterior margin (Fig. 28), of larger specimens with numerous coarser pits some of which exceed the ocelli in size and many of which coalesce to form an irregular emargination posteriorly (Fig. 29); more apical terga with sparse medium pitting and fine reticulate sculpturing, strongest on terga 4 to 6. Pubescence generally sparse, white and inconspicuous, longest on sides of metasoma and hind tibiae; dorsal areas of metasomal terga lacking thickened or conspicuous setae.

Head and body black; clypeus with a full length T-shaped white mark; labrum, mandibles and legs largely or wholly orange-brown; medium and large females usually have diffuse orange-brown patches on mesepisterna, metasternum and anterior metasomal sterna.

The specific name refers to the 3-pointed margin of the 6th metasomal tergum of the female.

Distribution

Semi-arid regions of South Australia and southern Western Australia (the mallee *Eucalyptus* belt and bordering areas).

Specimens examined: The holotype and the following. *S. AUST.*: 1 ♂ and 14 ♀ (all paratypes), Corunna Hills, N. of Iron Knob, 19.iv.1971, ex nest (SAM); 4 ♀, S. of Iron Baron, Eyre Peninsula, 30.xi.1971, on *Eremophila* (HC); 40 ♂ (paratypes), 26 ♀ (including allotype and 22 paratypes), Lake Gilles National Park, 30–31.xii.1973, 11–16.iv.1974, 14–17.vi.1974, 29.viii–1.ix.1974 and 27.x.1974, ex nests in hollow *Heterodendron* twigs, *C. A. & T. F. Houston* (ANIC, HC, KU and SAM —some in alcohol); 1 ♂ (paratype), 3 ♀, northern Middleback Ranges (137°9′E, 33°3′S), 7–8.x.1973, ex hollow *Heterodendron* twigs, *C. A. & T. F. Houston* (HC, SAM); 7 ♀, 8 miles (13 km) E. of Poochera, 8.i.1970, on *Melaleuca pubescens* (HC); 1 ♀, 29 km NNW. of Pt Augusta, 29.ix.1972, on *Myoporum* (SAM); 3 ♀, 2 miles (3.2 km) N. of Port Germein, 7.i.1970, on *Loranthus miraculosus* and *Melaleuca pubescens* (HC); 1 ♀, 30 miles (48 km) NNW. of Renmark, 22.i.1972, on mallee *Eucalyptus* (SAM). *W. AUST.*: 1 ♂, 27 miles (43 km) W. of Coolgardie, 18.i.1970, on *Eucalyptus* (HC); 1 ♀, 25 miles (40 km) E. of Kalbarri, 6.iii.1974, *K. T. Richards* (WADA); 1 ♀, 8 miles (13 km) S. of Wanoo, 7.v.1974, *K. T. Richards* (WADA).

Size-correlated variation in E. tridentata

As noted in the above description, females of *E. tridentata* vary markedly in size and form and slightly in coloration. Some of this variation is correlated with size and since it is significant in terms of the bionomics of the bees it is detailed below.

Individual size has been judged according to head capsule width. Measurements of fore wing lengths were made but proved unnecessary since the ratio of fore wing length to head width remained approximately constant over a range of measurements.

With increasing size, the following changes occur.

(1) The head capsule becomes increasingly more quadrate, the inner orbits changing from slightly converging to slightly diverging below and the clypeus becoming wider relative to its length (cf. Figs 20, 21).

(2) The metasoma becomes relatively larger (especially in length). In the smallest females the apex of the metasoma does not extend beyond the tips of the reflexed fore wings whereas in the largest females it protrudes beyond them by about 1/3 of its length (cf. Figs 22, 23). This increase in relative size is not due to extension of the telescopic segments but reflects an increase in size of all the component parts including the sting.

(3) The latero-apical projections of the 6th metasomal tergum become relatively larger, more obtuse and further apart (cf. Figs 24, 25). This variation is quantified in Figure 30.

(4) The 1st metasomal tergum becomes increasingly more coarsely and deeply pitted and in the larger females the pits along

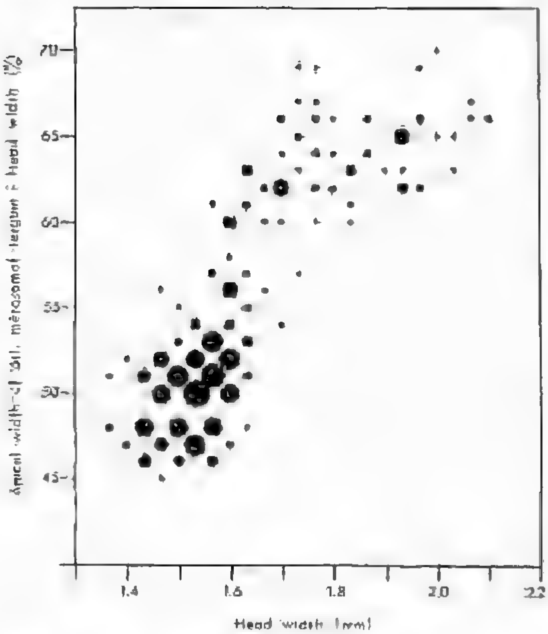


Fig. 30. Allometry in females of *Exoneura* (*Exoneurella*) *tridentata*. Scatter diagram showing how relative width of apex of sixth metasomal tergum increases with size of individual. The number of individuals represented by spots increases with their size in the order 1, 2, 3, 4, 5, 6–10, 11–15, 16–20 and 21–25.

the posterior margin coalesce to form an irregular emargination (cf. Figs 28, 29).

(5) The integument of the metasoma becomes relatively thicker and more brittle and the apodemes become relatively larger (cf. Figs 26, 27). The sturdier anterolateral apodemes are associated with relatively larger extensor muscles.

(6) Orange-brown patches with diffuse borders appear on the thorax and metasoma of medium and large females. They occur on the mesepisterna, mesosterna and anterior metasomal sterna. The larger the individual, the more extensive are the maculations.

(7) A small median spine develops from the gradulus of the 4th metasomal tergum in medium and large females.

This variation appears to be unique amongst allodapine bees and in the family Anthophoridae as a whole. Michener (1965*a*) discussed size variation amongst females of the social Australian bee, *Exoneura* (*E.*) *variabilis* Rayment. In this species, egg layers average larger than workers but no structural differences or allometry has been reported. The degree of size variation in this species is also less than in *E. tridentata*, the largest known females having head widths only 1.28x as great as the smallest females (cf. 1.54x in *E. tridentata*).

THE IMMATURES

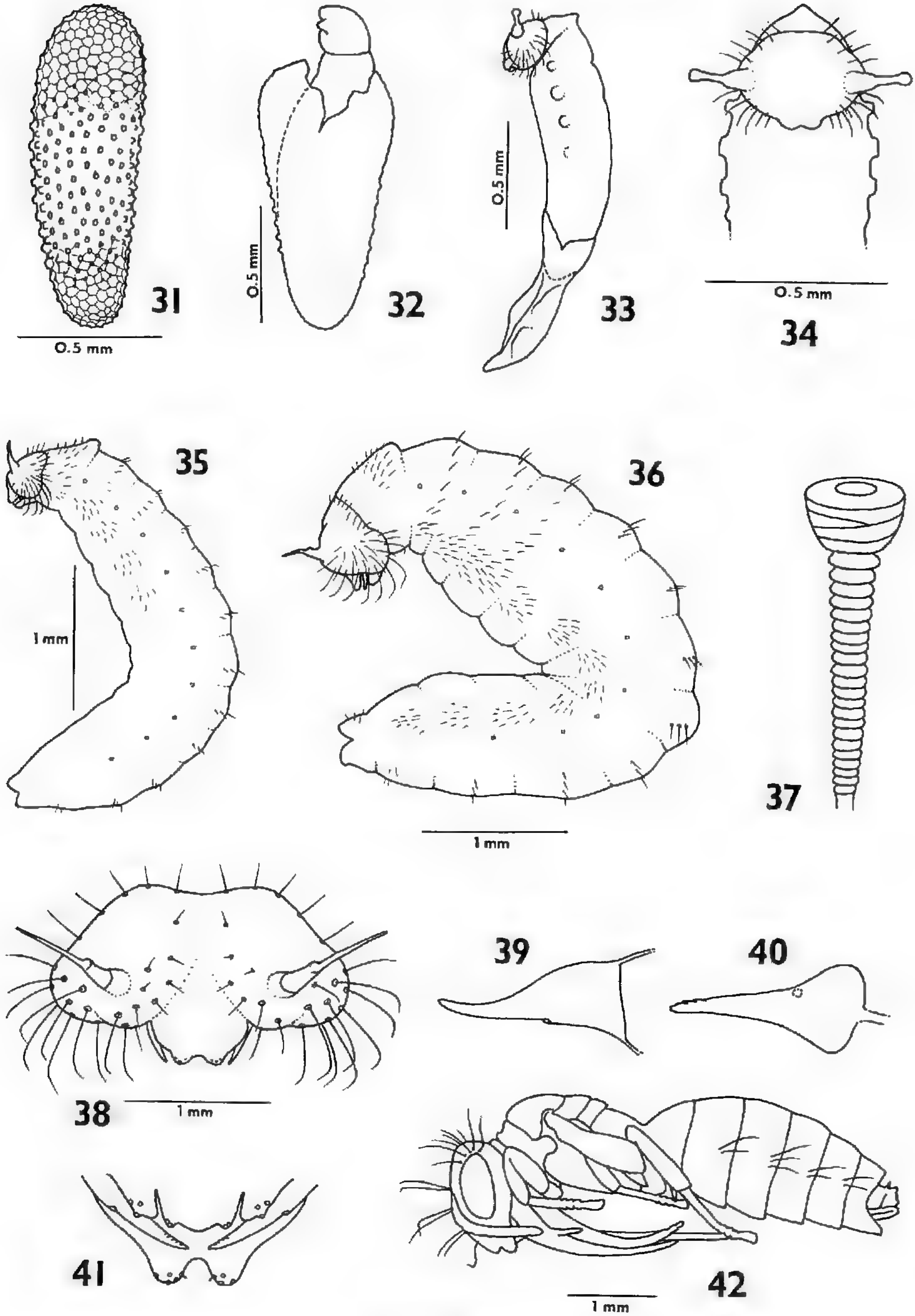
The immatures studied were preserved by dropping them live into either Kahle's solution or 75% ethyl alcohol and were stored in the latter.

Syed (1963) described 4 larval instars of *E. lawsoni* from preserved material and Michener (1964) described and figured live specimens of probable 2nd, 3rd and 4th instars as well as the egg, prepupa and pupa. However, the identity of the material studied and described by these authors is subject to a little uncertainty because a few of the nests from which it was derived have proven to belong to *E. setosa* (C. D. Michener—personal communication). Professor Michener confirms that the bulk of the adult material on which he based his 1964 studies is clearly *E. lawsoni* and in all probability the immatures described by him would be of the same species.

Four morphologically distinct larval instars can be recognised in each of the known species of *Exoneurella* without recourse to histograms of head width frequencies. Indeed, with *Exoneura tridentata* there is such marked size variation within each instar and such wide overlap in size between them that the histogram of head width frequencies was of no help at all in determining the number of instars.

The terminology employed in the following descriptions of larvae follows that of Michener (1953).

Figs 31–42. Immatures of *Exoneura* (*Exoneurella*) *eremophila*. Fig. 31.—Egg. Fig. 32.—First instar partly enclosed in chorion (left lateral view). Fig. 33.—Second instar with chorion still attached (left lateral view). Fig. 34.—Ventral view of head and fore body of second instar. Figs 35, 36.—Third and fourth instars, respectively (left lateral views). Fig. 37.—spiracle of fourth instar. Fig. 38.—Head of fourth instar (anterior view). Figs 39, 40.—Left mandible of fourth instar, anterior and ventral views, respectively. Fig. 41.—Mouthparts of fourth instar (posterior view). Fig. 42.—Female pupa (left lateral view).


31
0.5 mm
32
0.5 mm
33
0.5 mm
34
0.5 mm
35
1 mm
36
1 mm
37
38
1 mm
39
40
41
42
1 mm

FIGS 31–42

E. (E.) eremophila

Egg. (Fig. 31). About 1.1 mm long and 0.4 mm in maximum width; white, sausage-shaped and with a coarse reticulate sculpturing each end, the middle portion being tuberculate.

In some eggs from Queensland nests the sculpturing was weak or absent.

First instar.—(Fig. 32). Remains almost wholly within chorion; head of very simple form, lacking lateral lobes, antennae and setae; mouthparts hardly developed, lobe-like and probably non-functional; body sac-like without obvious segmental lines, tubercles or setae.

Second instar.—(Figs 33, 34). Chorion remains attached to abdomen; head relatively broader than in 1st instar but with no obvious lateral lobes; antennae well-developed, capitate and laterally directed; mouthparts well-developed and functional; head capsule with numerous moderately long setae; body without setae and distinct segmental lines but with 4 tubercles each side anteriorly and a middorsal tubercle on prothorax.

Third instar.— (Fig. 35). Entirely free of chorion; head relatively very broad with well developed ventrolateral lobes; antennae very slender and acute apically; body gently curved with distinct intersegmental lines, no anterolateral tubercles or ventrolateral swellings but prothorax with a distinct middorsal tubercle; anal slit moderately deeply incised; setae numerous on head and body, longest on ventrolateral lobes of head; patches of small setae occur dorsally and laterally on the prothorax, laterally on the following 4 segments and transverse rows of short stiff setae occur dorsolaterally on the 2nd to 12th body segments.

Fourth instar.—(Figs 36-41). Head relatively very broad with conspicuous ventrolateral swellings and slender acute antennae (Fig. 38); labrum bilobed apically with a few sensoria, not delimited from distinctly sunken clypeal region; mandibles slender apically with only a few minute spines subapically and a single sensorium ventrally (Figs 39, 40); maxillae shorter than labium, their palpi consisting of indistinct tubercles bearing a few sensoria (Fig. 41); labium bearing tubercle-like palpi latero-apically; body strongly bent at 5th abdominal segment (Fig. 36); prothorax with an obtuse mid-dorsal tubercle; intersegmental lines weak; ventrolateral body swellings absent; terminal segment of abdomen strongly laterally compressed with anal slit deeply incised; setation much as in 3rd instar but all body segments have ventrolateral patches of setae; atrial and primary tracheal openings of spiracles circular; atria without spines but with a few branching and anastomosing sculptural lines; subatria relatively long (Fig. 37).

Prepupa.—Similar to 4th instar except that the body is straight and swollen anteriorly.

Pupa.—(Fig. 42). Conforms essentially to features of the adult but the following special pupal structures were noticed: all coxae with ventro-apical spines (very short and inconspicuous on mid and hind coxae of females); vertex (across full width), interantennal area, upper, middle and lower clypeus with extremely long setae; 2nd to 5th metasomal segments also with 2 or 3 long setae each side; in some specimens the more apical metasomal terga bear a few tiny setae dorsally.

Material examined.—155 eggs, 109 larvae and prepupae and 46 pupae, New Kalamurina HS, S. Aust., 9-11.iii.1972, ex dead stems of *Myriocephalus*; 7 eggs, 48 larvae and prepupae and 2 pupae, 4.8 km W of Windorah, Qld, 17.iv.1969, ex dead stems of *Crotalaria*.

E. (E.) setosa

Egg.—(Fig. 43). About 1.0 mm long and 0.4 mm in maximum width; white, sausage-shaped and with a reticulate sculptural pattern (finer than that of *E. eremophila* eggs.)

First instar.—Not observed.

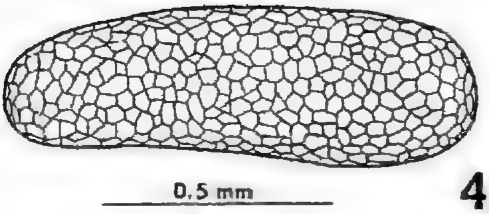
Second instar.—(Fig. 44). Similar to that of *E. eremophila* except that antennae are not capitate; 1st and 2nd body segments with a few small setae dorsally.

Third instar.—(Fig. 45). Similar to that of *E. eremophila* but with more distinct intersegmental lines and moderately developed ventrolateral body swellings. Of 4 specimens examined, 2 lacked dorsal abdominal setae and 2 slightly larger ones had setae on all but the terminal segment.

Fourth instar.—(Fig. 46). Generally similar to that of *E. eremophila* except as follows: intersegmental lines more distinct; ventrolateral swellings moderately developed; 5th abdominal segment slightly more protuberant dorsally; labial palpi situated more posteriorly on labium and further from apex.

Prepupa.—Like 4th instar but body straight and swollen anteriorly.

Pupa.—Generally similar to that of *E. eremophila* (allowing for differences correlated with



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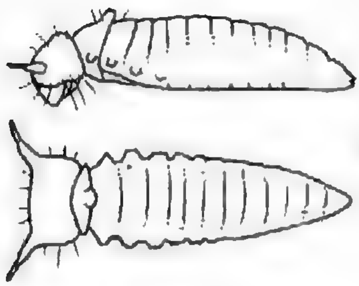

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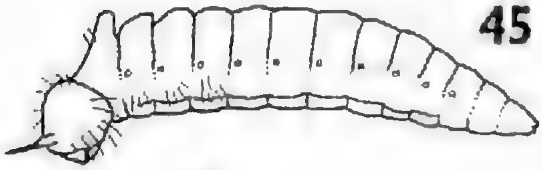

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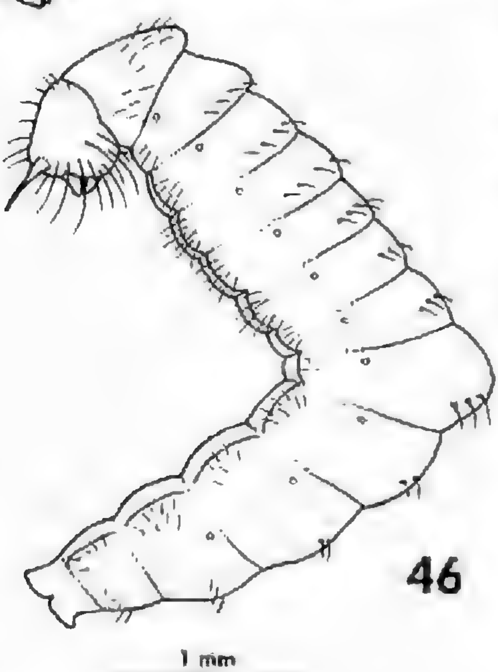

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Figs 43–46. Immatures of *Exoneura* (*Exoneurella*) *setosa*. Fig. 43.— Egg. Fig. 44.—Second instar in left lateral (upper) and dorsal (lower) views. Figs 45, 46.—Third and fourth instars, respectively (left lateral views).

adult form); 3rd to 5th metasomal terga with a few short setae dorso-apically.

Material examined.—21 eggs, 32 larvae and prepupae and 12 pupae, West Beach, Adelaide, S. Aust., Feb.–Oct. 1965, ex dead stems of *Euphorbia*; 14 eggs, 28 larvae and prepupae and 3 pupae, 4.8 km N. of Peregian Beach, Qld. 9.xii.1966.

E. (E.) tridentata

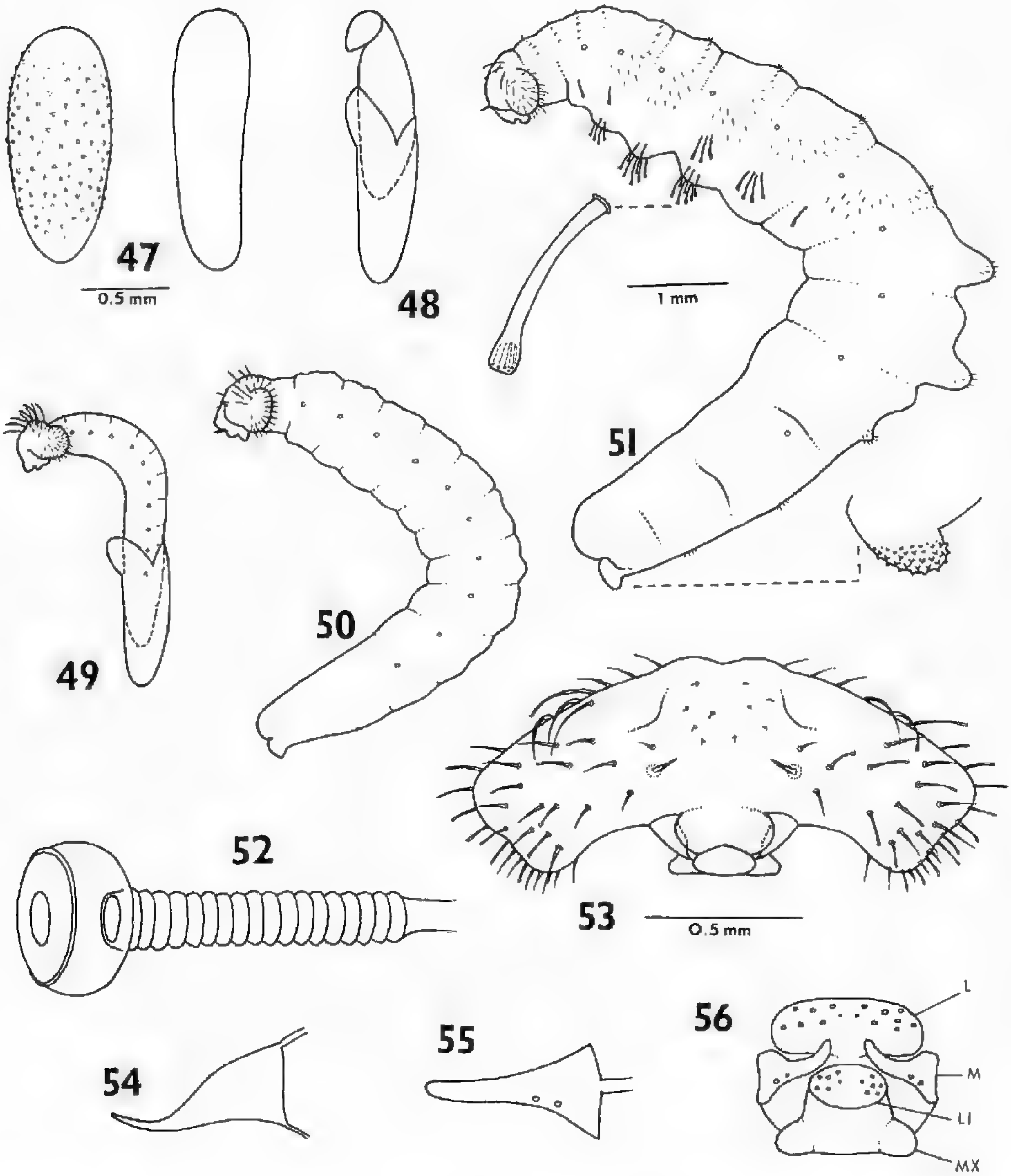
Egg.—(Fig. 47). Size variable ranging from 1.3–2.0 mm in length and 0.43–0.70 mm in maximum width; white, sausage-shaped to elongate ovoid; chorion entirely smooth to finely granular (except at the ends).

First instar.—(Fig. 48). Remains largely within chorion; head capsule smooth and appoximately circular in anterior view; antennae, mouthparts and setae absent; body sac-like without intersegmental lines, tubercles and setae.

Second instar.—(Fig. 49). Retains chorion on apex of abdomen; head broad with distinct lateral lobes which are usually reflexed against sides of prothorax; antennae absent; mouthparts developed and functional; body sausage-shaped, curved, lacking tubercles and with weak intersegmental lines; head with numerous setae, longest on vertex where they are thick throughout their length; body lacking setae.

Third instar.—(Fig. 50). Head relatively extremely broad with laterally extended lobes; antennae present, relatively short (compared with those of other *Exoneurella*) and medially directed; body curved, without tubercles (except dorso-apically on terminal segment) and with weak intersegmental lines; head with almost a complete covering of short blunt setae; body without setae.

Fourth instar.—(Figs 51-56). Head with exceptionally large quadrate lateral extensions (Fig. 53); antennae short, slender, acute and medially directed; labrum broad and bilobed with several sensoria ventrally (Fig. 56), not delimited from clypeo-frontal area; mandibles (Figs 54-56) slender, tapering and compressed apically, each with a pair of sensoria ventrally but lacking spines; labium rounded and lobe-like, bearing 2 patches of sensoria which may represent obsolescent palpi (Fig. 56); a transverse, laterally projecting lobe behind the labium probably represents degenerate maxillae (Figs 53, 56); body strongly bent at 5th abdominal segment which, like the 6th, bears a prominent dorso-median tubercle (Fig. 51); 7th abdominal segment with a small dorsal tubercle; terminal abdominal segment broad



Figs 47–56. Immatures of *Exoneura* (*Exoneurella*) *tridentata*. Fig. 47.—Eggs showing extremes of form and sculpturing. Figs 48, 49.—First and second instars with chorion attached (left lateral views). Figs 50, 51.—Third and fourth instars, respectively (left lateral views), with enlargements of capitate seta and spinose apical tubercle. Fig. 52.—Spiracle of fourth instar. Fig. 53.—Head capsule of fourth instar (anterior view). Figs 54, 55.—Left mandible of fourth instar in anterior and ventral views, respectively. Fig. 56.—Mouth parts of fourth instar (ventral view. L, labrum; LI, labium; M, mandible; MX, maxilla?). Figs 48–51 are drawn to same scale.

with a moderately large spinose tubercle just above the anus (Fig. 51); head with numerous short obtuse setae; body with short setae disposed in transverse bands on prothoracic to 4th abdominal segments and small dorsal patches on the 5th to 9th; relatively large thick capitate setae occur ventrally in clusters on the metathoracic to 2nd abdominal segments and singly or clustered laterally on the mesothoracic to 4th abdominal segments; spiracles (Fig. 52) not protruding above body wall; atrial and primary tracheal openings circular; atria subspheroidal without spines or other sculpture; subatria slender with about 18 annulations.

Prepupa.—Similar to 4th instar but body straight, swollen anteriorly and with reduced dorsal tubercles.

Pupa.—Similar to that of *E. eremophila* differing as follows. Head with fewer setae, a pair being situated low on the clypeus and several across the vertex, the more lateral ones being much longer than more medial ones; metasoma with short setae dorsally on segments 2-5 (females) and 2-6 (males) (in addition to the long lateral setae).

Material examined.—200+ eggs, 125 larvae and prepupae and 73 pupae, Lake Gilles National Park, S. Aust., 30.xii.1973-27.x.1974, ex dead stems of *Heterodendron oleifolium*.

Discussion

Regarding adult features, the 3 new species agree almost totally with the diagnosis of *Exoneurella* given by Michener (1965*b*, p. 223). The only points of disagreement relate to *E. tridentata*: in this species the eyes of males are conspicuously swollen, the apex of the 6th metasomal tergum of females is simple, not bifid, and the costal margin of the 2nd cubital cell of the fore wing of both sexes is at least as long as the 1st transverse cubital vein, not much shorter. In these respects *E. tridentata* is rather more like bees of the subgenus *Exoneura* than are other *Exoneurella*. It is also unlike its closest relatives in the constricted mandibles, angular genae, pronounced size variation and allometry of females.

Eggs of *Exoneurella* are unusual amongst those of allodapines (Michener 1973, p. 281) in having sculptured chorions. The sculpturing forms a delicate reticulum in *E. lawsoni* and *E. setosa*, fine granules in *E. tridentata* (absent in some specimens) and a combination of coarse reticulum and distinct tubercles in *E. eremophila*.

Similarities in larval form between the 4 species of *Exoneurella* correspond to similarities in adult form. Thus, larvae of *E. setosa* are most like larvae of *E. lawsoni* as described and figured by Michener (1964, pp. 422-424, figs 13-20) and larvae of *E. eremophila* differ from these 2 species in only a few minor features. On the other hand, larvae of *E. tridentata* are highly distinctive: the head capsule of 2nd to 4th instars is extraordinarily produced and quadrate laterally, the antennae are comparatively tiny, the maxillae and labium are strongly modified, 2nd instars lack lateral body tubercles but 4th instars have large dorsal tubercles on the 5th and 6th abdominal segments, spiny apical tubercles and peculiar thickened setae on the thoracic and anterior abdominal segments.

The features which will distinguish *Exoneurella* larvae from those of other groups are the following. Head capsule (of more mature instars) relatively broad with distinct hairy ventrolateral or lateral expansions; antennae (except in *E. tridentata*) of 2nd to 4th instars relatively long, slender apically, thickened basally and directed anterolaterally; no separation of clypeus and labrum; mandibles strongly tapered with slender simple apices; body of 4th instar conspicuously bent at 5th abdominal segment which protrudes dorsally; 3rd and 4th instars lacking lateral or ventrolateral extensions of body segments such as occur in other *Exoneura* (Syed 1963).

The pupae of *Exoneurella* differ from species to species in conformity with adult differences but otherwise are fairly uniform. Of the various specialized pupal structures occurring in Apoidea (Michener 1954) the only ones occuring in *Exoneurella* are long thick setae on the head and metasoma, fine short setae on the metasomal terga, and coxal spines. Michener (1964, p. 424) remarks on the absence of coxal and trochanteral spines in *E. lawsoni* but I have seen no material which could confirm this. Specific differences were noted in the number and arrangement of setae.

Exoneurella, originally established as a genus, was relegated to subgeneric status in Michener's (1965*b*) classification of Australian bees but has continued to receive generic status (Michener 1971, 1973). The taxon with its new additions remains distinctive and well defined. I consider it a purely arbitrary matter whether one recognizes it at generic or subgeneric level and have preferred to follow

Michener's (1965*b*) arrangement since it expresses the obvious affinity between *Exoneurella*, *Exoneura s. str.* and *Brevineura*.

Acknowledgments

I wish to thank my wife, Carol Houston, for assisting with collection of some of the material described below, Ms J. C. Cardale (ANIC) for providing some critical details of the type specimen of *Exoneura lawsoni*, and Professor C. D. Michener (KU) for advice concerning material used in his studies of *Exoneurella*.

Some of the material listed herein was collected during field work funded by the Royal Society of South Australia.

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FAULTING CONTEMPORANEOUS WITH UMBERATANA GROUP SEDIMENTATION (LATE PRECAMBRIAN), SOUTHERN FLINDERS RANGES, SOUTH AUSTRALIA

BY P. S. PLUMMER AND V. A. GOSTIN**

Summary

PLUMMER, P. S., & GOSTIN, V. A. (1976).-Faulting contemporaneous with Umberatana Group sedimentation (Late Precambrian), southern Flinders Ranges, South Australia. *Trans.* R. *Soc,* S. *Aust.* **100**(1), 29-37, 28 February, 1976.

Interglacial sedimentation within the Late Precambrian Umberatana Group (Adelaide System) was greatly influenced locally by contemporaneous faulting along the Spring Creek Mine Fault. Stratigraphic study both sides of the fault and of the fault zone has revealed a variable sequence of elastics and carbonates. Lithological correlation across the fault zone suggests two periods of faulting contemporaneous with deposition, followed by a phase of downwarping of the area north of the fault along a hinge line coinciding with the earlier fault zone. This activity resulted in a thickness increase of approximately 750 m in the sequence north of the fault when compared with that of the more stable sequence to the south. Three varieties of stromatolites occur within the area studied, displaying distributions which were influenced by varying water depths. Palaeoenvironmental interpretations based on vertical and lateral lithological associations, palaeocurrent analysis and studies of the contained stromatolites reveal that sedimentation south of the fault occurred within shallow marine, intertidal and supratidal environments resulting from the prevailing regional regressive-transgressive-regressive marine cycle. Modification of this cycle north of the fault zone was influenced by contemporaneous faulting.

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Palaeoenvironmental interpretations based on vertical and lateral lithological associations, palaeocurrent analysis and studies of the contained stromatolites reveal that sedimentation south of the fault occurred within shallow marine, intertidal and supratidal environments resulting from the prevailing regional regressive-transgressive-regressive marine cycle. Modification of this cycle north of the fault zone was influenced by contemporaneous faulting.

Introduction

This paper deals with Umberatana Group sedimentation in a region of contemporaneous faulting on the western flank of the Flinders Ranges, 12 km NNW. of Melrose (Fig. 1). This is in the southeast quadrant of the ORROROO 1:250,000 geological sheet mapped by Binks (1968). Deposits of the Sturtian and Elatina glaciations form the basal and capping components, respectively, of the Umberatana Group. The intervening period is represented by a variable sequence of clastic and carbonate sediments of non-glacigene origin (Thomson 1969).

The study area is divided by a fault zone into two subareas of differing stratigraphies. These reflect penecontemporaneous movement on the east-west Spring Creek Mine Fault (new name). The regional pattern of the area was one of a regressive-transgressive-regressive marine cycle, represented by the stratigraphy of the southern subarea (Fig. 7). However, fault rupture and subsequent subsidence north of the fault zone produced a short transgression within the initial regressive phase, but the main sedimentation cycle regained dominance as the sedimentation rate exceeded the rate of subsidence.

Time-stratigraphic relationships, as shown in Fig. 7, are based on the assumption that the fault zone can be interpreted as in Fig. 5. The nature of outcrop is not sufficent, however, to fully confirm this interpretation, and the possibility of complex fault slices of the stratigraphy contained within the fault zone is not discounted.

Stratigraphic nomenclature (Fig. 2) is that of Thomson *et al.* (1964) and Thomson (1969). Detailed geology is described in Plummer (1974)[1].

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[1] Plummer, P. S. (1974).—The stratigraphy, sedimentology and palaeoenvironments of Late Precambrian Umberatana Group in the Mount Remarkable-Alligator Gorge area, South Australia. Univ. Adel., unpublished Honours thesis.

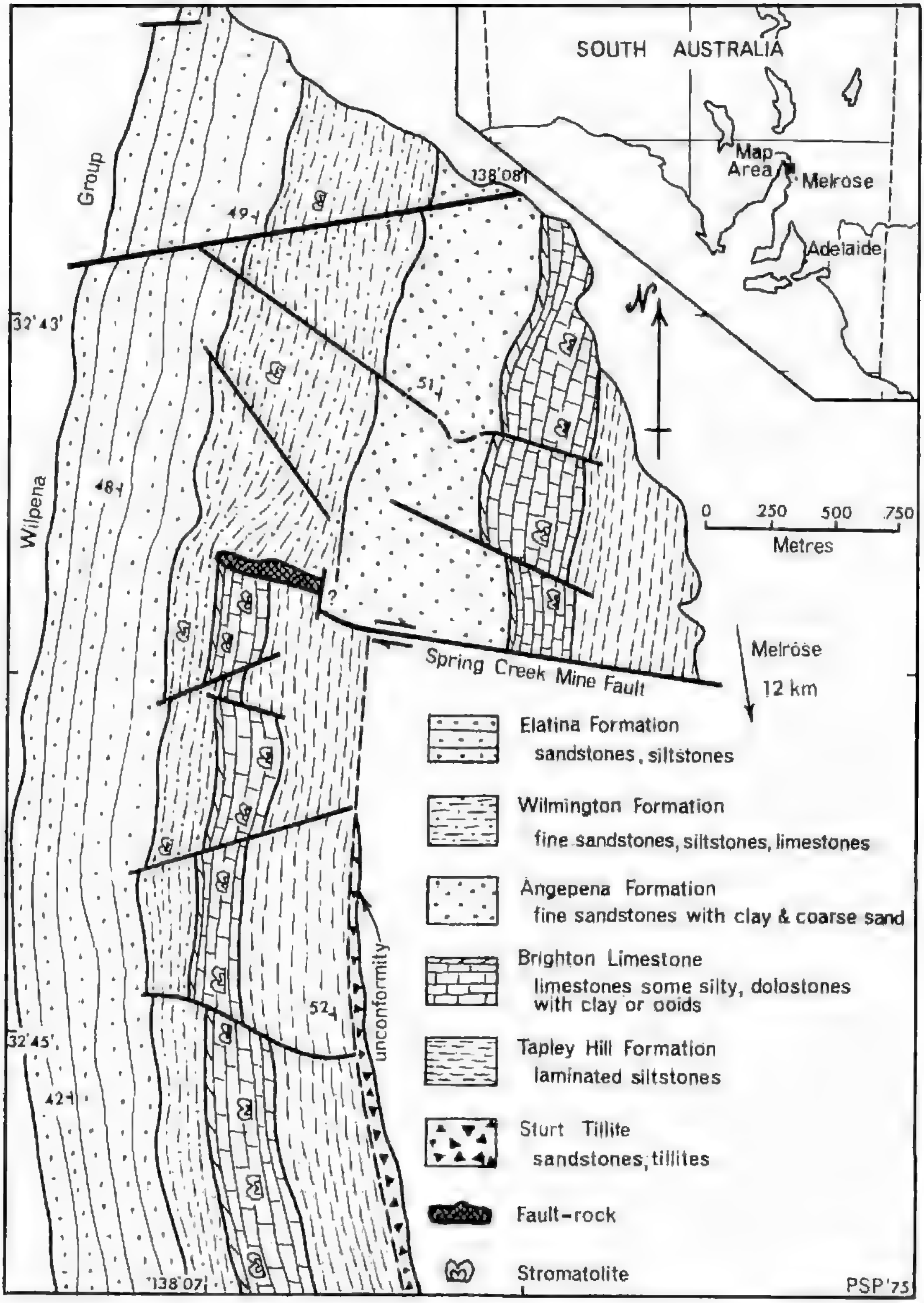

Fig. 1. Generalized geological map of the Umberatana Group in the study area.

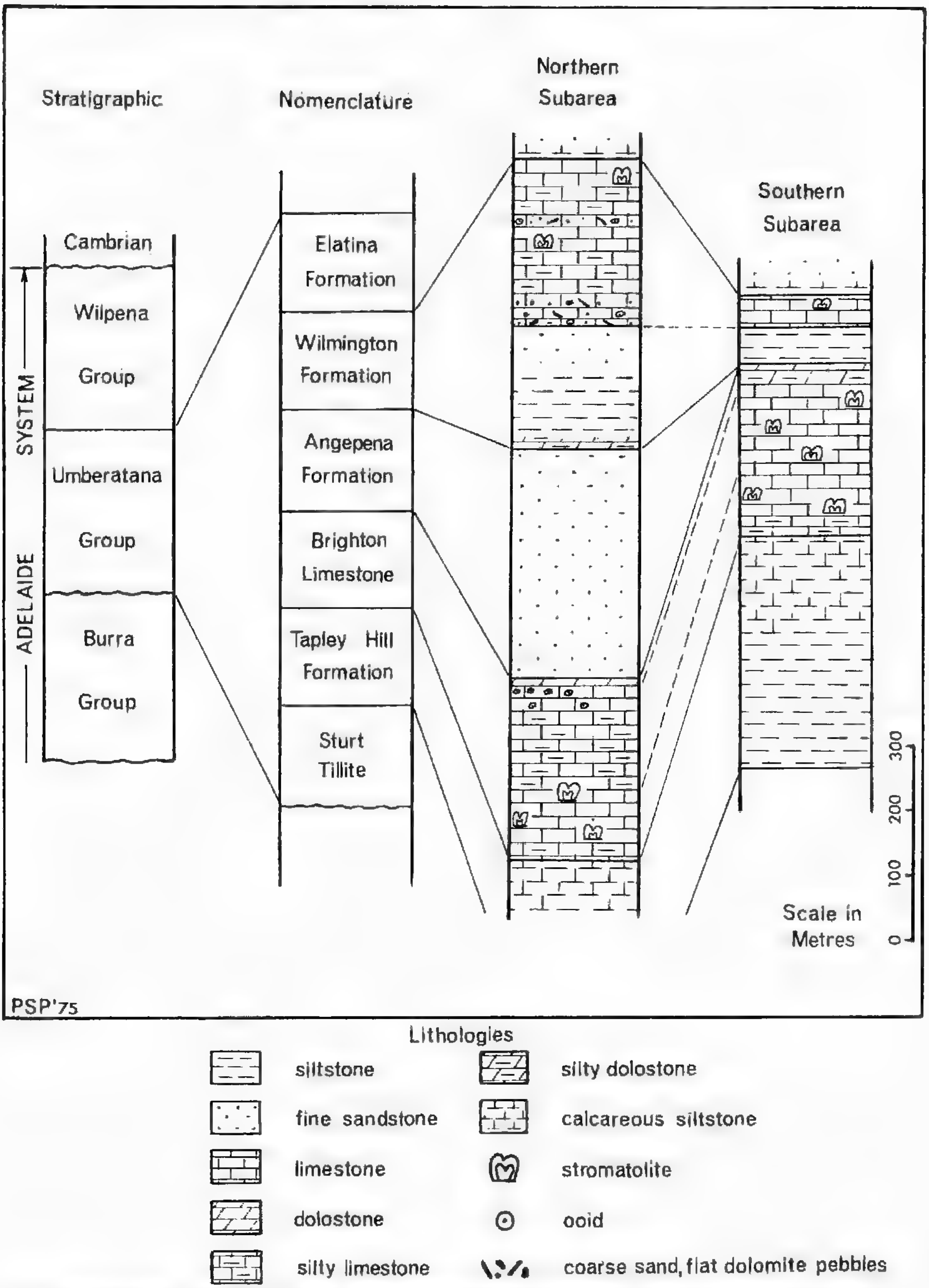

Fig. 2. Stratigraphic nomenclature and general stratigraphic columns of the two subareas divided by Spring Creek Mine Fault. Thickness variations controlled by subsidence north of the fault.

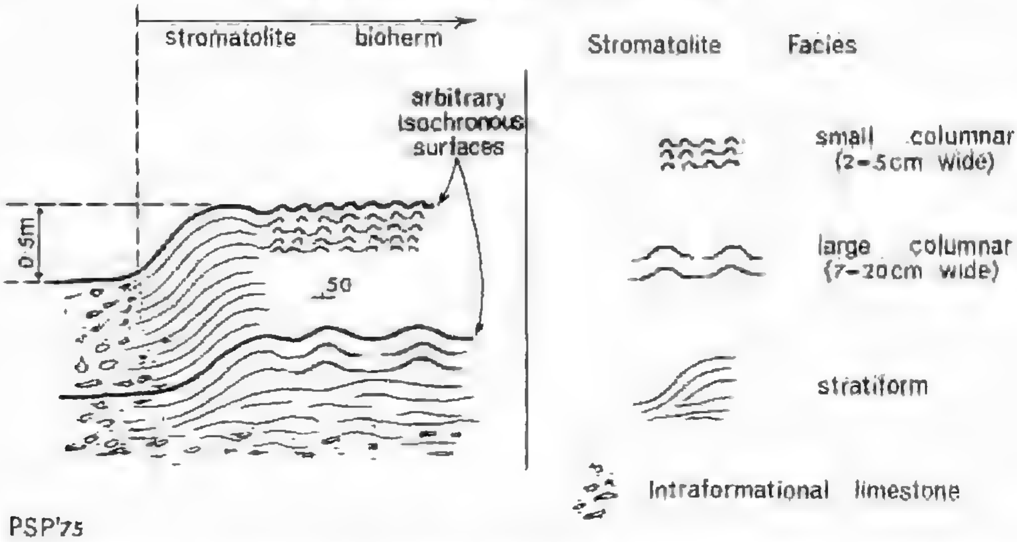

Fig. 3. Diagramatic facies sketch of the base and edge of a stromatolite bioherm, Middle Brighton Limestone, southern subarea.

Sedimentation prior to faulting

Following the Sturtian glaciation, interglacial sedimentation began in a marine basin below the wave base, outside the zone of carbonate deposition, and under reducing conditions. The resultant lithologies, namely black, finely laminated pyritic quartzose shales grading upward into well laminated dark grey quartzose siltstones, form the Tapley Hill Formation (Howchin 1904; Thomson *et al.* 1964). Gradually the sediment surface rose into the zone of carbonate deposition, resulting in an increase in carbonate content toward the top of this formation. Eventually carbonate became dominant as a well laminated dark grey silty limestone was deposited (basal Brighton Limestone—Howchin 1904). Above this, the presence of large dendroid branching stromatolites, set in a blue-grey limestone, testify to the basin floor rising above the level amenable to stromatolite growth. Current activity during this initial period of uniform sedimentation was minimal, the dominant direction initially being from the north-west, but later swinging to flow from the south-west (Fig. 6). A gradual increase in current intensity is suggested by the change from rare small cross-laminations (lower Tapley Hill Formation) to more common shallow ripple marks (basal Brighton Limestone).

Faulting with sedimentation

Movement along the Spring Creek Mine Fault ended Lower Brighton Limestone sedimentation and produced variations in lithologies across the fault. A sketch of the fault zone is shown in Fig. 5. Tentative correlations of rocks in this zone with adjacent lithologies suggest two periods of faulting (Fig. 7), the total stratigraphic throw being approximately 750 m. Fault-zones facies 1 (FF1)—a dark grey micritic limestone (brecciated in places), with stromatolitic limestone megaclasts (up to 0.5 m long) of the previously deposited Brighton Limestone—suggests initial rupture along the fault, whereas subsequent facies lacking megaclasts (and FF2 lacking brecciation) imply warping due to very gradual subsidence.

Southern Subarea

South of the fault, shallowing steadily continued. At, or just after the time of initial faulting, the blue-grey stromatolitic limestones of the preceding period grade slowly upward into massive deep reddish-purple intra-formational limestones containing abundant buff-yellow stromatolite bioherms, displaying large furcate to small digitate branching columns, as the sedimentation surface rose into the zone of wave agitation, oxygenation and tidal activity.

Within these bioherms, a zonation based on stromatolite morphology occurs (Fig. 3), suggesting a series of growth stages resulting from energy fluctuations within the depositional environment, indicating emergence of the bioherms through the intertidal zone in the following manner:

(a) basal stratiform mats trapped sediment forming a stable layer within the high-

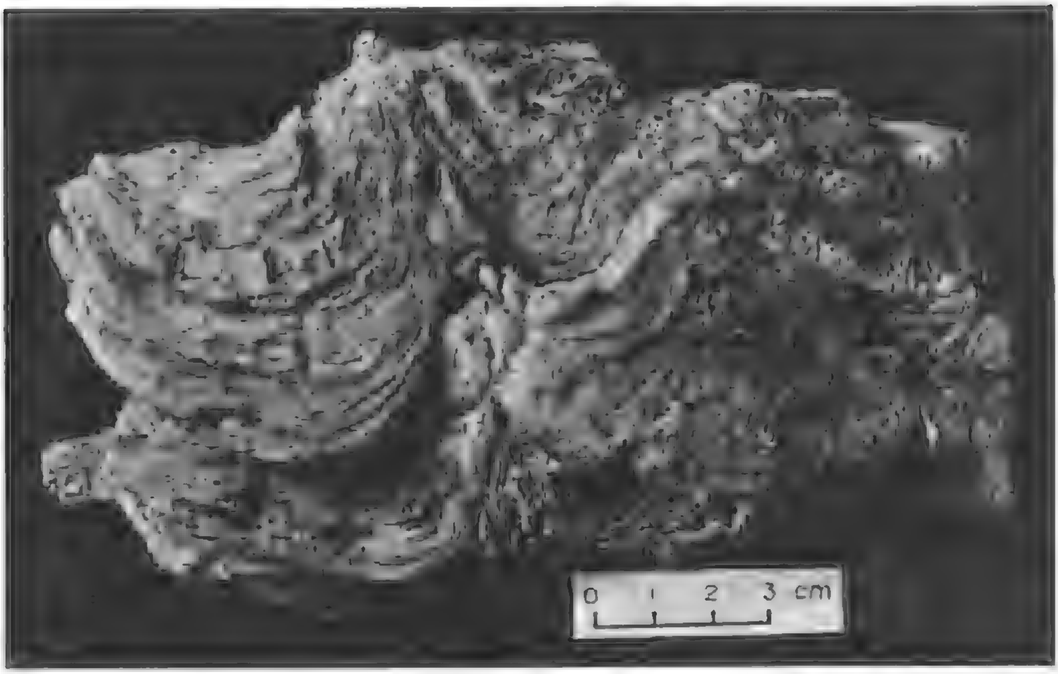

Fig. 4. Tepee structure, Upper Brighton Limestone, northern subarea.

energy subtidal to low intertidal zone;

(b) 'large' columns (7-20 cm wide) then developed within the lower to middle intertidal zone. Abundant carbonate flakes, originating from disruptive wave and tidal action, lodged between these columns;

(c) 'small' columns (2-5 cm wide) cap the bioherms in the high intertidal zone. Rare disruption of laminae, or an efficient drainage of debris from the intercolumn maze explains the relative lack of carbonate flakes in this zone; and

(d) stratiform layering on the bioherm flanks encasing both facies (b) and (c) enhanced drainage from the centre of the bioherm.

Fault-zone facies 2, a yellow dolostone, lacking brecciation and in places sandy, suggesting gradual subsidence and warping of the still soft sediment, and FF3, a brecciated pale yellow dolostone, were probably deposited during this period of stromatolite proliferation.

Continued shallowing then produced a supratidal environment of deposition and completed the initial regressive sequence of the interglacial period south of Spring Creek Mine Fault. A purple dolostone, with disrupted clay laminae and lenticular beds of quartz sand, caps the Brighton Limestone. Fault-zone facies 4 and 5—brecciated purple dolostones (with clay in the former)—are the time equivalents of this unit, although north of the fault these two facies possibly represent the time equivalents of two very different lithologies (uppermost Brighton Limestone and Angepena Formation).

Northern Subarea

At the time of initial rupture along Spring Creek Mine Fault. the northern block was downthrown below the depth amenable to stromatolite growth, yet remaining within the zone of carbonate deposition, resulting in flaggy grey limestones bearing a minor quartz silt fraction. The thickness (125 m), and uniformity of this unit is a result of equivalent rates of subsidence and sedimentation. Rare large scale ripple marks (wavelength 50 cm, amplitude 8 cm) and cross-bedding (up to 2.5 m per set with foreset slopes between 15° and 40°), plus the more abundant small scale current-ripples and cross-stratification, suggest an increase in current activity attributed to the change in seafloor topography. Palaeocurrent analysis reveals several modes as shown in Fig. 6. Rare lenticular outcrops of grey stromatolitic and purple intraformational limestones

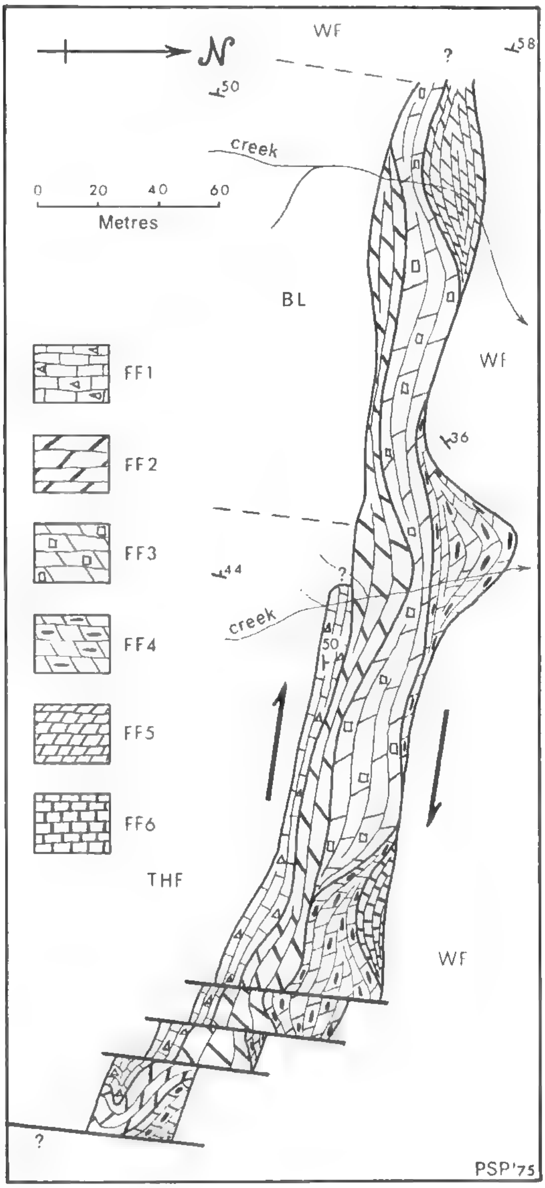

Fig. 5. Facies sketch map of the fault zone, Spring Creek Mine Fault.
FF1: dark grey micritic limestone with some megaclasts, brecciated in places
FF2: yellow dolostone, sandy in places.
FF3: brecciated pale yellow dolostone.
FF4: brecciated purple dolostone with clay.
FF5: brecciated purple dolostone.
FF6: grey silty limestone.
Formation symbols as in Fig. 7.

suggest that the depths of oxygenation, agitation and stromatolite growth were almost juxtaposed.

Above this unit a change in colour and lithology suggests shallowing of the basin to an oxygenated wave agitated depositional environment, within which a 20 m thick unit was deposited. This unit exhibits facies variation from pink dolomitic oolites with birdseye structures, and sandy dolostones near the fault grading northward into white limestones with dolomite flakes, generally graded within trough cross-beds, and rare ooids. A gentle palaeoslope northward away from the fault is therefore suggested. A supratidal environment followed, depositing a 5 m thick purple dolostone with clay laminae exhibiting tepee structures (Fig. 4) in the vicinity of the fault. This unit, possibly equivalent to fault-zone facies 4 (and ? 5), caps the Brighton Limestone north of Spring Creek Mine Fault as does its counterpart to the south. It therefore appears that supratidal deposition occurred uniformly over the entire area at this time, suggesting a temporary quiescence of fault activity (Fig. 7).

These purple dolostones were overlain by 350 m of the greyish-red fine sandstones of the Angepena Formation (Thomson 1969). These contain abundant purple clay laminae providing excellent bedding plane partings revealing a wealth of ripple marks and both polygonal and sinuous mudcracks. Lenses of coarse-grained rounded sand are common, often graded and draped with clay. These sedimentary structures typify a vast tidal flat to distal fluviatile depositional environment. The abundance of desiccation cracks, some reaching 1 cm in width, favours a non-marine influence. Palaeocurrent analysis reveals a dominant easterly drainage pattern with minor southern and western components (Fig. 6).

This dominantly regressive sequence north of Spring Creek Mine Fault was then overlain by the transgressive grey-green deposits of the lowermost Wilmington Formation (Thomson 1969). Siltstone pillows in dolostone are overlain by grey slightly calcareous siltstones with chloritic wavy laminae, ripple marks and rare sinuous mudcracks. These in turn are overlain by a massive grey calcareous siltstone bearing pillow structures, slump beds and lenticular beds of olive green-brown oolitic limestone. A very shallow, yet wholly submerged environment is therefore suggested. Fault-zone facies 6, a grey silty limestone, is possibly the equiva-

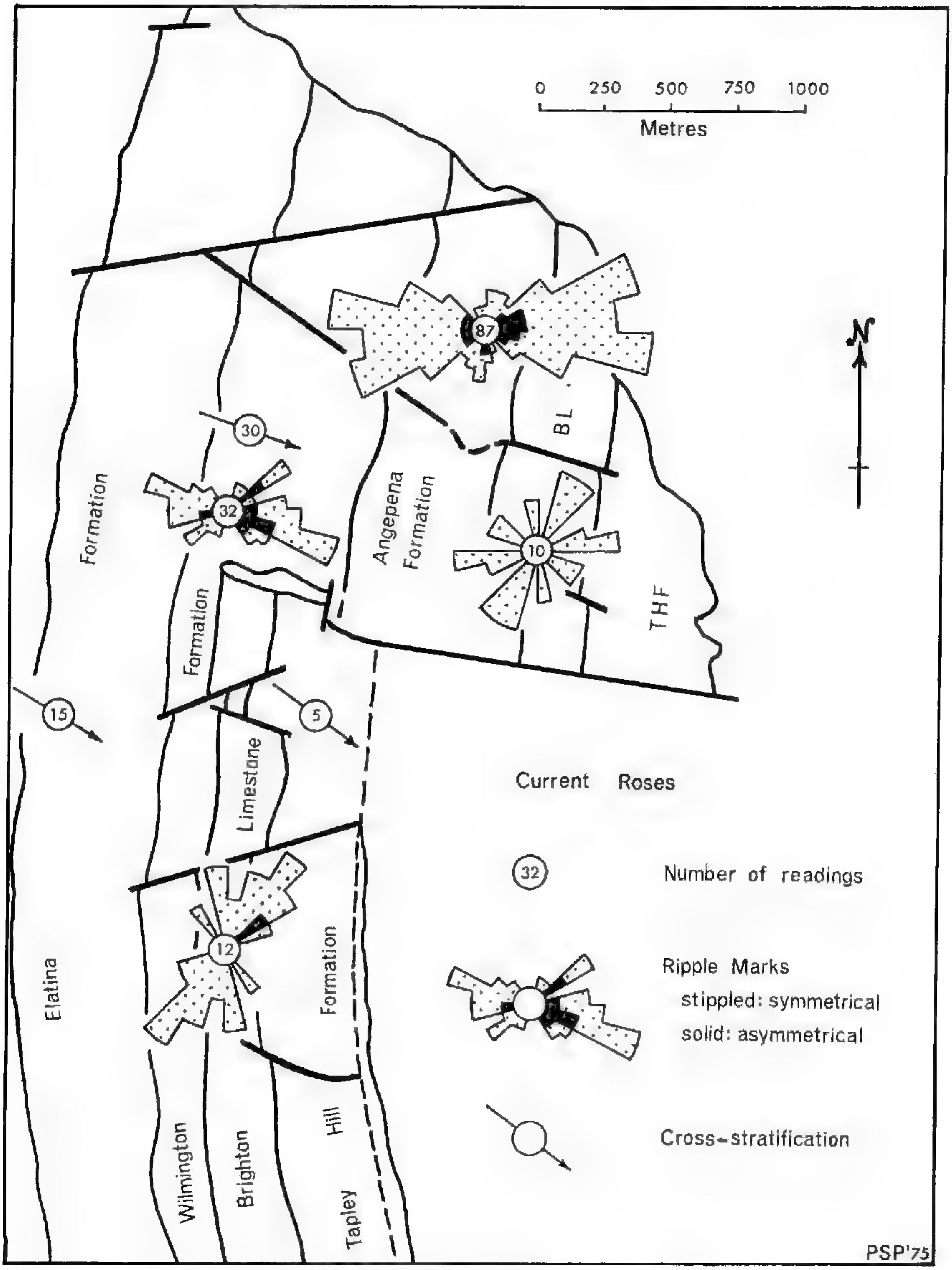

Fig. 6. Palaeocurrent analysis of the Umberatana Group in the study area.

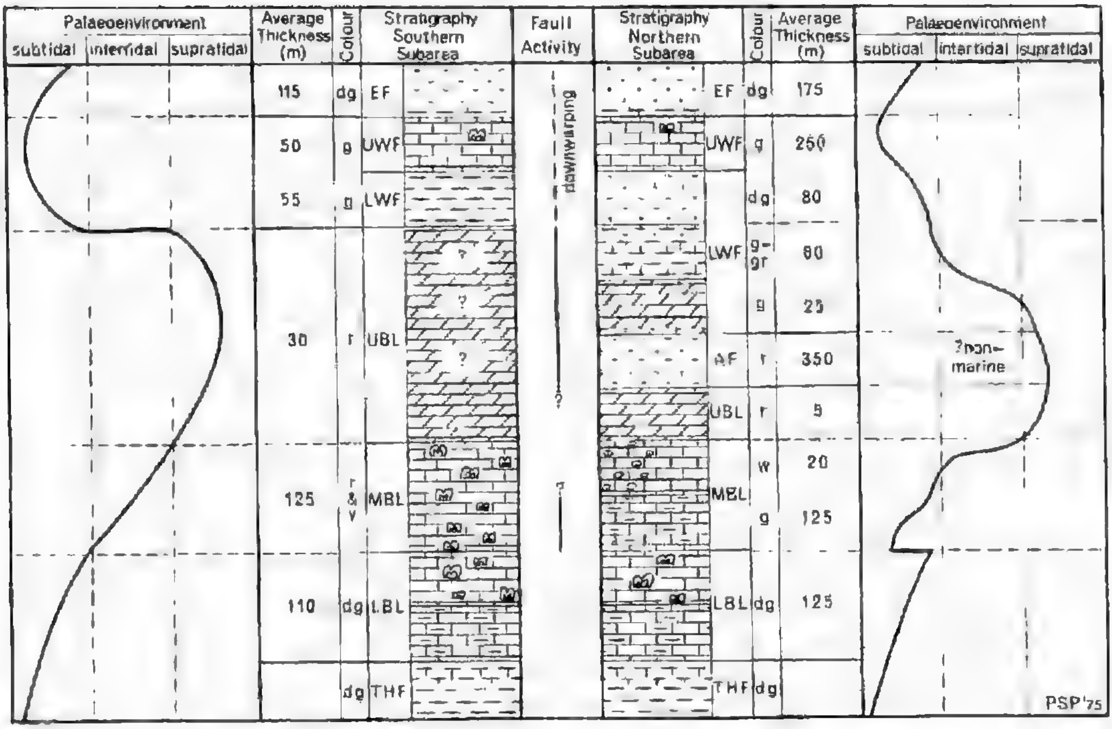

Fig. 7. Time-stratigraphic summary chart of lithologies, fault activity and palaeoenvironments. Lithologies as in Fig. 2. THF: Tapley Hill Formation; BL: Brighton Limestone; AF: Angepena Formation; WF: Wilmington Formation; EF: Elatina Formation; L: Lower; M: Middle; U: Upper; dg: dark grey; g: grey; gr: green; r: red and purple; w: white and pink; y: yellow.

lent of this period, and represents the final phase of faulting (Fig. 7).

South of the fault, the Angepena Formation and the two lower parts of the Wilmington Formation are absent. The contact between the Upper Brighton Limestone and the Lower Wilmington Formation is nowhere visible. It is suggested that either an hiatus in deposition occurs between the Upper Brighton Limestone and Lower Wilmington Formation, or alternatively the Upper Brighton Limestone deposition continued in a restricted, slightly elevated environment, whilst to the north the much thicker Angepena Formation and the two lower units of the Wilmington Formation were laid down.

Continued warping

Deposition was dominantly terrigenous as Spring Creek Mine Fault evolved from a zone of separation of the two subareas into a flexure with more marked subsidence of the northern subarea. The fault zone was still a major influence of Wilmington Formation sedimentation as facies changes and thickness variations occurred above, or immediately adjacent to it. Massive dark grey very fine sandstones overlain by brown fine and medium sandstones of the lower Wilmington Formation grade southward into flaggy grey siltstones supporting the palaeocurrent data of a west-north-westerly source area. Widespread slumping and cross-bedding within included sandstone beds imply a palaeoslope (possibly submarine deltaic) away from this source region.

The ensuing calcareous member of the uppermost Wilmington Formation (herein regarded as the equivalent of the Trezona Formation of Thomson *et al.* 1964) represents the maximum transgressive phase of deposition. Flaggy grey silty limestones and massive grey, in places stromatolitic, limestones in the south thicken rapidly north of the fault zone (by up to 5 times) and interdigitate with a buff coarse sandy cross-bedded limestone bearing ooids and imbricated dolomite intraclasts. The repetitive nature of this interfingering, which commences directly above the fault zone (Plummer 1974[1], Fig. 10), probably resulted from fluctuating rates of sedimentation and subsidence within a shallow sea.

The final regressive coarsening upward sequence of laminated siltstones to fine and coarse sandstones suggest prograding deltaic sedimentation. Ripple marks, cross-bedding and some slide-slump bedding support a west to east palaeoslope, (Fig. 6). Capping the Umberatana Group are the massive purple siltstones of the Elatina Formation bearing (?ice-rafted) erratics. Equivalents of these siltstones elsewhere in the Flinders Ranges are distinctly glacigene in origin (Elatina glaciation of Mawson 1949).

Conclusion

Stratigraphic study south of the Spring Creek Mine Fault reveals that a regressive-transgressive-regressive cycle of marine sedimentation took place during the deposition of the interglacial portion of the Late Precambrian Umberatana Group. The sedimentary structures and presence of stromatolites within these sediments indicate that environmental conditions ranged from shallow subtidal, through intertidal to supratidal, then back to a shallow subtidal environment.

To the north of the Spring Creek Mine Fault, two periods of faulting contemporaneous with deposition caused water depth fluctuations during the initial period of shallow subtidal deposition, then rapid shallowing through intertidal and supratidal conditions to a marginal marine (possibly distal floodplain) environment. This faulting and later subsidence hinged along the fault zone, caused a 750 m thickening of the succession to the north of the fault.

Acknowledgments

The authors wish to thank Dr B. Daily for critical examination of this text and helpful discussion in the field. Acknowledgment is also made to the Australian Research Grants Committee for supporting the research of Dr V. A. Gostin.

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SMALL FOSSIL VERTEBRATES FROM VICTORIA CAVE, NARACOORTE, SOUTH AUSTRALIA IV. REPTILES

BY MEREDITH J. SMITH

Summary

SMITH, Meredith J. (1976) .-Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. *Trans.* R. *Soc. S. Aust.* **100**(1), 39-5 1, 28 February, 1976.

Reptile fossils have been found at Naracoorte, South Australia, in a Pleistocene cave deposit that is rich in marsupial and rodent remains. Reptile vertebrae are abundant and a few jaws and limb bones have been recovered. The diagnostic features of these bones are described.

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The remaining species is a boid snake, described here as a new genus and species, *Wonambi naracoortensis.* The eight vertebrae recovered are large, suggesting a length of at least 5 m for the whole snake. Morphologically, the vertebrae differ strongly from those of other Australian boids in having a high but back-sloping neural spine, paracotylar foramina present, accessory processes absent, and, particularly, in having large paradiapophyses that extend further laterally than the zygapophyses. These vertebrae closely resemble those of *Madstoia bai* Simpson from the Eocene of Patagonia, but without cranial remains of both species, no relationship can be postulated between *Wonambi* and *Madstoia.*

SMALL FOSSIL VERTEBRATES FROM VICTORIA CAVE, NARACOORTE, SOUTH AUSTRALIA
IV. REPTILES

by MEREDITH J. SMITH

Summary

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Reptile fossils have been found at Naracoorte, South Australia, in a Pleistocene cave deposit that is rich in marsupial and rodent remains. Reptile vertebrae are abundant and a few jaws and limb bones have been recovered. The diagnostic features of these bones are described.

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Introduction

The reptile faunas of Australian fossil deposits have rarely been completely analysed. For some deposits, the presence of unidentified reptiles has been noted (e.g. Archer 1974, Dortch & Merrilees 1971, Gill & Banks 1956, Lundelius 1963); for other deposits, the most distinctive species have been identified, but often to genus only (e.g. Merrilees 1968; Thorne 1971). Exceptions are the carpet snake, *Python variegatus* (=*Python spilotus variegatus*) associated with the extinct marsupial, *Thylacoleo* sp., and other marsupial remains at Marmor Quarry, Queensland (Longman 1925) and the sleepy lizard, *Trachydosaurus rugosus*, at Gore Limestone Quarries, Queensland (Longman 1945). Remains of a large extinct varanid lizard, *Megalania prisca*, have been found in Pleistocene deposits in Queensland, New South Wales and central Australia (Fejervary 1918, 1935; Hecht 1975).

The deposit in Victoria Cave at Naracoorte, South Australia, is probably of Pleistocene age (Smith 1971). Among the large animals, extinct species are common (van Tets & Smith 1974; Wells, pers. comm.), but, in contrast, the small marsupials and small birds are referrable to modern species, though not all of them occur in the Naracoorte area now (Smith 1971, 1972; van Tets & Smith 1974).

For identifying reptile species, characteristics of skull fragments, jaws and teeth are of less value than they are for mammals. As reptiles grow throughout life and are polyphyodont, the "adult" dention cannot be defined as it can in mammals. The variations in dentition between species in many genera is no greater than within species. Fortunately the vertebrae of reptiles are of diagnostic value and Auffenberg (1963) was able to identify single vertebrae of North American snakes to genus and often to species. Diagnostic vertebral characters have

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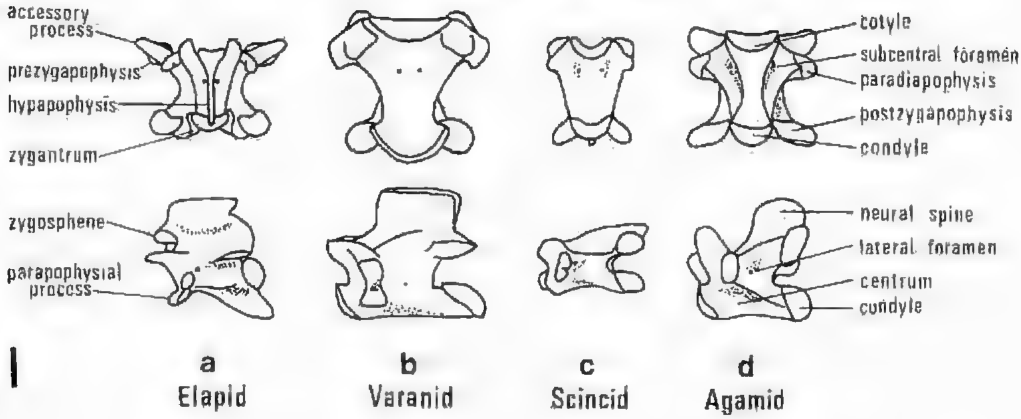

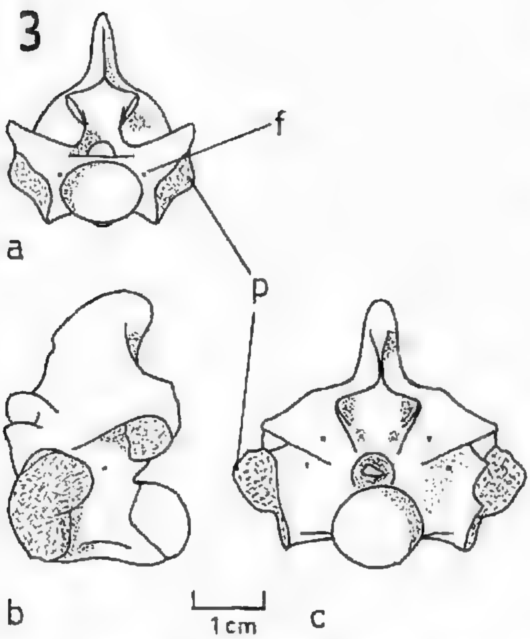

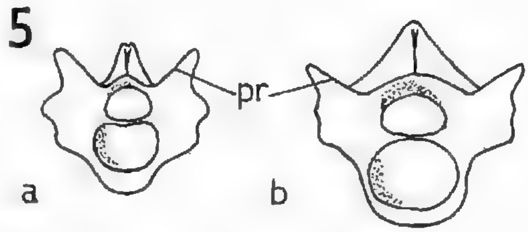

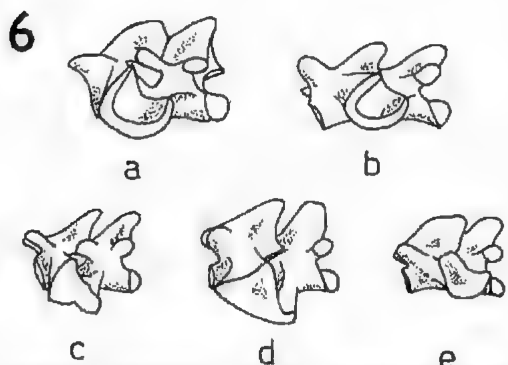

Fig. 1. Ventral (above) and lateral views of precaudal vertebrae of (a) *Pseudonaja nuchalis* (Elapidae), (b) *Varanus gouldii* (Varanidae), (c) *Tiliqua occipitalis* (Scincidae), (d) *Amphibolurus barbatus* (Agamidae).

Fig. 3. Vertebrae of *Wonambi naracoortensis* are distinguished by their wide paradiapophyses (p) and presence of paracotylar foramina (f) as seen in (a) anterior view of P16144k and (b) lateral, and (c) posterior view of P16144s.

Fig. 5. The prezygapophysial facets are less upturned in *Trachydosaurus rugosus* (b) than in *Tiliqua nigrolutea* (a).

Fig. 6. Distally, the fused sacral pleurapophyses are cup-shaped in *Trachydosaurus rugosus* (a) and *T. occipitalis* (b) but are triangular in *T. nigrolutea* (c), *T. scincoides* (d) and *Egernia cunninghami* (e).

not been established precisely for any Australian snake species (Smith 1975). Fossil remains of lizards include not only skull bones and vertebrae but also some limb bones and some elements of pectoral and pelvic girdles. These are briefly described, and their diagnostic values assessed in this paper.

Methods

Methods of collection and preservation follow Smith (1971).

The present maximum depth of excavation is 80 cm, although bone chips occur in cores taken as deep as 2.5 m.

TABLE 1

Some dimensions of the holotype (P16168) and the seven paratype vertebrae of Wonambi naracoortensis *(Dimensions in mm)*

	Specimen							
	P16168	P16170a	P16166	P16129t	P16144k	P16144s	P16167	P16170b
Length between zygapophyses	16.5	15.4	18.1	16.4	19.3	21.8	23.4	19.6
Height (centrum + neural spine)	32.3	34.1*	40.8*	33.1	38.4	37.1	41.0	36.2
Width across prezygapophyses	25.6	21.1	27.7	25.8	30.4	33.0	35.5	29.5
Width across paradiapophyses	28.5	22.3	29.7	27.7	33.2	41.1	43.7	33.0
Minimum width of centrum	18.6	15.9	21.2	19.1	22.7	24.1	27.1	21.8
Width of zygosphene	9.2	8.4	11.8	9.3	12.6	10.9	12.4	11.3
Width of condyle	10.8	8.2	10.6	10.3	12.6	12.3	12.7	12.4
Length of prezygapophysis	8.1	6.1	7.5	7.4	8.9	11.8	12.8	10.9

* Height includes length of hypapophysis.

Skull and jaw elements of all but the most robust species were rarely recovered from the Victoria Cave deposit, whereas vertebrae were common. Consequently, for the diagnosis of reptile species in this fauna, vertebrae have been considered in detail and other bones more briefly. Comparisons have been made with dry, disarticulated skeletons, and occasionally with cleared, alizarin-stained whole specimens.

Descriptive terms (Fig. 1) follow Auffenberg (1963). The "length" referred to in descriptions of vertebrae is the greatest distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis (Pr-Po of Smith 1975). The ranges of lengths are given, with mean and standard error. Measurements were made to the nearest 0.1 mm, with dial-reading, needle-point calipers. The fossil specimens are lodged in the South Australian Museum (SAM).

Results

Family BOIDAE

Boid vertebrae lack parapophysial processes, the accessory processes are very short or absent and the vertebrae lack hypapophyses on the posterior two thirds of the precloacal column (Hoffstetter & Gasc 1969).

Wonambi n. gen.

Definition: Vertebrae characterized by a high, backwardly-sloping neural spine; slightly upturned zygapophysial facets; large paradiapophyses extending laterally beyond the zygapophyses; and a pair of paracotylar foramina.

Type species: Wonambi naracoortensis

Content: W. naracoortensis is the only known species in the genus.

"*Wonambi*" is derived from an aboriginal name for the mythical rainbow serpent (Elkin 1964).

Wonambi naracoortensis n. sp.

Holotype: SAM, P16168. A dorsal vertebra collected in Fossil Chamber, Victoria Cave, Naracoorte, S. Aust., at a depth not greater than 30 cm below the surface of the cave earth.

Definition: The same as for the genus *Wonambi* until other species are described.

Description: The neural spine is high (Fig. 2C); its anterior edge begins near the rim of the zygosphene and rises obliquely to the horizontal dorsal edge of the spine. The spine overhangs slightly posteriorly. The zygosphene is narrow (Table 1) but it is so heavily thickened that it is as deep in dorsoventral extent as it is broad. The zygosphenal facets are almost vertical (c. 70° to horizontal) (Fig. 2D). The relatively small zygapophyses are slightly upturned (c. 25° from horizontal). Accessory processes are completely absent. The paradiapophyses are large (Table 1); the upper part of the articular facet is convex and protrudes so far from the centrum that the maximum width of the vertebra is the width measured across the paradiapophyses; the lower part of the articular facet is flat. The cotyle and condyle are slightly depressed (Fig. 2A) and the top of the condyle is tilted forwards at c. 75° to the vertical. The ventral surface of the centrum is smoothly rounded, with weak subcentral ridges and a low median ridge that terminates posteriorly as a blunt haemal keel, notched in the midline (Fig. 2B).

Each foramen of the subcentral pair is located close to the median ridge at about mid-centrum; each foramen of the lateral pair lies on the neural arch pillar about halfway between paradiapophysis and postzygapophysis. There appear to be two pairs of parazygantral foramina, but, as the bone is pitted in this region,

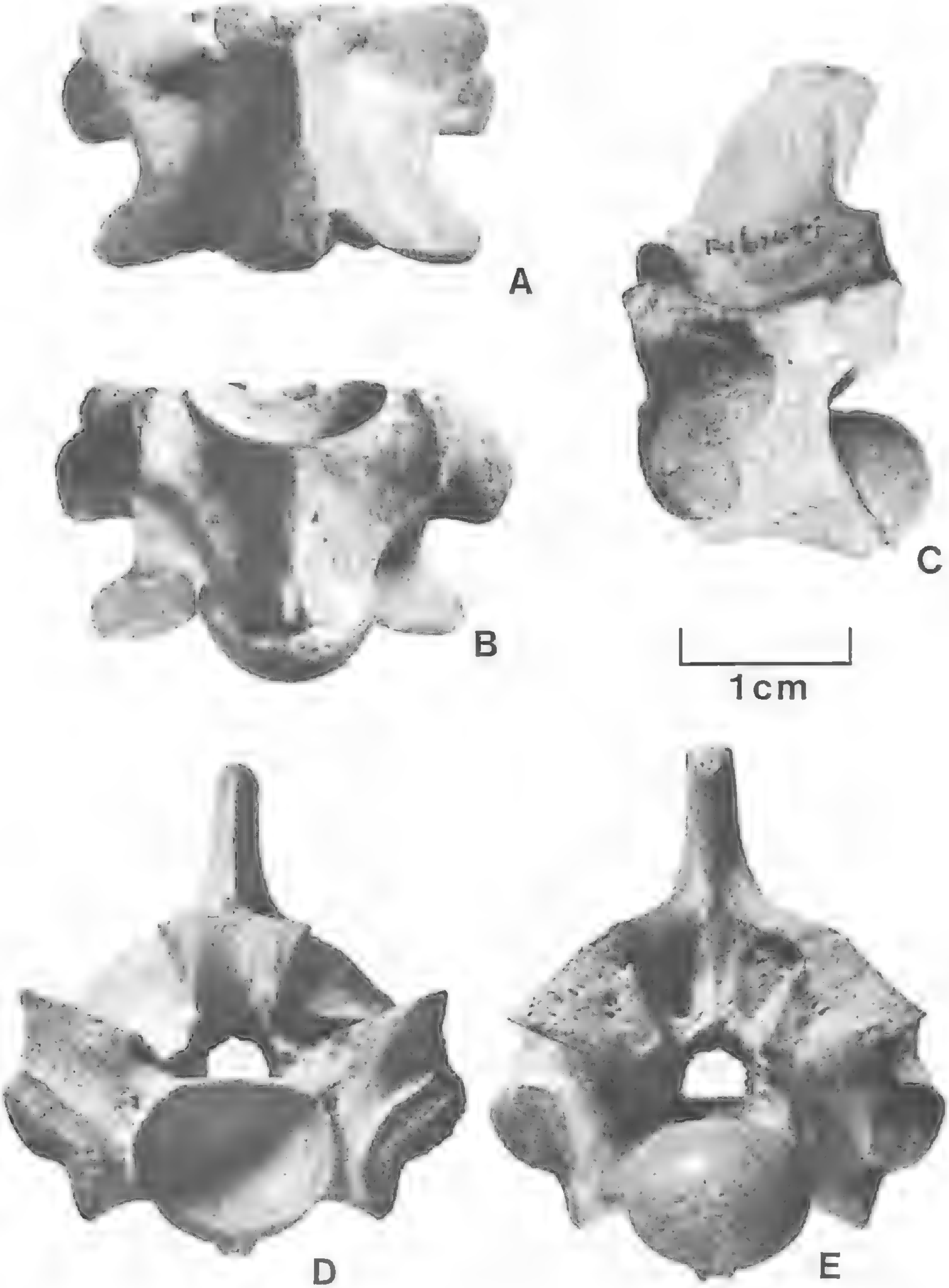

Fig. 2. The holotype of *Wonambi naracoortensis* (P16168) in dorsal (A), ventral (B), lateral (C), anterior (D), and posterior (E) views.

foramina are distinguished with difficulty from pits. The two foramina of a paracotylar pair lie close to the rim of the cotyle near the top of the centrum.

Variation: The paratype series consists of seven dorsal vertebrae: P16129t, P16144k,s, P16166–7, and P16070a, b all but one of which were found in the top 30 cm of the cave earth of Fossil Chamber, Victoria Cave. All specimens share with the holotype the diagnostic features, especially the widely spaced paradiapophyses (Table 1, Fig. 3). The parazygantral foramina consist of a single pair which are sunk into hollows in P16129s, P16167 and P16170b; and in P16144k the single pair of zygantral foramina can be seen clearly. The haemal keel is notched posteriorly in P16129s, P16167 and P16170b (as in the holotype), these vertebrae having occurred nearer the tail than the others, as judged from their lower neural spines. P16166 bears a small hypapophysis, and P16170a a longer hypapophysis.

Associated material: A fragment (P16170c) from near the anterior end of a left maxilla with three teeth, curved backwards. Each tooth is approximately 7 mm long.

Assuming that P16167 represented the largest vertebra of the specimen of *Wonambi naracoortensis*, and assuming that the largest vertebrae of *W. naracoortensis* and *Python spilotus*, respectively, occupy the same proportion of the length of the vertebral column, then P16167 would have been derived from a snake of total length about 5.0 m.

Comparison with other species: Of the eight Australian species of Boidae, vertebrae of *Python spilotus* (4 specimens), *P. amethistinus* (2), *Liasis childreni* (1), *Chondropython viridis* (1) and *Aspidites melanocephalus* (3) have been examined.

The vertebrae of these extant boids are characterized by the presence of small, pointed, accessory processes beneath the prezygapophyses, by having large outwardly-directed zygapophyses extending further laterally than the paradiapophyses (Table 2) and the neural spine hatchet-shaped, and by the absence of paracotylar foramina. Subcentral ridges are strongly developed. The general shape of the vertebra is similar among all the species (Tables 2, 3). *Chondropython viridis* differs in having the neural spine bifurcate anteriorly.

Python spilotus and *P. amethistinus* resemble each other in having a pair of foramina at the base of the neural spine, while *Aspidites melanocephalus*, *Chondropython viridis* and *Liasis childreni* lack this pair of foramina.

Wonambi naracoortensis differs from all other Australian boids in lacking accessory processes, in having the neural spine sloping backwards, in having weak subcentral ridges, and in the presence of paracotylar foramina. It shares with *Aspidites melanocephalus*, *Chondropython viridis* and *Liasis childreni* the absence of foramina at the base of the neural spine. The total height (relative to length) of the vertebrae is greater in *W. naracoortensis* than in other Australian boids, the paradiapophyses extend further laterally than the zygapophyses, the condyle (relative to vertebra length) is wider and the zygosphene (relative to vertebra length) is narrower (Table 2). On the other hand, width across prezygapophyses, minimum width of centrum, and length of prezygapophysis (all relative to vertebra length) fall within the ranges of the extant species, as does height/width of condyle (Table 3).

Paracotylar foramina are generally absent in extant boids, and occur only in the genera *Constrictor* and *Tropidophis* (Boinae) and *Enygrus* (Erycinae) (Hoffstetter & Gayrard 1964). They are found, usually as two pairs, in the fossil genera *Gigantophis* and *Madstoia* (Hoffstetter 1961a, b), and as a single pair in *W. naracoortensis*.

Whereas the lengths of vertebrae of *Wonambi naracoortensis* (relative to width across prezygapophyses) fall within the ranges of those of the extant Australian boids, including *Liasis* (Table 3), six vertebrae from the Wellington caves of New South Wales were longer than vertebrae of *Liasis* (Lydekker 1888, p. 256).

There is a striking resemblance between *Wonambi* vertebrae and those of *Madstoia hai* (Palaeocene-Eocene of Patagonia) and *M. madagascariensis* (Cretaceous, Madagascar) (Hoffstetter 1961a, Simpson 1933), particularly in the back-sloping neural spine, broad paradiapophyses and absence of accessory processes. Hoffstetter (1961a, b) included *Madstoia* and *Gigantophis* (from the Eocene of Egypt; Andrews 1906) in a sub-family Madstoiinae. The diagnostic features were: (a) accessory processes absent; (b) a pair of parazygantral foramina present and opening into deep hollows; and (c) paracotylar foramina always present, usually as two pairs. The two genera were distinguished by the form of the ventral surface of the centrum, *Gigantophis* having an undivided haemal keel, and *Mad-*

stoia having the haemal keel distinctly divided into two. All *W. naracoortensis* vertebrae conform with character (a) and differ from other boids, all of which have accessory processes (Hoffstetter 1961a); and the more posterior vertebrae conform with (b). However all the vertebrae have distinct parazygantral foramina (even though they emerge through the characteristic deep hollow only in the posterior vertebrae) and such foramina in modern boids are minute, irregular and inconstant (Hoffstetter 1961a). *W. naracoortensis* vertebrae differ slightly from (c) in having a single pair of paracotylar foramina, but their presence at all is rare in boids (Hoffstetter & Gayrard 1964). The form of the ventral surface of *W. naracoortensis* vertebrae ranges from hypapophysis present (P16166) or haemal keel undivided (P16129t, P16144k), to haemal keel notched (P16168) and finally to haemal keel distinctly divided (P16129s and P16167); thus it encompasses the form of both *Madstoia* and *Gigantophis*. *Madstoia* differs from *Gigantophis* also in the greater development of neural spines and paradiapophyses (Simpson 1933). In these features *W. naracoortensis* closely resembles *Madstoia*.

When *Madstoia* was compared with many boids, both recent and fossil, the resemblance of *Madstoia* to *Gigantophis* was found to be closer than to other known genera. However it was impossible to conclude that the two were definitely more closely related to each other than to other fossil boids (Simpson 1933). Similarly the relationship of *Wonambi* to *Madstoia* or any other boid will remain obscure until the skull is known.

The presence of *Madstoia* in Patagonia and Madagascar has been regarded as evidence of former continuity of the southern continents (Hershkovitz 1972, p. 316).

Family ELAPIDAE

Elapid vertebrae have conspicuous accessory processes and hypapophyses on all precloacals (Fig. 1).

Pseudonaja c.f. P. nuchalis Gunther

Material: Vertebrae (566 precloacal, 25 caudal); dentaries (6).

The vertebrae have been described (Smith 1975). The largest with a length of 11.1 mm between zygapophyses would have been derived from a snake about 190 cm long.

The dentary of *P. nuchalis* is almost straight posteriorly, but anteriorly it curves outwards then inflects sharply. The teeth are strong and curve backwards very slightly. They are separated by a distance equal to c. 2/3 of the adjacent teeth. The second tooth is the longest but the succeeding teeth along the dentary decrease in size only slightly. The fossil dentaries are similar.

Notechis c.f. N. scutatus (Peters)

Material: Vertebrae—precloacal (13, length 6.3–9.9 mm, mean 7.6 ± 0.35).

These vertebrae differ from *P. nuchalis* and resemble *N. scutatus* in having a relatively short neural spine overhanging both anteriorly and posteriorly (Smith 1975).

Pseudechis c.f. P. porphyriacus (Shaw)

Material: Vertebrae—precloacal (55, length 4.1–9.5 mm, mean 6.3 ± 0.13); maxillae (2); dentary (1).

Both *Notechis* and *Pseudechis* have 3–5 small teeth, whereas *Pseudonaja* has 8–10 (Worrell 1963; pers. observ.). A left maxilla (P16164a) bears a curved fang, followed after a diastema, by three small, curved teeth and is consistent with *P. porphyriacus* in size and shape. A smaller fragment of a right maxilla (P16164b) is probably from the same skull, having been taken from the same sample.

P. porphyriacus dentaries differ from *P. nuchalis* and *N. scutatus* dentaries in being more sharply curved anteriorly; the teeth are fine, backwards-curving and closely-set. A right dentary (P16132c) conforms with *P. porphyriacus*.

The vertebrae have the long, acute, accessory processes (Smith 1975) typical of *P. porphyriacus* but they differ in having these processes directed more anterolaterally than in the *P. porphyriacus* available for comparison.

Undetermined

An unidentified elapid group contains 40 vertebrae (length 3.8–7.8 mm, mean 6.0 ± .15) characterized by the short, blunt hypapophysis.

Family VARANIDAE

Varanid vertebrae are distinguished by the overhanging condyle (Fig. 1).

Varanus varius (Shaw)

Material: Vertebrae—cervical (4, lengths 18.7–26.3 mm, mean 21.35 ± 1.76), dorsal (17, lengths—Table 4), sacral (3), caudal (26, lengths 7.9–19.2 mm, mean 12.3 ± .53); maxilla (1); dentaries (5); parietal (1).

The dorsal vertebrae of *Varanus giganteus* are readily distinguished by their broad centra [ratio of width across prezygapophyses (Pr–Pr) to minimum width of centrum (BW) ≤ 1.6 (Table 4)] and long neural spines, vertical both anteriorly and posteriorly. But the vertebrae of *V. varius* and *V. gouldii* are similar morphologically—there is overlap in the relative width of centrum, relative width of condyle (CW) and relative width across prezygapophyses (all relative to the length, Pr–Po) and also in the ratio of width across prezygapophyses to minimum centrum width (Table 4). These values overlap even when the comparison is made between vertebrae from the same position in the column. The neural canal, viewed from the front, is slightly depressed in *V. gouldii* but is round in *V. varius*.

The fossil dorsal vertebrae are consistent with both *V. varius* and *V. gouldii* in their proproportions and have the neural canal round anteriorly, as in *V. varius*.

Like the dorsals, the cervical and caudal vertebrae of *V. varius* and *V. gouldii* are almost (or quite) indistinguishable as to species, but the first sacral vertebrae are distinctive. The transverse processes of the first sacral of *V. gouldii* (2 specimens examined) bear several low ridges— one such ridge from the anteriormost point of the lateral surface of the transverse process extends towards the cotyle; a diagonal ridge passes from the prezygapophysis to the lateral postero-dorsal tip of the transverse process and a ridge from the lateral antero ventral tip of the transverse process to the condyle makes the posterior surface of the transverse process slightly concave. In contrast, the transverse processes are smoothly-rounded and convex in *V. varius* (3 specimens examined). Similarly in the fossils (P16135r, P16169a) the transverse processes are smoothly rounded. The fossil conforms with *V. varius* and differs from *V. gouldii* also in having the neural canal round anteriorly and the transverse processes at their lateral extremities flared to below the level of the centrum (whereas in *V. gouldii* the flaring extends more dorsally).

In *Varanus varius* the parietal foramen lies in the middle third of the length of the parietal plate (Mertens 1942), whereas in *V. gouldii* and *V. giganteus* it is in the anterior third (pers. observ).

Laterally compressed, recurved, pleurodont teeth with striated bases are characteristic of varanids (Edmund 1969). The teeth of *V. giganteus* are fine and thin, but in *V. varius* and *V. gouldii*, and in the fossils, the lateral compression is less extreme, and a labial and a lingual ridge ascend each tooth. The basal fluting extends about 1/3 of the way up the tooth.

The length of the larger fossil first sacral vertebra (18.8 mm Pr–Po) indicates a total length of c. 1.6 m for the animal.

Varanus gouldii (Gray)

Material: Humerus (1).

The shaft of the humerus is smoothly rounded in *V. varius* (2 specimens) but in *V. gouldii* (3 specimens) a distinct ridge extends from the proximal termination of the supinator crest to a muscle scar (presumably for the humeroradialis muscle) near the proximal expansion. Anteroventrally, the deltopectoral crest is prominent in both *V. varius* and *V. gouldii*, but in *V. gouldii* the crest extends further proximally than in *V. varius*. The fossil humerus (P16146b) conforms with *V. gouldii* and differs from *V. varius* in having a ridge extending proximally from the supinator crest and apparently also in the proximal development of the deltopectoral crest, although most of the proximal articular facet of the fossil humerus has been lost. The fossil has a distinct tubercle at the proximal termination of the supinator crest. Such a distinct tubercle was seen only in one modern specimen of *Varanus* species, viz. a very large *V. gouldii*. No tubercle could be distinguished in two *V. gouldii* comparable in size with the fossil, nor in two *V. varius*.

Family SCINCIDAE

In scincid vertebrae the centrum tapers, in ventral outline, from broader anteriorly to narrower posteriorly, and there is no precondylar constriction. The ventral surface of the centrum is smoothly rounded (Fig. 1).

Trachydosaurus rugosus (Gray)

Material: Osteoderms (several hundred); vertebra—cervical (10, lengths 5.2–7.0 mm, mean 6.0 ± 0.21), dorsal (46, lengths 6.1–10.7 mm, mean 8.9 ± 0.17), sacral (5 pairs), pygal (6, lengths 6.7–10.0 mm, mean 8.0 ± 0.53), caudal (5, lengths 5.0–7.0 mm, mean 6.3 ± 0.37); maxillae (5); premaxillae (2); dentaries (6); humeri (3); femur (1); frontals (2).

Osteoderms: In *Trachydosaurus*, the osteoderms are thick and coarsely pitted, whereas in *Tiliqua nigrolutea*, *T. occipitalis* and *T. scincoides* the osteoderms are thinner and finely pitted; in *Egernia cunninghami* the dorsal osteoderms bear a posterior median tooth; and in

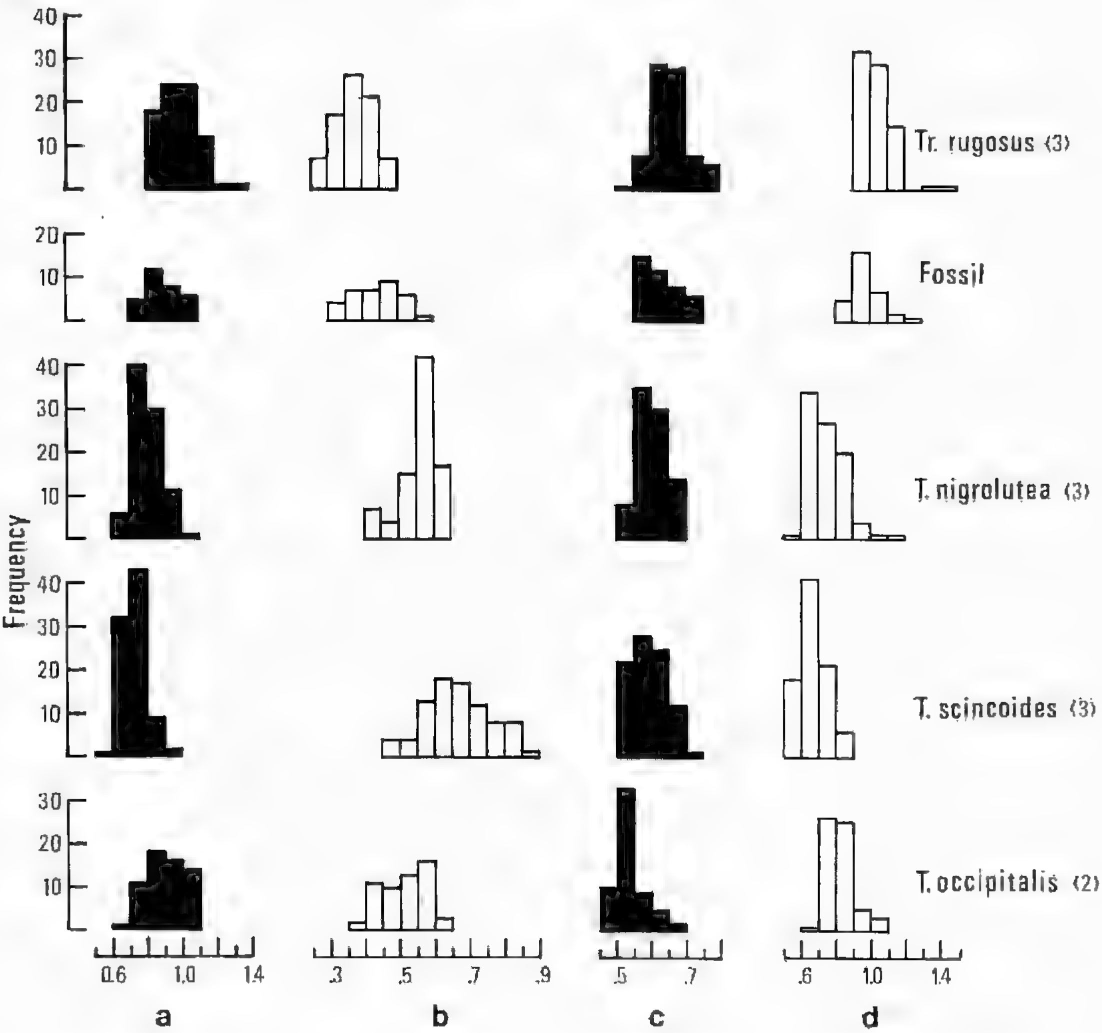

Fig. 4. Frequency distributions of some dimensions of dorsal vertebrae in which *Trachydosaurus rugosus* differs from *Tiliqua* species. The sample of fossil vertebrae assigned to *T. rugosus* has frequency distributions similar to the modern sample. (a) width across prezygapophyses divided by length between zygapophyses, (b) width across prezygapophyses divided by maximum width across paradiapophyses, (c) width of condyle divided by width across postzygapophyses, (d) height of condyle divided by width of condyle. Although the number of presacral vertebrae without a hypapophysis is 30–32, not all vertebrae could be measured in every specimen.

most other skinks the osteoderms are thin and almost smooth, except over the head of some.

Cervical vertebrae: Cervical vertebrae of scincids have the hypapophysis sutured or fused to the posterior part of the centrum whereas in agamid cervical vertebrae the hypapophyses are sutured or fused to the anterior part of the centrum (Hoffstetter & Gasc 1969). Cervicals of *Trachydosaurus rugosus* have broad, roundish zygapophysial facets whereas in *Tiliqua* species and *Egernia* species the zygapophyses are usually anteroposteriorly elongated and narrow.

Dorsal vertebrae: Cervical vertebrae are defined as those anterior to the first vertebra of which the rib joins the sternum (Hoffstetter & Gasc 1969), but because this distinction cannot be applied to isolated vertebrae, I have included in the discussion of dorsal vertebrae all the presacral vertebrae that do not bear a hypapophysis. Dorsal vertebrae of *T. rugosus* are squarish in dorsal outline, i.e. the width across the zygapophyses approximately equals the length between the zygapophyses, whereas dorsals of *Tiliqua* species are longer than wide (Fig. 4a). In other skinks also, and even in the largest Australian skink, the heavily-built *Egernia bungana* (only one specimen examined), the vertebrae are longer than wide. In *T. rugosus* vertebrae, the neural spine is low, slopes backwards and overhangs posteriorly. At its posterior termination, the neural spine is thickened and marked by a short median groove. The pre-zygapophysial facets are directed dorsally at an angle to the horizontal of about 20–40° (although in the anterior 3 or 4 dorsals the angle may be as great as 60° in some specimens (Fig. 5)). The prezygapophysial facets extend laterally nearly as far as, or further than, the paradiapophysial convexities (Fig. 4b). The zygapophysial facets are almost round in contrast with the outwardly directed zygapophyses of agamids. The condyle is narrow (Fig. 4c) and slightly depressed (Fig. 4d). Except for the neural spine and slight zygapophysial ridges, the centrum is smoothly rounded, again in sharp contrast with agamids where not only are the lateral ridges strong, but also a wide midventral ridge is conspicuous (Fig. 4d). The ventral surface of the centrum is triangular in *T. rugosus* (as in agamids) whereas in other skinks, ventrally the sides of the centrum are almost parallel behind the paradiapophyses.

Sacral vertebrae: The pleurapophyses of the sacral vertebrae are fused distally for about one third of their length. The facet for articulation with the ilium is cupped and differs from the triangular facets of *Tiliqua* species (except *T. occipitalis*) and *Egernia* species (Fig. 6). In *T. occipitalis* where the lateral articulation is cupped (as in *T. rugosus*), the zygapophysial facets are sharply upturned, at an angle of about 40–50°, as in other *Tiliqua* species, whereas in *T. rugosus* the facets are only slightly upturned (angle c. 20°). The condyle is narrower in *T. rugosus* than in *Tiliqua* species.

Caudal vertebrae: T. rugosus caudals are robust and the transverse processes project only slightly ventrally, much less ventrally than in *T. scincoides*, *T. occipitalis* and *T. nigrolutea*.

Teeth and tooth-bearing bones: The teeth of *Trachydosaurus* resemble those of *Tiliqua* species in having conical tips, whereas teeth of *Egernia* species are laterally compressed at the tips (Mitchell 1950). Usually the teeth of *T. rugosus* are broad and blunt, but in some specimens the teeth are longer, thinner and sharper. These latter overlap in form with those of the larger *Tiliqua* species. In *T. gerrardii* one tooth in each jaw is very large, about four times the thickness of the others, which are fine, with rounded tips. The maxillary bone of *T. rugosus* is robust. Beneath the orbit, a strong bone ridge runs parallel to the jaw margin and extends posteriorly beyond the level of the end of the tooth row. In *Tiliqua* species, this ridge is weaker and shorter, not extending beyond the end of the tooth row, and often ending still more anteriorly. The dentaries, too, are robust, and are thicker and deeper, especially anteriorly, near the symphysis, than are those of *Tiliqua* species.

Frontals: Two frontal bones were each characterized as of *T. rugosus* by the thick, coarsely-pitted osteoderm fused with the bone.

Limb bones: Humerus and femur have relatively thick shafts in *T. rugosus*.

Tiliqua nigrolutea (Quoy & Gaimard)

Material: Vertebrae—dorsal (6, lengths 6.0–8.9 mm, mean 7.8 ± 0.44), pygal (2, lengths 5.0, 6.2 mm), caudal (3, lengths 5.6, 6.4, 6.8 mm); maxillae (4); dentaries (3); parietal bone (1).

The size of the fossil dorsal vertebrae indicates that they were derived from a lizard at least 22 cm in snout-vent length. Such size is reached by the larger species of *Egernia* and *Tiliqua*, but not by *T. casuarinae*, *T. branchiale*, *T. petersi* nor *T. wood-jonesii*.

In *Tiliqua* species, the prezygapophyses are dorsally upturned at an angle of 35–55° (Fig. 5a) or even greater in the first two or three dorsals. The dorsal vertebrae of Australian skinks, other than *Trachydosaurus*, are longer than wide, except sometimes the last presacral which may be slightly wider than long (Fig. 4a). In *T. scincoides*, most of the dorsal vertebrae (except for the first two or three and last two or three) are extremely elongated (Fig. 4a) and this species is further characterized by the broad, depressed condyle (Fig. 4c, d) and narrow zygapophyses directed almost anteroposteriorly. In *T. scincoides*, the paradiapophyses extend laterally well beyond the lateral edges of the zygapophyses (Fig. 4b). In *T. nigrolutea* and *T. occipitalis* the zygapophysial facets are slightly wider (though the width never equals nor exceeds the length) and are directed antero- or postero-laterally; hence the width across the zygapophyses is greater (relative to, e.g., the length between zygapo-

TABLE 2

Vertebral proportions of Wonambi naracoortensis *compared with those of four extant boids. Ten vertebrae were measured from the post-hypapophystal region of modern specimens. The range is followed by mean ± standard error in parenthesis.*

Specimen	Length (mm)	Total height/length	Width across paradiapophyses/Width across pre-zygapophyses	Width condyle/Length	Zygosphene width/Length
W. naracoortensis					
P16168	16.5	1.95	1.11	0.65	0.55
P16144k	19.4	1.99	1.09	0.65	0.65
P16144s	21.8	1.70	1.24	0.56	0.50
P16129t	16.4	2.02	1.07	0.63	0.57
P16167	23.4	1.76	1.23	0.54	0.53
P16170b	19.6	1.85	1.12	0.63	0.58
Liasis childreni	4.3–5.2 (4.9 ± .09)	1.01–1.33 (1.17 ± .03)	0.80–0.91 (0.85 ± .01)	0.36–0.52 (0.47 ± .02)	0.59–0.74 (0.66 ± .02)
Python spilotus					
23	7.5–8.5 (8.1 ± .09)	1.01–1.29 (1.17 ± .03)	0.70–0.77 (0.73 ± .01)	0.47–0.55 (0.50 ± .01)	0.57–0.72 (0.66 ± .02)
2*	8.1–8.8 (8.4 ± .08)	1.24–1.47 (1.36 ± .02)	0.78–0.80 (0.79 ± .002)	0.53–0.58 (0.56 ± .01)	0.65–0.76 (0.71 ± .01)
3*	11.4–12.0 (11.6 ± .07)	1.53–1.71 (1.61 ± .02)	0.70–0.73 (0.71 ± .002)	0.47–0.51 (0.49 ± .003)	0.78–0.90 (0.85 ± .01)
Python amethistinus					
1*	14.5–15.5 (14.9 ± .08)	1.32–1.45 (1.38 ± .01)	0.75–0.78 (0.77 ± .003)	0.47–0.51 (0.49 ± .004)	0.68–0.72 (0.69 ± .004)
16*	10.1–10.5 (10.3 ± 0.4)	1.42–1.49 (1.45 ± .01)	0.79–0.82 (0.80 ± .003)	0.59–0.62 (0.60 ± .003)	0.63–0.65 (0.64 ± .002)
Aspidites melanocephalus					
3	5.7–6.5 (6.3 ± .07)	1.37–1.54 (1.46 ± .02)	0.79–0.83 (0.82 ± .004)	0.55–0.62 (0.59 ± .01)	0.70–0.77 (0.73 ± .01)
13	5.5–6.4 (6.1 ± .10)	1.29–1.55 (1.43 ± .03)	0.80–0.86 (0.83 ± .01)	0.52–0.62 (0.58 ± .01)	0.58–0.67 (0.63 ± .01)
Chondropython viridis	5.5–6.9 (6.4 ± .14)	0.95–1.35 (1.22 ± .04)	0.73–0.83 (0.78 ± .01)	0.40–0.49 (0.46 ± .01)	0.52–0.64 (0.59 ± .01)

* Specimen incomplete: only about one quarter of the precloacal vertebrae were studied.

TABLE 3

Vertebral proportions of Wonambi naracoortensis *compared with those of four extant boids. Ten vertebrae were measured from the post-hypapophysial region of modern specimens. The range is followed by mean ± standard error in parenthesis.*

Specimen	W. across pre-zygapophyses/Length	Min w. centrum/Length	Height condyle/Width condyle	L. pre-zygapophysis/Length
W. naracoortensis				
P16168	1.55	1.12	0.82	0.49
P16144k	1.57	1.17	0.81	0.46
P16144s	1.51	1.10	0.84	0.54
P16129t	1.58	1.16	0.79	0.45
P16167	1.52	1.16	0.96	0.55
P16170b	1.50	1.12	0.88	0.56
Liasis childreni	1.30–1.71 (1.52 ± .04)	0.78–1.05 (0.93 ± .03)	0.77–1.01 (0.88 ± .02)	0.34–0.46 (0.40 ± .01)
Python spilotus				
23	1.48–1.71 (1.60 ± .02)	0.91–1.10 (1.01 ± .02)	0.76–0.92 (0.84 ± .01)	0.40–0.49 (0.45 ± .01)
2*	1.53–1.77 (1.66 ± .03)	1.01–1.18 (1.10 ± .03)	0.75–0.96 (0.85 ± .02)	0.46–0.54 (0.50 ± .01)
3*	1.74–1.88 (1.81 ± .02)	1.14–1.25 (1.20 ± .01)	0.96–1.04 (0.99 ± .01)	0.54–0.59 (0.56 ± .01)
Python amethistinus				
1*	1.69–1.76 (1.72 ± .01)	1.16–1.21 (1.18 ± .005)	0.88–0.90 (0.89 ± .004)	0.48–0.53 (0.51 ± .005)
16*	1.59–1.65 (1.62 ± .01)	1.10–1.14 (1.12 ± .005)	0.76–0.83 (0.80 ± .01)	0.41–0.45 (0.43 ± .005)
Aspidites melanocephalus				
3	1.62–1.74 (1.67 ± .01)	1.06–1.12 (1.09 ± .01)	0.69–0.87 (0.82 ± .02)	0.42–0.47 (0.45 ± .004)
13	1.53–1.63 (1.58 ± .01)	0.99–1.08 (1.03 ± .01)	0.75–0.82 (0.78 ± .01)	0.40–0.46 (0.42 ± .01)
Chondropython viridis	1.13–1.44 (1.34 ± .03)	0.75–0.99 (0.91 ± .03)	0.75–0.83 (0.99 ± .01)	0.27–0.43 (0.37 ± .01)

* Specimen incomplete: only about one quarter of the precloacal vertebrae were studied.

TABLE 4

Length and proportions of dorsal vertebrae of specimens of three species of Varanus. *The ultimate presacral vertebra of each specimen is excluded. The range is followed by mean ± standard error in parenthesis.*

Specimen	Numbers of vertebrae	Pr–Po (mm)	BW/Pr–Po	CW/Pr–Po	Pr–Pr/Pr–Po	Pr–Pr/BW
V. giganteus	20	24.5–27.1 (25.7 ± .14)	0.54–0.64 (0.58 ± .005)	0.55–0.63 (0.59 ± .006)	0.88–1.01 (0.92 ± .007)	1.51–1.64 (1.58 ± .008)
V. gouldii						
Specimen 1	20	12.4–13.6 (13.2 ± .07)	0.48–0.60 (0.52 ± .005)	0.52–0.56 (0.54 ± .002)	0.86–1.00 (0.90 ± .007)	1.68–1.78 (1.73 ± .006)
Specimen 2	20	17.5–19.6 (18.5 ± .09)	0.47–0.59 (0.55 ± .007)	0.48–0.54 (0.52 ± .004)	0.85–1.02 (0.97 ± .009)	1.70–1.88 (1.77 ± .011)
Specimen 3	20	14.7–15.8 (15.4 ± .07)	0.43–0.54 (0.49 ± .006)	0.44–0.53 (0.49 ± .006)	0.82–0.95 (0.91 ± .007)	1.70–1.97 (1.85 ± .013)
V. varius						
Specimen 1	19	16.7–18.5 (17.9 ± .09)	0.48–0.59 (0.51 ± .005)	0.56–0.59 (0.58 ± .002)	0.87–0.92 (0.90 ± .004)	1.61–1.85 (1.76 ± .012)
Specimen 2	16	13.9–15.4 (15.0 ± .10)	0.45–0.57 (0.51 ± .007)	0.53–0.57 (0.55 ± .004)	0.84–0.96 (0.91 ± .009)	1.70–1.88 (1.78 ± .011)
Specimen 3	19	21.2–23.7 (22.9 ± .17)	0.47–0.64 (0.51 ± .009)	0.47–0.51 (0.49 ± .002)	0.82–1.00 (0.89 ± .011)	1.57–1.84 (1.73 ± .015)
V. varius						
(fossil)	13	13.1–21.8 (16.3 ± 0.67)	0.47–0.55 (0.51 ± .007)	0.48–0.57 (0.52 ± .007)	0.84–0.98 (0.91 ± .010)	1.69–1.87 (1.78 ± .015)

physes or to the condyle) than in *T. scincoides*. In *Tiliqua* species and *Egernia* species the tip of the neural spine may be thickened and sometimes marked with a shallow median groove, but in *T. nigrolutea* (four specimens examined) the median groove is so deep that the spine terminates in a double tip.

Three incomplete dentaries (P16124z, P16126w, and P16128h) resemble *T. nigrolutea* dentaries in shape, and four maxillae (P16125s, P16128n, P16128w and P16157z) are consistent with *T. nigrolutea* (and also with *T. scincoides* and *T. occipitalis*) in the slight suborbital ridge. A parietal bone (P16127d) is probably also of this species although the sides are slightly less constricted than in modern *T. nigrolutea*.

c.f. Sphenomorphus tympanum (Lönnberg & Andersson)

Material: Two fused sacral vertebrae.

In *Sphenomorphus tympanum*, the transverse processes of the first sacral vertebrae (S1) are strong and slant backwards only a few degrees. The transverse processes of S2 are thinner and are directed forwards to join and fuse with those of S1 at their lateral expansions. The sacral fossae between the transverse processes are wide. *S. tympanum* sacral vertebrae differ from those of *Egernia striolata* in having relatively wide fossae, and differ from *E. whitei tenebrosa* where the transverse processes of S1 are angled backwards and the transverse processes of S2 are perpendicular to the long axis of the vertebra. The fossil (P16146r) has a total length (from prezygapophysis of S1 to postzygapophysis of S2) of 3.7 mm.

Egernia, c.f. E. whitei (Lacepede)

Material: Vertebrae—dorsal (2, lengths 3.4, 2.7 mm), caudal (1, length 2.4 mm); maxillae (5 left, 5 right); dentaries (8 left, 6 right); frontals (1).

The Meckelian groove in the lower jaw is closed anterior to the splenial in *Egernia* but it is open forward to the symphysis in *Sphenomorphus*. The dentary of *E. whitei* is deeper than the slender dentary of *S. tympanum*, and the notch in the posterior lateral surface of the dentary is higher (i.e. nearer the tooth row) than in *S. tympanum*. The fossils are consistent in shape and size with E. *whitei*.

The fused frontal bones of *E. whitei* differ from those of *S. tympanum* in their gradual taper, both anteriorly and posteriorly.

Family **AGAMIDAE**

Agamid vertebrae are characterized by their triangular ventral outline and strong subcentral ridges.

Amphibolurus c.f. A. barbatus

Material: Maxillae (1); dentaries (7).

Agamids are the only Australian reptiles with acrodont tooth implantation. The largest fossil, a right dentary (P16132b) with length of tooth row 14.5 mm, closely resembles *A. barbatus*. The other specimens, two of them fragments, may be of a smaller species.

Faunal change

The two reptiles most common in the Victoria Cave deposit, *viz. Pseudonaja* c.f. *P. nuchalis* and *T. rugosus* were represented at all depths in similar abundance. The less common species, except for *W. naracoortensis* were also found at various depths from the surface to the present maximum depth of excavation. Seven vertebrae and the tooth fragment of *W. naracoortensis* were near the surface and all within 2 metres of each other. Hence the reptile fauna does not change remarkably with depth in the deposit.

Discussion

The small marsupial remains, together with abundant rodent remains, were probably brought into Victoria Cave by owls (Smith 1971, 1972), and the small lizards may also have been the prey of owls. Among the larger species, *Trachydosaurus rugosus* is a clumsy, short-legged, heavy-bodied lizard which might easily fall into sinkholes or caves and would have little chance of escaping. This species has been recorded from several cave deposits (e.g. Cook 1963, Finlayson 1933, Longman 1945). The snakes may have actually inhabited the cave, as live brown snakes (*Pseudonaja* sp.) are found in the limestone caves in south eastern South Australia (Wells, pers. comm.) and *P. nuchalis* has been classified as an occasional trogloxene (Richards 1971).

In any measurements of the bones of reptiles, intraspecific variances are large because reptile growth is asymptotic. When vertebrae are the bones measured, changes along the column further increase the variation. In the identification of isolated vertebrae of some groups (e.g. the snake family Crotalidae), these inherent large variances can be offset by considering several dimensions simultaneously and in comparison with their previously determined inter-relationships along the entire column of reference skeletons (Brattstrom

1964). Nevertheless, when the reptile remains are abundant or include a qualitatively diagnostic bone (e.g. the first sacral vertebra of *Varanus*), the species can be diagnosed with confidence.

Of the 5 species confidently determined, 4 are still found in south-eastern Australia, and all but *Varanus varius* have been found near Naracoorte. All 6 additional species tentatively identified have been found near Naracoorte. The large boid is the only Pleistocene species absent now. Hence, among the reptiles, the small species have survived from Pleistocene to present without detectable change of the characters available in fossil material, whereas the large species has become extinct. Similarly with the marsupials; while many large species have become extinct [e.g. several *Sthenurus* species, *Thylacoleo* c.f. *T. carnifex* (Wells, pers. comm.), *Palorchestes* sp., (Pledge, pers. comm.)], the small species, e.g. *Bettongia* spp., *Perameles* spp., *Antechinus* spp. and *Petaurus breviceps* are indistinguishable from modern species, many of which still survive near Naracoorte (Smith 1971, 1972). Among the birds, the only species now extinct, *Progura naracoortensis*, was a large bird, while all of the small species are extant. The factors that caused the extinction of so many large vertebrate species have had little perceivable effect on the small vertebrates.

The presence of *Varanus varius* together with *V. gouldii* in this Pleistocene deposit does not support the suggestion (King & King 1975) that the *indicus* karyotype (represented by *V. varius*) invaded south-eastern Australia after the separation of Kangaroo Island from the mainland, 8,000–10,000 years ago.

Most of the extant species of the Victoria Cave reptile fauna are wide-ranging with broad habitat tolerances. *Varanus gouldii* occurs in most parts of mainland Australia but is most common in sandy areas, where it lives in sand burrows (Worrell 1963). The tree-climbing species *V. varius*, occurs throughout eastern Australia inside the 20" (508 mm) isohyet (Rawlinson 1969). *Trachydosaurus rugosus* is found in inland areas of all mainland states, while *Pseudechis porphyriacus* lives in coastal to mountainous forests and swamps of eastern Australia, but does not extend into dry inland areas (Worrell 1963). The ranges of *Pseudonaja nuchalis* and the morphologically similar *P. textilis* together include most of mainland Australia (Worrell 1963), and *P. textilis* occurs also in New Guinea (McDowell 1967). None of these species extend into the cool temperate zone of the Bassian zoogeographical subregion (Rawlinson 1974). Conversely, *Tiliqua nigrolutea* is confined to the cool temperate zone, its range extending from the extreme south-east of South Australia and southern Victoria to the islands of Bass Strait and Tasmania. Naracoorte is close to the north-western limit of its range (Rawlinson 1974). *Egernia whitei*, *Sphenomorphus tympanum* and the genus *Notechis* occur in all zones of the Bassian but not in other subregions (Rawlinson 1974). Hence little palaeo-ecological information can be gleaned from them. The presence of a large proportion of the Pleistocene reptile fauna in the area at present does suggest that climatic changes during the last 30,000 years have been slight in south-eastern South Australia.

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MIOCENE MARSUPICARNIVORES (MARSUPIALIA) FROM CENTRAL SOUTH AUSTRALIA, *ANKOTARINJA TIRARENSIS* GEN. ET SP. NOV., *KEEUNA WOODBURNEI* GEN. *ET* SP. NOV., AND THEIR SIGNIFICANCE IN TERMS OF EARLY MARSUPIAL RADIATIONS

*BY M. ARCHER**

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Keeuna woodburnei is a small marsupicarnivore which is more similar to dasyurids than is A. tirarensis. It resembles species of *Phascolosorex* Matschie, 1916, *Neophascogale* Stein, 1933, *Murexia* Tate & Archbold, 1937, and some *Antechinus* Macleay, 1841. More distant relationship to didelphids is suggested.

Resemblance of both of these fossil marsupicarnivores to modern New Guinean highland rainforest dasyurids rather than to more arid-adapted Australian dasyurids, is regarded as evidence suggesting that central Australia was less arid during Etadunna time than it is now.

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Introduction

In 1971 W. A. Clemens, M. O. Woodburne, C. Campbell and the author recovered fossil mammal remains from a site known as Tedford Locality, on the west side of Lake Palankarinna, Etadunna Station, South Australia. These fossils come from the Etadunna Formation which is now regarded (W. K. Harris, pers. comm.) as being approximately middle Miocene in age. In 1972 M. O. Woodburne, P. Lawson, W. Head, E. Archer and the author extensively quarried and screen-washed Tedford Locality. From the concentrate, two marsupicarnivores, as well as other mammal remains, were recovered.

Stirton, Tedford, & Miller (1961) briefly describe a third marsupicarnivore from the Etadunna Formation.

Terminology of individual teeth is that used by Thomas (1887) and Archer (1974). Terminology of tooth crowns is shown in Figure 1 and follows that used by Archer (1975a). Comparisons with other marsupicarnivores are based in large part on Archer (1976b).

Specimens with prefix P are in the fossil collection of the South Australian Museum; F in the fossil collection of the Queensland Museum; UCR in the University of California at Riverside; AMNH in the Archbold Collections of the American Museum of Natural History; J and JM in the modern collections of the Queensland Museum; and WAM in the modern collections of the Western Australian Museum.

Species names of modern Australian marsupials are those employed by Ride (1970), Laurie & Hill (1954) or Archer (1975b). Other modern marsupial names are those employed by Collins (1974). Names of Cretaceous didelphids are mainly those used by Clemens (1966). Fossil marsupial names are those employed by the most recent reviewer of those particular groups.

Taxonomy

Genus ANKOTARINJA nov.

Type species: Ankotarinja tirarensis sp. nov. (by designation and monotypy).

Generic diagnosis: Differs from other Australian and New Guinean dasyurids in having, as

* Queensland Museum, Gregory Terrace, Brisbane, Qld 4006.

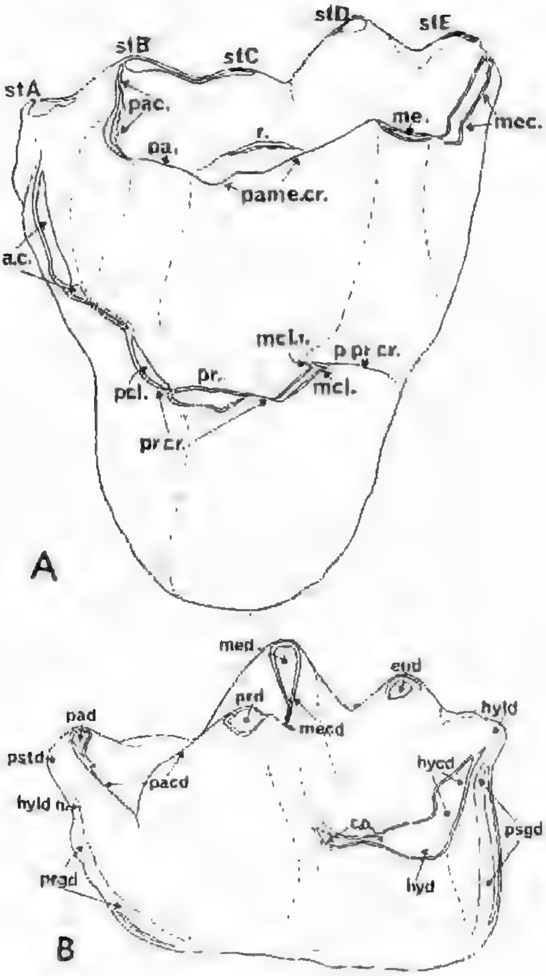

Fig. 1. Terminology of molar cusps and crests (based on *Ankotarinja tirarensis*). 1*A*, upper molar. 1*B*, lower molar. a.c., anterior cingulum; *c.o.*, cristid obliqua; *end*, entoconid; *hycd*, hypocristid; *hyd*, hypoconid; *hyld*, hypoconulid; *hyld n.*, hypoconulid notch; *mcl.*, metaconule; *mcl.r.*, metaconular ridge; *me.*, metacone; *mec.*, metacrista; *mecd*, metacristid; *med*, metaconid; *pa.*, paracone; *pacd*, paracristid; *pad*, paraconid; *pame. cr.*, para-metacone crest; *pcl.*, protoconule; *pprcr.*, postprotocrista; *prcr.*, protocrista; *prd*, protoconid; *prgd*, precingulid (or anterior cingulum); *psgd*, postcingulid (or posterior cingulum); *pstd*, parastylid; *r.*, ridge mesial to stC; stA-E, stylar cusps A-E.

a combination of characters, relatively unreduced talonid on $M_{/4}$ with well-formed hypoconid, hypoconulid and entoconid and relatively unreduced $P_{/4}$.

Origin of generic name: An allusion to *Ankotarinja*, a dreamtime ancestor (Robinson 1966, p. 26) who, having remained buried a long time as bones in the earth, resurrected himself in a small watercourse. *Ankotarinja* is here given masculine gender.

Ankotarinja tirarensis sp. nov.

FIGS 1–5

Holotype: P18190, right dentary fragment with $M_{/2-/4}$.

Type locality: Tedford Locality, Etadunna Formation, Lake Palankarinna, Etadunna Station, S.A. (28°47'S, 138°25'E).

Diagnosis: That of genus. Features likely to be of specific value include very small size, relationship of hypocristid to entoconid, size and width of anterior and posterior cingula, relative size of paraconid on $M_{/1}$, and relative size of stylar cusps.

Origin of specific name: Specific name refers to the Tirari Desert, the portion of the Simpson Desert containing Lake Palankarinna.

Referred specimens: UCR, 15340, dentary fragment with $LM_{/1}$; UCR, 15341, dentary fragment with $LM_{/2-/3}$; UCR, 15342, dentary fragment with $RM_{/4}$; F7331, dentary fragment with $LM_{/3-/4}$; UCR, 15343, maxillary fragment with alveoli for $LM^{3/-4/}$; UCR, 15308, $LM^{?3/}$; F7332, $LM^{?3/}$.

Description

Maxillary fragment (UCR, 15343) referred to this species on basis of size, has alveoli for $M^{3/-4/}$ and posterior root of $M^{2/}$. $M^{4/}$ appears to have been as wide as $M^{3/}$, presumably with relatively little reduction of protocone. $M^{4/}$ length less than that of $M^{3/}$, metacone root being reduced and displaced antero-lingually relative to metacone root of $M^{3/}$. Zygomatic root of maxilla arises buccal to region between $M^{3/}$ and $M^{4/}$. Numerous small interdental fenestrae in palate between $M^{2/}$ and $M^{3/}$, and between $M^{3/}$ and $M^{4/}$.

Upper teeth represented by two isolated molars, probably $LM^{2/}$ and $LM^{3/}$. Although possible that these teeth actually represent $M^{1/}$ and $M^{2/}$, improbable for following reasons. Stylar cusps (UCR, 15308) much more reduced than those cusps on $M^{2/}$ in all other dasyurids but not so strikingly reduced when compared with $M^{3/}$ in some dasyurids such as *Keeuna*, described below, or some species of *Planigale* Troughton, 1928. Also, notch in antero-buccal cingulum of F7332 for reception of metastylar corner of preceeding tooth suggests F7332 is posterior molar. However, it is also true that in some dasyurids and didelphids with large $P^{3/}$, such a notch sometimes exists

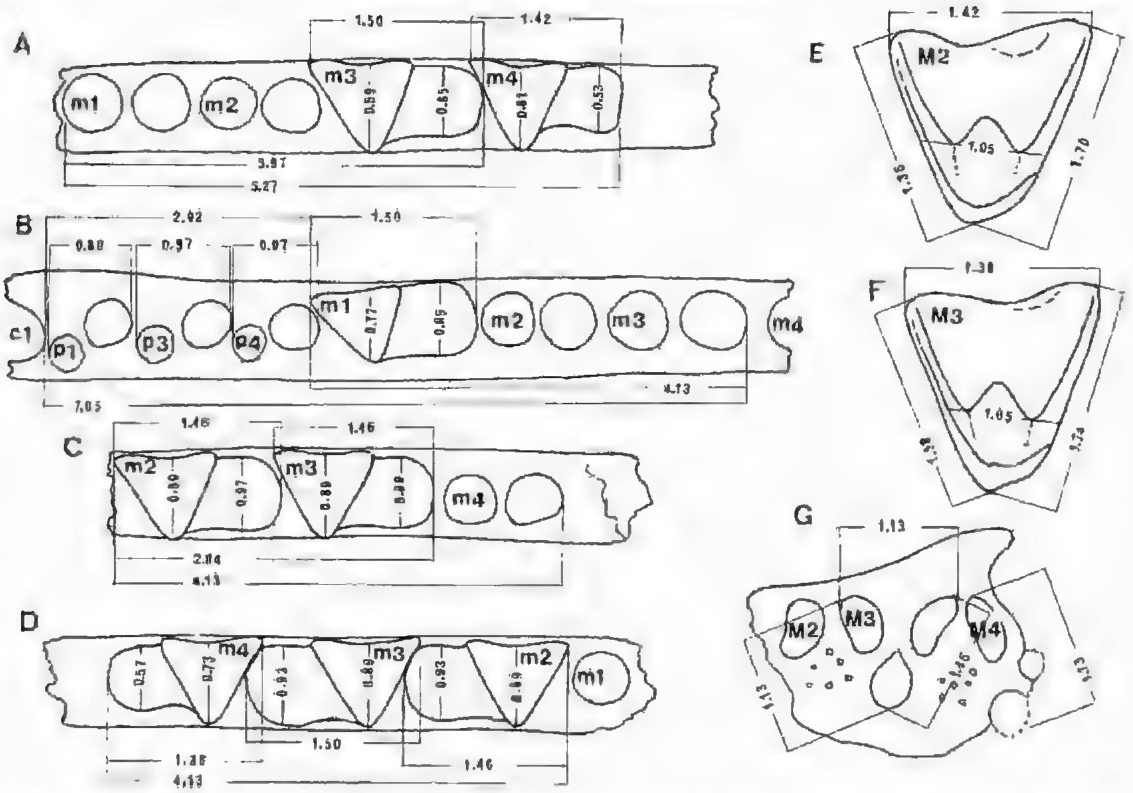

Fig. 2. Specimens of *Ankotarinja tirarensis* and their measurements (mm). *A*, F7331, LM$_{3-4}$. *B*, UCR. 15340, LM$_{1}$. *C*, UCR. 15341, LM$_{2-3}$. *D*, Holotype, P18190, RM$_{2-4}$. *E*, F7332, LM^{2}. *F*, UCR. 15308, LM^{3}. *G*, UCR. 15343, maxillary fragment with alveoli for M$^{2-4}$.

in antero-buccal cingulum of M^{1}. Probable that F7332 and UCR. 15308 represent M^{2} and M^{3} respectively rather than M^{1} and M^{2}.

F7332 has at least three stylar cusps. StB connects to parastylar corner of tooth which may be distinguishable as discreet stA. Parastylar blade very short. Ectoloph crest descends gently from posterior flank stB, then rises gently, to form long low ridge-like stC. Posterior point of this cusp marked by beginning of rise in ectoloph which forms tall stD. StD has minor ectoloph crest on posterior flank which descends towards metastylar corner of tooth. Very minute rise in crest on posterior flank of stD may represent stE. Ectoloph posterior to this point very low, extending to metastylar corner of tooth. Paracone taller than stylar cusps but subequal in crown height to, or shorter than, protocone. Metacone tallest cusp. Prominent protoconule and metaconule. Ectoloph continuous on buccal edge of crown. Buccal concavity in crown outline slight. Paracrista just longer than half length metacrista. Paracrista extends from paracone to anterior half of stB. Although slightly worn, paracrista appears to curve at buccal end to contact stB. Paracrista apparently transverse to imaginary long axis of toothrow. Para-metacrista continuous. Slight protoconule ridge may be present linking base of paracone to preprotocrista. Clear metaconular ridge present linking base of metacone to postprotocrista. Metaconular ridge extends short way up base of metacone causing bulge in base of that cusp. Metaconular ridge bounds marked declivity between posterior portion of steeply inclined postprotocrista and posterior base of metacone. Anterior cingulum complete, linking preprotocrista and antero-buccal cingulum to parastylar corner of tooth. No posterior cingulum present. Pre- and postprotocrista form large but acute angle.

UCR. 15308 has at least four stylar cusps. Possible stA as in F7332. Posterior crest from stB descends steeply to base of stC. Between stC and D, and connected by crests, another smaller stylar cusp of uncertain homology. StD small and connected to metastylar corner of tooth by low ectoloph crest. Paracone and protocone subequal in crown height. Protoconule absent and protoconule swelling only just present. Metaconule large. Buccal concavity in crown outline deeper than in F7332. Paracrista almost three-quarters length metacrista. Paracrista worn but appears to intersect ectoloph on anterior flank of stB. No clear protoconule ridge present. Metaconular ridge small but present. Metaconular ridge does not clearly extend up base of metacone. Otherwise morphology of UCR, 15308 as in F7332.

Meristic gradients from M^{2} to M^{3} may be summarized as follows. Tooth length decreases Width increases. Ectoloph becomes more evenly and deeply concave. Stylar cusps, particularly D, become smaller. Paracrista and metacrista increase in length. Para-metacrista becomes more symmetrical. Protoconule decreases in size. Angle formed by pre- and postprotocrista becomes slightly more acute. Antero-buccal cingulum increases slightly in length.

Dentary fragments indicate premolar size. UCR, 15340 has alveoli for C_{1}-P_{4}. Premolar alveoli subequal in size, indicating little or no reduction in tooth size from P_{3} to P_{4}. P_{4} presumably had posterior cingular cusp which corresponds with hypoconulid notch of M_{1}. P_{1} anterior alveolus slightly crowded out of alignment but (as evidenced in modern species of *Planigale*, Archer 1976a), does not necessarily mean P_{1} crown out of alignment. Judging from proximity of premolar and canine alveoli, premolars and canine presumably contacted one another antero-posteriorly. C_{1} alveolus suggests C_{1} width exceeded that of any premolar, but because of relatively unreduced P_{1}, C_{1} probably not greatly enlarged and comparable with canine of *Ningaui* Archer, 1975b.

M_{1} talonid wider than trigonid but trigonid not as compressed laterally as in most modern dasyurids. Well-developed anterior cingulum, which terminates lingually for hypoconulid notch. Parastylid corner of tooth most anterior portion of crown. Posterior cingulum comparable in length to anterior cingulum and terminates buccal to posteriorly projecting hypoconulid. Basal cingulum absent beneath postero-buccal corner of protoconid and hypoconid. Roughened enamel suggests cingulum present between base of protoconid and hypoconid. No lingual cingulum. Paraconid low, approximately same height as hypoconulid. Protoconid tallest cusp of trigonid. Metaconid just shorter than protoconid. Hypoconid just taller than entoconid which is taller than paraconid. Paracristid complete between protoconid and paraconid but almost vertical from protoconid to shallow paracristid fissure and horizontal between paracristid fissure and paraconid. Metacristid steeply inclined on both sides of metacristid fissure. Metacristid and hypocristid approximately transverse to long axis of dentary. Cristid obliqua (damaged) extends from hypoconid to trigonid intersecting latter at point below protoconid tip, well buccal to metacristid fissure. Hypocristid extends from hypoconid to hypoconulid, without approaching entoconid. Entoconid and hypoconulid not connected by crest. Entoconid and metaconid connected by high crest.

M_{2} talonid wider than trigonid. Anterior and posterior cingulum as in M_{1}. Buccal cingulum between protoconid and hypoconid less developed (absent in P18190). No lingual cingulum. Paraconid smallest trigonid cusp but subequal in height to hypoconid and entoconid. Metaconid much taller than hypoconid and just shorter than protoconid. Hypoconid and entoconid subequal in height. Entoconid not connected to hypoconulid by crest, but connected to metaconid as in M_{1} except that crest interrupted by shallow transverse groove. Paracristid from paracristid fissure to paraconid, inclined, not horizontal. Crista obliqua extends to base of protoconid as in M_{1} but anterior end appears to be distinct contribution from trigonid with slight fissure where talonid and trigonid parts meet. Trigonid portion thicker and more bulbous. Otherwise morphology M_{2} as in M_{1}.

M_{3} talonid just wider than trigonid. Anterior and posterior cingulum as in M_{2}. Buccal cingulum confined to area between base of protoconid and hypoconid, as thickened bulge of enamel, clearly less well-developed than anterior and posterior cingula. No lingual cingulum. Paraconid smallest trigonid cusp but taller than any talonid cusp. Entoconid not connected to hypoconulid by crest, but connected to metaconid, as in M_{2}. Unlike cristid obliqua in M_{2}, this structure in M_{3} appears to lack transverse fissure separating crest into hypoconid and trigonid portions. This difference between M_{3} and M_{4} notable in P18190. Cristid obliqua also intersects trigonid in slightly more lingual position than in M_{2}. Otherwise morphology M_{3} as in M_{2}.

M_{4} trigonid wider than talonid, but talonid wider than that structure in most modern dasyurids. Anterior cingulum as in M_{3}. Posterior cingulum absent. Buccal cingulum confined to area between protoconid and hypoconid. Paraconid just shorter than metaconid. Entoconid and hypoconid reduced relative to M_3, but larger relative to most modern dasyurids. Entoconid connected to base of metaconid via low crest. Entoconid also connected to hypoconulid by low crest. Hypocristid convex anteriorly. Hypoconulid subequal in height to entoconid. Cristid obliqua intersects trigonid base immediately buccal to point below metacristid fissure, this being markedly more lingual than similar intersection of cristid obliqua in M_3. Otherwise morphology of M_4 as in M_3.

Meristic changes along tooth row as follows. Paraconid increases in height from M_1 to M_4. Metaconid height M_{1-4} subequal but metaconid length at base of cusp decreases markedly from M_1 to M_4, result of reduction in size of minor crest on posterior slope of metaconid which links with entoconid. Entoconid M_{1-3} subequal and larger than entoconid of M_4. Hypoconulid M_{1-3} subequal in height and shorter than that cusp in M_4. Protoconid M_1 shorter than protoconid M_2 which is subequal to that cusp in M_3 which is larger than that cusp in M_4. Hypoconid decreases in height from M_1 to M_4. Talonid M_{1-3} wider than trigonid. Talonid M_4 narrower than trigonid. Paracristid M_{1-2} subequal and subequal to (P18190) or just shorter than (UCR, 15341) that crest in M_3. Paracristid M_4 shorter than that of M_3. Metacristid increases in length from M_1 to M_3. Metacristid M_4 shorter than metacristid M_3. Cristid obliqua intersects trigonid in progressively more lingual position from M_1 to M_4. Hypocristid M_{1-3} subequal in length and longer than hypocristid M_4. Anterior cingulum decreases in length slightly from M_1-M_4. Posterior cingulum M_{1-3} subequal in length (absent in M_4).

Discussion and comparison

Ankotarinja is a metatherian because it has four molars, a large stylar shelf, and an approximated entoconid and hypoconulid. It is also a marsupicarnivore because it has tribosphenic molars lacking hypocones.

Dental characteristics of known dasyurids, peramelids, thylacinids, didelphids, and related marsupicarnivores have been reviewed (Archer 1976b) and, to avoid repetition, it is sufficient to point out here that *Ankotarinja* can only be regarded as either a dasyurid or didelphid. Because morphological variation of teeth exhibited by didelphids and dasyurids overlaps, only incisor number and possibly dP4 cusp number permit diagnosis at the family level. All dasyurids have three lower incisors and four upper incisors on each side, whereas almost all didelphids have four lower and five upper incisors (exceptions may include *Derorhynchus singularis* Paula Couto, 1952, species of *Eodelphis* Matthew, 1916). The premaxilla and anterior region of the dentary of *Ankotarinja tirarensis* are unknown. Therefore, this marsupicarnivore cannot at present be referred conclusively to either the Dasyuridae or the Didelphidae.

Modern and fossil didelphid subfamilies exhibit greater morphological variation than dasyurids. Most are so distinct that their mere subfamilial status has been questioned, and the reasons they are doubtfully referred to the Didelphidae are also the reasons they cannot be related to *Ankotarinja tirarensis*. Only didelphines warrant closer comparison.

Some North and South American didelphines are adequately illustrated (such as the Paleocene forms described by Paula Couto 1952, 1962, 1970) but most are not. Archer (1976b) summarizes the most striking characteristics of these forms. Only species of *Coona* Simpson, 1938, *Marmosopsis* Paula Couto, 1962, *Mirandatherium* Paula Couto, 1970, *Monodelphopsis* Paula Couto, 1952, *Derorhynchus* Paula Couto, 1952, *Ischyrodidelphis* Paula Couto, 1952, *Didelphopsis* Paula Couto, 1952, *Minusculodelphis* Paula Couto, 1962 and an M^1 listed by Paula Couto (1962) as *incertae sedis* are similar to *A. tirarensis*. Among Cretaceous didelphines, species of *Alphadon* Simpson, 1927, and *Pediomys* Marsh, 1889, warrant comparison. Modern didelphines used here for comparison include two species of *Marmosa* Gray, 1821, *M.* sp. and *M. mitis* Bangs, 1898, *Monodelphis dimidiata* (Wagner, 1847), *Metachirus nudicaudatus* (Geoffroy, 1803), *Philander opossum* Gray, 1843, and *Didelphis marsupialis* Linnaeus, 1760. Of these, species of *Marmosa*, *Monodelphis* Burnett, 1830 and *Didelphis* Linnaeus, 1758 warrant closer comparison with *Ankotarinja*.

Characters of *Ankotarinja* which are unusual among dasyurids and invite broader comparison within the Marsupicarnivora (the didelphine forms noted above) are as follows: 1, large M_4 talonid; 2, relatively uncompressed M_1 trigonid; 3, buccal position of anterior end of cristid obliqua; 4, transverse orientation of metacristid; 5, large P_3; 6, large M^4; 7, stylar

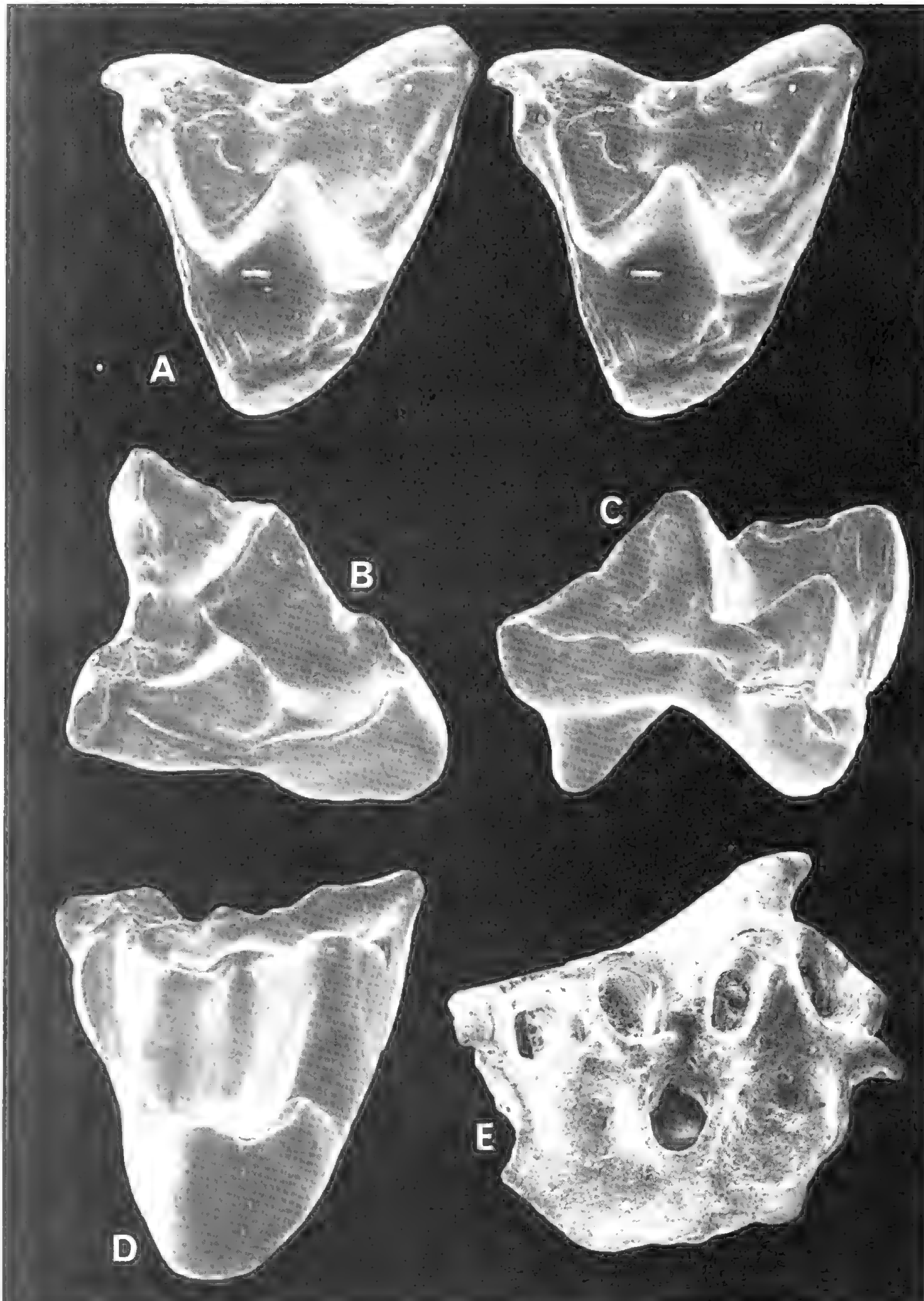

FIG. 3.

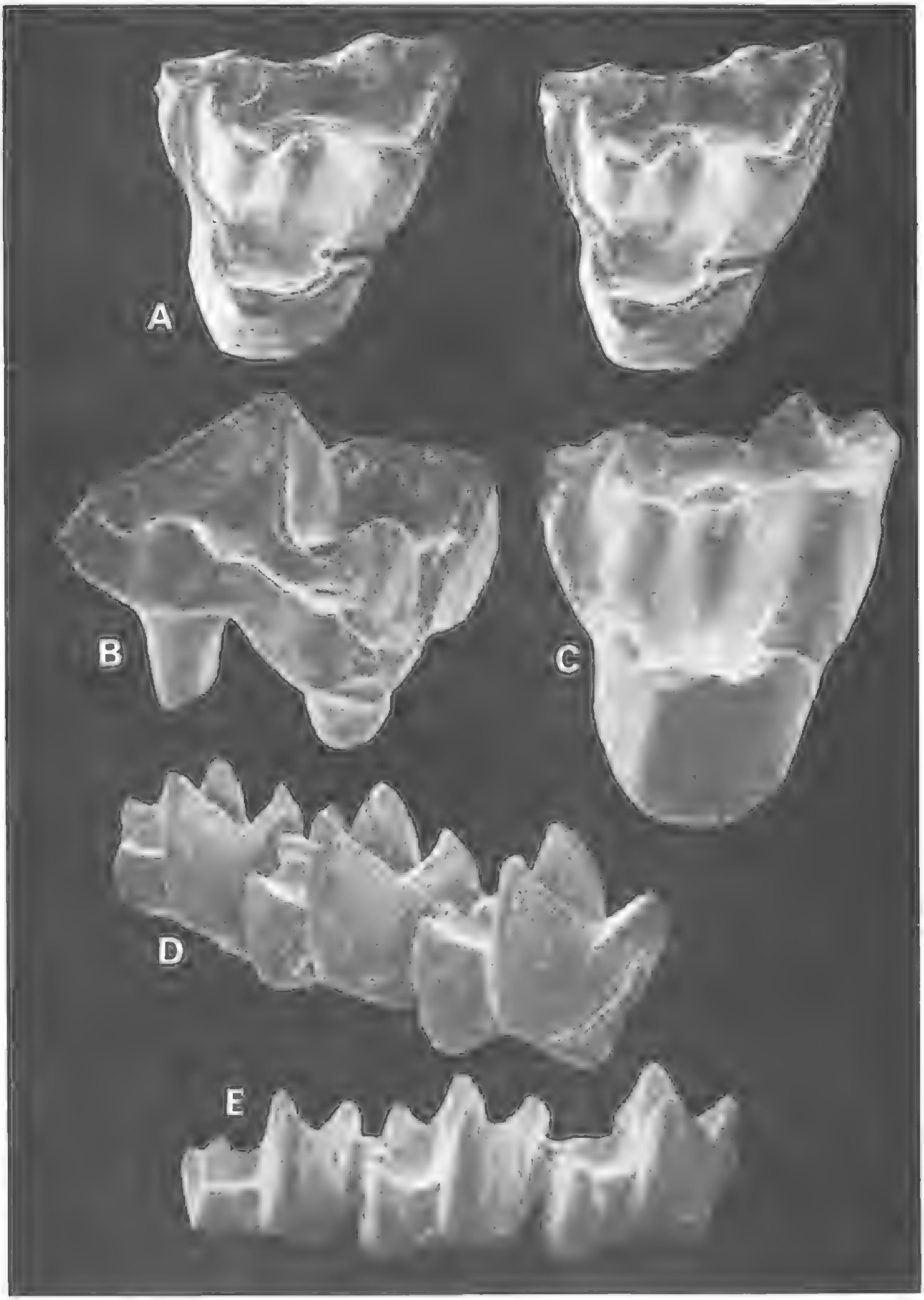

FIG. 4.

FIG. 5.

TABLE 1

Unusual characteristics of *Ankotarinja*	*Ankotarinja*	*Coona*	*Marmosopsis*	*Mirandatherium*	*Monodelphopsis*	*Derorhynchus*	*Ischyrodelphis*	*Didelphopsis*	*Minusculodelphis*	*Incertae sedis* LM?	*Peradectes*	*Alphadon*	*Pediomys*	*Marmosa*	*Monodelphis*	*Didelphis*	*Murexia*	*Neophascogale*	*Phascolosorex*	*Sminthopsis*	*Ningaui*	*Antechinus*	*Phascogale*	*Keeuna*
1. M_4 talonid large	+	+	—	?	—	+	?	+	—	?		+	—	+	+	+	—	+	+	—	—	—	—	?
2. M_1 trigonid wide	+	?	+	+	+	+	—	+	?	?	+	+	+	+	+	+	+	—	—	+	—	—	—	—
3. C.o. buccal position	+	+	+	—	+	+	+	—	+	?	+	—	+	+	+	+	—	+	—	—	—	—	—	+
4. Transverse metacristid	+	+	+	—	—	—	—	—	+	?	+	+	+	+	+	+	—	—	—	+	—	—	—	—
5. Large P_4	+	+	+	+	+	—	—	+	+	?	+	+	+	+	+	+	+	—	—	+	—	—	—	?
6. Large M^4	+	?	?	?	?	?	?	—	?	?	+	+	+	—	+	+	—	+	+	—	—	—	—	+
7. stD small and posterior	+	?	?	?	?	?	?	?	?	?	+	+	+	+	+	+	—	—	—	—	—	—	—	+
8. Metaconule prominent	+	?	?	?	?	?	?	+	?	?	+	+	+	—	—	—	+	+	+	—	—	+	—	+

cusp arrangement with reduced and posteriorly positioned stD; and 8, prominent metaconule. These characters are compared in Table 1 for non-dasyurid marsupicarnivores noted above, as well as dasyurids which provide the closest approximations to *Ankotarinja*. In this Table, characters 1–8 are the same as noted above. A "+" records a condition similar to or which approaches the condition found in *Ankotarinja*. A "?" indicates either that the requisite part of the dentition is unknown or not adequately preserved. A "—" indicates a character condition unlike that in *Ankotarinja*. In some genera noted, some species may be similar to, while others differ from, the condition in *Ankotarinja*. In this case, a "+" only is recorded.

M_4 and M^4 size

Large M^4 and M_4 talonid are related characters and more common among structurally ancestral didelphines than dasyurids. Very few dasyurids have the M_4 talonid as relatively large as it is in *Ankotarinja*. The M_4 talonid of most dasyurids is laterally compressed with one or at most two cusps present, the hypoconid and entoconid or hypoconid and hypoconulid. In this character, *Ankotarinja* is most similar (among dasyurids) to *Neophascogale* and to a lesser extent *Phascolosorex*. Three distinct cusps may sometimes be present on the M_4 talonid of other dasyurids such as *Murexia*; *Myoictis* Gray, 1858 and some *Antechinus* but in these forms the M_4 trigonid is relatively larger than in *Ankotarinja*, while the talonid is transversely compressed. Relatively large M_4 talonids characterize many didelphine groups. For example, the talonid of M_4 in *Marmosa* is only slightly more reduced than that of *Ankotarinja*. However, in *Marmosa* the whole M_4 is not as reduced relative to M_3 as it is in *Ankotarinja*. *Philander* Brisson, 1762 (J3460), and *Metachirus* Burmeister, 1854 (J3461) also show a relatively unreduced M_4 talonid. *Coona* and *Guggenheimia* Paula Couto, 1952 have M_4 talonids even wider than the trigonids. Extremely narrow M_4 talonids (comparable with the condition in most dasyurids) are found among didelphines in species of *Minusculodelphis* and and *Marmosopsis*.

Overall reduction of M_4 relative to M_3, such as occurs in *Ankotarinja*, does not occur in any modern dasyurids. It is common only to some didelphoids. M^4 of *Ankotarinja* is unknown but maxillary fragment UCR, 15343 indicates that this tooth was as wide but not as long antero-posteriorly as M^4 of most didelphids. It was comparable in length to M^4 of some modern dasyurids such as *Neophascogale*, but wider than that tooth in most modern dasyurids. Size of M^4 in modern dasyurids

Fig. 3. *A-E*, scanning electron microscope photographs of *Ankotarinja tirarensis*. *A-D*, UCR, 15308, LM^3. *A*, stereophotographs. *E*, UCR, 15343, maxillary fragment with alveoli for LM^{3-4}.

Fig. 4. *A-E*, scanning electron microscope photographs of *Ankotarinja tirarensis*. *A-C*, F7332, LM^3. *A*, stereophotographs. *D-E*, Holotype, P18190, RM_{2-4}, entoconid broken off RM_1.

Fig. 5. *A-E*, scanning electron microscope photographs of *Ankotarinja tirarensis*. *A-B*, UCR, 15340, dentary fragment with LM_{2-3}. *D*, UCR, 15341, dentary fragment with LM_{2-4}. *E*, F7331, dentary fragment with LM_{3-4}.

appears to be related to relative length of the cheek-tooth row, being shorter and more reduced in forms with more compressed tooth rows. This compression commonly occurs in more strictly carnivorous forms where emphasis is on development of metacrista-paracristid shearing elements. In more insectivorous forms, paracrista-metacristid shearing elements are relatively less reduced, resulting in a relatively more functional M^4 paracrista and larger M_4 talonid.

Reasons for overall reduction of M_4 relative to M_3 are not easy to interpret. In some diprotodont marsupials where reduction of M_4 is advanced, sometimes even involving loss, P_3 is developed as a large sectorial or even plagiaulacoid tooth, possibly reflecting a shift anteriorly in shearing emphasis, reducing the importance of M_4. In *Ankotarinja*, although P_3 is large, the size is not particularly different from that of some didelphines which lack a reduced M_4.

M_1 trigonid width, paraconid reduction, and size of P_3

Reduction of the M_1 paraconid and P_3 are related characters and often accompanied by transverse compression of the M_1 trigonid and increase in relative importance of the protoconid. The relatively large P_3 and wide trigonid of M_1 in *Ankotarinja* are unmatched among living dasyurids. Even in *Neophascogale* the M_1 trigonid is transversely compressed with gross reduction of the paraconid. In *Ankotarinja* the M_1 paraconid is very low on the trigonid but not strongly deflected out of alignment with the other lingual cusps such as occurs in most dasyurids. The closest match among dasyurids is found in species of *Sminthopsis*, *Murexia*, and *Keeuna* but even here, the M_1 paraconid is shifted anteriorly relative to that cusp in *Ankotarinja*. A relatively wide trigonid on M_1 occurs in most didelphoids, and in part, reflects the relatively large P_3 in most of these forms. In dasyurids which show premolar reduction, it is P_3 which is reduced or lost in the lower dentition (including the interesting case of *Planigale gilesi* Aitken, 1972; Archer 1976a), while in didelphoids and borhyaenids it is P_1 which is normally reduced. The only marked exception are species of *Zygolestes* Ameghino, 1898, which are unique among didelphids in having an extremely reduced, although two-rooted, P_3. Reig (1957) notes that in the M_1 the paraconid is more buccal in position than is normal for the group. This modification is much less than that seen in the trigonid of dasyurids with a comparably reduced P_3. Reduction of P_3 normally occurs among dasyurids which exhibit a compressed cheek-tooth row, increased carnassiality as judged by proportionate increase in metacrista-paracristid length, enlarged canines, etc. (Archer 1976b). Attendant reduction of the M_1 paraconid and increase in size of the M_1 protoconid shift the premolariform-molariform boundary posteriorly. The M_1 trigonid functions as a stabbing, piercing premolar rather than a sectorial trigonid. Further, in dasyurids which have lost P_3, such as *Dasyurus* Geoffroy, 1796 and *Sarcophilus*, the metacrista-paracristid length of M_3 is greater than that of M_2 or M_1. The net effect is to concentrate the sectorial function of the molars at a point posterior of the middle of the molar row. Posterior shift of the premolariform-molariform boundary may be seen in this way as merely maintaining the structurally ancestral relationship between these two types of teeth.

Ankotarinja is clearly structurally ancestral in this regard and more similar to didelphids than dasyurids.

Position of the cristid obliqua

The M_3 cristid obliqua of *Ankotarinja tirarensis* is unlike almost all dasyurids in that it intersects the trigonid at a point so far buccal to the metacristid carnassial notch. This condition is approached in *Neophascogale* and to a lesser extent in *Keeuna*, while in other dasyurids the cristid obliqua tends to intersect the trigonid just buccal to the carnassial notch. In some dasyurids (e.g. *Neophascogale* and *Dasyurus*) the protoconid flank contributes to the cristid obliqua on M_{1-3}, and this same condition occurs in *Ankotarinja*, at least on M_3. Clemens (1966) suggests that lower teeth (except perhaps dP_4) of pediomyids can be distinguished from species of *Alphadon* in that the crista obliqua in pediomyids intersects the base of the trigonid well buccal to the metacristid fissure. This pediomyid condition is also present in all modern didelphids examined in the present study and appears to be present in illustrations of species of many of the South American fossil didelphines. The condition in *Ankotarinja* is closer to this pediomyid and didelphine condition than it is to most modern dasyurids or *Alphadon*.

Although the functional significance of this difference is not clear, a relatively more buccal position produces a larger talonid basin. Position of the cristid obliqua must also reflect position of the paracone, a more buccal position indicating a relatively reduced or more buccally situated paracone.

The condition found in *Ankotarinja* and some dasyurids (e.g. *Dasyurus*) of a small anterior component of the cristid obliqua formed by the protoconid flank results in the development of a small accessory carnassial notch against which shears the paracone. This makes an effective point-cutting unit that supplements those developed on the trigonid.

Transverse metacristid

In *Ankotarinja* the metacristids are transverse to the long axis of the dentary. In dasyurids, this condition is present only in species of *Sminthopsis*, *Antechinomys* Krefft, 1867, and to a lesser extent, species of *Ningaui* and some species of *Planigale*. In other dasyurids, the metaconid is displaced posteriorly relative to the protoconid resulting in the metacristid and paracristid forming a more obtuse angle. The transverse condition is present among some but not all modern didelphines, some Cretaceous didelphoids, and many Tertiary didelphids.

Among dasyurids, markedly non-transverse metacristids occur only in the more carnivorous forms. This structural trend is noted by Bensley (1903) who regards it as modification towards longitudinal and away from transverse shear. In this respect, the lower molars of *Ankotarinja* demonstrate the structurally primitive insectivorous condition, which is more common among didelphids.

Stylar cusp size and position

Terminology of the stylar cusps of *Ankotarinja* used here is set out elsewhere (Archer 1976b).

The stylar cusp condition in *Ankotarinja* is closer to that of didelphids than dasyurids in having a large stylar cusp posterior to stB, anterior to stD and buccal to the low point in the para-metacrista of M^3, which is the homologue of the normal didelphid and variably present, but invariably small, dasyurid stC. Further, stD in *Ankotarinja* is smaller and slightly more posterior in position than that cusp in modern dasyurids. These non-dasyurid-like features are common among Cretaceous didelphines such as glasbiines, some species of *Alphadon* and *Pediomys*.

Stylar cusps do not have occlusal counterparts in lower molars, yet they clearly sustain wear. This wear must result from food abrasion during initial puncturing prior to the cutting or shearing occlusal phase. As the dentary closes, force is applied to food trapped between teeth by the lower molars in opposition to the whole of the upper molars including the stylar shelf. The area of the crushing or puncturing surface is increased by larger stylar cusps. In marsupicarnivores, stylar cusp reduction occurs in the more carnivorous forms such as *Sarcophilus*, *Thylacinus* Temminck, 1824, and borhyaenids where perhaps the puncturing value of these cusps is overshadowed by the need to have large and sturdy shearing crests. The stylar cusp size and arrangement in *Ankotarinja* may therefore be interpreted as evidence for insectivorous rather than carnivorous habits.

Metaconule development

In *Ankotarinja* the metaconule of the upper molars is a prominent feature, while the protoconule is not present in M^3. Conule development is present in some dasyurids and many didelphids. It is well-developed in most Cretaceous didelphines where both protoconules and metaconules occur. Simpson (1928) notes that these cusps in recent didelphids are represented at most by vestiges.

The possible functional significance of metaconules is discussed elsewhere (Archer 1971). In addition, well-developed metaconules may serve as shearing counterparts for the hypoconid and buccal edge of the hypocristid.

Summary

The dentition of *Ankotarinja* resembles that of many didelphids, and some dasyurids such as *Neophascogale*, *Murexia*, and *Sminthopsis*. Because of the middle Miocene age of the deposit, as well as the fact that two relatively more modern-type dasyurids (*Keeuna* and an unnamed form noted by Stirton, Tedford, & Miller 1961) are in the same deposit, it would be absurd to regard *Ankotarinja* as the ancestral dasyurid. However, it does preserve characters which could be regarded as structurally ancestral to modern dasyurids. It is clear that many South American Tertiary didelphines of Paleocene age (Graham & Ride 1967) share characters with *Ankotarinja* which it does not share with modern dasyurids. Taking into account all available morphological characters together with what is currently known of their distribution, and recognizing that the characters (incisor number and dP4 morphology) which will distinguish between the two lineages Dasyuroidea and Didelphoidea are not preserved, one cannot avoid concluding that the data available indicate a marsupicarnivore, probably belonging to the Dasyuroidea, but which, like the slightly older phalangeroid *Wynyardia* Spencer, 1900 (Ride 1964b), also

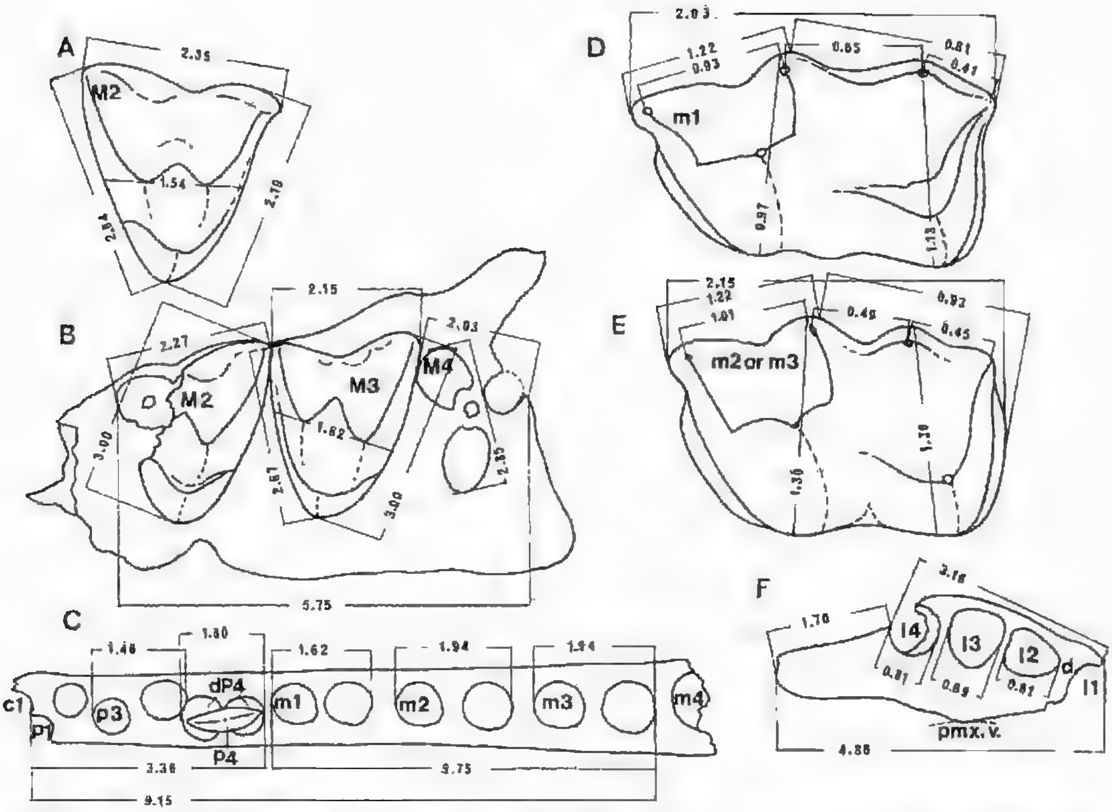

Fig. 6. Specimens of *Keeuna woodburnei* and their measurements (mm). *A*, Holotype, P18191, RM^{2}. *B*, F7333, maxillary fragment with LM^{2} (broken), LM^{3} and alveoli for LM^{4}. *C*, UCR, 15346, dentary fragment with LP$_{4}$ erupting and alveoli for LC$_{1}$-M$_{4}$. *D*, F7334, LM$_{1}$. *E*, UCR, 15344, LM$_{2}$ or M$_{3}$. *F*, tentatively referred to *K. woodburnei*, UCR, 15347, premaxillary fragment, with alveoli for RI^{1}-^{4}: d represents diastema between alveoli for RI^{1} and RI^{2}; pmx.v. represents edge of premaxillary vacuity.

retains a number of characters of a sort which reveals its derivation from early Tertiary didelphoids or the didelphoid-dasyurid stem. If it should be discovered that *Ankotarinja* possesses a didelphoid incisor number, the author will have no hesitation in describing it as a didelphoid with characters foreshadowing dasyurids, but it is clear that it is far too late in time to be an ancestor to the whole dasyurid family. For the present, it is listed as ?Dasyuridae.

Genus KEEUNA nov.

Type species; Keeuna woodburnei sp. nov. (by designation and monotypy).

Generic diagnosis: Differs from other Australian and New Guinean dasyurids including *Ankotarinja* in combining relatively reduced stD on M^{2}-^{3}, large M^{4}, antero-posteriorly shortened M^{4}, and virtually absent posterior cingulum on M^{2}-^{3} (although mild posterior cingular swelling present on holotype), and relatively unreduced P$_{4}$.

Origin of generic name: Kee, central Australian Aboriginal word for wild cat; *una*, central Australian Aboriginal word for forgotten (Smith 1880). *Keeuna* is here given masculine gender.

Keeuna woodburnei sp. nov.

FIGS 6–8

Holotype: P18191, isolated RM^{2}.

Type locality: Tedford locality, Etadunna Formation, Lake Palankarinna, Etadunna Station, S.A. (28°47′S, 138°25′E).

Diagnosis: That of genus. Relative development of entoconids, stylar cusps, and size may prove to be diagnostic species characters.

Origin of specific name: The specific name is in honour of Dr M. O. Woodburne who helped find all of the material referred to this species and who, with Dr W. A. Clemens, gave the author his first opportunity to study Australian Tertiary fossils.

Referred specimens: UCR, 15271, RM^{4}; F7333, left maxillary fragment with M^{3} and part of M^{2}; UCR, 15347, right premaxillary fragment; UCR, 15344, isolated LM_{1}; UCR, 15348, left dentary fragment; UCR, 15286, trigonid RM_{1}; UCR, 15269, trigonid RM_{4}; UCR, 15274, isolated M_{2}; UCR, 15345, left dentary fragment; UCR, 15346, dentary fragment with LP_{4} erupting; F7334, isolated LM_{1}.

Description

Maxillary fragment (F7333) has LM^{3}, posterior part LM^{2}, and alveoli for LM^{4}. M^{4} narower than M^{3} but relatively little reduced antero-posteriorly, being only slightly shorter than M^{3}. Metacone root M^{4} large, equivalent in size to protocone root, and only just smaller than paracone root. Interdental fenestrae occur between M^{2} and M^{3} and between M^{3} and M^{4}. Maxillary root of zygomatic arch arises buccal to M^{3-4}. Infraorbital canal opens on anterior edge of maxillary fragment, dorsal to anterior end M^{2}.

Premaxillary fragment (UCR, 15347) may represent *K. woodburnei* on basis of size, because larger than would be expected for other known Ngapakaldi forms. Four alveoli present. Largest represents RI^{1} (alveolus broken). This alveolus separated from alveolus for RI^{2} by very short diastema. Alveoli for RI^{2-4} contact one another. RI^{1} alveolus inclined posteriorly and suggests RI^{1} inclined antero-ventrally. Based on alveolar size, RI^{1} largest incisor, RI^{2} exceeded RI^{4} in length which exceeded RI^{3} in length. This may be misleading since posterior lobe of RI^{4} (occurrence of which is not uncommon among modern dasyurids) may have caused this tooth to be longer than RI^{2}. Also, root for RI^{1} commonly large in modern dasyurids, while crown may be very reduced. Posterior to RI^{4} alveolus, premaxillary wall descends into pit which is occlusal counterpart of RC_{1}, indicating RC_{1} large and caniniform.

M^{2} with continuous anterior cingulum connecting parastylar corner of tooth to preprotocrista (piece of enamel missing from anterior cingulum of holotype). Posterior cingulum absent (F7333) to doubtfully present (P18191) as swelling at base of crown above metacone root. Swelling not continuous with postprotocrista whereas this is the case in modern dasyurids with undoubted posterior cingula. Five distinct buccal cusps present. StA occurs at buccal end of anterior cingulum, between parastylar corner of tooth and stB. Almost vertical, minor crest connects stA to parastylar corner of tooth, that part of tooth which would overlap postero-buccal edge of P^{4}. Very minor, more gently inclined crest conects stA to stB. StB connected to paracone by long paracrista. Buccal crest extends posteriorly from stB to contact small, low stC which is adjacent to another small low stylar cusp of uncertain homology. These two stylar cusps not connected by crest. The posterior small cusp connects to larger stD by minor, inclined crest. StD largest stylar cusp, but smaller than that cusp in M^{2} of modern dasyurids. StD connects to metastylar corner of tooth by long, low crest. No evidence of stE. From metastylar corner of tooth, three crests radiate: buccal crest to stD; metacrista to metacone; and minor short crest that extends antero-lingually from metastylar corner and ends within short distance of tooth corner. Crescentic enamel ridge occurs lingual to mid-point of ectoloph, and buccal to mid-point of para-metacrista. Ridge may represent cusp analogous to similar structure in some specimens of *Sminthopsis virginiae* Tarragon, 1847. Paracone shorter than metacone, and two cusps widely separated. Small but clear metaconular ridge extends from base of metacone to middle of postprotocrista. Postprotocrista terminates as steep-sided crest adjacent to base of metacone. Deep pyramid-shaped fossa exists between bases of paracone and metacone and buccal flank of protocone. Metacrista approximately 1.5 times length paracrista. Ectoflexus in ectoloph slight, point of inflection immediately posterior to stC.

M^{3} with continuous anterior cingulum. Posterior cingulum absent. At least four stylar cusps present. Parastylar extension of tooth small and accordingly little overlap of metastylar corner of M^{2} occurs. StC connected to stB as in M^{2}. On anterior flank of cusp called stC (F7333), small, possibly distinct swelling occurs which may be homologous with stC of M^{2}. If so, cusp posterior to that cusp in M^{2} might be homologous with single conspicuous cusp in this position on M^{3}. Posterior to stC of M^{3} is slightly larger stD. Posterior to stD, and connected to it by crest, is stE. This cusp extends posteriorly as ridge which terminates short of metastylar corner of tooth. Only metacrista radiates from metastylar corner of tooth. Lingual to stC, as in M^{2}, crescentic ridge occurs which may be distinct cusp. In addition

TABLE 2

Unusual characters of *Keeuna*	*Keeuna*	*Didelphopsis*	*Peradectes*	*Alphadon*	*Pediomys*	*Marmosa*	*Monodelphis*	*Didelphis*	*Murexia*	*Neophascogale*	*Phascolosorex*	*Sminthopsis*	*Ningaui*	*Antechinus*	*Ankotarinja*
1. Large M$^4_4$	+	+	+	+	+	+	+	+	—	+	+	—	—	—	+
2. M^x lack post. cing.	+	+	+	+	—	+	+	+	—	—	—	+	+	+	+
3. Small stD	+	+	+	+	+	+	+	—	—	—	—	—	—	—	+
4. Compressed M$^4_4$	—	—	—	—	+	+	+	—	+	—	—	—	+	+	—

to metaconular ridge, as in M^2, clear metaconular swelling present on postprotocrista. No clear protoconule or protoconular ridge present. Metacrista less than 1.5 times length paracrista. Ectoflexus M^3 broad and relatively deep. Point of inflection in ectoflexus occurs anterior to stC. Otherwise morphology of M^3 as in M^2.

Dentary with two branches of inferior dental canal, one emerging at point level with middle of M$_1$ on buccal surface of dentary while other emerges at point beneath posterior root P$_1$ (latter condition determined from juvenile dentary, UCR, 15346). UCR, 15346 only specimen with premolar alveoli preserved. P$_3$ erupting in this specimen. As result, apparently crowded premolar condition may become less crowded in adult dentary. Premolar gradient suggested by alveoli; P$_1$ shorter than P$_3$ which is subequal in length to P$_1$. DP$_4$ alveoli suggest tooth as large as P$_3$ and two-rooted. P$_1$ alveoli acutely oblique with anterior root postero-buccal to C$_1$ alveolus. Posterior root P$_1$ immediately posterior to C$_1$ alveolus. P$_3$ and dP$_4$ alveoli suggest teeth only mildly out of alignment (although crown alignment need not be reflected in root alignment). C$_1$ alveolus relatively small, suggesting tooth no wider than P$_3$.

P$_3$ partly erupted and partly obscured. Tooth single-cusped with tall protoconid. Paracristid steep. No anterior cingulum cusp. Metacristid more gently inclined and appears to directly contact very small posterior cingulum cusp. No buccal or lingual cingula evident.

M$_1$ talonid wider than trigonid, and trigonid more laterally compressed than that structure in *Ankotarinja*. Anterior cingulum relatively well-developed, terminating lingually with hypoconulid notch, and terminating buccally anterior to buccal base of protoconid. Posterior cingulum slightly shorter than anterior cingulum and extends to contact hypoconulid. Pronounced cingulum development, as bulge between bases of protoconid and hypoconid. No lingual cingulum. Paraconid low on crown, approximately same height as entoconid. Protoconid tallest trigonid cusp. Metaconid just shorter than protoconid. Hypoconid subequal to entoconid in height. Paracristid complete between protoconid and paraconid, and anterior part of crest steeply inclined. Metacristid and apparently paracristid fissures extend below cutting edges of crests. Crest descends from posterior wall of metaconid and meets crest from anterior wall of entoconid. Two crests meet with shallow, open fissure. Crest development from posterior wall of entoconid slight to absent. No crest links entoconid and hypoconulid. Hypocristid extends posterolingually from hypoconid to hypoconulid. Both hypocristid and metacristid clearly not transverse to long axis of tooth. Cristid obliqua intersects trigonid well buccal to point below metacristid fissure.

Isolated molars posterior to M$_1$ not been positively identified. UCR, 15274 and UCR, 15344 tentatively regarded as representing M$_2$ and M$_3$ respectively. This conclusion based on trigonid width and paraconid height. Both increase posteriorly in most modern dasyurids between M$_1$ and M$_4$.

UCR, 15274, LM$_2$, trigonid just narrower than talonid. Hypoconulid notch between parastylid and lingual end of anterior cingulum larger than in M$_1$. Cingulum development between base of protoconid and hypoconid does not produce buccal convexity in crown outline. Paraconid higher on crown than in M$_1$. Paracristid fissure well-developed below crest. Cristid obliqua intersects trigonid and extends short way up trigonid wall at point lingual to point of same intersection in M$_1$. Otherwise morphology UCR, 15274 same as M$_1$.

UCR, 15344, LM$_3$, trigonid and talonid subequal in width. Hypoconulid notch larger than in M$_1$ but subequal to that of M$_2$. Posterior cingulum less convex posteriorly than in $M_{/1}$ or $M_{/2}$. Also, posterior cingulum extends lingually and contacts hypoconulid rather than stopping short of it as in $M_{/1}$ and $M_{/2}$. Basal cingulum between protoconid and hypoconid well-developed but does not cause buccal convexity. Crests linking metaconid and entoconid less-developed than in $M_{/1}$ and $M_{/2}$ (although $M_{/3}$ damaged in this region). Cristid obliqua intersects trigonid as in $M_{/2}$. Otherwise morphology $M_{/3}$ as in $M_{/1}$.

Discussion and comparison

A summary of important dental characters in marsupicarnivores in general is given elsewhere (Archer 1976b) and to avoid repetition, discussion of dental characters of *Keeuna* is largely restricted to those characters which either make *Keeuna* unusual among the Dasyuridae or suggest affinities outside of that family. Comparison within the Marsupicarnivora is restricted to the Dasyuridae and Didelphidae, because no other families contain forms even remotely similar to *Keeuna*.

Keeuna cannot be referred conclusively to the Dasyuridae for the same reasons given above in the discussion of *Ankotarinja*. However, the features of *Keeuna* are more suggestive of known dasyurids than didelphids. If the referred premaxilla does in fact represent *Keeuna*, there is no reason to doubt its reference to the Dasyuridae. This specimen shows alveoli for four incisors. The diastema behind the anterior alveolus confirms that the anterior alveolus represents $I^{1/}$. No dasyurid or didelphid known to the author has a diastema within the incisor row posterior to $I^{3/}$ or anterior to $I^{5/}$, other than a variably present diastema between $I^{1/}$ and $I^{2/}$.

Although the dental characters of *Keeuna* are all present in one dasyurid or another, considered together: 1, the large $M^{4/}$ (inferred from alveoli); 2, virtual lack of a posterior cingulum on the upper molars; 3, relatively reduced stD on $M^{3/}$; and 4, antero-posteriorly shortened $M^{3/}$; they make *Keeuna* unique among dasyurids. These characters are compared in Table 2 for didelphids and dasyurids which provide the closest similarities in upper molar morphology to *Keeuna*. Many South American Tertiary didelphids which have a lower molar morphology (e.g. *Mirandatherium*, Paula Couto 1962, fig. 4) similar to that of *Keeuna*, are unrepresented by upper molars and not included in Table 2. Characters 1–4 are the same as noted above. A "+" records a condition similar to or closely approaching that found in *Keeuna*. A "?" indicates either that the dentition is too incomplete or poorly preserved to enable determination. A "—" indicates a condition unlike that in *Keeuna*. Polytypic genera which have some forms similar to but others differing from *Keeuna* are recorded only as "+-". M^x indicates any or all upper molars.

$M^{4/}$ size

The possible significance of a large $M^{4/}$ is discussed above. *Keeuna* exhibits similarities in this regard to many didelphids but only a few structurally ancestral dasyurids, including *Ankotarinja*.

Posterior cingula on upper molars

Elsewhere (Archer (1976b) it has been noted that cingula have the effect of increasing molar surface area. It is also possible that posterior cingula on upper molars act as supplementary shearing crests in opposition to the paracristids which come into effect after the paracristids shear past the metacrista. Distribution of this character in modern dasyurids (Archer 1976b) does not appear to lend itself to phylogenetic interpretation, being present in some but not other species of single genera such as *Antechinus*. Absence in *Keeuna*, although perhaps phylogenetically unimportant, is useful in combination with other characters for differentiating the genus.

Stylar cusp D

Small size of this cusp allies *Keeuna* with *Ankotarinja*, as well as with many didelphids.

The possible significance of stylar cusp size is discussed above in regard to *Ankotarinja*.

Compressed $M^{3/}$

$M^{3/}$ of *Keeuna* is longitudinally compressed in comparison with structurally ancestral dasyurids such as *Neophascogale* but not in comparison with structurally derived dasyurids such as *Sminthopsis* whose molars are even more compressed. Bensley (1903) notes relative compression in some dasyurids and regards this as a more insectivorous than carnivorous adaptation. Extremes of non-compression, such as occur in *Sarcophilus*, result in shearing crests which approach longitudinal rather than a transverse orientation.

Detailed comparisons

Overall, *Keeuna* more closely resembles some dasyurids including *Phascolosorex*, *Neophascogale*, some *Antechinus*, *Murexia*, and *Ankotarinja*, than it does didelphids. Particular similarities and differences are noted below.

Similarities which extend to all dasyurids are not noted.

Phascolosorex: Similarities include relatively large $M^4/$ and metaconule. Upper molars of *Keeuna* differ from those of *Phascolosorex* (e.g. AMNH. 109758, 151992, 101975 and 109757) in that stylar cusps much closer to buccal edge of crown; small stylar cusp occurs lingual to stC (although in some specimens of species of *Phascolosorex* such as AMNH, 151992, this cusp suggested on $M^3/$); $M^3/$ shorter antero-posteriorly; paracrista and metacrista enclose more acute angle; and $M^1/$-$^4/$ lack clear posterior cingula. In lower molars of *Keeuna*, trigonid and paraconid of $M/_1$ much less reduced; crests from posterior face of metaconids much better-developed; talonid $M/_1$ relatively slightly wider.

Neophascogale: Large $M^4/$ of *Keeuna* similar to that of *Neophascogale* (e.g. AMNH, 109524). Differences in upper molars of *Keeuna* include those noted above in comparison with *Phascolosorex* as well as lack of distinct antero-lingual low crest developed on base of protocone (which has nothing to do with preprotocrista); ectoloph and para-metacrista relatively more widely separate at their closest point; protoconule slightly better-developed. Lower molars *Keeuna* differ in having less reduced $M/_1$ trigonid; relatively shorter, wider molars; cristid obliqua which intersects trigonid in relatively more lingual position (notable in $M/_2$-$/_3$); lack of post-entoconid crest which directly connects to hypoconulid; relatively lower talonids, higher trigonids; relatively shorter talonids.

Antechinus: Resemblance with some *Antechinus* (e.g. *A. mayeri* (Rothschild & Dollman, 1930), AMNH, 109816, *A.* sp., AMNH, 190877 from New Guinea, and *A. melanura* (Thomas, 1899), WAM, M5517) considerable including overall proportions of $M^2/$-$^3/$; somewhat similar reduction of stD on $M^3/$; relatively unreduced $P/_4$. Upper molars *Keeuna* differ in that stD relatively slightly more reduced on $M^3/$; stB relatively more posterior on ectoloph; all stylar cusps relatively smaller; $M^1/$-$^3/$ somewhat shorter antero-posteriorly; $M^4/$ notably longer in proportion to length of $M^3/$; posterior cingula absent; metacone and paracone $M^2/$-$^3/$ relatively closer in height; larger, more conspicuous cusp or crest occurs lingual to stC; ectoflexus in relatively more posterior position; protocone shorter antero-posteriorly at its longest point. Lower molars *Keeuna* differ in having less-compressed trigonid on $M/_1$ with larger paraconid; relatively wider talonid on $M/_3$; lack complete buccal cingulum such as occurs on $M/_1$-$/_4$ of some *Antechinus* species (e.g. *A. mayeri*); lower molars relatively shorter, wider; entoconids $M/_2$-$/_3$ relatively taller; hypoconulid wider and extends farther from postero-lingual corner of $M/_1$-$/_3$.

Murexia: Similarities between species of *Murexia* (e.g. *M. longicaudata* (Schlegel 1866) (AMNH, 101972 and 152035)) include comparable relative length of $M^3/$; relatively unreduced $P/_4$. Upper molars of *Keeuna* differ in same features from *Murexia* as they do from molars of *Antechinus* except as follows. In *Keeuna*, all stylar cusps except C relatively smaller; posterior cingulum of upper molars virtually undeveloped (although only slight posterior cingular development occurs in species of *Murexia*); $M^3/$ relatively longer; metaconular crest from base of metacone less well-developed and lacks low, minor crest linking stD with metacone (latter observed only in unworn specimens of *Murexia* examined in this study, AMNH, 152035). Lower molars of *Keeuna* differ in same features from teeth of *Murexia* that differentiate teeth of *Antechinus*, except as follows. In lower molars of *Keeuna* entoconids relatively shorter antero-posteriorly, and higher; buccal cingulum absent (occurs in one specimen of *Murexia*, AMNH, 152035); low direct crest linking posterior face of entoconid with hypoconulid absent.

Ankotarinja: Comparison with much smaller *Ankotarinja* demonstrates that both forms similar in having relatively small stylar cusps (particularly stD); stylar cusp(s) present between B and D; no posterior cingulum; complete anterior cingulum; slightly smaller paracones than metacones; lack of direct crest linking entoconid with hypoconulid; relatively large $P/_4$; unreduced trigonid and paraconid of $M/_1$. Upper molars of *Keeuna* differ from those of *Ankotarinja* in larger size and more anterior position

Fig. 7. *A-E*, scanning electron microscope photographs of *Keeuna woodburnei*. *A*, Holotype, P18191, $RM^2/$, stereo photographs. *B*, tentatively referred to *K. woodburnei*, UCR, 15347, premaxillary fragment with alveoli for $RI^2/$-$^3/$ and posterior edge of alveolus for $RI^4/$. *C*, F7334, $LM/_4$. *D*, UCR, 15344, $LM/_2$ or $LM/_3$. *E*, UCR, 15346, dentary fragment with unerupted $LP/_4$ and alveoli for $LP/_1$-$M/_3$ and edges of alveoli for $LC/_1$ and $LM/_4$.

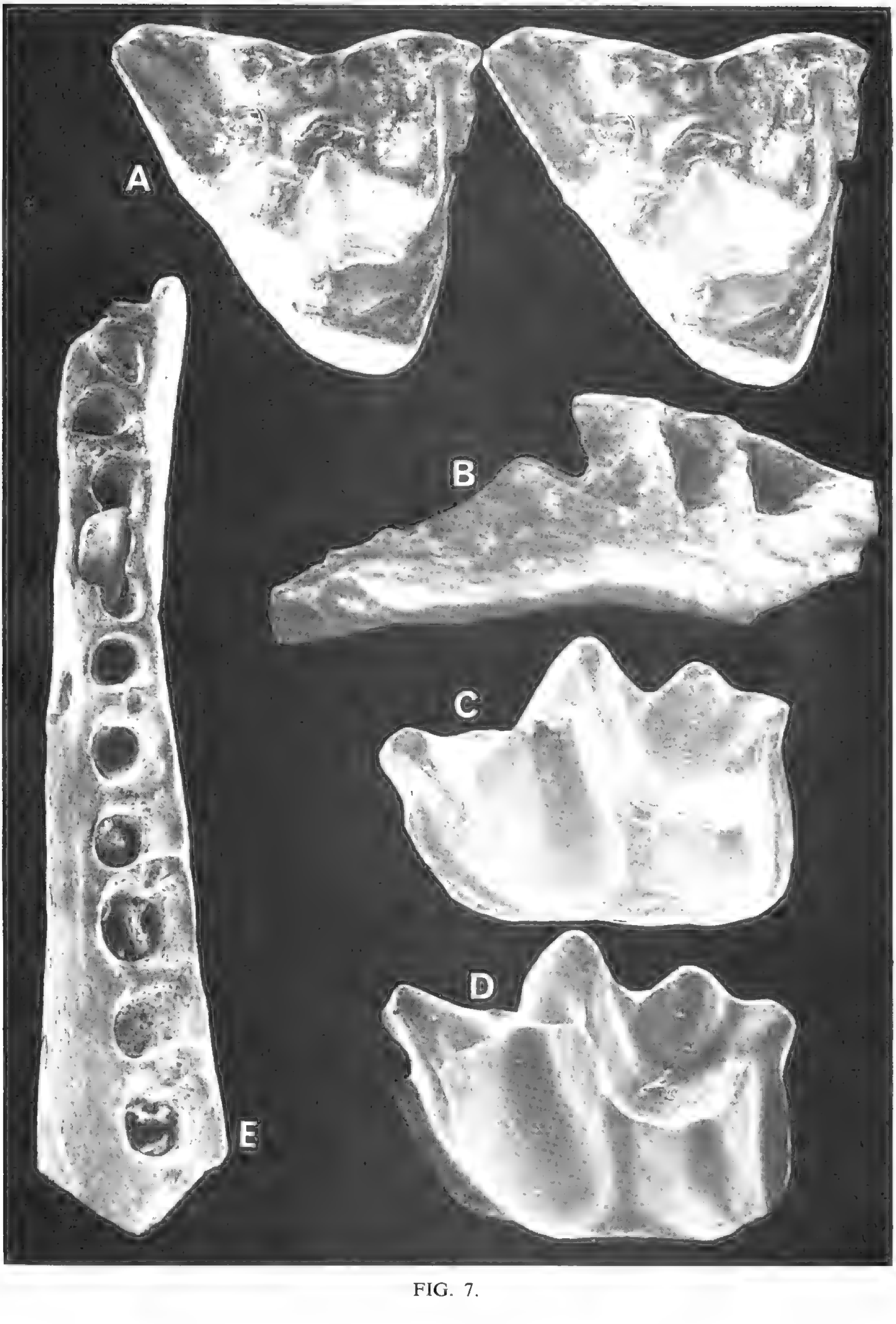

FIG. 7.

FIG. 8.

of stD on $M^{2/\text{-}3/}$; number of cusps in position of stC; presence of stylar crest lingual to stC; less well-developed metaconule; presence of deep pit between bases of paracone and metacone. Lower molars of *Keeuna* differ in having longer metacrista; relatively larger $M^{4/}$; more lingual intersection of cristid obliqua and trigonid; non-transverse metacristid and hypocristid; large hypoconulid of $M_{/4}$; antero-posteriorly non-compressed trigonids; relatively unequal heights of the paraconids and metaconids. Differences in position of intersection of cristid obliqua and trigonid in *Ankotarinja* and *Keeuna* not one of kind, but degree, position being relatively more lingual in *Keeuna*.

Other comparisons: No other dasyurids warrant detailed comparisons. Most didelphids reveal fewer similarities, particularly if the referred premaxillary fragment of *Keeuna* does in fact belong to this form. General similarities with Cretaceous didelphines (e.g. some species of *Alphadon* such as *A. rhaister*) include the paracone, which although smaller than the metacone, is not markedly so. Other similarities between *Keeuna* and species of *Alphadon* include relatively reduced stylar cusps (except B), particularly D on $M^{3/}$ of species such as *A. rhaister* and *A. lulli* Clemens, 1966, and presence of stylar cusp or crest lingual to stC in *A. rhaister*. Marked differences in upper molars of *Keeuna* include much smaller proto- and metaconules; less-deeply concave and symmetric ectoloph of $M^{3/}$; smaller stB; and absent posterior cingulum (present in some species of *Alphadon*). In lower molars, similarities between *Keeuna* and species of *Alphadon* include relatively unreduced trigonid of $M_{/1}$. Differences in lower molars of *Keeuna* include much smaller paraconid relative to metaconid in $M_{/2\text{-}/3}$ as opposed to specimens referred to species of *Alphadon* (Clemens 1966, Lillegraven 1969).

Compared with holarctic Tertiary didelphines, relative size of paracone in *Keeuna* is similar to condition seen in species of *Peradectes* and *Peratherium*. Other similarities include relatively low stylar cusps; unreduced condition of $P_{/4}$ (and presumably $P^{4/}$) and $M_{/1}$ paraconid; lack of posterior cingulum on upper molars; relatively shallow indentation of ectoloph; extreme buccal position of stylar cusps; and evidently non-transverse orientation of metacristid and hypocristid. Differences in *Keeuna* include relatively larger stylar cusps (particularly D); relatively poorly-developed metaconule; non-pediomyid-like cristid obliqua orientation; relatively taller metaconid and entoconid, and shorter paraconid; and presence of rudimentary buccal cingulum between bases of protoconid and hypoconid. Despite these differences, *Keeuna* more closely resembles these didelphines than any others for which good illustrations or photographs are available.

Close similarities may exist between *Keeuna* and some Paleocene (Riochican) didelphids. Unfortunately very few are known from upper teeth and few are adequately illustrated. As noted above, all modern didelphines examined, and most Tertiary didelphines exhibit a pediomyiid type of cristid obliqua, which differs from *Keeuna*. Of all Paleocene forms illustrated by Paula Couto (1952, 1962, 1970) and Simpson (1947), *Mirandatherium* is perhaps most like *Keeuna*. *Keeuna* differs from this didelphid in relatively smaller size of $P_{/4}$ and presence of buccal cingulum developed between bases of protoconid and hypoconid. Upper molars of *Mirandatherium* are unknown.

Other didelphids do not reveal enough similarities to warrant separate comparisons.

Summary

Teeth of *Keeuna*, although resembling teeth of some Tertiary didelphines such as species of *Peratherium*, *Peradectes*, and *Mirandatherium*, are broadly similar to teeth of some modern dasyurids such as New Guinean *Antechinus*. In view also of the Australian locality of *Keeuna* it seems most logical to regard this form as a somewhat unusual dasyurid, probably without direct descendants in the modern dasyurid fauna. Resemblances between upper molars of *Ankotarinja* and *Keeuna* further suggest the possibility that these two forms are more closely related to each other than either is to other dasyurids, thereby placing *Keeuna* in a structurally intermediate position between *Ankotarinja* and modern dasyurids.

Discussion of Etadunna marsupicarnivores

Stirton, Tedford, & Miller (1961, p. 35) briefly describe (but not name) another carnivore from the Etadunna Formation. According to their description "The size of the animal is comparable to *Dasyurus quoll* . . . The three

Fig. 8. *A-C*, scanning electron microscope photographs of *Keeuna woodburnei*, F7333, maxillary fragment with partial $LM^{2/}$, $LM^{3/}$ and alveoli for $LM^{4/}$. *C*, stereo photographs.

premolars with gradation in size from $P_{/1}$ to $P_{/3}$ and the absence of the metaconid on $M_{/1}$ suggests that this animal may not be far removed from the ancestry of *Thylacinus*". The author has seen drawings and photographs of this specimen (courtesy Dr W. A. Clemens and Mr C. Campbell) and it is clear that nothing else about the specimen, including the morphology of the upper molars, shows any similarity to *Thylacinus*. On the contrary, it appears to represent another dasyurid lineage (perhaps related to *Dasyurus*) in which metaconid reduction has occurred only on $M_{/1}$. This unnamed dasyurid and *Keeuna* are the only Etadunna carnivores which can be referred with some confidence to the Dasyuridae.

Ankotarinja is either a didelphid or dasyurid. Compared with known didelphoids, dasyuroids and perameloids, the preserved portions of *Ankotarinja* do not enable confident reference to a particular marsupial family. It is referred to here as ?Dasyuridae.

Ankotarinja and *Keeuna* compared with modern dasyurids, share most dental characters with living New Guinean species of *Neophascogale*, *Phascolosorex*, and *Antechinus*. Similarities with Australian forms are fewer and those that do exist are with forms found in generally non-arid Australian habitats. Broad $M_{/4}$ talonid, large $M^{1/}$, narrow and relatively uncrowded premolar row, and large entoconids are characters either lacking or rare in Australian arid-adapted dasyurids. Several authors (e.g. Woodburne 1967, Schodde & Calaby 1972, Stirton, Tedford, & Woodburne 1968) indicate that New Guinea has many mammals (e.g. species of *Dendrolagus* Muller, 1839, *Dorcopsis* Schlegel & Muller, 1839, *Distoechurus* Peters, 1874, *Microperoryctes* Stein, 1932, *Murexia*, *Myoictis*, *Neophascogale* and *Phascolosorex*) from highland rainforest habitats which appear to be structurally ancestral within their respective families.

Evidence for a less-arid central Australia during Ngapakaldi time is reviewed by Stirton, Tedford, & Woodburne (1968). In addition, pollen from the base of the Etadunna Formation, recently obtained from bores in South Australia, has been found to include *Nothofagus* sp. (pers. comm., W. K. Harris, South Australian Department of Mines), a genus of plants presently restricted in the Australian region to the high-rainfall habitats of eastern Australia, New Guinea and New Zealand. Resemblance between Ngapakaldi marsupicarnivores and living New Guinean dasyurids, suggests these living highland New Guinean dasyurids may have avoided certain selective pressures brought to bear on marsupicarnivores living in central Australia, following Ngapakaldi time. These pressures may have included progressive deterioration of climate with increasing aridity. Elsewhere, as part of revision of the dasyurid genus *Sminthopsis*, the author has given evidence for believing that several Australian dasyurid lineages underwent arid-adaptation. Arid-adapted forms now dominate the majority of Australia and are in clear contrast to the marsupicarnivores of the Ngapakaldi local fauna described here.

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SOUTHERN AUSTRALIAN SPECIES OF *CHAMPIA* AND *CHYLOCLADIA* (RHODYMENIALES: RHODOPHYTA)

BY D. J. REEDMAN AND H. B. S. WOMERSLEY*

Summary

REEDMAN, D. J., & WOMERSLEY, H. B. S. (1976).-Southern Australian species of *Champia* and *Chylocladia* (Rhodymeniales: Rhodophyta). *Trans.* R. *Soc. S. Aust.* **100** (2), 75-104, 31 May 1976.

Five species of *Champia* are recognised on southern Australian coasts. *C. viridis* C. Ag. (including *C. tasmanica* Harvey, *C. oppositifolia* J.Ag., and *C. verticillata* J.Ag.) resembles the type species *C. lumbricalis* (L.) Desvaux from South Africa] in having numerous scattered longitudinal filaments passing through the diaphragms of the thallus. *C. insignis* Lucas from Tasmania also has scattered longitudinal filaments. Three other species, *C. affinis* (Hook. & Harv.) J. Ag. (including *C. obsolete.* Harvey), *C. zostericola* Harvey (including var. *arcuata* Hook. & Harv. of *C. affinis)* and *C. parvula* (C.Ag.) Harvey var. *amphibolis* var. nov., have only peripheral longitudinal filaments in the thallus. Australian records of the South African *C. compressa* Harvey probably apply to juvenile *C. tasmanica* or to a probably undescribed species on the N.S.W. coast.

One species of *Chylocladia,* C. *grandis,* is newly described. Other Australian species previously referred to *Chylocladia* belong to *Lomentaria* or are relegated to synonyms.

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One species of *Chylocladia*, *C. grandis*, is newly described. Other Australian species previously referred to *Chylocladia* belong to *Lomentaria* or are relegated to synonyms.

Introduction

Champia Desvaux is in general a well characterised genus (Kylin 1956) of the family Champiaceae Kuetzing (1843) (syn. Lomentariaceae Naegeli 1847) of the Rhodymeniales and includes numerous species from most coasts of the world. Some 9 species have been credited to southern Australia, and as with so many Australian genera, taxonomic distinctions are uncertain and in some cases the earliest valid names are not in current use.

Chylocladia Greville has been credited with several Australian species, all of which are synonyms of species of *Champia* or other genera. One new species of *Chylocladia* has, however, been found in South Australian waters.

The type species of *Champia* is *C. lumbricalis* (L.) Desvaux (1808, p. 246), from the Cape of Good Hope, South Africa. Although a well-marked species, *C. lumbricalis* has never been studied in detail, and the generic concepts of structure and reproduction are based largely on the European *C. parvula* (C. Agardh) Harvey which has been investigated most recently by Bliding (1928) who reviews earlier studies. The thallus construction and reproduction of the type species do, however, appear to conform with those of *C. parvula*, and a brief account of the type species is given below.

Champia is characterised by a multiaxial, hollow but septate and thus segmented, usually much-branched thallus which originates from a ring of apical cells (or a ring plus several central cells). These apical cells each cut off a filament of cells which runs longitudinally through the thallus, and from the peripheral filaments the continuous cortical layer of cells originates close to the apex. If a group of central apical cells is present (as in the type species), then longitudinal filaments also occur in the central region throughout the "hollow" thallus. The characteristic transverse diaphragms in the thallus are derived from the longitudinal filament cells very close to the apex, and originate either from alternate cells or ones 2–3 cells apart. Each longitudinal filament cell cuts off cells laterally in one transverse plane, and these link up and divide further to form the characteristic 1 cell thick diaphragm, the peripheral filaments being adjacent to the cortex or sometimes separated by

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one diaphragm cell. The longitudinal filament cells lying between the diaphragms usually cut off one (–3) gland cells. Outer cortical layers may be formed, and in some species an inner cortex of rhizoidal filaments develops.

Most species are much branched, and the branches arise from the regions of the diaphragms by development of a ring of apical cells from cortical cells of the parent branch.

Reproductively *Champia* is fairly distinctive. The procarp consists of a 4-celled carpogonial branch borne on a supporting cell (a cortical cell), together with a 2-celled auxiliary cell branch present before fertilisation. The cystocarps are external and sub-spherical to urceolate, ostiolate, containing a carposporophyte with a basal fusion cell and much branched gonimoblast filaments with terminal carposporangia. The inner cells of the pericarp become stellate and form a network ("tela arachnoidea").

Spermatangia are cut off from mother cells derived from the outer cortical cells, and may cover extensive areas of the branches.

Tetrasporangia develop by enlargement of inner cortical cells, they are tetrahedrally divided and occur scattered over the branches.

Species of *Champia* are moderately common along most of the coast of southern Australia, and are commonly mentioned in ecological accounts. In general, however, they do not characterise any communities, though *C. affinis* may be common in shallow water on rock platforms (Womersley 1948, p. 158).

Chylocladia Greville differs from *Champia* in that the cystocarps do not have an ostiole and the carposporophyte consists of a large, basal fusion cell giving rise directly to carposporangia. The thallus construction of the two genera is similar.

CHAMPIA Desvaux

The structure and reproduction of the type species, *Champia lumbricalis*

Champia lumbricalis (L.) Desvaux (1808, p. 246) is based on *Ulva lumbricalis* Linnaeus (1771, p. 311) from the Cape of Good Hope. The species is a distinct one, and material from Camps Bay, Cape Town, South Africa (*G. Dieckmann*, 31.viii.1973) has been studied to check on the generic characteristics.

C. lumbricalis is a robust species forming clumps with numerous axes to 15 cm high, arising from an entangled, stoloniferous base. The axes are 2–4 mm thick, terete and linear, with occasional basally constricted branches with rounded apices. The diaphragms are regular in position, ½–1(–1½) mm apart and largely obscured below by the thick cortex.

The apices have a central group of 7–8 initials and peripheral ring of about 14 initials, resulting in longitudinal filaments passing through the inner part of each diaphragm as well as 14–20 around the periphery. One complete (rarely 2) and two part longitudinal filament cells occur between the diaphragms, bearing 1–3 gland cells. The cortex close to the apex becomes 3–4 cells thick, with a dense outer cortical layer of anticlinally elongate cells. In old axes the cortex increases to about 8 cells thick, and a weft of rhizoids also develops as an internal layer to the cortex.

The reproductive organs occur on tufts of short, adventitious, branchlets (5–10 mm long and 1–1½ mm thick) formed on the upper half of the axes. Usually the tufts are dense, with numerous, curved (concave adaxially) fertile branchlets, but in some plants cystocarps are borne on single lateral branchlets.

Cystocarps are borne mainly on the adaxial (concave) side of the curved branchlets, often with 2–4 grouped together; they are ovoid with a small ostiole, 1–2 mm in diameter and high. The carposporophyte arises from a basal fusion cell, with a much-branched gonimoblast bearing terminal carposporangia; subterminal cells probably also mature into carposporangia after loss of the terminal ones. The inner cells of the pericarp become stellate, forming a loose tissue, and the outer wall is comparatively thick. Carpogonial branches and early post-fertilisation stages have not been observed.

Spermatia form a continuous covering all around the branchlets, or sometimes largely on the adaxial sides, with the outer cortical cells cutting off 2–4 elongate spermatangial mother cells which then cut off several ovoid spermatangia.

Tetrasporangia occur densely in the branchlets and are transformed from most of the large inner cortical cells; they are slightly pyriform to ovoid, about 100 μm long, and tetrahedrally divided.

The above description of *C. lumbricalis* agrees well in essential generic details with that of Bliding (1928, p. 5) for *C. parvula*, though the latter is much smaller and slenderer, with a much thinner cortex, and has only peripheral longitudinal filaments. There is thus no reason to doubt the generic concept of *Champia* as recognised by Bliding and by Kylin (1956, p. 346).

Key to southern Australian species of Champia

1. Thallus with longitudinal filaments scattered through the diaphragms as well as peripheral filaments; branches usually linear, basally constricted or not, not or slightly constricted at the diaphragms; branching irregular or distichous ... 2
1. Thallus with peripheral longitudinal filaments only; branches usually tapering to base and apex, usually slightly to moderately constricted at the diaphragms; branching irregular or radial ... 3
   2. Branching irregular, often distant; branches linear, (½–)1–2½ mm broad ...... *C. viridis* (p. 77)
   2. Branching subdistichous, fairly regularly pinnate; branches 2–5 mm broad, with a basal slender stalk .... *C. insignis* (p. 81)
3. Thallus segments obscured; hooked branches absent; usually epilithic; cortical cells cutting off, near branch apices, usually several small outer cortical cells at first around their margins, later becoming almost continuous over the thallus as an outer layer and in older parts cutting off further outer cortical cells; inner primary cortical cells, which thus become obscured, are ovoid, 1½–2 times as long as broad, and 20–30 μm broad .... *C. affinis* (p. 82)
3. Thallus segments clearly defined throughout most of thallus; usually epiphytic on seagrasses or larger algae; cortical cells each cuting off usually only 1(–2) small cells from their corners, so that the single layer of large cortical cells remains clearly defined throughout most of the thallus; cortical cells usually angular, 2–3(–4) times as long as broad 4
   4. Branchlets ½–1 mm, branches 1–2 mm, in diameter; cortex essentially single layered throughout; usually one complete longitudinal filament cell between diaphragms; ultimate branchlets often hooked; usually epiphytic on *Posidonia*, *Amphibolis* or larger algae ... *C. zostericola* (p. 87)
   4. Branchlets 1/3–½ mm, branches ½–1 mm, in diameter; cortex mostly single layered but 2–4 cells thick in oldest axes; usually two complete longitudinal filament cells between diaphragms; ultimate branchlets usually linear, rarely hooked; epiphytic on *Amphibolis* ... *C. parvula* var. *amphibolis* (p. 91)

Champia viridis C. Agardh 1828: 115. Kuetzing 1849: 862.

Corinaldia viridis (C. Agardh) Trevisan 1848: 108.

Champia tasmanica Harvey 1844a: 407, pl. 19; 1847: 78; 1859: 307. J. Agardh 1852: 370; 1876: 306; 1879: 67, pl. 19, figs 10–12. De Toni 1900a: 79; 1900b: 563. Guiler 1952: 95. Hooker & Harvey 1847: 402. King *et al.*, 1971: 122(?). Kuetzing 1849: 861; 1865: 30, pl. 84g. Kylin 1931: 29. Lucas 1909: 34; 1929a: 19; 1929b: 50. Lucas & Perrin 1947: 207, fig. 72. May 1965: 362. Okamura 1904: 88. Reinbold 1897: 53; 1899: 45. Shepherd & Womersley 1970: 134; 1971: 165. Sonder 1846: 177(?); 1853: 682; 1855: 518; 1880: 17. Tate 1882: 18. Tisdall 1898: 506. Wilson 1892: 180. Womersley 1950: 176; 1966: 151.

Champia tasmanica var. *gracilis* Harvey 1863, synop.: 27. Sonder 1880: 17. Tate 1882: 18.

Corinaldia tasmanica (Harvey) Trevisan 1848: 108.

Champia oppositifolia J. Agardh 1901: 27. De Toni 1924: 309. Kylin 1931: 29, pl. 16, fig. 37. May 1965: 362.

Champia verticillata J. Agardh 1901: 26. De Toni 1924: 309. Kylin 1931: 29, pl. 17, fig. 39. May, 1965: 362.

Champia compressa sensu Harvey 1863, synop.: 27 (at least in part—see below).

FIGS 1, 2*A–D*, 10

Thallus (Fig. 10) usually with several main axes from a stoloniferous base, forming a dense, spreading tuft commonly 5–15(–20) cm high, moderately or slightly adhering to paper, medium to dark red or red-purple in colour. *Axes* (1–)2–3 mm broad, usually with numerous irregular branches in 2–4 orders, often subopposite, usually less than 1 cm (sometimes 2–4 cm) apart, in older or grazed plants often verticillately branched. All branches terete to slightly compressed, (½–)1–2½ mm broad, linear to slightly curved, basally constricted and with rounded apices. *Diaphragms* ½–1(–1½) mm apart, regular and usually conspicuous in surface view of thallus. *Cortex* of a single layer of compact cells, polygonal and 25–40 μm across in surface view, with an inner cortex of rhizoidal filaments in older parts of robust plants. *Longitudinal filaments* both peripheral and central, with one complete and two part filament cells between each diaphragm.

Cystocarps scattered over young branches, globular to urceolate, ostiolate, ½–1 mm in diameter. Apparently very few cystocarpic plants have been collected.

Spermatangia forming a continuous layer over branchlets.

Tetrasporangia scattered in young branches, 60–120 μm in diameter.

Type locality. W. Aust.

Type. Herb. Agardh, LD, 26112.

Distribution. From Rottnest I., W. Aust. around southern Australia and Tasmania to Gabo I., Vic., usually on rough-water coasts or in strong currents, from shaded pools to 28 m deep, with a slender form on *Posidonia* in more sheltered waters.

The type specimen of *C. viridis* C. Agardh consists of 8 small branches on mica, and is identical with the later described *C. tasmanica* Harvey (type from Tasmania, in TCD), under which name most specimens of this taxon have been known.

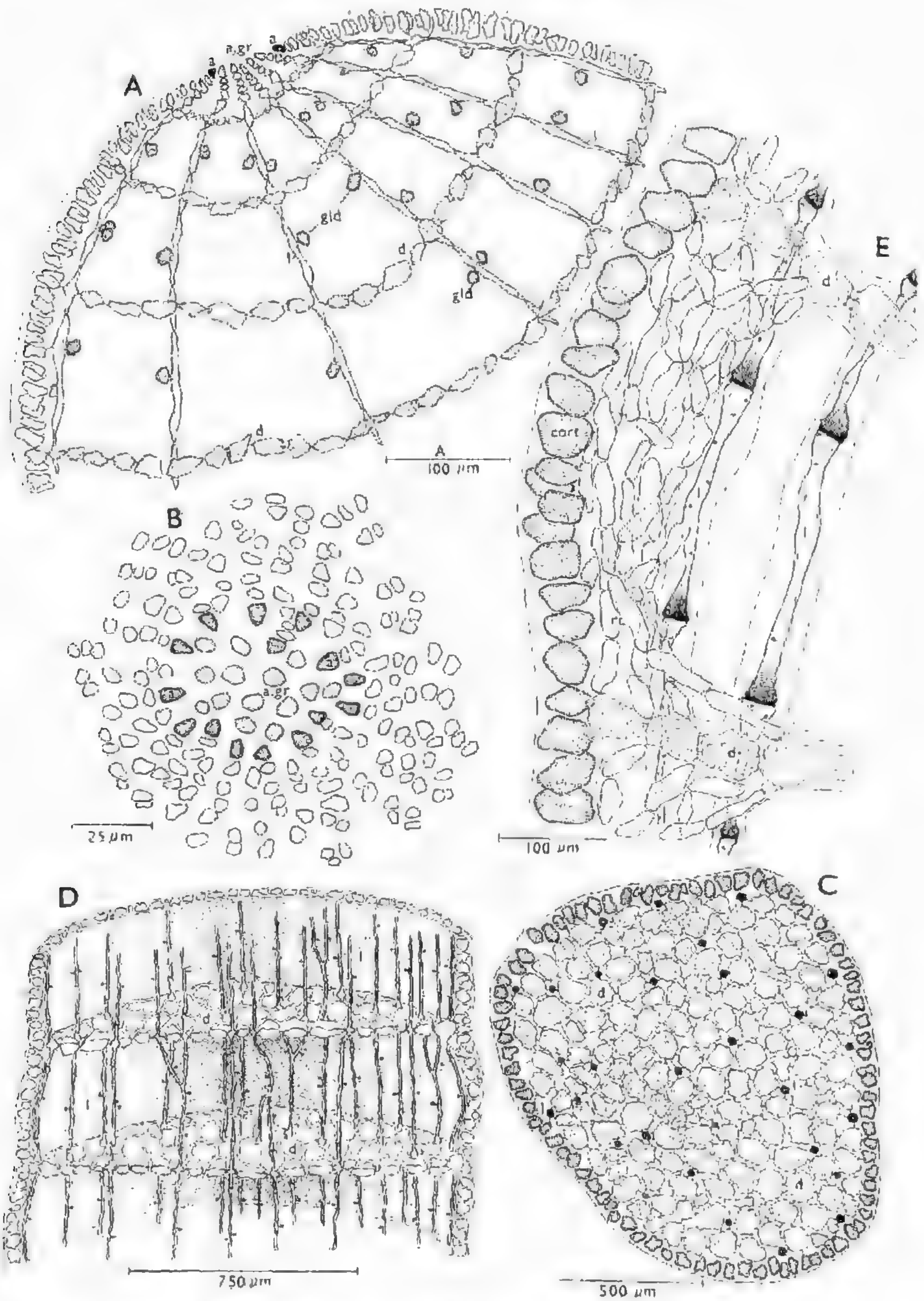

Fig. 1. *Champia viridis*. *A*. Longitudinal section of a branch apex showing the development of cortex, longitudinal filaments and diaphragms (A42995). *B*. Surface view of a branch apex showing central and peripheral apical cells (A42991). *C*. Cross section of a young branch showing a diaphragm with peripheral and scattered longitudinal filaments (A42991). *D*. Three dimensional view of thallus showing diaphragms and longitudinal filaments with gland cells (A42991). *E*. Longitudinal section of an older axis showing development of rhizoids from the peripheral diaphragm cells (A30550).

Harvey (1863, synop. p. 27) described var. *gracilis* of *C. tasmanica*. A suitable lectotype is probably Harvey's, Alg. Aust. Exsicc. 251, in TCD, from Port Phillip, Vic., and specimens in MEL (45227) from Brighton, Port Phillip, Vic. (Harvey, Trav. Set 483), named var. *fracta*, are probably the same. These are small, slender forms, often found on *Posidonia* under moderate conditions of water movement (e.g. Port Phillip, Vic., St Vincent Gulf, S. Aust.) in early summer, and doubtfully justify a varietal name. The thallus is usually 4–10 cm high, densely tufted with an entangled base, irregularly branched, with occasional curved branch apices, branches mostly ½–1 mm broad and segments ¾–1 times as long as broad, slightly constricted at the diaphragms. The cell structure is very similar to larger forms typical of the species, with cells about 40 µm broad, (1–)2–3 times as long as broad, angular with small cells cut off from the corners (about as many small cells as parent cells). While extremes of this sheltered-water form and the robust rough-water form appear relatively distinct, a good range of intergrades does occur.

C. verticillata J. Agardh (1901, p. 26) is based on a specimen (type in LD, 26078) from Port Elliot, S. Aust. (*Hussey*) and is an older plant of *C. viridis* with verticillate branching, and *C. oppositifolia* J. Agardh (1901, p. 27), with type in LD (26148) is a plant with somewhat more distinct opposite branching.

C. viridis is a distinctive species in size, form, and in having central as well as peripheral longitudinal filaments. It varies considerably in robustness and thickness of branches and in branching, with frequent occurrence of proliferous branches giving a subverticillate arrangement. These variations are either ecological or due to the age of the plant.

C. viridis is most closely related to the type species, *C. lumbricalis*, from South Africa, but is distinct in being a less robust plant and not developing a cortex several cells thick.

A Preiss specimen in MEL (45206) is *C. zostericola*, not *C. viridis*, but a small form of the latter does occur in Western Australia.

C. viridis (as *C. tasmanica*) has been recorded from New Zealand by Naylor (1954, p. 658). This record has not been checked, but may apply to the closely related but distinct *C. novae-zelandiae* Hooker & Harvey, which has central longitudinal filaments but a many layered cortex.

STRUCTURE AND REPRODUCTION

Material studied: Nora Creina, S. Aust., uppermost sublittoral (*Reedman*, 12.ii.1973; ADU, A42995); Cape Lannes, S. Aust., under ledges (*Reedman*, 10.ii.1973; ADU A42991); and Stapleton Point, Prosser Bay, Tas., 8–12 m deep (*Olsen*, 21.vi.1966; ADU, A30550).

Thallus development. The apex of a branch (Fig. 1*A*; *B*) includes both a central group of 12–16 initials and a peripheral ring of initials, producing longitudinal filaments passing through the central as well as the peripheral regions of the diaphragms (Fig. 1*C*, *D*), as in the type species. The number of central longitudinal filaments is commonly greater than the number of apical initials, due apparently to division of the initials and consequent branching of the filaments and subsequent loss of some initials and termination of some filaments at diaphragms. The apical initials of the peripheral ring divide transversely, and within 2 or 3 cells of the apex divide periclinally forming cortical cells which then divide anticlinally to form the single-layered cortex (Fig. 1*A*). Alternate cells of the longitudinal filaments cut off cells laterally which join to form the single-layered diaphragms (Fig. 1*A*), after which the longitudinal filament cells become very elongate. The alternate cells of the longitudinal filaments, lying between the diaphragms, form 1(–2) gland cells (Fig. 1*D*). Only the cortical cell formed directly from the longitudinal fila-

Abbreviations used in Figures 1–9.

a	— apical cell	f.c.b	— fused carpogonial branch	o	— ostiole
a.gr.	— apical group	fu	— fusion cell	per	— pericarp
a.m.c	— auxiliary mother cell	g1, g2	— gonimoblast cells	r.c	— rhizoidal cell
aux	— auxiliary cell	gl	— gonimolobe	sp	— spermatangium
c.b	— carpogonial branch	gld	— gland cell	sp.m	— spermatangial mother cell
co	— outer cortical cell	l	— longitudinal filament	su	— supporting cell
cort	— inner cortical cell	l.c	— lateral connecting cell	t	— tela arachnoidea
csp	— carposporangium			tr	— trichogyne
d	— diaphragm			tspg	— tetrasporangium

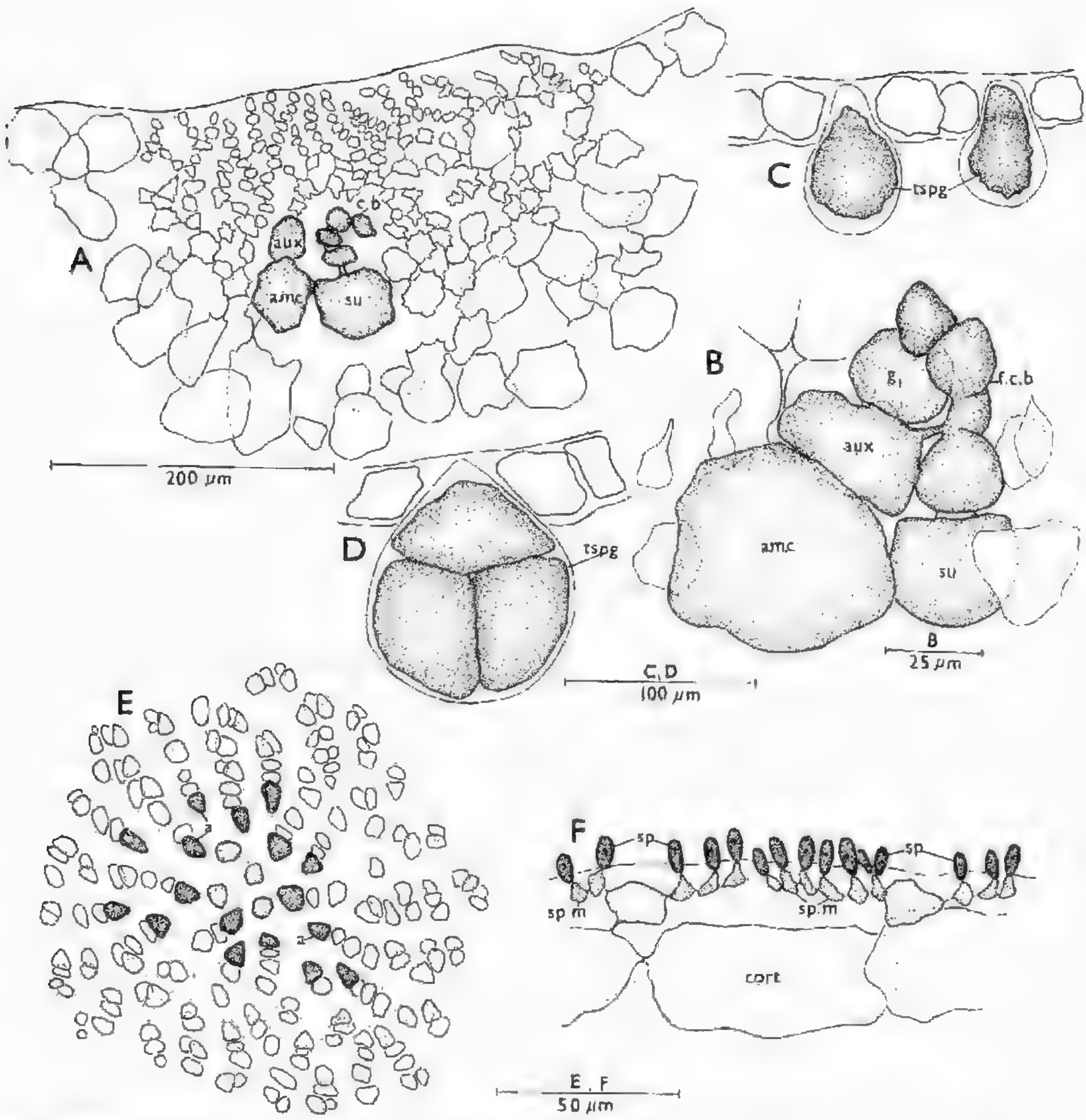

Fig. 2. *Champia viridis*. *A*. An early post-fertilisation stage showing supporting cell with auxiliary cell branch and carpogonial branch with fusions occurring between the cells. Considerable cortical proliferation has occurred towards formation of the pericarp (A30550). *B*. A post-fertilisation stage showing a connection between the fused carpogonial branch and the auxiliary cell, and formation of the first gonimoblast initial (A30550). *C*. Development of tetrasporangial initials (A30550). *D*. A mature tetrasporangium (A30550). *Champia insignis*. *E*. Surface view of a branch apex showing initials (A12237). *F*. Section of male thallus showing development of spermatangia (A12237).

ment cell is in pit-connection with it. In older parts, some cortical cells may produce small outer cells from their corners, but the cortex remains essentially only one cell thick.

In older branches, rhizoidal cells develop from peripheral diaphragm cells and form a loose layer lining the inner side of the cortex (Fig. 1*D*), as in the type species.

Branches arise from the region of the diaphragms, following development of a group of apical initials from the cortical cells.

Procarp and carposporophyte

Cystocarpic specimens appear to be rare, and only one female specimen with very young carposporophytes has been available. The carpogonial branch is 4-celled and borne on a supporting cell which also bears the auxiliary mother cell with its auxiliary cell (Fig. 2*A*). Following fertilisation, the cells of the carpogonial branch fuse and a connection between the fused carpogonial branch and the auxiliary cell is formed (Fig. 2*B*), and the first gonimoblast cell is cut off from the auxiliary cell. Early post-fertilisation development is accompanied by division of the surrounding cortical cells to form the pericarp (Fig. 2*A*), and in the one specimen (Stenhouse Bay, S. Aust., 3–7 m deep, *Kraft*, 18.ix.1973; ADU, A44564) observed with cystocarps, the structure of the pericarp and carposporophyte is typical of *Champia* and very similar to the illustrations of Bliding (1928) for *C. parvula*.

Spermatangia

Spermatangial plants have not been observed.

Tetrasporangia

Tetrasporangia develop by enlargement of cortical cells (Fig. 2*C, D*) and are tetrahedrally divided, 60–120 µm in diameter when mature, and scattered in younger branches.

NOTES ON *CHAMPIA COMPRESSA*

Champia compressa Harvey (1838: 402; 1847: 78, pl. 30) was first recorded from Australia by Harvey (1863, synop.: 27) on the basis of specimens from Western Australia (*Clifton*, and Alg. Aust. Exsicc. 250A) and from Port Fairy, Vic. (Alg. Aust. Exsicc. 250D). Since then, *C. compressa* has been recorded from Australia by the following authors, probably largely on the basis of Harvey's records: Garnet 1971: 96. Lucas 1909: 34. Lucas & Perrin 1947: 206. May 1947: 275; 1965: 362. Sonder 1880: 17(?). Tisdall 1898: 506.

However, comparison with material of *Champia compressa* from St James, Simonstown, S. Africa (*G. Dieckmann*, 29.iii.1973; ADU, A44601) shows that the Australian records almost certainly are not *C. compressa*. The South African species has strongly compressed branches with numerous central longitudinal filaments scattered across the diaphragms. Harvey's Western Australian specimens also have central longitudinal filaments but the branches are only slightly compressed. They agree in these features with *C. viridis* C. Agardh, and are very similar to young, well displayed, specimens of this species from elsewhere in southern Australia. Harvey's Alg. Aust. Exsicc. 250D (in TCD) from Port Fairy, Vic., includes *C. viridis* as well as some plants which are not a *Champia*, and one specimen of 250D in BM is *C. zostericola*.

Other records of *C. compressa* from southern Australia probably apply to *C. viridis* if the specimens have central longitudinal filaments, but the records of May (1947, p. 275; 1965, p. 362) from N.S.W. apply to a separate species which may be unnamed. This small, irridescent species, with branches attached to others by haptera, does not have central longitudinal filaments and is only slightly compressed. It is thus distinct from both *C. viridis* and *C. compressa*, and also differs from the very strongly flattened subtropical *C. vieillardii* Kuetzing, which from material from the Solomon Islands (Womersley & Bailey 1970, p. 321) is so strongly flattened that the diaphragms are only 2–4 cells across in the direction of flattening of the thallus, and longitudinal filaments are almost entirely around the periphery.

It is therefore considered that *Champia compressa* does not occur on Australian coasts. Other records of this species from outside South Africa also need checking; the record of Weber van Bosse (1928, p. 477) from Borneo is probably *C. vieillardii*, and that of Joly (1965, p. 176) from Brazil probably applies to a different species.

Champia insignis Lucas 1931: 409, pl. 25, fig. 1. Guiler 1952: 94. Lucas & Perrin 1947: 207. May 1965: 362.

FIGS 2*E, F*, 11*A*

Thallus (Fig. 11*A*) with one to several main axes to 18 cm high, arising from a small, discoid to slightly lobed holdfast on pebbles or shells; branches of pyramidal form, with lower laterals often similarly branched; thallus adhering closely to paper, colour red-brown (herbarium specimens) to "bright purple" (Lucas). *Axes* 3–5 mm in diameter, subterete (possibly slightly compressed), linear, bearing alternate or opposite laterals mostly ½–1 cm apart and sub-distichously arranged along the axes, often somewhat denuded towards the base. Main lateral branches usually with a slender stalk (Fig. 11*A*), then broadening, linear or gently tapering, usually 3–5 mm in diameter, with a rounded apex. Lesser branches similar but slenderer and shorter. *Diaphragms* apparent throughout most of the thallus, 2–3(–4) mm apart in older parts, 1–2 mm apart in younger branches which are slightly constricted at the diaphragms. *Cortex* essentially one cell thick, the cells subpolygonal in surface view, mostly

50–100 μm long and 35–50 μm broad, cutting off 1–3 small cells from their outer corners and more numerous such cells near the thallus base. *Longitudinal filaments* scattered throughout the diaphragms, consisting of several (?) cells between diaphragms.

Cystocarps scattered over the lesser branches, conical to urceolate, ostiolate, 1–1½ mm in diameter; carposporophyte branched with lower sterile cells and terminal carposporangia.

Spermatangia cut off from cortical cells (Fig. 2F) and forming collar-like patches on either side of the diaphragms of lesser branches.

Tetrasporangia scattered over the lesser branches, tetrahedrally divided, 80–100 μm in diameter.

Type locality. R. Derwent Estuary, Tas. ("Sandy Bay, Hobart. Oct. 1925" on type sheets.)

Lectotype. Herb. Lucas, NSW, 136559. Syntypes (♂) in NSW (136558) and ADU (A12237).

Distribution. Only known from the type collection and the following Tasmanian collections: D'Entrecasteaux Channel, Nov. 1910 (NSW, 136561); Browns River, *Lucas*, Oct. 1923 (NSW, 136562); and Snug, *Lucas*, Aug. 1925 (NSW, 136560). Two specimens in the BM, labelled "Tas. *Oldfield*", one numbered 81, are probably also from the Derwent Estuary. The species appears to be known only from, or just south of, the Derwent Estuary.

Lucas did not specify type material, but the one now selected as lectotype is the cystocarpic specimen illustrated by Lucas (1931, pl. 25, fig. 1).

The above description is compiled from that of Lucas (1931, p. 409) and study of the type and other material in NSW and ADU. *C. insignis* has apparently not been collected recently, but it seems to be a quite distinct species. It resembles *C. viridis* in having peripheral and central apical cells (Fig. 2E) producing longitudinal filaments scattered across the diaphragms, but differs in form and dimensions and in being essentially distichously branched. Lucas (1931, p. 409) refers to the whole plant as being "compressed". It is desirable, however, that liquid preserved collections should be studied to confirm such aspects.

The BM specimens agree well with the type collection though the lateral branches do not appear to be themselves distichously branched, and the main braches are basally constricted but scarcely stalked; they are cystocarpic. In carposporophyte structure and the ostiolate cystocarp, *C. insignis* appears to conform well with *Champia*.

Champia affinis (Hooker & Harvey) J. Agardh 1876: 304. De Toni 1900a: 75, pl. 5, fig. 2; 1900b: 559; 1924: 307. Guiler 1952: 94. Harvey 1855a: 545(?); 1859: 307; 1863, synop.: 27. Kylin 1931: 28. Lucas 1909: 34; 1929a: 19; 1929b: 50. Reinbold 1897: 53; 1899: 45. Sonder 1880: 17. Tisdall 1898: 506. Wilson 1892: 180.

Chylocladia affinis Hooker & Harvey 1847: 402. Harvey 1847: 79, pl. 29(?).

Lomentaria affinis (Hooker & Harvey) Kuetzing 1849: 863. J. Agardh 1852: 730. Sonder 1853: 693.

Gastroclonium affine (Hooker & Harvey) Kuetzing 1849: 866.

Chylocladia kaliformis sensu Harvey 1844b: 444.

Champia obsoleta Harvey 1859: 307; 1863, synop.: 27. J. Agardh 1876: 304. De Toni 1900a: 75, pl. 5, fig. 3; 1900b: 559; 1924: 307. Guiler 1952: 94. Kylin 1931: 28, pl. 15, fig. 35. Lucas 1909: 34; 1929a: 19; 1929b: 50. Lucas & Perrin 1947: 206. May 1965: 362. Reinbold 1898: 46. Sonder 1880: 17. Wilson 1898: 506. Womersley 1950: 176; 1966: 150.

FIGS 3, 4, 11B, 12

Thallus (Figs 11B, 12A, B) erect, usually 4–15(–40) cm high, with one to several main axes from a small discoid holdfast, grey-red to purple in colour, adhering to paper; usually growing on rock or on *Amphibolis*, rarely on *Posidonia*. *Axes* usually densely and irregularly radially branched for 3 or 4 orders, branches of pyramidal form (more spreading in plants on seagrasses), often denuded below; axes 1–3½ mm, branches ½–1½ mm, and lesser branches ⅓–½ mm, in diameter, all branches slightly basally constricted and tapering to rounded apices. *Diaphragms* usually fairly distinct in lesser branches, obscured on older axes, (½–)1–1½(–2) mm apart (segments (½–)1–1½ times as long as broad), thallus constricted at diaphragms except on older axes. *Cortex* of a layer of large sub-ovoid cells, (20–)25–40(–60) μm across, and a sparse layer of outer small cells around margins of inner cells in young branches (Fig. 3F, I), becoming more or less continuous on older parts (Fig. 3G–I) and near bases of old plants 2–4 cells thick (Fig. 3E). *Longitudinal filaments* usually confined to periphery of the diaphragms (Fig. 3C), rarely with 1 or 2 within the periphery, usually with two (occasionally

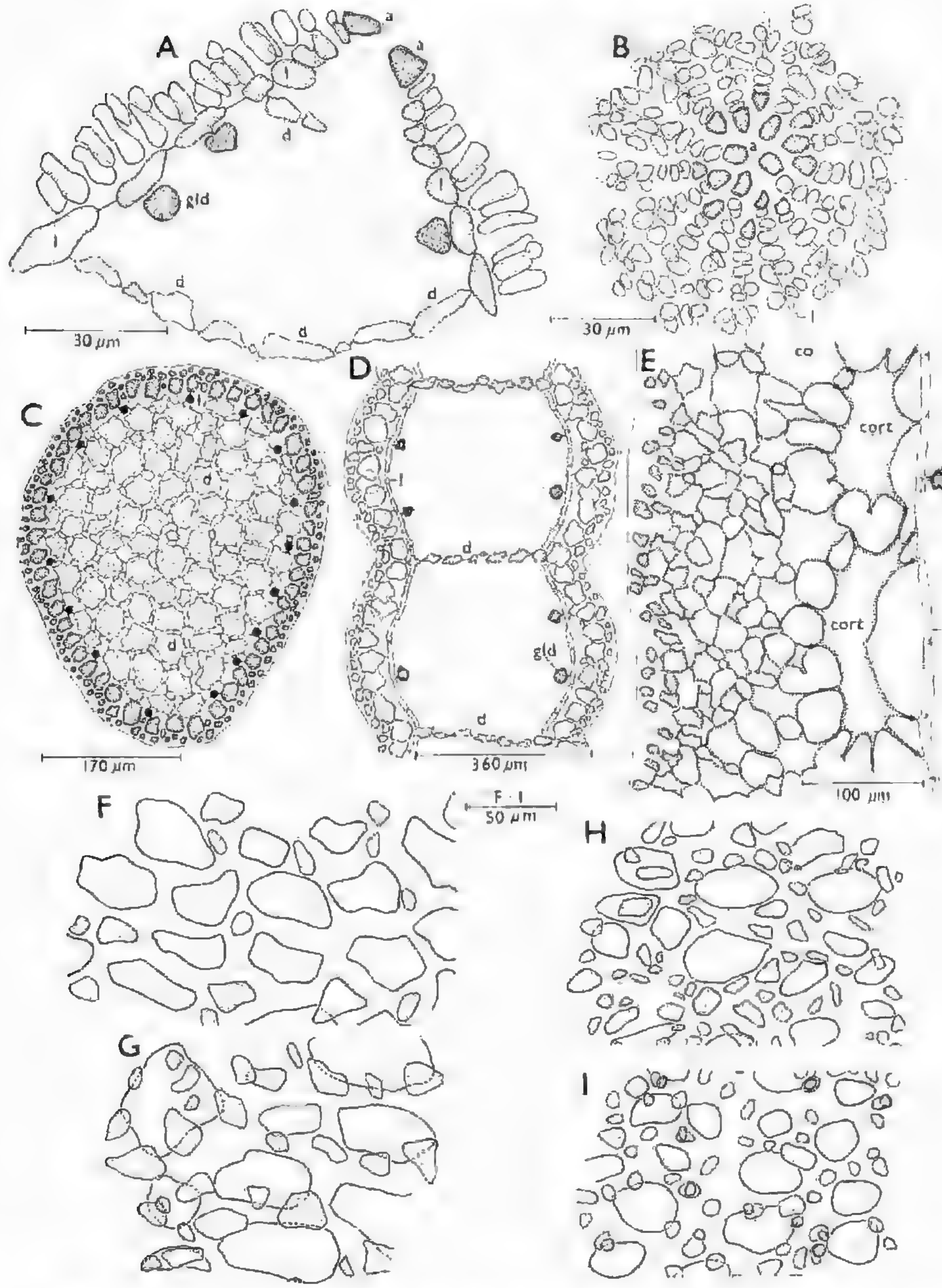

Fig. 3. *Champia affinis*. *A*. Longitudinal section of a branch apex showing the development of cortex, longitudinal filaments and diaphragms (A42994). *B*. Surface view of a branch apex showing apical cells (A42994). *C*. cross section of a mature branch showing a diaphragm with peripheral longitudinal filaments and small outer cortical cells (A42994). *D*. Longitudinal section of mature branch (A42993). *E*. Longitudinal section of an old axis showing several layers of cortical cells (A42997). *F*. Surface cell pattern of type specimen (*Gunn*, in BM) 10 segments from a branch apex. *G*. Ditto, 30 segments from a branch apex. *H*. Ditto for Harvey, Alg. Aust. Exsicc. 252I from Georgetown, Tas., as *C. obsoleta*, 30 cells from a branch apex. *I*. Ditto for A42990, 10 segments from a branch apex.

one or three) complete cells and two part cells between the diaphragms.

Cystocarps single, scattered over lesser branches, subspherical to urceolate, 1–1½ mm long, ½–1½ mm in diameter, with a distinct ostiole (Fig. 4*C*).

Spermatangia (Fig. 4*E*) in patches around branchlets on either side of diaphragms, often covering most of the segments.

Tetrasporangia scattered over branches, 60–80 μm in diameter (Fig. 4*F*).

Lectotype locality. Georgetown, Tas. (*Gunn*).

Lectotype. BM.

Distribution. From King George Sound, W. Aust. to Western Port, Vic., and around Tasmania. Generally found in shallow water on reefs on rough-water coasts, rarely epiphytic on *Posidonia* or robust algae.

C. affinis was reported from New Zealand by Harvey (1855b, p. 236) and recently by Chapman & Dromgoole (1970, p. 145). There are also specimens in BM from New Zealand, but while they appear closely related to *C. affinis* there are differences in form. Detailed comparisons of liquid-preserved material are needed to establish the relationships of the New Zealand plant.

Hooker & Harvey (1847, p. 402) based *C. affinis* on plants from Georgetown, and a cystocarpic plant in BM has been selected as lectotype (Fig. 11*B*). Other specimens in BM and in TCD are syntypes. The type specimens are of loose, spreading form and typical of plants from moderately sheltered conditions: the diaphragms are not conspicuous and the wall has an outer layer of small cells which becomes continuous in older parts.

Some of these Georgetown specimens are referred by Harvey to *C. obsoleta*, which he described (1859, p. 307) on the basis of thallus structure and cystocarpic plants, referring to "Alg. Exsic. n. 252" and the following localities:

"HAB. Georgetown. Southport, *C. Stuart.*

DISTRIB. Port Fairy, Victoria. *W.H.H.*"

The critical specimens in TCD include

1. "Georgetown. Sept. 1848. 252 I". This specimen (Fig. 12*A*) was previously considered the lectotype (by H.B.S.W. in 1952), but is tetrasporangial and has no name on the sheet; it is an old plant but is *C. affinis*, being very similar to the type of this species. Another specimen labelled "Georgetown, V.D.L. 252 I" is also an old, battered specimen, probably of *C. affinis*.
2. "Southport, V.D.L. *C. Stuart*"—four specimens, two with "*C. obsoleta*" on the sheets, and which are *C. affinis*. They are all tetrasporangial and do not match the type description at all well.
3. "Port Fairy, Vic. *W.H.H.* 252 D"—five specimens, 3 tetrasporangial and 2 cystocarpic: these match the description well and include the only cystocarpic specimens in TCD. One tetrasporangial specimen has "*Champia obsoleta*" on the sheet.

On the basis that the lectotype specimen of *C. obsoleta* should have Harvey's number 252 on it and should also agree well with the type description and be cystocarpic, one of the two Port Fairy specimens (Fig. 12*B*) is now selected as the lectotype and the other Port Fairy specimens are then syntypes.

In describing *C. obsoleta*, Harvey (1859, p. 307) stated "perhaps only a variety of *C. affinis*", and Kylin (1931, p. 28) doubted that they were distinct species. Study of Harvey's Georgetown material, the Port Fairy specimens of *C. obsoleta*, and knowledge of this common species along southern Australian coasts, suggests strongly that only one species is involved, and *C. obsoleta* is therefore reduced to synonymy. *C. affinis* occurs mainly on rocks and platforms at about low tide level, and under rough-water conditions in such habitats it is of pyramidal form and grey-purple in colour, as Harvey (1859, p. 307) noted. While normally epilithic, it occasionally occurs on other robust algae or on the seagrass *Amphibolis*, and some of Harvey's Georgetown specimens were growing on *Posidonia*. While there appear to be no structural differences between these forms on seagrasses and the rough-water forms, the former are more loosely branched and of more spreading habit.

The type specimen of *C. affinis* shows numerous small outer cells cut off from the primary cortical cells (Fig. 3*F*, *G*), but not as many as in rough-water forms (Fig. 3*I*). However, the habit, lack of clearly visible primary cortical cells and obscuring of the diaphragms in most of the thallus, are features of *C. affinis* as understood here, and differentiate this species from *C. zostericola* (see below). The type of *C. affinis* and other specimens (e.g. in ADU) from Georgetown in Tasmania, Port Phillip Heads in Victoria, and near American River inlet on Kangaroo Island, appear to represent relatively calm water forms of the species.

and the type of *C. obsoleta* to represent rough-water forms of more pyramidal habit and with more prominent outer cortical cell layers.

Some specimens of *Champia*, epiphytic on *Posidonia*, resemble *C. affinis* in that the segments are not distinct and a moderate number of outer cortical cells are present. The segments are, however, often distinctly longer than in the type of *C. affinis*, being 2–3(–4) times as long as broad. The longitudinal filaments often consist of 2–3 complete cells between the diaphragms, and the primary cortical cells are moderately conspicuous. Most of the plants with these characteristics are small and possibly young, though often fertile. For the present they are regarded as probably a form of *C. affinis*, but further studies on their seasonal growth and variation is needed. The specimens concerned include: Port Lincoln, S. Aust., 4–12 m deep, on *Posidonia* (*Shepherd*, 23.viii.1975; ADU, A46561, A46567, A46570), and Pig I., American R. inlet, Kangaroo I., S. Aust. (*Womersley*, 17.i.1947; ADU, A4467).

C. affinis differs from the other common southern Australian species, *C. zostericola*, in its habit, lack of hooked branches, and thick (2–3 layered) cortex which obscures both the diaphragms and the large primary cortical cells. The latter species is discussed further below, but very occasional plants with intermediate characters do occur. Harvey's Alg. Aust. Exsicc. 253H, distributed as *C. affinis*, is typical *C. zostericola*, and this has led to considerable confusion.

J. Agardh (1876, p. 304) distinguished two varieties of *C. affinis* (var. α *affinis* and var. β *intermedia*) on the proportions of the articulations and density of tetrasporangia. Both these features are unsatisfactory characters to separate varieties, and Kylin (1931, p. 28) considered var. *intermedia* as intermediate between *C. affinis* and *C. obsoleta*. These varieties do not appear worth distinguishing from the species.

Hooker & Harvey (1847, p. 402), following description of *C. affinis*, also described var. *arcuata*. This variety is considered specifically distinct and is relegated below to the synonymy of *C. zostericola* Harvey.

STRUCTURE AND REPRODUCTION

Material studied: Cape Lannes, S. Aust., low eulittoral (*Reedman*, 10.ii.1973; ADU, A42993 and 12.ii.1973; ADU, A42990); Nora Creina, S Aust., lower eulittoral (*Reedman*, 12.ii.1973; ADU, A42994); and Pennington Bay, Kangaroo I., S. Aust., low eulittoral on reef (*Reedman* 13.iv.1973; ADU, A42997).

Thallus development

There are 12–16 apical initials (Fig. 3*B*) which form a peripheral ring of longitudinal filaments; only very occasionally have filaments been seen within the periphery of the diaphragms. The initials segment (Fig. 3*A*) as do the peripheral apical initials in *C. viridis*, but the cortical layer of large cells cuts off small outer cells, at first around their outer margins, but a more or less continuous layer of small cells occurs on mature parts (Fig. 3*G–I*), and near the base (especially in older plants) a cortex several cells thick is developed (Fig. 3*E*). Hairs are commonly formed from outer cortical cells near branch apices. The diaphragms are formed usually by every third or fourth cell of the longitudinal filaments (Fig. 3*A*, *D*), leaving usually two or three complete cells between the diaphragms, each cell commonly bearing a gland cell. Rhizoidal development within the cortical layer has not been observed.

Branches arise from the region of the diaphragms, where a ring of outer cortical cells becomes meristematic and forms the apical initials of the branch. Branching occurs irregularly and often densely on all sides.

Procarp and carposporophyte

The supporting cell (Fig. 4*A*) is a large cortical cell in primary pit-connection with a longitudinal filament, and is generally attached opposite a gland cell. The cystocarps thus lie between the diaphragms of a branch, and cystocarpic plants are common. The supporting cell is multinucleate and densely cytoplasmic, and cuts off a 4-celled, curved, carpogonial branch (Fig. 4*A*), of which the first cell is binucleate and the other three uninucleate.

The supporting cell also produces a multinucleate, densely cytoplasmic auxiliary mother cell (Fig. 4A), which produces a uninucleate auxiliary cell just prior to fertilisation.

Following fertilisation, the pit-connections of the carpogonial branch cells enlarge (Fig. 4*B*) and the cells tend to fuse. Following presumed diploidisation of the auxiliary cell, first and then second gonimoblast cells are produced, and the latter divides further to produce a cluster of branched gonimoblast filaments (Fig. 4*C*, *D*), which terminate in uninucleate, ovoid carposporangia. The carposporangia mature simultaneously, but a new gonimolobe commonly develops from the basal cell of the gonimoblast and produces a secondary, later maturing, smaller cluster of carposporangia.

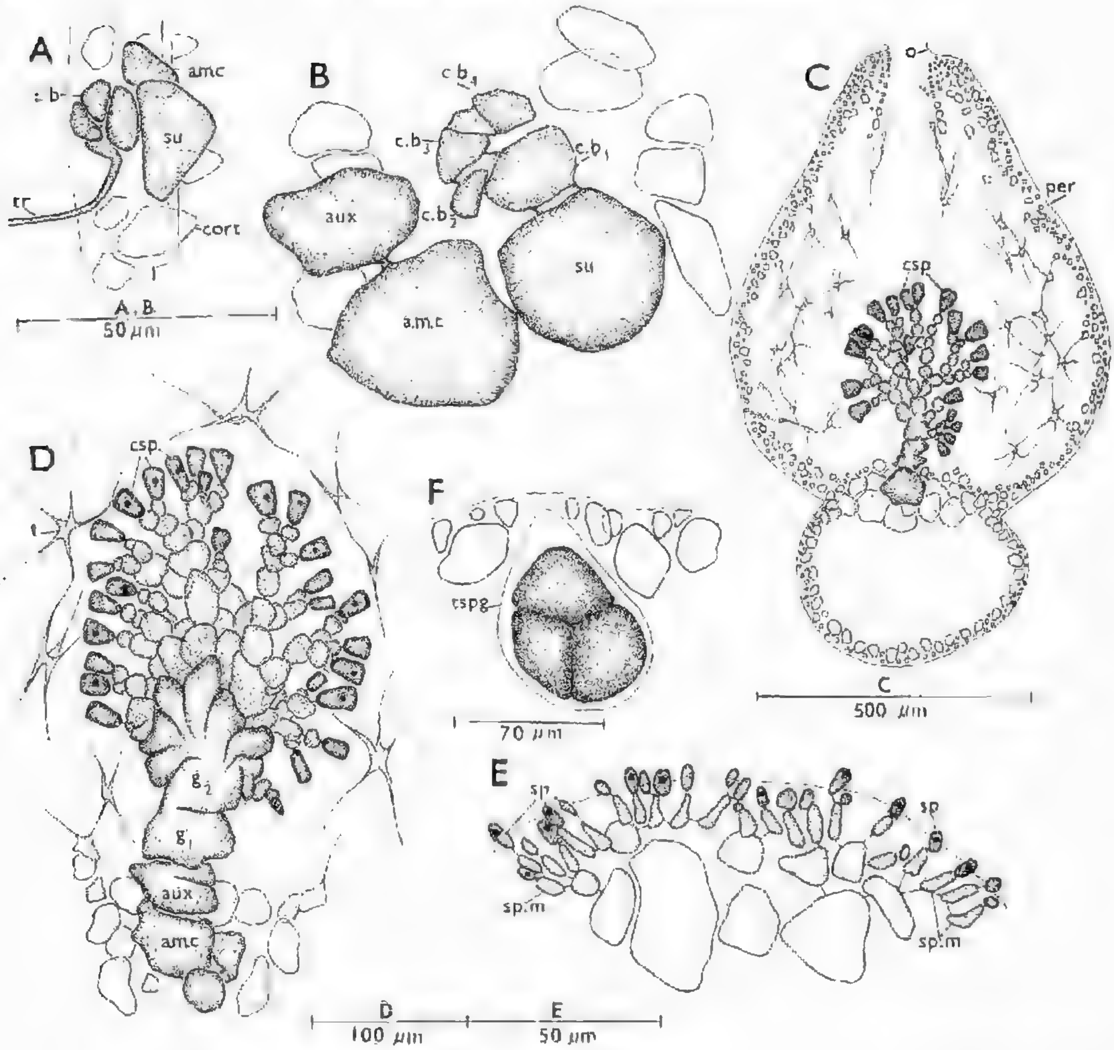

Fig. 4. *Champia affinis*. *A*. Supporting cell with auxiliary mother cell and carpogonial branch (A42990). *B*. Post-fertilisation stage with cells of carpogonial branch fusing (A42990). *C*. Section of an immature cystocarp showing development of carposporophyte from old auxiliary cell (A42997). D. A mature carposporophyte showing much-branched gonimoblast with terminal carposporangia, surrounded by cells of the "tela arachnoidea" (A42990). *E*. Section of male thallus showing development of spermatangia (A42997). *F*. Section with a mature tetrasporangium (A42993).

Vegetative cells adjacent to the auxiliary mother cell becomes densely cytoplasmic, and assist nutrition of the developing carposporophyte. Pit-connections between the lower cells of the gonimoblast enlarge considerably but the cells do not fuse completely.

As the gonimoblast develops, vegetative cells around its base divide to produce the pericarp. Inner cells of this form the cell reticulum, with an outer wall several cells thick (Fig. 4*C*). The mature cystocarp has a well-defined ostiole.

Spermatangia

Spermatangial mother cells are cut off from the small outer cortical cells to form a continuous layer over the branches, and each cuts off 2–3 ovoid spermatangia (Fig. 4*E*). Usually the entire spermatangium is shed.

Tetrasporangia

Tetrasporangia (Fig. 4*F*) develop by enlargement of inner cortical cells which develop several secondary pit-connections with adjacent cells. They are tetrahedrally divided.

with a thick gelatinous sheath, and usually densely scattered over the branches.

Champia zostericola (Harvey) comb. nov.

Lomentaria zostericola Harvey 1855a: 545; 1863, synop.: 26. J. Agardh 1876: 632.

Gastroclonium (?) *zostericolum* (Harvey) De Toni 1900b: 567.

Chylocladia zostericola (Harvey) Kylin 1931: 30.

Chylocladia affinis var. *arcuata* Hooker & Harvey 1847: 402. Womersley 1966: 150.

Lomentaria affinis sensu Kuetzing 1865: 31, pl. 86d–f. Sonder 1855: 523.

Champia affinis sensu King *et al.*, 1971: 122. Lucas & Perrin 1947: 206, fig. 71. May 1965: 362. Shepherd & Womersley 1971: 165. Womersley 1950: 176.

Champia parvula sensu Harvey 1855a: 545 (in part).

FIGS 5, 6, 12*C*, 13

Thallus (Figs 12*C*, 13) usually spreading and forming irregular clumps with several branches from the entangled base, sometimes with one or more erect axes and spreading laterals, commonly 6 to 20 cm high, grey-red to red in colour, normally epiphytic on the seagrasses *Posidonia* and *Amphibolis* or on larger algae, possibly on rock; attachment at first by means of a small discoid holdfast with one to several axes, later attaching by small adventitious multicellular pads to the seagrass or itself. *Axes* usually 1½–3(–5) mm in diameter, branches only slightly slenderer and ultimate branches ½–2 mm in diameter, branches slightly basally constricted and with rounded apices; mature plants normally with some to many branches ending in recurved ("hooked") tips (Fig. 13); young branches distinctly constricted at diaphragms, segments mostly (½–) 1–1½ times as long as broad. *Diaphragms* distinct except in oldest parts of some plants, ½–1½(–2) mm apart. *Cortex* single layered, of relatively large angular cells [40–60(–75) μm across and mostly (1½–)2–4 times as long as broad] which are usually arranged more or less in longitudinal rows (Fig. 5*E–H*). Near the apices, each cell usually cuts off a single, relatively small cell from near a corner, and further such cells develop on older parts; however, the essentially single layered cortex of large cells is maintained throughout most of the plant (Fig. 5*F*, *H*). *Longitudinal filaments* confined to periphery of the diaphragms, rarely with odd ones more centrally placed, with generally one complete cell and two part cells between the diaphragms (Fig. 5*C*).

Cystocarps subspherical to slightly conical, base broad and slightly constricted, ¾–1 mm in diameter.

Spermatangia scattered over smaller branchlets, as extensive patches or collar-like sori around the diaphragms.

Tetrasporangia scattered over branches, 60–100 μm in diameter.

Type locality. Rottnest I., W. Aust.

Type. TCD (Harvey, Trav. Set 195).

Distribution. From the Abrolhos Islands, W. Aust. around southern Australia to Kiama, N.S.W. and around Tasmania. Generally epiphytic on seagrasses or other algae, from low tide level to 41 m deep, generally under slight to moderate water movement.

C. zostericola is based on small plants 3–4 cm high, growing on *Posidonia* (not *Zostera*). The type is No. 195 in Harvey's "Travelling Set", and his Alg. Aust. Exsicc. 294A (MEL 45197) from Fremantle (Fig. 12*C*) is very similar. Harvey was in the vicinity of Fremantle from April to June 1854, and during this period the plants are young (though often fertile), but may not show the typical hooked branches. Later in the year, especially in spring and early summer (September to November) the plants reach 20 cm in height and nearly all plants develop the hooked branches.

The lectotype (Fig. 13*A*) of var. *arcuata* Hooker & Harvey of *C. affinis* has been selected from several specimens in BM. It is a well-developed specimen, attached to stems of *Heterozostera* (?) and with numerous hooked branches. Whereas the type of *C. zostericola* is a young, small plant, that of var. *arcuata* is an older, larger plant of the same species.

The general confusion between *C. affinis* and *C. zostericola* (or *C. affinis* var. *arcuata*) is probably largely due to Harvey in his Alg. Aust. Exsicc. listing 253H from Western Port, Vic. as *C. affinis*, whereas these specimens are typical *C. zostericola*.

In contrast to *C. affinis* which is usually epilithic on rough-water coasts and only occasionally occurs on robust algae or on seagrasses, *C. zostericola* is a common epiphyte on *Posidonia* and on some larger algae, usually in conditions of slight to moderate water movement and extending into deeper water.

The presence of hooked branches, the clearly septate thallus almost throughout, the essentially one cell thick cortex throughout the

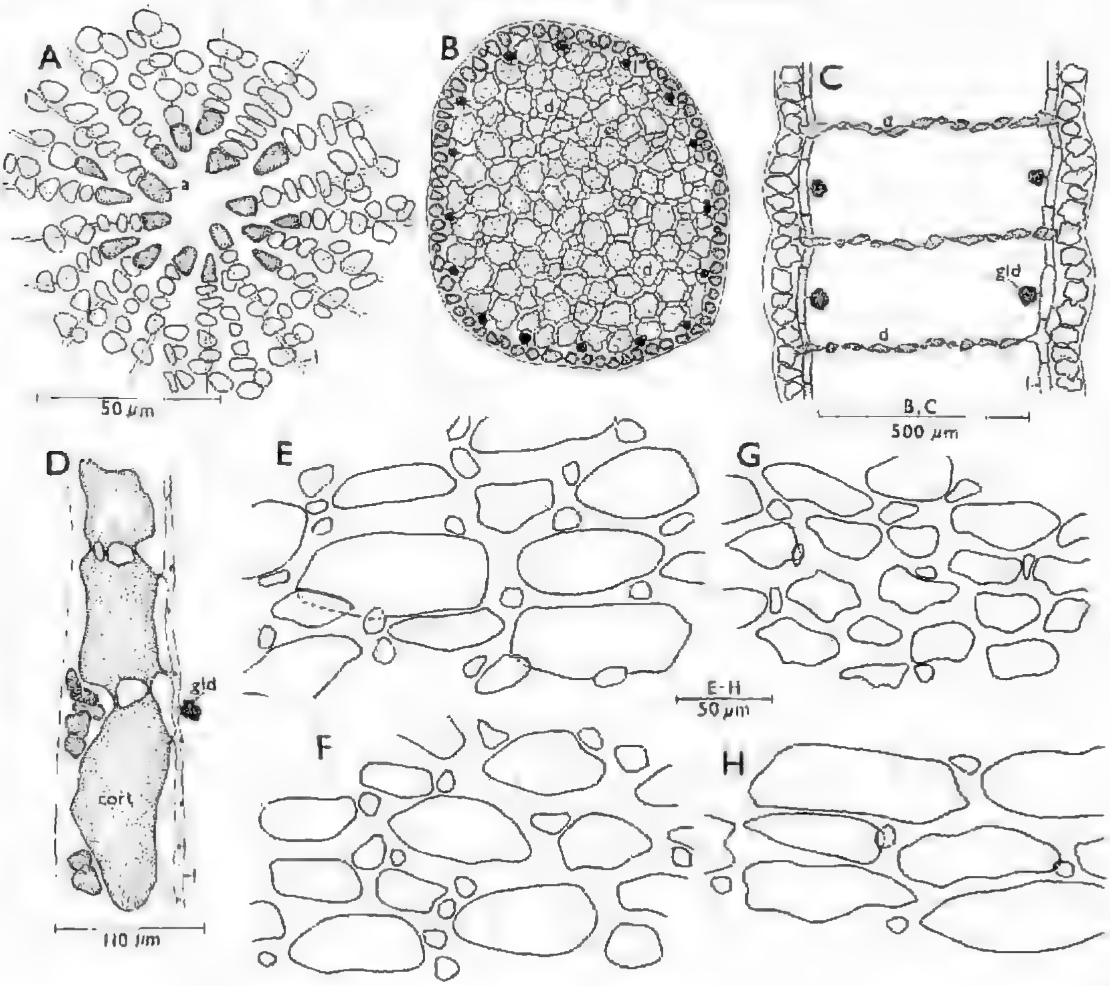

Fig. 5. *Champia zostericola*. *A*. Surface view of apex of branch showing apical cells (A43556). *B*. Cross section of branch showing cortex, diaphragm and peripheral longitudinal filaments (A43556). *C*. Longitudinal section of mature branch showing single layered cortex, diaphragms and longitudinal filaments with gland cells (A43556). *D*. Longitudinal section of an old axis showing slight development of small outer cells (A8944). *E*. Surface cell pattern of Harvey Alg. Aust. Exsicc. 249A (MEL. 45197), 10 cells from branch apex. *F*. Ditto, 30 cells from a branch apex. *G*. Surface cell pattern of the type specimen in BM of *C. affinis* var. *arcuata*, 10 cells from a branch apex. *H*. Ditto, 30 cells from a branch apex.

plant with few small cells lying largely between the primary ones, and the cortical cell dimensions and arrangement, characterise this species, but occasional plants occur without hooked branches. While most mature plants have several vague axes from their entangled bases, some (from Tasmania and Port Phillip Heads in particular) do have well developed main axes with abundant laterals. Such plants commonly (but not always) have hooked branches and have the single-layered, large-celled cortex typical of *C. zostericola*. However, the number of small cortical cells cut off from the larger ones does vary somewhat, and very occasionally plants intermediate in this respect with *C. affinis* are found (see under *C. affinis*).

C. zostericola shows the variation in form which occurs in many other algal species distributed along all of southern Australia, i.e. the western specimens are generally smaller and less robust, and in the east, especially near Port Phillip Heads and in Tasmania, larger and more robust plants occur.

Variation in diameter of the branches and axes is considerable, probably largely dependent on age, but branches are normally over 1 mm thick. However, new growth on older denuded branches may be slender and only about ½ mm thick, as shown on several collections from Pearson I., S. Aust. in ADU.

Many references to *Champia affinis* apply, at least in part, to *C. zostericola* rather than to true *C. affinis* (see above). Probably most Australian records of *C. parvula* also apply to young plants of *C. zostericola*, though some may apply to slender *C. viridis*.

STRUCTURE AND REPRODUCTION

Material studied: Point Peron, W. Aust., drift (*Gordon*, 15.xi.1968; ADU, A34256); Port Noarlunga, S. Aust., 6–7 m deep on jetty piles (*Johnson*, 15.ii.1973; ADU, A43556); Marino, S. Aust., drift (*Womersley*, 26.x.1975; ADU, A46646).

Thallus development

There are 14–20 apical initials (Fig. 5*A*) which form a peripheral ring of longitudinal filaments (Fig. 5*B*), with only occasionally an odd inner one. The initials segment as in *C. affinis* and a single layer of large cortical cells is formed, arranged more or less in longitudinal lines (Fig. 5*E–H*). Fairly near the apices, these cortical cells become angular and cut off from a corner a smaller cell, which remains essentially in the layer of larger cells (Fig. 5*E–H*). The smaller cells are at first similar in number to the larger primary cortical cells, but later more may be formed; however, the cortex remains essentially only one cell thick througout most of the thallus (Fig. 5*C, D*). The diaphragms are formed usually from alternate longitudinal filament cells, so that there is one complete longitudinal filament (with a gland cell) and two part ones between successive diaphragms (Fig. 5*C*). The relatively thin, essentially single layered cortex results in the primary cortical cells being visible throughout most of the plant, and the diaphragms are also conspicuous. Rhizoidal development within the cortex does not occur.

Branches arise from the region of the diaphragms, with their apical cells differentiating from the cortical cells. Near the base of entangled thalli, small branches may develop into haustorial pads of tissue and attach to other branches or to the host.

Many of the branch apices are curved or hooked (Figs 13*B*, 14*A*), and in some cases these aid in attachment. The only structural difference in hooked branch ends appears to be that on the convex side each segment has a greater number of cells than on the concave side.

Procarp and carposporophyte

From the limited female material available, the supporting cell of the procarp appears to be a large cortical cell, which produces the carpogonial and auxiliary cell branches (Fig. 6*A*). Following fertilisation, the pit-connections of the carpogonial branch cells enlarge (Fig. 6*B*) and the cells fuse, with a connection forming from the old carpogonium to the auxiliary cells (Fig. 6*C*).

The diploidised auxiliary cell cuts off a first gonimoblast cell which divides again (Fig. 6*D*) to initiate several branched gonimoblast filaments with the mature filaments terminating in single carposporangia (Fig. 6*E*) which mature simultaneously. New gonimolobes are produced from the base of the gonimoblast and mature later. Some darkly-staining and possibly nutritive cells occur around the base of the old auxiliary mother cell.

At an early stage in development of the procarp, cells are cut off from the surrounding cortical cells to form the protective pericarp (Fig. 6*D*). The inner cells of the pericarp form a reticulum (the "tela arachnoidea") which is gradually absorbed by the developing carposporophyte (Fig. 6*E*), and the outer 2–3 layers remain as the cystocarp wall, with a distinct apical ostiole.

Spermatangia

Spermatangia are formed as in other species, with small cells being cut off around the margins of the cortical cells and then producing branched chains of spermatangial mother cells over the surface, from which the elongate spermatangia develop.

Tetrasporangia

The tetrasporangia develop by enlargement of cortical cells (Fig. 6*F*) which protrude within the cortical layer, and they divide tetrahedrally (Fig. 6*G*).

Champia parvula (C. Agardh) Harvey 1853: 76. J. Agardh 1876: 303. De Toni 1900b: 558. Newton 1931: 439, fig. 263. Gayral 1966: 485, pl. 134.

Chondria parvula C. Agardh 1824: 207.

Chylocladia parvula (C. Agardh) Hooker. Harvey 1849: pl. 210.

Type locality. Gades (Cadiz), Spain.

Type. Herb. Agardh, LD, 26022.

Distribution. *C. parvula* appears to be the only species of *Champia* known from European coasts, and has been recorded from most temperate and tropical coasts of the world.

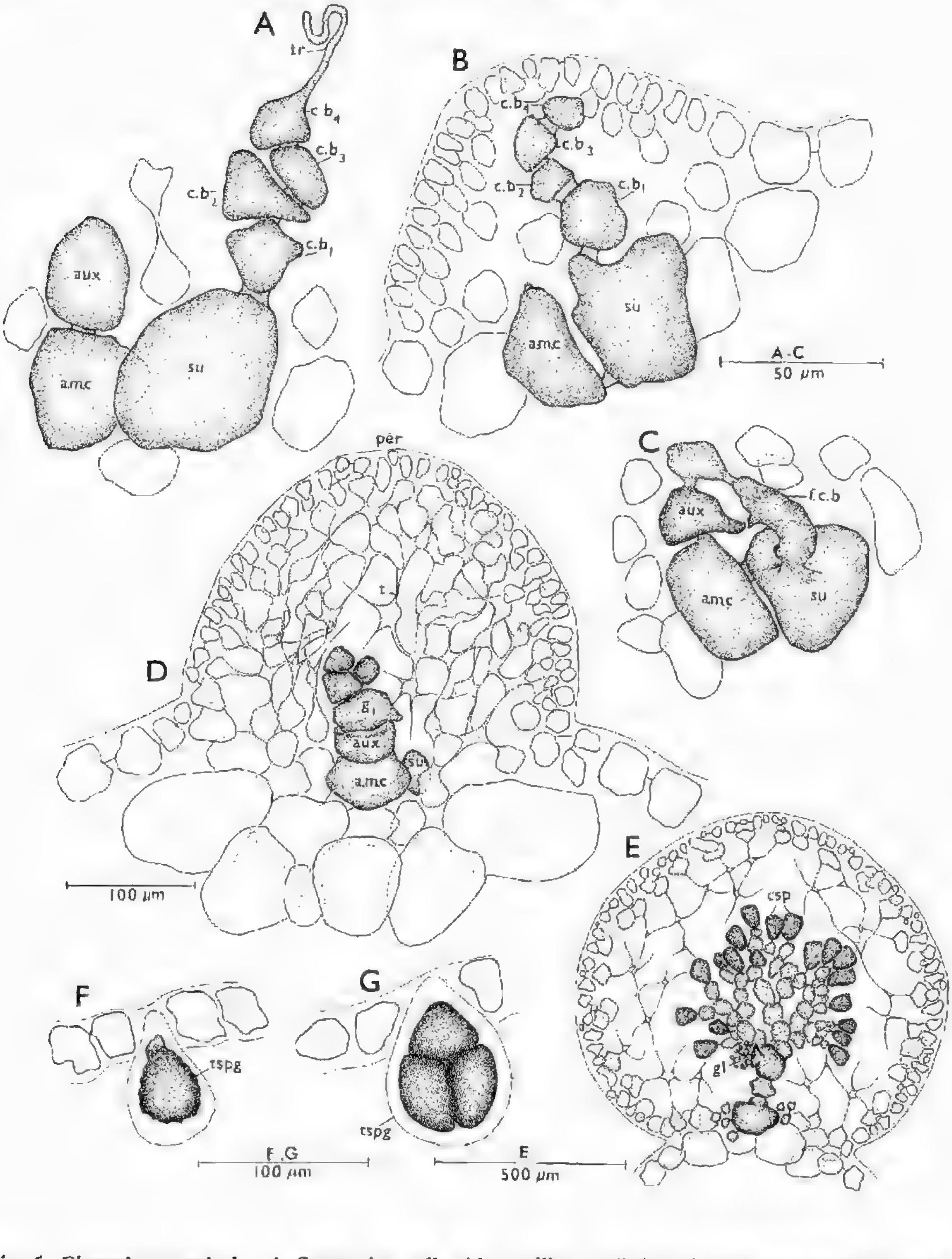

Fig. 6. *Champia zostericola*. *A*. Supporting cell with auxiliary cell branch and carpogonial branch (A43556). *B*. An early post-fertilisation stage showing fusions between cells of carpogonial branch (A43556). *C*. Post-fertilisation stage with fused carpogonial branch and connections to auxiliary cell (A43556). *D*. Young gonimoblast within developing pericarp (A43556). *E*. Older carposporophyte with terminal carposporangia, within pericarp (ostiole not in section) (A43556). *F*. A young tetrasporangium (A34256). *G*. Mature tetrasporangium (A34256).

The following references credit *C. parvula* to southern Australia, but probably all apply to other species, mainly to small specimens of *C. zostericola*; in most cases it is not possible to clarify these references

Guiler 1952: 94. Harvey 1855a: 545; 1859: 307. Lucas 1909: 34; 1929a: 19; 1929b: 50. Lucas & Perrin 1947: 206, fig. 70. May 1965: 362. Reinbold 1897: 53. Sonder 1846: 176; 1880: 17. Tate 1882: 18. Tisdall 1898: 506. Wilson 1892: 180.

C. parvula is generally recognised as a relatively small and variable species, and herbarium specimens credited to it vary in size, degree of branching, proportions of the segments and distinctness of the diaphragms, and in the size of the cortical cells and degree of outer cortical development. Harvey (1849, pl. 210; 1853, p. 76) commented on the variability of this species. In comparisons with southern Australian taxa, liquid preserved material from Ile Verte, Roscoff, France (*J. Feldmann*, 14.x.1974; ADU, A46057) has been taken as representing the species in western Europe. This specimen has longer segments (about as long as broad) than shown by Gayral (1966, pl. 134) but distinctly shorter than illustrated by Harvey (1849, pl. 210), and the diaphragms and cortical cells are distinct throughout the plant, with relatively slight development of small outer cells. There are usually two complete longitudinal filament cells between the diaphragms, and the longitudinal filaments are confined to the periphery of the diaphragms. The most detailed account of *C. parvula* is by Bliding (1928) who studied material from Woods Hole, U.S.A. Bliding's description and illustrations appear to agree with the Ile Verte specimen.

In spite of the several references to *C. parvula* in southern Australia, it now seems clear that typical forms of this species do not occur here. Young and small plants of *C. zostericola* do show some similarities, but are generally broader, more robust, and when mature have numerous hooked branches. Also, *C. zostericola* has usually only one complete longitudinal filament cell between the diaphragms, and the cortical cells are larger. Some small forms of *C. affinis* also approach *C. parvula* but can be distinguished on their greater outer cortical development. Harvey's specimens referred to *C. parvula* appear to be slender forms of either *C. zostericola* or *C. viridis*.

However, a distinctive taxon occurs epiphytic on *Amphibolis* at Tipara reef in Spencer Gulf, South Australia, and it appears best to designate this as a distinct variety of *C. parvula*, to which it seems more closely allied than to the larger *C. zostericola*. Future studies may show that it should be recognised as a distinct species.

Champia parvula var. **amphibolis** var. nov.

FIGS 7, 14*A*

Thallus (Fig. 14*A*) erect, spreading, 3–11 cm high, with one to several much-branched main axes arising from a small discoid holdfast on stems of *Amphibolis*, red to red brown in colour, adhering to paper; occasional attachments by haustorial pads occur. *Axes* densely and irregularly radially branched to 3 or 4 orders, with alternate, opposite or occasionally whorled branches; axes 1–1½ mm in diameter below, tapering gradually to branchlets 1/3–½ mm in diameter. Young branches slightly constricted at diaphragms, segments 1–1½ times as long as broad, branch ends usually straight but rarely hooked, apices rounded. *Diaphragms* distinct throughout most of the thallus, somewhat obscured near bases of older plants. *Cortex* of a layer of angular cells 25–40(–50) μm across and (1–)2–3(–4) times as long as broad, with small cells cut off from their corners, and on older axes developing a continuous outer cortical layer (Fig. 7*D*) which in old plants may be 3 cells thick. *Longitudinal filaments* confined to periphery of diaphragms, developed from 10–15 apical cells, usually with two (–3) complete cells and two part cells between the diaphragms (Fig. 7*C*).

Cystocarps single, subspherical to urceolate, scattered over younger branches, ¾–1¼ mm long and ¾–1 mm in diameter, ostiolate.

Spermatangia forming sori over several segments near the apices of young branches.

Tetrasporangia scattered in young branches, 75–120 μm in diameter.

Thallus erectus, effusus, 3–11 cm altus ex haptere parvo discoideo in Amphibole. Axes irregulariter ramosi, 1–1½ mm in diametro, ramuli 1/3–½ mm in diametro; segmenta 1–1½ plo longiora quam lata. Diaphragmata conspicua nisi prope bases plantarum veterum. Cortex compositus cellularum angulosarum 25–40(–50) μm latarum, (1–)2–3(–4) plo longiorum quam latarum, parvas cellulas in angulis ferens, ad 3 cellulas crassus in partibus veteribus crescens. Filamenta longitudinalia tantum in margine, 2(–3) cellulas totas inter diaphragmata habentia. Cystocarpia subglobosa vel urceolata, dispersa, ¾–1¼ mm longa et ¾–1 mm in diametro, ostiolata. Spermatangia in soris fasciculata prope apices ramulorum. Tetrasporangia 75–120 μm in diametro dispersa.

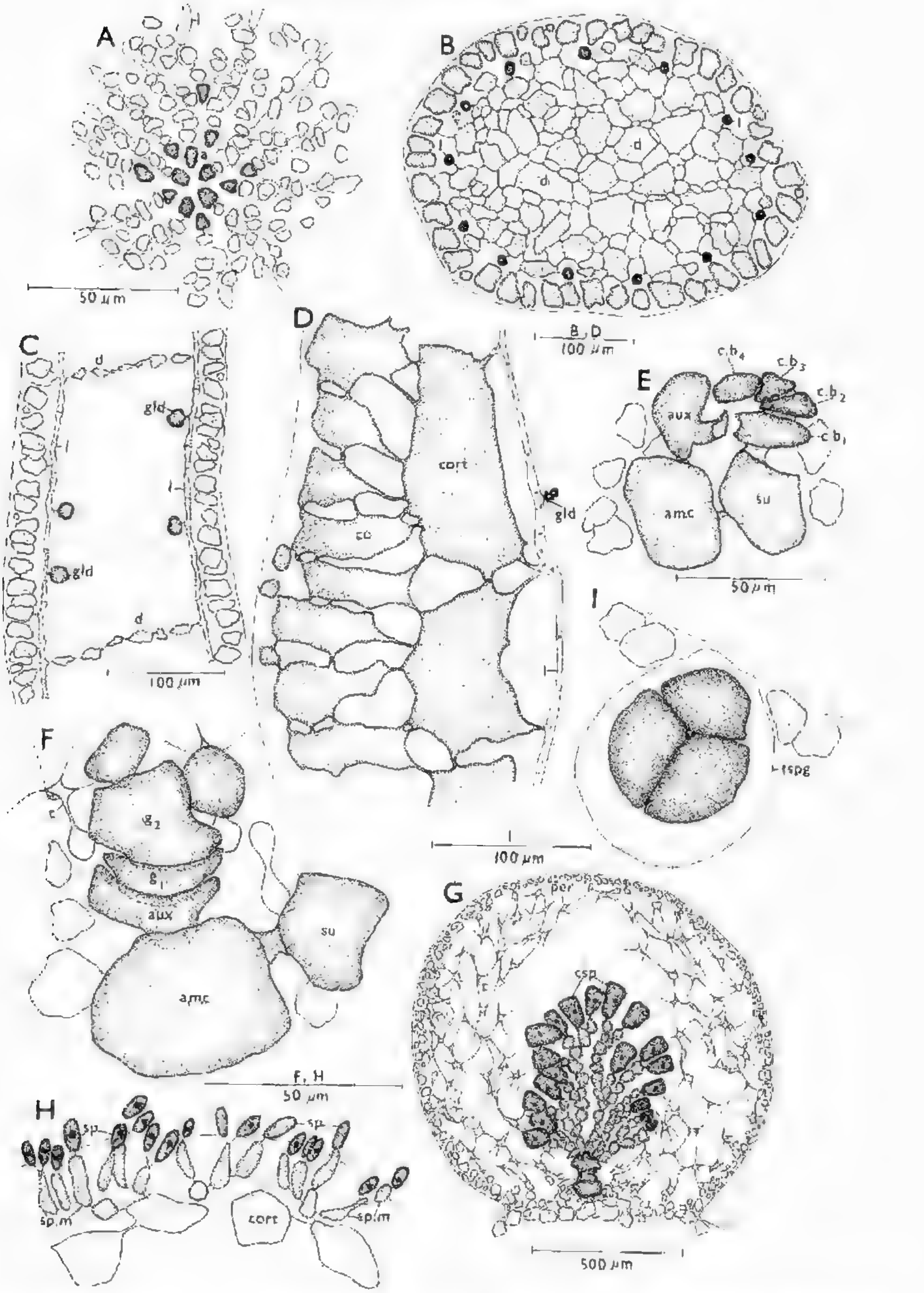

Fig. 7. *Champia parvula* var. *amphibolis*. *A*. Surface view of branch showing apical cells (A41276). *B*. Cross section of branch showing diaphragm, cortex and peripheral longitudinal filaments (A41276). *C*. Longitudinal section of a branch showing single-layered cortex, diaphragms, and longitudinal filaments with gland cells (A41276). *D*. Longitudinal section of older axis showing two (-3) layered cortex (A37291). *E*. Post-fertilisation stage showing fusions between carpogonial branch cells and connection to auxiliary cell (A38255). *F*. Young gonimoblast (A38255). *G*. Mature cystocarp (ostiole not in section) with carposporophyte bearing terminal carposporangia (A38255). *H*. Section of male thallus with spermatangia (A41276). *I*. Mature tetrasporangium (A37291).

Type locality. Tipara reef, Spencer Gulf, S. Aust. (*Shepherd*, 23.xii.1970).

Type. ADU, A38255.

Distribution. Known from several collections from Tipara reef, on *Amphibolis antarctica* and *A. griffithii*, 5–11 m deep. Young plants occur in June, maturing to bushy plants up to 11 cm high in December.

Var. *amphibolis* resembles the more typical forms of *Champia parvula* in being a relatively slender plant, mostly irregularly alternately branched, with diaphragms distinct throughout most of the plant and segments as long to slightly longer than broad, with the primary cortical layer of cells cutting off relatively few outer cells (except in old parts), and with usually two complete longitudinal filament cells between the diaphragms. Reproductively it is similar to the account of Bliding (1928) and at least superficially to the Ile Verte material.

It differs from European forms in being slenderer than some, more profusely branched, and in growing on *Amphibolis* as erect tufted plants. Future collections may show that it is not confined to this sea-grass and some specimens of Harvey (in TCD & MEL) from Fremantle and King George Sound, W. Aust. (e.g. Alg. Aust. Exsicc. 254B in MEL, 45307) need careful comparison with this variety and with *C. zostericola*.

This Australian variety shows slight similarity to *C. zostericola* but is very much slenderer than most plants of the latter, only rarely has hooked branches, has longer segments close to the apices and has two complete longitudinal filament cells between the diaphragms rather than the usual one in *C. zostericola*. *C. zostericola* does occur on *Amphibolis*, but is more characteristically associated with *Posidonia*.

STRUCTURE AND REPRODUCTION

Material studied: Tipara reef, Spencer Gulf, S. Aust., on *Amphibolis*, *Shepherd*. The type, A41276 (13.xii.1971) and A37291 (30.ix.1970).

Thallus development

The thallus has 10–15 apical cells (Fig. 7*A*) which segment as in other species to form a peripheral ring of longitudinal filaments (Fig. 7*B*), with diaphragms forming usually from each third cell and thus with two (occasionally three) complete longitudinal filament cells (usually each with a gland cell) between successive diaphragms (Fig. 7*C*). The cortex is one cell thick (Fig. 7*C*) except on older axes (Fig. 7*D*) and the elongate cortical cells cut off, from their corners, small cells (usually only one per cell) which lie more or less in the layer of primary cortical cells. These small cells commonly bear a hair in young branches, but such hairs are lost from older branches.

On old axes, the primary cortical cells cut off an outer, continuous, layer of cells (Fig. 7*D*) and this may become two or three cells thick, the outermost layer being of small cells.

Branching occurs from the regions of the diaphragms. Most branches are linear to the apex, but occasionally a curved or slightly "hooked" branch end occurs.

The holdfast remains small and discoid, but several new axes may develop from it. Small, pad-like haustoria also develop from branches of some plants, attaching mainly to other branches.

Procarp and carposporophyte

The multinucleate supporting cell develops from a cortical cell and bears both carpogonial and auxiliary cell branches as in other species. Following fertilisation, the carpogonial branch cells begin to fuse (Fig. 7*E*) and a connection forms between the fertilised carpogonium and the auxiliary cell. The diploidised auxiliary cell forms a first gonimoblast cell which divides again (Fig. 7*E*), and the upper cell forms the branched gonimoblast filaments (Fig. 7*G*) which bear terminal carposporangia.

Following fertilisation, some vegetative cells around the supporting cell become darkly-staining, apparently as nutritive cells. Other vegetative cells divide to form the pericarp (Fig. 7*G*) which develops as in other species, with the inner cells forming the "tela arachnoidea" which is broken or absorbed by the developing carposporophyte. A well-defined ostiole occurs at maturity of the cystocarp.

Spermatangia

The small outer cortical cells, or further cells cut off from the primary cortical cells, divide to form branched filaments of cells covering the surface of one to several segments close to the apices of young branchlets. Each cell of these filaments functions as a spermatangial mother cell which cuts off outwardly 2–3 elongate-ovoid spermatangia (Fig. 7*H*), which appear to be shed entire.

Tetrasporangia

Tetrasporangia (Fig. 7*I*) develop within cortical cells which enlarge greatly and bulge within the segments of the thallus.

CHYLOCLADIA Greville

Chylocladia Greville (*in* Hooker 1833, p. 297), with the type species *C. kaliformis*, is conserved over *Kaliformis* Stackhouse 1809, and is distinguished from *Champia* by the formation of carposporangia directly from a large basal fusion cell (without branched gonimoblast filaments as in *Champia*) and by the cystocarps being non-ostiolate. Otherwise, *Chylocladia* is similar structurally to *Champia*.

While numerous Australian taxa have at some time been referred to *Chylocladia*, most have been placed in other genera (see Kylin 1931) or can now (see below) be excluded from *Chylocladia*.

However, a very distinctive species of *Chylocladia*, known from only a few deep-water collections, has recently been discovered in South Australian waters.

Chylocladia grandis sp. nov.

FIGS 8, 9, 14*B*

Thallus (Fig. 14*B*) erect, red-brown to red-purple, 20–50 cm high, with one to several axes arising from a hard, branched, perennial base to 5 cm high and 1/3–¾ cm thick, attached to rock by a discoid holdfast to 1½ cm across. Axes with opposite or usually whorled lateral branches to 10 cm long, similarly branched (mainly oppositely or alternately) to a second or third order; axes often denuded below, 2–7 mm in diameter, branches 1½–2½ mm in diameter tapering to ¾–1 mm in diameter in branchlets; all branches slightly basally constricted, tapering gently to a rounded apex, segments ½–1½ times as long as broad; branches slightly constricted between segments, but diaphragms conspicuous. *Cortex* in branchlets 1 cell thick (Fig. 8*D*), in older branches thicker and in axes to 8 cells thick (Fig. 8*E*); cortical cells ovoid, 25–35(–40) μm across and 1–2 times as long as broad in surface view. *Longitudinal filaments* scattered throughout diaphragms, with (1–)2(–3) complete cells and two part cells between the diaphragms (Fig. 8*B*), with each peripheral filament cell connected to the cortical cells by a lateral filament.

Cystocarps scattered over lesser branches, spherical to slightly ovoid, ¾–1(–1¼) mm across, broad based, without an ostiole; carposporangia borne directly on the large, basal, fusion cell.

Spermatangia unknown.

Tetrasporangia scattered over branches, tetrahedrally divided, mostly 150–200(–250) μm in diameter.

Thallus erectus ad 20–50 cm altus, uno vel pluribus axibus ex base dura ramoso et perenni ad 5 cm altis et 1/3–¾ cm latis ortis, haptere discoideo. Rami laterales in verticillum vel opposite dispositi, ad 10 cm longi et similita ramosi; axes 2–7 mm, rami 1.5–2.5 mm et ramuli 0.7–1 mm in diametro, segmentis ½–1½ plo longioribus quam latis, plus minus constrictus, diaphragmalibus conspicuis. Cortex ad unam cellulam in ramulis crassus, ad 8 cellulas crassus in axibus crescens. Filamenta longitudinalia dispersa, plerumque 2 cellulas totas inter diaphragmata habentia. Cystocarpia subglobosa ¾–1(–1¼) mm lata, haud osteolata, dispersa; carposporangia in coalescenti cellula ipsa magna basali portata. Tetrasporangia in ramis dispersa, 150–200(–250) μm in diametro.

Type locality. Tapley Shoal, Edithburg, S. Aust., 15 m deep (Shepherd, 2.ii.1969).

Holotype. ADU, A33515. Isotypes to be distributed under this number.

Distribution. Only known from the type collection from Tapley Shoal, and Investigator Strait, S. Aust., *Watson*, 11 m deep (20.i.1971: ADU, A40995), 23 m deep (28.i.1971; ADU, A41010), and 34 m deep (20.i.1971; ADU, A39197).

Chylocladia grandis appears to be quite distinct in its form, large size, dense branching, and in the perennial base which appears to last for several years, producing one to several fronds annually (probably in spring and lasting through summer).

STRUCTURE AND REPRODUCTION

Material studied: The type and Investigator Strait collections.

Thallus development

The multiaxial apex of a branch (Fig. 8*A*, *B*) includes both a central group of apical cells which give rise to the scattered longitudinal filaments, and outer apical cells which produce the peripheral longitudinal filaments and the cortex.

Fig. 8. *Chylocladia grandis*. *A*. Surface view of an apex showing peripheral and central apical cells (A33515). *B*. Longitudinal section of a branch apex showing development of cortex, diaphragms, and longitudinal filaments with gland cells (A33515). *C*. Cross section of a branch showing a diaphragm with sub-peripheral and central longitudinal filaments (A33515). *D*. Longitudinal view of outer part of a mature branch, showing the lateral connecting filaments between the longitudinal filaments and the cortex (A33515). *E*. Longitudinal section of an axis showing the multi-layered cortex (A33515).

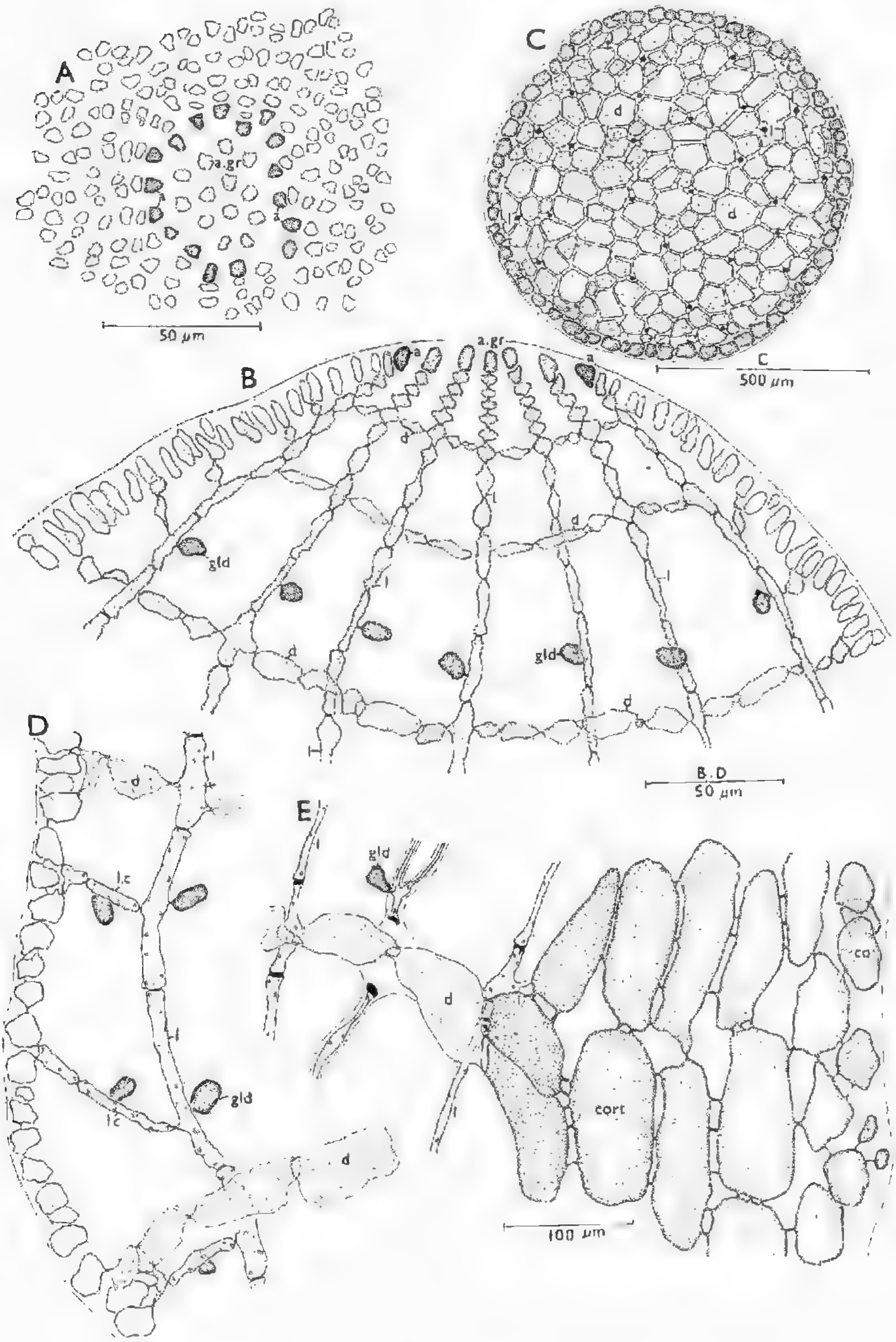
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FIG. 8.

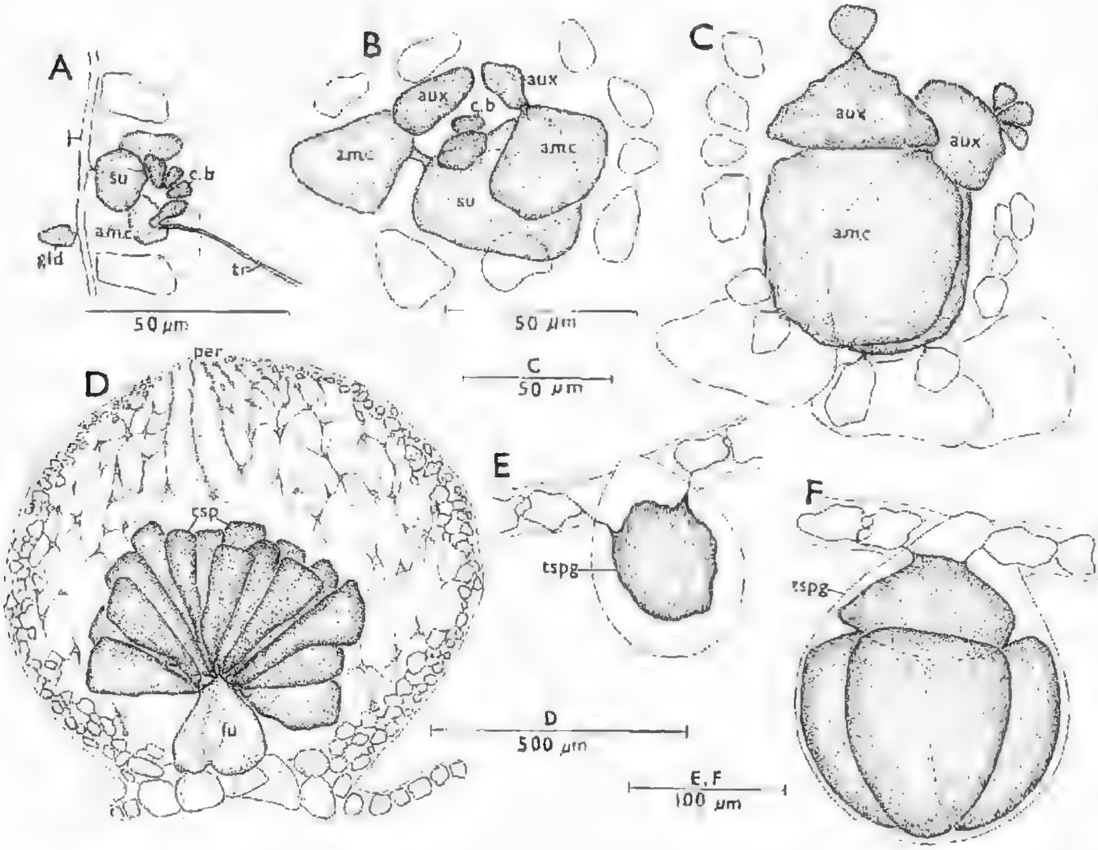

Fig. 9. *Chylocladia grandis*. *A*. Longitudinal section showing supporting cell with auxiliary mother cells and 4-celled carpogonial branch (A33515). *B*. Post-fertilisation stage showing two auxiliary cell branches and remnants of carpogonial branch (A33515). *C*. Post-fertilisation stage with auxiliary cells bearing young carposporangia. The supporting cell, auxiliary mother cells and auxiliary cells are partly fused (A33515). *D*. A cystocarp with mature carposporangia formed directly from the fusion cell, the lobes of which probably indicate the original auxiliary mother cells (A33515). *E*. A young tetrasporangium (A39197). *F*. A mature tetrasporangium (A39197).

The 12–16 central apical cells (Fig. 8*A*, *B*) divide transversely and the cells elongate to form longitudinal filaments. Each third cell usually produces a whorl of diaphragm initials which divide further to join with similar adjacent cells to form the single-layered diaphragms (Fig. 8*B*, *C*). The longitudinal filament cells between the diaphragms generally produce a single spherical to slightly pyriform gland cell (Fig. 8*B*).

The 15–20 outer apical cells divide transversely to form the peripheral ring of longitudinal filaments, but each of these cells, close to the branch apex, divides periclinally to form an outer primary cortical cell initial (Fig. 8*B*). This cell divides periclinally again once or twice and then the outer cell divides anticlinally to form the primary cortical layer, but the later formed cells are not in pit-connection with the longitudinal filaments (Fig. 8*B*). The periclinal division of the cortical initial is followed by the inner one or two cells elongating to form a bridging filament between each cell of the peripheral longitudinal filaments and the cortical cells (Fig. 8*D*). This feature is not found in the Australian species of *Champia*. The peripheral longitudinal filament cells cut off diaphragm cells which join with those from the inner filaments. The peripheral filaments are usually separated by one diaphragm cell from the cortex (Fig. 8*C*).

Many of the primary cortical cells cut off a small outer cell which produces a hair; these hairs form a dense felt over most of the thallus.

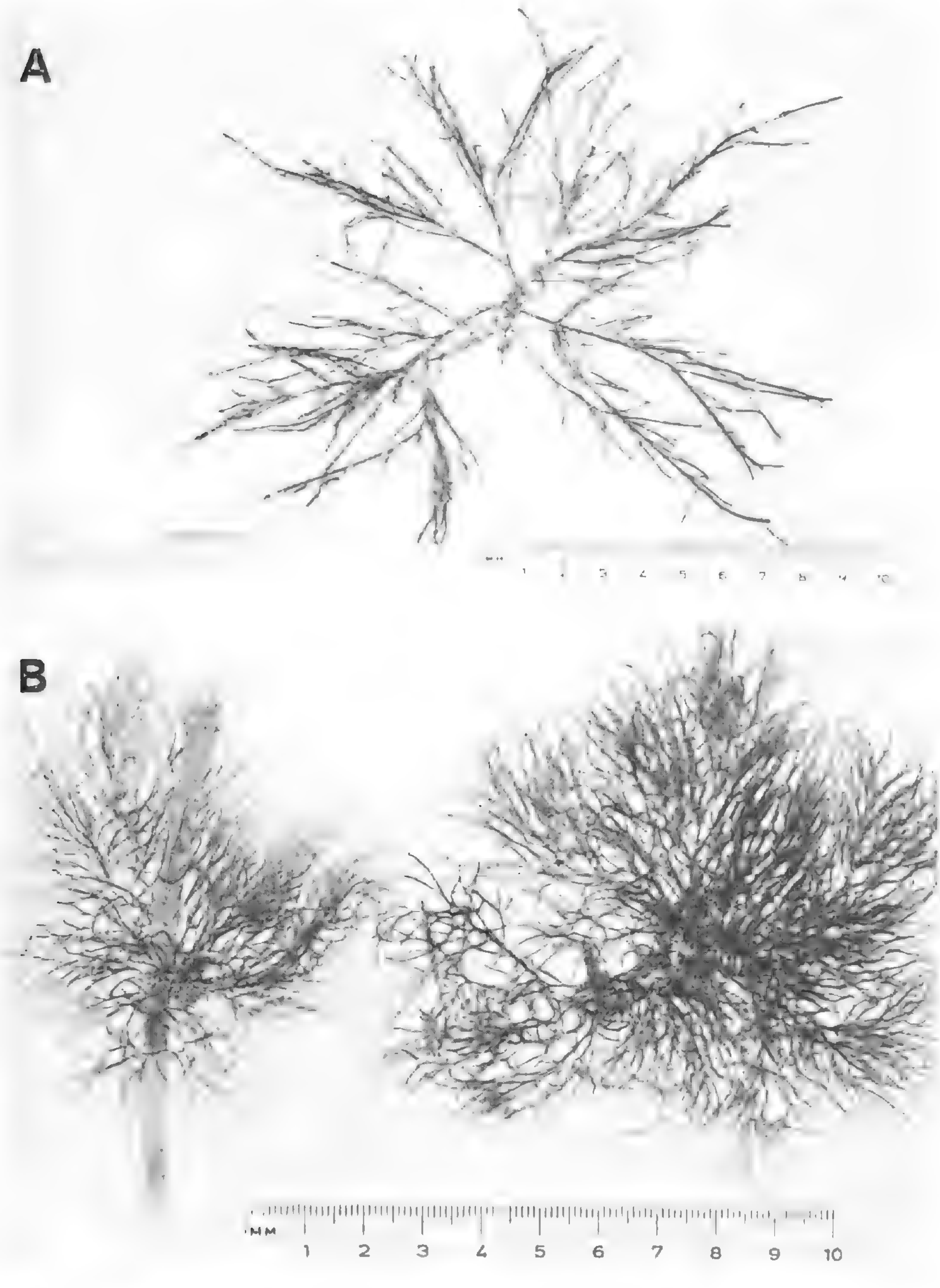

Fig. 10. *Champia viridis*. *A*. Type of *C. tasmanica* Harvey in TCD. *B*. A slender form (var. *gracilis* Harvey) on *Posidonia* (Marino, S. Aust. Drift. *Womersley*, 26.x.1975; ADU, A46651).

As the branch matures, the primary cortical cells cut off outer layers of cells, and in old axes the cortex may be up to 8 cells thick (Fig. 8*E*).

Branches originate from the region of the diaphragms, when a group of apical initials develops from the cortical cells.

The basal part of the thallus is clearly perennial, being hard and resistant, up to 5 cm high with irregularly placed, lateral propections representing the bases of previous axes. From the number and position of branch bases, some perennial bases appear to be 4–5 years old, and the axes are probably newly formed in spring and lost by the following winter. The branches probably decay rapidly since this plant has never been collected in the drift.

Procarp and carposporophyte

The supporting cell is a large primary cortical cell in pit-connection with a peripheral longitudinal filament (Fig. 9*A*). The supporting cell is multinucleate and cuts off outwardly a small cell, the carpogonial branch initial, and two larger cells, the auxiliary mother cells. The carpogonial branch (Fig. 9*A*) is 4-celled, curved, with an outwardly directed trichogyne. Prior to fertilisation, each auxiliary mother cell produces a uninucleate auxiliary cell (Fig. 9*B*).

Following fertilisation, a connection forms between the fertilised carpogonium and each auxiliary cell, and carposporangia are formed directly from the auxiliary cells (Fig. 9*C*). Fusion occurs between the auxiliary cells and auxiliary mother cells (Fig. 9*D*), forming a large basal fusion cell bearing the carposporangia directly. The supporting cell and some vegetative cells may be incorporated into the fusion cell.

Concurrent with the early development of the carposporophyte, vegetative cells around the supporting cell divide to produce erect chains of cells which cut off outer cells and form the pericarp (Fig. 9*D*), as in *Champia*. The inner cells of the pericarp form the "tela arachnoidea", but no ostiole is produced. When the carposporangia are mature, the top of the pericarp ruptures.

Tetrasporangia

The tetrasporangia develop by enlargement of the primary cortical cells (Fig. 9*E*), which have several pit-connections with adjacent cells. The tetrahedrally divided sporangia (Fig. 9*F*) develop a thick gelatinous sheath.

Relationships

Chylocladia grandis agrees well with *Chylocladia* and its type species, *C. kaliformis*, in thallus structure and in reproduction. However, it has not been established whether one or two auxiliary cell branches occur in *C. kaliformis*. *Champia* has only one auxiliary cell branch as far as is known, but the type of *Gastroclonium* Kuetzing (*G. ovale* (Hudson) Kuetzing) has two auxiliary cell branches (Bliding 1928, p. 27).

The thallus structure of *Chylocladia grandis* differs from that of the Australian species of *Champia* in that the initial cells of the primary cortex are connected to the longitudinal filament cells via a filament of one or two cells, not directly. Whether this occurs in *C. kaliformis* has not been established.

SPECIES EXCLUDED FROM CHYLOCLADIA

Apart from the various *Chylocladia* names which have been shown previously to be synonyms of species of *Champia* or other genera, the following names are now referred to other genera.

Chylocladia fruticulosa (Reinbold) De Toni 1900b: 576.

Lomentaria fruticulosa Reinbold 1899: 46.

Type locality. Investigator Strait, S. Aust. (*Davey* 148).

Type. Herb. Reinbold, M. Isotype in ADU, A1553.

The thallus of the isotype is on *Posidonia* (not *Amphibolis antarctica* as in Reinbold). It is hollow and without diaphragms, and the tetrasporangia are grouped in sori around depressions in the wall of the branches. These features are typical of *Lomentaria*, and the isotype (a small, bleached specimen) appears similar to the earlier described *Lomentaria australis* (Kuetzing) Levring 1946, p. 223 (*Chondrothamnion australe* Kuetzing 1865, p. 29, pl. 82 d–f). The southern Australian species of *Lomentaria* are in need of detailed study.

Chylocladia gelidioides Harvey 1863, synop.: 46. De Toni 1900b: 578; 1924: 312. Gepp & Gepp 1906: 257. Okamura 1904: 88.

Type locality. Twofold Bay, N.S.W. (*F.v. Mueller*).

Type. Herb. Harvey, TCD.

Although cystocarpic material has not been studied, the hollow thallus construction without single layered diaphragms, and sori of tetrasporangia, are typical of *Lomentaria*. The

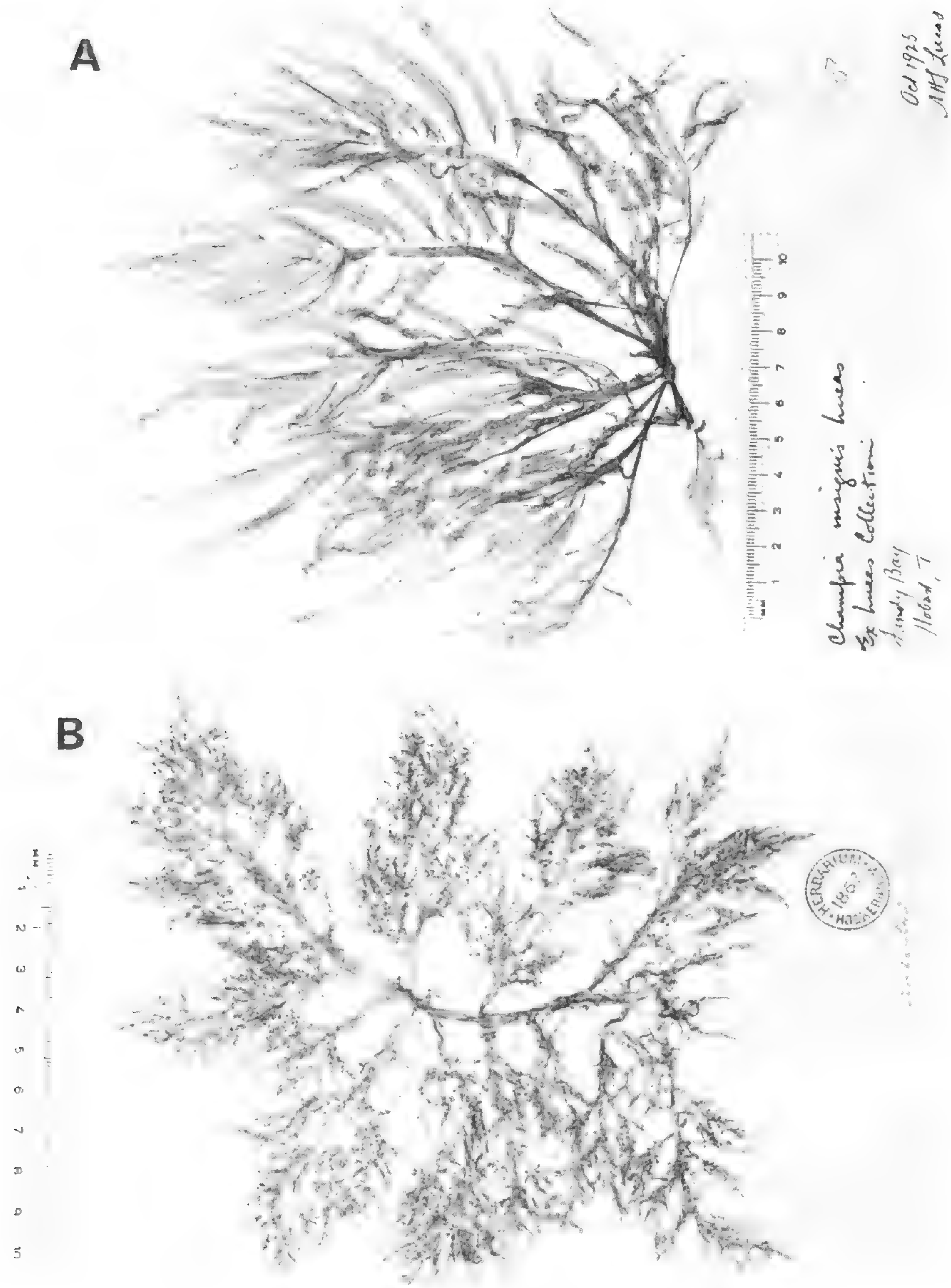

Fig. 11. *A*. *Champia insignis*. Isotype male specimen (ADU, A12237). *B*. *Champia affinis*. Lectotype specimen in BM.

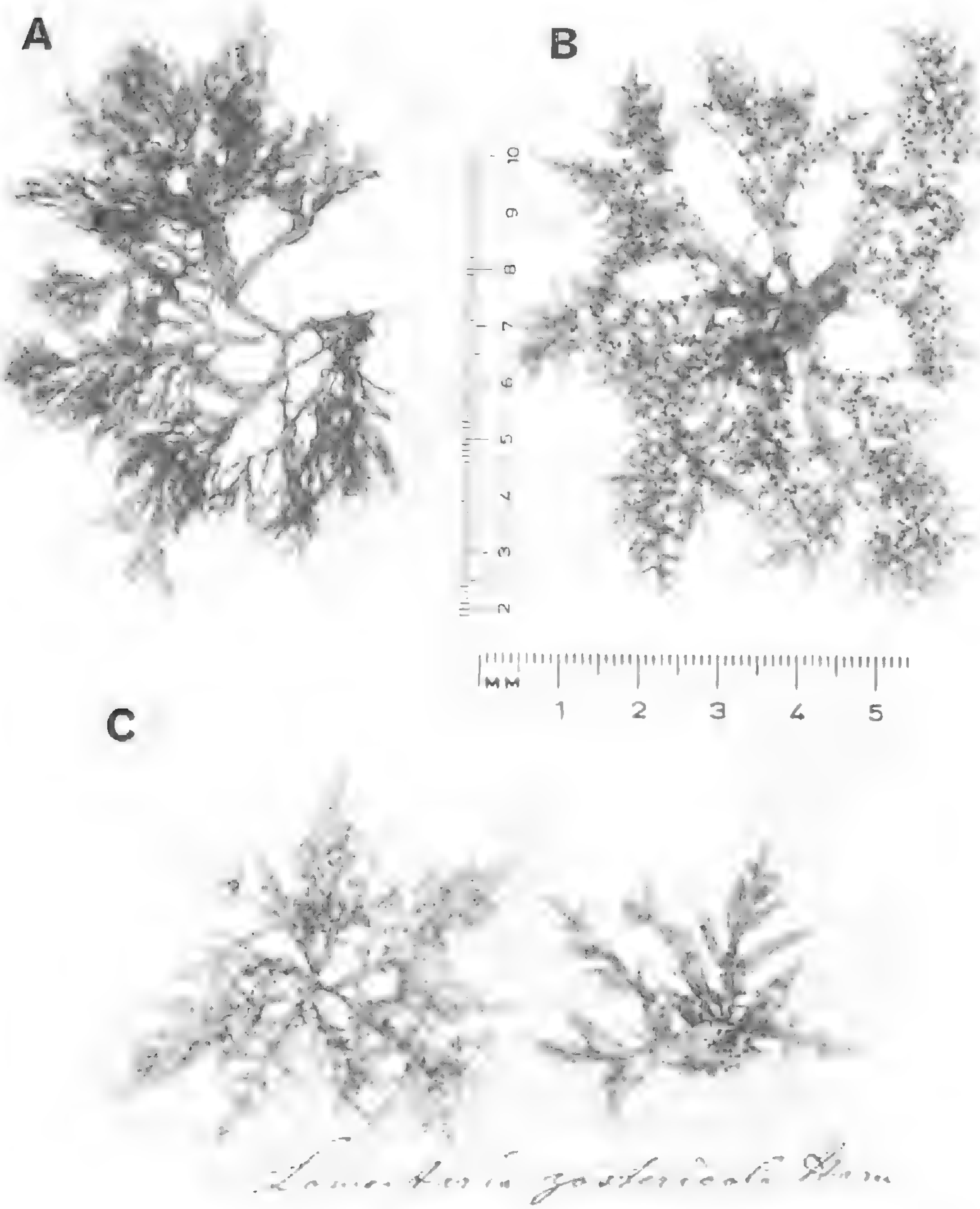

Fig. 12. *Champia affinis*. *A*. Harvey's Alg. Aust. Exsicc. 252I (as *C. obsoleta*) from Georgetown, Tas. (in TCD). *B*. Lectotype of *C. obsoleta* (Port Fairy, Vic. Harvey's, Alg. Aust. Exsicc. 252D) —a rough-water form. *Champia zostericola*. *C*. Harvey's Alg. Aust. Exsicc. 249A, Fremantle, W. Aust.

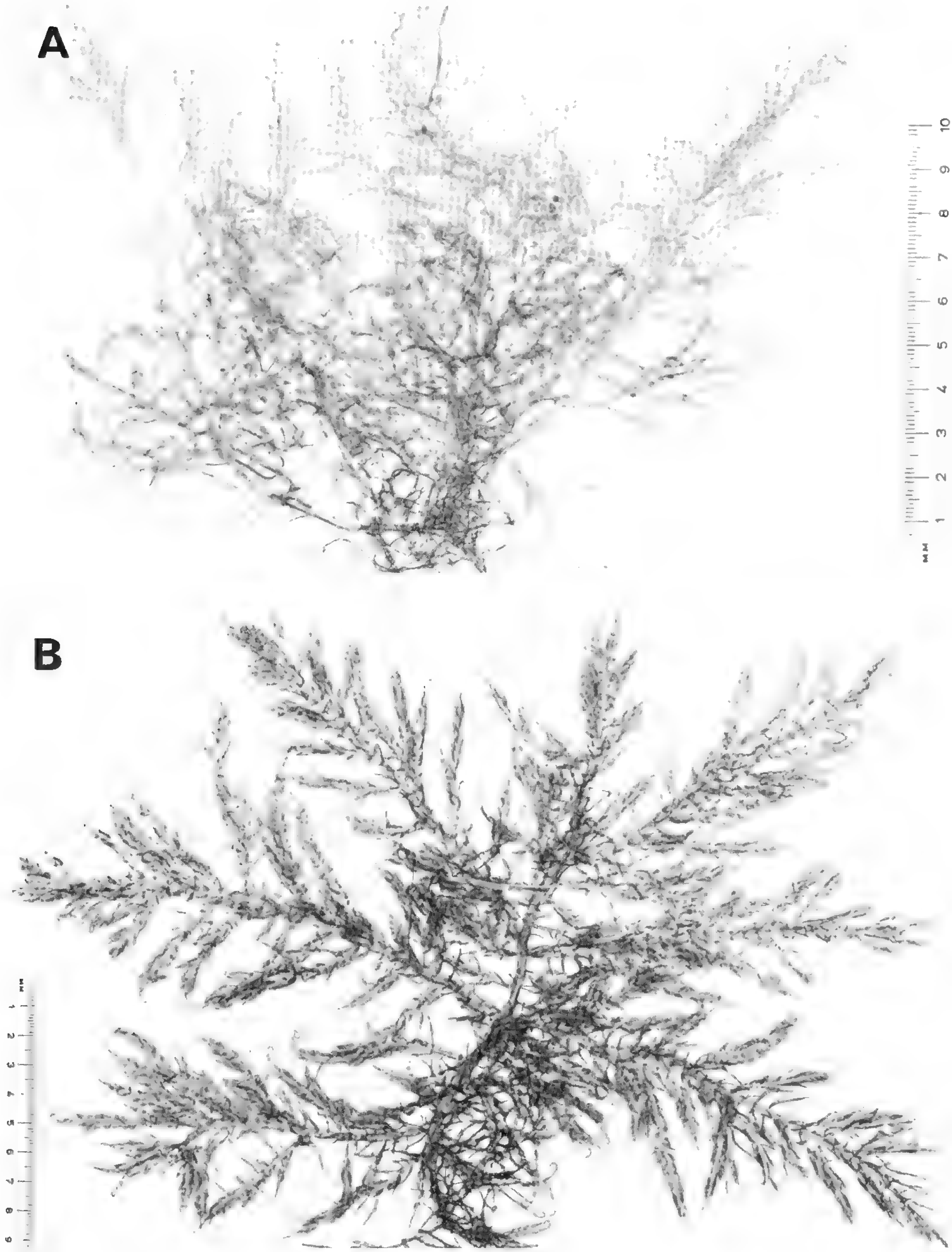

Fig. 13. *A*. Lectotype of *C. affinis* var. *arcuata* Hooker & Harvey. *Gunn* 1332, in BM. *B*. *Champia zostericola*. Musselroe Bay, Tas. *Perrin*, March 1937 (MEL 45252)—plant with well-developed axes.

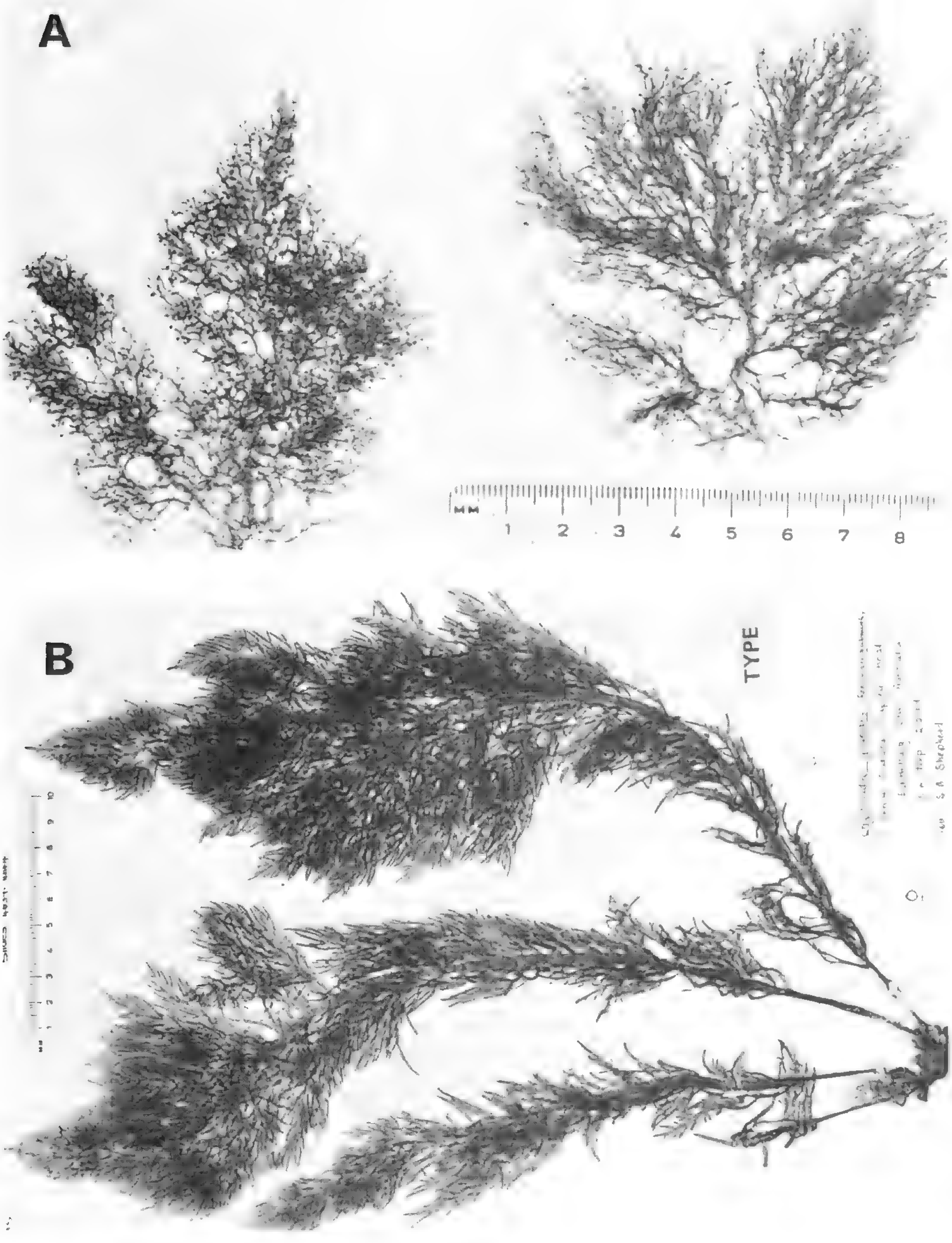

Fig. 14. *A*. *Champia parvula* var. *amphibolis*. Type specimen of variety.
B. *Chylocladia grandis*. Holotype specimen.

thallus habit, cell detail, and tetrasporangial sori are very similar to *Lomentaria catenata* Harvey from Japan (as noted by Harvey 1863 and Okamura 1904), and the N.S.W. plant may be a slightly less robust form of the Japanese species, which is also recorded from Pacific Mexico by Dawson (1963, p. 465, pl. 92). It appears to be closely related to *Lomentaria ramsayana* (J. Agardh) Kylin (1931, p. 27, pl. 14, fig. 33).

Chylocladia multiramea Sonder 1853: 681.

Type locality. Lefevre Pen., S. Aust.

Type. MEL, 45196.

The type specimen (female) in MEL is a slender, much branched, bleached plant of *Dasyphloea insignis* Montagne.

Acknowledgements

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LEGGADINA LAKEDOWNENSIS, A NEW SPECIES OF MURID RODENT FROM NORTH QUEENSLAND

BY C. H. S. WATTS*

Summary

WATTS, C. H. *S.* (1976).-*Leggadina lakedownensis*, a new species of Murid rodent from north Queensland. Trans. R. Soc. *S.* Aust. **100**(2), 105-108, 31 May, 1976.

Leggadina lakedownensis, a new species of murid rodent from northeastern Queensland is described and figured. Morphologically it most closely resembles *L. forresti* (Thomas).

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by C. H. S. WATTS*

Summary

WATTS, C. H. S. (1976).—*Leggadina lakedownensis*, a new species of Murid rodent from north Queensland. *Trans. R. Soc. S. Aust.* **100**(2), 105-108, 31 May, 1976.

Leggadina lakedownensis, a new species of murid rodent from northeastern Queensland is described and figured. Morphologically it most closely resembles *L. forresti* (Thomas).

Introduction

A pair of small rodents from Cape York, examined during the course of a broader investigation into the karyotypes of Australian rodents, was found to differ in karyotype, blood proteins, and cranial morphology from the otherwise similar *Leggadina forresti*, as well as all other murids examined.

Leggadina lakedownensis n.sp.

FIGS 1, 2, and 3

Holotype: Qld Mus. JM1192, ♀. Received from Queensland Museum in May 1975, killed August 1975. The parents of this specimen were received by the Queensland Museum from Mr C. Tanner in August 1973; these were offspring of animals collected at Lakeland Downs, 110 km S of Cooktown, Queensland by Mr R. Buckley in 1973.

Description: (Colour after Ridgway 1912). Head relatively narrow and pointed as in *L. deliculata* and *L. hermannsburgensis*. Eyes not as prominent as in those species or in *L. forresti*. Ears small and broad, proportionately smaller than in *L. forresti*. Feet narrow. Hairs on back with tips buffy brown grading to pale olive-buff on sides, bases of hairs blackish brown which shows through giving back a brindled look. Underside white, hairs white to base, as are hairs on upper surface of feet. Face with suggestion of darker central stripe and lighter ring around eyes. Tail sparsely haired with light-coloured hairs.

Skull flat on top, rostrum short, interorbital region broad. Interparietal wide, short. Zygo-

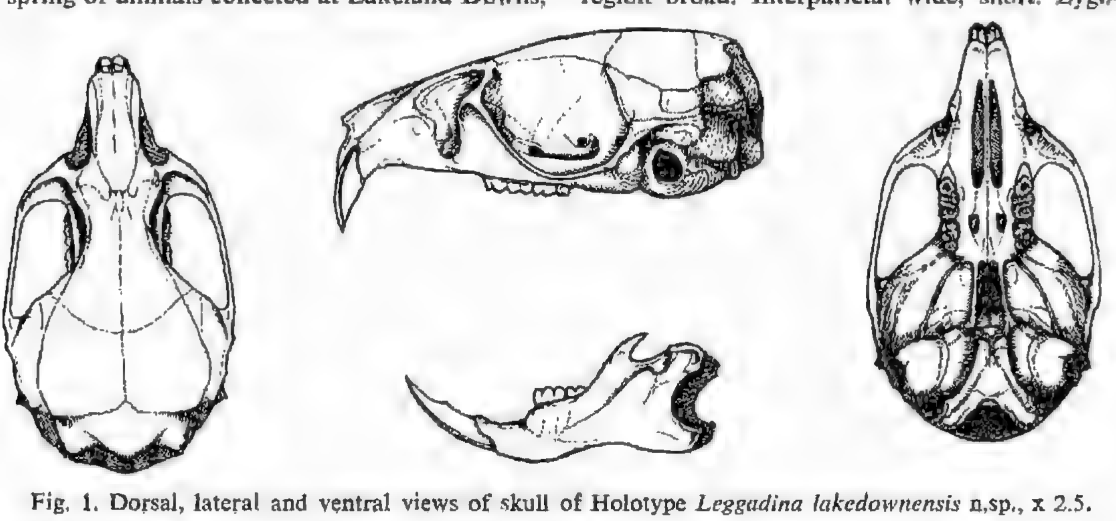

Fig. 1. Dorsal, lateral and ventral views of skull of Holotype *Leggadina lakedownensis* n.sp., x 2.5.

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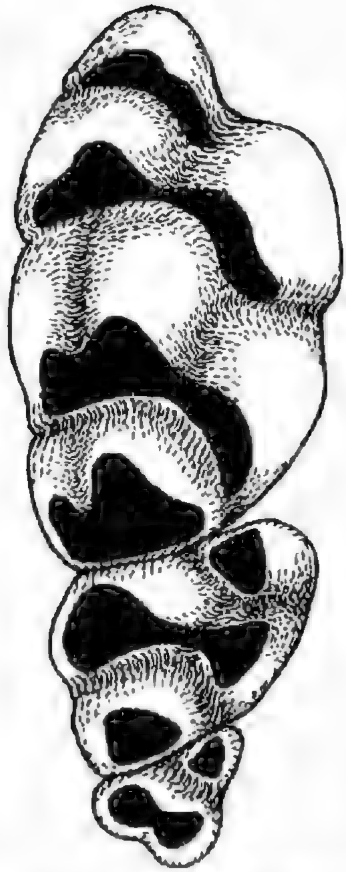

Fig. 2. Upper right molar tooth row of holotype of *Leggadina lakedownensis* n.sp.

matic plates moderate, minimum width equal to length of M^1_1. Lacrimals small. Nasals short, not exceeding premaxillae anteriorly. Incisive foraminae longer than tooth row, reaching beyond anterior end of M^1_1, broad, slightly wider posteriorly, broadly rounded posteriorly, more pointed anteriorly. Posterior palatal foraminae oval, about length of M^3_3. Mesopterygoid fossae narrow, their width about equal to length of M^3_3. Bullae moderately developed about size of occipital foraminae, the distance between them about equal to combined lengths of M^2_2 and M^3_3. Upper incisors forward pointing. Molars as in Figure 2, anterior ligual cusp of M^1_1 blade-like and strongly developed. M^1_1 large, approximately 65% of tooth row, M^3_3 small, approximately 15% of tooth row.

Specimens examined: Paratypes: Qld Mus. JM1293 ♀, JM1294 ♀ bred in captivity; collection details as for Holotype. Referred specimen. Qld Mus. J.17919, Williams Id, Queensland (35°S; 135°E), 1969, coll. Mr. C. Tanner.

Diagnosis

(Head and body 60–70 mm, Tail 40–50 mm, Ear 10–12 mm, Skull length 20–23 mm). Incisive foraminae reaching beyond anterior end of M^1_1, rounded and slightly widened posteriorly. Upper incisors forward pointing. Upper molar tooth row 3.7–4.2 mm long. Anterior ligual cusp of M^1_1 blade-like and strongly developed. M^1_1 4 to 5 times length of M^3_3.

Systematic position

Leggadina lakedownensis is separated from all named forms within the genus *Leggadina*, as recognised by Tate (1951), except *L. forresti* (Thomas), *L. waitei* (Troughton) and *L. messoria* (Thomas), by the short tail, small ears, long incisive foraminae, and large molar tooth row with M^1_1 large and with a strongly developed anterior ligual cusp.

These three taxa, *L. forresti*, *L. waitei* and *L. messoria*, were considered to be very closely related by Tate (1951) and were synonymised under the name of *Pseudomys forresti* by Ride (1970). My examination of the types of all three supports this view that only one species is involved, characterized by downward pointing upper incisors and long incisive foraminae narrowing posteriorly and about 3 times the length of M^3_3. Measurements of the Holotypes are included in Table 2.

Leggadina lakedownensis differs from *L. forresti* (and the Holotypes of *L. waitei* and *L. messoria*) in having the incisive foraminae widening rather than narrowing posteriorly, a slightly larger M^1_1 (in comparison to total tooth row), a smaller M^3_3 and forward pointing upper incisors. On the limited evidence available it is

TABLE 1

Measurements of specimens of L. lakedownensis *(mm)*

	1	2	3	4
Head and body	72	—	—	64
Tail	45	—	—	41
Hind foot (S.u.)	15	—	—	14
Ear (from notch)	11	—	—	11
Greatest length of skull	23.0	21.9	—	20.4
Zygomatic breadth	12.5	11.4	12.0	10.8
Interorbital breadth	3.6	3.5	3.4	3.6
Depth of brain case, including bullae	8.4	—	—	7.6
Length of nasal	7.3	7.3	7.3	6.7
Length of ant. palatal foramina	5.7	5.2	5.4	4.8
Crown length of molar row	4.0	3.9	3.7	4.2
Crown length of M^1_1	2.7	2.7	2.4	2.6
Crown length of M^3_3	0.6	0.5	0.5	0.7

1. Qld Mus. JM1292 ♀, Lakeland Downs, Qld, 1973. Holotype.
2. Qld Mus. JM1294 ♀, Lakeland Downs, Qld, 1973.
3. Qld Mus. JM1293 ♀, Lakeland Downs, Qld, 1973.
4. Qld Mus. J17919, Williams Id, Qld, 1969.

Fig. 3. *Leggadina lakedownensis*, n.sp.

a slightly smaller animal. In my opinion the scale of these differences indicate a form specifically distinct from *L. forresti* or any other described rodent.

Support for the distinctiveness of *L. lakedownensis* from *L. forresti* comes from studies of the chromosomes and blood proteins of these and some related species (Baverstock *et al.* 1976). These studies suggest that *L. forresti* and *L. lakedownensis* form a distinct group within *Pseudomys sensu lato*. The morphological characters (cf. above) tend to support this view and it seems prudent at this stage to retain the genus *Leggadina* at least for these two species.

Habitat and distribution

The Williams Island locality is an area of short grassland surrounded by scrub. (The locality is illustrated as Lakefield Station, by Covacevich (1974, p. 7).) Lakeland Downs is on an isolated area of basalt-derived red and brown soil supporting a natural vegetation of Box woodland (*E. leptophleba*), and deciduous scrub with kangaroo (*Themeda australis*) and spear (*Heteropogon contortus*) grass. At the time of collection however, sorghum covered the whole area. Rainfall is between 100 cm and 130 cm per year, occurring mainly in the summer (J. Covacevich, personal communication).

At present the species is only known from the above 2 localities on the eastern side of Cape York. *Leggadina forresti* has a much greater distribution in inland Australia and is known from W.A., S.A., N.T. and N.S.W. as well as western Queensland. From specimens in the Australian Museum and Queensland Museum (Table 2) it appears that there is a considerable gap between the distribution of the two species.

Acknowledgments

Miss Jeanette Covacevich kindly sent the animals on which the descriptions are based. Curators in the Queensland Museum, Australian Museum and South Australian Museum kindly sent material or allowed me access to specimens of *Leggadina* in their care. I am also grateful to Miss Heather Aslin for drawing the skull and teeth of the type specimen.

TABLE 2

Measurements of specimens of L. forresti *from Qld, S.A. and N.T. including Holotypes of* L. waitei, L. forresti *and* L. messoria *(mm)*

	AM M5194, Hart Range, N.T. *L. waitei* Holotype	BMNH 6.3.9.39, Alexandria, N.T., 1905 *L. forresti* Holotype	BMNH 25.4.9.1, Melrose, S.A., 1922 *L. messoria* Holotype	AM M9208, Mt Isa, Qld, 1968	AM M5165, Burketown, Qld, 1931	QM J5113, Barcardie, Qld	SAM M6344, SW Mann Range, S.A., 1966	SAM M6345, SW Mann Range, S.A., 1966	SAM M2958, Macdonald Downs, S.A., 1930	SAM M2405B, Horn Exp. (Waite)	SAM M2405, Horn Exp. (Waite)	SAM M6350, 60 km N Birdsville, Qld, 1966	SAM M6351, 60 km N Birdsville, Qld, 1966	SAM M6352, 48 km N Oodnadata, S.A., 1966	SAM M9481, 20 km W Innamincka, S.A., 1973
Head and body	77	104	67	84	83	—	88	100	—	—	—	80	90	89	80
Tail	55	72	53	53	—	—	59	69	—	—	—	56	61	—	59
Hind foot (S.u.)	—	19	17	18.7	17.2	—	17	17	—	—	—	18	18	19	18
Ear (from notch)	—	15	13	13.2	12.3	—	15	14	—	—	—	12	14	15	14
Greatest length of skull	22.4	24.9	23.3	—	—	23.5	23.4	24.6	25.2	24.4	24.3	23.6	24.8	25.2	23.4
Zygomatic breadth	12.0	—	12.4	—	13.8	12.6	12.1	13.2	14.0	12.9	13.1	13.1	13.2	13.0	12.7
Interorbital breadth	3.5	3.6	3.4	3.4	4.0	3.7	3.6	3.3	3.6	3.8	3.6	3.7	3.6	3.7	4.0
Depth of brain case, including bullae	8.5	8.9	8.1	7.8	8.6	8.7	8.6	9.2	8.8	8.9	8.6	—	8.8	8.9	8.9
Length of nasal	7.6	8.5	7.7	9.0	—	—	7.7	9.1	8.3	7.8	8.4	7.7	7.7	7.6	7.5
Length of ant. palatal foramina	5.8	5.3	5.6	6.0	5.0	5.2	5.4	5.6	5.7	5.0	5.5	5.2	5.3	5.6	5.4
Crown length of molar row	4.0	4.3	4.2	4.6	4.5	4.6	4.6	4.3	4.4	4.0	4.5	4.3	4.6	4.4	4.4
Crown length of M1	2.4	2.5	2.5	2.7	2.7	2.7	2.7	2.5	2.6	2.3	2.7	2.6	2.6	2.7	2.5
Crown length of M3	0.9	1.0	0.9	0.9	0.9	0.9	1.0	0.8	0.8	0.8	0.9	0.9	0.8	0.8	1.0

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BAVERSTOCK, P. R., HOGARTH, J. T., COLE, S., & COVACEVICH, J. (1976).—Biochemical and Karyotypic evidence for the specific status of the rodent *Leggadina lakedownensis* Watts. *Trans. R. Soc. S. Aust.* **100**(2), - .

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BIOCHEMICAL AND KARYOTYPIC EVIDENCE FOR THE SPECIFIC STATUS OF THE RODENT *LEGGADINA LAKEDOWNENSIS* WATTS

BY *P. R. BAVERSTOCK*, J. T. HOGARTH*, S. COLE** AND *J. COVACEVICH†*

Summary

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Introduction

In 1973 several specimens of a species of small rodent were collected from Lakeland Downs in northeast Queensland and described as a new species, *L. lakedownensis*, by Watts (1976). The morphological differences between *L. lakedownensis* and its apparent nearest relative *L. forresti* are, however, minor. Because speciation is the result of the accumulation of many genetic differences and because morphology alone reflects only part of these genetic differences, it seems desirable in such cases to assess other aspects of genetic differences between allopatric populations. The present study was undertaken to determine whether the karyotypic and biochemical differences between *L. forresti* and *L. lakedownensis* substantiated the recognition of the latter as a distinct species.

Methods

Sources of animals: The sources of animals utilized in the present study are shown in Table 1, along with their Institute of Medical and Veterinary Science number. When these animals die their skull and skin will be submitted to a Museum and given a Museum number. Museum numbers corresponding to IMVS numbers will be available from the IMVS or the South Australian Museum.

Chromosome preparations: Chromosome preparations were made from 8 *L. forresti* and 3 *L. lakedownensis*. Animals were bled by cardiac puncture under ether anaesthesia and leukocytes cultured for 3 or 4 days. Slides were prepared by means of the routine

TABLE 1

Reference numbers and sources of animals

Species	IMVS No.	Sex	Locality
(a) Chromosomes			
L. forresti	1	F	Coorabulka, SW Qld
	2	M	19 km W Innamincka, S.A.
	3	F	19 km W Innamincka, S.A.
	5	F	19 km W Innamincka, S.A.
	6	M	Fowlers Gap Stn, N.S.W.
	7	M	Fowlers Gap Stn, N.S.W
	8	M	Fowlers Gap Stn, N.S.W.
	9	M	Mt Sarah Stn, S.A.
L. lakedownensis	10*	F	Lakeland Downs Stn, Qld
	11	M	Lakeland Downs Stn, Qld
	12	M	Lakeland Downs Stn, Qld
(b) Electrophoresis			
L. forresti	3	F	19 km W Innamincka, S.A.
	5	F	19 km W Innamincka, S.A.
L. lakedownensis	10*	F	Lakeland Downs Stn, Qld
L. delicatula	13	M	Fairbairn Dam, 22 km SW Emerald, Qld
	14	M	Fairbairn Dam, 22 km SW Emerald, Qld
L. hermannsburgensis	14	M	Lab. stock
P. novaehollandiae	15	M	Port Stevens area, N.S.W.
P. australis		M	Lab. stock

* Holotype—Queensland Museum JM1292.

* Institute of Medical & Veterinary Science, Frome Rd, Adelaide, S. Aust. 5000.
† Queensland Museum, Gregory Tce, Fortitude Valley, Qld 4006.

TABLE 2

Electrophoretic buffer and staining systems used for proteins examined

Enzyme/Protein	Buffer system	Stain
E.E. 1.1.1.49 Glucose 6-Phosphate dehydrogenase (G 6-PD)	Brewer (1970)	Brewer (1970)
6-Phosphogluconate dehydrogenase E.C. 1.1.1.44 (6-PGD)	Brewer (1970)	Brewer (1970)
Phospho-hexose isomerase E.C. 5.3.1.9. (PHI)	Selander *et al.* (1971) 7	Brewer (1970)
Phosphoglucomutase E.C. 2.7.5.1. (PGM)	Selander *et al.* (1971) 7	Brewer (1970)
Lactate dehydrogenase E.C. 1.1.1.27 (LDH)	Holmes *et al.* (1973) TEB*	Brewer (1970)
NAD-Malate dehydrogenase E.C. 1.1.1.37 (NAD-MDH)	Holmes *et al.* (1973) TEB*	Brewer (1970)
Leucine aminopeptidase E.C. 3.4.1.1 (LAP)	Selander *et al.* (1971) 2	Brewer (1970)
Glyceraldehyde 3-Phosphate dehydrogenase GA 3-PD E.C. 1.2.1.12	Brewer (1970)	Brewer (1970)
Tetrazolium oxidase	Brewer (1970)	Scored from gels stained from GA 3-PD
Esterase (Est)	Soln A: 0.08M. tris-citrate pH 8.6 Soln B: 0.06 M. Li-borate-pH 8.8 Gel: 337.5 ml Soln A: 62.5 ml Soln B in 400 ml B. Electrode: Soln B.	Brewer (1970)
Albumin (Alb.)	as for Est	Amido Black
Haemoglobin (Hb)	as for G 6-PD	Amido Black
Transferrin (Tf)	as for Est	Amido Black

* TEB — Tris-EDTA-Borate

air-dry method. For karyotypes, slides were stained with 2% Giemsa. C-staining was conducted by the method of Arrighi and Hsu (1971) except that the RNase step was omitted. Slides were then stained with 10% Giemsa.

Electrophoresis: In addition to *L. forresti* and *L. lakedownensis*, specimens of *L. delicatula*, *L. hermansburgensis*, *Pseudomys novaehollandiae* and *P. australis* were studied. Blood was collected by cardiac puncture under ether anaesthesia in syringes containing a dried film of heparin and centrifuged immediately at 2,000G for 10 minutes at room temperature. Plasma was pipetted off and stored at −20°C. The red cells were washed 3 times in 2 volumes of isotonic saline and lysed in an equal volume of distilled water containing 1/5 volume of toluene. Cell walls were centrifuged out and the clear supernatant stored at −20°C for a maximum period of 3 weeks.

Horizontal starch gell electrophoresis was used. Gel slabs 300 mm x 150 mm x 6 mm were prepared from 12.5% (50g/400 ml buffer) starch using a perspex mould. Gels were run in a refrigerator to minimize heating. After electrophoresis a section approximately 90 mm x 120 mm was cut from the gel slab, sliced into two separate halves, and these halves then incubated in the appropriate staining solutions (Table 2).

Results

Chromosome studies: Fig. 1a shoks the karyotype of a female *L. forresti*. The diploid number was 2N = 48. The largest chromosome, designated pair 1, was acrocentric in IMVS 1, 2, 5, 7, 8 and 9. However, in IMVS 3 and 6, pair 1 was heteromorphic, one member being acrocentric and the other being subacrocentric with a distinct short arm. Pairs of 2 to 21 were acrocentric forming a series graded in size. Pairs 22 and 23 were small metacentrics. The presumed X-chromosome was an acrocentric representing about 6% of the total chromosome length and the Y-chromosome an acrocentric.

The C-staining technique (Fig. 1b) showed that although the centrometric area of some chromosomes were C-banded, only in the small metacentric pairs 22 and 23 was this marked. In many preparations the presumed Y stained slightly more intensely than other chromosomes over its entire length.

Chromosomally *L. lakedownensis* differs from *L. forresti* in possessing only one pair of small metacentrics (Fig. 1c). Also, in the three individuals karyotyped, pair 1 was always acrocentric. Centromeric C-banding of *L. lake-*

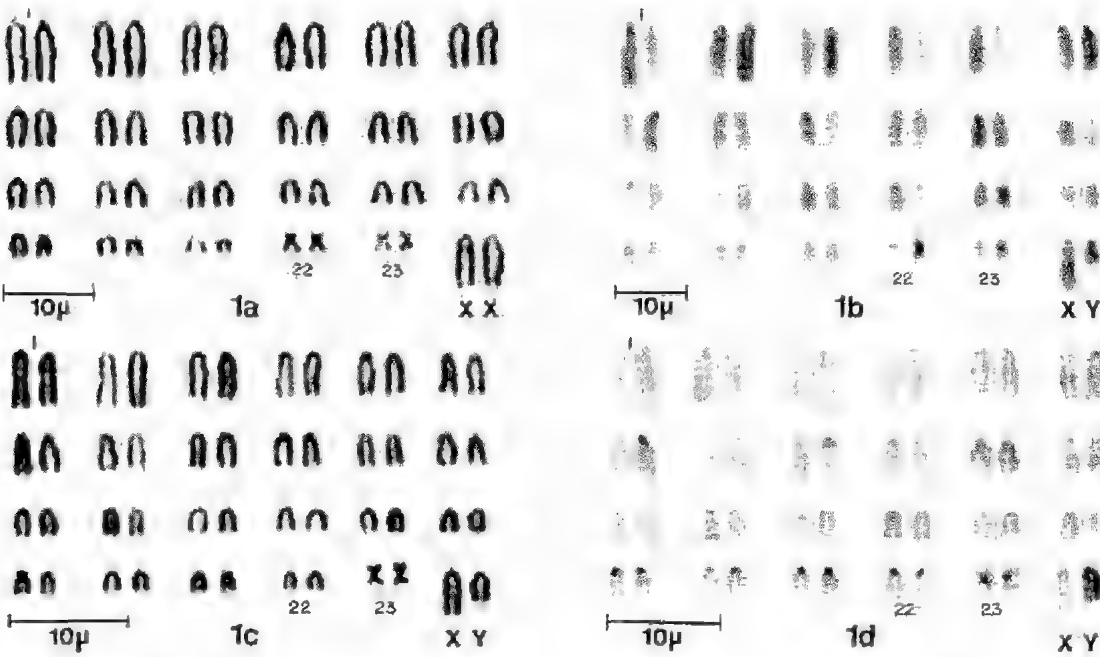

Fig. 1. Karyotype and C-banding of *L. forresti* and *L. lakedownensis*. 1a, Karyotype of female *L. forresti* (IMVS 3) heteromorphic for pair 1; 1b, C-banding of male *L. forresti* (IMVS 6) heteromorphic for pair 1; 1c, Karyotype of male *L. lakedownensis* (IMVS 11); 1d, C-banding of male *L. lakedownensis* (IMVS 12).

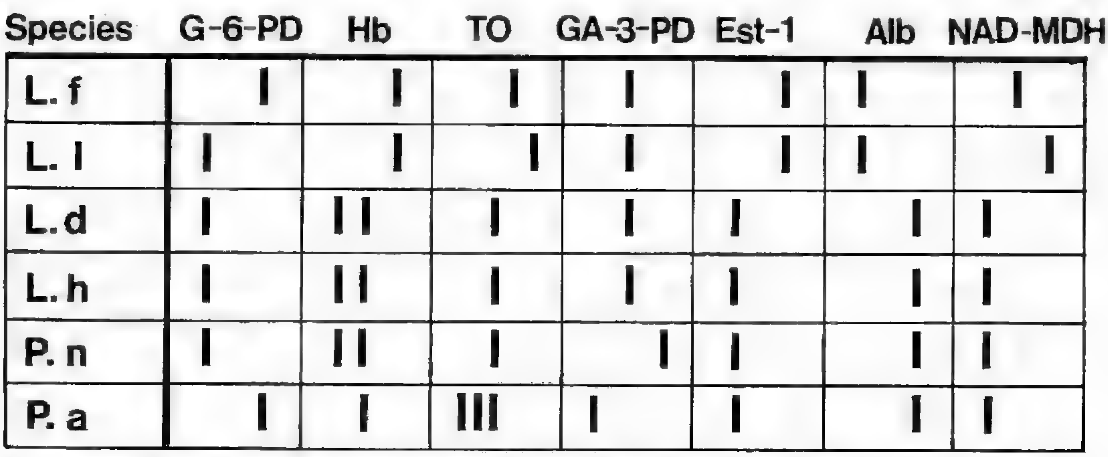

Fig. 2. Representation of electrophoretic patterns observed for seven useful proteins in six pseudomyin species. In each case the origin is to the left, and fastest migrating bands to the right (cathodal). Key—*L.f.* = *Leggadina forresti*; *L.l.* = *L. lakedownensis*; *L.d.* = *L. delicatula*; *L.h.* = *L. hermannsburgensis*; *P.n.* = *Pseudomys novaehollandiae*; *P.a.* = *P. australis*.

downensis (Fig. 1d) was evident only in the smaller chromosomes. The presumed Y was slightly more intensely C-banded than other chromosomes over its entire length.

Electrophoresis: Of the 16 proteins studied (Table 2), LAP, PHI, Tf, Est. 2 and Est. 3 showed evidence of polymorphism in at least one species, and 6-PGD, LDH A & B and PGM were identical for all species. This left seven of the proteins studied that were consistent within species but varied between species. The electrophoretic results for these seven proteins are shown in Fig. 2, and the resulting difference matrix in Table 3.

TABLE 3
Difference matrix for data in Figure 2
(Key as in Figure 2)

	L.f.	*L.l.*	*L.d.*	*L.h.*	*P.n.*	*P.a.*
L.f.	0					
L.l.	3	0				
L.d.	6	5	0			
L.h.	6	5	0	0		
P.n.	7	6	1	1	0	
P.a.	6	7	4	4	4	0

Discussion

Most *L. forresti* were found to possess the same karyotype, although two were heteromorphic for a sub-acrocentric pair 1. C-banding showed that the short arm on the sub-acrocentric member was not heterochromatic, suggesting that the sub-acrocentric was related to the acrocentric by a pericentric inversion.

L. lakedownensis, however, had a pair of small metacentrics converted to a pair of acrocentrics, presumably by a pericentric inversion. Although a single fixed chromosomal difference between *L. forresti* and *L. lakedownensis* is insufficient in itself to indicate a species difference, taken in the context of the very low karyotypic variation of the whole of the pseudomyinae (unpublished data), a single chromosomal rearrangement probably indicates reasonable differentiation.

The biochemical data are more convincing. Of the seven useful proteins studied, *L. forresti* and *L. lakedownensis* differ in 3 (Table 3). This is considerable compared to the biochemical differentiation between 3 "good" species—*L. delicatula* and *L. novaehollandiae* (1 difference), and *L. novaehollandiae* and *L. hermannsburgensis* (1 difference). These results suggest that *L. forresti* and *L. lakedownensis* may have been separated from each other for at least as long as have *L. delicatula*, *L. novaehollandiae* and *L. hermansburgensis*.

Phenetically *L. lakedownensis* and *L. forresti* are biochemically more similar to each other than either is to any other pseudomyin studied (Table 3). Although more data are needed these results support the maintenance of *Leggadina* as a separate genus which at this time would include only these two species.

Acknowledgments

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CORYSTUS DYSASTEROIDES, A TERTIARY HOLASTEROID ECHINOID FORMERLY KNOWN AS *DUNCANIASTER AUSTRALIAE*

BY R. J. FOSTER* *AND* G. M. PHILIP†

Summary

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CORYSTUS DYSASTEROIDES, A TERTIARY HOLASTEROID ECHINOID FORMERLY KNOWN AS *DUNCANIASTER AUSTRALIAE*

by R. J. FOSTER* and G. M. PHILIP†

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Introduction

Holasteroid echinoids are not abundantly represented in the diverse Tertiary echinoid fauna of southern Australia, but there is one common species which, for the last eighty years has been known as *Duncaniaster australiae* (Duncan). The purpose of this note is to review the complex nomenclatural history of the species and to decide on its correct designation. Also, photographs of the type material of four nominal species proposed by Duncan (1877, 1887) and Cotteau (1890) are published for the first time.

The species is known from the Tertiary coastal basins of southern Australia from Eucla Basin in the west to Torquay Embayment in the east, and from New Zealand. The earliest known Australian occurrence is in the Middle or early Late Eocene; it is present in the Wilson Bluff Limestone at the Bluff and in Abrakurrie Cave, and in the Tortachilla Limestone and equivalents of the St Vincent Basin. It makes its last Australian appearance in the late Early Miocene (uppermost Longfordian) Watacpoolan Limestone at Koonalunda in western Victoria. The species also occurs in the South Island of New Zealand; it appears first near the base of the Weka Pass Limestone in the Early Oligocene (questionable Whaingaroan), and last in the Gee Greensand in the Late Oligocene or Early Miocene (Waitakian-Otaian). More stratigraphic details are given in a separate paper (Foster and Philip, in press).

Historical review

Duncan (1877, p. 49) described the species *Rhynchopygus dysasteroides* from Castle Cove, Victoria (Late Eocene Castle Cove Limestone) and (1877, p. 51) described a further species, *Holaster australiae* from the same locality. The holotype of *R. dysasteroides* is crushed, and it was presumably for this reason that Duncan regarded the specimen as a cassiduloid. Pomel (1883, p. 61) proposed the genus *Corystus* for *R. dysasteroides* because of its intercalary apical system. In his revision of the Australian echinoid fauna Duncan (1887, p. 421(provided a corrected woodcut of the apical system of the holotype of *H. australiae*. He recognised that he had misinterpreted the species *R. dysasteroides* and been mistaken about its affinities. As a consequence he renamed it *Holaster difficilis*. Pomel's work was not well known at the time and it is no doubt because of this Duncan made no mention of the genus *Corystus*.

Cotteau (1890, p. 548) described *Galeraster australiae* from Mount Gambier (Early Miocene Gambier Limestone) as a new genus and species, placing the genus *Galeraster* close to *Holaster*. Tate (1891, p. 276) first suggested that *H. difficilis* and *H. australiae* were the same species. In 1892 Bittner (p. 359) rejected the

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genus *Corystus*, noting Gregory's (1890, p. 490) reference to *H. difficilis* as an "unsatisfactory species". Also, in 1892 Tate published his strongly worded criticism of Bittner's paper but in regard to these species he followed Bittner, although he suggested that *Galeraster australiae* was an additional synonym of *Holaster australiae*.

Lambert (1893, p. 97) transferred *H. australiae* to Pomel's genus *Lampadocorys* but later (1896, p. 317) made it the type species of his new genus *Duncaniaster* which he placed close to *Stegaster*. Thus was created the widely used name *Duncaniaster australiae*. In 1903 Lambert (p. 32) grouped the genus with *Lampadocorys*, *Stegaster*, *Tholaster* and *Offaster* in his subfamily Echinocorynae.

Lambert & Thiery (1921, p. 332) recognised *Galeraster* as a valid genus in the Echinogalerinae, stating (1924, p. 408) that Tate was mistaken when he made *Galeraster australiae* a synonym of *Holaster australiae*. They (1921, p. 364) reinstated the species *Rhynchopygus dysasteroides*, and made *Corystus* Pomel a synonym of *Rhynchopygus* d'Orbigny. Last of all (1924, p. 408), they relegated *Duncaniaster* Lambert to a sub-genus of *Cibaster* Pomel.

H. L. Clark (1946), in his review "The Echinoderm Fauna of Australia" mentioned neither *Corystus* nor *Galeraster*. He maintained *Duncaniaster* as a separate genus (p. 361), but did not consider it far removed from *Cardiaster*; the only species he listed was *D. australiae* (Duncan). Mortensen (1948, p. 84) retained Cotteau's genus *Galeraster* in the family Echinoneidae Wright and close to *Pyrina*, but (p. 203) considered *Corystus* to be a synonym of *Cassidulus*. He confirmed (1950, p. 74) *Duncaniaster* in the Holasteridae close to *Cibaster*. Wagner & Durham (1966, pp. U445 U528) in the Treatise followed Mortensen in their placement of *Galeraster* and *Duncaniaster*, and *Corystus* was tentatively placed among the cassiduloids as a doubtful nominal genus.

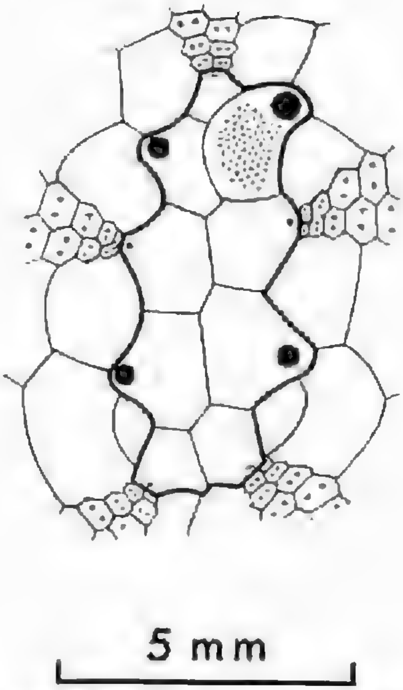

Fig. 1. Plating of apical system of holotype of *Holaster australiae* Duncan (BM E31067).

Type material

The holotype of *Rhynchopygus dyasteroides* is BM, E42418 (Fig. 2 C, E, F) and that of *Holaster australiae* is BM, E31067 (Fig. 2 A, B, D). Both are lodged in the British Museum (Natural History), and both were collected from the "No. 5 Upper Coralline Beds, Castle Cove, near Cape Otway" in Victoria. This is the old locality AW5 of Wilkinson (1865) in the Castle Cove Limestone, which Carter (1958, p. 21) refers to as his Foraminiferal Units 2 and 3. The echinoids are probably from the upper part of the formation in the latest Late Eocene.

As indicated above, the type specimen of *R. dysasteroides* is badly crushed, although the adapical surface shows an holasteroid apical system, similar to that of *H. australiae* (Fig. 1). In both specimens the adoral surface is poorly preserved, and the plastronal plating is obscure. Because of the state of preservation, the presence or absence of a subanal fasciole could not be established.

The holotype of Cotteau's *Galeraster australiae* is an unnumbered specimen in the Ecole des Mines, Paris, in the Cotteau Collection (Fig. 2 G, H, I). Its locality is "Mount Gambier, Australia" and doubtless is from the Gambier Limestone. The type section in the sinkhole at Mt Gambier town is of Longfordian (Early Miocene) age, and Janjukian (Late Oligocene) outcrops are limited to restricted areas NW and SW of the town. The precise locality of Cotteau's type, and of the only other representatives of the genus from this formation (P20456 from the National Museum of Victoria and T267a from the Tate Collection labelled "*Holaster woodsii* Mt Gambier"), is

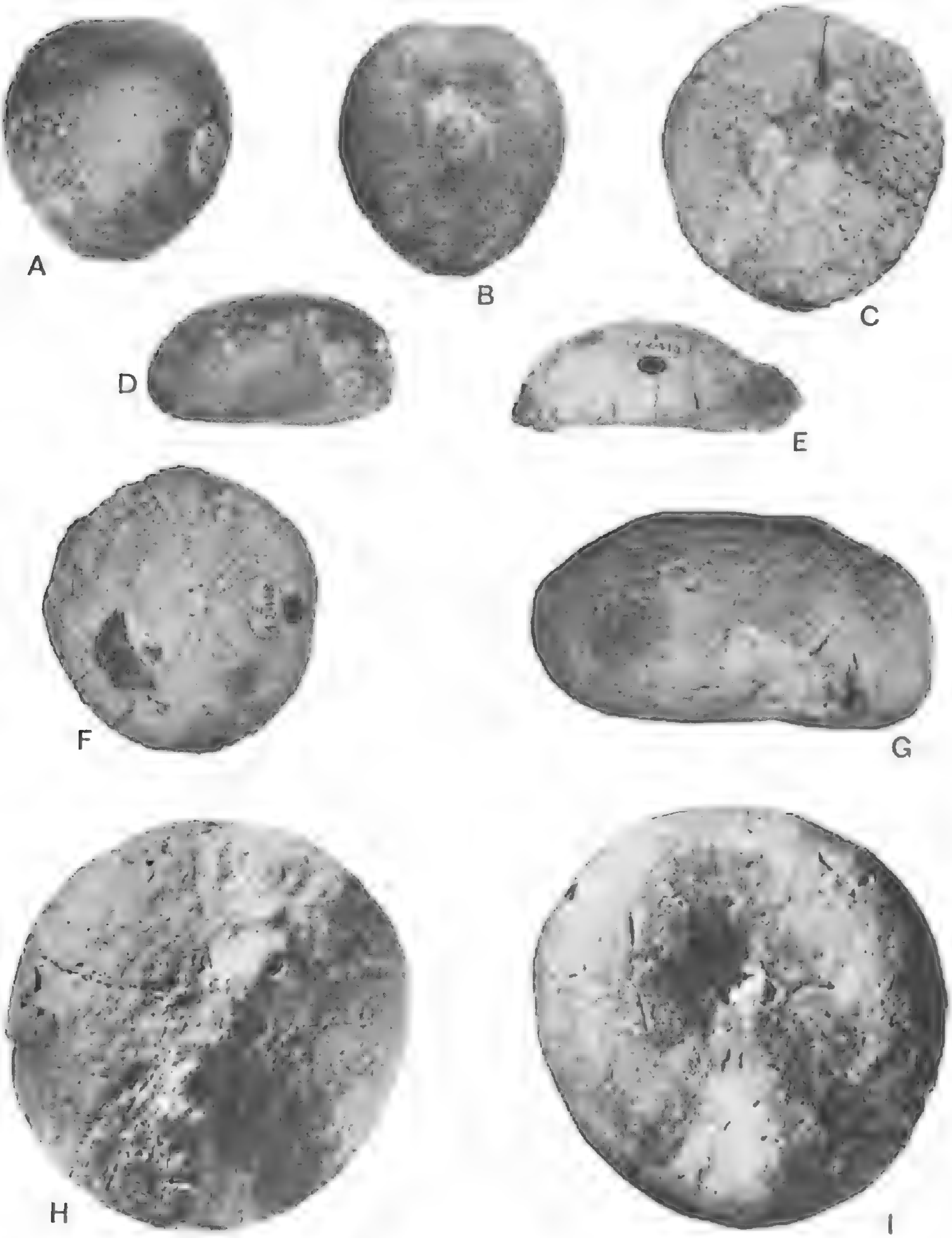

Fig. 2. All natural size. *A, B, D.* Adapical, adoral, and lateral views of holotype of *Holaster australiae* Duncan (BM E31067). *C, E, F.* Adoral, lateral and adapical views of holotype of *Rhynchopygus dysasteroides* Duncan (BM E42418). *G, H, I.* Lateral, adapical and adoral views of holotype of *Galeraster australiae* Cotteau.

not known. The general echinoid fauna presently available from the Gambier Limestone appears to have its closest affinities with that of the Longfordian Mannum Formation of the River Murray cliffs. In particular, T267a the only well-preserved specimen of *Corystus* from Mount Gambier was elsewhere (Foster & Philip, in press) compared statistically with the populations from a number of south-eastern Australian localities ranging from Late Eocene to Early Miocene, and its parameters correlated best with samples of populations from the Mannum Formation and the Longfordian portion of the Port Vincent Limestone. It is therefore concluded that the holotype is probably from the Early Miocene. Again the holotype is a poorly preserved specimen. It is worn and cracked and a number of borings occur in parts of the test. Surface detail is obscured by matrix and secondary calcite to the degree that even the paths of the ambulacra are difficult to trace. Preparation of the apical region of the specimen showed the widely separated oculars typical of an holasteroid apical system.

Conclusions

Despite the unsatisfactory nature of the type material, we conclude that all specimens are conspecific. We base this conclusion on the large collections of the species available to us from various localities in south-eastern Australia. We here choose *dysasteroides* as the valid name for the species as it has page precedence over *australiae* which was introduced by Duncan in the same publication. Pomel's genus *Corystus* has priority over *Duncaniaster* Lambert. Thus the valid Linnean species is *Corystus dysasteroides* (Duncan).

In a further paper (Foster & Philip, in press) we present a statistical analysis of samples of *Corystus* populations ranging from Late Eocene to Early Miocene in age. This analysis is designed to depict the morphological trends apparent in the evolution of the species. We also have in preparation a taxonomic study of all the holasteroid echinoids known from the Tertiary rocks of Australia (including Western Australia) and New Zealand. In this latter article we will review the affinities of the genus *Corystus*.

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REDISCOVERY OF *ACACIA BARATTENSIS* J. M. BLACK (MIMOSACEAE) IN SOUTH AUSTRALIA

*BY M. D. CRISP**

Summary

CRISP, M. D. (1976).-Rediscovery of *Acacia barattensis* J. *M.* Black (Mimosaceae) in South Australia. *Trans.* R. *Soc. S. Aust.* **100**(3), 117-120, 3 1 August 1976.
Acacia barattensis, previously known only from the type collection, has been rediscovered near the type locality in the Flinders Ranges, South Australia. It is described in more detail than previously, the legumes and seeds for the first time. Its taxonomic affinities and the type material are discussed. Possible reasons for the species remaining "lost" for so long are suggested, and its state of preservation is discussed in relation to its distribution and ecology.

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Introduction

Recently I rediscovered *Acacia barattensis* in the Flinders Ranges, South Australia. In so doing I established that the species was not extinct as previously supposed (Specht et al. 1974, p. 304), and that the locality information given by its author was inaccurate. The following formal taxonomic treatment contains new information about its morphology, type material, affinities, ecology and distribution.

Taxonomy of *Acacia barattensis*

Acacia barattensis J. M. Black in *Trans. R. Soc. S. Aust.* 56:42, t.1, fig. 2 (1932); *Flor. S. Aust.* ed. 2:419, fig. 578 (1948).

Somewhat diffuse, spreading *shrub* 2–3 m tall with several slender branches arising at or near the base. *Branchlets* slender, glabrous, gently curved so that the tips stand erect; strongly angular and very viscid towards the tips; becoming terete, less viscid and faintly striate towards the bases; greenish-brown but usually covered with a black incrustation. Foliage with a strong odour of resin acids when dry†. *Stipules* absent. *Phyllodes* erect, narrow-linear but tapering slightly towards both ends, vertically flattened, never terete, gently incurved, abruptly rostrate-uncinate at the apices, (3)5–8 cm long, 0.8–1.5 mm broad, 3-nerved on each face, 1-nerved on each margin (8-nerved in all); with a narrow groove which is usually filled with brown resin above and along each nerve; often shallowly and irregularly sulcate between the nerves; very sparsely and minutely pusticulate, initially very viscid. *Marginal gland* scarcely visible, 2–3 mm above the base of the phyllode. *Peduncles* 1–2 in the axils, each with a minute narrow-triangular basal bract (0.5 mm long), slender (0.2–0.3 mm diam.), terete, ± papillose-viscid, 8–13 mm long. *Heads* globular, 5–7 mm diam. at anthesis, ca 20-flowered *Floral bracts* navicular with long (ca 0.5 mm) triquetrous claws and with extended acute apices, 0.8–0.9 mm long and 0.2 mm broad, densely papillose-viscid, the margins scarious, ± entire. *Flowers* 4-merous. *Calyx* ca 1/3 length of corolla, consistently divided for 1/4 its length into triangular and barely acute lobes with entire margins, papillose-viscid. *Petals* oblong, recurved at the acute tips, 2 mm long, faintly uninerved, ± papillose-viscid, loosely connate for ca ½ their length. *Ovary* ± sessile, densely papillose-viscid. *Legume* narrow-linear, ±coriaceous, straight or slightly curved, stipitate, contracted to ½ its width between the seeds, (6)8–10(15) cm long, 2.5–3.5 mm broad, often with a very narrow (1 mm) and elongate (up to 1 cm) black sterile tip. Surface of the legume initially very viscid, finally not viscid, dark brown, with anastomosing raised veins between the seeds, irregularly colliculate over the seeds. Margins of the legume much thickened, straw coloured. *Seeds* longitudinal, oblong-elliptic, smooth, dark brown, ca 2.5 x 4.5 mm. *Aril* much dilated, with

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† Personal communication: J. Elix, Dept of Chemistry, Australian National University, A.C.T.

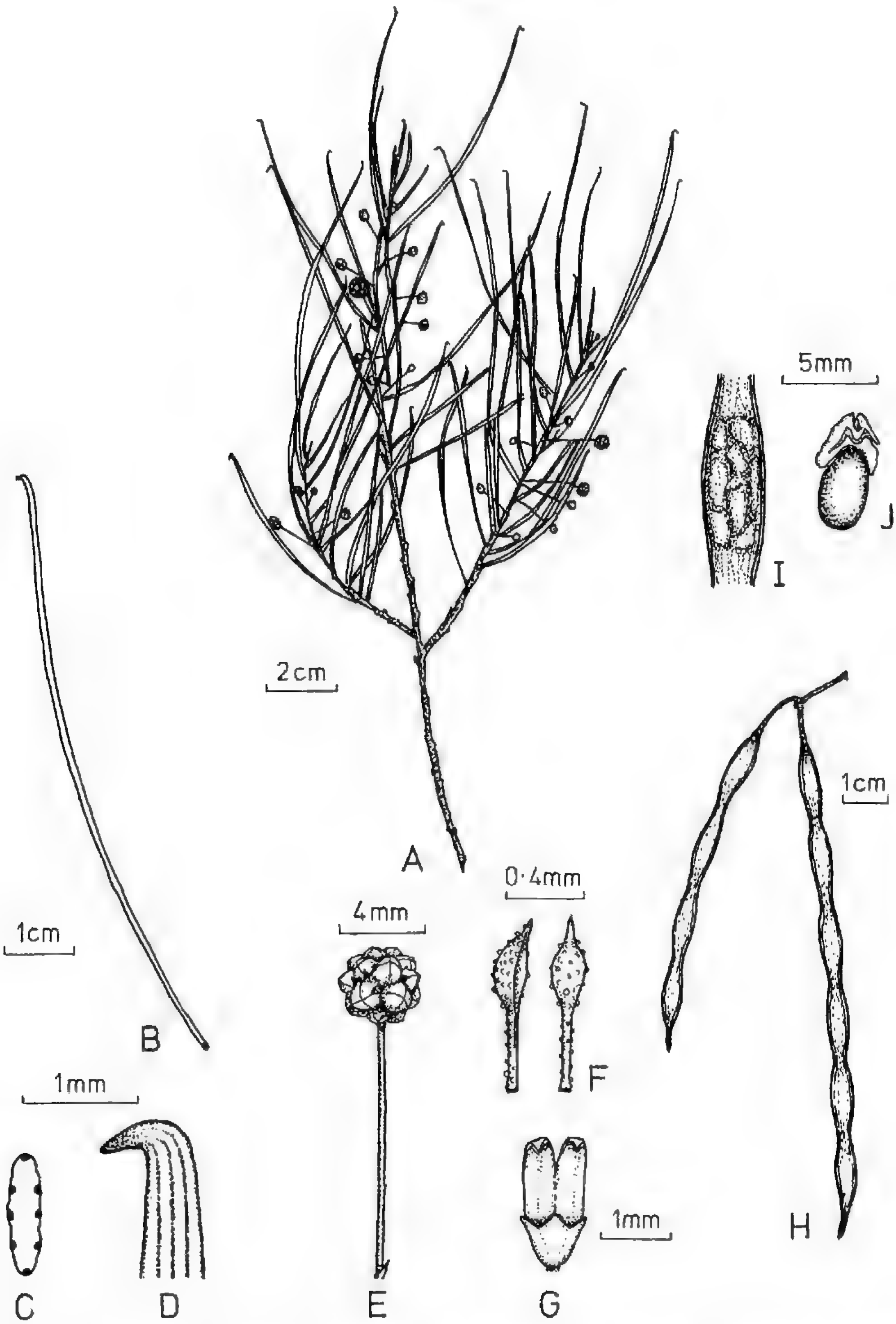

Fig. 1. *Acacia barattensis*. A. Portion of branch in bud and flower. B. Phyllode. C. Transverse section of phyllode, taken near the centre, showing resin-filled grooves. D. Apical portion of phyllode. E. Inflorescence (note basal bract). F. Floral bract in lateral (left) and ventral (right) view. G. Calyx and corolla. H. Legumes and peduncle. I. Exterior view of portion of legume over seed. J. Seed, aril and funicle. A-E from *M. D. Crisp* 889; F-G from *M. D. Crisp* 731; H-J from *M. D. Crisp* 890.

hyaline wings, once-bent above the seed and gradually contracted through a sharp bend into a thrice-folded *funicle*.

Type citation: "Near Baratta head-station, on a branch of the Siccus River and 20 miles west of Koonamore."

Holotypus: J. B. Cleland, 3.xii.1930, "North of Baratta Head Statn." (Baratta is at 31°59'S, 139°06'E), AD 97338071 (fl.)! *Isotypi:* AD 96247254 ("belongs to AD 97338071") (fl.)!, K.

Distribution: South Australia: Flinders Ranges. Apparently restricted to the deep gullies of an unnamed range forming the northern and western boundaries of Bibliando Station, ca 55 km E of Hawker and 16 km NW of Baratta head station. All recent collections have been made in the vicinity of the peak known as "The Bluff".

Ecology: Apparently confined to near-vertical gorge walls, from just above creek level to ca 30 m above, on skeletal soils between outcropping quartzite. Flowering is apparently irregular, having been observed in April, October, November and December; fruiting in October (immature) and November.

Additional specimens examined: Bibliando Stn, ca 2 km N of New West Bore (31°52'S, 139°03'E), *M. D. Crisp* 731, 13.iv.1974, fl., fr. & photo. (AD; CBG 060871—orig. spec.); Bibliando Stn, southern slopes of The Bluff, West Bore Pdk (31°51'S, 139°00'E), *M. D Crisp* 889, 20.x.1974, fl. & fr. (CBG 060873—orig. spec.; NSW); ibid., *M. D. Crisp* 890, 20.x.1974, fl. & fr. (CANB, CBG 060872—orig. spec., NSW, TL, US); Between Willipa and Bibliando, *M. G. Catford* s.n., 2.xi.1974, fl. & fr. (AD 97448228—pro parte); ibid., *M. G. Catford* s.n., 23.xi.1974, fr. (AD 97448228—pro parte)

Affinities: In his original description of *Acacia barattensis*, Black placed it next to *A. subporosa* F. Muell. (the now segregated *A. cognata* Domin). I consider it to be much closer to the group *A. gracilifolia* Maiden et Blakely, *A. wilhelmiana* F. Muell., *A. helmsiana* Maiden and *A. menzelii* J. M. Black, which apparently belongs in Bentham's series *Calamiformes*. However it differs from all these in its 4-merous flowers and in being totally glabrous. Maiden & Blakely (1927) describe a 4-partite corolla for *A. gracilifolia*, but both their illustration and material examined by myself have a 5-partite corolla. In SE Australia the most similar relative of *A. barattensis* is apparently *A. menzelii*, which has similar phyllodes, glands, peduncles, legumes, seeds and arils. However the latter differs in having phyllodes shorter and usually terete, 2 fewer nerves per phyllode, bracts larger, cucullate and prominently ribbed, flowers 5-merous, floral bracts with short claws.

Discussion

The type material at AD consists of 2 sheets, both annotated by Black. One of these (AD 97338071) has two twigs of material and two locality labels in Black's handwriting. One label,

> "North of Baratta
> Head Statn 3/12/30
> (J. B. Cleland)
> label marked 'Kew 137' ",

appears to be the original information received from Cleland, while the other,

> "Baratta H.S. (on a branch of the Siccus River & 20 miles W of Koonamore.)",

is Black's transcription of the former for publication. There is no evidence to suggest that the two twigs are separate collections. Both twigs are identical in all respects, particularly in the stage of flowering. The sheet also bears extensive descriptive notes and drawings, and a bold label "*Acacia barattensis* J. M. Black", all in his hand. Clearly this sheet is the holotype.

The second sheet (AD 96247254), originally kept separately in Herb. J. B. Cleland but later transferred to AD, carries a locality label similar to that on the holotype, and a twig identical to the others, indicating that this sheet is an isotype. The label is marked "Kew 137" by an unknown writer, and

> "Apparently a new sp., but if sent to Kew, I scarcely know what to do—J.M.B."

by Black. Clearly it was after he wrote this note that Black decided to describe and name the *Acacia* from the duplicate (holotype) material. If any specimen had been sent previously to K, it must have been returned, because the only specimen of *A. barattensis* now there is endorsed

> "comm. J. M. Black, Jan. 1933"

i.e. it was sent there *after* publication of the new species by Black. This third specimen appears in all respects to be a duplicate of the holotype collection, and must be regarded as a second isotype.

The above discussion shows clearly why many attempts to relocate *Acacia barattensis* failed. Whereas Cleland's field locality was

"North of Baratta" (in the ranges where it presently occurs and only about 10 km distant from Baratta), Black's published locality erroneously focussed attention on the head station itself, where it does not occur. The populations of the *Acacia* are in fact restricted to specific sites in the deep gorges of the range at Bibliando. However, where populations do occur they are fairly extensive and protected by the inaccessibility of their habitat. Provided that no major disturbance occurs in this range, *Acacia barattensis* is probably safe from the threat of extinction for the immediate future.

Acknowledgments

I wish to thank the staff of the State Herbarium of South Australia (AD) for the loan of specimens and for assistance received. I am also grateful to Dr Hj. Eichler of Herbarium Australiense (CANB), who offered some useful comments about the type material and read the manuscript. Mr A. B. Court of the Herbarium, Canberra Botanic Gardens (CBG) offered many helpful suggestions. Dr A. Kanis kindly located and supplied data from the specimen at the Herbarium, Royal Botanic Gardens, Kew (K).

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WOODWARDOSTRONGYLUS OBENDORFI NEW SPECIES (NEMATODA: AMIDOSTOMATIDAE) FROM KANGAROOS

BY PATRICIA M. MAWSON*

Summary

MAWSON, P. M. *(1976).-Woodwardostrongylus obendorfi* new species (Nematoda: Amidostromatidae) from Kangaroos. *Trans.* R. *Soc. S. Aust.* **100**(3), 121-123, 3 1 August 1976.

Woodwardostrongylus obendorfi n.sp. is described from the oesophagus of *Macropus parryi* (type host), *M. robustus,* and *M. rufogriseus.* It is distinguished from *W. woodwardi* (Wood) chiefly in having only 6 pairs of oral denticles instead of 16. *Woodwardostrongylus* Wahid is transferred to the family Amidostomatidae, and the genus *Cristaceps* Mawson is placed as a synonym of *Woodwardostrongylus.*

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Introduction

The genus *Woodwardostrongylus* was erected by Wahid (1964, p. 184) for *Pharyngostrongylus woodwardi* Wood, 1931. Mawson (1971, p. 174) not having seen Wahid's work, proposed the genus *Cristaceps* for the same species, pointing out that this genus was close to *Filarinema* in the family Amidostomatidae (sensu Inglis 1968). *Cristaceps* now falls as a synonym of *Woodwardostrongylus*, but the latter must be transferred to Amidostomatidae.

Nematodes recently taken from the oesophagus of three species of macropods have been identified as a new species of *Woodwardostrongylus*. In all three cases the worms were threaded through the oesophageal epithelium so that care was needed to collect them entire. This situation is similar, though in the oesophagus instead of the stomach, to that occupied by *W. woodwardi* in the two recorded findings (Wood 1931; Mawson 1971). It is a locale which is likely to escape all but the most careful dissections, so it is possible that species of the genus are more widely distributed than the records indicate.

I am very grateful to Dr Brian Coman and Dr Tom Kirkpatrick who shot the kangaroos and to Mr David Obendorf who first noticed the presence of the worm.

The micrographs (Figs 10, 11) were taken by E.T.E.C. Autoscan in the Central Electron Optical Laboratory of the University of Adelaide. I am indebted to Dr Karl Bartusek of this Laboratory for help in taking the micrographs, and to P. G. Kempster for developing and printing them.

Woodwardostrongylus obendorfi n.sp.

FIGS 1–11

Host and Locality: *Macropus parryi* (Bennett) (type host and *M. robustus* (Gould), from Dorrigo, N.S.W.; *M. rufogriseus* (Desmarest) from Warwick, Qld.

The worms are thin and elongate, the males 15.9–16.7 mm, the females 24–26 mm in length. The body, especially of the female, is widest in its posterior part. The rounded anterior end bears a small round mouth, on each side of which lie six prominent denticles each associated with a plate-like sclerotisation in the cuticle. The mouth leads to a thick-walled buccal capsule or vestibule. The lumen of this is narrow but wider dorsoventrally than from side to side. The walls are faintly striated transversely (more distinctly in some specimens than others), and are distinctly thicker posteriorly than anteriorly. The cephalic papillae and amphids are very small.

The oesophagus widens in its posterior half to a very slight terminal swelling. It is 800–900 μm long in the male, 900–1050 μm in the female. In the male the distance from the anterior end of the worm to the nerve ring is 320–400 μm, to the cervical papillae 300–460 μm, and to the excretory pore 440-510 μm; in the female these distances are respec-

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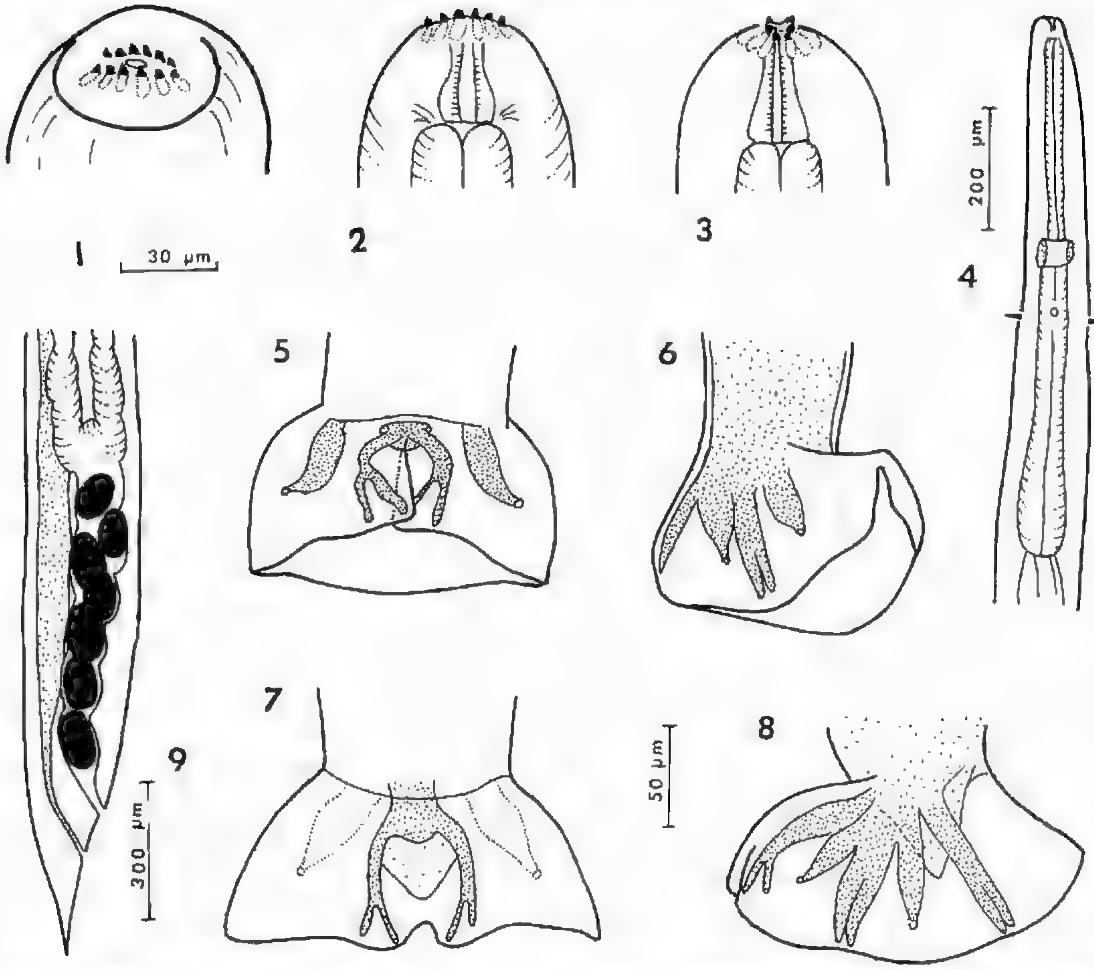


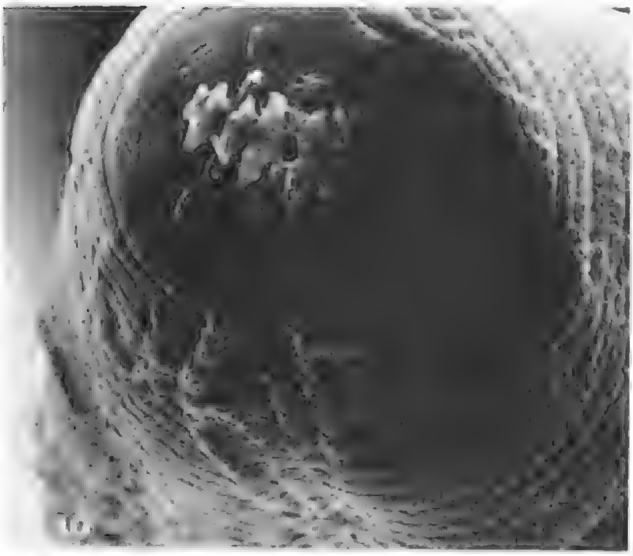
Figs 1, 2 and 3—Head, in semi-en face, lateral and ventral views respectively. Fig. 4—Oesophageal region. Figs 5, 6, 7, and 8—Views of bursa. Fig. 9—Posterior end of female. Figs 1-3 to same scale. Figs 5-8 to same scale.

tively 360–400 µm, 560–600 µm, and 500–550 µm.

The bursa is only slightly lobed, closed ventrally, and somewhat voluminous dorsally where it extends so that the dorsal ray for most of its length lies at right angles to the long axis of the body. The arrangement of the rays is shown in Figs 5–8. The genital pore is of medium size, apparently without accessory lobes. The spicules are 1700–2100 µm long, the ratio body length: spicule length being 9.9–12.8. A gubernaculum is present.

In the female the tail is 180–220 µm long, conical and pointed. The vulva is shortly in front of the anus, 300–350 µm from the posterior end. The vagina is relatively long, up to 800 µm. Vaginal eggs measure 140-150 x 70–80 µm.

The species is distinguished from *W. woodwardi* mainly by the presence of only six pairs of oral denticles instead of sixteen pairs, and by the presence of the associated basal plates, which are not seen in the type species. There is also a difference in the site in which the species occur in the body, *W. woodwardi* in the stomach and the new species in the oesophagus. In *M. parryi* and *M. rufogriseus* the worms were numerous, but only one was found in *M. robustus*.



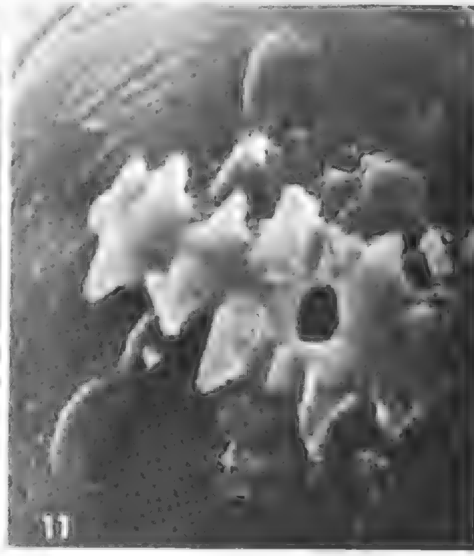


Fig. 10. S.E. Micrograph, anterior end almost en face (x 1500).
Fig. 11. S.E. Micrograph, part of region around mouth, showing two of the submedian papillae, the mouth, and some of the oral denticles (x 3 500).

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NEW LATE CAINOZOIC ROCK UNITS AND DEPOSITIONAL ENVIRONMENTS, LAKE FROME AREA, SOUTH AUSTRALIA

BY R. A. CALLEN AND R. H. TEDFORD†*

Summary

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Introduction

Mapping on the FROME (Callen 1975), and CURNAMONA 1:250 000 geological sheets has resulted in differentiation of several Tertiary and Quaternary rock units which can be traced throughout the Lake Frome area (the region south of Lake Callabonna between the Flinders, Barrier and Olary Ranges). The Eyre Formation has been defined previously (Wopfner *et al.* 1974). It lies immediately beneath the units described here for the Lake Frome area and can be recognised over a much wider region. The other units are at present restricted to the Lake Frome region, though correlation with units elsewhere, especially in the Lake Eyre Basin, is generally possible on a firm basis.

There was a low divide between the depositional areas of Lakes Frome and Eyre, suggested by the distribution of arenaceous material in the Miocene rocks. The development of this divide is clearly described by Wopfner (1974, p. 6). Thus the Lake Eyre and Lake Frome areas formed two distinct depositional basins during late Tertiary times; different sets of formal names are used for rock units in each. In late Tertiary and Quaternary times the Flinders Ranges achieved their present dimensions, completely separating the two basins by a range of mountains.

This paper describes five rock units requiring formalization under the Australian Code of Stratigraphic Nomenclature (1973), commenting on the paleo-environmental inferences to be drawn from them. The nomenclature supersedes that shown on the FROME geological map, relationships between units now being on firmer basis. The paper is divided into two parts, dealing with essentially Tertiary and Quaternary units respectively. New geographic names have been formalized with the Geographic Names Board of South Australia

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(pers. comm. 1973) and are designated with a superscript wherever they first appear, thus: Lake Namba[x]. Geologic names have been cleared with the Central Registry (Canberra, 1973). The paper derived from a report by Callen (1974)[1] and an M.Sc. thesis (Callen, 1976)[2]. Additional stratigraphic data may be found in this thesis.

Previous work includes the early geological surveys of Selwyn (1860), Brown (1884) and later of Jack (1930) and Kenny (1934). More recently Ker (1966), Krinsley *et al.* (1968) and Draper & Jensen (1975, in prep.) have reported on hydrology and geology. The margins of the basin have been the subject of regional mapping programmes by the South Australian and New South Wales geological surveys, on 1:250 000 scale. Relevant to this report are Leeson (1967)[3], Firman (1971)[4] and Coats (1973). A detailed basin study of the older unit NAMBA FORMATION is in progress and will be reported at a later date. A preliminary account of the stratigraphy is presented in Callen (1976), which gives the structural and tectonic setting.

The terms used to describe the sedimentary rocks are those of Folk *et al.* (1970), unless indicated otherwise. Colours are given symbolically in terms of Munsell Colour Code (Geological Society of America 1951). A relative scale was used for designating the thickness of cross-bedding, as follows: very small <1 cm, small 1–5 cm, medium 5–50 cm, large 0.5–2 m; very large >2 m. In the designation of contact features, core width places a limit on the interpretation, as it does on maximum grain size: cobbles and boulders are interpreted from the proportion and shape of fragments ground down and broken by the drilling operation, and nature of petrophysical log response.

The older units (Pt I) were described mainly from bores, the younger (Pt II) from outcrop. Knowledge of the younger units was derived from detailed investigation of over 100 trenched outcrop sections. Where possible units were traced between sections. Fossil soils were an aid to stratigraphic interpretation.

The location of the sections is shown in Fig. 1, Tables 1 and 3 summarizing rock unit properties, palaeontology and geomorphology. Symbols are in Fig. 2.

The subsurface sections were studied from cores derived from bores drilled by the South Australian Department of Mines and private companies. Some percussion and rotary cutting were used to assist correlations, but those utilized for type sections were cored continuously, and are available for inspection at the South Australian Department of Mines Core Laboratory. Petrophysical logs were run in all cases. The lithological descriptions were supplemented by binocular microscope examination, and clay (x-ray diffraction) and grain size (sieve and pipette) analyses were performed by Drs R. N. Brown and B. G. Stevenson respectively of the Australian Mineral Development Laboratories.

The text is regarded as a supplement to the diagrams and tables; descriptions in Tables 1 and 3 should be read first. Complete descriptions of each section are given in the appendices, wherein the sequences are described as they occur on the earth's surface—i.e. youngest at top, oldest at base. Depths to the top of each unit or bed from the bore collar are given, and the thickness is placed at the start of its description. In each unit, description of the dominant lithology is capitalized; followed by qualifying descriptors referring to each lithology in the same order.

Division into units in the reference sections is intended as an aid to identification of the appropriate intervals in the descriptions (Section 12, Fig. 3), not a formal subdivision. Core loss is indicated in the bore logs (Fig. 3 sections 10, 11 & 12).

Pt. I—Older Cainozoic Rock Units

A general definition of each unit giving salient features, age and geomorphic setting is presented in Table 1, representative sections in Fig. 3. Appendix 1 gives detailed descriptions of individual units.

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[1] Callen, R. A. (1974).—New Rock Units and Climate of the Cainozoic, Lake Frome area, South Australia. *S. Aust. Dept. Mines Rept.* 74/75 unpub.

[2] Callen, R. A. (1976).—Stratigraphy, sedimentology and uranium deposits of Tertiary rocks, Lake Frome area, South Australia. M.Sc. thesis, University of Adelaide (unpublished).

[3] Leeson, B. (1967).—Geology of *Balcanoona* 1:63 360 map area. *S. Aust. Dept. Mines Rept.* RB 64/92 unpub.

[4] Firman, J. B. (1971).—Regional stratigraphy of surficial deposits in the Great Artesian Basin and Frome Embayment in South Australia. *S. Aust. Dept. Mines Rept.* RB 71/16 unpub.

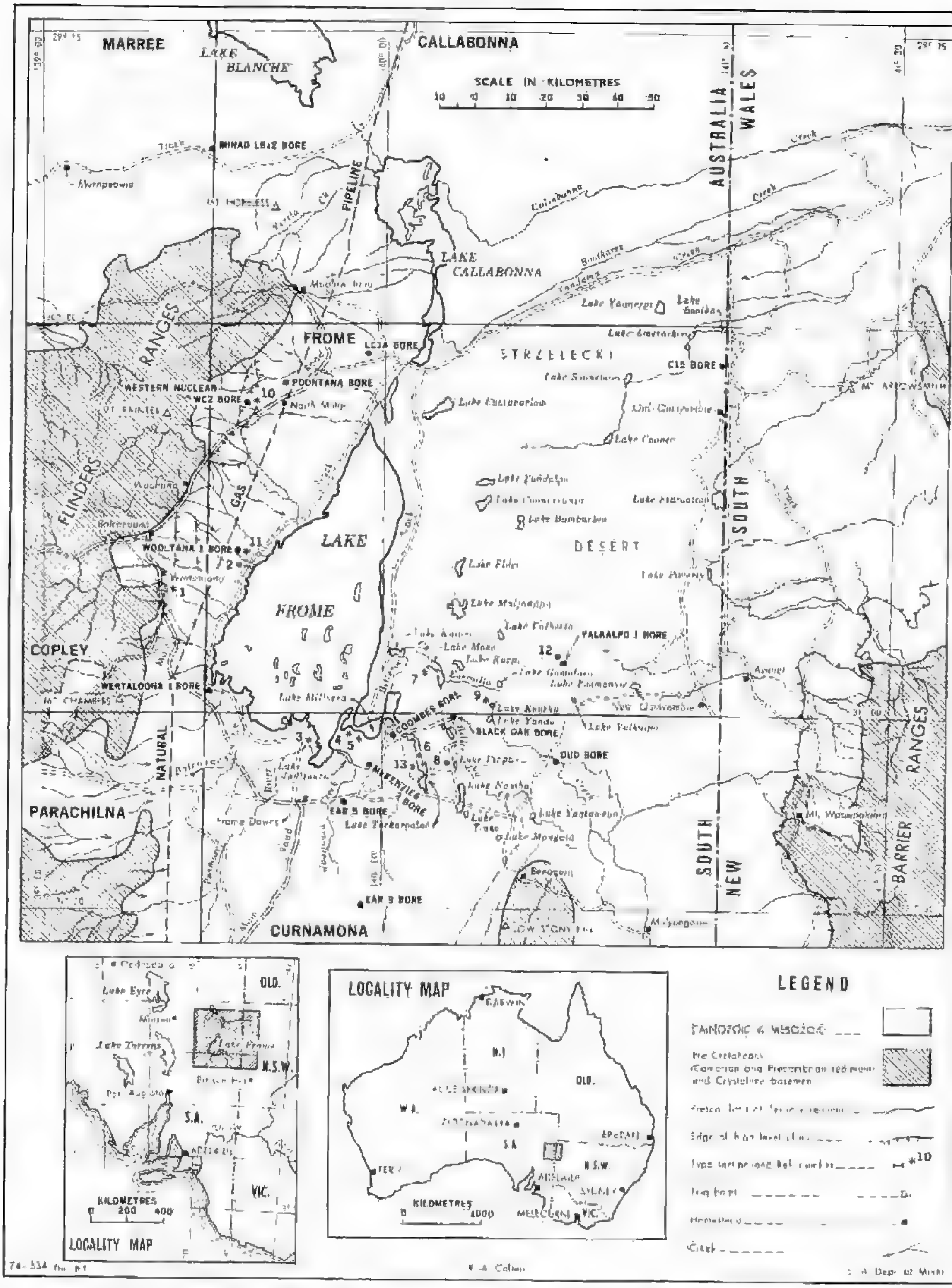

Fig. 1. Locality map, Lake Frome area—location of type sections. Numbered sections shown in Figs 3, 14, 15.

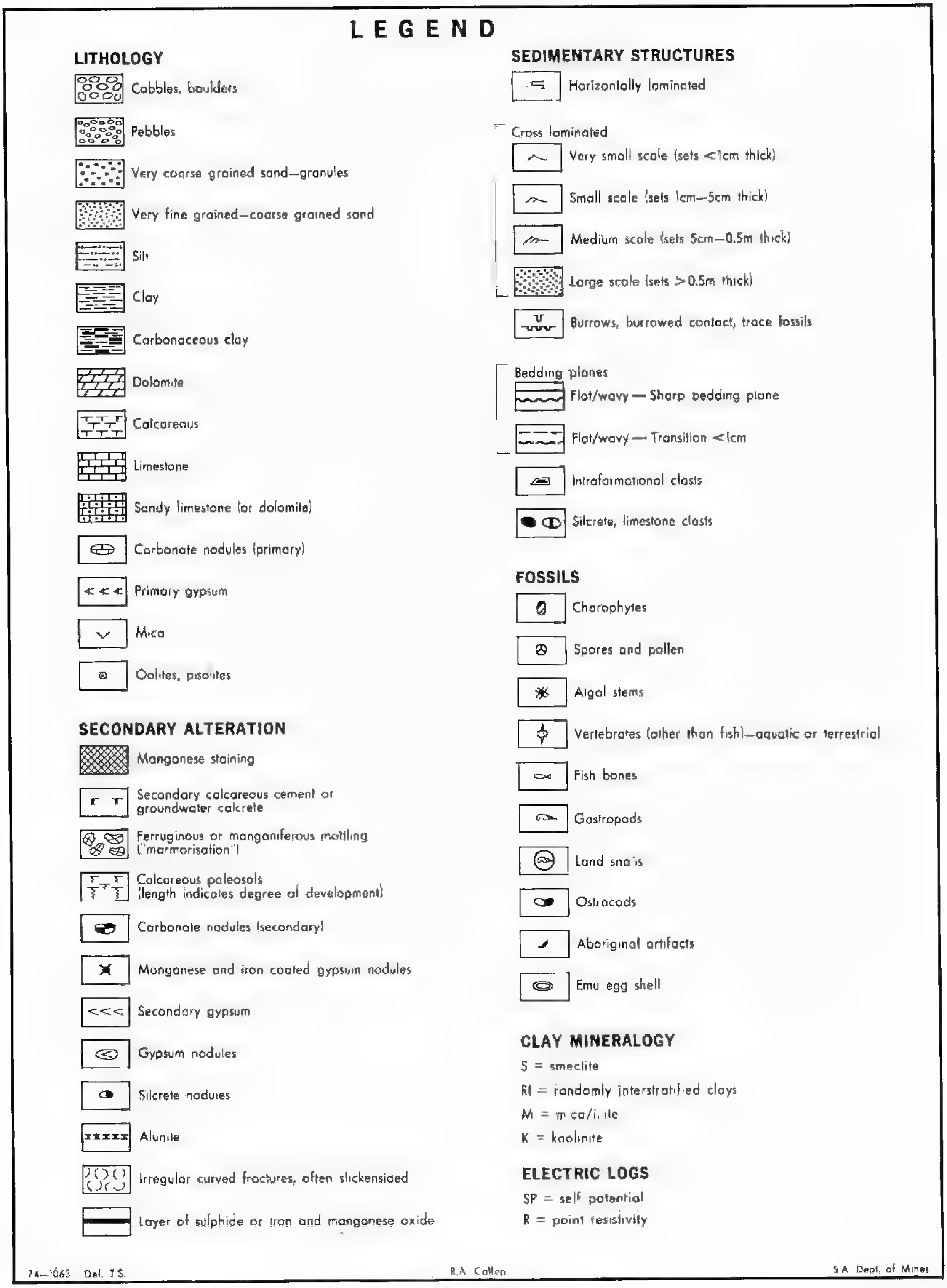
LEGEND
LITHOLOGY
Cobbles, boulders
Pebbles
Very coarse grained sand—granules
Very fine grained—coarse grained sand
Silt
Clay
Carbonaceous clay
Dolomite
Calcareous
Limestone
Sandy limestone (or dolomite)
Carbonate nodules (primary)
Primary gypsum
Mica
Oolites, pisolites
SECONDARY ALTERATION
Manganese staining
Secondary calcareous cement or groundwater calcrete
Ferruginous or manganiferous mottling ("marmorisation")
Calcareous paleosols (length indicates degree of development)
Carbonate nodules (secondary)
Manganese and iron coated gypsum nodules
Secondary gypsum
Gypsum nodules
Silcrete nodules
Alunite
Irregular curved fractures, often slickensided
Layer of sulphide or iron and manganese oxide
SEDIMENTARY STRUCTURES
Horizontally laminated
Cross laminated
Very small scale (sets <1cm thick)
Small scale (sets 1cm—5cm thick)
Medium scale (sets 5cm—0.5m thick)
Large scale (sets >0.5m thick)
Burrows, burrowed contact, trace fossils
Bedding planes
Flat/wavy — Sharp bedding plane
Flat/wavy — Transition <1cm
Intraformational clasts
Silcrete, limestone clasts
FOSSILS
Charophytes
Spores and pollen
Algal stems
Vertebrates (other than fish)—aquatic or terrestrial
Fish bones
Gastropods
Land snails
Ostracods
Aboriginal artifacts
Emu egg shell
CLAY MINERALOGY
S = smectite
RI = randomly interstratified clays
M = mica/illite
K = kaolinite
ELECTRIC LOGS
SP = self potential
R = point resistivity
74—1063 Del. T.S.
R.A. Callen
S.A. Dept. of Mines

Fig. 2. Legend.

LITHOLOGY

NAMBA FORMATION (Derivation, Lake Namba*, CURNAMONA map sheet: "Namba" is the Jadliaura aboriginal tribal word for bone-fish).

The type section is Yalkalpo No. 1 bore (section 12, Fig. 3) drilled by the South Australian Department of Mines. Though not typical in some respects, this is the only section demonstrating the relationship to the Eyre Formation (Appendix 1). The sequence is of reduced thickness (56.60 m) compared with that of the reference section in Wooltana No. 1 bore (170.09 m, Section 11, and Appendix 1, excluding unit 4 which is 68.26 m thick). Section 11 also contains a microflora important in the age determination of the unit. The most extensive outcrops are on the west shore of Lake Tarkarooloo* (Fig. 14), where 26 m are exposed, and at the south and north ends of Lake Namba (e.g. Section 8, Fig. 15). These are unsuitable for designation as type sections, as only the uppermost beds are represented.

The type section consists of a series of cyclic sand/clay sequences in the lower part totalling 32 m of interbedded yellowish silt and dark grey or olive clay. This is overlain by 24.8 m of burrowed yellowish silt and intraformationally brecciated light olive clay. The cyclic sequences constitute the following, from the base of each set upwards:

(a) Fine to medium-grained sand with small to medium scale cross stratification.
(b) Laminated silt to very fine sand with very small scale cross-lamination.
(c) A zone of dolomite or calcite patches or a bed of dolomite.
(d) A relatively thick dark grey clay with irregular shiny-surfaced fractures (skew planes of Brewer 1964) and scattered patches and wisps of fine to coarse sands, in which grains are polished.

In this sequence (a) and (b) may alternate, or either (a) or (b) may be absent. Unit 5 of the type section represents a relatively complete cycle:

1.70 m Alternating CLAY and SILT to SAND. Sand very fine grained moderately sorted, percentage increasing upwards. Grains very angular, with crystal faces developed on quartz. Becomes calcareous at top. Bedding lenticular, with sedimentary brecciation and possible burrowing activity. Obscure horizontal lamination at top. 7% carbonate grains, rare mica. Colour 5Y6/1 mottled 10YR6/6.

0.75 m SANDY CLAY. Vertically streaked transition zone from sand to clay. Fine sand forms streaks and patches in clay. Very poorly sorted medium silt, with modes in clay and very fine sand sizes.

4.10 m CLAY, black (5Y1/1) and tough, with characteristic irregular shiny-surfaced fractures, and streaks of white carbonate. Mottled with orange brown colours which suggest an irregular microstructure. Many brown patches have well defined straight boundaries, producing angular blocks with dendritic or patchy internal structure. Unoxidized clay in these blocks is greenish grey. Scattered patches of silt and very fine sand are present. Upper contact sharp, but disturbed, with partial mixing into overlying sand.

The burrowed silt is very finely laminated, but this is often disrupted by burrowing. Very fine sand sized material is the coarsest grain size encountered. Colours are mainly yellowish grey to yellowish-white for silt or light olive for clays, having a greasy lustre. Fractures do not reach the degree of development of comparable structures in the black clays of the lower part of the sequence.

The burrow structures are a few millimetres in diameter, containing convex-down lamellae usually less than 0.5 mm thick. They are irregular and often branch, tending to be concentrated in certain horizons. Many of the homogenized clays have a churned structure suggestive of bioturbation.

The top of unit 9 marks the last appearance of the tough black clays characteristic of the lower part of the formation (Fig. 4). Frequently alunite ($KAl_3(SO_4)_2(OH)_6$) is developed as lustrous white particles or patches within the clay at the top of this unit. Above unit 9, silts dominate over clay, and burrows (Fig. 9) are more common.

The outcrop at Lake Tarkarooloo (section 13, Fig. 14) is situated on the western cliff face, immediately north of the track-crossing, on the route from "Frome Downs" to Black Oak Bore. The lower part of the section is a few tens of metres south of this track. The two parts were correlated using continuously traced bedding planes, and levelled with an Abney hand level. The strata are essentially horizontal, as are those in the type section.

Notable features of this outcrop are the interbedded gypsum nodules in the upper part of the section, the presence of ostracode-bearing oolitic dolomite associated with palygorskite, burrowed fine sand beneath the upper clay-dolomite sequence, the finely laminated calcareous silt near the base of the sequence, and the sharp contact with the upper tough black clay. These features, particularly the last mentioned, are useful in correlation. In section 12, the petrophysical logs indicate the interval between units 12 and 13, which lacks core, is probably silcrete, calcrete or dolomite. The absence of palygorskite beneath it suggests it may not be dolomite (this clay mineral is invariably associated with dolomite elsewhere in the basin). A turtle shell fragment in unit 10 supports a lithological correlation with section 8, if the black clay and ?dolomite are also correlated, but this is not in agreement with the clay mineralogy. Section 13 shows the typical dolomite—palygorskite association, and trend towards illite domination in member two.

Typical of the Namba Formation outcrop are the brown chert nodules which cover the breakaway slopes, and black manganese oxide coating on the grains in sand beds. Microscopically, the chert nodules have structures indicative of shrinkage and formation from accretionary silica gel. The black stain is manganese. Both these secondary effects are localized, occurring in sands cropping out in the banks of stream valleys eroded in the Namba Formation, prior to the deposition of the

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Figs 4–9. Older units. Examples of Namba Formation lithology. Scales in mm and cm. Core sections. Arrows point to top of section.

Fig. 4 Section 12, Yalkalpo 1 bore, 125.00 m Core. Dark grey clay with streaks of carbonate, darker and lighter clay, and sand, some filling burrows or root holes. Vertical disposition of patches well-displayed. Represents swamp deposition or a lake deposit which has been subject to subaerial exposure. Centripetal orientation of streaks is result of expansion of clay as it enters the core barrel.

Fig. 5. Section 11. Wooltana 1 bore, 218.68 m. Section through core, showing upper contact of laminated dolomite bed. Shrinkage and cracking of the dolomite has occurred, allowing penetration of the semi-fluid overlying clayey lime (C). Represents chemical sedimentation in a lacustrine or marginal marine environment. Boundaries of carbonate fragments and laminae emphasized by inking.

Fig. 6. Section 11, Wooltana 1 bore, 58.72 m. Core. Calcareous claystone with numerous burrows infilled with green-grey clay. Irregular shrinkage crack (C) has been infilled with semi-liquid clay which carries carbonate particles. The clay-filled crack is itself burrowed, indicating genesis soon after deposition. Represents combined chemical and detrital deposition in a marginal marine lagoon or lacustrine environment, with burrowing organisms.

Fig. 7. Section 11, Wooltana 1 bore, 122.00 m. Core. Fine lamination with typical alternation of silt and sand. Very fine scale trough cross-lamination. Quiet water deposition (migrating ripples) in a tidal, lacustrine or floodplain environment.

Fig. 8. Wertaloona 1 bore, 152.00 m. Araldite peel of sectioned core. Typical example of small scale cross-lamination in medium grained sand, partly disrupted by burrowing in upper part. Clayey laminae alternate at base. Relief coincides with porosity, though affected by varying thickness of core across section. Cross bedding formed by ripple migration, in an offshore bar or channel.

Fig. 9. Section 12, Yalkalpo 1 bore, 22.61 m. Core. Top of bedding plane. Shows burrows along bedding plane, with concave internal lamination (I). Represents quiet water deposition with burrowing organisms.

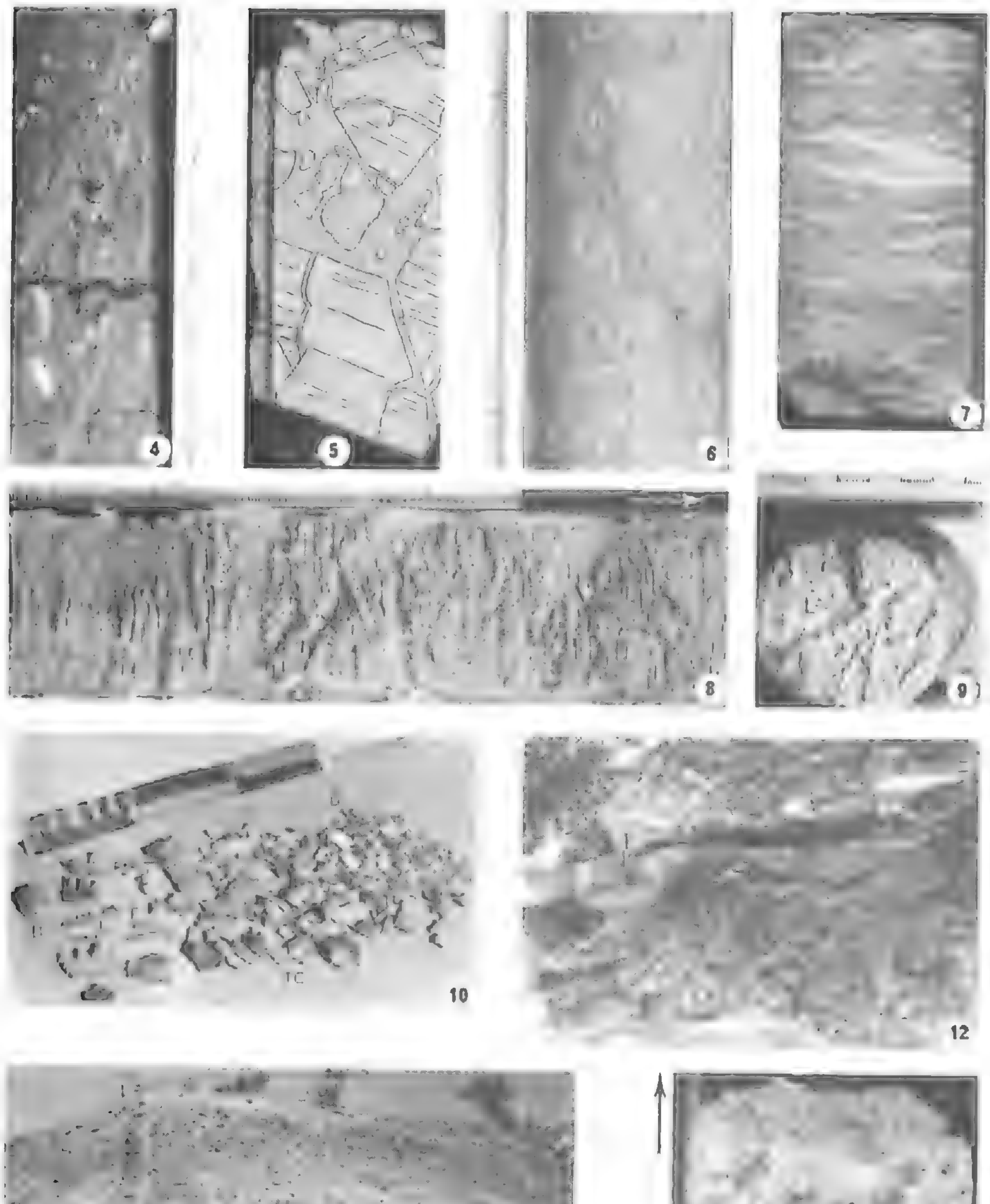
Figs 10–13. Outcrop of Namba Formation and Willawortina Formation, core of Willawortina Formation.

Fig. 10 Vertebrate fossil float from the Namba Formation of L. Yanda on Euriodlla Creek. Vertebra on far left (D) is riverine dolphin, on its right (L) are lungfish teeth and two fish spines (F). In centre (T,C) are mainly crocodile scutes and turtle plates. A fragment of bird bone (B) is on upper right corner. From base of upper unit of Namba Formation. Scale 30 cm.

Fig. 11. South end of Lake Namba. Typical outcrop of Namba Formation. Gypsum nodule capping (G) overlies thin nodular dolomite (white: LS), Greyish olive silty clay (grey) occupies most of section. Grassed white bench at base of slope is very fine grained laminated sand (S). 30 cm scale rests on upper contact in trench. Outcrop surface is covered by gypsum nodules and weathered clay. Sand represents channel or floodplain deposition, clay and dolomite probably lacustrine.

Fig. 12. Balcanoona Ck, Willawortina Formation. Calcified medium crossbedded sand lens in calcareous reddish brown very poorly sorted clay-silt. Note thin bedding in silt. Sand lens represents deposition from higher powered streams, fine sediments are floodplain deposits. Scale 30 cm.

Fig. 13. Section 10, WC2 bore, 68.75 m, section of core. Willawortina Formation shows large pebbles, granules, very coarse silty and clayey sand. Extremely poor sorting. Represents deposition in an alluvial fan environment. Scale in mm.



Millyera Formation and *Eurinilla Formation* (new names see Pt. II).

Wooltana No. 1 bore (Fig. 3, Section 11 and Appendix 1), drilled by the Australian Department of Mines is an important supplementary section, exhibiting a thicker sequence, lithologically more typical of the Namba Formation than the type section. It also demonstrates the intertonguing relationship with the *Willawortina Formation* (new name Pt. 1).

The base of the Namba Formation was not penetrated, though cuttings from old Pootana bore (Fig. 1, 50 km north-north-east of Wooltana No. 1 bore) indicate a total thickness of 190 m. This compares with 54.40 m in Yalkalpo No. 1 bore (Section 12). The sediments have been divided into six informal units. The lowest of these (unit 1) consists of 8.5 m of laminated black and dark olive carbonaceous clays with characteristic fauna and microflora (discussed later). Laminae containing ostracodes of early Neogene aspect (including cypridids—pers. comm. K. McKenzie 1973), and fish spines are present. Protoconchs of a small gastropod (*Potamopyrgus* s.l., see Ludbrook 1972)[5], are scattered through the clay and ?gastropod tracks and burrows of other organisms are common on bedding planes. These sediments are restricted to the Poontana Sub Basin west of Lake Frome.

Unit 2 (40 m) is dominated by white, frequently oolitic, dolomite beds (Fig. 5) containing characteristic branching pores 0.5 mm diameter, alternating with clay, and sometimes interbedded with silt and fine sand. The carbonates have unusual transitional or irregular upper boundries: in some beds spherical zones delineated by colour variations develop, which pass upwards into discrete carbonate lumps within the matrix of overlying unit. These are thought to be diagenetic features associated with lithification possibly resulting from intermittent exposure. Other beds (Fig. 5) show shrinkage cracks, into which the overlying clay penetrates. Particles of carbonate are included and flow lines occur, indicating liquefaction resulting from thixotropic transformation. The lack of rounding of the clasts derived from cracking, and gradation to uncracked material, suggests sinking of carbonate plates into underlying liquid clay. The cracking may be a syneresis phenomena, which occurred during or shortly after deposition of the overlying clay. Occasionally the clasts have been rounded, and incorporated in the overlying unit: current or wave action has been effective in some cases. Other beds show wispy carbonate and clay intermixed at the contact, interpreted as flame structures which have transformed by thixotropic changes, to flow as a semi-liquid. Bioturbation is frequently associated with these structures, and is common throughout (Fig. 6).

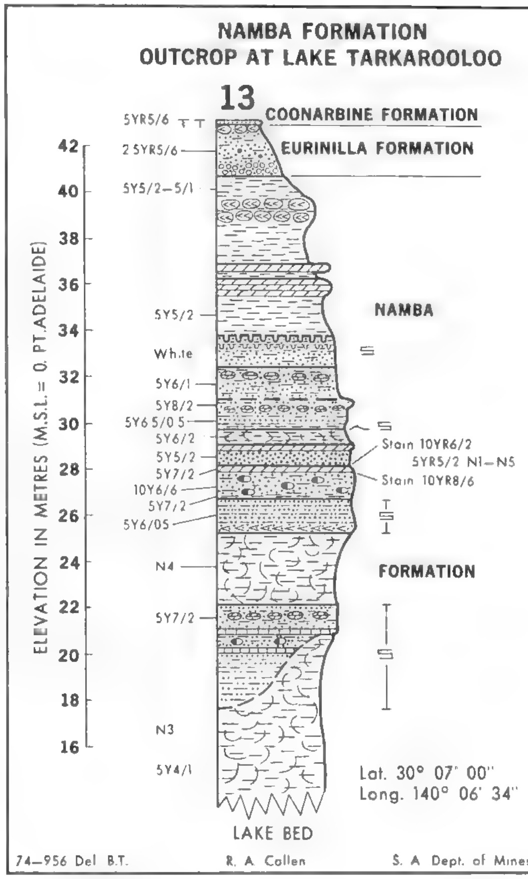


Fig. 14. Namba Formation—outcrop reference section.

Unit 3 (49.7 m) is very similar to the lower part of the Type Section (section 12, units 1–9), exhibiting similar cyclic deposition, in which cross-stratified sands (Fig. 8) grade up into tough black clays with pockets of medium sand, often with polished grains (see description of unit 4, section 12). The black clays are identical to those in section 13, Fig. 14. Analyses showed the black colour does not

[5] Ludbrook, N. H. (1972). Age and environment of deposition of a sample from Yalkalpo No. 1 Bore, Lake Frome area, South Australia. *S. Aust. Dept. Mines Rept.* RB 72/207 unpub.

result from anomalous concentration of carbonaceous matter, sulphides or manganese. Iron-rich montmorillonite or humic acid staining are alternative explanations. A bed of dolomite or limestone nodules is often present at the contact between the sand and black clay. Lamination (Fig. 7) is generally not as prominent as in the equivalent strata in the type section, and the sand beds are often burrowed.

The cross-bedded sand sequence of unit 4 (49.2 m total thickness) grades up into a uniform olive clay with churned structure. The sand bed is a prominent horizon west of Lake Frome, and is being prospected for sedimentary uranium of the geochemical cell type. The dark sandy clays with skew planes are rather weakly developed in this unit.

The upper carbonate horizon, unit 5, is 23.7 m thick, has a much higher proportion of clay than unit 2, and is intensely burrowed. Sedimentary gypsum laminae are present.

The uppermost part of the section (unit 6) in which the Namba and Willawortina Formations intertongue is more conveniently described when discussing relationships between units.

The Namba Formation has been broadly divided into two informal members (1 and 2) of regional extent, on the basis of the presence or absence of the tough black sandy clays with skew planes. The lower member (e.g. units 1–4, section 11, Fig. 3) is characterized by these clays, and cyclicity is more prominent. It was later found that this subdivision closely coincided with the change from smectite to illite-kaolinite dominated clay mineral suites (inset, Fig. 3), except in Yalkalpo 1 bore (Fig. 3, section 12). In this bore it is uncertain whether the dominance of smectite throughout the sequence represents a local variation in clay mineralology or whether the upper part has been wrongly assigned to member 2 (which may have been eroded). The mineralogy in Yalkalpo 1 bore is remarkably uniform, smectite almost the only component. The higher proportion of silt is also unusual.

An interesting, varied vertebrate fauna is found in the upper part of member 1 and the base of member 2 of the Namba Formation in various small saltpans southeast of Lake Frome, in the vicinity of Eurinilla and Billeroo Creeks. One of these localities is at Lake Pinpa (Section 8; Fig. 15).

WILLAWORTINA FORMATION (Derivation—Willawortina Creek, passing south of "Wertaloona" on the Balcanoona High Plains, in the vicinity of the outcrop reference section).

The type section for this unit is Western Nuclear's sedimentary uranium test hole WC2 (Fig. 3, section 10 and Appendix 1) cored from 8 m to base. The hole was drilled on the uplifted plains flanking the Flinders Ranges, near Paralana, where a continuous sequence of coarse poorly sorted sediments is encountered. A detailed division is not possible as a result of moderate recovery and gradational contacts. Three members are recognized, members 1 and 2 (16.4 m and 17.0 m thick respectively) have less mica and sand in the matrix than the overlying beds, and are less oxidized. Member 2 has finer overall grain size than member 3 but is comparatively coarser than member one. Members 1 and 2 are equivalent to unit 6 of section 11.

Although bedding planes are very indistinct, transitions in grain size are often abrupt (Fig. 13). Secondary alteration with production of red mottling is common throughout. Feldspars are generally more abundant than in the Namba Formation. Sandy beds have matrix-supported framework with a high proportion of framework compared with the Namba Formation.

The Formation crops out along creeks incised into the high level plains flanking the Flinders Ranges, along the southern shore of Lake Frome, and along the Siccus-Pasmore River. The section (Fig. 3 section I, Appendix I) in a low range of hills, 3.7 km on 22°T, north of Prism Hill and south of "Wertaloona" (Air photo reference: S. Aust. Dept. Lands Svy. 803, *Balcanoona* Run 7, photo 0014), is an important supplementary section, as it is the only outcrop in which the contact with the Namba Formation can be observed. The sequence is 140 m thick and dips 30–50° east, in accord with the remainder of the Cainozoic section. The whole rests with angular unconformity on Middle Cambrian rocks. Exposure is moderate to poor, necessitating reconstruction from several scattered outcrops, particularly through the Namba Formation. This sequence was first mapped by Leeson (1967)[a] who referred the conglomerate to the Telford Gravel (Firman 1963, 1964, 1966b, 1967a, 1970) and the underlying clays to the Avondale Clay (Firman 1967a). Subsequently Callen (in Coats 1973) remapped the area during 1970–1 for the COPLEY 1:250 000 geological map sheet, and the sequence was assigned to an undifferentiated Tertiary-Quaternary unit.

Elsewhere on the eastern portion of COPLEY, green clay, now known to belong to the same sequence, was called Avondale Clay.

In Section 1 (Fig. 3) the base of the Willawortina Formation is placed at the base of the lowest conglomerate. Beds below this unit include poorly sorted sandy clays, but with interbedded micritic white dolomite, fine yellow-green sand, and pale grey and olive clay, closely resembling the Namba Formation. Below these beds, resting with angular unconformity on the gently folded Middle Cambrian red beds, is coarse sand with polished pebbles and ?ferricrete clasts resembling the Eyre Formation.

Another section regarded as equivalent to the Willawortina Formation, but of overall finer grainsize, is exhibited by unit 6 of Wooltana No. 1 bore (Fig. 3, section 11). It shows a prominent alternation of sand and clay in fining upwards sequences, each separated by sharp contacts. Sorting is uniformly very poor, and mottled green and brown colours common. Secondary carbonate nodules are present, and also beds of lacustrine dolomite. Toward the top of the section the fining upwards sequences become poorly defined. The top is capped by a thin dolomite bed, overlain by cobble conglomerate and sandy clay silt, representing the Eurinilla Formation and "unnamed conglomerate" (probably equivalent to the Millyera Formation).

Upstream from section 2 along Balcanoona Creek, excellent exposures (e.g. Fig. 12) of the upper part of the sequence seen in section 11 are displayed in cliffs. One of these exhibits a hiatus—limestone and conglomerate in the lower part have been faulted before deposition of the overlying silts. Subsurface (below soil) karst structure is present.

RELATIONSHIPS BETWEEN FORMATIONS

The nature of the contact between the Namba and Eyre Formations, and difficulties associated with differentiation when both units are sandy, have been discussed by Wopfner *et al* (1974). The disconformable relationship is demonstrated palynologically by W. K. Harris (pers. comm. 1974, see section on AGE, this paper).

The intertonguing relationship between the Willawortina and Namba Formations is illustrated by Fig. 3 (inset), a section across the Paralana High Plain, on which Wooltana 1 bore has been superimposed. A similar section showing the same features can be drawn across the Balcanoona High Plain through WT3, WT5 and WT4 bores (Mines Administration Pty Ltd) and Wooltana 1 bore. The decrease in coarse clastics proceeding east from the Flinders Ranges is demonstrated. The lower boundary of the Willawortina Formation has been drawn at the base of the characteristic mottled, immature, poorly sorted sediments. Note the varying electric log response to similar lithological differences between bores, which results from differing drilling mud properties and sensitivity, and in the case of WC2 bore, different instrumentation. Holes F22–20 and E20–13 however, are not affected by these variables and are directly comparable.

In Wooltana 1 bore (section 11 Fig. 3) intertonguing with the Namba Formation is exhibited by unit 6. The typical Namba Formation lithology of sharply differentiated relatively better sorted clay and silt beds grades to the extremely to very poorly sorted coarse grained Willawortina Formation. The two units alternate to some extent. Essentially there is a gradual upward increase in the coarser grained fraction, though an isolated pebbly bed appears low in the sequence. Clays are rich in illite (muscovite) and feldspar is abundant, compared with the bulk of the Namba Formation where these minerals are minor components and smectite the dominant clay mineral.

Unit 6 of section 11 is therefore interpreted as the equivalent of the lower part of the Willawortina Formation in section 10, a relationship suggested by the correlation lines drawn in Fig. 2 of Callen (1976). The criteria chosen here to identify the base of the Willawortina Formation are those readily mappable: the base of the consistently coarse-grained poorly sorted sediments. Thus unit 6 as shown on Fig. 3 is regarded as mainly Willawortina Formation, though it contains tongues of lacustrine dolomite like those in the Namba Formation. The contact is readily recognizable from petrophysical logs (Callen 1976 Fig. 2) and can partly be explained by the degree of secondary alteration (carbonate nodules, iron oxide mottling) stratigraphically associated with the Willawortina Formation. These secondary effects alternated with deposition, and are an integral part of the unit.

Support for the intertonguing relationship between Namba and Willawortina Formation is also derived from clay mineral analyses (Callen 1976)[2]. Results are shown diagrammatically on the inset of Fig. 3 demonstrating the abrupt change from rocks dominated by smectite and randomly interstratified clay, to illite (largely well crystallized muscovite), randomly interstratified clay and kaolinite. This change corresponds to the position of the alunite horizon within the Namba Formation, and is widespread throughout the basin, having been located in 14 bores and in outcrop. The change was probably initiated by uplift of the Flinders Ranges, probably with climatic variation from high to low rainfall as indicated by clay minerology and colour change (see later). It is therefore regarded as an approximate time marker, and is coincident with the boundary between members 1 and 2 of the Namba Formation, and with the base of the Willawortina Formation in its type section. The change corresponds with the base of the Willawortina Formation identified in WC2 and Wooltana 1 bore.

Alunite is recorded near the top of member 1 of the Namba Formation, forming a series of nodular horizons associated with sharp bedding planes. The nodules ramify through the clay and resemble calcareous hardpans of soils in their manner of development. The horizons are widely developed in the Paralana High Plains area, but are also found in the eastern part of the basin in C15 bore. Here, they are overlain by a relatively thicker sequence of member 2 than in the high plains. The horizons are regarded as soils, associated with a well developed hiatus or disconformity formed during uplift of member 1. This emphasizes the time significance of the clay mineral change recorded earlier.

Silcrete has been identified by one author (R.A.C.) in the interval 72–94 m from cuttings of bore LB12, drilled by Mines Administration Pty Ltd. It is developed on clay, and overlain by greenish-red mottled sandy calcareous clay resembling the Willawortina Formation. A number of closely spaced bores between "Murnpeowie" and Reedy Springs, drilled by Pechiney Exploration (Australia) Pty Ltd (Mannoni & Barral 1972)[6] suggests a similar relationship. The silcrete varies from the red and grey mottled chalcedonic and opaline "puddingstone" to the grey microcrystalline quartz "grey billy" type, according to whether clay or sand is silicified. This is displayed by Mannoni & Barral in their cross-section, and can be observed in outcrop. The same silcrete horizon forms a cap to the dipping Eyre Formation at Reedy Springs (Wopfner *et al.* 1974 Fig. 2). The silcrete is thought to represent a soil horizon, and therefore marks a disconformity (Callen 1976)[2].

Thus there is evidence supporting a disconformity between the Namba Formation and rocks resembling the Willawortina Formation in this area. Although the silcrete has not been identified in the high plains regions, it is apparent that the Willawortina Formation, as defined, may contain some younger material.

The brown silcrete and ferruginous material developed on sandy facies of the Namba Formation exposed at Lake Tarkarooloo, and around other saltpans east of Lake Frome, are thought to be equivalent to that just described. Cementation certainly occurred prior to deposition of the Millyera Formation, as indicated by abundant silcrete nodules and ferruginized Namba Formation clasts in the base of the channel facies in Lake Tarkarooloo.

AGE

The flora of member 1 of section 11 (Fig. 3) indicates an early to middle Miocene age for the base of the Namba Formation (Batesfordian-Balcombian—pers. comm. W. K. Harris 1974). Harris states the flora is similar to that of the Munno Para Clay of Lindsay & Shepherd (1966), and Lindsay (1969, p. 38) in the Adelaide Plains Sub-Basin. An assemblage of the same age was found in Mines Administration Pty Ltd LC1A bore (for lithological description see Wopfner *et al.* 1974) to the north of section 11, and also in Lake Eyre 20 bore (Johns & Ludbrook 1963) in the Etadunna Formation.

The age of the Willawortina Formation, accepting a conformable relationship with the Namba Formation, is therefore medial Miocene or younger. Its upper age limit, as for the Namba Formation, is deduced from relationship to the Millyera Formation, and Eurinilla Formation (Pt II) indicating a minimum age in excess of 40 000 years B.P., possibly pre-Pliocene.

[6] Mannoni, N., & Barral, J. M. (1972).—Murnpeowie Project S.M.L. 373 (South Australia) drilling program report R/72-21-U, *S. Aust. Dept. Mines envelope* 1327, Unpub.

TABLE 1. SUMMARY OF ROCK UNIT PROPERTIES

ROCK UNIT	SECTION (Fig. 3)	LITHOLOGY	SEDIMENTARY STRUCTURES	CRITERIA FOR CORRELATION	FOSSILS	AGE	GEOMETRY	GEOMORPHIC EXPRESSION	ASSOCIATED SOILS
WILLAWORTINA FORMATION	10 (1, 11)	Extremely to very poorly sorted bouldery to pebbly silt clay with numerous greenish carbonate nodules enveloping matrix and skeleton grains in southern areas. Lenses and sheets of pale greenish white dolomite with scattered pebbles, bouldery dolomite near ranges. Lenses of pebbles to large boulders common near Flinders Ranges, sand beds further east 2.5-7YR3-8/1-8, 5-7Y6-8/1-8.	Crude wavy and lenticular horizontal lamination. Well defined medium scale cross beds, Beds ½–4m thick, fining upwards cycles in lower part, finer facies	Greenish clays with very poorly sorted sand to boulder content, usually matrix supported framework. Greenish silty carbonates. Red brown mottling common.	Rare vertebrates.	LATE MIOCENE-PLIOCENE possibly to EARLY PLEISTOCENE (from relationship to NAMBA FORMATION)	Wedge shapes mass, thinning east, between Lake Frome and Flinders Ranges, and to south. 0 – 150m	Forms basic landscape of uplifted "high plain" flanking Flinders Ranges, where it supports growth of *Eucalyptus gillii*. Crops out as vertical or overhanging cliffs along creeks. Cliffs along Siccus Pasmore Rivers and along south shore of Lake Frome.	Well developed massive white hard carbonate developed in long cylindroids or horizontal sheets, pisolitic structures. Hard butt groundwater calcrete cements porous sediment. Massive crusts of gypsum rosettes. Red green mottling, green colour increasing with depth, black patch stain on fractures.
NAMBA FORMATION	12 (11)	Alternating fine to medium poorly sorted sands silt and clay, thin dolomite and limy dolomite beds, often oolitic. Sands generally angular of high sphericity. Clays may be black (ferrous iron) and tough with characteristic irregular shiny-surfaced fractures, or pale green or grey. Sands and clays may be carbonaceous. Dolomites often have nodular structure, and are penetrated by branching pores lined with manganese. Rare Charales limestone. 10YR2-9/0.25-6, N0-N9, 10YR2-7/1-2, rarely 5B5 7/1, 5-10R3-3.5/3-4, 5GY4-7/0.5-1 and 5G6/1	Horizontal lamination common, especially in silt and very fine sand. Very small to medium scale cross bedding common in silts and sands, irregular ooliths in carbonates, often rod shaped. Intraformational brecciation, quick flow structures common. Bioturbation common. Rare shrinkage (?subaqueous) cracks and slumps. Cyclic deposition prominent	Pale grey green clays and fine silts and sands, dolomites, tough black clay with irregular fractures. Fish spines in lower beds. Vertebrates—lung fish teeth.	Ostracoda (Cyprididae), Charales oogonia and stem moulds. *Potamopyrgus* s.l. Dipnoi, Teleostei, Chelonia, Crocodilia, Aves, Monotremata, Marsupialia, Cetacea. Plant spores: *Nothofagus*, *Dacrydium*, *Podocarpus*, *Eucalyptus*, Gramineae, Restionaceae, Casuarinaceae, *Pediastrum*	MEDIAL MIOCENE (BATESFORDIAN-BALCOMBIAN) from plant spores and pollen	Thin widespread blanket and shallow basins 20 – 250m	Sloping cliffs often capped by dolomite, gypcrete or secondarily carbonate cemented younger units, along edges of dry lakes and creeks, east and south east of Lake Frome. Less commonly as dipping sequences uplifted along western margin of Flinders Ranges. Mainly subsurface	Sometimes capped by ferruginous yellow brown orthoquartzite silcrete. Alunite soil like horizons associated with uppermost black clay.

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REGIONAL CORRELATION

Relationships with other units used on adjacent South Australian Department of Mines Geological Atlas Series map sheets (COPLEY, PARACHILNA) and in other basins, are shown in Table 2.

Equivalence between the Etadunna and Namba Formations is demonstrated by lithological similarity, similar flora, and occurrence of species of fossil marsupials previously known only from the Etadunna Formation. Both contain the unusual dolomite-palygorskite mineral assemblage.

A sequence penetrated during drilling operations by Carpentaria Exploration Pty Ltd immediately west of the Ediacara Fault (Binks 1972) is very similar to that encountered in Wooltana No. 1 bore (section 11, Fig. 3) in the Lake Frome area. The section in Binks' Fig. 3 has been interpreted by one of us (R.A.C.) thus: 0.0 to 94.8 m ?Willawortina Formation equivalent, 94.8 to 121.0 m—unnamed beds, 121.0 to 233.2 m—Etadunna Formation equivalent, 233.2 to 298.7 m—Eyre Formation. The sequences in the intermontane Walloway and Willochra Basins (Howchin 1909, 1913; O'Driscoll 1956) are more difficult to compare lithologically, but palynology (Harris 1970)[7] from 30 m in Willochra No. 2 bore suggests most of the sequence is equivalent to the Eyre Formation.

On the northwestern side of the Flinders Ranges is the Avondale Clay (Firman 1967a) of similar lithology and mineralogy to the green clays of the Namba Formation and Willawortina Formation, particularly where they intertongue (unit 6, section 11, Fig. 3). The type section is affected by secondary iron oxide mottling, and the "clay" is actually a clayey fine sand, with angular shiny grains. The relationship between Avondale Clay and Etadunna Formation is unknown at the type area: the base is not exposed, and the unit is unconformably overlain by the Telford Gravel and "Conglomerate at Lyndhurst" (Firman 1969). The "Conglomerate at Lyndhurst" resembles conglomerates in the Willawortina Formation (Fig. 12 this paper). Kaolinite is the dominant clay in the Avondale Clay type section, and is abundant in the upper part of the Namba Formation, and the Willawortina Formation.

A section of Yerila Creek in the Mooloowatana area of the northern Flinders Ranges was described and figured by Firman (1971, Fig. 12)[8] as Avondale Clay. Upstream from this site, a lower part of the section is exposed, connected by continuous outcrop. This exhibits micritic carbonate nodules, underlain by silty olive grey clays similar to the upper part of the section. The clay is capped by a well-developed hard white fine grained carbonate soil horizon, comparable to that developed on the Willawortina Formation at Balcanoona Creek. It is overlain by the Eurinilla Formation. The lithology is identical to the transition beds between the Namba and Willawortina Formations (section 11, unit 4).

The Avondale Clay is regarded by Firman as much younger than the Etadunna Formation, hence younger than the Namba Formation. However, the comments above suggest it could either be part of the Etadunna Formation, equivalent to the lower part of the Willawortina Formation or upper Namba Formation.

The lower part of the Telford Gravel (Firman 1967a) may be equivalent to at least part of the Willawortina Formation.

ENVIRONMENT

Consideration as to whether the Namba Formation sediments are marine, marginal, or non-marine was a prime objective. The most conclusive indicators of marine influence are marine fossils and glauconite, hence samples were investigated for foraminifera, and any green pellets or clays were studied by x-ray diffraction. A variety of lithological types from subsurface and outcrop were examined by J. M. Lindsay who found no foraminifera. Non-marine gastropods and pelecypods (pers. comm. N. H. Ludbrook 1973–4) are present, as are non-marine ostracodes (pers. comm. K. McKenzie) and the fresh water algae *Pediastrum* (pers. comm. W. K. Harris) and charophytes. All green clays proved to be montmorillonite, and green pellets found in the eastern areas were dolomite, associated with non-marine pelecypods.

Other evidence for non-marine origin is derived from the terrestrial vertebrate remains (e.g. Fig. 10). Several skeletons were found in a partly articulated state. Delicate bones are

[7] Harris, W. K. (1970).—Palynology of Lower Tertiary sediments, South Australia. M.Sc. thesis. University of Adelaide (unpublished).

[8] Firman, J. B. (1971).—Regional stratigraphy of surficial deposits in the Great Artesian Basin and Frome Embayment in South Australia. *S. Aust. Dept. Mines Rept.* RB 71/16.

TABLE 2 CORRELATION CHART – OLDER UNITS

TIME / UNIT	LAKE FROME AREA: CALLEN & TEDFORD, This paper	SUGGESTED EQUIVALENTS – ADJACENT MAP SHEETS AND OTHER BASINS: FIRMAN, N. Western Flinders Ranges	COATS et al. COPLEY 1:250 000 map sheet	WOPFNER, 1974, Strzelecki Desert and northeastern South Australia	STIRTON et al., 1961 Lake Eyre
LATE MIOCENE to EARLY PLEISTOCENE	Ferricrete	Ferruginous horizon (of Karoonda surface)	BUNGUNNIA LIMESTONE equivalent; Conglomerates, clays "T–Q"		
	WILLAWORTINA FORMATION	AVONDALE CLAY and "Conglomerate at Lyndhurst"	AVONDALE CLAY		MAMPUWORDU SAND; WIPAJIRI FORMATION
	? Puddingstone and grey billy silcrete, on ferricrete ?	FERRICRETE			
MEDIAL to LATE MIOCENE	NAMBA FORMATION			ALBERGA LIMESTONE; DOONBARA FORMATION	ETADUNNA FORMATION
OLIGOCENE to EARLY MIOCENE	Massive columnar 'grey billy' silcrete	SILCRETE		SILCRETE OF CORDILLO SURFACE	
MEDIAL EOCENE AND PALEOCENE	EYRE FORMATION		EYRE FORMATION		EYRE FORMATION

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well-preserved, and abrasion due to transportation in currents virtually absent. The sediments in which they occur are fine sand, clay, and dolomitic clay. A nearshore marine environment therefore seems untenable, though a lagoonal or upper estuarine environment is possible. A non-marine environment is preferred, though presence of Cetacean remains (a platanistid dolphin) indicates a link to the sea at some stage.

More specifically, environments are (i) Micritic dolomitic carbonates with irregular ooliths, suggesting low energy shallow lake or shoreline conditions. (ii) Black, laminated fossiliferous clay of Wooltana No. 1, unit 1, suggesting a well developed lake: the fine laminae resemble varves, but have been disrupted by diagenesis and bioturbation. (iii) Sedimentary structure types, abundance of fines, and very poor to poor sorting support a low energy environment for the whole unit. This may explain the apparent lack of well-developed beach sands, which would be poorly developed and poorly sorted along a low energy shoreline.

The environments represented by the cyclic sequence described earlier are in ascending order: (a) channels: small to medium scale cross-bedded fine to medium sand (Fig. 8). (b) flood plain, estuarine or lacustrine: finely laminated silt, often burrowed and with very small to small scale cross-bedding (Fig. 7), and olive clay. (c) lacustrine: patchy carbonate, oolitic dolomite (Fig. 5) and clay (Fig. 6). (d) swamp or mud flat with occasional channels: hard, black, mottled clays with irregular fractures and sand patches (Fig. 4), interpreted as vertisols. The cyclic sequences are of 1–20 m thickness, averaging 9 m, well-developed in most parts of the basin, except the northwest where uniform clay sections dominate. The cyclicity suggests a depositional process resulting in a particular sequence of facies, but with inherent instability. Some examples applicable to the Namba Formation are (1) a delta building into a shallow lake or estuary (necessarily shallow because the cyclic sequences are thin), (2) repetitive transgression and regression of a shallow lake shore in response to fluctuations in water level (3) repetitive avulsion of a meandering stream, (4) bars associated with development and abandnoment of portions of river channel.

The abundant bioturbation, and its occurrence in medium-scale cross-bedded coarse channel sands, and basal parts of laminated silt beds, is inconsistent with river channel origin of these facies. These sands more likely represent offshore lacustrine bars. Lenses of the coarser sand facies at the base of, or within, the tough dark grey clays are also difficult to explain in terms of a river and flood plain relationship: channels cutting across a tidal or deltaic mud-flat are more acceptable. Subsequent intensive bioturbation or rheotropic flow has partly destroyed bedding, distributing the sand in irregular patches. In the estuarine case, the absence of any evidence for a marine influence, particularly in the microfauna, indicates deposition in the uppermost reaches of the estuary. In sequences where coarser channel sands are interbedded with non-burrowed laminated silts, the river-channel and flood-plain relationship is still applicable.

Fluviatile deposits are abundant, and fossils (e.g. Fig. 10) of aquatic vertebrates (Dipnoi, Teleostei, Chelonia, Cetacea) suggests a permanent water supply, and fossil plants (*Nothofagus* and *Podocarpus*) indicate high rainfall. The distribution of lenses of channel sands within an essentially clayey sequence is typical of meandering rivers. Although only 42 current directions were measured (mostly in the Lake Tarkarooloo area) results suggest a southerly component of transport direction for the upper part of the Namba Formation, in marked contrast with the north-easterly direction of overlying units.

Dense vegetation is suggested by the palynology of the basal unit 1: the modern descendants of the species represented typify rainforests. Abundant grass pollen are evidence that grassland occupied extensive areas. Thus rainforest was not continuous in the early lacustrine phase of deposition. The relative abundance of arboreal marsupials in the upper part of the Namba Formation indicates the presence of gallery forests along the watercourses.

Apparently at variance is the smectite—dolomite—palygorskite association, frequently recorded from arid soils, playa lakes and warm hypersaline waters (e.g. McLean *et al.* 1972, Bentor *et al.* 1963, Meester 1971, Singer *et al.* 1972). At present dolomites and high-Mg calcite are forming in hot arid or semi-arid hypersaline lagoons (e.g. Von der Borch 1965, Von der Borch *et al.* 1975, Friedman *et al.* 1973) though some magnesium-rich sediments are found in latitudes as high as 48°N (Muller *et al.* 1972).

Millot (1964) indicates the montmorillonite—palygorskite—sepiolite association is the result of offshore lacustrine or marine chemical deposition. This took place adjacent to a lateritized land mass of low relief and dense vegetational cover, in a subtropical or tropical climate. Sepiolite is absent in the Lake Frome area, but this may be an affect of degree rather than basic difference. The hypothesis as applied to the Namba Formation overcomes the difficulty of evoking evaporative conditions in a high rainfall climate.

Millot's hypothesis has been applied in a similar manner to the Cainozoic rocks of the Jordon Valley (Wiersma 1970). These sediments contain a remarkably similar sequence of clays to the Namba Formation. Particularly relevant are Wiersma's comments regarding the origin of palygorskite (p. 88). He concluded that intensive weathering on the hinterland under warm humid conditions was necessary for liberation of the elements essential to the genesis of palygorskite and its associated sediments, and that evaporation in the sedimentation basin should be such annually as to provide the necessary concentration of chemical elements. He deduced that evaporation must prevail over precipitation and fluviatile and/or marine supply of water to the basin. In many places in the present tropics evaporation can exceed annual precipitation, with resultant formation of evaporites in favourable locations. Palygorskite was of detrital origin in the late Tertiary and Quaternary of the Jordon Valley, having been derived from Cretaceous and early Tertiary rocks in which it originated by chemical sedimentation. In the Lake Frome area no pre-existing rocks rich in palygorskite were present: rather kaolinite, smectite and illite are abundant. Palygorskite can be formed in soils (Singer & Norrish 1974) but only in relatively low proportion, thus it must have originated within the depositionary basin during sedimentation.

It is notable that Millot's (1964) ideas as applied to deposition of Namba Formation sediments require an equivalent Miocene lateritization on adjacent land masses. In this context Wopfner's (1974) conclusions regarding an Oligocene-Miocene "ferralitization" are of interest. Although the evidence he gives for age of the Doonbara Formation is inconclusive, some additional observation are made here. Firstly clasts identified with the Doonbara Formation (by R.H.T.) are found in the Wipajiri Formation (Stirton *et al.* 1967) of Miocene age. Secondly the ferruginization in Lake Eyre Bore 20, doubtfully equivalent to the Doonbara Formation, is recorded by Callen (Wopfner *et al.* 1974, Fig. 17) *within* the lower part of the Miocene Etadunna Formation. Others have also recorded an older Tertiary ferricrete (Firman 1967b). Therefore lateritization (or at least, ferruginization) could have been proceeding in uplands adjacent to the basins in which the Etadunna Formation and Namba Formation sediments were being deposited.

The main carbonate horizons occur a few metres above unit 1 of section 11, with its rainforest flora, and above the vertebrate zone with its indications of seasonal climate with abundant water supply. The presence of these carbonates can be explained in terms of protracted arid phases superimposed on a subtropical or warm temperate climate.

In addition the presence of detrital feldspars must be explained, particularly in view of the abundance of plagioclase and association with smectite.[11] The possibility of addition of volcanic material from eastern Australian must be considered, the Miocene being a period of maximum vulcanism (Sutherland *et al.* 1973). However, the percentage of feldspar is not large. Preliminary studies of feldspars in the Namba and Willawortina Formations suggest relative proportions of feldspar types and compositions of plagioclases are similar to an unmodified contribution from nearby Precambrian crystalline basement rocks. On present evidence there is apparently no change in relative abundance and type of feldspars in the illite-kaolinite rich zones of the Tertiary, in comparison with the smectite zones. This suggests abundance is not tied to smectite occurrence, as would be expected if these minerals originated from volcanic ash falls. The presence of feldspar presents a problem considering the evidence for a humid climate. Possibly seasonal aridity and nearby source permitted preservation. In addition Todd (1968) has shown plagioclase is more stable than orthoclase under conditions of restricted leaching, in a tropical climate. Thus smectite (montmorillonite) is unlikely to have originated from volcanic ash falls.

[11] The mineral group smectite, but R. N. Brown recognized dioctahedral montmorillonite in several instances.

In the final analysis, the Namba Formation was thought to be deposited in a warm temperate to subtropical climate. The landscape had a savannah aspect, with gallery forests around permanent rivers and lakes. Periods of aridity occurred.

High average temperature, invoked to explain the mineralogy of the Namba Formation, is in accordance with marine paleotemperature measurements in southern Australia (Gill 1968) and New Zealand (Devereux 1968, Jenkins 1968) of 18-22°C for the Miocene. Considered in the light of continental drift data, which suggest Australia was closer to Antartica (though drifting rapidy northward: Wellman *et al.* 1969), and data which indicate the cooling of Antarctica was underway (Hayes *et al.* 1973), the temperature can be explained in terms of greatly expanded subtropical climatic zones during early and middle Miocene times.

Deposition of the Namba Formation in the central part of the Lake Frome area was followed by widespread ferruginization and silicification (opal, and quartz overgrowths) and development of cryptocrystalline silica nodules, particularly in the coarser Namba Formation sands. These processes were the result of widespread groundwater movements. Formation of duricrusts and related phenomena had a locus in river valleys cut into the Namba Formation, prior to deposition of the Millyera Formation.

No evidence for a major period of Oligocene to early Miocene "ferralitization" suggested by Wopfner (1974) was found in the Lake Frome area, though there is abundant evidence for late Miocene to Pliocene ferruginization and orthoquartzite silcrete Formation. This does not necessarily negate Wopfner's climatic evidence, since two periods of ferruginization are probable (Firman 1967b, 1971[b]; Jessup & Norris 1971). The older Tertiary ferruginization would presumably not be manifested in the Lake Frome area, where chemical and detrital deposition were proceeding.

The coarse detritus in the Willawortina Formation has clasts derived from Cambrian and Precambrian rocks in the Flinders Ranges. When considered in combination with poor sorting and abundant feldspar content, vigorous uplift of the Ranges is indicated. This was accompanied by movement on the Poontana Fault. A similar conclusion has been drawn by Binks (1972) from evidence on the western side of the Ranges. Ironstone and silcrete pebbles from pre-Willawortina Formation (?pre-Namba Formation) duricrust are present. However, laterite clasts are not as abundant in the overlying Willawortina Formation as one would expect in a sequence supposedly derived from erosion of a laterized land mass. Presumably this is because the Flinders Ranges were virtually non-existent at the time of deposition of the Namba Formation, presenting only a small area for laterization. Alternatively, in keeping with the suggested warm-temperate to sub-tropical climate, ferruginization may not have developed an extensive laterite crust.

Deposition in an alluvial fan environment is suggested for the Willawortina Formation by the presence of extremely poor sorting (Fig. 13), numerous channels (Fig. 12) with medium scale cross-bedding, and laminated calcareous silts (Fig. 12) with red-mottling and carbonate concretions typical of flood plain deposits. Fining upwards sequences are typified in section 11, suggesting bar deposition. The deposits coarsen very rapidly close to the Flinders Ranges. The extremely poor sorting, coarse grain-size and matrix-supported texture in some beds may be the product of mud-flows. The red mottling ('marmorization') and carbonate soils are similar to those described by Freytet (1971) in association with alluvial deposits, and typically form in the inactive parts of fans (Blissenbach 1954, p. 185; Denny 1967, p. 105). These features resemble modern fan deposits.

In sections 1 and 10 there is a tendency for overall coarsening upwards, suggesting increasingly rapid uplift of the Flinders Ranges. The uplift deluged the former lakes and swamps of the Namba Formation with detritus, reducing their extent. Thin dolomite lenses in the sequence (section 11, and Balcanoona Creek) represent lacustrine or playa lake phases similar to those of the Namba Formation. Petrological investigation shows these contain a much higher proportion of sand (much of it unstable mineral grains) than the Namba Formation carbonates.

During deposition of the Willawortina Formation, oxidizing conditions became prevalent, through accumulation of the sedimentary column above the water table. This contrasts with the sub-water table reducing environment of deposition of the Namba Formation. Abundant potash feldspar and plagioclase can be attributed to rapid deposition and possibly semi-arid climate. Presumably uplift of the

Flinders Ranges would have had a strong effect on local climate, but this cannot be assessed at present.

Following deposition of the Willawortina Formation, ferricrete and calcrete formation occurred, particularly in marginal areas.

The absence of surficial cementation of coarse sediment in the type section of the Willawortina Formation and nearby outcrop, contrasts with the ubiquitous cementation in southern areas (sections 1, 11, Fig. 3). An explanation in terms of a carbonate rich source area for groundwater or sediment, or abundance of limestone clasts in southern areas, does not explain the widespread distribution of surficial carbonate cementation in rocks of various ages throughout the Flinders Ranges. Indeed, many fans in semi-arid areas throughout the world are similarly cemented. Enough calcium is produced by weathering, or deposited from wind-born dust, to provide sufficient carbonate material for cementation anywhere. Therefore in the case of the Willawortina Formation adjacent to Mount Painter, absence of carbonate is a local phenomenon, the explanation of which is unknown.

Pt. II—Younger Cainozoic Rock Units

Type and reference sections are shown in Fig. 15, and described in detail in Appendix 2. Table 3 summarizes the lithological and other properties of the rock units dealt with in the text.

LITHOLOGY

MILLYERA FORMATION (Derivation: Lake Millyera[x], near the mouth of Billeroo Creek. Millyera is local aboriginal word for water. Map reference: *Siccus* map sheet, FROME).

The name is proposed for a sequence of interbedded greenish ostracode-bearing clays, thin limestone of charophyte algal remains, and fine sand. The sediments occur in Lake Frome or in small lakes close to its margin. The name is also applied to a coarse cross-bedded or conglomeratic sand, regarded as a fluviatile equivalent of the clays, where these contain interbedded charophyte limestones.

The type section at Lake Millyera (Fig. 15, section 4) is located 69.2 km on 320°T, northwest of Low Stony Hill (map reference *Telechie)* on the *Siccus* map sheet (Air Photo ref.: Dept. Lands Svy. 361, *Siccus* Run 1, Photo 4460).

The section consists of 4.3 m of laminated green ostracode bearing clay with a thin bed (40 cm) of laminated charophyte limestone near the top, overlain by alternating clay and fine sand. An abbreviated description is given in Table 3.

The type section was not located at the thicker section 5, where there is intertonguing with red beds. This avoids confusion which might arise should the red beds, which have affinities with certain fluviatile equivalents (e.g. the Eurinilla Formation—see later), be formalized as a distinct unit.

The contact with the Namba Formation was not exposed, but can be observed in the supplementary section located about 2 km east (Fig. 15, section 5, 68.7 km on 327.5°T northwest of Low Stony Hill—air photo reference S. Aust. Dept. of Lands Svy. 361, *Siccus* Run 1, Photo 4461).

In section 5, the Millyera Formation is 8.5 m thick, cropping out below a thick exposure of Eurinilla Formation. Here thin charophyte limestone in the Millyera Formation grades laterally into gypsum, often ripple marked (Fig. 16), intercalated in an essentially sandy sequence. Sometimes botryoidal structures are present on the surface of the gypsum layer, similar to those found on the floor of Lake Frome. Scattered very coarse polished sand grains are present on top of the gypsum, where it is in contact with the overlying red sand lens.

The red sand lens consists of a thin bed of bright red-brown coarse silt with basal granule layers impregnated with secondary gypsum, closely resembling the Eurinilla Formation in lithology. It grades by alternation to greenish very fine sand with coarse sand, silt and clay laminae (yellowish grey). The greenish sand bed is fossiliferous, with numerous charophyte oogonia and stem moulds, fish verebrate and spines, and 'Coxiella'.

The contact with the Namba Formation was exposed by trenching. Orange and yellow sands of the Millyera Formation contain reworked and oxidized tough grey sandy clay clasts from the underlying Namba Formation. The Namba Formation is more indurated and darker coloured.

The top of the sequence is marked by a strongly developed soil, also observed elsewhere affecting the Namba Formation. The soil has a crumbly texture, with peds of irregular shape about 0.5–2 cm across. A well developed black mangans is present, and reddish-to yellowish-brown iron oxide patches are developed in the clay. A similar horizon is

TABLE 3 SUMMARY OF ROCK UNIT PROPERTIES
YOUNGER UNITS

ROCK UNIT	SECTION (Fig. 15)	LITHOLOGY	SEDIMENTARY STRUCTURES	CRITERIA FOR CORRELATION	FOSSILS	AGE	GEOMETRY	GEOMORPHIC EXPRESSION	ASSOCIATED SOILS
COONARBINE FORMATION	7 (5,2,9)	Sand to silty or clayey sand, poorly to moderately sorted, usually fine grained with subangular to sub rounded grains. 2.5-10YR7-8/4-6	Weak horizontal lamination, lenses large scale cross-stratification (rarely well-defined)	Weakly developed bedding, moderate sorting, light brown colour, absence of gypcrete and large carbonate nodules. Locally abundant land snails. Typical soil horizon at top	Snail shells, emu shell, aboriginal artifacts. Charales oogonia (rare). Rare vertebrates. Burrows	EARLY PLEISTOCENE–RECENT? (From relationship to EURINILLA FORMATION)	Thin blanket 0 — 2m	Flat low lying plains, dominates landscape of plains and seif dunes. Crops out in creeks as vertical faces with columnar jointing.	Weakly developed carbonate cylindroids, weathering as hard granules. Discontinuous. Rectangular blocky structure, forming columns of sediment.
EURINILLA FORMATION	7 (5,3,9)	Clay-sand to sand, with interbeds of silt and clay in upper part, lower part sand often with pebbles. Very poorly sorted grains may be moderately rounded but rough and pitted, or rounded and frosted. Upper part 2.5-5YR4-9/4 7. Sandy lower part 7.10YR5-7.5/2-6. Clays 5Y7/1 2. Basal conglomerates and coarse sand with quartz pebbles and locally derived carbonate and ferruginous sandstone clasts. Coarse gypsum sands.	None or crude horizontal stratification well developed horizontal lamination (2-10cm). Sometimes developed into large scale low angle sets. Basal sands trough or planar cross bedded on medium scale. Rarely lower part horizontal wavy laminae with load casts. Low angle lunette-type cross-bedding in gypsum sand.	Poor sorting, fine upper part, coarse lower part. Upper part lacks bedding or more rarely has well-defined sub-horizontal cross-stratification. Lower part cross bedded. Upper part reddish brown, lower yellowish brown. Typical soil horizons, ground water calcrete and gypcrete (in basal part). Gypsum sand	Insect burrows and nests. Vertebrates basal channels including *Diprotodon* sp. *Procoptodon goliah* *Macropus* sp. Basal layer of gastropods and lamellibranchs "Coxiella" near edge of Lake Frome. Numerous Charales oogonia, especially in coarse sand.	LATE PLEISTOCENE (vertebrate fauna C_{14} dating)	Thin tabular widespread sand sheet, fills hollows 0 — 20m	Flat low-lying plains cropping out as low slopes around depression and watercourses. Lower part often cemented by gypcrete or calcrete, producing bench or massive cap to cliff. Frequently basal channels approximate present clay drainage. Islands and mounds along S.E. shore Lake Frome, gypsum lunettes	Several well developed horizons of carbonate and gypsum cylindroids may be presented at top, soft large nodules in some areas. Frequently weather out as granules or sheets on surface. Lower sand weakly to strongly cemented with crystalline white calcite. Also with massive or layered gypsum rosettes. Mottled in shades of red brown and white. Basal conglomerate solidly cemented with white hard to soft carbonate and gypsum of groundwater type.
MILLYERA FORMATION	4 (5,6)	Pale green laminated clay, conchoidal fracture with thin Charales limestone (5Y9/1) laminae at top, interbedded with fine well-sorted sand (2Y7/4 5Y7/2). Limestone may grade to thin ripple-marked gypsum beds. Sand grains angular to well rounded. Reddish to white fine sand with basal pebble beds and interbedded hard thin Charales limestone beds. Algal limestone of mound springs. Clay 10YR5/2, 5Y5/6, 5Y8 9/1 4. Fine sands white to 2.5Y7/2-4. Channel Sand 5-10Y6 8/2 5 10YR5-8/4 7. Medium to fine greenish clayey sands.	Fine horizontal lamination in clays and limestone, assymetric small scale ripples and botryoidal blister on gypsum, oriented Charales tubules. Trough cross-bedded channel sands. Small scale cross lamination wavy bedding	Charales tubule limestone, greenish ostracod-bearing clay, fine sand with Charales oogonia	Charales stem moulds and oogonia. Spiral gastropods 'Coxiella' sp., burrows (spiral along bedding planes), silicified wood (pebbles and tree trunks [illegible]) Ostracodes. Bivalves, fish vertebrae.	MIOCENE-EARLY PLEISTOCENE (From position relative to other units).	Shallow basin discontinuous linear deposits. 0.2 — 10m	In bed of Lake Frome and cropping out around edge, occupying old deeply eroded stream channels, now represented by linear lakes associated with Billeroo-Eurinilla Creek System. Mound spring limestone.	Massive white groundwater calcrete in sands, bright orange stain in basal coarse sands. Red-orange-brown mottling

74—959 Del. B.T R. A. Callen S. A. Dept. of Mines developed on the Millyera Formation in Section 7 of Fig. 15.

The distinction between the lacustrine facies of the Millyera Formation and the superficially similar Namba Formation can be demonstrated from Lake Millyera and Lake Tarkarooloo. In Lake Millyera, the north shore is formed by cliffs of Namba Formation clay and dolomite showing no facies changes throughout the length of the continuous outcrop. The south shore has sporadic outcrops of Millyera Formation, also unchanged along strike, traced to the junction of Billeroo Creek and Lake Tarkarooloo. These relationships suggest a disconformity between the two units. The Millyera Formation also occurs on the north shore of Lake Millyera at its eastern end, but a covered interval prevents direct establishment of a relationship with the nearby Namba Formation. The contact between the units can be observed by trenching the base of the supplementary section 5, where the erosional contact and weathered top of the Namba Formation support a disconformity.

Similar laminated ostracode-bearing clay and gypsum laminae are found beneath the base of the gypsum dunes constituting the islands of Lake Frome. These grade down to ostracode and charophyte-bearing indurated clays, without sedimentary structures, beneath the lake bed. Fine sand interbeds are present. These beds are equated with the Millyera Formation, but most sediment flooring Lake Frome, though of similar lithology, is younger and less consolidated.

Along the eastern edge of Lake Frome is a series of eroded mound springs, exhumed by deflation of the modern lake floor. These are built of saucer-shaped carbonate layers, partly algal in origin, which intertongue with the clays. These spring deposits are partly equated with the Millyera Formation.

In Lake Tarkarooloo, reddish-brown silt and conglomerate is inter-bedded with the charophyte limestone. Proceeding south along this linear lake, the coarse facies eventually dominates, the limestones being absent. The Millyera Formation is no longer identifiable, having graded into an entirely fluviatile facies of conglomerate 2–3 m thick, cemented with massive white secondary carbonate (henceforth referred to as the 'unnamed conglomerate' equivalent to the Millyera Formation). Section 6 (Figs 15, 17) shows an intermediate stage in this transition. Numerous well developed channels exhibiting π cross stratification (Allen 1963) are present, exhumed on the lake floor. They often contain clasts of fossil wood, Namba Formation dolomite, ferruginized Namba Formation sand, and milky quartz at the base, demonstrating a disconformable relationship with the Namba Formation. There is little facies change along the length of Lake Tarkarooloo in the Namba Formation, whereas the Millyera Formation varies considerably, though retaining its identity as a unit.

Two charophyte limestone horizons were developed in the southern part of Lake Tarkarooloo, instead of one as at Lake Millyera. Since they must have once represented a horizontal lake shoreline, and are equivalent to the horizon at Lake Millyera, structural deformation (?faulting) is required to account for their relatively higher position in the landscape. Barometric levelling, tied in with South Australian Department of Lands bench marks, established the height difference (see Sections 5 and 6, Fig. 15). Comparison of the heights of equivalent Namba Formation carbonates, between Lake Millyera and the Namba Formation reference section in Lake Tarkarooloo (Fig. 14) also supports downfaulting of the Lake Millyera region.

The "unnamed conglomerate" channel equivalent of the Millyera Formation can be traced throughout the area southeast of Lake Frome, where it is invariably overlain by the Eurinilla Formation. The disconformity is difficult to detect away from low-lying areas such as Lake Tarkarooloo, where well-developed greenish carbonate nodules and cylindroids of a soil calcrete mark the contact, and massive white groundwater carbonate cements the conglomerates in the Millyera and Eurinilla Formations. Elsewhere the conglomerate has a weak earthy carbonate cement and interbedded secondary gypsum layers, interpreted as groundwater phenomena rather than soils. The contact with Eurinilla Formation appears gradational (e.g. units 1 and 2 of the Eurinilla Formation in section 8, Fig. 15), and it is not possible to establish a disconformity. An additional problem in the Millyera Formation is the repetition of red sand facies resembling those of the Eurinilla Formation. This suggests it may be possible to have two red facies superimposed. The contact between unit 2 and 3 in section 8 may represent such a boundary (i.e. the lower part of this section may correlate with the Millyera Formation).

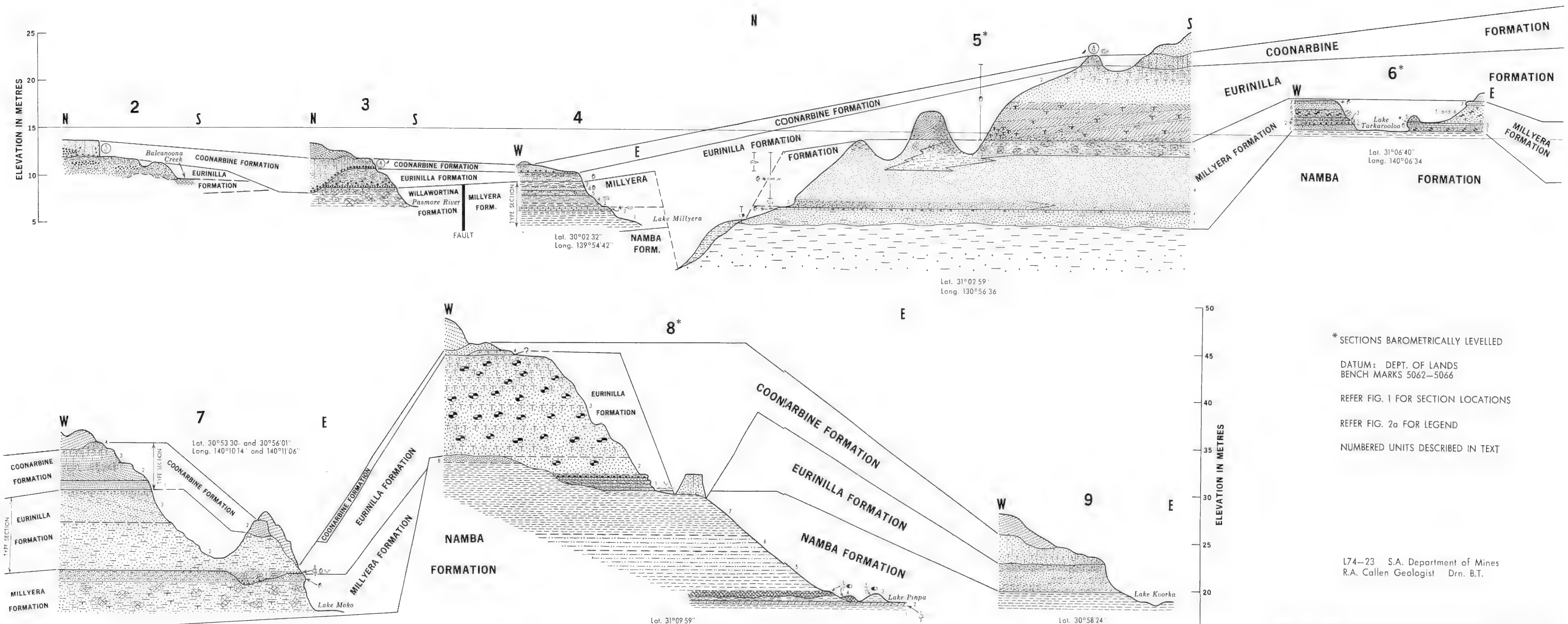

Fig. 15 YOUNGER CAINOZOIC UNITS, LAKE FROME AREA
TYPE AND REFERENCE SECTIONS

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Current directions were recorded from a variety of cross-bedding types in widely scattered localities in the basal channel facies (both sands and conglomerates), though with a bias towards the Lake Tarkarooloo area, but are sufficient (45 measurements) to record a north to northeasterly transport direction. Conglomerates such as those of section 8, where no disconformity between the Eurinilla and Millyera Formation was established, were not included in this analysis.

EURINILLA FORMATION (Derivation, Eurinilla Creek, *Eurinilla* map sheet, CURNAMONA).

The type section (section 7, Fig. 15) is located at Lake Moko[x] on the junction between Billeroo and Eurinilla Creeks (Air Photo Ref. —S. Aust. Dept. Lands Svy. 395, *Coonarbine*, Run 3, Photo No. 9637). The locality is 45.8 km on 332°T from Billeroo Waterhole (CURNAMONA—Billeroo Creek), and the outcrop (Fig. 20) occurs in an amphitheatre, formed by gullies draining into the north end of the lake. The upper fine grained facies is well developed. The complete section is described in Appendix 2. Section 7 was constructed from two outcrops 200 m apart, correlated by following the beds along strike.

This sequence consists of three units, separated by a weak carbonate soil horizon. The lower unit, exposed in the southern outcrop, consists of 1.8 metres of white well sorted medium grained channel sand. It is cross-bedded, and contains some vertebrate remains, clasts of underlying units, and charophyte oogonia. The sands have features similar to channel sands elsewhere at or below the base of the Eurinilla Formation. An interesting feature is the presence of biotite, suggesting nearby crystalline basement outcrop at the time of deposition. Unit 1 is overlain by the much more widespread and typical red, silty and sandy facies of units 2 and 3, respectively 5.3 and 5.5 m thick. These units are separated by a weak carbonate soil horizon. The lower is paler than the upper, and shows no evidence of bedding. It grades to clay-silt at the base. The upper unit has diffuse large scale cross-bedding, is sandy, and orange-coloured throughout. It is capped by a well-developed fossil soil horizon with nodules and cylindroids of carbonate and some gypsum.

The sequence is overlain above the fossil soil by a horizontally laminated sand, similar to that at the top of Unit 2, but with more pronounced bimodality. Since the soil represents a disconformity, these sands are excluded from the definition, and placed in the Coonarbine Formation.

Another section 8 m thick (section 5, Fig. 15) is situated on a steep bluff facing north, on the southern side of Lake Millyera, close to the Millyera Formation type section 4. A detailed description is in Appendix 2. The sands are paler than those of the type, and contain low angle cross-bedding at the base. The overall two-fold division (of units 2 and 3) in the type section is retained. A diffuse thin bedding dips toward Lake Millyera. Considered with the geometry of the outcrop, the sequence is interpreted as a small delta.

The upper part of this sequence has tubules and cylindroids of soft white carbonate and gypsum, several centimetres diameter, forming several inter-related horizons representing a fossil soil complex. The tubules weather out as hard cylinders. The lower part of the sequence is partly cemented with sheets of soft white carbonate, and with pink carbonate nodules. The base is solidly cemented with gypsum, partly derived from the dissolution of gypsum lunettes (represented by low angle cross-bedding).

A third reference section of 3 m thick is located at Lake Koorka[x] (Fig. 23), a small claypan on Eurinilla Creek, close to the boundary between FROME and CURNAMONA on *Eurinilla* map sheet. The western edge of the pan is formed by a cliff 6 m high, where section 9 (Fig. 15) was measured (Appendix 2). Here, the Eurinilla Formation is represented by mottled very pale orange and strong brown clayey silt without stratification, capped by a massive gypsum horizon with 0.5 cm rosettes of gypsum crystals developed in red-brown silt and gypsum flour. It disconformably overlies the Namba Formation.

Burrowed horizons and gypsified roots are locally common in the Eurinilla Formation, though not represented in the sections described here.

The carbonate zones at the top of the Eurinilla Formation in sections 5 and 7 are regarded as a single widespread paleosol. They differ from the soil developed on the overlying Coonarbine Formation by having larger patches of carbonate segregation, often in several horizons, frequently weathering out as solid sheets or lumps. In the Arboola Claypan[x] large soft calcareous "biscuits" are developed, in which the original lamination of the cemented sediment is visible. This paleosol has been identified along Balcanoona and Poontana Creeks, on the west side of Lake Frome (Figs 1, 15, section 2) where it is developed in coarser grained sediments.

The Eurinilla Formation is often underlain by a coarse cross-bedded sand or conglomerate, ?'unnamed conglomerate' usually partly cemented with hard white lime. The beds are light pinkish brown, from iron-staining on sand grains. A typical sequence including this facies occurs at Lake Pinpa reference section (section 8, Fig. 15, and Appendix 2). The basal conglomerate often contains clasts of Namba Formation dolomite or Willawortina Formation carbonate nodules. At Lake Tarkarooloo the islands on the lake floor (especially near section 6, Fig. 15, where massive carbonate cemented pink sands and conglomerates are interbedded with the charophyte limestone), demonstrate the gradation to the Millyera Formation.

The disconformity between the Millyera and Eurinilla Formations is exemplified in sections 5 and 7, but is not at all obvious in section 8, or elsewhere away from the vicinity of Lake Frome. The relationship can, however, be observed along the Pasmore River, particularly where the main Yunta to Flinders Ranges road crosses. Here, two terraces of secondary carbonate-cemented conglomerate occur, interbedded with yellowish sands containing greenish white carbonate nodules at the top. The nodules are interpreted as a paleosol, and occur in similar yellowish sands of the Millyera Formation in Lake Tarkarooloo. Therefore the unnamed conglomerate and associated sands are regarded as Millyera Formation equivalents.

The red brown silty Eurinilla Formation with its characteristic soil developed at the top, infills a valley cut into the 'unnamed' conglomerate, and associated sediments. The whole is cut into Willawortina Formation sandy clays. Light brown sands of the Coonarbine Formation disconformably overlie all units at various levels in the landscape.

The relationships between the Eurinilla and Willawortina Formations is also exhibited in section 3 at the mouth of the Pasmore River (Fig. 15 and Appendix 2) where reddish-brown pebbly silt with a basal conglomerate (Eurinilla Formation) rests with sharp erosional disconformity on pale green and red-brown mottled clay (Willawortina Formation).

On a regional scale the disconformity surface between the Eurinilla Formation and Coonarbine Formation is flat, but locally, river valleys are developed.

Within Lake Frome are several islands consisting of up to 10 m thick of coarse well rounded gypsum sand with minor quartz, and interbeds of clay pellets. These exhibit the low angle cross-bedding, lithology and geometry of lunettes described by Bowler elsewhere in Australia (pers. comm. 1974, J. M. Bowler). The sands rest disconformably on the Millyera Formation indurated clays, and are tentatively correlated with the Eurinilla Formation. Similar lunettes flank the eastern shore of Lake Frome.

COONARBINE FORMATION (Derivation Lake Coonarbine, *Coonarbine* map sheet, FROME).

The type section is located at Lake Moko section 7, Fig. 14 and Appendix 2), mentioned earlier. The sequence (Fig. 20), resting disconformably on the Eurinilla Formation, consists of three parts—a basal 1.0 m of a red brown indistinctly laminated sand, overlain by 3.3 m of light brown dune sand (two large scale cross-bed sets are represented) with a carbonate soil horizon at the top. This is overlain by 0.6 m of light brown sand with carbonate patches and rhizondules. The laminated sand at the base of this sequence may be a distinct unit in its own right, since it has features different from the remainder of the Coonarbine Formation. Its disconformable relation with the Eurinilla Formation has been established.

The carbonate soil horizons are much weaker than those of the Eurinilla Formation in the same section and at section 5 (Fig. 15). The upper more prominent horizon is correlated with that at the top of section five. The Coonarbine Formation in this section exhibits the typical blocky joint pattern, producing 5 x 10 cm columns of sediment (large ped structures). Land-snail shells occur here, and at other widely separated localities, being characteristic of the unit. The uppermost layer is associated with aboriginal artifacts and emu shell fragments. The Formation can be traced west to the Pasmore River (e.g. section 3) where it overlies the Eurinilla Formation.

An important supplementary section (section 2, Figs 15, 21 and Appendix 2) representing a coarser facies of the Coonarbine Formation of western Lake Frome, is found in Balcanoona Creek, near the natural gas pipeline (Air Photo Ref.: S. Aust. Dept. Lands Svy. 394, *Arkaroola* Run 3, Photo No. 0078). At this site the old land surface on top of the Eurinilla Formation is exposed. The overlying beds of the Coonarbine Formation consist of 1.70 metres of dark brown, sandy silt, with a basal pebble bed, moderately poorly sorted. No bedding planes are visible, and columnar ped structure is well-developed.

Immediately downstream the surface of the Coonarbine Formation is scattered with aboriginal artifacts, the colour is redder, and land snail shells are present. Upstream, near Mulga Bore on "Balcanoona", the basal pebble bed has 0.5–1 m thick lenses, cutting into the Eurinilla Formation. Carbonate nodules from the soils developed in the Eurinilla Formation are eroded and incorporated into the basal Coonarbine Formation.

East of Lake Frome the fluviatile facies of the Coonarbine Formation gives way to aeolian seif dunes, forming the partly indurated cores of the modern dunes of the southern Strzelecki Desert. Exposures occur along the flanks of the modern dunes. The gypsum lunettes of the islands have a deposition break within them, the significance of which is uncertain: it is likely that the part above the break corresponds to the Coonarbine Formation.

RELATIONSHIPS BETWEEN FORMATIONS

The Millyera Formation rests disconformably on the Namba Formation in Lakes Millyera and Tarkarooloo, but its relationship to the Willawortina Formation is less clear. The correlation of conglomerates and sands at the Pasmore River Section with similar facies at Lake Tarkarooloo has been mentioned, and suggests the Millyera Formation conglomerate equivalent is also disconformable on the Willawortina Formation. The relationship is similar to that at the "Wertaloona" section. Further support is derived from the presence of bright orange to red-brown silt and sand, similar to that in the Millyera Formation of section 5, intertonguing with the conglomerate around the mouth of Balcanoona Creek.

At the "Wertaloona" section (section 1, Fig. 3) the dipping sequence of Willawortina Formation is overlain with angular unconformity by a small patch of horizontal conglomerate and yellow sand, regarded as Millyera Formation equivalent. The conglomerate contains pebbles of ferruginized material, derived from what was probably a widespread surface, now exhibited as small remnants in the same valley. This ferruginization is correlated with that beneath the Millyera Formation at Lake Tarkarooloo, and elsewhere. Deformation of the Tertiary sequence occurred before deposition of the Millyera Formation and development of the ferruginous horizon.

The disconformity between the Eurinilla Formation and Willawortina Formation can be seen in cliffs along the Pasmore River. The clearly disconformable relationship between the Millyera Formation and Eurinilla Formation is seen in section 5 (Fig. 15). The disconformity is less obvious for its equivalent, the "unnamed conglomerate" of Lakes Tarkarooloo, Pinpa (?units 1 and 2 of section 8, Fig. 15), and elsewhere.

Relationship between Eurinilla and Coonarbine Formations can be easily observed (for example in sections 2, 3, 7 and 9, Fig. 15). The Coonarbine Formation can be frequently seen cutting into the Eurinilla Formation, and the two units usually have contrasting lithology. The soil carbonate at the top of the Eurinilla Formation may be completely eroded and reworked into the younger unit.

Rock relationships are summarized in Fig. 24.

AGE

The Millyera Formation has equivalents at the southern edge of Lake Callabonna, and northern end of Lake Frome. It closely resembles laminated green clays and sands bearing *Diprotodon* found in the main part of Lake Callabonna. The temporal range of *Diprotodon* is Pliocene to late Pleistocene. A wood radiocarbon age of >40 000 years B.P. (Daily 1960) from these beds has lately been confirmed by another wood radiocarbon date of >39 900 years B.P. (Tedford 1973). At the mouth of Poontana Creek, on the Lake Frome—Lake Callabonna confluence, dates from shells in sands equated with the Millyera Formation give ages of >33 400 years B.P. and 35 200 ±1 200 years B.P. (GaK–4949, GaK–4948). This shell material has been affected by younger pedogenesis, converting them to calcite (assuming the shells were originally all aragonite as are most non-marine molluscs). Therefore the dates are minimal, and the Millyera Formation has an age in excess of 34 200 years B.P., probably >40 000 years B.P. Similar shell beds in a similar stratigraphic sequence were recorded at Lake Eyre, and gave a date of 39 200 ± 1 300 years B.P (Johns & Ludbrook 1963).

The Eurinilla Formation contains late Pleistocene vertebrate fossils, somewhat different in generic composition to those at Lake Callabonna. The fauna occurs in channels at the base of the unit, along Billeroo Creek east of Lake Pinpa.

The overlying Coonarbine Formation is probably late Pleistocene or early Recent.

REGIONAL CORRELATION

Equivalents of Millyera Formation are little known at present, though the sequence described immediately above the Etadunna Formation in the Madigan Gulf region of Lake Eyre North is apparently very similar (King 1956, Ludbrook 1956, Johns & Ludbrook 1963). The lithological similarity between the fossiliferous greenish sands containing *Coxiella gilesi* in Madigan's Gulf, and those in the Millyera Formation of section 5 (Fig. 15) is marked. All these beds are close to or beyond the limits of radiocarbon dating, but the closely comparable micro-fauna (including *Elphidium* spp., *Ammonia beccarii*, *Nonion* sp: pers. comm. J. M. Lindsay 1974), charophytes and molluscs tend to support correlation. The Lake Eyre sequence rests on the Etadunna Formation, and is overlain by rocks resembling the Tirari Formation.

The Eurinilla Formation closely resembles the Tirari Formation of the Lake Eyre Basin, in lithology, stratigraphic position and topographic expression. Vertebrate faunas in basal Eurinilla Formation channels indicate equivalence with the youngest Katapiri Sand (Stirton *et al.* 1961) of the same basin.

Other possible equivalents are indicated in Table 4. The Pooraka Formation (Firman 1966a) supposedly rests on Telford Gravel (Firman 1963) on the west side of the Flinders Ranges, and is overlain by the Lake Torrens Formation (Williams & Polach 1971). The unnamed conglomerate equivalent of the Millyera Formation lithologically resembles the Telford Gravel at Telford open cut, Leigh Creek. The Eurinilla Formation, lithologically resembling the Lake Torrens Formation, overlies the Millyera Formation, and is in turn overlain by the Coonarbine Formation. The latter is similar to the Thomson Creek Formation of Williams & Polach. There also are similarities in the calcareous soil horizons of each, in the same geomorphic situation.

The Pooraka Formation, Telford Gravel and "unnamed conglomerate" of Lake Frome area are probably equivalents. It has been suggested by Firman (1971)[a] that the Telford Gravel is equivalent to the whole of the Tirari Formation (Eurinilla Formation correlative), but this cannot be the case in the Lake Frome area. The youngest *probable* equivalents here are the conglomerate at the base of the Eurinilla Formation, and the most *likely* correlative the "unnamed conglomerate" equivalent of the Millyera Formation.

The unit mapped as Pooraka Formation on COPLEY (Coats 1973) is Coonarbine Formation. During mapping COPLEY, Callen & Williams (in Coats 1973) recognized a unit of reddish brown sand and cobbles which covered most of the surface of the high level plains flanking the eastern Flinders Ranges. The unit was later named the Arrowie Formation by Coats (1973): subsequently mapping for FROME has shown it is probably partly equivalent to the Coonarbine Formation. The two units both contain land snail shells, and appear to grade laterally into one another at the break in slope at the base of low hills south of "Wertaloona." However, Coats seems to include some younger and older gravels in his definition, with ?disconformable relationships.

ENVIRONMENT

The Millyera Formation constitutes three facies groups: the most typical and widespread are the laminated ostracode clay and charophyte limestones (Fig. 18), with associated charophyte oogonia-bearing fine sand. Fine lamination, ostracodes, and distribution of sediment, indicate they are undoubtedly of lacustrine origin. The fine sands are well rounded and smooth and may therefore be aeolian, having been blown into the lake, or carried by floods. Drying of the lake is indicated by the charophyte limestone and equivalent gypsum lamellae (Figs 16, 18; cf. Reeves 1968, p. 57, 58). Similar modern calcareous algal deposits (Fig. 19), grading to rippled gypsum crusts, are present in Lake Kuturu". Waves acting on the very shallow water bodies break up the filaments and orient them in crescent like ripples, sometimes resembling the oriented structures in their fossil equivalents. The gypsum laminae may have botryoidal surfaces that are reminiscent of similar forms

TABLE 4 CORRELATION CHART – YOUNGER UNITS

TIME UNIT	LAKE FROME AREA: CALLEN & TEDFORD This paper		SUGGESTED EQUIVALENT - ADJACENT MAP SHEETS AND OTHER BASINS: FIRMAN, N. Western Flinders Ranges, Lake Eyre Basin	COATS et al., COPLEY 1:250 000 map sheet	WILLIAMS and POLACH, 1971, Western Flinders Ranges	STIRTON et al., 1961, Lake Eyre	TEDFORD (1973, pers. com.) Lake Callabonna
RECENT	Modern dunes Lake deposits Stream bedload	Mound spring deposits	SIMPSON SAND CALLABONNA CLAY	?— —?	THOMSON CREEK F. (upper part)		
PLEISTOCENE–RECENT	Fossil calcareous soil horizon		LOVEDAY SOIL	ARROWIE FORMATION	NACOONA PALEOSOL		
	COONARBINE FORMATION includes gypsum lunettes		POORAKA FORMATION	?—? POORAKA FORMATION	THOMSON CREEK FORMATION (lower part)		COONARBINE FORMATION Equivalent (Fossil bird-bearing unit)
PLEISTOCENE	Fossil calcareous soil horizon		LOVEDAY SOIL		MOTPENA PALEOSOL		
	GYPCRETE and CALCRETE of basal Eurinilla Formation (Stratigraphic significance uncertain)		?BAKARA SOIL	GYPCRETE AND BAKARA SOIL			
	EURINILLA FORMATION ? ? CALCRETE		POORAKA FORMATION BAKARA SOIL		LAKE TORRENS FORMATION WILKATANA PALEOSOL	TIRARI FORMATION and KATAPIRI SAND	
	UNNAMED CONGLOMERATE / MILLYERA FORMATION		TELFORD GRAVEL	TELFORD GRAVEL			MILLYERA FORMATION Equiv. (Diprotodon bearing unit)
LATE TERTIARY TO EARLY QUATERNARY	WILLAWORTINA FORMATION	?	—?— —?—	'T–Q' Unnamed conglomerates and clays		—?— —?— MAMPUWORDU SANDS —?— —?—	

74—421 R.A.Callen S.A. Department of Mines on the surface of modern Lake Frome, produced by crystallization pressure buckling the surficial crusts.

The second facies group is the channel facies (Fig. 17), of conglomerate/sand which exhibits features of meandering streams of large size containing bed-forms of slightly crescent-shaped aqueous dunes. The streams carried pebbles from the Olary Ranges, and eroded valleys into the Namba Formation. These deposits are lateral equivalents of the "unnamed conglomerate" which is so extensive along the Siccus—Pasmore River System.

The third facies group are the greenish fossiliferous sands, which (Section 5, Fig. 15) are cross-bedded on a small to medium scale, and contain shell beds and fish vertebrate. Similar shells are also abundant in a narrow zone along Billeroo Creek between Lakes Kuturu and Tarkarooloo. These deposits are interpreted as shoreline facies of the Pleistocene Lake Frome.

These sediments, and equivalents at the northern end of Lake Frome, contain the foraminiferal assemblage mentioned earlier (p. 147). Similar species were also recorded by Ludbrook (Ker 1966, p. 94) in equivalent strata in McKenzie Bore, 7.5 km south south-east of section 5. The presence of several species of foraminifera over a wide area in the same sediments can be explained in terms of Ludrook's (1965) hypothesis of transport to salt lakes on the feet of seabirds, with subsequent survival for a period. The species present are mostly Rotaliina with a wide salinity tolerance, and diversity is low. Such a situation is typical of inland saline lakes (Resig 1974), where foraminifera have been introduced by some dispersal mechanism from coastal areas. Species such as *Ammonia beccarii* are common in these environments. Although the assemblages found at Lake Eyre and Lake Frome are considerably different in content from those listed in Table 4 of Resig's paper (e.g. *Nonion* spp. are not recorded, though common at Lakes Frome and Eyre) this does not detract from the dispersal hypothesis because each locality cited in her paper has high endemism. The Coorong area contains a similar assemblage (pers. comm. J. M. Lindsay 1975), though its low diversity is probably the result of high salinity, even though it has a connection with the sea.

Another explanation is that there was a distant connection to the sea, implying a high sea level during the Pleistocene prior to 40 000 years B.P.

The detrital component of the lacustrine Millyera Formation sediments were brought to the ancestral Lake Frome by large braided streams with a pebble bed load ("unnamed conglomerate") approximately following the channels of present day watercourses such as the Pasmore-Siccus River system, and the Lake Tarkarooloo-Billeroo Creek system. They were much more extensive than their modern counterparts. The clasts indicate a provenance similar to the modern streams, in the Olary

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Figs 16-19. Younger Units. Structures in Millyera Formation.

Fig. 16. Millyera Formation. Laminated ripple-marked gypsum and clay (Fig. 15, section 5). Scale 30 cm.

Fig. 17. Plan view of cross-stratified channel sand in Millyera Formation channel facies, bed of Lake Tarkarooloo near Section 6, Fig. 15. Approximates Pi cross-stratification. Current direction (arrowed) is to north. Hammer handle 25 cm long. Laminae emphasized by inking.

Fig. 18. Algal tubules showing rough orientation. Same locality as Fig. 22. Scale in cm.

Fig. 19. Modern calcareous charophyte algal filaments, Lake Kuturu, showing crude orientation. Thin crust of gypsum (G) in upper central part of photograph.

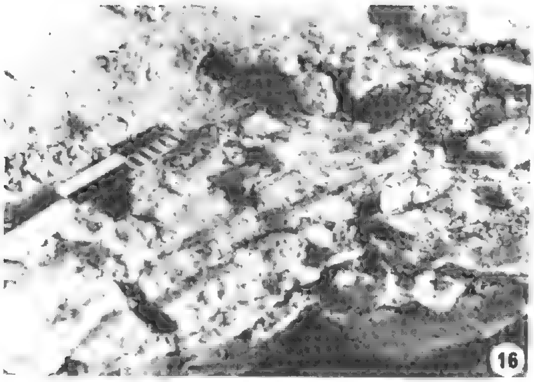
Figs 20-23. Outcrop.

Fig. 20. Upper part of section 7, Fig. 15, showing dune sand facies of Coonarbine Formation (two upper benches), basal laminated sand (bench just above contact), and upper part of Eurinilla Formation with calcareous paleosol (just below contact).

Fig. 21. Section 2, Fig. 15, Columnar-structured sand of Coonarbine Formation overlying Eurinilla Formation. Surface in foreground shows carbonate patches of paleosol, and represents the pre-Coonarbine Formation land surface slightly modified by present erosion. Scale 30 cm.

Fig. 22. Coonarbine Formation sand with columnar jointing, overlying Millyera Formation which in turn overlies Namba Formation. Millyera Formation shows upper algal limestones and lower massive sandy limestone (prominent benches) with intervening clayey sand. Lake Tarkarooloo, near Coombes Bore. Scale 30 cm.

Fig. 23. Section 9, Fig. 15 (lower part). Coonarbine Formation, disconformably overlying Eurinilla Formation which has its upper surface cemented with secondary gypsum (prominent bench). Black clay of Namba Formation at base (30 cm scale crosses contact).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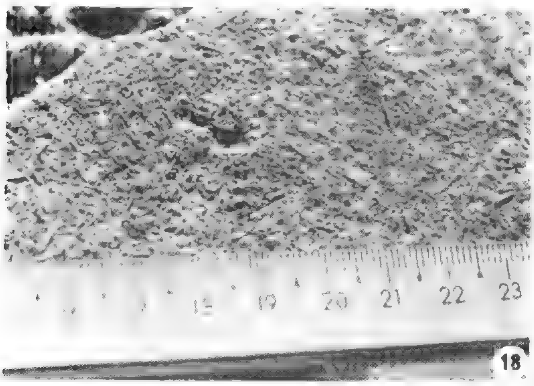
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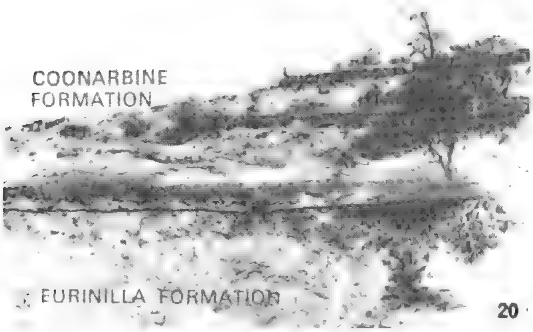
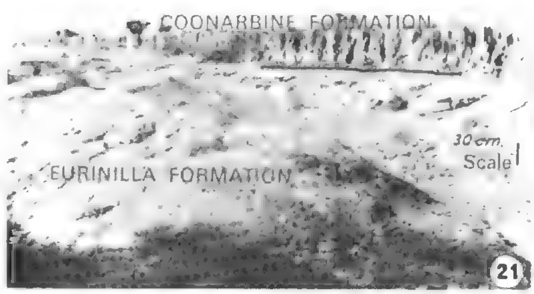
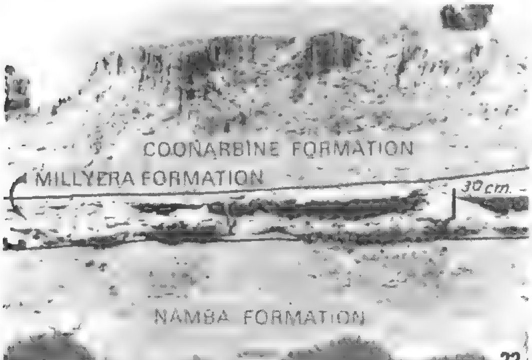

COONARBINE FORMATION
EURINILLA FORMATION
20


COONARBINE FORMATION
30 cm. Scale
EURINILLA FORMATION
21


COONARBINE FORMATION
MILLYERA FORMATION
30 cm.
NAMBA FORMATION
22


COONARBINE FORMATION,
EURINILLA FORMATION
23

Ranges and southern Flinders Ranges. Large straight-crested aqueous dunes typified the streams with coarse sandy and pebbly bed loads, whereas crescentic dunes characterized the streams with a finer sand-bed load. The eastern shore of Lake Frome was estimated to be about 10 km further east than at present.

The Eurinilla Formation contains channel deposits, exemplified by coarse sand with parting lineation and cross-bedding, in troughs and point bar deposits along Billeroo Creek. The meandering form of these channels can sometimes be seen on aerial photographs. The pebbles have sources in the Flinders Ranges or Olary Ranges, or have been eroded from the underlying Tertiary units. Flood-plain deposits are represented by the finer facies, which is sometimes laminated. The initially fluviatile phase (basal coarse grained sands) gave way to a more complex environment with finer fluviatile deposits and large scale cross-bedded aeolian deposits, including huge gypsum lunettes along the south western shore and on the islands. Some possible loess (massive silt and very fine sands) is present. These sediments transgressed over the older lake deposits of the Millyera Formation. The ancient Lake Frome therefore decreased in size in medial Pleistocene times, being somewhat smaller than at present.

The plains of this essentially fluviatile environment were inhabited by large marsupials (*Diprotodon* sp., *Procoptodon goliah*, *Sthenurus* sp. and *Macropus* sp.) Rivers followed approximately the same coarses as the present day drainage. The distribution of lunettes indicates a dominant wind direction from the west and a strong westerly component still characterizes this region.

The overlying Coonarbine Formation includes fluviatile braided stream environments west of Lake Frome, and dominantly aeolian east of the lake. The fluviatile sediments have less defined channels than the Eurinilla Formation, pebble sheets being more common. East of Lake Frome longitudinal dunes were developed, and another minor phase of gypsum lunettes built up along the lake shore. Land snails probably lived around water holes.

Conclusions

The new rock units in the Lake Frome area record a history of intermittent deposition through Miocene to late Pleistocene-Recent times. During this interval the extensive rivers, lakes and possibly estuarine environments of the Miocene Namba Formation drained areas of low relief in a climate of high rainfall, and of higher annual temperature than the same latitude today. At times, seasonal dry periods became a part of the weather pattern. A connection with the sea was established at some stage, probably to the Murray Basin. Some conflicting climatic evidence is partly resolved by applying the continental lessivage hypothesis (Millot 1964, as modified by Wiersma 1970) in relation to the smectite—dolomite—palygorskite mineral suite. Thus warm tem-

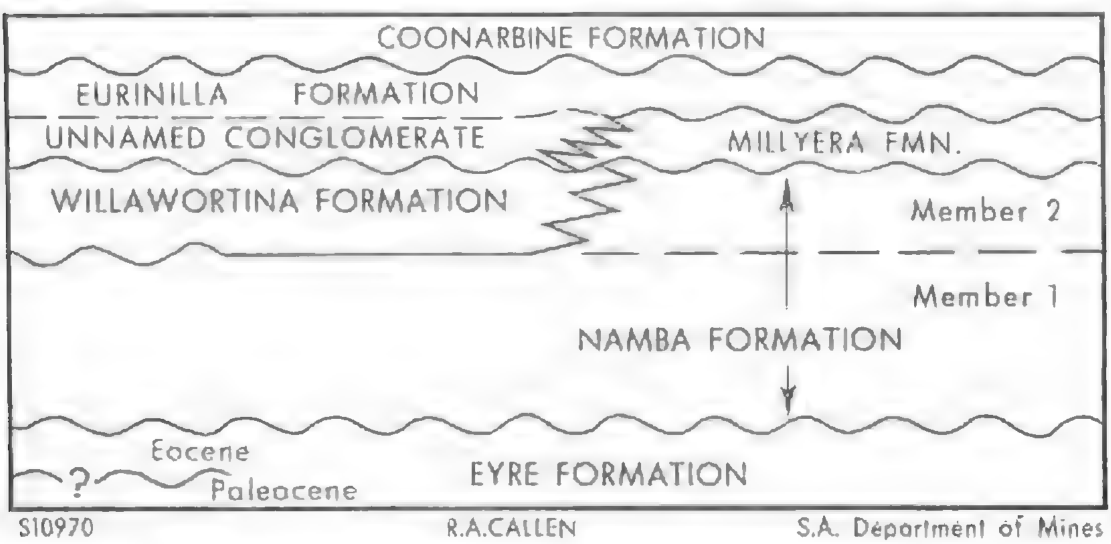


Fig. 24. Cainozoic rock stratigraphic relationships, Lake Frome.

perate to subtropical conditions prevailed, with savannah landscape, and gallery forests around the large permanent streams and lakes.

Uplift of the Flinders Ranges occurred at the earliest during late Miocene times, continued through the Pliocene intermittently into the Quaternary, and is still proceeding at present. Prior to this, at least during the Cainozoic, the Flinders Ranges were virtually non-existent. The sediments deposited during the Pliocene-early Pleistocene Epochs record the change from the earlier Miocene palaeogeography to the very different landscape approximating that of the present. Lakes and swamps during Tertiary times disappeared during the Pleistocene, as tectonism and climatic change altered the depositional regime. Drainage resembled that of the present during the late Pleistocene, indicating the basin was approaching its present configuration.

The Millyera Formation indicates active deposition on a playa lake somewhat larger than the present. The changing character of the sediments from Millyera to Coonarbine Formation suggests overall increasing aridity, probably seasonally distributed during Eurinilla Formation times, as exemplified by the formation of the gypsum lunettes. Marked climatic fluctuations were superposed on this overall climatic trend. Uplift of the ranges continued, alternating with periods of stability during which soils developed.

Rock relationships are summarized in Fig. 24.

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Appendix 1

OLDER CAINOZOIC UNITS

Fig. 3, sections 1, 10, 11, 12, Fig. 14, section 13

NAMBA FORMATION TYPE SECTION

SADM Yalkalpo No. 1 Stratigraphic Bore. Fig. 3 Section 12

COONARBINE FORMATION

2.00. SAND, medium grained, strong reddish brown (2.5YR4/6). Subrounded grains. Rectangular joint pattern and carbonate cylindroids in upper part.

— Disconformity —

NAMBA FORMATION

Unit 18. 3.40 — 1.40 CLAY, slightly silty, with scattered gypsum spots. Light grey (N.4) with moderate yellowish orange (10YR5/6) patches. Sharp upper contact.

Unit 17. 4.75 — 1.35. Interbedded SAND and CLAY overlain by SILT. Sand is very fine grained, laminated and small scale cross laminated, as are the silt beds at the top of the unit. Lower beds have structure destroyed by secondary gypsification. Contacts between sand and clay beds are sharp and flat. Sand-filled shrinkage cracks extend down from the wavy irregular upper contact.

Unit 16. 12.00 — 6.45. SILTY CLAY. Poorly sorted, diffusely laminated. Two silt beds with gradational to sharp contacts near the top, lower 1 m burrowed and bioturbated with wavy irregular upper bedding plane separating it from the remainder of the sequence. Irregular shiny fracture planes (crumbly texture) and gypsum nodules developed in upper part. Light to moderate olive grey (5Y4/2–5Y5/1, 5–5Y6/1). Mottled black and yellow (5Y4/0.5) in lower silt.

0.60. No recovery.

0.20. As before. Shrinkage cracks filled with sand extend down from upper unit—wavy irregular contact. Light olive grey (5Y5/2).

Unit 15. 12.20 — 0.20. SILT. Laminated, very fine cross-laminated, burrowed in part. Very pale yellowish grey (N1 to 5Y9/1). Upper contact sharp and flat, burrowed.

Unit 14. 15.20 — 3.00 SILTY CLAY. Intraformationally brecciated. Burrowed and bioturbated in lower half, upper half with angular clay clasts and slump structures. Upper contact sharp, flat.

Unit 13. 17.30 — 1.70. CLAY SILT and CLAY. Poorly sorted. Clay beds near centre. Burrowed at top, intraformational brecciation common. Pale to light olive clay (10Y6/2 to 6/4), silt pale grey to pale yellowish grey (5Y8/1 to N7). Upper contact sharp and flat.

0.40. SAND and SILT, interbedded, weakly laminated, wavy sharp contacts between interbeds. Sand is very fine, very angular (quartz crystal faces—overgrowths on rounded grains, contacts between overgrowth and grain visible).

Unit 12. 19.59 — 1.05. No recovery.

1.24. SAND, grading up to CLAY SILT and SILT. Sand has small-scale cross lamination with heavy mineral laminae.

Unit 11. 21.52 — 0.05. CLAY, black as below. Contact with overlying bed sharp and flat.

1.13. No recovery.

0.75. SAND, grading up to CLAYEY SILT. Sand very fine, wavy lamination. Colour 5Y6/4.

Unit 10. 26.82 — 0.20. SILT and CLAY, interlaminated, flame structures on contacts. Light olive grey (Clay 5Y6/1, Silt N9). Contact with unit 11 sharp and flat.

2.30. SILT, lower bed laminated and cross-bedded, with scattered burrows.

result of bioturbation and extensive burrowing. Upper contact wavy and irregular.

0.30. CLAY, laminated, colour NO, 4Y4/2. With CHELONIA scute at 24.21 m. Upper contact sharp, with flame structures.

1.40. SAND, fine grained in lower 1/5 grading up to laminated and burrowed light grey (N5) SILT. Sand grains smooth and shiny, angular, some well rounded and frosted, many with crystal faces and re-entrants. Upper contact wavy and irregular. Grading down to . . .
1.10. SILT, laminated and small scale cross-bedded, with scattered burrows.

Unit 9. 35.52 — 3.20. CLAY, black (N1) mottled light olive brown (5Y5/6), with sand patches and other features as before. Contact with sand lower in unit gradational. Large sand grains in the patches are polished, rounded to well rounded, smaller grains being angular to subangular with overgrowths(?). Some of the larger grains show rounded crystal forms.
0.35. No recovery.
3.60. SAND, as below. Calcite patches and very coarse mica common. Polymodal, poorly sorted overall. Small sizes angular, coarse are rounded, some doubly terminated crystals. Interbedded light grey (N7) clay in centre of unit. Becoming well sorted and fine grained at top with mixed well rounded and angular grains. Obscure small scale cross bedding and lamination.
0.60. No recovery.
0.95. SAND. Coarse to medium grained, slightly calcareous. Large grains polished, others with crystal faces (overgrowths?) which give stepped shiny surfaces. Many grains show original elongate quartz prism shape.

Unit. 8 36.22 — 0.70. Alternating SAND and CLAY. Sand very fine grained with small scale trough cross-lamination. Clay olive to medium grey (5Y5/0.5).

Unit 7. 39.22 — 0.30. Clay as below. Sharp wavy upper contact.
1.25. No recovery.
1.45. Alternating SAND-CLAY fining upwards sequences. Several thin beds, beginning with very fine grained sand at base. Sharp flat contacts, grading to black (N2, 5YR2/1) clay with orange brown specks and sand patches in top 20 cm.

Unit 6 40.79 — 0.94. SANDY SILT, grading up to CLAY. Black (N2) clay as for unit 5, with fine sand patches, 1/3 of sequence. Sharp wavy upper contact.
0.58. No recovery.
0.05. SILT with slump structures.

Unit 5. 47.44 — 6.55 SAND, SILT and CLAY alternating in lower 1/3, grading to CLAY at top. Lithology as for unit 4. Obscurely laminated in lower part, lenticular bedding. Light olive grey (5Y6/1) with oxidised brown patches (10YR6/6). Calcareous at transition (25 cm) to dark clay. Sand distributed in vertical streaks and patches through the dark olive clay (5Y5/1). Irregular wavy upper contact.

Unit 4. 50.84 — 3.30. SILT, grading up to CLAY. Lower 1/3 laminated silty and clay with very-small to small scale cross bedding at base, some burrows. Pale yellowish grey (5Y9/1) and pale olive (10Y6/2). Grades rapidly into sandy clay with vertically oriented structure and lime streaks, yellowish grey to pale olive (5Y7/2 to 9Y8/2). This grades to tough black (N1) clay with orange brown dendritic mottling and patches of fine sand. A thin brown band of iron oxides is present. Upper contact wavy, irregular.

Unit. 3. 52.04 — 1.20. SAND, grading to CALCAREOUS CLAY. Lower 40 cm very fine grained, loosely cemented by quartz overgrowths (original grains rounded) calcareous at base. Heavy minerals 1%. Dusky yellow (5Y4/1). Clay is olive grey (5Y4/1) and has white vertically oriented streaks and sheets of carbonate. Contact with overlying unit is sharp and wavy.

Unit 2. 56.60 — 1.94. No recovery.
0.22. SAND, very fine grained as for base unit. Contact with underlying clay irregular, with mixing.
1.10. CLAY, as for base unit 1, silty top, with moderate yellow green clay patches which become dull on exposure (7GY4/1, 5Y5/2, 5Y4/2). Obscure lamination.
1.00. No recovery.
0.20. SAND, very fine grained, scattered medium, polished grains. Opaques common. Some patches moderate yellow green clay (7GY4/1–5Y4/2).

Unit 1. — 1.20. CLAY, waxy lustre on curved irregular fractures. Rare angular white carbonate lumps and streaks. Olive grey (5Y5/2).

NAMBA FORMATION

Supplementary Section Outcrop, West Side Lake Tarkarooloo, Section 13, Fig. 14

Section 13A, north of the northern track crossing Lake Tarkarooloo.

COONARBINE FORMATION

0.10 SAND. Very calcareous, with numerous 1-5 cm dolomite nodules and ferruginous sandstone lumps (reworked from Namba Formation), 5YR8/6.

— Disconformity —

EURINILLA FORMATION

2.30. CLAY-SILT-SAND. Silt (dominant) to fine grained sand, poorly sorted. Lower 10 cm moderately sorted medium grained sand. Up to 50% reworked dolomite nodules (pisolitic) of granule to pebble size in lower part, 7½ x 5 cm maximum size, and little evidence for abrasion. Upper 10–70 cm with gypsum nodules and carbonate patches. Green-black ferruginous and manganiferous stain, otherwise light red-brown 2.5YR5/6.

— Disconformity —

NAMBA FORMATION

3.85. CLAY, GYPSUM. Slightly silty clay, very hard, light weight, crumbly with greasy lustre. Colour

5Y5/2 to 5/1, mottled red-brown, yellow brown and black, specked with white gypsum flour. 80 cm horizon of cauliflowercoid gypsum nodules 1.10 m from top. Nodules 0.25–0.50 cm diam. with clay cores, not associated with any porosity change in host sediment.

1.25. DOLOMITE, CLAY. Lower dolomite 0.60 m clay 0.50 m upper dolomite 0.15 m. Lower dolomite nodular (intraformational conglomerate) at top, manganese dendrites throughout. White, very fine grained, with 5% angular silt. Upper dolomite contains ostracodes. Clay as above.

1.95. CLAY. 5% angular silt to very fine sand, grading to sand at base and dolomite at top. Very hard, light, dry and crumbly, with manganese stain.

1.45. SILT. Silt and very fine sand, becoming clayey at top. Bioturbated at top, 2–3 cm burrows, otherwise finely laminated. Minor bright green clay laminae. Top 40 cm impregnated with gypsum, mottled orange brown. Very light grey to white overall. Lower contact sharp, flat.

1.70. CLAY-SILT, DOLOMITE. Clay with 40% silt, 5–10% very fine sand. Arenaceous fraction of moderately sorted, angular grains. Colour 5Y6/1, orange to orange-brown mottling. Nodules and patches of greenish-white very fine grained sandy dolomite, weathering as 2 cm granules at top and bottom. Black stained.

0.78. Alternating SAND and CLAY. Sand beds range from silt to very fine sand, colour 5Y8/2. Clay is sandy. Individual beds 2–27 cm. Lower beds have sharper contacts and are laminated, very finely cross-bedded and lensing. Orange brown mottling and gypsum in upper part of section. Minor nodular dolomite.

0.80. SILTY CLAY. Silt to very fine sand 10–20% subangular frosted grains. Clay has greasy lustre and 5Y6/2 colour. Upper contact very sharp, flat.

1.00. SAND and DOLOMITE. Sandy clay and clayey sand with dolomite nodules 2–30 cm thick at top and bottom. Sand is subangular to subrounded, moderately well sorted, with frosted grains. Weathers to hard light brown sandstone, base cemented with gypsum. Sandy clay is 5Y5/2, clayey sand 5Y7/3, mottled with yellow green patches, and black patches at base (N1–N5). Very sandy parts are 10YR6/2–5YR5/2 at base.

Dolomite is very fine grained with botryoidal upper surface, in way, lensing beds. Greenish upper surfaces.

0.30. SAND. As above.

0.33. CLAY. Mottled clay and very fine sand, finely laminated beds which are irregular and lenticular, and have yellow green (10YR6/6) clay patches and, cross-cutting brown (10YR8/6) patches with black centres. Sand (5Y7/2). Basal 2 cm fine white sand. Gradational upper contact. Contains dark brown to yellow-orange irregular silcrete and ironstone nodules.

0.02-0.03. CLAY. As above. Sharp contacts.

0.23. SAND. Very fine, yellow green clay lamellae. Obscure medium cross bedding, straight foresets. Stained greenish black. Sharp upper contacts.

0.25. CLAY. As higher in the sequence. Upper 5-10 cm dolomitic, yellow-green and brown mottled.

0.10. SAND. As above. Obscurely cross-bedded, selenite cement at base.

1.30. CLAY. Silty. Very finely laminated, with very small scale cross-bed sets. Colour 5Y6/0.5, occasional black and brown patches. Upper contact sharp, flat.

0.70. CLAY. Slightly silty, hard, with sub-conchoidal fracture and greasy lustre. Selenite on contact with overlying unit. Slight greenish brown tint, otherwise N4.

Section 13B, south of the northern track, crossing Lake Tarkarooloo (200 m south of section 13A). Constructed from a series of breakaway slopes, and a scoured channel in the centre of the lake. Beginning from the top of the black clay, as at the base of the previous section, the sequence is as follows (from gully sequence):

3.5. CLAY. Dark grey clay with irregular shiny surfaced fractures, becoming lighter coloured towards base. Crops out poorly, forming low angle vegetated slopes. Upper contact sharp, flat. Lower contact moderately sharp to disturbed.

2.1. SAND. Very fine to fine grained, black stained. Thin 5 cm beds and fine laminate. Brown silcrete nodules throughout. Thin horizon of DOLOMITE nodules at top. About 20 cm above the base are 10 cm of laminated silty limestone with low amplitude symmetrical ripples, mud cracks, and 1–3 mm long tubules of organic origin. Sharp basal contact with . . .

0.25. CLAY. As at top of sequence (13B).

On a small noll isolated near the edge of the lake, the sequence continues as follows, with some overlap:

0.55. DOLOMITE. Sandy nodular white dolomite. Impregnated with gypsum and calcite, plus tabular black manganese concretions.

0.95 SAND. Fine grained, well sorted, laminated and silty at base. Cemented by gypsum and calcite in part. Numerous carbonate nodules exhibiting concentric structure. Some have vertical tubular disposition with an internal structure suggestive of shrinkage (c.f. silcrete nodules). Black and brown stain at base, with orange brown and yellow green patch stain. This, and the previous unit are equivalent to the 2.1 m of sand described above, with its bed of dolomite nodules.

2.5. CLAYEY SILT. Alternating hard clay and clayey silt in very fine lamellae (varve-like). Silty grey clay lenses. Yellow green patches with waxy lustre. Clay dominant at base. N5, 10Y5/4 to 6/6. Contact with underlying unit sharp, undulating: same contact as at base of 2.1 m sand described in gully section above.

0.5. CLAY. Hard, greasy lustre, irregular fracture. N3 at top grading down to 5Y4/1.

This clay crops out across the bed of the lake to its centre, where a scour next to a salt spring exhibits a further 2.5 m of massive hard grey clay.

NAMBA FORMATION *SUPPLEMENTARY SECTION*
SADM Wooltana 1 Stratigraphic Bore. Section 11, Fig. 3

?EURINILLA FORMATION

0.0 to 5.2 m No core

5.2 0.9 COBBLE CONGLOMERATE. Cemented with red-brown carbonate. Mica schist, gneiss, quartzite. Sandy (medium grained), with subrounded to well rounded, grains.

— ?Disconformity —

WILLAWORTINA FORMATION AND NAMBA FORMATION (intertonguing)

Unit 6

6.1 1.1 DOLOMITE. Sandy, clayey at base. 5YR6/4 to N6. Sharp upper contact, gradational lower contact.

7.2 3.8 CLAY. Slightly sandy, with dolomite nodules. Clay 7Y7/2 with red-brown vertical pipe structure. Sand subangular to subrounded. Some gypsum patches in lower part. Lower contact gradational. 50 cm core missing.

11.0 0.65 SAND. Fine sand, very poorly sorted, subangular to subrounded. Thin dolomite beds. Dolomite nodules. Clay at base.

11.65 to 12.50 No core

12.50 16.15 CLAY grading to SAND at base. Numerous dolomite nodules and some beds. Extremely poorly sorted medium sand to coarse silt. Some gypsum patches at top. Green and red-brown pipe structure. Sand subangular to well rounded. Sharp basal contact. 40 cm core missing in sand interval.

28.65 4.35 CLAY grading to SAND at base. As above. Mica in basal sand. 2.5YR/4–6, 5Y6/1 mottles. Sharp wavy basal contact.

33.00 5.6 CLAY, and DOLOMITE grading to SAND at base. As above, but dolomite beds in upper clayey part. Dolomite is 20% clay. Medium silt, extremely poorly-sorted. Sand subangular to rounded. Gradational wavy lower contact.

38.6 4.45 CLAY, grading to SAND at base. As above. Dolomite beds (brown) and nodules throughout. Sand patches at top. Lower contact gradational.

43.05 4.95 CLAY grading to DOLOMITE then SAND at base. As above. Mottled red-brown, green and yellow grey. Very poorly sorted. Minor core loss. Lower contact gradational.

48.00 5.15 SANDY CLAY grading to SAND at base. As above. Dolomite beds and nodules throughout. Sand laminated, micaceous. Intraformational clay and carbonate at base. Sand reaches medium grain size. Subangular to rounded. Disturbed irregular basal contact.

53.15 14.50 CLAY cf. NAMBA FORMATION. Patchy sand and carbonate near top, Reticulate network of carbonate "veins". Lower part with limonite nodules, irregular shiny black-stained fractured clay. Obscurely laminated in middle part. Sand very fine, angular to subrounded. 5Y6/1, 2.5YR6/2–8, 10YR8/2, 2.5YR5/6, 5Y7/1.5, 5Y6/1, 5Y5/5. 2–3 m core missing, mainly in upper part.

67.65 6.7 SANDY CLAY. Micaceous finely laminated silt becoming pebbly at 72 m, reverting to clay at base. Extremely poorly sorted. Granite, quartzite, shale, quartz and gneiss pebbles. Very angular to subrounded. Clay intraformationally brecciated and burrowed in lower part. Minor carbonate, c.f. WILLAWORTINA FORMATION. Gradational lower contact.

NAMBA FORMATION

Unit 5

74.35 4.9 Alternating DOLOMITE and CLAY Dolomite (5–10 cm thick), oolitic white, aphanitic, with charophytes, ostracodes, molluscs and unidentified calcareous ?plant fossils. Numerous burrows in clay beds (all about 1 m thick). Micaceous silt in part. Bioturbated. Laminated at base. Sharp basal contact.

79.25 7.9 CLAY, minor DOLOMITE. Upper part similar to above, laminated and burrowed. Clay 6Y6/1+2.5YR4/6, becoming sandy at base, with rounded clay clasts. Basal contact gradational.

87.15 1.75 SANDY CLAY. Calcareous. 5Y5/1 to 5Y6/1. Sharp basal contact.

88.90 0.10 CLAY. Sharp contacts.

89.00 2.00 Interbedded DOLOMITE and CLAY. Dolomite as above. Very finely interlaminated with brittle, swelling clay. Shrinkage cracks common. Burrowed. Contacts on carbonate beds sharp and wavy to disturbed irregular. 7Y571, 5Y6/1, N3.5, 5Y4/2.

91.0 2.55 MARL and GYPSUM. Alternating thin selenite and calcareous clay. Sharp contacts on gypsum. Gradational lower contact. Black to dark olive.

93.55 4.60 CLAY grading to DOLOMITE and MARL at base. Numerous gypsum nodules, 4Y5/1, 5Y8/2. Mottled 5YR6/7. Minor gypsum laminae. Contacts wavy gradational to disturbed irregular. Intraformational brecciated.

98.15 3.55 CALCAREOUS CLAY. Irregular shiny fractures, oxidized red-brown patches. Swelling, very porous. Subaqueous shrinkage cracks.

101.7 9.15 CLAY. Sandy in centre, with selenite veins infilling slickensided joints. Sand laminated. Clay with irregular shiny surfaced fractures as above. 10–15% very fine sand to silt. Alternating colour pattern—oxidized red-brown clay passes down to 3Y4/2 to 6Y7/1 clay, has sharp upper surfaces. Basal contact irregular, disturbed.

110.85 7.1 CLAY. As above. Basal thin white dolomite. Churned structure suggests bioturbation.

118.00 7.45 CLAY grading to SILT in lower half. Silt well laminated, micaceous, very small scale cross-laminated. Grains very angular to sub-rounded Silt moderately sorted. Lower contact moderately sharp.

125.45 4.55 Alternating SAND, CLAY. Sand very fine, micaceous, small scale cross bedded, laminated. Lower contact moderately sharp.

129.00 1.80 As above. Lower contact irregular, wavy.

130.80 9.00 SAND, interbedded CLAY. Sand fine to medium, well sorted, small to medium scale cross-bedded. Micaceous and with clay balls. Grains very angular to subrounded. Sharp wavy contacts.

138.00 2.60 SAND. As above. Upward fining. Some clay at top, burrowed. Poorly sorted, average very fine grained. Wavy moderately sharp lower contact.

140.60 6.70 Alternating SAND, SILT, CLAY, CARBONATE. Sand as above. Carbonate nodular. Clay dark grey. Bioturbated and intraformationally brecciated. Mainly fining upward sequences. Sand dominant. Contacts irregular, disturbed.

Unit 3

147.30 26.10 CLAY grading to SAND in lower 1.5 m. Manganese nodules above sand. Minor sand bed at 157 m. Clay N5, numerous irregular shiny fractures. Sandy, averaging very fine silt, very poorly sorted. Sand and very fine silt, very poorly sorted. Sand very fine, burrowed and laminated. Very angular to angular grains. Irregularly disturbed lower contact.

163.40 1.80 SILT. 5Y6.5/0.25, orange brown mottles, obscure lamination, bioturbated. Sharp wavy lower contact. Grades to very fine sand at base.

165.20 3.4 SAND. Fining upwards from fine sand to clay. Thin clay bed with sharp contacts near top. Medium scale cross-bedded. 6Y6/1 to 5Y7/2. Sand poorly sorted. Moderately sharp wavy lower contact.

166.80 4.00 CLAY grading to SAND at base. Upper 1 m sandy, lower very fine obscurely laminated sand. Clay with irregular fractures, 5Y4/1. Sand beds have gradational contacts.

170.80 4.50 AS ABOVE. Minor sand at 172.2 m. Basal very fine sand, moderately sorted, obscurely small scale cross laminated, burrowed. Gypsum nodules. Clay as above with fractures and orange to red-brown mottles. Sand very angular to angular.

175.30 7.4 Silt. Laminated fine, very poorly sorted silt, gypsum nodules at top. very small scale cross-bedded, some burrows. 3 m missing in central part. Sharp wavy lower contact.

182.7 4.6 SANDY CLAY, grading to SAND at base. Cycle as above. Some calcareous zones, 5Y5/1, 5Y3/4. Sandy at 185 m. Basal sand fine grained, sub-rounded. Moderately sorted. Lower contact moderately sharp.

187.3 8.8 SANDY CLAY, SAND at base. Upper 3/4:N2 to 5GY7/0.5 clay as above with fractures and sandy patches. Dolomite nodules at contact with sand. Sand very fine to fine, very poorly sorted, 5Y6/1 to N8. Burrowed near top sand, rest bioturbated, obscurely cross-stratified.

196.10 0.9 SILT. Minor alternating clay and sand, sharp contacts. Silt laminated. Lower contact sharp and wavy.

Unit 2

197.0 14.0 Alternating DOLOMITE, CLAY, SILT and SAND. Complex inter-relationship between clay-dolomite cycles and sand and clay beds c.f. above. Contacts variable. Dolomite intraformationally brecciated. Silt laminated. Bioturbated and burrowed horizons. Clays with irregular fractures and orange mottles. Beds 40 cm–1·5 m thick.

211.0 16.3 Alternating LIMESTONE, DOLOMITE and CLAY. Consists of 1–2 m carbonate beds grading up to clay via disturbed zone. Clay beds burrowed or bioturbated, 10Y5/2 to 10YR7/2. Base of dolomite beds sharp and wavy. Dolomite aphanitic, white laminated, with oolitic zone. Ostracodes common, algal mats present. Zone 215–217 m of very narrow clay filled cracks. Irregular shiny fractures dominate in clay near base, otherwise absent. At top of this sequence is 5 cm goethite-limonite crust.

227.3 8.7 CLAY. Calcareous, intraformationally brecciated with numerous white carbonate specks. Irregular shiny surfaced fractures. N1 to olive green. Quartz rare, very fine to fine, angular. Lower contact gradational.

236.0 8.45 CLAY. Fissile pyritic carbonaceous very finely laminated clay with silt parting. Fine laminae of N1 to dark olive or 5Y2/1 colour. Numerous plant stem and leaf impressions or fruiting bodies, fish spines and scales, ostracodes (often in pure layers), gastropod protoconchs, spores and pollen. Burrows (pyrite filled) and bedding plane traces. Numerous pyrite-marcasite nodules. Some subaqueous shrinkage cracks.

WILLAWORTINA FORMATION *TYPE SECTION*

Western Nuclear WC2 Bore. Section 10, Fig. 3

?COONARBINE FORMATION and ?EURINILLA FORMATION

0.00 to 7.05 Cuttings only. SANDY PEBBLES, SAND. Micaceous, calcareous, impregnated with gypsum (except sand). Angular to very angular, 2.5YR4/8, 2.5YR3/6.

— Disconformity —

WILLAWORTINA FORMATION—MEMBER 3

7.45 0.44 No recovery.

7.89 1.65 SAND as below, 1–3% muscovite.

9.54 0.30 No recovery.

9.84 3.95 SAND grading to SILT. Sand very poorly sorted and very fine grained, silt coarse, pebbly and micaceous. Thin pebble bed grading up to sand at base. Porous zones impregnated with gypsum.

13.79 0.25 No recovery.

14.04 1.21 PEBBLY CLAY SILT, poorly sorted, with basal pebble bed, impregnated with gypsum.

15.25 1.50 No recovery.

16.75 0.24 PEBBLES, subrounded to rounded. Coarse feldspathic gneiss, fine biotite quartz feldspar gneiss, purple stained coarse feldspar.

16.99 0.68 No recovery.

17.67 0.13 SAND, pebbly, coarse grained. Feldspars, muscovite, biotite

17.80 1.98 No recovery—a few abraded pebbles.

19.95 0.24 SAND, fine grained and micaceous.

20.19 0.22 No recovery.

20.41 0.38 GRANULES grading up to PEBBLES.

20.79 1.45 No recovery.

22.24 0.28 GRANULES to SAND, medium grained. Larger grains subrounded. Mica 5%, pink potash feldspar 15–20%.

22.52 0.64 No recovery.

23.16 0.33 CLAYEY SAND, very fine grained and micaceous, sharp wavy content with overlying 20 cm of COBBLES. 5–10% muscovite, pink potash feldspar. Yellowish grey (5Y7/2).

24.4 1.49 No recovery.

24.98 0.11 SAND, grading up to GRANULES. Sand medium grained with dull, pitted or shiny surfaced, angular to subangular grains. 15–20% feldspar (mostly pink potash variety). Muscovite and biotite flakes in the quartz.

25.09 0.80 No recovery.

25.89 0.20 SAND, pebbly, micaceous and overall fine grained.

26.09 0.72 No recovery.

26.81 0.14 COBBLES, sandy.

26.95 0.47 No recovery.

27.42 0.17 Pebbly micaceous coarse sand.

27.59 1.00 No recovery.

28.59 0.27 SAND, grading over short interval to COBBLES at top. Sand is poorly sorted and micaceous, medium grained.

28.86 1.61 No recovery.

30.47 0.27 COBBLES, passing over short interval to medium micaceous SAND.

30.74 0.72 No recovery.

31.46 0.53 SAND, grading to COBBLES in upper half. Sand micaceous and poorly sorted, medium grained. Clasts pink quartzite with micaceous hematite, purple fine quartzite, vein quartz, large potash feldspar pebbles.

31.99 1.00 No recovery.

32.99 0.26 SANDY PEBBLES, micaceous.

33.20 0.58 No recovery.

33.78 0.30 SAND, coarse and poorly sorted, micaceous.

34.08 0.30 No recovery.

34.40 0.39 PEBBLY SAND, very poorly sorted, micaceous, coarse grained. Dusky yellowish grey (5Y6/2).

34.79 0.57 No recovery.

35.36 0.24 CLAY, sandy, micaceous.

35.60 0.62 No recovery.

36.22 0.13 PEBBLY SAND, fine grained, moderate reddish brown (2.5YR5/6 to 4/6).

36.35 2.00 No recovery.

38.35 0.30 COBBLES and PEBBLES overlain by fine grained CLAYEY SAND.

38.65 0.20 No recovery.

38.85 0.56 GRANULE bed, thin, overlain by thick SANDY COBBLY PEBBLE bed (white vein quartz, pink potash feldspar, pink ferruginous quartzite, coarse siliceous gneiss or granite, dark grey shale, weathered fine gneiss).

39.41 0.77 No recovery.

40.18 0.20 SAND as before, with clayey sandy cobble bed at top.

40.38 0.71 No recovery.

41.09 2.46 SAND, coarse at base, grading up to extremely poorly sorted fine sand. Vertically oriented reddish brown pipes.

43.55 0.29 No recovery.

43.84 0.53 PEBBLY SAND, sand medium grained.

44.37 0.23 No recovery.

44.65 2.77 Fine SAND as before, grading up to pebbly medium grained sand in upper 1/3.

47.42 0.18 No recovery.

47.60 1.47 SAND, poorly sorted and very fine grained, micaceous, with scattered granules, two thin pebble beds at base.

49.07 0.63 No recovery.

49.70 0.35 PEBBLES, passing over short interval to SAND, clayey, micaceous and fine grained, poorly sorted.

50.05 1.64 No recovery.

51.69 0.34 CLAYEY SAND, coarse and very poorly sorted, grading to boulders. Metaquartzite clasts.

52.03 1.23 No recovery.

53.26 0.29 SAND, micaceous and very fine, light yellow-brown (7YR5/6). Very poorly sorted.

53.55 1.25 No recovery.

54.80 0.50 SAND, very micaceous, very fine grained. Pebble bed in centre (granite, banded pink and white quartzite).

55.30 0.58 No recovery.

55.80 0.63 SAND, fine, grading up to fine grained with scattered granules.

56.43 0.30 No recovery.

56.73 0.44 SAND, as above. Feldspathic quartzite pebbles.

57.17 0.48 No recovery.

57.65 0.40 SAND, as above, pebble-cobble bed in centre.

58.05 0.49 No recovery.

58.54 0.84 CLAY, and pebbly SAND, coarse grained. Grades rapidly to micaceous CLAYEY SAND, fine grained, in upper 30 cm.

59.38 0.69 No recovery.

60.07 0.56 SAND, as below, fining to fine grain size at top.

MEMBER 2

60.63 0.66 No recovery.

61.29 0.54 SAND, as below, no granules.

61.83 1.43 No recovery.

63.26 0.99 SAND, slightly clayey, medium grained, with granules. Coarsening upwards.

64.25 1.50 No recovery.

65.75 0.23 COBBLES: massive pink granite, very fine dark quartzite, pink feldspar with ?hornblende.

65.98 1.30 No recovery.

67.28 0.10 SAND, medium micaceous and clayey.

67.38 0.19 No recovery.

67.57 0.34 GRANULES, grading to CLAY-SILT.

67.91 0.84 CLAYEY SAND, coarse, pebble interbeds.

68.75 0.05 No recovery.

68.80 0.47 SAND, coarse and poorly sorted, pebbly. Pebbles of quartz and gneiss.

69.27 0.14 No recovery.

69.41 0.41 SANDY CLAY, as before grading up to COBBLY SAND.

69.82 0.12 No recovery.

69.94 0.18 SANDY CLAY, as before. Micaceous.

70.12 0.25 No recovery.

70.95 0.85 Silty clay grading up to cobbles.

71.82 0.33 No recovery.

72.15 0.27 SAND, medium, grading up to CLAY.

72.42 0.13 No recovery.

72.55 4.07 SILT, extremely poorly sorted, medium size.

76.62 0.11 No recovery.

76.73 1.40 SAND, very fine, pebbly, grading to SANDY SILT CLAY.

78.13 0.95 No recovery.

79.08 0.85 GRANULES (lower 20 cm) grading up over short interval to SAND, clayey, medium grained, very poorly sorted.

79.93 0.17 No recovery.

80.10 1.68 SAND, very fine, grading to very coarse at top. 1% muscovite and biotite, 10–15% potash feldspar. Grains very angular to subangular and dull. Small grains shiny and faceted. Extremely poor sorting.

81.78 0.15 No recovery.

81.93 0.25 SAND, fine grained, very poorly sorted.

82.18 0.16 No recovery.

82.34 0.85 GRANULES, basal bed, grading over short interval to very poorly sorted CLAY, very sandy.

MEMBER 1

83.18 0.06 No recovery.

83.24 0.76 CLAY, lower 10 cm sharp contact with SAND, coarse grained to granule sized. CLAY thin bed at top. Extremely poorly sorted.

84.00 0.37 No recovery.

84.10 0.10 SAND, fine grained, clayey.

84.47 1.37 No recovery.

85.84 1.50 SILTY CLAY. Very poorly sorted, with thin coarse sand beds.

87.34 2.03 No recovery.

89.37 5.74 SILT, SILTY CLAY. Extremely poorly sorted coarse silt, silty clay micaceous. Thin coarse grained sand bed (91.2 m), above which the sediment coarsens from clay to very fine grained sand.

95.11 0.45 No recovery.
95.56 1.81 SAND, grading to CLAY at top. Sand very coarse, clay silty and micaceous with a thin granule bed near the top. Yellowish grey (5Y8/1).
97.37 0.26 No recovery.
97.63 3.79 SANDY CLAY, SAND. Sandy clay has medium grained sand fraction, very poorly sorted, grades to clayey coarse sand, with very angular to subangular pitted to shiny grains. Feldspar is common. The base of this interval is taken as the base of the WILLAWORTINA FORMATION.
101.42 1.08 No recovery.

—?Disconformity—

NAMBA FORMATION

102.50 2.30 CLAY. 15–20% subangular to subrounded sand, minor mica. Sand patchy near base, with irregular shiny-surfaced fractures (skew-planes). 5Y6.5/2 to 4Y5/1. Basal contact sharp. 30 cm core missing near base.
104.80 1.10 CLAY. As above. 10% sand, no mica, nodular and swelling with well developed fractures. Alunite mottles at base, 20 cm core missing in centre of interval. 1Y4/1, to 6YR6/1 at base. Sharp basal contact.
105.90 4.90 CLAY, grading to SILT in basal 60 cm. Intraformationally brecciated and burrowed (at 109 m) with some laminated intervals. Well developed alunite streaks, which decrease in abundance with depth, being absent at the base. 6YR6/1–6/2 grading to N8 at base. 70 cm core missing at various intervals, mainly near top. Basal contact irregular, disturbed.
110.80 10.50 CLAY grading to SILT at 144.4 m and SAND at 119.4 m. Clay intraformationally brecciated, 15–25% very angular to subrounded sand. Silt micaceous. Sand micaceous, cross bedded in 30 cm sets, and laminated, fine grained, well sorted. Grains angular to subrounded. Basal contact gradational. Weak alunite horizon 50 cm below top of unit, absent at 115 m. Colour 5YR5/1 above alunite, N8 below. 2.1 m core missing in silt and sand beds. Wavy indistinct lower contact.
121.20 0.70 SILT.
121.90 1.45 SAND. Micaceous, laminated, obscurely cross-bedded. Fine grained and moderately well sorted. Sharp lower contact. 70 cm core missing in centre of unit.
123.35 3.10 SAND. Minor clay at top, fine grained micaceous sand in centre, lower half grading to very coarse sand at base. Subangular to subrounded, large grains highly polished composites. Mostly no core, there being 50 cm recovered. Basal contact sharp.
126.45 9.45 SILT and CLAY (below 129 m). Clay, nodular, dark brown, silt greenish white. Sandy patches. Sand grains often show crystal faces—bipyramids. Indistinct contacts observed at 129.25, 129.4, 129.6 associated with weak alunite horizon. Colour 10YR6/2–5Y8/1 in this zone. Below 131.80 irregular shiny surfaced fractures and some alunite specks. Colour 5Y5/1–4, 5Y3/1. 17% silt. Grains very angular to angular. Much core missing throughout. recovery 40%.

WILLAWORTINA FORMATION *SUPPLEMENTARY OUTCROP SECTION*

"Wertaloona" Homestead Area. Section 1, Fig. 3

WILLAWORTINA FORMATION

Unit 9. 37.9 COBBLES. Brown quartzite cobbles in a matrix as for unit 6. Basal bed of almost 100% grey-blue limestone cobbles. Rare red sandstone, quartz and yellow-brown silicified carbonate cobbles in float. Exposure poor, top not exposed.
Unit 8. 37.9 49.2 SANDY CLAY, red brown.
Unit 7. 87.1 20.8 COBBLE to BOULDER beds. Matrix as for unit 6, cemented with secondary white carbonate which may be powdery and soft, or hard vughy and crystalline. Cobbles of brown quartzite with 20% blue-grey limestone (resembling Cambrian limestones). Rare very large boulders of grey massive microcrystalline quartzitic silcrete with large milky quartz pebbles.
Unit 6. 107.0 13.0 (approx.) CLAY SAND. Red brown very poorly sorted and calcareous.
Unit 5. 2.0 (approx.) COBBLES. Brown quartzite cobbles scattered through matrix as for unit 4. Lenses out along strike.
Unit 4. 7.0 (approx.) CLAYEY SILT SAND. As for unit 2.
Unit 3. 1.0 (approx.) PEBBLY COBBLES. As for unit 1. more matrix, thin and lensing along strike.
Unit 2. 5.5 (approx.) CLAYEY SILT SAND. Red brown, with a calcareous matrix, sometimes thinly laminated.
Unit 1. 140.1 4.0 (approx.) COBBLES. Brown quartzite pebbles and cobbles in calcareous red-brown silty sand, lenses of calcareous medium sand at base. The sandstone fills channels, which have groove casts on the base. Cementation is weak, and pebbles weather out readily with thin calcareous crusts. Proportion of matrix low. The unit cuts into deep red brown clayey silt, probably Namba Formation. Although the contact here is sharp, there may be an intertonguing relationship along strike. The unit grades laterally to the south into pebbly clayey sandstone.

The following part of the section is poorly exposed, and is yet to be fully described:

—Disconformity—

?NAMBA FORMATION

12.0 SAND. Very fine greenish sand grading up into silty grey-green clay with gypsum patches.

7.2 CALCAREOUS SANDSTONE. Very angular sand with soft crystalline carbonate cement. Contains pebbles of very angular sandstone, carbonate, rounded brown quartzite, polished milky quartz, chert granules.
51.2 CLAY. Dark green-grey clay with greenish-yellow-stained patches, slightly sandy. Thin white nodular dolomicrite is present near the base, and may be a facies variant of the previously described unit.
8.2 SAND. Reddish to greenish silty fine to medium sand.
8.2 CALCAREOUS SANDSTONE. Essentially a sandy limestone with about equal quantities of medium grained angular sand and lime. Weathers grey, with a sculptured rough surface.
144.7 CLAY. Grey green to olive, greasy irregular fracture, sandy and silty. Minor dark olive to grey clay. Mottled with red-brown iron oxides. The interval 430–350 m (measured from top of the unit 9 in the Willawortina Formation section) is very poorly exposed and deeply weathered.
Near the top of these beds in the northern part of the area, is a thin white dolomicrite bed.

— Disconformity —

?EYRE FORMATION
2.0 SANDSTONE. Massive calcareous medium grained sandstone, partly silicified, and capped by remnant silcrete, dipping with the section.
2.0 CONGLOMERATE. Granule to pebble-sized polished white quartz, grey chert, ironstone. Pebble to cobble-sized angular Middle Cambrian sandstone. All in medium well-rounded sand matrix, cemented by calcium carbonate. Pebbles are patchily distributed, and the whole crops out as a low ridge with cavernous weathering and of brownish grey colour. Medium scale cross-bedding is prominent. The unit has an angular unconformable relationship with the underlying Middle Cambrian red-beds, though dips are similar.

Appendix II

YOUNGER CAINOZOIC UNITS
FIG. 15 SECTIONS 2–9
(See Fig. 1 for locations, and main text for access and photo points)
SUPPLEMENTARY SECTION, COONARBINE FORMATION
SECTION 2

COONARBINE FORMATION
1.7 SANDY SILT, with basal pebble bed. Sand dark brown (5YR3/5). Size varies from silt to very fine sand, moderately poorly sorted. No bedding planes visible. Columnar structure well developed. Basal clasts may be small cobble size, and are of metamorphic rocks and quartz.

— Disconformity —

EURINILLA FORMATION
2.2–2.5 CLAYEY SILT-SAND. Very poorly sorted, with irregular-shaped frosted or pitted grains. Contains pebble lenses (though not in the figured section) and large irregular aphanitic greenish white sandy carbonate lumps. The latter are probably derived from the upper carbonate in Wooltana 1 bore (section 11, Fig. 3). At top of 0.5–1 cm diameter branching vertically oriented cylindroids of pinkish "chalky" textured carbonate, representing a fossil soil horizon.

— Disconformity —

0.2 CALCAREOUS SAND. Pebbly sand (coarse grained), solidly cemented by pinkish buff (5YR7/2) carbonate. Colour derived mainly from orange-stained quartz grains. Laminated and thin bedded. Beds dip, suggesting cross-bedding is present (outcrops seen in plan only, in creek bed).
Possibly represents Willawortina Formation, or unnamed conglomerate equivalents of Millyera Formation.

SUPPLEMENTARY SECTION, COONARBINE FORMATION, EURINILLA FORMATION
SECTION 3

Location, Curnamona *Sìecus* map sheet. Air photo ref.: S. Aust. Dept. Lands Svy. 361, run 2, photo no. 4442. The section is situated on the northwestern bank of the Pasmore River, close to the point where it debouches in to Lake Frome.
RECENT
0.00–1.20 Mobile bright red-brown dune sand, sharp erosional contact with underlying units.

— Disconformity —

COONARBINE FORMATION
1.00–3.50 SAND. Yellow-brown, with large scale dune-type cross-bedding. Sharp erosional basal contact. A lag of pebbles (eroded from the Eurinilla Formation) is at the base.
Numerous broken mature snail shells are present in the upper part of the unit. Aboriginal artifacts, calcified tree roots, emu shell, and vertebrate bones occur in the uppermost level (or possibly on the upper surface in the case of the artifacts and emu shells).
Strongly developed columnar structure is present (resulting from soil processes).

— Disconformity —

EURINILLA FORMATION
1.80 PEBBLY CLAY-SILT and SAND. Sand at base, medium-grained, yellow brown, numerous pebbles and rare flat cobbles, cemented by gypsum. Pebbles are milky and clear quartz, and very angular fragments of calcite-cemented conglomerate, overlain by bright red-brown silty clay

Unnamed Conglomerate (?Millyera Formation equivalent)

0.15 CONGLOMERATE. Thin, calcite cemented. Pebbles weather out without adhering crust. Pebbles as for overlying unit plus ?Namba Formation dolomicrite, and brown carbonate nodules from Willawortina Formation. Carbonate penetrates into top of underlying bed.

— Disconformity —

WILLAWORTINA FORMATION

2.05 SILTY CLAY. Sandy, greenish-brown with red-brown mottles, hard. Patches of gypsum nodules. Partly calcified at top. Blocky columnar structure visible (resulting from soil processes). Upper contact sharp, undulating.

MILLYERA FORMATION TYPE SECTION
SECTION 4

0.30 SAND. Reworked from older unit into base of dunes.

0.70 SAND. Coarse grained, with many gypsum grains and anomalous pebble sized angular quartz (milky). Powdery hummocky gypsum often developed at top (soil profile).

— Disconformity —

EURINILLA FORMATION

1.10 CLAYEY SAND. Very fine-grained, sub-rounded to rounded, good sphericity, moderate sorting. Numerous charophyte oogonia. Many greenish, yellow and brown grains, Colour 5YR5/6. Capped by gypsum crust, of gypsum nodules in clayey sand (groundwater deposit).

— Disconformity —

MILLYERA FORMATION

Unit 7. 0.50 CLAY. Soft, conchoidal fracture. Contact with overlying Eurinilla Formation sharp and flat. Very dark yellowish brown. The oxidized crumbly appearance and shiny surfaces (cutans) on crumbs suggest soil processes have operated, and indicate a disconformity between Millyera and Eurinilla Formations.

Unit 6. 0.40 SAND. Very fine to medium grained. Grains subangular to rounded and frosted. Charophyte oogonia .5%. Grades by alternation, to . . .

Unit 5. 0.50 CLAYEY SAND. Sand fraction well-sorted, with subangular to angular rounded grains, sharp flat upper contact. Greenish yellow (10Y7/2).

Unit 4. 0.70 CLAYEY SAND. Interbedded thin clay and very fine to fine clayey sand 0.25–0.50 mm thick. The sand is very well sorted, with subrounded to rounded high sphericity frosted grains. Darker oxidized clay present. Yellowish grey (5Y7/2). Lower contact gradational.

Unit 3. 0.30 CLAY as for unit 1.

Unit 2. 0.40 LIMESTONE and CLAY. Near the top of the sequence each clay lamina grades up to charophyte stem-mould limestone (up to 1 cm thick). These limestone beds harden on weathering, producing sheets and slabs with a metallic ring when struck. Intervening lamellae are 0.5–2 cm thick. Some of the Charales tubules are oriented and small turreted gastropods aff. "*coxiella*" are present (henceforth referred to as "*Coxiella*"). An oxidized zone exists beneath the limestone. The limestones form a distinctive marker horizon 20–30 cm thick. Contact with unit 1 and unit 3 are gradational by alternation.

Unit 1. 0.10 CLAY, brittle, soft, waxy lustre. Distinctly laminated and thin bedded (1–5 cm), each lamina grades up to a thin fine silt layer with charophyte oogonia and Ostracoda. White carbonate granules occur near the base of the sequence. Scattered medium polished or frosted quartz grains, sometimes up to 40% of the rock, occasionally forming sand lenses. Yellowish grey (5Y6/2—clay, lighter for sand). Base not exposed.

SUPPLEMENTARY SECTION, COONARBINE FORMATION, EURINILLA FORMATION, MILLYERA FORMATION
SECTION 5

0.00–3.50 SAND. Red brown sand of modern dunes reworked from Coonarbine Formation.

COONARBINE FORMATION

1.00 SAND. Light brown. Numerous vertically oriented small cylindroids of soft white carbonate, of soil profile. Emu shell, aboriginal artifacts and rare mature snail shells occur in uppermost level. Forms longitudinal dunes.

— Disconformity —

EURINILLA FORMATION

Unit 2. 4.00 SAND, fine to medium grained, with subangular rough or pitted grains, poorly sorted. Stratification absent. Grades to unit 1 over short distance. Light brown (5YR4/7).

Unit 1 4.00 SAND, medium grained, brown (5YR6/6), lighter coloured beds alternate near base. Cross-bedded, sets 40 cm, lensing, gently curved coarse and fine laminae, sharp eroded upper contacts, assymptotic bottomsets. Laminae 0.5–1 cm, by variation in clay content. Sets are gently inclined toward Lake Millyera. Numerous charophyte oogonia.

Lightly cemented with clear or white finely crystalline carbonate. Pinkish irregular nodules, weathering as brown lumps and slabs on surface. Carbonate gives white cast to this part of the section, and causes slight benching. Partly cemented with massive gypsum in the basal layers.

— Disconformity —

MILLYERA FORMATION

Unit 5. 1.60–2.50 CLAY. Very hard, shiny irregular fractures, coated with black iron oxide and white carbonate at top (soil horizon). Impregnated with vertically oriented gypsum masses, in 5–10 cm columns (fossil groundwater horizon) at top. No silt content. Colour 10Y6/2. Similar to Willawortina Formation. Upper contact sharp, flat. Grades down to light green soft clay interbedded with very fine grained white sand rich in charophyte oogonia. Intertongues with unit 4.

Unit 4. 4.00–5.00 SAND. Silt to very fine grained sand, with coarse lenses. Numerous thin 0.5–5 cm clay beds and lamellae near top, which are crowded with algal tubules (charophytes). Some rare massive charophyte crusts consisting entirely of strap-like algal forms with numerous large oogonia. Charophyte oogonia common in upper sands. Clay pellet layers common. Sand grains are subrounded to well-rounded smooth or frosted, with moderate sorting. Small scale cross-laminated sets, 10 cm thick, with curved laminae.
Upper surface may be cemented with gypsum of a fossil groundwater horizon.

Unit 3. 0.00–0.93 SAND. Very fine grained, well sorted. Colour 5YR6/8. Impregnated with massive gypsum and disc-shaped crystals of gypsum. Grades by alternation of 1–4 cm thick beds into overlying unit, in which it forms a lense. Contacts between lamellae are wavy, lenticular, and rippled in some cases. Resembles Tirari Formation. Basal angular quartz granule layer, often resting directly on underlying gypsum sediment.

Unit 2. 0.25 LIMESTONE-GYPSUM. Greenish slightly sandy clay with 20 cm of interbedded thin (0.5 cm) gypsum laminae at top, which grades laterally into laminated algal stem (tubules of charophytes) limestone. The limestone and gypsum contain charophyte oogonia. The gypsum contains scattered very coarse sand grains, and surfaces are assymetrically ripple-marked, or have botryoidal "puff" structure.

Unit 1. 0.70 SAND. As for unit 4. Orange and yellow stained, especially near base, greenish where unoxidized. Reworked distorted clay fragments from underlying units at base.

— Disconformity —

NAMBA FORMATION

3.28 SILTY CLAY, grey to black, tough. Grading down to grey, clayey, poorly sorted fine sand. Greasy lustre on iregular fracture surfaces. Gypsum patches and cracks at top infilled with overlying sand.

SUPPLEMENTARY SECTION, MILLYERA FORMATION

SECTION 6

EURINILLA FORMATION

At least 2.0 bright red brown SANDS.

— Disconformity —

MILLYERA FORMATION

Unit 7. 0.20 CALCAREOUS SANDSTONE. Very fine to medium grained moderately sorted sand, 30% carbonate. Grains pitted or frosted, subrounded to rounded, alternates with very fine sand. Coarser sand contains charophyte tubules and rare oogonia. Some pink and black sand grains, rare carbonate grains. Weathered colour white (N10), unweathered greyish yellow (5Y8/4).
Elsewhere passes to hard platy limestone identical with 2. Impregnated with numerous white gypsum cylindroids. Gradational contact with 6.

Unit 6. 0.62 SAND. As for sand in 3 but uncemented, distinct contact with 5. Colour moderate reddish yellow (2Y7/4).

Unit 5. 1.20 CLAYEY SAND. Moderately sorted, with black and orange grains scattered throughout. Irregularly cemented into very hard massive nodules and sheets by fine grained white to pink carbonate. Yellow and brown mottling common near base, white gypsum and carbonate spots throughout. Yellowish grey (5Y6/2).

Unit 4. 0.25 SAND, SILTY CLAY. Grades from clay to very fine sand, grains poorly rounded. Colour yellowish (5Y7/2) oxidized to moderate brown (5YR6/7) in patches.

Unit 3. 0.5 LIMESTONE, CALCAREOUS CLAY. Varies laterally from burrowed soft calcareous clay, with 30% silt to fine sand, to hard sandy white limestone. The former has 1–2 mm diameter vertical burrows (insects?) and the latter has scattered charophyte oogonia and shrinkage cracks. The base of the burrowed horizon is gradational, and lumps of the underlying unit are worked into it.

Unit 2. 0.10–0.20 LIMESTONE. Laminated, platy, hard, metallic ring when struck. Constitutes numerous tubules of charophytes, and patches of "Coxiella". Contact with 4 not observed, contact with 1 distinct, undulating.

Unit 1. 0.50. On east side of channel, SAND, very fine grained, nodular white carbonate at lower contact. Pale grey. Massive carbonate-cemented at top with shrinkage phenomena apparently related to drying of carbonate.
On west side of channel. CLAYEY SAND. Moderate to well sorted, angular grains. Yellowish grey (5Y6/1) but speckled yellowish green. Grades up into unit 3.

NAMBA FORMATION

0.10 Black tough clay. Sharp flat upper contact.

EURINILLA FORMATION AND COONARBINE FORMATION TYPE SECTIONS; MILLYERA FORMATION SUPPLEMENTARY SECTION

SECTION 7

Modern dune sands

— Disconformity —

COONARBINE FORMATION

Unit 4. 0.70 SAND, very fine to medium grained, silty. Fine size dominant, well sorted, well rounded, frosted. Light brown (5YR5/6). At top is 20 cm of soft white carbonate, consisting of 0.5 cm cylindroids and tubules (plant roots?) with 1–2 cm lumps at the top, grading to blotchy white carbonate as for unit 2.

Unit 3. 1.62 SAND, bimodal, medium-coarse and very fine to fine. Bimodality disappears downward, grain size becomes finer, and sorting poorer. Some patches of white sand are present in the essentially moderate yellowish orange (9YR5/6) coloured sequence. Top is moderate reddish brown (3YR5/6). Large scale cross-bedding is just visible. A well developed fossil carbonate-rich soil horizon marks the top. It is 50 cm thick and consists of moderately hard rather irregular nodules and cylindroids, and gypsum cylindroids.

Unit 2. 1.80. SAND, fine-grained ranging to coarse, grades down to CLAY-SILT. Moderately poor sorting. No signs of stratification. Colour light brown to reddish yellow (6YR5/6–3YR5/6). Weakly developed whitish carbonate patches at top (soil horizon).

Unit 1. 1.00 SAND. Bimodal, on medium-coarse grained and very-fine grained boundaries. Dark red brown (2YR4.5/6). Indistinctly horizontally laminated, upper contact sharp and flat, lower contact obscure, apparently gradational.

— Disconformity —

EURINILLA FORMATION

Unit 3 3.50 SAND, as above. Solour light brown (7YR6/4). Constitutes a single cross-bed set. Contact with unit 1, sharp, inclined, flat. Irregular gypsum as for unit 1 at base. Upper 10–20 impregnated with carbonate (10YR7/3) of a fossil soil horizon.

Unit 2. 4.00 SAND, friable, fine to medium grained, bimodal. Coarse fraction well rounded, dominant, colour light brown (6YR5.5/6). Constitutes a single cross-bed set, with low angle cross-bedding. Contact with underlying unit sharp, undulating, cuts well down into unit 1. Patches of very irregular tubules, nodules and cylindroids of gypsum occur at the top.

Unit 1. 0.88 SAND. Medium grained, sub-rounded to well-rounded grains with very fine grained angular proportion (bimodal). Numerous coloured grains, opaques and biotite present. Silty brown clay with gypsum forms pebble sized clasts, and clasts of underlying limy sandstone are present. Cross bed sets planar, 8–10 cm. Charophyte oogonia very common, and fragmental vertebrate bones present. White colour. Lower contact erosional.

— Disconformity —

MILLYERA FORMATION

1.1 LIMY SANDSTONE. Very fine to medium grained moderately sorted clear-grained quartz sand with 30–40% finely crystalline soft carbonate cement. Sand grains pitted or shiny, angular to sub-rounded. Some grains of feldspar and ferruginous sandstone, flakes of hematite. Thin section shows carbonate has recrystallized into radiating spherules, resembling some groundwater carbonates.

2.8 SAND, SILT. Silt to fine sand, 1–5% clay-carbonate matrix, forms strong cement by reason of poor sorting of framework grains. Very poorly sorted with sub-rounded to very angular grains. Hard and red-white mottled.

SUPPLEMENTARY SECTION, EURINILLA FORMATION

SECTION 8

Locality: CURNAMONA, *Eurinilla* map sheets. Air photo ref.: S. Aust. Dept. Lands Svy. 361, run 3; photo no. 4396. The section is situated on the west side of Lake Pinpa, approximately 50 m north of the only track crossing the lake.

Modern sand dunes

0.0–4.0 SAND. Fine to medium grained, moderately sorted. 5YR5/8. Strongly erosional base.

— Disconformity —

?COONARBINE FORMATION

0.50 SAND. Very fine to medium (averaging fine grained), poorly sorted, with sub-angular to sub-rounded polished or frosted grains (4YR5/8). Erosional basal contact.

This unit may represent the Coonarbine Formation. It forms the basis of the longitudinal dunes.

— Disconformity —

0.25 SAND. Very fine to fine, rather poorly sorted, clayey. Grains irregular, subangular, rough. Colour 5YR5/7. Soft patchy carbonate well developed, with pipe like structure 5 cm diameter. This is a soil horizon, and has a similar development to those of the Eurinilla Formation. The lithology is also similar but there is a distinct contact at the base which appeared slightly erosional. The unit may be part of the EURINILLA FORMATION.

— Disconformity? —

EURINILLA FORMATION

Unit 3. 1.00 SAND. Clayey, very fine to fine, poorly sorted. Angular to sub-rounded frosted and coarsely pitted sand grains. Colour 3YR5/8. Well developed secondary carbonate profiles constituting soft sandy pinkish white lime in lumps and cylindroids 1–5 cm across which weather out. In lower part of sequence fractured lumps 10–20 cm are common. The carbonate profiles form numerous layers, concentrated toward the top of the unit, and represent soil development (hence intermittent deposition is indicated).

Unit 2. 5.33 SAND. Poorly sorted silty, slightly clayey fine grained, rounded (2.5YR4/8). Grades imperceptibly into overlying unit.

UNNAMED CONGLOMERATE (?MILLYERA FORMATION equivalent)

Unit 1. 0.8 Interbedded CONGLOMERATE, SAND and CLAY. Consists of basal sand loosely cemented with calcium carbonate, cross-bedded on medium scale. Micaceous. At the base of this sand bed are granule size quartz (grey, clear, dark grey, yellow), pebble size clasts of grey clay and subrounded calcareous orange-brown clay. Also large grains of brown perthite feldspar. Maximum grain size is 1.5 x 2 cm.

Overlying this is an uncemented medium to coarse sand layer, which is capped by coarsely crystalline gypsum nodules and plates, weathering to a powdery crust.
The gypsum is followed by coarse grained to medium grained moderately sorted sand as below, with scattered very coarse grains. Grains are dull and subrounded to rounded.
The uppermost calcareous sand (5YR8/4) alternates with thin SILTY CLAY (10YR6/2) with irregular patches of 5YR6/2 coarse grained very poorly sorted clayey sand. All contact are distinct and flat. Apparently grades into overlying unit over short distance and by intertonguing—no disconformity observed.

—Disconformity—

NAMBA FORMATION

Unit 8. 0.40 SAND. Very fine grained. Yellowish white.
Unit 7. 3.85 CLAY. Puggy, soft, with powdery gypsum stringers at top. N5.
Unit 6. 0.85 CLAYEY SILT. Colour 5Y6/1 with 10Y6/2 patches.
Unit 5. 2.23 CLAY. Hard, greasy, Colour 5Y6/1 (silty) to 5Y4/1 becoming 5Y6/0.5 at base. Contact with 4 gradational.
Unit 4. 0.20 SILTY CLAY. Finely laminated, dark and bright orange brown siliceous limonite nodules, dense masses of manganese oxide. Bright yellow green patches in clay. Basal contact sharp, undulating, indicates an hiatus. Rare vertebrates.
Unit 3. 0.22 CLAY. Dark olive (5Y4/1) greasy. Sharp basal contact. Numerous vertebrates as for unit 2.
Unit 2. 0.12 DOLOMITIC CLAYSTONE. Pale green (5Y8/2) with black patches. Subconchoidal fracture, hard. Sharp contact with overlying units. Numerous vertebrates include lungfish, crocodiles, turtles and marsupials.
Unit 1. 0.18 CLAY. Light green.

In addition to this sequence, an erosional remnant of Coonarbine Formation is superposed on the top of the Namba Formation-Eurinilla Formation disconformity. The description is:
1.18 SAND. Yellow brown (7YR6/7) with prominent columnar jointing (15 cm rectangules) typical of Coonarbine Formation. Fragments of Eurinilla Formation carbonate nodules occur at the base.
Also along the lake shore is reworked material from all the above units, forming outwash and aeolian mounds of sub-Recent origin. This material is slightly older than the red brown dunes.

SUPPLEMENTARY SECTION, EURINILLA FORMATION

SECTION 9

Location: FROME, Coonarbine map sheets. Air photo ref.: S. Aust. Dept. Lands Svy. 395, Run 4, Photo no. 9597. The section is situated on a cliff on the western edge of a small claypan on Eurinilla Creek.

RECENT SAND DUNES

0.0–2.2 SAND. Very fine to fine grained, well sorted, with subrounded grains. Large scale dune cross-bedding.

— Disconformity —

COONARBINE FORMATION

1.7–3.5 SAND. Clayey, up to medium grained, mostly fine grained, grains subrounded. Moderately sorted. Weak thin horizontal bedding at base. Spotted with white carbonate patches, tending to 0.5 cm diameter cylindroids near base (weakly developed soil profile). Colour 6YR5/7.

— Disconformity —

EURINILLA FORMATION

3.05 CLAYEY SILT. No sedimentary structure. Oxidized dark orange brown (5YR4/7)—original colour (new patches) pale orange (10YR8/2). Gypsum beds several centimetres thick occur in lower part, as for cap of 95 cm of massive disc shaped (0.5 cm) gypsum rosettes in red brown silt and white gypsum flour.

— Disconformity —

NAMBA FORMATION

1.8 CLAYEY SILT. Very soft, 5Y5/0.5 with 5YR4.5/4 patches.

A NEW GENUS OF LATE PRECAMBRIAN POLYCHAETE WORMS FROM SOUTH AUSTRALIA

BY *M. F. GLAESSNER**

Summary

GLAESSNER, M. F. (1976).-A new genus of Late Precambrian polychaete worms from South Australia. *Trans.* R. *Soc. S. Aust.* **100**(3), 169-170, 31 August 1976.
New material indicates differences between *Spriggina floundersi* Glaessner and *S.? ovata* Glaessner & Wade which are comparable with those between genera of living polychaete annelids. Accordingly, a new genus *Marywadea* is proposed for *ovata.* The evolutionary significance of the Sprigginidae is discussed briefly.

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Introduction

The representatives of the Family Sprigginidae Glaessner (1958) are among the most remarkable elements of the Ediacara fauna from the Pound Quartzite of South Australia. The Late Precambrian age, stratigraphic position and geographic distribution of this rock unit and its fauna need no further discussion (Wade 1970; Glaessner 1971, 1972). The arthropod-like appearance of *Spriggina* is attracting increasing attention (Cisne 1975, p. 61; Stanley 1976, p. 58). The reconstruction of an ancestral crustacean by Hessler & Newman (1975) shows startling resemblances with *Spriggina*. Notwithstanding these, no convincing evidence has been discovered which would justify the transfer of the Sprigginidae from Annelida to Arthropoda or prove a transitional position of this family between two phyla. New discoveries have, however, clarified and emphasized the differences between the type speies *S. floundersi* and the species described *S.? ovata* described by Glaessner & Wade (1966). Its diagnostic characters have at least the same significance as those distinguishing genera of living Polychaeta and for this reason the following new genus is proposed. It differs from *Spriggina* in all characters listed in the diagnosis.

Taxonomy

Genus **Marywadea** nov.

Type species: Spriggina? ovata Glaessner & Wade 1966.

Fig. 1. *Marywadea ovata* (Glaessner & Wade). Latex mould of specimen from the Late Precambrian Pound Quartzite of Ediacara, S. Aust. x 2. (Outlines and surface slightly distorted during fossilization; anterior margin of the head pushed back causing truncation of the outline and wrinkling of the surface; some ventral structures may be obscurely visible. Note that all other specimens have smoothly curved anterior outline and smooth surface.)

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Diagnosis: Prostomium half-moon-shaped, not wider than the body with its appendages. Integument thin, wrinkled and possibly showing some underlying structures when compressed. Body consisting of up to 50 short, broad segments, occasionally with impressions of bundles of long, curved setae. A pair of oval impressions behind the prostomium suggests the presence of teeth. The posterior end of the body is broadly rounded.

Derivation of generic name: After Dr Mary Wade who earlier expressed the view that *ovata* may be generically distinct from *floundersi;* this has now been confirmed by new finds.

Localities: Ediacara Hills, Brachina Gorge, Bunyeroo Gorge, Mayo Gorge.

Number of specimens of *M. ovata:* 16.

Remarks

The Sprigginidae are not arthropods as the head did not consist of the appropriate number of appendage-bearing segments and the trunk appendages are not distinctly jointed and end in acicular setae. The mouth was probably not directed posteriorly, there was no labrum and there is no evidence of antennae or a caudal furca. On the other hand the head was conspicuous and relatively larger than in any known annelid and its integument was more strongly sclerotized in *Spriggina* (apparently less so in *Marywadea*). There is evidence of a simple pharynx in *Spriggina* and of two simple teeth in *Marywadea,* suggesting relations to Phyllodocemorpha; otherwise the Sprigginidae are unlike living Annelida. Some evolutionary advance in the direction of a primitive arthropod is indicated, particularly in cephalization. It may be parallel to the unknown evolutionary lineage which had produced the two primitive arthropods known from the Ediacara fauna (*Praecambridium* and *Parvancorina*).

Acknowledgments

The specimen illustrated here was found by Mr D. Westlake in August 1975 at Ediacara. I am grateful to Mr J. Gehling, Murray Park College of Advanced Education, who presented to me casts and moulds of this and other specimens.

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THE VERTEBRATE FAUNA OF NUYTS ARCHIPELAGO, SOUTH AUSTRALIA

BY A. C. ROBINSON* AND M. E. B. SMYTH†

Summary

ROBINSON, A. C. & SMYTH, M. E. B. (1976).-The Vertebrate Fauna of Nuyts Archipelago, South Australia. *Trans.* R. *Soc.* S. *Aust.* **100**(4), 171-176, 30 November, 1976.
The St Francis group of islands in Nuyts Archipelago was visited by a joint Royal Society of South Australia and Fisheries Department of South Australia expedition in January, 1971. Seven species of mammals, twenty-seven species of birds and sixteen species of reptiles are recorded, together with comments on their habitat and abundance. The potential of the islands for fauna conservation is briefly considered.

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Introduction

The study of the fauna of islands can provide useful insights into the biogeography of the fauna on the adjacent mainland. Many islands along the southern coast of Australia were connected to the mainland when sea level fell during the Pleistocene glaciations, and samples of the coastal flora and fauna were preserved on these islands as the sea level rose during the interglacial periods (Main 1961). With the accumulation of information on the flora and fauna of these islands and the adjacent mainland, including the palaeofaunas and floras, it may eventually be possible to reconstruct the biological history of southern Australia from the Pleistocene to the present. Further, as information is assembled on the present habitat preferences and tolerances of mainland species, data on island faunas may assist the construction of a palaeoclimatic history for southern Australia. Another important aspect of islands is their suitability for conservation. Many of the islands around southern Australia preserve relict populations of species that are rare or extinct on the mainland. Studies such as this should therefore contribute to the management of these islands as fauna sanctuaries maintaining these important populations.

This paper discusses the species of mammals, birds and reptiles recorded from the St Francis Island group of Nuyts Archipelago during the joint Royal Society of South Australia and Fisheries Department of South Australia expedition there in January, 1971, together with some additional information gathered by subsequent visitors to the islands.

The expedition visited four islands: St Francis, Masillon, Fenelon and Dog. Mammal trapping was carried out on St Francis I. (4 nights), Dog I. (1 night) and Masillon I. (1 night). Since then trapping has been carried out on Egg I. (D. Murray, pers. comm.). Data were obtained from animals caught in traps or observed by spotlight, from collection of bones and from signs of mammal activity. Sherman and wire cage traps were used in trap lines for a total of 153 trap nights (St Francis I. 105, Dog I. 19, Masillon I. 19, Egg I. 10). Traplines and spotlight surveys covered all vegetation associations on the islands and gave a wide coverage of the areas. Specimens have been lodged in the South Australian Museum (SAM); registration numbers are cited.

The bird list is based on the observations of all members of the expedition and compiled by Mr P. Macrow. The records generally represent sight records, but where doubt existed as to the identity of a species, a specimen was shot for a positive identification.

The reptile list is primarily from collections made on St Francis I. Only part of a day was spent looking for reptiles on Dog, Masillon and Fenelon Is.

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MAMMALS

Mammals previously recorded from St Francis I. include the bandicoot *Isoodon obesulus nauticus* and a rat kangaroo, presumed to be a species of *Bettongia*, which had become extinct by the 1920s (Wood-Jones 1924; Verco 1935). Three terrestrial and two marine species are now added, and these are marked by an asterisk in the list which follows. In addition, skulls collected on the island enabled identification of the species of *Bettongia*.

Family PERAMELIDAE

Isoodon obesulus (Shaw). SAM, M8546-M8549. *Short-nosed bandicoot*. St Francis I.

A common animal preferring the grassy areas on the higher parts of the island but also occurring in the saltbush steppe association covering the remainder of the island. These bandicoots have survived the introduction of cats and the conversion of a large part of the island to grassland by cultivation. *I. obesulus* remains common in south-eastern and south-western Australia and there are populations on Kangaroo I. (Andrewartha & Barker 1969) and Franklin I. (Watts 1974).

Family MACROPODIDAE

Bettongia penicillata (Gray). SAM, M8353. *Brush-tailed bettong*. St Francis I.

Fragments of skulls were found in the sandhills behind Petrel Cove, but living animals were not observed. Bettongs were reported to be very common when St Francis Island was first settled. Wood-Jones (1924) and Verco (1935) reported that the settlers introduced cats to the island to exterminate the bettongs which were causing damage to vegetable gardens. It seems likely that alteration of habitat may have also played a part in their decline, as this species nests in dense cover such as that formerly provided by the sclerophyll shrub community on the higher parts of the island. The settlers completely destroyed this habitat through clearance for wheat growing. *B. penicillata* was formerly widespread throughout the southern half of Australia but now appears to be confined to southwest Western Australia.

***Macropus eugenii** (Desmarest). SAM, M8575. *Tammar wallaby*. St Francis I.

A single tooth row of this species was found in the sandhills behind Petrel Cove. No living animals were found. The settlers did not report tammars on the island and it is possible that they were either already extinct, that the individual collected was introduced at some time, or that it was left by sealers known to have collected large numbers of wallabies on other islands (N. Wace pers. comm.). They were formerly widespread on the south and south-west Australian mainland and populations were recorded from Kangaroo I., Flinders I., St Peters I., and a number of Western Australian islands. Today, in South Australia, tammars remain common only on Kangaroo I. and on Greenly I. where they were introduced (Mitchell & Behrndt 1949); the St Peters I. population is extinct, the Flinders I. one is almost extinct and the mainland population is reduced to a remnant on Eyre Peninsula (P. Aitken pers. comm.).

Family MURIDAE

***Rattus fuscipes** (Waterhouse). SAM, M8541-M8545, M8598-M8600. *Bush rat*. Masillon and Dog Is.

This species appeared to be common on these islands, where it nested in limestone crevices and, possibly, mutton bird burrows. It seems unlikely that the smaller islands of Nuyts Archipelago ever supported mammals larger than *R. fuscipes*. Its absence from Egg Island suggests that this island may be too small to support a population of *R. fuscipes*. We did not see or collect this rat on St Francis I. where there are extensive areas of suitable habitat, but again they may have been exterminated by cats.

***Rattus rattus** (Linn.). SAM, M8551. *Black rat*. St Francis I.

Two lower jaws of this introduced species were collected in the sandhills behind Petrel Cove. No living animals were caught. *R. rattus* was undoubtedly introduced by the early settlers to St Francis I. and has since become extinct.

Family OTARIIDAE

***Neophoca cinerea** (Peron & Lesueur). *Australian sea lion*. Fenelon I.

This species visits all the islands and there is a breeding colony on the beach of Fenelon Island. In January 1971 this colony numbered approximately 50 individuals, including a number of pups. D. Murray (pers. comm.) provided the following estimates of the size of this colony in February 1973: mature bulls 7, pups 8, cows and immature bulls 36. The number of individuals in the vicinity of the beach was 56-58

A South Australian National Parks and Wildlife Service expedition in June 1975 was unable to land on Fenelon I., but a count from the boat showed mature bulls 4, pups 5, cows and immature bulls 3. They also noted a possible breeding colony of this species on Dog I. Numbers recorded for this colony were bulls 3, cows and immature bulls 10. In addition 20 sea lions were seen on Freeling I.

***Arctocephalus forsteri** (Lesson). *New Zealand fur seal.* Fenelon I.

The South Australian National Parks and Wildlife Service expedition in June 1975 noted 40 fur seals on Fenelon I. No evidence of breeding was observed. They also noted 5 fur seals on Freeling I.

BIRDS

No systematic list of the birds of the St Francis Group has been compiled. The following list contains comments on habitat and abundance of birds observed during the 1971 expedition.

Family SPHENISCIDAE

Eudyptula minor (Stephens). *Little penguin.* St Francis I.

Common around the shores of Petrel Bay; most of the birds were in a heavy moult.

Family PROCELLARIIDAE

Macronectes giganteus (Gmelin). *Giant petrel.* Dog I.

Beach washed specimen.

Puffinus tenuirostris (Temminck). *Short-tailed shearwater.* All islands visited except Fenelon.

Nesting burrows were found wherever sufficient soil depth allowed excavation. Approximately one-third of St Francis I. was covered by the burrows. During the day most burrows contained one adult bird and one egg in an advanced stage of incubation. At approximately 20.00 hours each evening vast numbers of birds returned to the island from feeding at sea.

Family OCEANITIDAE

Pelagodroma marina (Latham). *White-faced storm petrel.* Dog and Fenelon Is.

Dried remains and wings were found. Small burrows on Fenelon I. may belong to this species.

Family PHALACROCORACIDAE

Phalacrocorax varius (Gmelin). *Pied cormorant.* St Francis I.

A small number of birds were fishing in Petrel Bay and roosting in company with black-faced cormorants at the eastern end of the bay.

Phalacrocorax fuscescens (Vieillot). *Black-faced cormorant.* St Francis I.

Approximately 20 birds roosted on the eastern headland of Petrel Bay.

Family ANATIDAE

Cereopsis novaehollandiae (Latham). *Cape Barren goose.* St Francis I.

Approximately 50 geese were observed and flocks of 3 to 20 were seen feeding on the eastern end of the island near the lighthouse. The geese congregated around three small fresh water soaks above granite boulders on the eastern end of the island. Goose droppings were also found on Masillon I.

Anas sp. Unidentified teal. Egg I.

One bird was seen at sea near this island.

Family ACCIPITRIDAE

Haliaetus leucogaster (Gmelin). *White-breasted sea eagle.* St Francis and Masillon Is.

Several adults and one immature bird were observed flying over St Francis I. and three adult birds were seen flying over Masillon I.

Family PANDIONIDAE

Pandion haliaetus (Linn.). *Osprey.* St Francis I.

One or two birds were observed on most days at the eastern end of the island near the lighthouse. Old nests of sea eagles or ospreys were found on the eastern side of Dog I. and the southern side of St Francis I.

Family FALCONIDAE

Falco peregrinus (Tunstall). *Peregrine falcon.* Masillon I.

Only a single bird was observed.

Falco cenchroides (Vigors & Horsfield). *Nankeen kestrel.* St Francis, Dog and Masillon Is.

Several pairs on St Francis I.

Family PHASIANIDAE

Coturnix pectoralis (Gould). *Stubble quail.* St Francis I.

Several birds were flushed in the grassy area near the lighthouse.

Family RALLIDAE

Rallus philippensis (Linn.). *Banded landrail.* St Francis and Dog Is.

This species appeared common on St Francis I. and two specimens were collected. Only two birds were sighted on Dog I.

Family **HAEMATOPODIDAE**

Haematopus fuliginosus (Gould). *Sooty oystercatcher.* All islands visited.

A common bird of the rocky shorelines.

Family **CHARADRIDAE**

Vanellus miles novaehollandiae (Stephens). *Spur-winged plover.* St Francis I.

Eight to ten birds were observed feeding around the shores of Petrel Bay.

Charadrius rubricollis (Gmelin). *Hooded dotterel.* St Francis I.

From two to ten birds were seen on the beach in Petrel Bay each day.

Charadrius alexandrinus (Linn.). *Red-capped dotterel.* St Francis I.

One bird was observed on the beach in Petrel Bay in company with four Red-necked stints.

Family **SCOLOPACIDAE**

Calidris ruficollis (Pallas). *Red-necked stint.* St Francis I.

Four to eight birds on the beach in Petrel Bay. One specimen collected.

Family **LARIDAE**

Larus novaehollandiae (Stephens). *Silver gull.* St. Francis I.

Nine to ten birds on the beach in Petrel Bay.

Larus Pacificus (Latham). *Pacific gull.* All islands.

A common bird of these islands. Adults and immature birds were present in about even numbers. Approximately 20 birds foraged along the shores of Petrel Bay.

Hydroprogne tschegrava (Lepechin). *Caspian tern.* St Francis and Dog Is.

Two birds noted on each island.

Family **PSITTACIDAE**

Neophema petrophila (Gould). *Rock parrot.* Found on all islands visited.

Numerous small flocks were flushed while walking on St Francis I.

Family **HIRUNDINIDAE**

Hirundo tahitica neoxena (Gould). *Welcome swallow.* Found on all islands visited.

A common bird. Old nests in houses, lighthouse shed and caves.

Family **MOTACILLIDAE**

Anthus novaeseelandiae (Gmelin). *Pipit.* All islands visited.

Abundant.

Family **MELIPHAGIDAE**

Meliphaga virescens (Vieillot). *Singing honeyeater.* All islands visited.

A very common bird. Eight to ten birds were present in the camp area at all times.

Family **CORVIDAE**

Corvus coronoides (Vigors & Horsfield). *Australian raven.* St Francis I.

Common; a flock of approximately 30 birds was observed as the expedition landed. Small flocks were seen daily, foraging amongst the mutton bird burrows. The lighthouse tower was a favoured roost, and nest remains were found here. Other nests were found on low bushes.

REPTILES

Eleven species of reptiles are listed or mentioned for Nuyts Archipelago by Proctor (1923), Waite (1923) and Worrell (1963). Our expedition added another five species; these are indicated by an asterisk in the list below. The islands of the group from which each species is now known is also recorded. Some contrasts between the abundance of several species on St Francis and other offshore islands in the Bight are noted in the list below. Possibly the drier climate of the Nuyts Group is responsible.

Family **GEKKONIDAE**

***Underwoodisaurus milii** (Bory). SAM, R12858, R12863, R12870, R12876, R12889. St Francis, Masillon, Fenelon, Dog Is.

Common under limestone boulders or in burrows in the sand by day.

***Heteronotia binoei** (Gray). SAM, 12878. St Francis I.

Common under stones by day.

***Phyllodactylus marmoratus** (Gray). SAM, R12865, R12877. St Francis, Fenelon Is.

Surprisingly uncommon, for this is a very abundant species on some other off-shore islands. Found only under aeolianite slabs on exposed coastal areas.

Family **PYGOPODIDAE**

Lialis burtonis (Gray). SAM, R12896. St Francis I.

Only one seen during the visit.

Aprasia striolata (Lutken). Recorded for St Francis I. by Kluge (1974); this is the specimen referred by Proctor (1923) to *Delma fraseri*. No *Aprasia* was collected in 1971.

Family **AGAMIDAE**

Amphibolurus fionni (Proctor). SAM, R12874, St. Francis I.

Found only among the exposed granite around the edges of the island. Wood-Jones did not find it (Proctor 1923), but Worrell (1963) has recorded it from St Francis I.

Family **SCINCIDAE**

Hemiergis peronii (Fitzinger). SAM, R12862, St Francis, Dog and Fenelon Is.

Surprisingly infrequently seen; like *P. marmoratus*, this is a common species on other off-shore islands.

Egernia multiscutata (Mitchell & Behrndt). SAM, R12857, R12861, R12873, R12888. St Francis, Dog, Masillon and Fenelon Is.

A very common species on the sandier parts, burrowing under rocks or bushes and using the mutton-bird burrows for quick retreats.

Lerista frosti (Zietz). SAM, R12859. Masillon I.

Another species usually common on off-shore islands but very scarce in the Nuyts group.

***Lerista** sp. **(near picturata)**. SAM, R12880. St Francis I.

A large member of the genus, with forelimbs reduced to dimples and two toes on each hind limb. Commonly found buried in sand under stones.

***Menetia greyii** (Gray). SAM, R12875. St Francis I.

Rarely seen, probably because it is small, quick and secretive.

Morethia obscura (Storr). St Francis I.

Again, rarely seen and very difficult to catch, no specimens collected.

Tiliqua branchiale (Gunther). SAM, R12864, R12879, St Francis, Fenelon Is.

Common in litter and around the buildings.

Family **BOIDAE**

Morelia spilotes variegata (Gray). *Carpet snake*. St Francis I.

Commonly seen in the morning and late afternoon, no specimens collected.

Family **ELAPIDAE**

Drysdalia coronoides (Gunther). SAM, R12860, R12881. *White-lipped snake*. St Francis, Masillon and Fenelon Is.

Not frequently seen, but probably quite common.

Notechis ater (Krefft). SAM, R12895. *Tiger snake*. St Francis I.

Usually common on mutton-bird islands, yet only a few were seen even at night.

Discussion

The vertebrate fauna of the St Francis I. group of Nuyts Archipelago is quite diverse and remains relatively undisturbed and relatively free from introductions. The fauna of most South Australian islands and indeed of the mainland adjacent, is still incompletely known, and so biogeographical interpretations are difficult at this stage. However, some comments may be made on the importance of these islands in conservation.

Island faunas are extremely vulnerable to man's interference, and the fate of *Bettongia penicillata* on St Francis I. illustrates this point If further work there definitely establishes that this species is extinct, the opportunity exists to re-establish dense vegetation on the island and introduce *B. penicillata* from Western Australia. This should succeed as cats are no longer present on the island. It is obviously a long-term project but it merits consideration because the island population could ultimately serve as a reservoir of animals for release in suitable areas of their former mainland range. In addition, if *Rattus fuscipes* is absent from St Francis I. it could be re-introduced from neighbouring islands.

The majority of the birds observed are common on all islands in the area and on the adjacent coast, but a notable exception is the Cape Barren goose. The total world population of this endemic Australian species, although it is increasing, is still dangerously low, and so every attempt should be made to conserve the known populations from disturbance.

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THE SUBTIDAL ALGAL AND SEAGRASS ECOLOGY OF ST FRANCIS ISLAND, SOUTH AUSTRALIA

BY S. A. SHEPHERD AND H. B. S. WOMERSLEY†*

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In the sheltered Petrel Bay- communíties of the seagrasses *Amphibolis antarctica* and *Posidonia* occur.

An algal species list is appended.

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An algal species list is appended.

Introduction

The marine flora of the Great Australian Bight is little known. Apart from the intertidal region, which has been briefly discussed by Womersley & Edmonds (1958), the subtidal region is known only from various drift collections and the ecological account of Shepherd & Womersley (1971) of Pearson Island, towards the eastern limit of the Bight.

An expedition to the Isles of St Francis, lying off Ceduna, supported by the then Fisheries and Fauna Conservation Department and the Royal Society of South Australia, visited the islands from 4–11 January, 1971. This provided the opportunity for a brief survey of the subtidal ecology of selected sites subject to varying degrees of water movement. Although limited in time, these studies provide the first such information from the northern part of the Great Australian Bight.

The Isles of St Francis comprise nine small islands, the largest of which, St Francis I. (Fig. 1) is about 4 km across and lies at 32°31'S, 133°18'E, about 56 km from the mainland. The islands are granitic, rising steeply from the sea-floor, and subtidally the topography consists of massive blocks and sheets of rock. In sheltered areas (e.g. Petrel Bay), the sandy sea-floor slopes more gently into deeper water.

The short stay on the island prevented a detailed survey, but three survey sites were chosen on St Francis I., subject to different degrees of water movement. One site was chosen on nearby Masillon I., and collections were also made at Egg I.

The field work was limited to the subtidal region, but brief observations of the intertidal region indicated that the organisms and zonation present were similar to those described by Womersley & Edmonds (1958) for such granitic steeply sloping coasts.

Methods

The following transects (Fig. 1) were chosen, and in each case the transect ran normal to the coast, from low water level down the slope to the depth where rock was buried by sand, except for transect D which was predominantly on sandy bottom.

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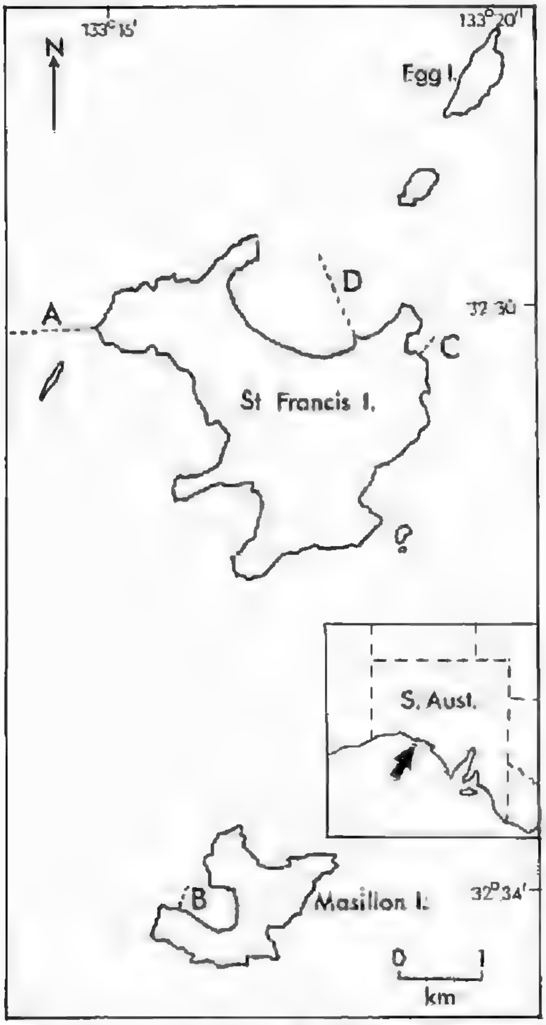

Fig. 1. Map of four of the isles of St Francis showing the position of the four transects (A–D). Inset shows the situation of the islands in the northern Great Australian Bight.

Transect A was on the NW corner of St Francis I., under conditions of strong water movement, and terminated at 57 m depth. A sampling gap (32–38 m deep) in this transect was filled by collections from a similar site on Egg I.

Transect B was on Masillon I., subject to moderate water movement, and terminated at 33 m depth.

Transect C on St Francis I., was subject to relatively slight water movement, and descended to 20 m.

Transect D in Petrel Bay on St Francis I., was the most sheltered site, with a gently sloping, sandy, sea-floor dominated by seagrasses.

On transects A, B and C, the diver first swam about 2 m above the bottom along the transect, estimating the percentage cover and recording the vertical range of the prominent brown algae. This was then repeated on two parallel lines, one each side of the first transect and about 15–20 m distant. Estimates of cover for particular depths are given as the average of these three values, which were made subjectively as a percentage on a scale of 0–10. Many species vary considerably in percentage cover over a horizontal distance of some metres, but the figures given provide an overall assessment of the cover along the transects.

Communities were recognised by the upper stratum dominants, this being the most satisfactory method on such surveys. At the depths studied, algae were dominant except at 50–57 m on transect A, and within each community quantitative samples of the upper stratum were taken for biomass estimates. This was done by counting the plants in a hoop of ⅛ m^2 area, placed sequentially along a horizontal line some 16–24 times, so as to give a total sampling area between 2 and 3 m^2, and the number of plants per m^2 calculated. The average weight of an individual plant was determined by weighing a random sample of 10 plants, and the biomass per m^2 then calculated. The other strata were sampled by means of 4 to 8 sequential samples, each of ⅛ m^2.

On transect D in Petrel Bay, a diver was towed on an underwater sled behind a boat, and the distribution and depth range of the seagrasses were noted, and photographs taken.

The algal samples were preserved in 4% formaldehyde-sea water, and taken to the laboratory for determination and analysis. Biomass figures are based on the wet weight of the preserved collections after removal of surface water. These estimates should be taken as examples only of the size and variation in biomass of the community dominants, since the restricted diving time on a short expedition such as this limits the range of transects, and the number of samples that can be taken. The transect samples were supplemented by other general observations and collections, and by photography.

Depths were measured by capillary and mechanical depth gauges, and the results averaged and adjusted to approximate low tide level.

Environmental factors

The short duration of the survey precluded detailed studies on environmental factors, but the following information is available. The Isles of St Francis rise from a maximum water depth of about 60 m at the southwest of St Francis I. and are comparable to the Pearson Islands in their distance from the mainland and in their topography.

Water movement

St Francis I. is subject to a strong southwesterly swell of 10–12 second period, prevailing throughout the year, similar to that at Pearson I. and West I. (Shepherd & Womersley 1970, 1971). In summer, a short southerly swell is generated by the strong southerly winds which blow for about 12 hours each day and are characteristic of this part of the Great Australian Bight. Wave action on all parts of the islands facing south to west is strong in the intertidal region.

Temperature, salinity and nutrients

Sea surface temperatures range from 18–20°C in summer to 14–15°C in winter, according to Vaux (1970) and data obtained from various oceanographic stations in the vicinity (C.S.I.R.O. 1967a, 1967b, 1968, 1969). In summer, bottom temperatures at 50 m depth are 2–3°C lower than sea-surface temperatures. During the study, the surface temperature was 18°C off the island and about 20°C inshore in Petrel Bay.

Salinity, phosphate, nitrate and oxygen levels are similar to those for Pearson I., viz. salinity 35.6–36.2‰; inorganic phosphate 0.09–0.17 μg atom/litre; nitrate about 0.3 μg atom/litre; and oxygen saturation 93–103%.

Submarine light intensity

Light penetration was not measured, but according to H. Jitts (pers. comm.) it corresponds to that for Type II oceanic water of Jerlov (1968), and is thus only slightly less clear than the waters about Pearson I.

The algal and seagrass ecology

The algal-dominated subtidal photic zone at other localities in South Australia has been found to present three main zones, designated as the upper, mid, and lower sublittoral zones (Shepherd & Womersley 1970, 1971). These zones are also apparent in the areas studied at St Francis I.

Communities of the rocky coast will be described first, including those on both horizontal and sloping rock but not those in crevices or under overhangs, followed by the sea-grass and algal communities of sheltered, sandy areas. The communities studied are essentially those subject to sufficient light intensity to be plant dominated, but prominent animal species are mentioned where present.

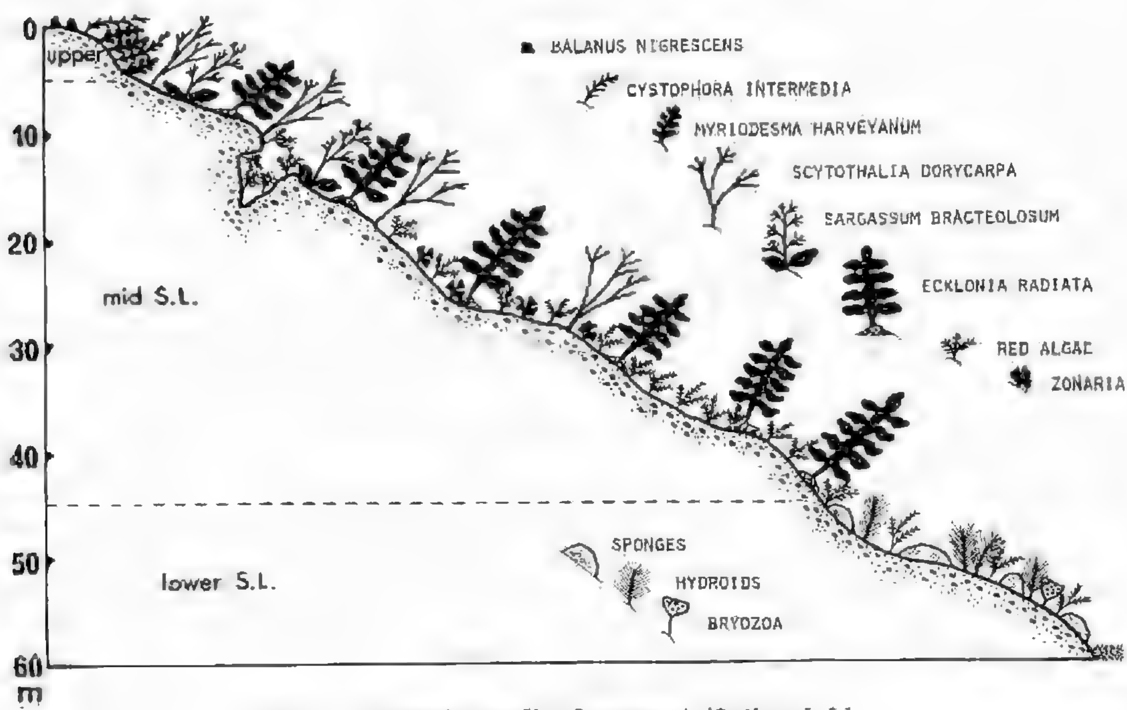

Fig. 2. A vegetation profile of transect A (St Francis I.).

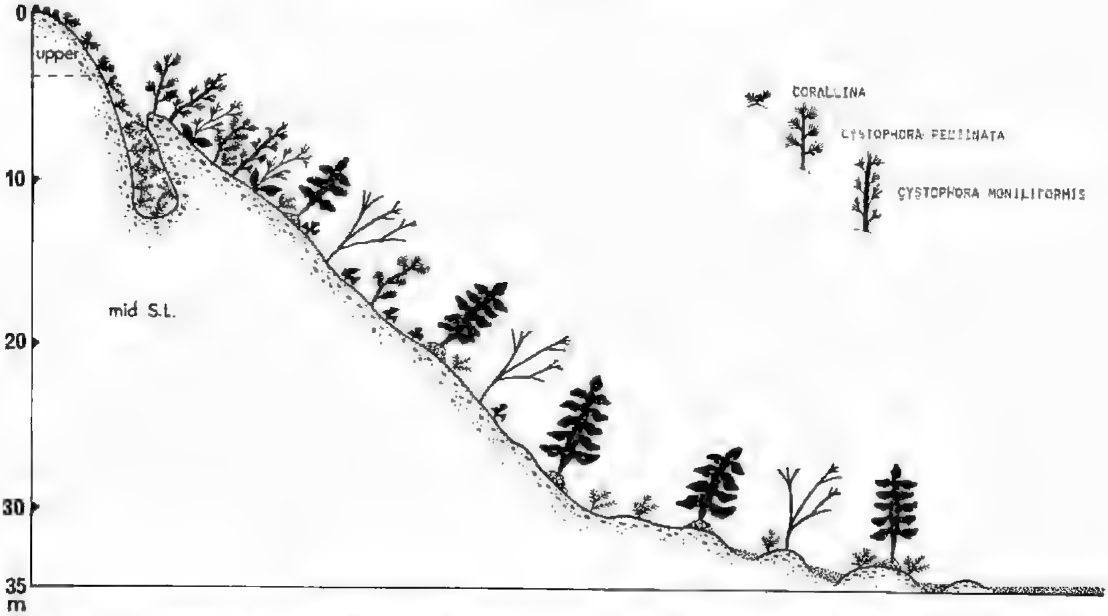

Fig. 3. A vegetation profile on transect B on Masillon I. See legend on Fig. 2 for other algal taxa.

Fig. 4. A vegetation profile of transect C on St Francis I. See legend on Fig. 2 for other algal taxa.

A. ROCKY COASTS

Transects A, B, and C traverse rocky areas, generally steeply sloping and including both horizontal and sloping rock surfaces. The marked light gradient with depth, coupled with the considerable gradient in water movement within each transect (especially A) and also between the transects, gives rise to a fairly distinct zonation of algae. Profiles for transects A, B, and C are given in Figs 2–4, and the depth relationships of the communities to water movement are given in Fig. 5.

1. *Upper sublittoral zone*

This zone is subject to the most intense water movement, and varies in vertical width from 5(–7) m on rough-water coasts (transect A, Fig. 2) to 2(–3) m on sheltered coasts (transect C, Fig. 4). Communities of this zone typically have a single, dense, stratum of fairly uniform height, ranging from 15–20 cm for the *Cystophora intermedia* community to 2–3 cm for the *Jania* community.

Corallina cuvieri, in high-light situations (i.e. especially horizontal surfaces and those facing

TABLE 1

Species and biomass (g/m²) composition of upper sublittoral communities in samples taken at about 1(–1.5) m depth on transects A, B and C. "P" indicates sparse occurrence although not present in sample.

Transect	A	B	C	
Area sampled (m²)	0.25	0.25	0.37	
Water movement	Strong	Moderate	Slight	
Dominant Species				
Cystophora intermedia	**1,280**	P	30	
Myriodesma harveyanum	**1,400**			
Corallina cuvieri f. *crispata*		**2,800**	**4,200**	
Jania fastigiata				**[1,900]***
Other Species				
Caulerpa brownii	70			
Caulerpa papillosa	140			
Cystophora gracilis	<10			
Lobospira bicuspidata	40		40	
Pachydictyon paniculatum	50	20	50	
Sargassum spp.		<10		
Callophyllis rangiferinus	280	15		
Champia obsoleta	80			
Dasya clavigera			<10	
Griffithsia teges	260			
Hypnea sp.	40			
Laurencia filiformis f. *heteroclada*	290			
Lenormandia harveyiana	<10			
Polysiphonia nigrita	<10			
Total coverage	100	100	100	
Biomass g/m²	3,950	2,840	4,330	[1,900]
Number of species	14	4	5	

In each case the biomass value of the species characterising the community is in bold type.

* This sample was taken from a distinct *Jania* community at a depth of about 0.5 m (see Fig. 4).

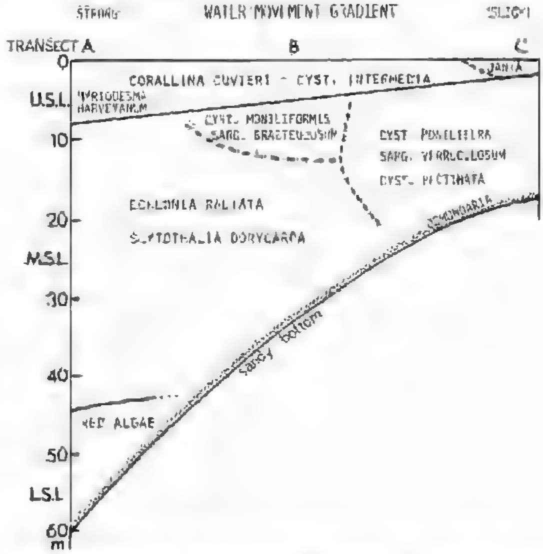

Fig. 5. Change in vegetation patterns along water movement and depth gradients.

north or east) and subject to strong to moderate water movement, forms an almost pure community completely covering the rock surface. In calmer areas a *Jania fastigiata* community, presenting a somewhat similar aspect of short, tufted plants, replaces the *Corallina*. The *Corallina cuvieri* community extends upwards into the lower eulittoral zone of the intertidal in rough-water situations, as described by Womersley & Edmonds (1958, p. 232).

Cystophora intermedia forms a fairly pure community under slightly less extreme water movement than *Corallina*, and also on sloping (rather than horizontal) surfaces subject to somewhat lower light intensity. While *Cystophora intermedia* may be dominant in such situations, in lower light intensity *Myriodesma harveyanum* becomes co-dominant, with numerous associated species of green, brown and red algae (see Table 1).

Cystophora intermedia is rare within the *Corallina cuvieri* community, but may be common near the upper and lower boundaries of this community. Its occurrence at the upper limit (i.e. near low tide level) agrees with the observations of Womersley & Edmonds (1958) that it marks the sublittoral fringe, but at St Francis I. it is not confined to this zone, occurring also as deep as 3 m.

2. Mid sublittoral zone

As at West I. and Pearson I., this zone on St Francis I. is characterised by larger brown algae 30 cm–1 m in height, forming an upper canopy or stratum over a lower stratum mainly of red algae 5–25 cm in height. The upper limit of this zone depends on the intensity of water movement as described for the upper sublittoral zone, and the lower limit on the limiting depth of large brown algae; this is about 45(–47) m deep on transect A. The vegetation profiles of Figs 2–4 represent the appearance of this zone on transects A, B, and C and the relations of the vegetation patterns with water movement are shown in Fig. 5. The average cover of the important upper stratum species is given in Fig. 6.

Several communities could possibly be recognised in this zone, but more extensive studies than were possible in the time available are needed to establish their validity. The dominants and understorey species will therefore be discussed more generally.

Ecklonia radiata and *Scytothalia dorycarpa* (Fig. 9) dominate this zone under conditions of considerable water movement at the rough-

TABLE 2

Biomass (g/m²) composition of mid sublittoral species in samples taken at certain depths on 3 transects. Further data on the vertical range of the species is given in the appendix

Transect	A			B			C			
Depth (m)	6	13	35	6	22	32	6	13	19	20
Area sampled (m²)	0.5	1	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Upper stratum										
**Ecklonia radiata*	2,200	300	1,800	450	900	1,200	—	1,050	250	740
**Scytothalia dorycarpa*	2,300	2,560	200	50	1,380	2,500	—	1,245	200	—
Cystophora pectinata	75	600	—	400	—	—	—	1,910	720	—
Cystophora moniliformis	—	—	—	420	—	—	—	—	—	—
Myriodesma harveyanum	—	—	—	250	—	—	—	—	—	—
Sargassum bracteolosum	—	315	P	510	180	—	—	P	15	90
Sargassum varians	75	—	200	120	—	—	10	250	340	—
Sargassum verruculosum	—	—	10	—	—	—	800	90	320	—
Sargassum linearifolium	—	—	—	P	—	—	390	—	10	—
Sargassum heteromorphum	—	—	—	—	—	—	210	—	—	—
Sargassum decipiens	—	—	—	50	—	—	950	210	92	—
Cystophora brownii	—	—	—	P	—	—	110	P	—	—
Cystophora subfarcinata	—	—	—	P	—	—	220	720	280	—
Cystophora monilifera	—	—	—	—	—	—	560	330	710	—
Upper stratum coverage (%)	100	95	35	90	50	60	80	100	80	75
Upper stratum biomass (g/m²)	4,650	3,775	2,210	2,250	2,460	3,700	3,250	5,805	2,937	830
Lower stratum										
Brown algae										
Dictyopteris muelleri	—	—	P	—	30	—	5	P	6	—
Dictyota diemensis	—	—	P	30	—	—	10	—	5	—
Dictyota prolifera	—	—	50	—	130	—	—	—	5	—
Chlanidophora microphylla	—	—	—	—	180	—	—	—	25	80
Glossophora nigricans	—	—	P	—	90	—	—	—	—	—
Hydroclathrus clathratus	—	—	—	—	—	—	—	—	5	50
Lobospira bicuspidata	—	—	5	<5	—	—	610	75	6	—
Pachydictyon paniculatum	—	—	5	25	P	—	P	60	10	—
Zonaria spiralis	—	20	50	25	P	—	—	40	8	—
Zonaria sinclairii	—	—	50	—	600	—	—	—	4	—
Zonaria turneriana	—	30	P	—	—	—	—	—	—	—
Red algae										
Austrophyllis alcicornis	—	—	4	—	—	5	—	—	—	—
Ballia callitricha	—	—	4	—	—	40	—	—	—	—
Botryocladia obovata	—	—	—	—	—	—	—	—	50	60
Champia affinis	—	—	100	—	—	—	—	—	5	—
Cliftonaea pectinata	—	—	60	—	—	—	—	—	5	—
Delisea hypneoides	—	—	30	—	—	—	—	—	5	—
Delisea pulchra	—	—	105	340	P	—	—	—	—	—
Kallymenia cribrosa	—	—	20	—	—	—	—	—	—	—
Laurencia filiformis f. dendritica	—	—	80	—	—	—	—	—	—	—
Laurencia spp.	—	—	—	—	—	—	—	—	36	25
Osmundaria prolifera	—	—	—	—	—	—	410	40	1,020	3,400
Plocamium angustum	P	P	10	10	50	80	P	P	4	—
Plocamium cartilagineum	P	—	P	—	90	5	—	—	—	—
Plocamium mertensii	P	P	300	25	180	—	P	P	6	—
Plocamium preissianum	P	20	5	20	150	10	5	P	4	—
Pterosiphonia sp.	—	—	—	680	—	—	—	—	—	—
Rhodophyllis membranacea	—	—	5	—	50	—	—	—	—	—
Sonderophycus australis	—	—	—	—	10	10	—	—	—	—
Webervanbossea kaliformis	—	—	5	—	50	—	—	P	5	—
Biomass	—	70	888	1,160	1,610	150	1,040	215	1,214	3,615
Total number of species in sample	4	7	25	24	22	12	11	16	29	7
Total Biomass	4,650	3,845	3,098	3,410	4,070	3,850	4,290	6,020	4,151	4,445

* Values for *Ecklonia* and *Scytothalia* are mean values over 2–3 m².

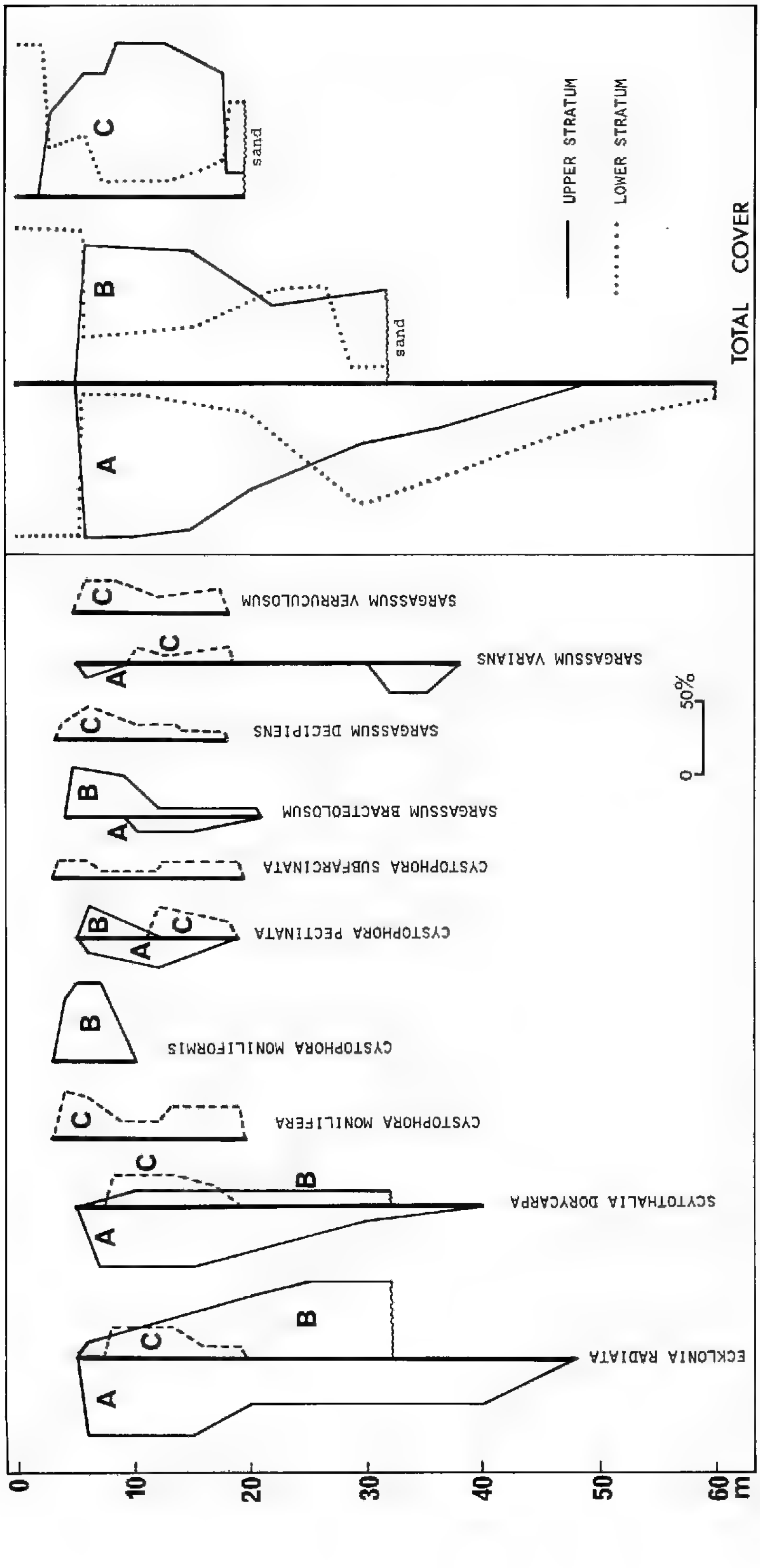

Fig. 6. Vertical distribution of % cover of prominent upper stratum species of the mid sublittoral zone, and total % cover of upper and lower strata on transects A, B and C.

water site (transect A, Fig. 2), but with less water movement (transect B, Fig. 3) other species of brown algae (*Sargassum bracteolosum* and *Cystophora moniliformis*) also become prominent. With greater shelter (transect C, Figs 4, 7, 8), *Cystophora monilifera*, *C. pectinata* and *Sargassum verruculosum* are common, together with *C. subfarcinata*, *Sargassum decipiens* and *S. varians*. These species are most common in the upper part of the mid sublittoral, with *Ecklonia* and *Scytothalia* still common in the lower part of this zone (Fig. 6).

Sargassum bracteolosum and *Cystophora moniliformis* on transect B, and *S. verruculosum* and *C. monilifera* on transect C, have similar vertical distributions, enabling field recognition of algal subzones dominated by these species pairs.

Understorey species are sparse over much of transects A and C, and moderately common only on transect B where the canopy is less dense. The distribution of many understorey species is too patchy to show any obvious relationship with either the distribution of upperstorey species or with apparent environmental factors.

The commonest understorey species are of *Plocamium* (*P. angustum*, *P. mertensii* and *P. preissianum*). They occurred on all three transects, with a vertical depth range of as much as 50 m; where they are rare or absent on horizontal surfaces, they are usually present on vertical ones.

Other species with a wide vertical range are *Caulerpa brownii*, *Lobospira bicuspidata* and *Pachydictyon paniculatum*; these species are known to be tolerant to a wide range of light intensity and of water movement. Some other species (e.g. *Glossophora nigricans*, *Austrophyllis alcicornis*, *Cliftonaea pectinata* and *Delisea hypneoides*) were found only in deeper water; most of these species occur also at West I. and Pearson I., with similar distribution in conditions of low light (and slight water movement at depth).

On transect C at 17–18 m depth (Fig. 4), there is an abrupt decline in the number of upper stratum species and their coverage, and an increase in coverage of several species of the lower stratum, e.g. *Osmundaria prolifera*, *Botryocladia obovata* and *Hydroclathrus clathratus*. This community forms a band 1–2 m wide lying immediately above the sandy bottom at about 20 m depth, and the species are apparently tolerant of the sedimentation which is pronounced over this narrow band.

The cover of upper and lower stratum species, with depth, is given in Fig. 6. Upper stratum cover is highest between 5 and 15 m depth, declining with depth, whereas lower stratum cover is lowest where the upper stratum is most dense, and in general increases with depth until light becomes limiting.

3. Lower sublittoral zone

Only on transect A does rocky substrate descend to sufficient depth for the lower sublittoral zone dominated by red algae (Shepherd & Womersley 1970, 1971) to occur. On this transect, a community (Fig. 10) of red algae together with bryozoa, sponges and hydroids, occurs between 47 and 57 m deep. The community is rich in algal species (but of low biomass), the most common being *Plocamium angustum*, *P. mertensii* and *P. preissianum*; several other species (*Rhodymenia australis*, *Gattya pinnella*, *Rhodocallis elegans* and *Kallymenia spinosa*) were found only in this collection. Algal cover in this community is low, averaging 10% (5-15%), indicating that 57 m is close to the depth (i.e. light) limit for most algae in this region.

B. THE SEAGRASS COMMUNITIES IN PETREL BAY

Three seagrass communities occur in this sheltered bay, forming bands around the bay dependent on substrate and depth.

Amphibolis antarctica fringes the shore from low water mark to 0.5 m below, attached by its rhizome-root system to calcareous reefs of low relief. Below these reefs the bottom is sandy, and at a depth of about 2 m, *Posidonia ostenfeldii* forms a fringe community about 20 m wide around the bay. Beyond this, descending to 22 m deep, *Posidonia australis* (narrow leaf form) is dominant in fairly continuous beds. Beyond about 22 m deep, *P. australis* becomes sparse, and at the time of the survey a loose-lying but apparently healthy community of the red alga *Hennedya crispa* occurred at this depth.

Fig. 7. Algal community at 8 m depth on transect C. Note *Cystophora monilifera* (top left), *Scytothalia dorycarpa* (top right) and several species of *Sargassum* (centre and lower right).

Fig. 8. Algal community at 10 m depth at transect C. Note species of *Sargassum* (centre left), *Ecklonia radiata* (top right) and *Cystophora monilifera* (centre and lower right).

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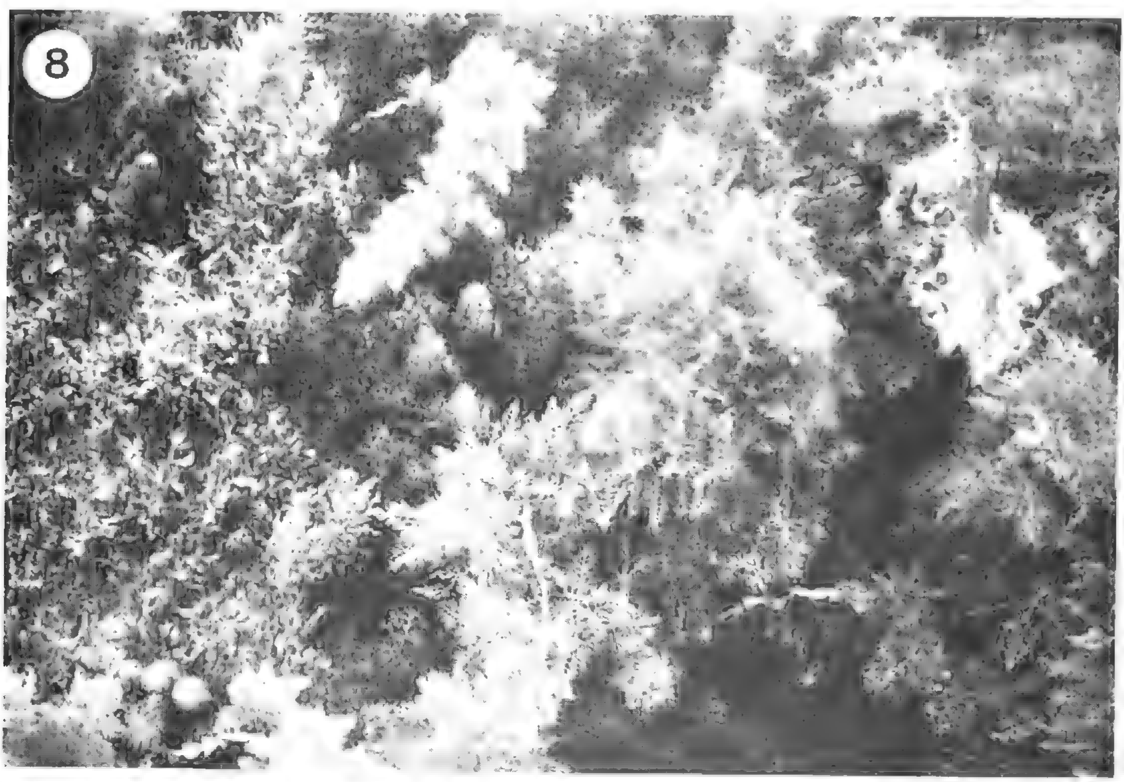

Discussion

Algal zones within the sublittoral, and the distribution, cover and biomass of the component species, have been described for many coasts elsewhere in the world. Recent accounts are those of Lüning (1970) from Helgoland, Boudouresque (1971) from the Mediterranean, and Mann (1972) from the Atlantic coast of Canada. These and other accounts show that broad algal zones, correlated with light intensity and the degree of water movement, occur in the photic zone on most coasts.

Although limited in extent, this survey of the subtidal algal vegetation of St Francis I. shows a similar zonation pattern to that at West I. and Pearson I. (Shepherd & Womersley 1970, 1971). As at these islands, the vertical extent of the upper sublittoral zone, and to a lesser extent the mid sublittoral, is dependent on the degree of water roughness (with which light penetration is also associated). The extent of the upper sublittoral zone probably corresponds with the depth to which "white water" (i.e. turbulent water carrying air bubbles) penetrates under average swell conditions. Riedl & Forstner (1968) considered the vertical height of their "inner surf zone" (Riedl 1971) to correspond to 2.5 x wave height, and this could also be applied to the upper sublittoral zone on South Australian coasts where wave heights are 1.5–2 m in a moderate swell. Chapman (1967) in discussing the presence of a sublittoral fringe in many parts of the Pacific is largely referring to this upper sublittoral zone. The term "sublittoral fringe" is best restricted to the zone emergent during suck back of waves at low tide, when this zone is ecologically distinctive (Womersley & Edmonds 1952).

The mid sublittoral zone at St Francis I. shows similar features to this zone at West I. and Pearson I., being dominated by the larger brown algae and with an understorey of mainly red algae. Further studies may show that distinct communities could be recognised in this zone, since competition between the various dominant species is apparent, and, over the considerable depth range, both light intensity and degree of water movement vary considerably. While most species show typical "bell-shaped" distribution patterns (as discussed by Whittaker 1967), some (e.g. *Cystophora monilifera, C. subfarcinata*) apparently show slightly bimodal distributions (Fig. 6), probably due to competition with other species better suited to the environment within their extremes.

The lower sublittoral zone of red algae was observed only in depths of 47–57 m at St Francis I., corresponding to the situation at Pearson I. rather than at West I., and reflecting the clarity of the water. This zone lies below the light intensity necessary for the larger brown algae and grades to the lower photic levels of the red algae. At St Francis I., intermixing of lower sublittoral red algae with fauna such as bryozoa, sponges and hydroids, was more prominent than at West I.

Although sublittoral zones are well defined at St Francis I., this characteristic is emphasized by choice of transects on steeply sloping shores involving steep light and water movement gradients. On more irregular shores, distinct zonation is less apparent.

Apart from ecological differences associated with depth, which reflect mainly the decrease in light intensity, light relationships are apparent in the mid sublittoral zone where a dense upper canopy may reduce the light reaching the lower stratum by up to 95%. This effect was well shown on transect A at 5–15 m depth and transect C at 7–13(–15) m depth, where a dense canopy covered a sparse understorey. Where a dense canopy exists with considerable water movement, reduction of the understorey may also be due to the physical effect of the larger fronds sweeping over the rock.

The effect of sediment (fine sand or silt stirred up in stormy weather and settling on the seabed under calmer conditions) was evident in two places. Near the end of transect B, at about 30 m depth, sediment is present on rocky surfaces and here there is an abrupt decline in cover of the lower stratum. At the end of transect C at 18(–20) m depth, where sediment also covers the rocky bottom, there is a distinctive community of certain red algae (*Botryocladia obovata, Osmundaria prolifera*) which can tolerate sediment. The effect of sedi-

Fig. 9. Algal community at 16 m depth on transect C. Note *Ecklonia radiata* (top right and lower left) and *Scytothalia dorycarpa* (centre).

Fig. 10. Sparse red algal community at 57 m depth on transect A.

ment in inhibiting algal colonisation and growth has been recently discussed by Grigg & Kiwala (1970).

The survey of St Francis I. was limited in time, the area covered, and in the variety of habitats sampled. Nevertheless, the subtidal algal flora appears fairly rich, with some 138 species recorded, compared to 160 for Pearson I. and 132 for West I. Further studies would certainly extend this number considerably.

Appendix: Algal species list

Identifications are by H. B. S. Womersley, Dr G. T. Kraft (Mychodeaceae, Dicranemaceae and Acrotylaceae) and Dr E. M. Wollaston (Crouanieae).

CHLOROPHYTA	
Caulerpales	
Caulerpa brownii (C.Ag.) Endlicher	A, 0–2, 32–38; B, 4–7; C, 2–6, 19
Caulerpa cactoides (Turn.) C. Agardh	A, 32–38; D, 2
Caulerpa flexilis Lamouroux	A, 32–38; D, 2
Caulerpa flexilis Lamouroux var. *muelleri* (Sond.) Womersley	B, 6–18; C, 6, 19
Caulerpa hedleyi W. v. Bosse	A, 32–38, 55
Caulerpa longifolia C.Ag. f. *crispata* (Harv.) Womersley	D, 2
Caulerpa obscura Sonder	D, 2
Caulerpa papillosa J. Agardh	A, 2; D, 2
Caulerpa scalpelliformis (R.Br.) C. Agardh	A, 35; B, 13–18; C, 19; D, 2
Caulerpa simpliciuscula (Turner) J. Agardh	A, 32–38; C, 10–13
PHAEOPHYTA	
Dictyotales—Dictyoteae	
Dictyota diemensis Kuetzing	A, 32–38; B, 6; C, 6, 19
Dictyota furcellata (C.Ag.) J. Agardh	A, 35
Dictyota prolifera Lamouroux	A, 32–38; B, 13–22; C, 19
Dilophus fastigiatus Sonder	B, 22; C, 19
Dilophus robustus (J.Ag.) Womersley	A, 32–38; B, 13–18
Pachydictyon paniculatum J. Agardh	A, 2, 35; B, 0–7, 22; C, 2–19; Masillon I. in bay, 1–4
Pachydictyon nov. sp?	B, 13–18
Glossophora nigricans (J.Ag.) Womersley	A, 32–38, 55; B, 13–22
Lobospira bicuspidata Areschoug	
Zonarieae	A, 2, 35; B, 6, 13–18; C, 6–19
Chlanidophora microphylla (Harv.) J. Agardh	B, 22; C, 19–20
Dictyopteris muelleri (Sond.) Reinbold	A, 32–38; B, 22; C, 6–19
Lobophora variegata (Lamx.) Womersley	B, 13–18
Zonaria crenata J. Agardh	A, 32–38
Zonaria sinclairii Hooker & Harvey	A, 10, 32–38; B, 13–22; C, 19
Zonaria spiralis (J.Ag.) Papenfuss	A, 13, 32–38; B, 6–22; C, 10–19
Zonaria turneriana J. Agardh	A, 13, 32–38
Nov. gen?	A, 32–38
Chordariales—Chordariaceae	
Corynophlaea cystophorae J. Agardh	C, 10–18, on *Cystophora brownii*
Bactrophora filum (Harv.) J. Agardh	C, 19–22; D, 3, 4, on *Posidonia australis* and *P. ostenfeldii*
Bactrophora vermicularis J. Agardh	C, 6
Polycerea nigrescens (Harv. ex. Kuetz.) Kylin	C, 6, 19–20; D, 3, 4, on *Posidonia australis* and *P. ostenfeldii*
Sporochnales—Sporochnaceae	
Bellotia eriophorum Harvey	A, 32–38; B, 13–18
Sporochnus comosus C. Agardh	A, 32–38
Dictyosiphonales—Giraudyaceae	
Giraudya sphacelarioides Derbes & Solier	D, 3, on *Posidonia australis*
Punctariaceae	
Hydroclathrus clathratus (C.Ag.) Howe	C, 19–20
Laminariales—Alariaceae	
Ecklonia radiata (C.Ag.) J. Agardh	A, 5–38; B, 5–32; C, 8–20
Fucales—Cystoseiraceae	
Scytothalia dorycarpa (Turn.) Greville	A, 6–38; B, 4–32; C, 8–19, Masillon I. in bay, 1–4
Cystophora brownii (Turn.) J. Agardh	B, 4–7; C, 2–13
Cystophora intermedia J. Agardh	A, 0–2; C, 0–3

Cystophora gracilis Womersley & Nizamuddin	B, 4–7
Cystophora monilifera J. Agardh	A, 0–2; C, 2–19
Cystophora moniliformis (Esper) Womersley & Nizamuddin	B, 4–7
Cystophora pectinata (Grev. & C.Ag.) J. Agardh	A, 6, 13; B, 6–18; C, 10–19
Cystophora subfarcinata (Mert.) J. Agardh	B, 6; C, 0–13, 19. Masillon I. in bay, 1–4
Myriodesma harveyanum Nizamuddin & Womersley Sargassaceae	A, 2; B, 4–7
Phyllotrichia	
Sargassum decipiens (R.Br.) J. Agardh	B, 6; C, 2–19
Sargassum heteromorphum J. Agardh	C, 2–4, 6
Sargassum varians Sonder	A, 6, 32–38; B, 6–18; C, 6–19
Sargassum verruculosum (Mert.) Agardh	A, 35; B, 13–18; C, 2–19
Arthrophycus	
Sargassum bracteolosum J. Agardh	A, 13, 32–38; B, 4–22; C, 10–19; D, 2
Sargassum lacerifolium (Turn.) Agardh?	A, 12, 32–38
Sargassum tristichum Grev. & Agardh ex Sonder	Masillon I. in bay, 1–4
Eusargassum	
Sargassum linearifolium (Turn.) Agardh?	B, 4–7; C, 6, 19
Sargassum podacanthum Sonder?	A, 32–38
Sargassum spinuligerum Sonder	A, 35
Sargassum distichum Sonder	A, 35
Sargassum (Eusargassum, tribe Glomerulatae?)	C, 10–13
RHODOPHYTA	
Nemaliales—Chaetangiaceae	
Galaxaura spathulata Kjellman	A, 32–38; B, 22. Masillon I. in bay, 1–4
Helminthocladiaceae	
Liagora harveyiana Zeh	A, 2
Bonnemaisoniaceae	
Asparagopsis armata Harvey	A, 10, 32–38; B, 4–18
Delisea hypneoides Harvey	A, 32–38; B, 13–18; C, 19
Delisea pulchra (Grev.) Montagne	A, 10, 32–38; B, 6–22
Gelidiales—Gelidiaceae	
Pterocladia lucida (R.Br.) J. Agardh	B, 4–7, Masillon I. in bay, 1–4
Cryptonemiales—Dumontiaceae	
Acrosymphyton taylori Abbott	A, 32–38
Squamariaceae	
Sonderophycus australis (Sond.) Denizot	B, 13–32
Corallinaceae (excluding encrusting taxa)	
Amphiroa anceps (Lamarck) Decaisne	A, 32–38; B, 13–18, 32; C, 10–19
Jania fastigiata Harvey	C, 0–2
Jania micrarthrodia Lamouroux?	D, 3 on *Posidonia australis*
Jania pusilla (Sond.) Yendo	B, 4–7; Masillon I. in bay 1–4 on *Cystophora subfarcinata*
Jania sp.	A, 32–38
Corallina cuvieri Lamouroux	B, 6
Corallina cuvieri f. crispata Lamouroux	B, 0–6; C, 0–6; D, 2
Metagoniolithon charoides (Lamx.) W. v. Bosse	C, 6–19
Metagoniolithon stellifera (Lamarck) W. v. Bosse	D, 2 on *Amphibolis antarctica*
Polyporolithon patena (H. & H.) Mason	B, 13–18 on *Ballia callitricha*
Cryptonemiaceae	
Carpopeltis phyllophora (H. & H.) Schmitz	A, 32–38, Masillon I. in bay, 1–3
Cryptonemia undulata Sonder	D, 2
Halymenia harveyana J. Agardh	B, 13–18; C, 10–13
Thamnoclonium dichotomum (J.Ag.) J. Agardh?	A, 32–38
Grateloupiaceae	
Gelinaria ulvoidea Sonder	C, 19–20
Kallymeniaceae	
Austrophyllis alcicornis (J.Ag.) Womersley & Norris	A, 32–38; B, 13–18, 32
Callophyllis rangiferinus (Turn.) Womersley	A, 2–10; B, 0–7; C, 10–13
Callophyllis lambertii (Turn.) J. Agardh	A, 55
Kallymenia cribrosa Harvey	A, 32–38; B, 13–22
Kallymenia spinosa Womersley & Norris	A, 55
Thamnophyllis lacerata Womersley & Norris	A, 32–38
Gigartinales—Plocamiaceae	
Plocamium angustum (J.Ag.) Hooker & Harvey	A, 6–55; B, 6–32; C, 6–19

Plocamium cartilagineum (L.) Dixon	A, 6–10, 32–38, 55; B, 13–22, 32
Plocamium leptophyllum Kuetzing	A, 55
Plocamium mertensii (Grev.) J. Agardh	A, 6–55; B, 6–22; C, 6–19
Plocamium preissianum Sonder	A, 6–55; B, 6–32; C, 6–19
Solieriaceae	
Solieria robusta (Grev.) Kylin	A, 32–38; C, 20; D, 4
Rhabdoniaceae	
Areschougia congesta (Turn.) J. Agardh?	A, 32–38
Rhodophyllidaceae	
Rhodophyllis membranacea (H. & H.) Harvey	A, 35; B, 13–22
Rhodophyllis ramentacea (C.Ag.) J. Agardh	A, 32–38; B, 32
Hypneaceae	
Hypnea episcopalis Hooker & Harvey	B, 6; C, 10–13
Hypnea sp.	A, 2; B, 4–6
Mychodeaceae	
Mychodea pusilla (Harv.) J. Agardh	D, 2, on *Amphibolis antarctica*
Mychodea ramulosa J. Agardh	B, 4–7
Mychodea carnosa Hooker & Harvey	A, 32–38
Neurophyllis australis Zanardini	C, 19–20
Dicranemaceae	
Dicranema revolutum (C.Ag.) J. Agardh	D, 2, on *Amphibolis antarctica*
Acrotylaceae	
Hennedya crispa Harvey	D, 24, loose-lying
Rhodymeniales—Rhodymeniaceae	
Fauchea?	A, 32–38
Webervanbossea kaliformis (J.Ag.) J. de Toni	A, 32–38; B, 22; C, 10–13, 19
Webervanbossea splachnoides (Harvey) J. de Toni	A, 32–38; C, 19–20
Botryocladia obovata (Sonder) Kylin	C, 19–20
Coelarthrum cliftonii (Harv.) Kylin	A, 32–38
Coelarthrum meulleri (Sond.) Boergesen	A, 35
Gloiosaccion brownii Harvey	B, 13–18; C, 10–13
Rhodymenia australis (Sond.) Harvey	A, 32–38, 55; D, 2
Lomentariaceae	
Champia affinis (H. & H.) J. Agardh	A, 32–38; B, 13–18; C, 19
Champia obsoleta Harvey	A, 2
Champia tasmanica Harvey	A, 32–38
Ceramiales—Ceramiaceae	
Crouanieae	
Gattya pinella Harvey	A, 55
Gulsonia annulata Harvey	C, 19–20
Antithamnieae	
Acrothamnion preissii (Sond.) Wollaston	B, 13–18, on *Ballia callitricha*
Antithamnion divergens (J.Ag.) J. Agardh	A, 55
Ballia ballioides (Sond.) Wollaston	A, 55
Ballia callitricha (Ag.) Kuetzing	A, 35; B, 13–18, 32
Ballia mariana Harvey	A, 55
Platythamnion nov. sp?	A, 55
Griffithsieae	
Griffithsia teges Harvey	A, 2
Callithamnieae	
Callithamnion sp.	A, 32–38
Callithamnion sp.	A, 55
Dasyphileae	
Rhodocallis elegans Kuetzing	A, 55
Delesseriaceae	
Apoglossum tasmanicum (F.v.M.) J. Agardh	B, 32
Dasyaceae	
Dasya clavigera (Wom.) Parsons	C, 0–2; D, 2–4
Dasya naccarioides Harvey?	C, 19–20
Rhodomelaceae—Polysiphonieae	
Polysiphonia nigrita Sonder	A, 2
Pterosiphonieae	
Pterosiphonia sp.	B, 6
Herposiphonieae	
Dipterosiphonia? nov. sp?	B, 13–18
Herposiphonia nov. sp?	A, 55

Polyzonieae	
Cliftonaea pectinata Harvey	A, 32–38; B, 13–18; C, 19
Amansieae	
Osmundaria prolifera Lamouroux	B, 13–18; C, 6–20
Laurencieae	
Laurencia elata (Ag.) Harvey	B, 13–18
Laurencia filiformis (Ag.) Montagne f. *dendritica* Saito & Womersley	A, 32–38
Laurencia filiformis (Ag.) Montagne f. *heteroclada* Saito & Womersley	A, 0–2; C, 19–20
Laurencia paniculata (Ag.) J. Agardh	C, 19–20
SPERMATOPHYTA—seagrasses	
Potamogetonaceae	
Heterozostera tasmanica (Mart. ex Aschers) den Hartog	D, 3
Posidonia australis J. D. Hooker—narrow and broad forms	C, 19–22; D, 3–4
Posidonia ostenfeldii den Hartog	D, 3, Masillon I. in bay 6–9
Amphibolis antarctica (Labill.) Sonders ex Aschers	D, 2

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BREEDING BIOLOGY AND LARVAL DEVELOPMENT OF *LITORIA VERREAUXI* (ANURA: HYLIDAE)

BY MARION ANSTIS**

Summary

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Introduction

Litoria verreauxi (Duméril), previously included in *Hyla ewingi* Duméril & Bibron (see Littlejohn 1963, 1965; Tyler 1971) is a hylid frog found along the coast of eastern Australia from Victoria to southern Queensland (Littlejohn 1965; Straughan 1966)†. Adult morphology in the Sydney area has been described by Copland (1957) as *H. ewingi verreauxi*, and by Moore (1961) as *H. ewingi*. Fletcher (1889) and Harrison (1922) provided some data on the breeding season, ova and larvae, while Moore (1961) briefly described advanced embryos and larvae. Martin (1965) described tadpoles from the Melbourne area but did not discuss embryonic development. Martin & Watson (1971) mention some life history characteristics. The present paper provides data on breeding biology and larval ecology and includes a detailed description of embryos and larvae.

L. verreauxi appears to be related to a complex of species including *L. ewingi*, *L. paraewingi*, *L. jervisiensis*, and possibly *L. burrowsi* (Martin & Littlejohn 1966; Martin 1967a; Watson, Loftus-Hills & Littlejohn 1971). Where data are available, comparisons are made with these taxa.

Material

Six egg masses of *L. verreauxi* laid in the laboratory, together with samples of larval material from the field, form the basis of the study. Egg masses came from an adult population, originally collected at Darke's Forest in 1970 and released in a garden at Penshurst. Frogs from adjacent areas in Penshurst may also have joined the population.

An egg mass from a pair of *L. ewingi* captured in amplexus at Lobethal, S. Aust. on 30.viii.1972, was maintained to hatching stages. Larvae of *L. paraewingi* from 2 km N of Glenburn, Vict. were examined for comparison. Collecting localities and dates are listed in Table 1.

Methods

A series of outdoor aquaria containing rainwater and vegetation was maintained at Penshurst and checked regularly for the presence of spawn. Three pairs (one in amplexus) were captured in the vicinity of the aquaria (two on 11.ix.1972 and one on 20.ii.1974) and placed in plastic bags containing water, twigs and vegetation. Oviposition behaviour of these three pairs was studied.

Embryos were maintained up to stage 25 in shallow water ranging from 14°–21°C. Larvae from the various localities were maintained separately in open outdoor aquaria, and individuals from some were reared to metamorphosis. The behaviour of larvae was studied both in aquaria and at field collecting sites. Food provided consisted of algae and other water plants, commercial fish food, boiled lettuce and occasionally meat. Water temperature during larval development ranged 8°–27°C. Specimens from each group were fixed at inter-

* 630 King George's Road, Penshurst, N.S.W. 2222.

† Straughan, I. R. (1966).—An analysis of species recognition and species isolation in certain Queensland frogs. Ph.D. thesis, University of Queensland (unpubl.).

TABLE 1

Breeding sites of Litoria verreauxi

Locality	Description of habitat	Collecting date	Stages	Other larvae present
Menai, 34°02′ S 151°01′ E	1. Permanent dam in dry sclerophyll bushland. Surface vegetation, rooted plants, mud substratum.	21.ii.1971	34–42	*Litoria aurea* *L. latopalmata* *Uperoleia marmorata* *Ranidella signifera*
	2. Concrete water vessel, permanent water, surface vegetation, mud substratum	16.ix.1972	34–41	
Penshurst, 33°58′ S 151°05′ E	Permanent outdoor aquaria in suburban garden. Surface and rooted plants	Numerous dates, 1970 to 1974	1–46	
Darke's Forest, 34°12′ S 151°58′ E	1. Permanent flowing stream, sandstone base, fast flowing sections, deep pools in dry sclerophyll bushland.	16.ix.1972	16–18	*Litoria jervisiensis*
	2. Permanent dams, little rooted and no surface vegetation, mud substratum	24.ix.1972 30. x.1972 2.xi.1972 6.xi.1972	26–40	*Limnodynastes peroni* *Litoria peroni* *Ranidella signifera*
Ourimbah, 33°22′ S 151°22′ E	Semi-permanent, small, slowly flowing creek, shallow pools, rooted vegetation, mud substratum. Cleared farmland in wet sclerophyll forest	19.ix.1973	25–33	*Ranidella signifera*
Glen Alice, 33°02′ S 151°12′ E	Semi-permanent, shallow pond, grass bottom, in open cleared farmland with surrounding woodland	1.vi.1974	25–28	*Limnodynastes tasmaniensis*
Spring Creek, 30°29′ S 152°24′ E	Permanent creek, slowly flowing small pools, sandy and basalt substratum. Wet sclerophyll forest, partly cleared	25.i.1973 25.xii.1973 18.iv.1973	30–46 25–42	*Mixophyes balbus* *Ranidella signifera* *Litoria glandulosa* *L. pearsoni*
Dorrigo, 30°20′ S 152°43′ E	Small, slowly flowing creek, surface vegetation, mud substratum. Cleared rainforest farmland	26.xii.1974	28–43	*Mixophyes fasciolatus* *Adelotus brevis*
Rouse Hill, 33°42′ S 150°55′ E	Permanent waterhole in cleared paddock. Dry sclerophyll bushland area, farmland	19.xii.1972	27–42	*Litoria caerulea* *Ranidella signifera*

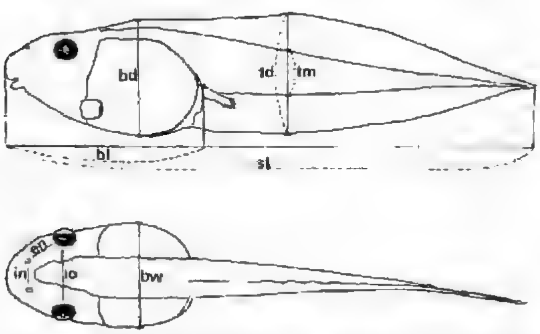


Fig. 1. Lateral and dorsal views of larva showing measurements for morphometric characters.

vals in 4% formalin, after being relaxed in 1% chlorbutol solution; larger specimens were injected with a small quantity of formalin before final fixation.

Measurements were taken with vernier callipers reading to 0.1 mm or an ocular micrometer (reading to 0.01 mm). Drawings were made using a drawing tube attached to a stereoscopic microscope. All measurements and drawings are based on preserved specimens, while descriptions are of both preserved and live material. The staging system used is that of Gosner (1960). Abbreviations and definitions of larval morphometric characters (Fig. 1) are: ST—total length (tip of snout to tip of tail); BL—body length (tip of snout to junction of body wall and tail musculature); BW—maximum body width; BD—maximum body depth; TD—maximum tail depth; TM—depth of tail musculature (measured in line with TD); IO—inter-orbital span (minimum distance between the eyes, measured at the central inner edge of each eye); IN—internarial span (minimum distance from eye to naris); EN—distance from eye to naris; MW—maximum width of oral disc.

Results

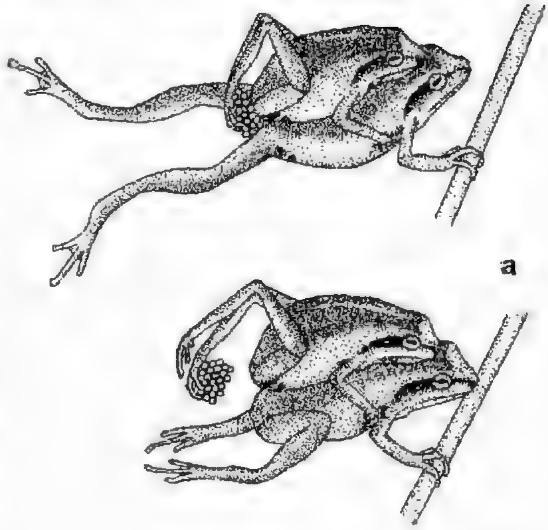
Calling activity: The mating call has been described by Littlejohn (1965). Males at Penshurst call throughout the year, with the most intense activity on mild, wet nights during spring and summer. Diurnal calling mostly occurs during and after rain. Males call while afloat near the edge of ponds by night, or from low vegetation or ground near the water by night or day. At 2300 hrs on 20.ii.1974 at Penshurst, during light rain, a silent male surfaced in an aquarium about 4 cm from a calling male. The latter turned to face the former and, after a brief pause, swam slowly towards him, calling in softer, separate notes (quite distinct from the mating call) and attempted amplexus. The silent male immediately swam off. The calling male did not follow, but resumed a normal mating call.

A similar behavioural sequence preceded amplexus in one of the pairs captured on 11.ix.1972, the male emitting soft, separate notes as he approached the female.

Oviposition: Oviposition at Penshurst has been observed in February, March, June and September–December. The following description is a composite of observations of the three pairs studied.

When frogs were collected on 11.x.1972, air temperatures 2 cm above water were 18°–19°C and surface water temperatures 19°–23°C. Amplexus commenced in these pairs at 2000 and 2325 hrs. Eggs were laid in separate batches attached to twigs or reeds over a period of hours (Table 2). Before oviposition, the female showed lateral abdominal contractions, either simultaneously or alternately. These contractions usually became more powerful as oviposition was near and lasted about one second, with two or more occurring in succession.

In a typical behavioural sequence, a pair submerged and the female grasped a twig with one hand. She dorsiflexed her body with the hind limbs extended and, as the batch emerged, the male lowered his vent towards the eggs and cupped his feet around, so holding them (Fig. 2a). The sides of the male then undulated and his feet moved up and down in a brief fanning motion over the eggs. This process of oviposition and fertilisation lasted 3 sec. The female ventriflexed, drawing her legs back under her body, and the male rolled the batch down to her feet (Fig. 2b). The female held the batch motionless for 40 sec. She then pulled herself around the twig in spiral fashion, wrapping the eggs round it with her feet. The pair left the eggs and returned to the surface. After 1.5–7.5 min. the entire process was repeated, and 5 min.–2 hr elapsed before further batches were laid.



a

b

Fig. 2a. Oviposition with the male receiving and fertilising the eggs.
Fig. 2b. The male pushes the batch down to the female's feet.

Variations were: (1) Nearing the end of amplexus, two or three batches were laid in very close succession, each being held by the feet of the female for 40–60 sec. before the ensuing one was laid. The resulting composite batch was then attached to supporting material. (2) Females varied in their attempts to spread

TABLE 2
Oviposition behaviour

Pair	Total duration of Amplexus	Duration of egg-laying period	Duration of single batch oviposition	Batch holding time (female)	n	Total eggs laid
1	5 hr 15 min.	2 hr 18 min.	2–4 sec.	35–60 sec.	15	757
2	Unknown	3 hr 47 min.	2–4 sec.	35–60 sec.	23 or 24	1,011

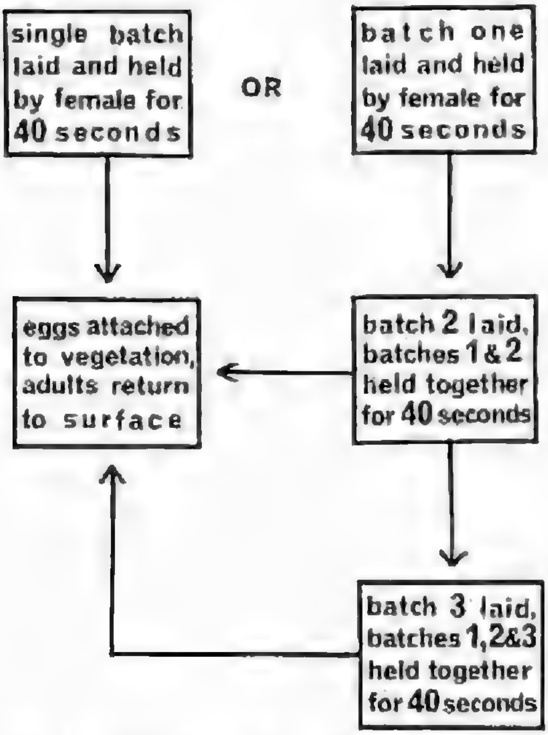


Fig. 3. Oviposition cycles during which a single batch is laid and attached to vegetation, or two or three are laid in close succession before attachment.

out the eggs in spiral fashion, sometimes swivelling around the twig only once or not at all, resulting in thicker clumps of eggs. (3) One female used her left hand to grasp and pull free some eggs which had adhered to her venter, before attaching the batch to vegetation.

Females had more difficulty in wrapping a composite batch around a twig, and often abandoned the eggs as a thick mass. In aquaria lacking vegetation or twigs, egg masses have been found in thick clumps on the substratum, in water up to 50 cm deep.

The final stages of amplexus in one pair were: at 0100 hrs the female made movements similar to the croaking motions of males, but produced no sound. At 0108 hrs she submerged and both male and female began typical ovipositional behaviour, but the female remained in the dorsiflexed position for 7.7 sec. (4.7 sec. longer than average) and produced no eggs. Two sec. later the pair fell apart, both floating motionless on their sides just under the surface, with limbs tightly adpressed against the body. After 10 sec., the male

Fig. 4. Two batches of eggs joined and attached to a stem. Filamentous algae are entwined amongst the egg mass.

recovered from this state of suspension and surfaced, the female doing so 5 sec later. A second pair behaved similarly, except that the period of motionless suspension was shorter. The basic cycle of oviposition behaviour is shown in Fig. 3. Laying of all eggs comprises a number of such cycles.

Ova: In natural environments egg masses are attached to submerged reeds, twigs or grasses usually close to the surface (Littlejohn 1963). The eggs cohere and the inner ones stick to the supporting material. There is a single layer of jelly around each egg, but within a mass the individual capsules merge and are not clearly defined (Fig. 4).

The mean diameters of eggs and capsules in stages 1 and 8 are shown in Table 3. Ova generally have a dark brown animal pole and an off-white, yellow or orange vegetal pole. All ova from a single female are the same colour. The animal pole gradually lightens from gastrulation onwards.

The number of eggs in 20 single batches ranged from 1–52 (mean 30). Three "double" batches contained 64, 78 and 79. The total complements of four females were 1,011, 757, 632 and 522.

Development of embryos: After fertilisation there is no distinct grey crescent. Cell division appears normal, although not as symmetrical as in Gosner's (1960) diagrams. The vegetal pole always divides later than the animal pole. At stage 17 (tail bud: Fig. 5a), the head region is well defined, showing optic bulges, gill plates, U-shaped adhesive organ and a slight stomodaeal pit. The posterior crescent of the adhesive organ is less distinct. In some embryos the visceral arches and a slight pronephric bulge are discernable. The tail bud is straight and points dorsally, with no obvious tail fin rudiment. In late stage 17, just before muscular movement begins, the tail bud extends and points either to the right or to the left, and the posterior crescent of the adhesive organ almost disappears, yielding two separate organs which are heavily pigmented. Embryos in stages 17 to 20 have a yellow yolk sac and are light brown elsewhere.

The embryos begin hatching when they have reached stages 19 and 20. At stage 20 (Fig. 5b) the gills are small, just functional and non-pigmented. The optic bulges are more defined, and there is a small crescent of melanophores around the anterior edge of each. The stomodaeal pit has deepened and the adhesive organs are prominent. The yolk sac has elongated and is generally narrow, and there are small areas of pigment along its dorsal edge, and between the optic bulge and olfactory pit. The area above the olfactory pit is clearing and the tail fins are a translucent milky white.

With the temperature regime prevailing during early development, hatching was complete after 147 hr when most embryos were in stages 21–23. The external gills are fully developed in stage 21 (Fig. 5c). The tail fins and cornea clear during stage 22; the operculum partly covers the gills, and the distribution of melanophores increases over the yolk sac, beneath the eyes, around the nares and along the dorsal surface of the tail musculature. At stage 23 the gills are reduced, the external nares are open, the stomodaeal pit deepens further and the oesophagus begins to differentiate. The anal tube is developing and the fins, now transparent, take on their characteristic arched shape. Generally, pigmentation increases, dispersing into the pattern typical of the larva. The yolk sac is pale yellow beneath the layer of melanophores, while other dorsal and lateral areas surrounding the pigment, become transparent. However one group of embryos at this stage lacked dark pigment (except for the eyes), and appeared yellow. These embryos did not develop melanophores until stage 25.

At stage 24 the mouth-parts have developed oral ridges and a small non-keratinised beak, the oral suckers have diminished, and the operculum closes on the right side. The anal tube is partly open in some embryos. During stage 25 the formation of mouthparts is virtually completed, the beak becoming keratinised and

TABLE 3

Dimensions in mm of embryos and larvae of L. verreauxi *from Penshurst*
(means, with ranges in brackets)

Embryos Stage	n	Embryo diam.	Capsule diam.
1	10	1.23 (1.19–1.23)	4.31 (3.53–4.92)
8	8	1.20 (1.15–1.23)	4.55 (4.26–4.92)
9 & 10	9	1.28 (1.23–1.39)	3.88 (3.44–4.35)
14	9	1.55 (1.48–1.64)	4.28 (3.74–4.92)
15	9	1.74 (1.68–1.80)	4.41 (4.10–4.92)
17	10	2.11 (1.85–2.30)	4.39 (3.61–6.40)

Stage	n	Embryo diam.
20	10	5.83 (5.62–5.99)
21	10	6.27 (6.07–6.44)
22	10	6.40 (6.15–6.64)
23	10	6.98 (6.23–7.30)
24	9	7.26 (6.72–7.71)
25	10	8.45 (7.87–9.18)

Larvae Stage	n	Body length	Total length
26	10	10.16 (9.02–12.79)	23.6 (19.0–31.4)
27	10	11.11 (10.50–11.64)	24.2 (21.2–27.2)
28	10	10.85 (9.68–11.91)	24.0 (21.0–27.6)
29	9	11.16 (10.33–11.97)	24.5 (24.0–27.2)
30	10	12.88 (11.15–13.78)	29.1 (25.2–31.5)
31	10	13.65 (12.30–15.42)	33.6 (27.5–39.4)
32	7	13.40 (11.91–14.27)	30.5 (27.0–33.2)
33	8	14.31 (13.94–15.58)	32.6 (31.0–34.0)
34	8	14.85 (13.12–15.74)	34.7 (30.1–37.6)
35	10	16.65 (14.76–19.68)	41.1 (33.0–48.8)
36	10	16.15 (15.35–18.61)	41.4 (34.8–47.2)
37	8	16.22 (14.92–17.22)	39.5 (36.4–44.8)

Stage	n	Body length	Total length
38	6	16.84 (15.00–18.00)	43.2 (39.6–46.0)
39	6	17.27 (16.73–18.32)	45.6 (42.0–51.9)
40	10	16.87 (14.76–18.37)	46.6 (39.2–52.2)
41	10	17.09 (16.56–18.20)	48.2 (45.0–52.9)
42	3	16.13 (14.27 17.38)	43.1 (40.5–45.1)
43	4	14.51 (14.27–14.92)	38.6 (37.4–39.7)
45	10	16.3 (14.9–18.6)	—
46	18	15.3 (13.2–17.3)	—

labial teeth developing on the oral ridges. The labial papillae may not reach their total number until stage 26 or later. The spiracle becomes functional and the anal tube is fully open. The remnant adhesive organs gradually disappear during this stage.

Measurements of embryos are shown in Table 3.

Larvae: A composite description of 10 larvae at stage 35 (Figs 5d–f) from Penshurst follows: Body widest across the mid region of the abdomen and ovoid. Snout evenly rounded in dorsal view and tapers to a truncate edge in lateral view. Nares dorsal and raised on very short tubes which open antero-laterally. Eyes lateral and relatively large. Spiracle sinistral, ventrolateral and not visible from above. It opens in a porstero-dorsal direction and diameter of the spiracular tube decreases slightly from its origin to its opening. Anal tube dextral, very short, of small diameter and opens about halfway up the ventral fin. Tail fins arched and taper to a fine point. Dorsal fin extends midway up the body, deepest approximately halfway along its length. Ventral fin deepest along its anterior third. Tail musculature moderately thick, narrowing to a fine point posteriorly.

Mouth antero-ventral in position and has border of papillae around all but the anterior margin (Fig. 6). In some specimens there is also a median gap along the posterior margin (possibly caused by damage). Papillae most numerous laterally. Two upper and three lower rows of labial teeth, two upper being of approximately equal length in most specimens. First two rows in the lower labium are also about equal, third lower row is usually the shortest. In some specimens a partial median gap occurs in second lower row and other rows may be interrupted at various points, probably through damage. Beaks of moderate proportions, serrations fine on inner edge of lower beak and very fine on the upper beak.

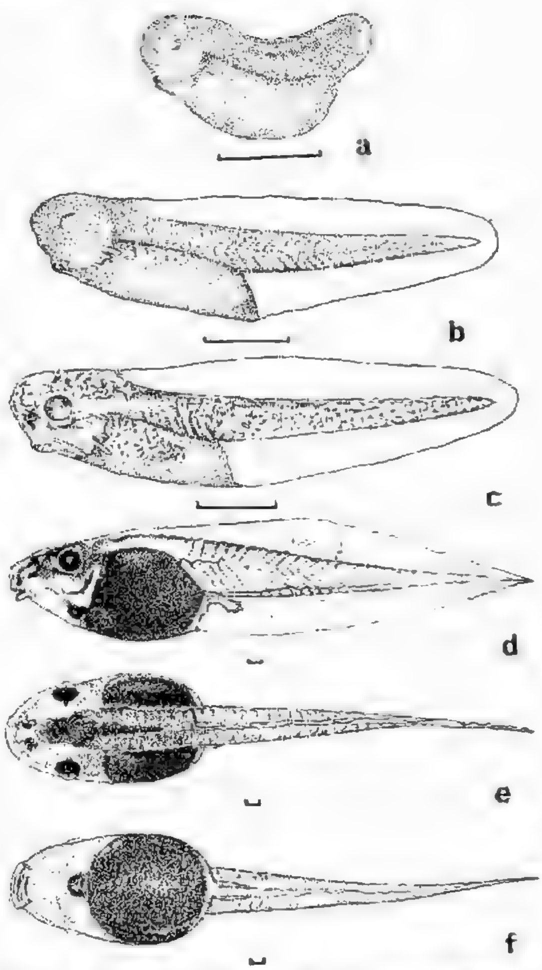


Fig. 5. Embryological and larval development of *Litoria verreauxi*, Penshurst. (Bar represents 1 mm). Stages: a—17, b—20, c—21, d—36, e—36, f—36.

The only consistent geographic variation noted was in specimens from Spring Creek, most of which had more massive beaks and two pigmented areas below the lower beak (Fig. 6b). Specimens from Dorrigo also showed a tendency towards more massive beaks. It was noted that specimens from the northern localities generally had shallower fins than most southern specimens (Table 4). Body dimensions of larvae are given in Table 3.

In life the dorsal surface varies amongst individuals from light golden to a very dark

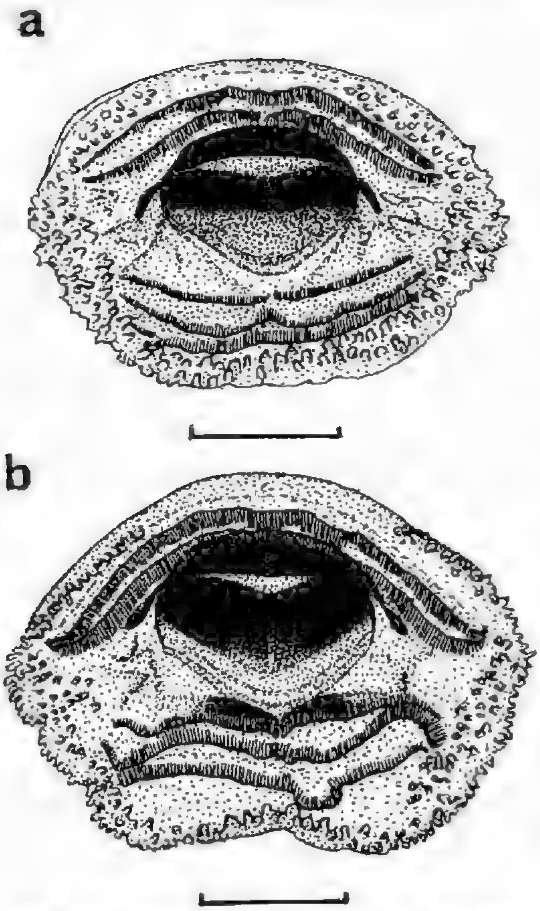


Fig. 6. Mouthparts of *L. verreauxi*. a, from the southern site of Penshurst; b, from the northern site of Spring Creek (bar represents 1 mm).

brown (almost black). In some specimens the pigment is mottled. The areas of skin over the trabeculae cornua, central nervous system (brain and spinal cord to base of tail), the abdomen and surrounding the nares, are darker. There is a copper-gold sheen ventrally and laterally over the abdomen. In lateral view the areas covering the pharynx and buccal cavity (excluding eyes) are transparent (except for some melanophores between the eye and naris); and the gills, heart and developing forelimbs are visible. From the ventral aspect the areas over the gills, heart and buccal cavity are unpigmented.

The tail musculature is cream with irregular dark blotches over the dorsal surface, and partly over the lateral surface. In generally darker larvae the musculature may be uniformly pigmented. The dorsal and ventral fins

TABLE 4

Proportions in mm of L. verreauxi *larvae from different localities*

(means, with ranges in brackets)

	Northern (Spring Creek, Dorrigo)	Southern (Penshurst)
Stage	35 & 36	35 & 36
n	7	10
ST	35.1 (30.9–41.2)	43.1 (36.3–48.8)
BL	13.69 (12.46–16.56)	17.27 (15.58–19.68)
BW	7.74 (6.72–8.86)	10.26 (8.69–11.48)
BD	7.79 (6.56–9.35)	10.50 (8.86–12.14)
TD	7.98 (6.48–9.68)	10.19 (8.53–12.30)
TM	2.68 (2.13–3.28)	3.60 (2.79–4.59)
IO	3.92 (3.44–4.55)	5.53 (4.66–6.40)
IN	2.01 (1.72–2.21)	2.64 (2.40–2.95)
EN	2.25 (2.13–2.69)	2.69 (2.38–3.12)
MW	2.03 (2.95–4.43)	4.10 (3.61–4.66)

vary from dusky (in dark larvae) to almost transparent (lighter larvae), with parts of the tail vascular system pigmented. Larvae with mottled pigmentation over the body also have mottled tails. The iris is golden.

Specimens which were dark in life may retain much of this pigment in preservative. Those which were light golden become an off-white colour in all but the darker areas, and the skin is clearer than in life. The copper-gold sheen is lost and the abdomen may appear dark shiny blue for some time in preservative, then eventually turn black. The iris loses its golden colour and also appears black.

Larval behaviour: After hatching the embryos remain close to the egg capsules until about stage 24. During stages 25 to about 27, the larvae are most often found in the shallow areas of ponds, particularly near the edge, but beyond this stage a much greater water space is utilized.

The larvae are of the active, nektonic type (Orton 1953) and spend much of their time hovering in the water by rapidly oscillating the tail tip (flagellum). They frequently cruise slowly to the surface with head uppermost at about a 45° angle, using only the flagellum for propulsion. When feeding at the surface, they often position themselves almost vertically and can remain suspended at this, or any level in the water. They are capable of sudden spurts of speed (during which they may use the entire tail and body), and rapid changes of direction (making use of the deep fins), when disturbed. As well as feeding at the surface, the larvae graze on vegetation and other material in any zone of the pond and scavenge in bottom sediments. The variation in larval pigmentation appears to be related to characteristics of the habitat. Specimens in muddy water, or clear water over a dark substratum, usually range from dusky brown to almost black, while those in clear water over a light substratum tend to be golden, with the darker areas contrasting, but less pronounced.

Larval life span and metamorphosis: Metamorphosis of larvae reared from eggs laid at Penshurst on 11.ix.1972 began on 10.xii.1972, giving a spring-summer larval life span of 90 days. Metamorphosis of larvae from egg masses laid on 23.x.1971 occurred from late December to early March. Metamorphosis was also recorded at Penshurst in September 1972 and at Menai from 27–29.ix.1972. It is therefore known to occur from September–March, but probably takes place at other times because egg masses have been found in most months of the year.

The body lengths of 10 juveniles at stage 45 and 18 at stage 46 are shown in Table 3. At these stages the juveniles closely resemble the adults in colour, but lack the deep orange on the anterior and posterior surfaces of the thigh, and the black spots in the groin. Pale orange thigh colouration is visible in some juveniles at stage 46.

Discussion

Calling activity: Fletcher (1889) and Harrison (1922) noted that calling occurs throughout the year, and Moore (1961) observed calling activity from the end of July 1952 to late April 1953. Watson *et al.* (1971) record calling activity in all months except July and found that *L. verreauxi* males when sympatric with *L. ewingi* usually call on land up to 25 m from water, and only rarely in water. This latter behaviour contrasts with that of males at Penshurst and Darke's Forest which commonly call in water.

A call distinct from the mating call, given by the male on approaching a potential rival or mate, has been observed; its function is not known. More observations are necessary to establish the extent of behavioural variation in this species. A similar call has been observed in *L. ewingi* (Anstis 1976).

Oviposition: Harrison (1922) found spawn in Sydney every month of the year, and Moore (1961) collected embryos in August, 1952 at Killara. Fletcher (1889) found a pair in amplexus in June, 1885 and stated that the species "probably breeds nearly throughout the year". This agrees with the oviposition dates recorded at Penshurst.

Oviposition has been observed in few Australian hylids. Watson *et al.* (1971) described part of the behaviour associated with egg-laying in *Litoria paraewingi*, and I have observed oviposition in *L. citropa*, *L. dentata*, *L. freycineti* and *L. glauerti*. Some of the ovipositional patterns in *L. verreauxi* are unique, notably the action of the male pushing the clutch down to the feet of the female where the eggs are held motionless for a short period.

The behaviour of the male in cupping his feet around the batch and rapidly "fanning" the eggs may serve to distribute the seminal fluid around the eggs within a more confined space and thus aid fertilisation. A similar although somewhat briefer process occurs in the ovipositional behaviour of *L. citropa*, *L. dentata* and *L. glauerti* (Anstis unpubl.). By holding the batch still for a period of some seconds, the female may also aid fertilisation in allowing time for sperm penetration before the eggs are attached to supporting material.

It is not known whether the abdominal contractions in the female prior to egg-laying were the sole factor in extruding the eggs, or whether the pressure exerted by the clasp of the male aided the process.

The attachment of eggs to vegetation in a spiral movement has been recorded by Harrison (1922) for *L. verreauxi* (as *H. ewingi*) and by Watson *et al.* (1971) for *L. paraewingi*. Harrison's statement that the female moved "right around the stalk at the moment of laying" is not borne out by the present study, but it is possible that Harrison did not see the entire egg-laying procedure. Watson *et al.* (1971) state that a female of *L. paraewingi* observed in the field "held onto a submerged grass stem, and pressed the cloaca to the stem as the eggs were extruded; then the pair pivoted around the stem while attaching the eggs". Such behaviour would appear to be similar to that of *L. verreauxi* except that in the latter, the female holds the eggs still before attachment and was not observed pressing the cloaca to the stem during egg extrusion. In the three oviposition sequences observed in this species, the extent to which batches of eggs were spread around the supporting vegetation varied. Observations have indicated that the mortality rate of embryos is lower in smaller well-spread batches attached to a stem. Larger masses of eggs on the bottom of aquaria without vegetation suffer high mortality from about stage 9 onwards, possibly due to inadequate oxygenation resulting from the thickness of the egg mass and the depth of the water where they lay. The attachment of two or three batches together as one also tends to increase mortality. After death of an embryo, a fungus develops over the egg capsule.

The manner of termination of amplexus varies amongst hylids, but often the last ovipositional sequence is longer than any other and is followed by separation either immediately or a few seconds later, e.g. in *Hyla versicolor* (Fouquette & Littlejohn 1960), and *Litoria dentata*, *L. glauerti* and *L. citropa* (Anstis unpubl.). *L. verreauxi* also follows this pattern; however, the brief period of total immobility of both male and female after separation has not been recorded in other species.

Ova: The significance of eggs being deposited in small batches has been discussed by Pyburn (1963) and Martin & Littlejohn (1966). Harrison's (1922) observation that the eggs are "attached in a cylindrical mass numbering upwards of a hundred eggs to grass stalks and similar submerged objects" is probably based on cases where two or three batches were attached as one.

The ovidiameter in stages 1–8 (1.21 mm) is in agreement with Harrison's figure of 1.2 mm. The ovidiameter of *L. ewingi* has been recorded as 1.65 mm (Martin & Littlejohn 1966) and that of *L. ewingi* and *L. verreauxi* as 1.7 mm (Martin, Littlejohn & Rawlinson 1966). A series of eggs of *L. ewingi* laid in Adelaide during September 1972, have mean diameters of 1.18 mm (at stage 1), 1.20 mm (stage 5) and 1.68 (stages 12–13); measurements similar to embryos of *L. verreauxi* at the same stages (Table 3). It would seem likely therefore that measurements by Martin *et al.* may have been taken from embryos at about stages 11–13.

The eggs of *L. paraewingi* are similar to those of *L. ewingi* (Watson *et al.* 1971). Those of *L. jervisiensis* can readily be distinguished from other members of the complex by the larger ovidiameter (2.33 at stage 10: Martin & Littlejohn 1966). Eggs of *L. burrowsi* can be distinguished from those of the *L. ewingi* group by the presence of two jelly layers around the ovum. The ovidiameter of this species at stage 14 is close to that of *L. jervisiensis* at the same stage.

Embryos and larvae: The larvae of the *L. ewingi* complex are of the common hylid type (Martin 1967b) as is *L. burrowsi*. The drawings by Martin (1967a) of *L. burrowsi* larvae show a tail not as finely pointed and fins not as deep as in members of the *L. ewingi* complex. The body shape also appears somewhat different. *L. paraewingi* larvae are similar to those of *L. ewingi* "except that the tail fins (especially the dorsal fin) . . . are more heavily pigmented" (Watson *et al.* 1971). Specimens of this species examined are more uniformly pigmented than *L. verreauxi*, and three specimens at stage 26 (mean total length 12.9 mm; body length 7.02 mm) are much smaller than *L. verreauxi* at the same stage. Such size differences may be related to environmental factors.

The mouthparts of the group are basically similar, having a formula of

$$\frac{\begin{matrix} & 1 & \\ 1 & & 1 \end{matrix}}{\begin{matrix} 1 & & 1 \\ & 2 & \end{matrix}}$$

All have a median gap in the papillae on the upper lip, the extent of which varies amongst individuals of the same species. The number and size of the papillae is variable between species: those of *L. jervisiensis* are more numerous and tightly grouped than in *L. verreauxi*, while those of *L. paraewingi* are a little larger and less numerous. The larvae of *L. jervisiensis* possess larger, darker and more massive beaks than *L. verreauxi* and in a number of specimens of the former species from Darke's Forest, the central edge of the upper beak curves slightly below the level of the rest of the edge, unlike *L. verreauxi*. The two pigmented areas below the lower beak in *L. verreauxi* from Spring Creek, are not found in other members of the *L. ewingi* complex.

Larval behaviour and adaptation: All the larvae of the *L. ewingi* group are nektonic and generally exhibit behaviour patterns similar to those described for *L. verreauxi*. However, differences occur in the larvae of *L. jervisiensis* which have been observed schooling together in groups of 20 or more in the mid-level of the water. Individuals from the group move at different times to the surface where they may take air (Anstis, unpubl.). Larvae of *L. verreauxi* were never observed congregating in this manner.

Larval life span and metamorphosis: Data on larval life span are mainly limited to specimens in captive conditions. Moore (1961) records a laboratory life span of three months for *L. verreauxi* which agrees with one of the groups raised at Penshurst. Harrison (1922) found that larvae in aquaria "required upwards of three months" to reach metamorphosis, but believed seven to eight weeks to be normal life span in the field during summer. This is considerably less than the approximate minimum of 79 days for one group in the present study, but this difference may simply reflect different culture and temperature conditions. Further observations are necessary to ascertain the average life span of this species in the field.

Moore (1961) records the body lengths of 11 newly metamorphosed *L. verreauxi* as 14.3–17.00 mm: consistent with measurements of specimens in the present study (Table 3). Martin (1965) gives a range 11.1–13.6 mm for newly metamorphosed *L. ewingi*, which are generally smaller than *L. verreauxi*, and Martin & Littlejohn (1966) 15.6–19.7 mm for *L. jervisiensis*. No data on *L. burrowsi* and *L. paraewingi* are available.

The overall life cycle of *L. verreauxi* appears quite similar to that of other members of the *L. ewingi* complex in the adaptations to still water situations, although *L. jervisiensis* differs noticeably in the details of its life history (Martin & Littlejohn 1966). More data are necessary before useful comparisons can be made between the life histories of *L. burrowsi* and the *L. ewingi* complex.

Acknowledgments

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RESTRICTION OF THE CHIRIDOTID GENUS *TROCHODOTA* LUDWIG (1891) (HOLOTHURIOIDEA: APODIDA), WITH THE DESCRIPTION OF A NEW SPECIES FROM SOUTH AUSTRALIA

*BY F. W. E. ROWE**

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Trochodota Ludwig (1891) is restricted to the type-species *T. purpurea* (Lesson), and three other species, including a new species from South Australia. The generic significance of scattered or heaped wheels, used in separating *Trochodota* from *Taeniogyrus* Semper, 1868, is disputed. The distribution of serrations on the inner margin of the wheels is regarded a more reliable generic character; on this basis seven species included in *Trochodota* by H. L. Clark (1921) and subsequent authors are referred to *Taeniogyrus.*

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Introduction

Among the holothurians collected at Port Lincoln, South Australia during 1975 by Mr S. A. Shepherd are six belonging to an undescribed species congeneric with *Trochodota purpurea* (Lesson), type-species of *Trochodota* Ludwig (1891).

In one important character, the new species falls into an intermediate position between the genera *Trochodota* and *Taeniogyrus* Semper (1868), as currently diagnosed (H. L. Clark 1921; Pawson 1964). A review of the two genera has revealed that they are not based upon reliable characters; in this paper they are redescribed and a list of species given for each.

It is not appropriate to discuss in this paper the validity of all species now included in *Taeniogyrus;* since many species require re-examination and material is not available: H. L. Clark (1921); Pawson (1964). However, the differences between the four well documented species in *Trochodota*, including the new species described below, are tabulated.

Taxonomic account

H. L. Clark (1921), revising the chiridotid genera, separated *Taeniogyrus* Semper (1868) and *Trochodota* Ludwig (1891) from other genera, because they possess a combination of wheel and sigmoid ossicles. On the basis of having the wheel ossicles actually collected into sharply defined papillae of the body wall, *Taeniogyrus* was considered generically distinct from *Trochodota*. Small accumulations of wheels were considered indicative of *Trochodota*. Subsequent authors have rigidly adhered to this recognition of the two genera (A. M. Clark 1966; Hickman 1962; Pawson 1964, 1970; Heding 1928; Cherbonnier 1952). Although several new species of *Taeniogyrus* have been described since 1921, no new species of *Trochodota* have been found.

With the arrangement of wheels in large groups, though not in papillae, the new species described below falls into an intermediate position between *Taeniogyrus* and *Trochodota*. In my view, this shows the unreliability of using such a character for generic distinctions, particularly when H. L. Clark (1921) used the similar grouping of sigmoid ossicles for species determinations. A difficulty then arises in deciding the relative merits of the importance of wheels versus sigmoid ossicles in the recognition of the generic taxa, for which no sound argument has so far been advanced. One character which does so easily distinguish *T. purpurea*, *T. allani*, *T. maculata* and the new species not only from those in *Taeniogyrus*, is the arrangement of the serrations on the inner margin of the wheels. In the absence of any other reliable internal or skeletal character, I believe that this is a much more significant

* Australian Museum, P.O. Box A285, Sydney South, N.S.W. 2001.

character on which to place generic weight. It also accords with the use of spicule form in the recognition of generic taxa within other orders of holothurians (Panning 1949; Rowe 1969).

Trochodota is herein restricted to that discrete group of species with serrations of the inner rim of the wheels arranged in groups. The remaining seven species included by H. L. Clark (1921) in *Trochodota* are referred to *Taeniogyrus*.

Trochodota is now considered to be restricted to the southern hemisphere, with representative species ranging from the colder waters of the southern tip of South America to the more temperate waters of southeastern Australia, including Tasmania, and the tropical waters of the Torres Strait between Papua New Guinea and the northeastern tip of Australia. The genus is found from shore-line to depths of about 50 m.

Taeniogyrus Semper, 1868

Taeniogyrus Semper 1868: 23.
?*Sigmodota* Studer 1876: 454.
?*Trochodota* Ludwig 1891: 358 (part).

Diagnosis: Chiridotid genus with wheels and sigmoid ossicles present, scattered, or in groups or clustered into papillae; wheels with serrations continuous around the inner margin; tentacles 10 or 12.

Type-species: Chiridota australianus Stimpson 1856.

Other species: T. contortus (Ludwig 1874); *T. cidaridis* Oshima 1915; *T. dubius* H. L. Clark 1921; *T. keiensis* Heding 1928; *T. clarus* Heding 1928; *T. dunedinensis* (Parker 1881); *T. diasema* (H. L. Clark 1921); *T. roebucki* (Joshua 1914); *T. rosea* (Oshima 1914); *T. japonica* (von Marenzeller 1881); *T. dendyi* (Mortensen 1925); *T. dayi* (Cherbonnier 1952); ?*T. venusta* Semon 1887.

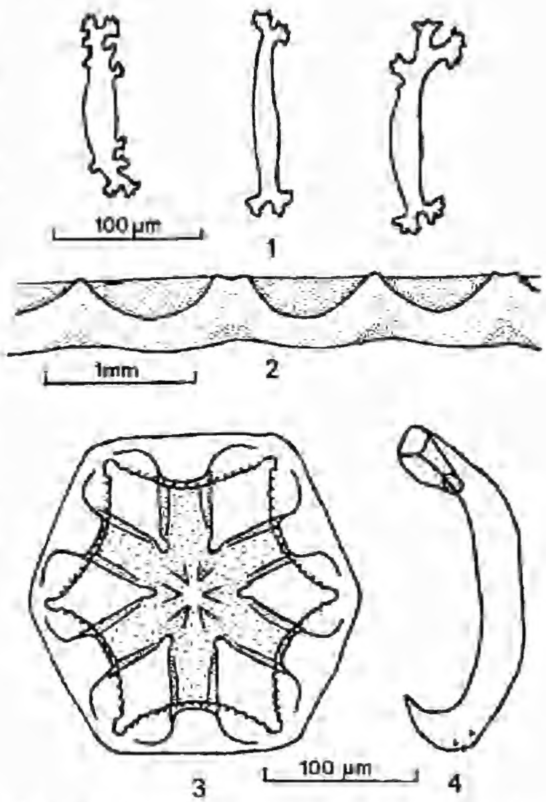
Trochodota Ludwig, 1891

Trochodota Ludwig 1891: 358 (part).

Diagnosis: Chiridotid genus with wheels and sigmoid ossicles present scattered or in groups, wheels with serrations on the inner margin in well defined groups; tentacles 10.

Type-species: Holothuria (Fistularia) purpurea Lesson 1830.

Other species: T. allani (Joshua 1912); *T. maculata* H. L. Clark 1921; *T. shepherdi* n. sp.



Figs 1-4. *Trochodota shepherdi* n.sp. Fig. 1—Tentacle rods; Fig. 2—Two radial and two interradial plates of the calcareous ring; Fig. 3—Wheel ossicle; Fig. 4—Sigmoid ossicle.

Trochodota shepherdi n. sp.

T. allani, Joshua & Creed, 1915: 21 (non *T. allani* Joshua).

Types: Holotype (Australian Museum J9467) and 5 paratypes J9796 (2) J9797 (1); South Australian Museum K1366 (2)); Proper Bay, Port Lincoln, Spencer Gulf, S. Aust., among algae growing on *Pinna dolobrata* at 10 m depth. Collected by S. A. Shepherd, 23.viii.1975.

Diagnosis: Large spicules, wheels 55–226 µm diameter; serrations on inner margin of wheels in 6 groups of about 16; sigmoid ossicles 144–190 µm long, outer curve of hook of sigmoid ossicle with minute thorns; colour in life, black.

Description of holotype (which has been dissected): The holotype is 60 mm long, of which the anterior 20 mm is contracted. Body diameter 5–8 mm along its length, tapering only at the posterior end. Ten strongly contracted tentacles, each with about 3 pairs of digits.

TABLE 1

Differences between species of Trochodota

Species	Sigmoid ossicles			Wheel ossicles		Colour	Distribution
	Grouping	Hook	Length	Grouping	Diameter		
maculata	in papillae and scattered	smooth	66-77 μm	scattered	50-100 μm	pink with darker spots	Torres Strait, Qld
allani	scattered perpendicular to longitudinal body axis	smooth	120-150 μm	scattered singly or at most in small groups of 5-6	33-216 μm	purple	Port Phillip, Vic.—S.E. Tas.
purpurea	scattered	smooth	125-150 μm	scattered	154-182 μm	purple	Southern Ocean, Falkland Island southern coast of South America
shepherdi	scattered perpendicular to longitudinal body axis	with thorns	144-190 μm	discrete, large groups (not in papillae) arranged uniserially along each interradius	84-216 μm	black	Port Lincoln and Kangaroo I., S. Aust.

Spicules in tentacles comprise slightly curved rods dichotomously branched at each end, and usually have a series of thorny knobs projecting laterally along shaft (Fig. 1).

Calcareous ring comprises 10 pieces fused, with a straight anterior and a slightly undulating posterior margin. Radial pieces each have a small anterior notch. Each piece of the ring is 1 mm x 0.5 mm (Fig. 2).

There is one ventral polian vesicle and the dorsally placed madreporite is very small and hook-shaped (0.5 mm x 0.25 mm).

Long, unbranched gonad on either side of the dorsal mesentery, joined anteriorly to a single, dorsal gonoduct. Gonads extend for about two-thirds of the body length and are packed with eggs.

Ciliated funnels numerous: on either side at base of dorsal mesentery in mid-dorsal interradius in mid-interradial line of interradius adjacent to, and to left of mid-dorsal interradius, and in ventral interradius directly opposite to those two dorsal interradii. Body wall translucent; radial muscles, lines of ciliated funnels, and outline of internal organs can be seen through it.

Calcareous spicules of body wall comprise wheels and sigmoid ossicles. Wheels restricted to discrete groups but not accumulated into papillae. These groups form a single line along each of the interradii, except in the posterior 1/3 of body where the groups possess smaller numbers of wheels, and form two irregular lines per interradius. Wheels have six spokes. Inner margin of each wheel has six discrete groups of about 16 serrations (Fig. 3). Wheels are 55 μm–226 μm in diameter. Sigmoid ossicles evenly scattered throughout the body wall and lie perpendicular to longitudinal axis of body. Shaft of each is smooth except that on the outside curve, at the attenuated hook end, there are 2–4 minute spines or thorns (Fig. 4). The sigmoid ossicles are 144–190 μm in length.

The animal in life is black. Besides the holotype 5 other specimens, similar in all respects, were collected and these are considered as paratypes.

Distribution: Port Lincoln, Spencer Gulf and Kangaroo Island, South Australia.

Etymology: The species is named after the collector, Mr Scoresby A. Shepherd.

Remarks: Differences between *T. shepherdi*, *T. maculata*, *T. allani* and *T. purpurea* are listed in Table 1.

Acknowledgments

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