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CONTENTS

PLANETARY SCIENCE

OPERCULA OF TWO GASTROPODS FROM THE LILYDALE LIMESTONE (EARLY DEVONIAN) OF VICTORIA, AUSTRALIA

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Abstract

Specimens of both *Cyclonema lilydalensis* and *Oriostoma northi* are known which show the operculum in life position. Additional loose opercula contribute to knowledge of the geometry of fossil paucispiral and multispiral opercula respectively. Various considerations, including the characters of the opercula, suggest that neither species is correctly assigned to genus; no convenient taxa are available for these forms. The opercula show a number of distinctive features and hold potential for stratigraphic and biologic discrimination.

Introduction

Gastropods have been known to occur in the Lilydale Limestone for more than 75 years (Etheridge 1890, 1891, Cresswell 1893) and opercula for almost the same length of time (Cresswell 1894, Etheridge 1894). These opercula have not been studied in detail in recent times, though several taxa of the gastropod fauna known only from their shells have been redescribed (Philip and Talent 1959). Now through the kindness of Mr Edmund D. Gill, Deputy Director, National Museum of Victoria, we have been able to study a large collection of opercula from the well-known Cave Hill locality in Victoria, Australia. In turn, examination of the specimens necessitated an investigation of the widely scattered literature on Palaeozoic gastropod opercula, and some examples from living forms.

Acknowledgements

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Prevalence and association of gastropod opercula

It is generally accepted that all living prosobranch gastropods develop opercula (Fretter and Graham, 1962, p. 77; Kumé and Dan, 1968, p. 513). Many of the living forms considered to be more advanced lose this structure in post-larval life, and a few others, which are less advanced but have specialized in a clinging mode of life, also lose the operculum. These exceptions reinforce the reasonable assumption that the presence of an operculum is primitive, and therefore that virtually every known Palaeozoic gastropod had an operculum; it is further likely that almost all the animals retained them throughout life.

When one deals with fossil gastropods, the association of a loose operculum with any given shell is always a matter of uncertainty, even if both are from the same stratigraphic interval

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and from the same locality. For some genera, such association has been a matter of controversy which is still not fully resolved, as for example with the Early Ordovician *Ceratopea* (Yochelson and Bridge 1957). Palaeozoic gastropods with opercula in place are among the rarest of fossils. Indeed, the collections of the U.S. National Museum of Natural History contain only one such specimen, an Ordovician *Maclurites*. Thus it is surprising that the Lilydale Limestone has yielded two different forms of opercula, both represented by specimens in which association of shell and operculum is as it was in life. These quite different forms in the Lilydale Limestone extend considerably the knowledge of Palaeozoic opercula *in situ*.

Although the upper part of the Early Ordovician has yielded a large number of opercula, especially of the genus *Ceratopea* (Yochelson and Bridge 1957), the post-Ordovician Palaeozoic record of opercula is exceedingly poor. Each new occurrence adds significantly to a meagre record, and we hope that this paper may bring others to the attention of palaeontologists.

One might assume that shells and opercula will occur in a one-to-one ratio, but Hadfield (1970, pp. 307-308) observed that the vermetid gastropod *Petuloconchus montereyensis* (Dall) (1919) periodically moults its operculum and generates a new one. Because of the highly specialized nature of the Vermetidae, this may well be a unique feature. Post-mortem sorting and differential preservation are sufficient as mechanisms to explain deviation of fossil gastropods from the theoretical one-to-one ratio.

Geometry of opercula

Cox (1960, pp. 1124-1126), in a brief but general review, illustrated a variety of opercular shapes. He noted that although at least 20 types have been distinguished, they may be grouped as spiral, concentric, or lamellar in growth plan. Typically, gastropods grow following a logarithmic spiral pattern in the formation of their shells. This growth pattern is also represented in most spiral opercula. Even opercula which complete only part of

one whorl grow logarithmically. Taki (1950) divided recent spiral opercula into the broad groups of subspiral, paucispiral, and multispiral; no clear dividing line distinguishes these groups, and terminology is arbitrary. Two of these three types occur in the Lilydale Limestone. We have called the opercula form of *Cyclonema lilydalensis* paucispiral, but another worker might argue that it should be more properly called multispiral, for the operculum does contain a fair number of volutions.

The essence of the logarithmic spiral is that width increases at an increasing rate. A fundamentally different mode of coiling is that of a spiral of Archimedes. In that mode of expansion, the width of each volution remains constant. Some Holocene opercula appear to follow an Archimedian spiral, but have relatively few volutions. Taki (1950, p. 34) may have emphasized the spiral of Archimedes, but his text is in Japanese, and this point is not mentioned in his English summary. However, his classification of opercula does not take any apparent change away from the logarithmic pattern to an Archimedian pattern into account. Thompson (1942, pp. 772-778) discussed the geometry of opercula in terms of logarithmic growth only.

The multispiral form of the *Oriostoma northi* operculum, the second type found in the Lilydale Limestone, may represent growth following the pattern of a spiral of Archimedes. Although there is some slight variation in the width of individual opercular volutions, this is a relatively minor point, particularly when judged against the impressively large number of volutions. Because the number of volutions is very large, there has been confusion with opercula characterized by concentric growth. No convenient term has been proposed for opercula characterized by so many narrow volutions. 'Multispiral' will continue to be used here purely for convenience, but it may be an inappropriate term.

Multispiral opercula, in which the volutions are not so close that their spiral course is difficult to observe, are well known in the Silurian. Lindström (1884, Pl. 17, figs. 32-47) illustrated a variety of multispiral opercula from Gotland. In some instances the opercula

are in life association within the aperture of various species of *Oriostoma*. The occurrence of generally similar opercula in *Oriostoma* and unrelated genera in the Devonian demonstrates that a large number of volutions forming the operculum is most assuredly not in itself an indication of close phyletic relationships; the number may well be critical, but when the volutions become so numerous that they prevent ready observation, all forms tend to be lumped simply as 'numerously volute'.

No data exist on such a fundamental question as whether in the formation of opercula gradation is continuous between the Archimedian and logarithmic spirals. If the two kinds are discontinuous, they may be of use in higher classification; we do not know for certain whether any Holocene opercula are rigidly Archimedian in pattern. It is theoretically possible that true Archimedian growth—within the limits of biological variation—is confined to extinct gastropods. Study of additional Palaeozoic fossil opercula, such as are available in the Silurian, eventually may lead to a more clear-cut distinction between Archimedian and logarithmic growth.

Comparison of the two opercula in the Lilydale fauna is particularly instructive in pointing out the difference between the external shape and internal configuration of a gastropod whorl. Though one might assume from the generally rounded profile of the shell exterior that the Devonian *Cyclonema* might have a nearly circular operculum, it obviously is elongate. On the other hand, the subquadrate external profile of *Oriostoma* belies the circular internal section. Even though there is an apparent lack of fit when viewing the external whorl profile, an inspection of the apertural shape of the two shells shows that the fit of each operculum is very good indeed.

In general, the only shell form which could accept an Archimedian-like spiral or a true multispiral operculum would be one which has an essentially circular aperture. This necessitates a shell with an entire lip and no interference in its outline from preceding whorls. The only shell forms which satisfy this criterion are those with a circular internal whorl profile and whose axis of the generating curve

expands outward away from the axis of coiling, or downward along the axis of coiling in pace with the rate of expansion of the generating curve (Raup and Michelson 1965). Among Palaeozoic gastropods, shells like the Euomphalidae or Oriostomatidae primarily possess these characters, and these are the shells known for their calcified multispiral opercula.

In shells where the displacement away from or down the axis of coiling does not keep pace with the rate of expansion of the generating curve, the earlier whorls will interfere with the shape of the aperture. In such cases the shape of the aperture tends to an elongate oval, the parietal lip disrupting the circular shape. The elongated paucispiral operculum is an ideal form to fit within this aperture. The relation between the operculum and the aperture will place theoretical restrictions on opercular form, and obviously many apertural shapes could not be sealed off by spiral growth. In these shells, the opercula characterized by concentric or lamellar growth will be found.

Calcification of opercula

In spite of the large number of opercula which must have been produced in more than 500 million years, remarkably few are preserved as fossils. Typically, the Holocene gastropod operculum is a plate of organic conchiolin (Fleishmann 1932, Kessel 1941), and is unsatisfactory raw material for fossilization. Only in rare instances among the great variety of living gastropods does this organic material serve as a matrix for calcification. Calcified opercula are prominent only in some members of the Trochacea, especially the Turbinidae, and among the Neritacea; these are accepted generally as primitive prosobranchs. Some, though far from all, *Natica* species also have calcified opercula. *Turbo* is a characteristic reef-dweller and is found most commonly on the seaward side. Most members of the family seem to occur in this habitat. *Nerita*, a typical neritacean, lives on both ocean and lagoon sides of reefs, at or above high tide level but most commonly in a rocky intertidal habitat. (For a summary of living reef-dwelling gastropods, see Demond 1947). Species of *Natica*,

some with calcified opercula and some with 'horny' opercula, are primarily sand or mudflat dwellers. Other living gastropods function in all these habitats equally as well without calcification of their opercula. Just why some forms do calcify this structure is not at all clear; at present there is no obvious answer based on physical characteristics of the environment.

No non-calcareous opercula of Palaeozoic age are known to us. One is faced with a record which may be incomplete on two counts. The palaeontologist must accept the normal vagaries of preservation and recovery of fossils. In addition, he must deal with gaps imposed by the paucity of calified opercula, for phylogenetic distribution of calcified opercula was probably as erratic in the past as now. These factors make it most unlikely that a phylogenetic sequence of opercula will ever be recovered.

Functional morphology and evolution of opercula

Among the molluscs, opercula occur in living and fossil gastropods, fossil hyolithids (an extinct group of class rank) and fossil cephalopods. Opercula of living gastropods are used to close the aperture, and in many forms they are also employed as a pad on which to rest the shell during movement. Both functions are important, but the general prevalence of opertural closings among representatives of several mollusc classes suggests that the closure function is the more primitive.

The operculum has been variously modified in different groups and, as noted, even lost in some, but there seems little question that the sealing of the aperture is its prime function (Cox 1960, p. 1125). Adaptations in shape and reduction in size are particularly noteworthy among the more advanced living gastropods. However, opercula of most living snails fit the aperture of the shell closely when retracted. In viewing the Palaeozoic gastropods collectively, the most logical supposition is that the operculum fitted the aperture closely.

In a sense, the operculum is a defence mechanism. The soft parts of the animal must be extended for locomotion and feeding, but if they are retracted and the aperture sealed, the shell is a formidable fortification against predators. A calcareous plug rather than a horny one would increase the strength of the defence. However, it may be even more important to view the operculum as a significant defence against the environment, rather than against predation. Gastropods are not noted for rapid movement such as characterizes coral polyps or tube-dwelling worms, who withdraw almost instantaneously when a shadow falls on them. It would seem *a priori* that a fast-moving carnivore would find a gastropod to be vulnerable. Nevertheless, *Turbo* and *Trochus* may retract at a rapid rate when a shadow passes over them (J. Rosewater oral communcation 1969).

Hedley (1917, p. 98) suggested, and Taki (1950, p. 47) fully supported, the notion 'that the multispiral type of operculum seen in *Pleurotomaria* and Trochidae is the most primitive'. In the scheme of operculum evolution proposed by Taki (1950, fig. 12), calcification is shown occurring at various stages, an overlay, as it were, to changes in shape. He stated (Taki 1950, p. 46) that 'The evolution of operculum types begins with the retardation of its rotation with its growth. The calcification of opercula is of secondary origin, which also slows down its rotation. Thus, a calcified operculum belongs to a more advanced type than the ordinary non-calcified one.'

Speculation on evolution of the operculum cannot be supported from the fossil record, for the earliest known calcified operculum, that of the late Early Ordovician *Ceratopea*, emphasizes growth in the third dimension, the specimens being horn shaped (Yochelson and Bridge 1957). More plate-like opercula, which complete less than one volution, have long been known to occur with shells in the Middle and Late Ordovician *Maclurites*; Salter (1859, pp. 7-10, Pl. 1) gives an excellent description and outstanding illustrations of the shell and operculum. Yochelson (1966a) described a more typically paucispiral operculum from Middle Ordovician which he attributed to *Helicotoma*. Because of the presence of subspiral to paucispiral calcified opercula in these early gastropods, the basic concept that a calcified operculum is an 'advanced type' is a dubious concept and may be spurious.

Gratacap (1907) has pointed out both the

utility of opercula in classifying some Holocene gastropods and some of the dangers inherent in placing too great a weight on them. These mid-Palaeozoic Lilydale opercula, when compared with other opercula, show that different opercular forms may often converge. However, the opercula offer a new line of evidence on classification. This must be treated with extreme caution, but data on distribution of opercula form could be significant in corroborating new concepts of gastropod arrangement at the familial level.

Stratigraphic and ecologic setting of Lilydale Limestone

The Lilydale Limestone constitutes the third youngest of four formations forming the Yering Group (Gill 1965). Although classically this group was considered to be Silurian in its entirety, now only the basal Christmas Hills Sandstone is judged to be Siluro-Devonian. The overlying Ruddock Siltstone and Lilydale Limestone are generally accepted as Lower Devonian. Talent (in Talent and Banks 1967, p. 151) considered the Lilydale Limestone to be Emsian, and possibly lower Emsian. Philip (1967, p. 918), following Gill (1965), considered the unit to be Siegenian; Edmund D. Gill (written communication 1969) judges that the formation is most likely of upper Siegenian age. This is actually only a minor difference in age, and is not surprising that workers considering a richly fossiliferous thick unit should have minor differences in interpretation. The opercula contribute no data to the question of the age of the Lilydale Limestone, but the fact that the Lilydale is Devonian rather than Silurian is highly significant for better understanding of the record of opercula.

The Lilydale Limestone is about 700 feet thick. Regarding its general character, Edmund D. Gill (written communication 1969) notes:

'Proximity to a large city of a deposit of good limestone has led to the extensive working of the Lilydale Limestone and so the opportunity for its study. It is a lenticle of recrystallized limestone well stratified and dipping 60°E. with beds mostly 6 in. to 3 ft thick. The formation is richly fossiliferous, with corals and stromatoporoids predominating. Mollusca are represented chiefly by gastropods, which are common, but pelecypods and cephalopods are comparatively rare. Brachiopods and trilobites are very rare. Foraminifera, Ostracoda and *Girvanella* are present. No fish have been discovered.

'The sediment types vary from low energy lime muds (grading into noncalcareous silts in places) to high energy conglomerates of water-worn pebbles of coral, stromatoporoids, and such. No reefs or organisms in position of growth have been recognized. The formation as exposed is a coral-stromatoporoid biostrome. In some places, the gastropod shells are worn while in others they are excellently preserved. The gastropod with the operculum appears to have come from such a low energy environment.'

Except for the opercula assigned to the early Ordovician *Ceratopea*, the most abundant Ordovician calcareous operculum is that of *Maclurites*. In the Silurian, the *Oriostoma-Poleumita* generic complex is noteworthy for the abundance and variety of calcified opercula. Although no palaeoecologic studies *per se* have been done of these three genera, they are readily interpreted as having lived in a near-reef, shallow-water, and possibly high-energy environment. It may be more than coincidence that both kinds of operculate Lilydale snails lived in a similar environment.

Operculum of *Cyclonema lilydalensis* and similar paucispiral forms

The Australian literature during 1893 and 1894 contains several references to gastropod opercula from the Lilydale Limestone. However, the only description and illustration of an operculum is that of Etheridge (1894) for *Oriostoma* which is discussed below. Sufficient vagueness surrounds the discussion of a paper given at the Royal Society of Victoria (Hall and Pritchard, in Anonymous 1893, p. 260) to suggest that one person may have been commenting on the operculum of *Cyclonema* while another commented on that of *Oriostoma*. On the other hand, Etheridge (1894, p. 154) indicated that only one specimen was in question.

The description below is based on twelve free opercula of *Cyclonema lilydalensis* ranging from 9 to 23 mm in greatest length. These specimens supplement one shell with the operculum in life position within the aperture.

The operculum of *Cyclonema lilydalensis* is paucispiral, expanding in the characteristic counter-clockwise direction, with all volutions observable on the external surface. Its overall general shape is that of a wide oval disc. Growth is accomplished by adding increments which are essentially tangent to the rim; the increments are inclined at an oblique angle to the plane of the operculum. Were it not for the one specimen in place it would be difficult to assign this operculum to a shell, for the whorl profile of *C. lilydalensis* follows essentially the arc of a circle. The similarity of apertural shape and opercular shape are not at all obvious, and the confusion in the literature as to which shell this operculum should be assigned is perfectly understandable.

The first four observed volutions on most specimens lie in essentially one plane, though one specimen suggests that the first two observed are slightly depressed (Pl. 1, fig. 2a); the nucleus of the operculum is unknown. The individual volutions have a flattened exterior surface (Pl. 1, figs. 1a, 2a). With increasing size, perhaps beyond six volutions, the axis of the volutions is displaced toward the inner surface of the operculum, so that large opercula are very slightly convex in cross-section (Pl. 1, fig. 3c). In spite of this gradual slight inclination, the individual segments remain flattened, rather than convex. The suture on the outer face is distinct, but not deep.

As seen from the side, the operculum is a moderately thin plate, the thickness seemingly increasing in direct proportion to increasing diameter. In the early growth stages, the periphery is close to the outer surface and may protrude as a very narrow flange so that the profile is step-like. In larger specimens the periphery is near the middle, and the profile is well rounded (Pl. 1, fig. 3c).

The inner face also shows volutions, but as they are approximately twice as wide as those on the exterior surface, much of the surface area of the earlier whorls is covered (Pl. 1, figs. 1b,

2b, 3b). The inner surface of each volution is as flat as the exterior, the only exception being near the rim at the zone of growth; this growth edge thins toward the periphery so that it is blade-like (Pl. 1, fig. 3b). The zone of growth occupies roughly one-eighth of the circumference of the operculum.

The flat inner surface of each volution uniformly occupies about one-half of the total width at every growth stage. The inner edge of each volution abruptly bends downward to an eccentric depression in which the more central portions of the earlier whorls are seen. This inner edge of the inner surface—that is, the area of the operculum that would be analogous to the umbilicus of a widely phaneromphalous gastropod shell—has the sides of the depression perpendicular in the early stages of growth. However as the operculum increases in size, the inner edge of the inner surface becomes more and more rounded and protruding as an overhang, thus producing below it an 'umbilical suture' of increasing depth (Pl. 1, fig. 3d). This suture would enlarge the area of opercular surface available for attachment of the retractor muscle. There is no indication of any central boss or shell thickening within the central depression. The outer surface of the operculum irregularly shows growth lines which are tangent to the preceding whorl, following the shape of the growing edge (Pl. 1, figs. 1a, 3a), but these growth lines are not visible on the inner surface because the layers are deposited parallel to the plane of the operculum.

The operculum in place (Pl. 1, figs. 4a-c) rests tightly within the shell only just behind the apertural opening and is not retracted, its outer edge and surface being just within the outer lip. The growth edge of the operculum is at the upper part of the opening, the farthest point being below the suture, that is, at the juncture of the parietal and the upper part of the outer lips. The straight growing edge itself lies parallel to the parietal lip.

When the shell is held with the columellar axis perpendicular, the plane of the operculum is inclined at an angle of 50° to the columellar axis. Our interpretation is that the operculum of this gastropod is held in place only by force of the retractor muscle. Although there may be

development of grooves, teeth or ridges on the columellar margin of the aperture, as occurs in more advanced forms such as the Neritacea, it seems most unlikely. The only specimen in our possession is that illustrated with the operculum in place.

Most of the opercula are broken or fragmentary; the thin inner whorls are particularly an area of weakness. The opercula are relatively soft, and more difficult to clean than the shell. Essentially no preparation was possible. The free specimens may be weathered or they may be softer because calcium carbonate was more porous in the operculum than in the shell.

The type specimen of *Cyclonema lilydalensis* Etheridge (1891, p. 128, Pl. 19, fig. 3), at the Australian Museum, has not been studied and compared by us. However, because of its globose profile and numerous, evenly-spaced, uniformly-rounded spiral cords (Pl. 1, fig. 4a) the operculate specimen is probably conspecific with this species rather than with *Cyclonema australis* Etheridge, 1890 (p. 63-64, Pl. 9, figs. 4-5), the type specimen of which is also at the Australian Museum. That species has fewer spiral elements and a less globose whorl profile. The illustration of *C. australis* given at the time *C. lilydalensis* was described, indicates more clear-cut differences between the two taxa than does the 1890 drawing. When these two species were described, their opercula were unknown. This report appears to be the first presenting the operculum of either form.

Like all other Devonian species which have been assigned to the genus *Cyclonema*, both species of the genus described from the Lilydale Limestone probably are not members of that genus. True *Cyclonema* has a calcitic shell, as well as imperfections in its spiral ornament as a consequence of sedentary life habit at maturity. The operculate Lilydale specimen is recrystallized, and its soft, powdery texture suggests to us that it may have been aragonite originally. The mid-Palaeozoic assemblage of spirally ornamented globose gastropods, into which the Lilydale taxa fall, have not been critically studied. Correct assessment of the taxonomic position of both species would be premature at this time, and beyond the scope of this paper. The operculated form is referred

to as *Cyclonema lilydalensis* purely in quotational sense.

It cannot be assumed that a paucispiral operculum is confined to the Devonian or restricted to a particular shape of shell. In addition to Yochelson's (1966a) report of a paucispiral operculum with *Helicotoma*, Teller (1910) illustrated a Silurian shell from the Racine Dolomite (Niagaran) of Wisconsin with a paucispiral operculum in place; this is probably the same as the form described by Whiteaves (1891; 1895, p. 96) from the Guelph Formation, but we have not compared specimens from the two units. Though this Silurian operculum is paucispiral, it expands at a more rapid rate than that of the Australian Devonian *Cyclonema*. Teller's form has a gently concave outer surface rather than convex and perhaps it is relatively thinner. Still, the similarity to the Australian form is interesting.

What is perhaps even more interesting is that this operculum occurs within the aperture of a moderately high-spired pleurotomariecean gastropod. Teller (1910) incorrectly assigned his shell to *Murchisonia conradi* Hall, but the operculate form has a more prominent upper shoulder than true *Murchisonia*. This may be another example of convergence in opercular form, such that lower-spired shells (*Helicotoma*) and moderately high-spired shells with striking differences in external forms (*Murchisonia* and *Cyclonema*) all have similar opercula. No other examples of paucispiral opercula in the Palaeozoic are known to us.

Lindström (1884) assigned several Silurian opercula to *Cyclonema*. So far as it can be determined from his illustrations, none were actually found in life position. These opercula are multispiral and are relatively thick. Apparently they are more similar to Silurian opercula of *Oriostoma* illustrated by him than to either of the Devonian forms described herein. At least some of the Silurian shells which Lindström described originally as *Cyclonema* might better be transferred to *Oriostoma* or to *Poleumita*. Should study of his specimens support this suggestion, evidence on classification from the shape of the shell and the operculum would tend to reinforce one another rather than be at variance.

Operculum of *Oristoma northi* and its distribution

Two specimens identified as *Oriostoma northi* Etheridge (1890, p. 64-65, Pl. 9, figs. 6-7), which have the operculum within the aperture, are available for study. One is only a fragment of the final conch whorl, and the outer surface of the operculum is badly weathered. This specimen from the Pritchard collection could be the one mentioned, but apparently not seen by Etheridge (1894, p. 154). Etheridge also noted a large operculated specimen in the collection of Rev A. W. Cresswell (National Museum of Victoria no. P1107). We have also examined 21 isolated opercula, one of which was donated by Cresswell. It is a minor footnote to history that two of the specimens figured herein (a large operculum, and a fine specimen with the operculum in place) were donated to the National Museum of Victoria by him in 1902.

In marked contrast to the operculum of *Cyclonema lilydalensis*, this operculum is virtually circular in plan and is of the multispiral type with extremely narrow volutions. The statements and drawings given by Etheridge (1894) suggested incorrectly that it is made of concentric increments. The individual volutions may be seen only on the exterior surface (Pl. 2, figs. 1a, 2a, 3a, 5a). All specimens are somewhat weathered, and the spiral course of the volutions cannot be traced readily; no doubt this misled Etheridge in his interpretation. Forty volutions were counted on a specimen 1·8 cm in diameter, but the actual number is probably closer to 60. The whorls are not of constant width, nor is increase in width completely uniform, for several specimens have volutions of very slightly greater width between the central portion and the rim. In the large specimens there appears to be a narrowing of the volutions near the mature rim. This can be seen fairly well in thin section (Pl. 1, figs. 6a-d). The slight variation or ontogenetic change is far less significant than the very large number of volutions.

The overall shape of the operculum is such that, as Cresswell (1894, p. 157) remarked, originally there was controversy as to the origin of the fossil, 'some taking for a nummulite, and some for the lid of a coral, others for the vertebrae of a fish'. Most specimens are concave on the outer surface and so resemble fish vertebrae. Although all specimens have the central area sunken relative to the rim, individual variation is considerable. Among specimens of similar diameter, some individuals will be twice as thick as others (Pl. 2, figs. 1c, 2c, 3c, 5b). However, on all specimens the inclination of the outward-facing surface appears uniform throughout growth, though this may be masked by differential erosion of the central area. Chapman (1916, p. 90) indicated that the exterior of the operculum is concave; Cresswell (1894, p. 158) stated the operculum to be 'plano-concave', an accurate description of the form.

Both the outer and inner edges of the rim are relatively sharp. The rim is straight in profile but inclined slightly inward, the inner opercular surface being a bit narrower than the outer. No ontogenetic change in the profile has been observed, and there does appear to be a difference in inclination of the rim between the thinner and the thicker opercula.

The inner surface is smooth, being built of laminae deposited at almost right angles to the rim, each lamina completely covering the one previously laid down (Pl. 2, figs. 1b, 2d, 3d, 5c). The surface varies from almost horizontal to distinctly inclined inward. The thicker opercula may be more strongly inclined, but the inclination of this surface varies considerably with individuals. There is no indication that this is an ontogenetic change.

Approximately one-third of the inner surface is occupied by the central depression, presumably the point of attachment of a retractor muscle. Each lamina bends down gently to form this concavity. However, in weathered specimens, the depression appears to a flat-based pit, the walls of which are nearly vertical except at the uppermost rounded edge. Such a configuration would impose impossible mechanical problems in increasing the size of the depression as each succeeding lamina was deposited. Thin sectioning (Pl. 1, fig. 6d) shows the central depression to be shallow.

One large specimen has a mound within

the central depression (Pl. 2, fig. 5c). It is not possible to determine whether this is a gerontic feature or whether it is a result of weathering and subsequent preparation by another worker of the soft material forming the laminae. A thin section of another specimen suggests that this feature may be spurious (Pl. 1, fig. 6c), but it cannot be entirely ruled out, for comparable thickening of the attachment area has been observed in unusually large Pennsylvanian neritacean opercula.

Although these opercula are generally thick, they are also as soft as those of *Cyclonema lilydalensis*; a number has been modified in details by weathering. Specimens vary in diameter from the smallest 1·2 cm, to the largest just over 3 cm (Pl. 2, fig. 5). The ratio of width to thickness means little because of the likelihood of modification of the inner surface, in particular by weathering. Variation in the slope of the outer surface cannot be attributed to weathering.

The operculum fits tightly into the shell aperture. The well-preserved shell which has a portion of the aperture unbroken, shows that the operculum is essentially not retracted for more than two millimetres at the inner lip (Pl. 2, figs. 4 b-c). It may be withdrawn a slight distance more at the outer lip (Pl. 2, fig. 4a), but even here this cannot be more than a few millimetres. The interior of the aperture of several specimens examined shows no indication of any sort of groove or teeth to assist in holding the retracted operculum. However, the thinning of the shell toward the aperture is a perfect match for the inclination of the opercular rim.

Oriostoma northi Etheridge (1890, p. 64-65, Pl. 9, figs. 6-7) is a common species in the Lilydale gastropod fauna; the type specimen is housed in the Australian Museum. This species was redescribed by Philip and Talent (1959) who assigned it to *Straparollus (Euomphalus)*; we prefer to use the original generic name in a quotational sense, for reasons noted below. They not only discussed the general external form and ornament of the shell in considerable detail but also demonstrated the spurious nature of the genus *Liomphalus* Chapman (1916, p. 90), which had been based on steinkerns of this species. They figured a number of shells, but no opercula. As noted by Philip and Talent (1959) both Hall and Pritchard (in Anonymous 1893, p. 260), when commenting on a paper by Cresswell (1893), discussed the occurrence of opercula *in situ* at Lilydale, though Cresswell (1894, pp. 157-158) was the first to exhibit such a specimen at a public meeting. It remained for Etheridge (1894) to describe the operculum itself, which he illustrated by line drawings of isolated examples. So far as we have been able to determine, in spite of the report by Cresswell (1894) of a specimen showing the operculum in place, none has been figured.

Spitz (1907, Pl. 14, fig. 1a-c) recovered one operculum from the Lower Devonian of Austria which is remarkably similar to that of *O. northi*. Comparison of an Austrian specimen with the Australian specimens reveals no obvious difference, and were the opercula presented without locality data they would immediately be judged to be conspecific. Part of this Early Devonian gastropod fauna has recently been redescribed (Jhaveri 1969), while other parts and opercula are still under investigation. It seems highly probable that *Straparollus (Euomphalus) carnicus* (Frech) is the host shell for this operculum. The similarity in both shell and operculum between this species, as illustrated by Jhaveri (1969, Pl. 21, fig. 8), and *Oriostoma [Straparollus (Euomphalus)] northi* (Etheridge), as illustrated by Philip and Talent, is striking.

In general shape and ornament, the shell of *Oriostoma northi* is also similar to species of *Omphalocirrus* from the Middle Devonian of Germany (see Yochelson 1966b). This raises yet another interesting point. In connection with redescription of *Omphalocirrus manitobensis* (Whiteaves 1890) from the Middle Devonian Winnepegosan of Manitoba, Canada (Geological Survey of Canada No. 4174), Whiteaves (1890, Pl. 6, figs. 3-3a) figured an apparently free convex operculum. The operculum actually is in a shell some distance within the aperture. Considerable uncertainty has surrounded this material, for the operculum has appeared to be exceptionally thin and in an unusual orientation. In the light of the Lilydale specimens, it is now readily interpreted as the impression

of the concave external surface of a multispiral operculum slightly out of life position and pushed or retracted a short distance into the aperture. Additional closely similar opercula have been found in *Omphalocirrus*-like shells in the Middle Devonian Rogers City Limestone of Michigan (R. M. Linsley, unpublished).

The shell of *Omphalocirrus manitobensis* has slightly less prominent collabral ornamentation on the basal surface but is still impressively similar to that of *Oriostoma northi* and *Straparollus* (*Euomphalus*) *carnicus*. All three probably form a closely allied group almost certainly within the same subfamily. Similarity in opercular type thus has led to reinterpretation of phyletic relationships which were not suspected earlier because of the scattered nature of the literature. So far as we can determine, no operculum has yet been reported for the type species of *Omphalocirrus*. The currently accecpted classification of Euomphalacea (Knight, Batten and Yochelson 1960, pp. 1189-1196), does not include *Omphalocirrus*. However, to engage in a major reorganization of the Euomphalacea at this time would greatly exceed the scope of this discussion of opercula.

When one considers the paucity of mid-Palaeozoic opercula, it is remarkable that specimens have been found from Australia and Canada, let alone within shells. This geographic range rivals that of the late Early Ordovician *Teiichispira* opercula known from Malaya and the United States (Yochelson and Jones 1968); none of them has been found in life position. The Austrian and Australian occurrences constitute a remarkable range.

Allied genus *Cyclospongia*

In his description of the operculum of *Oriostoma northi* Etheridge (1894) noted its similarity to *Cyclospongia discus* Miller (1891) described from Indiana. The observation that the taxon described by Miller is based on a gastropod operculum rather than a sponge has only recently been documented by Solem and Nitecki (1968); Miller's work appeared in a more formal format in 1892 (Solem and Nitecki 1968, p. 1007), which would have allowed a full year for it to come to Etheridge's attention before his paper on the Australian

fossil. Solem and Nitecki demonstrated that *C. discus* was characterized by narrow, closely spaced, multispiral volutions, rather than concentric growth. In a sense, this indicates the perception shown by Etheridge, but it is a case of arriving at the right answer for the wrong reason, for Etheridge believed that the operculum was formed by concentric growth.

Although these two forms are generally similar, as was observed by Etheridge, the differences certainly warrant retention of *Cyclospongia* as a distinct gastropod genus, which was known originally only from its operculum. Opercula of that genus differ from those of *Oriostoma* in being relatively thinner, having relatively fewer whorls, having a rounded rim, and having a convex outer surface.

Tyler (1965) recently described a multispiral operculum in the gastropod fauna from the Middle Devonian Four Mile Dam Limestone of Michigan; a thin section of one of his specimens is figured for comparison (Pl. 1, fig. 5) to *O. northi*. He assigned this operculum to his species *Turbinilopsis anacarina* (Tyler 1965, p. 348, Pl. 48, figs. 19-25). The shell is moderately low spired with a well-rounded whorl profile. Examination of shells and opercula of this species indicates that the presumed association morphologically is likely; the geologic evidence further supports the inference of a life association. However, comparison of Tyler's holotype with a cast of *T. inconspicua* De Koninck, the type species, suggests that the taxa are not congeneric.

This operculum of *Turbinilopsis anacarina* and *Cyclospongia discus* are impressively similar in terms of general shape, number of volutions, and details of the rim and attachment pit. This similarity in overall form reinforces the suggestion of Solem and Nitecki (1968) that the poorly documented *Cyclospongia discus* occurs in rocks of Middle Devonian age rather than Silurian.

Further, if generic characters can be inferred from these opercula, it would suggest that *Turbinilopsis anacarina* be transferred to *Cyclospongia* Miller. Some may judge this to be too large a step to contemplate seriously at the present stage of our knowledge, but careful comparison of opercula of both species has

convinced us that at least a questioned transfer of Tyler's species is warranted.

From horizon 11 of the Dalhousie beds in Gaspé, Clarke (1909, p. 25, Pl. 1, figs. 10-12) briefly described and figured several specimens of opercula. One specimen in the collections of the U.S. National Museum (USNM 56745) indicates that these opercula are close to *Cyclospongia*; the material is not well enough preserved to demonstrate that they are congeneric. Although they are questionably ascribed to *Euomphalus*, it seems more likely that these opercula are to be associated with one or more of the species in the fauna placed by Clarke under *Holopea*. *Holopea* as used by Clarke and *Turbinilopsis* as used by Tyler are simple shells of similar form.

In addition to an operculum referred to *Oriostoma*, Spitz (1907, p. 139) recovered at least two other different isolated opercula. An impression of the inner surface (Pl. 13, fig. 9) of one specimen is at least suggestive of *Cyclospongia*. Another form (Pl. 13, figs. 22a-c, 23) is similar to that of *O. northi* in shape but may have fewer whorls.

Koken (1889, Pl. 12, figs. 11-12) illustrated two specimens which appear to be external views of *O. northi* opercula, *Cyclospongia*, or closely similar forms. Unfortunately, these figures are neither mentioned on the plate description nor noted in the text. Their source and significance remain an enigma.

Finally, Wright (1915, p. 71) lists an 'operculum' from the Lower Devonian of Alaska. The specimens are distinct from both those of *Oriostoma northi* and *Cyclospongia*. It is evident from the scattered literature that a variety of generally similar multispiral opercula occur in the Devonian. Considerable care will have to be taken in the future to differentiate them.

Summary

Few mid-Palaeozoic opercula are known, and the literature is scattered. We have exceeded the limits of describing two Australian forms by drawing together these scattered references, but we believe that it is appropriate to use the remarkable Lilydale specimens as a basis from which to draw more general conclusions as to the form and function of opercula.

If there is one lesson in the subject of Palaeozoic opercula, it is that convergence among diverse groups is considerable, for in only a limited number of ways can an operculum be constructed. At the same time, we have attempted to demonstrate that when one interprets the opercula in a rigorous fashion, then similarity of opercula may be useful in associating shells. This is particularly evident with the multispiral opercula.

Although there might be some relationship at the superfamily level between the shells of *Oriostoma* and *Omphalocirrus*, the Silurian opercula of *Oriostoma* collectively show differences in external profile, rim, and inner surface which may be of a greater order of magnitude than those between the Devonian *Cyclospongia* and the Devonian *Oriostoma-Omphalocirrus* complex. Etheridge (1894, p. 154) pointed out the difference between the Silurian and Devonian opercula and questioned the generic placement of *Oriostoma northi*. However, the shells of *Oriostoma* and *Omphalocirrus* have more in common than either has with the shells of the species questionably assigned here to *Cyclospongia*. Classification based on shell form and that based on opercular form are still disjunct rather than coordinate. Finer discrimination within the 'multispiral' group of opercula may resolve this problem. Collectively, these three groups prove that convergence in opercular form has occurred in the fossil record more than once. We certainly concur with Etheridge's (1894, p. 154) remark that 'the subject is too long and complex to be considered now'.

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Explanation of Plates

PLATE 1

Figs. 1-4—Operculum and shell of *Cyclonema lilydalensis* Etheridge Jr., from the Lilydale Limestone quarry, Lilydale, Victoria, Australia.
1. Relatively large operculum × 1·5, NMV P26889, (a) exterior, (b) interior.
2. Smallest available operculum ×3, NMV P26889, (a) exterior, (b) interior.
3. Largest available operculum × 1·5, NMV P26889, (a) exterior, (b) interior, (c) side view to show ontogenetic change in profile, (d) portion of oblique interior view × 4 to

show overhang, and at lower right start of taper toward growing edge.

4. Shell with operculum in place $\times$ 1, NMV 26888, (a) side, note that specimen is partially broken and obscured with matrix so that juvenile whorls appear isolated from body whorl, (b) apertural view, (c) view of shell with outer operculum face at right angles to camera.

Fig. 5—Thin section of ?*Cyclosponiga anacarina* (Tyler) for comparison. Museum of Paleontology, University of Michigan no. 57302d, $\times$ 5. Collected by J. M. Tyler from the Four Mile Dam Limestone, at Four Mile Dam on Thunder River, Michigan.

Fig. 6—Thin sections made from one large operculum of *Oriostoma northi* Etheridge Jr., NMV P26890. (a) portion of section parallel to outer face $\times$ 5, (b) same $\times$ 1, (c) right-central portion of a transverse section $\times$ 10, (d) same $\times$ 5. Note short recrystallized portion to left.

PLATE 2

Figs. 1-5—Operculum and shell of *Oriostoma northi* Etheridge Jr. from the Lilydale Limestone at Cave Hill quarry, Lilydale, Victoria, Australia.

1. Relatively thick operculum $\times$ 1·5, NMV P26890, (a) exterior, (b) oblique exterior, (c) unbroken side.
2. Thin operculum $\times$ 1·5, NMV 26890, (a) exterior, (b) oblique exterior, (c) side, (d) interior.
3. Thick operculum, somewhat weathered $\times$ 1·5, NMV P26890, views comparable to fig. 2 to illustrate especially differences in width and slope of outer operculum face.
4. Shell with operculum in place $\times$ 1, NMV P1107, presented A. W. Cresswell July 1902, (a) view at right angles to operculum, (b) very slightly oblique top view, (c) apertural view.
5. Largest available operculum $\times$ 1·5, NMV P26890, (a) exterior, (b) side, (c) interior.
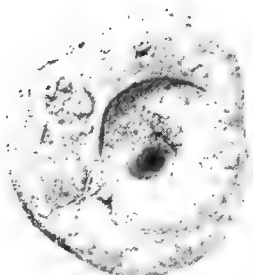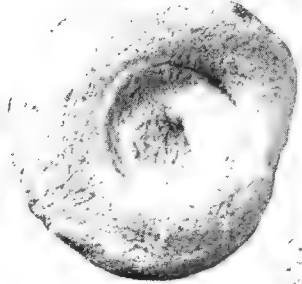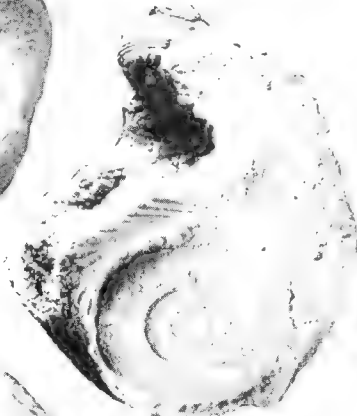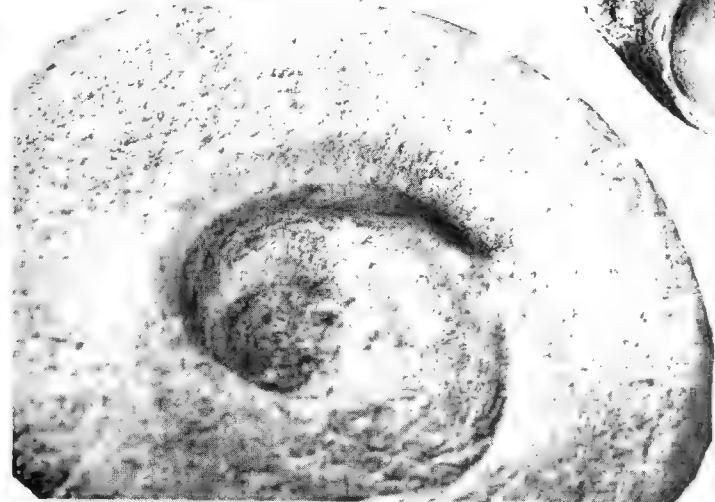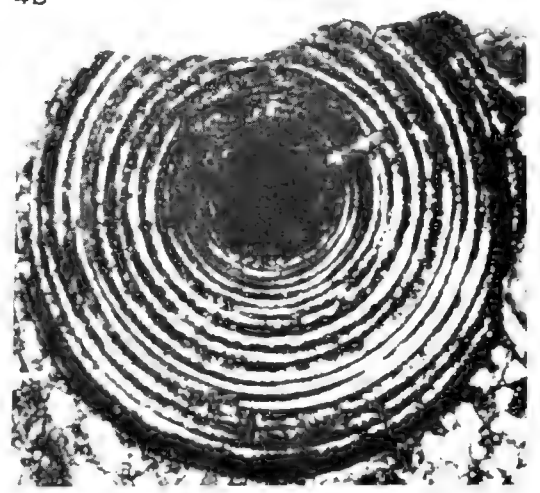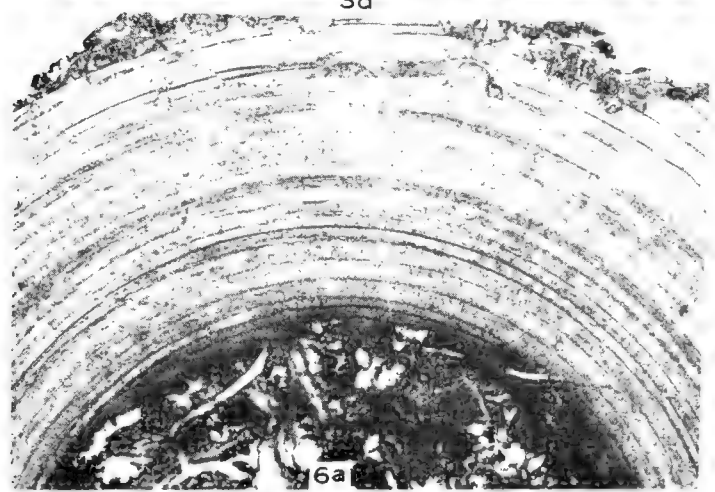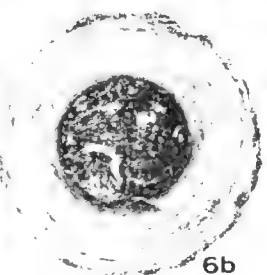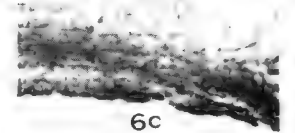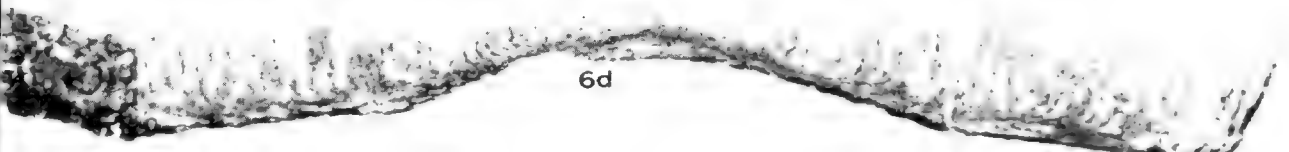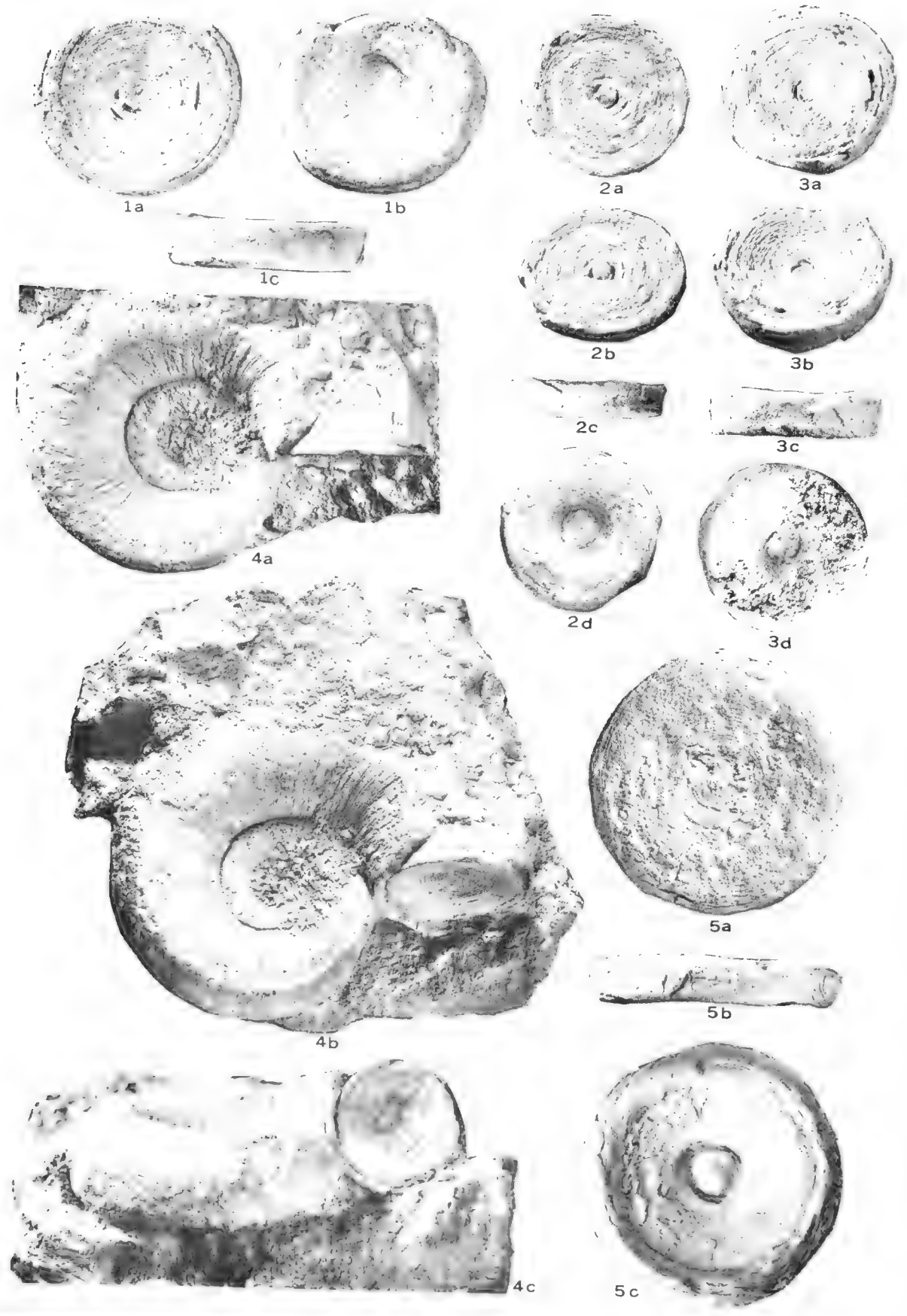
STUDIES IN AUSTRALIAN MURIDAE: REVIEW OF *MASTACOMYS FUSCUS*, AND DESCRIPTION OF A NEW SUBSPECIES OF *PSEUDOMYS HIGGINSI*

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Abstract

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Data are presented of cranial and dental characters of series of *Mastacomys* from extant populations and from fossil deposits of Holocene and of late Pleistocene ages. It is considered that *Mastacomys* is a monotypic genus, that the species, *M. fuscus* Thomas, comprises two subspecies—*M. f. fuscus* of Tasmania and *M. f. mordicus* Thomas of the Australian mainland —and that *M. f. brazenori* Ride and *M. wombeyensis* Ride are synonyms of *M. f. mordicus*. *Pseudomys higginsi* (Trouessart) is recorded from the Australian mainland, from fossil material of late Pleistocene age. The Australian population is distinguished from the nominate Tasmanian race and is described as *P. higginsi australiensis*, a new subspecies. *P. h. australiensis* is compared with *P. oralis* (Thomas) and *P. australis* Gray.

Introduction

This paper is adapted from part of the taxonomic section of a document (Wakefield 1969) summarizing an investigation of mammal fossils from SE. Australian caves. Other sections of the document, dealing with palaeo-ecology and age of the fossils, have been incorporated in a separate paper (Wakefield, in press). Another part of the taxonomic section of the document, dealing with subspecific grouping of populations of *Rattus*, is currently being extended by further study.

Dimensions used in this paper, and their abbreviations, are as follows:

BL. Basal length of skull, from anterior margin of foramen magnum to anterior ends of premaxillae.

IC. Interorbital constriction: least width.

PL. Palatal length, along mid-line.

ZPH. Zygomatic plate height, from anterior-most alveolus of M^1 to junction of plate with zygomatic arch.

ZPL. Zygomatic plate length: Minimum antero-posterior length of plate.

FL. Foramen length: Mean length of incisive foramina.

FW. Foramen width: Maximum lateral extent of the two incisive foramina.

DL. Dentary length, from posterior end of condylar process to anterior end of dentary.

RD. Ramus depth: Minimum dorso-ventral depth of ramus in vicinity of M_3.

$M^{1-3}L$, $M_{1-3}L$. Antero-posterior length of upper and lower molar row, respectively, at alveolar level.

M^1W, M_1W. Maximum crown width of the tooth specified, irrespective of which cusps are involved.

I^1W, I_1W. Width of upper and lower incisor, respectively, at anterior edge of alveolus.

Measurements were made correct to 0·1 mm, using Helios dial calipers or cross-over vernier calipers.

Proportions such as ZPL/ZPH, I_1W/DL and RD/DL were computed, and these are expressed as percentages in this paper.

The Student's *t* test was used for most statistical comparisons, with probability values computed correct to the third decimal place. In some other cases the *t* test was applied, and less precise assessments of probability obtained. In certain cases involving small series, the Mann-Whitney U test was used, as in Siegel (1956).

The following abbreviations are used for institutions:

AM. Australian Museum, Sydney.

BM. British Museum (Natural History), London.

FM. Field Museum of Natural History, Chicago.

FWD. Fisheries and Wildlife Department, Melbourne.

QVM. Queen Victoria Museum, Launceston.

TM. Tasmanian Museum, Hobart.

WRD. Wildlife Research Division, CSIRO, Canberra.

The Pyramids Cave deposit referred to in this paper was an accumulation of bones of small animals, essentially the prey of owls, located four miles NNE. of Buchan, E. Vict. Material from the deposit was divided, according to texture and colour of the bones, into two fractions which are referred to as Holocene and Pleistocene respectively. Age of the Holocene fraction has not been assessed, and the Pleistocene fraction is considered to have accumulated mainly during the recession of the main Würm glaciation. (Wakefield, in press).

The bulk of the Pyramids Cave collection is to be placed in the National Museum of Victoria. Specimen numbers prefixed with P, in this paper, refer to registrations in the palaeontological department of that museum. The sources of other specimens are set out in Appendix 2 of this paper; locality data are provided in Appendix 3.

Delimitation of subspecies

Concerning subspecies taxonomy, the following principles have been observed in the present studies:

When the geographic range of a species is found to comprise major subdivisions, and the populations of these subdivisions are found to differ significantly from each other in one or more morphological features (at or beyond a probability level of 0·05), then each of these populations should be identified as a subspecies and recognized taxonomically by a distinguishing trinomen.

The geographic subdivisions should represent primary subdivisions of the gene pool of the species. Thus, as a taxon, subspecies should be meaningful biologically, and should have genetic, zoogeographic and evolutionary significance. Minor, or secondary, subdivisions of a species population should not be recognized as subspecies, because the significance of the primary subdivisions would then be obscured and the taxon become less meaningful biologically.

This subspecies concept is essentially that defined and discussed by Mayr (1969) except that, surprisingly, Mayr denies evolutionary significance of the taxon.

In these studies, it has not been accepted that populations which have attained a particular degree of morphological differentiation must necessarily be classified as different subspecies. This course is demanded by the gross dissimilarities in patterns and degrees of morphological divergence found in different species which have closely similar patterns of distribution and subdivision of population and therefore, presumably, analogous zoogeographic histories.

Problems inherent in the statistical approach to taxonomy are demonstrated by the following data concerning species of *Rattus* (Muridae) and *Antechinus* (Dasyuridae):

Horner and Taylor (1965) demonstrated by interbreeding experiment, that population groups, which on the evidence of general morphology had been classified as distinct species (Troughton 1941, Tate 1951), were in fact subspecies of the one species—*Rattus fuscipes*. Further, on the evidence of sympatric occurrence, they concluded that *R. lutreolus* was correctly classified as a species distinct from *R. fuscipes*.

Cranial and dental morphology of the three major population groups of *R. fuscipes* and of two groups of *R. lutreolus* have been compared, using 18 linear dimensions and 8 proportions. No character was found for which mean differences between specifically distinct populations were consistently greater than those between conspecific populations. The degree of difference, in cranial and dental morphology, between major population aggregates (i.e., subspecies) of *R. fuscipes*, was found to be of the same order as that between the nominate subspecies of *R. fuscipes* and the subspecies *velutinus* of *R. lutreolus*. (Wakefield 1969).

Unpublished data from an extension of this study of *Rattus* show that there are a number of small local populations of *R. fuscipes greyii* in the Central Division of S. Aust., which differ

significantly from each other in cranial and dental morphology.

A different situation pertains with certain species of *Antechinus*.

A. minimus and *A. swainsonii* are distinguishable only on minor morphological characters, but sympatric occurrence demonstrates that these two are in fact distinct species (Wakefield and Warneke 1963). Likewise, *A. flavipes* and *A. stuartii* are specifically distinct though closely similar morphologically (Wakefield and Warneke 1967). Depending on morphology, Thomas (1888) and Troughton (1941) regarded *stuartii* and *flavipes* as conspecific. Finlayson (1958) did likewise and in addition named the S. Australian population of *A. minimus* as a subspecies of *A. swainsonii*.

The dental and cranial differences which distinguish *Antechinus swainsonii* from *A. minimus*, and *A. stuartii* from *A. flavipes*, are of the order of those which distinguish subspecies within *Rattus fuscipes* and *R. lutreolus*. The order of morphological divergence found between primary population subdivisions of *Antechinus flavipes, A. swainsonii* and *A. minimus*, is less than that found between adjacent local populations of *R. fuscipes greyii*. The application of an arbitary statistical subspecies formula to these species of *Rattus* and *Antechinus* would produce an artificial classification with very little biological significance.

While there may be little similarity between patterns of divergence in species of unrelated genera such as *Rattus* and *Antechinus*, degrees of morphological variation within species of the Muridae have been found to be generally similar (Wakefield 1969). Further analogy has been assumed within the Muridae in connection with interpretation of certain data in the present paper. In this connection, patterns within *Rattus fuscipes* are considered to be very relevant, in view of the biological relationships established by the work of Horner and Taylor (*loc. cit.*).

A. Review of *Mastacomys fuscus* Thomas

Materials and Method

The following specimens of *Mastacomys* are included in the study:

(a) SE. Aust. series. 34 skulls of modern museum specimens: 12 from Whites River, Kosciusko State Park, S. N.S.W.; 13 from Otway Ranges, W. central Vict., including holotype of *M. fuscus brazenori*; 5 from Loch Valley, E. central Vict.; 4 from other Victorian localities. (See Appendix 2).

(b) Tasm. series. 27 skulls of modern museum specimens: 11 from Waratah, 9 from Mt. Kate, 7 from other Tasmanian localities (See Appendix 2).

(c) Pleist. Pyramids series. 21 right maxillae and 57 right dentaries, each with complete molar row, selected from Pleistocene fraction of Pyramids Cave deposit. (P20674-751).

(d) Holocene Pyramids series. 67 cranial specimens each with right molar row and zygomatic plate, and 59 right dentaries each with molar row, selected from Holocene fraction of Pyramids Cave deposit. (P20752-877).

(e) Fern Cave series. 12 cranial specimens, and 12 right dentaries, from Fern Cave, near Portland, SW. Vict. (P20985-21008).

(f) Holotype of *M. wombeyensis* (AM, F47322).

(g) Holotype of *M. mordicus* (BM, 22. 10. 1. 3). The specimen was not seen but measurements were communicated by J. E. Hill (letter, 12 March 1965), and photographs were seen.

(h) Carrieton series (see Appendix 2).

Each series was sorted into subseries according to tooth-wear, using the system of Ride (1956):

Subseries A. With distinct cusps on all molars.
Subseries B. With wear beginning to unite cusps into laminae.
Subseries C. With cusps united into transverse laminae but still discernible.
Subseries D. With cusps no longer discernible.

General data of the series were determined by combining data of subseries B and subseries C in each case, thus eliminating all or most specimens of very immature animals and of aged animals. Such restricted data of the main series studied, and similarly restricted data of series from specific localities, are set out in Tables 1 and 2. Data of subseries A and B of certain of the main series are set out in Table 3.

This system of tooth-wear categories has been used in the present paper in connection

with *Mastacomys* so that relevant comparisons could be made with data documented by Ride and others who adopted the system. However, in the series of *Mastacomys* which have been studied, tooth-wear is more advanced in certain small skulls than it is in certain larger and presumably older skulls. Moreover, tooth-wear is usually much more advanced on third molars than it is on first molars of the same specimen. In these circumstances degree of tooth-wear is not regarded as a wholly reliable key to age-grouping.

RESULTS AND DISCUSSION: It is assumed that the Tasm. series represents the *Mastacomys fuscus* of Thomas (1882) and thus the nominate race, *M. fuscus fuscus*. Compared with this series, the SE. Aust. series has these features:

Size (indicated by BL and DL) similar.

I^1W 10 percent greater, I_1W 13 percent greater, I_1W/DL greater (p= 0·003, 0·000, 0·000).

RD 3 percent greater, RD/DL greater (p = 0·022, 0·001).

Comparisons of the Tasm. series with the two Pyramids series, the Fern Cave series, and the Carrieton series, show that all the mainland Australian series which have been studied differ similarly from the Tasm. in having incisors 10-13 percent wider, ramus 3-5 percent deeper, and the proportions I_1W/DL and RD/DL greater. In all cases the differences are significant. Tasmanian specimens differ further from those of the mainland in having the posterior portions of the incisive foramina comparatively broad and obtuse (Plate 3, figs. 2-3).

Fig. 1 illustrates the relationship of I_1W and DL, in both the Tasmanian and the mainland Australian populations of *Mastacomys*.

Brazenor (1934) stated that tail length averaged 64 percent of head-body length in Tasmanian specimens. However, Green (1968) found that this proportion averaged 70·8 percent for 20 adult males and 72·0 percent for 17 adult females of the nominate Tasmanian race, and he observed that these figures were very similar to the 74 percent and 71 percent noted by Calaby and Wimbush (1964) for series from Loch Valley, Vict., and Whites River, N.S.W., respectively.

Significant differences occur between the two
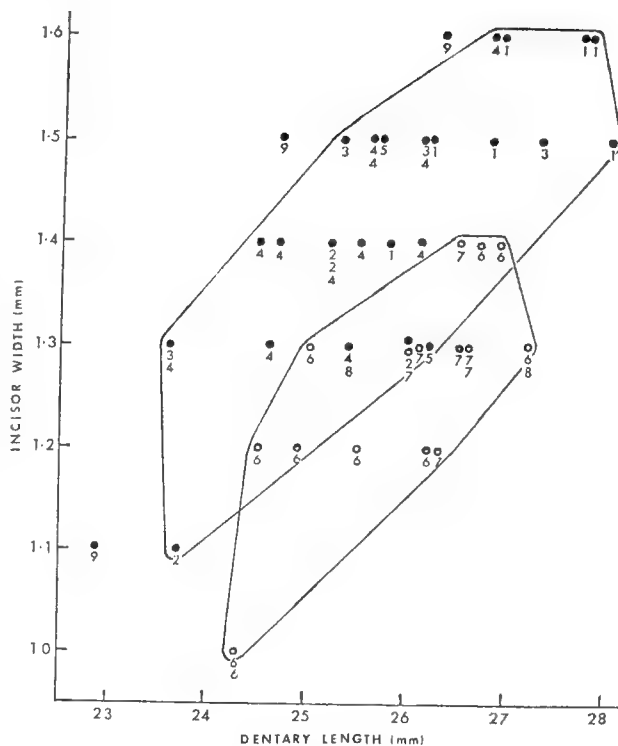
FIGURE 1

Relationship of I_1W and DL in subspecies of *Mastacomys fuscus*. The data apply to specimens of the restricted series, comprising tooth-wear categories B and C only.

   ⬤ *M. f. mordicus*   O *M. f. fuscus*

The boundary shown for *M. f. mordicus* applies to all modern and Holocene series studied. Points for the 59 specimens of the Holocene Pyramids series are not shown, but all would fall within the boundary.

Each plotted point shows dimensions of one or more specimens (as indicated by the number of figures beneath each plot). The figures refer to the source of each specimen, as follows:

1.	Whites River	5.	Other Vict. localities
2.	Otway Ranges	6.	Waratah
3.	Loch Valley	7.	Mt. Kate
4.	Fern Cave	8.	Other Tasm. localities

The figure 9 indicates dimensions of three exceptional specimens of the Pleistocene Pyramids series. The points for the other eight specimens of this series would fall within the boundary indicated for *M. f. mordicus*.

main local populations represented in the Tasm. series, and between two of the three main local populations of the SE. Aust. series, according to the data shown in Table 2.

Compared with the Mt. Kate series, the Waratah series differs as follows:

ZPL 10 percent less, and ZPL/ZPH less.

FW 8 percent greater but FL 7 percent less, so FW/FL greater.

RD/DL greater.

($0.01 < p < 0.05$, in each case).

Compared with the Otway Ranges series, the Whites River series has the incisors broader by 12-18 percent, dentaries longer by 8 percent, and the proportion I_1W/DL greater ($0.01 < p < 0.05$, in each case).

Some of the above differences observed between local populations may be due to age bias in these small samples. (See tooth-wear groupings in Appendix 2). In any case, these differences are of the same order as those found between local populations of *Rattus greyii* (See comments in Introduction).

Compared with data of the composite SE. Aust. series (Table 1), the $M^{1-3}L$ is 3 percent less in the Holocene Pyramids series and 5 percent less in the Pleist. Pyramids series ($p = 0.014$, 0.002). Except for the differences in molar sizes, means of the dimension and proportions for each of the Pyramids series are very similar to those of the SE. Aust. series.

The Fern Cave series differs significantly from the SE. Aust. series only in the shorter incisive foramina and the proportion FW/FL. It does not differ significantly in any observed character from either of the Pyramids series.

The holotype of *M. mordicus* is a maxilla with molar row, originating from the Mount Gambier area, S. Aust. Thomas (1922) designated it a distinct species on the evidence of the very short crown length of the molar row and the small zygomatic plate. The specimen belongs to tooth-wear category A, and the supposed diagnostic characters are due to its immaturity.

The geological age of the *mordicus* holotype is not known, but it is most likely to have originated from a Holocene deposit. There are numerous Holocene deposits, in which *Mastacomys* is represented, about the lower Glenelg River in the Mount Gambier area (Wakefield, unpublished data), and the Fern Cave deposit (Wakefield 1963) is typical of these.

In the holotype of *mordicus*, $M^{1-3}L$ (alveolar) is 9.0 mm, which is not significantly different from the mean for any of the series discussed above. With ZPL 3.1, ZPH 5.6, and ZPL/ZPH 55.4, the holotype of *mordicus* is comparable with a similarly immature specimen (NMV, C5539) from the Otway Ranges, Vict., which has ZPL 3.3, ZPH 5.9, and ZPL/ZPH 55.9. Moreover, the 55.4 of the holotype is identical with the mean ZPL/ZPH for subseries A of the Holocene Pyramids series, and very close to the means for subseries A of the Tasm., SE. Aust. and Pleist. Pyramids series (Table 3).

The evidence which has been outlined indicates that the extant SE. Australian population of *Mastacomys fuscus*, and the populations represented by the Fern Cave series, the Holocene Pyramids series, and the Pleist. Pyramids series, collectively represent a subspecies distinct from the Tasmanian *M. fuscus fuscus*. As pointed out by Troughton (1941), the valid name for this mainland subspecies is *M. fuscus mordicus*. Geographically, the holotype of *mordicus* belongs to the mainland subdivision of the species, and morphologically it is not separable from the mainland series which have been studied.

Ride (1956) suggested that 'the name *M. fuscus mordicus* should be restricted to the ?Pleistocene S. Australian populations of *M. fuscus*', and he proposed the name *M. fuscus brazenori* for the extant mainland population, depending on the supposed difference in tail length to distinguish it from the nominate race. The holotype of *brazenori* (NMV, C199, Beech Forest, Otway Ranges, Vict.) is a badly broken specimen, but details available ($M^{1-3}L$ 9.6 mm, ZPH 8.9 mm, ZPL 4.4 mm, $M_{1-3}L$ 8.7 mm, ZPL/ZPH 49.4) distinguish it in no way from the extant mainland race (Table 1). With the application of the name *M. fuscus mordicus* to this race, the name *brazenori* becomes a subjective synonym of *mordicus*.

Tate (1951) treated the Carrieton specimens as topotypical of *M. mordicus*, but as pointed out by Ride (1956), this is not so. Carrieton is 610 km. from Mt. Gambier, and *Mastacomys* has not been recorded between these two localities.

In depth of ramus and width of incisors, as well as in the proportions examined, the Carrieton series is not separable from the SE. Aust. series. Mean lengths of molar rows are 6 percent less in the Carrieton series than in the SE. Aust. series (significantly, with $p = 0.000$,

0·012). The smaller tooth-size probably represents the lower limit of a clinal gradient occurring when wetter climatic conditions provided tolerable habitat for *Mastacomys* as far inland as Carrieton. On present evidence, the Carrieton series is included in *M. fuscus mordicus*.

The holotype of *M. wombeyensis* is a maxilla with molar row. In describing the specimen, Ride (1956) assessed the tooth-wear in his category B. The $M^{1-3}L$ (8·9 mm) is smaller by 5-9 percent than the means for the series of *M. fuscus* under review (Table 1), but in no case is the difference significant ($0·17 > p > 0·05$, in each case). Minimum observed values of $M^{1-3}L$ are 8·6 mm for P20788 of the Holocene Pyramids series, 8·7 mm for NMV no. C200 of the Tasm. series, and 8·8 mm for P20675 and P20689 of the Pleist. Pyramids series.

The ZPH of the holotype of *wombeyensis* (8·3 mm) is close to the mean for each of the series studied (Table 1). However, the ZPL (5·0 mm) is 15-23 percent greater than means of ZPL for those series, though the difference is in no case significant ($0·12 > p > 0·05$, in each case). The 5·0 is 19-27 percent greater than the means for the subseries B of those series (see Table 3), the differences being barely significant for the comparisons with the Tasm. and the Holocene Pyramids series ($p = 0·045, 0·040$) and not significant for the comparisons with the SE. Aust. and the Pleistocene Pyramids series ($p = 0·08, 0·12$).

The proportion ZPL/ZPH (60·2) in the *wombeyensis* holotype is greater than the mean for each of the principal series studied (Table 1), not significantly in the case of the Pleist. Pyramids series, the SE. Aust. series or the Tasm. series ($p = 0·168, 0·079, 0·111$), and barely significantly in the cases of the Holocene Pyramids and Carrieton series ($p = 0·036, 0·047$). The 60·2 is not significantly greater than the mean for subseries B of any of these series (Table 3), all probability values lying between 0·1 and 0·3. High individual values for this proportion occur as follows: 60·5 for P20708 in subseries C of the Pleist. Pyramids series, 60·9 for a specimen in subseries A of the Carrieton series, 62·5 for P20761 in subseries A of the Holocene Pyramids series, and

63·6 for QVM 1963.1.306 in subseries B of the Tasm. series.

The holotype of *wombeyensis* possesses 'a small additional cusp on the third molar, internal to and lying between the innermost cusp of the last two rows' (Ride 1956). An additional cusp occurs in the same position in QVM 1963.1.262 of the Tasm. series (on left M^3 only), in FWD R2954 (on right M^3 only) and NMV C134 (on both M^3s) of the SE. Aust. series, and in P20778 (right maxillary piece) of the Holocene Pyramids series (Pl. 3, fig. 1). Additional cusps of similar size occur in other positions on various molars, in some specimens on each of two opposite teeth but in other specimens on one tooth only. For example, the additional cusp on M^1, as illustrated in Pl. 3, fig. 2, occurs occasionally in *M. fuscus fuscus* and in *M. fuscus mordicus*, and an additional cusp on the mid-posterior of M^3 has been observed in several specimens of *M. f. mordicus* but not in *M. f. fuscus*.

On the average, additional cusps have been found in approximately 4 percent of the specimens of each of the larger samples of *Mastacomys* which have been studied. Some are distinct and functional, with the apex worn, while others are merely small non-functional lobes fused to the side of a normal cusp. The occurrence of such additional cusps appears to be due to comparatively uncommon alleles distributed widely amongst the various major populations, and they thus appear to be of no taxonomic significance.

Schram and Turnbull (1970) provide data of two further cranial specimens of *Mastacomys* obtained from the Wombeyan Caves bone breccia. The following details are included:

FM, PM5861—M^{1-3}, alveolar length, 9·3 mm; M^1W 3·2 mm.

AM, F52303—M^{1-3}, alveolar length, 8·3 mm; M^1W 2·8 mm; ZPL 4·1 and 4·2 mm; IC 3·4 mm; PL 16·2 mm.

The two measurements for PM5861 are not significantly different from means for the various series studied (Tables 1-3).

Schram and Turnbull placed F52303 in tooth-wear category B, but their photograph of it shows very little tooth-wear and indicates

a much younger state than that of the holotype of *wombeyensis*. The measurements given for F52303 may be compared with data of subseries A and B in Table 3. The teeth measurements, IC and PL, of F52303, are significantly less than means observed for the respective features in the subseries tabulated, but ZPL is greater than the observed means in all but one case. This indicates that, as in the holotype of *wombeyensis*, the ZPL in F52303 is proportionately great.

F52303 and PM5861 each has the additional cusp on M³, as in the holotype of *wombeyensis*. In F52303 it is of medium development on the right M³ and is less developed on the left, and in PM5861 it is partially fused to the hypocone on the one M³ present (Schram and Turnbull Pl. 1).

The three Wombeyan specimens of *Mastacomys* appear to represent a population with comparatively small teeth, proportionately long zygomatic plate, and a comparatively high incidence of the additional cusp on M³. Ride (1960) considered the Wombeyan deposit to be essentially an owl pellet accumulation, and he suggested 'an age somewhat later that the last pluvial period of the Pleistocene'. Subsequent work (Wakefield, in press) supports both contentions and indicates that all components of the Wombeyan faunal assemblage are identifiable with modern species.

The diagnostic characters of *M. fuscus mordicus*, being present in the Pleist. Pyramids series, were established at least as long ago as the main Würm glaciation. As certain forest species such as *Petaurus breviceps* and *Rattus fuscipes* were plentiful in the Pleistocene fraction of the Pyramids Cave deposit (Wakefield, in press) but are not indigenous in Tasmania, conditions on the Bass Strait land bridge during the main Würm glaciation evidently did not favour the crossing of it by forest animals, so it is highly unlikely that there was intercommunication at that time between Tasmanian and Australian mainland populations of *Mastacomys fuscus*.

Whilst the Pleist. Pyramids and the Carrieton series differ little from the Holocene and modern *M. fuscus mordicus*, there is suggestion of greater differentiation in the case of the Wom-

beyan group. Even if confirmed by study of further specimens, such differentiation is what might be expected within a primary population subdivision of a murid species. Therefore, on present knowledge, the Wombeyan *Mastacomys* cannot justifiably be classified other than in *M. fuscus mordicus*.

In summary, this study indicates the following taxonomy of *Mastacomys fuscus*:

(a) **Mastacomys fuscus fuscus**

(*Mastacomys fuscus* Thomas, 1882; Tasmania)
Tasmania. Holocene.

(b) **Mastacomys fuscus mordicus**

(*Mastacomys mordicus* Thomas, 1922; Mt. Gambier district, S. Aust.; subfossil).
Central and E. Vict., SE. N.S.W. (subfossil or fossil in SE. Aust., SW. Vict., E. N.S.W.). Pleistocene to Holocene. Subjective synonyms: *Mastacomys wombeyensis* Ride, 1956; Wombeyan Caves, E. N.S.W.; fossil. *Mastacomys fuscus brazenori* Ride, 1956; Beech Forest, W. central Victoria.

B. *Pseudomys higginsi australiensis*,
new subspecies

Diagnosis

A population of *Pseudomys*, presumably extinct, represented by fragmentary subfossil specimens of late Pleistocene age, from Pyramids Cave (lat. 37°27′, long. 148°13′) near Buchan, E. Vict., identified at species level as *P. higginsi* (Trouessart) and distinguished from the nominate Tasmanian race by smaller mean tooth-size and the zygomatic plate generally of less height and greater length.

Holotype

NMV, P20903—a right maxilla with M¹⁻³ (Pl. 3, fig. 9).
M¹⁻³L 6·0 mm, M¹W 2·0 mm, ZPH 7·0 mm, ZPL 3·7 mm.

The M¹ has a small auxiliary cusp anterior to the anterolingual conule, and a very slight anteromedian cingular ridge.

Upper anterior edge of zygomatic plate is pointed; posterior end of incisive foramen is level with middle of anteriormost root of M¹.

Paratypes

P20878-902, P20904-13—right maxillary specimens with teeth; used, together with holotype, for measurement and estimation of population parameters.

P20914—edentulous right maxilla with alveoli of molars.

P20915—incomplete right dentary with incisor, M^{1-2}, and the coronoid process entire.

P20916-83—right dentary specimens, used for measurement and estimation of population parameters.

P20984—incomplete right dentary, with condylar and angular processes entire.

General data

The holotype and paratypes were selected from 230 maxillary and 330 dentary specimens of the subspecies, found in the Pleistocene fraction of the Pyramids Cave deposit. Series of these specimens were identified originally (Wakefield 1960) as 'Pseudomys oralis', and later (Wakefield 1967) as 'Pseudomys sp.'.

Data of the 36 maxillary specimens (P20878-913) and the 68 dentary specimens (P20916-83), which were used for measurement and estimation of parameters, are set out in Table 4. This series constitutes all available right-hand specimens in which the three molars were present. Such specimens are mature in dentition, all molars being fully developed in both crown and roots. (In immature specimens the M^3, and often the M^2 also, become detached owing to incomplete formation of their roots).

Photographs of the holotype and of five of the paratypes comprise figs. 7-12 of Pl. 3.

In the Pyramids Cave deposit, *P. higginsi australiensis* was associated with wet forest species such as *Burramys parvus*, *Gymnobelideus leadbeateri* and *Schoinobates volans*. It was absent from the dry sclerophyll forest and woodlands faunal assemblage of the Holocene fraction of the deposit. Its habitat tolerance appears to have been limited to wet forests of the kind which occur today in E. central Victoria where mean annual rainfall is 100 cm or more (Wakefield, in press).

P. higginsi australiensis has not been found in any Holocene fossil deposit. Evidently it became extinct several thousand years ago.

Comparison with P. higginsi higginsi

A series of 49 skulls of *Pseudomys higginsi* from Tasm. (Appendix 2) was taken to represent the nominate race. Only mature specimens (with BL > 27 mm) were included. Data of this series are set out in Table 4. Compared with those of this series, means for *P. higginsi australiensis* differ as follows:

$M^{1-3}L$ 8 percent greater, M^1W 12 percent greater, $M_{1-3}L$ 8 percent greater, M_1W 8 percent greater (p = 0·000 in each case).

ZPH 5 percent less and ZPL 12 percent greater, so ZPL/ZPH much greater (p = 0·000 in each case).

Mean ZPL/ZPH is 45·9 for the *P. higginsi higginsi* series, and 53·4 for the *P. higginsi australiensis* series; but this divergence does not deny conspecificity. Greater divergence is observed with this proportion in *Rattus fuscipes*: 53·5 for a series of *R. f.greyii* from SW. Vict., and 61·7 for a series of *R. f. assimilis* from the Pleistocene fraction of the Pyramids Cave deposit (Wakefield 1969).

Mean DL is the same for each series of *P. higginsi*, indicating closely similar skull size for each population. In both series the coronoid process is well developed (fig. 10), the upper anterior edge of the zygomatic plate is pointed (figs. 6, 8-9), and the posterior ends of the incisive foramina are level, on the average, with the middle of the anteriormost root of the M^1 (figs. 5-9).

Occasionally in *P. higginsi higginsi*, the M^1 has a well developed low cusp or cingular ridge extending from the anterior face of the anterolingual conule to the anteromedian end of the tooth; for example, in TM nos. 0191 and 0816. Such well developed cusp or ridge was not observed in any of the Pyramids series of *P. higginsi australiensis*, though four of the paratypes (P20879, P20883, P20893, P20908) show what appears to be a modification of the feature in the form of a small auxiliary cusp anterior to the anterolingual conule, and the holotype (P20903) has both the auxiliary cusp and a slight cingular ridge.

All known occurrences of *P. higginsi higginsi* have been in or near rainforest, in areas with mean annual rainfall from about 125 to over 250 cm. (Green 1968). This habitat is gener-

ally similar to that which *P. higginsi australiensis* is believed to have occupied.

Comparison with P. oralis

To represent the Pyramids Cave *Pseudomys oralis*, 97 cranial specimens (P21009-21105) and 84 dentary specimens (P21106-21189) were selected. The selection was limited to those having the right-side molar row complete. Data of the series are summarized in Table 4. In this series the means of DL, $M^{1-3}L$ and $M_{1-3}L$ are each approximately 10 percent greater, and mean I_1W 26 percent greater, than in *P. higginsi australiensis*.

P. oralis is absolutely distinguished from *P. higginsi* by the rounded upper anterior edge of the zygomatic plate, and the much smaller (obsolete) coronoid process. It is distinguished further by the lesser posterior extent of the incisive foramina, the ends of which are, on the average, level with the anterior edge of the anteriormost root of M^1.

P. oralis occurred in the Holocene fraction of the Pyramids Cave deposit and was absent from the Pleistocene fraction, so it and *P. higginsi australiensis* were not associated in either faunal assemblage.

Comparison with P. australis

Two series of *Pseudomys australis* were used:

(a) A series of 21 specimens (P21190-21210) from Fern Cave, SW. Vict., comprising 12 right-side maxillary pieces each with complete molar row and zygomatic plate, and nine right-side dentary specimens each with complete molar row.

(b) A series of six cranial specimens from central Australian localities (Appendix 2).

In comparison with these series of *P. australis*, the *P. higginsi australiensis* series differs as follows:

Size, as evidenced by DL, ZPH and lengths of molar rows, is approximately 6 per cent less than for the Fern Cave series and 8 percent greater than for the central Australian series.

ZPL/ZPH is greater than in either series of *P. australis* (p. < 0.001 in each case).

No anteromedial cingular ridge has been observed on M^1 in any specimen of *P. australis*, though occasionally there is a small auxiliary cusp anterior to the anteromedian style.

The incisive foramina do not extend as far posteriorly as in either series of *P. australis*. This is the key morphological feature upon which the identification of the Pyramids Cave series as *P. higginsi*, rather than as *P. australis*, depends.

This identification is supported by the fact that *P. australis* is a species of habitats much drier than that of the faunal assemblage in which the Pyramids Cave population, now identified as *P. higginsi australiensis*, occurred. See Appendix 1 for relevant details of morphology and habitat of *P. australis*.

Occurrence at Wombeyan Caves

Ride (1960) reported a small series of *Pseudomys oralis* from bone breccia obtained at Wombeyan Caves, E. N.S.W. Three of these specimens were examined during the present study. One (Ride's B 58/6), with $M^{1-3}L$ and M^1W 7·4 and 2·3 mm respectively, and a second (B 58/C), with M_1W 1·8 mm, are correctly identified as *P. oralis*. The third (B8/g) is a dentary with teeth dimensions ($M_{1-3}L$ 6·0 mm, M_1W 1·7 mm, and I_1W 0·8 mm) and other features typical of *P. higginsi australiensis*.

Schram and Turnbull (1970) identified as *P. oralis* a series of specimens which they extracted from Wombeyan Caves breccia. The mean which they report for M^1W (2·10 mm), and the presence of 'a clearly defined antero-medial style' on the M^1 of some specimens, indicates that at least part of this series is *P. higginsi* rather than *P. oralis*.

The faunal assemblage represented in the Wombeyan Caves breccia includes *Burramys parvus*, *Gymnobelideus leadbeateri* and *Schoinobates volans*; it was a wet forest fauna very similar to, and most probably contemporaneous with, the fauna represented in the Pleistocene fraction of the Pyramids Cave deposit (Wakefield 1969). Therefore it must be expected that the Wombeyan specimens which are similar to *P. higginsi* are in fact this species rather than *P. australis*. Furthermore, as Wombeyan Caves and the Pyramid Cave are both in the highland region of SE. Aust., it must be expected that

the specimens in question should be *P. higginsi australiensis*.

Addendum

While this paper was in press, *Mastacomys* and *Pseudomys* material was examined from a cave deposit ('Wombeyan Quarry') located approximately 1·6 km. W. of Broom's Wombeyan Caves site and at the same elevation. The deposit includes remains of extinct animals such as *Sthenurus* and *Thylacoleo*, indicating that it is of Pleistocene origin. Absence of arboreal mammals suggests that the vegetation was montane shrubbery associated with colder climatic conditions than at present. Remains of *Burramys* were present.

The specimens examined include 20 left maxillae and 20 incomplete left dentaries of *Mastacomys*, and four maxillae (two left, two right) of *Pseudomys* cf. *higginsi*. This material has not yet been allocated to a museum but is part of a collection being studied by Dr Jeannette Hope, Department of Prehistory, Australian National University. I am indebted to Dr Hope for the loan of the murid specimens and for information about the quarry site.

Of the *Mastacomys* maxillae, two were of tooth-wear category B and 15 of category C, and of the dentaries, six were of category B and 13 of category C. Data of these specimens are as follows, the three figures in each case being number of observations, mean value, and standard deviation:

$M^{1-3}L$—17, 9·45 mm, 0·23
ZPH—17, 8·06 mm, 0·56
ZPL—16, 4·48 mm, 0·33
ZPL/ZPH—16, 56·0 percent, 4·18
I_1W—16, 1·38 mm, 0·09
RD—19, 6·44 mm, 0·18

Of the 20 *Mastacomys* maxillae, the small auxiliary cusp of *M. wombeyensis* was present in two specimens and absent in 16. Teeth in the other two specimens were too worn for the occurrence of the cusp to be assessed. These details, in a series of late Pleistocene *Mastacomys* from the Wombeyan area, tend to confirm the suggestion in this paper that presence of the auxiliary cusp is not of taxonomic significance.

Mean incisor width in the Wombeyan Quarry *Mastacomys* is 10 percent greater than in the Tasmanian *M. fuscus fuscus* (significantly with $p < 0.02$) but not significantly different from means for the mainland Australian *M. f. mordicus* (Table 1). In size (as evidenced by $M^{1-3}L$, ZPH and RD) the Wombeyan Quarry *Mastacomys* is essentially similar to the other major series studied. These details lead to the identification of the Wombeyan Quarry series as *M. fuscus mordicus*, and this supports the same identification for the Wombeyan Caves specimens otherwise classified as *Mastacomys wombeyensis*.

Mean ZPL/ZPH is significantly greater for the Wombeyan Quarry series than for the SE. Australian series and the Holocene Pyramids series ($p < 0.001$ in each case), but is closely similar to that of the Pleistocene Pyramids series. This supports the suggestion that the Wombeyan *Mastacomys fuscus* had a proportionately long zygomatic plate, and the similar character of the older Pyramids series suggests that the long zygomatic plate may have been general in late Pleistocene populations of the species in SE. Australia.

Data of the series of *Pseudomys* cf. *higginsi* (giving number, mean and standard deviation) are:

$M^{1-3}L$—4, 5·95 mm, 0·18
ZPH—4, 6·24 mm, 0·16
ZPL—3, 3·30 mm, 0·10
ZPL/ZPH—3, 52·5 percent, 1·87

The posterior end of the incisive foramen is level with the anterior edge of the anteriormost root of the M^1 in two of the specimens, and with the middle of the same root in the other two. This distinguishes these specimens from *P. australis*. The distinction is supported by the evidence indicating that the Wombeyan Quarry fauna belonged to a cold montane habitat.

The upper anterior edge of the zygomatic plate is pointed in the two specimens which have this feature unbroken. This, together with the linear dimensions, distinguishes the series from *P. oralis* (Table 4).

The proportion ZPL/ZPH in the Wombeyan Quarry sample is significantly greater than in the Tasmanian *P. higginsi higginsi* ($p < 0.02$) but is closely similar to that of the Pleistocene Pyramids series.

The foregoing details indicate that the Wombeyan Quarry *Pseudomys* is taxonomically the same as the *P. higginsi australiensis* of the Pleistocene fraction of the Pyramids Cave deposit.

APPENDIX 1: Data of *Pseudomys australis*

Incisive foramina

Thomas (1921) included the following comment in his original description of *Pseudomys australis oralis* (now *Pseudomys oralis*):

'Palatal foramina proportionately shorter, not or scarcely penetrating between the molars, while in *australis* they reach to the level of the middle of m^1'.

Proportionately long and narrow incisive foramina comprise a diagnostic character which distinguishes *P. australis* from other species, including *P. higginsi*. For example, the central Australian series of *P. australis* (see Appendix 1) and the Tasmanian series of *P. higginsi* (see Appendix 1) compare as follows:

In *P. australis*, mean FL/BL is 24·9 percent (n = 5, SD = 0·6), and mean FW/FL is 23·3 percent (n = 6, SD = 2·0).

In *P. higginsi*, mean FL/BL is 23·5 percent (n = 47, SD = 1·1), and mean FW/FL is 28·4 percent (n = 49, SD = 3·0).

In these proportions, the differences between the two series are highly significant, with p = 0·008 in the case of FL/BL and 0·000 in the case of FW/FL.

The greater proportionate length of the foramina of *P. australis* results in their extending farther posteriorly than in *P. higginsi*. In *P. australis*, the posterior end of each foramen is level, on the average, with the anterior edge of the middle (internal) root of the adjacent M^1. This feature is diagnostic in maxillary specimens, such as those in the Fern Cave series of *P. australis*, in which the foramina are incomplete.

Habitat

Data on the habitat of *Pseudomys australis* are noted by Gould (1863) as follows:

Under the synonym *Hapalotis murinus* (Gould's Pl. 7)—'Plains bordering Namoi and Gwydir', NE. N.S.W., and 'on edge of dry salt water lagoon of Plains' near Lake Albert, S. Aust.

Under the synonym *Mus lineolatus* (Gould's Pl. 18)—Darling Downs, SE. Qd., on 'all open parts of the grassy plains'.

Further distributional and habitat data of *P. australis* are provided by Troughton (1941), under the synonym *Pseudomys minnie*. These include the occurrence at Minnie Downs, NE. S. Aust., and 'on well-timbered sand ridges', 220 km. S. of Longreach, Qd.

P. australis has been recorded (in some cases under the synonym *Pseudomys auratus*) from several Holocene subfossil deposits in W. Vict. (Wakefield 1964). In one case (at Mount Hamilton) some of the remains appeared to be quite modern, but in all other cases the specimens were of unknown age.

The foregoing data indicate that *P. australis* was an animal of comparatively dry habitats, in which the range of mean annual rainfall was from 15 cm. (at Minnie Downs) to 60 or 75 cm. (in SE. Qd. and W. Vict.).

P. australis did not occur either in the dry forest and woodland faunal assemblage of the Holocene fraction of the Pyramids Cave deposit (Wakefield 1967) or in other Holocene deposits in the same district (Wakefield 1960). The habitat data of *P. australis*, together with the fact that *P. higginsi australiensis* also was absent from the Holocene fraction of the Pyramids Cave deposit, demonstrate that these two *Pseudomys* were separated by a habitat tolerance gap of substantial width.

APPENDIX 2: Data of series of *Mustacomys* and *Pseudomys*

Mustacomys fuscus

Whites River, Kosciusko Park, SE. N.S.W.

Subseries A—WRD: CM408, CM595, CM-608.

Subseries B—WRD: CM405-6, CM409, CM411.

Subseries C—WRD: CM402, CM404, CM-607. AM: M7170.

Subseries D—WRD: CM622.

Otway Ranges, SW. Vict.

Subseries A—NMV: C849-50, C903 (Beech Forest); C5539 (Lavers Hill).

Subseries B—NMV: C848, C893, C896, C900 (Beech Forest); C5540 (Lavers Hill).

Subseries C—NMV: C199 (Beech Forest).

Subseries D—NMV: C842, C902 (Beech Forest); C5541 (Lavers Hill).

Loch Valley, EC. Vict.

Subseries B—FWD: R2220-2.
Subseries C—FWD: R2693.
Subseries D—FWD: R2219.

Other Vict. specimens

Subseries B—FWD: R2954 (Kalorama).
Subseries C—NMV: C134-5 (no precise locality); C8146 (Leongatha).

Waratah, NW. Tasm.

Subseries B—QVM: 1963:1:116, 121-2, 130-1, 133, 140.
Subseries C—QVM: 1963:1:135, 145, 160, 173.

Mt. Kate, NW. Tasm.

Subseries B—QVM: 1963:1:82, 88, 262-4.
Subseries C—QVM: 1963:1:256, 259-60, 270.

Other Tasm. specimens

Subseries A—QVM: 1963:1:71, 78-9, 309 (Cradle Mt.).
Subseries B—QVM: 1963:1:306 (Cradle Mt.).
Subseries C—QVM: 1963:1:74 (Cradle Mt.). NMV: C200 (Swan Id.).

Carrieton, S. Aust.

Subseries A—1 maxillary specimen.
Subseries B—2 max., 2 dentary specimens.
Subseries C—3 max., 8 dent. specimens.
Subseries D—2 max. specimens.
These 18 specimens, each with molar row complete, were selected from 93 fragments which comprised collectively, MCZ no. 7049.

Pseudomys higginsi (Tasm. series)

QVM: 63:1:251-2, 254-5; 64:1:257-9, 300, 314; 65:1:23 (Mt. Kate). 63:1:159, 181-6, 231; 64:1:29, 226, 230; 65:1:87, 128-9, 229 (Waratah). 65:1:251-2 (Golden Valley). 65:1:38-9, 48, 55, 130-2 (Renison Bell). 65:1:74 (Corinna).

TM: A76, A78 (Florentine Valley); A479-81 (St. Valentine Peak); A79 (Junee).

Pseudomys australis (C. Aust. series)

NMV: C4883-5 (Mulka, S. Aust.); C157, C161 (Charlotte Waters, C. Aust.); C4885-6 (Brighton Downs, Qd.).

APPENDIX 3: Locality Data

Locality	Latitude (S)	Longitude (E)
Brighton Downs	23°30′	141°30′
Buchan	37°30′	148°10′
Carrieton	32°26′	138°32′
Charlotte Waters	25°55′	135°46′
Corinna	41°40′	145°06′
Cradle Mt.	41°40′	145°56′
Darling Downs*	28°	150°
Fern Cave	38°04′	141°10′
Florentine Valley	42°40′	146°28′
Glenelg River (lower)*	38°	141°
Golden Valley	41°38′	146°43′
Gwydir River*	29°30′	150°
Junee	42°45′	146°39′
Kalorama	37°48′	145°22′
Lake Albert	35°42′	139°10′
Lavers Hill	38°40′	143°24′
Leongatha	38°29′	145°57′
Loch Valley	37°47′	146°01′
Longreach	23°26′	144°15′
Minnie Downs	26°30′	140°
Mount Gambier	37°50′	140°46′
Mount Hamilton	37°47′	143°00′
Mount Kate	41°37′	145°55′
Mulka	28°18′	138°38′
Namoi River*	30°30′	150°
Pyramids Cave	37°27′	148°13′
Renison Bell	41°48′	145°26′
St. Valentine Peak	41°20′	143°48′
Swan Island	40°45′	148°07′
Waratah	41°27′	145°32′
Whites River	36°18′	148°23′
Wombeyan Caves	34°19′	149°59′

* The position indicated is at about the middle of the feature.

Acknowledgements

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PLATE 3

Details of *Mastacomys* and *Pseudomys*

Fig. 1. P20778. *Mastacomys fuscus mordicus*, with additional cusp of M³ indicated by arrow.

Fig. 2. P20799. *M. f. mordicus*, with additional cusps of molars indicated by arrows. Note posteriorly narrow incisive foramina.

Fig. 3. NMV, C200. *M. f. fuscus*, illustrating posteriorly broad incisive foramina.

Fig. 4. NMV, C4884. *Pseudomys australis*, illustrating posterior extent of incisive foramina.

Fig. 5. NMV, C7884. *P. higginsi higginsi*, illustrating posterior extent of incisive foramina.

Figs. 6-8. P20914, P20908, P20880 respectively. Maxillary paratypes of *P. higginsi australiensis*. Arrow indicates an additional cusp on M¹.

Fig. 9. P20903. Holotype of *P. higginsi australiensis*.

Figs. 10-12. P20915, P20940, P20984 respectively. Dentary paratypes of *P. higginsi australiensis*.

Enlargements: Figs. 1-2 × 5, figs. 3-5, 10-12 × 3, figs. 6-9 × 4.

TABLE 1

Data of series of *Mastacomys*

Each group comprises from top to bottom, number of observations, mean, and standard deviation.

Series	Tasm.	S.E. Aust.	Fern Cave	Holocene Pyramids	Pleist. Pyramids	Carrieton
$M^{1-3}L$	23 9·49 0·37	22 9·78 0·41	12 9·58 0·29	37 9·52 0·34	12 9·34 0·26	5 9·26 0·20
M^1W	23 3·33 0·10	21 3·25 0·16	12 3·33 0·12	36 3·36 0·13	12 3·23 0·14	5 3·14 0·06
I^1W	23 1·37 0·12	21 1·50 0·15	12 1·43 0·10	15 1·41 0·16		
ZPH	23 8·08 0·60	22 8·32 0·76	12 8·26 0·62	37 8·22 0·89	12 8·10 0·48	5 8·26 0·51
ZPL	23 4·13 0·42	22 4·14 0·44	12 4·33 0·51	37 4·23 0·47	12 4·33 0·34	4 4·05 0·51
FL	21 7·80 0·50	21 8·12 0·61	12 7·28 0·69	19 7·55 0·73		
FW	21 1·74 0·17	21 1·90 0·16	12 1·94 0·32	19 1·92 0·20		
BL	14 34·66 1·45	17 34·82 2·25		5 35·74 1·02		
DL	19 25·90 0·91	19 25·86 1·54	12 25·31 0·86	59 25·62 1·02	22 25·31 0·69	
RD	22 6·22 0·21	21 6·43 0·36	12 6·45 0·31	59 6·51 0·19	57 6·40 0·26	10 6·41 0·20
$M_{1-3}L$	22 8·71 0·20	22 8·96 0·28	12 8·81 0·26	59 8·87 0·27	57 8·60 0·28	10 8·40 0·25
L_1W	22 1·26 0·12	21 1·42 0·16	12 1·42 0·09	59 1·41 0·10	18 1·39 0·07	7 1·37 0·11
ZPL/ZPH	23 51·2 5·3	22 50·0 5·4	12 52·7 6·2	37 51·6 3·9	12 53·6 4·3	4 47·8 3·4
FW/FL	21 22·4 2·6	21 23·5 2·9	12 26·9 3·5	19 25·6 3·4		
I_1W/DL	19 4·9 0·3	19 5·5 0·4	12 5·6 0·3	59 5·5 0·3	11 5·5 0·3	
RD/DL	19 23·9 1·0	19 25·1 1·1	12 25·6 1·0	59 25·4 1·1	22 25·2 1·3	

TABLE 2

Data of local populations of *Mastacomys*

Each group comprises, from top to bottom, number of observations, mean, and standard deviation.

	Tasmania		Australian Mainland		
	Mt. Kate	Waratah	Otway Ranges	Loch Valley	Whites River
$M^{1-3}L$	9 9·66 0·27	11 9·36 0·33	5 9·76 0·23	4 9·85 0·54	7 9·81 0·35
M^1W	9 3·37 0·10	11 3·31 0·08	4 3·30 0·00	4 3·35 0·10	7 3·26 0·08
I^1W	9 1·38 0·08	11 1·33 0·14	4 1·43 0·22	4 1·48 0·10	7 1·60 0·06
ZPH	9 8·13 0·42	11 8·00 0·75	5 8·00 0·76	4 8·65 0·51	7 8·64 0·51
ZPL	9 4·29 0·21	11 3·87 0·41	5 4·18 0·40	4 4·33 0·55	7 4·17 0·50
FL	9 8·04 0·46	9 7·52 0·40	4 8·38 0·21	4 8·15 0·52	7 8·04 0·61
FW	9 1·64 0·05	9 1·78 0·17	4 1·83 0·22	4 1·98 0·26	7 1·93 0·17
BL	7 35·30 0·68	5 33·68 1·99	2 33·60 2·26	3 35·07 2·25	7 36·07 1·10
DL	7 26·37 0·24	10 25·55 1·12	4 25·00 1·00	4 25·58 1·55	7 27·03 0·84
RD	9 6·21 0·22	11 6·23 0·22	4 6·33 0·25	4 6·55 0·37	7 6·61 0·24
$M_{1-3}L$	9 8·76 0·18	11 8·67 0·23	5 8·92 0·19	4 9·00 0·40	7 9·03 0·14
I_1W	9 1·26 0·10	11 1·24 0·14	4 1·30 0·14	4 1·45 0·10	7 1·53 0·08
ZPL/ZPH	9 52·8 3·3	11 48·6 5·0	5 52·4 5·0	4 50·7 4·9	7 48·3 5·8
FW/FL	9 21·4 1·7	8 23·5 2·5	4 21·8 2·5	4 24·3 2·0	7 24·0 1·9
I_1W/DL	7 4·9 0·2	10 4·8 0·4	4 5·2 0·5	4 5·7 0·2	7 5·7 0·3
RD/DL	7 23·2 0·7	10 24·3 0·2	4 25·5 1·5	4 25·6 1·0	7 24·5 1·6

TABLE 3

Data of subseries of *Mastacomys*

Each group comprises, from top to bottom, number of observations, mean, and standard deviation.

	Series	Tasmania	S.E. Aust.	Holocene Pyramids	Pleist. Pyramids	Carrieton
Subseries A	$M^{1-3}L$	4 9·60 0·25	7 9·50 0·43	14 9·31 0·30	4 8·97 0·17	1 8·80 —
	M^1W	4 3·40 0·16	7 3·31 0·07	13 3·36 0·10	4 3·22 0·05	1 3·20 —
	IC	4 4·20 0·28	7 4·19 0·18	4 4·57 0·71		
	PL	4 20·95 0·95	7 20·71 1·15	4 20·57 0·84		
	ZPH	4 7·35 0·72	7 6·83 0·62	14 6·56 0·57	4 7·35 0·66	1 6·40 —
	ZPL	4 4·00 0·29	7 3·69 0·27	14 3·64 0·45	4 3·95 0·24	1 3·90 —
	ZPL/ZPH	4 54·6 2·8	7 54·1 2·8	14 55·4 3·7	4 53·9 2·3	1 60·9 —
Subseries B	$M^{1-3}L$	13 9·42 0·38	13 9·72 0·48	15 9·49 0·38	4 9·35 0·31	2 9·05 0·07
	M^1W	13 3·35 0·08	13 3·31 0·09	15 3·37 0·12	4 3·30 0·14	2 3·15 0·07
	IC	11 4·09 0·18	13 4·12 0·24	7 4·33 0·29		
	PL	11 21·93 0·79	13 22·45 1·48	6 21·50 1·42		
	ZPH	13 7·75 0·49	13 8·05 0·82	15 7·47 0·90	4 7·90 0·70	2 7·55 0·07
	ZPL	13 3·98 0·42	13 4·06 0·47	15 3·92 0·46	4 4·20 0·34	1 3·30 —
	ZPL/ZPH	13 51·4 5·4	13 50·7 5·6	15 52·7 4·2	4 53·4 5·1	1 43·4 —

TABLE 4

Data of series of *Pseudomys*

Each group comprises, from top to bottom, number of observations, mean, and standard deviation.

|	P. oralis	P. higginsi australiensis	P. higginsi higginsi	P. australis (Fern Cave)	P. australis (C. Aust.)
$M^{1-3}L$	97 6·88 0·19	36 6·19 0·17	49 5·73 0·24	12 6·49 0·19	6 5·84 0·34
M^1W	97 2·24 0·09	36 1·93 0·08	49 1·73 0·06	12 2·08 0·05	6 1·92 0·09
ZPH	96 7·38 0·48	29 6·50 0·37	49 6·84 0·35	11 6·91 0·16	6 6·03 0·48
ZPL	95 3·86 0·27	25 3·49 0·16	49 3·13 0·26	12 3·64 0·20	6 2·93 0·25
DL	83 22·88 0·68	8 20·54 0·64	48 20·54 0·66	5 21·42 1·16	6 18·88 1·29
RD	82 5·14 0·13	60 4·70 0·19	49 4·60 0·20	9 4·76 0·18	6 4·28 0·25
$M_{1-3}L$	84 6·58 0·18	59 5·94 0·19	49 5·61 0·20	9 6·67 0·17	6 5·56 0·32
M_1W	84 1·79 0·08	66 1·66 0·07	49 1·54 0·07	9 1·76 0·05	6 1·73 0·05
I_1W	83 1·06 0·06	14 0·84 0·06	49 0·84 0·06	8 0·90 0·03	6 0·83 0·08
ZPL/ZPH	94 52·5 3·7	24 53·4 2·5	49 45·9 4·4	12 48·3 3·7	6 48·6 2·2
I_1W/DL	82 4·7 0·3	2 4·2 0·5	48 4·1 0·2	4 4·3 0·2	6 4·4 0·5
RD/DL	81 22·5 0·7	7 23·3 0·7	48 22·4 1·0	5 22·2 1·7	6 22·7 1·0
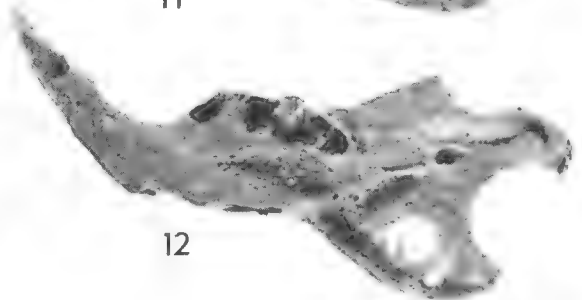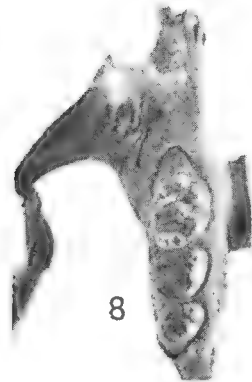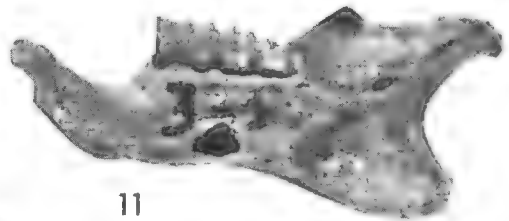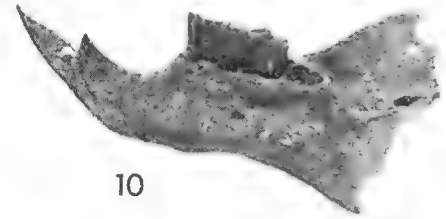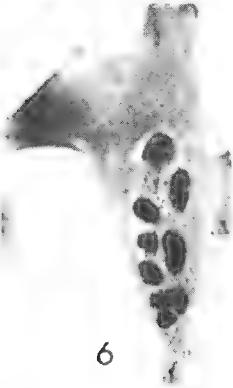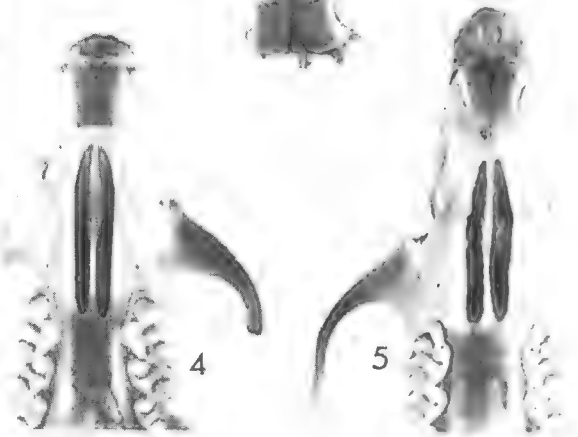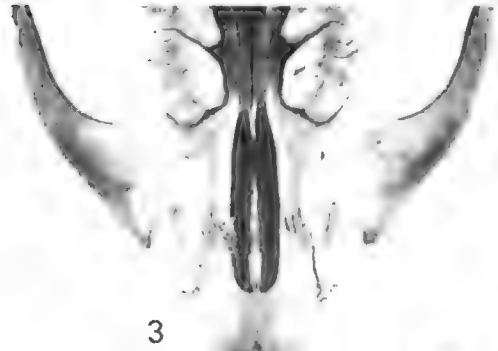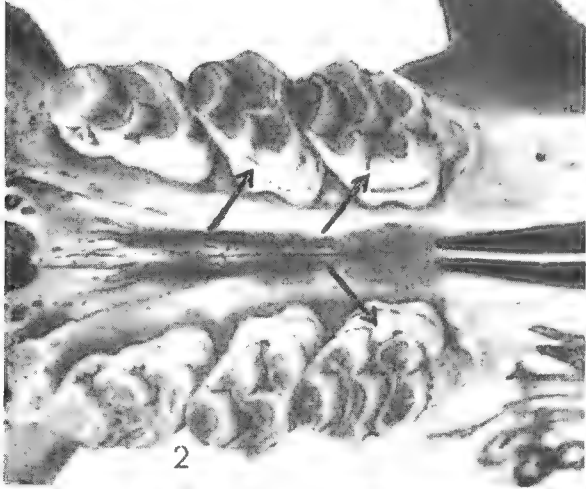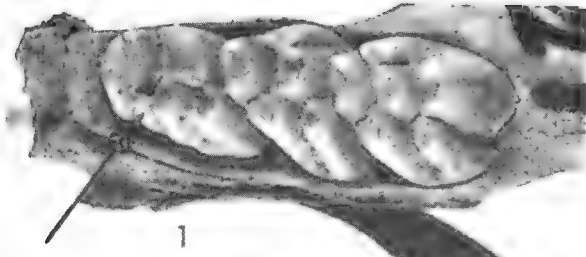
A NEW GUINEA FOSSIL MACROPODID (MARSUPIALIA) FROM THE MARINE PLIOCENE OF VICTORIA, AUSTRALIA

By M. PLANE

Bureau of Mineral Resources

Abstract

The discovery of a fossil macropodid skull fragment in Lower Pliocene (Kalimnan) marine rocks with associated shelly and microfossils provides a further cornerstone in the development of a time scale for the terrestrial Tertiary sequence in Australia and New Guinea. The fossil is *Protemnodon otibandus* Plane 1967, a species previously known only from the non-marine Pliocene of New Guinea, but as a result of this study now recognized from Victoria and SE. Queensland.

Introduction

In April 1969 Mr R. E. Hesselschwerdt of Melbourne discovered in the second headland north of Lake Tyers House, on the Nowa Nowa arm of Lake Tyers, Victoria, a fragment of bone and portions of teeth. He carefully extracted a large block and presented it to the National Museum of Victoria (P26893). The block contained not only the skull fragment but an abundant shelly and microfauna. The rock in which the fossil was found is portion of the Jemmy's Point Formation which has been described as a lithologically diverse series of marine calcareous sands (Wilkins 1963). The upper shell bed in which the fossil was found has been dated by the same writer as lower Pliocene at the top of the Kalimnan Stage. As pointed out by Warren (1965) the formation contains rounded pebbles and carbonaceous material, which together with faunal evidence is taken as indicating a near shore environment. It is not surprising that a fragment of a terrestrial animal should be found in these rocks and indeed Warren (1965) has described a fossil marsupial humerus from this formation, at a site near the Bunga Creek road cutting on the Princes Highway, Victoria.

The fossil includes portions of the left maxilla, palatine and frontal bones, the complete left lacrimal, the four molar teeth, and the posterior alveolus of the permanent premolar. The molars are in the LMEB wear stage of Tedford (1966). The fossil, although fragile, has not been greatly damaged apart from one large crack which extends anterodorsally in the maxilla from in front of the M^3, through the anterior opening of the infraorbital canal and back to the lingual side of the M^3. There has been some compression along the path of the infraorbital canal, which has collapsed.

Description

Maxillary: The bone is robust and is pierced just anterior to the orbital rim by the anterior opening of the infraorbital canal. The maxillary is produced laterally above the M^3 to form a strong base for the anterior root of the zygoma. The maxillary contribution to the masseteric process of the zygoma has been broken off but it does seem certain that the jugal made a long contact with the maxillary; this contact terminated at the ventral edge of the lacrimal. The maxillary contributes to the orbital surface. The postorbital surface is pierced by the posterior opening of the infraorbital canal and a small sphenopalatine foramen is situated on the palatine/maxillary suture behind the infra-orbital foramen. Both foramina lie in a deep broad groove and are separated by a low ridge within the groove.

Lacrimal: From its shape and position this bone would seem to make up the anterodorsal section of the orbit. There is a large orbital process. The infralacrimal foramen is approximately twice the diameter of the supralacrimal foramen. They are separated by a small rugose infralacrimal tuberosity and there is no supralacrimal tuberosity.
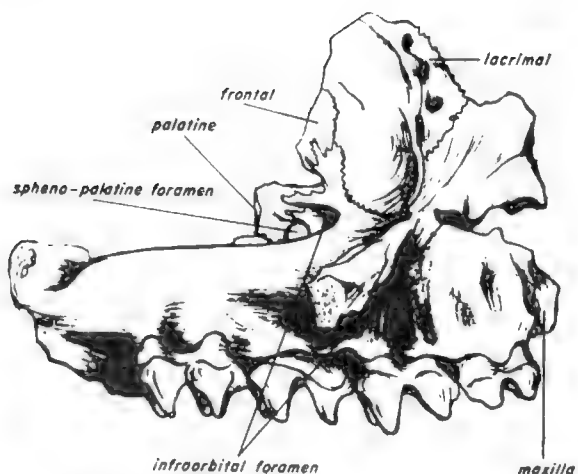
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Fig. 1—Hypotype of *Protemnodon otibandus* Plane.

Frontal: Only a small fragment is preserved (Fig. 1).

Palatine: Only a small fragment is preserved (Fig. 1).

Dentition: The molars, as with those of all protemnodonts, are alike in pattern and shape. They are rectangular, low crowned, and strong. The protoloph is slightly narrower than the metaloph in M^{1-2} while in M^{3-4} the metaloph is narrower than the protoloph. A low anterior cingulum extends nearly across the tooth. From the anterolingual side of the tooth this cingulum is formed by a crest which ascends to a point just lingual of the anteroposterior midline of the tooth then levels off to a position anterior to the paracone. A spur which ascends from the top of the paracone meets the cingulum at the anterolabial corner of the tooth, and behind this junction a small pocket is formed. This is particularly noticeable on the M^{2-3} of this specimen. No forelink is recognizable and the anterior transverse valley between the cingulum and the protoloph is shallow. The midlink is low and formed nearly equally by the dorsal end of the post protoconal spur and the median metaloph spur. This is best seen on M^{3-4}. A spur ascends from behind the paracone to a point just below the top of the transverse median valley then inflects for a short distance to cross the valley and connect with a similar spur which ascends from the metacone. This structure, particularly the spur which ascends anteriorly from the paracone, is best developed

in M^{1-2} but can still be seen in M^{3-4} while the other spur which ascends posteriorly from the metacone is reduced to a very thin line in M^{3-4}. The post paraconal and premetaconal spurs ascend to meet $\frac{1}{3}$ of the distance from the midline to the labial margin of the tooth in M^{1-2} while in M^{3-4} the premetaconal spurs are much weaker and become almost indistinct as they ascend into the transverse valley. A posterior spur ascends from the metacone and is separated by a slight commissure near the base of the tooth, from a sweeping spur which ascends dorsolabially from the hypocone. Stirton (1961) following Owen called this structure the hindlink. The posterior median spur on the metaloph is incipient on M^{3-4}, and M^{1-2} are too worn to show anything but the suggestion of a weak spur. The crests of the metaloph and protoloph are crescentic in occlusal view while in lateral view labial surfaces of the lophs of all molars tend to curve anteriorly.

Comparisons

On the completion of the preparation it was immediately apparent that the fossil was a protemnodont very like *Protemnodon otibandus* Plane 1967, from the Awe fauna of the Watut Valley, New Guinea. With the age of the fossil so firmly established relative to the marine sequence it was evident that the most meaningfull comparisons would be with Tertiary rather than Quaternary protemnodonts on the mainland. Mr Alan Bartholomai, Director of the Queensland Museum, made available to me the material from the Chinchilla Sand of the W. Darling Downs, SE. Queensland, and a striking resemblance to one of the species from that unit was apparent. Detailed comparisons were made with *P. otibandus* and the Chinchilla material which had been segregated under a new specific taxon. Morphologically the Victorian fossil can be matched in every feature with specimens from the Awe and Chinchilla faunas. The figured specimen of *P. otibandus,* U.C.M.P. 69857 (Plane 1967 fig. 7), a maxilla fragment with P^3M^{1-2}, was used in detailed comparisons with that species. While unfortunately there is no P^3 with the Victorian fossil it is clear from the worn nature of the anterior cingulum on the M^1 and the appression facet on the M^1 that this

tooth had contact with a P^3 similar to that observed in *P. otibandus*. The Awe maxilla is not as worn as the Victorian fossil and the post-paraconal and premetaconal spurs are unworn in the Awe specimen. However, apart from variations attributable to wear, all morphologic features are identical. Chinchilla specimens used for comparisons were Queensland Museum numbers F4665, 4686, 4721, 4688, 4684, 4702. The length of the molars measured along the midline of the tooth listed in Table 1, illustrates that the Victorian fossil lies within the range of measurements made on Awe fauna specimens. Table 2 demonstrates that there is a greater narrowing of the metaloph on the M^{3-4} on the new fossil than that observed within the Awe specimens. The measurements made on the Chinchilla specimens are biased in that the smallest individuals had only anterior molars. The Victorian specimen is outside the range of the Chinchilla grouping.

The new specimen is assigned to the species *Protemnodon otibandus* and it is concluded that the Chinchilla assemblage also represent a population of the New Guinea species, albeit a slightly larger form.

Geochronologic Interpretation

The discovery of a land mammal in a marine formation with a shelly and microfauna is of great interest as it provides an independent check on the Tertiary non-marine time scale which has been built up by fossil mammal workers (Stirton, Tedford and Woodburne 1968).

The Upper shell bed of the Jemmy's Point Formation has been assigned a lower Pliocene age by Wilkins (1963) and he puts it as the top of the Kalimnan Stage. This then makes the new specimen of *Protemnodon otibandus* early Pliocene in the time terminology of the molluscan workers. The Otibanda formation and its associated Awe fauna are assigned a Pliocene age on the basis of radiometric dating (Plane 1967). A new date from higher in the section in the Watut Valley which is associated with the occurrence of *P. otibandus* extends the range of dates for the formation from 3·9 to 7·6 m.y. B.P. The age of the Chinchilla fauna is not precisely known. It has been assigned both an early Pleistocene (Stirton, Tedford and Wood-

burne 1968) and late Pliocene age (Woods 1960).

The discovery of the new fossil provides an opportunity to re-examine the age of the Awe and Chinchilla faunas. Recently, radiometric dating has been carried out by McDougall and Page (1970) in an attempt to develop a time-scale for the Miocene of New Guinea. They suggest that the Miocene, as recognized in the Indo-Pacific, extends from 22·5 to 5·5 m.y. before present. This and present concepts of the Pleistocene has reduced the Pliocene to a short interval spanning 2·5 m.y. using the base of the Pleistocene at about 3 m.y. B.P., and a Miocene/Pliocene boundary at 5·5 m.y. B.P. On this scale the Otibanda formation ranges from late Miocene to late Pliocene and the species *P. otibandus* is present throughout the Pliocene. The new specimen of *P. otibandus* from the Kalimnan stage (lower Pliocene) of Victoria lies well within this range.

No firm date can yet be assigned to the Chinchilla population of *P. otibandus*. The larger size of the animals might be construed as indicating a younger age but may well be due to environmental factors. The evidence does suggest, however, that the Chinchilla fauna is of Pliocene age as claimed by Woods (1960) and Bartholomai (in press).

TABLE 1

	Awe (composite)		Lake Tyers	Chinchilla (composite)	
M^1	10·0-11·5	(4)	10·2	10·7-11·5	(3)
M^2	11·7-12·8	(6)	12·5	13·1-14·4	(4)
M^3	12·9-13·9	(5)	13·0	14·2-15·5	(4)
M^4	13·1-14·0	(3)	13·5	15·7-16·4	(3)

Table 1: length of molars measured at the midline. The Awe and Chinchilla composites indicate the extremes.

TABLE 2

		Awe		Lake Tyers	Chinchilla	
M^1	p	9·5-10·6	(4)	9·8	11·0-11·4	(3)
	m	10·6-11·0	(3)	10·0	11·7-11·9	(3)
M^2	p	10·3-12·4	(5)	11·5	12·6-13·7	(4)
	m	10·3-12·8	(6)	10·9	12·6-13·6	(4)
M^3	p	10·3-12·7	(5)	11·9	12·2-15·3	(4)
	m	11·7-12·5	(5)	10·7	11·9-12·9	(4)
M^4	p	12·4-13·1	(3)	11·7	13·0-13·2	(3)
	m	10·0-10·9	(3)	9·6	11·3-12·8	(3)

Table 2: width of protoloph and metaloph at base of enamel.

p = protoloph   m = metaloph
(4) = number of individuals measured

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1 cm

A DENDROID GRAPTOLITE FROM 'KILLARA', SEVILLE, VICTORIA, AUSTRALIA

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Abstract

A fragmentary dendroid graptolite from the Humevale Formation exposed at 'Killara', Seville, Victoria is assigned to the genus *Desmograptus* and compared with certain North American Early and Middle Devonian desmograptids. The dendroid occurs with a shelly fauna in the shelly faunal facies of the Humevale Formation recognized by Williams (1964).

Introduction

A single fragmentary specimen of a dendroid graptolite was collected by E. D. Gill from rocks assigned to the Humevale Formation (see Williams 1964) exposed at Syme's Homestead, 'Killara', Seville, Victoria. The locality from which the graptolite was obtained is that numbered 33 in Text fig. 2 in Gill's (1945) map of the Killara area. Gill (1945, p. 183) described locality 33 as 'an old water race near the Wandin Yallock Creek in front of the homestead [since demolished] of the Killara estate. The matrix is a fawn mudstone which has yielded a very rich Yeringian fauna'. The graptolite is associated with a rich shelly fauna of which certain calymenids and the brachiopod *Notoleptaena otophera* Gill have been described (see Gill 1939, 1945, 1951). Gill (1971, written commun.) commented that the siltstones in the Humevale Formation in the Killara area bear a relatively diverse branchiopod fauna as well as trilobites and certain land plants, including *Hedeia corymbosa*.

The dendroid graptolite occurs in the shelly faunal facies of the Humevale Formation recognized by Williams (1964). Primarily graptoloid graptolites have been found in the eastern, essentially graptolitic, faunal facies of the Humevale Formation (Williams 1964).

Williams (1964) indicated that the Humevale Formation ranges in age from Late Ludlow into the Early Devonian. Gill (1971, written commun.) suggested that the shelly fauna that occurs with the dendroid graptolite might be indicative of about Late Siegen age.

The dendroid graptolite from the Humevale Formation is similar to certain dendroids described by Ruedemann (1947) and Berry (1969) from Early and Middle Devonian age strata in the eastern and central parts of the United States. The dendroids occur there with diverse shelly faunas, in associations similar to that in the Humevale Formation with which the Victorian dendroid occurs.

The author is indebted to Mr. E. D. Gill for sending him the dendroid specimen for description and for his comments regarding the associated fauna and the stratigraphic relationships in the Killara district.

Taxonomic Relationship

Most of the specimen is preserved as a tan impression on a light grey matrix, but small parts of it are preserved in enough relief to determine certain details of thecal morphology. The stripes are undulose and appear to be united by relatively regular anastomosis. Thecae, possibly the autothecae, appear to have been relatively long and tubular and to have been clustered closely together. The specimen is crushed such that details of the budding pattern, thecal spacing, and nature of the thecal apertures may not be examined. The specimen appears somewhat similar to an apparently compressed specimen of *Reticulograptus tuberosus* (Wiman 1895, Pl. 12, fig. 9) in gross form. The specimen is too highly compressed to consider closely such relationship as it may have

with *Reticulograptus* because Bulman and Rickards (1966, p. 44) described conothecae and a stolonal system as characteristics of the Genus *Reticulograptus*. Neither conothecae nor the stolonal system may been seen in highly comcompressed specimens.

The closest affinities of the Victorian specimen appear to be with members of the genus *Desmograptus* because the stipes are flexed and united by anastomosis and the thecae are tubular. The gross similarities between certain specimens of the *Reticulograptus* and *Desmosograptus* may suggest that certain specimens assigned to *Desmograptus* could be assignable to *Reticulograptus* if all morphological details could be determined. At present, flattened specimens with undulose stipes that are united by anastomosis and in which the autothecae appear to have been tubular are considered members of the genus *Desmograptus*.

Elias (1971, p. 20) suggested that *Reticulograptus tuberosus sinclairi* Whittington and Rickards might be a bryozoan, primarily because he believed fusellar layer half-rings to be absent in the periderm of *Reticulograpus tuberosus sinclairi,* because of the similarity of the conothecae in *Reticulograptus* to brood chambers in certain modern cyclostomate bryozoans, and because of the gross similarity in colony form between *Reticulograptus tuberosus sinclairi* and certain modern bryozoans. Bulman and Rickards (1966, p. 53) and Whittington and Rickards (1968, p. 61, in press) indicated that conothecae had been observed in representative specimens of the genera *Discograptus* and *Idiotubus* as well as in *Reticulograptus* and that fusellar layer half-rings were present in the periderm of *Reticulograptus*. The partly sclerotized stolons in *Reticulograptus* and in other tuboid graptolites as well as the presence of fusellar layer half-ring bands in the periderm of *Reticulograptus* and other tuboid graptolites appear to more closely ally *Reticulograptus* and other tuboids with dendroid graptolites than with any bryozoan.

Class GRAPTOLITHINA Bronn, 1846

Order DENDROIDEA Nicholson, 1872

Family DENDROGRAPTIDAE Roemer in Frech, 1897

Genus **Desmograptus** Hopkinson, 1875

TYPE SPECIES: *Dictyograptus cancellatus* Hopkinson, 1875.

DIAGNOSIS: Conical, stipes flexuous and united by regular anastomosis, dissepiments rare, autothecae commonly tubular but rarely isolate.

Desmograptus sp.

Pl. 5, figs. 1-2

MATERIAL: One fragmentary specimen. National Museum of Victoria P27484.

DESCRIPTION: The shape of the fragment suggests that it was part of a relatively large, probably expanding rhabdosome. The fragment is approximately 4·5 cm long and 4·5 cm wide in its maximum dimensions. The stipes appear to bifurcate at relatively regular intervals, except perhaps in the distal part of the rhabdosome where orientation of the stipes suggests that certain stipes in that part of the rhabdosome occasionally failed to bifurcate. Each stipe diverges from the point of bifurcation to touch and apparently join with with a stipe developed from bifurcation of an adjacent stipe. The pattern of stipe bifurcation and subsequent join of stipes developed from bifurcation of two adjacent stipes as well as stipe flexure forms generally oval-shaped interspaces between stipes.

The stipes appear to be formed from bundles of relatively long thecae (probably autothecae). Bifurcation appears to involve splitting of the thecal bundle with some of the tubular thecae diverging in one direction and the others at an approximately 40-60 degree angle from them. Each set of thecae joins with thecae diverging from a similar splitting of the thecal bundle in an adjacent stipe.

The stipes are 0·5-1·0 mm wide. The individual, probable autothecal, tubes are approximately 0·1-0·2 mm in diameter in the small areas in which they may be observed. The ovoid interspaces are 3·0-5·2 mm long and 1·2-1·5 mm wide at their widest points. Six to seven stipes occur in 10 mm transversely across the rhabdosome. A 10 mm transect horizontally across the rhabdosome cuts parts of 6-7 interspaces and a 10 mm transect longitudinally

along the rhabdosome cuts parts of 2-3 interspaces.

REMARKS: The width of the stipes and size of the interspaces in the Victorian fragment are somewhat similar to these characters in *Desmograptus* sp. 1 described by Berry (1969. p. 706-707) from Middle Devonian strata in Illinois, U.S.A. The Victorian specimen is closely similar to medial-distal parts of the Illinois specimen in stipe width, nature of stipe bifurcation, and length and width of the ovoid interspaces. The Victorian specimen is too fragmentary to make closer comparison with the Illinois specimen and more of the rhabdosome is preserved in the Illinois specimen than in the Victorian. The Victorian specimen is also somewhat similar to *Desmogratus becraftensis* Ruedemann from Early Devonian strata in New York, U.S.A. Stipe width and interspace dimensions of the two are similar but stipe bifurcation appears to be less regular and the interspaces are slightly longer in the Victorian specimen. The Victorian specimen is too fragmentary to make significant comparison with other desmograptids.

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Explanation of Plate

Figs. 1, 2—*Desmograptus* sp. National Museum of Victoria P27484

Fig. 1—Entire specimen; tubular aspect of probable autothecae may be noted on stipes at upper-right margin of specimen, ×2·5.

Fig. 2—Portion of specimen showing some details of rhabdosome form, ×5.
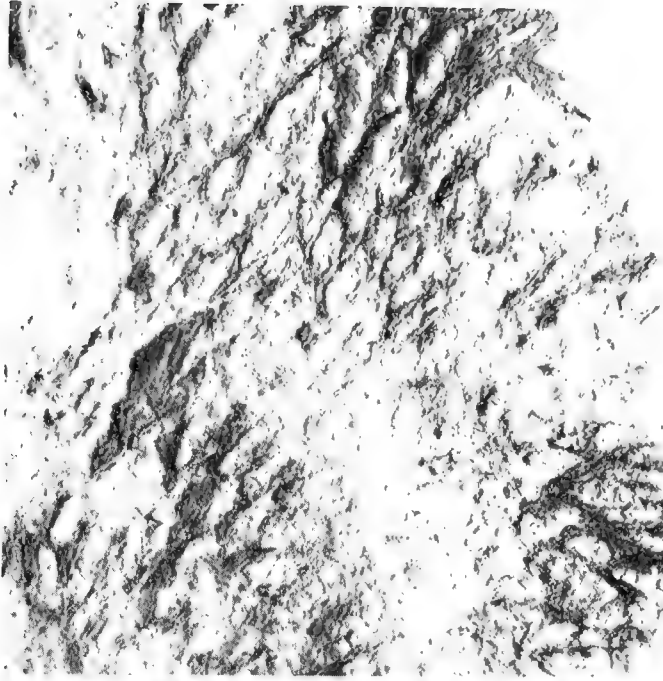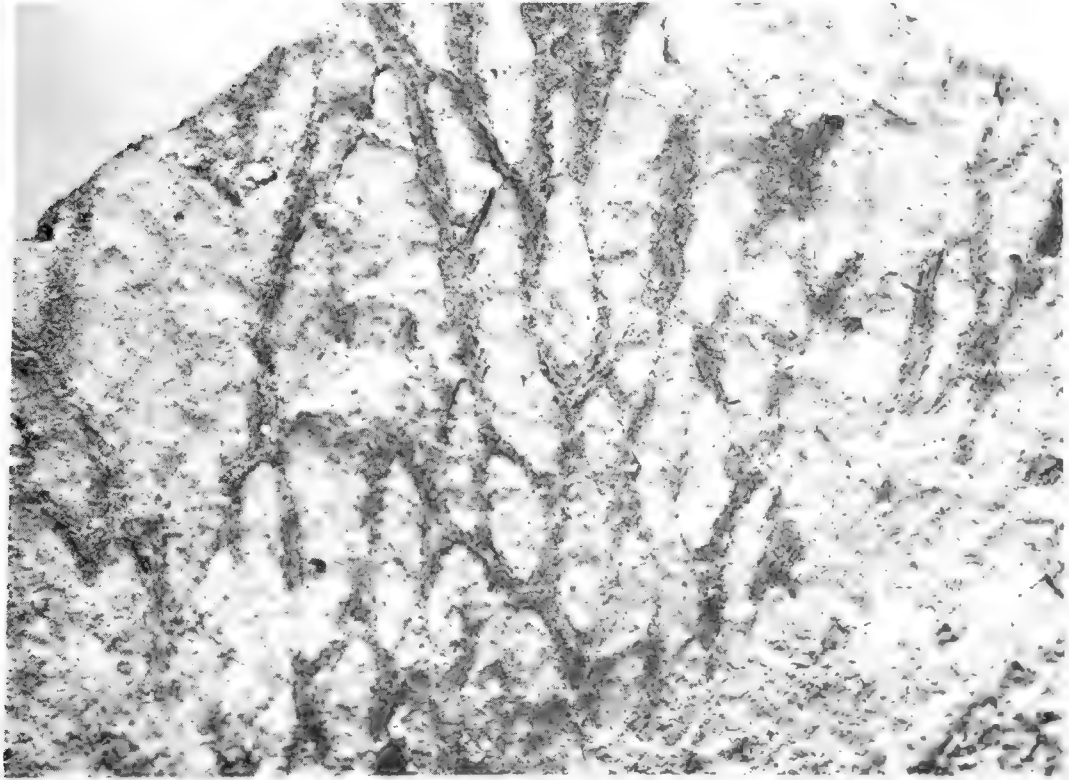
THE DUCK PONDS FOSSIL MARSUPIAL FAUNA, HOVELL'S CREEK, LARA, VICTORIA, AUSTRALIA

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Abstract

Fossil bones were obtained from depths of 6-14 m in excavations for the foundations for the railway viaduct at Duck Ponds (now Lara) in 1875. They came from fluviatile sediments overlying the Newer Volcanic lava flows, but underlying the freshwater Lara Limestone. The fauna contains *Thylacoleo, Diprotodon* and giant species of *Macropus* and *Protemnodon*. Stratigraphic and faunal considerations indicate that the Duck Ponds fauna is older than the Late Pleistocene Colongulac Fauna, but younger than the Chinchilla, Hamilton and Awe Faunas. The association of *Diprotodon* with the Lara Limestone (Keble 1945, Gill 1964) is shown to be incorrect.

Introduction

Duck Ponds Creek was the original name for Hovell's Creek, which flows into Corio Bay. The present town of Lara, which is situated on this creek about 6 km from its mouth, was originally known as Duck Ponds. In 1875 a viaduct was constructed to carry the railway across the creek, and in the excavations associated with this work, fossil bones were found.

The find was reported by Brough Smyth in 1876, and by Couchman in 1877. McCoy prepared a draft description of a jaw of *Thylacoleo carnifex* obtained from the excavations, but this was never published. Incisors of *Diprotodon* found at the same time were mentioned by Keble (1945) in his paper on the Diprotodontidae, but he was obviously unaware of the earlier references, and concluded, with some reservations, that the Duck Ponds *Diprotodon* came from the freshwater Lara Limestone. Gill (1964) used the supposed occurrence of *Diprotodon longiceps* in the limestone as part of his evidence for a probable Upper Pliocene age.

In fact, the bones came from fluviatile sediments which occur stratigraphically beneath the limestone. The National Museum archives and the labels on the specimens, in conjunction with the two contemporary published references given above, provide enough information to fully document the circumstances of discovery, and the provenance of the bones.

Growing interest in Australian mammal fossils, and the development of phylogenetic schemes, makes it important that all occurrences be dated as accurately as possible. There are relatively few localities older than Late Pleistocene, and 'Duck Ponds' appears to be at least Middle Pleistocene, or perhaps older. Since the opportunity to recollect may occur when the viaduct is duplicated, it seemed worthwhile to publish all the available information.

Opportunity is also taken to publish for the first time (Pl. 6) the superb plate of a jaw of *Thylacoleo carnifex* found at Duck Ponds, prepared for McCoy by Dr Wild. This was to be Plate LXX1 of Decade 8 of the Prodromus of the Palaeontology of Victoria, but along with a number of others which had reached page proof stage, was never published.

Discovery of the Bones

On 16 July 1875, T. Couchman (Secretary for Mines) wrote to McCoy as follows:

'Sir,
    Herewith are forwarded for examination fossils numbered 3451 obtained from near Duck Ponds Station, Geelong and Melbourne Railway.
    I shall be glad if you will be so good as to examine the specimens and report to this office the results of your examination'.

These were the specimens obtained by Mr Robert Watson C.E., referred to in Brough Smyth, 1876 (see below). On 13 August 1875, Mr James Blair of Lara wrote to McCoy about

the same discovery, with valuable information and an offer of further specimens:

'Sir,

I take the liberty of addressing you with reference to the specimens of bones recently discovered in this locality whilst sinking for the foundations of a new bridge for the railway.

The bones in question were found at a depth of 15 feet from the surface consisting of large joints, tusks etc. and appear to be in a state of petrefaction.

I have been informed that samples have been already forwarded to you for examination in order to ascertain to what species of animals they may have belonged, but if such is not the case I should find pleasure in furnishing you with a few pieces which are now in my possession.

You will be pleased therefore to signify at your earliest convenience whether you would wish that I so forward the specimens'.

No record exists that these specimens were ever received. Brough Smyth (1876, pp. 73-4) says:

'Mr Robert Watson C.E., Resident Engineer of the Victorian Railways Department, brought me lately a number of bones from a cutting near the Duck Ponds Station on the margin of Corio Bay, and Professor McCoy has found amongst them the os inominatum, several vertebrae, fragments of ribs, and molar and incisor teeth of the great extinct kangaroo, the *Macropus titan*'.

A footnote to this says:

'Mr James Wilkinson, who has charge of some of the works now being constructed at the Duck Ponds, has collected a great number of fossil bones from depths varying from twenty-five to thirty-three feet, and he has been so good as to present them to me. They are of great value, and this gentleman is deserving of the highest commendation for the care and trouble he has taken in procuring these specimens. Professor McCoy is now examining the collection'.

On 28 January 1876, Brough Smyth sent the collection made by James Wilkinson to Professor McCoy, and asked for a report. He remarked that Mr Wilkinson had been 'so good as to present all the bones to the Department except three which are specially labelled —to be returned'. McCoy was obviously a bit tardy in supplying the report, for Couchman wrote to him on 27 September 1876 asking for it. The original of the report, in McCoy's handwriting, is in the archives of the National Museum. It is dated 4 October 1876 and addressed to Couchman:

'Sir,

Referring to your letter of the 27th September, I beg to report that the specimens from the Duck Ponds forwarded to me 28-1-1876 were incisor tusks of *Diprotodon* and incisors and molars of the Gigantic Extinct Kangaroo *Macropus titan* and *M. atlas*, with numerous portions of the skeletons of these animals which mark the newer Pliocene Tertiary periods. One of these specimens is the leg of a horse, and no doubt was mixed with the others through some unintentional carelessness which might give rise to serious errors; this specimen is numbered 138 in the consecutive series of numbers from 1 to 142 on those specimens forwarded by Mr Wilkinson and is manifestly in a different state of preservation from the others, appearing to have been partially burnt'.

Couchman published his own version of this report in 1877 (p. 18), which deleted the reference to the horse bone, adjusted the number of specimens, and added the identification of a 'jaw of *Protemnodon*'. The reference to *Protemnodon* must have been added by McCoy before Couchman's report was published.

On 7 May 1877, the Rev. C.S.Y. Price presented a piece of macropod jaw to the National Museum. The label states that it was 'Obtained at Ducks Ponds 40 ft. deep in clay when digging for the foundations of the railway bridge'.

The upper and lower incisors of *Diprotodon* (NMV P1892-3), and the jaw of *Thylacoleo* (P5287, Pl. 6) from Duck Ponds, which McCoy intended to describe in the unpublished Decade 8 of the Prodromus, were also donated by the Rev. Mr Price, presumably at the same time.

In a paper on the freshwater limestones of the Geelong district (Pritchard 1895), the only fossil mentioned from the Lara Limestone is a freshwater mussel, although the marsupial fauna from the probably equivalent limestone at Limeburners Point is discussed in detail. Since the purpose of the paper was to document the known fauna of the limestones, the absence of a reference to *Diprotodon* at Lara can be taken as negative evidence that it was not found in the limestone there, since Pritchard would presumably have been aware of the true provenance of the Lara fossil marsupials.

Keble (1945) discussed this locality at some length. He assumed that the Duck Ponds specimens were obtained from the freshwater Lara Limestone, despite his own admission that there is little mineral replacement and an absence of adherent matrix, and his stated doubt as to whether they were *in situ*. His main reason

for this assumption was the occurrence of fossil bones in the lithologically similar freshwater limestone at Limeburners Point at Geelong. Keble presented detailed evidence to support his view that the limestone was of early Upper Pleistocene age, including data derived from logs of the bores put down by the Railways to test the foundations for the viaduct. These bores disclosed 'flood plain' sediments beneath the limestone, and it will be demonstrated below that this is the formation which yielded the bones.

Gill (1964) also thought the bones came from the limestone, but disagreed with Keble's age determination. He thought that the age was probably Upper Pliocene because the limestone infills a valley which was blocked by earth movements of that age. He used the fossils to support this contention: 'If one distinguishes between the fossils found in the limestone, and those found in cavities in the limestone, this also has a fauna older than the accepted Pleistocene one. The *Diprotodon* found in the Lara Limestone is not the Pleistocene *D. optatum,* but the related *D. longiceps'.*

The Geological Survey of Victoria adopted a position between these extremes and indicated an age of approximately Middle Pleistocene on the Geelong 1:63,360 geological map, 1963.

Stratigraphic Sequence

The oldest rocks exposed at Lara are the Newer Volcanic basalt flows. No radiometric dates are available as yet for the Lara-Werribee area, the nearest being at Albion and Newport, some 40 km NE. The Melbourne 1:250,000 geological map shows dates of 2·55 to 2·74 m.y. at Albion, and 2·49 to 2·50 m.y. at Newport, but basalt dates for the Melbourne area range from 4·55 to 0·79 m.y., so it would be unwise to place too much emphasis on a possible extrapolation from Albion and Newport to Lara.

Overlying the basalt flows in the Hovell's Creek valley are Keble's early 'flood plain' deposits, which consist of muds, clays, sands and gravel. The sequence is known from railway bores for the foundations of the viaduct. At

6·4 m below the creek, the bores disclosed a bed of 'quartz gravel and rotten shells' overlying 'stiff clay' (Keble 1945).

The interior of a macropod femur in the Wilkinson Collection contains clay, and coarse quartz sand with small molluscs up to about 5 mm diameter. There are small pelecypods, probably *Corbiculina,* and the gasteropods *Coxiella* and *Lenameria.* There is an admixture of ecologies here, since *Corbiculina* occurs in freshwater lakes and streams, *Lenameria* is normally a swamp dwelling gasteropod, and *Coxiella* is found in swamps and lakes in which the water ranges from slightly brackish to very salt. They were probably derived from varying ecologies marginal to Hovell's Creek. The material preserved in the femur almost certainly corresponds with the bed of 'quartz gravel and rotten shells' which was met in the railways bore 6·4 m under the bed of Duck Ponds Creek. A sample of matrix taken from the bones presented by Wilkinson is a clayey fine sand, probably corresponding to the 'stiff clay'.

The Lara Limestone is of freshwater origin, and contains small freshwater gasteropods, as well as the *'Unio'* recorded by Pritchard (1895). One of the railway bores disclosed 1·5 m of limestone, 1·5 m above sea level and 4·3 m above the layer of 'rotten shells' (Keble 1945). Thus the freshwater limestone overlies the post-volcanic, fluviatile sediments, and was in turn succeeded by calcareous clays, sands and gravel. Keble thought that regional subsidence on the Lovely Banks Monocline took place at the end of this cycle, with younger alluvial terrace sediments being deposited subsequently, which he correlated with his Braybrook and Maribyrnong cycles in the Maribyrnong valley.

Estuarine sediments with marine molluscs occur along the banks of the present Hovell's Creek, in places directly overlying the freshwater Lara Limestone, which is bored by marine molluscs. These beds were radiocarbon dated at 5,620 ± 90 B.P. (Gill 1961, 1971). They thus correspond to a mid-Holocene higher sea level. Fragments of mineralized bone occur in these beds, suggesting that the Pleistocene bone beds were subject to marine erosion during the higher sea level, and frag-

D

ments have been incorporated in the shell beds. A note by Daintree on Quarter Sheet 24 NE. referring to this deposit says 'The estuary deposit consists of shells, quartz gravel, nodules of limestone, and contains numerous fragments of bones'. This map was published in 1863, 12 years before the railway bridge work began.

Age of Marsupial Fauna

The Duck Ponds fauna contains giant forms only, and there is little adjustment needed to McCoy's original determinations, except for the apparent absence of *Sthenurus atlas*. The fauna has not yet been studied completely, but the provisional faunal list is as follows:

>*Thylacoleo carnifex* Owen
>*Diprotodon* cf. *longiceps* McCoy
>*Protemnodon* cf. *anak* Owen
>*Macropus titan* Owen

The National Museum collections include a probable topotype ramus of *T. crassidentatus* Bartholamai (P15921), which is labelled 'Darling Downs', but has the typical Chinchilla preservation and matrix. It is more complete than the holotype, and compares closely in tooth dimensions, and especially in the massiveness of the horizontal ramus, angle of elevation of the lower incisor, and more or less triangular cross section of that tooth. The *Thylacoleo* from Duck Ponds (P5287) was compared with this specimen, and a series of typical *T. carnifex,* and this clearly showed that its affinities were with the latter. The relatively slender ramus, more nearly rectangular incisor cross section, and steeper angle of elevation, of the lower incisor identify it as *T. carnifex.*

Diprotodon longiceps was maintained by Keble (1945) to be a valid species but this a matter in need of re-evaluation. Specimens of *Diprotodon* with narrower molars than typical *D. optatum* are known from North Melbourne and Footscray, as well as the type locality at Lake Ondit, near Colac. These are all from deposits which are probably of somewhat greater age than the Late Pleistocene deposits with typical *D. optatum,* so there is a likelihood that *D. longiceps* is an Early to Middle Pleistocene species.

The macropods do not seem to be very different from the Late Pleistocene forms, but this needs further study. Lack of adequately identified comparative material makes this difficult at this stage.

At a time when the radiometric age of the Plio-Pleistocene boundary is placed by various authors at from 3·5 m.y. to 1·79 m.y., the use of Lyellian ages is a source of confusion. However, if the 1·79 m.y. boundary proposed by Bandy and Wilcoxon (1970) is accepted, then the Duck Ponds Fauna is probably best described as Lower to Middle Pleistocene. This would fit the probable Plio-Pleistocene age of the underlying basalt, and the relative position of the fauna with respect to the definitely older Awe, Hamilton and Chinchilla Faunas. A recent discussion on these faunas is contained in Turnbull and Lundelius, 1970.

Since the limestone became exposed to solution by ground water, small caverns have developed, and bones are sometimes found in these when exposed by quarrying operations. Geological Survey localities Ad 33 and Ad 34 refer to such occurrences. A small collection of bones 'from a depth of nine feet in limestone in a quarry at Lara' was donated by F. Parsons on 19 July 1913. *Vombatus hirsutus, Dasyurus quoll* and *Rattus* sp. have been identified in this collection. On 7 November 1947, Mr Parsons presented two macropod molars from '10 feet below surface under solid limestone, Mitchells Quarry on Forest Road, Lara'. These are the 'bones in cavities in the limestone' referred to by Gill (1964), and represent the extant fauna. They are probably not older than very Late Pleistocene, and may be relatively recent in age.

Summary and Conclusion

The Duck Ponds Marsupial Fauna came from fluviatile sediments occupying a valley developed on Newer Volcanic lava flows, and underlying the Lara Limestone. The small fauna obtained from the railway viaduct foundation excavations in 1875 is of Pleistocene aspect. The presence of *Diprotodon* cf. *longiceps* in association with *Thylacoleo carnifex* supports the Early to Middle Pleistocene age suggested on stratigraphic grounds, rather than an Upper Pliocene one.

Until radiometric dates for the basalt become available, it is not possible to be more precise, but it does seem that the Duck Ponds fauna helps to fill in the gap between the Late Pleistocene faunas and the earlier Plio-Pleistocene ones. Therefore every effort should be made to obtain a good collection when the railway is eventually duplicated.

Acknowledgements

The putting in order of the Museum archives by Mr A. G. Parsons made possible the documentation used in this paper. Mr T. A. Darragh assisted with other information, and Mr E. D. Gill advised on the Plio-Pleistocene problem.

In anticipation of an obvious question, James Wilkinson was not, to the best of my knowledge, a relative.

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Plate 6

Reproduction of lithograph of incomplete right ramus of Thylacoleo carnifex Owen, P5287, from excavations for railway viaduct over Duck Ponds (= Hovells Creek, Lara, Victoria), prepared for Professor McCoy by Dr Wild as Pl. LXXI of the unpublished Decade 8 of the Prodromus of the Palaeontology of Victoria.
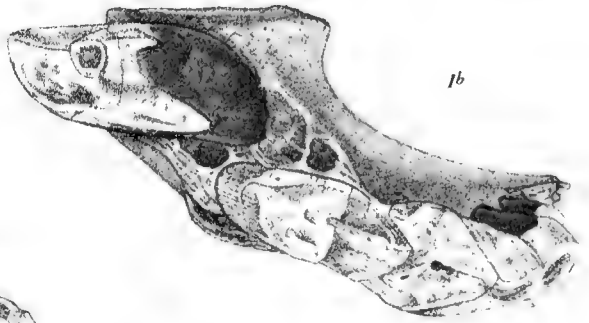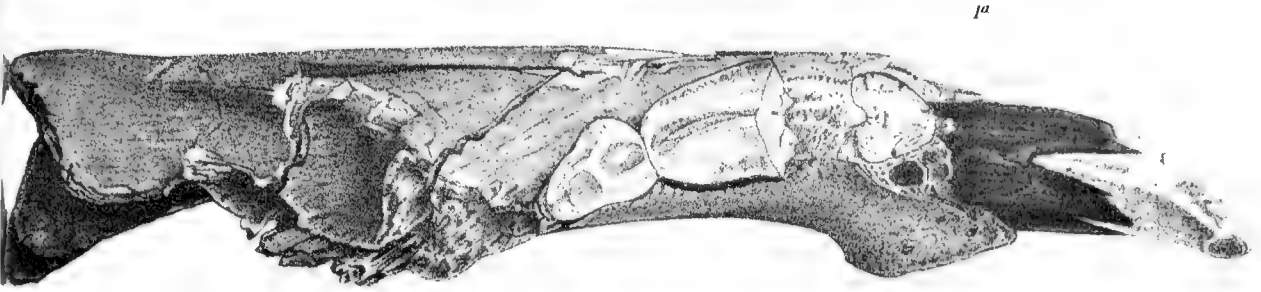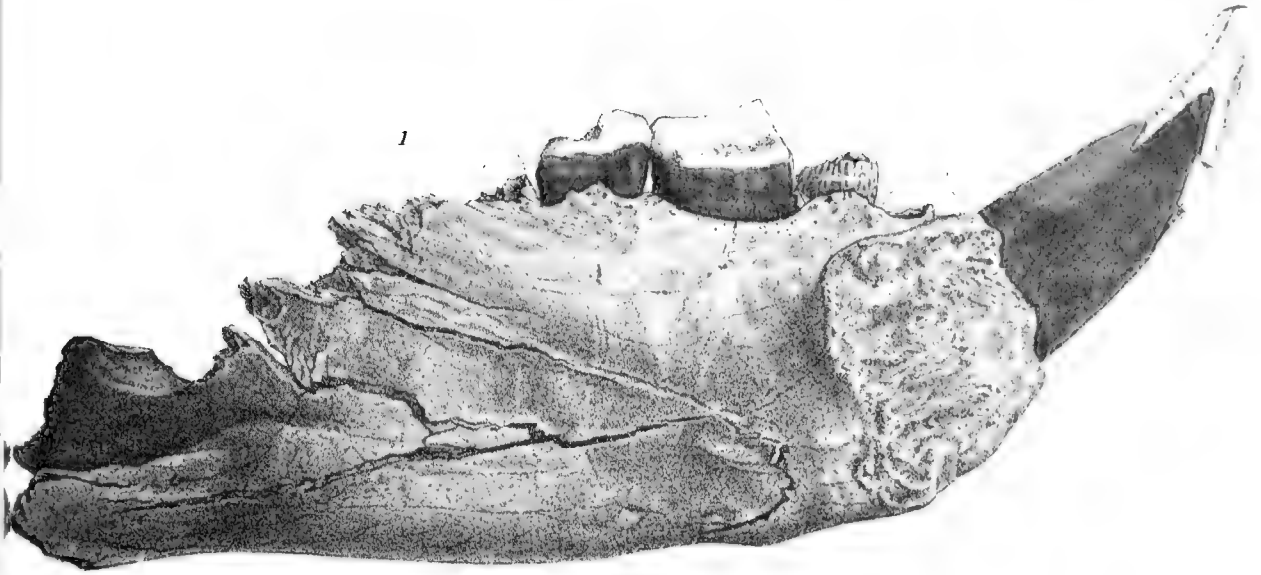
SANDS FROM THE SQUEAKY BEACH AREA, WILSONS PROMONTORY, VICTORIA, AUSTRALIA

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Abstract

The textural and constituent composition of eight sand samples from Squeaky Beach and adjacent beaches on Wilsons Promontory, and one sample from the Squeaky Beach foredune are described. The Squeaky Beach sands are composed almost entirely of quartz grains which are very uniform in size (of medium sand size), are mostly subrounded to rounded, and have a fairly high degree of sphericity. Sand samples from Picnic and Norman Bay beaches contain nearly 40 per cent of organogenic carbonate. They are not as well sorted as the Squeaky Beach sands, the grains have a lower degree of roundness, and their maximum size-grade is fine sand.

The squeaking sound emitted by the dry sand of Squeaky Beach when walked on results probably from shearing of successive layers of the regularly packed grains. The eroding Squeaky Beach foredune appears to be the immediate source of much of the sand of the adjoining beach. The primary source of the sand minerals is almost certainly the Wilsons Promontory Granite. The relatively high content of organogenic carbonate in the Picnic and Norman Bay sands has probably come mainly from the disintegration of local aeolianite.

The marked suitability of the Squeaky Beach sand for the preservation of flowers and foliage is apparently related to its composition of very uniform rounded quartz grains. They permit even contact between sand and plant plus adequate aeration for drying.

Introduction

Squeaky Beach is part of the shore of Leonard Bay (Fig. 1) and is so called because the dry sand squeaks when walked on. The sand belongs to the interesting type known as singing sands. However, it was not because of the sound phenomenon that the writer's attention was drawn to the Squeaky Beach sand; it followed an enquiry from our Senior Preparator as to why this sand was more suitable than most for the preservation of flowers and foliage. The drying of flowers and foliage in sand is a very old method of preservation, and it can give very good results.

In June 1970 mid-tide sand samples were collected from the middle and extreme S. and N. ends of Squeaky Beach, while low-tide, high-tide and backshore samples were taken from midway along the beach; also a sample from the crest of the foredune towards the N. end. As the Squeaky Beach sands are different from those of adjacent beaches, mid-tide samples were collected also from about midway along the beaches at Picnic Bay and

Norman Bay. Figure 1 shows the sample localities and details are given in the Appendix. Samples of approximately 400 g were obtained by pushing down a thin metal cylinder to a depth of 8 cm, removing the sand around the outside of the cylinder, and sliding a thin board underneath.

No comprehensive account of the sands of the Squeaky Beach region has previously been presented, but some earlier work has been conducted. Parsons (1966) stated that the Squeaky Beach sand 'is almost pure silica ($CaCO_3 = 0.1 - 0.6$ per cent)', but the sand on the adjacent Norman Bay beach is quite calcareous. He noted that the sand composing the foredune flanking Norman Bay beach has a relatively high content of calcareous (shell) material, and that high waves were eroding it. Work on the geomorphology of Wilsons Promontory has recently been carried out by Tuddenham, who (pers. comm.) considers that the sand of Squeaky Beach is derived mainly by marine erosion of the adjacent foredune. Two English research workers on singing sands, Thomas and Jones (1964)
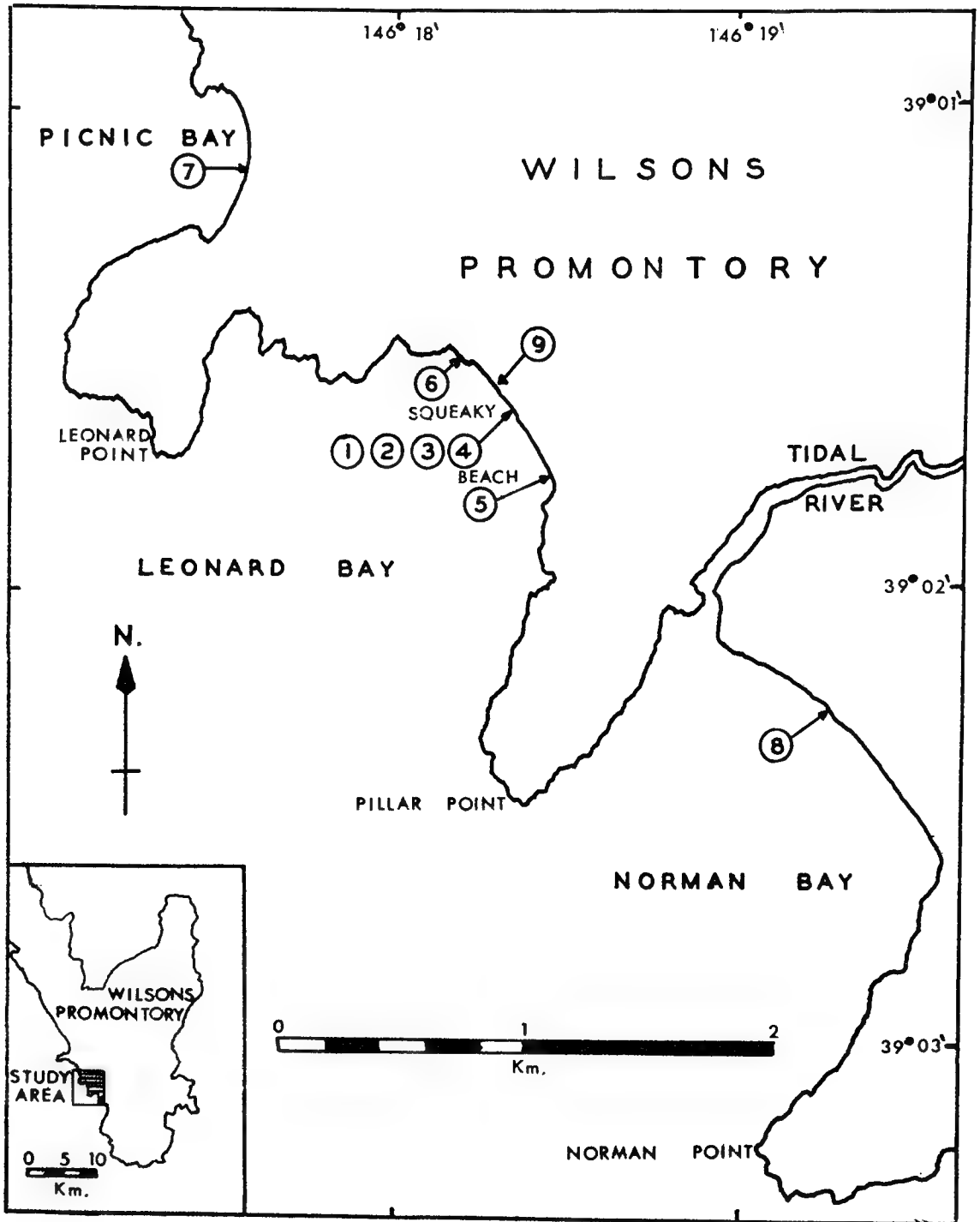
Fig. 1—Location of sample stations.

studied a number of Australian samples including one from Squeaky Beach, and found that, like the others, it has a high degree of uniformity of grain size.

Geomorphology, Geology and Environment

On the W. coast of Wilsons Promontory bays with sandy beaches alternate with cliffs. In length the beaches (Fig. 1) are approximately: Picnic Bay 594 m, Squeaky Beach 686 m, and Norman Bay 1,200 m.

The maximum width of sand on Squeaky Beach was 68 m, being widest near the ends where the angle of slope was small. The shore gradient was slightly steeper in the middle where the shore measured 39 m. Backshore width was generally small. Similar conditions were encountered on the Picnic Bay and Norman Bay beaches.

The bays are exposed to W. winds. Wind data from the Wilsons Promontory Lighthouse indicate that the monthly prevailing wind direcrection is W. for all months except July (NW), August (NW. and W.), and December (W. and NE.). As the bays have protruding headlands with deep water immediately offshore, it is probable that the sand moves to and fro within each bay, with little longshore drift. Coastline features show the results of the Flandrian Transgression. The cliffs plunge into the sea, and there are no shore platforms. Evidently the rock is too resistant for platforms to have developed within the relatively short period since submergence.

Wilsons Promontory is composed of ?Devonian granite (Reed 1959), with some Quaternary deposits. It is a coarse-grained porphyritic type containing feldspar crystals up to 10 cm long and 5 cm wide. Quartz, orthoclase, subordinate plagioclase, and biotite are the main minerals; black tourmaline is a widely distributed accessory mineral. Aeolianite of Pleistocene age is found along the coast at Darby River to the N., at Oberon Bay to the S., and a small outcrop overlies granite near the mouth of Tidal River (Parsons 1966).

Laboratory Procedure

Each sand sample was dried and reduced in bulk with a Jones splitter to about 75 g.

Soluble marine salts and plant matter were removed by decantation, and after drying the sample was sieved using Wentworth intervals. A cumulative frequency curve and a histogram were constructed for each sample; the median diameter and Trask's sorting coefficient were determined. Size fractions were examined under a binocular microscope. To determine the weight percentage of acid-soluble material, another split of about 75 g was made from each sample. Following washing, this was treated with dilute 1 : 2 hydrochloric acid and the acid-soluble matter was removed.

Heavy minerals were separated from the ·06 - ·25 mm size-grades of each sample using bromoform, and the weight percentage of heavy minerals (index number) for this size range was determined. The heavy mineral fractions of mid-tide samples 2 and 7, and of dune sample 9, were examined in detail. An Alnico hand magnet was used to detect the presence of magnetite; its relative abundance was estimated and the grains returned to the heavy mineral fraction prior to mounting in Canada balsam for examination under the microscope. Heavy mineral species were identified under the petrological microscope and their relative proportions were determined by counting random fields of grains in each microscope slide. Percentages were determined to the closest integer; less than 0·5 per cent was recorded as a trace.

Textural Composition of the Sands

Results of the mechanical analysis of the sands are presented in Table 1 and Fig. 2.

MEDIAN GRAIN SIZE: Median grain size of the beach sands ranges from 0·34 mm to 0·14 mm. The samples from Squeaky Beach vary little in their median grain size, and the three mid-tide samples have almost identical medians. Median grain size decreases slightly from low-tide through mid-tide level to high-tide mark in the row of samples taken midway along Squeaky Beach. The median grain size of the beach sand from Picnic Bay and Norman Bay is significantly lower than that from Squeaky Beach. Since wave energies and current velocities in the different bays vary little, a

TABLE 1 STATISTICAL CONSTANTS OF WILSONS PROMONTORY SANDS

Sample No.	Md (mm)	Q3 (mm)	Q1 (mm)	So	Acid-soluble per cent
1	0.34	0.41	0.28	1.21	0.7
2	0.32	0.37	0.27	1.17	0.4
3	0.29	0.34	0.25	1.17	0.6
4	0.33	0.40	0.28	1.19	0.5
5	0.30	0.34	0.26	1.14	0.4
6	0.31	0.37	0.25	1.22	1.0
7	0.20	0.29	0.16	1.35	37.6
8	0.14	0.18	0.11	1.28	39.0
9	0.26	0.35	0.20	1.25	0.7

Key: Md = Median, Q3, Q1 = Quartiles, So = Sorting coefficient

difference in source is suggested to account for the smaller medians. The Squeaky Beach dune sand has a median diameter lower than any of the adjacent beach sands, but the difference is not great.

Considering the proximity of granite cliffs, medians of the beach sands are all surprisingly small. The small median diameters of the Squeaky Beach samples suggest that most of the mineral grains had a relatively long detrital history. In fact, it seems probable that most of the terrigenous matter in the sands of the study area was liberated from the granite many thousands of years ago; with changes in sea level, it may have passed through the surf zone a number of times. Most of the marine skeletal material (common in the Picnic Bay and Norman Bay beach sands) probably has been through more than one cycle of erosion, and was incorporated in dunes during the Pleistocene. The similarity in median diameter of the Norman Bay and Picnic Bay sands suggests similar source materials and similar conditions of deposition.

SORTING: Trask's (1932) coefficient of sorting (So) of the samples are listed in Table 1. Sorting values range from 1·35 to 1·14; they are all well sorted. The beach samples from Squeaky Beach have sorting coefficients between 1·14 and 1·22, and have a higher degree of sorting than those from Picnic and Norman Bay beaches. The Squeaky Beach sample with the highest sorting is from the S. end and that with the lowest degree from the N. end; the difference presumably results from a variation in water turbulence related to coastline

configuration. Samples in the row taken midway along Squeaky Beach have sorting coefficients that are identical or almost so. The Squeaky Beach dune sand has a coefficient of sorting greater than any of the shore samples from that Beach, but the difference is not large.

The lower degree of sorting of the Picnic Bay and Norman Bay beach sands, when compared with those of Leonard Bay, is noteworthy, particularly in view of the smaller median diameters of the former sands. This relationship between sorting coefficient and median diameter is the opposite to that found by Beasley (1969) in a study of some Port Phillip Bay beach sands, where a decrease in the degree of sorting generally corresponds with an increase in median grain size. At Wilsons Promontory the relationship is apparently controlled mainly by source, since wave energies and current velocity conditions are similar.

Although the Squeaky Beach sands are very well sorted, beach sands on other parts of the Victorian coastline have an even higher degree of sorting (Beasley 1969).

HISTOGRAMS: Fig. 2 shows that all of the sand samples are unimodal. A conspicuous maximum size-grade occurs in the medium sand grade of the samples from Squeaky Beach, and fine proximate admixture exceeds coarse proximate admixture in each of them. The conspicuous maximum towering above the neighbouring grades, and the small spread of these samples, indicates a high degree of sorting. The sample from the foredune flanking Squeaky Beach also has its maximum in the
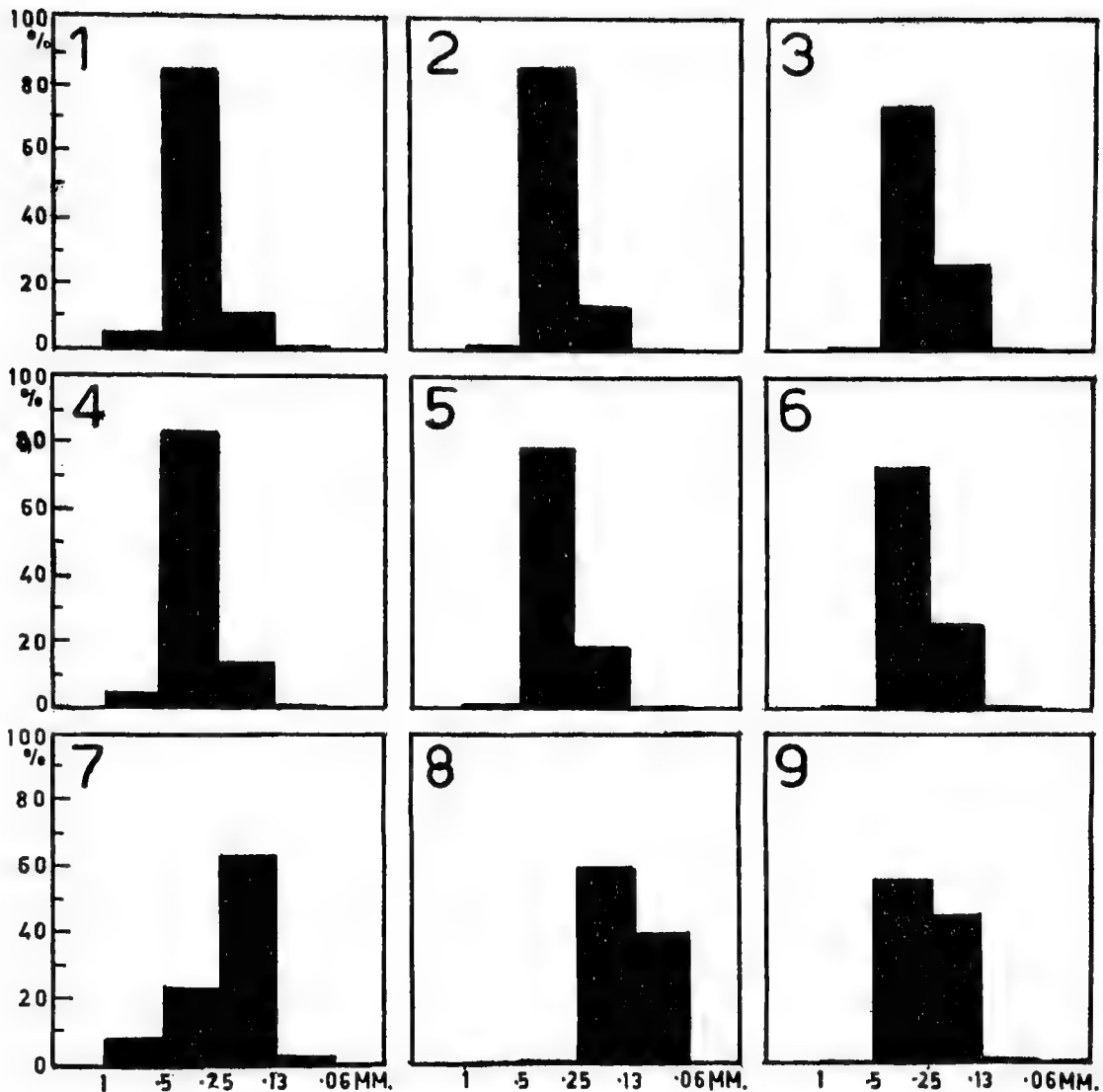
Fig. 2—Size-analyses of sands.

medium sand grade, with fine proximate the dominant admixture. In the dune sand, however, the maximum size-grade is not so conspicuous, and the amount of fine proximate admixture is greater than in the beach sands.

Unlike the Squeaky Beach sands, the samples from Picnic Bay and Norman Bay beaches have their maximum in the fine sand grade. The histograms reveal that these sands are finer in grain size than those of Squeaky Beach. Coarse proximate admixture exceeds fine proximate admixture in the Picnic Bay sample, but the fine proximate admixture is greater than the coarse admixture in the Norman Bay beach sand. In these two samples, the maxi-

mum size-grade is not so conspicuous as it is in the samples from Squeaky Beach, and the histograms also reveal a wider spread of size-grades; this indicates a lower degree of sorting. The shape of the histogram indicates that the beach sand from Picnic Bay has the lowest degree of sorting of the samples examined.

Constituent Composition of the Sands

The constituent composition refers to the acid-soluble (mainly organogenic carbonate) content and the content of terrigenous, mineral matter in the sands. Rock fragments were not present in any of the samples.

ACID-SOLUBLE CONTENT: Weight percent-

age of acid-soluble material in each sample is listed in Table 1, and ranges from 0·4 to 39·0 per cent. That of the Squeaky Beach samples is very small, varying from 0·4 to only 1 per cent. In the row of four samples taken midway along Squeaky Beach, that with most soluble material (0·7 per cent) is the low-tide one. The mid-tide samples from the S. end and midway along the beach have the same soluble content, but the sand from the N. end contains more. This higher content may be due to difference in water turbulence. The sample from the foredune flanking Squeaky Beach contains only 0·7 per cent. Both the Picnic Bay and Norman Bay beach sands have acid-soluble material approaching 40 per cent, which is considerably higher than that of the other samples.

Microscopic examination indicates that organogenic carbonate makes up almost all of the acid-soluble content. All size-fractions of the Picnic Bay and Norman Bay beach sands contain marine skeletal material, and it is abundant in most fractions. Shell material was observed in most of the size-fractions of the Squeaky Beach sands, usually being more common in the very fine fraction than in the others.

MINERAL CONTENT: The mineral content of the sands consists mainly of quartz, almost all of which is the transparent to translucent variety of granitic origin, but small amounts of opaque reef quartz occur. Feldspar grains are very rare in the Squeaky Beach sands, but more common in the Picnic and Norman Bay beach sands. Biotite occurs in small amounts in all samples, and is also more common in the Picnic and Norman Bay samples. Tourmaline is a conspicuous minor constituent; its abundance in the heavy fractions is indicated below.

Most quartz grains in the Squeaky Beach samples are colourless, but a few are yellowish and brownish from a thin coating of limonite. The grains in these samples are mostly rounded to subrounded, adopting Powers' (1953) roundness scale, but in the finer fractions they are commonly subangular with some angular. The degree of roundness of the grains is greater than that of the Picnic and Norman Bay sands. Many quartz grains in the Squeaky Beach samples have a high polish.

In general, the rounder a quartz particle, the longer its abrasion history. Accordingly, the lower degree of roundness of the quartz grains in the Picnic and Norman Bay beach sands suggests a shorter detrital history than those from Squeaky Beach; many grains are subangular to angular, and some are very angular. This shorter history is supported by the greater abundance of feldspar and small "books" of biotite. It seems that some of the grains have been liberated fairly recently from the nearby granite.

Although not abundant, ironstained quartz grains occur more frequently in the Picnic and Norman Bay sands, and the ratio of ironstained to colourless grains is similar in the samples from these two beaches. The ironstained grains usually exhibit a higher degree of roundness than the colourless ones; they appear to have experienced a longer abrasion history.

The mineral content of the Squeaky Beach dune sand is similar to that of the adjacent beach sand. The appearance of the grains, including their degree of roundness, is also similar. Most quartz grains are colourless and many have a fairly high polish.

Heavy Fractions

The index numbers (weight percentages of heavy minerals) for the ·06 - ·25 grades range from 0·97 to 0·19, viz: sample 1, 0·19; sample 2, 0·21; sample 3, 0·33; sample 4, 0·48; sample 5, 0·30; sample 6, 0·28; sample 7, 0·23; sample 8, 0·28; sample 9, 0·97. The values for the mid-tide samples are similar. In the row of samples taken midway along Squeaky Beach the index number increases in value from low-tide through mid-tide and high-tide to a maximum near the foot of the foredune. The backshore zone is inundated by exceptionally high tides and by large waves during storms. Of the beach sand samples, the backshore one has the highest index number. However, the Squeaky Beach dune sand has an index number higher than any of the beach sands. The heavy minerals must have been transported by strong wind action from the beach.

The index numbers of the sands are low, all being below unity. Beach samples from near the Mt. Martha Granodiorite in Port Phillip Bay (Beasley 1969) have much higher index numbers. It seems that the source rocks of the Wilsons Promontory sand do not have a high heavy mineral content.

Magnetite was detected in the heavy fraction of each sample. Its abundance is about the same in each, and was estimated at 5 - 10 per cent.

The heavy mineral fraction of sample 2 (Squeaky Beach) is made up of the following constituents, listed as grain number percentages and, when less than 0·5 per cent, as a trace: apatite, trace; biotite, 1; black opaques, 32; brown opaques, 1; cassiterite, trace; garnet, 2; leucoxene, 3; monazite, trace, others, 1; topaz, trace; tourmaline, 55; zircon, 5. In the above list and those below, "others" refers to grains which could not be positively identified, usually because their weathered condition obscured diagnostic optical properties. Black opaque minerals are mainly magnetite and ilmenite, while brown opaque minerals comprise limonite and other ferruginous minerals. The heavy fraction of sample 9 (Squeaky Beach dune) contains the following percentages of minerals: apatite, trace; black opaques, 35; brown opaques, 1; garnet, 2; leucoxene, 4; others, 1; topaz, trace; tourmaline, 48; zircon, 8. Mineral percentages in the Picnic Bay (sample 7) heavy fraction are: anatase, trace; biotite, 4; black opaques, 41; brown opaques, 1; cassiterite, trace; garnet, 1; leucoxene, 9; monazite, trace; others, 1; rutile, trace; topaz, trace; tourmaline, 25; white mica, trace; zircon, 15.

A close similarity exists between the heavy mineral assemblage of the sand from Squeaky Beach and that from the adjacent dune. Similar species are represented, and the amounts of the various minerals are similar. The assemblages are predominantly of tourmaline and black opaque minerals, ilmenite being more abundant than magnetite. Next in order of abundance are zircon, leucoxene and garnet, but the combined amount of these minerals is less than 15 per cent in both assemblages. The great abundance of tourmaline (more than 47

per cent) is noteworthy. Biotite is not common in the Squeaky Beach assemblage and was not recognised in the dune heavy fraction; the flaky nature of the biotite particles could have retarded its transport by wind action from beach to dune.

The heavy fraction of the Picnic Bay sample differs from the Squeaky Beach ones mainly in the percentages of the various mineral constituents. Black opaque minerals predominate, and tourmaline is next in order of abundance, followed by zircon, leucoxene and biotite. The tourmaline content is markedly lower than that of the Squeaky Beach assemblages, but the black opaques and tourmaline make up more than 65 per cent. Zircon, leucoxene and biotite contents are all higher than in the other samples. The Picnic Bay assemblage also differs by the presence of trace amounts of anatase, rutile and white mica; the white mica could be bleached biotite.

Heavy fractions of the samples consist predominantly of a granitic group of minerals, basaltic minerals such as augite and olivine being absent. The Wilsons Promontory Granite is naturally regarded as the primary source. Baker (1942) listed the heavy mineral assemblage in a representative sample of Wilsons Promontory Granite as: apatite (common), biotite (abundant), cassiterite (recorded in thin sections), chlorite (occasional), hematite (rare), magnetite (very rare), sulphides (very rare), tourmaline (recorded in thin sections), white mica (occasional), zircon (common).

The nature of the Picnic Bay heavy fraction suggests some difference in source from that of the Squeaky Beach assemblages. Some of the constituents may have come from aeolianite. However, the greater abundance of fresh biotite in the Picnic Bay assemblage, combined with the relatively slight abrasion of certain of the other mineral grains, suggests that at least some of the constituents were liberated recently from granitic rocks in the vicinity.

Sound Phenomenon

Squeaky Beach sand will emit a squeaking or singing sound when it is dry or nearly so. Such can be produced by walking on the sand, or striking it with the hand, foot or a stick.

When the sand is wet, it is silent. The sound phenomenon must be related to physical composition and textural characteristics. This sand is composed almost entirely of quartz grains, most of which are subrounded to rounded with a fairly high degree of sphericity. The degree of sorting is very high, more than 75 per cent of every sample falling into the medium sand size-grade. The sand is almost devoid of material less than 0·125 mm in diameter.

Conversely, the Norman Bay and Picnic Bay beach sands are silent. They contain a large percentage of shell material, and their degree of sorting is not as high. The sands contain an appreciable proportion of particles less than 0·125 mm in diameter. The roundness of the grains is also noticeably lower; many grains are angular.

The sound phenomenon is apparently connected with the nature of packing of the grains, which is controlled by size distribution and shape. Very fine particles have a clogging effect. Presumably, the pressure produced by walking on results in shearing, layers of the packed grains shifting over other grains. The character of the note is some function of friction.

Acknowledgement

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Explanation of Plate 7

Fig. 1.—Squeaky Beach from N. end with granite in foreground and background.

Fig. 2—Squeaky Beach with eroding foredune.

Fig. 3—Picnic Bay with wide, sandy beach.

Fig. 4—Looking S. along Picnic Bay beach, showing granite headland.

APPENDIX

Sample Stations

1. 358 m NW. from S. end of Squeaky Beach, low-tide.
2. 358 m NW. from S. end of Squeaky Beach, mid-tide.
3. 358 m NW. from S. end of Squeaky Beach, high-tide.
4. 358 m NW. from S. end of Squeaky Beach, backshore near foredune foot.
5. 23 m NW. from S. end of Squeaky Beach, mid-tide.
6. 23 m SE. from N. end of Squeaky Beach, mid-tide.
7. 311 m N. from S. end of Picnic Bay beach, mid-tide.
8. Midway along sandy beach fronting Norman Bay, mid-tide.
9. Crest of foredune towards N. end of Squeaky Beach.

1

2

3

4
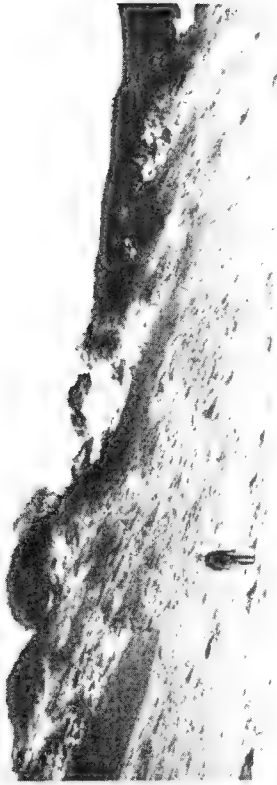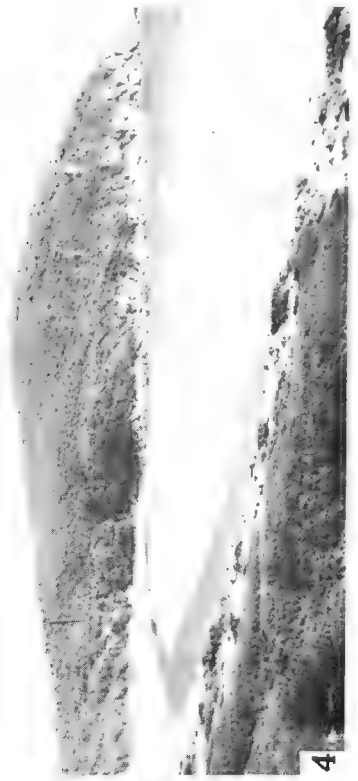
THE GREEN GULLY BURIAL LOCATION

By J. A. Blackburn

In February 1966 I was requested to provide a datum for levels, and to link together the various excavations carried out around the site (these *Memoirs* 30). As the area was being worked as a soil pit, it was considered advisable to record enough data to enable the exact site to be relocated on the ground in the future. Due to the absence of convenient co-ordinated points, permanent structures, or even defined property boundaries, this was not an easy task.

An outline of the method used will be given as a guide to others who may be faced with a similar problem.

Three steel rods were driven into the ground along a line leading to the most prominent and permanent mark visible in the area, the Keilor Church spire. At each of these steel rods, which were as far apart as circumstances permitted, angles were read to some ten or so well-defined objects such as power pylons, poles, chimneys, etc. The distances between the rods were measured, and the position of the centre of the burial relative to the nearest rod was determined. If one of the rods survives re-establishment will be simple and direct. However, angles read between only three of the referring objects will enable the site of the centre of burial to be relocated. This is an example of the 'Three Point Problem' well known to surveyors and navigators.

In April 1970 Mr K. A. Baker, L.S., established co-ordinated points at Keilor East and Keilor West, using a DI.50 Distomat which, by means of radio waves, measures distances up to 90 miles with an accuracy of $\pm$ 0·20 feet $\mp$ 3 parts per million. In August 1970 he traversed between the two with theodolite and DI.10 Distomat which uses infra-red rays with a range of 1 kilometre and accuracy $\pm$ 1 centimetre. One additional line with a closing angle as a check sufficed to fix the adjacent rod and centre of burial.

Co-ordinates of the key points on the Australian Map Grid Zone 55 are (in metres):

Centre of burial	E	308552·45
	N	5821781·00
Adjacent Steel Rod	E	308547·02
	N	5821783·04
Keilor Church Steeple	E	310126·65
	N	5822437·53

The latitude and longitude of the centre of burial was then calculated to be:

37° 43′ 52″·03 South
144° 49′ 38″·95 East

AMPHIBIANS AND REPTILES FROM SIMBAI, BISMARCK-SCHRADER RANGE, NEW GUINEA

By David S. Woodruff

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Abstract

Frogs: *Litoria angiana, L. arfakiana, L. micromembrana, Nyctimystes disrupta, N. foricula, N. kubori;* skinks: *Sphenomorphus flavipes, Emoia pallidiceps, Scincella stanleyana, S. prehensicauda;* and the snake *Natrix montana* are reported from Simbai (altitude 1770 m) in the Bismarck-Schrader mountains of New Guinea. Taxonomic problems associated with *N. disrupta* and the lygosomines are discussed but not resolved. *N. disrupta* is added to the list of montane, riparian anurans known to be host to endoparasitic leeches. Marked sexual dichromatism in *S. prehensicauda* is described and illustrated. The Simbai anuran fauna appears to be similar to that of the adjacent Kaironk Valley and to that of the Wahgi-Sepik Divide 40 km further S. Finally, Rappaport's study of the regulation of the consumption of small animals by natives, and Bulmer and Tyler's comparison of modern and native classifications of frogs in this area are discussed.

Introduction

This contribution to the herpetology of New Guinea concerns a small collection of six species of hylid frogs and five species of reptiles constituting the first collection reported from the Simbai Valley.

Simbai Patrol Post is located about 113 km W. of Madang on the NE. side of the Bismarck-Schrader mountain range (Fig. 1). The settlement lies in the upper valley of the Simbai River at an altitude of about 1740 m. The Schrader Range lies to the N. and W. of Simbai, the Bismarck Range to the S. and E. The SW. side of the ranges are drained at this point by the Kaironk River. The Simbai-Kaironk divide is about 2000 m above sea level, while in this region the ridges of the ranges vary from 2225 m to 2625 m. The lowlands on either side of the ranges are less than 600 m above sea level.

The climate and ecology of the neighbouring Kaironk Valley have been described by Bulmer and Tyler (1968). Conditions near the summit of Mt. Kominjim just north of Simbai have been described by Gilliard and Le Croy (1968), and Rappaport (1967) provides a detailed account of environmental conditions in the Bismarck Range a few miles S. of Simbai. The climate of this region is subtropical; annual rainfall varies between 2540-3810 mm. Originally the bases of the ranges were covered with lowland rainforest, the flanks of the ranges up to about 1825 m with lower montane rainforest, and the top of the ridge with montane or cloud forest. Today the valleys of the Simbai and Kaironk are populated by Karam and Maring horticulturalists and much of the lower montane forest has been cleared or disturbed (Pl. 8, fig. 2). Except in the main valleys where settlement occurs at higher altitudes, only remnants of virgin forest occur below about 1600 m. Above that level the forests are still relatively undisturbed along much of the Bismarck-Schrader Range (Pl. 8, fig. 3). At Simbai, however, the grasslands and cultivated areas are continuous from the Simbai to the Kaironk, so separating and effectively isolating the forests of the Schrader Range from those of the Bismarck and other ranges in the central highlands.

Although the Bismarck-Schrader Ranges are still relatively remote they have been visited by several biologists and anthropologists. Three parties collected amphibians and reptiles in the Simbai-Kaironk area prior to the author's visit. Undescribed collections made by H. G. Cogger in the upper Kaironk Valley and by the late E. T. Gilliard on Mt. Kominjim are in the collections of the Australian Museum and the American Museum of Natural History
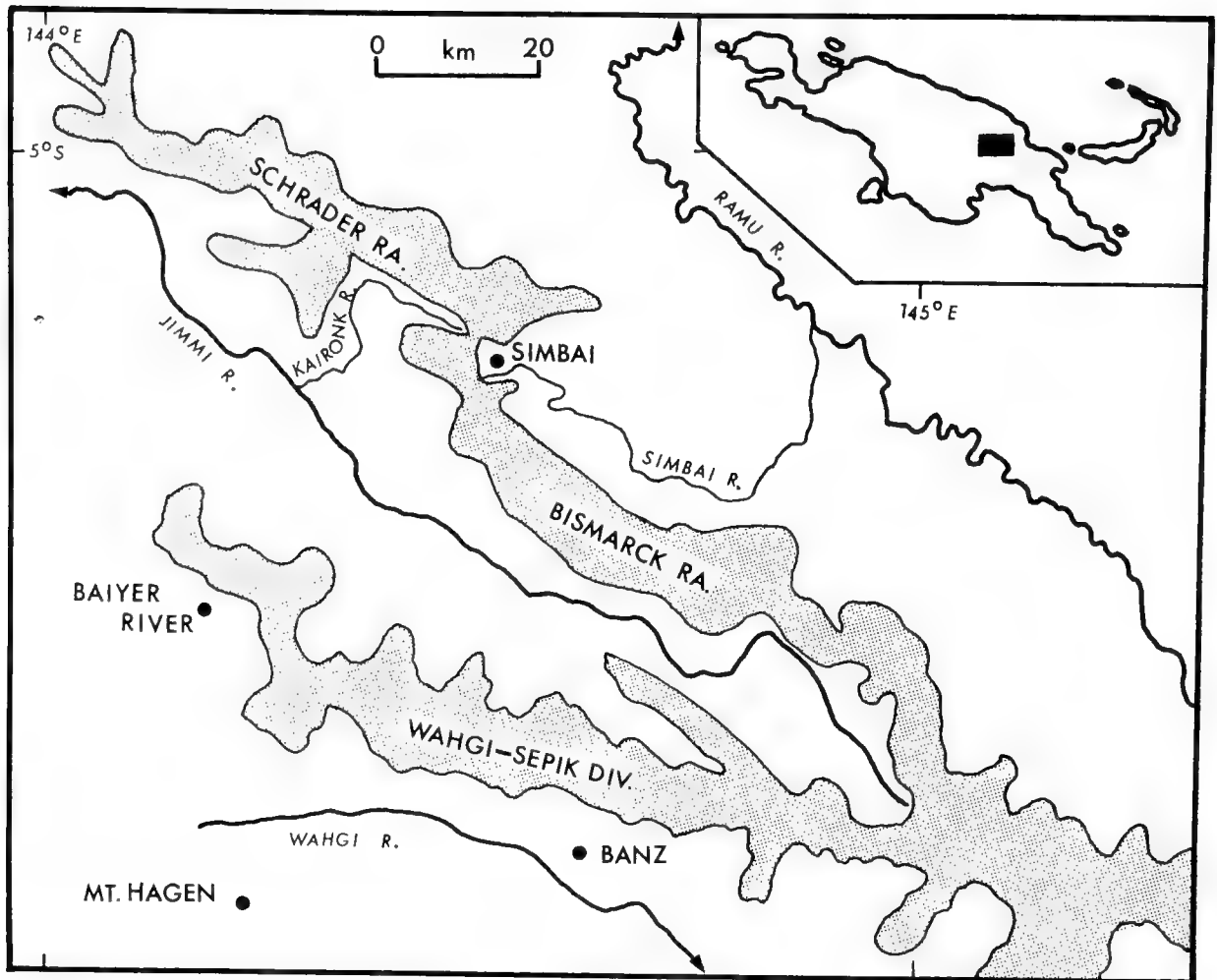
Fig. 1—Area of the central highlands of New Guinea discussed in the text showing the relationships of the main mountain ranges. Inset shows the location of the larger map.

respectively. R. N. H. Bulmer collected nearly 500 frogs in connection with a detailed study of the ecology of the Karam in the upper Kaironk. This collection, which contains at least 19 species, has been reported by Bulmer and Tyler (1968). The present collection was made at the Anglican Mission, Simbai, on 1 Jan., 1966. All specimens were collected during the day in nearby native gardens and along the banks of the swiftly flowing Simbai River, at an altitude of about 1770 m. The specimens have been deposited in the National Museum of Victoria; their registration numbers are indicated below.

Species Represented

ANURA

Litoria angiana (Boulenger)

Specimens: Two adult males (D 14472, 14478).

Discussion: These specimens agree with Tyler's (1968) description of this morphologically variable species. Both specimens have a continuous fold on the posterior surface of the forearms and nuptial pads a little larger but of the same shape of those illustrated by Tyler (1963, Fig. 3B). This species is now known throughout the mountains of New

Guinea, occurring near streams at altitudes of 1225-2750 m.

The Australian hylid frogs previously placed in the genus *Hyla* are here referred to the genus *Litoria* Tchudi on the authority of Tyler (1971).

Litoria arfakiana Peters and Doria.

Specimens: Three adult males (D14473, 14480-1).

Discussion: These males agree with those described by Tyler (1968). The long unwebbed fingers, tubercles on the upper eyelid, heel, and vent (absent from the tarsi), and the prominent pointed snout, appear to characterize this species. In life two of the males were brown dorsally, the other was olive green. *L. arfakiana* has been collected throughout the mountains of New Guinea at altitudes of 775-1825 m.

Litoria micromembrana (Tyler).

Specimens: 13 adults (D14462-71, 14475, 14477, 14479).

Discussion: These specimens agree closely with Tyler's (1968) description of this species. All of the specimens were collected in vegetation along the side of the river. This species is now known from a number of localities in the highlands of central New Guinea at altitudes of 1225-2450 m.

Nyctimystes disrupta Tyler.

Specimen: One adult male (D14218).

Discussion: Tyler (1963c) distinguished this species from the morphologically similar *N. papua* on the basis of differences in palpebral venation, the degree of webbing on the fourth finger, and the ratio of the eye-nostril to internarial distance. While the above specimen agrees closely with the description of Tyler's holotype it is intermediate between these two taxa in all three diagnostic characters. Specimens collected by H. G. Cogger (pers. comm. 1966) were also morphologically intermediate between *N. disrupta* and *N. papua* as presently defined.

N. disrupta was previously known from the Kaironk Valley and from near Baiyer River, about 50 km to the SW. (Tyler 1963c). *N. papua* was described from specimens collected on Mt. Victoria in the Owen Stanley Range (Boulenger 1897) and is widespread in the highlands between 1525 and 2275 m (Zweifel 1958, Tyler 1963b). One of the five syntypes of *N. papua* in the British Museum has subsequently been referred to *N. semipalmata* (Parker 1936). More recently Tyler (1963b) has suggested that the type series may still not be conspecific. The validity of *N. disrupta* may therefore depend, in part, on the selection of a lectotype from among the four remaining syntypes in the British Museum and a single syntype in the Museum of Comparative Zoology. As Boulenger's original description of *N. papua* includes an illustration of one individual (1897, Pl. 1, fig. 5) the specimen represented should become the lectotype. Until such a lectotype is designated *N. disrupta* must be regarded as a species of doubtful validity possibly synonymous, in part, with *N. papua*.

When captured this frog exuded a slimy secretion with a sickly odour. A large endoparasitic leech was found in the dorsal lymph sac. Although such parasitism has not been reported previously in this species, these unusual infestations are now known to occur in most of the common riparian anura in the New Guinea highlands: *Rana grisea, Litoria angiana, L. arfakiana, L. micromembrana, N. kubori,* and *N. papua* (Mann and Tyler 1963, Tyler, Parker and Bulmer 1966, Tyler 1968).

Nyctimystes foricula Tyler.

Specimens: One adult male and one juvenile (D14030-1).

Discussion: The specimens agree closely with Tyler's (1963c) original description, being green above and yellow below in life. The palpebral venation differs from that of the sympatric *N. kubori* in that the veins are broad, parallel, and oblique. This species has been reported previously only from the Kaironk Valley.

Nyctimystes kubori Zweifel.

Specimens: Four adult males (D14214-7).

Discussion: This species was described by Zweifel (1958) and subsequently by Tyler (1963b, c). The present series conform closely to the males described by Tyler (1963b). This

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species is now known from a number of localities in the central highlands of New Guinea at altitudes between 1525 and 1975 m.

REPTILIA: SQUAMATA

Scincella stanleyana (Boulenger).

Specimens: Seven adults and four juveniles from Simbai (D14018-28). An additional individual was collected in montane forest at about 2130 m on the trail between Simbai and Kundan (D14029).

Discussion: This small, ground dwelling skink was common beneath rotting vegetation in the gardens around Simbai. Adults have snout-vent lengths of 48-59 mm. All specimens have a dark brown lateral line separating the copper coloured back from the cream undersurface. In immature individuals there is also a broken, white, dorso-lateral line extending from the upper eyelid onto the flanks. This species is widespread in the mountains of New Guinea (Loveridge 1948, and undescribed collections in the Museum of Comparative Zoology).

Scincella prehensicauda (Loveridge).

Specimens: Six females (D14012-7) and four males (D14008-11).

Discussion: This small arboreal skink with striking white eyelids is unusual in possessing marked sexual dichromatism (Pl. 8, fig. 1). In life, females are brown dorsally with darker brown crossbars and small paler patches, particularly on the sides. There are conspicuous dark stripes on the sides of the neck. This colouration is little changed on preservation. In contrast the males, which are uniformly green in life, are a pale golden brown colour in alcohol. The females are also slightly larger than the males, as indicated by the following measurements of individuals with undamaged tails (data in mm).

	No.	Total-length	Tail length
Females	4	135-151	70-76
Males	3	121-125	63-68

The Karam natives are well aware of this dimorphism, pointing out to the author in pidgin English that: 'dispela man bilong dispela mari' and *vice versa.*

Greer and Raizes (1969) have shown how the green colour of the males of this species is due to the presence of a pigment in the blood plasma, which gives the muscles, bones, and other tissues a striking green colour. They report that females are similarly coloured internally but do not appear green externally because of the presence of brown pigment in the scales.

This species is now known from several localities in the central highlands of New Guinea.

Sphenomorphus flavipes (Parker).

Specimen: One adult (D14005).

Discussion: This handsome arboreal skink has a body length of 90 mm and a total length of 180 mm. Dorsal surfaces are dark brown with cream spots while the belly is a fine mosaic of cream, yellow, and brown. The tail is marked with 6-7 longitudinal brown stripes. The specimen was collected 4 m above the ground in a small *Casuarina* tree.

Greer and Raizes (1969) note that the predominant ground colour of both sexes of this species is brown, and that there are three distinct colour morphs: crossbanded, striped, and plain. The present specimen belongs in the last group. Loveridge (1948, p. 354) was therefore mistaken in describing the variation in his three specimens (referred to *Lygosoma (Leiolopisma) flavipes*) as a case of sexual dichromatism.

As in *Scincella prehensicauda* this species also possesses a green blood pigment (Greer and Raizes 1969). According to these authors this phenomenon is known in only one other amniote: *Leiolopisma virens anolis,* an arboreal skink from New Guinea and the Solomon Is. The apparent uniqueness of the green blood pigment, coupled with certain morphological features and similarity of distribution patterns, indicate that these three species should probably be placed in a single genus (Greer, in preparation).

Emoia pallidiceps De Vis.

Specimens: One adult and one juvenile (D14006-7).

Discussion: Loveridge (1948) treated this species as a race of *E. baudini.* Brown (1953), in a subsequent revision of the *baudini* com-

plex resurrected *E. pallidiceps* as a distinct species. The specimens from Simbai agree closely with Brown's description. The adult measures 53 mm from snout to vent and is 128 mm in total length. It is dark brown dorsally with black sides and there is a white lateral line running from the ear to the shoulder, continuing as a series of spots to the hind limb.

Natrix montana Jeude.

Specimen: One juvenile (D14004).

Discussion: The specimen has a total length of 190 mm, a tail length of 43 mm, divided anal and subcaudal scales, and 15 rows of scales at the mid-body. It was collected beneath a log on the river bank.

Discussion

ANURANS OF THE BISMARCK-SCHRADER RANGE

Collecting over a period of several years, Bulmer and Tyler (1968) were able to report 19 species of anurans from the upper Kaironk Valley and the adjacent forests of the Schrader Range. Ten species of hylids, eight microhylids, and one ranid occur in that area:

Litoria angiana, L. arfakiana, L. bulmeri, L. micromembrana, L. modica, Nyctimystes disrupta, N. foricula, N. kubori, N. narinosa, N. sp. indet., *Sphenophryne brevicrus, Cophixalus parkeri, C. riparius, C. shellyi, C. variegatus, Asterophrys wilhelmana, Xenobatrachus rostratus, Barygenys* sp., and *Rana grisea.*

This is essentially a montane fauna: most of these species are not known from below 1200 m and all are restricted to altitudes of more than 600 m. Generally speaking the hylids are the dominant group in the cleared areas along the valley floor while the microhylids are restricted to the forests.

On the basis of present knowledge, the adjacent Simbai Valley contains the six hylids reported above and *Litoria bulmeri* which Gilliard collected at 2530 m on Mt. Kominjim (Tyler 1968). All species reported from the Simbai watershed are represented in the larger Kaironk collection. The absence of microhylids in the Simbai collection is probably due to the fact that the collection was made in native gardens near the river, rather than in the lower montane or montane forest. At this time, therefore, the data suggest that the anuran fauna of these two areas on either side of the mountain range are probably very similar.

Although herpetological exploration of the New Guinea highlands is still in its infancy the anurans of the Wahgi-Sepik Divide, about 40 km south of Simbai, have been the subject of a number of recent papers by Tyler (1963a, b, c, 1968) and Zweifel (1956a, b, 1958, 1962). It can be seen in Fig. 1 that the Bismarck-Schrader Range and the Wahgi-Sepik Divide converge near Mt. Wilhelm in the E. The forested ridges of these ranges, which are still largely unsurveyed, vary in altitude between 2100-3100 m with summits rising up 4510 m. As the lower montane and montane forests appear to be continuous along these mountain ranges, it might be expected that the fauna of the Bismarck-Schrader Range near Simbai would be similar in species composition to that of the Wahgi-Sepik Divide near Banz or Nondugl.

The comparison of the faunal lists of these two areas shows that in fact the two are remarkably similar. Sixteen of the 18 described species collected in the upper Kaironk Valley are known from elsewhere in the central highlands. All but one of these 16 *(Cophixalus variegatus)* have been collected on the Wahgi-Sepik Divide. Only two taxa *(Litoria bulmeri* and *Nyctimystes foricula)* have not yet been reported from outside the Kaironk-Simbai area. On the other hand, there are five species *(L. becki, L. darlingtoni, L. iris, Metopostira ocellata,* and *C. darlingtoni)* known from the Wahgi-Sepik Divide which so far have not been found on the Bismarck-Schrader Range. More detailed comparison of the two faunas will have to await the availability of data derived from additional field work, and the clarification of a number of distributional and taxonomic problems.

ANURANS AND MAN IN THE BISMARCK-
SCHRADER RANGE

Finally attention is drawn to the work of two anthropologists who have studied the relations

between the natives of this area and the non-domestic fauna. Rappaport (1967) studied the role of ritual in the ecology of the Tsembaga group of the Maring people who live about 10 km south of Simbai. Rappaport (1967) and Bulmer (pers. comm. 1966) have drawn attention to the fact that frogs, lizards, and other small animals constitute a small but important part of the diet of the Maring and Karam people. On several occasions the author saw children carrying home frogs wrapped in leaves or secured by the legs. Although children in this area do not exhibit symptoms of severe protein deficiency, Rappaport presented evidence suggesting that their protein intake may be inadequate. It is very interesting, therefore, that in the Tsembaga he found that taboos operated to make most of the subsidiary sources of animal protein available to women and children but precluded them from adolescents and adult males. He concluded that such ritualistic regulation maximizes the value of such foods for the population as a whole.

It is partly because of the dietary importance of small animals like frogs to the natives of this area that their knowledge of the natural history of such animals is so remarkable. Bulmer, in his field study of the Karam in the upper Kaironk Valley, recorded the native names of all specimens he received. He was subsequently able to show that the Karam classification of frogs is very similar to that adopted by trained herpetologists (Bulmer and Tyler 1968). The exceptions to this generalization are particularly interesting as they involve *Litoria angiana* and *Nyctimystes disrupta*, taxa which have troubled museum workers. In the case of *L. angiana* the Karam, like the museum taxonomists, have attempted to describe the variation of this highly variable species by reference to a series of taxa. In the second case Bulmer and Tyler note that the Karam recognize two speciemes as being equivalent to the taxon *N. disrupta*. It may well be that future studies will reveal the presence of sibling species presently confused under this name. Linguistic studies of the type carried out by Bulmer may guide biologists to a number of hitherto unrecognised species complexes.

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Explanation of Plate 8

Fig. 1—Sexual dichromatism in *Scincella prehensicauda*. The upper two specimens are females, the lower pair are males.

Fig. 2—Simbai Patrol Post (altitude 1740 m) and 600 m airstrip near the headwaters of the Simbai River. Note that the forest has been cleared from the valley floor and lower ridges.

Fig. 3—Montane or cloud forest 20-30 m high on the trail between Simbai and Kundan at an altitude of about 2100 m.

2 cm
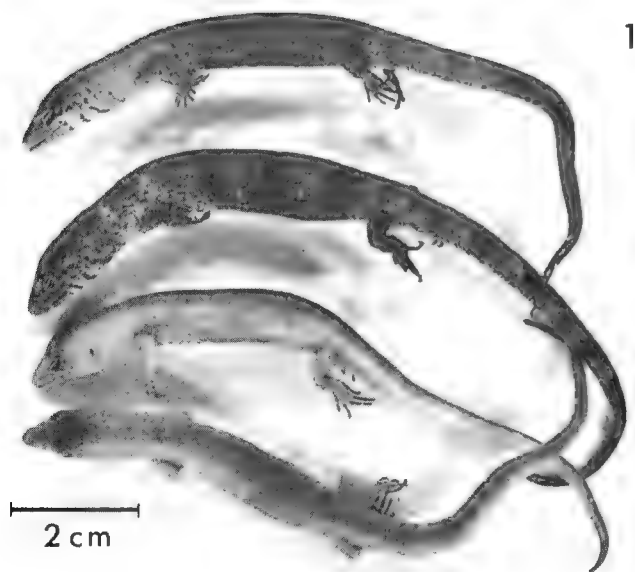
QUANTENOBDELLA HOWENSIS RICHARDSON 1969 OF LORD HOWE ISLAND, WITH COMMENT ON DISPERSAL BY PASSIVE TRANSPORT (HIRUDINOIDEA: RICHARDSONIANIDAE)[1]

By Laurence R. Richardson[2]

Abstract

Distinct in having 16 5-annulate somites, salivary gland papillae, elongate cylindrical ejaculatory bulbs and a simple fusiform vagina with a long vaginal duct. Adequate systematization gives evidence of diversity in leech faunas, not the widespread uniformity associated with dispersal by passive transport.

Introduction

The elongate cylindrical ejaculatory bulb folding lengthwise in contraction and in male maturity, had not been recognized as a distinctive morphological form at the time when the original description of the g. *Quantenobdella* was prepared (Richardson 1969a), and at that time I failed to detect the minute salivary gland papillae reported here on the jaws.

With the combination of these papillae and 16 complete 5-annulate somites, elongate cylindrical ejaculatory bulbs as in bassianobdellids (Richardson 1970a) and a simple fusiform vagina, poorly defined internal muscular ridges on the wall of the pharynx, *Quantenobdella* now stands apart from the other genera of aquatic jawed sanguivores known in the Australian Region, but otherwise the morphology retains it fully within the Richardsonianidae.

The inadequately known *Hirudo catenulata* Johansson 1918 of the New Hebrides resembles *Q. howensis* in having 16 complete 5-annulate somites, a small posterior sucker about half of the maximum width of the body, and a small number of teeth, but differs in pattern, and Johansson states that there are no salivary gland papillae (which may or may not be correct for his specimens were small, 20·0 mm in length).

The presence of salivary gland papillae on the jaws is known in aquatic jawed sanguivores of the tropical-subtropical belt, essentially between the latitudes of 35° N. and S. Others lacking such papillae occur in this belt and in the temperate regions. The present indications are (1) that *Quantenobdella* is part of the tropical-subtropical component in the Australian leech fauna, and (2) in favour of the probability of isolation over a period of biological time sufficient for the appearance of distinctive generic characteristics.

The occurrence of leeches on oceanic islands has been long known. Moquin-Tandon (1846) records leeches in the East Indies and the West Indies. By 1900 Blanchard (e.g. 1897) had reduced many early described species in the East Indies to a relatively few species widely distributed through the archipelago. Since 1900 leeches have been recorded on many remote high oceanic islands: Madagascar, Juan Fernandez, Samoa, Hawaii, Fiji, etc. The knowledge of these more isolated leech faunas is commonly incomplete, inadequate (even for Hawaii), and confused within the earlier simple classification based essentially on readily accessible external morphological features with the recognition of relatively few genera, some being widespread, and a small number of species.

These leeches are without close marine relationship, are intolerant of saltwater, and are freshwater dependent. The distribution of a few genera throughout an archipelago and the appearance of a uniformity in the fauna, are suggestive of the possiblity of passive transport by other animals or through the agency of man, as proposed by Darwin as a dispersal mechan-

ism leading to the uniformity of freshwater faunas over wide areas. The few authors who have concerned themselves with the distribution of leeches on oceanic islands have relied on passive transport as the dispersal mechanism.

For example, Moore (1901) recognized the resemblance in the morphology of the reproductive systems, somital annulation, pattern, etc. of a leech from Porto Rico, the West Indies, to a leech in the Oriental g. *Hirudinaria*, gave the leech from the West Indies the name of *Hirudinaria blanchardi*, and suggested that it had been transported to the West Indies by man. Moquin-Tandon (1846) records shipments of medicinal leeches from Europe to the West Indies, but not from the Oriental Region. Notes associated with later specimens of *blanchardi* now in the Smithsonian Institution, show that Moore continued strongly of his earlier opinion. In 1946, Moore considered that the presence of *Gastrostomobdella quinqueannulata, Glossiphonia weberi lata*, and *Barbronia weberi formosana* in Hawaii was probably due to human agency and to transport by birds. Otherwise the g. *Gastrostomobdella* was known in Indo-Malay, *G. weberi lata* in China, and *B. weberi formosana* in Formosa.

The only previous knowledge of the nature of the leech faunas of the high oceanic islands adjacent to the E. coast of Australia is given by Johansson (1918), who described *Glossiphonia novaecaledoniae* and *Barbronia rouxi* from New Caledonia, and *Hirudo catenulata* from the New Hebrides; and by Moore (1944) who described *Chtonobdella parva* from the New Hebrides. This illustrates the nature of the leech faunas of high oceanic islands with representation of glossiphonids, erpobdellids, and aquatic jawed sanguivores, with the addition of terrestrial jawed sanguivores in the Oriental and Australian Regions, including Polynesia.

Passive transport is seemingly possible for jawed sanguivores which attach as adults and young to birds and other animals, but not for long periods, for when engorged, the leech departs the host. The cocoons are deposited loose in wet mud and could conceivably adhere to the feet of birds. This possibility cannot be simply dismissed, but it is questionable that cocoons could be carried for any lengthy time across the open ocean. Young of the Australian *Aetheobdella hirudoides* perforate the conjunctiva at the outer corner of the eye in some bush birds, including the White-eye, and remain for some weeks in the subcutaneous pocket lateral to the bony orbit (Richardson 1969a). Something possibly of this nature is recorded in Moquin-Tandon for *Hirudo ardeae* at Martinique, but the habit is most rare. The erpobdellids are macrophagous, do not attach to other animals, and fasten the cocoon securely to aquatic plants, sticks, and stones. The glossiphonids take body fluids from aquatic molluscs and other invertebrates, some from amphibia, and brood the young attached to the venter of the adult. Invasion of the nasal chamber of aquatic birds is known for the glossiphonid g. *Theromyzon*.

Prince Edward Island in the Gulf of St. Lawrence has gained a leech fauna since the last glaciation. It was pointed out in a study of the leeches of this island (Richardson 1943) that a possibility of passive transport might be accepted for *Theromyzon* and for the jawed sanguivorous *Macrobdella*, transport of cocoons is a possibility for the macrophagous haemopids, but passive transport was beyond probability for the macrophagous erpobdellids and for the glossiphonids in this fauna. The possibility for passive transport as a mechanism of dispersal is outweighed by the improbabilities. It is necessary to seek a dispersal mechanism which is available to the erpobdellids, the haemopids, and the majority of the glossiphonids. It can be reasonably anticipated that when such a mechanism is found, it will be equally available to *Theromyzon* and *Macrobdella*. The proposal applies also to the leech faunas of high oceanic islands.

More adequate systematization points to dispersal in more remote biological time, a period of such length as has produced diversity at the generic level. Families of regional status, and genera of sub-regional status are now demonstrated for the aquatic jawed sanguivores (Ringuelet 1968, Richardson 1969a). It is possible to show (Richardson 1970c) that the Oriental *Barbronia weberi* is not congeneric with *Barbronia rouxi*, the type species of the genus, that *Hirudo catenulata* does not belong

in the g. *Hirudo* (Richardson 1969a), that terrestrial jawed sanguivores of Java, Samoa, and Madagascar placed by Blanchard (1917) in the Australian g. *Philaemon* do not belong in this genus (Richardson 1969b). Also the terrestrial jawed duognathous sanguivore *Nesophilaemon skottsbergi* of Juan Fernandez and the trignathous g. *Mesobdella* of Chile and the Argentine (Richardson 1970a) belong to the Neotropical jawed sanguivores, not to the Haemadipsidae of the Oriental and Australian Regions. It will be shown later that *Chtonobdella parva* of the New Hebrides differs significantly from the leeches in the Australian g. *Chtonobdella,* that *Hirudinaria blanchardi* differs significantly from the leeches in the Oriental g. *Hirudinaria,* and from a recent study of gastroporous leeches, it is clear that Moore's *quinqueannulata* of Hawaii cannot be retained in the Oriental g. *Gastrostomobdella.*

For aquatic leeches, a measure of uniformity over a wide range is recognizable in those parts of the Western Palaearctic and Nearctic which were defaunated in the last glacial and repopulated by a limited immigrant fauna in the postglacial, a period still too brief in biological time for a diversification at specific and generic levels, and division into significant zoogeographic groupings.

In contrast, undisturbed by the last glacial, the aquatic jawed sanguivores of the Australian Region divide at the generic level into provincial faunas. They exhibit not only the diversity of a fauna continuous with the fauna of the long preglacial period, but also the persistence of zoogeographic groupings. Both these features contraindicate dispersal by passive transport.

The progressive displacement of apparent uniformity in distribution by the demonstration of diversity, lowers to improbability the general operation of a dispersal mechanism formerly proposed on the basis of a wide uniformity in distribution.

Genus *Quantenobdella* **Richardson 1969** (Amended)

Monostichodont; 16 5-annulate somites (ix to xxiv); xxv, 4-annulate; somital sense organs, minute; jaws small, resting in shallow open recesses; teeth, about 40, minute, acute, spaced; salivary gland papillae, sparse, minute; dorsal salivary glands diffuse, with weakly developed columns of aggregated ducts; entrance to pharynx and lumen of pharynx, narrow; weakly defined muscular ridges on the inner surface of the pharynx; pharynx small, terminating in ix; crop compartments in x to xix each with a small pair of simple secondary anterior caeca and larger caeca at the median level, the latter extending into the paramedian chamber and those of xix forming postcaeca extending to xxvi; no copulatory gland pores; genital pores xi and xii b_5/b_6; testes, simple saccular; number of testes, ?; anterior region of male paired duct without a primary flexure, epididymis in xii posterior to the elongate cylindroid ejaculatory bulb in xi, the relationship linear; ejaculatory ducts, very short; median reproductive regions, bimyomeric, mesomorphic, both formed on a posteriorly directed primary loop; male median region short, reflected at xi/xii; oviducts, very short; female median region reflected at xiii/xiv; female atrium continuous with the long common oviduct; vagina caecate, transverse, fusiform, vaginal duct long. Size, ? medium, pattern, continuous longitudinal dark bands and light stripes, aquatic, sanguivorous. Australian Region.

Type species: *Quantenobdella howensis* Richardson 1969.

Holotype G850, National Museum of Victoria, 38·0 mm long, from Lord Howe Island, January 1903. W. Baldwin Spencer collector. Right ventrolateral jaw removed, mounted separately.

Quantenobdella howensis **Richardson 1969**
Fig. 1 a-g

Preserved, moderately contracted so that the annuli are low-ridged, the velum obtuse, the aperture of the anterior sucker transverse, and generally the animal strongly depressed, low convex above, the margins obtusely rounded, the venter slightly concave. Quite typically aquatic, sanguivorous, excepting that the posterior sucker is unusually small. The dorsum divided by narrow light stripes into a median
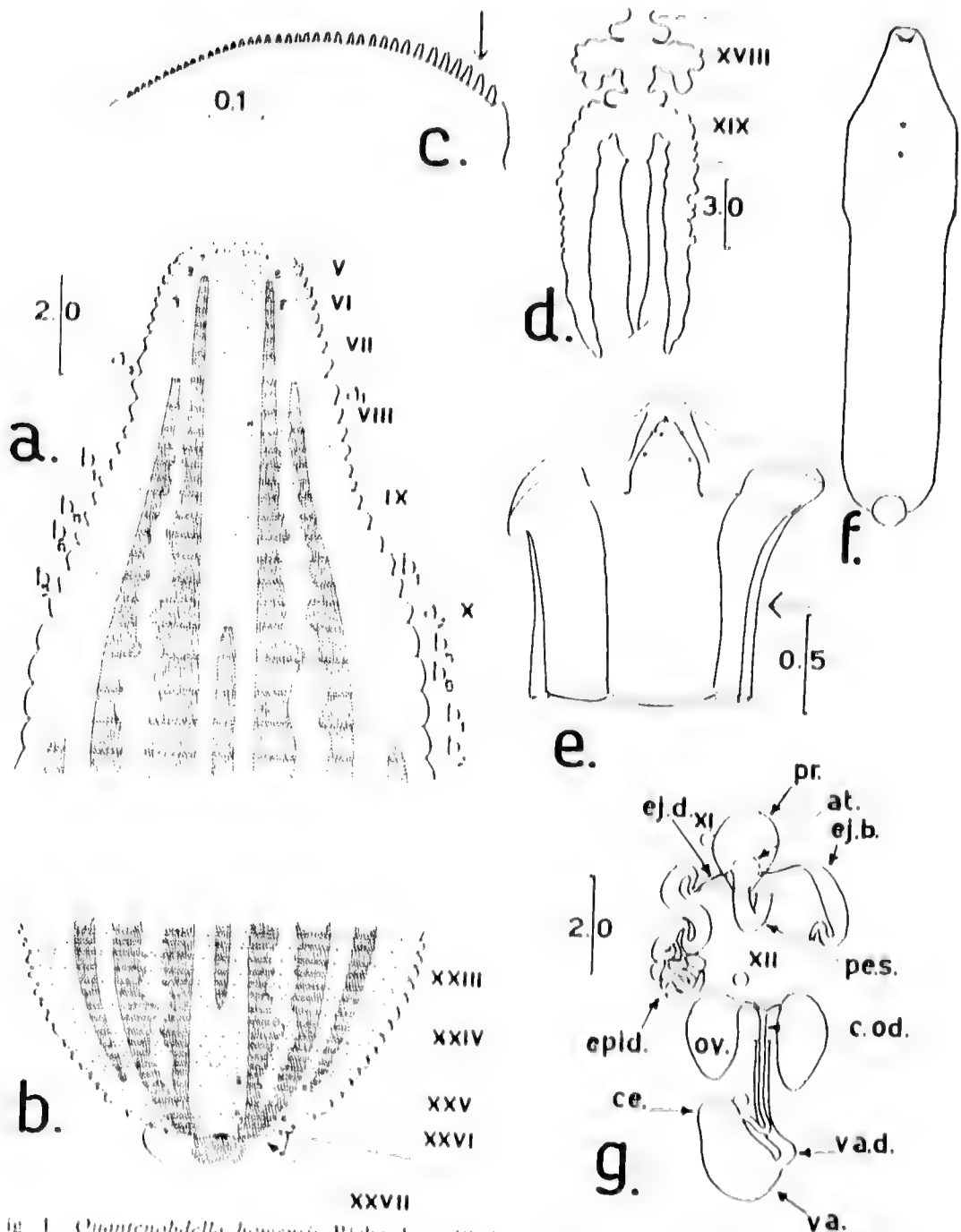
Fig. 1. *Quantenobdella howensis* Richardson 1969. a. Dorsal aspect, somites i to x, and b. somites xxiii to xxvii and sucker, to show annulation and pattern. c. Right ventro-lateral jaw and dental ridge (arrow marks medial end). d. crop, somites xvii and xix, caecation and intestine. e. Jaws and pharynx opened along midventral line to show internal surface (arrow marks midpoint in length of pharynx). f. Ventral view of entire animal showing the small posterior sucker. g. Anterior region male paired ducts (medial aspect, the dorsal aspect is lateral in the figure), male median region, and female reproductive system.

Somites and somital ganglia indicated by Roman figures; annuli, 'a', etc.; somital ganglia shown at relative size. Abbreviations: at., atrium; c.od., common oviduct; ce., vaginal caecum; ej.b., ejaculatory bulb; ej.d., ejaculatory duct; epid., epididymis; ov., ovary; pe.s., penis sheath; pr., prostate; va., vagina; va.d., vaginal duct.

All scales in millimetres. All drawings from the holotype.

narrow, wider inner and narrower outer dark bands. The margins light and continuous with the immaculate venter.

The anterior end obtusely rounded, narrow, the preclitellar region widening rapidly to the clitellum, slightly narrower behind this along the postclitellar region with parallel sides to the postnephric region which narrows abruptly to the base of the unusually small cupped sucker with the diameter about ⅓rd of the maximum width of the body.

The male pore opens at the end of a low truncate cone formed by the margin of the genital aperture.

Total length, 38·0 mm; width at iv/v, 2·75 mm, at vii/viii, 4·0 mm, and the depth 2·0 mm increasing to 3·0 mm along the nephric region; width at x/xi, 8·0 mm and of this width along the clitellum and then briefly narrower to xxiv/xxv, rounding to form the base to the sucker, 2·0 mm, and the diameter of the sucker about 3·0 mm.

Colour

Preserved in alcohol: generally pale bluish grey with yellowish longitudinal stripes, the margin paler and continuous with the pale yellowish venter. Dorsum of the posterior sucker with a median dark patch, the sucker elsewhere of the colour of the venter.

The specimen has been long preserved. There is no indication of brownish or greenish tones, and the colour in life may possibly be blackish above, the light stripes, margins and venter all yellow.

Pattern Fig. 1 a-b

Preserved, faded. There is no indication of an ocular band, the ocular arch and margin of the velum are continuous with the margins. The somital sense organs are rarely detectable, nowhere as a series, and the topography of the pattern can only be estimated as:

(1) A light stripe occupying the median field and the paramedian line of sense organs (confirmed in viii) continues from the edge of the velum to the posterior border of xxvii. In this stripe there are faint indications of an interrupted narrow median dark band of the

width or narrower than the light stripes on either side between x and xv, and almost continuous from xv to xxiv.

These represent a dark median band and an inner pair of light stripes.

(2) An inner pair of dark bands fill the paramedian fields, extend from v/vi back to xxvii, being much clouded with paler colour along the middle of the band and to such a degree that this band appears along most of its length as composed of an inner and an outer band with erratic opposing margins; but this is a single band as shown by the fusion posteriorly in xxvii.

These correspond to paired bands of the paramedian fields, and as usual increase in width along the body as the fields widen.

(3) An outer pair of narrow light stripes of uniform width, generally a little wider than the inner pair, extend along the line of the intermediate sense organs and briefly into the fields on either side from about the middle of xi to xxiv or xxv.

(4) An outer pair of narrow dark bands define the outer pair of light stripes between the above levels and are generally of the width of the adjacent light stripe. It is possible that these bands include the supramarginal sense organs and extend briefly into the supramarginal field, but this could not be confirmed.

(5) The marginal stripe, wider than the other dorsal stripes, extends across the supramarginal field and is continuous on to the submarginal field.

Annulation Fig. 1 a-b

Interannular and intersomital furrows well-defined, equivalent, and the somital limits not directly recognizable along most of the body. Somital sense organs, small, rarely detectable; no obvious sensillae. Nephropores generally large, open, obvious.

The velum contracted, the margin thick, low convex, obtusely rounded, carrying the 1st and 2nd pairs of eyes in ii and iii; the first furrow iv a_1 a_2/a_3, so that a_1 a_2 with the 3rd pair of eyes is not defined anteriorly and is continuous with the velum and a_1 a_2/a_3 extends across the

median and paramedian fields, not to the margin of the sucker and there is no well-formed dorsolateral lobe; v, 2-annulate above, the 4th eyes in $a_1 \, a_2 < a_3$, $a_1 \, a_2/a_3$ reaches to the marginal line, and below this uniannulate v forms the lateral and ventral margin of the sucker; vi, 3-annulate above, $a_1 < a_2 < a_3$, the 5th eyes in a_2, and vi 2-annulate below with $a_1 \, a_2 > a_3$; vii, 3-annulate above and below, $a_1 < a_2 < a_3$; vii a_3 and viii a_1, subequal; viii, 4-annulate, $a_1 > a_2 > b_5 = b_6$, 1st nephropores on a_1; ix to xxiv, 5-annulate (total 16); ix, $b_1 = b_2 < a_2 > b_5 > b_6$; x, $b_1 = b_2 < a_2 < b_5 < b_6$, with b_5 the 1st annulus of the clitellum; xi, $b_1 = b_2 = a_2 < b_5 > b_6$; xii, $b_1 = b_2 < a_2 > b_5 > b_6$; xiii to xxii, the relative lengths of the annuli cannot always be determined with confidence on the dorsum, but these appear to be $b_1 = b_2 < a_2 = b_5 = b_6$ in the midnephric group; xxiii and xxiv, $b_1 = b_2 > a_2$ slightly $> b_5 = b_6$, the last nephropore on xxiv b_2; xxv, 4-annulate, $b_1 = b_2 = a_2 < a_3$, and xxv a_3 reduced but complete across the venter; xxvi, 2-annulate, somital organs posterior in $a_1 \, a_2 > a_3$; xxvi/xxvii, incomplete across the median field; xxvii, uniannulate; the anus at the posterior border of xxvii: dorsum of the posterior sucker showing three concentric furrows, and one pair of paramedians.

Alimentary tract Fig. 1 c-e

Jaws small, compressed, the dorsomedian as high ($0 \cdot 35$ mm) as wide at the base, narrowing to be subacute at the dental margin, housed in open recesses or grooves with such poorly defined margins as to be non-morphological; the dental margin very low convex, almost straight, $0 \cdot 60$ mm long; 39 teeth, strong, a gradually diminishing row, the teeth at the medial end, 20 microns high.

Salivary gland papillae present as a row of spaced small papillae parallel to the dental margin, and a few papillae scattered over the surfaces of the jaws.

The mouth and lumen of the pharynx slightly wider than usual, the mouth being distinctly wider than the base of the dorsomedian jaw; the lumen not obviously tapering; the wall of the pharynx, thin, smooth internally with no indications of grooves dividing off muscular ridges (refer to the other material). Salivary glands diffuse, simple glands, ducts of the dorsal group aggregated into poorly defined columns of ducts. Radial muscles, an obvious sparse system.

The crop is swollen with consolidated blood. It is fragile and hinders dissection in the postclitellar region.

The pharynx, short, terminating in the anterior annuli of ix at b_2/a_2 with a short acaecate compartment as the first portion of the crop in ix; x, a short compartment with a pair of minute caeca in the median position; xi to xiii, the compartments reduced by the heavily developed glandular layer of the clitellum, and almost tubular; xiv, a well formed compartment with obvious small paired caeca in the anterior position and larger paired caeca in the median position which extend into the paramedian chamber, as also in xv to xviii with the median caeca extending posteriorly to be lateral to the anterior caeca of the following somite; xix, with small anterior caeca and the caeca at the median level extending as postcaeca at least to xxv/xxvi; the compartment in xix is broad behind the origin of the postcaeca, connects terminally to the intestine which is tubular, inflated. The dissection was not continued to the rectum.

Reproductive system Fig. 1g

The indications are that the specimen is fully female mature with enlarged thin-walled ovaries, the vagina mucus-filled and swollen, and a heavy development of clitellar glands.

The genital pores are at xi b_5/b_6 and xii b_5/b_6. The male aperture terminal on a wide-based low fleshy truncate papilla.

The organs on the anterior region of the male paired duct are in a linear relationship; the median regions, bimyomeric, mesomorphic, the female median region with a caecate vagina and vaginal duct.

The 1st testes are at xiii/xiv (dissection was not taken beyond this owing to the fragility of the crop). The vasa deferentia could not be examined anteriorly owing to the development of the clitellar glands. The convoluted folded epididymis consists of a narrow posterior

portion and a more broadly tubular anterior portion in the paramedian chamber in the anterior half of xii; the anterior portion of the epididymis tapering into the muscular ejaculatory bulb which is elongate cylindroid and the left partly folded on itself; ejaculatory bulbs taper into delicate ejaculatory ducts which pass into the median chamber and join independently into the ventral aspect of the muscular atrium which is continuous with the muscular penis sheath formed on a posteriorly directed primary loop reflecting at xi/xii so that the penis sheath is short, sturdy, relatively wide, and the initial recurrent limb dorsal to the terminal procurrent limb.

The enlarged ovaries are in the contiguous halves of xii and xiii; a short oviduct passes from the medial aspect of the anterior end of each ovary, the two joining together but without an indication of an atrium distinct from the common oviduct. The female median region formed on a posteriorly directed primary loop reflecting at xiii/xiv; common oviduct occupying nearly the entire length of the recurrent limb, is unusually wide, of uniform width and appearance along its length, and extends along and is intimately associated with the dorsal aspect of the vaginal duct, departing this posterior to the level of junction of the common oviduct with the vagina, and then briefly anteriorly to enter the vagina subterminally; the vaginal caecum, broad, shorter than wide; the vagina thin-walled, swollen, fusiform, terminating abruptly in the vaginal duct which is strongly muscular, continues directly to the genital pore without folds or convolutions, and occupies the procurrent loop.

The indications are that the vagina forms across the elbow of the primary loop, the common oviduct and vaginal duct occupying almost the entire length of the recurrent and procurrent limbs of the loop.

Other material

One specimen, Australian Museum, Sydney, G 11217, Lord Howe Island. Collector, Saunders, 1908.

Total length, 25·0 mm. Clitellum not evident, otherwise depressed and form as in the type with the margins parallel from xii to xxiv;

posterior sucker distinctly small, the diameter 2·5 mm and less than half the maximum width (6·0 mm) of the body.

Preserved, completely decolourized without any indication of eyes or pattern. Somital sense organs, not detectable; nephropores, minute.

General annulation as in type on the prenephric and postnephric somites; annulation of the midnephric somites, $b_1 = b_2$ slightly $< a_2 = b_5$ slightly $> b_6$ but while with the differences can be determined by measurement, they are so small that a_2 is not recognizable with confidence by length alone, i.e. the annuli are essentially equivalent in length; xxvi/xxvii, incomplete across the median field.

Alimentary tract: Jaws, as in the type; papillae, very minute; internal surface of the pharynx with distinct dorsolateral grooves defining a dorsomedian ridge and the dorsal margins of the ventrolateral ridges, but these ridges are not further subdvided. The crop unsuitable for further detail.

Reproductive system, approaching male maturity. Regional and general morphology as in the type. Ejaculatory bulbs distinctly elongate cylindroid, each closely folded lengthwise into subequal limbs; male median region cylindrical, sturdy, reflected as a short loop in the contiguous halves of xi and xii. Oviducts, very short; no obvious atrial chamber and the atrium smoothly continuous with the wide oviduct; vagina, transverse, the caecum narrower than the body of the vagina, small and the length about twice the width; vaginal duct, heavily muscular, straight.

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THE AUSTRALIAN EARTHWORM GENUS *SPENCERIELLA* AND DESCRIPTION OF TWO NEW GENERA (Megascolecidae: Oligochaeta)

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Abstract

A neotype is designated for a rediscovered specimen of *Diporochaeta notabilis*, the only known material of the type-species of *Spenceriella* Michaelsen. The genus appears to belong to a *Dichogaster-Megascolides* group of genera, though poor preservation precludes certain demonstration of the stomate median meronephridia diagnostic of the group. Specimens from Lord Howe Island are shown to merit recognition of a new genus and species, *Paraplutellus insularis*, closely allied to *Heteroporodrilus* Jamieson and *Plutellus* Perrier on the Australian mainland. The new genus *Simsia* is established to receive six Victorian species assignable in former classifications to *Plutellus*, including the new species *Simsia longwarriensis*. The type-species *S. tuberculata* (Fletcher) is shown to be a senior synonym of *Megascolides roseus* Spencer. *Paraplutellus* and *Simsia* are members of a *Perionyx* group of genera.

Introduction

The author is currently studying the Baldwin Spencer earthworm collection through the kind co-operation of Dr B. J. Smith and the authorities of the National Museum of Victoria. Attention has initially been directed to resolving the heterogeneous and clearly polyphyletic assemblages *Plutellus* and *Diporochaeta* into distinct and individually more homogeneous groupings. This paper is confined to consideration of four species which in previous classifications would have been assignable to *Plutellus* or *Diporochaeta* but which represent three distinct genera of which two are new to science.

Diporochaeta notabilis Spencer, 1900, was made the type-species of a new genus *Spenceriella* by Michaelsen (1907). With *D. notabilis* were included the two Victorian species, *D. maplestoni* Spencer, 1900, and tentatively *Perichaeta lateralis* Spencer, 1892b, and also the two New Zealand species *Diporochaeta gigantea* Benham, 1906, and *D. shakespeari* Benham, 1906. *S. shakespeari* was shown by Lee (1962) to be a junior synonym of *S.* (formerly *Megascolex*) *antarctica* (Baird, 1871). Lee (1959) added two further species from New Zealand, *S. argillae* and *S. pallida*, bringing the generic total to seven species.

Michaelsen erected *Spenceriella* for species with more than eight setae per segment, one to three pairs of spermathecal pores, a gizzard in segment V, meronephridia, and tubular prostate glands with unbranched lumen. This superficial definition (which ignored morphological heterogeneity in other respects) and the disjunct geographical distribution, has resulted in a polyphyletic genus. Revision of the genus and elucidation of the affinities of the included species necessitates examination of the type-species. Jensz and Smith (1969) stated that the type specimens had presumably been lost and no other specimens of the species were known. The author has examined an unidentified perichaetine specimen from the type locality, Dimboola, Victoria, and finds it to be unequivocally identifiable as *Spenceriella* (= *Diporochaeta*) *notabilis*. As it is not possible to prove indisputably that it is part of the lost type series, and because of its significance for revision of the genus and for nomenclatural stability, it is here designated a neotype. This specimen is described below, and its significance discussed.

It has been shown (Jamieson 1970, 1971b) that the large circummundane genus *Plutellus* must be restricted to only two of the known species, *Plutellus heteroporus* Perrier, 1873, and *Plutellus manifestus* (Fletcher, 1889). Resolution of the remaining congeries has been commenced (Jamieson 1971a) by resurrection of *Fletcherodrilus* Michaelsen, 1891. In the present study a group of Victorian species which were formerly ascribable to *Plutellus* will be

shown to warrant recognition as a distinct new genus.

A previously unidentified species from Lord Howe Island, assignable to *Plutellus* sensu Stephenson 1930, will be shown to represent a new monotypic genus allied to *Heteroporodrilus* Jamieson, 1970, and to *Plutellus* s. str.

Systematics

Genus Spenceriella Michaelsen, 1907
Spenceriella notabilis (Spencer, 1900)
Fig. 1 D-H.
Diporochaeta notabilis Spencer, 1900: 57-58, Pl. 10, figs. 76-78.
Spenceriella notabilis; Michaelsen, 1907: 161.

l = 36 mm, w (midclitellar) = 3 mm, s = 116. Form fairly stout, circular in transverse section throughout, lacking secondary annulation. Prostomium epilobous 3/4 open and almost parallel-sided, the lateral margins perhaps continuous as faint grooves to intersegment 1/2, i.e. possibly tanylobous. First dorsal pore 4/5 (?), as noted by Spencer. Setae perichaetine commencing in II, the setal rings interrupted dorsally and ventrally in the midline except posteriorly where *b* lines become irregular. Numbers of setae in XII: 11 (left), 11 (right); in XXV: 11 (left), 10 (right); at the posterior end 12 (left), 10 (right). Nephropores not externally visible. Clitellum poorly developed, annular, on XIV-XVI but intersegments 13/14 and 16/17, like those between, are faint, suggesting that when fully developed the clitellum would occupy at least part of XIII and XVII; dorsal pores, intersegmental furrows and setae retained. Male pores represented by a pair of indistinct papillae on XVIII approximately in *a* lines. Accessory genital markings a pair of elliptical dark glandular areas in X, XIX, XX immediately lateral of *a* lines, those in X and XX with depressed elliptical centres with narrow pale rims, possibly also represented on XVIII in *b* line on the right side. Female pores minute orifices median and slightly anterior of setae *a* of XIV in a common elliptical slightly tumid field. Spermathecal pores represented by a single pair of elliptical intersegmental markings in 7/8, about as wide as *ab* in which their centres lie very slightly median of *b*.

Septal thickening: 5/6 and 6/7 slight, 7/8 and 8/9 moderate, 9/10—12/13 fairly strong, 13/14 and 14/15 slight, the remainder thin. Last pharyngeal glands in V, overlying the gizzard. Dorsal blood vessel single, fragmented but apparently continuous onto the pharynx. Dorsoventral commissural vessels paired in VI-XII; those in X-XII forming rather narrow hearts, each of which is latero-oesophageal, arising from the dorsal vessel but also receiving a connective from a calciferous vessel where the latter joins a narrow supra-oesophageal vessel. The calciferous vessel circumscribes and receives vessels from the corresponding calciferous gland. Supra-oesophageal restricted to X-XII. A latero-oesophageal vessel on each side supplies the calciferous glands. Gizzard large, firm and barrel shaped, in V. Calciferous glands four pairs, in X-XIII, each a large anteroposteriorly depressed lobe filling the space between the hearts and the oesophagus in X-XII and communicating with the oesophagus by the narrowed ventromedian portion of the gland, which forms a short duct; each gland with approximately 24 radial septa most of which unite centrally. Intestine commencing, with abrupt expansion and a narrow oesophageal valve, in XV. Typhlosole and muscular thickening absent.

Nephridia: meronephridia, not sufficiently well preserved to allow confirmation of Spencer's observation of pharyngeal nephridia. At the posterior end of the body preservation is generally inadequate for determination of nephridial morphology beyond recognition of several rows of meronephridia on each side but in one segment the nephridium nearest the nerve cord was observed to have a preseptal funnel. Testes and funnels not visible but holandry indicated by the presence of racemose seminal vesicles in IX and XII. Prostates racemose, bipartite with a small anterior and larger posterior lobe and short muscular duct; surface slightly lobulated; the exact form uncertain owing to partial fragmentation; no central lumen detectable in transverse serial sections. Ovaries (elongate wisps consisting of several chains of oocytes) and funnels in XIII. Spermathecae a single pair, in VIII; each with a sac-like ampulla approximately four times as long as wide, which is joined ectally, without the intervention of a

separate duct, by a lateral digitiform diverticulum which is longer than the ampulla. Length of right spermatheca = 0·98 mm; ratio of total length: length of diverticulum = 0·7.

Material examined: A single imperfectly clitellate specimen labelled only 'Dimboola, Victoria, Oct. 1892', Nat. Mus. Vict. G353, here designated a neotype.

Remarks: The above account considerably augments and closely accords with that of Spencer (1900). The only noteworthy departures of the newly examined material from Spencer's description are the racemose as opposed to tubular prostates and the intestinal origin in XV and not in XVI.

There is no evidence that Michaelsen examined specimens of *Diporochaeta notabilis* and his characterisation of the genus by tubular prostates presumably derived from Spencer's description of these glands as 'coiled, tubular'. Their lobular ('racemose') nature has been demonstrated above. Branching of the prostatic lumen renders *Spenceriella* indistinguishable from *Megascolex* as defined by Michaelsen (1907) but there is no reason to consider that *S. notabilis* is in fact congeneric with the type-species of *Megascolex, M. caeruleus* Templeton, 1844, from Ceylon. *Spenceriella* is therefore retained. It is questionable, however, whether other species assigned to the genus are congeneric with the type species.

Simsia* gen. nov.

Prostomium variable, epilobous to tanylobous. First dorsal pore in or behind 4/5. Setae eight per segment, commencing on segment II, the rows sometimes becoming irregular posteriorly, ventral setal couples (*ab*) wide (the median ventral interval *aa* < 3 *ab*), dorsal setal couples (*cd*) wider than *ab* but much narrower than the distance (*bc*) between the two setal couples, dorsal median intersetal distance (*dd*) 0·3 — 0·5 of the circumference (*u*). Nephropores inconspicuous, or unrecognizable, in approximately straight series on each side in the vicinity of *c* lines but those of the tufted nephridia typically further dorsally. Clitellum

* The genus is named after my friend and colleague, R. W. Sims, Curator of annelids, British Museum (Natural History).

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annular, not extending behind the male pores. A pair of combined male and prostatic pores on XVIII; the prostates thickly tubular, sometimes with lobulated surface; prostate duct muscular, lacking distinct ectal dilatation. Penial setae present or absent. Accessory genital markings present. Spermathecal pores two ventral pairs, segmental or at the anterior border of their segments, the posterior pair on IX.

Some preclitellar septa thickened. Gizzard well developed, in V. Oesophagus strongly dilated in XV and XVI to form two unpaired annular (calciferous?) glands, sometimes with lesser dilatation in XVII, intestine commencing in XVIII, XIX or XX; muscular thickening absent, lamelliform dorsal typhlosole present. Supra-oesophageal vessel present. Dorsal vessel single. Dorsoventral commissural vessels extending from the gizzard, or anterior to this, to XII; those in X-XII forming latero-oesophageal hearts, receiving connectives from the supra-oesophageal and the dorsal vessel. Nephridia stomate, avesiculate holonephridia with the exception that those in a few anterior segments are tufted, meronephric (always?) and typically, at least, have composite ducts; the tufts sometimes preceded by one or two pairs of small holonephridia. Testes and funnels free in X and XI; seminal vesicles in IX and XII; or the first pair of testes, funnels and seminal vesicles reduced or absent. Ovaries and funnels in XIII. Ovisacs in XIV (not known in *eucalypti*). Spermathecae with saccular ampullae at the ectal limit of which is a sessile internally multiloculate subspherical diverticulum (In *S. narrensis* possibly shortly clavate and not known to be multiloculate); the duct long and coiled, or concealed in the body wall.

DIAGNOSIS: Nephridia stomate avesiculate holonephridia except in a few anterior segments which have tufted nephridia with (always?) composite ducts. Nephropores of holonephridia in a single series on each side. Unpaired annular (calciferous?) dilatations of the oesophagus in XV and XVI, XVII. Dorsal intestinal typhlosole present. Spermathecae two pairs, each with a small sessile internally multiloculate diverticulum.

DISTRIBUTION: Eastern Subregion, Koscius-

kan Division, S. Southern Faunal Province of Kikkawa and Pearse (1969), in the vicinity of Warragul, Victoria, between lat. 145° and 146° S., long. 38° and 39° W.

TYPE SPECIES: *Notoscolex tuberculatus* Fletcher, 1888a. (syn. *Megascolides roseus* Spencer, 1892a)

OTHER SPECIES:

Megascolides eucalypti Spencer, 1900
Cryptodrilus intermedius Spencer, 1892
Simsia longwarriensis n. sp.
Megascolides manni Spencer, 1892
Cryptodrilus narrensis Spencer, 1892

The diagnosis indicates the striking morphological homogeneity of the species here included in *Simsia*. The phenetic unity of the group is unquestionable and, notwithstanding the acceptability of polythetic groups, future inclusion in the genus of species departing in one or more characters from the diagnosis would probably require recognition of separate subgenera if it were indeed justifiable.

Simsia differs from *Plutellus* s. str. in numerous respects, including the absence of stalked calciferous glands, of a complex alternation of nephropores, of nephridial bladders and in the presence of tufted (and apparently meronephric) nephridia and of a typhlosole. From the N. American species of *Plutellus* (other than the supposedly Pennsylvannian *P. heteroporus*) *Simsia* differs in the location of the oesophageal dilatations, presence of tufted nephridia and the more regular arrangement of nephropores. The N. American species will have to assume the oldest available generic name, *Argilophilus* Eisen, after restriction of *Plutellus* to *P. heteroporus* (the type species) and *P. manifestus*.

The frequent alternation or irregularity of nephropores in *Argilophilus*, especially the regular alternation in *b* and *d* beginning with segment IX in *Plutellus davisi* MacNab and McKey-Fender, 1953, suggests affinity of *Argilophilus* with the *Plutellus* s. str.—*Heteroporodrilus*—*Paraplutellus* group of genera despite the presence of nephridial bladders in the latter group. On the other hand the general anatomy of *Argilophilus* is sufficiently close to indicate an affinity with *Simsia* closer than that with

other megascolecoid genera despite separation of the two groups by the Pacific. The diversity of plutelloid genera in Australia, considered with the Pacific seaboard focus of endemicity of *Argilophilus*, perhaps suggests invasion of America from Australia or its vicinity. If this were by a Gondwanaland connection, the failure of *Argilophilus* to subsequently spread more widely in America is remarkable. The alternative of recent invasion across the Pacific (for instance by rafting or transportation) may be rejected in view of the diversity of species and evidence of subspeciation in America (MacNab and McKey-Fender 1960).

Simsia tuberculata (Fletcher, 1888)

Figs. 2 A-C, 3 A-B, E, H-I, L-N

Notoscolex tuberculatus Fletcher, 1888, pp. 611-614.
Megascolides tuberculatus; Spencer, 1892a: 156; Beddard 1895, p. 494.
Plutellus tuberculatus; Michaelsen, 1900, p. 168.
Megascolides roseus Spencer, 1892a, pp. 153-154, Pl. 18, figs. 58-60, Pl. 19, fig. 81, Beddard 1895, p. 491, Sweet 1900, p. 112.

$1 = 140$ mm ($160 +$ mm in the posterior amputee of *M. roseus*), w (segment XVIII *tuberculatus*, or midclitellar, *roseus*) $= 7$ mm, s $= 165$ (*tuberculatus*), 88 (*roseus*). Circular in cross section throughout, posterior end clubbed, secondary annulation very distinct commencing in IV. Pigmentless buff in alcohol with the exception of the clitellum which is pigmented pale reddish brown. Prostomium epilobous 1/2, or (*roseus*) pro-epilobous, but connected with intersegment 1/2 by two longitudinal grooves which would confer a tanylobous condition on the prostomium were other longitudinal grooves not present on the peristomium. First dorsal pore 12/13. Setae indistinct, in eight regular longitudinal rows throughout, beginning on II; the ventral couples absent in XVIII.

Nephropores not externally visible (*tuberculatus*) or (*roseus*) visible in a single series on each side, in *cd* nearer *c*, near the anterior borders of their segments, from IV posteriorly. Clitellum not developed in *tuberculatus*; in *roseus* annular, strongly protuberant, embracing the posterior 1/3 XIII to the anterior 1/3 XVIII but interrupted ventrally by the genital markings in XVII and XVIII; intersegmental

TABLE 1

INTERSETAL DISTANCES IN SEGMENT XII
IN *Simsia tuberculata*

	aa *		ab		bc		cd		dd		dd:u
	mm	st	mm	st	mm	st	mm	st	mm	st	
N. tuberculatus	2·21	13·64	0·61	3·79	2·33	14·39	0·88	5·41	6·35	39·18	
intervals/ab		3·60		1·00		3·80		1·43		10·34	0·39
M. roseus	2·29	12·12	0·71	3·79	2·43	12·88	0·89	4·73	8·50	45·08	
intervals/ab		3·20		1·00		3·40		1·25		11·90	0·45

* Standardized to a periphery of 100.

furrows indicated, though weakly; setae and nephropores retained; dorsal pores absent. Male genital field: male pores a pair in XVIII, minute points in *ab* (*tuberculatus*) or one in *b* and the other lateral of *b* (*roseus*), each on a small, low papilla; accessory genital markings consisting of a large median boss in XVIII between the male pores and paired markings with peripheral rim and raised central area the centre of which usually displays a pore or slit, located presetally in XVII and XX, XXI and XXII (*tuberculatus*) or XVII and XX only (*roseus*; observed in XVII, XX-XXIII by Spencer); the markings in XVII and XX in *ab*, those in XXI centred on *a* lines and those in XXII with their centres slightly median of *a* lines; the two presetal markings on each segment impinging slightly on the preceding segment and connected by a transverse glandular band. Female pores a pair in XIV, immediately in front of the setal arc and separated by about 1/3 *aa*, both in a common glandular field. Spermathecal pores two pairs, located segmentally, in VIII and IX immediately in front of the setal arc shortly lateral of *a* lines; each on a small elliptical papilla.

Septa: 3/4-5/6 very thin, 5/6 being displaced posteriorly by the gizzard; 6/7 slightly (*tuberculatus*) to moderately strongly thickened (*roseus*), 7/8-12/13 strongly thickened, 9/10 being the thickest; 13/14-14/15 (*roseus*), 15/16 (*tuberculatus*) slightly thickened; the remainder thin. Last septal (pharyngeal) glands anterior in IV. Dorsal blood vessel single, continuous onto the pharynx, dorsoventral commissurals in (IV?) V-XII; those in X-XII forming three pairs of large latero-oesophageal

hearts, each receiving a connective from the dorsal vessel and from a supra-oesophageal vessel. Supra-oesophageal present in VIII (?) (*tuberculatus*)—or IX (*roseus*)—XIII, seen in *tuberculatus* to be double in XI-XIII, and to receive in each of XII and XIII two pairs of large vessels running circumferentially on the oesophagus which is here vascularized though not widened. In XIV one pair of thick vessels from the vascular and dilated oesophagus joins the dorsal vessel and an indistinct anterior pair of oesophageal vessels probably feeds the supra-oesophageal vessels which abut on septum 13/14 (*tuberculatus*). Subneural vessel absent (both specimens). Large posteriorly running latero-parietals originating below the oesophagus in XIII (*roseus*).

Pharynx abutting posteriorly on septum 3/4; a croplike muscular but compressible proventriculus in IV; gizzard large, firmly muscular, elongate-globose in V (septum 5/6 so attenuated over the gizzard as to be almost unrecognizable). Oesophagus narrow to XIV, greatly dilated and strongly vascularized in XV and XVI to form two unpaired annular calciferous (?) glands each of which gives two pairs of vessels to the dorsal blood vessel, the dilatations thin walled, with internally low longitudinal vascular folds surrounding the capacious oesophageal lumen; the glands not constricted off or separated from the oesophagus. Oesophagus wide and vascularized throughout XVII, though narrower than in XVI, the intestine commencing in XVIII (both specimens). Intestine lacking muscular thickening but with a thickly laminar dorsal typhlosole commencing in segment XXIX-XXX.
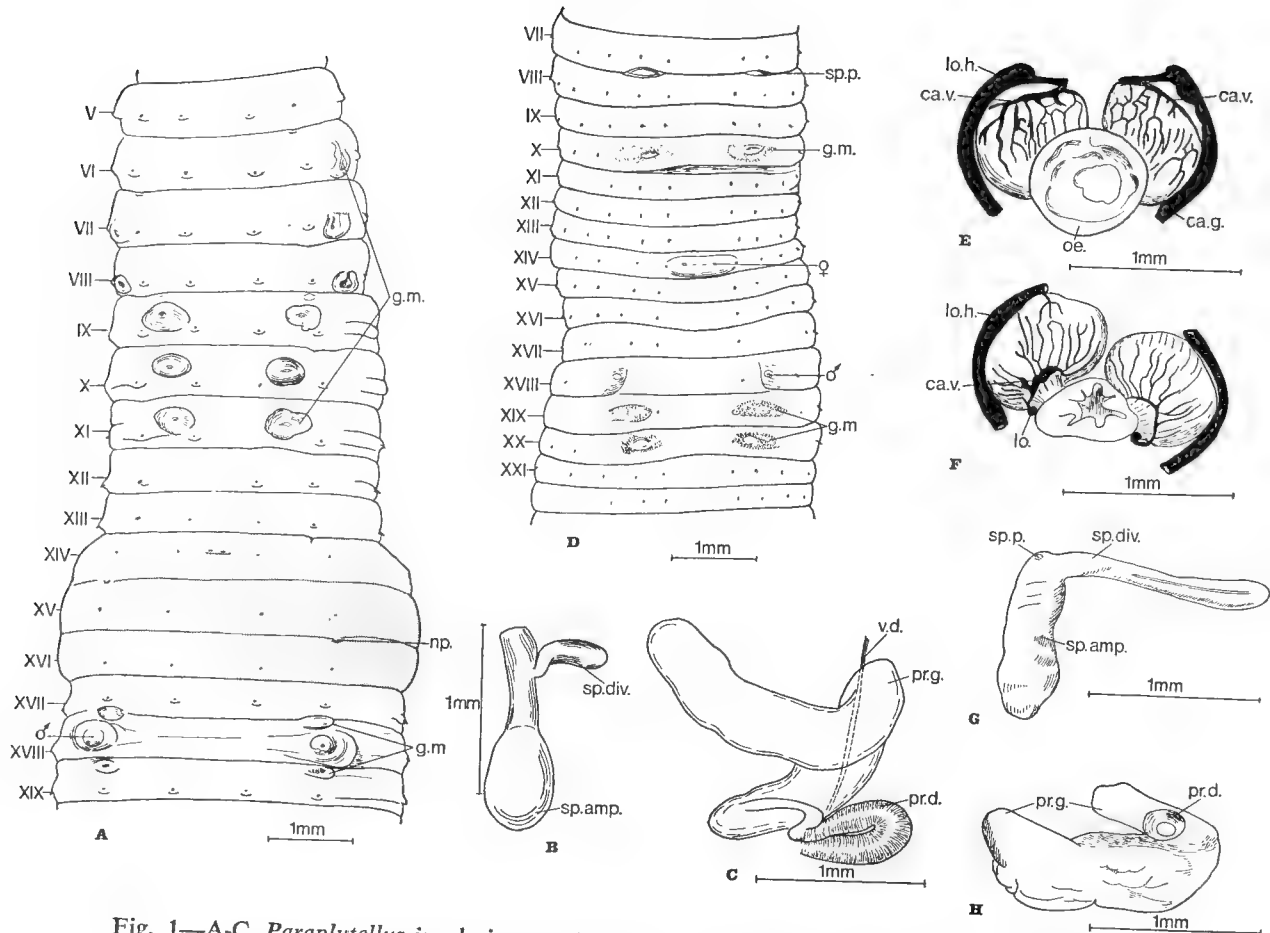
Fig. 1—A-C, *Paraplutellus insularis* gen. et sp. nov. Holotype G416. A, ventral view of genital fields. B, right spermatheca of segment IX. C, right prostate gland. D-H, *Spenceriella notabilis* neotype G353. D, ventral view of genital fields. E-F, anterior and posterior aspects respectively of the calciferous glands of X. G, right spermatheca of VIII. H, ventral aspect of right prostate; part of the anterior lobe has detached. All by camera lucida. Clitellum shaded.

Nephridia not observable in II, in III nephridia small exonephric holonephridia, those in IV, V and VI paired (stomate?) exonephric tufted nephridia with composite ducts and approximately six loops in IV, 20 loops in V and 40 loops in VI, those in VII much coiled but each with a simple duct. The ducts of the nephridia of IV discharge anteriorly in III while those of the nephridia of V and VI discharge anteriorly in their respective segments. Nephridia in VIII and succeeding segments stomate, exonephric, avesiculate holonophridia; all pre-intestinal nephridia considerably coiled; intestinal nephridia not coiled; those of the last 20 segments (approximately) thicker than the

preceding nephridia, and with larger funnels, but with no other variation from the usual form (*tuberculatus*) (Horan pers. comm.). Nephridia in *roseus* similar (personal observations).

Small testes and large, convoluted iridescent sperm funnels free in X and XI; racemose seminal vesicles in IX and XII. Prostates much coiled, the coils with flattened faces and closely adpressed; limited to segment XVIII which they expand longitudinally or in *roseus* extending into XIX; the relatively short duct slender and twisted; the two vasa deferentia of a side completely separate, joining the glandular portion of the corresponding prostate shortly ental

of the duct. Penial setae slender, ectally slightly curved, the tip pointed in profile but fairly broad when viewed from above; the ectal region bearing scattered cicatricing; lengths of two setae 0·95 and 1·2 mm, width of the shafts at the ectal fourth 20 μ (*tuberculatus*). In *roseus* the penial setae are closely similar; the cicatricing of the ectal sixth consists of a series of several notches each of which corresponds with an irregular transverse serration encircling half or less of the circumference of the seta; length of a mature seta 1·05 mm, width shaft 20 μ. Bushy ovaries (with many strings of large oocytes) and delicate pleated funnels in XIII; ovisacs present on the anterior face of XIV (*roseus*).

Spermathecae each wih a large saccular ampulla and well demarcated, narrow, tortuous, muscular duct which extended approximately equals the ampulla in length, and a subspherical somewhat lobulated diverticulum sessile on the duct shortly ectal of the ampulla. Uniform in size, in IX (right side) length extended = 4·3 mm, ratio total length: length duct = 2·1, ratio total length: length diverticulum = 9·4 (*tuberculatus*).

Material examined: A mature but aclitellate undissected specimen labelled 'Megascolides tuberculatus Fletcher. Jar 5', Nat. Mus. Vict. G172, probably part of the type series which is missing from the Australian Museum; here designated a lectotype. An aclitellate undissected specimen labelled (apparently in Spencer's writing) 'Megascolides roseus', Victoria, and curatorially 'Plutellus roseus', Australian Museum Sydney W1278, probably part of the type series which Jensz and Smith (1969) were unable to locate in the National Museum of Victoria.

Simsia intermedia (Spencer, 1892)

Fig. 2E, 3F-G, K.

Cryptodrilus intermedius Spencer, 1892a, pp. 133-134, Pl. 14, figs. 4-6, Pl. 19, fig. 64.
Cryptodrilus intermedius, Beddard 1895, p. 492.
Plutellus intermedius, Michaelsen 1900, p. 170.
Megascolides intermedius, Sweet 1900, pp. 110-111.

l = 98, 220 and 105 mm, w (midclitellar) = 5, 5 and 4 mm, s = 172, 175 and 178 (G58, G86 and G1406 respectively). Form moderately slender, posteriorly clubbed, segments of the forebody at first biannulate, and subsequently triannulate to quadriannulate. Pigmentless buff in alcohol. Prostomium epilobous < 1/3 closed (G86 and G1406; indeterminable in G58). First dorsal pore 4/5 (imperforate G1406), or 5/6 (G58, G86, perforate as in G1406). Setae eight per segment, commencing on II, all rows except *a* irregular at the posterior end; *ab* absent, *cd* present, in XVIII; individual setae sporadically displaced in some anterior segments in some specimens.

Nephropores not externally visible (G58, G1406) or visible in *c* lines (G86). Clitellum not developed (G58, G1406) or well developed, annular, on the posterior 1/3 XIII to anterior 1/3 XVIII; nephropores, dorsal pores, setae and intersegmental furrows retained. Male pores minute slits on dome-shaped papillae in *ab* of XVIII, both surrounded by a median tumescent genital marking which extends from 1/4 XVII to 1/3 XX (G86) or to 2/3 XX (G58, G1406) and slightly above *b* in XVII, XVIII and XIX and barely reaching *a* or *b* in XX. Intersegmental furrows and secondary annulation continuous across the genital marking though weak when this is well developed. Female pores minute transverse slits median to and slightly anterior to setae *a* of XIV, on the anterior region of the setal annulus. Spermathecal pores on two pairs of small hemis-

TABLE 2

INTERSETAL DISTANCES IN SEGMENT XII IN

Simsia intermedia

	aa		ab		bc		cd		dd		dd:u
	mm	st	mm	st	mm	st	mm	st	mm	st	
G58	1·29	9·82	0·57	4·34	1·79	13·60	0·71	5·41	5·71	43·49	0·43
G1406	1·29	10·69	0·50	4·14	1·50	12·43	0·54	4·47	5·71	47·31	0·47
G72	1·29	9·71	0·64	4·82	1·50	11·29	0·79	5·94	6·14	46·20	0·46
G86	1·29	10·62	0·50	4·12	1·57	12·93	0·64	5·27	5·43	44·73	0·45
mean st.		10·21		4·36		12·56		5·27		45·43	0·45
mean/ab		2·34		1·00		2·88		1·21		10·42	

pheroidal papillae at the anterior borders of segments VIII and IX but displaced into intersegments 7/8 and 8/9 in *a* lines; the preceding setal annulus slightly bowed anteriorly in their vicinity (all examined specimens).

Internal anatomy (G1406, G86). Septal thickening: 5/6 extremely thin; 6/7-12/13 very strong, 6/7 and 12/13 less strong than the others; 13/14 moderate; 14/15 and 15/16 slightly thickened. Last pharyngeal glands anterior in IV. Dorsal blood vessel single. Dorsoventral commissural vessels in VI-XII; those in VI-IX originating only from the dorsal vessel; those in X-XII forming large latero-oesophageal hearts arising from the supra-oesophageal vessel and from the dorsal vessel. Supra-oesophageal vessel in VIII-XIII. Subneural vessel (?). Gizzard large, barrel shaped, strongly muscular though fairly easily compressible, in V; preceded in IV by a muscular compressible proventriculus (crop) which is gizzardlike in appearance. Oesophagus not evidently vascularized in VI and VII; from VIII-XIV moniliform and with circumferential vascular striae; in XV and XVI greatly widened and vascularized giving in each segment two pairs of large vessels to the dorsal vessel and conspicuously visible on opening the animal whereas the preceding region of the oesophagus is concealed in thick funnel shaped septa; the internal walls of these dilatations covered by innumerable large rounded villi; oesophagus in XVII similarly dilated in its anterior half but narrow in the posterior half and in XVIII. Intestine commencing in XIX with abrupt expansion; muscular thickening absent; a deep dorsal typhlosole present, commencing at approximately segment XXVI (G1406, G86).

Nephridia exonephric holonephridia throughout with the exception of those in II, III and IV which form exonephric meronephric tufts with composite ducts; those in V-VII large and coiled but with simple ducts; preseptal funnels demonstrated for nephridia of VIII posteriorly but septal connectives (necks of nephrostomes?) observed from segment II; bladders absent (G1406—Horan pers. comm.).

Moderately large iridescent sperm funnels in XI, very small non-iridescent funnels in X, racemose seminal vesicles in XII only (G1406), the anterior sperm funnels absent in G86. Prostates short tortuous tubes with adpressed coils of irregular cross section, in XVIII and XIX; each with a very short muscular duct the surface of the gland in G1406 minutely and copiously lobulated. Penial setae absent, unpaired glandular masses present medianly and partly obscuring the prostate ducts, correspond with the external genital markings. Ovaries (large, palmate, with many terminal chains of large oocytes) and funnels in XIII, ovisacs present in XIV. Spermathecae two pairs, uniform in size, discharging anteriorly in their segment; the ampulla elongate-ovoid, about four times as long as wide, almost sessile on the body wall, there being virtually no extramural spermathecal duct; a large subspherical but dorsoventrally depressed multioculate iridescent diverticulum present at the ectal end, and as wide as the ectal end of the ampulla (G1406, G86). Length of the anterior spermathecae of VIII = 2·3 mm; ratio length spermatheca: length diverticulum = 8.5 (G1406).

Material examined: From S. Warragul, Vict., coll. W. Mann, July 1891: Nat. Mus. Vict. G58 (one aclitellate specimen); G1406 (six aclitellate specimens of which one was used for the above description); July 1892, G86 (four clitellate and six aclitellate specimens plus fragments). Locality unknown, G72 (two much dissected clitellate specimens).

Remarks: G58 was designated the lectotype and G1406 paralectotypes by Jensz and Smith (1969). G58 and four of G1406 have male genital fields which agree closely with the above description, while one has a weakly developed field which is not certainly identifiable and the sixth lacks a field. Specimens of both species differ from the type description (Spencer 1892a) in being aclitellate and in being shorter than the seven inches given by Spencer. A label with G58 in Spencer's writing reads 'Young of *C. intermedius*'. Designation of G58 as lectotype and of G1406 (from the same original series) as paralectotypes is therefore invalid.

The series G86, consisting of clitellate specimens which conform in size and anatomy with Spencer's account and which are referred to in Spencer's manuscript notes as 'MSS', would
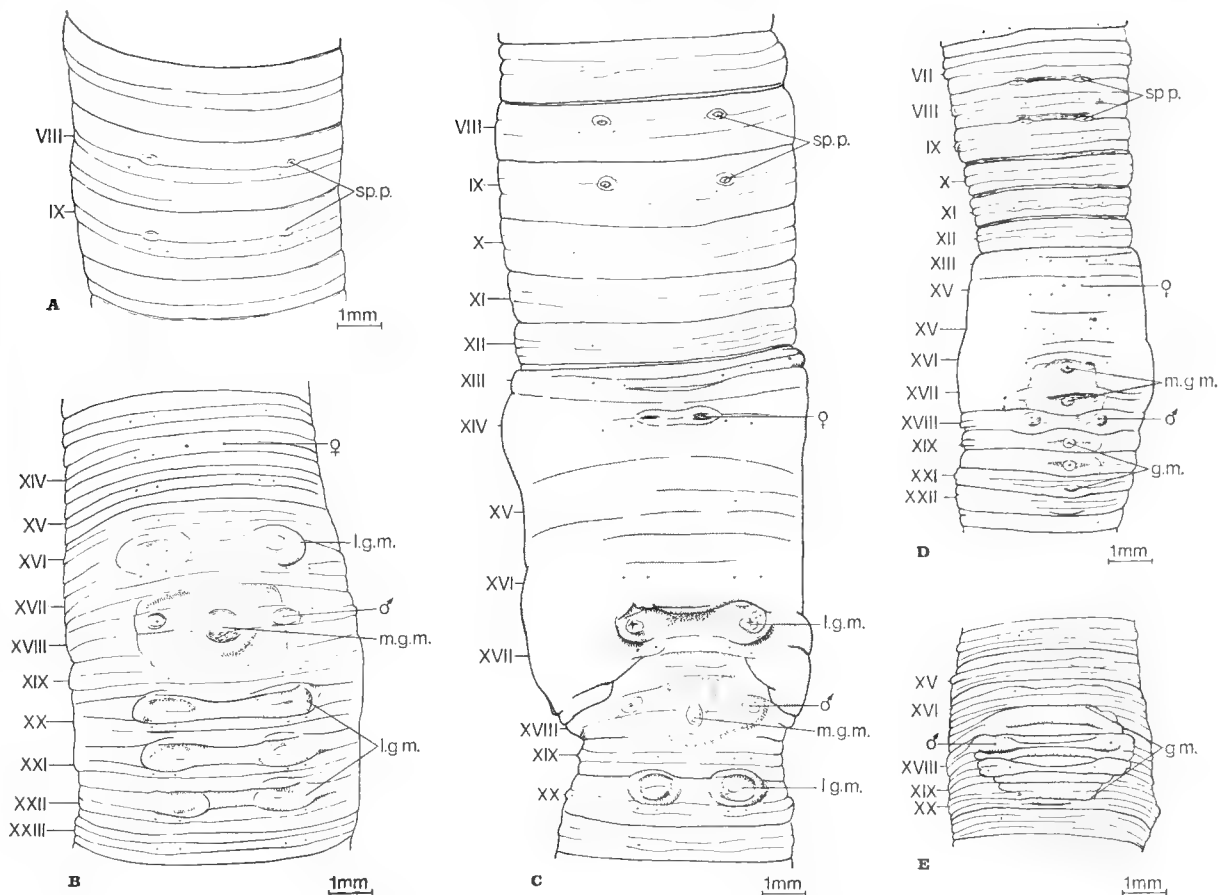
Fig. 2—A-C, *Simsia tuberculata* lectotype G172. A, spermathecal pores. B, male genital field. C, junior synonym *Megascolides roseus* W1278, ventral view of genital fields. D, *Simsia longwarriensis* n. sp. Holotype, ventral view of genital fields. E, *Simsia intermedia* paralectotype G58, male genital field.
All by camera lucida. Clitellum shaded.

appear to be the type series. The series cannot at present be considered lectotypic, however, as a museum label gives the data 'South Warragul, July 1892', post-dating the type description. It is nevertheless probable that the date is an error of transcription for July 1891.

A specimen of G72 has been examined externally and agrees closely with the above description. Only its intersetal ratios have, however, been included therein. This material would not appear to be part of the type series as it includes a label in Spencer's hand which reads 'C. intermedius (?) two different forms? . . . .', the remainder being only partly legible. There are two further specimens of *C. intermedius* in the Australian Museum (W1284) which have

not been seen by the author. These were identified by Spencer and are possibly part of the type series, although not so designated.

Simsia longwarriensis n. sp.

Fig. 2D, 3C-D, J.

1 = 62 mm, w (midclitellar) = 4.6 mm, s = 129. Pigmentless, buff in alcohol. Form moderately stout, circular in cross section throughout, the posterior end clubbed. Prostomium very wide, parallel-sided, tanylobous; not canaliculate; the peristomium short. First dorsal pore 11/12. Setae in eight regular longitudinal lines throughout, commencing on II; setae *ab* absent, *bc* present in XVIII.

TABLE 3

INTERSETAL DISTANCES IN SEGMENT XII
IN *Simsia longwarriensis* (holotype)

	aa		ab		bc		cd		dd		dd:u
	mm	st	mm	st	mm	st	mm	st	mm	st	
	0·88	8·19	0·50	4·59	1·53	14·26	0·95	8·85	3·9	36·39	
intervals/ab		1·79		1·00		3·10		1·92		7·93	0·36

Nephropores not externally visible. Clitellum annular, moderately protuberant; embracing XIII—XVII and dorsally 1/3 XVIII, paler (and weaker?) ventrally between setae *b* of XVI and XVII. Male genital field, a pair of small male porophores in *b* lines and equatorial in XVIII; median genital markings consisting of single, median circular papillae each with a central pore, equatorial in each of segments XVI, XVII, XIX-XXI, and a slight corresponding tumescence in XXII. A suggestion of paired markings in XVI and XVII behind setae *a*. Female pores minute, anteromedian to setae *a* of XIV (seen on right only). Spermathecal pores 2 pairs of conspicuous ellipses in *a* lines, in 7/8 and 8/9.

Septa: 3/4-7/8 thin; 8/9 moderately thickened; 9/10-13/14 fairly strongly thickened, the thickness increasing to 11/12 and then decreasing; the remainder thin. Pharyngeal glands large lobes excepting the last which are small masses in IV (?). Dorsal blood vessel single, very narrow at the pharynx. Dorsoventral commissural vessels in IV (ventral connection verified) to XII; those in IV-XI slender, though increasing in thickness posteriorly; those in X-XII forming large latero-oesophageal hearts, each receiving a connective from the dorsal vessel and from a supra-oesophageal vessel where this receives a pair of circum-oesophageal intramural vessels. Supra-oesophageal vessel single, in X-XII and receiving a pair of vessels posteriorly from circum-oesophageal intramural vessels in XIII. Subneural vessel absent.

Gizzard large, globose and strongly muscular in V (septum 5/6 so attenuated as to be almost unrecognizable); proventriculus absent. Oesophagus supressed by backward extension of the gizzard in VI and VII; narrow in VIII; moniliform and vascularized, though narrow, in IX-XIV; greatly expanded in XV and XVI to form two annular (calciferous?) glands; the walls of each gland thrown into numerous ridges, which end freely in the cavity of the gland; the glands not subdivided from the narrow oesophageal lumen. Oesophagus narrow in XVII; intestine beginning, with abrupt expansion, in XVIII; a very large thickly laminar dorsal typhlosole present, filling almost the entire height of the intestinal lumen, commencing in XXI; muscular thickening and caeca absent.

Nephridia in VI, posteriorly, stomate avesiculate holonephridia with preseptal funnels, the slender ectal ducts penetrating the parietes in *c* lines. Large tufted nephridia consisting of many spiral loops in *V* anteriorly, the entire mass apparently discharging by a single (composite?) duct on each side well above *d* lines, at intersegment 2/3 (1/2?). Testes, non-iridescent funnels and copious free sperm masses in X and XI; seminal vescicles elongate, strongly racemose, in IX and XII. Prostates restricted to an enlarged segment XVIII; tubular and very tortuous, the folds lobulated, adpressed and flattened in contact so that the gland is compacted into a single mass which bears a superficial resemblance to a racemose prostate and, from its lobulation and the irregularity of the cross section, may be considered intermediate in form between the tubular and racemose types. Vasa deferentia joining the gland shortly ental of its junction with the muscular duct which is looped once. Penial setae absent. Accessory genital markings represented internally by villous median glandular masses in XVI-XXI. Ovaries bushy masses in XIII together with small funnels; ovisacs large laminae, with several chains of large oocytes in XIV well above the oviducal funnels on the anterior septum of XIV. Spermathecae two pairs, relatively very large, the anterior pair reflexed into VII, each with an ovoid ampulla and a narrow coiled

almost equally long duct, a multiloculate sessile iridescent diverticulum attached to the junction of ampulla and duct. Posterior spermathecae larger than the anterior. Length of right spermatheca of IX (extended) = 4·3 mm, ratio total length spermatheca: length duct = 2·2, ratio total length: length diverticulum = 18·6.

Material examined: A single specimen, here designated the holotype, Longwarry S. via Drouin, Vict., coll. J. T. Ryan, 14 Aug. 1904, *Nat. Mus. Vict.* G1552.

Paraplutellus gen. nov.

Prostomium tanylobous. Dorsal pores present. Setae eight per segment, in regular longitudinal rows, commencing on II; ventral setal couples (*ab*) wide, dorsal setal couples (*cd*) at least twice as wide, and wider than the intervening distance (*bc*); dorsal median setal distance (*dd*) 0·2 of the circumference (*u*). Nephropores large, first in *d* lines (segments II-IV); then in *c* lines for one or two segments; thereafter alternating between *d* and *b* lines. Clitellum annular, on XIV-XVI. A pair of combined male and prostatic pores on XVIII in *b* lines: the prostates with thickly tubular glands and muscular, ectally dilated ducts. Penial setae and accessory genital markings present. Spermathecal pores five pairs, the last at the anterior margin of IX.

Some preclitellar septa thickened. Gizzards absent. A pair of sessile extramural calciferous glands in XIII; intestine commencing in XVI; muscular thickening and typhlosole absent. Supra-oesophageal vessel present. Dorsoventral commissural vessels in VI-XII; those in X-XII forming large latero-oesophageal hearts which receive connectives from the supra-oesophageal vessel and from the dorsal vessel. Nephridia stomate holonephridia; the duct of each with a large diverticulate ectal bladder. Testes and funnels free in X and XI; seminal vesicles in IX and XII. Ovaries and funnels in XIII; ovisacs absent. Spermathecae discharging anteriorly in their segments; each with a single diverticulum.

DIAGNOSIS: Holonephric with large nephridial bladders; nephropores in a few anterior segments in *d* lines, then in *c* lines, and thereafter (from VI or VII) alternating from *d* to *b* lines. Sessile calciferous glands present. Combined pores of a pair of (tubular) prostates and the vasa deferentia in XVIII.

DISTRIBUTION: Lord Howe Island, lt. 31° 31′ S., long., 159° 04′: E.

TYPE SPECIES: *Paraplutellus insularis* n. sp. *Remarks:* Lord Howe Island is 700 km. NE. of Sydney, Australia, but is a true oceanic island separated from the mainland by the Tasman Abyssal Plain at a depth of 4,900 m. It lies on a rise which is covered by about 1,200 m. of water and which joins the Coral Sea Platform in the N. and the S. Island of New Zealand in the South. It is largely volcanic, with lavas considered to be of Pliocene to Pleistocene age but even with the post-glacial rise in sea level much of the island remained exposed (Standard 1967) and therefore the terrestrial fauna may date at least from the Pleistocene and possibly from an earlier period. Endemicity of *Paraplutellus* on this isolated island is, however, questionable and the possibility of introduction from E. Australia, where its near relatives *Plutellus manifestus* and *Heteroporodrilus* are endemic, cannot be dismissed.

Paraplutellus forms with *Plutellus* s. str. (Jamieson 1971b) and *Heteroporodrilus* Jamieson (1970) a highly distinct group characterized by a more or less complex alternation of nephropores on each side of the body and presence of very large subspherical nephridial vesicles. The alternation of nephropores in *Paraplutellus* is distinctive of the genus and yet is intermediate between the arrangements in the other two genera. Like *Heteroporodrilus*, the pores lie in *d* lines in segments II-IV or V and then in *c* lines for a few segments but whereas in *Heteroporodrilus* alternation from *b* to *d* lines commences within one or two segments of X, it commences in VI or VII in *Paraplutellus* as in *Plutellus* s. str. In the latter genus the pores in V or VI anteriorly are in *c* lines only.

Paraplutellus also resembles *Plutellus* in possessing tubular prostates (these glands are racemose in *Heteroporodrilus*) and in the ectal dilatation of their ducts.

Setal ratios are closely similar in the three genera; the ventral setae (*ab*) are widely paired
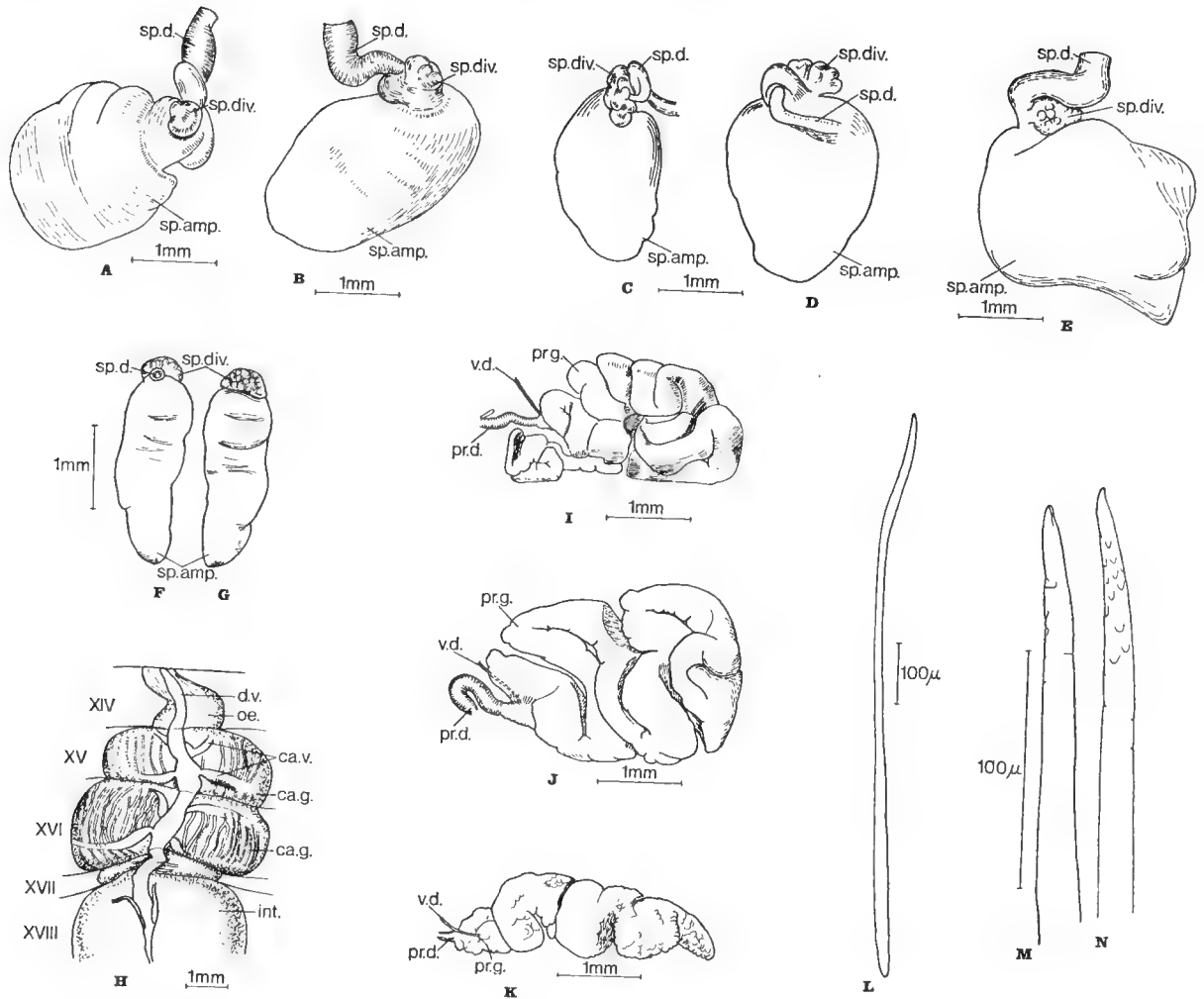
Fig. 3—A-B, *Simsia tuberculata* lectotype G172 left and right spermathecae of IX. C-D, *Simsia longwarriensis* n. sp. right spermatheca of VIII and IX. E, *Simsia tuberculata* (junior synonym *Megascolides roseus* W1728) right spermatheca of IX. F-G, *Simsia intermedia* paralectotype G58, ventral and dorsal aspects of right spermatheca of VIII. H, *Simsia tuberculata* (junior synonym *Megascolides roseus* W1728) califerous glands. I-K, right prostate glands of the above specimens of I, *Simsia tuberculata* G172, J, *Simsia longwarriensis* and K, *Simsia intermedia*. L-N, *Simsia tuberculata* G172. L, penial seta. M, tip of same. N, tip of further penial seta. All by camera lucida.

or distant and the dorsal setae (*cd*) are more widely separated, the interval between them being greater than or only slightly smaller than the interval (*bc*) between the two setal couples; the dorsal median intersetal distance (*dd*) is only 0·2-0·3 of the body circumference (all ratios in segment XII).

Paraplutellus differs from the other two genera in having calciferous glands in XIII only (in IX-X or XI-XIII in *Heteroporodrilus*, X-XIII in *Plutellus*) and in the absence of a gizzard. Individuals of *Heteroporodrilus tryoni* are known in which the gizzard is rudimentary but the difference in arrangement and form of the calciferous glands in both *Heteroporodrilus* and *Plutellus*, together with the peculiar arrangement of the nephoropores in each, leaves no doubt that *Paraplutellus* is distinct.

Paraplutellus insularis n. sp.

Fig. 1A-C.

$1 = 28$ (paratype) and 46 mm (holotype), w (midclitellar) $= 4.5$ mm, s $= 68$ (posterior regenerate) and 98. Form moderately stout, circular in cross section throughout, setal annuli moderately prominent but distinct secondary annulation lacking. Pigmentless buff in alcohol. Prostomium tanylobous, with very narrow, almost parallel-sided dorsal tongue; not canaliculate. First dorsal pore 6/7, setae in eight regular longitudinal rows, commencing on II; *ab* absent, *bc* present, in XVIII.

Nephropores sporadically visible externally, anterior in their segments in more than one series on each side, from internal distribution of vesicles in *d* lines in segments II-IV, in *c* lines in V or in V and VI, alternating from *b* to *d* lines in successive segment from VI or VII posteriorly.

Clitellum annular and very strongly protuberant as a conspicuous narrow band around the body, embracing XIV-XVI; dorsal pores, nephropores, setae and intersegmental furrows retained. Male genital field: male pores on XVIII in *b* lines on large, prominent porophores which extend from 1/3 XVIII-18/19. Very small eye-like accessory genital markings in *b* lines, a pair anteriorly in XVIII impinging on intersegmental furrow 17/18 and a pair anteriorly in XIX, impinging slightly on furrow 18/19. Further accessory genital markings large paired oval glandular areas with depressed centres, occupying the posterior halves of segments VI, VII and VIII in *bc* (that in VI not represented on the right side); in IX in front of setae *b,* and in X and XI presetally in *ab* (holotype). In the paratype the male porophores are similar, but only the accessory genital markings in XVIII and XIX are present. Female pores a pair in XIV, very near the midventral line immediately in front of the setal arc. Spermathecal pores inconspicuous, five pairs, in 4/5-8/9, in *c* lines.

Septal thickening: 3/4-6/7 thin, 7/8-8/9 slightly, 9/10-14/15 moderately, 15/16 slightly thickened, the remainder thin. Pharyngeal glands five pairs of large lobes, the last in VII. Dorsal blood vessel single, continuous onto the pharynx. Dorsoventral commissural vessels in VI-XII; those in IX, anteriorly, slender and arising from the dorsal vessel only; those in X-XII forming three pairs of large latero-oesophageal hearts each of which receives a connective from the dorsal vessel and one from a paired circum-oesophageal vessel shortly before this joins a single, midorsal supra-oesophageal vessel which occupies segment IX-XII. Subneural vessel absent.

Oesophagus in V-VII enveloped by the pharyngeal glands and moniliform and extremely thin walled. Similar but not obscured, in VIII and IX, a gizzard being totally absent. In X expanded and croplike with a pair of circumferential vessels, in XI and XII segmentally dilated and similarly vascularized. In XIII the oesophagus bears a pair of large lateral reniform calciferous glands sessile on the oesophagus over half of its circumference, the two glands merging middorsally and midventrally. The cavity of each gland is occupied by lamellae orientated radially relative to the oesophagus and with their greatest widths longitudinal. Each gland sends an anterior and a posterior calciferous vessel to the dorsal blood vessel. Oesophagus in XIV and XV narrow but still moderately vascular and sending paired vessels to the dorsal vessel. Intestine commencing with abrupt

TABLE 4

INTERSETAL DISTANCES IN SEGMENT XII IN
Paraplutellus insularis

	aa		ab		bc		cd		dd		dd:u
	mm	st	mm	st	mm	st	mm	st	mm	st	
holotype	0.84	9.24	0.57	6.22	1.11	12.16	1.37	15.02	2.18	23.98	
intervals/ab		1.49		1.00		1.95		2.41		3.86	0.24
paratype	0.77	9.46	0.58	7.13	1.02	12.53	1.23	15.50	1.72	21.13	
intervals/ab		1.33		1.00		1.76		2.17		2.96	0.21

expansion and narrow oesophageal valve in XVI, typhlosole and muscular thickening absent.

Nephridia stomate vesiculate exonephric holonephridia throughout. The ectal duct of each nephridium entering the side of a large elongate bladder the opposite side of which projects as a wide diverticulum; the diverticulum median if the nephropore is in *b*, lateral if it is in *d*.

Testes and large iridescent funnels free in X and XI; seminal vesicles elongate, racemose, in IX and XII. Prostates tubular, restricted to XVIII in which the glands run laterally and then for an equal distance medially; the duct tortuous and about half as long, its ental half narrow, its ectal half wide and with a strong muscular sheen. Vasa deferentia double on each side, joining the prostate glands ental of the ducts. Penial setae present in XVIII; whiplike, with moderately stout basal portion and longer, slender undulating region which bears sparsely scattered inconspicuous teeth or spines; length ca. 1 mm (uncertain owing to fragmentation) width of shaft 8μ; greatest width of base (terminally) 12μ.

Ovaries (consisting of many egg-strings) and moderate sized funnels in XIII. Ovisacs absent. Spermathecae five pairs, discharging anteriorly in their segments; each with an ovoid ampulla, somewhat longer narrow cylindrical duct and a small clavate sperm-filled lateral diverticulum joining the duct slightly ectal of its middle. Length of right spermatheca of IX $= 1\cdot2$ mm, ratio total length: length of duct $= 2\cdot1$; ratio total length: length of diverticulum $= 2\cdot7$.

Material examined: Two clitellate specimens, here designated holotype and paratype (new registration numbers G1543 and G1544 respectively); collector?, Baldwin Spencer collection. The sample includes two labels, both giving the locality as Lord Howe Island, one bearing the date Jan. 1903 but no registration number, the other Jan. 1906 and the number G416. With the two syntypes is a specimen of a large perichaetine worm.

Discussion

Paraplutellus and *Simsia*, in having male and

prostatic pores restricted to segment XVIII and holonephridia, are placeable in a *Perionyx*-group which is composed of the genera *Perionyx* Perrier, 1872, *Comarodrilus* Stephenson, 1915, *Diporochaeta** Beddard, 1890, *Diplotrema* (part, New Caledonian species only) Spencer, 1900, *Fletcherodrilus** Michaelsen, 1891, *Heteroporodrilus** Jamieson, 1970, *Plutellus** Perrier, 1873; *Pontodrilus** Perrier, 1874; *Pseudoperichaeta** Jamieson, 1970 and *Woodwardiella** Stephenson, 1925.

Spenceriella belongs to a distinct group of megascolecid genera which are meronephric with (in each prostate segment) an exonephric, stomate meronephridium median to astomate micromeronephridia. This *Dichogaster*-group (Jamieson 1971a) contains many genera, notably *Dichogaster* Beddard, 1888, *Didymogaster** Fletcher, 1887a, *Digaster** Perrier, 1872, *Eutyphoeus* Michaelsen, 1900, *Megascolides** McCoy, 1878, *Notoscolex** Fletcher, 1887a, s. str. Jamieson 1971c, and *Spenceriella** Michaelsen, 1907 (typical part).

* Genera indigenous in Australia.

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LIST OF ABBREVIATIONS USED IN THE ILLUSTRATIONS

ca.g., calciferous glands; ca.v., calciferous vessel; d.v., dorsal vessel; ♀, female pore; g.m., accessory genital marking; int., intestine; l.g.m., lateral accessory genital marking; lo, latero-oesophageal vessel; lo.h., latero-oesophageal heart; ♂, male pore; m.g.m., median accessory genital marking; np., nephropore; oe, oesophagus; pr.d., prostate duct; pr.g., glandular part of prostate; sp.amp., spermathecal ampulla; sp.d., spermathecal duct; sp.div., spermathecal diverticulum; sp.p, spermathecal pore; v.d., vas deferens.

FURTHER SPECIES OF THE VICTORIAN EARTHWORM GENUS *SIMSIA* JAMIESON, 1972 (MEGASCOLECIDAE: OLIGOCHAETA) WITH A NUMERICAL ANALYSIS OF INTERSETAL RATIOS

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Abstract

Four further species formerly assigned to *Plutellus* s. Michaelsen are transferred to *Simsia,* viz. *Cryptodrilus minor, Megascolides attenuatus* and *M. incertus,* all of Spencer, 1892, and *M. steeli* Spencer, 1900. *M. steeli* and *M. attenuatus* are relegated to junior synonymy in *Simsia manni* and *S. minor* respectively. A new species, *S. multituberculata,* brings the generic total for *Simsia* to nine valid species. A new subspecies, *S. intermedia papillata* is described and two species formerly assigned to *Simsia, S. eucalypti* (Spencer, 1900) and *S. manni* (Spencer, 1892) are revised. The genus is redefined and a key to species given. Intersetal ratios, which are known to yield groupings which correlate well with supra-generic taxa based on general anatomy, are shown to be of limited value for specific identification of individual specimens of *Simsia.* The poor specific segregation of ratios reflects the exceptional morphological homogeneity of this genus.

Introduction

The genus *Simsia* was erected by Jamieson (1972) for reception of seven species of which six had been assigned by Michaelsen (1900) to *Plutellus* and one was new. One of these, *Megascolides roseus* Spencer, 1892, was shown to be a junior synonym of the type species, *Simsia tuberculata* (Fletcher, 1888). Further revision of *Plutellus* reveals that four additional species of *Plutellus* s. Michaelsen must be transferred to *Simsia,* namely *Cryptodrilus minor, Megascolides attenuatus* and *M. incertus,* all of Spencer, 1892, and *M. steeli* Spencer, 1900. *M. steeli* is included here as a junior synonym of *Simsia manni* and *M. attenuatus* as a junior synonym of *Simsia minor.* A new species, *Simsia multituberculata* is erected for material wrongly identified by Spencer as *Megascolides incertus.* The generic total for *Simsia* is thus raised to nine valid species.

Material of the species added here to *Simsia* will be described below, together with that of species formerly referred to the genus which have not previously been revised. A new subspecies will also be defined. The value of intersetal ratios for estimation of intra- and interspecific affinities within *Simsia* will be examined taxonometrically.

Systematics

The material described in this paper requires a slight modification of the diagnosis of *Simsia* given by Jamieson (1971). Thus genus nevertheless remains very homogeneous both morphologically and geographically.

Genus **Simsia** Jamieson, 1972

Nephridia stomate, avesiculate holonephridia throughout or preceded in a few anterior segments by tufted nephridia which (always?) have composite ducts. Nephropores of holonephridia in a single series on each side (in setal lines *c* or *cd*) though pores of tufted nephridia may lie in *d* lines. Unpaired, annular, or paired sessile, (calciferous?) dilatations of the oesophagus in (XIV), XV-XVI (XVII). Dorsal intestinal typhlosole present though sometimes rudimentary. Spermathecae 2 pairs, each with a small, sessile, internally multiloculate diverticulum.

Key to the species of **Simsia**

1. One or more midventral circular or oval papilla-like genital markings present, each restricted to one segment or adjacent parts of two segments. Paired markings present or absent   2

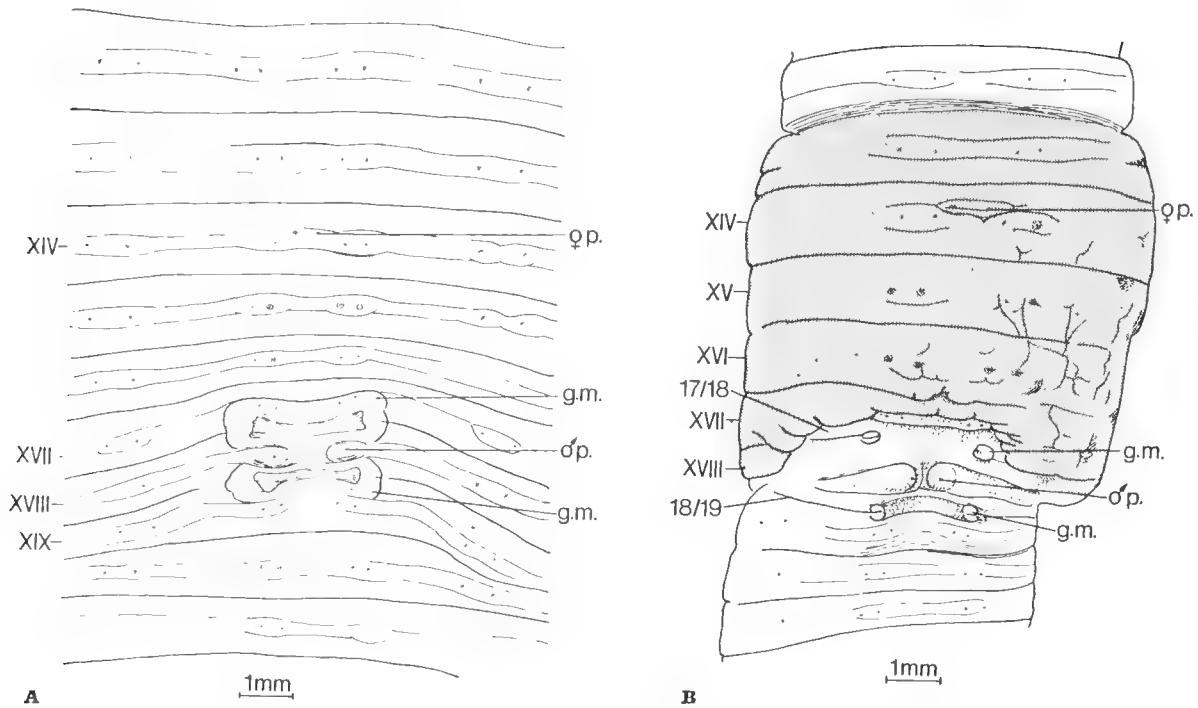—Midventral unpaired genital markings absent

Fig. 1—Male genital field of *Simsia eucalypti* (Spencer, 1900). A, paralectotype of *Megascolides eucalypti* Spencer 1900, Nat. Mus. Vict. G1440. B, new record from Longwarry. Both by camera lucida. Clitellum shaded.

or forming a single indefinite glandular area extending over more than two segments. Paired markings rarely present   5

2. Circular midventral genital markings present in front of and behind the male pores. None present on XVIII though a marking may occur at 18/19. Paired markings absent or inconspicuous   3
—Midventral genital marking present on XVIII and on a variable number or no other segments. Several pairs of well developed paired markings present   4

3. Two circular midventral genital markings present, one posteriorly in XVII, the other at 18/19. Paired markings absent

S. narrensis (Spencer, 1892)

—Circular midventral genital markings present in XVI, XVII, XIX, XX and XXI. Lateral markings poorly developed in XVI and XVII

S. longwarriensis Jamieson, 1971b

4. A single midventral genital marking present, forming a large raised oval area on XVIII. Paired markings present at the anterior margin of XVII and XX and a vari-

able number of, or no, adjacent segments

Simsia tuberculata (Fletcher, 1888)

—Genital markings three longitudinal rows of oval tubercles in the four intersegments, 17/18-20/21

S. multituberculata sp. nov.

5. Paired genital markings, or a transverse depression with glandular margins, in each of intersegments 17/18 and 18/19. Spermathecal pores median to *a* lines   6

—Paired genital markings absent, or poorly developed at 17/18 and anterior XIX. Spermathecal pores in *a* lines or between *a* and *b* lines   7

6. Nephridia in the clitellar region discharging in *c* lines

S. eucalypti (Spencer, 1892)

—Nephridia in the clitellar region discharging between setal lines *c* and *d*

S. manni (Spencer, 1892)

7. A smooth midventral area, with transverse furrows suppressed, lying between the setal annulus of XVII, which forms the posterior margin of the clitellum, and the male pores.

Spermathecal diverticulum multiloculate and discrete but almost hidden in the duct wall

<div align="right">S. lucasi (Spencer, 1892)</div>

—A glandular midventral field present in the vicinity of the male pores and adjacent segments but differing from that of *lucasi*. Spermathecal diverticulum protuberant from the duct 8

8. Tufted nephridia present in anterior segments, from II; followed by simple holonephridia 9

—Tufted nephridia absent. All nephridia simple holonephridia.

<div align="right">S. minor (Spencer, 1892)</div>

9. Paired genital markings at 17/18 and anterior XIX

<div align="right">S. intermedia papillata subsp. nov.</div>

—Paired genital markings absent

<div align="right">S. intermedia intermedia (Spencer, 1892)</div>

Simsia eucalypti (Spencer, 1900)

Figs. 1A-B, 5A, 6A-B

Megascolides eucalypti Spencer, 1900: 35-36, Pl. 5, figs. 13-15.
Simsia eucalypti, Jamieson 1972.

$1 = 82$ mm, $s = 88$. Form circular in cross section, clubbed at the posterior end. Prostomium? (damaged, tanylobous, Spencer). First dorsal pore indeterminable (most anterior 4/5, first one visible usually further back, often at 12/13, Spencer). Setae in eight regular longitudinal rows throughout, commencing on II, *a* and *b* absent in XVIII. Intersetal distances (Table 1). Nephropores fairly conspicuous on the clitellum, in a single series on each side in *c* lines near the anterior borders of their segments, only sporadically recognizable elsewhere. Clitellum annular, XIII-1/3XVIII, intersegmental furrows retained but only ventrally fully developed, setae and nephropores clearly visible, dorsal pores recognizable but occluded. Combined male and prostatic pores a pair in *ab* equatorially in XVIII, each on a small papilla. Genital field ill-defined; an approximately oblong glandular area present in XVII, extending laterally beyond *b* lines, posteriorly to abut on the male porophores, and anteriorly to include setae *a* and *b* of XVII; a similar area extending from the male porophores as far as, but not including, the setal annulus of XIX; each tumid

area with a deep transverse linear depression corresponding with intersegment 17/18 or 18/19. No other accessory genital markings present (see Remarks). Female pores a pair of small orifices anteromedian of setae *a* of XIV at about 1/3 *aa*. Spermathecal pores two pairs of faint, slitlike depressions shortly median to *a* lines and near the anterior borders of VIII and IX.

Septa 10/11 and 11/12 the thickest (strongly thickened). Septal glands invest the pharynx but do not extend appreciably behind it. Gizzard in V large and strongly muscular, preceded by a muscular but easily compressible gizzard-like proventriculus in IV. Sessile vascular swellings of the oesophagus very pronounced in XV and XVI, smaller in XIV, that in each segment grooved dorsally by the dorsal blood vessel which receives a conspicuous circumferential vessel on each side from the dilatation. Intestine commencing, with abrupt expansion, in XIX; a fairly low but distinctly developed rounded dorsal typhlosole present, beginning abruptly in anterior XXV. Dorsal blood vessel single, continuous onto the pharynx. Dorsoventral commissural vessels in VII-XII (vessels on the gizzard joining the dorsal vessel do not have recognizable connections with the ventral vessel); those in VIII and IX although valvular give off a lateral vessel to the parietes before joining the ventral vessel, and are very slender or slender respectively; those in X-XII form large latero-oesophageal hearts, each arising from the dorsal vessel and from the supra-oesophageal, and are otherwise unbranched. Supra-oesophageal vessel in X-XIII, bifurcating in the last segment. Subneural vessel absent. Lateroparietal vessels run from XII to the prostates.

Nephridia simple exonephric holonephridia in (II?) III and IV; those in V and VI forming two pairs of very large tufts with apparently composite ducts which enter the body wall in *c* lines; succeeding nephridia small, exonephric, holonephridia; all nephridia avesiculate and, with the exception of the tufted nephridia, stomate. Testes and funnels not detectable; seminal vesicles a single, racemose pair, on the anterior septum of XII. Ovaries not recognizable; small masses on the posterior septum of XIII presumably are oviducal funnels. Prostates large, tu-

G
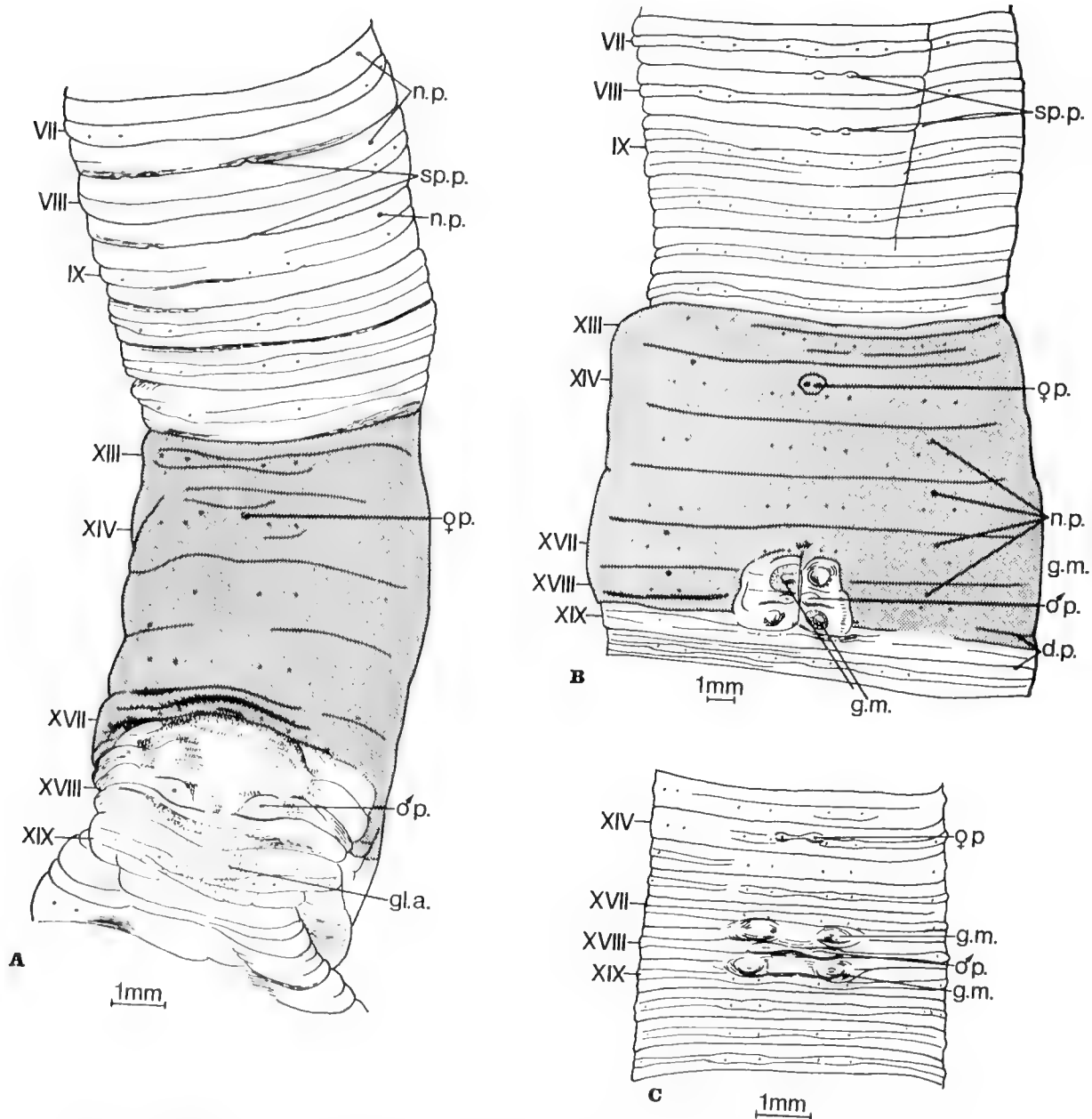
Fig. 2—Male genital fields. A, *Simsia lucasi* (Spencer, 1892), lectotype of *Cryptodrilus lucasi* Spencer, 1892, Aust. Mus. W1282. B-C, *Simsia manni* (Spencer, 1892). B, lectotype of *Megascolides manni* Spencer, 1892, Nat. Mus. Vict. G158. C, lectotype of junior synonym, *Megascolides steeli* Spencer, 1900, G168. All by camera lucida. Clitellum shaded.

bular, much coiled laterally in XVIII to which they are restricted. Vasa deferentia not visible. Penial setae not recognizable possibly owing to previous dissection as these setae are reported by Spencer. Spermathecae discharging anteri-

orly in VIII and IX, each with a large ovoid-saccular ampulla, a shorter but nevertheless unusually long and slender duct, and a multi-loculate diverticulum attached dorsolaterally near the ental end of the ducts; size uniform,

length (right spermatheca of IX) = 4·9 mm; ratio of total length of spermatheca: length duct = 2·3; ratio total length: length diverticulum = 6·3.

Material examined: an imperfectly clitellate previously dissected paralectotype, Nat. Mus. Vict. G1440 from Noojee, S. Warragul (Jensz and Smith 1969). A fully clitellate specimen from Longwarry S. via Drouin, Victoria, coll. J. T. Ryan, 14 July 1904, Nat. Mus. Vict. G1553.

Remarks: Spencer (1900) gives the type localities as 'Neerim and South Warragul'. His illustration shows two pairs of eye-like genital markings, both in *ab*, one pair at intersegment 18/19

the other at 19/20. This constitutes a notable difference from the paralectotype as does the reported presence of penial setae. Agreement of the anatomy of the paralectotype with Spencer's description is otherwise very close, even extending to restriction of the seminal vesicles to XII. It is possible that Spencer had two species before him and henceforth the characteristics described in the present account should be regarded as typical of the species.

The previously unidentified specimen from Longwarry, sympatric with *Simsia longwarriensis* Jamieson, 1972, is here considered to be indubitably conspecific with *S. eucalypti* as exemplified by the paralectotype described. The presence of eye-like accessory genital markings
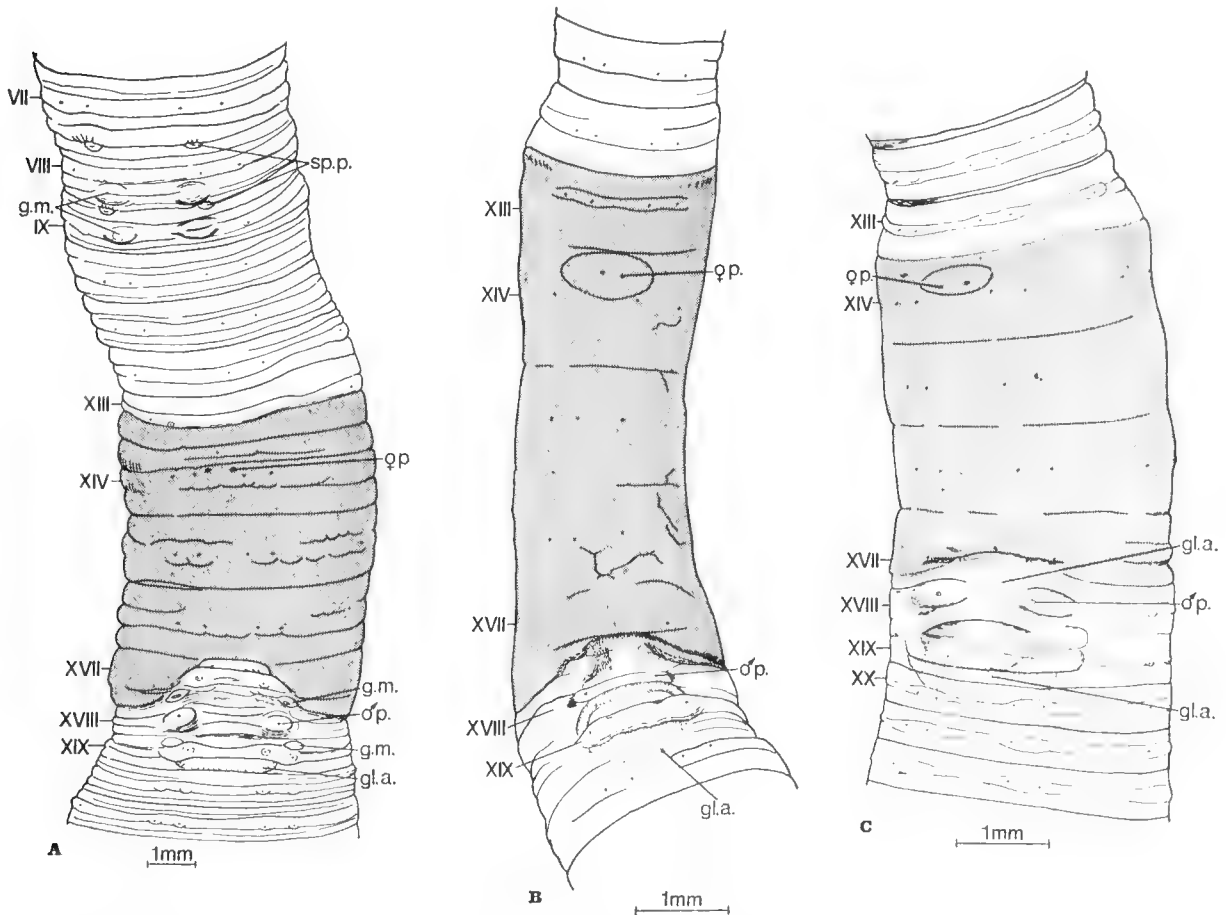

Fig. 3—Male genital fields. A, *Simsia intermedia papillata* subsp. nov. Nat. Mus. Vict. holotype G52. B-C, *Simsia minor* (Spencer, 1892). B, lectotype of junior synonym *Megascolides attenuatus* Spencer, 1892, Nat. Mus. Vict. G176. C, probable syntype of *Cryptodrilus minor* Spencer, 1892, Aust. Mus. W1283. By camera lucida. Clitellum shaded.

in intersegmental tranverse depressions accords both with the new description and that of Spencer, although in the latter account both pairs of markings were stated to be posterior to the male pores. The depressions were so deeply recessed in the paralectotype that eye-like markings if present would have been indetectable.

The Longwarry specimen agrees in all respects with the description of the paralectotype with the following reservations or additions: 1 = 93 mm, w (midclitellar) = 6 mm, s = 93 (posterior amputee?) Prostomium apparently tanylobous. First visible dorsal pore 11/12 but pores poorly visible throughout the body. Intersetal distances (Table 1). Clitellum XIII-2/3 XVIII, interrupted ventrally from 1/3XVII posteriorly. Genital field with a pair of eye-like accessory genital markings in each intersegmental depression, those in 17/18 immediately lateral to *b* lines, those in 18/19 in *b* lines. Spermathecal pores a little further median at 1/4 *aa* from *a*. Typhlosole well developed, although not high, a broad ridge commencing at anterior XXIII and at first low. A pair of large latero-oesophageal vessels visible in VI anteriorly. Ovaries, large fan-shaped laminae with many chains of large oocytes, and funnels in XIII; small ovisacs in XIV. Vas deferens joining the ental end of the prostate duct. Penial setae absent. Spermathecae as in the paralectotype; length of right spermatheca of IX = 4·4 mm; ratio of total length: length duct = 2·3; ratio of total length: length diverticulum = 5·6.

Simsia intermedia (Spencer, 1892)
Simsia intermedia papillata subsp. nov.
Figs. 3A, 5F, 6F

Cryptodrilus willsiensis, Jensz and Smith 1969, p. 93 *(non) Cryptodrilus willsiensis* Spencer, 1892, p. 140.

1?, s? (fragmented), w (midclitellar) = 5 mm. Circular in cross section, canalicula absent. Prostomium prolobous (?, damaged), peristomium with numerous longitudinal grooves. First dorsal pore (?). Setae in eight longitudinal rows; *b, c* and *d* lines very irregular in the detached posterior ends. Intersetal distances (Table 1). Nephropores moderately conspicuous whitish points in *c* lines near the anterior borders of their segments, observed from VII

posteriorly. Clitellum annular, posterior 1/3 XIII-XVII, but interrupted ventrally in *aa* in XVII by the male genital field; intersegments, setae and nephropores visible; dorsal pores not determinable owing to previous dissection. A pair of combined male and prostatic pores on XVIII in *ab*, on moderately large papillae. The midventral surface from the anterior margin of XVII to the posterior margin of XIX forming an indistinct glandular area bearing the male porophores laterally. A pair of small elliptical genital markings present at 17/18, and a further pair anteriorly in XIX, in *b* lines. Female pores inconspicuous, anteromedian of setae *a* of XIV. Spermathecal pores two pairs, in 7/8 and 8/9, in *a* lines; paired suggestions of elliptical genital markings accompanying them, posteriorly in VIII and anteriorly in IX.

Septa: 9/10 and 10/11 the thickest (very strong). Last evident septal glands in IV. Brain at the junction of II and III, mainly in the latter segment. Dorsal blood vessel single; commissural hearts of IX slender and dorsoventral only; those of X-XII large, latero-oesophageal hearts; supra-oesophageal vessel indistinct, not certainly continuous intersegmentally, in IX-1/2 XIII. Subneural vessel absent. Gizzard large in V; oesophagus intact only from IX posteriorly; in IX-XV with encircling vascular striae but no extra-mural dilatations or calciferous glands apparent, possibly owing to damage; intestine?

Nephridia: a pair of large tufts in II, exonephric, each with a composite duct discharging in *c* line; smaller but similar nephridia in III and IV; ducts passing anteriorly and slightly laterally to enter the body wall; possibly no simple holonephridia until VII; these stomate and avesiculate. Small testes and iridescent sperm funnels in XI only; seminal vesicles racemose, restricted to XII in both specimens. Ovaries, consisting of many chains of large oocytes in XIII; no ovisacs seen. Prostates tubular but with the walls very thick relative to the almost unrecognizable central lumen and superficially minutely lobulated; long, with several, tightly adpressed bends; the short muscular duct almost as wide as the glandular portion. Between and partly obscuring the prostate ducts is a very conspicu-
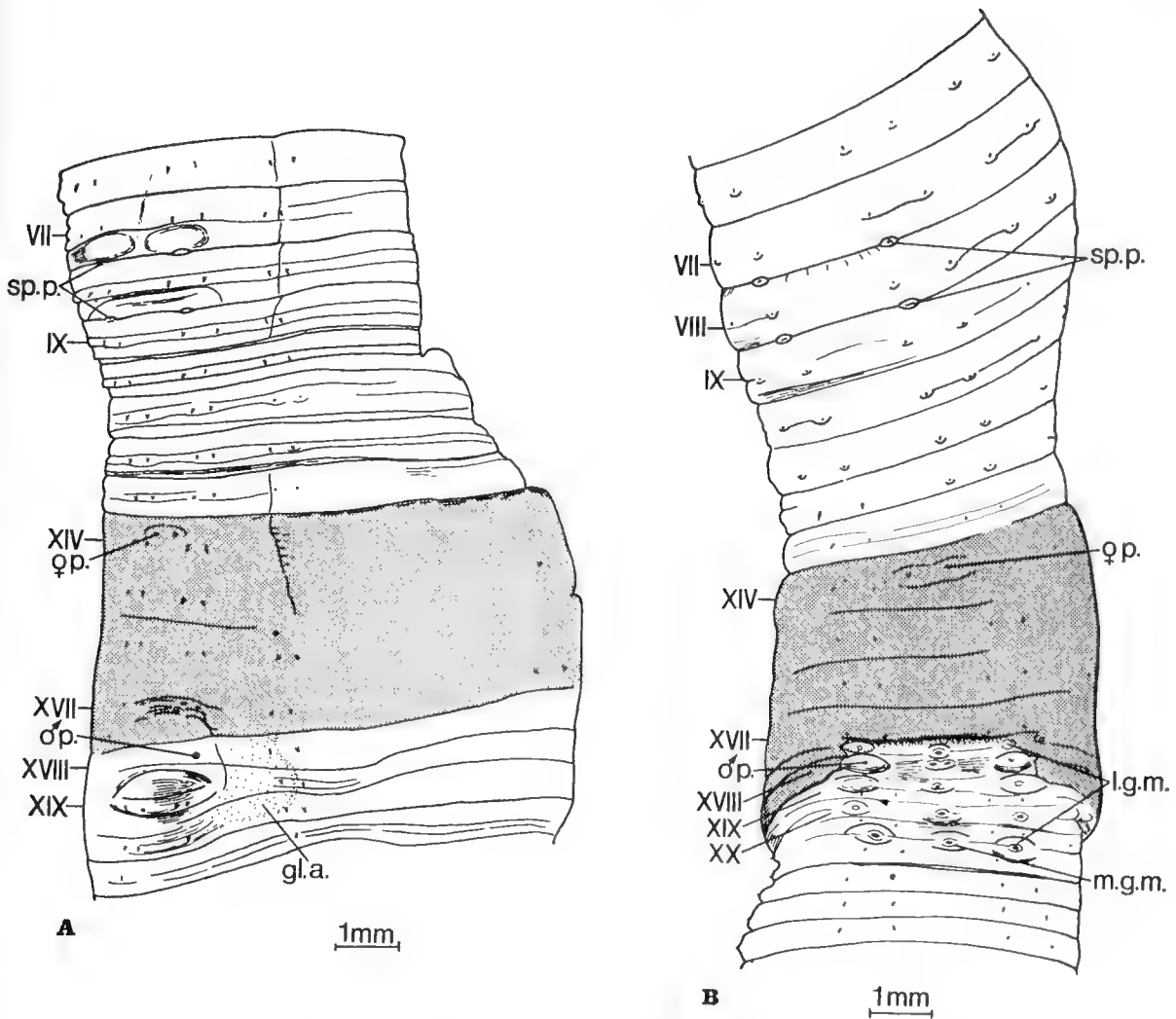
Fig. 4—Male genital fields. A, paralectotype of *Simsia minor* (Spencer, 1892), Nat. Mus. Vict. G1435. B, *Simsia multituberculata* sp. nov., holotype, G175. All by camera lucida. Clitellum shaded.

ous hemispheroidal racemose genital marking gland, filling segments XVII, XVIII and XIX. Spermathecae two uniform pairs, discharging anteriorly in VIII and IX, each with a bent, elongate saccular ampulla, and sessile, sub-spheroidal, multiloculate diverticulum at the junction of the ampulla and the very short, narrow duct. Length of right spermatheca of IX = 4·5 mm; ratio of total length: length duct = 12·5; ratio of total length: length diverticulum = 7·4.

Material examined: Five fragments, of which two are heavily dissected clitellate portions (one

of these lacking the anterior segments) stated by Jensz and Smith (1969) to be syntypes of *Cryptodrilus willsiensis* Spencer, 1892, Nat. Mus. Vict. G52. Although from the type locality (undated), the specimens were unaccompanied by a Spencer label and do not accord with the type description of *C. willsiensis* which is a plutelloid distinct from the genus *Simsia*. The complete anterior portion is here designated the holotype and the anterior amputee the paratype.

This entity is imperfectly described because of the poor condition of the two known speci-

mens. Description was warranted by its mis-identification as *Cryptodrilus willsiensis*. It has close similarities with both *Simsia minor* and *Simsia intermedia,* both of Spencer, 1892 but the presence of anterior tufted nephridia supports identification with *S. intermedia.* The presence of paired accessory genital markings is here considered to merit separate subspecific status but the paucity of our knowledge of variation in the population of *S. intermedia* from the type locality, and of the anatomy and variability of the Mt. Wills morph leave the status of the latter material uncertain.

Simsia lucasi (Spencer, 1892) n. comb.

Figs. 2A, 5E, 6C

Cryptodrilus lucasi Spencer, 1892, p. 143, Pl. 16, figs. 28-30, Pl. 19, fig. 72.
Megascolides lucasi; Beddard 1895, p. 489.
Plutellus lucasi; Michaelsen 1900, p. 168; Jamieson 1972, p. 88.

1 = 102, w (midclitellar) = 5·7 mm, s = 150. Form moderately stout, slightly clubbed posteriorly, circular in cross section throughout; segments distinctly triannulate after the first two, excepting the clitellum. Only the clitellum pigmented (brown) in alcohol. Pigment spots present laterally and dorsally in some anterior and posterior segments. Prostomium epilobous 1/3, dorsal tongue wedge shaped, closed by a transverse furrow; peristomium with many longitudinal grooves. First dorsal pore 4/5. Setae in eight longitudinal rows, becoming irregular posteriorly; *a* and *b* absent in in XVIII. Intestal distances (Table I). Nephropores anterior in their segments, in *d* lines in each of II-VI, thereafter in *c* lines throughout. Clitellum annular XIII-2/3 XVIII; dorsal pores suppressed, intersegmental furrows and nephropores present although faint. Combined male and prostatic pores equatorial in *a* lines of XVIII on a pair of small inconspicuous papillae. The setal annulus of XVII forming an arch-shaped thickening bounding a smooth unsegmented depressed area which extends to the male porophores; the entire ventral surface from 1/2 XVII-XIX appearing glandular. Female pores shortly anteromedian of setae *a* of XIV. Spermathecal pores visible as two pairs of low papillae in

7/8 and 8/9, slightly embaying the preceding segment, in *ab* shortly lateral of *a* line.

Septa 5/6-9/10 very strongly, 10/11 and and 11/12 strongly thickened; 12/13 and 13/14 slightly thickened; the remainder thin. Last septal (pharyngeal) glands in IV. Dorsal blood vessel single, continuous onto the pharynx; dorsoventral commissural vessels in V-XII; all valvular, increasing in thickness posteriorly; those in VIII-IX moderately thick and heart-like, dorsoventral only; those in X-XII forming three pairs of large latero-oesophageal hearts, each receiving a connective from the dorsal vessel and the supra-oesophageal vessel. Supra-oesophageal vessel in IX-1/2 XIII; single anteriorly; posteriorly double segmentally, single intersegmentally. Subneural vessel absent. Gizzard very large and firmly muscular in V, stoutly fusiform and enveloped anteriorly by a rim-like posterior fold of the crop-like oesophagus. Oesophagus almost suppressed in VI and VII by backward extension of the gizzard; moderately moniliform, vascularized and internally rugose in IX-XIII; similar but narrow in XIV; in each of XV and XVI bearing a conspicuous outpouching on each side which, although sessile, has a restricted opening into the oesophagus; the internal wall of each pouch forming numerous high, fairly thin lamellar folds which touch but do not unite across its lumen; each pouch sending a conspicuous circumferential vessel to the dorsal vessel. Oesophagus in XVII narrow and thin walled. Intestine commencing in XVIII; a high, wide, rounded dorsal typhlo-sole occupying about one third of the intestinal lumen commencing in XXV.

Nephridia in II-VI much coiled to the extent of forming conspicuous tufts, though with only a few convoluted loops, in II; ducts (apparently simple) opening anterior to seta *d* in the same segment as the nephridium. In VII posteriorly the nephridia discharge in *c* lines; all are avesiculate. Small preseptal funnels were demonstrated in XII posteriorly but necks connecting nephridia with the preceding septum were demonstrated forward into the region of tufted nephridia; all nephridia are probably, therefore, stomate. (Testes?), sperm masses and weakly iridescent sperm funnels in X and XI; seminal vesicles racemose, in IX and XII.

Large diffuse stalked ovaries with many rows of large oocytes and small funnels in XIII; large racemose ovisacs pendant from the posterior face of septum 13/14 into XIV, not directly associated with the oviducal funnels. Prostates thickly tubular, with several closely adpressed coils and a short muscular duct, restricted to XVIII. Penial setae absent. Spermathecae uniform; two pairs opening anteriorly in VIII and IX each with an elongate
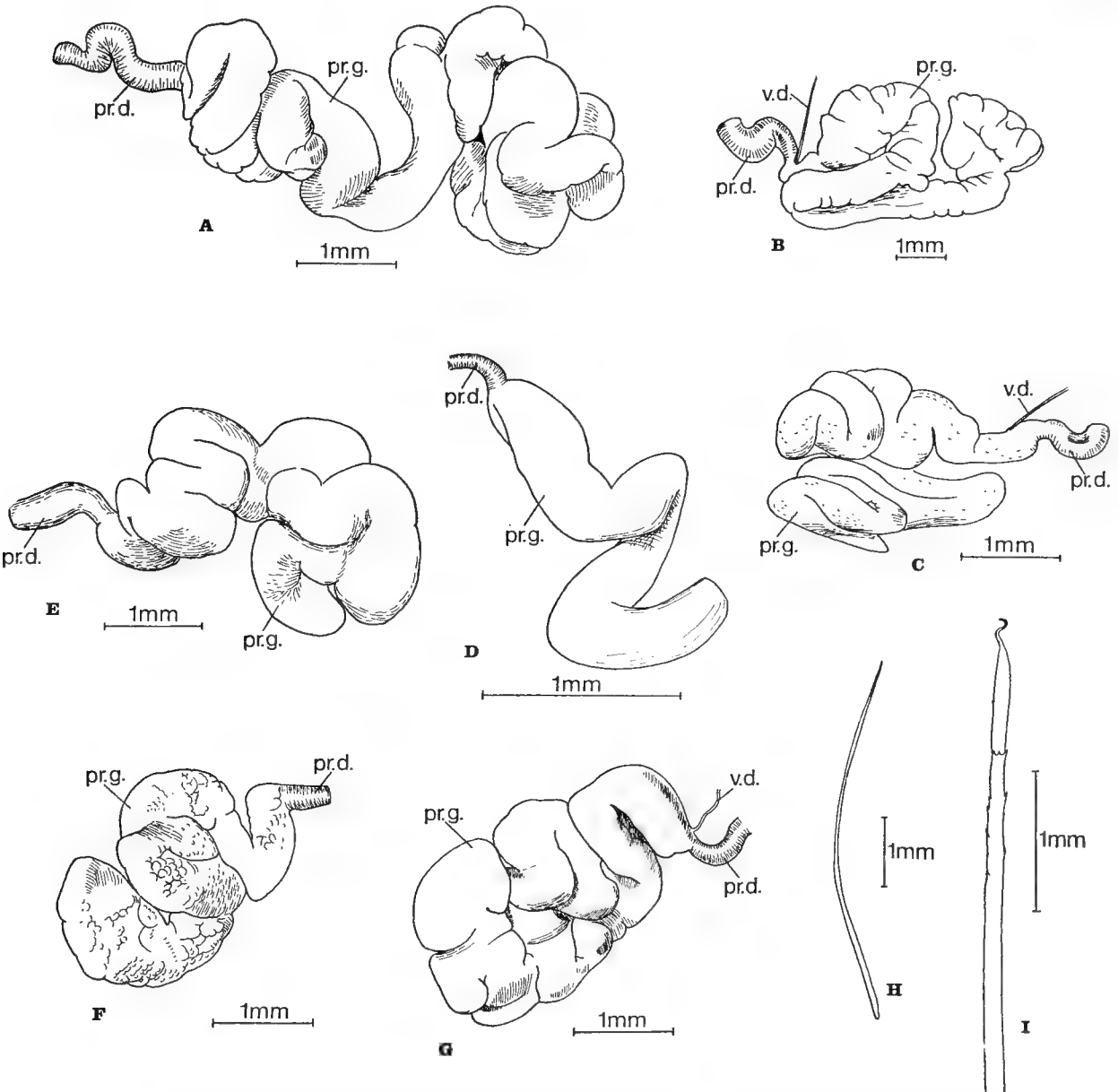
Fig. 5—Prostate glands. A, *Simsia eucalypti* (Spencer, 1900), paralectotype of *Megascolides eucalypti* Spencer, 1900, Nat. Mus. Vict. G1440. B-C, *Simsia manni* (Spencer, 1892). B, lectotype of *Megascolides manni* Spencer, 1900, G158. C, lectotype of junior synonym, *Megascolides steeli* Spencer, 1900, G168. D, *Simsia minor* (Spencer, 1892), lectotype of junior synonym, *Megascolides attenuatus* Spencer, 1892. E, *Simsia lucasi* (Spencer, 1892), lectotype of *Cryptodrilus lucasi* Spencer, 1892, Aust. Mus. W1282. F, *Simsia intermedia papillata* subsp. nov. Nat. Mus. Vict. holotype, G52. G-I, *Simsia multituberculata* sp. nov., holotype, G175. G, prostate gland. H-I, a penial seta. All by camera lucida.

saclike ampulla and externally wide, poorly demarcated duct which bears at mid length an iridescent multiloculate, rosette like diverticulum which is embedded in the external wall of the duct though separable from it by dissection. In a cleared mount the duct is seen to consist of an ental wide half and a narrow tortuous tube forming the ectal half, which is concealed in a glandular (?) and vascular investment which latter constitutes the externally observable duct. Length left spermatheca of VIII = 3·6 mm; ratio of total length of spermatheca: length duct = 2·4; ratio of total length: length diverticulum = 7·3.

Material examined: Three clitellate specimens labelled 'Crypto lucasi. Tallarook, Goulbourn R. Jan 92, A.M.S.L.', Aust. Mus. Sydney, W1282. This label indicates that the specimens are part of the type-series. Only one specimen, here designated the lectotype, was used for the above account but the other two specimens were observed to be closely similar, in external and internal anatomy, including intersetal ratios, and are here designated paralectotypes.

A single fragmented heavily dissected specimen with no locality data, Nat. Mus. Vict. G84, according in general anatomy with the lectotype but yielding no data as to extent of supra-oesophageal vessel, details of excretory system, form of alimentary canal behind XIV and morphology of the female gonads and ducts.

Remarks: Demonstration for the first time of calciferous dilations in XV and XVI and an intestinal typhlosole; and confirmation of the presence of multiloculate rosette-like spermathecal diverticula on two pairs of spermathecae, indicate that *Megascolides lucasi* must be transferred to *Simsia*. Its assignment to the latter genus is supported by general morphology, including the setal ratios.

Simsia manni (Spencer, 1892)

Figs. 2B-C, 4B-C, 6D-E

Megascolides manni Spencer, 1892, pp. 149-150, Pl. 17, figs. 46-48, Pl. 19, fig. 78.
Megascolides manni, Beddard 1895, p. 490.
Plutellus manni, Michaelsen 1900, p. 169.
Simsia manni, Jamieson 1972.
Megascolides steeli Spencer, 1900, p. 34, Pl. 4, figs. 10-12.

l = 250 mm, 120 mm; w (midclitellar) =

? mm, 6 mm, s = 280, 327 (*manni* and *steeli* respectively). Form elongate or moderately stout, circular or trapezoidal in cross section respectively; secondary annulation well developed. Prostomium canaliculate and with a transverse groove at about 1/4 peristomium. First dorsal pore indeterminable. Setae in eight regular longitudinal rows throughout; *a* and *b* absent in XVIII. Intersetal distances (Table 1). Nephropores anterior in their segments, observable in *d* lines in III-VIII (*manni*) or III-VII (*steeli*) and seen in mid *cd* in VIII-XIV and in XX posteriorly in *steeli* but recognizable at this site only on the clitellum in *manni*. Clitellum annular, strongly developed and prominent, embracing XIII-XVIII (= six segments); intersegments represented only by transverse lines, setae and nephropores visible; dorsal pores obscured (*manni*); not developed in the lectotype of *steeli*. Combined male and prostatic pores a pair in XVIII on small papillae in *a* lines. Accessory genital markings two pairs of elliptical low mounds, usually with pore-like centres visible, in 17/18 and 18/19 in *ab* (both taxa); the markings and male pores lying on an approximately rectangular tumid area at maturity (*manni*). Female pores shortly anteromedian to setae *a*; closer together in *manni* than in *steeli*. Spermathecal pores inconspicuous, two pairs, in 7/8 and 8/9, median of *a* lines (*manni*), not visible in the lectotype of *steeli* but stated by Spencer to be in *a* lines.

Septa: 10/11 and 11/12 the thickest (very strong). Dorsal vessel single; commissurals of IX forming slender hearts which are dorsoventral only; those of X-XII forming three pairs of large latero-oesophageal hearts; latero-oesophageal hearts, like those of IX each sending a branch basally to the parietes (both taxa); supra-oesophageal observable in X-XII in *steeli* but not distinguishable in the lectotype of *manni*. Gizzard large and firmly muscular, apparently in VI; dorsal typhlosole represented only by a slight internal ridge (both taxa); alimentary canal otherwise too severely macerated for description in *steeli*. In *manni* oesophagus conspicuously dilated (calciferous?) in XV-XVI and grooved middorsally; still wide in XVII; very narrow in XVIII; intestine commencing at 18/19.
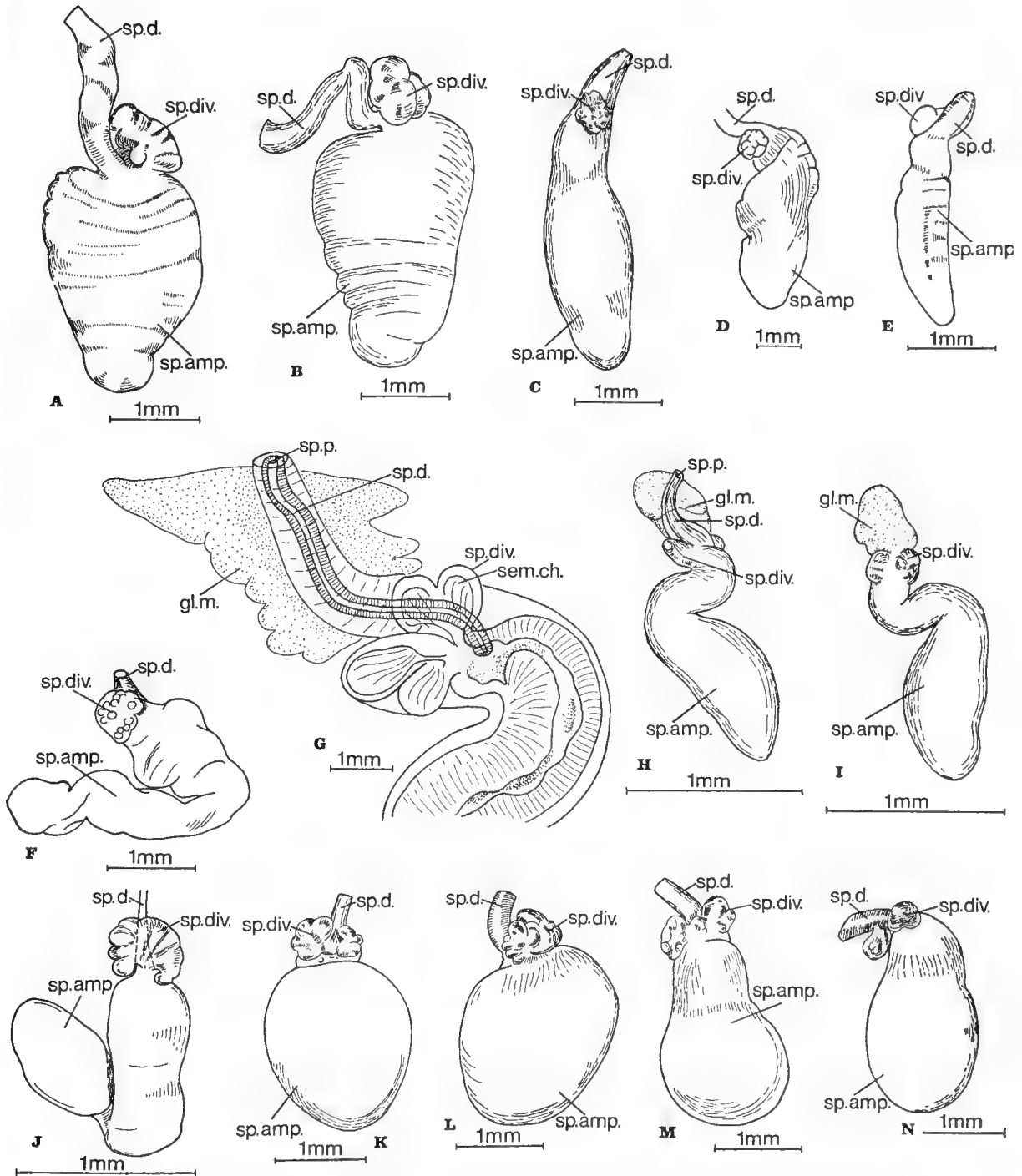
Fig. 6—Spermathecae. (R = Right, L = Left, roman numerals indicate segment). A-B, *Simsia eucalypti* (Spencer, 1900). A, new record from Longwarry (R. IX). B, paralectotype of *Megascolides eucalypti* Spencer, 1900, Nat. Mus. Vict. G1440 (R. IX). C. *Simsia lucasi* (Spencer, 1892), lectotype of *Cryptodrilus lucasi* Spencer, 1892, Aust. Mus. W1282 (L. VIII). D-E, *Simsia manni* (Spencer, 1892). D, lectotype of *Megascolides manni* Spencer, 1892, Nat. Mus. Vict. G158 (R. VIII). E, lectotype of junior synonym, *Megascolides steeli* Spencer, 1900, G168 (L. IX). F, *Simsia intermedia papillata* subsp. nov. (R. IX), Fig. 5F. G-J, *Simsia minor* (Spencer, 1892). G-I, lectotype of junior synonym, *Megascolides attenuatus*, duct and ventral and dorsal views respectively of a spermatheca (R. VIII). J, paralectotype of *Cryptodrilus minor* (Spencer, 1892), G1435 (R. IX). K-N, *Simsia multituberculata* sp. nov. holotype, G175 (R, L. VIII; R, L. IX, respectively).

Nephridia avesiculate a pair of small exonephric holonephridia in IV; large paired stomate tufts, in each of segments V-VII, each tuft with approximately 100 loops and discharging through the parietes by a double terminal duct; nephridia in this region apparently discharging a segment or more anterior to their main bodies. Nephridia in VIII posteriorly, simple, exonephric stomate, avesiculate holonephridia discharging to the exterior in the segment containing the post-septal body (*manni*, data of Horan, pers. comm.; *steeli* reported to be similar but additional simple nephridia demonstrated in II and III). Large much divided laminar testes and large iridescent sperm funnels free in X and XI, racemose seminal vesicles in XI and XII (*manni*), iridescence confined to the funnels of XI in *steeli* and anterior testes not recognizable. Laminar ovaries with many chains of oocytes and funnels in XIII (both taxa), ovisacs in XIV in *manni* but not in *steeli*. Prostates long, much coiled, depressed tubes with sinuous muscular ducts which receive the vasa deferentia entally. Penial setae absent. Spermathecae two pairs, discharging anteriorly in VIII and IX, one or more reflexed into the preceding segment; ampulla elongate ovoid, more or less sacculated; duct shorter, bearing a small multiloculate diverticulum near its ental end (both taxa). Dimensions of right anterior and left posterior spermatheca of *manni* and *steeli* respectively: = 5 mm, 2·8 mm; ratio of total length of spermatheca: length duct = 2·8, 3·5; ratio of total length: length diverticulum = 7·0 (both taxa).

Material examined:

The previously dissected, clitellate lectotype of *Megascolides manni*, S. Warragul, Victoria, coll. W. Mann July 1891, Nat. Mus. Vict. G158.

The aclitellate, macerated lectotype of *Megascolides steeli*, Warragul, coll. T. Steel April 1892, Nat. Mus. Vict. G168.

Remarks: M. *steeli* is here synonymized with M. *manni* on the grounds of general similarity, including the unusual disposition of the nephropores, in conjunction with close agreement of intersetal ratios. M. *manni* var. *variabilis* Spencer, 1892, requires no separate status, its supposedly distinctive male genital field being characteristic of the lectotypes of both M. *manni* and M. *steeli*.

Simsia minor (Spencer, 1892) n. comb.

Figs. 3B-C, 5D, 6G-J

Cryptodrilus minor Spencer, 1892, p. 144, Pl. 16, figs. 31-33, Pl. 19, fig. 73.
Megascolides attenuatus Spencer, 1892, p. 155, Pl. 19, figs. 61-62, 82.
Megascolides minor, Beddard 1895, pp. 489-490.
Megascolides attenuatus, Beddard 1895, p. 491; Sweet 1900, p. 112.
Plutellus attenuatus, Michaelsen 1900, p. 169.
Plutellus minor, Michaelsen 1900, p. 170.

External morphology: (Specimens previously referred to *C. minor*, only): 1?, 83 mm; w (midclitellar) 3 mm (both specimens); s = ?, 121 (G1435 and W1283 respectively). Form circular in cross section throughout; weakly triannulate. Pigmentless buff in alcohol. Prostomium epilobous 1/3, a deep middorsal furrow running from the prosotomium to 1/2 segment II. First dorsal pore 5/6. Setae in eight longitudinal rows, regular except on the posterior 14 segments where all rows become irregular (W1283); *ab* absent in XVIII (both specimens).

Nephropores sporadically visible, at the anterior borders of their segments in *c* lines (both specimens). Clitellum annular slightly protuberant, embracing XIV-XVII, with some clitellar modification of XIII in W1283; dorsal pores occluded but faintly visible; setae and nephropores retained; intersegmental furrows faint or obscured.

Male genital field: male pores a pair of minute apertures at the sites of the absent setae *ab* of XVIII, in W1283 on transversely elliptical papillae extending somewhat beyond *a* and *b* lines medianly and laterally. An approximately circular midventral area, extending from the setal zone of XVII to that of XX and laterally attaining a maximum width, in XVIII or XIX of slightly less than or slightly more than *bb*; this glandular field interrupted centrally from approximately 18/19 to the anterior limit of the setal annulus of XIX in such a way that a tumid, glandular arc is evident behind the male pores. Female pores anteromedian of setae *a* of XIV, on minute papillae. Spermathecal pores two pairs of minute ellipses in *ab* of 7/8 and

8/9; each in G1435 preceded by postsetal tumescence of the preceding segment.

Some anterior septa thickened; 9/10 the thickest, being quite strong. Dorsal blood vessel single, continuous onto the pharynx. Hearts well developed in X-XII. Supra-oesophageal vessel visible in XII but supra-oesophageal connectives to hearts not verifiable owing to poor condition of material. Subneural vessel absent. Gizzard large and cylindrical, in V; oesophagus vascular and moniliform in XII-XVII, and narrow in XVIII, in G1435; in W1283 large annular dilatations in 1/2 XIV, XV, XVI and XVII, have the appearance of sessile unpaired calciferous glands. Intestine beginning in XIX, with a large constricted oesophageal value; dorsal typhlosole present, a rounded tortuous ridge beginning at 19/20; muscular thickening absent (both specimens).

Nephridia: all simple exonephric, avesiculate holonephridia; funnels not observed in nephridia of the forebody but connections with the anterior septum of each segment clearly visible. Terminal ducts of nephridia of segments II-V all enter the parietes anteriorly in II; composite ducts and pronounced coiling or tufting of nephridia not developed. In the posterior 13 or so segments, nephridia are thicker and slightly more coiled and the single funnels are easily detectable (W1283, Horan pers. comm.). Metandric; iridescent convoluted male funnels seen only in XI and small, racemose seminal vesicles only in XII. Ovaries consisting of united long chains of fairly large oocytes; ovisacs absent. Prostates coiled, tubular with distinct muscular duct (W1283); similar in G1435 but precise form indeterminable owing to previous damage. Penial setae absent. Spermathecae discharging anteriorly in their segments, each with a broadly digitiform sometimes reflexed ampulla and a much shorter, slender duct; a multiloculate iridescent dorsoventrally depressed diverticulum lying dorsally over and joining the junction of duct and ampulla; approximately uniform in size, length (G1435, right spermatheca of IX) = 2·5 mm; ratio total length: length duct = 5·8; ratio total length: length diverticulum = 9·1.

Material examined: A single, much dissected paralectotype, Ellinbank, S. Warragul, coll. W.

Mann Aug. 1891, Nat. Mus. Vict. G1435. A previously undissected clitellate specimen, used for the above account, and a dissected aclitellate specimen used only for setal ratios, Aust. Mus. W1283; this material is labelled *Cryptodrilus minor,* apparently in Spencer's handwriting, and is probably part of the type-series.

Remarks: It is here considered that *Megascolides attenuatus* Spencer, 1892, is a junior synonym of *Cryptodrilus minor* Spencer, 1892. The following description of the lectotype of *M. attenuatus* allows comparison of the two entities.

Megascolides attenuatus Spencer, 1892
Figs. 3B, 5D, 6G-I

$1 = 122$ mm, w (midclitellar) $= 1·9$ mm, $s = 166$. Circular in cross section throughout. Pigmentless buff in alcohol, clitellum dark brown (worms grey in life, Spencer). Prostomium prolobous. First dorsal pore very conspicuous, 4/5. Setae small, in eight longitudinal rows, commencing in II, which become irregular posteriorly (in last 15 segments); *ab* absent in XVIII. Intersetal distances (Table 1).

Nephropores in *c* lines but only sporadically visible. Clitellum annular, well developed but not protuberant, embracing XIII-XVIII dorsally but interrupted ventrally in 1/2 XVII-XVIII; dorsal pores present in a middorsal furrow extending from XII-XIX; setae retained but less distinct; intersegmental furrows weak. Male pores equatorial in *ab*, nearer *a* of XVIII on a transverse band; the midventral region from the male pores almost to the setal annulus of XX glandular and tumid, the glandular field extending maximally, at the equator of XIX, to shortly beyond setae *b*. Female pores a pair of small orifices at about 1/3 *aa*, midway between the setal arc and the anterior border of XIV, in a common glandular field. Spermathecal pores two pairs, minute, on minute almost inappreciable papillae near the posterior limits of VII and VIII, in *ab* nearer *a*.

Septal thickening: 4/5 and 5/6 very delicate; 6/7-11/12 progressively thickened but 11/12 still only moderately thick, 12/13 and 13/14 moderately thickened but less than 11/12; the remainder slightly thickened to unthickened. Last septal (pharyngeal) glands anterior in IV.

Dorsal vessel single, continuous onto the pharynx. Dorsoventral commissural vessels in V-XII; those in V-IX progressively wider posteriorly, those of IX still, however, only about half as wide as those of X-XII which form three pairs of latero-oesophageal hearts each of which is attached directly to the dorsal vessel and receives a connective from the supra-oesophageal vessel. The latter vessel well developed, and free from the oesophagus, in X-XII, exceedingly thin in IX; not represented in other segments. Subneural vessel absent.

Gizzard large, almost cylindrical and firmly muscular, in V; oesophagus narrow and thin walled, not forming a proventriculus, in IV; its surface in VII, VIII and IX drawn out into innumerable long, fine (glandular?) processes which form in each segment a tuft obscuring the gut. Oesophagus narrow and chloragogenous-looking in X-XVIII, especially so in XIII posteriorly; lacking appreciable dilatation but with two pairs of conspicuous vessels to the dorsal vessel in XV and XVI (damaged in XVII) which are presumed to represent homologues of the (calciferous?) dilatations of other *Simsia* species. Intestine commencing with abrupt expansion in XX, the gut in XIX with deeply folded internal walls and externally distinguished by the opacity of its walls from the thin walled intestine and pinched off at each border of the segment; a deep tortuous narrow lamelliform dorsal typhlosole commencing in XXI; muscular thickening of the intestine absent.

Nephridia large, thickly tubular avesiculate (stomate?) holonephridia, the postseptal bodies commencing in II; the slender ducts entering the parietes in front of setae c. Testes, free sperm masses and large robust iridescent sperm funnels free in X and XI; seminal vesicles two pairs, in IX and XII, racemose, the posterior the larger. Prostates a pair of stout tubes, bent twice, in XVIII and XIX, each with a short, narrow muscular duct. The duct embedded in glandular masses which extend on the ventral body wall from posterior XVII-posterior XIX and correspond with the external genital field. (The two vasa deferentia of each side remain separate, running up within the muscular wall of the spermiducal duct, and entering the duct as it leaves the gland, Sweet 1900). Penial setae not recognizable (see Remarks). Ovaries very large firm laminae, each consisting of many rows of large oocytes, radiating laterally from basal strands attached near the ventral nerve cord; they and the funnels in XIII; ovisacs absent. Spermathecae two pairs, discharging anteriorly, the ampulla an elongate bent sac the narrow ectal end of which joins a narrow much shorter duct; 2 multiloculate diverticula, with spermatozoal iridescence, present one on each side at the junction of duct and ampulla; the duct embedded in a glandular mass. Size uniform, length of right spermatheca of VIII $= 1.9$ mm; ratio total length: length duct $= 3.9$; ratio total length: length diverticulum $= 8.3$.

Material examined: Lectotype, a previously undissected clitellate specimen, from Warragul, Nat. Mus. Vict. G176.

Remarks: Sweet (1900) noted on each side just behind the opening of the prostate duct a slightly muscular sac enclosing a long curved penial seta. Neither follicles nor penial seta are visible in the lectotype despite exhaustive examination. The possibility that the genital marking glands have obscured these cannot, however, be rejected.

Simsia multituberculata n.sp.

Figs. 4B, 5G, I, 6K-N

$1 = 49$, ?, 80 mm, w (midclitellar) $= 4$-5 mm, s $= 126$, ?, 137 (holotype and two paratypes, respectively). Form moderately stout; circular in cross section throughout; anterior segments widest. Colour in alcohol pale brown (but unpigmented?); clitellum pigmented. Prostomium tanylobous, with faint median dorsal groove (three specimens). Setae in eight regular longitudinal rows throughout, commencing on II; *ab* absent in XVIII.

Nephropores visible (preclitellar to about segment V, clitellar and occasionally postclitellar) on the anterior borders of their segments, in *c* lines. Clitellum annular, moderately protuberant, embracing XIV-XVIII (three specimens) with some clitellar modifications of XIII in the holotype; interrupted ventrally posteriorly from the setal arc of XVII by the male genital field. Male pores approximately equatorial on XVIII, in *ab*, on oval porophores

which extend slightly beyond *a* and *b* lines, medianly and laterally. Accessory genital markings three longitudinal rows of oval tubercles in the four intersegments 17/18, 18/19, 19/20 and 20/21, each intersegment thus with a pair of tubercles (in *ab* or, in 19/20 in *b*) and a median tubercle; an additional unpaired median tubercle present in approximately the same transverse line as the male pores in XVIII; the median and right marking of intersegment 20/21 not developed in paratype 2. Each tubercle has a pore-like central area which is transversely duplicated in that of XVIII in the holotype. Female pores small slits anteromedian of setae *a* of XIV. Spermathecal pores two pairs on small but conspicuous papillae in *a* lines of 7/8 and 8/9.

Internal anatomy (holotype). Septal thickening: 3/4-7/8 thin, 5/6 being so attenuated by the gizzard as to be barely perceptible; 8/9 moderate; 9/10-13/14 fairly strong; the remainder thin. Last pharyngeal glands in IV. Dorsal blood vessel single; continuous onto the pharynx. Dorsoventral commissural vessels in IV-XII; those in IV to IX slender, though increasing in thickness posteriorly; those in X to XII forming large latero-oesophageal hearts, each connected with the dorsal vessel and receiving a connective from a supra-oesophageal vessel which is visible in VIII-XII. Subneural vessel absent. Oesophagus unusually long and tortuous in front of the gizzard. Gizzard large, globose, and strongly muscular, in V; oesophagus greatly expanded in XV and XVI to form two unpaired annular (calciferous?) dilatations; moniliform and vascularized, though narrow, in IX-XIV; narrow in XVII. Intestine beginning, with abrupt expansion, anteriorly in XVIII; a thickly laminar dorsal typhlosole commencing in XXIV. Nephridia small tufts in II and III; avesiculate holonephridia in succeeding segments which are slightly more coiled in the anterior few segments; the tufts in II discharging by a wide duct anteriorly, at furrow 0/1 in or above *d*; exit of those of III not seen; the remaining nephridia with ducts entering the parietes in *c* lines. Testes, large lobed iridescent sperm funnels and free sperm masses in X and XI; seminal vesicles in IX and XII, those in IX small and only slightly racemose, those in XII

larger, elongate and lobulated. Prostates restricted to an enlarged segment XVIII; very much coiled tubes, the folds adpressed, irregular in cross section and entally fused; vasa deferentia joining the gland shortly ental of its junction with the curved, relatively short, muscular duct. Penial setae gently bowed, the ectal end with a few scattered anteriorly directed minute spines some of which near the tip form a single serrated annulus; the tip of the seta drawn out into a very slender S-shaped process. Length of a well developed seta, 0·51 mm, width of the shaft generally 7 μ, slightly wider entally. Ovaries large folded laminae with many strings of large oocytes in XIII; ovisacs large laminae with several chains of oocytes on the anterior septum of XIV. Spermathecae two pairs; each with an ovoid or bulbous ampulla, a narrow short duct, and two lateral multiloculate diverticula which are not completely separate one from the other. Size of the spermathecae approximately uniform; length (four spermathecae of holotype) $= 2 \cdot 6$-$3 \cdot 2$ mm; ratio of total length: length duct $= 2 \cdot 7$-$3 \cdot 2$; ratio total length: length diverticulum $= 7 \cdot 4$-$8 \cdot 5$.

Material examined: the holotype, a complete specimen which had previously been dissected; and two paratypes of which one (paratype 1) is a previously dissected posterior amputee and the other an undissected complete specimen; all specimens clitellate; labelled in Spencer's hand 'Megascolides incertus Black Spur, Oct. '95', Nat. Mus. Vict. G175.

Simsia tuberculata (Fletcher, 1888)

Notoscolex tuberculatus Fletcher, 1888, p. 611-614.
Megascolides tuberculatus, Beddard 1895, p. 494; Spencer 1892, p. 156.
Plutellus tuberculatus, Michaelsen 1900, p. 168; Jamieson 1971a, p. 88.
Megascolides roseus Spencer, 1892, pp. 153-154, Pl. 18, figs. 58-60; Pl. 19, fig. 81; Beddard 1895, p. 491; Sweet 1900, p. 112.
Plutellus roseus, Michaelsen, 1900, pp. 167-168; Jamieson 1971a, p. 88.
Simsia tuberculata, Jamieson 1972. This volume.
Megascolides incertus Spencer, 1892, pp. 151-152, Pl. 18, fig. 52-54; Pl. 19, fig. 80.
Megascolides incertus, Beddard 1895, p. 490.
Plutellus incertus, Michaelsen 1900, p. 167; Jamieson 1971, p. 87.

Prostomium tanylobous. First visible dorsal pore 18/19. Setae small and difficult to discern;
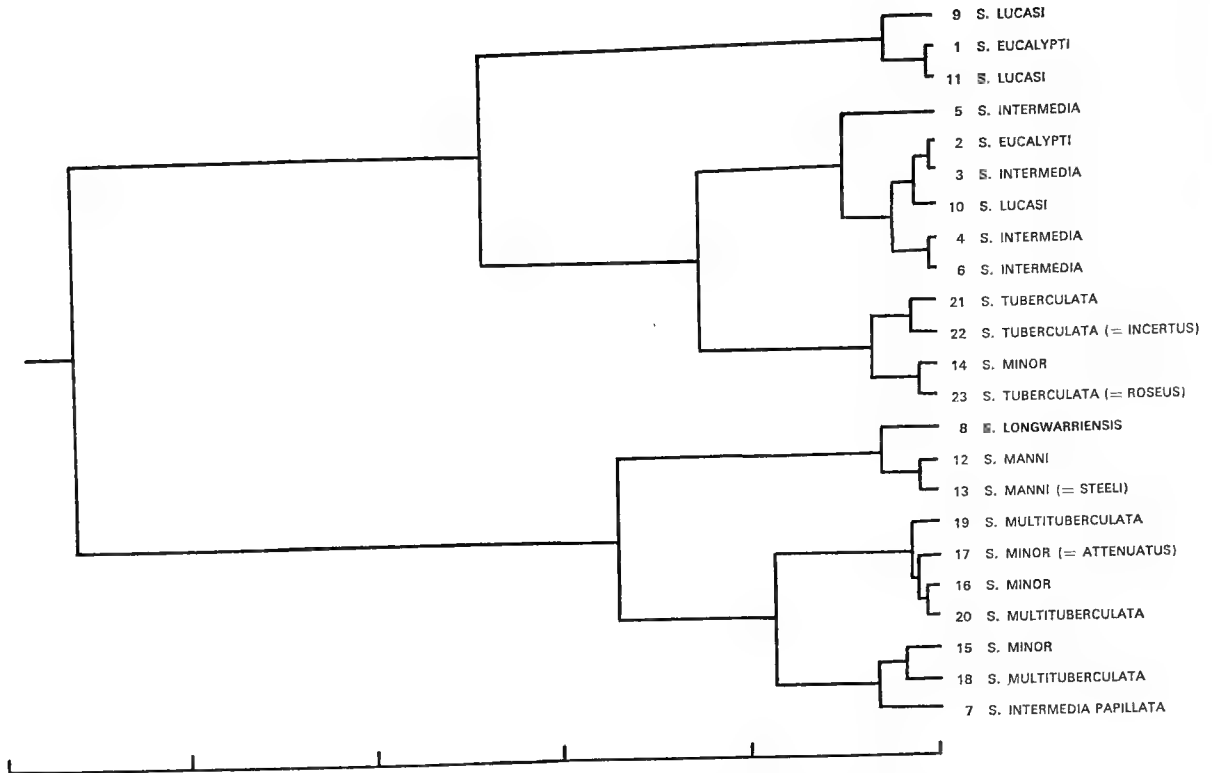
B. G. M. JAMIESON

Fig. 7—Dendrogram of intertaxon (inter-ratio) distances in the genus *Simsia*.

in eight regular longitudinal rows (throughout?), commencing in II; *a* and *b* absent in XVIII. Intersetal distances (Table 1). Nephropores not visible. Clitellum annular, embracing 1/2 XIII-2/3 XVIII; setae and intersegmental furrows retained but less distinct; dorsal pores not recognizable. Combined male and prostatic pores a pair on XVIII in *a*. Paired eye-like accessory genital markings presetally in *ab* in XV, XVI, XVII, XX, XXI and XXII in all of which they impinge on the anterior intersegment; a single midventral marking in XVIII. Female pores small slits anteromedian of setae *a* of XIV. Spermathecal pores not visible. General internal anatomy as for *S. tuberculata* (Jamieson 1971b).

Material examined: A clitellate posterior amputee with the registration 'Megascolides incertus, now *Plutellus incertus* (Sp.), Victoria, presented by J. J. Fletcher (Nov. 1924), identified by Prof. B. Spencer', Aust. Mus. Sydney, W1276; here designated the lectotype of the junior synonym *Megascolides incertus* Spencer.

Remarks: The above brief account, coupled with Spencer's description, is sufficient to leave no doubt that *Megascolides incertus* is a junior synonym of *Simsia tuberculata*. Location of additional paired accessory genital markings in the specimens of *incertus* in XV and XVI is a not unexpected extension of the genital field of *S. tuberculata*.

Intersetal Ratios

Table 1 lists intersetal distances for species of *Simsia* described here and in Jamieson (1971b). These are subjected to numerical analysis below.

Methods

The four setae on each side of a segment are designated, in the ventral to dorsal direction, *a*, *b*, *c*, and *d*. The distances *aa: ab: bc: cd: dd: dc: cb: ba* are measured by means of a camera lucida (alternatively a graticule or scale in the occular may be used). The specimen is held down by a glass slide or coverglass, avoiding

TABLE 1
Intersetal distances in the genus *Simsia*

		aa			ab			bc			cd			dd			dd:u	
		mm	st	st/ab	mm	st	st/ab	mm	st	st/ab	mm	st	st/ab	mm	st	st/ab		
S. eucalypti	1	1·39	10·12	2·78	0·50	3·64	1·00	2·14	15·58	4·28	0·71	5·17	1·42	5·64	41·07	11·28	0·41	G.1440 Paralectotype
S. eucalypti	2	1·72	10·36	2·33	0·74	4·44	1·00	2·25	13·53	3·05	0·91	5·50	1·24	7·09	42·71	9·62	0·43	G.1553
S. intermedia	3	1·29	9·82	2·26	0·57	4·34	1·00	1·79	13·60	3·13	0·71	5·41	1·25	5·71	43·49	10·02	0·44	G.58
S. intermedia	4	1·29	10·69	2·58	0·50	4·14	1·00	1·50	12·43	3·00	0·54	4·47	1·08	5·71	47·31	11·43	0·47	G.1406
S. intermedia	5	1·29	9·71	2·01	0·64	4·82	1·00	1·50	11·29	2·34	0·79	5·94	1·23	6·14	46·20	9·59	0·46	G.72
S. intermedia	6	1·29	10·62	2·58	0·50	4·12	1·00	1·57	12·93	3·14	0·64	5·27	1·28	5·43	44·73	10·86	0·45	G.86
S. papillata	7	1·72	13·49	2·50	0·70	5·51	1·00	1·54	12·12	2·20	0·91	7·16	1·30	4·70	36·91	6·70	0·36	G.52 Holotype
S. longwarriensis	8	0·88	8·19	1·79	0·50	4·59	1·00	1·53	14·26	3·10	0·95	8·85	1·92	3·90	36·39	7·93	0·36	G.1552 Holotype
S. lucasi	9	1·23	8·66	3·18	0·39	2·72	1·00	2·18	15·35	5·64	0·53	3·71	1·36	6·77	47·77	17·56	0·48	G.84
S. lucasi	10	1·58	8·91	2·25	0·70	3·96	1·00	2·42	13·66	3·45	0·84	4·75	1·20	8·21	46·34	11·70	0·46	W.1282 Lectotype
S. lucasi	11	1·82	10·24	3·06	0·60	3·35	1·00	2·81	15·75	4·70	0·77	4·33	1·29	7·65	42·91	12·81	0·43	W.1282 Paralectotype
S. manni	12	1·29	9·57	1·64	0·79	5·85	1·00	2·07	15·43	2·64	1·07	7·98	1·36	4·29	31·91	5·45	0·32	G.158 Lectotype
syn. steeli	13	1·30	9·08	1·69	0·77	5·38	1·00	2·07	14·46	2·69	1·09	7·61	1·41	5·16	36·03	6·70	0·36	G.168 Lectotype
S. minor	14	0·95	12·55	2·97	0·32	4·23	1·00	0·95	12·55	2·97	0·46	6·08	1·44	3·16	41·74	9·87	0·42	G.1435 Paralectotype
S. minor	15	0·70	11·13	1·80	0·93	6·20	1·00	0·81	12·88	2·08	0·42	6·68	1·08	2·35	37·36	6·03	0·37	W.1283(1)
S. minor	16	0·67	10·79	2·39	0·28	4·51	1·00	0·84	13·53	3·00	0·42	6·76	1·50	2·46	39·61	8·78	0·40	W.1283(2)
syn. attenuatus	17	0·56	10·59	2·43	0·23	4·35	1·00	0·75	14·18	3·26	0·42	7·94	1·83	1·93	36·48	8·39	0·36	G.176 Lectotype
S. multituberculata	18	1·47	11·76	2·07	0·71	5·68	1·00	1·66	13·29	2·34	1·07	8·56	1·51	4·14	33·14	5·83	0·33	G.175 Holotype
S. multituberculata	19	1·47	12·36	2·89	0·51	4·28	1·00	1·65	13·87	3·24	0·89	7·48	1·75	4·32	36·33	8·49	0·36	G.175 Paratype
S. multituberculata	20	1·61	11·63	2·37	0·68	4·91	1·00	1·84	13·29	2·71	1·07	7·73	1·57	5·05	36·48	7·43	0·36	G.175 Paratype
S. tuberculata	21	2·21	13·64	3·60	0·61	3·79	1·00	2·33	14·39	3·80	0·88	5·41	1·43	6·35	39·18	10·34	0·39	G.172 Lectotype
syn. incertus	22	2·57	11·76	3·00	0·86	3·92	1·00	3·14	14·38	3·67	1·07	4·90	1·35	9·14	41·83	10·67	0·42	W.1276 Lectotype
syn. roseus	23	2·29	12·12	3·20	0·71	3·79	1·00	2·43	12·88	3·40	0·89	4·73	1·25	8·50	45·08	11·90	0·45	W.1278

undue compression. When each intersetal distance is to be measured the glass is depressed sufficiently to flatten the body surface between the two adjacent setae. A measurement of the arc rather than the chord between the two setae is thus obtained. Very large intersetal distances, for instance *dd*, which may exceed one half of the circumference, are measured in two or more sections. Intersetal distances are expressed in millimetres and, to allow comparison between specimens, are also expressed relative to a constant total (periphery) of 100. Direct comparison of ratios between individuals without recourse to additional computations is also facilitated by stating the distances as ratios relative to one of the distances (*ab*) expressed as unity and by giving the ratio of the dorsal median intersetal distance (*dd*) to the circumference of the segment (*u*). In the computer study, paired intersetal distances (*ab, bc, cd*) were each averaged and *dd* was omitted as it was assumed that for *n* intervals the degrees of freedom were *n*-1. Four attributes (*aa, ab, bc*, and *cd*) were therefore used in the computations.

Inter-taxon (i.e. inter-ratio) distances were calculated after standardization of attributes (setal ratios) according to the Euclidean model of Burr (1968); the subsequent fusion strategy was the same author's 'incremental sum of squares' (Burr 1970), which minimizes the increase in within-group sum of squares at each fusion.

Results. The dendrogram representing relative distances of intersetal ratios is given in Fig. 7. *Conclusions.* The morphological homogeneity of the genus *Simsia* is reflected in the intersetal ratios of the constituent species. Thus overlap of ratios between unquestionably distinct morphospecies is frequent and suggests that ratios of individual specimens would be of limited value for specific identification in this genus. Whether intersetal ratios of the constituent species form parameters diagnostic of each species requires investigation of larger samples than are at present available. From the dendrogram some differentiation of intersetal ratios can nevertheless be seen to have accompanied speciation as only two of the eight species studied occur on both branches of the major dichotomy (final fusion at greatest 'intertaxon'

distance) and, usually, individuals or representatives of synonyms of a single species fuse at small intertaxon distances. One of the taxa, *S. intermedia*, which appears to cross the major dichotomy does not indisputably do so as only its subspecies *S. i. papillata* occurs on one of the branches and the affinity of this subspecies with *S. intermedia*, as adjudged from general anatomy, cannot be considered settled. It shows close general resemblance to *S. minor*, with which it clusters in the dendogram. Identification with *S. intermedia* was determined by the mutual possession of tufted nephridia which are not known in *S. minor*. Specific distinction from both *S. minor* and *S. intermedia* cannot be ruled out on present evidence.

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Abbreviations used in figures

d.p. = dorsal pore, ♀ p. = female pore, g.m. = accessory genital marking, gl. a. = glandular area, gl. m. = glandular (?) mass, l.g.m. = lateral accessory genital marking, ♂ p. = male pore, m.g.m. = median accessory genital marking, np. = nephropore, pr.d. = prostatic duct, pr.g. = glandular portion of prostate, sem. ch. = seminal chamber, sp. amp. = spermathecal ampulla, sp.d. = spermathecal duct, sp. div. = spermathecal diverticulum, sp.p. = spermathecal pore, v.d. = vas deferens.

H

CORRECTION AND ADDITIONS TO REVISION OF AUSTRALIAN SPECIES OF THE GENUS *STENUS* LATREILLE (COLEOPTERA; STAPHYLINIDAE)*

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In my 'Revision of the Australian Species of the Genus *Stenus* Latreille' (*Mem. nat. Mus. Vict.* 31: 55-80) there is a misprint on page 55 line 20 from below—'any of the collections quoted below.' should be followed by the whole text of p. 56 from line 16 from above ('This species must be regarded . . .') to line 9 from below ('but are only helpful for identification').

After finishing the manuscript of the revision I obtained some supplementary material from the UMQ and SAM; also I had the opportunity to revise the BM-collection in London, and the collection of the Field Museum of Natural History, Chicago. The total number of Australian specimens is 194.

Stenus cupreipennis Macleay 1 ♂ Melbourne, E. Fischer; 1 ♂, 1 ♀ Richmond, Bryant; 2 ♂ ♂, 5 ♀ ♀ N. Sydney, Bryant; 1 ♀ Gayndah, coll. Sharp, all BM; 2 ♀ ♀ Neu-Holland (FMCh).

S. janthinipennis Lea 2 ♂ ♂, 3 ♀ ♀ Kimberley, Mjöberg (FMCh).

S. olivaceus Macleay 1 ♂ Clarence River (BM); 1 ♂, 1 ♀ Cairns; 1 ♀ Brisbane; 1 ♂ Maryborough; 1 ♀ Black Rgs. (all FMCh).

S. atrovirens Fauvel 1 ♀ Qd. (FMCh).

S. macellus Fauvel 1 ♀ King George's Sound (BM).

S. convexiusculus L. Benick 1 ♀ Clarence River; 1 ♀ Maryborough (FMCh).

S. caviceps Fauvel 1 ♂, 3 ♀ ♀ Lockerbie, Cape York, 6-10.6. 1969, Monteith (UMQ coll. m.).

S. villosiventris Lea 2 ♂ ♂, 2 ♀ ♀ N.S.W. (BM FMCh); 1 ♀-cotype (BM); 1 ♂, 2 ♀ ♀ Windsor (FMCh).

S. cursorius L. Benick 3 ♂ ♂, 2 ♀ ♀ Adelaide River (BM).

S. gayndahensis Macleay 1 ♀ Moreton Bay (BM).

S. piliferus obesulus Fauvel 2 ♂ ♂ Australia (BM); 2 ♂ ♂, 1 ♀ Clarence River, Lea (SAM); 1 ♂, 4 ♀ ♀ Tweed River, Lea (SAM); 1 ♂ Richmond River (SAM); ♂-type and 3 ♀ ♀-paratypes (BM); 1 ♂, 3 ♀ ♀ Blackall (FMCh); 1 ♂ Townsville (BM); 2 ♀ ♀ Brisbane (BM FMCh); 1 ♀ N-Qd., Blackburn (SAM); 1 ♂ Bowen, A. Simson (SAM); 1 ♀ Magnetic Is., Lea (SAM); 15 ♂ ♂, 9 ♀ ♀ Bamaga, Cape York, 15-18.6. 1969, G. Monteith (UMQ coll. m.).

S. coeruleus Waterhouse 1 ♀ N.S.W. (FMCh); 6 ♂ ♂, 2 ♀ ♀ Ourimbah, Bryant (BM); 7 ♂ ♂, 5 ♀ ♀ Richmond River (BM FMCh); 1 ♀ Clarence River (BM); 1 ♂ Malanda, Mjöberg (FMCh); 2 ♀ ♀ Gosford (BM); 3 ♂ ♂ Sydney distr. (BM); 1 ♀ Sydney (FMCh); 1 ♂, 2 ♀ ♀ Nov. Holl., Simson (BM); 1 ♂, 1 ♀ Port Bowen, coll. Sharp (BM); 1 ♀ Kuranda, Dodd (BM), 1 ♂ Bellenden Ker (FMCh); 2 ♂ ♂, 2 ♀ ♀ Blackall Ra. (BM FMCh); 2 ♂ ♂, 3 ♀ ♀ Cairns distr., Lea, Dodd (SAM FMCh).

S. pseudocoeruleus Puthz 1 ♂, 1 ♀ Hambledon (FMCh); 1 ♀ Bellenden Ker (FMCh).

S. improbus Puthz 2 ♂ ♂, 2 ♀ ♀ N. Qd., Blackburn (SAM coll. m.).

S. platythrix Puthz 1 ♂ Kuranda; 1 ♀ Cairns; 1 ♀ Bellenden Ker (all FMCh).

S. bifenestratus L. Benick 2 ♂ ♂, 1 ♀ W. Aust. BM FMCh).

S. guttulifer Waterhouse 5 ♂ ♂, 6 ♀ ♀ King George Sound, coll. Sharp (BM); 1 ♂ Mun-

daring, Bryant (BM); 5 ♀ ♀ Albany, J. J. Walker (BM FMCh).

S. maculatus Macleay 1 ♀ Australia, coll. Sharp; 1 ♂ Qd.; 1 ♀ Blackall Ra., Wilson; 2 ♂ ♂ Clyde River, coll. Sharp; 1 ♂, 1 ♀ Tambourine Mts., R. E. Turner; 1 ♀ Wide Bay, coll. Sharp; 2 ♂ ♂ Moreton Bay, coll. Sharp (all BM); 1 ♂ Millstream Falls via Ravenshoe, 9.8.1968, T. Weir (UMQ); 1 ♂, 1 ♀ Richmond River; 5 ♂ ♂, 3 ♀ ♀ Sydney, coll. Sharp; 1 ♂ N. Sydney Ryde, Bryant (all BM).

S. pustulifer Fauvel 1 ♂ Blue Mts., Bryant; 1 ♂ Illawarra, Bryant; 1 ♀ Nat. Pk. N.S.W., Carter; 1 ♀ (cf.) Ourimbah, Bryant (all BM).

TASMANIAN SNAIL REFERRED TO THE GENUS *VICTAPHANTA* (STYLOMMATOPHORA: PARYPHANTIDAE)

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Abstract

The genus *Melavitrina* Iredale (1933) is placed in the synonymy of *Victaphanta* Iredale (1933) and the distribution of the three species of *Victaphanta* is discussed. The anatomy of the Tasmanian species *Victaphanta milligani* (Pfeiffer 1853) is described.

Introduction

Following recent work on the Victorian paryphantid genus *Victaphanta* Iredale 1933 (Smith 1969, 1970), the closely similar group of snails from W. Tasmania belonging to the genus *Melavitrina* Iredale 1933 were considered. Two species are described for the genus, *M. milligani* Pfeiffer (1854) and *M. fumosa* Tenison-Woods (1878) and these have often been closely compared to the *Victaphanta* species (Tenison-Woods 1878, Murdoch 1904, Cox and Hedley 1911, Davies 1912). Iredale's (1933) description of *Melavitrina* was not considered sufficient to separate these species from *Victaphanta* and Tenison-Wood's description of *M. fumosa* was not considered sufficient to separate this species from *M. milligani*. The object of this paper is to establish *Victaphanta milligani* as the single Tasmanian species of this genus, and to relegate *Melavitrina* and *fumosa* to the synonymy of these taxa.

Generic Placement

The genus *Victaphanta* was redescribed by Smith (1969). Both Iredale's scant description of the genus *Melavitrina*, and the shell and other anatomical features of the type species *M. milligani* fall within that description. Iredale (1933) differentiates the genus from *Helicarion* Ferussac and *Paryphanta* Albers because the last whorl is large with an 'open mouth' and the surface is shining black. However, the slight enlargement of the last whorl compared to the two Victorian *Victaphanta* species is here considered of specific significance. The shell being thin, composed mainly of conchin with very little calcareous material, umbilicus nearly closed, glossy with the inner whorls white to yellow and outer whorl dark brown, are all features of the genus *Victaphanta*.

With the inclusion of the Tasmanian species in *Victaphanta,* the number of species increases to three and gives a circum-Bass Strait distribution for the genus (Pl. 9, fig. 7). This is further reinforced by the discovery of sub-fossil shells very similar to *V. milligani* in the dunes of Flinders Island giving a date for the existence of this fauna of up to at least 6,000 years ago (E. D. Gill pers. comm.). All three species are confined to the wet temperate rain-forest areas.

Victaphanta **milligani** (Pfeiffer, 1853)
(Pl. 9, figs. 1-6)

Vitrina milligani Pfeiffer, 1853, *Monographia Heli-ceorum Viventium*, Lipsiae 3: 4

Vitrina milligani Pfeiffer, 1954, *Proc. zool. Soc. Lond.* 20 (1852): 56

Helicarion milligani Gray, 1855, *Cat. Br. Mus. nat. Hist., Pulmonata* 1: 68

Vitrina milligani Pfeiffer, 1856, *Malakozoologische Blatter,* Cassel, 2: 116

Vitrina milligani Shuttleworth, 1856, *Notitiae Malacologicae*, Leipzig, 1: 16

Paryphanta milligani Albers, 1861, *Die Heliceen.* Leipzig, p. 48

Vitrina milligani Reeve, 1862, *Conch. Icon.* 13, *Vitrina* sp. 18

Vitrina milligani Cox, 1868, *Monograph of Australian Land Shells*, Sydney, p. 82, pl. 14, figs. 2-2a

Helicarion fumosa Tenison-Woods, 1878, *Proc. Linn. Soc. N.S.W.* 3: 124, pl. 12, figs. 3-3a

Helicarion milligani Tryon, 1885, *Man. Conch.* (2) 1: 172, pl. 26, figs. 11-12

Paryphanta fumosa Murdoch, 1904, *Trans. Proc. N.Z. Inst.* 36: 156, pl. 6

Paryphanta milligani Petterd and Hedley, 1909, *Rec. Aust. Mus.* 7 (4): 287

Paryphanta fumosa Petterd and Hedley, 1909, *Ibid.*, p. 287

Paryphanta milligani May, 1921, *Check-list of the Mollusca of Tasmania*, p. 92.

Paryphanta milligani var. *fumosa* May. 1921, *Ibid.*, p. 92

Melavitrina milligani Iredale, 1933, *Rec. Aust. Mus.* 19 (1): 40

Melavitrina milligani Iredale, 1938, *Aust. Zool.* 9 (2): 116

Melavitrina fumosa Iredale, 1938, *Ibid.*, p. 116

Melavitrina milligani Macpherson, 1958, *Illustrated Index of Tasmanian Shells*, p. 46, pl. 42, fig. 13

DIAGNOSIS Paryphantid snail, shell depressedly globose, thin, composed mainly of conchin, glossy, inner whorls white to yellow to dark blown, spire nearly flat, suture deeply impressed, last whorl wide, aperture large, oblique, umbilicus almost closed, fine concentric lines on upper surface, lower surface almost smooth. Animal black with orange foot and mantle edge. Pharynx long, cylindrical, radula spatulate, without rachidian, teeth aculeate, unicuspid, approximate formula 38-0-38 to 41-0-41, of 78-86 rows. Reproductive system simple, vas deferens free from common duct, attached to outer wall of vagina, running in a loop past genital atrium and entering penis at posterior end, penis longer than vagina.

TYPE MATERIAL Lectotype, here designated, and two paralectotypes in the British Museum (Natural History) No. 1969265 collected from a small island in Macquarie Harbour, Tasmania (probably by a Mr. Milligan). Dimensions of lectotype (from photograph), max. diam. 21.9 mm, min. diam. 15.8 mm.

DISTRIBUTION The animal appears to be confined to the W. or N.W. portion of Tasmania but the lack of comprehensive collecting makes a precise statement of locality impossible. Specimens are in museum collections from the forest areas of the Duck River, Montague River and Arthur River of the N.W. corner of Tasmania, and from a wide area to the N. and E. of Strahan and Queenstown. In this latter area specimens were collected from Mt. Zeehan, Mt. Farrell, Mt. Pelion as well as around Queenstown and Macquarie Harbour. They also presumably occur at localities between these two areas but more collecting is needed. Specimens have also been reported (A. J. Dartnall pers. comm.) from the Port Davey area of S.W. Tasmania so the species may occur in all the wet forest areas of the W. half of that State.

ANATOMICAL NOTES Four specimens were used in this study, two collected from near Montague River by R. C. Kershaw, one Australian Museum specimen collected near Zeehan, and one from A. J. Dartnall, collected between Queenstown and Zeehan. The anatomy of *M. fumosa* has been described by Murdoch (1904) and both his findings and the present study show the anatomy to be very similar to that described for the other two species of *Victaphanta* (Smith 1970). It was therefore considered necessary to describe only those aspects of the anatomy which differ from those described for *V. atramentaria* and *V. compacta*.

PALLIAL REGION This region is similar to that of the other species, with the lappets around the pulmonary orifice, the termination of the rectum in a deep groove just posterior to the orifice, and the pseudoureter running along side of the rectum. The kidney appears larger than in *V. atramentaria* and there is no sign of the mantle gland on the posterior margin of the collar as suggested for that species by Smith (1970).

ALIMENTARY SYSTEM The only difference in the alimentary system between this species and the two Victorian species is in the radula. The radula is spatulate, without a rachidian and the teeth are aculeate, unicuspid with oblong base plates. The teeth formula is

38-0-38 to 41-0-41 x 78 to 86 rows. The teeth increase in size from the margins to a maximum about four teeth from the centre, and then decrease sharply. This compares with teeth formula of 64-0-64 to 67-0-67 x 102-105 rows for *V. atramentaria* and 60-0-60 to 63-0-63 x 99-103 rows for *V. compacta*.

The pharynx is very large and muscular, filling the head-foot cavity. The oesophagus arises as a narrow tube from the dorsal surface of the pharynx about a third of the way along its length. The salivary glands are fused into a single almost ovoid body, although its origin as two separate bodies can be seen by the lobing.

REPRODUCTIVE SYSTEM This system differs from that of the other two *Victaphanta* species in three respects (Pl. 9, fig. 6). 1. The common duct is similar but the prostate gland is mainly confined to the anterior end of the duct with only a small amount at the posterior? end. 2. In the Tasmanian species the spermathecal duct is short. The simple sac-like spermatheca is situated in a fold of the anterior end of the common duct immediately posterior to a point where the vas deferens emerges from the common duct to run freely along the outside of the vagina to the posterior end of the penis. 3. The penis is a long, uniformly thin tubular structure approximately 1·5 times longer than the vagina.

The three species appear very similar in:
1. The structure of the hermaphrodite gland and the receptaculum seminalis.
2. The internal surface of the penis which consists of a covering of conical papillae with grooves running from the point of entry of the vas deferens.

REMARKS The original description of *Victaphanta milligani* Pfeiffer is here recorded as 1853, *Monographia Heliceorum Viventium*, Lipsiae, 3 : 4. Most authors, including Pfeiffer himself in the above reference, state the original reference as *Proc. zool. Soc. Lond.* 20 (1852): 56. However, the publication date for the latter reference is March 22nd, 1854; thus the former reference has priority. This probably occurred through an oversight by the editor of the *Proceedings* as it appears that Pfeiffer

expected the description to appear in the issue prior to the publication of the third volume of his *Monographia*. The descriptions in both references are identical, but this priority should be borne in mind when dealing with other species described in these papers.

H. fumosa Tenison-Woods 1878 is here reduced to the synonymy of *V. milligani* as the minute differences used to separate it from *milligani* fall within the intraspecific variation of that species. One of us (RCK) has collected a series of specimens from the one locality on the Montague River which show all stages of variation between the two 'forms'.

Victaphanta milligani differs from the two Victorian species of the genus in the size and shape of the shell, the number of teeth per row in the radula, and the structure of the reproductive system. The shell is smaller (maximum diameter approximately 24 mm), and characterised by its brown colour, the extreme enlargement of the last whorl, and the wide oblique aperture approaching that of a vitrinid. The radula averages only 38-41 teeth per half row compared to 60-63 for *V. compacta* and 64-67 for *V. atramentaria*. The reproductive system differs from the Victorian species of the genus in two important respects. The spermathecal duct is short terminating in a simple sac-like spermatheca situated in the region of the junction of the common duct with the vagina. The other species have long spermathecal ducts, equal in length to the common duct. Secondly, the penis is approximately 1·5 times the length of the vagina instead of being equal to or shorter than the vagina as in the other species.

It was suggested by Solem (1959) that the genus *Melavitrina* could be referable to *Wainuia* Powell 1930 from New Zealand. However, the anatomy differs from that of the type species *Wainuia urnula* (Pfeiffer 1855) as described by Murdoch (1903). The radula of *W. urnula* has a teeth formula of 14-0-14, much less than *V. milligani* and the teeth have no distinct oblong base plate.

In *W. urnula* the second tooth from the margin in each row is the largest and the remainder diminish in size towards the centre. In all three *Victaphanta* species the largest

tooth is the fourth or fifth from the centre and the teeth diminish in size from this point. The other main differences are seen in the reproductive system. *Wainuia* has a finger-like, tubular appendage to the posterior end of the spermatheca, and the posterior part of the penis is expanded into a sac-like portion. These two characters are not seen in *V. milligani.*

Acknowledgements

We thank the Mollusc Section of the British Museum (National History) for providing photographs of the lectotype of *Vitrina milligani*, Dr. W. F. Ponder of the Australian Museum for the loan of the type of *Helicarion fumosa* and a large collection of dry and spirit specimens, and Mr. A. J. Dartnall and Mrs. E. Turner of the Tasmanian Museum for information and specimens.

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Explanation of Plate 9

Fig. 1-2—Lectotype of *Vitrina milligani* Pfeiffer, dorsal and ventral views, BM (NH) Reg. No. 1969265.

Fig. 3-5—Holotype of *Helicarion fumosa* Tenison-Woods, dorsal, lateral and ventral views, AM. C78335. (Photo by E. Rotherham).

Fig. 6—Diagram of reproductive system of *Victaphanta milligani.*

Fig. 7—Distribution map of the three species of *Victaphanta.* SF on Flinders Island denotes the site of subfossils similar to *V. milligani.* (Drawn by Miss R. Plant).
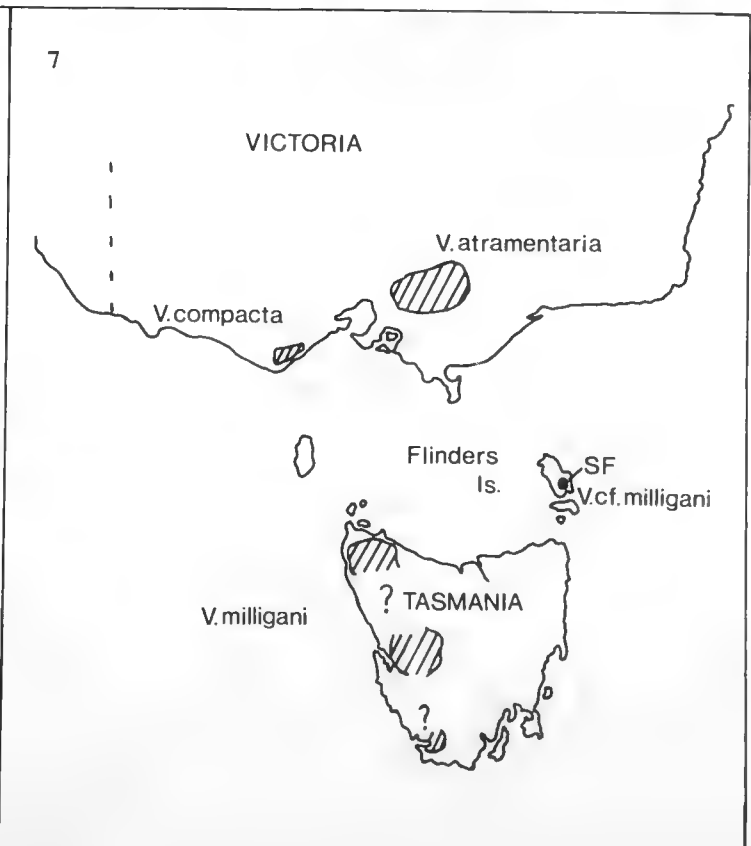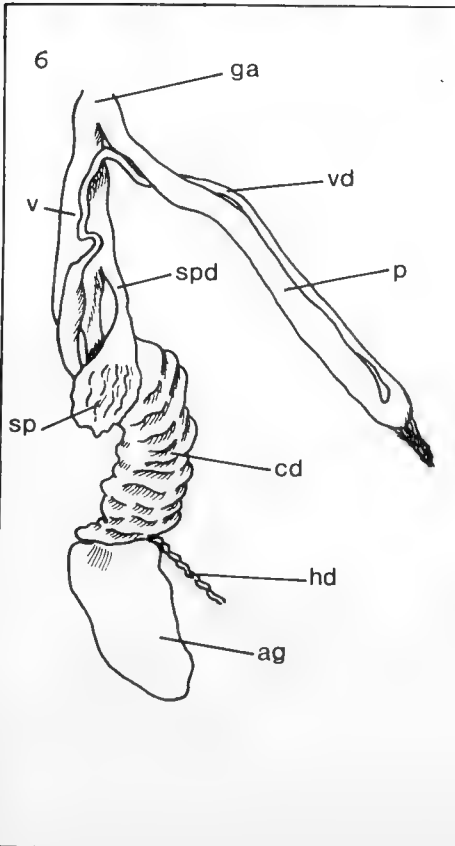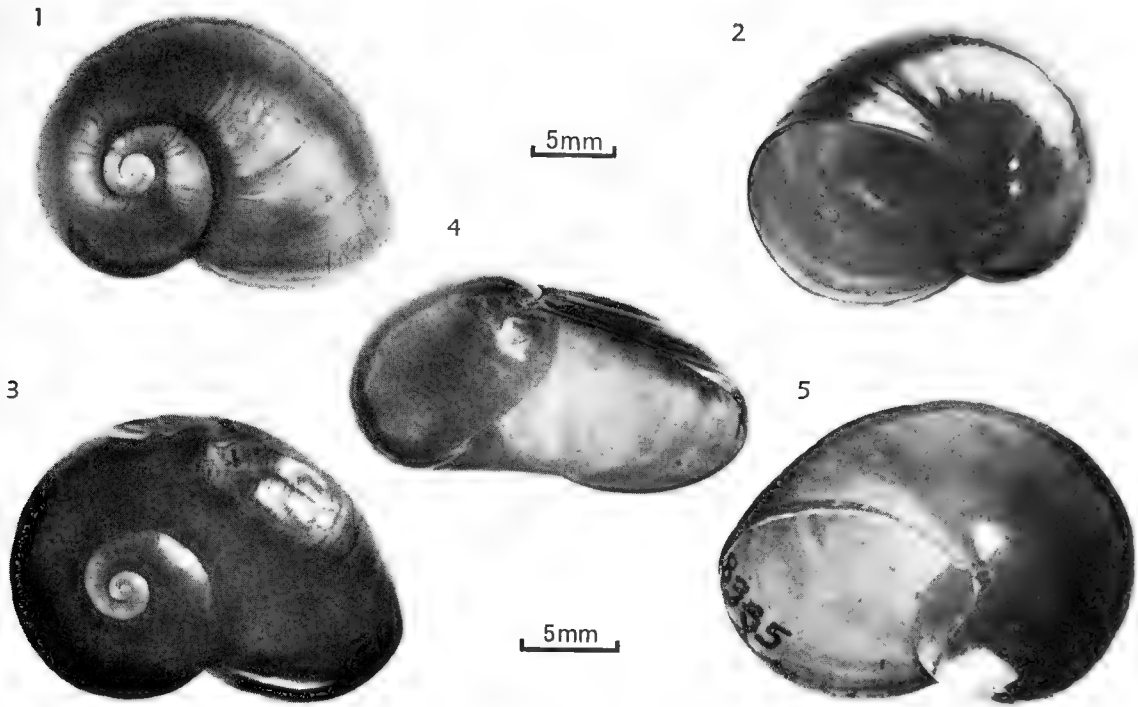
ZONITID SNAILS (GASTROPODA : PULMONATA) INTRODUCED INTO VICTORIA

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Abstract

Five species of European zonitid snails are listed as having been introduced into Victoria, one as early as 1850. Two species, *Vitrea contracta* (Westerlund, 1873) and *Oxychilus draparnaldi* (Beck, 1837) are recorded from Australia for the first time. Three of the five species have become established.

Introduction

This paper reviews knowledge of introductions of zonitid snails into Victoria and assists field collectors to identify them. It is based on an examination of the collections in the National Museum of Victoria and on the writer's field work from August 1969 to the end of 1970.

The Zonitidae is a widespread family of pulmonate land snails, generally small to medium sized (2 to 20·0 mm diam.) with low-spired, thin, transparent to translucent shells, hiding under stones and litter by day, and eating non-green vegetable matter or small animals such as other snails and slugs. Several species have been introduced by European man into America, Africa and Australasia (Ellis 1951, pp. 193-195).

Five species of European Zonitidae have been identified as introductions: *Euconulus fulvus* (Müller, 1774), *Vitrea contracta* (Westerlund, 1873), and three species of *Oxychilus* (Fitzinger, 1833), viz. *O. cellarius* (Müller, 1774), *O. draparnaldi* (Beck, 1837) and *O. alliarius* (Miller, 1822). *Vitrea contracta* and *Oxychilus draparnaldi* are here recorded from Australia for the first time. In addition, *Zonitoides nitidus* (Müller, 1774) has been recorded (Musson 1890, p. 894 and Taylor 1914, p. 150) but the records are probably in error for *O. alliarius* which was erroneously recorded from N.S.W. and New Zealand (Taylor 1914, p. 66). *Z. nitidus* is an obligate hygrophile (Boycott 1934, p. 13) and therefore an unlikely candidate for successful introduction to Australia.

Identifications in this paper are based on shell characters and the external features of the animal when available. Where possible the descriptions are based on Victorian specimens; otherwise they are taken from Taylor (1914), Janus (1965) or Kuiper (1964, *V. contracta*). Zilch (1959, p. 277) has placed *Euconulus* in the family Euconulidae, but its inclusion in the Zonitidae by Ellis (1951) is adopted. Distributions outside Australia are taken from Ellis (1951) unless otherwise stated. The references given under each species cover (a) The original description and (b) The introduction into the various States of Australia.

Abbreviations:

H. = height, W. = width (diameter), WH. = number of whorls, NMV = National Museum of Victoria.

Key to Field Identification of Zonitids Introduced into Victoria

This key separates the various species from each other, and from other similar snails in the Victorian fauna.

Land snails with glossy, semi-transparent or translucent more or less smooth shell; animal with pedal groove defining the foot margin and capable of complete withdrawal into shell.

1. Shell turbinate 2
1. Shell depressed helicoid 3
2. Umbilicus present, W. under 4·0 mm
    Laoma penolensis
2. Umbilicus absent, W. under 3·0 mm
    Euconulus fulvus
3. Umbilicus present 4
3. Umbilicus absent, W. under 4·0 mm
    Prolesophanta dyeri
4. Shell W. under 4·0 mm 5

4. Shell W. over 4·0 mm   8
5. Shell whitish or colourless   6
5. Shell horn coloured   7
6. Umbilicus regular spiral   ..   *Vitrea contracta*
6. Umbilicus irregular spiral   ..   *Vitrea crystallina*
7. Aperture elongate ellipse, montane
                                            Delos nelsonensis
7. Aperture rounded ellipse, settled areas
                                            juvenile *Oxychilus?*
8. Shell yellowish or horn coloured   9
8. Shell greenish white, hyaline
                        Oxychilus alliarius var. *viridula.*
9. Shell polished with faint growth lines,
      colour paler below   11
9. Shell striated above, smooth below   10
10. Regularly striated above to periphery *Strangesta*
10. Irregular striae and close spiral lines above
                                    Echotrida strangeoides
11. Shell horn coloured   12
11. Shell greyish yellow, animal with brown
      spots on mantle edge   ..   *Oxychilus cellarius*
12. Shell W. 10·0-14·0 mm, animal deep blue
      grey   ..   ..   *O. draparnaldi*
12. Shell W. 4·0-7·0 mm, animal blue-black
      above, grey below, garlic odour. ..   *O. alliarius*

Family ZONITIDAE

Zonitids have a simple aperture to the spirally coiled shell. The animal has the foot margin defined by a pedal groove which may form a caudal mucus gland. The marginal teeth of the radula are aculeate, and the jaw is oxygnathous. The ovotestis is usually imbedded in the liver (Taylor, 1914, p. 1).

Genus **Euconulus** (Reinhardt, 1883)

Euconulus fulvus (Müller, 1774)
Figures 1-3

Helix fulva Müller, 1774, *Verm. Hist.* 2: 249.

Hyalina (Euconulus) fulva, Müller. Gabriel, 1928, p. 133.

DESCRIPTION: Shell very small, glossy, turbinate, reddish brown, no umbilicus, semi-transparent, last whorl with a blunt peripheral keel. Animal grey-black. H. 2·0-2·3 mm, W. 2·5-3·0 mm, WH. 5-6 (Janus 1965, p. 112).

DISTRIBUTION: Holarctic (Ellis 1951, p. 193). Introduced, Cann River, Victoria.

MATERIAL EXAMINED: Two shells in NMV collected at Cann River by J. Clark in March 1928 (Gabriel 1928, p. 133).

NOTES: Not to be confused with *Laoma penolensis* (Cox 1867), a native species, which is not glossy, has an umbilicus, and is common in coastal areas in Victoria.

Genus **Vitrea** (Fitzinger, 1833)

Vitrea contracta (Westerlund, 1873)
Figures 4-6

Zonites crystallina var. *contracta* Westerlund, 1873, Faun. Moll. Suec. p. 56.

DESCRIPTION: Shell very small, semi-transparent, milk-white (yellowish in life), spire depressed umbilicus small and regular, last whorl 0·3 larger than the penultimate. Animal greyish white.

H. 1·25 mm, W. 2·52 mm, WH. 4·5 (Kuiper 1964, p. 278).

H. 1·0 mm, W. 2·7 mm, WH. 4·5 (Geelong, Vict.).

DISTRIBUTION: Europe (Ellis 1951, p. 193). Introduced into Victoria and collected at Geelong.

MATERIAL EXAMINED: Two shells in NMV collected in garden, Geelong, 15 Oct. 1967 by R. Burn, identified by Dr. M. P. Kerney (in lit.).

NOTES: *V. contracta* is a new record for Australia, and is closely related to *V. crystallina* (Müller, 1774) which is recorded as introduced into 'S. Africa, New Zealand, Tasmania, etc.' (Ellis, 1951, p. 193). As *V. contracta* has been included in *V. crystallina* in the past (Taylor 1914, p. 113, etc.) some of these records may refer to *V. contracta. V. crystallina* is recorded as collected in gardens at Hobart by W. F. Petterd (Petterd and Hedley, 1909, p. 303).

Genus **Oxychilus** (Fitzinger, 1833)

DESCRIPTION: The three *Oxychilus* species identified in Victoria are small to medium sized snails with depressed spired, polished, semi-transparent shells of various shades of horn colour, paler below than above, and with a wide umbilicus.
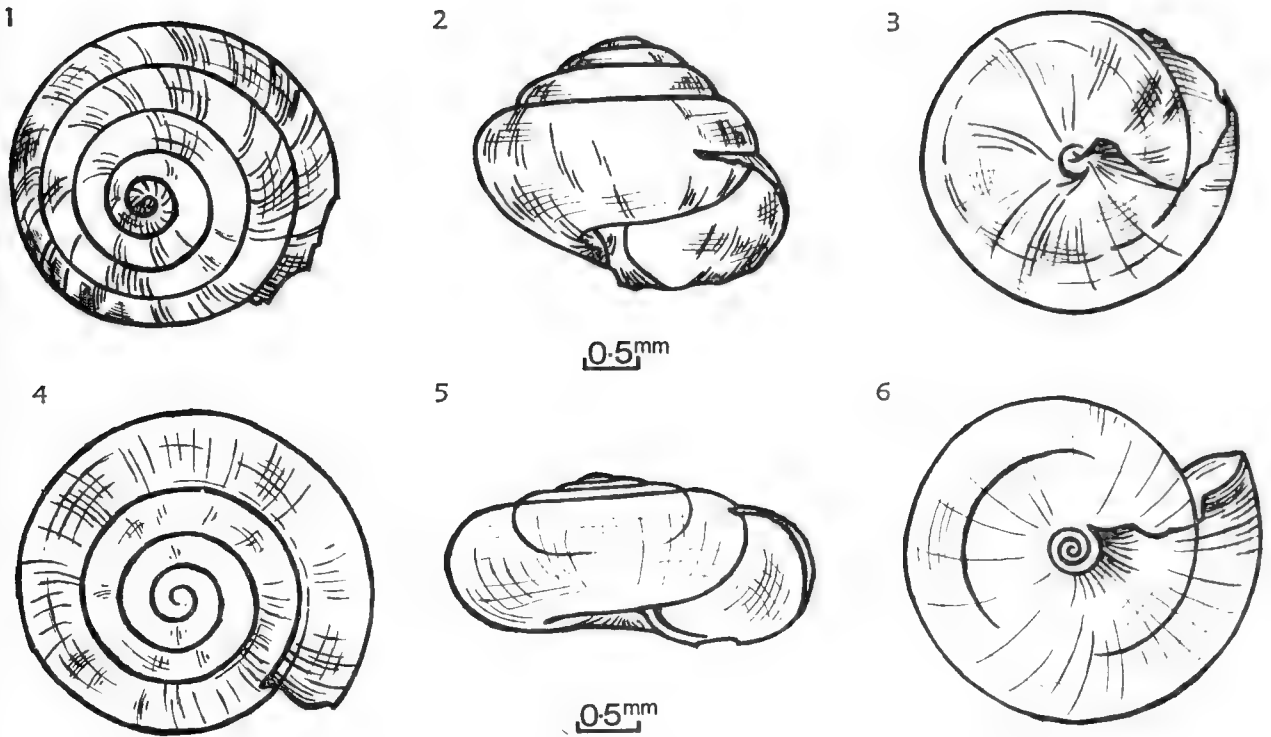
Figs. 1-3—*Euconulus fulvus* (Müller), Cann River, Vict. Dorsal, lateral, and ventral views.
Figs. 4-6—*Vitrea contracta* (Westerlund) Geelong, Vict. Dorsal, lateral and ventral views.

NOTE: Live specimens are preferable for identification. Empty shells (especially if not fresh) may present difficulties, and so may preserved animals to a lesser extent, as some colours fade in alcohol and it is not always possible to get the animals fully relaxed.

Oxychilus cellarius (Müller, 1774)
(O. c. f. cellarius, Plate 10, figures 1-3)

Helix cellaria, Müller, 1774, *Verm. Hist.* 28 : 230.

Helix sydneyensis, Cox, 1864, p. 37.

Helix (Hyalina) sydneyensis, Cox. Legrand, 1871: 63.

Helix cellaria. Petterd, 1879, p. 96.

Zonites cellarius, Müller, 1774. Musson, 1890, p. 893.

DESCRIPTION: Shell medium sized, spire low, umbilicus 0·17-0·14 of shell diameter, colour greyish yellow and paler below than above, surface polished, growth lines faint, suture may appear channelled, aperture elliptical. Animal pale grey, foot nearly white, darker with a bluish grey tinge on the head and above the lateral line, mantle edge grey speckled with brown, spots vary from a stipple to well marked mottled but they may disappear in spirit specimens, mantle edge slightly yellowish compared with the body.

H. 5·0 mm, W. 10·0 mm, WH. 5-6 (Taylor 1914, pp. 31-32) but up to H. 4·0 mm, W. 9·0 mm, WH, 4-5 in Victoria, (Mt. Dandenong, 18 Oct. 1970).

DISTRIBUTION: Britain, Central Europe, W. Mediterranean; introduced to Scandinavia and Finland, N. America, S. Africa, Australia (N.S.W., Vict., Tasm.), New Zealand, etc. (Ellis 1951, p. 194).

MATERIAL EXAMINED: In NMV seven empty shells of *O. cf. cellarius* from S. Melbourne, coll. C. J. Gabriel, no date. Six living specimens from a garden, S. Camberwell, coll. Mrs. M. Turnbull with one *O. alliarius*, 27 Aug. 1970. One living specimen from a road verge, coll. D. C. Long, 5 Sept. 1970. Six living specimens from the base of grass tufts, road

verge, Mt. Dandenong, coll. D. C. Long, 18 Oct. 1970. Four living specimens and one dead shell near Mansfield school, coll. Sacred Heart College students, 9 Nov. 1970.

NOTES: Though there is no dated pre-1970 Victorian material in NMV, Musson (1890 p. 893) gives it from Melbourne on the authority of Kershaw, and Taylor verified specimens collected from Port Melbourne in October 1896 by J. H. Gatliff (Taylor 1914, p. 44). *Helix sydneyensis* Cox, 1864 has been identified as a synonym for *O. cellarius* (Cox 1909, p. 76), but following his original description Cox (1864, p. 37) remarked on differences of colouring and spire height between his specimens and *O. cellarius*. It would be useful to re-examine Cox's type specimens. One of the six *O. cellarius* collected at Mt. Dandenong on 18 Oct. 1970, laid eggs in the NMV on 21 Oct. 1970 (per Dr. B. J. Smith). The maximum shell size of these specimens is given above.

Oxychilus draparnaldi (Beck, 1837)
Pl. 10, figures 4-6

Helicella draparnaldi Beck, 1837, *Index Moll.* 6.

DESCRIPTION: Shell medium sized, polished with a slightly raised conical spire, last whorl slightly dilated at the aperture, twice as broad as the penultimate whorl, aperture elliptical (more elongate than *O. cellarius* and *O. alliarius*), whorls with irregular growth lines (more prominent than *O. cellarius* and *O. alliarius*), colour pale to dark horn and paler below, umbilicus about 0·13 of shell diameter. Animal blue-grey, including the foot of which the central zone is paler, mantle edge dark grey and unspotted, appears dark through the shell.
H. 6·0 mm, W. 15·0 mm, WH. up to 7 (Taylor 1914, p. 20) up to H. 6·0 mm, W. 13·0 mm, WH. 6 in Victoria (Murrumbeena 28 Apr. 1970).

DISTRIBUTION: Europe (introduced in N.), British Isles but mostly in S. and W., introduced in N. America and S. Africa (Ellis 1951, p. 194), Morocco, Algeria, W. Asia (Taylor 1914, p. 29).

Introduced into Victoria; coll. various Melbourne suburbs out to Mt. Dandenong, and possibly Mansfield.

MATERIAL EXAMINED: In NMV 24 collections from 22 localities in the Melbourne area, one possible coll. near Mansfield School by Sacred Heart College students, 9 Nov. 1970.

NOTES: This species has not been previously recorded from Australia. Specimens in the NMV collected prior to 1970 were all identified as *O. cellarius*. *O. draparnaldi* seems to be especially frequent in the outer suburbs of Melbourne. The earliest dated NMV shell was collected by 'J.D.' at Richmond in 1902. Three undated specimens were collected by C. J. Gabriel in his glasshouse at Abbotsford and six undated specimens from his fernery. Four dead shells were found with two living specimens (now in NMV) at Beaumaris on 28 Mar. 1970 by the writer, and sent to Dr. M. P. Kerney who commented 'The *Oxychilus* you send look to me exactly like *O. draparnaldi*' (in lit. 14 Apr. 1970). Taylor (1914, p. 22) states that each row of the radula of British specimens of *O. draparnaldi* typically has three tricuspid lateral denticles on either side of the median tooth, though some continental writers give the number as two to four. Dr. B. J. Smith prepared the radulae of two snails, one from Ivanhoe (coll. Gunner, 11 May 1970), and one from Greensborough (coll. G. Robertson 4 July, 1970). Both these radulae have two tricuspid lateral denticles per row. Some caution is therefore necessary about the identity of this introduced snail, even though its external features are in close agreement with *O. draparnaldi*. One possibility is that there are regional variants of *O. draparnaldi* and that the Victorian introductions are not from a British source. More radulae need to be examined.

Oxychilus alliarius (Miller, 1822)
Pl. 10, fig. 7-9

Helix alliaria Miller, 1822, Ann. Phil. N.S. 3: 379.
Zonites nitidus Müller, 1774, Musson 1890, p. 893.
Zonitoides nitidus Müller, Gabriel 1930, p. 187.
Zonitoides nitidus (Müller) 1774, Cotton 1954, p. 183.
Oxychilus alliarius (Miller) 1822, Cotton 1954, p. 183.
Oxychilus alliarius (Miller), Laws 1966, pp. 257-260.

DESCRIPTION: Shell similar in shape but smaller than the preceding two species, horn coloured, slightly paler round the umbilicus, glossy with regular week striations, convex above, flattened below, umbilicus 0·17 of shell width, aperture slightly elliptical (rounder in outline than *O. cellarius* and *O. draparnaldi),* spire slightly higher than *O. cellarius.* Animal slaty blue-black on head and above lateral groove, grey below groove, paling towards the foot which is grey, mantle edge grey, appears thinly edged dark grey through the shell.

H. 2·5 mm, W. 5·0-6·0 mm, WH. 4-4·5 (Taylor 1914, p. 59) up to H. 2·5 mm, W. 7·5 mm, WH. 5 in Victoria, waste ground, Oakleigh 5 July 1970).

DISTRIBUTION: Britain, Europe (Iceland, Scandinavia, Estonia to France and Poland), introduced into N. America, St. Helena, S. Africa, Juan Fernandez, Australia, and New Zealand (Ellis 1951, p. 194). Introduced into N.S.W., S. Australia, and Vict. where widespread. Common around Melbourne. Extremes are Hamilton (undated), Irymple (*O.* cf. *alliarius,* 1970), Bairnsdale (undated), and Rutherglen (*O.* cf. *alliarius,* 1954).

MATERIAL EXAMINED: In NMV numerous dead shells and preserved animals from 26 localities in Victoria.

NOTES: *O. alliarius* has not been formally recorded from Victoria before, though it is the most widespread introduced zonitid in Victoria and apparently the earliest introduced. Seven shells of this species from the R. A. Bastow Collection in NMV are labelled '*Zonites alliarius* Mull. 1850 Fitzroy Gardens' an ascription apparently overlooked for the last 120 years. The snail has been found mainly in gardens, under dwellings, and in cleared land, but there are two records of it in open sclerophyll forest with a mixed native and introduced mollusc fauna at Linton, 23 Nov. 1969 (Long 1970, p. 171). and "under stones in open forest," N. Ringwood, coll. B. Fuhrer 22 June, 1970.

O. alliarius emits a smell of garlic on withdrawing into its shell when alarmed, and when crushed alive, a feature not shared by *O.*

cellarius and *O. draparnaldi,* hence the specific name (Latin : allium = garlic) and the vernacular Garlic Snail. A variety with a greenish white shell (var. *viridula* Jeffreys, 1862) has been found in a garden at Oakleigh by the writer (Sept. 1969 - Apr. 1971). Laws (1966) noted differences between the first and second radula teeth and the spermatheca of S. Australian *O. alliarius* and the material described by Taylor (1914) and commented that the S. Australian introduction may be from a source outside the British Isles. The relative roundness of the shell aperture may be the cause of earlier mis-identifications of this species in Australia as *Z. nitidus.*

Discussion

The identification of introduced Zonitidae, especially *Oxychilus* spp., requires caution. Cox (1864) and Laws (1966) have remarked on differences between the specimens they examined and the descriptions available for European (mostly British) material. Externally the three *Oxychilus* spp. identified in Victoria resemble specimens of those species encountered by the writer in the course of local recording for the Conchological Society of Gt. Britain and Ireland's Census of Non-marine Mollusca in Britain from 1966 to 1969, but the apparent radula difference in *O. draparnaldi* has already been noted, and the maximum size of *O. alliarius* exceeds that published elsewhere (Taylor 1914, Janus 1965). Whether this is because the species encounters optimum conditions here or because the published dimensions are taken from a small sample is unknown. Evidence exists for suspecting that some of the Victorian introductions of *Oxychilus* are not from Britain but from mainland Europe, possibly the Mediterranean, though little is known of regional variation of *Oxychilus* spp. in Europe.

Field observations have so far indicated that the habits of *Oxychilus* in Victoria are similar to those of the genus in Britain. Most collections of *Oxychilus* in Victoria have been of one species, but all three were found by the writer within 200 m of each other at Mt. Dandenong on 18 Oct. 1970. Fifteen of the 72 collections of *Oxychilus* examined were not

fully identifiable, mostly because of poor or insufficient material, but in at least two cases species other than the three identified may be involved. Three living specimens were collected at Redcliffs on 1 Jan. 1970 by A. Borlace, and one dead shell, Mt. Buffalo Chalet, altitude 1,370 m, 14 Feb. 1970, coll. writer.

Little can be said about the introductions of *E. fulvus* and *V. contracta*. They do not appear to be widespread, though both being small could easily be overlooked. The dimensions of the Victorian *V. contracta* are larger than those given by Kuiper (1964, p. 278). In Feb. 1971 a brief search of the strawberry bed where *V. contracta* had been found in 1967 failed to produce any specimens.

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Explanation of Plate 10

Figs. 1-3—*Oxychilus cf. cellarius* (Müller), S. Melbourne, Vict. The spire is higher than typical *O. cellarius.*

Figs. 4-6—*O. draparnaldi* (Beck), Abbotsford, Vict. from C. J. Gabriel's glasshouse. Note typical dilation of last whorl.

Figs. 7-9—*O. alliarius* (Miller), Kew, Vict. 10 June 1941.
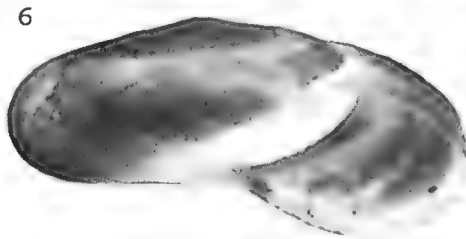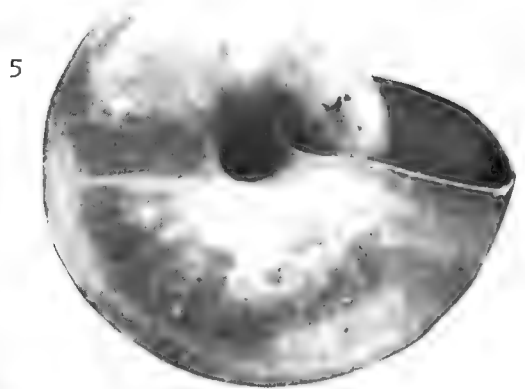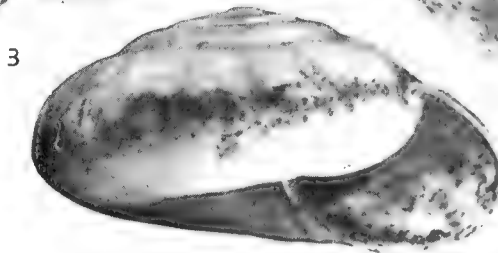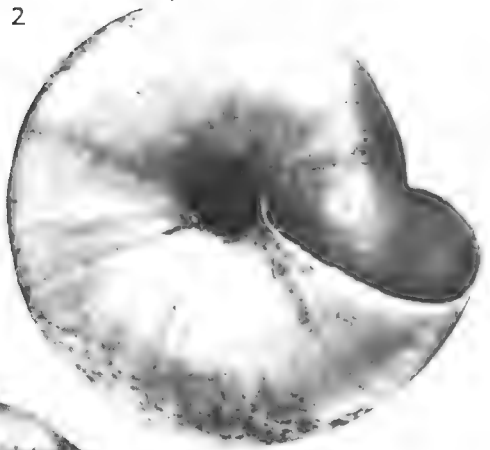
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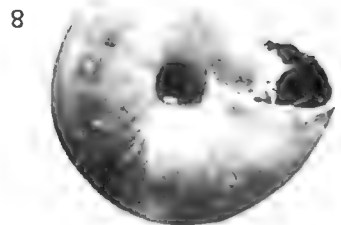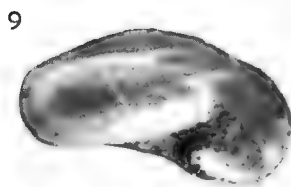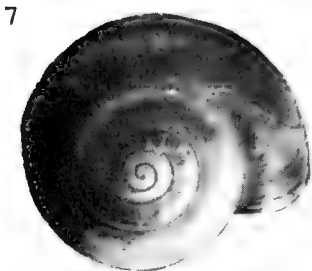
CATALOGUE OF GALAXIID TYPES (PISCES: GALAXIIDAE) IN THE NATIONAL MUSEUM OF VICTORIA, AUSTRALIA

By Joan M. Dixon
Curator of Vertebrates

Introduction

Fishes of the family Galaxiidae are found in Australia, New Zealand, South Africa and South America. As there is wide interest in the systematics of the family, this small catalogue has been prepared. Among the galaxiid types held in this museum are specimens of historical and scientific significance. It is important that the repository of such types be known. The condition of the types varies, but vertebral and fin features can be examined in the museum's X-ray apparatus.

The galaxiid collection other than types is extensive and in good condition. A wide range of species from within and outside Australia is held. Most of the specimens were donated by Dr R. Frankenberg, and have detailed labels. M.U.Z.D. = Museum of the Zoology Department, University of Melbourne. All are spirit specimens unless otherwise stated.

Order GALAXIIFORMES
Family GALAXIIDAE
Genus **Galaxias** Cuvier, 1816
Galaxias fuscus Mack, 1936

Mem. natn. Mus. Vict. 9: 100, fig. 1.
HOLOTYPE: A96, Rubicon R., Vict., donated A. C. Payne 18 Apr. 1935.
PARATYPE: A99, ditto.

Galaxias nigothoruk Lucas, 1892

Proc. R. Soc. Vict. 4: 27-28.
= *Galaxias coxii* Macleay, 1880

SYNTYPES: A408-11, Lake Nigothoruk, above the head of the Wellington R., Gippsland, Vict., coll. A. H. S. Lucas, M.U.Z.D. 197.

Galaxias ocellatus McCoy, 1866

Intercol. Exhib. Essays No. 7:18 (French ed.)
= *Galaxias truttaceus* (Cuvier, 1816).

?SYNTYPE: A444, River Yarra near Studley Park, Vict., June 1864. Labels enclosed with the above specimen correspond to Nat. Mus. Vict. specimen, old no. 56308, which appears to belong to the type series.

Galaxias parrishi Stokell, 1964

Rec. Dom. Mus., Wellington 5 (6): 47-48, fig.
HOLOTYPE: A242, Lake Bullenmerri, Vict., coll. R. H. Parrish, pres. 8 June 1964.

Galaxias parvus Frankenberg, 1968

Aust. Zool. 14: 270-274, Pl. 15.
PARATYPES: A392-400; A401-407 stained specimens, coll. Lake Peddar, S. Tasm., near mouth of the inflowing stream from Lake Maria, and including the stream itself up to 30 m from the mouth, Feb. 1967 by R. Frankenberg.

Galaxias pedderensis Frankenberg, 1968

Aust. Zool. 14: 268-270, Pl. 14.
PARATYPES: A379-387. Data as for *G. parvus*.

Galaxias pusillus Mack, 1936

Mem. natn. Mus. Vict. 9: 101, fig. 2.
= *Brachygalaxias pusillus*, Eigenmann, 1928
HOLOTYPE: A97, Cardinia Creek, Vict. about 50 km E. of Melbourne, Vict., obtained by A. Massola, 22 May 1936.
PARATYPES: A98, A388-90, ditto.

Genus **Paragalaxias** Scott, 1935
PARAGALAXIAS SHANNONENSIS Scott, 1935

Pap. Proc. R. Soc. Tasm. 1935: 41-6, Pl. 3.
PARATYPE: A413, Shannon R., Tasm., coll. 3 Dec. 1933.

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A NEW SPECIES OF *THALAINODES* (LEPIDOPTERA: GEOMETRIDAE-ENNOMINAE) FROM CENTRAL AUSTRALIA

By J. O. WILSON

42 Wilson Tce., Glenelg E., S. Australia 5045

A single female (the holotype) of this striking geometrid was collected by Mr Noel McFarland on 26 April 1966, 148 km S. of Alice Springs in Northern Territory, Central Australia. In late May, 1967, Mr McFarland and Mr T. R. Newbury collected a series of 14 more specimens of the same species (10 males, four females). This moth does not appear to be highly variable in colour or maculation. The most variable feature of its maculation is the black blotching on the hindwing. Males and females are similar in colour, maculation, and wing shape, but males have pectinate antennae, and most of the male specimens in the present series are smaller than the females.

Genus **Thalainodes** Lower (1902)

Trans. R. Soc. S. Aust. 1902, 26: 231.

Allied to *Thalaina;* differing in the frontal process in both sexes, and pectinate antennae in the male.

Type species: *Amelora tetraclada* Lower

Thalainodes tetraclada (Lower) 1900

Amelora tetraclada Lower, 1900, *Proc. Linn. Soc. N.S.W.,* 25: 406.

Locality: Broken Hill, N.S.W.

Thalainodes paronycha (Lower) 1900

Amelora paronycha Lower, 1900, *Proc. Linn. Soc. N.S.W.,* 25: 407.

Locality: Broken Hill, N.S.W.

Thalainodes nessostoma Turner 1919

Proc. Linn. Soc. N.S.W., 44: 386.

Locality: Bourke, N.S.W.

Thalainodes allochroa Lower (1902)

Trans. R. Soc. S. Aust., 26: 232.

Localities: Broken Hill, Bourke, N.S.W.

This genus appears to be confined to the dry country of the interior. Further collecting may show a much greater distribution for some of the species.

Thalainodes macfarlandi sp. nov.

Head (between antennal bases) white or greyish-white, with a prominent forward-projecting, bifurcate, heavily sclerotized frontal process (Pl. 11). Frontal process 1 mm max. length, deep brown, shiny, devoid of scales. Antennae pale brown; finely-pectinate in δ. *Thorax* and patagia unmarked, white to greyish-white. Legs and abdomen unmarked, dull whitish with a satiny sheen.

Length of forewing from base to tip (along costal margin), varies from 21 to 23 mm in the ♀ (based on five specimens); length of forewing in the δ varies from 17 to 20.5 mm (based on 9 specimens).

Forewing (upperside δ, ♀). Outer margin strongly convex from M1-M3; margin just below apex slightly excavated, producing a moderately falcate tip, which is slightly more evident in the ♀ (Pl. 11). Ground colour opaque pure white with a satiny sheen, contrastingly marked with pale to medium brown lines which are narrowly and sharply bordered with black; a line along costal margin from base to $\frac{1}{4}$, bending downward at $\frac{1}{4}$, crossing wing and bifurcating at discal cell, one branch extending directly to outer margin along M3, the other extending diagonally downward to fuse with a wide, pale grey-tinged brownish line along inner margin near anal angle; line along inner margin abruptly terminated (usually truncate) at 1-2 mm short of wing base; distally it continues for full length of outer margin to apex, becoming narrower from M2 to Cu1; a second short but prominent line along costal margin from $\frac{3}{4}$ to approximately 2 mm short of apex, bending abruptly down-

J

ward and outward, from ¾, to fuse with median line and M3 at outer margin; cilia pale brown shading to pale greyish near anal angle.

Hindwing (upperside ♂, ♀). Outer margin rounded. Translucent pure white with a faint sheen (less shiny than forewing); usually two variable, irregular, large dull black blotches at outer margin, which can be entirely separated or somewhat joined together (no two specimens are identical in these markings); cilia white.

Forewing (underside ♂, ♀). Costal and outer margins narrowly bordered by brown, but for a small break on costal margin just short of apex, where the satiny pure white ground colour reaches the margin; brown lines of upperside here mostly retraced with dull black; in some specimens this maculation faint or lacking along line which follows M3 from discal cell to outer margin; no maculation along inner margin.

Hindwing (underside ♂, ♀). Translucent pure white; black blotches of upperside roughly retraced here, with some small parts missing, and often with an upward extension of the upper-most blotch (not repeated on upperside).

Locality Records:

N. TERRITORY, 148 km. S. of Alice Springs, near the Palmer River crossing, on the main road, 26 April 1966, N. McFarland, at uv. light (♀ HOLOTYPE); 45 km WSW. of Alice Springs, near the Hugh River crossing, on the main road, 30 May 1967, at uv. light, N.M. and T. N. (♀ PARATYPE); 19 km E. of Alice Springs, near Jessie Creek, 28 May 1967, at uv. light (3 ♀ ♀, 7 ♂ ♂, PARATYPES). S. AUSTRALIA 160 km NNW. of Coober Pedy, near Wintinna on the main road, 25 May 1967, N. McFarland and T. Newbury, at uv. light (1 ♂ PARATYPE); 61 km S. of Kulgera (N.T.), S. of Sundown, near the Alberga River crossing, on the main road, 26 May 1967, N. McFarland and T. R. Newbury, at uv. light (♂ ALLOTYPE).

Specimens are deposited in the following institutions:

HOLOTYPE, ALLOTYPE, and 3 PARATYPES (1 ♀, 2 ♂ ♂). S. Australian Museum (20,628), Adelaide; 2 ♂ ♂ (PARATYPES) J. O. Wilson collection; 1 ♂, 1 ♀ (PARATYPES) T. R. New-bury collection; 2 ♂ ♂ (PARATYPES) Australian Museum, Sydney; 1 ♂ (T-4235) 1 ♀ (T-4236) (PARATYPES) National Museum, Melbourne; 1 ♀ (PARATYPE) British Museum (Nat. Hist.), London.

Remarks

Thalainodes macfarlandi is readily separated from other described species of the same genus by its very different maculation and its somewhat larger size. It is the only *Thalainodes* species having forewing maculation superficially very similar to that of *Thalaina angulosa* Walker, a well known species abundant in some areas of the Mt. Lofty Range, S. Australia. It is, however, easily distinguished from *T. angulosa* by the prominent frontal process on the head in both sexes, by the more attenuate forewing apex, by the pale drab brown lines on the forewing (lines rich rust-brown in *T. angulosa*), by the white or pale grey head (head rich orange-brown in *T. angulosa*), and by the pectinate antennae in the male.

Adults of *T. macfarlandi* are on the wing during autumn and early winter (April to June), probably reaching a peak during May. They often fly on rather cold nights, and come to light early in the evenings, before it gets still colder.

This species is almost certainly single-brooded. Eggs were obtained by Mr McFarland in May, 1967, and larvae were subsequently reared to final instar, at Blackwood, S.A., on a substitute foodplant, the coastal *Acacia pycnantha* Benth. (Mimosaceae). According to Mr McFarland, they were 'close to *Thalaina angulosa* larvae in general appearance but less colourful, having a ground colour of deep green, and a strong white and pale yellow spiracular line, which is on a crenulate ridge, slightly raised above the surrounding skin surface'. Photographs and preserved stages of the life history are under the McFarland code number 'G.180', at the S. Australian Museum, Adelaide.

Explanation of Plate

Thalainodes macfarlandi, n. sp.

Upper figure female paratype (NMV Coll.)
Lower figure male allotype (SAM Coll.)

LARGEST AUSTRALITE FROM VICTORIA, AUSTRALIA

By George Baker

Honorary Associate in Mineralogy

Abstract

The largest australite so far discovered in Victoria is a boat-shaped specimen weighing 173·621 gm and with a specific gravity of 2·417. It was found about the year 1900, and has only recently been brought to scientific notice. Found in the Connangorack Swamp area, Western Victoria, it was regarded for many years as 'some blackfellow's stone'.

Introduction

The largest australite collected to date in Victoria was recently (10 August 1970) added to the rock and mineral collection of the National Museum of Victoria (E4753). It is the heaviest of six australites found in Victoria that weigh over 100 gm. The specimen is a somewhat asymmetrical boat-shaped form (Pl. 12, figs. A-D) weighing a little over 173·5 gm, sixth heaviest of 23 australites weighing over 100 gm from the extensive Australian strewn-field of over 5×10^6 km² (Baker, 1969, Table 1).

Donated by Mr Alexander S. McDonald of 'Strathalbyn'. Cavendish, this australite came from the E. bank of Connangorack Swamp (or Ten Mile Swamp) 11 km E. of Toolondo on the Natimuk-Hamilton Railway Line, and 40 km SW. of Horsham (Fig. 1).

The specimen was found by the late Mr G. A. McDonald about the year 1900 while ploughing on a sand hill. It was regarded by him as 'some blackfellow's stone' until he saw the aus-

tralites on display in the National Museum of Victoria in Melbourne.

Known Large Boat-Shaped Forms

Only four large boat-shaped australites of over 100 gm have so far been located. Two of these are from Victoria, one from S. Australia, and one from W. Australia. Their weights, dimensions, and specific gravity values are listed in Table 1.

The specimen from Karoonda has been considerably abraded (Baker 1969, p. 61), while the Narembeen australite has been significantly etched so as to form numerous deep, solution grooves (Baker 1961a, Pl. 1). The specimen from Port Campbell (190 km SSE. of Connangorack Swamp) is the best preserved, with much less etching and no signs of abrasion (Baker 1969, Pl. 5, 9). The Connangorack Swamp specimen is also relatively well-preserved (Pl. 12) with few signs of abrasion and no significant loss from terrestrial etchants since its flaked equatorial zone was produced after landing on the earth's surface.

Table 1

BOAT-SHAPED AUSTRALITES OVER 100 GM

Locality	Weight (gm)	Measurements* (mm)	Specific Gravity	Reference
1. Karoonda, S.A.	208·9	82 × 46·8 × 37·9	(not given)	Fenner 1955
2. Connangorack Swamp, Vic.	173·621	78·9 × 47·6 × 34	2·417†	(this paper)
3. Port Campbell, Vic.	141·575	86·2 × 41·3 × 30·5	2·414	Baker 1969
4. Narembeen, W.A.	107·46	64 × 37 × 30·5	2·431	Baker 1961a

† Temperature of distilled water = 19°C
* Measurements are length width depth

The 23 largest known australites range from 101 gm to 265 gm (Baker 1969), and vary in shape from round cores through oval cores to boat-shaped and dumbbell-shaped forms. As noted for australites generally, the specific gravity values for the large boat-shaped forms increase from the most easterly (Port Campbell) through the Connangorack specimen to the most westerly occurrence (Narembeen).

As the sixth heaviest australite the Connangorack Swamp specimen is approximately 92·5 gm lighter than the heaviest, which is an oval core from Warralakin, W. Australia (Baker 1962). It is 69·5 gm lighter than a round core from Newdegate, W. Australia (McCall 1965), 45·5 gm less than a round core from Lake Yealering, W. Australia (Fenner 1955), 35 gm less than an abraded boat-shaped form from Karoonda, S. Australia (Fenner 1955), and only 2·5 gm less than the largest known dumbbell from Cuballing, W. Australia (Baker 1966). It is thus the second heaviest boat-shaped australite known (Table 1).

Other Australites from Horsham Region

A considerable number of smaller australites, mostly 1-40 gm, have been recorded from the region shown in the map (Fig. 1) of c 10,000 km² during the past 75 years at the following localities: Grampian Mountains (Dunn 1912, Tilley 1922), around Balmoral (Dunn 1912, Baker 1964), Horsham (Walcott 1898, Dunn 1908, 1912, Baker 1959b, 1961b), Hamilton (Dunn 1912, Baker 1959b), Harrow (Baker 1940, 1955), Glenthompson and Murtoa (Baker 1957), Dunkeld (Baker 1957, 1959b), Polkemmet East (Baker 1959b), Kanagulk, Telangatuk East, and Mt Talbot near Toolondo (Baker 1959a), Nurrabiel (Baker 1964), Lower Norton (Baker 1964, 1969), and Noradjuha (Baker 1964).

The specific gravity values for 140 or so australites from this region have been determined thus: Balmoral (14 determinations), Hamilton (10), Harrow (2), Mt William (2), Polkemmet East (1), Stony Creek Basin, Grampians (2), and Telangatuk East (9). See Baker and Forster (1943). Later 34 specific gravity determinations were made for australites from Harrow (Baker 1955), followed
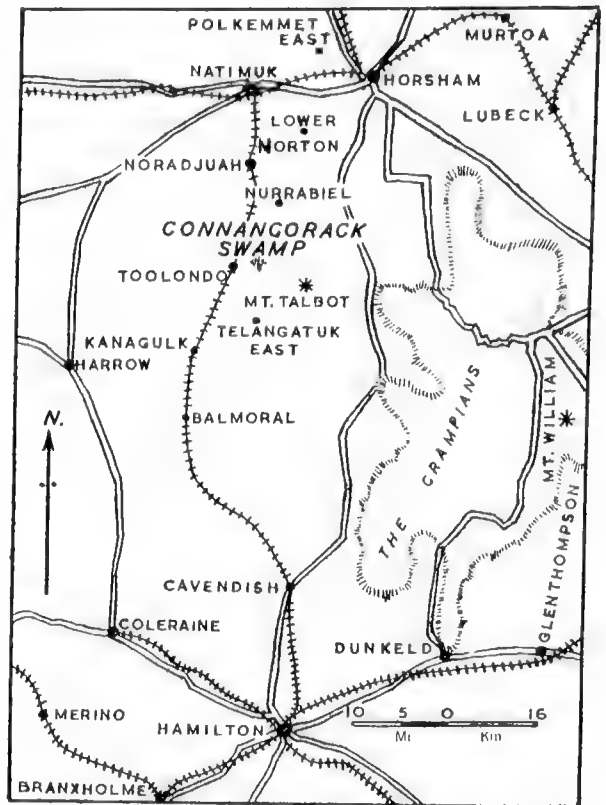

Fig. 1—Sketch map of part of W. Victoria showing discovery site of australite at Connangorack Swamp and other australite localities in the Horsham region.

by 29 from Kanagulk and five from Mt Talbot (Baker 1959a), one from Lower Norton (Baker 1964), and 33 from Nurrabiel (Baker 1964). The average is 2·408, a little lower than for the Connangorack Swamp australite (2·417). The overall range from this region is 2·335-2·468, disregarding specimens known to contain sizable internal cavities (Baker 1961b). The total weight of australite glass involved in the determinations is approximately 1,238 gm, and the Connangorack Swamp specimen contributes a little over one sixth of this weight. The ranges in specific gravity for the localities in this region are set out in Table 2.

The two entries for Hamilton, Balmoral, and Harrow arise from discoveries at different times having been studied by different authors, resulting in somewhat divergent average specific gravities and, in some, omission of the details of weights in the papers describing the specimens. There is mainly a random distribution

TABLE 2

SPECIFIC GRAVITY VALUES FOR AUSTRALITES IN THE HORSHAM REGION

| Locality	No. of spec.	Total Wt. (gm)	Range in S.G.	Average S.G.
Stony Cr. Basin, Grampians	2	0·782	2·335–2·376	2·356
Hamilton	4	8·824	2·339–2·459	2·378
Balmoral	8	14·516	2·356–2·428	2·389
Harrow	2	135·056	2·391	2·391
Hamilton	6	?	2·395–2·406	2·400
Kanagulk	34	314·577	2·380–2·441	2·404
Telangatuk E.	9	60·232	2·378–2·437	2·408
Mt. Talbot	5	14·840	2·392–2·424	2·410
Nurrabiel	34	63·048	2·374–2·462	2·410
Balmoral	6	?	2·389–2·455	2·411
Connangorack Swamp	1	173·621	2·417	2·417
Mt. William, Grampians	2	?	2·393–2·462	2·418
Harrow	34	305·050	2·386–2·468	2·420
Lower Norton	1	115·920	2·429	2·429
Polkemmet E.	1	31·885	2·433	2·433
TOTALS	149	1,238·351	2·335–2·468	2·408
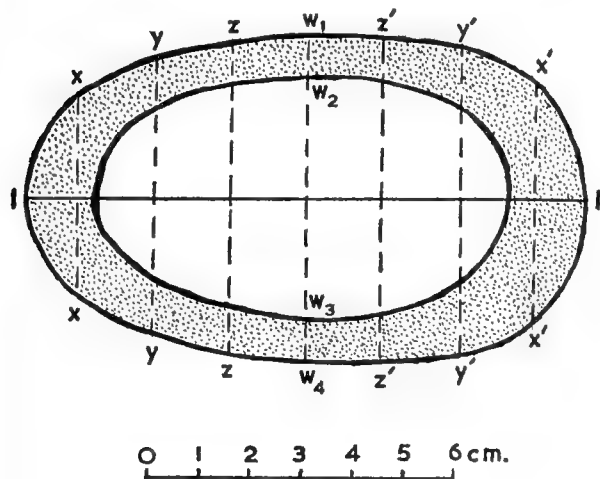
Fig. 2—Plan showing restored primary form of the Connangorack Swamp australite.

$w_2w_3 = 47·6$ mm = width of secondary form as found

$w_1w_4 = 64$ mm = width of primary form by reconstruction

$11 = 110$ mm = length of reconstructed primary form

xx and x'x' = 39 mm and 48 mm respectively

yy and y'y' = 54 mm and 61 mm respectively

zz and z'z' = 61 mm and 64 mm respectively

Dotted area represents tektite glass lost from the primary form on production of the secondary boat-shaped form.

through this region of specific gravity values whose average tends to increase from N. to S., but this is scarcely significant when superposed upon the general specific gravity increase from SE. to NW. across 4,000 km of the australite strewnfield (Baker 1959b).

Description of Form

The large boat-shaped australite from Connangorack Swamp is slightly asymmetrical in plan and elevation. It has a well-developed flaked equatorial zone (Pl. 12, figs. B, D) carrying a few etch pits up to 1 mm diameter, occasional flow lines (schlieren) accentuated by natural etching, and occasional shallow etch grooves trending parallel with the depth of the flaked zone. These grooves range up to 10 mm long and 1 mm wide; in cross section they are generally U-shaped and up to c. 0·25 mm deep.

A sharply marked rim separates the equatorial zone from the convexly curved posterior surface, and this delineates the limits of post-landing exfoliation (spalling) of tektite glass constituting the aerothermal strained zone (cf. Baker 1963) that arose as a secondary feature during hypersonic transit through the earth's atmosphere. As a consequence, the transition from anterior surface to equatorial zone is relatively smoothly rounded, and not demarked by a sharp rim as for the posterior surface. The

resultant configuration below the rim region (Pl. 12, figs. B, D) fundamentally represents the basal surface of the aerothermal strained zone, and hence indicates the depth of penetration of aerodynamic heating from the anterior surface inwards.

A few solution etch grooves also occur on the posterior and anterior surfaces, mostly short (Pl. 12, fig. C), but a longer one on the posterior surface (Pl. 12, fig. A) is arcuate in outline and up to 0·5 mm deep.

The posterior surface of the specimen (Pl. 12, fig. A) tends to be smoother than the anterior surface (Pl. 12, fig. C) due to less frequent etch pits and etch grooves. Flow swirls are just detectable and not pronounced as on some australites (e.g. Baker 1969, Pl. 5A). The vague flow swirl on the posterior surface of the Connangorack Swamp australite measures approximately 30 mm by 20 mm, and is made faintly evident by soil etchants. Arcuate to subcircular pits about 2·5 mm across are evidently chatter or percussion marks subsequently modified by solution etching.

Dimensions of Specimen

The length is 78·9 mm but the width ranges from 47·6 in the central regions to 39 mm towards the broader and 28·5 mm towards the narrower end. The depth ranges from 34 mm in the central regions to 32·5 mm towards the deeper end and 28·5 mm towards the shallower. One side is approximately parallel with the long axis, as seen from the top edge of Pl. 12, fig. A and the bottom edge of Pl. 12, fig. C, whereas the opposite side is significantly curved, as revealed by the bottom edge of Pl. 12, fig. A and the top edge of Pl. 12, fig. C. Although shorter than the large boat-shaped australite from Port Campbell (Baker 1969), the Connangorack Swamp specimen is significantly broader and deeper (cf. Table 1), thus accounting for the form being a little over 32 gm heavier. No attempt was made to determine a radius of curvature for either surface along the elongated axis. Across the short diameter the arcs of curvature are R_F 27 mm and R_B 32 mm.

The arc and radius of curvature R_B of the posterior surface provides some concept of the
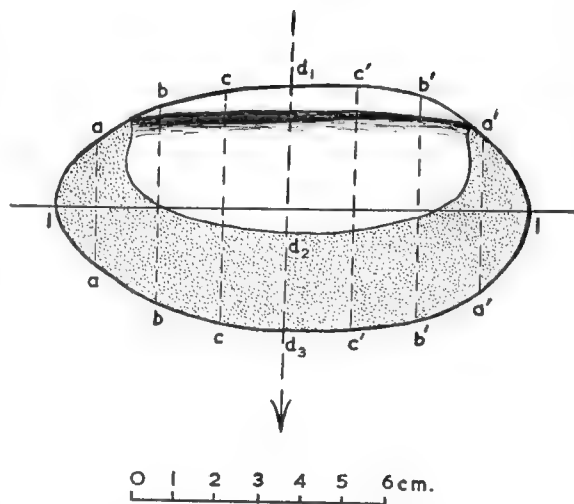

Fig. 3—Side elevation to show restoration of the primary form from the residual boat core (boat-shape obtained from trace of side elevation in Pl. 12, fig. B). Posterior surface uppermost.
$d_1d_2 = 34$ mm = depth of secondary form as found
$d_1d_3 = 56·5$ mm = depth of reconstructed primary form
$d_2d_3 = 22·5$ mm = depth of ablation along the polar axis combined with glass lost by subsequent terrestrial spallation
$11 = 110$ mm = length of reconstructed primary form
aa and a'a' = 27 mm and 37 mm respectively
bb and b'b' = 45 mm and 52 mm respectively
cc and c'c' = 53·5 mm and 56 mm respectively
Arrow points down the flight path earthwards. The specimen trimmed in flight with its long axis normal to the flight direction. Dotted areas represent australite tektite glass lost from the primary form on production of the secondary form.

nature of the primary form, while that of the anterior surface gives an approximate concept of the way the primary form has been secondarily modified. With the boat-shaped form trimmed in a stable position during earthward flight, which was one of aerodynamic equilibrium with the long axis of the specimen normal to the flight direction earthwards and the shorter of the two lateral axes (for a triaxial ellipsoid) parallel with the flight path, the amount of ablation from the forward surface of the specimen was quite significant. This and exfoliation of the forward surface resulted in a loss of c. 23 mm depth of the australite.

Reconstruction results in the outline forms depicted in Figs. 2 and 3. From these it is esti-

mated that the dimensions of the primary ellipsoid were approximately 110 mm by 64 mm (width) by 56·5 mm (depth). Loss during earthward flight and from terrestrial agencies resulted in a reduction of c. 32 mm in length, c. 16 mm in width, and c. 22·5 mm in depth.

Description of Plate 12

Boat-shaped australite from Connangorack Swamp (natural size)

Fig. A—Posterior surface with ill-defined flow swirls, distinct etch pits, and chatter (or percussion) marks.

Fig. B—Side elevation showing flaked equatorial zone with natural solution etch grooves (posterior surface uppermost).

Fig. C—Anterior surface with short natural solution etch grooves, a few etch pits, and several chatter (or percussion) marks.

Fig. D—End elevation showing flaked equatorial zone and nature of arcs of curvature of the two surfaces (posterior surface uppermost).

Acknowledgements

The author is grateful to Dr A. W. Beasley for drawing attention to this recent addition.

Addendum

An oval australite core recently described by W. H. Cleverly from Lake Ballard, Western Australia (*Jl R. Soc. West. Aust.* 54: 14-16, 1971) measures 60 × 57 × 44 mm and weighs 202·29 gm. It is the fourth australite from Western Australia weighing over 200 gm and the fifth heaviest australite known to science, as a heavier one weighing over 200 gm is recorded from Karoonda, South Australia.

Consequently, the Connangorack Swamp ralite brought to scientific notice.
specimen becomes the seventh heaviest aust-

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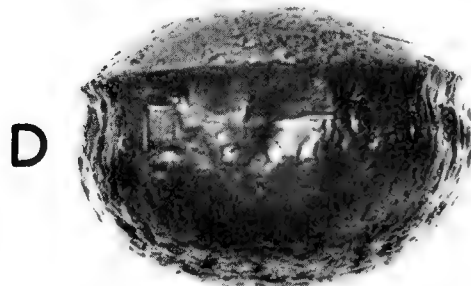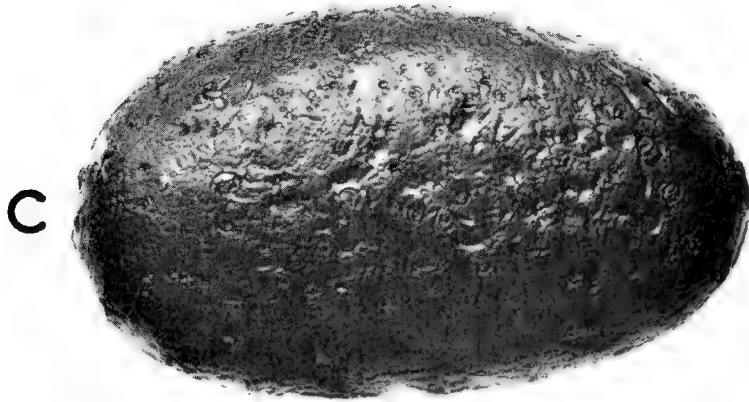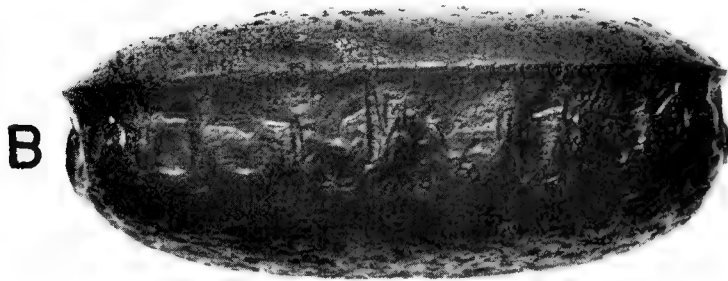
SMALLEST KNOWN COMPLETE AUSTRALITE

By George Baker * and William J. Cappadona †

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Abstract

The smallest known complete Australian tektite, recently discovered 10 km NNE. of Princetown, Western Victoria, is a minute oval, bowl-shaped australite weighing only 0·026 gm, with a specific gravity of 2·410. It is practically a complete form shaped and sculptured by aerodynamic processes at hypersonic speeds, and subsequently subjected to relatively minor losses by terrestrial natural solution etching. Virtually no effects of terrestrial mechanical abrasion are detectable.

Introduction

A recently discovered australite having the least weight of the 45,000 or so australites so far brought to scientific notice is an elongated, bowl-like specimen from the Fergusons Hill area some 10 km NNE. of Princetown on the S. coast of W. Victoria. It was discovered by W. J. Cappadona on 10 February 1971 resting with its anterior surface uppermost on light greyish to white, leached sandy clay on the W. side of a new access road in the closer settlement region opened up in the past few years between Princetown and Simpson.

The location is 143°10'30" E. and 38°36'45" S. in the region whence seven australites were described by Baker (1968a) during the early phases of road formation. Some 400 or so australites have been discovered in this area since the virgin bush country was cleared for closer settlement. Unfortunately very few of these have been submitted for scientific investigation. Among those examined is another small, shallow, oval dish-like form weighing 0·097 gm and constituting the third lightest complete australite known. It was also found by W. J. Cappadona, in September 1970. Both of these small bowl-shaped to dish-like australites are lodged in the private collection of W. J. Cappadona of Dandenong, Victoria.

Dimensions, Weight, and Specific Gravity

Although the dimensions of the australite from Fergusons Hill are shown in Table 1 in round figures, it is worth noting, by virtue of its minute size and weight, that the actual measurements are length = 4·9 mm, width = 2·9 mm, depth = 2·1 mm. The thickness of the glass averages 0·6 mm. The form is comparable in size with an ordinary match head (4·5 mm × 3·0 mm × 2·5 mm).

The specimen weighs 0·026 gm, and the specific gravity averaged from five determinations using distilled water (20°C) is 2·410, which is not much different from that of the mode for australites in the Port Campbell region (Baker 1968a, p. 25). It should be pointed out that the weight and specific gravity values are affected by small amounts of adventitious matter embedded in schlieren accentuated by natural solution etching inside the shallow bowl (Pl. 13 fig. E.). The adventitious matter consists of leached clay with minute quartz grains, and is partially cemented. In the interests of keeping the specimen intact, it was not subjected to ultrasonic cleaning.

A quarter of a century ago, the lightest known australite was 0·0645 gm (Baker 1946), so the complete form now recorded is only one third its weight. The heaviest australite (265 gm) so far recorded (Baker 1962) is 10,000 times its weight. The heaviest recorded tektite from all strewnfields weighs 3,200 gm (Laos, Indo-China) which is some 121,000 times heavier.

For purposes of comparing and contrasting some of the physical properties of the known lightest bowl-shaped and dish-like aus-

TABLE 1

BOWL-SHAPED AND DISH-LIKE AUSTRALITES IN ORDER OF INCREASING WEIGHT

	Weight (gm)	Specific Gravity	Diameter (mm)	Length (mm)	Width (mm)	Depth (mm)	Thickness (mm)	Reference
1	0·026	2·410	—	5	3	2	0·5	This paper
2	0·065	2·406	—	9	6	1	0·5	Baker 1963a
3	0·097	2·410	—	8·5	7	1	0·25–0·5	This paper
4	0·100	2·422	—	12·5	2–3	2	0·25–0·5	Baker 1964
5	0·123	2·431	7·5	—	—	1·5	1	Baker 1963a, 1963b
6	0·135	2·410	—	7·5	5	3	0·5	Baker 1940, 1946, 1963a
7	0·149	2·442	—	9	4	3	0·5–0·75	Baker 1940
8	0·154	2·406	—	8	7·5	2	1	Baker 1963a
9	0·177	2·408	—	12	5	2	0·5	Baker 1963a
10	0·230	2·421	—	9	7	2·5	0·75	Baker 1963a, 1963b
11	0·245	2·414	—	10·5	6·5	4	1	Baker 1963a, 1963b
12	0·276	2·400	—	9	8	2·5	0·75–1	Baker 1963a
13	0·305	2·440	10	—	—	3	1	Baker 1963a
14	0·371	2·441	—	14·5	13	1–3	1	Baker 1963a, 1963b

Key: 1 = oval shallow bowl, 10 km NNE. of Princetown.
2 = oval shallow bowl, Port Campbell.
3 = oval shallow bowl (dish-like), 6·5 km NNE. of Princetown.
4 = elongated bowl, Nurrabiel.
5 = round shallow bowl, Port Campbell.
6 = elongated deep bowl, Port Campbell.
7 = elongated deep bowl, Kalgoorlie.

8 = oval shallow bowl.
9 = elongated bowl.
10 = elongated deep bowl.
11 = elongated deep bowl.
12 = oval shallow bowl.
13 = round shallow bowl.
14 = oval shallow bowl.
All localities are in Victoria except 7 which is in W. Australia. 8-14 are from Port Campbell.

tralites, 14 are listed in Table 1. Among these, elongated specimens exceed round specimens in the ratio 7 to 1.

Range in weight of the australites in Table 1 is 0·026 gm to 0·371 gm, their average weight is 0·175 gm, and their specific gravity values range from 2·400 to 2·441 with an average of 2·419.

Three other similar forms have been figured by Dunn (1916, Pl. 23, figs. 6, 8, 9) but no details of weight or measurements were given, except that the smallest example (fig. 9) weighed 0·2044 gm; measurement of the photograph gives its diameter as 8 mm. In weight, this round shallow bowl fits into Table 1 between specimens 9 and 10, but its inclusion is not warranted in view of paucity of data.

Four small dish-like forms have been figured by Fenner (1940, figs. 18, 21-22, 27), but no details were given. A few specimens included

in other private collections were not available for study.

Within the weight range of the australites in Table 1 there occurs a small number of flat disc- and plate-shaped australites from 0·112 gm to 0·308 gm (Baker 1963a p. 38, Skeats 1915 p. 362), and two or three slightly heavier specimens weigh up to 0·636 gm.

Description of Features

In reflected light, the colour of the glass is black in the thickest portion of the specimen, but in transmitted light is yellowish-green to brownish-green, typical of Australian tektite glass generally. The lustre is characteristically vitreous, and as far as its diaphaneity is concerned, the glass is translucent throughout because of its thinness.

The specimen is oval in plan although not perfectly so (Pl. 13, figs. A, C). The broad arc

of curvature of the anterior surface is evident from its side elevation (Pl. 13, figs. B, F), while the rather steeper arc of curvature of the end-on aspect is shown in Pl. 13, fig. D. The posterior surface is concave, while the anterior surface is convex, and was faced down the flight path earthwards during high velocity transit through the earth's atmosphere. Fig. E shows the posterior surface with its somewhat shallow curvature; Fig. G is a plan view of the convex surface.

The radius of curvature of the anterior surface (R_F) along the long axis is 2·6 mm, while that along the short axis is 1·2 mm. As the posterior surface is hidden within the bowl-shape, its arc of curvature (R_B) cannot be precisely determined. However, there is a back curvature of some regularity for the end-on aspect of the specimen, as revealed in Pl. 13, fig. D; this represents the curved character of the lip of the bowl arising from the backward bending of plastic glass during the end phases of atmospheric transit. This curvature is negative in sense relative to the aerodynamic orientation of the form, and is 2·75 mm radius.

The surficial sculpture pattern is a consequence of burial in moist soil for a considerable period of time, with resultant differential etching from slight chemical variations within the streaky, rather inhomogeneous tektite glass.

Effects of Natural Etchants

The principal effect of natural solution etching of the glass has been the accentuation of its schlieren. This is a tertiary phase, commencing only after earth landing, and it has the effect of slightly modifying the secondary aerodynamic form shaped from the primary form during atmospheric transit.

The somewhat complex flow-line pattern evident in Pl. 13, figs. B-C, and shown in more detail in figs. E-G, is a consequence of minute differential etching of adjacent streaks of glass of slightly varying chemical composition by soil etchants. The strength and quantity of the etching solutions would vary significantly from time to time throughout the period of burial, and after exhumation, the upwardly exposed anterior surface would be less etched than the still partially buried posterior surface. It is therefore

not surprising to find that the schlieren trends on the posterior surface (Pl. 13, fig. E) are more overdeepened than those on the anterior surface (Pl. 13, fig. G).

Of less significance in the sculpture pattern are the etch pits, which are rare and small. They range up to 0·25 mm across, and are discernible in the side elevation shown in Pl. 13, fig. F; they are also very shallow. More outstanding are two prominent etch craters on the posterior surface which are somewhat deeper and up to c. 1 mm across. There is one at each end of Pl. 13, fig. E. Both reveal schlieren trending across their walls, while the one at the bottom, right-hand side of Pl. 13, fig. E reveals a smaller etch pit on the crater floor.

The rather irregular posterior surface is evidently a result of two effects (1) a 'hummocky' build-up of plastic glass on bending back into the bowl-shape, combined with (2) accentuation of the irregularity of the surface by differential etching, some overdeepening occurring in the small depressions separating the minute 'hummocks'.

It is difficult to assess the loss of glass by etching, but it has not been of any great significance. From detailed examination under $\times$ 10 magnifications, it is evident that virtually nothing has been removed by subaerial mechanical abrasion. This leads to the important conclusion that the specimen has not been transported into the area by any known terrestrial agency, and that it was found substantially where it fell. The general geomorphology supports this conclusion, the locality being at the summit of an interfluve.

Origin of Bowl-Shaped Australite

It is concluded this australite was aerodynamically shaped and sculptured in the manner set out in detail by Baker (1958, pp. 380-382) for other bowl-shaped and dish-like australites of small size. The most interesting point is that the secondary shape was evidently derived from the smallest spheroid of primary glass in the australite swarm that survived aerodynamic ablation. The small primary ellipsoid of tektite glass was ablation-reduced to a thin, flattened oval disc-like form near the end stage of transit through the earth's atmosphere. Dur-

ing this phase of earthward flight, depth of penetration of aerothermal heating would be sufficient to render the thin form plastic throughout, and under such circumstances, with frontal shock waves perpendicular and frontal pressures increased by up to 50 per cent, increased drag on the surface pointed down the flight path would cause the softened material to bend backward into a bowl-shaped form. As the specimen was evidently solid and cold on reaching the earth, the backward bending is deemed to have occurred at the very end of hypersonic flight or during the transonic period, because once it had passed into subsonic flight, all aerodynamic heating, ablation and sculpturing would have ceased (cf. Baker 1959, pp. 159-173).

One effect of the australite becoming non-elastically flexed is that the flow schlieren in the thin glass became differentially contorted, as indicated after accentuation of the schlieren by etching (Pl. 13, fig. G).

Contrast with Microbeads from Oceanic Sediments

The smallness of this australite has significance for the origin of microbeads of glass recovered from oceanic sediments (Glass 1967, 1969). The lightest australite is 10,000 times lighter than the heaviest (Baker 1962), but the largest of the microbeads obtained off the coasts of Australia and the Ivory Coast (Africa) is only 34 times lighter than the lightest known australite. Of particular significance is the marked contrast between the form of this australite and that of the glass microbeads. The australite has a form produced by the secondary effects of aerodynamic processes acting upon a small primary spheroid of tektite glass traversing earth's atmosphere with a single pass entry (Baker 1958). On the other hand, the forms of the microbeads (spheres, spheroids, ellipsoids, etc.) are all fundamentally those of primary forms. None of these microbeads reveals any evidence of the secondary effects of hypersonic flight through the earth's atmosphere.

On this basis alone, we have a pointer to the minute bowl-shaped australite being within the lowest possible size range for tektites generally.

Primary forms smaller than that from which this australite was produced should be completely ablated during hypersonic flight through the earth's atmosphere, and hence leave no micro-residual secondary forms. It should be borne in mind that every australite in each of the known shape groups, no matter what its weight, is a secondary form. Throughout the whole weight range from 265 gm down to 0·026 gm not one australite possesses a complete primary shape any more, for the reason that all the original primary shapes have been severely modified by aerodynamic ablation and sculpture, some more so than others. On the other hand, not a single glass microbead from the oceanic sediments reveals any evidence of secondary shape development from the primary forms, and no sign of aerodynamic sculpture arising from hypersonic passage through the earth's atmosphere. The size of these glass microbeads, ranging up to about 800 microns in diameter, is evidently such that they would not survive the effects of such severe conditions as suffered by australites whilst travelling earthwards.

The conclusion is that there are no such objects as microtektites with primary shapes, the nearest object to a microtektite being the minute australite described herein. The microbeads called microtektites (Glass 1967, 1969) are more likely minute beads of wood silica glass, many of which have now been observed by incinerating certain Australian timbers rich in opal phytoliths. These are comparable in size, shape, colour, and other characteristics described for microbeads generated from the burning of haystacks (Baker 1968b), and generally comparable with the glass microbeads recovered from oceanic sediments.

Description of Plate 13

Smallest known complete australite

Fig. A—Oval outline in plan aspect; posterior surface view.

Fig. B—Slightly undulating edge of lip of bowl-shaped form on posterior surface (uppermost) and more open nature of curvature of anterior surface (lowermost in photo) compared with that in Fig. D.

Fig. C—Oval outline in plan aspect; anterior surface view.

Fig. D—Compressed, steep arc of curvature of anterior surface (lowermost) in end-on aspect, and more open nature of arc of curvature of the lip edge on the posterior surface (uppermost) of the bowl-shaped form.

Fig. E—Interior of the bowl-shaped form (i.e. posterior surface view) showing schlieren (flowlines) accentuated by natural solution etching, and two relatively deep etch craters at left- and right-hand ends of photo. White streak represents leached clay with minute quartz grains embedded in overdeepened portions of etched-out schlieren.

Fig. F—Side elevation (reverse to that shown in fig. B) showing irregularity of lip of bowl due to differential natural solution etching. The etch crater at the top left-hand edge of the photo is the same as that at the bottom right-hand corner of fig. E.

Fig. G—Twisted, complex schlieren trends revealed by natural etching of the anterior surface.

(Photos A—D by Mr S. Jame, Monash University; Photos E—G by Mr W. A. Jackson, R.M.I.T.)

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A

B

C

D

E

F

G

0 1 2 3 4 5

millimetres

0 1 2 3 4 5

millimetres

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