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Cover motif: head of female signal fly Rhytidortalis averni by J. Bowley from the paper by D.K. McAlpine this volume.
Editorial

In this issue we revive several features that have appeared in the Proceedings of the Linnean Society of New South Wales at various times in its 130 years of continuous publication. There is a book review (‘The Yponomeutinae of the world exclusive of the America’ reviewed by Courtney Smithers), and anyone wishing to submit book reviews in future is most welcome to do so. There is a section of ‘News and Notes’ for which submissions are also invited. And there is a presidential address, which, like a few in past issues, is in fact a scientific paper including original, unpublished material. In early volumes presidential addresses were often a summary of the activities of the society and its members, but such matters are now covered in the society’s newsletter which is distributed several times during the year to all members and associate members.

The Presidential Address by Dr Armstrong Osborne has undergone the complete referee process required by the society’s editorial policy, as has the paper of which the editor is an author (Augee and Ford). The latter paper was edited by a member of council who is a past editor of this journal. Every paper submitted is refereed by two scientists. At least one referee is a specialist in the topic concerned, and the second referee is usually a scientist in a related field. Overall journal policy and the final acceptance of individual papers is in the hands of the Editorial Committee. Because this journal covers an unusually wide range of research topics, including all earth sciences and biological sciences, the Editorial Committee is comprised of all council members, since the council of the society includes a sufficiently wide range of scientific expertise and experience.

The role of research journals published by societies and other non-profit publishers will, I believe, increase with the advent of new technology. Most scientists are aware of certain commercial journals, usually European, whose extraordinary prices serve actually to restrict the dissemination of scientific information and research results. The role of non-profit publishers is to facilitate the dissemination of such material and the web now provides a means to greatly expand this role. The council of the Linnean Society of NSW has been exploring the means by which we can take advantage of the opportunities offered by electronic publication and vastly increase the distribution potential for our authors. Initially we are placing the abstracts from this volume on our website. It is likely that with the next issue we will be providing complete text electronically.

The Linnean Society of NSW website also contains an index to past issues of the Proceedings. This is being prepared by J.C. Herremans and at present volumes 1–29 and 108–120 are on the site. Another important feature of our website is information about research grants offered by the Linnean Society of NSW.

M.L. Augee
Editor
Presidential Address for 1998–1999

The Origin of Jenolan Caves: Elements of a New Synthesis and Framework Chronology

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Jenolan Caves are Australia’s premier show caves. It has proved difficult to explain the origin and development of these caves. A new synthesis and framework chronology is proposed involving at least ten distinct phases of development beginning in the Carboniferous and extending until recent times.

Key elements of this new synthesis are Carboniferous and Peronian palaeokarst, exhumation of palaeokarst, hydrothermal speleogenesis, the influence of steeply dipping limestone on morphology, complex hydrology, sediment blockages and paragenesis. Many significant features of the caves are not the products of solution by meteoric water.

This new synthesis and framework chronology challenges not only the accepted scientific view of the caves, but also the way in which they are conserved, managed and interpreted.

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KEYWORDS: caves, hydrothermal, Jenolan, karst, paragenesis speleogenesis


INTRODUCTION

Jenolan Caves, located 100 km due west of Sydney (Fig. 1), are Australia’s best-known and most-visited limestone caves. With a history of tourist development and conservation beginning in the 1860s, one might expect that their origin would have been the subject of much speculation, research and publication. Surprisingly this is not the case. While there has been a significant amount of work on the palaeontology and structure of the Late Silurian Jenolan Caves Limestone, and some speculation on the age of the caves (e.g. Sussmilch and Stone 1915), there has been little or no serious consideration given to how the caves formed.

The most widely known explanation for the origin of the caves is found in the eleven editions of Dunlop’s guidebook published between 1950 and 1979. In summary, Dunlop stated that, “The caves owe their existence to the two facts that calcium carbonate.... dissolves slightly in river waters and the limestone.... is traversed by fine cracks.... which admit water to all parts of the rock and thus enable solution to proceed” [p 18] and “the caves are the channels of three streams which flow through the limestone” [p 23] (Dunlop, 1979).

Much of the more scientific discussion that has occurred to date is to be found in Steve McClean’s unpublished honours thesis (McClean 1983) and in the unpublished
portions of my own PhD thesis (Osborne 1987). Kiernan (1988a) provided a good summary of the various karst features at Jenolan and the role of geological structure in guiding their development. He only gave a brief account of the evidence for the origin and development of the caves, noting that “in the absence of a suitable map the origin of the caves has not yet been fully resolved”.

My own published work has largely concentrated on palaeokarst at Jenolan and its likely age and role in cave development (Osborne 1984, 1991, 1993, 1995). I have only discussed possible mechanisms of cave development at Jenolan quite recently (Osborne 1996, 1999).

The general lack of attention to the problem of the origin and history of Jenolan Caves may be due to a number of factors. One was a management policy between 1915 and 1983 that kept scientists out of the show caves. Another was a serious lack of scientific interest in the science of caves in Australia. I believe, however, that an additional important factor has been the failure of conventional approaches to explain many of the significant features and characteristics observed at Jenolan.

FEATURES OF JENOLAN CAVES REQUIRING EXPLANATION

There are a number of features of the caves and surrounding landscape at Jenolan which cannot be accounted for by any simple interpretation of landform development, or by any single phase, entirely meteoric cave development process. Eight of these features are outlined below.
Figure 2. Evidence for landscape age; Camp Creek and Jenolan River South. A) Deposit of Permian conglomerate located within the valley of Camp Creek; B) Saddle south of Lucas Rocks; C) Saddle above Grand Archway; D) Carlotta Arch; E) 900 m bench at Jenolan Village; F) 900 m bench north of Jenolan Village.
Seemingly Contradictory Evidence For Landscape Age

Sussmilch and Stone (1915) provided the first reasoned approach to the question of cave and landscape ages at Jenolan. Using the then accepted timing for the uplift of the eastern Highlands (2 million years ago), Sussmilch and Stone applied a simple incision approach which led them to conclude that the highest levels of the present caves could be no more than 500,000 years old. A similar approach using modern incision rates derived from workers such as Bishop (1985) and Young (1977) would suggest that old high level caves, such as Carlotta Arch, could be at least eight million years old.

Field evidence, however, suggests that such simple approaches have little validity at Jenolan. Doughty (1994) found a conglomerate deposit in Camp Creek 1.9 km south of the Grand Archway. This deposit sits unconformably on the Jenolan Caves Limestone and has a base elevation of 1040 m, well within the valley of Camp Creek (Fig 2). The valley lip at that point is defined by the 1180 m contour. Doughty correlated these conglomerates with the Permian Snapper Point Formation, outliers of which are found at various levels in the landscape near Jenolan Caves (Gostin and Herbert 1973). Similar conglomerates with a base elevation of 1220 m occur 1.4 km further south near the Kanangra Walls Road (Fig 2). If we assume that the base of these deposits approximates the gradient of a Permian valley floor and extrapolate north to near Lucas Rocks, a base elevation of 810 m would be expected, well below the 910 m elevation of the limestone outcrop forming Lucas Rocks.

Kiernan (1988a) and I (Osborne 1987) recognised two distinct erosional benches in the landscape at Jenolan Caves. The higher bench has an elevation of 900–930 m at Jenolan Village (E & F in Fig 2) and can be traced north, up the Jenolan River Valley. The lower bench has an elevation of approximately 830 m and includes the flat area near Carlotta Arch (D in Fig 2) and the saddle above the Grand Archway (C in Fig 2). The northward slope of the Permian base level between Kanangra Road and Doughty’s outcrop would allow either or both of these benches to have Permian origins. North of Jenolan Caves the Jenolan River Valley has a distinct valley-in-valley structure. The 900 m bench forms the floor of the upper, broad valley, while the lower narrow valley results from incision below the 900 m bench. I (Osborne 1995) noted that Dreamtime Cave, developed below the 900 m bench, contains conglomerate likely to be of Permian age.

These observations suggest that a valley with a floor level at least as low as 900 m existed at Jenolan during the Permian and that the valley was filled, exhumed and then incised. It is clear, however, that the situation is not that simple. Resting on, and exposed in, the saddle above the Grand Archway are not only conglomerates of probable Permian age, but also what are clearly Cainozoic (probably Pleistocene) bone-bearing gravels. Any new synthesis must account for this and other seemingly contradictory occurrences.

Parallel Surface and Underground Drainage

One striking feature of Jenolan Caves is the development of parallel surface and underground drainage paths (both active and fossil) through the limestone. The semi-dry valleys of Camp Creek and Jenolan River are paralleled at a lower level by the conduits presently carrying underground drainage and at a higher level by both surface palaeochannels and underground palaeoconduits (air-filled and sediment-filled caves) (Fig. 3). Caves, some of which contain bone-bearing sediment, are intersected by the walls of the limestone gorges of the Jenolan River, upstream of the Devils Coach House.

Cave sediments containing large boulders indicate that at times in the past the northern show caves carried much of the flood load of the Jenolan River, while at present this flows overland, except for its short underground path through the Devils Coach House. Any new synthesis must account for the development of these parallel systems of drainage.
Figure 3. Caves and surface drainage, upstream of the Grand Archway, after Welch (1976).

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Complex Drainage

Careful examination of cave maps, many years spent by cavers attempting unsuccessfully to find new sections of cave by following streams and the findings of cave divers all indicate that the geometric pattern and hydrology of Jenolan Caves is far from simple. It could in no way represent the simple path of three underground streams as suggested by Dunlop (1979). The more we know of present and past drainage, the more it becomes clear that pattern of drainage at Jenolan is quite complex and has been complex in the past. While there are stream passages in Jenolan Caves, and the caves do capture streams underground, the path of these streams and the passages in which they flow are neither simple nor continuous.

A good example of this situation has been the long search by cavers and cave divers for the section of the “Jenolan Underground River” known as the “Hairy Diprotodon” connecting Slug Lake in Mammoth Cave with the stream passage in Spider Cave. Although cavers, cave divers and geophysical investigations (T. Hubble, pers comm) have located cave passages in the area between the northern end of Spider Cave and the southern extremity of Mammoth Cave, there is no single large “river” passage linking Slug Lake with Spider Cave. The Jenolan Underground River rather takes a complex route, in places reaching depths of more than 90 m below its surface level.

Any new synthesis must account for the development of complex drainage patterns and the presence of large chambers extending to great depths below the water table.

Exposure of Palaeokarst Deposits in Caves

Palaeokarst deposits at Jenolan Caves, and many other places in eastern Australia, are exposed in and intersected by caves. In some places palaeokarst deposits have guided cave development. This is unlike the situation described in the international literature and observed by me in 1997 during fieldwork in Europe (Bosak et al. 1989, Ford 1995 and Osborne in press). In many karst areas palaeokarst deposits are evident and often abundant as in the classical karst of Slovenia. There palaeokarst deposits are found exposed in natural outcrops at the surface, in quarry faces and in motorway cuttings, but rarely, if ever, are they exposed in caves. Ford (1995) noted that it was unusual for modern caves to intersect and exhume filled palaeokarst cavities, except where the modern caves were the result of per ascensum (caused by water rising from below) hydrothermal, artesian or stratiform karstification.

The presence of palaeokarst in the Jenolan Caves Limestone is neither surprising nor difficult to explain, however, the exposure of palaeokarst and the role it has played in guiding cave development in Jenolan Caves does require explanation and must be addressed in any new synthesis.

Cupolas and Halls

Some of the most striking morphological features of Jenolan Caves are the large dome-shaped chambers (cupolas) found in the southern show caves (Temple of Baal, Persian Chamber, Queen Esther’s Cave) and in Mammoth Cave (Oolite Cavern, The Oval, and Pisa Chamber). Apart from commenting on the size and shape of these features (a height of 45 m being cited for the Temple of Baal by Dunlop 1979) there is little or no comment about their origin in the literature. Dunlop (1979) described the Persian Chamber as “a deep, symmetrically scoured pothole” and, in the absence of any contrary explanation, this has been taken by some cave guides to mean that the cupolas were eroded by vast underground whirlpools. This explanation, however, does not accord with the available evidence.

Another possible explanation for the development of cupolas would be to attribute
Figure 4. Simplified map of the Jenolan Tourist Cave System after unpublished compilation map by K. Oliver. A) Southern, Orient-Baal-River Cupola Cluster; B) Northern, Cerebus-Cathedral Cupola Cluster; C) Jubilee Cave; D) Imperial Cave; E) Spider Cave; F) Barrelong Cave; H) Halls in the Jenolan Underground River; S) Sumps in the Jenolan Underground River.
Figure 5. Mammoth Cave, after Welch (1976). Note location and distribution of cupolas; Pisa Chamber, The Oval and Oolite Cavern and of other isolated chambers.

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them to mixing corrosion or convection in meteoric water. Dublyansky (1980) noted that cupolas produced by these types of processes show deep penetration into a guiding joint. While some small-scale cupolas at Jenolan do show penetration into guiding joints or bedding planes, the ceilings of the large cupolas do not penetrate into structural planes in the limestone, but truncate them. The large cupolas are therefore unlikely to have been produced by mixing corrosion or convection currents in meteoric water.

There does not appear to be any discernible pattern to the distribution of cupolas within the cave system, nor does there appear to be any obvious genetic relationship between the cupolas and the cave passages with which they connect. In the southern show caves cupolas occur in two distinct clusters, a southern Orient-Baal-River cluster (A in Fig. 4) and a northern Cerebus-Cathedral cluster (B in Fig 4). The low-level connection between the Orient-Baal-River cluster and Lucas Cave appears to have formed after the cupolas. In Mammoth Cave (Fig. 5) cupolas such as Pisa Chamber, The Oval and Oolite Cavern are connected by lower-level passages that have been guided by geological structures and appear to have formed after the two cupolas.

Halls are elongate structurally guided cavities named after Caesars Hall in Wyanbene Cave, New South Wales (Osborne, 1996). The height of halls generally exceeds their width and they either have blind terminations along strike or are partially closed along strike by significant constrictions called “narrrows”. The passages through which the Jenolan Underground River flows between sumps are examples of halls (e.g. the Imperial Streamway, H in Fig. 4) and the sumps in the river are narrow (“S” in Fig 4). I (Osborne 1993, 1996) described how vadose weathering of unstable minerals resulted in halls being exhumed, but did not explain how the halls formed in the first place.

Any new synthesis must account for origin and distribution of cupolas and halls and how they were able to form before the passages that now connect them to the cave system as a whole.

**Conduits with Wall Niches**

Cave passages with a roughly rectangular cross-section, often 6 m high by 3 m wide, are found in a number of parts of the cave system (e.g. Madonna Cave in Chifley Cave, the Tower Chambers-Pool of Reflections passage, Fig. 6, and Mons Meg in River Cave). These passages have essentially flat ceilings that have been cut directly across bedding. A series of curved indentations are developed in the walls of these passages. The uppermost indentation is usually the widest. The passage floor is frequently sediment; however, in rare cases there is a sloping bedrock floor with a narrow, sometimes meandering, slot cut in its centre. Both Kiernan (1998a) and I (Osborne 1987) interpreted these passages as large phreatic conduits in which later vadose incision had cut deep, wide floor canyons. The floors and ceilings of these passages rise and fall in a loop-like fashion. This was interpreted as evidence for the development of phreatic loops.

This interpretation however ignored some simple facts:

i. Where the floors rise they are often made of sediment, not bedrock

ii. The passages are developed in almost vertically bedded limestone (unlike passages of similar cross-section shown in textbooks)

iii. The wall niches do not slope gently downstream, as would be expected if they resulted from vadose incision, but instead rise and fall in fold-like patterns.

Any new synthesis must account for the origin of these striking passages. Recently I (Osborne 1999) proposed an alternative interpretation of these passages involving parasogenesis (see below).
Figure 6. Section of loop between Pool of Reflections and Tower Chambers, River Cave, looking north. Note niches and planes of repose in right (eastern) wall. Second niche above path rises towards, and then falls after bend in path. Narrow slot in floor is visible to the left of path in mid-field.

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Secondary Mineralisation of Palaeokarst and Bedrock, Deposition of Coarse Calcite Crystals and Emplacement of Dolostone

I have described how weathering of pyrite-bearing dolomitic palaeokarst deposits at Jenolan Caves resulted in ancient filled cave passages being exhumed (Osborne 1984, 1991, 1993, 1996). I noted that aragonite and sulfate speleothems were preferentially deposited on a substrate of weathering dolomitic palaeokarst (Osborne 1994). It was proposed that dolomitisation and pyrite emplacement could have been caused by basinal fluids originating in the Sydney Basin sequence which overlay the Jenolan Caves Limestone for much of the Mesozoic and into the Tertiary.

Recent detailed fieldwork has shown that there are three distinct types of yellow-coloured dolomitic material exposed in the caves:

i. dolomitised and pyritised bedrock structures (e.g. algal mats),

ii. dolomitised and pyritised laminated carbonate and crinoidal calcarenite palaeokarst, and

iii. cavity-filling crystalline dolostone.

All three types of dolomitic material occur as remnant deposits and form roof pendants in the caves.

Some of the material previously interpreted as dolomitised palaeokarst has now been found to be either dolomitised bedrock or crystalline dolostone. Dolomitic roof pendants in Ribbon Cave, formerly thought to be dolomitised palaeokarst, have now been found to be algal mats in the bedrock which have been dolomitised. The dolomitic palaeokarst I (Osborne 1993) described as being exhumed from Barrelong Cave (F in Fig. 4) and some of the dolomitic roof-pendants near the Pool of Cerebus (Fig. 7) have now been found to be cavity-filling crystalline dolostone.

While the dolomitised bedrock and palaeokarst deposits are the result of an alteration process, the crystalline dolostone fills spar-lined voids or is separated from bedrock by a zone of ferruginous alteration. This suggests that it was deposited in preexisting cavities.

In a number of places, particularly in the northern part of Imperial Cave (D in Fig. 4), cave passages intersect masses of coarse calcite crystals. These crystals line cavities, which in places have open cores. I interpreted these crystals as palaeokarst deposits (Osborne 1984, 1991). Crystals with a similar habit are found both as wall coatings and lining open cavities in River Cave and Oolite Cavern, Mammoth Cave. In River Cave the crystals overlie both bedrock and laminated carbonate palaeokarst and in places the crystal-lined cavities are filled with crystalline dolostone (Fig. 8).

Any new synthesis must account for the alteration of the bedrock and carbonate palaeokarst, the excavation of the cavities into which the crystalline dolostone was deposited, the deposition of the coarse calcite crystals and the deposition of the crystalline dolostone.

Deposition of Aragonite, Dolomite and Sulfate Speleothems

Some of the most highly regarded speleothems in Jenolan Caves are composed of aragonite (Fig. 9). The deposition of aragonite speleothems in caves is usually attributed to the “poisoning” effects of magnesium ions on the calcite crystal lattice (Hill and Forti 1997). Work in progress with R. Pogson and D. Colchester of the Australian Museum has found that magnesium-rich phases, huntite, dolomite and ferroan dolomite have been and continue to be deposited in close association with the aragonite speleothems.

The Jenolan Caves Limestone, however, contains little magnesium and almost no pyrite. Of two bulk analyses reported by Carne and Jones (1919), one shows a “trace” and the other a nil result for MgCO₃. I noted the close association between the aragonite
Figure 7. Roof Pendant of crystalline dolostone, adjacent to Pool of Cerebus, Pool of Cerebus Cave. Circular artifacts are light reflectors. Note small complex aragonite speleothems in upper left and right of photo.

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and sulfate minerals and deposits of dolomitic palaeokarst (Osborne 1994). Weathering of the dolomitic palaeokarst and dolostones is the most likely source of the magnesium, and weathering of secondary pyrite the most likely source of the sulfate. The continuing deposition of huntite, dolomite and ferroan dolomite, usually associated with evaporative conditions, in the extremely wet conditions of Ribbon Cave requires further investigation and explanation.

ELEMENTS OF A NEW SYNTHESIS

My aim here is to identify those factors and processes that may account for the particular features and characteristics of Jenolan Caves. These factors will then be used to form the elements of a new synthesis and framework chronology. Much of the evidence for these factors and processes is derived from observations in the southern show caves and their major southerly extension, Barrelong Cave. It has proved much more difficult to unravel the events and processes that have occurred in the northern show caves due to the volume and complexity of fluvial sediments in them, which obscures evidence for other processes.
Multiple Karstification

Jenolan Caves are not the product of a single recent event during which a single process operated, but, rather, are the product of a number of different events, during which a variety of processes operated. These events took place over a geologically significant period of time (Osborne 1984).

The features we see in the caves today can only be understood, and the evolution of the caves deciphered, if we recognise from the outset that they result from the overprinting of a range of different events and processes. It is clear that unraveling these events is, and will continue to be, difficult, requiring a very significant commitment to detailed field investigation.

Hydrothermal/Per Ascensum Processes

Conventional models for the excavation of limestone caves (speleogenesis), e.g. Ford and Williams (1989), have stressed the dominant role of meteoric water sinking into the limestone (per decensum) as the agent of solution. Recently there has been increasing discussion in the international literature about the role played in speleogenesis by hydrothermal, artesian and interstratal waters; that is water rising into the limestone body

Figure 9. The Lyrebirds Nest, a complex aragonite helictite, Ribbon Cave. Spirals and spikes are aragonite; white cauliflower-like growths are composed of hunte in a pasty from, similar to ricotta cheese.
from below (per ascensum). Dublyansky (1980) listed four morphological criteria that strongly indicate a hydrothermal origin for caves.

1. They lack a genetic relationship to the surface topography.
2. They are largely or entirely devoid of fluvial sediments.
3. They display a three-dimensional rectilinear maze form guided by major fracture systems and, more rarely, by bedding planes, indicative of excavation by slowly flowing ascending waters.
4. The highest parts may display cupola-form solutional pockets.

While morphological characteristics are indicative of non-meteoric origins, the most reliable indicators of a non-meteoric origin are; high temperature minerals, clay minerals deposited in low pH conditions (Hill 1987; Hill and Forti 1997 and Forti 1996), stable isotope ratios and fluid inclusion thermometry (Bakalowicz et al. 1987 and Cilek et al. 1994).

Ford (1995) stated that caves formed by meteoric waters flowing downwards are the global norm, while ascending (per ascensum) waters and gases create few caves. He noted that per ascensum caves are more likely to intersect or be guided by palaeokarst than meteoric caves.

Many of the world’s largest and most spectacularly mineralised caves, e.g. Carlsbad (Hill 1987) and Lechuguilla Cave, New Mexico, Wind & Jewel Cave South Dakota (Bakalowicz et al. 1987) and the gypsum caves of the Ukraine (Klimchouk 1996), are now thought to have formed by the action of rising hydrothermal or artesian waters. Significant hydrothermal caves occur in Hungary and the Czech Republic. The role played by hydrothermal processes in the development of the World Heritage Listed Ochtinska Aragonite Cave in Slovakia remains controversial (Cilek et al. 1997).

While much research internationally has focused on caves that have formed solely or principally by hydrothermal or artesian processes, Ford (1995) noted that “multi phase cave systems of the general character of meteoric-hydrothermal-meteoric are probably far more common than generally realised”.

Jenolan Caves are clearly not solely the product of hydrothermal or artesian processes. Many of the unusual features of the caves such as intersection of palaeokarst, formation of cupolas and halls, alteration of bedrock and palaeokarst and the deposition of coarse calcite crystals and crystalline dolostones probably, however, result from one or more phases of per ascensum hydrothermal/artesian development.

Studies that could provide more direct evidence for the role of hot or warm non-meteoric water have only just begun. Reconnaissance fluid inclusion investigations suggest that the waters depositing the coarse calcite crystals were neither particularly saline, nor very hot, and suggest, along with the available mineralogical evidence, that the per ascensum processes at Jenolan may have been somewhat different from those described from North America and central Europe.

**Inception Horizons**

The inception horizon hypothesis (Lowe 1992; Lowe and Gunn 1997) seeks to explain the development of the initial conduits in karst rocks from which caves later develop. It postulates that initial conduits are most likely to form in particular lithostratigraphic features called inception horizons. Lowe (1992) defined inception horizons as “any lithostratigraphically controlled elements of a carbonate sequence that passively or actively favours localised inception of dissolitional activity, by virtue of physical, lithological or chemical deviation from the predominant carbonate facies within the sequence.”
Figure 10. Cross-sections showing development of passages in horizontal and steeply-dipping limestone after Osborne (1999a). A, B and C = horizontally-bedded limestone. Thick horizontal lines are inception horizons. A) Elliptical phreatic passages developed below inception horizons, axis of ellipse is horizontal, parallel to bedding. B) Keyhole passages produced by vadose incision in floor of phreatic passages. Axis of canyon is perpendicular to bedding. C) Paragenetic development of ovate phreatic passages excavates upwards, above the level of the inception horizons. Result is broad passage with wall morphology influenced by variable solubility of bedding. D, E and F = steeply-dipping limestone. D) Elliptical phreatic passage developed in steeply-dipping limestone. Axis of ellipse is vertical, parallel to bedding. E) Keyhole passages produced by vadose incision at lowermost point of phreatic passage. Axis of canyon is parallel to bedding; F) Paragenetic development of ovate phreatic passages excavates upwards producing conduit with relatively planar walls, guided by bedding.
Like most research and discussion about the formation and development of limestone caves, Lowe’s work has been largely concerned with phenomena occurring in horizontal to gently dipping limestone. I (Osborne 1999) have recently discussed how inception horizons may behave in limestone that is vertically to steeply dipping. While it is clear that bedding does play a role in guiding cave development at Jenolan, there has yet to be any detailed study of the lithostratigraphic features that initiated and guided cave development there.

Morphology of Caves Developed in Steeply Dipping Limestone

Most textbook diagrams showing cave cross-sections and their likely origin (e.g. Figure 52 of Jennings 1985) assume that the limestone has horizontal or near-horizontal bedding. At Jenolan, however, the bedding is steeply dipping and close to vertical, making these diagrams, and the inferences attached to them, inapplicable.

Figure 10, after Osborne (1999), shows some of the differences in cave cross-section that are likely to occur when caves develop in vertical to steeply dipping, rather than horizontally-bedded limestone. Phreatic tubes in vertical to steeply-bedded limestone will be ovoid with vertical axes of symmetry and tubes incised by vadose canyons will not have the classic keyhole shape as found in horizontally-bedded limestone. Passages developed in steeply-dipping limestone that have the same or similar cross-section to those shown in the classic textbook diagrams (Fig. 11) are most likely not to have been produced under the same conditions. As a consequence previous assumptions made that passages at Jenolan are either vadose, phreatic, pressure tubes or canyons etc. all require detailed reevaluation.

Sediment Blockages and Flow-Shifting

In impounded karsts, like Jenolan, water sinking into the karst drainage system carries with it significant amounts of insoluble sediment such as mud, sand, gravel and cobbles derived from the surrounding non-limestone catchment. At Jenolan the sediment
contains considerable quantities of quartz sand and volcaniclastic cobbles and boulders. I proposed that in impounded karsts with steeply to vertically dipping limestone, major flow paths for water through the limestone could become blocked with sediment, shifting flow from below ground to the surface (Osborne 1999).

During periods of blockage the stream will shift to the surface and then could incise into the limestone producing gorges that parallel (and in places intersect) former underground flow paths. This process may account for the contradictory evidence for landscape age given by the presence of high-level gravels of differing ages at the same elevation. A relatively recent blockage of the Grand Archway could result in the valley upstream being filled with sediment to the level of the saddle. Young fluvial sediment could then be deposited on the saddle adjacent to, and at the same level as, much more ancient sediment which was deposited well before the limestone became breached by the Grand Archway.

Following the blockage the stream may again be captured underground by the same inception horizon at a level below that of the blockage, providing another mechanism for intersection of palaeokarst by more recent caves.

Paragenesis

Paragenesis, described by Renault (1968), is the process of limestone dissolution at the upper limestone-water interface above an accreting sediment mass in a cave. As the sediment continues to be deposited, water is forced upwards against the passage ceiling which it dissolves away. As a consequence paragenetic passages tend to have relatively flat ceilings. As solution proceeds above the accreting sediment, lower sections of the walls are protected from solution by the sediment, resulting in the development of an inward-sloping planar profile in the lower wall, above which sideways dissolution produces a concave wall niche. Lange (1963) and Goodman (1964) called these inward-sloping planes in the lower walls of passages “planes of repose”.

By forcing aggressive water up against the cave ceiling, paragenesis allows relatively small and slow water flows to produce high cave passages with a large cross-section. Osborne (1999) proposed that the large conduits with wall niches at Jenolan (Fig.
11) are not the result of large phreatic flows followed by massive incision, but are exhumed paragenetic passages.

The rising and falling wall niches and the apparent "phreatic loops" are now interpreted as paragenetic in origin. The idea that the passages in River Cave were phreatic loops probably had its origin in the cross-section provided by Trickett (1925) (Fig. 12) which shows Mons Meg as a large loop. Trickett did not show, however, that the floor of this loop consists of sediment extending to a great depth, rather than bedrock, which a simple reading of his section might imply. Observations in the Tower Chambers-Pool of Reflections passage in River Cave (Fig. 13) showed that these loops are better interpreted as paragenetic features, resulting from the partial blockage of an original passage.

If the large conduits are paragenetic in origin there is no need to infer that significantly larger underground stream flows occurred in the past.

**Vadose Weathering and Secondary Mineralisation**

Deposits emplaced in hydrothermal cavities are likely to contain minerals, such as pyrite, which will decompose when exposed to oxygenated vadose seepage water. I proposed that weathering and underhand stoping of deposits that are unstable in vadose conditions are significant mechanisms for the exhumation of some large chambers (halls) in eastern Australian caves (Osborne 1996). It was also recognised that this process was currently taking place in parts of the Barrelong Cave and in the Imperial Streamway at Jenolan.

There is increasing evidence to suggest that stoping of hydrothermal deposits is widespread at Jenolan. Evidence for both past and presently active stoping is found in
some cupolas and in smaller passages, such as those in the western parts of Pool of Cerebus Cave.

The role of the hydrothermal dolostones and altered rocks containing dolomite and pyrite as substrata and sources for aragonite and sulfate speleothems is now more clearly established, however it is equally clear that this is not the whole story and that much more work is needed in this area.

**A FRAMEWORK CHRONOLOGY**

The chronology presented below is the first attempt to bring together the ideas I have previously published about the likely age of palaeokarst at Jenolan (Osborne 1995) and the mechanisms discussed above. The aim is to produce a framework chronology for the development of Jenolan Caves, which can form the basis for subsequent investigation and discussion. Jenolan Caves have a complex history. It is more likely than not that many of the events described here as occurring once, will, with further examination, be found to have taken place on a number of occasions during the hundreds of millions of years that caves have existed in the Jenolan Caves Limestone.

It is highly likely that there have been many phases of sediment blockage leading to flow shifting and paragenesis during the Cainozoic history of the caves. There is some

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**Table 1.**

A Framework Chronology for Jenolan Caves

<table>
<thead>
<tr>
<th>Geological Era/Period</th>
<th>Phase</th>
<th>Event/Process</th>
<th>Feature</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present</td>
<td>10</td>
<td>Stability</td>
<td>Low Mg Calcite Speleothems</td>
<td>Orient Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Continued Weathering</td>
<td>Ribbon Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mg Rich Minerals</td>
<td>Ribbon Cave</td>
</tr>
<tr>
<td>Quaternary</td>
<td>9</td>
<td>Meteoric Speleogenesis 5 Exhumation</td>
<td>Nick Point Sediment Cliffs Breakdown</td>
<td>The Ladder, River Cave Exhibition Chamber, Lucas Cave</td>
</tr>
<tr>
<td>A number of Cainozoic Phases</td>
<td>8</td>
<td>Meteoric Speleogenesis 4 Paragenesis</td>
<td>Conduits</td>
<td>The Slide, Lucas Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Loops</td>
<td>Mons Meg, River Cave</td>
</tr>
<tr>
<td>? Tertiary</td>
<td>7</td>
<td>Meteoric Speleogenesis 3 Invasion Caves</td>
<td>Crystal-lined Cavities</td>
<td>Baal-River Passage</td>
</tr>
<tr>
<td>? Late Cretaceous</td>
<td>6A</td>
<td>Hydrothermal Speleogenesis 2 Hydrothermal Fills &amp; Alteration</td>
<td>Dolomite Crystal</td>
<td>Mud Tunnels, River Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Altered Algal Mats</td>
<td>Pool of Cerberus Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Altered Palaeokarst Non-Detrital Clay</td>
<td>Ribbon Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Olympia Steps, Ribbon Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>River Letha, River Cave</td>
</tr>
<tr>
<td>? Late Cretaceous</td>
<td>6</td>
<td>Hydrothermal Speleogenesis 2 Evacuation</td>
<td>Cupolas</td>
<td>Persian Chamber, Orient Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Halls</td>
<td>Jenolan Underground River Ribbon Cave</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Tubes</td>
<td></td>
</tr>
<tr>
<td>Permian</td>
<td>5</td>
<td>Cave fill &amp; Landscape Burial</td>
<td>Fluvial Sediments</td>
<td>Dreamtime Cave</td>
</tr>
<tr>
<td>Permian</td>
<td>4</td>
<td>Meteoric Speleogenesis 2</td>
<td>Large Caves</td>
<td>Dreamtime Cave</td>
</tr>
<tr>
<td>? Early Permian</td>
<td>3</td>
<td>Hydrothermal Speleogenesis 1 Crystal-lined Cavities</td>
<td></td>
<td>Lucas Cave Entrance</td>
</tr>
<tr>
<td>? Latest Carboniferous</td>
<td>2</td>
<td>Marine Transgression and filling</td>
<td>Crinoidal and Laminated Carbonates</td>
<td>Olympia Steps, Ribbon Cave</td>
</tr>
<tr>
<td>? Late Carboniferous</td>
<td>1</td>
<td>Meteoric Speleogenesis 1 Phreatic Caves</td>
<td></td>
<td>Olympia Steps, Ribbon Cave</td>
</tr>
</tbody>
</table>
evidence to suggest that two or more hydrothermal/per ascensum phases have occurred. I have indicated in the sub-heading of each phase the type of process involved and a number to indicate the number of times each process has taken place in the chronology. A summary of the chronology is given in Table 1.

**Maximum Age of Karstification**

Convincing evidence for karstification of the Jenolan Caves Limestone prior to the Kanimblan Orogeny has yet to be found, however recent fieldwork has identified possible solution cavities which appear to predate significant folding. All confirmed palaeokarst features so far described have an angular unconformity at their boundary with the Late Silurian Jenolan Caves Limestone and show no sign of having been effected by either Tabberabberan (Mid Devonian) or Kanimblan (Early Carboniferous) folding.

**Phase 1 Meteoric Speleogenesis 1**

This phase of cave development produced a major phreatic conduit in the south, now filled and exposed in Barelong and River Caves, and a network of smaller passages now filled and exposed in the Grand Archway, Devils Coach House and in surface exposures.

While it is difficult to come to any definitive conclusion about the nature and extent of this period of speleogenesis, the conduit in the south suggests the excavation of a significant phreatic cave system more than 100 m below the likely surface level. There is no evidence of vadose development.

**Phase 2 Marine Transgression and Filling**

Marine carbonate sediments forming a sequence of crinoidal grainstones and grad-ed-bedded lime mudstones filled the phase 1 caves. Detrital quartz is absent from these rocks which have been altered by the emplacement of secondary pyrite and dolomite. They are disconformably overlain by pyrite-bearing conglomerates in Arch Cave. Similar deposits are found at Bungonia Caves (N.S.W.) and Ida Bay (Tasmania) (Osborne 1995).

While there is no direct evidence for the age of these units, I argued that they are most likely Latest Carboniferous (Osborne 1995). The transgression must have occurred prior to deposition and filling of the Camp Creek and Jenolan River palaeovalleys by conglomerates of the Permian Snapper Point Formation. This may be a previously unrecognised event for which palaeokarst deposits are the only remaining evidence. Preliminary palaeomagnetic work by Dr Brad Pillans of the Research School of Earth Sciences, Australian National University, has confirmed that these strata have not been folded and are older than Latest Cretaceous.

**Phase 3 ? Hydrothermal Speleogenesis 1**

A spar-lined cavity, filled with carbonate-cemented sandstones and conglomerates containing secondary pyrite, is exposed in the entrance area of Lucas Cave. The spar is similar in habit to that found filling cavities in River and Imperial Caves, but is white in colour and not associated in any way with ferroan dolomite. Since the pyrite in the sandstone is thought to be a product of a later hydrothermal event (phase 6) it is possible that there may have been an early, possibly Permo-Carboniferous, phase of hydrothermal cave development. There is some other evidence also suggesting an early phase of hydrothermal development, but it requires much further investigation.

**Phase 4 Meteoric Sepeleogenesis 2**

Phase 4 caves developed at Jenolan prior to the deposition of the conglomerates in the Surveyors Creek and Jenolan River palaeovalleys. Although remnants of these caves are more difficult to recognise than phase 1 caves, their palaeogeographic relationships are much clearer. Phase 3 caves formed below the level of the 900 m bench and consist
of large conduits such as Dreamtime Cave with cross-sectional shapes strongly suggestive of paragenesis (Osborne 1995). These types of passages are consistent with development in a sediment-rich, high relief, fluvio-glacial depositional environment such as that associated with the Permo-Carboniferous Talaterang Group and the Permin Snapper Point Formation (Herbert 1972, 1980).

Phase 5 Cave Filling, Valley Filling and Burial

Phase 3 and 4 caves are filled with sandstones and conglomerates in which secondary pyrite has been emplaced. In addition to Dreamtime Cave, strongly-cemented pyrite-bearing conglomerates and sandstones are exposed at the surface in the saddle above the Grand Archway and underground in the northern parts of Lucas Cave (e.g. Wiburds Dig), in Arch Cave, Chifley Cave and Elder Cave.

These sediments are likely to represent the earliest stage of valley-filling associated with Sydney Basin sedimentation. As with other valley-fills in the Jenolan Caves area (Bembrick 1980), they should be included in the Late Carboniferous or very Early Permin Talaterang Group (Gostin & Herbert 1973). After the caves and valleys became filled, there seems to have been a general cloaking of the landscape by Permin strata such as the Snapper Point Formation. This would have buried the whole of the limestone mass. The period of burial is likely to have extended from the Mid Permian through most of the Mesozoic.

Phase 6 Hydrothermal Speleogenesis 2

At least one major hydrothermal, per ascensum, phase of cave development followed phase 5. This was responsible for the excavation of three types of void: cupolas (circular in plan), halls (rectangular to lens-shaped in plan) and tubes (passages with roughly circular cross-section). Halls were produced where hydrothermal excavation occurred along inception horizons. The rising water was able to excavate upwards, penetrate through and expose palaeokarst fills, which would have prevented the passage of descending meteoric water.

Cupolas, halls and tubes were filled with coarse calcite crystals, ferroan dolomite, clays and iron-rich phases. Secondary pyrite and dolomite were emplaced by the rising fluids in the sediments filling the phase 1, 3 and 4 caves.

Examples of phase 6 cavities include:

- **Cupolas:** Queen Esther’s Chamber, River Cave  
  The Temple of Baal  
  Persian and Egyptian Chambers, Orient Cave  
  Mud Tunnels, River Cave  
  Cathedral, Lucas Cave  
  Queens Diamonds, Imperial Cave  
  Oolite Chamber, Mammoth Cave

- **Halls:** Imperial Streamway  
  Barrelong Cave

- **Tubes:** Barrelong Cave (see Osborne 1993)  
  Ribbon Cave  
  Passages in River Cave near the Junction  
  Pool of Cerebus west, near Arabesque

This phase could have occurred at any time between the mid Permian and the initiation of the present phase of landscape development (Late Cretaceous to Early Tertiary), however there is yet no direct evidence for its timing. It could well be related to thermal activity associated with the Late Cretaceous uplift of the Eastern Highlands and the opening of the Tasman Sea.
Phase 7 Meteoric Speleogenesis 3  Invasion Meteoric Caves

Following the uplift of the Eastern Highlands most of the Snapper Point Formation was eroded from the high parts of the landscape and the Talaterang Group conglomerates were exhumed from the Jenolan River and Camp Creek valleys. Meteoric water was then able to enter the Jenolan Caves Limestone via those inception horizons (or levels within inception horizons) that were not blocked by deposits emplaced during phases, 2, 5 and 6.

When the phase 7 passages formed below hydrothermal cavities filled with pyrite-bearing deposits, the process of exhumation by vadose weathering was initiated. Ferroan dolostone and other deposits in the cupolas began to weather and the cupolas became sediment traps. Caves also began to form along horizontal inception horizons in the Carboniferous carbonate palaeokarst, particularly where more open beds had formed the focus for pyrite emplacement.

Examples of phase 7 cavities include:
- Barrelong Cave where it is developed in palaeokarst
- The Baal Dig and Baal-River connection
- The tourist path passages in Imperial Cave

Phase 8 Meteoric Speleogenesis 4  Paragenesis

Eventually the phase 7 caves were able to capture most of the flow of the Jenolan River and Camp Creek underground. The geometry of the system, with its lack of a simple stream path, the presence of now open cupolas acting as sediment traps and the high sediment load in the surface streams resulted in the caves becoming blocked.

Blockage of the Grand Archway resulted in the valley upstream of the being filled by sediment and water being re-directed over the Grand Arch saddle. Partial blockage of the subterranean pathways in the northern caves resulted in significant incision into the bed of the Jenolan River, as its underground capture became less and less efficient.

In the many parts of the caves large paragenetic conduits and paragenetic loops developed as local groundwater levels rose and water slowly flowed over the blockages.

Examples of phase 8 cavities include:
- Conduits: The Slide, Lucas Cave
- Lucinda Cave, Lucas Cave
- Madonna Cave, Chifley Cave
- Loops: Mons Meg, River Cave
- Pool of Reflections — Tower Chambers, River Cave

Phase 8 was most likely not a single event. It is highly likely that a whole series of events involving blockage, paragenesis and flow shifting occurred throughout the Tertiary and Pleistocene. Detailed stratigraphy and palaeomagnetic dating will be required to sort this out.

Phase 9 Meteoric Speleogenesis 5 Exhumation

Following incision, the surface streams became recaptured along inception horizons either at a level below the sediment-blocked caves or in adjacent, lower-level inception horizons. This produced the present conduits of the Styx and the Jenolan Underground River. In places these new conduits formed below halls (Jenolan Underground River). In some parts of the system the phase 9 passages took quite a different path through the limestone to the older, higher-level caves, e.g. the stream at the southern end of Barrelong Cave.

Fills of various ages including weathered hydrothermal deposits and fluvial sediments responsible for paragenesis were excavated as downstream blockages were removed and perched aquifers within the limestone fell.
Sediments eroded back to form nick points in south at Queens Canopy and The Ladder in River Cave. A similar process may have operated in the north, e.g. at Katies Bower, but the history of filling and exhumation is far more complex in north. The major breakdown forming Exhibition Chamber and breakdown due to crystal wedging in limestone adjacent to cupolas, e.g. 2nd Persian Chamber and Orient-River Connection, probably occurred or began towards the end of this phase. This phase probably came to an end quite recently.

Phase 10 Relative Stability

The caves, at least what we can see above water level, appear at present to be in a stage of relative stability. The nick points in the paragenetic sediments have been stabilised by flowstone. Breakdown and removal of remnants of hydrothermal deposits appears to be proceeding quite slowly. Speleothem, dominantly phosphorescent calcite, but also aragonite, continues to be deposited.

DISCUSSION

Scientific Implications

The synthesis and chronology outlined above suggest that Jenolan Caves are likely to contain features and information of scientific interest that would not have been previously expected, including:

- cavities dissolved by rising water
- minerals emplaced by “hydrothermal” waters
- sediments, including clays, of hydrothermal, rather than surficial, detrital origin
- cave morphologies formed in response to steeply-dipping bedrock
- cave morphologies resulting from paragenesis

It also suggests that:

- large passages and chambers that are out of scale with the size of present streams in the caves need not be indicative of larger stream flows and higher rainfall in the past, but may result from either hydrothermal solution or paragenesis under relatively low stream flow conditions.
- excavation and removal of palaeokarst deposits has not only resulted from fluvial erosion by meteoric water under vadose conditions, but may also have resulted from solution and upward stoping by rising hydrothermal waters and/or gravity stoping following weakening due to weathering of unstable minerals, such as pyrite, in the vadose zone.

This paper is the first step towards a new understanding the geological history and evolution of Jenolan Caves. All of the processes discussed, the attempt to bring them together into a framework chronology and the original observations on which these are based require a great deal of further investigation.

It is quite clear that further progress in understanding Jenolan Caves and other similar caves in eastern Australia requires:

- **people** able to undertake detailed field studies of features within the caves,
- **time** in sufficient quantity for undertaking detailed fieldwork,
- **laboratory studies** in areas such as mineralogy, isotopes, dating etc.,
- **teamwork**, between field workers and those undertaking laboratory studies, and
- **funds** to make it happen.

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Management Implications

Current conservation and management of Jenolan Caves, and most other limestone caves in Australia, assume that they were formed by sinking meteoric water. It follows the dictum of Kiernan that "Maintaining the hydrological system in a natural condition is the foundation stone of karst management" (Kiernan 1988b, p 43).

If many of the significant morphological (e.g. cupolas) and mineralogical features (e.g. aragonite and gypsum speleothems) of the caves are the products or by-products of past hydrothermal processes, they will require different conservation and management strategies from those applied to features produced by current meteoric solution and deposition.

The conservation and management of these hydrothermal and post-hydrothermal features is unlikely to be dependent on maintenance of hydrological conditions or water chemistry in the catchment in general. Much more emphasis will need to be given to identifying and documenting significant and vulnerable features within the caves and developing localised management strategies at a feature by feature level. This new type of management will require the sort of detailed fieldwork and documentation that is also necessary for progress in research.

Interpretative Implications

The lack of scientific research into the origins and development of Jenolan Caves has meant that there has been little scientific underpinning for interpretation. This new synthesis and chronology can form the basis of interpretation that is able to answer many of the questions asked by tourists that could not previously be addressed. Three underground rivers and giant underground whirlpools will no longer suffice. Central to any new interpretative program will be the recognition that our understanding of the caves will undoubtedly change as research progresses.

Implications for Cave Exploration

The 'cave river' theory which has guided cave exploration at Jenolan for at least 30 years has not proved particularly useful in finding new caves. The new synthesis suggests that large cupolas are likely to be distributed rather randomly through the limestone and may have little genetic relationship with and poor connections to the passages through which water currently flows. Orient Cave and The Temple of Baal were discovered by climbing up from low-level caves into cupolas. The best chance for finding new highly decorated chambers is probably to repeat this technique. Perhaps the Chief Guides at Jenolan in the late 19th and early 20th centuries, such as Vos Wibur and Jeremiah Wilson, knew much more about the caves and how they really worked than many of us do today at the end of the 20th century.

ACKNOWLEDGEMENTS

Many people have assisted with my research at Jenolan Caves over the last sixteen years. David Branagan supervised the initial work and supported the idea of old caves at a time when it was unpopular to do so. Ernst Holland, both as Chief Guide and more recently as Karst Resources Manager, has helped in many ways, most significantly by making Jenolan a place where scientists are welcome and research is valued.

The Jenolan Caves Reserve Trust permitted access to the caves and provided staff assistance and accommodation. Ernst Holland, Nigel Scanlan, Steve Riley and their families have helped enormously by sharing their extensive local knowledge and providing accommodation, sustenance and friendship.

Many of the ideas in this paper came together as a consequence of study leave in Europe during the second half of 1997. While many scientists and cave managers assisted both Penney and me in the field and with accommodation, some deserve special mention. In Slovenia, Dr Tade Slabe and the staff of the Karst Research Institute, Slovene Academy of Arts and Sciences, Postojna, particularly Bojan Otonicar, showed us lots of palaeokarst in surface outcrop and motorway cuttings, but none in caves. In Austria, Dr Robert Seemann of the
Natural History Museum, Vienna showed us the caves and palaeokarst at Dachstein. Drs Pavel Bosak and Václav Cílek of the Geological Institute, Czech Academy of Science, Prague generously arranged field trips to palaeokarst, hydrothermal karst and hydrothermal palaeokarst in Czech Republic and Slovakia. The Management of Slovak Caves and the staff of Ochtinská Aragonite Cave provided significant assistance.

Research at Jenolan has been greatly helped by recent funding from the Australian Museum Trust and by the enthusiasm of Ross Pogson and David Colchester of the Australian Museum Geodiversity Research Group. My family, Penney and Michael, have endured much and greatly supported my dedication to a field of research so professionally and financially unrewarding as cave geology.

REFERENCES


Winter Use of Large-leafed Privet *Ligustrum lucidum* (Family: Oleaceae) by Birds in Suburban Lismore, New South Wales

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A large proportion of non-sclerophyll forest regrowth in the former “big scrub” region of north-eastern New South Wales is dominated by exotic trees of camphor laurel (*Cinnamomum camphora*) and large-leafed privet (*Ligustrum lucidum*). The high abundances of these species and the widespread clearance of native rainforests has meant that bird species have had to adjust to the new suite of plant resources or be eliminated from the region. The aim of this study was to investigate the variety of birds that use *L. lucidum* during the fruiting season and the ways in which the resources of the privet trees are exploited. The study was conducted in forest stands with a range of relative privet abundances in and around Lismore, in north-eastern New South Wales. A total of 17 species of birds used the privet during this study. Most were frugivores, feeding on the abundant privet fruit, but significantly more insectivory took place at the site with lowest privet abundance. A significant difference was noted in the avifaunal species composition of each site. Privet trees in mixed stands supported a greater range of bird activity and were used by more species than privet trees in near-pure stands. Eradication programs aimed at trees such as privet and camphor laurel will further reduce the resources available to birds and other wildlife unless they are gradual and include replacement with suitable native species.

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INTRODUCTION

Prior to European settlement, forest comprising a mosaic of subtropical rainforest, wet sclerophyll forest, warm temperate and dry rainforest covered more than 75,000 ha in the vicinity of Lismore, north-eastern New South Wales (Holmes 1987; Gosper 1994). These forest types, collectively known as the ‘Big Scrub’, were cleared in the mid 19th century for agriculture. Native rainforest communities in the region are now limited to small, often isolated remnants and scattered regrowth. The majority of regrowth areas include high proportions of exotic tree species such as camphor laurel (*Cinnamomum camphora*) and large-leafed privet (*Ligustrum lucidum*). These two species are now abundant in the former Big Scrub, often forming mono-specific stands (Gosper 1994). In the absence of native trees, exotic species may provide substantial resources to remaining bird populations (Date et al. 1991).

*Ligustrum lucidum*, a member of the Oleaceae family, is a shrub or small tree that grows to a height of 10 m and favours a rich, clayey soil (Buchanan 1989a; Harden 1992). *Ligustrum lucidum* is widely distributed from the south coast of New South Wales to north-eastern Queensland. In Northern NSW it is distributed in degraded pasture that once supported rainforest (Anon. 1983; Williams et al. 1984). Fruiting occurs in autumn.
and winter, with an average of 400 fruits produced per square metre of canopy (Buchanan 1989a). *Ligustrum lucidum* can produce a total of 100,000 to 1,000,000 seeds on one plant (Westoby et al. 1983; Fox and Adamson 1986; Buchanan 1989a). Of these seeds, 90% are capable of germinating thereby guaranteeing high recruitment of *L. lucidum* in Big Scrub remnants (Dunphy 1991).

The main features of a forest that influence birds are the structure and composition of the vegetation (Ford 1985). These features determine the variety of food types and foraging sites offered by a forest and consequently, the diversity of bird species. The structure of the vegetation also determines the availability of nesting sites and safe refuges from predators (Ford 1985). Bird species diversity is generally higher in rainforest vegetation because it has a greater structural complexity than weedy regrowth areas (MacArthur and MacArthur 1961; Disney and Stokes 1976; Leach and Recher 1993; Gosper 1994).

When environmental weeds invade native vegetation, a shift in the bird species composition can occur (French and Zubovic 1997). Environmental weeds cause changes in food resources and habitat structure, usually resulting in a reduction of the diversity and abundance of bird species (MacArthur and MacArthur 1961). The importance of an introduced plant to birds can increase if it provides more food or cover at a particular place and time than the remaining native vegetation. This is evident in farmland and urban areas where thickets of exotic vegetation can provide the only source of cover for native birds to roost or nest (Loy and French 1991).

In north-eastern NSW, many birds cannot adjust to the intensively managed agricultural systems that replaced rainforest, so weed dominated regrowth on disused land may constitute an important habitat for their conservation (Gosper 1994). This is particularly evident with frugivorous pigeons in the area, which rely heavily on introduced plant species on farmland during the winter fruiting period (Date et al. 1991). Exotic trees such as *L. lucidum* and *C. camphora* provide an abundance of winter food (Gosper 1994) and act as “stepping stones”, facilitating the movement of these species between patches of rainforest (Date et al. 1991). Therefore, the clearing of these exotic plants has the potential to affect the long-term survival of many rainforest birds (Lott and Duggin 1993; Recher et al. 1995).

The aim of this study was to investigate the variety of birds that use *L. lucidum* during the fruiting season and the ways in which the resources of the privet trees are exploited by birds in and around Lismore, north-eastern New South Wales, by examining:

(i) the variation in bird assemblages across four study sites which differ in the proportion of *L. lucidum* in their closed forest communities; and

(ii) the behaviour of birds in *L. lucidum* at four study sites.

**METHODS**

**Study area**

The study was conducted in Lismore (28°49′S, 153°16′E) New South Wales, from 20 July to 22 August 1997. Four study sites were selected to represent the range of habitat types in which *L. lucidum* occurs (Fig 1). Sites 1, 3 and 4 were of similar size (4 ha) and were dominated by weed regrowth with high relative abundances of *L. lucidum*. Other weed species at the sites included lantana (*Lantana camara*), wild tobacco (*Solanum mauritianum*) and *C. camphora*. Site 3 had the greatest relative abundance of privet, which in places formed mono-specific stands. Sites 1 and 4 supported a mix of exotic and native dry rainforest trees. Site 4 is close to a large stand of native species dominated by brush box (*Lophostemon confertus*).

Site 2 is Wilson Park Nature Reserve, a 21 ha Big Scrub remnant containing subtropical and dry rainforest vegetation (Holmes 1987). The core of the remnant supports a
high diversity of native trees and shrubs including forest red-gum (Eucalyptus tereticornis), hoop pine (Araucaria cunninghamii), python tree (Austromyrtus bidwillii), giant water gum (Syzygium francisii), whalebone tree (Streblus brunonianus) and Moreton bay fig (Ficus macrophylla) (Holmes 1987) whilst exotic species L. lucidum, C. camphora, climbing asparagus (Protaasparagus africanus) and L. camara are common around the perimeter of the park.
Survey Techniques

The four study sites were surveyed for seven days each, making the total survey period 28 days. On each day observations were conducted for 2–3 hours after sunrise and 2–3 hours prior to sunset. Each site was only surveyed for a maximum of three consecutive days. Sampling was only undertaken on days with little wind and no rain. At each site four sample points were randomly selected within the area of greatest privet abundance and two mature privet trees were selected at each point for observation. The same trees were used for the duration of the study. Observations of both trees at each sample point were made simultaneously over a period of 30 minutes. In this period the behaviour of all bird species using each tree was observed using 8 x 30 mm binoculars from a stationary position approximately 25 m away from the trees. Thus, eight trees at four points were observed for 30 min each morning and afternoon for seven days at each site. Each site therefore received a total of 56 tree-hours of sampling effort over the duration of the study. Behaviour was categorised according to a modified scheme developed by Recher and Holmes (1985) which is summarised in Table 1.

**Table 1.**

<table>
<thead>
<tr>
<th>Behaviour Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perch</td>
<td>any bird which remains stationary on a perch and performs no other behaviour before leaving the <em>L. lucidum</em> tree or termination of observation</td>
</tr>
<tr>
<td>Call</td>
<td>a bird that makes a vocal noise whilst in <em>L. lucidum</em> (may be simultaneously performing any other behaviour)</td>
</tr>
<tr>
<td>Feed (Frugivory)</td>
<td>a bird that visits and removes one (or more) fruit from <em>L. lucidum</em></td>
</tr>
<tr>
<td><em>Glean</em></td>
<td>a bird which walks or hops along branches of <em>L. lucidum</em>, searching for and taking prey from short distances</td>
</tr>
<tr>
<td><em>Pounce</em></td>
<td>a bird which drops or flies down from a perch in <em>L. lucidum</em> to take prey from the ground or low vegetation</td>
</tr>
<tr>
<td><em>Hover</em></td>
<td>a bird in flight remains stationary for brief periods while taking prey from <em>L. lucidum</em></td>
</tr>
<tr>
<td><em>Probe</em></td>
<td>bird extracts from under or within a substrate on <em>L. lucidum</em>, e.g. from crevices in bark</td>
</tr>
<tr>
<td><em>Hawk</em></td>
<td>bird flies from a perch in <em>L. lucidum</em> to take prey (e.g. insect)</td>
</tr>
</tbody>
</table>

* Bird behaviour categories Hawk, Probe, Pounce, Hover and Glean were considered as various forms of insect feeding and were grouped under the heading "Insectivory" for simplicity of analysis.

During any single 30–minute observation period a single behaviour record consisted of one type of behaviour being performed at least once by one or more individuals of a species. It was possible for the same species to display several types of behaviour during the one observation period, thereby generating several records, but multiple displays of the same behaviour type by the same species resulted in a single record for each 30 minute period.

RESULTS

A total of 17 bird species were recorded using privet trees during the study (Table 2). All species were native Australian birds (Slater et al. 1988; Simpson and Day 1996; Pizzey and Knight 1997), and none are considered rare or endangered.
**Table 2.**
Species recorded using privet trees during this study, and their general dietary requirements.

<table>
<thead>
<tr>
<th>Species1</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 4</th>
<th>Diet2</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-headed Pigeon Columba leucomela</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>g, f</td>
</tr>
<tr>
<td>Varied Triller Loxa ge leucomela</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td>g, i, f</td>
</tr>
<tr>
<td>Lewin’s Honeyeater Meliphaga lewinii</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>g, i, f, n</td>
</tr>
<tr>
<td>Silvereye Zosterops lateralis</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>g, i, f, n</td>
</tr>
<tr>
<td>Figbird Sphecotheres viridis</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>g, i, f, h</td>
</tr>
<tr>
<td>Pied Currawong Strepera graculina</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>g, i, f, n</td>
</tr>
<tr>
<td>Eastern Yellow Robin Eos paltala australis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>g, i</td>
</tr>
<tr>
<td>Rufous Whistler Pachycephala rufiventris</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>g, i</td>
</tr>
<tr>
<td>Grey Fantail Rhipidura fuliginosa</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>i</td>
</tr>
<tr>
<td>Red-backed Fairy Wren Malurus melanocephalus</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>g, i</td>
</tr>
<tr>
<td>White-browed Scrubwren Sericornis frontalis</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>g, i, h</td>
</tr>
<tr>
<td>Large-billed Scrubwren S. magnirostris</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>i</td>
</tr>
<tr>
<td>Brown Gerygone Gerygone mouki</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>i</td>
</tr>
<tr>
<td>Brown Thornbill Acanthiza pusilla</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>g, i, n, h</td>
</tr>
<tr>
<td>Red-browed Finch Neochmia temporalis</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>g, i, f</td>
</tr>
<tr>
<td>Spangled Drongo Dicrurus bracteatus</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>i, n</td>
</tr>
<tr>
<td>Scarlet Honeyeater Myzomela sanguinolenta</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>g, i, n</td>
</tr>
</tbody>
</table>

Total number of species recorded using privet at each site in this study | 10 | 10 | 5 | 9 |

+ Denotes species using privet at this site

1 Nomenclature from Christidis and Boles (1994)
2 Feeding types from Barker and Vestjens (1989)
g= granivore; i= insectivore; f= frugivore; n= nectarivore; h= herbivore

The highest number of species was observed at sites 1 and 2 whilst the lowest number of species observed was at site 3. Bird assemblages differed at each site and only three species (brown thornbill, figbird and silvereye) were present at all four sites.

A high percentage of locally nomadic, generalist feeding birds were recorded in *L. lucidum*. A higher number of insectivores were recorded at the native-dominated site (site 2) and one species, large-billed scrubwren, an obligate insectivore, was only recorded at that site. No obligate frugivores were present in the study, although individual rose-crowned fruit-doves (*Ptilinopus regina*) were heard calling from the core of site 2 and small flocks of topknot pigeons (*Lopholaimus antarcticus*) were observed flying over the study area.

A total of 483 behaviour records (200 at site 1; 72 at site 2; 90 at site 3; and 121 at site 4) were noted during 224 tree-hours of survey. Four behaviour categories were observed across the study sites (Fig. 2), these were perching, feeding on privet fruit (frugivory), calling and various forms of insectivory (gleaning, probing, pouncing, and hawking).

![Figure 2. Frequency of each behaviour type as a percentage of total observations (n) across all sites.](image)
Frugivory was the most frequently observed behaviour, followed by perching. The frequencies of observations of calling and insectivory were comparatively low. A chi-squared test for heterogeneity of behaviour type shows that bird behaviour when pooled for all species at each site differed significantly across the four study sites ($C^2 = 52.26$, d.f. = 9, $P = 0.0001$). These differences are illustrated in Fig. 3.

Frugivory was most frequently observed at Site 3, whilst lowest frugivorous activity was at site 2. The most frequent observations of perching was at site 1, whilst the fewest records of perching activity was observed at site 3. Insectivory was most frequently observed at site 2 followed by site 4. A very low frequency of insectivory was recorded at sites 1 and 3.

**DISCUSSION**

**Species Assemblages Across the Study Area**

All species recorded in the study are common (Pizzey and Knight 1997). The presence of three species (figbird, silveryeye and brown thornbill) across all four study sites may be due, in part, to their generalist feeding and nomadic behaviour (Recher and Holmes 1985) and high population levels in the region (Ekert, pers. obs.).

Figbirds have been recorded to rely heavily on *C. camphora* and *L. lucidum* fruit as a food source in the region during the winter months when native fruit abundance is low (Gosper 1994; Hackett 1997). Their presence across the study area is likely to be related to the availability of *L. lucidum* fruit present at all study sites. Importantly, as the *L. lucidum* fruiting season follows the *C. camphora* fruiting season, the figbirds that are initially attracted by the *C. camphora* fruit may remain when the *L. lucidum* fruit ripens.

Figbirds were commonly found in flocks comprising 10–50 birds. Flocking may enable figbirds to occupy territories and exploit resources by displacing other frugivores.
During this study white-headed pigeons, were forced to leave fruiting privet trees on several occasions by flocking figbirds.

Another species that has been recorded feeding on the fruits of *C. camphora* and *L. lucidum* was the Silvereye (Loy and French 1991; Gosper 1994; Hackett 1997). In this study silvereyes were frequently observed feeding on *L. lucidum* fruit. Like the figbirds, silvereyes may remain in the area after the *C. camphora* fruiting season to take advantage of *L. lucidum* fruit.

The brown thornbill was another species present across all of the sites. Leach and Recher (1993) and Wood (1996) consider the species to be dependent on remnant vegetation, abundant in both small and large patches of rainforest in N.S.W. However, Gosper (1994) found that this species has broad habitat requirements in north-eastern NSW, enabling it to occur in any forest vegetation, and this seems to be supported by this study.

Privet trees in mixed stands with native plant species (sites 1 and 4) supported a similar number of bird species as privet adjacent to native-dominated remnant rainforest vegetation (site 2). A high percentage of the birds recorded using *L. lucidum* were locally nomadic or migratory within their range (Pizzey and Knight 1997), and the closeness of the study sites may facilitate the movement of these common species between sites. No sedentary bird species were recorded from weed-dominated or mixed forest sites, and the large-billed scrubwren and eastern yellow robin, both sedentary species, were only recorded in site 2. The lowest number of bird species was recorded at the privet-dominated site (site 3). All of them are widespread, generalist feeders (Table 2) and used privet at 3 or 4 of the study sites. This result suggests that isolated, near-pure stands of privet are of limited resource value, however, privet located near native forest provides supplementary resources for many more species.

Fruit pigeons, apart from the one record of a white-headed pigeon at site 1, were absent from *L. lucidum*. Both topknot and white-headed pigeons were observed flying in flocks above the study sites, whilst rose-crowned fruit-doves were heard calling from the core of site 2. There was no trace of other fruit pigeons (wompoo fruit-dove [*P. magnificus*] and superb fruit-dove [*P. superbus*]) that are within their known geographical range (Pizzey and Knight 1997). Their absence may have been due to the aggressive behaviour and dominance of figbirds. More importantly, the small size of the remnants and their isolation from other stands may not provide the amount of fruit nor afford the protection from predators needed for these species (Howe et al. 1981; Innis 1989).

Pied currawongs have been widely documented to incorporate the fruits of exotic species including *L. lucidum* as a major component of their diet, especially during the winter period (Rose 1973; Mulvaney 1986; Buchanan 1989b; Bass 1995, 1996; Wood 1998). During the winter months (non-breeding season), pied currawongs congregate in flocks and migrate from the higher altitudes on the northern tablelands of NSW and the Canberra region into the lower altitudes to take advantage of fruiting exotic plant species (Frith 1969; Bass 1995, 1996).

The few records of pied currawongs feeding on privet in this study are in contrast to other studies in south eastern Australia (Rose 1973; Mulvaney 1986; Buchanan 1989b; Bass 1995, 1996; Wood 1998). Unlike the more temperate regions of Australia, with marked cold and hot seasons and subsequent marked lean and high levels of food resources, the subtropical climate of north eastern NSW may provide pied currawongs with sufficient food resources all year round. This may not necessitate a switch in diet of pied currawongs to fruit and/or a widespread migration to the lower altitudes during the winter period in the region.

**Fruiting cycles and food selection**

Frugivory was the dominant behaviour of birds at all the study sites, and is likely to be related to the superabundance of fruit at the time of the survey. Similarly, Innis
USE OF PRIVET BY BIRDS

(1989), Gosper (1994) and Hackett (1997) found that frugivory peaked with the seasonal abundance of fruit. The high percentages of frugivory observations suggest that *L. lucidum* fruit is an important resource for some generalist feeders in the Lismore region. Unlike native members of the Oleaceae Family, *L. lucidum* has the ability to produce an abundance of fruit year after year (Innis 1989). Furthermore, it produces fruit during the lean period of winter and spring when other fruits are comparatively scarce in the region.

Perching appears to be related to the high frequency of feeding records. This is because birds were frequently seen perching before and after taking *L. lucidum* fruit. The perches provided by *L. lucidum* afford birds protection from predators and disturbance from humans. It may also allow frugivores time to process fruit after intense feeding bouts. This underscores the role of *L. lucidum* to act as a local ‘stepping stone’, facilitating the movement of common birds between fruiting trees.

Insect availability and food selection

A comparative study of spiders in *L. lucidum* and native rainforest remnants in suburban Lismore (S. Burns pers. comm., Southern Cross University), has shown that a greater diversity of spiders exists in native rainforest remnants. The absence of a loose or fissured bark and a low diversity of leaf litter (Amor and Piggan 1977) in *L. lucidum* may reduce the habitat for spiders and insects, thus reducing the availability of food for insectivorous birds. A study of weed-infested coastal vegetation indicated that some specialist leaf litter invertebrates may be strongly affected by such infestations (French and Eardley 1997). This may explain the comparatively low recordings of insectivory in *L. lucidum*, especially in sites 1 and 3, which had the highest relative abundance of privet. Conversely, the presence of fissured bark and a higher plant species diversity of the adjacent plant community at site 2 can provide for a greater diversity of insects and therefore support a greater diversity of insectivorous birds.

Insect availability varies as a direct result of changes in seasons, with insect abundance higher in the warmer months and lower in the cooler months (Ford 1985). This variability may be due to the seasonal flowering of many species rather than changes in temperature, especially in the subtropical climate of northern NSW, and could account for changes in foraging activity of insectivorous birds (Cale 1994). Like the fruit, the flowers of *L. lucidum* are profuse and attract many insects. Flowering of privet had finished prior to commencement of this study and there were few other species in flower during the study period. The lack of abundant flowers would have reduced the potential activity by insects. In addition, there was no opportunity for nectarivorous birds to feed in privet during this study. Further studies incorporating the flowering season of *L. lucidum* are recommended to ascertain the use of privet by insectivorous and nectarivorous birds.

Management Implications

The invasion of exotic species such as *L. lucidum* in areas that once constituted the area of the Big Scrub may be seen as reducing the intrinsic value of native vegetation (Holmes 1987). The supporters of the eradication of this species may need to understand the importance of *L. lucidum* to some native avifauna in the area (Date et al. 1991). With less than 1% of the Big Scrub remaining, *L. lucidum* and *C. camphora* regrowth now occupy large areas of former agricultural land, often providing the only remaining resource for birds. The scarcity of available fruits in the area may further increase if *C. camphora* is declared a noxious weed and removed on a large scale. This may place a greater reliance on *L. lucidum* as an annual food resource by birds in the region.

Eradication of these species would need to be carefully planned to ensure the least disruption to bird feeding patterns. In rural areas, *L. lucidum* regrowth may well be an important habitat and food source for rainforest pigeons. However, the small size of the

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study sites and their close proximity to urban areas of Lismore reduce the likelihood of pigeons using the sites in this study. Furthermore, the abundance of territorial and aggressive flocking birds may exclude pigeons from such sites.

Management of *L. lucidum* in Lismore must consider the diversity of avifaunal guilds, including migratory birds that may use *L. lucidum*. This may require retaining *L. lucidum* in the short term with the long-term objective of replacing it with native vegetation (Date et al. 1991). Replacement of *L. lucidum* must be gradual to ensure that the existing resources *L. lucidum* provides to birds are maintained. To adopt a complete eradication of *L. lucidum* without the replanting of native vegetation would further reduce the resources of the region.

The concept of bird conservation may not be compatible with weed control strategies. The conflict involves the provision of a valuable resource to birds, and the dispersal of *L. lucidum* seed. Gradual replacement of *L. lucidum* with native vegetation would mean that there need not be a rapid depletion in fruit availability. However, the continuing presence of mature privet trees results in the dispersal of seeds. This may mean that as areas of *L. lucidum* regrowth are replaced there is still the potential for other sites to be colonised or invaded by *L. lucidum* because of the availability of viable seeds (Loyn and French 1991; Buchanan 1989a).

**CONCLUSIONS**

The findings of this study suggest that *L. lucidum* provides a resource for a number of common native birds in Lismore. During the winter fruiting season, *L. lucidum* produces an abundance of fruit at a time when the availability of native fruits is comparatively low in the region. This abundance of fruit provides a resource for some generalist frugivores. The dense canopy of *L. lucidum* can afford birds the protection from predators, whilst the close proximity of similar sites in the Lismore area allows such small stands to act as stepping stones thereby facilitating the movement of many species between sites.

The results of this study indicate that privet trees in mixed stands support a greater range of bird activity and are used by more species than privet trees in near-monospecific stands. In particular, sedentary species and insectivores were absent in isolated privet forests. We conclude that eradication programs aimed at trees such as privet and camphor laurel will further reduce the resources available to birds and other wildlife unless they are gradual and include replacement with suitable native species.

**ACKNOWLEDGEMENTS**

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**REFERENCES**


Occurrence of the Parasite *Ergasilus intermedius* (Copepoda: Ergasilidae) on the Gills of Macquarie Perch, *Macquaria australasica* (Percichthyidae)

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The parasitic cyclopoid copepod *Ergasilus intermedius* is recorded for the first time on the threatened Macquarie perch, *Macquaria australasica*, which represents the most southerly record of this parasite. Infestations (up to 50 parasites per gill arch) have been observed on broodfish (310–360 mm total length, 270–750 g weight) held in earthen ponds; 47% of fish examined in 1987 and 24% of fish examined in 1988 were infested. Attachment of *E.intermedius* to the gills induced chronic, segmental branchitis, characterised by localised epithelial hyperplasia, lamellar fusion and mucous metaplasia adjacent to the constriction caused by the clasping antennae. Infested fish held in 2000 L tanks were successfully treated with a single application of 2.0 mg/L Dipterex® for 24 hours. Lower dosages of Dipterex (0.15 and 1.5 mg/L) and other chemicals, such as NaCl and NaCl plus methylene blue in tanks, and malachite green in ponds, failed to eradicate the parasite. Discrepancies in the identity and source of the type host of *E. intermedius* are discussed. Potential implications for *M. australasica* conservation programs are briefly outlined.

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KEYWORDS: Australian freshwaters, conservation, Murray-Darling river system, parasitic cyclopoid copepod, pathology, treatment.

INTRODUCTION

The cyclopoid copepod *Ergasilus* is an important ectoparasite of wild and farmed fish around the world (Amlacher 1970; Kabata 1970; Sarig 1971). In Israel, for example, over 150 ergasilid parasites per gill filament have been recorded on farmed mullet, *Mugil* spp. which have caused massive mortalities (Sarig 1971). In Australia, ergasilids have been reported from marine, estuarine and freshwater fishes (Cressey and Collette 1970; Roubal 1981; Byrnes 1986; Kabata 1992). Much of the lifecycle of ergasilids is spent in a non-parasitic planktonic phase. Only mature females are parasitic, attaching to the host following copulation, whereas males are non-parasitic (Kabata 1970).

The Macquarie perch (*Macquaria australasica* Cuvier) is a freshwater fish native to south-eastern Australia. The present distribution of Macquarie perch is restricted to small isolated populations in some tributaries of the Murray River system and some river systems of the South-East Drainage Division (Cadwallader 1981). Consequently, the species is classified nationally as vulnerable (Jackson 1998) and is the subject of several conservation management programs (Ingram et al. 1990).

During captive breeding trials at NSW Fisheries' Inland Fisheries Research Station (IFRS), Narrandera, *Ergasilus intermedius* Kabata was identified on Macquarie perch...
broodfish. This paper describes the occurrence of *E. intermedius* on Macquarie perch, including observations on the pathology associated with attachment and treatment of infestations. In addition, discrepancies in the identity and source of the type host for *E. intermedius* are identified and discussed.

**MATERIALS AND METHODS**

**Occurrence and identification**

Macquarie perch broodfish, which were collected from the wild, were maintained in earthen ponds at the IFRS. The source of these fish and conditions under which they were maintained were outlined in Ingram et al. (1994).

Between September to November each year, when the maximum water temperature measured near the bottom of the ponds was between 15°C and 21°C, broodfish were transferred to 2000 L tanks in the hatchery for breeding trials (described in Ingram at al. 1994). Each fish was anaesthetised with 0.1 g/L benzocaine (Sigma), and their total lengths, weights and general condition were recorded. After breeding trials, fish were returned to the ponds.

The gills of fish were examined macroscopically and individual gill filaments with attached parasites were removed and fixed in 5% phosphate-buffered formol-saline, dehydrated in alcohol and embedded in paraffin wax. Longitudinal and transverse sections, 5μ thick, were stained with haematoxylin and eosin and examined histologically. Whole preserved parasites were mounted on microscope slides in polyvinyl lactophenol (containing acid fuchsin) and identified using descriptions provided by Kabata (1992).

**Treatment of infestations**

In order to eradicate the ergasilids, infested fish were treated with a range of chemicals commonly used to control external parasites (Rowland and Ingram 1991). Chemicals and dosages applied to 2000 L tanks containing infested fish were 10.0 g/L NaCl (60 min.), 5.0 g/L NaCl plus 1.0 mg/L methylene blue (24 hour), 0.15 mg/L Dipterex® (0,0-Dimethyl 2,2,2-trichloro-1–hydroxyethyl phosphonate) (Bayer) (24 hours) and 1.5 mg/L Dipterex® (24hours). In addition, earthen ponds containing Macquarie perch broodfish were treated with 0.08 mg/L malachite green (Bayer).

**RESULTS AND DISCUSSION**

**Parasite occurrence and pathology**

*E. intermedius* was found on the gills of Macquarie perch broodfish during spring in two consecutive years, 1987 and 1988. *E. intermedius* was not recorded from other species of fish held at the IFRS.

In 1987, 14 of the 30 fish (47%) examined were infested. Infestations ranged from less than one to 50 parasites per gill arch. In 1988, fewer fish were infested and the intensity of infestation was lower; 7 of 29 fish (29%) were parasitised, with 0–10 (mean 2.25) parasites per gill arch. Infested fish were 310–360 mm (mean 314 mm) in total length and 270–750 g (mean 492 g) in weight. *E. intermedius* were attached 0.63–0.94 mm (mean 0.77 mm) from the tip of the gill filaments. The second antennae of the ergasilid encircled the gill filament causing constriction of tissue at the site of attachment (Fig. 1).

The branchial epithelium at the site of attachment was hyperplastic and had formed a cushion of proliferated epithelial cells adjacent to the site of constriction (Fig. 2). Adjacent
Figure 1. *E. intermedius* (Er) attached to the gill filament (Gf) of Macquarie perch. Arrow indicates second antennae (Sa) encircling the gill filament. (Scale bar length = 0.20 mm).

gill lamellae were fused. Epithelial cells in the cushion were polyhedral in deeper layers, but became more flattened superficially. The epithelium was vacuolated, oedematous and exhibited mucous metaplasia. Several cystic spaces had formed. Small numbers of lymphocytes and eosinophilic granular cells infiltrated the deeper layers of the epithelium (Fig.3).

The histological changes in the gills at the site of attachment of the ergasilid probably represented a localised reaction to irritation from the feeding of the parasite (Oldewage and van As 1987), as well as constriction of the epithelium by the modified antennae. Ergasilids secrete enzymes which digest tissues of the host externally, facilitating the ingestion of particulate material, and which may also contribute to the pathological effects of the parasite (Smith 1975; Oldewage and van As 1987). However, Roubal (1986) suggested that the effects of attachment were more damaging than those of feeding. Pathiratne (1992) attributed the decrease in oxygen consumption of the Asian cichlid, *Etroplus suratensis*, to extensive hyperplasia and hypertrophy of gill filaments infested with *Ergasilus ceylonensis*.

Eosinophilic granular cells are common in chronic parasitic infections of the gills (Ferguson 1988). Infiltrations of lymphocytes, eosinophilic granular cells, macrophages and neutrophils accompanied the proliferative response associated with attachment of *E. lizae* Krøyer to the gills of yellowfin bream, *Acanthopagrus australis* (Roubal 1989). Oldewage and van As (1987) described a hollow in the area of proliferated branchial epithelium opposing the mouthparts of *E. mirabilis* attached to the gills of fish, but in Macquarie perch in this study, there was only a mild indentation in the epithelial cushion adjacent to the attached parasite.

**Comparison of treatments**

During the 1987 breeding trials, while infested fish were held in 2000 L tanks, applications of 10.0 g/L NaCl (60 min.), 5.0 g/L NaCl plus 1.0 mg/L methylene blue (24 hours), and 0.15 mg/L Dipterex® (24 hours), all failed to eradicate *E. intermedius*.  

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However, these fish were subsequently treated with 1.5 mg/L Dipterex® (24 hours) which reduced the infestation by 30% after 24 hours. Three days later all the parasites appeared to be dead.

During the 1988 breeding trials, a single 24 hour treatment of 2.0 mg/L Dipterex® completely eradicated *E. intermedius*, and in 1989, the next time the fish were recovered from the ponds, no fish were parasitised by the ergasilids.

Between 1987 and 1988, ponds containing the Macquarie perch broodfish were treated with malachite green at 0.08 mg/L primarily to control ectoparasitic ciliates, but this treatment was not successful in eliminating *E. intermedius*, as infested fish were recovered from these ponds after treatment.

Previous studies have shown that treatment with Dipterex® was an effective method of controlling ergasilid infestations (Lahav and Sarig 1967; Sarig 1971). Sarig (1971) indicated that the minimum concentration of Dipterex® for killing Ergasilus was 0.15 mg/L. The ineffectiveness of salt treatments suggests that *E. intermedius* is tolerant to the salinity levels and exposure times normally used to treat external parasites on freshwater fishes. Indeed some ergasilids, such as *E. lizae* (Kelly and Allison 1962), are euryhaline.

### Records of co-hosts

This is the first time *E. intermedius* has been recorded from Macquarie perch, and represents the most southerly record of this parasite. Kabata (1992) recorded *E. intermedius* from *Maccullochella macquariensis* (Cuvier), the type host, collected from Moreton Bay (Queensland), and *Tandanus tandanus* Mitchell, *Nematalosa erebi* (Günther) and *Macquaria ambiguca* (Richardson), all collected from the Macintyre River in Queensland. Kabata (1992) concluded that, having such a wide range of hosts, *E. intermedius* was a successful parasite. The occurrence of *E. intermedius* on Macquarie perch
increases the number of known hosts to five, which further demonstrates the success of this species as a parasite. However, we consider that both the identity and the collection site for the type host are incorrect. At the time of collection (1967), *M. macquariensis* was the species name for Murray cod, a relatively common and widespread species endemic to the Murray-Darling River system, including the Macintyre River. In 1972, the species name *M. macquariensis*, was assigned to trout cod, while Murray cod was renamed *Maccullochella peeli* (Berra and Weatherley 1972), then later corrected to *M. peeli* peeli (Rowland 1993). Trout cod is known to have occurred in tributaries of the Macquarie, Murrumbidgee and Murray River systems only (Berra and Weatherley 1972). Therefore the type host is more likely to be Murray cod. Since Moreton Bay is outside the range of Murray cod, the type host may also have been collected from the Macintyre River where the species occurs naturally, and where all other co-hosts of *E. intermedius* were collected.

Because ergasilids have been responsible for massive losses of farmed fish in other parts of the world (Amlacher 1970; Sarig 1971), *E. intermedius* infestation is a potential threat to Macquarie perch held in captivity, as loss of valuable broodfish to outbreaks will hinder conservation efforts. Captive breeding programs have been developed, as a conservation measure, to produce seedstock for release into selected areas to re-establish populations. Loss of broodfish to parasitism reduces the number of seedstock available for release, and can lead to a reduction in genetic variability and a loss of rare alleles. In addition, due to the rarity of this species, replacement of broodfish can be costly and time consuming. Therefore, parasitic outbreaks should be promptly treated to prevent such losses occurring.

*B.A. INGRAM AND A.W. PHILBEBY*

**Figure 3.** Stained cross section showing a lymphocyte (Ly) and an eosinophilic granular cell (Egc) in the cushion of proliferated epithelial cells. (Scale bar length = 30 μm).
ACKNOWLEDGMENTS

The authors wish to thank staff at the Inland Fisheries Research Station for their assistance, D. Callinan (NSW Fisheries) for commenting on the manuscript, Z. Kabata for confirming the identification of the ergasilid, and L. Cannon, J. Bourke and Z. Kabata for comments on host records.

REFERENCES

Incubation Temperature and Growth of Brisbane River Turtle (Emydura signata) Hatchlings

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Eggs of the Brisbane river turtle *Emydura signata* were incubated at three different temperatures (26°C, 28°C, 31°C) and hatching size and growth over the first year post hatch measured in two individuals from each temperature. Hatchlings emerging from eggs at all temperatures had similar plastron lengths and head widths, but hatching mass was significantly greater at 26°C. 412 d post-laying hatchlings from 28°C were only slightly larger in mass and dimensions than hatchlings from other temperatures, suggesting that incubation induced differences in hatching size have minimal impact on post-hatch growth over the first year. However, incubation at higher temperature results in shorter incubation periods and early hatching may give an advantage to hatchlings when food is scare or when the immediate post hatching growth period is shortened by winter cold, causing cessation of feeding and growth.

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KEYWORDS: *Emydura*, growth, hatching, turtle, incubation, temperature.

INTRODUCTION

Incubation temperature of many oviparous reptiles is known to affect hatchling attributes including sex (e.g. Bull 1980), morphology and size (Webb et al. 1986; Gutzke and Packard 1987; Gutzke et al. 1987; Hutton 1987; Joaen et al. 1987; Packard and Packard 1987; Packard et al. 1987; Webb et al. 1987; Webb and Cooper-Preston 1989; Burger 1990; Whitehead and Seymour 1990; Brooks et al. 1991; Demming and Ferguson 1991; Van Damme et al. 1992; Janzen 1993a; Allsteadt and Lang 1995; Shine 1995; Shine et al. 1995), behavior (Burger 1989, 1990, 1991; Webb and Cooper-Preston 1989; Janzen 1995; Shine 1995), locomotor performance (Burger 1990, 1991; Van Damme et al. 1992; Janzen 1993a, 1995; Shine 1995; Shine et al. 1995) and post-hatch growth (Hutton 1987; Joaen et al. 1987; Webb and Cooper-Preston 1989; Brooks et al. 1991; Bobyn and Brooks 1994; Rhen and Lang 1995). In species with temperature dependent sex determination, some of the differences in hatchling attributes may be due to sex, although it has been argued that this is not the case (Webb et al. 1987; Webb and Cooper-Preston 1989) and manipulative experiments that separate the effects of sex from the effects of temperature support this argument (Rhen and Lang 1995).

Temperature-induced differences in hatchling attributes are also found in species that have genotypic sex determination (Gutzke and Packard 1987; Burger 1989, 1990, 1991; Van Damme et al. 1992; Janzen 1993a; Shine 1995; Shine et al. 1995, Booth 1998). Whether or not these incubation temperature induced attributes affect a hatchling’s long-term growth and/or survival is still a largely unanswered question, with few studies addressing this topic to date (Joaen et al. 1987; Webb and Cooper-Preston 1989; Brooks et al. 1991; Bobyn and Brooks 1994; Janzen 1995; Rhen and Lang 1995).
the results of a preliminary experiment designed to quantify the effects of incubation temperature over the first year of growth in hatchling Brisbane river turtles (*Emydura signata*), a species which exhibits genotypic sex determination are presented.

MATERIALS AND METHODS

An entire clutch of 21 eggs was collected from a single female Brisbane river turtle (*Emydura signata*) nest immediately after oviposition on 24 December 1995, at a lake in St. Lucia, Queensland (27°32'S, 155°00'E). The eggs were transferred to the laboratory where they were weighed and placed in three separate containers on moist vermiculite with a water potential of approximately −150 kPa. Seven randomly chosen eggs were placed in each container, and one container placed in incubators set at temperatures of 31°C, 28°C or 26°C. Temperature within incubators fluctuated by less than 0.5°C. Towards the end of incubation, containers were examined daily for hatchlings. At hatching, each hatchling was removed, brushed free of vermiculite, weighed on an electronic balance, and plastron length and head width at the level of the jaw articulation measured with calipers. Two hatchlings from each temperature were placed into a 50 cm x 35 cm plastic tub filled to a depth of 12 cm with water. The tub was placed on a bench in front of a window in the laboratory and the water changed daily during the time when turtles were active and weekly during the winter period of inactivity. The laboratory was not artificially heated or cooled during the period of raising. Turtles were fed frozen whole mosquito fish (*Gambusia* sp.) in excess of need daily when active, and uneaten food removed when the water was changed. Food was offered once weekly during the winter period, but was never eaten. Turtles were weighed and the plastron and head width measured once a month throughout the experiment. A miniature temperature data logger (Tidbit, stowaway) programmed to record temperature every 30 min was placed in the water throughout the experiment so that mean water temperature between measurements could be calculated.

Oneway ANOVA was used to analyse for treatment differences in fresh egg mass, hatchling mass, hatchling plastron length and hatchling head width. Where significant differences were found (P < 0.05), a post-hoc Tukey pairwise multiple comparison procedure was used to compare individual treatments. Because sample size was limited to two turtles from each temperature, statistical analysis was not undertaken for 352 day-old turtles.

RESULTS

Of the 7 eggs incubated at each temperature, 5, 7 and 6 hatched successfully at 31°C, 28°C and 26°C respectively and subsequent analysis only includes these successfully hatched eggs. Mass and dimensions of fresh eggs, hatchlings and 412 d post-laying turtles are listed in Table 1 and the growth profiles depicted in Figure 1. Incubation time was temperature-dependent, with eggs incubated at 31°C hatching after 43 d, those incubated at 28°C after 50 d and those at 26°C after 60 d. At any one temperature all eggs hatched within 24 h of each other. Fresh egg mass and hatchling dimensions were not significantly different between temperature treatments (Table 1), but hatchlings from 26°C had a significantly greater mass than those from 31°C or 28°C (Table 1). No difference in mass was found between hatchlings from 31°C and 28°C.

Hatchlings began feeding within 4 days of hatching and grew relatively slowly (~65 mg/d) until water temperature dropped below 20°C (130 d after incubation started) at which time turtles became inactive, stopped feeding and ceased growing (Fig. 1). Approximately 4 months later (270 d after incubation started) water temperature
Figure 1. Mean water temperature, body mass, plastron length and head width of *Emydura signata* emerging from eggs incubated at 31°C, 28°C and 26°C against days since laying. Lines represent mean data for 2 turtles.
rose above 20°C and turtles became active and began feeding again. From this time until the experiment ceased growth was rapid (~270 mg/d; Table 1). By the end of the experiment turtles had grown to approximately 13 times their hatching mass (Table 1). Patterns of growth of turtles hatched from all temperatures were similar resulting in similar mass and dimensions 412 d post-laying (Table 1). Interestingly, growth in turtles from the 26°C treatment slowed compared to turtles from other temperatures over the last month of the experiment.

### Table 1.

Mean mass and dimensions of fresh eggs, hatchlings and 412 d post-laying turtles and mean hatchling growth rates before and after winter of *Emydura signata* from constant temperature incubation. Numbers in parenthesis indicate sample sizes. ANOVA used for treatment comparisons. * Indicates treatment was significantly different from other treatments.

<table>
<thead>
<tr>
<th>Incubation temperature 8C</th>
<th>31</th>
<th>28</th>
<th>26</th>
<th>Comparison between treatments</th>
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</thead>
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<tr>
<td>Fresh egg mass (g)</td>
<td>7.100(5)</td>
<td>6.882(7)</td>
<td>6.998(6)</td>
<td>P = 0.216</td>
</tr>
<tr>
<td>Hatchling mass (g)</td>
<td>3.936(5)</td>
<td>3.908(7)</td>
<td>4.137*(6)</td>
<td>P = 0.007</td>
</tr>
<tr>
<td>Hatchling plasteron length (mm)</td>
<td>22.4(5)</td>
<td>22.2(7)</td>
<td>22.3(6)</td>
<td>P = 0.824</td>
</tr>
<tr>
<td>Hatchling head width (mm)</td>
<td>8.8(5)</td>
<td>8.9(7)</td>
<td>8.8(6)</td>
<td>P = 0.241</td>
</tr>
<tr>
<td>412 d post-laying mass (g)</td>
<td>43.3(2)</td>
<td>45.0(2)</td>
<td>43.2(2)</td>
<td></td>
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<tr>
<td>412 d post-laying plasteron length (mm)</td>
<td>52.7(2)</td>
<td>52.8(2)</td>
<td>52.3(2)</td>
<td></td>
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<tr>
<td>412 d post-laying head width (mm)</td>
<td>13.2(2)</td>
<td>13.8(2)</td>
<td>13.0(2)</td>
<td></td>
</tr>
<tr>
<td>Pre-winter growth rate (mg/d)</td>
<td>56(2)</td>
<td>74(2)</td>
<td>66(2)</td>
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<tr>
<td>Post-winter growth rate (mg/d)</td>
<td>264(2)</td>
<td>281(2)</td>
<td>210(2)</td>
<td></td>
</tr>
</tbody>
</table>

### DISCUSSION

Of the three growth parameters monitored during this experiment, body mass was chosen because it is the best overall indicator of body size, plastron length was chosen because it is the most reliable linear measurement of body size in hatchlings of this species (the carapace remains relative soft and still retains curled carapace edges for up to a week after hatching), and head width was chosen because it reflects bite size which may be important in determining what food is available to hatchlings. Hatchlings emerging from eggs incubated at 26°C were significantly heavier than hatchlings from 31°C or 28°C, but linear dimensions were similar across all three temperatures. This observation is consistent with previous studies which indicate incubation at lower temperatures results in longer incubation times and slightly larger hatchlings, as judged by either a length dimension, mass or both (Webb et al. 1986; Gutzke and Packard 1987; Gutzke et al. 1987; Hutton 1987; Joanen et al. 1987; Webb et al. 1987; Packard and Packard 1987; Whitehead and Seymour 1990; Brooks et al. 1991; Shine 1995). An exception to this generalization is the Smooth soft shell turtle (*Apalone mutica*) in which cooler incubation temperatures result in smaller hatchlings (Janzen 1993a).

Conventional wisdom suggests that bigger is better in survival stakes (e.g. Brockelman 1975; Janzen 1993b, 1997), so *E. signata* hatchlings from 26°C may have a
greater fitness compared to hatchlings from 31°C or 28°C. However, in snapping turtles (Chelydra serpentina), incubation temperature-induced larger hatchlings do not experience greater post-hatch growth or survival compared to their smaller siblings under laboratory conditions (Brooks et al. 1991; Bobyn and Brooks 1994), similar to those in the current study. On the other hand, the incubation period at 26°C was longer than eggs incubated at 28°C or 31°C (7 and 17 days respectively). If there is an advantage to hatching and entering the aquatic environment earlier (e.g., starting to feed earlier) then hatchlings from 26°C might be at a disadvantage, despite their larger hatching mass. Indeed, a close examination of the growth curves based on the time since hatching (Fig. 1) indicate hatchlings from 26°C have similar mass but slightly smaller plastron and head width dimensions compared to hatchlings from 31°C and 28°C which have been in water and feeding for several days by the time 26°C hatchlings emerged. However, the larger hatching size and slightly faster mean daily growth rate of hatchlings from 26°C compared to hatchlings from 31°C (Table 1) before the onset of winter inactivity, meant that turtles from these two temperatures were the same size at the onset of winter (Fig. 1) despite hatchlings from 26°C hatching 17 days later than hatchlings from 31°C. The faster growth rate of hatchlings from 28°C meant that they were slightly larger in mass than hatchlings from 26°C and 31°C at the onset of winter (Fig. 1). After winter hatchlings from 26°C grew slower than hatchlings from 28°C and 31°C, particularly during the last month of the experiment (Fig. 1, Table 1). Hatchlings from 28°C may have had an advantage over hatchlings from other temperatures because their growth rate was slightly faster both before and after winter (Table 1) which resulted in these turtles being slightly larger at the end of the experiment (Fig. 1, Table 1). Comparative data on the effects of incubation temperature on the post-hatch growth of reptiles are scarce and all of the studies have raised hatchlings under highly artificial conditions. In the Nile crocodile (Crocodylus niloticus) individuals hatching from eggs incubated at 34°C were smaller in length, than individuals hatching from eggs incubated at 31°C, but by three months individuals from 34°C eggs were slightly longer (Hutton 1987). In American alligators (A. mississippiensis) hatchlings emerging from eggs at high (32.8°C) and low (29.4°C) are larger than at an intermediate temperature (30.6°C), but after 18 months of growth, the hatchlings from the intermediate temperature were significantly larger than those from either 32.8°C or 29.4°C (Joanen et al. 1987). In snapping turtles (C. serpentina) hatchlings emerging from eggs incubated at 28.6°C were smaller compared to hatchlings emerging from eggs incubated at either 22.0°C or 25.6°C, but once again hatchlings from the intermediate temperature were larger than either of the other temperatures after 7 months (Brooks et al. 1991) and 11 months growth (Bobyn and Brooks 1994). In another experiment with C. serpentina, in which temperature effects were experimentally separated from sex effects by manipulating embryo sex via the application of sex hormones during development, hatchlings from an intermediate temperature of 26.5°C grew faster than hatchlings from either 24°C or 29°C during the first 6 months of post-hatching growth (Rhen and Lang 1995). Thus the general trend from all of the studies is for hatchlings emerging from intermediate temperatures to grow faster than hatchlings from either higher or lower temperatures, but this difference in growth is small. It is highly questionable whether trends from an artificial environment (no predators, excess food at all times) can be extrapolated to the natural environment, but if there is an advantage to hatchlings emerging from eggs incubated at a particular temperature, it is slight in terms of post-hatch growth performance. If in the natural environment food is scarce and therefore a potentially limiting factor on growth, then it is probably advantageous to hatch earlier rather than later so that the limited food resources can be exploited before hatchlings from other nests emerge. In such cases, hatchlings emerging from eggs incubated at higher temperatures would have a clear advantage over hatchlings emerging from eggs incubated at lower temperatures because they hatch earlier. Hatching earlier may also be advantageous because early hatchlings have a longer feeding period before the onset of cool winter temperatures cause a cessation of feeding activity.
Figure 2. A). Percentage increase in cube root of body mass, plastron length and head width in *Emydura signata* hatchlings emerging from eggs incubated at 31°C. Lines represent mean data for 2 turtles. B). Percentage increase in head width against percentage increase in plastron length in *Emydura signata* hatchlings emerging from eggs incubated at 31°C. Dashed line indicates relationship if head width growth rate was the same as plastron growth rate. Solid line indicates linear regression of actual data. The slope of the regression line is considerable less than the slope of the equal growth rate line indicating that head width growth is proportionally slower than plastron length growth.
Head width reflects jaw width which in turn reflects mouth size and presumably feeding ability. If feeding ability is of particular importance to small hatchlings, the rate of head growth might be expected to be different from that of the overall body (other factors such as rate of brain growth may also have an important influence on the pattern of head growth). A plot of the relative changes in body size parameters as growth proceeds should highlight any differences. Because body mass is approximately proportional to body volume, and volume is proportional to the cube of a body linear dimension, the best direct comparison is to compare the cube root of mass with linear dimensions. A plot of these variables in hatchlings that emerged from eggs incubated at 31°C reveals that the cube root of mass scalar and plastron length have a very similar pattern of increase (as expected), but that head width increases at a much slower rate (Fig. 2A). A plot of the proportional increase in head width against the proportional increase in plastron length (Fig. 2B) also indicates head growth increases at a slower rate than body growth. Similar plots for hatchlings that emerged from eggs incubated at 28°C and 26°C show the same pattern (not shown). These plots indicate that hatchlings have proportionally much larger heads and mouths than older individuals. As a consequence, hatchling have the potential to handle relatively large food items which should enable them to tackle a wider size range of food items and thus increase their chance of survival.

ACKNOWLEDGMENTS

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Size, Water and Energy Content of Eggs of the Freshwater Turtles, *Emydura signata* and *Chelodina expansa*

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The relationships between egg dimensions, fresh egg mass, eggshell mass, fractional water content of egg contents and energy density of dry egg contents were determined for two species of Australian freshwater turtles, the Brisbane river turtle (*Emydura signata*) and the Broad-shelled river turtle (*Chelodina expansa*). Egg mass varied between 4.7 g and 10.6 g for *E. signata* and 10.4 g to 24.9 g for *C. expansa*. Egg length and width were good predictors of fresh egg mass in both species. Shell mass averaged 12% of fresh egg mass but varied significantly with fresh egg mass from 13.2% in 5 g eggs to 11.4% in 10.5 g eggs in *E. signata*, and averaged 14.6% over the entire egg size range in *C. expansa*. Fractional water content of fresh egg contents averaged 80.1% over the entire egg size range in *E. signata*, and averaged 78% but varied significantly from 81.8% in 10.5 g eggs to 73.3% in 24 g eggs in *C. expansa*.

Energy density of dried egg contents did not vary significantly over the entire egg size range in either species and averaged 25.05 kJ/g in *E. signata* and 26.21 kJ/g in *C. expansa*.

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**KEYWORDS:** *Chelodina*, eggs, *Emydura*, energy, turtle, water.

**INTRODUCTION**

Reproduction is fundamental to the persistence of all organisms. Consequently many biologists are interested in the effort made by organisms to reproduce themselves. One approach to this field of research is to measure or estimate the energy expended by organisms during reproduction. In animals this can be quite a complex process because energy may be expended in defending territory, obtaining mates and caring for young as well as producing eggs. In oviparous reptiles such as turtles, a good index of energy expended on reproduction is the energy content of eggs within a clutch, because energy expenditure obtaining mates is thought to be small and there is no post-oviposition expenditure of energy (Congdon and Tinkle 1982, Congdon et al. 1983, Booth 1998).

The most accurate way to estimate clutch energy expenditure is to measure the energy content of eggs by bomb calorimetry. This is necessarily an invasive and destructive process and therefore not a viable method if the reproductive effort of entire populations is the focus of interest, as is frequently the case in ecological studies. However, if the relationship between egg size and energy content can be quantified for a species, then only egg size and clutch size are needed to estimate reproductive effort. In freshwater turtles, egg size and clutch size can be accurately determined by X-ray radiography of gravid females with oviducal eggs (e.g. Gibbons and Greene 1979, Congdon et al. 1983, Dodd 1997, Hintow et al. 1997). After X-ray radiography, females are returned intact to their place of capture. This relatively uninvasive method can be used to estimate the reproductive effort of a population without the need for destructive sampling once the
relationship between egg dimensions and egg energy content is determined. In this paper I present data on the relationships between egg dimensions (which can be measured from X-ray radiographs), egg mass, and egg water and energy content for two species of Australian freshwater turtles, the Brisbane river turtle (*Emydura signata*) and the broad-shelled river turtle (*Chelodina expansa*).

MATERIALS AND METHODS

Clutches of *E. signata* and *C. expansa* eggs were collected from breeding sites located around the University of Queensland St. Lucia campus waste water treatment ponds near Brisbane, Australia (27°32′S, 153°00′E) between 1994 and 1997. Daily searching of oviposition areas insured clutches were less than 24 h old when collected. These ponds were constructed in 1981 and colonized by turtles soon after construction. The source of colonizing animals is not known, but both species occur naturally in streams and ponds in the Brisbane area (Cann 1998, D. Booth pers. obs.). Both species emerge to oviposit after rain, *E. signata* between October and January, and *C. expansa* between March and June. Eggs were collected from nests and transported to the laboratory in moist paper towel lined plastic containers within 30 min of collection. Once in the laboratory, eggs were rinsed with tap water to remove any adhering soil and blotted dry with paper towel. Eggs were then weighed (±0.1 mg) with an electronic balance and their length and width measured (±0.1 mm) with calipers.

Samples of 2–4 eggs from 16 clutches of *C. expansa* and 8 clutches of *E. signata* were used for analysis of water and energy content. Eggs were cut open with scissors and the mass of the wet contents recorded. No attempt was made to separate the yolk from the albumen. The eggshell including the attached membrane was blotted dry and weighed. The contents were dried to constant mass at 60°C to determine water content and stored frozen at −20°C until bomb calorimetry was performed. For bomb calorimetry, samples were thawed, ground to a paste with a mortar and pestle, and then placed in an oven at 60°C for 24 h. From each sample 3 sub-samples (0.2–0.5 g) were ignited in an adiabatic bomb calorimeter (Gallenkamp auto bomb, England) previously calibrated by igniting pre-weighed samples of thermochemical standard benzoic acid (26.442 kJ/g). In all cases the 3 sub-samples gave energy densities within 2% of each other, so an average was calculated from all three values and this assigned to the egg from which the sub-samples were obtained.

Linear regression, multiple regression and Pearson product moment correlation analysis were used to determine descriptive relationships between fresh egg mass (FEM) and other variables. When analyzing the relationship between FEM and egg energy content, water content and eggshell mass, a single value was used for each clutch, and this value was derived from the average for all eggs sampled within the clutch. Results are presented as means ± standard errors of the mean. Energy density of egg contents was compared between *E. signata* and *C. expansa* using a Mann-Whitney Rank Sum test.

RESULTS

*Emydura signata*

A total of 385 *E. signata* eggs from 21 clutches were collected (Table 1). Eggs were oval in shape with egg length (EL) always exceeding egg width (EW). Multiple regression analysis indicated that EL (mm) and EW (mm) together were better predictors of FEM (g) (Eq. 1) than either EL or EW alone (Eqs. 2 and 3). EL was a slightly better predictor (as indicated by a higher R² value) of FEM than EW.
Eq. 1:
FEM = EL x 0.3232 + EW x 0.5471 – 13.532
R^2 = 0.98, P < 0.001, N = 385

Eq. 2:
FEM = EL x 0.5545 – 10.040
R^2 = 0.90, P < 0.001, N = 385

Eq. 3:
FEM = EW x 1.054 – 13.291
R^2 = 0.88, P < 0.001, N = 385

Water content of egg contents was independent of FEM (Pearson correlation: R^2 = 0.07, P = 0.52, N = 8) and averaged 80.1 ± 0.5%. Energy density of dry egg contents was independent of FEM (Pearson correlation: R^2 = 0.27, P = 0.27, N = 8) and averaged 25.05 ± 0.08 kJ/g. The fractional mass of the eggshell varied significantly with FEM with small eggs having proportionately more eggshell (Fig. 1). Egg energy content can be accurately predicted from FEM (Fig. 2).

**Table 1.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>E. signata</th>
<th>C. expansa</th>
</tr>
</thead>
<tbody>
<tr>
<td>clutch sample size</td>
<td>21</td>
<td>24</td>
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<tr>
<td>mean clutch size</td>
<td>18.3</td>
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<td>egg sample size</td>
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<tr>
<td>mean egg mass (g)</td>
<td>7.67</td>
<td>16.51</td>
</tr>
<tr>
<td>egg mass standard error (g)</td>
<td>0.08</td>
<td>0.18</td>
</tr>
<tr>
<td>egg mass range (g)</td>
<td>4.69–10.57</td>
<td>10.39–24.92</td>
</tr>
<tr>
<td>mean egg length (mm)</td>
<td>31.9</td>
<td>38.5</td>
</tr>
<tr>
<td>egg length standard error (mm)</td>
<td>0.1</td>
<td>0.2</td>
</tr>
<tr>
<td>egg length range (mm)</td>
<td>25.6–37.7</td>
<td>32.0–43.2</td>
</tr>
<tr>
<td>mean egg width (mm)</td>
<td>19.9</td>
<td>27.0</td>
</tr>
<tr>
<td>egg width standard error (mm)</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>egg width range (mm)</td>
<td>16.4–22.3</td>
<td>23.4–30.8</td>
</tr>
</tbody>
</table>

**Chelodina expansa**

A total of 359 *C. expansa* eggs from 24 clutches were collected (Table 1). Eggs were oval in shape with egg length always exceeding egg width. Multiple regression analysis indicated that EL and EW together were better predictors of FEM (Eq. 4) than either EL or EW alone (Eqs. 5 and 6). EW was a better predictor of FEM than EL.

Eq. 4:
FEM = EL x 0.4883 + EW x 1.135 – 32.956
R^2 = 0.99, P < 0.001, N = 359

Eq. 5:
FEM = EL x 1.044 – 23.713
R^2 = 0.83, P < 0.001, N = 359

Eq. 6:
FEM = EW x 1.724 – 30.016
R^2 = 0.91, P < 0.001, N = 359
Water content of egg contents varied significantly with FEM (Fig. 3). Energy density of dry egg contents was independent of FEM (Pearson correlation: \( R^2 = 0.03, P = 0.63, N = 16 \)) and averaged 26.21 ± 0.03 kJ/g. The fractional mass of the eggshell was independent of FEM (Pearson correlation: \( R^2 = 0.09, P = 0.25, N = 16 \)) and averaged 14.6 ± 0.4%. Egg energy content can be accurately predicted from FEM (Fig. 2).

**DISCUSSION**

By combining the relationships in Eqs. 1, 4 and figure 2 energy content of *E. signata* and *C. expansa* eggs can be reliably predicted from measurement of EL and EW.

For *E. signata*: Energy content (kJ) = 1.551 x EL (mm) x 2.626 – 68.563

For *C. expansa*: Energy content (kJ) = 3.645 x EW (mm) x 8.472 – 287.068

EL and EW can be accurately measured from X-ray radiographs if a known length metal object is placed beside the female turtle when she is being radiographed, and this measurement used to correct for the magnifying effect usually present in such radiographs. Hence X-ray radiographs of gravid females is a relatively uninvasive method to provide accurate data on reproductive energy expenditure in these two turtle species.

EW and EL alone were good predictors of FEM in both *E. signata* and *C. expansa*. In *C. expansa* EW was a slightly better predictor than EL, a finding consistent with studies of North American freshwater turtles (Congdon and Tinkle 1982, Proc. Linn. Soc. N.S.W., 121. 1999
Figure 2. Relationship between egg energy content against fresh egg mass for *E. signata* and *C. expansa* eggs.

Data points are mean values for eggs sampled from different clutches. Least squares linear regression for *E. signata* eggs:

Energy content (kJ) = 4.800 x FEM (g) - 3.609

$R^2 = 0.96, P < 0.001, N = 8$

Least squares linear regression for *C. expansa* eggs:

Energy content (kJ) = 7.464 x FEM (g) - 41.084

$R^2 = 0.97, P < 0.001, N = 16$

Schwarkopf and Brooks 1986, Iverson 1991, Iverson and Ewert 1991, Iverson and Smith 1993, Rowe 1994). In contrast, EL was as good a predictor of FEM as EW in *E. signata*.

Eggshell mass was a constant fraction (14.6%) of FEM over the entire egg size range in *C. expansa* but smaller eggs had proportionately heavier eggshells than larger eggs in *E. signata*. *C. expansa* eggs are generally larger than *E. signata* eggs (Table 1, Fig. 2). However in eggs of the overlapping size range (10–11 g), *C. expansa* have a heavier eggshell and thus lighter egg contents compared to *E. signata* eggs. The relative eggshell mass of both *E. signata* and *C. expansa* eggs is lighter than the hard-shelled eggs of pig-nosed turtle *Carettochelys insculpta* (16.5%) which have a FEM averaging 34 g (Webb et al. 1986).

Fractional water content of the contents of fresh *E. signata* eggs varied around a mean of 80.1% over the entire egg size range. In contrast, egg contents of smaller *C. expansa* eggs had a higher fractional water content than larger eggs (Fig. 3). This might be explained by smaller eggs having a higher albumen to yolk ratio than larger eggs (Booth 1998) because albumen has a higher water content than yolk. Interestingly, the fractional water contents of both *E. signata* and *C. expansa* eggs are greater than those found in 12 species of fresh water turtles than lay parchment shelled eggs (mean 69%, range 61%–73%) examined by Congdon and Gibbons (1985) but similar to the water content of the hard shelled eggs laid by the turtle *Trionyx triunguis* (78.6%, Leshem et al. 1991). Thus the ratio of albumen to yolk may also differ markedly between fresh water turtle...
species that lay hard and pliable shelled eggs. The biological significance of such a difference is obscure, but may reflect differences in incubation strategy, as the amount of water absorbed from or lost to the environment affects hatching size in species that lay pliable shelled eggs (e.g. Gutzke et al. 1987, Miller 1993, Packard 1999) but does not affect hatching size in species that lay hard shelled eggs (Martin 1999, Packard 1999).

The energy density (on a dry weight basis) of both E. signata and C. expansa egg contents was independent of FEM, but was significantly (P < 0.001) greater in C. expansa (26.21 kJ/g) compared to E. signata (25.05 kJ/g). This reflects a slightly higher lipid to protein ratio of C. expansa egg contents (D. Booth pers. data) as lipid has a higher energy density than protein.

Data on the energy density of dry contents of freshly laid freshwater turtle eggs are scarce. Values have been reported for Chyrsemys picta (26.4 kJ/g, Congdon and Tinkle 1982), Chelydra serpentina (28.5 kJ/g, Wilhoft 1986) and Trionyx triunguis (28.5 kJ/g, Leshem et al. 1991). These values are slightly higher than those for E. signata and C. expansa reported here. However, more data from other species are needed before any generalisations about egg contents energy density of freshwater turtles can be made.

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Radio-tracking studies of hand-reared grey-headed flying-foxes (*Pteropus poliocephalus*) released at the Gordon colony in the northern suburbs of Sydney have shown that successful integration of hand-reared bats with a wild colony depends on timing of release. Complete integration occurred when release was timed to coincide with independent foraging behaviour of wild juvenile bats. Radio-collared hand-reared bats were found to move between the colony at Gordon and colonies in the Royal Botanic Gardens Sydney and at Cabramatta Creek in the south of Sydney. Long distance movements of individuals along the coast as far as 310 km north and 279 km south of Gordon were recorded.

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KEYWORDS: bat migration, flying-foxes, hand-rearing, *Pteropus poliocephalus*, radio-tracking, rehabilitation.

**INTRODUCTION**

In recent years there has been a rapid growth in the number of wildlife rehabilitation groups, particularly along the east coast of Australia. The ultimate goal of such groups is to release rehabilitated and hand-reared native animals back into the wild. Indeed this is required by law in all Australian states.

In some states there are restrictions on conditions and sites of release, such as regulations prohibiting release in National Parks, but these criteria appear to be based on general conservation biology principles rather than data based on studies of individual species and specific sites. The few local studies that have been carried out to determine the fate of rehabilitated, captive-reared or relocated animals after release have provided only limited data (Gipps 1991; Hyman 1993; Kleiman 1989). The programs have usually been terminated by high rates of predation by foxes or other introduced carnivores. For example, in a release of captive-bred Parma Wallabies, 100% were killed by foxes shortly after release (Short et al. 1992). Similarly 26 out of 55 Rufous hare wallabies released with radio transmitters in the Northern Territory were killed by cats, and the total was probably much higher as the fate of some of the other radio-collared wallabies could not be determined (Gibson et al. 1994). In a long-term study of the fate of hand-reared ring-tail possums released into Ku-ring-gai Chase, Augee et al. (1996) found low levels of survival and high rates of predation by foxes and to a lesser extent cats. The only successful release programs have apparently been on islands, such as the establishment of brush-tailed bettongs (Delroy et al. 1986).
All the above studies of release programs in Australia have dealt with terrestrial mammals. However Australia has a diverse bat fauna, including six families of Microchiroptera with about 56 species and one family (Pteropidae, the flying-foxes) of Megachiroptera with 7 species. Because of their proximity to human habitation and the economic impact of their occassional attacks on fruit orchards, flying-foxes receive considerable human attention. The distribution of the grey-headed flying-fox, *Pteropus poliocephalus*, includes the major cities of Brisbane and Sydney, and to a lesser extent Melbourne, and therefore this is the bat species most commonly involved in rehabilitation and release programs. However the fates of hand-reared flying-foxes, their survival and behaviour after release remain unknown.

Here we report a study of radio-collared, hand-reared *P. poliocephalus* juveniles released at the periphery of a colony site in the northern Sydney suburb of Gordon. The four main objectives were to:

1) determine the degree to which released hand-reared juveniles integrated with the resident wild colony;
2) establish release procedures which maximise such integration;
3) track local movements within 50 km, which is the maximum range for nightly foraging flights determined for this species by Eby (1991); and
4) track long distance movements to other colony sites to the north and south of Sydney.

MATERIALS AND METHODS

The individuals radio-tracked in this study were orphans that had been hand-reared by trained carers belonging to the Ku-ring-gai Bat Conservation Society (KBCS). Several wild adults that were captured by C.R. Tidemann and the Cabramatta Bat Colony Committee at Cabramatta Creek were also fitted with radio transmitters.

Colony site

The colony is located in a narrow, steep-sided valley in the Sydney suburb of Gordon, 13 kilometres north of the Sydney Opera House, 33°45'16"S, 151°9'30"E. This valley is drained by Stoney Creek, a tributary of Rocky Creek, which flows into Middle Harbour, and which eventually runs into Sydney Harbour. The valley consists of tall open forest, much degraded with introduced vines and ground cover. The site is being regenerated by paid contractors and volunteers who have worked regularly on site since 1987.

Release protocol

The established procedure used by the Ku-ring-gai Bat Conservation Society for release of hand-reared flying-foxes is to place the animals in a large aviary (2.5 m high, 3.1 x 6.3 m base) near to the colony but well outside its perimeter. The colony can be heard from the cage but not seen. Wild juvenile and adult flying-foxes have been observed regularly visiting the aviary when the hand-reared animals occupy it.

In 1995, the first year of the study, the procedures for release used in previous years were followed and the hand-reared flying-foxes were placed into the aviary in late February. The aviary remained closed for a period of 28 days to allow the animals to become accustomed to the wild surroundings and to give them an opportunity for flight practice. Buckets of fruit with protein supplement were provided daily. On 18 March, a hatch in the aviary was opened and the animals were allowed to freely move in and out of the cage. Food was available from buckets hanging on the outside of the aviary for a further eight weeks.
In 1996 the flying-foxes were placed in the release aviary in late January, a month earlier than in 1995. The release hatch was opened 30 days later, on 26 February. Support feeding ceased after six weeks. In 1997, the earlier release time was repeated and the hatch opened on 21 February. Support feeding was gradually reduced, terminating completely after four weeks.

Radio transmitters

Radio transmitters were specially made for this project by Biotelemetry Tracking Australia, Kent Town, South Australia. A prime consideration for a radio-tracking system with flying-foxes is that there is virtually no prospect of recapturing the bat in order to remove expired transmitters. Therefore in 1995 transmitters were designed to be glued to the back of the animal so that they would fall off after a short period. The transmitters weighed 7 g and had a 26 cm trailing antenna. The range of the transmitters was good, at least 5 km line-of-sight, but after 20 days almost all of the transmitters had fallen off or were possibly removed by grooming.

In 1996 transmitters weighing 16 g with a shorter trailing antenna were attached to collars made from surgical tubing. This type of collar was designed for use on small marsupials (Soderquist 1993) where both stretch and limited life of the collar are required. Ultraviolet light destroys the rubber tubing, and in our experience the transmitter and collar fell off within 3–4 months. Prior to the 1996 release, prototypes of the collar were tested on captive flying-foxes and proved to be tolerated extremely well by the bats. The same system was used again in 1997.

Location techniques

The position of individual flying-foxes was determined by triangulation from three vantage points on the rim of the valley, above the colony. Bearings were determined using directional antennas and surveyors’ (magnetic) compasses and plotted onto a “radio map” (Gibson et al. 1994) of the resident colony which was established by multiple bearings taken on transmitters placed at various spots on the outer limits of the colony.

Several aerial surveys were made from a NSW National Parks and Wildlife Service fixed-wing aircraft along the coast to the north and south of Sydney. Directional antennas (Telonix, Mesa, Arizona, USA) were fixed to the wings and transmitter frequencies were scanned using a multichannel Telonix scanner.

Exit counts

The size of the Gordon colony was estimated by counting the number of bats flying out at sunset over points located below the three major exit routes (Rosedale Bridge to the W of the colony, Maytone Ave. to the SE, and Warandoo St. to the NE). Counts were carried out by trained volunteers using hand-held counters.

RESULTS

Integration

The only criterion for a “successful” release capable of quantitative assessment by the technique outlined above is integration into the resident colony. Locations of bats in the Gordon Valley determined by triangulation for the three year period of this study are shown in Fig. 1. As data could only be obtained for the first 20 days after release in
Figure 1. All roost sites determined by triangulation of signals from radio-collared grey-headed flying-foxes in the Gordon valley. The outline represents the maximum boundary of the resident, wild bat colony. The solid triangle indicates the position of the release cage.

1995, due to the subsequent shedding of the glued-on transmitters, Table 1 compares the location of daytime roost sites for all three years over that time period. In 1997, under conditions of relatively early release and cessation of post-release support feeding, integration was 100% by Day 20. By Day 20 in 1997 all the radio-collared bats were flying out from the valley with the nightly exit of the colony.

<table>
<thead>
<tr>
<th>Year</th>
<th>Release date</th>
<th>Number of hand-reared bats</th>
<th>Number of wild bats</th>
<th>Support feeding</th>
<th>Mean Wt. (g)</th>
<th>Integration (Day 20)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>18 Mar.</td>
<td>28</td>
<td>2</td>
<td>Long Term</td>
<td>463</td>
<td>45%</td>
</tr>
<tr>
<td>1996</td>
<td>26 Feb.</td>
<td>48</td>
<td>4</td>
<td>Long Term</td>
<td>402</td>
<td>67%</td>
</tr>
<tr>
<td>1997</td>
<td>21 Feb.</td>
<td>31</td>
<td>4</td>
<td>Short Term</td>
<td>384</td>
<td>100%</td>
</tr>
</tbody>
</table>

Local and long distance movements

Unfortunately interference within the scientific research UHF band (150–152 MHz) is so great in the Sydney urban area that signals from the radio-collars could only be picked up at very close range or on the city outskirts.

Local movements of radio-collared flying foxes are shown in Table 2. In 1995 several radio-collared bats which had not roosted within the colony left the valley and were found in nearby backyards or neighbouring suburbs. Bats that had roosted within the colony site and had departed with the rest of the colony at dusk, were found in 1996 and
1997 in the Royal Botanic Gardens, next to the Sydney Opera House (Table 2). On 26 March 1997 a male bat was shot while feeding in a cumquat orchard at Glenorie, about 28 km from the Gordon site. During a tracking flight in 1997 a signal was detected in Bankstown from a transmitter that had been attached to a bat at the Cabramatta colony, about 9 km away.

**Table 2.**

<table>
<thead>
<tr>
<th>Date</th>
<th>Sex</th>
<th>Location</th>
<th>Distance and direction from release cage</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 Mar. 95</td>
<td>M</td>
<td>Maytone Ave</td>
<td>0.8 km SE</td>
<td>remained for one week</td>
</tr>
<tr>
<td>24 Mar. 95</td>
<td>M</td>
<td>Warnando Ave</td>
<td>0.4 km NE</td>
<td></td>
</tr>
<tr>
<td>7 Apr. 95</td>
<td>F</td>
<td>Roseville</td>
<td>5.1 km S</td>
<td>electrocuted on power line</td>
</tr>
<tr>
<td>20 Apr. 95</td>
<td>M</td>
<td>Hornsby</td>
<td>11 km NW</td>
<td>also in Hornsby 27 Apr.</td>
</tr>
<tr>
<td>27 Apr. 95</td>
<td>M</td>
<td>Hornsby</td>
<td>11 km NW</td>
<td>many stamens on fur</td>
</tr>
<tr>
<td>28 Mar. 95</td>
<td>F</td>
<td>Botanic Gardens</td>
<td>13 km S</td>
<td>feeding</td>
</tr>
<tr>
<td>1 Apr. 96</td>
<td>F</td>
<td>St. Ives</td>
<td>3.1 km N</td>
<td></td>
</tr>
<tr>
<td>26 Mar. 97</td>
<td>M</td>
<td>Glenorie</td>
<td>28 km NW</td>
<td>feeding on cumquats</td>
</tr>
<tr>
<td>28 Mar. 97</td>
<td>F</td>
<td>Crows Nest</td>
<td>9.6 km SE</td>
<td>electrocuted (overhead wires), banded but not radio-collared</td>
</tr>
<tr>
<td>8 Apr. 97</td>
<td>F</td>
<td>Botanic Gardens</td>
<td>13 km S</td>
<td>collared at Cabramatta colony</td>
</tr>
<tr>
<td>13 Apr. 97</td>
<td>F</td>
<td>Botanic Gardens</td>
<td>13 km S</td>
<td>feeding</td>
</tr>
<tr>
<td>18 Apr. 97</td>
<td>F</td>
<td>Bankstown</td>
<td>9 km NE of Cabramatta</td>
<td>collared at Cabramatta colony</td>
</tr>
<tr>
<td>24 Nov. 97</td>
<td>F</td>
<td>Ryde</td>
<td>7.8 km SW</td>
<td>electrocuted (overhead wires), banded but not radio-collared</td>
</tr>
</tbody>
</table>

Individuals or small groups of grey-headed flying-foxes are frequently seen to roost for one to several days at various sites throughout metropolitan Sydney during summer, especially in large fig trees. During this study radio-collared bats were found to be absent from the Gordon colony for periods of one to 11 days before returning to it.

Interchange between the Cabramatta and Gordon colony sites was shown by the appearance of two female bats radio-collared at Cabramatta (weighing 375 and 490 g) at Gordon (9 April and 6–19 April respectively).

Bats detected more than 50 km from the Gordon colony site are listed in Table 3.

In 1996 signals from radio-collars that had been put on hand-reared bats were located north and south of Sydney. A signal from a radio-collar that had been put on a wild bat which was released at Gordon on 24 April 96 was found on 30 April at the same site near Raymond Terrace where signals were detected from two radio-collars that had been put on hand-reared animals (Table 3).

In 1997 several radio-collar signals were detected south of Sydney (Table 3), but flights to the north of Sydney on 18 April and 29 May 1997 failed to detect any signals. However a radio-collar from a female was found on the ground on 28 May 1997 at Sea Acres Reserve in Port Macquarie (310 km north of Sydney, Table 3), a known *P. poliocephalus* colony site.
Exit counts

The total number of bats counted exiting the colony at sunset in the years 1995–1997 are shown in Fig. 2. An increase in the number of bats exiting the colony shown in the period mid-Dec. to Feb. each year corresponds to the time at which young were first observed to fly independently from the site. Flightless juveniles remain at the colony site for about three months, usually November–January (Parry-Jones 1987).

The number of bats in the colony drop dramatically in June and July, although in most years a small group of bats remain over winter.

DISCUSSION

Integration

The degree of integration (Table 1) is taken from data shown in Figure 1. In evaluating Figure 1 it is important to note that the lines drawn as the colony boundary are based on signals from transmitters placed at the extreme edges when the colony was at its furthest expansion in each year during the study. Not only does the colony size and shape vary yearly as shown in Figure 1, but there is also some variation within each year. Points outside the boundaries in Fig. 1 can be taken with confidence as representing non-integrated roost sites, and the value “% integration” represents the minimum number of bats that did not integrate. Points within but close to the boundaries could represent sites that were not integrated.

Another feature of Figure 1 is that points outside the boundaries are concentrated in the vicinity of the release cage which was also the supplementary feeding station. This observation lead to the decreased period of supplementary feeding in 1997.
Each year is of course different, and we were unable to control variables such as weather, food supply, and colony size. Integration clearly increased from 1995 to 1996, and from 1996 to 1997. We conclude that this is likely to have been the result of altered release procedures, but we also acknowledge that it is impossible to rule out uncontrol- lable or even unknown environmental factors.

Local movements

In 1995 several radio-collared animals were recovered from backyards of houses at the edges of the colony (eg Maytone and Warandoor Avenues in Table 2). This did not occur in subsequent years and is most likely to be the result of failure of the juveniles to integrate into the wild colony in 1995.

Movement of individuals between the Gordon colony and the Royal Botanic Gardens Sydney have been demonstrated in this study (Table 2). The number of flying foxes in the Royal Botanic Gardens Sydney has increased from several hundred in 1991 to more than 4,000 in 1999. They are reported to be remaining for longer periods, and a “reasonably large number” was observed in the Royal Botanic Gardens Sydney throughout the winter of 1998 (Botanic Gardens Staff, pers. comm.). Due to the fact that the numbers present vary from day to day, it has been assumed that the Royal Botanic Gardens Sydney “colony” is simply an aggregation of bats from the Gordon Colony with continuing interchange. However the exact relationship remains uncertain and may be changing.

The Cabramatta colony site is different in that it is much further from Gordon than the Royal Botanic Gardens Sydney and contains far more bats than the latter; up to 30,000 (G.L. Newman, ANU, pers. comm.). The Cabramatta Creek site is continuously occupied from September through May (C.R. Tidemann and G.L. Newman, ANU, pers. comm). The numbers of bats recorded at this site and the persistence of the colony through the mating season indicate it is a separate colony from the one at Gordon, even though there is an interchange of individuals.
Other tracking results simply confirm that bats from the Gordon Colony forage throughout the Sydney metropolitan area, including fruit growing regions to the NW (Table 2). The small number of foraging locations fixed over the three years of the study is due to the immense area to be covered and the impossibility of sorting out the relatively weak radio-collar signals within a cacophony of radio interference in the urban area.

**Long distance movements**

If the dates of release (Table 1) and the dates when radio-collar signals were detected from the air (Table 3) are compared with counts of bats at the Gordon colony (Fig. 2), it is clear that the radio-collared bats did not leave the colony site at times of mass migration. In 1996 the radio-collared bats left during a period when colony numbers were increasing, not decreasing. Movements of bats from the Cabramatta colony into and out of the Gordon colony likewise do not correlate with mass movements to or from Gordon. These observations strongly suggest that the colony site at Gordon is in a constant state of flux, with individual bats coming and going continuously. The colony cannot be seen as a fixed population of individuals, moving in mass in response to conditions of food availability or requirements of reproduction. These factors no doubt determine the number of bats that are present at any one time in a colony site such as Gordon, but they do not lead to mass movements such as the migrations of many bird species. One animal (1.042, Table 2) was located at Nowra, 130 km south of Sydney, on 28 March but had returned to Gordon by 4 April. By 30 April he was in Nowra again. The constant movement of individuals or possibly small groups, rather than movement of a population as a unit, observed in this study, and also observed in a radiotracking study carried out in northern NSW (Eby 1991), provides a likely answer to the frequently raised question “How do flying-foxes know when and where an outbreak of blossom occurs?” If individual bats are always moving about within the core of the range, they will begin to congregate where food resources are plentiful. There is no need to postulate complex communication or super sensory capacities.

The opportunistic nature of movements and feeding congregations of *P. poliocephalus* is shown in 1996 by the fact that some bats flew north to an area around Raymond Terrace where *Melaleuca quinquinervia* was flowering while others went south to the Nowra region where *Eucalyptus longifolia* was flowering. In 1997 bats flew to several locations along the coast south of Sydney (Table 3) where *Corymbia gummifera* was flowering and where there was heavy but patchy flowering of *C. maculata*.

Unlike the irregular flowering cycles of food resources other than figs, the reproductive cycle of *P. poliocephalus* is regular and annual. The regularity of occupation of the Gordon site reflects this regularity of the reproductive cycle, with an early peak starting in September when the colony begins to function as a maternity site, and a later peak during the mating season in April-May (Fig. 2). Unfortunately the need to balance radio transmitter (battery) weight with signal strength, and transmitter life, limited the above study to a period of three months after release, and no data on bat movements could be related to reproductive behaviour. However this will be the subject of further radiotelemetry studies of flying-foxes.

**Release management**

Based on evidence from the exit counts (Fig. 2) that wild juvenile bats were flying independently from the colony at sunset from as early as mid-December, the release date was moved forward from 18 March to 21 February. By the criterion used in this study (the degree of integration of hand-reared grey-headed flying-foxes with the resident, wild colony), this earlier release of hand-reared animals combined with decreased post-release support was highly successful. As shown in Table 1, animals released on 21 February
integrated completely while most of those released 18 March remained outside the resident colony over a comparable time span. The animals released earlier weighed less (mean 384 g) than those released later (mean 483 g), which is in contrast to the widely accepted principle within wildlife care groups that the larger a bat is on release, the greater its chances of survival. In our interpretation of the above findings, body weight is not the important factor; behaviour and natural cycles have a much greater influence on survival. In this study we chose to release earlier than the traditional mid to late March period because observations of the colony over a number of years showed that resident juveniles begin to undertake independent foraging flights from the colony in January or early February; sometimes as early as December (Fig. 2). Before this time, the juveniles remain in the colony at night and are suckled by the mothers after the latter return from foraging flights for a period of about 3 months (Parry-Jones 1987). During this time they are scattered throughout the area occupied by the adult bats. However from late February and March juveniles have been observed in the Gordon colony (KBCS, unpublished observations) to begin to segregate into separate roosting trees at the outer edge of the colony. Although there is clearly a great deal of work that needs to be done in order to understand the social behaviour of *P. poliocephalus*, it seems likely that at the start of the mating season (from early March), there would be minimal tolerance of new juveniles at the colony site and even territorial exclusion due to mating behaviour.

Other factors that might contribute to the success of earlier release are reduced exposure to human contact, to a restricted environment and to an unnatural diet. The reduction in support feeding in 1997 might also have contributed to the rapid integration of the released animals into the wild colony. In 1996 radio-collared bats were still observed at the support feeding station (the release cage) at night for six weeks after release. Within two days of stopping support feeding (17 April 96) this behaviour had ceased.

In summary, we propose that release of hand-reared juvenile *P. poliocephalus* should be done as near as possible to the time when wild juveniles are starting to make independent foraging flights and that support feeding be reduced to less than 4 weeks after release.

ACKNOWLEDGEMENTS

We would like to thank Dr Chris Tidemann, Australian National University, without whose magnificent giant bat trap we would have been unable to radio-collar wild bats at Cabramatta Creek, and the volunteers from the Cabramatta Creek Flying-fox Committee. We thank Stefan Rose for help with statistical analysis and graphical representation. The aerial tracking would have been impossible without the expertise and assistance of Peggy Eby. The study would also have been impossible without the help of members of the KBCS who spent many hours trying to obtain bearings from erratic radio signals, especially Maree Treadwell, Sandy Richardson and Rhondda Retallack.

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Seasonal Ecology, Condition and Reproductive Patterns of the Smooth Toadfish *Tetractenos glaber* (Freminville) in the Hawkesbury Estuarine System, Australia

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Seasonal variation in population structure, diet, lipid condition and reproduction of the smooth toadfish, *Tetractenos glaber*, were monitored in Berowra Creek and Cowan Creek, two estuarine arms of the Hawkesbury River, New South Wales, Australia. *Tetractenos glaber* is site-specific, feeding on benthic mussels and crustaceans. Reproduction occurs in April–July (winter), preceded by a buildup of somatic lipids in both sexes in February–April (Autumn). The liver appears to be a major source of lipid mobilisation, with total lipids varying among individuals from 20 to 90% of liver dry weight, and from 6 to 30% for muscle tissue. Recruitment occurred in November, and populations were composed of individuals up to at least 13 years of age. Sex ratios fluctuated seasonally, with a higher proportion of females sampled in winter, and more males in summer. The site-specificity, high abundance and benthic foraging behaviour of *T. glaber* suggest that it is largely estuarine-resident, and make it a potential bioindicator of the effects of degraded water quality on estuarine biota.

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KEYWORDS: condition, deformities, diet, gonadosomatic index, lipid, sex-ratio, *Tetractenos glaber*, toadfish

INTRODUCTION

Estuaries provide organisms with many physiological challenges, including fluctuations of salinity, temperature, turbidity and dissolved oxygen, at a variety of temporal and spatial scales. Fishes are the major vertebrate taxon in estuaries and exhibit a wide range of life histories. Some are only seasonally resident, or pass briefly through as they migrate between fresh to marine waters (e.g., salmon, eels). Others spend most of their adult life in estuarine waters, taking advantage of high productivity and food levels, and many of these species are of commercial importance. Reduced water quality may affect community structure, populations and individual physiology of fishes. While lethal effects of point-sources of pollution on fishes have been demonstrated (e.g. Sakthivel and Gaikwad 1994), chronic, sublethal effects of degraded waterways may be of more widespread importance to estuarine communities. Species diversity of fish assemblages is often reduced in polluted waters, and population densities of some species may also be reduced (e.g., Lee et al. 1992). Lipid concentration is an important somatic measure of physiological condition in fishes, and may be influenced by seasonal changes in diet, reproduction or pollution level (Booth and Keast 1986; Fraser 1989; Suthers et al. 1992). A drop in the somatic condition (measured as lipid depletion) of individual fish in winter may interact with external stressors to cause increased mortality ("Winter Stress
Syndrome” (Lemly 1996). Fraser (1989) suggested that the quantity of storage lipids, such as triacylglycerides (TAG), are related to ambient pollution levels for clupeid larvae, while Wang and Stickle (1988) found that TAG quantity was inversely related to exposure concentration to crude oil for juvenile blue crabs (*Callinectes sapidus*).

The present study investigates seasonal changes in the ecology and physiology of a common fish, the smooth toadfish *Tetractenos glaber*, in Berowra Creek and Cowan Creek estuaries, on the northern outskirts of Sydney, Australia. The overall goals of the study were to determine seasonal patterns in the life history of a common estuarine inhabitant, and to assess its use as a bioindicator of degraded estuarine health. Specifically, we asked

- is the species resident at sites within the Creeks?
- do population structure and sex ratio change seasonally, and when does recruitment occur?
- what are the main dietary items, and do quantity and quality of diet change seasonally?
- are there links between seasonal reproductive cycles and somatic condition?
- would *T. glaber* be a useful biomonitor of estuarine health?

**MATERIALS AND METHODS**

**Study species**

*Tetractenos glaber* (smooth toadfish) is a small tetraodontid fish inhabiting estuaries and coastal bays on the south-east coast of Australia (Kuiter 1994). It is found in aggregations in mud-flat shallows in estuaries, and may enter freshwater, but is not fished commercially due to the toxin it carries on its skin and in its internal organs. Few studies have focussed on tetraodontid fish ecology, despite their major contribution to fish biomass in estuaries and other habitats (e.g., Thresher 1984). Toadfishes are known to forage on a range of estuarine benthic organisms, including gastropods and oysters, and may significantly affect inter- and subtidal assemblages through predation (Connell and Anderson 1999).

**Study sites**

Fish were sampled in two major estuarine arms of the Hawkesbury River (33°30'S, 151°10'E), Cowan Creek and Berowra Creek, from October 1995 to March 1997, with sampling carried out at six different sites (4 in Berowra Creek, 2 in Cowan Creek, see Fig. 1) every 1–2 months. The Hawkesbury River extends over 200 km and flanks the Sydney Basin to the north and west. It supports significant recreational and commercial fisheries, particularly prawns, and is used for mariculture of oysters along the foreshores (Mercer 1984).

Berowra Creek is a sheltered waterway with a limited tidal flow, and urban development which have generated considerable sediment movement. Its tributaries are sites for sewage treatment plants (Fig. 1). Urban and farm runoff cause significant pollution and may be major factors affecting the quality of the water and sediment (unpublished data). Cowan Creek, part of the Ku-ring-gai Chase National Park, is located on the southern side of Broken Bay, about 5 km east of Berowra Creek (Fig. 1). The major habitats found within this creek include mangroves and sandflats with sparse seagrass areas. While similar in morphology, Cowan Creek is generally cleaner and more saline than Berowra Creek, due to its closer proximity to the ocean, reduced urban and agricultural.
runoff, and lack of sewage treatment plant effluent (Hornsby Council, unpub. report). However, it receives considerable recreational boat traffic. Natural oysters are prolific along the rocky shores, compared to Berowra Creek, where rocky foreshores that once supported oysters, are now covered with green algae. Both creeks have sediment “hotspots” for contaminants such as DDD, and other derivatives of DDT along with high concentrations of nitrogen and phosphate nutrients (Birch et al. 1998).

**Field sampling**

Fish were taken using a 15.5 x 1.75 m beach-seine net with a mesh of 16 mm stretch. The method involved manually hauling the net across the bottom, covering a depth of up to 1.5 m and a width of about 8–10 m, encompassing an area of about 10–15 m². Sampling at all sites was carried out for 2 hours either side of the afternoon low tide (1400h to 1600h in winter, 1500h to 1700h in summer). From each haul, a random sam-
ple of up to ten *T. glaber* were kept on ice for further processing, and the remainder were measured (total length) tagged (dorsal fin clip) and returned to the water. Other species of fish captured were measured, identified and returned to the water. Water quality measurements were taken at each site using a Yeokel Water Quality Meter (Model 611, Yeokal Instruments Ltd.), measuring dissolved oxygen (mg.l\(^{-1}\), % sat.), salinity (ppt), turbidity (ntu), pH and temperature (°C). Continuous data on these parameters were obtained using similar apparatus for both creeks from Hornsby Council data for 1995–1997 (R. McPherson, Hornsby Council, pers. comm.).

**External and internal morphology**

Samples were frozen at -4°C until processed. When fish were thawed, standard length (SL, mm), total length (TL, mm) and wet weight (WW, g) were measured. The fish were dissected ventrally to expose the internal organs. The otoliths were removed from each fish and stored for aging analysis. The alimentary canal was removed and the contents analysed under the binocular microscope (see below). The gonads were removed and examined to determine the sex of individuals, with ovaries orange in colour with eggs visible, and testes creamy-pink. Wet weights (WW, grams) and dry weights (DW, grams) were obtained, the latter by drying samples at 60°C until a constant weight was obtained.

**Dietary analysis**

*Tetractenos glaber* had no obvious stomach, so the foregut contents were removed from the anterior 1/3 of the alimentary canal, and were assumed to represent recent food intake. Contents were blotted and weighed (WW, mg), then items sorted into major categories (algae, bivalves, crustaceans, fishes, sediment and other), and percentage volume of the total contents for each category determined using the points method (Hyslop 1980). Contents were spread evenly on a grid of 100 points, and prey types counted on each point. Items were identified to lower taxonomic levels where possible.

**Table 1.**

Variation in water quality parameters in Berowra Creek and Cowan Creek, February 1996 to March 1997 [mean (se), n=16 sampling times for Berowra, 7 for Cowan]. Ranges refer to data obtained over the study period (McPherson, pers. comm.) using similar apparatus on a continuous logging basis at a site in each creek from 1995–1997.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Berowra Creek</th>
<th>Cowan Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp (°C)</td>
<td>Mean (se):</td>
<td>21.1 (0.5)</td>
</tr>
<tr>
<td></td>
<td>Range:</td>
<td>14.8–28.0</td>
</tr>
<tr>
<td>Salinity (%)</td>
<td>Mean (se):</td>
<td>17.7 (1.3)</td>
</tr>
<tr>
<td></td>
<td>Range:</td>
<td>16.1–19.5</td>
</tr>
<tr>
<td>pH</td>
<td>Mean (se):</td>
<td>7.7 (0.05)</td>
</tr>
<tr>
<td></td>
<td>Range:</td>
<td>7.6–8.0</td>
</tr>
<tr>
<td>Dissolved O(_2) (mg/l)</td>
<td>Mean (se):</td>
<td>7.7 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Range:</td>
<td>7.4–8.0</td>
</tr>
<tr>
<td>Dissolved O(_2) (% sat)</td>
<td>Mean (se):</td>
<td>94.3 (2.2)</td>
</tr>
<tr>
<td>Turbidity (ntu)</td>
<td>Mean (se):</td>
<td>4.6 (1.1)</td>
</tr>
<tr>
<td></td>
<td>Range:</td>
<td>3.3–6.9</td>
</tr>
</tbody>
</table>

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Lipid analysis

Portions of two tissues (muscle and liver), were removed for lipid analysis. The liver of *T. glaber* is extremely large compared to its body size, while muscle tissue also represents a large proportion of the soft tissue mass of *T. glaber*. We extracted lipids from the caudal peduncle muscle mass. The samples were freeze-dried, homogenised and DW was obtained. Lipids were then isolated using chloroform-methanol extraction (Bligh and Dyer 1959; Mann and Gallagher 1985) and weighed.

Synthesis of data

Changes in population structure were monitored by following length/frequency distributions through successive samples. Sex ratios were tested against 50:50 using Chi-Square analysis. Reproductive cycles were estimated by plotting gonadosomatic index (GSI) versus time for males and females separately. Because GSI may be related to body weight, and may be underestimated when stomachs are full (De Vlaming et al. 1982), stomach contents weights were removed from body weights, and gonad weight and GSI were regressed against body weight. Lipid weights and liver weights were treated similarly. Relationships between age and body length, were evaluated using linear regression analyses (Zar 1996).

RESULTS

Water quality

Salinity was higher in Cowan Creek, while Berowra Creek was more turbid and slightly more acidic on average. Dissolved oxygen levels were high at both locations (Table 1). Water quality varied seasonally and between estuaries, with temperature ranging from 15°C to 28°C in Berowra Creek, and from 17°C to 26.5°C in Cowan Creek during sampling times (Table 1).

Population structure

During this study, 3552 fish comprising 45 species were caught. *Tetractenos glaber* was represented at all sites and times, and comprised 43% of the total fish catch (n=1527 fish). However, catches of *T. glaber* at each of the sites varied temporally, with very low numbers caught at some sites on some occasions, so data were pooled for Berowra Creek sites and for Cowan Creek sites. Although differences among sites within locations were therefore not assessed, the use of multiple sites in each Creek gave increased spatial generality to results within estuaries. Few *T. glaber* were caught during the study from Cowan Creek, partly due to the difficulty of accessing habitat using seine nets, but perhaps as a result of higher salinity there. Video observations on seine net operation in both creeks confirmed that net avoidance was rare for this species (unpublished data).

Fish ranged from 32 to 160 mm TL, with new recruits (<40 mm TL) appearing in November 1995 at Berowra Creek sites (Fig. 2). This cohort could be traced until March 1996, when it merged with the size classes above 80 mm TL. However, the November 1996 pulse was much smaller. There was a linear relationship between age (as determined from otoliths) and body length (r²= 0.89, n=8, p<0.05; Central Aging Service, pers. comm.), with the largest fish (160 mm TL) being 13 years of age, and the smallest (32 mm TL) being under one year old. Apart from recruitment pulses, the size-distribution of fish in Berowra Creek was similar throughout the study. Too few fish were caught in Cowan Creek, but ranges were similar to Berowra Creek samples.
Movement of tagged fish

Tagging of fishes in Berowra Creek indicated a 10–11% recapture overall of tagged fish (Table 2). This rate of recapture was highly variable among dates, suggesting mortality or some degree of emigration from sites, although no tagged fish were recovered at adjacent sites during the study. In addition, snorkeling surveys conducted during the study suggested that this species rarely inhabited deeper adjacent waters.

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TABLE 2.

Tagging and recaptures of *T. glaber* in Berowra Creek estuary. "Total % recap" refers to (a) the percentage of either fish tagged on the previous tagging date ("Last tag date"), the sum of the previous 2 dates ("Last 2 tags") or the sum of the previous 3 sampling dates ("Last 3 tags"), that were recaptured.

<table>
<thead>
<tr>
<th>Date</th>
<th># caught</th>
<th># tag/release</th>
<th># recap</th>
<th>Total % recap</th>
<th>Last tag date</th>
<th>Last 2 tags</th>
<th>Last 3 tags</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 April 96</td>
<td>42</td>
<td>34</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1 May 96</td>
<td>70</td>
<td>51</td>
<td>1</td>
<td>2.9</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>30 May 96</td>
<td>15</td>
<td>13</td>
<td>5</td>
<td>9.8</td>
<td>5.8</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>12 Sep 96</td>
<td>21</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>12 Nov 96</td>
<td>31</td>
<td>19</td>
<td>5</td>
<td>23.8</td>
<td>13.9</td>
<td>5.7</td>
<td></td>
</tr>
<tr>
<td>21 Jan 97</td>
<td>37</td>
<td>32</td>
<td>7</td>
<td>36.8</td>
<td>17.5</td>
<td>12.7</td>
<td></td>
</tr>
<tr>
<td>19 Mar 97</td>
<td>19</td>
<td>9</td>
<td>1</td>
<td>3.1</td>
<td>2</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>233</td>
<td>181</td>
<td>19</td>
<td>100</td>
<td>80</td>
<td>40</td>
<td>20</td>
</tr>
</tbody>
</table>

Figure 3. Sex-ratios of *T. glaber* from Berowra Creek estuary between October 1995 and March 1997. Asterisks indicate significant deviations from unity (Chi-squared tests, p<.05, 1:1 male:female, shown by solid horizontal line). Sample sizes indicated.
Figure 4. Seasonal variation in dietary composition of *T. glaber* in Berowra Creek estuary. [Dietary categories: Mollusca: bivalves Salatellina alba, Crassostrea sp., Tellina delloidalis; Crustacea: Ghost crabs, red rock crabs; Fishes: Gobiidae] (mean ± se, n).

**Sex differences**

Sex ratios in samples fluctuated seasonally, and were significantly skewed towards females on two occasions (both in winter), and males on one occasion, in summer (Fig. 3, \(\chi^2 = 10.3, 3.95, 13.71, n = 14, 13, 42, \) respectively, \(p<0.05\)). Females reached a slightly larger maximum size (160 mm TL, 84 g WW) than males (150 mm TL, 76 g WW), and gonad development occurred at 70–80 mm TL for both sexes.

**Diet**

Benthic organisms predominated in foregut contents, with bivalve remains (*Salatellina alba, Crassostrea sp., Tellina delloidalis*) the major food items across seasons in Berowra Creek (Fig. 4). Although only 18 fish were examined in Cowan Creek, they had a higher proportion overall of crustaceans in their diet than those from Berowra Creek (Chi-Squared test, \(\chi^2 = 12.55, p<0.05\)), particularly the soldier crab (*Mictyris longicarpus*) which was noted to be abundant in Cowan Creek, but rare in Berowra Creek. Stomach contents WWs were similar for males, females and juveniles across seasons, with means ranging from 1 to 5% of body weight. Stomach contents WWs were slightly higher in winter for males and females (Fig. 5).

**Reproduction**

For both males and females, gonad weight was related to DW (Males: \(r^2 = 0.13, p<0.001, n = 155\), Females: \(r^2 = 0.45, p<.001, n = 153\)), and both regressions passed
Figure 5. Seasonal variation in foregut contents weight (as a % of body weight) for female, male and immature *T. glaber* in Berowra Creek (mean ± se, n). No juveniles were caught in July. Vertical solid lines delineate winter period.
Figure 6. Seasonal variation in gonadosomatic index (gonad wet weight/total body wet weight) for female (solid circles, solid line) and male (open circles, dashed line) *T. glaber* (mean ± se, n).

through the origin (Males: t = -0.433, Females t=-1.44, both p>.05). Since GSI for both males and females was not related to DW (linear regression, p<0.05 for both sexes, see De Vlaming et al. 1982), GSI was plotted for each month for both males and females (Fig. 6). GSI was low for both males and females from October to February (Fig. 6). GSI increased to a maximum of 0.15 in females and 0.1 in males, with maxima in April-September. The large variation in GSI among individuals suggests that gamete production is not synchronous across the population.

**Somatic condition**

Lipid concentration of the liver of fish in Berowra Creek was higher than that of the muscle tissue at all times at both locations, peaking at a mean of 70% DW in February 1996 (Fig. 7a). This is the time that gonads increase in size (Fig. 6). Muscle tis-
Figure 7. Seasonal variation in (A) lipid content of liver as a % of dry weight (Berowra Creek: solid circles, unbroken lines; Cowan Creek: open circles) and muscle (Berowra Creek: solid squares, unbroken lines; Cowan Creek: open squares) of T. glaber. (B) Total weight of lipid in liver tissue (Berowra Creek: solid circles, unbroken lines; Cowan Creek: open circles), and (C) Weight of liver as a proportion of body weight (Berowra Creek: solid circles, unbroken lines; Cowan Creek: open circles). (mean ± se, n indicated, n for both sites indicated in top panel).
sue lipid, while lower overall in concentration, peaked at a mean of 25% DW in October 1995 and 18% in July 1996. Seasonal patterns of lipid content for liver did not correspond to those for muscle tissue. The percentage of DW of liver tissue also varied seasonally (Fig. 7b), accounting for significantly higher lipid storage in the liver in December-March than at other times (Fig. 7c, 7% DW vs. 2.4%, t-test, arc sine Vx transformed, p<0.05). While sample sizes were low, similar patterns of lipid deposition were seen for fish in Cowan Creek (Fig 7a–c).

**DISCUSSION**

This study determined that *T. glaber* is a site-specific benthic-feeding fish, with a primarily carnivorous diet consisting of benthic organisms. Reproduction occurred in winter, preceded by a buildup of storage lipids, especially in liver tissue.

**Diet and population structure**

In Berowra Creek, the main dietary item was the mussel *Solatellina alba* which is common in sediments (Edwards 1995), and in Cowan Creek the dominant food source was the soldier crab *Mictyris longicarpus*. The importance of mussels in the diet may have been overestimated, as it is likely that bivalve shells persist in the foregut. Higher stomach contents weights in winter may be partly due to slower rates of food evacuation at the lower winter temperatures (e.g., Booth and Keast 1986) rather than increased consumption rates. Tetraodontids have dentition that allows crushing of prey and they may therefore have access to the abundant benthic bivalves that are not available to other estuarine fishes. The high incidence of soldier crabs in diets of fish at Cowan Creek suggests that they may also be capable of capturing more active prey.

Size-distributions of fish from seasonal samples indicate that all age-classes are present throughout the year, although numbers of fish larger than 120 mm TL were low in July. Sex ratios in samples fluctuated during the study, suggesting sex-related movement among the study sites and adjacent deeper waters. Since sampling was conducted at standard times and tides, movement patterns are unlikely to be diurnal.

The smallest fish caught in this study were 30 mm TL, and although otoliths were unsuitable for daily ring counts, fish of this size were likely to be at most several months post-settlement, since nearshore plankton samples yielded individuals of 25 mm TL (unpublished data). Growth as estimated through otolith aging of known-length individuals was linear, but since only 8 fish were analysed, von-Bertalanffy growth cannot be rejected. The habitat and habits of smaller post-settlement fishes (<30 mm TL) is unknown, but samples taken from intertidal rockpools in nearby coastal areas yielded fish from 38–70 mm TL (Silberschneider and Booth, in press). Due to the fact that we recaptured a total of 11% of tagged fish over the sampling period, and recaptured fish were from all size classes, it is likely that at least some individuals do not migrate but are site-specific over monthly scales. In addition, snorkel surveys suggested that this species is confined to shallower waters as sampled by seine net (pers. obs.), despite fluctuation in sex ratios over the study. Although fish were not uniquely tagged, it is unlikely that clipped fish migrated between sites, since clipped fish were never found in areas where none had previously been clipped. Given the presence of all sizes of *T. glaber* in samples (apart from recruits below 30 mm TL), and the occurrence of reproduction at these sites, it is likely that this species completes most of its life cycle in estuaries.

**Reproductive and somatic condition**

The reproductive season appears to be protracted, with high mean GSI from April to September (winter), however individuals may be reproductively-active for a much

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shorter period. In contrast, most other temperate tetractenid fishes are reported to spawn in the warmer part of the year (e.g., Habib 1979; Thresher 1984). At the population level, mean male and female reproduction is synchronised, however high variation in GSI within sexes for fish captured at the same time suggests that individual reproductive cycles differ. Although sample size was low, GSI patterns were similar in Cowan Creek. Since gonad development began at similar sizes for both sexes, it is not consistent with protogamous sexual development, and this species is likely to be a gonochore. Histological examination of reproductive tissues and measurement of changes in egg diameter would be useful to further resolve patterns of reproduction in this species.

The build up of gonadal tissue is preceded by lipid increase in the liver. Both liver size and lipid concentration increased prior to GSI increase. Lipid in muscle also increased prior to GSI increase. This suggests that accumulated lipid in the liver is a major source of lipid energy for gonad development. Lipid in livers was comprised largely of triacylglycerides (unpub. data), which are known to be primary storage lipids (e.g. Fraser 1989; Suthers et al. 1992). Also, livers are known sites for concentration of lipid-soluble contaminants, such as polynuclear hydrocarbons (PAH’s), organometallics and chlorinated biphenyls (e.g., Harshbarger and Clark 1990). Preliminary analyses of lipids in livers on T. glaber in this study, using Gas-Chromatography Mass Spectrometry have revealed the presence of PAH’s and phenols for fish in both Creeks (unpublished data), and liver assays appear to be potentially useful biomonitor of sediment contaminant loads.

Lipids in livers were depleted during winter in this study in both Creeks, and it may be that at this time fish are most vulnerable to pollution stress. However, winter stress syndrome, as reported by Lemly (1996), occurs at water temperatures below 10°C, while temperatures in this study did not drop below 14°C. Livers fluctuated dramatically in size throughout the year, and liver WW, corrected for WW, may provide a reasonable index of the level of storage lipids in this species.

*Tetractenos glaber* as a biomonitor

This study has identified that *T. glaber* is potentially a useful organism for monitoring the impacts of pollution on estuarine biota. A good biomonitor species should: 

a) be site-specific. Tagging studies confirmed that a significant proportion of the *T. glaber* population remains resident for at least several months. Also, most of the size range of the species was represented at the study sites.

b) forage on prey that are resident. Prey items were largely sedentary benthic organisms, which would be subject to local patterns of water quality and sediment pollution load. Therefore, contaminants may be biomagnified through benthic diets to fish tissue (Frank, 1986). Toadfish livers are useful tissues for monitoring such contaminants.

c) be common throughout the year, and at all sites of interest. *Tetractenos glaber* was common at all times in Berowra Creek, although abundances fluctuated in Cowan Creek.

*Tetractenos glaber* is also very common around the southern Australian coastline and estuarine systems, where expanding urbanisation is rapidly occurring. However, this study suggests that *T. glaber* was not as common in Cowan Creek, which was more saline than Berowra Creek, suggesting that care must be taken in choice of sampling locations. By monitoring a suite of factors such as population structure, condition, reproduction and pollutant levels of fish, *T. glaber* may prove to be an important bioindicator of the effects of changes in water and sediment quality on marine life.

ACKNOWLEDGMENTS

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REFERENCES


Initial Report on Discovery of Ordovician Scolecodonts from Eastern Australia.

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Department of Environmental Sciences, University of Technology Sydney, P.O. Box 123, Broadway 2007, Australia


Scolecodonts recovered from conodont residues of a Late Ordovician (Eastonian) limestone block contained in the Wisemans Arm Formation include a range of elements and represent the first documented Ordovician scolecodont fauna from Australia.

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KEYWORDS: conodont, scolecodont.

INTRODUCTION

A clast of limestone from volcanioclastic conglomerate in the Wisemans Arm Formation (Leitch and Cawood 1980) at Roscommon, east of Manilla (Fig. 1) has yielded a small fauna of scolecodonts as a by-product of conodont extraction. The conodont fauna is Late Eastonian (Ea3) (Furey-Greig 1999), and correlates with faunas documented from Ea3 horizons in the Lachlan Fold Belt (eg. Trotter and Webby 1995; Zhen et al. 1999). Little has been published on Palaeozoic polychaete microfossils from Australia. The present report is provides documentation of a scolecodont fauna from a residue of known age.

The olistostromal Wisemans Arm Formation (Leitch and Cawood 1980) is a fault-bounded unit within the structurally complex Tablelands Complex of the New England Fold Belt (Fig. 1), that crops out between Nundle and Warialda. The Wisemans Arm Formation is characterised by volcanioclastic sandstone and siltstone, rare radiolarian mudstone, and conglomerates and olistostromes containing masses of mafic and intermediate volcanics, limestones of Late Ordovician and Early Silurian ages (Furey-Greig 1999; in press) and chert.

Standard acetic acid dissolution of limestones at the Macquarie University Centre for Ecosтратigraphy and Palaeobiogeography, and separation of residues using the method of Anderson et al. (1995), yielded scolecodonts and conodonts. Illustration was entirely digital using the method described by Furey-Greig (1999). Some vacuum-induced damage was sustained by the specimens, hence no attempt was made to re-position the fragile microfossils in case of further damage. Terminology used herein is based on that of Kielen-Jaworowska (1966).

FOSSIL POLYCHAETE TAXONOMY

Historically, the common occurrence of scolecodonts (the acid-resistant jaw elements of polychaete annelids) as disarticulated, dispersed elements in Palaeozoic acid-insoluble residues led to development of a complex form taxonomy along similar lines
to the early study of conodonts. This led to problems in reconciling that system with documented natural assemblages (eg., Jansonius and Craig 1974). The complication of early, premature attempts at reconciling the two systems, and subsequent advances in this area, were discussed in detail by Eriksson and Bergman (1998). Several multi-element scolecodont studies have provided a basis for improving the taxonomic situation (eg, Kielen-Jaworowska 1966; Jansonius and Craig 1974; Bergman 1989). It has been

Figure 1. A. Major structural elements of southern New England Fold Belt; B. Location of study area; C. Geological map of Roscommon olistostrome. Grid co-ordinates in Australian Metric Grid System.

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Figure 2. Scale bars items 2–8 = 100 microns, item 1 = 1 mm. 1. Right MI element, lateral view. 2. ‘broken MII element, lateral view. 3. M4 elements, lateral views. 4. ‘Basal plate, lateral view. 5. unassigned element, dorsal view. 7. M2 element, lateral and dorsal views. 8. broken element.

shown in these and other reports that only a small number of scolecodont elements, the MI and MII, are genus or species-diagnostic (see Szaniawski 1996 for a detailed review).

The stratigraphic value of Palaeozoic scolecodonts is hampered by their strong relationship with facies (Szaniawski 1996) and by the lack of stratigraphic information in many publications (Eriksson and Bergman 1998). One exception is Hints’ (1998) report on scolecodonts from the Caradoc of Estonia and the St. Petersberg region. It is hoped that this preliminary report on Late Ordovician scolecodonts from Australia, well constrained as to age, will lead to further documentation of such faunas, for scolecodonts are known to occur in other eastern Australian Late Ordovician conodont residues (Percival 1999; Zhen, pers. comm.).
DISCUSSION

The fauna from Roscommon numbers forty elements and includes only one broken dextral Mandible 1, generally accepted as being the genus-diagnostic element. This is insufficient for precise taxonomic assignment and the material is here left in open nomenclature. Nevertheless, some comparison with documented Ordovician material is appropriate. The M1 element (Fig. 2, item 1) features a pronounced falx and edentulate falcal arch and is comparable to jaws of Atraktoprionidae illustrated by Kielan-Jaworowska (1966, plates XXXI–XXXIV), and by Hints (1998, Fig. 16). The other elements may belong to one or more species and are illustrated for future comparison.

ACKNOWLEDGEMENTS

I thank my supervisor, Evan Leitch, for much support and material assistance during this research. Ian Percival and Theresa Winchester-Seeto are thanked for reviewing the manuscript. Theresa Winchester-Seeto was generous with some rare literature on fossil polychaetes and discussion. Ruth Mawson and John Talent are thanked for underwriting the acid processing of limestones at Macquarie University. My research benefitted from financial support from ARC Large Grant A39601646 (E.C. Leitch) and from a Doctoral Research Scholarship provided by the Faculty of Science, University of Technology Sydney. Noni Callan drafted the figure. Ambrose and Patricia Blanche, owners of Roscommon, are thanked for permitting access to their property.

REFERENCES


Fishes of the Nymboida, Mann and Orara Rivers of the Clarence River Drainage, New South Wales, Australia

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A six-month survey of fishes in the Nymboida, Mann and Orara Rivers in northeastern NSW was conducted from March–August, 1991. Forty collections at 12 sites yielded over 7000 specimens, representing 20 species and 15 families. Marjorie’s hardyhead (*Craterocephalus marjoriae*) accounted for 41% of the total specimens. Other numerical dominants included Douboulay’s rainbowfish (*Melanotaenia duboulayi*) 16%, firetailed gudgeon (*Hypseleotris galii*) 11%, western carp gudgeon (*H. klunzingeri*) 8%, Australian smelt (*Retropinna semoni*) and eastern mosquitofish (*Gambusia holbrooki*) with 6% each. Although not numerous in the sampling, the endangered eastern freshwater cod (*Maccullochella ikei*) was recorded from the Nymboida River and the Australian bass (*Macquaria novemaculeata*) from the three rivers sampled. Sampling also revealed the exotic species rainbow trout (*Oncorhynchus mykiss*) in the upper reaches of the Nymboida River and the goldfish (*Carassius auratus*) in the three rivers. The pattern of distribution includes longitudinal zonation in the upper reaches, where only five species were recorded; three of which were restricted to this region. This was followed by a rapid increase in species (11) beginning with the low gradient, less turbulent, middle section and then an addition of species (4) from the lower reaches of the system to the confluence with the Clarence River. Values for Jacard’s (J) and percent similarity (PSI) indices indicate the headwater fauna is highly dissimilar from the middle and lower reaches, while the three stations in the downstream section have similar faunas. The distribution pattern and results of the faunal similarity indices are corroborated by the results of detrended correspondence analysis (DCA).

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KEYWORDS: Clarence River drainage, freshwater fishes, instream distribution of fishes, Mann River, Nymboida River, Orara River.

INTRODUCTION

Australia’s freshwater fish fauna has been characterized as depauperate when compared to the richness of other continental assemblages (Allen 1989). The most recent compilations include only between 180–196 species of fishes living in Australian freshwater habitats (Merrick and Schmida 1984; Allen 1989), and the number of species completely restricted to freshwater is probably 20–25% less than the number usually reported (Allen 1989). However, the inventory of Australian freshwater fishes is far from completed. In the past several years populations of nominal species, such as Murray cod (*Maccullochella peeli*) (Rowland 1993), Macquarie perch (*Macquaria australasica*) (Duffy 1986), golden perch (*Macquaria ambigua*) (Musyl and Keenan 1992), blue-eyes (*Pseudomugil signifer*) (Ivantsoff et al. 1991), rainbowfish (*Melanotaenia fluviatilis*)
Figure 1. Map of Clarence River Drainage in northeastern NSW. Stations labeled 1–12 in the Nymboida, Mann and Orara Rivers were sampled during 1991. Closed circles, stations 1–5, were sites that were sampled monthly, March-August, 1991. Closed rectangles, stations 6–11, were sites that were sampled only once during the study and the closed rectangle on the Orara River, station 12, was sampled three times.
(Crowley et al. 1986), and freshwater catfish (Tandanus tandanus) (Musyl and Keenan 1996) have been identified as morphologically or genetically distinct and deserving of taxonomic recognition. It is also reasonable to expect the number of taxa of Australian freshwater fishes to increase as the faunas of individual rivers within major drainage divisions are better documented (e.g. Midgley et al. 1991). Stream surveys, as well as assessing genetic and morphological variation for wide ranging species, may reveal even more cryptic forms than listed above (Musyl and Keenan 1992). The Northern Rivers region in northeastern New South Wales (South-east Coast of Australian drainage division) includes four major basins, Tweed, Richmond, Clarence, and Bellinger rivers, that flow eastward into the South Pacific Ocean. Thus far 35 species of indigenous freshwater fishes have been reported from this area (Lake 1978; McDowall 1980; Merrick and Schmida 1984; Allen 1989), which gives it a greater overall species richness than 7 of the 12 commonly recognized drainage divisions in Australia (Lake 1978; Allen 1989). There is very little published material on the fishes of any of the individual rivers in the Northern Rivers region. Apparently the lower reaches or estuarine portions of these separate drainages have been well surveyed (D. Pollard, pers. comm.), but the fish communities in the upper, freshwater portions have only been studied sporadically (e.g., Llewellyn 1983; Bishop unpub. data). The objectives of this paper are to: a) document the fish species and their pattern of distribution over a six month period (March-August, 1991) in the Nymboida and Mann Rivers; b) prepare a preliminary list of fishes of the Orara River, another Clarence River tributary, based on three collections during 1991 and literature records; and c) compare community similarity and diversity among sites along the Nymboida and Mann Rivers and with one site in the Orara River.

MATERIALS AND METHODS

Description of Study Area

The Clarence River system, in northeastern NSW, is one of Australia’s largest and most important coastal drainages with a catchment area of approximately 22,400 square kilometers (Bucher and Saenger 1989). The catchment is characterised by high average annual rainfall averaging around 1400 mm with a distinct seasonal peak during the summer months (December-April), and drier and cooler conditions during winter, resulting in highly variable river flows. Only about a quarter of the catchment has been cleared, mostly for agricultural use (Bucher and Saenger 1989).

The Nymboida and Mann Rivers constitute an important tributary of the Clarence. The Nymboida River originates on the Dorrigo Plateau near Hernani, NSW, and becomes a 3rd order stream within its first 5 km. The river flows in an easterly then northeasterly direction for approximately the next 100km. Major tributaries to the Nymboida in this stretch include Little Murray, Blinks and Little Nymboida Rivers. After the junction with the Little Nymboida, the Nymboida turns almost due north for 30 km and then northeastward along the remainder of its course. The Boyd River is the next major tributary before the Mann River joins the Nymboida. From its junction with the Mann on to its confluence with the Clarence River, the river is known as the Mann despite the fact that the Nymboida is the larger stream course. The Nymboida after its junction with the Mann is a 5th order river, has a drainage area of over 10,000 sq km, and flows over 200 km from its origin on the Dorrigo Plateau to the junction with the Clarence River (Fig. 1).

Collection Sites

Five stations (Fig. 1, 1–5), roughly coinciding with changes in stream order, were selected for monthly sampling of fishes in the Nymboida and Mann Rivers. Another six
sites (Fig. 1, 6–11) were sampled only once. One station on the Orara River (Fig. 1, 12) was sampled three times. All sites listed below were sampled between March-August, 1991, except the Nymboida River at the confluence of the Little Nymboida (Fig. 1, 9), which was sampled on 17 December 1991. A total of 40 collections was made during this survey. The collecting sites and localities were as follows:

NYMBOIDA AND MANN RIVERS

1. Nymboida River above the Dorrigo-Ebor road bridge and about 8 km east of the junction of the Dorrigo-Grafton road (Station 1).
2. Nymboida River at Riverview on the Dorrigo-Tyringham road, 7 km SW of Bostobrick (Station 2).
3. Nymboida River at the Nymboida Coaching Station (Station 3).
4. Nymboida River at its confluence with the Boyd River (Station 4).
5. Mann River near the bridge at Jackadgerry (Station 5).
7. Nymboida River on Moon Par road, 3 km northwest of the Dorrigo-Tyringham road.
8. Nymboida River at Platypus Flats
10. Mann River at New Zealand Falls
11. Clarence River 1 km above the mouth of Mann River

ORARA RIVER

12. Orara River at Coutt’s Crossing, 17 km south of Grafton (sampled three times during the survey period).

Collection Methods

Specimens were collected during the day and at night by using 12 mm mesh seines, 75 mm and 112 mm mesh gill nets, eel lines, and traps. All types of collecting gear were employed during each sampling effort. Fish collections with seines and nets at each site were normally made for a period of 1.5 hrs. Traps and eel lines were set at dusk and checked every 4–6 hrs. All fishes collected were preserved in 10% formalin, returned to the University of New England-Northern Rivers (now Southern Cross University) for identification and then transferred to 50% isopropyl alcohol for permanent storage. Keys in Allen (1989) and Merrick and Schmida (1984) were used to identify specimens to species. Nomenclature in this paper follows Allen (1989).

All material collected was deposited in the Australian National Museum, Southern Cross University at Lismore, the University of New Orleans and Cornell University.

Physical-chemical Variables

Eleven physical and 19 chemical variables were measured at each of the permanent stations each time fish were collected. The methods used are given in Hawkes (1991) and are largely based on those of the American Public Health Association (1981) and Cole (1983). Ranges and means for 14 of the variables at stations 1–5 are presented in Table 1.
Table 1.
Ranges and means for 14 envirnontmental variables recorded at stations 1–5 in the Nymboida and Mann Rivers; March–August 1991

<table>
<thead>
<tr>
<th>Variable</th>
<th>Station 1</th>
<th>Station 2</th>
<th>Station 3</th>
<th>Station 4</th>
<th>Station 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp. (C)</td>
<td>9.0–16.7</td>
<td>11.6</td>
<td>11.9</td>
<td>15.7</td>
<td>17.9</td>
</tr>
<tr>
<td>Cond. (μS/cm)</td>
<td>20.7–25.5</td>
<td>22.6</td>
<td>32.2</td>
<td>44.4</td>
<td>75.1</td>
</tr>
<tr>
<td>pH</td>
<td>6.3–7.5</td>
<td>6.8</td>
<td>7.0</td>
<td>6.6</td>
<td>7.5</td>
</tr>
<tr>
<td>DO (% Sat)</td>
<td>73.3–121.0</td>
<td>95.3</td>
<td>81.3</td>
<td>89.3</td>
<td>79.5</td>
</tr>
<tr>
<td>NO3 @pm</td>
<td>0.1–0.3</td>
<td>0.2</td>
<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>PO4(ppm)</td>
<td>0.0–1.0</td>
<td>0.2</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Chlor. a (@g/L)</td>
<td>0.0–20.5</td>
<td>9.3</td>
<td>13.3</td>
<td>10.1</td>
<td>2.1</td>
</tr>
<tr>
<td>Total Alk. (mg/L)</td>
<td>22.5–240.0</td>
<td>67.7</td>
<td>71.7</td>
<td>48.7</td>
<td>56.7</td>
</tr>
<tr>
<td>TDS (mg/L)</td>
<td>11.0–69.0</td>
<td>38.8</td>
<td>39.2</td>
<td>42.2</td>
<td>44.2</td>
</tr>
<tr>
<td>TSS (mg/L)</td>
<td>0.6–5.2</td>
<td>2.4</td>
<td>1.9</td>
<td>1.8</td>
<td>2.2</td>
</tr>
<tr>
<td>Current (m/sec)</td>
<td>0.1–0.2</td>
<td>0.2</td>
<td>0.2</td>
<td>0.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Flow (ML/day)</td>
<td>25.9–69.1</td>
<td>55.3</td>
<td>343.9</td>
<td>1394.5</td>
<td>280.6</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>0.3–0.5</td>
<td>0.4</td>
<td>1.0</td>
<td>1.6</td>
<td>0.7</td>
</tr>
<tr>
<td>Width (m)</td>
<td>8.6–12.2</td>
<td>10.3</td>
<td>17.2</td>
<td>25.3</td>
<td>76.9</td>
</tr>
</tbody>
</table>

Data analyses
Comparisons of fish assemblages based only on the 1991 survey data among stations along the Nymboida and Mann Rivers and between these stations and the one site on the Orara River were made qualitatively using Jaccard’s Index (JI) (Ludwig and Reynolds 1988), and quantitatively by a percent similarity index (PSI) (Wolda 1981). Values for JI and PSI range from 0 (if no species are common to the two assemblages) to 1.00 (if all the species are identical between the two assemblages). Both indices have been used for fish community analysis and in studies of fish ecology (Lyons 1989; Cashner et al. 1994). Estimates of diversity were made using Shannon’s Index (Ludwig and Reynolds 1988). Stations 1 and 2 and three other sites (6–8) were combined as a more inclusive headwaters region for comparison with downstream regions.

Principal components analysis (PCA) of species presence and 19 environmental variables was used to correlate changes in physico-chemical characters and fish assemblages at different stations along the Nymboida and Mann Rivers. Detrended correspondence analysis (DCA; Gauch 1982) was used to examine faunal similarity among stations based on abundance of species at each station. DCA is an indirect gradient analysis that simultaneously ordinates sites and species in multivariate space, with site placements reflecting the weighted average of species abundance at that site, and species placements representing the centroid of species distribution among all sites. The placement of sites along axes in multivariate space is biologically interpretable because DCA axes are scaled in standard deviations of species abundance curves (with 100 units representing one SD) such that sites separated by 100 units on an axis have, on average, a 50% similarity in composition. A difference of 400 units along an axis represents a complete faunal turnover on that axis (Gauch 1982). All DCAs were performed with PCORD Version 3.0 (McCune and Mefford 1997). For stations with multiple collections, all collections were pooled for this analysis.

RESULTS AND DISCUSSION

Prior to 1991, there had been scant published information on the fishes of the freshwater portions of the Clarence River, and the upper Clarence, Nymboida and Mann Rivers had not been intensively sampled. Even Llewellyn’s (1983) comprehensive survey of the New South Wales freshwater fishes included only five localities (two of which overlapped with our sites) and recorded just six species from the Nymboida and Mann Rivers. In the study reported herein, over 7,000 specimens were collected during the 1991 survey of the Nymboida and Mann Rivers, which included 20 species, representing 15 families (Table 2). The numerically dominant species was Marjorie’s hardyhead (Craterocephalus marjo-riae), which accounted for 41% of all the specimens taken. Other species with relatively high abundance were Duboulay’s rainbowfish (Melanotaenia duboulayi) 16%, firetailed gudgeon (Hypseleotris galii) 11%, western carp gudgeon (H. kluunzingeri) 8%, Australian smelt (Retropinna semoni) and eastern mosquitofish (Gambusia holbrooki) 6% each. The other 14 species were relatively rare (<1%-2%), and one species, the shortfinned eel (Anguilla australis), was represented by only a single specimen. Four additional species have been documented from other sources (Llewellyn 1981; Harris unpub. data; Bishop unpub. data); the introduced brown trout (Salmo trutta), ornate rainbowfish (Rhadinocentrus ornatus), striped gudgeon (Gobiomorphus australis) and Cox’s gudgeon (G. coxii), which brings the total to 24 species for Nymboida and Mann Rivers.

Thirteen species were represented from over 750 specimens taken during three collections at a single site in the Orara River (Table 2). Australian smelt (Retropinna semoni), empire gudgeon (Hypseleotris compressa), and eastern mosquitofish (Gambusia holbrooki) were the most abundant. Seven more species were added based on earlier collections (Llewellyn 1981; Harris unpub. data; Bishop unpub. data). These included the non-native goldfish (Carassius auratus), fork-tailed catfish (Arius graeffei), ornate rain-
**Table 2.**
List of fish species for the Nymboida, Mann and Orara rivers collected during March-August, 1991. Numbers are sample sizes for each species. Records for other species are based on field data sheets of John Harris (MH). Reports by Llewellyn 1983 (LL) and Bishop 1991 (KB). Mnemonics used in Figure 4 are given next to each species name.

<table>
<thead>
<tr>
<th>NYMOIBIDA AND MANN RIVERS</th>
<th>ORARA RIVER</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anguilla australis (AAUS)</strong></td>
<td>Anguilla reinhardtii</td>
</tr>
<tr>
<td><strong>Anguilla reinhardtii (AREI)</strong></td>
<td>Potamalosa richmondia</td>
</tr>
<tr>
<td>34</td>
<td>3</td>
</tr>
<tr>
<td><strong>Potamalosa richmondia (PRIC)</strong></td>
<td>Retropinna semoni</td>
</tr>
<tr>
<td>144</td>
<td>235</td>
</tr>
<tr>
<td><strong>Retropinna semoni (RSEM)</strong></td>
<td>Carassius auratus JH</td>
</tr>
<tr>
<td>399</td>
<td></td>
</tr>
<tr>
<td><strong>Galaxias olidus (GOLI)</strong></td>
<td>Arius graefei LL</td>
</tr>
<tr>
<td>149</td>
<td></td>
</tr>
<tr>
<td><strong>Oncorhynchus mykiss (OMYK)</strong></td>
<td>Tandanus tandanus</td>
</tr>
<tr>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td><strong>Salmo trutta LL,KB</strong></td>
<td>Gambusia holbrooki</td>
</tr>
<tr>
<td>109</td>
<td></td>
</tr>
<tr>
<td><strong>Carassius auratus (CAUR)</strong></td>
<td>Craterocephalus marjoriae</td>
</tr>
<tr>
<td>3</td>
<td>86</td>
</tr>
<tr>
<td><strong>Tandanus tandanus (TTAN)</strong></td>
<td>Melanotaenia duboulayi</td>
</tr>
<tr>
<td>191</td>
<td>60</td>
</tr>
<tr>
<td><strong>Gambusia holbrooki (GHOL)</strong></td>
<td>Rhadinocentris ornatus LL</td>
</tr>
<tr>
<td>536</td>
<td></td>
</tr>
<tr>
<td><strong>Craterocephalus marjoriae (CMAR)</strong></td>
<td>Pseudomugil signifer LL</td>
</tr>
<tr>
<td>2887</td>
<td></td>
</tr>
<tr>
<td><strong>Melanotaenia duboulayi (MDUB)</strong></td>
<td>Macquaria novemaculeata JH</td>
</tr>
<tr>
<td>1121</td>
<td></td>
</tr>
<tr>
<td><strong>Rhadinocentris ornatus LL,KB</strong></td>
<td>Magil cephalus JH</td>
</tr>
<tr>
<td><strong>Ambassius agassizi (AAGA)</strong></td>
<td>Myxus petardi JH</td>
</tr>
<tr>
<td>142</td>
<td></td>
</tr>
<tr>
<td><strong>Maccullochella ikei (MIKE)</strong></td>
<td>Notesthes robusta (NROB)</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td><strong>Macquaria novemaculeata (MNOV)</strong></td>
<td>Gobiomorphus australis (GAUS)</td>
</tr>
<tr>
<td>29</td>
<td>8</td>
</tr>
<tr>
<td><strong>Bidyanus bidyanus (BBID)</strong></td>
<td>Gobiomorphus coxii (GCOX)</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><strong>Myxus petardi (MPET)</strong></td>
<td>Hypseleotris compressa (HCOM)</td>
</tr>
<tr>
<td>7</td>
<td>234</td>
</tr>
<tr>
<td><strong>Gobiomorphus australis LL,KB</strong></td>
<td>Hypseleotris galii</td>
</tr>
<tr>
<td><strong>Gobiomorphus coxii LL, KB</strong></td>
<td>Hypseleotris kluenzeri</td>
</tr>
<tr>
<td><strong>Hypseleotris galii (HGAL)</strong></td>
<td>5</td>
</tr>
<tr>
<td>740</td>
<td></td>
</tr>
<tr>
<td><strong>Hypseleotris kluenzeri (HKLU)</strong></td>
<td>6</td>
</tr>
<tr>
<td>578</td>
<td></td>
</tr>
<tr>
<td><strong>Philypnodon grandiceps (PGRA)</strong></td>
<td>18</td>
</tr>
<tr>
<td><strong>Philypnodon sp. (PSP)</strong></td>
<td>60</td>
</tr>
</tbody>
</table>

**Table 3.**
Number of species (n) captured and Shannon diversity index (H) for each site in parentheses. Headwater sites (Stations 1, 2, 6–8) combined for comparison. Jaccard’s index of similarity followed by percent similarity index for fish assemblages at headwater sites and stations 3–4 in the Nymboida, station 5 in the Mann River and one locality on the Orara River, based on collections made in 1991.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Headwaters</td>
<td>5</td>
<td>0.943</td>
</tr>
<tr>
<td>Nymboida 3</td>
<td>12</td>
<td>2.302, 0.13, 0.07</td>
</tr>
<tr>
<td>Nymboida 4</td>
<td>13</td>
<td>2.186, 0.13, 0.04, 0.77, 0.58</td>
</tr>
<tr>
<td>Nymboida 5</td>
<td>13</td>
<td>2.820, 0.13, 0.06, 0.69, 0.57, 0.79, 0.66</td>
</tr>
<tr>
<td>Orara R.</td>
<td>13</td>
<td>2.279, 0.13, 0.06, 0.45, 0.41, 0.53, 0.23, 0.61, 0.32</td>
</tr>
</tbody>
</table>

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bowfish (*Rhadinocentris ornatus*), Pacific blue-eye (*Pseudomugil signifer*), Australian bass (*Macquaria novemaculeata*) and two mullets, the sea mullet (*Mugil cephalus*) and the freshwater mullet (*Myxus petardi*), raising the total documented for the Orara to 20 species. The relative species richness for the Orara River is surprising considering the limited effort and the single site sampled.

The uppermost sites in the Nymboida River, stations 1 and 2 and 6–8 (Fig. 1), yielded only 1 shortfinned eel, 6 longfinned eels (*Anguilla reinhardtii*), 149 marbled galaxias (*Galaxias olidus*), 11 specimens of rainbow trout and 10 eastern mosquitofish during the survey. Jacard’s index of similarity (JI) and percent similarity index (PSI) were used to provide an estimate of community relatedness between adjacent sites in the Nymboida and Mann Rivers. Fish collection data for the two sites labeled as headwaters for the Nymboida River (sites 1–2) were pooled. Data for each of the three downstream stations (3–5) were treated separately, but data at each station were aggregated for the six month period. JIs ranged from 0.13–0.79 and PSI values were 0.04–0.66 (Table 3). These indices have been widely used to compare faunal similarities of different sites within and between streams. Values of 0.70 and higher for JI and ≥ 0.65 for PSI have been considered indicative of faunal similarity (Matthews et al. 1988; Cashner et al. 1994). Both JI and PSI indicate that the uppermost or headwaters region is highly dissimilar from the middle and lower reaches and that stations 3–5 have similar faunas. In this region, the values for PSI are generally lower than the values for JI, but do not reach the level of ≤ 0.40, which is generally accepted as low or dissimilar (Matthews et al. 1988).

The comparison of the three lower stations on the Nymboida and Mann Rivers with the single site on the lower Orara River clearly indicates that reaches at similar positions of different Clarence River tributaries are not faunistically identical (Table 3), because JI values ranged from 0.45–0.61 and PSI values were much lower at 0.22–0.41. The Shannon index of diversity was calculated for Nymboida River headwaters, stations 3–5, and the site on the Orara River. There was a sharp increase in species richness and diversity downstream between the headwater sites and station 3 on the Nymboida River, a pattern sometimes observed in North American streams, rather than a gradual downstream increase (Matthews 1997). The lower Orara River was similar in species number (though not composition) and diversity to the three lower Nymboida River sites (Table 3).

The pattern of longitudinal distribution of fishes within the Nymboida is one of apparent zonation in the upper reaches, where three species, *A. australis, O. mykiss*, and *G. olidus*, are restricted and only five species have been recorded (Fig. 2). The pattern does not persist, rather there is an abrupt increase in species (5 to 12), starting in the more placid waters of station 3. Thirteen species were recorded from stations 4 and 5, although not exactly the same ones. The restriction of *C. auratus, M. petardi* and *B. bidyanus* to the lower reaches probably does not reflect their true distribution in the Nymboida and Mann Rivers. All three likely extend upstream at least as far as station 3 which still has relatively placid waters. There may be replacement of upland forms in the middle and lower reaches, but basically, from station 3–5, there is an addition of deeper-bodied forms, benthic species and those preferring the conditions in the middle and lower reaches of lotic habitats.

Detrended correspondence analysis of stations, with the Orara River (station 12) included, confirmed the longitudinal pattern revealed from presence-absence of species. The DCA, which is based on abundance, produced a long gradient (>500 units) on the first axis, indicating a complete faunal turnover from upstream station 1 to downstream stations (3, 4, 5, 10, 11), with stations 2, 6, 8 intermediate (Fig. 3). The gradient on Axis 1 reflects longitudinal distribution of species in the Nymboida and Mann Rivers, and the gradient on Axis 2 reflects not only the downstream position of station 12 within the Orara river, but also the presence of four species in the Orara not found in the Nymboida (Fig. 4). Orara station 12 was aligned with downstream stations of the Nymboida on DCA Axis 1, but was distinctive on DCA Axis 2.
Figure 2. Longitudinal distribution of fishes collected in the Nymboida and Mann Rivers in 1991. Exotic species are marked with an asterix.

Figure 3. Station plot of Nymboida and Orara DCA. (Station identifications given in Fig. 1.)
Species richness and 19 physico-chemical parameters were analyzed by PCA to explain variation in fish assemblages. The first three PCA axes accounted for about 65% of the variance. Physical characters had the highest correlations with differences in the presence and absence of species and most of these characters were correlated with gradient and river distance. Factors with high loadings and positively correlated with gradient included altitude, hardness and alkalinity. Factors with high values and negatively correlated with gradient included river distance, physical factors such as width, depth, flow and temperature, as well as conductivity. One of the most striking physical features is the stream gradient in the Nymboida and Mann Rivers. Station 1 was located at an elevation of 1190 m and from station 1 to 2, a distance of 26 km, there was a 575 m drop in elevation, or a 22.1 m/km gradient in that section. There are waterfalls in excess of 10 m in the headwater tributaries of the Nymboida.

Several different analyses, using both presence-absence and relative abundance of fish species, revealed a strong longitudinal component to variation in assemblage composition in the Nymboida and Mann Rivers. The headwaters region yielded only five species, and at station 1 only O. mykiss, and A. australis were captured in six collections. Galaxius olidus was first encountered at station 2 and was fairly common at stations 6–8. The absence of G. olidus from station 1 is probably related to a combination of predation by the introduced O. mykiss and the inability of the galaxiid to overcome the waterfalls as a barrier to its dispersal. The fact that G. olidus was the only species recorded at station 2 may be the result of inappropriate gear or technique. Two other species, A. reinhardtii, and G. holbrooki, were collected at sites in close proximity to station 2, and there was a visual record of a third species, the eastern freshwater cod (M. ikei) at Platypus Flats (station 8). The occurrence of M. ikei at least as far upstream at Platypus Flats, if not actually at sta-
tion 2, is also supported by numerous reports from fishermen and maps provided by companies promoting white-water rafting. The overall downstream increase in richness and diversity reflect conditions more suitable for species associated with river sections that are deeper and wider, with appreciably less current, such as Australian bass (Macquaria novemaculeata), river herring (Potomalosa richmondia) and glassfish (A. agassizi). Softer substrates in the middle to lower reaches offer more suitable habitats for benthic forms such as freshwater catfish (T. tandanus) and various species of gudgeons (Hypseleotris spp. and Philypnodon spp.) (Fig.2). The downstream increase in species richness and diversity also is likely to reflect an associated increase in the diversity of habitat types.

A final observation on the Nymboida and Mann Rivers is that a surprisingly high percentage (>20%) of its fishes are non-native. Rainbow trout (O. mykiss), brown trout (S. trutta), goldfish (C. auratus) and eastern mosquiofish (G. holbrooki) are exotics. species non-indigenous to Australian freshwaters. The silver perch (B. bidyanus) is a transplant from the Murray-Darling drainage west of the Great Dividing Range. The Orara River, based on samples at just one locality, has only two documented exotics, C. auratus and G. holbrooki, however, a more intensive survey of the system would be likely to reveal more introductions.

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REFERENCES


The Psocoptera (Insecta) of Norfolk and Philip Islands: Occurrence, Status and Zoogeography

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This paper provides a list of the twenty-one species of Psocoptera known from Norfolk Island (29°04'S, 167°56'E) and nearby Philip Island, in the South Pacific, with records of localities, wider distributions and notes on habitat preferences. Their status as widespread species, species known from geographically adjacent areas or island endemics is noted. Local distributions are briefly discussed as a base line for future monitoring of the fauna. Conditions are expected to undergo rapid change on Philip Island resulting from environmental management practices as vegetation regenerates following removal of introduced mammals which had almost completely denuded the island of vegetation. Possible source areas for non-endemic species are suggested. The relationships of the eleven probably endemic species seem to lie with the faunas of the New Zealand subregion, New Caledonia and Australia rather than with Lord Howe Island. The affinities of four endemic species are not clear.

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INTRODUCTION

Psocoptera (commonly known as psocids, booklice or barklice) are usually small insects, 1–10 mm in length, mostly winged as adults, which occur in a variety of habitats, on bark and leaves, in ground litter, in stored products and domestic situations. They feed on fungi, algae, lichens and other elements of the microflora, some species being general feeders while others are specialists with a narrow range of acceptable habitats and food sources.

Hawkins (1943) was the first to record Psocoptera from Norfolk Island when he gave family or generic determinations for a few specimens in the British Museum. Between 1967 and 1972 one of us (CNS) paid several visits to the island, with two of us (CNS, IWBT) visiting in 1971. Study of the accumulated material resulted in a record of fourteen species from Norfolk and Philip Islands, eleven of which were previously undescribed. A fifteenth was added on the basis of material collected by Mrs Maurge Jowett (Smithers and Thornton 1974). Another species (Ectopocus richardi (Pearman)) was added from an unusual source, the result of examination of the stomach contents of a gecko, Phylloscopius guentheri Boul., from Philip Island (Smithers 1980). A substantial collection made in 1977 by Dr G.B. Monteith, of the Queensland Museum, included all but four of the previously recorded species, and localities recorded from this material were included, with a key to species, in Smithers (1981). An even larger collection, made by entomologists from the Australian National Insect Collection, Canberra, in 1984, resulted in two further species being recorded from Norfolk Island and one from Philip Island (Smithers 1986), bringing the number of species from the islands to nineteen. A remarkable, almost colourless, previously undescribed, prognathous species was collected from the crown of a
Kentia palm by Mr. N. Tavener in 1986 (Smithers 1994). Intensive collecting of Psocoptera on Norfolk and Philip Islands by two of us (CNS, JVP) between the 12th and 25th January, 1998 resulted in a collection which included all but five of the previously recorded species and in the addition of only one widespread tropical species, bringing the total number now known to twenty-one. Records of Norfolk and Philip Island Psocoptera are included in Smithers (1996) and a list of the Psocoptera recorded up to the end of September, 1996 is included in a catalogue of insects recorded from Norfolk Island (Smithers 1998).

Pigs, goats and rabbits were introduced onto Philip Island during an early period of human settlement on Norfolk Island, resulting in almost complete denudation of Philip Island. Goats and pigs eventually died out. Rabbits survived and only through a long and energetic, not to mention sometimes risky, program of extermination by personnel of the National Parks and Wildlife Service and some of the island’s residents were they finally eliminated in February, 1988. Since the earliest collections and publications on Norfolk Island Psocoptera there have been considerable changes of consequence to fauna and flora conservation on the two islands. Fundamental to these changes has been the long-awaited establishment of the Norfolk Island National Park and the formal environmental protection of Philip Island as well as selected areas of Norfolk. Programs involving deliberate rehabilitation of native vegetation have been initiated. Some results of this activity are apparent on Norfolk Island and some obvious natural revegetation of Philip Island has already taken place. Removal of rabbits has permitted gradual regeneration of plant cover and two species of plants, *Elymus multiflorus* var. *kingianus* (Endl.) Connor (Poaceae) and *Abutilon julianae* Endl. (Malvaceae), both thought to be extinct on Philip, have been rediscovered there (Green 1994). It is hoped that the revegetation processes will continue and that many microhabitats that were lost will be restored and become available for recolonisation by native species of insects.

**LIST OF SPECIES OF PSOCOPTERA RECORDED FROM NORFOLK AND PHILIP ISLANDS**

The following list gives localities from which each species has been taken (data from all collections), their known distribution beyond Norfolk and Philip Islands, and which species are probably endemic. In the list PI=Philip Island, NI=Norfolk Island and an asterisk indicates previously unrecorded localities. Where the name of the island is in inverted commas specimens exist which are labelled with the name of the island only as the locality. There has been no detailed study of the ecology of any of the species on Norfolk or Philip, but the list indicates what appear to be their preferred habitats, based on collecting experience and some limited references in the literature for other areas. Some of the locality records are based on trap catches, e.g. Malaise traps and pan traps, and do not provide ecological information. Data on habitat preference may need modification if more detailed ecological studies are carried out.

**LEPIDOPSOCIDAE**

*Echmepteryx madagascariensis* (Kolbe)

NI: Duncombe Bay Road*, Steel’s Point*. **Wider distribution:** A very widespread species. Known from Madagascar, Africa, Chagos Archipelago, Hong Kong, North America, West Indies, Chile; widespread through the Pacific, New Zealand, Australia, Indonesia. **Habitat:** Frequently found on dried leaves of bananas. This was the only unrecorded species to be taken in the most recent field work.
Lepolepis graeemi Smithers and Thornton


**Habitat:** Mainly an inhabitant of leaf litter; has been taken from dead leaves on trees.

Pteroxanium ralstonae Smithers and Thornton


**Wider distribution:** None recorded, endemic. 

**Habitat:** On tree trunks, branches and in leaf litter. The least common of the three species of *Pteroxanium*; not taken in the most recent collections.

Pteroxanium evansi Smithers and Thornton

NI: Bumbora, Collin’s Head, Mount Pitt Reserve, Point Blackbourne, Point Hunter Reserve, Rocky Point Reserve, Selwyn Reserve, Stockyard Creek. PI: “Philip Island”, South east slopes*. 

**Wider distribution:** None recorded, endemic. 

**Habitat:** On tree trunks, branches and in leaf litter.

Pteroxanium insularum Smithers and Thornton

NI: Anson Bay Reserve*, Botanic Gardens*, Broken Pine Track*, Burnt Pine, Captain Cook Monument, Cascade-Red Road, Collin’s Head, Jonneniggabunnit, Highlands Guest House*, Melanesian Mission, Mission Road, Mount Pitt Reserve, Palm Glen, Pitt-Bates Track, Point Blackbourne, Point Ross, Red Road Track*, Rocky Point Reserve*, Selwyn Pine Road, Selwyn Reserve*, Stockyard Creek, South Spur Track*. 


**Wider distribution:** None recorded, endemic. 

**Habitat:** On twigs and branches of trees. Has been taken from under a stone. The commonest of the three species of *Pteroxanium* on *Araucaria* but not restricted to it.

**TROGIIDAE**

Cerobasis guestfalica (Kolbe)

PI: “Philip Island”, Upper Long Valley*. 

**Wider distribution:** A very widespread species. Europe, North America, West Indies, Brazil, Argentina, Chile, Morocco, South Africa, Mauritius, Australia, Tasmania, Java, Hawaii, Robinson Crusoe Island, Azores, St. Helena, Canary Islands, St. Paul Is. 

**Habitat:** Occurs on bark of trees, coastal dune vegetation, in leaf litter, on fences and sometimes in buildings.

Lepinotus patruelis Pearman

NI: Broken Pine Track, Rocky Point Reserve. 

**Wider distribution:** A very widespread species. Europe, North America, Argentina, South Africa, New Zealand, Australia, Tasmania. 

**Habitat:** Occurs in buildings, in stored products, in termite nests, on twigs and branches of shrubs and trees.

Trogium evansorum Smithers

NI: Indoors, Colonial Hotel, Queen Elizabeth Avenue*. 

**Wider distribution:** None recorded, endemic. 

**Habitat:** Previously known only from the crown of a Kentia palm tree on Norfolk Island.
CAECILIUSIDAE

Caecilius insulatus Smithers and Thornton

NI: Bumbora, Captain Cook Monument, Cascade-Red Road, Mission Road, Point Blackbourne, Rocky Point Reserve, Selwyn Reserve. Wider distribution: None recorded, endemic. Habitat: Leaf dweller; beaten from both fresh and dead leaves, possibly also living on twigs.

Caecilius pacificus Smithers and Thornton


ECTOPSOCIDAE

Ectopsocus briggsi McLachlan

NI: Anson Bay*, Botanic Gardens*, Bullock’s Hut Road, Burnt Pine, Captain Cook Monument, Melanesian Mission, Mount Bates, Mount Pitt Reserve, Pitt-Bates Track, Palm Glen, Red Road Track, Rocky Point Reserve, Selwyn Pine Road. Wider distribution: Worldwide, likely to be found wherever habitat is suitable. Habitat: Lives on dead, dry leaves in litter and especially those hanging from woody plants.

Ectopsocus inornatus Smithers and Thornton

NI: Captain Cook Monument, Mount Pitt Reserve, Palm Glen, Rocky Point Reserve*, Red Road Track*, Botanic Gardens*. Wider distribution: None recorded, endemic. Habitat: Lives on dried leaves, including those of dead herbaceous plants, and in dead flowers and inflorescences.

Ectopsocus insularis Smithers and Thornton


Ectopsocus richardsi (Pearman)

PI: “Philip Island”. Wider distribution: Europe (introduced, in stored products), West Africa, Azores, Madagascar, North America, South America, Hong Kong, Australia, Galapagos, Hawaii. Habitat: In stored products; in the field in dead inflorescences.

PERIPSOCIDAE

Peripsocus milleri (Tillyard)

NI: Anson Bay Reserve, Botanic Gardens*, Collin’s Head*, Mount Pitt Reserve, Nobb’s Apartments, Palm Glen, Pitt-Bates Track*, Rocky Point Reserve, Steel’s Point*.
PI: “Philip Island”, Upper Long Valley. **Wider distribution:** Europe, Canary Islands, Azores, North America, Chile, Australia, Tasmania, Kermadecs, Auckland Islands, New Zealand, Hawaii, Robinson Crusoe Island. **Habitat:** On stems, branches and twigs of shrubs and trees.

*Peripsocus norfolkensis* Smithers and Thornton

**NI:** Anson Bay Road, Botanic Gardens*, Bullock’s Hut Road*, Burnt Pine, Captain Cook Monument, Collin’s Head, Filmy Fern Walk*, Highlands Guest House*, Jonnenigabunnit, King Fern Gully* Melanesian Mission, Mission Road, Mount Bates, Mount Pitt Reserve, Norfolk Island National Park, Pitt-Bates Track*, Palm Glen, Point Ross, Red Road Track*, Rocky Point Reserve, Selwyn Pine Road, Selwyn Reserve, South Spur Track*, Steel’s Point*, Stockyard Creek. **PI:** “Philip Island”, Upper Long Valley*. **Wider distribution:** None recorded, endemic. **Habitat:** On twigs and branches of trees and shrubs.

**PSEUDOCAECILIIDAE**

*Heterocaecilius variabilis* Smithers and Thornton

**NI:** Botanic Gardens*, Bullock’s Hut Road*, Bumbora, Burnt Pine, Captain Cook Monument, Highlands Guest House*, Mount Pitt Reserve, Nobb’s Apartments, Palm Glen, Pitt-Bates Track*, Red Road Track*, Rocky Point Reserve, Selwyn Pine Road, Selwyn Reserve*. **Wider distribution:** None recorded, endemic. **Habitat:** On green foliage of mainly large shrubs and trees.

**PHILOTARSIDAE**

*Haplophallus emmus* Smithers and Thornton

**NI:** Captain Cook Monument, Mount Pitt Reserve, Rocky Point Reserve, Ross Point. **Wider distribution:** None recorded, endemic. **Habitat:** On mature twigs and branches of trees, bark of Eucalypts.

**ELIPSOCIDAE**

*Propsocus pulchripennis* (Perkins)

**PI:** Moo-oo Beach, Upper Long Valley. **Wider distribution:** Africa, Chile, Mexico, Tasmania, Australia, New Zealand, Hawaii. **Habitat:** Inhabitant of dried leaves and especially of leaf litter.

**PSOCIDAE**

*Blaste lignicola* (Enderlein)

**NI:** Anson Bay Reserve*, Botanic Gardens*, Bumbora, Burnt Pine, Collin’s Head*, Highlands Guest House*, Melanesian Mission, Middlegate, Mount Pitt Reserve, Nobb’s Apartments, Palm Glen, Rocky Point Reserve, Ross Point, Selwyn Pine Road. **Wider distribution:** Australia, Tasmania. **Habitat:** On trunks and branches of trees and shrubs bearing lichen and algae.

**MYOPSOCIDAE**

*Myopsocus australis* (Brauer)

**NI:** Anson Bay Reserve*, Burnt Pine, Cascade, near Collin’s Head*, Point Blackbourne. **Wider distribution:** Australia, Tasmania, New Zealand, Lord Howe
Island, Kermadecs, Solomon Islands. Habitat: On trunks and branches of trees carrying fungi attacking bark. Also found on weathered paling fences.

DISTRIBUTION OF NORFOLK ISLAND PSOCOPTERA

Table 1 summarises the known distribution of species between Philip and Norfolk islands and indicates which species are considered to be endemic.

Jones and McDougall (1973) discuss the geological history of Philip and Norfolk Islands, providing a background against which the origins of the fauna can be considered. Holloway (1977), in an outstanding and scholarly treatment of the Lepidoptera of Norfolk Island based on a trapping program carried out by Mrs Maurge Jowett, has summarised this history. An essential point is that the Norfolk Island area was at one time below sea level. From this it is concluded that all elements of the Norfolk land biota are probably derived from transoceanic arrivals during about the past 2.3 million years, the nearest source areas being Australia, New Caledonia, Lord Howe Island and the New Zealand subregion.

When considering the wider geographical distribution of Norfolk Island Psocoptera they can be grouped into three categories.

1. Species which are widespread beyond Norfolk and Philip Islands.

These are species which appear to be highly vagile and have an ability to establish themselves with relative ease, probably because of the widespread availability of suitable habitats in newly colonised areas and, in some cases at least, with the assistance of people. These species, which may have arrived early or recently, are now widespread on Norfolk and Philip. \( E. \text{ madagascariensis} \) is closely associated mainly with dead banana leaves, a habitat available almost throughout the tropics. People, by taking bananas from island to island, have probably made suitable habitat more widely available than it would otherwise have been to naturally colonising individuals and have also physically assisted in their dispersal by carriage on leaf material. \( C. \text{ guestfalica} \) and \( \text{L. patrueris} \) are found in buildings and have also undoubtedly been introduced into many countries with widely differing climatic regimes. In many of the areas in which they occur they do, however, occupy a wider range of habitats than those provided in domestic situations. They appear not to be specialists in regard to habitat requirements. It is surprising that \( C. \text{guestfalica} \) has been taken on Philip Island but not yet on the larger Norfolk Island where human habitation has been available for so long. \( E. \text{ briggsi} \) is almost a worldwide species which usually inhabits dead glabrous leaves of woody, dicotyledonous plants, a habitat which, although somewhat ephemeral, is constantly replaced. In addition to dispersal by natural mechanisms their spread may have been assisted through the introduction of horticultural and possibly packaging material, such as straw. On Philip Island \( E. \text{ richardi} \) has been found only in the stomach contents of a gecko. Elsewhere, it is usually found in stored grains and other stored products but in the field occurs in dead inflorescences. Introduction in grain or dead plant material could easily have assisted its dispersal, with populations maintaining themselves in stored products in the colder climates in which it has also been found. In Britain it has been found in stored cacao imported from West Africa, from where it has also been recorded. \( P. \text{ milleri} \) occurs on twigs and branches of trees and appears also to be almost worldwide. It has the same status on twigs and branches as \( E. \text{ briggsi} \) does on leaves. \( P. \text{ pulchripennis} \) is an inhabitant of dead leaves and leaf litter. It is interesting to note that \( P. \text{ pulchripennis} \) does not often occur with species of \( Ectopsocus \), such as \( E. \text{ briggsi} \), which are the most frequently encountered species specialising in the use of the same habitat. This is probably because of subtle differences in habitat requirements, but relatively little is known of such factors as specific microfloral components of psocopteran food sources in the wild.
2. Species which are found in limited areas geographically adjacent to Norfolk and Philip Islands.

In addition to Norfolk and Philip Islands, *L. graemei* is known elsewhere only from Lord Howe Island. This Lord Howe Island record has not previously been published. Details of the many specimens taken there in surveys by Dr. T. Kingston and Dr G. Monteith in 1978 and 1979 will be provided in a forthcoming study of the Psocoptera of Lord Howe Island. Over the years there has been much exchange of vegetable and other material between the islands and there must have been ample opportunity for transfer from one to the other by this means or naturally. There is so far no way of knowing in which direction immigration might have taken place. *Blaste lignicola* has been found only in southeastern Australia and Tasmania and *M. australis* is known elsewhere from Tasmania, New Zealand, Lord Howe Island, Kermadecs and the Solomon Islands. It is very common in western, through southern and southeastern to northeastern Australia. Both species inhabit the bark of trees and by whatever route these two species might have arrived on Norfolk they probably have their origin in Australia. Wind assisted dispersal, as in the case of many species of Australian insects arriving in New Zealand (Tomlinson, 1973; Fox, 1978; Early et al. 1995 and many references therein), could easily account for the arrival of several of the non-endemics on Norfolk from source areas in Australia, New Caledonia or elsewhere at any time since the last exposure of Norfolk by lowering of sea level about 2 million years ago (Holloway, 1977). A high proportion of the non-endemics of Norfolk are found in the New Zealand subregion.

3. Species so far found only on Norfolk and Philip Islands.

Eleven species are considered at present to be endemics, a high percentage of the known fauna. Five of these are known to occur on both islands (*P. evansi, P. insularum, C. pacificus, C. insulatorus, P. norfolkensis*). The remaining six endemics are known from Norfolk only (*P. ralstonae, T. evansi, E. insularis, E. inornatus, H. variabilis, Hap. emmus*). There are no endemics known only from Philip.

**AFFINITIES OF ENDEMIC ELEMENTS OF THE FAUNA**

The probable affinities of the endemic species are summarised in the following list. Apparent near relatives are known to occur in the areas given for each species. Comparisons are based on limited knowledge of several of the families in such areas as New Caledonia and it should be noted that the fauna of Lord Howe Island is not yet as well known as that of Norfolk.

*P. evansi*: Chatham Islands
*P. insularum*: Chatham Islands
*P. ralstonae*: Chatham Islands
*C. pacificus*: New Zealand, Australia
*C. insulatorus*: New Zealand, Australia
*P. norfolkensis*: Australia, New Caledonia
*T. evansi*: ?
*E. insularis*: Philippines, Samoa, Micronesia
*E. inornatus*: ?
*H. variabilis*: ?
*Hap. emmus*: Lord Howe Island, Australia, New Zealand, New Caledonia

Six species of the Norfolk endemics seem to have affinities with the New Zealand subregion, two with New Caledonia, four with Australia, one with other Pacific island
groups and one with Lord Howe. The affinities of three species are not clear. Seven of the eleven endemics have relatives in areas lying on the Norfolk Ridge. Ties with Lord Howe Island seem limited, through one species only (H. emmus) other than L. graemei, the only shared species, which could have originated on either island. On balance it appears that the New Zealand subregion has had the greatest influence in providing the source of endemic species on Norfolk and could well be the area from which several of the more widespread non-endemics have come. This is interesting in light of the fact that moths regularly or sporadically immigrant into New Zealand and Norfolk Island are predominantly of Australian origin (Holloway 1977).

**DISTRIBUTION OF SPECIES BETWEEN NORFOLK AND PHILIP ISLANDS**

Out of a total of 21 species of Psocoptera, 18 have been recorded from Norfolk Island and ten from Philip Island. Eleven species have been found on Norfolk which have not been found on Philip and there are 3 known from Philip but not yet found on Norfolk. Not one of these (C. guestfalica, E. richardsi, P. pulchripennis) is endemic, all three being widespread in other parts of the world.

Considering the 5 non-endemics which have not been found on Philip, E. madagascariensis (on dead banana leaves), L. patruelis (brachypterous mostly in human habitation), E. briggsi (mainly on dead leaves) and B. lignicola and M. australis (associated with lichens and algae or fungus on trunks and branches of trees), it is possible that these species have not yet been found on Philip because of current lack of narrow niche requirements in the habitat. E. briggsi, however, is a surprising absentee from Philip because its habitat is available, especially since the gradual revegetation of the island has been in progress. Dead leaves form a habitat which is continuously being replenished and so is always available for colonization by E. briggsi and other species which prefer it.

Although it can never be known with certainty how many, and which, species were originally on Philip, it seems highly unlikely that the six endemics on Norfolk Island not yet recorded from Philip were not present there prior to the almost total destruction of vegetation of Philip which resulted from introduction of herbivorous mammals. Norfolk Island has an area of about 34 square kilometres and rises to a height of over 300 metres at Mt Pitt (316 m) and Mt Bates (308 m). Philip Island, which is much smaller, covers about 2 square kilometres and is about 280 metres at its highest point. Although differing considerably in size, the two islands, at about 6.5 km apart, are very close to one another. The vegetation on Philip may never have been as dense as that on Norfolk and by 1830 it had certainly been reduced enough to permit some obvious erosion (Green 1994). The island must, however, have been at one time (prior to human influence) substantially clothed in forest, enough to prevent erosion and support the development and maintenance of forest communities which included large trees such as Araucaria heterophylla (Salisb.) Franco (Norfolk Island Pine) (Araucariaceae) and Lagunaria patersonia (Andrews) G. Don. (White Oak) (Malvaceae) as well as other endemic and indigenous species. Interchange of insects between the islands would have been, and must still be, frequent. It seems likely that the “missing” endemics disappeared as a result of the denudation and loss of suitable habitat rather than that they were never present. Possibilities for interchange have not diminished. Despite the presence of substantial populations on Norfolk which could serve as a source of recolonisers of “missing” endemics, six of them have not, apparently, so far reestablished themselves in response to the present increasing levels of revegetation. Adequate niche features of the habitats required by them may, of course, still not be available on Philip.

Now that substantial collections of Psocoptera have been made on the islands between 1967 and 1998, the fact that only one species, a pantropical inhabitant of dead banana leaves, was added in the intensive recent field work strongly suggests that most
of the species have probably been recorded. It would be useful to be able to quantify the collecting effort which has been put into Psocoptera collection over time. Unfortunately, although some of the collections were made by specialist collectors concentrating on the group continuously for a known number of days, several of the collections have been the result of general trapping programs undertaken for various periods, and a few species have been added through casual collecting. It is, therefore, not possible to produce a meaningful discovery curve. It is, however, timely to provide this summary of present knowledge in the hope that subsequent reestablishment and turnover of species will be more easily followed and documented.

It will be interesting to see if, and when, recolonisation of Philip by the presumably "lost" endemics and other species "missing" from Philip, but present on Norfolk, takes place. Frequent, long term, detailed monitoring of vegetational changes and reestablishment of Psocoptera (and other insect groups) on the island could be instructive in giving an insight into the processes of recolonisation by a partially eliminated fauna during a period of reestablishment of vegetation.

At the same time it should be noted that Norfolk has an area of just under 35 square kilometres and supports 18 recorded species of Psocoptera. Philip Island, with an area of about 2 square kilometres apparently supports 10 species. Considering the small areas involved and small numbers of species recorded these numbers are probably tolerably close to the expected relative number of species in terms of the Equilibrium Theory of Island Biogeography. Perhaps Philip Island is already at maximum expected "carrying capacity" and little long term increase should be expected.

ACKNOWLEDGEMENTS

We would like to thank the Director of the Australian National Parks and Wildlife Service for permission to work in Service areas on Norfolk and Philip Islands, and the officers of the Service on Norfolk Island for their help and advice, Owen and Beryl Evans for their ever-ready willingness to share their knowledge of the island and its natural history, Maurge Jowett for providing us with work space in her home, Merval Hoare for help with historical information and Angela Guymer and other members of the Norfolk Island Flora and Fauna Society for their help with information and literature on the islands' faunas.

REFERENCES


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The Stratigraphic Palynology of the Macquarie River Valley, Central Western New South Wales

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School of Biological Science, University of New South Wales, Sydney 2052, Australia


The palynology of samples from bores in the Macquarie River Valley has provided evidence of the age of the sediments. The Neogene-Quaternary valley fill is underlain by Mesozoic sedimentary rocks and possibly older units. Upstream of Narrmome, the basement is Triassic, and downstream, it is Jurassic-Cretaceous. Late Miocene-Pliocene assemblages are found over the whole region, and there are a few occurrences of early and mid Miocene assemblages. Most of the Neogene assemblages occur at relatively shallow depths, but west-southwest of Narrmome, they are found at greater depths of about 100 m, suggesting that this is the region of the palaeovalley of the Macquarie River. Identification of the important aquifer, the Pilliga Sandstone, should be based on evidence of lithology, hydrology etc., in addition to palynological age, for extensive units such as this are not necessarily the same age over the whole of their extent.

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KEYWORDS: Cainozoic, Macquarie River Valley, Mesozoic, palynology, Pilliga Sandstone, stratigraphy.

INTRODUCTION

The allocation of water resources between competing interests in the semi-arid regions of western New South Wales is at times controversial. Groundwater is an important component of the resource, and knowledge of the geology is necessary for proper management. The Tertiary alluvial fill of the river valley is a source of groundwater, but it may overly a basement of older sediments that may be virtually indistinguishable on lithologies alone. The Macquarie River Valley in central western New South Wales extends across the southern edge of the Middle to Late Jurassic Pilliga Sandstone, a well known aquifer. Palynology is essential for the identification of these different units. This paper reports the stratigraphic palynology of bores in the Macquarie River Valley (Fig. 1).

MATERIALS AND METHODS

Samples of sediment from bores (Figs 1, 2) were supplied by the Department of Land and Water Conservation. The samples are first soaked in water, then treated with hydrochloric acid to remove all carbonates, if present. They are then treated with hydrofluoric acid to remove silicates. These two acids together remove all mineral matter. If sand and/or gravel are present, they are removed by decanting early in the treatment. Processing times and concentrations vary, depending on the nature of the sample.

The organic residues are oxidised with Schultz solution (nitric acid saturated with potassium perchlorate) to dissolve degraded organic matter. Treatment with an alkaline solution, sodium carbonate, then removes the dark coloration, making the residues suitable for examination under the microscope. Again, times and concentrations vary,
Figure 1. Locality map. For legend to bore symbols, see Fig. 2.

Figure 2. The area of detailed study. For a more precise age of the bores, see Table 1 in the Appendix.
depending on the nature of the sample, and the final treatment with an alkali may be omitted on highly oxidised samples. The residues are then mounted on a microscope slide in glycerine jelly.

The pollen and spore assemblages are matched with descriptions in the literature of palynological zones which have been dated. The most recent zonations are used here (Figs 3, 4, 5). Some older, unpublished reports may be based on older zonations, but they have been updated to the most recent ones used here. The change makes no difference to the age, or a very slight difference if the ranges of diagnostic species have been modified.

Good assemblages with some diagnostic species may be assigned to a zone, but if diagnostic species are not present, then the general abundance of some species may indicate a superzone. With very poor assemblages, even a superzone may not be possible, but as there are hardly any species common to the Mesozoic and the Tertiary, then even a few grains will distinguish these two ages.

GEOLOGY

A complex sequence of Paleozoic rock units underly this region (Sherwin 1996). Mesozoic sediments of the Coonamble Lobe of the Surat Basin, part of the Great Australian Basin, overry the Paleozoic sequence. Narromine and Dubbo are close to the southern limits of widespread Mesozoic sediments, although small remnants of Mesozoic sediments may be found further south near Trundle (Hawke et al. 1975) and Molong (Gibson and Chan 1999). The Middle Jurassic Purlawaugh Formation, the Middle-Late Jurassic Pilliga Sandstone and possibly the Late Jurassic-Early Cretaceous Keelindi Beds are found in this area. Upstream from Dubbo, there is some Triassic of the Gunnedah Basin (Raymond et al. 1997). Cainozoic sediments fill the valley and may form a thin veneer elsewhere (Raymond et al. 1997; Sherwin 1996).

STRATIGRAPHIC PALYNOLOGY

A summary of the results for each bore is given in Table 1 of the Appendix. Many more samples and bores have been examined, but they proved barren, and are not included here.

Triassic assemblages

Triassic palynomorphs are very poorly preserved, with only a few of the most robust forms identifiable. The species identified in selected assemblages are presented in Appendix Table 2. Falcisporites australis is common and this places it in the Triassic Falcisporites Superzone (Helby et al. 1987). Aratrisporites spp. are present, indicating a mid Triassic age, possibly the A. parvispinosus Zone, or even the A. tenuispinosus Zone (Fig. 3). These data show that the basement upstream from Dubbo, where intersected, is Triassic, and there is one occurrence of a Triassic assemblage between Dubbo and Narromine (Fig. 2).

Late Jurassic to Early Cretaceous assemblages

The species identified in selected assemblages are presented in Appendix Table 3. Following Helby et al. (1987), the Jurassic Callialasporites dampieri Superzone (Fig. 4) is recognised by an abundance of Callialasporites spp. Microcachryidites antarcticus first appears in the mid Jurassic, but it is not common. An abundance of M. antarcticus is characteristic of the overlying Microcachryidites Superzone which begins at the base of the Tithonian in the Late Jurassic, and continues into the Early Cretaceous (Helby et al.
If diagnostic species (Fig. 4) are present, then the assemblage may be placed in a Zone. The sediments range in age from the Mid-Late Jurassic Murospora florida Zone to the earliest Cretaceous Cicatricosisporites australiensis Zone. All of these assemblages were deposited in non-marine environments. Late Jurassic to Early Cretaceous sediments are found north, west and southwest of Narromine (Fig. 2).
<table>
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<td>Berriasian</td>
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</tr>
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<td>R. watheroensis</td>
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<tr>
<td>Kimmeridgian</td>
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<td>M. florida</td>
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</tr>
<tr>
<td>Aalenian</td>
<td>C. turbatus</td>
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</table>

Figure 4. Range chart for the Mid-Late Jurassic and Early Cretaceous. From Helby et al. (1987).

North of the area of intensive investigation, sediments of the earliest Cretaceous C. australiensis Zone occur in the Macquarie Marshes region, and deposits of the Aptian Cyclosporites hughesi Zone is found near Bourke (Fig. 1). Both assemblages contain dinoflagellates and acritarchs (Table 2), which indicate marginal marine environments of deposition.
### Figure 5. Range chart for the Neogene and Pleistocene.


### Tertiary and Pleistocene assemblages

The species identified in selected assemblages are presented in Appendix Table 4. The early Miocene Upper *Proteacidites tuberculatus* Zone (Stover and Partridge 1973) is marked by the first appearance of *Acaciapollenites myriospora* (Fig. 5), and is found
west of Narromine. *Haloragacidites haloragoides*, *Rugulatisporites micraulaxus* and *Tubulifloridites antipodica* denote the Mid-late Miocene *Canthiumidites (=Triporopollenites) bellus* Zone (Stover and Partridge 1973), which occurs near Narromine. The probable assemblage of the *C. bellus* Zone near Mudgee has an appreciable *Nothofagidites* spp. content, which is more typical of older assemblages, but which may be found occasionally throughout the Neogene. *Monotocidites galeatus* and *Cingulatisporites bifurcatus* indicate the late Miocene-Pliocene *Monotocidites galeatus* Zone (Macphail and Truswell 1993), which may be found west of Narromine, but it is most common upstream of Dubbo (Fig. 2).

*Tubulifloridites pleistocenicus* (Asteraceae) and *Fenestrites* sp. (Tribe Cichoreae of the Asteraceae) mark the top of the *M. galeatus* Zone, and the Pleistocene Asteraceae/Poaceae assemblage (Fig. 5). Other Asteraceae (*Tubulifloridites antipodica/simplis*) and Poaceae (*Graminidites monoporites*) are usually abundant also. Other characteristics of Pleistocene assemblages include a very reduced spore and gymnosperm content and an overall reduction of species diversity.

**DISCUSSION**

The stratigraphic palynology and ages reported here rely on diagnostic species which are not common, and, if the assemblage is not very diverse, may be based on only one key species. For example, 9 samples between 120 m and 175 m in bore DLWC1 yielded assemblages which are generally similar, and have been assigned to the *Murospora florida* Zone. However, only two of the diagnostic species, *M. florida* and *Retitriletes facetus* which demarcate the base of the *M. florida* Zone, are found, and
then only in 3 of the samples. The other six samples lack diagnostic species of the zone. When there is a sequence from the one bore in which the assemblages and sediments are all similar, as in bore DLWC1, then it is reasonable to assume they all belong to the same zone.

With single samples from a bore, difficulties may arise. For example, bores NADC9 and NAD104 are close to each other (Fig. 2), and very similar assemblages were recovered from the 104–126 m level in the former, and the 94–97 m level in the latter. A single grain of *Cicatricosisporites australiensis* in the 104–126 m level places the assemblage in the younger *C. australiensis* Zone, whereas the lack of this species in the 94–97 m level places that assemblage in the older *M. florida* Zone (Table 1, Fig. 4). In this case, other evidence should be considered, along with the palynological age, to arrive at a satisfactory outcome.

The identification of the Pilliga Sandstone is critical, because of its importance as a regional aquifer. The Pilliga Sandstone is generally regarded as Late Jurassic (Hind and Helby 1969; Sherwin 1996), based on palynological evidence from bores more than 200 km to the northeast. The palynology of a sandstone at Spring Ridge, which has all the lithologic and hydrologic characters of the Pilliga Sandstone and was mapped as Pilliga Sandstone, was however found to be Early Cretaceous (Martin 1981) *Foraminisporis wonthaggiensis* Zone (Fig. 4), based on the most recent zonations used here. Experience has shown that formations which may be identified on grounds of lithology, hydrology, etc., over large areas, are not necessarily the same palynological age over the whole of the area, i.e. are time transgressive, and this applies particularly to the margins of the unit. Spring Ridge is near the eastern edge of the Pilliga Sandstone, and Narramine is near the southern edge. Other evidence, as well as palynology, should be taken into account to identify the Pilliga Sandstone.

The same problem of scarcity of diagnostic species applies to the Neogene assemblages. There is an overall trend of loss of rainforest taxa, and a lower diversity of species throughout the Neogene, but this trend is extremely variable geographically. For example, the *C. bellus* assemblage at Mudgee has an appreciable content of the rainforest taxa *Nothofagidites* spp. (Table 4), whereas at Narramine it is minimal. This difference may be attributed to a geographic difference in the source vegetation. In New South Wales, increasingly dry climates through the Neogene (Martin 1998) forced a retreat of rainforest taxa from the drier, western regions first, restricting them eventually to the eastern highlands. Assemblages with appreciable *Nothofagidites* spp. are found at Lake George in the Highlands, in the latest Pliocene, just below Asteraceae-Poaceae assemblages (McEwen Mason 1989), but a high content of *Nothofagidites* spp. is more typical of Palaeogene assemblages in the western regions of New South Wales. Some of the assemblages have a high content of *Araucariacites australis*, representing araucarians such as hoop pine, bunya pine, kauri, which are now found in the drier rainforest habitats. The variability in the palynology reflects the patchiness of the vegetation.

An increase of Asteraceae, the daisy family (collectively *Tubulifloridites antipodica/simplis*, *T. pleistocenicus* and *Fenestrides* sp.), and Poaceae, grasses (*Graminidites media*) is a palynostratigraphic marker horizon that can be recognised over much of New South Wales. Accompanying this change, is a reduction of the spore content (chiefly ferns) and also in the gymnosperm pollen, most of which represents rainforest species (Table 4). This change, which represents the opening up of the forests and the development of grasslands and herbfields/shrublands, has been palaeomagnetically dated as 2.5–2.9 million years at Lake George (McEwen Mason 1989, 1991). It is assumed the same ecological trend occurred at about the same time elsewhere.

Fig 6 shows a cross-section west of Narramine. The southern end of the transect shows Tertiary assemblages occurring at depths of more than 100 m, whereas at the northern end, the Jurassic/Cretaceous basement may occur at depths as shallow as 40 m.
This suggests that the old Tertiary palaeovalley of the Macquarie River probably continued in a westerly direction after Narromine, instead of turning north, as it does today. The depth to pre-Tertiary bedrock contour map, based on hundreds of bores drilled in the area west of Narromine (S. Haridhanan, pers. comm.) supports this conclusion.

ACKNOWLEDGEMENTS

I am indebted to the New South Wales Department of Land and Water Conservation for the materials of this project, and to Mr. S. Haridhanan, of the DLWC, Dubbo, for advice and comments about the manuscript.

REFERENCES


### APPENDIX

#### Table 1.
Summary of results. Bores arranged approximately W to E, then N to S (see Figs 1, 2).

<table>
<thead>
<tr>
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<td>79–80</td>
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<td>36965</td>
<td>110–132</td>
<td>A few long ranging Mesozoic spp.</td>
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**North of the detailed area (Fig. 1)**

- Early Cretaceous (Aptian)
- Early Cretaceous (Berriasian)
- Mesozoic
- Late Jurassic (Tithonian)
- Tertiary
- Early Cretaceous (Berriasian)
- Mesozoic
- Mid–late Miocene
- Mesozoic
- Late Jurassic
- Mid–late Miocene
- Earliest Cretaceous
- Late Jurassic
- Mid–late Pliocene
- Late Miocene–Pliocene
- Late Miocene–Pliocene
- Mid Triassic
- Late Miocene–Pliocene
- Pliocene
- Late Miocene–Pliocene
- Pleistocene
- Mid Triassic
- Late Miocene–Pliocene

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PROC. LINN. SOC. N.S.W., 121, 1999
Table 2.
Triassic assemblages. Taxonomy follows Helby (1973) and Helby et al. (1987).

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**H.A. MARTIN**
### Table 3.


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PROC. LINN. SOC. N.S.W., 121. 1999
I. punctatus + + + + +

Kluksaporites scaberis + + + + +

Krauselisporites linearis +

Leptolepidites verrucatus + +

Lycopodiacidites asperatus + + + + +

Microchacryidites antarcticus + + + + + ++

Murospora florida + + +

Neoraistrikia truncatus + + + + + + +

Osmundacites wellmanii + +

Pilosporites notensis +

P. parvispinosus +

Polycingulatisporites sp. +

Podocarpidites spp. + ++ ++ ++ + + ++ ++

Reticuloidosporites arcus +

Retitriteles austroclavatidites + + + + + +

R. circulamens + + + + + + +

R. facetus + + + +

R. nodosa + + + +

Retitriteles spp. ++ + + + +

Schizosporits reticulatus + +

Sestrostipites pseudoalveolatus + +

Stereisporites antiquasporetes +

Todisporites minor +

Triletes cf. T. tuberculiformis + + + +

Trilobosporites purveulentus +

Triporoletes sp. +

Dinoflagellates and acritarchs

Adanatosphaeridium sp. +

Cleistosphaeridium ancorferum +

Cyclonophelium densibartarum +

Cyclonophelium sp. +

Hestertonia cf. H. striata +

Kiokansium polypes +

Micrhystridium sp. + +

Nummus monoculus + +

Oligoshaeridium complex +

O. pulcherrinnum + +

Spiniferites sp. +

Stephanodium sp. +

Tenua hysterix + ++
TABLE 4.

Selected Tertiary assemblages. Identifications follow Martin (1973), Stover and Partridge (1973) and Macphail and Truswell (1993). Where percentages from counts of about 150 grains are not available, + = present, or present but not in the count, and ++ = common. Zones: 1. Upper Proteacidites tuberculatus, early Miocene. 2. Canthiwnidites bellus, late early-late Miocene. 3. Monotocidites galeatus, late Miocene-Pliocene. 4. Asteraceae/Poaceae, Pleistocene.

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**Spores**

- Baculatisporites disconformis 0.7
- Cingulatisporites bifurcatus 0.7 2.3 3.2 0.9
- Cyathacoidites annulatus + +
- Cyathidites paleospora + 3.7 ++ + 5.6 3.1
- C. subtilis 0.7
- Deltoideospora inconspicua 1.5 0.7 5.5 0.8 0.9
- Gleicheniidites cirrinulides + 0.7 + 2.2 1.6
- Klukisporites lachlanensis 0.7
- Laevigatosporites ovalis + 11.0 + 2.2 1.6
- Matonisporites ornamentalis + 1.4
- Polyplodiates sp. 0.7
- Reticulidosporites minispuria 2.3
- Rouseisporites sp. 1.8
- Rugulatisporites mallatus +
- R. trophus + +
- Stereisporites sp. 0.7

**Gymnosperms**

- Araucariacites australis ++ 2.2 + ++ 36.2 3.1
- Cupressaceae 1.5 0.8 0.9
- Dacrycarpus australiensis + 2.2 + + 2.9 7.8
- Lygistepollenites florinii + 0.7 + 0.8
- Phyllocladidites palaeogenicus 0.8
- Podocarpidites spp. + 3.7 + + 6.5 14.8

**Angiosperms**

- Acaciapollenites myriosporites + 0.7
- Chenopodiapollenites myriosporites + 0.7
- Cunoniaceae/Elaeocarpaceae 2.2
- Cupanioiidites orthoteichus 2.2
- Cyperaceae pollen sp. + 1.6 1.6 5.3
- Dodonaea sphaerica 0.7
- Ericites crassiusxenis + 0.7
- Fenestrites sp. 0.8
- Glencopollis ornatus + 0.8 0.9
- Graminidites media 1.4 6.4 12.5
- Guettardidites sp. +
- Gyrostemonaceae +
- Hakea sp. 0.7

PROC. LINN. SOC. N.S.W., 121. 1999
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**Reworked Permian forms**

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<td><strong>Protohaploxypinus sp.</strong></td>
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<tr>
<td><strong>Striatoabies multistriatus</strong></td>
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Leporillus (Rodentia: Muridae) from Madura Cave, W.A.

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1Department of Geological Sciences, University of Texas, Vertebrate Paleontology Laboratory, Texas Memorial Museum, University of Texas, Austin Texas 78712, USA; 2Department of Geology Field Museum of Natural History, Chicago Illinois, USA


Two species of the genus Leporillus are represented in the Pleistocene-Holocene sediments of Madura Cave. Leporillus conditor is abundant and ranges from the surface to the deepest level (38,000 BP). L. apicalis is less abundant and appears to be restricted to levels dating from 7,500 to 22,400 BP.

Most of the specimens are dissociated because they are derived from owl pellets and thus specific identification is difficult. Many of the dimensions of the teeth of the two species overlap and there are few diagnostic features that separate them. Watts and Aslin gave criteria for the genus based on modern material. We have attempted to evaluate features that would separate the species on the basis of incomplete cranial and dental materials.

We describe a few of the better specimens, discuss their morphologic features and historic distributions. From this work we are able to document the time span of their presence on the Roe Plain, that part of the Nullarbor Plain south of the Hampton Scarp. The species do not show any significant evolutionary changes during these intervals.

Manuscript received 28 July 1999, accepted for publication 15 December 1999.

KEYWORDS: Australia, dentition, Holocene, Leporillus apicalis, Leporillus conditor, Muridae, Nullarbor Plain, Pleistocene, Rodentia.

INTRODUCTION

This report is abstracted from an ongoing study of the rodents from Madura Cave, Part VIII of THE MAMMALIAN FAUNA OF MADURA CAVE. Here we report the presence of both species of the murid rodent genus Leporillus; L. conditor, the greater sticknest rat, or Walpilkara, and L. apicalis, the lesser sticknest rat, or Tchujalpi, Turulpa, Twealpi and show their chronologic distributions within the cave deposits. There are well over 1,700 specimens of L. conditor ranging from the surface, all units between Unit 1, dated at 7,500 BP, to the bottom unit of the deepest trench, Unit 7, dated at 38,000 BP. L. apicalis is much less abundant; 59 specimens were recovered, none from the surface, most (38) from Unit 1 and 21 from the upper part of Unit 2. (15,600 to 22,400 BP).

Madura Cave is located on the Roe Plain, the area on the southern edge of the Nullarbor Plain, six miles south of Madura, 110 miles west of Eucla. A fuller description of the cave is given in Lundelius and Turnbull (1973). The earlier illustrations of the cave map and trench sections are repeated here (Figs. 1–4) to give the reader convenient access to the stratigraphy encountered in each trench.

AGE OF DEPOSITS

Five radiocarbon dates from Trench 4 span a 30,000 year period between 7,470 ± 129 BP (TX 1146) and 37,880 ± 3,500 BP (TX 1143). Two radiocarbon dates from Trench 3 are 15,600 ± 250 BP (TX 1145) from the top of the second unit (red clay) and
LEPORILLUS (RODENTIA: MURIDAE) FROM MADURA CAVE, WA

Figure 1. Map of Madura Cave showing the central doline, the northern and southern tunnels, and the positions of the excavations.

Figure 2. Stratigraphic section exposed in Trench #3.

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Section A-A', Middle Trench, 4.

Figure 3. Stratigraphic section exposed in Trench #4.

Figure 4. Cross section of northern tunnel at Trench #5 showing the stratigraphic section exposed in this trench.
22,400 ± 580 BP (TX 1142) from the bottom of that unit. Correlations with the upper two units in Trenches 3 and 4 and Trench 1 (Lundelius 1963) can be made with reasonable confidence, but no firm correlations can be made for the lower units of the trenches.

MATERIALS AND METHODS

Measurements, abbreviations and statistical and dental terminology are either those in standard use or they are defined where used. Specimen numbers beginning with PM are in the Field Museum of Natural History collection. Specimen numbers beginning with TMM are in the collection of the Texas Memorial Museum, University of Texas. The TMM designation is omitted from the number in the material lists. Measurements of the dentition were taken with a microscope reticle and with micrometer calipers calibrated to .01 mm.

Cusp identifications and homology designations of murid upper molars have not been satisfactorily resolved. Hence it seems best to utilize a simple cusp designation scheme that makes no pretense at implying cusp homologies. Therefore we avoid using the Cope-Osborn scheme, or Vandebroek 1966, Hershkovitz 1971, Engesser 1972 or Jacobs 1977 and instead utilize that of Miller (1912, p. 801) as modified by Misonne (1969, p. 36) and here, so as to eliminate the remaining Cope-Osborn implied homologies. In Miller’s scheme the upper molar cusps are designated by t1 through t9 notations. This gives an unambiguous designation to each major cusp without any implied homology. Further, we follow Michaux’s (1971) and Jacobs’ (1977) use of the term “chevron” for each transverse row of cusps (Fig. 5A, left side).

Most workers have used the Cope-Osborn terminology for the lower molars. We do not consider the implied homologies to be certainties but use the terms rather than introduce new terms which would only add confusion (Fig. 5B and C, center and right). The cusps labeled Prd, Hyd, End and Hyld probably are the Cope-Osborn homologues of protoconid, hypoconid, entoconid and hypoconulid respectively. The homologies of those labeled Pad (paraconid) and Med (metaconid) however are dubious. For example, Misonne used Pad, which he states is more distal than the Prd. However that is the more usual position of the Med. Engesser (1972) uses Med for a cusp that is more mesial than the Prd., i.e. is in the usual Pad position. Our use of these terms is simply as cusp identifiers without any implied homologies. For the variable additional elements we use the designations Misonne employed (following Van de Broek 1966): sm, sl, and sv.

The homology of the cusps of the upper teeth of murids with those of other rodents is uncertain. The terminology used here is that of Miller (1912) as modified by Michaux (1971).

ORDER RODENTIA BOWDICH, 1821:7, 51
FAMILY MURIDAE ILLIGER, 1811:84
SUBFAMILY MURINAE ILLIGER, 1811:84
LEPORILLUS THOMAS 1906:83

Watts and Aslin (1981) gave features of the skull that distinguish Leporillus from other genera of Australian rodents. In addition to size Table 1 summarizes the outstanding cranial and dental differences between L. conditor and L. apicalis.

Leporillus conditor (Sturt 1848)

Most of the hundreds of specimens are fragmentary, and are most likely derived from owl pellets.
Figure 5. Diagrams of murid dentitions (modified from Misonne 1969), showing cusp terminology (modified from Misonne 1969). Upper teeth are shown in A on left, lower teeth in B and C, center and right. Numbers 1–9 indicate the cusps (or tubercles of some authors) of the upper molars, a-lab = anterolabial cusp, a-ling = anterolingual cusp, end = entoconid, hyd = hypoconid, med = metaconid, pcd = postcingulid, and prd = protoconid. For the lower teeth we show different age/wear stages. In B, the younger of the two, a post-cingulid cusp is present (pcd of m1, m2), and in C those cusps have worn away so that their bases are fused with the posterior lophids. For lower teeth, Misonne followed Vandebroek (1966) adding the Cope-Osborne equivalents, a few of which we question (see text).

Table 1.

Size, cranial and dental features that differentiate the species of *Leporillus*.

<table>
<thead>
<tr>
<th>Feature</th>
<th><em>Leporillus apicalis</em></th>
<th><em>Leporillus conditor</em></th>
</tr>
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<tbody>
<tr>
<td>Body size</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>Lower molars, median longitudinal groove</td>
<td>shallow</td>
<td>deep</td>
</tr>
<tr>
<td>m1, anterior lophid</td>
<td>nearly evenly rounded</td>
<td>decidedly V-shaped, opening forwards, sometimes with a central cusp</td>
</tr>
<tr>
<td>m2, posterior (3rd) lophid (chevron)</td>
<td>located in a central position</td>
<td>central, but more tied to lingual end of 2nd lophid</td>
</tr>
<tr>
<td>m3, posterior cuspid</td>
<td>narrow base; does not reach to labial side</td>
<td>base broad; swings to lingual side of tooth</td>
</tr>
<tr>
<td>Posterior loph of M1 and M2</td>
<td>length &amp; width approx. equal</td>
<td>wider than long</td>
</tr>
<tr>
<td>Anterior palatal foramen</td>
<td>ends at front of M1</td>
<td>usually extends to widest part of anterior loph of M1</td>
</tr>
</tbody>
</table>

Position of mental foramen: just at front of masseteric tubercle well anterior to masseteric tubercle

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Material

Surface
2 specimens, a skull in 3 pieces (TMM 41106-28, Fig. 6 A-D); and a left maxilla with M1-3

Trench 1, Unit 1, top 1 foot
Skull
4 partial skulls including PM 6195 (Fig. 7)
Upper dentition
35 left and 35 right specimens with teeth
5 left and 6 right edentulous maxillae
Lower dentition
8 left and 15 right rami with i - m3, including PM 6181 (Fig. 6 E-G)
32 left and 22 right rami with teeth, 1 edentulous right ramus

Trench 1, top 30 inches
Lower dentition
1 left ramus with i, 1 edentulous left ramus

Trench 1, 30 inches below surface
Upper dentition
3 partial right maxillae with teeth
Lower dentition
5 left and 4 right partial rami with teeth

Trench 2, Unit 1, Level 1
Upper dentition
1 right maxilla with M1-3
Lower dentition
1 left and 2 right partial rami with teeth

Trench 2, 2 1/2 feet below surface
Upper dentition
3 right maxillae with teeth, 1 edentulous right maxilla
Lower dentition
2 left and 5 right rami with teeth, 1 edentulous right ramus

Trench 3, Unit unknown
Upper dentition
1 left maxilla with M1

Trench 3, Unit 2, Level unknown
Skull
1 with left and right M1-3, 1 with right M2-3
Upper dentition
94 left and 108 right specimens with teeth, 6 isolated molars
Lower dentition
134 left and 129 right rami with teeth
16 left and 16 right edentulous rami

Trench 3, Unit 2, Level 2
Upper dentition
33 left and 33 right maxillae with teeth, 1 right 1
15 left and 12 right edentulous maxillae
Lower dentition
6 left and 19 right rami with teeth, 2 left and 7 right edentulous rami

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Trench 3, Unit 3
  Upper dentition
    14 left and 22 right maxillae with teeth, 35 edentulous maxillae
  Lower dentition
    13 left and 10 right rami with teeth, 6 edentulous rami

Trench 4, Unit 1, Level 1 (top 1 foot)
  Skull
    1 edentulous, lacking back of braincase
  Upper dentition
    10 left and 9 right maxillae with teeth, 5 edentulous maxillary fragments
  Lower dentition
    21 left and 15 right rami with teeth
    14 left and 9 right edentulous rami

Trench 4, Unit 2, Level 1
  Upper dentition
    24 left and 38 right maxillae with teeth
    6 left and 3 right edentulous maxillae
  Lower dentition
    53 left and 63 right rami with teeth
    4 left and 8 right edentulous rami

Trench 4, Unit 2, Level 1 (Middle Pit, top 6 inches of red)
  Upper dentition
    4 left and 2 right maxillae with teeth, and 2 edentulous left maxillae
  Lower dentition
    8 left and 8 right rami with teeth, 3 edentulous rami

Trench 4, Unit 2, Level 2
  Upper dentition
    22 left and 25 right maxillae with teeth
    10 left and 14 right edentulous maxillae
  Lower dentition
    79 left and 56 right rami with teeth
    12 left and 13 right edentulous rami

Trench 4, Unit 2, Level 3
  Upper dentition
    1 left and 1 right maxillae with teeth, 2 edentulous maxillary fragments
  Lower dentition
    1 left and 8 right rami with teeth, 2 left and 4 right edentulous rami

Trench 4, Unit 4–5
  Upper dentition
    9 left and 16 right maxillae with teeth, 24 edentulous maxillary fragments
  Lower dentition
    6 left and 11 right rami with teeth
    12 left and 11 right edentulous rami

Trench 4, Unit 7, Level 1
  Upper dentition
    2 left and 3 right maxillae with teeth, 1 edentulous maxillary fragment
  Lower dentition
    2 left and 1 right rami with teeth
Figure 6. *Leporillus conditor*. A–D, TMM 41106-28, a nearly complete skull shown in A, anterior; B, left lateral; C, dorsal; and D, ventral stereo views; E–G, PM 6181, left mandibular ramus with I, m1-3 shown in E, left lateral; F, occlusal; and G, lingual views. Scale bars are 2 cm. long. FMNH negative numbers are G 85962-85967.
Figure 7. *Leporillus conditor*. A–D, PM 6195, a nearly complete skull shown in A, anterior; B, dorsal; C, left lateral; and D, ventral stereo views. Scale bars are 2 cm long. FMNH negative numbers are G 85954-85958.
Trench 4, Unit 7, Level 2
Upper dentition
5 left and 14 right maxillae with teeth, 6 edentulous maxillary fragments
Lower dentition
11 left and 8 right rami with teeth, 9 left and 8 right edentulous rami

Trench 4, Unit 7
Upper dentition
2 left and 3 right maxillae with teeth, 6 edentulous right maxillae
Lower dentition
6 left and 3 right rami with teeth, 9 left and 4 right edentulous rami

Trench 5, Lower Red Unit
Upper dentition
5 left and 5 right maxillae with teeth
15 left and 21 right edentulous maxillae
Lower dentition
2 left and 3 right rami with teeth, 9 left and 10 right edentulous rami

Trench 5, Laminated Unit
Upper dentition
1 right maxilla with M1-3, 1 edentulous left maxilla
1 right M1, and 1 left M2

Descriptions

Skull
The skulls have the normal murid form. They have the myomorphous enlargement of the infraorbital foramina for the transmission of a part of the M. maxillomandibularis. It is more oval, less circular than in Rattus norvegicus. There is an enlargement of the anterior face of the zygomatic arch for the origin of the anterior part of the M. masseter, pars profunda. The anterior edge of the zygomatic plate is straight. At its ventral end there is a small tubercle that marks the origin of the M. masseter, pars superficialis and probably also the M. masseter, pars reflexa. There is no spine on the dorsal end. In anterior view the zygomatic plate of L. conditor tends to be relatively broader dorsally rather than in L. apicalis. The anterior part of the zygomatic arch is not broadened as in Notomys.

In dorsal view the interorbital width is narrow compared with the width of the braincase which is expanded laterally. This is true for both species but is more extreme in L. conditor. There are no raised supraorbital ridges on the frontal bone, although it turns ventrally very abruptly to form the medial side of the orbit. The dorsal margin of the area of origin of the M. temporalis closely corresponds to the suture between the parietal and squamosal.

The incisive foramen is large and is located at the front of the palate, immediately posterior to the upper incisors. The anterior palatal foramina are long, extending forward from just posterior to the anterior end of the M1 three fourths of the distance to the upper incisors. They have the shape of long ovals and are about equally contained by the maxillary and premaxillary bones. The median parts of the maxillaries and the premaxillaries are expanded to nearly fill the anterior three fourths of the foramina. The palate has shallow lateral grooves that connect the anterior and posterior palatine foramina. These grooves are separated from the alveoli by a ridge which is especially well defined in younger individuals. The posterior palatal foramina are oval in shape and are located opposite the M2. The post palatine spine is larger than that of Rattus norvegicus.

The cranial foramina are similar in their arrangement to those of Rattus norvegicus. The foramen ovale is about the same size in L. conditor as in R. norvegicus.
and is located low on the outer edge of the entopterygoid fossa (entire pterygoid fossa of some authors). In R. norvegicus the foramen ovale is more inclined upwards anteriorly and is entirely above the entopterygoid fossa. Further, in R. norvegicus there is variation, probably age related, in the extent of its ventral exposure. Musser (1981, p. 235, Fig. 5) shows it to be partly hidden and partly confluent with the median lacerate foramen based on AMNH 207554, while in a Field Museum specimen, FMNH 154733, it is seen to lie anterior to the median lacerate foramen, bridged over and partly obscured by the pterygoid ridge.

The entopterygoid fossa is triangular and shallow but is broader and deeper than in R. norvegicus. It is bordered internally by a more prominent descending internal pterygoid process than in R. norvegicus. This process (entopterygoid crest of some authors) differs from that of R. norvegicus in its larger size and in its sinus development which is lacking in R. norvegicus. On the posterolateral corner of the fossa in R. norvegicus there is a large foramen that joins the foramen ovale dorsally, but in L. conditor the lateral edge of the fossa is anterolateral to the foramen ovale so that the foramen ovale opens first into the fossa, then in a slit-like opening to the anterior lateral face of the alisphenoid. The anterior part of the pterygoid fossa in R. norvegicus is more fenestrated than in L. conditor, with a large interpterygoid (sphenopterygoid) foramen located at the base of the internal pterygoid process. In L. conditor this foramen is small. In the more extended work the cranial foramina are dealt with more extensively.

The optic and sphenopalatine foramina are larger than in Rattus and about equal in size. Tate (1951) reported the same condition in L. jonesi (now synonymized with L. conditor by Watts and Aslin 1981). The orbital portions of both the maxillary and the pre-sphenoid extend farther dorsally than in Rattus. From the Watts and Aslin (1981) figures, the rostrum of L. conditor is broad relative to its length, while that of L. apicalis is narrow (Table 2).

**Mandible**

Mandibles were found articulated with skulls in the Madura Cave deposits. Mandibles were assigned to L. conditor on the basis of size, morphology and comparison with other more complete material from other localities. The mandible is shallowest under m2 and is much deeper posteriorly to the end of the angular process. The ventral border is slightly irregularly concave beneath the molars. The ascending ramus and the angular process are in essentially the same plane. The coronoid process is reduced to a small spine on the anterior edge of the ascending ramus. The condyle is rounded in lateral view and is laterally compressed. There is a low rounded ridge on the lateral surface of the ascending ramus that extends from the condyle into the masseteric fossa where it disappears. The expanded angular process is smoothly rounded ventrally. The posterior margin of the mandible is a smoothly rounded re-entrant extending from the posterior end of the angular process to the condyle. The masseteric ridge extends along the ventral edge of the angular process and ends in a tubercle on the lateral edge of the jaw below the m1 and just posterior to the mental foramen. The small mandibular foramen is well posterior to the m3 just dorsal to a prominent thin ridge that extends posteriorly and upwards from the alveolus of m3 towards the condyle and forms the dorsal edge of the pterygoid fossa. The diastema is about equal in length to that of the lower molar row. The mental foramen lies just anterior to the masseteric tubercle and to the m1.

**Dentition**

The upper incisors are opisthodont and relatively narrow for the size of the skull (Fig. 6). They are so narrow that it is difficult if not impossible to assign isolated incisors to this species or to L. apicalis. The cutting edges are straight and oriented with the lateral end slightly posterior to the medial. The upper incisors of L. conditor are narrower than those of L. apicalis (Table 2).
The upper molars have three antero-posterior rows of cusps with the buccal row significantly smaller than the other two. The teeth are high crowned. The M1 is made up of three transverse rows of cusps termed chevrons by Michaux (1971) and Jacobs (1977). The first chevron is made up of three cusps, with the largest being t2, followed by t3 and t1. The t1 and t3 are located slightly behind the t2. The three cusps of the second chevron are close to the same size. The t4 is located farther posterior to the t5 and is better separated from it than is the t6. The posterior end of the tooth has two cusps, a large centrally located cusp (t8) and a much smaller cusp, the t9, located buccally to it. With wear the buccal cusps join the central cusps before the lingual cusps (Fig. 5A).

The M1 has three roots of subequal size. One is located at the anterior end of the tooth, one at the posterobuccal corner and one lingually at the midpoint of the tooth. The M2 and M3 also have three roots each. Those of the M3 form the apices of an equilateral triangle with the posterior one located at the posterior end of the tooth.

The M2 has six cusps. The t4, t5 and t6 form a well-defined chevron. The centrally located t5 is slightly larger than the other two cusps which are located posterior to it. A t1 is present on the anterolingual corner of the tooth. It is the same size as the t4 and t6 and is well separated from the t5. An incomplete chevron is formed at the posterior end of the tooth by a large t8 and a very small t9 which is not completely separated from the latter.

The M3 has one well-developed chevron made up of t4, t5 and t6. The t5 is the largest followed by the t4 and the t6. The t4 is more separated from the t5 than is the t6, which merges with it soon after wear starts. A t1 is present on the anterolingual corner of the tooth. It is about the diameter of the t5 and is separate from the other cusps to the base of the tooth. The posterior chevron is elliptical in shape and is made up of the joined t8 and t9.

The lower incisor is narrow with the cutting edge gently rounded and oriented at about 60 degrees in the vertical plane to the long axis of the tooth.

As noted above, we do not consider the homologies of the cusps of the lower teeth to be secure, although they are derived from the cricetid plan. Like the upper molars, the lowers are high crowned. The m1 has six main cusps that are arranged in two longitudinal rows. The pairs of cuspids (and associated crests) are joined to form chevrons. The

### Table 2.
Measurements of skull and upper teeth of *Leporillus* (mm).

<table>
<thead>
<tr>
<th></th>
<th><em>Leporillus conditor</em> Madura Cave</th>
<th><em>Leporillus apicalis</em> Webb’s Cave</th>
</tr>
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<tbody>
<tr>
<td>Width of rostrum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>sample size</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
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<td>4.75</td>
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<tr>
<td>range</td>
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<td>4.45-4.90</td>
</tr>
<tr>
<td>Width zygomatic plate</td>
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<tr>
<td>sample size</td>
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<td>5</td>
</tr>
<tr>
<td>mean</td>
<td>8.86</td>
<td>6.96</td>
</tr>
<tr>
<td>range</td>
<td>8.63-8.98</td>
<td>6.80-7.12</td>
</tr>
<tr>
<td>Length M1-3</td>
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<tr>
<td>sample size</td>
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<td>5</td>
</tr>
<tr>
<td>mean</td>
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<tr>
<td>range</td>
<td>8.03-8.18</td>
<td>6.79-7.14</td>
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<tr>
<td>Width upper incisor</td>
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<td>mean</td>
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</tr>
<tr>
<td>range</td>
<td>.783-.957</td>
<td>.986-1.015</td>
</tr>
</tbody>
</table>

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wings of the chevron formed by the anterior pair, the antero-labial and antero-lingual cuspids, project anteriorly. The wings of the other chevrons project posteriorly. A round postcingulid is present between the wings of the posterior chevron. With wear this cusple merges with the hypoconid and entoconid to form a posterior lophid (Fig. 5B, C).

The m2 has four principal cuspids of about equal size that form two chevrons with backward projecting wings. A circular postcingulid is present between the wings of the posterior chevron. As in the m1, this cusple merges with the hypoconid and entoconid with wear to form a posterior lophid.

The m3 has two anterior cuspids, the protoconid and ‘metaconid’, that are joined to form a chevron. The two posterior cuspids, the hypoconid and entoconid, are joined to form an elliptical cusp at the posterior end of the tooth. In both the upper and lower molar series the third molars are equal in width to the first molars, in contrast to *L. api- calis* in which the third molars are narrower than the first molars.

### Table 3.

Statistical data for the lower teeth of *Leporillus conditor* from Madura Cave (mm).

<table>
<thead>
<tr>
<th>STRATIGRAPHIC UNIT</th>
<th>Trench 1 Unit 1</th>
<th>Trench 4 Unit 2</th>
<th>Trench 4 Unit 7</th>
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<tbody>
<tr>
<td><strong>m1-3 Length</strong></td>
<td></td>
<td></td>
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<tr>
<td>Sample size</td>
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<tr>
<td>Mean</td>
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<tr>
<td>Sample size</td>
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<tr>
<td>Mean</td>
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<td>3.71</td>
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<tr>
<td>Standard deviation</td>
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<td>.126</td>
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<td>.191</td>
<td>.199</td>
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<td>Mean</td>
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<td>Standard deviation</td>
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<td>.071</td>
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<td>2.14–2.67</td>
<td>2.18–2.44</td>
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<tr>
<td><strong>m3 Ant. Width</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Sample size</td>
<td>18</td>
<td>14</td>
<td>6</td>
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<td>Mean</td>
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<td>1.98</td>
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<td>.089</td>
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<td>8.198</td>
<td>4.37</td>
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<tr>
<td>Range</td>
<td>1.42–2.29</td>
<td>1.59–2.18</td>
<td>1.89–2.12</td>
</tr>
</tbody>
</table>

*Proc. Linn. Soc. n.s.w.*, 121. 1999
Discussion

Data on the historic distribution of this species have been summarized in maps by Robinson in Strahan (1995), Copley (1999), and Baynes (1979). According to Watts and Aslin (1981) it was widely distributed in southern Australia from the lower Darling River of New South Wales through South Australia into the eastern part of the Nullarbor Plain. Its presence on the Nullarbor Plain of South Australia suggests that it probably was present to the west in Western Australia as well. This is supported by its presence in Holocene deposits from the Nullarbor Plain in Western Australia (Lundelius 1957, 1963; Baynes 1987; Archer 1970, 1974). It is also known from Holocene deposits along the west coast of Western Australia from Jurien Bay to Shark Bay (Baynes 1979) and in the Flinders Ranges of South Australia (Smith 1977). The available information indicates that it was distributed along the southern edge of the arid zone (Copley 1999). Its presence throughout the stratigraphic sequence in Madura Cave demonstrates its presence on the Roe Plain for at least the last 38,000 years. Measurements of the midwidth of M1 and length of M3 show no changes in size over the last 38,000 years (Table 3).

*Leporillus apicalis* (Gould 1853)

Material

Trench 1, Unit 1, Level 1 (top 1 foot)

Upper dentition

3 left, 1 right maxillae with M1-3, including PM 6140, 6146, and 25520 (Fig. 8A-G), 2 left and 1 right maxillae with some teeth

Lower dentition

1 left ramus with i - m3, PM 6185 (Fig. 8H-J), 4 left and 7 right rami with teeth, 1 edentulous ramus fragment

Trench 2, 2 1/2 feet below surface

Lower dentition

3 left, 5 right rami with teeth, 1 incisor

Trench 3, Unit 2, Level 2?

Upper dentition

5 left and 1 right maxillae with teeth, 1 right M2, 2 edentulous right maxillae

Lower dentition

2 rami with m1

Trench 4, Unit 1, Level 1, top 1 foot

Upper dentition

1 left and 1 right maxillae with teeth, 2 edentulous left maxillae

Lower dentition

6 left and 8 right rami with teeth

Trench 4, Unit 2, Level 1, top 1 foot

Upper dentition

1 M2

Descriptions

Skull

The skull of *Leporillus apicalis* differs from that of *Leporillus conditor* mainly in size. Wood Jones (1925) and Watts and Aslin (1981) have stated that the bullae of *Leporillus apicalis* are smaller than those of *Leporillus conditor*. In none of the Madura
Figure 8. *Leporillus apicalis*. A–C, PM 6146, left maxilla with ml–3 shown in A, anterior; B, occlusal; and C, left lateral views. D and E, show PM 25520 a left maxilla with ml–3, and PM 6140 a right maxilla with ml–3 posed together to simulate the appearance of a partial palate. In D they are shown in anterior view and E stereoscopically in ventral view. F, PM 25520 left lateral view; G, PM 6140 right lateral view. H–J, PM 6185, left mandibular ramus with I, ml–3, H, left lateral; 1, occlusal; and J, left lingual views. Scale bar is 2 cm. The FMNH negative numbers are G86189.1–3, G86191.1&.3&.4 for A–G, and G85959-85961 for H–J.
Cave material are these structures preserved, so this feature cannot be determined. The rostrum of *L. apicalis* is narrower than that of *L. conditor*. This is true of the width taken directly over the upper incisor capsules and the width across the tubercles at the base of the zygomatic plate (Table 2). Although the samples are small there is no overlap in the ranges of the two species.

**Dentition**

As in the skulls, *Leporillus apicalis* and *Leporillus conditor* differ in the size of their dentitions. They also differ in that the lower third molars of *Leporillus apicalis* are narrower than the first (Table 4) whereas in *L. conditor* the m3s are about the same width or slightly wider (Table 3). The incisors of *L. apicalis* are broader than those of the larger *L. conditor* (Table 2).

**Table 4.**

Statistical data for measures of *Leporillus apicalis* from Madura Cave (mm).

<table>
<thead>
<tr>
<th>STRATIGRAPHIC LEVEL</th>
<th>Trench 1</th>
<th>Trench 2</th>
<th>Trench 3</th>
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<tr>
<td></td>
<td>Unit 1</td>
<td>Unit 2</td>
<td>Unit 2</td>
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<td>Level 1</td>
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</tr>
<tr>
<td><strong>m1–3 Length</strong></td>
<td></td>
<td></td>
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<tr>
<td>Sample size</td>
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<td>—</td>
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<tr>
<td>Coeff. variation %</td>
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<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Range</td>
<td>6.83–7.25</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>m1 Length</strong></td>
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<tr>
<td>Sample size</td>
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</tr>
<tr>
<td>Mean</td>
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<td>3.11</td>
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</tr>
<tr>
<td>Standard deviation</td>
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<td>.135</td>
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<td>Coeff. variation %</td>
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<td>4.35</td>
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</tr>
<tr>
<td>Range</td>
<td>2.95–3.33</td>
<td>2.90–3.24</td>
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</tr>
<tr>
<td><strong>m1 Mid Width</strong></td>
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<td>Sample size</td>
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<tr>
<td>Mean</td>
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<tr>
<td>Standard deviation</td>
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<td>.094</td>
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<tr>
<td>Coeff. variation %</td>
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<td>Range</td>
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<td>Mean</td>
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<tr>
<td>Standard deviation</td>
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<td>Coeff. variation %</td>
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<td>—</td>
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<tr>
<td>Range</td>
<td>2.088–2.349</td>
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<tr>
<td><strong>m3 Ant. Width</strong></td>
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<tr>
<td>Sample size</td>
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<td>Mean</td>
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<td>Range</td>
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</table>
Discussion

The distribution of this species prior to European settlement is uncertain. According to maps by Robinson in Strahan (1995), and Copley (1999), wild caught specimens are known from a few localities in western New South Wales, southern Northern Territory and northern South Australia. Nests attributed to this species have been found in the eastern part of Western Australia. It is known from Holocene deposits in a number of caves on the Nullarbor Plain (Lundelius 1957, 1963; Archer 1970, 1974;), the Flinders Ranges in South Australia (Smith 1977; McCarthy et al. 1996) and from cave deposits on the west coast of Western Australia (Baynes 1979, 1987). The record from Madura Cave demonstrates that it was an inhabitant of the area around the cave from 22,400 years ago to 7,500 years ago. Its absence from the lower levels (Unit 7) of Pit 4 is problematical. It is possible that its absence is an accident of sampling as the total amount of material recovered from Unit 7 is small.

SUMMARY AND CONCLUSIONS.

Two species of Leporillus, L. conditor and L. apicalis, are represented in Quaternary deposits in Madura Cave. Leporillus conditor is represented by a large amount of material, L. apicalis by much less. Leporillus conditor is found in all stratigraphic levels, spanning a time interval from 38,000 to 7,500 years before present (and from the surface and top levels of this and other Nullarbor caves). Leporillus apicalis is absent from the lowest level and from the surface although it is represented in the top units. Its absence from the lower level may be an accident of sampling as it is much less abundantly represented than L. conditor in all units and the total amount of material from the lowest unit (Unit 7) is small in comparison with the higher units. It could be argued that its absence from the surface is also a sampling accident as it is present in surface deposits in caves on the nearby Nullarbor Plain. However a sampling of the surficial deposits of the Nullarbor Region by Baynes (1987) indicates that there are few records from the Roe Plain. In addition, Boscacci et al. (1987) have demonstrated that the Roe Plain has a somewhat different modern mammal assemblage than the Nullarbor Plain proper.

ACKNOWLEDGMENTS

We thank Dr. Alex Baynes of the Western Australian Museum for allowing access to material, for much information on the distribution of Australian rodents and for helpful comments on the manuscript. We thank Mark Widhelm, Photography Department, Field Museum of Natural History and Lori Grove for help with the illustrations. Judith Lundelius and Hedy Turnbull provided editorial assistance. Support came from the National Science Foundation, the Field Museum of Natural History, and The Geology Foundation, Department of Geological Sciences, The University of Texas at Austin.

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Australian Signal Flies of the Genus *Rhytidortalis* (Diptera: Platystomatidae)

DAVID K. MCALPINE

Australian Museum, 6 College St, Sydney 2000


The genus *Rhytidortalis* Hendel is characterised. The Australian species and the Oriental type species of *Rhytidortalis* are keyed and described. *Rhytidortalis acme*, *R. averni*, *R. browni*, *R. cteis*, *R. kelseyi*, and *R. perforata*, are new species. *Duomyia rugifrons* (Thomson) (from *Senopterina, Rhytidortalis*) and *Duomyia solocifemur* (Enderlein) (from *Pseudepicausta, Rhytidortalis*) are new combinations. Sexual dimorphism in these flies is discussed with reference to its possible biological significance, particularly with regard to pre-mating recognition signals, and compared with sexual dimorphism in other platystomatid flies, particularly species of *Euprosopidia* Macquart.

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INTRODUCTION

The Platystomatidae form a major family of the superfamily Tephritoidea and are one of the five most species-rich families of acalyprate flies in the Australasian Region. There are about 483 valid described species in this Region (Evenhuis 1989; McAlpine 1994, 1995, this publication), and at least 235 additional species have been observed in collections (author’s counts). The present paper treats the small Australian genus *Rhytidortalis* Hendel, which occurs also in the Oriental Region.

The species of *Rhytidortalis*, in common with other small, inconspicuous flies, have not been well collected in many parts of Australia. The apparently endemic Western Australian species *R. acme* and *R. kelseyi* have been collected only once, and no species are known from Victoria. From these facts it can be inferred that additional species are likely to be discovered, and that the known range of the described species is likely to be extended with future collecting.

The term ‘signal flies’ has recently been used as a family-level common name for platystomatids, in reference to the many and diverse morphological and behavioural devices utilised in communication between conspecifics in many genera (see Whittington 1998; McAlpine 1998). One common form of signalling, found also in some other families, consists of the continuous waving of conspicuously marked wings while walking or while stationary. This behaviour is very noticeable in *Cleitamia astro-labei* (Macquart), *Pogonortalis doclea* (Walker), *Lamprogaster* spp., *Lenopilia* spp., *Rivella* spp. etc., and must affect the way the fly is perceived by potential predators, as well as conspecifics. Despite the significance of this family in Old World tropical faunas, no common name is in use for Platystomatidae, perhaps because before about 1950 the family was often merged with the Otitidae (Ulidiidae or picture-winged flies), and because the rarely used name broad-mouthed flies has not been deemed generally applicable.
METHODS

The morphological terms used here are those previously employed by me for platystomatids (McAlpine 1973a), and most are also explained by Harrison (1959) and Crosskey (1973). In addition, the cell-4 index is the ratio of the length of the antepenultimate section of vein 4 to the full length of the discal cell on vein 4. The stigmatal index is the ratio of the length of costa on the subcostal (stigmatal) cell to the length of costa on the marginal cell. Lengths of sections of veins do not include the thickness of those veins bounding measured sections, except that, for practical reasons, length of costa on marginal cell is taken from the distal extremity of the subcostal cell to the distal extremity of the marginal cell. The nomenclature of the thoracic bristles is shown in Fig. 6 below.


The following abbreviations refer to institutions housing specimens:

- **AM**: Australian Museum, Sydney
- **ANIC**: Division of Entomology, CSIRO, Canberra
- **AWA**: Department of Agriculture, Western Australia, South Perth
- **BM**: The Natural History Museum, London
- **MNB**: Museum of Natural Science at Humboldt University, Berlin
- **MNK**: Hungarian Natural History Museum, Budapest
- **NRS**: Naturhistoriska Riksmuseet, Stockholm
- **QM**: Queensland Museum, Brisbane
- **UQ**: University of Queensland Insect Collection, Brisbane
- **USNM**: National Museum of Natural History, Washington
- **WM**: Natural History Museum, Vienna
- **ZMC**: Zoological Museum, Copenhagen

ECOLOGY AND HABITS

Material of *Rhytidortalis* spp. that I have collected has been found in sandy habitats near the sea shore, and label data on most other material appear to support the generally coastal distribution of the genus. *R. averni*, the best known species, is often found at the edge of dune scrub, but this species and *R. perforata* were taken ‘at light’ in the rain forest at Iluka, which borders on sandy coastal scrub. On Nullica Beach, near Eden NSW in November 1997, *R. averni* was found to be abundant on the grass *Spinifex hirsutus* (Poaceae), but was apparently absent on the nearby low (almost prostrate) *Acacia* shrubs to the landward side of the *Spinifex* habitat. These coastal dune habitats are shared with some other platystomatids, including species of *Microepicausta* Hendel, *Rivellia* Robineau-Desvoidy, and some little known species of *Duomyia* Walker. At Buffalo Creek, Darwin, specimens of *R. browni* were collected in a clearing bordering sandy scrub and mangrove. The records of *R. browni* from several inland districts in Queensland indicate that the species is not restricted to coastal habitats.

Many specimens of *Rhytidortalis* spp. have been collected ‘at light’. This indicates at least some nocturnal activity.

In *Rhytidortalis* spp. the wings are folded roof-wise along the abdomen as in cicadas, with their posterior margins uppermost and almost meeting above the median line of the abdomen, when the insect is at rest (McAlpine 1973a and author’s observations). Similar carriage of the wings occurs in *Duomyia, Microepicausta*, and some other platystomatids, and aids group identification of these flies in the field, but comparison of
Figures 1, 2. Antennae of *Rhytidortalis averni*: 1, male; 2, female.

numerous living examples of *R. averni* and *Microepicausta* sp. at Nullica Beach showed that, in the former, the wings are less steeply sloped and slightly more spread. Wing carriage in *R. cteis* is similar to that of *R. averni*. None of the wing-waving, so characteristic of *Rivellia* and *Pogonortalis* spp., was observed in these taxa.

The larval stages of *Rhytidortalis* are unknown.

**SEXUAL DIMORPHISM**

Platystomatid flies of many genera are noted for their sexual dimorphism in numerous external features in addition to that in structures directly concerned with copulation and oviposition. I have described some of these dimorphic features (McAlpine 1973a, 1982, 1994; McAlpine and Kim 1977), and commented on their relation to specific behaviour patterns (McAlpine 1973b, 1975, 1979). Variation in many of these dimorphic structures provides some of the sharpest visible distinctions between closely related species, perhaps because they are often concerned with the signals by which the flies recognize their own species in nature. I have therefore classed some such features as potentially components of specific mating mechanisms, as distinct from isolating mechanisms (McAlpine 1988).

In females of *Rhytidortalis averni*, *R. cteis*, and *R. kelseyi* antennal segment 2 has a comb of relatively long bristles on its inner surface, while the males of these species (male unknown in *R. kelseyi*) have only the usual short setulae on this segment as in both sexes of other known species of *Rhytidortalis* (Figs. 1, 2). The frequently observed damage to setulae and bristles on antennal segment 2 is perhaps caused by probing in attempts to escape from collecting containers. I have no evidence as to any biological significance of the dimorphism.
Figures 3, 4. Left mesopleural region of *Rhytidortalis averni*: 3, male; 4, female.
In those species of *Rhytidortalis* for which both sexes are known, antennal segment 3 is larger in males than in females. In these males the paired antennal grooves are more capacious than in the females, as an obvious adaptation to accommodate the antennae. The enlargement of the groove is generally associated with a narrowing of the facial carina and parafacial which flank the groove.

Similar sexual dimorphism in the size of antennal segment 3 occurs in a number of taxa of Platystomatinae, including some species of *Duomyia* Walker, *Euprosopina* Macquart, and *Microepiecausta* Hendel. The biological significance of the dimorphism is not established. It may be that the enlarged male antenna has increased olfactory ability which could be of importance in females, if they produce a sex pheromone. There could thus be a parallel with saturniid and other moths, which have an elaborate male antenna whereby the pheromone-producing female is detected at a distance (summary in Common 1990). Antennal segment 3 in *Euprosopina anostigma* McAlpine has a very complex array of sensilla on its surface (McAlpine 1973a, figs 109, 110) some of which are likely to be olfactory as in *Drosophila* spp. (Begg and Hogben 1946).

Greater size or complexity (the latter increasing the surface area) of antennal segment 3 in males of schizophoran flies, as compared with females, occurs in taxa of several families. It is particularly notable in some taxa of Tachinidae (Wood 1987) and in the Axiniidae (Colless 1994). Wood indicates that tachinid species in which males do not rely on vision to find females (species having no sexual dimorphism in eye size) have the third antennal segment (not ‘third flagellomere’ — Wood’s lapsus) of the male longer or more complex than that of the female. He infers that, in these species, males use their antennae rather than their eyes in recognizing a potential mate.

In *Rhytidortalis averti* and related species most major bristles on the thorax are significantly longer in males than in females. *R. averti* has the hairing on the humeral callus longer in the male than the female, and there is a smaller degree of difference in length in some other species of *Rhytidortalis*. The mesopleuron and pteropleuron of male *R. averti* have fine to moderately fine pale hairs of moderate length (Fig. 3). In the female most of the mesopleural hairs are extremely short so that the basal sockets are often as conspicuous as the hairs (Fig. 4). The pteropleural hairs of the female are mostly converted into short, stout, black setulae.

In *Rhytidortalis cteis*, the female shows similar shortening of the humeral hairs to that sex of *R. averti*, but the macrotrichia of the mesopleuron and most of those of the pteropleuron are stout, moderately short, and black. The male is essentially similar to that of *R. averti* and most other *Rhytidortalis* species in these features, and only the female shows these modifications that are characteristic of this species.

Previously (McAlpine 1973a) I have recorded sexual dimorphism of thoracic vestiture in certain species of *Euprosopina*, which resembles to a certain extent that here recorded for *Rhytidortalis* spp. The particular modifications of the female thorax recorded include, inter alia, reduction of the humeral bristle and hairing, reduction or other modification of the notopleural bristles, reduction of mesopleural hairs to minute stumps, and reduction of bristling on the fore femur. As in some *Rhytidortalis*, the precise manifestation of the female modification can provide very decisive criteria for specific identification in this sex.

The wing of *R. cteis* shows sexual dimorphism in length of vein 6 and in microtrichiation, as described under that species. Similar sexual dimorphism does not appear to be recorded in other platystomatids.

The female of *R. cribrata* has a pleural sclerite of variable size on each side of abdominal segment 4 (see Fig. 24 below), but there is no such sclerite in the male of this species or in either sex of any other known *Rhytidortalis* species. Abdominal pleural sclerites are present in a few very specialised flies (e.g. the family Braulidae) but are absent in most families of Schizophora. Among platystomatid flies, the female of an undescribed species of *Duomyia* (‘sp. 19’ in AM) has a large pleural sclerite in the vicin-
ity of segments 3 and 4 (probably absent in the unknown male), and, in females only of some species of the taxonomically unelucidated group of species near *Euprosopia impingo*

 gens* (Walker), there is a sclerite or subsclerotised zone in the region of segment 4.

Remarkable differences in the position of the female preabdominal spiracles (particularly those of segments 3 to 5) exist between the six species of *Rhytidortalis* for which the female is known (see Figs 17, 18, 21, 22, and 26 below), with the exception of the pair *R. cteis* and *R. kelseyi*, which are remarkably similar in this respect. There is also some specific difference in the shape of tergites 3 to 5 round which or on which the spiracles are situated. Diversity of a similar kind to that in *Rhytidortalis* occurs among species of the platystomatine genera *Microepicausta* Hendel, *Plagiostenopterina* Hendel, *Rivellia* Robineau-Desvoidy, *Senopterina* Macquart, and *Euprosopia* Macquart, and is particularly great in the last (McAlpine 1973a and further unpublished examples). In the males of these taxa, the spiracles appear to be consistently in the presumed plesiomorphic position in the pleural membrane below the lateral margins of their respective tergites. However, in both sexes the abdominal spiracles are often undetectable in dried specimens because of shrinkage and infolding of the cuticle, so that relevant data are still incomplete for many species.

In seeking a reason for similar patterns of variation in placement of female abdominal spiracles in different platystomatine genera, I incline towards the hypothesis of their functioning as specific recognition marks during courtship (elements of specific mating mechanisms). The possibility that males of *Rhytidortalis* and other genera are, through their antennal development, adapted to detect female pheromones, has already been mentioned. The abdominal spiracles of females would often appear appropriate for exhalation of gaseous pheromones, particularly when located on or near the dorsal surface, as is the case in so many platystomatine species. The marked specific differences in position of the spiracles could themselves contribute to specific recognition by the males at close range.

Courtship behaviour in *Rhytidortalis* is unrecorded. In both *Euprosopia tenuicornis* Macquart and *E. anostigma* McAlpine there is tapping or probing on the female abdomen by the male before mounting (McAlpine 1973b), but this is performed with the male fore tarsi or proboscis, not the antenna, according to the recorded observations. In both these *Euprosopia* species there is significant difference between the sexes in size of antennal segment 3, but the difference is less than in *Rhytidortalis* species. Females of *E. tenuicornis* and *E. anostigma* have the spiracles of segments 4 and 5 more or less dorsal in position (readily accessible from above).

In *Euprosopia subula* McAlpine antennal segment 3 is of similar size in both sexes, but the male has the palpus significantly larger. The female has the spiracles of segments 4 and 5 conspicuously dorsal in position. While under observation, this species (McAlpine 1973b) showed no premating probing of the female abdomen by the male, though there was contact between the sexes for up to 30 minutes before mounting. However, the male mounted the female from behind.

The above observations indicate that the connection between sexual dimorphism and behaviour in platystomatids should be a fertile field for future research.

Conventional cladistic reasoning, with its heavy reliance on parsimony, might treat as plesiomorphic the condition of the female spiracles present in *Rhytidortalis perforata* (see Fig. 21 below), which is most like that of *Rhytidortalis* males, and which must also resemble that of the female of early ancestral platystomatids. On the other hand interspecific variability in position of female abdominal spiracles occurs in numerous other genera of Platystomatidae as indicated above. Therefore it is probable that this kind of variation is a quite ancient feature of platystomatid evolution, and that present diversity (for instance in *Rhytidortalis* spp.) is the result of numerous sequential diversification processes. Hence there is no assurance that the male-like arrangement of female abdominal spiracles is the plesiomorphic state within any modern group of species, as the occur-
rence of numbers of cycles of diversification is likely to have involved numbers of reversals of character polarity. A similar argument applied to other secondary sexual modifications and to variation in male genitalia suggests that restraint should be observed in using these characters for reconstructing phylogenies.

SYSTEMATIC TREATMENT

Genus Rhytidortalis Hendel

Rhytidortalis Hendel 1914a: 14, 66–68. Type species R. cribrata Hendel (original designation).

Description

Head compact, slightly wider than high, usually obliquely squarish in lateral aspect, and usually angular in profile at junction of postfrons and face; postfrons almost smooth to coarsely rugose-pitted; cheek region with strongly raised but not sharp oblique ridge; lateral arm of ptillinal fissure long; parafacial with fine hairs (socket-based macrotrichia) near middle, in addition to pruinosence (microtrichia); median facial carina strongly raised, but not sharply margin, face thus usually very broadly visible in front of antennal groove in profile; the following bristles present: inner and outer ventrals, divergent postvertical, usually 2 pairs of small fronto-orbitals, small ocellar, sometimes a lateral occipital and a small postgenal. Antenna: segment 1 very short; segment 2 short, dorsally cleft, not convexly cap-shaped; segment 3 long, usually potentially reaching to or beyond median point of lower margin of face, generally larger in male; arista apparently bare under moderate magnification, but sometimes with very minute decumbent pubescence on basal swelling of segment 6. Prelabrum reduced, not prominent, not joined medially to lower margin of face by a well developed shining quadratic sclerite (rudimentary such sclerite visible in R. acme); palpus of moderate size, compressed.

Thorax elongate (compared with typical Rivellia spp.), almost parallel-sided, with largely blackish ground colour; mesoscutum about 1.2 to 1.3 times as long as wide, extensively pale grey-pruinose, with numerous bare black dots, each of which surrounds the base of a hair, without long, dense hairing-bristling in prescutellar area; scutellum rounded, longer than a semicircle, thinly grey pruinose, without setae; sternopleuron with pale-pruinose, ventral zone, or more extensively pruinose; suprasquamous ridge with short pubescence/pruinosence and no longer hairs or setae; prothorax trapezoid, setulose, isolated from propleura; metathoracic postcoxal bridge absent; the following thoracic bristles present (see Fig. 6): humeral, 1+1 notopleurals, 1+1 or 1+0 or 0+0 supra-alar (i.e. there is a supra-alar close behind transverse suture, unless supra-alars are altogether absent), postalar (on postalar callus), intra-alar, sometimes a variably developed bristle approximating in position to a presumeral, dorsocentral, prescutellar acrostichal, usually 3 pairs of scutellars, all long and inserted near margin (only 2 pairs in R. acme), well developed mesopleural; scapular and sternopleural bristles absent. Legs moderately short; fore coxa rather short and broad; femora not remarkably thickened; fore femur with long posteroverentral bristles and shorter dorsal bristles, at least in males; mid femur with long posterior hairs/bristles, more distal ones becoming more bristle-like and uniseriate; hind femur sometimes with distinct seriate anteroventral bristles; mid tibia with one large apical ventral spur; tarsi entirely yellow to tawny orange, or with one or more segments partly browned; hind tarsus somewhat depressed and often slightly broadened. Wing moderately elongate, with predominantly yellow veins and often yellow subcostal cell, usually without other markings (apical brown spot present in submarginal cell in R. cribrata); membrane entirely or predominantly microtrichose (least so in R. averni); section of costa on subcostal cell shorter than that on marginal...
cell; vein 2 nearly straight; veins 3 and 4 slightly divergent to almost parallel apically; second section of vein 4 with slightly concave curvature, dipping into discal cell, its third (penultimate) section longer than discal crossvein; anal cell distinctly broader than second costal cell, less than half as long as discal cell; squama forming a small, distinct lobe, no larger than axillary lobe. Capitellum of halter pale yellowish.

Abdomen ovoid, not attenuated anteriorly; tergites 4 and 5 as large as tergite 3 or almost so in both sexes. Male postabdomen: surstyli rather short, distal section of outer one short and rounded, without notable modifications; preglands of aedeagus forming short, convex, well defined sclerite, separated from stipe by a membranous collar; glans stoutly ovoid; paired terminal filaments fused basally, not or only slightly longer than glans; cerci moderately large, joined to proctiger for most of their length. Female postabdomen: spiracles of segment 5 situated near posterolateral angles of tergite 5 (which may be rounded), or (in R. averni) approximated dorsomedially within posterior margin of tergite 5; tergite 6 very small, usually concealed below tergite 5; tergosternite 7 (ovipositor sheath) not noticeably longer than tergite 3; aculeus slender distally, obtuse, not compressed.
Notes

As here defined *Rhytidortalis* includes seven easily recognised species: the type species *R. cribrata* Hendel from Southeast Asia and six newly described Australian species. There is also evidence of an additional species, ‘sp. 7’, inadequately known for formal description. Distribution of these species is shown in Fig. 5.

Evenhuis (1989) listed the following three species of *Rhytidortalis* for the Australasian region: *R. conformis* (Walker), *R. rugifrons* (Thomson), and *R. solocifemur* (Enderlein). The two latter are here placed in *Duomyia* Walker (see below). The species originally described as *Ortalis conformis* Walker, 1853, was referred with doubt to *Rhytidortalis* by Hendel (1914a,b) on the basis of the original description. This description of a damaged specimen from Van Dieman’s Land (Tasmania) is too brief to indicate the taxonomic position of the species, though it could refer to a platystomatid. Walker does not mention the mesoscutal colour pattern, which is diagnostic in *Rhytidortalis*, but gives the wing veins as black, which is in disagreement with this genus. I treat *Ortalis conformis* as a nomen dubium, as I have not found the type. Designation of a neotype is not permissible under Article 75 of ICZN, as the name is not in current use for a recognised species.

*Rhytidortalis* belongs in the subfamily Platystomatinae as defined by McAlpine (1973a). Within the subfamily, it most resembles the genera *Scotinosoma* Loew and, to some extent, *Pseudepicausta* Hendel and *Duomyia*. The species of *Rhytidortalis* have a consistent condition not found in these other genera, viz. the extensive grey pruinescence on the mesoscutum penetrated by a black dot at the base of each hair. This is apparently a synapomorphy for these species and could be an indicator of monophyly, if there is no other taxon derived from within the genus which has lost the condition.

Another unusual condition of *Rhytidortalis* species is the presence of two pairs of supra-alar bristles — an anterior and a posterior bristle on each side, the 1+1 condition (Fig. 6, sa). This condition is not absolutely consistent in *Rhytidortalis*, as supra-alar

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Figure 6. *Rhytidortalis averni*, female, dorsolateral view of thorax showing nomenclature of bristles. ac, prescutellar acrostichal. dc, dorsocentral. h, humeral. ia, intra-alar. m, mesopleural. n, notopleural (2 pairs). pa, postalar. prs, presutural. sa, supra-alar (2 pairs). scl, scutellar (3 pairs).
bristles are absent in *R. browni*, only the anterior one is present in *R. cteis* (1+0 condition), and occasional specimens of *R. perforata* have only the posterior bristle present (0+1 condition). The outgroups to *Rhytidortalis* (e.g. the genus *Scotinosoma*) generally have only one supra-alar bristle which appears to be homologous with the posterior one in *Rhytidortalis* (i.e. 0+1 condition, which occurs in *Rhytidortalis* only as an infrequent variant). Some *Duomyia* species are also without supra-alar bristles, but this is a convergent condition with *R. browni* and certainly not a synapomorphy. The presence of an anterior supra-alar bristle may be a groundplan condition for *Rhytidortalis*, but occurrence of the condition in a very few species of *Duomyia* and *Scotinosoma* prevents its being classed as a primal autapomorphy for the former genus.

*Rhytidortalis* differs from most other elongate, *Senopterina*-like Australasian platystomatines (the tribe *Stenopterininia* of Hendel 1914a, e.g. *Scotinosoma*, *Microepicausta, Elassogaster, Plagiostenopterina* Hendel, the vast majority of *Duomyia* species) in the presence of hairs near the centre of the parafacial. In this character, however, *Rhytidortalis* resembles *Pseudepicausta*. Australasian species of the latter genus differ from *Rhytidortalis* in the broad, little elevated facial carina and other features of head shape, absence of the characteristic mesoscutal pattern of *Rhytidortalis*, the more elongate hind basitarsus, the presence of brown wing markings, the smaller alula, and the very long ovipositor sheath.

Other unifying character states for *Rhytidortalis* include the heavy oblique cheek ridge, and the features of the aedeagus, in particular the quite separate sclerotisation of the preglands from the stipe, the small, compact glans, and remarkably short terminal filaments. It is difficult to determine to what extent these characters involve autapomorphies for the genus.

The southern African genus *Sphenoprosopa* Loew has a superficial resemblance to *Rhytidortalis* which is enhanced by the black spotting on grey-pruinsect cuticle, though this coloration is not restricted to the mesoscutum in the former. In both genera the prelabrum is much reduced. *Sphenoprosopa* differs from *Rhytidortalis* in having the anterior and discal crossveins approximated, the anal cell narrower, and the wing with heavy dark markings. Hendel (1914a) thought that *Sphenoprosopa* was related to *Platystoma*, because of its habitus, while Enderlein (1922) placed it in the tribe *Plastoptephritinae*. The latter opinion is certainly erroneous, but my own brief study of material (at MNB in 1973) led me to think that relationship with *Rhytidortalis* is more probable.

Two species recently referred to *Rhytidortalis* (e.g. in McAlpine 1973a; Evenhuis 1989) are *Duomyia rugifrons* (Thomson) and *Duomyia solocifemur* (Enderlein) n. combs., both from New South Wales. These lack the significant diagnostic features of *Rhytidortalis* discussed above, and I have given careful consideration as to whether they and two or more undescribed species from south-western Australia should constitute a small new genus, perhaps closely related to *Rhytidortalis* and *Scotinosoma*. *D. rugifrons* and *D. solocifemur* differ from more typical *Duomyia* spp. in having the squama relatively small, the suprasquamal ridge without a group of somewhat elongate erect hairs, the facial carina rounded and not prominently margined, a shining quadrate sclerite present between face and prelabrum, the mesopleural bristle usually distinct, the mid femur without distinct posterior bristles distally (though it has relatively long posterior hairs), the distal section of vein 4 apically not curved forward nor converging with vein 3. However, the southwestern species of the *D. rugifrons* alliance are not consistent in some of these characters, and *D. solocifemur* has the squama about as large as that of a few species previously included in *Duomyia* s.str. (e.g. *D. capitalis* McAlpine). Several species accepted as *Duomyia*, e.g. *D. capitalis* McAlpine, *D. parallela* McAlpine, and *D. adelaidae* McAlpine, show various combinations of characters resembling those of the *D. rugifrons* alliance, but appear to be related to other species, e.g. *D. iris* McAlpine, which are reasonably typical *Duomyia* spp. Perhaps the only consistent feature in which the *Duomyia rugifrons* group differs from the rest of the genus is the absence, in the for-
mer, of the group of erect hairs on the supersquamal ridge. We thus have a large genus *Duomyia* (about 100 species now known to me), which shows a wider range of morphological variation than previously recorded (McAlpine, 1973a), and does not appear easily divisible into smaller natural groupings.

The known species of *Rhytidortalis*, except for the oriental *R. cribrata*, are apparent Australian endemics. As *R. browni* has a wide distribution in far northern Australia, it would not be surprising if it were found to occur outside Australian limits.

**Key to species of *Rhytidortalis***

1 Scutellum with only two pairs of bristles, both located near its apex; sternopleuron almost entirely grey-pruinose; Western Australia .............................................. *acme*
   – Scutellum with three pairs of bristles, the foremost much closer to scutellar suture than to apex; sternopleuron with large subshining brown-black zone .......................... *2*

2 Fore coxa and all femora and tibiae yellow; supra-alar bristles absent; Queensland and Northern Territory ............................................. *browni*
   – Fore coxa and all femora and tibiae partly or extensively brown to blackish; one or two supra-alar bristles present between postalar bristle and transverse suture ............. *3*

3 Wing with brown spot filling apex of submarginal cell; female: abdominal segment 4 with pair of sclerotised pleural plates; Southeast Asia .............................................. *cribrata*
   – Wing without apical spot; female: segment 4 without pleural plates; Australia .......... *4*

4 Wing margin without distinct incision at end of vein 5; black markings of mesoscutum consisting mainly of minute dots at bases of hairs; ♀: setulae on medial surface of antennal segment 2 not enlarged, all much shorter than segment 2; setulae on mesopleuron nearly all pale, only moderately short; New South Wales, southern Queensland................................................................. *perforata*
   – Wing margin with distinct incision at end of vein 5; black markings of mesoscutum consisting of many larger spots, sometimes merging, the diameter of each mostly greater that distance between spots (except in *R. kelseyi*); ♀ (unknown in *R. sp.7*): antennal segment 2 with some enlarged setulae on medial surface as long as segment (Fig. 2); setulae on mesopleuron variable, but generally not as above ........ *5*

5 Males (unknown in *R. kelseyi*) ................................................................. *6*
   – Females (unknown in sp.7) ................................................................. *8*

6 Anal cell bare, except at base; fore tarsus tawny, with at most faint brown suffusion; New South Wales, Tasmania, South Australia ............................................. *averni*
   – Anal cell microtrichose, at least on extensive anterior zone; fore tarsus variably pigmented ................................................................. *7*

7 Fore tarsus brown, except for paler basal part of segment 1; fore femur with all posteroventral bristles black; anal cell bare on central zone; South Australia, Western Australia ............................................. *ceis*
   – Fore tarsus entirely fulvous; fore femur with mixed pale and dark posteroventral bristles; anal cell microtrichose on whole width; Western Australia .......... *sp. 7*

8 Fore femur with several long posteroventral bristles; anal cell largely bare; setulae on mesopleuron pale, minute (Fig. 4); spiracles of abdominal segment 5 located within posterior margin of tergite, thus readily visible in dorsal view (see Fig. 13 below); New South Wales, Tasmania, South Australia ............................................. *averni*
   – Fore femur with posteroventral bristles short or vestigial; anal cell entirely microtrichose; setulae on mesopleuron coarse, black; spiracles of segment 5 located at margin of tergite or in membrane, usually concealed in dried specimens .......... *9*
9 Distal section of vein 6 traceable almost to margin, though gradually weakened distally; thickened basal section of costa with fine black setulae and a ventral brush of longer whitish setulae; fore femur without posterior and posteroventral bristles, with only few minute hairs in their place; tergite 5 with all setulae quite small; Western Australia .............................................................. kelseyi

– Distal section of vein 6 abruptly discontinued about halfway to margin; thickened basal section of costa with short rather coarse black setulae only; fore femur with few short, spinescent posteroventral bristles and numerous spinescent posterior bristles; tergite 5 with group of enlarged black setulae on each side; South Australia, Western Australia .............................................................. cteis

**Rhytidortalis acme** n.sp.
(Figs 7–9)

**Material examined**

**Holotype.** ♂ (unique), Western Australia: Mount Claremont, Perth, 10.iv.1968, I.F.C., M.S.U. (ANIC).

**Description (♂; ♀ unknown)**

Agreeing with that of *R. averni*, except as indicated below.

**Coloration.** Ground colour of head much less extensively darkened on occiput than in *R. averni*, but this region similarly covered with grey pruinescence. Prelabrum brown to tawny. Thorax with slightly bronze-tinted reflections; scutellum with round smooth shining black mid-dorsal zone; pale grey pruinescence on mesoscutum thick and extensive, extending almost to pronotum, but less evenly distributed than in *R. averni* and similar species, the black spots relatively small, more crowded on pair of paramedian longitudinal bands, but not coalescing in linear series; pleura almost uniformly grey-pruinescent except as follows: narrow shining blackish vertical mark and bronzy subshining posterior zone on mesopleuron, subshining dark brony mark on sternopleuron just below sternopleural suture. Fore coxa fulvous-yellow, with the usual shining pruinescence; fore basitarsus fulvous basally, brown on about apical fifth, other segments fused with brown; posterior hairs and bristles on mid femur nearly all yellow. Wing: veins yellowish brown, i.e. distinctly darker than in *R. averni* and most other species. Halter pale yellow. All preabdominal tergites extensively but not completely grey-pruinescent; many hairs on tergites 4 and 5 with dark dot at base.

**Head** in profile not angular at junction of postfrons and face; vertex more rounded off than in other species; postfrons coarsely rugose-pitted; facial carina less elevated than in other species, less attenuated between antennal sockets, somewhat depressed slightly above epistomal margin, with shallow median sulcus near middle; outer vertical bristle not more than half as long as inner vertical; anterior fronto-orbital bristle very small. Antennal segment 2 with setulae on inner surface numerous, quite short.

**Thorax.** Presutural bristle absent; other thoracic bristles, including both supra-alars, quite large; scutellum with only two pairs of bristles, apical pair and a slightly shorter subapical pair placed well behind mid-length of scutellum; humeral callus and mesopleuron with numerous fairly long whitish hairs; pteropleuron with long hairs — white ones posteriorly and black ones anteriorly. Wing: veins 3 and 4 more strongly divergent apically than in other species; second section of vein 4 (before anterior crossvein) more strongly curved than in other species; basal crossvein oblique, making posterobasal angle of discal cell remarkably acute; anal crossvein straight, almost transverse; bases of submarginal and discal cells, about distal two thirds of first basal cell, and almost whole of second basal and anal cells bare.
Figures 7–9. *Rhytidortalis acme*: 7, wing; 8, scutellum; 9, distal part of aedeagus, scale = 0.4 mm. c, membranous caecum. f, terminal filament (paired). g, glans. pg, preglans. st, stipe.

**Abdomen.** Tergite 5 with posterior marginal series of bristles; epandrium with dorsal hairs; surstyli not examined; glans without distinct distal lobe; each terminal filament about 1.0 times as long as glans; a slender membranous caecum arising between filaments.

**Dimensions.** Total length 3.8 mm; length of thorax 2.6 mm; length of wing 5.8 mm; length of glans of aedeagus 0.32 mm.

**Distribution.** Western Australia — near Perth. Map reference 2L (Fig. 5).

**Notes.**

*R. acme* is morphologically the least typical species of *Rhytidortalis*. In addition to the characters given in the key, it has the head much less angular and the facial carina less broadly visible in profile than in other species, the contour of the second section of vein 4 is distinctive, and the terminal filament of the aedeagus is as long as the glans. On the other hand, the carina on the cheek is very oblique, the mesopleural bristle is large, there are two supra-alar bristles, the mesoscutum is extensively spotted, the anal cell is rather broad distally, the squama is scarcely larger than the axillary lobe, and the aedeagus has the glans small and ovoid and has a distinct convex sclerite distad of the
preglands. Because of this combination of characters, I place the species in *Rhytidortalis*, but there is a possibility that it forms a sister group to the rest of the genus.

The specific epithet is a Greek noun meaning ‘apex’, in reference to the apical position of the scutellar bristles.

*Rhytidortalis averni* n.sp.

(Figs 1–4, 6, 10–17)

Material examined


Paratypes. Tasmania: 18 ♂, 27 ♀, same data as holotype (AM, BM, USNM); 3 ♂, 3 ♀, Badger Beach, Asbestos Range National Park, 4.i.1988, A.D., G.D. (AM); 1 ♂, 1 ♀, Poole, via Gladstone, 1.i.1988, A.D., G.D. (AM); 1 ♂, 1 ♀, Stumpy’s Beach, Mount William National Park, 21.i.1992, A.D., G.D. (AM); 1 ♂, 2 ♀, 1 mile (about 1.6 km) N of Scamander, 18.i.1948, Key, Carne, and Kerr (ANIC); 1 ♀, Henty’s Dunes, N of Strahan, i.1992, A.D., G.D. (UQ).

Other material. New South Wales: Iluka, (near) Clarence River (AM); Red Rock, near Woolgoolga (AM); Bundagen, Coffs Harbour district (AM); Tucker’s Rock, near Repton (AM); North Beach, Bellinger River (AM); Snapper Beach, near Urunga (AM); Woy Woy (ANIC); North Cronulla (AM); Broulee, Moruya district (ANIC); Ocean Beach, Merimbula (AM); Nullica Beach, near Eden (AM, BPB, CNC, MNM, NRS, UQ, ZMC). South Australia: Long Gully and Little Dip, Robe district (AM).

Description (♂, ♀)

Coloration. Head orange-fulvous in ground colour, becoming blackish on occiput; following zones silvery-grey pruinescent: almost entire occiput, broad fronto-orbital band extending on to upper and posterior part of parafacial, lining of antennal groove, postgenal region. Antennal segments 1 and 2 orange-fulvous; segment 3 brownish-grey pruinescent. Prelabrum brown-black; palpus orange-fulvous. Thorax with almost entirely black to brown-black ground colour with green to yellow-green tinted reflections where cuticle is exposed; humeral callus, notopleuron, scutellum, and most of mesoscutum pale grey pruinescent, most of latter with pattern of numerous black spots, each surrounding base of hair; spots on dorsocentral line and a few intradorsocentral spots tending to coalesce into longitudinal black lines; much of propleuron, less than upper half of mesopleuron, much of pteropleuron, pleurotergite, and hypopleuron, and lower paramedian part of sternopleuron grey-pruinescent. Coxae fulvous with some brown suffusion and grey pruinescence; fore coxa with dense pale pruinescence on anterior surface, giving silvery sheen in anterior aspect; femora brown-black, narrowly fulvous apically; tibiae brown black, usually narrowly fulvous at each end; tarsi fulvous-yellow, usually with little or no brownish suffusion. Wing without dark markings. Halter tawny to yellowish. Abdomen largely black and non-pruinescent; tergites largely shining, with yellow-green tinted reflections; tergite 1 and part of tergite 2 with thin grey pruinescence; tergites 3 to 5 not grey-pruinescent on lateral margins.

Head squarish in profile, outline of face meeting that of postfrons approximately at a right angle; facial carina narrow, especially so above, in male with median sulcus for most of length, in female rugose on lower part, with less developed median sulcus; outer vertical bristle nearly as long as inner vertical; usually two short fronto-orbital bristles present. Antennal segment 2 in male with only quite short setulae, in female with several enlarged setulae on inner part of distal margin some of which are usually about as long as segment 2; segment 3 almost as long as antennal groove in female, fully as long as groove in male, though the groove itself is longer in male.
Figures 10–11. *Rhytidortalis averni*: 10, wing, showing distribution of microtrichia; 11, head of female.

**Thorax.** Major bristles generally longer in male than in female; presutural bristle ranging from large to vestigal in both sexes; both anterior and posterior supra-alar bristles present; humeral callus in male with numerous fine pale hairs of moderate length, in female with hairs relatively short and inconspicuous; mesopleuron in male with numerous moderately long, fine, rather pale hairs, in female with hairs minute and often less conspicuous than their basal sockets; pteropleuron in male with moderately long and fine hairs, some yellowish and some black, in female with short thick black setulae and few fine, pale hairs. Fore femur with a series of long posteroventral bristles in both sexes. Wing: margin strongly incised at end of vein 5; anal cell wider near its distal end than second basal cell; anal crossvein oblique, but curved through most of its length; vein 6 in both sexes traceable to margin, but unpigmented distally; all of anal cell, except for small basal zone, and much of distal part of first basal cell bare; rest of wing membrane almost entirely microtrichose.
Abdomen. Male: tergites 3 to 5 with mostly moderately short hairs, not forming specialised groups; spiracles 1–3 and 5 in pleural membrane below lateral margins of tergites; spiracle 4 placed on posterior margin of tergite 4 just above posterolateral angle; epandrium with dorsal setulae, some nearly as long as epandrium; outer surstylus as long as epandrium, broad, obtuse, its apex only slightly exceeding that of inner surstylus; glans of aedeagus with very small distal lobe; terminal filament about 0.85 as long as glans. Female: tergites 4 and 5 with moderately short hairs on central parts, giving way to very short, rather fine, not remarkably crowded hairs on lateral parts, without stouter or more crowded lateral

setulae; pleural sclerites absent; spiracles 1 and 2 in pleural membrane below lateral margins of their tergites; spiracle 3 on posterior margin of tergite 3, closer to lateral margin of tergite than to median line (Fig. 17); spiracle 4 just within posterior margin of tergite 4, much closer to median line than to lateral margin; spiracles 5 closely approximated middorsally within posterior margin of tergite 5 (thus generally easily visible in dried specimens); spiracles of segment 6 moderately approximated on posterior margin of tergite 6.

**Dimensions.** Total length, ♂ 4.0–4.8 mm, ♀ 4.2–5.5 mm; length of thorax, ♂ 1.6–2.1 mm, ♀ 1.9–2.6 mm; length of wing, ♂ 4.0–4.4 mm, ♀ 4.4–5.8 mm; length of glans of aedeagus 0.25–0.27 mm.

**Distribution**

New South Wales — widely distributed in coastal districts; Tasmania — coasts generally; South Australia — south-east coast. The absence of records from Victoria probably indicates a gap in collecting effort. Map reference 14O, 17R, 18Q, 18R, 19O, 19Q, 20M, 20N (Fig. 5).
Notes

*R. averni* is distinguished from other species of *Rhytidortalis*, except *R. acme*, by the largely bare anal cell, but differs from *R. acme* in having three pairs of scutellar bristles, the head subquadrate in profile, and the anal crossvein very oblique. It agrees only with *R. cteis* and *R. kelseyi* in having enlarged setulae on antennal segment 2 of the female. The position of spiracle 5 in the female is apparently unique (Fig. 17), and, unlike that of other species, it is easily visible in dried specimens (female of *R. acme* and sp. 7 unknown). Separation of the males of *R. averni* from those of *R. cteis* can be difficult, and is discussed under the latter species.

The specific epithet refers to Geoffrey Avern in recognition of his help with electron microscopy in this and numerous other projects.

*Rhytidortalis* sp. 7

Material examined


Description

In the absence of females, naming and formal description of this species are deferred.

Notes

The available males very probably represent a distinct species, but as specific differences are generally much smaller in males of this group than in females, and because, in the related species *R. kelseyi*, only the female is known, I refrain from naming the species at present.

The male of sp. 7 resembles that of *R. cteis* in many characters, including shape of head and markings on the mesoscutum. It differs in the entirely fulvous foretarsus, in having some or most of the posteroventral bristles of the fore femur pale (yellowish brown to whitish), and in having the anal cell microtrichose on its entire width. It differs from the male of *R. averni* in having some of the posteroventral bristles on fore femur pale, in the entirely microtrichose anal cell, and in having the anal crossvein much less oblique and more curved. I do not think these males represent the other sex of *R. kelseyi* (known only from the female), because the pattern on the mesoscutum is different, and the head is not much prolonged in front of the eye or rostrate as in that species. Also, the genoparafacial region of sp. 7 has an oblique rounded ridge, as in *R. averni* and *R. cteis*, whereas in *R. kelseyi* this region is anteriorly almost planate, and the postgenal region is simply convex.

*Rhytidortalis cteis* n.sp.

(Figs. 18, 19)

Material examined


Paratypes. South Australia: 1 ♂, 1 ♀, same data as holotype (AM, ANIC).

Other material: Western Australia: 187 km E of Esperance (AWA); Conspicuous
Cliff, S of Normalup (AM); Long Point, 9 mi (about 14 km) SW of Walpole (AM); Crystal Springs, 7 mi (about 11 km) W of Walpole (AM); Canal Rocks, near Yallingup (AM); Meelup Beach, near Dunsborough (AM, ANIC, USNM).

Description (♂, ♀)

Agreeing with that of R. averni, except as indicated below.

Coloration. Thorax with green to bronzy tinted reflections; mesoscutum with black spots on intradorsocentral zone with stronger tendency to form longitudinal series than in R. averni; mesopleuron with grey pruinose generally extending well below middle, on posterior margin extending below centre and often almost to sternopleural suture. Fore coxa largely or entirely dark brown, with extensive grey pruinosecence; tarsi usually with extensive brown suffusion, generally fulvous basally.

Head. Facial carina with median sulcus on most of length in both sexes.

Thorax. Presutural bristle distinct in male, usually short or poorly differentiated in female; humeral callus extensively haired in male, distinctly haired only on anterior part in female; mesopleuron in male with extensive long, fine hairing, in female with numerous short, thick, black setulae, absent from most of anterior part; pteropleuron, in female only, with most hairs reduced to short, thick black setulae. Fore femur with long posteroventral bristles in male, but these quite short and spinescent in female. Wing with marginal notch at end of vein 5 shallower than in R. averni, but more distinct than in R. perforata; distal section of vein 6 extending to margin or almost so in male, abruptly discontinued about halfway to margin in female; anal cell entirely microtrichose in female, more or less bare in centre but microtrichose anteriorly along vein 5 and posteriorly near vein 6 in male.

Abdomen. Male: approximately as described for R. averni; terminal filament of aedeagus about 0.74x as long as glans. Female: tergite 4 with many long black hairs on central part; tergite 5 moderately haired in centre, laterally with rather dense, moderately long, coarse black hairs; spiracle of segment 4 placed just within posterior margin of tergite 4 at about three quarters distance from median line to lateral margin of tergite; spiracle 5 placed at (not within) posterior margin of tergite 5 and much closer to lateral margin than to median line; spiracle 6 more laterally placed that in R. averni.

Dimensions. Total length, ♂ 3.8 mm, ♀ 3.7–5.1 mm; length of thorax, ♂ 1.9 mm, ♀ 1.6–2.4 mm; length of wing, ♂ 4.0 mm, ♀ 3.8–5.1 mm; length of glans of aedeagus 0.31 mm (range for specimens from Western Australia 0.26–0.30 mm).

Distribution

South Australia — Kangaroo Island; Western Australia — southern coasts, as far north as Geographe Bay. Map reference 2M, 6M, 3N, 13N (Fig. 5).

Notes

Females of R. cteis are easily distinguished from those of other species of Rhytidortalis by the shortened vein 6 and from species other than R. kelseyi by the black spinescent setulae on the mesopleuron. They share with R. averni the same, unusual modification of the antenna, but have the posteroventral bristles of the fore femur quite short, the anal cell entirely microtrichose, and abdominal spiracle 5 differently situated. None of the above characters is available for determination of males, because of an unusual degree of sexual dimorphism in R. cteis.

The most reliable character for distinguishing males of R. cteis from those of R. averni is the extent of microtrichiation in the anal cell. In R. cteis there is a broad tract of microtrichia along the full length of the anterior margin of the anal cell near vein 5 as well
as a variable tract near or behind the middle of this cell. In males of *R. averni* microtrichia are restricted to the base of the anal cell. Also, the extent of the pale pruinosecence on the mesopleuron of *R. cteis* is greater than in *R. averni*, as described above, but the pruinosecence is sometimes abraded in carelessly handled specimens. The tarsi of *R. cteis* are generally darker than those of *R. averni*, except at their bases.

Differences in the aedeagi of the two species are slight. Also males of *R. cteis* show a stronger tendency for the thoracic intradorsocentral black spots to be arranged in longitudinal series, have usually a slightly narrower scutellum, and average a greater extent of microtrichiation in the distal part of the first basal cell than in *R. averni*. However, these differences are not sufficiently constant for reliable determination.

The available data suggest an east-west separation in the distributions of *R. averni* and *R. cteis* at about 138° E longitude.

The specific epithet is a Greek noun meaning a comb, in reference to the armature of antennal segment 2 in the female.
Material examined

**Holotype**. ♀ (unique), Western Australia; Arrowsmith River, 20 km N of Eneabba, on heath, 13.x.1981, L.P.K. (ANIC).

**Description** (♂; ♀ unknown)

Agreeing with that of *R. averni*, except as indicated below.

**Coloration.** Palpus fulvous, lightly browned distally. Mesoscutum with numerous black non-pruinescent spots which are mostly much smaller than in *R. averni* and *R. cteis*, only very few of them coalescing, not tending to form longitudinal lines, those near centre of mesoscutum largest. Tarsi fulvous basally, lightly browned on distal segments, not as dark as in *R. cteis*. Halter tawny.

**Head.** More elongate and produced at bases of antennae than in *R. averni* and *R. cteis*; facial carina with narrow median sulcus, not rugose; outer vertical bristle about as long as inner vertical; eye markedly higher than long. Antennal segment 2 with two enlarged setulae on medial surface.

**Thorax.** Mesoscutal setulae markedly smaller than in female of *R. cteis*, more as in *R. averni*; dorsocentral and prescutellar acrostichal bristles smaller than in female of *R. cteis*, at least as small as in female of *R. averni*; humeral bristle vestigial; presutural and anterior supra-alar bristles absent; mesopleuron and pteropleuron with all setulae moderately short, thick and black, approximately as in *R. cteis*. Fore femur with no bristles, and with setulae reduced to minute hairs, all except a few dorsal ones much smaller than...
setulae on fore tibia. Wing: thickened basal section of costa with fine black setulae and a ventral brush of longer, whitish setulae; anal crossvein curved, less oblique than in *R. averni*; vein 6 traceable approximately to margin; marginal, submarginal, and second basal cells with bare basal zones; first basal cell with extensive bare zones; anal cell almost entirely microtrichose, with small bare zone near base.

**Abdomen.** Tergites 4 and 5 with almost uniformly short fine hairs, the latter tergite considerably shorter; positions of spiracles 3, 4, and 5 approximately as in *R. cteis* (see Fig. 18).

**Dimensions.** total length 5.0 mm; length of thorax 2.2 mm; length of wing 4.6 mm.

**Distribution**

Western Australia – temperate west coast. Map reference 2K (Fig. 5).

**Notes**

Although it is desirable that the male be made known, the unique female type provides good evidence of the distinction of this species. The head is more prolonged in front of the eyes (as viewed in profile) than in other species (except the shallow-eyed *R. brownii*), and the greatly reduced armature of the fore femur is unique in the genus. Judging from sexual dimorphism in *R. cteis*, I think the latter character is unlikely to be available for distinguishing males, as are the other characters used in my key.

The specific epithet refers to L.P. Kelsey, who collected the holotype and much other interesting material now in ANIC.

*Rhytidortalis perforata* n.sp.

(Fig. 21)

**Material examined**


**Description (♂, ♀)**

Agreeing with that of *R. averni*, except as indicated below.

**Coloration.** Thorax with yellow-green to bronzy reflections; black spots of mesoscutum numerous and small, not tending to coalesce into lines, diameter of each spot in general much smaller than distance between spots. Fore tibia often paler than that of *R. averni*, but variable; tarsi often lightly browned distally.

**Head** less nearly square than in *R. averni*, because of its shorter ventral outline; facial carina with median sulcus not more distinct in male than in female. Antennal segment 2 with only quite short setulae in both sexes.

**Thorax.** Presutural bristle usually distinguishable; anterior intra-alar bristle usually present, sometimes reduced; posterior intra-alar consistently present; humeral callus with hairing about as well developed in female as in male, usually including a number of black
hairs; mesopleuron on central part less smooth and glossy than in *R. averni*, with minute sculpturing and/or dark pruinose; in male fine, pale mesopleural hairs much as in *R. averni*, in female hairs similar to but slightly shorter than those of male; pteropleuron in male with moderately long, fine mostly pale hairs, in female with mostly shorter mixed black and pale hairs. Wing: margin not incised at end of vein 5; anal crossvein curved, usually less oblique than in *R. averni*; first basal and anal cells entirely microtrichose.

**Abdomen.** Male: preabdomen resembling that of *R. averni*; epandrium with somewhat shorter dorsal setae than that of *R. averni*; outer surstylus gibbous anterobasally; glans with prominent distal lobe; length of terminal filament about 0.8 of length of glans. Female: hairs on tergites 4 and 5 not becoming remarkably short, thickened, or crowded on lateral parts, a few of those near posterolateral angle of tergite 5 longer and bristle-like; spiracles 3, 4 and 5 all situated in pleural membrane below posterior part of lateral margins of tergites; spiracle 6 situated at posterior side of lateral extremity of tergite.

**Dimensions.** Total length, ♂ 4.4–5.1 mm, ♀ 4.5–4.9 mm; length of thorax, ♂ 1.8–2.1 mm, ♀ 2.1 mm; length of wing, ♂ 3.7–4.5 mm, ♀ 4.5–4.7 mm; length of glans (without distal lobe), 0.22 mm.

**Distribution.**

Queensland — southern coast, Bribie and Stradbroke Islands; New South Wales — coastal districts. Map reference 20N, 21J, 21K, 21M (Fig. 5).

**Notes**

*R. perforata* differs from the other species of *Rhytidortalis* in the much smaller black spotting on the mesoscutum. It differs from *R. averni* in its microtrichose anal cell. The female also differs from those of *R. averni, R. kelseyi* and *R. cteis* in the absence of enlarged setulae on antennal segment 2 and the moderately fine hairing of the mesopleuron. This is the only species of *Rhytidortalis* known to have the spiracles of abdominal segment 3, 4, and 5 all situated in the pleural membrane below the lateral margins of tergites in the female (Fig. 21), but this sex is unknown in *R. acme* and sp. 7.

The name *perforata* is a Latin adjective, referring to the small perforations in the covering of pale pruinose of the mesoscutum.

*Rhytidortalis browni* n.sp.

(Figs. 22, 23)

**Material examined**


Other material. Northern Territory: 3 ♀, Buffalo Creek. Darwin. (AM, NTM); 7 ♂, 1 ♀, Horn Islet, Sir Edward Pellew Group (AM, UQ). Queensland: 2 ♂, Kennedy River, 30 km W of ‘Fairview’, Laura district (UQ); 2 ♂, 1 ♀, Laura River, Kennedy Creek junction, Laura district (UQ); Mount Moffat, via Carnarvon Ra (QM); 1 ♀, 5 km N of Leyburn (AM).

**Description** (♂, ♀)

Agreeing with that of *R. averni*, except as indicated below.

**Coloration.** Occipital region with large brown-black zone on each side, not concealed by pale pruinose. Prelabrum usually orange-fulvous. Mesoscutum with black spots smaller than in *R. averni*, some coalescing on dorsocentral lines; only upper part of
humeral callus grey-pruinescent, about lower half shining to subshining brown-black; posterior notopleural callus fulvous to brown, pruinescent; mesopleuron with small grey-pruinescent zone on upper margin only. Legs entirely fulvous-yellow; fore coxa with very slight silvery sheen. Abdominal tergites 3–5 without grey pruinescent markings.

Head less nearly square in profile than in *R. averni* because of its more rounded ventral outline; facial carina with median sulcus in both sexes; fronto-orbital and postvertical bristles minute. Antennal segment 2 with setulae on medial surface all small in both sexes.
Figures 24–26. Rhytidortalis cribrata: 24, distal part of aedeagus of lectotype (scale = 0.25 mm); 25, left lateral parts of segment 4 of female, including median sternite 4; 26, diagram of segments 3 to 6 of female abdomen. p, pleural sclerite. s4, sternite 4. t3, t6, tergites 3 and 6. t4, margin of tergite 4.

Thorax. Presutural and supra-alar bristles absent; humeral callus with few hairs in male, with shorter hairs in female; in female posterior sternopleural longer than anterior one and strongly curved; mesopleuron with hairs only slightly shorter in female than in male; pteropleuron with relatively few short, fine yellow hairs in both sexes. Wing: anal crossvein strongly curved, its general direction less oblique than in R. averni; first basal and anal cells entirely microtrichose.

Abdomen. Male: tergite 5 with posterior marginal series of bristles; outer surstylus somewhat gibbous basally; glans with prominent distal lobe; length of terminal filament about 0.85 of that of glans. Female: tergites 4 and 5 with numerous moderately short hairs not becoming shorter on sides; tergite 5 with hairs not denser laterally, but with several posterior marginal bristles; spiracle of segment 3 placed at summit of deep lateral incision in tergite 3; spiracle of segment 4 placed well within anterior part of lateral margin of tergite 4; spiracle 5 placed in pleural membrane below anterior part of lateral margin of tergite 5; spiracle 6 near posterior margin of tergite 6, well removed from median line.

Dimensions. Total length, ♂ 4.1–4.9 mm, ♀ 3.8–4.3 mm; length of thorax, ♂ 1.6–2.0 mm, ♀ 1.7–1.8 mm, length of wing, ♂ 3.4–3.9 mm, ♀ 3.5–3.7 mm; length of glans of aedeagus (without distal lobe) 0.23–0.24 mm.

Distribution

Queensland — northern and southern districts, inland ranges and coast; Northern Territory — Darwin district and Sir Edward Pellew Group. This is the only species of Rhytidortalis known from the Australian tropics. Map reference 10C, 13D, 16D, 17D, 19I, 20H, 20J (Fig. 5).

Notes

R. browni differs form other species of Rhytidortalis in the absence of supra-alar bristles and the entirely pale legs. In the female, the posterior notopleural bristle is longer.
and strongly curved, and spiracles 3 to 5 are situated much further forward than in other species for which this sex is adequately known; the position of spiracle 3 is very distinctive (Fig. 22).

The specific epithet refers to Graham R. Brown, who greatly assisted the author’s field work in Northern Territory.

*Rhytidortalis cribrata* Hendel

(Figs 24–26)


**Material examined**

Lectotype (here designated). ♂, Taiwan (Formosa): Takao, ‘1907.vi.20’ (i.e. 20.vi.1907), H. Sauter (WM). Aedeagus extended.

Paralectoty pes. Taiwan: 1 ♀, Takao, 23.vi.1907, H. Sauter (WM). There are also 6 specimens of this species labelled ‘typus’ in MNM, but, as Hendel’s type series included only four specimens, I cannot determine which of these are genuine types.

**Other material.** Taiwan: Takao (AM). Vietnam: Namo Beach, Quang Nam Province (AM).

**Description (♂, ♀)**

The following notes supplement the description of Hendel (1914b).

**Coloration** generally resembling that of *R. averni*. Wing: apical dark brown spot in submarginal cell extending slightly over veins 2 and 3.

**Head.** Chaetotaxy as in *R. averni*. Antennal segment 2 without specially enlarged setae in female.

**Thorax.** Chaetotaxy generally as in *R. averni*; presutural bristle similarly variable; hairs or setae on humeral callus moderately developed in both sexes; mesopleuron with numerous moderately long, mainly dark hairs in both sexes; pteropleuron with moderately long, mainly dark hairs, apparently not showing much sexual dimorphism. Wing: anal crossvein strongly curved, its general direction only slightly oblique; first basal, second basal, and anal cells entirely microtrichose.

**Abdomen.** Male: spiracles not observed; postabdominal parts resembling those of *R. averni*; glans with large distal lobe. Female: tergites 4 and 5 normally haired, hairs not particularly shortened on sides; segment 4 with rather variable transversely grooved sclerite on each side; spiracle 3 in pleural membrane below anterior part of lateral margin of tergite 3; spiracle 4 immediately behind posterolateral angle of tergite 4; spiracle 5 similarly situated in relation to tergite 5, but a little more removed from posterolateral angle; spiracle 6 behind lateral part of tergite 6.

**Dimensions.** Length of glans of aedeagus (lectotype) 0.25 mm.

**Distribution**

Taiwan. Vietnam: coast of Quang Nam Province.

**Notes**

This Oriental species is the only species of *Rhytidortalis* yet known from outside Australia. Its morphology generally resembles that of Australian species, the most outstanding differences being the possession of an apical wing-spot and, in the female, of a pleural sclerite on abdominal segment 4. The size of the pleural sclerite and number of grooves are remarkably variable, but, as this variation is apparent even among the female topotypes, it does not seem to indicate specific heterogeneity, and may be age-related.
Hendel (1914a) first published the name *Rhytidotalis cribrata* without formal description, but (1) gave illustrations of the head and wing, and (2) included in his detailed generic description mention of several features in which *R. cribrata* differs from the other included species. Both these actions constitute indications under Article 12 of the ICZN for making available the name *R. cribrata*, and the type series consists of all specimens on which these actions were based. The only locality given was 'Formosa'.

Hendel (1914b) gave a description of *R. cribrata* n.sp., which is not technically the original description, as the name was already available. He listed the material as '4 ♂ ♀ aus Formosa, Takao, Juni und August, leg. Sauter, im Ungar. Nationalmuseum', i.e. MNM. As this work was prepared more or less simultaneously with that containing the original publication of the name *R. cribrata*, I regard it as giving the best available evidence as to what material was before the author at the time, i.e. the syntypic series. Other specimens collected by Sauter in Taiwan are therefore not considered to be types. The fact that the lectotype and paralectotype (both subsequently labelled 'paratype') are in Hendel's own institutional collection, WM, and not in MNM, simply means that he retained half the type series at WM.

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REFERENCES


The Occurrence and Distribution of the Tube-nosed Insectivorous Bat (Murina florium) in Australia

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A comparison of specimens (n=14) of the Tube-nosed Insectivorous bat, Murina florium, from the wet tropics (15°30'–19°20'S) and an outlying specimen from Cape York Peninsula, suggests that a single species exists in Australia. A total of 26 localities have been identified using capture records and acoustic detection (echolocation and social calls). Sites occur between 60–1120 m above sea level, in rainforest or wet sclerophyll forests. A common feature at each site, or in close proximity (within 4 km), is the presence of mixed wet sclerophyll forest or a close structural equivalent. BIOCLIM modelling was used to describe the climate variation between sites and predict a distribution. The climate profile suggests that M. florium prefers forested areas with the following key parameters (annual average); precipitation 1852 mm (range 1197–2574 mm), rainfall in the driest period 39 mm (range 20–59 mm), temperature range of 17.7°C (range 13.9–19.0°C), maximum temperature of the warmest period 28.6°C (range 27.3–31°C). The predicted distribution of M. florium in the wet tropics is restricted to a relatively narrow, elongated band running approximately north-south. It corresponds to regions with a steep rainfall gradient, largely on the western side of mountainous areas and several plateaus, and encompasses the upland wet sclerophyll forests.

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KEYWORDS: Australia, bats, BIOCLIM, capture, climate, distribution, echolocation call, ecotone, Murina florium, rainforest, social call, tube-nosed insectivorous bat, wet sclerophyll, wet tropics.

INTRODUCTION

The microchiropteran bat Murina florium was described originally from a specimen collected on the Isle of Flores in Indonesia by A.R. Wallace (Thomas 1908). Subsequently, M. florium has been found on numerous islands, largely to the east of Wallace’s Line, as far as Papua New Guinea but records are sparse (Laurie and Hill 1954; Hill 1983; Koopman and Danforth 1989; Corbet and Hill 1992; Koopman 1993; Flannery 1995a, 1995b). M. florium was not discovered in Australia until 73 years after its description, when it was captured on Mount Baldy (17°17’S 145°25’E) at the western edge of the Atherton Tableland in north Queensland, during a national survey of rare and endangered bats sponsored by the World Wildlife Fund (Richards et al. 1982; Hall 1983). Then a few years later in 1986, a second locality was found nearby at Mt. Hypipamee National Park, from bats captured along a walking track (G.A. Hoye, pers. comm.; see Winter 1991). Unfortunately with only two known sites, Nix and Switzer (1991) were
unable to predict the distribution of *M. florium* through climate modelling. Despite this problem, it was speculated that the species may be restricted to high altitudes such as “misty, mountainous, tropical rainforest” (Richards 1983), thereby evading capture by inhabiting areas hitherto rarely sampled for bats. A single *Murina* specimen was collected near sea level at Iron Range (12°40'S 143°21'E) in 1983 (Queensland Museum Specimen No. JM4423, collectors S. Flavel, M. Adams and C.H.S. Watts), and although not identified formally as *M. florium*, it possibly belongs to the subspecies *M. f. lanosa* (Hill and Rozendaal 1989).

The paucity of records for *M. florium*, and its perceived rarity, initially resulted in a conservation status of ‘critically endangered’ within the boundaries of the Wet Tropics World Heritage Area (WTWHA), from recommendations to a regional action plan (Nias et al. 1993). However, the number of records for this species have increased significantly over the last decade or so (Spencer et al. 1992; Clague et al. 1995; Kutt and Burnett 1995; Whybird 1996; Schulz and Hannah 1996) due to focussed interest in the bat fauna of the Australian wet tropics, and the refinement of capture and observational techniques (Clague 1998; 2000). As a consequence, *M. florium* has now an IUCN conservation rating of Lower Risk, near threatened (for definition, see IUCN 1994) in the recently published Action Plan for Australian Bats (Duncan et al. 1999).

The number of capture records for *M. florium* in the wet tropics region (as defined by Nix and Switzer 1991) has now reached a point where it is useful to compare the data for specimens and the biogeography of collecting localities. The aim of this paper is to present new data on the occurrence of *M. florium* in Australia, and to re-assess existing records in order to describe the known distribution. In addition, any habitat preferences for the species have been examined, and the bioclimatic modelling program BIOCLIM has been used to generate a climate profile and hence a map of predicted distribution.

**METHODS**

**Records of Murina florium**

Records of *M. florium* were obtained from museum specimens (Queensland Museum and Australian Museum), external measurements taken, and where possible details relating to the collecting locality (Table 1). Additional records were obtained by personal communication with collectors or by reference to the literature and unpublished reports.

New observations reported here were obtained from general bat surveys carried out by the authors in the Wet Tropics World Heritage Area (WTWHA) through Project Gondwana (Clague et al. 1995) and as a result of other research projects in the region (Clague 1998). Data collected during these studies were obtained from bat capture using conventional harp traps and mist nets, and by acoustic survey methods. In the latter case, the echolocation call of *M. florium* and its species specific ‘audible’ social call have been recorded and analysed in detail (Coles et al. 1998). Both of these vocalisations can be used to identify individual bats flying and foraging at night, and positive observations (from the analysis of tape recordings) have been used to provide ‘acoustic detection’ sites, in addition to ‘capture’ sites (listed in Table 2).

**Site localities and vegetation**

All sites recorded for *M. florium* in Australia were visited during this study, to establish or confirm the precise location by grid reference and altitude, using satellite positioning (GPS) and topographic map sheets. The biogeography was described for new sites established in this study and, if necessary, re-assessed for the existing sites (Table 3).
Table 1.

External measurements of *Murina florium* specimens from Australia, Papua New Guinea (PNG) and Indonesia (Indo). Sources: Australian Museum M, Queensland Museum JM, British Museum BM, Rijksmuseum Leiden RMNH; 1 Schulz and Hannah (1996), 2 Kutt and Burnett (1995), 3 specimen measured before loss, 4 G.A. Hoyle pers. comm., 5 holotype *M. f. florium* (Thomas 1908). See Table 2 for details of Australian localities and site No. For other localities see 6 Hill (1983); 7 Hill and Rozendaal (1989); 8 Flannery (1995a); 9 Flannery (1995b). Abbreviations: forearm FA, humerus Hum, thumb Th, 3rd metacarpal mc3, femur Fem, tibia Tib, hindfoot HF, head-body HB, head-body-tail HBT, ear EL, tragus Tr; measurements in mm, weight (Wt) in g.

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<td></td>
</tr>
</tbody>
</table>

¹ released, ² released without measurements, ³ released without sex, ⁴ released without age, ⁵ released without notes, ⁶ released without details, ⁷ released without comments, ⁸ released without additional information, ⁹ released without observations, ¹⁰ released without records, ¹¹ released without particulars, ¹² released without information, ¹³ released without remarks, ¹⁴ released without specifications.
A description of the vegetation types at each site was based on Tracey (1982), and the wet sclerophyll vegetation types were defined by Harrington and Sanderson (1994) criteria, as shown in Tables 3 and 4.

Climate analysis and predicted distribution

An Arcview 3.1 (Environmental Systems Research Institute, Inc., http://www.esri-au.com.au) emulation of the predictive climate modelling program BIOCLIM (Busby 1986), was used to predict the distribution of potential *M. florium* habitat. Climate surfaces were generated, using the ESOCLIM module of ANUCLIM (http://cres20.anu.edu.au/software/anuclim.html) and a Digital Elevation Model (DEM) with a resolution of approximately 250 m. The model was run for a region extending between 15°30’-19°20’S and 144°20’-147°00’E. This area encompasses the ‘wet tropics’ and the WTWHA as illustrated by Nix and Switzer (1991).

A maximum of 35 bioclimatic parameters can be used for a BIOCLIM analysis (see http://cres20.anu.edu.au/software/anuclim.html) and these are created from the climate surfaces output by ESOCLIM. The model was run for all 35 climate parameters (see Table 5) and a grid surface representing each parameter was generated for the region of interest (illustrated in Fig. 1) in order to predict the distribution of *M. florium*. Previous BIOCLIM modelling for the distribution of vertebrates the same region (Nix and Switzer 1991) suggests that there are several important rainfall and temperature parameters determining forest structure in the wet tropics. On this basis, a subset of seven parameters were selected (see Table 5) and also used to predict the distribution for *M. florium* (see Figs 1 and 2).

The complete wet tropics data set comprised 25 discrete records where individuals of *M. florium* have been either captured (n=11) or detected by acoustical monitoring (n=14) at a given locality (Table 2). Using the seven selected bioclimatic grid surfaces (parameters listed in Table 5), the distribution of *M. florium* was modelled for all localities (Fig.1), capture records only (Fig. 2a) or observations by acoustic detection only (Fig. 2b).

In the present study, each modelled distribution (Figs 1 and 2) represents the total area of grid cells that are common to all of the selected climate parameters and all of the sites. The range in value for each climate parameter generated by the DEM, across all sites used in this study, produces the complete climate profile for *M. florium* (Table 5).

The single capture site at Iron Range on Cape York Peninsula (Table 2) was regarded as an outlier for the purposes of the current BIOCLIM analysis and will be treated separately. This approach is prudent as, at present, all other known records for *M. florium* are confined to a circumscribed region in the wet tropics (see Table 2 and Fig.1) which appears to be a core of its distribution in Australia.

RESULTS

External morphology

Table 1 summarises the measurements available for a range of morphological characters obtained from 14 specimens captured in Australia and nominated as *Murina florium*. A complete set of measurements is not available for all specimens due to variation in the source of the material (identified in Table 1). From the data available, all specimens conform to the key diagnostic characters of the genus *Murina* by having extended tube-like nostrils and a pelage with relatively long woolly fur, including an extension of hair onto the uropatagium especially and the wing membranes, and a relatively long thumb (Richards 1983; Koopman 1993; Richards et al. 1995; Churchill 1998). The fur colour of
Table 2.

Australian localities for Murina florium based on 25 sites in the wet tropics and a single site on Cape York Peninsula (Iron Range), identified by the nearest named feature. The type of record (Rec.) at each site is capture (c) or acoustic detection by echolocation call or social call (a). Altitude in metres (m) above sea level.

<table>
<thead>
<tr>
<th>No.</th>
<th>Site name</th>
<th>Rec</th>
<th>Latitude degrees S</th>
<th>Longitude degrees E</th>
<th>altitude (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Shipton’s Flat</td>
<td>c</td>
<td>15°46’</td>
<td>145°13’</td>
<td>245</td>
</tr>
<tr>
<td>2</td>
<td>Gap Creek</td>
<td>c</td>
<td>15°48’</td>
<td>145°19’</td>
<td>245</td>
</tr>
<tr>
<td>3</td>
<td>Mt. Windsor Tableland</td>
<td>a</td>
<td>16°17’</td>
<td>145°05’</td>
<td>840</td>
</tr>
<tr>
<td>4</td>
<td>Mt. Carbine Tableland</td>
<td>a</td>
<td>16°27’</td>
<td>145°11’</td>
<td>914</td>
</tr>
<tr>
<td>5</td>
<td>Gordonvale</td>
<td>a</td>
<td>16°57’</td>
<td>145°49’</td>
<td>70</td>
</tr>
<tr>
<td>6</td>
<td>Chalumbin–Woree</td>
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<td>16°58’</td>
<td>145°39’</td>
<td>650</td>
</tr>
<tr>
<td>7</td>
<td>Mt. Baldy</td>
<td>c</td>
<td>17°16’</td>
<td>145°25’</td>
<td>1090</td>
</tr>
<tr>
<td>8</td>
<td>Mt. Baldy</td>
<td>a</td>
<td>17°16’</td>
<td>145°25’</td>
<td>1000</td>
</tr>
<tr>
<td>9</td>
<td>Mt. Baldy</td>
<td>c</td>
<td>17°16’</td>
<td>145°25’</td>
<td>1120</td>
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<tr>
<td>10</td>
<td>Mt. Baldy</td>
<td>c</td>
<td>17°19’</td>
<td>145°26’</td>
<td>1100</td>
</tr>
<tr>
<td>11</td>
<td>Mt. Baldy</td>
<td>a</td>
<td>17°19’</td>
<td>145°24’</td>
<td>1100</td>
</tr>
<tr>
<td>12</td>
<td>Mt. Baldy</td>
<td>a</td>
<td>17°19’</td>
<td>145°24’</td>
<td>1080</td>
</tr>
<tr>
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<td>Moomin</td>
<td>a</td>
<td>17°22’</td>
<td>145°26’</td>
<td>1060</td>
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<tr>
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<td>Tinaroo</td>
<td>a</td>
<td>17°22’</td>
<td>145°35’</td>
<td>850</td>
</tr>
<tr>
<td>15</td>
<td>Mt. Hypipamee</td>
<td>c</td>
<td>17°25’</td>
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<td>Mt. Fisher</td>
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<td>Mt. Fisher</td>
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<td>145°35’</td>
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<td>17°43’</td>
<td>145°31’</td>
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<td>145°32’</td>
<td>762</td>
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<td>17°51’</td>
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<td>145°33’</td>
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<td>Dalrymple Gap</td>
<td>a</td>
<td>18°23’</td>
<td>146°04’</td>
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<td>145°47’</td>
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<td>19°01’</td>
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<td>c</td>
<td>12°40’</td>
<td>143°20’</td>
<td>60</td>
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Australian *M. florium* ranges from russet brown to grey in living specimens, but preservation in alcohol makes it difficult to determine accurately. Living specimens have been noted to have fawn to bronze fur dorsally, and bicoloured fur with a black base and grey tips on the ventral surface (see also Schulz and Hannah 1996). The uropatagium is always hairy but the hairs vary in density between individuals, having a golden brown appearance.

The most complete measurements (Table 1) yield the following average values for *M. florium* specimens from the wet tropics region of Australia: forearm length 34.7 mm,
### Table 3.

Vegetation description for 26 *Murina florium* sites (listed in Table 2). Forest type is based on the classifications of Tracey (1982) and Harrington and Sanderson (1994) where possible. Otherwise, an equivalent (equiv.) forest type, and/or distance to the nearest Harrington and Sanderson (1994) forest type is indicated. Harrington and Sanderson (1994) forest types were assessed for each site in this study. For Tracey (1982) descriptions, the source references (Ref.) are: 1, this study; 2, Richards et al. 1982; 3, Spencer et al. 1992; 4, Kutt and Burnett 1995; 5, Schulz and Hannah 1996, 1998 (description varies, see text); 6, Kutt and Williams unpublished record; 7, Whybird 1996; 8, M. McLaughlin pers. comm.; 9, J. Clarkson pers. comm. See Table 4 for summary.

<table>
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<tr>
<th>No.</th>
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<th>Vegetation Description</th>
<th>Tracey 1982</th>
<th>Ref.</th>
<th>Harrington and Sanderson 1994</th>
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<tr>
<td>1</td>
<td>Shipton’s Flat</td>
<td>Complex notophyll vine forest [Type 5b], near open <em>Eucalyptus tesselaris</em> forest [cf Type 16h]</td>
<td>3</td>
<td>3</td>
<td>&lt;1 km from Type 4 equiv.</td>
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<td>2</td>
<td>Gap Creek</td>
<td>Complex mesophyll vine forest [Type 1a]</td>
<td>3</td>
<td>3</td>
<td>~2.5 km from Type 2 equiv.</td>
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<td>3</td>
<td>Mt. Windsor Tableland</td>
<td>[Type 14b] near Complex notophyll vine forest [Type 6]</td>
<td>1</td>
<td>1</td>
<td>Type 4 and 5</td>
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<tr>
<td>4</td>
<td>Mt. Carbine Tableland</td>
<td>[Type 14] near Simple notophyll vine forest [Type 8]</td>
<td>1</td>
<td>1</td>
<td>Type 5, &lt;200m from Type 4</td>
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<td>5</td>
<td>Gordonvale</td>
<td>Mesophyll vine forest with dominant fan palms [Type 3b] near [Type 12c]</td>
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<td>7</td>
<td>&lt;1 km from Type 2, 4 and 5 equiv.</td>
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<td>Chalumbin-Woree power corridor</td>
<td>Mesophyll vine forest [Type 2a], fringing [Type 13c] vine forest; emergent <em>Eucalyptus grandis</em> on ridges</td>
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<td>&lt;1 km from Type 3, &lt;2 km from Type 4 equiv.</td>
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<td>Simple notophyll vine forest [Type 8]</td>
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<td>&lt;1 km from Type 1, 2, 4 and 5</td>
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<td>Mt. Baldy</td>
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<td>1</td>
<td>Type 5, &lt;250m from Type 4</td>
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<td>Mt. Baldy</td>
<td>Simple microphyll vine-fern forest [Type 9], surrounded by tall <em>Eucalyptus</em> forest [Type 14]</td>
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<td>2</td>
<td>&lt;1 km from Type 1, 2, 3, 4 and 5</td>
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<tr>
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<td>[Type 14b]</td>
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<td>1</td>
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<td>Mt. Baldy</td>
<td>Simple notophyll vine forest [Type 8]</td>
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<td>&lt;1 km to Type 1 and Type 4</td>
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<td>Moomin</td>
<td>[Type 14b] near Simple notophyll vine forest [Type 8]</td>
<td>1</td>
<td>1</td>
<td>Type 4</td>
</tr>
<tr>
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<td>Tinaroo</td>
<td>[Type 14]</td>
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<td>1</td>
<td>Type 5, &lt;100m from Type 4</td>
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<td>Mt. Hypipamee</td>
<td>Complex notophyll vine forest [Type 5a]</td>
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<td>1</td>
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<td>Mt. Fisher</td>
<td>Complex mesophyll/notophyll vine forest [Type 1b/5b]</td>
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<td>&lt;4 km from Type 1, 2, 4 and 5</td>
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<td>1</td>
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<td>Nitchaga</td>
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<td>20</td>
<td>Koombboolamba</td>
<td>Simple notophyll vine forest [Type 8] with patches of flooded gum emergent on acid plutonic soil [Type 13c]</td>
<td>1, 5</td>
<td>5</td>
<td>Type 3, &lt;800 m from Type 1 and Type 4</td>
</tr>
<tr>
<td>21</td>
<td>Koombboolamba</td>
<td>[Type 13c]</td>
<td>1</td>
<td>1</td>
<td>Type 2, &lt;500m from Type 1 and Type 4</td>
</tr>
<tr>
<td>22</td>
<td>Dalrymple Gap</td>
<td>Mesophyll vine forest [Type 13f] close to [Type 15b]</td>
<td>1</td>
<td>1</td>
<td>&lt;100m from Type 4 equiv.</td>
</tr>
<tr>
<td>23</td>
<td>Wallaman Falls</td>
<td>Simple notophyll vine forest [Type 8]</td>
<td>6</td>
<td>6</td>
<td>&lt;4 km from Type 4 and 5</td>
</tr>
<tr>
<td>24</td>
<td>Paluma</td>
<td>[Type 14a]</td>
<td>1</td>
<td>1</td>
<td>Type 1, &lt;100m from Type 4</td>
</tr>
<tr>
<td>25</td>
<td>Paluma</td>
<td>[Type 14]</td>
<td>8</td>
<td>8</td>
<td>Type 5, &lt;100m from Type 4</td>
</tr>
<tr>
<td>26</td>
<td>Iron Range</td>
<td>Mesophyll vine forest</td>
<td>1, 9</td>
<td>9</td>
<td>&lt;1 km from Type 4 equiv.</td>
</tr>
</tbody>
</table>
Figure 1. Map of all recorded sites (n=25) for *Murina florium* in the wet tropics region of Australia (listed in Table 2) shown as filled dots. Grey area is the total predicted distribution for *M. florium* using a BIOMC model based on the seven climate parameters listed in Table 5 for all localities. The BIOMC climate model covers a land surface area (including islands) bounded approximately by the map (Cape Bedford to Cape Cleveland) and up to 120 km inland. This area contains the wet tropics region of Australia as defined by Nix and Switzer (1991).
Table 4.

Summary of the major forest structures encountered at Murina florium sites, taken from the detailed descriptions in Table 3. Examples of Forest Type are taken from Table 3 using Tracey (1982) and Harrington and Sanderson (1994) classifications. Site numbers (Site No.) are identified in Tables 2 and 3.

<table>
<thead>
<tr>
<th>Forest Structure</th>
<th>Forest Type</th>
<th>Site No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microphyll vine-fern forest</td>
<td>Tracey 1982</td>
<td>9</td>
</tr>
<tr>
<td>Notophyll vine forest</td>
<td>Harrington and Sanderson 1994</td>
<td>9</td>
</tr>
<tr>
<td>Meso/notophyll vine forest</td>
<td>5a, 5b, 8</td>
<td>1, 7, 12, 15, 18, 23</td>
</tr>
<tr>
<td>Mesophyll vine forest</td>
<td>1b/5b</td>
<td>16, 17</td>
</tr>
<tr>
<td>Eucalyptus grandis forest with a rainforest substory or understory</td>
<td>1a, 2, 3b</td>
<td>2, 5, 6, 21</td>
</tr>
<tr>
<td>Mixed upland wet sclerophyll forest with a rainforest substory or understory</td>
<td>13c, 3, 4</td>
<td>19, 20, 21</td>
</tr>
<tr>
<td>Lowland equivalent of mixed upland wet sclerophyll forest with a rainforest substory or understory</td>
<td>14, 5</td>
<td>4, 8, 14, 25</td>
</tr>
<tr>
<td>Mixed upland wet sclerophyll forest with a grassy ground layer</td>
<td>13f</td>
<td>22</td>
</tr>
<tr>
<td>Eucalyptus grandis forest with a grassy ground layer</td>
<td>14b, 4</td>
<td>3, 10, 11, 13</td>
</tr>
<tr>
<td></td>
<td>14a, 1</td>
<td>24</td>
</tr>
</tbody>
</table>

range 32.6–35.6 mm (n=14); body weight 7.4 g, range 5.8–9.0 g (n=13); tail length 33.9 mm, range 30.8–37.0 mm (n=11); thumb length 8.8 mm, range 6.8–10.1 mm (n=8); 3rd metacarpal 31.6 mm, range 29.2–34.8 mm (n=8); tibia length 16.9 mm, range 15.2–18.8 mm (n=8); ear length 12.5 mm, range 10.5–13.7 mm (n=8). Compared to the holotype of M. f. florium (Thomas 1908; Hill 1983), these Australian specimens are similar in the length of the forearm, 3rd metacarpal and tail, but apparently the thumb is longer in the holotype which is also much lower in body weight (see Table 1).

Also shown in Table 1 are measurements of M. florium specimens from Papua New Guinea, representing the closest region of collection to Australia. From a very limited sample, their size is generally in agreement with the Australian specimens, and any differences are not consistently larger or smaller. Specimens collected from several Indonesian islands, including the type locality (Flores Is.), are shown in Table 1, but only body weight and forearm length are useful for comparison.

Finally, measurements from a single Murina specimen collected at Iron Range (Table 2) generally fall within the range of the other M. florium from Australia, and Papua New Guinea, but notably it has a lower body weight and shorter head-body length (Table 1).

Identification of M. florium sites, vegetation and forest type

A total of 25 discrete localities for M. florium have been found in the wet tropics region of Australia, as listed in Table 2. One subset of records (n=11) is based on captures where individual bats have been trapped and taken as voucher specimens, or released. The second subset of records (n=14) is based on the presence of M. florium at a
Figure 2. (a) capture localities (n=11) of Murina florium for wet tropics sites listed in Table 2, shown as filled dots. Grey area is the total predicted distribution for M. florium using a BIOCLIM model based on the seven climate parameters listed in Table 5 for capture sites only. (b) acoustic detection localities (n=14) of M. florium, details as in (a). Predicted distribution applies to acoustic detection sites only. For further details see Fig.1.

given site, having been detected acoustically by its echolocation call or social call. Both of these sounds are produced by M. florium leaving the diurnal roost or flying in the foraging area at night (Coles et al. 1998). Sound recordings were made at ground level as well as from canopy towers with microphones elevated into the forest strata at various heights (e.g Sites 5 and 17 in Table 2; see Whybird 1996, 1998). Echolocation calls can be used to positively identify free flying M. florium by reference to tape recordings (and analysis) from captured, and then released, individuals (Coles et al. 1998). A distinctive social call used by M. florium can be recognised in the field with practice, since it is audible to the unaided ear (Winter 1991; Schulz and Hannah 1996; Coles et al 1998). The same call is used by captive bats and released individuals, and it has been recorded and analysed as a means of identifying flying M. florium, but its function remains
DISTRIBUTION OF *MURINA FLORIUM* IN AUSTRALIA

**Table 5.**  
The climate profile for *Murina florium* generated by BIOCLIM using a full set of 35 parameters (see [http://cres.anu.edu.au/software/anuclim.html](http://cres.anu.edu.au/software/anuclim.html)) and based on 25 locations (see Table 2). The predicted distribution of *M. florium* (Figs. 1 and 2) is generated by using a subset of seven key parameters marked by an asterisk (*). For details see text. Temperature in °C, Precipitation in mm, Radiation in m/m²/d.

<table>
<thead>
<tr>
<th>Climate parameter</th>
<th>mean</th>
<th>SD</th>
<th>maximum</th>
<th>minimum</th>
<th>range</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Annual Mean Temperature*</td>
<td>20.1</td>
<td>1.64</td>
<td>24.3</td>
<td>18.6</td>
<td>5.7</td>
</tr>
<tr>
<td>2 Mean Diurnal Range*</td>
<td>9.6</td>
<td>0.91</td>
<td>10.4</td>
<td>7.1</td>
<td>3.3</td>
</tr>
<tr>
<td>3 Isothermality*</td>
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<td>0.02</td>
<td>0.57</td>
<td>0.5</td>
<td>0.07</td>
</tr>
<tr>
<td>4 Temperature Seasonality</td>
<td>1.01</td>
<td>0.08</td>
<td>1.15</td>
<td>0.82</td>
<td>0.33</td>
</tr>
<tr>
<td>5 Maximum Temperature of Warmest Period*</td>
<td>28.6</td>
<td>1.13</td>
<td>31</td>
<td>27.3</td>
<td>3.7</td>
</tr>
<tr>
<td>6 Minimum Temperature of Coldest Period</td>
<td>10.9</td>
<td>2.12</td>
<td>16.7</td>
<td>9.2</td>
<td>7.5</td>
</tr>
<tr>
<td>7 Annual Temperature Range*</td>
<td>17.7</td>
<td>1.48</td>
<td>19.0</td>
<td>13.9</td>
<td>5.1</td>
</tr>
<tr>
<td>8 Mean Temperature of Wettest Quarter</td>
<td>22.9</td>
<td>1.57</td>
<td>26.8</td>
<td>21.4</td>
<td>5.4</td>
</tr>
<tr>
<td>9 Mean Temperature of Driest Quarter</td>
<td>17.7</td>
<td>2.01</td>
<td>21.9</td>
<td>15.4</td>
<td>6.5</td>
</tr>
<tr>
<td>10 Mean Temperature of Warmest Quarter</td>
<td>23.3</td>
<td>1.52</td>
<td>27</td>
<td>21.8</td>
<td>5.2</td>
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<tr>
<td>11 Mean Temperature of Coldest Quarter</td>
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<td>1.81</td>
<td>21.1</td>
<td>14.6</td>
<td>6.5</td>
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<tr>
<td>12 Annual Precipitation*</td>
<td>1852</td>
<td>333</td>
<td>2574</td>
<td>1197</td>
<td>1377</td>
</tr>
<tr>
<td>13 Precipitation of Wettest Period</td>
<td>384</td>
<td>73</td>
<td>558</td>
<td>287</td>
<td>271</td>
</tr>
<tr>
<td>14 Precipitation of Driest Period*</td>
<td>39</td>
<td>11</td>
<td>59</td>
<td>20</td>
<td>39</td>
</tr>
<tr>
<td>15 Precipitation Seasonality</td>
<td>85</td>
<td>9</td>
<td>100</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>16 Precipitation of Wettest Quarter</td>
<td>1063</td>
<td>188</td>
<td>1486</td>
<td>766</td>
<td>720</td>
</tr>
<tr>
<td>17 Precipitation of Driest Quarter</td>
<td>127</td>
<td>37</td>
<td>203</td>
<td>64</td>
<td>139</td>
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<td>18 Precipitation of Warmest Quarter</td>
<td>869</td>
<td>137</td>
<td>1123</td>
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<td>19 Precipitation of Coldest Quarter</td>
<td>168</td>
<td>59</td>
<td>290</td>
<td>79</td>
<td>211</td>
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<td>20 Annual Mean Radiation</td>
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<td>0.18</td>
<td>20.1</td>
<td>19.3</td>
<td>0.8</td>
</tr>
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<td>24.9</td>
<td>0.23</td>
<td>25.2</td>
<td>24.4</td>
<td>0.8</td>
</tr>
<tr>
<td>22 Lowest Period Radiation</td>
<td>14.6</td>
<td>0.27</td>
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<td>14.2</td>
<td>1</td>
</tr>
<tr>
<td>23 Radiation Seasonality</td>
<td>18</td>
<td>0.79</td>
<td>19</td>
<td>16</td>
<td>3</td>
</tr>
<tr>
<td>24 Radiation of Wettest Quarter</td>
<td>19.7</td>
<td>0.48</td>
<td>20.8</td>
<td>18.9</td>
<td>1.9</td>
</tr>
<tr>
<td>25 Radiation of Driest Quarter</td>
<td>19.7</td>
<td>1.37</td>
<td>21.4</td>
<td>18.2</td>
<td>3.2</td>
</tr>
<tr>
<td>26 Radiation of Warmest Quarter</td>
<td>21.7</td>
<td>0.42</td>
<td>22.6</td>
<td>20.9</td>
<td>1.7</td>
</tr>
<tr>
<td>27 Radiation of Coldest Quarter</td>
<td>16.5</td>
<td>0.24</td>
<td>17</td>
<td>16.1</td>
<td>0.9</td>
</tr>
<tr>
<td>28 Annual Mean Moisture Index</td>
<td>0.82</td>
<td>0.07</td>
<td>0.93</td>
<td>0.65</td>
<td>0.28</td>
</tr>
<tr>
<td>29 Highest Period Moisture Index</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>30 Lowest Period Moisture Index</td>
<td>0.31</td>
<td>0.14</td>
<td>0.59</td>
<td>0.14</td>
<td>0.45</td>
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<tr>
<td>31 Moisture Index Seasonality</td>
<td>33</td>
<td>11.5</td>
<td>58</td>
<td>14</td>
<td>44</td>
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<td>32 Mean Moisture Index of Highest Quarter</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>33 Mean Moisture Index of Lowest Quarter</td>
<td>0.43</td>
<td>0.16</td>
<td>0.74</td>
<td>0.14</td>
<td>0.6</td>
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<tr>
<td>34 Mean Moisture Index of Warmest Quarter</td>
<td>0.91</td>
<td>0.03</td>
<td>0.94</td>
<td>0.8</td>
<td>0.14</td>
</tr>
<tr>
<td>35 Mean Moisture Index of Coldest Quarter</td>
<td>0.92</td>
<td>0.13</td>
<td>1</td>
<td>0.54</td>
<td>0.46</td>
</tr>
</tbody>
</table>
unknown. It should be noted that the acoustical structure of the social call is different to a superficially similar vocalisation often used by Nyctimene robinsoni in the same areas (Coles et al. 1998).

Vegetation structure at each site was assessed using the Tracey (1982) classification scheme, either directly by visitation, or by reference to previous descriptions (Tables 3 and 4). As well, the scheme proposed by Harrington and Sanderson (1994) for wet sclerophyll forests was used at each site, and where possible, the forest type or an equivalent was defined. The forest in the vicinity of the site was assessed for example, by estimating the distance to the nearest wet sclerophyll forest type or that of an equivalent structure (Harrington and Sanderson 1994).

The rationale for using each classification scheme is that forest types in the humid tropics were defined originally by Tracey (1982), reflecting a combination of the general structure with a finer resolution based on floristics and geological components. Tracey (1982) forest structural types at M. florium sites encompass a range of canopy leaf size from 2.5–7.5 cm long (microphyll), up to 12.5–25 cm long (mesophyll). More recently, Harrington and Sanderson (1994) have defined forest types restricted almost entirely within Tracey (1982) forest Type 14 (tall open forest). Harrington and Sanderson (1994) definitions include other Tracey (1982) forest types (e.g. Type 13), but their scheme is based on the successional change from wet sclerophyll forest to rainforest as a function of fire regime. The Harrington and Sanderson (1994) classification scheme can be considered to be both floristic and structurally based, emphasising the dominant living tree species and the status of the forest understory.

Detailed site descriptions using these two schemes are shown in Table 3 and summarised in Table 4. In terms of major forest type, 10 out of 25 sites occurred in rainforest described as notophyll or mesophyll vine forest, whilst five sites (Sites 3, 10, 11, 13 and 24) were located in wet sclerophyll forests. Seven out of 25 sites occurred in forests derived from the invasion of wet sclerophyll forests by rainforest tree species. One site (Site 22) belongs to a lowland equivalent of the upland wet sclerophyll forests. The remaining site (Site 9, Tables 2 and 3), which is the original M. florium capture site on Mt. Baldy, was described as microphyll vine-fern forest by Richards et al. (1982), but this description could not be confirmed during the present study. Another nearby capture site on Mt. Baldy (Site 7, Tables 2 and 3) was first described as simple mesophyll vine forest (Schulz and Hannah 1996) but later described as simple microphyll vine-fern forest (Schulz and Hannah 1998; see also Site 20, Table 3). It is difficult to assess the forest types at the Mt Baldy sites, as the published locations are within areas of notophyll vine forest, where smaller patches of Type 9 (microphyll) forest (Tracey 1982) may well exist. The sites established on Mt. Baldy in this study (Sites 8, 11 and 12, Tables 2 and 3) are definitely in notophyll vine forest (Tracey 1982: Type 8) or in wet sclerophyll forests (Harrington and Sanderson 1994: Types 4 and 5).

Considering capture records only (refer to Table 2), only two out of the 11 sites were located within the wet sclerophyll forests as defined by Harrington and Sanderson (1994), but a further six sites were located within 4 km of these forest types (Tables 3 and 4). This means that a high proportion (73%) of capture sites involve tropical upland wet sclerophyll forest. More specifically, it should be noted that all of the eight sites mentioned above are within 4 km of Harrington and Sanderson (1994) Type 4 forest (mixed wet sclerophyll forest with a grassy understory). A similar trend can be found for acoustic detection records (refer to Table 2), where 12 out of 14 sites (86%) either belong to a wet sclerophyll forest type as defined by Harrington and Sanderson (1994), or they are located within 4 km of these forest types (Tables 3 and 4).

Considering all sites presented in this study, almost half (48%) are located within a Harrington and Sanderson (1994) defined wet sclerophyll forest type (summary in Table 4), but this proportion increases substantially to 84%, if the presence of wet sclerophyll forest types within a 4 km radius of the sites are included, particularly Type 4.
(Table 3). This forest type is one of the most common representatives of upland tropical wet sclerophyll forest in the region, and forms part of a well defined transitional zone (Harrington and Sanderson 1994; Williams and Marsh 1998); the sites in question range in altitude from 580 m to 1120 m above sea level (refer Tables 2, 3 and 4).

Localities at Shipton’s Flat, Gap Creek, Gordonvale and Dalrymple Gap (Table 3) appear to be exceptions as they are all lowland sites, ranging from 70 m to 245 m above sea level. However, each site is within 1 km of areas dominated by either acacia or eucalyptus forest that are structurally analogous to the Types 4 and 5 upland mixed wet sclerophyll forests of Harrington and Sanderson (1994).

**Climate modelling**

**Predicted distributions**

A BIOCLIM analysis was performed for all site localities (Table 2) using the full set and a subset of seven climate parameters, as listed in Table 5, to generate a prediction for the preferred habitat of *M. florium*. The subset was chosen by reference to the previous BIOCLIM analysis by Nix and Switzer (1991) and produced a predicted distribution being closely matched to the parent distribution (all parameters) but less restricted in some regions. The predicted area (Figs 1 and 2) is described below, with reference to geographical landmarks and relevant *M. florium* sites (see Tables 2 and 3).

The main feature of the predicted distribution (Fig. 1) is a series of more or less contiguous zones forming an elongated band along a relatively narrow north-south axis. This band is about 30 km wide at its maximum in the north but mostly it is less than 15–20 km wide and contains numerous discontinuities. In the north, the main zone starts at the approximate latitude of Helenvale (Sites 1 and 2) and then runs west of the Thornton Range incorporating the periphery of the Mt. Windsor and Mt. Carbine Tablelands (Sites 3 and 4), before narrowing through the MacAlister Range (known as the Black Mountain Corridor). The predicted zone extends further southwards into the Lamb Range (Site 6) to the west of Cairns, but it also spreads (patchily) directly to the east into the northern end of the coastal Malbon Thompson Range (Site 5). The main band of prediction continues south through the Atherton Tableland (Site 14) and most of the Evelyn Tableland (Sites 16 and 17), including the Herberton Range to the west (Sites 7–13). Then, the distribution extends in a restricted band along the Cardwell Range, initially rather narrow at the northern end (Sites 18–21), but widens to 20 km or so at the southern end of the range. At this point, the predicted distribution bifurcates, with the main arm heading south eastwards to the coast near Cardwell (Site 22) to include Hinchinbrook Island; some smaller islands are predicted, such as Goold, Brook and the Palm Islands group. At this latitude, the second branch of the predicted distribution remains about 50 km from the coast, proceeding southwards into parts of the Seaview Range (Site 23) and then finally to sections of the Paluma Range (Sites 24 and 25).

In order to validate the use of acoustic detection records for determining *M. florium* localities, a comparison was made between the two methods of observation as they are independent (capture being definitive for this species). The results are shown in Fig. 2 and the predicted map generated by a BIOCLIM analysis for acoustic detection records (Fig. 2b) is quite similar to the one for capture records (Fig. 2a). Both methods of determining the location of *M. florium* in the wet tropics can be seen to augment the ability to predict its habitat.

However, there are significant differences; for example the acoustic detection records available for this study (Table 2) fail to predict substantial areas of lowland forest north of the Mt. Windsor Tableland and to the west of the Thornton Range (compare Figs 2a and 2b). The existence of capture sites at Shipton’s Flat and Gap Creek (Table 2, Sites 1 and 2) provide the basis for predicting the lowland distribution of *M. florium* north of
the Mt. Windsor Tableland. On the other hand, two acoustic detection sites on the Mt. Windsor and Mt. Carbine Tablelands independently confirm predictions made from capture records alone (Fig. 2b). Similarly, the lowland acoustic detection sites at Gordonvale and Dalrymple Gap (Table 2, Sites 5 and 22) are predicted by the distribution generated from capture records (see Fig. 2a).

A further comparison between the predicted distributions in Fig. 2 reveals that capture records suggest a wider area in the MacAlister Range compared to acoustical detection records. Capture records predict a possible discontinuity between the Herberton and Cardwell Ranges, but *M. florium* was detected acoustically in this area. Interestingly, acoustical records alone did not predict suitable habitat for *M. florium* in the Seaview Range, but there is a capture record in this region at Wallaman Falls (Fig. 2a; Site 23, Table 2). *M. florium* has been reported from the Paluma Range by both capture and acoustical detection (Table 2), but capture records alone predict a greater area of potential habitat (compare Figs 2a and 2b).

Within the boundary of the present BIOCLIM model and predicted distribution (Fig. 1), there are a few isolated areas of potential significance: the Lookout Range, west of Cooktown; an unnamed range west of the Mt. Windsor Tableland and just east of the Peninsula Developmental Road; a possible presence at Baker’s Blue Mountain and Hanns Tableland.

The climate profile for *Murina florium*

The climate surfaces that generate a predicted distribution for *M. florium* (Figs 1 and 2) are based on variations in rainfall and temperature for seven out a possible 35 parameters (Table 5, see Methods). These parameters appear to have the greatest predictive value (see also Nix and Switzer 1991) and thus the distribution shown in Fig. 1 is determined by a combination of annual precipitation and precipitation in the driest period, together with the annual mean temperature and the maximum temperature of the warmest period. In addition, the derived variables of annual temperature range, mean diurnal range and isothermality contribute significantly to the predicted distribution. It should be noted that the climate model proposed here, and its predictions, take into account all the variation between the known localities for all seven parameters. This is in contrast to specifying a bioclimatic ‘core’ and ‘margin’ to predict the distribution of vertebrates endemic to the same region (Nix and Switzer 1991).

The climate profile produced by the present study (Table 5), at least in the wet tropics of Australia, suggests that *M. florium* is likely to be found in regions with a moderate to high annual rainfall varying between 1197 mm and 2574 mm, and areas where rainfall over the driest period ranges from 20 mm to 59 mm. *M. florium* appears to prefer an annual mean temperature between 18.6°C to 24.3°C with an average annual and diurnal range of 13.9°C to 19.0°C and 7.1°C to 10.4°C respectively.

The Iron Range locality

As the identity of the *Murina* specimen collected from Iron Range is similar in many respects to *M. florium* (see above for description, below for Discussion; also Hill and Rozendaal 1989), it is considered here as an outlier to the main population in Australia. Limited by dealing with a single specimen, it is nevertheless useful to consider the climate and vegetation that apply to the collecting site.

The site locality is known (Table 2) and the closest available climate measurements come from the Lockhart River Airport (12°47'S 143°18' E, elevation 17.4 m) located at a distance of 10 km. Climate statistics (Bureau of Meteorology 1999; for the period 1956 to 1999) are: mean annual rainfall, 2087 mm; precipitation for the driest period, 30 mm; mean daily maximum temperature for warmest quarter 31.7°C; mean annual temperature, 25.8°C. On this basis, the Iron Range collecting locality appears to fall within the maximum and minimum values for two of the most important rainfall and temperature conditions.
parameters determined by the climate profile in the wet tropics (Table 5). The maximum
temperature of the warmest period and annual mean temperatures are higher but never-
thelss close the climate profile (Table 5).

Vegetation at the capture site is an area of mesophyll vine forest (Tracey 1982),
and it is located within 1 km of wet sclerophyll forest, equivalent to a Harrington and
Sanderson (1994) Type 4 (J. Clarkson, pers. comm., see Table 3). This locality is thus
similar to other M. florium sites in the wet tropics region, such as Gap Creek (Site 2) and
Dalrymple Gap (Site 22); for details see Tables 2, 3 and 4, and Fig.1.

DISCUSSION

The occurrence of Murina florium in Australia

From a comparison of the measurements obtained from Murina specimens listed in
Table 1, it is most likely that a single species, Murina florium, occurs in Australia. At
present, the known populations occur in the wet tropics region (Fig. 1, Table 2; see Nix
and Switzer 1991) although tentatively, a single specimen collected from Iron Range on
Cape York Peninsula may be the same species (cf. Richards et al. 1995), representing a
northern Australian population. To confirm this view, more specimens are needed for a
detailed morphometric and genetic analysis. At present, it seems reasonable to conclude
that the Australian M. florium population represents the south eastern distributional limit
of the species, as part of a continuum with the Papua New Guinea population. It is not
possible to say conclusively if the Australian population differs significantly from the
holotype (Thomas 1908) or other specimens collected from a number of eastern
Indonesian islands (Table 1). The question of subspecies can not be resolved here,
beyond the opinions of Van Deursen (1961) who considered that possibly only one
species of Murina exists east of Wallace’s Line, and that of Hill and Rozendaal (1989)
who suggested one subspecies, M. f. lanosa, to be valid in this region. However, it can be
stated that M. florium is not confined to high altitude forests in Australia as previously
believed (Richards 1983, 1991) because specimens have been collected at elevations
below 300m (Tables 1 and 2). Elsewhere, M. florium has been collected from localities
close to sea level (Ambon Is. Indonesia; see Table 1; Flannery 1995b) although the
species certainly inhabits high altitude areas as well e.g. at 1480 m on Mt. Somoro,
Papua New Guinea (see Table 1 and Flannery 1995a).

The distribution of Murina florium in Australia

Habitat preference and climate

Despite a relatively limited sample of sites in Australia, it would appear that M.
florium is found in tropical forests that share several notable features (Tables 3 and 4). Of
course, each site in this study identifies M. florium only at a single point in the forest, but
the location is useful to describe at least part of its habitat. Despite some variability in
forest structure at the site (Tables 3 and 4), M. florium is found predominantly in rainfor-
est where wet sclerophyll forest is in close proximity, or in wet sclerophyll forest itself
(Table 3). This finding is consistent for upland areas containing wet sclerophyll forest
and extends to their counterparts in lowland forest. It suggests that M. florium may show
some association with a transitional zone involving Type 4 mixed wet sclerophyll forest
(Harrington and Sanderson 1994) or its structural equivalent (see Tables 3 and 4). The
distribution of these forest types is limited in the wet tropics of Australia and often the
forest boundaries are sharply demarcated (Harrington and Sanderson 1994). Within this
ecotone, vertebrate diversity has been found to change significantly across the transition
from open forest into rainforest (Williams and Marsh 1998). In the case of bats in general, diversity has been found to be high in Type 4 forests in the region compared to rainforest, and in fact, the northern populations of species such as *Tadarida australis*, *Nyctophilus gouldi* and *Scoteanax rueppellii* appear to be restricted to these wet sclerophyll forests (Clague 1998).

Interestingly, both the distribution of tall open forest types (Harrington and Sanderson 1994) and the predicted distribution for *M. florium* (Fig. 1) tend to be adjacent to the wettest areas in the region experiencing a significantly lower rainfall regime (Nix and Switzer 1991). For example, all *M. florium* sites studied here, except Dalrymple Gap and the Chambullan-Woree power corridor site (Table 2), are located on the western slopes or plateaus of mountainous areas (Fig. 1 and see Nix and Switzer 1991). Climatically, these sites occur in a steep rainfall gradient: refer to Table 5, and compare Fig. 1 in this study with Fig. 11 of Nix and Switzer (1991). In this respect, the Dalrymple Gap site (Site 22, Table 2, and see Fig. 1) is most likely within a rain shadow caused by its proximity to the mountainous Hinchinbrook Island. Likewise, the Chambullan-Woree power corridor site (Site 6, Table 2, and see Fig. 1) is likely to receive less precipitation compared to adjacent peaks in the Lamb Range, due to the convoluted topography of the area (see Fig. 11 in Nix and Switzer 1991).

Modelling the variation between sites via BIOCLIM produces a climate profile that can be defined by as few as seven parameters of rainfall and temperature (Table 5). Each climate surface has been used to find an area that is common to all sites and the model predicts a highly restricted distribution for *M. florium* (Fig. 1), one that appears to encompass most, if not all, of the 'preferred' habitat described above (see Tables 3 and 4). Of course, the reliability of the predictions are unknown, due to limited and potentially biased sampling. If the predictions are accurate, then it suggests that the distribution of *M. florium* in Australia is clearly influenced by the climate which must exert a major control over suitable forest habitat.

Although not specifically included in this study, it would seem that the outlying Iron Range capture site is a reasonable match to the climate and vegetation pattern established for *M. florium* in the wet tropics (Tables 3 and 5). Extending the BIOCLIM analysis to include the entire Cape York Peninsula would be of great interest, to see if suitable habitat can be predicted, and to serve as a focus for future field surveys. It was noted that a number of coastal continental islands are predicted (see Results and Fig. 1), the largest of these being Hinchinbrook Island. The predicted islands in this vicinity all contain mesophyll vine forest, as well as equivalent mixed wet sclerophyll (Harrington and Sanderson 1994). Therefore, it would not be surprising to find *M. florium* on these islands, none of which have been surveyed for bats in any detail (see Myroniuik 1988).

Roost preference

A comparison of site vegetation (Tables 3 and 4) and a climate analysis (Figs 1 and 2, Table 5) support the idea that *M. florium* may show a habitat preference. Whilst the localities identified in the present study are likely to be part of an individual bat's foraging area, a given forest type or combination of forest types might also provide suitable diurnal roosts. There are no data on the exact foraging range of *M. florium*, but Schulz and Hannah (1998) report roosts to be located within 150–900 m of capture sites. Since almost all of the sites in this study have been found in close proximity to Type 4 (Harrington and Sanderson 1994) forests (see Table 3), forest type might have an important bearing on roost selection. In this regard, *M. florium* has been found to roost in trees 'externally', under foliage such as dead epiphytic fern fronds (Type 2 forest of Harrington and Sanderson 1994) and palm leaves, as well as in the abandoned nests of *Sericornis citreogularis* and *Oreoscopus gutturalis* (Schulz and Hannah 1998). A tendency to roost in suspended bird nests may be an important clue, as it has been suggested that the northern population of *S. citreogularis* may be restricted to upland wet sclero-
phyll forests (Harrington and Sanderson 1994), and the distribution of this scrub wren may well coincide with that of *M. florium*. Moreover, the predicted distribution of *O. gutturalis* is remarkably similar to that predicted for *M. florium*, at least for upland areas (compare Fig.1 this study, with page 60 in Nix and Switzer 1991). Other bird nests may prove suitable as well and recently *M. florium* has been found roosting in the nest of *Todiramphus sanctus* burrowed into a termite mound, suspended in a tree, in mixed sclerophyll forest (Type 4) on Mt. Baldy (Clague, unpublished observations).

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REFERENCES


A Record of Hastings River Mouse (*Pseudomys oralis*) in a Fox (*Vulpes vulpes*) Scat from New South Wales

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The Hastings River mouse (*Pseudomys oralis*) is a threatened Australian mammal listed as endangered on the ‘NSW Threatened Species Conservation Act 1995’ and ‘Commonwealth Endangered Species Protection Act 1992’ and vulnerable on the ‘Queensland Nature Conservation Act 1992’. Predation by the fox (*Vulpes vulpes*) is identified as one of the key threatening processes although there has been no evidence to support this theory. Despite many predator scat surveys having been conducted throughout the geographical range of the species, only recently has any evidence of *V. vulpes* predation on the species been determined. This short note describes the first published record of *P. oralis* in a *V. vulpes* scat, collected in Marengo State Forest, NSW.

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KEYWORDS: fox, Hastings River mouse, predation, scat analysis.

INTRODUCTION

*Pseudomys oralis* only occurs in New South Wales and Queensland in tall open eucalypt forests at altitudes between 410–1250 metres above sea level (A.P. Smith unpub. data). Evidence suggests that the species was once more widely distributed along the east coast of Australia (NPWS unpub.). The main threats to the species are unknown and ecological research to study the biology of the species has been hampered by low capture success, low abundance and a patchy distribution (Read 1993; King 1984). A draft recovery plan has been prepared for this species in NSW (NPWS unpub.) where it is proposed that *V. vulpes* predation is one of five threatening processes. To date these threatening processes have been unproven and there has not been any evidence of *P. oralis* in *V. vulpes* scats although the species is considered to be in the critical weight range (after Burbidge and McKenzie 1989) vulnerable to *V. vulpes* predation.

The only record of *P. oralis* in mammalian predator scats has been recorded in a study of the diet of *Canis lupus familiaris* in the Oxley Wild Rivers National Park (Robertshaw and Harden 1985). Evidence of forest owl predation has been reported by Kirkpatrick (1995) and Read (1987). The occurrence of *P. oralis* in predator scats and owl pellets is not conclusive evidence that predation is a key threat to the species, and given the rarity of the occurrence and the difficulty in trapping this species, it is likely that quantifiable threats will be extremely difficult to accurately determine.

METHODS

In May 1999, as a part of pre-logging surveys, a State Forest employee (Bill Browning) collected numerous *V. vulpes* scats along a forestry road in Marengo State Forest, NSW.
RESULTS

Analysis determined that the scat was composed of hair from a *Pseudomys* sp., although the distinguishing features were difficult to identify accurately using cross-section analysis. The structure of the hair mounts in the *Pseudomys* spp. are very similar and overlapping diagnostic features between *P. oralis*, *P. gracilicaudatus*, *P. novaehollandiae* and *P. australis* can complicate accurate identification (Fig. 2). These *Pseudomys* species all have oval guard hairs and circular overhairs that can only be distinguished by measuring the maximum diameter of the hairs and the width of the hair cortex. Precise identification can also be complicated by damage to the hair’s outer scales and distortion of hair shapes caused by the digestive processes of the predator. In this investigation the hairs were damaged and confirmation of the species using dentition analysis was referred to the Queensland Museum. Results from the examination of the lower jaw and teeth revealed that the distinctive high molar crowns (upper and lower) and independent lophs were apparent, typical of *P. oralis* (Fig. 3), therefore distinguishing it from the other *Pseudomys*.

DISCUSSION

*P. oralis* is believed to be at risk of extinction due to a number of threatening processes including predation by *V. vulpes* (NPWS unpub.). This record of *P. oralis* in a
Figure 2. Cross-section of hair from *P. oralis* (above) and *P. novaehollandiae* (below) showing similar diagnostic features.
Figure 3. Lower jaw and teeth of *P. oralis*, note the distinctive high molar crowns and independent lophs.

*V. vulpes* scat and a second occurrence in a fox scat from the Border Ranges (D. Charley pers. comm. 1999) indicate that foxes could pose a threat to *P. oralis* although there is no conclusive evidence of predation. *V. vulpes* are scavengers and the interpretation of scat survey data should acknowledge that not all food items of *V. vulpes* are the result of predation (Meek and Triggs 1998).

More information is still needed to clarify all the causal factors influencing the low abundance of the species in the eastern states. Recent studies (S. Townley pers. comm. 1999) suggest that a major threat could be posed by grazing and/or increased fire frequency, although this theory is yet to be tested. Experimentally designed studies are needed to assess what threatening processes affect this species and to make recommendations for the protection of the remaining populations based on a test-of-hypothesis based inquiry. An investigation of grazing and burning practices and their effect on *P. oralis* may be the key to learning more about this cryptic species. Predator-prey experiments to determine whether foxes are a threat can be very difficult to conduct and it is questionable whether this is more important than issues associated with burning and grazing.

State Forests are planning predator suppression programs in areas of high species richness to reduce the potential threats to all threatened species, including *P. oralis* (P. Meek and J. Shields unpub). This may have value in suppressing predators but the ability to test *V. vulpes* impacts is limited by low target population density and compounding effects of other predators, competitors and the availability of food and shelter.
ACKNOWLEDGMENTS

The authors would like to thank Bill Browning for collecting the scats during the pre-logging surveys. Steve Van Dyck kindly identified the lower jaw and provided helpful information on the dentition structures. Wayne Longmore and Sandy Ingleby of the Australian National Museum organised excellent photographs of the dentition. I also sincerely thank Rob Kirwood for producing Figure 1. David Charley kindly supplied information on his unpublished record.

REFERENCES

Book Review

*The Yponomeutinae (Lepidoptera) of the World exclusive of the Americas.*

This book provides an overview of the species of moths of the subfamily Yponomeutinae, other than those occurring in the Americas. It is based on study of descriptions, type material and other material in major collections supplemented by that in some smaller collections. As a result 231 species, grouped in 25 genera, are considered to be appropriately included in the subfamily from areas other the Americas. There is a brief abstract and acknowledgements of help followed by an introduction and a section listing the sources of material used in the study.

To provide the background leading to the present state of knowledge of the species currently considered to be includable in the Yponomeutinae, the “Historical review” of the study of the “small ermine moths” starts with reference to the early work of Réaumur (1738), provides an outline of subsequent work on Yponomeutoidea in general and ends with reference to recent studies in New Zealand by Dugdale.

The basic information on the morphology of adults required as an introduction to initial taxonomic investigation is provided in a short, illustrated account. Similar information for immature stages, which are, as in the case with so many groups of insects, less well studied than the adults, is given in more abbreviated form but a useful entry to the relevant literature is given through appropriate references.

There is a substantial list, in tabular form, of host plants on which larvae are known to develop, which include members of more than twenty families, mostly of dicotyledonous angiosperms. The list is somewhat ambiguously stated not to include "introduced plant species" or "cultivars".

A synopsis of the distribution of the genera through zoogeographic regions, in areas other than the Americas, is also given in tabular form.

A section on the classification of the subfamily includes a brief statement that the authors agree with the conclusion that the subfamily is a monophyletic assemblage (placed at various taxonomic levels by earlier authors) having as its sister group the subfamily Saridoscelinae. A commitment is given by the authors to pursue the matter of the relationships of the genera within the Yponomeutinae and the position of the subfamily within the family in future publications. It might have been preferable to include their findings in the present book rather than delay publication to some future unspecified work. The subfamily is briefly defined and there is a list of non-American genera and species. There is also a list of those genera listed as Yponomeutids by Nye and Fletcher, in their 1991 "Generic names of Moths of the World", which the authors consider not to be Yponomeutines. A note beside each name in the list gives the reason for its exclusion. Two keys to the non-American genera are provided, one based on external features and another on male genitalia.

A list of references concludes the general part of the work which occupies almost a third of the book.

The remainder of the work (from page 59 onwards) is devoted to a more detailed treatment of the non-American Yponomeutines at generic and specific level. These are dealt with genus by genus, in alphabetical order, with species being treated alphabetically within each genus. There is a reference to the original description of each genus and the type species is given. Under each species there is a reference to the original description...
and information on synonyms, the location of the type material, distribution of the species, months in which adult flight has been observed and on host plants. Synonymic information could have been arranged in a way which would be easier to use. There are illustrations of more than 20 species of which genitalia have not previously been illustrated in the literature. There are three keys to the species of the large genus *Yponomeuta*, one based on external characters, one based on male genitalia and another on female genitalia. All three keys, unfortunately, exclude a number of species. This limits their usefulness to the uninitiated. Keys are lacking altogether for other genera, even the larger genera, such as *Zelleria* and *Kessleria*, for which they would be most useful. In addition to line drawings scattered through the text there are three coloured plates depicting more than 60 set specimens and six black and white plates of photographic illustrations of genitalia preparations.

The book itself is hard covered and well bound and has a simple, pleasantly coloured cover based on the three coloured plates of set specimens.

So much for the dry bones of the book. A reader of a review has, however, some right to expect an answer to the question, “Should I bother to have a closer look at the book to see if it will be of use to me”? The writer of a review has some obligation to attempt to provide an opinion on the position which the work holds in the literature. He can also be expected to suggest the value of the work to the various kinds of readers who might have an interest in it, even if, like me, he cannot claim to have been at any time seriously steeped in the study of the Yponomeutinae. On the other hand, perhaps this makes it easier for me to give advice from the point of view of a potentially interested person rather than someone who is already a fanatical enthusiast of the group. For the latter the book provides a useful synopsis of the present state of opinion and knowledge of the non-American species, and all specialists will no doubt already have a copy on hand. An experienced specialist would already be familiar with the literature and the inadequacy of those keys which are provided will not be too much of a hindrance, although even the specialist would undoubtedly appreciate a more complete coverage of the species. Looking at the work from the point of view of a potentially interested newcomer to the group or even someone who has some thoughts of looking at one of the groups of smaller moths for the first time, the book would certainly be useful as an introduction. The historical section gives a clear background to tracing the development of the study of the group and of the intricacies of opinions and their changes. The fact that the classification of the Yponomeutidae has, like so many insect families, been through a long series of changes, in whole or in part, and is still not stable shows that there is still much to be done and problems to be solved. This is confirmed by the fact that the authors of the book have decided to remove a great many genera from the subfamily Yponomeutinae in their reassessment of its constitution. This has implications in relation to the Australian fauna. Several of the genera included by Ted Edwards in his contribution to the “Checklist of the Lepidoptera of Australia” as Yponomeutines are on the “excluded” list and there are also a few differences at species level. Clearly, as pointed out in the “Catalogue” by Edwards, this group is in need of further study and revision in Australia. Work here promises the reward of interesting discoveries for the enterprising entomologist.

The morphological section gives enough information and guidance on what to look for in preliminary work and the systematic sections give enough information and guidance through the literature to enable anyone other than the complete novice to make early progress in his studies. Even so, perseverance and a little help from an experienced lepidopterist would soon overcome any “teething” problems. From then on the delight of working with such beautiful, if small, insects would surely provide the impetus for long term interest — even if society might not be forward-thinking enough to pay for benefits of the work!

Taken in the wider context, the increasing demands for taxonomic work, especially
on relatively poorly studied faunas of large land masses, such as Australia, Africa or Asia, make it important that those able to do so should provide works which will enable enthusiastic newcomers to become familiar with the fauna quickly and enable them to make contributions to knowledge themselves as soon as possible. This treatment of the Yponomeutinae is an example of just such a work. It is an example of the kind of publication which could well be produced for many other groups in our fauna.

Here, in Gershenson and Ulenberg's book, is a neat introduction to the Yponomeutinae. Is there anyone prepared to take a ride on its back into the fascinating unknowns of the microlepidoptera? You could do worse!

Before I forget — I must, because most reviewers seem to do it, point out that there is a least one spelling mistake. I doubt that this is as important as the many words which are correctly spelt!

_Courtenay Smithers,_
_Australian Museum,_
_Sydney._
News and notes

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