Additions to knowledge about ektopodontids (Marsupialia: Ektopodontidae): including a new species *Ektopodon litolophus*

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Abstract – Information about the extinct phalangeroid family Ektopodontidae has been increased following the discovery of new material from several localities. A new species, *Ektopodon litolophus*, described on the basis of an M[1] from the Leaf Locality, Lake Ngapakaldi, Lake Eyre Basin, is characterized by the extremely simple structure of the crests. Ektopodontids are recorded for the first time from the northern half of the Australian continent through discovery of a tooth fragment at Wayne's Wok Site, Riversleigh World Heritage area, northwestern Queensland. Comparisons of M[1] of *Chunia* and *Ektopodon* species now allow evolutionary trends of simplification to be discerned.

INTRODUCTION

Ektopodon is a genus of extinct possum-like marsupials established by Stirton *et al.* (1967) on isolated teeth found at the Early to Middle Miocene Leaf Locality (Kutjamarpu Local Fauna) at Lake Ngapakaldi, northeastern South Australia (Figure 1). Further specimens from this locality were described and interpreted by Woodburne and Clemens (1986b), together with new, slightly older Oligocene species in the plesiomorphic genus *Chunia* (*C. illuminata*, *C.* sp. cf. *C. illuminata* and *C. omega*) from sites in the Lake Eyre Basin (e.g. Tedford Locality, Lake Palankarinna, Ditjimanka Local Fauna) and the Frome Embayment (e.g. Tom O's Quarry, Lake Tarkarooloo, Tarkarooloo Local Fauna). A second Late Oligocene species *Ektopodon stirtoni* was described by Pledge (1986) from Mammalon Hill, Lake Palankarinna (Ngama Local Fauna), with a referred form from Tom O's Quarry. Rich (1986) described *Darcius duggani* from Hamilton, western Victoria, a deposit radiometrically determined to be Pliocene in age (ca. 4.46 Myr).

By 1986 the rich deposits of Riversleigh, northwestern Queensland, were beginning to yield many new species including an ektopodontid. This Riversleigh taxon as well as a new, second, ektopodontid from the Kutjamarpu Local Fauna are described in this paper.

Age

Although Stirton (Stirton *et al.* 1961, 1968) initially assessed the age of the Etadunna Formation and its faunas to be Oligocene, it became customary to interpret these central Australian deposits as Middle Miocene in age (approximately 12–15

million years; Woodburne *et al.* 1985), following preliminary analyses by W.K. Harris of pollen from the Etadunna Formation at Mammalon Hill, Lake Palankarinna. Subsequent work with
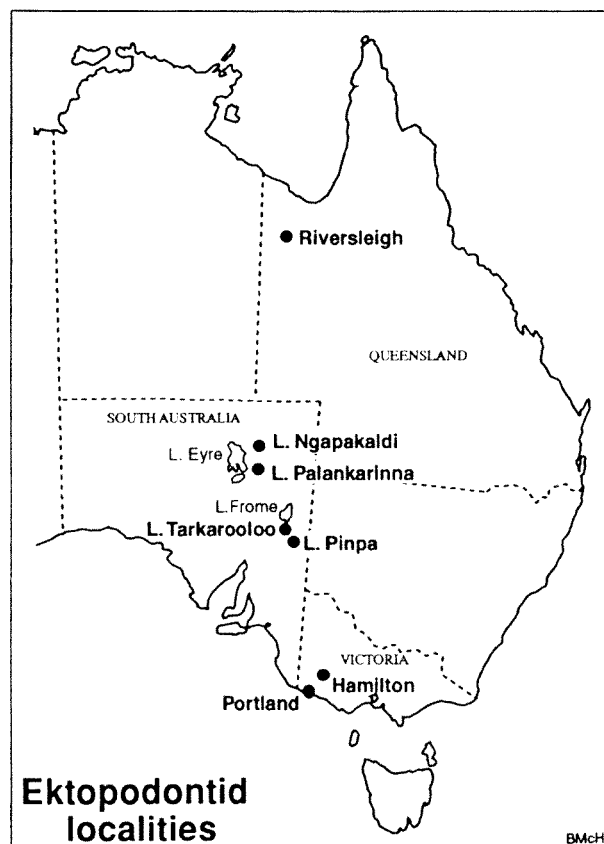
Figure 1 Locality map of central and eastern Australia, showing all localities from which ektopodontids have been recorded.

foraminiferans from underlying lacustrine dolomites (Lindsay 1987) suggested that at least some of these deposits might be as old as Late Oligocene. This assessment was based on the abundant presence of the foraminiferan *Buliminoides* sp. cf. *B. chattonensis*. The older age is also supported by Truswell *et al.* (1985) on the basis of pollens from the Geera Clay (which appears to be a lithological equivalent of basal Namba Formation, itself correlated with the Etadunna Formation); by Norrish and Pickering (1983) who reported a Late Oligocene Rb-Sr date for illite from the Etadunna Formation; and Woodburne *et al.* (1994) reporting the palaeomagnetic results of Bruce MacFadden.

The Wipajiri Formation (Stirton *et al.* 1967) occupies a channel cut into the underlying Etadunna Formation, and contains partly lithified pebbles of the latter sediments. The contained mammalian fauna is similar enough to the Ngapakaldi and other local faunas of the Etadunna Formation for Woodburne *et al.* (1994) to suggest closely similar ages for the two formations. This was predicated on a perceived brief span of time (about 2 million years) for the fossiliferous part of the Etadunna Formation, which one of us (Pledge) considers too short because of the numerous lacunae and erosional surfaces that can be discerned within the sequence. Pledge's estimate for the age of the Wipajiri Formation is Early to Middle Miocene.

The age of the Wayne's Wok *Ektopodon* from Riversleigh is equally contentious. At present, because of a majority of shared species, we conclude that the Wayne's Wok Local Fauna is approximately equivalent in age to Riversleigh's Upper Site Local Fauna which Archer *et al.* (1989) have concluded is probably Late Oligocene to Early Miocene in age. In part, this estimate is based on intercontinental comparisons of the Riversleigh hipposiderid bats (including *Brachipposideros nooraleebus* from Microsite) with their European congenors (Sigé *et al.* 1982). The Nooraleeba Local Fauna thus appears to be most probably Aquitanian (Late Oligocene) to Burdigalian (Early Miocene) in age.

Approximate correlation of the Upper Site and Wayne's Wok Local Faunas from Riversleigh with local faunas from northern South Australia (Figure 2) is based on shared faunal elements including closely-related species of *Namilamadeta* (Upper Site, Wayne's Wok, Tarkarooloo [Namba Formation] and Ngama [Etadunna Formation] Local Faunas); *Wakiewakie* (Upper Site and Kutjamarpu Local Faunas); and *Neohelos* (Wayne's Wok and Kutjamarpu Local Faunas).

Collection methods
Specimens from the Leaf Locality were found by

excavation of the fossiliferous horizons or by screen-washing the dried sediment through fine screen with mesh of 6 x 6 wires per cm², and picking the concentrate. The Riversleigh specimen was obtained by acetic acid digestion of the limestone matrix, after masses of fossiliferous rock had been blasted from the outcrop.

Terminology
Dental homology follows Luckett (1993). The terminology for the crown morphology of ektopodontid teeth used here is that of Woodburne and Clemens (1986a) with modifications recommended by Tedford and Woodburne (1987). Museum abbreviations are as follows: SAM, South Australian Museum; QM, Queensland Museum; NMV, Museum of Victoria; UCB, University of California, Berkeley; UCMP, University of California Museum of Paleontology locality number; SAM PL, South Australian Museum palaeontological locality.

SYSTEMATIC PALAEONTOLOGY

Supercohort Marsupialia (Illiger, 1811) *sens.* Cuvier (1817)

Order Diprotodontia Owen, 1866

Superfamily Phalangeroidea (Thomas, 1888) *sens.* Aplin and Archer (1987)

Family Ektopodontidae Stirton, Tedford and Woodburne, 1967

***Ektopodon litolophus* sp. nov.**
Figure 3

Material Examined

Holotype
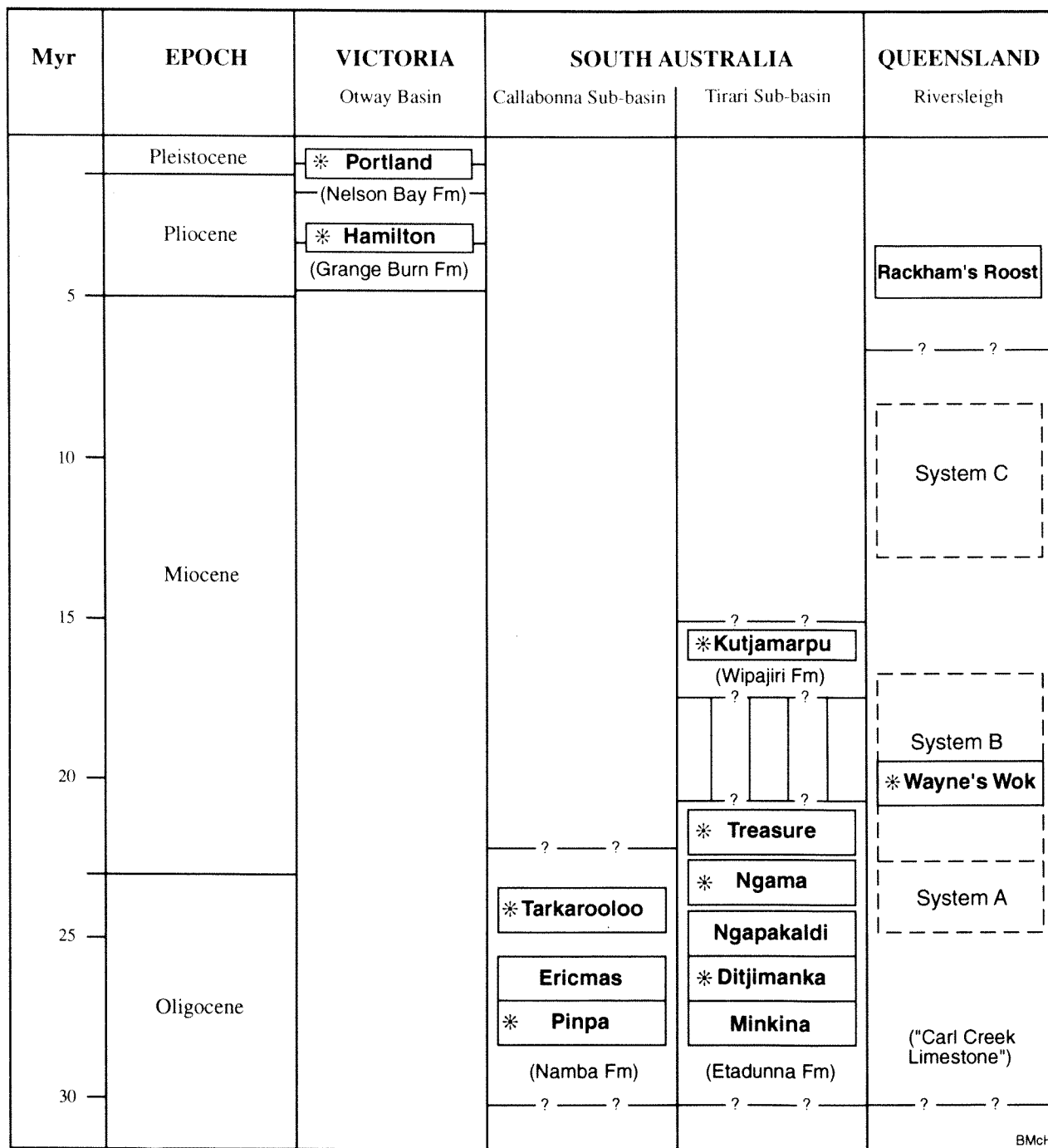SAM P30176, an isolated right M^1 collected by M. Archer, S. Hand and others in 1982.

Type Locality and Age
Basal coarse clastic unit, Leaf Locality (UCMP V-6213, SAM PL 7014), Wipajiri Formation, eastern strand, Lake Ngapakaldi, Etadunna Station, South Australia. Kutjamarpu Local Fauna of approximately Early Miocene age (see above).

Diagnosis
Ektopodon differs from the other ektopodontids, *Chunia* and (presumably) *Darcius*, in having anterior molars wider than long, more than 6 cusps on the protolophs, and with the accessory crests not radiating from the cusps but arranged more-or-less longitudinally.

Ektopodon litolophus differs from all other

Myr	EPOCH	VICTORIA Otway Basin	SOUTH AUSTRALIA Callabonna Sub-basin	SOUTH AUSTRALIA Tirari Sub-basin	QUEENSLAND Riversleigh
	Pleistocene	✳ **Portland**			
		(Nelson Bay Fm)			
	Pliocene	✳ **Hamilton**			**Rackham's Roost**
5		(Grange Burn Fm)			
					? —— ?
10	Miocene				System C
15				? —— ?	
				✳**Kutjamarpu** (Wipajiri Fm) ? —— ?	System B
20				? —— ?	✳**Wayne's Wok**
		? —— ?		✳ **Treasure**	
25			✳**Tarkarooloo**	✳ **Ngama** **Ngapakaldi**	System A
	Oligocene		**Ericmas**	✳ **Ditjimanka**	
30			✳ **Pinpa** (Namba Fm) ? —— ?	**Minkina** (Etadunna Fm) ? —— ?	("Carl Creek Limestone") ? —— ?

BMcH

Figure 2 Stratigraphic distribution of ektopodontids. Occurrences indicated by ✳. '?' indicates formation boundary age uncertainty. Modified in part from Woodburne *et al.* (1994). Local fauna names are shown in bold. 'Minkina' is the new name for the 'Wynyardiid', pre-Ditjimanka local fauna.

Ektopodon species in the following features: larger size; M^1 relatively and absolutely wider than that tooth in all species except *E. serratus* and 40% larger overall than that species; parastyloph more regular, with cusps of more uniform size; more cusps (10) on main lophs; cusps of more uniform size and with simple pre- and postcristae, without obvious ribs, struts or bifurcation (except on buccal-most cusps); reduced posterior cingulum.

Etymology

Specific name from the Greek *litos* (plain or simple) combined with *lophos* (a crest, mane or ridge), referring to the simple morphology of the crests on the molar cusps, relative to those of other species of *Ektopodon*.

Description

The holotype is a first upper molar, which has been
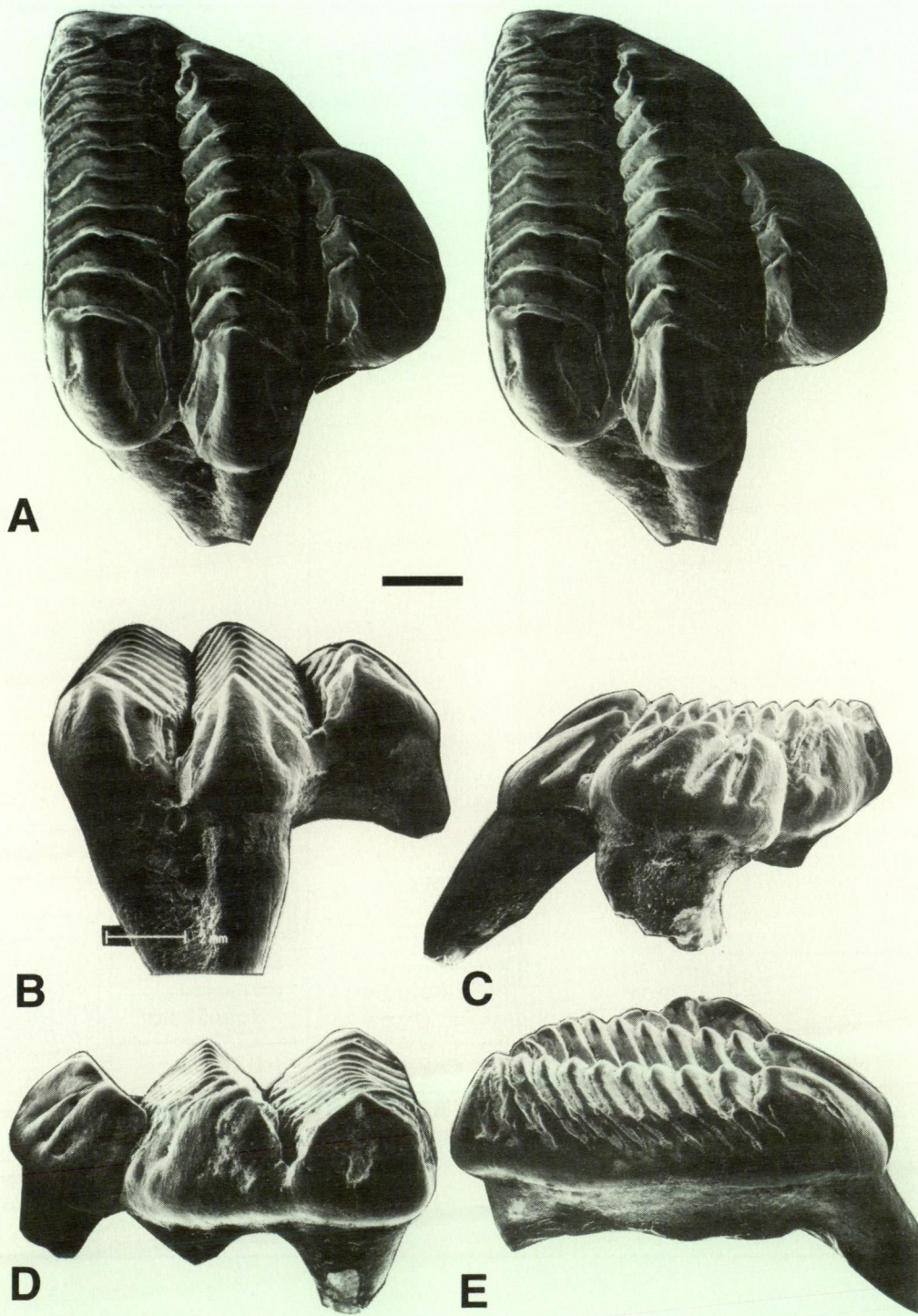
Figure 3   *Ektopodon litolophus* sp. nov., right M¹, SAM P30176, Leaf Locality, Lake Ngapakaldi, Kutjamarpu Local
Fauna. A, stereopair of occlusal surface, buccal side at top, anterior to right; B, lingual; C, anterior; D, buccal;
E, posterior views. Scale bar = 2 mm.

somewhat abraded, is relatively and absolutely
larger than that of any other known species (see
Table 1) and has a smoother, more triangular outline
(Figure 3). The truncated buccal face is also smoother
and more regular than in other species.

The crest of the metaloph is straight and
transverse while that of the protoloph curves
backwards buccally and would intersect, just

beyond its buccal end, a line extrapolated from the
curving parastyloph. Protoloph and metaloph are
about equal in length, but slightly offset.

The parastyloph is about half the width of the
protoloph, with four cusps. The first cusp has a
short postcrista joining a lingual cingulum that
crosses the end of the transverse valley to the
anterior base of the protocone. It is separated from

the slightly larger and bladed second cusp by an anterolingual crevice and a posterior crevice. The crest of the second cusp extends anterolingually to the anteriormost point of the tooth and there is a short postcrista. The third cusp is similar to the second but minute and squeezed between the second and fourth. The fourth cusp has a precrista from its lingual side, a very short postcrista and a short curving posterobuccal crest. The transverse valley is short, and none of the crests except the lingual cingulum crosses it.

The protoloph is almost straight, but its apical crest curves posterobuccally. There are 10 cusps. The protocone is by far the largest and is marked by a deep anterolingual groove and a slightly larger posterolingual groove. The pre- and postcristae thus formed are inclined apically to the buccal side of the tooth and are simple with no bifurcations, ribs or struts. Cusp 2 is simple with single, plate-like unornamented pre- and postcristae. The precrista curves lingually at the base of the anterior transverse valley. The succeeding 3rd to 8th cusps are similar with their subparallel and imbricated pre- and postcristae. The postcrista of cusp 3, however, differs in being bifurcated at its base. Cusp 9 is slightly smaller. Its precrista merges into the buccal face of the tooth and the postcrista is shorter because the apex is more posteriorly positioned. Cusp 10 shows a very short precrista and postcrista, and a buccal crest that curves backwards. None of the postcristae crosses the main transverse valley.

The metaloph is almost straight with a slightly sinuous posterior face, and 10 cusps. The metaconule is not as large as the protocone but is rounder. The apices of these two cusps are level. There is a deep anterolingual groove and a finer posterolingual one which apically tends to be more transverse. Cusps 2–9 are similar in form and become closer and slightly smaller buccally. There is a distinct flexure of the precristae (as in those of the protoloph) near the base of the transverse valley and of the postcristae at the posterior edge. In contrast to those of the protoloph, the cristae show a tendency to bifurcate and very weak ribs are developed. Cusp 10 may be interpreted as a fusion of two cusps because it has two diverging precristae and two diverging postcristae with an intermediate crest. The two buccal cristae are thickened basally. A remnant postcingulum is preserved buccally between the postcristae of cusps 9 and 10 but interdental appression has obliterated it lingually.

The tooth shows considerable, although not extensive, wear and most cristae have wear facets. The transverse valleys are deep and very narrow at the bottom but the lophs themselves are broader, their crests subtending an angle of about 90°, partly as a result of the degree of wear.

The roots of the holotype specimen are better preserved than those described by Stirton *et al.* (1967) for the holotype of *E. serratus*, but the configuration is basically the same. There is a bladed, slightly crescentically cross-sectioned root under the parastyloph, parallel to its buccal face. This fuses basally with a smaller laterally-compressed root under the buccal end of the protoloph. A broad, thin, transverse root supports the bulk of the metaloph. The best-developed root supports both protocone and metaconule. This root is a fusion of two structures, indicated on the lingual face by a deep groove and on its buccal face by a shallower groove. It leans anterolingually and tapers rapidly but only the last 1–2 mm of its estimated 7–8 mm length are missing. The tip of the root is below the protocone. This root configuration differs slightly from that inferred for *Chunia illuminata*, on the basis of maxilla fragment QM F10641, where the bone lamina buccal to the roots has been partly broken away. There the posterior transverse root is thicker and the anterior buccal root seems to be transverse and thicker than the small parastyloph root to which it appears to be fused.

Remarks

The holotype and only known specimen of *Ektopodon litolophus* was found in the same coarse basal unit of the Wipajiri Formation and the same quarry (the Leaf Locality) as the holotype and all other specimens of *E. serratus*. Although this conjunction suggests that the two species may have been sympatric, there is no way of being certain that the single tooth of *E. litolophus* had not been transported from some distance away. Its very rarity might be taken as evidence that it was not normally encountered in the same environment as *E. serratus*. However, the significant size difference (Figure 4) would probably have been sufficient to have enabled these species to be members of a single ecological guild in the same way that different-sized but comparably-shaped congeneric dasyurids are known to coexist (e.g. *Antechinus swainsonii* and *A. stuartii*).

A strong molar gradient is apparent in the maxilla of *Chunia illuminata* (QM F10641), and a lesser gradient may be seen in the maxilla SAM P35309, and inferred from the dentaries SAM P19509 and P29577, of *Ektopodon stirtoni*. It is probable then that *E. serratus* would show even less molar gradient and, in fact, the isolated upper molars referred to *E. serratus* do not differ greatly in size (Woodburne and Clemens 1986b). In view of this, and the differences in morphology (cusp number and complexity), it is unlikely that Leaf Locality specimens previously referred to *E. serratus* include examples of *E. litolophus* posterior molars.

For the same reasons SAM P30176 is almost certainly not an extreme variant of *E. serratus*. The

size difference alone is beyond that shown by the comparable teeth of natural species. Nor is the tooth likely to be an abnormal tooth of *E. serratus*. Its regular wear facets indicate that it occluded with a lower counterpart of similar size and shape, a situation so far unknown in marsupials exhibiting abnormalities on such a scale (Archer 1975).

In representing a fourth species of *Ektopodon*, the tooth shows that some phylogenetic trends can be discerned within both the family and the genus, viz. a general increase in size, increase in number of cusps and decrease in complexity of structure. Also, it shows that the genus was still diversifying during the Miocene.

Ektopodon sp. cf. *E. serratus*
Figure 5

Material Examined

QM F36365, a fragment of a right upper molar, comprising a quarter of the protoloph and most of the metaloph of M^2 or M^3. Collected by M. Archer, H. Godthelp, S.J. Hand and others in May 1986.

Locality and Age

Wayne's Wok Site is in an unnamed freshwater limestone, "System B Sediments" (Archer *et al.* 1989, 1991), Hal's Hill, Riversleigh Station, northwestern Queensland. The Wayne's Wok Local Fauna, a member of Riversleigh System B, is presently interpreted to be between Late Oligocene and Early Miocene in age on the basis of biocorrelation (Archer *et al.* 1989, 1991), and shares many elements with the Upper Site Local Fauna (Godthelp Hill, Riversleigh), which in turn has taxa that are congeneric and (in some cases) conspecific with forms in the Kutjumarpu and Tarkarooloo Local Faunas of northern South Australia (see Introduction).

Description

Although not greatly worn, this specimen has been badly corroded and broken and lacks the buccal edge of the crown. The transverse rather than oblique nature of the lophs indicates that it is an upper molar. A full cusp count cannot be made. Most of the protoloph, including the protocone, is missing but it would have borne at least six cusps. The metaloph bears six cusps with evidence of a seventh on the buccal end. The metaconule is rounded with an anterolingual groove and a bifurcated premetaconulecrista. The precrista of cusp 2 also bifurcates lingually. Cusps 3 and 4 are similar with single cristae. Their precristae each have three small lingual ribs towards the anterior end. The cristae of cusps 5 and 6 are single and simple with no obvious ribs or divisions. Cusps are linked apically with single deep-set fine struts. The buccal face is damaged or missing.

Remarks

QM F36365 is the first ektopodontid described from the northern half of Australia and the only ektopodontid specimen yet recovered from the otherwise richly fossiliferous Riversleigh deposits. Its referral to *E. serratus* is on the basis of similar crestal spacing and development. The relative rarity of the species suggests that ektopodontids were uncommon in the Riversleigh rainforests in Oligo-Miocene times. The damaged nature of the tooth might be seen as support for the hypothesis that this specimen was transported to the Riversleigh area, perhaps by a bird of prey. However, to date several other Riversleigh animals (e.g. yalkaparidontids, Archer *et al.* 1988) were first discovered as small fragments and only much later appeared in abundance when other sites representing slightly different habitats or depositional environments were explored. Thus, it
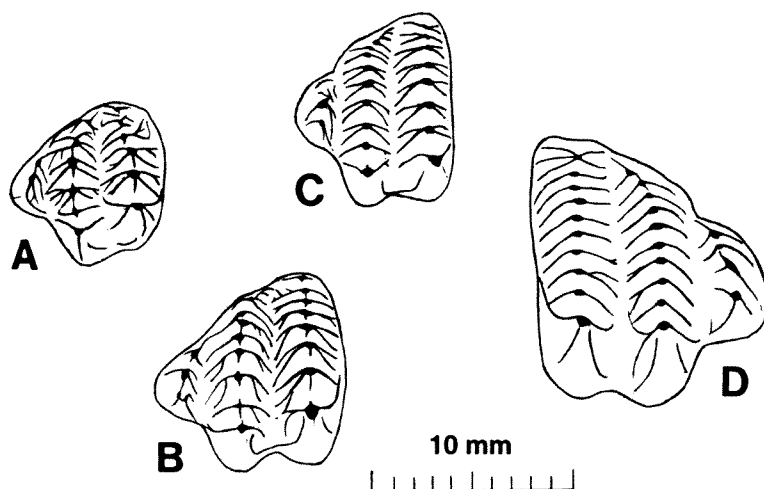
Figure 4 Comparison drawings of known ektopodontid M^1s in occlusal view. A, *Chunia illuminata*; B, *Ektopodon stirtoni*; C, *E. serratus*; D, *E. litolophus*. Scale = 10 mm.
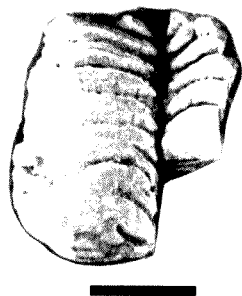
Figure 5 *Ektopodon* sp. cf. *E. serratus*, upper molar fragment QM F36365, Riversleigh, Wayne's Wok Local Fauna. Scale bar = 2 mm.

is probably too early to conclude anything about the significance of the apparent rarity of ektopodontids in the Riversleigh deposits. Further, investigation of the Wayne's Wok Site material is in its early stages with many kilograms of limestone blocks still remaining to be prepared.

The relative simplicity and regular spacing of cusps on this tooth fragment most closely match the condition seen in *E. serratus*, but too little of the tooth is preserved to exclude the possibility that it represents a distinct taxon.

In view of many other overlaps in taxa between the Kutjamarpu Local Fauna and various Riversleigh local faunas (e.g. *Neohelos tirarensis, Wakiewakie lawsoni, Wakaleo* sp. cf. *W. oldfieldi, Emuarius gidju,* and the lungfish *Mioceratodus anemosyrus*) (Archer *et al.* 1989, Kemp 1997), it is not improbable that this Riversleigh ektopodontid will be confirmed as representing another Kutjamarpu taxon.

DISCUSSION

The family Ektopodontidae is now known to contain three to five species of *Ektopodon* (*E. serratus,*

E. stirtoni, E. litolophus, E. sp. cf. *E. stirtoni,* and the Riversleigh taxon), two or three species of *Chunia* (*C. illuminata, C.* sp. cf. *C. illuminata, C. omega*), and *Darcius duggani.* No ektopodontid species occurs in more than a single local fauna and in all but two local faunas (Tarkarooloo and Kutjamarpu) there is only a single ektopodontid species. Further, most are not common in their respective local faunas and three (*E. litolophus, C. omega* and the Riversleigh taxon) are known only from single teeth. In the faunas where more than one species occurs, the sympatric forms are distinct in terms of size and morphology, a situation that may indicate ecological partitioning of species into feeding guilds. Food preferences for these possums are unclear but possibilities include seeds or grains, nuts and insects (Pledge 1982, 1986, 1991).

Species of *Ektopodon* range in age from Late Oligocene to ?Middle Miocene. The oldest (*E.* sp. cf. *E. stirtoni*) occurs in the Tarkarooloo Local Fauna of probably latest Oligocene age and the two youngest (*E. serratus* and *E. litolophus*) in the Kutjamarpu Local Fauna of possible Early to Middle Miocene age. The age of the Riversleigh ektopodontid has been interpreted by Archer *et al.* (1989) to be most probably Early Miocene. Species of *Chunia* range in age from Late Oligocene (Ditjimanka Local Fauna) to latest Oligocene (Tarkarooloo Local Fauna) in age. *Darcius duggani* is only known from the Early Pliocene Hamilton Local Fauna, although an undescribed ektopodontid ascribed tentatively to *Darcius* (T.H. Rich, pers. comm.) is reported in passing by Archer *et al.* (1997) from the Early Pleistocene Nelson Bay Local Fauna.

The *Ektopodon serratus*-like ektopodontid from the Wayne's Wok Local Fauna supports previous suggestions that Riversleigh's System B local faunas share taxa with the Kutjamarpu Local Fauna (Archer *et al.* 1989).

Table 1 Measurements (in millimetres) of ektopodontid upper molar teeth (M^1).

Specimen number	Tooth	Length	Anterior width	Posterior width
Ektopodon litolophus sp. nov.				
SAM P30176	RM^1	10.6	11.7	12.1
Ektopodon serratus				
SAM P13847	LM^1	7.1	7.8	8.4
Ektopodon stirtoni				
SAM P22504	RM^1	8.7	8.9	9.2
SAM P35309	LM^1	8.8	8.3	9.0
Ektopodon sp. cf. *E. stirtoni*				
NMV P48750–1	LM^1	8.5	8.0	–
SAM P19962	RM^1	8.5	–	–
Chunia illuminata				
SAM P29081	LM^1	7.3	6.3	7.0

Chunia
illuminata

Ektopodon
stirtoni

8   **7**

Ektopodon
serratus

6

Ektopodon
litolophus

Darcius
duggani
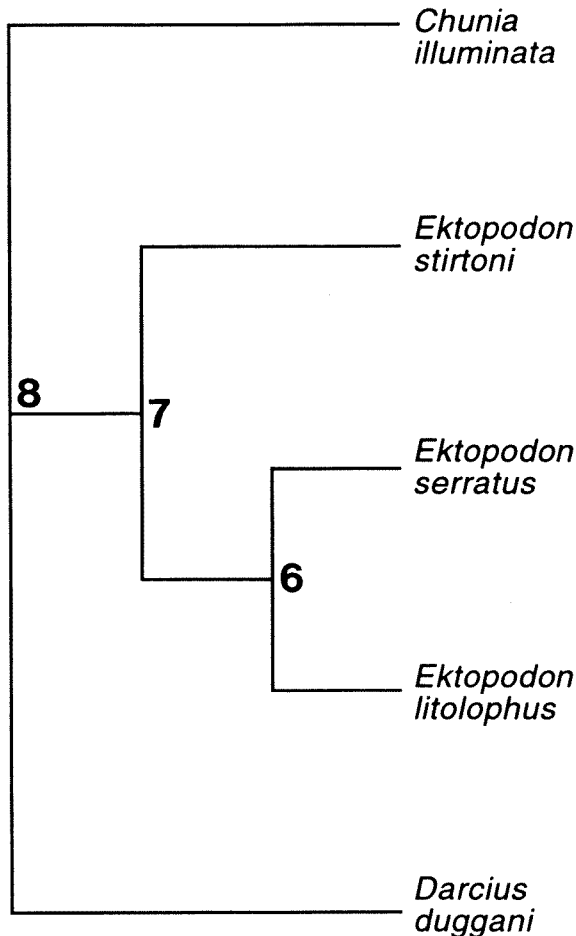
Figure 6   PAUP-derived   cladistic   tree   for
ektopodontids, based on morphology of M¹s.
At node 6, synapomorphic characters are: **1,
3, 15**; at node 7: **4, 7, 14**; and at node 8: **2, 6, 9,
11.**

(and extrapolating for *Darcius* from its lower molars by comparison with *E. stirtoni*) (Table 2), and the nature of the crests and overall proportions of these teeth (Table 3), using PAUP 3.1 (Swofford 1993), gave a single simple tree (Figure 6). Because of the unique morphology of the M¹, no meaningful outgroup could be chosen, so the tree is unrooted.

We suggest here that the new species *Ektopodon litolophus* is best regarded as a sister taxon of *E. serratus* and that both may have been derived from an *E. stirtoni*-like ancestor. This conclusion follows from the observation that *E. litolophus* and *E. serratus* share the evidently synapomorphic condition of transversely widened lophs which also contain a relatively larger number of cusps. Considering that both of the more derived species are contemporaneous, neither is likely to be the other's ancestor. Because of the poor preservation of the Riversleigh tooth fragment, it is not possible to be confident about its affinities, although it appears to be more similar to *E. serratus* in style of crista development and spacing.

ACKNOWLEDGEMENTS

Woodburne and Clemens (1986c) interpreted the phylogenetic relationships of ektopodontids then known. Analysis of the four known ektopodontid species M¹s in terms of cusp and crest numbers

Table 2   Comparison of cusp and crest numbers on M¹ of different ektopodontids. Abbreviations: a = approximate count because of complexity of tooth morphology; e = estimated number by comparison with lower molar.

M¹	*Chunia illuminata*	*Ektopodon stirtoni*	*Ektopodon serratus*	*Ektopodon litolophus*	*Darcius duggani*
Parastyloph					
precristae	1	3	4	4	?
cusps	3	3	4	4	?
postcristae	6	6	5	6	?
Protoloph					
precristae	11	11	13	11	e5
cusps	6	8	8	10	e4
postcristae	13a	14	16	13	e8
Hypoloph					
precristae	14	15	15	13	e7
cusps	7	8	8	10	e5
postcristae	12	13	14	13	e7

Table 3 Matrix of character states in M¹ of different ektopodontids. Plesiomorphic character states indicated by '0'. **1**, three or fewer parastyloph cusps; **2**, four or less protoloph cusps; **3**, six or less protoloph cusps; **4**, seven or less protoloph cusps; **5**, eight or less protoloph cusps; **6**, five or less hypoloph cusps; **7**, seven or less hypoloph cusps; **8**, eight or less hypoloph cusps; **9**, generally more than two precristae per cusp; **10**, generally two or more precristae per cusp; **11**, crests radiating from cusps; **12**, crests bifurcating, parallel; **13**, generally more than one pre- or postcrista; **14**, length equals or exceeds overall width; **15**, l:w ratio more than 0.9; **16**, l:w ratio more than 0.85.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Darcius	?	0	0	0	0	0	0	0	1	0	1	0	0	?	0	0
Chunia	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
E. stirtoni	0	1	1	1	0	1	1	0	1	0	1	0	0	1	0	0
E. serratus	1	1	1	1	0	1	1	0	1	0	1	0	0	1	1	0
E. litolophus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

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