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# New specimens of ektopodontids (Marsupialia: Ektopodontidae) from South Australia

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Abstract

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Knowledge about the extinct phalangeroid family Ektopodontidae is increased by the discovery of new material from several localities. Previously unknown teeth of *Chunia illuminata* and *Ektopodon stirtoni* are described respectively from White Sands Basin and Mammalon Hill, Lake Palankarinna, Lake Eyre Basin, South Australia, with M<sup>1</sup> being recorded for the first time for any species of *Chunia*, and a full maxilla of *Ektopodon stirtoni* showing the positional relationship between P3 and M1 for the first time; this is even more extreme than the arrangement postulated previously. Another species *Ektopodon litolophus* has been described on the basis of an M<sup>1</sup> found at the Leaf Locality, Lake Ngapakaldi, Lake Eyre Basin. Material from Lake Tarkarooloo, referred to *Ektopodon stirtoni*, is redescribed as a new species *Ektopodon tommosi*. Comparisons of M<sup>1</sup> of *Chunia* and *Ektopodon* species now allow evolutionary trends, such as increasing number of cusps on the molar lophs, and simplification of the cusps, to be discerned.

Keywords Marsupialia, Ektopodontidae, *Chunia, Ektopodon*, Ditjimanka, Ngama, Kutjamarpu, Etadunna Formation, Wipajiri Formation, Tertiary, Oligocene, Miocene, Lake Eyre Basin, Australia.

## Introduction

*Ektopodon* is a genus of extinct possum-like marsupials established by Stirton et al. (1961) for isolated teeth found at the early Miocene Leaf Locality at Lake Ngapakaldi, northeastern South Australia. Further specimens from this locality were described and interpreted by Woodburne and Clemens (1986b), together with new, slightly older late 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) and the Frome Embayment (e.g. Tom O's Quarry, Lake Tarkarooloo). A second, later Oligocene species of *Ektopodon* (*E. stirtoni*) was described by Pledge (1986) from Mammalon Hill, Lake Palankarinna (fig. 1.), and specimens also from Lake Tarkarooloo were also referred to *E. stirtoni*.

Rich (1986) described *Darcius duggani* from Hamilton, western Victoria, a deposit radiometrically determined to be Pliocene in age (ca. 4.46 Ma), and *E. paucicristata* from Pliocene sediments near Portland, also in western Victoria (Rich et al., 2006). By 1986 the rich deposits of Riversleigh, northwestern Queensland, were beginning to yield many new species including an unidentifiable ektopodontid, and a second species of *Ektopodon* was found in the Kutjamarpu Local Fauna of South Australia (Pledge et al. 1999). New specimens from Lake Palankarinna referable to *Chunia illuminata* and *Ektopodon stirtoni* are described in this paper. The status of the Tarkarooloo specimens referred to *E. stirtoni* is re-evaluated and a new species erected.

#### Age

Although Stirton (Stirton et al., 1961) 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 Ma; Woodburne et al., 1985), following preliminary analyses by W. K. Harris of pollen, wrongly identified as grasses, from the Etadunna Formation; this was amended to Restionacea (sedge) pollen by Martin (1990). Later work with foraminiferans (Lindsay 1987) suggested that at least some of these deposits may 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), and by Norrish and Pickering (1983) who reported a Late Oligocene Rb-Sr date for authigenic illite from the Etadunna Formation.

## **Collection methods**

Specimens from the Lake Eyre Basin were found by excavation of the fossiliferous horizons or by screen-washing the dried sediment through window screen with mesh of  $6 \times 6$  wires per cm<sup>2</sup>.



Figure 1. Locality map. Ektopodontid localities.

## Terminology

Molar homology follows Luckett (1993). The terminology for the crown morphology of ektopodontid teeth used here is that of Woodburne & Clemens (1986a) with modifications to cusp homology as recommended by Tedford & Woodburne (1987).

#### **Museum abbreviations**

SAM, South Australian Museum; NMV, Museum Victoria; UCMP, University of California, Berkeley; UCMP V, University of California Museum of Paleontology locality number; UCR, University of California, Riverside; SAM PL, South Australian Museum Palaeontological locality.

### Systematic Palaeontology

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

Diprotodontia Owen, 1866

Phalangeroidea (Thomas, 1888) sens. Aplin & Archer (1987)

Ektopodontidae Stirton, Tedford & Woodburne, 1967

## Chunia Woodburne & Clemens, 1986

Chunia illuminata Woodburne & Clemens, 1986

## (Figs. 3A-D)

*Holotype*. SAM P17997. In their original description of *Chunia illuminata*, Woodburne & Clemens (1986b) described the  $RM^2$  holotype SAM P17997 (=  $RM^3$  in their notation following Archer 1978), together with QM F10641 (maxilla fragment with partial  $LM^2$ ), UCR 15228 ( $LM_2$ ) and UCR 15227 ( $LM_2$ ).

*New Specimens*. SAM P29081, left M<sup>1</sup> (figs. 3A–D) collected by J. McNamara 9 July 1987; also SAM P33944, left M<sup>3</sup>, collected by J. Case and J. Clemitson, June 1992, from Tedford Locality.

*Locality.* White Sands Basin (SAM locality PL 7719), 200 m south of Tedford Locality (UCMP V5375, the Type Locality for the species).

*Stratigraphy and Age*. Stratigraphically, White Sands Basin is about one metre below the sandy clay layer in Tedford Locality that produced the holotype. This fauna from the Etadunna Formation is considered to be Late Oligocene in age (see above).

*Revision of specific diagnosis.* In addition to the features noted by Woodburne & Clemens (1986b), including the upper dental formula I<sup>?</sup>, C<sup>1</sup>, P<sup>1.3</sup>, M<sup>1.4</sup>, the M<sup>1</sup> of *Chunia illuminata* differs from that tooth in all other ektopodontids in being smaller, having fewer cusps on its lophs and in having a parastyloph that is less loph-like and more cusp-like than that structure in any known species of *Ektopodon*. The face is 'longer' and less obtuse than that of *Ektopodon stirtoni*.

*Description.* The  $M^1$  of *Chunia illuminata* has the same basic outline as that tooth in other species of *Ektopodon* but differs in several ways noted below. The cusps on the 'protoloph' and 'metaloph' are all worn apically, so some detail has been obscured.

The parastyloph ("paraloph" of Pledge, 1986) is simpler than that structure in other species, being an oblique blade confluent with the buccal face of the tooth and having three cusps. The minute lingual cusp is offset posteriorly from the end of the loph and gives rise to a pair of postcristae that initially diverge, then converge slightly linguad. A weak precrista descends basally from the point of inflection of the loph. The central cusp is by far the largest of the three but, apart from the loph crest, gives rise only to a short postcrista at right angles to it. However, a strong postcrista arises from near the buccal end of the cusp and continues transversely to almost meet the converging postcristae from the lingual cusp. The buccal cusp is separated from the median cusp by a narrow crevice. There are two postcristae, a buccal one forming part of the "parastyloph" and a lingual one that curves transversely and extends half the width of the loph.

The protoloph has four distinct cusps and a complex structure at the buccal end that could represent either two or three smaller cusps. The lingual cusp, the protocone, is a trigonal pyramid with the precrista being stronger than either the postcrista or the lingual extension of the loph crest. Cusp 2 is the smallest with a short precrista cut off by converging precristae from the protocone and cusp 3. Its postcrista is the



Figure 2. Stratigraphic distribution of named ektopodontid species.



Figure 3. *Chunia* spp. teeth: **a-d**. *Chunia illuminata*, Woodburne and Clemens, 1986. **a**. right maxilla. QM F10641, mirror-imaged to show angle of face, Tedford Locality; **b**. M<sup>1</sup> SAM P29081, White Sands Basin; **c**. SAM P17997, (type) M<sup>2</sup> Tedford Locality; **d**. M<sup>3</sup> SAM P33944, Tedford Locality, Lake Palankarinna, Ditjimanka Local Fauna; **e**. *Chunia omega* Woodburne and Clemens, 1986, half of M3? (type) SAM P23065, Tom O's Quarry, Lake Tarkarooloo, Tarkarooloo Local Fauna. Abbreviations: mel, metaconule; pastl, parastyloph; pr, protocone; prl, protoloph; 3, cusp 3; 5, cusp 5.

simplest (after that of the protocone) and extends to the transverse valley; a weak lingual spur arises about halfway along its length and the distal (posterior) end curves lingually to parallel the transverse valley. Cusps 3 and 4 are basically similar, each being large and having a pair of subparallel precristae and postcristae that are angled slightly linguad. Cusp 3, however, also has a third slightly sinuous precrista, two weak ribs on the buccal face of the outermost precrista and a bifurcation of the buccal postcrista. Cusp 5 shows two strong postcristae reaching the transverse valley and a shorter, bifurcating buccal postcrista. Anteriorly, two sinuous precristae are linked by two or more near-apical struts and a basal strut. The lingual precrista bifurcates just below a strut linking it with the buccal precrista of cusp 4. All cusps (1-5) are linked apically by a fine transverse strut. Cusp 6 is displaced posteriorly and is a small trigonal structure with pre-, post- and transverse cristae.

The transverse valley is deep, trenchant, slightly curved and anteriorly convex. No structures cross it except at the lingual end where there is a notched cingulum. Buccal to this are three weak irregular postcristae at the base of the protocone and four irregular precristae on the metaconule, none of which cross the valley. The lingual cingulum curves and extends up the lingual face of the metaconule (i.e. the posterolingual cusp of diprotodontians previously called the hypocone; see Tedford & Woodburne, 1987).

The metaconule is stronger and more bulbous than the protocone. Besides the irregular basal precristae, there are two short postcristae that form a small pocket on the posterior face. The main precrista is aligned with the main postcrista and with the postcrista of cusp 2 of the protoloph. Cusp 2 of the metaloph is similar in size to cusp 3 of the protoloph. Besides the strut linking it to the metaconule, both of the pre- and postcristae bear several transverse ribs on the lingual face of the lingual cristae and the buccal cristae bifurcate basally. Cusp 3 is similar but with fewer and weaker ribs; only its buccal postcrista bifurcates. However, the apex of the cusp appears to be a triangle of short crests with its base aligned with the buccal cristae. Buccally from here, the structure is unclear. Cusp 4 appears to be a relatively simple structure with a single precrista and a postcrista bearing several weak lingual ribs. Near its apex, however, a short crest leaves posterobuccally to join one coming anterolingually from another, posteriorly offset cusp. A short postcrista arises at the junction of these crests but does not reach the posterior cingulum. This posterior cusp also bears four other radiating crests, two being aligned longitudinally and the others antero- and posterobuccally. Buccal to cusp 4 are three or four weak cusps defined by four simple precristae alternating with three short postcristae that do not meet the cristae from the posterior cusp. At the base of these precristae a low transverse crest parallels the transverse valley. A distinct postcingulum extends from the buccal-most postcrista to the metaconule. Pledge (1986) attempted to equate these buccal structures (in species of Ektopodon) with the cusp and crest patterns common in diprotodontians but it now appears, even in this relatively plesiomorphic species, that the homology of these cusps in ektopodontids is unclear.

M<sup>3</sup>. The new specimen found by Case and Clemitson SAM P33944 is almost identical to, but the mirror image of, the holotype SAM P17977, and paratype SAM P22722 M<sup>2</sup>s from

the same locality. It differs in being slightly longer and narrower, with slightly more prominent equiradial development of crests and struts, and is thus accorded here a more posterior position. This tooth bears some resemblance to the incomplete type specimen of *Chunia omega* (fig. 3E) from the Tarkarooloo Local Fauna (Woodburne and Clemens 1986).

Ektopodon Stirton, Tedford & Woodburne, 1967.

*Distribution.* Kutjamarpu Local Fauna, Wipajiri Formation, Lake Ngapakaldi; Ngama Local Fauna, Etadunna Formation, Lake Palankarinna; Tarkarooloo Local Fauna, Namba Formation, Lake Tarkarooloo; Portland Bay Local Fauna, Whalers Bluff Formation, Portland.

Age. Late Oligocene to early-mid Miocene, Pliocene.

*Diagnosis (revised).* As for Woodburne and Clemens (1986b) but with the revision of the dental formula which is now understood to be: I?/1, C1/1, P3/3, M1-4/1-4. This revision involves recognition of the presence of only a single premolar.

Ektopodon serratus Stirton, Tedford & Woodburne, 1967.

Holotype. SAM P 13847. (Fig. 6B).

#### Ektopodon tommosi sp. nov.

*Ektopodon* sp. cf. *E. stirtoni* Pledge 1986, pls 3.1D, F, G; 3.2; 3.3D-E (fig. 4).

Holotype. SAM P19962 (RM1).

*Paratypes.* NMV P48750-48751 (LM<sup>1</sup>), SAM P19963 (RM<sup>2</sup>), SAM P19950 (RM<sub>1</sub>), NMV P48752 (LM<sup>2</sup>), NMV P48753 (LM<sup>3</sup>), NMV P48757 (LM<sup>4</sup>), NMV P48764 (LM<sub>2</sub>), NMV P48765 (RM<sub>3</sub>), NMV P48766 (RM<sub>4</sub>).

*Referred specimens*. NMV P48758 (right lower incisor), NMV P48769 (partial LP<sup>3</sup>), SAM P19965 (RP<sub>2</sub>).

*Locality*. Tom O's Quarry, western shore of Lake Tarkarooloo, Callabonna Basin. 31°8.5'S., 140°6.3'E.

*Horizon*. A sandy channel deposit within the Namba Formation (Callen & Tedford, 1976).

Age. Late Oligocene, Tarkarooloo Local Fauna. Biocorrelation suggests this is faunistically equivalent to the Ngapakaldi Local Fauna of the Lake Eyre Basin (Rich and Rich, 1987), which is a little older than the latest Oligocene Ngama L.F. of Lake Palankarinna, but younger than the Pinpa L.F. from Lake Pinpa.

*Diagnosis.* The molar teeth are generally 5–10% smaller than comparable elements of *E. stirtoni*, and the loph(id)s generally have one less cusp. The protostyloph on  $M^1$  is shorter and less loph-like with two cusps, one less than in *E. stirtoni*. The P<sup>3</sup> is larger than that tooth in *E. stirtoni*. The mandible is slightly larger than in other species, with a longer diastema.

*Etymology.* The species name reflects the source of these specimens, Tom O's Quarry site, (discovered by Cpl. John Thompson – 'Tom O' to distinguish him from Tom Rich – of  $3^{rd}$  RAAME which provided logistic support for Rich's 1974 expedition; Rich and Archer, 1979), at Lake Tarkarooloo.



Figure 4. Dentition of *Ektopodon tommosi* nom. nov. **a**. composite upper dentition, anterior at left: LM<sup>1</sup> fragment (NMV P48750), partial RM<sup>1</sup> (SAM P19962), LM<sup>2</sup> (NMV P48752), RM<sup>2</sup> (SAM P19963), LM<sup>3</sup> (NMV P48753), LM<sup>4</sup> (NMV P48757); **b**. LM<sup>3</sup> (NMV P48753); **c**. RM<sup>2</sup> (SAM P19963); **d**. RI<sub>1</sub> (NMV P48758); **e**. RM<sub>1</sub> (SAM P19950. Tom O's Quarry, Lake Tarkarooloo; Tarkarooloo Local Fauna. Abbreviations: mel, metaconule; pastd, parastylid; pastl, parastyloph; pr, protocone.



Figure 5. *Ektopodon stirtoni* Pledge, 1986, holotype dentary and new material. **a-c**. new maxilla (SAM P35309): **a**. lateral; **b**. dorsal; **c**. palatal; **d**. RM<sup>2</sup> (P23854); **e**. LM<sup>3</sup> (P30175); **f**. LM<sup>3</sup> (SAM P30156); **g**. right dentary (SAM P29577), lateral aspect; **h**. right dentary with  $M_{2.4}$  (SAM P29577) stereo pair; **i**, **j**. holotype right dentary with  $P_3$ ,  $M_{1.3}$  (SAM P19509); **k**. LM<sub>3</sub> (P31638); **l**. RM4 (SAM P33451). Ngama Quarry, Mammalon Hill, Lake Palankarinna; Ngama Local Fauna.



Figure 6. Ektopodontid spp.; comparison of first upper molars. **a**. *Chunia illuminata* SAM P29081 (left); **b**. *Ektopodon serratus* SAM P13847 (left); **c**. *Ektopodon stirtoni* SAM P22504 (right); **d**. *Ektopodon litolophus* SAM P30176 (right); **e**. *Ektopodon tommosi* NMV P48750-1 (left); **f**. *Ektopodon tommosi* SAM P19962 (right); **g**. *Ektopodon ulta* (from Megirian et al. 2004:719, fig. 15A); **h**. *Ektopodon paucicristatus* (from Rich et al. 2006:137, fig. 3D). Scale bar approximately 1 cm, for a-d; others about same scale. Abbreviations: ca, canine alveolus; fo, infraorbital foramen; mjs, maxillojugal suture; pastl, parastyloph.

*Description.* See Pledge (1986: 53–60) for a more-complete description. The following is abbreviated and has updated terminology.

P<sup>3</sup>. There are still only two fragments known; the incomplete specimen (NMV48769) referred to this taxon by Pledge (1986) is correctly ascribed. It agrees morphologically with the P<sup>3</sup> of *E. stirtoni* (see below) as far as can be compared, but is noticeably larger (length >5.6, width 4.1 vs. length 5.5, width 3.4). The curving longitudinal crest extends from a conspicuous anterior cusp at the anterolingual corner of the tooth. At the midway point, a deep angular saddle divides the crest, separating the anterior cusp from two closely-linked larger posterior cusps. The latter are separated by a deep narrow crevice. The crest ends at the posterolingual corner of the tooth. Its lingual face has a weak basal cingulum with two small cusps.

 $M^1$  (fig. 4A). Only three fragmentary teeth have been found, the holotype, SAM P19962 being one of them. The latter is quite worn and lacks the lingual margin, but compares well with P22504, the M1 of *E. stirtoni* from Mammalon Hill. However, it differs, apparently, in having one less cusp on each loph and a shorter protostyloph with only two well-developed cusps and the trace of an incipiently-developed third cusp.

M<sup>2</sup> (figs. 4A, C). This molar is broad, roughly trapezoidal, and the largest of the upper molars having only two lophs. The protoloph, with eight cusps, is slightly longer than the metaloph, which has seven, and the crests of the lophs slightly twisted rather than being in the same plane. The crests are also not as sharp as those structures on M<sup>1</sup>, nor the transverse valley as deep. On the protoloph, the protocone bears a pair of deep grooves on its anterior and posterior sides, but the resulting ridges do not bifurcate. Similarly, the cristae of the second protoloph cusp do not bifurcate, but those of the 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> cusps do (the last only on the posterior side). Similarly on the metaloph, the metaconule has a pair of deep grooves, and the 2<sup>nd</sup>, 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> cristae bifurcate, the last only on the anterior side. The posterior groove of the protocone joins with the anterior one on the metaconule to form a deep buccal pocket. All cusps on a loph are joined by a fine, deepset apical 'strut' along the axial plane of the loph. All cristae are cut off by the pre- and post-cingula.

M<sup>3</sup> (figs. 4A, B). This tooth is of similar length to M<sup>2</sup> but is noticeably narrower, and therefore trapezoidal in outline. The protoloph has eight cusps and extends beyond the metaloph at each end. The metaloph probably has seven cusps, but the count is uncertain because of the difficulty in distinguishing between primary cristae and bifurcations. Fine linking struts between cristae increase in number buccally to at least four at the paracone.

 $M^4$  (fig. 4A). This tooth appears to be a stunted version of  $M^3$ . It is triangular, and bears only the protoloph which is of low relief and has seven or eight cusps (number uncertain because of the irregular bifurcation of the cristae). The missing metaloph is replaced by the third corner of the triangle: an inchoate network of low crests. The metaconule appears to have merged into the protocone, and that combination presents as a square extension of the protoloph.

Dentaries. Three dentaries are known, one retaining a fragment of the hypolophid of  $M_3$ ; the others may be a pair. They

are relatively massive, are slightly larger than those of *E. stirtoni*. Compared with the latter, they have a more convex ventral profile, and a longer diastema, but the alveolar cheek-tooth length is shorter. A minute alveolus (for a canine?) immediately follows that of the incisor on its dorso-lateral corner.

 $I_1$  (fig. 4D). An isolated right incisor is referred to this position, based on size and its semicircular cross-section to fit the alveolus. It is short, high and somewhat spatulate, but it cannot be proven to relate to this species.

 $P_3$ . This tooth is represented by three specimens. It is smaller than the  $P_3$  of *E. stirtoni*, and more subdued in its features, but otherwise similar. It is ovate in outline, and has on the lingual side a longitudinal cristid that bears four cuspids. An isolated anterior cuspid is followed by a central slightly larger one, then a third even larger one to which is appressed a smaller fourth cuspid. A posterobuccal cingulum forms a small pocket.

 $M_1$  (Fig. 4E). SAM P19950 is the only complete specimen of this tooth known. It can be recognised by its distinctive 'parastylid'. The tooth is roughly rhomboid in outline and wider than long. The 'parastylid', at the anterolingual corner of the tooth, is more prominent than that structure in *E. stirtoni*. The lingual face of the tooth is relatively flat; the buccal ends of the lophids are quite swollen. Lophid crests are sharp and parallel to themselves, but not to the anterior and posterior faces of the tooth. The six protolophid cuspids are not as well-graded as in *E. stirtoni*. The two most buccal are very closely appressed, while the other four are well-spaced. The same pattern of distribution of cuspids characterizes the hypolophid. The precristids of cuspids 2–4 on the protolophid bifurcate. The same occurs for cuspids 1–3 on the hypolophid.

 $M_2$ . This tooth is relatively longer than  $M_1$  and has a more open transverse valley. Each lophid has seven cuspids, the inner-most two being combined. On the protolophid, only the precristid of the protoconid divides, and its lingual branch divides again. On the hypolophid, the hypoconid and cuspid 2 divide on both sides. Although this occurs on cuspid 3, it does so only on the precristid. The precristid of the metaconid has a small notch, as it does in  $M_1$ , but it does not develop a 'parastylid' at the precingulum.

 $M_3$ . This tooth is not represented by a complete specimen. A fragment of hypolophid is preserved in the dentary NMV P48767, Although another  $M_3$ , NMV P48765, is more complete, it lacks the protoconid and hypoconid. Based on what is preserved, these specimens show a morphology similar to that of *E. stirtoni*, with low lophids and a wide transverse valley. On both lophids, the postcristids of cuspids 2 and 3 divide, and on the hypolophid, the precristids also. The lingual part of the crown develops into a network of fine cristids and struts, which differs in the extent of this network development from that in the  $M_2$  of *E. stirtoni*.

 $M_4$ . Despite their superficially different appearances, two specimens, SAM P19966 and NMV P48766, have been identified as  $M_4$ s. The former is incomplete and slightly more worn than the other; both are from right dentaries. They are roughly triangular as a result of reduction of the entoconid, and are low-crowned with very low, broad lophids. There are six to seven cuspids on each lophid, the number uncertain because of similarities and irregularities of cristids and ribs. The transverse valley is an irregular network of anastomosing cristids and ribs. These teeth are elongate (length:width ratio about 1.14). NMV P48766 fits the alveolus of jaw NMV P48767.

Ektopodon stirtoni Pledge, 1986.

(Fig. 5)

Pledge (1986) named this taxon on the basis of a right dentary with  $P_3 M_{1-3}$  (SAM P19509) and an isolated RM<sup>1</sup> (P22504). The new material described here adds considerably to knowledge about this species.

New specimens, SAM P23854, RM<sup>2</sup> with lingual root, collected by J. McNamara, 13 July, 1981; SAM P24541, LM, hypolophid, collected by N. Pledge, August, 1983; SAM P23989, RM, hypolophid with root, collected by N. Pledge on 5 September, 1982; SAM P23988, LM, crown, collected by N. Pledge, 5 September, 1982. All the above were noted (per measurements only) in Pledge (1986). The following have not previously been noted. SAM P29577, right dentary with M<sub>2.4</sub>, collected by D. Williams, 3 July, 1988; SAM P30156, LM<sup>3</sup>, collected by H. Aslin, 1 September, 1989; SAM P30175, LM<sup>3</sup>, found by J. Thurmer, 1 November, 1989 (fig. 4); SAM P31637, left maxilla with M<sup>2</sup>, found by J. McNamara, 27 July 1990; SAM P31638, a left M, found by B. McHenry, August 1990; SAM P33451, a right M<sub>4</sub> collected by G. Aldridge, October 1991; and SAM P35309, a left maxilla, with P<sup>3</sup>M<sup>1-3</sup> but missing the canine and M<sup>4</sup>, collected by N. Haines, 8 August, 1995.

*Locality*. Mammalon Hill (SAM locality PL7611; the Type Locality for the species), northwestern shore of Lake Palankarinna, South Australia.

*Age.* The Ngama Local Fauna comes from the Mammalon Hill beds (zone D) of the Etadunna Formation. The age of this horizon is uncertain but considered to be Late Oligocene (Pledge, 1984; Woodburne, 1986; Woodburne et al., 1994).

*Revision of specific diagnosis.* In addition to the diagnostic features noted by Pledge (1986), these additional specimens of *Ektopodon stirtoni* demonstrate that this species differs from *E. serratus*, in greater size, greater length/width ratio of the molars and fewer cusp(id)s. It differs from *E. litolophus* (Pledge et al., 1999) in its smaller size, relatively narrower M<sup>1</sup>, relatively less regular parastyloph with less uniformly sized cusps, fewer and less uniformly-sized cusps on main lophs with obvious ribs and struts, presence of posterior cingulum. The face is blunter than that of *Chunia illuminata* (compare figs. 3A and 5B, C).

The original description of *E. stirtoni* (Pledge 1986) dealt with the holotype dentary and an M<sup>1</sup> (ibid. plate 3.1B). In the dentary, only the P<sub>3</sub> and M<sub>1</sub> were complete. The present work includes descriptions of the other lower molars (M<sub>2.4</sub>) as well as that of P<sup>3</sup>, M<sup>2</sup> and M<sup>3</sup>. These descriptions incorporate specimens previously noted only in the table of measurements (ibid. table 3.1).

*Descriptions*. Maxilla. Although the (mostly edentulous) maxilla of *Chunia illuminata* had been known for some time (Woodburne and Clemens, 1986b), it did not fully prepare us for the morphology shown by the new specimen of *Ektopodon*.

SAM P35309 is virtually complete, lacking only the thin bone on the medial edge of the palate at the midline suture, the dorsal wing of the maxilla with the nasal contact, the small canine, and the last molar  $M^4$  (figs. 5A-C).

However, part of the jugal which forms the lower border of the orbit and part of the zygomatic arch is also present. This enables us to form a picture of the face of Ektopodon. The orbits had an estimated diameter of up to 15 mm, and were directed forwards and upwards in a wide (est. 50 mm across cheekbones) flat face with a short, narrow muzzle. The lateral face of the maxilla is gently convex, almost flat, from canine to malar process of the zygomatic arch. There is no malar depression or fossa. The maxillo-jugal suture is gently sinuous from just behind the malar to the anterior 'corner' of the orbit, with the jugal tapering from less than 3 mm below the orbit and being a uniform 3 mm wide inside the edge of the orbit. The bottom edge of the eye socket is 5.5 mm above the molar occlusal surface. The infraorbital foramen is ovate and situated about 4 mm behind the canine and 3-4 mm above the diastemal crest; it emerges 12 mm posterior in the orbital floor.

The molar occlusal surface shows a slight torsion along its length. The combined length of the cheektooth row,  $P^3$  to  $M^3$  is 23.2 mm. The maximum bone length, from canine alveolus to posterior extremity of the palate, parallel to the molar toothrow, is 37.3 mm. The width of the maxillary palate to the lingual margin of the molars is (2x) 12.7 mm. The maximum palate width measured to the buccal edge of the molars is 22.2 mm.  $M^4$  is represented by three alveoli.

Canine. Not much can be said of this tooth based on its alveolus, apart from its existence and its gingival diameter: maximum 2 mm. The alveolar depth of 5 mm suggests it was neither a large nor particularly functional tooth. It is situated at the extreme corner of the maxilla, next to the premaxillar suture.

 $P^3$  (fig. 5C). Previously, the ektopodontid  $P^3$  was known only from two referred fragments from Lake Tarkarooloo (Pledge, 1986). These have here been reinterpreted (below) to represent *E. tommosi* n. sp.

The P<sup>3</sup> of SAM P35309 is somewhat recumbent, with its anterior root extending well into the diastema. However, it is almost transverse to the long axis of the molar-row, and its posterolingual corner is tucked neatly into the angle formed by the 'protostyloph' and the protoloph of the first molar. The tooth is fairly typical of the permanent premolars of many diprotodontans: somewhat rectangular with a longitudinal ridge just buccal of the centre-line bearing two major cusps, and a shorter, lower lingual cingular ridge with an anterior expansion that forms a prominent anterolingual corner and is the base for a strong transverse ridge ascending to the anterior cusp. Anterior to this ridge is a slightly weaker and shorter one, midway between the transverse ridge and the trenchant anterior extension of the longitudinal ridge. The longitudinal ridge is crossed by a deep valley that separates the anterior cusp from the slightly lower, double, posterior cusp; the crest from the hind part of this cusp curves around to connect with the posterior end of the lingual cingulum. There are two or three small transverse crenulations in the cingular valley. The longitudinal crest is slightly convex buccally, and is almost perfectly aligned with the anterior transverse crest (the 'parastyloph') of M<sup>1</sup>.

M<sup>1</sup>. This tooth in SAM P35309 is almost identical to the paratype SAM P22504 described by Pledge (1986).

M<sup>2</sup>. In Pledge (1986), the M<sup>2</sup> of *Ektopodon tommosi* from Lake Tarkarooloo was depicted for purposes of illustrating morphology in Text Fig 3.5 (ibid.) as that of *E. stirtoni*, the tooth having not then been found at Mammalon Hill. This deficiency has now been rectified with discovery of specimen SAM P23854 – an RM<sup>2</sup> still partly *in alveolo* in a fragment of maxilla (it lacks only the buccal face of the tooth), SAM P31637 with a complete LM<sup>2</sup> in most of the maxilla, and SAM P35309, an almost complete maxillary dentition (figs. 5A–C).

This bilophodont tooth is wider than long. The protoloph is slightly wider transversely than the metaloph. The tooth's length is 6.8 mm; its maximum width is 9.5 mm.

The protoloph has eight distinct cusps and an indication of at least one more (as does the metaloph). This is more than in E. tommosi (from the slightly older Tarkarooloo LF). The apices of the protocone and metaconule are equal in height, but the lingual extremity of the base of the former is more acute and thus extends slightly farther in a lingual direction. There is a large, deep groove on the anterior face of the protocone and a slightly weaker posterolingual one that extends into the pocket formed by the short but strong lingual cingulum at the end of the transverse valley. Strong pre- and postprotocristae extend in a slightly buccal direction (in the same way that comparable crests extend from the metaconule) giving a hint of remnant selenodonty. The preprotocrista meets the lingual end of the anterior cingulum. The other precristae do not join or only just contact the precingulum. Cusp 2 is smaller and simpler than either the protocone or cusps 3 or 4. It has a single undivided longitudinal crest and is linked to the protocone by an apical strut and a basal strut from the postcrista. Cusp 3 has a strong pre- and postcrista, with a somewhat weaker parallel set arising lower on the lingual face. It is linked to cusps 2 and 4 by a fine low apical strut. Cusp 4 is similar but the lingual pair of cristae is slightly stronger. Cusps 5 to 8 bear undivided pre- and postcristae which are linked by 2 or 3 subapical struts and several short basal ribs. The extent of the median valley indicates at least one more cusp and possibly two.

In occlusal view, only the metaconule on the metaloph is opposite its counterpart cusp (the protocone) on the protoloph. The metaconule is rounder than the protocone and the two grooves diverge antero- and posterolingually, the anterolingual groove running cingular into the pocket. The postmetaconulecrista runs into a very narrow postcingulum to which the other postcristae are weakly joined. Cusp 2 is large and well-spaced from both the metaconule and cusp 3. Its precrista bifurcates basally, with the new rib extending lingually towards the thickened basal ends of the premetaconulecrista and the postprotocrista. Short struts link it anterobasally and apically to the metaconulecrista and there is a short lingual rib from the postcrista. Cusp 3 is similar to that of the protoloph. Cusp 4 is finer with a bifurcating precrista and a short basal lingual rib from the postcrista. It is linked by an apical strut to cusps 3 and 5. Cusps 5 and 6 are similar with undivided cristae that bear a few short irregular ribs. Cusp 6 joins apically to cusps 5 and 7 with a fine strut. Cusp 7 is irregular, having a fine wavy crista bearing several short ribs or broken struts that link with the remnants of cusp 8.

Of the roots, only the double lingual one supporting the protocone and metaconule is preserved, although its tapered tip is missing. Anterior and posterior transverse roots are represented by their bases which support the buccal ends of the protoloph and metaloph respectively.

SAM P 23854 (fig. 5D) is similar in appearance and construction to the M<sup>2</sup> referred by Pledge (1986) to *E*. sp. cf. *E*. *stirtoni* (=*E*. *tommosi*) from the Tarkarooloo LF. It differs in two obvious respects: (1) the relatively and absolutely greater width of the Mammalon Hill M<sup>2</sup> resulting from (2) at least one extra cusp at the buccal end of each loph. In these features, it appears to be autapomorphic within the genus. In P 31637, by some aberrant occlusal wear or damage, cusps 2–4 on the protoloph and cusp 3 on the metaloph are exceedingly worn, far more so than the other cusps.

 $M^3$ . This tooth is represented by two specimens, SAM P 30156 (fig. 5F) and SAM P 30175 (fig. 5E), both slightly damaged by the loss of enamel on the buccal face. The former is the better preserved.  $M^3$  has been described from *E. tommosi*, e.g. NMV P48753, at Lake Tarkarooloo, hence a direct comparison is possible with these two additional specimens.

The  $M^3$  of *Ektopodon stirtoni* is slightly larger than that of *E. tommosi* and in occlusal outline is less tapered posteriorly since the metaloph is relatively longer and less acutely truncated. The detailed structure of cusp ribs and struts is also less complex. The tooth is 6.7 mm long.

The protoloph is 8.9 mm wide and has eight distinct cusps. It is similar in most respects to that of  $M^2$ , differing in that the posterolingual groove of the protocone does not flow into a pocket formed by a lingual cingulum, and in that there are more links joining the crests of cusps 7 and 8. By the same token, the protoloph differs from that of *E. tommosi*, in having fewer subapical links and struts between the crests of cusps 5 to 8. They are similar in lacking the lingual basin.

The metaloph is 7.6 mm wide with six distinct cusps and a buccal complex. The metaconule is situated somewhat more buccally than the protocone, but not level with cusp 2 of the protoloph. However, the crests of the metaconule do align with those of protoloph cusp 2. Similarly the cristae of metaloph cusps 2 and 3 align with those of protoloph cusps 3 and 4. The pre- and post-cristae of cusp 2 each have an accessory crista that is rather sinuous and arises from further down on the lingual face, parallel to the main crista. This is similar to cusp 3 of the protoloph. Cusp 3 is a smaller version of cusp 2; both have a basal bifurcation of the precrista. Cusp 4 is smaller still, with both pre- and post-cristae bifurcating. The cristae of cusp 5 do not bifurcate, but have several struts and/or ribs on the buccal face alongside the fine apical strut linking the cusp to cusp 6. The cristae of cusp 6 are rather zig-zag because of the several struts linking them to cusp 5 and to the missing buccal face. The putative apical strut linking to cusp 7 is displaced anteriorly and there is a short simple precrista from the apex. Parallel to this is an even shorter precrista (half the length of that of cusp 7), which would arise from the buccal edge of the tooth.

The metaloph thus differs from that of  $M^2$  in ways consistent with the posterior narrowing of the tooth and the molar gradient. It differs from that of *E. tommosi* in its greater relative and absolute width, and lesser buccal angular truncation, with consequent better development of the postcristae of cusps 5 to 7.

The maxilla of *Chunia illuminata* (QM F10641) (fig. 3A) suggests from its alveoli that there is a steep molar gradient in that species. The dentary of *Ektopodon stirtoni* (SAM P19509) indicates that the gradient is less in this species. The new specimens of M<sup>3</sup> described in this paper confirm that it is also less than in *E. tommosi*, although the alveoli preserved in maxilla P31637 are too damaged to enable tooth gradients to be determined with confidence.

The maxilla SAM P31637 is damaged on all sides. The root of the zygoma is split and the maxilla is broken anteriorly through the alveolus of  $M^1$ . The alveolus of  $M^3$  is damaged buccally and that of  $M^4$  is broken across, while the medial edge of the fragment is irregular with no part of the median suture being preserved. While the endocranial surface of the palatal wing of the maxilla is smooth and relatively flat (slightly concave anteriorly), the oral (ventral) surface is noticeable convex anteroposteriorly, rather as it is in *Phascolarctos cinereus*. This characteristic is not evident in *Chunia illuminata* where the palate is relatively flat.

Lower dentition. Dentary, SAM P29577, (figs. 5G, H) is broken off just anterior to the position of  $M_1$ , which is missing. It preserves molars  $M_{2.4}$  in good but more-worn condition than the holotype. The horizontal ramus is torted, and the toothrow lies at an angle of about 30° to this portion of the dentary.

 $M_2$ . In the holotype, this tooth is incomplete, having been reconstructed from numerous tiny fragments. Dentary SAM P29577 presents a complete but worn  $M_2$ , while SAM P24541 is a slightly worn hypolophid of an  $M_2$  and SAM P31638 a perfect  $M_2$  crown. The following description is based on the last, with additional comments on the others where appropriate.

The  $M_2$  is somewhat rhomboidal in occlusal outline with protolophid and hypolophid having about the same transverse width. In P29577, both protoconid and hypoconid are extremely worn with the enamel breached and the dentine deeply excavated, but only a few of the adjacent cuspids have been breached. In contrast, P31638 is virtually unworn.

The protolophid in P31638 has seven cuspids (eight in P29577) with the protoconid being much larger than the others. Its crest is oblique (at about 80°) to the lingual face. The protoconid in P29577 is so deeply worn that it merges with the second cuspid and the two are difficult to distinguish. In P31638, as in the holotype SAM P19509, cuspid 2 is a single, simple plate closely appressed to the protoconid. On the protoconid, the anterobuccal groove is flanked buccally by a low crest and lingually by a parallel crest that seems (in P29577) to arise from the precristid of cuspid 2. The precristid curves buccally to merge with the remnant of the precingulid. Posteriorly the posterobuccal groove of the protoconid is flanked by a fine cristid arising from the postprotocristid. The postcristid of cuspid 2 has a short buccal rib. The enamel of cuspids 3-6 of P29577 is breached, leaving a thicker and higher ridge on the buccal side. Precristids of cuspids 3-5 are simple but divide slightly as they merge with the precingulid. Their postcristids expand slightly in the base of the transverse valley and each has a minor buccal rib. Cristids of cuspid 6 (and 7 in P29577) are simple. The innermost cuspid (7 of P31638 and 8 of P29577) has a bifid precristid with a basal cuspule (homologous with the larger structure in  $M_1$  of the holotype) developed at the lingual corner of the precingulid.

The hypolophid parallels the protolophid. The hypoconid has deep anterobuccal and posterior grooves separating the bulbous buccal part from the rather sinusoidal cristid. The precristid curves buccally and the postcristid lingually to merge with the postcingulid. All six cuspids of P29577 have breached enamel. Precristid 2 has a weaker buccal rib and an expanded base; postcristid 2 is bifid at its base. On cuspid 3, the precristid is trifid with a weak buccal rib, a stronger lingual rib and the main crest expanded in the bottom of the transverse valley. The postcristid is bifid at its base. Cuspids 4 and 5 are similar, with simple undivided cristids. Cuspid 6 is complex with three parallel anterobuccal cristids which decrease rapidly in size lingually as they are truncated by a low, transverse cristid in the transverse valley. There are two parallel postcristids, the lingual one of which is shorter and cut off by the curving end of the postcingulid. The postcingulid is well developed.

The hypolophid (SAM P24541) has a transverse width (i.e. normal to the lingual face) of 6.4 mm. Characteristically for lower molars of Ektopodon spp., the lophids are oblique to the tooth row with an acute anterolingual corner. There are seven cuspids, the inner two being combined. The hypoconid is large, its apex just buccal of the mid-line of the tooth. It has a deep anterobuccal groove that swings out basally and an almost longitudinal posterobuccal groove. The cristid obliqua curves buccally and divides basally. The posthypocristid is longitudinal. Cuspid 2 is on the midline of the tooth. Its preand postcristids parallel those of the hypoconid and give rise to shorter, basal supplementary cristids on the buccal side. A notched apical strut links the cuspids. Cuspid 3 is more complex with the precristid bifurcating and the postcristid trifurcating. Cuspids 4 and 5 are similar, simple cuspids, linked apically by fine struts. Their cristids do not divide. Cuspids 6-7 are complicated in being almost inseparable but having two diverging pre- and postcristids. The lingual-most precristid is short and notched to produce a basal cusp that extends as a "cingulum" along the transverse valley to the precristid of cuspid 4. All but the penultimate postcristid merge into the postcingulum.

This tooth fragment is similar to that of *E. tommosi* (NMV P48764) but its ornamentation is less developed. It is smaller than both that specimen and the holotype of *E. stirtoni* but larger than  $M_3$  of *E. stirtoni*.

 $M_3$ . This tooth is incomplete in the holotype and poorly known in *E. tommosi*. It is now represented, however, by a complete (but worn) tooth in dentary SAM P29577 and by hypolophid SAM P23989.

The  $M_3$  resembles that of P29577 except for its lesser degree of wear. Only cuspids 1–3 of the protolophid and cuspids 1–5 of the hypolophid have been breached. There are eight protolophid cuspids and six or seven hypolophid cuspids. The anterolingual cuspule is smaller than in  $M_2$  but slightly larger than in  $M_4$ . The tooth is smaller than  $M_2$  and less rhomboid in outline, with the hypolophid narrower than the protolophid.

Hypolophid SAM P23989 is rectilinear and orientated obliquely at about 75-80° to the longitudinal axis of the tooth. The width of the hypolophid is 5.6 mm. There are seven cuspids. The buccal-most cuspid, the hypoconid, is at about one quarter the distance from the buccal end. It has a broad, shallow anterobuccal groove and a shallower posterior groove. The cristid obliqua is longitudinal but swings buccally at the base as it joins a basal strut from the second precristid. The posthypocristid curves lingually and joins the well-developed postcingulum. Cuspid 2 has simple undivided pre- and postcristids; the precristid of cuspid 3 divides halfway; and cuspids 4 and 5 have simple undivided cristae. Cuspid 6 lacks a postcristid but has a short precristid, parallel to that of cuspid 5, that divides basally. Cuspid 7 is displaced anteriorly and gives rise to two slightly diverging postcristids, the lingual one of which merges with the postcingulum. Its precristid is short and apparently joins the last postcristid of the protolophid.

This specimen preserves the posterior root, a long, tapering transverse fang-like structure, 9.8 mm long on the lingual side.

 $M_4$ . Three teeth represent  $M_4$ . Apart from its high degree of wear, which has reduced the crest angle of the protolophid to 140° or more and almost flattened the hypolophid, SAM P29577 from the dentary (fig. 5H) is virtually identical to the unworn SAM P23988 and P33451 (fig. 5I). Our description of this tooth will be based on the second specimen.

Previously,  $M_4$  was only known from *E. tommosi* from Lake Tarkarooloo. The new specimens should, therefore, be compared with NMV P48766 (Pledge, 1986, plate 3.2H), NMV P160517 and SAM P19966. SAM P23988 is less worn than the Tarkarooloo specimens and shows a similar occlusal outline although with more buccal constriction at the transverse valley. The lophids are low and broad, though possibly higher than in *E. tommosi*. The primary cuspids, the protoconid and hypoconid, stand markedly higher than their subordinate cuspids.

The protolophid is much wider than the hypolophid and its crest is orientated at about  $60^{\circ}$  to the lingual face. The anterior edge of the tooth is convex and has a widening precingulid extending from the anterolingual corner, curving backwards, almost to the inner preprotocristid. The protolophid has seven cuspids, as in *E. tommosi*. The protoconid is situated about one third the distance from buccal end of the lophid. It is relatively high and lacks the obvious buccal grooves present on the protoconids of more anterior teeth. Instead, it has a strong anterobuccal preprotocristid and a subordinate lower cristid parallel to it on the lingual side. A pair of subparallel postprotocristae extends posterolingually to the transverse valley, with the lingual one having two buccally directed ribs.

Cuspid 2 is plate-like. Its precristid almost meets the precingulum at a cuspule but instead swings buccally and parallels it (as a rib) almost reaching the lesser preprotocristid. The postcristid bifurcates basally. Cuspid 3 is also plate-like, its precristid being simple and undivided and its postcristid only thickening at the posterior end. Cuspid 4 is a weaker irregular plate, thick anteriorly, with several minor ribs. It is

shorter than cuspid 3 and larger than cuspid 5, which is otherwise similar although posterobuccally curved. Most cuspids are linked by fine, deep-set, apical struts, but on cuspid 6 these are as strong as the pre- and postcristids. The precristid is short and rather bulbous while the postcristid is finer and longer and curves buccally to join distally at the transverse valley the postcristids from cuspids 4 and 5. Cuspid 7 is low and on the extreme edge of the tooth. It is linked to cuspid 6 by a strut stronger than its pre- and postcristids. The precristid is short and merges into the precingulum. The postcristid is little more than a lingual cingulum with several strong basal ribs that increase in size towards the transverse valley. No postcristids actually cross the transverse valley.

The hypolophid is short with only five distinct cusps fewer than in E. tommosi. The hypoconid is rounder than the protoconid and has a small anterobuccal groove that joins a larger posterobuccal groove on the protoconid to form a shallow pocket. There is no buccal cingulid. The cristid obliqua curves almost in a semicircle to a small basal cusp in the transverse valley, where it joins the precristid from cuspid 2. The posthypocristid curves lingually to join the short postcingulid. Cuspid 2 is a simple cristid with no discernable apex. Posterolingually, it joins the postcingulid at a small cuspule. Cuspid 3 is also a simple cristid bifurcating at the anterior end and not reaching the postcingulid. Cuspid 4 is irregular and links with a transverse cristid in the transverse valley. It is posteriorly short. Cuspid 5 is very low; its cristid is irregular and buccally curved. It converges with but does not meet ribs from the lingual cingulum and posteriorly parallels the postcingulid.

Morphologically SAM P23988, P29577 and P33451 are similar to the  $M_4$ s of *E. tommosi* but the fine ornamentation of cristids, ribs and struts is simpler. The teeth are also marginally larger.

*Remarks.* Overall, these newly described teeth of *E. stirtoni* confirm the distinction of this taxon from *E. tommosi* from the Tarkarooloo LF and appear to represent a relatively derived species. This is in keeping with the perceived greater age of the Tarkarooloo LF (e.g. Woodburne et al., 1985).

#### Ektopodon litolophus Pledge et al. 1999.

Holotype. SAM P30176, an isolated right M1 (fig. 6D).

*Locality*. Leaf Locality (UCMP V-6213), Wipajiri Formation, eastern edge of Lake Ngapakaldi, South Australia.

*Local Fauna and Age.* The Kutjamarpu Local Fauna is estimated to be approximately early Miocene (see above).

*Remarks.* This unique specimen is noticeably larger than its contemporary *E. serratus*, and has a simpler morphology, with a longer, more loph-like parastyloph, suggesting that it is the most autapomorphic member of the family.

#### Discussion

There are now at least five known species of *Ektopodon* (*E. serratus, E. stirtoni, E. litolophus, E. tommosi*, a Riversleigh taxon, and *E. paucicristata*); two or three species of *Chunia* 

(C. illuminata, C. sp. cf. C. illuminata, C. omega); and the monotypic Darcius duggani. No ektopodontid species, except *E. paucicristata* and *D. duggani*, 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 a single tooth. 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 grains, nuts and insects/grubs (Pledge, 1982, 1986, 1991).

Species of Ektopodon range in age from late Oligocene to late Pliocene. The oldest (E. tommosi) occurs in the Tarkarooloo LF of late Oligocene age. Ektopodon serratus and E. litolophus in the Kutjamarpu LF are probably Early to Middle Miocene in age. Ektopodon ulta (Megirian et al., 2004; fig. 6G) from the Kangaroo Well LF of the Northern Territory may be slightly younger than E. stirtoni. The age of the Riversleigh ektopodontid has been interpreted by Archer et al. (1989) to be most probably Early Miocene. The youngest reported Ektopodon is E. paucicristata (Rich et al., 2006) from the Pliocene Whalers Bluff Formation (Dutton Way, Portland) and Childers Cove of southwestern Victoria. This species is a temporal anomaly, in so far as its authors regarded it to be relatively plesiomorphic. In its short protostyloph with few cusps, low number of deeply bifurcated cusps on the lophs, and equidimensional molars, it resembles species of *Chunia*. While the original authors considered the teeth of *E*. paucicristata to be upper molars, their outline suggests they may in fact be lower molars. Species of Chunia range in age from Late Oligocene (Ditjimanka LF) to latest Oligocene (Tarkarooloo LF) in age. Darcius duggani (Rich, 1986) is known from the Early Pliocene Hamilton LF, and from the apparently early Pleistocene Nelson Bay Formation (Rich et al., 2006), both in southwestern Victoria. Rich (1986) regards D. duggani to be structurally intermediate between the species of Chunia and Ektopodon.

The fragmentary *Ektopodon serratus*-like ektopodontid tooth from the Wayne's Wok LF (Pledge et al., 1999) confirms previous suggestions that Riversleigh's Faunal Zone B local faunas share taxa with the Kutjamarpu LF (Archer et al., 1989). A *Darcius*-like form, also from one of the numerous Riversleigh localities, is noted by Long et al. (2002: 142) but is yet to formally described.

Woodburne & Clemens (1986c) interpreted the phylogenetic relationships of ektopodontids known at the time. Now, *Ektopodon litolophus* (Pledge et al., 1999) is best regarded as a sister taxon of *E. serratus*, and 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 apparently contemporaneous, neither is likely to be the other's ancestor.

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Table 1. Measurements (in mm) of recently discovered ektopodontid molar teeth. Pstl = parastyloph width.

| Specimen<br>Number   | tooth                      | length | Pstl | Anterior<br>width | Posterior<br>width |  |  |  |  |
|----------------------|----------------------------|--------|------|-------------------|--------------------|--|--|--|--|
| Ektopodon stirtoni   |                            |        |      |                   |                    |  |  |  |  |
| SAM P35309           | LP <sup>3</sup>            | 5.5    |      | 3.4               |                    |  |  |  |  |
| (left maxilla)       | $LM^1$                     | 8.8    | 3.2  | 8.5               | 9.1                |  |  |  |  |
| "                    | $LM^2$                     | 6.9    |      | 9.3               | 8.7                |  |  |  |  |
| "                    | LM <sup>3</sup>            | 6.3    |      | 8.2               | 6.5                |  |  |  |  |
| SAM P31637           | LM <sup>2</sup>            | 6.8    |      | 9.3+              | 8.7                |  |  |  |  |
| SAM P23854           | RM <sup>2</sup>            | 7.9    |      | 9.5+              | 9.2+               |  |  |  |  |
| SAM P30156           | LM <sup>3</sup>            | 6.7    |      | 8.9               | 7.6                |  |  |  |  |
| SAM P30175           | LM <sup>3</sup>            | 6.7    |      | 8.5+              | -                  |  |  |  |  |
| SAM P31638           | LM <sub>2</sub>            | 7.7    |      | 7.0               | 6.7                |  |  |  |  |
| SAM P29577           | RM <sub>2</sub>            | 8.1    |      | 7.8               | 7.5                |  |  |  |  |
| (right dentary)      | RM <sub>3</sub>            | 8.0    |      | 6.9               | 6.1                |  |  |  |  |
| "                    | RM <sub>4</sub>            | 7.5    |      | 5.5               | 4.3                |  |  |  |  |
| SAM P24541           | LM <sub>2</sub>            | -      |      | -                 | 6.4                |  |  |  |  |
| SAM P23989           | RM <sub>3</sub>            | -      |      | -                 | 5.6                |  |  |  |  |
| SAM P23988           | LM <sub>4</sub>            | 6.8    |      | 5.95              | 5.0                |  |  |  |  |
| SAM P33451           | RM <sub>4</sub>            | 6.7    |      | 6.0               | 5.1                |  |  |  |  |
| Ektopodon litolophus |                            |        |      |                   |                    |  |  |  |  |
| SAM P30176           | $\mathbf{R}\mathbf{M}^1$   | 10.6   | 6.0  | 11.7              | 12.1               |  |  |  |  |
| Chunia illuminata    |                            |        |      |                   |                    |  |  |  |  |
| SAM P29081           | $\mathbf{L}\mathbf{M}^{1}$ | 5.0    | 1.9  | 4.5               | 4.8                |  |  |  |  |

Table 2. Dimensions (in mm) of check teeth in maxilla, *Ektopodon stirtoni* SAM P35309. Molar row length, 26.0; preserved molar length, 21.7; preserved check row length, 23.5; half-palate width, 22.0; clear half palate, 13.2; angle of premolar crest to inner line of molar row, 65°. 'Stylewidth' = parastyloph width.

| Tooth                 | Length | Stylewidth | Ant. Width | Post. Width | Ant. Cusps | Post. cusps |
|-----------------------|--------|------------|------------|-------------|------------|-------------|
| P <sup>3</sup>        | 5.00   | N/A        | 3.20       | 3.20        | 1.00       | 1.00        |
| $M^1$                 | 8.50   | 3.2        | 8.50       | 9.10        | 7.00       | 8.00        |
| M <sup>2</sup>        | 6.50   | N/A        | 9.10       | 8.25        | 9.00       | 8.00        |
| <b>M</b> <sup>3</sup> | 5.70   | N/A        | 8.00       | 6.70        | 8.00       | 7.00        |
| $M^4$                 | _      | -          | -          | -           | -          | _           |