Mayigriphus orbus gen. et sp. nov., a Miocene Dasyuromorphian from Riversleigh, northwestern Queensland

S. Wroe


Mayigriphus orbus gen. et sp. nov., an enigmatic Miocene dasyuromorphian from Riversleigh, is described from dental material. The tiny Mayigriphus orbus shows a number of derived character-states for Dasyuromorphia and two of these derived features may signify a special relationship with Planigale (Dasyuridae). However, no specialised features shown by M. orbus are unique to dasyurids within the order and M. orbus also possesses derived characters shown by basal thylacinids. Because previous investigation has indicated that Dasyuridae is not currently defined by any dental synapomorphies, caution is demanded regarding allocation of M. orbus at the family level. Problems associated with the phylogenetic placement of M. orbus portend a story of growing complexity for dasyuromorphian phylogeny—a story progressively being revealed in the Tertiary limestones of Riversleigh.

Mayigriphus, dasyuromorphan, Miocene, Riversleigh.

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The fossil record for Dasyuromorphia is reviewed by Wroe (1996b, 1997b). Until recently the pre-Pliocene fossil record for Dasyuromorphia was limited to five described taxa, all from deposits in central Australia (Ankotarinja tirarensis and Keeuna woodburnei (Archer, 1976a), Wakamatha tasselli (Archer & Rich, 1979), Dasyurinja kokuminola (Archer 1982a) and Thylacinus potens (Woodburne, 1967). With the exception of Thylacinus potens, investigation has failed to unequivocally link these fossil taxa with elements of modern dasyuromorphian radiations. More recently, the fossil-rich middle to late Tertiary deposits of Riversleigh have yielded six new thylacinid species: Nimbacinus dicksoni (Muirhead & Archer, 1990), Thylacinus macknessi (Muirhead, 1992; Muirhead & Gillespie, 1995); Wabulacinus ridei (Muirhead, 1997), Ngamalacinus timmulvaneyi (Muirhead, 1997), Badjcinus turnbulli (Muirhead & Wroe, in press), and Muribacinus gadiyuli (Wroe, 1996b). However, only two un-named taxa have been assigned to Dasyuridae: a possible phascogaline taxon known from a single M1 or M2 (Archer, 1982a) and an un-named ‘An-techinus-like’ species from Riversleigh (Van Dyck, 1989). Wroe (1996b, 1997b) investigates problems with dasyurid phylogeny, concluding that Dasyuridae is currently defined by possibly three basicranial, but no dental synapomorphies. A new dasyuromorphian described here shows an enigmatic combination of features within Dasyuromorphia and can not be unequivocally assigned at the family level.

Dental nomenclature follows Flower (1867) and Luckett (1993). Taxonomic terminology for Dasyuromorphia follows Wroe (1996b), with three subfamilies recognised within Dasyuridae (Sminthopsinae, Phascogalinae [including Murexia], Dasyurinae [including Neophascogale and Phascolosorex]) and the following taxa considered Dasyuromorphia incertae sedis: Ankotarinja tirarensis, Keeuna woodburnei, Wakamatha tasselli and Dasyurinja kokuminola. Higher level marsupial系统atics follows Marshall et al. (1990). Material is housed in the Queensland Museum (QMF).

SYSTEMATICS

Order DASYUROMORPHIA Gill, 1872
Family INCERTAE SEDIS

Mayigriphus gen. nov.

TYPE AND ONLY SPECIES. Mayigriphus orbus gen. et sp. nov.

GENERIC DIAGNOSIS. Mayigriphus orbus differs from all dasyurids in the following combination of features: Premolar row compressed longitudinally, P1 very small; P3 reduced but with two roots; M1 compressed on long axis with protoconid central on long and transverse axes with paraconid tiny; M1,4 metaconids and metaconids reduced; M1 metaconid not differentially reduced relative to M2-4 metaconids;
lingual anterior termination of cristid obliqua on M1-4, with M3 cristid obliqua terminating beneath metacristid carnassial notch; M1-4 protoconids lingually shifted and recurved; M1-3 entoconids small to tiny, M4 talonid reduced with entoconid absent. Mayigriphus orbus can be distinguished from known thylacinids by the following combination of features: M1 shows a greatly reduced paraconid but only moderately reduced metaconid; clearly defined hypoconulid notch in anterior cingulid of lower molars; very small size; reduction of P3 relative to P2; lack of diastema between P1 and P2. Mayigriphus orbus differs from known bandicoots in possession of the above combination of features, a well-defined posterior cingulid and more buccally shifted hypoconulid.

**ETYMOLOGY.** Wanyi mayi, tooth; Latin griphus, puzzle; refers to the enigmatic combination of dental features. Masculine.

Mayigriphus orbus sp. nov.

(Fig. 1)

**ETYMOLOGY.** Latin orbus, orphan, refers to its uncertain phylogenetic position.

**MATERIAL.** Holotype, QMF23780, right dentary with partial anterior alveolus of P1, P1 posterior root, P2-3, M1-4; Paratype QMF22791, right dentary fragment containing M3 and alveolus for M4. All from early late Miocene Encore Site, Riversleigh.

**DESCRIPTION.** Dentary broken away anteriorly from midpoint of P1 anterior root alveolus and posteriorly from about 1mm along ascending ramus; dentary almost uniform in depth, slight tapering anteriorly from beneath P3 protoconid; mental foramen beneath M1 hypoconid.

P1. P1 crown missing, only posterior half of anterior root alveolus and posterior root remain; based on root and alveolus size P1 small, less than half P2 length; anterior alveolus buccally displaced.

P2. No diastema between P1 and P2; twin rooted; P2 largest premolar in height and length; protoconid moderately worn; buccal cingulid runs posteriorly from midpoint between anterior and posterior roots to small posterior central cuspule on heel; another cingulid circumscribes the lingual crown base from this cuspule to anterior margin of posterior root.

P3. no diastema between P2 and P3; twin rooted; P3 morphology similar to P2 but differs in possession of continuous cingulid circumscribing base of entire crown and smaller size (P3 around 30 percent smaller in height an length).

M1. no diastema between P3 and M1; M1 unworn; principal cusps in order of decreasing height; protoconid, metaconid, paraconid, hypoconid and entoconid; entoconid tiny, closely abutting posterior face of trigonid adjacent to metaconid; paraconid damaged, but from basal dimensions was clearly small; metaconid small and shifted posteriorly; protoconid dominant cusp, lingually recurved, occupying almost central position on tooth; M1 reduced on the long axis; talonid small, slightly wider transversely than trigonid but shorter on long axis; paracristid parallel to, and cristid obliqua shows slight lingual inflection at anterior end; metacristid and hypocristid parallel and angled at about 20° to transverse axis of dentary; cristid obliqua terminates beneath apex of protoconid; anterior cingulid runs basally from paraconid to beneath protoconid; posterior cingulid weakly developed.

M2. M2 differs from M1 as follows; M2 much larger; paraconid much larger; metaconid relatively and absolutely larger though still small compared to protoconid; talonid shorter on long axis; cristid obliqua terminates against posterior face of trigonid in more lingual position, with angle formed between cristid obliqua and hypocristid more acute; metacristid and hypocristid run closer to transverse axis of dentary; entoconid relatively larger than in M1 though still small; posterior cingulid more strongly developed; M2 paracristid runs at about 30° to long axis of dentary, with angle between paracristid and metacristid slightly less than 90°.

M3. M3 differs from M2 as follows; protoconid larger; on transverse axis trigonid wider and talonid shorter; entoconid on M3 smaller; cristid obliqua terminates in a more lingual position against posterior face of trigonid beneath carnassial notch of metacristid.

M4. M4 similar to M3 except: metaconid smaller than paraconid; protoconid less lingually recurved; talonid greatly reduced, entoconid absent, hypoconid and hypoconulid small; no posterior cingulid.

Meristic gradients from M1-4. orientation of metacristid and hypocristid to long axis of dentary increasingly transverse from M1-2, departs away from transverse from M2-3, then back to more transverse orientation from M3-4; orientation of paracristid to long axis of dentary increas-

ingly transverse from M1-3, termination of cristid obliqua against posterior face of trigonid increasingly lingual M1-4; reverses departing from transverse for M3-4; protoconid and metaconid height increases M1-3, decreases M3-4; paraconid height increases M2-4; talonid width increases M2, decreases M3-4.

**CHARACTER ANALYSIS**

Wroe (1996b, 1997b) discusses taxa considered appropriate in the reconstruction of a dasyuromorphian morphotype (i.e., peradectids, didelphoids, microbiotheriids, peramelemorphians). Similar methodology is used for characters treated here to assess character-state polarities (Tables 2, 3). Within Dasyuromorpha *Ankotarinja tirarensis* is the least derived taxon and a possible outgroup to remaining dasyuromorphians. *Muribacinus gadiyuli* and *Badjcinus turnbulli* are the least derived thylacinids. For Dasyuridae the following taxa are considered plesiomorphic for their respective subfamilies: *Murexia longicaudata* (Phascogalinae), *Neophascogale lorentzii* (Dasyurinae) and *Sminthopsis leucopus* (Sminthopsinae).

**TABLE 1. Mayigriphus orbus, dental measurements (mm.), l=anteroposterior dimension, w1=maximum transverse dimension of trigonid, w2=maximum transverse dimension of talonid.**

<table>
<thead>
<tr>
<th>Ref. no</th>
<th>P2</th>
<th>P3</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
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</table>

**Character Analysis.**

**M1 paraconid.** The M1 paraconid is not reduced in dasyuromorphian outgroups and *A. tirarensis*, *W. tasselli*, moderate reduction is shown by thylacinids (excepting *B. turnbulli* which shows marked reduction) and plesiomorphic Sminthopsinae (*Sminthopsis leucopus*), Phascogalinae (*Murexia*) and Dasyurinae (*Neophascogale*). M1 paraconid reduction in *M. orbus* is less marked than in all Dasyurinae excepting *Neophascogale*. For *M. orbus* M1 shows greater reduction of the paraconid than for all Phascogalinae and Sminthopsinae except *Planigale*.

**M4 talonid.** The M4 talonid is unreduced in basal taxa for Dasyuromorphan outgroups and bandicoots (e.g., *Yarala burchfield*, Muirhead & Filan, 1995). Within Dasyuromorpha *A. tirarensis*, basal phascogaline (*Murexia*) and dasyurine (*Neophascogale*) taxa show slight reduction for this feature. The M4 talonid is greatly reduced on the plesiomorphic dasyuromorphian condition for *W. tasselli*, most dasyurines and phascogalines, and all sminthopsines. For thylacinids the M4 talonid is unreduced for basal taxa (*Muribacinus, Badjcinus*), but significantly reduced for derived species (*Thylacinus, Wabulacinus*). Even for specialised *Thylacinus* M4 talonid reduction does not approach that of derived dasyurids which show far greater diminution on the transverse axis. The degree of reduction for this feature in *M. orbus* is closest to that shown in *Phascogale*, but less than for most Dasyurinae, and all Sminthopsinae.

**Cristid obliqua orientation.** A buccal position for the anterior termination for the cristid obliqua relative to the carnassial notch of the metaconid is common to most dasyuromorphian outgroup taxa. This feature is associated with cristid obliqua orientation and formation of a right angle between the cristid obliqua and hypocristid. Most outgroup taxa to Dasyuridae and Thylacinidae show a cristid obliqua aligned closely with the long axis of the dentary and a 90° angle is formed between the cristid obliqua and hypocristid. In the
character-analysis (Table 2) only M3 is considered. Buccal termination is shown by A. tirarensis and, to a lesser degree, by K. woodburnei and W. tasselli. Basal thylacinids show relatively lingual anterior termination for the cristid obliqua, but a more buccal position is apparent in Thylacinus. Basal dasyurines show lingual termination for the cristid obliqua (Neophascogale, Myoictis, Dasyurus hallucatus), but more specialised taxa show buccal termination (other Dasyurus, Dasyercus, Dasyuroides, Sarcophilus). All phascogalines show lingual termination. Sminthopsines show buccal termination. Mayigrimus orbus shows lingual termination.

Orientation of the cristid obliqua correlates with other features of both the upper and lower molars. These include the angle between the postparacrista and premetacrista (together termed the centrocrista), the relative size of the protoconid and metaconid and, the occlusal surface area presented by the protocone and talonid basin. Scoring of character states for cristid obliqua without consideration of these associated features may be phylogenetically misleading. For example, derived Thylacinus and some dasyurines show longitudinal alignment for the M3 cristid obliqua (unspecialised didelphids, microbiotheriids and A. tirarensis), but for these derived dasyuromorphians this feature correlates with protoconid hypertrophy, metaconid reduction or loss, and a linear centrocrista. These character-states are all associated with the dominance of longitudinally oriented vertical shearing crests.

The basal position for Sminthopsinae within Dasyuridae indicated by molecular analyses (Kirsch et al, 1990; Krajewski et al., 1993; 1994) supports the contention that a buccal point of termination for the cristid obliqua is a plesiomorphic for the clade. However, dental features of Sminthopsinae are products of a different selective regime and transverse rather than longitudinal vertical shearing crests dominate. Archer (1976) noted that a buccal position for the cristid obliqua may be associated with reduction of the paracone or a lingual shift in the carnassial notch (of the metaconid). Both derived features are shown by sminthopsines and it is probable that cristid obliqua position represents a correlated apomorphic feature. A further derived feature shown by sminthopsines is gross reduction of the talonid on the anteroposterior axis which may also impact on cristid obliqua orientation. For sminthopsines and derived dasyurines and thylacinids, a buccal position for the cristid obliqua is treated as derived relative to that of microbiotheriids, unspecialised didelphids, bandicoots and A. tirarensis (Tables 2, 3). A relatively more lingual termination for the cristid obliqua, as shown by most dasyurids and basal thylacinids, is also considered derived. The character complex associated with most dasyurids (a relatively lingual anterior termination point and acute angle formed between the cristid obliqua and hypocristid) is scored as ‘a’. Buccal termination and formation of 90° between the cristid obliqua and hypocristid may be associated with increased transverse vertical shear (b) or increased longitudinal vertical shear (c).

Angle between paracristid and metacristid. For dasyuromorphian outgroups an acute angle is formed between the paracristids and metacristids (mirrored by an equivalent angle formed between the postmetacristae and preprotocristae with which they occlude in the upper dentition). Similar morphology is shown by A. tirarensis, W. tasselli and sminthopsine dasyurids. All dasyurines, phascogalines, basal thylacinids for which a metacristid is retained, and M. orbus show a relatively obtuse angle between paracristids and metacristids. Widest paracristid-metacristid angles are in Sarcophilus, Glaucodon and D. maculatus among dasyurids and Ngamalacinus among thylacinids. This phenomenon is correlated with carnivory and the development of longitudinally aligned vertical shearing crests.

Hypoconulid notch. Many marsupials have a distinct notch in the anterior cingulae of their lower molars to receive the hypoconulid of the preceding tooth. Outgroup data for Dasyuromorphia regarding this feature is equivocal. Some outgroup taxa (e.g., some peradectids) show a well-developed hypoconulid notch, but among other possible outgroups this feature is absent (e.g., peramelemorphs). Within Dasyuromorphia this feature is well-developed for Ankotarinja tirarensis and Keeuna woodburnei, but poorly defined for Wakamatha tasselli (see Wroe (1996b) re arguments for possible bandicoot affinities of this taxon). Among thylacinids, a well-developed hypoconulid notch is present for Muribacinus and Badjcinus, weakly-defined in Ngamalacinus, and absent in all other taxa. A well-developed hypoconulid notch occurs in all dasyurids excepting Dasyurus maculatus (reduced), and Glaucodon and Sarcophilus (absent). Mayigrimus orbus has a well-defined hypoconulid notch. Wroe (in press b) infers that loss of the hypoconulid notch is a function of ad-
TABLE 2. Characters and character-states used in phylogenetic analysis.

C1. P3 size relative to P2. 0. larger. 1. reduced. 2. intermediate. 3. tiny. 4. absent.
C2. M1 paraconid size. 0. large. 1. reduced. 2. tiny. 3. absent.
C3. M4 talonid size. 0. large. 1. moderately reduced. 2. markedly reduced. 3. tiny.
C5. Angle between paracristid-metacristid. 0. acute. 1. intermediate. 2. obtuse.
C6. Hypoconulid notch. 0. well developed. 1. intermediate. 2. absent.
C7. Metaconid morphology. 0. no clear differential between M1 and M2-4. 1. clear differential.
C8. M2-4 metaconid size. 0. large. 1. reduced. 2. greatly reduced. 3. absent.
C9. M3 entoconid size. 0. large. 1. reduced. 2. absent.

* Three derived states recorded for this character (see text).

Localised metaconid reduction (i.e., a clear differential shown between M1 and M2-4 metaconid reduction) as shown by some dasyurines, sminthopsines and Badjcinus, is probably related to brachycephalisation, shortening of the tooth row on the anteroposterior axis and concomitant premolarisation of M1 (Archer, 1976).

Generalised metaconid reduction (M1-4) correlates with increased size of the protoconid and primacy of the paracristid and postmetacristae in vertical shear. For carnivorous dasyurids and thylacinids these derived features are associated with alignment of the vertical shearing crests with the long axis of the tooth row.

Entoconid. Large entoconids are plesiomorphic for dasyuromorphian outgroups, A. tirarensis, K. woodburnei and W. tasselli. All thylacinids show marked reduction or loss of the entoconid on all lower molars. Among Dasyuridae this feature is variable. Plesiomorphic taxa for each subfamily show no reduction of the metaconids. However, specialised dasyurines and sminthopsines show derived character-states. Derived dasyurines show a reduced M1 metaconid, but less reduction for M2-4 metaconids (Dasycercus, Dasyuroides, Dasyurus, Sarcophilus). In Planigale metaconid diminution is less advanced on M1 and more uniform through M2-4. This phenomenon shown for Planigale is also common to thylacinids which retain metaconids (except Badjcinus turnbulli which shows the typical dasyurine condition). Mayigriphus orbitus shows uniform reduction of M1-4 metaconids, the character-state common to Planigale among dasyurids and Muribacinus, Nimbaclinus and Ngamalacinus among thylacinids.

Archer (1982b) regarded a hypoconulid notch in the anterior cingulum as a possible dasyurid synapomorphy. But Wroe (1997) concludes that it may have been in the common ancestor of Dasyuromorphia and was almost certainly in the common ancestor of Dasyuridae-Thylacinidae. For specialised dasyurids (Sarcophilus and Glauodon) and thylacinids (Thylacinus, Waburacinus) loss of the hypoconulid notch correlates with advanced carnassialisation.

Advanced carnassialisation for derived dasyurids and thylacinids, noting that the shift to a predominance of longitudinal vertical shear in marsupial carnivores diminishes the requirement for a brace against transverse forces (i.e., the likely role for the hypoconulid notch).

Archer (1981) and Sanson (1985) note that no clear form-function relationship explains the distribution of entoconid reduction and loss among dasyurids, but note that this reduction is greatest for arid-adapted species (some Sminthopsis, Antechinomys, Dasyuroides, Dasycercus, Dasykaluta, most Dasyurus (excepting D. hallucatus), Sarcophilus and Glauodon). All thylacinids show some entoconid reduction, with the least reduction in Muribacinus and the greatest by Thylacinus. Mayigriphus orbitus shows moderate reduction for this feature. Archer (1981) and Sanson (1985) note that no clear form-function relationship explains the distribution of entoconid reduction and loss among dasyurids, but note that this reduction is greatest for arid-adapted species (some Sminthopsis, Antechinomys, Dasyuroides, Dasycercus). However, considerable reduction or loss is shown for some species found in less extreme environments and for large dasyurid and thylacinid carnivores this phenomenon is likely associated with carnivory. More form-function data is required here.
TABLE 3. Character/taxon matrix.

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<thead>
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<th>Character/taxon matrix</th>
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**DISCUSSION**

**BIOSTRATIGRAPHY AND ECOLOGY.** To date, *M. orbus* is restricted to early late Miocene. Encore has produced a fauna that includes several unique taxa, including a large dasyuromorphian of uncertain affinity (unpubl. data), a giant *Ekaltadeta* (Wroe, 1996a), a derived koala (Black, pers. comm.), a palochevitid structurally intermediate between species from Riversleigh System C and the late Miocene *Palarcohes* *painei* of Alcoota (Black, 1997) and a *Warenjali* like wombat (Archer et al., 1995). The rootless teeth of this wombat (unknown for other species at Riversleigh) and the relatively low abundance of the frog *Lechriodus intergervis*, common in other Miocene Riversleigh deposits (Godthelp, pers. comm.) indicate that climatic conditions may have been drier for the depositional episode during which Encore was produced. Tentative support for a relatively late age for Encore site, is also forwarded by Wroe (1997a). If *M. orbus* is a dasyurid then the derived dentition (relative to other Miocene dasyurids) might also suggest a late age for Encore site. As noted above for small dasyurids, circumstantial evidence correlates en- toconid reduction with adaptation to relatively dry environments.

*Mayigriphus orbus* is the smallest dasyuro- morphian from the Oligocene and Miocene of Riversleigh and is comparable to *Planigale maculatus* in size. Only one other marsupial insectivore has been identified that might have competed closely with *M. orbus*, the diminutive bandicoot *Yarala burchfieldi* (Muirhead, 1995). As with modern *Planigale* (Denny, 1982) the diet of *M. orbus* probably included invertebrates, frogs, small lizards and or small mammals.

**PHYLOGENY.** *Mayigriphus orbus* shows a unique mosaic of features among dasyuro- morphians. Two features of *M. orbus* may indicate a relationship with *Planigale* (the greatly reduced M1 paraconid concurrent with a moderately reduced M1 metaconid, and relatively uniform diminution of the M1-4 metaconids). Although a comparable degree of M1 paraconid reduction is also common to many derived dasyurines (e.g., *Pseudantechinus*), in these taxa diminution of the M1 metaconid is far more advanced and a clear differential is produced between that shown by M1 and M2-4. Additional apomorphies shared by *M. orbus* and *Planigale* (e.g., reduction of M4 talonid, entoconid and P3), are also found in other specialised dasyurid taxa. On the basis of cytochrome-b data, Painter et al. (1995) estimate the oldest branchings within *Planigale* at 11-15 mya, thus the possibility that *M. orbus* represents an early branch of this radiation can not be discounted. However, *M. orbus* shows at least 2 derived features not in *Planigale* (wide angle formed between the paracristid, metacristid, a buccal shift in the point of termination of the cristid obliqua). The oldest material clearly attributable to *Planigale* is Pliocene (Archer, 1982a). Based on available data, a sister taxa association for *M. orbus* with *Planigale* is considered equivocal.

Even at the family level, the phylogenetic position of *M. orbus* is considered uncertain, because it has a number of features that might be interpreted as synapomorphies for either derived dasyurid or thylacinid clades, but no unequivocal synapomorphies (within Dasyuro-
M. orbus: reduction of P3 (Tate, 1947; Archer, 1982b; Marshall, 1990) and the hypoconulid notch in the lower molars (Archer, 1982b). Status of both as shared-derived features for Dasyuridae is questioned by Wroe (1996b, 1997b). Reduction of P3 is certainly common within Dasyuridae which culminates in the loss of this tooth among specialised taxa. However, reduction or loss of P3 may have occurred independently at least 3 times in the Dasyuridae (Archer, 1981). A further argument against the phylogenetic value of this character at the family level is the P3 smaller than P2 in 2 thylacinids from Riversleigh (Muirhead & Wroe, in press; Wroe, 1996b, 1997b). The status of the hypoconulid notch as a shared derived feature for dasyurids has been undermined by the discovery of plesiomorphic thylacinids with a well-defined hypoconulid notch in the lower molars (Wroe, 1997b; Muirhead & Wroe, in press). Marked reduction of the M1 paraconid in M. orbus is common to specialised dasyurids but not thylacinids, excepting Badjcinus turnbulli (Muirhead & Wroe, in press). None of these features represent unequivocal synapomorphies for Dasyuridae and each have been independently derived within specialised dasyurid lineages. At least 3 features in M. orbus suggest a possible alliance with thylacinids. Firstly, the lack of a clear differential between metaconid reduction on M1 and M2-4 in M. orbus is known only for Planigale among dasyurids but common to plesiomorphic thylacinids. In all dasyurids except Planigale, M1 metaconid reduction clearly exceeds that of M2-4. Although reduction of the M2-4 metaconids is less pronounced in M. orbus than in known thylacinids, excepting Murhabinus, it is greater than for most dasyurids except D. maculatus, Sarcophilus and Planigale. Secondly, the wide angle formed between the parasphenid and metacristid in M. orbus is found in basal thylacinids, but only D. maculatus, Sarcophilus and Glaucodon among dasyurids. Thirdly, among specialised dasyurids, reduction of the M1-4 talonids and metaconids is commonly associated with a buccal shift in the point of termination of the cristid obliqua. In both M. orbus and plesiomorphic thylacinids this is not the case, with the cristid obliqua terminating in a relatively lingual position. Ultimately, this may be related to Ride’s (1964) observation of a difference between Thylacinus and specialised dasyurids in the composition of the principal posterior shearing crest. Ride pointed out that, in Thylacinus, the posterior shearing crest runs from the protoconid directly to the hypoconid, while in derived dasyurids (especially Sarcophilus) the posterior shearing crest connects the protoconid and metaconid.

CONCLUSIONS

If M. orbus is a dasyurid it represents the most derived member of the family known from pre-Pliocene times, with the possible exception of the Miocene Dasylurinja kokuminola (Archer, 1982a) from Lake Yanda in central Australia. A special relationship between these two taxa can not be discounted, with both showing specialisations associated with carnassialisation (the much larger size of D. kokuminola precludes the possibility that the 2 taxa are conspecific). D. kokuminola is known only from a single upper molar and direct comparisons with M. orbus cannot be made. Among known dasyurids M. orbus shares the greatest number of derived features with Planigale: two character-states (disparate reduction of the M1 paraconid and metaconid and uniform reduction of the M1-4 metaconids) suggest the possibility of a special relationship for the 2 taxa. However, uniform diminution of the M1-4 metaconids is also shown by some basal thylacinids.

Mayigriphus orbus shows no unequivocal synapomorphies for either dasyurid or thylacinid clades. For Dasyuridae, unique derived-features (within Dasyuromorphia) are only found in the basicranium (Wroe, 1996b, 1997b). Unique derived features (within Dasyuromorphia) unifying Thylacinidae have been identified only in the upper dentition (Wroe, 1996b). Neither region is known for M. orbus. Confident phylogenetic assignment for M. orbus has been further tempered by the identification of possible thylacinid apomorphies in this taxon, which must be considered in the following context: investigation of Oligocene and Miocene material from Riversleigh is revealing a complex dasyuromorphian phylogeny dominated by a diverse thylacinid clade, showing greatly expanded intrafamilial variation (Muirhead, 1992, 1997; Muirhead & Archer, 1990; Muirhead & Wroe, in press; Wroe, 1996b, 1997b) a close relationship between Dasyuridae and Thylacinidae has been established by molecular studies (Lowenstein et al., 1981; Sarich et al., 1982; Thomas, 1989; Krajewski et al., 1992), and a relatively recent genesis for Dasyuridae has been suggested (Archer, 1982a; Krajewski, 1992; Wroe, 1996b,
equivocally associated with elements of the now known taxon has yet been described which can be unambiguously placed within either family impossible, particularly as this decision must currently be based solely on elements of the lower dentition. Problems associated with determining the phylogenetic position of *M. orbus* highlight an unexpected phylogenetic scenario. Despite an abundance of dasyuromorphian material from Oligocene-Miocene deposits of Riversleigh no taxon has yet been described which can be unequivocally associated with elements of the now ubiquitous dasyurid radiation.

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