

A new genus and species of dasyuromorphian from the Miocene of Riversleigh, northern Australia

STEPHEN WROE

WROE, S., 2001:12:20. A new genus and species of dasyuromorphian from the Miocene of Riversleigh, northern Australia. *Memoirs of the Australian Association of Palaeontologists* 25, 53-59. ISSN 0810-8889

Joculusium muizoni, new genus and species, is the least derived dasyuromorphian yet described from the Oligocene-Miocene deposits of Riversleigh in northwestern Queensland. Within Dasyuromorphia, *J. muizoni* is plesiomorphic for all dental features examined excepting metacristid orientation. Oblique alignment of this cristid with respect to the long axis of the dentary in *J. muizoni* is an apomorphy within Dasyuromorphia shared with some representatives of both Thylacinidae and Dasyuridae. Consequently, placement of this new taxon at the family level is untenable. Analysis of the material draws attention to the absence of well supported synapomorphies for the dasyuromorphian order. Considered together with temporal as well as geographic position, the presence of a feature which is possibly synapomorphic with some Thylacinidae or Dasyuridae, is treated as a reasonable basis for the placement of *J. muizoni* within Dasyuromorphia.

S. Wroe, (s.wroe@unsw.edu.au) School of Biological Sciences, University of Sydney, New South Wales, 2006 and School of Biological Science, University of New South Wales, New South Wales, 2052. Received 4 June 2000

Keywords: *Joculusium muizoni*, Dasyuromorphia, Miocene, Riversleigh

DASYUROMORPHIANS have been suggested to be structurally ancestral to the remainder of the Australian marsupial radiation (Bensley 1903, Ride 1964, Szalay 1994). However, the factor often flagged to support a basal position for the clade, that is, the retention of essentially primitive marsupial morphology, hinders attempts to demonstrate a special relationship between dasyuromorphians and any specific South American clade. The discovery and interpretation of new Australian fossil material has added new dimensions to debate on the topic of dasyuromorphian evolution (Wroe 1998, 1999a). Archer (1976b, 1982), Wroe (1996, 1997a, 1997b, 1999b, in press), Wroe *et al.* (2000) and Wroe & Nasser (2001) have demonstrated that even generalised dasyurids, commonly thought to approximate the plesiomorphic australidelphian state for many features, are highly derived in their cranial morphology. Moreover, Wroe (1999b) argues that although the family Dasyuridae can not be defined by the presence of dental synapomorphies, shared derived basicranial features demonstrate a special relationship between the middle Miocene dasyurid, *Barinya wangala*, and all 'modern Dasyuridae' (*sensu* Wroe 1999b), with 'modern Dasyuridae' united by a further suite of synapomorphic basicranial features.

Recently discovered material from early Tertiary deposits of Murgon, southeastern Queensland (Godthelp *et al.* 1999) has added further complexity to our understanding of dasyuromorphian evolution. Australia's oldest marsupicarnivore, *Djarthia murgonensis*, may be referable to either Didelphidae (*sensu* Marshall *et al.*, 1990) or Australidelphia on the basis of dental evidence. If the latter is ultimately supported by the unambiguous association of *D. murgonensis* with australidelphian tarsal material, then it becomes more difficult to define Australidelphia, Dasyuromorphia or Didelphidae on the basis of dental morphology alone. A conservative approach is required in the taxonomic placement of generalised Australian fossil taxa, such as that described below, particularly in the absence of basicranial material.

SYSTEMATIC PALAEONTOLOGY

Order DASYUROMORPHIA Gill, 1872

***Joculusium* gen. nov.**

Type species. Joculusium muizoni sp. nov.

Diagnosis. Joculusium muizoni differs from all

known dasyurids and thylacinids in the following combination of features: P_3 equal to or exceeding P_2 dorsoventrally; M_1 paraconid large, circumscribed by a well defined anterior cingulid; cristid obliqua terminates just buccal to the carnassial notch of the metacristid on M_{2-4} ; trigonid shorter, anteroposteriorly, than the talonid on M_{1-4} ; metacristid almost equal to the paracristid in length on M_{2-4} ; postprotocristid-metacristid and hypocristid strongly torsioned away from transverse orientation to dentary on M_{1-4} ; posterior face of the trigonid on M_{1-4} is anteriorly inclined; entoconid large on M_{1-3} and distinct on M_4 ; hypoconulid notch present in the anterior cingulid of M_{2-4} , but not deeply recessed. *Joculusium muizoni* can be distinguished from known bandicoots (peramelomorphians) by the above combination of characters and possession of a well defined posterior cingulid, a more buccally positioned hypoconulid and a less lingually positioned cristid obliqua.

Etymology. From the Latin *joculus*, meaning 'a little joke', in reference to the type locality (Gag Site).

***Joculusium muizoni* sp. nov. (Fig. 1)**

Diagnosis. As for the genus.

Etymology. After French palaeontologist Christian de Muizon, in recognition of his great contribution to marsupial palaeontology.

Holotype. QM F36442, a left dentary containing the posterior root of P_1 , P_2 (excepting the occlusal tip), and P_3 , M_{1-4} .

Locality and age of material. Gag Site, Riversleigh World Heritage fossil property, Lawn Hill National Park, northwestern Queensland. The fossil material recovered from Gag Site is interpreted to be middle Miocene in age on the basis of the site's stratigraphic relationships to other Riversleigh deposits and its contained (Dwornamor) local fauna (Archer *et al.* 1995, Creaser 1997).

Description. In buccal view the dentary is roughly uniform in depth posteroanteriorly from M_4 to beneath anterior root of M_1 , but tapers from M_1 to beneath the posterior root of P_1 , and is broken away from 2 mm posterior of M_4 and 1 mm anterior of P_1 root.



Fig. 1. *Joculusium muizoni* gen. et sp. nov., QM F36442, holotype, left dentary containing the posterior root of P_1 , P_2 (excepting the occlusal tip), and P_3 , M_{1-4} . Stereopair in occlusal view. Scale bar indicates 2 mm.

The crown of P_1 , the anterior root, and the lingual portion of the anterior root alveolus are broken away. Only the posterior root remains. A small diastema separates P_1 and P_2 .

In P_2 a portion of the crown is missing anterior to the posterior root. A clearly defined cristid ascends the posterior face of crown, from a small central cusplule on the heel to where the crown is broken away. Another cristid continues from the posterocentral cusplule along the buccal crown margin to a point between the anterior and posterior roots. From the distance between the anterior and posterior roots it is inferred that P_2 is the longest premolar anteroposteriorly.

P_3 is wider than P_2 transversely and gently recurved in lateral view. A cingulid circumscribes the heel and is bisected by another cristid which ascends the posterior face of the principal cusplule from the small, posterocentral cusplule. The principal cusplule and M_1 protoconid are of nearly equal height. It is inferred that P_3 probably exceeds P_2 in height, but damage to P_2 precludes certainty.

In M_1 the paracristid is the main vertical shearing crest. Principal cusplules in order of

decreasing height are: protoconid, paraconid, metaconid, entoconid, hypoconulid and hypoconid. Although taller than the metaconid, the paraconid is the smaller of the two with the protoconid the largest cusp of the M_1 trigonid. The metaconid is large and positioned posterolingually with respect to the protoconid. A right angle is formed between the paracristid-preprotocristid and the postprotocristid-metacristid. An acute internal angle is formed between the cristid obliqua and hypocristid. Both the metacristid and hypocristid are oriented at about forty-five degrees to the long axis of the dentary. The cristid obliqua terminates anteriorly just buccal to the 'carnassial notch' separating the metacristid and postprotocristid. In occlusal view the surface area of the talonid is much greater than that of the trigonid. The posterior face of the trigonid is inclined. A well defined anterior cingulid runs anteriorly from the buccal base of the protoconid to beneath the carnassial notch of the paracristid, where a small notch accommodates the heel of P_3 . The posterior cingulid is well-developed, running from the hypoconulid to the base of the hypoconid. A distinct buccal cingulid is almost continuous with the anterior and posterior cingulids. The hypoconulid is not deeply recessed into anterior cingulid of M_2 .

M_2 differs from M_1 in the following ways: the metacristid is almost as long as the paracristid; the trigonid is longer than the talonid; the trigonid and talonid are about equal in width; in occlusal view the internal angles formed by the paracristid and metacristid, and the cristid obliqua and hypocristid, are more acute; the entoconid larger; and a distinct hypoconulid notch beneath the anterior face of the paraconid accommodates the M_1 hypoconulid.

M_3 morphology is similar to that of M_2 except as follows: the trigonid is wider but more compressed anteroposteriorly, with the angle between the paracristid and metacristid more acute; on the transverse axis the talonid width is less in both absolute terms and relative to that of the trigonid; the anterior end of the cristid obliqua terminates in a more buccal position and the entoconid is smaller.

The tip of the M_3 protoconid is broken off. M_4 differs from M_3 as follows: both the talonid width and the hypoconid are reduced; the paraconid is larger, the entoconid and metaconid are smaller; anteriorly, the cristid obliqua terminates at a point lingual to the carnassial notch of the metacristid; and the angle formed between paracristid and metacristid is more acute.

Meristic gradients from M_{1-4} . The orientations of the paracristid, metacristid and hypocristid are increasingly transverse with respect to the long axis of dentary; the angle formed between the paracristid and metacristid is increasingly acute; protoconid height increases M_{1-3} (M_4 protoconid tip missing); metaconid height increases from M_1 to M_3 , then decreases for M_4 ; the metaconid is larger than the paraconid on all molars but decreases in size for M_{1-4} ; talonid width increases from M_{1-2} , but decreases from M_{3-4} .

CHARACTERSTATE POLARITIES

Method. Most features considered in the present study have been examined by Archer (1976a, 1976b), Reig *et al.* (1987), Marshall *et al.* (1990), Wroe (1996, 1997a, 1997b, 1999b), Wroe *et al.* (2000) and Godthelp *et al.* (1999). Further details regarding their distribution among dasyuromorphians and relevant outgroup taxa (i.e. Peradectidae, Didelphidae, *Djarthia murgonensis* (Marsupialia *incertae sedis*), Microbiotheriidae, Peramelemorphia) is contained therein. Systematic nomenclature for Dasyuromorphia follows Wroe (1996) with higher level marsupial systematics after Marshall *et al.* (1990). Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, such that the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3 and M1-4.

Morphology of P_3 . A P_3 that equals or exceeds P_2 in height is plesiomorphic for Marsupialia (Archer 1976a, Muirhead & Wroe 1998, Wroe 1996, 1997a, 1997b, 1999b). Marked hypertrophy of P_3 , as in some Thylacinidae (i.e. *Thylacinus*) and Borhyaenidae, as well as reduction or loss as in some Dasyuridae (e.g. *Dasyurus*) are derived. *Joculusium muizoni* is plesiomorphic for this feature.

Morphology of the M_1 paraconid. The paraconid is well developed on M_1 in unspecialised representatives of outgroups to Dasyuromorphia (Archer 1976a, Wroe 1996, 1997a, 1997b), and many dasyurid and thylacinid taxa. This cusp is small to absent in some dasyuromorphians, especially among carnivorous Dasyuridae (e.g. *Dasyurus* spp.). The large M_1 paraconid of *J. muizoni* represents a plesiomorphy within Dasyuromorphia.

Morphology of the metaconid. Metaconids which are well developed on M_1 as well as M_{2-4} , are treated as plesiomorphic for Dasyuromorphia by

Archer (1976) and Wroe (1996, 1997a, 1997b). Both uniform reduction of the metaconids on M_{1-4} (e.g. in most thylacinids), and differential reduction, with reduction of the M_1 metaconid greatly exceeding that of M_{2-4} (e.g. in species of *Dasyurus*, *Sarcophilus*), are derived. *Joculusium muizoni* exhibits the plesiomorphic state.

Orientation of the metacristid. This cristid (protocristid of Marshall *et al.* 1990) is oriented transversely with respect to the long axis of the dentary in most representatives of dasyuromorphian outgroup clades, *Ankotarinja tirarensis* and *Wakamatha tasselli* (both Dasyuromorphia *incertae sedis*), and among dasyurids, most sminthopsines. Previous authors have treated this character state as plesiomorphic for Marsupialia and Dasyuromorphia (Archer 1976a, 1976b; Van Dyck *et al.* 1994; Godthelp *et al.* 1999). The derived state for this feature (i.e. oblique orientation of the metacristid) is present in some Peradectidae and Didelphidae (Archer 1976a), at least one taxon treated as plesiomorphic for most dental characters within Dasyuromorphia (i.e. *Keeuna woodburnei*), thylacinids which retain a metaconid (e.g. *Muribacinus gadiyuli*, *Badjcinus turnbulli*), and all Phascogalinae and Dasyurinae. In the present study it is accepted that transverse orientation of the metacristid is plesiomorphic for Dasyuromorphia. However, pervasive homoplasy must be acknowledged regardless of the polarity decision taken. Thus, within Dasyuromorphia, the derived state (oblique alignment) must have evolved independently within Thylacinidae and Dasyuridae, unless the presence of transversely aligned metacristids in most Sminthopsinae is treated as an apomorphic reversal to a primitive state. Even among sminthopsines oblique orientation of this cristid is present in *Sminthopsis leucopus* requiring acceptance of at least three independent derivations of this feature within the order. *Joculusium muizoni* is apomorphic for this character among dasyuromorphians, which represents a possible synapomorphy with any of three taxa within the order.

Relative lengths of trigonids and talonids. The trigonid may be anteroposteriorly longer, equal to, or shorter than the talonid. The distribution of this feature among polyprotodont marsupials is considered by Reig *et al.* (1987), Marshall *et al.* (1990), Marshall & Muizon (1995), Springer *et al.* (1996) and Godthelp *et al.* (1999). Some Peradectidae (e.g. *Alphadon*), Didelphidae (e.g.

Caluromys) and all Microbiotheriidae have talonids that are clearly longer than the trigonids on all lower molars. In many marsupials trigonid and talonid lengths are almost equal, including in some Didelphidae (e.g. *Didelphis*), some Dasyuromorphia (e.g. *Ankotarinja tirarensis*) and Peramelemorphia (e.g., *Peroryctes*), *Djarthia murgonensis* and *Joculusium muizoni*. Among these taxa, slight variation in subjective determination of the trigonid-talonid boundary might result in their receiving either 'trigonid longer than talonid' or 'talonid shorter than trigonid' status. Because of variation among outgroup taxa and disagreement between authorities, Godthelp *et al.* (1999) were non-committal regarding the assignment of polarity for this feature among Marsupialia. However, the presence of trigonids and talonids of 'sub-equal' length in the least derived Australian marsupial (*Djarthia murgonensis*) as well as other generally unspecialised fossil taxa (e.g. *Ankotarinja tirarensis*, *Keeuna woodburnei*), supports the view that this represents the plesiomorphic condition for Dasyuromorphia. Consequently, *J. muizoni* is treated as plesiomorphic within the order for this feature.

Anterior point of termination of the cristid obliqua. The distribution of this feature is considered by Archer (1976a, 1976b), Marshall *et al.* (1990), Muirhead & Filan (1995) and Godthelp *et al.* (1999). Termination of this cristid beneath the carnassial notch of the metacristid is probably plesiomorphic for metatherians and the presence of both buccal (e.g. *Djarthia murgonensis*, *Joculusium muizoni*, most Didelphimorphia and Dasyuromorphia) and lingual placement (e.g. most Peramelemorphia) are derived (Godthelp *et al.* 1999). Termination of the cristid obliqua just buccal to the carnassial notch, evident in *Joculusium muizoni*, represents a likely dasyuromorphian plesiomorphy.

Position of the hypoconulid. Placement of the hypoconulid slightly posterobuccal to the entoconid is plesiomorphic for Dasyuromorphia and Didelphimorphia. Presence of a hypoconulid directly posterior to the entoconid is a peramelemorphian synapomorphy (Muirhead & Filan 1995). *Joculusium muizoni* shows the plesiomorphic condition.

Development of the anterior cingulid. A distinct anterior cingulid is present in peradectids, microbiotheriids, peramelemorphians, *Djarthia*

murgonensis, and most Ameridelphia and Dasyuromorphia. This feature is often poorly developed or absent in large carnivorous taxa (e.g. *Borhyaena*, *Thylacinus*). In a number of omnivorous taxa the anterior cingulid is markedly hypertrophied (e.g. *Didelphis*, *Wakamatha tasselli*, and Peramelemorphia). Both hypertrophy and hypotrophy of this feature, relative to that evident in peradectids, are apomorphic for both Metatheria and Dasyuromorphia. *Joculusium muizoni* is plesiomorphic for this feature.

Morphology of the M₄ talonid. A well developed M₄ talonid with the hypoconid, entoconid, and hypoconulid each present, is common to Peradectidae, most Didelphidae, some Peramelemorphia, *Djarthia murgonensis*, some Dasyuridae and Thylacinidae, and *Joculusium muizoni*. Reduction of one or more of these cusps is evident in microbiotheriids, some didelphids and peramelemorphians, and most dasyurids and thylacinids. Presence of a well developed M₄ talonid has commonly been treated as a dasyuromorphian plesiomorphy (Archer 1976a, 1976b). Reduction has clearly occurred independently within several marsupial lineages and at least twice within Dasyuromorphia (i.e. Dasyuridae and Thylacinidae). *Joculusium muizoni* is plesiomorphic among dasyuromorphians for this feature.

DISCUSSION

Many researchers in the field of dasyuromorphian phylogeny have treated the order as indefinable on the basis of dental morphology (Ride 1964, Archer 1976b, Szalay 1994), with the possible exception of a reduction in incisor formula to 4/3. Marshall *et al.* (1990) put forward two additional dental features as synapomorphic for the clade, that is, M₄ preparacrista elongated and talonids reduced relative to the trigonids. None of these putative synapomorphies are unequivocal within Marsupialia. Four upper and three lower incisors are found in some borhyaenoid and peramelemorphian taxa, as well as all Dasyuromorphia. While there can be little doubt that loss of I³ occurred independently in each of these three clades, this is not necessarily true with respect to loss of I₄. The fourth lower incisor is absent in all Australian taxa and therefore represents a possible synapomorphy for the Australian marsupial radiation. Polarity determinations for the additional features proposed by Marshall *et al.* (1990) are debatable.

Hypertrophy of the M⁴ preparacrista, although certainly derived within Marsupialia and common to most dasyuromorphians, is not present in some generalised dasyurid taxa (e.g. *Neophascogale*). However, it is present in some possible sister taxa to Dasyuromorphia (i.e. *Djarthia murgonensis*, Peramelemorphia). Regarding the relative sizes of the trigonid and talonid, there is disagreement over which constitutes the plesiomorphic marsupial condition (Godthelp *et al.* 1999).

Within a phylogenetic framework the elucidation of higher level relationships for *J. muizoni* is problematic at both the familial and ordinal levels. In terms of overall similarity, this species could be placed within Dasyuridae, but only on the basis of symplesiomorphy. Whilst some dasyurids retain a dentition that may be plesiomorphic for a higher clade within Dasyuromorphia, if not Dasyuromorphia itself, all Dasyuridae can be defined by a number of basicranial synapomorphies, as demonstrated by Wroe (1996, 1997a, 1999b) and Wroe *et al.* (2000). The single derived dasyuromorphian feature identified in *J. muizoni*, oblique orientation of the metacristid, is shared with some thylacinids and dasyurids. Consequently, in the absence of cranial material, it is impossible to position *J. muizoni* within the order. Even at the ordinal level circumspection is required. Loss of I³ remains the only well supported dental synapomorphy for Dasyuromorphia, a feature not yet known in *J. muizoni*. However, the presence of a derived feature that may indicate special relationship with either some Thylacinidae or Dasyuridae, in conjunction with stratigraphic and geographic position, are together treated as a reasonable basis for the placement of *J. muizoni* within Dasyuromorphia.

ACKNOWLEDGEMENTS

I am indebted to M. Archer and R. Cifelli for their constructive criticism and comment on drafts of this manuscript. Funding was provided to S. Wroe through grants from the following institutions: University of Sydney (U2000 Postdoctoral Research Fellowship), French Ministry of Foreign Affairs, Linnean Society of New South Wales, Australian Geographic Society, Institute of Wildlife Research, and the University of New South Wales. Support has also been given by the Australian Research Council (to M. Archer); National Estate Grants Scheme (Queensland) (grants to M. Archer and A. Bartholomai); Department of Environment, Sports and Territories; Queensland National Parks and Wildlife Service;

Commonwealth World Heritage Unit (Canberra); ICI Australia Pty Ltd; Queensland Museum; Australian Museum; Century Zinc Pty Ltd; Mt Isa Mines Pty Ltd; Surrey Beatty and Sons Pty Ltd; Riversleigh Society Inc.; Royal Zoological Society of New South Wales and many private supporters. Skilled preparation of most Riversleigh material was carried out by Anna Gillespie.

REFERENCES

- ARCHER, M., 1976a. The dasyurid dentition and its relationship to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peramelids (Peramelina: Marsupialia). *Australian Journal of Zoology, Supplementary Series* 39, 1-34.
- ARCHER, M., 1976b. Miocene marsupicarnivores (Marsupialia) from central South Australia, *Ankotarinja tirarensis* gen. et. sp. nov., *Keeuna woodburnei* gen. et. sp. nov., and their significance in terms of early marsupial radiations. *Transactions of the Royal Society of South Australia* 100, 53-73.
- ARCHER, M., HAND, S. & GODTHELP, H., 1995. Tertiary environmental and biotic change in Australia. 77-99 in Vrba, E.S., Denton, G.H., Partridge, T.C. & Burkle, L.H. (eds), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven.
- BENSLEY, B.A., 1903. On the evolution of the Australian Marsupialia with remarks on the relationships of marsupials in general. *Transcripts of the Linnean Society of London (Zoology)* 9, 83-217.
- FLOWER, W.H., 1867. On the development and succession of teeth in the Marsupialia. *Philosophical Transactions of the Royal Society of London* 157, 631-641.
- GILL, T., 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collection* 2, 1-98.
- GODHELP, H., WROE, S. & ARCHER, M., 1999. A new marsupial from the early Eocene Tingamarra local fauna of Murgon, southeastern Queensland: the prototypical Australian marsupial? *Journal of Mammalian Evolution* 6, 289-313.
- LUCKETT, W. P., 1993. An ontogenetic assessment of dental homologies in therian mammals. 182-204 in Szalay, F.Z., Novacek, M.J. & McKenna, M.C. (eds), *Mammal Phylogeny; Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*. Springer-Verlag, New York.
- MARSHALL, L. G., CASE, J.A. & WOODBURN, M.O., 1990. Phylogenetic relationships of the families of marsupials. 433-502 in Genoways, H.H. (ed.), *Current Mammalogy, Vol. 2*. Plenum Press, New York.
- MARSHALL, L.G. & MUIZON, C.de., 1995. *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. Part II. The Skull. *Mémoires du Muséum National d'Histoire Naturelle* 165, 21-90.
- MUIRHEAD, J. & FILAN, S., 1995. *Yarala burchfieldi* (Peramelemorphia) from Oligo-Miocene deposits of Riversleigh, northwestern Queensland. *Journal of Paleontology* 59, 127-134.
- MUIRHEAD, J. & WROE, S., 1998. A new genus and species, *Badjcinus turnbulli* (Thylacinidae: Marsupialia), from the late Oligocene of Riversleigh, northern Australia, and an investigation of thylacinid phylogeny. *Journal of Vertebrate Paleontology* 18, 612-626.
- MUIZON, C.de., 1994. A new carnivorous marsupial from the Palaeocene of Bolivia and the problem of marsupial monophyly. *Nature* 370, 208-211.
- RIDE, W.D.L., 1964. A review of Australian fossil marsupials. *Journal of the Royal Society of Western Australia* 47, 97-129.
- SPRINGER, M.S., KIRSCH, J.A.W. & CASE, J.A., 1997. The chronicle of marsupial evolution. 129-161 in Givnish, T.J. & Sytsma, K.J. (eds), *Molecular Evolution and Adaptive Radiation*. Cambridge University Press, Cambridge.
- SZALAY, F.S., 1994. *Evolutionary history of the Marsupialia and an analysis of osteological characters*. Cambridge University Press, New York. 455p.
- VAN DYCK, S.V., WOJNARSKI, J.C.Z. & PRESS, A.J., 1994. The Kakadu Dunnart, *Sminthopsis bindi* (Marsupialia: Dasyuridae), a new species from the stony woodlands of the Northern Territory. *Memoirs of the Queensland Museum* 37, 311-323.
- WROE, S., 1996. *Muribacinus gadiyuli* (Thylacinidae, Marsupialia), a very plesiomorphic thylacinid from the Miocene of Riversleigh, northwestern Queensland, and the problem of paraphyly for the Dasyuridae. *Journal of Paleontology* 70, 1032-1044.
- WROE, S., 1997a. A reexamination of proposed morphology-based synapomorphies for the families of Dasyuromorphia (Marsupialia): Part I, Dasyuridae. *Journal of Mammalian Evolution* 4, 19-52.
- WROE, S., 1997b. *Mayigriphus orbus*, a new genus and species of dasyuromorphian (Marsupialia) from the Miocene of Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41, 429-438.
- WROE, S., 1998. A new genus and species of 'bone-cracking' dasyurid (Marsupialia) from the Miocene of Riversleigh, northwestern Queensland. *Alcheringa* 22, 277-284.

- WROE, S., 1999a. Killer kangaroos and other murderous marsupials. *Scientific American*, May, 68-74.
- WROE, S., 1999b. The geologically oldest dasyurid, from Miocene deposits of Riversleigh, northwestern Queensland. *Palaeontology* 42, 501-527.
- WROE, S., in press. *Maximucinus muirheadae*, gen. et sp. nov. (Thylacinidae: Marsupialia), from the Miocene of Riversleigh, northwestern Queensland. *Australian Journal of Zoology*.
- WROE, S., EBACH, M., AHYONG, S., MUIZON, C. de & MUIRHEAD, J., 2000. Cladistic analysis of dasyuromorphian (Marsupialia) phylogeny using cranial and dental features. *Journal of Mammalogy* 81, 1008-1024.
- WROE, S. & MUSSER, A., 2001. The skull of *Nimbacinus dicksoni* (Thylacinidae: Marsupialia). *Australian Journal of Zoology* 49, 1-29.