

Postcranial morphology of *Ganguroo bilamina* Cooke, 1997
(Marsupialia: Macropodidae) from the middle Miocene of Riversleigh,
northwestern Queensland

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Postcranial remains of the early to middle Miocene bulungamayine kangaroo *Ganguroo bilamina* Cooke, 1997 are described. This is one of only two reports (see also Kear *et al.* this volume) of bulungamayine postcrania and describes some of the oldest postcranial material known for macropodoids. Functional analysis suggests a hopping gait, though the well developed forelimbs and scapular morphology indicate consistent use of more quadrupedal progression. Phylogenetic analyses using postcranial characters place *G. bilamina* as the sister taxon to macropodids. This supports the conclusions of Case (1984), Woodburne (1984), Cooke (1997a, b), Kear (1998), Cooke & Kear (1999) and Kear & Cooke (this volume) in advocating a revised position for Bulungamayinae.

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A PARTIAL juvenile skeleton and skull of the bulungamayine kangaroo *Ganguroo bilamina* Cooke, 1997 was collected from AL90 Site, System C deposits (Archer *et al.* 1994; Archer *et al.* 1997; Black 1997). This material, along with that reported by Kear *et al.* (this volume), is the only definite postcranial remains for bulungamayines and some of the oldest known for macropodoids.

Bulungamayines are small to large extinct kangaroos known from the late Oligocene to early late Miocene. Flannery *et al.* (1983) placed them as the sister group to potoroinae. Case (1984), Woodburne (1984), Cooke (1997a, b), Kear (1998), Cooke & Kear (1999) and Kear & Cooke (this volume), however, suggested macropodid affinity on the basis of synapomorphies present in *G. bilamina*, other derived bulungamayines and plesiomorphic macropodids such as *Dorcopsoides fossilis*, species of *Dorcopsis* and *Dorcopsulus* and *Hadronomas puckeridgei*. The possibility of bulungamayine paraphyly (Cooke 1997a, b) or polyphyly (Kear 1998; Kear *et al.* this volume) has also been proposed.

The postcranial anatomy of *G. bilamina* is similar to that of potoroinae and macropodids in exhibiting features indicative of hopping gaits. Forelimb morphology comparable to the

predominantly quadrupedal *Hypsiprymnodon moschatus* (Johnson & Strahan 1982), however, suggests consistent use of more quadrupedal modes of progression. This paper describes postcranial remains of *G. bilamina* and analyses bulungamayine phylogeny and functional anatomy using postcranial features.

Skeletal and myological terminology follows Elfman (1929), Hopwood (1974), Hopwood & Butterfield (1976, 1990), Murray (1995), Wells & Tedford (1995) and Bishop (1997). The abbreviation QMF refers to the fossil collection of the Queensland Museum, Brisbane. All measurements were made using digital callipers and are in millimetres (mm).

SYSTEMATIC PALAEONTOLOGY

Superfamily MACROPODOIDEA Grey, 1821

Family MACROPODIDAE Grey, 1821

Subfamily BULUNGAMAYINAE Flannery, Archer & Plane, 1983

Genus *Ganguroo* Cooke, 1997

Type species. Ganguroo bilamina Cooke, 1997

CERVICAL VERTEBRAE

- Centrum height: 2.59
- Centrum width: 4.33
- Body height (inc. neural spine): 9.34, 9.38, 9.58, 9.87, 10.48, 10.71
- Width across postzygapophyses: 9.47, 10.04, 10.46, 10.67, 10.87, 10.91

THORACIC VERTEBRAE

- Centrum height: 3.16, 3.22, 3.25, 3.35, 3.57, 3.63, 4.16
- Centrum width: 4.3, 4.4, 4.49, 4.57, 5.38, 5.39, 6.18
- Width across postzygapophyses: 5.53, 5.58, 6.01, 6.12, 6.19, 6.37, 6.59, 7.95, 8.86

LUMBAR VERTEBRAE

- Centrum height: 4.08, 4.87
- Centrum width: 6.37, 6.51
- Maximum height: 11.66, 13.62
- Width across postzygapophyses: 6.18, -

CAUDAL VERTEBRAE

- Centrum height: 1.43, 4.29, 4.96
- Centrum width: 2.41, 5.31, 6.02
- Maximum length: 7.07, 10.18, 13.57
- Minimum width: 1.09, 3.24, 3.8

SCAPULA

- Glenoid fossa diaphysis height: 5.15
- Glenoid fossa diaphysis width: 3.46
- Glenoid neck height: 5.99
- Maximum blade height: 14.17
- Supraspinous fossa height: 4.31
- Infraspinous fossa height: 7.84

HUMERUS

- Maximum distal width: 9.31
- Supinator crest height: 8.86
- Supinator crest width: 1.19
- Deltoid crest length: 16.78
- Total length: 33.39

ULNA

- Width across coronoid process: 3.46
- Olecranon process depth: 3.91
- Total length (estimated): 36.74

RADIUS

- Distal facet height: 3.24
- Distal facet width: 4.8
- Total length (estimated): 36.4

METACARPAL

- Maximum length: 5.87
- Maximum proximal width: 2.02
- Minimum shaft width: 1.47

DISTAL MANUAL PHALANGE

- Maximum length: 4.16, 4.08
- Ungual process width (at base): 1.61, 1.54
- Ungual process depth (at base): 0.73, 0.78

ILIUM

- Maximum ilial blade length: 28.33
- Minimum ilial blade width: 8.05
- Distal apex height: 10.79
- Total length: 38.98

FEMUR

- Maximum distal epiphysis width: 13.06
- Intercondylar notch width: 3.92

TIBIA

- Shaft circumference: 20.29
- Proximal epiphysis width: 11.66
- Intercondylar eminence height: 3.1

FIBULA

- Distal epiphysis width: 6.3
- Distal epiphysis ant./pos. length: 3.41
- Peroneal tendon sulcus width: 2.17

NAVICULAR

- Maximum height: 5.86
- Dorsal surface length: 3.81
- Plantar surface length: 5.24
- Astragalar facet height: 5.21
- Astragalar facet width: 2.19

ECTOCUNEIFORM

- Maximum height: 7.25
- Plantar process length: 2.77
- Dorsal surface length: 4.17
- Navicular facet height: 4.31
- Navicular facet width: 2.77
- Metatarsal III facet height: 3.42
- Metatarsal III facet width: 1.36

Table 1. Measurements of postcranial elements included in this study. (all measurements in mm).

Age and distribution. Early to middle Miocene of northern Australia.

Diagnosis. As for *G. bilamina* until postcranial material of other species recovered.

Ganguroo bilamina Cooke, 1997

Holotype. QMF19915, left dentary.

Additional Material. Additional material includes an associated juvenile partial skeleton and skull (skull not described here) QMF30845. Postcranial elements include: cervical vertebrae 1-6; thoracic

vertebrae 2-9, 12 and 13; lumbar vertebrae 1 and 2; caudal vertebrae 3 and 5; ribs left and right 1-12; left and right clavicle; manubrium and sternbra 5; fragmentary left and partial right scapula; complete left and right humerus; partial left and right ulna; partial left radius; left metacarpal II; two distal manual phalanges; right ilium; right distal femoral epiphysis; left proximal epiphysis and distal section of tibia (lacking epiphysis); left distal fibula; complete left navicular and ectocuneiform.

Supplemental Diagnosis. Lumbar vertebrae with strong mid-ventral keel; scapula broadly

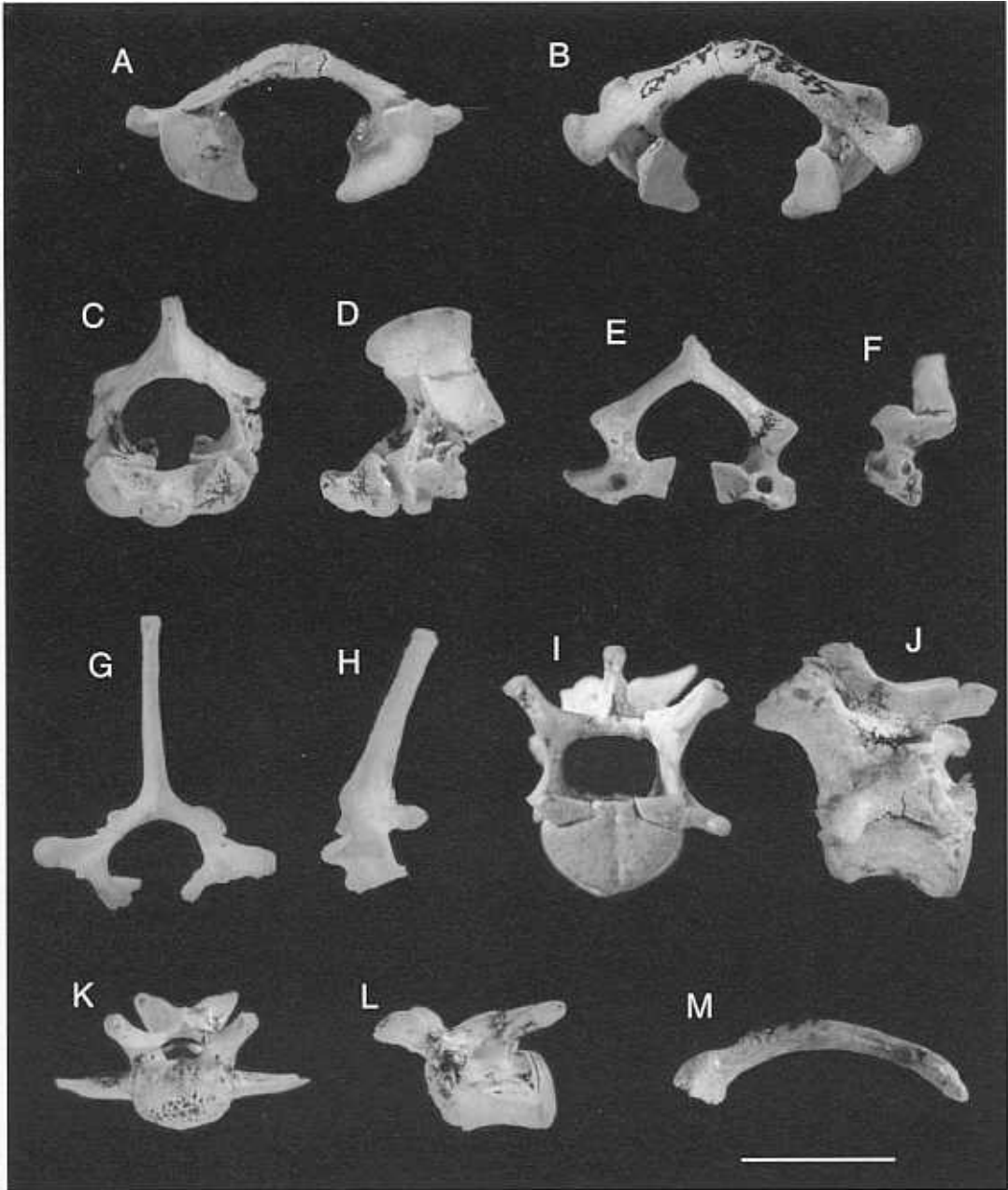


Fig. 1. Vertebral elements of juvenile *Ganguroo bilamina* Cooke, 1997 (QMF30845). A, B, atlas; A, anterior view; B, posterior view. C, D, axis; C, anterior view; D, lateral view. E, F, cervical vertebra; E, anterior view; F, lateral view. G, H, thoracic vertebra; G, anterior view; H, lateral view. I, J, lumbar vertebra; I, anterior view; J, lateral view. K, L, anterior caudal vertebra; K, anterior view; L, lateral view. M, posterior view of clavicle. Scale bar is 10 mm.

rectangular in outline with supraspinous fossa equal in length to infraspinous; acromion process reduced and rounded; humerus straight and slender with reduced supinator and long, distally low deltoid crests; lateral teres tuberosity poorly developed; entepicondyle closely abuts trochlea;

coronal depression deeply excavated and strongly delineated; capitellum and trochlea unevenly sized; ulna robust with straight ventral edge; olecranon process well developed and bears distinct transverse dorsal crest; distal apex of ilium dorsoventrally elongate and transversely



Fig. 2. Scapula fragment of juvenile *Ganguroo bilamina* Cooke, 1997 (QMF30845). Scale bar is 5 mm.

compressed; navicular large and crescentic with well developed plantar eminence; astragalar facet on navicular transversely broad;

Additional material locality distribution and age. AL90 Site, southern section Gag Site Plateau, Riversleigh World Heritage area, northwestern Queensland. AL90 Site is correlated with System C (early middle Miocene) deposits (Black 1997). Type locality is Wayne's Wok Site (System B, early Miocene; Cooke 1997c). Paratype and additional cranial/dental material is known from Bitesantennary Site, System A/B and Wayne's Wok, Camel Sputum, Mike's Menagerie and Upper sites, all System B (Archer *et al.* 1994).

Description

Axial skeleton

Cervical vertebrae (Fig. 1A-F, Table 1). Complete axis, atlas and cervicals 3-6 preserved. Centrum from second or third cervical present. Atlas tall and arched in anterior view; ventral arch not closed by neurapophyses. Condylar cusps reniform and transversely narrow. Transverse processes short, spatulate and anteriorly inclined. Transverse foramen small and laterally opening. Axis transversely narrow and tall with massive, lobate and anteroposteriorly elongate neural spine. Neural arch tall and transversely narrow. Prezygapophyses ovoid; odontoid process short and dorsally inclined. Postzygapophyses transversely narrow and subhorizontal; transverse foramen laterally opening. Cervical vertebrae anteroposteriorly short and dorsoventrally tall. Neural canal highly arched, becoming lower in successive vertebrae. Neural spines tall and tapering at apex. Pre/postzygapophyses subovoid and slightly concave. Centrum platycoelous.

Thoracic vertebrae (Fig. 1G-H, Table 1). Thoracic vertebrae 2-9 and 12, 13 preserved. Eight unfused thoracic centra present. Anterior thoracics low

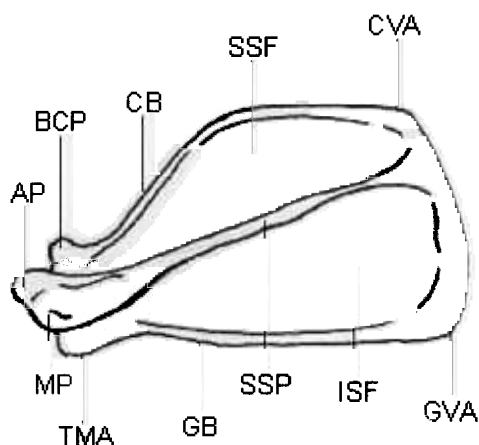


Fig. 3. Reconstructed scapula (lacking epiphysis) of juvenile *Ganguroo bilamina* Cooke, 1997 (QMF30845). Scale bar is 10 mm. Abbreviations: AP, acromion process; BCP, base of coracoid process; CB, coracoid border; CVA, coracovertebral angle; GB, glenoid border; GVA, glenovertebral angle; ISF, infraspinous fossa; MP, metacromion process; SSF, supraspinous fossa; SSP, scapular spine; TMA, triceps muscle attachment.

with tall neural spines becoming shorter and more inclined in successive vertebrae. Transverse processes robust with costal fovea shallowing posteriorly and being lost in fourth or fifth vertebra. First thoracic lacks transverse foramen. Pre/postzygapophyses prominent, becoming larger and more elevated in posterior vertebrae. Parapophyses on first thoracic subtriangular and well-developed, becoming reduced in posterior vertebrae. Neural canal arched and wider than tall, becoming narrower posteriorly. Centra deep and slightly opisthocelous; weak mid-ventral keel present on all thoracics.

Lumbar vertebrae (Fig. 1I-J, Table 1). Represented by lumbar 1 and 2 only. Transverse processes present only as a low crest in lumbar 1, becoming spatulate and subhorizontally oriented in lumbar 2. Anapophyses moderately large and lobate; metapophyses very weak. Pre/postzygapophyses large and laterally flaring. Prezygapophyses with indistinct and flat articular facets. Neural spine moderately tall. Sulci for ligamentum flavum very weakly developed. Centra slightly opisthocelous with distinct mid-ventral keel.

Caudal vertebrae (Fig. 1K-L, Table 1). Represented by caudals 3 and 5 only. Vertebral body ovoid in cross-section and dorsoventrally tall. Low neural canal present in both vertebrae. Third caudal exhibits large pre/postzygapophyses; fifth caudal exhibits large prezyg-

apophyses only. Transverse processes of third caudal narrow and wing-like; more anteroposteriorly elongate and extending the full length of centra in caudal five.

Ribs. Left and right ribs 1-12 present. Preservation ranges from complete to fragmentary. Rib shaft anteroposteriorly compressed being thicker towards vertebral extremity. Tuberculae subcircular and posteriorly offset in posterior ribs. Capitulae spatulate and ovoid in outline, being anteroposteriorly elongate.

Clavicle and Sternebrae (Fig. 1M, Table 1). Complete left and right clavicle present; manubrium and penultimate sternebrae present. Clavicle large with anteroposteriorly compressed shaft. Sternal extremity spatulate and flattened; external surface slightly concave. Vertebral extremity is a subtriangular lobe with dorsal edge bearing an elongate oblique costal fovea facet. Coracoclavicular ligament tubercle reduced to a raised crest on ventral edge of vertebral extremity lobe. Manubrium (not figured) kite-shaped with prominent posterior facet for articulation of sternebra. Penultimate sternebrae (not figured) short and distinctly waisted. Articular facets rectangular in outline.

Appendicular skeleton

Scapula (Fig. 2, 3, Table 1). Material consists of right glenoid (lacking epiphysis) and anterior scapular spine, and fragmentary left scapular blade. Scapular blade (Fig. 3) subrectangular in outline with obtuse glenovertebral angle and straight glenoid border; coracoid border inclined; coracovertebral angle near perpendicular; supraspinous and infraspinous fossae extensive; supraspinous fossa equal to infraspinous in length though dorsoventrally narrower posteriorly. Anterior portion of scapular spine deep and rounded; acromion process poorly developed; metacromion process dorsoventrally deep and semicircular in outline. M. triceps attachment deeply hollowed. Glenoid fossa and coracoid process broken away in specimen.

Humerus (Fig. 4A-C, Table 1). Both left and right humeri preserved, left lacking distal trochlea. Humeral shaft straight and slender; supinator crest weakly developed and low; deltoid crest long, low and blade-like. Teres tuberosity weakly developed. Glenoid large and globular; epiphysis missing. Greater and lesser trochlea transversely narrow;

distal trochlea with widely spaced capitulum and trochlea. Capitulum globular and larger than the more cylindrical trochlea. Medial and lateral epicondylae reduced. Olecranon depression low, wide and weakly defined dorsally. Coronoid fossa deep and extensive, separated from shallower trochlear depression by distinct inter-fossa ridge. Entepicondylar foramen dorsoventrally long and anteroposteriorly narrow. Entepicondylar buttress robust, D-shaped in cross-section.

Ulna (Fig. 4D-F, Table 1). Left and right ulnae present, left lacking most of shaft, right represented by distal extremity only. Ulna large with slender shaft and straight ventral edge. Proximal extremity deep with a broad, shallow depression for insertion of m. flexor digitorum profundus. Olecranon process large, being dorsoventrally tall and antero-posteriorly short when ulna is horizontally oriented. Process base transversely broad, narrowing dorsally and terminating in a distinct dorsal crest. Semilunar notch medially pinched; capitular facet open and separated from narrow trochlear facet by a low ridge. Radial facet narrow and also separated from trochlear facet by a low ridge. Capitular and radial facets strongly laterally sloping with low, weak buttressing. Coronoid process tall and laterally flaring. Anconeal process less distinct and anteroposteriorly thick. Subtriangular rugose insertion for m. brachialis and gleno-ulnar divisions of the m. biceps brachii present immediately anterior to the coronoid process. Depression for radial bursa elongate and indistinct; interosseous ridge long and low.

Radius (Table 1). Left radial shaft preserved. Lacks distal epiphysis, proximal articular facet and neck. Radial shaft D-shaped in cross-section over much of its length becoming more dorsoventrally flattened distally and circular proximally. The interosseous ligament groove is well developed and extends along the flattened proximolateral surface; the crest-like ventral border of the groove represents the interosseous membrane attachment (which joins the radial and ulnar shafts together). Adjacent to the interosseous ligament groove and situated on the dorsolateral surface is an elongate, arched depression for attachment of the m. adductor digit I longus. Distal apex of the radial shaft is both broad and deep relative to shaft length; distal facet surface trapezoidal in outline. Distal ulnar articulation forms shallow lateral groove.





Fig. 5. Hindlimb elements of juvenile *Ganguroo bilamina* Cooke, 1997 (QMF30845) A, B, ilium; A, lateral view; B, ventrolateral view. C, plantar view of distal femur epiphysis. D, dorsal view of proximal tibia epiphysis. E, anterior and posterior views of distal fibula. Scale bar is 10 mm.

Metacarpals (Table 1). Left metacarpal II present only; lacks distal epiphysis. Metacarpal shaft oval in cross-section, dorsoventrally compressed and distinctly waisted. Proximal trapezium facet trapezoidal in outline, tapering plantarly and shallowly concave. Metacarpal I and III facets broad and triangular; bordered dorsally by low ridges. Proximal plantar surface raised into a rounded node for interosseous ligament attachment.

Distal manual phalanges (Table 1). Two complete distal manual phalanges preserved. Ungual process elongate relative to plantar process length. Process slightly downcurved and dorsoventrally flattened with oval cross-section; elongate and parallel sided in dorsal view with tapered tip. Posterior articular facet shallow and oval in outline; borders produced into laterally flaring crests. Plantar process oval in outline and transversely narrow.

Pelvis (Fig. 5A-B, Table 1). Represented by complete right and distal extremity of left ilium, both unfused. Ilium outwardly flared (approximately 20° from vertebral plane); sacroiliac articulation situated far back on ramus. Distal ilial apex spatulate, being dorsoventrally elongate and transversely compressed. Iliac blade broad with low anteriorly flattened iliac crest. M. gluteus medius/m. gluteus profundus portion of blade shallowly concave, becoming slightly narrower anteriorly; m. iliacus portion narrow and flattened becoming broader anteriorly. M. rectus femoris scar forms prominent triangular rugosity immediately anterior to acetabulum border. Iliopectineal process large and subcylindrical.

Femur (Fig. 5C, Table 1). Represented by right distal epiphysis only. Condyles smooth and separated by a deep U-shaped intercondylar fossa. Lateral condyle transversely broad and ventrally flattened; medial condyle transversely narrow and rounded ventrally. Anterior condylar crests widely spaced and low.

Fig. 4 (opposite). Forelimb elements of juvenile *Ganguroo bilamina* Cooke, 1997 (QMF30845). A-C, humerus; A, anterior view; B, lateral view; C, posterior view. D-F, ulna; D, lateral view; E, dorsal view; F, medial view. Scale bar is 10 mm.

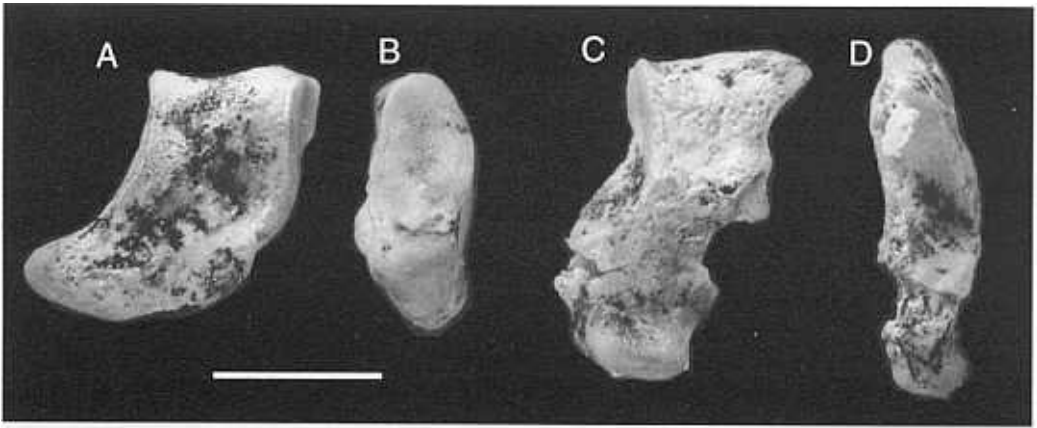


Fig. 6. Tarsal elements of juvenile *Ganguroo bilamina* Cooke, 1997 (QMF30845) A, B, navicular; A, lateral view; B, posterior view. C, D, ectocuneiform; C, lateral view; D, anterior view. Scale bar is 5 mm.

Tibia (Fig. 5D, Table 1). Represented by right distal shaft section lacking epiphysis, and left proximal epiphysis. Distal shaft section oval in cross-section, with flattened medial edge for fibula contact. Proximal epiphysis with transversely broad, flat and circular, lateral condylar surface; medial condylar surface transversely narrow and concave. Intercondylar eminence tall with wide transverse ligament attachment. Depression for anterior cruciate ligament shallow and indistinct. Shallow posterior cruciate ligament depression present on medial edge of intercondylar eminence.

Fibula (Fig. 5E, Table 1). Left distal fibular shaft and epiphysis present. Shaft slender and D-shaped in cross-section. Lateral peroneal tendon groove shallow; bordered anteroposteriorly by low tuberosities for attachment of superior peroneal retinaculum. Peroneal tendon groove terminates in a circular pit. Medial malleolar fossa of distal epiphysis shallowly inclined and slightly concave. Anterior edge of epiphysis produced into a rounded node.

Navicular and ectocuneiform (Fig. 6, Table 1). Complete left navicular and ectocuneiform recovered. Navicular (Fig. 6A, B) transversely compressed and crescentic in lateral view. Astragalar facet transversely wide and dorsoventrally elongate; facet occupies entire posterior surface of navicular. Posteriormost facet extremity slightly medially offset. Plantar tuberosity shallow and transversely narrow. Entocuneiform facet small and oval; ectocuneiform facet large, bilobed; mesocuneiform contact absent. Low, broad anterior lateral crest bears cuboid facet. Ectocuneiform (Fig. 6C, D)

transversely compressed and dorsoventrally tall; plantar tuberosity well developed and oval. Navicular facet dorsoventrally elongate, reniform and concave. Metatarsal III facet small, dorsoventrally elongate and crescentic. Cuboid articulation formed by a low lateral crest.

COMPARISONS AND FUNCTIONAL INTERPRETATION

The following are functional interpretations and comparisons of the postcranial elements preserved for *Ganguroo bilamina* with other macropodoids. Definitions of macropodoid gaits follow Windsor & Dagg (1971) and are as outlined in Kear *et al.* (this volume).

Vertebrae (Fig. 1A-L, Table 1). Cervical vertebrae in *G. bilamina* resemble those of sthenurines (Wells & Tedford 1995) in the presence of a massive neural crest on the axis and tall successive neural spines. Elongation of neural spines is associated with enlargement of the nuchal ligament and epaxial muscles, increasing strength and mobility in the neck (Finch & Freedman 1986). Lengthening of the cervical neural spines is also associated with increased attachment area for the m. trapezius (Wells & Tedford 1995), a major manipulator of the forelimb. This indicates increased strength in the forelimb for either locomotion (providing forelimb extension during the propulsive stroke) or browsing (elevating the limb).

The thoracic vertebrae of *G. bilamina* resemble those of other macropodoids with tall, slightly caudally directed neural spines and outwardly slanted prezygapophyses. This suggests restricted dorsoventral movement in the thoracic region, and saltating locomotion, as rigidity in the

head and thoracic region stabilizes the body (and raises the centre of gravity) during hopping (Christian & Preuchtoft 1996).

Lumbar vertebrae in *G. bilamina* are similar to those of other macropodoids in possessing ventrally deflected transverse processes and steeply oriented prezygapophyses. Ventral deflection of the transverse processes implies enlargement of the m. erector spinae, involved in flexing the lumbar region during hopping (Elftman 1929). Orientation of the zygapophyses also suggests considerable lumbar flexibility necessary for generating power for the initial upward and anterior propulsive thrust (Elftman 1929).

Scapula (Fig. 2, 3, Table 1). The scapular blade in *G. bilamina* resembles that of the phalangerid *Trichosurus vulpecula*, the hypsiprymnodontid *Hypsiprymnodon moschatus* and the potorine *Potorous tridactylus* in being subrectangular in outline. *Ganguroo bilamina* differs from these taxa, however, in possessing a more acute coracovertebral angle (a feature of macropodids related to reduction of the attachment area for the m. supraspinatus, and thus, extensor power of the forelimb, see below; Murray 1995). The supraspinous and infraspinous fossae in *G. bilamina* are large and subequal in anteroposterior extent suggesting powerful m. supraspinatus (an extensor of the forelimb) and m. infraspinatus muscles (rotator of the forelimb on the scapula). In macropodids the supraspinous fossa is much reduced anteroposteriorly and the infraspinous fossa becomes dorsoventrally more extensive (this development is most extreme in derived sthenurines, e.g. *Simosthenurus occidentalis*; Murray 1995). The condition in *G. bilamina* therefore suggests powerful extensors and rotators were present as in *T. vulpecula*, *H. moschatus* and *P. tridactylus*, in which they act to extend and rotate the forelimb during locomotion. The condition in macropodids indicates reduced emphasis on extension and development of a more extensive limb-rotating musculature possibly for manipulation of food and grooming.

The acromion process in *G. bilamina* is large and lobate similar to that of macropodids. The acromion process anchors the spino-acromiodeltoid portion of the m. deltoideus which serves to abduct the humerus. In forms consistently using quadrupedal gaits such as *T. vulpecula*, *H. moschatus* and *P. tridactylus* the process is massive and steeply inclined indicating considerable humeral abduction. The reduced

acromion of *G. bilamina* and macropodids (with the exception of *Hadronomas puckridgi*; Murray 1995) therefore may be related to a reduced locomotory role for the forelimb.

Humerus (Fig. 4A-C, Table 1). The humeral shaft in *G. bilamina* resembles that of *H. moschatus* and the propleopine *Propleopus oscillans* (Ride *et al.* 1997) in being relatively straight and slender, characteristics indicative of quadrupedal cursors (Ride *et al.* 1997). The deltoid crest is narrow and extends far down the shaft as in *T. vulpecula*, species of *Dendrolagus* and *Dorcopsis* and sthenurines (Murray 1995; Wells & Tedford 1995). Crest form in *G. bilamina*, species of *Dorcopsis* and sthenurines, however, differs in being uniformly low along its length. Lengthening of the deltoid crest corresponds to elongation of the m. deltoideus muscle (divided into anterior abducting and posterior retracting segments respectively) lever arm, thus increasing the muscle's range of action and strength. Enlargement of the clavicle in *G. bilamina* (with its correspondingly lengthened m. clavodeltoid attachment) similarly suggests extensive m. deltoideus musculature. Reduction of deltoid crest height is a feature of quadrupedal cursors (Ride *et al.* 1997), however, its reduction in bipedal sthenurines suggests the feature may also be related to forelimb browsing.

The condition of the supinator crest in *G. bilamina* resembles that of *H. moschatus*, *P. oscillans* (Ride *et al.* 1997) and species of *Dorcopsis* in being tall and transversely narrow. This would reduce area of attachment for the m. supinator longus (= m. brachioradialis which rotates the forearm and flexes the carpal digits), a common condition in quadrupedal cursors (Ride *et al.* 1997).

The teres tuberosity in *G. bilamina* is reduced as in *T. vulpecula*, *H. moschatus* and *P. oscillans* (Ride *et al.* 1997) suggesting reduction of the m. latissimus dorsi and m. teres major respectively. Both these muscles act as humeral retractors and are minimally developed (as in *G. bilamina*) in cursorial mammals (Ride *et al.* 1997).

The distal extremity of the humerus in *G. bilamina* is similar to that of potorines and macropodines (except species of *Dendrolagus*) in reduction of the medial entepicondyle. This limits the attachment area for the digital flexors and indicates reduced strength in the digits of the hand. In climbing marsupials such as *T. vulpecula* and species of *Dendrolagus*, the entepicondyle is strongly projecting and bears a prominent

anterior groove (accommodating the flexor tendon). Absence of these features in *G. bilamina* suggests insufficient gripping strength (in the hand), to support the body weight, and thus probably largely terrestrial habits.

The capitellum and trochlea in *G. bilamina* are unequal in size, a feature also occurring in *T. vulpecula*, *H. moschatus* and *P. tridactylus*. This may be an adaptation towards increasing rotational flexibility of the elbow and/or concentrating body weight through the more robust capitellar facet (on the ulna) during quadrupedal progression.

Ulna (Fig. 4D-F, Table 1). The ulna in *G. bilamina* resembles that of *T. vulpecula*, *H. moschatus*, potorines and sthenurines (Wells & Tedford 1995) in bearing a dorsoventrally deep olecranon process and pronounced transverse dorsal crest. This suggests enlargement of the m. triceps brachii and m. anconeus muscles (which extend and retract the ulna during elbow flexion) and strengthening of the forelimb for locomotion (e.g. *T. vulpecula*, *H. moschatus*) and/or browsing (e.g. sthenurines; Wells & Tedford 1995).

The m. flexor digitorum profundus attachment in *G. bilamina* is reduced in its depth and width similar to that of many macropodines. The m. flexor digitorum profundus serves to flex the wrist and metacarpals, therefore its reduction may be related to stiffening of the wrist and limitation of the manus to a more locomotory role.

The m. biceps brachii attachment is well developed in *G. bilamina* and, as in all macropodoids (Dawson *et al.* 1989), would have formed a powerful flexor of the elbow.

Pelvis (Fig. 5A-B, Table 1). The ilium in *G. bilamina* is similar that of other macropodoids in being laterally flared relative to the long axis of the vertebral column, and having the sacro-iliac contact situated far back on the iliac blade. This suggests enlargement of the erector spinae which support the upper half of the body during hopping (Elftman 1929) and may also have acted to raise the torso during browsing. The m. gluteus medius, m. gluteus profundus and m. iliatus (which act to extend/vert the hip and abduct/vert the thigh) attachments are large, representing the common condition in macropodoids. Enlargement of these muscle groups is indicative of saltating gaits (Elftman 1929; Alexander & Vernon 1975).

The anterior ilial apex in *G. bilamina* resembles that of *T. vulpecula*, *H. moschatus*, species of *Dorcopsis* and *Dendrolagus* and ambulating

marsupials such as *Sarcophilus harrisii* and *Thylacinus cynocephalus* in being transversely compressed and spatulate in lateral view. This increases the attachment area for the m. sartorius which acts to extend the upper portion of the hindlimb.

The pectineal process is well developed and subcylindrical in *G. bilamina*, resembling that of macropodids (except species of *Dorcopsis* and *Dendrolagus*, *Protemnodon tumbuna*; Menzies & Ballard 1994, and *H. puckridgi*; Murray 1995). An extended pectineal process increases the area for attachment of the m. psoas minor and m. pectineus (which act to flex the spine and hip and extend the pelvis), a common feature of macropodoid species which consistently use saltating gaits (pers. obs.).

The area of m. rectus femoris scarring in *G. bilamina* is anteroposteriorly extensive, similar to that of potoroids and macropodids in which m. rectus femoris abducts the femur anteroposteriorly. Scarring is extensive in all macropodoids but is anteroposteriorly reduced in species of *Dorcopsis* and *Dendrolagus*, *H. puckridgi* (Murray 1995) and *Protemnodon hopei* (pers. obs., suggesting that reduction of the rectus muscle may be related to the reduced abductive stresses of more quadrupedal modes in these taxa).

Tibia and fibula (Fig. 5D-E, Table 1). The possibility of limited movement between the tibia and fibula in *G. bilamina* is suggested by: the large posterior process of the proximal fibula epiphysis; prominent fibular sulcus on the lateral femoral condyle; and width of the tibial facet on the proximal epiphysis of the fibula. These features are also found in species of *Dendrolagus* (in which the tibia and fibula move freely relative to each other, Flannery & Szalay 1982; Flannery *et al.* 1996; Bishop 1997) in which they facilitate lateral mobility in the lower hindlimb for quadrupedal locomotion and climbing.

Pes (Fig. 6, Table 1). The elongate, condyle-like navicular facet of *G. bilamina* resembles that of *H. moschatus* and *P. tridactylus* in which it provides flexibility to the navicular/cuneiform complex and hence the medial digits of the foot (digits I-III). This condition is unlike that in the majority of potorines and macropodids in which the facet is shorter and more laterally oriented. This arrangement reduces lateral flexibility in the pes, stiffening it for more effective saltation. The loss of a mesocuneiform/navicular contact suggests the pes in *G. bilamina* was, as in all macropodoids, narrowed to some extent.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>B. parvus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>T. vulpecula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. moschatus</i>	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
<i>P. tridactylus</i>	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0
<i>G. bilamina</i>	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	1	1
<i>D. atrata</i>	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1
<i>D. goodfellowi</i>	1	1	1	1	1	1	0	0	1	0	0	1	0	0	1	0	1
<i>P. penicillata</i>	1	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	1
<i>T. thetis</i>	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1
<i>W. bicolor</i>	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1
<i>M. parryi</i>	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1
<i>S. stirlingi</i>	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	1	0

Table 2. Character state distribution for phylogenetic analysis of *Ganguroo bilamina* relationships. Plesiomorphic state = 0; apomorphic state = 1.

CHARACTER ANALYSIS

Seventeen postcranial characters were selected for phylogenetic analysis. Character selection was limited by specific element type preserved in the *G. bilamina* specimen. Because the specimen represents a juvenile, comparison was made with juvenile specimens of *Macropus parryi*, *Aepyprymnus rufescens* and *Potorous tridactylus* to screen for ontogenetic variability within characters. Character polarity was established by comparison with outgroup taxa. Determination of the plesiomorphic state follows Hennig (1966) and Wiley *et al.* (1991) with reference to the immediate sister taxon to the ingroup (represented herein by the phalangeriform *Trichosurus vulpecula*; Aplin & Archer 1987; Flannery 1987). The burramyid *Burramys parvus* was included to aid in resolving character polarities within the ingroup (see Stevens 1980; Simmons 1993).

Character states were determined by examination of representative specimens in the collections of the Australian Museum and National Museum of Victoria. No single complete specimen of *Sthenurus* was available for study. Character state determination for this taxon was therefore made by reference to published descriptions and figures of Wells & Tedford (1995).

The following is a list of character definitions and interpretations. Character distributions are listed in Table 2.

1. Proportions of navicular. The navicular in *S. stirlingi* and macropodines (represented herein by *Dendrolagus goodfellowi*, *Dorcopsis atrata*, *Petrogale penicillata*, *Thylogale thetis*, *Wallabia bicolor* and *Macropus parryi*) is subrectangular in lateral view having dorsal edge

longer or subequal to ventral edge (1). *Burramys parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus* and *G. bilamina* all exhibit a crescentic navicular in lateral view with the ventral edge longer than dorsal (0). A subrectangular navicular is considered derived relative to a crescentic form and represents a synapomorphy for *S. stirlingi* and macropodines.

2. Form of navicular plantar eminence. Eminence form in *S. stirlingi* and macropodines is reduced (1) unlike that of *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus* and *G. bilamina* which is condyle-like and prominent (0). A reduced eminence is considered derived relative to prominent and condyle-like and is synapomorphic for *S. stirlingi* and macropodines.

3. Length and width of astragalar facet of navicular. Astragalar facet in *G. bilamina*, *S. stirlingi* and macropodines is transversely wide and dorsoventrally shortened (1) relative to facet form in *B. parvus*, *T. vulpecula*, *H. moschatus* and *P. tridactylus* which is transversely narrow and dorsoventrally elongate (0). A wide short facet is considered derived relative to the narrow, elongate form and represents a synapomorphy uniting *G. bilamina*, *S. stirlingi* and macropodines.

4. Mesocuneiform/navicular contact. The mesocuneiform does not contact the navicular (1) in macropodoids (evidenced in *G. bilamina* by the absence of a mesocuneiform facet on the navicular) unlike *B. parvus* and *T. vulpecula* which exhibit a clear mesocuneiform-navicular contact (0). Absence of contact between the mesocuneiform and navicular is considered derived relative to contact presence and is a macropodoid synapomorphy.

5. Form of acromion process of scapula. The acromion process of the scapula in *G. bilamina*,

S. stirlingi and macropodines is poorly developed and rounded (1) unlike *B. parvus*, *T. vulpecula*, *H. moschatus* and *P. tridactylus* in which the acromion is well developed and anterodorsally produced (0). A poorly developed and rounded acromion process is considered derived relative to one which is well developed and anterodorsally produced. Condition (1) represents a synapomorphy for *G. bilamina*, *S. stirlingi* and macropodines.

6. Condition of supraspinous fossa of scapula. The supraspinous fossa in *S. stirlingi* and macropodines is anteroposteriorly shortened relative to the infraspinous fossa (1); supraspinous fossa is anteroposteriorly elongate and subequal in length to the infraspinous fossa (0) in *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus* and *G. bilamina*. An anteroposteriorly shortened supraspinous fossa is considered derived relative to an elongate fossa and represents a synapomorphy for *S. stirlingi* and macropodines.

7. Condition of supinator crest on humerus. The supinator crest in *G. bilamina* and *D. atrata* is reduced and transversely narrow with a rounded apex (1). The crest is well developed and transversely broad with distinctly pointed apex (0) in *B. parvus*, *T. vulpecula* and all other macropodoids. A reduced and narrow crest with rounded apex is considered derived relative to a well developed and broad crest with distinctly pointed apex. The latter condition appears to be independently derived in *G. bilamina* and *D. atrata*. However, the condition may also represent a plesiomorphic state for macropodids which has been subsequently lost in all other taxa. The character is uninformative because it represents an autapomorphic state in this phylogeny.

8. Height of deltoid crest of humerus. The deltoid crest is of uniform height along its length with the distal extremity forming a shallow incline (1) in *H. moschatus*, *G. bilamina* and *S. stirlingi*. The crest is of non-uniform height with its distal extremity forming a steep incline which may bear a rugose boss at its apex (0) in *B. parvus*, *T. vulpecula*, *P. tridactylus* and macropodines. A uniform crest with shallowly inclined distal extremity is considered derived relative to a non-uniform crest with steeply inclined distal extremity. Condition (1) is autapomorphic in *H. moschatus*, *G. bilamina* and *S. stirlingi* and is thus uninformative.

9. Condition of lateral deltoid ridge of humerus. The lateral deltoid ridge is well developed and prominent (1) in *P. tridactylus*, *S. stirlingi* and

macropodines; ridge is weakly developed and poorly evident (0) in *B. parvus*, *T. vulpecula*, *H. moschatus* and *G. bilamina*. A well developed ridge is considered derived relative to a poorly developed ridge and represents a synapomorphy for *S. stirlingi* and macropodines. The condition in *P. tridactylus* may be autapomorphic or represent a synapomorphy uniting *P. tridactylus*, *S. stirlingi* and macropodines which has been secondarily lost in *G. bilamina*.

10. Condition of entepicondyle of humerus. The entepicondyle closely abuts the trochlea (1) in *H. moschatus*, *P. tridactylus*, *G. bilamina* and *D. atrata* unlike *B. parvus*, *T. vulpecula*, *S. stirlingi* and macropodines in which the entepicondyle is widely separated from the trochlea by a distinct groove (0). A closely abutting entepicondyle and trochlea is considered derived relative to their being widely separated by a distinct groove. Condition (1) may represent a synapomorphy for macropodoids which has been secondarily lost in *S. stirlingi* and macropodines (except *D. atrata*). Loss of the feature may thus represent a synapomorphy for this latter group. The absence of the derived state in *D. atrata* may be a further secondary reversal or, more parsimoniously, a retention of the state present in plesiomorphic macropodoids. Phylogenetic significance of this character is equivocal because placement of the shared derived state can not be resolved.

11. Development of coronal depression on humerus. The coronal depression is deeply excavated and strongly delineated (1) in *G. bilamina*, *T. thetis*, *W. bicolor* and *M. parryi* unlike *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus*, *S. stirlingi*, *D. atrata*, *D. goodfellowi* and *P. penicillata*, all of which exhibit a shallowly excavated and weakly delineated (0) coronal depression. A deeply excavated and strongly delineated depression is considered derived relative to a shallowly excavated and weakly delineated depression. Condition (1) is a synapomorphy for the clade containing *T. thetis*, *W. bicolor* and *M. parryi* and is autapomorphic in *G. bilamina*.

12. Condition of capitellum and trochlea of humerus. The capitellum and trochlea are subequal in size (1) in *S. stirlingi* and macropodines; but are of distinctly unequal size with the capitellum larger than the trochlea (0) in *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus* and *G. bilamina*. Similarity in size of the capitellum and trochlea is considered derived relative to dissimilarity in size, and is a synapomorphy for *S. stirlingi* and macropodines.

13. Condition of ulna shaft. The shaft of the ulna in *S. stirlingi* and macropodines (except *D. goodfellowi*) has a distinctly sinuous ventral edge profile in lateral view (1) unlike *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus*, *G. bilamina* and *D. goodfellowi* in which the ulna shaft has a straight ventral edge profile in lateral view. A sinuous ventral edge profile is considered derived relative to a straight ventral edge profile and is synapomorphic for *S. stirlingi* and macropodines (except *D. goodfellowi*). The condition in *D. goodfellowi* may represent an autapomorphic secondary reversal or a retained plesiomorphy.

14. Form of olecranon process of ulna. The olecranon process in *S. stirlingi* and macropodines (except *D. goodfellowi*) is dorsoventrally short (when element is horizontally oriented), and rounded in lateral view (1). Those of *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus*, *G. bilamina* and *D. goodfellowi* are dorsoventrally tall (when element is horizontally oriented) with a distinct, transverse dorsal crest (0). A dorsoventrally short and rounded olecranon process is considered derived relative to a tall, distinctly crested process. The derived condition represents a synapomorphy for *S. stirlingi* and macropodines with the condition in *D. goodfellowi* being a retained plesiomorphy or a secondary reversal to the plesiomorphic state.

15. Shape of distal apex of ilium. The distal apex of the ilium in *P. tridactylus*, *S. stirlingi* and macropodines is transversely broadened by contribution of the raised distal end of the iliac crest (1); the apex is transversely narrowed by a poor contribution of the distal end of the iliac crest (which is reduced in height, making the distal ilial apex spatulate in lateral view; 0) in *B. parvus*, *T. vulpecula*, *H. moschatus* and *G. bilamina*. A transversely broad, distal ilial apex is considered derived relative to one which is transversely narrow and is a synapomorphy for *S. stirlingi* and macropodines. The condition in *P. tridactylus* may be autapomorphic or represent a synapomorphy shared with *S. stirlingi* and macropodines which has been secondarily lost in *G. bilamina*.

16. Development of the ilio-pectineal process of ilium. The iliopectineal process in *P. tridactylus*, *G. bilamina*, *S. stirlingi* and macropodines (except *D. goodfellowi*) is prominent and subcylindrical (1; more transversely compressed in *S. stirlingi*). The process in *B. parvus*, *T. vulpecula*, *H. moschatus* and *D. goodfellowi* is reduced and if present, restricted to a slight ridge (0). A

prominent subcylindrical iliopectineal process is considered derived relative to a reduced process and is a synapomorphy for *P. tridactylus*, *G. bilamina*, *S. stirlingi* and macropodines (except *D. goodfellowi*). The condition in *D. goodfellowi* represents an autapomorphic secondary reversal to the plesiomorphic state.

17. Ventral profile of anterior lumbar centra. The ventral profile bears a distinct median keel (1) in *G. bilamina* and macropodines and is unlike *B. parvus*, *T. vulpecula*, *H. moschatus*, *P. tridactylus* and *S. stirlingi* in which ventral profile is smooth and rounded (0). A distinct ventral keel is considered derived relative to a smooth and rounded surface and is a synapomorphy for *G. bilamina* and macropodines. The condition in *S. stirlingi* is an autapomorphic secondary reversal to the plesiomorphic state.

RESULTS

The analysis produced two equally parsimonious trees (Fig. 7A, B.), both of 27 steps with CI of 0.63 (expected CI = 0.667), RI of 0.818 and RCI of 0.515. Tree topology is identical for heuristic and branch-and-bound search options. Below expected consistency index values are produced by a polytomy including *S. stirlingi* and macropodines (except *D. goodfellowi* and *D. atrata* in tree 2; Fig. 7B.). Comparison with 'next-best' trees indicates polytomy resolution decreases with additional steps making interpretation of relationships within the *S. stirlingi*/macropodine group tentative.

Discussion

Macropodoid monophyly is unequivocally supported in this phylogeny by an apomorphic absence of contact between the mesocuneiform and navicular. Potoroids (*sensu* Flannery 1989) do not form a discrete clade, with *H. moschatus* placed as the sister taxon to all other macropodoids and *P. tridactylus* the sister taxon to *G. bilamina*, *S. stirlingi* and macropodines (unequivocally united by the presence of a prominent, subcylindrical iliopectineal process). *Ganguroo bilamina* is placed with *S. stirlingi* and macropodines on the basis of: a transversely wide and dorsoventrally shortened astragalar facet on the navicular; a rounded and weakly developed acromion process on the scapula; and presence of a distinct ventral keel on the anterior lumbar vertebrae (not present in *S. stirlingi*).

Unequivocal apomorphies uniting *S. stirlingi* and macropodines include: navicular rectangular in lateral view with dorsal edge longer than or

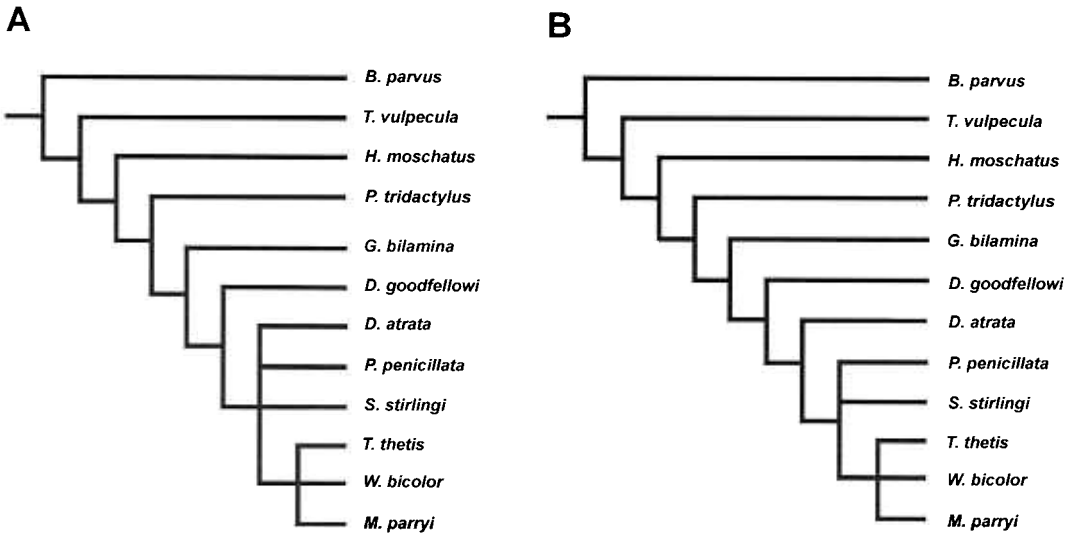


Fig. 7. Results of phylogenetic analyses. A, tree 1 topology includes *D. atrata* within the *S. stirlingi*/macropodine polytomy. B, tree 2 topology includes *D. atrata* as sister taxon to the *S. stirlingi*/macropodine polytomy. For both trees, length = 27, CI = 0.63, RI = 0.818, RCI = 0.515.

subequal to ventral edge; reduction of the navicular plantar eminence; anteroposteriorly shortened supraspinous fossa; and subequally sized capitellum and trochlea on the humerus.

Dendrolagus goodfellowi forms the sister taxon to a polytomy including *S. stirlingi* and the remaining macropodines, united by: a sinuous ventral edge to the ulnar shaft; and dorsoventrally short and rounded olecranon process. Separation of *D. atrata* from the *S. stirlingi*/macropodine polytomy in tree 2 (Fig. 7B) is based on an equivocal character state (a closely abutting entepicondyle and trochlea on the humerus) and cannot be substantiated in this phylogeny. The terminal clade formed by *T. thetis*, *W. bicolor* and *M. parryi* is united by an apomorphic deeply excavated and strongly delineated coronal depression on the humerus. This contradicts the immunological and DNA hybridisation data of Baverstock *et al.* (1989), Baverstock *et al.* (1990) and Kirsch *et al.* (1995) respectively, who include species of *Thylogale* as the sister group to those of *Petrogale*.

The inclusion of *S. stirlingi* within the macropodine complex may support the conclusions of Woodburne (1967), Archer (1984), Szalay (1994) and Cooke (1997a) who suggest origin of Sthenurinae from within a paraphyletic Macropodinae. The lack of resolution in this phylogeny, however, makes any conclusion extremely tentative.

Recognition of the bulungamayine *G. bilamina* as the sister taxon to *S. stirlingi* and macropodines

supports the conclusions of Case (1984), Woodburne (1984) and Cooke (1997a, b) who regard bulungamayines as basal to Macropodidae. This arrangement also supports Ride (1993), Cooke (1997a) and Wroe *et al.* (1998) in regarding Potoroidae (*sensu* Flannery 1989) as polyphyletic. The possibilities of a sister group relationship of potorines to both bulungamayines and macropodids, or a polyphyletic Bulungamayinae, however, are plausible. Separation of *H. moschatus* from potoroids (Ride 1993; Szalay 1994; Cooke 1997a; Wroe *et al.* 1998; Burk *et al.* 1998) may also be suggested by the absence of any clear synapomorphy.

CONCLUSIONS

1. *Ganguroo bilamina* was most likely partly quadrupedal, although bipedal saltation was probably used at higher speeds (as in species of *Dendrolagus*; Windsor & Dagg 1971 and *Potorous*; Buchmann & Guiler 1974).

2. Bulungamayinae, represented herein by *G. bilamina*, is the sister group to macropodids. This supports the conclusions of Case (1984), Woodburne (1984) and Cooke (1997a, 1997b).

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