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Ankle bones: The Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny

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Abstract. Szalay's (1982a) arrangement of the Marsupialia into cohort Ameridelphia encompassing all New World marsupials except Microbiotheriidae, and cohort Australidelphia containing all Australian and the American Microbiotheriidae, based primarily on the pattern of articulation between the foot bones astragalus and calcaneus, has no leg to stand on. It is shown here that joint patterns of these ankle bones are variable and intergrading, and that the derived "continuous" joint patterns attributed exclusively to Australidelphia, evolved independently more than once from "separate" joint patterns attributed exclusively to Ameridelphia, and that both patterns occur in both hemispheres. Morphology of astragalus and calcaneus of the Chilean opossum, *Dromiciops gliroides* Thomas (*D. australis* Philippi, preoccupied), Szalay's australidelphian "morphotype", is essentially ameridelphian or didelphoid, and little if at all different from that of some didelphoid mouse opossums of the family Marmosidae. On the other hand, special characters of *Dromiciops* revealed here are such that this lone survivor of the Microbiotheriidae, cannot be ancestral to or descended from any known non-microbiotheriid. The arrangement of living American marsupials proposed here recognizes two major subdivisions of infraclass Marsupialia (Metatheria): cohort Microbiotheriomorpha with distinctive characters shared with living eutherians and monotremes, and the younger, independently evolved, cohort Didelphimorpha with the American orders Didelphida and Paucituberculata, and the Australian superorder Dasyuomorpha.

Key words. Marsupial phylogeny; Australidelphia; Ameridelphia; Microbiotheriidae; *Dromiciops*.

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Introduction

The significance of the ankle bones astragalus and calcaneus in marsupial phylogeny and classification as conceived by Szalay (1982a, b) is critically examined. Szalay distinguished two morphological patterns (Plates I—IV). The first or primitive pattern, typified by ankle bones of early Cenozoic pelyomyids and Recent didelphoids, is characterized by two separate facets on the calcaneal dorsal surface that articulate with a corresponding pair of separate facets on the astragalar plantar surface (Plates I, II, a, b). This pattern, said to be restricted to all living and known extinct American marsupials except the Microbiotheriidae, is the primary basis for Szalay's cohort Ameridelphia. The second or derived pattern, typified by the sole surviving microbiotheriid, the Chilean "monito del monte", *Dromiciops gliroides* Thomas (*D. australis* Philippi preoccupied), and morphotype of Szalay's cohort Australidelphia, is marked by coalescence of the once dual facets of each bone into a single continuous facet (Pls. III, IV, a, b). This pattern is, according to Szalay, the exclusive hallmark of all known Australian marsupials as well as the American Microbiotheriidae first known from the Oligocene. The family supposedly includes a number of referred extinct taxa which date back to the late Cretaceous (fide Marshall et al. 1990).

The acronym for the primitive, or separate lower ankle joint pattern, in Szalay's terminology, is SLAJP; and for the derived continuous lower ankle joint pattern, CLAJP. Of the two ankle bones in question only the astragalus articulates with the tibia and fibula for ankle joint movement. Variation within, or possible intergradation between the patterns, is not mentioned in Szalay's text. His concept of polarity is absolute and all American or Australian marsupials are explicitly included within their respective geographically restricted cohort. Other characters of possible phylogenetic significance, including the dental, are perfunctorily discussed and dismissed as comparatively unimportant.

The response by students of marsupial morphology and phylogeny to Szalay's interpretation has been mixed but with passive acceptance by most, and by others with uncritical incorporation of Szalay's cohorts into their respective phylogenetic arrangement of the Marsupialia. Strong objections to the classification raised by Reig et al. (1987, pp. 70, 77) seem to have passed unheeded by one coauthor in a subsequent publication (Marshall et al. 1990) and by the others in a later work (Kirsch et al. 1991). None compared marsupial ankle bones.

Material

The astragali and calcanei of 102 living American and Australian marsupials have been studied. All but those of 1 (*Lestodelphys*) are preserved in the Field Museum of Natural History (FMNH). They represent five of the six families and 18 of the 19 genera (*Glironia*, **Glironiidae**, lacking) of living American marsupials, and 6 (of ca 15) families, and 17 of

the total number of genera of living Australian taxa. The ankle bone data for two representatives of the American Miocene Borhyaenidae have been taken from the literature. The material is listed in Table 1.

Tarsal bones of right, left, or of both feet of the same animal, were examined. Most bones were individually disengaged from dry, articulated foot skeletons or liquid-preserved specimens, hand cleaned by scraping after water softening of the dry overlying tissue.

Foot bone data were supplemented by examination and comparison of cranial and dental characters of living and extinct mammals. Selected nonskeletal traits, particularly urogenital features of specimens examined, and others described in the literature were taken into account.

Material borrowed from other institutions for use in this study are indicated by the abbreviations USNM (National Museum of Natural History, Washington, D. C.), PU (Princeton University, Peabody Museum), and UWMZ (University of Wisconsin Museum of Zoology).

Contemporaneous classifications

In the same symposium volume with Szalay's (1982a, p. 621) new appraisal of marsupial phylogeny and classification, is an article by Kirsch & Archer (1982, p. 595) on an interpretation of the relationships of carnivorous marsupials using "polythetic cladistics". The 54 characters of 71 living and fossil marsupial species listed in their Wagner tree and analyses include 37 dental, 17 basicranial, and no tarsal characters. The uniquely constructed hyper-inflated auditory bulla of *Dromiciops gliroides* is mistakenly characterized in their Wagner tree analysis as primitive ("0.0") with components "alisphenoid and perioticum not or little expanded" (Kirsch & Archer 1982, p. 600). A number of their Wagner tree characters, they note, are overlapping or not discriminating. I find many, like the one attributed to *Dromiciops*, inaccurate. The authors conclude, nevertheless, that their cladistic manipulations clarified or resolved some problems of dasyurid taxonomy.

Aplin & Archer (1987) offer a "syncretic classification" fashioned from their attempt to reconcile or reinterpret the oft conflicting or redundant systematic arrangements proposed by various authors during the last two centuries. Their product is a classification top heavy with higher categories beginning with Subclass Theria and continuing through the descending ranks of Superlegion, Legion, Sublegion, Infralegion, Infraclass, Superdivision, Division, Supercohort, and a rest stop at Szalay's cohorts Ameridelphia and Australidelphia. Characters of those cohorts are discussed or cited, but not verified. Special attention is given to the pros and cons of the position of the microbiotheriid *Dromiciops* as an australidelphian with Microbiotheria Ameghino included in that cohort as an order.

In their systematic rearrangement of American marsupials (Reig et al. 1987, p. 78) they find Szalay's conclusions in direct conflict with their own as well as other arrangements. They question Szalay's identifications of some early fossils used in the construction of his branching classification of ameridelphians based on tarsal bone morphology, and note inconsistencies and contradictions in some of his data. Regarding *Dromiciops*, they declare that it "is clearly a didelphimorph, although belonging to a taxon within Didelphimorphia well-differentiated on the basis of several dental, soft part anatomical, and biochemical features; it shows no special similarities to Australian marsupials and indeed represents the most derived taxon in a lineage that is continuously documented from the earliest didelphimorphs onward" (Reig et al. 1987, p. 71). As for Australian marsupials, Reig et al. contend that the likely ancestor was a *Monodelphis*-like didelphoid, not a microbiotheriid. Their ar-

range of American marsupials, borhyaenoids excepted, is contained within the Order Polyprotodonta Owen, 1866, with its American suborder Didelphimorphia Gill, 1872, subdivided into superfamilies Microbiotherioidea Ameghino, 1887, and Didelphoidea Osborn, 1910. Their phylogram (Reig et al. 1987, p. 80, plate 69) shows the Microbiotherioidea as the upper Cretaceous stock from which American and Australian marsupials diverged. Foot bones were not examined or mentioned.

Marshall (1987), in a report on Itaboraian (Middle Paleocene) marsupials, reconsidered the systematics of American marsupials just proposed by Reig et al. (1987, p. 81). He allowed, in partial agreement with Szalay (1982a), that the Microbiotheriidae might represent the ancestral stock for at least some Australian marsupials. Fundamental to Marshall's (1987, p. 90) thinking is that South America was the primary area of early marsupial cladogenesis, "and that all basic aspects of marsupial evolution and distribution can be explained envisioning initial dispersal of stocks from, and not to, that continent."

The dissertation on phylogenetic origins, relationships and classification by Marshall et al. (1990, p. 457) is based entirely on molar morphology. The authors adopt without reservation Szalay's cohorts Ameridelphia and Australidelphia, based primarily on tarsal bone morphology. Differences between their and the Aplin & Archer (1987) classifications are explained. It appears that Szalay's (1982a) clear and unequivocal description of late Cretaceous pediomyids as didelphoid, and installation of the group within the Ameridelphia, was misread, misunderstood or somehow confounded by Marshall et al. (1990, p. 457). Their inclusion of the pediomyids within the Australidelphia is misguided. Their newly proposed cohort Alphadelphia includes *Peradectes elegans* Matthew & Granger. As depicted by Fox (1983, p. 1575), the species appears to be marked by a staggered is, a didelphoid autapomorphy.

Separation of all American from all Australian marsupials has long been recognized by systematists. Szalay's (1982a, b) classification founded primarily on tarsal bone morphology is, however, the first to treat the American Microbiotheriidae as australidelphian. To my knowledge, no authors following Szalay (1982a) have actually compared the astragalus and calcaneus of *Dromiciops* with those of other marsupials for verification of the characters said to distinguish cohort Ameridelphia from cohort Australidelphia.

Discussion

The revision of marsupial classification by Szalay (1982a) contains no list of specimens examined or the documentation for any in the form of catalog number or specific institution where preserved. Tarsal bones actually described and figured diagrammatically, ostensibly the ones examined, are of the following taxa, lettering and mix of names for astragali and calcanei are Szalay's (1982a text, and Figs 1 through 9).

AMERIDELPHIA: Left astragalus and calcaneus with articular facets separate; identified in text as SLAJP or "separate lower ankle joint pattern" (Szalay, Fig. 6, A-H).

- A. pediomyid
- B. borhyaeniform
- C. borhyaeniform

D. *Caenolestes*

E. *Thylacosmilus*

F. *Didelphis* “*patagonicus*” (right foot bones, Szalay 1982a, Fig. 1)

G. *Chironectes*

H. *Glironia*

The following mentioned in text:

Marmosa sp. (Szalay 1982a, Fig. 3, p. 625)

Prothylacinus patagonicus (fossil, Szalay 1982a, p. 628)

“*Sipalocyon*” (fossil, Szalay 1982a, p. 628)

Cladosictis patagonica (fossil, Szalay 1982a, p. 628).

AUSTRALIDELPHIA: Left astragalus and calcaneus with articular facets continuous as one; identified in text as CLAJP or “continuous lower ankle joint pattern” (Szalay, Fig. 6, I–Q).

I. *Dromiciops australis*

K. *Neophascogale*

L. *Myrmecobius*

M. *Thylacinus*

N. *Perameles*

O. *Notoryctes*

P. *Distoechurus*

Q. *Hypsiprymnodon*

— *Cercartetus* (Szalay, Figs 4, 5)

In a second review of the same data Szalay (1982b) adds to his Ameridelphia the figures of the right astragalus and calcaneus of *Philander opossum*, *Caenolestes* sp., and a pediomyid. To the Australidelphia are added the right astragalus and calcaneus of a *Notoryctes*, a *Neophascogale*, and a *Dromiciops* “representative of the australidelphian morphotype.” Specimens described in that work are documented by catalog number and institution. Whether or not the left bones described or figured in the original work (Szalay 1982a) are mates of the right foot bones figured in the second (Szalay 1982b) is speculative.

The total number of Ameridelphia ostensibly examined by Szalay represent only 6 living and 6 extinct species. All 9 species of Australidelphia examined are Recent.

Szalay’s descriptions of the tarsal bones may have been entirely derived from the 17 figured or their diagrammatic representations, and 5 mentioned in text. There is no indication in the text that more than a single astragalus or calcaneus per taxon (many polytypic) had been examined. Nothing is said of variation although no two bones of the same taxon are exactly alike, some grossly different.

As seen by Szalay (1982a, p. 634; 1982b, p. 187), the similarity in tarsal bone morphology and other shared characters of his australidelphians “firmly points to the origin of the protodasyurid if not from a didelphid (*sensu stricto*) or pediomyid (*sensu lato*) but from an australidelphian source which is perhaps best estimated to be a dromiciopsion.” The only “dromiciopsion” with known tarsal bone morphology is the living American *Dromiciops gliroides*. Szalay’s reasoning here regarding possible australidelphian origins seems convoluted and is anachronistic.

Most parsimonious interpretation of tarsal bone similarities between marsupials as widely separated as *Dromiciops* is in time and place from present and past

Australian marsupials, is, as shown beyond, the independent evolution in each lineage of CLAJP from SLAJP which, according to Szalay (1982a, pp. 625, 630, caption Figure 6), and as seen in nearly all other mammals, is the primitive therian pattern. Other shared similarities, if not metatherian plesiomorphs, and most are, may also have evolved independently or in parallel. Most important and entirely ignored by Szalay are certain unique characters that stamp *Dromiciops gliroides* as sole survivor of a lineage derived independently from a species near the ancestral metatherian.

Evidence revealed by skeletal material at hand completely confirms not only the interpretation of a number of independent derivations of CLAJP from SLAJP, but also the occurrence of both patterns among both Australian and American marsupials (Table 1, Plates I, II, III, IV).

In living American marsupials the continuous ankle bone pattern of astragalus and calcaneus (CLAJP) or simply C, is seen in *Dromiciops* but with some evidence of intermediacy between it and SLAJP, or simply S, of other American marsupials. The C pattern appears in all calcanei of the Marmosinae (Marmosidae) examined but only to variable degrees in the astragalus. The calcaneus of the Caluromyidae, like that of the preceding, is also CLAJP or C, the astragalus, however is unmodified S in the few specimens examined.

Dominant among Australian marsupials is the continuous or C ankle bone pattern. In all Peramelidae and Macropodidae examined, however, the separate or S pattern prevails. Representatives of the many more Australian taxa not examined may reveal more samples of S with consistency at the generic if not family level.

Tarsal bone patterns of each foot skeleton examined are listed in Table 1. Characters of those of living American marsupials are summarized below. For the classification see page 208.

Table 1: Articular facets between facing surfaces of astragalus and calcaneus, S = separate; C = continuous; M = intermediate; L = left foot; R = right foot.

| Name | FMNH | Astragalus | Calcaneus |
|-----------------------------|--------------------|------------|-----------|
| AMERICAN | | | |
| MARMOSIDAE | | | |
| Marmosinae | | | |
| <i>Gracilinanus marica</i> | 18907 | C (L) | C (L) |
| <i>Marmosa chapmani</i> | 61878 | S (L) | C (L) |
| <i>Marmosa robinsoni</i> | 121547 | C (R) | C (L) |
| <i>Marmosa robinsoni</i> | 34898 | S (R) | C (R) |
| <i>Marmosa robinsoni</i> | 58817 | S (R) | C (R) |
| <i>Marmosa robinsoni</i> | 58818 | S (L) | M (L) |
| <i>Marmosa robinsoni</i> | 58819 | S (R) | M (R) |
| <i>Marmosops noctivagus</i> | 70946 | S (L) | C (L) |
| <i>Marmosops noctivagus</i> | 70952 | S (R) | C (R) |
| <i>Micoureus demerarae</i> | 18904 | S (L) | C (L) |
| Lestodelphyinae | | | |
| <i>Lestodelphys halli</i> | 22422 ¹ | S (L) | C (L) |
| Thylamyinae | | | |
| <i>Thylamys elegans</i> | 119487 | S (L) | M (L) |
| <i>Thylamys palliolatus</i> | 22178 | S (L) | S (L) |

| Name | FMNH | Astragalus | Calcaneus |
|---|--------------------|------------|-----------|
| Monodelphinae | | | |
| <i>Monodelphis touan</i> | 94018 | S (L) | S (L) |
| Metachirinae | | | |
| <i>Metachirus nudicaudatus</i> | 94287 | S (R) | S (R) |
| <i>Metachirus nudicaudatus</i> | 70988 | S (L) | S (L) |
| <i>Metachirus nudicaudatus</i> | 70988 | S (R) | S (R) |
| <i>Metachirus nudicaudatus</i> | 70989 | S (L) | S (L) |
| <i>Metachirus nudicaudatus</i> | 69806 | S (L) | S (L) |
| CALUROMYIDAE | | | |
| Caluromyinae | | | |
| <i>Caluromys philander</i> | 61877 | S (L) | C (L) |
| <i>Caluromys lanatus</i> | 60598 | S (L) | C (R) |
| <i>Caluromys lanatus</i> | 60588 | S (R) | C (L) |
| <i>Caluromys lanatus</i> | 124595 | S (L) | M (L) |
| <i>Caluromys lanatus</i> | 60697 | S (R) | C (R) |
| <i>Caluromys lanatus</i> | 49337 | S (L) | C (L) |
| <i>Caluromysiops irrupta</i> | 121522 | S (R) | C (L) |
| <i>Caluromysiops irrupta</i> | 60698 | S (L) | C (R) |
| DIDELPHIDAE | | | |
| <i>Chironectes minimus</i> | 58807 | S | S |
| <i>Chironectes minimus</i> | 60576 | S (R) | S (R) |
| <i>Chironectes minimus</i> | 60517 | S (R, L) | S (R, L) |
| <i>Chironectes minimus</i> | 122156 | S | S (R) |
| <i>Chironectes minimus</i> | 127356 | S (R, L) | S (R, L) |
| <i>Chironectes minimus</i> | 60091 | S (R, L) | S (R, L) |
| <i>Chironectes minimus</i> | 121639 | S (R, L) | S (R, L) |
| <i>Didelphis albiventris</i> | 75103 | S (R, L) | S (R, L) |
| <i>Didelphis albiventris</i> | 75104 | S (R, L) | S (R, L) |
| <i>Didelphis albiventris</i> | 124596 | S (R) | S (R) |
| <i>Didelphis albiventris</i> | 124600 | S (R, L) | S (R, L) |
| <i>Didelphis marsupialis</i> | 128386 | S (R, L) | S (R, L) |
| <i>Didelphis marsupialis</i> | 128387 | S (R, L) | S (R, L) |
| <i>Didelphis marsupialis</i> | 128388 | S (R) | S (R) |
| <i>Didelphis virginiana</i> | 42697 | S (R, L) | S (R, L) |
| <i>Didelphis virginiana</i> | 60363 | S (R, L) | S (R, L) |
| <i>Didelphis virginiana</i> | 108696 | S (R, L) | S (R, L) |
| <i>Didelphis virginiana</i> | 122152 | S (R, L) | S (R, L) |
| <i>Lutreolina crassicaudata</i> | 60730 | S (R) | S (R) |
| <i>Lutreolina crassicaudata</i> | 22419 ¹ | — | S (L) |
| <i>Philander andersoni</i> | 70986 | S (R) | S (R) |
| <i>Philander opossum</i> | 50576 | S (R) | S (R) |
| <i>Philander opossum</i> | 60097 | S (R) | S (R) |
| <i>Philander opossum</i> | 69805 | S (R) | S (R) |
| <i>Philander opossum</i> | 60501 | S (R) | S (R) |
| <i>Philander opossum</i> | 121525 | S (L) | S (L) |
| BORHYAENIDAE | | | |
| <i>Prothylacinus patagonicus</i> ² | Princeton U. | S | — |
| <i>Cladosistis lustratus</i> ³ | Princeton U. | — | S |
| CAENOLESTIDAE | | | |
| <i>Caenolestes fuliginosus</i> | 18604 | S (R) | S (R) |
| <i>Caenolestes fuliginosus</i> | 18604 | S (L) | — |
| <i>Lestoros inca</i> | 75123 | S (L) | S (L) |
| <i>Rhyncholestes raphanurus</i> | 22423 | S (R) | M (R) |

| Name | FMNH | Astragalus | Calcaneus |
|---------------------------------|--------|------------|-----------|
| MICROBIOTHERIIDAE | | | |
| <i>Dromiciops gliroides</i> | 129804 | C (R, L) | C (R, L) |
| <i>Dromiciops gliroides</i> | 50072 | C (L) | C (L) |
| <i>Dromiciops gliroides</i> | 127453 | — | C (L) |
| <i>Dromiciops gliroides</i> | 127453 | C (R) | C (R) |
| <i>Dromiciops gliroides</i> | 129808 | — | M (L) |
| <i>Dromiciops gliroides</i> | 129809 | C (R) | — |
| <i>Dromiciops gliroides</i> | 134556 | C (R) | M (R) |
| AUSTRALIAN | | | |
| DASYURIDAE | | | |
| <i>Dasyuroides byrnei</i> | 127359 | C (R) | C (R) |
| <i>Dasyurus viverrinus</i> | 121206 | C (L) | M (L) |
| <i>Dasyurus viverrinus</i> | 42159 | C (L) | C (L) |
| <i>Dasyurus viverrinus</i> | 57209 | C (R) | C (R) |
| <i>Dasyurus viverrinus</i> | 57526 | C (R) | C (R) |
| <i>Dasyurus hallucatus</i> | 119803 | C (R, L) | C (R, L) |
| <i>Dasyurus hallucatus</i> | 119806 | C (R, L) | C (R, L) |
| <i>Dasyurus hallucatus</i> | 119808 | C (R) | C (R) |
| <i>Sarcophilus harrisii</i> | 127266 | C (R, L) | C (R, L) |
| <i>Sarcophilus harrisii</i> | 129428 | C (R, L) | C (R, L) |
| <i>Sarcophilus harrisii</i> | 47166 | C (R, L) | C (R, L) |
| <i>Sarcophilus harrisii</i> | 46006 | C (R, L) | C (R, L) |
| MYRMECOBIIDAE | | | |
| <i>Myrmecobius fasciatus</i> | 35259 | C (R) | C (R) |
| PERAMELIDAE | | | |
| <i>Echymipera</i> sp. | 60525 | S (R, L) | S (R, L) |
| <i>Echymipera</i> sp. | 60701 | S (R, L) | S (R, L) |
| <i>Echymipera</i> sp. | 121679 | S (R, L) | S (R, L) |
| <i>Isoodon obesulus</i> | 98899 | S (R, L) | S (R, L) |
| <i>Isoodon obesulus</i> | 98901 | S (R, L) | S (R, L) |
| PHALANGERIDAE | | | |
| <i>Phalanger orientalis</i> | 104803 | C (R) | C (R) |
| <i>Phalanger orientalis</i> | 60402 | C (R) | C (R) |
| <i>Trichosurus vulpecula</i> | 60389 | C (L) | C (L) |
| <i>Trichosurus vulpecula</i> | 57174 | C (L) | C (L) |
| PETAURIDAE | | | |
| <i>Petaurus australis</i> | 58964 | C (L) | M (L) |
| <i>Petaurus australis</i> | 60927 | C (L) | C (L) |
| <i>Petaurus breviceps</i> | 129430 | C (R) | C (R) |
| <i>Pseudocheirus peregrinus</i> | 134502 | C (R) | C (R, L) |
| <i>Schoinobates volans</i> | 60908 | C (R) | C (R) |
| MACROPODIDAE | | | |
| <i>Aepyprymnus rufescens</i> | 121645 | S (L) | S (L) |
| <i>Macropus fuliginosus</i> | 129434 | S (L) | S (L) |
| <i>Macropus robustus</i> | 104674 | S (R, L) | S (R, L) |
| <i>Macropus stigmaticus</i> | 60886 | S (R) | S (R) |
| <i>Macropus stigmaticus</i> | 60884 | S (R, L) | S (R, L) |
| <i>Potorous tridactylus</i> | 57805 | C (R) | S (R) |
| <i>Thylogale brunii</i> | 60682 | S (R) | S (R) |
| <i>Setonix brachyurus</i> | 135038 | S (L) | S (L) |
| <i>Dendrolagus matschiei</i> | 44428 | S (L) | S (L) |

¹ University of Wisconsin Museum of Zoology² Sinclair (1906, pl. 54, figure 29) Miocene (Santa Cruz Formation)³ Sinclair (1906, pl. 54, figure 3) Miocene (Santa Cruz Formation)

Marmosidae (New)

Marmosinae (10 specimens). This presently established subfamily includes all mouse opossums historically included within the composite genus *Marmosa* currently divided into genera *Gracilinanus*, *Marmosops*, *Marmosa* and *Micoureus*.

Astragalus (Plates II, IV): Articular facets generally separate but those of the single available *Gracilinanus marica* (FMNH 18907) are continuous and practically indistinguishable from those of *Dromiciops*. The facets of *Marmosa robinsoni* (FMNH 121547) appear to be continuous but much of the appearance may have been caused by wear. In any event the pattern is more like the C of *Dromiciops* (cf. FMNH 129804) than intermediate between S and C.

Calcaneus (Plates I, III): Facets generally continuous but those of *Marmosa robinsoni* (FMNH 58818) nearer C than S, whereas those of FMNH 58819 are nearer S than C.

Remarks: The evolutionary trend in the Marmosinae has been toward the continuous ankle bone pattern or C, with that of the calcaneus already continuous except for occasional signs of intermediacy. The astragalar pattern is one of intergradation between S and C.

Lestodelphyinae (1 specimen)

Astragalus: S

Calcaneus: C

Remarks: Important external, cranial and dental differences between the Marmosinae and Lestodelphyinae suggest that the shared calcaneal joint pattern was independently evolved in each group. Likely, *Lestodelphys* represents a distinct family.

Thylamyinae (1 specimen)

Astragalus: S

Calcaneus: M (= intermediate) or S

Remarks: *Thylamys*, sole genus of the Thylamyinae has generally been treated as either subgenerically distinct from or strictly congeneric with *Marmosa*. Its in-crassate tail, stout manual claws, unflared nasal bones at the nasomaxillary suture, and large third premolar, are, among other characters, distinctive. The separate astragalar pattern and intermediate calcaneal joint pattern not only add distance between *Thylamys* and the Marmosinae but emphasize the peculiarity of the latter. Present treatment of *Thylamys* within the family Marmosidae is uncertain.

Monodelphinae (2 specimens)

Astragalus (Plate II): Definitely S

Calcaneus (Plate I): Narrowly S

Metachirinae (5 specimens)

Astragalus (Plate II): S, the facets well separated

Calcaneus (Plate I): S

Caluromyidae

Caluromyinae (8 specimens)

Astragalus (Plate IV): Consistently S

Calcaneus (Plate III): C in 7 specimens, and one *Caluromys lanatus* (FMNH 124595) that appears to be more nearly S than C.

Remarks: The Caluromyinae have travelled their own pathway of tarsal bone evolution from S to C to nearly the same grade attained by the Marmosinae.

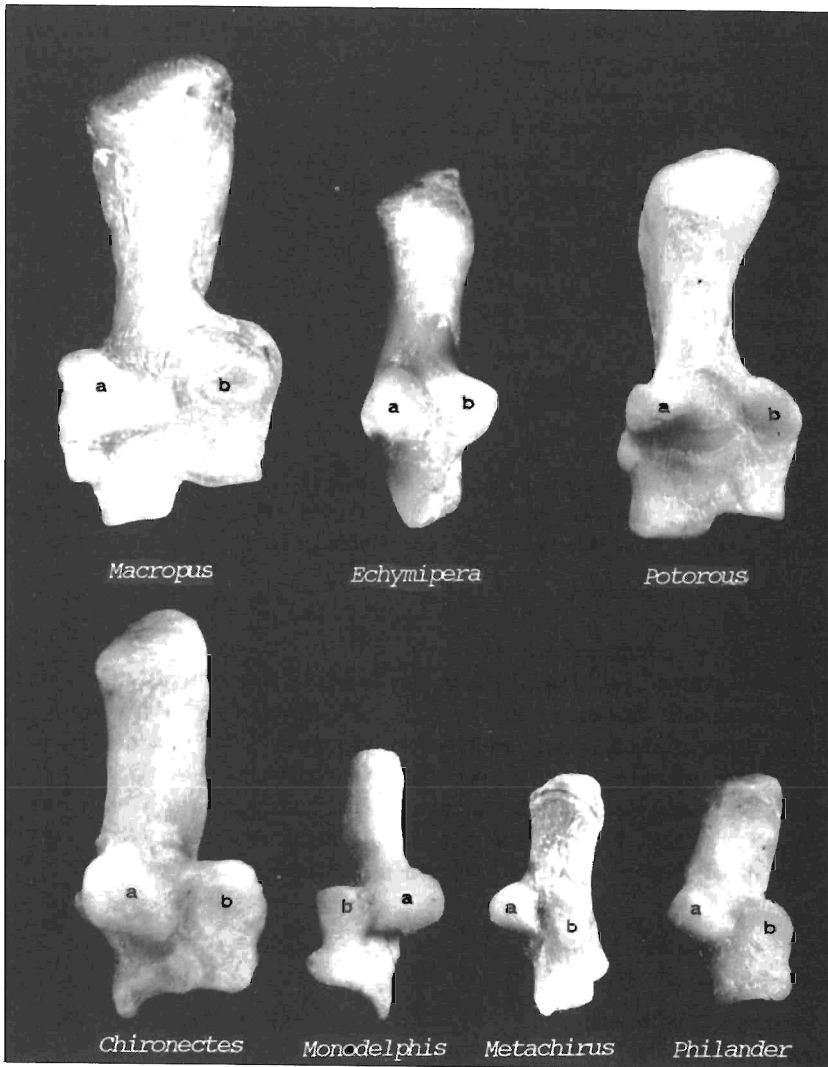


Plate I: Calcanei, dorsal surface with separate joint pattern (a, b) of Australian (upper row) and American (lower row) marsupials; not to scale, greatest length in mm [brackets]; R = right bone, L = left bone; all specimens preserved in FMNH: *Macropus stigmaticus* (60884R) [25.8]; *Echymipera* sp. (60701R) [14.8]; *Potorous tridactylus* (57805R) [14.4]; *Chironectes minimus* (60576R) [12.9]; *Monodelphis palliolatus* (22178L) [4.6]; *Metachirus nudicaudatus* (70988R) [8.4]; *Philander opossum* (60576R) [8.3].

Didelphidae (26 specimens)

Astragalus (Plate II): S

Calcaneus (Plate I): S

Remarks: In his legend for *Philander opossum*, Szalay (1982b, p. 180, Fig. 2) described the facet labelled “f” as a “distally extended medial cuboid facet extension, sharply angled from distal calcaneocuboid facet, diagnostic of Didelphidae, sensu stricto.” It might be assumed that “Didelphidae sensu stricto” implies Didelphinae but Szalay’s use of the family rank term is consistent, often as the equivalent of Didelphoidea. In any case, the described and figured calcaneal facet extension is present in all 11 specimens of *Didelphis* examined, the 3 of the didelphid *Philander opossum* and in one *Lutreolina*. It is absent in the 7 specimens of the didelphid *Chironectes minimus* at hand. All other didelphoids examined lack the facet as described but its presence is noted in the calcaneus of the Australian *Phalanger orientalis* (FMNH 60402) (Plate V).

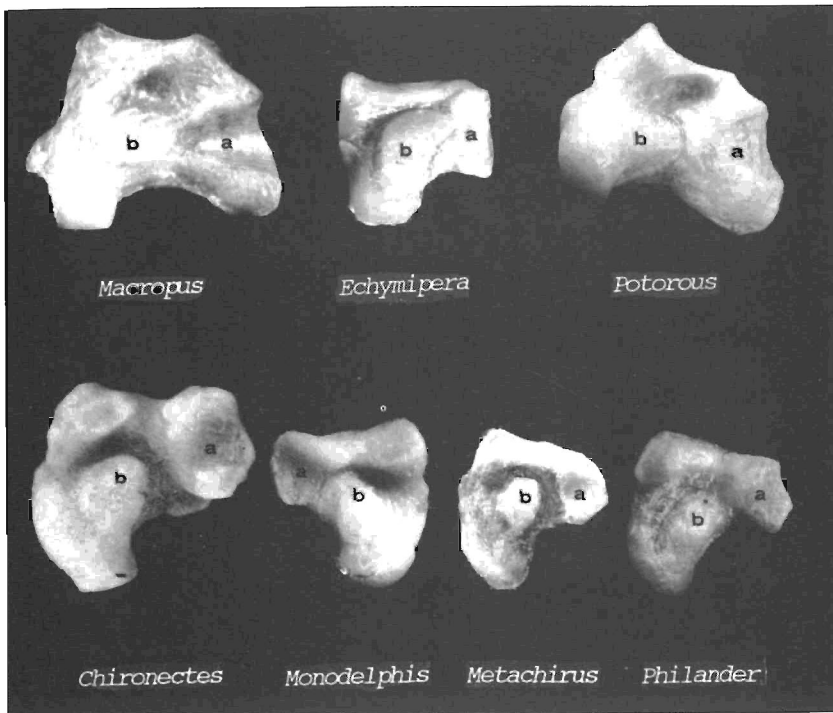


Plate II: Astragali, plantar surface with separate joint pattern (a, b) of Australian (upper row) and American (lower row) marsupials; not to scale, greatest length in mm [brackets]; R = right bone, L = left bone; all specimens preserved in FMNH: *Macropus stigmaticus* (60884R) [14.8]; *Echymipera* sp. (60701R) [6.3]; *Potorous tridactylus* (57805R) [8.3]; *Chironectes minimus* (60576R) [6.7]; *Monodelphis palliolatus* (22178L) [2.6]; *Metachirus nudicaudatus* (70988R) [5.1]; *Philander opossum* (60501R) [5.5].

Caenolestidae (3 specimens)

Astragalus (Plate IV): S

Calcaneus (Plate III): Strongly S in *Caenolestes fuliginosus* and *Lestoros inca*, intermediate between S and C in *Rhyncholestes raphanurus*.

Remarks: The astragalus with sharply angled proximal border narrower than long, differs markedly from that of all other marsupials examined. Significance of the character, however, cannot be properly assessed where samples are few and in-



Plate III: Calcanei, dorsal surface with continuous joint pattern (a, b) of Australian (upper row) and American (lower row) marsupials; not to scale, greatest length in mm [brackets]; R = right bone, L = left bone; all specimens preserved in FMNH: *Trichosurus vulpecula* (57174L) [17.6]; *Myrmecobius fasciatus* (35259R) [10.8]; *Dasyurus viverrinus* (57209R) [16.0]; *Dromiciops gliroides* (129804R) [3.1]; *Gracilinanus marica* (18107L) [2.6]; *Marmosa robinsoni* (121547L) [3.5]; *Caluromysiops irrupta* (121572L) [8.3]; *Rhyncholestes raphanurus* (22423R) [3.7].

dividual variability great. *Lestoros inca* Thomas includes *Caenolestes gracilis* Bublitz as a synonym.

Microbiotheriidae (7 specimens)

Astragalus (Plate IV): C in all *Dromiciops gliroides*

Calcaneus (Plate III): C with one sample intermediate between S and C, the pattern is very near that of *Gracilinanus marica* (FMNH 18907) and *Marmosa robinsoni* (FMNH 121547) both labelled C in Table 1.

Remarks: The pattern of all ankle joint bones of *Dromiciops* is essentially didelphoid. In most, the sustentacular facet of the calcaneus is larger than the coalesced opposite facet. In all other American marsupials, this facet is smaller or about equal in bulk to the other one. The size appraisal however is rough and where the C facet appears twisted, may be misleading.

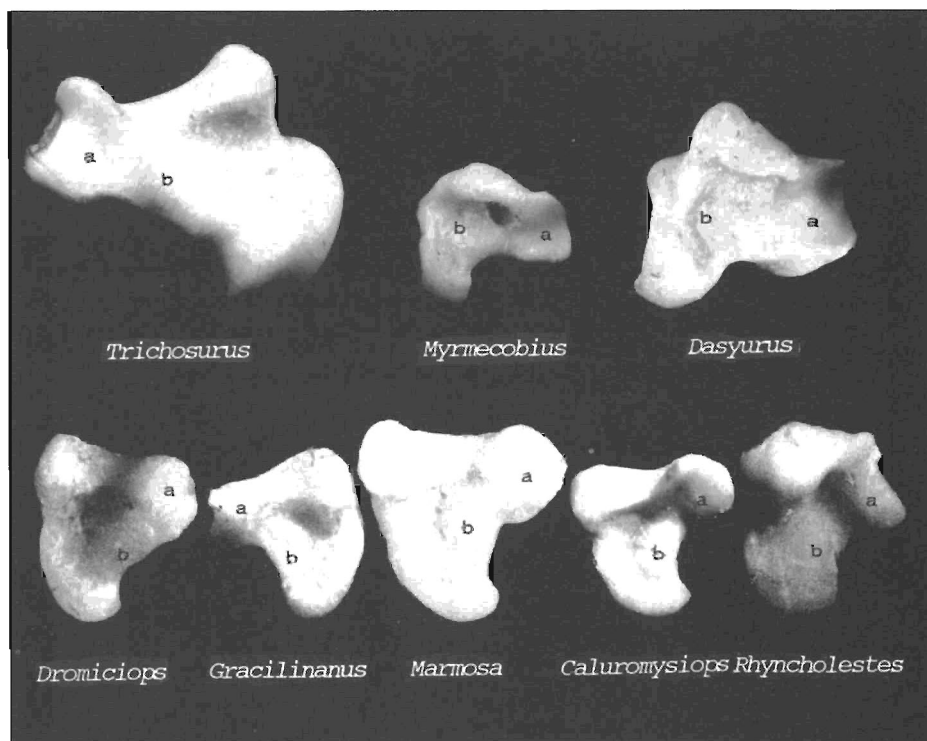


Plate IV: Astragali, plantar surface with continuous joint pattern (a, b) of Australian (upper row) and American (lower row) marsupials with continuous and separate patterns; not to scale, greatest length in mm [brackets]; R = right bone, L = left bone; all specimens preserved in FMNH: *Trichosurus vulpecula* (57174L) [11.7]; *Myrmecobius fasciatus* (35259R) [6.6]; *Dasyurus viverrinus* (57209R) [8.7]; *Dromiciops gliroides* (129804R) [2.4]; *Gracilinanus marica* (18907L) [2.0]; with separate joint pattern: *Marmosa robinsoni* (121547R) [2.7]; *Caluromysiops irrupta* (121522R) [5.9]; *Rhyncholestes raphanurus* (22423R) [2.6].

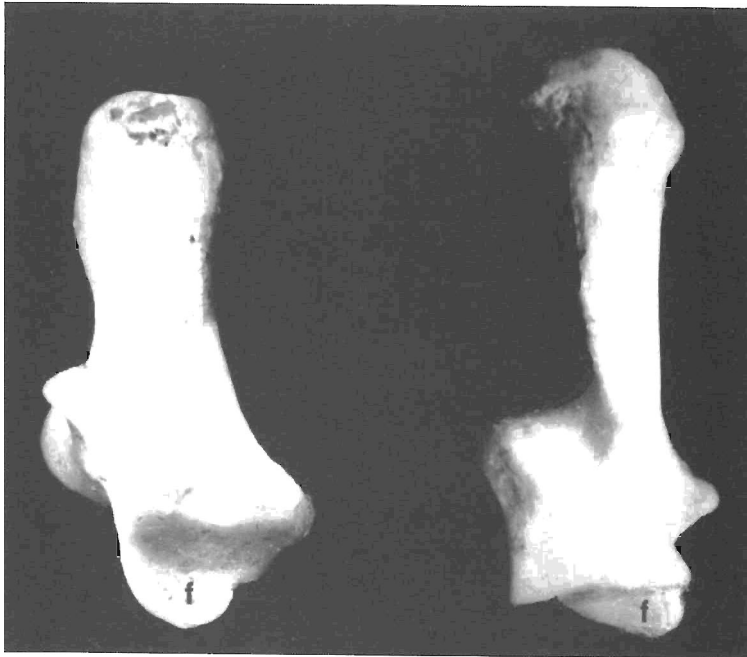


Plate V: Calcanei, not to scale, greatest length in mm [brackets]; right calcaneus of *Didelphis virginiana* (FMNH 108696) [12.8] and right calcaneus of *Phalanger orientalis* (FMNH 60402) [17.9]; f = medial cuboid facet extension.

Taxonomic and locomotor significance of ankle bone articular patterns

Confutation of ankle joint bone patterns as criteria for separation between Szalay's concept of Ameridelphia and Australidelphia does not invalidate those patterns as taxonomic states of lower hierarchies of marsupials. Both patterns, it is shown (Table 1), occur among Australian marsupials. The S pattern present in astragalus and calcaneus of the Peramelidae and Macropodidae supports separation of those two Australian families from others where the C pattern prevails. Modifications of the pattern of each bone within each family group may also prove distinctive at subfamily or generic levels.

The virtually consistent presence of pattern C in the calcaneus of the American Marmosinae distinguishes that taxon from nearly all other marmosids. The same may be said for the peculiar Lestodelphyinae (1 species) also with a C calcaneal pattern but differing most notably by its short, incrassate, nonprehensile tail, and complete tympanic bulla. The Caluromyidae depart widely from the Didelphidae with its C pattern calcaneus combined with a suite of distinctive non-tarsal characters including distinct karyotype and retention of the cloaca (eliminated in Didelphidae). Persistence of the primitive S or intermediate pattern in calcanei and S pattern in astragali of the otherwise grossly different *Thylamys*, *Metachirus* and *Monodelphis*, does not reflect on the taxonomic disassociation of one from the

other, and each from the Marmosinae. Their respective characters are given elsewhere (HersHKovitz, in press).

A spot check among eutherians of at least one representative of each living order and most major subdivisions, all in the Field Museum osteological collections, reveals basic similarities of the articular patterns of astragalus and calcaneus. In nearly all samples, the patterns are separate as described for marsupials irrespective of the morphological diversity of individual foot bones and taxa. The continuous pattern was found only in two fruit bats of the suborder Megachiroptera (Order Chiroptera), one *Pteropus giganteus* (FMNH 57666), the other *Eidolon helvum* (FMNH 42379). The S pattern persistent in all orders, appears to be a mammalian plesiomorphy. Not enough specimens were examined, however, to assure that the continuous pattern is confined to certain marsupials and some fruit bats of the suborder Megachiroptera.

Ankle bone joint patterns appear to be independent of any particular locomotor form, type or gait. The absence of correlation may be a factor of the immobility of the articulation between astragalus and calcaneus, gross morphological differences between bones from individual to order, ubiquity of the primitive S pattern, and evidence of intergradation between it and the derived C pattern. As an example, the similarity between the S patterns of the American didelphid *Didelphis* and Australian peramelid *Echymipera* (Plate VI), stands in sharp relief to gross differences in their respective metatarsals, digits, and locomotor forms.

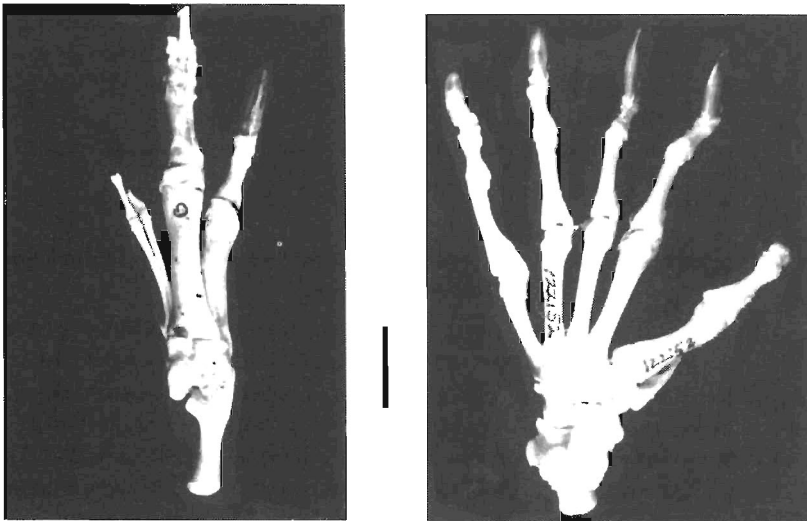


Plate VI: Right foot skeleton of Australian *Isoodon obesulus* (Peramelidae, FMNH 98900), and left foot skeleton of American *Didelphis virginiana* (Didelphidae, FMNH 122152); ankle bone joint patterns are similarly "separate" in both species (Table 1); about natural size; black bar = 1 cm.

Microbiotheriidae: Characterizations and Wagner trees

The genus *Dromiciops* Thomas with its only known species, the extant *D. gliroides* Thomas, is marked by a number of characters shared with no other living marsupial, and insofar as known with certainty, with no extinct marsupial save those of the genus *Microbiotherium* Ameghino as typified by the Miocene *M. patagonicum* Ameghino. The family Microbiotheriidae, treated at the time as didelphoid, had been systematically reviewed by Marshall (1982). He included a detailed life history of *Dromiciops gliroides* compiled from published sources, chiefly Mann (1955; 1958, but see also Mann 1978, and B. D. Patterson & Rogers, in press). Marshall's otherwise excellent and detailed account is devoid of any verifiable characters unique to *Dromiciops*.

A check of the 54 Wagner tree traits for 72 living and extinct American and Australian marsupial species analyzed by Kirsch & Archer (1982, p. 596) reveals none by which *Dromiciops australis* (now *D. gliroides*) may be distinguished from the others. Excepted may be character 49 "Otic region I" erroneously scored as 0 for *Dromiciops* but which should have been the number 3 misplaced in the adjacent *Notoryctes typhlops* column. The character described is an enlarged bulla composed of alisphenoid, petrous and mastoid bones, a character shared by *Dasyuroides* and other Australian marsupials.

Scrutiny of the 45 Wagner tree characters for 33 species of living and fossil American marsupials examined by Reig et al. (1987, p. 15) reveals four scored for *Dromiciops* only. These are character 28, which refers to the large complete bulla which is shared as noted above; character 32, "pars mastoidea expanded;" is shared with Australian forms; character 34, scored "1" for *Dromiciops* reads "antigens as shared by all didelphoids . . . except *Ancestor*" (Reig et al. 1987, p. 14), is presumably correct if "*Ancestor*" is a lapsus for *Dromiciops*, but the unverified distinction is one of degree; character 38 refers to absence of a median vaginal septum as unique for *Dromiciops*. The source given for the information is Mann (1955; 1958) who described and figured the median vagina.

A few outstanding characters unique to *Dromiciops* are described under the next heading.

Some symplesiomorphic and autapomorphic characters of *Dromiciops* (Microbiotheriidae)

The living *Dromiciops gliroides* (Plates VII, VIII) is the summation of all known of its phylogeny. It appears to have evolved independently from a metatherian stock not necessarily the same and likely a predecessor of a stock that presumably gave rise to all other known marsupials. Its origin must have been at a stage before certain archaic characters seen only in *Dromiciops* had disappeared, were in the course of disappearing or had been suppressed in the nearest ancestry of the other known marsupials. Those characters are among the deeply rooted autapomorphies that absolutely and decisively separate the Chilean "monito del monte" from all other marsupials, American and Australian. Any one of those cranial, dental, urogenital, and serological characters described below invalidates the postulate that a *Dromiciops*-like morphotype may be ancestral to Australian marsupials.



Plate VII: *Dromiciops gliroides*, natural size; note incrassate prehensile tail in lower photograph. Animal captured in Chile by Dr. Bruce Patterson and donated to the Chicago Zoological Society. Photographs by Mike Greer, courtesy of the Chicago Zoological Society.

(a) Entotympanic component of auditory bulla (Plates VIII, IX)

The large, globular bulla of *Dromiciops* is composed of the tympanic wing of the alisphenoid, the tympanic wing of the petrous bone, greatly pneumatized mastoid bone with paraoccipital or mastoidal process absorbed, a narrow lamina of the basisphenoid, and a ventromedial bone between alisphenoid and petrous wings, identified as an entotympanic bone, an element not present in any other marsupial. The bone is wide-spread among eutherians.

Van der Klaauw (1931, p. 267) had already suggested that a part of the tympanic process of the petrous bone in the Miocene *Microbiotherium tehuelchum* figured by Sinclair (1906, p. 410, Pl. 62, Figure 7) might be an entotympanic.

Segall (1969, p. 489, Figure 1) noted the similarities between the auditory bullae of Sinclair's *M. tehuelchum* and *Dromiciops gliroides* (his *D. australis*) and identified an entotympanic bone in both. His figure of the *Dromiciops* bulla, however, includes the inflated tympanic wing of the petrous with the entotympanic although the illustration clearly shows sutural separation between the two bones. According to Patterson (1965, p. 7) who may have examined the same specimens at an earlier date, Segall's entotympanic is the petrous and the true petrous is the mastoid, a sequential association which makes for an anatomical anomaly. The bone labelled "pars petrosa" in the bulla of *Dromiciops* by Reig et al. (1987, p. 48, Figure 45) is the entotympanic; lateral to it and barely indicated is the ventral process of the pars petrosa. The supposed entotympanic reported in certain dasyuroids (cf. Carlsson 1926) fits Patterson's description in being either petrous or mastoid elements of the inflated bulla.

Among eutherians, Van der Klaauw (1929) described two entotympanic bones in the auditory bulla of the insectivore-like Macroscelididae (Macroscelidea), one rostral and the other caudal, both independent of the petrous bone. Judged by orientation and relationship to other bullar parts, neither appears to be homologous with the *Dromiciops* entotympanic. A study of the auditory bulla of the tree shrew *Tupaia glis* led Spatz (1966, pp. 45, 48) to conclude that "all fusions of the entotympanicum with other elements of the skull are regarded as secondary. It is suggested that the entotympanicum (and also the cartilage of the auditory tube) is a new acquisition of mammals with no genetic relation to any other structures."

The foregoing suggests that the *Dromiciops* entotympanic may be (a) the homologue of a developmental stage of the independent tupaiid entotympanic; (b) a pneumatized derivative of the pars petrosa; (c) more or less like either of the two macroscelidid entotympanics; (d) an adventitious element which, in the evolving marsupial tripartite auditory bulla, filled the midventral and medial gaps before they might otherwise have been closed by junction of alisphenoid and petrous bones, as occurred in other marsupials.

In addition to the above taxa, Van der Klaauw (1931, p. 266) commented on those reported present in tupaiids (Scandentia), fruit bats (Megachiroptera) and microbats (Microchiroptera), pangolin (Pholidota), edentates including armadillos, anteaters, tree and extinct ground sloths (Xenarthra), all families of Carnivora, seals (Pinnipedia), manatees (Sirenia), tapirs and rhinoceroses (Perissodactyla), and hyrax (Hyracoidea). Van der Klaauw questioned reports of an entotympanic bone in marsupials other than in *Microbiotherium*.

Whatever the homology of the *Dromiciops* entotympanic, it exists as a bone suturally distinct from alisphenoid, petrous and basisphenoid bones in all 47 *Dromiciops* skulls examined. It may well be a hyperinflated cell of the petrous, as is the mastoid, but both bones are distinct entities in *Dromiciops* as is the mastoid alone in all marsupials. An entotympanic occurs in no other marsupial, and with the form and orientation as in *Dromiciops*, in no other mammal.

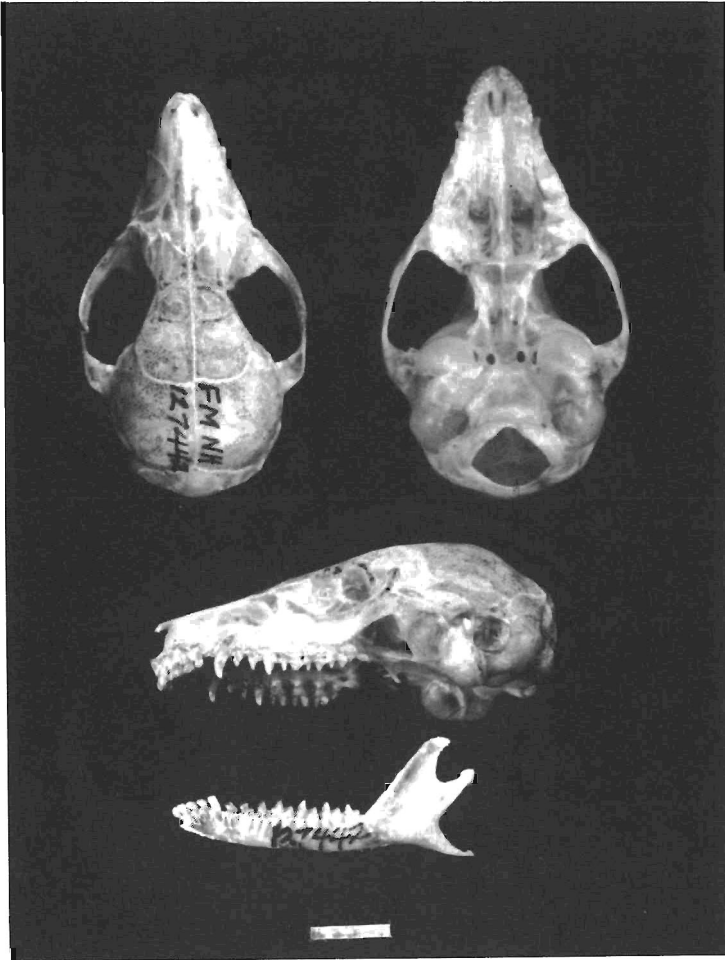


Plate VIII: *Dromiciops gliroides* skull (FMNH 127442); dorsal, ventral, left lateral tilted, and left mandible; bar = 2 cm.

(b) Sagittal crest of the mesopterygoid fossa (Plates VIII, IX)

A prolongation of the nasal septum or vomer extends through the mesopterygoid fossa as a low sagittal crest of the presphenoid and forepart of the basisphenoid in *Dromiciops*, and in no other marsupial.

The sagittally keeled mesopterygoid fossa present only in *Dromiciops* among marsupials is widely distributed among eutherians. It has been seen in the holotype of the plesiadapiform *Plesiadapis tricuspidens* (personal observation). It is figured in the basicranium of the related early Eocene *Ignacius grabullianus* by Kay et al. (1990). Kay & Cartmill (1977, p. 34, Figure 4) described the feature in the Paleocene *Palaechthon nasimienti* as "a midventral ridge or keel, with extends back from the vomer along the entire length of the basicranium becoming more pronounced

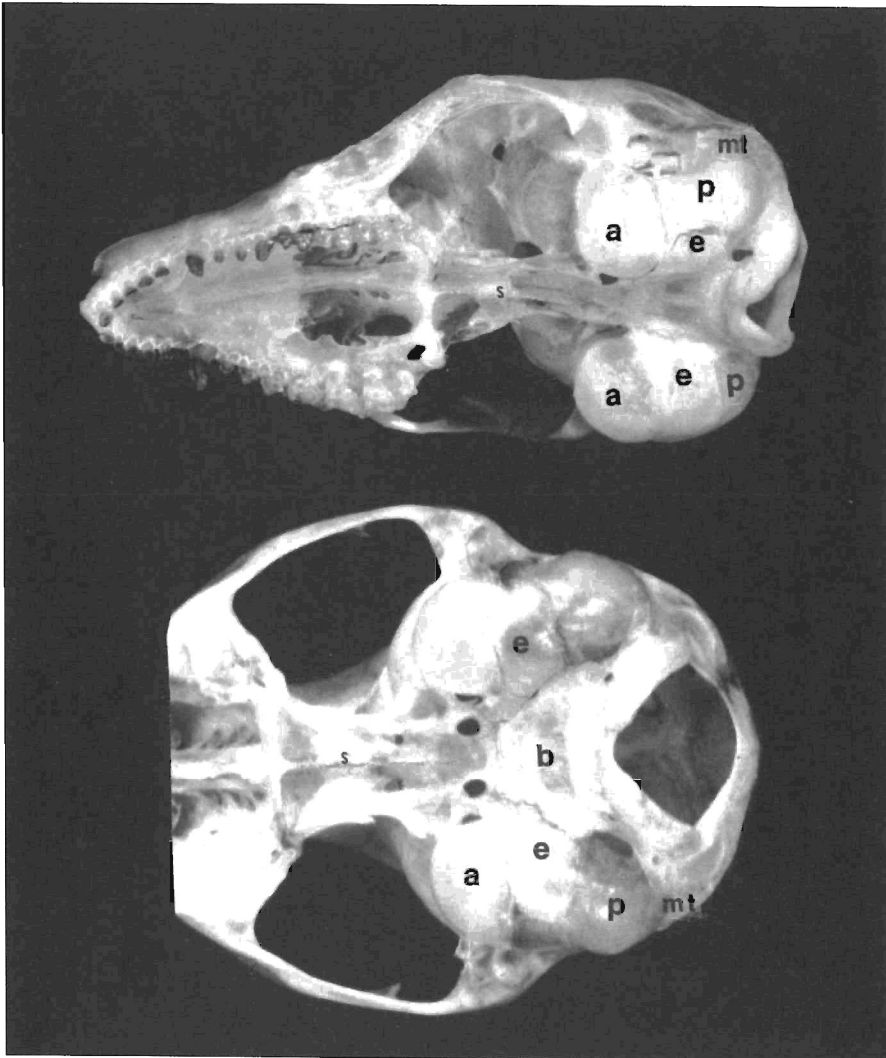


Plate IX: *Dromiciops gliroides*; basicranium tilted (FMNH 129804, x 3.34) and prone (FMNH 127449, x 4) showing sagittal crest of mesopterygoid fossa, and auditory bulla: a, alisphenoid; b, basioccipital; e, entotympanic; mt, mastoid; p, petrous; s, sagittal crest of mesoterygoid fossa.

posteriorly.' They added, "We have seen nothing much like this in any other mammals [sic], fossil or extant, and therefore cannot offer any testable hypothesis concerning its significance."

A spot check of skulls of all major categories of living eutherians and representatives of most of their families in the Field Museum collection reveals the mesopterygoidal sagittal crest as common in the strepsirhine *Galago* (Primates),

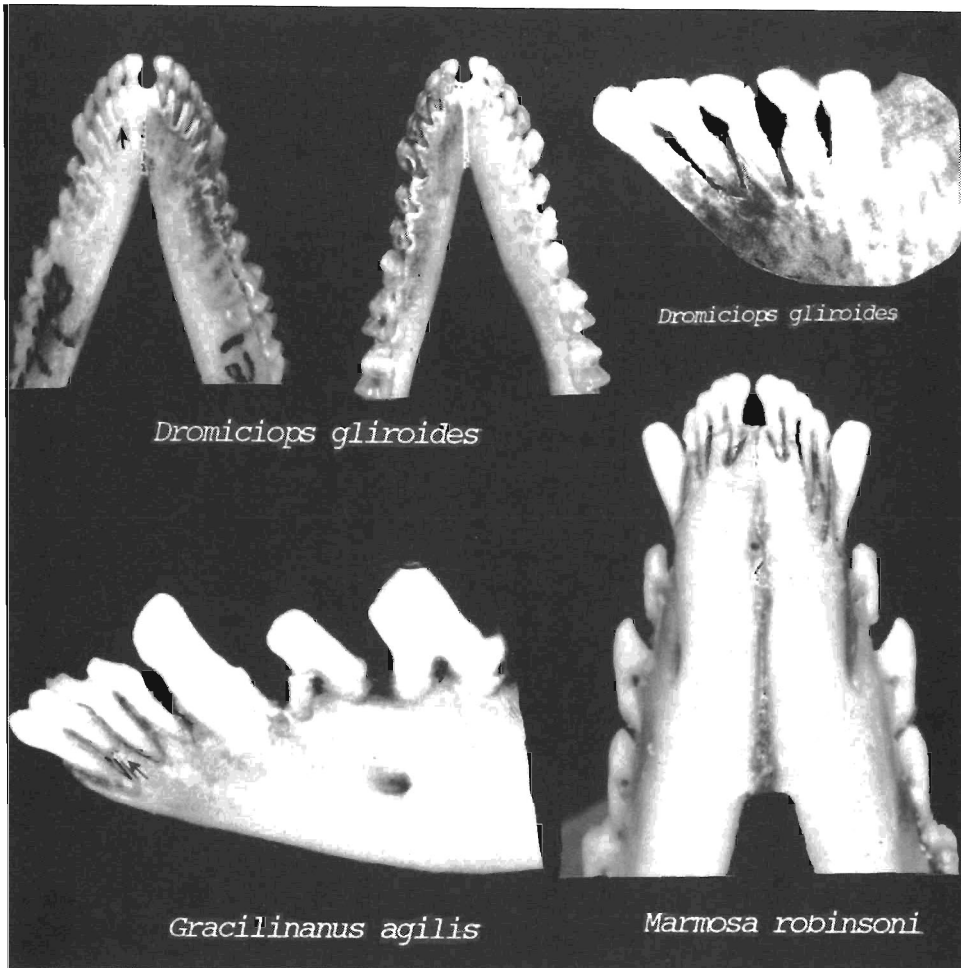


Plate X: Short symphysis menti in *Dromiciops gliroides*, buccal and lingual aspects (FMNH 127448); long in *Marmosa robinsoni*, buccal aspect (USNM 280869); non-staggered i_3 (arrow) in *Dromiciops gliroides*, left lateral aspect (FMNH 127440); staggered i_3 and buttress (arrow) in *Gracilinanus agilis*, left lateral aspect (FMNH 114663).

variable among lorises (Lorisidae, Primates), tree shrews (Tupaiaidae, Scandentia), megabats (Megachiroptera), certain families of microbats (Microchiroptera), flying lemurs (Dermoptera), some Mustelidae, Procyonidae, and Viverridae among the Carnivora, in some deer, sheep, camels, swine, and some antelopes among the Artiodactyla, and in the rhinoceros of the Perissodactyla; it is present in manatees (Sirenia) and hyraxes (Hyracoidea), absent in whales, rodents, and no doubt others.

(c) Symphysis menti (Plate X)

The incisive arch of *Dromiciops* is rounded, the mandibular symphysis shallow and

extends back to a line between $i_{4,5}$, sometimes between i_{5-c} . In all other marsupials examined, the arch and symphysis are angular the latter terminating behind at a line between lower canine and premolars or an equivalent point in the diastema. In eutherians, the symphysis also extends back to a line between lower canine and premolars but the comparison is academic. Dental formulae and diastemata of eutherians and marsupials are different with dental points of reference not strictly comparable.

Of the four mandibles of *Microbiotherium* from the Patagonian Santa Cruz (Miocene) formation, described and figured by Sinclair (1906) the symphysis is complete only in *M. tortor* (Sinclair 1906, p. 313, Plate 62, Figures 2, 2a). It agrees with that of *Dromiciops* but "terminates inferiorly in a prominent tubercle." The right mandible of *M. tehuelchum* (Sinclair 1906, p. 363, Figures 4, 4a) with nearly complete symphysis lacks the tubercle. Apart from the prominent tubercle of the left mandible of *M. tortor* Ameghino, most if not all differences between the fragmentary mandibles of *M. gallegosense* Sinclair, *M. tehuelchum* Ameghino, and *M. patagonicum* Ameghino as described by Sinclair, may be individual variables.

No postsymphyseal tubercle occurs in any of the 47 pairs of *Dromiciops* mandibles in the FMNH collection. However, in a new species of the didelphoid *Gracilinanus* (FMNH 89991), the left mandible is similar to that of *Microbiotherium tortor* even to the post-symphysial tubercle. The right mandible lacks the tubercle. In the case of the left it is obvious that the tubercle is a mended fracture that had extended across the ramus between canine and first premolar. The incisors are broken to the roots, presumably a result of the same injury.

The short *Dromiciops* symphysis menti, not matched in any other living mammal, may hark back to the therian stock from which presumably the metatherian-eutherian line and the prototherian line arose.

(d) Four lower incisors evenly spaced (Plate X)

The maximum $\frac{5}{4}$ incisor formula of marsupials including *Dromiciops* is believed to result from loss of the first lower incisor at the threshold of or prior to metatherian differentiation (Hershkovitz 1982, p. 195 et seq.).

In all living didelphoids and polyprotodont Australian marsupials, crowding of the lower incisors, a consequence of mandibular contraction, forced the numerical second lower incisor, or phylogenetic third, out of line with adjacent incisors 2 and 4. A bony upgrowth of the alveolus on the buccal side of the staggered tooth appears as a buttress. The staggered, buttressed condition is present in all Cenozoic and Cretaceous didelphoids and borhyaenoids known to me that have at least three lower incisors or their intact alveoli (Plates X, XI), (Hershkovitz 1982, and in preparation). Loss of additional lower incisors because of attenuation of the mandibular body secondarily reduces or eliminates the staggered condition.

The staggered incisor had already been noted by Sinclair (1906, p. 348, Plates XL, XLV, Figure 3) in his description of the Patagonian Santa Cruz (Miocene) *Borhyaena*. The lower incisors he remarked, "are closely crowded and the root of the second [i_3] is displaced posteriorly with reference to the median and lateral teeth, as in *Thylacinus* [Australian Thylacinidae] and the Santa Cruz [marsupial] genera in general?"

Opossums of the family Microbiotheriidae possess the same derived dental formula as didelphoids but with lower canine smaller, the four lower incisors uncrowded, evenly spaced and in line (Plate X), a condition Sinclair (1906, p. 409) also noted in the Miocene Microbiotheriidae. This may well be the primitive metatherian state retained in the Microbiotheriidae but by no other marsupials. Among eutherians with two or three lower incisors, a non-staggered morphology is the rule but the adult second generation or replacement teeth are not comparable in number, placement, or ontogeny with the adult first generation teeth of marsupials.

(e) Rete testis and related characters

According to Wooley (1987, pp. 221, 226, Figure 6) the *Dromiciops* rete testis differs from that of all other marsupials in the structure of the rete, greater number of tubules, and encasement in a mediastinum.

The rete testis as described from one specimen has the appearance of an autapomorphic character complex. It is part, however, of one of the reproductive organs requiring more study. Other seemingly unique elements of the urogenital system include the sessile scrotum and possibly undivided glans penis of adult *Dromiciops* like those of unweaned pouch young marsupials.

(f) Cloaca basicaudal (Fig. 1B)

The basicaudal location of the cloaca in both sexes of *Dromiciops* is a character shared only with monotremes among mammals, and with reptiles. The trait, a legacy from the reptilian ancestry points to the greater antiquity of the microbiotheriian clade than might have been inferred on the basis of shared eutherian symplesiomorphies alone.

The cloaca is present in all mammals at least during late embryogenesis, and persists in newborn and adult stages of monotremes, most marsupials, and certain eutherians. Among the latter the precaudal type cloaca persists in *Ochotona* (Lagomorpha), the African Insectivora *Setifer*, *Microgale*, *Tenrec*, *Hemicentetes*, *Oryzoryctes* and *Potamogale*, and likely in all Tenrecidae.

A spot check of other Insectivora suggests that the precaudal cloaca is present in most if not all adults in one or another of the three intergrading evolutionary stages outlined below.

Marsupials:

1. Cloacal: Common chamber for discharges of male and female rectal and urogenital ducts.
 - (a) Cloaca basicaudal:
 - American: Microbiotheriidae (*Dromiciops*)
 - Australian: Monotremata (Zaglossidae; Ornithorhynchidae)
 - (b) Cloaca precaudal:
 - American: Caenolestidae; Caluromyidae (except *Caluromysiops*); Marmosidae (except *Metachirus*, *Marmosops*, *Micoureus*)
 - Australian: Dasyuridae; Peramelidae
2. Cloacal-perineal: Male urogenital and rectal ducts separated by perineum, cloaca eliminated; female ducts of same species empty into persistent cloaca.

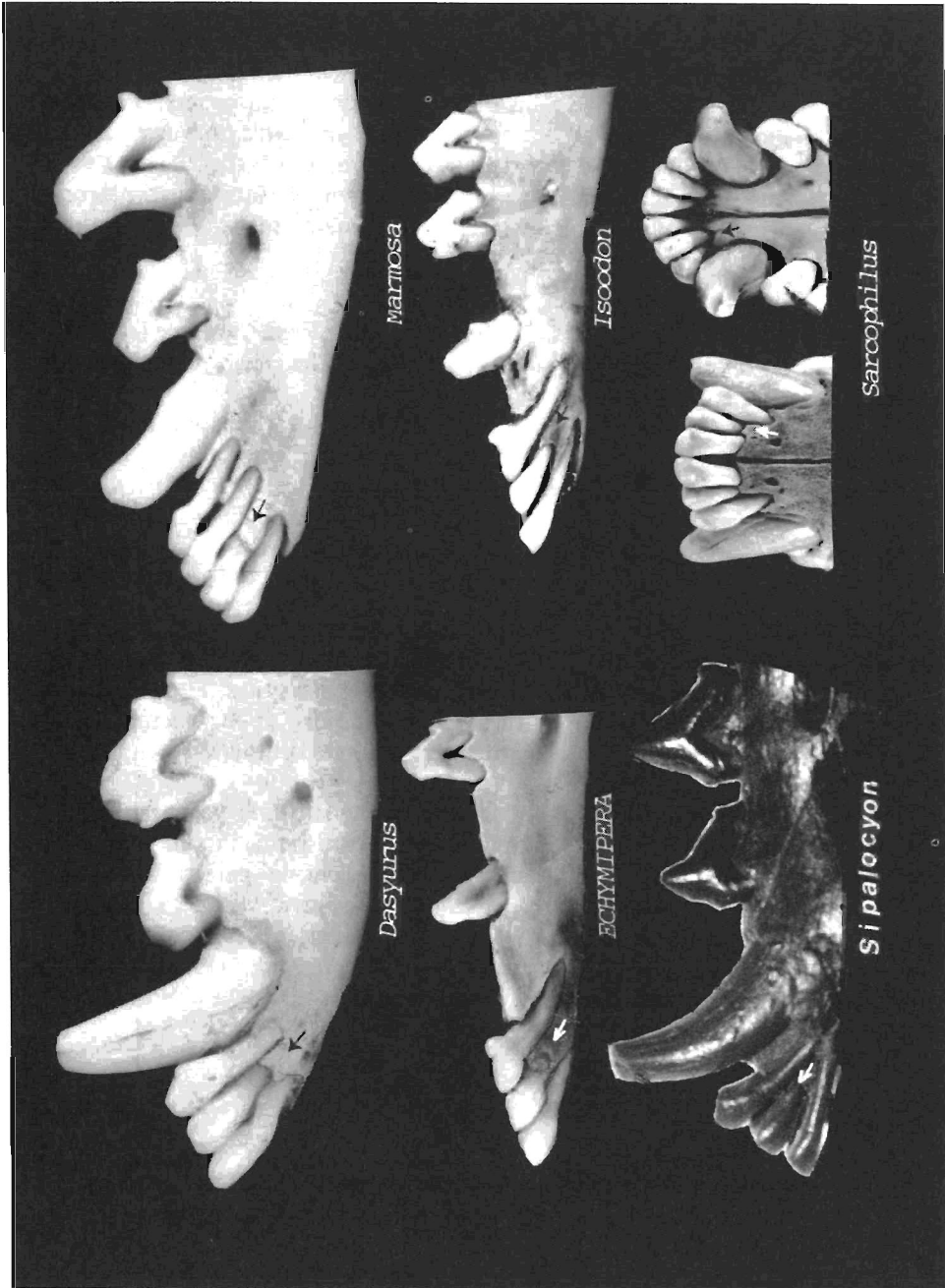


Plate XI: Staggered is and butress (arrow) left lateral aspect in *Dasyurus viverrinus* (FMNH 34718); *Marmosa robinsoni* (USNM 280872); *Echymipera* sp. (FMNH 56367); *Isoodon obesulus* (FMNH 60949); *Sypalocyon gracilis* (Borhyaenidae) cast of Miocene fossil (PU153373); *Sarcophilus harrisi*, buccal and lingual aspects (FMNH 57801).

American: Marmosidae (*Metachirus*, *Marmosops*, *Micoureus*);
 Caluromyiidae (*Caluromysiops* only)

Australian: Phalangeridae; Macropodidae (*Dendrolagus*)

3. Perineal (non-cloacal): Mouth of rectal and urogenital ducts of both sexes completely separated by perineum, occasional individual exceptions or integrades between stages 2 and 3 may occur.

American: Didelphidae

Australian: Macropodidae; Phalangeridae.

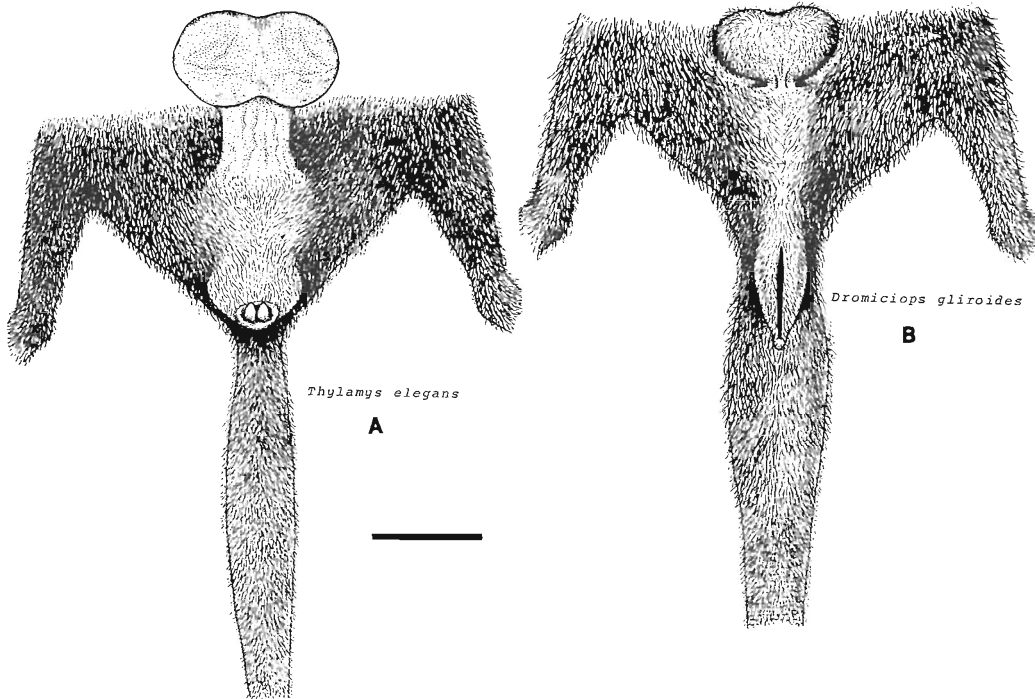


Fig. 1: A: Precaudal location of the cloaca of incrasate tailed *Thylamys elegans*, bifid glans penis partially everted. B: Basicaudal location of the cloaca of *Dromiciops gliroides* on incrasate tail. Scrotum of each species raised to show attachment. Bar = 3 cm.

(g) Serology

The first, and so far only, comprehensive serological tests of marsupial interrelationships are by Kirsch (1977). His techniques of antisera prepared in marsupials were used for comparison of about 100 species representing all major supergeneric marsupial categories. His (1977, p. 1) most comprehensive grouping "contrasts the

Australian forms with two equally distinct American groups, the Didelphidae and Caenolestidae. However, *Dromiciops* probably represents a third American family, the otherwise extinct Microbiotheriidae, which is closer to Didelphidae." Notwithstanding his assertions of a closer relationship between *Dromiciops* and didelphids than with caenolestids and Australian marsupials the serological results deny the bias. As determined by Kirsch (1977, p. 95) *Dromiciops* consistently reacts as a taxon distinct from the didelphids, and in fact, seems very little more like them than do the Australian or caenolestid marsupials. Nonetheless, because of his adherence to what may now be regarded as obsolete concepts of marsupial interrelationships, Kirsch (1977, p. 111) treats the Microbiotheriidae as a family coordinate with the Didelphidae within the superfamily Didelphoidea.

The serological distance between *Dromiciops* and other marsupials shown by Kirsch are differences of degree and not necessarily autapomorphic. Nevertheless, the possibility of absolute serological separation cannot be ruled out and may even be demonstrated in future assays with more or other material and advanced techniques. Kirsch (1977, p. 95) adverts that only a single sample of *Dromiciops*, a female, was available for study.

Marsupial evolution: Sequence of major events leading to living forms

Data accumulated in the preparation of this report together with other information provide the basis for a time scale perspective of the major events, or phylogenetic markers, in the differentiation of microbiotheriids, didelphoids, and dasyuroids. The markers appeared, disappeared, or persisted through the following stages.

- I. Differentiation of nearest marsupial ancestor from transitional therian to metatherian grade; stock characterized by retention of epipubic bones; viviparity; double vagina; undivided glans penis; basicaudal cloaca; digits unguiculate; presumed karyotype, $2n = 14$; dental formula $i \frac{1, 2, 3, 4, 5}{1, 2, 3, 4, 5}$, $pm \frac{1, 2, 3}{1, 2, 3}$, $m \frac{1, 2, 3, 4, 5}{1, 2, 3, 4, 5}$; molars tritubercular, eutheromorphic.
- II. Mandible contracted; first alveolar space with i_1 lost; differentiation of subclass Marsupialia or Metatheria with incisor formula $\frac{1, 2, 3, 4, 5}{(1), 2, 3, 4, 5}$.
- III. Muzzle foreshortened, m_1 lost in adult, molar formula, $\frac{(1), 2, 3, 4, 5}{(1), 2, 3, 4, 5}$, hallux inunguiculate, opposable or reduced.
- IV. Symphysis menti rounded; entotympanic bone present; cloaca basicaudal; rise of North American cohort MICROBIOTHERIOMORPHIA; pouch and hallucial opposability later developments.
- V. Independent (not dichotomous) origin of nearest anonymous didelphimorph ancestor; symphysis menti elongate, angular; entotympanic bone absent; cloaca precaudal.
- VI. Continued contraction of incisor field with i_3 and alveolus crowded into staggered position; residual prototherian-metatherian-eutherian characters suppressed or lost; differentiation of cohort DIDELPHIMORPHIA with entotympanic bone absent; hallux reduced or opposable.
- VII. Incisor formula $\frac{1, 2, 3, 4, 5}{(1), 2, 3, 4, 5}$; molars tritubercular, eutheromorphic with dilambdomorphic derived; glans penis undivided with bifurcation derived; pouch present or not; differentiation of order DIDELPHOIDEA; radiation with con-

- tinued loss of incisors (cf. Marshall et al. 1990, p. 46 for dental formulae).
- VIII. Differentiation of Australian order Dasyuroidea from colonizing American didelphimorphs; hallux reduced; i_3 lost, lower incisor formula (1), 2, 3, 4, (5); molars dilambdomorphic, tritubercular, the quadritubercular derived; modifications of primitive diploid chromosome number by fission or fusion; radiation with modifications of urogenital system and cloaca, sequential loss of incisors 3, 4, after loss of i_5 .
- IX. Epididymal pairing of spermatozoa in American DIDELPHIMORPHIA; karyotypes, $2n = 14, 18, 22$; persistence of incisor formula $\frac{1, 2, 3, 4, 5}{(1), 2, 3, 4, 5}$; precaudal cloaca persistent, modified, or eliminated (see p. 203 above); caudal prehensility and opposability of hallux derived.
- X. Differentiation of order PAUCITUBERCULATA; karyotype, $2n = 14$; precaudal cloaca unmodified; pouch absent; inunguiculate pollex derived; tail non-prehensile, hallux non-opposable; phylogenetic dental formula: $i \frac{1, 2, 3, 4, (5)}{(1), 2, 3, 4, 5}$, $c \frac{1}{1}$, $pm \frac{1, 2, 3}{(1), 2, 3}$, $m \frac{(1), 2, 3, 4, 5}{(1), 2, 3, 4, 5}$; molars euthemorphic, m^{1-2} quadritubercular, m^{3-4} tritubercular.

Duration of each event is relative but measured in millions of years and with extensive time, stage, and character overlaps. Cohort Microbiotheriomorphia with its particular residuum of prototherian and metatherian-eutherian grade characters must have arisen earlier than the Didelphimorphia, possibly in middle Jurassic, either in South America or North America. The autapomorphic staggered i_3 of didelphimorphs was already present in late early Cretaceous (Hershkovitz 1982) and introduced into Australia by one or more adventurous didelphoids via the Antarctic bridge, perhaps during late Cretaceous. Richardson's (1987, p. 73) suggestion that microbiotherioids were already there as part of an older Australian fauna is conceivable. Absence of a fossil record or living Australian descendants makes the hypothesis appear unlikely.

The unique didelphimorph paired spermatozoan system derived from the common single system appeared in American didelphoids after colonization of Australia where it does not occur. Caenolestoids with both staggered i_3 and paired epididymal spermatozoa either branched off later, or less likely, evolved the paired system independently from an earlier didelphimorph ancestor. In any case, according to Roger (1982), who examined 10 specimens, *Caenolestes obscurus* may be unique in the shape and presumed secretory function of its distal ductus deferens.

The marsupial pouch, present only in the monotreme echidna, and marsupials including *Dromiciops*, among mammals, evolved independently and differently in all major categories from the pouchless condition still preserved in most didelphoids, all caenolestoids and a few dasyuromorphs. The genetic potential for pouch development in marsupials, and monotremes (*Zaglossidae*) was probably inherited from preprototherian grade stock which presumably may have included temporarily pouched, quasi-pouched, incipiently or potentially pouched or absolutely pouchless species. Only the last type could feature in eutherian ancestry.

The hallux of the stock from which metatherians and eutherians diverged must have been unguiculate. The digit in living marsupials, however, retains neither claw

nor nail. The hallux became opposable in didelphoids and microbiotheriids, reduced, vestigial or absent in all other marsupials.

The basic 14 diploid number of chromosomes, as in *Dromiciops*, was inherited by dasyuromorphs from their didelphoid progenitors and is the same basis from which all other chromosomal complements of American or Australian marsupials can be derived, at least initially, by fission (Hayman 1990). Findings by Sharman (1982) of chromosomal similarities, banding unknown, between *Dromiciops* and Australian *Isoodon* (Peramelidae), *Cercartetus* (Burrmyidae), and *Vombatus* (Vombatidae) suggested a common ancestry "since they diverged from other marsupials" Which others is not clear but the tarsal bone joint patterns cited for support, following Szalay (1982a), are contradictory (Table 1). Other characters are discussed elsewhere (Hershkovitz, in press.).

The *Dromiciops* molars retain the early mammalian high cusped tritubercular eutheromorphic crown pattern with buccal shelf narrow, stylocone (cusp B or j of authors) diminutive or hardly more than suggested. Although primitive in design no feature of the *Dromiciops* molars is peculiar to the genus. Molars of caenolestids and the didelphoid *Caluromysiops* are also eutheromorphic but more molarized. Molar crown patterns of all other marsupials including *Caluromys* are dilambdomorphic with the W-shaped eocrista secondarily derived from the eutheromorphic pattern (cf. Hershkovitz 1977, p. 279), buccal shelf variably developed, the stylocone absent in some.

Classification of living New World marsupials (Fig. 2)

The condensed and simplified arrangement of living New World marsupials to the genus presented below takes into account those of Simpson (1945), Aplin & Archer (1987, p. xxi), Reig et al. (1987, p. 81), and Marshall et al. (1990, p. 479), new assessments of ankle bone joint patterns, and previously ignored cranial, dental, external, and urogenital characters. Passed over are the extinct forms. In our present state of ignorance, filling gaps in knowledge of gross and comparative morphology will contribute more to a definitive classification of marsupials than any amount of serological, molecular, and abstruse methodological investigations. The ill-conceived cohorts Ameridelphia for the American marsupials less Microbiotheriidae, and Australidelphia for the Australian marsupials with the microbiotheriids are rejected. Bibliographic references to all named forms and synonyms will be found in Marshall et al. (1990) and other works cited above. For a chronological review of marsupial classifications see Marshall (1981). Cohort Didelphimorphia includes the superorder Dasyuroidea, with order Dasyuroidea Gill and other orders of Australian marsupials following Marshall et al. (1990, p. 488).

Class Mammalia Linnaeus, 1758

Subclass Theria Parker and Haswell, 1897

Infraclass Marsupialia Illiger, 1811 (Metatheria of authors)

Cohort Microbiotheriomorphia Ameghino, 1887

Order Microbiotheria Ameghino, 1887

Family Microbiotheriidae Ameghino, 1887

Dromiciops Thomas, 1894

- Order Didelphoidia Gray, 1821
 - Superfamily Didelphoidea Gray, 1821
 - Family Marmosidae (new)
 - Subfamily Marmosinae Reig et al., 1985 (new rank)
 - Gracilinanus* Gardner & Creighton, 1989
 - Marmosops* Matschie, 1916
 - Marmosa* Gray, 1821
 - Micoureus* Lesson, 1842
 - Subfamily Thylamyinae (new)
 - Thylamys* Gray, 1843
 - Subfamily Lestodelphyinae (new)
 - Lestodelphys* Tate, 1934
 - Subfamily Metachirinae Reig et al., 1985 (new rank)
 - Metachirus* Burmeister, 1854
 - Subfamily Monodelphinae (new)
 - Monodelphis* Burnett, 1830
 - Family Caluromyidae Kirsch, 1977
 - Subfamily Caluromyinae Kirsch, 1977
 - Tribe Caluromyini (new)
 - Caluromys* J. A. Allen, 1900
 - Tribe Caluromysiopsini (new)
 - Caluromysiops* Sanborn, 1951
 - Family Glironiidae (new)
 - Glironia* Thomas, 1910
 - Family Didelphidae Gray, 1821
 - Subfamily Didelphinae Gray, 1821
 - Philander* Tiedemann, 1808
 - Didelphis* Linnaeus, 1758
 - Chironectes* Illiger, 1811
 - Lutreolina* Thomas, 1910
- Order Paucituberculata Ameghino, 1894
 - Superfamily Caenolestoidea Trouessart, 1898
 - Family Caenolestidae Trouessart, 1898
 - Subfamily Caenolestinae Trouessart, 1898
 - Caenolestes* Thomas, 1895
 - Lestoros* Oehser, 1934
 - Rhyncholestes* Osgood, 1924

Conclusions

The monophyletic cohort Ameridelphia and the monophyletic cohort Australidelphia with morphotype the American *Dromiciops gliroides*, constructed by Szalay (1982a, b), stand or fall on the postulate of an absolute difference between the separate astragalar and calcaneal articular pattern of American marsupials and the continuous astragalar and calcaneal pattern of Australian marsupials. It is shown here that the tarsal bone patterns are variable, that the continuous lower ankle joint

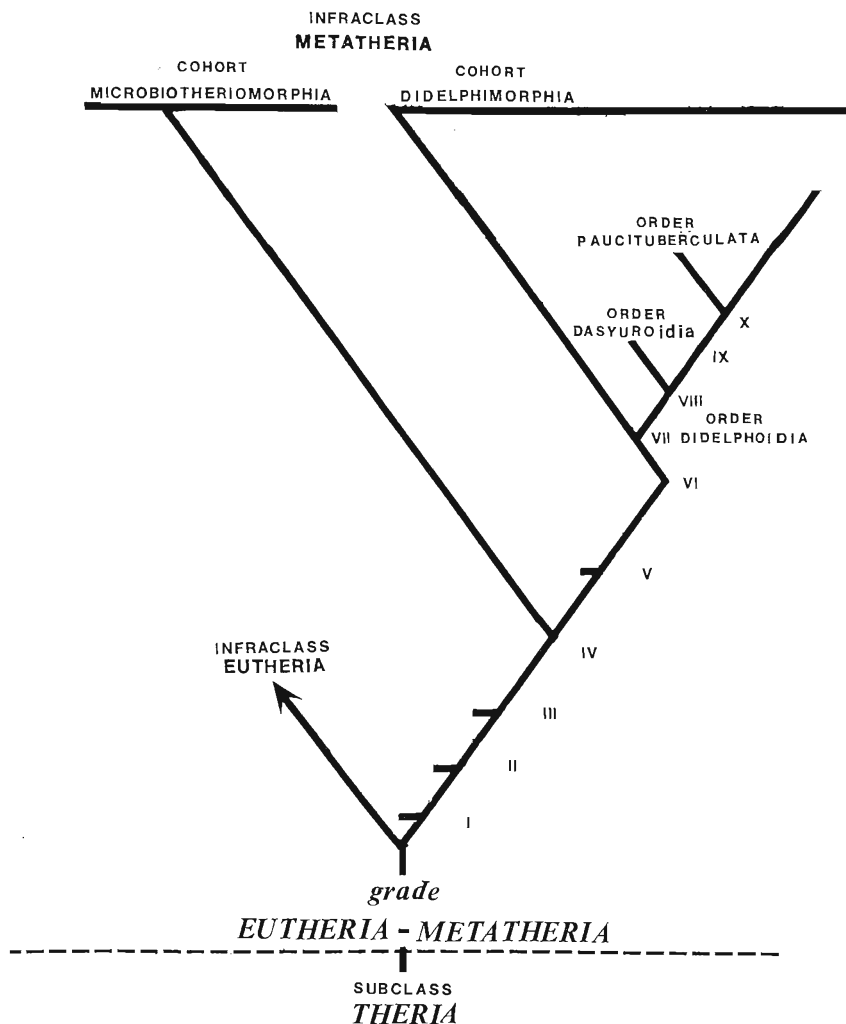


Fig. 2: Diagram representing phylogenetic relationship of living cohorts and orders of Marsupialia (Metatheria). See page 206 for explanation of evolutionary markers I—X. Bar = 3 cm.

pattern evolved independently from the separate lower ankle joint pattern more than once, and that both patterns are present in more than a single line of both American and Australian marsupials. It is also shown that the morphology of the *Dromiciops* astragalus and calcaneus is essentially didelphoid or ameridelphian, and little different from that of the American mouse opossum *Gracilinanus marica*. Contrary to Szalay, a postulated Cretaceous or Paleocene marsupial with the distinctive characters of *Dromiciops* could no more be ancestral to modern Australian mar-

supials, than the relict *Dromiciops* itself. Because of its untenable base, Szalay's concept of Ameridelphia and Australidelphia is scrapped.

The relationship between American didelphoids and Australian dasyuroids is more likely a continuum but with each geographically isolated line pursuing its own course with some parts of the one in parallel with parts of the other. Australian dasyuroids can be derived from didelphoids through an early Cenozoic or late Mesozoic Patagonian founder that colonized Antarctica and spread into Australia. The founder need not have been more than a single gravid pouchless marmosid-like marsupial. The possibility of more than one founder at the same or widely separated times, however, cannot be excluded. The poor Australian early fossil record casts little light on the marsupial history of that continent.

The phylogenetic history of *Dromiciops* is clearer. Its entotympanic bone, sagittal crest of the mesopterygoid fossa, unstagged lower incisors unique among marsupials but the rule among eutherians, its basicaudal cloaca shared with monotremes, crocodiles and turtles, and oddly short, shallow symphysis menti, attest to its independent origin before those characters were lost, suppressed, or were never present in other marsupials, and before the staggered is appeared in cohort Didelphimorphia. In sum, *Dromiciops* is a highly derived opossum cast in an archaic mold, the lone survivor of the earliest known branch of metatherian stock.

Addendum

A report by Kirsch et al. (1991, p. 10465) on Australian marsupial affinities of *Dromiciops*, based on DNA hybridization experiments, appeared while the present paper was under review. In support of their argument, the authors point to ankle bone morphologies demonstrated by Szalay (1982), chromosome comparability noted by Sharman (1982), spermatozoan morphology described by Temple-Smith (1987), and discovery by Gallardo & Patterson (1987) of male-sex chromosome mosaicism in *Dromiciops* previously recorded only among Australian marsupials.

The cited characters have been reviewed here and elsewhere by Hershkovitz (in press), and dismissed as either erroneously-founded phylogenies, shared primitive, or parallelisms. Results of the DNA experimentations as interpreted by Kirsch et al., are in the same vein. Among other discrepancies, they find "a most unexpected linkage" between the highly derived polyprotodont *Dromiciops* and the highly derived diprotodont *Phalanger*, "rather than with marsupials as a whole." Their experimental DNA revelation of a grossly discordant connection between the South American shrew-like *Caenolestes* and the Australian *Echymipera* is equally disturbing. Such findings raise questions regarding the aptness or accuracy of procedures employed by Kirsch et al. (1991).

From their molecular systematics, carefree of morphology, Kirsch et al. (p. 10468) turn to biogeography with the speculation that the "*Dromiciops*-Diprotodont separation represents a late dispersal or vicariant event". The microbiotheriine dispersal, they add "would likely have been from [Australia] rather than to Australia." Available morphological evidence and biogeographical reconstructions reveal that Australian marsupials are derived from didelphoid colonizers from South America. Although microbiotheriines are not didelphoids, dasyuroids, or diprotodonts, there is no in-

dication that they, their ancestor or putative descendents ever lived in Australia or any part of Gondwanaland before or after it broke up into Antarctica and Australia.

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