Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria

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ABSTRACT

Over 130 specimens of metatherian bones (predominantly long bones, one scapula, and several innominates and unguals) from the Palaeocene Itaboraí fissures of Brazil are described and analyzed from a functional-adaptive perspective, in order to 1) understand the adaptations of species they represent; 2) obtain taxonomic properties of the species taxa they represent; and 3) estimate their phylogeny within the Metatheria. To provide context for the analysis, the descriptions are preceded by a survey of postcranial variation in the extant *Didelphis virginiana* Kerr, 1792, together with an examination of a number of heritage and habitus properties in several extant species designated as models. The study of extant models served as the basis for explanations of locomotion-related form-function features that predict a range of positional behaviors ranging from arboreal to terrestrial in the fossils. The purpose of such adaptation-oriented character analysis is to differentiate causally-related adaptive aspects of a species in its realtime (the entire life history of the individual organisms) from features retained from its ancestry, i.e. those that were contingent in the past of its lineage. Such level-specific primitive attributes, *while fully adaptive*, are less directly related to the more recently acquired adaptive strategies of the species taxa analyzed, the derived attributes. This procedure allows the ordering and polarization of lineage- and taxon-specific properties. As a cornerstone of our methodology, prior to the analyses of didelphid variation, the model species, and the fossils, we examined 1) the general theoretical issues that relate to adaptations in fossils; 2) some of the competing views of what functional biology is supposed to be in relation to phylogenetic analysis; and 3) the connections between a broad concept of functional biology and phylogenetic analysis. Model construction for character state evaluations, using extant marsupials, was a basic part of our methodology. The medium-sized models employed were the didelphids *Caluromys derbianus* (Watrhouse, 1841) and *Metachirus nudicaudatus* (Demarest, 1817) and the small models were the microbiotheriid *Dromiciops gliroides* Thomas, 1894 and the caenolestid *Rhyncholestes raphanurus* Osgood, 1924. In each group the former species are arboreal and the latter terrestrial. The attributes of the models were explained in the light of locomotor and myological attributes, joint mechanics, as well as substrate preference. The various attribute-related hypotheses were tested by comparisons with the extant *Didelphis virginiana* and *Monodelphis domestica* (Wagner, 1842), as well as behaviorally less well-known species of *Marmosa* Gray, 1821, *Micoureus* Lesson, 1842, *Chironectes* Illiger, 1811, and *Lutreolina* Thomas, 1910. This permitted us to ascertain and extend, and thus generalize in a metatherian context: 1) the close causal association of many of these attributes with similar or divergent adaptations in other taxa in addition to the models; 2) their consolidation into robust character complexes; and 3) an understanding of which are primitive or advanced didelphid, didelphimorph, or didelphidan and/or sudameridelphian characters. In addition to the living species, the nearly complete skeletal remains of early Palaeocene Tiupampa *Pucadelphys* Marshall & Muizon, 1988 and *Mayulestes* Muizon, 1994 provided complete skeletal comparisons and therefore increased confidence in the evaluation of isolated fossil bony element, although fossils are not proper tests of the models, as there is no direct information about their habits. Following description and analysis of the extant and fossil specimens, a variety of phylogenetic proposals based mostly on genetic and molecular evidence have been examined in light of the morphological evidence. Together with an examination and critique of the recent contributions of Kirsch *et al.* (1997) and Springer *et al.* (1998) on metatherian phylogeny and biogeography, some aspects of the nature of morphological and fossil evidence are highlighted, and marsupial suprafamilial relationships outlined. Biogeographic implications of the phylogeny presented are also detailed, particularly the Gondwanan distribution of lineages and taxa and their various possible interpretations.

KEY WORDS
Metatheria
Palaeocene,
Itaboraí,
Brazil,
functional analysis,
adaptations of fossil species,
extant models,
Marsupiala,
phylogeny,
biogeography.

RÉSUMÉ

Analyse modélisée du squelette postcrânien des marsupiaux du Paléocène d'Itaboraí (Brésil) et la phylogénie et biogéographie des Metatheria.

Plus de 130 pièces osseuses de métathériens (essentiellement des os longs, une omoplate, plusieurs bassins et des phalanges terminales) provenant des fissures d'Itaboraí du Paléocène du Brésil ont été décrites et analysées dans une perspective d'anatomie fonctionnelle. Notre but était 1) de comprendre leurs adaptations ; 2) de repérer les caractéristiques taxonomiques des taxa qu'ils représentent ; et 3) d'évaluer leur position phylogénétique au sein des métathériens. La description de ces pièces est précédée d'un bref exposé de la variation existant au niveau du postcrânien chez l'espèce actuelle *Didelphis virginiana* Kerr, 1792, ainsi que de l'examen d'un certain nombre de caractères hérités ou acquis chez plusieurs espèces actuelles choisies comme modèles. L'étude de modèles actuels a servi de fondement à l'explication de complexes forme-fonction reliés à la locomotion chez les fossiles, qui prédisent une gamme de comportements répartis entre arboricoles et terrestres. Le but d'une telle analyse de caractères liés à l'adaptation est de distinguer les caractères adaptatifs d'une espèce déterminés par son mode de vie des caractères issus d'un ancêtre commun, contingents au passé de la lignée. De tels caractères, primitifs pour l'espèce, *bien que pleinement adaptatifs*, sont moins directement reliés aux stratégies adaptatives acquises plus récemment par les espèces des taxa analysés qui représentent les caractères dérivés. Cette procédure permet d'ordonner et de polariser les caractères taxonomiques et spécifiques aux lignées. Comme fondement de notre méthodologie et avant l'analyse de la variation chez les didelphidés, des espèces-modèles et des fossiles, nous avons examiné 1) les conclusions générales théoriques relatives aux adaptations observées chez les fossiles ; 2) certains points de vue concurrents portant sur ce que la « biologie fonctionnelle » est censée être d'un point de vue phylogénétique ; et 3) les relations existant entre la biologie fonctionnelle et l'analyse phylogénétique au sens large. La construction de modèles ayant pour but l'évaluation des états de caractères et reposant sur les didelphidés actuels a représenté une part fondamentale de notre méthodologie. Les modèles de taille moyenne employés ont été les didelphidés *Caluromys derbianus* (Watrhouse, 1841) et *Metachirus nudicaudatus* (Demarest, 1817), et les modèles de petite taille ont été le microbiotheriidé *Dromiciops gliroides* Thomas, 1894 et le caenolestidé *Ryncholestes raphanurus* Osgood, 1924. Dans chaque groupe, la première espèce citée est arboricole et la seconde est terrestre. Les caractéristiques de ces modèles ont été expliquées fonctionnellement à la lumière d'études portant sur la locomotion, la myologie et la mécanique articulaire, et ont été associées sans équivoque à un substrat et à un mode de locomotion préférentiels. Les différentes hypothèses reliées à ces caractéristiques ont été testées en comparant les espèces actuelles *Didelphis virginiana* et *Monodelphis domestica* (Wagner, 1842), ainsi que les taxons au comportement moins bien connu, *Marmosa* Gray, 1821, *Micoureus* Lesson, 1842, *Chironectes* Illiger, 1811 et *Lutreolina* Thomas, 1910. Cela nous a permis de constater et de généraliser à l'ensemble des métathériens : 1) l'association étroite entre certaines de ces caractéristiques et des adaptations similaires ou divergentes existant dans des taxa autres que les modèles choisis ; 2) le regroupement de ces caractères en complexes robustes ; et 3) dans le même temps, cela nous a permis de comprendre quels caractères de didelphidé, didelphimorphe ou didelphidien et/ou sudaméridelphien étaient primitifs ou dérivés. Outre les espèces vivantes précédemment décrites et analysées, les restes squelettiques très complets des marsupiaux du début du Paléocène de Tiupampa, *Pucadelphys* Marshall & Muizon, 1988 et *Mayulestes* Muizon, 1994, ont complété les comparaisons squelettiques et ont donc accru la sûreté de l'examen critique des pièces fossiles isolées. Évidemment, les fossiles eux-mêmes ne permettent pas de tester de façon appropriée les modèles choisis, puisqu'il n'existe pas d'informations directes concernant leur mode de vie. Poursuivant la description et l'analyse des spécimens actuels et fossiles, diverses hypothèses phylogénétiques basées principalement sur des données génétiques et moléculaires ont été examinées à la lumière de données morphologiques. Associés à l'examen critique des récentes contributions de Kirsch *et al.* (1997) et Springer *et al.* (1998) portant sur la phylogénie et la biogéographie des métathériens, certains aspects caractéristiques des données morphologiques et fossiles sont mis en lumière et les relations entre marsupiaux à un niveau supra-familial sont rapidement esquissées. Les implications biogéographiques de la phylogénie présentée ici sont également détaillées, en particulier la distribution gondwanienne des lignées et taxa, ainsi que leurs diverses interprétations possibles.

MOTS CLÉS
Metatheria,
Paléocène,
Itaboraí,
Brésil,
analyse fonctionnelle,
adaptations des espèces fossiles,
modèles actuels,
Marsupia,
phylogénie,
biogéographie.

CONTENTS

INTRODUCTION

"If two or more instances in which the phenomenon occurs have only one circumstance in common, while two or more instances in which it does not occur have nothing in common save the absence of that circumstance, the circumstance in which alone the two sets of instances differ is the effect, or the cause, or an indispensable part of the cause, of the phenomenon."

John Stuart Mill (1872, reprinted 1967: 263)

The fundamental and recurrent challenge of all phylogenetic systematics, the *sine qua non* of a biologically meaningful character analysis, is the conceptual partitioning of features that are adaptive results due to the realtime habitus of a species from those equally adaptive heritage attributes that constrained and guided the expression of the most recent consequences of selection. While such aims can rarely be accomplished fully or adequately, every effort in that direction can have potentially far reaching consequences on both microtaxonomic, as well as macroevolutionary conclusions. Phylogenetic estimations that have been subjected to tests are obviously included in the latter.

Research projects in palaeontology that involve descriptions and analyses of a large number of specimens will occasionally push the investigators to an increasingly detailed reexamination of a whole variety of assumptions that form the cornerstone of such undertakings. Our project was one of these. Because we believed that this collection of Palaeocene marsupials was potentially important for an understanding of the evolutionary beginnings of the living Metatheria, we also came to the conclusion that some of the relevant theoretical issues that formed the foundations of our conceptual methodology for the analysis of morphology on various levels should be reexamined within the context of this work. Just as empirical work without supporting theory is often questionable, theory about systematic practice without supporting epistemological demonstrations is also unconvincing.

Our aims are to describe and understand both the adaptive and phylogenetic significance of the isolated postcranial remains of fossil marsupial species from Itaboraí. To communicate the results of our analytical procedures we find it necessary to dwell into aspects of methods for adaptive and phylogenetic analysis, their relationship to evolutionary theory, and comment on some aspects of the expression of tested aspects of phylogenetic hypotheses.

The fossils from the mid to late Palaeocene Itaboraí fissures of Brazil, along with the spectacularly complete specimens of the early Palaeocene Tiupampa locality of Bolivia, represent the most important sources of information for an understanding of the beginning of therian mammal radiations in South America (see Simpson 1948, 1967; Muizon 1992; and references therein). The most comprehensive analysis to date on the postcranial osteology of eutherian mammals of Itaboraí is by Bergqvist (1996; and references therein), and the most recent accounts of Marshall & Sigogneau-Russel (1995), Muizon (1992, 1995, 1998), and Muizon *et al.* (1997) present the appropriate background for the general faunal, stratigraphic, systematic, and morphological context of our study. In addition to the general accounts of the whole fauna at Itaboraí, prior to Bergqvist's (1996) study of condylarths and other archaic ungulates, the studies of Cifelli (1990a-e, 1993a, b), Clemens (1966, 1979) and Lillegraven (1969), papers by Muizon & Marshall (1992; see comprehensive list of references in Muizon 1998 on the mammals from Tiupampa, Bolivia), numerous papers by Paula Couto and by Simpson (see references in Szalay 1994), and Szalay & Trofimov (1996) are some of the primary sources on metatherians and relevant eutherians from the Cretaceous and Early Tertiary in North and South America.

The collection studied here represents a selection from the large samples taken from the fissures by a number of collectors before the Itaboraí area was flooded (Bergqvist 1996). The selection and identification of the remains as marsupials was done in 1981 by one of us (FSS), and the tarsal specimens were described and discussed by Szalay (1994). The collection represents a series of phena for various elements of the postcranium. We have attempted, after documenting some aspects of variation in several living species of marsupials, to sort the specimens into designated groups which we believe probably correspond to valid biological species taxa.

Samples that were judged to be conspecific specimens of humeri, ulnae, innominates, femora, and tibiae, along with a single scapula, were designated on an increasing size scale with Arabic numerals as various clusters (e.g., IMG Humerus 1). In the future these may be allocated to Itaboraí Metatherian Groups (IMGs) designated with Roman numerals in Szalay (1994), that stand for species taxa. Some of our designations in this paper could be assigned with confidence to the same species (e.g., IMG Humerus 2, IMG Ulna 3, IMG Femur 5, IMG Tibia 1, IMG Calcaneus 3, and IMG Astragalus 4, all of which probably belong to IMG II, a species undoubtedly known by name and based on dental features; see pertinent discussions in Szalay 1994). Association of these Itaboraí samples with the appropriate IMG groups (surrogates for the formally named taxa based on dental specimens) remains fundamentally problematic, as *in situ* or complete skeletal associations are lacking (additional details are given below).

In light of a gratifyingly growing interest in the history and adaptations of both living and fossil marsupials during the last several decades, it has become obvious to us that additional information and proper phylogenetic analysis of relatively early and biogeographically important remains of marsupials hitherto undescribed should be carried out. Thus, although we have undertaken some variational and functional-adaptive studies as a necessary minimum background, we hasten to add that these are not the primary emphases of this paper. Detailed investigation dealing with intraspecific and interspecific variation, age and/or sex-dependent, or population differences, and comparative studies on the postcrania of closely related marsupials species for systematic purposes in the broadest sense are very few in the literature. Similarly, functional-adaptive evaluations of the ecological morphology of closely related species with distinctive habitus are desperately in need of detailed analyses. We could not possibly hope to remedy, to any significant extent, such a state of affairs in one publication. Nevertheless, our preliminary accounts in these areas are vital both for our taxonomic hypotheses regarding the phena without the customary taxonomic precedence of dental or cranial attributes, and for what we consider the theoretically most complete and valid analysis of traits against which the phylogeny of taxa should be tested.

The taxonomic designations used in the comparisons follow the higher taxon nomenclature in Szalay (1994). The concept "didelphid", and the other higher taxon designations are used in the strict sense as diagnosed there. The Didelphida is the only order in the cohort Ameridelphia. Within it the paraphyletic suborder Didelphimorphia (derived from a sudameridelphian ancestry) includes the Didelphidae, whereas the suborders Sudameridelphia paraphyletic and Glirimetatheria (holophyletic) contain the remaining many distinctive groups of ameridelphians. The cohort Australidelphia includes two orders, the Gondwanadelphia (Microbiotheria and Dasyuromorphia, both holophyletic) and Syndactyla (the remaining Australasian marsupials, the semiorders Peramelina and Diprotodontia).

ABBREVIATIONS

Specific joints are abbreviated by the combination of the first letters of the names of those units which contribute to the joint in capitals, and the letter J for joint. The combination of adjectives which designate two articulating bones usually stands for particular articular facets. Abbreviations entirely in lower case designate landmarks on specific bones, anatomical directions, ligaments, tendons, or muscles. These abbreviations are listed under two separate headings in order to facilitate retrieval of information. Most of the characters abbreviated here and used on the figures and in the text are specific homology designations rather than just topographically descriptive terms.

Bones, Joints, and Joint Facets

ACJ	astragalocuboid joint
ACu	astragalocuboid
AFi	astragalofibular
AN	astragalonavicular
ANJ	astragalonavicular joint
As	astragalus
ATi	astragalotibial
ATip	posterior astragalotibial
ATil	lateral astragalotibial
ATim	medial astragalotibial
Ca	calcaneus
CaA	calcaneoastragalar
CaCu	calcaneocuboid
CaCua	auxiliary calcaneocuboid (australidelphian)
CaCud	distal calcaneocuboid (didelphid)
CaCul	lateral calcaneocuboid (australidelphian)
CaCum	medial calcaneocuboid (australidelphian)
CaCup	proximal calcaneocuboid (didelphid)
CCJ	calcaneocuboid joint
Ce	centrale
CLAJP	continuous lower ankle joint pattern
CMcJ	carpometacarpal joint
Cn	cuneiform (in carpus)
Cu	cuboid
Ec	ectocuneiform
En	entocuneiform
Ep	epipubic
Fe	femur
FeFi	femorofibular
FePf	femoroparafibular
FeTil	lateral femorotibial
FeTim	medial femorotibial
Fi	fibula
HRJ	humeroradial joint
Hu	humerus
HUJ	humeroulnar joint
HuRa	humeroradial
HuRal	lateral humeroradial
HuRam	medial humeroradial
HuRas	humerus-radial sesamoid
HuRaz	zonal humeroradial (for eutherians)
HuUl	humeroulnar
HuUlm	medial humeroulnar
HuUlr	radial humeroulnar
HuUlz	zonal humeroulnar (primitive therian condition)
Il	ilium
IlFe	iliofemoral
Is	ischium
LAJ	lower ankle joint
Lu	lunate
Mc	mesocuneiform
Mcp	metacarpal
Mg	magnum
Mt	metatarsal
Na	navicular
Pa	patella
Pf	parafibula
PfFi	parafibulofibular
Ph	prehallux
Pi	pisiform
Pp	prepollex

PTFJ	proximal tibiofibular joint
Pu	pubis
Ra	radius
RCJ	radiocarpal joint
RaLu	radiolunate
RaSc	radioscaphoid
RaScCe	radioscaphocentrale
Ras	radial sesamoid
RaRas	radius-radial sesamoid
RaUlp	proximal radioulnar
Sc	scaphoid (scaphocentrale of metatherians on Fig. 69)
ScCe	scaphocentrale
ScHu	scapulohumeral
Su	sustentacular
TF	tibiofibular
Ti	tibia
TiFid	distal tibiofibular
TiFip	proximal tibiofibular
Tm	trapezium
TMtJ	tarsometatarsal joint
Tr	trapezoid
TTJ	transverse tarsal joint
UAJ	upper ankle joint
UCJ	ulnocarpal joint
Ul	ulna
UlCn	ulnocuneiform
UWJ	upper wrist joint (**RCJ** + **UCJ**)

Topographical bony details, ligaments, tendons, muscles, and anatomical directions

ac	astragalar canal
actb	acetabulum
ampt	astragalar medial plantar tuberosity
asisp	anterior superior iliac spine
cdpt	calcaneal distal plantar tubercle
cpp	calcaneal peroneal process
ct	calcaneal tuber
eppl	epiphyseal plate
eppup	proximal epipubic facet
ffoc	femoral fovea capitis (for ligamentum teres)
fft	flexor fibularis (= flexor hallucis longus) tendon
fhd	femoral head
fhdn	neck of femoral head
ficfo	femoral intercondylar fossa
fihd	fibular head
fgqf	femoral groove for quadriceps femoris
fgtr	femoral greater trochanter
flc	femoral lateral condyle
fltr	femoral lesser trochanter
fmc	femoral medial condyle
fptcr	femoral paratrochanteric crest
fptgr	femoral patellar groove
fsotbr	fibular soleus tuberosity
ftf	femoral trochanteric fossa
fthtr	femoral third trochanter
ftt	flexor tibialis (= flexor digitorum longus) tendon
gpbt	groove for peroneus brevis tendon
gtfa	groove for flexor accessorius tendon
gtpl	groove for tendon of peroneus longus
hbgr	humeral bicipital groove
hcap	humeral capitulum
hcfo	humeral coronoid fossa
hdldcr	humeral distolateral deltoid crest
hdps	humeral deltopectoral shelf
hdtt	humeral deltoid tubercle
hhd	humeral head
hlec	humeral (lateral) ectepicondyle
hlecr	humeral (lateral) ectepicondylar crest
hlfcap	humeral lateral flange of capitulum
hltub	humeral lateral (greater) tuberosity
hplcr	humeral posterolateral crest
hpmcr	humeral posteromedial crest
hmec	humeral (medial) entepicondyle
hmtub	humeral medial (lesser) tuberosity
hofo	humeral olecranon fossa
hpcr	humeral pectoral crest or ridge
hplcr	humeral posterolateral crest
hrfo	humeral radial fossa
hscf	humeral supracondyloid foramen
hscr	humeral supracondyloid ridge
htr	humeral trochlea
hzcon	humeral zona conoidea
ilcrf	ilial crest for quadriceps femoris
issp	ischial spine
l	lateral
lu	lunula
m	medial
mc	meniscus
p	proximal
pbt	peroneus brevis tendon
plt	peroneus longus tendon
ppl	process for peroneus longus on Mt 1
rasgr	groove for radial sesamoid
rbbrt	radial biceps brachii tuberosity
rcefo	radial central fossa
rcpr	radial capitular process
rdm	radial distal malleolus
rlcr	radial lateral crest
rgedc	radial groove for tendon of extensor digitorum communis
rgecr	radial groove for tendon of extensor carpi radialis
rmcr	radial medial crest
rn	radial notch
sa	sulcus astragali
sacpr	scapular acromion process
sc	sulcus calcanei
scopr	scapular coracoid process
sdtr	scaphoid tubercle
sglfo	scapular glenoid fossa
spsp	scapular spine
sup	sustentacular process
tat	tibialis anterior tendon
tilc	tibial lateral condyle
tilic	tibial lateral intercondylar tubercle
timic	tibial medial condyle

timit	tibial medial intercondylar tubercle
tmm	tibial medial malleolus
trmgr	tibial retromalleolar groove (for tpt and ftt)
tps	tibial distal posterior shelf
tpt	tendon of tibialis posterior
tst	tendon of triceps surae
tqf	tendon of quadriceps femoris
tqfcr	tibial crest for quadriceps femoris
ulalfo	ulnar annular ligamentous fossa
ulcolr	ulnar cranial olecranon ridge
ulco	ulnar coronoid process
uldtc	distal ulnar trochlear crest
ulfofdp	ulnar fossa for flexor digitorum profundus
ulfoa	ulnar fossa for anconeus
ulgr	ulnar guiding ridge
ulol	ulnar olecranon process
ulppr	ulnar proximal process
ulptc	ulnar proximal trochlear crest
ulptcl	ulnar lateral proximal trochlear crest
ulptcm	ulnar medial proximal trochlear crest
ulscs	ulnar subcutaneous surface
ulst	ulnar styloid process
ultrn	ulnar trochlear notch
utfdp	ungual tubercle for flexor digitorum profundus

RELEVANCE OF FUNCTIONAL AND SELECTIONAL ANALYSIS FOR PHYLOGENETICS

It is generally understood that the relationship between what an animal does and its inherited morphology presents one of the more complex set of issues in evolutionary theory. But equally important is that this relationship is directly relevant to how we test phylogenetic hypotheses against morphological attributes. As stated by many, the morphology (and its mechanical consequences) of an animal is to a large degree the result of the heritage (selective demands of the past manifest, but also adaptively significant, in the descendant organism). The animal's structure/function is also partly the driving force of its actions. What an animal has, its form-function complexes, will "force" or influence it in its pursuit of a certain habitus beyond the selective demands that are driven both by the animal's cognitive behavior and the environment. These are, simply, the theoretical positions we hold regarding the concepts of adaptation and adaptedness.

There is need for an explicit theoretical position regarding the meaning of function and phylogeny in (individual) organisms in their "realtime" (Szalay 1999a), and therefore the role of functional analysis in a broad sense in phylogeny estimation. We try to explain this briefly below. Much has been written about the theoretical issues of functional biology, in a broad sense, as these pertain to the study of living organisms, but very little has been written regarding the relevance and significance of function and adaptation for phylogenetic understanding of fossil and living organisms. Furthermore, although most ideas of function have been tied to adaptations (e.g., Pranger 1990), there has also been a general belief among many neontologists that (past) adaptations of fossil organisms really cannot be ascertained (see especially Lauder 1995). Like so many foci of debate in systematics, this one also should be about appropriate levels of applicability, but these are often unspecified. Little attention has been paid to different levels of adaptations within lineages and species tied to their phylogeny, beyond Gould & Vrba's (1982) taxic and punctuationist conceptualization (and proposed vocabulary that reflects that perspective)[1]. Much of systematic literature itself is both equivocal and confused regarding the role of functional biology and its relationship to the estimation of phylogeny of lineages. This is peculiar because what the process of phylogeny is should have a significant bearing on the methods we use to reconstruct it. It is for this reason that we draw attention to some theoretical and methodological relationships (both ontological and epistemological) between functional analysis (*sensu lato*) and phylogenetics (see Szalay 2000).

BACKGROUND AND STATEMENT OF THE PROBLEM

As a necessary preamble, it should be recalled that each organism (an ontogeny) is a phylogenetically (as encoded in its genotype) and developmentally (in realtime) intertwined individual of specific duration. (In sexually reproducing organisms the ovum itself represents a probably critical component of the phylogeny beyond genetics; Raff 1996). The evolutionary fate of demes or species depends on the interplay of both the physical and biological world in a Darwinian context, the consequence of natural and sexual selectional imperatives effecting the individuals that make up such evolutionary units. It should be obvious that ancestrally mediated descent with modification is an equally and quintessentially Darwinian component of tested evolutionary theory, in addition to adaptations through natural selection or modifications through sexual selection. Modal patterns of the various frequencies of these variant ontogenies become fixed differently in populations or species, and these variably persist and change in lineages. So phylogeny is a succession of successful ontogenies in the context of ecology, what we may dub here as the Darwinian context. Nevertheless, both ontological and epistemological issues of contention remain[2].

As a rule neontologists have doubts about the legitimacy of adaptational assessment of fossil species, and the use of adaptational analysis for phylogenetics is all but ignored. It should not need repeating here that science is a probabilistic enterprise with equal doses of deductive and inductive activities, *contra* axiomatized Popperian views. Its various problems can be "solved" or even "resolved" only with varying degrees of success, and any phylogenist must be acutely aware of this. Yet some of the least "falsifiable" (but often well-corroborated, or "verified") answers to questions can be the most important for understanding causes, attributes, and history of lineages (these often being the least logical in a linear sense).

Adaptations in fossil taxa cannot ever be fully understood, but it is also questionable, to a lesser degree, whether they can be fully understood for most living species as well. The reason for the latter is partly theoretical in nature, but also because the operational difficulties can be enormous. But to make categorical statements that because we have no "behavior" preserved for fossils (therefore we cannot understand their adaptations) is somewhat equivalent to stating that we have no time machines as a means of observing historical character transformations or lineage evolution in geological time. We need to remind ourselves at this point that one should be equally aware of the fact that, while phylogeny resides in the past, we nevertheless pursue it. Should we not, therefore, do the same with regard to functional and adaptive analysis for both fossils and living species, particularly as evolutionary (hence systematic) theory requires such methodology?

So ontological issues that surround adaptation as a process at times seem unresolvable because of the thorny issue of "current utility" (see below). Such philosophical conundrums, however, do not make the adaptive process and its results, or those of sexual selection, any less real. But it should be realized, although it is not widely appreciated, that explanation of adaptations in fossils (independent only to the degree that the concept of adaptation can be of phylogenetic ties, and *vice versa*), is often less of an epistemological problem than attempts at valid testing (i.e. corroboration) of many phylogenetic hypotheses. The currently dominant view of parsimony cladistics eschews the relevance of selectional analysis and its usefulness for phylogenetics, if not for "scenario" concoction. According to this well-known view, cladograms, based on parsimony-driven distributional analyses of "synapomorphies" (i.e. untested homology hypotheses of uniquely shared similarities between taxa), should represent the "foundations" of all other historically relevant analysis (e.g., Eldredge & Cracraft 1980; Simmons 1993).

FUNCTIONAL BIOLOGY AND TERMINOLOGY

To most naturalists (in a broad sense), functional biology has a unifying significance for evolutionary biology. This is in contrast to a narrow taxonomic tradition that attempts to keep functional, adaptational, and historical research programs separate, as if their domains were theoretically unrelated. The holistic and Darwinian perspective of naturalists, however, should axiomatically apply for the study of phylogenetics (Fig. 1).

In an attempt to unwrap the several meanings of the term function, a more restrictive usage was suggested for "function" by Bock & Wahlert (1965; see also Bock 1977) in their paper regarding adaptation and the form-function complex. They refined the distinction between the mechanical/physiological and environment-related aspects of features of organisms, and distinguished these from the selection-caused (heritage-mediated) biological role (biorole or role; or adaptive or biological function). Such a conceptual difference was previously well understood by a number of biologists and paleontologists, but not by many others to judge from the literature. The concepts of *mechanical* and *biological* functions (i.e. *function* and *biorole*) have not only been clearly differentiated by Bock & Wahlert (1965), but were presented in a theoretically detailed functional and ecological context. This clarification of terms had salutary consequences on evolutionary conceptualization and consequently theoretical perspectives.

We and others (Dagosto *et al.* 1999; Szalay & Lucas 1993, 1996; Szalay & Schrenk 1998) have since followed that terminology as such practice had the salutary consequence of forcing one to think more clearly of the complexity of functional and evolutionary issues. Yet in any meaningful, "real world", sense, mechanical and biological functions are inseparable, as they both reflect the same history, and therefore, epistemic factors clearly drive this theoretical differentiation of wholly interdependent processes and causalities [3].

CAUSALITY AND FUNCTION

An issue of seemingly remote importance to theoretical notions regarding "function" is the "proximate" *vs* "ultimate" dichotomy in biological explanations. Mayr's (1961) early and much repeated thesis (Mayr 1982) was that there are proximate and ultimate causes (and this subsequently became a nearly universally endorsed stance). The former was to be pursued by the "functionalists" and the latter by the "naturalist-evolutionists", and it was implied that sharply different *conceptual approaches* were necessary to understand these two causalities. We take the contrary position that the concept of causality in realtime should play a fundamental role in theoretically important connections between the various components of holistic functional biology (e.g., Szalay 1999a; see level-specific definitions of "realtime" of life histories, populations, and species there as distinct from "real time"). Therefore a loose designation of "cause" is obfuscating when it comes to either functional or evolutionary analysis, both in a broad sense (see below). Causes affecting organisms occur in realtime (and that rules out "causal" past history), although the initial and boundary conditions of organisms living in a particular moment in time play a significant constraining and facilitating role in their entire life history. We second, and generally adopt the view of Mahner & Bunge (1997) on causality (with some exceptions) [4]. Their arguments render meaningless the notion of "ultimate causality" out of the context of realtime causality in any lineage.

A lineage does not have "causes" acting on it beyond those that acted on the aggregate of individuals that made up each segment, in realtime, in the past (a species in an instant in time, not a species taxon; see discussion in Bock 1979; and Szalay 1999a). Real causes that affect, for example, the becoming (not merely origin) of a single organism are demonstrated by the newly emerging "hybrid" fields (e.g., developmental genetics, often called "evo-devo", and other novel approaches), namely how inseparable functional explanations are not only from history but also adaptive existence. Mutations and their developmental consequences are inseparable from the context of a particular genotype. This is well beyond the occasionally agenda-laden and quasi-engineering concepts of function that eschew the full meaning of adaptations and adaptedness, a "functional" conceptualization advocated by Cummins (1975), Lauder (1981, 1995), and Amundson & Lauder (1994) [5].

ONTOLOGICAL PERSPECTIVES ON FUNCTIONAL BIOLOGY, AND THE OMISSION OF "WHAT FOR"

We fully endorse the epistemologically important distinction in practical research programs that pursue sundry important functional aims in the laboratory (as we did to some degree in this study) without immediate concern for specifically field related bioroles. But one is repeatedly reminded by one's own practice and the literature of the fact that the concept of function is understood very differently by many who consider themselves either structuralists, functionalists, phylogenists, or adaptationists, a somewhat unfortunate but perhaps necessary compartmentalization of what should be at least a theoretically cohesive area of study.

But beyond the basic epistemological issue that a changing field of morphological studies entails, there has been an increasing conceptual redefinition and narrowing, as well as an ontological confusion, concerning the theoretical meaning of functional studies. Theoretical positions have been taken by authors proposing various exclusive meanings for the concept of function. While some of these positions are largely epistemological in nature, some have taken on the cloak of ontological propositions in claiming some special theoretical virtue for them.

For example, in a series of papers going back two decades Lauder has been advocating a rather narrow view of the discipline of functional morphology itself (see Amundson & Lauder 1994; Lauder 1996; and references therein). This particular advocacy seeks connections between parsimony-generated cladograms of systematists and quasi-engineering type of functional analyses, devoid of input from selectional perspectives. In fact, Amundson & Lauder (1994) claim that adaptations are all but impossible to identify and therefore the search for the "why" of attributes, namely what selectional causes molded a feature, is doomed to failure. Their justification for this narrow view of "functionalism" (in fact a form of structuralism, see below) is that they believe that the mechanical transformation of structures is what "functional" biology is about, without regard for the specific contextual role of natural and sexual selection (resulting in adaptations on one hand and complex behaviors and display paraphernalia on the other). Yet this theoretically restricted perspective does not prevent Amundson & Lauder from calling their conceptualization, inexplicably, "causal role function". Such conceptualization sidesteps the selection mediated origin and "becoming" of a given form-function complex [6].

This "causal role function" perspective (with its patronizing tone regarding the research aimed at uncovering adaptive functions, the "old adaptationism" of Rose & Lauder 1996) is a direct outgrowth of the "cladogram first" research program (pattern over process; Eldredge & Cracraft 1980; Lauder 1981). Such theory would render biological character analysis subservient to taxic schemes of bifurcations, and forego the necessary prerequisite of testing character transformations and synapomorphies. The latter is accomplished with the aid of methods derived from tested evolutionary theory, i.e. the phyletics of features. Yet any evolutionary scheme, or theory, is unrealistic without adaptation (and/or results of sexual selection) as an integral part of the process [7]. Ironically, patterns of cladogeny are just as unknowable with certainty as is adaptive function jettisoned by Lauder and others. In fact, as we noted, there are gradational or incremental probabilities in the testing procedure (corroboration), often with a considerable overlap between both phylogenetic and adaptational hypotheses.

Functional (*sensu lato*), phyletic, as well as cladistic evaluations of attributes to yield character states (distributional data) are integral parts of phylogenetics. Both the establishment and the explanation of patterns require: a) ecological and other selectional assessment; b) phyletics of features to determine polarities; as well as c) stratigraphic and biogeographic contexts, all at a level that information and the applications of valid methods permit. These structures apply proportionately to the degree to which any of these activities can be brought to bear, which obviously depends on the nature of available evidence (including both deductive and inferential information). But the various levels of inference permitted by data and context do not alter the force of a conceptual methodology derived both from descent, and natural and sexual selection, in specific space and time. To claim theoretical "primacy" for a phylogeny based on any presorting of structural patterns, combined with only a *sensu stricto* functional analysis (that would transfer functional evolution into a non-Darwinian vacuum), is a flawed epistemic prescription for attaining understanding of "functional evolution" [8].

The combined "logical primacy" perspectives of parsimony and engineering approaches that claim adaptational understanding to be unattainable, however, are being made obsolete by many "multidisciplinary" efforts (resulting from the fusion of genetic, morphological, developmental, ecological, and paleontological perspectives and practices, to mention only a few [9]. The pivotal role of contingency-based evolutionary analysis means dependence on selection-related considerations, manifested in palaeontology mostly as structural patterns of the skeleton itself. Without the fundamental Darwinian context brought to bear on a problem the functional protocol of Lauder and associates assures no deep insight for evolutionary transformations. This purely deductive approach to mechanical function is tied to equally deductive, but deeply flawed, attempts at "transformational analysis" that map traits onto taxograms [10]. So, in contradistinction to the paradigm of "causal role function" advocated by Amundson & Lauder (1994), it appears to us that that approach, without the ecological and other selectional components, lacks the required framework for estimating evolutionary history, as vague as adaptive meaning may be in some instances in phylogenetic analysis.

We note here a singularly relevant query that is omitted from the "new adaptationism". What does the comparative assessment of engineering parameters mean without any conceptual room left for the reasons for these differences? When engineers plan the construction or analysis of structures, there is always a particular goal in mind. That goal is the Aristotelian "final cause", namely "what something is for". This implicit factor is absolutely and fundamentally connected to any engineering (mechanical) enterprise, and if such an effort is separated from its context, then it loses not only its directives and limits, but also its meaning [11]. This does not, however, translate into any of the goal directed teleologies of the past. It is hard to contemplate how a particular observed biorole (or one inferred with a lesser degree of probability, based on modeling, than direct observations can provide), correlated with form-function, would not have played a major causal evolutionary role in the becoming of that complex, except in a strongly structuralist conceptualization of biodiversity. An increasingly narrow emphasis on engineering function results in an evolutionary conceptualization of function in biology that brings into question the simplistic and truncated view of its definitions, of evolutionary process, not to mention the problem of discordant semantics. Is such conceptualization really "good" biological theory? Lamarck's insight, reworked within Darwinian theory, namely that the combined function and role of attributes is part of the causal interaction responsible for their evolution, has been pursued by many biologists and philosophers, and its theoretical consequences will not be discussed further here [12]. In a definitional sense, at any moment in lineage history, a form-function complex that exists is a set of initial conditions, and the sundry causes that act on the organisms are, strictly speaking, the causes that mediate subsequent survival and resulting fitness differences. But it cannot be overlooked that the very phenotype-based activities of organisms generate a great deal of the specific causal forces acting on them. The feedback loop is mutually dependent, and the understanding of the workings of this process fully justifies an expansion of conceptual methodologies based on it.

But what about real evolutionary goals or explanations in research protocols, ones that should rest on conceptual foundations different from those of engineering considerations only? Purely functional explanations, while they may justify deductive issues dealing with features, are incomplete ones (to recast and paraphrase Dobzhansky) for species specific phenotypic attributes. These lack explanations for their species-specific, hence idiosyncratic, workings. The perspective of "new adaptationism", repeated for decades both by doctrinaire cladists, as well as by the pure "functionalists" such as Lauder and co-authors, is quite different from Bock's frequently taken stance (e.g., Bock 1988). Bock & Wahlert (1965) held that functional (*sensu stricto*) and selectional components of features are (conceptually) independent and complementary. Still, Bock does profess belief that a sharp, theoretical dichotomy should apply to function and adaptations, and particularly that the investigations of the latter should depend on the former [13]. Bock's (1999) theoretical perspective appears to be tied to Mayr's (1961) claim regarding distinct "proximate" (what Bock calls functional) and "ultimate" (what Bock calls evolutionary) causes (and what Bock more meaningfully, and astutely, prefers to call explanations). Bock (1999) maintains that functional morphology answers "how" questions, namely how things work. We do not disagree with that, but the questions and problems of functional biology (*sensu lato*, the sense endorsed here) arise from a much broader context than just statics and mechanics, or chemistry. Bock's view on evolutionary explanations, namely that these are responses to questions of "[…] why attributes of organisms came into being originally and have modified [= evolved] over historical time" (Bock 1999: 49), indicates, however, that a certain critical theoretical perspective is missing, a link that might not justify his particular dichotomous and hierarchic view.

A "functional" *vs* "evolutionary" theoretical dichotomy lacks the formal recognition that in any evolutionary change the usual "why" question alone is not an adequate formulation of the nature of evolutionary explanations. Similarly, functional questions also have an ineluctable lineage-based transformational component (not a taxic one) that renders answers to these incomplete in mechanical terms. In fact, any attempt at full evolutionary explanation that deals with specific lineages involves the issue of: a) how something works (in light of); b) what it is for; which in turn c) is critically dependent on how a particular trait of organisms came to be historically transformed; and d) how it was ontogenetically constructed that way. At first this may appear to be either overcomplicating matters or insignificant. But on second thought it should be realized that contingent, lineage-specific changes are not "merely what happened" (*contra* Bock 1999: 56). Such changes, the selectional guidance notwithstanding, were profoundly influenced or guided by preexisting stages (as they will have influenced subsequent changes). There is virtually universal agreement that these contexts (the heritage) guide both the nature of transformations as well as their adaptive "goodness", "latitude", and even the built in seeds of doom (in retrospect) or new opportunities of given lineages in the particular environmental or competitive contexts they will encounter [14]. Realtime constraints (rooted in history) do not only constrain, but also direct and facilitate subsequent modifications.

Such conceptualization should have implications for methodologies that aim to decipher evolutionary history, ones that can produce probability-based truth content (*vs* parsimony tested-consistency, or congruence, of diverse classes of features). For example, the literature on the history of understanding of tribosphenic teeth of therian mammals and the subsequent evolutionary patterns constrained by the original molar system supply some of the most numerous and persuasive examples on the meaning of constraint as these affected morphology, function, and biological roles. Other examples abound in virtually all systems of vertebrates, the skeleton being perhaps the richest storehouse for this (e.g., transformational aspects of the therian tarsus; Szalay 1994).

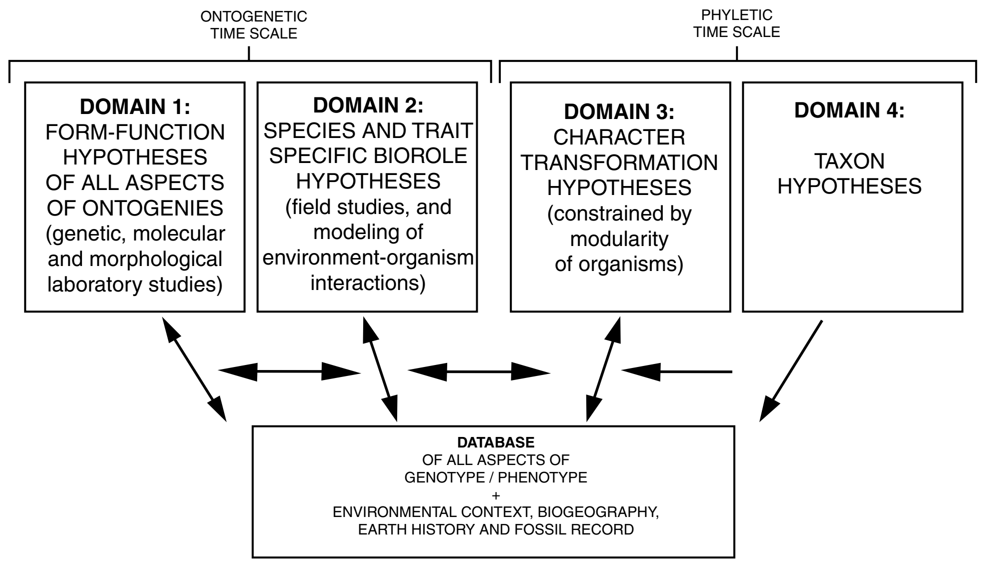
Bock's (1988: 207) view that adaptational explanations are not evolutionary but functional, therefore, is also problematic. This is so particularly as he (Bock 1999) continues to maintain the legitimacy of theoretical independence of functional (proximate) and evolutionary (ultimate) explanations. We believe, however, that explanations of results of selectional processes are in fact inseparably both. They are "temporally-looped", rather than hierarchically and dependently related to form-function. While natural and sexual selection are law-like explanations, their consequences in lineages are fundamentally historical and time dependent processes that cannot be disembodied from the particular lineage histories (e.g., Szalay & Costello 1991). As Bock (1993) so aptly emphasized, natural selection as a nomological explanation is cause, mechanism, as well as process, depending on our usage and the context of the concept. Acquisition of new adaptations (a process) is a large component of evolutionary history, and much of phenotypic evolution, as most evolutionists suspect (and long championed by Bock), is fully Darwinian.

Ecomorphology (or any aspect of the phenotype-related bioroles) is conceptually very much part of this endeavor, as it forms the context with its inseparable feedbacks into the "purely" functional (nomothetic) efforts in laboratories. The deductive base of the latter does not make it "superior" or axiomatically antecedent to the former, as noted. While Bock (1999) argues for the distinction of ecological morphology from functional morphology, and the notion that the former should always be built on the latter, he nevertheless fully endorses the importance of adaptational analysis in contrast to Lauder and others. When it comes to extinct organisms, however, Bock (e.g., 1977, 1981), in spite of his firm holistic view that connects function and bioroles, applies what we consider a neontologist's bias. We believe that his theoretical stance on extinct species and their adaptations is somewhat narrow, restrictive, and linear in its logic. A model- and probability-based perspective offers a more realistic epistemology. Given good and complete specimens, specific adaptive strategies (at an appropriately designated level) can be understood in fossil taxa with high probability. The judicious and phyletically contextual use of combined mechanical, adaptational, and ecological models of living organisms can render great certainty to this type of paleobiological analysis. Modeling through the use of carefully delineated aspects of living species yields important and necessary dimension to the practice of both adaptational and phylogenetic analysis.

We reemphasize that often one can corroborate far better the adaptive strategies of fossil species than their phylogenetic affinities. We suggest, therefore, that perhaps the construction of completely deductive, syllogism-like, ontological statements (i.e. those that carry well-corroborated theoretical concepts to their extreme logical exegesis), such as the construction of theory from the logical consequences of clear definitional differences between function and biorole, is not the most useful approach to theorizing in this area of evolutionary analysis. Both an unnecessarily restrictive deductive approach and the variable epistemological limitations, as in the case of strict functionalist practice, are unjustified theoretical grounds for truncating the domain of evolutionary explanations (see Fig. 1, this schema is in agreement with all the major points discussed by Bock 1981).

Let us also reiterate the obvious first, namely that the level at which results of selection may be ascertained in organisms is unequivocally the highest for living species observed in nature. But lest one forgets, it is equally obvious that existing features in an organism may reflect causal correlations between these form-function complexes and the use they had in the past rather than at the time of study. In fact, deductive consequences of descent with adaptive modification demands that it be understood clearly, given the ongoing temporal nature of the evolutionary process, that current attributes of organisms are the products of selectional forces acting on past generations. Activities in a given point in time (in the particular context of the total environment) generate the selectional forces that transform the frequencies of "fit" individuals in the succeeding populations. This temporal relationship is critically important and renders all static definitions theoretically unacceptable.

The only factor that is likely to assure successful programs in adaptational studies (those with high truth content), however, is that the rate of environmental change: a) is usually slow (certainly gradual short of extraterrestrial impacts or violent local disturbances); or b) often approaches zero (in generational terms), resulting in either stabilizing selection or often in a fully Darwinian progressive change of features (not a goal directed teleology) for the same biological functions. What most organisms do in their currently observed environment, therefore, is probably causally connected to their features.


OUTLINE OF CONCEPTUAL RELATIONSHIPS BETWEEN CONNECTED DOMAINS OF RESEARCH DERIVED FROM AN EXPANDING DARWINIAN SYNTHESIS TO YIELD TESTED TRANSPECIFIC HISTORICAL EXPLANATIONS (i.e. PHYLOGENY)

Hypotheses of Domains 1-3 are tested against data they generate and against well-tested hypotheses of the other two domains. Hypotheses of Domain 4 are tested against all data and the tested hypotheses generated by the other domains. Because lineages (and taxa) are recognized based on research in Domains 1-3, data and tested hypotheses of these domains or transformation hypotheses are not tested against supraspecific taxon hypotheses of Domain 4. Species taxa are recognized based on field data (reproduction, ecology, behavior) and their genetic and phenotypic expressions. Supraspecific taxa are delineated monophyletically (recognizing both paraphyla and holophyla).

(Szalay F. S. 1999; prepared by Warshaw J. S.)

FIG. 1. — The conceptual relationships of four domains of research, and the valid and noncircular methodological links between them for reconstructing phylogeny. These interrelationships are in accordance with the evolutionary process based on modern Darwinian theory (the expanding Synthesis). The directional arrows indicate the domains, databases, and tested hypotheses within these domains, and the causal interdependency of the first three domains for both generating data and testing hypotheses. Note that while the interrelationships for the first three domains are in reality “temporally-looped”, they are not circularly dependent on Domain 4. It is against these former domains that phylogenetic and taxonomic hypotheses are tested.

The foregoing general theoretical point should caution everyone regarding the allegedly unequivocal nature of Recent organisms over fossil ones when it comes to their understanding. For example, the statement of Bock (1999: 55) that the “study of biological roles must be done by observations of the organism living naturally in its environment – they cannot be determined by observations made in the laboratory or other artificial conditions” is a case in point. But such implied dismissal of the fossil record does not reflect the realities of much highly corroborated paleontological research. No one would argue that information from the natural setting is critical for highly specific activities contained within the form-function features of living organisms for the reasons pointed out above. A host of highly relevant explanations about fossil taxa, using rigorously selected and explained extant model species, are equally justified, with virtually the same degree of probability as explanations made concerning numerous aspects of living organisms. In fossil mammals, based on this type of rigorous and relevant modeling, there are such role related attributes as cursorial modifications, aquatic adaptations, digging and burrowing adaptations, traits related to habitual hanging, obligate arboreality or terrestriality, and hosts of obligate dietary adaptations such as grazing, myrmecophagy, piscivory, hypercarnivory, and numerous others on a level of generality that can be securely ascertained (Court 1994; Szalay 1994; Szalay & Lucas 1993, 1996; Szalay & Schrenk 1998; and many others). Such model-based assessments that employ ecologically and functionally well understood living species that cross size and higher taxon limits, provide a high degree of adaptational assessment. This is accomplished through the convergence method that is not only highly reliable, but which forms a critical link to other activities such as phylogenetic estimations (e.g., Szalay 1981). Like any other methodology that is axiomatically derived from underlying tested theory, none of this is linearly full proof, but probability-based.

Therefore no valid theoretical justifications exist for excluding fossils from adaptational analysis. To hold that ecological morphology is applicable to living species only is an unfortunate and monotonic logic-bound view. It unnecessarily truncates adaptational, as well as phylogenetic, analysis. It also unjustifiably limits valid epistemological methods in testing a tremendous range of issues in macroevolution. We emphasize again: in general, survival and sexual selection related assessment of well-represented fossils is not any less dependent on probability judgements than is phylogenetic estimation (see also Szalay 2000).

DEVELOPMENT, LOCOMOTION, AND INTRASPECIFIC VARIATION OF POSTCRANIAL ATTRIBUTES IN LIVING MARSUPIALS

Without some guide posts gleaned from living species, a collection of postcranial remains of a large number of species of fossil marsupials would be extraordinarily difficult either to interpret in terms of their ecological significance, or to assign to species taxa (named or unnamed). For the former task ecologically meaningful assessment of skeletal aspects of living models is needed. For alpha taxonomy of fossils an appreciation of variation needs to be gleaned from samples of extant species. But first and foremost we need to highlight at the outset a number of differences in skeletal development between metatherians and eutherians. This discussion, in turn, should give some context to both the similarities and differences between the two major groups of therians.

DEVELOPMENTAL AND PHYSIOLOGICAL BACKGROUND

In the placental neonate the ossification centers are usually present, although the forelimb develops slightly earlier than the hindlimb prenatally, a pattern that becomes reversed by birth (Patton & Kaufman 1995). This sequence and reversal are a phylogenetically revealing signal. In fact by birth the hindlimb of placentals are larger and faster growing than the forelimb (Watkins & German 1992). In metatherians, however, the skeleton of the mobile and crawl-capable "embryonic" neonate (the embryonic designation is from a eutherian perspective), with its hypertrophied head and pectoral girdle, is completely cartilaginous with some exceptions in the oral region. Furthermore, the ossification of the long bones of the forelimb of marsupials well precedes that of the pelvic girdle (McCrady 1938; Klima 1987; Hughes & Hall 1988; Frigo & Woolley 1996). The adaptive explanation of this pattern resides in the marsupial neonate's need to make its way to the nipple, using its relatively well-developed hands with a complete internal cartilaginous framework and external deciduous claws. This pattern is an adaptive imperative that affects postnatal growth patterns, with developmentally and phylogenetically constraining consequences. Such a growth pattern, rooted in the adaptations of the neonate, limits those kinds of adult locomotor strategies in marsupial lineages that would require a drastic adult alteration of the pentadactyl grasping pattern of the neonate's hand early enough to be effective following weaning (Lillegraven 1975; Szalay 1994). We add here that the early, *in utero,* developmental similarity of the placental pattern to a marsupial neonate suggests that the protoplacental had an ancestor with a marsupial-like developmental system. Such an assessment does not imply the dental formula-based notion of a metatherian mammal, a taxic- rather than lineage-based concept. (For the concepts of the taxa Theria, Tribotheria, Metatheria, and Eutheria see Szalay 1994; and Szalay & Trofimov 1996). Furthermore, the marsupial ancestor probably did not have the an effective trophoblast (Lillegraven 1985; Lillegraven *et al.* 1987). This was a feature that probably evolved in the protoplacental embryo and which allowed the subsequent rapid and extended development of eutherian embryos. As a consequence, protoplacental neonates could be left in a nest while the unburdened mother foraged (Szalay 1994: 58; 59).

A number of significant recent studies have close conceptual bearing on the analytical perspective we employ in the assessment of the fossils from Itaboraí. One of these is by Maunz & German (1997) on the ontogeny of limb bone scaling in *Monodelphis domestica* Wagner, 1842 and *Didelphis virginiana* Kerr, 1792. While *M. domestica* is a highly terrestrial species, *D. virginiana* is only partly terrestrial in habitus (*contra* Maunz & German 1997: 128, who mistakenly consider the latter "[…] the most adapted to arboreality of the Didelphidae […]"). These two species are born near 1 g in size but on reaching adulthood *D. virginiana* is about 50 times larger than *M. domestica*. Interesting patterns of heterochrony were observed by Maunz & German (1997), both between the forelimb and hindlimb, and in the proximodistal heterochronic parameters of the limbs. All of the information provided by these authors need to be viewed in the context that *D. virginiana* grows 100-150 days longer than *M. domestica*. But in spite of the fact that the larger didelphid grows longer before reaching adult size, there appear to be few scaling differences over time in the ratios of limb bone length to width. These relatively unchanged proportions of their long bones are in direct contrast to the differences in the scaling of their hands and feet.

Maunz & German (1997: 118) note that "proximodistally, there is variation in growth rate within the bones of each limb. Several hypotheses exist to explain this pattern. It is possible that the more distal elements are less subjected to developmental constraints therefore having more variation […]. Or it may be the converse of this […] there may be selection pressures for specific sizes of each bone that must be reached in a given amount of time, therefore confining bones to certain growth rates". We should add here that a selectionist explanation, rather than a perhaps excessively constraint-evoking structuralist perspective when specific evidence is lacking, may be more likely. Such appears to be more realistic in light of the prevalent and highly corroborated patterns in mammals where the ubiquitous correspondence between habitus and the length and shape of cheiridia in both the hands and feet is the repeatedly observed norm. Yet specific, vertebrate chondrogenic, anlage-related constraints may also be operating. But the constraint supplied by the necessities of marsupial birth is a functionally mediated one, obviously produced by selection. It appears that the substrate demands on the adult animal (in as much as the compromise with the neonatal biorole permitted) was one of the major determining factors of the adult substrate-related adaptive patterns.

LOCOMOTOR STUDIES ON RELEVANT EXTANT MARSUPIALS

The most significant studies on marsupial locomotion (and on a monotreme and a range of eutherian mammals as well) and their skeletal dynamics are those of Jenkins (1971, 1973). Pridmore's (1992, 1994) studies on locomotor behavior of two marsupial species are also important additions to that literature. These works can be closely correlated with the anatomical evidence and have fundamental relevance to explanations of morphology in both extant and fossil taxa. Jenkins' (1971) experimental study of cineradiographically monitored positional behaviors was broadly comparative; it included *Didelphis virginiana*, *Tachyglossus aculeatus* (Shaw, 1792), *Tupaia glis* (Diard, 1820), *Mesocricetus auratus* (Waterhouse, 1839), *Rattus norvegicus* (Berkenhaut, 1769), *Mustela putorius* Linnaeus, 1758, *Heterohyrax brucei* (Gray, 1868), and *Felis catus* Linnaeus, 1758. In that study Jenkins concluded that the posture and limb movements, positions, and excursions during locomotion of the species he considered "non-cursorial" (all but *H. brucei* and *F. catus*) displayed characteristics much more similar to an inferred primitive ancestral therian than to what had been considered to be "typical" mammalian postures and locomotor attributes. Jenkins stated that the ancestral therian locomotor mode was far better reflected in the "non-cursorial" locomotion of opossums and tree shrews than in the textbook-designated "typical" mammalian condition of mammalian cursors.

Pridmore's studies on *Dromiciops gliroides* Thomas, 1894 and on the trunk movements of *Monodelphis domestica* during locomotion represent another set of contributions bearing on the assessment of ecological morphology of marsupials. Pridmore (1992: 138-141) found that there are three consecutive modes of locomotion: slow to fast walking, troting, and half-bounding. *M. domestica* uses what he called a lateral sequence walk that turns into a trot at faster speeds when "[…] the diagonal limb pairs function in synchrony". During slow walk the trunk of *Monodelphis* "[…] undergoes significant lateral bending [while during] faster walk, the magnitude of lateral bending is reduced. At both speeds, one complete bending cycle occurs with each locomotor cycle. Regardless of walking speed, the trunk shows maximum bending at the stage in the locomotor cycle in which the hindfoot on the concave side of the trunk is being set down. Dorsal views of animals trotting show very little lateral bending […]. There is no evidence of lateral bending during half-bounding […]." Pridmore notes (p. 142) the findings of Jenkins & Camazine (1977), namely that raccoons show "[…] considerably greater rotation in the plane of yaw of the pelves […] walking at 3.2 km/hr than in those of more erect-limbed carnivores (a fox and cats) walking at the same speed. In these three carnivores, the amount of horizontal rotation of the pelvis during walking correlates with the extent to which the femur is abducted". Pridmore makes the final suggestion that lateral bending, contrary to previous suggestions in the literature, was never really lost in either metatherian or eutherian mammals, and that the sagittal bending of the vertebral column was an addition in conjunction with asymmetrical gait and the ability to gallop and bound, rather than a complete replacement of the ancestral tetrapod pattern of lateral bending during locomotion. The locomotor modes and relative degrees of lateral bending in the terrestrial *Monodelphis* are also discussed by Pridmore (1992). We find it significant that, while the locomotor repertoire of *Monodelphis* is not different from that of other "small to moderate sized therians […] that use a lateral sequence walk as their slowest gait" (Pridmore 1992: 141), including a variety of eutherian mammals that also trot and then half-bound or bound at higher speeds, the fundamental morphology of *Monodelphis* is of course that of a didelphid.

Pridmore's (1992) conclusions regarding the persistence of symmetrical gaits in *Dromiciops* on narrow substrates across a range of speeds, and the conclusion that this pattern is shared with arboreal didelphids (and we may add, most arboreal syndactylans; koalas are likely to be secondarily fully arboreal), is significant in several respects. As he suggests, this appears to be a characteristic of the last common ancestor of living metatherians (we exempt the Caenolestidae from this generalization only because information is lacking). It is suggestive that small, terminal branch locomotion favored this mode of progression where pedal grasping had a major role. This appears to be in accord with the notion that the Didelphidae represented a departure in the Palaeocene from other didelphidan marsupials and that the australidelphians (including the microbiotheriids) are derived from that *sensu stricto* didelphid pattern (Szalay 1994). Pridmore's finding that *Dromiciops* also displays two typical asymmetrical gaits, such as half-bound and transverse gallop, does not negate his conclusions regarding the shared and persistent symmetrical pattern of locomotion in arboreal marsupials.

LOCOMOTOR DESIGNATIONS

There is no question that what we consider today to be a cursorial locomotor strategy, displayed by mammals such as canid and felid carnivorans, artiodactyls, and perissodactyls, is a proper designation of the adaptations for gallop-sustaining running behavior of these mostly medium to large eutherians. It is also true that this designation, as it stands at one extreme, denoting fast and sustained running abilities and their attendant skeletal adaptations, becomes problematic when we try to apply it to some adaptive shifts among early therians.

Stein & Casinos (1997) have recently reexamined the notion of cursoriality in mammals and concerned themselves especially with the incorporation of biomechanical techniques into terminology. As they stated, their quantitation-based definition of cursoriality is inapplicable to fossil taxa or even to most living forms. Our particular concern with their use of locomotor terms such as cursorial is the omission of any reference to the history of lineages regarding the role of ancestral adaptations, new ones derived from these, and their morphologically constraining and facilitating influence on the evolution of that lineage. We prefer the heritage-imbued concept of what has been called *morphotype locomotor mode* (Szalay & Dagosto 1980). This is a concept applicable to a group in which the ancestor and at least some of its descendants (the former inferred from the latter) practiced a particularly characteristic pattern of locomotor behavior in an obligate manner more often than other behaviors, and this obligate locomotor behavior is clearly manifested in the skeleton. Szalay (1994: 187-189) has discussed the meaning and overlap (and hence occasional ambiguity), of the terms grasp-climbing, scansorial, scampering (arboreal or terrestrial), and semicursorial or subcursorial. This will not be repeated here [15].

INTRASPECIFIC VARIATION AND SOME ATTRIBUTES OF *DIDELPHIS VIRGINIANA*

Variational studies on the postcrania of therian mammals are few. One of the most comprehensive is that of Grulich (1991) who studied metric osteological variation in an extensive sample (over 1 000 individuals from the youngest ossified stage to the oldest) of the rodent *Cricetus cricetus* (Linnaeus, 1758). Nothing comparable exists in the literature on metatherians. We are not aware of qualitative studies of taxonomically useful postcranial attributes either. The most available sample to us for assessing and illustrating some limits of population variation in an extant marsupial species was a variety of skeletal elements of *Didelphis virginiana.* These skeletons were collected in New Jersey during the past 20 years and prepared by one of us (FSS). Our variation-oriented study was checked against samples of skeletal specimens of *Caluromys derbianus*, *Metachirus nudicaudatus*, *Monodelphis domestica,* and *Marmosa elegans*, but particularly against very large samples (up to 25 specimens each) of *Dromiciops gliroides* and *Rhyncholestes raphanurus.* We have selected and illustrated five specimens of *D. virginiana* (Figs 2-6) representing an increase in size from “juvenile” to “large adult” for each of those long bones that we have represented by samples of more than one specimen in the Itaboraí sample, namely the humerus, ulna, innominate, femur, and the tibia. A similar assessment of *Didelphis* was done for the tarsus by Szalay (1994).

Our primary intent here is to assess and illustrate the extent to which qualitative attributes can be judged and recognized as distinctly genus- or species-specific, given size and age variation within a species. Furthermore, it was considered important to determine the degree to which morphological attributes of specimens of one species either overlap or are consistently distinct from those of other extant species. Clearly, taxonomic properties of significance are attributes which are consistently distinct from those of other taxa of the same categorical level. In assessing the postcranial characteristics of various species and fossil samples, we particularly searched for those attributes that showed wide-ranging differences and size extremes in their adaptive complexes. Such traits are the shared heritage properties that are fundamentally useful for character analysis, and, hence, phylogeny estimation, as we discuss below.

As it will become obvious in the ensuing discussions, the taxonomic separation and the functional assessment of the individual fossil marsupial speci-

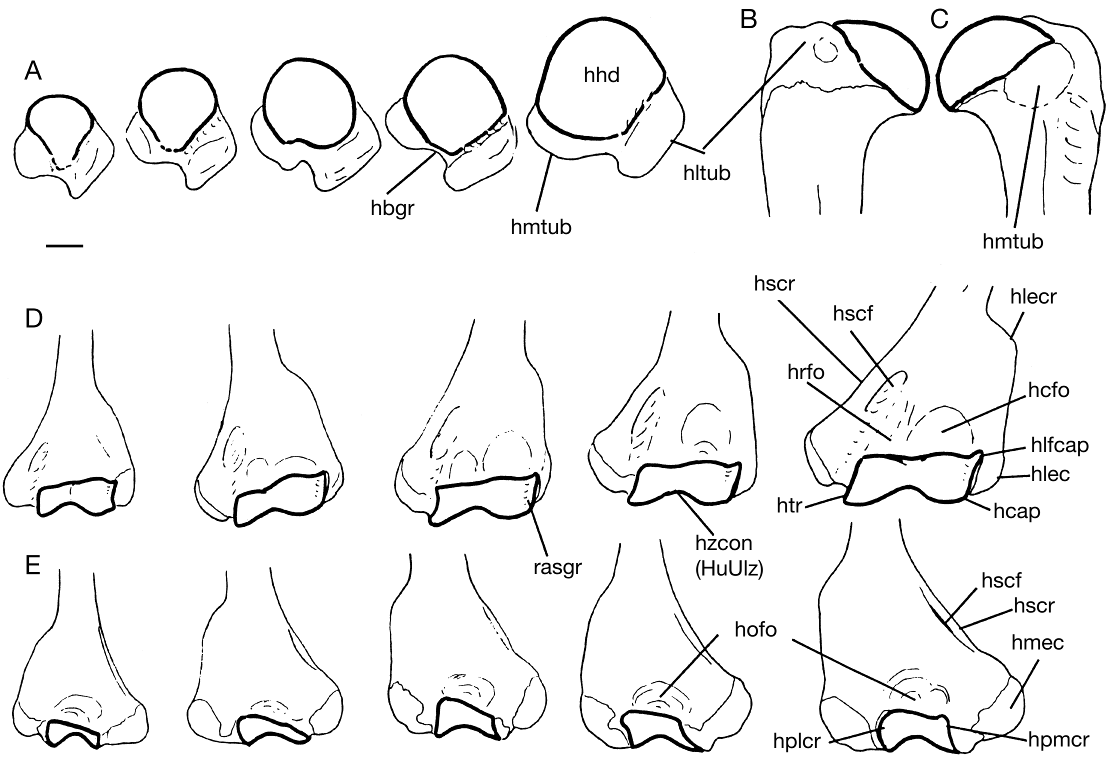


FIG. 2. — Juvenile to adult ontogenetic series, from left to right, of five left humeri of *Didelphis virginiana*; **A**, proximal ends; **B**, lateral view of proximal end of largest specimen; **C**, medial view of proximal end of largest specimen; **D**, anterior view of distal ends; **E**, posterior view of distal ends. Abbreviations: **hbgr**, humeral bicipital groove; **hcap**, humeral capitulum; **hcfo**, humeral coronoid fossa; **hhd**, humeral head; **hlec**, humeral (lateral) ectepicondyle; **hlecr**, humeral (lateral) ectepicondylar crest; **hlfcap**, humeral lateral flange of capitulum; **hltub**, humeral lateral (greater) tuberosity; **hmtub**, humeral medial (lesser) tuberosity; **hmec**, humeral (medial) entepicondyle; **hofo**, humeral olecranon fossa; **hplcr**, humeral posterolateral crest; **hpmcr**, humeral posteromedial crest; **hrfo**, humeral radial fossa; **hscf**, humeral supracondyloid foramen; **hscr**, humeral supracondyloid ridge; **htr**, ; **HuUlz**, zonal humeroulnar facet; **hzcon**, humeral zona conoidea; **rasgr**, groove for radial sesamoid. Scale bar: 4 mm.

mens were ultimately based on the qualitative evaluations, particularly in light of the knowledge we gained about intraspecific variation and functional inter-connections. This was so in spite of the hundreds of measurements we took and the numerous indices we constructed. There are a number of fundamental reasons for this. We list a few:

– attributes chosen reflect our ecology- and adaptive model-based notions (see below) of what should be (and actually were) taxon-specific identifying features. We consider this approach objective in the full sense of that concept, as it is properly steeped in the fundamental theoretical considerations that led us to the discovery of what we regard as well-tested taxonomic properties;

– many of the fossils, most of which are quite small, displayed enough broken or abraded surfaces to make primary reliance on the measurements inappropriate, and scrutiny of the joint surfaces, proportions, and muscle attachments particularly important. In other words, informed judgement based on the nature of variation in the living species studied and the adaptive differences in the models used offered criteria that were constantly utilized when examining, describing, and measuring any of the critical areas of the specimens.

The most significant aspect of what we consider to be intraspecific variation in metatherian postcranials is best considered as "ontogenetic"

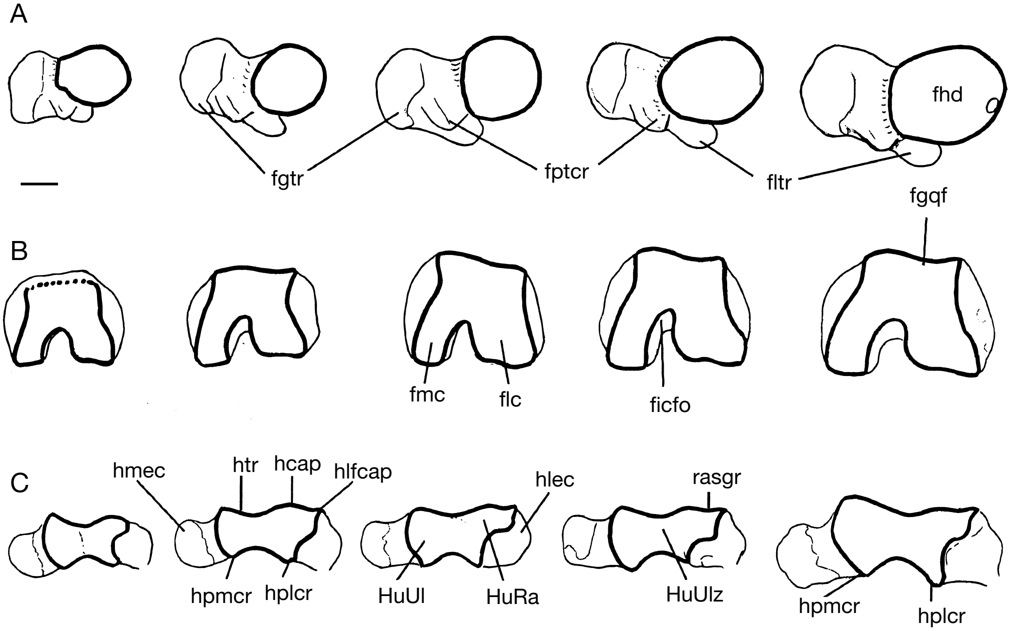


FIG. 3. — Juvenile to adult ontogenetic series, from left to right, of five left femora and humeri of *Didelphis virginiana*; **A**, proximal view of femora; **B**, distal view of femora; **C**, distal view of humeri. Abbreviations: **fgqf**, femoral groove for quadriceps femoris; **fgtr**, femoral greater trochanter; **fhd**, femoral head; **ficfo**, femoral intercondylar fossa; **flc**, femoral lateral condyle; **fltr**, femoral lesser trochanter; **fmc**, femoral medial condyle; **fptcr**, femoral paratrochanteric crest; **hcap**, humeral capitulum; **hlec**, humeral (lateral) ectepicondyle; **hlfcap**, humeral lateral flange of capitulum; **hpmcr**, humeral posteromedial crest; **hmec**, humeral (medial) entepicondyle; **hplcr**, humeral posterolateral crest; **htr**, humeral trochlea; **HuRa**, humeroradial facet; **HuUl**, humeroulnar facet; **HuUlz**, zonal humeroradial; **rasgr**, groove for radial sesamoid. Scale bar: 4 mm.

variation. These differences are in reality size-based assessments that nevertheless track post-neonate "ontogenetic" changes (life history attributes), as these animals steadily increase in size from self-sufficient juveniles to adults along a growth trajectory distinct from eutherians. What is significant in the brief descriptions below regarding the various bones of *D. virginiana* is how consistent a number of functionally significant, species-specific features are in this scansorial animal, one that is equally at home on the ground, as well as in the trees. The descriptions below also serve the purpose to initiate our focus on attributes that are discussed in detail when the accounts of the models and the fossils are presented, and when adaptational or phylogenetic assessments are tested.

The epiphysial plates (**eppl**) that remain discernable on marsupial long bones at all ages are shown with irregular outlines; they appear as patches at their customary locations on the proximal and distal ends of the bones.

Humerus (Figs 2; 3C)

Figs 2 and 3C depict selected aspects of a sample of five different sized specimens of *Didelphis virginiana* from the smallest to the largest. The proximal end (Fig. 2A-C), particularly the relative dimensions of the humeral head (**hhd**) is generally, but perhaps not very reliably, an indicator of the relative angular distances in habitual excursions of the forelimb on the shoulder. The head starts out in the juvenile as distinctly longer anteroposteriorly than wide mediolaterally, but becomes increasingly the widest at the anterior limit of the medial (lesser) and lateral (greater) tuberosities (**hmtub** and **hltub**). In addition, the head has a well-developed neck which allows the articular area to "hang back", the proximal end of the humerus giving the impression of a "beak" when viewed either medially or laterally (we will use the term "beaking" below as a relative indication of this overhang). The relatively much greater development of the lateral tuberosity leading distally into the deltoid crest is constant from the smallest juvenile to the largest adult specimen.

The distal end (Figs 2D, E; 3C) reflects the nature of ulnar movement on the humeral trochlea (**htr**) particularly well, as well as whether the joint is stabilized medially and laterally to a greater or lesser extent. In the juvenile condition the trochlea is relatively shorter mediolaterally than the rounded capitulum (**hcap**), although the basic conformation of these articular areas is consistent throughout the sample. In the subsequent larger and more mature conditions, the dimensions of these two articular surfaces are nearly equal in linear dimensions anteriorly. As skeletal maturity proceeds, the trochlea, particularly its weight bearing distal surface (Fig. 3C) significantly hypertrophies compared to the capitular dimensions that are relatively small distally. The curvature (concavity) between the humeral posteromedial crest (**hpmcr**) and humeral posterolateral crest (**hplcr**) on the posterior articular surface of the distal humerus is much more pronounced in adult specimens than in juveniles. In *Didelphis* the **hplcr**, in spite of the pronounced concavity on the posterior surface of ulnar articulation, does not extend past the articular surface, unlike in other taxa where it can border the olecranon fossa.

The relative robusticity of the humeral (lateral) ectepicondylar crest (**hlecr**), a proximal continuation of the ectepicondyle, appears to be ontogenetically controlled as it becomes more developed from the juvenile to adult conditions. In general, the morphology of the articular surface of the distal end shows no significant qualitative variation from the juvenile to adult conditions. The relatively well-developed humeral (medial) entepicondyle (**hmec**), the persistent humeral supracondyloid foramen (**hscf**), the humeral lateral flange of the capitulum (**hlfcap**) that articulates with a sesamoid in the elbow joint, and the humeroulnar zonal articulation in the zona conoidea (**HuUlz** and **hzcon**) are ubiquitous attributes of the didelphids, microbiotheriids, caenolestids, and most other metatherians. The pronounced groove for the radial sesamoid (**rasgr**) between the capitulum proper and the **hlfcap** is both a specific and an adaptively significant feature of mature specimens of *Didelphis* (not as well-developed in juveniles) that these appear to share with other terrestrial didelphids.

The following is a summary of the characteristic ranges of variation in the properties of the humerus of *D. virginiana*:

1) the head (**hhd**) is more circular than oblate in mature specimens, and there is a predominant development of the lateral tuberosity;

2) beaking of the head is pronounced, indicating an angular excursion of approximately 80°+;

3) the shaft is slightly bowed and not slender;

4) the relative size and conformation of the **hdps** appears to be similar in the sample. The pectoral crest extends distally about two thirds of the length of the humerus. The Humeral Deltopectoral Shelf Index (HDSI = length of **hdps**/length of humerus × 100) is consistent throughout our ontogenetic sample (see comments below on this index). HDSI ($n = 6$) is 58;

5) the relative size of the humeral medial epicondyle (**hmec**) is moderate; in powerful graspers like *D. virginiana* the area for large digital flexors is reflected by the relative size of this process;

6) the humeral (lateral) ectepicondylar crest (**hlecr**) is well-developed but is not retroflexed. It extends proximally about one third of the length of the humerus;

7) the trochlea is well-developed and extends proximally, and the capitulum is relatively small. The **HuUl** facet extends well proximally on the posterior side of the humerus. Ventrally the trochlea is very wedge-shaped, wide medially, and extremely narrowed towards the middle of the articular surface;

8) the humeral posterior lateral crest (**hplcr**) is moderately developed next to the deep **hofo**, aiding the stabilization of the elbow joint significantly;

9) groove (**rasgr**) for the radial sesamoid (**Ras**) is well-developed. It manifests itself in the lateral border of the articular area turned anteriorly; this is particularly clear when the bone is examined in distal view.

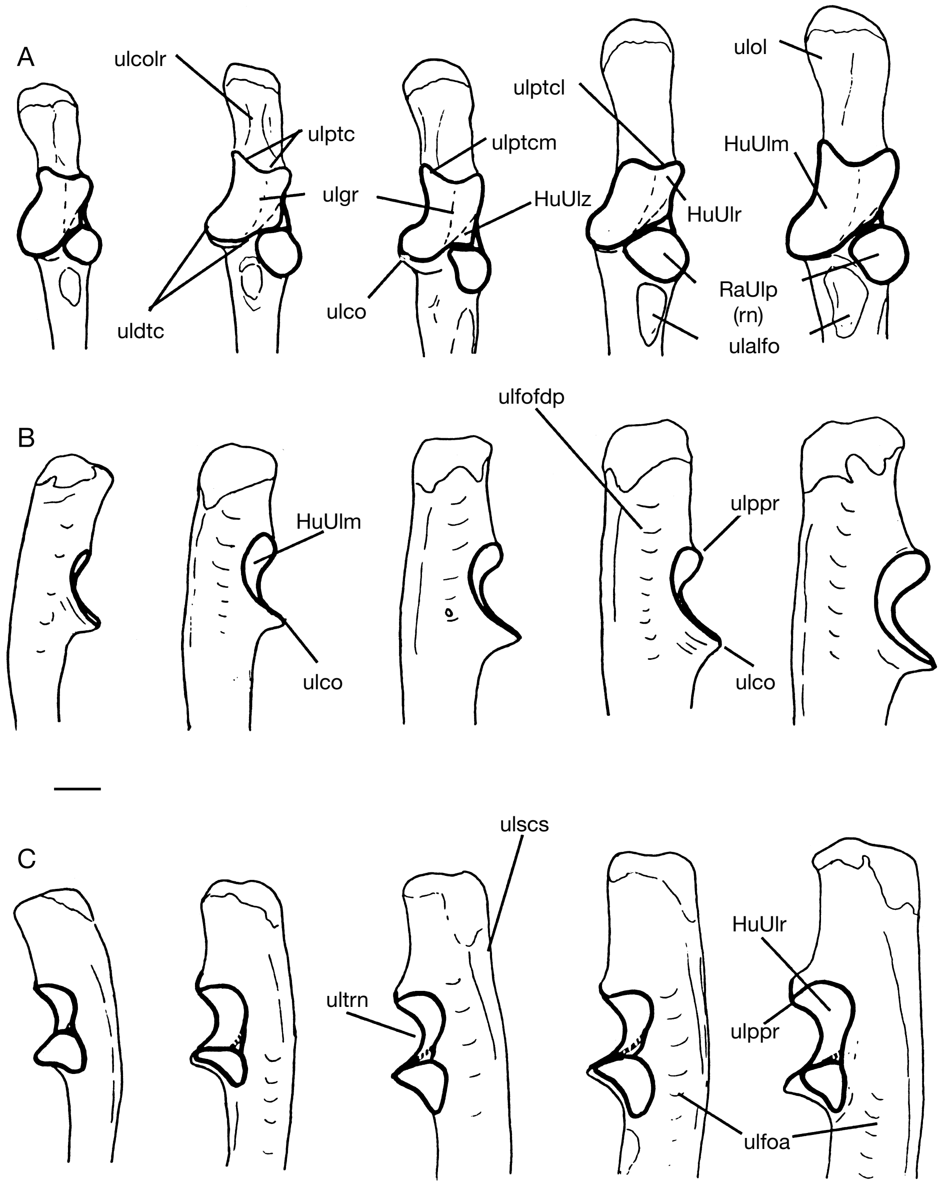


FIG. 4. — Juvenile to adult ontogenetic series, from left to right, of five left proximal ulnae of *Didelphis virginiana*; **A**, anterior view; **B**, medial view; **C**, lateral view. Abbreviations: **HuUlm**, medial humeroulnar; **HuUlr**, radial humeroulnar; **HuUlz**, zonal humeroradial; **RaUlp**, proximal radioulnar facet; **rn**, radial notch; **ulalfo**, ulnar annular ligamentous fossa; **ulco**, ulnar coronoid process; **ulcolr**, ulnar cranial olecranon ridge; **uldtc**, distal ulnar trochlear crest; **ulfoa**, ulnar fossa for anconeus; **ulfofdp**, ulnar fossa for flexor digitorum profundus; **ulgr**, ulnar guiding ridge; **ulol**, ulnar olecranon process; **ulppr**, ulnar proximal process; **ulptc**, ulnar proximal trochlear crest; **ulptcl**, ulnar lateral proximal trochlear crest; **ulptcm**, ulnar medial proximal trochlear crest; **ulscs**, ulnar subcutaneous surface; **ultrn**, ulnar trochlear notch. Scale bar: 4 mm.

Ulna (Fig. 4)

Most of the variation in the ulna of *D. virginiana* (Fig. 4), much of it obviously quantitative and continuous, is within the qualitatively set, species-specific limits we employ for the fossils, as in the humerus. The olecranon process (**ulol**) is consistently long from juvenile to adult in contrast to fully arboreal didelphids, and is in line with the part of the ulna immediately distal to the articular surfaces for the humerus and radius; namely, bowing is minimal compared to many other didelphids. While the olecranon process slightly and gradually increases in size as the animal gets larger (older), it remains relatively constant in its linear proportion in relation to the distance between the coronoid process (**ulco**) and the most proximal extent of the medial ulnar proximal trochlear crest (**ulptcm**) proximally, or the diagonal distance from the **ulco** to the lateral ulnar proximal trochlear crest (**ulptcl**). In *Didelphis*, the **ulptcm** and the **ulptcl** are approximately equal in size, and the **ulptcm** extends slightly more proximally than the **ulptcl**. The ulnar cranial olecranon ridge, located between the proximal end of the olecranon and the ulnar trochlear (semilunar) notch (**ultrn**), is oriented medially towards the **ulptcm**. This orientation is probably indicative of the direction of loading of the olecranon.

The point where the two proximal crests of the trochlear notch (**ultrn**) create an angle is a recognizable landmark on the ulna. This ulnar proximal process (**ulppr**) represents the centrally located proximal point of the ultrn opposite the coronoid process, the two points delimiting the "gape" of the **ultrn**. The relief from the **ulppr** to the **ulco** forms a ridge, the ulnar guiding ridge (**ulgr**). The latter is a raised area that is essentially the stabilizing wedge of the humeroulnar articulation. This ridge divides the humeroulnar articulation into radial and medial components (**HuUl** facets). Because of the characteristic medial twist of the (radial) **HuUlr** facet, the medial facet (**HuUlm**) is significantly larger than the **HuUlr** facet. A small sliver of the articular area between the humerus and ulna is consistently identifiable as the zonal articulation (**HuUlz**) when the two bones are brought into articular contact. The distal ulnar trochlear crest (**uldtc**) comes to a rounded point distolaterally on the ulco. The proximal radioulnar facet (**RaUlp**), the radial notch (**rn**), consistently faces more cranially than laterally, with no special peduncular support. The ulnar subcoronoid fossa (**ulalfo**) for the attachment of brachialis is well-developed. The **ultrn** is shallow in the juvenile, but deepens to a characteristically open condition where the **HuUlm** slopes about 45° from the horizontal (Fig. 4).

The following is a summary of the characteristic ranges of variation in the properties of the ulna of *D. virginiana*:

1) in the older, compared to an earlier juvenile stage, when the bone is well-ossified the **ulol** is consistently longer in length than the gape of the **ultrn**. The **ulol** is of nearly equal width along its length with a well-developed shelf radially, the **ulscs**. The **ulcolr** runs from the proximal tip towards the medial side of the proximal crest;

2) the **ultrn** is deep with an Ulnar Trochlear Notch Index (UTNI = chord of depth/length of opening × 100) of 32 (n = 6). The coronoid process (**ulco**) projects well forward and medially;

3) medial and lateral wings of the proximal trochlear crest of the ulna (**ulptc**) are approximately subequal;

4) bowing of the ulna is minimal, particularly in light of the slight retroflexion of the olecranon process;

5) the radial notch faces more cranially than laterally, and the **RaUlp** facet extends onto the radial edge of the protruding **ulco**;

6) on the proximal medial ulnar surface the fossa for the flexor digitorum profundus (**ulfofdp**) is moderate to shallow. The fossa on the radial side for the insertion of the anconeus (**ulfoa**) is also shallow;

7) ulnar styloid process is deep, rather than wide and well-rounded, with **UlCn** facet facing medially.

Carpus

Intraspecific variation in different aged individuals of *D. virginiana* is reflected in the extent to which fusion of the centrale with the scaphoid has occurred, although a fully unitary scaphocentrale is the fixed adult condition in didelphids and all other living marsupials.

Femur

As in the long bones of the pectoral girdle described above, the juvenile condition is somewhat different

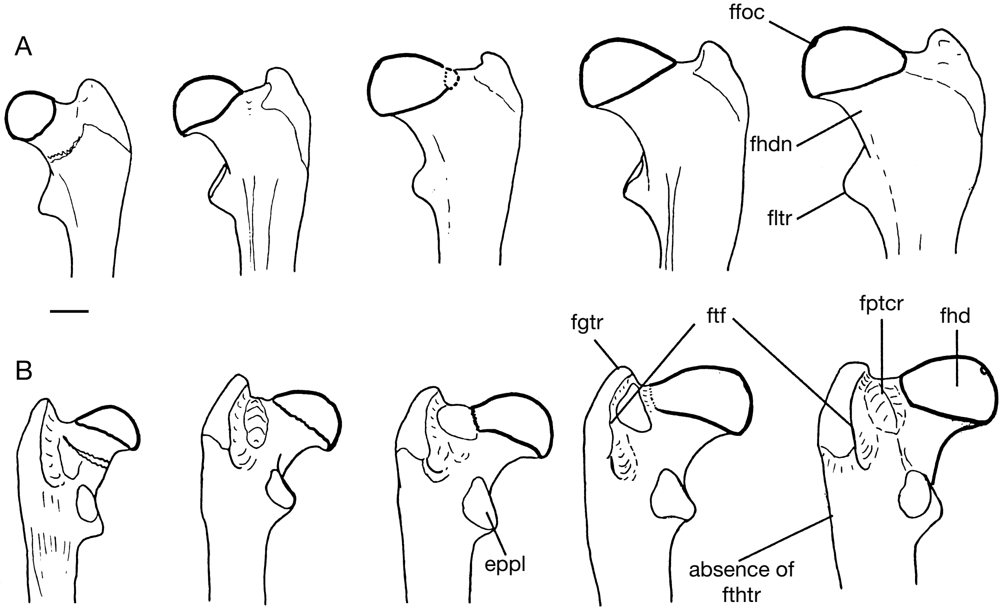


FIG. 5. — Juvenile to adult ontogenetic series, from left to right, of left proximal femora of *Didelphis virginiana*; **A**, anterior view; **B**, posterior view. Abbreviations: **eppl**, epiphyseal plate; **ffoc**, femoral fovea capitis (for ligamentum teres); **fgtr**, femoral greater trochanter; **fhd**, femoral head; **fhdn**, neck of femoral head; **fltr**, femoral lesser trochanter; **fptcr**, femoral paratrochanteric crest; **ftf**, femoral trochanteric fossa; **fthtr**, femoral third trochanter. Scale bar: 4 mm.

in shape and outline compared to more mature specimens (Figs 3A, B; 5).

Due to the less complete development of the articular surface of the femoral head (**fhd**), the mediolateral elongation that results in a considerable medial and distal extension of the articular area occurs only in larger, more mature, specimens. The femoral head extends well past the medial limit of the diagnostically small lesser trochanter (**fltr**). The greater trochanter (**fgtr**) is slightly taller in the juvenile conditions than in the fully grown adults; in the former it is slightly above the head, while in the latter it is lower or at the same level as the head. *Didelphis*, like all living marsupials except for caenolestids, has no third trochanter (**fthtr**), a point of some significance discussed below. The femoral trochanteric fossa (**ftf**) is well-developed, and the femoral paratrochanteric crest (**fptcr**), the area of attachment for the ischiofemoral ligament, is present in most specimens. However, it is best developed in older individuals.

The distal femur (Fig. 3B) is typically metatherian in having unequal-sized condyles (a condition that is probably primitive for the Theria, *sensu stricto*), and it probably closely reflects the locomotor repertoire of the ancestral metatherians. Yet the relative dimensions of the distal femur are highly species-specific in the Didelphidae, as proportions and conformation of the condyles closely reflect the nature of motions possible between the thigh and the crus, as well as the nature of loading in the knee joint and the femur itself. This area is a sensitive tracker of adaptively critical locomotor attributes and substrate preference. It is also one of those characters that is useful for adaptive assessment among metatherians, but is without any meaningful phylogenetic significance by itself[16].

There is no patella in the knee joint (except a small ossification in some older individuals; see below), although the tendon of the quadriceps femoris is guided in a shallow groove distally (**fgqf**) and the bone on the distal epiphysis has a somewhat similar surface to that of patellate eutherians and caenolestids. In the more mature specimens, the medial side of the distal femur is higher than the lateral one, and, in general, the distal anteroposterior dimensions of the medial side are greater than that of the lateral side, as in other metatherians.

The medial condyle, from juveniles to adults, is consistently quite narrow, while the lateral one is not only much wider, but it is concave on its posterior surface. This minor but significant feature indicates the habitual and stabilized articulation of the posterior side of the condyle with the convex lateral condyle of the tibia. This stability-related feature in the metatherian knee attests to the highly flexed position of the lower leg on the femur when the latter is in its habitually flexed position during locomotion (see discussion below). On the distolateral side of the femur there is the femorofibular articular facet (**FeFi**). On the proximal and lateral surface of the lateral condyle a distinct triangular shaped facet is the femoroparafibular articulation (**FePf**; for general characteristics of the didelphid knee see Fig. 20).

The following is a summary of characteristic ranges of variation in the properties of the femur of *D. virginiana*:

1) beaking, or medial projection of the head, is highly developed, and the articular facet extends laterally and distally on an epiphysis that has its distal edge cranially close to horizontal. Extremes of abduction and hindfoot reversal require such articular contacts;

2) relative height of the greater trochanter is somewhat variable, but in several individuals it extends above the level of the head, representing a terrestrial feature in didelphids;

3) lesser trochanter is very small and it is retroflexed (as in terrestrial forms);

4) femoral paratrochanteric crest (**fptcr**) on the posterior side is very prominent and robust in larger and older individuals; it is part of the medioproximal epiphysis of the femur;

5) there is a complete absence of the third trochanter, as in all other didelphids and australidelphians;

6) no particular shaft characters can be discerned except for the small but distinct spinous rugosity (often double within a depression) for the tendon of what may be the equivalent of the human adductor magnus (see also Coues 1869). Femoral Midshaft Diameter Index (FMDI = anteroposterior midshaft length/mediolateral midshaft length × 100) is 83 (n = 4) with a range of 67-91;

7) there is only a slight sulcus proximal to the distal epiphysis for the tendon of the quadriceps femoris. In older individuals there is occasionally an elongated and small sesamoid ossification within the tendon of the quadriceps femoris where it crosses the knee joint when the crus is flexed;

8) Femoral Distal Height Index (FDHI = medial condyle depth/distal end width × 100) is 72 (n = 4), with a range of 69-79, and the Femoral Condyle Width Index (FCWI = medial condyle width/lateral condyle width × 100) is 59 (n = 4), with a range of 55-61.

Tibia and fibula

The tibia, and to some extent the fibula, are the last of the long bones of *Didelphis* studied for variation that has representation in the Itaboraí collection. These bones show some characteristic didelphid taxonomic properties compared to those of the Palaeocene specimens and of the caenolestids, as we discuss below.

The shaft of didelphid tibiae displays the characteristic lateral bowing, a sigmoid curvature in the mid-shaft. Accounting for this phenomenon is difficult (but see discussion below). The bone is mediolaterally compressed along the entire shaft and it is convex laterally, a condition that appears pathological, at first, to those unfamiliar with metatherian osteology. The proximal surface of the tibia displays an extensive insertion surface for the tendon of the quadriceps femoris (**tqfcr**) in all three of the growth stages illustrated (Fig. 6A-C). The torque generated by that muscle, given its more distant (anteriorly-placed) position from the knee articulation, appears to be relatively greater than that in similar sized eutherians. But all placentals have patellae which alter the mechanics of the knee. The medial and lateral

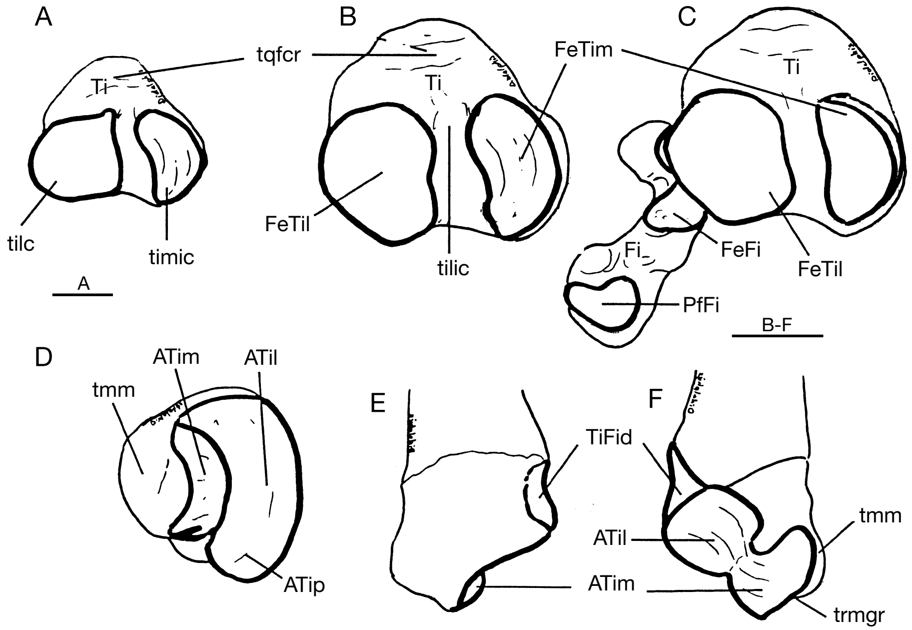


FIG. 6. — Details of juvenile and adult left tibiae and fibula of *Didelphis virginiana*; **A**, proximal view of juvenile tibia; **B**, proximal view of adult tibia; **C**, proximal view of adult tibia and fibula; **D**, distal view of adult tibia showing astragalar articulation; **E**, posterior view of specimen shown in D; **F**, anterior view of specimen shown in E. Abbreviations: **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **ATip**, posterior astragalotibial facet; **FeFi**, femorofibular facet; **FeTil**, lateral femorotibial facet; **FeTim**, medial femorotibial facet; **Fi**, fibula; **PfFi**, parafibulofibular facet; **Ti**, tibia; **TiFid**, distal tibiofibular facet; **tilc**, tibial lateral condyle; **tilic**, tibial lateral intercondylar tubercle; **timic**, tibial medial condyle; **tmm**, tibial medial malleolus; **tqfcr**, tibial crest for quadratus femoris; **trmgr**, tibial retromalleolar groove. Scale bars: 4 mm.

tibial articular surfaces (**FeTim** and **FeTil**) reflect the morphology described for the articular surface of the distal femur. Although menisci moderate and accommodate the loads in the knee joint as in all known therians, the medial tibial condyle is concave and the lateral one is both convex and much wider than the medial one.

The peculiar sigmoid curvature of the didelphid tibia with its medial concavity is a primitive therian or pretherian feature, not unique to the didelphids. This shape also characterizes the known microbiotheriids and the caenolestids, although the condition of the latter is complicated by the fact that the distal two-thirds of the crus is fused. The curvature can be clearly detected on *Henkelotherium* Krebs, 1991 as well, a Jurassic eupantothere (Krebs 1991: fig. 10, pl. 3; Szalay pers. obs.). As we discuss it the sections on models and phylogeny, this phenomenon, in spite of its taxon-specific and therefore variable aspect, is not likely to be reliably indicative of functional attributes that can be tied to ecological conditions, particularly substrate preference or locomotor mode. Its phylogenetic significance is equally moot as it can be absent in some Palaeocene metatherians like *Pucadelphys* Marshall & Muizon, 1988 while present in others like *Mayulestes* Muizon, 1994 (see Muizon 1998).

The wide, fan-shaped, and laterally concave proximal surface of the fibula articulates laterally with the underside of the proximal tibia and the femur, as well as with the parafibula (as noted above). The parafibula articulates with the fibula on the proximolateral surface of the latter (Fig. 6C).

The distal tibia of *Didelphis* consistently has the highly characteristic wide didelphid articular contact with the astragalus (a derived condition compared to other ameridelphians), via an elongate and crescent shaped lateral astragalotibial contact (**ATil**; one that has a posterior astragalotibial extension, **ATip**; Fig. 6D, F; for a discussion of this area see Szalay 1994). Offset from the **ATil** at an angle on the inside of the tibial medial malleolus (**tmm**) is the medial astragalotibial facet (**ATim**), which is anteroposteriorly less extensive than the lateral articulation.

The medial malleolus itself is angular, as the medial and proximal borders of the upper ankle joint articulations form a right angle, and the distal tibial tibiofibular articulation (**TiFid**) is concave laterally. These aspects of didelphid tibiae are highly adaptive. Yet they are also phylogenetically significant in a manner that is complementary to their functional aspect. These distinctions are discussed below.

Tarsus

Szalay (1994) briefly discussed intraspecific variation in astragali and calcanea of *Philander*, and these bones are reliable indicators of specific (perhaps more often generic) differences. Aspects of didelphid tarsal attributes are treated below in the context of the phylogenetic discussion of the Itaboraí phena.

EXTANT SPECIES AS MODELS FOR ADAPTATIONAL AND PHYLOGENETIC ANALYSIS

MODELING IN SYSTEMATIC BIOLOGY

Modeling is a scientific endeavor with many differences in various disciplines. In general, models tend to be constructs that aim to represent some aspects of reality in order to analyze various manifestations of that reality more effectively. In a variety of disciplines in natural history, such as ecology, paleobiology, or the designations in sundry models of evolutionary change from population genetics to specific character transformations, the concept of a model is used rather loosely. Nevertheless it is usually clear in individual contributions what is meant by it. Often it may be a mathematical construct, a particular null hypothesis, with which real empirical observations are contrasted or examined as to the degree of their conformity to a set of hypothesized conditions. In that sense the concept is close to the notion of a hypothesis, the framework within which certain researches are undertaken.

Modeling in systematics plays an important role in not only delimiting extant models for alpha taxonomy for fossil species taxa, but also for biomechanical analyses of all sorts. These model construction activities, when properly applied, are central to a whole host of specifically paleobiological researches. Modeling is critical, we believe, in setting the framework for an understanding of different kinds of properties of organisms. Modeling based on living species and their attributes, as a fundamental method, allows the recognition and usage of adaptively significant attributes. Consequently, it enables one to identify the more ancient, less species-specific and more channeling attributes that are useful for phylogenetic analysis.

Such method-driven analysis allowed us to make model-based judgements about homologous attributes in different groups. This activity is the essence of character analysis beyond an obligatory distribution analysis for all systematic undertakings. It allows one to distinguish homologous from homoplasious aspects of the features examined at the designated levels of comparisons. We emphasize that this is character, and not taxic, analysis [17].

In this study we aim to connect the patterns, and their highly corroborated causal assessment from ecological morphology, of a variety of chosen extant species with the facts we ascertain from the fossils, into a cohesive explanatory framework. The matching of morphological similarities between homologous bones in itself is not a particularly challenging activity, as recognition of similar landmarks on bones is a relatively pedestrian exercise. Homologies of the synapsid and mammalian bones and their general attributes extend back to deep time to the point that we easily identify most such equivalents back to the Triassic. What we intend to do beyond the mere conceptual connection of landmarks, however, is a theoretically meaningful appraisal of the specific modifications of these landmarks (subtle similarities and differences) that denote mechanical and adaptive solutions. In using the modeling approach we describe, one that is compliant with the basic axioms of adaptive descent with the subsequent constrained (and facilitating) modification, we aim to employ a valid methodology with which to place character analysis on some theoretically consistent foundations in contradistinction to practices we discuss below.

Use of living organisms as surrogates for interpreting aspects of extinct entities is obviously complicated by the fact that all lineages are unique because of their phylogenetic history. There are no "exact match" models. Nevertheless, as in the case of all other surrogates used in modeling, there are some basic biomechanical generalities, such as the loading of a given area of the skeleton that correlate strongly with some basic activities in extant forms that may be used with high probability for the interpretation of fossils [18].

However, it should be noted that using either reasonably well studied living whole organisms as surrogates for interpreting fossil organisms, or using specified parts of these extant forms and their relationships to the total environment, is somewhat different in its specifics from other types of model construction and use. There is a critical difference in the reliability of interpretation that resides in the manner of how living models are used to evaluate fossil taxa. This reliability is in the degree to which attributes of living species are, or are not, consistently evaluated regarding the interaction of their taxon-specific form, mechanics, and ecological context. As examples for this widely used methodology in palaeontology, there is the: a) functional relationship between specifically shaped teeth and jaw mechanics, and the frequency and consistency of specific food resources; or b) correlation of postcranial features and their mechanical correlates with any mode of specific activity such as a substrate preference or a type of locomotion. It is important to repeat that such comparisons go far beyond a mechanical modeling of forces and loads (i.e. function in a narrow sense), as such "causal role function" is advocated by Amundson & Lauder (1994). Different organisms perform their survival-related tasks differently because of taxon-specific constraints, with a consequence of generating selectional forces of their own making in that process. (Lineages, circumstances permitting, may also track their most recent habitus environments, slowing down change).

Our primary interest in using a model-driven approach to conduct our comparative analysis was simply to increase our understanding of the selectionally causal, as well as historical (i.e. constrained), meaning of metatherian osteology. Coupled to this is the aim to understand the fossil taxa as fully as we could, given availability of the record and material limitations. In employing (either implicitly or explicitly) a model-based methodology to interpret aspects of extinct organisms there are at least two ways to proceed. One may simply pick living analogs to find a similarity-match of some sort for fossil morphology without giving functionally, and therefore causally, meaningful reasons for suggesting that the matching morphologies do indicate not only strictly functional but also adaptive (ecological) similarities between the model and the fossil. This can supply some meaning for paleobiological assessment if a whole skeleton is available for the fossil. Without complete specimens, however, the modularity-based and well-corroborated patterns of mosaic evolution (note discussion below) render such assessments problematic for individual elements.

Such general similarity evaluation is a fairly common procedure, one that, unfortunately, can be confounded by the same problems that parsimony analysis of indiscriminate "synapomorphous" attributes poses. It lacks the necessary character analysis that aims to test the nature of similarities before these are used either for paleobiological assessment or phylogenetics. It is well to consider that the degree of confidence (probability) that may be attached to adaptive assessment of fossil taxa using the most appropriate comparisons is not qualitatively different from that in the estimation of phylogeny (i.e. phylogenetic analysis).

Both phylogenetic estimates and adaptive assessments can be more or less convincing depending on the completeness of material, level of inquiry, and the nature of understanding of the character complexes themselves.

In our view a far more desirable, albeit more difficult, procedure is the construction of mechanically and adaptively meaningful relationships in character complexes in a number of not particularly closely related species that display attributes which are more likely convergent than homologous (see Szalay 1981). We may call this the "modular-function" approach. It is important to have some strong ecologically compelling evidence that certain recurrent attributes, given a similar level of basic mechanical organization of the skeletal biology, are under strong selectional imperatives for their recurrent developments. An understanding of functional-adaptive significance (and consequently the probability of convergence *vs* homology of properties) is decisive in establishing a list of tested taxonomic properties (e.g., Argot 2001). This approach has both an inductive component in using the recurrent correlations between morphology and mechanics and the ecological context, as well as a deductive one in applying the correlations to the fossil taxa [19].

All models for use in paleobiological assessment will be necessarily limited in scope. The initial and boundary conditions of any lineage, the ancestral strategy of a group, will necessarily channel what mechanically and adaptively may be a significant change in the descendant lineages. In fact, even most allometric conclusions regarding morphology should be couched both in phylogenetic as well as behavioral contexts, as Biewener's (1989, 1992) studies have emphatically demonstrated. Similarly, even highly and validly corroborated phylogenetic relatedness alone does not solve problems of causality regarding adaptations, although this is often mistakenly implied [20].

Unlike others (e.g., Coddington 1988), we do not question the fact that primitive features are just as adaptive as derived ones. Four chambered hearts still continue to render the same service as the original models. But such hearts are unlikely to help with the prediction of differences in habitus between camels and hippos, for instance. However, uncovering consistently convergent derived features in the skeleton of mammals that have strong functional associations with either feeding or positional strategies, does supply us with powerfully modeled "postdictors" for adaptations in the fossil record.

The use of habitus-related derived modifications of a character complex (and these are usually few at any moment in a lineage) as more reliable predictors of biological roles for fossils than the heritage traits may be, has been suggested by Szalay (1981) [21]. If the probability is high that one or more aspects of properties in two or more taxa examined are the result of phyletically independent adaptive responses rather than ancestral constraints, then such convergent attributes should not be considered taxonomic properties. These characters, however, become excellent indicators of ecologically meaningful aspects of the fossils under study. Once the initial and boundary conditions (both phyletic and adaptive) are established for extant model species, and the fossils can be placed in a particular ecologically meaningful framework, then further analysis of attributes of these fossil taxa becomes properly constrained for phylogenetically useful character analysis.

Darwinian phylogenetic analysis is predicated on the closely interwoven practice of adaptive- and contingency-based evaluation of properties of organisms, an activity theoretically and operationally primary to the estimation of lineage and taxon phylogeny or taxic analysis (Bock 1981, 1991; Szalay & Bock 1991; Szalay 1994; Szalay & Lucas 1996; Szalay & Schrenk 1998). It follows, therefore, that a function and selection oriented analysis of morphological properties is an essential component of that analytical framework. While the degree of adaptive assessment that can be realized for extant species is obviously often not attainable for poorly known fossil taxa, we believe that it has great value nevertheless. This is true not only for the sake of the attempted ecological understanding, but also for establishing the context for a (tested) approximation of what are likely to be homoplasious aspects of characters.

Models are particularly significant as they represent results of surrogate evolutionary processes for a particular set of adaptive transformations. Such tested models, like all models, can never be a complete match for the organisms, or their aspects, that are subjected to analysis. Nevertheless, when size is controlled for, and functional (mechanical) attributes are correlated with some well understood adaptations in the living models, many behaviors can be inferred for those fossils that share these features (see Cifelli & Villarroel 1997 for a detailed example for the interpretation of a fossil mammal). Such procedures provide a corroborated (to varying degrees) level of character explanation, both functional (nomological in essence) and evolutionary (historical). We believe this to be the case in our use of selected osteological attributes of the four living models (boosted by numerous other examples examined here in less detail) for an understanding of the Early Tertiary metatherians we describe.

Modeling relies heavily on theoretical perspectives, as well as the experiences of the modelers with the subjects that they are focused on. In our efforts to use the specific living models to better understand a series of archaic species we freely eliminated details that were not relevant to our fundamental interests. We focused on two extremes of locomotor behavior found in a forest habitat that characterized Itaboraí (Bergqvist 1996; and references therein).

In our initial effort to establish with some certainty general features of our models for either mostly (obligate) arboreal or terrestrial locomotion we knowingly (and probably also inadvertently) ignored details that are clearly part of a more refined future understanding of these model species. Our goal was to ascertain those attributes that yielded relatively invariant (hence highly reliable) correlations between the bony morphology and its mechanics and the positional behavior (related to ecology) of our model species. We had to choose those attributes (and ignore some others in the process) that gave us the appropriate constellation for trying to establish for the fossil elements (and for the taxa they represent) where they fit in the continuum between the extremes of the models regarding substrate preferences. In fact, so little is known of the extant model species regarding the frequency and range of their positional behaviors, the specific details of certain habitats, etc., that it would be difficult to gain additional insights into their still poorly studied variation and morphological details. This is true for almost all extant American species of marsupials. Nevertheless, we are confident that the shared attributes culled from our models are valid yardsticks for our evaluations of the fossils. Furthermore, we are confident that in the future such modeling, of both narrower and wider perspectives on a variety of mammals, will yield meaningful taxonomic properties of both extant and fossil taxa, and subsequently produce evolutionary histories (phylogenies) that are robustly tested morphologically.

Finally, we would like to note that the models we used and tested (as those by Argot 2001) have been amply validated. Specifically, those morphological attributes that we (and Argot) chose because they correlate, among the living forms, with mechanical and adaptive solutions, appear to hold true for living metatherians even across highly significant body size differences. Our conclusion that the modeled traits have been well-chosen for the task we intended them for is supported by: a) qualitative assessments of osteology and its mechanical consequences; b) the comparative biometric analysis of specific indices based on measurements that reflect these attributes; and c) some additional and independent evolutionary explanations concerning eutherian mammals. These attributes, therefore, are “predictors” (“postdictors”) with a high degree of probability, ones which allow an unusually high degree of modular reliability for the limits of assessment we sought for the fossil taxa.

MODELS FOR THE ASSESSMENT OF HERITAGE AND HABITUS OF FOSSIL MARSUPIALS

Our aim in this study was to obtain some objective standards that reflected functionally understood, and adaptively correlated, attributes in living marsupials that could be applied with some confidence to the fossils. While pursuing our qualitative and quantitative examinations of the living and fossil samples, a number of attributes that did not reflect adaptive imperatives in the living forms became obvious. These attributes on the femora and tibiae, for example, have consequences for the ongoing arguments about the phylogeny and biogeographic history of living and fossil marsupials. We pursue this topic in detail below.

In selecting our models for this study we were faced with the realities of current knowledge about the positional behavior and habitat preferences of relevant living species, and the subsequent difficult choices. Postcranial analyses of living marsupial species are very few, and field-based knowledge of the animals are rare. Given the species that are reasonably well studied in the field, we had to choose models that well-reflected unambiguous and well-corroborated poles of locomotor strategies, such as being either fully arboreal or terrestrial (see also Argot 2001). We are fully aware that such designations are never totally accurate. Given the species where our correlations of habit and substrate (and habitat) with morphology stand a very good chance to be a reflection of causes that originate from habitual postures and attendant mechanics, we are also aware that many species between the "extremes" represent complex mosaics of habitat preference and behavioral strategy. Nevertheless, with fossils that are not complete skeletons but merely individual bony elements, we had to rely on the unequivocal models. This allowed us to judge the extremes, as well as appreciate, in light of our models, the equivocal character combinations found in many of the fossil specimens. So choices had to be made in selecting certain species that we could conduct pilot studies on for the purposes of giving a context to the description and analysis of the fossils.

Two didelphid species were selected because they are unequivocally either primarily arboreal or terrestrial in their locomotor habits, and they are similar in size. *Caluromys derbianus* (Waterhouse, 1841) and *Metachirus nudicaudatus* (Desmarest, 1817) met these criteria (Atramentowicz 1982, 1988; Charles-Dominique *et al.* 1981; Streilein 1982; Charles-Dominique 1983; Grand 1983; Leite *et al.* 1996). Another consideration was the effect of size on aspects of bone morphology. Reports on body size ranges vary to an extreme in the literature. What remains from an assessment of both published and visually examined skeletal remains is that: a) *Didelphis virginiana* is the largest species we studied; b) *Caluromys* and *Metachirus* were smaller and close to subequal in size; and c) *Dromiciops*, *Rhyncholestes*, *Monodelphis*, and *Marmosa elegans* were in the smallest size range of the American marsupials. While *Didelphis virginiana* has a reported average around 2.5 kg, adult *C. derbianus* is said to weigh between 245-370 g, whereas adult *M. nudicaudatus* is reported to be between 300-480 g. We have also studied the small didelphids *Marmosa* (*Thylamys*) *elegans* (20-50 g) and *Monodelphis domestica* (60-150 g) [22].

Two other American families of marsupials in addition to the Didelphidae, the Microbiotheriidae and Caenolestidae, have also played a large role in our modeling effort. Not only were both of these in the low size range for marsupials that represented different substrate related adaptations, but they were also available in large numbers of superbly prepared osteological specimens. These taxa had the additional advantage to have figured largely in the various debates of metatherian phylogeny over the past decades. So the examination of *Dromiciops gliroides* (approximately 22 g; n = 78) and the similarly sized *Rhyncholestes raphanurus* (approximately 28 g; n = 48) were obligatory for phylogenetic reasons, and they also represented two distinctive adaptive types. The former is arboreal and the latter terrestrial, and both are of approximately the same body mass. We have also examined a relatively large number of additional didelphids, dasyurids, peramelids, a constellation of small and large phalangeriforms, and the postcranially representative basal kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876, although we have few occasions to specifically refer to these here in our model oriented interspecific comparisons [23].

Forelimb morphology and function

The cineradiographic studies of Jenkins (1971), and Jenkins & Weijs (1979), the latter using cineradiography coupled with electromyography, have provided descriptions and figures of forelimb movements on level ground by *D. virginiana*. In addition to these experimental studies, Jenkins (1973) has also proposed a suite of functional explanations for the major patterns that occur in the synapsids and mammals, with a general scheme on the probable routes of transformations of the elbow joint in a number of selected types and specific taxa.

The beginnings of what may be considered as the primitive condition of the therian elbow joint involves changes from one that Jenkins (1973) called the condylar type of articulation. In that antecedent stage (and not an evolutionary grade that has been independently attained by several lineages), the distal and medial articular surface on the humerus is condylar (with a helical component) and articulates with an ulnar depression medial to a ridge that does not as yet resemble the trochlear notch of either metatherians or eutherians. Judged from the shared attributes of all unequivocal therians (the tribosphenic stem and descendants), the humerus of the therian stem lineage had a trochlea-like medial condyle that still retained a helical component. The capitulum was laterally restricted. In this transformation sequence to the ancestor of Metatheria and Eutheria, the differentiation of the lateral and medial halves of the ulnar articulations greatly stabilized the elbow joint, given the particular pattern of locomotion. This is probably sufficiently well-modeled by the limb movements seen in *Didelphis*. We suspect that the changing loads from both the medial and lateral sides, as the humerus and the forearm were both abducted and then adducted, were driving this particular transformation that resulted in the development of the medial side of the trochlear notch on the ulna in therians.

The so called "zona conoidea" (unlike in extant, and at least in Cenozoic, fossil eutherians) primitively articulated with the ulna in the stem therians, and in living metatherians it is still an area of humeroulnar contact (Szalay & Trofimov 1996). This is in contrast to that noted for the eutherian condition, where the medially extended radial head has come to articulate with the "notch" between (what has been generally perceived by students of eutherians as the extension of) the capitulum on one hand, and the trochlea on the other. It is likely that this change came about as a particular adaptive trait in the (or a particular, later) eutherian stem, whereby reduced radial angular excursion (and a restricted range of pronation-supination) was tied to terrestrial habitus. While the reacquisition of a round radial head and a consequently enhanced mobility of the forearm and manus occurred in the stem, and retained in most but not all descendant, of Archonta, or in particular lineages of arboreal Carnivora, for example, the eutherian or placentalian zonal articulation was retained.

The single most important message of Jenkin's (1971) experimental analysis of locomotion was that early therian as well as stem metatherian and eutherian lineages did not have the "classical mammalian" parasagittal posture and locomotion (of eutherian cursors). Such a condition was previously often assumed (particularly in textbooks) to be part of the stem therian, or at least eutherian, complex. His study demonstrated that considerable excursion of the upper limb and the antebrachium occurred at different stages of the locomotor cycle, and that the same was also true, in a hindlimb-specific manner, for the femur and the crus as well.

There is a discrepancy in the depiction of the angle of the antebrachium compared to the humerus between Jenkins (1971: fig. 1c) and Jenkins & Weijs (1979: fig. 5c). In the latter, the lower arm is more in line with the humerus (i.e. more extended) than in the former at the end of the stride during push-off, the difference in the two figures being about 35°-40°. In general, the figure in Jenkins (1971) shows substantially greater adduction of the upper arm during locomotion than that depicted by Jenkins & Weijs (1979). The figures in the 1971 paper also show a less forwardly extended phase I in the stride than the 1979 rendition where the humerus is shown at about 80° from the horizontal (a near vertical position), and the manus and antebrachium are well forward at the beginning of the stride. (The 1979 drawings of the lateral view are strongly substantiated by an excellent series of cineradiographic images in plate 1 of that paper.)

The description and illustrations both from above and lateral to the positions of the elements of the pectoral girdle, in what Jenkins (1971) named phases I-IV during walking, give an excellent idea of the range of movements, at least in terrestrial locomotion, of *D. virginiana*. Phase IV represents the recovery phase when the limbs are drawn up and move forward after the push-off (phase III). Jenkins & Weijs (1979: 391) defined the stride as "[…] a single, complete cycle of forelimb movement, and includes a propulsive phase [foot in contact with the substrate] and a swing phase [foot not in contact with the substrate]". The stride is the distance between two successive footfalls of the same limb (see also Pridmore 1994).

One of the more interesting aspects of the cineradiographic studies of terrestrial walking in *Didelphis* for our study is the recorded angles of articulating long bones that are in contact during the stride. During the first contact of the manus with the substrate, the articular contact between the proximally elevated humerus and the elevated but dorsocaudally oriented scapula is roughly on the proximal surface of the humeral head (phase I). Halfway between the initial contact and the push-off (i.e. phase II), the elbow becomes slightly abducted from its previous position while the manus is under the body. At the point of push-off (phase III) the scapula is lowered and becomes vertical, and the humerus, now adducted and inclined past the horizontal with its distal end well above the proximal one, contacts the scapula with its dorsocaudal surface, what we have called the "beak" (in fact it is here that the scapula and humerus "lock" and the joint becomes most stable). During the recovery phase (phase IV) both the humerus and antebrachium are abducted, the latter flexed to the extreme on the former before the manus makes contact again, while the scapula comes to lean caudally again. While the flexion (angular excursion) of the humerus on the scapula is considerable (as ascertained by Jenkins & Weijs 1979; from an initial angle of 120° at the most cranial extent of the hand to about 70° at push-off), the movement of the forearm on the humerus (like the movement of the scapula) is quite restricted during the stride. While flexion on the humerus is limited during the stride, it is mostly in the recovery phase (swing phase of Jenkins & Weijs) that the forelimb is drawn up against the upper limb. As Jenkins & Weijs (1979: 401) note: "Thus, the entire forelimb [including the scapula] can be regarded as an extensible strut or lever, and the principal action of muscles crossing the shoulder and elbow joints appears to be that of stabilization". They add that "[…] the body appears to be accelerated forward relative to the intrinsically stabilized scapula and forelimb principally by the actions of the pectoralis and posterior part of the latissimus. The vertebral border of the scapula acts as a fulcrum for the lever-like limb, and is stabilized by the rhomboid, anterior trapezius, and serratus ventralis".

At least in *D. virginiana*, as reported by Jenkins (1971) and Jenkins & Weijs (1979), the forelimb does not seem to be extended past the long axis of the humerus more than 90° during the stride. Given a) the correlation of these parameters with the known scansorial habits of the relatively slow moving *D. virginiana*; b) the differences and similarities in these joint contact relationships in the models used and studied below; and c) the fossils described, these parameters represent significant empirical cornerstones regarding the positional behaviors of the fossil species. Consequently, there is a robust functional context within which the features of the fossils may be evaluated.

Hindlimb morphology and function

Unlike the detailed study by Jenkins & Weijs (1979) of the electromyography of the forelimb coupled with cineradiography, the patterns of hindlimb positions and bone relationships are known only from the cineradiographic study of Jenkins (1971). This study has the advantage of a comparative perspective that provides data on monotremes and eutherians as well.

The position of the head of the femur, when viewed laterally during the stride, varies from about 10° below the knee at the horizontal during phase I, to about 30° above the knee during the horizontal in phase III. The 20° difference between the extended positions of the crus on the femur (at about 80° at phase I to a flexion of about 60° when it reaches phase III) is small compared to the range of femoral extension on the ilium (during the same time) from a position of about 30° when the thigh is drawn up to the body to 90° when push-off occurs. During the recovery or swing phase (phase IV) the crus is further flexed on the femur, as the femur is flexed on the ilium.

The movements within the hindlimb from the dorsal view are particularly interesting, inasmuch as the angular distance of the femur from the ilium goes from 30° at phase I (while flexed on the hip) to be abducted (while extended) to about 50° at phase III, the push-off. The crus, however, from an essential alignment with the femur at phase I, through slight medial adduction placing it under the body (phase II), is abducted from the femur at push off to about 35°, and thereafter returns during the recovery phase to its alignment with the femur. Therefore, during the most heavily loaded moment of the knee, the ground forces are being transmitted to the femur itself through a crus more abducted than the femur, just as the forces emanating from the animal's mass are transmitted through an abducted femur in relation to the hip. It is equally interesting to note that the innominate of *D. virginiana*, as later indirectly confirmed by Pridmore's (1992) studies on trunk movements in *Monodelphis*, is pushed towards the opposite side by the active femur during propulsion, and is rotated toward the active side. In light of this pattern of skeletal dynamics during locomotion when their interaction during propulsion is understood, the role and articular relationships of the fibula, parafibula, and femur become clear. Furthermore, the shared changes in the relationship of these bones in highly terrestrial species of marsupials and the last common ancestor of extant eutherians lead to an appreciation of the changes in not only the knee complex, but in key areas of the skeleton as well that reflect the interface of bone mechanics, substrate, and locomotion (Szalay 1994) [24].

Differences in the morphology of the marsupial models

In this section we examine, in addition to our assessment of the scansorial *D. virginiana* (where intrademic variation was the focus), the various aspects of the osteology of our designated model species in order to lay foundations for the evaluation of the various fossil "unknowns". A recent study by Argot (2001) of the forelimb of *Caluromys* and *Metachirus*, undertaken to understand the Tiupampa fossil marsupials, is the most comprehensive comparative account in the literature of that area of the anatomy in these two extant didelphids, and in didelphids in general [25].

We have constructed, following our qualitative assessments, a number of indices based on measurements (taken with the aid of a 3-D Mitutoyo stage microscope and Measure Graph 1-2-3 measurement software). These provide us with quantitative data with which to consider the functional-adaptive and taxonomic aspects of our conclusions regarding the various proposed Itaboraí Metatherian Groups (IMGs) for the long bones, so that these groups are probably reasonable approximations of extant species taxa. The various plots that are shown for both the fossil and the model species reflect in some measure attributes that are probably reliable indicators of substrate preference in most cases on the Y-axis, and some surrogate of body size on the X-axis. The regression lines were derived from the extant models only, without any values from the fossils, then they were imported and superimposed onto the plots that include the fossils and extant taxa. The regression lines were generated using the extant arboreal and terrestrial models to provide an admittedly very rough division between arboreal and terrestrial species for certain features. The lines served the purpose of evaluating where the fossils fell relative to a divide between our model species. We state

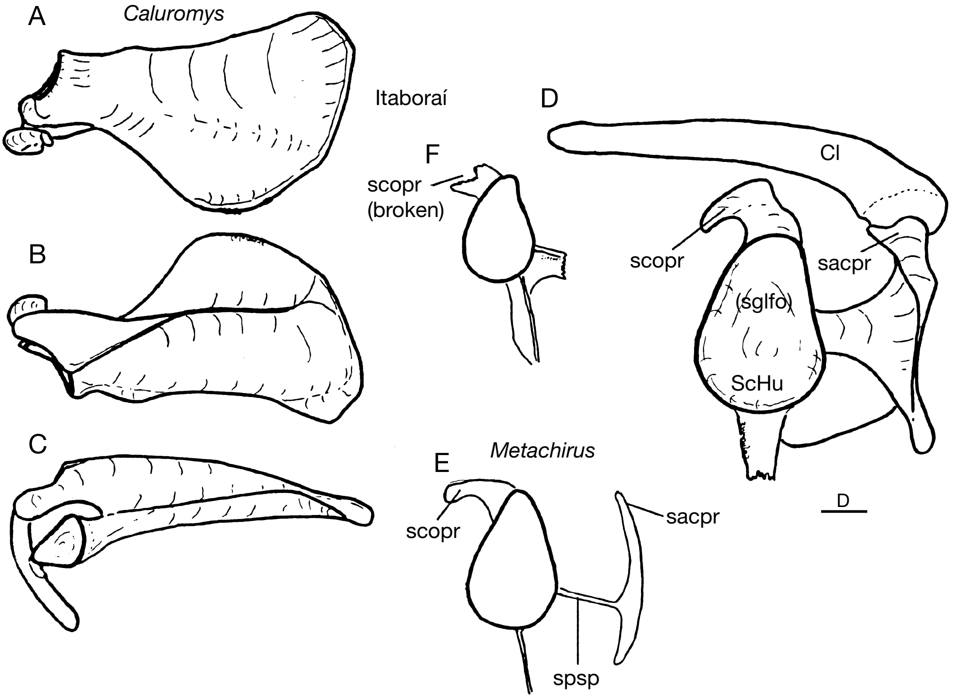


FIG. 7. — **A-D**, *Caluromys derbianus*, left scapula; **A**, medial view; **B**, lateral view; **C**, anterior veiw; **D**, ventral view; **E**, *Metachirus nudicaudatus*, left scapula, ventral view; **F**, left scapula of the Itaboraí specimen (reversed), ventral view. Abbreviations: **Cl**, clavicle; **sacpr**, scapular acromion process; **ScHu**, scapulohumeral facet; **scopr**, scapular coracoid process; **sglfo**, scapular glenoid fossa (within which ScHu is located); **spsp**, scapular spine. Scale bar: D, 4 mm.

emphatically that this line was not considered to be axiomatically a line of demarcation between arboreal and terrestrial adaptations. Consequently we would not assume that any of the fossil groupings were either arboreal or terrestrial based solely on these plots, as our discussions of the fossils below bear make clear. This regression line is considered by us a very fuzzy and vacillating one. Our aim was largely to determine if certain quantitative data supported our qualitative assessment of substrate preference in the fossils.

Scapula. Roberts (1974) gave a comprehensive analysis of the forces affecting the morphology of the scapula. Our treatment of it here is severely restricted, as there is only one scapular fragment available from Itaboraí, although it is interesting on several accounts and merits a brief discussion of this bone in the models (Fig. 7). First, the anterior portion of the fossil unmistakably shows that it was far deeper dorsoventrally and more rounded in its overall morphology than that of the highly arboreal *Caluromys* (Fig. 7). In spite of this obvious difference in general outline, the scapulohumeral articulation (ScHu), the glenoid fossa of the fossil, is essentially of the same outline and proportions as those of both *Caluromys* and *Metachirus*. From this it appears clear that the shape and width/length ratio of the glenoid fossa itself is of little predictive value regarding locomotor behavior and substrate preference, at least for didelphids. It also suggests that, even in very differently adapted taxa like *Caluromys* and *Metachirus*, the habitual loading of the glenoid, if not the stability or associated muscular origins, is substantially the same. Unfortunately the acromion process, the proportions of which show functionally diagnostic differences between *Caluromys* and *Metachirus* (Argot in press), is not preserved in the fossil.

The scapula of *Caluromys* is characterized by a relatively narrow neck area behind the glenoid, an area that widens more gradually than that seen in *Didelphis* or *Metachirus* (or in the only Itaboraí fossil scapula). The angle of articulation of the glenoid surface, with its very small arc, is about 40° to the scapular spine itself. The clavicle of *Caluromys* is exceptionally stout, but there is no comparative data available, corrected for size, that would allow any estimate of the significance of relative clavicle size, articulation with the acromion process (**sacpr**; Fig. 7A-D), and the relevance of these factors for positional behavior and substrate preference. The scapular spine (**spsp**) is long and high, tapering caudally only gradually. The acromion process in *Caluromys* is broad based and robust, this being attributed to the importance of the part of the deltoid attached to the acromion (Argot 2001). But surprisingly, we find this pattern equally well-developed in the specimens of *Metachirus* that we examined. In other specimens of *Metachirus* this process may well be more slender and cranially directed, as suggested by Argot. As noted, the supraspinatous attachment area in *Metachirus*, as well as in *Didelphis*, broadens quickly behind the glenoid neck, a condition shared with the only Itaboraí scapula. This aspect of the scapula in both *Metachirus* and in the partial fossil specimen gives the impression of a nearly rectangular, rather than triangular, bone. As Argot (2001) noted, the supraspinatous component of the rotator cuff complex aids in the prevention of the dislocation of the shoulder. A distal extension of the area of origin of this muscle that attaches to the greater tuberosity suggests that a hypertrophy in that area of the scapula is positively correlated with stabilizing and restricting the shoulder.

In *Dromiciops* and *Rhyncholestes,* however, the habitus-related correlations of the didelphid scapulae do not appear to apply in the same manner as in the didelphids, at least at the level that we have examined this. Both of these very small mammals have long and attenuated scapulae, that of *Rhyncholestes* being relatively longer. Nevertheless, as Argot (pers. comm.) has pointed out to us, the relative size of the infraspinatous fossa and the extension of the of the posterior angle (site of origin for the teres major) show differences. The acromion process is robust in the terrestrial form, perhaps even more so than in *Dromiciops*. Our observations only reinforce the need for a detailed musculoskeletal analysis of these important South American families.

Humerus. This bone is replete with useful attributes for functional-adaptive and habitus related assessment. A précis of some of the functional literature above regarding the dynamics of pectoral limb during level locomotion provides critical context for the taxon specific differences. There are, however, no detailed cineradiographic observations of didelphids or other marsupials on arboreal substrates comparable to those conducted on level ground by Jenkins (1971) and Jenkins & Weijs (1979). Therefore much of the associated morphology is interpreted in the framework provided by these authors with some additional inferences from the morphology itself. Figs 2 and 8-10 indicate the various attributes that may be useful traits for differentiating between form-functional differences in differently adapted extant species. In general, uniform numbers are used on homologous skeletal elements to label characters in both the text and the figures. The configurations of the numerically labeled characters are largely, but certainly not exclusively, habitus-dependent.

The following features of the humerus hold potentially significant adaptive (or possibly phyletically important) information:

1) head and the surrounding tuberosities;
2) “beak”-like projection the head;
3) shaft shape and robusticity;
4) relative size and conformation of the deltopectoral shelf and crest. This area is possibly indicative of a considerable distal extension of the major flexor, abductors, and rotators of the humerus (the deltoid and pectoralis major);
5) relative size of the humeral medial epicondyle (**hmec**). In powerful hand graspers (most marsupials) the area for major hand flexors (flexor carpi ulnaris, flexor carpi radialis, flexor digitorum profundus) is reflected by the relative size of this process. As Argot (pers. comm.) pointed out, while

the flexor carpi radialis is not well-developed, the relatively larger flexor digitorum profundus well reflects the adaptive differences;

6) conformation of the humeral lateral epicondylar crest (**hlecr**) is related to the origin of the brachioradialis, which is related to the flexion of the antebrachium (digital extensors attach to the distal tip of **hlecr**);

7) relative size and configuration of the trochlea and the size of the capitulum are critically important areas where (habitual) loading is reflected. The extent of the **HuUl** facet on the posterior side of the humerus, its distal shape, and its distal extension medially are all important indicators;

8) degree of development of the posterior lateral crest (**hplcr**) next to the olecranon fossa (**hofo**);

9) extent of grooving on the facet lateral to the capitulum for the radial sesamoid (**Ras**), when present (as in caenolestids), or for the radius itself.

Before we examine these features (see below, same numbering), we note that the generally similar loading of the glenoid fossa in didelphids raises some questions regarding the range and extent of movements of the humerus and the scapula, queries that cannot be definitively answered here. The similarity of the shape and proportion of the glenoid of didelphids and other basal metatherians may be due to the extent to which the humerus is flexed on the scapula, either a) to a lesser degree, as in a form like *Caluromys* where there is no "beak" on the caudal end of the humeral head; or b) to a greater degree, as in terrestrial forms. The morphology of the humeral head (if not the scapular glenoid) certainly suggests that there is this difference in the degree of humeral flexion on the scapula during the push-off phase of the stride. It is also possible that the limits of humeral excursion are not different but that the shoulder in *Caluromys* is more mobile, and, hence, less vertical and more cranially oriented during push-off. In general, it is clear that the position of the humerus in relation to the scapula is distinct in *Caluromys* vs *Didelphis* and *Metachirus* when the loads are transferred from the humerus to the glenoid.

The humeri of *Caluromys* and *Dromiciops*, in spite of their more remote affinities and their discrepancies in size, are consistently similar to one another (unlike the morphology of their scapulae), and differ in what we consider adaptively significant attributes from those of *Metachirus* and *Rhyncholestes* (taxa that resemble one another in these features). The similarities and differences between these unequal-sized genera reflect, of course, the general resemblance of their skeletal adaptations due to differential substrate use. *Caluromys* and *Dromiciops* are far more arboreally adapted, particularly to a small, terminal branch milieu, than are the nearly obligate terrestrial *Metachirus* and *Rhyncholestes* (as well as *Caenolestes*).

1) While the humeri of the two didelphid models are similar in size, the relative size of the head on *Metachirus* is far greater, both in length and breadth. Both the medial (lesser) and lateral (greater) tuberosities are somewhat more developed in *Metachirus* than in *Caluromys*. These are conditions that apply equally to the caenolestids (that resemble *Metachirus*) and to *Dromiciops*, which is *Caluromys*-like (Figs 9; 10). Equally distinctive is the hypertrophied greater tuberosity that extends higher than the head in the terrestrial and cursorial didelphid, and the terrestrial bounding-leaping caenolestids. While the lower height of the tuberosities in the arboreal forms aid mobility in the shoulder, the functional explanation for the pattern in the terrestrial cursors is probably related to the increased need for stabilization of the shoulder. The latter is a derived condition in *Metachirus* compared to other didelphids, but is probably primitive in Caenolestidae in regards to its ancestral root.

2) The head in *Metachirus* is exceptionally "beaked" in contrast to *Caluromys*, where the caudal extension of the "beak" is minimal among didelphids (Fig. 8). The same dichotomy in the expression of this feature applies to the caenolestids *vs* the microbiotheriid.

3) The shaft is relatively straight in both didelphids. In *Dromiciops* it is relatively straight, but in caenolestids, perhaps because of the extreme development of the area of origin for the deltopectoral complex, the proximal half is bowed.

4) We found that the shape and conformation of the deltoid shelf and deltopectoral crest, while a

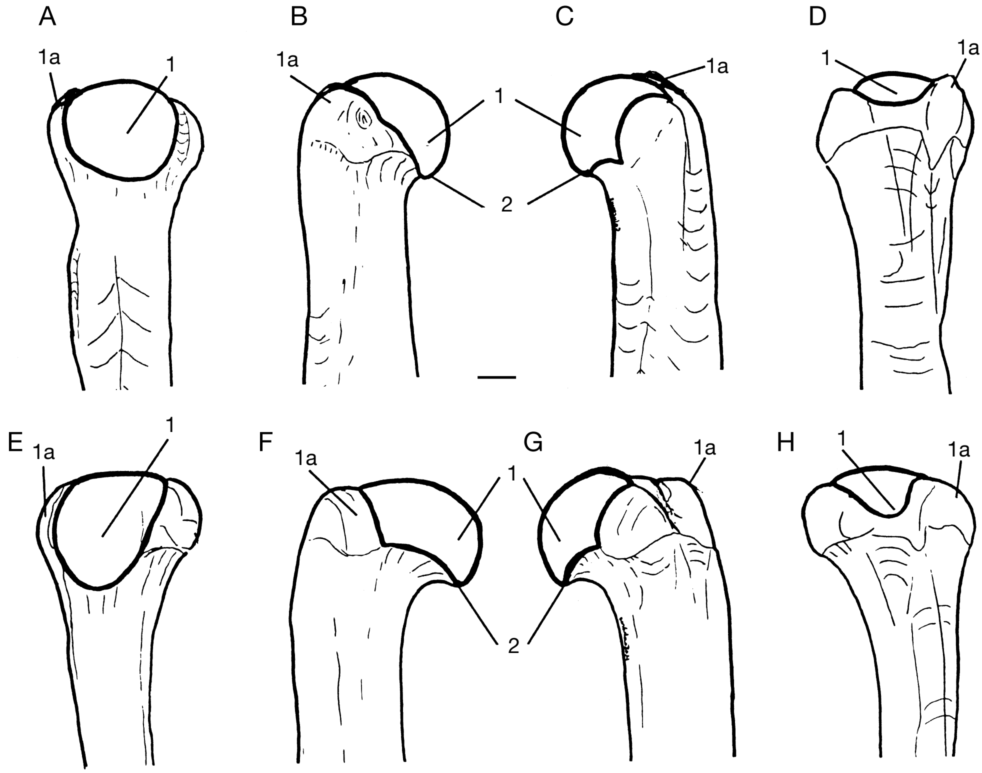


FIG. 8. — Details of proximal left humeri; **A-D**, *Caluromys*; **A**, posterior view; **B**, lateral view; **C**, medial view; **D**, anterior view; **E-H**, *Metachirus*; **E**, posterior view; **F**, lateral view; **G**, medial view; **H**, anterior view. For numbered designations of specific characters see text. Scale bar: 2 mm.

tantalizingly well-preserved part of most of our fossil humeri, is difficult to interpret functionally (for a thorough discussion of the myology of this area of attachment see Argot 2001). While there are some differences between the arboreal and terrestrial didelphids that can be explained by the myological patterns, we found that the osteological expression, the deltoid area, reflects these either poorly or not at all. In general, we found all extant South American marsupials to be well-endowed with a long and extensive deltopectoral crest. There is enough variation within *Didelphis* and within clusters of equally arboreal animals to make us suspect that its predictive value is low. In *Caluromys* the deltopectoral crest is far sharper than in *Metachirus*. In *Dromiciops*, the crest is also sharp and similar to *Caluromys*. In *Rhyncholestes*, however, a fully developed robust shelf, rather than a crest, predominates.

An interesting point, one in support of our failure to functionally discriminate based on the deltopectoral area, is the superficial pattern of consistency of the Humeral Deltopectoral Shelf Index, (HDSI; see definition above under *Didelphis*). In *Caluromys* it is 54 and in *Metachirus* 55, while in *Dromiciops* it is 47 and in *Rhyncholestes* it is 48. The didelphid values fall within the range for *Didelphis*. The values we obtained for the fossils are equally inconclusive. There is a vague suggestion that at least this index may scale with body size, but is independent of any adaptive imperatives that we may be aware of.

5) It is difficult to make a judgment on the relative size of the medial epicondyle because of the distinctly greater size of the distal articulation in the terrestrial cursors. Both *Metachirus* and *Rhyncholestes* have a considerably hypertrophied trochlea, most especially distally and posteriorly

where this expansion projects onto the medial epicondyle itself.

6) Laterally the distal half of the shaft is characterized by a well-developed epicondylar crest in *Caluromys* and *Dromiciops*, in contrast to a somewhat reduced condition in *Metachirus* and *Rhyncholestes*. In didelphids the anterior portion of this area is the place of origin for the more proximal brachioradialis and the more distal extensor carpi radialis. The posterior portion is for the extensive lateral head of the triceps brachii and distal to this the anconeus. While the size of the crest is variable in didelphids, it is particularly well-developed in *Caluromys*, but also in terrestrial genera such as *Monodelphis*. It was undoubtedly well-developed in the last common ancestor of living and better known fossil metatherians. It may be that the well-developed crest is a strong indication of the arboreal and manipulative ability of the manus in the last common ancestor of postcranially known fossil and extant marsupials. Its mechanical significance is probably related to an ancestral arboreal habitus. Its variable expression in various lineages is not a very reliable predictor in fossils, although its extreme reduction suggests more cursorial and terrestrial mechanics for the manus.

7) The condition of the trochlea was mentioned above. In *Caluromys* and *Dromiciops* the anteriorly and distally relatively long, cylindrical and slender trochlea is relatively small compared to the large capitulum. This relationship is reversed in the terrestrial forms. In the latter the trochlea is not only expanded both anteriorly and posteriorly at the expense of the capitulum, but the distal articular surface has transformed from the more cylindrical condition to a medially very broad and wedge-shaped form (compare character states of trait 7a on Figs 9 and 10). This change is related to an increase of the surface during close packing of the elbow joint, an adaptive response to repetitive high impact loading during rapid running. In a highly characteristic manner, the distal trapezoid-shaped surface of the trochlea has a medial border that is far wider than the lateral one. In both the didelphid and caenolestid cursors the posterior and lateral edge of the **HuUl** articulation is hooked, and is continuous with the posterior lateral crest (**hplcr**). This configuration is not only indicative of greater load absorption than in the arboreal forms, but it also provides great stability in the joint during full extension.

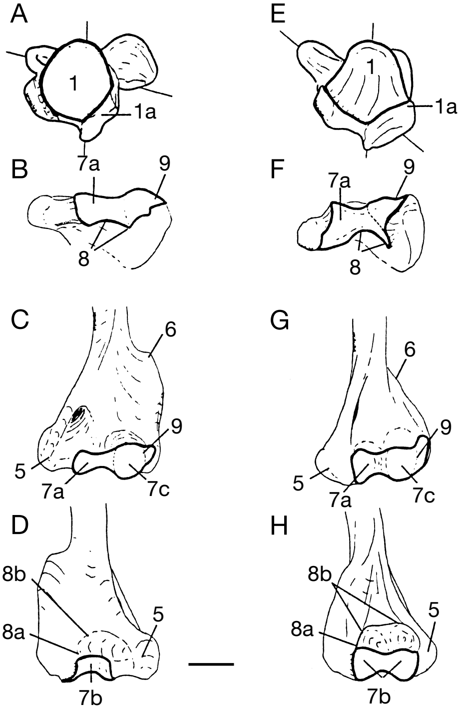


FIG. 9. — Details of left humeri; **A-D**, *Caluromys*; **E-H**, *Metachirus*; **A**, **E**, proximal view of head and distal outline (axes show an approximate degree of torsion between proximal and distal ends); **B**, **F**, distal view of distal end; **C**, **G**, anterior view of distal third; **D**, **H**, posterior view of distal third. For numbered designations of specific characters see text. Scale bar: 4 mm.

Significantly, given the higher level taxon-specific ancestral configuration, the difference in the (equally taxon-specific) mechanics of trochlear configuration of terrestrial *vs* arboreal species is nearly universal in both metatherians and eutherians (see also Szalay & Dagosto 1980). The patterns are usually related to the form of the **HuUl** articulation in terrestrial forms that both restricts and stabilizes this joint during extreme extension of the forearm on the humerus during half-bounding or bounding locomotion. This is in contrast to the more flexed and less extended condition in arboreal species. Exceptions, of course, exist in

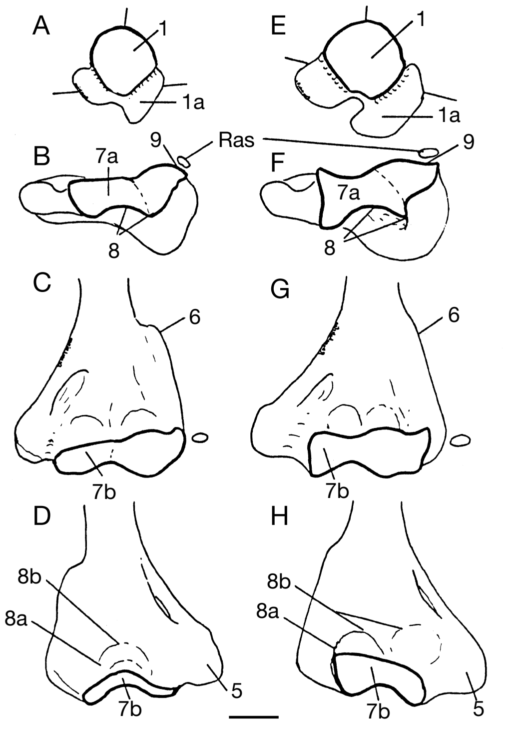


FIG. 10. — Details of left humeri; **A-D**, *Dromiciops*; **E-H**, *Rhyncholestes*; **A**, **E**, proximal view of head and distal outline (axes show an approximate degree of torsion between proximal and distal ends); **B**, **F**, distal view of distal end; **C**, **G**, anterior view of distal third; **D**, **H**, posterior view of distal third. For numbered designations of specific characters see text. Abbreviation: **Ras**, radial sesamoid. Scale bar: 1 mm.

suspensorial species where locking of the elbow in tension is at an adaptive premium.

It is obvious that the loads incurred at this articulation in terrestrial forms, and the relatively larger surface of the articulation with the ulna distally, as well as cranially and caudally, is an interdependent causal relationship. The specifics of this relationship constitute a character complex. A larger surface both dissipates loads more efficiently and reflects the locking of the joint in close-packed conditions for stability. The condition of the olecranon fossa on the posterior surface of the humerus is particularly revealing in regards to the close packed articulation of the mediolaterally widened proximal ulnar trochlear crest. Caudally the ulnar facet is more concave in the terrestrial forms, a property tied to the stabilization of this joint. This correlation between morphology and function of the **HuUl** articulation is further emphasized below in our discussion of the ulna.

8) In terrestrial genera where the trochlea is medially restrictive and deep, the surface of the trochlear contact with the ulna is extensive both anteriorly and posteriorly, and the olecranon fossa is deep. Sometimes the fossa is somewhat divided. In the arboreal taxa, the olecranon fossa mirrors this condition where the articular areas with the radius and ulna are characterized by a medially less restrictive trochlear border that is shallower, and a trochlear articulation with the ulna that is less extensive both cranially and caudally. The shallower olecranon fossa has a less extensive posterolateral crest (**hplcr**), and the distal surface of the trochlea is relatively smaller and less cylindrical than in the terrestrial genera.

The posterior surface of the distal humerus is highly informative with regard to elbow extension and stabilization, correlated with a more extended forearm in terrestrial forms. Unlike in *Caluromys* or *Dromiciops*, both in *Metachirus* and *Rhyncholestes* the humeral olecranon fossa (**hofo**) is deep and widened due to the closely fitting and mediolaterally spread proximal trochlear crest of the ulna (**ulptc**). As a direct consequence of this extension and stability related attribute, the posterolateral crest of the humerus (**hplcr**) that laterally borders the **hofo** is developed into a robust and sharp crest for the insertion of a hypertrophied and heavily stressed joint capsule. This osteological emphasis laterally is probably the result of the slightly abducted stance at the elbow when contact with the substrate occurs.

9) A radial sesamoid (**Ras**), when present, in both arboreal and terrestrial genera (or in its absence, the radial head) articulates with the lateral flange of the capitulum (**hlfcap**) and with the radius. Correlated with this contact is a ubiquitous, but functionally variably expressed, feature on the distal articular end of the humerus of the model species, other metatherians, and a host of eutherians. This sesamoid, not invariably present in all species, however, is rarely preserved in skeletal preparations (but see Fig. 10B, F), and it is obviously even more scarce in the fossils. The radial sesamoid (or

TABLE 1. — Functional differences (or lack there of) in the humerus of arboreal (*Caluromys derbianus* [Watrhouse, 1841], *Dromiciops gliroides* Thomas, 1894) and terrestrial (*Metachirus nudicaudatus* [Demarest, 1817], *Rhyncholestes raphanurus* Osgood, 1924) species of extant marsupials that were employed as models in this study.

Traits	Arboreal	Terrestrial
1. Articular surface of head	Length-width ratio is not definitive	Length-width ratio is not definitive
2. Extent of "beaking" (overhang) of head	Very little beaking	Pronounced beaking
3. Shaft characteristics	Unclear	Unclear
4. Conformation of deltopectoral shelf	Not consistent	Not consistent
5. Relative size of medial epicondyle	Tends to be large, related to large digital flexors	Highly reduced
6. Relative size of lateral epicondylar crest	Not consistent	Not consistent
7. Distal articulation with radius and ulna:		
a) relative size of trochlea compared to capitulum;	a) relatively small;	a) relatively large
b) distal width of trochlear facet	b) relatively narrow	b) wide, particularly medially, resulting in a triangular outline
8. Condition of posterior lateral crest bordering olecranon fossa	Low and nondescript	Sharp and proximally extended
9. Groove for radial sesamoid	Usually, but not always, poorly defined	Usually, but not always, well defined and visible when the humerus is viewed distally

the equivalent area of the radius) mediates motion and stabilizes the radius during its flexion on the humerus and rotation on the ulna. It also provides additional stability in a close-packed elbow joint, particularly in rapidly bounding terrestrial forms like *Metachirus* and caenolestids where a variably deep sulcus separates the capitulum from the lateral flange (see trait 9 on Figs 9B and 10B). The groove greatly improves stability of the rapidly sliding sesamoid in the small cursors.

Table 1 summarizes a list of characteristic differences (as well as relatively invariant similarities) of the humerus of the four model species. These attributes are employed in judging both adaptively and phylogenetically significant information gleaned from the fossils.

Ulna and Radius. The ulnae and radii (Figs 11-14) offer a great range of distinctive traits, and the following are characteristic properties that help diagnose the adaptive and taxonomic differences between different species. More specifically, the areas of significance for ulnae are:

1) shape, dimensions, and configurations of the olecranon process, particularly in relation to the muscles attached to it, and related to some of the articular aspects reflected in the trochlear notch;
2) shape of the trochlear notch and its articulating facets (including the trochlear notch index), in particular as these permit associations between humeri and ulnae;
3) differences between the length and orientation of the medial and lateral wings of the ulnar proximal trochlear crest (**ulptc**);
4) bowing, or lack of it, in the ulna, particularly the proximal section;
5) position of the radial notch and attributes of the shaft of the ulna distal to the trochlear notch;
6) surface of the ulna proximally for various muscle attachments;
7) configuration of the distal ulna, particularly the styloid process. The specific adaptive differences in the model species require a detailed discussion of these areas. Also of particular significance to this discussion is Argot's (2001) detailed treatment of the interrelationships between the myology and the bones of the elbow in didelphids.

Due to the vulnerability of the complex elbow joint, where both pronation and supination of

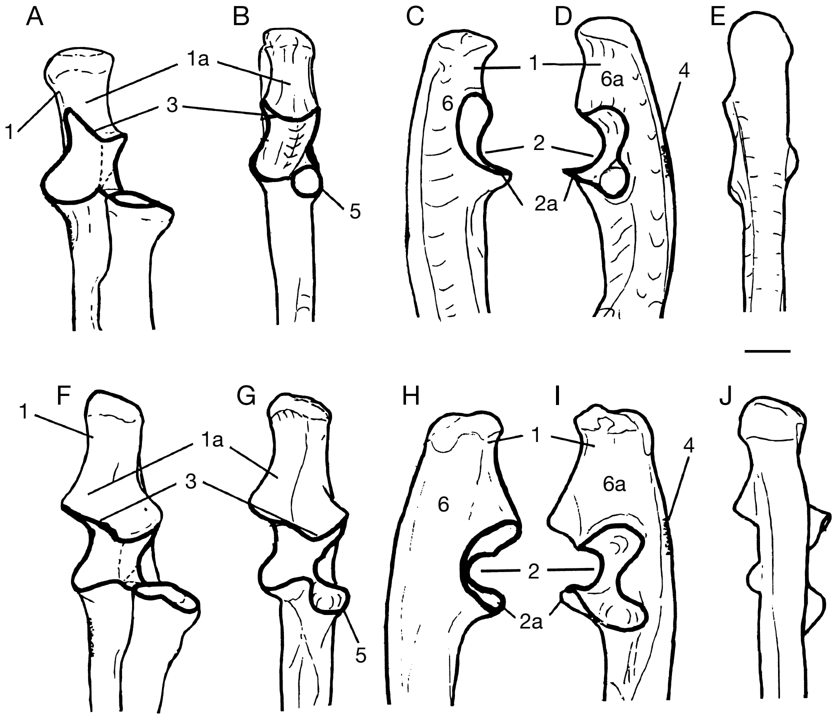


FIG. 11. — Details of left proximal ulnae and radii; **A-E**, *Caluromys*; **F-J**, *Metachirus*; **A**, **F**, anterior view of ulna and articulating radius; **B**, **G**, anterior view of ulna; **C**, **H**, medial view of ulna; **D**, **I**, lateral view of ulna; **E**, **J**, posterior view of ulna. For numbered designations of specific characters see text. Scale bar: 2 mm.

the hand as well as the flexion and extension of the forelimb on the humerus occur, the differences in the structural and functional needs between obligate arboreal forms and committed terrestrial species is usually adaptively accentuated, although without any particularly obvious phyletic significance on the level that we sought in this study. In the arboreal group there is a premium on both the flexibility for positioning the hand and the need to maintain the forearm in a relatively flexed position. In the terrestrial species the optimal solution is to maintain stability while the forearm is maximally extended (and shock-loaded) during the frequent bouts of rapid galloping and scurrying that are necessary in a terrestrial habitat.

1) As a general rule gleaned from the model species and other relevant taxa, the olecranon process (the lever of the various heads of the triceps brachii around the humeroulnar articulation) shows differential widening and narrowing in the arboreal and terrestrial groups, and, perhaps also significant relative length differences between the didelphid arboreal and terrestrial species. In didelphids the arboreal forms appear to have relatively shorter olecranon processes.

We find the olecranon process to be relatively longer (slightly) and anteroposteriorly broader in *Metachirus*, and longer in *Didelphis* and *Monodelphis* than in *Caluromys*. The length differences may be of no biological significance for *Metachirus* because it is a particularly long-limbed animal, and, therefore, close-grained qualitative comparisons, such as relative length of part of a bone, may be of little meaning without a complex comparative and quantitative analysis that would involve body mass, lengths, and proportions.

The deepening of the process, particularly at its base in *Metachirus*, and along its length in caenolestids, however, is significant. It may be related to the hypertrophy of the triceps (lateral and long heads), but is more likely due to the extreme widening of the proximal part of the trochlear notch in both *Metachirus* and caenolestids.

2) The general conformation of the ulnar trochlear notch appears to be a significant indicator of the degree of stability of the elbow joint, and therefore potentially of the speed of travel. It is consequently an indicator of either an arboreal, terrestrial, or scansorial emphasis in the habitus. It cannot be axiomatically tied to any one particular substrate. The depth of the trochlear notch in *Metachirus* appears be deeper and more restrictive than that in caenolestids. Generally, the arboreal *Caluromys* and *Dromiciops* have wider distal halves of the notch, perhaps a reflection of less emphasis on elbow joint locking onto the humerus than load bearing. In contrast, the extreme expressions of a proximally wide trochlear notch in the two model cursors is related to the emphasis on stability of the elbow in extension. While the arboreal forms tend to have more open trochlear notches, the anterior extension of the coronoid process (**ulco**) compared to the proximal trochlear crest assures stability for this joint that is usually not fully extended in these animals.

The trochlear notch index (UTNI, see definition above under *Didelphis*) in the two didelphids is 36 in *Caluromys* and 58 in *Metachirus*. In *Dromiciops* it is 36, whereas it is 44 in *Rhyncholestes*. The mean of 32 for *Didelphis* emphasizes the arboreal capabilities of this scansorial genus.

As discussed by Szalay & Trofimov (1996), the zona conoidea on the humerus articulates with the ulna in basal and most other marsupials, unlike the more advanced therian condition of placentals where the radius displaces the ulna in the zona (see **HuUlz** facet in Fig. 2D). While this change does not invariably occur with a change to a terrestrial habitus in metatherians, it does appear to be a concomitant of such a shift in the eutherian ancestry, where a premium on vertical support and stability resulted in the mediolateral expansion of the proximal surface of the radius. Furthermore, there appears to be no reversion in the condition of the zona in the secondarily arboreal radiations of the Eutheria (Szalay 1984), with the possible exception of some highly derived xenarthran vermilinguas (Szalay & Schrenk 1998). Even in obligate terrestrial taxa such as *Metachirus* or caenolestids, the radially extended distal corner of the humeroulnar joint reflects the unmistakably metatherian (and therian) **HuUlz** facet. This difference can be readily seen when comparing otherwise similar metatherian and eutherian ulnae.

3) In addition to the relative width of the proximal and distal sections of the trochlear notch, the proportions of the medial and lateral segments of the ulnar proximal trochlear crest (**ulptc**) are also significant. In *Metachirus* the proximal trochlear crest is disproportionately widened, particularly its medial limb (**ulptcm**), compared to *Caluromys* (Fig. 11). This widening has the consequence of providing an extremely stable cradle for the humeral trochlea through its entire range of angular displacement in addition to highly stabilized locking at full extension of the lower arm where the two wings of the proximal trochlear crest come in full contact with the caudally concave distal humerus. This condition is completely convergent with caenolestids (Fig. 12), undoubtedly an identical functional response for the same bioroles. Correlated with this is the medial displacement of the cranial ridge of the olecranon process (**ulcolr**) at its distal extremity where it joins the medial limb of the crest. This modification indicates a shifting of the loads on the ulna, both from the joint and the triceps, during the stable position of the joint in extension. Although in such totally obligate terrestrial species such as *Metachirus* and caenolestids the extreme proportions of the proximal and distal segments of the trochlear notch are clearly predictive, application of this criterion alone to such differences in fossil ulnae does not necessarily give clear signals.

4) The bowing of the ulna is an expression of a complex set of myological factors related to the

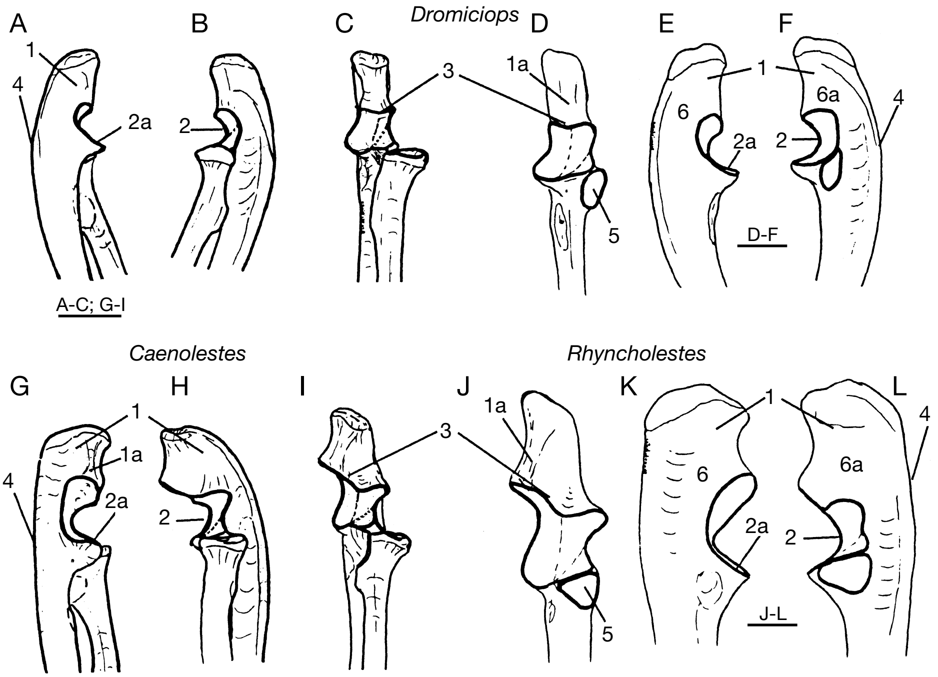


FIG. 12. — Details of left proximal ulnae and radii; **A-F**, *Dromiciops*; **G-I**, *Caenolestes*; **J-L**, *Rhyncholestes*; **A**, **G**, medial view of ulna in articulation with radius; **B**, **H**, lateral view of the same; **C**, **I**, anterior view of the same; **D**, **J**, anterior view of ulna; **E**, **K**, medial view of ulna; **F**, **L**, lateral view of ulna. For numbered designations of specific characters see text. Scale bars: 2 mm.

degrees of habitual flexion as well as to load resistance associated with the proximal half of the ulna, particularly the olecranon process. The extreme expressions of this attribute in eutherians is well-known. Arboreal forms often have short and anteriorly bent olecranon processes that result in a variably bowed, posteriorly convex proximal ulna. Terrestrial forms, on the other hand, have a relatively straight or even concave proximal ulna which is related to the well-understood lever mechanics of the elbow. In fact, in such cursors as lagomorphs or various caviid rodents (that are extremely lagomorph-like in their cursorial adaptations) the shaft of the ulna distally is anteriorly bowed and deeply concave posteriorly. In contrast, in the relatively primitive Itaboraí taxa the distinctions were rarely clear. The terrestrial marsupial models we studied have a slightly less bowed curve to the ulna proximally than the arboreal species.

5) The radial notch appears to be interestingly dichotomous in the arboreal *vs* terrestrial models. In arboreal forms the notch faces more anteriorly, while it is offset more laterally in the terrestrial ones. In the former there appears to be no continuous articular surface onto the lateral side of the coronoid process, whereas this continuity is clear in the latter.

A deep and oblique groove lateral and distal to the insertion of the brachialis and distal to the radial notch is a strong distinguishing feature of *Metachirus* compared to *Caluromys*. In the microbiotheriid and *Rhyncholestes* such differences are not obvious. It appears that in didelphids this depression on the ulna is to accommodate both the radial tuberosity for the attachment of the biceps brachii, as well as the muscle itself. The relatively more constant pressure of a habitually pronated hand in the terrestrial forms may account for the much more excavated condition of the ulna than in the arboreal forms which have more variably positioned forearms and hands.

6) The medial surfaces of the proximal ulnae (in addition to the hmec) are places for the origin of the flexor digitorum profundus that extends far distally on the shaft. The insertions of the anconeus on the lateral side of the olecranon, beginning behind the trochlear notch and continuing down the shaft, and the deep flexor digitorum on the medial side, result in variable excavations of the two sides of the ulna. Keeping in mind the caveats regarding muscle insertions raised by Bryant & Seymour (1990) that closely parallel our own observations, the significance of the degree of excavation of the sulci on the two sides of the ulna is difficult to understand for the fossils as yet. Nevertheless, the medial side of the ulna is far more deeply excavated in *Caluromys*, and the crest posteriorly and laterally for the origin of flexor carpi ulnaris is much more developed than in *Metachirus*. A myological study might result in more firmly based correlations of the relative importance of these muscles, their osteological expression, and their adaptive significance in marsupials.

7) The distal configuration of the ulna is discussed below under the radius, together with the configuration of the radioulnar contact with the wrist. Both of these bones show a similar mobility-related pattern in the arboreal forms and a more restrictive stability-related modification in the terrestrial taxa.

Although we only have one radius in the Itaboraí collection, the intimate relationship of this bone with the humerus and ulna mandated its close examination in the models. The most significant diagnostic aspects of the radius are manifested in the differences that favor either mobility or stability. A rounded capitular contact enables the rotation of the radius on both the humerus and the ulna. This mobility allows the manus to accomplish different degrees of pronation and supination. At the other extreme, when stability is required for load bearing and compressive force accommodation, as in running and bounding forms (e.g., most eutherians), the elliptical enlargement of the **HuRa** articulation is the mechanically relevant adaptive response. Such distinctive patterns are usually reflected on the head of the radius in Cenozoic eutherians whose ancestral adaptation was almost certainly to a terrestrial habitus.

In the didelphids examined, however, the differences are far more subtle and less extreme between terrestrial and arboreal species. Contrary to expectations from any preconceived notions based on eutherian analogs, there is no major difference in the mediolateral dimensions of the head of the radius between *Caluromys* and *Metachirus*. Both of these taxa, like other didelphids, have a rounded radial head. Nevertheless, a more rounded and deeper, as opposed to a more oblate and shallower, articular facet with the humeral capitulum (which is only a part of the proximal radius) is an indication of functions in arboreal behaviors (Fig. 13).

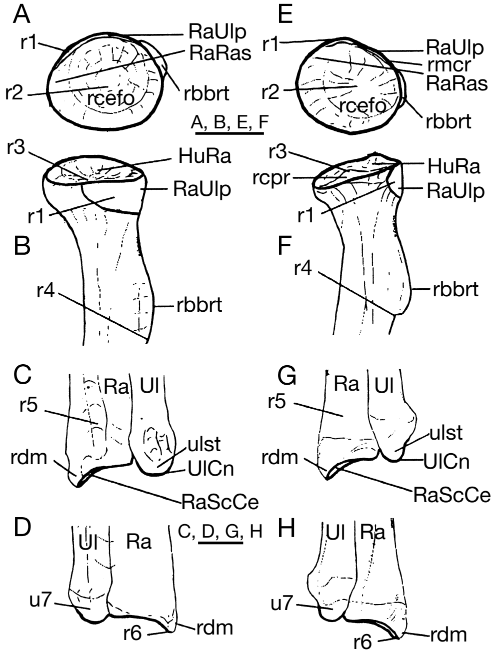


Fig. 13. — Details of left radii and ulnae; **A-D**, *Caluromys*; **E-H**, *Metachirus*; **A**, **E**, proximal view of radius; **B**, **F**, medial view of proximal radius; **C**, **G**, anterior view of radius and ulna; **D**, **H**, posterior view of radius and ulna. For numbered designations of specific characters see text. Prefixes before the numbers: **r**, radial; **u**, ulnar. The scales are for the proximal and distal ends, respectively. Abbreviations: **HuRa**, humeroradial facet; **Ra**, radius; **RaRas**, radius-radial sesamoid facet; **RaScCe**, radioscaphocentrale facet; **RaUlp**, proximal radioulnar facet; **rbbrt**, radial biceps brachii tuberosity; **rcefo**, ; **rcpr**, radial capitular process; **rdm**, radial distal malleolus; **rmcr**, radial medial crest; **Ul**, ulna; **UlCn**, ulnocuneiform facet; **ulst**, ulnar styloid process. Scale bars: 2 mm.

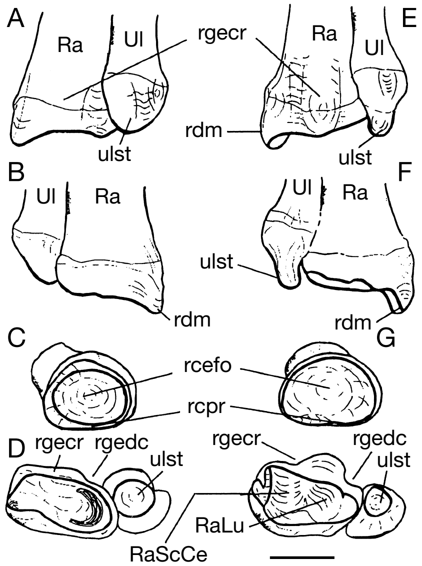


FIG. 14. — Details of left radii and ulnae; **A-D**, *Dromiciops*; **E-H**, *Caenolestes*; **A**, **E**, anterior view of distal radius and ulna; **B**, **F**, posterior view of distal radius and ulna; **C**, **G**, proximal view of radius; **D**, **H**, distal view of distal radius and ulna. Abbreviations: **Ra**, radius; **RaLu**, radiolunate; **RaScCe**, radioscaphocentrale facet; **rcefo**, radial central fossa; **rcpr**, radial capitular process; **rdm**, radial distal malleolus; **rgecr**, radial groove for tendon of extensor carpi radialis; **rgedc**, radial groove for tendon of extensor digitorum communis; **Ul**, ulna; **UlCn**, ulnocuneiform facet; **ulst**, ulnar styloid process. Scale bar: 1 mm.

This **HuRa** articulation is noticeably shallower in the terrestrial species than in the arboreal one. Another reflection of this dichotomy is the extent of the facet that articulates with the ulna (**RaUlp**). Furthermore, *Metachirus* and *Didelphis* have a well-developed central process (**rcpr**) for stabilizing the humerus anteriorly, compared to an all but unobstructed and smooth rim of the head in *Caluromys*. As expected from their commitment to different substrates and differences in the extent and frequency of pronation and supination, *Caluromys* has a more extensive proximal radioulnar (**RaUlp**) articulation (Fig. 13A, B, E, F).

Both taxa have an extensive, ledge-shaped articulation for the radial sesamoid (**RaRas**). The tuberosity for the biceps brachii in *Metachirus* (**rbbrt**) is both more proximal and more sharply delineated distally than in *Caluromys*. It is also more proximally located in caenolestids than in *Dromiciops*.

Strikingly different is the medial edge of the radius, where the origin of the flexor digitorum profundus anteriorly and the abductor pollicis longus posteriorly create a sharp and prominent ridge for most of the length of the radius below the **rbbrt** in *Caluromys*. Among the didelphids, neither *Metachirus* nor *Didelphis* display this distinct sharp ridge. Both *Dromiciops* and *Rhyncholestes* have relatively unmodified radial shafts, although this does not preclude some significant differences in their musculature.

Distally the radius is wider mediolaterally in *Caluromys* than in *Metachirus*. This is congruent with the notion that in an arboreal didelphid species the mobility in the upper wrist joint (**UWJ**) is more extensive than in a terrestrial one. The shape of the ulnar styloid process (**ulst**) and its mobility- *vs* stability-related mechanics well reflect the habitus differences in the two didelphids (see ulst on Fig. 13C, D, G, H). In *Caluromys* the ulnocuneiform (**UlCn**) facet occupies the entire distal surface of the ulna without any narrowing of the tip of the ulnar styloid process. In *Metachirus* the styloid is considerably narrowed into a tip compared to the bulbous distal part of the ulna, and is somewhat pointed (the **UlCn** articulation on the styloid faces laterally; in the anatomically correct position of a quadruped standing). The only significant sign of a stability-related structural difference on the distal radius in *Metachirus*, compared to that of *Caluromys*, is the slightly more robust and more distally extended radial distal malleolus (Fig. 13C, D, G, H; **rdm**).

In contrast to the didelphid variation related to stability in the upper wrist joint (**UWJ**, comprised of the **RCJ** and **UCJ**), the caenolestids, compared and contrasted to the similarly sized *Dromiciops*, while exhibiting deep ulnar styloid and radial distal malleolus, opted for a substantially widened (and also sharply angled) contact between the distal radius and the scaphocentrale and lunate. Thus, in addition to the interlocking and sharply angled **rdm**, the additional distal extension of the part of the radius articu-

TABLE 2. — Functional differences (or lack there of) in the ulna of arboreal (*Caluromys derbianus* (Watrhouse, 1841), *Dromiciops gliroides* Thomas, 1894) and terrestrial (*Metachirus nudicaudatus* (Demarest, 1817). *Rhyncholestes raphanurus* Osgood, 1924) species of extant marsupials that were employed as models. For definition of UTNI see text.

Traits	Arboreal	Terrestrial
1. Olecranon process	Shorter and narrower proximally	Longer and broader proximally
2. Trochlear notch and related attributes	Shallower and less restrictive; UTNI is relatively low	Deeper and more restrictive; UTNI is relatively high
3. Conformation of the ulnar proximal trochlear crest (**ulptc**)	Nearly equal medial and lateral limbs of crest	Disproportionate widening of medial segment of crest
4. Condition of the posterior border of proximal ulna	Slightly bowed posterior border	Straight to concave posterior border
5. Radial notch and shaft characteristics	Faces more anteriorly; facet usually not connected to coronoid process	Slightly offset laterally; facet is usually extended onto coronoid process
6. Muscle attachments to proximal ulna	No clear differences	No clear differences
7. Configuration of distal end	Broad styloid process for full ulnocuneiform articulation	Narrowed styloid process and pointed ulnocuneiform articulation

lating with the lunate assures extreme interlocking stability with the proximal row of carpals (Figs 14; 15). Table 2 summarizes a list of characteristic differences (as well as relatively invariant similarities) in the ulna, and Table 3 summarizes differences for the radius of the four model species. These attributes are employed in judging both adaptively and phylogenetically significant information gleaned from the fossils.

Carpus and hand. Carpal patterns for fossils are rare and usually incomplete (see Szalay & Trofimov 1996, for that of *Asiatherium*). But because of their relatively slow rate of evolution (Szalay 1994), particularly in the Metatheria, the complete patterns (when available) can be extremely useful tests of both adaptational and phylogenetic hypotheses. We suspect that the bradytelic evolution of the carpus in metatherians is closely related to the nearly universal retention of a grasping hand with convergent digits (see Haines 1958). Species-specific patterns in marsupials must contain compromise functions and roles for both neonate adaptations for reaching the nipples, as well as the subsequent life history adaptations that appear to be severely constrained in most marsupial lineages compared to eutherians (Lillegraven 1975; Lillegraven *et al.* 1987; Szalay 1994).

We briefly comment here on the adaptive differences between the hand structure of *Dromiciops* and *Caenolestes* Thomas, 1895 (the latter representing caenolestids in general). Below, under phylogenetic considerations, we reiterate the historically relevant details. The highly mobile radioulnar articulation with the proximal row of carpals, as well as the sliding and mobile contact between the unciform and cuneiform in the microbiotheriid, are in sharp contrast to the highly restricted and locked **UWJ** and the stepped articulations between the scaphocentrale and the trapezium and trapezoid of caenolestids (Fig. 15).

These clearly adaptive differences in the **UWJ** articulation and general mobility- *vs* stability-related modifications in the two groups are superimposed on two otherwise stage- (rather than taxon-) specific patterns. The pattern in caenolestids (and didelphids), where the scaphocentrale is in lateral contact with a magnum that contacts the lunate, is likely to be an ancestral metatherian pattern either in the Sudameridelphia, or deeper in the Metatheria. In *Dromiciops* (and dasyurids) the lateral extension

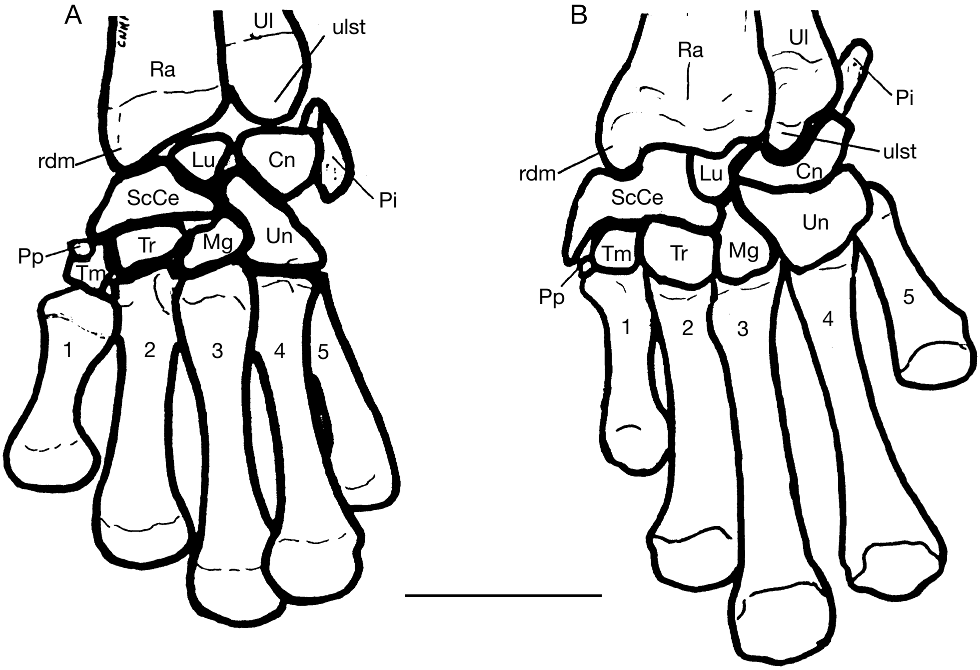


FIG. 15. — Anterior view of left distal antebrachium, carpus, and metacarpus; **A**, *Dromiciops*; **B**, *Caenolestes*. Abbreviations: **Cn**, cuneiform; **Lu**, lunate; **Mg**, magnum; **Pi**, pisiform; **Pp**, prepollex; **Ra**, radius; **rdm**, radial distal malleolus; **ScCe**, scaphocentrale; **Tm**, trapezium; **Tr**, trapezoid; **Ul**, ulna; **ulst**, ulnar styloid process; **Un**, unciform. Scale bar: 2 mm.

of the scaphoid (scaphocentrale) is retained from the more primitive didelphid pattern, but it is interposed between the magnum and lunate.

Pelvis. Elftman's (1929) classic study is still the most broadly comparative and functionally-oriented effort on the osteology and myology of the os coxae of metatherians. It provides a useful basic account of the myology and osteology of the pelvis in *Didelphis*, *Pseudocheirus* Ogilby, 1837, *Petauroides* Thomas, 1888, *Macropus* Shaw, 1790, *Perameles* É. Geoffroy, 1804, *Phascolarctos* Blainville, 1816, *Vombatus* É. Geoffroy, 1803, and *Sarcophilus* F. G. Cuvier, 1837. Muscle attachments and lever relationships, as well as the morphology of the acetabula are discussed. A more recent, analytical and probing study of the possible functions of the epipubic bones in mammals is by White (1989), and commented on by Szalay (1994: 57-59). These bones have been long associated with marsupials ("marsupial bones"), although they are obviously ancient synapsid attributes. Their primary role, as suggested by Elftman, was probably related to the support of the abdomen. The cineradiographic study of ambulatory and cursorial carnivorans by Jenkins & Camazine (1977) has probed some of the fundamental questions regarding the functional connections between the construction of components of the hip joint and locomotor behavior. Kielan-Jaworowska (1975), reporting on the diagnostic hip attributes of the Cretaceous eutherian *Barunlestes*, made it obvious that this bone has been retained in some early clades identified as eutherians on dental and cranial grounds (see also Novacek *et al.* 1997). The exact role of epipubic loss, if any, in the origin of placentalian in utero growth-acceleration of the embryo, and the probably concurrent loss of the nipple-attached phase of neonate development, however, is unclear.

The modifications of the pelvis in extant marsupials, as those of the scapula, is ripe for a major

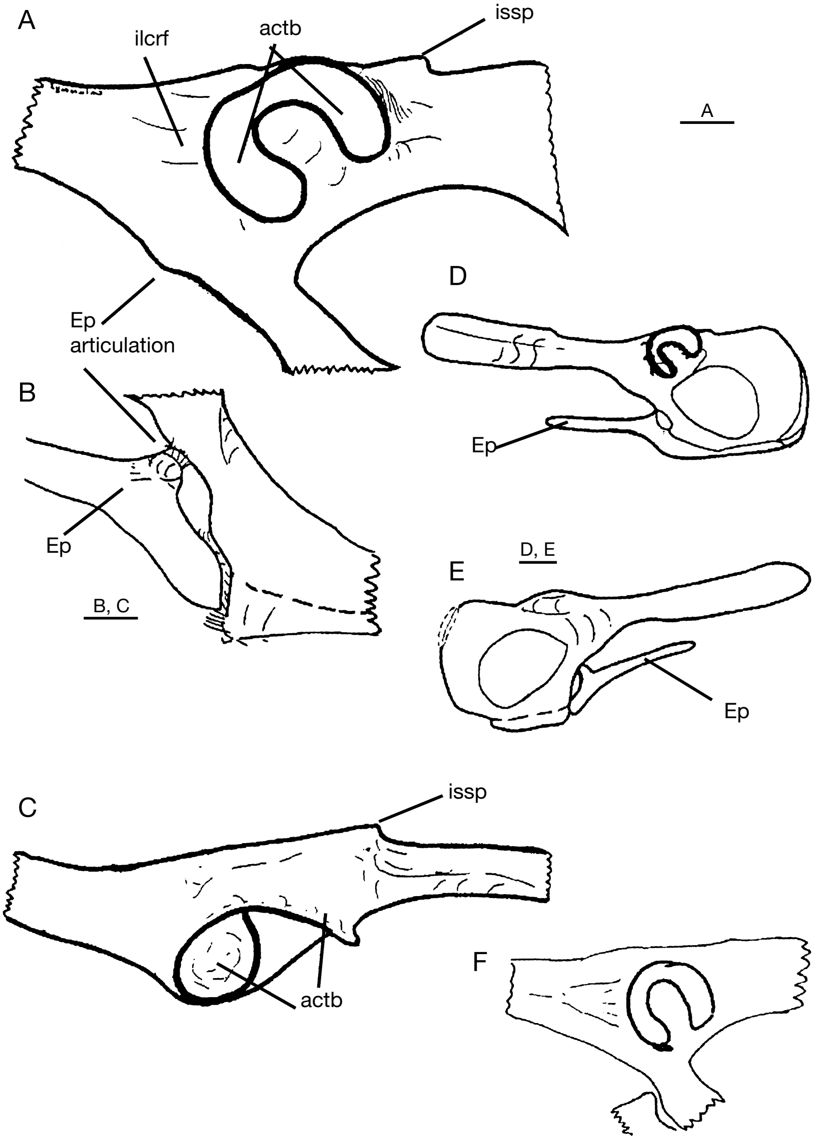


FIG. 16. — Details of innominates; **A-E**, *Caluromys*; **A**, **B**, **D**, lateral view; **C**, dorsal view; **E**, medial view; **F**, *Metachirus,* lateral view. Abbreviations: **actb**, acetabulum; **Ep**, epipubic; **ilcrf**, iliac crest for quadriceps femoris; **issp**, ischial spine. Scale bars: A-C, 2 mm; D, E, 5 mm.

analysis. This would require not only a size- and ecology-related assessment, but also the details of the exact myological differences that undoubtedly govern the osteological characteristics. Until such a study is undertaken, only a very limited understanding of the few partial specimens from Itaboraí is possible.

Figs 16 and 17 depict selected details of the osteology of the innominate and epipubic bones of *Caluromys*, *Metachirus*, *Dromiciops*, *Caenolestes*, and the small phalangeriform *Cercartetus*. The more ventral of the two articular contacts of the epipubic with the pubis is the more extensive. But for fossils that are missing the ventral and

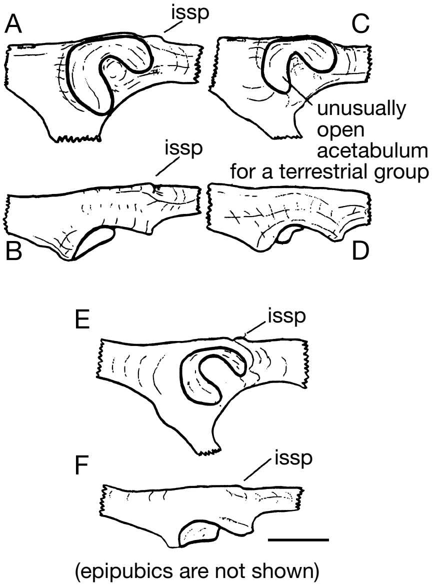


FIG. 17. — Details of innominates; **A**, **B**, *Dromiciops*; **A**, lateral view; **B**, dorsal view; **C**, **D**, *Caenolestes*; **C**, lateral view; **D**, dorsal view; **E**, **F**, *Cercartetus*; **E**, lateral view; **F**, dorsal view. Abbreviation: **issp**, ischial spine. Scale bar: 2 mm.

caudal parts of the hip (along with the borders of the obturator foramen), the prominent tuberosity for the dorsal wing of the epipubic establishes the presence of this bone.

Attachment of the quadriceps femoris on the area cranial to the acetabulum is indicative of the relative importance (i.e. size) of this extensor of the knee and flexor of the hip, and its attachment on the cranioproximal edge of the tibia should be correlated. For fast and powerful extension in either terrestrial forms that scamper, or leapers of all sorts, this tuberosity should be large. Slow arborealists do not show much of this. The muscle is present, but it is not one that heavily and intermittently stresses its origin and insertion. The fact that it also flexes the hip is perhaps less important (see Muizon 1998).

The only suggestion of a useful difference between *Caluromys* and *Metachirus* is in the shape and morphology of the acetabulum itself. As expected, that of the arboreal didelphid is more oblate and elongated, making it less restrictive of the movements of the femoral head. The terrestrial *Metachirus*, like small terrestrial eutherians, has a circular and tightly articulating (restrictive) acetabulum. This generalization, however, does not appear to hold for either *Caenolestes* or *Rhyncholestes*. Surprisingly, both of these taxa show a relatively oblate acetabulum where the anterior and dorsal articular area is enlarged. This condition, interestingly, is not unlike the ones encountered in vertical climbers, in spite of the fact that most caenolestids have been collected on the ground and have been observed to be rapid terrestrial cursors.

Femur. Perhaps more than any other part of the mammalian skeleton, the femur has been extensively studied as to its micro- and macro-morphological manifestation of the functional forces that reflect primarily propulsion-, digging-, suspension-, or sundry other positional behavior-related biological roles. A multitude of different types of studies abound on eutherians, but metatherians have not been discussed adequately in the literature.

The hindlimb reflects locomotor and substrate commitment far better than the forelimb. In light of the relative abundance of fossil specimens of whole femora as well as proximal and distal ends, an adaptive understanding of this bone reveals some important ecological and phylogenetic aspects of the marsupial fauna from Itaboraí. In general, we found the areas of significance to be: a) the head of the femur; b) the trochanteric fossa and the area surrounding it, including the trochanters; c) some attributes of the shaft; and d) the complex distal femur, both its attachment areas for tendons and ligaments and its articular relationship with the tibia, fibula, and parafibula (fibular fabella). The specific adaptive and a few phyletic differences in the femora require a more detailed discussion below (see also Table 4 and Figs 18-20).

In mature specimens of the models the following attributes may reflect adaptational and taxonomic differences between species:

1) size and shape of the head and its orientation, particularly the extent of the articular facet dorsally because it reflects habitual contact with the acetabulum, and, therefore, the extent of taxon-specific abduction possible for the femur;

2) relative height of the greater trochanter;
3) size and orientation of the lesser trochanter;
4) extent and development of the femoral paratrochanteric crest (**fptcr**);
5) absence or presence of the third trochanter (**fthtr**; related to gluteus superficialis, a fast extensor of the thigh across the hip joint), and its lateral extent when present (this feature, present only in caenolestids among extant species, is ubiquitous in the Itaboraí femora);
6) shaft characters related to muscle insertions or loading. Differences in the Femoral Midshaft Diameter Index (anteroposterior midshaft length/mediolateral midshaft length × 100), FMDI;
7) attributes of the groove for either the tendon of the quadriceps femoris or a patella;
8) differences and comparative aspects of the Femoral Distal Height Index (medial condyle depth/distal end width × 100), FDHI, and the Femoral Condyle Width Index (medial condyle width/lateral condyle width × 100), FCWI.

1) In general, the head of the femur in *Caluromys* is both relatively larger and more cylindrical than that of *Metachirus* (Fig. 18). The same relationships are true when we compare *Dromiciops* and *Caenolestes* (Fig. 19E, M). This general comparison is probably also valid for *Dromiciops* vs *Rhyncholestes*, although statistically valid samples of the measurements of the head were not collected for these comparisons. Nevertheless, the slightly smaller microbiotheriid has a femoral head distinctly larger than that of the larger *Rhyncholestes* (Fig. 19L).

The lateral and posterior extension of the femoral head articulation of *Caluromys* reflects the extreme abduction capability of the leg while it is extended posteriorly. The larger size of the overall articular area of the head is related to the lateral extension of the articular surface. In *Metachirus* the articular surface of the head is very close to spherical on its dorsal aspect (Fig. 18). This dichotomy is consistent with the smaller models (Fig. 19). While *Caenolestes* has a spherical femoral head, that of *Rhyncholestes* is more oblate anteroposteriorly, suggesting an extreme specialization for contact exclusively during flexion and extension of the femur.

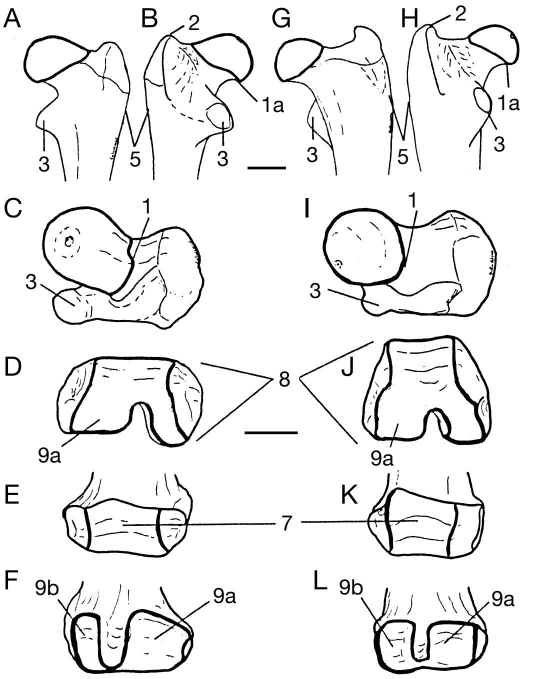


Fig. 18. — Details of left (A, B, G, H) and right (C-F, I-L) femora; **A-F**, *Caluromys*; **G-L**, *Metachirus*; **A**, **G**, anterior view of proximal third; **B**, **H**, posterior view of proximal third; **C**, **I**, proximal view of proximal end; **D**, **J**, distal view of distal end; **E**, **K**, anterior view of distal end; **F**, **L**, posterior view of distal end. For numbered designations of specific characters see text. Scale bars: 4 mm.

2) There is a noticeable difference in the height of the greater trochanter between the two groups. As expected, the terrestrial forms have a somewhat larger trochanter than the arboreal species, but the difference is not great.

3) The lesser trochanter of the models is consistently relatively larger in the arboreal species *vs* the terrestrial forms. This difference in the insertion of the hip flexor iliopsoas, as well as the slightly more caudal orientation of the trochanter in the terrestrial forms, strongly suggests more powerful abduction in the arboreal species, and an emphasis on greater speed rather than power in the terrestrial forms. Other features discussed below support these conclusions. Arboreal animals like *Caluromys* and *Dromiciops* resort to a greater range of habitual abduction and flexion when climbing and positioning themselves in a

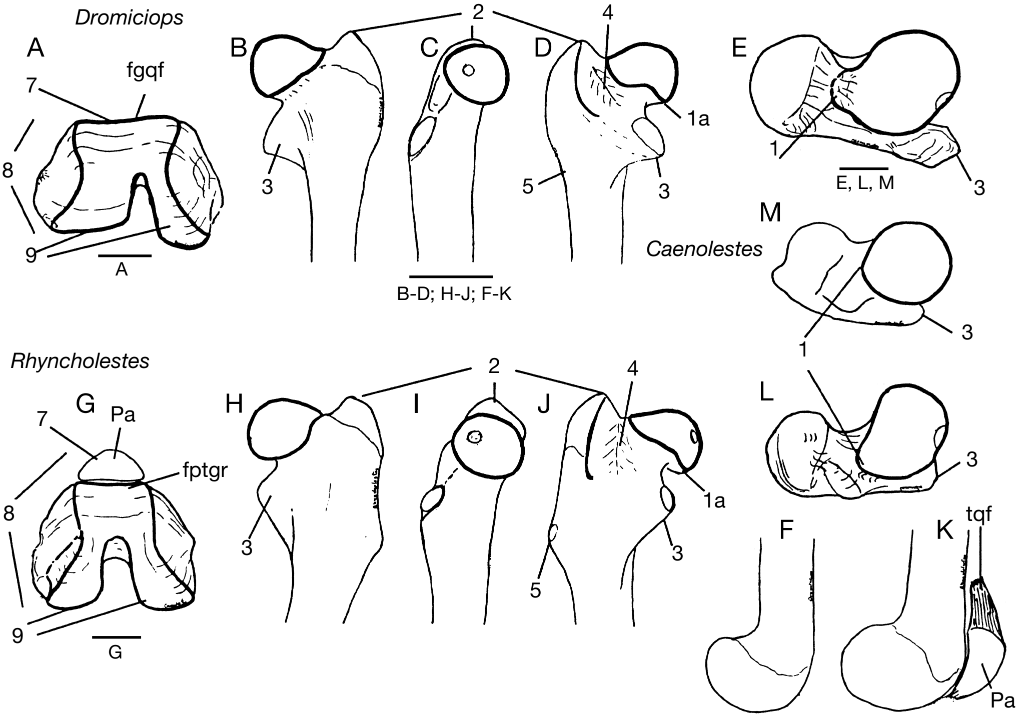


FIG. 19. — Details of left femora; **A**-**F**, *Dromiciops*; **G**-**L**, *Rhyncholestes*; **M**, *Caenolestes;* **A**, **G**, distal views; **B**, **H**, anterior views; **C**, **F**, **I**, **K**, medial views; **D**, **J**, posterior view; **E**, **L**, **M**, proximal views. For numbered designations of specific characters see text. Abbreviations: **fgqf**, femoral groove for quadriceps femoris; **fptgr**, femoral patellar groove; **Pa**, patella; **tqf**, tendon of quadriceps femoris. Scale bars: A, E, G, L, M, 1 mm; B-D, H-J, F-K, 2 mm.

small branch milieu, than predominantly terrestrial forms like *Metachirus* and caenolestids.

4) The often well-developed paratrochanteric crest within the trochanteric fossa, and the attendant differences between the taxa, while undoubtedly related to the ischiofemoral ligament, is difficult to interpret.

5) It should be noted here that while glirimetatherian caenolestids, like archimetatherians (e.g., peradectids from Messel) and sudameridelphians, have a well-developed third trochanter, didelphids and the didelphid-derived australidelphians lack this process regardless of their habitus. This is a significant phylogenetic, rather than functional, attribute. Although the origin of the diagnostic loss of the third trochanter for living metatherians (except for caenolestids) is undoubtedly related to the adaptive shift of the protodidelphid, subsequent habitat and locomotor diversity apparently has not altered this condition.

6) The significant attributes of the shaft relate primarily to various cross-sectional dimensions. The FMDI, taken at midshaft, shows some interesting differences between the arboreal and terrestrial forms, independent of size or phyletic factors. In *Caluromys* and *Dromiciops* the index is 103 and 102, respectively, whereas it is 82 and 90 in *Metachirus* and *Rhyncholestes*. The usefulness of this index is strengthened by the mean value of 83 for the scansorial and terrestrial *Didelphis*.

7) Possibly as a direct consequence of the usual lack of a patella in metatherians, there is a groove, developed to various degrees in different taxa, for the tendon of the quadriceps femoris as it crosses the knee, starting on the distal shaft of the femur and continuing across the distal epiphysis. Caenolestids, however, as peramelids and noto-

ryctids, as well as the stem placentalian, evolved an exceptionally well-developed patella independently. The patella significantly extends the lever of the quadriceps. But in addition to having a substantial patella, the height of the distal femur anteroposteriorly is also far greater in caenolestids than in *Dromiciops*. A similar proportional relationship exists between the distal femora of the larger model species, although the patella is lacking in *Metachirus*. Thus the deep distal femur of metatherians and the near equality of the proportions of the distal condyles strongly support the combination as an indicator of terrestriality. In general, however, this proportional difference can be a significant indicator of leaping ability, and it is not a feature directly predictive of terrestrial substrate-related modification. The inferred ancestry of the highly arboreal, grasp-leaping, Euprimates had an anteroposteriorly very deep distal femur, along with their placentalian condylar proportions.

8) The articular condyles likely reflect the habitual positioning of both the femur and the crus, particularly the relation of the crus to the distal femur during obligate postures and locomotion (Figs 18; 19). We have discussed this relationship above. The relative mediolateral dimensions of femorotibial articular surfaces (**FeTim** and **FeTil**) are highly characteristic of both fossil and extant marsupial species, and are presumably related to their locomotor regimes, but less directly with substrate preference. Therefore a direct causal association with arboreality, however, without a consideration of the positional mechanics based on other factors may be spurious, as the position and mechanics of the hindlimb are probably responsible for the relative differences in the articular surfaces. The inferred primitive therian condition probably consisting of a marked asymmetry between the sizes of the medial and lateral femoral condyles (but not in anyway corroborated by a largely missing fossil record), is present in *Didelphis* and *Caluromys*, as well as in *Dromiciops*[26].

The difference in the proportion of the condyles between our terrestrial and arboreal models consistently highlights the recurrent near-equality between the two distal femoral condyles in habitually terrestrial marsupials. Such proportions, seen in placentals, are due to the selectively mediated reduction of the lateral condyle in obligate terrestrial species (as probably in the protoplacentalian; *contra* Martin 1990). A modification of the extensive crural abduction seen in most didelphids during push-off (discussed above) brought about the reduction of the lateral femoral condyle relative to that of the medial one in order to bring the hindlimb faster under the body. As a result of this transformation, the shape is cylindrical rather than conical. Selection for a more adducted and parasagittal position of the crus in line with the knee during push-off (less abducted than that described by Jenkins 1971, for *Didelphis*) necessitated the morphological change. In the derived position the loads are relatively evenly distributed in the knee. Such a condition in extant eutherians is one of the strongest tests of the hypothesis that their last common ancestor (Szalay 1984, 1994).

The distal ends of femora of the model species, therefore, offer some highly significant functional-adaptive attributes that are probably universally applicable for fossil metatherian phena, and strongly corroborate paleobiological hypotheses based on these. In general, the height of the distal femur (anteroposteriorly measured) compared to its width (mediolaterally measured) is invariably greater in the terrestrial model species. This ratio is independent of the unusual presence of a patella in caenolestids. This difference has been attributed to the "slow" *vs* "fast" (or less *vs* more stabilized) flexion and extension of the lower leg (due to the action of the quadriceps femoris) in the literature (e.g., Tardieu 1981; Kappelman 1988). Cifelli & Villarroel (1997) have pointed out, however, that the proportions of the distal femur are a somewhat more complex issue. These proportions appear to be related to the relative length of the femur and tibia. They contend that a deeper distal femur places the action of the quadriceps farther from the axis of rotation. This arrangement gives the muscle greater mechanical advantage (i.e. more power) rather than speed. Arboreal species that do not travel particularly

TABLE 3. — Functional differences (or lack there of) in the radius of arboreal (*Caluromys derbianus* [Watrhouse, 1841], *Dromiciops gliroides* Thomas, 1894) and terrestrial (*Metachirus nudicaudatus* [Demarest, 1817], *Rhyncholestes raphanurus* Osgood, 1924) species of extant marsupials that were employed as models.

Traits	Arboreal	Terrestrial
1. Shape of head and articular contact with capitulum (former is circular in *Dromiociops* and all Didelphidae)	Articular contact is deeper, more circular, and more extensive	Articular contact is shallower and more oblate. Head is elliptical in caenolestids.
2. Central process	Poorly developed or absent	Well-developed
3. Proximal radioulnar articulation	More extensive in angular distance	Less extensive in angular distance
4. Medial edge of shaft	In *Caluromys* origin for well developed flexor digitorum profundus anteriorly and abductor pollicis longus posteriorly form sharp ridge	No sharp ridge
5. Distal end	Radial distal malleolus shallower and smaller	Radial distal malleolus deeper and larger

rapidly abduct-adduct their hindlimb considerably more than terrestrial forms which restrict limb movements more to the parasagittal plane. The adaptive importance of knee joint modification is also well-illustrated in the comparisons of *Dromiciops* with caenolestids (Fig. 19). Even without the added increase in the leverage of the quadriceps femoris with the addition of the patella (depth of the knee), a feature lacking in didelphids and *Dromiciops*, the distal femur is still considerably deeper than wide in caenolestids than in *Dromiciops*. Patellae, of course, are ubiquitous in eutherians.

Correlated with the "slow" *vs* "fast" knee joints (a simplified assessment, as noted above), the femoral groove for the quadriceps femoris (**fgqf**) is wider and not particularly concave in the arboreal *Caluromys*, whereas it is narrower and slightly concave in *Metachirus*. These subtle differences indicate stability-related properties in these opossums. Another interesting correlate on the distal femora in these species (related to the degree that crural abduction occurs during the push-off phase of locomotion) is the morphology of the surface of the distal femoral condyles. As evident on Fig. 18F, L, the caudal view of the distal femur in *Caluromys* shows the lateral condyle to be conical in shape, in contrast to that of *Metachirus* where this structure is cylindrical[27]. Table 4 summarizes a list of characteristic differences (as well as relatively invariant similarities) in the femur of the four model species. These attributes are employed in judging both adaptively and phylogenetically significant information gleaned from the fossils.

Tibia and fibula. A number of attributes of the proximal crus (Figs 20-22) also closely reflect many of the differences noted under the discussion of the distal femora of the model species. The distal crus has additional significant attributes that appear to predict habitus. The following areas of tibiae have useful properties that permit both taxonomic and functional-adaptive characterization of the models and other metatherians:

1) proximal surface of tibia, specifically the proportions of the medial and lateral condyles which show significant adaptive differences. The Tibial Proximal Articular Index (medial condylar width/lateral condylar width × 100), TPAI, reflects these differences that, in turn, are indicative of mechanics related to the range of arboreal to terrestrial habits;

2) extent of quadriceps femoris insertion anterior to the femoral articulation; this is a probable indication of the lever function of the quadriceps femoris, that can be expressed as the Tibial Proximal Depth Index (width of proximal

TABLE 4. — Functional differences (or lack there of) in the femur of arboreal (*Caluromys derbianus* [Watrhouse, 1841], *Dromiciops gliroides* Thomas, 1894) and terrestrial (*Metachirus nudicaudatus* [Demarest, 1817], *Rhyncholestes raphanurus* Osgood, 1924) species of extant marsupials that were employed as models. For definitions of FDHI, FCWI, and FMDI see text.

Traits	Arboreal	Terrestrial
1. a) Size, shape, orientation of head; b) articular surface.	a) Larger, more cylindrical as a rule; b) Pronounced lateral and posterior extension of articular surface.	a) Smaller and more spherical; b) Little extension of articular surface laterally and posteriorly.
2. Height of greater trochanter.	Somewhat lower.	Somewhat higher.
3. Size and orientation of lesser trochanter.	Consistently larger and not retroflexed.	Consistently smaller and retroflexed.
4. Extent and development of paratrochanteric crest.	Equivocal.	Equivocal.
5. Third trochanter (absent in all didelphids); more of a heritage than habitus feature in Metatheria (see Table 13).	Absent.	Absent in *Metachirus* but present in *Rhyncholestes* (and in all caenolestids, as well as all other Cretaceous-Cenozoic non-didelphid Didelphida).
6. a) Shaft characteristics; b) FMDI.	a) Equivocal; b) Higher (anteroposteriorly deeper shaft).	a) Equivocal; b) Lower (mediolaterally wider shaft).
7. Groove on distal end.	Equivocal.	Equivocal.
8. a) FDHI; b) FCWI.	a) Distal height is shallow; b) lateral condyle is much wider.	a) Distal height is pronounced; b) lateral condyle is narr owed, to various degrees.

tibia/depth of proximal tibia × 100), TPDI, which is indicative of the degree of deepening and/or narrowing of the proximal tibia;
3) relative depth of the medial malleolus, expressed as the Tibial Medial Malleolar Index (depth of medial malleolus medially/anteroposterior depth of distal tibia × 100), TMMI, it demonstrates a relationship that is indicative of the relative degree of stabilization of the upper ankle joint medially;
4) presence of a sigmoid curvature of the tibia medially (tibia convex laterally); this is an enigmatic, yet often characteristic trait;
5) nature of the astragalar articulations; these reflect the extent of the rotation of the foot in the upper ankle joint during inversion-eversion by the foot. This rotation (or its lack) is mirrored by the relative proportions of the **ATim** facet, the extent of the **ATip** facet in most ameridelphians, its absence in caenolestids, and its presence or absence in different groups of australidelphians. These are all good character combinations for both adaptive and phyletic evaluation.

Although there are no fibulae known to us from Itaboraí, attributes of this bone are closely relevant to an evaluation of the other elements of the metatherian (and therian) knee complex. This knee complex in *Caluromys* (Fig. 20) is highly characteristic of not only didelphids but probably also of more ancient taxa of the Metatheria.
1) The larger lateral femorotibial (**FeTil**) articulation of the tibia in *Caluromys* with its slight convexity compared to the smaller and concave medial femorotibial facet (**FeTim**), closely mirrors the proportions, and, to some degree, the general shape of the femoral condyles. The slight concavity of the mediolaterally extensive conarticular **FeTil** facet of the femur, together with the tibial attributes, exhibit the range of abduction of the lower leg during push-off (as repeatedly noted above). In contrast to *Caluromys*, the homologous attributes of *Metachirus* reflect the decided shift towards more equal dimensions of the medial and lateral femorotibial articulation. The differences in the proportions of the femorotibial facets between *Dromiciops* and caenolestids also

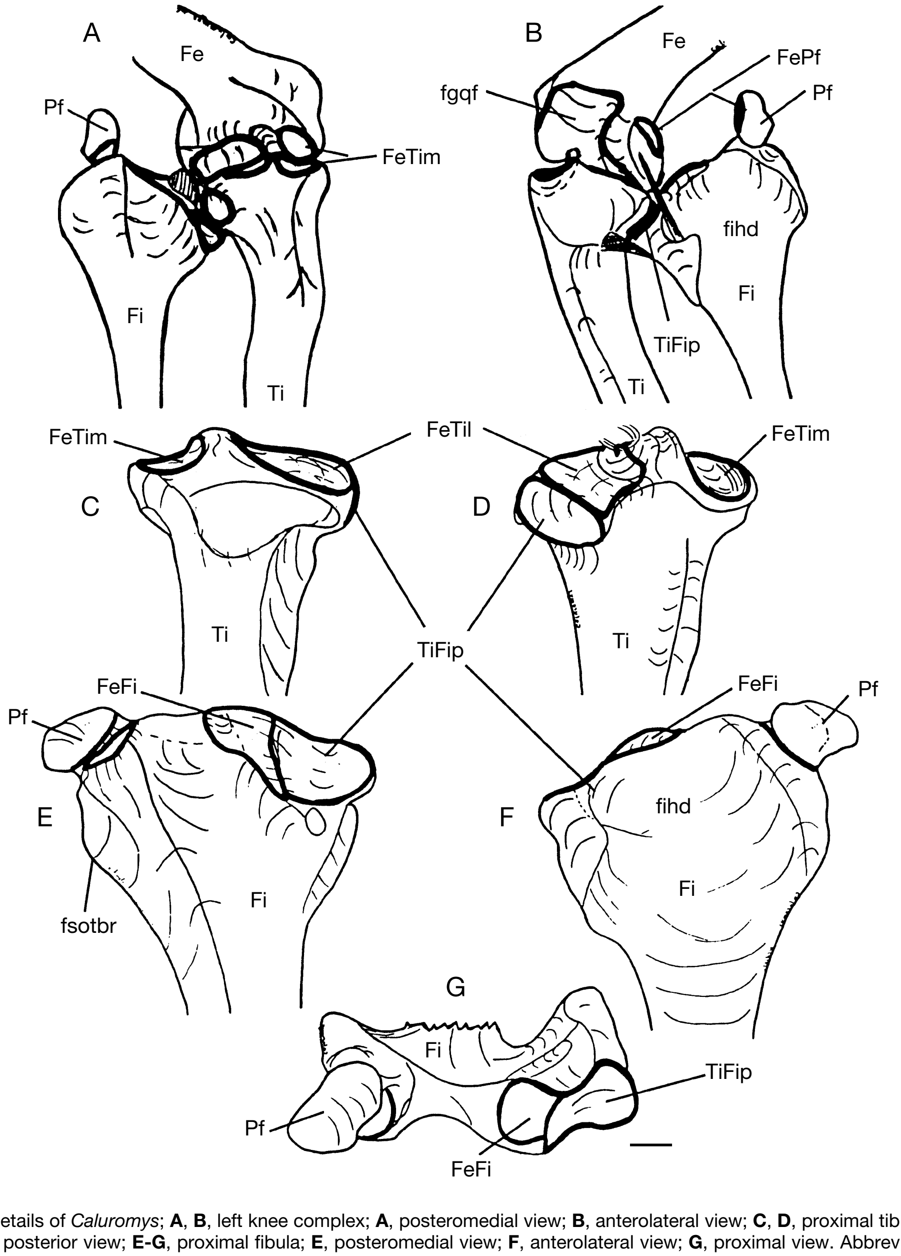


FIG. 20. — Details of *Caluromys*; **A**, **B**, left knee complex; **A**, posteromedial view; **B**, anterolateral view; **C**, **D**, proximal tibia; **C**, anterior view; **D**, posterior view; **E-G**, proximal fibula; **E**, posteromedial view; **F**, anterolateral view; **G**, proximal view. Abbreviations: **Fe**, femur; **FeFi**, femorofibular facet; **FePf**, femoroparafibular facet; **FeTil**, lateral femorotibial facet; **FeTim**, medial femorotibial facet; **fgqf**, femoral groove for quadriceps femoris; **Fi**, fibula; **fihd**, fibular head; **fsotbr**, fibular soleus tuberosity; **Pf**, parafibula; **Ti**, tibia; **TiFip**, proximal tibiofibular facet. Scale bar: 2 mm.

mirror the contrast between the arboreal and terrestrial didelphids (Fig. 22).

2) The place of attachment of the quadriceps tendon (**tqfcr**) is more craniad in *Metachirus* than in *Caluromys*, suggesting an increased mechanical advantage for the powerful lower leg extensor and hip flexor (Fig. 21A, E). The lack of a commensurate anterior extension of the area of quadriceps

attachment in caenolestids compared to *Metachirus*, however, may be related to the presence of the large patella that considerably increases the leverage of the quadriceps.

3-5) The distal tibia offers a number of significant attributes that are both functionally revealing as well as phylogenetically important (we discuss the latter under phylogenetics). In *Caluromys* the tibial medial malleolus is relatively shorter, and the surface area of the **ATim** facet is relatively smaller than these in *Metachirus* (Fig. 21C, D, G, H). These attributes are correlated with the greater need for medial buttressing of the **UAJ** in a terrestrial cursor and the need for greater mobility in that joint in an arboreal didelphid. In most marsupials the major tarsal adjustments for inversion occur in the **UAJ** (Szalay 1994).

While the distal tibia of *Dromiciops* is essentially similar to that of didelphids, the ultimate source of the Australidelphia, hence Microbiotheriidae (Szalay 1994), caenolestids display what may be considered to be a major modification of the primitive metatherian condition (Fig. 22) that resembled the condition retained in didelphids. As discussed in Szalay (1994), the caenolestids (as well as dasyuromorphians, peramelids, macropodoids, and possibly the eutherians if their source was metatherian-like in that respect) independently eliminated the posterior extension of the astragalotibial articulation (**ATip**) on the tibia. The glirimetatherian caenolestids and sudameridelphians show a considerably distinct **ATim** facet. The latter condition, of course, may well be primitive in the group that was the source of sudameridelphians. Didelphids departed from a basal sudameridelphian cruropedal stage but retained a large **ATip** facet. Nevertheless, the remnant of a posterior buttress for such a facet in caenolestids, as well as the condition in some borhyaenids, suggests the presence of a large **ATip** facet on the tibia in the ancestral sudameridelphian (Szalay 1994: 201-206). Both of these reduced conditions are undoubtedly related to obligate terrestriality. They represent parallel (or possibly homologously shared) adaptive shifts, similar to the independent protoeutherian condition, where movement is generally restricted to flexion and extension of the foot in the **UAJ**. A particularly revealing testimony to the direction of this transformation, that of the derived metatherian elimination of the **ATip** facet in caenolestids, is the posterior shelf that persists on the distal tibia. This area appears to have been the bony base of the eliminated part of the posterior segment of the astragalotibial facet.

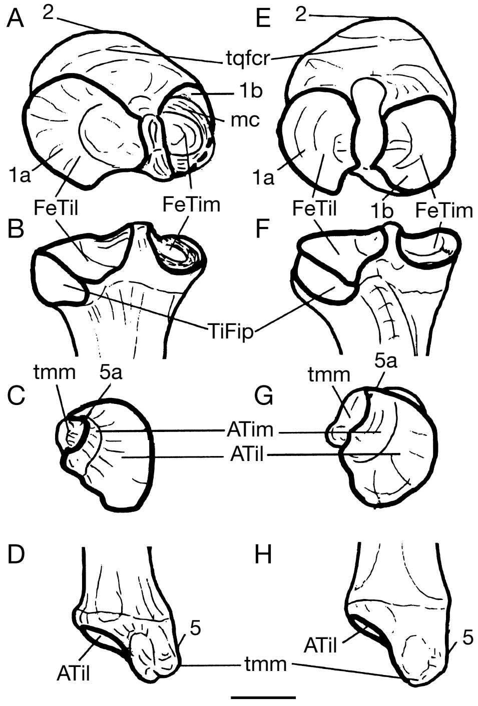


Fig. 21. — Details of left tibiae; **A-D**, *Caluromys*; **E-H**, *Metachirus*; **A**, **E**, proximal view of proximal end; **B**, **F**, posterior view of proximal end; **C**, **G**, distal view of distal end; **D**, **H**, posteromedial view of distal end. For numbered designations of specific characters see text. Abbreviations: **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **FeTil**, lateral femorotibial facet; **FeTim**, medial femorotibial facet; **mc**, meniscus; **TiFip**, proximal tibiofibular facet; **tmm**, tibial medial malleolus; **tqfcr**, tibial crest for quadriceps femoris. Scale bar: 2 mm.

Although the fibula is not represented in the Itaboraí collection we describe, we treat some aspects of the proximal fibula in the models here, as this has relevance to both the femoral and tibial morphology discussed (Figs 20-22). The most characteristic aspect of interspecific fibular differences is the extent to which the proximal fibula is

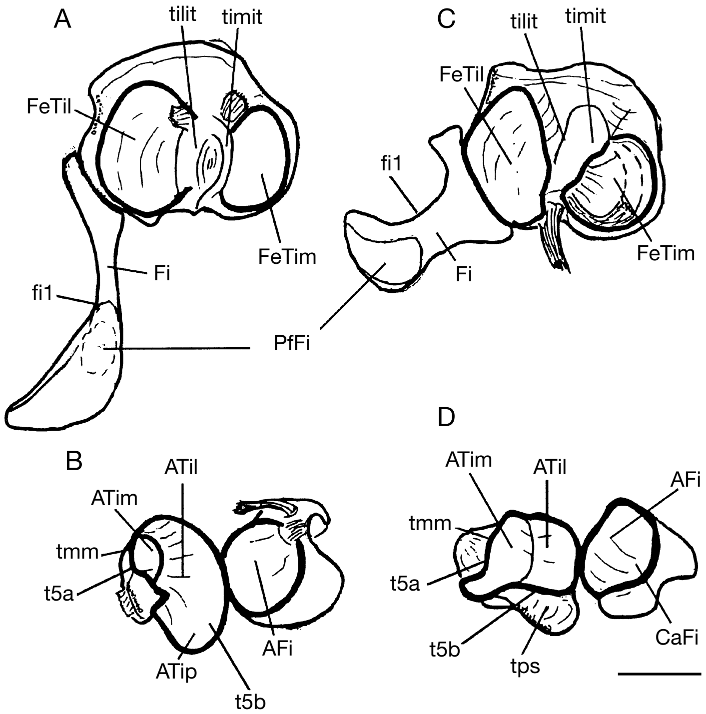


FIG. 22. — Details of left crus; **A**, **B**, *Dromiciops*; **C**, **D**, *Caenolestes*; **A**, **C**, proximal view of proximal ends; **B**, **D**, distal view of distal ends. For numbered designations of specific characters see text. Prefixes before the numbers: **t**, tibial; **fi**, fibular. Abbreviations: **AFi**, astragalofibular facet; **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **ATip**, posterior astragalotibial facet; **CaFi**, calcaneofibular facet; **FeTil**, lateral femorotibial facet; **FeTim**, medial femorotibial facet; **Fi**, fibula; **PfFi**, parafibulofibular facet; **tilit**, tibial lateral intercondylar tubercle; **timit**, tibial medial intercondylar tubercle; **tmm**, tibial medial malleolus; **tps**, tibial distal posterior shelf. Scale bar: 1 mm.

either broad and palmate, or narrowed, the latter approaching the extant eutherian condition. Szalay (1994) has given descriptive accounts of most of the distal crural variation in extant marsupials in conjunction with analyses of the upper ankle joint. It is probably true that a wide and flat proximal fibula is characteristic of the primitive therian condition, and that it is generally retained, particularly in arboreal didelphids and *Dromiciops*. The fibula articulates with the tibia, femur, and the parafibula. The latter, in turn, has an additional articular contact with the femur (**FePf** facet) proximal to the **FeFi** facet on the femur. These relationships are detailed in Fig. 20 for *Caluromys*. Argot (2001) also noted that a wide proximal fibula is related to a well-developed peroneus longus. This is related to the ability to grasp by abducting the hallux widely. It is a functional solution different from that seen in euprimates.

In addition to its role in the mechanics of the hallux, the proportions of the proximal fibula (Figs 20; 22) appear to be closely correlated with the biomechanics of bracing the knee during abduction and extension of the lower leg during push-off, and, therefore, also with the degree to which this function is performed (and differs) in an arboreal *vs* habitually terrestrial metatherian. Both *Metachirus* and caenolestids, like the protoplacentalian, have considerably reduced the dimensions of the fibula proximally. Interestingly, however, in spite of the reduction of the head of the fibula in caenolestids, a relatively enormous parafibula is retained. Retention of a small parafibula in extant eutherians is not uncommon (e.g., pangolins, *Ptilocercus* Gray, 1848, etc.).

Tarsus and foot. Tarsal bones also closely mirror adaptive demands, but within well understood heritage contexts of the specific taxa. In general, the relationship between their mechanics and roles is well understood among extant metatherians and eutherians. Because, and not in spite, of this well understood relationship of the complex interacting network of bones (as well as ligaments and muscles), their phylogenetic information content is exceptionally high. Usage of functionally and phyletically unanalyzed attributes from the tarsus in the literature has often led to irrelevant character information fed into equally irrelevant parsimony algorithms, with predictable results.

We do not discuss here in detail the complex adaptive attributes of the tarsus and the foot (which are strikingly constrained by heritage), as these topics have been treated in some detail by Szalay (1994). A study of some excellent undescribed tarsal remains from the Tiupampa locality of Bolivia by Szalay, Muizon, and Argot is in progress, in which additional details are reported. Nevertheless, because there is evidence that the importance of the ecomorphological aspect of the tarsus for phylogenetics has been either overlooked, not understood (Kirsch *et al.* 1997; Springer *et al.* 1998), or, in general, considered to be not particularly relevant to phylogenetic analysis, we discuss below certain adaptively and phyletically important differences between extant marsupials, the Itaboraí specimens, and some of the previously described Tiupampa marsupials. We discuss and summarize the relevance of important differences between the sudameridelphian stem, didelphid, caenolestid, and protoaustralidelphian conditions.

TESTS OF THE MARSUPIAL MODELS

It is instructive to see how a relatively complete representation of the osteology in extant species ("unknowns") other than the ones designated as models can give a high degree of confidence in the models for paleobiological assessment. We used two living species as tests of the traits that indicate certain mechanical and ecological attributes in the model taxa, and also checked the evidence offered by two exceptionally complete fossil taxa. While the value of the fossils as tests of living models is nonexistent, evaluation of (near) complete fossil skeletal material does provide an opportunity to make us of the models for fossil species rather merely aspects of these. This is preliminary to our description and quasi-ecological evaluation of the collection of unassociated fossils we describe.

Didelphis virginiana is an ecologically interesting species, representative of its genus in many respects. It is probably the largest of living didelphids, and it appears to be equally at home on the ground as it is in trees. In fact, its scansorial, quasi-terrestrial predisposition was probably a likely key to its unprecedented success in the temperate and only partially wooded areas of North America during the last century, where it has come to colonize virtually all habitats (Gardner 1973). As the figures documenting some aspects of intraspecific variation (Figs 2-6) and the description and discussions above suggest, most of the information on the joint complexes of the skeleton are indicative of those widespread attributes that occur in didelphids, regardless of substrate related specializations in any one species. Nevertheless, a certain ecomorphologically significant pattern emerges from the following attributes of *D. virginiana*: a) disproportionate enlargement of the humeral lateral tuberosity (**hltub** on figures) compared to the medial one; b) overhanging head of the humerus on a slightly elongated neck ("beaking"); c) decidedly conical and relatively very large humeral trochlea (**htr**) that is wide medially and very narrow at its zonal lateral extremity (Fig. 4C); d) well-developed radial central process (**rcpr**); e) deep radial distal malleolus (**rdm**); f) exceptionally elongated ulnar olecranon process (**ulol**); g) overhanging and medially extended femoral head; h) somewhat reduced lesser trochanter (**fltr**) compared to *Caluromys* and *Dromiciops*; i) less mediolaterally extensive development of the lateral femorotibial contact (as evidenced by the relative size of the lateral femoral and tibial condyles in the adults, **flc** and **tilc** on Figs 3B and 6, respectively) than in *Caluromys*.

The terrestrial features in the postcranium of *Didelphis* appear to be a decidedly derived constellation in light of universal didelphid adaptations that almost certainly indicate arboreal beginnings. Such is the transformed pedal complex of the stem didelphid from an ancestral sudameridelphian stage. Similar to this is the highly adapted carpometacarpal complex of didelphids. It is particularly derived in the articulation of the lateral metacarpals with the unciform (Szalay 1994), closely paralleling the grasping related attributes of the didelphid calcaneocuboid joint. How ancient the didelphid carpal complex is within the Metatheria, however, is not known, and, therefore, its taxonomic value is still equivocal.

The skeletal traits of the small terrestrial *Monodelphis domestica* (Figs 23; 45G, H) also support the recurrent reliability of the mechanical attributes we explored. These appear to be strongly and probably causally correlated with primarily non-arboreal positional behaviors. The following characters give a morphological profile of a small animal whose skeleton, given its didelphid heritage, has mechanically optimized those areas that are subjected to the forces habitually incurred on a terrestrial substrate, without impairing at least its general arboreal abilities: a) humeral lesser (medial) tuberosity hypertrophied as in the terrestrial models; b) complete absence of humeral torsion (the transverse axis of the distal humerus forms 90° with the craniocaudal alignment of the humeral head); c) robust extension of the hplcr proximally as in the terrestrial models; d) humeral trochlea broad medially and narrowed in the zonal area when examined distally; e) disproportional medial and lateral crests of the ulnar proximal trochlear crest, the medial portion (**ulptcm**) being at least twice as long as the lateral one (**ulptcl**), as well as proximodistally aligned, as in the terrestrial models; f) relatively long olecranon process of the ulna; g) head of the femur somewhat medially extended; h) femoral lesser trochanter relatively small and caudally oriented; i) proportions of the condyles of the distal femur and proximal tibia are like those of the terrestrial models; and j) medial malleolus of the tibia is deep.

We include in this section a brief overview of some aspects of two very complete fossil marsupial skeletons, *Pucadelphys* and *Mayulestes*, respectively, for which greatly detailed descriptions were made available by Muizon (1995), Marshall & Muizon (1995), Marshall & Sigogneau-Russell (1995), and Muizon (1998). We briefly consider information from these specimens in light of our arboreal and terrestrial models described above, although neither *Pucadelphys* nor *Mayulestes* are either didelphids, microbiotheriids, or caenolestids, nor are they, in our view, especially related to the Didelphidae in exclusion of other probable sudameridelphian ties. Our functional assessment of the two fossil taxa is in concordance with the detailed analyses of Muizon (1998).

The biggest problem in analyzing such ancient genera is the difficulty of separating attributes that may have been ancestral sudameridelphian features from those that are species-specific habitus traits. This is not a trivial task when one realizes that in a relatively well-known extant radiation such as the Didelphidae one can with ease point to features in a number of terrestrial forms such as *Didelphis*, *Metachirus*, *Monodelphis*, or *Chironectes* that are didelphid plesiomorphies associated with the fundamentally arboreal shift of the stem of this family, and/or anagenetic improvements in the adaptations of the protodidelphid. In spite of the presence of the highly specialized tarsal and pedal attributes (and probably those of the carpus and manus as well) of all didelphids that were arboreal adaptations of a level that set them apart from their more ancient relatives known from Tiupampa and Itaboraí, there are also new habitus-related adaptations that attest to a terrestrial shift (to various degrees) in the didelphids listed.

So it is obvious that, on one hand, any adaptational assessment of even such nearly complete specimens as those from Tiupampa can pose formidable analytical problems. On the other hand, as we discuss under phylogenetics below, the completeness of the specimens allows us to rule

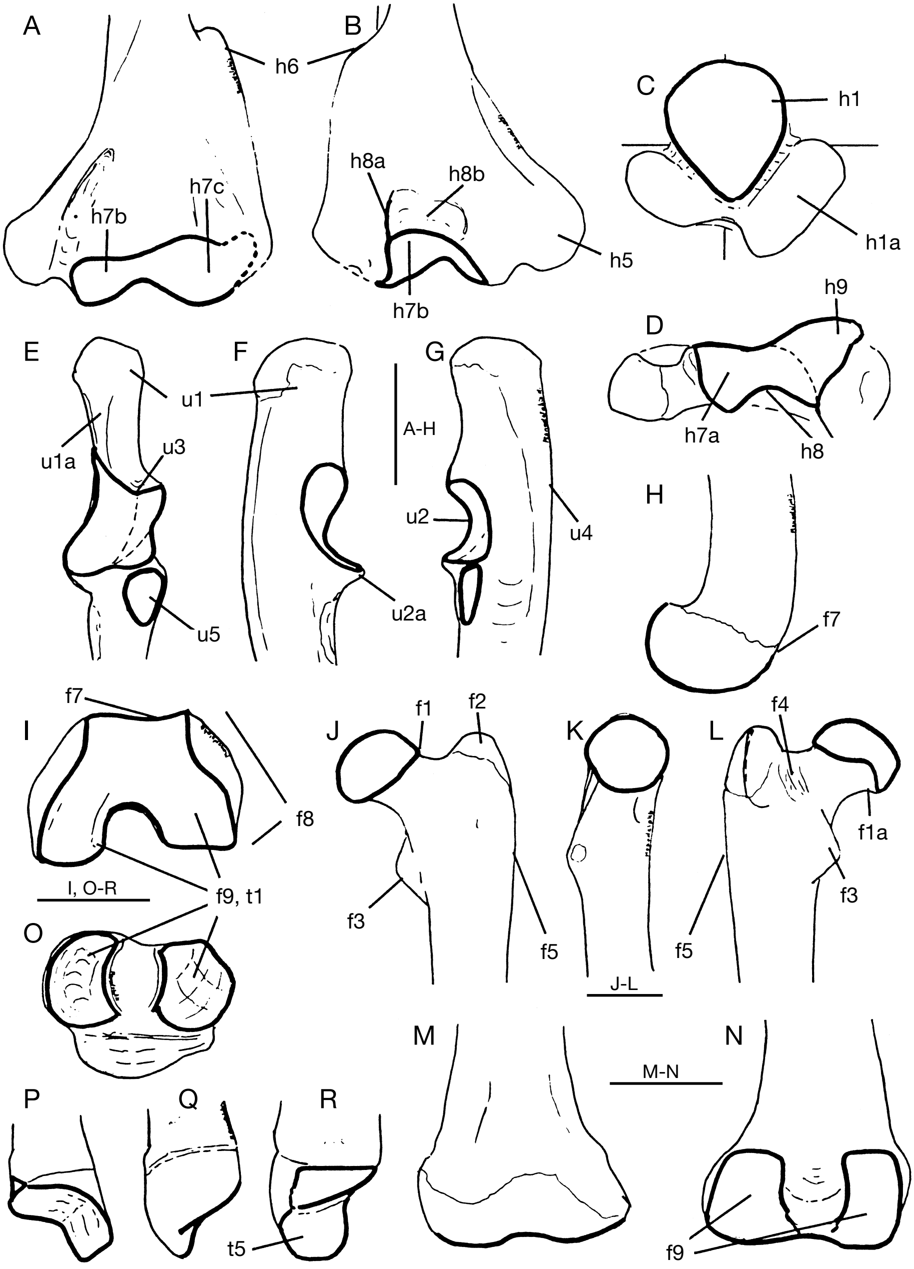


FIG. 23. — Details of *Monodelphis domestica* (Wagner, 1842); **A-D**, left humerus; **A**, anterior view; **B**, posterior view; **C**, proximal view; **D**, distal view; **E-G**, ulna; **E**, anterior view; **F**, medial view; **G**, lateral view; **H-N**, femur; **H**, medial view; **I**, distal view; **J**, anterior view; **K**, medial view; **L**, posterior view; **M**, anterior view; **N**, posterior view; **O-R**, tibia; **O**, proximal view; **P**, posterior view; **Q**, anterior view; **R**, lateral view. For numbered designations, see text. Letters in front of the numbers pertain to the initials of the bones for which numbers are shown: **f**, femoral; **h**, humeral; **u**, ulnar; **t**, tibial. Scale bars: 2 mm.

out special synapomorphous similarities in any part of the postcranium with either didelphids or australidelphians, beyond sudameridelphian heritage. The most difficult task regarding the Palaeocene fossils is, therefore, to ascertain the range of substrate preferences, and the extent to which the ancestor of South American marsupials was adapted for these. This may seem to be an impossible task even with the use of models. In general, it is a good guess, predicted from evolutionary theory, that shortly after entry into South America, populations of the stem species (or those of a genus, at most) experienced a classical ecological release. Thus, the great metatherian radiation got under way, and a complex and highly adaptation-driven niche differentiation was the compelling factor in their lineage and taxic differentiation.

A series of attributes in *Pucadelphys andinus* would seem to suggest that its obligate predilection was perhaps for a terrestrial, rather than habitually arboreal, substrate, although a number of serious caveats are hidden in this interpretation (as astutely pointed out by Muizon 1998). We note at the outset that the drawings of some critical areas of the skeleton in Marshall & Sigogneau-Russel (1995) correspond poorly with the excellent stereophotos in that monograph. The humerus of this species is puzzling, and conveys equivocal signals in its characteristics (Fig. 24A-D). While the "waisting" in the zonal area is not as extreme as in *Metachirus*, the difference in the medial *vs* the zonal width of the trochlea distally is more similar to that of *Didelphis* than to that of *Caluromys*. Furthermore, the lateral edge of the somewhat deep humeral olecranon fossa is well-accentuated, suggesting a condition more similar to the terrestrial model species than to the arboreal ones. The lateral tuberosity is not particularly indicative of either substrate-related extremes of the model species.

The ulna of *Pucadelphys* strongly suggests similarities to the derived condition among didelphids associated with rather full extension, with an ulnar proximal process well offset radially, resulting in a disproportional size difference between the medial and lateral proximal trochlear crests (Fig. 24E). The olecranon, while not particularly long, is not bowed as the drawing in Marshall & Sigogneau-Russel (1995: fig. 40) mistakenly depict it.

The femur of *Pucadelphys* is particularly interesting (Fig. 25A-D). It appears that the distal femur is relatively much smaller than the proximal femur when compared to the extant didelphids, a proportionality perhaps representative of an archaic metatherian or therian condition. The femoral head overhangs medially and the greater trochanter is especially large, both conditions strongly suggesting a terrestrial substrate preference. Added to these attributes is the relatively small and posteriorly flexed lesser trochanter, the distally placed third trochanter, and the proportions of the mediolateral dimensions of the medial and lateral condyles. Although the lateral femoral condyle is certainly wider than the medial one, the difference in the dimensions of the two is relatively small, suggesting minimal abduction of the crus during the push-off phase. Equally significant is the relatively deep distal femur that is more similar in its proportions to *Metachirus* than to *Caluromys*. The dimensions of the femoral condyles are also reflected on the proximal condyles of the tibia. The medial malleolus of the tibia is exceptionally deep. Nevertheless, the femoral midshaft diameter index (not a reliable measure for locomotor prediction) is very high, 109, well within the values of arboreal didelphids. The relatively small proximal third of the fibula also strongly suggests the mechanics noted above regarding the differences in the femoral condyles, and the correlated association among living didelphids with terrestriality.

We have no knowledge of the form and function of the unciform-metatarsal articulations in *Pucadelphys* and the attendant differences or similarities to didelphids. We did, however, have the opportunity to study in detail the tarsus of this Tiupampa genus. The tarsus, as we discuss below under our phylogenetic analysis, is entirely unlike the derived condition of didelphids, or those of microbiotheriids. The total lack of didelphid complexity of the calcaneocuboid articulation,

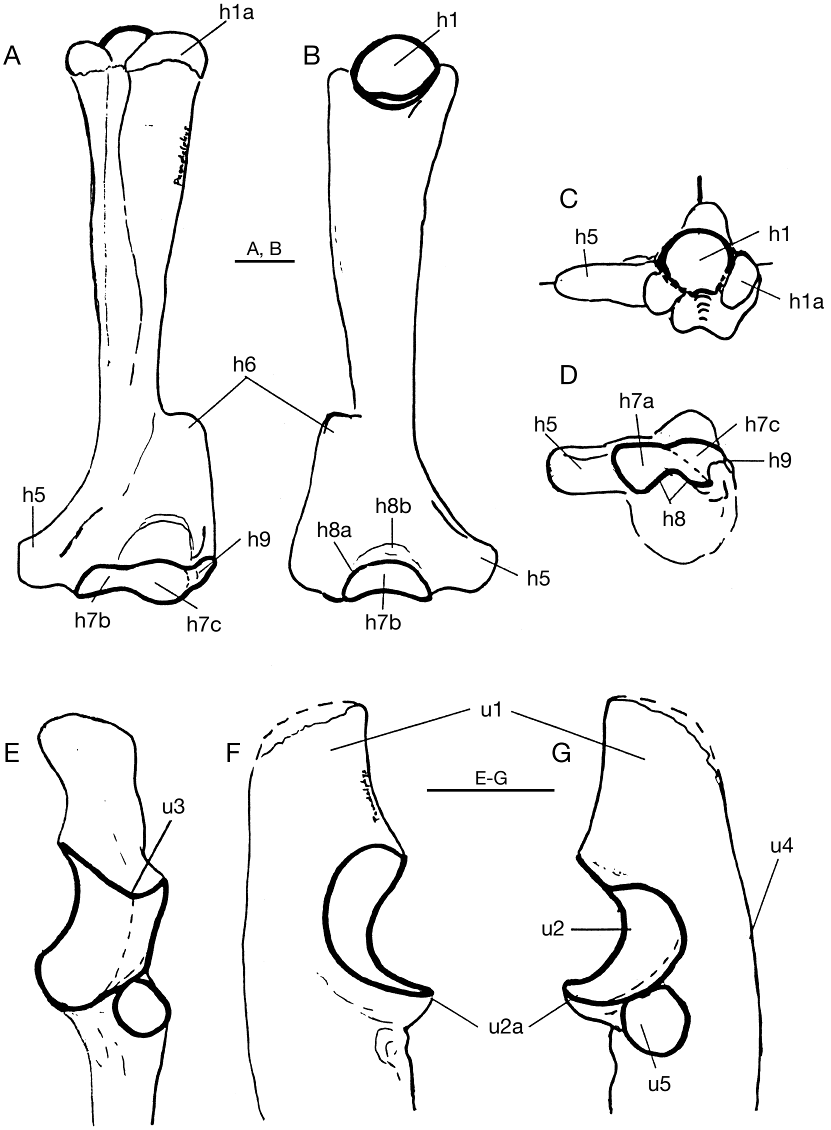


FIG. 24. — Details of *Pucadelphys* (Marshall & Muizon, 1988); **A-D**, left humerus; **A**, anterior view; **B**, posterior view; **C**, proximal view; **D**, distal view; **E-G**, ulna; **E**, anterior view; **F**, medial view; **G**, lateral view. For numbered designations of specific characters see text. Prefixes before the numbers: **h**, humeral; **u**, ulnar. Scale bars: 2 mm.

the narrow **ATil** facet bordered by a sharply angled **ATim** facet (in keeping with the exceptionally deep tibial medial malleolus), the narrow **AFi** facet and the huge astragalar medial plantar tuberosity (**ampt**), and the proximodistally long sustentacular facet extending dorsal to the ampt have the unmistakable stamp of the primitive sudameridelphian pattern (Szalay 1994). This tarsal pattern, judged from the upper ankle, lower ankle and astragalonavicular articulations, is primarily suited for flexion-extension rather than either upper or lower ankle accommodations for

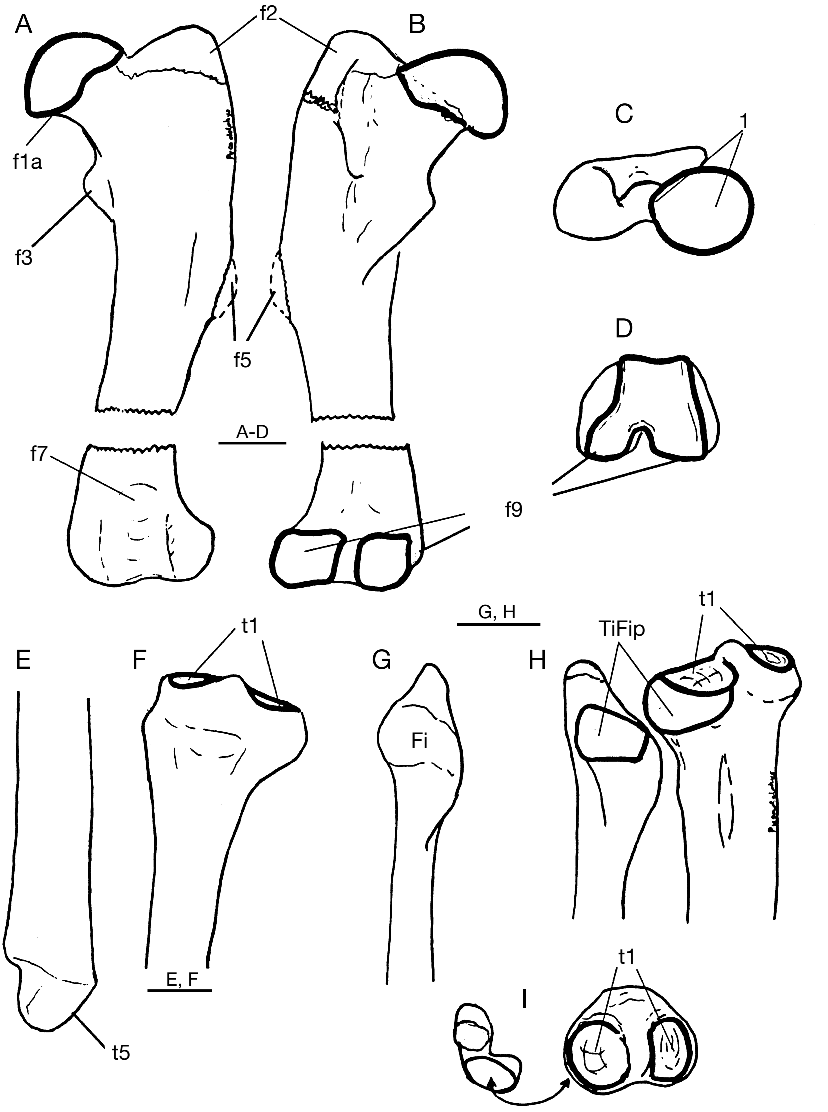


FIG. 25. — Details of *Pucadelphys* (Marshall & Muizon, 1988); **A-D**, left femur; **A**, anterior view; **B**, posterior view; **C**, proximal view; **D**, distal view; **E**-**I**, crus; **E**, lateral view; **F**, anterior view; **G**, medial view; **H**, posterior view, fibula is rotated laterally; **I**, proximal view, fibula is rotated laterally. For numbered designations of specific characters see text. Prefixes before the numbers: **f**, femoral; **t**, tibial. Abbreviations: **Fi**, fibula; **TiFip**, proximal tibiofibular facet. Scale bars: 2 mm.

inversion. This pattern, in contrast to the protodidelphid one, suggests a set of adaptive joint restrictions that a terrestrial substrate requires.

To sum up our analysis based on the models we selected, *Pucadelphys* appears to have been primarily a terrestrial species, as concluded by Muizon (1998). The reflection of terrestriality in its tarsus, however, is within the morphological limits of the Itaboraí pattern, rather than the didelphid one. Neither the postcranial morphology nor the dentition give support for a special phylogenetic relationship between this genus and Didelphidae.

Mayulestes ferox, the near-basal borhyaenid from Tiupampa (monographed in detail by Muizon

1998; see copious illustrative coverage there), is an especially interesting species that shows a suite of attributes in its postcranium that reflect both its sudameridelphian ancestry, as well as its habitus. One question raised by such a complete, but temporally remote, fossil species relates to its traits, namely which reflect its heritage and which mirror its habitus? While we strongly concur with Muizon's (1998) detailed assessment of the habitus of this genus, we consider it to be important to list our reasons in light of the models we examined.

We list a number of attributes that we believe to be associated with a terrestrial substrate preference in marsupials. These were either fully heritage features present in the first South American sudameridelphians from a more ancient lineage, and/or were adaptations in *Mayulestes* in its realtime existence. This list does not in any way negate the great likelihood that this taxon was an excellent climber, as Muizon (1998) states. It should be kept in mind that while the protodasyurid was undoubtedly a terrestrial species, the outstanding and sometimes obligate climbing ability of the smaller species of extant dasyurids is well-known. *Mayulestes* also possessed several traits that, in the light of the total Tiupampa and Itaboraí information available, are likely to be derived and associated with an at least partially arboreal habitus.

1) The proportions of the humeral medial and lateral tuberosities (Muizon 1998: fig. 19) suggest a sharp difference from the condition seen in *Caluromys*, but they are quite similar to those of *Didelphis virginiana*. The latter, while generally a terrestrial species, is also an excellent climber.

2) The distal view of the humerus shows the extraordinary difference in the medial and zonal width of the trochlea, as well as the robust humeral posterolateral crest. These attributes, along with the differences in the length of the medial and lateral proximal trochlear crests of the ulna, suggest strong locking of the elbow during the push-off phase.

3) The head of the radius and the articular contact with the humerus are exceptionally wide mediolaterally, noncircular (Muizon 1998: fig. 26), and unlike the condition even in such a terrestrial didelphid as *Metachirus* (Fig. 13). Taken at its face value it very strongly implies terrestriality. The question is whether the general shape is a heritage feature or not, and whether the **HuRa** facet would tell another story of realtime adaptation if one had the opportunity to compare it with other Tiupampa marsupials. It is almost certain that such a humeroradial articulation indicates lesser rotational (supination and pronation) ability of the forearm compared to that seen in didelphids, which are usually, but not invariably, associated with an arboreal substrate preference. The conformation of the head of the radius, at least the oblate outline of it, as in the specimen we describe below, may well represent the ancestral sudameridelphian condition, and may not allow any general predictions concerning associated habit.

4) The radial tuberosity for the biceps brachii is close to the head of the radius, and the radial distal malleolus (Muizon 1998: fig. 26) is exceptionally well-developed, more so than in *Metachirus* (Fig. 13). Both of these conditions are associated with functions related to terrestrial substrates.

5) The femoral head is somewhat medially displaced and the lesser trochanter is small and slightly posteriorly rotated.

6) The **ATil** articular area of the distal tibia in *Mayulestes* (Muizon 1998: fig. 35F) is even less extensive than in *Metachirus* among the didelphids (Fig. 21). This suggests less rotation of the tibia on the astragalus when the foot is engaged on the substrate, and, therefore, probably a smaller range of foot movements in the upper ankle joint. The astragalus is not known to us so we cannot further comment on this attribute.

7) The groove on the distal femur for the tendon of the quadriceps femoris (or a patella) is relatively deep compared to didelphid marsupials, and it presents a difficult condition to judge in any mechanical or adaptive sense. While the relatively shallow distal femur suggests slow movements as a rule, the deep distal groove on the femur is indicative of a powerful quadriceps in need of great stability during its contraction. This feature is equivocal as to its suggestion of habitual substrate preference.

On the other side of the ledger, there are also attributes that suggest a strong arboreal component to the habitus of *Mayulestes*, as emphasized by Muizon (1998).

8) The proportions of the distal femoral condyles are primitively unequal, and the vertical dimension of the distal femur is relatively low compared to its width. The former condition indicates considerable crural abduction during locomotion, an attribute modified in the extant didelphid and caenolestid terrestrial models we studied. These features, in combination with a calcaneus that may or may not have had a fibular contact (the facet lateral to the **CaA** one may represent a ligamentous contact) and which has a dorsoventrally deep tuber, strongly suggest at least a partly arboreal habitus.

MODELS, LONG BONE CURVATURE AND SHAPE IN THERIANS, AND CONNECTIONS BETWEEN THEIR FUNCTIONAL, ONTOGENETIC, AND PHYLOGENETIC SIGNIFICANCE

It is probable that the peculiar bowing of the tibia in most metatherians was, at its phylogenetic inception (as well as in the realtime of species that posses it), functionally determined, based on the resolution of mechanical issues regarding some homeostatic aspects of the musculoskeletal system. Lanyon (1980) and Bertram & Biewener (1988) have addressed this problem, yet the specific and unique lateral bowing of the tibia as seen in didelphids and others is admittedly not fully explicable by the suggestions made by these authors. Lanyon (1980: 457) first cites the epigenetics-slanted hypothesis offered by Frost (1973) that "[…] long bone curvatures are developed largely to minimize bending moments and so ensure that the bone shaft is loaded axially". Lanyon (1980: 457) then adds the following caveat: "However, strain recordings during locomotion have shown not only that bones are normally subjected to bending, but that there is no consistent relationship between the direction of a bone's curvature and the direction in which it is customarily deformed. In sheep the longitudinally convex surface of the radius is the tension surface. […] while in the distal tibia of the same species the tension surface is longitudinally concave. This disparity indicates either that the establishment of bone curvatures is largely unaffected by customary loading, or that the relationship between mechanics and structure varies between different bones". Lanyon (1980: 465-4666) goes on to offer two possible hypotheses regarding the processes that control bone curvature: 1) "[…] that long bone curvatures are established to accommodate local musculature and are engendered as a result of local pressure on the periosteum"; and 2) (which he examines in that paper) "[…] that certain levels of intermittent bone strain may benefit the tissue's physiology and that the establishment of bone curvatures may be a device to induce bending and generate physiologically optimum high strains in situations where functional loading of a straighter bone would fail to do so". Lanyon's conclusion (1980: 466) is that "[n]either of these hypotheses seem satisfactory alone and it is proposed that long bone curvatures may result from an equilibrium in which a trend toward greater curvature induced by adjacent musculature is arrested at the stage when a further increase results in excessive functional bone strain". Bertram & Biewener (1988: 76), dealing with bone curvature again, however, considered that "[…] no sound evidence exists either for or against these hypotheses, and so, they must remain speculative." They develop the idea that: "As few long bones are straight and capable of maintaining overall axial compression in their cortices […], the possibility exists that bone curvature, and some degree of bending, is in fact, a mechanically desirable loading configuration." Their subsequent analysis and discussion makes the case as to why this may be the correct explanation. The following is an encapsulated version of their view (1988: 76): "The hypothesis argues that bending optimizes bone form to meet the conflicting demands for bone strength *vs* the predictability of the pattern of the stresses within the bone, achieved through control of the direction of load-induced bending ([…]'load predictability'). Load predictability is likely an important factor in the design of a structure that must support dynamically variable loads. […] and has been argued as a key determinant of structure's safety factor to failure. […] Axial compression, in contrast to bending, we show to be a metastable loading configuration (that is the system remains stable only under narrowly defined circumstances and failure predictability is low) and hence, this loading mode has not been selected for."

As Bertram & Biewener note (1988: 88), "[m]any factors will influence the precise degree of curvature suitable for a particular animal and limb element. The final result will most likely be the 'best' compromise between many of these competing factors." They suggest three of these that they consider to be the most important in influencing curvature: 1) loading variability and body size; 2) controlled eccentric loads; and 3) cross-sectional shape.

We suspect that the complex, cyclic, and recurring positions of the limbs (as well as other elements of the body) during positional behaviors (driven by the general dynamics of competitive interactions of species sharing ecological space, a well-founded Darwinian assumption) are key selecting factors that provide the forces which are likely to shape what may be optimally predicted designs under given circumstances. This adaptive-role (and phylogenetic) perspective encompasses a reasonable general view (but not a wholly epigenetic and physiologically causal explanation for taxon specific bone configuration), be it designed for axial compression or axial bending. It has specific bearing on the functionally mediated causal origin of some unusual features in a number of therian lineages. Thus, for example, the nearly pathological-appearing condition of the didelphid tibia (from a eutherian perspective) is probably originally related to the loads incurred in a lower leg performing a specific regime of locomotion while it is considerably abducted in comparison to a more adducted femur (see above). Just as the relatively wider and conical lateral condyle of the distal femur (and the corresponding proportions on the articular condyles of the proximal tibia) is an expression of loading in the knee joint due to an abducted cruropedal complex during locomotion, the tibial curvature also may have had its origins based on such a selective regimen. It was, and continues to be, the direct result of selectional factors (hence phylogenetic as well), and remains an important design improvement in those extant metatherian mammals that continue to have the abducted cruropedal complex during the push-off phase. Its disappearance (or retention from a more ancient ancestry) in some taxa such as *Pucadelphys* may be an adaptive alternative given the positional behaviors of a more terrestrial form with altered femorocrural articular dynamics. Alternatively, its persistence from a didelphid ancestry in a form like *Metachirus*, which has certainly altered its knee complex as a consequence of substrate preference and locomotion, may well represent a failure in the selectional readjustment of the various genetic and epigenetic factors responsible for the shape of the tibia.

Nevertheless it is not clear why and how this tibial shape continues to be maintained in the terrestrial taxa, such as *Metachirus* and the caenolestids. These latter appear to have reduced the extent of cruropedal abduction (as this is judged not by actual observations, but by the symmetry of the condylar articulations in the knee). So, judged from the distribution of femorocrural characteristics in either fully arboreal, scansorial, or obligate terrestrial didelphids, this attribute of bending, or its absence in more axially loaded tibiae, is not a good predictor of substrate preference. Yet, in *Pucadelphys*, which reduced the ancestral disproportion of the articular condyles in the knee and was probably mostly terrestrial, the sigmoid curvature of the tibia is absent (Muizon 1998: fig. 37). The possibility should not be overlooked that the ancestry of sudameridelphians had a highly terrestrially constrained heritage in which there was no tibial curvature, and that *Pucadelphys* retained that condition for adaptive reasons.

One cannot but tentatively conclude that in spite of clear modifications of the knee for rapid terrestrial scampering or galloping as in *Metachirus* (probably in *Pucadelphys* with its straight tibia, as well), the morphological parameters of tibial shaft configuration may be *genotype-based* rather than *epigenetic* (as certainly are the habitus-reflecting knee morphologies coupled with the reduced proximal fibula, or the attributes of the astragalus; Szalay 1994). One may also speculate that *Metachirus* is a very recent terrestrial offshoot from an arboreal ancestor, although the same cannot be assumed for caenolestids.

When examining loading variability and body size, Bertram & Biewener (1988: 89-90) note under the discussion of causal factors responsible for long bone curvature (and we assume that they consider genetics, and not only epigenetics), that two factors are responsible for the optimal compromise between predictability and structural strength: "These are (1) the peak loads encountered relative to the limits of the bone tissue (the safety factor) and (2) the degree of variability in loading orientation over a species' normal range of activity". In terrestrial cursors, as pointed out in a number of studies, there has been a tendency to decrease bone curvature as body mass is increased. The straighter long bones, while increasing the structural strength of these elements, have a reduced range of predictability, as the model advanced by Bertram & Biewener predicts. It appears to us that this is a result of a long range selection-mediated phenomenon (phylogeny) rather than just a physiological response within the lifetime of an animal.

The issue of phylogenetic patterns of curvatures in therian long bones, particularly in the antebrachium and crus, is an important one for an understanding of the balance between genetics and epigenetics in shape determination of long bones. While Bertram & Biewener (1988: 91) conclude that "[...] the precise biological role of mechanical load predictability [...] remains unclear", we believe that a general adaptive advantage tied to a range of motions (positional behaviors) is evident. This is another "predictability" issue related to causal ecological aspects of morphology. Quite simply, a variety of permissible loads within a fundamentally skeletally-guided regime of motions is likely to select for such long bone curvatures. The odd curvature of the tibia in a number of metatherians, in contrast to the condition in eutherians, provides some understanding of this problem, as well as the probable transformational history of this bone. In most eutherians, in the almost completely propulsion-oriented hindlimb, the straight lines of the crural elements are in sharp contrast to an usually curved ulna and radius in the same animals. Even in arboreal euprimates, with their obvious terrestrial eutherian heritage beyond their arboreal archontan roots (Szalay & Lucas 1993, 1996), the mechanisms of leaping are intimately tied to both a relatively straight femur and a straight crus. In the metatherians, however, the usually slow climbing activities of species of such a relatively primitive extant family as the Didelphidae (the source of all other extant marsupials) display curvature in the tibia (and to some degree in the fibula as well) as well as in the long bones of the antebrachium. In particular, the hand and foot morphology of didelphids is so fundamentally grasping-related that a contemplation of terrestrial origins of the extant marsupials other than caenolestids is, in our view, extremely unlikely. So from all corners there is strong evidence that not only the didelphids, but also a number of the postcranially known other metatherian lineages had this type of ancestral tibial construction. But slow moving propulsion systems, or rather a skeletal morphology that appears to have a great range of load predictability, is unlikely to have been successful on the ground given the limited options of escape from predators[28].

As we observed, retention of a bowed tibia in an obligate terrestrial galloping form like *Metachirus* does hamper the prediction of arboreality in a fossil with such a tibia. The general pattern is such, however, that at least in early therians the primitive condition may have been an arboreally adapted skeleton. This was retained in the last common ancestor of the Metatheria, and was quite terrestrially modified in the ancestral lineage of the extant Eutheria. As discussed elsewhere, the small size of a mammal species does not in any way determine that such a form was, or is, biomechanically destined for a kind of obligatory scansoriality (*contra* Jenkins 1974, whose view has been followed unquestioningly in the literature). As shown repeatedly (Szalay 1984; Sargis

2001) the physics-based selectional demands operate with the same stringency on small mammals as they do on the larger ones.

We strongly believe that a conceptually fundamental idea such as that of "load predictability" as advanced by Bertram & Biewener (1988) and Biewener (1989) is a critical link between highly functional explanations emanating from the mechanical and ecological analysis of skeletal structure, and the attempts to ferret out the historically-embedded aspect of morphological properties. The selectionally constructed and genotype-embedded stable designs of musculoskeletal systems are the ones that set the mechanical limits for the dynamics of these entities in an ecological setting. These heritage patterns allow the directed changes, through *evolutionary time* and not *ontogeny*, that the differential survival of the variants can bring about. The basic design parameters (the ancestral conditions), when either fossil continuity or synchrony of multiple related lineages sharing these properties is available, are reflected in most such skeletal systems. These allow analyses of transformations when a variety of skeletal states are available.

It is clear, that at the moment, there is no simple, linear explanation possible for the nature of long bone shape, nor is there an exact explanation of the particulars of specific lineages. But it would be unwise to assume that historically contingent, and subsequently genotype-embedded, factors will ever be exiled from explanations of osteological morphology and its causal correlates. Yet no one should doubt that the functionally and experimentally exacting studies applied to bone shape are of fundamental importance and greatly aid morphological analysis. These occasionally yield hypotheses of great generality from which many sound deductive explanations are possible (e.g., see Biewener's 1989 account on the significance of body size increase and functional equivalence of long bones mediated by altered behavioral-cum-locomotor strategies). Genotype-based (phylogenetic) constraints (the initial and boundary conditions) for stable designs continue to add an element of lineage specificity that simply cannot be accounted for either by ontogeny-mediated functional adjustments or adaptive explanations alone, without the appropriate historical context. The past failure of allometric explanations that considered body mass as the single driving factor of bone shape in lineages (as thoroughly discussed and refuted by Biewener's various contributions) attest to the unacceptability of simplistic (either structuralist or ahistorical physiological adaptationist) explanations.

PALEOBIOLOGICAL MODELING OF SKELETAL FEATURES IN THE RELEVANT LITERATURE

We briefly comment here on a previous attempt to use *Caluromys*, and various concepts of the didelphid ancestry, as models for interpreting the origins of a group of eutherians, the euprimates and their relatives, the plesiadapiforms. Morphology is the only point of reference that fossils can offer for analysis. This must be connected with functionally well understood similar, or instructively contrasting, morphology in proper models. Modeling, in our view, should not consist of picking a living species based on some behavioral criterion, and stating categorically that its behavioral or physiological state (or another attribute) was probably similar to that in a postulated fossil taxon. This is done not infrequently, even when the morphology of the designated extant "model" in no way resembles the unknown or inferred fossil condition. Rasmussen (1990), in choosing the didelphid *Caluromys* (called "primate-like" by him) as a surrogate "model" for the protoeuprimate, followed this flawed protocol. Similarly, Martin (1990), based on the thesis of Lewis (1989; see references therein for earlier papers dealing with the same issues), has employed the concepts that supposed to correspond to metatherian morphology in his attempts to interpret Palaeocene plesiadapiform evidence. In light of the fact that primates, like other extant and fossil placentalians, show unmistakable signs of having originated from a terrestrial ancestry (beyond their more proximal arboreal archontan roots), such use of metatherians is particularly misleading and does not conform to what we consider appropriate modeling.

According to Rasmussen (1990), the relatively large brain and eyes, small litters, slow development (meaning postpartuition because prepartuition development is nearly uniform in all didelphids and fundamentally different from the universally "accelerated" condition of eutherians when compared to metatherians), and agile locomotion (compared to clumsier arboreal didelphids such as the scansorial *D. virginiana*) represent a suite of attributes that is convergent to the euprimate ancestor. He stated (1990: 263) that these "analogous […] selection pressures […] represent an independent test of the arboreal hypothesis, […] the visual predation hypothesis, […] and the angiosperm exploitation hypothesis of primate origins". However, the prehensile-tailed *Caluromys* has not the slightest special similarity in its osteological properties to a condition that can be confidently inferred for the ancestry of euprimates. Unlike the clawed *Caluromys* (which occasionally indulges in small leaps), the protoeuprimate had nails. The early euprimates also had fast and highly stabilized patellate knee joints superbly constructed for powerful leaping in conjunction with a foot that had an equally speed-adapted upper ankle joint capable of rapid flexion, totally unlike didelphids. But this latter joint is a eutherian one, and the manner of adjustments to it for the use of arboreal substrates evolved in the lower ankle joint within the highly constrained cruropedal contact that characterizes eutherians. Neither arboreality nor visual predation account for the transformation of claws into nails, but the evolution of powerful *pedal* grasping coupled with mechanical solutions of the entire pelvic limb does, as these features are clearly to explosive long jumps combined with grasping branches when landing (Szalay & Delson 1979; Szalay & Dagosto 1988).

In fact, there are no osteological attributes of *Caluromys* that parallel euprimate osteological features (related to grasp-leaping), and therefore this genus (or any didelphid) is an entirely inappropriate model for early primates known from bones alone. A strong case can be made that, osteologically, *Caluromys* probably approximates a good model for the arboreal protodidelphid (but not didelphidan or sudameridelphian ancestry), one that significantly differed in its advanced arboreal abilities from the postcranially more primitive sudameridelphians of the Palaeocene (Szalay 1994). The well-known agility of *Caluromys* compared to forms like *Didelphis*, which is quite scansorial and is at home on terrestrial substrates, does not provide evidence for the argument that the agile arboreality of *Caluromys* is a derived condition within the Didelphidae. Many smaller species of didelphids are also quite agile and quick in an arboreal environment, this almost certainly being the initial and boundary condition for the first didelphid (see discussion of the Didelphidae in Szalay 1994). Unfortunately, a model like *Caluromys* tells us little or nothing about the origins of euprimate skeletal morphology (and therefore inferred habits from that), which was transformed from an essentially terrestrial eutherian heritage, via a still poorly understood arboreal archontan heritage into the relatively well understood primitive euprimate postcranial state (Szalay *et al.* 1987; Dagosto 1988; Dagosto *et al.* 1999).

In attempting to explain arboreal attributes of the inferred common ancestry of euprimates, Lewis (1989; and references to his previous papers therein) has derived the various primate attributes from an essentially didelphid condition, the latter standing in as a surrogate for a "marsupial stage" prior to eutherian arboreality. Neither the phylogenetically troubling details that primates are eutherians with their own highly specific constraining heritage that circumscribes their morphology, nor the fact that didelphids appear to be a derived arboreal clade among South American Metatheria, have constrained Lewis' explanation. His transformational analysis, unfortunately, lacked the necessary context that is provided by a corroborated phylogeny of the character complexes he studied, and the implication of this for the taxa. Furthermore, many of the problems with his proposed transformations were also due to a lack of ecomorphologically meaningful assessment of details. Modeling of ecomorphologically tested attributes coupled with a reasonably tested phylogenetic perspective (that should automatically disavow the notion that all attributes of an outgroup are necessarily plesiomorphous) would have resulted in a clear recognition that all the transformational association of didelphid and primate attributes was entirely inappropriate. The general notion that some aspects of marsupials are probably primitive (e.g., reproductive or developmental patterns) compared to their eutherian homologues does not mean that there is a general functional similarity (certainly not morphological in its complex details) between eutherian attributes and those of didelphid marsupials (Szalay 1984, 1994). Hence, the same could be stated even more emphatically concerning an attempt to understand euprimate origins based on didelphids.

Another inappropriate use of various modeled conditions of aspects of metatherian and eutherian skeletal adaptations was made by Martin (1990). This was the consequence of a lack of familiarity with both the fossil and relevant extant skeletal evidence, as well as their functional significance for positional behaviors, and therefore the theoretical context of modeled living forms. The explanations advanced by Martin heavily relied on implicit assumptions about the relevance of didelphid attributes for evaluating fossil eutherians. Martin confused the application of modeled properties in his text, where he presented a lengthy analysis of selected osteological attributes of euprimates and their possible closest relatives, specifically the plesiadapiforms, colugos, and tupaiids. In writing about the evolution of mammalian locomotion, primate arboreality, and the specifics of the osteological evidence retrieved from the literature, a number of issues that relate to modeling and phylogenetic analysis of the metatherian-eutherian dichotomy framed his account.

Views of the alleged homology of arboreality in marsupials and extant eutherians, the supposed primitiveness of the cheirogaleid primates (which do have a predilection for terminal or small branch locomotion), and the various didelphid attributes for such habitat preferences have provided confusing examples of modeling. These flawed studies spawned further confusion about both the alleged arboreality of the protoplacentalian, and that how some arboreality-related therian traits, lost in other eutherian lineages, are preserved in the primates [29].

THE ITABORAÍ METATHERIAN POSTCRANIALS

There are approximately 19 or 20 species, based on dental material, reported from Itaboraí (Szalay 1994: 158-162; and references therein). Our description of the postcranial fossils (the entire collection is listed in Table 5) is selectively documented in the figures, as well as on the comparative plots of those indices of the extant model taxa and the fossils that have some perceived significance for the evaluation of the latter. It should be kept in mind that the rare dental taxa are unlikely to be represented by postcranials. Yet preservational happenstance allows no nomothetic conclusions. It is obvious, however, that none of the various postcranial elements show the kind of taxonomic diversity displayed by the dental material. The most diverse group is the ulnae of which we recognize 11 different types. In spite of the relative taxonomic shortfalls of the postcranials compared to the dental record, the paleobiological understanding of diversity at Itaboraí is greatly enhanced by these fossils, and valuable phylogenetic insights are gained as well.

We try to avoid excessive detailing of the various breaks, missing pieces, and areas of bad erosion, as accounts of these often overwhelm what should be the establishing of taxonomic properties of newly described fossils. These details of preservation can be important, of course, and when they are relevant for the characterization of attributes and our interpretations of the various elements, we give accounts of them.

After repeated bouts of close inspection we have sorted the fossils into phena (presumably representing species-level taxonomic units), which was an ongoing exercise that modified the groupings a number of times. Stability of our views (if not complete certitude) was attained largely through the norms established by realistic ranges

TABLE 5. — List of metatherian postcranial specimens allocated to Itaboraí Metatherian Groups (IMG) represented by the various elements. There is no taxonomic concordance between the same group numbers of various skeletal elements. The numbered sequences within each homologous postcranial group represent size- and morphology-based taxonomic separations that reflect, presumably, species level differences.

Itaboraí Metatherian Groups	**N**	**Specimen numbers**
IMG Scapula		
IMG Scapula 1	1	DGM 1763PV
IMG Humeri		
IMG Humerus 1	12	DGM 1.191A-M ->C-M, DGM 1.192a-m ->j-m
IMG Humerus 2	12	DGM 1.193A-M ->L-M
IMG Humerus 3	8	DGM 1.194A-M ->H-M
IMG Humerus 4	9	DGM 1.197A-M ->H-M, 2001M
IMG Humerus 5	4	DGM 1.195A-M ->D-M
IMG Humerus 6	2	DGM 1.196F-M ->G-M
IMG Humerus 7	5	DGM 1.196A-M ->E-M
IMG Ulnae		
IMG Ulna 1	1	DGM 1.150I-M
IMG Ulna 2	1	DGM 1.150II-M
IMG Ulna 3	4	DGM 1.150IIIA-M ->B-M, DGM 1.150IVA-M ->B-M
IMG Ulna 4	3	DGM 1.150VA-M ->C-M
IMG Ulna 5	2	DGM 1.150VIA-M ->B-M
IMG Ulna 6	2	DGM 1.150VIIA-M ->B-M
IMG Ulna 7	2	DGM 2020M, DGM 1.150VIII-M
IMG Ulna 8	2	DGM 1.150IX-M, 1.150X-M
IMG Ulna 9	2	DGM 1.150XIA-M ->B-M
IMG Ulna 10	3	DGM 1715PV, DGM 2078M, DGM 1362M
IMG Ulna 11	1	DGM 2069M
IMG Radius		
IMG Radius 1	1	DGM 1.125-M
IMG Innominates		
IMG Innominate 1	4	DGM 1.145A-M ->D-M
IMG Innominate 2	2	DGM 1.146A-M,1.146D-M
IMG Innominate 3	2	DGM 1.146B-M ->C-M
IMG Femora		
IMG Femur 1	1	DGM 1.185IB-M
IMG Femur 2	2	DGM 1.185IA-M, 1.185II-M
IMG Femur 3	6	DGM 1.201A-M ->C-M, DGM 1.201E-M ->G-M
IMG Femur 4	11	DGM 1.201D-M, DGM 1.202A-M ->J-M
IMG Femur 5	3	DGM 1.203VA-M ->C-M
IMG Femur 6	7	DGM 1.203VI-M, DGM 1.203VIIIA-M ->C-M DGM 1.203VII-M, DGM 1.203IXA-M ->B-M
IMG Femur 7	3	DGM 1.203XA-M ->B-M, DGM 1.203XI-M
IMG Femur 8	2	DGM 1.203XIII-M, 1887M
IMG Femur 9	2	DGM 1.203XIIA-M ->B-M
IMG Femur 10	2	DGM 2040M, DGM 1886M
IMG Tibiae		
IMG Tibia 1	3	DGM 1.188A-M ->C-M
IMG Tibia 2	2	DGM 1.189-M, 1952M
IMG Tibia 3	2	DGM 1.200-M, 1731PV
IMG Unguals		
IMG Ungual Type 1	6	DGM 1.198A-M ->F-M
IMG Ungual Type 2	4	DGM 1.199A-M ->D-M

of variation of given bones in living species of didelphids. The designations we have come to use for these quasi-species level taxa dovetail with and complement the convention initiated by Szalay (1994) for Itaboraí postcranials lacking clear association with dental material. The acronym IMG is usually followed by a designation of a particular bone, as well as by an Arabic numeral representing a distinct sample of a phenon as far as that particular bone is concerned (see Introduction). Because of the uncertainty of associating different bones with, and allocating them to, quasi-species level groups, we have used Arabic numerals to distinguish this grouping within specific bone groups from the quasi-taxonomic designations of the Roman numerals used in Szalay (1994). Thus, humeral and femoral samples with different numbers may well belong to the same quasi-species level group of as yet unspecified designation, just as those with the same number do not necessarily belong to the same species. In fact it is almost certain that such samples of different elements designated with the same or different Arabic numbers may eventually be allocated to IMG with a specific Roman numeral. These samples can potentially be allocated to already described and named species (based on dental criteria) within the Itaboraí fauna, as this was attempted for the tarsal groups in Szalay (1994).

Our practice here complements, but differs slightly from the IMG groupings in Szalay (1994), out of the necessity that these elements of the skeleton pose different problems of association. Dealing with different tarsal elements that could be more easily allocated to the same species because of their characteristic conarticular relationships, Szalay's (1994) emphasis was on the allocation of the various tarsal samples to the same species taxa. The Roman numerals in Szalay (1994) referred to the quasi-species level groups of the functionally associated tarsal samples. The samples of homologous tarsal elements of various species, after scrutiny, were given designations as discrete numerical samples in Szalay (1994), arranged as specific astragalar and calcaneal entities judged to belong to specific IMG groups. These associated designated samples were given consecutive odd and even Roman numerals. The sequential arrangement was basically dictated by size, as it is in this study, and this had (and has) no other significance beyond the potentially interesting correlates of body size. As in that paper, we also designated the various samples of specific bones of increasingly different size and morphology with Arabic numerals. The museum numbers for all the fossil specimens we have examined and included in this study are given in Table 5.

In summary, the designation IMG and the name of the bone (or its initial) followed by Arabic numerals (in an arbitrary sequence of increasing numbers to stand, approximately, for increasing size) designate (samples of) phena of homologous bones. Differently numbered groups of the different skeletal elements can belong to the same species (e.g., IMG Humerus 2, IMG Ulna 3, IMG Femur 5, and IMG Tibia 1 are almost certainly of the same species, and furthermore, they are with near certainty conspecific with IMG II based on Itaboraí tarsal samples 3 and 4, calcanea and astragali, and allocated cuboids, respectively; see Szalay 1994).

Much of the description of the fossils is directed towards the detailed appraisal of subtle osteological features on the bones that can be explained functional-adaptively and phylogenetically. This is a necessity, as any assessment must be inferential based on these features and proportions. So the (numerically-) designated attributes of the various bones attempt to render relatively objective accounts of those features in order to facilitate comparative descriptions and illustrations. These numerically designated attributes are, in combination, diagnostic of the particular phena. They are also the bases for any functional-adaptive and phylogenetic appraisals that we present. Unfortunately, many aspects of the bones are often not sufficiently well-preserved to draw some critical paleobiological conclusions. For example, the subtle morphological details of the proximal end of the ulnar olecranon are often obscured for such reasons, so confident inferences about the various heads of the triceps cannot be

TABLE 6. — Measurements of scapula and innominates from Itaboraí (all DGM numbers).

Group	Specimen number	Glenoid width	Glenoid height	Acetabulum width	Acetabulum height
IMGS 1	1763PV	6.09	7.52		
IMGI 1	1.145A-M			2.25	2.26
IMGI 1	1.145B-M			2.59	2.11
IMGI 1	1.145C-M			2.51	2.30
IMGI 1	1.145D-M			2.21	2.20
IMGI 2	1.146A-M			3.34	2.65
IMGI 2	1.146D-M			3.07	2.86
IMGI 3	1.146B-M			3.43	3.17
IMGI 3	1.146C-M			2.88	2.88

FIG. 26. — Itaboraí partial right scapula (DGM 1763PV); **A**, lateral view; **B**, medial view. See also Fig. 7. Scale bar: 3 mm.

drawn. But the greater is the taxon specific detail that we can extract from the phena of various elements, the more complex, and, therefore, more reliable becomes the matrix of unique species specific attributes which can be explained with high probability.

SCAPULA (TABLES 5; 6)

IMG Scapula 1 (Figs 7F; 26)

There is only a single partial scapula (DGM 1763PV), a relatively large right specimen with interesting post-glenoid proportions. The size of the specimen indicates an individual that had the body mass of an average-sized adult female Virginia opossum, hence it was among the largest of the fossil marsupials from Itaboraí (such as *Patene* and *Zeusdelphys*). However, there are some interesting differences from *Didelphis*. The scapular spine of the fossil forms about 65° of arc with the plane of the scapula compared to nearly 90° in *Didelphis*. Judged from the intact superior border, the supraspinous fossa was significantly wider than that of *Didelphis*, and quite different from the didelphid models. The shape and proportions of its glenoid fossa are similar to those of both *Metachirus* and *Caluromys,* with some potentially significant small details that seem to differentiate it from the latter. The articular portion of the scapular glenoid fossa is more similar to that of *Metachirus*, in that it is narrower than that of *Caluromys*. This may mean that at full extension the humeral head is more securely locked (wedged in) between the lateral (greater) and medial (lesser) humeral tuberosities than in *Caluromys*. The postglenoid proportions of the fossil are strikingly different from either of the two arboreal models, but resemble strongly those of *D. virginiana* and *Metachirus*. This similarity is in the forward extension of the supraspinous portion of the bone, suggesting a terrestrial animal. This condition is also similar to *Pucadelphys* (Marshall & Sigogneau 1995), but not to *Mayulestes*, which is more *Caluromys*-like (Muizon 1998).

HUMERI (TABLES 5; 7; 9)

IMG Humerus 1 (Figs 27-30; 34-35; 68)

Of the 12 specimens we judge to belong to this group, four are almost certainly juveniles with their epiphyseal plates missing, whereas eight are probably fully adult. Two of them are particularly complete. The larger of the two is DGM 1.192A-M and the smaller is DGM 1.192F-M.

The following represent characteristic properties of this group:

1) the head (**hhd**) is poorly preserved and the surface morphology is not revealing but it appears that the head was more circular than oblate, with a predominant development of the lateral tuberosity;

2) beaking of the head is pronounced, indicating an angular excursion of this tiny humerus on the scapula near to that of *D. virginiana,* approximately 80°;

3) shaft is bowed and not particularly slender;

4) the relative size of the **hdps**, the Humeral Deltopectoral Shelf Index (HDSI = length of **hdps**/length of humerus × 100), with a mean of 44.3, confirms our suspicion that this index is generally size related in marsupials;

5) the relative size of the humeral medial epicondyle (**hmec**) cannot be determined; in powerful graspers the relative size of this process reflects the area of origin for large digital flexors;

6) the humeral lateral epicondylar crest (**hlecr**) is the origin of the brachioradialis, and hence related to the flexion of the antebrachium (digital extensors attach to the distal tip of **hlecr**). It is not only well-developed, but it is also considerably retroflexed. It is about one third of the length of the humerus;

7) the trochlea is well-developed and extends proximally, and the capitulum is large. The **HuUl** facet extends well proximally on the posterior side of the humerus;

8) the humeral posterior lateral crest (**hplcr**) is well-developed next to the deep hofo, reflecting the significant stabilization of the elbow joint;

9) the groove for the radial sesamoid (**Ras**), if there was one, is not accentuated for the level of stability seen in caenolestids.

The morphological analysis that was carried out independently of plotting the various chosen parameters suggests conclusions that are corroborated by the metrics. The functional properties of this humerus place it almost in the middle of the arboreal-terrestrial continuum, and this is where this group falls on the plots. Fig. 34 depicts the relation of mediolateral trochlear length/trochlear anteroposterior width on the vertical axis against the length of the humerus on the horizontal axis. While the length of the bone is a quasi-surrogate for the body mass of the animal (almost all of the Itaboraí species are known by isolated bones only), the ratio of length *vs* depth of the trochlea clearly places the living arboreal models above, and the terrestrial ones below, the regression line calculated for them. The fossils of IMG Humerus 1 straddle this line. Similarly, in Fig. 35, where the horizontal axis has been changed to depict mediolateral distal articular surface length (another, probably poor, surrogate for body size) against the same vertical axis as in Fig. 34, we find this morph on both sides of the model-derived regression line.

While the humero-ulnar joint strongly recalls the attributes of *Rhyncholestes,* and to some degree *Metachirus*, some other traits are more similar to those of the arboreal models. The extensively developed trochlear articulation is well-extended posteriorly, and a strong **hplcr** past the articulation itself, together with a deep **hofo** and a retroflexed **hlecr**, all suggest an exceptionally braced elbow during extreme extension of the forearm. While this complex is related to stabilization of the forearm, it is not at all certain that this can be causally correlated with terrestrial locomotion in all instances. In fact, it is almost certainly

TABLE 7. — Measurements of humeri from Itaboraí (all DGM numbers) and from the model species.

Group	Specimen number	Humeral head		Delto-pectoral crest length	Humerus length	Humeral distal end width	Humeral distal articular surface width
		Length	Width				
IMGH 1	1.191 A-M	1.65	1.74		10.62		
—	1.191 B-M	1.59	1.73		10.13		
—	1.191 C-M			4.83	10.73	3.04	
—	1.192 A-M	1.73	2.16	6.79	14.07	3.82	2.42
—	1.192 C-M	1.60	1.96	5.88	12.79	3.49	2.48
—	1.192 D-M	1.61	1.85	4.99	12.25	3.54	2.32
—	1.192 F-M	1.69	2.01	5.01	12.06	3.34	2.39
IMGH 2	1.193 A-M	2.40	2.59		20.86	3.62	2.83
—	1.193 B-M	2.39	2.48		20.57	3.59	2.85
—	1.193 C-M					3.52	2.76
—	1.193 D-M					3.53	
—	1.193 E-M					3.51	2.83
—	1.193 G-M					3.25	2.60
—	1.193 H-M					3.38	2.77
—	1.193 I-M					3.41	2.77
—	1.193 J-M					3.53	2.93
IMGH 3	1.194 A-M	3.21	3.04	6.33	16.50	5.72	4.17
—	1.194 B-M					5.16	
—	1.194 C-M	2.65	2.87	7.98	16.45	5.30	2.94
—	1.194 D-M	2.69	3.32	7.88	18.04	5.78	4.04
—	1.194 E-M			8.40	18.43	5.05	
—	1.194 F-M			8.41	17.70	4.94	
—	1.194 G-M					5.64	
—	1.194 H-M	2.27	2.64	9.17	15.89	5.89	
IMGH 4	1.197 A-M	3.60	4.03	15.18	24.09	7.09	4.64
—	1.197 B-M					6.15	4.31
—	1.197 C-M					6.19	3.68
—	1.197 D-M	3.11	3.47		19.96	5.58	4.26
—	1.197 E-M					6.37	4.00
—	1.197 F-M					6.71	4.21
—	1.197 G-M					6.05	3.86
—	2001 M	3.26	3.58	9.33			
IMGH 5	1.195 A-M	4.38	4.05	13.10			
—	1.195 B-M						4.93
—	1.195 C-M					8.69	5.32
—	1.195 D-M					9.06	5.25
IMGH 6	1.196 F-M						
—	1.196 G-M	5.86	5.49	19.13	31.74	11.16	6.66
IMGH 7	1.196 A-M	7.24	6.20	21.64	36.42	13.13	8.49
—	1.196 B-M					13.48	8.41
—	1.196 C-M						9.14
—	1.196 D-M					10.68	7.55
—	1.196 E-M					11.41	7.66
Caluromys derbianus		6.46	5.61	21.26	39.37	11.54	7.54
Metachirus nudicaudatus		6.57	6.71	22.95	41.35	9.94	7.07
Rhyncholestes raphanurus		2.11	1.99	6.47	12.73	4.17	2.79
—		2.40	2.30	6.07	13.21	4.37	2.95
Dromiciops gliroides		1.88	1.55	5.38	12.55	3.66	2.94
—		2.20	2.01	7.04	14.13	4.42	2.60

Group	Specimen number	Capitulum width	Zona conoidea width	Trochlea width	Capitular tail width	Capitulum height
IMGH 1	1.191 A-M					
—	1.191 B-M					
—	1.191 C-M					
—	1.192 A-M	1.01	0.26	0.81	0.30	0.87
—	1.192 C-M	0.89	0.29	0.94	0.37	0.83
—	1.192 D-M			0.96		
—	1.192 F-M	0.88	0.25	0.85	0.43	0.87
IMGH 2	1.193 A-M				0.41	1.04
—	1.193 B-M				0.47	1.05
—	1.193 C-M	1.09	0.41	0.83	0.33	1.01
—	1.193 D-M	1.07	0.33	0.95	0.28	1.00
—	1.193 E-M	1.10	0.22	1.10	0.33	1.04
—	1.193 G-M					
—	1.193 H-M	0.98	0.39	1.11	0.33	0.96
—	1.193 I-M	1.04	0.34	1.19	0.27	1.03
—	1.193 J-M	1.28	0.34	1.00	0.36	1.09
IMGH 3	1.194 A-M	1.47	0.46	1.59	0.61	1.59
—	1.194 B-M					
—	1.194 C-M	1.05	0.39	0.94	0.58	1.05
—	1.194 D-M	1.56	0.44	1.50	0.49	1.58
—	1.194 E-M					
—	1.194 F-M			1.48		
—	1.194 G-M					
—	1.194 H-M					
IMGH 4	1.197 A-M	1.95	0.65	1.65	0.46	1.85
—	1.197 B-M	1.88	0.58	1.57	0.24	1.60
—	1.197 C-M	1.63	0.49	1.26	0.21	1.45
—	1.197 D-M	1.65	0.52	1.48	0.62	1.55
—	1.197 E-M	1.88	0.47	1.62		1.46
—	1.197 F-M	1.71	0.47	1.60	0.44	1.82
—	1.197 G-M	1.76	0.31	1.50		
—	2001 M					
IMGH 5	1.195 A-M					
—	1.195 B-M	1.97	0.47	1.72	0.95	1.70
—	1.195 C-M	1.99	0.57	2.03	0.82	1.85
—	1.195 D-M	2.30	0.68	1.66	0.84	1.93
IMGH 6	1.196 F-M					
—	1.196 G-M	3.02	1.10	2.00	0.57	2.50
IMGH 7	1.196 A-M	3.66	0.90	2.75	1.16	3.04
—	1.196 B-M	3.89	0.70	2.61	1.20	2.99
—	1.196 C-M					
—	1.196 D-M	3.12	0.98	2.39	0.97	2.69
—	1.196 E-M	3.07	0.88	2.62	1.02	2.83
Caluromys derbianus		2.84		2.55	0.92	3.04
Metachirus nudicaudatus		2.61		2.44	1.36	2.78
Rhyncholestes raphanurus		1.30		0.91	0.33	1.03
—		1.48		0.79	0.39	1.16
Dromiciops gliroides		1.10		1.14	0.41	1.07
—		0.94		0.94	0.24	1.00

Group	Specimen number	Capitulum length	Trochlea length	Inter-condylar groove height	Trochlea height	Inter-condylar groove depth
IMGH 1	1.191 A-M					
—	1.191 B-M					
—	1.191 C-M					
—	1.192 A-M	1.14	1.11	0.30	0.85	0.36
—	1.192 C-M	1.04	1.11	0.24	0.93	0.31
—	1.192 D-M		1.01		0.75	
—	1.192 F-M	0.96	1.01	0.26	0.79	0.29
IMGH 2	1.193 A-M	1.18	1.30			0.51
—	1.193 B-M	1.09	1.32	0.32	1.12	0.43
—	1.193 C-M	1.10	1.31	0.37	1.16	0.38
—	1.193 D-M	1.15	1.26	0.36	1.10	0.42
—	1.193 E-M	1.17	1.28	0.32	1.09	0.41
—	1.193 G-M					
—	1.193 H-M	1.20	1.32	0.30	1.10	0.45
—	1.193 I-M	1.06	1.31	0.43	1.20	0.58
—	1.193 J-M	1.11	1.36	0.36	1.19	0.41
IMGH 3	1.194 A-M	1.85	1.79	0.41	1.25	0.49
—	1.194 B-M					
—	1.194 C-M		1.52	0.35	1.11	0.68
—	1.194 D-M	1.89	1.85	0.56	1.32	0.67
—	1.194 E-M					
—	1.194 F-M		1.49		1.05	0.54
—	1.194 G-M					
—	1.194 H-M					
IMGH 4	1.197 A-M	2.03	2.15	0.68	1.33	0.75
—	1.197 B-M	1.84	2.03	0.58	1.34	0.71
—	1.197 C-M	2.05	1.82	0.48	1.14	0.76
—	1.197 D-M	2.23	1.73	0.61	1.25	0.59
—	1.197 E-M	2.04	1.92	0.49	1.45	0.71
—	1.197 F-M	2.28	1.96	0.65	1.61	0.67
—	1.197 G-M	2.19	1.87		1.41	0.66
—	2001 M					
IMGH 5	1.195 A-M					
—	1.195 B-M	2.44	2.09	0.57	1.32	0.89
—	1.195 C-M	2.50	2.25	0.67	1.85	0.87
—	1.195 D-M	2.49	2.71	0.68	1.83	0.93
IMGH 6	1.196 F-M		2.87	0.90	1.62	0.87
—	1.196 G-M	3.20	2.78	1.04	1.89	0.84
IMGH 7	1.196 A-M	3.96	3.23	0.97	1.79	1.05
—	1.196 B-M	4.33	3.27	1.22	2.12	0.88
—	1.196 C-M					
—	1.196 D-M	3.55	3.11	1.08	1.93	0.81
—	1.196 E-M	2.27	3.10	1.11	2.09	0.82
Caluromys derbianus		3.30	2.73	1.10	2.35	0.63
Metachirus nudicaudatus		2.58	3.52	0.80	3.02	0.59
Rhyncholestes raphanurus		0.87	1.36	0.33	0.98	0.43
—		0.92	1.60	0.39	1.19	0.47
Dromiciops gliroides		1.09	0.86	0.29	0.69	0.26
—		1.19	0.92	0.28	0.69	0.30

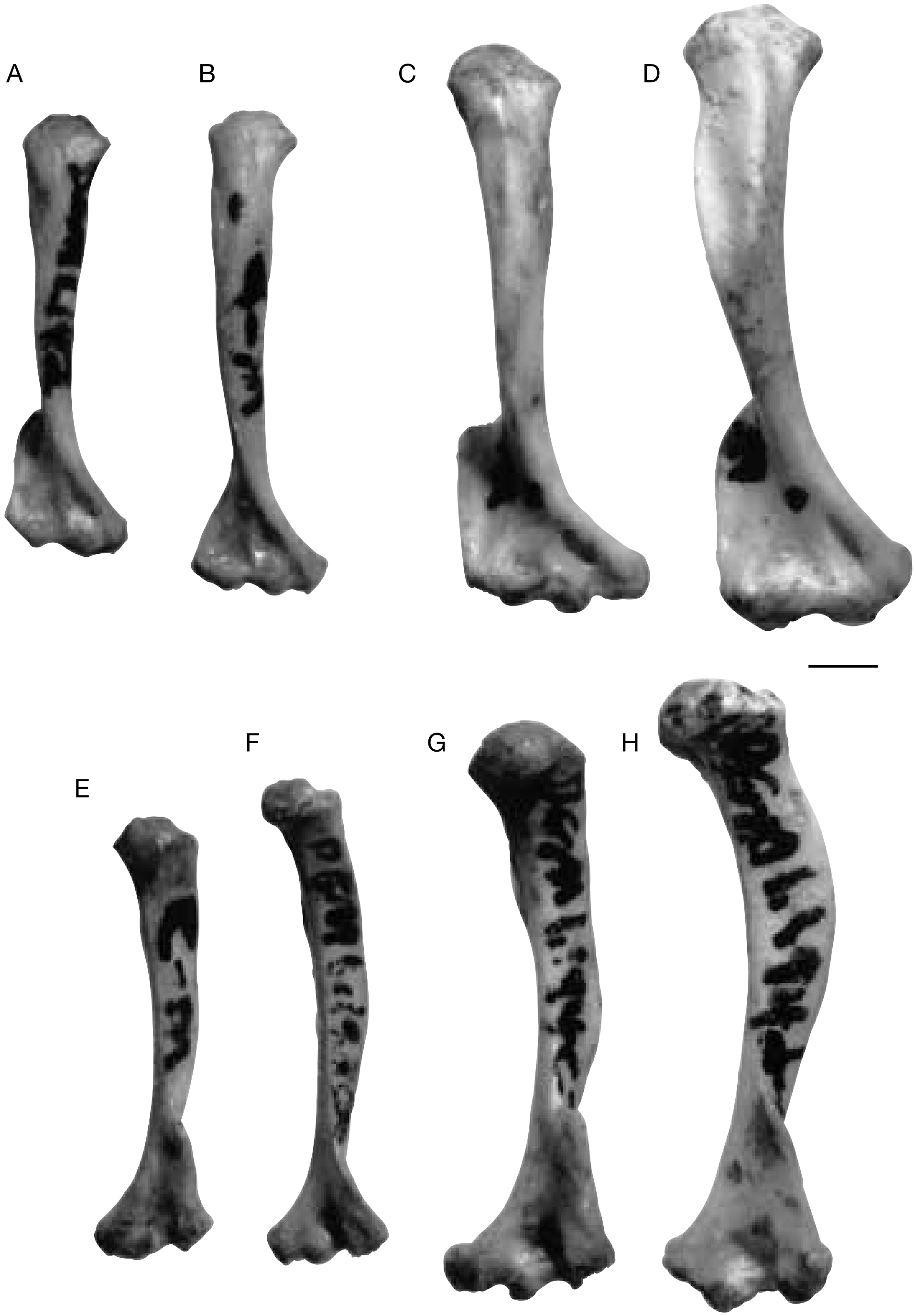


FIG. 27. — **A**, **B**, **E**, **F**, right IMG Humeri 1; **A**, **E**, DGM 1.192C-M; **A**, anterior view; **E**, posterior view; **B**, **F**, DGM 1.192A-M; **B**, anterior view; **F**, posterior view; **C**, **D**, **G**, **H**, right IMG Humeri 3; **C**, **G**, DGM 1.194C-M; **C**, anterior view; **G**, posterior view; **D**, **H**, DGM 1.194D-M; **D**, anterior view; **H**, posterior view. Scale bar: 2 mm.

FIG. 28. — IMG Humerus 4; **A**, **D**, DGM 1.197A-M, right specimen; **A**, anterior view; **D**, posterior view; **B**, **E**, DGM 1.197D-M, left specimen; **B**, anterior view; **E**, posterior view; **C**, **F**, DGM 2001M, right specimen; **C**, anterior view; **F**, posterior view. Scale bar: 3 mm.

applicable in some cases to an obligate arboreal habitus. The relatively poorly developed **hplcr** in the terrestrial models is in sharp contrast to the condition in IMG Humerus 1, and the latter may have been at least partly, but perhaps fully arboreal. The properties of this particular humeral type present serious challenges to the use of models based on the extremes of locomotor type. Yet at the same time this approach also points out the usefulness of this method of evaluation for isolated fossil bones.

IMG Humerus 2 (Figs 31A-G; 34; 35; 53; 68)

There are 12 specimens allocated to this group, and they are preserved to various degrees, with some being complete. The two best ones are DGM 1.193B-M (with a less abraded head) and DGM 1.193A-M. In general, the humerus is exceptionally long, strait, and slender relative to its articular dimensions at its extremities. These humeri represent the most distinctive type within the entire marsupial fauna of Itaboraí, as do IMG Ulna 3, IMG Femur 5, and IMG Tibia 1 within their own designated bone groups. The latter three groups are almost certainly conspecific elements with IMG Humerus 2, as are the tarsals (calcanea, astragali, and a cuboid) assigned to IMG II by Szalay (1994).

The following represent characteristic properties of this group:

1) the head is anteroposteriorly elongated and is relatively small. The lateral tuberosity is far more robust than the medial one;

2) the head is not beaked, that is, not overhanging or leaning caudally. In fact, the articular surface of the head is extremely close to the shaft at its posterior and distal border. In spite of the lack of overhang, the craniocaudally oblate head allowed an angular travel of the humerus on the scapula that exceeded that measured on *Didelphis* and other didelphids;

3) shaft is long and straight and relatively slender compared to its length;

4) the **hdps** is poorly developed and its length is not well-indicated on the shaft, so we did not measure it;

5) the **hmec** is exceptionally reduced;

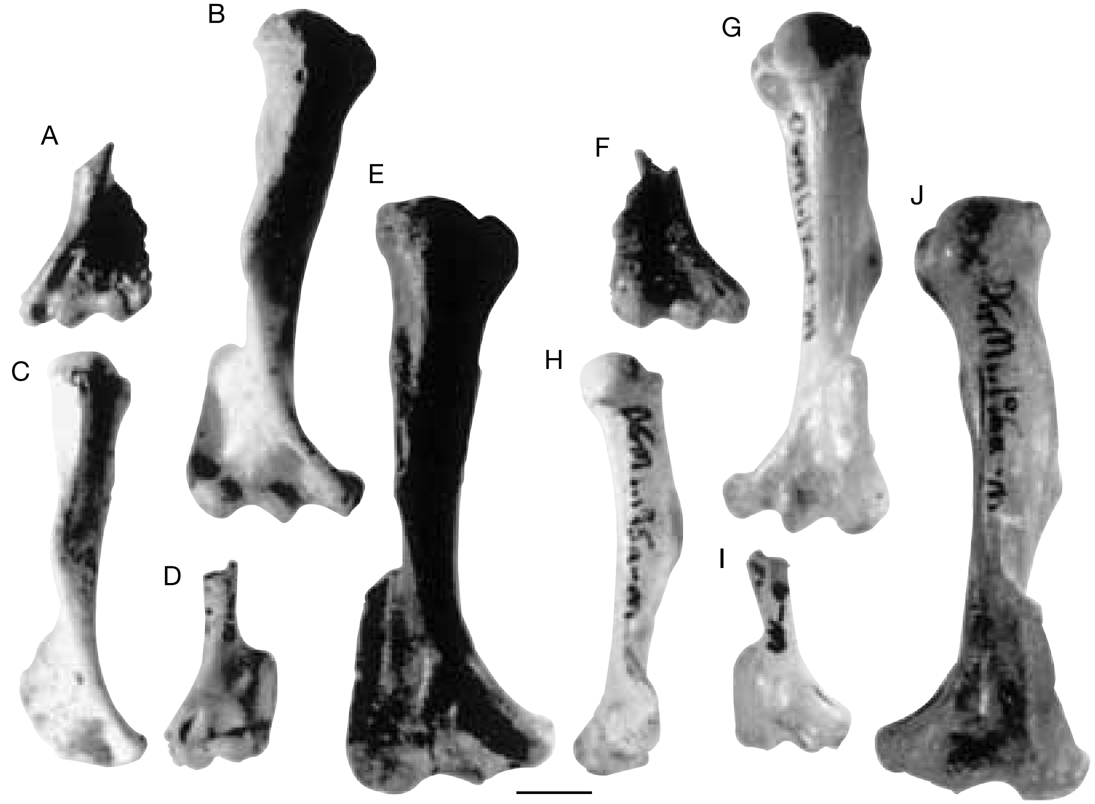


FIG. 29. — **A**, **F**, IMG Humerus 5 (DGM 1.195C-M), left specimen; **A**, anterior view; **F**, posterior view; **B**, **G**, IMG Humerus 6 (DGM 1.196G-M), right specimen; **B**, anterior view; **G**, posterior view; **C**, **H**, IMG Humerus 5 (DGM 1.195A-M), right specimen; **C**, anterior view; **H**, lateral view; **D**, **I**, IMG Humerus 5 (DGM 1.195B-M), left specimen; **D**, anterior view; **I**, posterior view; **E**, **J**, IMG Humerus 7 (DGM 1.196A-M), right specimen; **E**, anterior view; **J**, posterior view. Scale bar: 5 mm.

6) the **hlecr** is reduced (it is probably not more than a sixth of the total length of the humerus, and it is not retroflexed;
7) the trochlea and capitulum, although their spread is relatively short mediolaterally compared to the length of the humerus, are extensively developed both cranially and caudally. The articular facets of both extend well proximally, and the **HuUl** facet is particularly extensive posteriorly;
8) the **hplcr** bordering the deep and double-pitted **hofo** is so strongly developed that it extends proximally past the level of the proximal limit of the supracondyloid foramen (**hscf**);
9) there is no prominent groove for the radial sesamoid, if present, although the facet is well-developed.

The functional significance of these attributes above can be summed up as follows. The relatively long shaft, craniocaudally elongated head, and strongly interlocking elbow joint suggest construction for sustained tensile loads in contrast to the variety of loads encountered in either scansorial or arboreal animals. The deltoid shelf/crest, a complex area for attachment of the pectoralis medially and the acromial and clavicular parts of the deltoid laterally, is poorly developed. While the former muscle is a powerful adductor and rotator, the latter is an abductor. This complex is well-developed in extant didelphids regardless of a variety of substrate usage and locomotor preferences, and this is reflected in their uniformly well-developed deltoid crests

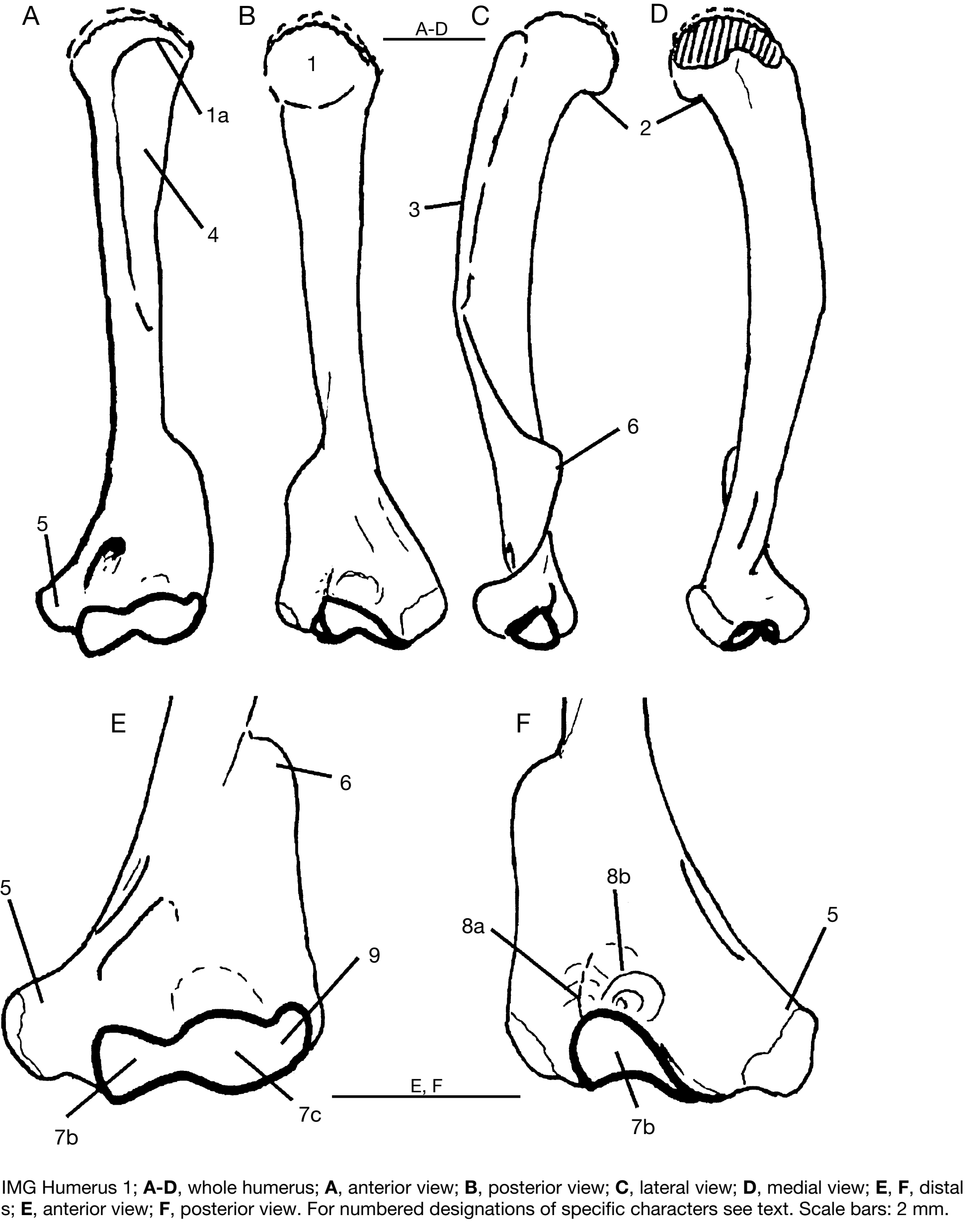


FIG. 30. — Left IMG Humerus 1; **A-D**, whole humerus; **A**, anterior view; **B**, posterior view; **C**, lateral view; **D**, medial view; **E**, **F**, distal third of humerus; **E**, anterior view; **F**, posterior view. For numbered designations of specific characters see text. Scale bars: 2 mm.

or shelves. While some interesting differences exist in this area in didelphids, as explored by Argot (2001), the significance of the underdeveloped condition of this area in this morph is difficult to ascertain.

On Fig. 35 where the mediolateral length/anteroposterior width of the trochlea on the vertical axis is plotted against the mediolateral length of the distal articular surface, the specimens of this phenon fall on both sides of the regression line based on the living models. Nevertheless there is a clear preponderance below the line dividing the arboreal models above and the terrestrial ones below. This pattern for these fossils, however, is far more

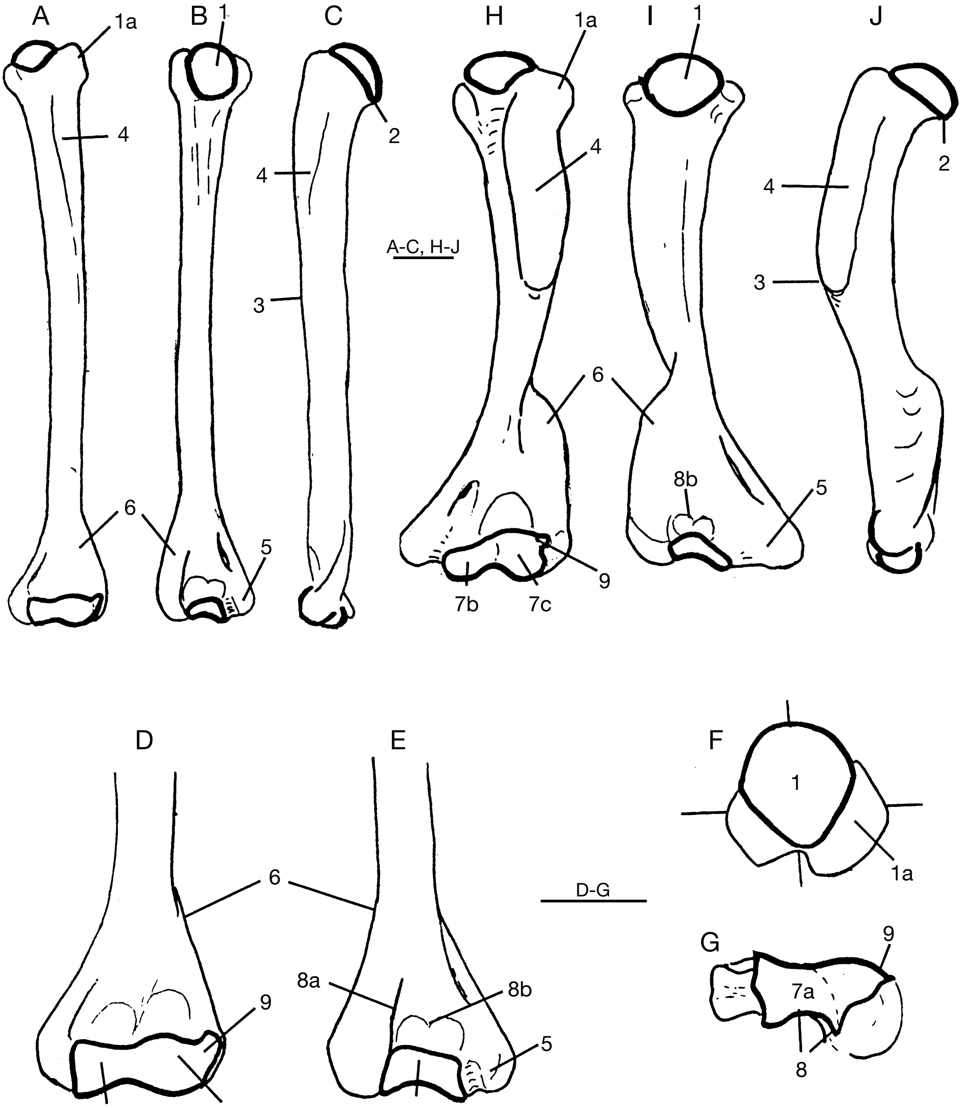


FIG. 31. — **A-G**, left IMG Humerus 2; **A**, anterior view; **B**, posterior view; **C**, lateral view; **D**, **E**, distal third of the humerus; **D**, anterior view; **E**, posterior view; **F**, proximal view; **G**, distal view; **H-J**, left IMG Humerus 3; **H**, anterior view; **I**, posterior view; **J**, lateral view. For numbered designations of specific characters see text. Scale bars: 2 mm.

complicated than an "arboreal" *vs* "terrestrial" issue. The plots (i.e. all of them in this paper) depict morphological relationships that reflect mechanics, and only secondarily associations with biological role. Thus, specimens of the morphologically very distinct IMG Humerus 2, from both IMG Humerus 1 and IMG Humerus 3 (which are dissimilar from one another), show a distribution pattern on these plots that is deceptively similar to that of these other two groups. The particular elbow characteristics that we plotted in this case are simply not indicative of existing and significant real differences between these groups because other factors of the humeri alter

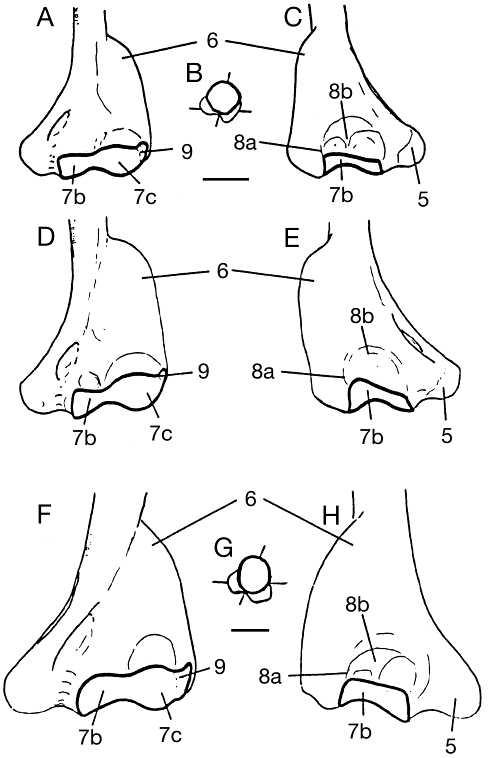


FIG. 32. — **A-E**, left IMG Humerus 4; **A**, **D**, anterior view of the distal third; **B**, proximal view of the head with the approximate axes of orientation of the head and distal end; **C**, **E**, posterior view of the distal third; **F-H**, left IMG Humerus 5; **F**, anterior view of the distal third; **G**, proximal view of the head with the approximate axes of orientation of the head and distal end; **H**, posterior view of the distal third. Scale bars: 2 mm.

the perspective of evaluation. These other factors of the bones are critical as their osteological (and therefore myological and mechanical) contexts render the interpretation of the distal end radically different.

It appears that this humerus was involved in a biological role distinct from the known quadrupedal didelphids living today which usually excel in climbing. We suggest perhaps a particular suspension-related activity that may be tied even to the functional demands of a stretched patagium for gliding. In fact, the angular distance of the head of the humerus in a craniocaudal direction is so extensive that it recalls the similar morphological pattern of dermopteran and anomalurid humeral heads that we have examined in detail (see also Stafford 1999). The discussions under IMG Ulna 3, IMG Femur 5, and IMG Tibia 1, and in Szalay (1994: 166-168) are highly pertinent, as we believe these to be conspecific elements.

IMG Humerus 3
(Figs 27C, D; 31H-J; 34; 35; 68)

There are eight specimens included in this group. Two of them are complete with abraded heads (DGM 1.194A-M and DGM 1.194D-M) and while DGM 1.194H-M is completely lacking distal morphology, it has a well-preserved proximal end. Compared to IMG Humerus 2, this morph is a shorter but far more robust bone, with much larger proximal and distal articular areas.

The following represent characteristic properties of this group:

1) the head is rounded and extensive, with a relatively modest development of the lateral tuberosity;
2) the head is beaked;
3) shaft is relatively short and robust with the bone bowed laterally and cranially;
4) the **hdps** is extensively developed distally, and unlike many of the IMG humeri, it is shelf-like and not crestate; the HDSI index is 47 (n = 6), suggesting a faster rather than slower action for the flexors, adductors, and rotators;
5) the **hmec** is extensive medially, indicative of well-developed digital flexors. It is probably unreduced (i.e. probably close to the morphotypic sudameridelphian condition);
6) the **hlecr** is probably also near the sudameridelphian morphotypic condition, and extends over one third of the length of the humerus;
7) trochlea and capitulum are well-developed, and the **HuUL** facet extends only slightly onto the posterior surface of the bone;
8) the **hplcr** is weekly developed, bordering a double pitted but small and shallow **hofo**;
9) there is no appreciable groove for the radial sesamoid (**Ras**), if it was present, and the **HuRas** facet (or an extension of the **HuRa** facet) is very small.

There are no apparent significant functional specializations on this bowed and ruggedly sculpted humerus that would suggest any other functions than those associated with arboreal generalists.

IMG Humerus 4 (Figs 28; 32A-E; 34; 35; 68)
There are nine specimens allocated to this phenon, one of which (DGM 2001M) may represent another species. Unfortunately, the distal ends are broken on this specimen, but its exceptionally shelf-like and extremely well-developed deltopectoral ridge, in spite of its similar size to the other specimens, hints at taxonomic distinction. The most complete specimen of the entire sample is DGM 1.197A-M that has a ridge-like deltopectoral crest, and the morphology displayed by the specimen is supplemented by very well-preserved distal thirds of three specimens, as well as four other nearly complete humeri.

The following represent characteristic properties of this group:

1) because the head is not well-preserved, little can be said about it. However, the lateral tuberosity is moderately developed;
2) the beaking of the head is similar to that of *Didelphis*;
3) the moderately robust shaft is not bowed, although the hypertrophied deltopectoral ridge does give that impression;
4) the **hdps** is ridge-like with little shelving, and the HDSI of the complete specimen is 63, which is unusually high given that this index appears to correlate with body size;
5) the **hmec** is moderate, not really reduced, and similar in proportions to IMG Humerus 3;
6) the **hlcer** is well-developed, not particularly retroflexed, and it is about a fourth of the proximodistal length of the humerus;
7) the trochlea is modestly developed compared to the capitulum; it is not as extensive proximally on the anterior face as the capitulum;
8) the posterior extent of the **HuUl** facet is moderate with only a barely noticeable **hplcr** bordering the shallow, slightly double pitted **hofo** (the double pitting being present in only two out of the eight specimens);
9) there is no significant groove for the radial sesamoid (if present), and this facet is exceptionally small.

The points for IMG Humerus 4 on the plots of Figs 34 and 35 fall either on the model-generated regression line, or well below it on Fig. 35. The latter has distal articular mediolateral length on the horizontal axis. This distribution is anomalous, in our view, as the articular pattern of the distal humerus suggests a highly arboreal animal. This case underscores the difficulty of finding easily applicable ratios, measurements, or indices for diversely preserved fossils of highly disparate-sized species. Alternatively, it is possible that this animal may have been scansorial.

IMG Humerus 5
(Figs 29A-D, F-I; 32F-H; 34; 35; 68)
Of the four specimens representing this sample, three are exceptionally well-preserved distal thirds, whereas the fourth (DGM 1.195A-M), while lacking the distal articular surfaces, has the proximal end well-preserved. Because the distal end is poorly preserved, this last specimen is allocated to this group based on size alone. It is both conspicuously larger than IMG Humerus 4 and smaller than IMG Humerus 6. Remarks about the morphology of the shaft and the head are based on this specimen.

The following represent characteristic properties of this group, but attributes of the head and shaft should be considered with the caveat expressed above regarding allocation:

1) the head is well-rounded, not oblate, and the lateral tuberosity is marginally developed, perhaps equivalent to the medial tuberosity in overall size;
2) beaking of the head is well-developed;
3) shaft is slightly bowed and not slender;
4) the **hdps** is long, high, but relatively slender, and crest-like distally;
5) the **hmec** is well-developed but not excessively so, similar in its proportions to most Itaboraí didelphidans;
6) the **hlcer** is well-developed with the characteristic proximolateral slight bulge that is present in many living didelphids and Itaboraí didelphidans; it is somewhat retroflexed;
7) the trochlea is especially well-developed compared to the capitulum, and the **HuUl** facet extends well proximally on the posterior side where it is very concave;
8) the **hplcr** is well-developed and the **hofo** is double pitted in two of the three specimens with well-preserved distal ends;

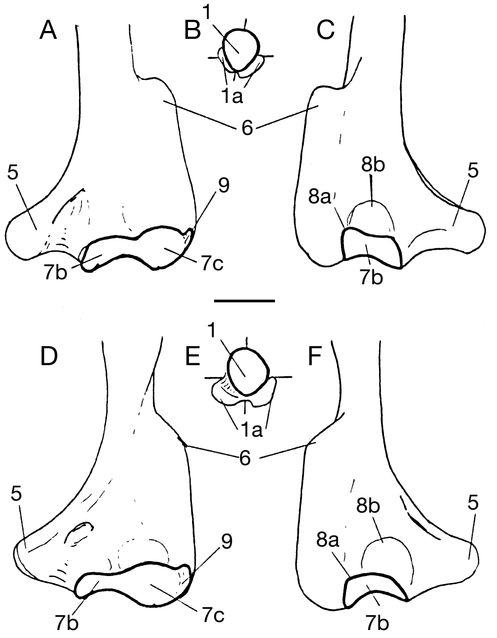


FIG. 33. — **A-C**, left IMG Humerus 6; **A**, distal third, anterior view; **B**, proximal view of the head with the approximate axes of orientation of the head and distal end; **C**, distal third, posterior view; **D-F**, left IMG Humerus 7; **D**, distal third, anterior view; **E**, proximal view of the head with the approximate axes of orientation of the head and distal end; **F**, distal third, posterior view. For numbered designations of specific characters see text. Scale bar: 4 mm.

9) the groove for the radial sesamoid (if present) is pronounced and the facet itself is large.

The distal half of the bone suggests a well-stabilized elbow joint, with features more characteristic of terrestrial animals than obligate arboreal forms. The spread on Fig. 35 shows two specimens closely above and below the model-based regression line, and one specimen well down in the "terrestrial range". Scansorial behavior, with a strong terrestrial component, was a probable locomotor pattern.

IMG Humerus 6 (Figs 29B, G; 33A-C; 34; 35; 68)

This sample is represented by two specimens, a single perfect right humerus of light color (DGM 1.196G-M), the one whose values are plotted, and another with the head and tuberosities completely missing.

The following represent characteristic properties of this group:
1) the head is rounded;
2) beaking of the head is well-developed;
3) shaft is slightly bowed;
4) the **hdps** is long and flat proximally for half of its length, but it becomes crestate distally. The HDSI is 60;
5) the **hmec** is especially well-developed on the complete specimen, but somewhat abraded on the other;
6) the **hlcer** is well-developed with the characteristic proximolateral peaking described above, but it is not retroflexed at all;
7) both the trochlea and capitulum are well-developed, and the **HuUl** facet extends well proximally on the posterior side where it is very concave;
8) the **hplcr** is not extended proximally, and the hofo is relatively shallow;
9) there is no groove for the radial sesamoid, if present, and the facet itself is very small.

This humerus falls below the model-based regression line on Figs 34 and 35. Its distal articulation, characterized by a wide and posteriorly highly concave trochlea, as well as the large and somewhat distally extended trochlea anteriorly, suggests a terrestrial component to its habitus.

IMG Humerus 7 (Figs 29E, J; 33D-F; 34; 35; 68)

This phenon consists of five specimens. DGM 1.196A-M is a perfectly preserved right specimen, and DGM 1.196B-M is a left distal half that is not only exceptionally preserved, but is also a mirror in most ways of DGM 1.196A-M.

The following represent characteristic properties of this group:
1) the head is slightly oblate craniocaudally, and is bordered by a hypertrophied medial tuberosity that is situated well medially;
2) the beaking of the head is pronounced;
3) the shaft is minimally bowed;
4) the hdps is long and exceptionally well-developed at its distal extremity where it is crest-like, rather than shelf-like. The HDSI is 59;
5) the **hmec** is well-developed, although not beyond what one finds in most of the IMG humeri;

6) the **hlcer** is well-developed, not retroflexed, and has the proximolateral extension described for several of the other groups;
7) the trochlea is relatively very small compared to the large and slightly oblate capitulum, and it has a not particularly concave **HuUl** facet that is only moderately extended onto the posterior surface;
8) the **hplcr** is not extended past the articulation, and the variably shaped hofo is small and shallow;
9) there is a slight groove on the moderately sized facet for the radial sesamoid.
Characteristics of this relatively large humerus suggest a fully arboreal animal. The relatively shallow **HuUl** articulation posteriorly and the disproportionately large capitulum, as well as the distribution of the specimens on the plots of Figs 34 and 35, strongly support this hypothesis. The HDSI is high simply because this was a large species (and apparently for no other reason).

ULNAE (TABLES 5; 8; 9)
IMG Ulna 1 (Fig. 38A-C)
A single tiny ulna (DGM 1.150I-M), with only its proximal half preserved that is no more than 3 mm in length, belonged to a species far smaller than either *Monodelphis*, *Dromiciops*, or any caenolestid specimen analyzed by us. In spite of its small size, the specimen is robustly constructed. The following represent characteristic properties of this ulna:
1) olecranon process (**ulol**) is slightly shorter in length than the opening of the trochlear notch between the ulnar coronoid process (**ulco**) and the most proximal extent of the medial proximal trochlear crest of the ulna (**ulptcm**). The **ulol** is tapered proximally, and has a well-developed subcutaneous surface (**ulscs**);
2) trochlear notch is relatively shallow, and the Ulnar Trochlear Notch Index, UTNI (chord of depth/length of opening × 100), is 24, a value lower than that in either *Dromiciops* or *Caluromys*;
3) medial and lateral wings of the proximal trochlear crest of the ulna (**ulptc**) are subequal;

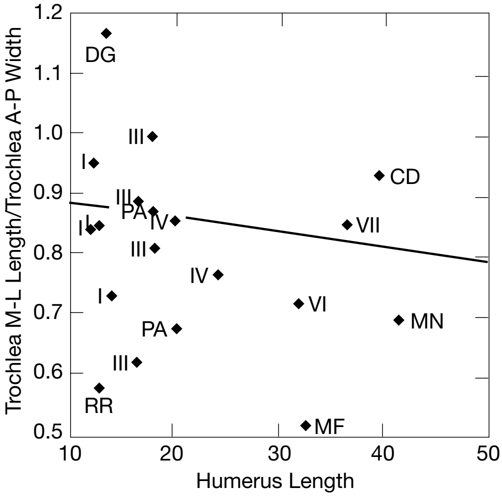


FIG. 34. — Plot of a humeral index against a quasi-surrogate measure of body weight (given the isolated nature of specimens) on the horizontal axis. Regression line was drawn for living models only, and the fossil values were plotted subsequently in order to gauge some measure of their relationship to the arboreal-terrestrial dichotomy between models. Abbreviations: **CD**, *Caluromys derbianus*; **DG**, *Dromiciops gliroides*; **MF**, *Mayulestes ferox*; **MN**, *Metachirus nudicaudatus*; **RR**, *Rhyncholestes raphanurus*; **PA**, *Pucadelphys andinus*. Roman numerals stand for Itaboraí Metatherian Group designations of humeri.

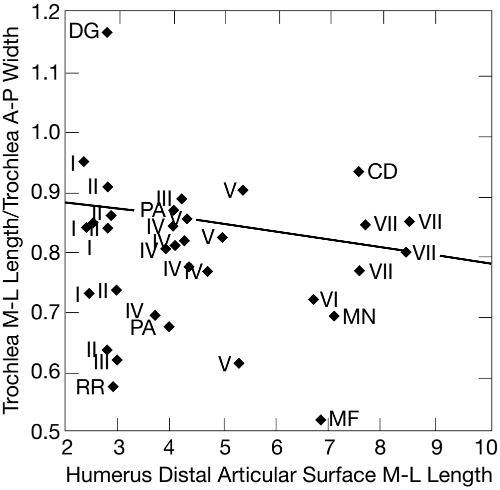


FIG. 35. — Same as for Fig. 34, but with a different body weight surrogate that allows the inclusion of more (fragmentary) fossils.

4) ulna appears to be caudally bowed;
5) radial notch is not clearly visible, but the peduncle that was undoubtedly backing the **RaUl**

TABLE 8. — Measurements of ulnae from Itaboraí (all DGM numbers) and from the model species.

Group	Specimen number	Olecranon process length	Medial length of trochlear notch	Proximal width of trochlear notch	Distal width of trochlear notch	Midline length of trochlear notch	Lateral olecranon beak length	Ulnar proximal end length
IMGU 1	1.150I-M	0.85	1.06	0.66		0.81		1.91
IMGU 2	1.150II-M	1.39	1.63	1.01	1.36	0.88	0.76	3.02
IMGU 3	1.150IIIA-M	1.18	1.85	1.14	1.64	1.53	0.40	3.05
—	1.150IIIB-M	1.07	1.97	1.38	1.71	1.41	0.63	3.11
—	1.150IVA-M	1.31	1.76	1.39		1.68		3.07
—	1.150IVB-M	1.15						
IMGU 4	1.150VA-M							
—	1.150VB-M		2.42	1.52	1.93		0.54	
—	1.150VC-M	2.13	2.05	1.41	1.88	2.05	0.53	4.21
IMGU 5	1.150VIA-M		3.19	2.16	2.15	1.65	0.54	
—	1.150VIB-M	2.82	3.16	2.00	2.43	2.25	0.79	6.05
IMGU 6	1.150VIIA-M		3.91					5.98
—	1.150VIIB-M	2.56	2.53	0.94	2.45	2.57	1.18	6.06
IMGU 7	2020M	4.01	3.93	2.77	2.67	3.09	0.84	8.00
—	1.150VIII-M	4.08	3.30	2.51	2.76	3.04	1.79	7.37
IMGU 8	1.150IX-M	2.83	5.38	3.09	3.61		1.06	8.22
—	1.150X-M	3.44	4.26	3.26	4.25	3.45	1.42	7.72
IMGU 9	1.150XIA-M	4.46	6.51	3.27	4.87	5.01	1.33	10.96
—	1.150XIB-M							
IMGU 10	1715PV	6.52	6.88	4.90	6.10	5.84	2.29	13.42
—	2078M	6.55	6.71	4.21	5.39	5.62	1.68	13.23
—	1362M		7.18	4.00	5.30	4.73	2.20	
IMGU 11	2069M	7.78	8.37	5.20	6.78	6.89	2.05	16.17
Caluromys derbianus		3.42	3.98	2.71	4.99		1.39	7.40
Metachirus nudicaudatus		5.22	4.22	5.13	4.67		2.13	9.45
Rhyncholestes raphanurus		2.29	1.91	1.81	1.72		0.76	4.22
—		2.01	2.24	1.78	1.63		0.78	4.23
Dromiciops gliroides		1.42	1.39	1.03	1.58		0.36	2.82
—		1.60	1.36	0.96	1.65		0.50	2.95

Group	Specimen number	Ulnar proximal shaft width	Trochlear notch depth	Medial olecranon beak length	Olecranon process angle	Ulnar proximal shaft depth
IMGU 1	1.150I-M	0.39	0.25		65.00	0.71
IMGU 2	1.150II-M	0.69	0.28	0.44	65.00	1.23
IMGU 3	1.150IIIA-M	0.86	0.74	0.91	71.00	1.40
—	1.150IIIB-M	0.75	0.78	1.24	74.00	1.50
—	1.150IVA-M		0.74		74.00	
—	1.150IVB-M					
IMGU 4	1.150VA-M	0.90				1.53
—	1.150VB-M	0.85		1.09	70.00	1.63

Group	Specimen number	Ulnar proximal shaft width	Trochlear notch depth	Medial olecranon beak length	Olecranon process angle	Ulnar proximal shaft depth
—	1.150VC-M	0.92	0.71	0.99	75.00	1.98
IMGU 5	1.150VIA-M	1.11	0.90	2.24	77.00	2.15
—	1.150VIB-M	1.14	1.06	1.64	80.00	2.20
IMGU 6	1.150VIIA-M					
—	1.150VIIB-M	2.04	0.86	1.24	60.00	1.63
IMGU 7	2020M	1.53	1.07	2.62	78.00	2.37
—	1.150VIII-M	1.60	0.83	0.75	73.00	2.41
IMGU 8	1.150IX-M	1.46	1.12	3.05	57.00	2.96
—	1.150X-M	1.54	1.14	2.27	74.00	3.36
IMGU 9	1.150XIA-M	2.17	1.72	2.60	78.00	3.97
—	1.150XIB-M					3.44
IMGU 10	1715PV	2.40	2.65	3.68	74.00	5.14
—	2078M	2.52	2.21	3.21	75.00	4.75
—	1362M	2.82	1.78	2.84	72.00	4.93
IMGU 11	2069M	3.42	2.41	3.57	72.00	6.40
Caluromys derbianus			1.44	1.38		
Metachirus nudicaudatus			2.45	3.56		
Rhyncholestes raphanurus			0.91	1.36		
—			0.91	1.19		
Dromiciops gliroides			0.45	0.70		
—			0.54	0.66		

facet is convex, process-like, and projects well laterally. The robusticity of the process (the convexity is a probable artifact due to weathering) does suggest that the radius was well-removed laterally, indicating a wide articular surface on the humerus. The radial notch appears to have faced cranially;

6) on the proximal and medial ulnar surface, the fossa for the origin of the flexor digitorum profundus (**ulfofdp**) is shallow and poorly developed. The lateral fossa for the insertion of the anconeus (**ulfoa**) is moderately excavated.

This robust yet tiny ulna appears to be functionally distinctive inasmuch as it resembles most arboreal didelphids and *Dromiciops*. It is far more like *Dromiciops* than either *Monodelphis* or *Rhyncholestes*, yet this similarity cannot be considered anything but a functional, rather than phylogenetic, one. While *Monodelphis* and caenolestids have a relatively straight proximal third of the ulna with an olecranon process expanded proximally, this fossil is bowed with a tapered olecranon. A characteristic of the arboreal didelphids and the microbiothere is the slightly greater separation of the **RaUl** facet from the lateral border of the coronoid process, which is suggestive of a lesser restriction of the rotating radius than what occurs in terrestrial forms like *Metachirus*, caenolestids, and *Didelphis*. In these terrestrial forms the radial contact tends to be closely abutted against the coronoid process.

IMG Ulna 2 (Figs 38D-F; 42-44)

This group is represented by a single specimen (DGM 1.150II-M), the proximal half of the bone, which is preserved to the same degree as IMG Ulna 1. It is also similar in its morphology to IMG Ulna 1, although it is twice the length of that specimen.

TABLE 9. — Comparisons of a humeral and an ulnar index in *Didelphis virginiana* Kerr, 1792, the model species, Itaboraí specimens (all DGM numbers), and taxa from the Paleocene of Tiupampa, Bolivia. For a definition of indices see text.

Group	Group means	Specimen number	HDSI	UTNI
IMGH 1		1.191 C-M	45.01	
—		1.192 A-M	48.26	
—		1.192 C-M	45.97	
—		1.192 D-M	40.73	
—		1.192 F-M	41.54	
	IMGH 1 (n = 5)		**44.30**	
IMGH 3		1.194 A-M	38.36	
—		1.194 C-M	48.51	
—		1.194 D-M	43.68	
—		1.194 E-M	45.58	
—		1.194 F-M	47.51	
—		1.194 H-M	57.71	
	IMGH 3 (n = 6)		**46.89**	
IMGH 4		**1.197 A-M**	**63.01**	
IMGH 6		**1.196 G-M**	**60.27**	
IMGH 7		**1.196 A-M**	**59.42**	
IMGU 1		**1.150 I-M**		**23.58**
IMGU 2		**1.150 II-M**		**17.18**
IMGU 3		1.150 III A-M		40.00
—		1.150 III B-M		39.59
—		1.150 IV A-M		42.05
	IMGU 3 (n = 3)			**40.55**
IMGU 4		**1.150 VC-M**		**34.63**
IMGU 5		1.150 VIA-M		28.21
—		1.150 VIB-M		33.54
	IMGU 5 (n = 2)			30.88
IMGU 6		1.150 VIIB-M		33.99
IMGU 7		2020 M		27.23
—		1.150 VIII-M		25.15
	IMGU 7 (n = 2)			**26.19**
IMGU 8		1.150 IX-M		20.82
—		1.150 X-M		26.76
	IMGU 8 (n = 2)			**23.79**
IMGU 9		**1.150 XIA-M**		**26.42**
IMGU 10		1715 PV		38.52
—		2078 M		32.94
—		1362 M		24.79
	IMGU 10 (n = 3)			**32.08**
IMGU 11		**2069 M**		**28.79**

Genus	Species means	Species	HDSI	UTNI
Caluromys		*derbianus*	**54.00**	**36.18**
Metachirus		*nudicaudatus*	**55.50**	**58.06**
Didelphis	**n = 6**	*virginiana*	**58.35**	**31.56**
Rhyncholestes	**n = 2**	*raphanurus*	**48.34**	**43.86**
Dromiciops	**n = 2**	*gliroides*	**46.55**	**36.00**
Mayulestes		*ferox*	**55.01**	
Pucadelphys	**n = 2**	*andinus*	**49.91**	

The following represent characteristic properties of this ulna:

1) the **ulol** is slightly shorter in length than the opening of the trochlear notch between the **ulco** and the **ulptcm**, as in IMG Ulna 1. The **ulol** is tapered proximally, with a well-developed **ulscs**;
2) trochlear notch is relatively very shallow and the UTNI is 17, which is a very low value;
3) medial wing of the **ulptc** is somewhat longer than the lateral one;
4) ulna is caudally bowed;
5) while the peduncle that supported the radial head is robust and well-separated from the ulnar shaft, the orientation of the notch itself is cranial. There is no evidence, however, that the **RaUl** facet was adjacent to the **HuUlm** facet and the coronoid process itself is poorly preserved;
6) the medial **ulfofdp** is poorly developed whereas the lateral **ulfoa** is moderately excavated.

For the same reasons as the ones given for IMG Ulna 1, attributes of this group suggest that it was a small arboreal animal. Yet the animal represented by this ulna was probably almost twice the body mass of the one individual in the preceding group. In Fig. 42, where the ratio of the proximal trochlear notch width over the distal trochlear notch width is plotted against ulnar trochlear notch length, IMG Ulna 2 falls just below the model-based regression line, along with the arboreal models. In Fig. 43, where the same ratio is plotted against ulnar proximal end length, this group falls right on the model-based regression line. In Fig. 44, where the critical ratio of ulnar trochlear notch depth over ulnar distal trochlear notch width is plotted against the length of the proximal ulna, this specimen falls well below all other samples plotted, reflecting the extreme shallowness of its trochlear notch.

IMG Ulna 3 (Figs 38G-I; 39; 42-44; 53)

Four specimens represent this phenon, an ulnar group that we have allocated above to be conspecific with IMG Humerus 2, IMG Femur 5, and IMG Tibia 1, as well as with the tarsals described by Szalay (1994) as representing IMG II. The best of these ulnae is DGM 1.150IIIA-M. The size of these specimens is smaller than that of *Rhyncholestes raphanurus*.

The following represent characteristic properties of these specimens:

1) the olecranon process is less than half the length of the opening of the trochlear notch between the **ulco** and the most proximal extent of the **ulptcm**. The **ulol** is substantially expanded proximally, and it has a well-developed ulscs;
2) trochlear notch is very deep and the UTNI is 41;
3) medial and lateral wings of the **ulptc** are unequal, the medial portion being substantially longer;
4) ulna appears to be slightly caudally bowed;
5) condition of radial notch is highly diagnostic of this animal. The caudal part of the **RaUl** facet is flat and faces cranially, rather than laterally as it does in all the other phena. It is crowded against the base of the coronoid process next to the sliver of this facet that is along the lateral face of the coronoid process. There is no appreciable supporting peduncle. Immediately distal to the **RaUl** facet, a broad and diagonal groove is apparently present to allow broad access of the biceps onto the radius;
6) there is no appreciable medial **ulfofdp**, but the **ulfoa** is well-excavated proximally and laterally.

As we noted above, there is little doubt that these ulnae are conspecific with IMG Humerus 2. The general conformation of the ulna, as with that of the humerus, suggests great stability in its construction and conarticulation with the distal humerus. The robust but mediolaterally narrowed articular areas of the elbow account for the close proximity of the **RaUl** facet to the coronoid process, but caudally recessed aspect of this facet, along with the groove distal to the facet, is not the condition we have encountered in our terrestrial models. This phenon, therefore, while reflecting the stability related features of the terrestrial models, is distinct from them.

The most interesting mechanical aspect of this sample is the combination of a short lever provided by the olecranon process with the pronounced stability-related conformation of the humeroulnar articulation. In spite of the short olecranon process, the robust areas of insertion for the heads of the triceps are obvious on the bones. Judged from the lack of a peduncle of the radial articulation, the radioulnar joint was not heavily stressed in compression. However, the obvious stability related humeroulnar articulation suggests tensile loading, an explanation in keeping with the slender and long IMG Humerus 2, IMG Femur 5, and IMG Tibia 1.

As expected from the description, the plotted values for these ulnae on Figs 42 and 43 fall near the model-based regression line. In Fig. 44, however, because of the combination of extreme brevity of the olecranon with the great depth of the trochlear notch, the specimens fall above the line together with the terrestrial models.

IMG Ulna 4 (Figs 36; 38J-L; 42-44)

This phenon is represented by three specimens; two are the proximal thirds of the ulnae, whereas DGM 1.150VC-M is a nearly complete one. These ulnae are in the size range of those of *Rhyncholestes*.

The following represent characteristic properties of these specimens:

1) the olecranon process is the same length as the opening of the trochlear notch between the **ulco** and the most proximal extent of the **ulptcm**. The **ulol** is tapered proximally and has a well-developed **ulscs**;

2) trochlear notch is somewhat deep with a highly characteristic cranial projection of the **ulco**. UTNI is 35, which is within the range of *Dromiciops*;

3) the **ulptcm** and **ulptcl** are subequal;

4) ulna appears to be relatively straight;

5) the concave radial notch extends onto the entire lateral face of the coronoid process, although only as a small proximal ribbon. The supporting peduncle for the somewhat laterally facing **RaUl** facet is minimal;

6) the **ulfofdp** is well-excavated, and has a diagonal partition trending proximodistally at the proximal end of the olecranon process;

7) the distal fourth of the shaft is triangular, and has a flattened medially facing surface. This may be for the pronator quadratus or part of the interosseous ligaments between the ulna and radius.

The morphology, inferred mechanics, and similarities to the arboreal models all indicate a small arboreal animal. Nevertheless, the plotted values of these specimens fall very close to or onto the model-based regression lines in Figs 42-44.

IMG Ulna 5 (Figs 36; 40A-C; 42-44)

Two partial specimens represent this phenon. The better of the two is DGM 1.150VIB-M because it has a complete olecranon process. It is a distinct possibility that this sample is from the same species as IMG Ulna 4. But because of some of the differences noted below, as well as the consistently larger olecranon notch and olecranon process, we treat it separately from the sample discussed above. In general, the articulating area of the proximal ulna is robustly delineated by the hypertrophy of the edges of its articular surfaces.

The following represent characteristic properties of this group:

1) the olecranon process is about the same length as the opening of the trochlear notch between the ulco and the most proximal extent of the ulptcm. The **ulol** is not tapered proximally, and it is moderately expanded craniocaudally with a well-developed **ulscs**;

2) trochlear notch is somewhat deep, and has a cranially projecting **ulco** similar to that in IMG Ulna 4. UTNI is 31;

3) the **ulptcm** is distinctly longer than the **ulptcl**, and the **HuUlm** facet extends well proximally on the medial side of the bone;

4) ulna appears to be relatively straight judged from the preserved proximal half;

5) the radial notch is well-recessed caudally and faces laterally, but it is not displaced laterally; peduncular support is minimal. There is no appreciable extension of the radial notch onto the lateral side of the **ulco**, although the process is laterally narrowed probably to accommodate the head of the radius;

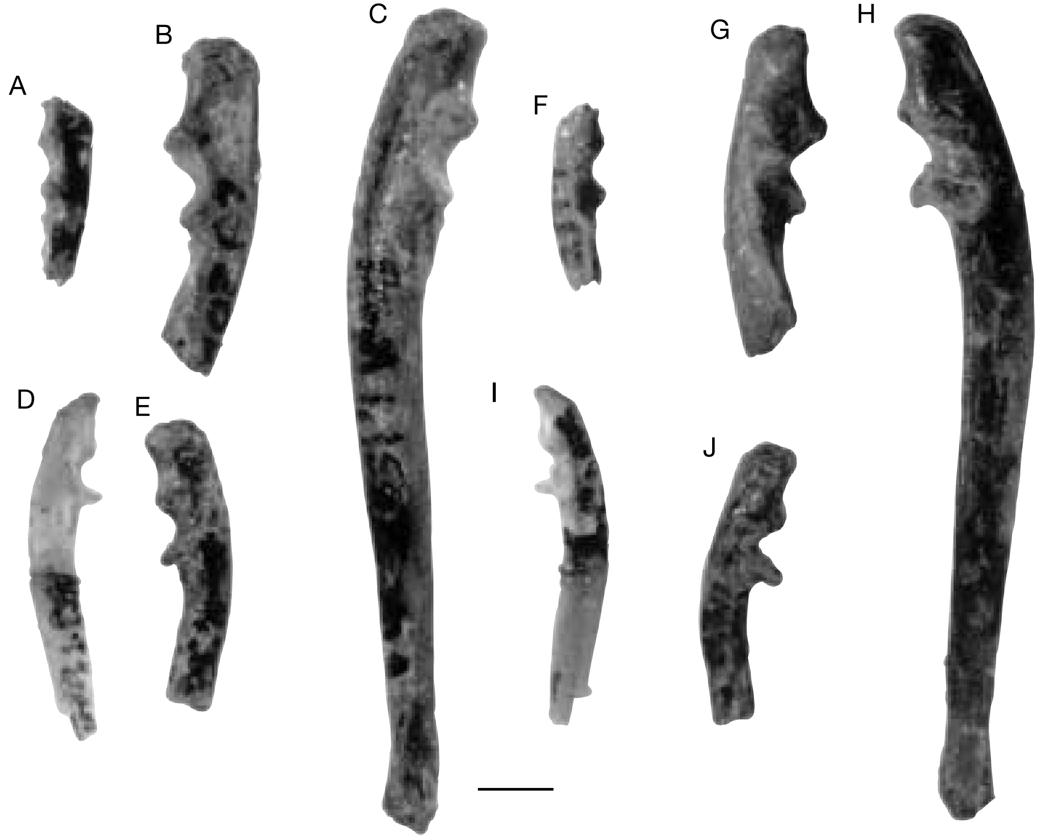


FIG. 36. — **A**, **F**, IMG Ulna 4 (DGM 1.150VB-M), right specimen; **A**, medial view; **F**, lateral view; **B**, **G**, IMG Ulna 7 (DGM 2020M), right specimen; **B**, medial view; **G**, lateral view; **C**, **H**, IMG Ulna 8 (DGM 1.150X-M), left specimen; **C**, medial view; **H**, lateral view; **D**, **I**, IMG Ulna 5 (DGM 1.150VIB-M), left specimen; **D**, medial view; **I**, lateral view; **E**, **J**, IMG Ulna 6 (DGM 1.150VIIB-M), right specimen; **E**, medial view; **J**, lateral view. Scale bar: 3 mm.

6) the medial **ulfofdp** is well-excavated and, as in IMG Ulna 4, there is a similar proximodistally trending partition in the excavated areas.

In Fig. 42, one of the two specimens falls well above the model-based regression line, and it is found slightly above the line in Fig. 44. But even in Fig. 42, as in Fig. 43, the other specimen is on the line. This is an ambiguous ulna in terms of substrate preference, suggesting either a scansorial animal, or an animal whose substrate preference could only be determined using additional postcranial elements. This, again, highlights the difficulty of trying to determine biological roles based on single elements. Animals will show compromise morphologies in one area of the skeleton, whereas they may have highly specialized adaptive solutions in another area.

IMG Ulna 6 (Figs 36; 40D-F; 43; 44)

Two specimens, one slightly more complete than the other, represent the proximal third of this bone. DGM 1.150VIIB-M is the more complete of the two.

The following represent characteristic properties of these specimens:

1) the olecranon process is substantially shorter than the opening of the trochlear notch between the **ulco** and the most proximal extent of the **ulptcm**. The **ulol** is expanded craniocaudally, and has a well-developed **ulscs**;

2) trochlear notch is somewhat deep with a characteristic minimum of **ulco** projection. UTNI is 34, which is well within the range of the arboreal models;
3) medial and lateral wings of the **ulptc** are subequal, and the humeroulnar articulation is rotated somewhat radially;
4) ulna appears to be relatively straight due to the expansion of the olecranon process;
5) the flat **RaUl** facet is closely nestled against the distal part of the ulnar guiding ridge (**ulgr**); it faces laterally, but has minimal peduncular support;
6) the medial surface for the **ulfofdp** is not excavated, which is in sharp contrast to the previously described ulnae. In fact, the preserved proximal shaft of the bone is rounded. The area of insertion for the brachialis, the ulnar annular ligament fossa (**ulalfo**) is exceptionally long and deeply excavated, again in contrast to the expression of this feature on the Itaboraí ulnae described above. The **ulfoa** is not noticeable, although undoubtedly the anconeus was present. Attributes of the trochlear notch (shallow depth, subequality of the wings of the **ulptc**) suggest an arboreal form. But its expanded **ulol**, the somewhat laterally rotated articular area, and the great proximodistal extent of the **ulalfo** all suggest a somewhat enigmatic combination. As far as the plotted values on Figs 42-44 are concerned, however, this group plots squarely with the arboreal models.

IMG Ulna 7 (Figs 36; 40G-I; 42-44)
Two nearly identically preserved incomplete specimens, representing the proximal third of the ulna, comprise this phenon.
The following represent characteristic properties of this group:
1) the olecranon process is slightly longer than the opening of the trochlear notch between the **ulco** and the most proximal extent of the **ulptcm**. The **ulol** is tapered proximally and has a well-developed **ulscs**, and the **ulcolr** is thin, sharp, and deviated to the medial limit of the trochlear notch;
2) trochlear notch is relatively shallow at the **ulgr**, but it is extensive when considering the radially extended **HuUlr** facet. UTNI is 26;
3) medial and lateral wings of the **ulptc** are substantially unequal with the medial wing predominating;
4) ulna appears to be only very slightly bowed caudally;
5) the radial notch faces laterally and it is closely pressed against the bone. Peduncular support for it is minimum, and the **RaUl** facet does not extend onto the **ulco**;
6) both the medial **ulfofdp** and the lateral **ulfoa** are moderately excavated.
The critical distinguishing marks of this sample are the conformation of the ulnar cranial olecranon ridge (**ulcolr**) and the degree of medial extension of the coronoid process. The former feature is sharp and runs diagonally towards the medial side of the **ulol**. The **ulco** is relatively less extended medially than in IMG Ulna 8. In Figs 42 and 43, IMG Ulna 7 plots unambiguously with the terrestrial forms, but in Fig. 44, where the ratio of ulnar trochlear notch depth over ulnar distal trochlear notch width is plotted against the long ulnar proximal end of these specimens, this group falls below the model-based regression line, with the arboreal models. This latter anomaly is due to the apparent shallowness of the trochlear notch. The standard measurements taken at the same points could not account for the medial twisting of the trochlear notch. Consequently the linear metrics do not reflect the complex adaptive pattern of this group. There is little doubt in our minds that these ulnae belonged to a terrestrial, possibly scansorial, animal.

IMG Ulna 8 (Figs 36C, H; 41A-C; 42-44)
This phenon is represented by two nearly complete ulnae with shafts. The better preserved of the two is DGM 1.150X-M. These specimens are similar in size to the two IMG Ulna 7 representatives, but they are nevertheless consistently distinct in what we consider to be systematically important attributes.
The following represent characteristic properties of this group:
1) the **ulol** is substantially shorter than the opening of the trochlear notch between the **ulco** and

the most proximal extent of the **ulptcm**. The process is tapered proximally, has a robust **ulcolr** deviated to the medial side, and has a well-developed **ulscs**;
2) trochlear notch is relatively shallow, and has considerable cranial and distal extension of the ulco. UTNI is 24.
3) medial and lateral wings of the **ulptc** are substantially unequal, with the medial wing predominating;
4) ulna is caudally bowed;
5) the radial notch faces laterally, and it has minimal peduncular support. The **RaUl** facet does not extend along the distal half of the lateral border of the prominent coronoid process that is deflected medially;
6) both the medial **ulfofdp** and the lateral **ulfoa** are well-excavated;
7) the distal fourth of the shaft is triangular, with the medial surface being slightly hollowed. This may be for the pronator quadratus or part of the interosseous ligaments between the ulna and radius, as noted above for some phena with adequate preservation, such as IMG Ulna 4.
The triangular distal shaft and well-delineated medial surface of that triangle is present in *Caluromys*, but not in *Metachirus*. *Didelphis* shows some expression of this distal medial surface, but not to the extent seen in either *Caluromys* or IMG Ulna 8. Both the morphology and the plots on Figs 42-44 strongly suggest an animal that was at least scansorial, but more likely arboreal.

IMG Ulna 9 (Figs 37; 41D-F; 42-44)
Two specimens make up this phenon. The better preserved and nearly complete specimen is DGM 1.150XIA-M, which only has its distal and proximal epiphyses missing.
The following represent characteristic properties of this group:
1) the **ulol** is substantially shorter than the opening of the trochlear notch between the **ulco** and the most proximal extent of the **ulptcm**. The process is not tapered but is slightly expanded proximally, has a robust **ulcolr** deviated to the medial side of the **ulptcm**, and has a well-developed **ulscs**;

FIG. 37. — **A**, **D**, IMG Ulna 9 (DGM 1.150XIA-M), left ulna; **A**, medial view; **D**, lateral view; **B**, **E**, IMG Ulna 10 (DGM 1715PV), right ulna; **B**, medial view; **E**, lateral view; **C**, **F**, IMG Ulna 11 (DGM 2069M), left ulna; **C**, medial view; **F**, lateral view. Scale bar: 5 mm.

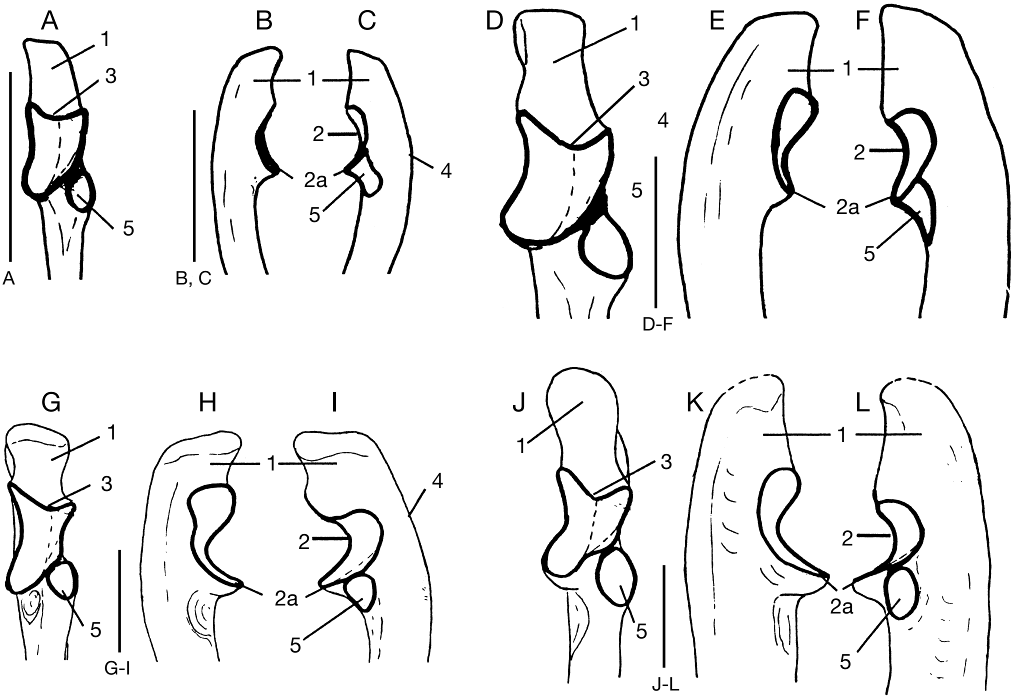


FIG. 38. — **A-C**, left IMG Ulna 1; **A**, anterior view; **B**, medial view; **C**, lateral view; **D-F**, left IMG Ulna 2; **D**, anterior view; **E**, medial view; **F**, lateral view; **G-I**, left IMG Ulna 3; **G**, anterior view; **H**, medial view; **I**, lateral view; **J-L**, left IMG Ulna 4; **J**, anterior view; **K**, medial view; **L**, lateral view. For numbered designations of specific characters see text. Scale bars: 2 mm.

2) trochlear notch is relatively shallow, but with considerable cranial extension of the **ulco**. UTNI is 26;
3) medial and lateral wings of the **ulptc** are unequal, with the medial wing predominating;
4) ulna appears to be slightly bowed caudally;
5) the radial notch faces laterally, and has minimal peduncular support. The **RaUl** facet appears well-separated from the **ulco**, but it is possible that the fully preserved facet extends far along the coronoid process, the latter being considerably deflected medially;
6) while the lateral **ulfoa** is shallow, the medial **ulfofdp** is well-excavated.
The shallow trochlear notch and the consistent plotting of this group well below the model-based regression line on Figs 42-44 suggest arboreality. The slightly expanded olecranon process, on the other hand, may hint that this animal was scansorial.

IMG Ulna 10 (Figs 37; 41G-I; 42-44)
Three specimens represent this second largest ulnar phenon. DGM 1715PV is the most complete and best preserved of the three.
The following represent characteristic properties of these specimens:
1) the **ulol** is probably the same length as the opening of the trochlear notch between the ulco and the most proximal extent of the **ulptcm**. The process is tapered, has a robust ulcolr deviated to the medial side of the **ulptcm**, and has a well-developed laterally offset **ulscs**;

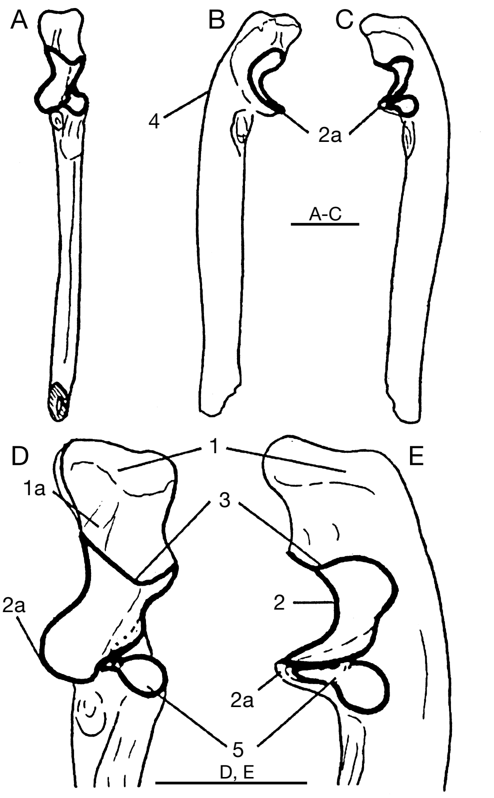


FIG. 39. — Left IMG Ulna 3; **A-C**, nearly complete specimen; **A**, anterior view; **B**, medial view; **C**, lateral view; **D**, **E**, details of the proximal end and trochlear notch; **D**, anterior view; **E**, lateral view. For numbered designations of specific characters see text. Scale bars: 2 mm.

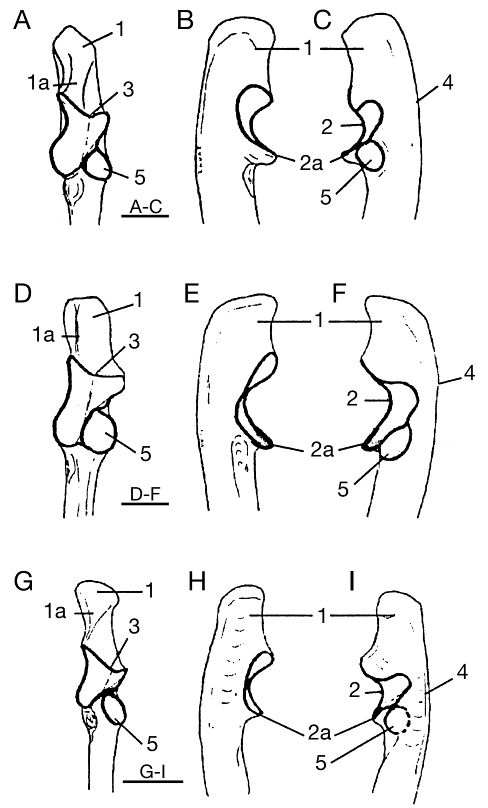


FIG. 40. — **A-C**, left IMG Ulna 5; **A**, anterior view; **B**, medial view; **C**, lateral view; **D-F**, left IMG Ulna 6; **D**, anterior view; **E**, medial view; **F**, lateral view; **G-I**, left IMG Ulna 7; **G**, anterior view; **H**, medial view; **I**, lateral view. For numbered designations of specific characters see text. Scale bars: A-F, 2 mm; G-I, 4 mm.

2) trochlear notch is relatively deep, and has a large cranially projecting ulco. UTNI is 32;
3) medial and lateral wings of the **ulptc** are subequal, despite the fact that from the cranial view of the illustration it looks as if the medial wing was longer; it is not;
4) ulna is bowed;
5) the radial notch faces more craniad than laterally, and it has minimal peduncular support. The **RaUl** facet is well-separated from the **ulco,** but the facet (reconstructed) does extend along the coronoid process that is considerably deflected medially;
6) while the lateral **ulfoa** is shallow, the medial **ulfofdp** is well-excavated.

The plotted values of the three specimens allocated to this group closely cluster well below the model-based regression line, among the arboreal models (Figs 42-44). There is little doubt that IMG Ulna 10 represents an arboreal species.

IMG Ulna 11 (Figs 37; 41J-L; 42-44)

This is the largest of the ulnae, represented by a single poorly preserved specimen.

The following represent characteristic properties of this specimen:
1) as in the preceding phenon, the **ulol** is probably the same length as the opening of the trochlear notch between the **ulco** and the most proximal extent of the **ulptcm**. The process is not tapered (and appears to have been the same width all along its length), has a robust **ulcolr** deviated

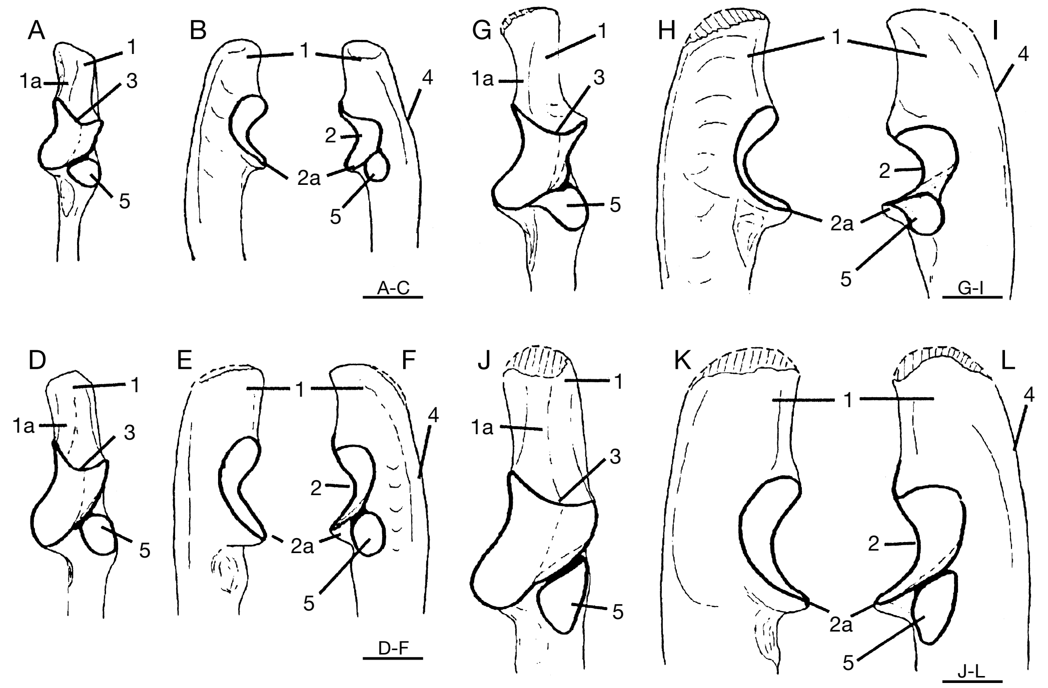


FIG. 41. — **A-C**, left IMG Ulna 8; **A**, anterior view; **B**, medial view; **C**, lateral view; **D-F**, left IMG Ulna 9; **D**, anterior view; **E**, medial view; **F**, lateral view; **G-I**, left IMG Ulna 10; **G**, anterior view; **H**, medial view; **I**, lateral view; **J-L**, left IMG Ulna 11; **J**, anterior view; **K**, medial view; **L**, lateral view. For numbered designations of specific characters see text. Scale bars: 4 mm.

to the medial side of the **ulptcm**, and has a well-developed laterally offset **ulscs**;
2) trochlear notch is less deep than in IMG Ulna 10, and has a large cranially projecting **ulco**. UTNI is 29;
3) medial and lateral wings of the **ulptc** are subequal, although, as stated above, from the cranial view of the illustration it looks as if the medial wing was longer, even though it is not;
4) unlike IMG Ulna 10, this ulna is straight;
5) the radial notch faces laterally, and it has minimal peduncular support. The **RaUl** facet is well-separated from the **ulco**, but the facet (reconstructed) may have extended along the coronoid process that is considerably deflected medially;
6) as in IMG Ulna 10, the lateral **ulfoa** is shallow, and the medial **ulfofdp** is well-excavated.

As stated for IMG Ulna 10, the plotted values of the specimen allocated to this group are well below the model-based regression line, among the arboreal models (Figs 42-44). There is little doubt that IMG Ulna 11 also represents an arboreal species.

RADIUS (TABLE 5)

IMG Radius 1 (Fig 45A-D)

Only a single specimen of a radius is known to us from the entire Itaboraí metatherian fauna. Nevertheless, together with information from the fossil remains of the Tiupampa *Pucadelphys* and *Mayulestes*, some significant information can be gleaned both about forearm function, as well as its possible general heritage significance for the early stocks of sudameridelphians (or possibly even more broadly, in early didelphidans). The very oval head (but not necessarily the **HuRa** articulation itself), of both the Itaboraí and Tiupampa specimens (as well as caenolestids) is distinct from that of known didelphids and *Dromiciops*, which both have a nearly circular radial head.

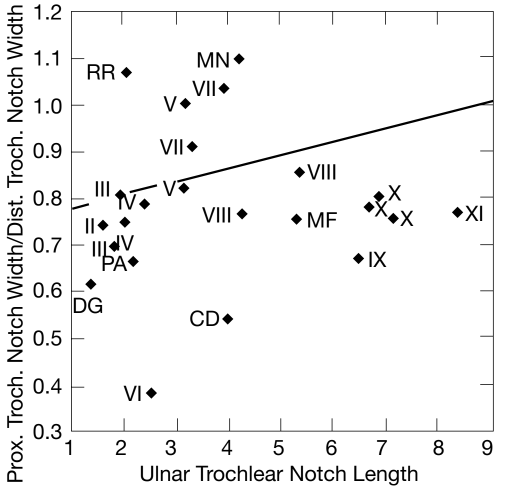


FIG. 42. — Plots of ulnar parameters. Regression line was drawn for living models only, and the fossil values were plotted subsequently in order to gauge some measure of their relationship to the arboreal-terrestrial dichotomy. The extremes of the living range are represented by the modern species. Abbreviations: **CD**, *Caluromys derbianus*; **DG**, *Dromiciops gliroides*; **MF**, *Mayulestes ferox*; **MN**, *Metachirus nudicaudatus*; **RR**, *Rhyncholestes raphanurus*; **PA**, *Pucadelphys andinus*. Roman numerals stand for Itaboraí Metatherian Group designations of ulnae.

The following represent characteristic properties of this radius when compared with a diversity of didelphids and caenolestids:

1) head is exceptionally wide compared to the shaft. It is distinct from a caenolestid like *Rhyncholestes* that has an overlapping lip proximal to a much slimmer shaft. The Itaboraí specimen, unlike caenolestids, has a broad neck distal to the head;

2) distally the radius is not particularly broad, unlike the condition seen in terrestrial forms.

When the possible influence of heritage is considered, in spite of its wide and elliptical head, this radius may well have belonged to an arboreal animal. The only confirmation of such a hypothesis would be the discovery of an arboreal caenolestid with its family-specific radial head. Alternatively, this radius could represent a terrestrial animal (based on the outline of its head), and the differences between it and that of caenolestids may represent heritage features rather than functional ones.

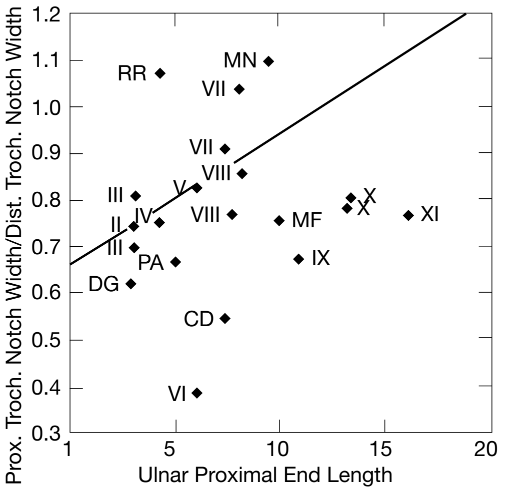


FIG. 43. — Same as Fig. 42, but with a different body weight surrogate on the x-axis.

INNOMINATES (TABLES 5; 6)

IMG Innominate 1 (Figs 46; 47A, B)

There are four specimens that probably belong to this phenon, and the two best ones, DGM 1.145A-M and DGM 1.145B-M, are shown in Fig. 47A and B.

The following represent characteristic properties of this group:

1) the acetabulum is circular rather than oblate, and the cranial and caudal portions of the articulations are quite close to one another ventrally;

2) there is a well-developed and crestate area on the lateral side for the origin of the quadriceps femoris (**ilcrf**), immediately cranial to the acetabulum;

3) the angle between the ilium and pubis appears to be about 90°.

There are few, if any, meaningful attributes that can add to the comparative understanding of the scarce Itaboraí innominates. That they are metatherian is incontestable, based on the clear presence of the articular facets for at least the dorsal limb of the epipubic attachment. This is a reliable identifying feature (in the Itaboraí context) for their metatherian rather than eutherian status, in spite of the fact that epipubes are obviously primitive mammalian (synapsid) attributes.

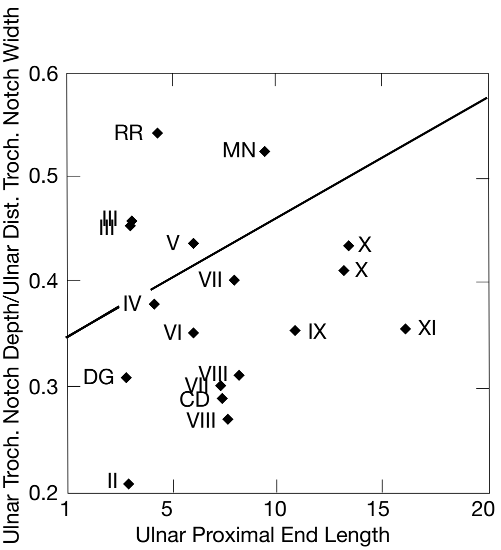


FIG. 44. — Same as Fig. 43 but with a different index on the y-axis.

The usefulness of the shape and morphology of the acetabula of the various specimens have been somewhat equivocal. While in *Metachirus* an almost circular acetabulum with its nearly continuous articular surface is in noticeable contrast to the more oblate condition and ventrally more separated facets of *Caluromys*, the distinction is less clear in such small forms as the obligate terrestrialist caenolestids on the one hand, and the arboreal *Dromiciops* on the other. In fact, the acetabula of caenolestids are oblate rather than circular, and the cranial and caudal wings of the articular surfaces are widely separated ventrally. Interestingly, the differences between the ilia of larger terrestrial forms like *Metachirus* and smaller ones like caenolestids defy any simple categorization of pelvic characters. In *Metachirus* the superior iliac surface is hypertrophied. This is presumably for the enlarged gluteus medius, in contrast to the condition in more arboreal and less terrestrial didelphids. Note that the outward deflection of the iliac blade is related to the hypertrophy of the epaxial musculature, particularly the longissimus dorsi (Argot pers. comm.). The arboreal didelphids retain an essentially triangular cross section of the ilium, the primitive therian condition, without any hypertrophy of that jumping- and bounding-related musculature. Unlike caenolestids, but like the larger *Metachirus*, the innominates of this phenon display a circular pattern of the acetabulum, suggesting a tightly contained femoral head and probably terrestrial locomotion. The latter does not require the extremes of abduction and flexion of the femur in relation to the pelvis that arboreal locomotion does.

IMG Innominate 2 (Figs 46; 47C)

The best specimen of the two in this group is DGM 1.146A-M.

The following represent characteristic properties of this group:

1) the acetabulum is oblate;
2) the ilcrf is not crestate, and presumably relatively less important than in IMG Innominate 1;
3) the angle between the ilium and pubis appears to be about 90°. Judged from the condition of the acetabulum, this form was probably arboreal.

IMG Innominate 3 (Figs 46; 47D)

The best specimen of the two in this group is DGM 1.146B-M.

The following represent characteristic properties of this group:

1) the acetabulum is oblate, with the cranial articular portion predominating, and the cranial and caudal articular segments are rather well-separated ventrally;
2) the **ilcrf** is not crestate;
3) the angle between the ilium and pubis appears to be about 65°. As with the prior group, the acetabulum of this phenon suggests arboreality.

FEMORA (TABLES 5; 10; 11)

The first two groups are poorly represented and equally poorly preserved. Several of the significant areas that probably characterized these phena could not be ascertained. Nevertheless, as for the long bones described above, for the sake of ease of comparisons in the text, we list attributes in a numerical and consecutive manner that correspond throughout the femoral accounts, even if preservation does not allow comment on some of these features.

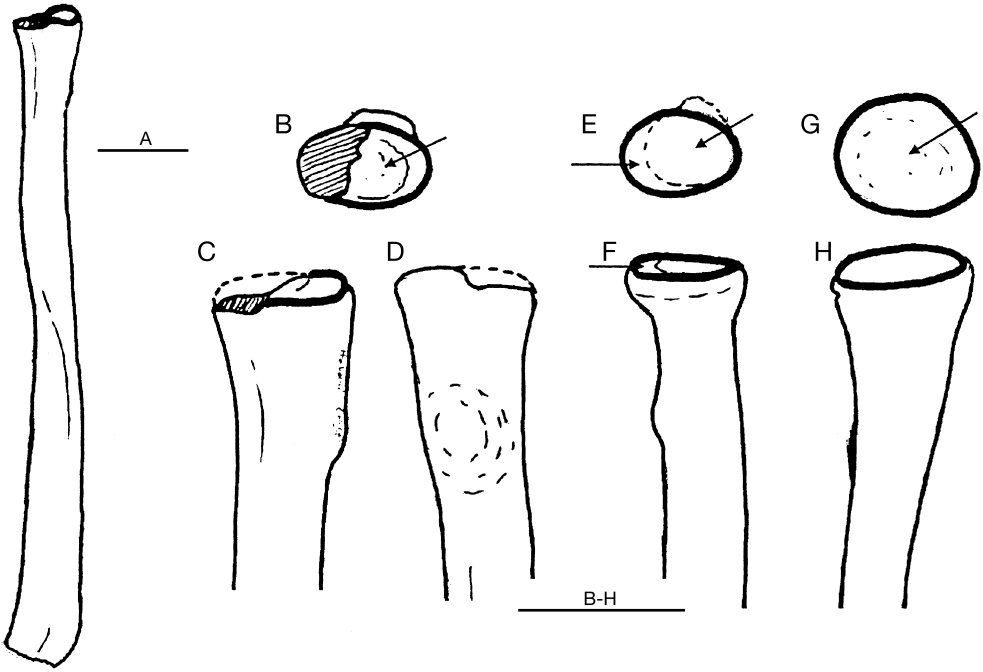


FIG. 45. — Radii of *Rhyncholestes* (**E**, **F**) and *Monodelphis* (**G**, **H**) compared to the IMG specimen (**A-D**); **A**, anterior view of complete radius; **B**, **E**, **G**, proximal views of proximal radius; **C**, **F**, **H**, anterior views of proximal radius; **D**, posterior view of proximal radius. Note the elliptical outline of the head in both the IMG specimen (**B**) and the caenolestid (**E**), compared to the rounded head of the terrestrial didelphid (**G**). Scale bars: 2 mm.

IMG Femur 1 (Fig. 50A, B)

This smallest of the femoral groups is represented by a single specimen, DGM 1.185IB-M, the right proximal half with a poorly preserved head. The following represent a few of the characteristic properties of this specimen:

1) the head is poorly preserved, so no articular characteristics can be ascertained. Beaking or medial projection of the head appears to have been extensive;

2) relative height of the greater trochanter is unavailable as the specimen is abraded in this area;

3) size of the lesser trochanter is relatively very small (as in terrestrial forms), and, significantly, it is retroflexed;

4) femoral paratrochanteric crest (**fptcr**) on the posterior side is not preserved;

5) the third trochanter (**fthtr**; related to gluteus superficialis, a fast extensor of the thigh across the hip joint) is well-developed and relatively close to the proximal end of the shaft; its lever value (expressed as distance from **fgtr** to **fthr**/length of femur) cannot be ascertained because of lack of preservation of the distal half of the femur;

6) no particular shaft characters can be discerned. Femoral Midshaft Diameter Index (anteroposterior midshaft length/mediolateral midshaft length × 100), FMDI, could not be determined due to poor preservation;

7) groove for patella or quadriceps femoris tendon cannot be ascertained due to lack of preservation of the distal half;

8) Femoral Distal Height Index (medial condyle depth/distal end width × 100), FDHI, cannot be ascertained, and Femoral Condyle Width Index (medial condyle width/lateral condyle width × 100), FCWI, is equally unavailable. It is our tentative judgement, as we cannot take adequate measurements of the distal end, that this tiny marsupial was terrestrial.

TABLE 10. — Measurements of femora from Itaboraí (all DGM numbers) and from the model species.

Group	Specimen number	Femur length	Distal extent of lesser trochanter	Femoral head height	Proximal femur width	Femoral head width	Distal extent of trochanteric fossa
IMGF 1	1.185 I B-M		1.99	0.71	1.92	0.94	1.13
IMGF 2	1.185 I A-M						
—	1.185 II-M		3.16				2.01
IMGF 3	1.201 A-M	14.71	2.95	1.09	3.11	1.58	1.79
—	1.201 B-M	14.51	2.76	1.13	3.12	1.69	1.97
—	1.201 C-M	12.45	2.90	1.23	3.22	1.63	1.61
—	1.201 E-M	12.77	2.52	1.10	2.92	1.64	1.43
—	1.201 F-M	12.08	2.54		2.84	1.72	1.43
—	1.201 G-M		2.31	0.82	2.67	1.27	1.66
IMGF 4	1.201 D-M	13.27	2.77	1.09	2.97	1.87	1.63
—	1.202 A-M	16.82	3.73	1.68	3.77	1.94	2.20
—	1.202 B-M	16.55	3.34	1.56	3.55	1.89	1.92
—	1.202 C-M	18.15	3.65	1.39	4.08		2.88
—	1.202 D-M	17.92	4.17	1.19	3.84	1.95	2.65
—	1.202 E-M	16.73	3.29	1.35	3.72	1.88	1.92
—	1.202 F-M	15.66	3.22	1.26	3.50	1.59	1.99
—	1.202 G-M	16.68	3.15	1.35	3.66	1.92	2.23
—	1.202 H-M	16.54	3.21	1.39	3.53	1.71	2.25
—	1.202 I-M	15.54	3.02	1.16	3.37	1.55	1.97
—	1.202 J-M	15.69	3.21		3.35		2.19
IMGF 5	1.203 VA-M						
—	1.203 VB-M						
—	1.203 VC-M						
IMGF 6	1.203 VI-M	19.87	4.51	1.77	4.60	2.54	2.13
—	1.203 VIIIA-M	23.68	5.31	2.28	5.63	2.97	3.20
—	1.203 VIIIB-M	22.81	5.89	2.34	5.25	3.34	4.91
—	1.203 VIIIC-M	24.41	5.39	2.32	5.72	2.80	3.23
—	1.203 VII-M		6.02	2.29	5.94	2.92	3.20
—	1.203 IXA-M	25.83	5.92		6.03		4.03
—	1.203 IXB-M	28.33	6.24		6.03	3.14	5.47
IMGF 7	1.203 XA-M	27.57	6.40		6.24		3.96
—	1.203 XB-M	27.92	8.05		6.93		4.06
—	1.203 XI-M	31.36	8.70	2.89	7.17	3.64	7.41
IMGF 8	1.203 XIII-M	30.38	8.28		7.04		5.07
—	1887 M		8.66		8.05		4.57
IMGF 9	1.203 XIIA-M	37.06	10.44	3.71	8.01	4.18	5.80
—	1.203 XIIB-M		8.00	3.01	6.78	3.91	5.04
IMGF 10	2040 M				8.93	5.20	
—	1886 M		9.91		10.50		5.75
Caluromys derbianus		51.59	12.63	4.75	10.40	5.87	7.53
Metachirus nudicaudatus		56.35	11.93	4.37	11.39	5.17	8.20
Rhyncholestes raphanurus		14.10	3.58	1.49	3.25	1.73	2.16
—		14.91	4.14	1.64	3.48	1.74	2.41
Dromiciops gliroides		15.74	3.41	1.55	3.42		1.90
—		18.78	4.31	1.66	4.18	2.51	2.15

Group	Specimen number	Femoral AP midshaft diameter	Femoral ML midshaft diameter	Femoral distal end width	Femoral head depth	Femoral medial condyle height	Femoral lateral condyle height
IMGF 1	1.185 IB-M				0.85		
IMGF 2	1.185 IA-M	0.85	0.87	1.77			
—	1.185 II-M	1.14	1.31				
IMGF 3	1.201 A-M	1.05	1.20	2.57	1.33		
—	1.201 B-M	1.14	1.23	2.50	1.22		
—	1.201 C-M	1.20	1.33	2.68	1.61		
—	1.201 E-M	1.09	1.13	2.67	0.98		
—	1.201 F-M	1.03	1.21	2.28	1.07		
—	1.201 G-M				1.07		
IMGF 4	1.201 D-M	1.06	1.15	2.57	1.19		
—	1.202 A-M	1.25	1.39	2.98	1.61		
—	1.202 B-M	1.15	1.33	2.90	1.73		
—	1.202 C-M	1.64	1.71	3.43	1.74		
—	1.202 D-M	1.40	1.48	3.01	1.49		
—	1.202 E-M	1.30	1.30	3.19	1.52	1.27	1.36
—	1.202 F-M	1.34	1.31		1.35		
—	1.202 G-M	1.33	1.46		1.51		
—	1.202 H-M	1.34	1.36		1.55		
—	1.202 I-M	1.11	1.32	2.82	1.40		
—	1.202 J-M	1.28	1.39				
IMGF 5	1.203 VA-M	1.77	1.83				
—	1.203 VB-M	1.49	1.59				
—	1.203 VC-M	1.47	2.02	3.71		2.00	2.03
IMGF 6	1.203 VI-M	1.85	2.04	3.96	2.23		
—	1.203 VIIIA-M	1.97	2.02	4.14	2.51		
—	1.203 VIIIB-M	2.04	2.00	4.05	2.77		
—	1.203 VIIIC-M	2.12	1.99	4.16	2.61	1.81	1.75
—	1.203 VII-M				2.76		
—	1.203 IXA-M	2.19	2.30		2.50		
—	1.203 IXB-M	2.13	2.46		2.76		
IMGF 7	1.203 XA-M	2.50	2.25				
—	1.203 XB-M	2.61	2.77		3.52		
—	1.203 XI-M	2.62	2.63	6.44	3.27	2.73	2.75
IMGF 8	1.203 XIII-M	2.88	2.82				
—	1887 M						
IMGF 9	1.203 XIIA-M	2.73	2.86	6.55	4.26	3.02	2.76
—	1.203 XIIB-M				3.13		
IMGF 10	2040 M	3.08	3.34		4.25		
—	1886 M						
Caluromys derbianus		3.30	3.20	9.06	4.80	4.45	4.52
Metachirus nudicaudatus		3.30	4.00	7.96	4.90	4.01	3.78
Rhyncholestes raphanurus		1.10	1.23	2.95	1.63	1.52	1.33
—		1.22	1.32	3.49	1.77	1.76	1.56
Dromiciops gliroides		1.18	1.20	2.97	1.61	1.55	1.40
—		1.46	1.40	3.42	2.01	1.65	1.55

Group	Specimen number	Femoral medial condyle width	Femoral lateral condyle width	Femoral medial condyle depth	Femoral anterior groove width	Femoral lateral condyle depth	Distal extent of third trochanter
IMGF 1	1.185 IB-M						2.57
IMGF 2	1.185 IA-M				0.94	1.14	
—	1.185 II-M						5.30
IMGF 3	1.201 A-M	0.99		2.03	1.05	1.87	4.40
—	1.201 B-M			2.02	0.94	1.74	4.49
—	1.201 C-M			1.98	1.19	1.80	3.31
—	1.201 E-M	1.00	1.26	1.87	1.08	1.80	3.76
—	1.201 F-M			1.65	1.06	1.63	3.89
—	1.201 G-M						
IMGF 4	1.201 D-M			1.91	1.39	1.89	4.18
—	1.202 A-M				1.09		5.31
—	1.202 B-M				1.12		5.41
—	1.202 C-M				2.02		5.92
—	1.202 D-M				1.75		5.65
—	1.202 E-M	1.08	1.30	2.56	1.40	2.45	5.02
—	1.202 F-M						4.65
—	1.202 G-M				1.54		5.06
—	1.202 H-M				1.55		5.22
—	1.202 I-M				1.47		4.16
—	1.202 J-M				1.63		5.05
IMGF 5	1.203 VA-M						4.80
—	1.203 VB-M						
—	1.203 VC-M	1.22	1.29	3.37	1.31	3.33	
IMGF 6	1.203 VI-M			2.66	1.59	2.63	5.91
—	1.203 VIIIA-M						5.90
—	1.203 VIIIB-M				1.88		6.28
—	1.203 VIIIC-M			2.85	2.11	2.76	6.90
—	1.203 VII-M						6.76
—	1.203 IXA-M						7.45
—	1.203 IXB-M						7.46
IMGF 7	1.203 XA-M						7.19
—	1.203 XB-M						7.20
—	1.203 XI-M	1.84	2.87	4.58	2.79	4.42	7.86
IMGF 8	1.203 XIII-M						11.26
—	1887 M						10.15
IMGF 9	1.203 XIIA-M	2.48	3.22	4.94	3.94	4.35	9.77
—	1.203 XIIB-M						
IMGF 10	2040 M						9.03
—	1886 M						9.73
Caluromys derbianus		2.27	4.50	5.55	4.80	5.10	
Metachirus nudicaudatus		2.60	3.60	7.00	4.20	5.95	
Rhyncholestes raphanurus		1.11	1.19	2.28	1.85	2.13	
—		1.26	1.31	2.53	1.68	2.34	
Dromiciops gliroides		0.78	1.53	2.15	1.80	1.97	
—		0.89	1.68	2.43	1.86	2.26	

TABLE 11. — Comparisons of three femoral indices in *Didelphis virginiana* Kerr, 1792, the model species, Itaboraí specimens (all DGM numbers), and taxa from the Paleocene of Tiupampa, Bolivia. For a definition of indices see text.

Group	**Group means**	**Specimen number**	**FDHI**	**FCWI**	**FMDI**
IMGF 2		1.185 IA-M			97.70
—		1.185 II-M			87.02
	IMGF 2 (n = 2)				**92.36**
IMGF 3		1.201 A-M	78.99		87.50
—		1.201 B-M	80.80		92.68
—		1.201 C-M	73.88		90.23
IMGF 3		**1.201 E-M**	70.04	**79.37**	96.46
—		1.201 F-M	72.37		85.12
	IMGF 3 (n = 5)		**75.21**		**90.40**
IMGF 4		1.201 D-M	74.32		92.17
—		1.202 A-M			89.93
—		1.202 B-M			86.47
—		1.202 C-M			95.91
—		1.202 D-M			94.59
IMGF 4		**1.202 E-M**	80.25	**83.08**	100.00
—		1.202 F-M			102.29
—		1.202 G-M			91.10
—		1.202 H-M			98.53
—		1.202 I-M			84.09
—		1.202 J-M			92.09
	IMGF 4 (n = 2)		**77.28**		
	IMGF 4 (n = 11)				93.38
IMGF 5		1.203 VA-M			96.72
—		1.203 VB-M			93.71
IMGF 5		**1.203 VC-M**	**90.84**	**94.57**	72.77
	IMGF 5 (n = 3)				87.73
IMGF 6		1.203 VI-M	67.17		90.69
—		1.203 VIIIA-M			97.52
—		1.203 VIIIB-M			102.00
—		1.203 VIIIC-M	68.51		106.53
—		1.203 IXA-M			95.22
—		1.203 IXB-M			86.59
	IMGF 6 (n = 2)		**67.84**		
	IMGF 6 (n = 6)				**96.42**
IMGF 7		1.203 XA-M			111.11
—		1.203 XB-M			94.22
IMGF 7		**1.203 XI-M**	**71.12**	**64.11**	99.62
	IMGF 7 (n = 3)				**101.65**
IMGF 8		**1.203 XIII-M**			**102.13**
IMGF 9		**1.203 XIIA-M**	**75.42**	**77.02**	**95.45**
IMGF 10		**2040 M**			**92.22**
Caluromys derbianus			**61.26**	**50.44**	**103.13**
Metachirus nudicaudatus			**87.94**	**72.22**	**82.50**
Didelphis virginiana	**n = 4**		**72.26**	**58.76**	**82.81**
Rhyncholestes raphanurus	**n = 2**		**74.69**	**94.80**	**90.98**
Dromiciops gliroides	**n = 2**		**71.67**	**52.02**	**101.54**
Mayulestes ferox				**88.65**	**75.41**
Pucadelphys andinus			**82.56**	**90.26**	**109.05**

IMG Femur 2 (Figs 50C-F)

There are two specimens of somewhat unequal size yet the pattern of preserved morphology suggests that they might be conspecific. They represent different growth stages, or, less likely, dimorphism. It is, of course, entirely feasible that these two specimens represent two distinct species. If the preservation of the specimens was better, then some of these doubts could be removed. DGM 1.185IA-M is a nearly complete right specimen with its head and the details of its distal end missing. DGM 1.185II-M is a partial left specimen with its head and distal end missing. The following represent characteristic properties of this group:

1) the head is not preserved, so related characteristics cannot be ascertained;
2) relative height of the greater trochanter is unavailable;
3) size of the lesser trochanter is relatively small, but it is not retroflexed;
4) femoral paratrochanteric crest (**fptcr**) on the posterior side is not preserved;
5) the third trochanter is about one third the distance down the shaft from the proximal end on DGM1.185IA-M, but appears to be relatively more distal in the larger of the two specimens assigned to this phenon. Its lever value cannot be ascertained because of lack of preservation of the entire length of the femur;
6) no particular shaft characters can be discerned. FMDI is 98 for the smaller specimen, and 87 for the larger specimen;
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is well-emphasized;
8) accurate measurements to calculate the FDHI could not be made. The FCWI cannot be ascertained accurately due to abrasion. Yet, in spite of the poorly preserved end of the smaller femur, it appears that it had a low and relatively wide distal end. The proportions of the condyles cannot be estimated. This was probably an arboreal group.

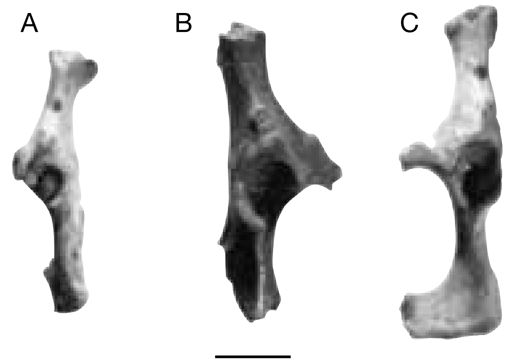


FIG. 46. — **A**, lateral view of IMG Innominate 1 (DGM 1.145A-M), specimen from the left side; **B**, lateral view of IMG Innominate 3 (DGM 1.146B-M), specimen from the right side; **C**, lateral view of IMG Innominate 2 (DGM 1.146A-M), specimen from the left side. Scale bar: 4 mm.

IMG Femur 3 (Figs 48; 51A-C; 61-64)

Of the six specimens assigned to this phenon, a nearly completely preserved left femur, DGM 1.201B-M, has poorly preserved head morphology and a broken distal end. We do not have full confidence in the separation of IMG Femora 3 and 4, although we decided to treat them as two phena because of some of their differences. These two groups probably belonged to well-represented species in the Itaboraí collections, judged from a total of 17 relatively well-preserved femora. The following represent characteristic properties of this group:

1) the head shows an articular facet that extends laterally onto the neck. Beaking or medial projection of the head appears to have been extensive;
2) relative height of the greater trochanter is difficult to judge as the specimens are abraded in this area;
3) size and medial projection of the lesser trochanter is pronounced;
4) the **fptcr** is prominent in all specimens except where visibly abraded;
5) the **fthtr** is very close to the proximal end of the shaft;
6) no particular shaft characters can be discerned. FMDI is 90 (n = 5);
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is well-emphasized;
8) FDHI is 75 (n = 5). FCWI is 79.4 for one specimen.

For a discussion, see IMG Femur 4.

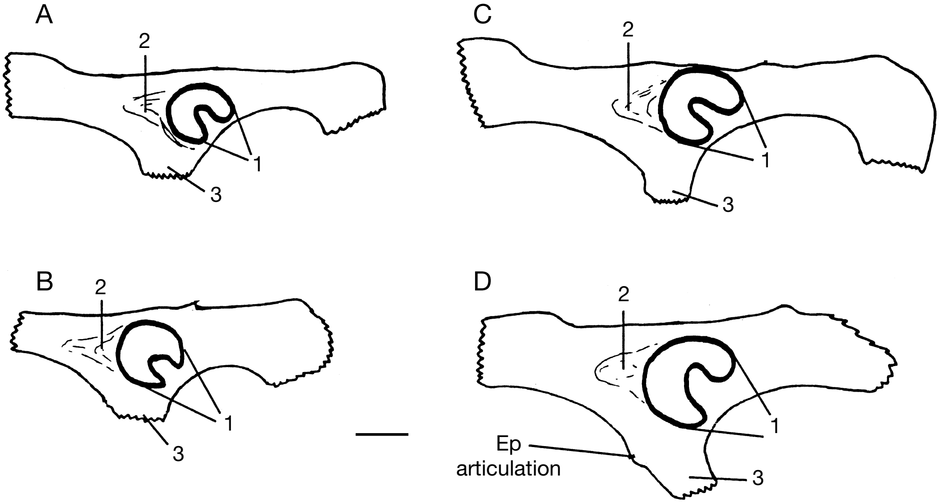


FIG. 47. — **A**, **B**, lateral view of IMG Innominates 1; **A**, DGM 1.145A-M; **B**, DGM 1.145B-M; **C**, lateral view of IMG Innominate 2 (DGM 1.145A-M), reversed; **D**, lateral view of IMG Innominate 3 (DGM 1.146B-M). For numbered designations of specific characters see text. Abbreviation: **Ep**, epipubic. Scale bar: 2 mm.

IMG Femur 4 (Figs 48; 51D-F; 52; 61-64)
There are 11 nearly complete specimens. One of these has a well-preserved right proximal end (DGM 1.202A-M), whereas DGM 1.202E-M is a left specimen with the femoral condyles completely preserved. As we noted above, this phenon may represent the same species as IMG Femur 3. The following represent characteristic properties of this group:

1) the articular characteristics of the head cannot be ascertained. Beaking or medial projection of the head appears to have been extensive;
2) relative height of greater trochanter is unavailable as the specimens are abraded in this area;
3) size and orientation of the lesser trochanter is relatively very small (as in the terrestrial models), and, significantly, it is retroflexed;
4) femoral paratrochanteric crest (**fptcr**) on the posterior side is not preserved;
5) the third trochanter is relatively close to the proximal end of the shaft;
6) no particular shaft characters can be discerned. The FMDI is 93 (n = 11);
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is well-emphasized;
8) the FDHI for one specimen is 80, and the FCWI is 83.

The distal height of the femur, together with the near subequality of the two condyles, are very strong indicators that IMG Femur 4 represents an animal that was more terrestrial than arboreal. In many ways, the femur has proven to be the most reliable indicator of substrate preference when analyzing our model species. This reliability probably carries over to the fossils as well. The four plots, Figs 61-64, have various parameters on their x-axes. These are femur length, femoral midshaft anteroposterior width, femoral midshaft mediolateral width, and distal femur width, respectively. All of these measures represent surrogates for body weight. While none of these is really adequate (and some are probably better than others), they are the best we could find for use with fossils of isolated (and often fragmentary) limb elements. On the y-axis, we plotted medial condyle width/lateral condyle width against all four body weight surrogates. Without exception, IMG Femur 3 and 4 specimens plotted relatively close to one another above the model-based regression line with the terrestrial species. We have little doubt that these two femoral phena represent terrestrial animals.

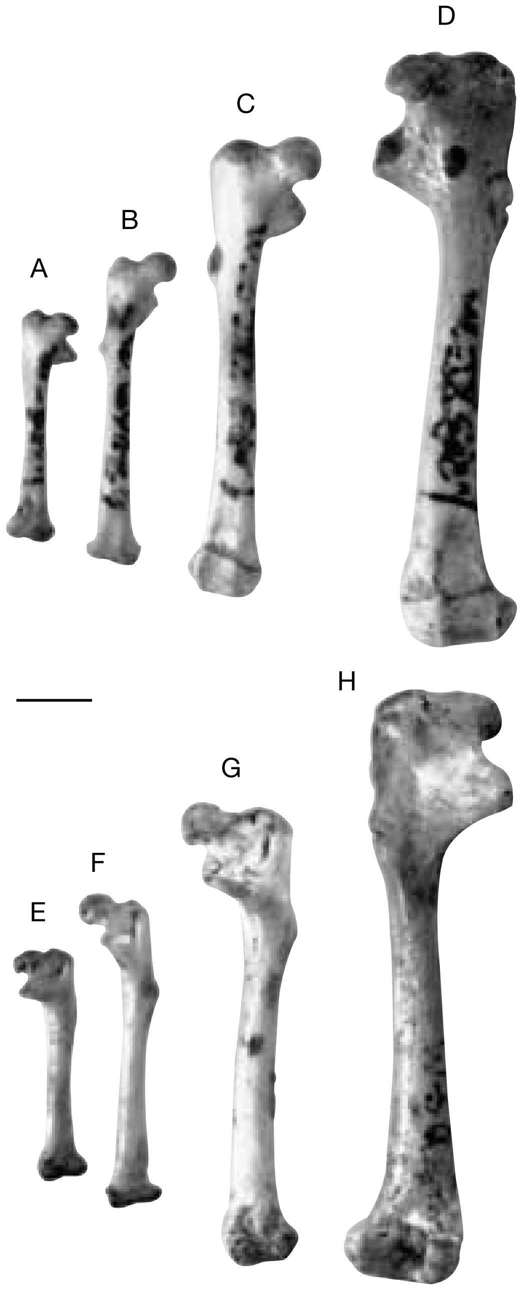


FIG. 48. — **A**, **E**, IMG Femur 3 (DGM 1.201A-M), right specimen; **A**, anterior view; **E**, posterior view; **B**, **F**, IMG Femur 4 (DGM 1.202A-M), right specimen; **B**, anterior view; **F**, posterior view; **C**, **G**, IMG Femur 6 (DGM 1.203VIIIC-M), right specimen; **C**, anterior view; **G**, posterior view 6; **D**, **H**, IMG Femur 7 (DGM 1.203XI-M), left specimen; **D**, anterior view; **H**, posterior view. Scale bar: 4 mm.

IMG Femur 5 (Figs 53-55; 62-64)

There are three specimens in this group, one a nearly complete left femur with the distal epiphysis missing (DGM 1.203VA-M), another is a left specimen with its proximal half missing but its distal half perfectly preserved (DGM 1.203VC-M), and the third is a nearly complete right specimen missing the epiphyses of the two extremities (DGM 1.203VB-M), although it is unquestionably part of this phenon.

The following represent characteristic properties of this group:

1) the head is not well enough preserved, so critical articular characteristics cannot be ascertained. Although the articular surface is gone, the general morphology suggests a much more cylindrical than rounded head surface. Beaking or medial projection of the head is well-developed;

2) relative height of the greater trochanter is unavailable as the specimen is abraded in this area;

3) size of the lesser trochanter is relatively small, and it is well medial to the projecting head and slightly retroflexed;

4) femoral paratrochanteric crest (**fptcr**) on the posterior side is lacking, although a very slightly raised surface can be discerned on one of the specimens;

5) the pronounced **fthtr** peaks at the point level with the lower limit of the lesser trochanter, suggesting very fast extension of the thigh;

6) the shaft is exceptionally long and straight. On the distal shaft the lateral side is raised into a rugose and prominent crest, probably for a hypertrophied lateral head of the gastrocnemius. FMDI is 88 (n = 3);

7) sulcus for the tendon of the quadriceps femoris is long, and there is no indication for the presence of a patella;

8) the FDHI on one specimen is 90.84, and the FCWI on the same specimen is 95.

We suspect that whenever a broad sulcus is discernable above the epiphysis on the distal femur in fossil metatherians it is indicative of the lack of a patella. However, the absence of this feature is no indication for the presence of a patella, as extant metatherians make clear. While there is no

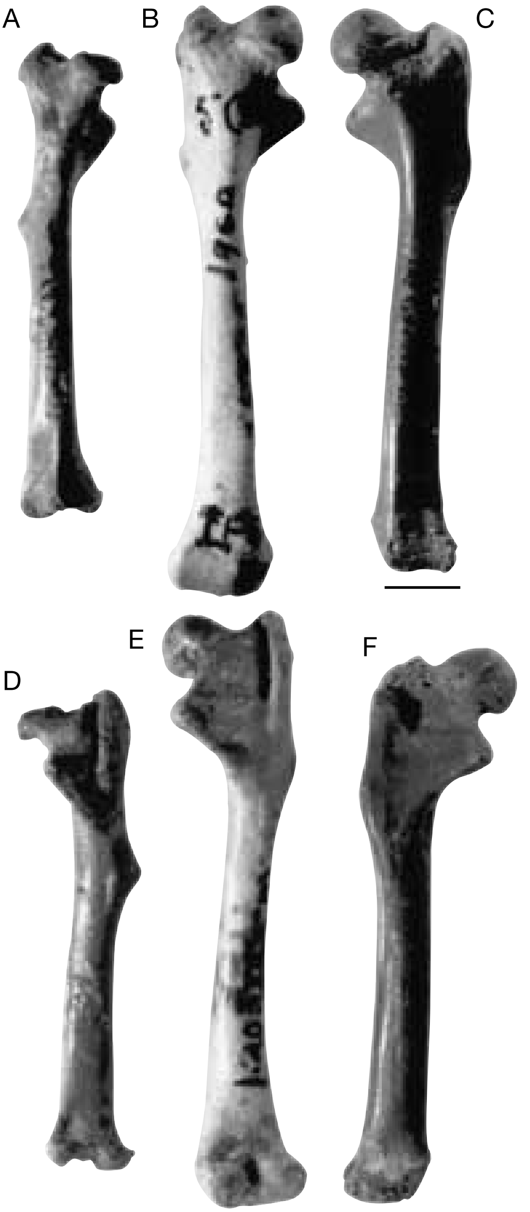


FIG. 49. — **A**, **D**, IMG Femur 8 (DGM 1.203XIII-M), specimen from the right side; **A**, anterior view; **D**, posterior view; **B**, **E**, IMG Femur 9 (DGM 1.203XIIA-M), specimen from the right side; **B**, anterior view; **E**, posterior view; **C**, **F**, IMG Femur 10 (DGM 2040M), specimen from the left side; **C**, anterior view; **F**, posterior view. Scale bar: 5 mm.

trace of this sulcus on the patellate *Rhyncholestes*, it is also absent *Dromiciops* which lacks a patella. The presence and absence of this sulcus varies in different species of *Monodelphis*, a primarily terrestrial genus. IMG Femur 5 has a long groove for the quadriceps femoris tendon, and therefore almost certainly lacked a well-developed patella. It should be noted, however, that in occasional specimens of *Didelphis virginiana* (probably old individuals of a species with a short life span) an elongated, slender, and curved ossification inside of the tendon can be seen.

In general, the attributes of this femur fall among those parameters that characterize the terrestrial models, regardless of size. This is clearly reflected in Figs 62-64. This group is missing from the plot in Fig. 61 because our most complete specimen (Figs 53C; 54A) lacks the distal epiphysis. Nevertheless, it is obvious that if we were to plot it, even with its incomplete length, it would fall near or above *Rhyncholestes*. The features of the distal end of this bone alone would not suggest anything other than that of a leaper (usually indicator of a strong terrestrial adaptations). Nevertheless, these features together with this bone's straightness and unusual length may be the hallmarks of an arboreal leaper. In spite of the plots of IMG Femur 5, as we indicated above (and in preparation), we have some reasons to suspect that this animal was probably not terrestrial. The composite of IMG Group II, to which we believe this femoral group belongs along with IMG Humerus 2, IMG Ulna 3, IMG Tibia 1, as well as IMG tarsal samples 3 and 4 (and the cuboid allocated with these) described in Szalay (1994), suggests a unique adaptive locomotor complex among the Itaboraí metatherians. This morphological complex appears to belong to a small, unique arboreal marsupial glider.

IMG Femur 6 (Figs 48; 56)

There are seven specimens in this phenon and all but one of them have complete shafts, but with differential preservation of the proximal and distal epiphyses. The best of the lot is DGM 1.203VIIIC-M, towards the large end of the size range of the femora, and is a right specimen, with the distal end somewhat preserved. The smaller one illustrated is a right femur, DGM 1.203VI-M.

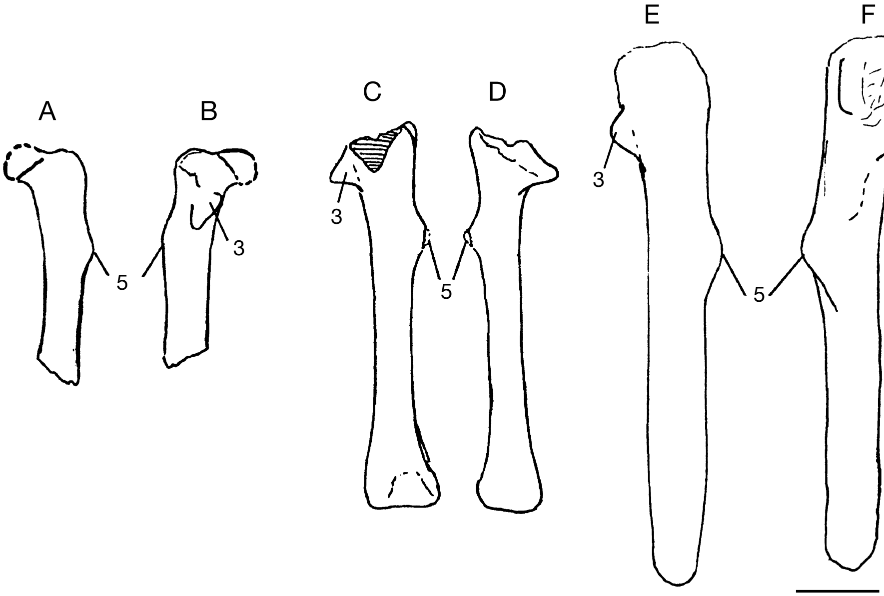


Fig. 50. — **A**, **B**, left incomplete IMG Femur 1; **A**, anterior view; **B**, posterior view; **C-F**, left incomplete IMG Femur 2; **C**, **E**, anterior view; **D**, **F**, posterior view. For numbered designations of specific characters see text. Scale bar: 2 mm.

The latter has the extremities poorly preserved. Another one figured, a left specimen, is DGM 1.203IXB-M. It is possible that this last specimen represents a species different from the rest of the femora in this not excessively variable phenon, although in our judgement it does not.

The following represent characteristic properties of this group:

1) the rounded head (when viewed anteriorly) shows a laterally and distally expanded articulation. Beaking or medial projection of the head is moderate;
2) relative height of the greater trochanter was probably not higher than the head, although abrasion in this area on all of the specimens is a problem;
3) size and orientation of the lesser trochanter is relatively very large, and it is not retroflexed;
4) the **fptcr** on the posterior side is well-developed;
5) the **fthtr** is relatively close to the proximal end of the shaft at the level where the lesser trochanter ends;
6) no particular shaft characters can be discerned. The mean of FMDI is 96 (n = 6);
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is well-emphasized;
8) the FDHI is 68 (n = 2). The FCWI could not be accurately determined.

The combination of attributes of this femur indicates a primarily arboreal animal. The FDHI value of 68 suggests that this animal, with its low knee index, was a slow climbing form.

IMG Femur 7 (Figs 48; 57; 61-64)

There are three specimens assigned to this phenon. Two of these, a right (DGM 1.203XA-M) and a left (DGM 1.203XB-M) femur, are nearly complete, both lacking only the femoral condyles. The right specimen served as the basis of the illustration, with some information reinforced from the other. A single left, complete femur (DGM 1.203XI-M), with the usual abrasion of the greater trochanter seen in most Itaboraí femora, is the largest and best preserved of the three specimens.

The following represent characteristic properties of this group:

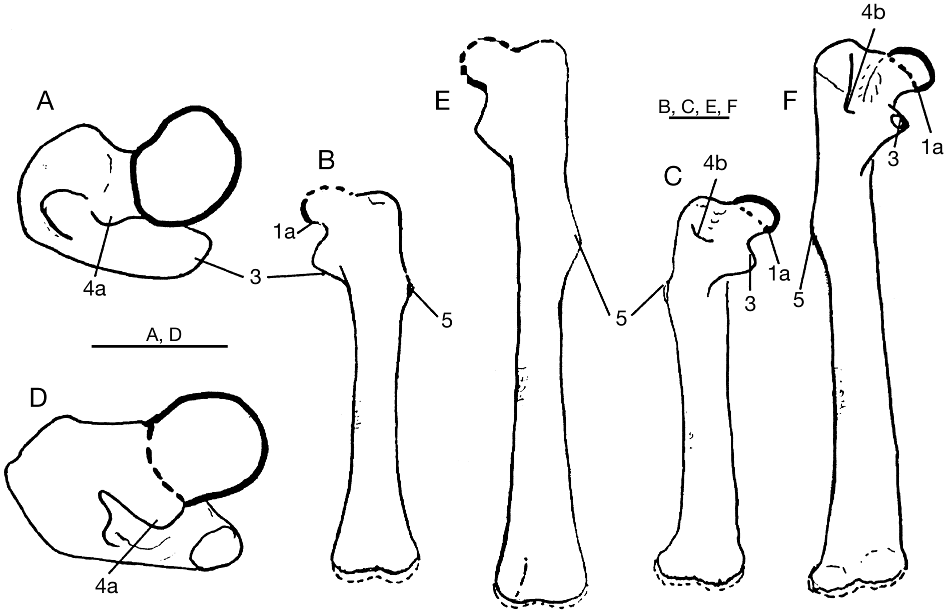


FIG. 51. — **A-C**, left nearly complete IMG Femur 3; **A**, proximal view; **B**, anteroir view; **C**, posterior view; **D-F**, left nearly complete IMG Femur 4; **D**, proximal view; **E**, anteroir view; **F**, posterior view. For numbered designations of specific characters see text. Scale bars: 2 mm.

1) the head is not adequately preserved, although there is little doubt that the articulation extended well onto the neck laterally and posteriorly. Beaking or medial projection of the head is minimal;
2) relative height of the greater trochanter was probably below the head, although abrasion in all three specimens makes this assessment uncertain;
3) the lesser trochanter is relatively enormous, and is not retroflexed;
4) the **fptcr** is low;
5) the **fthtr** is distinct, small, and it is relatively close to the proximal end of the shaft. It is within the linear limits of the distal extent of the lesser trochanter;
6) no particular shaft characters can be discerned. The FMDI is 102 (n = 3);
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is well-emphasized;
8) the FDHI is 71 (n = 1), and the FCWI of the same specimen is 64.

Judged from the huge lesser trochanter, head characteristics, and the distal end, this animal was probably highly arboreal. The plots on Figs 61-64 support an arboreal, if not "highly arboreal", assessment.

IMG Femur 8 (Figs 49; 58; 60A-D)

There are two right specimens in this group. One has a complete shaft and a reasonably well-preserved proximal extremity, as well as a critical, although poorly preserved, distal end (DGM 1.203XIII-M). The other specimen is a proximal half (DGM 1887M).

The following represent characteristic properties of this group:
1) the head is poorly preserved; its articular surface is abraded, although it appears that, as in the other Itaboraí metatherians, it was somewhat oblate. Beaking or medial projection of the head is extreme;
2) relative height of the greater trochanter was probably at a level higher than the head, but there is abrasion in that area;
3) the lesser trochanter is not particularly small, but it is almost completely retroflexed;

4) the **fptcr** is robustly developed, immediately in front of the fossa itself;
5) the **fthtr** is both small and well-removed towards the middle of the shaft: it is more than a third of the way down the shaft. The lever value of the **fthtr** is obviously greater than that of any of the other metatherians described here;
6) no particular shaft characters can be discerned. The FMDI is 102, inexplicably very close to the values of the arboreal models;
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is long and well-emphasized, in a manner characteristic of most metatherians;
8) the FDHI and the FCWI cannot be estimated as the distal end is considerably abraded. Nevertheless, the distal femur was relatively high.

DGM 1.203XIII-M is a specimen that is critical in a number of ways. Its badly abraded distal end, in spite of its poor preservation, suggests that this phenon, despite its convergence with several eutherian small condylarths at Itaboraí, may be a metatherian. Its distal end appears to be flared in a manner typical of metatherians; it is as craniocaudally long as it is in terrestrially adapted didelphids and didelphidan sudameridelphians. In spite of the single index that may suggest an arboreal animal, this femur is extremely unlike any arboreal marsupial. The relatively small and retroflexed lesser trochanter, the distally displaced third trochanter, and the relatively great height of the distal end all suggest a terrestrial habitus. We have strongly contemplated the possibility that these specimens represent one of the small Itaboraí condylarths that may have been mixed in with our sample. *The allocation of this sample of two specimens to the Metatheria should, therefore, be considered with caution as these specimens may well be eutherian.* There is a distinct possibility that these femora, if they represent a small condylarth, a group with unmistakable terrestrial heritage attributes, show modifications for arboreality.

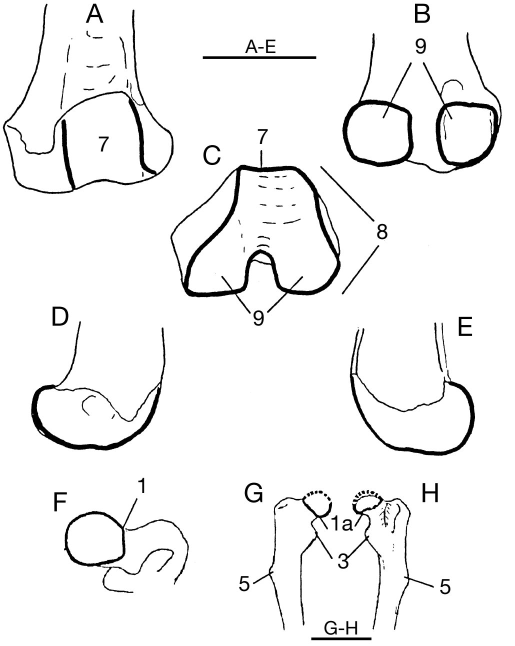


Fig. 52. — Details of specimens of IMG Femur 4; **A-F**, left specimen; **A-E**, distal end; **A**, anterior view; **B**, posterior view; **C**, distal view; **D**, lateral view; **E**, medial view; **F**, proximal end, proximal view; **G**, **H**, right specimen, proximal half, **G**, anterior view; **H**, posterior view. For numbered designations of specific characters see text. Scale bars: 2 mm; 4 mm.

IMG Femur 9 (Figs 49; 59; 61-64)

There are two specimens in this group. One is a complete right femur (DGM 1.203XIIA-M), and the other is an equally well-preserved but fragmentary, unabraded, right proximal end (DGM 1.203XIIB-M).

The following represent characteristic properties of this group:
1) head is large, and its articular surface extended well onto the neck laterally and posteriorly. Beaking or medial projection of the head is minimal;
2) relative height of the greater trochanter was almost exactly at the level of the head; there is no appreciable abrasion in that area;
3) as in IMG Femur 7, the lesser trochanter is enormous, and is not retroflexed;
4) the **fptcr** is low;
5) the **fthtr** is both small and relatively close to the proximal end of the shaft; it is at the same level as the distal limit of the lesser trochanter;
6) no particular shaft characters can be discerned. The FMDI of the well-preserved specimen is 95, an ambiguous value when compared to the models;

FIG. 53. — Itaboraí Metatherian Group II, selected specimens; **A**, **F**, IMG Ulna 3 (DGM 1.150IIIA-M); **A**, anterior view; **F**, posterior view; **B**, **G**, IMG Humerus 2 (DGM 1.193B-M); **B**, anterior view; **G**, posterior view; **C**, **H**, IMG Femur 5 (DGM 1.203VA-M); **C**, anterior view; **H**, posterior view; **D**, **I**, IMG Femur 5, distal half (DGM 1.203VC-M); **D**, anterior view; **I**, posterior view; **E**, **J**, IMG Tibia 1 (DGM 1.188C-M); **E**, anterior view; **J**, posterior view. Distal femur and proximal tibia are shown in near articular contact as on Fig. 54. Scale bar: 3 mm.

7) sulcus above the epiphysis for the tendon of the quadriceps femoris is not well-emphasized;
8) the FDHI is 75, and the FCWI is 77.

In spite of the fact that the plotted values of this group fall very close to *Metachirus*, lying above the model-based regression line, the morphology of this specimen suggests arboreality or scansoriality. The knee indices suggest the terrestrial component in the habitus.

IMG Femur 10 (Figs 49; 60E-H)

A left femur (DGM 2040M), missing the distal epiphysis and the greater trochanter, is the smaller of the two specimens representing this phenon. The larger, left proximal femur (DGM 1886M) is missing its distal third, has a heavily abraded head, and has considerably larger greater trochanter. In our view, it is of the same species as the smaller specimen.

The following represent characteristic properties of this group:
1) the head shows the lateral and distal extension of the articular surface. Beaking or medial projection of the head is minimal;
2) relative height of the greater trochanter is unavailable as both specimens are abraded in this area;
3) size of the lesser trochanter is relatively very large and it is not retroflexed;

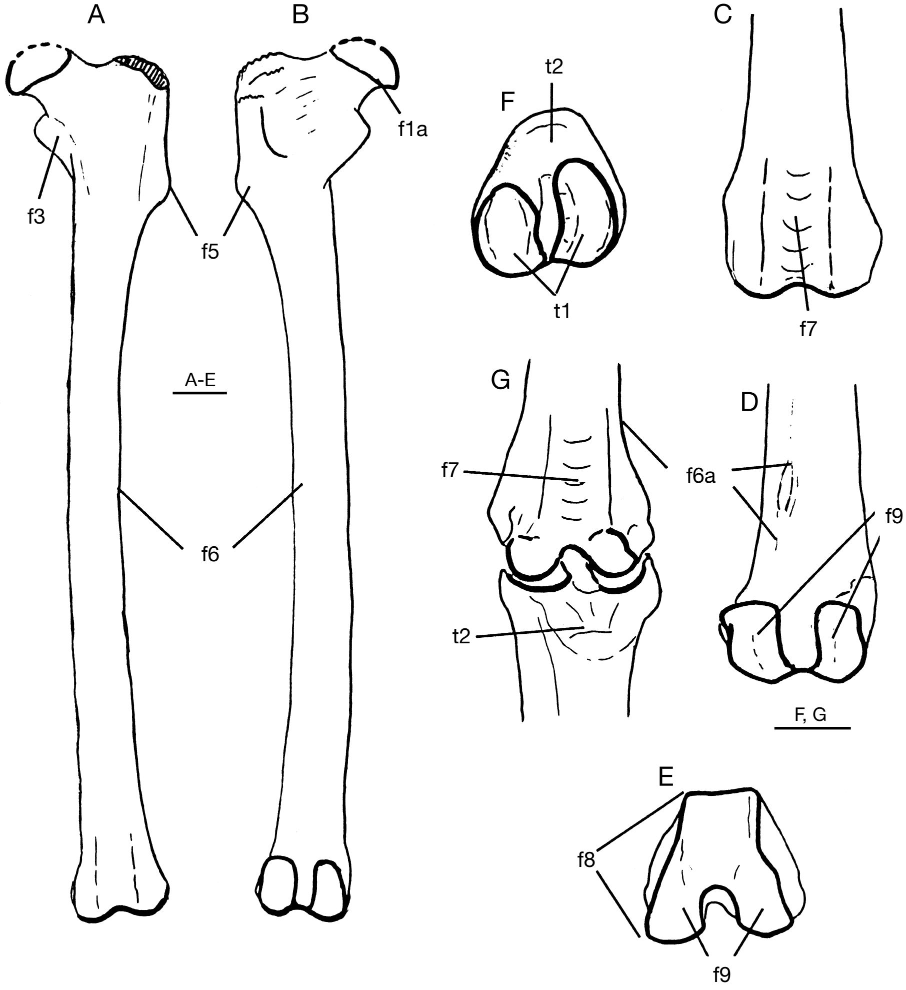


Fig. 54. — Left IMG Femur 5 and Tibia 1; **A**, **B**, reconstructed complete femur; **A**, anterior view; **B**, posterior view; **C-E**, distal femoral details; **C**, anterior view; **D**, posterior view; **E**, distal view; **F**, tibia, proximal view; **G**, distal femur and proximal tibia in articulation. For numbered designations of specific characters see text. Prefixes before the number: **f**, femoral; **t**, tibial. Scale bars: 2 mm.

4) the **fptcr** is low and barely visible;
5) the **fthtr** is both small and relatively close to the proximal end of the shaft;
6) no particular shaft characters can be discerned. The FMDI is 92;
7) sulcus above the epiphysis for the tendon of the quadriceps femoris is well-emphasized;
8) the FDHI and the FCWI cannot be determined as the distal end of the more complete fossil is missing.

This femur has all the hallmarks of an arboreal animal, judged by its large lesser trochanter that shows no retroflexion, as well as its third trochanter that is close to the head. Yet, compared to IMG Femur 9 that has a relatively larger lesser trochanter and a similar FMDI index, its adaptive affinities are as elusive as that of the previously discussed phenon.

TIBIAE (TABLES 5; 12)

IMG Tibia 1 (Figs 53; 54F, G)

There are three specimens in this group. The one left proximal tibia (DGM 1.188C-M), with its condyles perfectly preserved, articulates with one of the specimens of IMG Femur 5.

TABLE 12. — Measurements of tibiae from Itaboraí (all DGM numbers) and from the model species.

Group	Specimen number	Tibia length	Tibial proximal end width	Tibial distal end width	Tibial AP midshaft diameter	Tibial ML midshaft diameter	Medial malleolus length	Tibial proximal end depth
IMGT 1	1.188A-M		3.36	2.23	1.65	1.52		
—	1.188B-M		3.38		1.62	1.66		
—	1.188C-M		3.56					3.78
IMGT 2	1.189M		5.52					5.33
—	1952M		5.41		2.80	2.08		
IMGT 3	1731PV	40.24	8.98	4.51	4.18	2.56	1.42	6.77
—	1.200M			4.85			1.71	

Group	Specimen number	Tibial lateral condyle length	Tibial lateral condyle width	Tibial medial condyle length	Tibial medial condyle width	Tibial distal end depth	Tibial distal articular surface width	Medial malleolus width
IMGT 1	1.188A-M							
—	1.188B-M							
—	1.188C-M	2.07	1.38	2.18	1.16			
IMGT 2	1.189M	2.83	2.24	3.26	1.73			
—	1952M							
IMGT 3	1731PV	4.26	3.77	4.10	3.10	4.31	2.76	2.13
—	1.200M					4.00	2.47	2.09

The following characterize this group:
1) the proximal surface of the tibia, namely the proportions of the medial and lateral condyles, shows only a slightly wider lateral articular surface compared to the medial one. The TPAI (Tibial Proximal Articular Index, the ratio of the medial condyle width/lateral condyle width × 100) is 84, showing a close similarity between the two condylar widths;
2) the extent of the quadriceps femoris insertion is well anterior to the limits of the femorotibial contacts. The proportions are more similar to those of *Metachirus* than *Caluromys*. The TPDI (Tibial Proximal Depth Index, the ratio of proximal tibial width/proximal tibial depth × 100) is 94, a low value, indicative more of mobility in flexion-extension than stability;
3) no data can be retrieved from the distal ends of these tibiae;
4) of the other two specimens, both undoubtedly part of this phenon, the longer right specimen (DGM 1.188B-M) shows beyond any doubt that the tibial shaft was unusually long and slender, without any suggestion of the tibial sigmoid curvature seen in didelphids;
5) distal articular areas of these tibiae are unknown.
Both the articular fit between this proximal tibia and IMG Femur 5, and their joint inclusion in IMG II, have been discussed above. The locomotor assessment, with all its caveats that a single are of the skeleton requires, is essentially the same as that we have considered above for the distal end of IMG Femur 5.

IMG Tibia 2 (Figs 65; 66A)
Two left specimens make up this groups. One has a well-preserved proximal articular surface

(DGM 1.189-M), whereas the other has the entire length of the shaft with a poorly preserved proximal surface, and it is missing the distal epiphysis (DGM 1952M).

The following represent characteristic properties of this group:

1) the suggestion from the proximal surface is that the lateral, **FeTil**, facet was not particularly wide, although the medial facet was not only relatively narrow, but also anteroposteriorly long. The proportions of these facets, while not as derived as those of the previous tibial group, are unusual. The TPAI index is 77, showing somewhat disparate values between the widths of the condyles;

2) the quadriceps femoris insertion is not extreme, unlike in IMG Tibia 1. The TPDI is 104, which is a relatively large value indicating a wide proximal end (but narrower than that of IMG Tibia 3);

3) there is no information about the distal end;

4) no sigmoid curve is noticeable;

5) the distal articular area is unknown.

As Fig. 65 shows, the proximal proportions and conformation of this group are not similar to those of IMG Tibia 3. The lack of sigmoid curve certainly suggests a terrestrial habitus (but see caveats discussed above regarding the heritage and habitus factors in tibial curvature).

IMG Tibia 3 (Figs 65; 66B-E, K, L)

This group is represented by two specimens, a perfectly preserved right tibia (DGM 1731PV) and a distal tibia (DGM 1.200-M). The size of the former is very similar to that of the Tiupampa *Pucadelphys* (see Muizon 1998: fig. 37).

The following represent characteristic properties of this group:

1) the TPAI of the complete specimen is 82, suggesting near subequality and terrestriality;

2) the TPDI is 132, indicating a wide proximal tibia suggestive of stability more than anything else;

3) the TMMI (Tibial Medial Malleolar Index, the ratio of the depth of the medial malleolus medially/anteroposterior depth of the distal tibia × 100) is 31.5 for the more complete specimen and 35.2 for the other. In contrast, the value for *Caluromys* is 11.7, whereas for *Metachirus* it is 28.8. These data, together with the extremely *Pucadelphys*-like morphology of these tibiae (compare with Fig. 66F), leave little doubt that this animal, like *Pucadelphys*, was quite terrestrial. These values also raise some interesting issues regarding Itaboraí, as well as Tiupampa, marsupials, and the adaptations of their last common sudameridelphian ancestor that entered South America;

4) this tibia shows no appreciable lateral convexity of the shaft;

5) unlike the homologous area in didelphids, the distal end of the bone is laterally extended, and the facet indicating articulation between the distal extremities of the crus, the **TiFid** facet, has a convex, as opposed to concave, surface. The shape of the **TiFid** facet represents a sharp distinction between the few known Itaboraí specimens and didelphids.

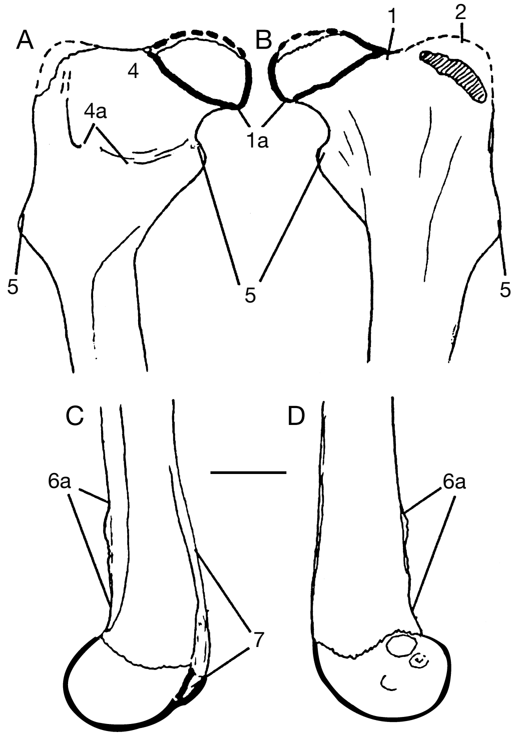


FIG. 55. — Details of left IMG Femur 5; **A**, **B**, proximal third; **A**, posterior view; **B**, anterior view; **C**, **D**, distal third; **C**, medial view; **D**, lateral view. For numbered designations of specific characters see text. Scale bar: 2 mm.

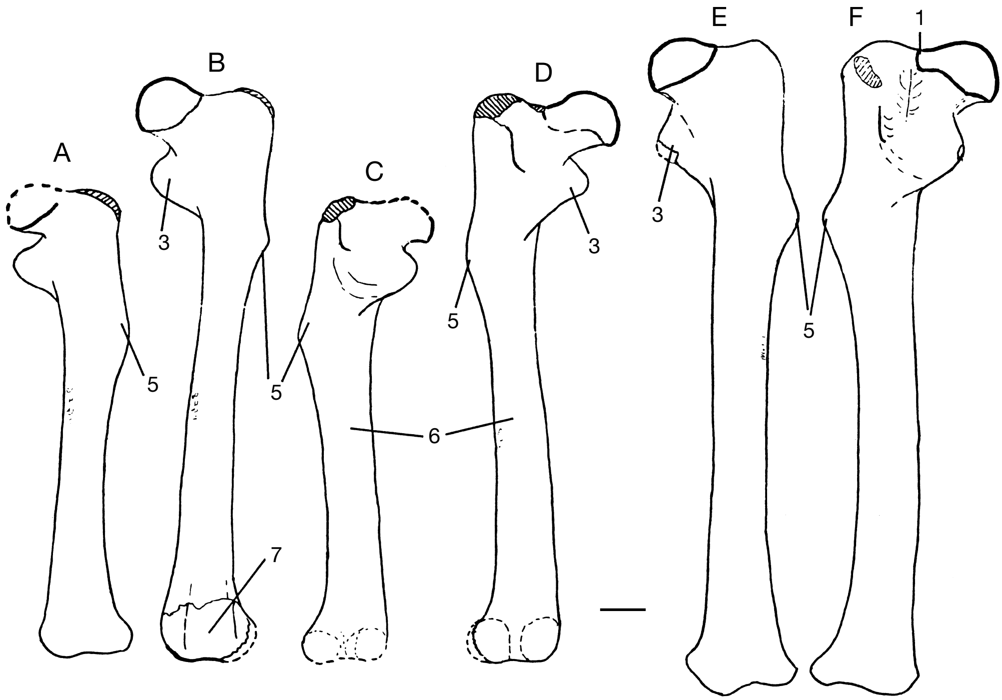


FIG. 56. — Left IMG Femur 6. Three specimens of different sizes; **A**, **B**, **E**, anterior view; **C**, **D**, **F**, posterior view. Distal ends are poorly preserved. For numbered designations of specific characters see text. Scale bar: 2 mm.

TARSUS

A total of 13 informal (unnamed) probable species groups were reported by Szalay (1994) based on tarsals. These groups were based on a nearly equal number of calcaneal and astragalar phena. What was particularly striking at that time, as it is now, was that with a few notable exceptions, the basic patterns of these specimens closely reflected what was considered to be the common ancestral sudameridelphian (and probably even more primitive) pattern (Szalay 1994). With the noted few exceptions, there was not much evidence from tarsal remains, at least not from these from early in the Cenozoic, for adaptive divergence beyond some recurrent patterns of mechanics pointing to either habitual eversion or inversion. The latter appeared to track, very convincingly, terrestriality and arboreality in the extant models used for tarsal attributes.

The outstanding exceptions were the tarsals of IMG II, as well as the calcaneal morphs of IMG V and XII. The latter two were suspected to belong to didelphids, but there were no astragali that would securely confirm this suggestion. In retrospect, we doubt their didelphid status. Concerning the specimens of IMG II, both their size and their highly suggestive aberrant and different adaptations strongly support the notion that they are conspecific with IMG Humerus 2, IMG Ulna 3, IMG Femur 5, and IMG Tibia 1.

UNGUALS

While the specimens of unguals are of limited value in this analysis, we included them because of their probable marsupial affinities. The two types described below show the size range expected for the Itaboraí marsupials described here and previously. Fig. 67 depicts the relatively clear juxtaposition of terrestrial *vs* arboreal types. This differentiation is based on the inferred loads incurred and resisted on the tip and base, respectively, of these bones. We make no attempt at grouping the few specimens into the type of "surrogate taxa" we used above to organize our other described specimens.

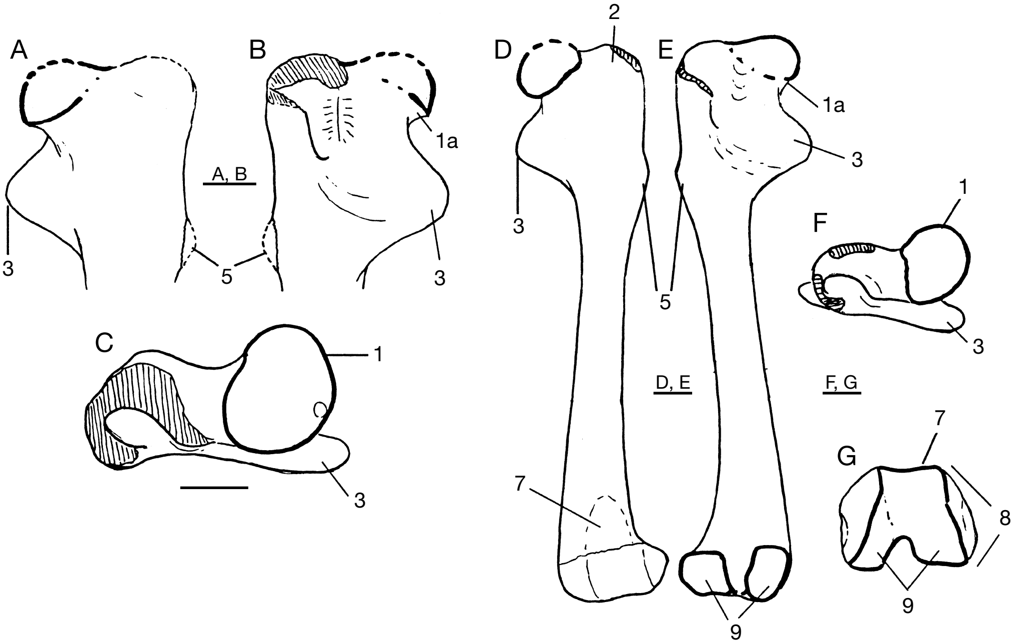


FIG. 57. — Left IMG Femur 7. Two specimens (**A-C** et **D-G**); **A**, **D**, anterior view; **B**, **E**, posterior view; **C**, **F**, proximal view; **G**, distal view. For numbered designations of specific characters see text. Scale bars: 2 mm.

IMG Ungual type 1 (Fig. 67A-F)

This type, although far from heterogeneous in morphology, represents several taxa that are considered "terrestrial" in conformation because of the morphology and ratios (depth/length) of their various parameters. They can be characterized as long and shallow. There are six specimens ranging in size from about 3 mm to 10 mm, representing a range of species.

IMG Ungual type 2 (Fig. 67G-J)

These specimens are considered "arboreal" in conformation because of the morphology and ratios (depth/length) of their various parameters. There are four specimens ranging in size from about 3 mm to 4.5 mm, representing a tight range. It is not clear whether several species are represented in this sample.

ASSOCIATION OF POSTCRANIALS AND DENTAL TAXA

In this study we have uncovered a series of inferred associations between some of the postcranials, as we commented above. The only such reliable association between bones belonging to different groups is based on size, functional factors, and the ephemeral notion of a high degree of apomorphy shared between well-represented clusters. There is only one group for which this approach yielded some secure inferences. This collection of postcranials are the samples of IMG Humerus 2, IMG Ulna 3, IMG Femur 5, IMG Tibia 1, IMG Calcaneus 3, IMG Astragalus 4, and an allocated cuboid; the tarsals were described in Szalay (1994) and were allocated to IMG II. All of these samples, together, point to a single small species of unusual marsupial. This uniqueness is not particularly pronounced in the name bearing dental taxon that may belong with this postcranial group. *Gaylordia macrocynodonta* Paula Couto, 1952 (including *G. doelloi* [Paula Cuoto, 1962]), is of the approximate size rank among Itaboraí dental taxa as the postcranial complex we associate with IMG II as a single species. The hypertrophied PM4 and the heavy premolar and anterior molar wear do not, of course, hint any of this association.

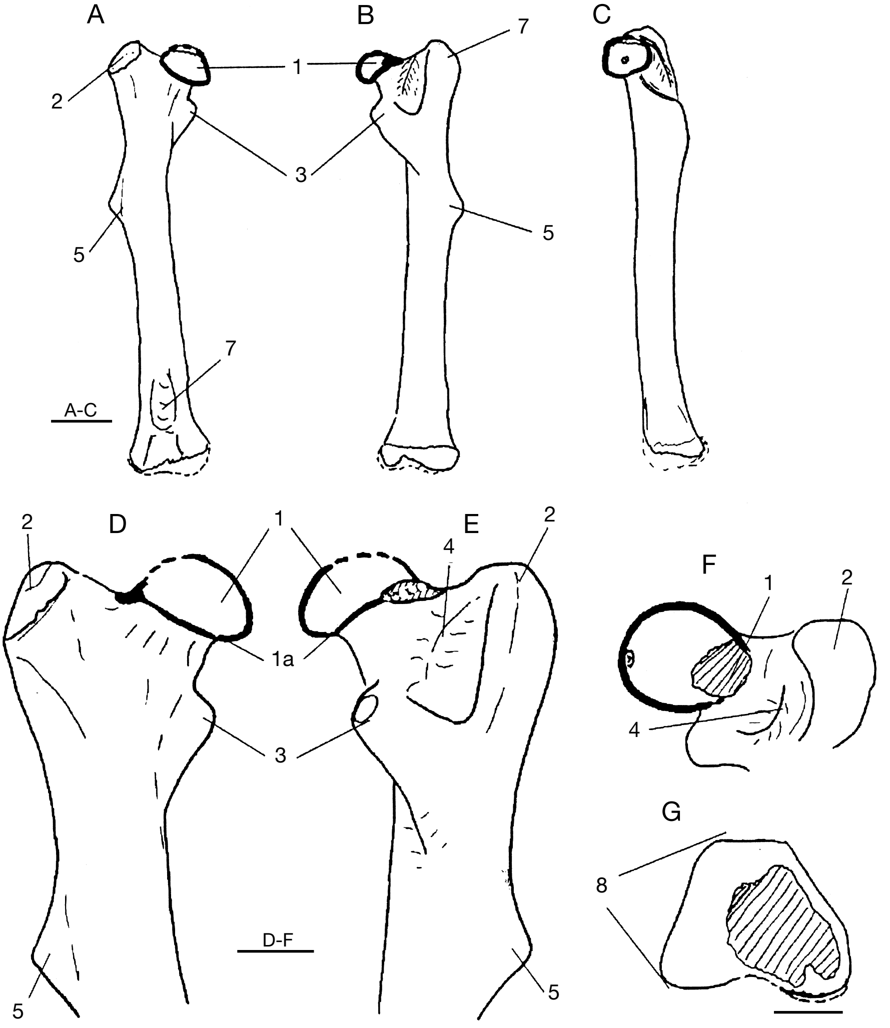


FIG. 58. — Right IMG Femur 8; **A-C**, the whole bone; **A**, anterior view; **B**, posterior view; **C**, medial view; **D-G**, details; **D**, anterior view; **E**, posterior view; **F**, proximal view; **G**, distal view. For numbered designations of specific characters see text. Scale bars: A-C, 4 mm; D-G, 2 mm.

The reasons for considering this postcranially delineated species taxon a glider are complex, yet compelling. Its humeri and femora are exceptionally long and slender compared to their articular areas, suggesting habitual tensile loading. The articulation of the elbow is rigid suggesting locking, yet far more advanced functionally in that respect than in the terrestrial *Metachirus*, *Monodelphis*, or caenolestids. The knee joint, along with attributes of the proximal femur, strongly predicts leaping behavior. The tarsals, while seemingly those of a hopper or leaper, show great mobility in the calcaneocuboid joint, an attribute usually absent in such terrestrial forms. Plotting various indices of this species with arboreal and gliding mammals (both metatherian and eutherian), bats, sloths, and *Cyclopes* shows that the Itaboraí species fall on the line with the gliders (Stafford 1999). There are no other associations that we are aware of among either the various groups of postcranials or between the dental specimens-based named taxa form Itaborai.

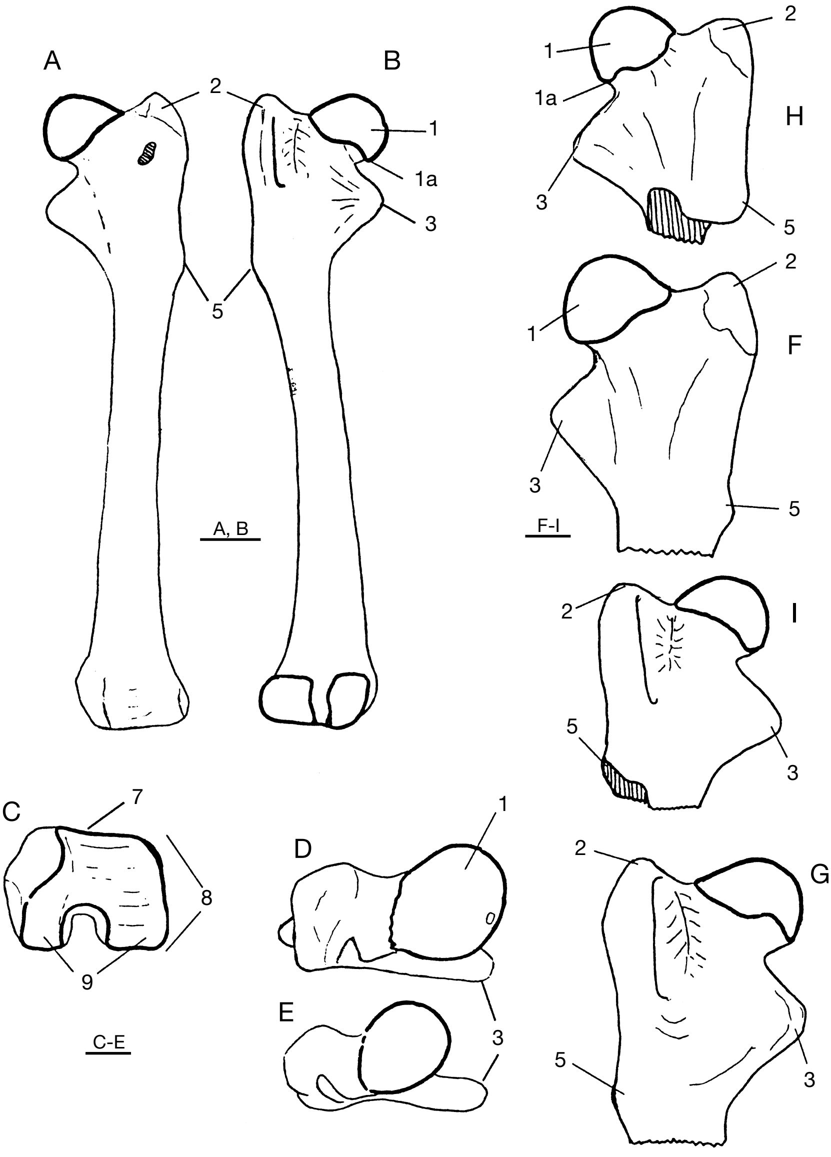


FIG. 59. — Left IMG Femur 9; **A-D**, **F**, **G**, first specimen; **A**, **F**, anterior view; **B**, **G**, posterior view; **C**, distal view; **D**, proximal view; **E**, **H**, **I**, second specimen; **E**, proximal view; **H**, anterior view; **I**, posterior view. For numbered designations of specific characters see text. Scale bars: A, B, 4 mm; C-I, 2 mm.

PHYLOGENETIC ANALYSIS AND BIOGEOGRAPHY

Evolution is descent with modification, an aspect of which is cladogenesis. This plain Darwinian dictum, one that is founded on ancestor-mediated anagenetic transformation even during any level of cladogenesis, is often completely ignored in systematics in light of the unbalanced emphasis on the search for cladogeny. Yet the complete theory has profound consequences for methods used in estimating the

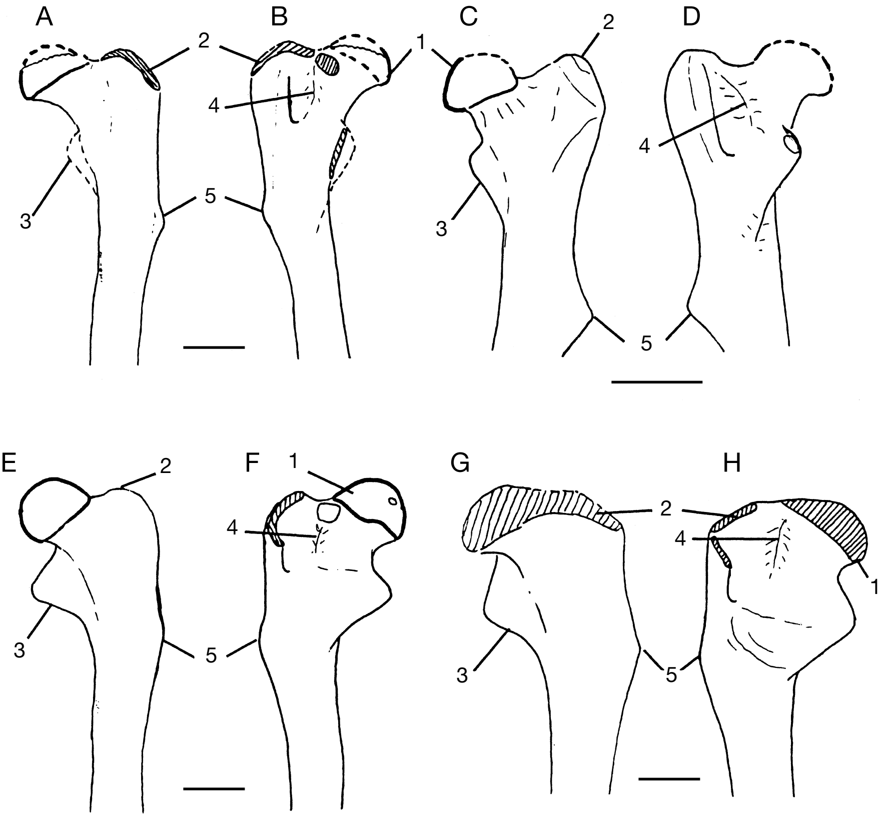


FIG. 60. — **A-D**, left IMG Femur 8, two specimens, proximal halves; **A**, **C**, anterior view; **B**, **D**, posterior view; **E-H**, left IMG Femur 10, two specimens, proximal halves; **E**, **G**, anterior view; **F**, **H**, posterior view. For numbered designations of specific characters see text. Scale bars: 4 mm.

evolutionary history of all organisms[30]. This is also a way of saying that there is no cladogenesis without anagenesis (Szalay 1999a). The character patterns that we recover reflect results of processes based on underlying contingent theory, and the methods to decipher these patterns, therefore, need to be theory-based. This is in contradistinction to the theoretical prescription of Eldredge & Cracraft (1980), a perspective widely followed by those who attempt to reconcile parsimony-driven cladistic operationalism with phylogeny. The patterns observed are the results of heritage-constrained and -facilitated adaptive descent in space and time, expressed either as transformation or stasis. But how do we pick the relevant? What is relevant for adaptational assessment is often phylogenetically only tangential. In phylogenetic analysis we need to know what is and what is not admissible into the relevant database when testing hypotheses against interpreted information[31].

CHARACTER ANALYSIS AND PHYLOGENETICS

Much of what has been discussed above regarding variation, models, and the analytical description of specimens naturally leads into both the theoretical issues of phylogenetic reconstruction, as well as the use of specifics of data and their interpretations as bases for metatherian phylogenetics. The discussions of the phylogenetics of character complexes lead into the phylogeny of lineages and taxa. The taxon phylogeny presented here is based on the character analysis of properties chosen *a priori* to taxic analysis. These choices are not driven by parsimony-based algorithmic processes.

Therefore, we take a different tack than that expressed in Novacek's (1993) reflections on higher mammalian phylogenetics. Novacek has been a prolific contributor to mammalian, higher level, taxonomy, and a committed practitioner of the taxic approach to phylogenetics of eutherian mammals. We comment on his theoretical stance because it is both often and conspicuously displayed (e.g., *Nature*) and is representative of cladists who reject pattern cladism, but also view paleontological and functional methods as contrary to parsimony-based analysis (for similar views to those of Novacek, see also Simmons 1993). Significantly, Novacek's approach attempts to reflect a balanced and deceptively even handed attitude towards a range of practices in phylogenetics. Yet, in his discussion of methods of analysis (as in that of Simmons 1993), Novacek eschews what we consider to be a Darwinian approach to character analysis-based phylogenetic estimation. Novacek attempts to justify the combined uses of parsimony and *a posteriori* weighting, but not consistently, however. Novacek (1993: 6) comments that in "the non-molecular world [i.e. in analyses of morphological attributes], a priori weighting is much less open to any kind of objective analysis." By stating this, he implies that occasionally such an approach is acceptable. Given *his* definition of objective, it appears that Novacek believes in a theory-free perception of structurally delineated traits. But shortly after this, he comments on the "[...] obvious circularity in applying weights based on the character behavior revealed in the same data set through unweighted analysis." (Novacek 1993: 7). So according to Novacek (and others), while *a priori* weighting is not objective when dealing with results of comparative and evolutionary analysis of morphology, *a posteriori* weighting is circular. While the latter is a position with which we strongly concur, we consider the explicit and contestable *a priori* analysis of attributes and their weighting to be useful characters the only theoretically meaningful approach to phylogenetics.

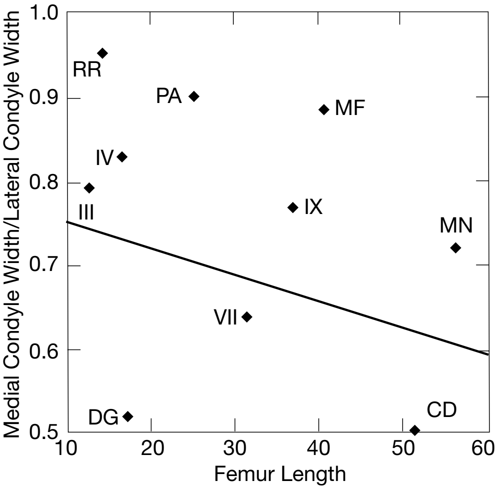


FIG. 61. — Plot of a femoral index against a quasi-surrogate measure of body weight (given the isolated nature of specimens) on the horizontal axis. Regression line was drawn for living models only, and the fossil values were plotted subsequently in order to gauge some measure of their relationship to the arboreal-terrestrial dichotomy between models. Abbreviations: **CD**, *Caluromys derbianus*; **DG**, *Dromiciops gliroides*; **MF**, *Mayulestes ferox*; **MN**, *Metachirus nudicaudatus*; **RR**, *Rhyncholestes raphanurus*; **PA**, *Pucadelphys andinus.* Roman numerals stand for Itaboraí Metatherian Group designations of femora.

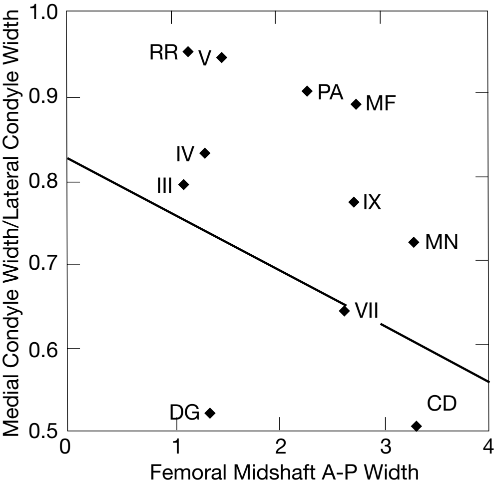


FIG. 62. — Same as Fig. 61 but with a different body weight surrogate.

In the following pages (in which Novacek further discusses taxic procedures that lead to the most parsimonious resolution of cladograms), he

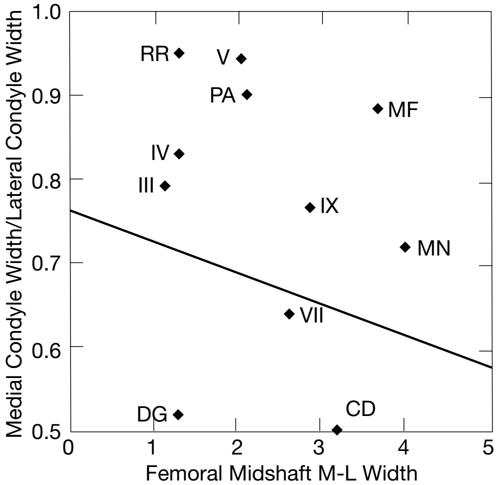


FIG. 63. — Same as Fig. 61 but with a different body weight surrogate.

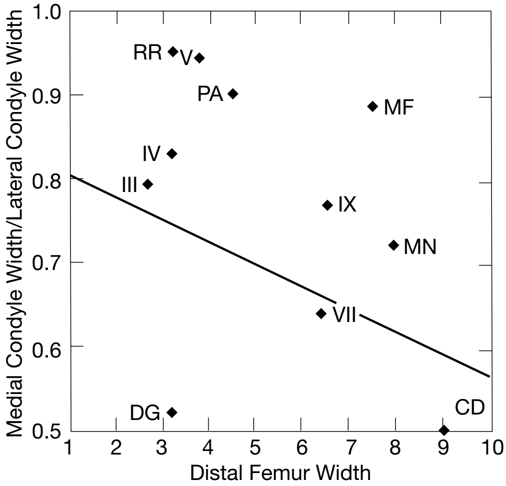


FIG. 64. — Same as Fig. 61 but with a different body weight surrogate.

regrettably omits the procedural details of how we gather and test the necessary characters and determine their polarities. The Darwinian context of phylogeny, within which selection is considered to be the main (but not only) engine of change (given initial and boundary conditions), is also omitted and in a diplomatic manner the issue of character analysis itself is sidestepped by reference to a few opposing approaches in the literature (Novacek 1993: 10; see also Novacek 1996, on adaptation).

In contrast to the openly expressed ambiguities and studied omissions of that approach, one that provides no theoretically sound guiding method to either character selection or the combined activity of character ordering and polarization, we are far less conciliatory and accommodating. We believe that a theoretically rigorous practice of systematics should be explicit regarding the routinely submerged issues about methods of character analysis. We consider an approach that attempts to reconcile morphological character ordering and polarization based on algorithms to be an essentially structuralist one. This is an inadequate, albeit widely accepted, practice among morphologists using parsimony algorithms in order to generate not only cladograms, but also circular "character transformation" schemes. How one garners objective observations into a theoretically well founded set of taxonomic properties and taxon phylogeny that are valid and not circular (e.g., *fide* Bock 1981) is critical for constructing hypotheses of taxon phylogeny.

We are obviously not against rigorous cladistic analysis (without parsimony criteria), based on biologically sophisticated horizontal comparisons. Cladistics and phyletics (the transformational assessment of attributes and lineages), together, constitute phylogenetic analysis. But we aim for temporal (geological) and/or functional-adaptive analysis-based *ordering and polarization* of chosen, and (whenever possible) functionally interrelated, characters that add the weight of probability to a database. Phylogenetic hypotheses about lineages should be tested against such data, and such a procedure does not require decisions by parsimony (an irrelevant statistical fiat in phylogenetic estimation), which is a last resort strategy at best [32]. We subsequently reject any procedure that considers parsimony analysis to be a "test" of the scientific reliability of taxon phylogeny hypotheses, let alone the application of such methods to produce reliable character polarities. Parsimony-based methods explicitly sidestep attempts at causal understanding of character evolution (i.e. transformational understanding), and hence render evolutionarily meaningful scientific treatment impossible. In fact, this practice positively discourages rational (as opposed to statistical) analysis, citing "consistency" and an idiosyncratic meaning of "objectivity" as the criteria. The "objectivity" of such references in relation to human observations is presumably some form of theory-free process, a procedure or phenomenon unknown to us[33].

In the briefest terms, our model based procedure is squarely rooted in the fundamental Darwinian precept of *descent with selection-based modifications, mediated and/or constrained and facilitated by heritage*, the methodological consequences of which can be outlined as follows:

1) collection of distributional data on attributes of significance pertaining to the living and fossil taxa under scrutiny, as well as their geographical and temporal framework;

2) variational, functional (mechanical), and adaptive assessment of character complexes of specific bones, or other integrated aspects of organisms, whenever possible (we realize the sometimes insurmountable empirical limitations);

3) subsequent choice of character constellations with several homologous states that allow some form of both ordered and polarized (transformational) understanding;

4) examination of the functional-adaptive context of the properties to allow one to differentiate, while obviously not perfectly, between what are likely to be convergently *vs* homologously shared attributes between taxa. In the case of fossils, this procedure involves a carefully chosen and contextually appropriate model-based assessment of attributes that may give a probabilistic overview of the adaptive aspects of the properties (discussed above);

5) construction of a database that consists of both transformational homologies, as well as genuine, preferably structurally complex synapomorphies (that are considered to be homologous either as a result of testing that convincingly rejected homoplasy, or because they are identical or nearly identical), against which various hypotheses of lineage and taxic relationships can be tested in both the best temporal and biogeographic framework available[34]. In particular, we note below the consequences of employing a combination of taxic and solely cladistic perspectives in biogeographic reconstruction. Such procedures often stand as substitutes for lineage-based thinking when grappling with a geographical historical narrative.

FIG. 65. — **A**, IMG Tibia 3 (DGM 1731PV), right specimen, anterior view; **B**, IMG Tibia 2 (DGM 1952M), left specimen, anterior view. Scale bar: 3.5 mm.

TRANSFORMATIONAL ANALYSIS, ADAPTATIONISM, AND THE CONCEPT OF MOSAIC EVOLUTION

As outlined elsewhere (Bock 1981; Szalay 1994), Darwinian phylogenetic analysis represents the combination of several research programs that are

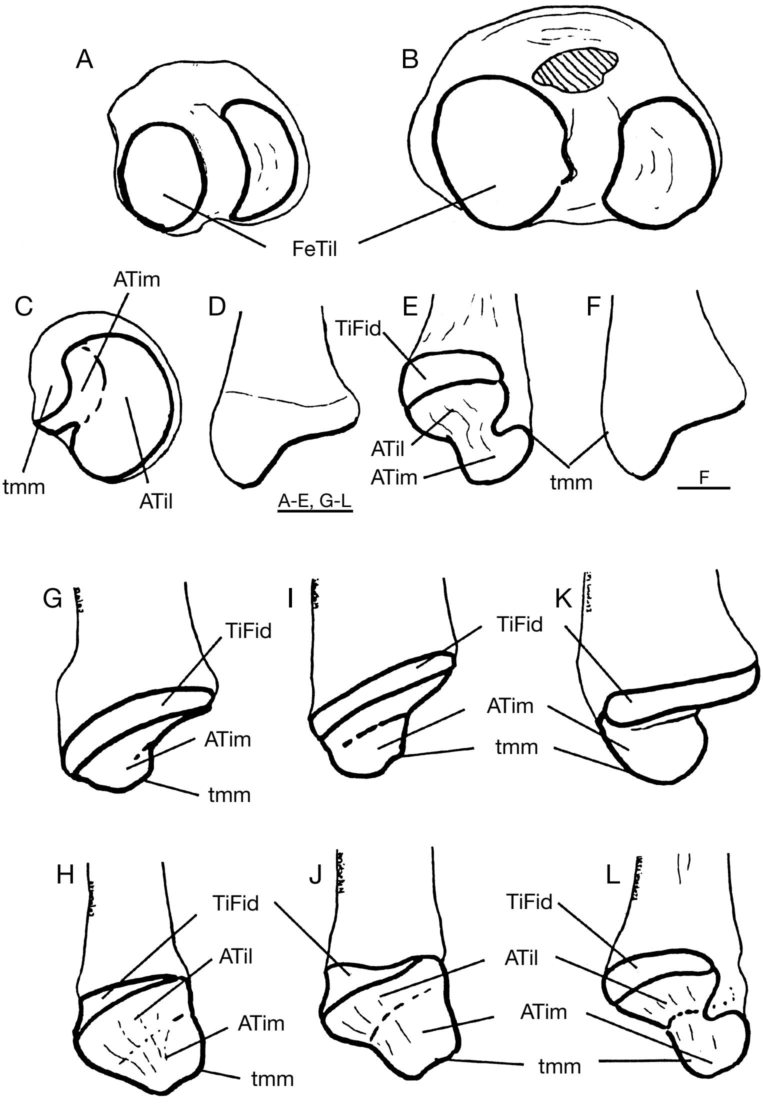


FIG. 66. — **A**, details of left IMG Tibia 2, proximal view; **B-E**, **K**, **L**, details of left IMG Tibia 3; **B**, proximal view; **C**, distal view; **D**, anterior view of distal end; **E**, posterior view; **K**, lateral view of distal end; **L**, posterior view of distal end; **F**, left distal tibia of *Pucadelphys*, anterior view; **G**, **H**, left distal tibia of *Caluromys*; **G**, lateral view; **H**, posterior view; **I**, **J**, left distal tibia of *Metachirus*; **I**, lateral view; **J**, posterior view. Abbreviations: **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **CaFi**, calcaneofibular facet; **FeTil**, lateral femorotibial facet; **TiFid**, distal tibifibular facet; **tmm**, tibial medial malleolus. Scale bars: 2 mm.

based on the information supplied by the fossil record, as well as the comparative developmental, functional, and ecological biology of extant and extinct organisms (see Fig. 1). This procedure results in an often small number of (preferably) complex and phyletically and functionally well understood attributes that are *objectively* judged to be tested transformational homologies (based on supporting research), which both root and give direction to phylogenetic reconstruction. There have been fundamentally flawed criticisms and axiom-driven misconceptions of what Darwinian transformational analysis entails. Equally misperceived is how transformational analysis is employed in estimating phylogenetics of lineages and their taxonomized chunks. Taxic analysis is often viewed as the proper starting point for both the phylogeny of the taxa themselves, and subsequently, the transformational understanding of the traits emanating from such analysis [35].

Taxogram-based "transformation" approaches decouple phylogenetic analysis from evolutionary theory, and advocate methods based on a perception of evolution that is derived from the practical procedures of delineating species and other taxa. Such views, we believe, improperly mix the conceptual foundations of evolutionary dynamics (tested theory-based) with practical necessity, and with various imperatives that are needed for taxonomic actions and the notions derived from them. In fact, taxonomists and punctuationists who consider the origin of a new lineage (i.e. also a new species taxon in the making) to be causally and processually distinct from anagenetic evolutionary change in general often reject the methods of transformational analysis [36].

Workers advocating specific taxic views of the evolutionary dynamic (perhaps the handle of taxism is not entirely out of place for that perspective), therefore, ignore the general guideline that methods of phylogenetic analysis of taxa should fall out of the underlying tested principles of the evolutionary dynamic, and not out of its shifting taxonomic perceptions. To us, the most fundamental of these principles is the incontrovertible view that all functionally meaningful properties of any organism, within the often strictly defined confines of their ancestry (i.e. constrained by the ovum and inherited genotype), are continually under the scrutiny of selection (the ideology of the advocates of "new adaptationism" notwithstanding).

Attacks similar to those on the practice of transformational analysis are correlated with ones on the phenomenon of mosaic evolution. The latter has been referred to as a "hoary old concept", in order to drive arguments against the straw man of transformationism. It is a mistake to believe that natural selection cannot favor individuals that retain traits that fulfill critical and persisting bioroles, while also being the source for newer traits for new roles. New traits can and do arise, unaffected by the persistence of other adaptations. To deny this makes one unobservant, but it also makes too much of the textbook concept of epistasis. *Such linear advocacy against mosaic evolution (modularity) misses the fundamentally pattern-based observation, repeatedly corroborated, that aspects of taxa evolve at different rates.* Such advocacies reject some of the great advances of both Darwinian evolutionism, as well as that of the Synthesis (Simpson 1953), yet also hastily strive under the same breath to accommodate the incontrovertible notion that adaptation is central in evolution. The very fact that highly functional and adaptively correlated attributes of one character complex may have remained stagnant while

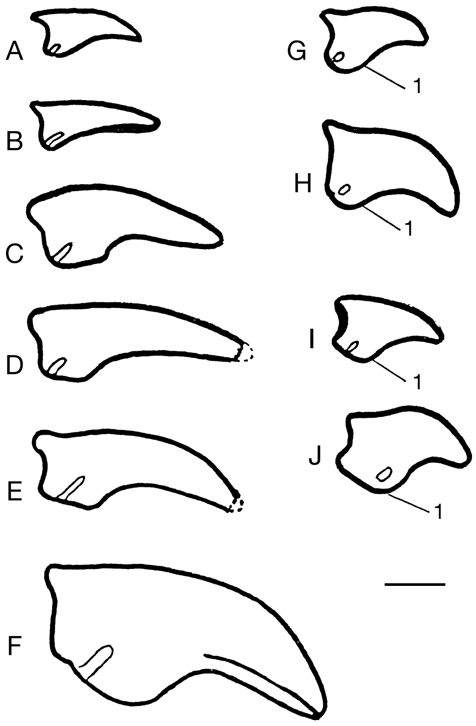


Fig. 67. — Unguals that probably belong to metatherians from Itaboraí; **A-F** likely represent terrestrial species, whereas **G-J** suggest arboreal forms. For numbered designations see text. Scale bar: 2 mm.

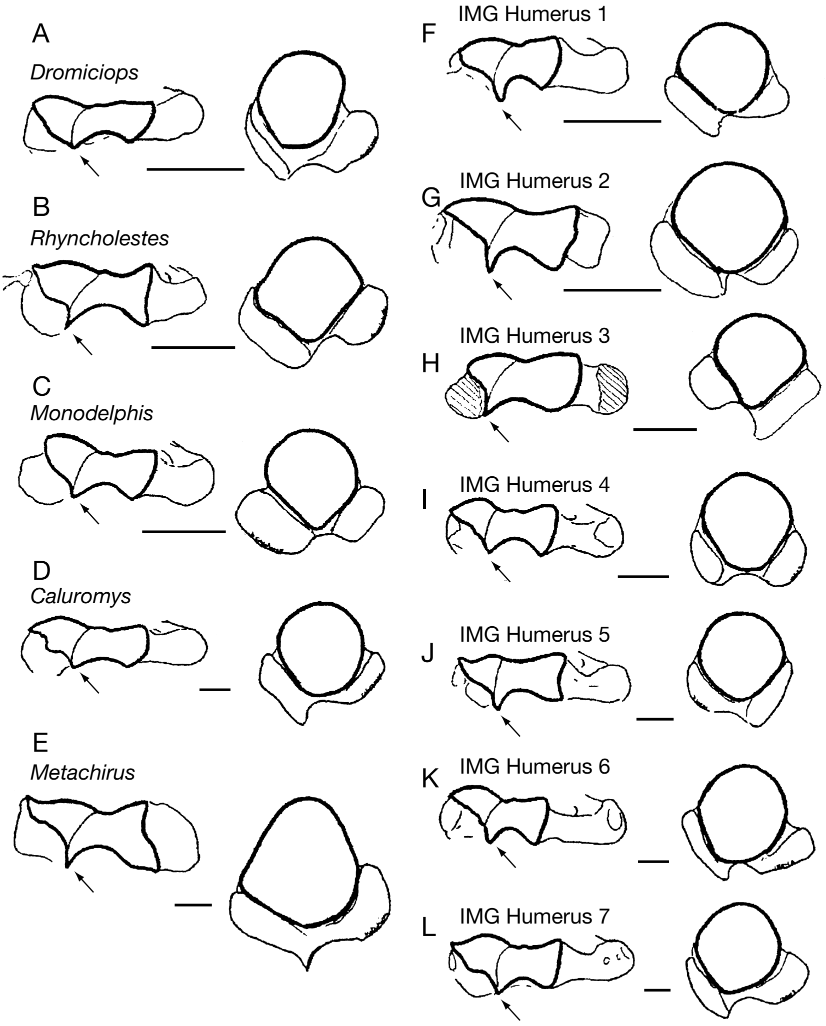


FIG. 68. — Comparisons of the distal end and head of the left humeri of the five extant didelphid species (**A-E**) with known habitus and the seven Itaboraí humeral groups (**F-L**); **A**, *D. gliroides*; **B**, *R. raphanurus*; **C**, *M. domestica*; **D**, *C. derbianus*; **E**, *M. nudicaudatus*. The drawings were prepared so that the distal width of the humerus was kept (approximately) constant, and the size of the head was then drawn at the same scale as the distal end of the same humerus. Anterior is toward the top of the page for the distal ends. From top to bottom, the size of the humeral groups (and possibly the body size as well) increases. Arrows point to the posterior and lateral extension of the curved (to various degrees) facet for the ulna. Scale bars: 2 mm.

others have evolved in various directions (even in populations of the same species) attests to the differential adaptedness of the same, or different, aspects of different lineages [37].

We reiterate that explicitly argued probability judgments about character transformations (including both the ordering and polarity of characters independent of taxogram patterns) are the core of phylogenetic analysis. As we outlined here (and elsewhere, see references in Szalay 1994, 2000), the Darwinian context of lineage transformation sets the boundaries within which contingent attributes of different lineages (or stages of the same ones) can be recognized and weighted, as well as judged to be either more probably homologous or homoplasious [38].

Any theoretically meaningful and operationally tested determination of which traits are either

TABLE 13. — Functionally based, but phylogenetically persistent, heritage retentions, or derived modifications (differences) in the postcranial skeleton in the ancestral sudameridelphian, the diagnostic stem didelphid (as well as the extant didelphids), and the australidelphian stem. The sudameridelphian conditions (inferred from those of Tiupampa and Itaboraí taxa, in their comparative contexts) are largely preserved in extant Caenolestidae, modified in the stem Didelphidae, and derived from a didelphid in the stem of Australidelphia. There is, therefore, a very real mosaic distribution of these traits in the taxa compared, either in their stasis or transformationally homologous manifestations. The direction of change is from the left column to the right one. Many minor characters of skeletal morphology in these higher taxa are subsequent to the adaptive modifications of the stems in various lineages, and the constraining heritage features cannot be recognized. In general, such traits (usually minor shifts in homologous character states) are poor or irrelevant tests of phylogenetic hypotheses of the known groups.

Characters (based on analysis of character complexes that they are parts of)	**Stem of Sudameridelphia**	**Stem of Didelphidae**	**Stem of Australidelphia**
1. Fusion of scaphoid and centrale (ScCe).	Unknown	Yes	Yes
2. Third trochanter.	Present	Absent	Absent
3. Astragalo-calcaneal position.	Astragalus lateral to calcaneus	Astragalus dorsal to calcaneus	Astragalus dorsal to calcaneus
4. Astragalar medial plantar tuberosity (ampt).	Very large	Small	Small
5. Sustentacular facet.	Tapers to ribbon above ampt on astragalus; extends onto proximal calcaneal surface of sustentaculum	Rounded and distinct on astragalus; elongated on calcaneus	Coalesces with calcaneoastragalar facet and is closely similar in size on both tarsals (Su + CaA = CLAJP)
6. Astragalofibular facet.	Narrow	Broad	Broad
7. Calcaneocuboid joint.	Simple shallow, nearly circular ovoid	Deep proximal extension of cuboid, and articular equivalent on calcaneus	Additional facet added to didelphid pattern results in three, stepped, articulations
8. Joint between hallux and first metatarsal.	Unknown	Hinge-type that allows guided, but extensive, abduction	Modified to saddle joint that allows disarticulation during extreme abduction; enhances mobility

homologous or homoplasious, or which are primitive or advanced in a given phyletic context, involves some sort of Darwinian transformational assessment. Transformational analysis, whether based largely or partly on the fossil record, or, given the lack of the latter, on purely developmental and functional-adaptive foundations, is the cornerstone of phylogenetic analysis. Beyond convincing stratophenetic data, transformational analysis requires either theoretical evolutionary modeling, or the use of model species that are as closely related as possible to the lineages investigated. While stratophenetic data are very rare for specific lineages, the context provided by a fossil record for analyses at sundry levels of structural organizations profoundly influences our perceptions of character change, even if this influence is rarely given any recognition (Szalay 1999b).

ROLE OF ANCESTRAL APOMORPHIES IN PHYLOGENETIC ANALYSIS

We add and emphasize the obvious, namely that the structural-functional solutions of different lineages, each with their own highly diagnostic taxonomic (but also functionally revealing) patterns, appear to be highly dependent on their heritage attributes. This also means that the nature of positional demands (or any other functionally-driven system of organisms), and hence loading on the whole musculoskeletal system (up to a significant point), results in adaptive modifications within the parameters of a heritage solution for some similar or divergent strategies. Therefore, even relatively small phyletic shifts in positional behavior leave recognizable traces on the skeleton. Such morphological distinctions allow fine grained recognition of distinct adaptive differences even among closely related fossil species taxa[39].

Nevertheless, certain basic adaptive patterns persist in groups of mammals even if the habitus of the descendants (their most recent adaptive modifications) varies considerably. There can be little question that such fundamental ancestral patterns, such as the musculoskeletal organization of the skeleton as it relates to positional (locomotor, etc.) behaviors, are adaptive. One would need to suspend the reality of a Darwinian world just to accommodate simplistic assumptions for equally simplistic taxonomic philosophies that either view ancestral attributes as non-adaptive, or consider adaptive assessment of features as methodologically unimportant. An understanding of ancestral attributes at given levels is necessary because these constrain the nature of adaptive transformation, and hence the possible directions of change (and therefore systematic understanding).

The (adaptive) persistence of heritage factors in the skeletal system also signals the fundamental importance of fossil skeletal morphology for phylogenetics, as stated so emphatically by Gregory (1910) regarding the central role of osteology in phylogenetics. Beyond the taxon specific stamps of the Metatheria and Eutheria, as well as the particulars of the various family and even genus level groups, functional-adaptive analysis based on the living models allows both paleobiological assessments of fossils, and the elimination of irrelevant functional attributes (habitus features) from phylogenetic analysis (see Szalay & Schrenk 1998).

“PHYLOGENETIC TAXONOMY OR NOMENCLATURE” (SENSU DEQUEIROZ & GAUTHIER) AND THE CAPTIVATING ILLUSION OF EXCLUSIVELY HOLOPHYLETIC CLASSIFICATIONS

In our analysis and conclusions below we deal with named taxa. Hence, we need to consider, even if briefly, some views recently introduced to classificatory practice and their applications to the metatherians.

Much of the systematic literature of the last decade has focused on the categorization of abstract models of cladistic-cum-taxonomic patterns. The discussions have centered on the laudable idea of separating the methods of historical analysis from classification itself, just as this has been practiced in the past (Simpson 1945). But this departure from the halcyon days of doctrinaire cladistics, when a cladogram was a “true” classification, is only apparent rather than real. The terminology in the discussions relating to “phylogenetic taxonomy” (a crown group and taxogram-based systematization), used to describe the various axiomatized taxonomic patterns of cladograms, as well as to redefine these concepts, has reached a state of rococo confusion (e.g., DeQueiroz 1992, 1994; DeQueiroz & Gauthier 1990, 1992; Rowe & Gauthier 1992; Sereno 1999). This is evident from Sereno’s (1999) instructive review and his tabulated list of definitions, although he continued to add to this list. Additionally, the specter of a strawman of “essentialistic perspective” was raised (and misunderstood) by DeQueiroz (1994) in order to justify this curious debate that consistently sidestepped biological meaning in the “definitional” approach to taxa.

It is ironic, that after extensive literature discussions on the merits of straightforward taxogram classifications, it should become obvious again that taxonomic expression without heuristics is an activity that creates confusion and does not serve the larger community (Szalay 1999b). We take this to mean that, for a useful taxonomy, some meaningful character constellation and practicable delineation is in order, as opposed to the practice of formalizing “ambitaxa” that the parsimony analysis of an unanalyzed data set will yield. As Sereno (1999: 350) concludes: “Survivorship, diversity, morphology, and tradition are heuristic criteria for placement of node-stem triplets”. But the concept of the “node-stem triplet” covers up a serious flaw in the conceptualization of the interface between lineages and created taxa.

The ongoing debate on the issues of various kinds of "phylogenies" that surround the new "phylogenetic taxonomy" misses a single and critical point. No matter what portion of a phylogeny is delineated as either a holophylon or paraphylon, all have (had) a real stem. These stems would be considered taxonomic species of specific lineages if we were to encounter them, and they would be named as real taxonomic entities. Nodes of taxograms do not depict any real phylogeny. Attempts at the reification of the node-based notion for the purposes of taxonomy (without taxonomic designation for that node) have all added a curious twist to this avenue of nomenclatorial exploration. The idea that only holophyla are "natural", and that such a particular methodological illusion coupled with the idea that cladistic analysis can stand alone without phyletics (the independent transformational analysis of traits) needs some serious reexamination.

The procedure of identifying clades through cladistic analysis has been declared by "phylogenetic taxonomists" to be distinct from their proposed "definitional" procedure of labeling with names. The latter procedure is said to have the merit of taxonomic stability, no matter what future research reveals (e.g., Flynn & Wyss 1999). In some ways, such claims go beyond the goals of the much maligned eclectic practices of "evolutionary taxonomists". It is not relevant here that it is widely, and mistakenly, taken for granted that these patterns are "tested" phylogenies (e.g., as claimed for "ambitaxa" in McKenna & Bell 1997), while they are really largely about node-based and algorithm-generated taxograms. Exclusive reliance on node-based concepts of taxa for the last three decades helped perpetuate a myth that the history of life can be realistically classified into holophyla only, without reasoned and justified cuts at specific and empirically accessible points. This taxogram view of evolutionary history, a direct outgrowth of doctrinaire parsimony cladistics, of a now axiomatized "crown-clade" perspective, and the ubiquitous and obligatory taxic iconography that the recent systematic literature promotes, was accompanied by the notion that nodes are the only "ancestries" needed, thus keeping at bay the specter of paraphyla [40].

In phylogeny all nodes represent splits in a previously single lineage. Furthermore, the characteristics of one of the lineages may retain all the noticeable attributes of a distant ancestry, while the new one altered these. Does this mean that future named descendants of these two lineage share a "common node?" Hardly, as such an event represents derivation from a specific ancestry. Lineage divergence is not equivalent to comparable rates of character divergence within these lineages. Paraphyletic species taxa, ancestors of clades, also have stems of their own, and of course all designated stems are derived from the previous stage of the same lineage or some other lineage. And we name recognized parts of lineages (or their clusters that do not yield to dichotomizing) as specific taxa, as we should. It follows that all node-based holophyla have stems derived from paraphyla. Stem-based taxa are phylogenetic (and not cladogenetic only) because the researched diagnoses (not definitions) of the character states of stems give phylogenetic meaning to the diverse modifications of lineages springing from that stem. A classification that aims to even come close to reflecting phylogeny, therefore, needs both holophyletic and paraphyletic groups, and no monotonic semantics used as a set of convenient axioms can change such descent-deduced evolutionary reality.

A case in point regarding the artifices of "phylogenetic taxonomy" is the concept of "Marsupialia" delineated with "considerable care" by Flynn & Wyss (1999: 534; 546). While they "define" this subset of marsupials as "[…] a crown-clade based definition, defined as the clade stemming from the most recent common ancestor of [all living groups]", they also "define" the Metatheria as the "[…] stem-based counterpart of 'Marsupialia'". It is defined as "all therians sharing a more recent common ancestor with Marsupialia than with Eutheria". Their remarks regarding "maximally precise" are noteworthy, but it is obvious that their "stem-based" notion, as with their node-based "definitions", is a mere mirror that is dependent on the extant crown-group, which is largely defined by extinction-criteria rather than by any significant, biologically meaningful diagnosis. Both their higher category designations of marsupials are devoid of a diagnostic stem-characterization. Stem-based monophyletic taxa should be delineated on the bases of characters that in some manner have been researched and proposed as present in that stem. Furthermore, as paleontologists, Flynn & Wyss must realize that not all stems represent points of furcations, even though they excise any hint regarding the necessity for paraphyla in phylogenetic delineations in their didactic notes on phylogenetic taxonomy. Wyss & Flynn's (1993) practice of leaving out the miacoid carnivorans from the crown group concept "Carnivora" is a good example of the sophistry that "phylogenetic taxonomy" leads to [41].

Rooting of taxa in stems should require, in our view, some biological statements about the taxonomic properties (and perhaps something of their fate) in the descendants. Flynn & Wyss (1999) present real node-based concepts of marsupial taxa (in spite of the mixed and complex terminology they employ) that are the direct outcome of taxogram practice. This method, through parsimony, attempts to render the spatiotemporal adaptive history of lineages into a monotonic construct of *ever shifting taxograms*. We consider such efforts to axiomatize taxonomy to be as flawed as the practice of algorithmic search for the most parsimonious model of cladogeny. The living marsupials (the "Marsupialia" of Flynn & Wyss 1998, 1999) stem from two of the multiple lineages that rapidly differentiated from somewhere within the Sudameridelphia which continues to resist dichotomizing. Sudameridelphia is a paraphyletic concept, based not only on geography, but on a reconstructed root as well. The two lineages were, one leading to the stem didelphid and the other to the stem caenolestid, two of many biologically similar clusters of species that derived from an ancestor, the various populations of which grasped a geographical opportunity upon entering South America.

By the implication of the "phylogenetic taxon" "Marsupialia", several of these early lineages in South America that are not in the ancestry of extant species were not "marsupialians". In that system they are rather divided by an unknown node. They are "basal" and excluded, and are part of the "Metatheria" of Flynn & Wyss. Meanwhile, practitioners will try to find a difference at that node on the two sides of the divide. To cite the intrusive reality of traits and organisms, there is no osteological evidence for the hypothesis that the Caenolestidae is more recently related to the Didelphidae than it is to any of the bushy lineages of the South American Palaeocene (and sperm-pairing cannot be detected in fossils). We may never know either who the "Marsupialia" is in deep time, or who belongs to the Metatheria. Rarely has the specter of a monotonic "node-based" taxonomic practice shown itself to be as egregiously non-heuristic and abiological as in the case of extinct and extant marsupials. "Phylogenetic taxonomy" (i.e. cladistic taxonomy), in spite of its claims to separate the heuristics of taxonomy from phylogenetics, is another monotonic practice in systematics. It is an attempt at legalistic solutions. It fails to track the real discoveries of phylogenesis, and blocks the unfolding of its biological meaning. Creation of holophyla based on crown groups and extinction criteria does not advance the understanding of evolutionary history. It may even convince some neomammalogists that the fossil record is really not very relevant for understanding the extant fauna.

As we explore below, node-based taxograms also pose considerable difficulties to biogeographic analyses. This is due to the fact that they often employ the taxogram-based approach rather than consider the complete phylogenesis of lineages.

RECENT VIEWS OF TAXON PHYLOGENY WITHIN METATHERIA

In the last decade, reconstructions of evolutionary trees by molecular systematists have been major components of the literature dealing with both metatherians and eutherians. In fact, the rate of contribution from laboratories generating DNA sequences, both mitochondrial and nuclear, and hybridizing the former, have been more numerous than morphological analyses.

While sundry molecule-based approaches have virtually the same options regarding a set of Darwinian strictures related to phylogenetics as morphological approaches do (even if this is rarely practiced), students of gene-based phylogenetics must use an algorithm-dictated approach to modern taxa and must therefore express their findings as node-based taxograms. Before we discuss some of these contributions we emphasize that we consider molecular and genetic findings often of exceptionally great value, particularly when utilized in the context of other information. But we also believe, that while placing great value on the contributions of molecular biology to systematics in general, DNA-based work, unless it is carefully tuned in some way to the realities of adaptive descent and the constraints of a well-analyzed and adequate fossil record, is incapable of dealing with issues of real lineage transformations in deep time.

A recent paper by Naylor & Brown (1997) has presented a thoughtful analysis. They indicated that a concerted effort to make sequence data that had been bootstrap-manipulated conform with an accepted set of evolutionary relationships yielded the "[...] resilient sites [...] associated with amino-acid residues important for tertiary protein structure" (p. 528). They added that this "information can be used both to refine phylogenetic models and to provide structural biologists with clues about the relative importance of particular co-varying combinations of residues for protein structure, function, and folding" (p. 528). In their brief, pithy, and far-reaching analysis, Naylor & Brown (1997: 528) conclude on a completely Darwinian note regarding molecular phylogenetics, by making an observation that has been heard occasionally since the rise of molecular phylogenetics, but which has been mostly overwhelmed by a variety of agendas: "Comparative morphologists have long acknowledged that character co-variation among organisms is affected not only by a shared history, but also by functional requirements. To work as an integrated unit, the sub-components of a complex morphological character must necessarily co-vary. There is every reason to believe that molecules are similar. As the database of protein structures continues to grow, and as sequences from an ever broader taxonomic range of organisms become available for a number of proteins, we can look forward to a better understanding of the historical and functional constraints that act on macromolecules and, as a consequence, to more realistic biochemically based models of change from which to infer evolutionary trees".

Laudably, a paper by Springer *et al.* (1997) on *Notoryctes* Stirling, 1891 shows an explicit recognition that molecular data should be interpreted with the same circumspection required in handling all phenotypic information (as they should be). It is also implied by this paper (unstated, however), that the genome itself is under the same adaptive constraints that the phenotype must contend with. They state (p. 13754): "Given that the interphotoreceptor retinoid binding protein gene is a single copy gene that functions in the visual cycle and that the marsupial mole is blind with degenerate eyes, this finding suggests that phenotypic degradation of the eyes is accompanied by parallel changes at the molecular level as a result of relaxed selective constraints". Clearly, molecule-based phylogenetics should also perform the necessary character analysis based on Darwinian precepts before their data can become a significant contribution to phylogenetics of higher taxa. Sequence data alone are not reliable without the appropriate analysis (and this is true for morphological data as well).

In addition to the recent description of new metatherian fossils and their analyses, there has been a plethora of recent analytical studies of DNA-hybridization (Kirsch *et al.* 1997; and references therein), amino acid sequences (Messer *et al.* 1998), combinations of mitochondrial and nuclear genes, RNA and cytochrome b sequences (Palma & Spotorno 1997, 1999; Springer *et al.* 1998; Burk *et al.* 1999; and references therein), and cytogenetics (Spotorno *et al.* 1997). We would like to comment below particularly on the work by Kirsch *et al.* (1997), who have made a number of general and highly contentious statements both about marsupial phylogeny and morphological evidence. Their assertions regarding:

a) marsupial phylogeny (cum taxonomy, in their usage); b) the significance of research and conclusions based on the morphology of fossils and extant skeletal evidence that they considered to be "opinions"; c) the alleged validity of a host of tree topologies that they somehow translated into "validated evidence" through jackknifing on taxa; and d) their subsequent "proper conclusions" in contrast to the "opinions" of others based on morphological analysis all require detailed examination.

Kirsch *et al.* (1997) present a view about the relevance and achievements of evolutionary morphology of marsupials that is deeply biased in its review of the morphological literature. It demonstrates a near complete lack of understanding of the nature of morphological evidence, the analytical approaches to it, and the testing of the critical transformational hypotheses that form the foundations of morphology-based phylogenies. But perhaps such misconceptions are understandable at some level, in light of the many high profile studies on mammal phylogeny that are studded with hosts of alternate taxograms. These latter studies often deal with largely unanalyzed morphological data fed into parsimony algorithms. Nevertheless, Kirsch *et al.* (1997) directed their discussion against analytical morphological studies not based on algorithmic analysis. They reviewed and reanalyzed previous DNA-hybridization work, which, combined with their own data, provided a sweeping set of conclusions. Their phylogenetic analyses, based on a number of trees, served as the bases for their biogeographic interpretation of the relationship between the marsupials of South America and Australasia. It is particularly interesting to note the extent to which Kirsch *et al.* (1997) had gone to homogenize (by filling, symmetrizing, and suturing) their hybridization data to make it resemble cladistic analyses of sequence data. In spite of claims that rate constancy assumptions were not required, it is noted that "[...] the foregoing points provide some justification for presenting a final, ultrametric tree, which in any case is necessary for computing average rates and divergence dates" (p. 217).

We cannot possibly comment here on the awesome minefield of assumptions that underlies both the data interdigitation and the various analytical runs that resulted in the "final" trees shown by Kirsch *et al.* (1997: fig. 13, a 102-taxon tree; fig. 15, a simplified version of fig. 13). The statement is made by Kirsch *et al.* (1997: 218) that: "We stress that the fig. 13 tree is only a 'template' for presenting the overall results, and was not separately validated. Indeed it would be pointless to do so, because there is no more-inclusive tree with which to compare fig. 13 (but see the discussion below on fig. 14 and the problem of rooting marsupial phylogeny)".

The trees of figs 13 and 15 of Kirsch *et al.* (1997) show the Caenolestidae to be the sister group of the remaining *living* metatherians (as strongly emphasized in Szalay 1994), but it also shows the Peramelidae (within which we include Thylacomyinae Bensley, 1903 and Peroryctinae Groves & Flannery, 1990) to be the sister group of all extant non-caenolestids. *Dromiciops* is stated and shown to be the sister of Diprotodontia, then the Notoryctidae is the next sister, and the Dasyuridae is designated to be the earliest group of the "Eometatheria" and the sister of the Didelphidae. When examining this tree (fig. 13), one that depends on the questionable practice of "suturing" otherwise useful assessments of small monophyletic clusters, it is imperative to pay attention to some of the remarks in the text. For example: "Apart from the effects of rate variation, these discrepancies occur because of the large number of species or subspecies in the 102-taxon tree, the short internodes associating some taxa, and *the consequent algorithmic compromises necessary in computing this and other large trees*" (italics supplied).

A large portion of their long paper is a series of caveat-ridden and laudably honest discussions of the pitfalls of technical and methodological procedures that beset such an attempt at combining DNA-hybridization data into a higher-level phylogenetic diagram. Subsequent remarks regarding the "intuitively satisfying" aspects concerning lower-level relationships of some groups, as well as the nature of this feedback to the sutured arrangements of *Dromiciops*, peramelids, dasyurids, and didelphids, makes us both curious and puzzled about the nature of the epistemic procedures used in their study. While their paper is obviously not about morphological, fossil, or geological evidence of any sort, Kirsch *et al.* note (1997: 235) that a "[...] 'timeline' to the left of the caption [of fig. 13, the sutured tree] lists some important events in marsupial history, with names proposed in our new classification [...]". These events include the postulated origins of fossil groups, and the highly specific paleogeographic history ranging from 104 to 3 my. The former date, according to the authors, is the time of the split between Metatheria and Eutheria.

There are a number of bold statements in Kirsch *et al.* (1997) that fly in the face of their own remarks on the history of publications about marsupial phylogeny. For example, the assertion that (p. 212) "[...] it remains true that marsupial classification since Ride [...] [has] built on an outline initially provided by molecular-systematic data" is a reference to Kirsch's (1977) major study. In that valuable contribution, however, the caenolestids were regarded as the sister group of a holophyletic *Dromiciops*-didelphid clade, and these, together, were depicted as the sister group of the remaining living marsupials. In light of the fact that no subsequent studies built on the contribution of Kirsch (1977), it must be pointed out that their claim overlooks explicit indications by Szalay (1982, 1994) concerning both the nature of microbiotheriid relationships and the independence of caenolestids from the last common didelphid ancestor of all living marsupials.

Similarly, a lack of understanding about the nature of morphological evidence and how it is combined with the fossil record is reflected when Kirsch *et al.* (1997: 242) state that "[...] the difficulty of rooting mammalian trees at the very highest levels obtains for sequence-based studies as well as for those on DNA hybridisation; it is likely to remain a problem for anatomical analyses as well" (spelling as in original). More morphological, geographical, and temporal data are becoming available through paleontological discoveries. The new fossils and analyses of extant species are constantly improving the accuracy of transformational analyses, and hence the understanding of morphoclines on which lineage reconstructions are based. In particular, causally estimated transformational hypotheses that employ judiciously constructed models from living forms can offer increasingly testable and corroborated adaptational hypotheses as the fossil record improves (as we suggest above). Against such growing morphological evidence, using theoretically refined methods, we can test increasingly more specific hypotheses within an actual temporal and biogeographic framework. *In that sense morphological analysis provides what genetic and molecular analysis cannot: a genuine, rather than surrogate, vertical dimension to an expanding data base that encompasses all hard morphology (as well as the inferable ligamentous and muscular anatomy, loading regimes of bones, etc.), together with a model-based understanding of extinct organisms.*

The casual, fundamentally ill-informed, and theoretically vacuous attitude about morphology and fossils is particularly explicit in the comments by Kirsch *et al.* (1997: 246) in the section following a new classification of marsupials down to the tribe level: "While we have made an attempt to integrate fossil taxa responsibly, the relationships of many of these are in dispute, and *our decisions frequently represent merely opinions about opinions*" (italics supplied). This quote also reflects the implicit attitude that morphological data (in all of their four dimensions) are somehow outdated in light of the laboratory advances related to the genetic and molecular data. This is not a unique attitude, one that is always emended in some form or another, namely that the fossils are necessary merely to assign primary ages to higher level taxa (often supraordinal designations) that are lately considered to be accurately determinable from molecular data [42].

POSTCRANIAL EVIDENCE BEARING ON MARSUPIAL PHYLOGENY RECONSTRUCTION

Many attributes of the long bones described here have proven to be revealing adaptations, but with no clearly recognizable heritage beyond the fact that they represent marsupials (Table 13). For example, the articular areas of the distal humerus

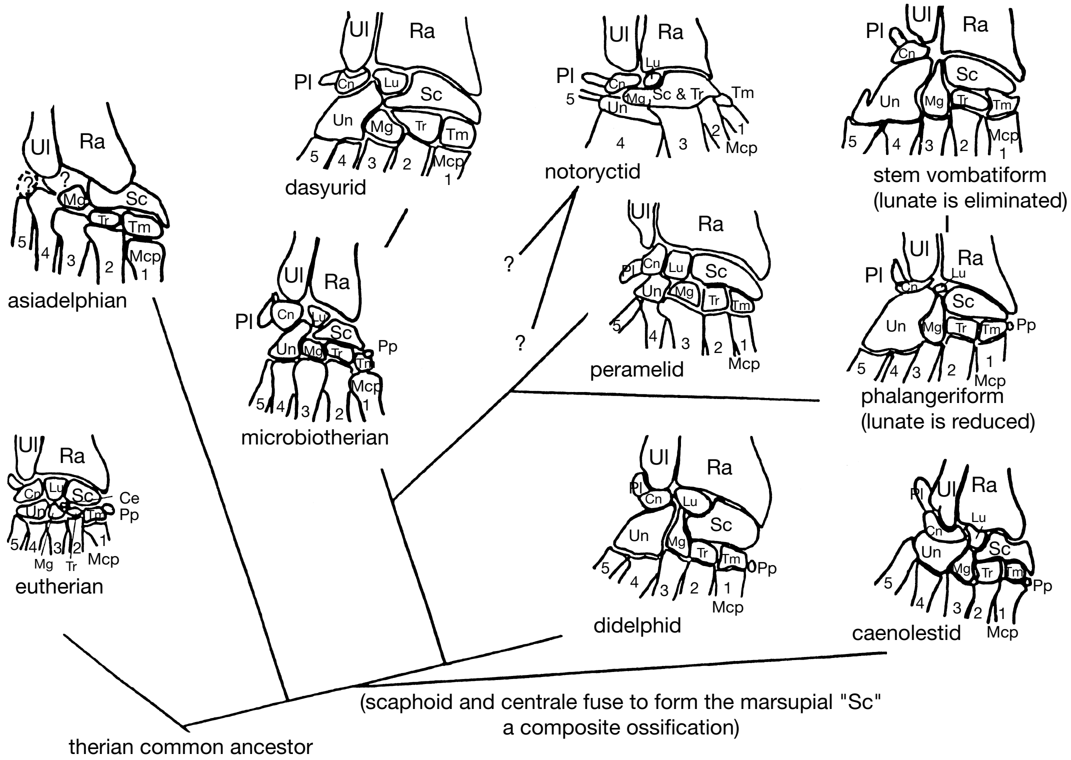


FIG. 69. — The patterns of bones in the carpus, viewed anteriorly, in some representatives of major groups of Metatheria. Lines between the patterns that can be found in the taxa (indicated under them by the taxonomic vernacular) represent approximate (or queried) transformations of these patterns. They do not stand for transformation of taxa from one into the other. Abbreviations: **Cn**, cuneiform ; **Lu**, lunate; **Mcp1-5**, metacarpals; **Mg**, magnum; **Pi**, pisiform; **Ra**, radius; **Sc**, scaphocentrale; **Tm**, trapezium; **Tr**, trapezoid; **Ul**, ulna; **Un**, unciform.

(Fig. 65) reflect some mechanical attributes, but not supraspecific taxonomic properties beyond the species they belong to. The oblate head of the radius of such skeletally known specimens as those of *Pucadelphys*, *Mayulestes*, and a single Itaboraí specimen, on the other hand, suggest a condition more primitive than that present in the Didelphidae. The reason for this is that didelphids, regardless of their locomotor and substrate preferences, have rounded radial heads, even though they are endowed with the subtle adaptive differences noted above.

In spite of all the caveats, several postcranial elements have proved to be particularly useful phylogenetically, largely because it is feasible to assess them functional-adaptively. As noted, that method allows the selection of phylogenetically significant traits in contrast to the adaptively independent, largely contingent, and habitus specific attributes in different taxa. The carpus and tarsus (Figs 69-73) in particular have provided a number of clear synapomorphies (*sensu stricto*), as well as some well-corroborated transformational sequences that strongly support specific associations and transformational relationships of lineages (and the known taxa based on these).

For example, there can be little doubt that certain characters in the tarsus of a terrestrial cursor like *Metachirus* compared to that of *Caluromys* are singularly derived and adaptive, but, at the same time, their similarities reflect their arboreal didelphid heritage. It is equally clear that the attributes of the tarsal joints of the extant caenolestids and a fossil like *Pucadelphys* (Fig. 70) represent the

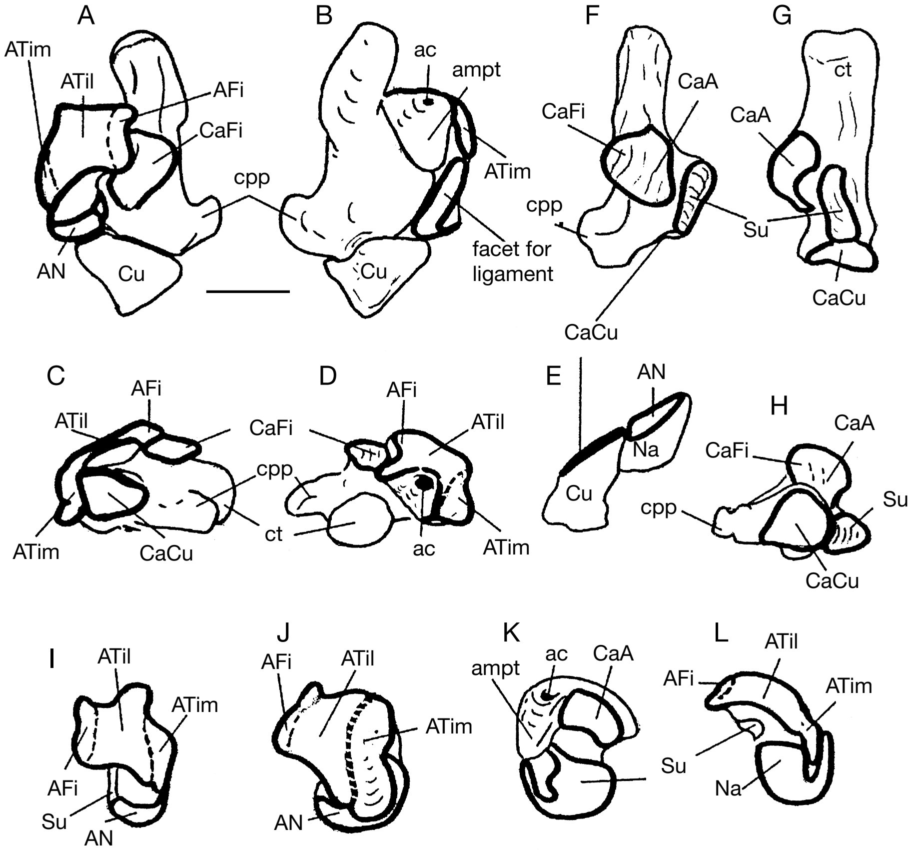


FIG. 70. — The calcaneus, astragalus, navicular, and cuboid of *Pucadelphys andinus*; **A**, **B**, a single left specimen, that has not been separated, of calcaneus, astragalus, and cuboid; **A**, dorsal view; **B**, plantar view; **C**, **D**, single left specimen of a calcaneus and an astragalus; **C**, distal view; **D**, proximal view; **E**, right specimen of a cuboid and navicular in articulation, dorsal view; **F-H**, right calcaneus; **F**, dorsal view; **G**, medial view; **H**, distal view; **I-L**, right astragalus; **I**, dorsal view; **J**, medial view; **K**, plantar view; **L**, distal view. Abbreviations: **ac**, astragalar canal; **AFi**, astragalofibular facet; **ampt**, astragalar medial plantar tuberosity; **AN**, astragalonavicular facet; **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **CaA**, calcaneoastragalar facet; **CaCu**, calcaneocuboid facet; **CaFi**, calcaneofibular facet; **cpp**, calcaneal peroneal process; **ct**, calcaneal tuber; **Cu**, cuboid; **Na**, navicular; **Su**, sustentacular facet. Scale bar: 2 mm.

basal condition from which didelphids were derived. But the ancestral sudameridelphians also exhibit a condition of the ANJ on which *Metachirus* has converged to a minor degree because of its habitus. Therefore the secondary acquisition of at least one aspect of an attribute prevalent in Palaeocene sudameridelphians (e.g., Fig. 70L), such as the dorsally turned astragalonavicular contact (a discrete "character"), in all terrestrial didelphids and the Dasyuridae (a terrestrial radiation at its inception), is significant to point out. As noted below, this is only a partial, but adaptively revealing, similarity that is related to mechanics, and not to a higher level taxon-specific configuration. Such ecologically correlated patterns allow these and other characters that may appear in lineages of Didelphida or Australidelphia to be rejected for phylogenetics because they are habitus-related modifications. In this instance of the tarsus, such a noticeable character is the mere consequence of the obligate mechanics necessary in a terrestrial and more cursorial animal.

While an analytical and narrative evaluation of similarities can be shown to be convergent, other similarities may be persistent ancestral features,

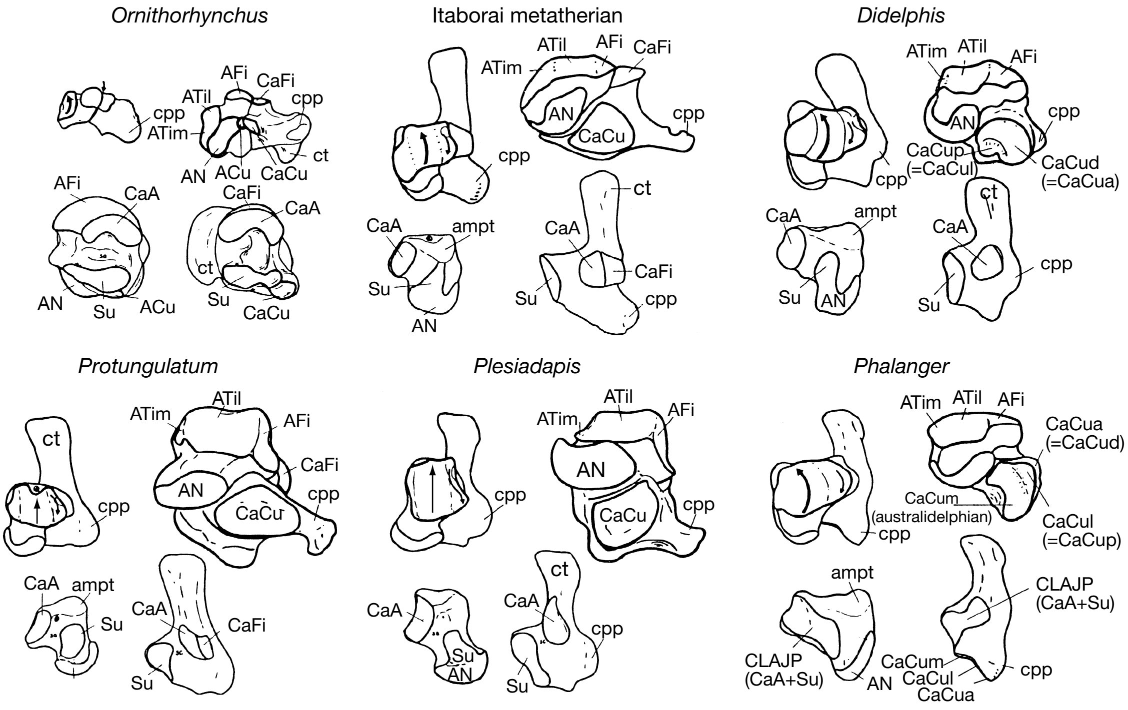


FIG. 71. — Comparisons of several stages of monotreme and therian astragalocalcaneal patterns and articular relationships. For each of the six taxa the dorsal and distal views are shown in articulation above, and the lower ankle joint surfaces for the two left bones are shown below. In the metatherians the movement of the tarsus on the crus has one degree of freedom in rotation and another in translation, whereas in eutherians the stabilized upper ankle joint usually only allows one degree of freedom in rotation. Arrows on the tibial facet of the astragalus show rotational (and translational) freedom in the upper ankle joint, whereas the slimmer arrow on the astragalar fibular facet shows rotation of the calcaneus under the astragalus (i.e. movement in the lower ankle joint). Abbreviations: **AFi**, astragalofibular facet; **ampt**, astragalar medial plantar tuberosity; **AN**, astragalonavicular facet; **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **CaA**, calcaneoastragalar facet; **CaCu**, calcaneocuboid facet; **CaCua**, auxiliary calcaneocuboid facet (australidelphian) **CaCud**, distal calcaneocuboid facet (didelphid); **CaCul**, lateral calcaneocuboid facet (australidelphian) **CaCum**, medial calcaneocuboid facet (australidelphian); **CaCup**, proximal calcaneocuboid facet (didelphid); **CaFi**, calcaneofibular facet; **cpp**, calcaneal peroneal process; **ct**, calcaneal tuber; **Su**, sustentacular facet.

or, clearly derived ones from another condition. Thus, the wide astragalar astragalofibular facet of didelphids (and their descendants) contrasts to that a very narrow facet of the sudameridelphians. The apomorphous wide facet, probably causally correlated with the elimination of a calcaneofibular facet in the didelphid ancestor, is retained in didelphids no matter how varied their habitus may be. These examples illustrate how combination of the fossil record, the total distribution of characters, the temporal values associated with the characters, the functional and ecological assessments of attributes, and the garnering of minor characters into complexes that make adaptive sense result in an understanding of character evolution and stasis. Such analysis is different from parsimony rulings on taxic patterns that consist of unanalyzed character matrices, often of bewildering provenance and numbers. Unless strong stratophenetic information is available, an axiomatized disregard for the understanding of attributes (functionally integrated complexes) makes the ordering and polarization of the characters for phylogenetics arbitrary.

Given these examples and caveats, we consider a couple of attributes below. The following traits, however, are clearly not useful taxonomic

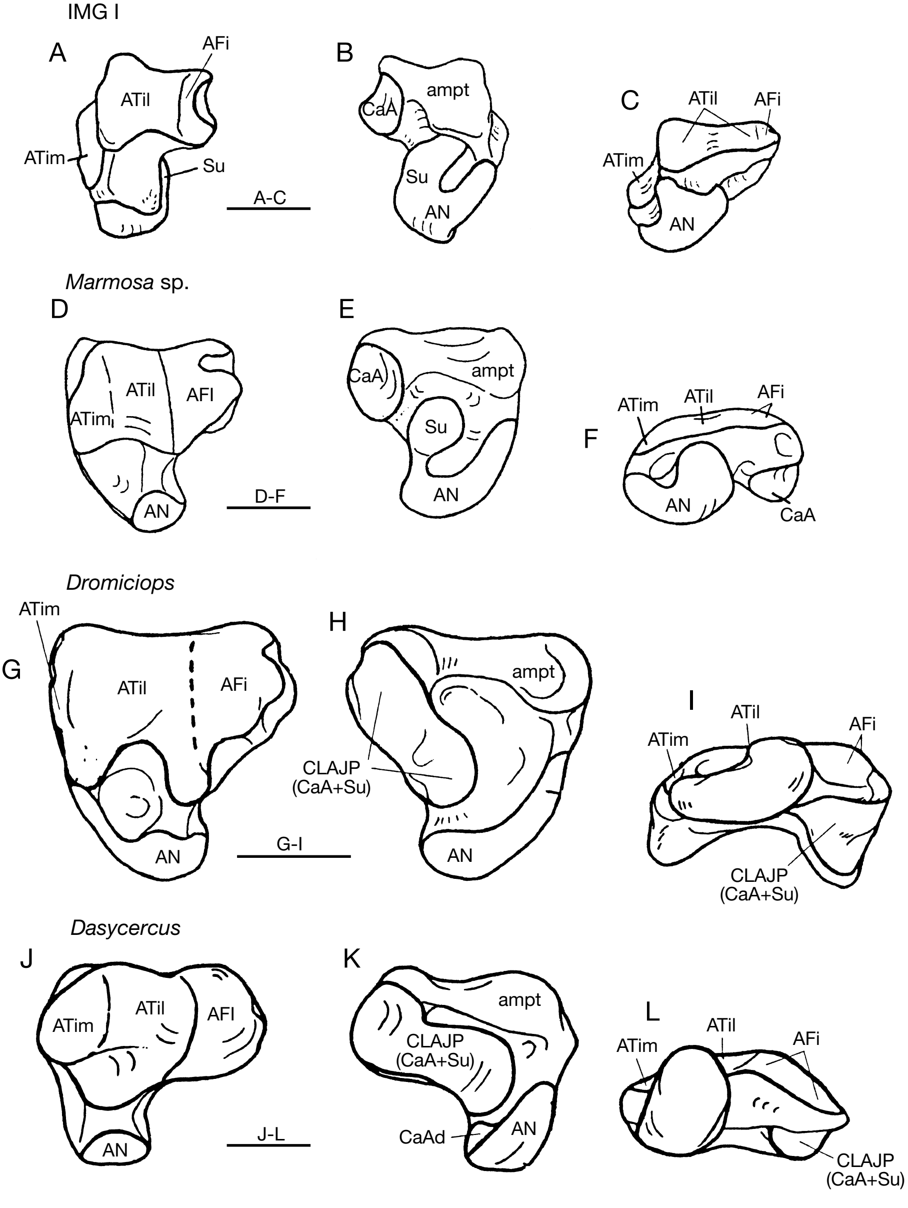


FIG. 72. — Comparison of left astragali and their articular patterns in selected metatherians to illustrate what were probably linear stages of transformation in the upper and lower ankle joints, as well as the astragalonavicular joint; **A-C**, a sudameridelphian (IMG I); **A**, dorsal view; **B**, plantar view; **C**, distal view; **D-F**, a didelphid (*Marmosa*); **D**, dorsal view; **E**, plantar view; **F**, distal view; **G-I**, a microbiothere (*Dromiciops*); **G**, dorsal view; **H**, plantar view; **I**, distal view; **J-L**, a dasyurid (*Dasycercus*); **J**, dorsal view; **K**, plantar view; **L**, distal view. Abbreviations: **AFi**, astragalofibular facet; **ampt**, astragalar medial plantar tuberosity; **AN**, astragalonavicular facet; **ATil**, lateral astragalotibial facet; **ATim**, medial astragalotibial facet; **CaA**, calcaneoastragalar facet; **CaAd**, distal calcaneoastragalar facet; **CLAJP**, continuous lower ankle joint pattern; **Su**, sustentacular facet. Scale bars: 1 mm.

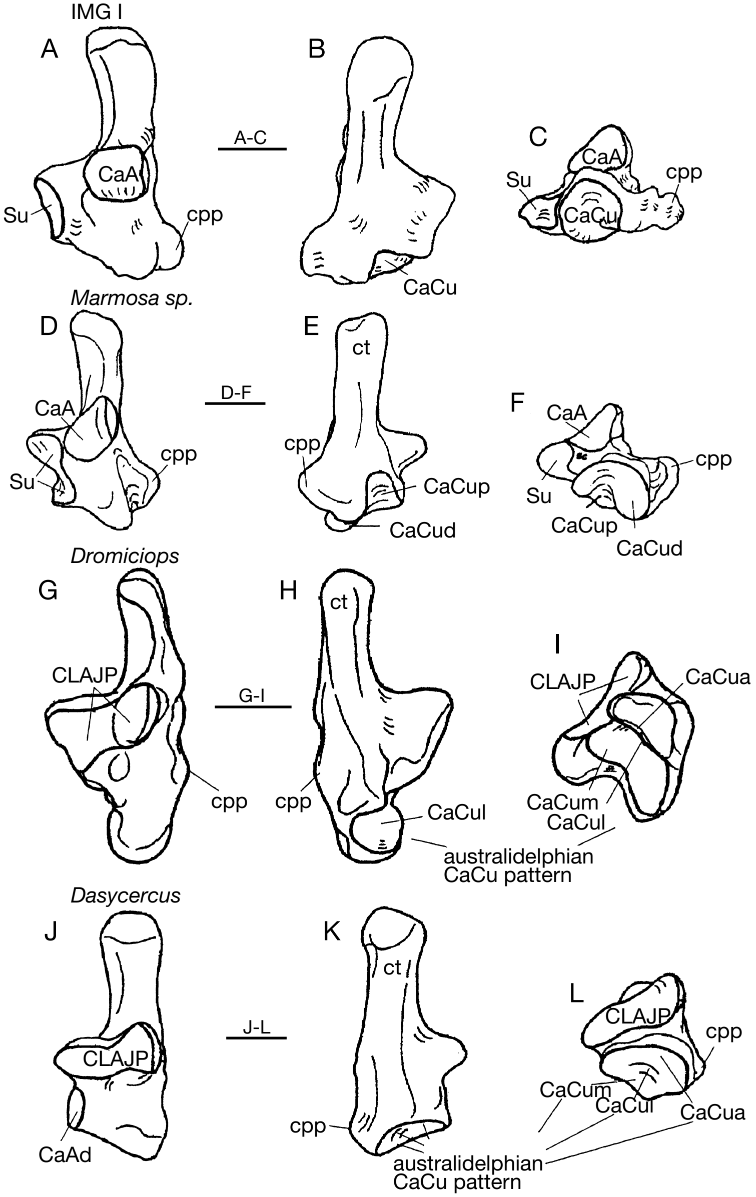


FIG. 73. — Comparison of left calcanea and their articular patterns in selected metatherians to illustrate what were probably linear stages of transformation in the upper and lower ankle joints, as well as the calcaneocuboid joints; **A-C**, a sudameridelphian (IMG I); **A**, dorsal view; **B**, plantar view; **C**, distal view; **D-F**, a didelphid (*Marmosa*); **D**, dorsal view; **E**, plantar view; **F**, distal view; **G-I**, a microbiothere (*Dromiciops*); **G**, dorsal view; **H**, plantar view; **I**, distal view; **J-L**, a dasyurid (*Dasycercus*); **J**, dorsal view; **K**, plantar view; **L**, distal view. Abbreviations: **CaA**, calcaneoastragalar facet; **CaAd**, distal calcaneoastragalar facet; **CaCu**, calcaneocuboid facet; **CaCua**, auxiliary calcaneocuboid facet (australidelphian); **CaCud**, distal calcaneocuboid facet (didelphid); **CaCul**, lateral calcaneocuboid facet (australidelphian); **CaCum**, medial calcaneocuboid facet (australidelphian); **CaCup**, proximal calcaneocuboid facet (didelphid); **CLAJP**, continuous lower ankle joint pattern; **cpp**, calcaneal peroneal process; **ct**, calcaneal tuber; **Su**, sustentacular facet. Scale bars: 1 mm.

properties when trying to assess similarities among taxa that may be loosely called "basal" metatherians: 1) relatively long tibial medial malleolus: a condition related to the need for increased medial bracing of the astragalus in a cursor; 2) orientation of the astragalonavicular facet proximodistally or craniocaudally: a condition necessitated by obligate and rapid flexion and extension at the midtarsal joint. This is related, at least in didelphids and eutherians in general, to mechanical resistance to loading associated with terrestriality during eversion, as noted above.

ON THE PROPOSAL THAT MONOTREMATA IS THE SISTERGROUP OF METATHERIA

Prior to our detailed discussion of some of the issues of metatherian systematics, we note the implications of several published molecular phylogeny-based proposals regarding the relationships of Metatheria to the monotremes. Such a node association implies that either: 1) monotremes and marsupials evolved from a level of organization known to us from the morphology of the inferred stem of living forms, a didelphid-like animal; 2) marsupials evolved their shared therian attributes with Eutheria in the dentition, skull, and skeleton independently, from a more monotreme-like base; or 3) both monotremes and marsupials have diverged from some common stage, hitherto unknown to us morphologically. This is, of course, a very awkward way of putting the phenotypic implications of these recent proposals, none of which are supported by morphological evidence, or any interpretation of this evidence that can be conceived by us. But this is exactly what is implied by the node-based iconography of the phenograms (presented as cladograms) that were proposed, on the bases of statistically manipulated mtDNA hybridization, by Janke *et al.* (1997), and others. If any of these propositions were true, then we would conclude, together with Gould's (1985, 1986) pessimistic comments that morphology and its methods are abject failures (in conjunction with hailing the promises of a panacea of molecular phylogenetics). If they are not, then a variety of "deep" genetic and molecular studies are exceptionally unreliable, as are the parsimony manipulations of inflated and unanalyzed morphological databases.

SUDAMERIDELPHIAN AND DIDELPHIMORPHIAN TAXONOMIC PROPERTIES, AND THE PHYLOGENY OF EXTANT MARSUPIALS

We discuss a number of taxonomic and phylogenetic propositions that were tested against morphological taxonomic properties. Our aim here is to address a number of questions regarding metatherian phylogeny and biogeography that are still puzzling for many. These questions may be grouped as follows:

1) did the Didelphidae derive from either a known or as yet unknown stock of didelphidans, specifically itaboraiforms, and what causality might have driven such an origin?;

2) is the Australidelphia derived from either *sensu stricto* Didelphidae (*fide* Szalay 1994), or some other group of marsupials? Or, should one, axiomatically in order to avoid a paraphyletic Didelphidae, consider the currently constituted family of opossums to be "unnatural" (a proposition based on an assumption regarding the "necessity" of "panholophyly" in taxonomy, a proposition both nonsensical and unacceptable to us)?;

3) which group of australidelphian marsupials is the most recent relative (sistergroup) of Microbiotheria (meaning *Dromiciops* and *Microbiotherium*, but not the various dental morphs attributed to this family)?;

4) what is the degree of relationship between a) Caenolestidae and *Dromiciops*; b) the former and Didelphidae; and c) Caenolestidae and other extant marsupials?;

5) is the Peramelidae the outgroup for all other living marsupials except the Caenolestidae?;

6) how can the morphological evidence outlined here be reconciled with hybridization or sequence data, and are "consensus" approaches justifiable for tree "resolution"?

Origins of Didelphidae

The morphological cohesiveness of the Didelphidae *sensu stricto*, which is not an anomalous dental concept based on metatherian plesiomorphies, and which includes both extant and extinct taxa, has been amply demonstrated elsewhere, so we will not dwell on it. The diagnostic postcranial attributes of this family, derived in contrast to the pervasive fossil evidence of other didelphidans, are the morphological complexes of the foot and hand (Szalay 1982, 1994). To this we may add the lack of a third trochanter of the femur in the protodidelphimorphian compared to its itaboraiform ancestry. The presence of a well-developed third trochanter in the South American basal groups, caenolestids, and of marsupials from Messel suggests this trait to be the primitive metatherian (and therian) condition. In contrast, all didelphids lack this trochanter, regardless of their substrate preference or locomotor propensities.

Unlike the fully habitus-related long bone features of species taxa, other attributes have proven to have remarkable consistency as supraspecific and lineage-specific (rather than closely adaptive) attributes. This clearly does not imply that the appearance of these higher taxon properties was not an adaptive response of the ancestral lineage when that attribute first appeared. The following areas of the tarsus reflect taxon-specific properties, as well as the nature of mechanics. We find such attributes of paramount significance when evaluating the morphology and attendant hypotheses regarding character evolution, lineages, and taxa.

Among these characters are a few that strongly reflect the evolution (and its causes) of the first Didelphidae from its more ancient probable root of itaboraiform sudameridelphians:

1) reduction of the **ampt** in didelphids in contrast to the huge tuberosity in sudameridelphian ancestry. The latter, primitive condition, probably related to the supporting (weight bearing) role of that tubercle in a foot in which astragalar superposition on the calcaneus has not as yet occurred (Szalay 1994);

2) modification of the sustentacular facet on the astragalus in the first didelphid, from the long, expanding, ribbon-like condition of sudameridelphians that extends above the large **ampt** and is continuous with the navicular facet. The didelphid condition is rounded and isolated. It is also in closer proximity to the **CaA** facet in relation to the change in the rotation of the calcaneus on the astragalus in the lower ankle joint;

3) expansion of the **AFi** facet is a direct consequence of increased mediolateral upper ankle joint mobility in didelphid ancestry, and the reduction of the **CaFi** contact. Nevertheless, calcaneofibular contact can disappear in sudameridelphians without an expansion of the **AFi** facet (Figs 72; 73);

4) a decrease in the angle between the **ATim** facet and the lateral tibial contact (**ATil** facet) is probably another consequence of increased mediolateral upper ankle joint mobility. The sudameridelphian condition displays a slab-sided astragalus medially where the medial malleolus restricts upper ankle joint motion mediolaterally;

5) rounding of the lateral and dorsal sides of the head of the astragalus (**AN** facet) in the protodidelphid, and extension of the head of the astragalus medially and horizontally for facilitating inversion. This condition is in contrast to the sudameridelphian one where the lateral and dorsal part of the head is "horned," and the more proximal extent of the **AN** facet is plantar rather than medial;

6) articular relationships of the calcaneus and cuboid are altered in the protodidelphid, where a highly stabilizing tongue-like projection of the cuboid articulates with the calcaneus (**CaCup** facets of the two bones).

Didelphidae and the relationships of Australidelphia

Recent studies by Palma & Spotorno (1997, 1999), based on the sequencing of mitochondrial gene base-pairs (using parsimony, distance and likelihood analyses; 800 bp in 18 genera in Palma & Spotorno 1999), suggest that *Dromiciops* shares affinities with the ancestors of both Didelphidae and the Australasian radiation. These results and analyses are somewhat consistent with the morphological interpretation that the stem lineage of the Australidelphia, originating from an early didelphid ancestry (Szalay 1994), gave rise to the

Microbiotheriidae and other australidelphians. Nevertheless, the results of these sequence analyses cannot as yet address the internal relationships of the Australidelphia, or even of the Ameridelphia as constituted here[43]. The studies of Hershkovitz (1992) on tarsals have been commented on by Szalay (1994). Hershkovitz (1999), in a review of a number of anatomical details in *Dromiciops*, raises no additional points that would in any way negate the structural, functional, or systematic conclusions drawn by Szalay (1994) regarding the whole tarsal complex of *Dromiciops* and other marsupials.

The postcranial evidence combined with the absence of therians in the Late Cretaceous (but probably not in the latest Cretaceous) strongly suggests that both the older Tiupampa and the younger Itaboraí assemblages from the Palaeocene reflect an adaptive radiation of metatherians that began just prior to the appearance of these two faunas, one that came from an ancestry that arrived to the then island continent of South America. We realize that, at the moment, this cannot be more conclusively corroborated, but we also note that there is no evidence that suggests multiple independent marsupial lineages entering that continent. Presence of shared primitive metatherian similarities with dental morphs from the Cretaceous of North America cannot meaningfully contradict this. All South American metatherians are considered to be derivatives of a single sudameridelphian stem. The ordinal concept Didelphida (see discussion in Szalay 1994) includes: a) the (probably paraphyletic) Archimetatheria of Holarctic distribution; b) Sudameridelphia (including the still phylogenetically poorly understood Itaboraiformes, Polydolopimorphia, and Sparassodonta); c) the holophyletic Glirimetatheria; and d) paraphyletic Didelphimorphia. The latter two taxa are likely derivatives of one of the early clusters of the Itaboraiformes[44].

The stem australidelphian condition of the tarsus represents a combination of retention, as well as an incremental modification, of the didelphid pattern. As we said before, this departure undoubtedly has its roots in an adaptive shift, and this shift has left fairly indelible marks on subsequent modifications.

The origin of the australidelphian stem (for an understanding of which, at least postcranially, one must rely largely on *Dromiciops*) from a morphologically unquestionable didelphid, and not some itaboraiform, has been discussed in detail, but we further discuss aspects of the evidence here. While the origin of the australidelphian lineage has not been contested with any phyletically meaningful evidence, the "cladistic" (phenetic) scheme offered by Kirsch *et al.* (1997) has *Dromiciops* as the sistergroup of the entire Diprotodontia. There is no corroborating evidence for this from any known aspects of either soft anatomy or skeletal morphology, and the tarsal similarities between the microbiotheriids and most diprotodontians are, to us, obviously primitive australidelphian features that permit no sistergroup association of any kind. Szalay (1994) and Szalay & Trofimov (1996) pointed out that the adult carpal patterns of *Dromiciops* and dasyuromorphians share a separation of the lunate and magnum by an ulnar projection of the scaphocentrale (the fused scaphoid and centrale of all living metatherians, and hence probably of the Sudameridelphia, if not of more inclusive groupings). This condition is in contrast to the syndactylan condition where this process is absent.

Given the caveat that no detailed comparative analysis exists as yet on the developmental and functional-adaptive aspects of the carpus in metatherians, the known carpal patterns (Fig. 69), together with similarities in incisor morphology, were the bases of the proposed Gondwanadelphia Szalay, 1993. The derived morphology of dasyuromorph tarsal patterns is not an impediment to this association with *Dromiciops* because the former pattern is clearly (structurally) derivable from the putative tarsal pattern of the stem Australidelphia. Nevertheless, as we show in Fig. 74, the Gondwanadelphia is only a weakly corroborated concept.

Aspects of the tarsus that reflect the departure of the stem Australidelphia from its more ancient didelphid (*sensu stricto*) roots are as follows:

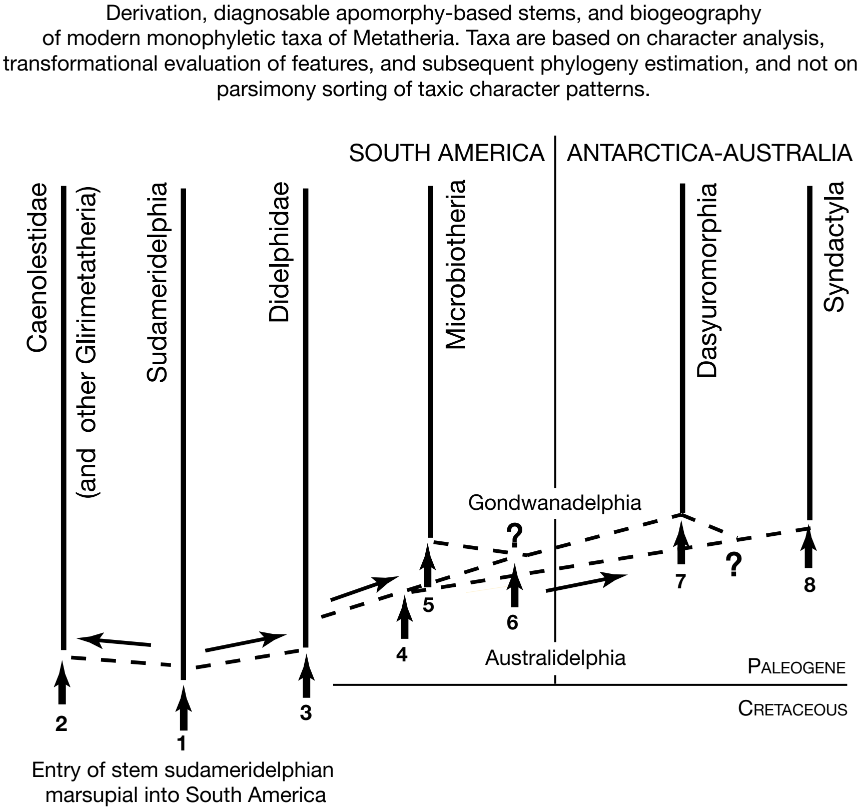


FIG. 74. — Simplified phylogeny of the taxa (thick vertical bars) and the hypothesized lineages leading to them (dashed lines). Numbered thick vertical arrows show points on the phylogeny where the stem of the various groups can be identified by diagnostic traits with respect to their ancestry. Only the entry of the stem of Sudameridelphia (**1**) is problematic in this regard because archaic metatherians outside of South America are less well known. Point **4** stands for the last common ancestor of Australidelphia, derivable from a *bona fide* didelphid (see text). Point **6** is the putative ancestry of the Gondwanadelphia, and as such it is queried. Thinner, and close to horizontal, arrows indicate both direction of phyletic derivations, as well as the direction of geographical dispersal. Note derivation and dispersal of australidelphians from a South American didelphid stem to Antarctica-Australia.

1) retention of the reduced **ampt** that is present in didelphids;
2) modification of the sustentacular facet on the astragalus in the protoaustralidelphian from the already reduced didelphid condition, that is rounded and isolated, through a merging with the **CaA** facet. This change (into the **CLAJP**) is the culmination of a functional modification that has come to characterize didelphids;
3) retention of the expanded **AFi** facet from the didelphid ancestry (Figs 72; 73);
4) retention of the increased alignment of the **ATim** facet with the lateral tibial contact (**ATil** facet) to assure mediolateral upper ankle joint mobility;
5) retention of the rounded lateral and dorsal side of the head of the astragalus, the **AN** facet, along with the medially and horizontally extended head of the astragalus;
6) lack of the **CaFi** facet, as in didelphid ancestry;
7) alteration of the articular relationship of the calcaneus and cuboid in the protoaustralidelphian, in a manner that reflects its transformation from the didelphid pattern. The change is probably a consequence of the extreme grasping ability that developed in the stem australidelphian lineage. As a consequence of grasping related change, as well as the attendant further improvement of hindfoot reversal ability, major modifications

occurred in the calcaneocuboid joint. The **CCJ** is particularly important in that regard because not only does the movement of the foot distal to the proximal tarsals depend on the position of the calcaneus in that joint (as well as the cuboid; Szalay 1994: chapter 4), but so does the resistance of loads in the foot in a particular dynamic grasp of a reversed hindfoot [45]. A new surface, the **CaCum** facet, develops, sharply angled against the **CaCul** facet (the didelphid **CaCup** facet), and the remaining narrow articulating surface, the **CaCua** facet (the didelphid **CaCud** facet), comes to supply the stable auxiliary surface in that mobile joint (Fig. 73; Szalay 1994: fig. 8.18 and relevant discussions);

8) modification of the basal articulation of the first metatarsal with the entocuneiform (**EMT1J**) adds additional mobility to the australidelphian grasp via its sellar modification of the didelphid hinge-like joint (Szalay & Dagosto 1988; Szalay 1994: fig. 8.17 and relevant discussions).

Without repeating the analysis of Szalay (1994), we note that there is no morphological evidence to support a microbiothere-diprotodontian clade in exclusion of the Peramelidae. The Syndactyla, as detailed below, appears to be a morphologically highly corroborated group based on cranial, dental, and postcranial synapomorphies and transformational assessments.

Who are the closest living relatives of Caenolestidae?

It appears that, beyond their cranial and dental autapomorphies, all postcranial attributes of these terrestrial animals are both deep ancestral adaptations to their cursorial and bounding locomotion, and retentions, with minor modifications, of attributes from a remote itaboraiform ancestry. Their carpal pattern is identical to that of the didelphids, which simply means that it is primitive on some unspecified sudameridelphian or even archimetatherian level. There is no skeletal evidence that would lend support to the notion that caenolestids are any more recently related to one extant group than to another. They are certainly not related to any member of what is considered to be a holophyletic Australidelphia, and they are not the sistergroup of the stem of that taxon either. Features of soft anatomy and sperm pairing may represent ancient metatherian attributes shared between didelphids and caenolestids, the relative recency of which cannot be judged.

Is the Peramelidae the sister to all other extant groups of Metatheria (and their extinct phyletic relatives) except the Caenolestidae?

One of the most jarring internal contradictions by Kirsch *et al.* (1997) regarding the phylogeny of marsupials is the treatment of the bandicoots, particularly when their proposed morphological evidence is considered. The sutured tree and discussions by Kirsch *et al.* (1997) show and advocate the peramelids to be the sister group of all other living metatherian taxa except the Caenolestidae. Yet, on p. 253 it is stated that: "We now agree with Szalay that the divided ankle-joint of kangaroos and perameloids are indeed reversions to (or more properly mimics of, because functionally different to) the relatively primitive (American) condition, because *Dromiciops* (with its undivided joint) clearly lies phyletically well within the Australian radiation and is sister to the tarsally polymorphic diprotodontians". First of all, if perameloids "reverted" (in fact, they never really did, except in a vaguely semantic sense that generally dominates reference to morphology in that paper), then they clearly shared the whole complex of traits (and not only the confluent facets) with other australidelphians, in exclusion of the Didelphidae. Secondly, all of the shared attributes of *Dromiciops* with diprotodontians are australidelphian plesiomorphies, which makes all of the statements of Kirsch *et al.* (1997) about the skeletal attributes of this taxon systematically imprecise and misleading.

The closing remark on perameloids by Kirsch *et al.* (1997: 255), stating that these "may well not be" Australasian in their affinities, is puzzling, particularly since they stated on p. 253 (quoted above) that they now agree with Szalay (while citing their "contradictory morphological evidence"). Equally revealing of the DNA-hybridization effort is their conclusion (p. 257) that: "A sister group relation between didelphimorphs and Australasian marsupials, so often stated by previous workers [...], although while implicitly or explicitly including perameloids among the latter metatherians, in fact seems to us to be unsupported by DNA-hybridisation data" (spelling as in original). Equally significant is their statement (p. 257; 258) regarding their strong biogeographic bias (note the use of the word myth) that: "Moreover, such a (mainly) American cohort would perpetuate the myth of a geographically based dichotomy within the Gondwanan marsupials that we are anxious to deconstruct". The result is a rationalized disregard for corroborated hypotheses, in favor of a tangled web of sutured distance data and its morphing into cladistic "trees".

There is not a single skeletal attribute that would support the hypothesis put forward by Kirsch *et al.* (1997: fig. 13). In fact, the most abundant fossil evidence, teeth, corroborates the transformation of the metaconule into the diprotodontian "hypocone" (*contra* Sánchez-Villagra & Kay 1996). The condition of the squamosal in the cranial base in relation to the alisphenoid is a strong character: peramelids show the beginnings of an intracranial extension of the squamosal, which is well-developed in diprotodontians (Murray *et al.* 1987). Similarly the contact of the lunate and magnum with a scaphocentrale that lacks an ulnar projection, the syndactylous foot, and the unique transformation of the tarsus from an australidelphian base corroborates this relationship (Szalay 1994). All of these point, *unequivocally*, to the validity of the Syndactyla. It seems to us that the mtDNA hybridization analysis of Kirsch *et al.* (1997) should be reexamined.

While the association of the Notoryctidae with the Peramelidae is tenuous, it is a fact that these fossorial forms are the only australidephians that have an ossified patella. The presence of a well-developed, eutherian-like patella in the Caenolestidae is not relevant here because this sesamoid is within a totally unique skeletal pattern that shows no derived resemblance to bandicoots. All of these metatherian terrestrial cursors and putative derivatives (*Notoryctes* is obviously not a cursor) probably developed this sesamoid as a means of lever arm improvement of the quadriceps complex that is useful in obligate terrestriality. So did the ancestral placentalian from a primitive therian, metatherian-like, condition. While a patella in the cursorial protoperamelid can be accounted for mechanically, its presence in the marsupial moles may represent a heritage feature from an ancestry that may have been derived from a bandicoot (Szalay 1994). While macropodids are cursors-jumpers *par excellence* and have stiff but flexible fibrous tissue in the tendon of the quadriceps femoris, they have no verified ossification (i.e. no patella) [46]. In addition, Gilkeson & Lester (1989), in their comprehensive survey of variation in the enamel patterns of Australian marsupials, identified a particularly unique prism-packing pattern shared between notoryctids and peramelids.

ON FLAWED BIOGEOGRAPHIC INTERPRETATIONS OF PATTERNS OF TAXIC DISTRIBUTIONS

Any discussion of biogeography needs, ideally, an agreed-upon level of understanding of the history of lineages, and not the node-based concepts of a taxogram. The latter (on meaningful theoretical grounds) should be a derivative of the best estimate of phylogeny. Nevertheless, we may ask: of the various historical-narrative explanations which we consider to be probable hypotheses for the biogeographic history of lineages of marsupials, which are the most probable? This question assumes that there is some agreement among those holding contending views that in addition to Recent distribution patterns, taxonomic properties and paleontological provenance are the proper databases against which these hypotheses should be tested. Such questions fundamentally rest on phylogenetic history and the fossil record, as well as on paleogeographic advances.

The major contention regarding the a biogeography of marsupials comes from Kirsch *et al.* (1997) and Springer *et al.* (1998). They suggested that *Dromiciops*, based either on its alleged sistergroup relationship with diprotodontians (Kirsch *et al.* 1997; Burk *et al.* 1999), or on its taxogram-nested inclusion within Australidelphia (Springer *et al.* 1998), represents a reversed migration into South America from Australia via Antarctica (for a prior review of marsupial biogeography see Szalay 1994; Szalay & Trofimov 1996).

First we briefly examine some of the arguments by Kirsch *et al.* (1997), aside from their mtDNA-based phylogeny, for such an assertion. In a reference to Ride (1993), Kirsch *et al.* (1997: 261) cite that author's "[...] demonstration that diprotodontian (specifically kangaroo) molars can be derived directly from those of microbiotheres". This evocation by Kirsch *et al.* (1997) of what we consider to be an *exceptionally uncorroborated* proposal of a morphological transformation (as some sort of evidence) is a good example of how they make use of morphology in their paper. Such references to skeletal morphology are profuse in Kirsch *et al.* (1997), and numerous fossil taxa are regularly shuffled from one postulated hypothesis to the other. These ventures into morphology are meant to imply that some sort of in-depth analysis has been performed, but without any evidence presented for such analysis. We reluctantly note that much of their invocation of skeletal evidence, and the various interpretations of it (which they use to support their mtDNA-based hypotheses), are not in any way critically understood by them. The use and misuse of skeletal evidence to bolster their views, therefore, is unfortunate. We add that such a poor level of understanding of the skeletal morphology of extant forms renders the fossil record all but unavailable for all intents and purposes.

What is not cited, or rather, what is ignored by Kirsch *et al.* (1997), regarding skeletal or any other morphological evidence, is the hitherto well-established *lack* of transformational continuity, or well tested synapomorphies, between *Dromiciops* and any of the diprotodontians (shared on the level of the latter taxon). Their shared similarities are the well-established australidelphian plesiomorphies. So the properties of the australidelphian tarsus mentioned above were regarded, rather than interpreted in any analytical sense, as a synapomorphy of the Diprotodontia by Kirsch *et al.* Consequently, we consider all of their assertions about the Australasian geographical origin of the Microbiotheria to be unsubstantiated.

Springer *et al.* (1998), using mitochondrial and nuclear genes in their recent analysis rejected, as Kirsch *et al.* (1997) did, the allocation of the peramelids to the Australidelphia, but they were equivocal on the exact relationships of *Dromiciops* within the Australasian complex. As in Kirsch *et al.* (1997), they sidelined or misunderstood the skeletal evidence, and this became a cornerstone of some of the more sweeping phylogenetic and biogeographic conclusions of their paper. In spite of their reluctance to accept the special ties of microbiotheriids to the Diprotodontia, their biogeographic conclusions were necessitated by a particular taxonomic logic they used. Their conclusions reflect node-based taxic propositions (the units of the taxograms they generated), as opposed to morphologically corroborated narrative accounts of evolving lineages with the attendant consequences. Their statement regarding possible lineage choreography (p. 2385; 2386) is flawed, we maintain, in that they claim that: "[n]esting of [*Dromiciops*] inside Australidelphia implies that the dispersal of a single marsupial ancestor into Australasia (with subsequent cladogenesis) can only account for the origin and distribution of australidelphians if the microbiothere lineage back-migrated to South America [...]. This scenario requires the occurrence of microbiotheres (or at least microbiothere ancestors) in Australia and Antarctica, with subsequent extinctions on both continents".

It certainly does not imply that. To begin with, the *nomen* Australidelphia does not imply ancestry outside of South America. But such a conclusion is symptomatic of the frequent exegesis of node-based taxograms, a practice of pure cladistics in biogeographic estimation (e.g., Nelson & Platnick 1984), as opposed to phylogenetic reasoning. The conclusions of Springer *et al.* (1998) are an example of how an inability to accept and accommodate both phyletic and cladistic components of evolutionary change often results in explanations that are flawed axiomatic translations of a taxogram. Regarding *Dromiciops* and the Australidelphia, there are two almost equally probable hypotheses that require no back-migration (and we obviously reject the notion that microbiotheriids are diprotodontian):

1) the endemic South American australidelphian common ancestor probably gave rise to a lineage leading to the common ancestry of Gondwanadelphia. Of that group, *Dromiciops* remained in South America and the stem of dasyuromorphians went over to more southern and eastern realms. This set of events would certainly have microbiotheriids nested within the Australidelphia. An earlier branch of this (South American) australidelphian ancestry, prior to the split of Gondwanadelphia, gave rise to another offshoot that left South America and gave rise to the remaining Australidelphia (Syndactyla);

2) if the microbiotheres are the sisters of all other Australasian metatherians and the Gondwanadelphia is not a clade (see our queried hypothesis on Fig. 74), then another offshoot of the South American australidelphian stem (the sister lineage of the one that would have given rise to microbiotheres only) simply entered the antipodean realm and split into the radiation we know from the fossil and extant faunas.

In either case, it is not probable that *Dromiciops* represents a back-migration. All phyletically interpreted (and not merely phenetically appraised) morphological attributes of the osteology show that it is highly unlikely that *Dromiciops* is a diprotodontian. Its special tarsal similarities to some of the small phalangers, as emphatically discussed by Szalay (1994), are primitive retentions, a mosaic pattern in small arborealists stemming from the same australidelphian source. And these traits are the solid and complex apomorphies evolved in the last common (South American) ancestor of Australidelphia. So we maintain that there is really no phylogenetic justification for the syllogisms and biogeographic scenarios advocated by Woodburne & Case (1996), Kirsch *et al.* (1997), or Springer *et al.* (1998) regarding the Australidelphia.

Evolutionary theory demands that one should use a mode of thinking essential to meaningful phylogenetic estimation, one that involves evolving lineages. Real phylogenetic reconstruction is founded on phyletics, which is based on a combination of transformational analysis coupled with cladistic analysis. It should not be based on an atemporal, cladistics-dictated, linear logic that invariably resorts to a two dimensional shuffling of taxic concepts, the node-based taxa. Biogeographic historical-narrative explanations need a stem-based mindset in the construction of higher taxa, in addition to the necessary awareness of the proper geological settings and the meaningful biological changes. The practice we advocate here is in contradistinction to the dichotomous dictates of cladistic reasoning, which is bereft of phyletics.

GENERAL CONCLUSIONS AND SUMMARY

As a corollary of our analysis of the marsupial postcranials from Itaboraí we have examined a number theoretical issues that are highly relevant to adaptational and phylogenetic analysis (Fig. 1). We have presented an outline of what we consider to be appropriate modeling methods for conducting analyses of fossils. In this process, we highlighted ecomorphological aspects of several living species that represented our models. Their ecologically correlated, and functionally appraised attributes formed the framework within which we described and interpreted the fossils. The use of modern Darwinian theory-derived methods were critical to our empirical evaluations. We briefly reiterate here the following theoretical points and conclusions regarding Itaboraí taxa, marsupials relationships and their taxonomic expression, and the biogeography of the Metatheria:

1) what phylogeny (but not classification) is has bearing on how one should try to recover it. Descent with ancestrally constrained (but also facilitated) adaptive and other modifications, largely through natural and sexual selection, contains, conceptually, a host of post-Darwinian advances in evolutionary biology that relate to a fundamentally Darwinian view of the evolutionary

process. This complex bundle of precepts is both the theoretical foundation of a Darwinian phylogenetic analysis, as well as the basis for any comprehensive theory of function (in a broad sense) and structure. Meaningful functional analysis-(in a broad sense) and phylogenetics-oriented systematic biology should focus on the study of the attributes of taxa (results of selection and other factors) and the acquisition and diversification of these attributes in lineages through phyletic processes and cladistic branching;

2) fundamentally structuralist approaches consider the goals of adaptational and other evolutionary analysis unattainable not only for fossils but for extant organisms as well. Yet adaptations or sexual selection-related paraphernalia in extinct species are often better understood than their phylogeny. Furthermore, a strictly functional and adaptational (ecologically utilitarian) assessment of traits in both extant and extinct organisms is necessary (whenever possible) in order to reliably establish polarities of homologous features. Such practice enables students of phylogeny to cull convergent attributes from a body of characteristic features. This in turn allows assembly of those taxonomic properties against which lineage and taxon phylogeny hypotheses may be tested;

3) an evolutionary explanation should embody both the causal and historically mediated components of a particular transformation (an evolutionary becoming). Its macrotaxonomic expression is constrained by heuristics which are not directly relevant to the theory and methods of phylogenetics. A sharp theoretical distinction between "functional" and "evolutionary" explanations should be replaced by less dichotomous and less hierarchic, and far more "temporally-looped" and interrelated, concepts regarding the relationship between the evolution of function and biorole of features in a lineage. Functional analysis (broad sense, Szalay 2000) and the biostratigraphic record are the valid bases of transformational analysis of organismal attributes in phylogenetics. The results of transformational analyses of features and the subsequent understanding of the relationships of lineages, independent of parsimony taxograms, are prerequisites for a meaningfully tested taxon phylogeny. Both adaptational and phylogenetic analyses are inferential about specific events in the past. Pairing the "causal role function" approach of Lauder and co-authors with parsimony cladistics, a structuralist perspective labeled the "new adaptationism", does not advance the cause of phylogenetic reconstruction;

4) an animal's range of positional (or feeding, etc.) behaviors is a direct consequence of its form-function complexes. But even a rather full understanding of an organism's functional attributes falls short of an adequate assessment of its specific adaptedness in its environment. While exact details of bioroles, possibly knowable in living forms, cannot be hoped for in fossils, it is unwarranted to state that "adaptations cannot be understood in fossils". Most scientific understanding is limited to some degree, most particularly that which deals with the past. A reasonably well-tested phylogenetic history cannot ever be known with a degree of accuracy similar to those sciences where deductive or experimental approaches predominate. Similarly to phylogenetic inference, assessment of adaptations in both extant and fossil taxa and lineages has its limits;

5) in spite of the noted limits we see no reason to reject either specific historical narrative explanations, their rigorous tests dealing with adaptations, or phylogenetic estimates of character transformations based on the fossil record. These activities are the core of comparative biology and macroevolutionary science, and the testing of phylogenetic hypotheses of lineages and taxa fundamentally relies on them (Fig. 1). Organisms are adapted ("fit" in a Darwinian sense), and an understanding of selection-produced attributes (mechanical adaptations or dimorphisms) can have a significant influence on choosing features against which phylogenetic estimates may be tested. Because of this we assume that an adaptational (i.e. ecomorphological), study of morphology, based on functional understanding, is essential in any estimation of descent with modification. We maintain that modeling based on attributes of selected extant species is a cornerstone of this activity;

6) node-based taxa, bereft of specific taxic derivation, are the results of purely cladistic analysis-generated taxograms, and they do not adequately reflect the lineage-based reality of phylogenetics. Axiomatized attempts to mirror the history of organisms as node-based holophyla without paraphyla is an illusory practice. It is contradicted by the continuity of all lineages in the evolutionary process. Taxograms, therefore, are not useful for the construction of tested biogeographic hypotheses. Description, analysis concordant with evolutionary theory, and historical narratives (tested against objective and interpreted evidence) are the valid probability-based foundations of both phylogenetic and biogeographic reconstruction;
7) the analysis of the Itaboraí postcranials has resulted in a number of well-tested explanations of many of the fossil samples. Both qualitative and quantitative analysis of the individual long bones suggests that some were clearly restricted either to an arboreal or terrestrial habitus. Many of the fossils, however, display ambiguous signals regarding the locomotor adaptations of the species they represent. A recurring pattern on the plots for many of the fossils suggests that the lineages of the Palaeocene marsupial radiation in South America, while perhaps reflecting a fundamentally arboreal heritage, were not as accomplished in their arboreal adaptations as the last common ancestor (and most of its descendants) of the Didelphidae;
8) we have also associated the postcranials of at least one skeletally unique type of small marsupial (IMG II, Szalay 1994) with an interim designation of "hanger-glider," a hypothesis that requires more rigorous testing (in preparation);
9) in addition to the phylogenetic significance of the tarsal and crural transformation series described in Szalay (1994) for marsupials, the study of the appendicular skeleton of extant and fossil metatherians yielded one unequivocally useful trait. As in extant caenolestids, the known fossil marsupials of South America (with the significant exception of didelphids and microbiotheres) have a well-developed third trochanter on the femur, independent of either arboreal or terrestrial adaptations. The same was true of the last common ancestor of the stem lineages of Cenozoic eutherian orders. This apparently primitive therian attribute, while present in the Itaboraí femora, was lost in the ancestor of Didelphidae, and is also absent in the didelphid-derived Australidelphia. While we do not doubt that this loss was adaptive in the stem Didelphidae (related to its probably obligate arboreality), its non-recurrence in highly terrestrial forms of marsupials represents another phylogenetically significant signal for the origin of the Australidelphia from a didelphid;
10) the more recent proposals of marsupial phylogeny and biogeography of Kirsch *et al.* (1997) and Springer *et al.* (1998), based on molecular analyses, were examined. We reject the inclusion of the microbiotheres within the Diprotodontia, and their suggested phylogenetic position for the Peramelidae and Caenolestidae. Bandicoots are part of the holophyletic clade Syndactyla. We also reject the proposed biogeographic hypothesis that would have the microbiotherians originate in Australasia and return to South America (Fig. 74).

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REFERENCES

Amundson R. 1996. — Historical development of the concept of adaptation, *in* Rose M. R. & Lauder G. V. (eds), *Adaptation*. Academic Press, San Diego: 11-53.

Amundson R. & Lauder G. V. 1994. — Function without purpose: the use of causal role function in evolutionary biology. *Biology and Philosophy* 9: 443-469.

Anthony M. R. L. & Kay R. F. 1993. — Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. *American Journal of Science* 293 (A): 356-382.

Argot C. 2001. — Functional anatomy of the forelimb in the Didelphidae and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology* 247: 51-79.

Atramentowicz M. 1982. — Influence du milieu sur l'activité locomotrice et la reproduction de *Caluromys philander* (L.). *Revue d'Écologie (la Terre et la Vie)* 36: 373-395.

Atramentowicz M. 1988. — La frugivorie opportuniste de trois Marsupiaux Didelphidés de Guyane. *Revue d'Écologie (la Terre et la Vie)* 43 (1): 47-57.

Benton M. J. 1987. — Progress and competition in macroevolution. *Biological Reviews* 62: 305-338.

Bergqvist L. P. 1996. — *Reassociação do pós-crânio às espécies de ungulados da bacia de S. J. de Itaboraí (Paleoceno), estado do Rio de Janeiro, e filogenia dos "Condylarthra" e ungulados Sul-Americanos com base no pós-crânio*. Ph.D., Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, 407 p.

Bertram J. E. A. & Biewener A. A. 1988. — Bone curvature: sacrificing strength for load predictability? *Journal of Theoretical Biology* 131: 75-92.

Biewener A. A. 1989. — Scaling body support in mammals: limb posture and muscle mechanics. *Science* 245: 44-48.

Biewener A. A. 1992. — *Biomechanics – Structures and Systems. A Practical Approach.* Oxford University Press, Oxford, 290 p.

Bock W. J. 1977. — Adaptation and the comparative method, *in* Hecht M. K., Goody P. C. & Hecht B. M. (eds), *Major Patterns in Vertebrate Evolution.* Plenum Press, New York: 57-82.

Bock W. J. 1979. — The synthetic explanation of macroevolutionary change – a reductionist approach. *Bulletin of the Carnegie Museum of Natural History* 13: 20-69.

Bock W. J. 1981. — Functional-adaptive analysis in evolutionary classification. *American Zoologist* 21: 5-20.

Bock W. J. 1988. — The nature of explanations in morphology. *American Zoologist* 28: 205-215.

Bock W. J. 1991. — Levels of complexity and organismic organization, *in* Lanzavecchia G. & Valvassori R. (eds), *Form and Function in Zoology.* Mucchi, Modena: 181-212.

Bock W. J. 1993. — Selection and fitness: definitions and uses: 1859 and now. *Proceedings of the Zoological Society,* Calcutta, Haldane Commemorative Volume: 7-26.

Bock W. J. 1999. — Functional and evolutionary explanations in morphology. *Netherlands Journal of Zoology* 49: 45-65.

Bock W. J. & von Wahlert G. 1965. — Adaptation and the form-function complex. *Evolution* 19: 269-299.

Bromham L., Phillips M. J. & Penny D. 1999. — Growing up with dinosaurs: molecular dates and the mammalian radiation. *Trends in Ecology and Evolution* 14: 113-118.

Bryant H. N. & Seymour K. L. 1990. — Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology* 206: 109-117.

Burk A., Westerman M., Kao D. J., Kavanagh J. R. & Springer M. S. 1999. — An analysis of marsupial interordinal relationships based on 12S rRNA, tRNA valine, 16SrRNA, and cytochrome *b* sequences. *Journal of Mammalian Evolution* 6: 317-334.

CHARLES-DOMINIQUE P. 1983. — Ecology and social adaptations in didelphid marsupials: comparison with eutherians of similar ecology. *The American Society of Mammalogists Special Publication* 7: 395-422.

CHARLES-DOMINIQUE P., ATRAMENTOWICZ M., CHARLES-DOMINIQUE M., GERARD H., HLADIK A., HLADIK C. M. & PREVOST M. F. 1981. — Les mammifères arboricoles frugivores nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. *Revue d'Écologie (la Terre et la Vie)* 35: 341-435.

CIFELLI R. L. 1990a. — Cretaceous mammals of Southern Utah. I: Marsupials from the Kaiparowits Formation (Judithian). *Journal of Vertebrate Paleontology* 10: 295-319.

CIFELLI R. L. 1990b. — Cretaceous mammals of Southern Utah. II: Marsupials and marsupial-like mammals from the Wahweap Formation (Early Campanian). *Journal of Vertebrate Paleontology* 10: 320-331.

CIFELLI R. L. 1990c. — Cretaceous mammals of Southern Utah. III: Therian mammals from the Turonian (Early Late Cretaceous). *Journal of Vertebrate Paleontology* 10: 332-345.

CIFELLI R. L. 1990d. — Cretaceous mammals of Southern Utah. IV: Eutherian mammals from the Wahweap (Aquilan) and Kaiparowits (Judithian) Formations. *Journal of Vertebrate Paleontology* 10: 346-360.

CIFELLI R. L. 1990e. — A primitive higher mammal from the Late Cretaceous of Southern Utah. *Journal of Mammalogy* 71: 343-350.

CIFELLI R. L. 1993a. — Early Cretaceous mammal from North America and the evolution of marsupial dental characters. *Proceedings of the National Academy of Sciences* 90: 9413-9416.

CIFELLI R. L. 1993b. — Theria of metatherian-eutherian grade and the origin of marsupials, *in* SZALAY F. S., NOVACEK M. J. & MCKENNA M. C. (eds), *Mammalian Phylogeny. Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials.* Springer-Verlag, New York: 208-215.

CIFELLI R. L. 1999. — Tribosphenic mammal from the North American Early Cretaceous. *Nature* 401: 363-66.

CIFELLI R. L. & VILLARROEL C. 1997. — Paleobiology and affinities of *Megadolodus*, *in* KAY R. F., MADDEN R. H., CIFELLI R. L. & FLYNN J. J. (eds), *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D. C.: 265-288.

CLEMENS W. A. 1966. — Fossil mammals of the Type Lance Formation Wyoming. Part II: Marsupialia. *University of California Publications in the Geological Sciences* 62: 1-122.

CLEMENS W. A. 1979. — Marsupialia, *in* LILLEGRAVEN J. A., KIELAN-JAWOROWSKA Z. & CLEMENS W. A. (eds), *Mesozoic Mammals: the First Two Thirds of Mammalian History.* University of California Press, Berkeley: 192-220.

CODDINGTON J. A. 1988. — Cladistic tests of adaptational hypotheses. *Cladistics* 4: 3-22.

COUES E. 1869. — The osteology and myology of *Didelphis virginiana. Memoirs of the Boston Society of Natural History* 2: 41-154.

COURT N. 1994. — Limb posture and gait in *Numidotherium koholense*, a primitive proboscidean from the Eocene of Algeria. *Zoological Journal of the Linnean Society* 111: 297-338.

CUMMINS R. 1975. — Functional analysis. *Journal of Philosophy* 72: 741-765.

DAGOSTO M. 1988. — Implications of postcranial evidence for the origin of euprimates. *Journal of Human Evolution* 17: 35-56.

DAGOSTO M., GEBO D. L., & BEARD K. C. 1999. — Revision of the Wind River faunas, Early Eocene of central Wyoming. Part 14: Postcranium of *Shoshonius cooperi* (Mammalia: Primates). *Annals of Carnegie Museum* 68 (3): 175-211.

DARWIN C. 1859. — *On the Origin of Species.* [Facsimile of the first edition published in 1964]. Harvard University Press, Cambridge, 490 p.

DEQUEIROZ K. 1992. — Phylogenetic definitions and taxonomic philosophy. *Biology and Philosophy* 7: 295-313.

DEQUEIROZ K. 1994. — Replacement of an essentialistic perspective on taxonomic definitions as exemplified by the definition of "Mammalia". *Systematic Biology* 43: 497-510.

DEQUEIROZ K. & GAUTHIER J. 1990. — Phylogeny as a central principle in taxonomy: phylogenetic definition of taxonomic names. *Systematic Zoology* 39: 307-322.

DEQUEIROZ K. & GAUTHIER J. 1992. — Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23: 449-480.

ELDREDGE N. & CRACRAFT J. 1980. — *Phylogenetic Patterns and the Evolutionary Process*. Columbia University Press, New York, 329 p.

ELFTMAN H. O. 1929. — Functional adaptations of the pelvis in marsupials. *Bulletin of the American Museum of Natural History* 58: 189-232.

FLYNN J. J. & WYSS A. R. 1998. — Recent advances in South American mammalian paleontology. *Tree* 13 (11): 449-454.

FLYNN J. J. & WYSS A. R. 1999. — New marsupials from the Eocene-Oligocene transition of the Andean Main Range, Chile. *Journal of Vertebrate Paleontology* 19: 533-549.

FRIGO L. & WOOLLEY P. A. 1996. — Development of the skeleton of the stripe-faced dunnart, *Sminthopsis macroura* (Marsupialia, Dasyuridae). *Australian Journal of Zoology* 44: 155-164.

FROST H. M. 1973. — *Bone Modeling and Skeletal Modeling Errors*. Charles C. Thomas, Springfield, Il.

GARDNER A. L. 1973. — The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. *Special Publications of the Museum of Texas Tech University* 4: 1-81.

GHISELIN M. T. 1997. — *Metaphysics and the Origin of Species*. State University of New York Press, Albany, xi + 377 p.

GILKESON C. F. & LESTER K. S. 1989. — Ultrastructural variation in enamel of Australian marsupials. *Scanning Microscopy* 3 (1): 177-191.

GOODWIN B. 1994. — *How the Leopard Changed its Spot. The Evolution of Complexity*. Charles Scribner's Son, New York, 252 p.

GOULD S. J. 1985. — A clock of evolution. *Natural History* 85 (4): 12-25.

GOULD S. J. 1986. — Evolution and the triumph of homology, or why history matters. *American Scientist* 74: 60-69.

GOULD S. J. 1988. — Trends as changes in variance: a new slant on progress and directionality in evolution. *Journal of Paleontology* 62: 319-329.

GOULD S. J. & VRBA E. S. 1982. — Exaptation – a missing term in the science of form. *Paleobiology* 8: 4-15.

GRAND T. I. 1983. — Body weight: its relationship to tissue composition, segmental distribution of mass and motor function. III: The Didelphidae of French Guyana. *Australian Journal of Zoology* 31 (3): 299-312.

GREGORY W. K. 1910. — The orders of mammals. *Bulletin of the American Museum of Natural History* 27: 1-524.

GRULICH I. 1991. — Variability of the ossa membri thoracici et pelvini of *Cricetus cricetus* (Rodentia, Mammalia). *Acta Scientiarum Naturalium Brno* 25: 1-63.

HAINES R. W. 1958. — Arboreal and terrestrial ancestry of placental mammals. *Quarterly Review of Biology* 33: 1-23.

HARVEY P. H. & PAGEL M. D. 1991. — *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, vii + 239 p.

HERSHKOVITZ P. 1992. — Ankle bones: The Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny. *Bonner Zoologische Beiträge* 43 (2): 181-213.

HERSHKOVITZ P. 1999. — *Dromiciops gliroides* Thomas, 1894, last of the Microbiotheria (Marsupialia), with a review of the family Microbiotheriidae. *Fieldiana, Zoology, New Series* 93: 1-60.

HOROVITZ I. 1999. — A report on "One day symposium on numerical cladistics". *Cladistics* 15: 177-182.

HU Y., WANG Y., LUO Z. & LI C. 1997. — A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature* 390: 137-142.

HUGHES R. L. & HALL L. S. 1988. — Structural adaptations of the newborn marsupial, *in* TYNDALE-BISCOE C. H. & JANSSENS P. A. (eds), *The Developing Marsupial: Models for Biomedical Research*. Springer-Verlag, Berlin: 8-27.

HULLEY P. E., WALTER G. H. & CRAIG A. J. F. K. 1988. — Interspecific competition and community structure. I: Shortcomings of the competition paradigm. *Rivista di Biologia* 81: 57-71.

JANKE A., XU X. & ARNASON U. 1997. — The complete mitochondrial genome of the wallaroo (*Macropus robustus*) and the phylogenetic relationship among Monotremata, Marsupialia, and Eutheria. *Proceedings of the National Academy of Sciences* 94: 1276-1281.

JENKINS F. A. Jr. 1971. — Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *Journal of Zoology* 165: 303-315.

JENKINS F. A. Jr. 1973. — The functional anatomy and evolution of the mammalian humero-ulnar articulation. *American Journal of Anatomy* 137: 281-298.

JENKINS F. A. Jr. 1974. — Tree shrew locomotion and the origins of primate arborealism, *in* JENKINS F. A. Jr. (ed.), *Primate Locomotion*. Academic Press, New York: 85-115.

JENKINS F. A. Jr. & CAMAZINE S. M. 1977. — Hip structure and locomotion in ambulatory and cursorial carnivores. *Journal of Zoology* 181: 351-370.

JENKINS F. A. Jr. & MCCLEARN D. 1984. — Mechanisms of hind foot reversal in climbing mammals. *Journal of Morphology* 182: 197-219.

JENKINS F. A. Jr. & WEIJS W. A. 1979. — The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). *Journal of Zoology* 188: 379-410.

JOLLY C. J. 1993. — Species, subspecies, and baboon systematics, *in* KIMBEL W. H. & MARTIN L. B. (eds), *Species, Species Concepts, and Primate Evolution*. Plenum Press, New York: 67-107.

KAPPELMAN J. 1988. — Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* 198: 119-130.

KAY R. F. & CARTMILL M. 1977. — Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ? Primates), with a description of a new genus and species. *Journal of Human Evolution* 6: 19-54.

KAY R. F. & COVERT H. H. 1984. — Anatomy and behaviour of extinct primates, *in* CHIVERS D. J., WOOD B. A. & BILSBOROUGH A. (eds), *Food Acquisition and Processing in Primates*. Plenum Press, New York: 467-508.

KIELAN-JAWOROWSKA Z. 1975. — Possible occurrence of marsupial bones in Cretaceous eutherian mammals. *Nature* 255: 698-699.

KIMBEL W. H. & MARTIN L. B. 1993. — *Species, Species Concepts, and Primate Evolution*. Plenum Press, New York, 560 p.

KIRSCH J. A. W. 1977. — The comparative serology of Marsupialia, and a classification of marsupials. *Australian Journal of Zoology supplementary series* 52: 1-152.

KIRSCH J. A. W., LAPOINTE F.-J. & SPRINGER M. S. 1997. — DNA-hybridisation studies of marsupials and their implications for metatherian classification. *Australian Journal of Zoology* 45: 211-280.

KLIMA M. 1987. — Early development of the shoulder girdle and sternum in marsupials (Mammalia, Metatheria). *Advances in Anatomy, Embryology and Cell Biology* 109: 1-91.

KREBS B. 1991. — Das skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal. *Berliner Geowissenschaftliche Abhandlungen* 133 (A): 1-116.

LANYON L. E. 1980. — The influence of function on the development of bone curvature. An experimental study on the rat tibia. *Journal of Zoology* 192: 457-466.

LAUDER G. V. 1981. — Form and function: structural analysis in evolutionary morphology. *Paleobiology* 7: 430-442.

LAUDER G. V. 1982. — Historical biology and the problem of design. *Journal of Theoretical Biology* 97: 57-67.

LAUDER G. V. 1995. — On the inference of function from structure, *in* THOMASON J. J. (ed.), *Functional Morphology in Vertebrate Paleontology.* Cambridge University Press, New York: 1-18.

LAUDER G. V. 1996. — The argument from design, *in* ROSE M. R. & LAUDER G. V. (eds), *Adaptation*. Academic Press, San Diego: 55-91.

LEITE Y. L. R., COSTA L. P. & STALLINGS J. R. 1996. — Diet and vertical space use of three sympatric opossums in a Brazilian Atlantic forest reserve. *Journal of Tropical Ecology* 12: 435-440.

LEROI A. M., ROSE M. R. & LAUDER G. V. 1994. — What does the comparative method reveal about adaptation? *American Naturalist* 143: 381-402.

LEWIS O. J. 1989. — *Functional Morphology of the Evolving Hand and Foot.* Oxford University Press, Oxford, 359 p.

LILLEGRAVEN J. A. 1969. — Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *University of Kansas Paleontological Contributions, Vertebrates* 12: 1-122.

LILLEGRAVEN J. A. 1975. — Biological considerations of the marsupial-placental dichotomy. *Evolution* 29: 707-722.

LILLEGRAVEN J. A. 1985. — Use of the term “trophoblast” for tissues in therian mammals. *Journal of Morphology* 183: 293-299.

LILLEGRAVEN J. A., THOMPSON S. D., MCNAB B. K. & PATTON J. L. 1987. — The origin of Eutherian mammals. *Biological Journal of Linnean Society* 32: 281-336.

MAHNER M. & BUNGE M. 1997. — *Foundations of Biophilosophy*. Springer-Verlag, New York, 423 p.

MARSHALL L. G. & MUIZON C. DE. 1988. — The dawn of the age of mammals in South America. *National Geographic Research* 4 (1): 23-55.

MARSHALL L. G. & MUIZON C. DE. 1995. — Part II: the skull, *in* MUIZON C. DE (éd.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Palaeocene of Bolivia. *Mémoires du Muséum national d'Histoire naturelle* 165: 21-90.

MARSHALL L. G., MUIZON C. DE & SIGOGNEAU-RUSSELL D. 1995. — Part I: the locality of Tiupampa: age, taphonomy and mammal fauna, *in* MUIZON C. DE (éd.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Palaeocene of Bolivia. *Mémoires du Muséum national d'Histoire naturelle* 165: 12-20.

MARSHALL L. G. & SIGOGNEAU-RUSSELL D. 1995. — Part III: Postcranial skeleton, *in* MUIZON C. DE (ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Palaeocene of Bolivia. *Mémoires du Muséum national d'Histoire naturelle* 165: 91-164.

MARTIN R. D. 1990. — *Primate Origins and Evolution*. Princeton University Press, Princeton, 804 p.

MASTERS J. C. & RAYNER R. J. 1993. — Competition and macroevolution: the ghost of competition yet to come? *Biological Journal of the Linnean Society* 49: 87-98.

MAUNZ M. & GERMAN R. Z. 1997. — Ontogeny and limb bone scaling in two New World marsupials, *Monodelphis domestica* and *Didelphis virginiana. Journal of Morphology* 231: 117-130.

MAYR E. 1961. — Cause and effect in biology. *Science* 134: 1501-1506.

MAYR E. 1982. — *The Growth of Biological Thought.* Harvard University Press, Cambridge, 974 p.

MCCRADY E. 1938. — The embryology of the opossum. *American Anatomical Memoirs* 16: 1-233.

MCKENNA M. C. & BELL S. K. 1997. — *Classification of Mammals above the Species Level.* Columbia University Press, New York, 631 p.

MCMAHON J. M. 1999. — *Nomological Mechanisms of Anthropoid Nasomaxillary Diversity*. Ph.D., City University of New York, New York, USA, 798 p.

MESSER M., WEISS A. S., SHAW D. C. & WESTERMAN M. 1998. — Evolution of the monotremes: phylogenetic relationship to marsupials and eutherians, and estimation of divergence dates based on a-lactalbumin amino acid sequences. *Journal of Mammalian Evolution* 5: 95-105.

MUIZON C. DE. 1992. — La fauna de mamíferos de Tiupampa (Paleoceno inferior, Formacíon Santa Lucía) Bolivia. *Revista Técnica de Yaciminentos Petrolíferos Fiscales de Bolivia* 12: 575-624.

MUIZON C. DE 1995 (éd.). — *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Palaeocene of Bolivia. *Mémoires du Muséum national d'Histoire naturelle* 165: 1-164.

MUIZON C. DE 1994. — A new carnivorous marsupial from the Paleocene of Bolivia and the problem of marsupial monophyly. *Nature* 370: 208-211.

MUIZON C. DE 1998. — *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. *Geodiversitas* 20 (1): 19-142.

MUIZON C. DE, CIFELLI R. L. & CESPEDES PAZ R. 1997. — The origin of the dog-like borhyaenoid marsupials of South-America. *Nature* 389: 486-489.

MUIZON C. DE & MARSHALL L. G. 1992. — *Alcidedorbignya inopinata* (Mammalia: Pantodonta) from the early Paleocene of Bolivia: phylogenetic and paleobiogeographic implications. *Journal of Paleontology* 66: 499-520.

MURRAY P., WELLS R. & PLANE M. 1987. — The cranium of the Miocene thylacoleonid marsupial *Wakaleo vanderleuri*: click go the shears – a fresh bite at thylacoleonid systematics, *in* ARCHER M. (ed.), *Possums and Opossums: Studies in Evolution*. Volume 2. Surrey Beatty & Sons, Sydney: 433-466.

NAYLOR G. J. P. & BROWN W. M. 1997. — Structural biology and phylogenetic estimation. *Nature* 388: 527-528.

NELSON G. J. & PLATNICK N. 1984. — Systematics and evolution, *in* HO M. W. & SAUNDERS P. T. (eds), *Beyond Neo Darwinism: an Introduction to the New Evolutionary Paradigm*. Academic Press, New York: 143-158.

NOVACEK M. J. 1993. — Reflections on higher mammalian phylogenetics. *Journal of Mammalian Evolution* 1: 3-30.

NOVACEK M. J. 1996. — Paleontological data and the study of adaptation, *in* ROSE M. R. & LAUDER G. V. (eds), *Adaptation*. Academic Press, San Diego: 311-359.

NOVACEK M. J., ROUGIER G. W., WIBLE J. R., MCKENNA M. C., DASHZEVEG D & HOROVITZ, I. 1997. — Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. *Nature* 239: 483-486.

NOWAK R. M. 1999. — *Walker's Mammals of the World*. 6th ed. Vol. I & II. The Johns Hopkins University Press, Baltimore, 1936 p.

O'SULLIVAN J. A. 1995. — *Skeletal Indicators of Arboreal and Terrestrial Positional behavior in Didelphid Marsupials*. MA Thesis, Hunter College, CUNY, USA, 145 p.

PALMA R. E. & SPOTORNO A. E. 1997. — Molecular phylogeny among American marsupial taxa: the molecular relatedness between *Dromiciops gliroides* and didelphid marsupials. *Noticiero de Biología* 5: 49.

PALMA R. E. & SPOTORNO A. E. 1999. — Molecular systematics of marsupials based on the rRNA 12S mitochondrial gene: the phylogeny of Didelphimorphia and of the living fossil microbiotheriid *Dromiciops gliroides* Thomas. *Molecular Phylogenetics and Evolution* 13 (3): 525-535.

PATTON J. T. & KAUFMAN M. H. 1995. — The timing of ossification of the limb bones, and growth rates of various long bones of the fore and hind limbs of the prenatal and early postnatal laboratory mouse. *Journal of Anatomy* 186: 175-185.

PRANGER R. 1990. — Towards a pluralistic concept of function statements in biology. *Acta Biotheoretica* 38: 63-71.

PRIDMORE P. A. 1992. — Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). *Journal of Morphology* 211: 137-146.

PRIDMORE P. A. 1994. — Locomotion in *Dromiciops australis* (Marsupialia: Microbiotheriidae). *Australian Journal of Zoology* 42: 679-99.

RAFF R. A. 1996. — *The Shape of Life*. University of Chicago Press, Chicago, 520 p.

RASMUSSEN D. T. 1990. — Primate origins: lessons from a neotropical marsupial. *American Journal of Primatology* 22: 263-277.

RAYNER R. G. & MASTERS C. J. 1995. — A good loser is still a loser: competition and the South African fossil record. *South African Journal of Science* 91: 184-189.

REDLINE A. D. 1997. — Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 13: Systematics and phylogenetic pattern of early Eocene *Hyopsodus* (Mammalia: Condylarthra). *Annals of Carnegie Museum* 66: 1-81.

RIDE W. D. L. 1993. — *Jackmahoneya* gen. nov. and the genesis of the macropodiform molar. *Memoirs of the Association of Australasian Palaeontologists* 15: 441-459.

ROBERTS D. 1974. — Structure and function of the primate scapula, *in* JENKINS F. A. Jr. (ed.), *Primate Locomotion*. Academic Press, New York: 171-200.

ROSE M. R. & LAUDER G. V. 1996.— Post-spandrel adaptationism, *in* ROSE M. R. & LAUDER G. V. (eds), *Adaptation*. Academic Press, San Diego: 1-8.

ROWE T. & GAUTHIER J. 1992. — Ancestry, paleontology, and definition of the name Mammalia. *Systematic Biology* 41: 372-378.

SALTHE S. N. 1989. — [Commentary], *in* HECHT M. K. (ed.), *Evolutionary Biology at the Crossroads*. Queens College Press, Flushing (NY): 175-176

SALTHE S. N. 1993. — *Development and Evolution: Complexity and Change in Biology*. The MIT Press, Bradford Books, Cambridge (Mass.), 400 p.

SÁNCHEZ-VILLAGRA M. R. & KAY R. F. 1996. — Do phalangeriforms (Marsupialia: Diprotodontia) have a "hypocone"? *Australian Journal of Zoology* 44: 461-467.

SARGIS E. J. 2001. — A preliminary qualitative analysis on the axial skeleton of tupaiids (Mammalia, Scandertia): functional morphology and phylogenetic implications. *Journal of Zoology, London* 253: 473-483.

SERENO P. C. 1999. — Definitions in phylogenetic taxonomy: critique and rationale. *Systematic Biology* 48: 329-351.

SILVA M. & DOWNING J. A. 1995. — *Mammalian Body Masses*. CRC Press, New York.

SIMMONS N. B. 1993. — The importance of methods: archontan phylogeny and cladistic analysis of morphological data, *in* MACPHEE R. D. E. (ed.), *Primates and their Relatives in Phylogenetic Perspective*. Plenum Press, New York: 1-61.

SIMPSON G. G. 1945. — The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 91: 1-232.

SIMPSON G. G. 1948. — The beginning of the age of mammals in South America. Part 1. *Bulletin of the American Museum of Natural History* 137: 1-260.

SIMPSON G. G. 1953. — *The Major Features of Evolution*. Columbia University Press, New York, 434 p.

SIMPSON G. G. 1967. — The beginning of the age of mammals in South America. Part 2. *Bulletin of the American Museum of Natural History* 85: 1-350.

SPOTORNO A. E., MARIN J. C. & YÉVENES M. 1997. — Comparative cytogenetics and phylogenetic relationships of the Chilean marsupials *Dromiciops gliroides* and *Thylamys elegans*. *Noticiero de Biología* 5: 48.

SPRINGER M. S., BURK A., KAVANAGH J. R., WADDELL V. G. & STANHOPE M. J. 1997. — The interphotoreceptor retinoid binding protein gene in therian mammals: implications for higher level relationships and evidence for loss of function in the marsupial mole. *Proceedings of the National Academy of Sciences* 94: 13754-13759.

SPRINGER M. S., WESTERMAN M., KAVANAGH J. R., BURK A., WOODBURNE M. O., KAO D. J. & KRAJEWSKI C. 1998. — The origin of the Australasian marsupial fauna and the phylogenetic affinities of the enigmatic monito del monte and marsupial mole. *Proceedings of the Royal Society of London* 265 (B): 2381-2386.

STAFFORD B. J. 1999. — *Ecological Morphology of the Flying Lemurs (Dermoptera, Cynocephalidae)*. Ph.D., City University of New York, New York, USA, 330 p.

STEIN B. R. & CASINOS A. 1997. — What is a cursorial mammal? *Journal of Zoology, London* 242: 185-192.

STREILEIN K. E. 1982. — Behavior, ecology and distribution of South American marsupials, *in* MARES M. A. & GENOWAYS H. H. (eds), *Mammalian Biology in South America*. Special Publication Series. Pymatuning Laboratory of Ecology, University of Pittsburgh: 231-250.

STUART MILL J. 1872. — *A System of Logic: Ratiocinetive and Inductive. Being a Connected View of the Principles of Evidence and the Methods of Scientific Investigation*. [Republished in 1967]. Logman, London.

SZALAY F. S. 1981. — Phylogeny and the problem of adaptive significance: the case of the earliest primates. *Folia Primatologica* 36: 157-182.

SZALAY F. S. 1982. — A new appraisal of marsupial phylogeny and classification, *in* ARCHER M. (ed.), *Carnivorous Marsupials*. Royal Zoological Society of New South Wales, Sydney: 621-640.

SZALAY F. S. 1984. — Arboreality: is it homologous in metatherian and eutherian mammals? *Evolutionary Biology* 18: 215-258.

SZALAY F. S. 1993. — Species concepts: the tested, the untestable, and the redundant, *in* KIMBEL W. H. & MARTIN L. B. (eds), *Species, Species Concepts, and Primate Evolution*. Plenum Press, New York: 21-41.

SZALAY F. S. 1994. — *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*. Cambridge University Press, New York, 481 p.

SZALAY F. S. 1999a. — Paleontology and macroevolution: on the theoretical conflict between an expanded synthesis and hierarchic punctuationism, *in* BROMAGE T. & SCHRENK F. (eds), *African Biogeography, Climate Change* & *Human Evolution*. Oxford University Press, Oxford: 35-56.

SZALAY F. S. 1999b. — Review of "classification of mammals above the species level" by McKenna M. C. & Bell S. K. *Journal of Vertebrate Paleontology* 19: 191-195.

SZALAY F. S. 2000. — Function and adaptation in paleontology: why omit Darwin? *Palaeontologia Electronica* 3 (2): 25 p., 366 KB; http://palaeo-electronica.org/paleo/2000_2/darwin/issue2_00.htm.

SZALAY F. S. & BOCK W. J. 1991. — Evolutionary theory and systematics: relationships between process and patterns. *Zeitschrift Zoologische Systematic und Evolutions-Forschung* 29: 1-39.

SZALAY F. S. & COSTELLO R. K. 1991. — Evolution of permanent estrus displays in hominids. *Journal of Human Evolution* 20: 439-464.

SZALAY F. S. & DAGOSTO M. 1980. — Locomotor adaptations as reflected on the humerus of Paleogene primates. *Folia Primatologica* 34: 1-45.

SZALAY F. S. & DAGOSTO M. 1988. — Evolution of hallucial grasping in primates. *Journal of Human Evolution* 17: 1-33.

SZALAY F. S. & DELSON E. 1979. — *Evolutionary History of the Primates*. Academic Press, New York, 580 p.

SZALAY F. S. & LUCAS S. G. 1993. — Cranioskeletal morphology of archontans, and diagnoses of Chiroptera, Volitantia, and Archonta, *in* MACPHEE R. D. E. (ed.), *Primates and their Relatives in Phylogenetic Perspective*. Plenum Press, New York: 187-226.

SZALAY F. S. & LUCAS S. G. 1996. — Postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. *New Mexico Bulletin of Natural History* & *Science* 7: 1-47.

SZALAY F. S., ROSENBERGER A. L. & DAGOSTO M. 1987. — Diagnosis and differentiation of the order Primates. *Yearbook of Physical Anthropology* 30: 75-105.

SZALAY F. S. & SCHRENK F. 1998. — The middle Eocene *Eurotamandua* and a Darwinian phylogenetic analysis of "edentates". *Kaupia* 7: 97-186.

SZALAY F. S. & TROFIMOV B. A. 1996. — The Mongolian late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *Journal of Vertebrate Paleontology* 16: 474-509.

TARDIEU C. 1981. — Morpho-functional analysis of the articular surfaces of the knee-joint in primates, *in* CHIARELLI A. B. & CORRUCINI R. S. (eds), *Primate Evolutionary Biology*. Springer-Verlag, Berlin: 68-80.

VRBA E. S. 1980. — Evolution, species and fossils: How does life evolve? *South African Journal of Science* 76: 61-84.

WALTER G. H. 1988. — Competitive exclusion, coexistence and community structure. *Acta Biotheoretica* 37: 281-313.

WATKINS M. A. & GERMAN R. Z. 1992. — Ontogenetic allometry of ossified fetal limb bones. *Growth, Development, and Aging* 56: 259-267.

WHITE T. D. 1989. — An analysis of epipubic bone function in mammals using scaling theory. *Journal of Theoretical Biology* 139: 342-357.

WOODBURNE M. O. & CASE J. A. 1996. — Dispersal, vicariance, and the late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. *Journal of Mammalian Evolution* 3: 121-161.

WYSS A. R. & FLYNN J. J. 1993. — A phylogenetic analysis and definition of the Carnivora, *in* SZALAY F. S., NOVACEK M. J. & MCKENNA M. C. (eds), *Mammal Phylogeny. Placentals*. Springer, New York: 32-52.

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ENDNOTES

1. The phylogenetic perspective of Simpson (1953) should be compared to the taxic theory and language presented by Gould & Vrba. Simpson envisages the adaptive process as an ongoing seamless relationship between a changing (total) environment and the evolutionary units at a given moment in time, the lineages (not species taxa) tracking it, where prospective functions become realized ones. Gould & Vrba base their theoretical discussions, implicitly, on the mysterious abrupt shifts of speciation (based on the evidence of paleontological species taxa) that is the encoded core of punctuationism.
2. The issues of contention in phylogenetics are neither "evolutionary" nor "cladistic" taxonomic expressions of phylogeny. The various caricatures of these schools of classification have been exhaustively portrayed in the partisan literature. Darwin himself fully understood that all information was to be used to test phylogenies (culminating in his theory of descent), and that the taxonomic expression of a phylogeny was fraught with the compromises that such heuristic activity must face. It is just as obvious now, as we noted above, as it was to Darwin, that what this phylogeny is (i.e. ancestry constrained and selectionally guided descent) should be the ontological core of methods, our epistemology, in order to recover it. As stated by Darwin (1859: 426, italics supplied). "We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, occur together throughout a large group of *beings having different habits*, we may feel almost sure, on the theory of descent, that these characters have been inherited from a common ancestor".
3. One should be reminded, again, however, that many researchers use the single term "function" with clear meaning where the context renders it obvious that they mean either mechanical or biological (adaptive) function. Others, however, continue to conflate the meanings at the expense of both operational, as well as explanatory clarity, so the conceptual and terminological differentiation introduced by Bock & Wahlert (1965), we believe, continues to serve a significant purpose in comparative biology.
4. Mahner & Bunge (1997) have a problem considering events in ontogeny as "causal". We prefer to consider all events in the realtime of an organism genuinely causal. Events in ontogeny have consequences well beyond the unfolding of the genetic blueprint or the heritage of the zygote.

5. Historical narratives are histories of successful and successive ontogenies wastefully managed by ecology, and ontologically lineages represent the past history of evolving populations or species (anywhere along that lineage in time). Ultrastructuralists who hope for a universal science of form miss the meaning of what phylogeny is. The descent of successful ontogenies should indicate that because of the differences, and not because of their universality, ontogenies succeed differentially through time. The historical and adaptive processes that Goodwin (1994, for example) tries to marginalize are an obvious threat to any Platonic universality that he attempts to deduce from the complexity of structural transformation of embryos. The commonality of patterns and processes of organization are not transcendental universal truths but the footprints of a phylogeny. For an extreme structuralist perspective by someone who considers Darwinism a reprehensible theory, see Salthe (1989, 1993).
6. In the significantly titled "Post-spandrel adaptationism" by Rose & Lauder (1996), and the introduction to their edited volume on adaptation that strongly reflects their particular perspective on phylogeny, these authors speak of the "rise" and subsequent impetus of cladistics, and the "new adaptationism". While they and others speak of "rigor" regarding interspecific comparisons (e.g., Harvey & Pagel 1991), they overlook the fundamental importance of an ancestral condition-centered tree for all valid non-independence methods (cf. McMahon 1999). This is relevant to the area of research that analyzes adaptations with statistics in multiple lineages. The output of parsimony cladistics, devoid of causally meaningful ancestral reconstruction and the phyletics of traits is, therefore, not amenable to such efforts.
7. The structuralist metaphysics of Lauder (1982: 57) is reflected in one of his early contributions: "The synthesis of a structural/phylogenetic approach to historical morphology with the analysis of extrinsic limits to form may provide the level of resolution needed to generate testable mechanistic hypotheses regarding the distribution of extant organismal forms in the hyperspace of possible morphologies". The adaptational vacuum is evident, the functional prescription is non-Darwinian, and the theoretical position is totally concordant with the exclusively character distribution-based paradigm of cladistics.
8. The concluding remarks of Leroi, Rose & Lauder (1994: 398) regarding phylogenetics is significant: "Such analyses will be all the more robust for lacking unsupported assumptions, unwarranted inferences, and untestable hypotheses about the history of evolutionary mechanisms". But such linear analyses of nonlinear relationships are not only appropriately sterile, but theoretically anemic as well.
9. "Multidisciplinary" in this case merely means that components of a research program represented "distinct" disciplines previously.
10. Such efforts, in light of the modularity of functional complexes in organisms, are particularly egregious when they map even functionally well-understood complexes onto a previously generated parsimony cladogram based on a different region of the organism. For example, even if a cladogram based on cranial and dental characters were true, superimposing postcranial traits on it does not necessarily yield meaningful transformational history for the latter. Demands and consequences of selection are different on different aspects of organisms (see below). A taxic perspective appears to assume that all character evolution is bound up in the concerted and magical origin of species taxa through speciation.
11. Unlike Lauder, Bock (1999), who maintains a sharp divide between function and adaptation epistemologically, makes the obvious connection, and in Bock's view functional and adaptational or utilitarian analysis come under the same conceptual and theoretical heading, i.e. functional explanations.
12. The philosophical literature on that one topic alone is enormous. Most of it is marred by a syllogistic presentation of issues about trait, function, and organism, the omission of the time sequential nature of the workings of selection, the consequently shifting base of what features and roles are from generation to generation, and a lack of consideration of selectionally mediated directional form-function changes for the same biological roles. For a review on the history of ideas on adaptation, but from a philosopher's perspective, see Amundson (1996). For antidotes see Darwin (1859) and Simpson (1953).
13. Bock (e.g., 1999) eschews the assessment of adaptations without previous mechanical analysis, and therefore implicitly rejects the proven value of correlating carefully selected variables in morphology with shared bioroles and ecological factors. The latter is the powerfully predictive convergence method. For example, detailed biometrical comparisons of osteological parameters of diversely adapted and unrelated species will often result in highly instructive clusters of both divergent and convergent complexes that can be strong indications of similar adaptations and multiple solutions for similar roles (e.g., Stafford 1999). Numerous selected comparisons based on massive samples and carefully derived indices can yield valuable correlations that are often proved to be causal regarding certain bioroles. Such correlation-based statistical studies often pave the way for more focused functional analyses. In general, attempted theoretical and semantic cubby-holing of dynamically inseparable evolutionary issues (that invariably grow out

of a search for increasingly complete explanations) are doomed to be reconstituted.

14. Studies such as those of Benton (1987), Walter (1988), Hulley *et al.* (1988), Masters & Rayner (1993), and Rayner & Masters (1995), for example, suggest or assert that the Darwinian imperatives of ecological competition are somehow not reflected in "objective" analyses of the fossil record or community structure, and that variance shifted punctuated trends (Vrba 1980; Gould 1988) are substitutes for most explanations of evolutionary progress driven by directional selection. Many such contributions are strongly driven either by political ideology or social dynamics, or a combination of both (see a review of some macroevolutionary dynamics in Szalay 1999a).

15. The area of study that attempts to relate phylogenetic and functional factors to the assessment of mammalian positional behavior and to the structure of the musculoskeletal system was strongly advocated by Gregory (1910), and has remained an active field of endeavor, often driven by paleobiological interests.

16. In Placentalia, on the contrary, differences in the proportions of the two femoral condyles is relatively fixed, and therefore not particularly indicative of substrate preference. The ancestral placentalian modification of the knee (reduction of the lateral condyle and the proximal fibula that primitively buttressed the knee via the parafibula) is a probable response to obligate terrestriality (Szalay 1994). It occurred either together or sequentially with a mediolateral restriction of the upper ankle joint. Following this event(s), subsequent substrate-related adaptations resulted in modifications of the lower ankle joint, but not of the proportions of the mediolateral widths of the femoral condyles and their conarticular facets on the tibia. Nevertheless, parafibular contact with the femur and fibula persists even in a number of extant placentalian eutherians (e.g., *Ptilocercus*).

17. Lest someone be confused, independent character analysis should not presuppose taxic considerations beyond the trivially obvious that traits are parts of real organisms that have names. Our view is contrary to that of Rieppel's (1993) thoughtful, but in our view flawed, theoretical analysis based on exclusively structuralist precepts.

18. Bone tissues and skeletal structures are a complex expression of the genome that reflects poorly understood stages of ancient phylogenetic history. They are also entities strongly channeled by developmental (ontogenetic) history. Growth rates and other organizational parameters in the genome, coupled with the level of homeostasis, endocrinology, and loading due to activity patterns and size become the final arbiters of both bone shape and microstructural tissue attributes. Ancient gene homologies reflect the expression along a range of these "gene/environment" factors. All genetically mediated aspects of this organization are guided by ecology (selection) through geological time. A holistic understanding of the specifics of such systems are one of the least trivial aspects of the science of form with obvious fundamental relevance for vertebrate paleontology. Loading of individual bones can now be determined quite accurately with computer assisted measurements of bone thickness and density. While hardware and algorithms that can digitize this information are not easy to obtain now, one may predict that in a relatively short time, such tools will be available to osteologists of extant and extinct species.

19. As and example of model-based paleobiological analysis, although not specified as such, Court's (1994) outstanding study of adaptations in the primitive fossil elephant *Numidotherium* from the African Eocene is conducted along similar theoretical paths to those we attempt to explicitly outline and implement here.

20. The fact, for example, that numerous small rodents feed on high energy concentrations like seeds negates an often cited "generality". Some statements assert that because many small living lipotyphlans or primates are insectivorous, all small fossil primates had to be as well. Many small fossil primates (as well as marsupials) with the appropriate dental and cranial attributes were probably oblivious to "Kay's rule" (*contra* Kay & Covert 1984) when it came to their dietary regimes. Morphological and functional patterns, in light of the appropriate models (but not size alone) supply convincing paleobiological explanations. The aim of modeling is to understand the obligate adaptations related to feeding, or positional behaviors, from the hard morphology of fossils. Such efforts relate only incidentally to the general environment of fossils. Monkeys and elephants can exist in the same environment. A derived trait is derived at its inception in a species, but if multiplication of that lineage follows, and modifications occur in those lineages then the ancestral condition is just that, and no longer derived in the descendants (*contra* the semantics offered by Anthony & Kay 1993: 374).

21. This was in juxtaposition to the practice of indiscriminate use of ancestral characters that could be correlated with some habitat in living animals (e.g., the relative size of the infraorbital foramen in archaic primates used by Kay & Cartmill 1977, to argue for terrestriality in paromomyid primates). While the persistence of functional correlates of even primitive traits can be useful in framing an adaptational analysis, primitive traits are often revealing of ancestral adaptations. The human thorax, shoulder complex, and elbow joint are good examples. These heritage traits, a group's synapomorphies, set the limits for various trajectories of the more derived features. For example, the contact of the fibula with the femur, and also via the parafibula (the fibular fabella), correlates only with some aspect of therian primitiveness in the knee complex, but no ecologically meaningful differentiating function can be associated with it in marsupials that show different habits today. Both the most arboreal and terrestrial forms have this as part of the knee complex. To the contrary, the extreme narrowing of the distal fibula (and attendant muscular and mechanical correlates) occurs only in highly terrestrial metatherians, as we discuss below. The repeated narrowing of the lateral femoral condyle in terrestrial didelphids, bandicoots, basal and all other kangaroos, as well as in the ancestral placentalian, however, closely predicts terrestriality. But this modification that also occurred in protoplacentalians does not widen again in arboreal eutherians. The latter, of course, are all derived from the terrestrially modified protoplacental.

22. All body weight measurements were from Silva & Downing (1995) and Nowak (1999), except for those of *Dromiciops* and *Rhyncholestes*, for which Dr. Gallardo graciously supplied numerous field based body weights.

23. We note here how unreliable isolated traits are either for making assessment of habitus, or for use as phylogenetically important characters, if one was to take them out of complete skeletal (phyletic and adaptational) context. For example, in the single specimen of the Mesozoic symmetrodont *Zhangheotherium* described by Hu *et al.* (1997) there are two postcranial traits that in isolation usually indicate two distinct particular functional complexes within the Didelphidae (an adaptively variable but phyletically constrained family). A long greater trochanter is invariably associated with terrestrial running, and a fast hip joint. A curved proximal ulna, however, is present in highly arboreal, relatively slow climbing, species. So what does the symmetrodont condition mean, if not genuine scansorial behavior?

24. The contribution of Jenkins & Camazine (1977) on the relationship of the hip and the proximal femur in a variety of diversely adapted carnivorans is an additional important study that greatly aids the understanding of femoral mechanics and its applicability to eutherian fossil specimens in general.

25. Bryant & Seymour (1990) render major service in their discussion regarding the reliability of muscle reconstructions in various groups of fossil vertebrates. According to these authors, in spite of the important caveats cited by them regarding this problem in reptiles and birds, there is greater reliability of inferring muscles and their orientation (if not their size) from bony topography in mammals than in nonmammals, particularly if these are attachments by aponeuroses or tendons. We note here a corroborated fact regarding the skeleton, however. Given that other factors are equal in related taxa, the relative size of crests, processes, proportions of articular relationships, particularly lever related distances of attachment surfaces from the appropriate fulcra, osteology alone can supply significant insights into the mechanics of various musculoskeletal, and certainly arthrological, adaptations. A related area of information gathering regarding loads on bones, based on cortical density, thickness, and trabecular patterns (all largely genotype-based patterns of a species), is rapidly expanding.

26. Selection for increased efficiency for terrestrial locomotion, both in lineages of marsupials and in the stem placentalians, probably resulted in limb posture differences and subsequent changes in the proportions of the articular facets from their similar ancestral conditions. The complex of attributes of the femorotibial articular surfaces, however, have a different meaning in subsequent eutherian lineages because the protoplacentalian had subequal medial and lateral condyles. This heritage condition in extant arboreal eutherians, as noted, has not reverted back to the prevalent primitive pattern seen in arboreal metatherians. The reason for this is simply a structural and functional reorganization of the hindlimb (on a heritable, and not epigenetic, level) in the protoeutherian lineage. In subsequent lineages arboreal reorganizations were based on that placental pattern that constrained taxon-specific joint-mechanics accordingly.

27. It bears emphasis that didelphid arborealists are drastically unlike a variety of explosive arboreal grasp-leapers encountered among, and probably in the very ancestry, of the Euprimates, particularly Strepsirhini. Small terrestrial marsupial species, while they cannot be technically considered “cursorial” in the traditionally accepted sense of the term, nevertheless show (as a result of enhanced stability for rapid flexion extension at the knee joint; more efficient abduction of the hindlimb, etc.) the incipient attributes that are also diagnostic properties of the placentalian ancestry. This is probably so because in a terrestrial habitat predation pressures on small mammals often result in strong selection for a musculoskeletal system that can sustain the necessary bursts of speed.

28. Slow locomotion in a complex environment like the canopy produces a complex system of loading. Similarly, the exploratory and manipulative abilities of such eutherians as tenrecoids, tupaiids, primates, a number of scansorial carnivorans like procyonids or the arboreal and swimming lineages of mustelids also produce such complex loading, to mention only a few taxa.

29. It may not seem so relevant here that, unfortunately, gross mistakes were committed when critical morphological details were misperceived from the literature. In addition, the account by Martin (1990) was based on the various hypothetical views of Lewis (1989) regarding the relevance of didelphids to alleged protoplacental arboreality. Furthermore, repetitions of mistaken interpretations of the literature about material (apparently unexamined) were repeated by Martin. But Martin's views, developed at great length in his textbook to shed doubt on the mechanical adaptations of the protoplacentals and the association of these with terrestrial locomotion, should be countered here because marsupials played an important role in his assessment. The great wealth of detail from the literature confusingly quoted by him (suggesting a failure to follow the specifics of the morphological arguments) was all interpreted in light of his ideas that ancestral placental arboreality framed the origin of the primate (and archontan) radiation.

The context of the issues discussed by him was based on evidence from ecological morphology, which forms the basis for the highly tested hypothesis for stem placentalian terrestriality. Unfortunately, Martin also published illustrations that do not represent the actual morphology that he used to support his views. He overlooked, and missed the significance of the fact, that unlike the relatively free upper ankle joint adjustments in such primitive living marsupials as didelphids, with their meniscus mediated fibular contact that puts little restraint on the upper ankle joint laterally, the protoplacentalian condition has evolved considerable tibial and fibular restraint for the upper ankle (the astragalus). Similar, independently evolved, ankle restriction patterns can be found in obligate terrestrial marsupials like peramelids or macropodids. Martin failed to recognize (even though this has been detailed in the literature) that the extensive lower ankle joint adjustments of plesiadapiforms, euprimates, and all other obligate arboreal eutherians became constrained by the ancestral adaptation, and that the most extensive adjustments to pedal inversion have invariably occurred in the lower ankle joint. As a result, evolution of a morphological complex in the lower ankle joint that facilitates inversion is invariably a derived condition among Cenozoic eutherians that show such morphotypic attributes, albeit convergently, such as archontans, some lipotyphlans, creodonts, carnivorans, and rodents.

30. An unfortunate consequence of the popularity of an axiomatized method of parsimony cladistics (and with it the neglected status of ancestor-descendant hypotheses, transformational analysis, etc.) is that the concept of phylogeny has been co-opted by cladogeny – but without phyletics even in the branching process. Reference to phylogenetic analysis is often only a term substituted for cladogeny of OTUs.

31. As stated in a *New York Times* review, in reference to the WWII trials at Blechley Park by the Allied experts assembled in England, the hunters for the code of the "Enigma" machine of Axis intelligence: "The world is an agglomeration of information, much of it seeming chaotic, some of it hidden, all of it requiring interpretation". So is all information we can retrieve from living and fossil organisms and their temporal and geographic contexts.

32. Greater reliability on biological research to order and polarize well chosen attributes should lead to the abandonment of the nomothetic panacea of parsimony algorithms. Subsequently, this should restore meaningful analysis to horizontal comparisons and cladistics. Thus cladistics in a renewed sense can become the theoretically robust part of phylogenetics.

33. Parsimony procedures and the attendant taxograms produced, aimed at character ordering and polarization (with their built-in circularity), are techniques that recall minimalist art which purports to present "essences". They fail to provide an epistemology that can struggle with lineage reconstruction (the representational reality). An estimation of the latter is attempted by the biologically and paleontologically meaningful testing of historical narrative accounts. Attempts to order and polarize character information through parsimony algorithm should be considered as the last resort of the systematist for classification but not phylogeny. The use of algorithms for character analysis is not a methodology concordant with tested Darwinian and neo-Darwinian theory, in spite of the increasing complexity in the use of these algorithms, escalation in the indices employed, as well as the explicit general taxic assumptions about various mathematical models rooted in node-based cladogeny (e.g., see Horovitz 1999). Such procedures, and many new ones being proposed with periodic regularity, are founded on an all but total theoretical elimination of the role of lineage specific adaptive change in anagenesis and the obvious methodological implications of this.

34. This is a historical narrative approach, and is highly idiographic depending on the organisms, character constellations, nature of the fossil record, and any and all justifiable initial and boundary conditions bearing on a specific investigation. Its aim is neither the deductive rigor attempting to imitate purely nomothetic science, nor is it "consistency" in the somewhat idiosyncratic and tautological sense applied to algorithmic procedures. In the latter, historical constructs are gauged not by probable truth content based on biology and paleontology but rather by the latest recastings of parsimony procedures. Darwinian phylogenetics is an induction-based and probability-based series of operations, with the deductive component being the applied knowledge of evolutionary mechanisms and selected and well understood specific relationships between the organisms and their structure, behavior, and environment. This applied knowledge is from the appropriately chosen models of evolutionary dynamics that appear to fit the problems investigated. These are, from the application of the relevant specifics of natural or sexual selection, or developmental factors, to constrained drift, etc., all explicitly detailed, and selected ecologically and functionally understood extant species models. We need to point out here some observations regarding the nature of character similarity in phylogenetic analysis. We are obviously not pheneticists, or quasi-pheneticist phylogenists who consider all untested "synapomorphies" of equal value in building taxograms (cf. Mahner & Bunge's 1997, designation of results of parsimony analysis as "pretheoretical classification"). Yet we note that a whole generation of taxonomists have been raised on the monotonic and linear paradigm of parsimony cladistics. In addition that school continues to teach an axiomatic scorn for the concepts of distance and intermediacy (and their biological meanings) in both the evaluation and polarizing of morphological attributes. The consequence has been an often grotesque shoe-horning of all degrees and minutiae of shared derived similarities into the loosely conceived, and subsequently abused, concept of synapomorphy. The fundamental role of the context and variations in these similarities has been largely ignored, resulting in, or rather becoming the consequence of, purely distributional assessment of variously perceived, and often unwisely divided, attributes.

For a full appreciation of the uniquely shared identical characters judged to be derived between taxa (the rigorous and necessary definition of synapomorphy), variously appraised distance and intermediacy measures are essential. This is needed either for morphologically similar taxa with attributes that sometimes cannot be meaningfully broken into components, or for those which do not lend themselves to vertical comparisons (see, for example, Cifelli's 1999, distance-based and clustered appraisal of the dental attributes of the early Cretaceous *Montanalestes* Cifelli, 1999; see also Bock 1977, for the conceptual foundations of horizontal and vertical comparisons). Without either a quantitative or a transformational (vertical) component in character analysis what is left is a distribution-appraising procedure that is incapable of providing theoretically realistic phylogenetic estimations of features (and, consequently, the taxa). But more importantly, this practice leads to a particularly pernicious form of linear logic that axiomatically results in the wrong conclusions (see an excellent analysis of the rich fossil record of *Hyopsodus* Leidy, 1870 by Redline 1997, and his discussion regarding a strict cladistic method when applied to a good fossil record). In our view a judicious and highly contextualized analysis of similarities requires the use of distance and intermediacy as applied to homologous traits.

35. Macrotaxonomic arrangements are (or should be) a consequence of an estimated delineation of evolved lineages. They are equally the results of microtaxonomic efforts to construct meaningful taxonomic species that gage organic diversity, and to study the history of life. The fossil (and often extant) species taxa are estimates by taxonomists. They are based on models of extant (and sub-Recent) species that have been studied regarding their geographic distributions, attributes and, (sometimes) genetics, as well as the various forms of intergradations of their populations that need to be applied to fossil phena (Jolly 1993; Szalay 1993, in press; and several other papers in Kimbel & Martin 1993). The fossil species taxa are certainly not all "new lineages", but many represent lineage segments as all taxonomic species do, including living ones into which taxonomists incorporate a fair chunk of precedent populations. Invariably, the latter view is tied to an ontological conception of "species" through time that in reality entails a segment of a lineage. The often asserted notion that species (and other taxa) are "individuals" is based on the conceptualizations of a flawed old metaphysics, Ghiselin's (1997) major and erudite efforts notwithstanding. We do not accept the notion that taxic "individuality" is the proper and decoupled way of looking at evolutionary dynamics, as it is considered to be in hierarchic punctuationism (Szalay 1999a).
36. For most parsimony cladists, transformational analysis represents a fundamental disagreement with both the tenets of a taxic view of life (as designated through taxograms), as well as hierarchic punctuationism. Evolution is lineage continuity and splitting, made to appear quite messy by both extinction and the incompleteness of the fossil record. These confusing paleontological facts permit a more extensive taxonomic carving up of the clades vertically than would be otherwise possible. This does not mean, however, that such holophyla alone do or can reflect evolutionary history.
37. How could we contemplate phylogeny without the persistence of homologous similarities of varying antiquity? Highly and causally corroborated correlations of homologies and synapomorphies in different lineages attest to the fact that mosaic evolution validates the transformational analysis of traits independent of a taxogram-driven "transformational" analysis that is *a posteriori*. Furthermore, whatever the rate of evolution of events that produce the mosaic patterns, these episodic changes are also gradual, as gradualism in the Darwinian

sense is rate-independent, as it has been pointed out too many times already (Szalay 1999a).

38. Employment of algorithms for decision making about "homology" *vs* "homoplasy" aim for a "falsifiable genealogy". This is done to fulfill perceived needs for notions of "consistency" and nomothetic legitimacy, a striving for a deductive "testing" of what is in fact a highly idiographic and idiosyncratic history of life. Such attempted expurgations of the fully Darwinian context of evolutionary change (often artfully returned through the back door) have been largely driven by a position which assumes that analysis of patterns "independent" of tested evolutionary theory will yield a theory of evolution of such generality that it will replace (as advocated by Eldredge & Cracraft 1980) an expanding Synthesis. Nothing of the sort has materialized. Yet parsimony cladists would have one believe that the Darwinian imperatives of ecological competition are somehow not reflected in "objective" analyses of the fossil record. "Objective" in their sense means theory free patterns that somehow supposed to yield new evolutionary generalities free of the encumbrances of tested Darwinian theory. Historical reconstruction is based on testing information against hypotheses.

39. Given either the spotty nature of the fossil record, differential extinction of lineages, or sudden adaptive shifts along with other factors, there are times in known clade histories when major skeletal reorganization becomes obvious. These differences can be between major groups, or, on lower levels, within a closely related cluster. These types of differences are the usually recognized gaps in the nature of skeletal morphology between genus and family level taxa, particularly when the fossil record is incomplete. These watershed points in time probably occur when certain new mechanical demands are coupled to a specific size, or to other biological factors such as novel behaviors. These may force a major readjustment of locomotor behaviors and their frequencies, and hence the attendant mechanical loads that supply the selectional parameters, given the initial and boundary conditions in the context of heritage. These events result in highly diagnostic morphological departures and their subsequent future constraints. The origin of the first mammal lineage, as well as that of the various major groups, was the result of such events. It makes sense to us to look for signatures of such reorganizations in order to delineate monophyletic taxa.

40. The doctrinaire practice of recovering cladogeny-cum-taxa through parsimony renders the striving for "holophyla only" approach to be a parallel to what the great 18th century Swedish taxonomist intended taxa to be. Namely, instead of all taxa having essences in pre-Darwinian times, now the vision of holophyla that do not come from other taxa (but share nodes) are now in vogue in taxic analyses. The additional consequence of the parsimony-based cladistic search for "all uniquely shared similarities" (and their putatively equal value regarding the use of such shared characters for algorithm mediated taxic analysis) has resulted in taxonomic rearrangements that cover up a confusion, differently, without attempting to clearly establish taxonomic properties that are not convergent (e.g., see the implied phylogeny in the classification of marsupials by McKenna & Bell 1997, or the classification in Kirsch *et al.* 1997).

41. Also note the designations of "Miacidae" and "Viverravidae" by these authors in their attempt at expurgation of suspected paraphyla.

42. As an example, this is stated by Bromham *et al.* (1999). These authors, following a number of molecular phylogenists, consider the monotremes and the Metatheria to be a clade, just as they consider Guinea pigs (exclusive of other rodents) and Primates to be a clade as well.

43. The study of Palma & Spotorno (1999) on a sequence of about 800 base pairs on the mitochondrial gene rRNA 12S in 18 genera confirms the australidelphian status of *Dromiciops*, but it is rather equivocal regarding other marsupials. Peramelids and caenolestids were considered to be sistergroups but without a firm position within the Metatheria.

44. All of these taxa are stem-based concepts because monophyletic groups (i.e. both paraphyletic and holophyletic ones) are clusters of lineages derived from a single stem. Adherence to an exclusive practice of node-based reconstruction of taxic history avoids the issue of evolutionary change from a specific (real) lineage-cum-taxon. To reiterate, were these lineage chunks known, they would be named as taxa and, therefore, would be paraphyletic.

45. Hindfoot reversal is highly characteristic of obligate arborealists (Jenkins & McClearn 1984) or groups that had an arboreal ancestry even if new lineages became terrestrial (e.g., dasyurids, tupaiids, marmots, ground squirrels, etc.). See the concept of morphotype locomotor mode in Szalay & Dagosto (1980).

46. Such a pattern in kangaroos may be a hitherto not understood adaptive aspect of their highly evolved locomotion.