

# Phylogenetic and functional affinities of *Babakotia* (Primates), a fossil lemur from northern Madagascar

(Palaeopropithecidae/primate evolution/postcranium)

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**ABSTRACT** Recent paleontological expeditions to the Ankarana range of northern Madagascar have recovered the partial remains of four individuals of a newly recognized extinct lemur, *Babakotia radofilai*. Craniodental and postcranial material serve to identify *Babakotia* as a member of the palaeopropithecids (also including the extinct genera *Palaeopropithecus*, *Archaeoindris*, and *Mesopropithecus*). Living indrids form the sister group to this fossil clade. The postcranial anatomy indicates that *Babakotia* was a medium-sized ( $\approx 15$  kg) indroid whose inferred positional behaviors were primarily slow climbing and hanging. Although it is probable that a leaping component typified the ancestral positional repertoire of all Malagasy lemurs, the mosaic nature of the locomotor skeleton of *Babakotia* further suggests that vertical climbing and hang-feeding rather than ricochet leaping were primitive for indrids and palaeopropithecids and that the dramatic saltatory adaptations of the living indrids postdate the divergence of these two lineages.

*Babakotia radofilai* is the first new genus of extinct "subfossil" lemur to be discovered in Madagascar since 1909 (1, 2). All of the fossil remains of this genus recovered to date were found in Antsiroandoha cave in the Ankarana Range of northern Madagascar (3). Field seasons from 1988 to 1990 have yielded parts of four individuals, including the type specimen at Antananarivo University (UA/LPV-8713; upper jaw plus postcranial fragments), another maxillary fragment [Duke University Primate Center (DUPC) 9144], numerous parts of a subadult (DUPC 9116), including craniodental fragments and many postcrania, and additional fragmentary postcrania (DUPC 9921). The dental formula  $2 \cdot 1 \cdot 2 \cdot 3$  and maxillary dental morphology clearly ally *Babakotia* with the indroid superfamily of Malagasy primates and more specifically with indrids (*Avahi*, *Propithecus*, and *Indri*) and palaeopropithecids (*Palaeopropithecus*, *Archaeoindris*, and *Mesopropithecus*) as opposed to archaeolemurids (*Archaeolemur* and *Hadropithecus*) (2). However, analysis of cranial and dental characters alone has proven to be inconclusive regarding the more precise affinities of *Babakotia* within the indrid-palaeopropithecid group. We believe that the postcranial evidence presented here serves to clarify the issue of phylogenetic affinities and offers an opportunity to assess the locomotor adaptation of this new genus. Taken together, the available information gleaned from the fossil remains of *Babakotia* leads us to offer a new phylogeny for indroid primates and an alternative hypothesis for the evolution of locomotion and skeletal design.

## Craniodental Anatomy and Tooth Shape

With an estimated body mass of just over 15 kg, *Babakotia* is a medium-sized indroid somewhat larger than the largest living indrid (*Indri*) but similar in size to several of the smallest extinct lemurs, *Mesopropithecus* and *Pachylemur* (4). A detailed description of the maxillary dentition of *Babakotia* exists (2), but several important features merit mention here (Fig. 1 compares the type maxilla of *Babakotia* to that of *Mesopropithecus*). *Babakotia* maxillae can be distinguished readily from other indroids by their possession of more laterally compressed and mesiodistally elongated postcanine teeth (with especially elongated upper premolars and third molar), a prominent mesial projection of the crown of the upper anterior premolar beyond the cervix, and incipient bilophodonty of the second molar. The palate also appears elongate, narrow, and squared off mesially. In this last respect, *Babakotia* exhibits a condition more fully developed in *Palaeopropithecus* and *Archaeoindris*. As in most indroids, the root of the zygoma begins between the first and second maxillary molars. The type specimen possesses a very prominent malar tubercle that is anteriorly situated (opposite the distal moiety of the first molar); in this last respect *Babakotia* is more similar to *Palaeopropithecus* than to either extant indrids or *Mesopropithecus*.

A few additional characteristics ally *Babakotia* generally with the palaeopropithecids and indrids but not specifically with any one species. The central upper incisors are larger than the lateral and separated by a small gap; the cheek teeth are laterally compressed, the premolars more so than the molars; the premolar series is about two-thirds as long as the molar series;  $M^2$  is squarer than  $M^1$  and possesses more transversely aligned mesial and distal pairs of cusps;  $M^3$  is smaller than  $M^1$  and  $M^2$ .

Similarity in overall tooth shape in *Babakotia* and all other indroids [except for the newly recognized *Propithecus tattersalli* (5)] was assessed by distance measures and clustering methods. We first created buccolingual/mesiodistal ratios for each tooth from the canine to last molar in all living and extinct indroids; the  $P^2$  of the three-premolar archaeolemurids was omitted to facilitate interspecific comparisons. Following standardization to Z scores to weight each ratio equally, mean shape variables for each species were used to compute average taxonomic distances among taxa, and this  $13 \times 13$  matrix was summarized using six different clustering algorithms (6, 7): UPGMA, WPGMA, single linkage, complete linkage, and  $\beta$ -flexible with  $\beta$  equal to 0.25 and 0.50. Most clustering methods did an excellent job of capturing the distance structure as reflected in cophenetic correlations

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Abbreviations: DUPC, Duke University Primate Centers; UA/LPV, Université d'Antananarivo/Laboratoire de Paléontologie des Vertébrés.

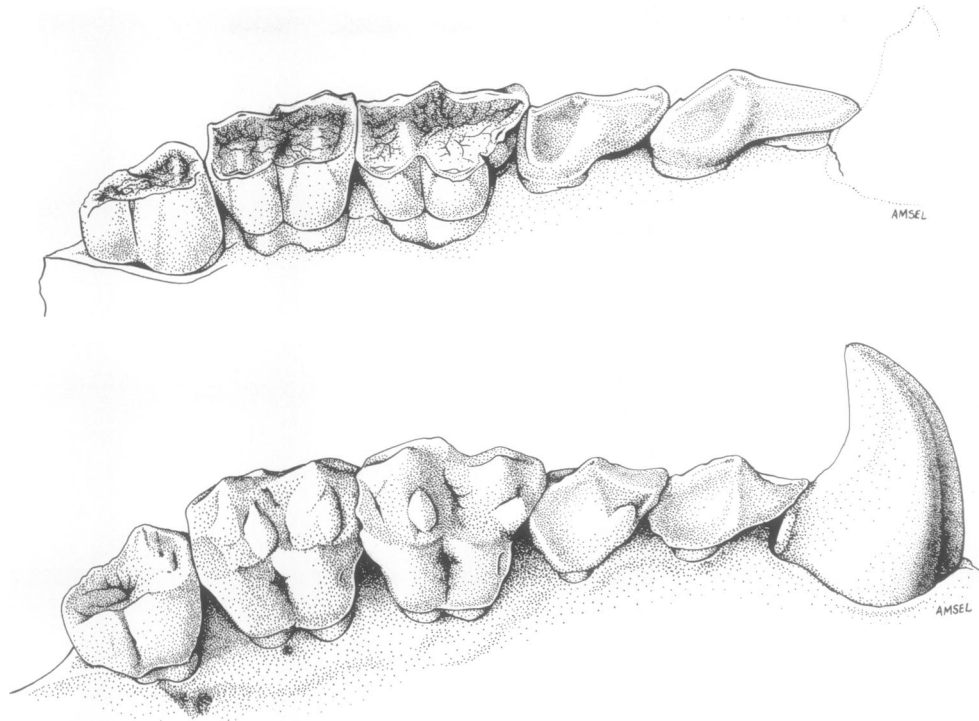


FIG. 1. Comparison (not to scale) of the maxillary dentition of the type specimen of *B. radofilai* (UA/LPV-8713; *Upper*) to *Mesopropithecus globiceps* (Laboratoire d'Anatomie Comparee, Paris; *Lower*). The postcanine tooth row of *Babakotia* is 45 mm long; that of the *Mesopropithecus* specimen is 31 mm long. Note the relatively long and narrow premolars of *Babakotia*.

around 0.9. Fig. 2 presents the strict consensus phenogram (Fig. 2A) of all six methods along with the UPGMA (Fig. 2B) and  $\beta(0.5)$ -flexible (Fig. 2C) solutions. The strict consensus phenogram underscores the distinctiveness of the archaeolemurids, which have relatively short and broad teeth. The second major cluster unites all other indroids, which have relatively longer and narrower postcanine teeth. Within this latter group, the extant indrids share enough similarity in tooth shape to form their own cluster regardless of method used (as do *Avahi* and *Indri* within this cluster). The two species of *Mesopropithecus* also always cluster together as do the large-bodied species of the *Palaeopropithecus*–*Archaeoindris* group. The findings most relevant to the issues at hand are that *Babakotia* either joins the nonarchaeolemurid cluster as its last member (e.g., UPGMA algorithm; Fig. 2B) or links to *Mesopropithecus* (e.g., the  $\beta$ -flexible algorithm; Fig. 2C). The former phenogram emphasizes the unique narrowing and elongation of the premolars and third molar in *Babakotia* (and it also allies *Mesopropithecus* with *Palaeopropithecus*–*Archaeoindris*), whereas the latter reflects the position of *Mesopropithecus* as the minimum link to *Babakotia*. In sum, although *Babakotia* is most similar in overall tooth shape to *Mesopropithecus*, the peculiarly buccolingually compressed and mesiodistally elongated premolars and last molar of *Babakotia* serve to distinguish this genus from all other indroids.

#### Postcranial Remains and Their Affinities

The only postcrania associated with the type specimen of *Babakotia* are portions of the shafts of a right femur and a left humerus (2). The subadult skeleton (DUPC 9116) recovered in the 1989 and 1990 field seasons includes craniodental remains (e.g., parts of the left and right petrous portions of the temporal bones, the right occipital condyle, an edentulous mandibular fragment, a left  $M^1$ , and some unidentified fragments), but its primary significance resides in the wide variety of postcranial elements preserved. These include elements of

the axial skeleton (two partial lumbar vertebrae, one cervical vertebra, and one caudal vertebra), parts of the upper extremity (medial portion of the right clavicle, most of the left ulna, distal third of the left radius, most of the left carpus, a complete right fourth metacarpal, a fragmentary left fourth metatarsal, a left pollical proximal phalanx, and distal parts of two proximal phalanges) and parts of the lower extremity (the distal end of the right femur, part of the left femoral diaphysis, a portion of the right greater trochanter, left fibular head and shaft fragments, a virtually complete right calcaneus, and the distal half of one metatarsal). The 1990 field season added other fragmentary shafts and right proximal femur (DUPC 9921) to the inventory of postcranial remains. Detailed descriptions of these remains will be presented elsewhere, but their implications for function and phylogeny serve as our focus here. Fig. 3 illustrates part of this postcranial sample.

Four regions of the locomotor skeleton are sufficiently complete to permit a multivariate assessment of the morphological affinities of *Babakotia*: proximal ulna, proximal femur, distal femur, and lumbar vertebra. To broaden the taxonomic and adaptive base of our comparisons, we contrast *Babakotia* with two relatively large-bodied living Malagasy species (*Indri indri* and *Varecia variegata*) and several extinct Malagasy lemurs, including three indroids (*Palaeopropithecus maximus*, *Mesopropithecus*, and *Archaeolemur majori*) as well as *Pachylemur jullyi*, and *Megaladapis edwardsi*. For each region a suite of measurements was taken, and shape measurements were created by dividing each variable by the geometric mean of the entire suite (8). This resulted in 25 region-specific shape variables: 5 for the proximal ulna (olecranon lever arm, span of the sigmoid notch, mid-sigmoid breadth, height of the proximal radioulnar facet, and breadth of the olecranon process); 5 for the proximal femur (average femoral head diameter, breadth of the greater trochanter, neck height, neck breadth, and biomechanical neck length), 7 for the distal femur (width of patellar groove, biepicondylar breadth, intercondylar width,

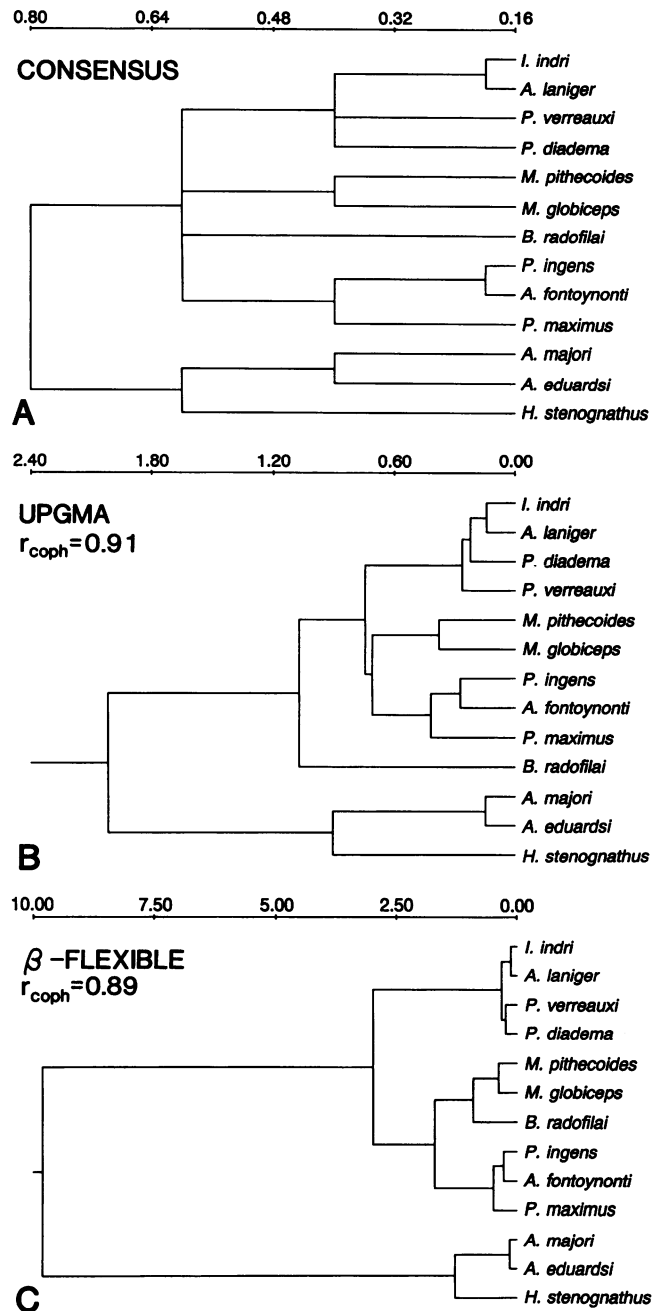


FIG. 2. Clustering of indroid taxa based on average taxonomic distances derived from maxillary tooth shape. (A) Phenogram is the strict consensus clustering from six different algorithms. (B) Phenogram is the UPGMA solution, which emphasizes the overall narrowness of the *Babakotia* dentition and places this species on the periphery of the cluster formed by indrids and the remaining palaeopropithecids. (C) Phenogram is the  $\beta(0.5)$ -flexible solution; this method reduces the impact of outliers on the resulting clusters and places *Babakotia* next to *Mesopropithecus* (which has the minimum spanning tree link to *Babakotia*). The cophenetic correlation between the original distance matrix and that implied by the phenograms is indicated by  $r_{\text{coph}}$ .

medial condyle breadth, lateral condyle breadth, anteroposterior projection of the medial condyle, and anteroposterior projection of the lateral condyle), and 8 for the lumbar vertebra (anterior height of the body, inferior width of the body, inferior anteroposterior diameter of the body, pedicle height, pedicle breadth, lamina height, lamina width, and spine length; the first three vertebral body measurements required some reconstruction in *Babakotia*).

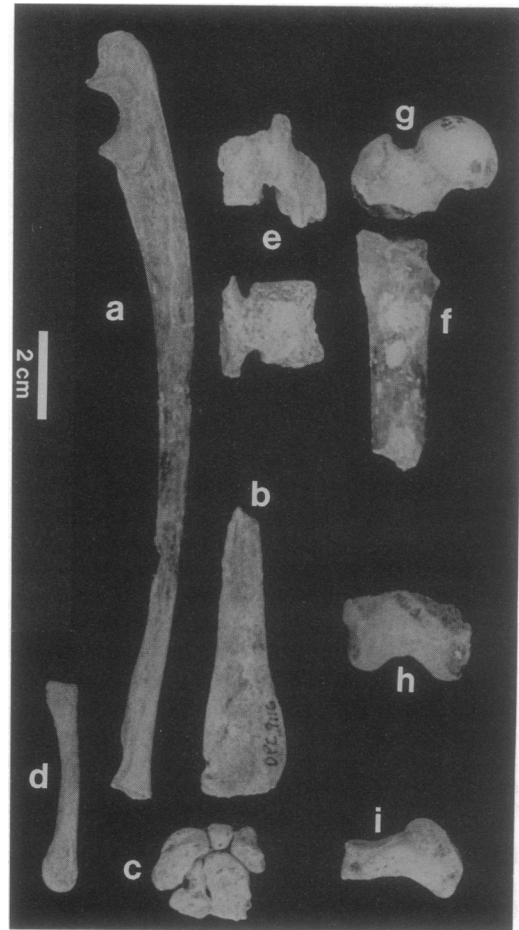


FIG. 3. Several of the most informative elements of the partial postcranial skeleton of *Babakotia*, including the ulna (a), distal half of radius (b), most of the carpus (c), the fourth metacarpal (d), two partial lumbar vertebrae (e), three femoral fragments (f-h), and a complete calcaneus (i).

Following standardization, the 25 shape variables were used to calculate an  $8 \times 8$  average taxonomic distance matrix. Because clustering did a poor job of summarizing this matrix, we present the results of a three-dimensional principal coordinates ordination in Fig. 4. The correlation between the distances implied by this three-dimensional representation and those of the original dissimilarity matrix is 0.97, indicating that most of the information is adequately summarized in this ordination space. These three axes account for  $\approx 80\%$  of the total variance (45.3%, 19.7%, and 14.5% for axes 1, 2, and 3, respectively).

Axis 1 separates *Indri* at one extreme from *Palaeopropithecus* at the other; in other words, leapers are maximally contrasted with and distinguished from nonleaping, suspensory forms along this most important axis. Correlations between shape variables and the scores on axis 1 indicate that animals with short lumbar spinous processes, short lumbar bodies, anteroposteriorly flattened and mediolaterally expanded distal femora, short biomechanical femoral necks, and short olecranon lever arms (i.e., *Palaeopropithecus*) are being differentiated from animals with the opposite characteristics (i.e., *Indri*). *Babakotia* occupies an intermediate position along this axis. Axes 2 and 3 do not lend themselves to easy functional interpretation but do highlight certain idiosyncratic features of several taxa. For example, *Archaeolemur* is separated maximally from *Varecia* along axis 2 primarily on the basis of neural arch shape (pedicle and lamina heights) versus relative breadth of the medial femoral

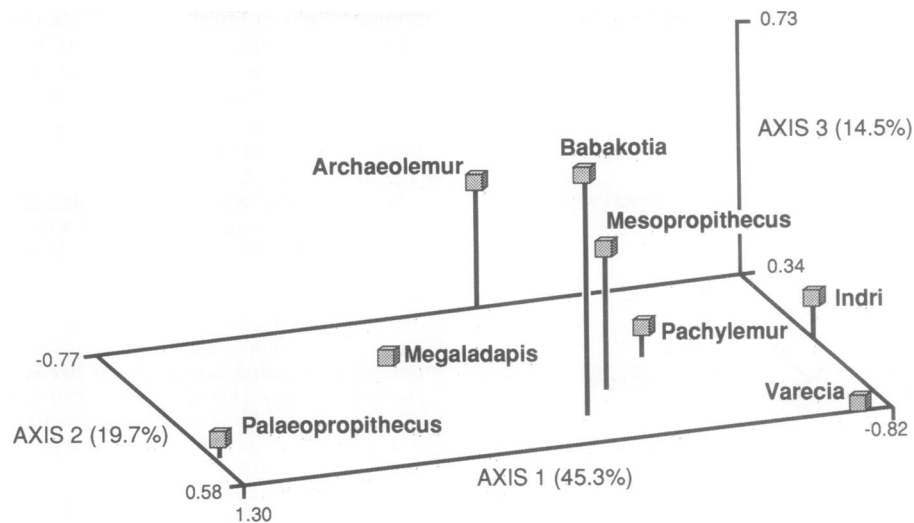


FIG. 4. The three-dimensional principal coordinates ordination of the average taxonomic distance matrix created from 25 region-specific shape variables. The percentage of variance explained by each axis is indicated. Axis 1 is the most important axis of shape variation and separates leapers (e.g., *Indri*) from suspensory species (e.g., *Palaeopropithecus*); *Babakotia* occupies an intermediate position along this axis and is most similar overall to *Mesopropithecus*.

condyle. Radioulnar facet height contributes significantly to axis 3 and is especially large in *Babakotia*. In overall phenetic terms, as judged again by minimum distance, *Babakotia* is most similar to *Mesopropithecus*; as such, this finding recalls the results of the dental shape analysis.

A closer focus on specific traits of clearcut functional significance (including some that do not appear in the phenetic evaluation because they are difficult to quantify) provides a clearer and complementary perspective on the adaptive and phylogenetic affinities of the postcranium of *Babakotia*. It also underscores the mosaic nature of indroid similarities and differences.

The forelimb of *Babakotia* is in many ways a more robust version of that seen in extant indrids—i.e., while widths and circumferences are consistently greater, absolute lengths of most of the forelimb elements of *Babakotia* fall well within the range of *Indri*. In other important aspects of its morphology, it is quite similar specifically to palaeopropithecids. Overall robusticity is most like that seen in *Mesopropithecus*; this generalization is clearly true for the humerus, ulna, radius, carpus, and metacarpus. The anteroposteriorly compressed radial shaft flares distally; its ventral surface is quite flat. In these features it resembles *Mesopropithecus* more than *Palaeopropithecus*, although some degree of flattening characterizes all indroids. The reconstructed maximum length of the nearly complete ulna of *Babakotia* is 189 mm, within the range of *Indri* in spite of its greater robusticity; it is slightly longer and more robust than an undescribed specimen of *Mesopropithecus* ( $\approx 174$  mm) from the same cave. The shaft of the *Babakotia* ulna also shares a marked ventral keel with *Mesopropithecus*. The carpus of *Babakotia*, represented by a scaphoid, lunate, triquetrum, hamate, and capitate, is slightly longer and much more robust than the same region in *Indri*, but the overall morphology is quite similar (e.g., exhibiting fusion of the os centrale and scaphoid, a relatively large hamate, and a strongly developed facet on the triquetrum for articulation with the ulnar head). The right fourth metacarpal and pollical proximal phalanx are more robust versions of the same bones in *Indri*, although, with a ratio of phalangeal length to metacarpal length of 0.48, the pollex of *Babakotia* may be slightly reduced in relative length (two *Indri* and two *Propithecus* specimens range from 0.50 to 0.57).

In other aspects of upper limb anatomy *Babakotia* is more similar specifically to *Palaeopropithecus* than to *Mesopro-*

*pithecus* or extant indrids. As in *Palaeopropithecus* the metacarpal heads possess a long curvilinear surface with maximum metacarpophalangeal curvature occurring in extreme flexion. This joint in *Babakotia*, however, lacks the highly derived wedge-like configuration typical of *Palaeopropithecus*. As in *Palaeopropithecus* and *Mesopropithecus* (9), the proximal phalanges (excluding the pollical one) are curved and bear marked flexor ridges.

The morphology of the hindlimb and lumbar vertebrae in *Babakotia* is even more similar to *Palaeopropithecus* and *Mesopropithecus* and diverges strongly from that seen in extant indrids. For example, the femoral head is relatively large and more cranially oriented; as a consequence, the greater trochanter appears reduced in height (and is relatively narrower). The femoral diaphysis is relatively flat anteroposteriorly; the distal epiphysis is also very expanded mediolaterally and flattened anteroposteriorly (exceeded only by *Palaeopropithecus* in this respect). The patellar articular surface of the distal femur is very broad and flat without elevated medial and lateral margins. The calcaneus is relatively short and possesses a prominent, plantar directed heel process like that of *Palaeopropithecus* (10). In virtually all of these respects, *Babakotia* is intermediate between *Mesopropithecus* and *Palaeopropithecus*.

We interpret this constellation of characteristics as strong evidence for a significant component of suspensory behavior (especially hindlimb suspension) in the positional repertoire of *Babakotia*. We also believe they constitute a suite of shared derived characters that places *Babakotia* firmly within the family Palaeopropithecidae.

## Conclusions

Within the palaeopropithecid clade, which we believe includes *Mesopropithecus*, *Palaeopropithecus*, *Archaeoindris* (11), and now *Babakotia*, we propose that *Babakotia* is the sister species of the *Palaeopropithecus*–*Archaeoindris* group and that *Mesopropithecus* joins this clade rather than that of the extant indrids (12). Despite radical differences in their hindlimb and lumbar morphology, the indrids and the newly constituted palaeopropithecids can be regarded as sister taxa distinct from the archaeolemurids. This phylogenetic hypothesis of relationships is depicted in the cladogram of Fig. 5.

The total morphological pattern of postcranial features seen in *Babakotia* points to a significant commitment to

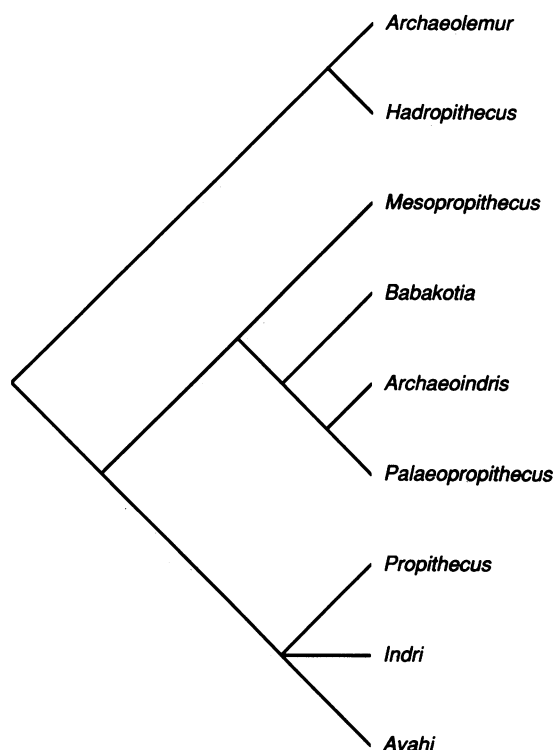


FIG. 5. This cladogram summarizes our current hypothesis as to phylogenetic relationships among the indroid primates of Madagascar. Note that *Babakotia* is depicted as the sister taxon of the *Palaeopropithecus*–*Archaeoindris* clade and that *Mesopropithecus* is considered a member of the palaeopropithecid rather than the indrid clade.

suspensory behaviors, especially those arboreal activities that involve hindlimb suspension but no leaping. Although not as specialized a suspensory form as the sloth-like *Palaeopropithecus* (13–15), *Babakotia* was clearly well along this adaptive path; as such, it provides a plausible structural model for the ancestral condition of the clade that includes *Babakotia*, *Palaeopropithecus*, and *Archaeoindris*. Unlike extant indrids, which climb upon, cling to, and leap between vertical supports and which also assume hang-feeding postures (10, 16), *Babakotia* had clearly sacrificed its leaping capability and instead emphasized climbing and hanging. Although we acknowledge the probability of a leaping component in the ancestral positional repertoire of Malagasy primates (17, 18), we propose that vertical climbing-clinging and hang-feeding rather than ricochetleaping and bipedal

hopping were primitive for indrids and palaeopropithecids. After the separation of the two lineages, thigh-powered vertical saltation developed as the dominant element in the locomotor repertoire of the Indridae (19), whereas adaptations for slow, quadrupedal suspensory progression evolved in the Palaeopropithecidae.

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