

Widanelfarasia, a diminutive placental from the late Eocene of Egypt

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Contributed by Elwyn L. Simons, December 15, 1999

The lower dentition of *Widanelfarasia* (new genus), a diminutive late Eocene placental from the Fayum Depression in Egypt, is described. *Widanelfarasia* exhibits a complex of features associated with incipient zalambdodonty and at least three unequivocal apomorphies [loss of P₁, an enlarged I₂ (relative to I₃), and a basal cusp on I₂], which provide weak support for its placement as a possible sister taxon of either a tenrecid–chrysochlorid clade or of solenodontids. The former hypothesis gains additional support from biogeographical evidence, but both scenarios are currently tenuous as *Widanelfarasia* is clearly not truly zalambdodont. Phylogenetic hypotheses positing affinities with tenrecids alone or chrysochlorids alone must invoke either convergent acquisition of zalambdodonty in these taxa or autapomorphic reversal in *Widanelfarasia*. Given these considerations, a relationship with more generalized taxa from the Laurasian Paleogene (e.g., geolabidids, nyctitheriids, leptictids) cannot yet be ruled out. Comparisons with other Paleogene Afro-Arabian forms are generally inconclusive. A relationship with the earlier Eocene *Chambilestes* from Tunisia—currently represented by a single specimen preserving P⁴–M³—seems possible based on the geometry and predicted occlusal relationships of these teeth, but cannot be confidently determined until these two taxa come to be represented by common diagnostic elements. *Todralestes* (late Paleocene, Morocco) exhibits general phenetic similarities to *Widanelfarasia*, but it is not yet known whether this taxon shares any of *Widanelfarasia*'s unequivocal dental apomorphies. Pending the recovery of more informative material, we tentatively refer *Widanelfarasia* to *Placentalia incertae sedis*. Truly zalambdodont placentals remain conspicuously absent from the Paleogene of Afro-Arabia.

Recent paleontological discoveries from the Cretaceous (1–4) and early Paleogene (5–10) of Morocco indicate that Afro-Arabia served as an important center for the early diversification of various mammaliaforms, including eutherians.[§] The evolution of primitive placentals of “insectivoran” grade remains poorly documented on this continent before the early Miocene, however, and only within the last decade have such mammals been described in any detail; most taxa are still represented almost entirely by isolated teeth. Eutherians formally or informally allocated to Lipotyphla [a potentially para- or polyphyletic assemblage (e.g., ref. 12) conventionally defined to include a crown clade of extant erinaceids, soricids, talpids, tenrecids, chrysochlorids, and *Solenodon*] have been recovered from five Paleogene localities on the Afro-Arabian plate—the Ouarzazate Basin [late Paleocene, Morocco (5–9)], El Kohol [early(?) Eocene, Algeria (13)], the Fayum Depression (late Eocene–early Oligocene, Egypt), Chambi [early(?) Eocene, Tunisia (14)], and Taqah [early Oligocene(?), Oman (15)]. As yet, Gheerbrant (9) has assigned the Moroccan Paleocene adapisoriculid *Afrodon* and possible representatives of *Adapisoriculus* and *Garatherium* to Lipotyphla with a query, as have Gheerbrant and Hartenberger (14) with *Chambilestes*, a newly described form from the Eocene of Tunisia; Mahboubi *et al.* (13) have noted similarities of a species from El Kohol designated “Lipotyphla indet.” to Laurasian geolabidids and nyctitheriids. A number of cimolestans or “proteutherians” of Laurasian affinities (*Palaeoryctes*,

Cimolestes, *Aboletylestes*, indeterminate didelphodontines) as well as a possible endemic form referred to Proteutheria, *Todralestes*, have also been described from the Ouarzazate Basin (5, 7, 8).

These diminutive north African eutherians have provided new evidence for the presence of intermittent biogeographical connections between Afro-Arabia and Laurasia during the early Cenozoic (16) and have helped to elucidate a considerable degree of biogeographical cosmopolitanism for palaeoryctoids through the late Cretaceous and early Paleogene (e.g., ref. 17). Due to the limited nature of the available material, however, it remains unclear just how the scarce Eocene Afro-Arabian “lipotyphlans” may relate to living and extinct Laurasian forms or to the extant tenrecs and golden moles—two groups whose fossil record appears to extend back only to the early Miocene (18), but which are generally considered to have had a long history of endemic evolution on the Afro-Arabian land mass. Here we report on the lower dentition of a late Eocene placental from the Fayum Depression which may prove to have a direct bearing on these issues.

Systematic Paleontology

Mammalia Linnaeus 1758. *Placentalia incertae sedis* Owen 1837. *Widanelfarasia*, new genus. Type species: *Widanelfarasia boweni*, new species. Age and distribution: Late Eocene, Jebel Qatrani Formation, Fayum Depression, Egypt.

Diagnosis. Differs from tenrecids, chrysochlorids, and other zalambdodont placentals (e.g., solenodontids, apternodontids) in having mesiodistally longer and buccolingually broader talonid basins on M₁–M₃ with three talonid cusps; the hypoconid is relatively well developed. Further differs from solenodontids in having a smaller I₂ with a pronounced posterior basal cusp, a presumably more caniniform canine, slightly more mesially oriented protoconids on P₂–P₃, and larger and more bulbous paraconid on P₄, and from apternodontids in having a relatively large I₂ with posterior basal cusp, less upright and complex P₃, P₄ less molariform and less compressed mesiodistally, no distal decrease in size or height of molars. Differs from most North American geolabidids in having a relatively large I₂ with a posterior basal cusp [as opposed to the bilobed condition of I₂ in *Centetodon* (19)], loss of P₁, lower and more distally placed metaconid on P₄, bulbous and somewhat more mesially oriented paraconid on P₄, well developed precingulid on P₄, slightly less crestiform cusps on lower molars, cristid obliqua which contacts

Abbreviations: DPC, Duke University Primate Center; CGM, Cairo Geological Museum.

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§We use Eutheria here as a stem-based taxon including all living or extinct taxa more closely related to extant placental mammals than to extant marsupials. *Placentalia* is used as a crown group that contains all extant eutherians and their last common ancestor and excludes all other eutherians [e.g., Asioryctitheria (11)].

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Article published online before print: *Proc. Natl. Acad. Sci. USA*, 10.1073/pnas.040549799. Article and publication date are at www.pnas.org/cgi/doi/10.1073/pnas.040549799

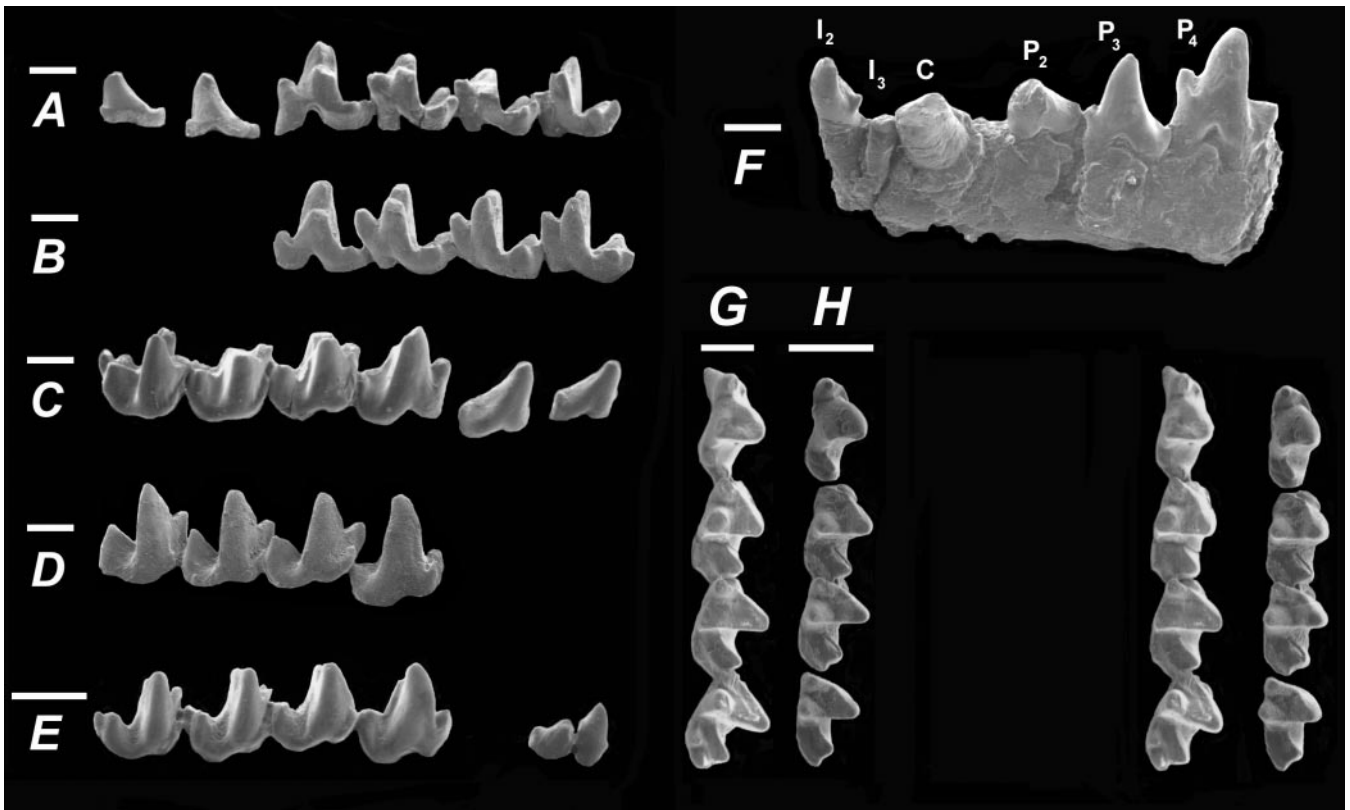


Fig. 1. Lingual views of DPC 15637, *Widanelfarasia bowni*, right P₂–M₃ (A), and cast of CGM 41878, *W. bowni*, left P₄–M₃ (reversed) (B). Labial views of DPC 15637, *W. bowni*, right P₂–M₃ (C); cast of CGM 41878, *W. bowni*, left P₄–M₃ (reversed) (D); and DPC 17427, *W. rasmusseni*, right P₂ and P₄–M₃ (note that labial views are taken from slightly different orientations) (E). (F) Labial view of DPC 17779 (*W. bowni*), left dentary containing I₂, root of I₃, and C–P₄. Note the loss of P₁, the large cross-section and slightly procumbent orientation of the broken canine, and the enlarged I₂ with posterior basal cusp. (G and H) Occlusal stereophotos of the holotypes of *W. bowni* (G, DPC 15637) and *W. rasmusseni* (H, DPC 17427). Note that a thin layer of matrix adheres to the hypoflexids of M₁–M₂ of DPC 17427. (Bars = 1 mm.)

the distal wall of trigonid at or slightly lingual to the metaconid–protoconid notch, slightly more defined entoconid on M₁–M₃, M₃ as large as M₁ and M₂. Differs from Laurasian nyctitheriids in having a relatively large I₂ with a single basal cusp, a presumably larger and more caniniform canine, loss of P₁, taller, less mesially oriented, and more upright premolars, shorter, narrower, and somewhat lower-crowned molar talonids with less sharply defined talonid cusps, taller and slightly more lingual paraconids on M₁–M₃, relatively tall protoconids on all molars (highest on M₃), less disparity in relative height of paraconids and metaconids, relatively larger P₄ with a taller protoconid. Differs from *Micropternodus* in the loss of P₁, having less mesiodistally compressed premolars, a well developed talonid on P₄, and less recumbent protoconids on P₄–M₃. Differs from *Butselia* most notably in having little or no size decrease from M₁–M₃, loss of P₁, a two-rooted P₂, larger paraconid on P₄, and slightly less lingual paraconids on molars. Differs from *Todrallestes* in having a stronger precingulid and a lower, more bulbous, and more mesially oriented paraconid on P₄ as well as more mesially placed metaconids on P₄–M₃ (and thus more labiolingually oriented protocristids). Differs from adapisoriculids such as *Afrodon* in the loss of P₁, having a larger paraconid on P₄, more acute paracristid–protocristid angle on molars, and a more mesially placed metaconid and buccolingually oriented protocristid as well as more pronounced precingulids and narrower talonids. Differs from most cimolestans (e.g., pantolestids, cimolestids) in the loss of P₁ (occurs in palaeoryctids) and in having a semimolariform P₄. Differs from leptictids in having a

relatively large I₂, loss of P₁, shorter and narrower talonids, and deeper hypoflexids.

Etymology. The genus is named for Widan el Faras, two hills which stand as a prominent geological feature in the Fayum Depression and which are capped by the Widan el Faras basalt. The name is Arabic for “ears of the mare.”

***Widanelfarasia bowni*, New Species.** *Holotype.* Duke University Primate Center (DPC) 15637, a right dentary preserving P₂–M₃ and complete ascending ramus, condyle, and angular process (Fig. 1 A, C, and G).

Hypodigm. The type specimen; DPC 17106, a right dentary preserving P₄–M₃ and complete ascending ramus; DPC 17779, a left dentary containing P₂–P₄, I₂, and the roots of the lower canine and I₃; Cairo Geological Museum (CGM) 41878, a left dentary containing P₃–M₃.

Locality and distribution. Quarry L-41, Late Eocene, Jebel Qatrani Formation, Fayum Depression, Egypt.

Diagnosis. Same as for genus.

Description. DPC 17779 (Fig. 1F) preserves the crown of I₂ and the root of I₃. I₂ preserves a posterior basal cusp, and the relative sizes of the roots of these teeth indicate that I₂ is larger than I₃. This specimen also preserves a single oval and somewhat procumbent canine root that is separated from P₂ by a diastema (suggesting the possible presence of a large upper canine).

P₂ is a two-rooted tooth with a mesially oriented protoconid, a very weak anterobasal cusp, and a stronger distal cusp. P₃ is morphologically similar to P₂ but is slightly larger and separated from P₂ by a short diastema (it is likely that the crowding of these

teeth in DPC 17779 is due to distortion; Fig. 1F). P₄ is separated from P₃ by a short diastema and is semimolariform, with a short talonid preserving a small entoconid and a more distal hypoconulid. The metaconid is unworn on DPC 17779 and is clearly intermediate in height between the bulbous and mesially oriented paraconid and the slightly more mesially placed protoconid. The P₄ protoconid is as high as or higher than the protoconids on M₁–M₃. The protoconids of P₄–M₃ are all somewhat labially convex, with this trend reaching its greatest extreme on M₃.

The lower molars are subequal in size. The protoconid is generally about two and a half times as high as the hypoconid on M₁–M₃ (highest on M₃), and the hypoconid is in turn somewhat elevated relative to the entoconid. This differential height relationship of the talonid cusps leads the entire talonid basin to be somewhat lingually canted in distal view. Molar paraconids are all oriented slightly labial to the metaconids and are elevated well above the talonid cusps of the mesially adjacent tooth on M₁–M₃. The roughly labiolingual orientation of the protocristids and slightly more oblique orientation of the paracristids leads to a fairly acute conformation of the trigonid cusps, similar to that seen in the geolabidid *Centetodon*. As is often the case in dentally primitive eutherians, this angle becomes more acute distally, reaching its greatest extreme on M₃. The metaconid is taller than the paraconid on all molars. The talonids are about one-half to two-thirds the length and about two-thirds to three-fourths the width of the trigonids on all molars and preserve three cusps, with the centrally placed hypoconulid being consistently more distal than the entoconid and hypoconid. The cristid obliqua runs mesiolingually to contact the distal trigonid wall at approximately the point of the metaconid–protoconid notch. Precingulids are present on all molars.

Mandibular condyle is transversely elongate and is positioned at or slightly above the occlusal surface of the lower teeth. Coronoid process is tall, rising at an angle of about 70° from the long axis of the dentary. Masseteric fossa tends to be well developed. Angular process is long and distinct, protruding almost as far caudally as the condyle. Position of the mental foramen varies.

Etymology. The species is named for Thomas M. Bown, who has made so many important contributions to our understanding of the geology, paleoenvironment, and vertebrate paleontology of the Jebel Qatrani Formation and who first discovered quarry L-41 with Mary J. Kraus.

***Widanelfarasia rasmusseni*, New Species.** *Holotype.* DPC 17427, a right dentary containing P₂, P₄–M₃, and alveoli for P₃, the canine and I₃ (Fig. 1 E and H).

Hypodigm. The type specimen; DPC 17396, a left dentary containing P₃–M₃.

Locality and distribution. L-41, Late Eocene, Jebel Qatrani Formation, Fayum Depression, Egypt.

Diagnosis. Same as for genus; differs from *W. bowni* in being much smaller (about 60% the size of *W. bowni* based on dental measurements), with slightly narrower talonids on M₂–M₃, particularly on M₃.

Description. Very similar to *W. bowni* in almost all respects; the alveolus anterior to P₂ is relatively large (quite a bit larger than the I₃ alveolus), suggesting that *W. rasmusseni* had a lower canine of approximately the same relative size as that seen in *W. bowni*. The dentary of the holotype has two major cracks, one between the canine alveolus and P₂ and one through the P₂ itself. The anterior half of this tooth has been twisted out of place, giving the P₂ the superficial appearance of being two small teeth.

Etymology. The species is named for D. Tab Rasmussen, in recognition of his many important contributions to our understanding of the vertebrate paleontology and paleoenvironment of the Fayum Depression.

Discussion

Among Paleogene eutherians, the geometry of *Widanelfarasia*'s lower molars (and, in most cases, P₄) exhibits the greatest resemblance to certain geolabidids, nyctitheriids, leptictids, and cimolestans, as well as more enigmatic forms such as the possible plesiosoricid *Butselia* and the late Paleocene *Todralestes* from Morocco. At present it is very difficult to determine, however, how many of the various similarities shared by these taxa are simply primitive features of the crown group Placentalia. As has been noted many times in the past (e.g., refs. 20–23), the polarity of dental characters in primitive Cretaceous and Paleogene eutherians is often ambiguous, and a healthy respect for homoplasy must lead to considerable caution when drawing phylogenetic interpretations from such material (particularly from teeth that tend to lack strong diagnostic features). As an exhaustive cladistic analysis of the available lower teeth of *Widanelfarasia* would be replete with characters of uncertain polarity, we feel that such an exercise is not yet likely to produce many compelling clues as to this taxon's true affinities. Furthermore, consideration of lower dental material alone fails to reflect the strong possibility (based on other morphological and molecular lines of evidence) that many striking dental apomorphies shared by higher taxa (e.g., those between Caribbean *Solenodon* and the Afro-Malagasy zambododonts) are not due to common ancestry (see discussion below). Thus, a brief consideration of *Widanelfarasia*'s few clearly derived features might be positively supplemented to a greater extent by consideration of other sources of data, including patterns of Paleogene biogeography and new molecular data bearing on the interrelationships of extant taxa traditionally placed in Lipotyphla.

Widanelfarasia exhibits three features of the antemolar dentition [loss of P₁, an enlarged I₂ (relative to I₃), and a posterior basal cusp on I₂] which are unequivocally derived within Eutheria. None of these characters provide particularly strong evidence for relationships at higher taxonomic levels, however. The loss of P₁ is not at all rare among “lipotyphlans” and other eutherians of relevance to this study, but retention of P₁ can often be observed in the close living or extinct relatives of those taxa which have lost the tooth, indicating that its loss in various taxa is generally only derived within some lower-level group (and, in most cases, was clearly lost after the acquisition of other apomorphies not seen in *Widanelfarasia*). For instance, while certain crown erinaceids have lost premolars (including P₁), it is evident from various other living and extinct erinaceids that retention of four premolars is a primitive feature within that clade and that premolar loss occurred in certain taxa only after the appearance of crown erinaceid synapomorphies (see, e.g., ref. 24). The same can be said of the common node of the talpid–soricid clade; as *Widanelfarasia* does not exhibit any of the probable dental synapomorphies of this clade (e.g., well developed dilambdodonty), a close relationship with these taxa does not seem likely. Tenrecids, chrysochlorids, solenodontids, and the subfossil nesophontids have all lost P₁, and all of these taxa share a similar pattern of premolar loss with *Widanelfarasia* in that P₂ remains two-rooted and premolars are occasionally separated by diastemata (as in *W. bowni*). Among relevant Paleogene taxa, *Butselia*, nyctitheriids, leptictids, and most geolabidids and cimolestans retained P₁, but this tooth was lost in apternodontids [a group which may also be closely related to the solenodontids (e.g., ref. 25)], in palaeoryctid palaeoryctoids such as *Aptoryctes* (26) and *Eoryctes* (27), and, among geolabidids, in certain species of *Centetodon* (28). Schlijker (25) suggested that *Micropternodus borealis* had lost P₁, but various authorities (29–31) have challenged this assertion; regardless, the affinities of *Micropternodus* arguably lie with Asian forms such as *Sarcodon*, *Prosarcodon*, *Sinosinopa*, and *Carnilestes* (refs. 32

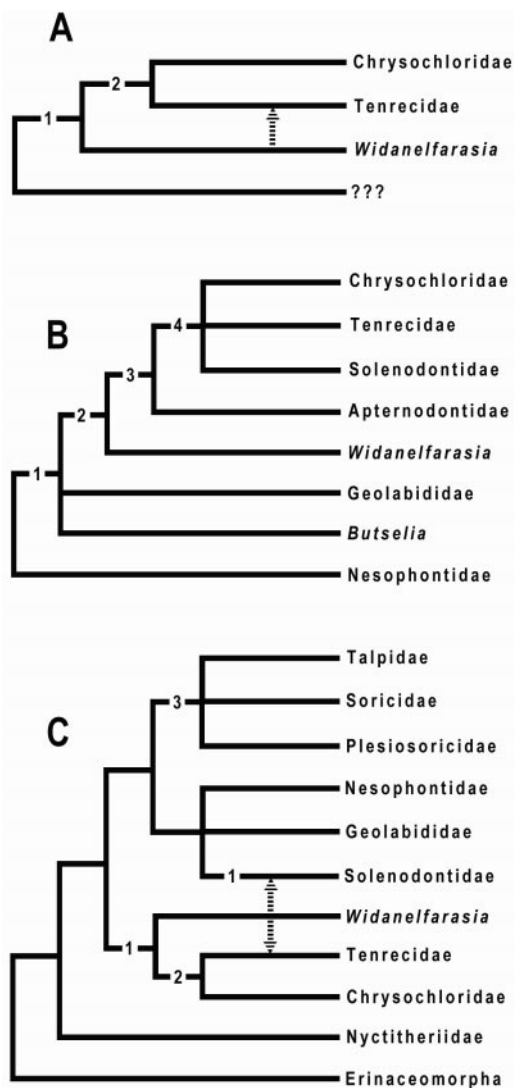


Fig. 2. Three of many feasible options for *Widanelfarasia*'s systematic position given differing assumptions of placental interrelationships. Possible lower dental synapomorphies are given at selected nodes. (A) The option preferred (but still weakly supported) by this study, under the assumption that tenrecids and chrysochlorids are sister taxa, *Solenodon* is unlikely to be the extant sister taxon of a tenrecid–chrysochlorid clade, and the extant sister taxon of the tenrecid–chrysochlorid clade is currently unclear—molecular data (e.g., ref. 12) suggest that it is some segment of “Afrotheria.” Nodes: 1, loss of P_1 , enlarged I_2 with basal cusp, possibly deep hypoflexids and a semimolariform P_4 ; 2, marked reduction of molar talonids, possibly a reduction of the lower canine. This option gains additional support from biogeographic considerations. (B) Possible relationships under the assumption that living and extinct zalambdodont placentals are monophyletic. Nodes: 1, semimolariform P_4 ; 2, loss of P_1 , increased depth of hypoflexids; 3, marked reduction of molar talonids; 4, relatively large I_2 . (C) *Widanelfarasia* mapped onto a cladogram of Lipotyphla as suggested (in part) by Butler (33). Lower dental features considered in this paper are quite labile given this scenario. Nodes: 1, loss of P_1 , enlarged I_2 with basal cusp, deep hypoflexids; 2, marked reduction of molar talonids, possibly a reduction of the lower canine; 3, increased dilambdodonty.

and 33, but see also ref. 34), all of which primitively retain P_1 . It is not yet known whether the Afro-Arabian todralestids retained P_1 .

An enlarged I_2 is seen in *Solenodon*, but not in *Nesophontes* [arguably one of *Solenodon*'s closer relatives (e.g., 31, 33)], which has bilobed incisors of subequal size. A trend toward subequal

polycuspidate incisors is also seen among geolabidids (19) and nyctitheriids (35), but it is not yet clear whether this morphology is derived from the sort of pattern seen in *Widanelfarasia*, chrysochlorids, and many tenrecids, which exhibit an enlarged I_2 relative to I_3 with a basal cusp. Crown soricids have enlarged incisors of uncertain homology, but this apomorphy clearly appeared after the talpid–soricid clade acquired various dental specializations which *Widanelfarasia* lacks. *Butselia* (36), *Plesiosorex* (37), the palaeoryctids *Palaeoryctes* (26, 38), *Aptoryctes* (26), *Eoryctes* (27), and possibly *Naranius* (39) all have an enlarged I_2 relative to I_3 ; apternodontids show a reversal of this trend in that I_2 is markedly reduced (31). *Micropternodus* has a slightly enlarged I_2 , but more primitive micropternodontids such as *Prosarcondon* and *Carnilestes* have somewhat spatulate incisors of approximately equal size, with I_2 being only slightly larger than I_3 (32, 34). This pattern is also seen among various leptictids (e.g., ref. 21) and many of the controversial “erinaceomorphs” [e.g., amphilemurids (40)], although *Litolestes* [an erinaceid according to Novacek (24); a possible dormaalid according to Butler (33)] has subequal trilobed incisors (41), and the sespedectine *Proterixoides* has an I_1 and I_2 that are enlarged relative to I_3 (42). Lower incisors of *Todralestes* have not yet been discovered.

These comparisons indicate that *Widanelfarasia*'s three unambiguously apomorphic dental features can only be matched by tenrecids, chrysochlorids, solenodontids (variably), and possibly palaeoryctids among the living and extinct eutherians considered. If other features of *Widanelfarasia*'s dentition are apomorphic within Eutheria (e.g., semimolariform P_4), support rises for a relationship with the extant zalambdodonts to the exclusion of palaeoryctids, which generally have a relatively simple P_4 . Other potentially derived features of *Widanelfarasia* are related to a pattern of incipient zalambdodonty which is also observable in other Paleogene taxa such as *Butselia* and various geolabidids. These forms tend to exhibit taller trigonids, relatively short and narrow talonids, deep hypoflexids (which accommodate a relatively large occluding paracone), well developed precingulids, and taller, more prominent (and more lingually placed) paraconids. Some or all of these features are exaggerated in true zalambdodonts such as the living tenrecids, chrysochlorids, and solenodontids and the extinct apternodontids, all of which have enlarged the paracone and lost the metacone on the upper molars [with the exception of the tenrecid *Potamogale*, whose small metacone is likely to be secondarily acquired (e.g., ref. 31)]. The polarity of the features associated with this pattern of incipient zalambdodonty are admittedly still unclear, however, due in part to the presence of some of these features in various cimolestans. Given these considerations, it can only be said with confidence that *Widanelfarasia* exhibits at least three apomorphic characters in the antemolar dentition and a suite of features in P_4 – M_3 that are more similar to dental patterns seen in certain lipotyphlan-grade placentals than in most “proteutherians,” and that the distribution of *Widanelfarasia*'s derived (and potentially derived) features among the former taxa most clearly supports (albeit weakly) affinities with either tenrecids, chrysochlorids, or solenodontids—all of which are, however, highly derived in being truly zalambdodont.

Various studies over the last half-century (31, 33, 36) have rejected the monophyly of living and extinct zalambdodont placentals and have supported a close relationship between *Solenodon* and the subfossil Caribbean dilambdodont *Nesophontes* (Fig. 2C), but there has been little consensus as to whether these latter taxa should be placed as sister to soricids (e.g., ref. 31) or to a talpid–soricid clade (e.g., ref. 33). Most recently, Asher (43) presented multiple phylogenetic analyses of morphological data which tended to support a clustering of solenodontids, apternodontids, and the Afro-Malagasy zalambdodonts to the exclusion of other “lipotyphlans.” Clearly, there is morpho-

logical support for various phylogenetic scenarios and, until recently, very little new data which could aid the resolution of this debate.

Importantly, the difficulties associated with phylogenetic analysis of living and extinct eutherian “insectivores” have been further compounded in recent years by molecular data which strongly suggest that Lipotyphla is para- or polyphyletic (e.g., ref. 12). Various nuclear and mitochondrial genes have supported a supraordinal clade of tenrecs, golden moles, elephant shrews, aardvarks, and paenungulates (“Afrotheria”) (12, 44, 45) and a tenrecid–chrysochlorid clade within Afrotheria for which Stanhope *et al.* (12) erected the new order “Afrosoricida.” These data also suggest that *Solenodon* joins talpids and soricids in a distantly related clade (12), but the position of erinaceids is less clear (46). These results clearly conflict with morphological studies supporting the monophyly of Lipotyphla (33, 47), as well as recent endorsements (47, 48) of earlier suggestions (49–51) that chrysochlorids and tenrecids do not share an exclusive relationship and that golden moles should be placed in their own order or suborder.

We opt to support phylogenetic hypotheses which receive reasonable support from morphological, molecular, and biogeographical data. Thus, we suggest that the association of *Solenodon* with the soricid–talpid clade already proposed on the basis of morphological evidence (and now supported by limited molecular evidence) is more likely to be correct than an association with the Afro-Malagasy zalambdodonts. Evidence for this solenodontid–soricid–talpid radiation can be found in the Laurasian fossil record, although it is not yet clear how or to what extent various geolabidids, plesiosoricids, nesophontids, apternodontids, or nyctitheriids might be involved. Regardless, this combined evidence indicates to us that the dental features of *Solenodon* are likely to be convergent on those of tenrecids and chrysochlorids, and that *Solenodon* and the Afro-Malagasy zalambdodonts are independently descended from more generalized forms which may have had dentitions similar to geolabidids and *Widanelfarasia*, respectively. This hypothesis is somewhat similar to that proposed by Butler (33), who suggested that an early African “nyctitheriid” branch gave rise to the tenrecid–chrysochlorid clade.

Although it has long been clear that faunal interchange between Afro-Arabia and northern continents was possible during the Eocene, the highly endemic nature of the Paleogene Afro-Arabian mammal fauna [as indicated directly by paleontological data (16) and indirectly by molecular data (12, 44, 45, 52)] provides supplementary evidence suggesting that the presence of a late Eocene Afro-Arabian taxon—*Widanelfarasia*—sharing apomorphic dental features with the endemic Afro-Arabian tenrecid–chrysochlorid clade is more likely to be a consequence of some phylogenetic relationship between the two groups than of an appearance by an otherwise endemic Laurasian form which coincidentally evolved the same apomorphic features convergently. As *Widanelfarasia* is not truly zalambdodont, however, this suggestion is not without its problems.

Dental convergence in tenrecids and chrysochlorids is a possibility which has been suggested (e.g., ref. 47), but for which there has, as yet, been little or no fossil evidence. It is a difficult hypothesis to test as the dentition of chrysochlorids is highly autapomorphic and possibly derived from a dental pattern resembling the zalambdodont morphotype of the extant tenrecids. As there is no known fossil record for tenrecids or chry-

sochlorids prior to the early Miocene, there is also little indication of a more conservative stage in either group’s ancestry [although early Miocene *Prochrysochloris* exhibits longer and more complex talonids and less molariform premolars than do crown chrysochlorids, and the contemporaneous tenrecid *Protenrec* retains a small metacone (18)]. The combined morphology, antiquity, and biogeographical provenance of *Widanelfarasia* raises the possibility that the dental similarities of tenrecids and chrysochlorids evolved convergently from what may have been an incipiently zalambdodont common ancestor. Considering the apparent reversal to tribospheny seen in extant *Potamogale*, however, it is, of course, entirely possible that (among other scenarios) *Widanelfarasia* is a tenrecid which exhibits a similar reversal from ancestral zalambdodonty.

The limited nature of the available material leaves open many other interesting phylogenetic options, including a possible relationship with the recently described *Chambilestes* (14) from the earlier Eocene of Tunisia (currently represented only by P⁴–M³). From what little can be determined based on the geometry and predicted occlusal relationships of these upper teeth, the morphology of *Chambilestes* does not appear to be entirely inconsistent with the lower dentition of *Widanelfarasia*. As *Widanelfarasia* exhibits relatively short and narrow talonids with well developed hypconids on M₁–M₃, and *Chambilestes* exhibits transversely elongate upper molars with well developed paracone and (reduced) metacone, the morphology of the Tunisian form certainly more closely approximates the predicted upper molar morphology of *Widanelfarasia* than does any known living or extinct tenrecid or chrysochlorid. In light of *Widanelfarasia*’s antemolar specializations, however, an allocation of *Widanelfarasia* to the Chambilestidae would be at odds with Gheerbrant and Hartenberger’s (14) suggestion that *Chambilestes* may be a primitive erinaceomorph. Clearly, much more complete material will be needed before the higher-level relationships of Afro-Arabian forms such as *Widanelfarasia*, *Chambilestes*, and *Todralestes* can be confidently resolved, but it is entirely possible that these taxa are all more closely related to each other than to any known Laurasian group. Until more informative material becomes available, we prefer to tentatively refer *Widanelfarasia* to *Placentalia incertae sedis*. This taxonomic decision is conservative, but we believe that it more accurately reflects current understanding of the true relationships of various extinct placentals traditionally placed in unstable taxa such as Insectivora or Lipotyphla.

We thank C. V. M. Simons for helpful discussion as well as editorial and research assistance and R. J. Asher, P. D. Gingerich, and J. G. M. Thewissen for providing a number of helpful comments and criticisms on earlier versions of this manuscript. The opinions expressed in this paper are, however, entirely those of the authors. We also thank L. Gordon and M. Carleton for access to specimens at the National Museum of Natural History; M. Godinot, E. Gheerbrant, and C. Berge for discussion, hospitality, and access to fossil material at the Muséum National d’Histoire Naturelle Institut de Paléontologie; and J.-J. Jaeger, S. Ducrocq, Y. Chaimanee, J. Sudre, and B. Marandat for discussion and hospitality while in Montpellier. Funds in support of this project have come from the U.S. National Science Foundation (BNS-91-08445 and SBR-95-07770) as well as from the Boise Fund, Oxford University, Gordon and Ann Getty, Margot Marsh, and Verna C. Simons. Specimens were prepared by P. Chatrath and D. DeBlieux. Scanning electron microscopy photos were taken by L. Eibest. This is DPC publication no. 697.

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