# On the question of the genus-name *Geogale aletris* Butler and Hopwood 1957 (Mammalia, Insectivora) from the East African Miocene.[†]

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*Zeitschrift fuer Saeugetierkunde* 50, 129-140.
1985.

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**Introduction**

When Butler and Hopwood (1957) named the fossil *Geogale aletris* from the Kenyan Miocene, congeneric with the recent Malagasy species *Geogale aurita*, they created a sensation by extending the distribution of *Geogale* into the African mainland, where it had been long extinct. Another discovery in 1969 included not only the fragment of a *G. aletris* maxilla but also a mandibular fragment with a tooth preserving a better-preserved molar talonid (Butler, pers. comm.). According to Butler (1978) *G. aletris* is too specialized to comprise a possible ancestor of the Tenrecidae prior to their radiation in Madagascar. For this reason Butler proposes a separate colonization event for *Geogale* apart from the remaining Tenrecidae.

The holotype of *G. aletris* was found on Rusinga Island in Kenya and consists of a damaged rostrum (Figs. 1-4). The cranial dermal bones are partially missing, exposing a large part of a natural cast of the maxillary recess. The holotype was originally accessioned in the Coryndon Museum in Nairobi (Rs 76 450) but is currently housed at the NHM London.

By comparing previous publications (Butler and Hopwood, 1958; Butler 1969, 1978) with our own observations, in this paper we try to answer the question whether or not the close relationship as proposed by Butler and Hopwood (1957) between *G. aletris* and *G. aurita* is in

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[†] Original citation: Poduschka, W. & C. Poduschka. 1985. Zur frage des Gattungsnamens von "*Geogale*" *aletris* Butler und Hopwood, 1957 (Mammalia, Insectivora) aus dem Miozän Ostafrikas. *Zeitschrift fuer Saeugetierkunde* 50:129-140. Figures and Literature Cited are not included in this translation.

[°] Comments from RA appear in brackets [].

fact real. We should note that in 1982 [*sic*] in an "in-press" manuscript (*Acta Zool. Fennica*), Butler himself proposed to place *G. aletris* in its own genus**.

Following Butler and Hopwood (1957), the Potamogalidae and Tenrecidae have a common ancestor in the Oligocene. In a later publication regarding *G. aletris* (Butler, 1969), Butler argued that the differences between these taxa preclude the fossil (*G. aletris*) comprising an ancestor of the living species (*G. aurita*). In the same work Butler considers the possibility that the similarities between the two taxa could result from parallel evolution, but nevertheless retains his opinion from the earlier publication (Butler and Hopwood, 1957): i.e., the fossil is a species of the living *Geogale* and differs from *G. aurita* by missing an anterior premolar, the larger posterobuccal lobe of M2, and the larger posterior extension of the palate behind the upper teeth. The skull is slightly larger than that of *G. aurita* and is broadly similar to the skull of *Microgale cowani*. The nasal portion of the skull is shorter than that of *G. aurita*. Butler and Hopwood (1957) arrive at the conclusion "none of the living African Tenrecidae resembles the Rusinga species as closely as the Madagascar *Geogale aurita*. The two forms agree with each other and differ from the other Tenrecidae in the short snout, the relatively long infraorbital canal, the presence of foramina in the maxilla in front of the infraorbital foramen, and the shape and degree of separation of the large anterior incisors. Because of these special resemblances, the fossil is placed in the genus *Geogale*" (1957: 21).

These and other details from the original description of the holotype are scrutinized in the following discussion.

## Material and Methods

For our comparisons, we considered material of recent Insectivora, possibly related to *G. aletris*, that was more diverse than the sample used by Butler and Hopwood (1957).

**list p. 132**

All skulls of these recent Tenrecidae and Potamogalidae were studied, measured, and photographed in collections in New York, Chicago, Cambridge MA, Stockholm, Vienna, Braunschweig, London, Washington, Paris, Leiden, and Amsterdam. *Echinops*, *Setifer*, *Nesogale* [sic] *talazaci*, and *N.* [*sic*] *dobsoni* were/are being bred and housed in our Insectivora-Station in Vienna.

## Critical Remarks on the Original Description

Butler and Hopwood show both similarities between *G. aurita* and *G. aletris* and differences to other Tenrecidae. Similarities include the short rostrum, the ** long infraorbital canal, the presence of foramina anterior to the infraorbital canal, and shape of the anterior incisors plus the inter-incisal diastema. Differences between the two species, following Butler and Hopwood

** note: paper cited as Butler "1982" *Acta Zoologica Fennica* "in press" was eventually published in 1985. It does not contain the skepticism of a relationship between Kenyan fossils and *Geogale* attributed to it by Poduschka [RA].

(1957), include a posterobuccal lobe of the M2, an indication of the fossil as more primitive than the living species. Further differences such as the lack of P2 and the posterior extension of the palate show the fossil to be more progressive than the living species.

However, examination of the original description shows that often only only one species of *Microgale*, namely *M. cowani*, plus the Potamogalidae, were used for comparisons. In addition the phrase “other Tenrecidae” was often used without mentioning countless differences in detail between the largest (*Tenrec ecaudatus*) and smallest (*M. pusilla*) species.

Butler and Hopwood cited just once the taxon *Micropotamogale lamottei* as an analogue to *G. aletris*, believing that **both lacked an M3. This is however incorrect; the adult *M. lamottei* indeed possesses an M3, as demonstrated by Kuhn (1964). Furthermore in his original description of *M. lamottei* Heim de Balsac (1954) clearly stated that he had available to him only a juvenile specimen, a fact obviously overlooked by Butler and Hopwood (1958).

An additional mistake is that *G. aurita*, as other Tenrecidae, lacks a fused tibia-fibula. In fact this could very well be the case in *Potamogale* and oryzorictines, but is however not a useful criterion, as it is dependent on the age of the individual.

Finally, the published figure showing the lateral aspect of the holotype (Butler and Hopwood, 1957: 18) does not show the "left lateral view" as claimed by the authors, but is rather a reconstruction based on the morphology of both sides. [footnote 2 says the same method was used in figuring Erythrozootes chamerpes.] Close inspection of the figure makes this is clearly evident: the largely intact right I1 (compare the palatal view) shows up (*wird eingezeichnet) in the figure of the lateral (left!) rostral skeleton. In addition the contours of the figure do not always correspond to the actual shape (Fig. 5). The interior contour of the intact alveolar maxilla does not run straight, but crooked (gekruemmt); the clearly visible root vestige of the right P3 of the holotype, and that (jener) of the rostral root of the left upper canine, are not illustrated; the very large block of roots and the tooth-base of the right P4 and right molars is completely missing from the figure, even though these are important to reconstruct the contours of the alveolar maxilla (Fig. 2).

## Discussion of details advanced by Butler and Hopwood

1. The relatively short rostral skeleton length. In comparison with the contours of the skull of *Setifer* and *Echinops*, the rostrum of *G. aletris* does not seem that short; this appearance is only evident in comparison with *G. aurita*. It must also be considered that the no-longer intact shape[**] of the right upper incisor is unknown. The root lies in the caudal half of the apparent incisive foramen--visible in palatal view---and permits recognition of a premaxilla that extends further anteriorly. In addition, Butler and Hopwood figure---randomly---an I1 crown estimated by them to show a curved profile. However, if this tooth were longer and more straight, as is the case in *G. aurita*, the alveolus could have reached much more farther anteriorly, corresponding with a considerably longer rostrum.

[**] *Ausdehnung*

2. The long infraorbital canal. This structure is certainly remarkably long in both *G. aletris* and *G. aurita*. On the other hand it is no criterium to rule out a relationship with other basal Insectivora. Long infraorbital canals are known in from the echinosoricines *Hylomys*, *Podogymnura*, and to a lesser extent *Echinosorex*.

3. The authors note that relative to *G. aletris*, the taxa *G. aurita*, *Microgale*, *Oryzorictes*, and *Centetes* [*sic*] possess a long, caudal extension of the palate (cf. Figs. 2 and 7). This extension is however present to varying degrees in *Echinops*, *Setifer*, and to a lesser extent in potamogalids. Setifer possesses the relatively longest palate (Fig. 6). Regarding this character, the comment of Butler and Hopwood (p. 19): "... unlike other Tenrecidae, it extends backwards for some distance (1.3 mm) behind M3..." is an inaccurate generalization.

4. Zygomatic width. This is estimated from the holotype to be 9.4 mm. Ignoring for a moment that becuase of the broken right maxillary process, this cannot be much more than a rough guess, the authors' comparison with "*Microgale*" is problematic because the species is not given. The authors' later comment (p. 18) "The skull is a little larger than in *G. aurita*, and resembles in size that of *M. cowani*..." can be interpreted to mean that *M. cowani* is the species in question.

5. The premaxillary suture is according to Butler and Hopwood, in contrast to other tenrecids, not closed; but this observation is hardly useful as a distinguishing character. The suture is clearly visible on the left side (Fig. 4), but runs on the upper third much more steeply than in *G. aurita* (Poduschka and Poduschka, 1983) and in potamogalines (Poduschka, unpub.). The suture changes course in the upper third of the bone in all tenrecs in a caudal-tending direction.

6. Butler and Hopwood state that the infraorbital foramen in *G. aurita* is situated before the last premolar, and in other oryzorictines [*sic*] over the first molar. But in *G. aletris* it is situated directly over the last premolar. Regarding the position the infraorbital foramen therefore shows an intermediate condition between *Geogale* and other oryzorictines [*sic*].

7. The "small foramen" in the maxilla clearly illustrated by Butler and Hopwood, described "shortly before the canine" is in fact barely recognizable in the actual specimen, and contrary to the authors comments is not "represented in this region by two small foramina." These are present in the recent *G. aurita*, but lie considerably farther caudally, on the anterior edge of the depression[*] of the maxilla leading to the anterior opening of the infraorbital canal. Whether or not these are actually foramina as mentioned in the original description of *G. aletris*, representing a growth-region of the bone or accessory infraorbital foramina, cannot be determined, particularly because only a small depression in the (exposed by the absence of dermal bone) nasal-capsule core of the holotype is evident.

8. Another foramen in the maxilla, similarly discussed by Butler and Hopwood as present in "other Oryzorictinae" and in *Potamogale*, could not be identified in *G. aletris*[*]. We assume Butler and Hopwood meant the prominent lacrimal foramen of *G. aurita*; however this foramen is not "usually over P4" but over M2 in this species (Fig. 7). Contrary to the comments of Butler

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[*] *Eindellung*
[*] another horrible German sentence paraphrased here [RA].

and Hopwood we could not identify the respective foramen[**] in *Potamogale*; alone in the type specimen (BMNH 19.5.9.17), 3 small foramina are located much more rostrally, above the alveolar edge between the upper canine and first two premolars. These are however individual, age-related bone-resorptions at the edge of the tooth-alveoli without morphological significance. They are present also in *Microgale pusilla*.

It must also be mentioned here that Mueller (1935) pointed out that within an order the structure of the orbitotemporal region can be highly variable. Its use in comparisons or diagnoses is therefore problematic. Mueller lists *Geogale aurita* in her list of examined specimens, but unfortunately does not elaborate further.

9. The distance between the anterior upper incisors. This detail can hardly be used as a character indicating relationship between the two *Geogale* forms, since it appears not only in these taxa but also in other tenrecids, namely *M. longicaudata*, *M. principula*, *M. sorella*, *M. majori*, *M. pusilla*, *Echinops telfairi*, as well as in erinaceines and echinosoricines. In soricids as well the roots of the anterior upper incisors are separated by a space, even when the crowns of the teeth tend toward each other at their apex.

10. Butler and Hopwood give the presence of P3 accurately in their figure, but assume the "absence of P2". In our opinion, however, this question must remain open:[***] between the P3 and canine a clear gap is evident. Because of the bad state of the holotype, neither suggestions of an alveolus nor root-remains of P2 are apparent. In no recent tenrecid is a gap evident in the toothrow [*sic*], at least anything between I3 and canine. Because *G. aletris* has such a diastema between the canine and the two present upper premolars, it seems to us likely that *G. aletris* also possessed a P2. If correct, then *G. aletris* would have had the same dental formula as *G. aurita* and *S. setosus*.

11. It is undisputed that the infraorbital canal in potamogalines is shorter than in *G. aletris* and *G. aurita*. However is must be noted that the upper edge of the maxillary zygoma in *G. aletris* reconstructed by Butler and Hopwood runs farther nasally than that of *G. aurita* (Fig. 7). Unfortunately, the accessory foramina easily seen in *G. aurita* are not evident in the figure and not easily recognizable in the holotype of *G. aletris*.

**Further comparisons not undertaken in the original description**

It is evident that Butler and Hopwood were not aware of probably the most conspicuous difference between *Geogale* and other tenrecids, namely, the abrupt narrowing of the facial skeleton just prior to the last premolars (Figs. 1, 2, 9). In their illustration, Butler and Hopwood extend this line, contrary to the visible contour on the object which is clearly mistaken on both sides: the right maxilla with a solid line, the left with a stippled line, presumably estimated by the authors. This change in the contour makes the illustration more similar to the two species of *Micropotamogale*, lamottei and ruwenzorii, as well as to juvenile *Potamogale*. Interestingly, Butler (1969) illustrates this contour, typically interrupted in *G. aurita*, in the dorsal view of

[**] lacrimal? foramen from first sentence? I don't know which one he means here [RA].
[***] whopper sentence here yet to be translated [RA].

*Erythrozootes chamerpes*; whereas in the coauthored publication with Hopwood this feature is less emphasized. Butler (1969) does not however consider *Erythrozootes*, also discovered by both authors, as a close relative or even ancestor of *G. aurita*.

Precisely this clearly degraded[*] contour[*] in occlusal view (figs. 2 and 9) would comprise an important argument for the hypothesized close relationship between *G. aurita* and *G. aletris* in the same genus. It must however also be pointed out that this kind of contour is not only present in *Geogale*, but also in distantly related Oligocene [*sic*] insectivorans, such as *C. marginalis* and *C. chadronensis* (Lillegraven et al. 1981). In spite of its clarity this character is not necessarily to be understood as evidence of relationship between *G. aletris* and *G. aurita*.

1. Based on the recently erupted[*] M3 in its final, slightly caudally facing crown, relative to a transverse plane (Poduschka and Poduschka, 1982), the holotype is an adult animal, whose visible and possibly not completely synostosed suture between the maxilla and premaxilla may justify identification as “early adult.”

2. The small, circular structures on the palate and maxilla in palatal view are, as the authors note, not perforations. On the holotype they can only be considered to be small excavations[*], and are probably impressions of palatal glands[*]. They are also evident in other tenrecids, such as *Potamogale*, *G. aurita* (Fig. 9), *M. pusilla*, *M. prolixicaudata*, *M. cowani*, *E. telfairi*, and *S. setosus*.

3. The smallest interorbital distance, situated in *G. aurita* and most other tenrecids just behind the zygomatic process of the maxilla, is in *G. aletris* approximately at the level of the choanae. This would correspond approximately to the smallest interorbital width of potamogalids.

4. An enlarged, backwards-curved root of I1 (following Butler and Hopwood “also in *Geogale*, *Limnogale*, and to a lesser extent in *Microgale*...”) is also evident in potamogalines; but it is not apparent in all members of the genus *Microgale*, in which the root of I1 extends curved barely visible backwards. In contrast to that of *G. aletris*, the I1 root is not appreciably larger than that of any other incisor. An appreciable curvature of the I1 root occurs only in those tenrecids in which the first upper incisor is enlarged and/or developed as a "capture-tooth" relative to more posterior incisors.

5. Concerning the strength and position of this root in *G. aletris* (Fig. 3), there is nothing comparable among recent tenrecids. Similarly diagonally positioned and strong roots are in any event present among the Soricidae.

**Results**

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[*] *abgesetzte*
[*] *Umrisslinie*
[*] *ausgetretenen*
[*] *Gruben*
[*] *Gaumendruesen*

We do not intend in this paper to reach a conclusion about the tenrecoid to which "*Geogale*" *aletris* is related. In our opinion, and recently also that of Butler himself [*sic*], Butler and Hopwood (1957) were too quick in making their decision.

Based on the differences demonstrated here between "*G. aletris*" and *G. aurita*, it does not seem to us productive to postulate a relationship between the Rusinga Island fossil and some other insectivoran. This is particularly true because of the certain similarities evident to other tenrecoids, but in no case to such an extent so as to justify assignment to another genus. In our opinion, the independence of the fossil shows that a close relationship to the recent genus *Geogale* is improbable.

The table shows that the characters used by Butler and Hopwood (1957) as proof of the membership of *G. aletris* to the living genus *Geogale* either inaccurately represent the morphology of *G. aurita* (chars. 1, 3, 4, 5 in the table), seem hardly useful (char. 6), or are not believable (char. 7). Only in characters 2 and 6 are the two forms similar, in addition to the rostral-contour character (10) not recognized by Butler and Hopwood. In any event, the last feature can to varying degrees also be found in other fossil and recent eutherians. Speaking against the assignment of the fossil to *Geogale* are other details found in other tenrecoids, but not in recent *Geogale* (chars. 1, 3, 4). The curvature and strength of the I1 root appears to us incomparable to anything shown by *G. aurita*.

In our opinion, the assignment by Butler and Hopwood of two species so widely separated to a single genus is doubtful, an opinion that Butler articulates in his most recent article (1982 [*sic*]), as among other things part of the original character comparisons are inaccurate and some important differences are present. It is unclear if the fossil relates to terecids, potamogalids, or some other insectivoran; the large I1 root and the doubly-interrupted contour of the maxillae in palatal view sufficiently distinguish *G. aletris* from all other comparable tenrecid and potamogalid genera. Additional characters show varaible similarities and differences with other genera (see Table). Joining the two taxa in a single genus does not therefore seem appropriate; and the previously published conclusions in relationships and distribution are invalid.

It is therefore necessary, following the rules for emendation from the ICZN, article 67 ii (1962) to assign the species "*G.*" *aletris* to a new species:

*Butleriella* nov. gen.

Derivation of the name: No one else seems more worthy to lend his name to this interesting fossil than Prof. P.M. Butler, as he not only first described it (along with A.T. Hopwood) but also continued to work on the fossil.

Generic diagnosis: Fossil zalambdodont insectivoran with the upper dental formula 2.1.?.3; I1 with conspicuously strong, curved root; both central upper incisors widely separated; M3 as in recent tenrecids proximally turned exteriorly; recognizable premaxilary suture; contour of the maxilla from dorsal or ventral view conspicuously narrowed just anterior to P4; remarkae caudal extension of the palate; long infraorbital canal.

Type species: *Butleriella* n.g. *aletris* (Butler and Hopwood) from Rusinga Island, Kenya, from the Rusingan [*sic*] (= *Geogale aletris* Butler and Hopwood, 1957).


**Acknowledgments**

We owe many thanks to the Volkswagen foundation, that along with the Austrain Academy of Sciences supported work on the revision of the Tenrecidae. We also thank Mr. Prof. Dr. Dr. h. c. Dietrich Starck[*] Frankfurt a. M. and Prof. Dr. Erich Thenius, Paleontological Institute of the University of Vienna, whose encouragement, constructive criticism, and corrections made this work possible. We thank Mr. Prof. Dr. Percy Butler, London for stimulating written and oral discussions over meetings in Helsinki and at the NHM London. We thank Mr. Dr. J. J. Hooker of the paleontological institute for his collegial help in accessing the type specimen. We thank Ms. Maria E. Rutzmoser and Prof. J. A. W. Kirsch, Museum of Comparative Zoology, Cambridge MA, Mr. Dr. Francis Petter MNHN Paris, and Ms. Paula Jenkins NHM London for making possible our study of collections in their care.


**Note added in proof**

While this article was in press we became aware that Prof. P. M. Butler suggested a new generic name for "*Geogale*" aletris, namely *Parageogale*, which did not correspond with the original publication (Butler and Hopwood, 1957). Hence our doubt as to the generic-level diagnosis of "*G.*" *aletris* postulated at that time has been confirmed. However, our new generic name *Butleriella* has now fallen into synonymy with the earlier-published name of Butler (1984).

**Summary**


The rostral fragment from Kenya discovered in 1957[*] was named by Butler and Hopwood *Geogale aletris*, thereby placing the fossil in the same genus as the living *G. aurita*. With this discovery it is inferred[*] that during the Miocene tenrecids exited in continental Africa.

The holotype of *G. aletris* was compared with multiple specimens of *G. aurita* and many other tenrecoids; the similarities with *G. aurita* are not of sufficient weight to support inclusion in the same genus. This is particularly so as many individual features are also apparent in many other insectivorans.

Hence we suggest a new generic name, *Butleriella*, in honor of its original describer, Prof. Dr. P. M. Butler.


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[*] not "Strack"-- but all the titles are in the original [RA].
[*] *sic*, published in 1957 [RA].
[*] *angenommen*