

Species limits and distribution of the Malagasy carnivoran genus *Eupleres* (Family Eupleridae)

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Abstract

A review was conducted of members of the endemic Malagasy carnivoran genus *Eupleres* (family Eupleridae) based on published and unpublished records and museum specimens. Classically, one species has been recognized in this poorly known genus – *E. goudotii*, divided into two geographical forms with non-overlapping distributions: *E. g. goudotii* distributed in the mesic forests of the east and *E. g. major* found in the dry areas of the northwest. Drawing on external and craniodental comparisons, we demonstrate that these two forms are highly distinctive morphologically and can be readily distinguished from each other. Furthermore, there is some evidence that they both can occur on the slopes of Montagne d'Ambre in the far north of the island. On this basis, we recognize these taxa as distinct species, *E. goudotii* and *E. major*.

Keywords: distribution; *Eupleres*; Madagascar; morphology; taxonomy.

Introduction

Until recently it was assumed that the native Carnivora of Madagascar represented several deeply divergent lineages within the order, and hence that they arrived on the island via multiple colonization events (Gregory and Hellman 1939, Simpson 1945). However, recent molecular comparisons have shown that all native Malagasy Carnivora genera (*Cryptoprocta*, *Fossa*, *Eupleres*, *Galidia*, *Galidictis*, *Saloia*, and *Mungotictis*) form a monophyletic group representing a single colonization event (Yoder et al. 2003) and all are now placed in an endemic family, Eupleridae (Wozencraft 2005). This family represents one of the more extraordinary adaptive radiations among the world's Carnivora (Goodman 2009). Although higher level systematics of the

Eupleridae are becoming reasonably well established (Yoder et al. 2003), the distribution and species limits of several genera remain poorly studied. Herein we address these aspects for the enigmatic genus *Eupleres* (the falanouc), which possesses a highly reduced dentition and other remarkable anatomical features (Gray 1870, Carlsson 1902, Pocock 1915, Scapino 1981, Popowics 2003, Gaubert et al. 2005) and for which little information is available regarding natural history and geographical distribution (Albignac 1972, 1973a, 1974).

In his extensive review of the Carnivora of Madagascar, Albignac (1973a) considered *Eupleres* to be monospecific and represented by two subspecies: *E. g. goudotii* Doyère, 1835, from the eastern wet forests and *E. g. major* Lavauden, 1929, from the transitional dry deciduous-humid forests of the northwest. Albignac (1973a) presented several external morphological characters to separate these two subspecies. In subsequent taxonomic reviews of the Carnivora of Madagascar, this monospecific arrangement for *Eupleres* has been followed (Wozencraft 1993, 2005), although there has been some indication that these geographical forms could warrant specific recognition (Lavauden 1929, Albignac 1973b). The purpose of this paper is to review morphological characters and measurements distinguishing these two forms, their geographical distribution, and to assess their specific status.

Methods and materials

Patterns of morphological variation

To assess patterns of morphological variation in the different recognized forms of *Eupleres* we examined and measured specimens in the following institutions: American Museum of Natural History (AMNH); Muséum national d'Histoire naturelle (MNHN); Museum of Comparative Zoology, Harvard University (MCZ); Natural History Museum, London [BMNH; formerly The British Museum (Natural History)]; Yale Peabody Museum (YPM), Yale University; Museum für Naturkunde, Humboldt Universität, Berlin (ZMB). Some of these specimens are incomplete, missing teeth or damaged in other ways. All craniodental measurements included herein were taken by the second author, at an accuracy of 0.1 mm for cranial variables and 0.01 mm for dental variables.

The following measurements were taken for all adult (and nearly mature subadult) specimens – skulls: greatest length of skull (GSL), condylobasal length (CBL), zygomatic breadth (ZB), breadth of braincase at zygomatic roots (BB), interorbital width (IOW), length of anterior palatal foramina

(APFL), maximum length of nasal bones (NL), palatal length (PL), auditory bulla length (AUDL), auditory bulla width (AUDW), and mandible length (ML); teeth – length of upper first molar (LM1); width of upper first molar (WM1); length of upper second molar (LM2); width of upper second molar (WM2); external alveolar distance between upper first molars (M1–M1); external alveolar distance between upper canines (C–C); length of maxillary toothrow (C–M2); width of lower first molar (wm1); length of second lower molar (lm2); length of third lower premolar (lp3).

Results

Morphology

External morphology External measurements tabulated both by Albignac (1973a) from non-cited sources and from museum study skins at MCZ (Table 1) demonstrate the consistently larger body size of *major* relative to *goudotii*. Another striking distinction between *major* and *goudotii* is in pelage coloration; *major* is distinctly darker brown than *goudotii*, which is paler and more fawn brown in overall coloration (both species are paler ventrally than dorsally). Albignac (1973a) noted sexual dimorphism in both of these forms, with males being slightly larger than females, but based on current limited sample sizes we are unable to test for these differences in a meaningful way.

Another consistent difference between these two forms is in the position and size of the foot-pads and fur cover on the distal portions of the fore and hind feet (see Albignac 1973a, Figures 9–12). On the palmar surface of the forelimb of nominate *goudotii* the digital pads are only moderately developed, and the interdigital and metacarpal pads are largely fused and form a large central surface, whereas in *major* the digital pads are markedly larger and inflated, and the hypothenar and thenar pads are notably separated from the inflated interdigital pads (terminology follows Brown and Yalden 1973). Furthermore, in *major* the palmar surface posterior to the metacarpal pads is largely naked and furred in *goudotii*. On the plantar surface of *goudotii*, the digital pads are reduced, and the largely fused interdigital pads form a central rounded unit with a notable separation from the digital pads, whereas in *major* the digital pads are conspicuously

inflated structures, the fused interdigital pads form a large proportion of the foot-pad surface, and the metatarsal pads (thenar and hypothenar) are more developed. Finally, a considerable portion of the plantar surface posterior to the metatarsal pads is naked in *major* and largely covered with fur in *goudotii*.

Cranial measurements and morphology There are several cranial and mandibular measurements that distinguish *goudotii* and *major* (Table 2, Figure 1). In general, *major* has a distinctly more robust skull, both in cranial length (e.g., greatest length of skull) and breadth (e.g., zygomatic breadth), as well as a longer and more robust mandible. In fact, there is a large discrepancy, with no overlap, in condylobasal length between adults of *goudotii* (≤ 87 mm) and *major* (≥ 90 mm), offering a convenient single metric for discriminating adult skulls. Furthermore, *major* has a distinctly longer palate, but shorter anterior palatal foramina than those of *goudotii*, an important cranioproportional distinction. One of the most noticeable diagnostic differences between these two animals is the much more expansive auditory bullae in *major*, as reflected both in average values for length and width dimensions (tabulated in Table 2), but most notably expressed by inflation of the bullae in the vertical (dorsoventral) dimension (difficult to measure consistently and not tabulated here).

Dental measurements Many of the specimens available for this study are missing teeth, so that there are numerous dental variables for which few measurements are available, particularly for *major*. In general, the upper molar teeth in *major* are more robust in length (e.g., length first upper molar, length second upper molar) and width (e.g., width first upper molar, width second upper molar) than in *goudotii*. The length of the maxillary toothrow in *major* is notably longer than in *goudotii*. Furthermore, the distance across the rostrum (e.g., distance outer C–C) and palate (distance outer M1–M1) are greater in *major* compared with *goudotii*. The lower molar measurements in *goudotii* show little overlap in length and width to those measurements of *major* (e.g., second to last lower width, second to last lower width, length of fourth to last tooth in lower jaw) (Table 3). Hence, animals assigned to nominate *goudotii* and *major* have conspicuously different dentitions, which in *major* are mainly more robust.

Taxonomic conclusions

Given the notable differences between the two *Eupleres* taxa in body size (as shown by external and skull measurements), pelage coloration, foot-pad morphology and flexor fur patterns, cranial-mandibular proportions and measurements, and dental measurements, as well as differences in their associated habitats, and some evidence (see below) that these taxa can occur in sympatrically (or in near sympatry), we suggest that these geographical forms should be elevated to the rank of species. Specimens of *Eupleres* are rare in museum collections, and to our knowledge no frozen tissue samples are available of both species to test easily this recommendation with molecular genetic data. Studies drawing on genetic sam-

Table 1 External measurements (in mm) of *Eupleres* taken from Albignac (1973a) and from linear measurements carefully estimated directly from study skins at MCZ by the second author.

| Form | Head and body length | Tail length | Hind foot length | Ear length |
|--------------------------|----------------------|-------------|------------------|------------|
| <i>Eupleres goudotii</i> | | | | |
| Albignac | 455–495 | 220–240 | 80–82 | 40–44 |
| MCZ (n=4) | 470–525 | 200–250 | | |
| <i>Eupleres major</i> | | | | |
| Albignac | 515–650 | 240–250 | 81–92 | 47–50 |
| MCZ (n=4) | 610–740 | 210–310 | | |

Table 2 Cranial and mandibular measurements (in mm) of *Eupleres* specimens based on age classes.

| Form and age class | GSL | CBL | ZB | BB | IOW | APFL | NL | PL | AUDL | AUDW | ML |
|--------------------|------------|------------|------------|------------|------------|----------|------------|------------|------------|------------|------------|
| <i>E. goudotii</i> | | | | | | | | | | | |
| Older subadult | 88.5, 89.2 | 84.0, 84.9 | 35.2, 35.4 | 31.7, 32.2 | 14.9, 15.3 | 6.3, 6.6 | 21.0, 23.5 | 41.2, 43.1 | 13.2, 15.8 | 8.8, 9.4 | 60.8, 61.6 |
| Adult | 88.5±2.51 | 84.0±2.13 | 35.3±1.61 | 32.0±1.01 | 14.3±0.79 | 6.3±0.51 | 21.6±1.45 | 42.5±2.12 | 14.9±0.82 | 9.3±0.56 | 61.5±2.26 |
| | 83.8–92.6 | 79.8–86.5 | 33.0–38.4 | 30.6–33.8 | 13.1–15.3 | 5.3–6.8 | 19.8–25.1 | 39.4–45.8 | 14.1–16.5 | 8.8–10.5 | 58.7–64.7 |
| n=12 | n=12 | n=10 | n=11 | n=11 | n=8 | n=7 | n=12 | n=8 | n=9 | n=8 | n=7 |
| <i>E. major</i> | | | | | | | | | | | |
| Older subadult | 92.1 | 89.8 | 35.9 | 32.2 | 14.5 | 5.7 | 25.6 | 45.6 | 15.2 | 10.2 | 65.0 |
| Young adult | 96.0 | 93.4 | 35.8 | 31.8 | 14.3 | 6.0 | 23.8 | 48.5 | 17.4 | 10.0 | 67.6 |
| Adult | 92.9, 97.0 | 91.3, 92.1 | 38.3, 39.4 | 32.7, 33.5 | 14.9, 17.0 | 4.7, 5.7 | 23.9, 26.5 | 46.5, 46.7 | 15.2, 16.0 | 10.0, 11.6 | 67.2, 67.7 |

For definitions of age classes and measurement acronyms see materials and methods section. Sample sizes of three or more specimens are presented as mean±standard deviation, minimum–maximum measurements, and number of specimens.

ples from specimens collected in the future or utilizing techniques for DNA extraction from museum skins and skulls (Helgen et al. 2008, 2009) are recommended to examine patterns of geographical variation between and within both *Eupleres* taxa; to test our hypothesis that *E. goudotii* and *E. major* each represent relatively deeply divergent evolutionary lineages; and to revisit the phylogenetic relationship of *Eupleres* with other Malagasy carnivoran genera (Yoder et al. 2003).

Geographical distribution

We present 40 records of *Eupleres* spp. from different regions of Madagascar based on a detailed survey of published and unpublished literature, as well as collections in different museums. Given the considerable amount of fieldwork and inventories conducted on the island over the past decades, it is clear that members of this nocturnal–crepuscular genus are notably rare or at least reclusive in their habits.

On the basis of specimen and sight records, *Eupleres* has a much broader distribution than previously understood (Albignac 1973a). *Eupleres goudotii* was previously known from the northern half of the eastern humid forest (Albignac 1973a, Figure 5), but its distribution extends the complete length of the eastern portion of the island to Andohahela (Figure 2, Appendix 1). The westernmost known record of this species in northern Madagascar is the montane forest of Montagne d'Ambre. Its documented elevation distribution is from approximately 50 to 1200 m. *Eupleres major* was considered by Albignac (1973a) to be restricted to the Sambirano region, i.e., the transitional humid-dry deciduous forests of northwestern Madagascar (Gautier and Goodman 2008). In fact, it also has a broader distribution in the west, reaching the middle portion of the central lowland zone, at least to the Parc National de Baie de la Baly, near Soalala (Figure 2). It has been documented across an elevational range from approximately 10 to 1500 m.

The northern portion of the island, within the Antsiranana Province, is a zone where the two *Eupleres* replace one another. *Eupleres major* lives in the transitional northwestern forests and associated marshlands east to the foothills of the Tsaratanana Massif (based on specimens with well-documented collection data). However, there is a specimen of *E. major* in the MCZ (45963) with the locality “Diego Suarez” [=Antsiranana] and collected by “M. Drouhard, inspecteur du Eaux et Forêts de Mad. nov. 1934”. Grandidier (1934) described two species of shrew tenrec (*Microgale*, family Tenrecidae) collected by M. Drouhard from “des environs de Diego-Suarez”. As with the *Eupleres* specimen under discussion, these type specimens are also part of the Grandidier Collection now housed in the MCZ (Helgen and McFadden 2001). On the basis of extensive small mammal inventories in the general vicinity of Antsiranana in both dry and humid forests (Raxworthy and Nussbaum 1994, Goodman et al. 1996, 1997, S.M. Goodman unpublished data), it can be con-



Figure 1 Views of skulls and mandibles of *Eupleres* spp. from Madagascar: left – *E. goudotii* (MCZ 45959) from the Forêt Sihanaka, right – *E. major* (MCZ 45963) from “Diego Suarez”. Views include (from top to bottom) dorsal view of cranium, ventral view of cranium, lateral view of cranium, lateral view of mandible, and dorsal view of mandible. Notable differences between these two taxa include the shape of the cranium and rostrum, as well as the size of the auditory bullae.

Table 3 Dental measurements (in mm) of *Eupleres* specimens based on age classes.

| | LM1 | WM1 | LM2 | WM2 | M1–M1 | C–C | C–M2 | Wm1 | Lm2 | Lp3 |
|--------------------|------------------------|------------------------|------------------------|------------------------|---------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| <i>E. goudotii</i> | | | | | | | | | | |
| Older subadult | 3.81, 4.23 | 3.61, 3.85 | 2.80, 3.18 | 3.20, 3.76 | 17.62, 18.77 | 8.20, 8.51 | 33.1, 32.0 | 1.92, 2.02 | 5.50, 4.83 | 3.20, 3.56 |
| Adult | 3.91±0.13 3.75–4.11 | 3.52±0.26 3.25–3.96 | 2.62±0.06 2.56–2.74 | 3.28±0.18 2.98–3.50 | 16.52±0.61 15.31–17.15 | 7.84±0.30 7.46–8.25 | 32.1±1.15 30.7–33.9 | 1.80±0.12 1.64–1.97 | 5.13±0.35 4.85–5.87 | 2.92±0.26 2.54–3.32 |
| | n=7 | n=6 | n=7 | n=7 | n=7 | n=8 | n=8 | n=6 | n=7 | n=7 |
| <i>E. major</i> | | | | | | | | | | |
| Adult | 4.2±0.28 3.9–4.5 | 3.8±0.07 3.8–3.9 | 2.6, 3.6 | 3.6, 3.7 | 18.3, 19.3 | 8.6±0.38 8.2–8.9 | 35.6±0.89 34.8–36.5 | 2.0±0.03 2.0–2.1 | 5.9±0.20 5.7–6.1 | 3.4±0.18 3.3–3.6 |
| | n=3 | n=3 | | | | n=3 | n=3 | n=3 | n=3 | n=3 |

Some examined specimens are missing teeth or are damaged. See Materials and methods section for definitions of measurement acronyms. Sample sizes of three or more specimens are presented as mean±standard deviation, minimum–maximum measurements, and number of specimens.

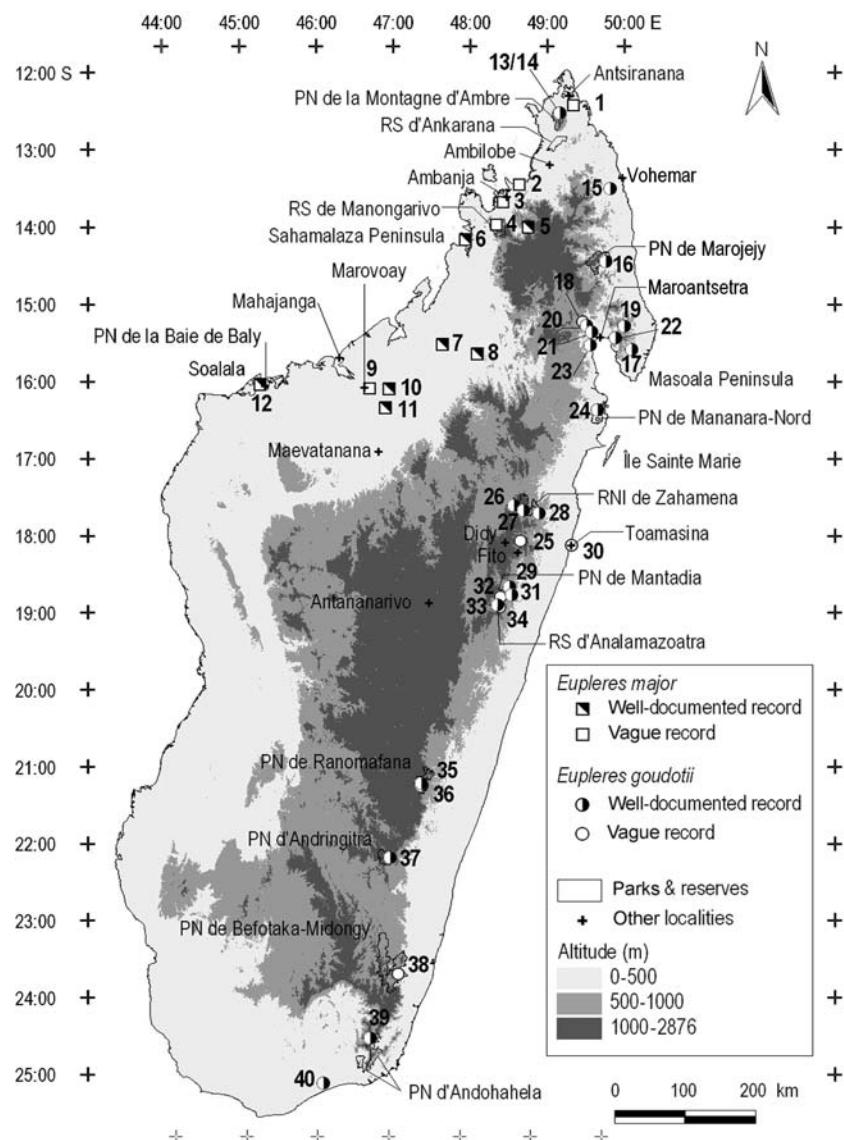


Figure 2 Map of the known distribution of *Eupleres*. The details for each numbered site can be found in Appendix 1. Sites with well-documented records are partially colored in black and those with vague or questionable records are completely in white. Other localities mentioned in the text are also shown on the map.

cluded that the type specimens of these two shrew tenrecs were almost certainly obtained in the humid forests on the upper slopes of Montagne d'Ambre (Jenkins et al. 1997). Hence, we presume that the *E. major* specimen in the Grandier collection (MCZ 45963) could have come from the same zone of Montagne d'Ambre. Given this supposition, both *E. goudotii* and *E. major* could occur on the slopes of this massif, although, direct sympatry cannot be confirmed. The lower slopes of this massif have dry deciduous forest and at around 900 m there is an ecotone to humid forest. *Eupleres goudotii* is known from this massif at 1000 m (Appendix 1; Sites 13 and 14). If indeed the Drouhard specimen of *E. major* was obtained on Montagne d'Ambre, it might have been obtained at a lower elevation in less mesic forest habitat. Clarifying the nature of geographical and ecological overlap or abutment between *E. goudotii* and *E.*

major at the interface of their distributions remains an exciting priority for further research.

Discussion

It was previously thought that the two *Eupleres* taxa, here recognized as distinctive species, have parochial habits with regard to habitat requirements, with *E. goudotii* being found in dense humid forests and associated marshlands and *E. major* in the Sambirano region, with its transitional humid and deciduous forests and marshlands (Albignac 1973a). Based on the distributional records tabulated here, we find that these characterizations do not always hold. For example, the habitat associated with the southernmost record of *E. goudotii*, along the Mandrare River (Site 40), is notably dif-

ferent from that of the majority of other sites where this species has been recorded from, being a mixture of spiny bush and gallery forest that receives less than 500 mm of annual precipitation and experiences a notable dry season (Chaperon et al. 1993). One of the principal branches of the Mandrare River has its origin in the Anosyenne Mountains, a zone to the east that receives at least 1500 mm of rain per year and which experiences a less pronounced dry season. Hence, the marshlands associated with gallery forest of the middle section of this river basin would remain mesic throughout the year. In the Forêt d'Andampy (Site 12), at the northern end of the distribution of this species, the natural forest habitat would be closer to a dry deciduous type, but with more mesic conditions than the Mandrare River basin; the nearby town of Vohemar receiving over 1600 mm on average of annual rainfall (Chaperon et al. 1993).

Across the known range of *Eupleres major* there is also a notable cline in annual rainfall and length of the dry season. This ranges from notably moist montane forest at 1500 m on the slopes of the Tsaratanana Massif (Site 4), where the syntypes of *E. major* were collected, to the largely dry deciduous forest at the Baie de Baly (Site 11) with annual rainfall of slightly more than 1000 mm per year and a notable dry season (Chaperon et al. 1993). Within the southern portion of range of *E. major*, there are considerable marshlands, which could be the mainstay of this species.

Members of the enigmatic genus *Eupleres*, which show remarkable adaptive and ecological parallels to the African aardwolf *Proteles*, a termite specialist (Matsebula et al. 2009), and remains one of the most poorly known carnivorans of Madagascar. Herein, using morphological data, we provide some details on the species limits of *Eupleres*, dividing the former monospecific genus into two separate species, which have broader distributions and more ecologically diverse habitat requirements than previously realized. Further fieldwork to collect tissue samples for molecular phyogeographical studies should provide further insight into the patterns of speciation in this genus. On the basis of site observations and specimen records, *E. major* appears to have the most limited distribution of the two species; it is currently only known from five specimens (all in the MCZ). *Eupleres goudotii sensu lato* is considered by the IUCN as Near Threatened (Hawkins 2008). With the taxonomic changes proposed here associated with splitting *E. goudotii* into two separate species, both the level of molecular divergence between them and their conservation status will need to be reassessed.

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Appendix 1

Localities from which *Eupleres goudotii* and *E. major* have been collected or reported. The individual sites have separate numbers, which are plotted in Figure 2, and are presented here by province (north to south), with supporting information and associated comments. Abbreviations for protected areas are: PN=Parc National, RNI=Réserve Naturelle Intégrale, RS=Réserve Spéciale. In a few cases, supplementary information is presented on unacceptable records.

Eupleres major

Province d'Antsiranana

Dollar (2000) noted this genus in the RS d'Ankarana; this record is incorrect and associated with a printing error (L. Dollar personal communication).

Site 1 In the MCZ (45963) there is a specimen collected near “Diego Suarez” (=Antsiranana). This might well have been taken from the slopes of Montagne d'Ambre. A note on the specimen label has inscribed on it “don de M. Drouhard, inspecteur du Eaux et Forêts de Mad. nov. 1934”. There are other cases of Drouhard specimens bearing the same collection locality and are probably from Montagne d'Ambre (see text).

Site 2 Albignac (1973a) mapped a record of this species approximately halfway between Ambilobe and Ambanja (estimated at 13°27'S, 48°40'E), but no precise detail is presented.

Site 3 Seven individuals were obtained from the region of Ambanja (Albignac 1973a, p. 85); the exact sites are not explicitly stated and this region is estimated to be located at 13°41'S, 48°27'E.

Site 4 Several authors have noted that this species might occur in the RS de Manongarivo (central point is 13°59'S, 48°22'E) (Schreiber et al. 1989, Dollar 2000, Conservation Breeding Specialist Group 2002). We are unaware of any definitive proof of its occurrence within this reserve despite several mammal expeditions to the site (Raxworthy and Rakotondraparany 1988, Goodman and Soarimalala 2002).

Site 5 The syntypes of *E. g. major* (MCZ 45961, 45962) were described by Lavauden (1929) based on specimens in the Grandidier collection that were subsequently transferred to the MCZ (Helgen and McFadden 2001, Helgen 2002). The material was collected north of Beangona, in the Upper Sambirano River Valley and at the foot of the Tsaratanana Massif at a site estimated to be 14°01'S, 48°47'E, 1500 m.

Province de Mahajanga

Site 6 There is a report by Schwitzer (2005) of this animal on the Sahamalaza Peninsula (central position of the associated forest block is at 14°06'S, 47°42'E).

Site 7 Albignac (1973a) noted that an individual was found in the region of Port Bergé (=Boriziny), estimated to be near 15°33'S, 47°40'E.

Site 8 Kaudern (1915) observed an individual at Andranolava (approximately at 15°40'S, 48°08'E, 200 m).

Site 9 An individual was found by Kaudern (1915) in a zone between Ste. Marie and Marovoay (approximately 16°07'S, 46°43'E).

Site 10 There are reports from Ste. Marie de Marovoay (Kaudern 1915) in an area estimated to be located at 16°08'S, 46°58'E, 50 m. Albignac (1973a, Figure 5) incorrectly reported this record from Île Ste. Marie, an eastern near shore island, based on Kaudern (1915).

Site 11 An animal in the MCZ (45964) was obtained 115 SE of Mahajanga (estimated to be 16°23'S, 46°56'E, 50 m), which would be in the region near Maevatanaana.

Site 12 An individual of *Eupleres* was observed in degraded deciduous forest in the PN de la Baie de Baly by Hawkins (1994) at 16°04'S, 45°16'E, 10 m.

Eupleres goudotii

Province d'Antsiranana

Site 13 There are numerous observations and photographs of this animal in close vicinity of the Station Forestière des Roussettes in the PN de la Montagne d'Ambre (12°31'37.3"S, 49°10'19.1"E, 1000 m) (Nicoll and Langrand 1989, Projet ZICOMA 1999, Dollar 2000, Goodman 2009).

Site 14 A specimen (AMNH 100461) was collected at Montagne d'Ambre, probably in close proximity to Site 13 (estimated at 12°31'S, 49°10'E, 1000 m).

Site 15 In the MNHN (1912.129) there is a fluid preserved specimen collected by G. Grandidier in the ‘Forêt d’Andampy, côte NE de Madag’. The inferred coordinates for this locality are 13°30'S, 49°51'E, approximately 100 m.

Site 16 Safford and Duckworth (1990) noted that local guides living close to the RNI de Marojejy (now a PN) reported a *Eupleres* from near Manantenina (14°29'S, 49°49'E, approximately 350 m).

Site 17 There are numerous reports of *Eupleres* on the Masoala Peninsula, which is a PN (Schreiber et al. 1989, R. Albignac personal communication). A portion of this reserve falls within the Province de Toamasina.

Province de Toamasina

Site 18 Golden (2009) has stated that people living in the Makira Forest (approximately centered at 15°14'S, 49°31'E) hunt *Eupleres* for bushmeat, although details of the specific sites were not cited.

Site 19 A specimen in the ZMB (44572) and another in the AMNH (188211) were collected at Ambatond’Radama (=Ambatondradama or Col de Radama) by H. Blüntschli (15°17'S, 50°04'E, 600 m).

Site 20 Two skin specimens in the BMNH (1932.3542, 35.1.8.310) were obtained by Rand at a site 40 km NW of Maroantsetra, near the village of Bevato and at approximately 15°17'S, 49°34'E, between 400 and 500 m (L. Wilmé personal communication).

Site 21 A specimen in the Grandidier Collection (MCZ 45965) was obtained at Fahampanambo, which is located at 15°22'S, 49°38'E and at approximately 100 m.

Site 22 A specimen was collected in 1878 (RMNH 34449) in the vicinity of Mahalevona at approximately 15°26'S, 49°57'E and at 1100 m (L. Wilmé personal communication), in probably lowland areas.

Site 23 Rand collected two individuals (AMNH 100484, 100462), 20 km SW of Maroantsetra estimated to be 15°32'S, 49°37'E, approximately 50 m. The site was along the coastal plain and in close proximity to the village of Manombia (Rand 1936).

Site 24 A specimen (RMNH 34450) was collected in 1876 by J. Audebert near Mananara (estimated locality at 16°23'S, 49°44'E). A number of modern reports of this taxon have come from the PN de Mananara-Nord, presumably in the same general area (Albignac 1973a, Nicoll and Langrand 1989, Projet ZICOMA 1999).

Site 25 A considerable number of specimens have been collected in the Sihanaka (=Sianaka) Forest (BMNH 1932.3540, 1932.3541, 35.1.8.308, 35.1.8.30935.12.10.2, 1962.16021962.2105; FMNH 30492; MCZ 27830, 45957, 45959; ZMB 43127), a region to the east of Lac Alaotra. Most, if not all, of these specimens were obtained by Hershell Chauvin, who collected many vertebrate specimens in the region. Numerous birds obtained by Chauvin are labeled “forêt de Sihanaka” and have secondary locality information making reference to the villages of Didy (18°7'S, 48°33'E) and Fito (18°05'S, 48°54'E). Hence, the Sihanaka Forest (sensu Chauvin) probably falls within the region between these two villages.

Site 26 Hoogstraal and Camicas (1977) noted that specimens of the tick *Haemaphysalis eupleres* (described by Hoogstraal et al. 1965) were collected at Manakambahiny Est, Andranomalaza (estimated coordinates at 17°38'S 048°38'E) and within the RNI de Zahamena. It is presumed that the ectoparasites were obtained from an individual of *Eupleres*, but this detail cannot be confirmed (Jean-Louis Camicas, personal communication).

Site 27 There are observations of this taxon from within the RNI de Zahamena at Volotsanganana (17°42'S, 48°46'E, 850–1000 m) (Anonymous 1995).

Site 28 Anonymous (1995) observed this species from within the RNI de Zahamena at Namarafana ($17^{\circ}44'S$, $48^{\circ}58.5'E$, 400–500 m).

Site 29 A specimen (BMNH 71.4.3.8) was collected by C.S. Webb at “12 mls NW Lohariandava”, which has been interpreted as being at $18^{\circ}42'S$, $48^{\circ}35'E$, 450 m (Carleton and Schmidt 1990).

Site 30 The holotype of *E. goudotii* was obtained by M. Goudot from local people “de Tamatave”, who indicated that this animal is found in areas with sand, where they dig burrows (Doyère 1835). The precise location of the collection site is unknown and is placed in close proximity to the city of Toamasina (=Tamatave) at $18^{\circ}09'S$, $49^{\circ}23'E$.

Site 31 There is a specimen in the MCZ (45958) collected near Rogez (=Ambatovola) (estimated at $18^{\circ}48'S$, $48^{\circ}37'E$, 450 m).

Site 32 The Conservation Breeding Specialist Group (2002) lists this species for the PN de Mantadia (centroid at $18^{\circ}50'S$, $48^{\circ}28'E$, 930–1040 m); the basis for this record is not known.

Site 33 There are numerous reports from the Périer area (Albignac 1973a, Nicoll and Langrand 1989, Dollar 2000), which are presumably within or in close proximity to the RS d’Analamaizaotra ($18^{\circ}56'S$, $48^{\circ}26'E$, approximately 900 m). A specimen was collected in the region of Périer on 6 May 1972 by R. Albignac (Hoogstraal and Camicas 1977).

Site 34 Albignac (1973a) plotted a record just to the south of Périer and on the southern side of Route National 2, linking Antananarivo to Toamasina. Based on the charted point, the site could be close to or within the Maromizaha Forest ($18^{\circ}57'S$, $48^{\circ}27'E$, 1000–1200 m).

Province de Fianarantsoa

Site 35 Observed at Vatoharanana ($21^{\circ}16'S$, $47^{\circ}26'E$, approximately 1125 m) within the PN de Ranomafana (Dollar 1999).

Site 36 Observed at Talatakely ($21^{\circ}14'S$, $47^{\circ}26'E$, approximately 850 m) within the PN de Ranomafana (Dollar 1999).

Site 37 An individual was observed in the RNI d’Andrinigitra (now a PN) ($22^{\circ}13'40"S$, $47^{\circ}00'13"E$, 810 m) (Goodman 1996).

Site 38 There is an undocumented report by Nicoll and Langrand (1989) of this species in the PN de Befotaka-Midongy du Sud ($23^{\circ}45'S$, $47^{\circ}07'E$).

Province de Toliara

Site 39 There is one record of *Eupleres* in parcel 1 of the RNI d’Andohahela (now a PN) ($46^{\circ}44.1'S$, $24^{\circ}35.0'E$,

1200 m) (Goodman and Pidgeon 1999), as well as other reports from this reserve pre-dating this record (Nicoll and Langrand 1989, Durban in Hawkins 1994).

Site 40 A specimen in the MCZ (45737) was obtained at Ambovombe (Androy) by Raymond Decary (estimated site details are $25^{\circ}10'S$, $46^{\circ}05'E$, 135 m). Decary (1950, p. 39) provides some further details on this record; he notes that this species occurs within the Androy, specifically the middle portion of the Mandrare River.

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